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PADRÕES DE DIVERSIDADE E VARIAÇÃO GENÉTICA DE AVES AO LONGO DA DIAGONAL SECA SUL-AMERICANA

HEVANA SANTANA DE LIMA

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Tese de Doutorado apresentada ao Programa de Pós-graduação em Biologia Animal da Universidade Federal de Pernambuco, como parte dos requisitos exigidos para obtenção do título de Doutora em Biologia Animal.

Orientador: Prof. Dr. Diego Astúa de Moraes
Co-orientador: Prof. Dr. Luciano N. Naka

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> “... Ele costumava sempre dizer que só havia uma Estrada, que se assemelhava a um grande rio: suas nascentes estavam em todas as portas, e todos os caminhos eram seus afluentes. "É perigoso sair porta afora, Frodo", ele costumava dizer. "Você pisa na Estrada, e, se não controlar seus pés, não há como saber até onde você pode ser levado..."
>
> J.R.R. Tolkien - "A Sociedade do Anel"

RESUMO

Entender e descrever os padrões de diversidade e de distribuição das espécies, e investigar os eventos e fatores que criaram estes padrões, é um dos grandes desafios da ciência. Na região Neotropical, múltiplos eventos climáticos e geomorfológicos são associados a história evolutiva das linhagens e são considerados responsáveis por moldar os padrões de diversidade e de distribuição de espécies atuais. Nesse estudo, usando diferentes conjuntos de dados, ferramentas e avaliando a história e os processos evolutivos, busquei entender o padrão de distribuição e diversidade de espécies de aves que habitam os domínios de vegetação aberta/seca da América do Sul. No primeiro capítulo, usando dados de censos de aves coletados em campo, apresento estimativas de abundância e produzi a primeira lista de aves que ocorrem em áreas de carrasco, uma fitofisionomia associada à Caatinga. Além disso, identifiquei que a avifauna dos carrascos representa uma parcela da avifauna da Caatinga, em um primeiro estudo visando descrever as afinidades biogeográficas entre Caatinga e Cerrado. No segundo capítulo, usando censos de aves de terceiros e dados de ciência cidadã realizados ao longo da Diagonal Seca Sul-Americana (DS) demostro que os domínios que compõem a DS representam três diferentes unidades em termos de avifauna. Identifiquei o *turnover* como o principal componente da β-diversidade atuando nas comunidades, sendo associado principalmente com a distância geográfica entre os pontos de amostragem, e com variáveis ambientais como temperatura, precipitação, aridez e altitude. No terceiro capítulo, usando genomas completos de 38 exemplares de diferentes subespécies de *Hemitriccus margaritaceinventer*, foi possível evidenciar a existência de dois principais grupos genéticos entre as subespécies, circundando o atual gradiente úmido da Floresta Amazônica, sugerindo assim a existência de uma antiga conexão entre os domínios de vegetação aberta/seca da América do Sul, corroborando a hipótese do Arco Pleistocênico. Também identifiquei para o clado *Hemitriccus* uma origem associada a habitats de floresta úmida, possivelmente com a Floresta Amazônica como fonte de diversificação. No quarto capítulo, usando filogenias para 39 táxons endêmicos de aves da Caatinga, elucidei que a história evolutiva dos endemismos da Caatinga está associada a eventos de vicariância e dispersão, com as florestas secas neotropicais atuando como principal fonte de espécies para a Caatinga, e evidenciando a influência de eventos climáticos históricos como facilitadores nos eventos de dispersão e diversificação de espécies.

Palavras-chave: Florestas Secas; β-Diversidade; Filogeografia; Genomas Completos; Biogeografia.

ABSTRACT

Understanding and describing patterns of diversity and distribution of species and investigating the events and factors that created these patterns is one of the great challenges of science. In the Neotropical region, multiple climatic and geomorphological events are associated with the evolutionary history of lineages and are considered responsible for shaping current species diversity and distribution patterns. In this study, using different sets of data and tools, I sought to understand the distribution pattern and diversity of species that inhabit the open/dry vegetation domains of South America, evaluating their history and evolutionary processes. In the first chapter, using bird census data collected in the field, we present abundance estimates and produce the first list of birds that occur in carrasco areas, a phytophysiognomy associated with the Caatinga, in addition, we identify that the carrasco avifauna represents a portion of the Caatinga avifauna, in a first study aiming to describe the biogeographical affinities between the Caatinga and Cerrado. In the second chapter, using third-party bird censuses and citizen science data carried out along the South American Dry Diagonal (DS), we demonstrate that the domains that compose the DS represent three different units in terms of avifauna, we identify turnover as the main component of β-diversity acting in communities, being mainly associated with the geographic distance between sampling points and environmental variables such as temperature, precipitation, aridity, and altitude. In the third chapter, using whole genomes of 38 specimens of different subspecies of *Hemitriccus margaritaceinventer*, we evidenced the existence of two main genetic groups between the subspecies, surrounding the current humid gradient of the Amazon Forest, thus suggesting the existence of an ancient connection between the open/dry vegetation domains of South America, corroborating the Pleistocene Arc hypothesis, we also identified for the *Hemitriccus* clade an origin associated with humid forest habitats, possibly with the Amazon Forest as a source of diversification. In the fourth chapter, using phylogenies for 39 endemic bird taxa from the Caatinga, we elucidate that the evolutionary history of Caatinga endemisms is associated with vicariance and dispersal events, with neotropical dry forests acting as the main source of species for the Caatinga and evidencing the influence of historical climatic events as facilitators in species dispersal and diversification events.

Keywords: Dry Forests; β-Diversity; Phylogeography; Whole Genomes; Biogeography.

SUMÁRIO

INTRODUÇÃO GERAL

Identificar e descrever os padrões atuais de diversidade e de distribuição de espécies é essencial não só para identificar os mecanismos que levaram aos atuais padrões de distribuição, mas também, para entender os processos de especiação ao longo de escalas espaciais e temporais (Byrne et al. 2008, Fine & Lohmann 2018, Werneck et al. 2012). É sabido que múltiplos eventos, sejam eles eventos históricos ou recentes, podem não só limitar a distribuição das espécies, mas também atuar como indicadores da história evolutiva das linhagens (Silva et al. 2021)

Para a região Neotropical, sabe-se que os padrões biogeográficos atuais da biota são o resultado de uma série de eventos evolutivos complexos que ocorreram durante a formação do continente (Corbett et al. 2020). Mudanças climáticas, tais como as flutuações de temperatura e a alternância entre períodos úmidos e secos, que ocorreram durante o Plioceno e Pleistoceno, influenciaram diretamente nos padrões de distribuição e na extensão das fitofisionomias existentes (Haffer 1969, Prado & Gibbs 1993, Fine & Lohmann 2018). Já eventos geomorfológicos, como o soerguimento dos Andes, a formação da bacia amazônica, e o fechamento do istmo do Panamá, impactaram diretamente na movimentação das espécies (Kattan et al. 2016). Essas modificações foram provavelmente responsáveis por eventos de extinção, substituição geográfica, especiação e estariam diretamente relacionadas com os padrões de distribuição das espécies (Sobral-Souza et al. 2015).

Em florestas úmidas da região Neotropical, como a Amazônia e a Mata Atlântica, a influência de processos históricos no atual padrão de distribuição de espécies já foi bem discutida ao longo do tempo (Sick 1967, Haffer 1969, Costa 2003, Ribas et al. 2012, Batata-Filho et al. 2013). Por outro lado, as comunidades associadas aos domínios de vegetação aberta, são ainda pobremente caracterizadas tanto em termos de padrões biogeográficos, como de estrutura genética das suas espécies (Werneck 2011). Uma das hipóteses mais comumente discutidas e que visa explicar os atuais padrões biogeográficos e de estruturação genética para espécies que habitam esses domínios de vegetação aberta/seca na América do Sul é a ‘Hipótese do Arco Pleistocênico’ (Prado & Gibbs 1993). De acordo com essa hipótese, os atuais fragmentos de vegetação aberta/seca que circundam a região Amazônica, e que estão distribuídos de forma disjunta na América do Sul, teriam sido conectados durante o Pleistoceno, facilitando eventos migratórios e expansão das distribuições das espécies (Prado & Gibbs 1993).

Na América do Sul, as maiores áreas compostas por domínios de vegetação aberta/seca se encontram nas costas caribenhas da Colômbia e Venezuela, em vales secos nos Andes na Colômbia, Peru, Equador e Bolívia, na costa do Equador e norte do Peru, e ao longo do maior bloco contínuo de áreas abertas da região Neotropical, conhecido como a ‘Diagonal Seca sul-americana’ (DS) a qual se estende diagonalmente em uma ampla faixa latitudinal do NE do Brasil até o N da Argentina (Prado & Gibbs 1993, Pennington et al. 2000) (Figura 1). Dentro de todas estas áreas, os domínios de vegetação aberta/seca se apresentam como um complexo de tipos de vegetação, que inclui vários domínios fitogeográficos, dependendo do clima local, do solo e das condições topográficas (Pennington et al. 2000). Como os Llanos (entre Colômbia e Venezuela), Savanas Rupununi (entre a Venezuela e Guiana), vales Andinos (entre Peru e Bolívia), Chiquitano (Bolívia), e os três domínios que compõem a DS, o Chaco, o Cerrado e a Caatinga, dentro da última, também sendo descrita fitofisionomias adjacentes como o Carrasco, que ocorre no topo de alguns platôs dentro dos limites da Caatinga (Araújo et al. 1998, Pennington et al. 2000).

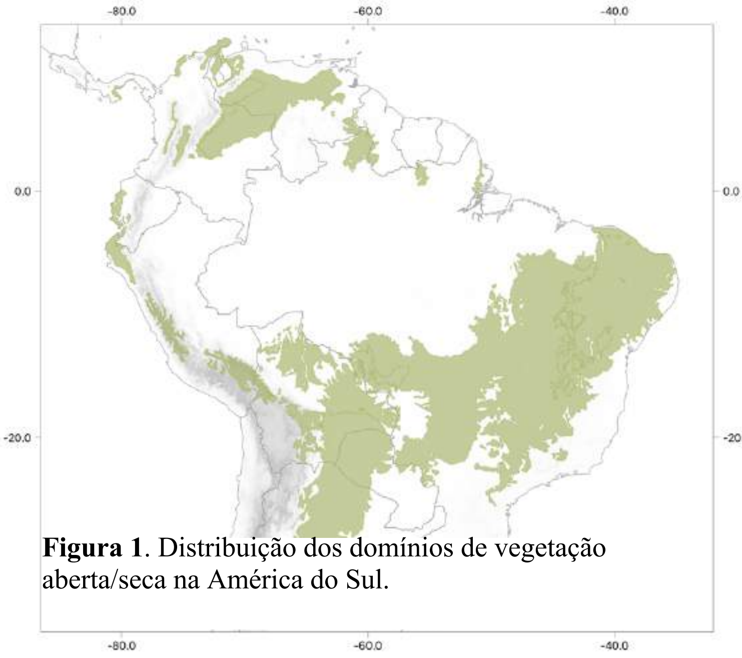

Figura 1. Distribuição dos domínios de vegetação aberta/seca na América do Sul.

Com o aumento na disponibilidade de informação sobre a distribuição geográfica, e as relações filogenéticas entre as espécies, estudos voltados a entender a história evolutiva e biogeográfica dos táxons que habitam esses domínios de vegetação aberta/seca vem sendo mais comuns (Werneck et al. 2012, Prieto-Torres et al. 2019, Corbett et al. 2020). No entanto, lacunas no conhecimento acerca das histórias filogeográficas, dos processos evolutivos, adaptativos e de diversificação que permitiram às espécies a explorar, ocupar e persistir nesses domínios abertos/secos ainda precisam ser preenchidas. Considerando ainda, os diferentes gradientes florísticos e climáticos encontrados ao longo desses domínios, investigar como a variação ambiental pode moldar os padrões de diversidade de espécies e entender como mudanças nas condições climáticas futuras podem levar a mudanças significativas na composição das espécies é extremamente necessário.

Nesta tese, usando diferentes tipos de dados, incluindo dados de distribuição, ecológicos, ambientais, e dados genômicos e filogenéticos, e usando as aves como modelo de estudo, procurei ao longo dos capítulos preencher as principais lacunas de conhecimento acerca da composição, ecologia, história biogeográfica, processos evolutivos e de diversificação das espécies que habitam os domínios de vegetação aberta/seca da América do Sul.

No primeiro capítulo, usando dados coletados em campo, caracterizei a avifauna encontrada em áreas de carrasco, um tipo vegetacional encontrado em platôs da Caatinga. Exploramos as afinidades biogeográficas entre a avifauna presente no carrasco, Caatinga e Cerrado, e identificamos os efeitos do manejo ambiental sob a avifauna. Nesse capítulo, além de produzir a primeira lista de aves que ocorrem em áreas de carrasco, também forneço dados base para futuros estudos de monitoramento que procurem entender os futuros impactos do manejo ambiental na área e descrevo de forma inicial os padrões de diversidade de aves e as afinidades biogeográficas entre Caatinga e Cerrado, dois domínios de vegetação aberta/seca que compõem a DS.

No segundo capítulo, complementei os dados do Capítulo 1 com dados de listas de espécies publicadas em artigos científico e em plataformas de ciência cidadã, buscando descrever os padrões de diversidade de aves ao longo da DS e suas associações com variáveis climáticas e ambientais. Nesse capítulo, descrevi a avifauna que ocorre ao longo do gradiente da DS e identifiquei não só quais os componentes da β-diversidade, mas também, quais variáveis ambientais são responsáveis por estruturar as comunidades de aves ao longo do gradiente Ambiental da DS. Identificando assim, os padrões e fatores responsáveis pelo atual padrão de distribuição das aves. Além disso, levantei informações sobre as relações históricas entre os domínios da Caatinga, Cerrado e Chaco e consequentemente a relação biogeográfica entre os domínios de vegetação aberta/seca da América do Sul.

No terceiro capítulo, busquei elucidar a relação biogeográfica entre os domínios de vegetação aberta/seca da América do Sul. Para isso, utilizei dados de genoma completo para investigar a história evolutiva de *Hemitriccus margaritaceinventer,* uma espécie de ave políptica, com uma ampla distribuição, e que habita de forma alopátrica domínios de vegetação aberta/seca da América do Sul. Nesse capítulo, busquei investigar os padrões de estruturação intraespecífica para elucidar não só a história biogeográfica do grupo como também das áreas de vegetação aberta/seca da América do Sul as quais essa espécie habita. Nesse capítulo, além de prover novos dados acerca das relações filogenéticas, e estrutura da população em *Hemitriccus margaritaceinventer*, forneço evidências sobre conexões históricas entre os atualmente fragmentados domínios de vegetação aberta/seca da América do Sul e o possível efeito que essas conexões desempenharam na diversificação de espécie no continente.

No quarto capítulo, para entender as relações biogeográficas entre os domínios de vegetação aberta/seca e os demais domínios da região Neotropical, utilizei os táxons endêmicos da Caatinga, para conduzir análises de reconstrução de área ancestral e entender os eventos de dispersão e os mecanismos por trás da avifauna endêmica da Caatinga. Nesse capítulo, apresentando um cenário nunca estudado para a evolução e diversificação biogeográfica da Caatinga, demonstrei que a história evolutiva da Caatinga foi influenciada por eventos de vicariância, e dispersão dirigidos pelas mudanças climáticas e geológicas que ocorreram no passado, e que conectaram a Caatinga com outras florestas secas e úmidas da América do Sul.

Dessa forma, em resumo, a obtenção e uso de diferentes níveis de dados nessa tese permitiu gerar informações a nível de espécie, de comunidades e de ecossistemas, preenchendo uma lacuna importante no conhecimento dos domínios de vegetação aberta/seca da América do Sul, sua relação com outros domínios Neotropicais e a influência de eventos climáticos históricos nos padrões de diversidade observados atualmente.

OBJETIVOS

Objetivo geral

Esta tese, através da integração de dados ecológicos, ambientais, e genômicos, tem como objetivo geral entender a história, os padrões e os processos evolutivos que atuaram e atuam na diversidade de espécies de aves observada nos domínios de vegetação aberta/seca da América do Sul.

Objetivos específicos

Especificamente, pretende-se:

i. Explorar as afinidades biogeográficas entre a avifauna presente nos domínios fitogeográficos do Carrasco, Caatinga e Cerrado.
ii. Descrever os atuais padrões de diversidade de aves ao longo da DS e entender como variáveis climáticas e ambientais afetam os componentes de diversidade e estruturam estas comunidades ao longo da diagonal seca sul-americana.
iii. Investigar padrões de fluxo gênico e estruturação genética em populações de uma espécie de ave com distribuição alopátrica em florestas secas da América do Sul.
iv. Entender os mecanismos que levaram aos atuais endemismos de aves da Caatinga e entender as relações biogeográficas entre os domínios de vegetação aberta/seca e os demais domínios da região Neotropical.

Capítulo II.

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Environmental gradients as drivers of avian diversity along the South American Dry Diagonal
Manuscrito submetido – Diversity and Distributions *A1*

Environmental gradients as drivers of avian diversity along the South American Dry Diagonal

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Abstract

Climatic conditions and geomorphological features are known as the main variables acting in the patterns of species distributions, but the way in which these conditions and features impact the structuring of communities across different biomes is not well explored. The South American Dry Diagonal (SADD), a corridor of open/semi-arid formations along the South American continent, exhibits unique environmental conditions throughout its extension representing an ideal place to assess how environmental condition structure the communities. Here, to elucidate the effects of environmental variables and geographic distance on total β-diversity and its components along the sampling points, we used bird species presence/absence data from 26 protected areas, distributed throughout the entire length of the SADD, in generalized dissimilarity models associated with environmental information. We compiled a bird list of 827 bird species along the SAAD gradient. Our results indicated that the avifauna of the three phytogeographic domains who compose the SADD represent three distinct units, in terms of avifauna, with a significant proportion of species been shared among all sampled sites. The spatial dissimilarity along the gradient and within the domains was explained by the turnover component. Geographic distance was the main predictor of total β-diversity and species turnover among SADD avian communities, followed by variation in the precipitation, temperature, and elevation. Considering the absence of main geographic barriers along the SADD gradient, our results indicate the importance of environmental variables in the structuring of bird communities along the SAAD and highlights the importance of developing conservation strategies to protect these domains under a scenario of future climate changes that could directly impact the communities that inhabit this system.

Keywords bird communities, biogeography patterns, beta diversity, species turnover, nestedness

Introduction

Identifying the factors that govern general patterns of species diversity is essential to understand ecological processes and ultimately conserving biodiversity. Large-scale global analyses have shaped our knowledge of how biological diversity is organized in space, pointing to interaction between latitudinal and altitudinal gradients, and environmental variables (Rohde 1992, Gaston 2000, Jetz et al. 2012). Contemporary climatic factors, such as temperature and precipitation, largely explain general patterns of Neotropical avian species diversity. Specifically, warmer, and wetter environments sustain more species than colder and drier ones (Hawkins et al. 2003). However, climate does not act alone, and a synergy with topographic complexity and ecosystem diversity primarily explains regional diversity (Rahbek & Graves 2001).

Multiple processes acting at different scales, such as historic climatic shifts, and/or recent anthropogenic changes, likely limit species distributions and represent a complex expression of species' ecology and evolutionary history (Ceron et al. 2021, da Silva et al. 2021). Whereas global or continental-scale meta-analyses offer important insights into general patterns across different biomes, they lack the necessary precision to identify changes at finer scales (i.e., within biomes) (Prieto-Torres et al. 2019). For instance, not only different variables, such as temperature, precipitation, and altitude, can affect patterns of species diversity, but they can do so in different manners across biomes (Pennington et al 2004, Neves et al. 2015). For instance, small changes in topography are known to affect avian species distributions within humid forests (Cintra & Naka 2012, Gerolamo et al. 2022), while their effect may be negligible in drier environments (Neves et al. 2015, Silva & Souza 2018). Furthermore, ecotones along environmental gradients play a critical role in determining species replacement patterns (Naka et al. 2020). Therefore, understanding the mechanisms driving assemblage composition across environment continuums and ecotones, may improve our knowledge of eco-evolutionary processes that determine range limits of species distributions (Miranda et al. 2018, McNew et al. 2021).

One region that is particularly interesting to assess the mechanisms behind patterns of alfa and beta diversity across biomes is the South American Dry Diagonal (hereafter SADD), a corridor of open/semi-arid formation that spans tropical and sub-tropical South America from Northeastern Brazil to Central Argentina (Prado & Gibbs 1993). The SADD covers a continental-scale gradient that includes three key Neotropical phytogeographic domains: i) the semi-arid thorny woodlands of the Caatinga dry forest of northeastern Brazil, ii) the fire-adapted seasonal woody savannas of the Cerrado in central Brazil, and iii) the Chaco dry woodlands from northeastern Argentina, western Paraguay, and south-eastern Bolivia (Miranda et al. 2018). Although much of the SADD is bounded by tropical or subtropical forests, such as the Amazon and the Atlantic Forest (Prado & Gibbs 1993, Carmignotto & Astúa 2022), environmental conditions differ among SADD domains. The Caatinga domain, for example, represents a semi-arid (< 1500 mm/year), highly seasonal (< 5 months of drought), tropical domain (monthly temperatures between 24 and 26°C) covering the interior of northeastern Brazil (Werneck 2011, Luebert 2021). The Cerrado, on the other hand, represents a fire-adapted ecosystem that receives larger amounts of seasonal rainfall (800-2000 mm/year) (Pennington et al. 2000, Werneck 2011, Luebert 2021). Finally, the Chaco has a semi-arid climate (500 -1000 mm/year), with high climatic seasonality (cold winters and very hot summers) (Pennington et al. 2000, Luebert 2021).

This mixture of unique environmental conditions makes the SADD an ideal place to address how environmental variation can shape species diversity patterns, as specific climatic changes (rainfall, aridity, temperature) can lead to significant changes is species composition (Silva & Souza 2018). Also, despite considerable advances in the last decade, patterns of species diversity remain poorly understood in open and drier environments, such as the SADD, relative to those in forested environments in the southern Hemisphere (Beheregaray 2008, Byrne et al. 2008), where few studies have focused on understanding general patterns of species richness in these open/dry domains (see Prieto-Torres et al. 2019).

The biological relevance of the SAAD is widely recognized, as it includes known biodiversity hotspots (Myers et al. 2000) and exhibits high levels of biological endemism (Werneck 2011). Despite its importance, this region continues to be severely impacted by the loss and fragmentation of natural habitats (Werneck 2011, Colevatti et al. 2013). Climatic models also suggest that the SADD will fare poorly under novel climate conditions due to climate change, which predict more extensive and devastating fires and more pronounced and prolonged droughts (Miranda et al. 2018, da Silva et al. 2021). Future environmental changes due to human interference can directly impact avian communities along these domains and may lead to changes in species distributions, local extinctions, and changes in patterns of species' functional and phylogenetic diversity (da Silva et al. 2021). Counting on accurate and comprehensive baselines of geographical patterns of biodiversity distribution is critical to shed light on the SADD's response to future climatic and environmental challenges (da Silva et al. 2021).

The SADD phytogeographic and climatic diversity represents an ideal system to study how phytogeographic domains can limit and structure biological communities. The structuring of biological communities can be analyzed in terms of total β-diversity (dissimilarity in species composition across communities), and its components, namely the spatial turnover (replacement of species across sites) and nestedness (related to the gain or loss of species in the communities, when the biota of one site is a subset of a more diverse site) (Baselga & Orme 2012). Recent studies have shown low numbers of shared species among SADD phytogeographic domains in plants (Neves et al. 2015) and marsupials (Carmignotto & Astúa 2022), resulting in high levels of species turnover among sites and ecosystems. For other taxa, even of well-known groups, such as birds, these questions remain unknown.

Here, we used avian community data from 26 well-sampled protected areas distributed along an environmental gradient of ~ 4,000 km, spanning from NE Brazil to C Argentina, to describe avian diversity patterns along the SADD and their associations with geographical and climatic variables. Specifically, we aim to i) describe how avian species composition varies across different phytogeographic domains (Caatinga, Cerrado, and Chaco), ii) evaluate species turnover and nestedness to describe spatial patterns of β-diversity, and iii) investigate how avian species composition responds to climatic variation along the SADD. We built a species presence/absence data matrix for each locality and used generalized dissimilarity models (GDM) and environmental information to map avian β-diversity components and identify overlap and transition hotspots. We show that the three domains that form the SADD represent three different units in terms of their avifauna. Species turnover is the main component of total β-diversity ruling bird communities, with the differentiation between sites increasing primarily in association with geographic distance and influenced by environmental variables such as temperature, precipitation, aridity, and elevation. Our study provides novel data into the factors and patterns leading to current avian distribution patterns along the SADD and the historical relationship between the Caatinga, Cerrado, and Chaco and sheds light into the importance to formulate conservation plans to protect the endangered phytogeographic domains, who compose the SADD, to the potential impacts that anthropogenic disturbances and climate change will have on its avifauna.

Methods

Avian inventories

We compiled avian community composition for 26 well-sampled protected areas along the SADD (Figure 1), covering nearly 37° of latitude (~4,000 km), from the northernmost Parque Nacional de Ubajara, in northeastern Brazil (latitude 3°50' N), to the southernmost Parque Nacional Traslasierra, in central Argentina (latitude 31° S). Sampled localities had a minimum distance of about 1 latitude degree (~110 km). This latitudinal transect covers the entire precipitation and seasonality gradient found along the SADD. We selected protected areas to minimize confounding effects of human activities on avian community composition. When no protected areas were available at a particular latitude, we selected preserved areas with minor environmental and human interference. Sampled localities included 12 sites in the Caatinga, seven in the Cerrado, and seven in the Chaco (Figure 1).

Avian community composition

To build our dataset, we included published avian inventories and third-party observations available in citizen science databases, such as ebird (https://ebird.org/) and Wikiaves (www.wikiaves.com.br), complemented by our own field observations, when available. We carefully curated the dataset to avoid misidentifications and followed the taxonomic classification and nomenclature by Pacheco et al. (2021) for species that occur in Brazil and the nomenclature of the ebird/Clements Checklist (Clements et al. 2022) for species occurring exclusively outside Brazil. For published avian inventories, we used species listed within the boundaries of the protected areas. For lists obtained from citizen science platforms, we selected only species identified as occurring within the boundaries of our sampling localities. Species were assigned to specific ecosystems – Caatinga, Cerrado, and Chaco – according to the predominant biome classification of each of our sampling localities (ICMBIO 2023, UC Socioambiental 2023).

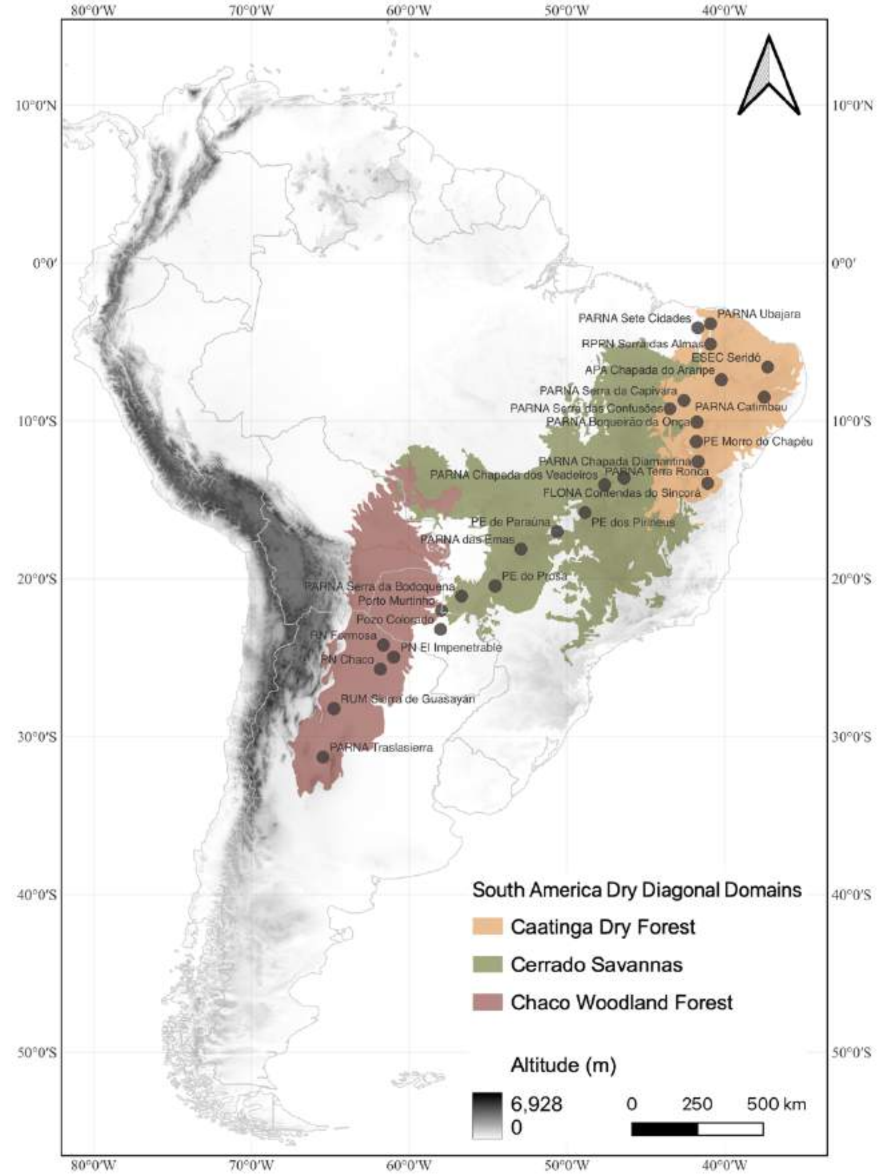

Figure 1. Location of the South American Dry Diagonal (SADD) and its three main ecosystems: Caatinga – orange, Cerrado – green, and Chaco –brown. Black dots denote the 26 protected or well-preserved areas used as sampling localities to conduct diversity spatial analyses. Sampled localities had a minimum distance of about 1 latitude degree (~110 km). Acronym locality names in English stand for: APA –Environmental Protection Area; ESEC – Ecological Station; FLONA – National Forest; PARNA – National Park; PE – State Park; RN – Natural Reserve; RPPN – Private Reserve of Natural Patrimony; RUM – Multiple Use Reserve. Localities without acronyms do not have an official protection status.

Avian similarity and β-diversity

We used the "*iNEXT*" R package (Hsieh & Chao 2016) to evaluate sample coverage, species diversity, and to apply species richness estimators for each locality in the presence/absence matrix. To understand patterns of avian community composition along the SADD, we first used Jaccard's dissimilarities distance (Sneath 1957), as the dissimilarity metric, to create a pair-wise dissimilarity matrix between sampled localities. Values in the dissimilarity matrix range from 0 to 1, with 0 representing complete similarity and 1 representing lack of species in common. We used the dissimilarity matrix to perform a hierarchical cluster analysis and a non-metric multidimensional scaling (NMDS) (Gower 1966) to visualize similarities or not between sampling localities. We applied a permutational analysis of variance (PERMANOVA) (Anderson 2001) to compare groups based on species composition. We created interaction networks between sampling localities using the proportion of shared species obtained from the Jaccard matrix to explore avian interactions between sampling localities using packages "igraph" (Csardi & Nepusz 2006), "ggraph" (Pedersen et al. 2017) and "network" (Butts 2008).

We also used a presence/absence locality matrix to estimate the β-diversity, including its turnover and nestedness components, and to create a pair-wise site dissimilarity matrix containing dissimilarity values for each β-diversity component between sampling localities. We calculated total β-diversity, turnover, and nestedness using the *beta.pair* function in the "*betapart*" R package (Baselga & Orme 2012). To compare spatial patterns of total β-diversity within and among ecosystems (Caatinga, Cerrado, and Chaco), we evaluated the contribution of turnover and nestedness components in each domain. All statistical analyses and networks were performed in R 4.2.1 (R Core Team 2022).

Environmental data

To characterize climatic variation and test the effect of environmental variables and geographic distance on total β-diversity and its components (turnover and nestedness) along the SADD and within the Caatinga, Cerrado, and Chaco, we extracted 14 environmental variables from WorldClim 2.0 (Fick & Hijmans 2017) at a 2.5-arc minute (5km) resolution, which included: i) Elevation, ii) Annual mean temperature (BIO1), iii) Temperature seasonality (BIO4), iv)

Maximum temperature of warmest month (BIO5), v) Minimum temperature of coldest month (BIO6), vi) Mean temperature of wettest quarter (BIO8), vii) Mean temperature of driest quarter (BIO9), viii) Annual precipitation (BIO12), ix) Precipitation of wettest month (BIO13), x) Precipitation of driest month (BIO14), xi) Precipitation Seasonality (BIO15), xii) Precipitation of wettest quarter (BIO16), and xiii) Precipitation of driest quarter (BIO16). We also obtained a layer for aridity V3 from Trabucco & Zomer (2022). We estimate geographical distance between sampled localities using each site's geographic coordinates (see Table 1). The center of each sampling locality was estimated considering a minimum distance of about 1 latitude degree (~110 km) between each one of the sites (Figure 1).

To minimize the effects of highly correlated environmental variables and to extract and summarize precipitation and temperature variables, we ran principal components analyses on these variables to create composite measures along the SADD using the package "*raster*" (Hijmans et al. 2015) (Figure S1). Values were obtained from the centroid of each sampling locality. We then used temperature and precipitation values using the values from the first PC axis (PC1) for each sampling locality. Similarly, we also used the centroides of each locality to extract aridity and elevation mean values, using the "*raster*" package (Figure S1).

Generalized dissimilarity models

We tested the relative contributions of each environmental variable and the geographic distance between sampling localities for predicting avian species β-diversity, turnover, and nestedness using Generalized Dissimilarity Models (GDM) from the R "*gdm*" package (Ferrier et al. 2007, Fitzpatrick et al. 2020). We fit separate models predicting taxonomic total β-diversity (using Jaccard's dissimilarity matrix), species turnover, and nestedness (using the turnover and nestedness pair-wise site distance matrices obtained from the function *beta.pair* on *betapart* package) as response matrices.

We first fit full models using all our selected environmental variables (geographic distance, temperature (first PCA axis), precipitation (first PCA axis), elevation, and aridity) as variables that could possibly predict β-diversity, turnover, and nestedness along the SADD. After fitting full models, we selected the most informative models to explain the greatest amount of variance with the fewest predictors using the backward-elimination selection strategy following the model fitting steps proposed by Ferrier et al. (2007). Model fitting and the importance of the predictors were evaluated by summarizing the GDMs, where the predictor importance is quantified as the percent change in deviance explained between a model fit with all variables and without each one of the predictors used (Ferrier et al. 2007, Fitzpatrick et al. 2011). We then checked the height of the splines to understand the effect of each environmental variable on the β-diversity components. We also created maps of species dissimilarity and species turnover using best GDMs which we projected back onto *rasters* of the predictor environmental variables following Mokany et al. (2022) and an adapted code from McNew et al. (2021). All environmental and modeling were performed in the software R 4.2.1 (R Core Team 2022).

Results

Avian inventories

In total, we compiled occurrence records for 826 bird species across the 26 sampling localities, representing 28 Orders and 80 avian families (Table S1). The number of species was relatively similar across ecosystems, including 506 species in the Caatinga (104 exclusive, only recorded in this domain), 554 in the Cerrado (94 exclusive, only recorded in this domain), and 527 in the Chaco (150 exclusive, only recorded in this domain) (Table S1). Extrapolation and mean values of rarefaction percentages of sampling coverage were high for the three domains, including 95% for the Caatinga, 94% for the Cerrado, and 93% for the Chaco (Figure S2).

Avian similarity and β-diversity patterns

Our results indicate that the avifauna of the phytogeographic domains investigated (Caatinga, Cerrado and Chaco) represent three distinct units, grouped into three independent clusters (PERMANOVA, $F=7.3756$, $R^2=0.390$, $p<0.01$), according to pair-wise Jaccard dissimilarity values (Figure 2a). Similarity values among ecosystems were relatively high, including 56% similarity between the Caatinga and the Cerrado (0.434, Jaccard index), 49% similarity between the Cerrado and Chaco (0.503, Jaccard index), and 40% similarity between the Caatinga and the Chaco (0.591, Jaccard index) (Figure 2b).

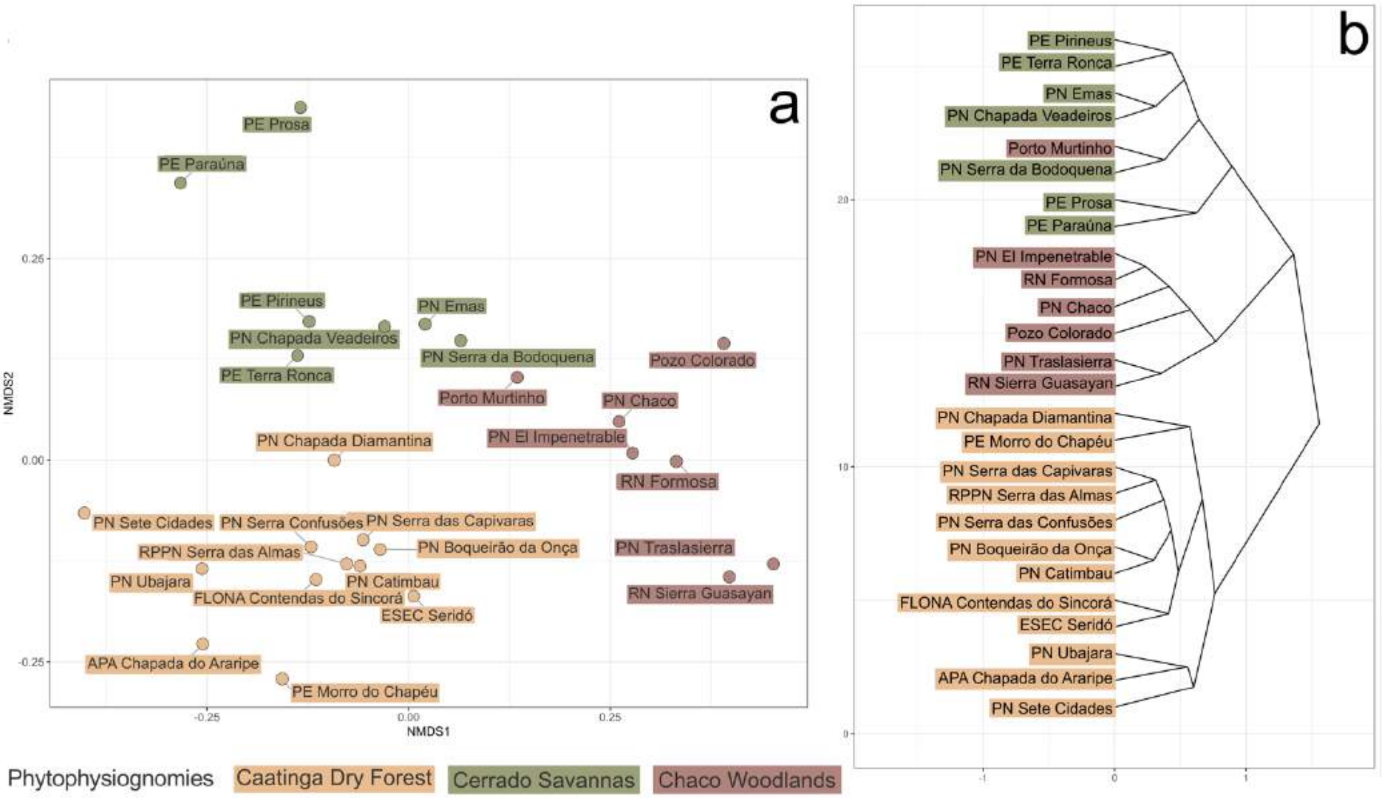

Figure 2. Species composition similarity of bird communities along the South American Dry Diagonal (SADD) recover three distinct units that primarily mirror the Caatinga, Cerrado and Chaco. a) Multidimensional scaling and b) Hierarchical cluster analysis showing spatial similarity between bird communities according to Jaccard's dissimilarity values.

Despite the separation in three distinct groups, the proportion of shared species between localities was high and all localities shared species with one another. A total of 282 (34%) species were recorded at all sampling localities. The number of shared species ranged from 37, between Pozo Colorado (Chaco) and Sete Cidades National Park (Caatinga locality), to 334, between Emas National Park (Cerrado) and Chapada dos Veadeiros National Park (Cerrado) (Figure S3, Table S2). The proportion of shared species ranged from 12.6%, between Traslasierra National Park (Chaco) and Sete Cidades National Park (Caatinga), to 76.4%, between El Impenetrable National Park (Chaco) and Formosa Natural Reserve (Chaco) (Figure 3, Table S3).

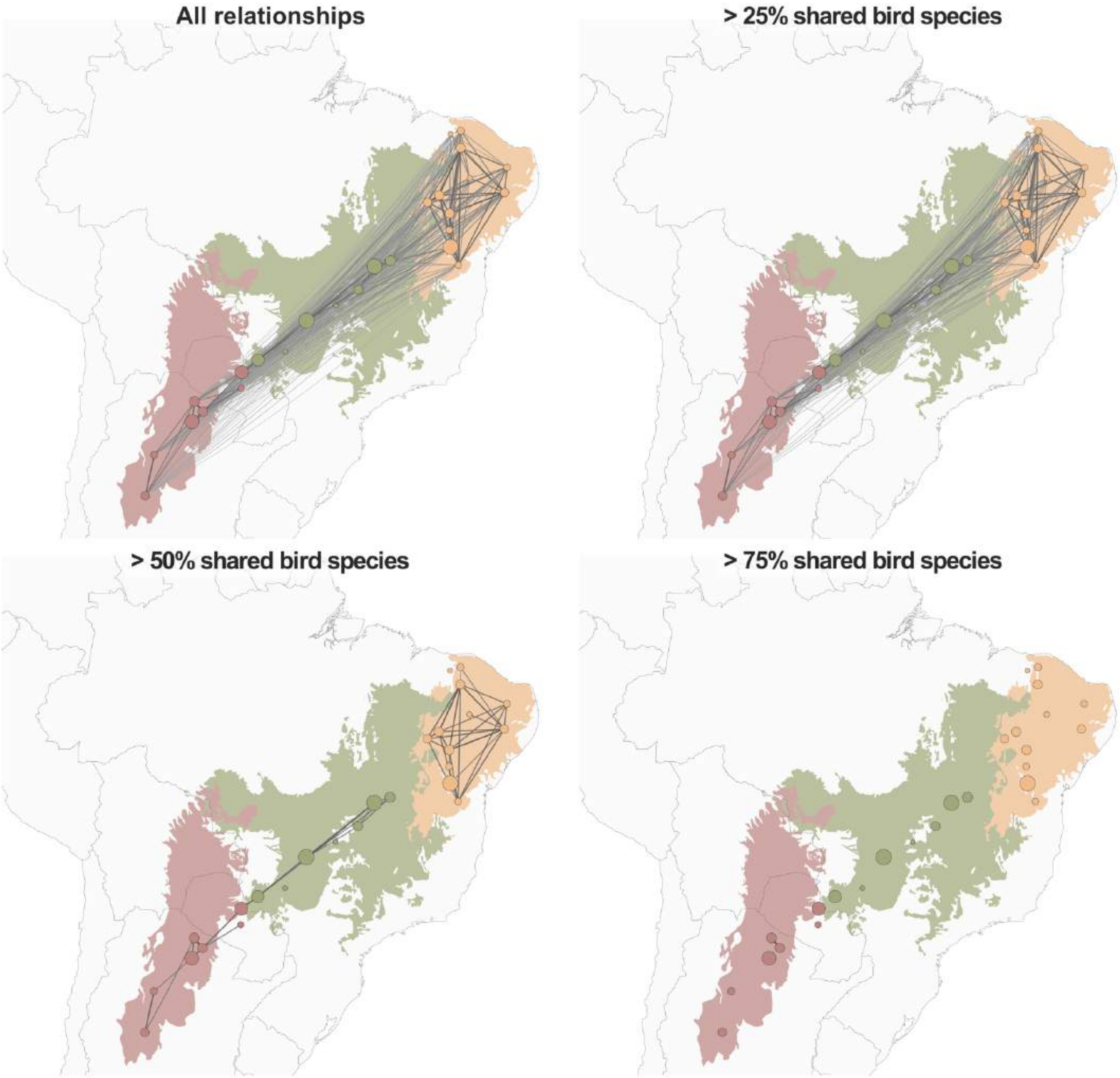

Figure 3. Proportion of shared species between 26 sampling localities along the South American Dry Diagonal (SADD). Circles correspond to sampling localities. Circle color denote phytogeographic domains (see Figure 1). Circles sizes represent the number of species recorded in each sampling point (Table S2). Line colors and thickness represent the proportion of shared species among localities. Light grey and thinner lines represent fewer proportion of shared species and dark grey and thicker lines represent higher proportion of shared species.

In relation to the β-diversity components, sampling localities also grouped communities in three different clusters (Figure S4). The complete multiple-site dissimilarity (overall β-diversity) in species composition along the SADD was high (~93%), and was dominated by turnover, which represented ~89% of the spatial dissimilarity (Figure S4), while nestedness represented less than 5% of the spatial dissimilarity (Figure S4). Within ecosystems, multiple-site dissimilarity (overall β-diversity) remained relatively high, including 82% in the Caatinga, 76% in the Cerrado, and 75% in the Chaco (Figure S5). The turnover/nestedness rate within the ecosystem was larger for the Caatinga (5.8; 70/12), than for the Cerrado (4.0, 51/25), and the Chaco (2.04, 60/15) (Figure S5).

Avian similarity and environmental variables

Despite the large latitudinal gradient investigated (spanning ~28° of latitude), climatic and topographic variation along the SADD is relatively low. Mean altitude ranged from 74 to 1,261 m asl (± 1,187 m), mean precipitation ranged from 536 to 1,676 mm (1,140 mm variation) and mean temperature ranged from 19.7 to 26.7 (7 °C variation) (Table 1, Figure S1).

In general, our results indicate that geographic distance was the strongest and most important predictor of both total β-diversity and species turnover among SADD avian communities (Figure S6). Precipitation variation, temperature variation, and elevation were also important variables to explain both total β-diversity, species turnover, and nestedness patterns along the SADD, but with different importance rates (Figure S6). Aridity was also selected as an important variable, but only to explain species turnover within avian communities (Figure S6).

When considering explanatory variables of avian β-diversity, turnover, and nestedness within the three phytogeographic domains investigated, we found that the main drivers differed among them. For instance, elevation was the most important predictor of total β-diversity for the Caatinga Dry Forest, whereas temperature appeared as the most important predictor of total β-diversity for the Cerrado and the Chaco (Figure S6). On the other hand, variation in aridity, geographic distance, and temperature were the strongest predictors of species turnover for the Caatinga, Cerrado and Chaco, respectively (Figure S6). Variables associated with environmental conditions, such as elevation, temperature and precipitation were the most important predictors for nestedness within phytogeographic domains (Figure S6). Because at least three different variables are required to build GDMs, we did not build a nestedness model for the Chaco.

Table 1. Values of environmental variables used to predict total β-diversity and species turnover and nestedness in 26 localities along the South American Dry Diagonal, ordered by latitude. Temperature (Temp.), precipitation (Prec.) and elevation (Elev.) represent median annual values and were obtained from Wordclim 2.0 (Fick & Hijmans 2017); aridity information was obtained from Trabucco & Zomer (2022).

Sampling localities	**Ecosystem**	**Lat**	**Long**	**Temp. (°C)**	**Prec. (mm)**	**Elev. (m)**	**Aridity Index**
PN Ubajara	Caatinga	-3.84	-40.91	22.36	1,402	724	0.89
PN Sete Cidades	Caatinga	-4.32	-42.02	26.77	1,574	126	0.83
RPPN Serra das Almas	Caatinga	-5.14	-40.92	23.26	950	643	0.58
ESEC do Seridó	Caatinga	-6.60	-37.26	26.60	760	206	0.43
APA Chapada do Araripe	Caatinga	-7.30	-39.55	21.46	1,003	914	0.61
PN do Catimbau	Caatinga	-8.51	-37.46	22.81	536	541	0.35
PN Serra da Capivara	Caatinga	-8.70	-42.59	25.17	758	549	0.38
PN Serra das Confusões	Caatinga	-9.22	-43.49	24.35	795	671	0.44
PN Boqueirão da Onça	Caatinga	-10.07	-41.78	24.63	630	602	0.33
PE Morro do Chapéu	Caatinga	-11.31	-41.80	22.69	622	762	0.34
PN Chapada Diamantina	Caatinga	-12.58	-41.70	20.56	696	1,013	0.42
PE Terra Ronca	Cerrado	-13.62	-46.39	24.43	1,352	639	0.72
FLONA Contendas do Sincorá	Caatinga	-13.94	-41.09	23.43	624	372	0.38
PN Chapada dos Veadeiros	Cerrado	-14.04	-47.62	20.82	1,676	1,261	1.28
PE dos Pirineus	Cerrado	-15.80	-48.87	20.89	1,632	1,204	1.07
PE Paraúna	Cerrado	-17.00	-50.63	23.06	1,664	670	0.91
PN das Emas	Cerrado	-18.12	-52.91	21.38	1,612	854	0.99
PE do Prosa	Cerrado	-20.45	-54.56	23.04	1,466	647	0.92
PN Serra da Bodoquena	Cerrado	-21.09	-56.69	22.21	1,328	605	0.84
Porto Murtinho	Chaco	-22.01	-57.96	24.60	1,134	74	0.80
Pozo Colorado	Chaco	-23.21	-58.01	23.98	1,169	86	0.71
RN Formosa	Chaco	-24.20	-61.64	22.92	677	173	0.39
PN El Impenetrable	Chaco	-24.96	-60.98	22.45	822	141	0.48
PN do Chaco	Chaco	-25.73	-61.82	22.20	672	168	0.39
RN Sierra Guasayan	Chaco	-28.22	-64.77	19.77	667	413	0.38
PN Traslasierra	Chaco	-31.30	-65.47	19.85	578	330	0.33

Total avian β-diversity and species turnover increase with geographic distance along the SADD, in general, and within the Caatinga and Chaco in particular (Figure 4). Within the Cerrado, geographic distance seems to influence total β-diversity at meso-scales (~400km), a distance that correspond to ~60% of the Cerrado. Beyond this distance, geographic distance appears to saturate and no longer acts as a main driver of total β-diversity in Cerrado (Figure 4).

Precipitation and temperature played different roles on β-diversity patterns. Both precipitation and temperature increase β-diversity and nestedness along the gradient, but temperature seem to rapidly saturate and no longer influence β-diversity components. We observed a similar pattern on species turnover, suggesting that the effects precipitation and temperature variation were primarily local (Figure 4). Elevation affected total β-diversity along the SADD, increasing gradually until 1,000 m, and saturating above this value. In the Caatinga, elevation showed a linear relationship with an expressive increased effect from 800m (Figure 4). In the SADD, the effect of elevation in species turnover reaches a threshold at 400m. The same pattern was observed for nestedness in the Caatinga (Figure 4). In the Cerrado, elevation influenced species turnover at 600m, after which, it saturates, whereas in the Chaco, species turnover increased linearly over the elevation gradient (Figure 4). Along the SADD, the Caatinga, and the Chaco, total β-diversity and species turnover increased nearly linearly along the aridity gradient, where, apparently, with the increase of humidity (from 0.5 in the aridity index) acting more quickly in the total β-diversity and species turnover (Figure 4).

Our geographic projection of the GDMs for total β-diversity showed a continuous variation in β-diversity, turnover, and nestedness (Figure 5), highlighting the importance of ecotones between phytogeographic domains. Also, the three ecosystems appear as three distinct groups varying with the latitudinal gradient along the SADD (Figure 5). Areas of high β-diversity and species turnover, represented by contrasting colors, can be seen at the western limit of the Cerrado and the Southern Chaco, where these regions are in contact with other domains with characteristics that are more dissimilar to those of the dry diagonal (i.e., Pantanal and Monte Desert) (Figure 5). Our map projections also highlight known topographic features, such as high elevation areas in the Caatinga, denoting the high species turnover that occurs in high elevation environments (Figure 5).

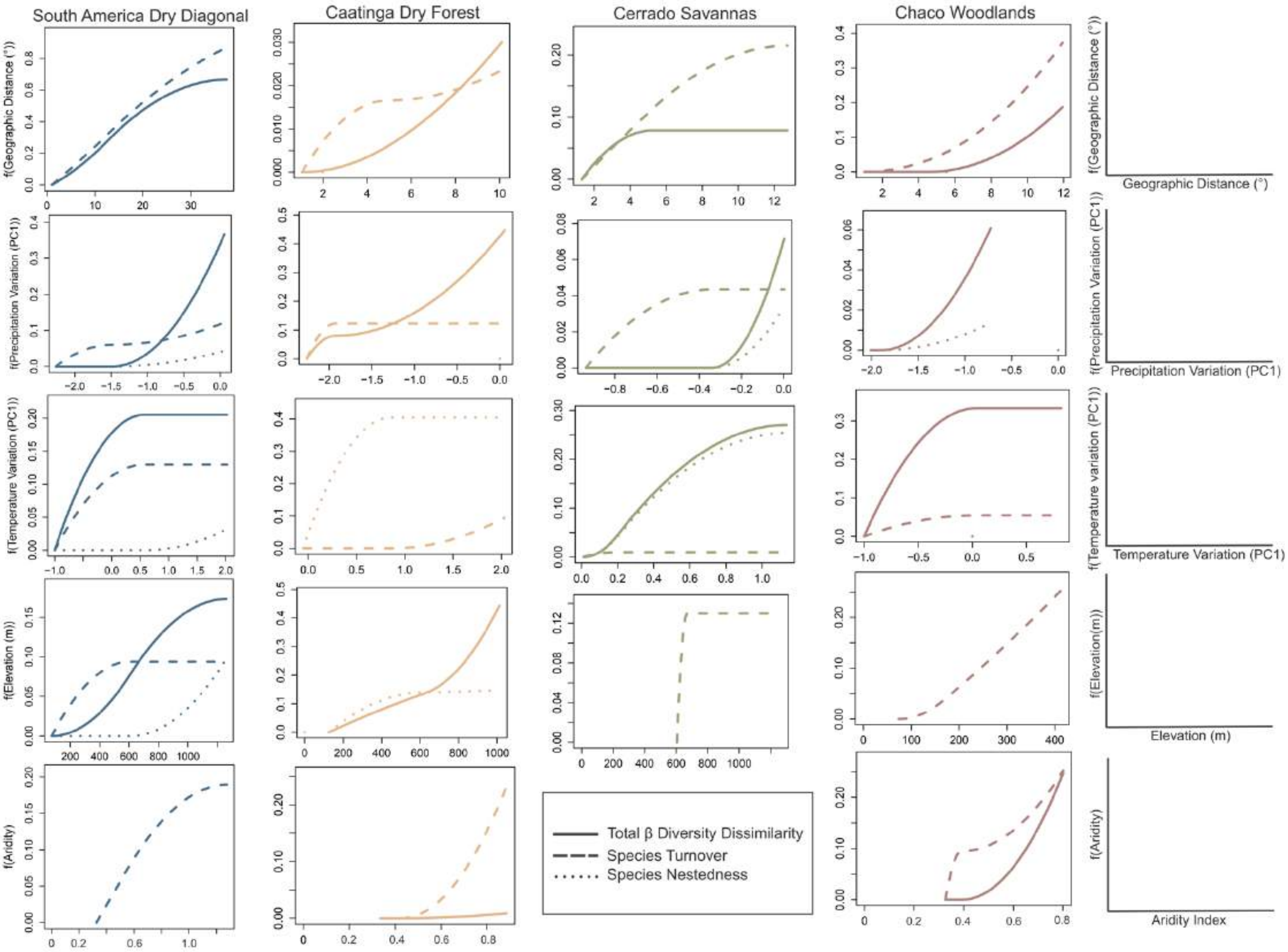

Figure 4. Best predictors and I-splines of species total β-diversity, species turnover and nestedness components along the South America Dry Diagonal communities, and individually for the Caatinga, Cerrado and Chaco. The I-splines show the fitted relationship between GDMs predictor variables and total β-diversity components. Predictor variables are on the x axis, and model tranformed values of that predictor are on the y axis. The maximun height of each spline panel indicates the magnitude of total biological change along that gradient and the relative importance of each environmental variable in contributing to total β-diversity, species turnover and nestedness. Splines are only shown for factors included in the best model for each turnover measurement.

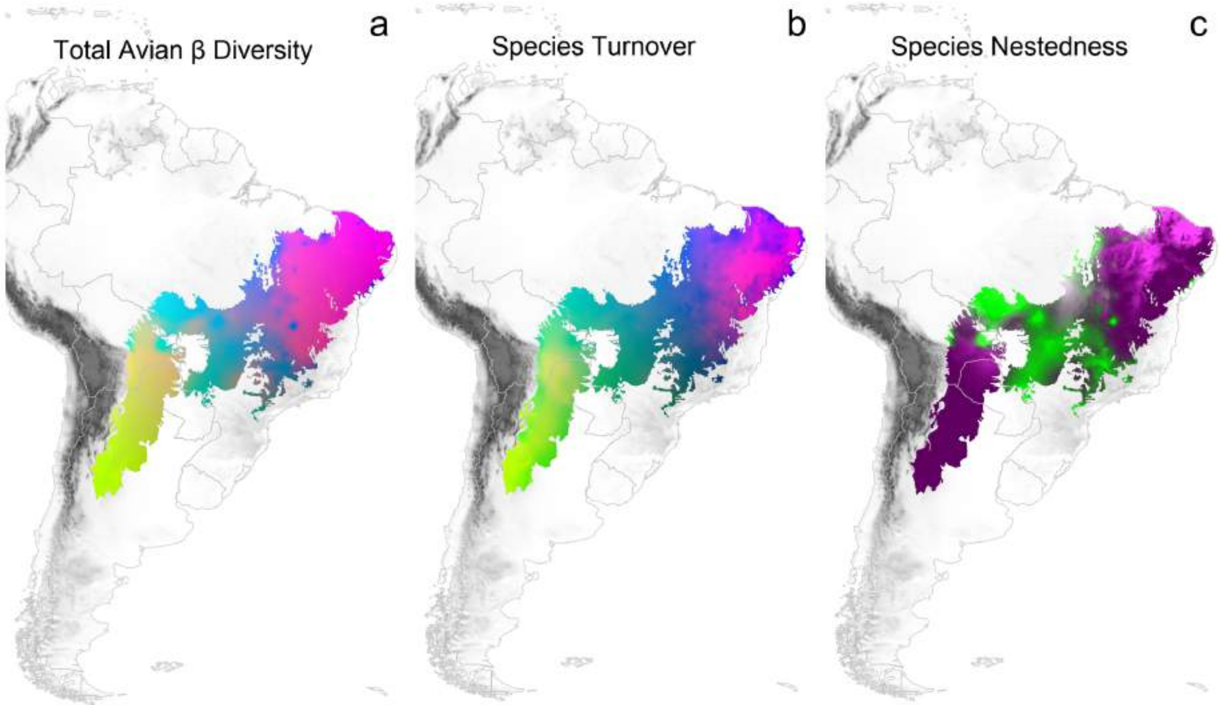

Figure 5. Maps depicting total avian β-diversity (a), species turnover (b), species nestedness (c), created using the best evaluated GDMs models (Figure S6) onto the raster of the best predictor variables for each β-diversity component. Similar colors in the maps indicate areas expected to have similar bird species composition or similar communities.

Discussion

In this study, we used avian community composition data to investigate how environmental condition are acting on the structure avian species diversity and assess patterns of total β-diversity, and its turnover and nestedness components, along the South American Dry Diagonal. We observed that the Caatinga, Cerrado, and Chaco represent three different units in terms of their avifauna, albeit they share many species. This is particularly interesting given the lack of geographical barriers between the three ecosystems, suggesting that their delimitation is mostly defined by environmental variables, such as climate, seasonality, and elevation. Species turnover clearly represents the main component of total β-diversity across avian communities, with both the total dissimilarity between avian composition and species turnover increasing primarily in association with geographic distance and influenced by temperature, precipitation, aridity, and elevation. Our results are indicating that the SADD is formed by three distinctive ecosystems contrast with earlier studies that interpreted the SADD as a single complex of low-diversity open formations, without regionally distinct biotas (Werneck 2011, Werneck et al. 2012).

Avian diversity patterns across the SADD

With almost 900 species of birds, the SADD is a region of high biogeographical importance, not only by dissecting the two main humid forest at the continental scale (the Amazon and the Atlantic Forest), but by representing a main corridor for open habitats in the continent. Despite lacking humid tropical forests, which are known for hosting a disproportionately high number of species, the SADD includes nearly a third of the avian diversity of South America. According to our data, the three phytogeographic domains have a relatively similar avian species richness with more than 500 species, with a slightly larger number in the Cerrado (554) than the Chaco (527) and the Caatinga (506). These figures are in concert with recent estimations obtained using different methodologies for the Caatinga (e.g., Araujo & Silva 2017, Lima 2021, and Leandro-Silva, in prep.), but seem to underestimate species richness for the Cerrado, for which, recent studies estimate around 700 species (Leandro-Silva, in prep.), this is likely due to the subsamples that we used in our analyses, which do not include ecotone areas or marginal and migrant species.

Although we found that each phytogeographic domain represents an independent biogeographical unit, we found clear avian similarities along the SADD, with over 30% of shared species among all sampling localities. Both, the Caatinga and the Cerrado, and the Cerrado and the Chaco shared over half of their bird species. The number of species in common drops to 40% between non-adjacent ecosystems (Caatinga and Chaco), despite their similarities in climate and vegetation structure, with common floristic adaptations to draughts (Pennington et al. 2000, Werneck 2011, Neves et al. 2015). The high number of shared species along the SADD's avifauna is similar to previous floristic studies, which found a similar pattern of shared species between sampling localities (Neves et al. 2015).

Avian similarities along the SADD could be explained by at least three different non-exclusive hypotheses. On the one hand, it is possible that current avian similarities are the result of current environmental conditions and the relatively low climatic and topographic variation found along the SADD. However, given the relatively large number of endemic species and lineages that thrive along the SADD, it is likely that history has played a key role in the structuring of current avian communities. If history has indeed played a role, then remains to be understood how and when. Current avian diversity patterns could be attributed to recent Pleistocene history (Prado & Gibbs 1993). According to the Pleistocene Arc Hypothesis (hereafter, PAH) put forward by Prado & Gibbs (1993), the SAAD represented a climatically stable area during most of its history, but dramatically changed its climate and vegetation boundaries during glacial/interglacial fluctuations during the Late Pleistocene (Mayle 2004, Werneck 2011). According to this model, the Chaco and Caatinga expanded during glacial periods forming a once continuous patch of Dry Forest, which retracted during interglacial periods. Although this idea offers a credible background to explain species similarities between the Caatinga and the Chaco, it neglects to explain how the Cerrado avifauna persisted through time in the landscape. However, since the SAAD's avifauna seems to have different evolutionary histories, it is possible to assume that current avian diversity gradient found are the result of more ancient evolutionary and biogeographic processes which occurred along the evolutionary history of this region (Arango et al. 2021). Therefore, it is possible that ancient events of *in situ* diversification and subsequent dispersal among the three domains facilitated by common climatic conditions, have defined major avian distribution patterns in this region. This hypothesis is based on the structural and vegetation similarities and relatively low climatic and topographic variation found along the SADD (Mayle 2004). According to this model, niche conservatism, rather than fragmentation of a once-continuous dry forest could explain current patterns (Mayle 2004). Recent studies on plant assemblages traced evolutionary and biogeographic processes at deeper time scales, pointing cases of local diversification and subsequent dispersal as playing major roles in current patterns of species richness (Arango et al. 2021). Unfortunately, we currently lack the phylogenetic data to test these hypotheses, but to further understand the effects of lineage diversification and dispersal on current avian distribution patterns along the SAAD, we are estimating the biogeographical origins and the history of endemic avian taxa along the SADD, which will be explored elsewhere (Lima et al. in prep.).

Underlying factors driving β-diversity along the SADD

Our results indicate that species turnover is the main β-diversity component structuring avian communities both along the SADD and individually within all three ecosystems that are part of the Dry Diagonal. Nestedness was low across our gradients, agreeing with previous studies that found similar patterns in multiple species inhabiting South America (Nascimento et al. 2020). Whereas turnover is known to be associated with environmental changes or spatial constraints, nestedness reflects that certain localities lack species that are available elsewhere, probably due to a lack of niches available or extinctions (Silva & Souza 2018). Here, we found that both geographic distance and small environmental changes act in structuring species turnover along the SAAD.

Environmental and topographic variables such as temperature, precipitation, aridity, and elevation represented significant factors explaining total β-diversity, species turnover, and nestedness along the latitudinal gradient. This is hardly surprising since these variables are strongly associated with the distribution of phytogeographic formations and plant species composition (Oliveira-Filho et al. 2006). Temperature and water availability have been indicated to influence evolutionary processes and diversification of trees in South America, representing barriers to evolutionary shifts (Oliveira-Filho et al. 2006, Jaramillo 2023). Precipitation regimes and seasonal droughts, in particular, are often considered key factors determining lineage establishment and diversification in plant communities (Neves et al. 2015, Pinho et al. 2019, Arango et al. 2021). And have been associated with historical processes of biome formation in South America (Arango et al. 2021, Jaramillo 2023). This suggests that environmental variables not only responsible for delimiting current species distributions but may also be behind the historical structuring of avian communities along the SADD.

We detected a latitudinal gradient in total β-diversity, species turnover, and nestedness with increasing latitude being one of the main factors responsible for the change of species in communities. Similar to our observed patterns, latitudinal gradients, and geographical distance have been shown to play an important role to determine the floristic relationships in Neotropical Seasonally Dry Forests (Oliveira-Filho et al. 2006). Many environmental variables can change along a latitudinal gradient crossing more than half of the South American continent, including year-round variation in daylight hours, soil, vegetation cover, and climatic variables, all of which can potentially influence the biota. The geographical distance acting on the substitution of species between communities, as the high spatial correlation found in avian composition along the SADD, it is expected, given the environmental changes, produced by the environmental gradient formed by the three phytogeographical domains. The geographical distance acts directly not only on the structuring of communities but also restricting contact between more distant sampling localities. The high number of shared species between sampling localities despite the geographical distance between them, suggests that the history of the bird species occupation in the SADD is likely a combination of local adaptive radiation and subsequent dispersal and species interchange between these three adjacent ecosystems as discussed before (Prieto-Torres et al. 2019, Corbett et al. 2020).

Therefore, diversification and species distribution along the SADD seems to be a combination of both vicariance events, local radiation, and dispersal resulting from a combination of ancient climatic conditions, changes in geomorphological conditions, and more recent climatic conditions that played a role in the evolutionary history of SAAD acting in different ways. Ancient climatic conditions were responsible for the formation of the three domains. Recent climatic conditions, such as the Quaternary climatic fluctuations are associated with not only vegetational shifts but also, the presence of connections between suitable habitats that could have allowed transition and dispersal events within the SAAD domains, which can be associated with the high number of shared species found in our results. Changes in geomorphological conditions, such as the final uplift of the central Brazilian plateaus, that formed mountain ranges and plateaus along the SAAD (Carmignotto & Astúa 2022) which can be associated with the high turnover of species at high latitudes that we found here.

Implications for Conservation

Information on patterns of species richness, avian distributions, and species composition (including β-diversity components such as species turnover, nestedness, and the historical relationship among regions), have been identified as important metrics for estimating not only the species diversity but also the conservation value of different areas (Prieto-Torres et al. 2019).

As observed in previous studies, conservation efforts should consider regional patterns of diversification in order to ensure representation not only of the present biological diversity but also of the evolutionary processes that gave rise to this diversity (Kattan et al. 2004). Considering the complexity of the phytogeographic domains that compose the SADD, future conservation plans for the SADD should consider at least three perspectives when elaborating conservation strategies: i) the individuality of each ecosystem (as areas with distinct avifauna and communities), ii) paying special attention to ecotone areas since these are floristic and faunistic transitional sites who might be particularly resilient, and thus important under future climate change, and they may require their own conservation actions (Miranda et al. 2018), and iii) also to consider the extension of the SADD as a great environmental continuum that allowed species exchanges throughout its biogeographical history.

Despite their relevance to global biodiversity, the Caatinga, Cerrado, and Chaco, the three phytogeographic domains who composed the SADD have been continuously and severely impacted by the loss and fragmentation of natural habitats, mainly due to the expansion of livestock and agricultural landscapes (Leal et al. 2005, Werneck 2011, Prieto-Torres et al. 2019). Individually, less than up to ~2.5% of the total area in each phytogeographic domain is strictly protected in protected areas (Werneck 2011). It is known that protected areas are considered cornerstone of the biodiversity conservation (Gonçalves-Souza et al. 2021). Although these areas can serve as an essential regulator of carbon emission, water control, and play a major role in mitigating habitat loss and climate change, conservation projects in South America continue to be undeveloped. An integrated evaluation for conservation purposes, as the expansions of protected areas remain to be done, especially in a scenario where an increase in land use and the impact of climate change in these environments is expected (Werneck 2011, Gonçalves-Souza et al. 2021).

Special attention needs to be given to areas of ecotone between the domains when developing conservation initiatives. Ecotones along the SADD are areas of extreme importance, with high species diversity, including species from adjoining domains. Therefore, understanding environmental requirements of species across the SADD and also considering the importance of ecotone areas, as important areas for speciation (Pennington et al. 2004) is urgent to improve conservation actions along the SADD. Understanding the patterns leading to current species composition along the SADD can also provide insights into how species may respond to large-scale environmental changes, such as anthropogenic use of the environment and future climate changes.

For upcoming decades, it is predicted more pronounced and prolonged droughts, with the rise in temperature and extreme events (Pennington et al. 2004, da Silva et al. 2021). It is expected that the climate in the tropics will get warmer and drier, this will likely result in various drastic transformations, including losses of biodiversity components, species range shifts, altered tree productivity, and overall extinction risks to the already endangered species inhabiting in these highly fragmented environments (Siyum 2020).

Rises in temperature are associated with decreasing of photosynthetic activity, and also timing of flowering and pollen production, which could lead to intense changes in the constitution of SADD domains (Stan & Sanchez-Azofeifa 2019). Variations in rainfall and a possible increase in events of floods and tropical storms, frequent occurrences of extreme heat, and increasing aridity are expected to influence tree growth, leaf phenology, and survivorship through their impacts on photosynthesis, respiration, and nutrient dynamics having major impacts on the resilience in this open/dry environment (Stan & Sanchez-Azofeifa 2019, Siyum 2020). Changes in the rainfall regimes, recurrent drought events, increasing aridity are also expected to further exacerbate the current natural resources exploitation levels, thus resulting in more pressures on the remnant vegetation resources or total conversion to persistent agricultural lands (Siyum 2020).

Environmental degradation and climate change make the vulnerability of species across the SADD critical, with an expected increase in loss of species, functional diversity, and genetic diversity. Thus, the future of these domains remains uncertain in the backgrounds of the changing climate (Siyum 2020, da Silva et al. 2021). It is fundamentally important that best practices in forest management and legislation be developed considering the integrity of the system that compose the SADD and considering the environmental continuum that it represents. Under climate change scenarios is also crucial to understand the capabilities of resilience of each phytogeographic domain and how this will change under this future scenario (Stan & Sanchez-Azofeifa 2019).

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Supplementary Material

Table S1. Species recorded at the South America Dry Diagonal sampling localities. Values corresponds to the number of sampling localities in which each species was recorded.

Order	Family	Taxa	Caatinga	Cerrado	Chaco	Total
Rheiformes	Rheidae	*Rhea americana*	4	6	5	15
Tinamiformes	Tinamidae	*Tinamus solitarius*	0	1	0	1
		Crypturellus soui	0	1	0	1
		Crypturellus undulatus	0	7	2	9
		Crypturellus zabele	4	0	0	4
		Crypturellus noctivagus	5	0	0	5
		Crypturellus parvirostris	11	6	1	18
		Crypturellus tataupa	10	1	6	17
		Nothoprocta pentlandii	0	0	2	2
		Nothoprocta cinerascens	0	0	5	5
		Rhynchotus maculicollis	0	0	1	1
		Rhynchotus rufescens	6	5	3	14
		Nothura darwinii	0	0	2	2
		Nothura boraquira	9	0	1	10
		Nothura minor	0	2	0	2
		Nothura maculosa	5	6	6	17
		Eudromia formosa	0	0	2	2
		Eudromia elegans	0	0	3	3
		Taoniscus nanus	0	2	0	2
Anseriformes	Anhimidae	*Anhima cornuta*	0	2	0	2
		Chauna torquata	0	0	5	5
	Anatidae	*Dendrocygna bicolor*	2	0	4	6
		Dendrocygna viduata	9	4	6	19
		Dendrocygna autumnalis	5	4	5	14
		Coscoroba coscoroba	0	0	2	2

		Neochen jubata	0	0	1	1
		Cairina moschata	7	6	5	18
		Sarkidiornis sylvicola	3	1	3	7
		Callonetta leucophrys	0	0	5	5
		Amazonetta brasiliensis	9	3	6	18
		Spatula versicolor	0	0	3	3
		Spatula platalea	0	0	2	2
		Spatula cyanoptera	0	0	2	2
		Anas bahamensis	3	0	1	4
		Anas georgica	0	0	2	2
		Anas flavirostris	0	0	1	1
		Netta erythrophthalma	3	0	0	3
		Netta peposaca	0	0	2	2
		Mergus octosetaceus	0	2	0	2
		Nomonyx dominicus	3	1	2	6
Galliformes	Cracidae	*Penelope superciliaris*	10	6	1	17
		Penelope jacucaca	8	0	0	8
		Aburria cumanensis	0	1	1	2
		Ortalis canicollis	0	1	7	8
		Ortalis guttata	1	0	0	1
		Ortalis araucuan	3	0	0	3
		Crax fasciolata	0	6	2	8
	Odontophoridae	*Odontophorus capueira*	0	1	0	1
Phoenicopteriformes	Phoenicopteridae	*Phoenicopterus chilensis*	0	0	1	1
Podicipediformes	Podicipedidae	*Rollandia rolland*	0	1	4	5
		Tachybaptus dominicus	6	3	6	15
		Podilymbus podiceps	8	2	6	16
		Podicephorus major	0	0	1	1
Columbiformes	Columbidae	*Columba livia*	4	6	4	14

		Patagioenas speciosa	0	2	0	2
		Patagioenas picazuro	9	7	7	23
		Patagioenas maculosa	0	0	6	6
		Patagioenas cayennensis	2	7	3	12
		Patagioenas plumbea	1	3	0	4
		Geotrygon violacea	0	1	0	1
		Geotrygon montana	1	1	0	2
		Leptotila verreauxi	11	7	7	25
		Leptotila rufaxilla	5	4	1	10
		Leptotila megalura	0	0	1	1
		Zenaida auriculata	9	7	7	23
		Claravis pretiosa	11	5	2	18
		Uropelia campestris	0	1	0	1
		Columbina passerina	1	1	0	2
		Columbina minuta	9	4	1	14
		Columbina talpacoti	12	7	5	24
		Columbina squammata	11	7	1	19
		Columbina picui	11	4	7	22
Cuculiformes	Cuculidae	*Crotophaga major*	7	3	4	14
		Crotophaga ani	11	7	6	24
		Guira guira	9	7	7	23
		Tapera naevia	10	5	7	22
		Dromococcyx phasianellus	4	3	0	7
		Dromococcyx pavoninus	0	3	0	3
		Neomorphus geoffroyi	1	0	0	1
		Micrococcyx cinereus	3	2	3	8
		Piaya cayana	12	6	5	23
		Coccyzus melacoryphus	10	4	6	20
		Coccyzus americanus	6	1	3	10

		Coccyzus euleri	4	1	0	5
Nyctibiiformes	Nyctibiidae	*Nyctibius grandis*	0	1	0	1
		Nyctibius griseus	10	4	6	20
Caprimulgiformes	Caprimulgidae	*Antrostomus rufus*	10	3	3	16
		Lurocalis semitorquatus	1	2	1	4
		Nyctidromus albicollis	11	5	2	18
		Nyctidromus hirundinaceus	7	0	0	7
		Hydropsalis parvula	8	4	7	19
		Hydropsalis candicans	0	1	0	1
		Hydropsalis longirostris	3	3	5	11
		Hydropsalis maculicaudus	0	2	1	3
		Hydropsalis torquata	10	4	6	20
		Nannochordeiles pusillus	9	1	0	10
		Podager nacunda	2	4	5	11
		Chordeiles minor	0	0	5	5
		Chordeiles acutipennis	4	2	1	7
		Cypseloides rothschildi	0	0	2	2
Apodiformes	Apodidae	*Cypseloides fumigatus*	2	2	0	4
		Cypseloides senex	1	2	0	3
		Streptoprocne zonaris	2	5	2	9
		Streptoprocne biscutata	5	2	0	7
		Chaetura cinereiventris	0	1	0	1
		Chaetura meridionalis	3	6	6	15
		Chaetura brachyura	0	2	0	2
		Aeronautes andecolus	0	0	1	1
		Tachornis squamata	9	5	0	14
	Trochilidae	*Florisuga fusca*	1	5	0	6
		Anopetia gounellei	8	0	0	8
		Phaethornis maranhaoensis	1	0	0	1

Phaethornis ruber	3	2	0	5
Phaethornis subochraceus	0	0	1	1
Phaethornis pretrei	9	6	0	15
Augastes lumachella	3	0	0	3
Colibri serrirostris	5	4	1	10
Colibri delphinae	1	0	0	1
Heliactin bilophus	2	3	0	5
Heliothryx auritus	0	1	0	1
Polytmus guainumbi	3	2	1	6
Polytmus theresiae	1	0	0	1
Chrysolampis mosquitus	10	3	0	13
Anthracothorax nigricollis	6	6	1	13
Lophornis magnificus	1	2	0	3
Heliomaster longirostris	2	0	0	2
Heliomaster squamosus	7	3	0	10
Heliomaster furcifer	0	3	6	9
Sappho sparganurus	0	0	2	2
Calliphlox amethystina	3	5	0	8
Chlorostilbon lucidus	12	7	7	26
Campylopterus largipennis	0	1	0	1
Campylopterus calcirupicola	0	1	0	1
Thalurania glaucopis	2	0	0	2
Thalurania furcata	2	6	1	9
Eupetomena macroura	11	6	1	18
Aphantochroa cirrochloris	1	3	0	4
Chrysuronia versicolor	5	4	0	9
Chrysuronia leucogaster	2	0	0	2
Leucochloris albicollis	0	0	1	1
Chionomesa fimbriata	10	5	0	15

		Chionomesa lactea	2	0	0	2
		Elliotomyia chionogaster	0	1	1	2
		Hylocharis sapphirina	1	2	0	3
		Hylocharis chrysura	0	3	5	8
		Chlorestes cyanus	2	1	0	3
Gruiformes	Aramidae	*Aramus guarauna*	6	2	5	13
	Rallidae	*Porphyrio martinica*	7	4	2	13
		Rufirallus viridis	2	2	0	4
		Laterallus flaviventer	0	0	1	1
		Laterallus melanophaius	3	1	5	9
		Laterallus exilis	1	0	1	2
		Laterallus leucopyrrhus	0	0	1	1
		Coturnicops notatus	0	0	1	1
		Micropygia schomburgkii	0	2	0	2
		Mustelirallus albicollis	2	3	3	8
		Neocrex erythrops	3	0	0	3
		Pardirallus maculatus	0	0	3	3
		Pardirallus nigricans	3	4	1	8
		Pardirallus sanguinolentus	0	0	2	2
		Amaurolimnas concolor	0	2	0	2
		Aramides ypecaha	0	0	5	5
		Aramides mangle	2	0	0	2
		Aramides cajaneus	8	7	6	21
		Porphyriops melanops	2	0	2	4
		Paragallinula angulata	1	0	0	1
		Gallinula galeata	10	3	7	20
		Fulica rufifrons	0	0	1	1
		Fulica armillata	0	0	1	1
		Fulica leucoptera	0	0	5	5

	Heliornithidae	*Heliornis fulica*	0	2	2	4
Charadriiformes	Charadriidae	*Vanellus cayanus*	6	1	1	8
		Vanellus chilensis	12	7	7	26
		Pluvialis dominica	1	2	1	4
		Charadrius semipalmatus	1	0	0	1
		Charadrius collaris	4	2	4	10
	Recurvirostridae	*Himantopus mexicanus*	7	2	7	16
		Himantopus melanurus	2	1	1	4
	Scolopacidae	*Bartramia longicauda*	0	1	2	3
		Limosa haemastica	0	0	1	1
		Calidris himantopus	0	0	1	1
		Calidris alba	1	0	0	1
		Calidris bairdii	0	0	2	2
		Calidris minuta	1	0	0	1
		Calidris minutilla	1	0	0	1
		Calidris fuscicollis	1	1	4	6
		Calidris subruficollis	0	0	1	1
		Calidris melanotos	0	1	4	5
		Gallinago paraguaiae	1	3	2	6
		Gallinago undulata	1	4	0	5
		Phalaropus tricolor	0	0	4	4
		Actitis macularius	3	4	2	9
		Tringa solitaria	8	4	6	18
		Tringa melanoleuca	0	2	5	7
		Tringa flavipes	1	3	6	10
	Thinocoridae	*Thinocorus orbignyianus*	0	0	1	1
	Jacanidae	*Jacana jacana*	9	3	5	17
	Rostratulidae	*Nycticryphes semicollaris*	0	0	1	1
	Laridae	*Rynchops niger*	1	3	3	7

		Chroicocephalus cirrocephalus	0	0	1	1
		Leucophaeus pipixcan	0	1	0	1
		Sternula superciliaris	1	0	4	5
		Phaetusa simplex	1	1	5	7
		Sterna hirundo	0	0	1	1
Eurypygiformes	Eurypygidae	*Eurypyga helias*	0	1	0	1
Ciconiiformes	Ciconiidae	*Ciconia maguari*	0	2	6	8
		Jabiru mycteria	1	3	5	9
		Mycteria americana	3	3	7	13
Suliformes	Anhingidae	*Anhinga anhinga*	2	3	4	9
	Phalacrocoracidae	*Nannopterum brasilianum*	8	3	7	18
Pelecaniformes	Ardeidae	*Tigrisoma lineatum*	7	4	5	16
		Tigrisoma fasciatum	0	1	0	1
		Cochlearius cochlearius	0	1	1	2
		Botaurus pinnatus	0	0	2	2
		Ixobrychus exilis	0	0	2	2
		Ixobrychus involucris	1	0	1	2
		Nycticorax nycticorax	5	4	6	15
		Butorides striata	8	5	7	20
		Bubulcus ibis	9	6	4	19
		Ardea cocoi	6	3	7	16
		Ardea alba	9	6	7	22
		Syrigma sibilatrix	1	6	6	13
		Pilherodius pileatus	1	4	1	6
		Egretta thula	8	3	6	17
		Egretta caerulea	0	1	0	1
	Threskiornithidae	*Plegadis chihi*	0	1	5	6
		Mesembrinibis cayennensis	0	7	2	9
		Phimosus infuscatus	1	5	5	11

		Theristicus caerulescens	0	1	5	6
		Theristicus caudatus	1	7	5	13
		Platalea ajaja	1	0	6	7
Cathartiformes	Cathartidae	*Sarcoramphus papa*	11	5	6	22
		[Vultur gryphus]	0	0	2	2
		Coragyps atratus	12	7	7	26
		Cathartes aura	12	7	7	26
		Cathartes burrovianus	11	4	6	21
Accipitriformes	Pandionidae	*Pandion haliaetus*	4	2	2	8
	Accipitridae	*Leptodon cayanensis*	1	4	3	8
		Chondrohierax uncinatus	1	1	2	4
		Elanoides forficatus	0	2	0	2
		Gampsonyx swainsonii	6	2	3	11
		Elanus leucurus	6	3	5	14
		Harpagus diodon	2	4	1	7
		Circus cinereus	0	0	2	2
		Circus buffoni	0	2	2	4
		Accipiter poliogaster	0	1	0	1
		Accipiter striatus	4	2	6	12
		Accipiter bicolor	5	1	5	11
		Ictinia mississippiensis	0	0	3	3
		Ictinia plumbea	3	7	3	13
		Busarellus nigricollis	0	1	5	6
		Rostrhamus sociabilis	6	1	5	12
		Geranospiza caerulescens	11	4	4	19
		Heterospizias meridionalis	10	5	7	22
		Amadonastur lacernulatus	1	1	0	2
		Urubitinga urubitinga	2	3	5	10
		Urubitinga coronata	1	3	5	9

		Rupornis magnirostris	12	6	7	25
		Parabuteo unicinctus	5	1	6	12
		Geranoaetus albicaudatus	9	6	6	21
		Geranoaetus melanoleucus	9	3	4	16
		[Geranoaetus polyosoma]	0	0	2	2
		Pseudastur albicollis	0	2	0	2
		Pseudastur polionotus	0	1	0	1
		Buteo nitidus	7	4	1	12
		Buteo brachyurus	10	7	1	18
		Buteo swainsoni	1	0	1	2
		Buteo albonotatus	5	3	3	11
		Harpia harpyja	0	1	0	1
		Spizaetus tyrannus	1	2	0	3
		Spizaetus melanoleucus	0	4	0	4
		Spizaetus ornatus	1	3	1	5
Strigiformes	Tytonidae	*Tyto furcata*	8	5	6	19
	Strigidae	*Megascops choliba*	11	5	6	22
		Pulsatrix perspicillata	3	1	1	5
		Bubo virginianus	2	2	4	8
		Strix chacoensis	0	0	5	5
		Strix rufipes	0	0	1	1
		Strix virgata	3	0	0	3
		Strix huhula Daudin	0	1	0	1
		Glaucidium minutissimum	2	0	0	2
		Glaucidium brasilianum	11	6	6	23
		Athene cunicularia	10	7	7	24
		Aegolius harrisii iheringi	2	0	1	3
		Asio clamator	3	1	2	6
		Asio stygius	1	0	1	2

		Asio flammeus	1	1	1	3
Trogoniformes	Trogonidae	*Trogon viridis*	0	1	0	1
		Trogon surrucura	2	3	2	7
		Trogon curucui	7	4	2	13
Coraciiformes	Momotidae	*Baryphthengus ruficapillus*	1	3	0	4
		Momotus momota	0	6	1	7
	Alcedinidae	*Megaceryle torquata*	6	4	6	16
		Chloroceryle amazona	8	4	5	17
		Chloroceryle aenea	0	2	1	3
		Chloroceryle americana	6	6	4	16
		Chloroceryle inda	0	2	1	3
Galbuliformes	Galbulidae	*Brachygalba lugubris*	0	1	0	1
		Galbula ruficauda	8	7	1	16
	Bucconidae	*Nystalus chacuru*	1	6	1	8
		Nystalus maculatus	12	5	6	23
		Nystalus striatipectus	0	1	1	2
		Malacoptila striata	1	0	0	1
		Nonnula rubecula	1	2	0	3
		Monasa nigrifrons	0	5	0	5
		Chelidoptera tenebrosa	1	3	0	4
Piciformes	Ramphastidae	*Ramphastos toco*	1	7	3	11
		Ramphastos vitellinus	0	4	0	4
		Ramphastos dicolorus	0	1	0	1
		Pteroglossus aracari	0	1	0	1
		Pteroglossus castanotis	0	5	1	6
	Picidae	*Picumnus pygmaeus*	10	0	0	10
		Picumnus cirratus	0	1	6	7
		Picumnus albosquamatus	0	7	1	8
		Picumnus limae	5	0	0	5

		Melanerpes candidus	2	6	7	15
		Melanerpes flavifrons	0	1	0	1
		Melanerpes cactorum	0	0	7	7
		Veniliornis affinis	1	0	0	1
		Veniliornis passerinus	12	6	2	20
		Veniliornis mixtus	0	3	6	9
		Campephilus rubricollis	0	1	0	1
		Campephilus melanoleucos	9	6	2	17
		Campephilus leucopogon	0	0	7	7
		Dryocopus lineatus	7	5	2	14
		Dryocopus schulzi	0	0	5	5
		Celeus ochraceus	9	3	0	12
		Celeus flavescens	7	2	0	9
		Celeus lugubris	0	1	3	4
		Celeus flavus	0	1	0	1
		Piculus chrysochloros	10	0	4	14
		Colaptes melanochloros	10	7	7	24
		Colaptes campestris	5	7	7	19
Cariamiformes	Cariamidae	*Chunga burmeisteri*	0	0	5	5
		Cariama cristata	11	6	5	22
Falconiformes	Falconidae	*Ibycter americanus*	0	1	0	1
		Caracara plancus	10	6	7	23
		Milvago chimachima	9	7	5	21
		Milvago chimango	0	0	3	3
		Herpetotheres cachinnans	12	5	4	21
		Micrastur ruficollis	7	3	2	12
		Micrastur semitorquatus	6	5	2	13
		Falco sparverius	9	6	7	22
		Falco rufigularis	6	4	2	12

		Falco deiroleucus	0	1	0	1
		Falco femoralis	8	7	7	22
		Falco peregrinus	4	0	3	7
		Spiziapteryx circumcincta	0	0	4	4
Psittaciformes	Psittacidae	*Anodorhynchus hyacinthinus*	0	2	1	3
		Anodorhynchus leari	1	0	0	1
		Ara ararauna	0	7	0	7
		Ara chloropterus	2	5	1	8
		Orthopsittaca manilatus	0	5	0	5
		Primolius maracana	5	1	1	7
		Primolius auricollis	0	1	1	2
		Diopsittaca nobilis	0	6	0	6
		Psilopsiagon aymara	0	0	1	1
		Thectocercus acuticaudatus	4	2	7	13
		Psittacara leucophthalmus	1	7	3	11
		Psittacara mitratus	0	0	1	1
		Aratinga nenday	0	0	3	3
		Aratinga auricapillus	1	2	0	3
		Aratinga jandaya	2	2	0	4
		Eupsittula aurea	2	7	1	10
		Eupsittula cactorum	12	1	0	13
		Pyrrhura devillei	0	1	1	2
		Pyrrhura frontalis	1	0	3	4
		Pyrrhura molinae	0	0	1	1
		Pyrrhura pfrimeri	0	1	0	1
		Cyanoliseus patagonus	0	0	1	1
		Myiopsitta monachus	0	0	7	7
		Forpus xanthopterygius	12	5	2	19
		Brotogeris tirica	1	0	0	1

		Brotogeris versicolurus	0	2	2	4
		Brotogeris chiriri	0	7	2	9
		Alipiopsitta xanthops	0	5	0	5
		Pionus menstruus	0	3	0	3
		Pionus maximiliani	1	4	5	10
		Amazona vinacea	1	0	0	1
		Amazona amazonica	2	5	0	7
		Amazona aestiva	6	7	6	19
Passeriformes	Thamnophilidae	*Myrmorchilus strigilatus*	10	0	3	13
		Formicivora iheringi	3	0	0	3
		Formicivora grisea	3	1	0	4
		Formicivora melanogaster	12	1	0	13
		Formicivora rufa	2	4	1	7
		Formicivora grantsaui	1	0	0	1
		Dysithamnus stictothorax	1	0	0	1
		Dysithamnus mentalis	1	5	0	6
		Herpsilochmus sellowi	10	0	0	10
		Herpsilochmus pileatus	2	0	0	2
		Herpsilochmus atricapillus	7	6	0	13
		Herpsilochmus pectoralis	1	0	0	1
		Herpsilochmus longirostris	2	7	0	9
		Herpsilochmus rufimarginatus	2	1	0	3
		Sakesphoroides cristatus	10	0	0	10
		Thamnophilus doliatus	0	6	5	11
		Thamnophilus capistratus	10	0	0	10
		Thamnophilus torquatus	6	4	0	10
		Thamnophilus punctatus	0	2	0	2
		Thamnophilus pelzelni	11	7	1	19
		Thamnophilus caerulescens	2	5	7	14

	Cymbilaimus lineatus	0	1	0	1
	Taraba major	10	6	7	23
	Hypoedaleus guttatus	1	0	0	1
	Mackenziaena severa	1	0	0	1
	Myrmoderus loricatus	1	0	0	1
	Pyriglena leucoptera	1	0	0	1
	Rhopornis ardesiacus	1	0	0	1
	Cercomacra brasiliana	1	0	0	1
	Cercomacra melanaria	0	0	1	1
	Drymophila ferruginea	1	0	0	1
	Drymophila ochropyga	1	0	0	1
Melanopareiidae	*Melanopareia maximiliani*	0	0	2	2
	Melanopareia torquata	1	4	0	5
Conopophagidae	*Conopophaga cearae*	2	0	0	2
	Conopophaga lineata	1	3	0	4
	Conopophaga roberti	2	0	0	2
Grallariidae	*Hylopezus ochroleucus*	9	0	0	9
Rhinocryptidae	*Scytalopus diamantinensis*	1	0	0	1
	Rhinocrypta lanceolata	0	0	5	5
Formicariidae	*Formicarius colma*	1	0	5	6
Scleruridae	*Sclerurus cearensis*	4	0	0	4
	Sclerurus scansor	2	1	0	3
	Geositta rufipennis	0	0	1	1
	Geositta poeciloptera	1	2	0	3
Dendrocolaptidae	*Dendrocincla turdina*	1	0	0	1
	Sittasomus griseicapillus	12	7	5	24
	Xiphorhynchus atlanticus	1	0	0	1
	Xiphorhynchus fuscus	3	2	0	5
	Xiphorhynchus guttatus	1	2	0	3

	Xiphorhynchus guttatoides	1	1	0	2
	Campylorhamphus falcularius	1	0	0	1
	Campylorhamphus trochilirostris	8	3	6	17
	Drymornis bridgesii	0	0	5	5
	Dendroplex picus	7	0	0	7
	Lepidocolaptes angustirostris	11	6	7	24
	Lepidocolaptes squamatus	1	0	0	1
	Dendrocolaptes platyrostris	6	5	2	13
	Xiphocolaptes falcirostris	4	0	0	4
	Xiphocolaptes albicollis	2	0	0	2
	Xiphocolaptes major	0	1	6	7
Xenopidae	*Xenops rutilans*	4	3	1	8
Furnariidae	*Berlepschia rikeri*	0	5	0	5
	Tarphonomus certhioides	0	0	5	5
	Cinclodes atacamensis	0	0	1	1
	Cinclodes comechingonus	0	0	1	1
	Cinclodes olrogi	0	0	1	1
	Cinclodes fuscus	0	0	2	2
	Furnarius figulus	12	0	0	12
	Furnarius leucopus	11	1	1	13
	Furnarius rufus	3	7	7	17
	Furnarius cristatus	0	0	5	5
	Phleocryptes melanops	0	0	2	2
	Lochmias nematura	1	2	0	3
	Dendroma rufa	0	4	0	4
	Clibanornis rectirostris	0	5	0	5
	Automolus leucophthalmus	1	2	0	3
	Megaxenops parnaguae	9	0	0	9
	Anabazenops fuscus	1	0	0	1

Syndactyla rufosuperciliata	0	1	1	2
Syndactyla dimidiata	0	3	0	3
Leptasthenura aegithaloides	0	0	1	1
Leptasthenura platensis	0	0	4	4
Spartonoica maluroides	0	0	1	1
Pseudoseisura cristata	8	0	0	8
Pseudoseisura unirufa	0	0	1	1
Pseudoseisura lophotes	0	0	4	4
Phacellodomus rufifrons	4	5	5	14
Phacellodomus sibilatrix	0	0	6	6
Phacellodomus striaticollis	0	0	1	1
Phacellodomus ruber	0	5	5	10
Anumbius annumbi	0	1	4	5
Coryphistera alaudina	0	0	6	6
Schoeniophylax phryganophilus	0	2	5	7
Certhiaxis cinnamomeus	9	4	5	18
Synallaxis hellmayri	11	0	0	11
Synallaxis cinerea	2	0	0	2
Synallaxis frontalis	12	6	6	24
Synallaxis albescens	10	4	5	19
Synallaxis spixi	1	0	2	3
Synallaxis hypospodia	2	3	1	6
Synallaxis albilora	0	0	1	1
Synallaxis scutata	8	5	0	13
Asthenes baeri	0	0	5	5
Asthenes modesta	0	0	1	1
Asthenes pyrrholeuca	0	0	4	4
Asthenes sclateri	0	0	1	1
Acrobatornis fonsecai	1	0	0	1

	Cranioleuca vulpina	0	2	1	3
	Cranioleuca pyrrhophia	0	0	6	6
	Cranioleuca semicinerea	5	0	0	5
	Thripophaga macroura	1	0	0	1
Pipridae	*Neopelma pallescens*	5	4	0	9
	Pipra fasciicauda	0	5	1	6
	Manacus manacus	1	0	0	1
	Machaeropterus regulus	1	0	0	1
	Ilicura militaris	1	1	0	2
	Chiroxiphia pareola	4	0	0	4
	Antilophia galeata	1	7	0	8
Oxyruncidae	*Oxyruncus cristatus*	1	1	0	2
Onychorhynchidae	*Myiobius barbatus*	2	1	0	3
	Myiobius atricaudus	4	1	0	5
Tityridae	*Schiffornis virescens*	1	4	0	5
	Iodopleura pipra	1	0	0	1
	Tityra inquisitor	3	3	2	8
	Tityra cayana	1	4	2	7
	Tityra semifasciata	0	3	0	3
	Pachyramphus viridis	9	3	4	16
	Pachyramphus rufus	0	1	0	1
	Pachyramphus castaneus	1	1	1	3
	Pachyramphus polychopterus	11	6	6	23
	Pachyramphus validus	10	3	4	17
	Xenopsaris albinucha	7	2	5	14
Cotingidae	*Phytotoma rutila*	0	0	5	5
	Phibalura flavirostris	1	0	0	1
	Pyroderus scutatus	2	1	0	3
	Procnias averano	1	0	0	1

	Procnias nudicollis	1	0	0	1
Platyrinchidae	*Platyrinchus mystaceus*	3	4	1	8
Rhynchocyclidae	*Mionectes rufiventris*	0	1	0	1
	Leptopogon amaurocephalus	5	6	2	13
	Corythopis delalandi	0	6	0	6
	Phylloscartes ventralis	0	0	1	1
	Phylloscartes beckeri	1	0	0	1
	Phylloscartes oustaleti	1	0	0	1
	Tolmomyias sulphurescens	3	7	5	15
	Tolmomyias flaviventris	11	3	0	14
	Todirostrum cinereum	11	7	1	19
	Poecilotriccus plumbeiceps	1	0	3	4
	Poecilotriccus latirostris	0	3	0	3
	Myiornis auricularis	1	2	0	3
	Hemitriccus diops	2	0	0	2
	Hemitriccus striaticollis	2	2	0	4
	Hemitriccus nidipendulus	2	0	0	2
	Hemitriccus margaritaceiventer	12	6	7	25
	Hemitriccus mirandae	1	0	0	1
	Hemitriccus furcatus	1	0	0	1
Tyrannidae	*Hirundinea ferruginea*	11	5	2	18
	Stigmatura napensis	10	0	0	10
	Stigmatura budytoides	5	0	5	10
	Inezia inornata	0	1	4	5
	Euscarthmus meloryphus	9	2	6	17
	Euscarthmus rufomarginatus	1	2	0	3
	Ornithion inerme	0	1	0	1
	Camptostoma obsoletum	11	7	7	25
	Elaenia flavogaster	10	6	2	18

Elaenia spectabilis	7	4	5	16
Elaenia chilensis	5	1	6	12
Elaenia parvirostris	1	3	6	10
Elaenia mesoleuca	3	2	1	6
Elaenia cristata	7	4	0	11
Elaenia chiriquensis	3	5	1	9
Elaenia obscura	1	4	0	5
Suiriri suiriri	3	4	7	14
Myiopagis gaimardii	0	6	1	7
Myiopagis caniceps	4	5	0	9
Myiopagis viridicata	10	5	3	18
Capsiempis flaveola	2	2	0	4
Phaeomyias murina	12	5	3	20
Phyllomyias reiseri	0	1	0	1
Phyllomyias fasciatus	10	5	0	15
Culicivora caudacuta	0	3	0	3
Polystictus pectoralis	0	2	1	3
Polystictus superciliaris	2	0	0	2
Pseudocolopteryx sclateri	0	1	1	2
Pseudocolopteryx acutipennis	0	0	1	1
[Pseudocolopteryx dinelliana]	0	0	2	2
Pseudocolopteryx flaviventris	0	0	3	3
Serpophaga nigricans	0	1	2	3
Serpophaga subcristata	9	2	6	17
Serpophaga griseicapilla	0	0	6	6
Attila phoenicurus	0	1	0	1
Legatus leucophaius	5	5	2	12
Myiarchus tuberculifer	1	1	0	2
Myiarchus swainsoni	9	5	7	21

Myiarchus ferox	10	5	2	17
Myiarchus tyrannulus	11	6	7	24
Sirystes sibilator	1	4	1	6
Casiornis rufus	0	5	5	10
Casiornis fuscus	11	1	0	12
Pitangus sulphuratus	12	7	7	26
Philohydor lictor	3	4	0	7
Machetornis rixosa	10	5	7	22
Myiodynastes maculatus	12	6	7	25
Tyrannopsis sulphurea	0	1	0	1
Megarynchus pitangua	12	7	4	23
Myiozetetes cayanensis	2	7	1	10
Myiozetetes similis	12	3	1	16
Tyrannus albogularis	3	7	1	11
Tyrannus melancholicus	12	7	7	26
Tyrannus savana	7	7	7	21
Tyrannus tyrannus	0	1	0	1
Griseotyrannus aurantioatrocristatus	1	5	7	13
Empidonomus varius	12	7	5	24
Guyramemua affine	0	3	0	3
Sublegatus modestus	9	3	6	18
Colonia colonus	1	5	0	6
Arundinicola leucocephala	10	3	2	15
Fluvicola pica	2	1	1	4
Fluvicola albiventer	9	4	7	20
Fluvicola nengeta	11	1	0	12
Pyrocephalus rubinus	0	4	7	11
Gubernetes yetapa	0	4	1	5
Heteroxolmis dominicanus	0	0	1	1

	Alectrurus tricolor	0	3	0	3
	Alectrurus risora	0	0	1	1
	Myiophobus fasciatus	8	5	7	20
	Cnemotriccus fuscatus	9	6	3	18
	Lathrotriccus euleri	5	5	3	13
	Empidonax alnorum	0	0	2	2
	Contopus cinereus	2	3	0	5
	Satrapa icterophrys	2	1	3	6
	Lessonia rufa	0	0	2	2
	Lessonia oreas	0	0	1	1
	Muscisaxicola capistratus	0	0	1	1
	Hymenops perspicillatus	0	0	7	7
	Knipolegus franciscanus	0	1	0	1
	Knipolegus lophotes	0	2	0	2
	Knipolegus nigerrimus	5	2	0	7
	Knipolegus cyanirostris	0	0	1	1
	Knipolegus striaticeps	0	0	5	5
	Knipolegus hudsoni	0	0	2	2
	Knipolegus aterrimus	0	0	3	3
	Xolmis cinereus	1	6	4	11
	Xolmis coronatus	0	0	5	5
	Xolmis irupero	8	1	7	16
	Xolmis velatus	0	6	1	7
	Agriornis montanus	0	0	1	1
	Agriornis micropterus	0	0	4	4
	Agriornis murinus	0	0	4	4
	Anairetes flavirostris	0	0	2	2
	Anairetes parulus	0	0	1	1
Vireonidae	*Cyclarhis gujanensis*	11	7	7	25

	Hylophilus amaurocephalus	10	1	0	11
	Hylophilus poicilotis	2	0	0	2
	Vireo olivaceus	7	3	5	15
	Vireo chivi	9	5	6	20
Corvidae	*Cyanocorax cyanomelas*	0	1	3	4
	Cyanocorax cristatellus	1	5	1	7
	Cyanocorax chrysops	0	2	6	8
	Cyanocorax cyanopogon	12	5	0	17
Hirundinidae	*Pygochelidon cyanoleuca*	7	4	3	14
	Pygochelidon melanoleuca	0	1	0	1
	Alopochelidon fucata	0	3	2	5
	Stelgidopteryx ruficollis	11	6	4	21
	Progne tapera	5	7	7	19
	Progne subis	1	0	0	1
	Progne chalybea	9	4	6	19
	Progne elegans	0	1	3	4
	Tachycineta albiventer	7	2	1	10
	Tachycineta leucorrhoa	1	2	7	10
	Tachycineta leucopyga	0	0	3	3
	Riparia riparia	0	1	4	5
	Hirundo rustica	2	1	4	7
	Petrochelidon pyrrhonota	0	1	3	4
Troglodytidae	*Troglodytes musculus*	12	7	6	25
	Cistothorus platensis	0	3	5	8
	Campylorhynchus turdinus	0	1	1	2
	Pheugopedius genibarbis	4	2	0	6
	Cantorchilus leucotis	0	5	0	5
	Cantorchilus guarayanus	0	0	1	1
	Cantorchilus longirostris	11	0	0	11

Donacobiidae	*Donacobius atricapilla*	3	3	3	9
Polioptilidae	*Ramphocaenus melanurus*	2	0	0	2
	Polioptila plumbea	12	0	0	12
	Polioptila dumicola	0	6	6	12
Turdidae	*Catharus fuscescens*	0	1	0	1
	Turdus chiguanco	0	0	2	2
	Turdus flavipes	1	0	0	1
	Turdus leucomelas	11	7	1	19
	Turdus rufiventris	12	7	7	26
	Turdus nigriceps	0	0	1	1
	Turdus amaurochalinus	11	6	7	24
	Turdus subalaris	0	1	0	1
	Turdus albicollis	1	4	0	5
Mimidae	*Mimus patagonicus*	0	0	1	1
	Mimus saturninus	11	7	7	25
	Mimus triurus	0	0	6	6
Estrildidae	*Estrilda astrild*	4	0	0	4
Passeridae	*Passer domesticus*	9	6	5	20
Motacillidae	*Anthus lutescens*	5	4	5	14
	Anthus furcatus	0	0	1	1
Fringillidae	*Spinus yarrellii*	5	0	0	5
	Spinus magellanicus	1	3	6	10
	Euphonia chlorotica	12	6	6	24
	Euphonia violacea	2	5	1	8
	Euphonia laniirostris	0	1	0	1
	Euphonia cyanocephala	1	1	0	2
	Euphonia pectoralis	1	0	0	1
	Geospizopsis plebejus	0	0	1	1
	Rhynchospiza strigiceps	0	0	2	2

Passerellidae	*Zonotrichia capensis*	12	5	7	24
	Ammodramus humeralis	11	6	5	22
	Ammodramus aurifrons	0	1	0	1
	Arremon taciturnus	6	4	0	10
	Arremon franciscanus	2	0	0	2
	Arremon flavirostris	1	5	4	10
	Arremon dorbignii	0	0	1	1
Icteridae	*Dolichonyx oryzivorus*	0	0	2	2
	Leistes loyca	0	0	1	1
	Leistes militaris	2	0	0	2
	Leistes superciliaris	9	5	6	20
	Psarocolius decumanus	2	4	2	8
	Cacicus solitarius	3	2	5	10
	Cacicus chrysopterus	0	0	5	5
	Cacicus cela	2	4	0	6
	Cacicus haemorrhous	1	3	1	5
	Icterus jamacaii	12	2	0	14
	Icterus croconotus	0	2	3	5
	Icterus pyrrhopterus	10	4	7	21
	Icterus cayanensis	5	2	1	8
	Molothrus rufoaxillaris	0	6	6	12
	Molothrus oryzivorus	0	4	1	5
	Molothrus bonariensis	12	7	7	26
	Amblyramphus holosericeus	0	0	4	4
	Gnorimopsar chopi	9	7	3	19
	Agelaioides badius	2	2	7	11
	Agelaioides fringillarius	9	0	0	9
	Agelasticus thilius	0	0	1	1
	Agelasticus cyanopus	1	1	5	7

	Chrysomus ruficapillus	10	2	5	17
	Pseudoleistes guirahuro	0	2	2	4
	Pseudoleistes virescens	0	0	1	1
Parulidae	*Setophaga pitiayumi*	8	4	7	19
	Geothlypis aequinoctialis	3	4	7	14
	Myioborus brunniceps	0	0	2	2
	Basileuterus culicivorus	4	7	4	15
	Myiothlypis flaveola	10	7	1	18
	Myiothlypis leucoblephara	0	0	3	3
	Myiothlypis leucophrys	0	4	0	4
	Myiothlypis rivularis	1	0	0	1
Cardinalidae	*Piranga flava*	6	5	6	17
	Pheucticus aureoventris	0	1	4	5
	Cyanoloxia glaucocaerulea	0	0	1	1
	Cyanoloxia brissonii	11	3	6	20
Thraupidae	*Charitospiza eucosma*	0	4	0	4
	Nemosia pileata	11	7	2	20
	Compsothraupis loricata	10	1	0	11
	Coryphaspiza melanotis	0	3	0	3
	Embernagra platensis	0	0	5	5
	Embernagra longicauda	2	0	0	2
	Emberizoides herbicola	1	4	2	7
	Emberizoides ypiranganus	0	1	1	2
	Rhopospina carbonaria	0	0	1	1
	Rhopospina alaudina	0	0	1	1
	Porphyrospiza caerulescens	1	3	0	4
	Hemithraupis guira	8	6	1	15
	Tersina viridis	2	6	1	9
	Cyanerpes caeruleus	0	1	0	1

Cyanerpes cyaneus	0	4	0	4
Dacnis cayana	6	6	0	12
Saltatricula atricollis	6	6	1	13
Saltatricula multicolor	0	0	6	6
Saltator maximus	1	4	0	5
Saltator coerulescens	0	3	7	10
Saltator similis	5	6	3	14
Saltator aurantiirostris	0	0	7	7
Coereba flaveola	12	7	1	20
Asemospiza obscura	0	0	3	3
Asemospiza fuliginosa	1	1	0	2
Volatinia jacarina	12	7	5	24
Conothraupis mesoleuca	0	1	0	1
Eucometis penicillata	0	7	1	8
Trichothraupis melanops	1	4	0	5
Loriotus cristatus	0	1	0	1
Coryphospingus pileatus	12	4	0	16
Coryphospingus cucullatus	0	5	7	12
Tachyphonus rufus	7	5	4	16
Tachyphonus coronatus	0	1	0	1
Ramphocelus bresilia	1	0	0	1
Ramphocelus carbo	2	5	1	8
Sporophila lineola	8	1	3	12
Sporophila plumbea	1	5	0	6
Sporophila collaris	1	3	5	9
Sporophila nigricollis	11	4	0	15
Sporophila ardesiaca	0	3	0	3
Sporophila caerulescens	0	5	7	12
Sporophila albogularis	10	0	0	10

Sporophila leucoptera	7	2	2	11
Sporophila bouvreuil	8	2	0	10
Sporophila pileata	0	2	0	2
Sporophila minuta	0	2	0	2
Sporophila hypoxantha	0	2	3	5
Sporophila ruficollis	0	2	2	4
Sporophila palustris	0	2	2	4
Sporophila hypochroma	0	1	0	1
Sporophila cinnamomea	0	3	1	4
Sporophila melanogaster	0	1	0	1
Sporophila angolensis	2	3	1	6
Sporophila maximiliani	0	1	0	1
Poospiza whitii	0	0	2	2
Poospiza ornata	0	0	2	2
Poospiza nigrorufa	0	0	2	2
Poospizopsis hypochondria	0	0	1	1
Thlypopsis sordida	6	2	1	9
Cypsnagra hirundinacea	1	4	0	5
Donacospiza albifrons	0	0	1	1
Lophospingus pusillus	0	0	2	2
Microspingus melanoleucus	0	0	7	7
Microspingus cinereus	0	3	0	3
Microspingus torquatus	0	0	5	5
Conirostrum speciosum	9	5	2	16
Sicalis citrina	3	4	0	7
Sicalis flaveola	10	7	7	24
Sicalis columbiana	1	2	0	3
Sicalis luteola	5	4	4	13
Haplospiza unicolor	0	1	0	1

Catamenia analis	0	0	2	2
Pipraeidea melanonota	0	2	1	3
Rauenia bonariensis	0	0	6	6
Neothraupis fasciata	2	4	0	6
Gubernatrix cristata	0	0	1	1
Diuca diuca	0	0	1	1
Cissopis leverianus	0	1	0	1
Schistochlamys melanopis	0	3	0	3
Schistochlamys ruficapillus	9	2	0	11
Paroaria coronata	0	1	7	8
Paroaria dominicana	12	1	0	13
Paroaria capitata	0	1	5	6
Thraupis sayaca	12	7	6	25
Thraupis palmarum	7	7	2	16
Stilpnia cyanicollis	0	1	0	1
Stilpnia cayana	11	6	1	18
Tangara seledon	1	0	0	1
Tangara cyanoventris	2	0	0	2

Table S2. Matrix of shared species between sampling localities in pair-to-pair comparisons. Numbers highlighted in orange indicate the number of species recorded for that locality. Number highlighted in blue and red indicate the maximum and minimum number of species shared between sampling localities, respectively.

Sampling localities	**01**	**02**	**03**	**04**	**05**	**06**	**07**	**08**	**09**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**
(01) APA Chapada Araripe	*148*																									
(02) PN Catimbau	134	*229*																								
(03) ESEC Serido	92	152	*182*																							
(04) PN Ubajara	107	145	111	*199*																						
(05) PN Sete Cidades	82	98	78	93	*129*																					
(06) RPPN Serra das Almas	130	186	157	156	103	*245*																				
(07) PN Serra Capivara	121	186	156	145	102	202	*251*																			
(08) PN Serra Confusões	125	172	134	143	107	184	189	*230*																		
(09) PN Boqueirão	130	200	165	145	101	195	199	182	*256*																	
(10) PE Morro do Chapéu	98	135	103	105	85	133	130	134	143	*185*																
(11) PN Chapada Diamantina	140	213	169	175	116	212	216	204	227	177	*407*															
(12) FLONA Contendas Sincorá	105	158	135	115	88	159	164	152	163	119	172	*183*														
(13) PE Terra Ronca	107	143	114	121	112	143	155	151	149	110	204	128	*277*													
(14) PN Chapada Veadeiros	112	170	142	144	113	178	184	181	187	128	261	143	241	*405*												
(15) PE Pirineus	97	132	101	108	92	124	131	125	140	101	191	112	188	227	*245*											
(16) PE Paraúna	48	72	61	57	60	71	78	74	76	65	98	70	117	123	112	*129*										
(17) PN Emas	110	175	141	145	109	181	190	174	191	127	269	147	241	334	230	124	*415*									
(18) PE Prosa	50	71	59	64	55	72	78	74	71	52	95	67	107	120	99	72	124	*135*								
(19) PN Serra Bodoquena	91	151	126	117	98	155	167	153	165	115	223	127	203	257	181	107	272	116	*332*							
(20) Porto Murtinho	98	160	140	123	95	168	177	157	177	111	216	134	188	254	169	103	275	112	264	*357*						
(21) Pozo Colorado	40	83	81	55	**37**	84	89	75	94	58	101	72	85	113	78	59	126	49	125	154	*167*					
(22) RN Formosa	73	118	109	83	51	118	124	107	129	80	142	94	110	152	104	61	166	70	165	202	141	*266*				
(23) PN El Impenetrable	74	123	114	84	53	124	132	112	138	84	146	99	120	159	114	68	171	71	173	210	150	226	*256*			
(24) PN Chaco	92	152	134	106	74	157	166	141	165	100	200	117	151	209	143	81	233	91	215	271	166	240	245	*372*		
(25) RUM Sierra Guasayan	61	95	82	66	45	91	94	83	100	67	107	76	92	104	91	49	116	52	114	132	92	152	152	164	*197*	
(26) PN Traslasierra	56	95	89	61	40	89	97	84	102	68	110	78	87	107	85	49	121	48	113	133	98	167	160	175	167	*228*

Table S3. Matrix of shared species proportion (%) between sampling localities in pair-to-pair comparisons. Number highlighted in blue and red indicate the maximum and minimum number of species shared between sampling localities, respectively.

Sampling localities	**01**	**02**	**03**	**04**	**05**	**06**	**07**	**08**	**09**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**
(01) APA Chapada Araripe	100																									
(02) PN Catimbau	55.1	100																								
(03) ESEC Serido	38.7	58.7	100																							
(04) PN Ubajara	44.6	51.2	41.1	100																						
(05) PN Sete Cidades	42.1	37.7	33.5	39.6	100																					
(06) RPPN Serra das Almas	49.4	64.6	58.1	54.2	38.0	100																				
(07) PN Serra Capivara	43.5	63.3	56.3	47.5	36.7	68.7	100																			
(08) PN Serra Confusões	49.4	59.9	48.2	50.0	42.5	63.2	64.7	100																		
(09) PN Boqueirão	47.4	70.2	60.4	46.8	35.6	63.7	64.6	59.9	100																	
(10) PE Morro do Chapéu	41.7	48.4	39.0	37.6	37.1	44.8	42.5	47.7	48.0	100																
(11) PN Chapada Diamantina	33.7	50.4	40.2	40.6	27.6	48.2	48.9	47.1	52.1	42.7	100															
(12) FLONA Contendas Sincorá	46.5	62.2	58.7	43.1	39.3	59.1	60.7	58.2	59.1	47.8	41.1	100														
(13) PE Terra Ronca	33.6	39.4	33.0	34.1	38.1	37.7	41.6	42.4	38.8	31.3	42.5	38.6	100													
(14) PN Chapada Veadeiros	25.4	36.6	31.9	31.3	26.8	37.7	39.0	39.9	39.5	27.7	47.4	32.1	54.6	100												
(15) PE Pirineus	32.8	38.6	31.0	32.1	32.6	33.9	35.9	35.7	38.8	30.7	41.4	35.4	56.3	53.7	100											
(16) PE Paraúna	21.0	25.2	24.4	21.0	30.3	23.4	25.8	26.0	24.6	26.1	22.4	28.9	40.5	29.9	42.7	100										
(17) PN Emas	24.3	37.3	30.9	30.9	25.1	37.8	39.9	36.9	39.8	26.8	48.6	32.6	53.4	68.7	53.5	29.5	100									
(18) PE Prosa	21.5	24.2	22.9	23.7	26.3	23.4	25.3	25.4	22.2	19.4	21.3	26.7	35.1	28.6	35.2	37.5	29.1	100								
(19) PN Serra Bodoquena	23.4	36.8	32.5	28.3	27.0	36.7	40.1	37.4	39.0	28.6	43.2	32.7	50.0	53.5	45.7	30.2	57.3	33.0	100							
(20) Porto Murtinho	24.1	37.6	35.1	28.4	24.3	38.7	41.1	36.5	40.6	25.8	39.4	33.0	42.2	50.0	39.0	26.9	55.3	29.5	62.1	100						
(21) Pozo Colorado	14.5	26.5	30.2	17.7	14.3	25.6	27.1	23.3	28.6	19.7	21.4	25.9	23.7	24.6	23.4	24.9	27.6	19.4	33.4	41.6	100					
(22) RN Formosa	21.4	31.3	32.2	21.7	14.8	30.0	31.6	27.5	32.8	21.6	26.7	26.5	25.4	29.3	25.6	18.3	32.2	21.1	38.1	48.0	48.3	100				
(23) PN El Impenetrable	22.4	34.0	35.2	22.6	16.0	32.9	35.2	29.9	36.9	23.5	28.2	29.1	29.1	31.7	29.5	21.5	34.2	22.2	41.7	52.1	54.9	**76.4**	100			
(24) PN Chaco	21.5	33.9	31.9	22.8	17.3	34.1	36.3	30.6	35.6	21.9	34.5	26.7	30.3	36.8	30.2	19.3	42.1	21.9	44.0	59.2	44.5	60.3	64.0	100		
(25) RUM Sierra Guasayan	21.5	28.7	27.6	20.0	16.0	25.9	26.6	24.1	28.3	21.3	21.5	25.0	24.1	20.9	25.9	17.7	23.4	18.6	27.5	31.3	33.8	48.9	50.5	40.5	100	
(26) PN Traslasierra	17.5	26.2	27.7	16.7	**12.6**	23.2	25.4	22.5	26.7	19.7	21.0	23.4	20.8	20.3	21.9	15.9	23.2	15.2	25.3	29.4	33.0	51.1	49.4	41.2	64.7	100

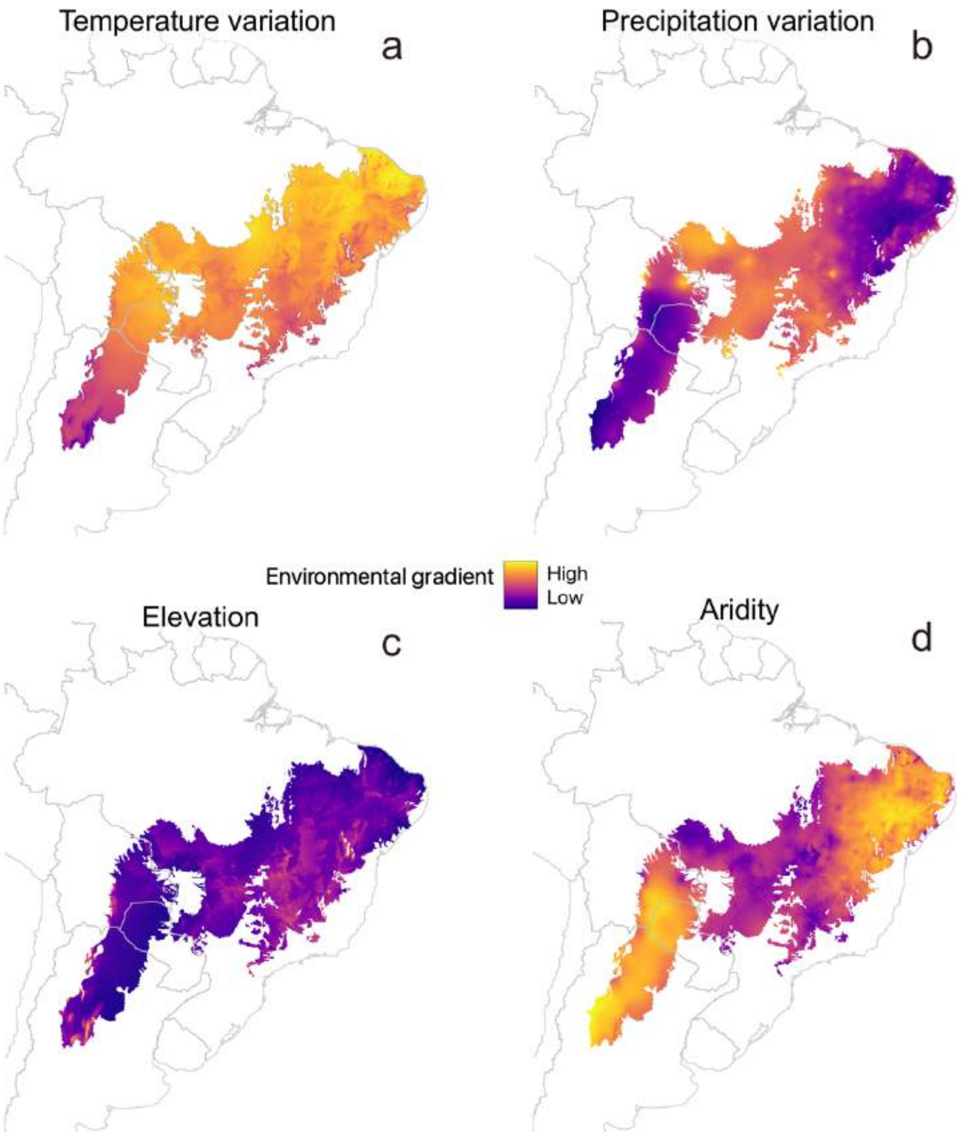


Figure S1. Environmental variables used to predict total β-diversity and species turnover along the SADD in the GDM models: (a) temperature variation (PC1, 81.97% of variance explained), (b) precipitation variation (PC1, 67.24% of variance explained), (c) elevation, and (d) aridity. Temperature, precipitation and elevation information were obtained from WorldClim 2.0 (Fick & Hijmans 2017). Aridity information was obtained from Trabucco & Zomer (2022). Environmental variables were cropped to the SADD area using QGIS 3.26.

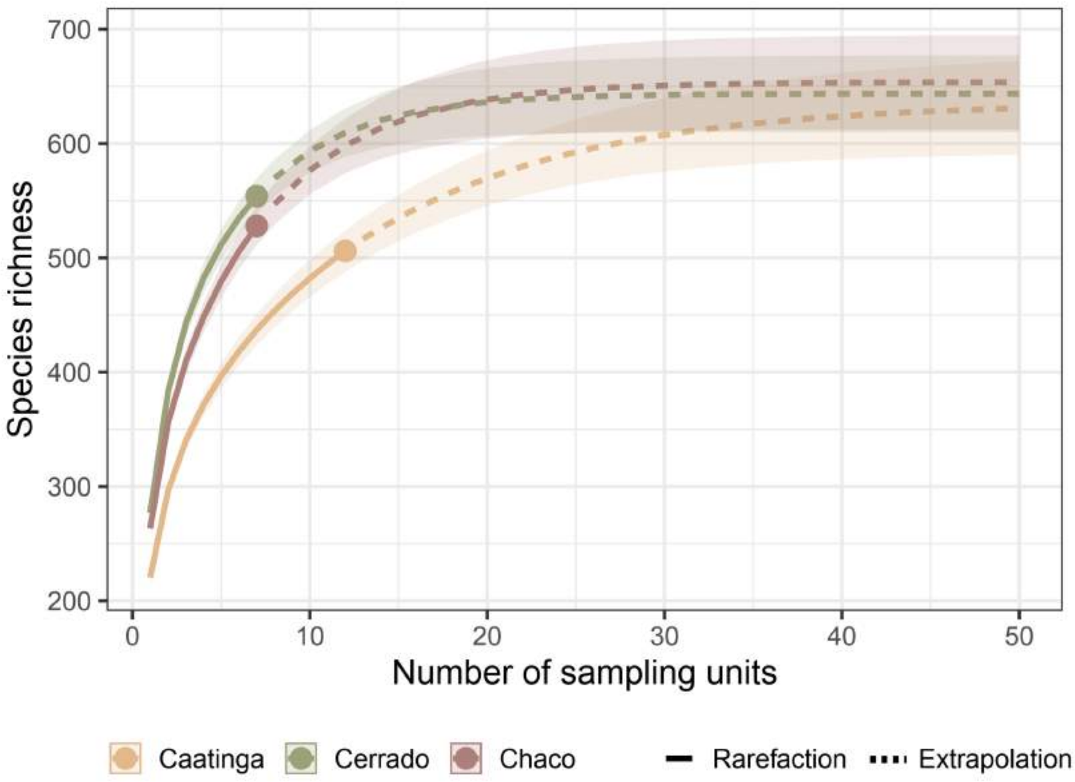
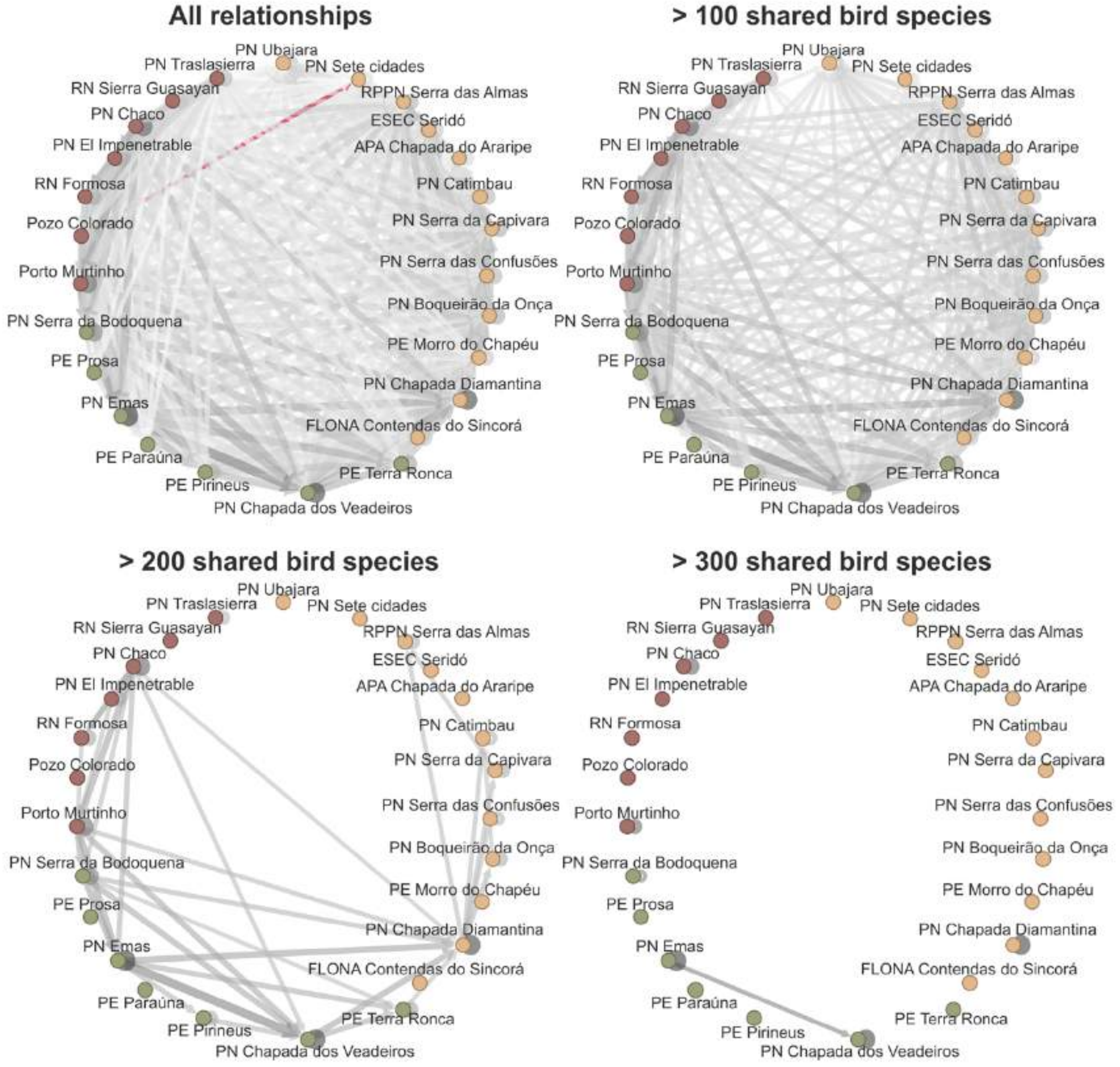


Figure S2. Sample-size rarefaction (solid line) and extrapolation (dotted line) sampling curves for species richness (q=0) with 95% confidence intervals (shaded areas) for the SADD sampling localities distributed in the Caatinga Dry Forests, Cerrado Savannas and Chaco Woodland Forest.



All relationships

> 100 shared bird species

> 200 shared bird species

> 300 shared bird species

Figure S3. Bird communities' similarities along the South American Dry Diagonal. Circles correspond to each sampling localities analyzed; circle's colors represent the ecosystems where the sampling localities is located (see Figure 1). Line colors describe the number of species shared species among localities; lighter lines represent fewer shared species and darker lines represent higher number of shared species.

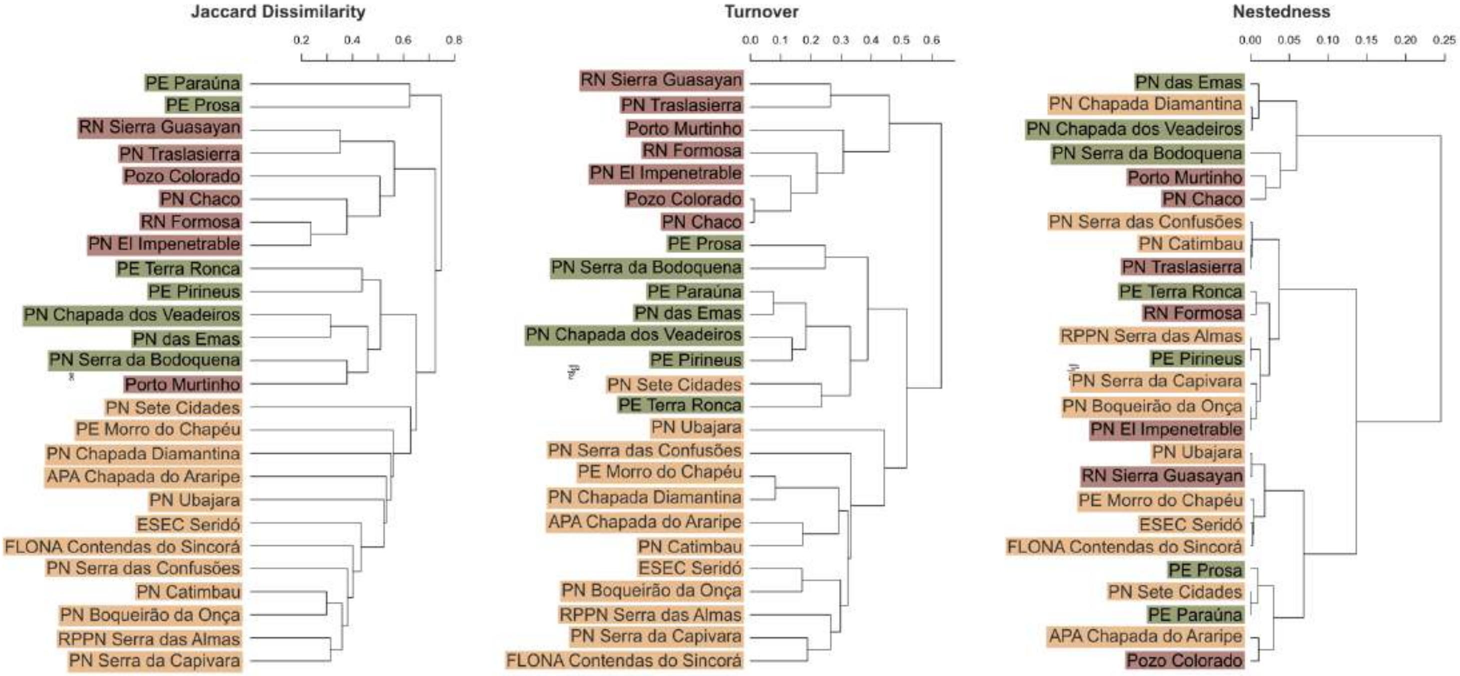


Figure S4. Total β-diversity (Jaccard's dissimilarity), Turnover and Nestedness percentual values between sampling localities along the South America Dry Diagonal grouped according to avian similarity.

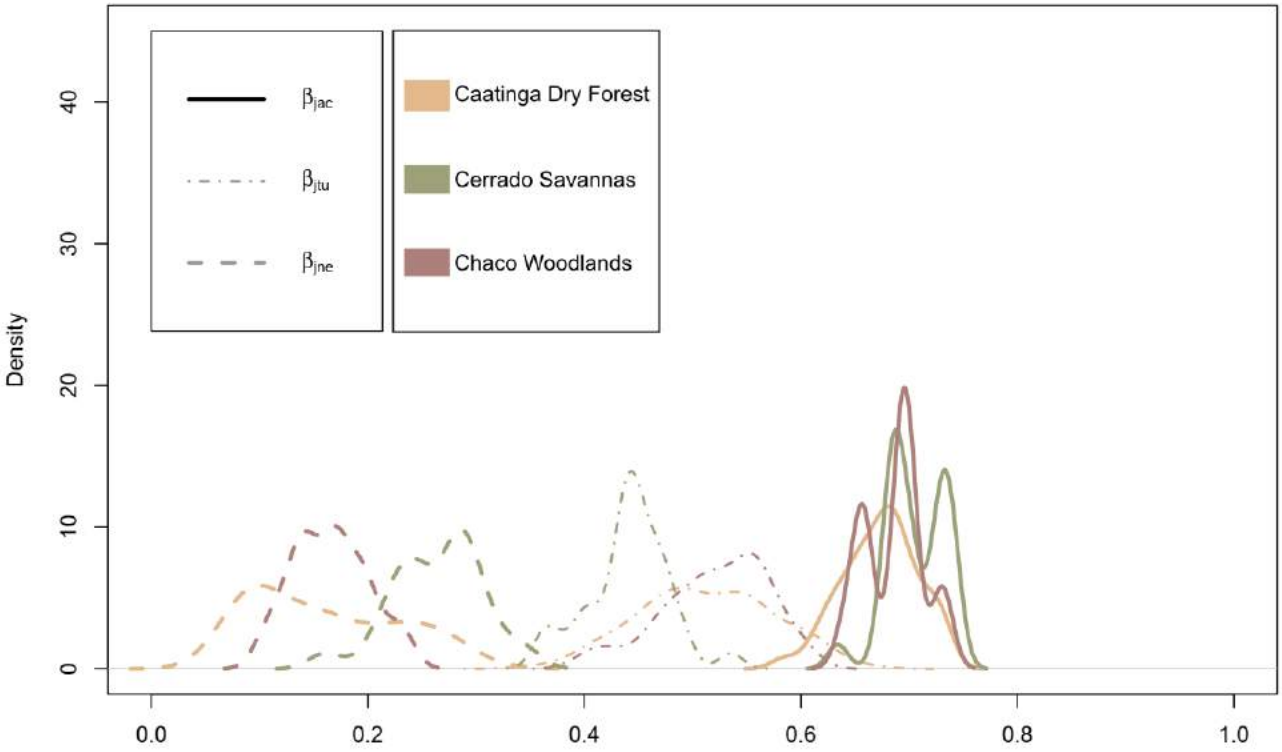


Figure S5. Values of β-diversity components within the ecosystem. β*jac* representing the total dissimilarity (total β-diversity) calculated by the Jaccard's index, β*jtu* representing the turnover component and β*jne* representing the nestedness component.

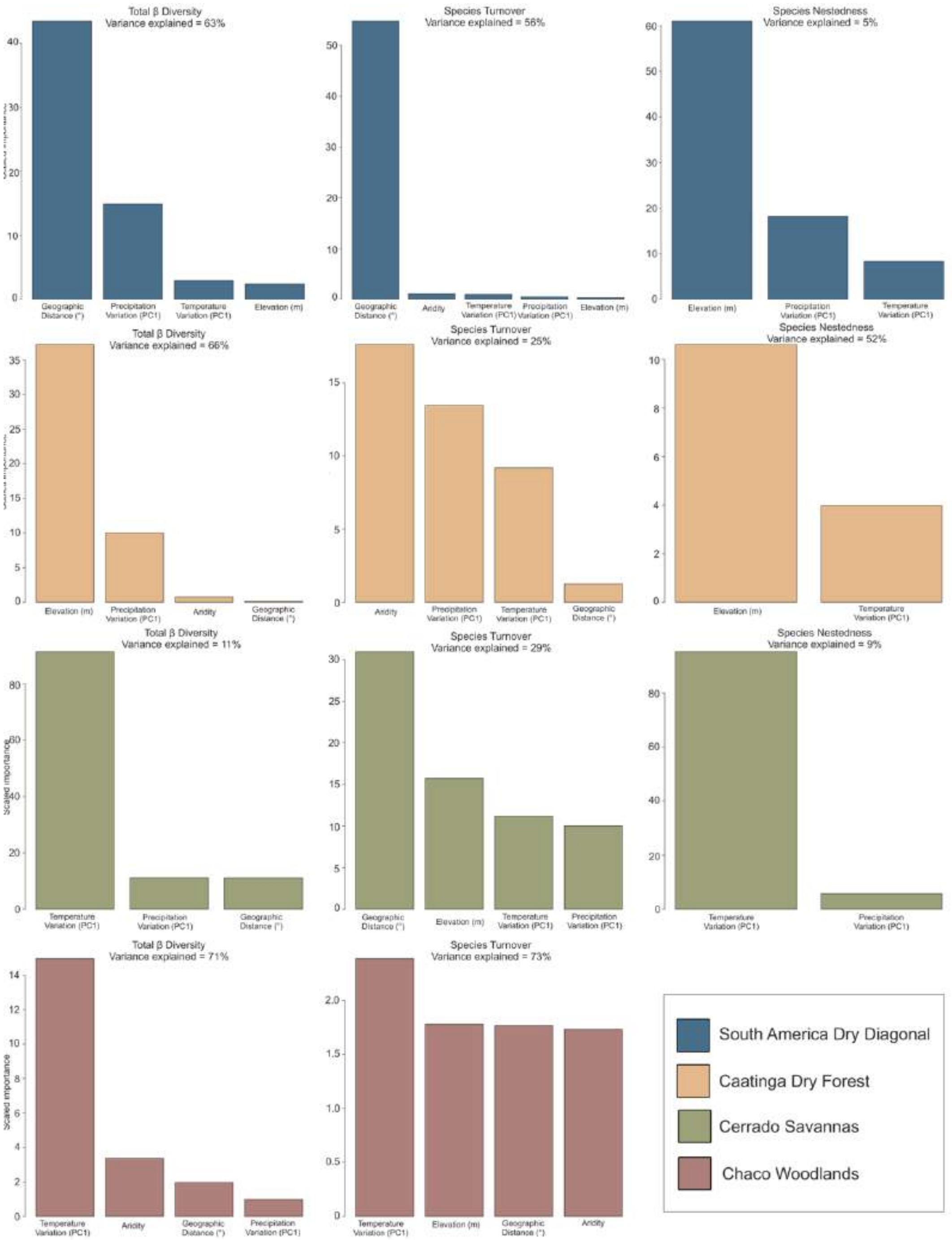


Figure S6. Best predictors of total β-diversity, species turnover, and species nestedness considering the whole SADD gradient, communities associated to the Caatinga Dry Forest, Cerrado Savannas and Chaco Woodlands. Predictor importance is the chance in total variance explained by the model when that predictor is randomized, here, the importance was scaled for comparison across models.

Capítulo III.

Lima, H. S.; Bravo, G. A.; Astúa, D.; Lopez, K.; Edwards, S.; Naka, L. N.

Phylogeography and biogeographic history of the Pearly-vented Tody-Tyrant (*Hemitriccus margaritaceiventer*) in South American open landscapes

Manuscrito à ser submetido – Molecular Ecology *A1*

Phylogeography and biogeographic history of the Pearly-vented Tody-Tyrant (*Hemitriccus margaritaceiventer*) in South American open landscapes

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Abstract

In the Neotropical region, the distribution and structuring of populations have been associated with climatic fluctuations and landscapes shifts during the Pleistocene. The influence of these climatic and landscapes shifts on South American biogeographic history and species distributions patterns of most clades remains unknown, especially for species that inhabit open/dry environments. Here, using whole genome data and a species-level phylogeny, we investigated the phylogeographic history and the ancestral habitats and range of the Pearly-vented Tody-Tyrant *(Hemitriccus margaritaceinventer*), a widespread species that inhabits South American open and dry environments. We retained a dataset with almost 19 million SNPs from 38 individuals from across its range representing all but three currently recognized subspecies. We uncovered a clear signal of genetic structuring among lineages and the existence of genetic clusters largely matching subspecific classification in both genome-wide population structuring analyses and mitogenomic phylogenetic inference. Tropical humid forests, such as Amazonia and the Atlantic Forest, were recovered as the most likely ancestral habitat for the *Hemitriccus* clade, with colonization of open/dry habitats occurring independently three times during the Pliocene and Pleistocene. This study represents the first comprehensive large-scale phylogeographic study of the *Hemitriccus* genus, including samples from a large part of the complex's distribution. The proposed scenarios corroborate previous studies and support the hypotheses that the currently fragmented open/dry environments of South America, were once connected, allowing species migration and diversification.

Keywords Whole genome, speciation, historical biogeography, dry environments

Introduction

Temporal and spatial processes are the main factors affecting the diversity, distribution, and structuring of species (Ricklefs 1987, da Silva et al. 2022). Within the Neotropics, the current diversity and structuring of species have been largely associated with major landscapes and/or climatic shifts, such as the uplift of the Andes, the formation of the Isthmus of Panama, the origin of Amazonian rivers, and a notable variation in climatic conditions during the Pleistocene (Chapman 1917, Sick 1967, Haffer 1969, Simpson 1980, Prado & Gibbs 1993). Whereas major landscape reconfigurations in South America covered most of the Neogene, it is generally accepted that the current landscape configuration of the continent was in place by the early Pleistocene (Werneck et al. 2012, Corbett et al. 2020, Buainain et al. 2022). Therefore, most biogeographic changes that can be traced down to the Pleistocene are generally attributed to climatic-driven expansion and contraction of vegetational formations during this Period, which likely led to events of expansion, isolation, and speciation (Prado & Gibbs 1993, Pennington et al. 2000).

The role of climatic fluctuations during the Pleistocene in the speciation process remains highly contentious, mostly due to the early work of Haffer (1969), who attributed most of the avian speciation in the Amazon to the formation of climatic forest refugia resulting from reduced precipitation and arid conditions. This idea, known as the ‘Pleistocene Refugia hypothesis’, lost track during the early 1990s due to the lack of evidence that the Pleistocenic climatic fluctuations were severe and frequent enough to fragment the core of the Amazon (Bush 1994, Colinvaux et al. 1996, Bush & Oliveira 2006, see Rocha & Kaefer 2019 for a careful reviews of this model). Whereas this hypothesis has been essentially abandoned for Amazonian taxa, the 'Pleistocene Arc hypothesis' formulated by Prado & Gibbs (1993) has gained traction during the last decades. This hypothesis states that the patches of dry/open vegetation formations currently surrounding Amazonia contracted and expanded during the Late Pleistocene forming a once contiguous 'arc' of seasonal dry woodland formation during a dry-cool climatic period.

The existence of this 'Pleistocene Arc' once connecting currently isolated patches of dry forests throughout South America currently represents the single-most important model supporting current distribution patterns of Tropical Dry Forest (hereafter TDFs) taxa in the Neotropics (Pennington et al. 2000, Prieto-Torres et al. 2019). Unfortunately, available data to test this hypothesis across a diverse array of taxa remains scarce, with limited studies either supporting or refuting this model. The age, phylogeographic history and divergence times of some Neotropical taxa represent the main line of evidence supporting this model, and they have been used as proxies to study the speciation process and phylogeographic history of species (Rojas et al. 2016, Corbett et al. 2020, Rocha et al. 2020). Gaps in the knowledge of the phylogeographic history of most clades that inhabit the open/dry domains still need to be filled (Werneck et al. 2012, Bolívar-Leguizamón et al. 2020). Only few phylogeographic studies of widespread dry forest species are available, and those have produced conflicting results regarding the existence of the Pleistocene Arc (Pennington et al. 2000, Werneck et al. 2012, Prieto-Torres et al. 2019, Corbett et al. 2020).

Historically, studies on avian historical biogeography have paved the way to test Neotropical evolutionary models (Remsen et al. 1991, Ribas et al. 2012, Smith et al. 2014, Naka & Brumfield 2018, Bolívar-Leguizamon et al. 2020, Harvey et al. 2020), but there is a relatively lack of studies on widespread lowland open habitat species to test alternative models. Ideally, we could look at widespread species or species complexes that cover distinct nuclei of TDFs throughout South America, with discrete and disjunct populations that could resemble an ancient 'arc'. By looking at the tempo and mode of diversification in those lineages, we could shed light into not only the diversification and phylogeography history of certain lineages, but also to understand the evolutionary history of the TDFs themselves. With enough replicates (different unrelated co-distributed groups), we will try to understand species-specific constrains and differences under common landscape scenarios. To date, only two avian groups have been studied in some detailed, including the Burnished-buff Tanager (*Stilpnia cayana*), and the Rufous-fronted Thornbird (*Phacellodomus rufifrons*), both of which show low levels of differentiation and somewhat different histories (Savit & Bates 2015, Corbett et al. 2020).

Here, we collected whole-genome data to investigate the evolutionary history of a third species, the Pearly-vented Tody-Tyrant *(Hemitriccus margaritaceinventer*), a tiny non-migratory suboscine passerine that inhabits open and dry domains in lowland South America, with a clear circum-Amazonian distribution. This polytypic species presents described phenotypic variation which resulted in the description of nine allopatric subspecies, ranging from the dry forests of N Colombia and Venezuela, with isolated populations along dry Andean valleys in Colombia and Peru, and a seemingly contiguous distribution covering Bolivia, Paraguay, Argentina, N Uruguay and eastern and northeastern Brazil, with some isolated populations in the Brazilian Amazon and at the base of the tepuis of Colombia, Venezuela and Guyana (Clock 2020) (Figure 1).

In this study, we used the entire genomes of 38 individuals of *Hemitriccus margaritaceinventer* from throughout its distribution and from six currently recognized subspecies to i) investigate patterns of phylogeographic structure; ii) elucidate the biogeographical history of this group in relation to the *Hemitriccus* clade, and iii) explore its historic area relationships and its possible association with major climatic events that occurred in the past.

Methods

Sampling

We sampled a total of 38 vouchered-tissue samples of six *Hemitriccus margaritaceiventer* subspecies from major natural history museums across the United States and Colombia. Our sampling spans 28 different localities, including individuals from subspecies *impiger* (7 samples), *septentrionalis* (4), *chiribiquetensis* (2), *duidae* (2), *rufipes* (4), *margaritaceinventer* (19) (Figure 1; Table S1). Unfortunately, for these analyses we had no access to samples of two-range restricted tepui populations (*auyantepui* and *brewreri*) and the subspecies *wuchereri* from Brazil.

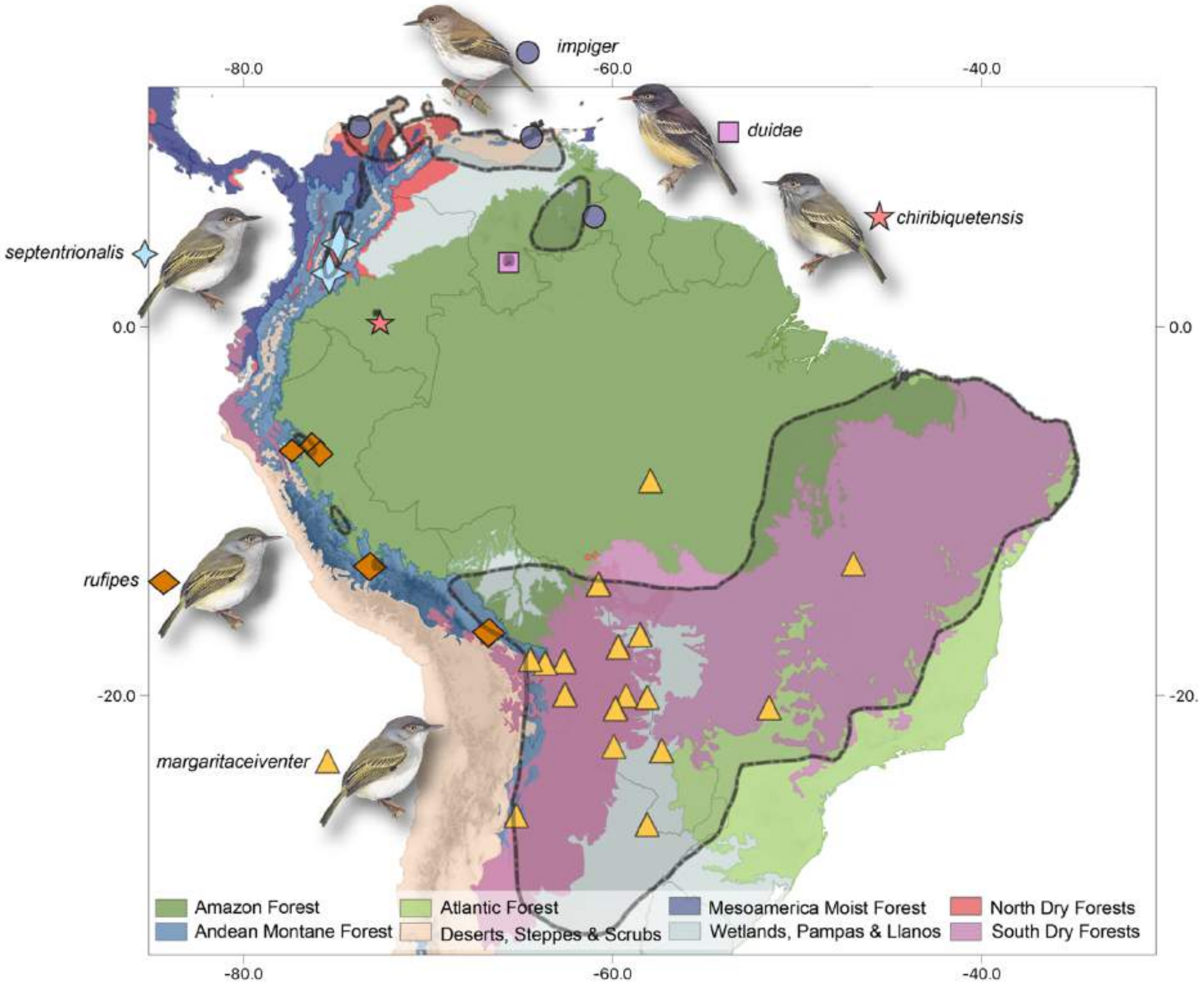

Figure 1. Distribution, phenotypic differentiation, and sampling localities of *Hemitriccus margaritaceinventer* subspecies samples obtained for this work. Shaded and dotted outlines represent the current distribution of the allopatric subspecies. Colors in the map represent the ecoregions classification used in BioGeoBEARS analysis. *Hemitriccus* subspecies illustrations are adapted from the Handbook of Birds of the World (Clock 2020).

Reference genome

We used a *de novo* reference genome (coverage ~30x) of *Hemitriccus margaritaceinventer wuchereri* (female, UFPE 6433, 9°13'S 43°28'W) assembled using long reads obtained via Pacific Biosciences High Fidelity technology (PacBio HiFi) and the SMRTbell prep kit 3.0 protocol at the Harvard University FAS Bauer Core Facility. The estimated genome size was ~1.1Gb and GC content was 42.8%. Preliminary annotation of this genome was done by homology through the alignment with the chicken (*Gallus gallus;* Genome Reference Consortium Chicken Build 6a, accession **GRCg6a** downloaded from NCBI) and zebra finch (*Taenopygia guttata;* Vertebrate Genomes Project, May 2021, accession **bTaeGut1.4** downloaded from NCBI) genomes. This annotation will be updated using RNA-seq data from *H. margaritaceiventer*. Genome assembly and annotation were conducted by C. Carvalho (Carvalho et al. in prep).

Whole-genome resequencing

We re-sequenced 38 individuals across the range of the *Hemitriccus margaritaceiventer* subspecies representing six of the nine currently-recognized subspecies (Clock 2020). The majority of samples represent fresh tissues preserved in ethanol or liquid nitrogen. Nine samples, however, came from toe pad clippings from museum specimens. Genomic DNA from fresh tissues was extracted using the DNeasy Blood and Tissue Kit (Qiagen) following the manufacturer's protocol. For toe pad samples, the isolation of DNA was conducted following the protocol by Harvey et al. (2020). We aimed for a fragment size distribution of 300 base pairs. Genomic DNA libraries were created using the Illumina DNA Kit - Quarter Volume or a Kapa HyperPrep Plus library preparation kit for tissue and toe pad samples, respectively. Genomic libraries were sequenced with 150 bp paired-end reads across a NovaSeq S4 single lane flowcell at the Bauer Core Facility at Harvard University.

Variant calling and filtering

We called variants using *snpArcher* (Mirchandani et al. 2023), a workflow designed specifically for the analysis of resequencing data in non-model organisms. *snpArcher* maps reads to the reference genomes and provides a standardized variant calling pipeline implementing GATK (McKenna et al. 2010) best practices. Variant Call Format (VCF) files were filtered using the VCFTools package (Danecek et al. 2011) keeping only sites with a minimum depth of coverage equal or greater than 10x. We also removed indels, missing data for more than 10% of individuals, and included only bi-allelic SNPs, the minimum quality score was defined to 30. The final dataset obtained after sequencing recovered 39,623,860 SNPs across 38 individuals. Average sequencing depth for resequenced individuals obtained a mean of 12.93X. After quality and coverage filtering, we retained a dataset consisting of 18,663,378 SNPs that were used in subsequent analyses.

Population structure analyses

We pruned SNPs to minimize the effects of linkage disequilibrium (LD) using PLINK 2.0 (Chang et al. 2015). We perform all population structure analyses using this set of 18,663,378 variant sites. Using this LD pruned dataset, we conducted principal components analysis also in PLINK and we visualized the PCA axis in R 4.3.1 (R Core Team 2023). We input filtered SNPs to further estimate population genetic structure with DAPC (discriminant analysis of principal components) in R, using the *adegenet* package (Jombart 2008), and using subspecies as *a priori* groups. We determined the best k values of DAPC analyses by evaluating BIC values. We also analyzed population structure using sNMF analyses (Frichot et al. 2014) implemented in the R package LEA (Frichot and François 2015). For sNMF analysis, we considered ancestral populations (K) ranging from 1:6 (where 1 represents absence of genetic structure and 6, represents populations divided by the subspecies already known). We used three different α regularization parameters (10, 50 and 100), to test the consistency of the model (Frichot et al. 2014). We perform 10 repetitions for each run, and we used the default value to the iteration number (200). We determined the best K values for each α by visualizing and identifying the decreasing point of the cross-entropy calculations values.

Mitochondrial genome assembly and alignment

We assembled *de novo* mitochondrial genomes using the default setting of NOVOPlasty 4.3.3 (Dierckxsens et al. 2016). Assemblies were aligned with MAFFT 7.0 (Katoh et al. 2019) and batch-annotated using GENEIOUS PRIME 2023.2.1 (https://www.geneious.com) once they were aligned. We used a *Mionectes oleaginous* as a reference sequence (Genbank accession number: KJ742591.1; Loaiza et al. 2014) for mapping and annotation. This sequence was also included in the alignment as an outgroup. We were able to successfully assemble the mitochondrial genome for 37 of the 38 sequenced individuals (*H. m. rufipes*, LSU46176 was unsuccessful), with final assemblies ranging in size from 17,023 – 17,326 base pairs in average.

Annotation identified 13 protein coding genes, of these, 10 were used in the phylogenetic inference analyzes (Table S2).

Phylogenetic inference and time-calibrated mitochondrial gene tree

We used 37 samples and *Mionectes oleaginous* as the outgroup to infer the mitochondrial gene tree. From the mitogenome alignment, we extracted sequences of protein-coding genes except for the very short ND4L, ND6 and ATP8 (following Nabholz et al. 2016). The optimal partitioning scheme was selected using Partition Finder under the Bayesian information criterion (BIC) (Lanfear et al. 2012). Then, we ran BEAST 2.7.5 (Bouckaert et al. 2019) for 50,000,000 generations, sampling every 5,000 generations, a strict molecular clock with a rate of 2.1% Myr (Weir & Schluter 2007), and assuming different substitution models for each one of the partitions schemes selected (Table S2). BEAST approximation of posterior tree distributions was obtained by Markov Chain Monte Carlo (MCMC). We assessed convergence (by examining ESS values), mixing of the MCMC chain and parameter posteriors using Tracer v1.7.2 (Rambaut et al. 2018), and we generated a maximum clade consensus tree using TreeAnnotator v.2.7.5 (Bouckaert et al. 2019) with 10% of burn-in.

Ancestral habitat and ancestral range estimation

To shed light on the evolution of habitat associations within the *Hemitriccus* radiation, we used the Harvey et al. (2020) phylogeny, which represents the most complete species-level phylogeny available and includes most Neotropical suboscine species. We edited this phylogeny using Mesquite 3.81 (Maddison & Maddison 2023) to extract the clade that contained all available *Hemitriccus* species. This resulted in a phylogenetic tree containing lineages not only of the genus *Hemitriccus*, but also members of the genera *Lophotriccus*, *Poecilotriccus* and *Oncostoma*. We will refer to this phylogenetic hypothesis hereafter, as the "*Hemitriccus* clade". Our goal in here, was to understand the history of the habitat association not only for our target species, the *Hemitriccus margaritaceinvente*r, but also to recover the history of the entire clade. We classified each species as: i) humid forest (species occurring in tropical humid forests, such as Amazon or Atlantic Forest), ii) montane (species that inhabits montane forest, such as Andes or Amazonian tepuis), ii) bamboo (species specialized in bamboo vegetation), iii) savannas (species associated with savannas and white-sand campinaranas), iv) dry forests (species that inhabit open areas and dry forests), based in data from literature. We used the function *make.simmap* in the *phytools* package (Revell 2012) in R, based in the best-fit transition rate model (evaluated by the value of AIC and AICc) to simulated a stochastic habitat history of the *Hemitriccus* clade on 1000 posterior distribution probabilities.

We also inferred the biogeographic history of the *Hemitriccus* clade, using the *BioGeoBEARS* package (Matzke 2014) in R. Our goal here, was to unveil the history of colonization of different biogeographic Neotropical domains of the *Hemitriccus* clade. We considered six areas: Amazon Forest (Am), Andean Montane Forest (Af), Atlantic Forest (At), Northern Dry Forests (Dr), Dry Diagonal (Dd), Mesoamerica (Me). All taxa were assigned to one or more of these areas. We set the maximum possible number of ancestral areas of occurrence of each species in the models to six, so each taxon could occur simultaneously in all pre-defined areas. We evaluated the fit of the data under six different models: DEC, DEC+J, DIVA, DIVA+J, BAYAREALIKE, and BAYAREALIKE+J, using AICc values.

Results

Population structure analyses and phylogenetic inference

Our population structure analysis shows genetic structure among populations of *H. margaritaceiventer*, with at least two main genetic clusters. The first population subdivision (K = 2) (Figure S2) discriminates a Northern (*chiribiquetensis*, *duidae*, *impiger*, and *septentrionalis*) and a Peruvian-South America Dry Diagonal (Peruvian-SADD, hereafter) (*rufipes* e *margaritaceinventer*) population, including individuals from savanna enclaves in Amazonia south of the Amazon River (Figure 2b). Inside these two main groups, individuals assigned to named subspecies showed varying degrees of mixed ancestry, particularly between subspecies *impiger* (from North Colombia), and *margaritaceinventer* (from Central Brazil) (Figure 2b). This subdivision into a Northern and a Peruvian-SADD populations is robust across markers and methodologies, including SNP analyses (PCA and sNMF, Figures S1 and S2) and also in our mitochondrial tree (Figure 2a).

Under a K = 3 scenario, our results were able to discriminate a subgroup within the Northern clade, including an Magdalena Valley-Coastal Colombia and Venezuela group (including *septentrionalis* and some *impiger* populations) and a Northern Amazonian-Tepui-Guiana Shield group from Southern Colombia, Southern Venezuela and Guyana (including *chiribiquetensis*, *duidae*, and some *impiger* populations), with evidence of mixed ancestry between the *impiger* samples from the Magdalena Valley-Coastal Colombia and Venezuela group and Northern Amazonian-Tepui-Guiana Shield group (Figure 2b, Figure S2).

The results of DAPC found four genetic clusters (K = 4) (Figure 2b, S3, S4) three of the clusters recapitulated the same subspecies grouping as the sNMF (K = 3), but with an additional cluster composed but three individuals from the subspecies *margaritaceinventer* from Central Brazil, separating populations from the South American Dry Diagonal (Figure 2b).

Our mitochondrial gene tree showed a well-resolved phylogenetic hypothesis (Figure 2a). Coinciding with whole-genome structure analyses, the mitochondrial gene tree recovered Northern and Peruvian-SADD well-supported clades. In the latter, our mitochondrial gene tree recovered clade formed by the three individuals from the subspecies *margaritaceinventer* subspecies from Central Brazil, coinciding with structure analyses when k = 3 (Figure 2a). According to our time-calibrated gene tree, the split between the Northern and Peruvian-SADD main populations, occurred during middle Pleistocene (~1.93 Ma). This split was followed by the divergence and rapid diversification of the Northern population also during the middle Pleistocene (~1.27 Ma), separating the populations from Northern Colombia and Venezuela from the populations of Southern Colombia and Venezuela and Guyana. The separation between the Peruvian-SADD populations also occurred during the middle Pleistocene, but more recently (~0.84 Ma) (Figure 2a).

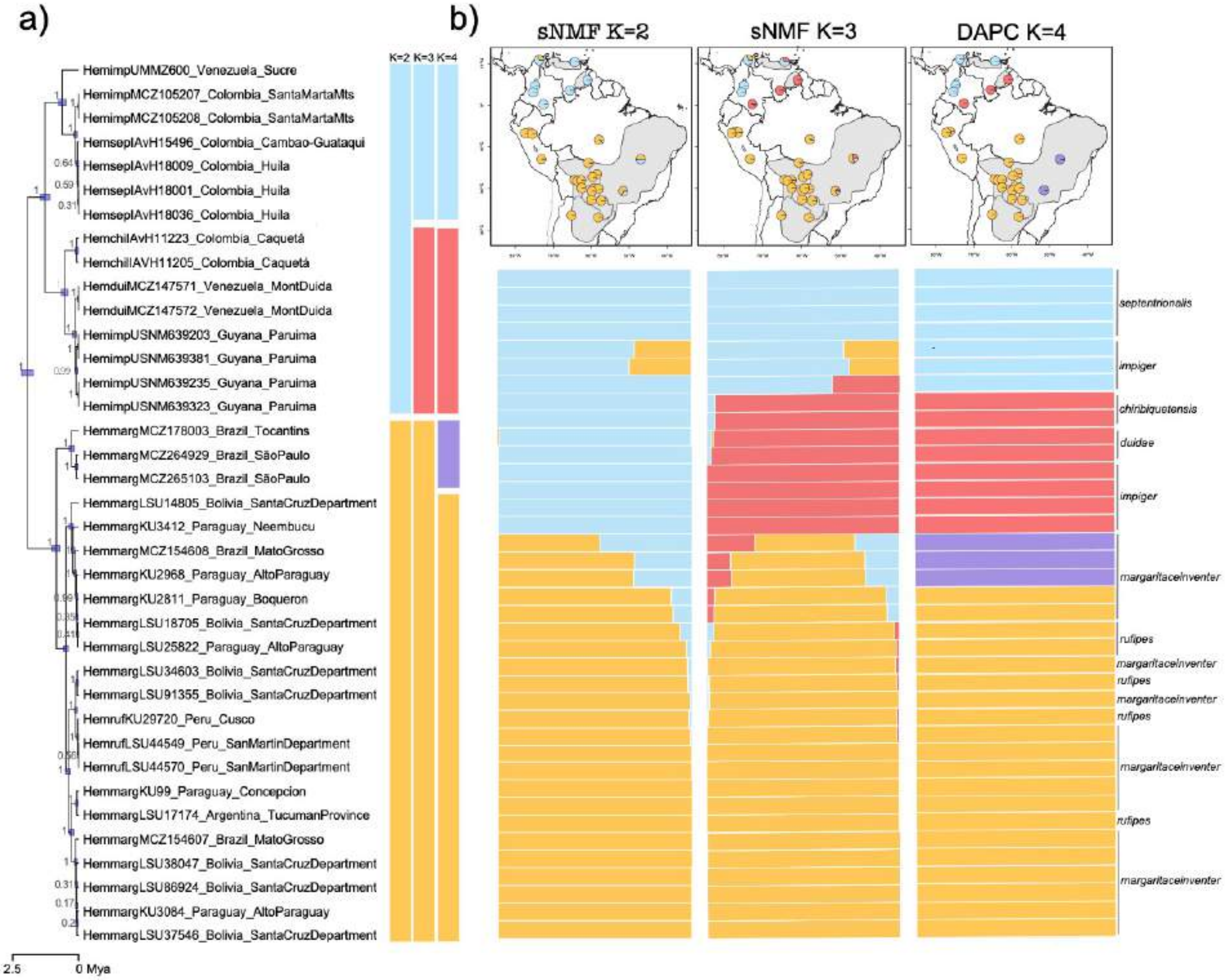

Figure 2. *Hemitriccus margaritaceinventer* time-calibrated mitochondrial genome tree and population structure results for sNMF and DAPC analyses. Colored bars next to the mitochondrial tree represent the structuring found by the sNMF and DAPC analyses considering different numbers of genetic clusters (a). Ancestral coefficients maps and side bar plots showing the genetic structure of *Hemitriccus margaritaceinventer* subspecies in sNMF and DAPC analyses (b).

Ancestral habitat and ancestral area estimation

The most informative ancestral reconstruction model was that of equal rates (ER) (AIC = 123.54, AIC.w = 0.99) (Table S3), which indicates that transitions between any of the habitats defined in here could occur with equal probability. According to our results, the most recent common ancestor of the *Hemitriccus* clade was most likely associated with tropical humid forests, such as Amazonia or the Atlantic Forest (Figure 3a). Colonization of bamboo and montane habitats took place early in the history of the clade and occurred subsequently multiple times. Dry/open habitats, such as the savannas and the dry forests occupied by *Hemitriccus margaritaceinventer,* only occurred within the Pliocene and Pleistocene (between 2.3 and 4.6 Ma) (Figure 3a). Colonization events of this open/dry habitats occurred independently when different lineages colonized these types of habitats six times since the Pliocene and during the Pleistocene (Figure 3a).

In relation to the ancestral range estimation, the most informative model was the DIVALIKEj (Dispersal-vicariance analyses) (AIC=175.4, AIC.w= 0.87) (Table S4). Under this reconstruction, the ancestral distribution area for the clade is Amazonia (Figure 3b). Expansion into other areas occurred during the Miocene, around 8 Ma, when early ancestors began to occupy the Atlantic Forest in eastern South America. The colonization of the Andes can also be tracked back to the Miocene, around 6.5 Ma, when different lineages (as *Poecilotriccus ruficeps*, *Poecilotriccus luluae*, *Poecilotriccus plumbeiceps*, *Hemitriccus rufigularis*, *Hemitriccus granadensis*, *Hemitriccus cinnamomeipectus*, *Hemitriccus spodiops* and *Lophotriccus pileatus*) colonized the Andes independently over the Miocene, Pliocene, and Pleistocene (between 2.1 and 6.4 Ma) from the Amazon or the Atlantic Forest (Figure 3b). The occupation of Mesoamerica seems to be the result of two independent colonization events from two different humid forest areas during the Pliocene around 3.04 Ma, when the ancestors of *Myiornis ecaudatus* / *atricapillus*, *Oncostoma cinereigulare*/*olivaceum* and *Lophotriccus pileatus* colonized this region from the Amazon (Figure 3b). According to our model, the occupation in dry forests habitats started during the Pliocene about 4.9 Ma giving origin to *Atalotriccus pilaris* from a humid forest Amazonian ancestor, and then again ~3.45 Ma to give origin to *Hemitriccus margaritaceinventer*, possibly also from an Amazonian ancestor (Figure 3b).

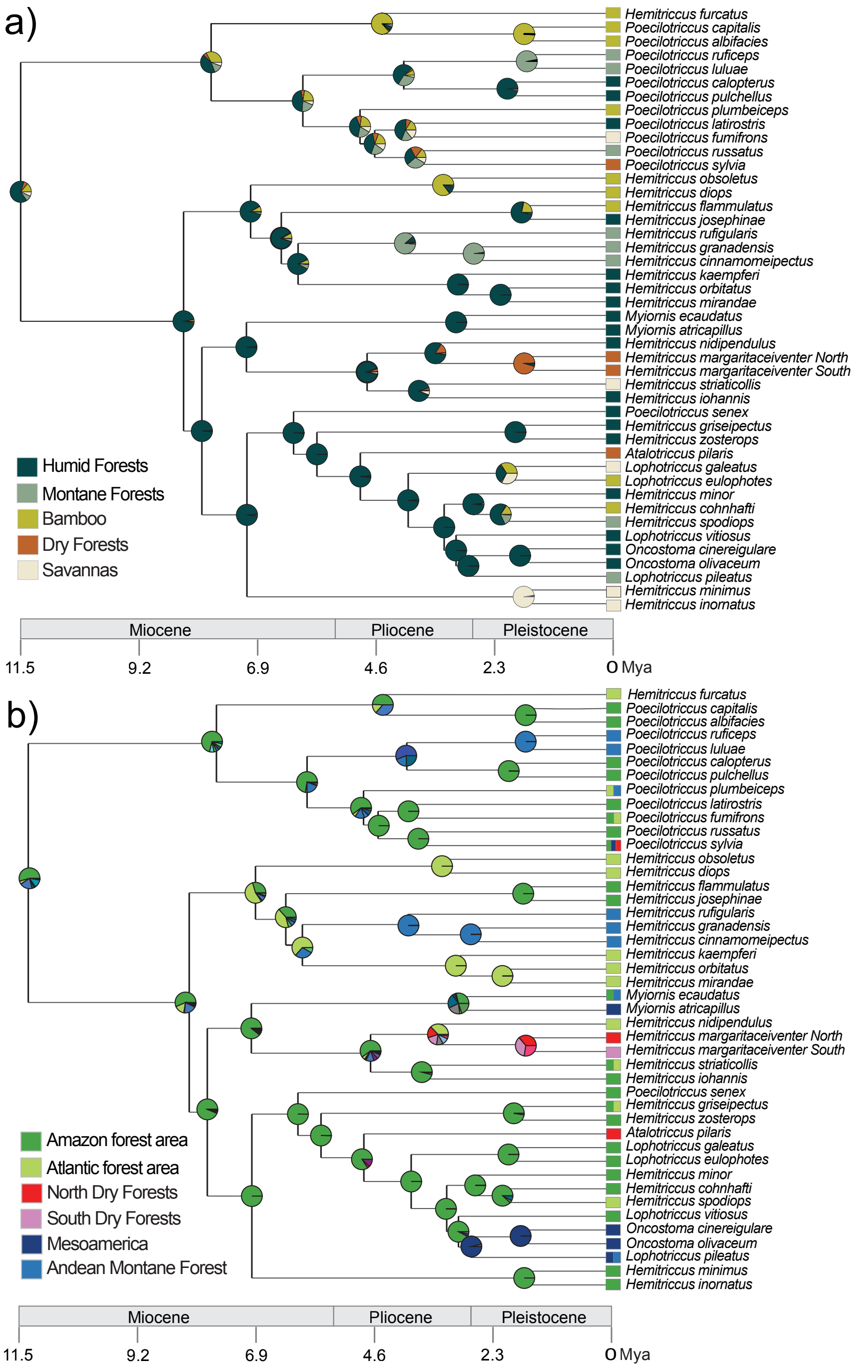

Figure 3. Ancestral habitat and ancestral range distribution estimation for the *Hemitriccus* clade. The topology shown in here is adapted from Harvey et al. (2020). Colors at the three tips represent the current habitat (a) and distribution (b) of each lineages, while pie charts colours in three nodes represent the posterior probabilities ancestral habitat sampled from 1000 simulations (a) and the most likely ancestral ranges estimated by the DIVALIKEj model in BioGeoBEARS (b). Geographic locations used in BioGeoBEARS analyses can be visualized in Figure 1.

Discussion

In this study, we provide results that increase the knowledge about population structure, phylogenetic relationships, and biogeographic history of *Hemitriccus margaritaceinventer* and the *Hemitriccus* clade. More broadly, our results provide a good starting point toward the understanding of the evolutionary history of species restricted to South American dry/open environments. Mainly, we recovered two main genetic clusters grouping subspecies along the humidity gradient surrounding Amazonia, with different levels of genetic structuring within each group. Moreover, we found that the *Hemitriccus* clade originated from humid forests habitats, possibly with Amazonia as the main source of the clade diversification.

Historical phylogeography of <u>Hemitriccus margaritaceinventer</u>

Despite the recent divergence time of the *Hemitricccus margaritaceiventer* subspecies, we found evidence of genetic structuring between disjunct populations/subspecies, with two geographically structured genetic clusters. The Northern cluster includes individuals identified as *chiribiquetensis*, *duidae*, *impiger*, and *septentrionalis*, whereas the Peruvian-SADD includes samples of *rufipes* and *margaritaceinventer*, comprising individuals from savanna enclaves in Amazonia south of the Amazon River (Figure 2b).

In the Northern cluster, subspecies *chiribiquetensis*, *duidae*, and *impiger* (from Guyana), clustered together in all K values. When described in 1995, *chiribiquetensis* was assumed to be closer to *septentrionalis*, from the Magdalena Valley, than to *duidae* and *impiger*, both restricted to nearby tepuis formations in Venezuela and Guyana, suggesting a long-distance dispersal from Andes to the Serranía de Chiribiquete, where have been isolated until recent times (Stiles 1995). Although we observed evidence of shared ancestry between *chiribiquetensis* and *septentrionalis* (K=3), our results suggest a major genetic affinity between *chiribiquetensis* and the near tepui subspecies. It is worth noting that the Serranía de Chiribiquete is an old formation of low elevation tepuis of Guianan origin (Huber 1994). Therefore, our results coincide not only with predictions based on the geological origin of populations located across the different formations of the Guiana Shield (Berry & Riina 2005, Kok et al. 2018), but also with floristic studies that observed a strong relationship between the vegetational formations of the open/dry domains from Northern South America (Linares-Palomino et al. 2011).

In the Peruvian-SADD cluster, despite long geographic distances of more than 200 km separating populations, the genomic affinity between subspecies *rufipes* and *margaritaceinventer,* also corroborates a pattern previously described for plants and birds, that suggested a strong relationship between plant species from dry/open environments of Brazil, Argentina, Paraguay and Bolivia, when compared with species from other biogeographic domains in South America (Linares-Palomino et al. 2011). Other bird species, such as *Thamnophilus caerulescens* (Bolívar-Leguizamón et al. 2020) and *Phacellodomus rufifrons* (Corbett et al. 2020), showed the same pattern for circum-Amazonian populations west and south of Amazonia. Altogether, these concordant results across co-occurring species offer evidence for the presence of an ancient corridor connecting those Peruvian populations with those in the SAAD, allowing dispersal events between these areas.

Despite the long distances and geographical isolation between some populations, distance does not seem to represent a barrier leading to increased genetic structure. For instance, in Northern populations, some individuals of *impiger* (from Northern Colombia) and *margaritaceinventer*, separated by more than 2,000 km, showed similar levels of mixed ancestry when compared with geographically closer populations such as *impiger* (from Southern Venezuela), *duidae*, and *chiribiquetensis*. It is not likely that these populations have gene flow currently. Thus, our results may be evidence of retained ancestral polymorphisms dating back to when ancient corridors allowed connections between *impiger* and *margaritaceinventer*. Further structure and demographic analyses with more complete sampling and accounting for potential effects of isolation by distance (IBD) will allow further insights into past connections between disjunct populations.

The proposed scenarios described above not only coincide with previous studies of bird species sharing similar circum-Amazonian distributions with widespread disjuncts ranges across dry forests (Bolívar-Leguizamón et al. 2020, Corbett et al. 2020), but also point to ancient connections during the Pleistocene. It is suggested that fragments of dry forest formed an interconnected belt that would later be fragmented, both due to cyclic climatic oscillations, and geomorphological changes leading to the repetitive separation and reconnection of populations in a non-gradual/simultaneous period, which may explain the differential levels of gene flow between subspecies (Haffer 1969, Prado & Gibbs 1993, Corbett et al. 2020, Buainain et al. 2022). Our results, then, can be considered as further evidence that the *Hemitriccus margaritaceinventer* populations were connected in the recent past, and the Pleistocene climatic oscillation and the connections among the dry forests patches influenced the diversification in this species and could have facilitated the expansion of this taxa across the continent, a pattern hypothesized by the Pleistocene Arc Hypothesis. All these postulations regarding the phylogeographical history of *Hemitriccus margaritaceiventer* and the historical connections between populations, however, need to be further explored with more detailed historical demographic analyses and improved geographic sampling.

Ancestral habitat and range reconstruction

Considering our population structure analyses, we found evidence of mixed ancestry between *rufipes* (Peruvian-SADD genetic cluster) and Northern populations and decreased levels of shared ancestry in the south (Bolivia, Paraguay, and Brazil). Furthermore, divergence between the Northern and Peruvian-SADD clades and the results of habitat and ancestral area reconstructions suggest a northern origin of *Hemitriccus margaritaceinventer*. The *Hemitriccus* clade originated predominantly in Amazonian humid forests, matching results from a wealth of animal and plat taxa (Antonelli et al. 2017). Colonization of different habitats occurred independently along the history of the clade, with humid forest habitats as one of the ancestral habitats for the clade, and occupation of bamboo, savannas, montane forests, and dry forests, occurring also independently along the clade since the Miocene.

Speciation in montane and open/dry habitats (such as savannas and dry forests), occurred mainly during middle Pliocene and Pleistocene. This more recent occupation could be associated with the environmental changes that occurred during the Pleistocene climatic oscillations, which led to changes in the distribution patterns of many phytophysiognomies, causing extensive habitat configurations. Ultimately, climatic changes caused extinctions, shifts in species distribution, and invasions into new habitats and areas (Haffer 1969, Fine & Lohmann 2018, Buainain et al. 2022, Lima et al. in prep).

Diversification of the *Hemitriccus* clade started in the Miocene, about 11.5 Ma, in Amazonia. Colonization of the Atlantic Forest in eastern South America started in the Miocene, and subsequent independent colonization events took place throughout the history of the clade.

The Miocene period coincides with a decrease in global temperature, a fragmentation of tropical biomes and the expansion of more open and drier environments (Claramunt & Cracraft 2015, Castro et al. 2021, Buainain et al. 2022). These changes in climate and in the arrangement of available phytophysiognomies and habitats during the Miocene, may have favored the isolation of these lineages in humid areas and may have caused strong selective pressures to develop traits better suited for survival in drier habitats, which may have allowed their dispersal into drier environments (Fine & Lohmann 2018).

We uncovered biotic interchange between Amazonia, the Atlantic Forest, and Andean Montane forests during the Miocene and Pliocene in the *Hemitriccus* clade. The occurrence of theses shifts has been previously described for other taxa, which may be the effect of various climatic changes and multiple instances of expansions/contractions of habitats throughout this period of climatic instability in South America. Also, colonization into new areas may have been favored by significant geomorphologic changes, such as the uplift of Central and Northern Andes, that promoted the diversification and speciation of both montane and lowland South America biota (Antonelli et al. 2017, Buainain et al. 2022).

Occupation of dry forested areas, both in north and central South America and Mesoamerica, occurred during the Pliocene and Pleistocene from ancestors restricted to Amazonia. The occupation of dry forests occurred independently during the Pliocene and Pleistocene, coinciding with a climatic oscillation period when disjunct dry forest patches were connected, allowing that populations better adapted to drier conditions expanded and occupy drier areas (Corbett et al. 2020, Buainain et al. 2022, Lima et al. in prep). We also uncovered a dispersion event between Amazonia and Mesoamerica, coinciding with the estimated time of the Isthmus of Panama closure during the late Pliocene (Jaramillo 2018). Significant numbers of dispersion events between Meso and South America were already described elsewhere, reinforcing the idea of a long and continuous exchange of lineages with the North American continent (Antonelli et al. 2017).

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Supplementary Material

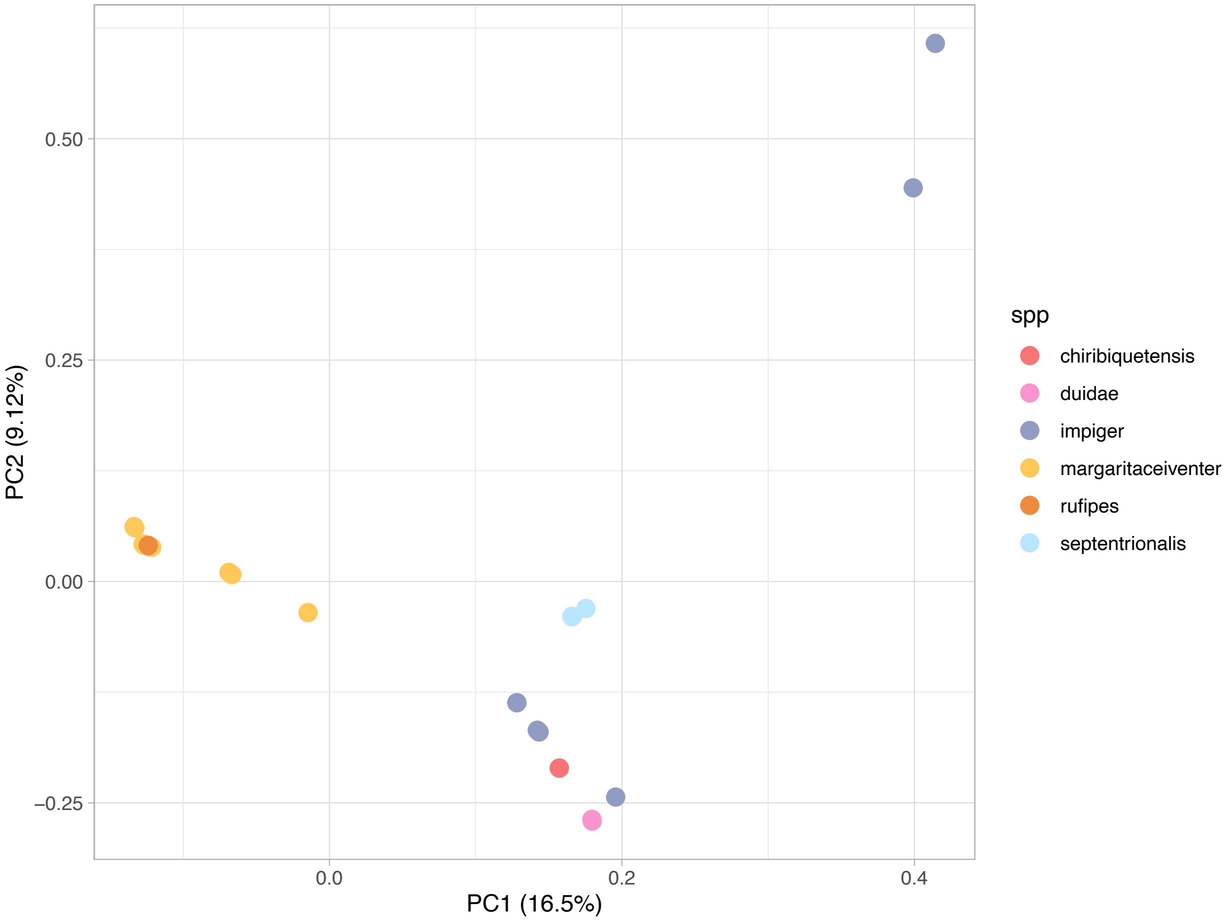

Figure S1. PCA analyses of SNPs data for the *Hemitriccus margaritaceinventer* subspecies. PCA analyses recovered primarily two main groups. Two *impiger* individuals were grouped separately in the PCA, but we believe this could be an effect of SNPs variation in these individuals, as the separation of these individuals was not found in any other test.

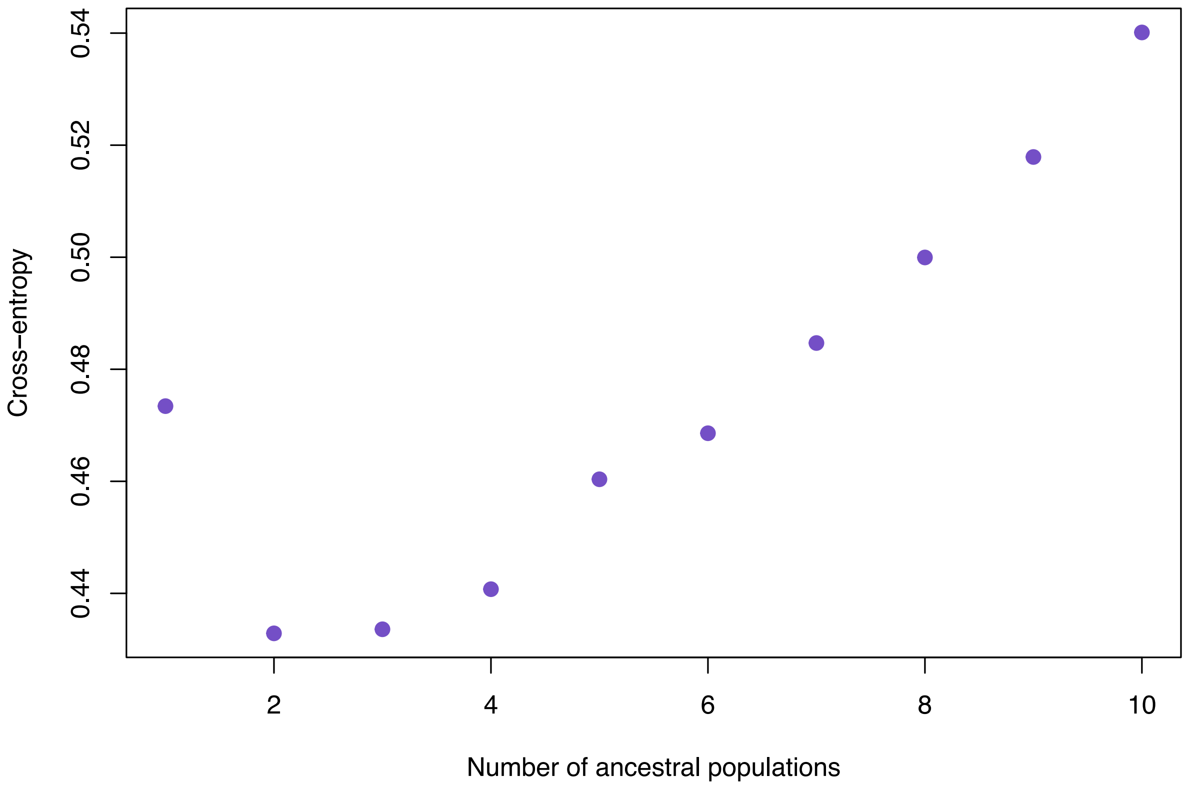

Figure S2. Cross-entropy values for the sNMF analyses of SNPs data for the *Hemitriccus margaritaceinventer* subspecies. We investigated both scenarios of K=2 and K=3 to understand the genetic structuring of the *Hemitriccus margaritaceinventer* subspecies.

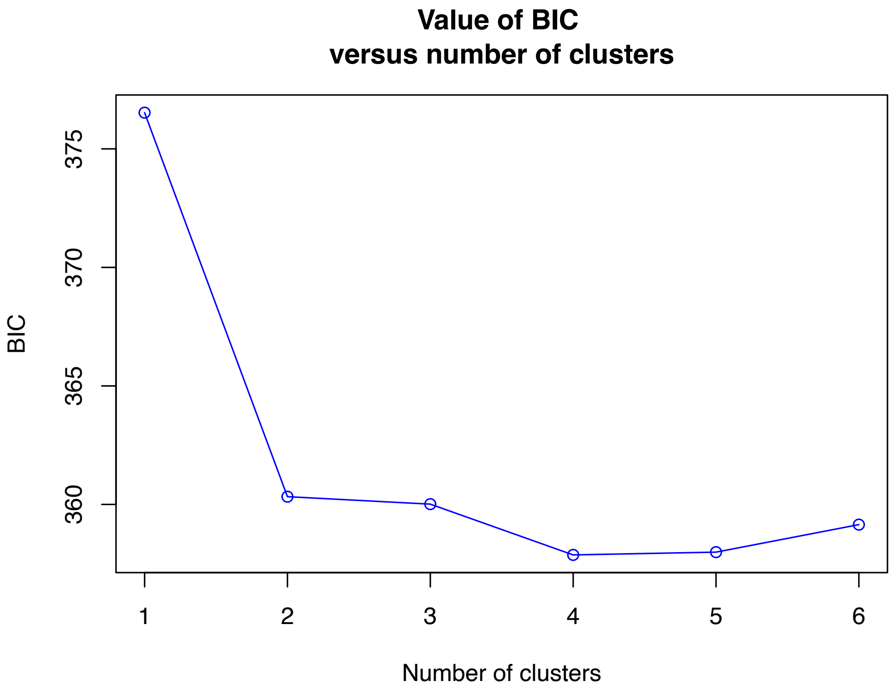

Figure S3. DAPC analyses of SNPs data for the *Hemitriccus margaritaceinventer* subspecies, recovered four genetic clusters. We selected the number of genetic clusters based in the lower BIC value.

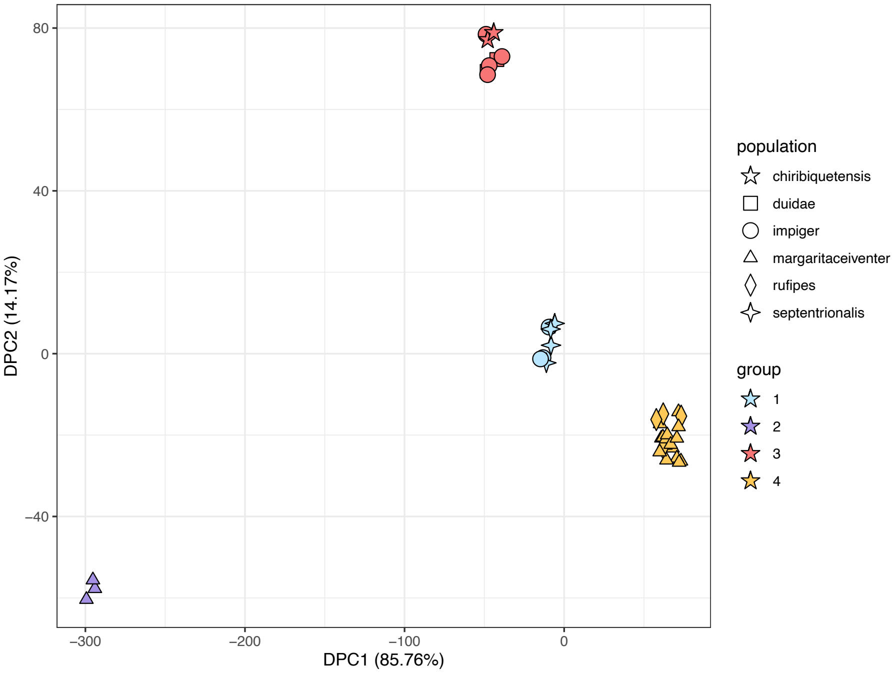

Figure S4. DAPC analyses of SNPs data for the *Hemitriccus margaritaceinventer* subspecies, DAPC recovered four genetic clusters.

Table S1. Samples obtained for *Hemitriccus margaritaceinventer* subspecies.

Tissue Sample	Museum	Taxa	Subspecies	Country	State	LONG	LAT	Data
KU2968	KansasU	*H. margaritaceiventer*	*margaritaceiventer*	Paraguay	Alto Paraguay	-59.26	-20	9/23/99
KU2811	KansasU	*H. margaritaceiventer*	*margaritaceiventer*	Paraguay	Boqueron	-59.93	-22.76	9/15/99
KU29720	KansasU	*H. margaritaceiventer*	*rufipes*	Peru	Cusco	-73.16	-13	10/14/12
KU3412	KansasU	*H. margaritaceiventer*	*margaritaceiventer*	Paraguay	Neembucu	-58.14	-27	10/31/99
KU3084	KansasU	*H. margaritaceiventer*	*margaritaceiventer*	Paraguay	Alto Paraguay	-58.13	-20.1	9/28/99
KU99	KansasU	*H. margaritaceiventer*	*margaritaceiventer*	Paraguay	Concepcion	-57.35	-23	10/23/96
LSU_17174	LSU	*H. margaritaceiventer*	*margaritaceiventer*	Argentina	Tucuman Province	-65.23	-26.51	11/26/96
LSU_91355	LSU	*H. margaritaceiventer*	*margaritaceiventer*	Bolivia	Santa Cruz Department	-62.62	-18.11	8/1/15
LSU_86924	LSU	*H. margaritaceiventer*	*margaritaceiventer*	Bolivia	Santa Cruz Department	-63.63	-18.20	7/26/13
LSU_38047	LSU	*H. margaritaceiventer*	*margaritaceiventer*	Bolivia	Santa Cruz Department	-58.5	-16.66	7/29/99
LSU_18705	LSU	*H. margaritaceiventer*	*margaritaceiventer*	Bolivia	Santa Cruz Department	-62.57	-19.92	9/9/90
LSU_37546	LSU	*H. margaritaceiventer*	*margaritaceiventer*	Bolivia	Santa Cruz Department	-59.68	-17.33	7/9/99
LSU_14805	LSU	*H. margaritaceiventer*	*margaritaceiventer*	Bolivia	Santa Cruz Department	-60.75	-13.92	7/5/89
LSU_34603	LSU	*H. margaritaceiventer*	*margaritaceiventer*	Bolivia	Santa Cruz Department	-64.43	-18.00	7/10/00
LSU_25822	LSU	*H. margaritaceiventer*	*margaritaceiventer*	Paraguay	Alto Paraguay Department	-59.83	-20.66	10/29/95
LSU_44549	LSU	*H. margaritaceiventer*	*rufipes*	Peru	San Martin Department	-76.31	-6.41	8/3/02
LSU_44570	LSU	*H. margaritaceiventer*	*rufipes*	Peru	San Martin Department	-76.23	-6.58	8/11/02
LSU_46176	LSU	*H. margaritaceiventer*	*rufipes*	Peru	San Martin Department	-77.38	-6.73	7/24/03
UMMZ600	Michigan	*H. margaritaceiventer*	*impiger*	Venezuela	Sucre	-64.34	10.34	1/27/89
IAvH-A-18036	IAvH	*H. margaritaceiventer*	*septentrionalis*	Colombia	Huila, Neiva	-75.38	3.06	8/9/21

IAvH-A-18009	IAvH	*H. margaritaceiventer*	*septentrionalis*	Colombia	Huila, Neiva	-75.36	3.06	8/4/21
IAvH-A-18001	IAvH	*H. margaritaceiventer*	*septentrionalis*	Colombia	Huila, Neiva	-75.36	3.06	8/3/21
IAvH-A-15496	IAvH	*H. margaritaceiventer*	*septentrionalis*	Colombia		-74.77	4.66	11/21/14
IAvH-A-11223	IAvH	*H. margaritaceiventer*	*chiribiquetensis*	Colombia	PNN Serranía de Chiribiquete	-72.60	0.18	4/18/00
IAvH-A-11205	IAvH	*H. margaritaceiventer*	*chiribiquetensis*	Colombia	PNN Serranía de Chiribiquete	-72.60	0.18	4/16/00
MCZ105207	MCZ	*H. margaritaceiventer*	*impiger*	Colombia	Santa Marta Mts	-73.72	10.86	13/1/1898
MCZ105208	MCZ	*H. margaritaceiventer*	*impiger*	Colombia	Santa Marta Mts	-73.72	10.86	11/1/1898
MCZ147571	MCZ	*H. margaritaceiventer*	*duidae*	Venezuela	Mount Duida	-65.62	3.51	15/2/1929
MCZ147572	MCZ	*H. margaritaceiventer*	*duidae*	Venezuela	Mount Duida	-65.62	3.51	7/2/29
MCZ154607	MCZ	*H. margaritaceiventer*	*margaritaceiventer*	Brazil	Mato Grosso	-57.95	-8.35	5/8/30
MCZ154608	MCZ	*H. margaritaceiventer*	*margaritaceiventer*	Brazil	Mato Grosso	-57.95	-8.35	7/8/30
MCZ178003	MCZ	*H. margaritaceiventer*	*margaritaceiventer*	Brazil	Tocantins	-46.95	-12.85	10/23/32
MCZ264929	MCZ	*H. margaritaceiventer*	*margaritaceiventer*	Brazil	São Paulo	-51.51	-20.66	11/10/38
MCZ265103	MCZ	*H. margaritaceiventer*	*margaritaceiventer*	Brazil	São Paulo	-51.51	-20.66	10/24/38
USNM_639203	Smithsonian	*H. margaritaceiventer*	*impiger*	Guyana	Cuyuni-Mazaruni	-61.04	5.98	2/22/07
USNM_639235	Smithsonian	*H. margaritaceiventer*	*impiger*	Guyana	Cuyuni-Mazaruni	-61.04	5.98	2/26/07
USNM_639323	Smithsonian	*H. margaritaceiventer*	*impiger*	Guyana	Cuyuni-Mazaruni	-61.04	5.98	2/19/07
USNM_639381	Smithsonian	*H. margaritaceiventer*	*impiger*	Guyana	Cuyuni-Mazaruni	-61.04	5.98	2/25/07

Table S2. Substitution models of each part of mitochondrial genes used to build the mitochondrial gene tree. The partition suggested by the Partition Finder method (Lanfear et al. 2012) was the one used in this work.

Protein Gene	Partition Finder	IQ-Tree	Model used in Beast
ND3	HKY+G+X	HKY+F+G4	HKY 4
ND4	HKY+G+X	HKY+F+G4	HKY 4
ND5	HKY+G+X	HKY+F+I	HKY 4
CYTB	HKY+G+X	HKY+F+G4	HKY 4 / GTR
ND1	HKY+G+X	HKY+F+I	HKY 4
ND2	HKY+G+X	HKY+F+G4	HKY 4
COX1	GTR+G+X	TIM2+F+I	GTR
COX2	GTR+G+X	TN+F+G4	GTR
ATP6	HKY+G+X	TPM2+F+G4	HKY 4
COX3	GTR+G+X	TIM2+F+G4	GTR

Table S3. AIC and AIC.w values for transition models used to reconstruct the ancestral habitat for the Hemitriccus clade. The ER transition model was the best-fitted model to our data.

Transition model	AIC	AIC.w
ER	*123.5415*	*0.99931376*
ARD	154.233	0.00000022
SYM	138.1093	0.00068602

Table S4. AIC and AICc. values for the BioGeoBEARS models used to reconstruct the ancestral area for the Hemitriccus clade. The DIVALIKEj model was the best-fitted model to our data.

BioGeoBEARS Model	LnL	d	e	j	AIC	AIC_wt	AICc	AICc_wt
DEC	-100.9	0.01	0.01	0	205.9	2.10E-07	206.2	2.40E-07
DEC+J	-87.1	0.0037	1.00E-12	0.067	180.2	0.079	180.8	0.079
DIVALIKE	-93.28	0.02	1.00E-12	0	190.6	0.0004	190.8	0.0005
DIVALIKE+J	-84.71	0.011	1.00E-12	0.037	175.4	0.87	176	0.87
BAYAREALIKE	-110.7	0.013	0.14	0	225.5	1.20E-11	225.8	1.40E-11
BAYAREALIKE+J	-87.54	0.0079	1.00E-07	0.047	181.1	0.051	181.7	0.051

Capítulo IV.

Lima, H. S.; Bravo, G. A.; Astúa, D.; Mariz, D.; Edwards, S.; Naka, L. N.
Origins and diversification of the Caatinga dry forest endemic birds
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Origins and diversification of the Caatinga dry forest endemic birds

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Abstract

Understanding the origins of biomes and their associated biota is key not only to comprehend the biogeographical histories and connections between them but also to predict the future of these environments and their associated biota in a future context of environmental change. The Caatinga dry forest, in Northeast Brazil, represents the largest and most biologically diverse patch of Seasonally Dry Tropical Forest in the Neotropics. Although the Caatinga was previously considered a species-poor domain with low levels of endemism, more recent studies have pointed out a rich avifauna and dozens of endemic taxa. Here, using published and time-calibrated phylogenies and ancestral habitat reconstruction analyses of 39 Caatinga avian endemic taxa we i) investigated the biogeographical origins and ii) the timing of diversification of the Caatinga endemic avifauna. Our results suggested a mixed origin of the Caatinga endemic avifauna, with cladogenesis events through the founder effect playing an important role in the colonization of the region. Although most avian endemics (22 taxa) are related to lineages from open habitats, including other dry forests or the savannas; a few species (9 taxa) likely colonized the Caatinga from adjacent humid forests. Whereas we detected relatively old lineages that likely occupied these dry landscapes before the Pleistocene, other endemics seem to represent new arrivals from adjacent habitats. This study represents the first effort to describe the biogeographical origins of the Caatinga avifauna, thus providing new data about the history of this endemic and threatened domain.

Keywords Caatinga, endemism, historical biogeography, semiarid environments

Introduction

The assemblage of current biotas is the result of several independent processes, which include speciation, extinction, and dispersal (Crisp et al. 2009). Whereas speciation and extinction are often considered as the main drivers of diversification, vicariance and dispersal can have long lasting effects on a region's biota (Smith et al. 2014). Therefore, understanding the origins of a biome's endemic taxa is key to recognize the factors involved in building and shaping current diversity patterns, offering insights into the role of these processes within and between biomes (Hausdorf & Hennig 2004, Byrne et al. 2008, Willis et al. 2014, Cai et al. 2020). In practical terms, investigating the mechanisms behind current biogeographic patterns is relevant to predicting how a given biota may behave under future environmental change (Byrne et al. 2008, Fine & Lohmann 2018). For example, a lineage well-adapted to hot and dry environments may fare relatively well under more extreme conditions, whereas poorly adapted species that manage to live in hot environments, may be close to their adaptive threshold and may not be able to survive under novel (and harsher) climatic conditions. Therefore, the fate of lineages may depend on their past history.

The assemblage of the Neotropical biota is the result of a series of complex evolutionary events following major geological, landscape, and climatic rearrangements, including the isolation of South America from other continents, the uplift of the Andes, the formation of the modern Amazon River basin, and the closure of the Panamanian isthmus (Kattan et al. 2016). This geological scenario established during the late Miocene (ca. X million years past) was likely influenced by floristic changes due to climatic fluctuations during the Plio-Pleistocene (ca. X million years past)(Fine & Lohmann 2018). Such modifications were likely responsible for extinctions and shifts in species distributions, probably resulting in the invasion of new ecosystems following historical range expansions (Sobral-Souza et al. 2015).

Recent studies have suggested that the Amazon, for example, was a key contributor to other Neotropical biomes, providing new plant and animal lineages via dispersal and ancient range expansions (Antonelli et al. 2018, Fine & Lohmann 2018). According to Antonelli et al. (2018) these contributions enriched the biota of other Neotropical biomes, not only of other humid tropical ecosystems, such as the Atlantic Forest, but also the biotas of open landscapes, such as the Cerrado and the Chaco. On the other hand, drier habitats, such as the Caatinga Dry Forest and the Patagonian steppes were considered less receptive to Amazonian lineages. These results are consistent with a phenomenon known as niche conservatism, which postulates that lineages track environmental conditions relatively similar to those found by their ancestors (Colwell & Rangel 2009, Peterson 2009), hindering invasions and exchanges between biomes. Data from woody plants seem to support the idea that intra-biome dispersal is quite rare worldwide due to the difficulties found by lineages to adapt to novel environments (Crisp et al. 2009). Therefore, the evolutionary influence of mesic environments on xeric biomes is highly contentious, remaining unclear whether the biotas of drier environments, such as the Seasonally Dry Tropical Forests (SDTFs), are the result of *in situ* adaptation and speciation, or whether they were enriched by the contribution of more humid environments (Byrne et al. 2008, Werneck 2011).

Seasonally Dry Tropical Forests, which are patchily distributed throughout the Neotropics, represent an evolutionary playground to test such hypotheses. The Caatinga dry forest, located in the semi-arid interior of northeastern Brazil and considered the largest and most biologically diverse patch of SDTF in the Neotropics (Pennington et al. 2000), represents an enlightening and unique case, as it is bounded by the two largest tracts of humid forest in South America (the Amazon and the Atlantic Forests), and the Cerrado savannas of central Brazil (Werneck 2011, Queiroz et al. 2017). Despite the importance of the Caatinga as the largest nucleus of Neotropical dry forest, we know very little about its endemic biota, and this includes conflicting biogeographical scenarios proposed to explain the origin and history of this domain (Oliveira et al. 1999, Pennington et al. 2000, Auler et al. 2004, Carmignotto et al. 2012, Thomé et al. 2016).

Early analyses suggested that the mammal fauna of the Caatinga, for example, originated from poorly adapted species from adjacent humid forests (Mares et al. 1985). More recent studies, however, consider that the extant mammal fauna of both the Cerrado and the Caatinga is made up of species strongly associated with open areas, most of which representing lineages that diversified in open formations (Carmignotto & Astúa 2022). However, the influence of humid forests on the complex history of mammal species diversity has not been completely ruled out (Carmignotto et al. 2012, Carmignotto & Astúa 2017). Paleopalynological data were interpreted as indicating the existence of a humid corridor through the Caatinga connecting the Amazon and the Atlantic Forests during the Late Pleistocene (Oliveira et al. 1999, Auler et al. 2004, Thomé et al. 2016). How such a corridor affected the biota of the Caatinga remains to be investigated, but it has been related to the genetic structuring in Caatinga frogs (Thomé et al. 2016), suggesting a main effect of the humid forests on speciation patterns in the Caatinga. Similarly, phytogeographical data seem to agree that the distribution of plant species was largely influenced by Pleistocene climatic fluctuations, including the Last Glacial Maximum (LGM) (Oliveira et al. 1999). These fluctuations have been pointed out as being responsible for the subsequent expansions and contractions of the dry forests, leading to current plant distribution patterns in the Caatinga (Prado & Gibbs 1993, Pennington et al. 2000, Auler et al. 2004, Medeiros et al. 2018). The biogeographical history of other groups such as birds, on the other hand, remains to be evaluated.

At least three putative origins have been suggested for the Caatinga avifauna, including: i) taxa originated in adjacent ecosystems (Amazon Forest, Atlantic Forest and Cerrado) which colonized the Caatinga during recent climatic fluctuations; ii) taxa originated in other Neotropical dry forests; and iii) taxa originated in situ, representing old ancestral lineages (Araújo & Silva 2017). To evaluate these hypotheses, we turned our attention to the Caatinga endemic avifauna. Studies on the Caatinga avifauna are relatively recent and somewhat controversial. For example, it is yet unclear how many species of birds occur in the Caatinga, ranging from 348 species (Pacheco 2004) to 548 (Araújo & Silva 2017), depending on whether species inhabiting humid enclaves at higher elevations are included in the species pool (Lima 2021, Araújo et al. 2022). The Caatinga was traditionally considered a domain with low levels of endemism (Mares et al. 1985), and the precise number of endemic species remains open to debate. Early studies indicated that between two and 13 species of birds were endemic to the Caatinga (Pacheco 2004, Marini & Garcia 2005, Lima 2021). However, preliminary data derived from evaluation of geographic species records suggest that these figures are grossly underestimated, and that at least 50 avian taxa (35 species and 15 subspecies), are either endemic or near endemic to the Caatinga (Mariz et al. 2015).

The increasing availability of information about the evolutionary history and genealogical relationships of avian lineages has allowed us to understand the evolutionary processes of speciation, diversification, and adaptation among species (Cavender-Bares et al. 2009). This new type of information has been used in recently developed methods based on models of geographic range evolution focused on understanding the processes leading to patterns of biogeographical history of species (Matzke 2013). Merging evolutionary history with information on geographic distribution of species is providing basic data needed to understand the biogeographic history of the species, and consecutively the history of connectivity of areas and their biotas (Leprieur et al. 2012, Batalha-Filho et al. 2013, Weeks et al. 2016).

Here, we use the endemic avifauna of the Caatinga to infer the biogeographic origins and time of divergence of these taxa, in relation to its closest relatives, investigating the relationship with taxa from other Neotropical vegetation domains. Specifically, we used molecular phylogenies including 39 avian Caatinga endemic lineages to conduct ancestral habitat reconstructions, estimate ancestral habitat parameters, and evaluate whether current endemic avian taxa derived from xeric lineages, represent dispersals events from mesic environments and to understand the mechanisms behind the Caatinga avian endemism. We used time-calibrated phylogenies to estimate the time of arrival in the Caatinga of these taxa and to shed light into the mode, time of evolution and conservation of the endemic avifauna of the Caatinga dry forest.

Methods

Caatinga avian endemic taxa

To determinate the Caatinga endemic taxa, we used published data and occurrence points obtained through specimens, vocalization records and photographs georeferenced. 56 endemic taxa (35 species and 21 subspecies) belonging to seven Orders and 22 Families were listed. According to the most recent list of threatened species in Brazil, six of these taxa are in danger of extinction, five of these taxa are Vulnerable and two are Critically Endangered (one of them, *Cyanopsitta spixii*, probably or extinct in the wild).

Phylogenies sampling

We collated the literature for the most updated and taxon-rich phylogenetic hypotheses published, based on molecular information. Up to the time of data compilation for this study, we retrieved phylogenies for 15 of 19 families, encompassing 39 endemic taxa (28 species and 11 subspecies) (Figure S1, Table S1). When necessary, to extract the clades of interest from larger phylogenetic trees, phylogenies were edited using Mesquite 3.61 (Maddison and Maddison 2019), and the *ape* package (Paradis *et al.* 2019). All the phylogenetic hypotheses used were constructed based on mitochondrial and/or nuclear genes. Except two of all the phylogenetic inference utilized were not time-calibrated (Table S1) and in this way, were not considered in the time related analyses.

Biogeographic areas and species distribution

To estimate the biogeographic history of the Caatinga endemic avifauna, we designated nine major biogeographic areas in the Neotropical region. Biogeographic areas were adapted from Olson et al. (2001) and included: Amazon Forest (Am), Andean Montane Forest (Af), Atlantic Forest (At), Caatinga (Ca), Cerrado (Ce), Dry Forests (Dr), Mesoamerica Moist Forests (Me), Pampas, Llanos & Wetlands (Pa) and Steppes, Scrubs & Deserts (St) (Figure 1, Table 1). To test the mesic or xeric origin of the Caatinga endemic avifauna we also grouped these nine biogeographic areas either as 'forested areas', which included humid forests (Am, Af, At, Me), or 'Open/Dry Forest areas', which included areas of open habitats (Ce, Pa, St) and Dry forests (Ca, Dr) (Figure 1, Table 1).

Figure 1. The Neotropical realm, based on nine biogeographic areas used to estimate ancestral habitat reconstruction of the Caatinga endemic avifauna. Biogeographic areas were adapted from Olson et al. (2001) and include: Amazon Forest (Am), Andean Montane Forest (Af), Atlantic Forest (At), Caatinga (Ca), Cerrado (Ce), Dry Forest (Dr), Mesoamerica Moist Forests (Me), Pampas, Llanos & Wetlands (Pa), and Steppes, scrubs & deserts (St).

All taxa present in the phylogenies were assigned to one or more biogeographic areas. Categorization was based on shapefiles of species' present-day distributions obtained from Birdlife International (2021), accounting the amount of overlap between them and the vectors corresponding to the biogeographic areas (we used a 20% of overlap between shapes to assigned one taxon to a biogeographic area) (Figure 1). These were accomplished using the functions *gIntersects* and *st_intersection* of packages *rgeos* (Bivand et at 2017) and *sf* (Pebesma 2018) for R (R Core Team

2021), respectively. We also verified the preferences of species' habitats and their geographic distributions in order to refine the boundaries of biogeographic areas and to determine which areas extant species occupy. We set the maximum possible number of ancestral areas of occurrence of each species in the models to nine, so each taxon could occur simultaneously in all pre-defined areas, thus, we could attribute a maximum number of possible areas where the Caatinga endemic lineages may have originated.

Table 1. Description of the biogeographic areas used in the study. Biogeographic areas are ecoregions or combinations of ecoregions based on Olson et al. (2001).

Biogeographic areas	Description
Open/Dry forests areas	
Ca	Caatinga dry forest, in Northeastern Brazil
Ce	Cerrado savannas, in Central Brazil
Dr	Dry forests from the Neotropical region, include Chiquitano Forest and Dry Chaco
St	Steppes, scrubs & deserts, include the Atacama Desert, Grasslands, Matorral shrubland, Paramo, Patagonia Steppes, Puna grasslands, Steppes, and Tundra
Pa	Pampas, Llanos & wetlands, include Beni Savanna, Espinal, Humid Chaco, Humid Pampas, Llanos, Mangroves, Panama flooded savannas, Pantanal, and Uruguayan savanna
Forested areas	
Am	Amazon Forest
At	Atlantic Forest
Af	Andean Montane Forest, include Andean humid montane forests, Magellanic subpolar forests, Valdivian Temperate Forests, and Yungas
Me	Mesoamerica Moist Forests, include humid forests of Mesoamerica such as Broadleaf Forests, and Pine Forests

Habitat reconstruction and biogeographic analyses

To reconstruct and infer the origins of the Caatinga endemic avifauna, we tested the fit of the data to six different models using the package BioGeoBEARS (Matzke 2013). These models included i) the Dispersal-Extinction Cladogenesis Model (DEC); ii) Dispersal-Extinction Cladogenesis Model with the founder parameter (DEC+J); iii) Dispersal-Vicariance Analysis (DIVA); iv) Dispersal-Vicariance Analysis with the founder parameter (DIVA+J); v) Bayesian inference of historical biogeography for discrete areas (BAYAREALIKE), and vi) Bayesian inference method with the founder parameter (BAYAREALIKE+J). Each model allows for a framework for comparing alternative biogeographic events that may occur at cladogenesis, including i) dispersal, where the ancestral range is copied by the new species; ii) sympatry, where a new species evolve in a subset of the ancestral range; iii) vicariance; iv) founder event, where a new species occupies a new area outside of its ancestral range; and v) extinction (Matzke 2013, Alfaro et al. 2015, Rojas et al. 2016).

These biogeographic processes are implemented in a maximum likelihood (DEC, DEC+J, DIVA, DIVA+J) or Bayesian (BAYAREALIKE, BAYAREALIKE+J) framework as free parameters estimated from the data (Alfaro et al. 2015). Reconstructions used a distance-dependent model so that dispersal probability was dependent on the distance between the centers of the 'locations' (Alfaro et al. 2015). We compared these six biogeographic models for statistical fit using the Akaike Information Criterion (AIC) and AICc (Akaike Information Criterion corrected for small-samples size), also implemented in the BioGeoBEARS package. The best models, those with lower AIC values, where used to interpret how well the different models fit the geographic distributions in the phylogenies. This allowed us to evaluate the possible geographic origins of the Caatinga endemic avifauna and to estimate the relative role of dispersal and vicariance events on these taxa.

After obtaining the most fitted biogeographic models suggested by BioGeoBEARS analyses, we computed the number of taxa that occupied the Caatinga from different origins and then constructed an interaction network between the biogeographic areas who acted as source areas for Caatinga endemic birds, using Gephi software (Bastian et al. 2009). For better visualization of the interaction network, and to understand the scenarios which led the occupation of the Caatinga, we used the classification of our biogeographical regions as described before (Forested areas, Open/Dry forest areas), and adding a 'Mixed area', 'Mixed Open/Dry forests area' and 'Mixed forested area' classification when the taxa were originated in a mix of i) forested and Open/Dry forests ecoregions, ii) Open/Dry forests ecoregions, and iii) forested ecoregions, respectively.

This classification was also used during the construction of a consensus tree, created for a better and broader visualization of the BioGeoBEARS results. The consensus tree was created using the 39 taxa analyzed on BioGeoBEARS and based on the phylogenies compiled from the BirdTree.org website. Nonetheless, we recovered the topology and relationships between species from the published phylogenetic hypotheses used in the analyses. As this tree was created only thought of as a better way to visualize the results, it does not reflect the actual branch lengths, or the time of diversification proposed for each taxon on the published manuscripts.

We also explored the BioGeoBEARS most fitted model united to the time-calibrated phylogenetic hypotheses to estimate the time of origin of these taxa and to shed light into the mode, tempo of evolution and conservation status of the endemic avifauna of the Caatinga dry forest. We compare, using ANOVA analysis, i) the time of occupation of the Caatinga between the different biogeographic areas and ii) whether the current threat status of endemic taxa, obtained from the IUCN red list (IUCN 2022), reflects some older history of occupation of the Caatinga. All analyses were performed in R 4.0.1 (R Core Team 2021).

Results

Our final dataset included 28 phylogenetic trees covering 15 families, 39 Caatinga endemic bird taxa, including 28 species and 11 subspecies (Table S1). The total number of taxa involved included 682, whose biogeographic history was recovered by the models tested. Dispersal-Extinction Cladogenesis Model with the founder parameter (DEC+J) was the best-fitted model for ~36% (10 trees) and BAYAREALIKE+J was the model with the best fit for ~32% (9) of the phylogenetic trees analyzed. Other models were the most adjusted in other phylogenies, including DIVALIKE+J (5 trees), DIVALIKE (3 trees), BAYAREALIKE (2 trees), and DEC (1 tree) (Table S2, Figure S3).

Except for Mesoamerican Moist Forests, all biogeographic regions were inferred as sources for at least one Caatinga endemic taxon (Figure 2, Figure S2-S3). More than half (22 taxa, 56% of the sample) of the Caatinga endemics were inferred to have originated primarily from Open/Dry domains, including *in situ* origins for eight taxa (20% of the sample), and taxa from the Cerrado (Ce) and Pampas, Llanos & Wetlands (Pa), each representing a source for one taxa. The remaining 12 taxa likely originated from mixed joint areas of Open/Dry domains. On the other hand, Neotropical forested areas were a source for 9 (~23%) endemic taxa, including 5 taxa form the Atlantic Forest (At), two taxa from the Amazon (Am), and one taxon from Andean Montane Forests (An). A set of different forested areas of the Neotropical region originated another endemic taxon. Areas with mixed, forested, and Open/Dry areas were a source for ~20% (8) of the Caatinga endemic lineages (Figure 2, Figure S2-S3).

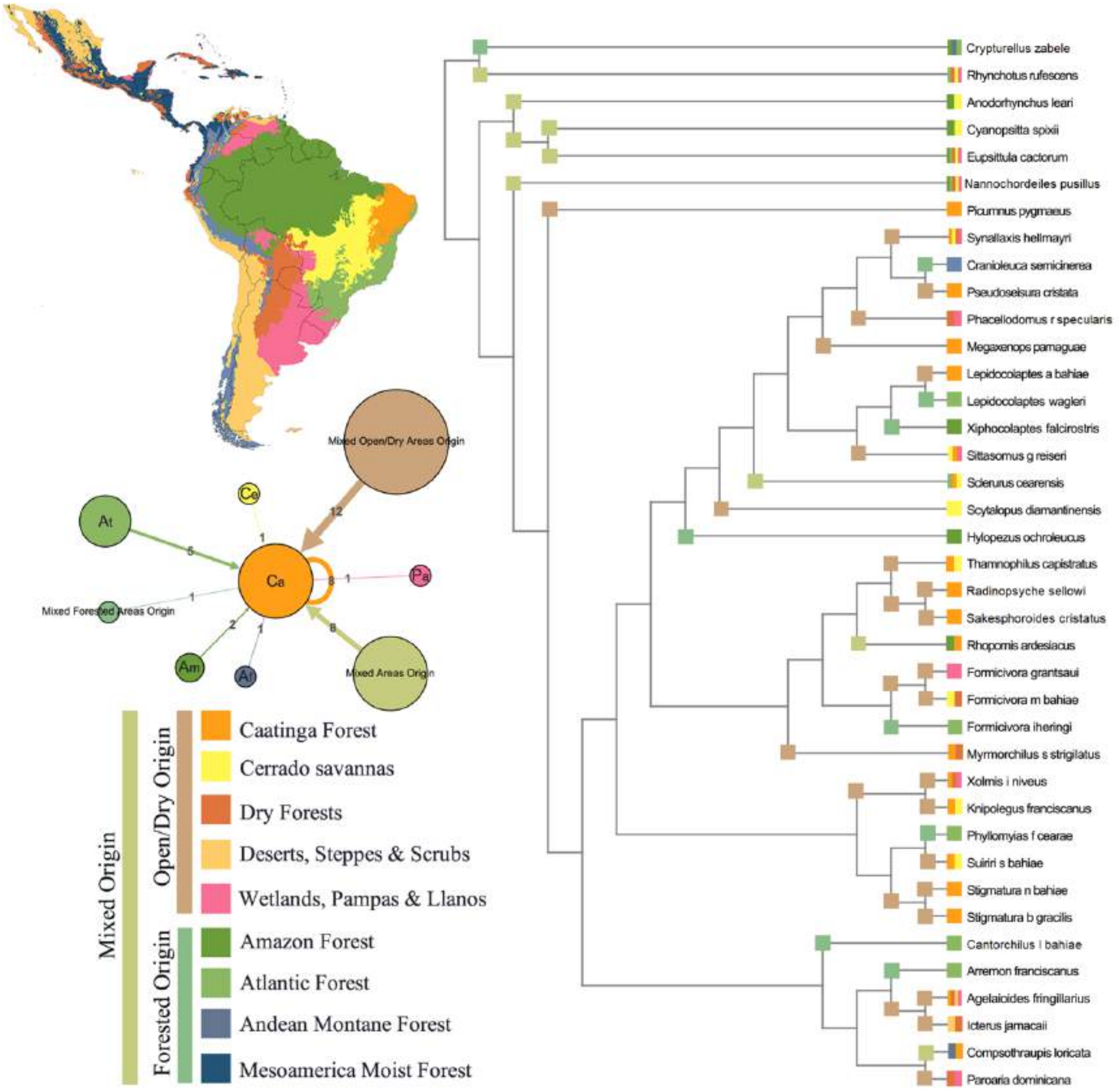

Figure 2. Ancestral range reconstruction of the Caatinga endemic birds and interaction network between areas. The tree topology shown was recovered from the phylogenies used in the analyses, the topology does not reflect the actual branch lengths or the time of diversification. Colors at the tree tips represent the current range of the lineages, and the color on the three nodes represents the most likely ancestral ranges estimated under the most fitted BioGeoBEARS model for each phylogeny.

Results of the BioGeoBEARS analyses suggest that the occupation and establishment of the avian endemic taxa evaluated in the Caatinga started during the Miocene at *ca*. 17 Ma, when representatives of the families Tinamidae, Psittacidae, Thamnophilidae, Grallaridae and Furnaridae restricted their range to the Caatinga from open/ dry (*Myrmorchilus strigilatus*, *Sakesphoroides cristatus*, *Radinopsyche sellowi*, and *Megaxenops parnaguae*), forested (*Crypturellus zabele*, *Formicivora iheringi, and Hylopezus ochroleucus*), and mixed forest/open areas (*Rhynchotus rufescens*, *Anodorhynchus leari, Eupsittula cactorum*, *Cyanopsitta spixii*, and *Rhopornis* *ardesiacus*) of South America (Figure 3, Table S1). Additionally, From the Miocene onwards (~11–6.5 Ma) lineages began to diversify within the Caatinga, giving rise to ancient endemic lineages of this biome such as *Sakesphoroides cristatus*, *Radinopsyche sellowi,* and *Megaxenops parnaguae*.

During the Pliocene, between 5.12 and 2.81 Ma, seven taxa representative of Thamnophilidae, Dendrocolaptidae, Furnariidae, Tyrannidae and Thraupidae established in the Caatinga (*Formicivora grantsaui*, *Thamnophilus capistratus*, *Lepidocolaptes wagleri*, *Synallaxis hellmayri*, and *Compsothraupis loricata)*, including two taxa *Stigmatura napensis bahiae* and *Stigmatura budytoides gracilis* which diversified within the Caatinga according with our results (Table S1). The Amazon Forest (Am) did not appear as a source area for Caatinga species during the Pliocene (Figure 3, Table S1).

We found a general increase in the number of biogeographic ranges restricted to the Caatinga region from the Pleistocene and towards the present, between 2.56 and 0.65 Ma. A total of 18 taxa, including members of the Picidae, Rhinocryptidae, Scleruridae, Passerellidae and Icteridae, established themselves into the Caatinga during this period (*Picumnus pygmaeus*, *Formicivora melanogaster*, *Scytalopus diamantinensis*, *Sclerurus cearensis*, *Sittasomus griseicapillus reiseri*, *Xiphocolaptes falcirostris*, *Lepidocolaptes angustirostris bahiae*, *Phacelllodomus rufifrons specularis*, *Cranioleuca semicinerea*, *Pseudoseisura cristata*, *Suiriri suiriri bahiae*, *Phyllomyias fasciatus cearae*, *Knipolegus franciscanus*, *Xolmis irupero niveus*, *Arremon franciscanus*, *Icterus jamacaii*, *Agelaioides fringilarius*, *Paroaria dominicana*) (Table S1). During the Pleistocene, the Amazon Forest (Am) reappeared as a source of species, and the Steppes, scrubs & deserts (St) appeared as a new source of species (Figure 3, Table S1). Diversification within the Caatinga continued to occur along the Pleistocene, with *Picumnus pygmaeus* appearing as the most recent lineage to diversify within the Caatinga (Figure 3, Table S1).

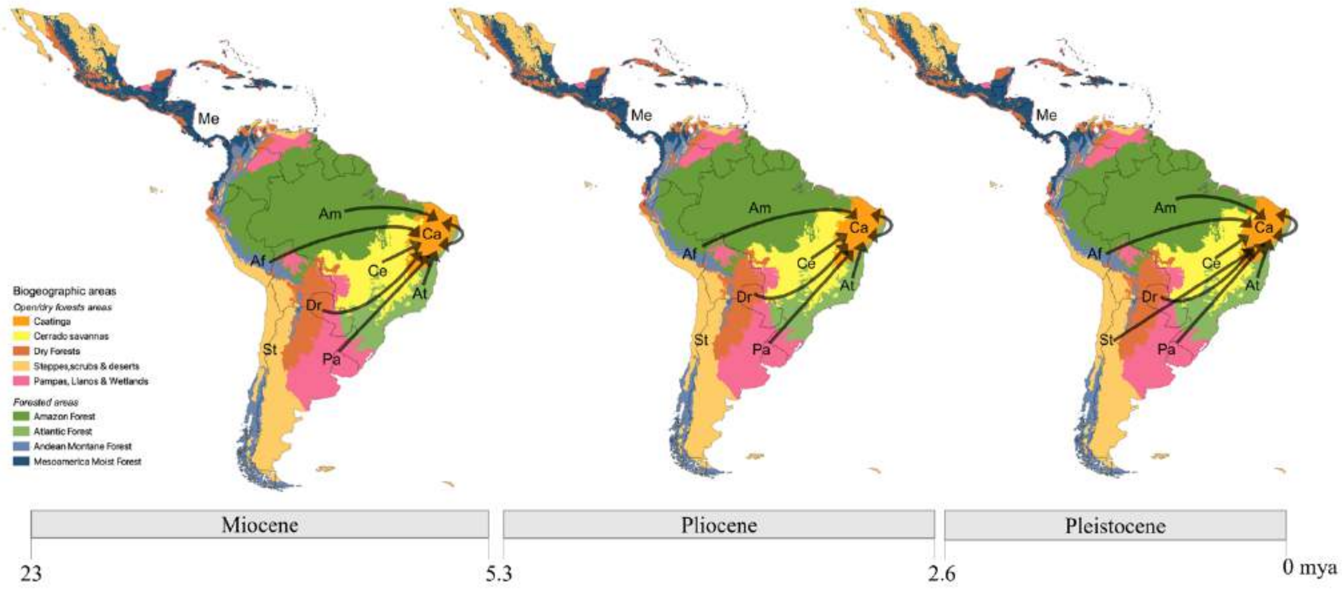

Figure 3. Hypotheses of Caatinga dry forest avian occupation from source areas over time, accordingly the results of the most fitted models on our BioGeoBEARS analyses. Solid lines represent the source area of Caatinga endemic birds. The estimated time of arrival in the Caatinga was obtained from each phylogenetic hypotheses used in the analyses.

Dispersal events towards the Caatinga occurred at different time periods, depending on the source. For instance, taxa from humid forests represent the oldest sources (4.65 Ma, ± 4.61), when compared to Open/Dry forests (3.38 Ma, ±3.03) (Figure 4a) of the Neotropical region (ANOVA, F = 2.94, p = 0.06) (Figure 4a). Regarding the Open/Dry environments of the Neotropical region, the Caatinga presented itself as the oldest source for the endemic lineages (4.91 Ma ± 4.22) when compared to other dry forests (2.51 Ma, ± 1.73) of the Neotropical region (Figure 4b).

Our results also pointed out a relationship between the degree of threat of the endemic taxa and the time of arrival in the Caatinga. Those taxa with some degree of threat were the oldest to occupy the Caatinga (3.49 Ma, ± 1.31) when compared to non-endangered taxa (3.37 Ma, ± 3.17) (ANOVA, F=7.92, p<0.05) (Figure 4c). According to our results, of the 10 threatened taxa in our analyses, 50% (5) came from humid forests in the Neotropics (*Crypturellus zabele*, *Formicivora iheringi*, *Hylopezus ochroleucus*, *Xiphocolaptes falcirostris*, *Arremon franciscanus*), 30% came from mixed origin (*Cyanopsitta spixii*, *Anodorhynchus leari*, *Rhopornis ardesiacus*) and only two taxa (20%) came from Neotropical Dry Forests (*Formicivora grantsaui*, *Scytalopus diamantinensis*).

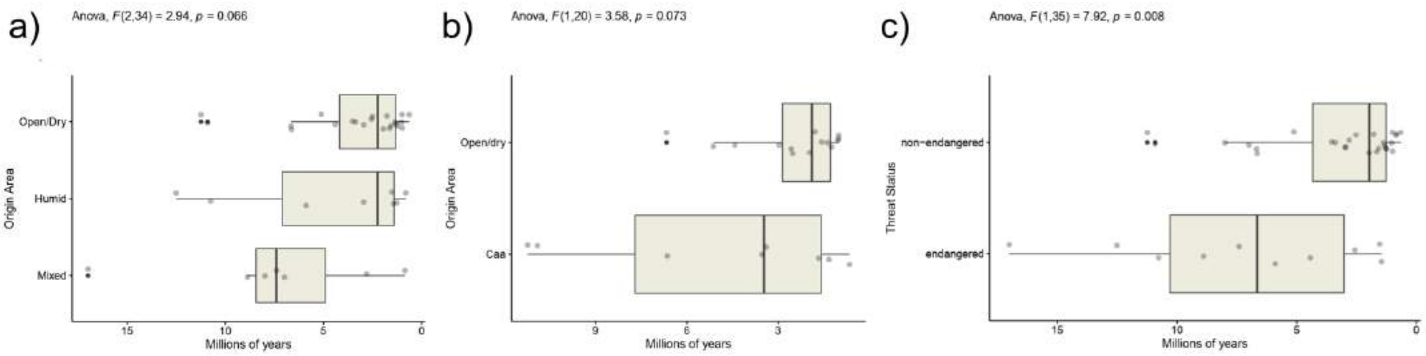

Figure 4. Comparisons of the different arrival times in the Caatinga for species that (a) originated in different biogeographical areas, (b) originated in dry forests and (c) species in some degree of conservation threat today. The boxplot shows the mean (boxes central lines) and standard deviation of the data (box limit lines), grey dots represent each of the 39 endemic taxa analyzed.

Discussion

Our results fill an important gap in the discussion about the biogeographic history of the Caatinga, suggesting that more than half of its endemic avifauna likely originated from Open/Dry domains, and about a fifth represent in-situ diversification events (*i.*e., ancient lineages that diversified within the Caatinga). Nevertheless, our results also recover the importance of adjacent humid forests, which were likely responsible for nearly a fourth of the Caatinga avian endemics. These include the Atlantic Forest, the Amazon and Andean Montane Forests. Perhaps one of our most striking findings was that every biogeographic region analyzed was likely responsible for adding specific lineages to the Caatinga avifauna, calling attention to the importance of biotic interchanges throughout the evolutionary history of South America. The time of diversification of the Caatinga endemics also seems relevant, as the establishment of extant lineages in that domain initiated as early as the Miocene around 17 Ma and continued as recently as the Pleistocene.

Biogeographic history of the Caatinga endemic avifauna

Our results pointed out that the occupation of the Caatinga started in the late Miocene, about 17 million years ago. During this period, intense environmental changes in the northern portion of the Andes and the Amazon Basin were occurring. This period is marked by the decrease in global temperature, fragmentation of tropical biomes, expansion of dry habitats, deserts, and grasslands, which is also coincident with a major peak in bird diversification around the globe (Claramunt &

Cracraft 2015, Castro et al. 2021, Buainain et al. 2022). The dynamic nature of forest expansion and contraction at different times in the past has contributed to complex patterns of interchange of humid-adapted versus dry-adapted taxa earlier in time (Willis et al. 2014, Fine & Lohmann 2018). These dynamics may have caused strong selective pressures for wet-adapted lineages to develop key characteristics associated with survival in dry microhabitats within humid regions, such as greater drought tolerance, which may have allowed their dispersal into drier environments (Willis et al. 2014, Fine & Lohmann 2018).

From the Miocene onwards, there was an increased exchange of animal and plant taxa between the Amazon Forest and other areas (Antonelli et al. 2018). Phylogeographical patterns of South American birds point to a connection between southern Atlantic Forest and western Amazonia since the Miocene through the ecotone Cerrado/Chaco. Changes in the Amazonian landscape in response to the Andes uplift could have favored these ancient links. This may have contributed not only to the Cerrado diversity, as discussed previously (Batalha-Filho et al. 2013, Sobral-Souza et al. 2015), but also contributed to avian dispersal into the Caatinga coming from forest and humid environments such as the Amazon, Atlantic Forest, and Andean Montane Forest. This could be observed in our results, where not only a portion of our taxa occupied the Caatinga coming from humid forests (12 taxa occupied the Caatinga, during this period), but also, the Amazon played an important role as a source of taxa for the Caatinga during the Miocene (Figure 2, Table S1, Figure S3).

The Miocene was followed by a period of climatic oscillation between glacial and interglacial cycles, during the Pliocene and Pleistocene, that likely provoked extensive shifts in habitat configuration (Prado & Gibbs 1993, Corbett et al. 2020, Buainain et al. 2022). Data from sediment and ice cores show that the Pliocene was a relatively warm period, with warmer mean temperatures. During this period seven taxa occupied the Caatinga, coming mainly from open and dry vegetation domains, among them two taxa that likely originated in the Caatinga. Whereas the earlier Pleistocene was a period of decreasing global temperatures with a 41,000-year glacial cycle, the Middle and Late Pleistocene were characterized by lower average temperatures and more pronounced glacial periods, including the Last Glacial Maximum (Clark et al. 2006).

The climatic fluctuations during the Pleistocene likely produced cycles of range contractions and expansions that resulted in fragmentation and isolation of populations, with subsequent speciation and radiation events (Kattan et al. 2004). Previously disjunct dry forest patches are most likely to have been connected during the coldest and driest periods of the Middle and Late Pleistocene. In species inhabiting mountain landscapes, such as the Andes, the Pleistocene climate changes caused repetitive range expansions and contractions of species distribution, allowing down-slope migration through lowland elevation barriers (Hazzi et al. 2018), and which may have colonized at that time fragments of dry forests. This period could have facilitated the expansion of widespread dry forest species across the continent (Corbett et al. 2020).

Based on plant distributions, some studies argued that the Caatinga could have been connected to dry forests in Bolivia and Argentina, or to dry forests on the Caribbean coast of northern South America (Magalhães et al. 2021). These connections would have taken place through the expansion of dry forests over areas now covered by mesic biomes (Magalhães et al. 2021). It was also during the Pleistocene that the South American dry diagonal was finally shaped, comprising the Caatinga, Cerrado, and Chaco biomes (Sobral-Souza et al. 2015). Consequently, this new open environment corridor may also have favored the dispersion of species to the Caatinga, mainly in groups with good dispersal ability, such as birds.

Ancient connections between the Caatinga and Northern South America dry forests imply a northern route passing through present-day Amazon; alternatively, the Caatinga could have been connected with southern formations, such as the Monte or the Chiquitano dry forests, passing through present-day Cerrado. It may be plausible that currently disjunct Neotropical dry areas might have gone through many periods of connections over the last 30 million years, and that groups with different dispersing capabilities could have responded idiosyncratically to such connections (Magalhães et al. 2021). We show that during the Pleistocene, 13 of the 18 species that occupied the Caatinga in this period came from other dry forests and/or open environments in South America, possibly indicating that the expansion of these dry forests and the presence of these ancient corridors interconnecting the dry forests patches may have favored the occupation of the Caatinga from other open environments during this period. These ancient connections may have allowed the arrival in the Caatinga, of species such as *Icterus jamacaii,* whose ancestors are mainly inhabitants of dry forests in Central America, and *Formicivora melanogaster bahiae*, whose ancestors reflect on a history of occupation of the dry forests of the Chaco and of the open formations of Cerrado savannas, according to our results (Figure S2).

Palynological data of central Caatinga from the Late Pleistocene revealed taxa currently found in the Amazon and Atlantic Forests, indicating the presence of forest vegetation in the Caatinga during the last glacial cycle, and a possible young corridor along the northern coast and through the current Central Caatinga linking the Amazon Forest and Atlantic Forest rainforests (Sobral-Souza et al. 2015, Thomé et al. 2016). These data may elucidate the importance of these connections across the Caatinga as corridors for dispersal events for species that occupied ancestrally humid and forested environments. They may also explain the Amazon Forest serving as a source of species to the Caatinga during the Pleistocene.

Long-distance dispersal is usually considered to have a minor role in structuring intracontinental species assemblages, and biotic dispersion is also considered historically constrained (Melo Santos et al. 2007). Yet, species within a bioregion do not necessarily share the same history of speciation because there are different events of isolation and diversification occurring several times and generating different evolutionary trajectories (Hazzi et al. 2018). As such, we believe that dispersal events played an extremely important role in the occupation of the Caatinga, and these events were influenced by major climatic and geological events that formed ancient corridors, allowing the connection of the Caatinga with other dry forests in South America and with other humid forests.

Origins of the Caatinga endemic avifauna

Understanding the time and mode of species assemblage offers important insights into the history of a biome and its associated biota. Like other Dry Tropical Forests, the Caatinga represents a highly seasonal environment, which likely acted as a strong filter to the species that were able to establish viable populations over time. The low annual precipitation, the occurrence of long draughts, and the unpredictability of the rainy periods (Ab'Saber 1974, Murphy & Lugo 1986) have selected a highly specialized plant community, which responds to water stress by physiological and anatomical adaptations such as small leaves, presence of thorns, water storage and other xerophytic characteristics (Prado & Gibbs 1993, Prado 2003), allowing them to withstand long periods without rain (Pennington et al. 2009). These specializations and the high level of plant endemism suggest a long story of adaptation and isolation (Mares et al. 1985). Discussions on the origins of the animal assemblage in the Caatinga, on the other hand, remain controversial. Previous analyses suggested that the mammal fauna of the Caatinga was mostly the result of recent invasions from mesic environments, such as the Amazon and Atlantic Forests, including a fauna generally devoid of evident adaptations to draught (Mares et al. 1985). A similar view was adopted for the Caatinga avifauna, suggesting that biotic interchange with adjacent humid forests were likely a more important biogeographic process than intra and inter-regional diversification within the Caatinga (Silva et al. 2003). More recent studies, however, questioned these viewpoints, suggesting that not only the animal fauna of the Caatinga, but also its flora, likely originated from both mesic and xeric environments, including older evolutionary lineages with a long history of adaptation to open and dry habitats (Carmignotto et al. 2012, Arango et al. 2021).

Among our results, the diversification models with stronger support were models of dispersal founder-events, which relate to the colonization of the Caatinga from other biogeographic regions (DEC+J and BAYAREALIKE+J), suggesting that important biotic interchanges occurred. Eight of the nine biogeographic areas considered acted as source areas for endemic avian taxa of the Caatinga. The Mesoamerica Moist Forests were the only area that did not directly contribute to the occupation of the Caatinga by avian taxa, although it was an area of early origin to related taxa. More than half of the Caatinga endemic lineages originated from other Open/Dry Forests of the Neotropics. This contrasts with previous results that highlight the importance of the Amazon Forest as a source of plant and animal taxa for other regions of South America (Antonelli et al. 2018). In our study, Neotropical Forested areas were recovered as the source for ~23% of the Caatinga endemic avifauna, whereas the Amazon contributed with less than 6%. These results are similar to those found marsupial' species that inhabits the Dry Diagonal on South America, which is considered to have ancestors that inhabited regions of the Atlantic Forest, Amazon Forest, Andes, as well as other areas of open formations (Carmignotto & Astúa 2022).

One fifth of the endemic lineages represent in-situ diversification events, likely indicating a long history of adaptation to the Caatinga dry forest. These include *Picumnus pygmaeus*, *Sakesphoroides cristatus*, *Radinopsyche sellowi*, *Lepidocolaptes angustirostris bahiae*, *Megaxenops parnaguae*, *Pseudoseisura cristata*, *Stigmatura napensis bahiae* and *Stigmatura budytoides gracilis*. Except for *Lepidocolaptes angustirostris bahiae*, these species were previously considered as species who originated in the Caatinga (see Araújo & Silva 2017). Birds have been considered conservative in maintaining similar habitats during diversification, indicating that major habitat shifts are not common during speciation events (Araújo & Silva 2017, Buainain et al. 2022). Such a view agrees with our results that point that Open/Dry areas were the main source for the endemic taxa of the Caatinga.

Conservation implications

For species that arrived in the Caatinga through biotic interchange events, it has expected them to be more numerous, along the boundaries between regions, and to have narrow and continuous ranges following the corridors that allowed them to expand, or to have isolated and patchy ranges, depending on the ecological conditions that enabled these species to expand into the Caatinga, conditions which currently no longer exist (Araújo & Silva 2017). In our results, we found not only a relationship between the time of occupation in the Caatinga with the threat status of the taxon but also with the area of origin, indicating that most of the threatened endemic taxa present in this study were the oldest to occupy the Caatinga, and mainly originated from humid forest environments. The threatened endemic species included in this study are primarily species of restricted distribution in the Caatinga, such as *Cyanopsitta spixii*, *Anodorhynchus leari*, *Rhopornis ardesiacus*, *Formicivora iheringi*, *Formicivora grantsaui*, *Scytalopus diamantinensis* and *Arremon franciscanus*, or are species dependent on specific environments, as *Crypturellus zabele*, *Xiphocolaptes falcirostris,* and *Hylopezus ochroleucus*, associated with more arboreal and conserved Caatinga environments (Figure S1) (Billerman et al. 2021, Lima et al. 2021). It is likely that the restricted distribution of these taxa within the Caatinga and, consequently, the degree of threat associated with them may be related to their biogeographic origin, as they may have suffered a distribution reduction as the environmental conditions that led them to occupy the Caatinga ceased to exist.

Approach and data limitation

In this study, we used phylogenetic trees collected from previously published studies. Although it would have been more desirable to perform the analyses with a single tree, constructed from a single method (single molecular marker), than with single phylogenies produced by multiple authors, we believe that our results present a strong biogeographic signal that overcomes the uncertainties of using multiple phylogenies. We believe that, considering the difference between the analyzed clades, we are taking into account the heterogeneity between the species and thus obtaining more realistic biogeographic signals. Although in this work we present a good sample of taxa related to endemic birds of the Caatinga, we believe that future studies should consider and obtain a larger sample of taxa, thus allowing an even more comprehensive biogeographic analysis.

We understand that extinction processes may have occurred during the colonization history of the Caatinga. If we consider that the Caatinga is an extremely inhospitable environment and that extinctions are expected to be very common, and that direct ancestors may have been lost in the trees we analyzed, this could impact the estimates for diversification times and times of occupation that we found, leaving a long-distance scattering signal. Although the question of the role of extinction is speculative, we believe it is worth mentioning the possible effect that events like this could have on the presented data. However, we believe that the congruence that we observed between the patterns of biotic exchanges among the analyzed clades indicates that possible extinction processes do not have a great influence on the general results presented here. Considering this, we believe that the results produced by this work are not affected by the data and methodology applied here.

Conclusions

Our analyses provided a new scenario for the evolution and biogeographic diversification of the Caatinga Forest. The spatio-temporal pattern recovered here for the Caatinga endemic taxa points to an evolutionary history of the Caatinga domain influenced not only by strict vicariance events but also by dispersal episodes that played an important role in the origin of its avifauna. These events were influenced by major climatic and geological events that formed ancient corridors, allowing the connection of the Caatinga with other dry forests in South America and with other humid forests. It is clear to us the major influence of other open and dry domains as the main sources for the Caatinga avifauna, not forgetting the role that humid forests played on the contribution of species to the Caatinga.

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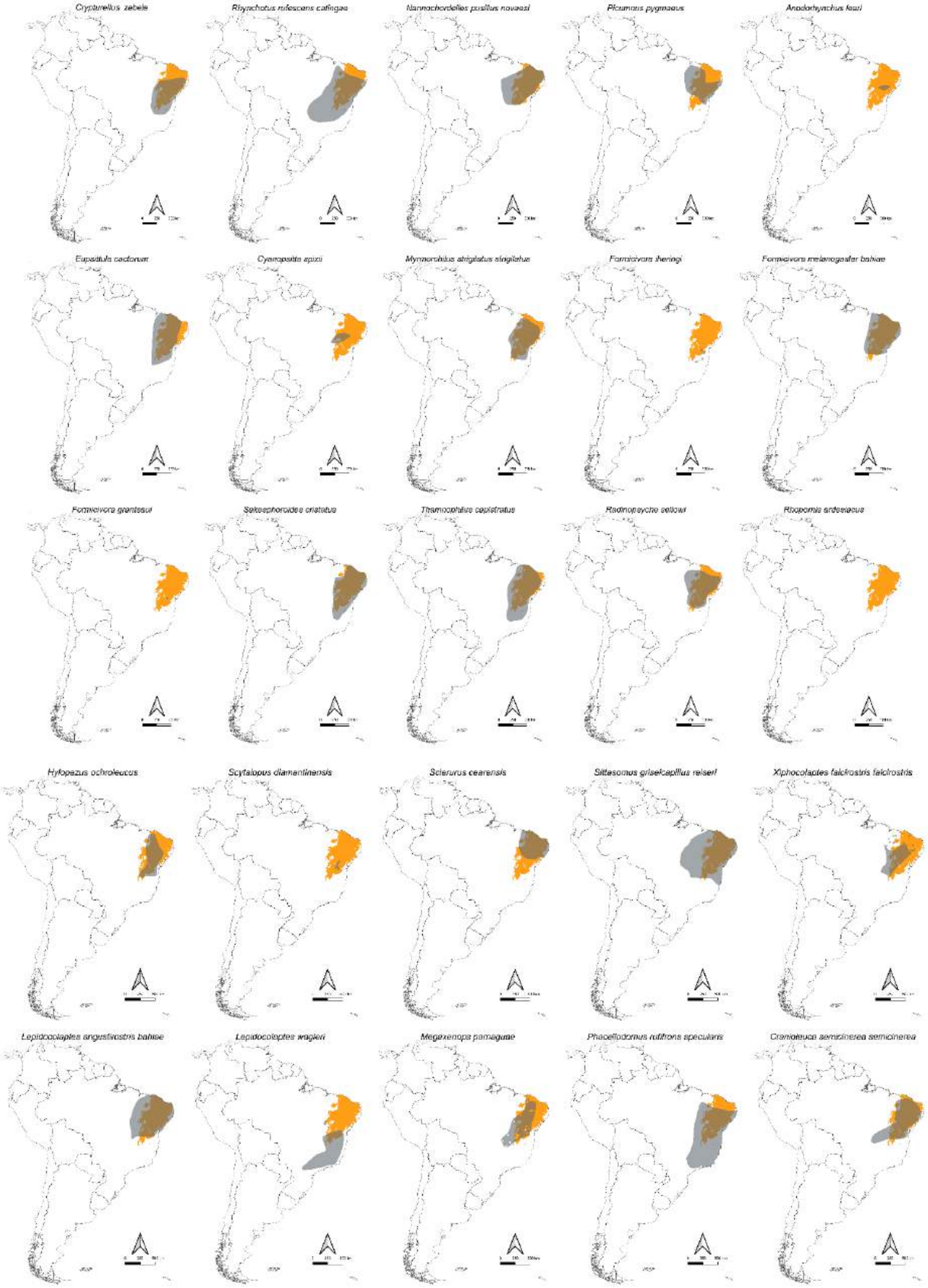
Supplementary Material

Figure S1. Distribution of the Caatinga endemic bird species used in the biogeographic analyses. On gray the current distribution of each taxon, orange indicates the Caatinga area.



Crypturellus zabele
Rhynchotus rufescens catingae
Nannochordeiles pusillus novaesi
Picumnus pygmaeus
Anodorhynchus leari
Eupsittula cactorum
Cyanopsitta spixii
Myrmorchilus strigilatus strigilatus
Formicivora iheringi
Formicivora melanogaster bahiae
Formicivora grantsaui
Sakesphoroides cristatus
Thamnophilus capistratus
Radinopsyche sellowi
Rhopornis ardesiacus
Hylopezus ochroleucus
Scytalopus diamantinensis
Sclerurus cearensis
Sittasomus griseicapillus reiseri
Xiphocolaptes falcirostris falcirostris
Lepidocolaptes angustirostris bahiae
Lepidocolaptes wagleri
Megaxenops parnaguae
Phacellodomus rufifrons specularis
Cranioleuca semicinerea semicinerea

Pseudoseisura cristata

Synallaxis hellmayri

Stigmatura napensis bahiae

Stigmatura budytoides gracilis

Suiriri suiriri bahiae

Phyllomyias fasciatus cearae

Knipolegus franciscanus

Xolmis irupero niveus

Cantorchilus longirostris bahiae

Arremon franciscanus

Icterus jamacaii

Agelaioides fringillarius

Compsothraupis loricata

Paroaria dominicana

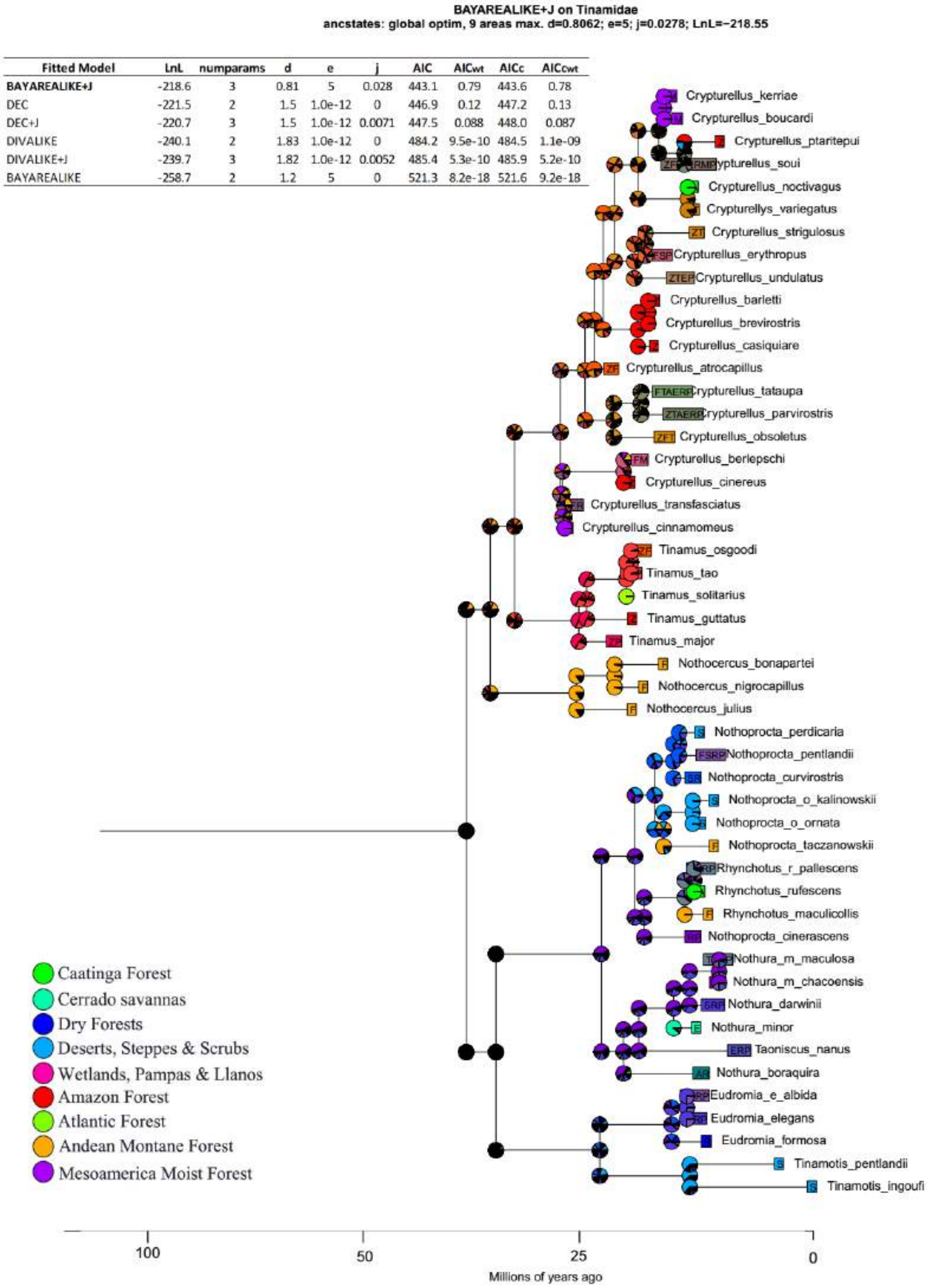
Table S1. Caatinga endemic avifauna and main results of the biogeographic analyses performed in this study for 39 Caatinga endemic bird species. Taxonomy and nomenclature used in this study follow the Brazilian Committee on Ornithological Records (Pacheco et al. 2021). Superscript description indicates the Conservation status of endangered species, following IUCN (2022). Acronymous as follow: A (Caatinga dry forest), E (Cerrado savannas), F (Andean Montane Forests), M (Mesoamerica Moist Forests), P (Pampas, Llanos & wetlands), R (Dry forests), S (Steppes, scrubs & deserts), T (Atlantic Forest), Z (Amazon Forest).

Taxa	Fitted Model	Caatinga Arrival (Ma)	Ancestor Origin	Ancestor Classification	Phylogeny utilized
TINAMIDAE					
Crypturellus zabele^{NT}	BAYAREALIKE+J	12.5	ZFT	Humid Forest	Almeida et al. (2022)
Rhynchotus rufescens	BAYAREALIKE+J	8.0	TERP	Mixed	Almeida et al. (2022)
CRACIDAE					
Penelope jacucaca^{VU}					
CAPRIMULGIDAE					
Nyctiprogne vielliardi					
Nyctidromus hirundinaceus					
Nannochordeiles pusillus	BAYAREALIKE+J		ZTERP	Mixed	White et al. (2016)
APODIDADE					
Streptoprocne biscutata seridoensis					
TROCHILIDAE					
Anopetia gounellei					
Augastes lumachella ^{NT}					
PICIDAE					
Picumnus limae					
Picumnus pygmaeus	BAYAREALIKE+J	0.65	A	Open/Dry	Shakya et al. (2017)
PSITTACIDAE					
Anodorhynchus leari ^{EN}	BAYAREALIKE+J	7.4	ZE	Mixed	Tavares et al. (2006)
Eupsittula cactorum	BAYAREALIKE+J	7.0	ZTERP	Mixed	Tavares et al. (2006)
Cyanopsitta spixii ^{EW}	BAYAREALIKE+J	17.0	ZE	Mixed	Tavares et al. (2006)

Thectocercus acuticaudatus haemorrhous					
THAMNOPHILIDAE					
Myrmorchilus s. strigilatus	DIVALIKE+J	6.66	AR	Open/Dry	Harvey et al. (2020)
Formicivora iheringi ^{NT}	BAYAREALIKE+J	5.89	T	Humid Forest	Harvey et al. (2020)
Formicivora melanogaster bahiae	BAYAREALIKE+J	1.57	ER	Mixed	Harvey et al. (2020)
Formicivora grantsaui ^{EN}	BAYAREALIKE+J	4.42	P	Open/Dry	Harvey et al. (2020)
Sakesphoroides cristatus	DEC+J	11.24	A	Open/Dry	Harvey et al. (2020)
Herpsilochmus pectoralis ^{VU}					
Thamnophilus capistratus	DIVALIKE	2.96	AE	Open/Dry	Harvey et al. (2020)
Radinopsyche sellowi	DEC+J	10.91	A	Open/Dry	Harvey et al. (2020)
Rhopornis ardesiacus ^{EN}	DIVALIKE	8.88	ZA	Mixed	Harvey et al. (2020)
GRALLARIDAE					
Hylopezus ochroleucus ^{NT}	DEC+J	10.76	Z	Humid Forest	Harvey et al. (2020)
RHINOCRYPTIDAE					
Scytalopus diamantinensis ^{EN}	DEC+J	2.56	E	Open/Dry	Harvey et al. (2020)
SCLERURIDAE					
Sclerurus cearensis	DIVALIKE	0.86	TAE	Mixed	Harvey et al. (2020)
DENDROCOLAPTIDAE					
Sittasomus griseicapillus reiseri	BAYAREALIKE+J	1.97	ERP	Open/Dry	Harvey et al. (2020)
Xiphocolaptes falcirostris ^{VU}	DEC+J	1.53	Z	Humid Forest	Harvey et al. (2020)
Lepidocolaptes angustirostris bahiae	DEC+J	1.66	A	Open/Dry	Harvey et al. (2020)
Lepidocolaptes wagleri	DEC+J	2.97	T	Humid Forest	Harvey et al. (2020)
FURNARIDAE					
Megaxenops parnaguae	DEC+J	6.64	A	Open/Dry	Harvey et al. (2020)
Phacelllodomus rufifrons specularis	BAYAREALIKE	1.37	RP	Open/Dry	Harvey et al. (2020)
Cranioleuca semicinerea	DIVALIKE+J	1.27	F	Humid Forest	Harvey et al. (2020)

Cranioleuca vulpina reiseri					
Pseudoseisura cristata	DIVALIKE+J	1.32	A	Open/Dry	Harvey et al. (2020)
Synallaxis hellmayri	BAYAREALIKE+J	5.12	AERP	Open/Dry	Harvey et al. (2020)
TYRANNIDAE					
Stigmatura napensis bahiae	DEC+J	3.38	A	Open/Dry	Harvey et al. (2020)
Stigmatura budytoides gracilis	DEC+J	3.53	A	Open/Dry	Harvey et al. (2020)
Suiriri suiriri bahiae	DIVALIKE+J	1.03	AE	Open/Dry	Harvey et al. (2020)
Phyllomyias fasciatus cearae	DIVALIKE+J	0.82	T	Humid Forest	Harvey et al. (2020)
Knipolegus franciscanus	DEC+J	1.79	AE	Open/Dry	Harvey et al. (2020)
Xolmis irupero niveus	DEC+J	1.00	ARP	Open/Dry	Harvey et al. (2020)
TROGLODYTIDAE					
Cantorchilus longirostris bahiae	DEC+J		T	Humid Forest	Mann et al. (2006)
MIMIDAE					
Mimus saturninus arenaceus					
PASSERELLIDAE					
Arremon franciscanus NT	DEC+J	1.45	T	Humid Forest	Barker et al. (2015)
ICTERIDAE					
Icterus jamacaii	BAYAREALIKE+J	1.00	ASRP	Open/Dry	Barker et al. (2015)
Agelaioides fringilarius	BAYAREALIKE	1.25	SR	Open/Dry	Barker et al. (2015)
THRAUPIDAE					
Compsothraupis loricata	DEC	2.81	FA	Mixed	Barker et al. (2015)
Paroaria dominicana	BAYAREALIKE+J	2.51	RP	Open/Dry	Barker et al. (2015)

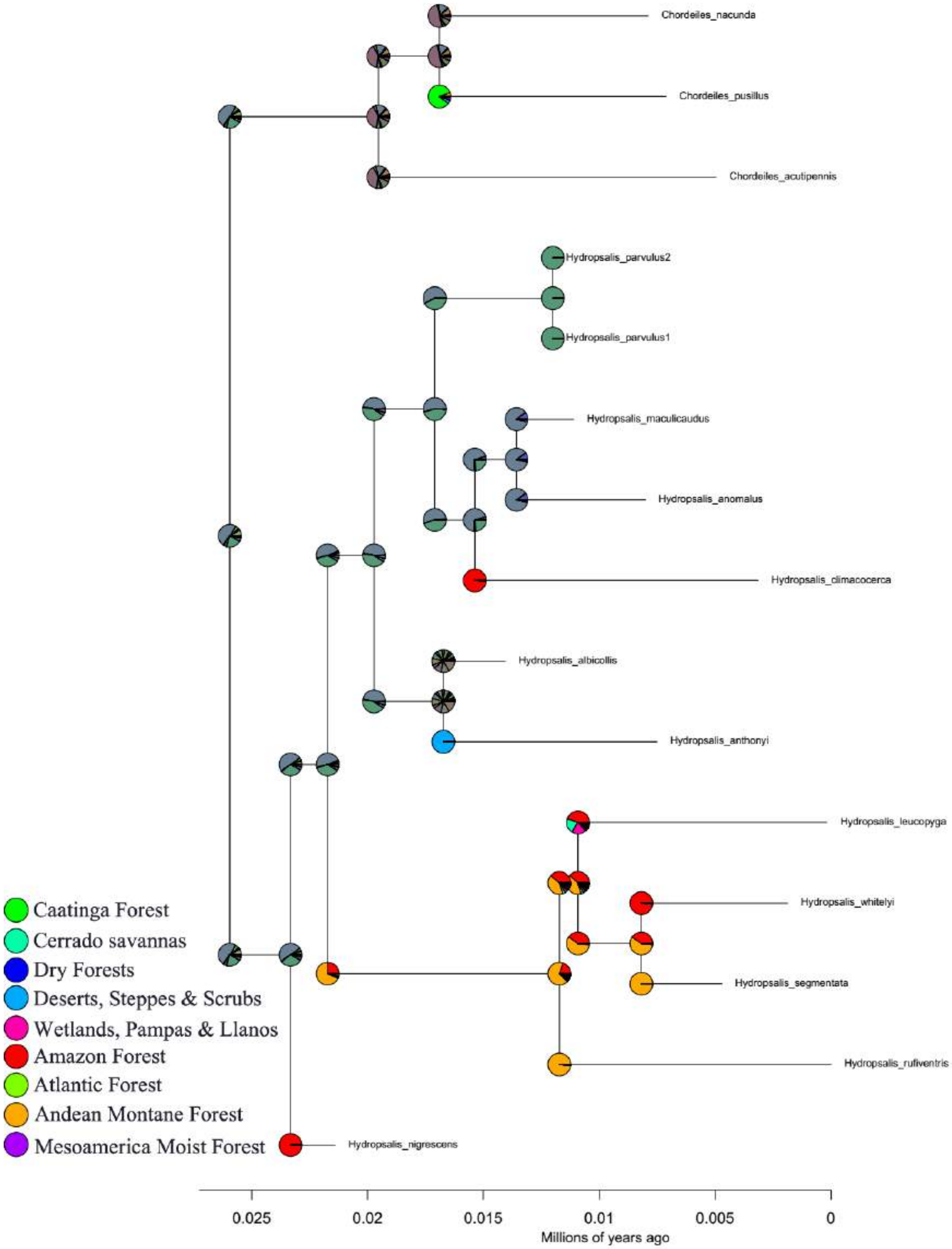
Figure S2. Plots of the phylogenies used in this study. The tips of the phylogenies indicate the current species distributions, while internodes represent the most likely ancestral area distribution inferred by BioGeoBEARS.

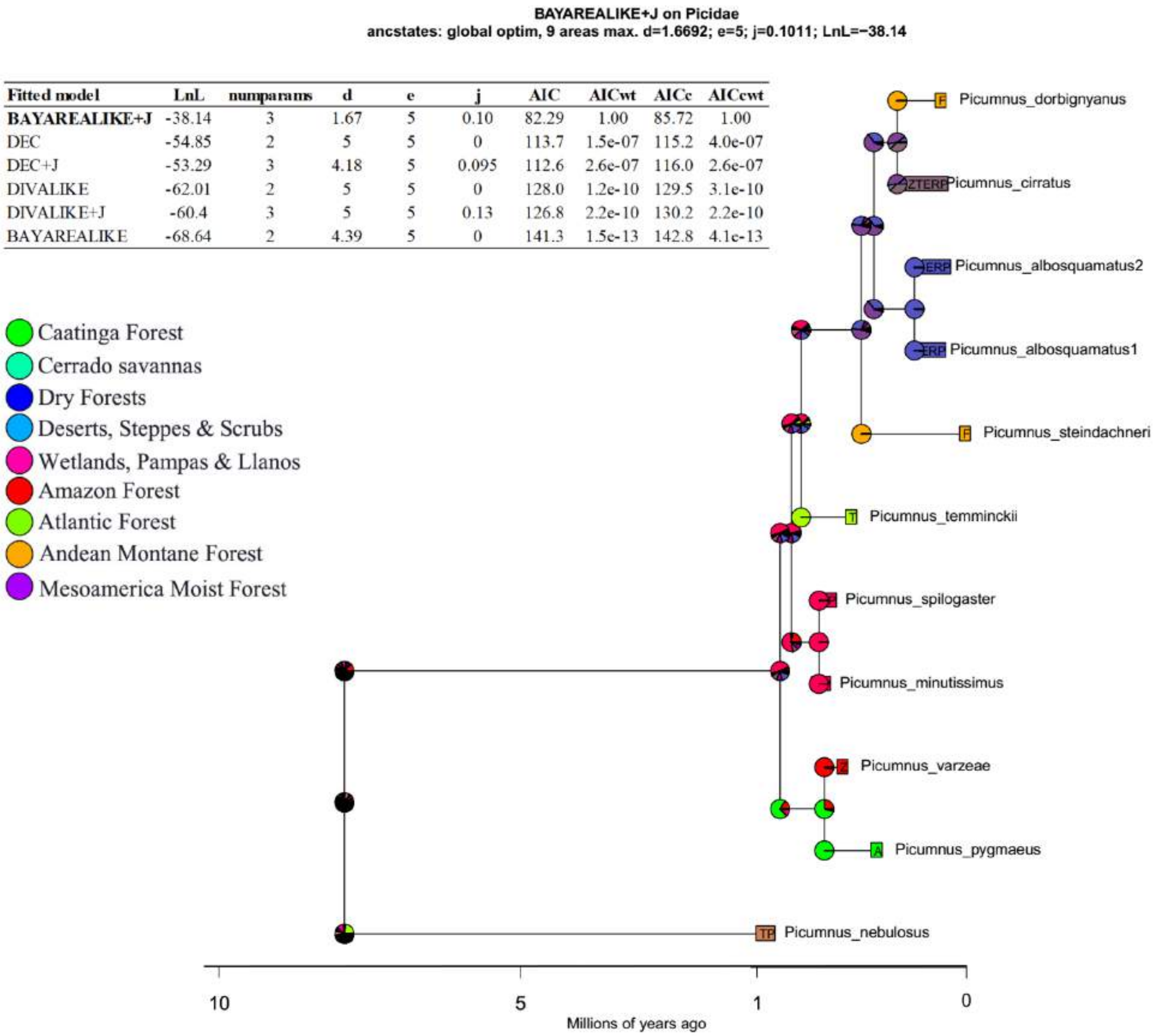


Fitted Model	LnL	numparams	d	e	j	AIC	AICwt	AICc	AICcwt
BAYAREALIKE+J	-218.6	3	0.81	5	0.028	443.1	0.79	443.6	0.78
DEC	-221.5	2	1.5	1.0e-12	0	446.9	0.12	447.2	0.13
DEC+J	-220.7	3	1.5	1.0e-12	0.0071	447.5	0.088	448.0	0.087
DIVALIKE	-240.1	2	1.83	1.0e-12	0	484.2	9.5e-10	484.5	1.1e-09
DIVALIKE+J	-239.7	3	1.82	1.0e-12	0.0052	485.4	5.3e-10	485.9	5.2e-10
BAYAREALIKE	-258.7	2	1.2	5	0	521.3	8.2e-18	521.6	9.2e-18

BioGeoBEARS BAYAREALIKE+J on Caprimulgidae M0_unconstrained
ancstates: global optim, 9 areas max. d=5; e=5; j=0.1164; LnL=−63.65

Fitted model	LnL	numparams	d	e	j	AIC	AICwt	AICc	AICcwt
BAYAREALIKE+J	-63.65	3	5	5	0.12	133.3	1.00	135.5	1.00
DEC+J	-78.87	3	5	1.0e-12	3	163.7	2.4e-07	165.9	2.4e-07
DIVALIKE+J	-79.41	3	5	1.0e-12	2	164.8	1.4e-07	167.0	1.4e-07
DEC	-83.55	2	5	1.0e-12	0	171.1	6.2e-09	172.1	1.1e-08
DIVALIKE	-97.03	2	5	8.6e-07	0	198.1	8.6e-15	199.1	1.6e-14
BAYAREALIKE	-106.5	2	5	5	0	217	6.6e-19	218.0	1.2e-18





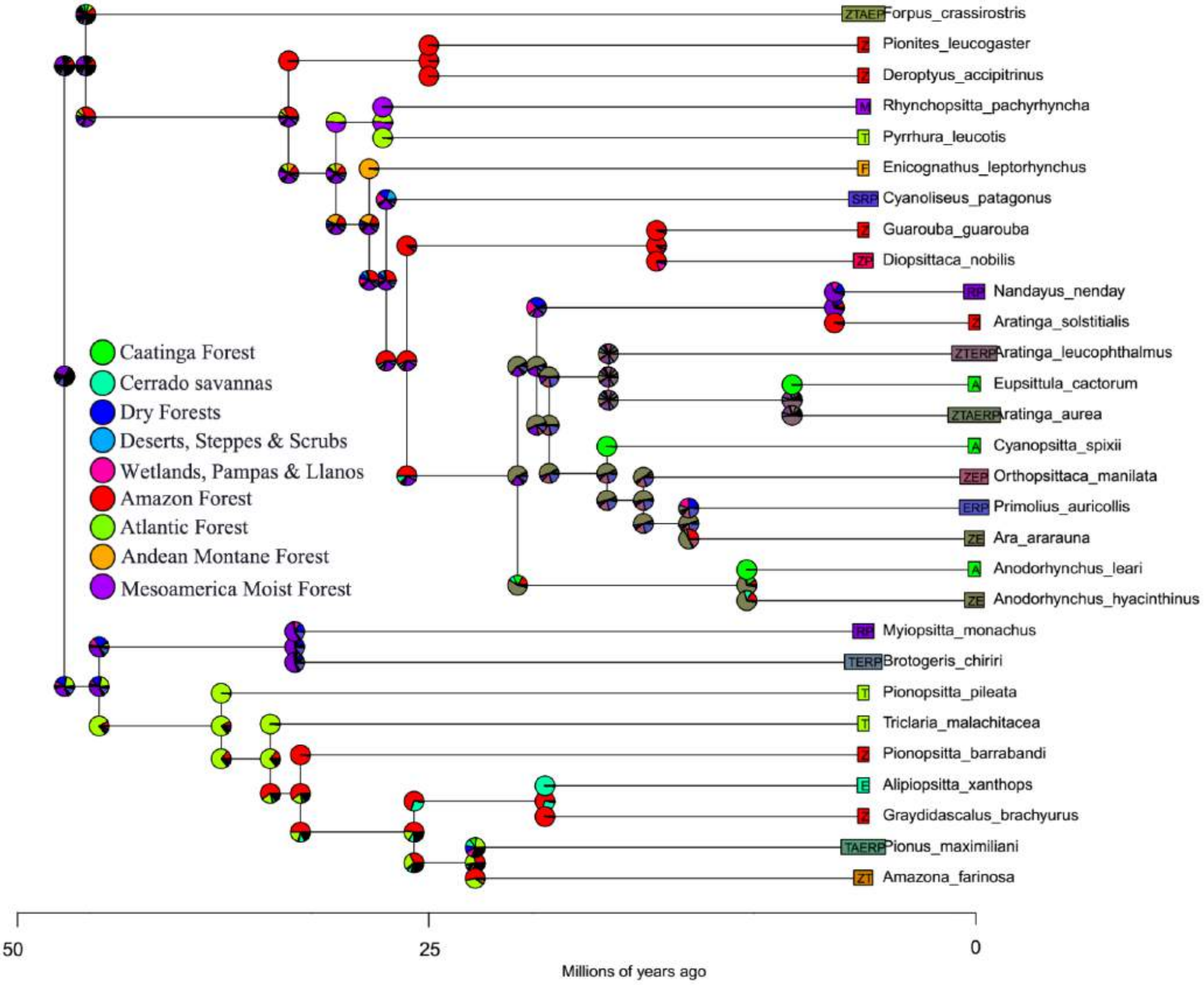
BAYAREALIKE+J on Picidae
ancstates: global optim, 9 areas max. d=1.6692; e=5; j=0.1011; LnL=−38.14

Fitted model	LnL	numparams	d	e	j	AIC	AICwt	AICc	AICcwt
BAYAREALIKE+J	-38.14	3	1.67	5	0.10	82.29	1.00	85.72	1.00
DEC	-54.85	2	5	5	0	113.7	1.5e-07	115.2	4.0e-07
DEC+J	-53.29	3	4.18	5	0.095	112.6	2.6e-07	116.0	2.6e-07
DIVALIKE	-62.01	2	5	5	0	128.0	1.2e-10	129.5	3.1e-10
DIVALIKE+J	-60.4	3	5	5	0.13	126.8	2.2e-10	130.2	2.2e-10
BAYAREALIKE	-68.64	2	4.39	5	0	141.3	1.5e-13	142.8	4.1e-13

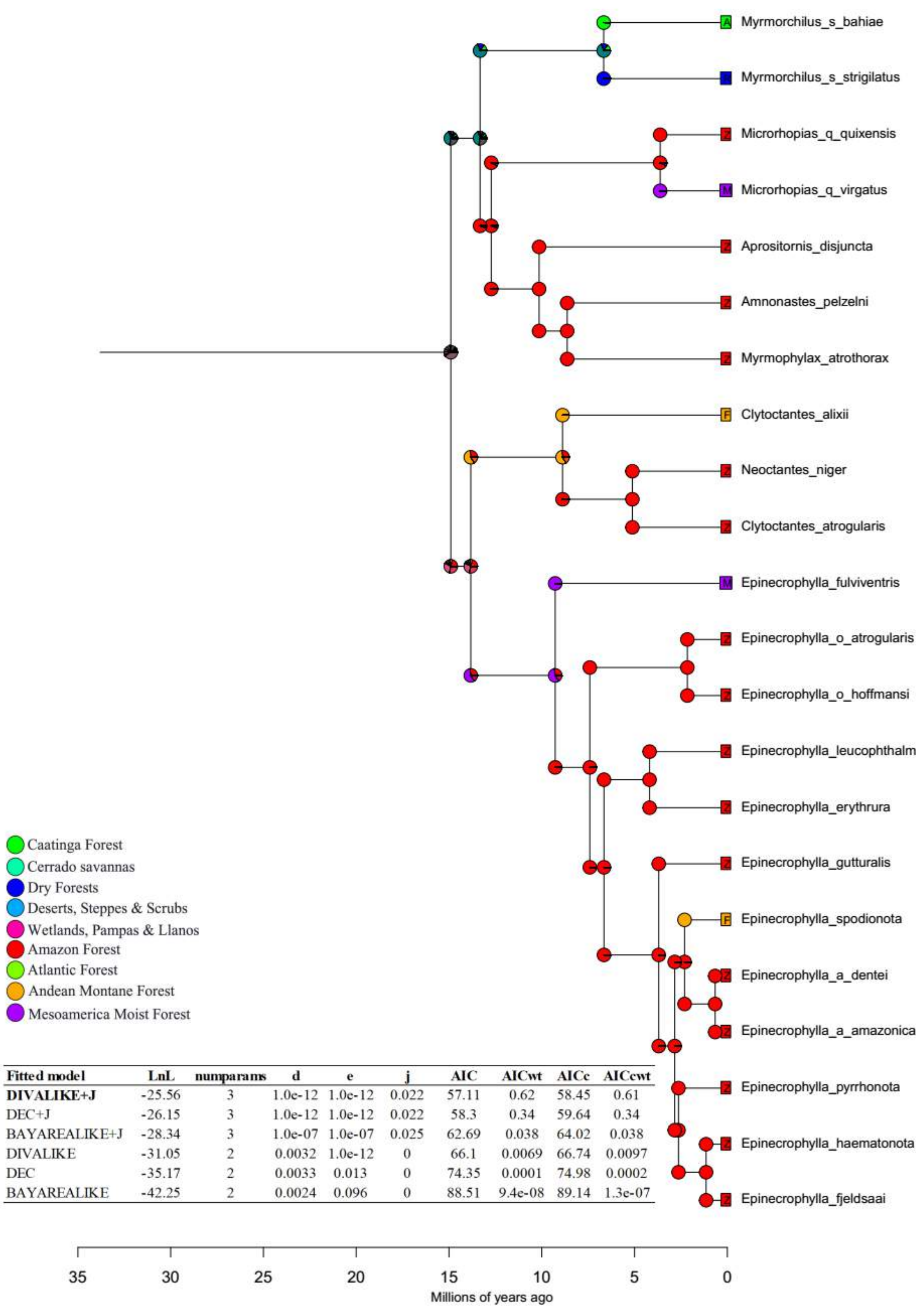
BAYAREALIKE+J on Psittacidae

ancstates: global optim, 9 areas max. d=1.7138; e=1.4858; j=0.1054; LnL=−126.09

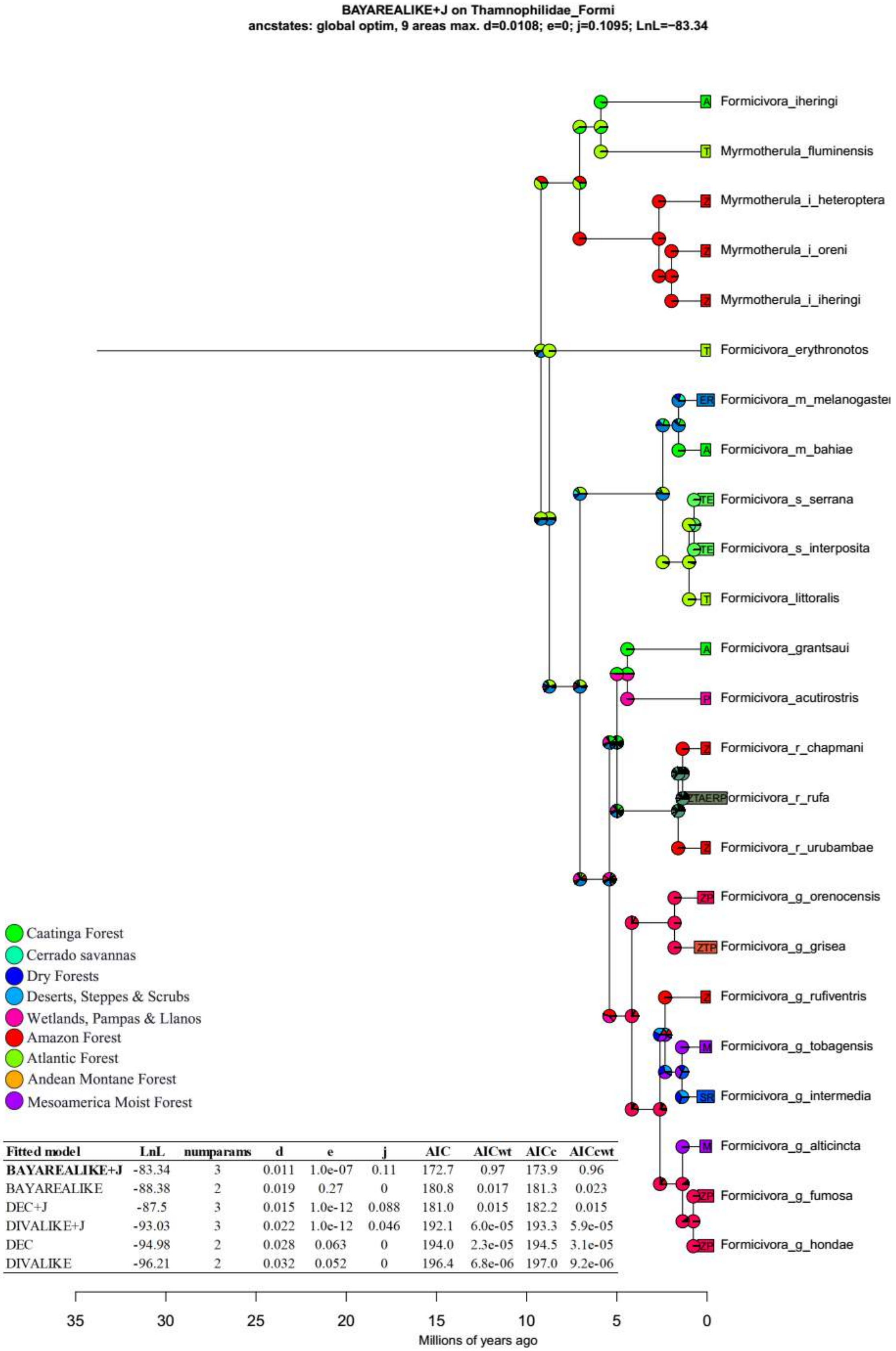
Fitted model	LnL	numparams	d	e	j	AIC	AICwt	AICc	AICcwt
BAYAREALIKE+J	-38.14	3	1.67	5	0.10	82.29	1.00	85.72	1.00
DEC	-54.85	2	5	5	0	113.7	1.5e-07	115.2	4.0e-07
DEC+J	-53.29	3	4.18	5	0.095	112.6	2.6e-07	116.0	2.6e-07
DIVALIKE	-62.01	2	5	5	0	128.0	1.2e-10	129.5	3.1e-10
DIVALIKE+J	-60.4	3	5	5	0.13	126.8	2.2e-10	130.2	2.2e-10
BAYAREALIKE	-68.64	2	4.39	5	0	141.3	1.5e-13	142.8	4.1e-13



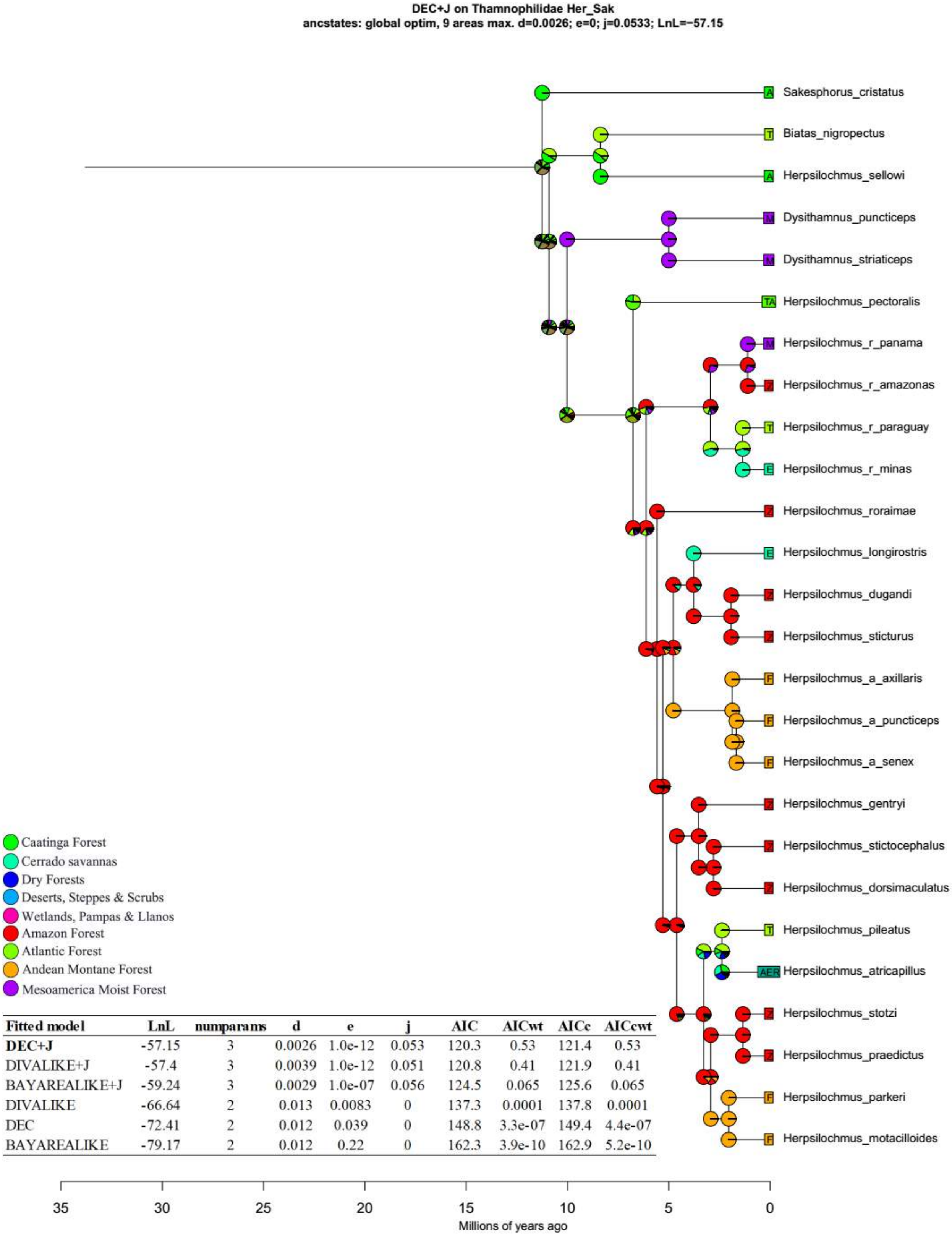
DIVALIKE+J on Thamnophilidae Myr str
ancstates: global optim, 9 areas max. d=0; e=0; j=0.0217; LnL=−25.56



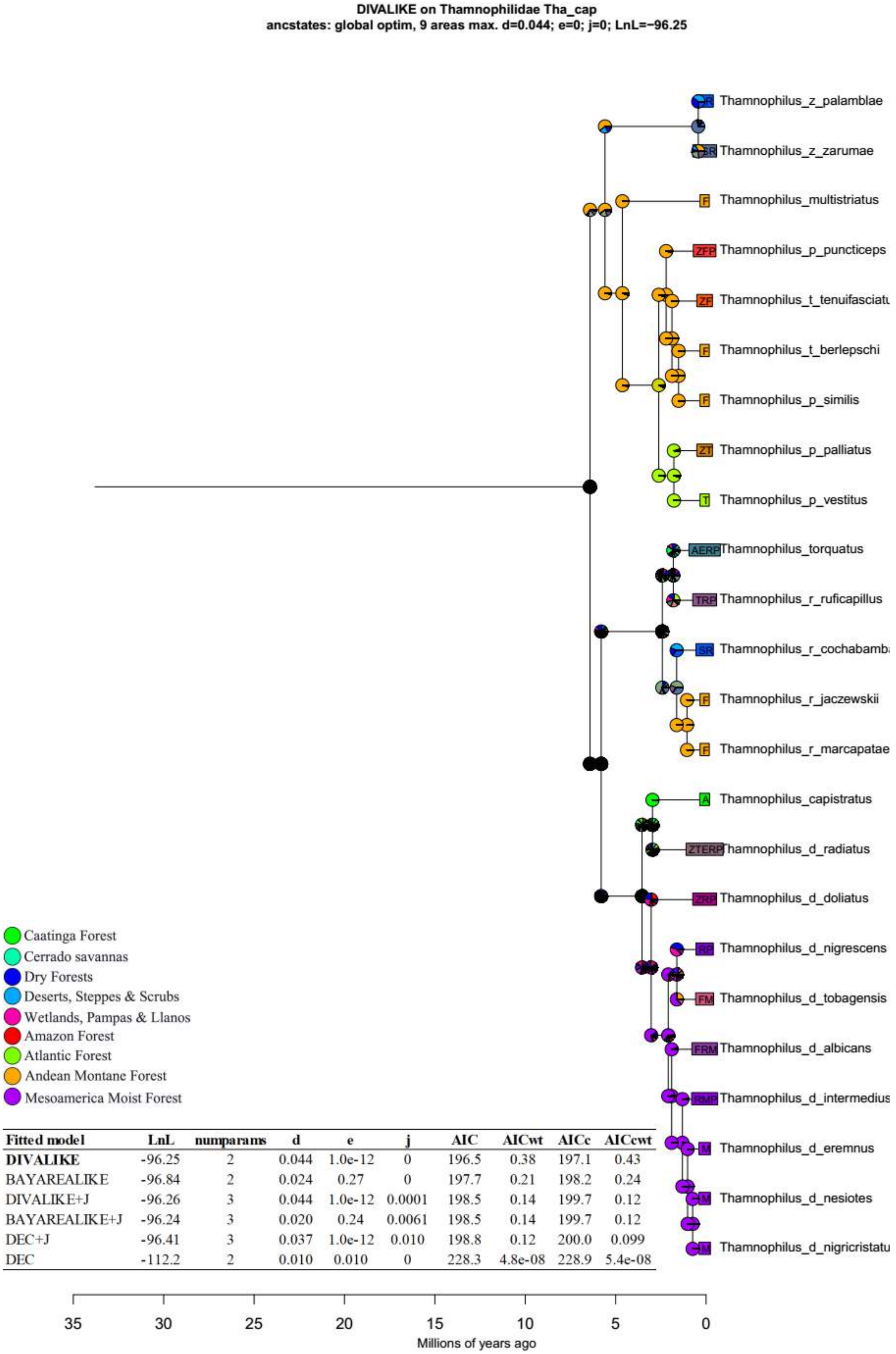
Fitted model	LnL	numparams	d	e	j	AIC	AICwt	AICc	AICcwt
DIVALIKE+J	-25.56	3	1.0e-12	1.0e-12	0.022	57.11	0.62	58.45	0.61
DEC+J	-26.15	3	1.0e-12	1.0e-12	0.022	58.3	0.34	59.64	0.34
BAYAREALIKE+J	-28.34	3	1.0e-07	1.0e-07	0.025	62.69	0.038	64.02	0.038
DIVALIKE	-31.05	2	0.0032	1.0e-12	0	66.1	0.0069	66.74	0.0097
DEC	-35.17	2	0.0033	0.013	0	74.35	0.0001	74.98	0.0002
BAYAREALIKE	-42.25	2	0.0024	0.096	0	88.51	9.4e-08	89.14	1.3e-07



Fitted model	LnL	numparams	d	e	j	AIC	AICwt	AICc	AICcwt
BAYAREALIKE+J	-83.34	3	0.011	1.0e-07	0.11	172.7	0.97	173.9	0.96
BAYAREALIKE	-88.38	2	0.019	0.27	0	180.8	0.017	181.3	0.023
DEC+J	-87.5	3	0.015	1.0e-12	0.088	181.0	0.015	182.2	0.015
DIVALIKE+J	-93.03	3	0.022	1.0e-12	0.046	192.1	6.0e-05	193.3	5.9e-05
DEC	-94.98	2	0.028	0.063	0	194.0	2.3e-05	194.5	3.1e-05
DIVALIKE	-96.21	2	0.032	0.052	0	196.4	6.8e-06	197.0	9.2e-06



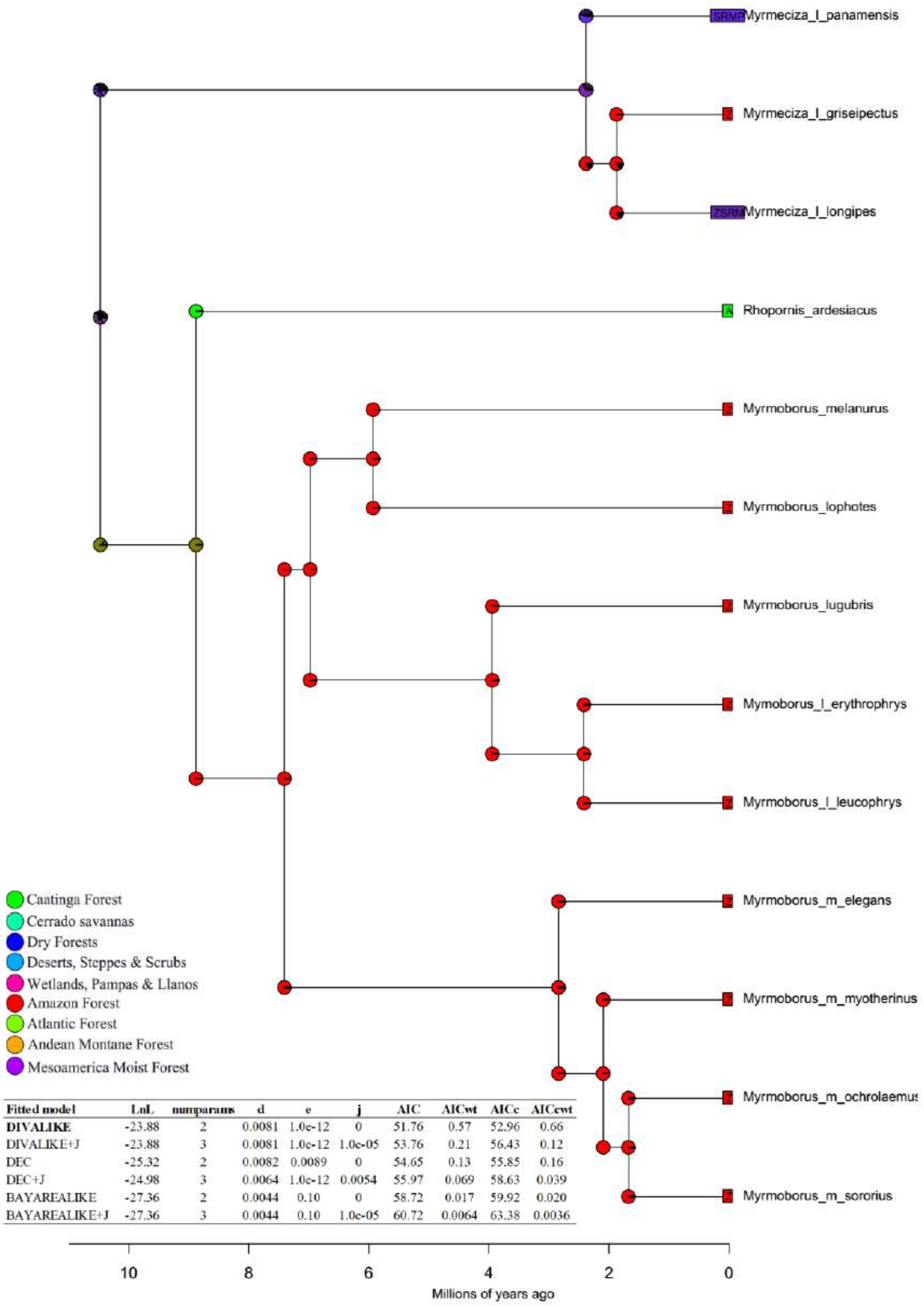
Fitted model	LnL	numparams	d	e	j	AIC	AICwt	AICc	AICcwt
DEC+J	-57.15	3	0.0026	1.0e-12	0.053	120.3	0.53	121.4	0.53
DIVALIKE+J	-57.4	3	0.0039	1.0e-12	0.051	120.8	0.41	121.9	0.41
BAYAREALIKE+J	-59.24	3	0.0029	1.0e-07	0.056	124.5	0.065	125.6	0.065
DIVALIKE	-66.64	2	0.013	0.0083	0	137.3	0.0001	137.8	0.0001
DEC	-72.41	2	0.012	0.039	0	148.8	3.3e-07	149.4	4.4e-07
BAYAREALIKE	-79.17	2	0.012	0.22	0	162.3	3.9e-10	162.9	5.2e-10



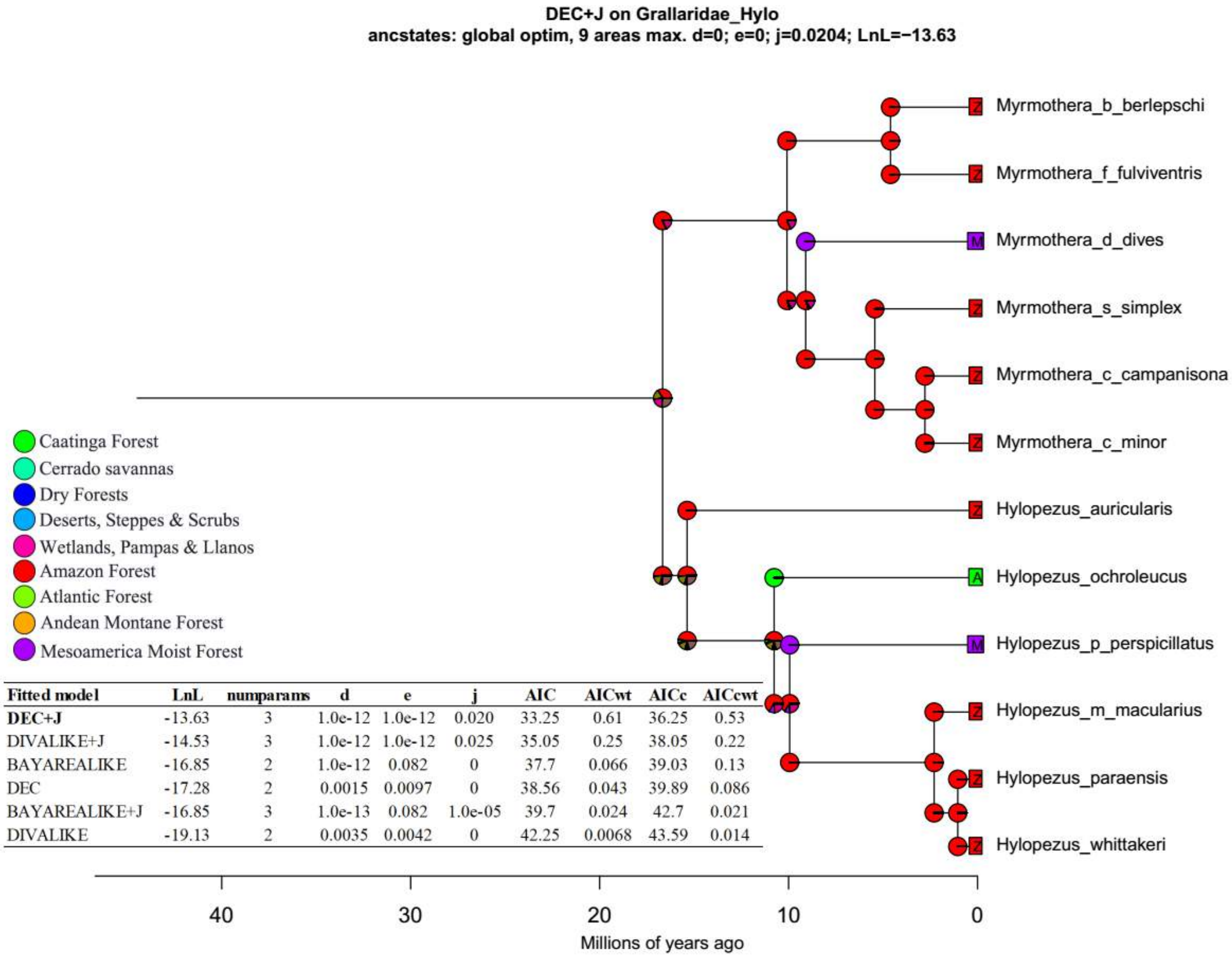
DIVALIKE on Thamnophilidae Tha_cap
ancstates: global optim, 9 areas max. d=0.044; e=0; j=0; LnL=−96.25

Fitted model	LnL	numparams	d	e	j	AIC	AICwt	AICc	AICcwt
DIVALIKE	-96.25	2	0.044	1.0e-12	0	196.5	0.38	197.1	0.43
BAYAREALIKE	-96.84	2	0.024	0.27	0	197.7	0.21	198.2	0.24
DIVALIKE+J	-96.26	3	0.044	1.0e-12	0.0001	198.5	0.14	199.7	0.12
BAYAREALIKE+J	-96.24	3	0.020	0.24	0.0061	198.5	0.14	199.7	0.12
DEC+J	-96.41	3	0.037	1.0e-12	0.010	198.8	0.12	200.0	0.099
DEC	-112.2	2	0.010	0.010	0	228.3	4.8e-08	228.9	5.4e-08

DIVALIKE on Thamnophilidae_Rho_ard
ancstates: global optim, 9 areas max. d=0.0081; e=0; j=0; LnL=−23.88

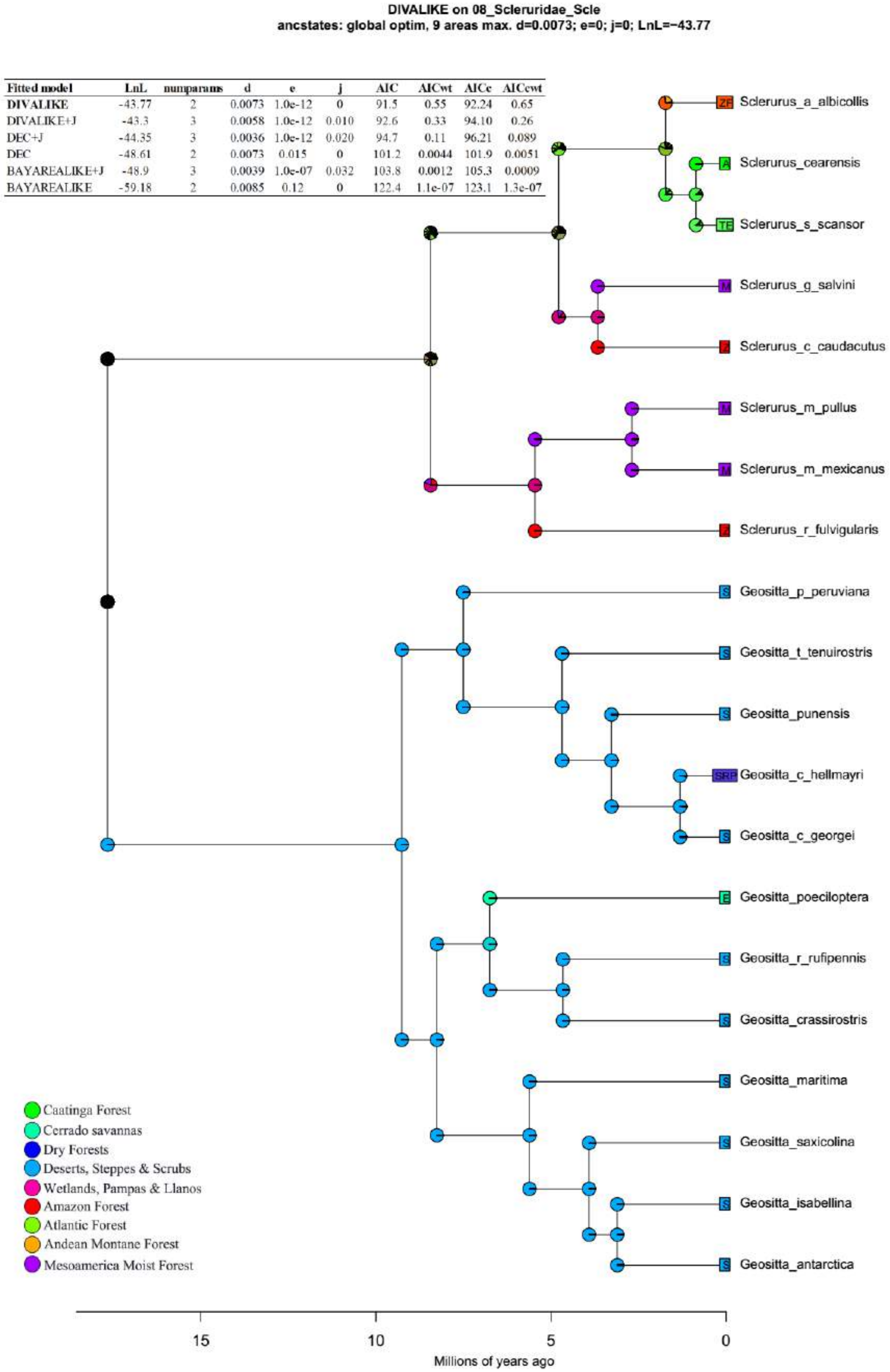


Fitted model	LnL	numparams	d	e	j	AIC	AICwt	AICc	AICcwt
DIVALIKE	-23.88	2	0.0081	1.0e-12	0	51.76	0.57	52.96	0.66
DIVALIKE+J	-23.88	3	0.0081	1.0e-12	1.0e-05	53.76	0.21	56.43	0.12
DEC	-25.32	2	0.0082	0.0089	0	54.65	0.13	55.85	0.16
DEC+J	-24.98	3	0.0064	1.0e-12	0.0054	55.97	0.069	58.63	0.039
BAYAREALIKE	-27.36	2	0.0044	0.10	0	58.72	0.017	59.92	0.020
BAYAREALIKE+J	-27.36	3	0.0044	0.10	1.0e-05	60.72	0.0064	63.38	0.0036

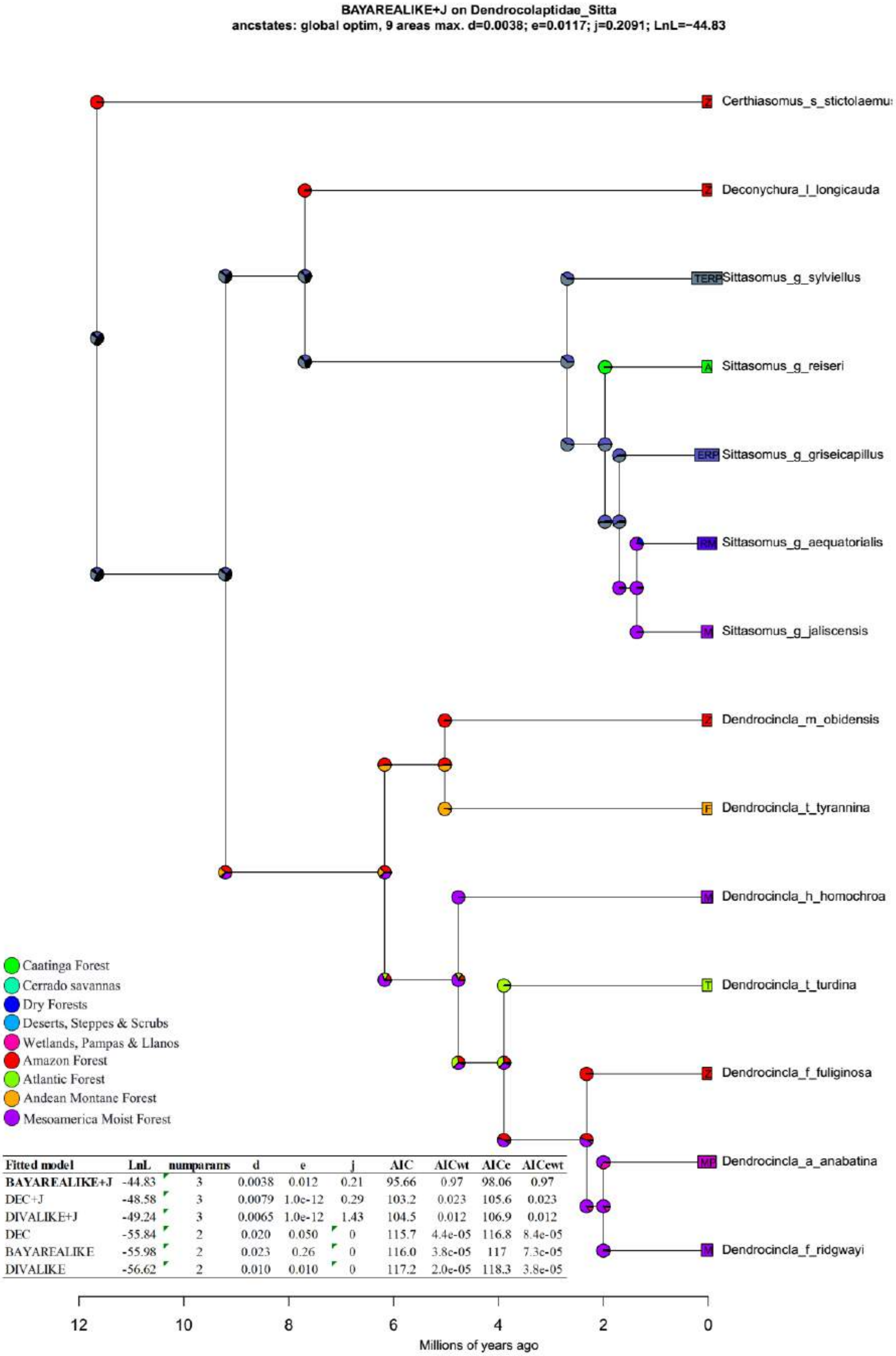

DEC+J on Grallaridae_Hylo
ancstates: global optim, 9 areas max. d=0; e=0; j=0.0204; LnL=−13.63

Fitted model	LnL	numparams	d	e	j	AIC	AICwt	AICc	AICcwt
DEC+J	-13.63	3	1.0e-12	1.0e-12	0.020	33.25	0.61	36.25	0.53
DIVALIKE+J	-14.53	3	1.0e-12	1.0e-12	0.025	35.05	0.25	38.05	0.22
BAYAREALIKE	-16.85	2	1.0e-12	0.082	0	37.7	0.066	39.03	0.13
DEC	-17.28	2	0.0015	0.0097	0	38.56	0.043	39.89	0.086
BAYAREALIKE+J	-16.85	3	1.0e-13	0.082	1.0e-05	39.7	0.024	42.7	0.021
DIVALIKE	-19.13	2	0.0035	0.0042	0	42.25	0.0068	43.59	0.014

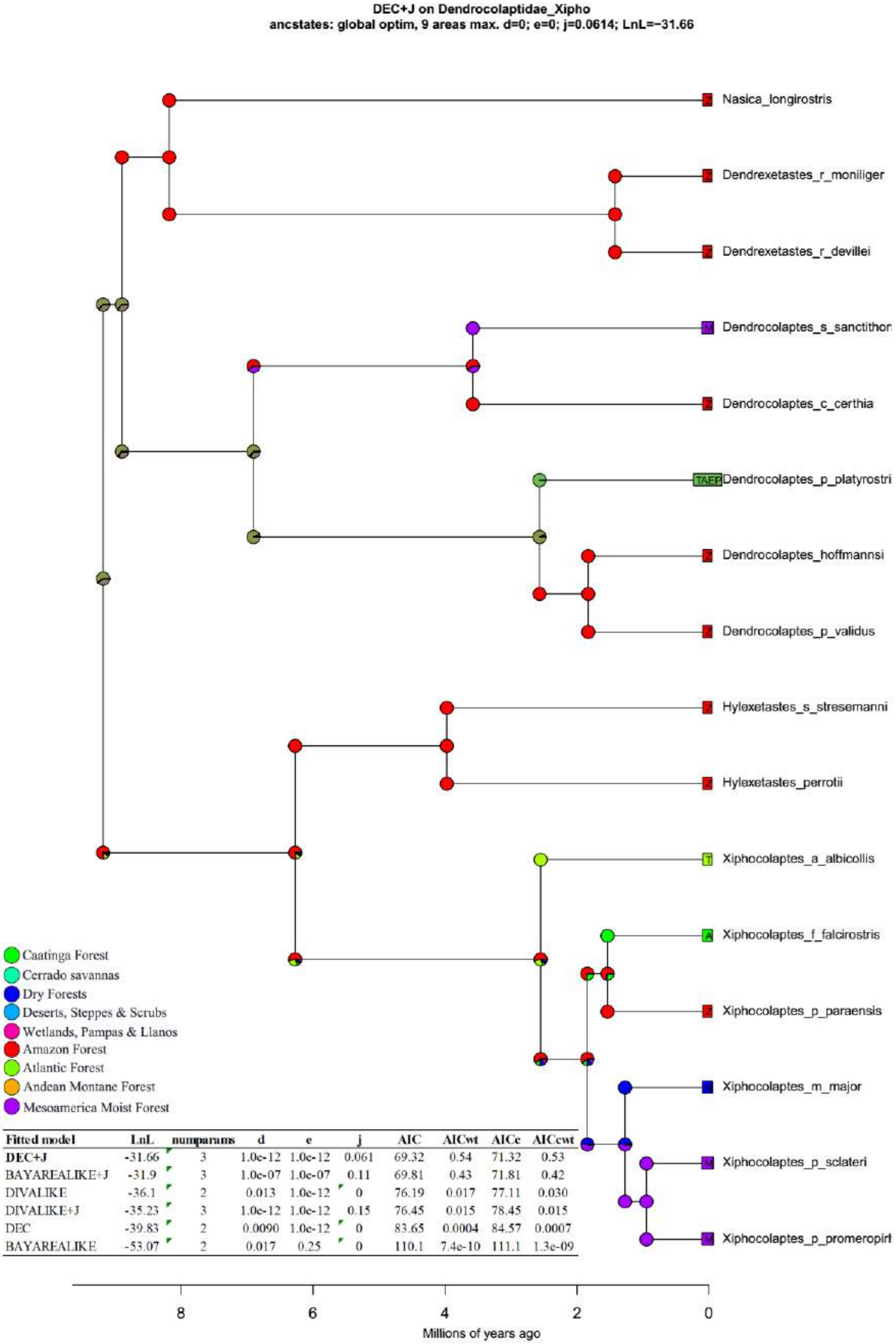
Fitted model	LnL	numparams	d	e	j	AIC	AICwt	AICc	AICcwt
DEC+J	-95.57	3	0.0084	1.0e-12	0.012	197.1	0.99	197.7	0.99
DEC	-101.3	2	0.011	0.0043	0	206.5	0.0091	206.8	0.011
BAYAREALIKE+J	-102.5	3	0.0079	1.0e-07	0.023	211.0	0.0010	211.6	0.0010
DIVALIKE	-106.6	2	0.010	0.010	0	217.2	4.3e-05	217.5	5.0e-05
DIVALIKE+J	-106.4	3	0.010	0.010	0.0001	218.8	2.0e-05	219.4	2.0e-05
BAYAREALIKE	-109.7	2	0.0014	0.23	0	223.4	2.0e-06	223.6	2.3e-06


DIVALIKE on 08_Scleruridae_Scle
ancstates: global optim, 9 areas max. d=0.0073; e=0; j=0; LnL=−43.77

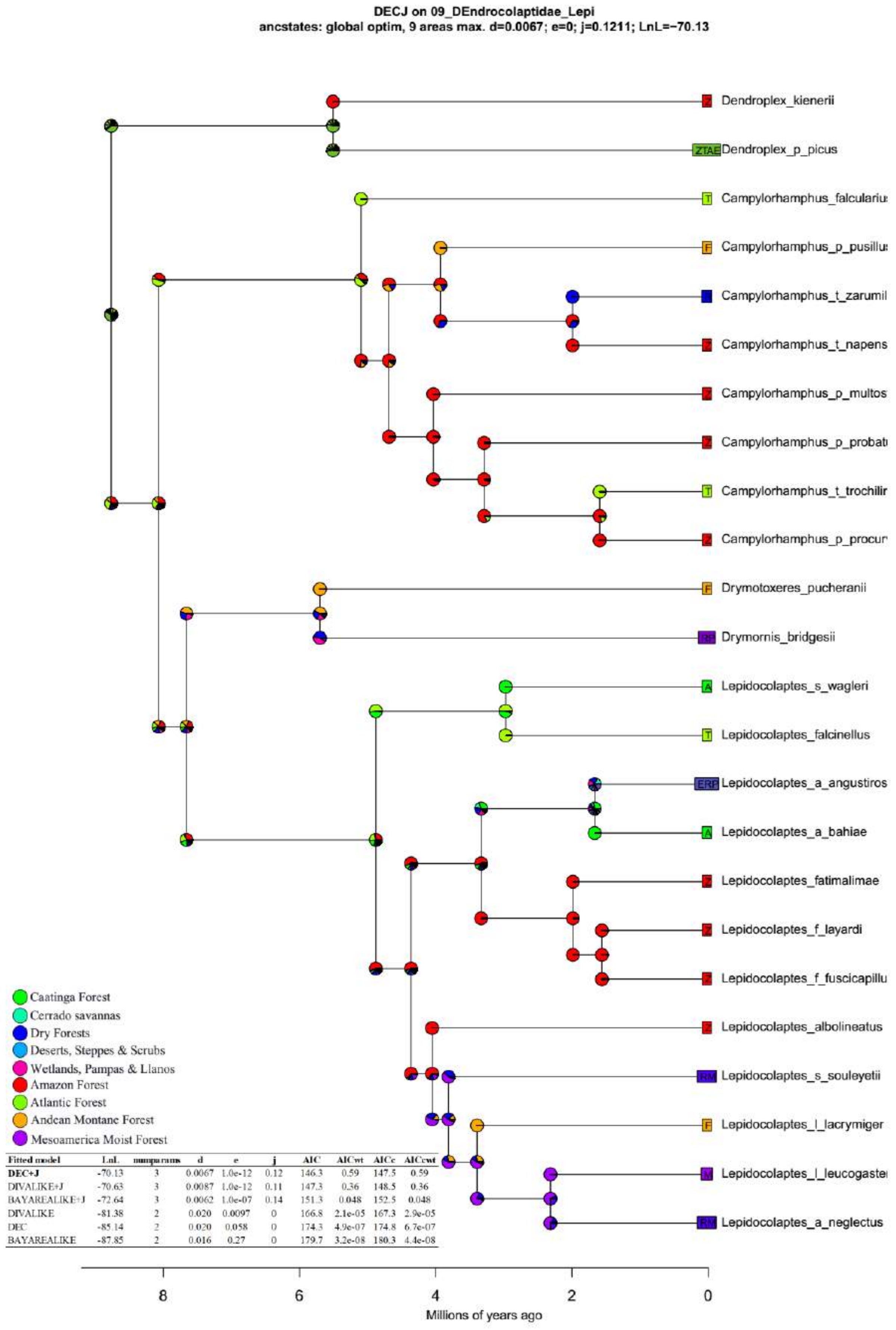
Fitted model	LnL	numparams	d	e	j	AIC	AICwt	AICc	AICcwt
DIVALIKE	-43.77	2	0.0073	1.0e-12	0	91.5	0.55	92.24	0.65
DIVALIKE+J	-43.3	3	0.0058	1.0e-12	0.010	92.6	0.33	94.10	0.26
DEC+J	-44.35	3	0.0036	1.0e-12	0.020	94.7	0.11	96.21	0.089
DEC	-48.61	2	0.0073	0.015	0	101.2	0.0044	101.9	0.0051
BAYAREALIKE+J	-48.9	3	0.0039	1.0e-07	0.032	103.8	0.0012	105.3	0.0009
BAYAREALIKE	-59.18	2	0.0085	0.12	0	122.4	1.1e-07	123.1	1.3e-07


BAYAREALIKE+J on Dendrocolaptidae_Sitta
ancstates: global optim, 9 areas max. d=0.0038; e=0.0117; j=0.2091; LnL=-44.83

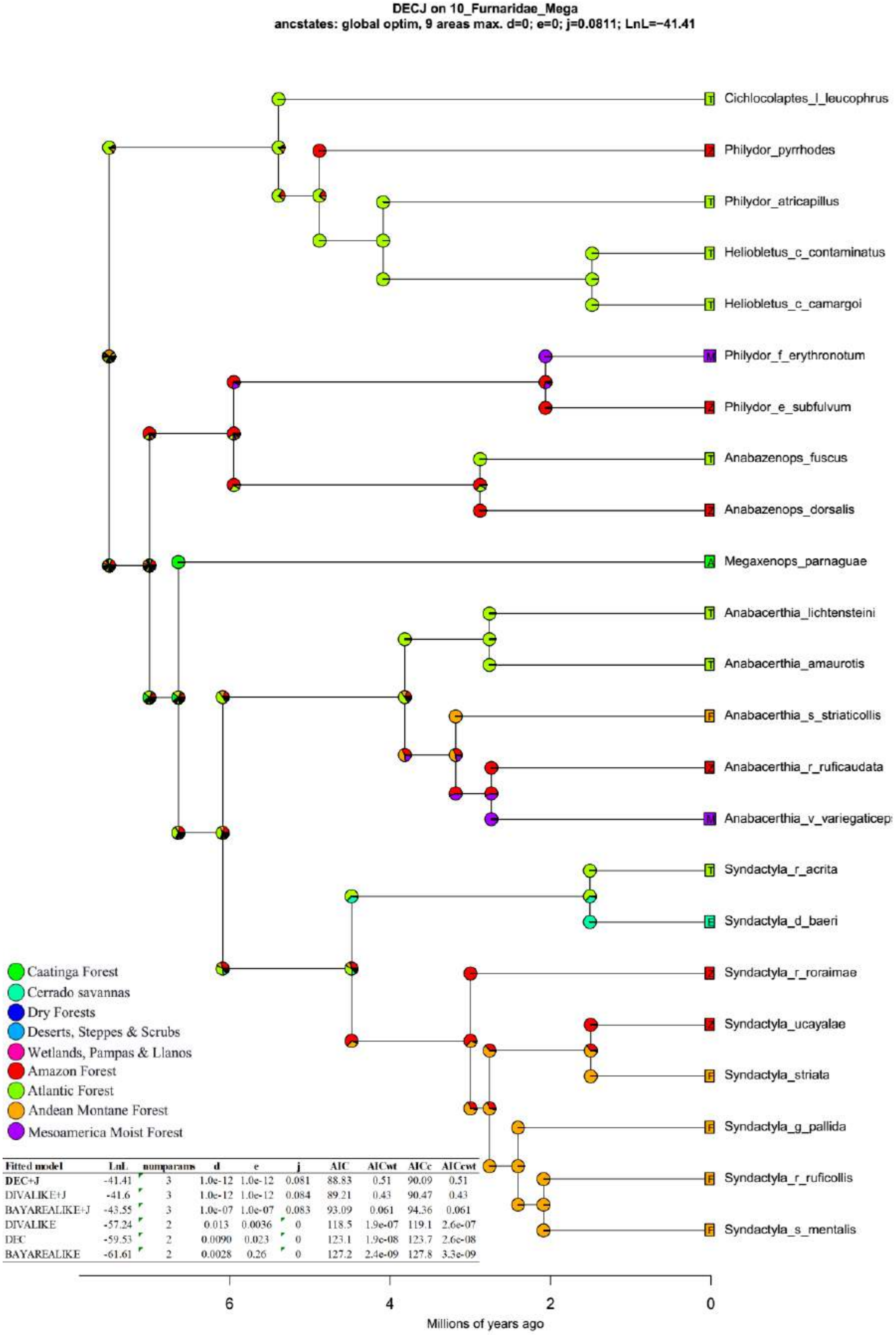
Fitted model	LnL	numparams	d	e	j	AIC	AICwt	AICc	AICcwt
BAYAREALIKE+J	-44.83	3	0.0038	0.012	0.21	95.66	0.97	98.06	0.97
DEC+J	-48.58	3	0.0079	1.0e-12	0.29	103.2	0.023	105.6	0.023
DIVALIKE+J	-49.24	3	0.0065	1.0e-12	1.43	104.5	0.012	106.9	0.012
DEC	-55.84	2	0.020	0.050	0	115.7	4.4e-05	116.8	8.4e-05
BAYAREALIKE	-55.98	2	0.023	0.26	0	116.0	3.8e-05	117	7.3e-05
DIVALIKE	-56.62	2	0.010	0.010	0	117.2	2.0e-05	118.3	3.8e-05



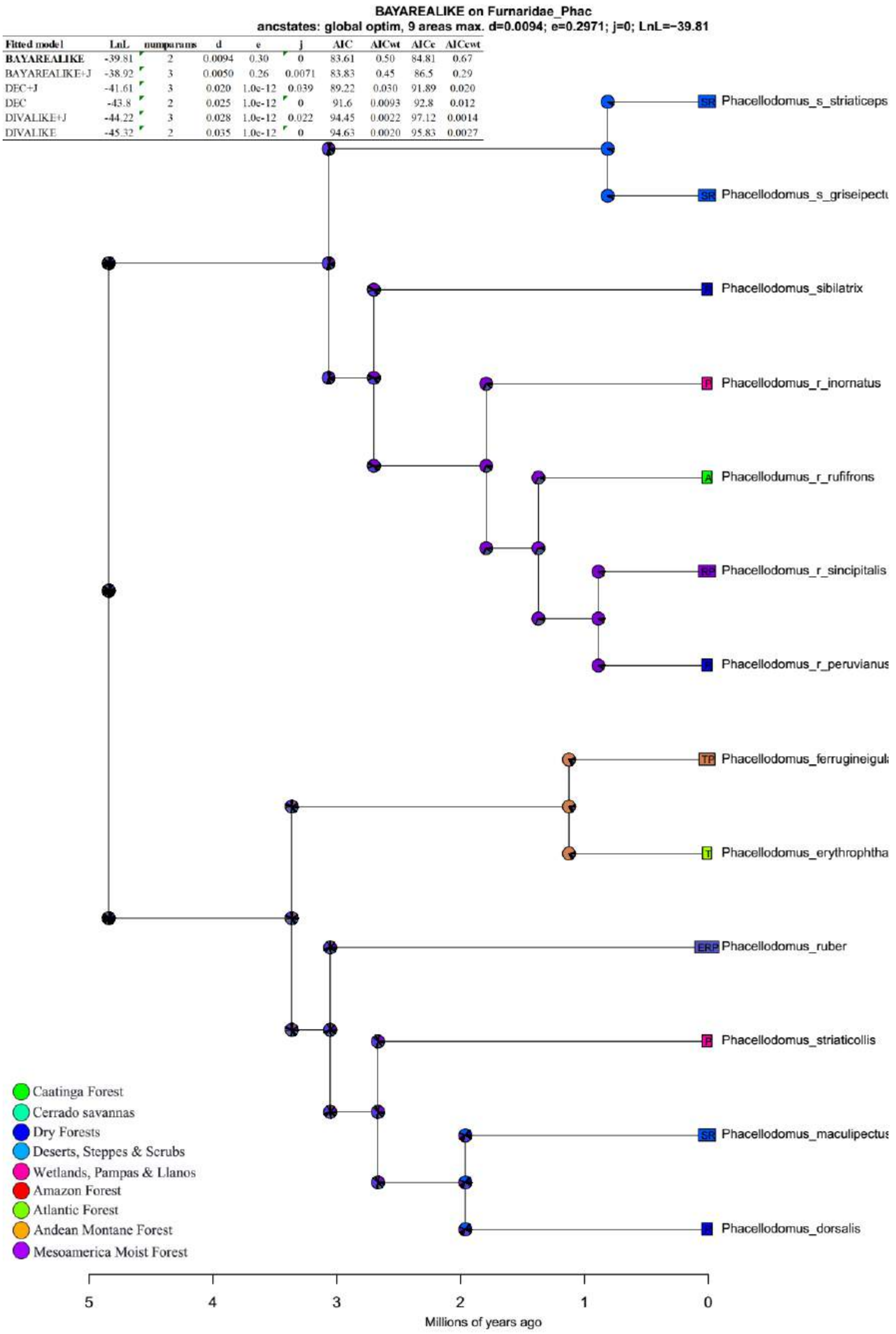
Fitted model	LnL	numparams	d	e	j	AIC	AICwt	AICc	AICcwt
DEC+J	-31.66	3	1.0e-12	1.0e-12	0.061	69.32	0.54	71.32	0.53
BAYAREALIKE+J	-31.9	3	1.0e-07	1.0e-07	0.11	69.81	0.43	71.81	0.42
DIVALIKE	-36.1	2	0.013	1.0e-12	0	76.19	0.017	77.11	0.030
DIVALIKE+J	-35.23	3	1.0e-12	1.0e-12	0.15	76.45	0.015	78.45	0.015
DEC	-39.83	2	0.0090	1.0e-12	0	83.65	0.0004	84.57	0.0007
BAYAREALIKE	-53.07	2	0.017	0.25	0	110.1	7.4e-10	111.1	1.3e-09



Fitted model	LnL	numparams	d	e	j	AIC	AICwt	AICc	AICcwt
DEC+J	-70.13	3	0.0067	1.0e-12	0.12	146.3	0.59	147.5	0.59
DIVALIKE+J	-70.63	3	0.0087	1.0e-12	0.11	147.3	0.36	148.5	0.36
BAYAREALIKE+J	-72.64	3	0.0062	1.0e-07	0.14	151.3	0.048	152.5	0.048
DIVALIKE	-81.38	2	0.020	0.0097	0	166.8	2.1e-05	167.3	2.9e-05
DEC	-85.14	2	0.020	0.058	0	174.3	4.9e-07	174.8	6.7e-07
BAYAREALIKE	-87.85	2	0.016	0.27	0	179.7	3.2e-08	180.3	4.4e-08

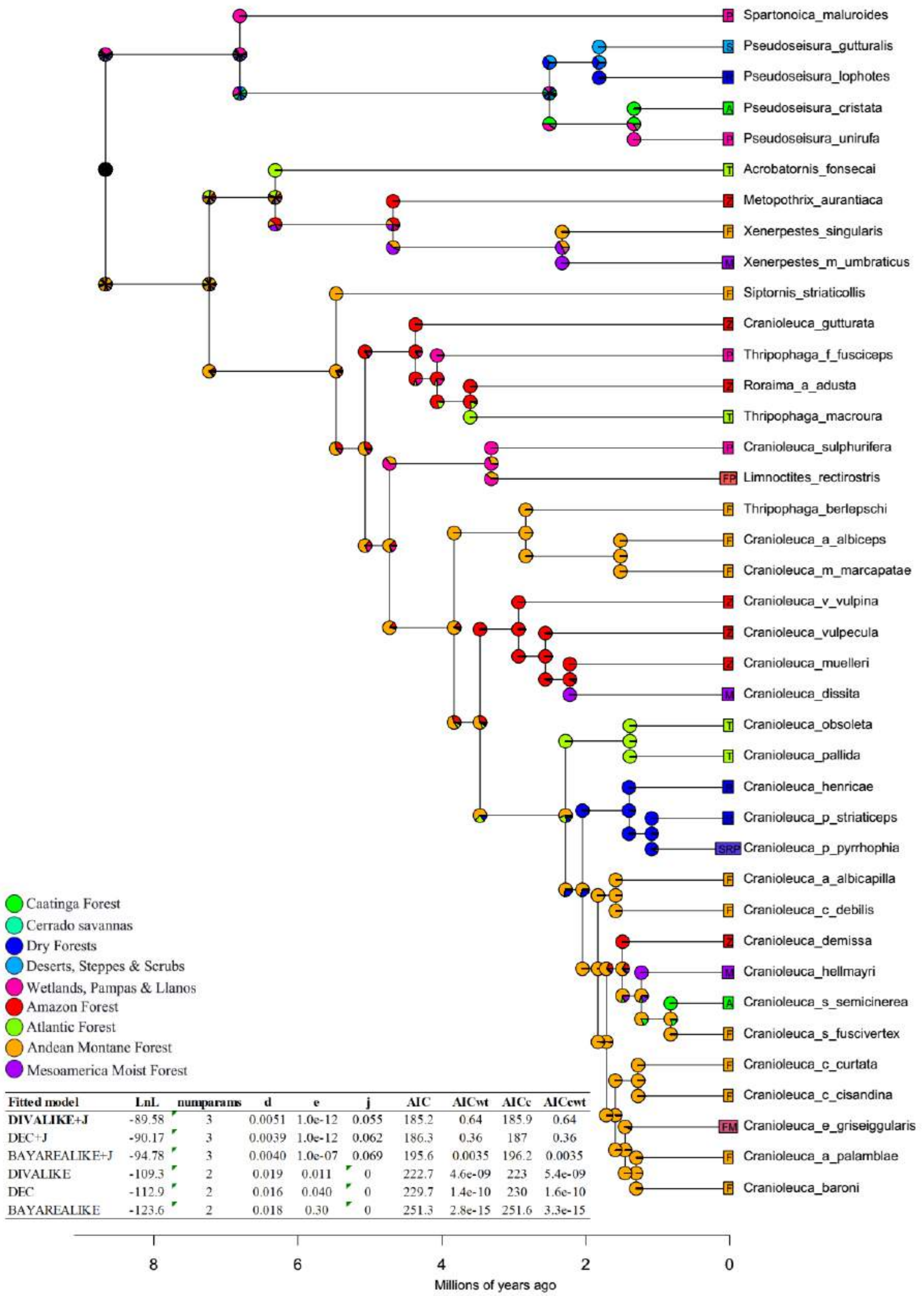


Fitted model	LnL	numparams	d	e	j	AIC	AICwt	AICc	AICcwt
DEC+J	-41.41	3	1.0e-12	1.0e-12	0.081	88.83	0.51	90.09	0.51
DIVALIKE+J	-41.6	3	1.0e-12	1.0e-12	0.084	89.21	0.43	90.47	0.43
BAYAREALIKE+J	-43.55	3	1.0e-07	1.0e-07	0.083	93.09	0.061	94.36	0.061
DIVALIKE	-57.24	2	0.013	0.0036	0	118.5	1.9e-07	119.1	2.6e-07
DEC	-59.53	2	0.0090	0.023	0	123.1	1.9e-08	123.7	2.6e-08
BAYAREALIKE	-61.61	2	0.0028	0.26	0	127.2	2.4e-09	127.8	3.3e-09

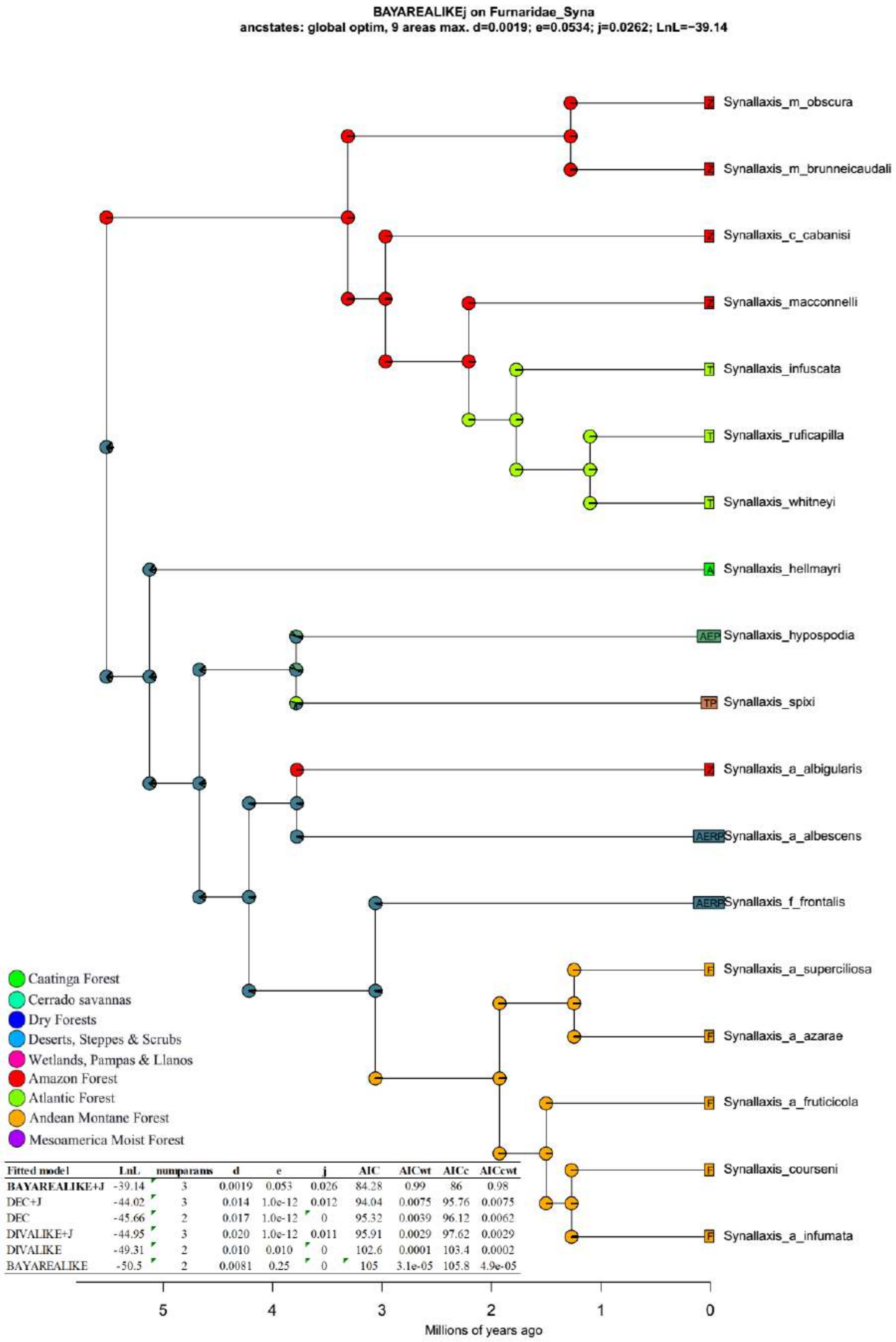


Fitted model	LnL	numparams	d	e	j	AIC	AICwt	AICc	AICcwt
BAYAREALIKE	-39.81	2	0.0094	0.30	0	83.61	0.50	84.81	0.67
BAYAREALIKE+J	-38.92	3	0.0050	0.26	0.0071	83.83	0.45	86.5	0.29
DEC+J	-41.61	3	0.020	1.0e-12	0.039	89.22	0.030	91.89	0.020
DEC	-43.8	2	0.025	1.0e-12	0	91.6	0.0093	92.8	0.012
DIVALIKE+J	-44.22	3	0.028	1.0e-12	0.022	94.45	0.0022	97.12	0.0014
DIVALIKE	-45.32	2	0.035	1.0e-12	0	94.63	0.0020	95.83	0.0027

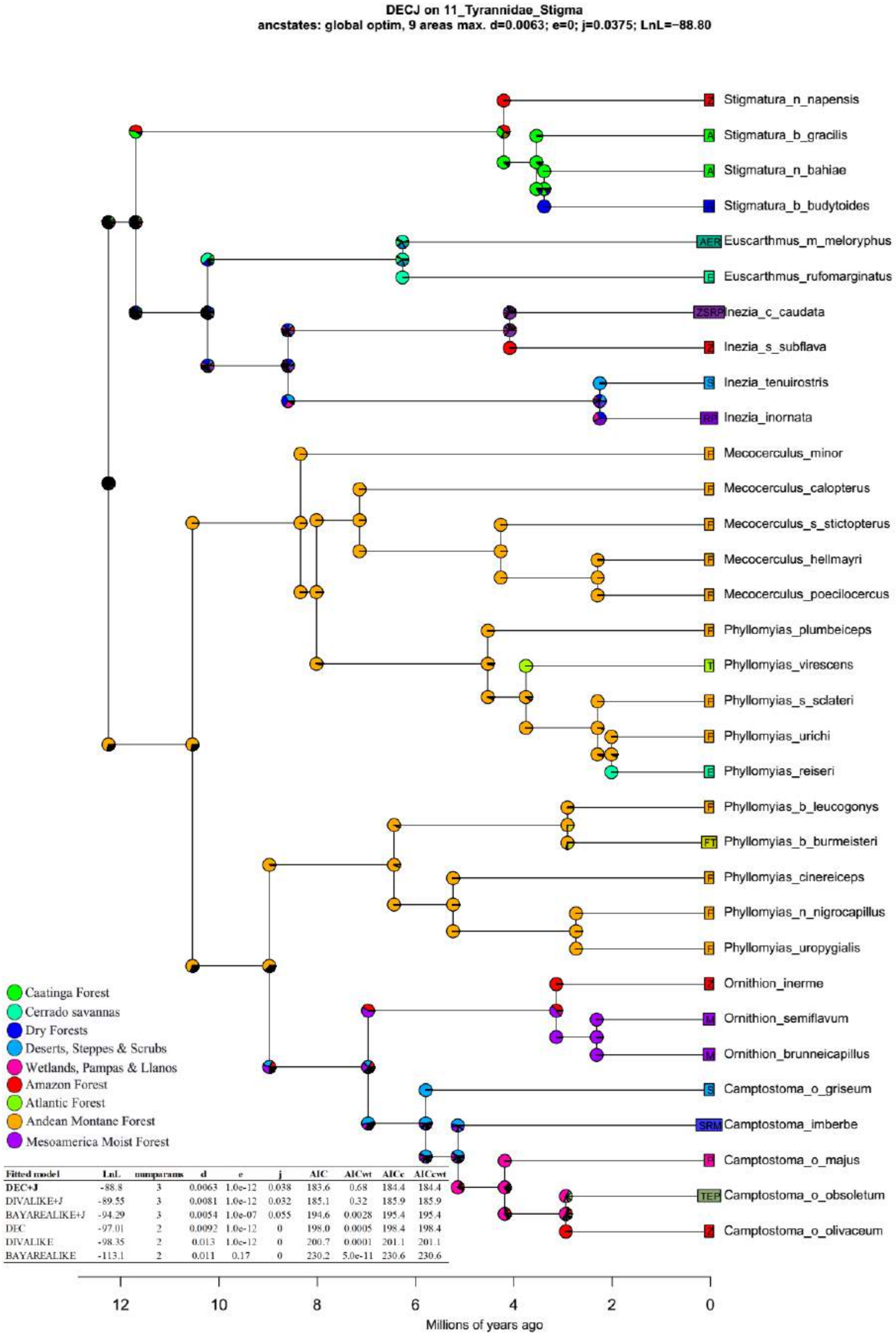
DIVALIKEJ on 10_Furnaridae_Crani_Pseu
ancstates: global optim, 9 areas max. d=0.0051; e=0; j=0.0552; LnL=−89.58



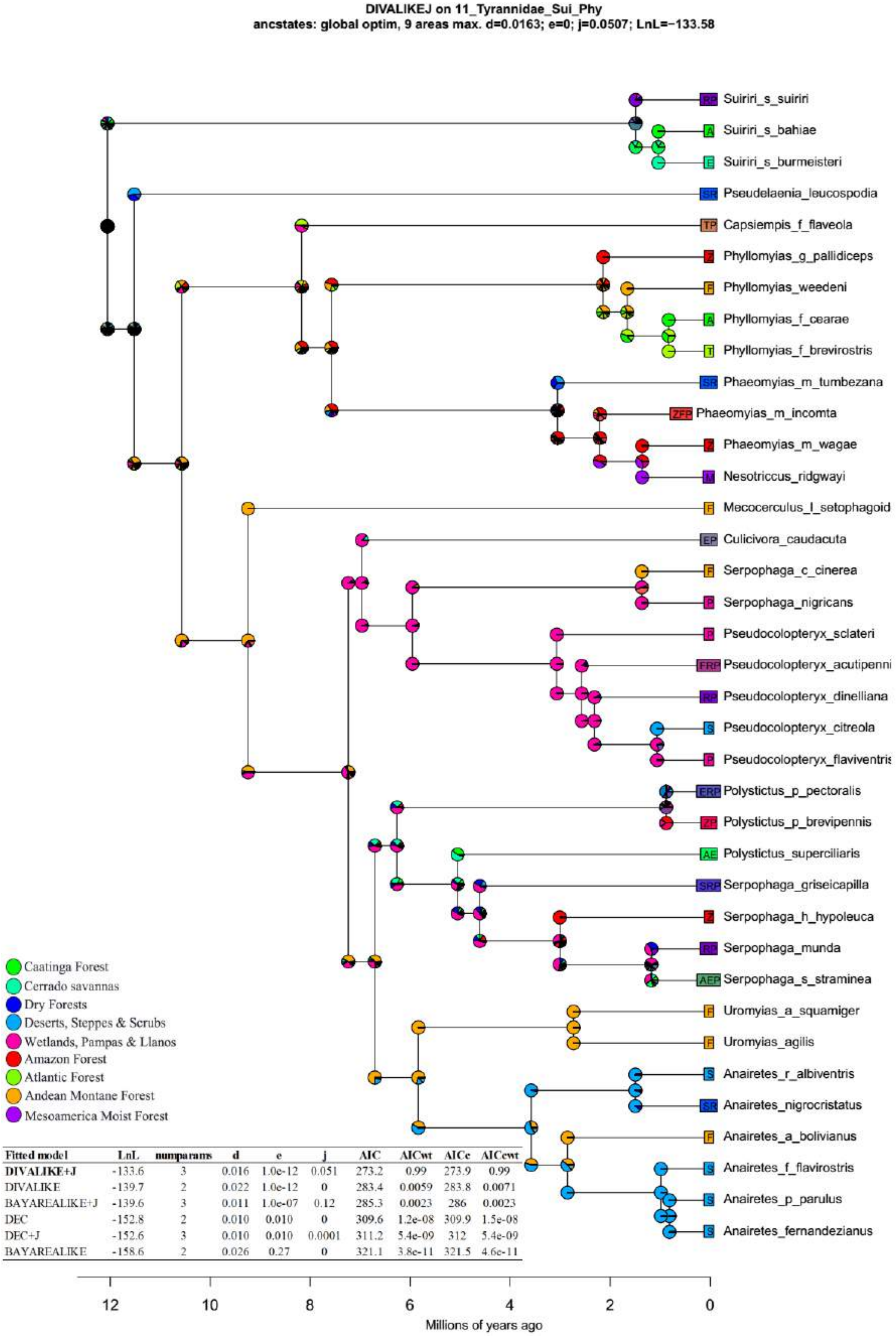
Fitted model	LnL	numparams	d	e	j	AIC	AICwt	AICc	AICcwt
DIVALIKE+J	-89.58	3	0.0051	1.0e-12	0.055	185.2	0.64	185.9	0.64
DEC+J	-90.17	3	0.0039	1.0e-12	0.062	186.3	0.36	187	0.36
BAYAREALIKE+J	-94.78	3	0.0040	1.0e-07	0.069	195.6	0.0035	196.2	0.0035
DIVALIKE	-109.3	2	0.019	0.011	0	222.7	4.6e-09	223	5.4e-09
DEC	-112.9	2	0.016	0.040	0	229.7	1.4e-10	230	1.6e-10
BAYAREALIKE	-123.6	2	0.018	0.30	0	251.3	2.8e-15	251.6	3.3e-15



Fitted model	LnL	numparams	d	e	j	AIC	AICwt	AICc	AICcwt
BAYAREALIKE+J	-39.14	3	0.0019	0.053	0.026	84.28	0.99	86	0.98
DEC+J	-44.02	3	0.014	1.0e-12	0.012	94.04	0.0075	95.76	0.0075
DEC	-45.66	2	0.017	1.0e-12	0	95.32	0.0039	96.12	0.0062
DIVALIKE+J	-44.95	3	0.020	1.0e-12	0.011	95.91	0.0029	97.62	0.0029
DIVALIKE	-49.31	2	0.010	0.010	0	102.6	0.0001	103.4	0.0002
BAYAREALIKE	-50.5	2	0.0081	0.25	0	105	3.1e-05	105.8	4.9e-05



Fitted model	LnL	numparams	d	e	j	AIC	AICwt	AICc	AICcwt
DEC+J	-88.8	3	0.0063	1.0e-12	0.038	183.6	0.68	184.4	184.4
DIVALIKE+J	-89.55	3	0.0081	1.0e-12	0.032	185.1	0.32	185.9	185.9
BAYAREALIKE+J	-94.29	3	0.0054	1.0e-07	0.055	194.6	0.0028	195.4	195.4
DEC	-97.01	2	0.0092	1.0e-12	0	198.0	0.0005	198.4	198.4
DIVALIKE	-98.35	2	0.013	1.0e-12	0	200.7	0.0001	201.1	201.1
BAYAREALIKE	-113.1	2	0.011	0.17	0	230.2	5.0e-11	230.6	230.6



DIVALIKEJ on 11_Tyrannidae_Sui_Phy
ancstates: global optim, 9 areas max. d=0.0163; e=0; j=0.0507; LnL=−133.58

Fitted model	LnL	numparams	d	e	j	AIC	AICwt	AICc	AICcwt
DIVALIKE+J	-133.6	3	0.016	1.0e-12	0.051	273.2	0.99	273.9	0.99
DIVALIKE	-139.7	2	0.022	1.0e-12	0	283.4	0.0059	283.8	0.0071
BAYAREALIKE+J	-139.6	3	0.011	1.0e-07	0.12	285.3	0.0023	286	0.0023
DEC	-152.8	2	0.010	0.010	0	309.6	1.2e-08	309.9	1.5e-08
DEC+J	-152.6	3	0.010	0.010	0.0001	311.2	5.4e-09	312	5.4e-09
BAYAREALIKE	-158.6	2	0.026	0.27	0	321.1	3.8e-11	321.5	4.6e-11
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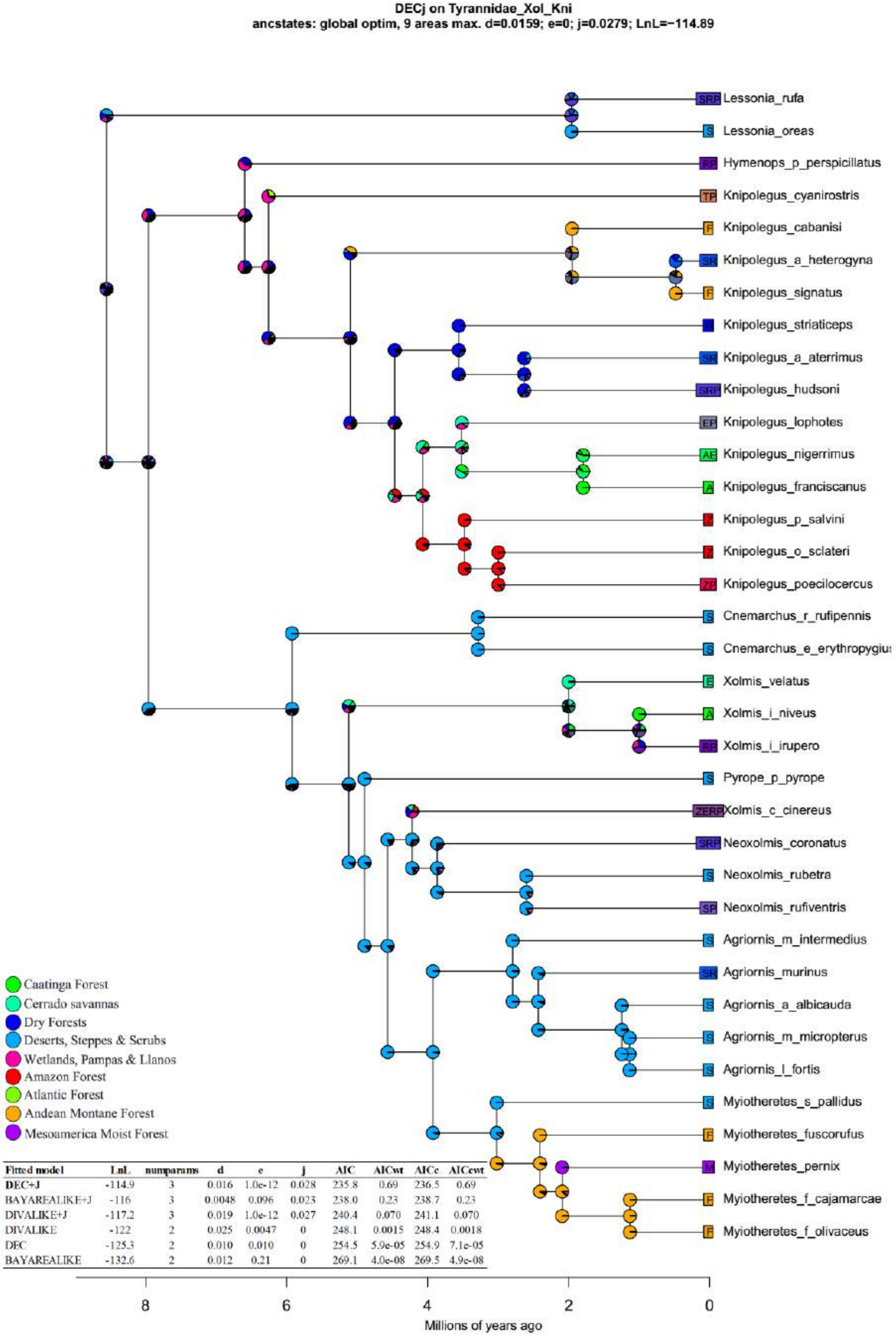


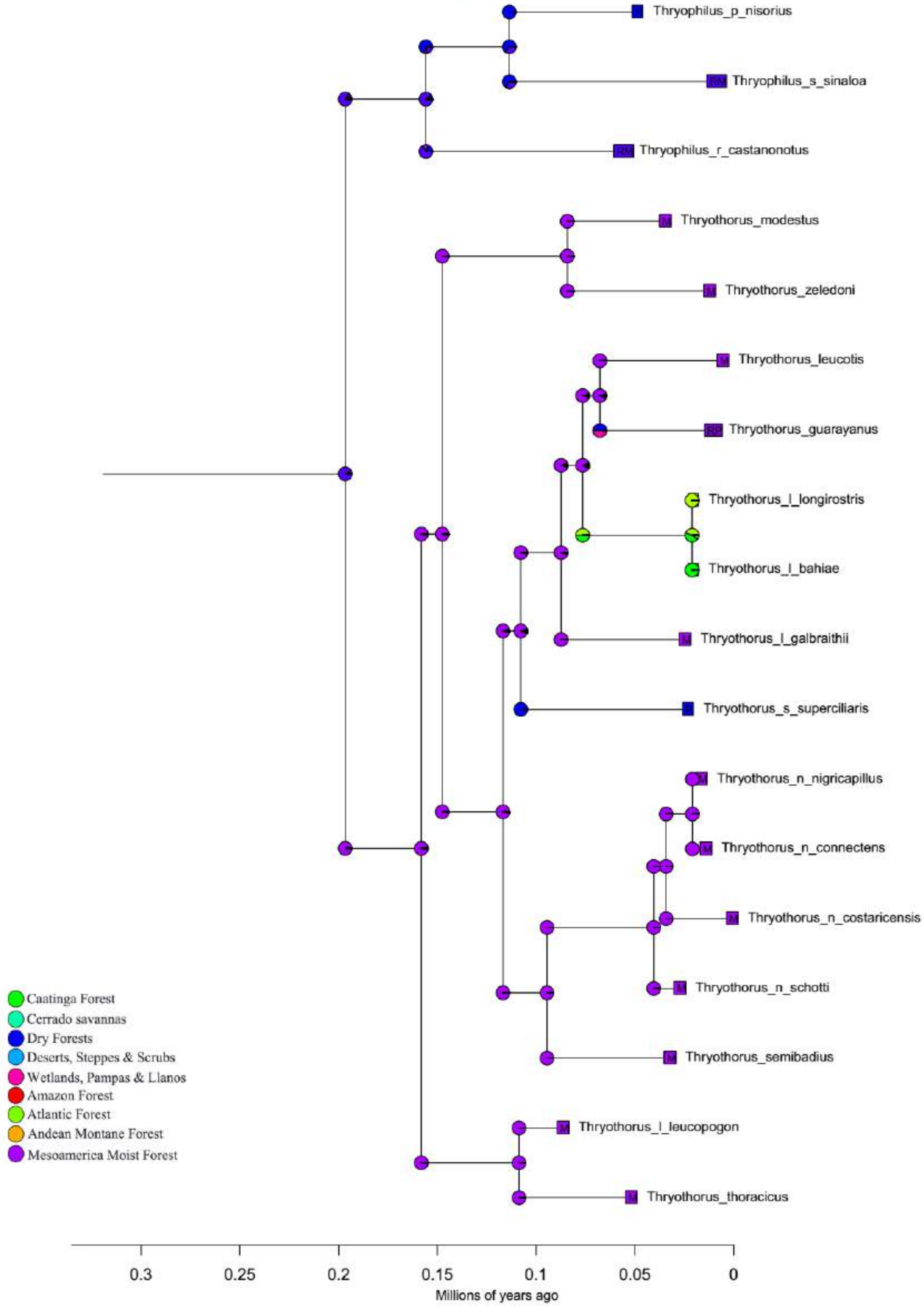
DECj on Tyrannidae_Xol_Kni

ancstates: global optim, 9 areas max. d=0.0159; e=0; j=0.0279; LnL=-114.89

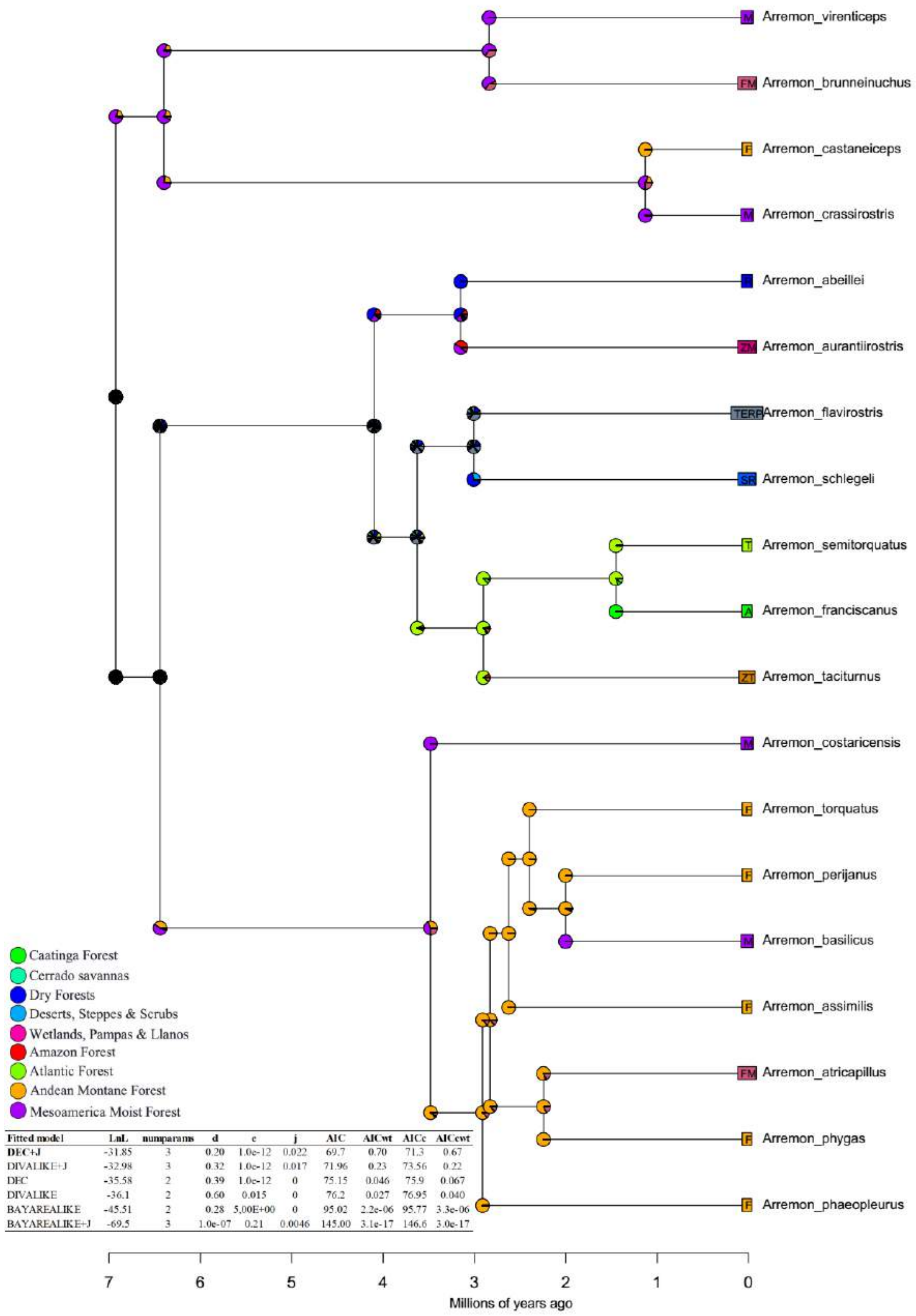
Fitted model	LnL	numparams	d	e	j	AIC	AICwt	AICc	AICcwt
DEC+J	-114.9	3	0.016	1.0e-12	0.028	235.8	0.69	236.5	0.69
BAYAREALIKE+J	-116	3	0.0048	0.096	0.023	238.0	0.23	238.7	0.23
DIVALIKE+J	-117.2	3	0.019	1.0e-12	0.027	240.4	0.070	241.1	0.070
DIVALIKE	-122	2	0.025	0.0047	0	248.1	0.0015	248.4	0.0018
DEC	-125.3	2	0.010	0.010	0	254.5	5.9e-05	254.9	7.1e-05
BAYAREALIKE	-132.6	2	0.012	0.21	0	269.1	4.0e-08	269.5	4.9e-08

DECJ on 12_Troglodytidae_Canto
ancstates: global optim, 9 areas max. d=0.195; e=0; j=0.022; LnL=−31.85

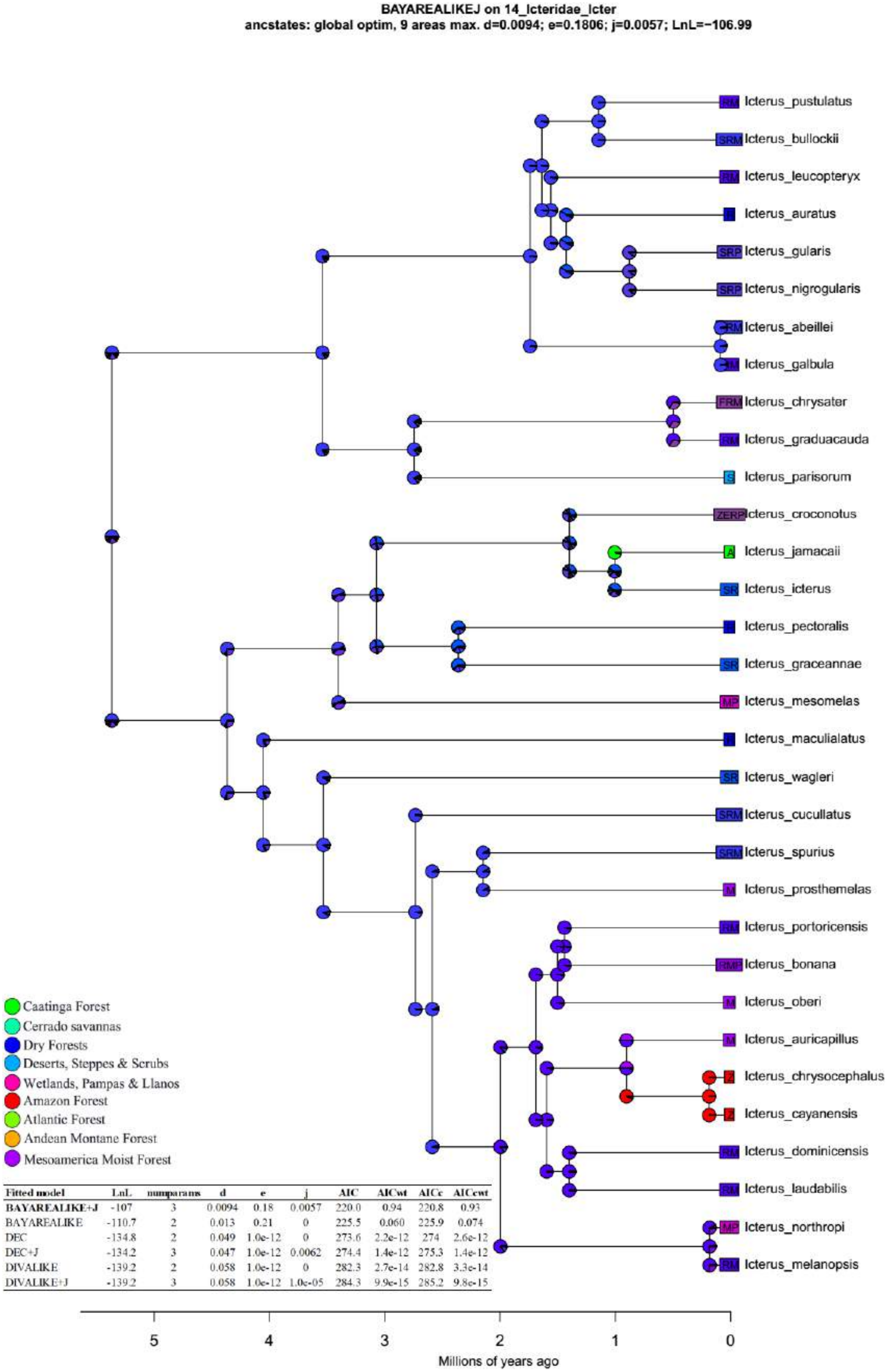
Fitted model	LnL	numparams	d	e	j	AIC	AICwt	AICc	AICcwt
DEC+J	-31.85	3	0.20	1.0e-12	0.022	69.7	0.53	71.41	0.52
BAYAREALIKE+J	-32.66	3	0.092	1.22	0.020	71.32	0.24	73.04	0.23
DIVALIKE+J	-32.98	3	0.32	1.0e-12	0.017	71.96	0.17	73.67	0.17
DEC	-35.58	2	0.39	1.0e-12	0	75.15	0.035	75.95	0.053
DIVALIKE	-36.1	2	0.60	0.015	0	76.2	0.021	77	0.032
BAYAREALIKE	-45.51	2	0.28	5	0	95.02	1.7e-06	95.82	2.6e-06



DECJ on 13_Passerelidae_Arrem
ancstates: global optim, 9 areas max. d=0.0112; e=0; j=0.041; LnL=−55.54



Fitted model	LnL	numparams	d	e	j	AIC	AICwt	AICc	AICcwt
DEC+J	-31.85	3	0.20	1.0e-12	0.022	69.7	0.70	71.3	0.67
DIVALIKE+J	-32.98	3	0.32	1.0e-12	0.017	71.96	0.23	73.56	0.22
DEC	-35.58	2	0.39	1.0e-12	0	75.15	0.046	75.9	0.067
DIVALIKE	-36.1	2	0.60	0.015	0	76.2	0.027	76.95	0.040
BAYAREALIKE	-45.51	2	0.28	5,00E+00	0	95.02	2.2e-06	95.77	3.3e-06
BAYAREALIKE+J	-69.5	3	1.0e-07	0.21	0.0046	145.00	3.1e-17	146.6	3.0e-17

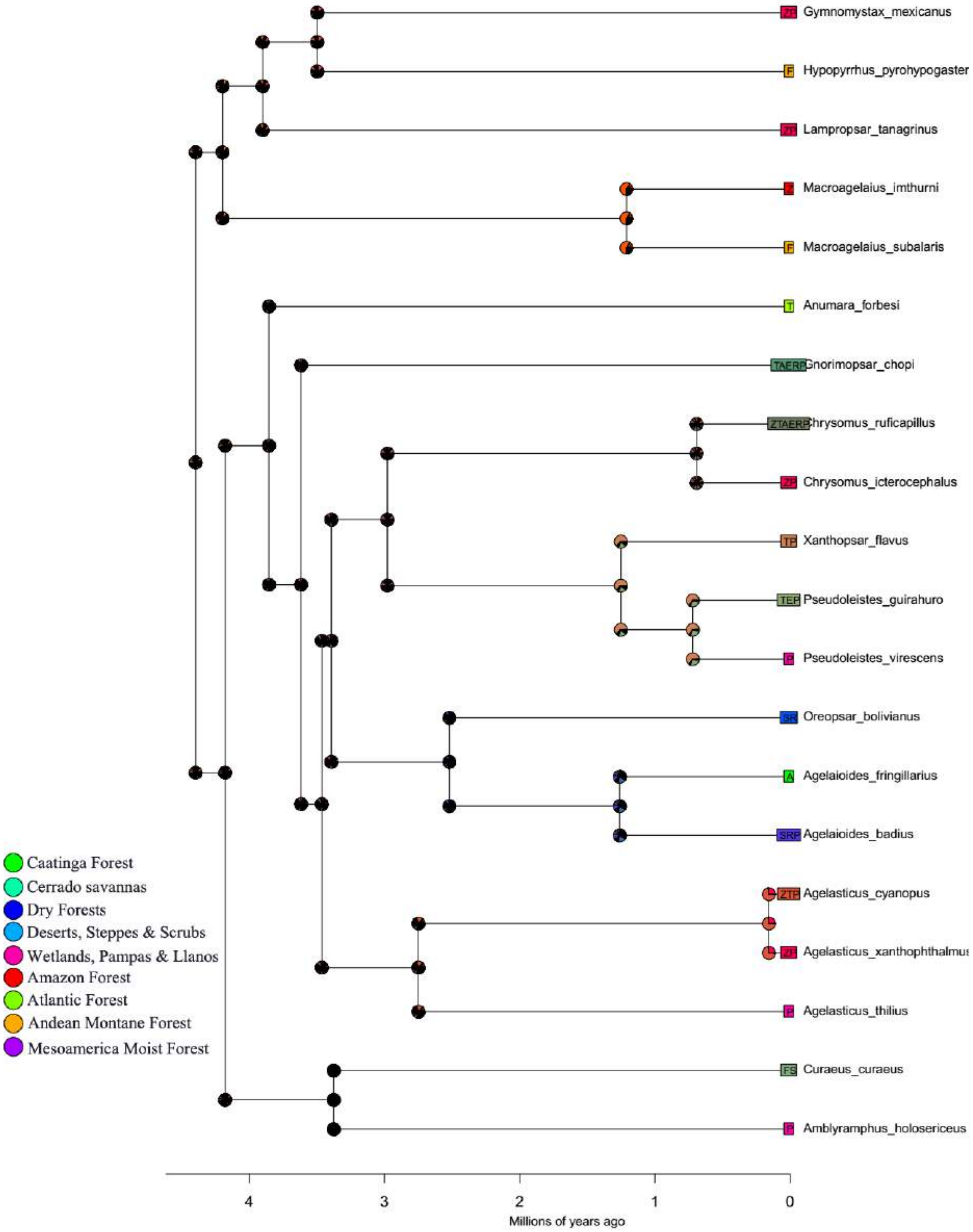


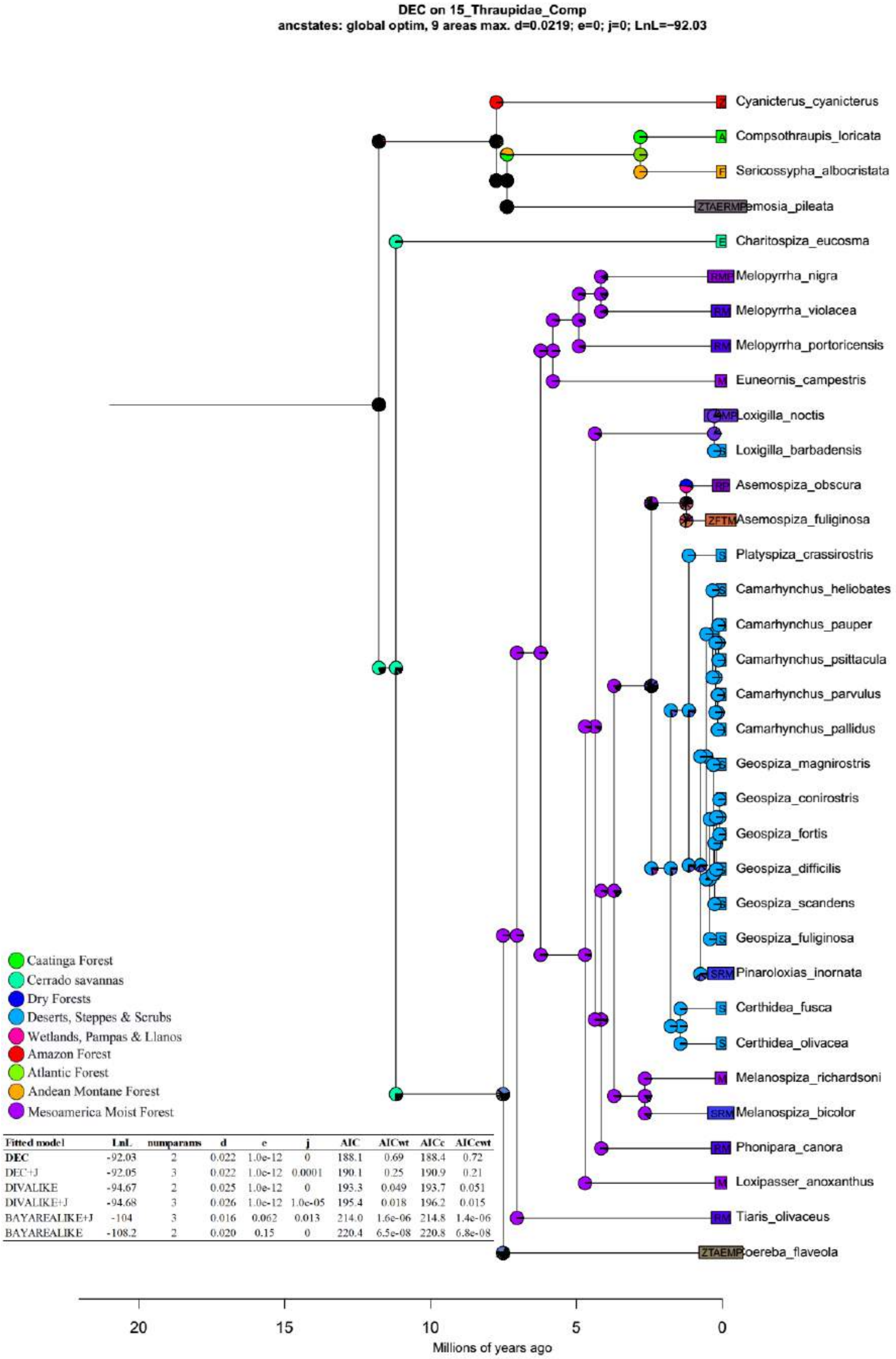
BAYAREALIKEJ on 14_Icteridae_Icter
ancstates: global optim, 9 areas max. d=0.0094; e=0.1806; j=0.0057; LnL=−106.99

Fitted model	**LnL**	**numparams**	**d**	**e**	**j**	**AIC**	**AICwt**	**AICc**	**AICcwt**
BAYAREALIKE+J	-107	3	0.0094	0.18	0.0057	220.0	0.94	220.8	0.93
BAYAREALIKE	-110.7	2	0.013	0.21	0	225.5	0.060	225.9	0.074
DEC	-134.8	2	0.049	1.0e-12	0	273.6	2.2e-12	274	2.6e-12
DEC+J	-134.2	3	0.047	1.0e-12	0.0062	274.4	1.4e-12	275.3	1.4e-12
DIVALIKE	-139.2	2	0.058	1.0e-12	0	282.3	2.7e-14	282.8	3.3e-14
DIVALIKE+J	-139.2	3	0.058	1.0e-12	1.0e-05	284.3	9.9e-15	285.2	9.8e-15

BAYAREALIKE on 14_Icteridae_Agela
ancstates: global optim, 9 areas max. d=0.0254; e=0.3515; j=0; LnL=−88.36

Fitted model	LnL	numparams	d	e	j	AIC	AICwt	AICc	AICcwt
BAYAREALIKE	-88.36	2	0.025	0.35	0	180.7	0.67	181.4	0.75
BAYAREALIKE+J	-88.06	3	0.021	0.31	0.0065	182.1	0.33	183.6	0.25
DIVALIKE+J	-95.58	3	0.045	1.0e-12	0.027	197.2	0.0002	198.7	0.0001
DEC	-109.4	2	0.010	0.010	0	222.8	5.0e-10	223.5	5.6e-10
DEC+J	-109.3	3	0.010	0.010	0.0001	224.5	2.1e-10	226	1.5e-10
DIVALIKE	-119.4	2	0.010	0.010	0	242.8	2.2e-14	243.5	2.5e-14





Fitted model	LnL	numparams	d	e	j	AIC	AICwt	AICc	AICcwt
DEC	-92.03	2	0.022	1.0e-12	0	188.1	0.69	188.4	0.72
DEC+J	-92.05	3	0.022	1.0e-12	0.0001	190.1	0.25	190.9	0.21
DIVALIKE	-94.67	2	0.025	1.0e-12	0	193.3	0.049	193.7	0.051
DIVALIKE+J	-94.68	3	0.026	1.0e-12	1.0e-05	195.4	0.018	196.2	0.015
BAYAREALIKE+J	-104	3	0.016	0.062	0.013	214.0	1.6e-06	214.8	1.4e-06
BAYAREALIKE	-108.2	2	0.020	0.15	0	220.4	6.5e-08	220.8	6.8e-08

Fitted model	LnL	numparams	d	e	j	AIC	AICwt	AICc	AICcwt
BAYAREALIKE+J	-63	3	0.0044	0.10	0.045	132.0	0.69	133.8	0.65
DEC+J	-64.11	3	0.012	1.0e-12	0.086	134.2	0.22	136.1	0.21
BAYAREALIKE	-66.07	2	0.013	0.22	0	136.1	0.086	137	0.13
DIVALIKE	-70.01	2	0.010	0.010	0	144.0	0.0017	144.9	0.0026
DEC	-70.18	2	0.010	0.010	0	144.4	0.0014	145.2	0.0022
DIVALIKE+J	-69.97	3	0.010	0.010	0.0001	145.9	0.0006	147.8	0.0006

CONSIDERAÇÕES FINAIS

Nesta tese, os resultados apresentados nos quatro diferentes capítulos se unem ao descrever e elucidar os diferentes padrões e mecanismos históricos e evolutivos envolvidos na atual configuração da distribuição e diversidade de espécies de aves que habitam os domínios de vegetação aberta/seca da América do Sul. Apresento aqui, evidências que corroboram as hipóteses discutidas em estudos anteriores e trago novas informações que servem de base para monitoramento futuros, em um cenário de mudanças climáticas que poderá afetar diretamente as espécies que habitam esses domínios de vegetação aberta/seca.

Nos capítulos 1 e 2, destaquei os fatores recentes que agem na estruturação das comunidades de aves e as relações biogeográficas entre os domínios fitogeográficos que compõem a Diagonal Seca Sul-Americana (SAAD). No primeiro capítulo, elucidei que a avifauna do carrasco, corresponde a uma parcela da avifauna da Caatinga, não possuindo relação significativa com a avifauna presente no Cerrado. No segundo capítulo, demonstrei que apesar do alto número de espécies compartilhadas entre os domínios que compõem a SADD, existem três diferentes unidades em termos de avifauna. O *turnover*, se apresentou como o principal componente da β-diversidade atuando nas comunidades ao longo da SADD, estando associado principalmente com a distância geográfica entre os pontos amostrados e sob influência de variáveis ambientais como temperatura, precipitação, aridez e altitude. Isso sugere uma provável mudança nos padrões de distribuição das espécies em um cenário de futuras mudanças climáticas, e emite um alerta para o desenvolvimento de estratégias de conservação voltadas a esses domínios.

Nos capítulos 3 e 4, destaquei os fatores e mecanismos históricos que agiram na diversificação das espécies que habitam os domínios de vegetação aberta/seca da América do Sul. No terceiro capítulo, apresentei o primeiro estudo filogeográfico da espécie *Hemitriccus margaritaceiventer*, demonstrando a existência de dois grupos genéticos principais separando as subespécies, circundando o atual gradiente úmido formado pela Amazônia, corroborando a hipótese dos Arcos Pleistocênicos. Também evidenciei a provável história evolutiva do Clado *Hemitriccus* associada a habitats de florestas úmidas como a Floresta Amazônica. No quarto capítulo, apontei a importância dos eventos de vicariância e dispersão na origem dos táxons endêmicos da Caatinga. Além disso, apontei as florestas secas neotropicais como principal fonte de espécies para a Caatinga, e a influência de eventos climáticos históricos na dispersão/diversificação das aves endêmicas da Caatinga.

De forma geral, essa tese preenche importantes lacunas no conhecimento não só corroborando estudos prévios que indicavam a influência de eventos climáticos históricos na diversificação das espécies na América do sul, como também investigando como características ambientais atuais podem estruturar as comunidades e podem ser usadas em estudos futuros, como indicadores de como essas comunidades se comportarão em um cenário de mudanças climáticas futuras.

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Apêndice A

Capítulo I.

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Lima, H. S.; Las-Casas F. M.; Ribeiro, J.; Girão, W.; Mariz, D.; Naka, L. N.
Avifauna and biogeographical affinities of a *Carrasco*-dominated landscape in northeastern Brazil: providing baseline data for future monitoring
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Avifauna and biogeographical affinities of a *carrasco*-dominated landscape in north-eastern Brazil: providing baseline data for future monitoring

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Summary

The *carrasco* is a dense, shrubby vegetation type that covers the higher parts of table-top mountains in north-eastern Brazil. The vegetation of this phytophysiognomy is often considered to have biogeographical and ecological affinities with the *cerrado* of Central Brazil, but the biogeographical affinities of its avifauna remain unclear. In recent years, deforestation due to local economic activities has been particularly severe in some *carrasco*-dominated landscapes. In 2013, we initiated avian surveys at the Fazenda Pau D'Arco, a privately owned property located on top of the Araripe Plateau, to evaluate the effects of a legal forest management program on the avifauna. Here, we present the results of four years of avian inventories to: i) characterize a well-preserved patch of *carrasco* vegetation; ii) assess avian biogeographical affinities of this vegetation type; iii) identify associations between managed/unmanaged areas and bird species; and iv) provide baseline data for future avian monitoring studies. Using different survey methods, we provide a list of 148 bird species, including several dry-forest specialists and *caatinga* endemics. Biogeographically, the avifauna of the *carrasco* represents a subsample of the *Caatinga* dry forest, lacking *cerrado* elements. Forest management significantly affected the distribution of several bird species in the study area. We found that 1/5 of the species (24) recorded during our standardized surveys were significantly associated with either unmanaged (14 species) or managed (10 species) areas. Species such as the Ceará Leaftosser *Sclerurus cearensis*, a globally vulnerable species, have only been detected in non-managed areas and therefore can be negatively affected by the management program. We also present data on 16 avian taxa with ecological and conservation concerns. By presenting a fairly complete and documented list of the avifauna, we characterize the *carrasco* avifauna and offer the tools to evaluate the effects of forest management on this poorly known vegetation type.

Keywords: logging, *Caatinga*, Brazilian dry forest, forest management

Introduction

The semiarid interior of north-eastern Brazil represents the largest and most biologically diverse block of seasonally dry tropical forest in the Neotropics (Pennington *et al.* 2009) and is a known area of avian endemism (Cracraft 1985, Haffer 1985). Part of this diversity is likely due to the *caatinga*'s vegetation heterogeneity, which represents a mosaic of different habitats, associated with varying degrees of topographic and edaphoclimatic conditions (Vasconcelos *et al.* 2010, Queiroz *et al.* 2017). Within the *caatinga*, there are several different phytophysiognomies, ranging from open and shrubby woodlands to ecologically more complex arboreal dry forests, and enclaves of wet forests (Giulietti *et al.* 2004, Queiroz *et al.* 2017).

While many of the *caatinga* avian endemics are restricted to the typical open shrubby woodlands found on the lowlands (<500 m above sea level), other endemics and dry forest specialists seem to favour denser forests, often present in higher plateaus (>600 m asl) and table-top mountains (known in Brazil as *chapadas*). On top of some of these plateaus, vegetation differs from that of the surrounding lowlands, including rocky outcrops (*campos rupestres*) and carrasco vegetation (Araújo *et al.* 1998, Alves and Kolbek 2010).

The *carrasco*, also known as sedimentary forest, is a dense shrubby vegetation type, with a xerophilous flora that grows on top of quartz sandy soils, generally between 700 and 900 m above sea level (Araújo *et al.* 1999). *Carrascos* are mostly found on the Ibiapaba and Araripe plateaus in the Brazilian semiarid region, although isolated patches are also present as far south as northern Minas Gerais (Araújo *et al.* 1999, Vasconcelos *et al.* 2010) (Figure 1). Despite being in the heart of the *caatinga* realm, this vegetation type has biogeographical and ecological affinities with both the

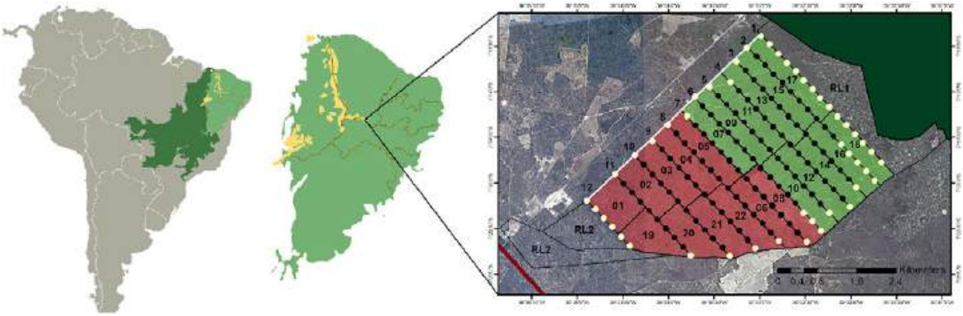

Figure 1. Map of South America, highlighting the *caatinga* Dry Forest (light green), the *cerrado* (dark green), and the distribution of the *carrasco* vegetation (in yellow); adapted from Araújo (1998). In detail, the Fazenda Pau D'Arco, with the 162 sampling points where we conducted point counts (all dots) and the 115 sampling points where we conducted mobbing experiments (black dots). The white line represents the main dirt road that gives access to the entire area, numbered lines (1 to 12) represent secondary roads that give access to the management plots. Red plots represent areas that had already been managed by the time of the beginning of our study (2014), whereas green plots represent unmanaged areas. RL1 and RL2 represent unmanaged control areas (*Reserve Legal*).

cerrado of central Brazil and the *caatinga* dry forests (Figueiredo 1986). These biogeographic affinities, however, remain poorly understood, particularly for animals (Araújo *et al.* 1999, Vasconcelos *et al.* 2010).

Worryingly, these thick patches of forest are under threat; anthropogenic disturbance includes extraction of wood for fuel, habitat conversion for crops, and grazing by goats (Chaves and Barros 2008). Some *carrascos*, such as those located on top of the Araripe Plateau are deforested due to local economic activities, such as gypsum mining and firewood gathering to feed industrial ovens. These kinds of anthropogenic disturbances are common in tropical dry forests and often lead to severe soil impoverishment and degradation (Shahabuddin and Kumar 2006, Venter *et al.* 2016). Such disturbances can cause local extinctions, changes in species composition, and alterations in important ecological processes and ecosystem services, such as pollination and seed dispersion, which in turn, may compromise the sustainability of native forests (Wiens 1994, Castelletti *et al.* 2003, Sekercioglu 2006).

The dense woodlands of the *carrascos* are also feeding the wood market as part of legal management logging programmes, allowed under Brazilian law. One such area is located at the Fazenda Pau D´Arco, a privately owned 2,125 ha property located on top of the Araripe Plateau, in the Brazilian state of Ceará. This area has been managed since 2001, with nearly 5% of the property logged every year and left to regrow for a new cutting cycle of 25 years. In 2013, we initiated avian surveys to evaluate the effects of this legal forest management programme on the avifauna. According to the management programme provided by the owners, by the end of our fieldwork, a total of 1,150 ha had already been logged, and another 520 ha are planned to be logged by 2026, when a new cutting cycle will be initiated. Due to the management programme, a network of dirt roads has been created in the area, resulting in ~40 km of roads, which offer access to an otherwise almost impenetrably dense thorny forest. From the original forest cover, nearly half of the area remains in a natural condition, offering a unique opportunity to sample its avifauna. Despite the longstanding interest in the effects of deforestation and forest fragmentation on tropical rainforest avian communities (Stouffer 2020), little attention has been given to evaluate the effects of anthropogenic changes in tropical dry forests (Shahabuddin and Kumar 2006).

In this article, our main goals are two-fold. First, we aim to describe in detail the avifauna of a well-preserved patch of *carrasco* dry forest, allowing us to better understand the ecological and biogeographical affinities of its avifauna. Second, we provide avian baseline data that will be useful to understand the effects of management on a forest that is currently being managed and will be almost completely converted into a secondary forest by 2026. To assess the biogeographical affinities of its avifauna, we provide a regional comparison of the *carrasco* avifauna, in relation to several areas of *caatinga* and *cerrado* along the South American Dry Diagonal. The avian baseline data provided is the result of a variety of sampling methods, resulting in what we believe is a fairly complete and well-documented inventory of its avifauna. We present abundance estimates based on quantitative surveys and use an indicator species analysis to evaluate associations between species and forest management. Finally, we provide details on the presence of 16 bird species that are either dry forest specialists, *caatinga* endemics, and/or threatened taxa. For these species, we include detailed maps of their presence in the study area. This represents the first avian inventory of an area exclusively dominated by *carrasco* vegetation that is also subject to a long-term forest management program and aims to provide the necessary grounds to establish a long-term species monitoring programme.

Methods

Study area

This study was conducted at the Fazenda Pau D´Arco (7°18′S, 39°33′W), located on top of the Araripe Plateau, in the municipality of Crato, in the Brazilian state of Ceará (Figure 1). The entire area of the Fazenda is covered by *carrasco* vegetation. Its north-eastern boundary is the Araripe-Apodi National Forest (FLONA Araripe-Apodi), which has a taller forest with a more open understorey locally known as *cerradão* and harbours a quite different set of bird species. The Fazenda Pau D´Arco covers 2,125 ha, 1,670 of which are part of a management programme aiming to provide charcoal and feed local industrial ovens. According to the management programme provided by the owners, nearly 425 ha were set aside as protected areas (*Reserva Legal*), which should go untouched under the management scheme proposed. Until 2017, when we conducted our last fieldwork in the area, a total of 1,240 ha had already been managed, and 90% of the area (excluding the *Reserva Legal*) will be logged by 2026. The region has a semiarid and hot tropical climate (mean annual temperature between 24 and 26° C), with a mean annual rainfall of ~1,090 mm, concentrated between January and May, with a peak in March (IPECE 2012).

Fieldwork and sampling of the avifauna

We conducted avian surveys at the Fazenda Pau D´Arco between 2013 and 2017 using multiple complementary methods, including: i) systematic surveys (point counts); ii) mobbing experiments; iii) mist-netting, and iv) opportunistic observations (Appendix 1). While opportunistic observations were conducted mostly along the main road and surroundings, point counts and mobbing experiments were conducted along secondary roads, covering the entire area (Figure 1).

We first visited the area in August 2013, when we made opportunistic observations and deployed mist-nets during field courses of the Federal University of Pernambuco (UFPE). In 2014, we initiated quantitative surveys, when we conducted a total of 295 5-min point counts at 162 points, systematically distributed every 250 m along the 12 parallel roads that cross the entire extension of the study area (black and white dots in Figure 1). Point counts started before sunrise (~05h00) and lasted till mid-morning (~ 09h00). A subset of these sampling sites (115 white dots in Figure 1) was surveyed through mobbing experiments. For the mobbing experiments, we excluded sites at the edges of each transect to avoid confounding variables, such as proximity to the main road. Mobbing experiments consisted of broadcasting the call of the Ferruginous Pygmy-Owl *Glaucidium brasilianum* for 5 mins to disclose the presence of birds in the thick vegetation (see Lima *et al.* 2018 for further details on this methodology). Each point was subject to these experiments twice (early morning and late afternoon) on different days.

Whenever possible, we documented our observations with photographs and audio recordings, and also collected a limited number of bird specimens to provide a reference collection of the study area. All specimens, collected under SISBIO license no. 36496, were captured using mist-nets, and are currently held at the UFPE Bird Collection (Appendix S1 in the online supplementary material). Voucher samples are now part of the permanent collection that aims to characterize and preserve morphological and genetic diversity in the Brazilian north-east, following the general guidelines extensively discussed by Collar (2000). Given that this area is often visited by birdwatchers, we also included documented material obtained by other people and available in public databases, such as Wikiaves (www.wikiaves.com.br) and eBird (https://ebird.org/), for audio recordings and photographs. Taxonomy and nomenclature follow the Brazilian Committee of Ornithological Records (Piacentini *et al.* 2015), and its forthcoming update (CBRO in prep). Endemism was classified based on Pacheco (2004) and Billerman *et al.* (2020), and threatened status according to Brazilian (MMA 2018, Machado *et al.* 2018) and global (IUCN 2020) Red Lists. The specific effects of forest management on species density and abundance and on avian species composition are being presented elsewhere (Ribeiro *et al.* in press a and b).

Carrasco avifauna affinities

In order to evaluate the biogeographical affinities of the avifauna of the Fazenda Pau D’Arco, in comparison with other dry forests in the Brazilian northeast and *cerrado* sites from central Brazil, we compiled bird species lists from 18 protected areas along the South American Dry Diagonal,

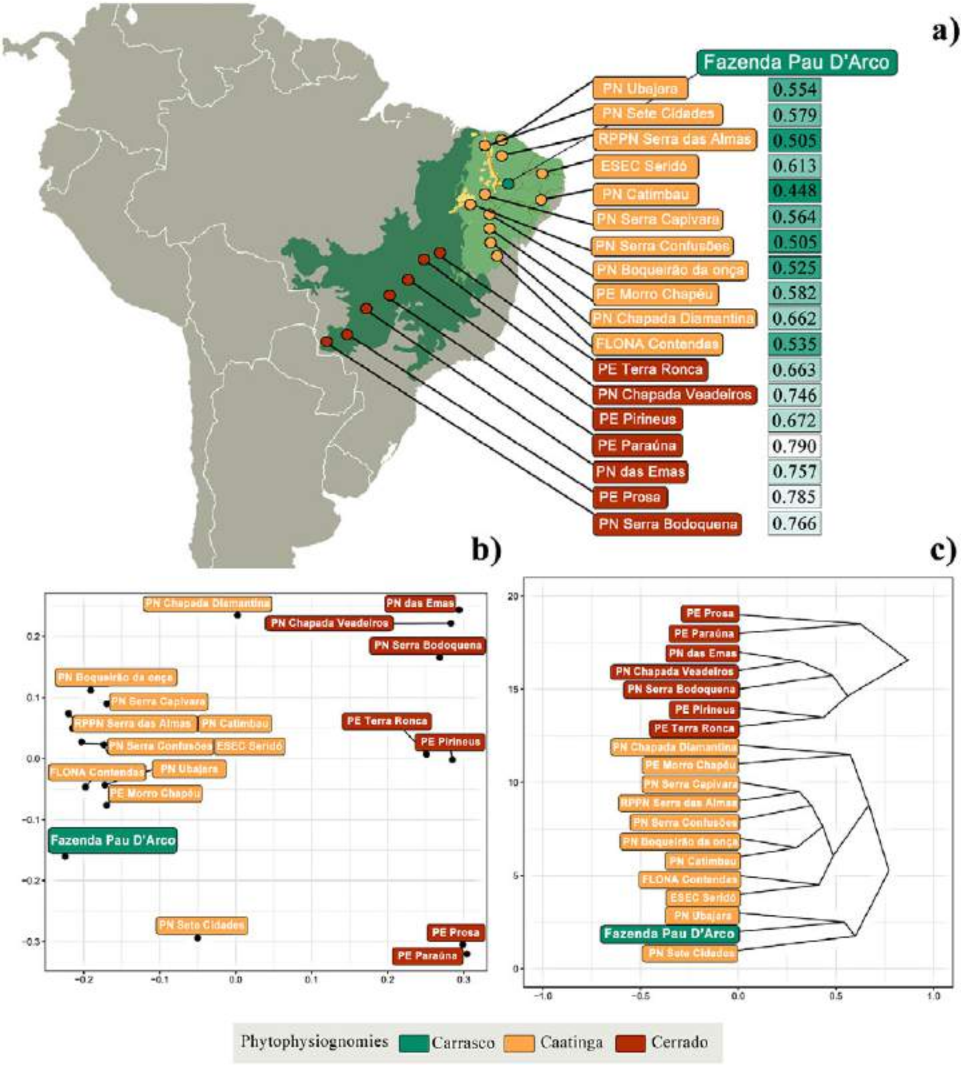

Figure 2. (a) Map of geographic localities selected to compare species similarity between and within biomes, (b) Multidimensional scaling, and (c) Cluster analysis showing the avian similarity between the Fazenda Pau D'Arco and 11 *caatinga* and seven *cerrado* localities. We indicate Jaccard's index values next to the localities' names (a). Dark green values represent more similar and light green values more dissimilar areas, in relation to *carrasco* avifauna.

including 11 *caatinga* and seven *cerrado* sites (Figure 2). We searched for published articles and complemented these from bird lists available in online databases, such as Wikiaves (www.wikiaves.com.br) and Ebird (ebird.org) (Table S1). For lists published in online databases, we double-checked the consistency of each record, ensuring its plausibility and preferably choosing lists that accurately discriminated its exact location. With this information, we generated a presence/absence matrix of species occurrence, which included a total of 677 bird species present in the *carrasco*, *caatinga*, and *cerrado* locations (Figure 2, Table S1). We then compared the bird species recorded at the Fazenda Pau D'Arco to evaluate biogeographical avian affinities. We used Jaccard's index

(Sneath 1957) to create a similarity matrix to compare sites. This index ranges from 0 to 1; values close to 0 indicate high composition similarity and values close to 1 indicate different communities. We then performed a hierarchical cluster analysis and a non-metric multidimensional scaling (NMDS) (Gower 1966) to visualize similarities. We also applied a permutational analysis of variance (PERMANOVA) (Anderson 2001) to verify the robustness of the groups formed. Although there are obvious sampling differences among sites, we believe that if biogeographical affinities are strong enough, they should be less influenced by sampling methods.

To detect a potential effect of isolation by distance, we calculated the correlations between geographic distance and bird species dissimilarity using Mantel tests (Smouse *et al.* 1986). For this, we used the geographic coordinates of each location and Jaccard's index as a response variable. We compared the effect of the geographic distance in the similarity of species between all locations and between *carrasco* and *caatinga* localities. All analyses were performed in the software R 4.0.1 (R Core Team 2020).

Management and bird species associations

We used all our standardized data (point counts and mobbing experiments) in both managed and unmanaged areas, to perform an Indicator Species Analysis (ISA) (Dufrêne and Legendre 1997) to identify those species that appear to have a tight relationship to habitat condition (managed or unmanaged). ISA can be used to objectively identify those species that present higher fidelity to one kind of habitat over another. This analysis generates values between 0 and 1, where 1 indicates complete fidelity to one of the groups and presence in every site in that given group. Statistical significance was obtained by conducting 9999 permutations. ISA was conducted using the multipart function of the *indicspecies* package in R (Cáceres and Legendre 2009). For this specific analysis, we used only 141 sampling points, 84 of them in unmanaged areas, and 57 in managed areas, excluding surveys conducted along trail 7 and half of trail 6, which had managed areas on one side and unmanaged areas on the other side of the trail.

Species accounts

Intending to provide baseline data for future studies, we also include a species accounts section, where we mapped results from point counts and mobbing experiments, for species that fulfill one of the requirements of being: i) globally or nationally threatened; ii) representative of *caatinga* or dry forest specialists (Stotz *et al.* 1996, Araújo and Silva 2017); or, iii) showed significant association with unmanaged areas in the ISA analysis. When appropriate, we included current threatened status at the Brazilian (MMA 2018) and global levels (IUCN 2020). Taxonomy and nomenclature follow the Brazilian Committee of Ornithological Records (Piacentini *et al.* 2015), and its forthcoming update (CBRO in prep).

Results

Avian surveys

A total of 148 species of birds have been recorded at the Fazenda Pau D´Arco, including 144 species recorded by ourselves and four species by other researchers/observers. Our most efficient surveying method was the opportunistic observations, which resulted in the detection of 129 species, including 36 species not detected by any other quantitative or standardized method (Appendix S1). Point counts were also quite effective, resulting in the detection of 108 species, and provided quantitative georeferenced data on individual species. Mobbing experiments also provided georeferenced data of 72 species (Appendix S1). With 44 species captured, mist-nets were an essential method for collecting specimens but did not contribute species solely recorded by this survey method (Appendix S1). We present documented evidence for more than half (95 spp or 64 %) of the species recorded, including 44 species with collected specimens, 59 with audio recordings, and 57 with photographs (Appendix 1). Unfortunately, we lack documented evidence for the Fazenda Pau D'Arco for a relatively large number of species (53), although most of these represent non-controversial records, and most of them are already known from and have been documented at the Araripe Plateau.

Species abundance and seasonality

Our quantitative surveys allowed us to offer a rough characterization of avian abundance at the Fazenda Pau D'Arco, which will be particularly important for future comparisons following the completion of the first management cycle. Only 18 species (12.1%) were fairly abundant, being recorded in more than 20% of our surveys (Appendix S1). On the other hand, 71 species (47.9%) were considered rare and were recorded in less than 1% of our systematic surveys or only recorded through opportunistic observations. Four species (2.7%) were detected and documented by other observers but not by any of our survey methods and were considered occasional (Appendix S1). We acknowledge that these categories are rather subjective, and present continuous abundance values in Appendix S1.

Most species (129 species or 87%) recorded at our study site are likely residents (Appendix S1). However, we recorded at least 19 species that are known to engage in some sort of seasonal movements in the Neotropics, including 18 austral migrants and one longitudinal migrant (Ash-throated Casiornis *Casiornis fuscus*). We recorded 23 Brazilian endemic species at our study site, including eight *caatinga* endemics and seven north-eastern Brazilian endemics (Appendix S1).

Dry forest avian affinities

The avifauna of the Fazenda Pau D´Arco represents a subsample of the *caatinga* avifauna, which is quite clear from our ordination and clustering analyses (Figures 2b and 2c). The avian composition of this *carrasco* site was significantly grouped with other *Caatinga* localities, rather than with *cerrado* localities (PERMANOVA, $R^2=0.26$, $P < 0.01$) (Figure 2b). The avifauna at the Fazenda Pau D'Arco is more similar (measured by Jaccard's Index) to the avifauna recorded in areas such as, the Catimbau National Park (0.448), Serra das Confusões National Park (0.505), and Serra das Almas Private Reserve (0.505), all of which harbour a mix of shrubby and arboreal *caatinga*, including *carrasco* vegetation (Figure 2a). On the other hand, the avifauna of the Fazenda Pau D'Arco is more different from Serra da Bodoquena National Park (0.766), Prosa State Park (0.785), and Paraúna State Park (0.790), areas where *cerrado* is predominant (Figure 2a, Table S1). Avian similarity, however, has a significant spatial autocorrelation (species dissimilarity and geographic distance), when both major biomes (*caatinga* and *cerrado*) are included (Mantel statistic, $r = 0.615$, $P < 0.001$) (Figure S1). When only the *caatinga* localities are included, this spatial correlation is no longer significant (Mantel statistic, $r = 0.174$, $P = 0.120$) (Figure S1), suggesting that other environmental or ecological variables may be important to define species composition.

Forest management and bird species associations

We found that 24 species of birds recorded during our standardized surveys (point counts and mobbing experiments) had significant associations with either unmanaged or managed areas (Table 1). Fourteen species showed significant associations with unmanaged areas, including six that were not recorded in managed areas at all. These numbers suggest that unless these species are able to colonize old-growth forests, they may go locally extinct when the management cycle is over

Table 1. Indicator Species Analysis (ISA) showing species with significant associations with unmanaged and managed areas, including individual records and p values. The total number of areas in our surveys included 84 unmanaged and 57 managed points. IndVal refers to the Indicator Value index measuring the association between a species and a site group.

			Number of records	
Species	IndVal	P-value	Unmanaged areas	Managed areas
Associated with unmanaged forests				
Thamnophilus pelzelni	0.78	0.001	159	24
Cranioleuca semicinerea	0.57	0.001	43	5
Trogon curucui	0.56	0.001	30	0
Cnemotriccus fuscatus	0.53	0.001	38	3
Myiothlypis flaveola	0.52	0.001	27	0
Neopelma pallescens	0.51	0.001	31	2
Tolmomyias flaviventris	0.49	0.012	33	7
Sclerurus cearensis	0.45	0.002	25	0
Leptotila verreauxi	0.44	0.002	19	0
Campylorhamphus trochilirostris	0.42	0.002	20	0
Myiopagis viridicata	0.42	0.006	30	3
Dacnis cayana	0.38	0.022	19	2
Synallaxis scutata	0.38	0.037	18	4
Sittasomus griseicapillus	0.29	0.036	8	0
Associated with managed forests				
Euscarthmus meloryphus	0.80	0.001	16	104
Chlorostilbon lucidus	0.64	0.001	31	51
Todirostrum cinereum	0.61	0.002	27	42
Elaenia chilensis	0.57	0.001	15	44
Thamnophilus capistratus	0.56	0.001	13	37
Phacellodomus rufifrons	0.54	0.001	6	27
Coryphospingus pileatus	0.52	0.005	18	39
Myiophobus fasciatus	0.49	0.001	11	28
Stigmatura napensis	0.42	0.001	0	15
Thamnophilus torquatus	0.27	0.023	0	7

(Table 1). On the other hand, 10 species showed significant associations with managed areas (Table 1), indicating that some of them may actually benefit from forest management.

Species accounts

We include species accounts for 16 avian taxa (species or subspecies), which include species that are most likely to be affected by forest management in the study area and which can be used as proxies to understand the influence of forest management on the avian community. We present species maps for 14 of those species, based on our quantitative censuses and mobbing experiments in the study area (Figure 3). We do not present occurrence maps for the Yellow-legged Tinamou *Crypturellus zabele* and Greater Wagtail-tyrant *Stigmatura budytoides* since neither of them was recorded during our standardized surveys.

Yellow-legged Tinamou *Crypturellus zabele* (NT/VU)

This taxon, recently elevated to full species (*C. zabele*) (Tomotani and Silveira 2016,CBRO, in prep.), is endemic to NE Brazil, and a rare inhabitant of *caatinga* and Atlantic Forests. Although we consider this species as being occasional at the Fazenda Pau D'Arco (Appendix S1), there are several records at this site (W. Girão, pers. obs.). The main threats to this taxon are hunting, trapping, and habitat loss, with population trends decreasing (IUCN 2020).

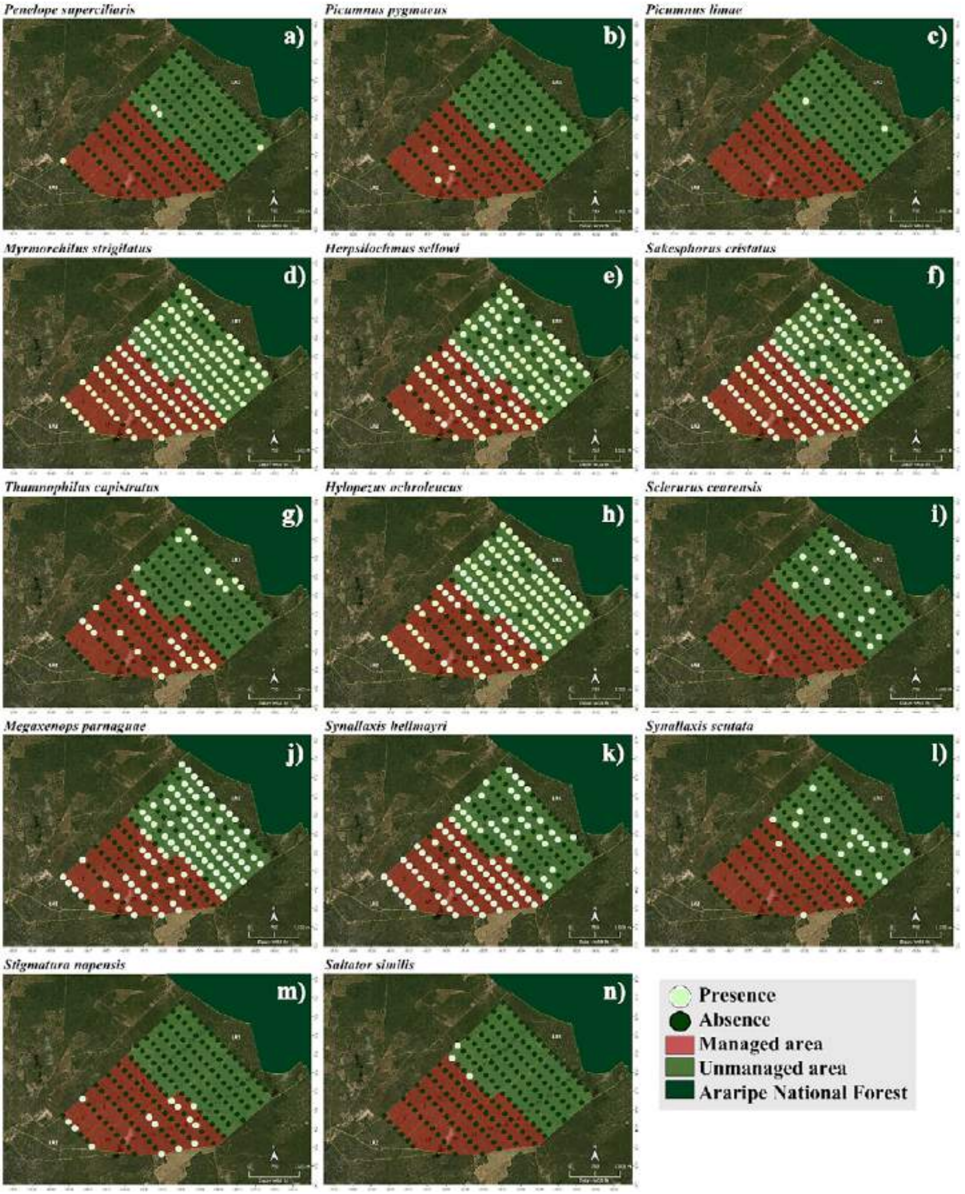

Figure 3. Local distribution maps of selected species at the Fazenda Pau D'Arco. Each point represents a sampling point surveyed by quantitative censuses (point counts) and mobbing experiments. Light green points with a white border represent presence points, whereas dark green points depict the absence of records.

Rusty-margined Guan *Penelope superciliaris*

Although this species is widespread in the Neotropics, several taxa have been described for eastern Brazil and the *caatinga* (del Hoyo and Kirwan 2020), where it is considered the main source of bushmeat for local human populations. Within the *caatinga*, the Rusty-margined Guan inhabits different types of phytophysiognomies, such as dry and gallery forests. This species was uncommon at the Fazenda Pau D'Arco, where we detected its presence in only a few of our surveys (5/162 points) (Figure 3a), mostly in unmanaged areas. One of our records, however, was obtained in an area that had been managed 12 years before our surveys, suggesting that this species may use second-growth forests. Although this species is not currently considered threatened, population trends appear to be negative (IUCN 2020). Being one of the few species at the site that is currently hunted for meat, we believe that the evidence of hunting found at our study site was likely targeting this species.

Spotted Piculet *Picumnus pygmaeus*

This *caatinga* endemic occurs in dry open and dense woodlands (Winkler *et al*. 2020a). The Spotted Piculet was uncommon at the Fazenda Pau D'Arco, where we detected its presence in only a few of our surveys (9/162 points) (Figure 3b), including unmanaged and relatively old (>10 yr) second-growth managed areas. It seems to avoid recently logged areas, where we failed to record this species.

Ochraceous Piculet *Picumnus limae*

This north-east Brazilian endemic inhabits deciduous, semi-deciduous, and secondary stands in the Atlantic Forest. Within the *caatinga*, it inhabits forested and shrubby dry forest vegetation up to ~1,000 m (Winkler *et al*. 2020b). This species was uncommon at the Fazenda Pau D'Arco, where we recorded it in only a few of our surveys (3/162 points) (Figure 3c), in both managed and unmanaged areas at low densities. Recent taxonomic studies have suggested that *P. limae* is conspecific with *P. fulvescens* and comprises a single species with a high degree of colour variation and a clinal distribution (Lima *et al*. 2020), a treatment adopted by the South American Classification Committee (SACC; https://www.museum.lsu.edu/~Remsen/SACCBaseline05.htm) and by the upcoming checklist of the Brazilian Committee of Ornithological Records (CBRO in prep).

Stripe-backed Antbird *Myrmorchilus strigilatus*

This dry forest specialist has two allopatric populations in the *caatinga* and the *chaco*. The nominate form, endemic to the *caatinga*, favours dry woodlands up to 1,200 m (Zimmer *et al.* 2020). With its constant vocalization, the Stripe-backed Antbird had the highest relative abundance at the Fazenda Pau D'Arco, where we detected its presence in most of our surveys (154/162 points) (Appendix S1, Figure 3d), both in managed and unmanaged areas.

Caatinga Antwren *Herpsilochmus sellowi*

Besides a few restricted Amazonian populations, this species favours the middle and upper strata of *Caatinga* scrub and deciduous woodlands up to 1,100 m (Zimmer and Isler 2020a). The Caatinga Antwren was abundant (among the 10 most frequent species) at the Fazenda Pau D'Arco, where we detected its presence in most of our surveys (139/162 points) (Figure 3e). Although it does occur in managed areas, our data suggest that this species is more abundant and presents higher individual densities in unmanaged forests (Ribeiro *et al.* in press a).

Silvery-cheeked Antshrike *Sakesphorus cristatus*

This *caatinga* endemic inhabits the understory and mid-storey of arid lowland *caatinga*, up to 1,100 m (Zimmer and Isler 2020b). The Silvery-cheeked Antshrike was abundant (being among the 10 most frequent species) at the Fazenda Pau D'Arco, where we detected its presence in most of our surveys (151/162 points) (Figure 3f), both in managed and unmanaged areas.

Caatinga Antshrike *Thamnophilus capistratus*

This *caatinga* endemic, sometimes considered conspecific with the Barred Antshrike *T. doliatus*, inhabits dense undergrowth and the mid-storey of deciduous woodland, second-growth forests, and dry scrub (Koloff and Mennill 2020). This species was among the 20 most abundant species at our study site, where we detected its presence at 50/162 points (Figure 3g). Although we detected this species throughout the study area, our data suggest that it is significantly associated with managed areas (Table 1), possibly benefiting from management conditions.

White-browed Antpitta *Hylopezus ochroleucus* (NT/-)

This *caatinga* endemic inhabits deciduous and semideciduous dry forests at ~400-1,000 m (Greeney 2020). We considered this species abundant at the Fazenda Pau D'Arco, where we detected its vocalizations in most of our surveys (144/162 points) (Figure 3h). Although it does occur in both managed and unmanaged areas, this species is more abundant and occurs in higher densities in unmanaged areas (Ribeiro *et al.* in press a). This species is not currently considered threatened by Brazilian authorities (MMA 2018), but the fragmentation of its populations and the transformation of natural habitats have rendered it a 'Near Threatened' global status (IUCN 2020).

Ceara Leaftosser *Sclerurus cearensis* (VU/VU)

This species, recently split from *Sclerurus scansor* based on biogeography, genetics, morphology, coloration, and vocalizations (d'Horta *et al.* 2013), is a NE Brazilian endemic that inhabits both humid and dry forests on a few 1,000-m high plateaus surrounded by *caatinga* scrub vegetation (del Hoyo *et al.* 2020). Its current 'Vulnerable' status is mainly due to having a highly fragmented population coupled with habitat loss through logging and wood harvesting. The Ceará Leaftosser was common at the Fazenda Pau D'Arco, where we detected its presence in about a fifth of our surveys (33/162 points) (Figure 3i), but only in areas that have not undergone any forest management (Appendix S1, Table 1). The local distribution at the study site suggests that this species has disappeared from managed areas, demonstrating the importance of forested vegetation patches and conserved areas to the species' occurrence and persistence.

Great Xenops *Megaxenops parnaguae*

This *caatinga* endemic occurs in the interior of north-eastern Brazil, where it favours humid and dense dry woodlands, between 200 and 1,100 m (Remsen 2020a). Great Xenops was abundant at the Fazenda Pau D'Arco, where we detected its presence in about a third of our surveys (55/162 points) (Figure 3j). Although it does occur in both managed and unmanaged areas, our data suggest that this species is more abundant in unmanaged taller forests (Ribeiro *et al.* in press a).

Red-shouldered Spinetail *Synallaxis hellmayri*

This *caatinga* endemic inhabits several types of dry forest throughout the Brazilian north-east (Remsen 2020b). The Red-shouldered Spinetail was abundant (among the 10 most frequent species) at the Fazenda Pau D'Arco, where we detected its presence in about a third of our surveys (56/162 points), in both managed and unmanaged areas (Figure 3k).

Ochre-cheeked Spinetail *Synallaxis scutata*

This species occurs in low dense forests in central and north-eastern Brazil up to 1,700 m (Remsen 2020c). The Ochre-cheeked Spinetail was uncommon at the Fazenda Pau D'Arco, where we detected its presence in about a fifth of our surveys (31/162 points) (Figure 3l), occurring mostly in unmanaged areas. Although it does occur in some previously logged areas, our data suggest that this species is significantly associated with unmanaged forests (Table 1), possibly avoiding management conditions.

Lesser Wagtail-Tyrant *Stigmatura napensis*

The subspecies *bahiae*, sometimes considered a full species, represents a Brazilian and *caatinga* endemic taxon that inhabits dense, brushy, low vegetation (Fitzpatrick *et al.* 2020). The Lesser

Wagtail-Tyrant was uncommon at the Fazenda Pau D'Arco, where we detected its presence in about a tenth of our surveys (15/162 points), mostly in managed areas of at least five years old. We found that the distribution of this species at our study site was significantly associated with managed areas (Table 1), suggesting that it may benefit from forest management (Figure 3m).

Greater Wagtail-Tyrant *Stigmatura budytoides*

The subspecies *gracilis* represents a Brazilian and *caatinga* endemic taxon that inhabits arid scrub, deciduous woodlands, from sea-level to ~1,000 m (Fitzpatrick 2020). The Greater Wagtail-Tyrant was rare at the Fazenda Pau D'Arco, where we detected its presence at a single managed site.

Green-winged Saltator *Saltator similis*

This species is widely distributed in South America occurring in Brazil, Bolivia, Paraguay, Argentina, and Uruguay (Brewer 2020). It is also widely distributed in Brazil, especially in the central-southern portion of the country, where it inhabits woodlands, gallery forests, forest edges, and clearings, up to 1,200 m. This species was first found and documented by FMGLC at the Fazenda Pau D'Arco in December 2014 (audio recording WA1550839), representing the first record for the state of Ceará. The Green-winged Saltator was uncommon at the Fazenda Pau D'Arco, where we detected its presence at only a few of our surveys (11/162 points) (Figure 3n), mostly in managed areas.

Discussion

This study represents the first attempt to offer quantitative data to characterize the avifauna of the *carrasco*, an often-neglected vegetation type within the *caatinga* dry forests. As far as we are aware, all previous ornithological studies conducted in the semiarid interior of north-eastern Brazil that included this vegetation type, also included other phytophysiognomies, preventing thorough analyses on this specific vegetation type (Nascimento *et al* 2000, Farias *et al.* 2006, Santos *et al.* 2012, Schunck *et al.* 2012, Sousa *et al.* 2012, Vasconcelos *et al.* 2012). Therefore, by sampling an area exclusively dominated by *carrasco* vegetation, with relatively low habitat heterogeneity, we can offer a clear description of what we believe is a typical *carrasco* avifauna. There are three key topics that are worth highlighting. First, despite the suggestion that the *carrasco* may be biogeographically related to the *cerrado* of central Brazil, we found that the *carrasco* avifauna actually represents a subsample of the *caatinga* one. Second, we obtained quantitative data suggesting that the kind of forest management being conducted at the Fazenda Pau D'Arco does affect its avifauna in significant ways. Third, while some non-forest bird species may benefit from forest management, we found that a larger number of bird species avoid managed areas, including species of conservation concern. Therefore, the results of our surveys are important for the understanding of the current and future effects of forest management, providing baseline data on an avian community that will have ~ 90% of its entire vegetation removed in the next decade.

Biogeographical affinities of the carrasco avifauna

The dense arboreal *carrasco* vegetation on top of the Araripe Plateau presents a relatively high species diversity for a 2,000-ha dry forest, composed of a typical arboreal *caatinga* avifauna. Based on our results, it is clear that the avifauna of the Fazenda Pau D'Arco shows biogeographic affinities with other *caatinga* sites, rather than to any *cerrado* locality (Figure 2). Although we found a significant spatial correlation (we cannot rule out the effect of distance on species composition; Figure S1), we recorded 19 avian taxa (including species and subspecies) endemic to the *caatinga* at the Fazenda Pau D'Arco (Appendix S1), and none that is generally considered a *cerrado* specialist. Interestingly, when considering only *caatinga* localities, we found no significant effect of distance on avian composition similarities, suggesting that unaccounted ecological factors, such as type of forest cover, altitude, or rainfall, may be involved in defining avian composition patterns. However, our results show the importance of the *carrasco* vegetation for the overall maintenance of avian *caatinga* diversity.

The presence of some species in our study area is as interesting as the absence of several others. Many *caatinga* endemics, which often dominate most of the lowland crystalline basin, were either completely absent (e.g. Caatinga Cacholote *Pseudoseisura cristata*) or rare (e.g. Red-cowled Cardinal *Paroaria dominicana*, Campo Troupial *Icterus jamacaii*, Pale Baywing *Agelaioides fringillarius*) on the top of the plateau dominated by denser forests. Similarly, dry forest specialists such as White-browed Antpitta *Hylopezus ochroleucus* or Great Xenops *Megaxenops parnaguae* (Stotz *et al.* 1996), which are often absent or hard to find in areas of open shrubby *caatinga* (Mazar Barnett *et al.* 2014), thrive at the Fazenda Pau D'Arco and even represent some of the most abundant species in our quantitative surveys.

Effects of forest management on the avifauna

The Fazenda Pau D'Arco is currently under a forest management program, under which its native vegetation cover will be completely removed from most of its area (except for ~425 ha of protected "legal reserve"). This means that by 2026, 75% of the original forest cover will be replaced by different levels of second-growth forest. While this represents a conservation issue, it also offers a unique opportunity to reach a better understanding of the effect of forest management on dry forest biodiversity.

Our results have shown that several species, such as the Ochre-cheeked Spinetail and the Great Xenops, are already suffering from this management, showing lower densities in managed areas or even being completely absent from them, as was the case of the Ceara Leaftosser (a globally 'Vulnerable' species) that was only recorded in areas that were not previously logged. We consider these results problematic, suggesting that the current management scheme may be further threatening degradation-intolerant species that are already threatened by forest loss (del Hoyo *et al.* 2020). Furthermore, our results suggest that even after a decade of forest recovery, the Ceara Leaftosser has not recolonized these areas. Although, we cannot rule out that this species may be able to recolonize forest patches after a 25-year recovery cycle, as planned by the management programme, there may not be many individuals left in the area to lead this hypothetical recovery. We believe that is more likely that this species will eventually be extirpated from the entire area unless more areas are left unmanaged at this specific site. The high level of habitat specificity showed by many bird species from other arid environments (Pavey and Nano 2009) could lead to further losses, including Blue-crowned Trogon *Trogon curucui*, Flavescent Warbler *Myiothlypis flaveola*, Red-billed Scythebill *Campylorhamphus trochilirostris*, or Olivaceous Woodcreeper *Sittasomus griseicapillus*, all of which are associated with arboreal environments and seem to be affected by the management programme and therefore may be extirpated from the area in the next few years.

On the other hand, we found that some species, such as the Caatinga Antshrike *Thamnophilus capistratus* and Lesser Wagtail-Tyrant *Stigmatura napensis*, apparently benefit from forest management. It is known that management frequently causes a reduction of habitat for arboreal species and also a reduction of the soil seed bank, which can directly affect species that are dependent on a dense environment, as well as granivorous species (Zwarts *et al.* 2018). Meanwhile, it may favour species from other guilds, as appears to be the case at the Fazenda Pau D'Arco.

By providing baseline data and documenting the avifauna before the complete exclusion of the original vegetation, we are providing the means for a full evaluation of the sustainability of this kind of forest management. Our preliminary results indicate that some bird species of conservation concern are significantly affected by forest management and point out the necessity of keeping unmanaged forest patches to avoid local extinctions. Therefore, our work represents an initial first step towards reaching a better understanding of the *carrasco* avifauna and evaluating the effect of forest management on its biodiversity.

Supplementary Material

To view supplementary material for this article, please visit http://dx.doi.org/10.1017/S0959270921000101.

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