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HUMBERTO COELHO NAPPO

O GRANDE INTERCÂMBIO BIÓTICO AMERICANO E A DIVERSIFICAÇÃO DE TEIIDAE

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RESUMO

Padrões de diversidade podem variar amplamente ao longo dos ramos de uma filogenia. Novidades evolutivas e eventos históricos como a colonização de novos ambientes e a interação com invasores podem fazer com que linhagens irmãs apresentem uma grande discrepância na riqueza de espécies. Um dos eventos históricos mais relevantes para a composição da fauna do Novo Mundo foi o Grande Intercâmbio Biótico Americano (GABI), que consistiu em pulsos migratórios de larga escala entre linhagens da América do Sul e da América do Norte após a formação do Istmo do Panamá. Apesar de existir uma extensa literatura descrevendo os padrões de migração e diversificação relacionados ao GABI, boa parte do entendimento sobre esse fenômeno foi construído com base no estudo de mamíferos. Neste trabalho, eu avaliei a variação nas taxas de diversificação de Teiidae, uma linhagem de lagartos neotropicais que migrou para a América Norte durante o Mioceno. Na sequência, eu testo se a diversificação desses lagartos está associada com a distribuição geográfica ou com algumas características fenotípicas como tamanho e temperatura corporal. Por fim, eu avalio a sobreposição de nicho entre o clado que colonizou a América Central, América do Norte e Antilhas e o seu grupo irmão na América do Sul. Os resultados mostram evidências de um aumento na taxa de diversificação em dois pontos na história do grupo, sendo um deles dentro do clado que dispersou para a América do Norte. Espécies com distribuição na América do Norte tiveram taxas de diversificação mais altas que as espécies sul-americanas. Tamanho e temperatura corporal, por sua vez, não influenciaram na taxa de diversificação. Os resultados da análise de sobreposição de nicho mostram que o clado que migrou pelo Istmo do Panamá apresenta um nicho ecológico mais amplo que inclui quase todo o nicho ocupado pelo grupo irmão na América do Sul somado a uma expansão para áreas mais áridas, o que é congruente com a hipótese de aproveitamento de oportunidades ecológicas em condições ambientais para as quais esses lagartos já estariam pré-adaptados.

Palavras-chave: diversificação, filogenia, oportunidade ecológica, sobreposição de nicho, Teiidae

ABSTRACT

Diversity patterns can vary widely across branches of a phylogeny. Evolutionary novelties and historical events such as the colonization of new environments and interaction with invaders can lead sister lineages to exhibit a significant discrepancy in species richness. One of the most relevant historical events for the composition of New World fauna was the Great American Biotic Interchange (GABI), which consisted of large-scale migratory pulses between lineages from South America and North America after the formation of the Isthmus of Panama. Despite extensive literature describing migration and diversification patterns related to GABI, a great portion of the knowledge about this phenomenon was built on the study of mammals. In this work, I assessed the variation in diversification rates of Teiidae, a lineage of Neotropical lizards that migrated toward North America during the Miocene. Subsequently, I tested whether the diversification of these lizards is associated with geographical distribution or some phenotypic traits such as body size and body temperature. Finally, I evaluated the niche overlap between the clade that colonized Central America, North America, and the Antilles, and its sister group in South America. The results show evidence of an increase in diversification rates at two points in the group's history, one of which occurred within the clade that reached North America. Species with distribution in North America had higher diversification rates than South American species. Body size and temperature, however, did not influence the diversification rate. The results of the niche overlap analysis indicate that the clade that migrated through the Isthmus of Panama occupies a broader ecological niche, which includes almost the whole niche occupied by the sister group in South America, along with a large expansion into more arid areas. This is consistent with the hypothesis of exploiting ecological opportunities in environmental conditions for which these lizards were already preadapted.

Keywords: diversification, ecological opportunity, phylogenetics, niche overlap, Teiidae

SUMÁRIO

INTRODUÇÃO GERAL

Ao longo dos últimos 3,5 bilhões de anos, a vida na Terra passou de organismos unicelulares muito simples para uma incalculável diversidade de formas. Todos os organismos conhecidos até então – deixando de lado os vírus, cuja origem ainda é debatida – traçam sua ascendência a um ancestral comum. A despeito de compartilharem a mesma origem, é notória a diferença de diversidade entre os herdeiros desse organismo ancestral. Isso porque a velocidade com que descendentes se acumulam pode variar extensamente até mesmo entre linhagens muito proximamente aparentadas. Essa disparidade é fruto de diferentes taxas de diversificação – definida como a diferença entre as taxas de especiação e extinção.

Inúmeros fatores podem afetar os valores dessas taxas. Já foi repetidamente demonstrado para diversas linhagens que a colonização de uma nova área pode contribuir para o aumento da diversificação (p. ex. Burress et al., 2017; Grant, 1999; Hou et al., 2011). A explicação mais clássica para esse fenômeno é que uma vez que uma linhagem ocupa uma nova área, ela pode se aproveitar de recursos que não estejam sendo utilizados pelos residentes originais ao mesmo tempo em que se evade de predadores, competidores e parasitas que a afligissem anteriormente (Schluter, 2000; Simpson, 1953). Essas condições favoráveis permitiriam um acelerado crescimento populacional e expansão da área de distribuição e dos nichos ecológicos ocupados, o que favoreceria o surgimento de novas espécies (Gillespie et al., 2020). Simultaneamente, a falta de predadores, competidores e parasitas adaptados aos colonizadores preveniria a extinção das linhagens, de modo que a taxa de diversificação tenderia a aumentar rápido.

Entretanto, essa não é a única explicação possível. Diversas linhagens proximamente relacionadas apresentam padrões de diversificação discrepantes sem uma justificativa biogeográfica aparente. Um exemplo familiar é o de Angiosperma, com folga o mais biodiverso grupo vegetal conhecido (Christenhusz & Byng, 2016). Neste caso, a explicação pode estar associada ao surgimento de fenótipos específicos – flores e frutos – que, de maneira similar ao que foi descrito acima, permitem que o organismo explore recursos subutilizados por seus competidores. Outras características fenotípicas, no entanto, podem afetar as taxas de diversificação por outros mecanismos. O tamanho corporal, por exemplo, há muito é sugerido como um preditor da diversificação por conta da relação inversa entre tamanho e diversidade que parece ocorrer em diversos grupos (Hutchinson & Macarthur, 1959). Frequentemente, porém, a mudança de um fenótipo pode estar associado a uma

mudança ecológica e à ocupação de uma nova área (Burress et al., 2017), o que torna indissociáveis os efeitos destes fatores.

Estudar a diversificação pode ser desafiador em função de alguns fatores. A profundidade temporal que estes estudos normalmente compreendem, a dependência do registro fóssil – que é incompleto por natureza – e principalmente a infinitude de fatores que podem afetar a diversificação fazem com que investigar o tema possa ser bastante desafiador. Como descobrir qual o maior responsável pelo padrão de diversificação de uma determinada linhagem se ela expressa incontáveis fenótipos e interage em uma teia complexa com inúmeras espécies em múltiplos contextos distintos ao longo de um extenso intervalo de tempo? Dadas as incertezas associadas, uma boa estratégia para investigar os determinantes da diversificação é buscar linhagens nas quais tenham ocorrido mudanças bruscas nas taxas de diversificação. Nestas linhagens, é provável que a alteração repentina seja devida a um número reduzido de variáveis, o que deve tornar a sua identificação mais fácil. Um bom lugar para procurar essas linhagens é em eventos de dispersão conhecidos. Tendo uma ideia de quando uma linhagem chegou a determinada região, pode-se determinar se houve uma mudança brusca na taxa de diversificação e posteriormente investigar o porquê.

Sem dúvidas, um dos maiores eventos de dispersão da história geológica recente – e consequentemente uma grande oportunidade para investigar a diversificação biológica e seus determinantes – foi o ocorrido entre Américas do Sul e do Norte após a reconexão destes dois continentes. Após a fragmentação da Pangeia, a América do Sul ficou isolada por algumas dezenas de milhares de anos, período durante o qual a biota sul-americana se desenvolveu com relativamente pouca influência de imigrantes. A situação mudou drasticamente após a formação do Istmo do Panamá, que criou uma conexão terrestre entre as duas regiões, facilitando a dispersão de uma série de linhagens (Montes et al., 2012; Montes et al., 2015). Às migrações massivas que se sucederam entre os dois continentes foi dado o nome de Grande Intercâmbio Biótico Americano – GABI (Bacon et al., 2015; Jaramillo, 2018).

O GABI teve implicações profundas na formação das comunidades em ambos os continentes, com diversas linhagens ganhando e perdendo espaço em função das migrações (Bacon et al., 2015; Jaramillo, 2018). Esse evento foi descrito inicialmente com base no estudo de mamíferos fósseis, e ainda hoje este é o grupo para o qual o fenômeno é mais conhecido. A partir do Pleistoceno, sucessivos pulsos migratórios culminaram com a chegada de linhagens como Carnivora, Artiodactyla e Perissodactyla na América do Sul e de Primates,

Xenarthra e Marsupialia na América do Norte (Webb, 2006; Woodburne, 2010). Para outros grupos no entanto, a história se deu de outra forma. Para répteis, a maior parte das migrações ocorreu ainda no Mioceno (Bacon et al., 2015; Estes & Báez, 1985).

Um dos grupos de répteis afetados pelo GABI foi Teiidae (Gray, 1827) uma linhagem de lagartos que provavelmente dispersou da América do Sul para a América do Norte e Antilhas em uma data próxima à formação do Istmo do Panamá (Giugliano et al., 2007; Scarpetta, 2020; Tucker et al., 2017). Esta família é composta majoritariamente por lagartos de médio a grande porte, heliófilos, forrageadores ativos e, em geral, predadores generalistas (Vitt & Caldwell, 2014). Duas peculiaridades se fazem notar neste grupo. A primeira é que apesar de terem se dispersado para a América do Norte e Antilhas há relativamente pouco tempo (Scarpetta, 2020; Tucker et al., 2017), o clado imigrante tem quase a mesma quantidade de espécies que as linhagens que permaneceram na América do Sul (Uetz et al., 2023). A segunda é que apesar da maior parte das espécies serem bastante similares em respeito à morfologia e ecologia, existe uma clara distinção de tamanho corporal e diversidade entre as duas subfamílias que é congruente com o esperado caso a primeira variável afete a última. Por estas razões, nós consideramos Teiidae um grupo interessante para investigar os determinantes da diversificação. A tabela 1 discrimina a riqueza de espécies seguindo a versão mais recente do *Reptile Database* (Uetz et al., 2023) e distribuição geográfica de todos os gêneros de Teiidae.

Nesta dissertação, meu objetivo é avaliar se a diversificação de Teiidae foi afetada pelo GABI e testar alguns de seus possíveis preditores. Conhecer os determinantes da diversificação é essencial para desvendar os processos responsáveis por moldar a biodiversidade em suas infinitas formas de grande beleza.

Tabela 1. Riqueza de espécies e distribuição geográfica dos gêneros de Teiidae.

Subfamília		Gênero	Riqueza de Espécies	Distribuição Geográfica
Tupinambinae		*Callopistes*	2	América do Sul transandina
		Dracaena	2	América do Sul cisandina
		Salvator	3	América do Sul cisandina
		Tupinambis	8	América do Sul cisandina e algumas ilhas do Caribe
		Crocodilurus	1	América do Sul cisandina
Teiinae		*Teius*	3	América do Sul cisandina
		Dicrodon	3	América do Sul transandina
	cnemidophorines	*Glaucomastix*	5	América do Sul cisandina
		Ameivula	11	América do Sul cisandina
		Contomastix	6	América do Sul cisandina
		Aurivela	2	América do Sul cisandina
		Pholidoscelis	21	Antilhas
		Holcosus	18	América Central e América do Sul transandina
		Aspidoscelis	45	América do Norte e Central
		Medopheos	1	América do Sul transandina
		Kentropyx	9	América do Sul cisandina e algumas ilhas do Caribe
		Cnemidophorus	19	América do Sul cisandina e algumas ilhas do Caribe
		Ameiva	14	América do Sul cisandina e algumas ilhas do Caribe

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CHAPTER 1

The Great American Biotic Interchange and teiid diversification

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The Great American Biotic Interchange and teiid diversification

Abstract

Aim: Diversification patterns may vary greatly through the branches of a phylogeny. Evolutionary novelties, interaction with the biotic and abiotic environment, and historical events such as the colonization of new areas may cause closely related lineages to present a significant disparity in species richness. One of the most relevant historical events for the New World fauna composition was the Great American Biotic Interchange (GABI), a massive migration movement between South and North America after the formation of the Isthmus of Panama. Although many have described migration and diversification patterns during the GABI, an earlier understanding of this phenomenon was heavily biased toward mammal fauna. Here, we assessed the variation in diversification rates of Teiidae, a Neotropical lizard lineage that migrated towards Central and North America and the Antilles during the Miocene.

Location: New World.

Taxon: Teiidae.

Methods: We constructed a dated phylogeny from GenBank sequences using a well-supported topology from the literature as a constraint. Then, we conducted diversification analyses using BAMM and ClaDS to estimate macroevolutionary rates and identify diversification dynamics shifts in the tree.

Results: The results show increased diversification rates at the base of cnemidophorines and within the clade that reached North America.

Main Conclusions: The formation of the Isthmus of Panama enabled teiids to colonize North America, where the lineage putatively seized ecological opportunities which allowed faster diversification. However, teiids migrating to the Antilles did not show increased diversification, which suggests that the diversification burst was due to factors related to the region instead of the organisms. Moreover, teiids had a diversification burst before the GABI, which we did not investigate but could be related to the emergence of morphological and ecological traits.

Keywords: diversification analysis, diversification rates, Great American Biotic Interchange (GABI), phylogenetics, Teiidae, whiptail lizards.

INTRODUCTION

Understanding which processes generate biodiversity is one of the primary goals of ecology, evolutionary biology, and biogeography. Diversification patterns may vary greatly through time, space, and the branches of a phylogeny. There are abundant examples of closely related lineages in the Tree of Life with significant diversity disparity between them. In mammals, for example, of 6,495 species, 94.09% are eutherians, 5.77% are marsupials, and only 0.08% are monotremes (Burgin et al., 2018). This disparity in diversification patterns between closely related lineages arises due to different diversification rates. The diversification rate consists of the speciation rate minus the extinction rate (net diversification = speciation – extinction). The evolution of traits (Pender et al., 2021) or the dispersal to new environments (Hou et al., 2011; Li et al., 2020) may increase the speciation rate, while the interaction with predators, competitors, and parasites (Bengtsson, 1989; Kehoe & van Veen, 2022) and the habitat loss and fragmentation may increase the extinction rate (Rybicki & Hanski, 2013).

The phenomenon of increasing diversification following the colonization of a new area is known as radiation, which can be adaptive or non-adaptive, depending on whether there is ecological differentiation or not (Gittenberger, 1991; Schluter, 2000; Simpson, 1953). One of the most prominent examples is the radiation of Darwin finches, which quickly evolved multiple species with marked morphological and ecological differences between them after dispersing to the Galapagos (Grant, 1999). Colonizing a new habitat enables the immigrants to explore ecological opportunities—that is, resources underused by other taxa— and escape predators, competitors, and parasites (Schluter, 2000). This setting favors the emergence of multiple novel species in a brief period. On the other hand, once a lineage has successfully established itself in a new area, direct and indirect interactions may cause important consequences to the local biodiversity. Since the resident species are not adapted to the pressures imposed by the immigrants, they may suffer high extinction rates (Stigall, 2019).

Dispersal to a novel environment may bring extensive implications for the speciation and extinction rates of the dispersers and resident lineages. Thus, sizeable biological dispersal events are unique opportunities to study the variation in diversification patterns. One of the most extraordinary dispersal events in recent geological history is the exchange of lineages between North and South America after the reconnection of these two land masses (Bacon et al., 2015; Jaramillo, 2018). South America was believed to have passed most of the Cenozoic in isolation from other landmasses until the reconnection with North America enabled

massive migrations starting around 3 Ma (Simpson, 1980). However, recent evidence indicates that the physical connection and migration dynamics between both continents are older and much more complex. Petrographic and thermochronological analyses show that sections of the Panama arc have already emerged in the late Eocene, and zircon sediments in the northern Andes suggest that by the middle Miocene, the Central American Seaway was already closed (Montes et al., 2012; Montes et al., 2015). This is supported by fossil and molecular data that indicate waves of migration between South and North America starting around 20 Ma (Bacon et al., 2015). This massive migration movement between both continents became known as the Great American Biotic Interchange (GABI). Albeit extensive literature addresses the dispersal patterns during the GABI and its implications for community assembly, an earlier understanding of this phenomenon was built heavily on the study of mammal fossils (Simpson, 1980; Webb, 2006; Woodburne, 2010). As for reptiles, dispersal rates estimated from molecular data point to migration increasing at the end of the Miocene (Bacon et al., 2015). Indeed, dating from this epoch are the oldest fossil of *Boa* in Central America (Head et al., 2012), Teiidae in North America (Scarpetta, 2020), and Viperidae (Albino & Montalvo, 2006) and Pan-Trionychidae in South America (Vitek & Joyce, 2015), for example.

One of the many reptile lineages affected by the GABI is Teiidae (Gray, 1827), a group composed of medium to large-sized lizards that occur naturally from central Argentina to middle North America (Vitt & Caldwell, 2014). Most of the 173 recognized species are terricolous, heliophilous, active foragers, and predators, although there are exceptions (Uetz et al., 2023; Vitt & Caldwell, 2014). After the reclassification of various taxa to Borioteiioidea (Nydam et al., 2007), the oldest fossil recognized as Teiidae dates from the early Eocene of Argentina (56.1-51.4 Ma) (Brizuela & Albino, 2016). Notwithstanding, molecular dating techniques estimate the origin of the group at 85 Ma, still during the Cretaceous (Tucker et al., 2017). Thus, despite likely having originated in North America, this lineage was extinct there shortly after its dispersal to South America, from where a single lineage recolonized teiid former home continent (Giugliano et al., 2007). Upon recolonizing North America and reaching the Caribbean islands, the dispersing lineage may have escaped predators, competitors, and parasites and encountered ecological opportunities that enabled it to diversify faster than its southern relatives—this northern radiation corresponds to approximately 48% of the family's diversity (Uetz et al., 2023). Indeed, this scenario is plausible since Cenozoic North American lizard fauna until then was dominated by groups

such as Iguanians, Scincomorphans, and Anguimorphans (Lofgren et al., 2020; Longrich et al., 2012; Smith, 2009)—most of them ecologically very distinct from teiids. Alternatively, this higher diversity of northern teiids could result from higher extinction rates in South American lineages due to interaction with establishing immigrants after GABI—such as carnivorans, for example.

This work aims to assess whether the formation of the Isthmus of Panama affected the diversification rates within Teiidae. We hypothesize that (1) lineages that migrated towards the Antilles, Central, and North America increased their diversification rates and (2) lineages that remained in South America experienced decreases in their diversification rates. These diversification shifts could be consequences of many different processes, such as seizing ecological opportunities, ecological release, and a succession of allopatric and parapatric speciation following colonization for (1) and interspecific interactions with northern immigrants for (2). However, in this chapter, we focus on identifying the pattern, rather than assessing its drivers. Our null expectation is that the formation of the Isthmus did not affect teiid diversification. Should this be the case, we may find uniform diversification rates for the whole family.

METHODS

Phylogenetic analyses

Diversification analyses are sensitive to incomplete sampling, especially because taxa are not sampled randomly (Cusimano & Renner, 2010; Höhna et al., 2011). Therefore, we followed a procedure to maximize the species included while avoiding using a low-support topology. First, we updated the sequences used by Tonini et al. (2016) for all Teiidae and two Gymnophthalmidae species (*Cercosaura ocellata* and *Potamites ecpleopus*) with new sequences published in GenBank for the same genes: mitochondrial ribosomal RNA 12S and 16S, brain-derived neurotrophic factor (BDNF), bone morphogenic protein 2 (BMP2), oocyte maturation factor *mos* (CMOS), cytochrome oxidase 1 (COI), cytochrome *b* (CYTB), NADH dehydrogenase subunits 1, 2, and 4 (ND1, ND2, and ND4), neurotrophin 3 (NT3), prolactin receptor (PRLR), G protein-coupled receptor 149 (R35), and recombination activating genes 1 and 2 (RAG1 and RAG2). Tonini et al. (2016) also used amelogenin (AMEL) and phosducin (PDC) sequences, but we did not include these genes since there were no available AMEL sequences and only one PDC sequence published in GenBank for Teiidae. The accession numbers for these sequences are in Appendix S1.

From these sequences, we produced a multiple sequence alignment for each gene using the MAFFT algorithm in Geneious Prime 2022.2 (Biomatters, 2022). After the automatic run, we checked and manually corrected all the alignments and excluded snippets with coverage lower than 80%. After this, we concatenated the alignments and subjected the full alignment to a constrained tree search in IQ-TREE, 2.2.2.6 (Minh et al., 2020) with the MP-EST topology from Tucker et al. (2016) as a constraint. Tucker et al. (2016) used a phylogenomic approach with many more loci and inferred highly congruent topologies with three different methods, albeit their analysis included only 56 species (32.4% of known diversity). Since we do not have the same quality of data, we chose to use their topology to constrain our search. Not all tips in the constraint tree were represented in our alignment since some of them did not have published sequences in GenBank. Because of this, we removed from the constraint tree tips that did not have counterparts in the alignment using ape's *drop.tip()* function (Paradis & Schliep, 2018). We used ModelFinder (Kalyaanamoorthy et al., 2017) to evaluate nucleotide substitution models separately for each gene and chose the best model for each one according to the Bayesian Information Criterion (BIC). We assessed node support by running 1000 iterations of ultrafast bootstrap (Hoang et al., 2017). The multiple sequence alignment, the file containing the partitions, the constraint used in IQ-TREE constrained tree search, and the maximum likelihood tree found are available in Appendixes S2-S5.

Then, we inferred divergence times for the maximum likelihood tree with RelTime implementation in MEGA11 (Tamura et al., 2021; Tamura et al., 2018) using default analysis settings for maximum likelihood branch lengths inference. We rooted the tree on the branch leading to *Cercosaura ocellata* and *Potamites ecpleopus* and calibrated it assigning exponential prior distributions for the ages of two nodes based on fossil evidence. We defined the offset age for *Callopistes* as 20.1 Ma (Quadros et al., 2018). For the origin of the clade *Pholidoscelis + Holcosus + Aspidoscelis*, we defined an offset age of 9.4 Ma (Scarpetta, 2020).

Diversification analyses

We removed the outgroup (Gymnophthalmidae) of the maximum clade credibility tree and subjected it to diversification analyses using BAMM, 2.5.0 (Rabosky, 2014) and ClaDS (Maliet et al., 2019). Both methods can handle heterogeneity in macroevolutionary rates, although they differ in some core assumptions, which may cause them to estimate

significantly different speciation rates (Martínez-Gómez et al., 2023). One of the main differences is that ClaDS assumes that all splits are associated with rate shifts, while BAMM assumes that shifts are rare events. BAMM has also been criticized for issues with its likelihood function (Laudanno et al., 2021), which justifies using a second method to validate its findings. For BAMM, we defined priors with the *setBAMMpriors()* function from the BAMMtools package (Rabosky et al., 2014) for R (R Core Team, 2023). To avoid biases derived from the non-random species sampling, we added a sampling fraction correction file that informed the algorithm of the proportion of sampled species for each genus separately. The MCMC analysis was run through ten million generations, sampled each thousand in four independent chains. The BAMM control and sampling fraction correction files are in Appendices S6 and S7, while the chain swap, event data, and MCMC output BAMM files are in Appendices S8-S10. We ran a diversification analysis with ClaDS on Julia 1.9.2 with the same tree and using the same sampling fraction correction used for BAMM. We ran three independent chains until convergence, defined as attaining a Gelman statistic lower than 1.05 after a 25% burn-in. ClaDS results are in Appendix S11.

The diversification analysis field has been turmoiled for the last few years with a rapid succession of papers questioning the reliability of inferences based on time-calibrated trees of extant species and how to properly handle them (e.g., Laudanno et al., 2021; Moore et al., 2016; Morlon et al., 2022; Rabosky et al., 2017). Most critically, if rates can vary unconstrained over time, infinite combinations of lineage-homogenous rate regimes can yield the same likelihood values, rendering it impossible to differentiate plausible estimated scenarios from biologically unrealistic ones—the congruency problem (Louca & Pennell, 2020). The congruency problem has only been demonstrated for homogenous-rate models so far (models in which all branches at each given time share the same rate), and although heterogenous-rate methods may also suffer from it, the methods we employ act to regularize this issue by favoring few rate shifts with large effects or frequent rate shifts with minor effects (Morlon et al., 2022). Moreover, despite the nonidentifiability of macroevolutionary rates, trends of rapid rate shift were shown to be robust to the congruence class; therefore, conclusions may be drawn from the estimated rate shifts even though the rates themselves cannot be identified (Kopperud et al., 2023).

RESULTS

Phylogenetic analyses

The expansion of the alignment in Tonini et al. (2016) for Teiidae resulted in the inclusion of 123 new DNA sequences. Our alignment included 106 teiid species—29 more than in Tonini et al. (2016)—corresponding to 60.3% of Teiidae diversity plus two gymnophthalmids as outgroup. We also replaced 36 sequences used by Tonini et al. (2016) with longer sequences for the same species and genes that were available on GenBank. Additionally, we removed one sequence for *Aspidoscelis tigris* (U71332.1) because it included several concatenated gene sequences and one for *A. velox* (EU116675.1) since the sequence seemed to be incorrectly named. Overall, our sequence matrix had 78.02% of missing data. The maximum likelihood tree has some differences when compared to the results from Tucker et al. (2016) probably due to the inclusion and exclusion of some species. First, the sister group to cnemidophorines in our tree is *Dicrodon* instead of *Teius* + *Dicrodon*. Second, the inclusion of *Glaucomastix venetacauda* and *G. cyanura* suggests the genus to be paraphyletic, with *Ameivula ocellifera* nested within it (Figure 1).

Diversification analyses

Estimates on speciation rate dynamics were similar between ClaDS and BAMM (Appendix S12); therefore, we focus the discussion on the latter. For BAMM, the ESS was high for both log-likelihood and number of shifts ($ESS_{log-lik}$ = 1606.848, $ESS_{Nshifts}$ = 2464.641). The convergence of the log-likelihood of the sampled models is in Appendix S13. The models with the highest posterior probability consistently showed two rate shifts (Figure 2): one at or next to the base of cnemidophorines and another within *Aspidoscelis*. Occasionally, only one of these shifts appears, albeit with a lower posterior probability. Two scenarios also sampled a third diversification rate shift within *Cnemidophorus* but with lower marginal probabilities. The average of all sampled configurations shows a shift at the base of cnemidophorines and another one within *Aspidoscelis*, at the base of the clade defined by the most recent common ancestor of *A. maximus* and *A. rodecki* (Figure 3). The diversification rates within these clades are markedly distinct from the other teiids in almost all scenarios sampled (Figure 4). These results corroborate our first hypothesis of increasing diversification within the migrating lineage, although we expected to observe an earlier diversification rate shift. South American lineages, on the other hand, did not have a diversification rate shift that could be attributed to the GABI.

Macroevolutionary BAMM analysis suggests that the increasing diversification within *Aspidoscelis* was due to a speciation burst, albeit followed by an increment in the extinction rate (Figure 5). Despite the confidence intervals (CI) for these two rates being ample, the CI for the speciation rate of the fast-diversifying *Aspidoscelis* was above the mean speciation rate of Teiidae. On the other hand, the extinction rate was more uncertain, and it is not possible to determine that it was higher than the rest of the tree.

DISCUSSION

We inferred a maximum likelihood tree for Teiidae constrained by a well-supported topology from the literature. In the light of recent phylogenetic inferences for this group, two points of our tree draw attention. The first one is the sister group of cnemidophorines, which was inferred as *Teius* + *Dicrodon* by Tucker et al. (2016) and as *Dicrodon* by us. This difference was possibly due to the lower sampling for these taxa by us—one species for each genus in our matrix *versus* three *Teius* species and two *Dicrodon* species in Tucker et al. (2016)—which could have prevented us from detecting the relationship between these genera. The second one was the inference of a paraphyletic *Glaucomastix*, with *Ameivula* nested within it. This does not contradict Tucker et al. (2016) because the paraphyly was only observed after the inclusion of a species absent from their matrix. However, this result goes against the findings of Arias et al. (2018), which found monophyletic *Glaucomastix* and *Ameivula*. Arias et al. (2018) used short sequences of 12S, 16S, and CYTB (similar to our approach) but sampled all known species of these genera to the date of their publication with the addition of some undescribed species. We had only one of the eleven known *Ameivula* species in our matrix so our inference could have been severely prejudicated by lack of data. Including more *Ameivula* sequences as the ones generated by Arias et al. (2018) in our matrix would be essential to test the monophyly of these genera, however, until the date of this publication— and opposite to what is declared in their paper—those sequences were not published in GenBank.

Regarding the diversification analyses, the average of sampled macroevolutionary dynamics configurations pointed to two diversification rate shifts in Teiidae, which is widely agreed between the sampled scenarios: one at the base of cnemidophorines and one within the clade that migrated toward North America. The first rate shift was estimated around 16 Ma and the second one around 7 Ma, both during the Miocene.

Teiidae has two subfamilies markedly distinct from each other in several aspects, including diversification patterns. While Tupinambinae has only 16 species, Teiinae has approximately ten times this number. This difference is almost entirely carried by the cnemidophorines, a clade that comprises all the subfamily excluding the basal genera *Teius* and *Dicrodon* (Reeder et al., 2002). Therefore, finding a diversification rate increment at the base of cnemidophorines was not unexpected. Whilst this difference cannot be readily assigned to be related to any biogeographic event, there are several differences between these subfamilies that could possibly contribute to differential diversification. One of the most evident differences between these lineages is body size: species in Tupinambinae are considerably larger (Meiri et al., 2018; Vitt & Caldwell, 2014). The association between body size and diversification has been suggested since long ago (Hutchinson & Macarthur, 1959) but studies with lizards have not found a significant relationship (Feldman et al., 2016; Li & Wiens, 2022). Teiinae and Tupinambinae also present some differences in ecology. While Teiinae species are mostly predators with highly similar morphology and ecology, Tupinambinae species are omnivorous and range from arid-adapted to semiaquatic species (Vitt & Caldwell, 2014). Contrary to what one would imagine, the least species-rich is the most ecologically diverse lineage. More in-depth investigations into the ecological requirements, evolutionary constraints, and trait-dependent diversification in this group are needed to unveil this pattern.

The genus *Aspidoscelis* is restricted to Central and North America, and it diverged around 11-10 Ma. The average model estimated with BAMM shows a rate shift within this genus around 7-6 Ma, temporally close to the estimated date for the formation of the Isthmus (Montes et al., 2012; Montes et al., 2015). However, the rate shift is way younger than the dispersal itself, which may have happened before the divergence of *Pholidoscelis* (Tucker et al., 2017). Based on our divergence times inference, the teiid migration should have happened before 12 Ma, which is congruent with the findings that reptile dispersal rates between North and South America increased greatly after 20 Ma (Bacon et al., 2015). However, the timing discrepancy between the dispersal and the diversification rate shift suggests that the colonization of a new area by itself was not enough to bolster teiid diversification. This diversification burst could have been furthered by the great extent of arid areas in western North America where teiids diversified extensively, although the simple range expansion was already shown to be related to squamate diversification (Li & Wiens, 2022), which could be explained, among others, by the rising of allopatric and parapatric speciation events following

a great range expansion. Notably, biotic interaction may also have played a role. If North American fauna lacked adapted predators and competitors, for example, the same pattern was to be expected. Assessing ancestral biotic interactions may be challenging, however, the fossil record gives us some leads. Most of the North American lizard fauna back then was composed of lineages that were both distantly related and ecologically distinct to Teiidae as Iguanians, Scincomorphans, and Anguimorphans, which would not likely dispute the same niches as the immigrants (Lofgren et al., 2020; Longrich et al., 2012; Smith, 2009). Indeed, this could also explain the rejection of our hypothesis of decreasing diversification rates in South American teiids: if there were no predators and competitors capable of threatening the persistence of teiids in North America, northern immigrants should not negatively affect teiid diversification in South America. These are not mutually exclusive possibilities, and both may be reasonable hypotheses of why this family diversified so swiftly in the newly colonized continent. Nevertheless, the pattern we found could have been influenced by the latitudinal taxonomy gradient (LTG)—the tendency of biodiversity to be better known at temperate latitudes than in the tropics (Freeman & Pennell, 2021). Since Teiidae spans a wide latitudinal range, this could be a pronounced issue if tropical teiid biodiversity is still largely unknown relative to temperate teiids. Notwithstanding, the LTG already shows signs of flattening in the New World (Costello et al., 2013) but until this gap is fully closed, this is an almost unescapable pitfall for studies aiming to compare diversity among different latitudes.

It draws the attention that none of the macroevolutionary dynamics configurations with the highest posterior probability pointed to increased diversification rates within *Pholidoscelis*. This genus is endemic to the Antilles and started diversifying around 11-9 Ma. Despite reaching novel environments where they could seize ecological opportunities and release ecological pressures (Schluter, 2000), colonizing the Caribbean did not seem to trigger a diversification burst. Island colonization is expected to accelerate diversification because of the reasons above and because it furthers reproductive isolation among islands. However, this was not the case here. Since all species in this genus are insular, habitat homogeneity, small population sizes, and restricted area availability may have prevented reproductive isolation within islands—inhibiting the emergence of new species—or increased extinction rates (MacArthur & Wilson, 1967; O'Grady et al., 2004). Indeed, threshold area values for *in situ* speciation were already observed for many taxa, including *Anolis* lizards in the same archipelago (Kisel & Barraclough, 2010; Losos & Schluter, 2000). As area thresholds for speciation are related to dispersal capability (Kisel & Barraclough, 2010), the greater body

size and home range of teiids could push the minimum area needed for *in situ* speciation towards a value so high that would prevent speciation within most of the Caribbean islands. This scenario seems plausible since most Caribbean islands tend to have only one or a few teiid species (Tucker et al., 2017). Besides that, the mere discontinuity of the colonized area could have prevented an explosive increase in diversification simply because of the longer time needed for the lizards to reach one island from another, as was suggested for Caribbean Alsophinii snakes (Burbrink et al., 2012). Alternatively, the apparent lack of diversification in the Antilles could be a product of a recent growth in extinction rates. European colonization was already shown to be the main driver behind the extinction of some *Pholidoscelis* species (Bochaton et al., 2019), and previous human occupations may also have affected ancient teiid populations in the islands.

Interestingly, *Anolis* lizards seem to show a different pattern than teiids, with higher diversification in islands than in similar-sized continental areas and possibly the mainland as a whole (Algar & Losos, 2011). It is possible, though, that this asymmetry in diversification patterns relates to factors other than the area itself since teiids and anoles are remarkably different in a multiplicity of aspects such as morphology, ecology, and behavior. The difference in these diversification patterns could also be due to the kinds of environments available. While North America possesses extensive open and arid areas—suitable for heliophilous teiids but prohibitive for the forest-adapted anoles—the Caribbean islands are characterized chiefly by forested formations (Areces-Mallea et al., 1999).

One limitation of this work is that the true Teiidae tree should be reticulated, instead of bifurcating due to hybridization on several teiiine genera (Barley et al., 2022; Reeder et al., 2002). However, since there are no current algorithms capable of estimating diversification rates on reticulated topologies, a bifurcating tree is a mandatory simplification. Hybridization has already been shown to increase diversification rates since no long reproductive isolation is needed (Moreira et al., 2021). However, its effect alone could not explain the higher diversification in *Aspidoscelis* since several South American teiid genera—including the species-poor *Kentropyx* and *Teius*—also have hybrid parthenogenetic species (Avila & Martori, 1991; Cole et al., 1995).

Rate shifts may help understand diversity disparities and are a first step to identifying factors affecting macroevolutionary dynamics. This framework ultimately sheds light on the formation of communities and might answer long-lasting questions about the composition of

biotas worldwide. We show that teiids underwent a rapid increase in diversification after the colonization of North America, although lineages that dispersed towards the Antilles or that remained in South America maintained their original diversification dynamics. Our findings underscore the importance of the GABI in the evolution of New World communities, which has not been investigated for most taxonomic groups. Naturally, since we identified the increase in diversification rate, the next step is to assess its drivers. Whether teiid diversification was driven by morphological, physiological, or ecological factors and whether the same pattern is replicated in other taxa with similar histories warrants further investigation.
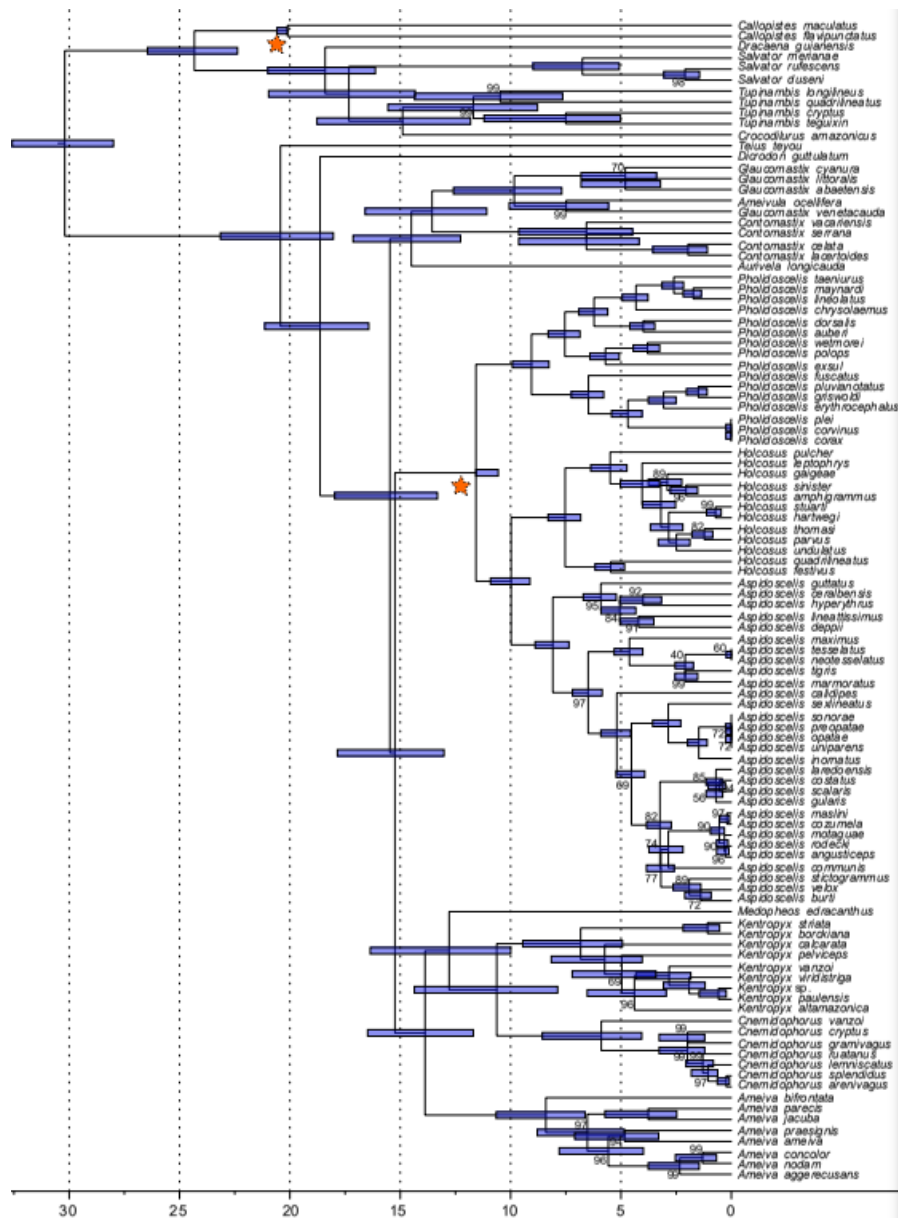
FIGURE 1 Teiidae chronogram built from fixed topology estimated with IQ-TREE and branch lengths optimized with RelTime. Bars represent the 95% confidence interval of node ages. Numbers correspond to the ultrafast bootstrap support values. Values of 100 are not shown. Note that nodes constrained by the monophyletic constraint will always show 100. Stars indicate nodes used for calibration.
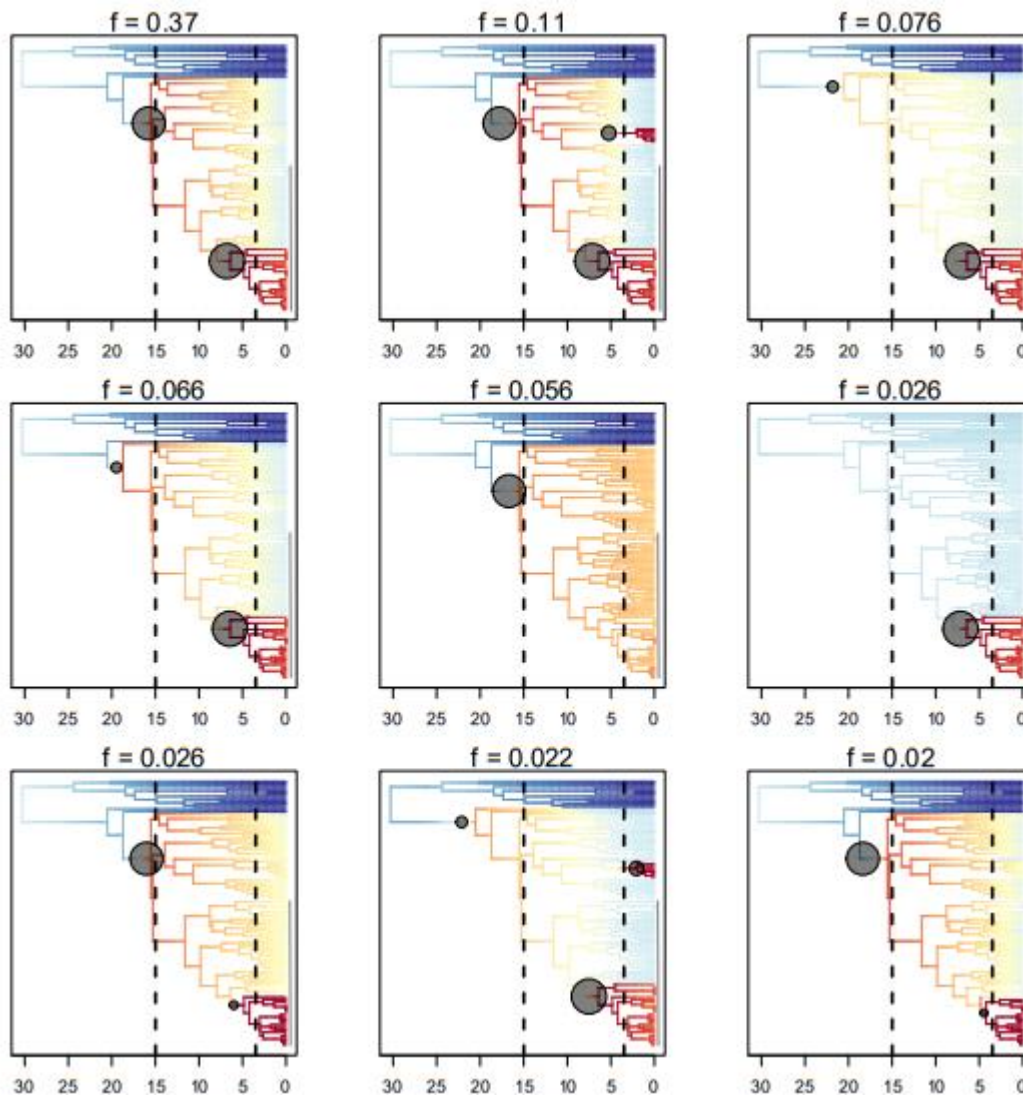
FIGURE 2 Set of highest posterior probability configurations for diversification rates. Circles indicate rate shifts, and circle size is proportional to the marginal probability of that shift occurring in that branch. Warmer colors indicate higher diversification rates, and cold colors indicate lower rates. The f values indicate the posterior probability for each configuration. The dashed lines correspond to the earliest estimated date of the closing of the Central American Seaway (15 Ma) and the full emergence of the Isthmus of Panama (3.5 Ma). The grey line marks the descendants of the North American radiation.
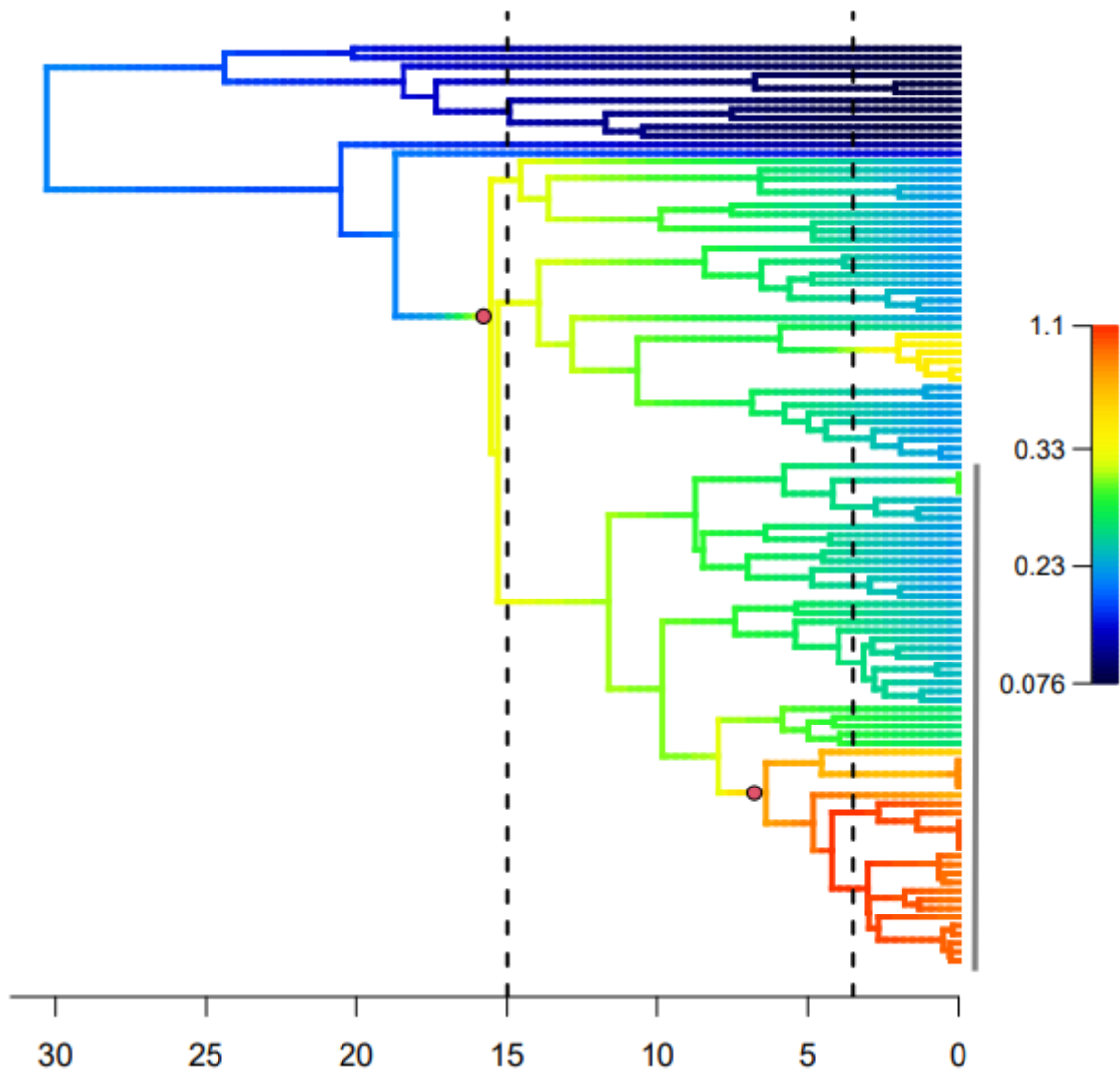
FIGURE 3 Average diversification rates between the models. Values in the horizontal axis correspond to the time before the present (Ma). Warmer colors indicate higher diversification rates, and cold colors indicate lower rates. Circles indicate shifts in the diversification rates calculated by the average of all models. The dashed lines correspond to the earliest estimated date of the closing of the Central American Seaway (15 Ma) and the full emergence of the Isthmus of Panama (3.5 Ma). The grey line marks the descendants of the North American radiation.

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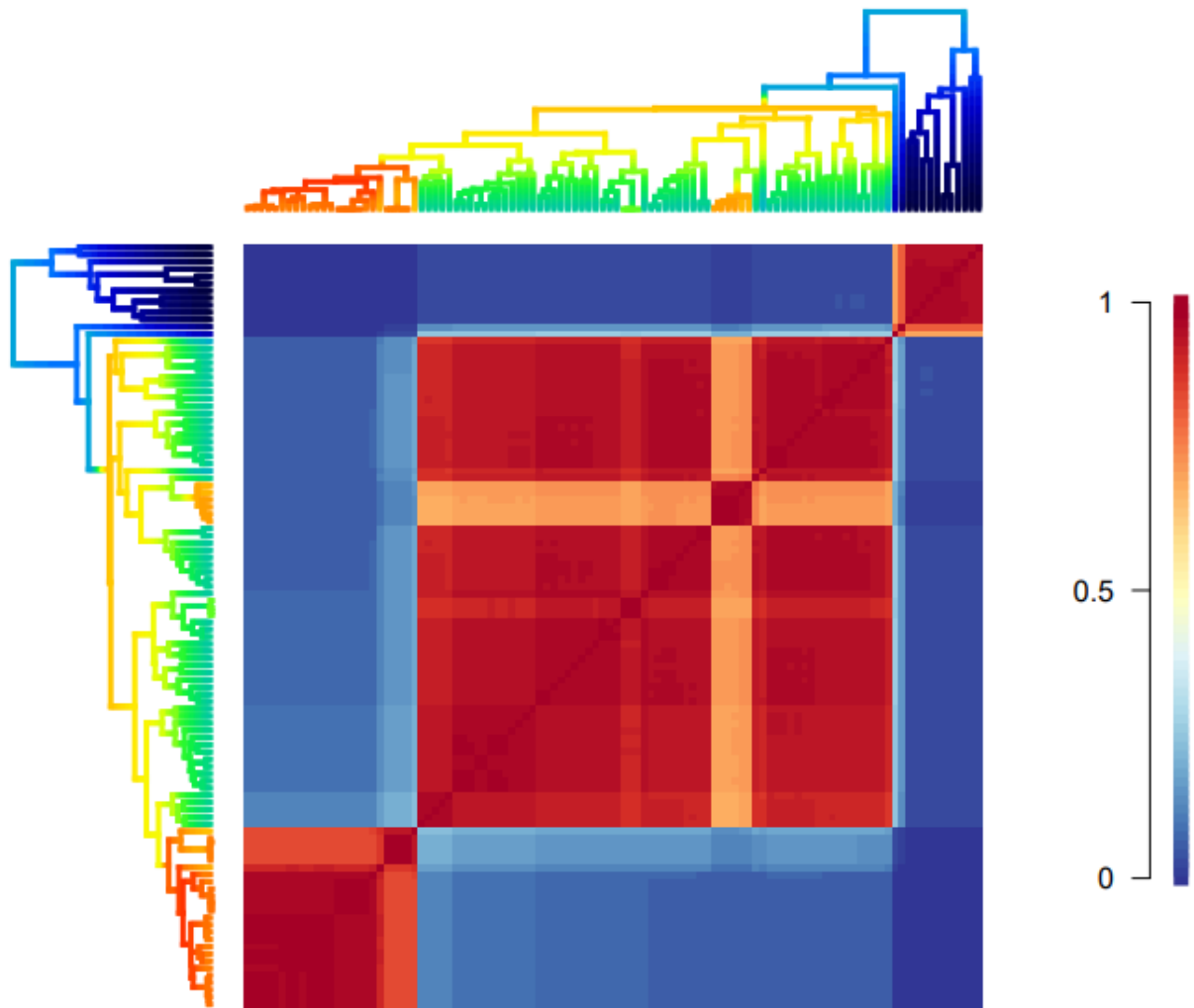
FIGURE 4 Teiidae macroevolutionary cohort matrix. The matrix is formed by lines that depart from each terminal and cross the lines from the mirrored tree. The color in each intersection corresponds to the probability that those two terminals present the same macroevolutionary dynamics. Warmer colors represent high probabilities. The matrix is mirrored in the secondary diagonal, where all the values are equal to 1 (since each terminal is being compared with itself). The legend to the right applies only to the colors in the matrix, not the colors in the trees.
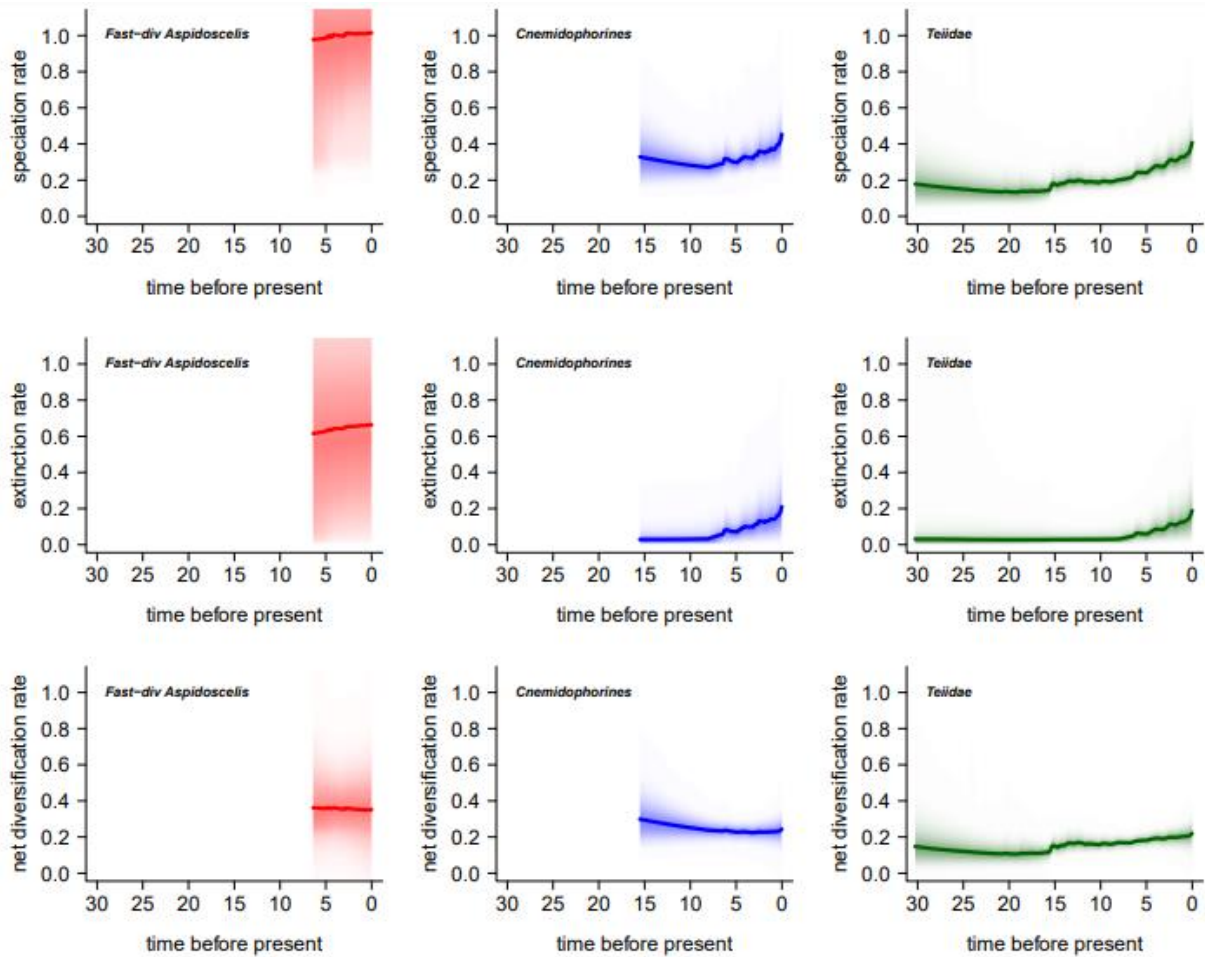
FIGURE 5 Speciation, extinction, and diversification rates (first to third rows, respectively) for the fast-diversifying *Aspidoscelis*—defined by the most recent common ancestor of *A. maximus* and *A. rodecki* (red), cnemidophorines—defined by all Teiinae excluding *Teius* and *Dicrodon* (blue), and Teiidae (green). Solid lines correspond to mean rates, and shaded areas correspond to 95% confidence intervals.

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CHAPTER 2

The drivers of teiid diversification

Whiptail lizard diversification was boosted by the colonization of North America

Abstract

Diversification is frequently associated with change—which could be anything from the colonization of a new area to the evolution of a new feature. Once a lineage changes, the organisms may be able to exploit ecological opportunities and release pressures from predators, parasites, and competitors, which may increase the rate of emergence of new species. Teiid lizards originated in South America but managed to colonize and diversify in North America. We assessed whether geographical distribution, body size, and body temperatures are associated with teiid diversification using GeoHiSSE and inverse equal-splits statistics with simulation tests. We also assessed the ecological niche overlap between North American (including Caribbean) teiids and their sister clade in South America. Our results show that only distribution range affected diversification, but we discuss that the available data might not have been enough to assess the effect of body temperatures. We also showed that these North American teiids have a wider ecological niche that encompasses almost all environmental conditions used by their sister clade in South America but with expansion mainly towards arid areas. Our results suggest that this expansion probably had a major impact on teiid diversification due to the seizing of ecological opportunities or ecological release but we do not discard possible effects of phenotypic evolution.

Keywords: diversification analysis, ecological niche overlap, habitat availability, state-dependent speciation-extinction, Teiidae.

INTRODUCTION

Phenotypic evolution is frequently evoked to explain diversification, even though the link may be context-dependent, and thus, not so easily identified (de Queiroz, 2002). Multiple studies have already reported shifts in diversification rates associated with the emergence of traits, which include morphological, physiological, ecological, and behavioral characteristics (e.g.: Biffin et al., 2010; Laserna & Herrera, 2017; Wessinger et al., 2019). However, the same has also been observed for less drastic changes as habitat shifts or the colonization of new areas, for example (Ballarin & Li, 2018; Hou et al., 2011).

The colonization of a new habitat enables the organisms to explore ecological opportunities—that is, resources underused by other taxa—and escape predators, competitors, and parasites (Schluter, 2000). This favorable scenario enables the expansion of niche breadth (Gillespie et al., 2020). Posteriorly, divergent selection acting upon populations in different environments generates specialized lineages that differentiate morphologically and ecologically from each other—which constitutes an adaptive radiation (Gillespie et al., 2020; Schluter, 2000). Indeed, the main drivers of diversification in squamates were shown to be range area expansion and arboreality—two predictors associated with the colonization of new habitats (Li & Wiens, 2022).

In addition to that, squamates are good candidates to show phenotypic evolution on physiological grounds associated with the colonization of new habitats thanks to their high dependence on environmental temperatures. Lizards are ectotherms and environmental temperatures directly influence their body temperatures, which play a key role in the colonization and persistence in novel environments (Lanna et al., 2022). Since these temperatures are associated with different types of habitats (Lanna et al., 2022), changes in body temperatures could be associated with habitat shifts and, therefore, diversification shifts. Body size was since long suggested to be a predictor for diversification, based on the idea that smaller organisms may have shorter generation times and thus, speciate faster (Hutchinson & Macarthur, 1959). However, this trait does not seem relevant for squamates (Feldman et al., 2016; Li & Wiens, 2022). Nonetheless, relevant drivers in smaller scales may be masked by general patterns, as was the case for the effect of body size in snake diversification (Feldman et al., 2016). Thus, testing these and other predictors in smaller phylogenetic scales may potentially unveil specific trait-diversification relationships.

An interesting group to test the drivers of diversification is Teiidae (Gray, 1827). Despite the origins of this family being probably in North America, all living teiids trace their history to a South American ancestor (Giugliano et al., 2007). These South American ancestors managed to disperse northwards and reached North America and the Antilles as early as the Miocene (Scarpetta, 2020; Tucker et al., 2017). Although most northern teiids descend from this single radiation, some scattered species managed to colonize areas in Central America and Caribbean islands more recently. This family is considerably conservative in ecology, with few scattered species deviating from the heliophilous, active forager, terricolous, and generalist predator pattern. There is, however, a notorious disparity in both species richness and body size between the two Teiidae subfamilies: Tupinambinae (Bonaparte, 1831) and Teiinae (Gray, 1827). While the former is composed of only 16 large-bodied species (mean maximum snout-vent length (SVL) = 379.1 ± 121.7 mm; range = 173 – 614 mm), the latter has over 150 smaller-bodied species (mean max SVL = 112.9 ± 37.79 mm; range = 52.4 – 250 mm) (Meiri et al., 2018).

A less conspicuous association could also link physiology and diversification. Teiidae maximum active body temperatures oscillate from low thirties to low forties (ºC), with the highest maximums within the desert-dwelling *Aspidoscelis* (Meiri et al., 2018; Meiri et al., 2013)—the most diverse genus in the family. The lower maximum temperatures, on the other hand, belong to species in less diverse genera, such as *Crocodilurus*, *Dracaena*, *Dicrodon*, and *Kentropyx*. However, body temperature is greatly affected by habitat, and semi-aquatic, arboreal, or forest-dwelling lineages as the ones cited above are expected to attain lower temperatures. Therefore, a correlation between diversification rates and body temperature could result from an effect of habitat, instead of a direct relationship between temperature and diversification.

Notwithstanding, if phenotype is conserved, diversification shifts could be a consequence of changes outside the organisms. This should happen if a lineage colonizes a new area that is environmentally similar to the center of origin or if it was already preadapted to the colonized area. Since no novel adaptation would be needed, descendants from the migrants should have very similar ecological requirements to their closest relatives. When this is the case, we should expect not to find any correlation between traits and diversification, and also observe high niche overlap between immigrants and their non-migrant relatives.

This study aims to assess whether diversification in Teiidae is associated with body size, body temperatures, and distribution range and to assess ecological niche overlap between North American (including Caribbean) teiids and its sister clade in South America. Since the colonization of new areas is frequently associated with increased diversification, we expect to observe higher diversification rates associated with a North American distribution. For phenotypic traits, we expect that higher diversification rates will be associated with smaller sizes and higher temperatures. Alternatively, if temperature is not related to diversification, this should mean that teiids did not need extensive physiological adaptations to colonize North America—either because the conditions in the new continent were similar to South America or because of preadaptation. In either case, we expect to find North American teiids occupying similar niches to their southern closest relatives.

MATERIALS AND METHODS

Data collection

We gathered data for maximum SVL, average minimum, average, and average maximum body temperature of active lizards, mostly from Global Assessment of Reptile Distributions (GARD) publications (Caetano et al., 2022; Meiri et al., 2018; Meiri et al., 2013; Roll et al., 2017) and complemented it with data published in later studies.

To assess ecological niche overlap we downloaded two sets of occurrence registers from the Global Biodiversity Information Facility (GBIF) (GBIF.org, 2023): one for the migrant clade, composed of *Aspidoscelis*, *Holcosus*, and *Pholidoscelis* and one for its South American sister clade composed by *Ameiva*, *Cnemidophorus*, *Kentropyx*, and *Medopheos*. We only used registers associated with preserved specimens from identified institutions after the year 2000, with individuals count different from 0. We also used the *clean_coordinates* function from the 'CoordinateCleaner' package, version 2.0.20 (Zizka et al., 2019) to identify and exclude potentially erroneous registers as coordinates falling in the sea or inside urban areas, coinciding with countries' centroids, next to biodiversity research institutions and other common spatial errors. Then, we generated random pseudoabsences for each clade in the corresponding continent using the *spatSample* function from the 'terra' package version 1.7.18 (Hijmans et al., 2023). We downloaded elevation and bioclimatic data from the Shuttle Radar Topography Mission and WorldClim 2.1 (Fick & Hijmans, 2017; Jarvis A. et al., 2008) at a resolution of 2.5 minutes. We also downloaded the normalized difference vegetation

index (NDVI) at a resolution of 0.05 degrees from the Terra satellite at EarthData (Didan & Huete, 2015). The NDVI is defined as the difference between near-infrared and visible spectral reflectance divided by their sum. This index is directly correlated with photosynthetic capacity and can be used for characterizing the environment. We downloaded monthly NDVI data from January 1st, 2001, to December 31st, 2020, and calculated mean values for each cell across all rasters. Since NDVI data is not available for high latitudes, we used the mean NDVI raster as a mask for transforming elevation and bioclimatic rasters so we could avoid dealing with empty cells. This should not impact our analyses since the maximum latitude limit for this data is way beyond the teiid distribution range. Then, we removed variables with a variance inflation factor (VIF) greater than 3.5 and extracted the values of each remaining variable for both presence and pseudoabsence coordinates.

Trait-dependent diversification

We updated teiid sequences in the multiple sequence alignment from Tonini et al (2016) and ran a constrained tree search in IQ-TREE, version 2.2.2.6 (Minh et al., 2020) using the topology from Tucker et al (2016) as a monophyletic constraint. Then, we ran a divergence time analysis in MEGA11 using the RelTime method (Tamura et al., 2021; Tamura et al., 2018). We used two fossils to calibrate the timetree. One at the base of *Callopistes* and another one at the base of cnemidophorines (Quadros et al., 2018; Scarpetta, 2020). More detailed explanations for the phylogenetic inference may be found in Chapter 1 and the resulting tree which we used in the diversification analyses is in Appendix S1.

We assessed whether diversification was associated with distribution range using GeoHiSSE, a modification of GeoSSE (Caetano et al., 2018; Goldberg et al., 2011). State-dependent speciation and extinction models (SSE) are models in which macroevolutionary rates depend on the state of a character. In GeoSSE models, species are allowed to have two states of a character (geographic distribution) simultaneously, in which case their rates will correspond to the summation of the effects of both areas. GeoHiSSE is essentially an expansion of GeoSSE to account for the effect of unmeasured variables (hidden states). Considering the effect of hidden states is essential in an SSE framework because otherwise, null models become trivial, which inflates the false positive rate (Beaulieu & O'Meara, 2016; Caetano et al., 2018). We implemented four GeoHiSSE models: range-independent diversification/without hidden states (1); range-dependent diversification/without hidden

states (2); range-independent diversification/with hidden states (3); range-dependent diversification/with hidden states (4). Distribution ranges for each species were classified as "North America" if restricted to Central and North America, including Caribbean islands; "South America" if restricted to mainland South America and islands outside the Caribbean Sea; or "both" if included mainland South America and North America/Caribbean islands. We accounted for the proportion of sampled species in each area, which were 0.527 (South America), 0.6556 (North America), and 0.8 (both). The area matrix with the classification of the distribution range for each species is in Appendix S2.

We used inverse equal-splits statistics and simulation-based significance tests (ES-sim) to assess whether speciation rates were associated with body size and body temperature (Harvey & Rabosky, 2018). The inverse equal-splits metric can be calculated through:

$$ES_i = \sum_{j=1}^{N_i} l_j \frac{1}{2^{j-1}}$$

ES_i corresponds to the diversification rate of tip i, N_i is the number of branches between tip i and the root, and l_j is the length of each branch j from the terminal branch to the root branch (Redding & Mooers, 2006). ES_i and trait values are then used to calculate Pearson's correlation coefficient, which is compared to the correlation coefficients of null simulations to assess significance. This method was shown to have similar statistical power to QuaSSE but with a lower false positive ratio (Harvey & Rabosky, 2018). Es-sim analysis does not handle missing trait data. Because of this, we ran ES-sim analyses twice for each trait. Once removed from the tree species for which we had missing trait data and once with the full tree and imputed trait data. Trait values were imputed accounting for tree branch lengths using the *phylopars* function from the 'Rphylopars' R package (Goolsby et al., 2017).

Niche overlap

We used environmental data for quantifying the ecological niche of the North American lineage and its sister group in South America using an ordination technique recommended by Broennimann et al. (2012). First, we conducted a principal component analysis (PCA) using the *dudi.pca* function from 'ade4' package version 1.7.22 (Dray & Dufour, 2007). Then, we calculated the ecological niche space in the ordination and tested for niche equivalency and similarity (Warren et al., 2008) using the 'ecospat' package, version 3.5 (Di Cola et al., 2017).

The niche equivalency test groups all the records together and splits them randomly into two data sets with the same size as the original ones and checks if overlap remains constant through iterations. The niche similarity test, on the other hand, shifts the occurrence density in one range and calculates the overlap between the simulation and the other observed niche. In both cases, the comparison between observed and simulated is made through Schoener's D overlap statistic, which ranges from 0 (no niche overlap) to 1 (identical niches). Each test was run twice, one for each alternative hypothesis (higher or lower equivalency/similarity), and 1000 replications were conducted in each case. All analyses were carried out in R, version 4.3.1 (R Core Team, 2023).

RESULTS

Trait-dependent diversification

The GeoHiSSE model that best explains teiid diversification includes the effect of distribution range without hidden states with a 0.69 AIC weight (Table 1). The second-best model was the null model with hidden states with a 0.31 AIC weight. The null model without hidden states and the alternative model with hidden states had negligible contributions. Figure 1 depicts diversification rates and distribution ranges for Teiidae species. Rates were estimated using the average of all models weighted by their AIC weights. The average model attributes higher speciation rates associated with a North American distribution, which corroborates our first hypothesis.

We gathered SVL data for 104 species, mean minimum and mean maximum active body temperature for 58, and mean body temperature for 56. These data and the corresponding references are in Appendix S3. ES-sim results showed that none of these predictors—either with imputed or unimputed trait data—had a significant correlation with diversification rates (Table 2). Our hypotheses were of inverse correlation with body size and direct correlation with body temperature.

Niche overlap

The variables used to represent the ecological niche were elevation, NDVI, and the bioclimatic variables from WorldClim: Bio2, Bio8, Bio9, Bio15, Bio18, and Bio19 (Mean Diurnal Range, Mean Temperature of Wettest Quarter, Mean Temperature of Driest Quarter,

Precipitation Seasonality, Precipitation of Warmest Quarter and Precipitation of Coldest Quarter). A correlation circle depicting all the environmental variables considered and the correlations between them is shown in Figure 2. The observed Schoener's D value for niche overlap was 0.16. Niche equivalency tests showed that niches had lower overlap than random but niche similarity tests showed that niches were as similar to each other as random simulations (Figure 3). These results seem to go against our hypothesis of high niche overlap. However, plotting the ecological niches reveals teiid's niche is broader in North America, and it encompasses most of the ecological conditions used by their sister clade, with only a small set of conditions used by the southern clade that are not colonized by the northern teiids (Figure 4). Figure 4 also shows that the highest density of teiid registers in North America comes from areas with different environmental conditions than the ones used by its sister lineage in South America. Overall, despite the low Schoener's D value, North American teiids had kept almost the entire ecological niche of their sister lineage—and putatively, their ancestors', which corroborates our last hypothesis, albeit in a way we did not anticipate.

DISCUSSION

We found teiid speciation rates to be associated with the distribution range, with the North American range associated with higher rates, according to our first hypothesis. Body size and body temperature, however, were not associated with diversification. Contrary to our expectations, ecological niche similarity between North American teiids and their closest relatives was no different from random simulations, and niche equivalency was lower than random. However, we found that North American teiids occupy a broader ecological niche that encompasses almost completely and extends beyond the niche of its sister clade—which is close to our hypothesis of maintenance of ecological niche requirements. These results suggest that the North American lineage expanded the ancestral ecological niche upon colonizing new environments. Beyond that, we showed that the highest occurrence density of teiids in North America is registered in different environments from the utilized by its sister lineage in South America.

Although richness and body size differences between the two Teiidae subfamilies seem to follow a predicted pattern of an inverse relationship between body size and diversification rate (Hutchinson & Macarthur, 1959), we did not find any relationship between them. Indeed, body size was shown previously not to be related to diversification in

squamates (Feldman et al., 2016; Li & Wiens, 2022). Our phylogeny is considerably comprehensive (over 60% of known teiid diversity) and we had a high coverage for this trait, so despite possible effects derived from incomplete taxon sampling, we think it is unlikely that body size influences diversification rates for this family. However, as body size is fairly simple to measure and easily available for a great number of species (e.g., Meiri et al., 2018), we encourage other researchers to keep including it in their analyses. As for body temperatures, on the other hand, our results are not so reliable. This is because these data were only available for a small subset of species, and for many of them, minimum and maximum active body temperatures were the same, indicating that the measures were taken from only one individual (Meiri et al., 2018). Body temperatures in ectotherms are associated with habitat (Lanna et al., 2022), and since we observed that North American teiids managed to colonize different environmental conditions from their southern relatives, shifts in body temperatures are to be expected. Another layer to this is that, unlike GeoHiSSE, ES-sim does not account for incomplete taxon sampling on the phylogeny, which could greatly bias the results especially if sampling is not random. Although our taxon sampling does not appear to be blatantly biased, the mere elongation of branch lengths derived from the exclusion of species could potentially diminish the diversification metric enough to affect the results.

The calculated Schoener's D statistic points to low niche overlap (0.16). However, this is almost entirely due to the expansion of the ecological niche instead of divergence. Since Shoener's D is a symmetrical index, its value will be the same for the compared taxa, even though they differ greatly in breadth. Because of this, a low value of D may hide a scenario of almost complete overlap for the narrower niche, as is the case for these teiids. Broadening of the ecological niche and subsequent rapid speciation is an expected pattern following the colonization of a novel environment (Schluter, 2000). However, the observed ecological differentiation was not accompanied by much phenotypical change, at least for the measured variables. Several hypotheses could be raised to explain this niche discrepancy, but we will highlight two of them. The first hypothesis is that the migrating teiids adapted to the new environment by evolving traits that relaxed their environmental requirements. Since North American teiids diversified so swiftly in arid areas, we would expect to find an effect of body temperature on diversification. However, as discussed above, available data on body temperature may not be enough to detect this influence. Setting aside data limitations, yet another factor prevents us from completely discarding the effect of phenotype on teiid diversification. Despite the best and averaged models having estimated higher speciation rates

for North America, since most teiids distributed in this region belong to a single clade, the emergence of a new adaptation at its base could have confounded the results. Indeed, this could be the reason why the null model with hidden traits attained a moderate AIC weight. Alternatively, the variables we measured may not be the most relevant ones for teiid diversification. Investigations focusing on more phenotypical traits such as limb length, head shape, sprint speed, and others would help to clarify this point.

Another—more convoluted—possibility is that migrating teiids were preadapted to a wider range of environmental conditions than the ones they had access to in South America. This seems at odds with our finding that the environmental conditions of most areas occupied by teiids in North America are also available in South America, albeit unoccupied by these lizards. This opens the question of why the closest relatives of the migrating teiids did not colonize these habitats if they were preadapted to them. A point could be made that these areas are inaccessible. We showed that most of the ecological niche expansion in the invaded continent was towards drier environments, where this lineage thrived the most. Whilst dry areas are easily reachable in North America from the Isthmus of Panama, arid South American environments at low latitudes can only be found West of the Andes, a kind of barrier shown to be untraversable for other lizards (Ghaedi et al., 2021; Smissen et al., 2013). On the other hand, at intermediate latitudes, the Patagonian arid plains are too cold, and the low temperatures probably constrain the geographical distribution of the family (Jarnevich et al., 2018). Nevertheless, other teiids inhabit arid environments in transandine South America with quite low diversity standards: only two species of *Callopistes* and three of *Dicrodon*. These genera, however, are more distantly related to the North American lineage, and other factors may play an important role—even more considering that the most diverse teiid genera can be grouped in a clade that does not include either. Another possibility though, would be that arid areas in transandine South America are not extensive enough to further the diversification of these lineages.

Another factor potentially affecting teiid diversification is the astonishing proportion of hybrid parthenogenetic species within Teiinae (Barley et al., 2022). Approximately 10% of the subfamily are exclusively parthenogenetic, and this proportion rises to 25% in *Aspidoscelis*. Unisexuality in squamates arises from hybridization (Fujita et al., 2020), which may generate novel species faster than cladogenesis—since no differentiation under reproductive isolation is required—which should inflate speciation rates. Moreover, parthenogenetic lizards were already suggested to have elevated speciation rates, albeit even

higher extinction rates due to a lack of genetic variability and mutation accumulation, which explains why parthenogenetic species tend to be younger (Fujita et al., 2020; Moreira et al., 2021). However, testing this hypothesis is not so straightforward since in this case, diversification would not be driven by a binary trait (sexual vs parthenogenetic) but rather by the propensity to hybridization, which is not so easily quantified. Speaking of hybridization, one criticism that may be raised against this work is that our analyses considered a bifurcating teiid tree—when in fact, hybridizations make it to be reticulated. This is very much true, but also is true that currently there are no algorithms able to run diversification analyses on reticulated trees, which makes the incorrect but useful model of a bifurcating tree, the only option for this kind of work.

Our results suggest that the teiid diversification burst after the colonization of North America was due to the great availability of suitable habitats. Faster diversification in newly colonized areas is congruent with the seizing of ecological opportunity and ecological release, and our results suggest that at least one of them took place at this point in teiid evolution. However, we do not feel confident about discarding an association between body temperature and diversification due to the low quality of the data. More insights on teiid diversification could come from assessing the effects of hybridization and other ecological variables related to physiology, morphology, and especially biotic interactions.

TABLES

Table 1. AIC weights for GeoHiSSE models.

Model	AIC weight
Range-independent	$2.4*10^{-5}$
Range-dependent	0.69
Range-independent + Hidden states	0.31
Range-dependent + Hidden states	$2.8*10^{-6}$

Table 2. Pearson's correlation coefficient *rho* between diversification rates and body size (snout-vent length—SVL), average minimum, average, and average maximum body temperature (Tb) of active teiids, and *P* values for the comparison between observed correlations and simulations. *P* values in the table do not correspond to the significance level of the correlations between diversification rates and traits. Results are shown for analyses with both imputed and unimputed data.
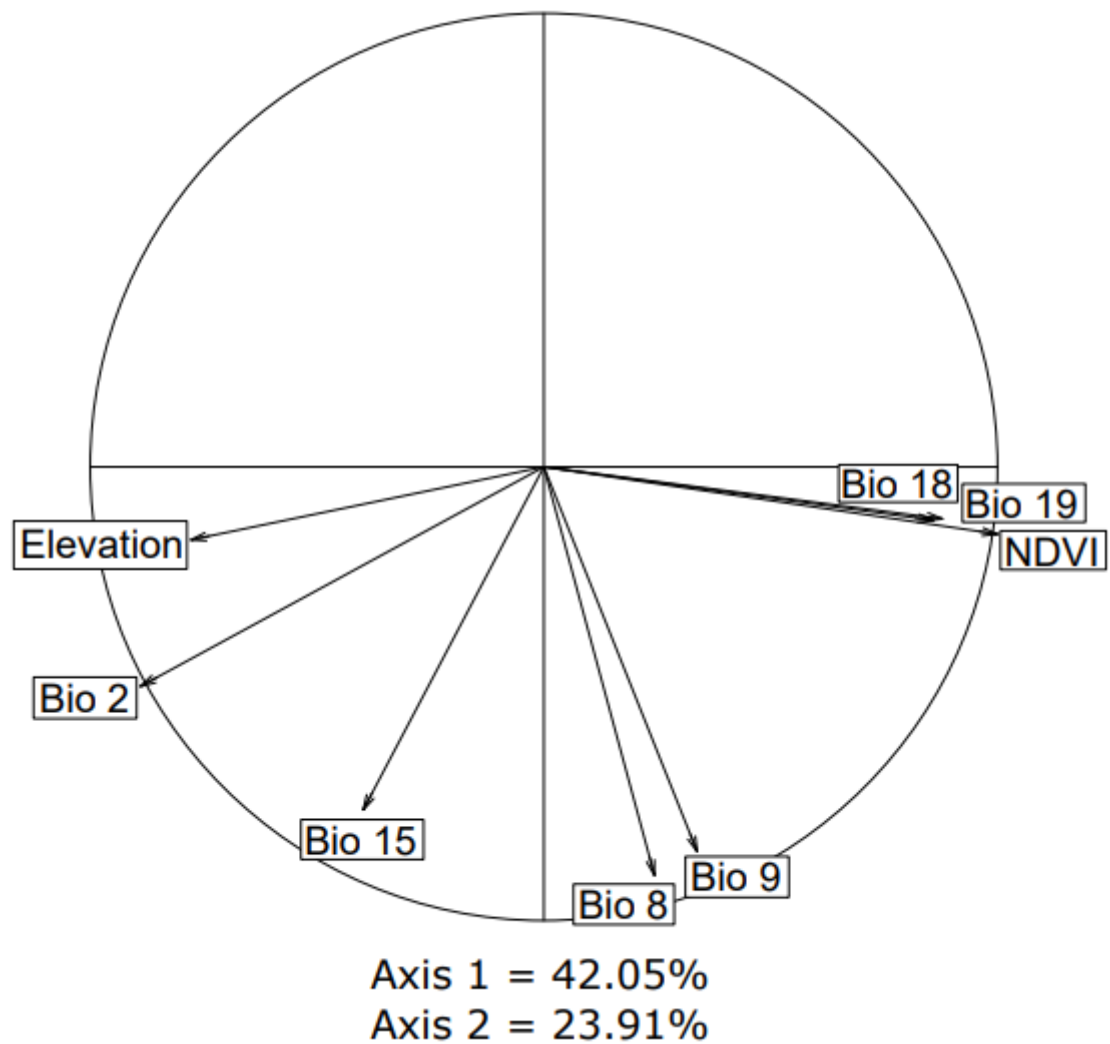
| Predictor	Rho	P
Maximum SVL (imputed)	-0.4075660	0.1818182
Average minimum Tb (imputed)	0.2050815	0.5074925
Average Tb (imputed)	0.2688443	0.3976024
Average maximum Tb (imputed)	0.3280758	0.2997003
Maximum SVL	-0.4040589	0.1658342
Average minimum Tb	0.3260446	0.3756244
Average Tb	0.4072709	0.3036963
Average maximum Tb	0.4133281	0.2417582
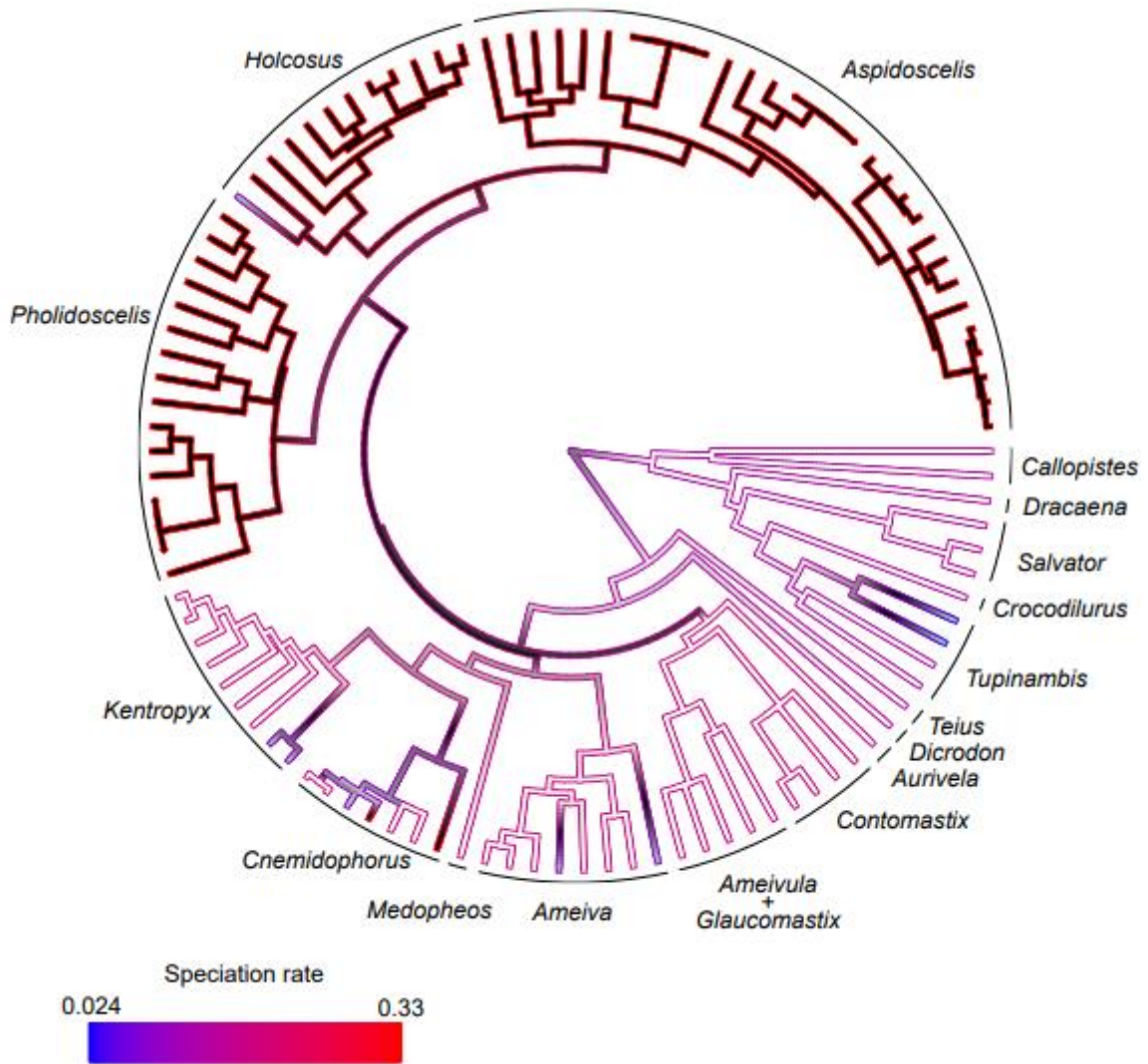
FIGURE 1 Distribution area and speciation rates estimated for Teiidae by GeoHiSSE. Branch colors correspond to the distribution range: white for South America, black for North America, and grey for both. Colors outlining the branches correspond to AIC weighted average speciation rates, following the legend on the inset.

Axis 1 = 42.05%
Axis 2 = 23.91%

FIGURE 2 Correlation circle derived from the principal component analysis of the environmental variables used to characterize the ecological niche of teiids. The angles between predictors correspond to the correlation between them and the projections of each vector on the axes are proportional to their contributions for each principal component.
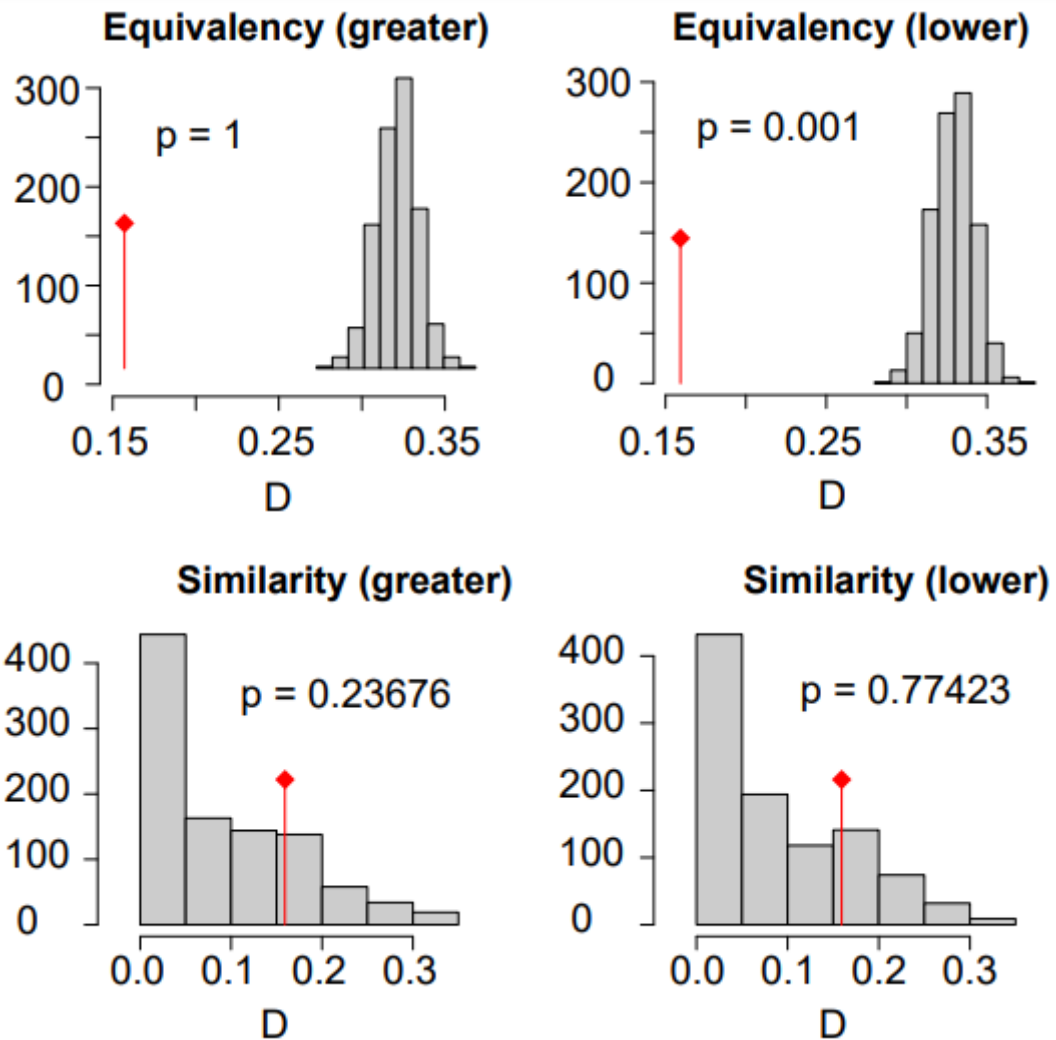
FIGURE 3 Histograms of simulated overlaps for equivalency and similarity tests. The text inside the parenthesis indicates the alternative hypothesis tested: "higher" stands for "niche equivalency/similarity is higher than random" and "lower" stands for "niche equivalency/similarity is lower than random". The red line represents the observed Schoener's D value. The respective p values are shown in each graph.
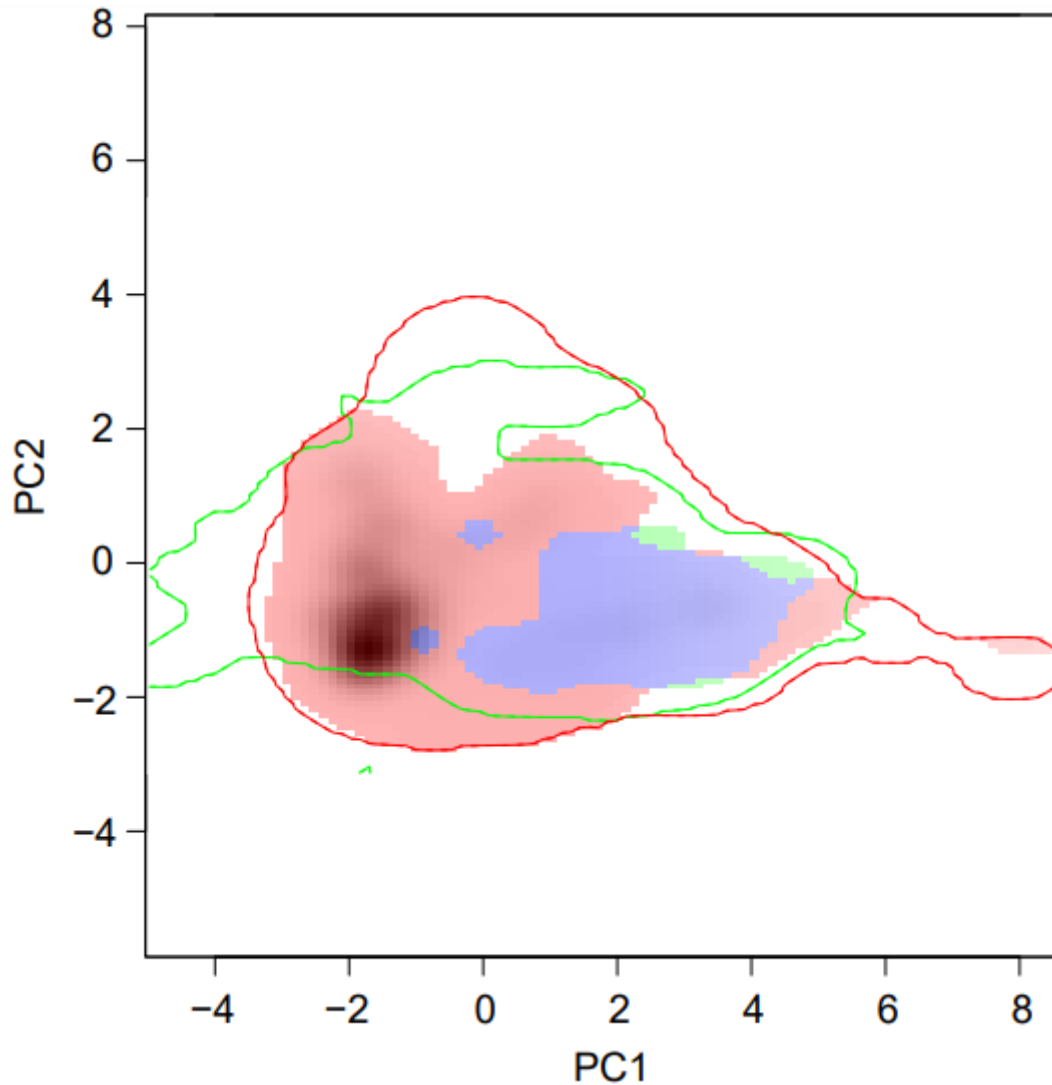
FIGURE 4 Niche overlap between North American teiids (*Aspidoscelis*, *Holcosus*, and *Pholidoscelis*) and their sister clade (*Ameiva*, *Cnemidophorus*, *Kentropyx*, and *Medopheos*). The axes depict the principal components of the environmental variables used to characterize the ecological niche. The lines represent the ecological conditions in North America (red) and South America (green). The blue stain corresponds to the niche overlap between both lineages, the red stain corresponds to the ecological niche exclusive to the northern lineage and the green stain corresponds to the ecological niche exclusive to the southern lineage. The shading indicates the density of registers of North American teiids.

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CONCLUSÃO

Os resultados apontam para aumentos da taxa de diversificação em dois pontos na filogenia de Teiidae. O primeiro antecede o GABI por alguns milhões de anos e deu origem ao mais diverso grupo dentro da família. O segundo ocorreu em um clado profundamente aninhado entre os descendentes da radiação norte-americana. Além disso, os resultados também mostraram que a distribuição na América do Norte está associada à diversificação mais rápida. O aumento da taxa de diversificação da linhagem que se dispersou através do Istmo do Panamá já era um resultado esperado – não apenas pela predição teórica, como também pela notável riqueza de espécies deste clado. Este resultado é congruente com a exploração de oportunidades ecológicas e liberação ecológica que comumente se seguem à colonização de uma nova área. Este quadro ganha cores ainda mais vivas quando analisamos o nicho ecológico dos imigrantes. A vultosa expansão para ambientes áridos e a profusão de registros nessas áreas mostram que esses lagartos encontraram na América do Norte uma terra onde puderam prosperar desimpedidos – uma espécie de destino manifesto ectotérmico, se me permitem o paralelo poético.

As linhagens que permaneceram na América do Sul, por outro lado, conservaram suas taxas de diversificação sem variações importantes, contrariando o cenário que sugeria reduções nas taxas de diversificação em consequência da interação com imigrantes. Os dois resultados juntos permitem especular que não havia entre a fauna norte-americana nenhum grupo que pudessem representar um risco para a sobrevivência de Teiidae enquanto linhagem – motivo pelo qual não foram negativamente impactados pelos imigrantes –, o que permitiu que esses lagartos expandissem sua distribuição e se diversificassem rapidamente no continente. Decerto que este ponto é mera especulação, mas uma que parece plausível em vista do registro fóssil conhecido.

Se a abundância de ambiente adequado é manifesta e a falta de predadores e competidores é suposta, o efeito do fenótipo na diversificação ainda permanece em grande parte inconclusivo. De mais seguro, temos a ausência de efeito do tamanho corporal na diversificação. Resultado que, apesar de contrariar a primeira impressão que se tem do grupo – além de uma hipótese clássica acerca dos determinantes da diversificação biológica – não se pode receber com surpresa dada a literatura disponível. Mais dúbia é relação entre temperatura corporal e diversificação. Dado que esses lagartos se diversificaram profusamente em ambientes desérticos, que estão associados a temperaturas corporais mais altas em animais

ectotérmicos, parece estranho não encontrar nenhum efeito significativo. Isso, porém, pode ser explicado pela baixa qualidade e abrangência dos dados disponíveis para esse preditor, que podem ter impedido as análises de acusarem um padrão.

Por fim, o GABI teve um amplo efeito sobre a diversificação de Teiidae, permitindo que essa linhagem atingisse áreas onde se diversificou profusamente. Não obstante, as minúcias desta história ainda permanecem desconhecidas. Há uma incalculável quantidade de variáveis que potencialmente afetam a diversificação de uma linhagem, rol que este trabalho apenas arranha. Morfologia, história de vida, dieta, genética e uma curiosa propensão à hibridização são apenas alguns exemplos de potenciais determinantes da diversificação que tiveram que ser deixados de fora desta dissertação em virtude da ausência de dados detalhados ou métodos adequados. Entretanto, como os modelos só são úteis na medida em que simplificam a complexidade real ao focar no essencial, minha sugestão para pesquisadores que se debrucem sobre essa questão no futuro é focar na fisiologia – para além das questões mais tradicionais envolvendo interações biológicas. Para tal, uma coleta de dados mais sistemática deve ser realizada, de preferência englobando outras variáveis associadas à temperatura corporal como velocidade de corrida e taxa metabólica.