



Vipers on the Scene: Assessing the Relationship Between Speciation and Climatic Niche Evolution in Venomous Snakes (Reptilia: Viperidae)

Citlalli Edith Esparza-Estrada¹ · Laura R.V. Alencar² · Levi Carina Terribile³ · Octavio Rojas-Soto⁴ · Carlos Yáñez-Arenas⁵ · Fabricio Villalobos¹

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Abstract

Evolutionary radiations have been a key paradigm in studying species richness and their temporal and geographic variation. These patterns have been associated with the interaction between the rate at which species originate and the rate at which phenotypic traits evolve. Nevertheless, despite extensive empirical testing, questions remain regarding the prevalence of the coupling between these rates within lineages. Climatic niche evolution is an important driver of speciation since niche divergence and niche conservatism may result in reproductive isolation. Here, we test whether the rate of climatic niche evolution influences the speciation rate for a globally distributed venomous snakes' clade, the Viperidae family. Contrary to expectations, we found no general relationship between climatic niche evolution rates and vipers' speciation rates. Our results showed that speciation during the radiation of vipers could have occurred without strong ecological niche divergence, perhaps through a non-adaptive process that could still include a complex pattern of iterated adaptive and non-adaptive radiations.

Keywords Viperidae · phylogenetic niche conservatism · richness · non-adaptive radiation · niche breadth · niche position

Introduction

Species diversification dynamics, namely the balance between speciation and extinction can reveal the timing and pathways that led to present-day patterns of species richness (Reznick & Ricklefs, 2009). These patterns have been associated with the interaction between the rate at which species originate and the rate at which phenotypic traits evolve (Cooney & Thomas, 2021). A positive association between these rates occurs during adaptive radiation when diversification is driven by speciation mediated by high rates of phenotypic evolution that result in different species adapted to distinct ecological niches (Losos, 2010; Schluter, 2009; Stroud & Losos, 2020). In contrast, non-adaptive radiations involve diversification with slight ecological divergence that results in species occupying similar ecological niches, but likely species can further diversify ecologically if conditions change (Czekanski-Moir & Rundell, 2019; Rundell & Price, 2009; Simões et al., 2016). Both adaptive and non-adaptive radiations can underlie the diversification of lineages belonging to the same clade resulting, for example, in a mixture of ecologically-similar allopatric

✉ Citlalli Edith Esparza-Estrada
calli.edithsita@gmail.com

✉ Fabricio Villalobos
fabricio.villalobos@gmail.com

¹ Laboratorio de Macroecología Evolutiva, Red de Biología Evolutiva, Instituto de Ecología, A.C, Xalapa, Veracruz, México

² Department of Ecology and Evolutionary Biology, Yale University, New Haven, CT 06511, USA

³ Laboratorio de Macroecología, Universidade Federal de Jataí, Goiás, Brasil

⁴ Laboratorio de Bioclimatología, Red de Biología Evolutiva, Instituto de Ecología, A.C, Xalapa, Veracruz, México

⁵ Laboratorio de Ecología Geográfica, Unidad Académica Sisal, Facultad de Ciencias, Unidad de Conservación de la Biodiversidad, Parque Científico y Tecnológico de Yucatán, Universidad Nacional Autónoma de México, Mérida, Yucatán, México

or parapatric species and highly ecologically-differentiated sympatric species (Rundell & Price, 2009). The prevalence of a positive association between speciation and phenotypic evolution leads us to assume that they are indeed typically coupled (Cooney & Thomas, 2021; Reis et al., 2018; Title & Burns, 2015). Nevertheless, speciation disassociated from phenotypic divergence has also been observed in several taxa (Crouch & Ricklefs, 2019; Koch et al., 2020; Lee et al., 2016; Maestri et al., 2017; Ramírez-Reyes et al., 2022); which has led to questioning which phenotypic aspects are actually related the speciation process.

Several factors have been proposed as correlates of speciation rates, including morphology (Mahler et al., 2010; Price et al., 2016; Rabosky & Adams, 2012), behavioral traits (Mason et al., 2017), and climatic niche (Folk et al., 2019; Reis et al., 2018). Climatic niches are represented by the multidimensional nature of the preferred climatic conditions that species occupy (Colwell & Rangel, 2009). Studying climatic niche evolution requires considering different aspects such as breadth and position that can be related to the mechanisms enabling lineages to diversify (Schnitzler et al., 2012; Velasco et al., 2016). For example, under climatic niche conservatism a relatively slow rate of change in species' niche breadth and position through time, geographic expansion may be prevented, leading to allopatric speciation (Fisher-Reid et al., 2012). In contrast, under climatic niche evolution, relatively high rates of change in species' niche breadth and position through time may allow the colonization of new environmental conditions in some populations but not others, facilitating reproductive isolation and, thereby, speciation (Hua & Wiens, 2013; Jezkova & Wiens, 2018). Both of these hypotheses are based on the assumption that speciation is directly influenced by the dynamics of climatic niche evolution (Cooney et al., 2016). Evidence about the relationship between climatic niche evolution rates and speciation rates is growing, with results implying different relationships. For instance, Seeholzer et al. (2017) and Cooney et al. (2016) found a positive relationship between climatic niche evolution and bird lineage speciation. In contrast, Folk et al. (2019) found that speciation rates were not coincident with rates of niche evolution in flowering plants. Thus, speciation rates may differ across clades in response to the specific environment experienced. As such, the existence of a widespread correlation between diversification rates and rates of climatic niche evolution at evolutionary timescales remains unclear.

Here, we test the hypothesis that the climatic niche evolution rate influenced the speciation rate in the family Viperidae (~380 species), a globally distributed venomous snakes clade. Vipers arose ~50 million years ago in the early Eocene, with a tropical origin (Alencar et al., 2016; Wüster et al., 2008). Most extant species of vipers are found

in the tropics, but numerous species are also occurring in temperate regions and almost in every terrestrial ecosystem (Terribile et al., 2009). Under this scenario, one possible explanation for their distributional pattern and spatial variation in species richness is the complex dynamics of climatic niche evolution, characterized by strongly conserved climatic niches among closely related species accompanied by shifts in niche breadth evolution that allowed them to occupy different regions of the world (Esparza-Estrada et al., 2022). Such explanations suggest that speciation and the dynamics of climatic niche evolution along the family history may be related. However, this relationship has only been implied but not explicitly tested. To address this issue, we assessed both rates of speciation and climatic niche evolution, considering niche breadth (NB) and niche position (NP), and tested whether these rates are correlated. We focused on species-level rates, also known as tip rates, derived from evolutionary models and on a recently proposed framework to correlate both rates based on simulation and phylogeny rescaling (Cor-STRATES; Cooney & Thomas 2021). We did not find an association between the rates of speciation and climatic niche evolution, suggesting that species diversification in vipers occurred without substantial climatic niche divergence.

Materials and Methods

Distributional Data and Phylogenetic Relationships

For our analyses, we gathered, evaluated and, if necessary, modified distributional data for 210 species of the Viperidae family from Roll et al. (2017) based on the known distribution of species. Range maps of each species were redrawn on a grid cell system of 1°x1° resolution and the presence or absence of each species in each cell was recorded with *letsR* package version 4.0 (Vilela & Villalobos, 2015). We used the maximum clade credibility (MCC) tree from Alencar et al. (2016).

Climatic Niche Characterization

To characterize the multivariate nature of species' climatic niches based on their range maps (Hutchinson's duality; Colwell & Rangel 2009), we assembled nine variables recognized as influential in determining the geographic distribution and richness pattern of vipers (e.g., Lourenço-de-Moraes et al., 2019; Terribile et al., 2009) and obtained their values across each species ranges (i.e., at each occupied grid cell). Variables came from WorldClim 2.0 online database (Fick & Hijmans, 2017). These were: Annual Mean Temperature (bio1), Isothermality (bio3), Temperature

Seasonality (bio4), Max Temperature of Warmest Month (bio5), Min Temperature of Coldest Month (bio6), Annual Precipitation (bio12), Precipitation of Wettest Month (bio13), Precipitation of Driest Month (bio14) and Precipitation Seasonality (bio15).

To obtain measures of niche position and niche breadth, we used the Outlying Mean Index (OMI; Dolédec et al., 2000). This is an ordination procedure that considers a theoretical niche that describes the climatic conditions occupied by the studied clade (i.e., Viperidae family) and determines how distant are each species' mean climatic conditions from the clade's average (i.e., a species' niche relative to the family's niche). This distance can be taken as a measure of niche position in the climatic hyperspace. We used OMI's first niche axis (PC1) scores to measure niche position. Using the same ordination procedure, we measured species' niche breadth (tolerance) as the variability of their occupied climatic conditions obtained by calculating the variance of the species occurrences in the climatic hyperspace (Gouveia et al., 2014; Peixoto et al., 2017).

Rates of Speciation and Climatic Niche Evolution

To assess the correlation between speciation rates and climatic niche evolution, we followed the Cor-STRATES approach recently developed by Cooney and Thomas (2021). First, we estimated the per-lineage rates of speciation using the Bayesian Analysis of Macroevolutionary Mixtures (BAMM v2.5.0; Rabosky 2014) method that has been previously tested for the highest degree of accuracy between methods for the estimation of tip rates in Cor-STRATES approach. BAMM is based on a reversible-jump Markov chain Monte Carlo (MCMC) method, the inference is based on the combination of prior and current information that is represented in the posterior distribution. The priors (i.e., speciation and extinction initial parameters) were estimated assuming a pure birth model and then parametrized under their individual probability distributions using the 'setBAMMpriors' function in the BAMMtools package for R (Rabosky, 2014). We then used these estimated parameters to run BAMM analyses and obtained the posterior probabilities of tip-based speciation rates. As incomplete taxon sampling may bias analyses of speciation from phylogenetic trees, BAMM allows the integration of an incomplete sample correction to account for incomplete taxa via a global sampling fraction parameter. When species are not randomly sampled, it is feasible to include various levels of non-randomness (Rabosky, 2014). We specified sampling fractions selecting 12 main clades of the phylogeny (SI Table 1), and sampling probabilities of each selected clade were specified according to the currently described diversity of Viperidae on the Reptile Database (Uetz et al., 2021).

We conducted BAMM analyses for 25 million generations, sampling every 10 000 generations, and 20% of the samples were discarded as burn-in to remove the lowest likelihood values. Mean per-branch speciation rates were calculated with 'getMeanBranchLengthTree' function in BAMM tools (Rabosky, 2014).

Second, to obtain the rates of climatic niche evolution, we first estimated the phylogenetic signal for each trait (NB $\lambda=0.45$, NP $\lambda=0.93$) and used a lambda transformation to rescale the phylogeny using the 'transformPhylo' function in MOTMOT package v1.1 (Puttick et al., 2020). We then calculated tip rates of phenotypic (climatic niche) evolution using the variable rates model in BayesTraits v.4 (Pagel & Meade, 2006), with the default priors. We ran the model for 25 million generations, sampling every 10 000 generations and 20% iteration burn-in to remove the lowest likelihood values. We estimated tip rates as a proportion of the expected rate of evolutionary change on each branch, dividing the output tree branch lengths by the original input tree branch lengths (Cooney & Thomas, 2021). Runs of each analysis were assessed for convergence using CODA package v0.19-4. Finally, to evaluate the correlation between rates, we log-transformed the rate estimates and tested for correlations between the rate of speciation and the rates of climatic niche breadth and climatic niche position evolution using a two-tailed Spearman's rank correlation.

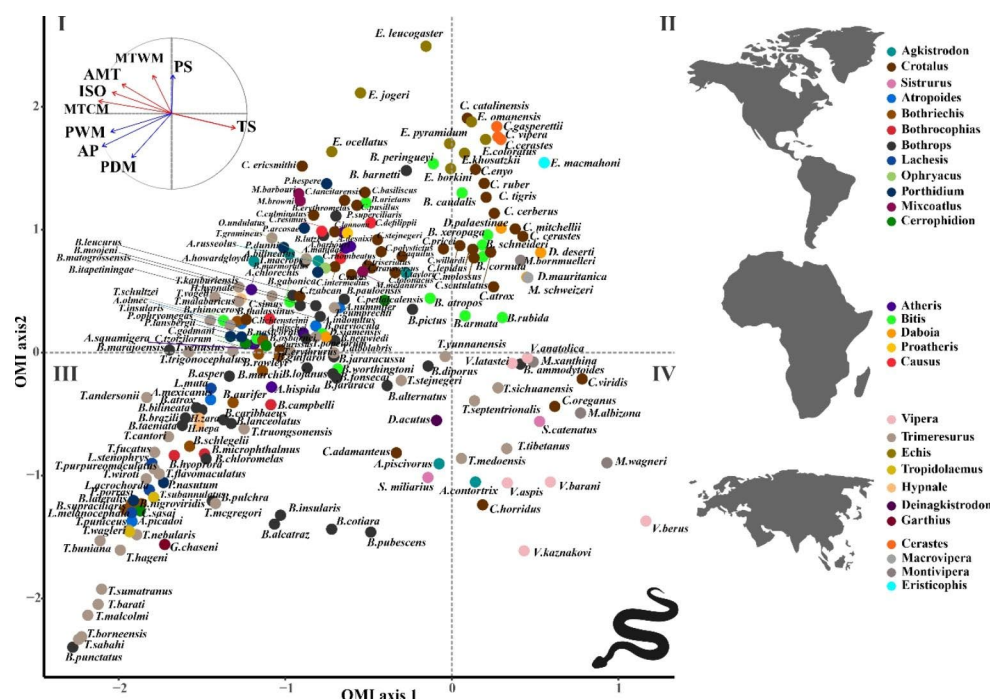
Results

Climatic Niche Characterization

The first two axes of the OMI accounted for 90% of the explained variability in climatic conditions occupied by vipers, with the first axis representing 68.95% of the variance and the second axis explaining 21.43%. The position of the species along the first two OMI axes is presented in Fig. 1. The multivariate climatic space of Viperidae species captured four main groups characterized by temperature, precipitation, precipitation seasonality, and temperature seasonality. The first group in quadrant I correspond to those species related to temperature variability and includes the greatest number of species. The second largest group of species in quadrant III is related to precipitation variability.

The third group in quadrant II is related to precipitation seasonality and corresponds closely to those species that inhabit mainly arid regions, for instance, *Crotalus enyo*, *C. ruber*, *C. tigris*, *C. mitchellii* found in the Sonoran Desert in northwestern Mexico. Similarly, rupicolous species endemic to southern Africa as *Bitis rubida*, *B. armata*, *B. caudalis*, *B. schneideri*, and *B. xerophaga*. The last group in quadrant IV corresponds with species related to temperature seasonality

Fig. 1 OMI analysis of Viperidae. Niche position of the species along the first two axes. Each colored dot on the right side indicates the genus included in the analysis. Each species is represented by colored dots within the axes. Red arrows indicate variables related to temperature and blue arrows variables related to precipitation



which represents species distributed in subtropical and temperate regions such as the *Vipera* genus distributed in North west of Africa, Europe, and central and eastern Asia. Also, the western North American rattlesnake *Crotalus oreganus* and *C. viridis* were found in the midwestern United States and extended from southern Canada.

Our estimates of OMI species tolerance indicated that 178 species showed low niche breadth values that imply that species occupy a limited range of environmental conditions (i.e., specialist species). In contrast, 32 species showed high values indicating that species are distributed across widely variable ecological conditions (i.e., generalist species). For instance, one species with the lowest values of tolerance *Crotalus tancitarensis* is a species distributed in upper elevations of the volcano Cerro Tancitaro in Michoacán, México. Another example is *Bothriechis supraciliaris*, which inhabits the mountains of Valle del General and the Coto Brus altiplano in the southwest of Costa Rica. On the other hand, we found species with high values of species tolerance, for instance, *Lachesis acrochorda* is found in western Panamá, Colombia and northeastern Ecuador from seal level to approximately 1600 mnsl where inhabits tropical forest with high levels of precipitation (SI Fig. 1; SI Table 2).

Speciation Rates and Climatic Niche Evolution Rates

We found that the speciation rate was very similar across the phylogeny (λ min = -0.93, λ max = -0.97; Fig. 2a-b). Our results for the niche breadth rate showed an acceleration

with the highest rate in *Bothrops*, *Lachesis*, and *Trimeresurus* lineages, but most of the rates have remained stable for long periods of time (Fig. 2a). Similarly, the niche position rate revealed the highest rate, particularly within *Bothrops*, *Agkistrodon*, and *Trimeresurus* lineages (Fig. 2b). Density plots for the relative evolutionary rates display the contrasting trends of the proportion of rates found across the phylogeny (Fig. 2c).

Comparing the relationship between the rate of speciation and the rates of climatic niche evolution, we discovered that the speciation rate varied independently of rates of evolution of niche position (Spearman's ρ = -0.13, P = 0.03) and the rate of evolution of niche breadth (Spearman's ρ = -0.09, P = 0.14) (Fig. 3).

Discussion

The evolutionary dynamics of Viperidae species' climatic niches suggests that such dynamics has being important in determining the geographic variation in species richness of the family, with more species in tropical than in temperate regions, and especially its wide spatial distribution across different environmental conditions (Esparza-Estrada et al., 2022; Terribile et al., 2009). This, in turn, suggests that climatic niche evolution could be related to the evolutionary diversification of Viperidae, namely the rate of species origination over its evolutionary history. Here, we found evidence against this relationship, showing that the speciation rate was not associated with the rate of climatic

Fig. 2 Phylogenetic patterns of evolutionary rates in Viperidae. Phylogenetic trees display mean per-branch rates. (a) speciation rate (λ BAMM left) and climatic niche breadth evolution (σ^2 BT, right) (b) speciation rate (λ BAMM left) and climatic niche position evolution (σ^2 BT, right) (c) Density plots of the relative evolutionary rates from left to right, speciation rate, niche breadth evolutionary rates and niche position evolutionary rate. Dark colors correspond to slow rates and light colors correspond to fast rates

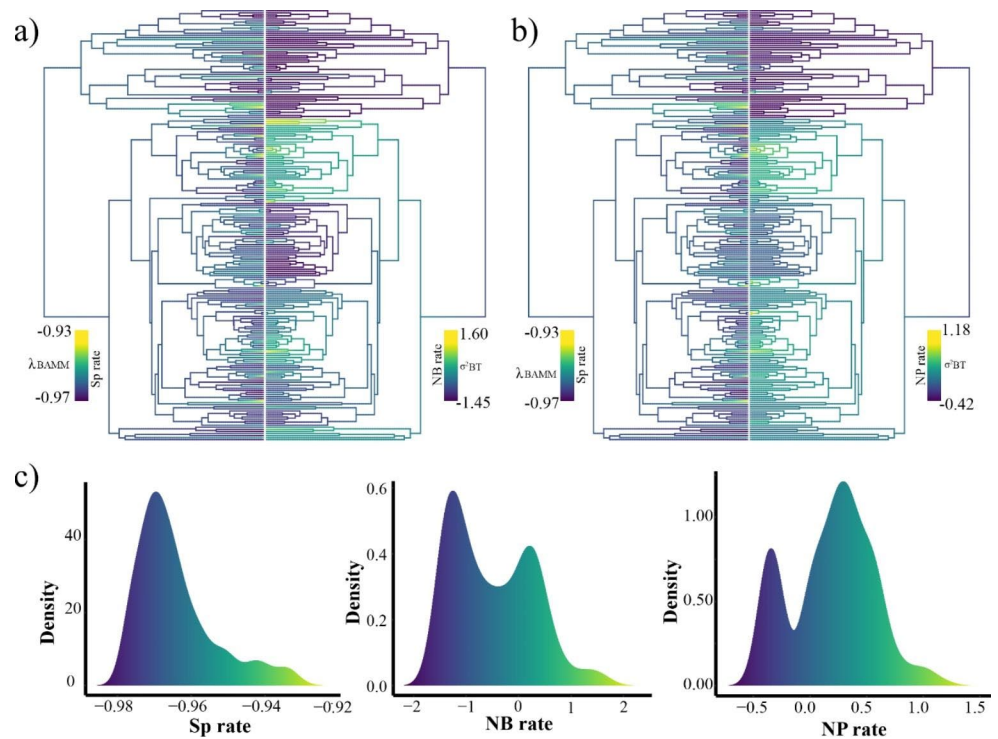
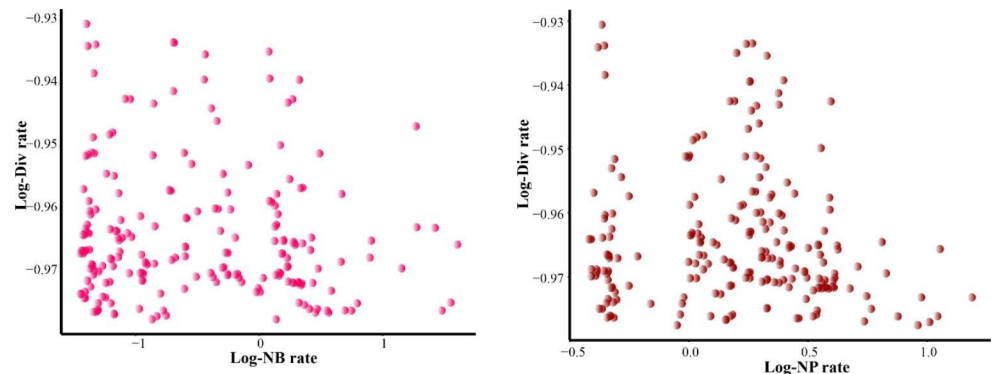


Fig. 3 Relationship between evolutionary rates. Scatter plots show the uncoupling between log-transformed tip-rates of speciation (λ BAMM) and climatic niche breadth (left) and niche position (right) evolutionary rates (σ^2 BT).



niche evolution along the family's history. This result suggests that speciation during the radiation of vipers appears to have been driven mostly without strong climatic niche divergence among species. These findings agree with previous research supporting phylogenetic conservatism in the evolution of vipers' climatic niches (Esparza-Estrada et al., 2022). Altogether, these findings support the notion of phylogenetic niche conservatism as a process for speciation (Pyron et al., 2015; Wiens, 2004), especially allopatric speciation (the most common mode of speciation; Coyne et al., 2004; Turelli et al., 2001) by favoring the formation of geographically isolated lineages given their retention of climatic preferences that do not allow them to adapt and/or disperse across geographic barriers with new environmental conditions (Wiens, 2004). A similar scenario has been suggested in other groups, such as geckos (Ramírez-Reyes et al., 2022), rodents (Maestri et al., 2017), and plants (Folk et

al., 2019), giving insights into the possibility that non-adaptive radiation that lacks accompanying phenotypic diversification occurs more often than expected in nature.

In non-adaptive radiations, emerging species often result from allopatric populations separated through dispersal or vicariance but occupying similar ecological niches (Svensson, 2012). It has been argued that allopatric speciation is the most frequent mode of speciation in squamates (Jezkova & Wiens, 2018), including various lineages of vipers (Ahmadi et al., 2021; Douglas et al., 2006; Martínez-Freiría et al., 2020). During allopatric speciation, genetic drift and natural selection may contribute to the development of reproductive isolation between incipient species, with genetic drift being more important at the initial stage of divergence and selection accelerating the process (Boucher et al., 2016) as incipient species must persist for the amount of time necessary to accumulate differences and become fully separated

from their ancestral populations (Vaux et al., 2016). In vipers, previous studies have shown the occurrence of natural hybrids in some lineages, particularly in contact zones (Burbrink & Guider, 2015; Guiller et al., 2017; Machado et al., 2014; Myers, 2021; Tarroso et al., 2014; Zinenko et al., 2016). This suggests that reproductive isolation between closely related species is frequently incomplete, which also indicates that genetic drift across hybridization may have played a role in the speciation, either through the formation of new hybrid taxa or with the addition of genetic variation that could promote adaptive divergence and facilitate speciation (Abbott et al., 2013). Conversely, if reproductive isolation does not complete, gene flow upon secondary contact will produce similar patterns of shared genetic diversity due to incomplete lineage sorting (D'Elia et al., 2019; Zhou et al., 2017). This pattern has been described for some viper lineages (Martínez-Freiría et al., 2020; Mason et al., 2019), which may result in a slow accumulation of differences between species. Nevertheless, these processes of selection and genetic drift can also interact with other processes, such as niche evolution in the emergence of new species.

It has long been recognized that during periods of environmental change, species are more likely to track the conditions more similar to their ancestral niche rather than adapting at the rate required by the new environmental conditions, i.e., phylogenetic niche conservatism (Peterson et al., 1999). Consequently, over evolutionary time, species tend to maintain their ancestral climatic niches and thus accumulate in regions with climates similar to those of their ancestors (Stephens & Wiens, 2003; Wiens & Donoghue, 2004). This is particularly true for vipers that show their highest species richness in the tropical region, which has been suggested as the region of origin for the family Viperidae in the early Eocene, 50 million years ago (Terribile et al., 2009; Wüster et al., 2008). Within the tropics, vipers also have a longitudinal pattern of species richness in three main regions: Neotropics and South-East Asia, with the greatest number of species, and tropical Africa, with fewer species (Terribile et al., 2009). One possible explanation for this pattern is that, since the Eocene, tropical forests have been relatively constant in size in the Neotropics and South-East Asia (Kissling et al., 2012). In contrast, in Africa, the tropical forest has experienced periods of expansion and reduction since the Oligocene (Couvreur, 2015). These oscillations may have led to the extinction of numerous taxa but also may induce allopatric speciation (Couvreur et al., 2008; Plana, 2004). Additionally, mountain building where viper species inhabit mountainous regions in Mexico (Birskis-Barros et al., 2019; Blair & Sánchez-Ramírez, 2016), the Andes in the Neotropics (Timms et al., 2019), Eastern Mediterranean mountains (Ahmadi et al., 2021), the Himalayan (Xu et al., 2021) created opportunities for allopatric speciation

(Antonelli et al., 2018; Hagen et al., 2021). During periods of environmental change, such as glacial and interglacial periods, erosion and relief formation are increased, the formation of valleys and glaciers promotes the separation of species that may go locally extinct or survive in refuges, and a second contact may occur when environmental conditions change during interglacial periods (Antonelli et al., 2018). As observed for some tropical viper lineages, geographic isolation during climatic cycles derived in allopatric speciation, where some species, even with the considerable geographic distances separating them, are found in similar climatic conditions (Ahmadi et al., 2021; Martínez-Freiría et al., 2017). Also, under allopatric speciation via niche conservatism, species can be found under similar environmental conditions on different parts of single mountain ranges or different ranges (Drovetski et al., 2013). In temperate regions, species exhibit patterns of behavior (e.g., hibernation or borrowing) that might compensate variability of seasonal environments (Mammola et al., 2019), and these patterns of activity may involve restrictions imposed by niche conservatism (Encarnación-Luévano et al., 2021). For instance, some temperate viper lineages exhibit a pattern of seasonal behavior through hibernation related to their physiological constraints (Bauwens & Claus, 2019; Nordberg & Cobb, 2016), suggesting that similarly to tropical regions, temperate lineages may have diverged under a non-adaptive process of climatic preferences.

During evolutionary radiations, lineages may experience adaptive and non-adaptive processes that can result in uncorrelated rates of speciation and ecological divergence given by discordant geographic and adaptive landscapes (Zelditch et al., 2015). For example, during the radiation of a lineage of mountain vipers (*Montivipera*), a mixed pattern of niche conservatism and niche divergence was observed across the clade, where species from the Raddei clade showed strong niche conservatism. In contrast, species from the Xanthina clade showed niche divergence, thus exhibiting a complex relationship between niche evolution and evolutionary radiation (Ahmadi et al., 2019). Similar patterns of ecologically differentiated and ecologically similar species have been observed in Hawaiian spiders' lineage (Rundell & Price, 2009). Indeed, derived lineages may adaptively radiate, whereas others may not, following a non-adaptive process regarding their climatic preferences. Under this scenario, considering radiations as a binary adaptive or non-adaptive process does not completely explain the complex processes that can lead to the contemporary patterns of species diversity, which is likely to be variable and clade-specific, and these complexities should be explored in future studies.

We acknowledge that our results are subject to possible caveats. First, several approaches have been used to estimate speciation rates leading to the possibility that alternative

approaches outperform our estimations, although without changing the overall pattern recovered here. Furthermore, we follow a method that previously tested for the highest degree of accuracy between methods for the estimation of tip rates (Cooney & Thomas, 2021), which might improve our ability to infer accurate relationships between evolutionary rates. Second, other factors (e.g., biotic interactions, morphological traits) may be involved in speciation, although, in vipers other traits such as body size and arboreality, were also not associated with speciation (Alencar et al., 2017; Cooney & Thomas, 2021). Altogether, these findings and ours seem to reflect a general evolutionary conservatism pattern that maintains the ecological similarity between viper species, even over large temporal and spatial scales (Moen et al., 2013).

Overall, our results reveal that there was no tendency for lineages with relatively faster rates of niche evolution to have higher rates of speciation during the radiation of vipers, possibly through a process that could still include a complex pattern of iterated adaptive and non-adaptive radiations among lineages. Such a complex pattern may explain the decoupling between the rates of speciation and niche evolution, which showed their heterogeneity. The complexity of non-adaptive radiations likely hides other patterns, such as at what phylogenetic scales and in which traits it is most common. All of these topics are worth further exploration not only in vipers but also in other groups with sufficient geographic and phylogenetic information.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s11692-023-09604-5>.

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Author Contributions CEEE and FV conceived and designed the study; CEEE collected and analyzed the data; CEEE led the writing with inputs from all authors. All authors contributed critically to the drafts and gave final approval for publication.

Declarations

Conflict of Interest The authors declare that they have no conflict of interest.

Competing Interests The authors declare no competing interests.

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