



Changing Only Slowly: The Role of Phylogenetic Niche Conservatism in Caviidae (Rodentia) Speciation

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Abstract

The dynamics of species diversification have attracted significant scientific attention in recent decades. Many lineages tend to maintain their niche characteristics over evolutionary time, a phenomenon known as phylogenetic niche conservatism (NC), which can slow the processes of ecological speciation by diversification selection. NC can, however, promote speciation through neutral evolution, favoring the geographic isolation of populations. Among the mega-diverse Rodentia group, the low species richness of the family Caviidae stands out. Here, we analyzed if the processes of climatic NC are related to the slow diversification observed in the Caviidae family. Locality data for 13 species and nine climatic variables were used to generate ecological niche models. Niche similarity was quantified using the Schoener D index and used to examine correlations between the times of species divergence and niche similarities, thus characterizing their niche occupation profiles (NOP). The NOP were subsequently used to perform phylogenetic niche reconstructions for these species. Niche models accurately described known distributions of species. The greatest niche overlap documented was between *Kerodon rupestris* and *Galea spixii* (0.86). The niche and species divergence times showed a negative correlation ($\beta = -0.013$; $p = 0.01$). These results support the existence of NC, with phylogenetically closer species occupying similar niches, and emphasize the importance of NC in diversification processes at continental scales in a slowly diversifying group.

Keywords Caviomorpha · Ecological niche models · Neutral evolution · Niche conservatism · South America

Introduction

John Haldane was once asked by theologians what his studies in science could indicate about the nature of God, and he

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responded that the Creator showed “An inordinate fondness for beetles” (Hutchinson 1959), reflecting the wide disparity of species richness found across the tree of life. The balance between speciation and extinction processes are key to determine the number of species found in each lineage over evolutionary time (Glor 2010). Extrinsic processes can promote increases in speciation rates. Evolutionary radiation, for example, can be driven by diverse processes such as climate change (Schluter 2000; Chaboureaud et al. 2014), competitor group extinctions (Silvestro et al. 2015), continental geomorphological changes (Zurano et al. 2017), and sea level alterations (Ruzzante et al. 2008). A high number of species can also emerge among some lineages as a response to low diversification in sister groups. The processes that can lead to decreases in speciation rates can be associated with resource environmental constraints or with niche saturation by a given lineage soon after an adaptive radiation event (McPeck 2008; Pyron and Burbrink 2013). Furthermore, some events like the rise of sea level, impact of asteroids on Earth, or paleoclimatic changes (Milankovitch cycles) may increase extinction rates,

which leads to low net diversification of the affected lineages (Urba 1992; Alroy 2008; Faith and Behrensmeier 2013).

A central point for understanding diversification rate dynamics requires examining the mechanisms that act in the formation of new species. The geographic isolation of a population can restrict genetic flow between individuals (de Queiroz 1998) and thus favor speciation. Speciation through the accumulation of neutral mutations is relatively frequent, albeit a very slow process (Wolf et al. 2010), that mainly occurs through reproductive isolation driven by population fragmentation due to geographic and/or climatic barriers (Wiley 1988). Speciation processes can also be driven by deterministic processes such as disruptive selection (ecological speciation), without the existence of vicariant barriers, with reproductive isolation being favored in that case by ecological niche differentiation (Rundle and Nosil 2005). That accumulation of differences can cause rapid isolation between individuals and impact genetic flux between them, thus resulting in strong ecological divergence even between phylogenetically closely related species (Pyron et al. 2015).

It is widely accepted that the climatic (Grinnellian) niches of species can have central roles in ecological speciation at broad geographic scales (Soberón 2007; Thomas 2010; Zurano et al. 2017; Reis et al. 2018). When selection acts as a promoter of speciation it would be expected that closely related species would show strong niche divergences over relatively short intervals of time (Rundle and Nosil 2005; Huang et al. 2017; Wang et al. 2017). Closely related species, however, tend to exhibit greater similarities in terms of their behaviors, morphologies, and ecologies than more distantly related taxa (Blomberg et al. 2003). Similarly, there is a natural tendency for species to conserve their ancestral climatic niches over evolutionary time – a tendency referred to as phylogenetic niche conservatism (PNC) (Peterson 1999; Wiens 2004; Losos 2008; Nyári and Reddy 2013). The PNC suggests that there is some process limiting the niche divergence among species, leading to more ecological similarity than expected by their phylogenetic relationships (Losos 2008).

When NC is strong, ecological speciation (through disruptive selection) can become difficult due to the incapacity of the taxa to adapt to new abiotic conditions. NC can, on the other hand, promote climatic isolation of incipient species, representing a key factor in the processes of allopatric speciation driven by neutral evolution (Wiens 2004; Wolf et al. 2010). As speciation through neutral evolution results from the accumulation of mutations over long periods of time, it would be expected to be a slower process than selection. The different processes of speciation (through neutral evolution or selection) leave different imprints on lineages. As such, examinations of the modes of niche evolution and the times involved become central to understanding diversification processes.

The Neotropical region is marked by a large climatic heterogeneity, diverse biomes (tropical and temperate forests, cold and hot deserts, etc.), and complex geomorphological patterns (Hoorn et al. 2010). Climatic heterogeneity has been documented to contribute to the diversification of plants (see, for example, Antonelli and Sanmartín 2011) and animals [including birds (Rocha et al. 2015), carnivorans (Zurano et al. 2017), and rodents (Parada et al. 2015; Reis et al. 2018)]. The wide variety of environments in the Neotropics provides unique opportunities for species diversification, promoting, in turn, niche diversification. Nonetheless, a tendency for niche conservatism among some sections of certain lineages could diminish diversification velocity (Wiens 2004). A better understanding of climatic niche evolution is therefore critical to understanding the forces that drive diversification. Neotropical rodents represent a mega-diverse group that inhabits a diversity of environments (Wilson et al. 2005). The Caviidae family is part of Caviioidea sensu stricto group, which presents a rich fossil record since the late Oligocene (Patton et al. 2015). It is estimated that the current members of Caviidae began to diversify at some time between the late Oligocene (Álvarez et al. 2017) and the middle Miocene (Pérez and Pol 2012). The Caviidae comprises six extant genera belonging to three subfamilies: *Cavia*, *Galea*, *Microcavia* (Caviinae), *Dolichotis* (Dolichotinae), *Kerodon* and *Hydrochoerus* (Hydrochoerinae). The subfamilies of Caviidae show large morphological and ecological disparity: (i) the Caviinae are usually small and inhabit different open environments, wetland, and forest edges, (ii) the Dolichotinae are large with elongated limbs, and show preference for arid environments, and (iii) the species of subfamily Hydrochoerinae are the largest living rodents of the world with preference for flooded areas (Nowak 1999).

Representatives of the Caviidae family are distributed from extreme southern to extreme northern Neotropical regions (Holt et al. 2013; Patton et al. 2015), and their low diversification, affinity for open environments, and widespread ranges make them an ideal group for studying connections between evolution, niche occupation, and diversification processes in the Neotropical region. Likewise, a possible hypothesis to explain the low diversification of the Caviidae is the existence of the NC, which may constrain or delay speciation processes. The goal of our work is to analyze, from ecological niche modelling, if the slow diversification of the Caviidae family is the result of neutral or deterministic processes.

Materials and Methods

Data Collection and Ecological Niche Models (ENM)

Geo-referenced occurrence data were gathered for 13 current species of the family Caviidae (~65% of the species) from the

Global Biodiversity Information Facility (<http://www.gbif.org>) database and through bibliographic consultations (Patton et al. 2015) (Table S1). Occurrence data were corroborated using Patton et al. (2015) and IUCN distribution maps. Duplicate points were eliminated based on the resolution of the climate data layers considered (~5 km). All the species analyzed had more than ten occurrence records covering their geographic distributions. Our analyses were performed with only current species, as the fossil species of Caviidae do not have enough occurrences to be used in the ENM, and the Pliocene/Miocene climatic layers are nonexistent. To define the geographic domains of the models (which represents a crucial step in the implementation of ENMs [refer to Barve et al. 2011]), we considered the areas occupied by the species (i.e., the “M” of the BAM diagram; Soberón and Peterson 2005) as those within the distribution polygons published by IUCN. The data of 19 climatic variables were obtained from Worldclim2 (2017), with a resolution of 2.5 arc-minutes (~5 km). To avoid redundancy among predictor variables, correlation tests were run among the 19 variables, allowing the selection of a subset demonstrating only low correlations ($r < 0.8$) (Table S2).

Ecological niche models (ENM) were generated for each species using *Maxent 3.4.1* software (Phillips et al. 2017). The optimal parameterization of the ENMs (i.e., using “features” parameters and “regularization multipliers” values of the *Maxent* configurations for the ENM of each species) was estimated using the ENM evaluate function of the ENMeval package, version 0.3.0 (Muscarella et al. 2014), in the R environment (version 3.4.4) (R Core Team 2018). The robustness of each model was evaluated through cross validation, partitioning their occurrences considering, first, two longitudinal blocks that were subsequently subdivided into latitudinal blocks – resulting in four geographically structured units. The ENMs were then calibrated using the data from three blocks, with the fourth block being used to validate the model projections. That procedure was repeated until each of the four blocks had been used as validation data. The blocks were obtained using the *get.block* function (SDMeval package; Muscarella et al. 2014). The use of blocks as a validation strategy has been shown to be a robust technique for evaluating the predictive performances of ENMs (Bahn and McGill 2007; Aiello-Lammens et al. 2015; Fourcade et al. 2017). In relation to false-absence data, we follow the recommendations of Phillips et al. (2009) and weigh the selection of those points using a sample bias layer that produced sampling effort data for the order Rodentia obtained from the GBIF platform (refer to the Supplementary Material).

The AUC (Area Under the ROC Curve) and TSS (True Skill Statistics) indices were used to measure the robustness of the models. High values (i.e., near 1) for both of those metrics are widely considered to indicate the efficiencies of the models (Warren et al. 2008).

Reconstruction, Similarities, and the Phylogenetic Signal of Climatic Niche

The niche occupation profiles (NOP) were characterized based on the ENMs generated. The optimum values for each species in relation to the climatic variables utilized in the ENMs were used to estimate each NOP. The NOP were then used to reconstruct the phylogenetic niches of each species in the Caviidae family using *phyloclim* package (Heibl 2012).

We used the approach of Broennimann et al. (2012) to estimate overlap between each pair. Background environmental data for South America were obtained by extracting the values of environmental layers (the same used for ENMs) from a sample of 1000 randomly chosen points. That information was aggregated to the set of presence points for each species to undertake a principal component analysis (PCA) for each. Then, we used principal components to estimate niche overlap between each of the species by calculating the Schoener’s D index (Schoener 1968; Warren et al. 2008). The significance of niche overlap estimates were evaluated by comparing the D values observed with null distributions (Warren et al. 2008), using the *ecospat.niche.equivalency.test* function (*ecospat* package version 3.0, Di Cola et al. 2017). The measures of niche overlap were used to evaluate the relationships between divergence times of species and the D index values using age-range correlation analysis (ARC, Fitzpatrick et al. 2006). We also analyzed the disparity through time (DTT) for each NOP of environmental variables with the *geiger* package (Harmon et al. 2016). The DTT analysis quantifies trait variations between and among clades over time, with values greater than 1 representing greater disparity within the clades, and values less than 1 indicating greater disparity between the clades (Harmon et al. 2003). We also estimated the Morphological Disparity Index (MDI) for each DTT to determine to what degree our results differed from neutral evolution over time (Harmon et al. 2003). One thousand simulations were used to evaluate if the MDI was different from a neutral model of evolution. All analyses were performed based on the molecular phylogeny described by Álvarez et al. (2017). The species *H. isthmius* was incorporated into the genus utilizing the phylogenetic position and temporal estimate proposed by Rolland et al. (2014). All the data used in this article are available upon contact with the authors.

Results

Maxent models demonstrated high performance (Table S1), with high AUC (0.75–0.97) and TSS (0.54–0.93) values. The variables that best explained species distributions were associated with thermal amplitude (BIO7, Table S3) and precipitation during the year (BIO13 and BIO19, Table S3). NOP analyses detected that phylogenetically closely related species

tended to inhabit regions with similar thermal amplitudes (BIO7) (Fig. 1a), with members of the Caviidae family occupying regions with relatively restricted thermal amplitudes, with an amplitude optimum (mean values) between 14 and 27°C (Fig. 1a). NOP analyses also demonstrated that the different species occupy different environments, with biases toward drier habitats with relatively high precipitation rates (< 350 mm) in the wettest months (BIO13). At one extreme, *Microcavia* species inhabit regions with < 125 mm of rainfall per month, while species of the genus *Hydrochoerus* demonstrate their best adaptations to higher rainfall levels (between 250 and 330 mm per month). Ancestral reconstructions (node values) indicate that their common ancestor had a clear preference for drier environments, with optimal precipitation levels below 100 mm/month during the rainiest month (BIO13, Fig. 1b). That preference is confirmed by rainfall during the driest period of the year (BIO14), as most species demonstrated optimal requirements near 20–40 mm/month (Fig. S6, Supplementary Material). Precipitation during the coldest season of the year (BIO19), demonstrated high variability, up to 1000 mm/month, although those species did show a preference for drier climates (Fig. 1c). Results for other variables are reported in the Supplementary Material section (Fig. S6).

The analyses of niche overlap indicated that six pairs of species demonstrated greater overlap than expected from the null model ($p < 0.05$): *C. aperea* and *C. fulgida* ($D = 0.59$); *C. aperea* and *H. hydrochaeris* ($D = 0.48$); *G. musteloides* and *G. leucoblephara* ($D = 0.57$); *G. leucoblephara* and *D. salinicola* ($D = 0.34$); *G. leucoblephara* and *M. australis* ($D = 0.46$); and *G. spixii* and *K. rupestris* ($D = 0.86$) (Table 1). The ARC analysis indicated the existence of a significantly negative correlation ($\beta = -0.013$; $p = 0.01$) between niche overlap and time of divergence (Fig. 2). As such, high climatic similarity was noted between phylogenetically closely related

lineages, with less niche overlap between more phylogenetically distant lineages (Fig. 2). The DTT analysis and the MDI index support these results, indicating that BIO7, BIO13, and BIO19 follow a model of neutral evolution over time ($p > 0.05$) (Fig. 3; Table 2).

Discussion

Our results show that the climatic niches of species in the family Caviidae evolve slowly, supporting the phylogenetic niche conservatism idea, based on the following evidence: (i) the existence of a negative correlation between time of divergence and climatic niche overlap; (ii) the NOP (niche occupation profiles) analyses indicated a tendency for the species to occupy predominantly dry areas; and, (iii) the DTT analyses evidenced the divergence of climatic optimum among clades is lower than between clades. These findings are indicative of the importance of niche conservatism in the diversification processes of caviids in the Neotropics. As such, there appear to be constraints that limit dispersal to humid zones, preventing diversification into the variety of environments available across the Neotropical region. Cavies show diversification in terms of their sizes and morphologies among their different lineages (Álvarez et al. 2013), although there appears to be considerable evolutionary constraints within clades in terms of morphological differentiation (Álvarez et al. 2011). That tendency for initial morphological diversity between clades indicates that body size and shape are strongly phylogenetically constrained in this family of rodents. As such, the Caviidae family shows phenotypic constraints (Álvarez et al. 2011) associated with strong niche conservatism. These results indicate that the processes of speciation driven by the accumulation of neutral mutations favored by vicariant barriers represent an important driver of the slow diversification,

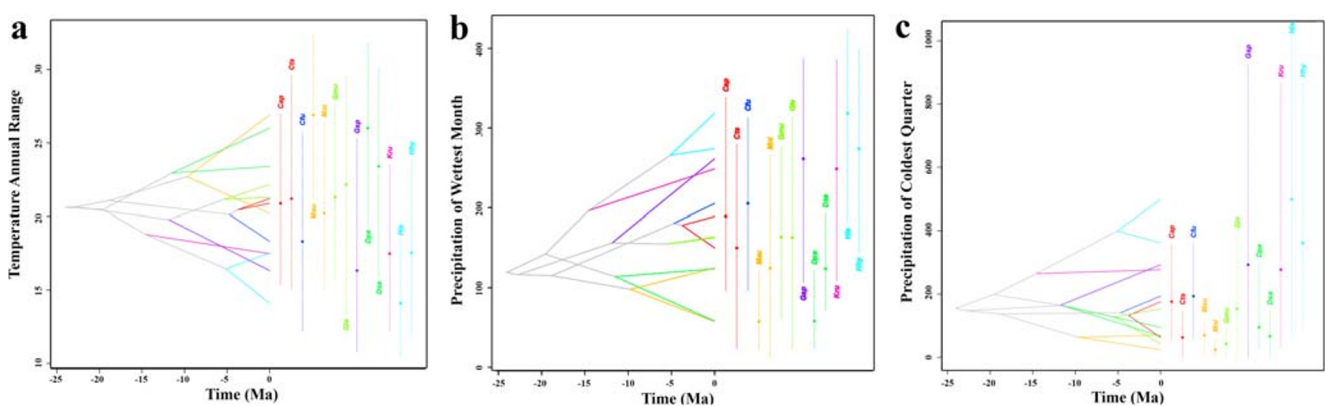
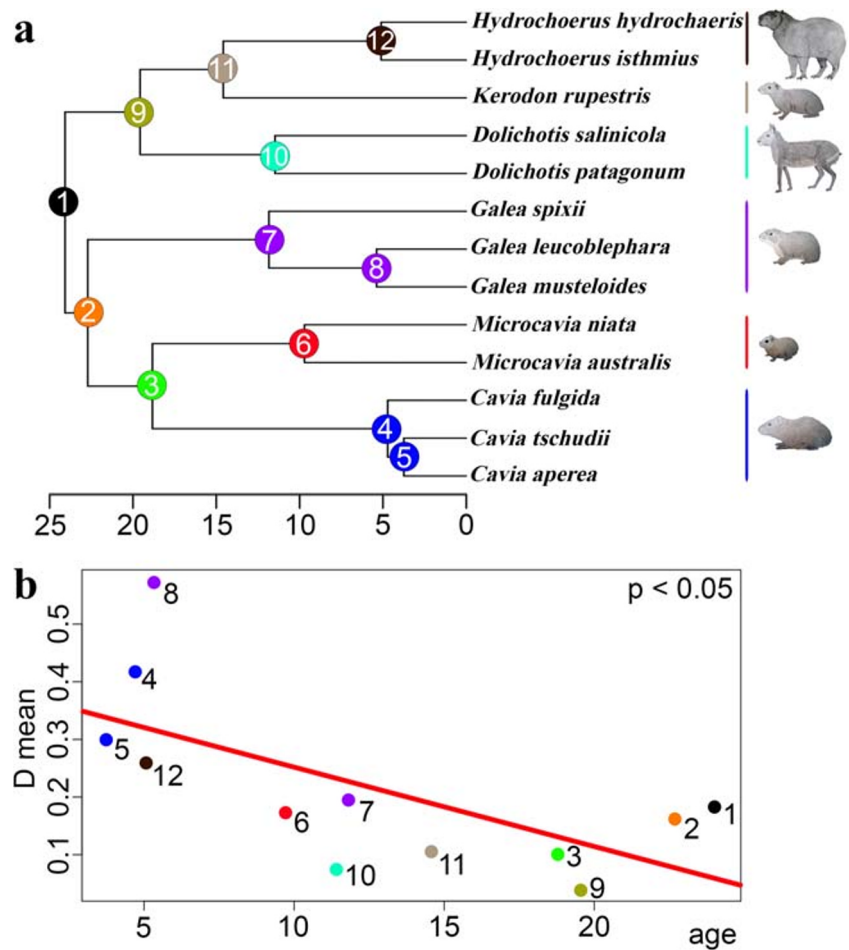


Fig. 1 Ancestral reconstructions (node values) of niche occupation profiles (NOP). The y axis demonstrates the amplitude of occupation of each climatic value for each species along its entire distribution (the point represents the mean value); the x axis represents time in millions of years. (a) Annual Temperature Range; (b) Precipitation of Wettest Month; and

(c) Precipitation of Coldest Quarter. Cap = *Cavia aperea*, Cfu = *C. fulgida*, Cts = *C. tschudii*, Dpa = *Dolichotis patagonum*, Dsa = *D. salinicola*, Gle = *Galea leucoblephara*, Gmu = *G. musteloides*, Gsp = *G. spixii*, Hhy = *Hydrochoerus hydrochaeris*, His = *H. isthmus*, Kru = *Kerodon rupestris*, Mau = *Microcavia australis*, Mni = *M. niata*

Fig. 2 **a** The phylogenetic hypotheses proposed by Álvarez et al. (2017); and **(b)** relationship between niche overlapping (D index) as a function of divergence time



when comparing with other extant caviomorph families, found among members of the Caviidae family.

Caviomorphs went through two high diversification events in their evolutionary history: the first one at the beginning of the Oligocene, and the second one at the beginning of the Miocene (Álvarez et al. 2017). In contrast to other

Neotropical rodents, the family Caviidae show low rates of speciation (Álvarez et al. 2017). Molecular and paleontological studies support the view that the Caviidae family arose at some time during the late Oligocene (~24 Ma; Álvarez et al. 2017) or the middle Miocene (~16.5 Ma) (Pérez and Pol 2012; Patton et al. 2015), although fossil data and molecular

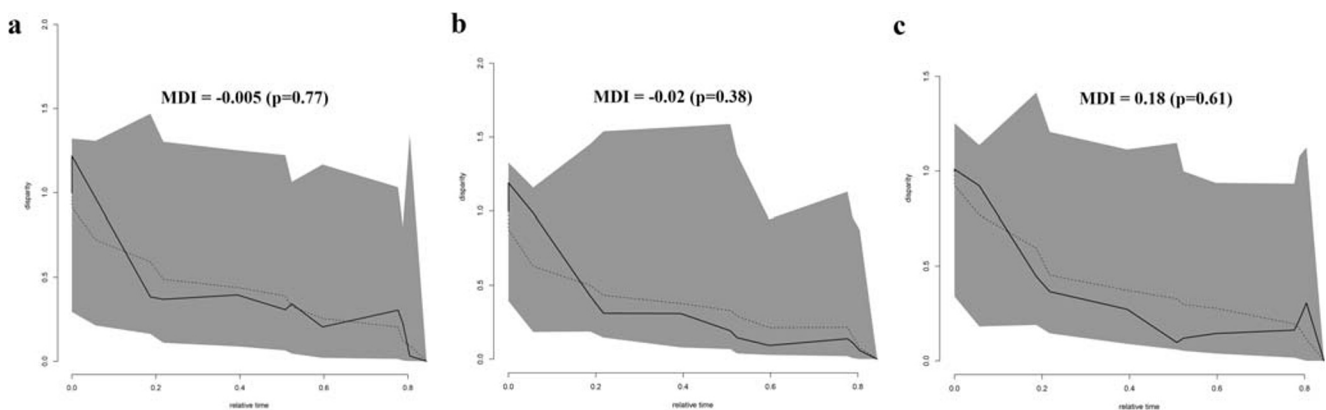


Fig. 3 Analyses of Disparity Through Time (DTT). The x axis represents the time elapsed since the origin of the group; the y axis represents the disparity. Continuous lines represent the data analyzed; dashed lines and gray zones represent the means of the data and the confidence interval

(95%) by a model of neutral evolution. **(a)** Annual Temperature Range; **(b)** Precipitation of Wettest Month; and **(c)** Precipitation of Coldest Quarter

Table 1 – Values of niche overlapping from Schoener's D index (lower diagonal) and p-values (upper diagonal)

	<i>C. aperea</i>	<i>C. fulgida</i>	<i>C. tschudii</i>	<i>D. patagonum</i>	<i>D. salinicola</i>	<i>G. leucoblephara</i>	<i>G. musteloides</i>	<i>G. spixii</i>	<i>H. hydrochaeris</i>	<i>H. isthmus</i>	<i>K. rupestris</i>	<i>M. australis</i>	<i>M. niata</i>
<i>Cavia aperea</i>	NA	0.02	0.24	0.23	0.22	0.10	0.44	0.24	0.03	0.27	0.24	0.28	0.50
<i>C. fulgida</i>	0.59	NA	0.12	0.34	0.15	0.20	0.25	0.15	0.10	0.33	0.15	0.43	1
<i>C. tschudii</i>	0.30	0.25	NA	0.20	0.06	0.09	0.09	0.30	0.30	0.41	0.24	0.16	0.14
<i>Dolichotis patagonum</i>	0.25	0.12	0.28	NA	0.17	0.11	0.21	0.55	0.32	1	0.48	0.07	0.09
<i>D. salinicola</i>	0.05	0.09	0.16	0.07	NA	0.01	0.10	0.19	0.22	1	0.22	0.06	0.18
<i>Galea leucoblephara</i>	0.27	0.18	0.34	0.26	0.34	NA	0.01	0.11	0.39	0.47	0.10	0.03	0.22
<i>G. musteloides</i>	0.10	0.14	0.40	0.13	0.30	0.57	NA	0.14	0.36	1	0.32	0.14	0.12
<i>G. spixii</i>	0.11	0.20	0.10	0.01	0.12	0.22	0.17	NA	0.22	0.18	0.01	0.56	1
<i>Hydrochaeris hydrochaeris</i>	0.48	0.32	0.17	0.13	0.05	0.07	0.08	0.14	NA	0.03	0.13	0.38	0.63
<i>H. isthmus</i>	0.03	0.04	0.02	0	0	0.02	0	0.12	0.26	NA	0.25	1	1
<i>Kerodon rupestris</i>	0.10	0.18	0.05	0.01	0.07	0.20	0.12	0.86	0.11	0.10	NA	0.43	1
<i>Microcavia australis</i>	0.20	0.09	0.33	0.66	0.12	0.46	0.27	0.02	0.08	0	0.01	NA	0.06
<i>M. niata</i>	0	0	0.09	0.11	0.06	0.11	0.25	0	0	0	0	0.17	NA

calibrations converge on the conclusion that current lineages of the family began diversifying during the late Miocene, at ~ 7 Ma (Pérez and Pol 2012). The caviids are predominantly granivores/grazers with some synapomorphies linked to grinding function during mastication (Álvarez and Pérez 2019). During the middle to late Miocene the Neotropical region was predominantly arid, largely dominated by grazing mammals (Ortiz-Jaureguizar 1998), which may have favored morphological adaptive changes in caviids (Álvarez and Pérez 2019). Speciation processes under neutral evolution are generally driven by geographic and/or climatic barriers (Schluter 2009). Diverse geological events during the Miocene could have acted as effective geographic barriers, provoking speciation in some lineages. At the end of the Miocene (~ 5 Ma) and through the Pliocene up to lower middle part of Pleistocene (~ 0.8 Ma), the sea level increased up to ~ 100 m leading to an extensive marine transgression in the Orinoco, Amazon, and Parana basins (Hernández et al. 2005; Hubert and Renno 2006). These transgressions resulted in the isolation of numerous species in the lowland regions of north and central South America (Hernández et al. 2005; Ottone et al. 2013) that favored the diversification of various animal groups (Ferretti et al. 2012; Rocha et al. 2015; Guarnizo et al. 2016). After that marine transgression, the then highly saline soils altered regional vegetation composition, and served as a probable geographic barrier to dispersal as well (Rocha et al. 2015). *Cavia aperea* and *C. tschudii*, for example, diverged at ~ 3.7 Ma (Álvarez et al. 2017), after the last Miocene marine transgression (Hernández et al. 2005), with *C. aperea* being most concentrated at lower elevations in northern Argentina, Uruguay, and Caatinga and Cerrado regions of Brazil, and with disjunct populations in Venezuela and Colombia; *C. tschudii* is found in highland areas in northeastern Argentina, Bolivia, and Peru (Dunnum and Salazar-Bravo 2010). These two species appear to be isolated within the current dry Chaco region that had been inundated by the Miocene marine transgression (Werneck et al. 2011).

Additionally, allopatric processes favored by climatic barriers could also have been driven by diversification processes in the Caviidae family. Historical climatic changes exercised a strong influence on the expansion and retraction of open vegetation areas (Werneck et al. 2011; Costa et al. 2017). Forest areas tended to expand during humid periods, diminishing connectivity between open areas (Werneck et al. 2011). These expansion and contraction dynamics created conditions for the appearance of the Seasonally Dry Tropical Forest (SDTF) vegetation that extends from northeastern Brazil to Argentina, Bolivia, Peru, and Ecuador – forming an vegetation arc within the South American continent (Mogni et al. 2015). Those events established landscapes that influenced the dispersal of many animal species in the late Cenozoic (Zanella 2002), and the fragmentation of those areas due to the expansion and retraction of dry forests would have

Table 2 – Values of MDI and p-values significance (p) from 100 permutation

Bioclim's code	Climatic variables	MDI	p
BIO2	Mean Diurnal Range	0.143	0.538
BIO3	Isothermality	0.159	0.385
BIO5	Max Temperature of Warmest Month	0.225	0.769
BIO7	Temperature Annual Range	-0.005	0.769
BIO13	Precipitation of Wettest Month	-0.025	0.385
BIO14	Precipitation of Driest Month	0.418	0.923
BIO15	Precipitation Seasonality	0.609	1
BIO18	Precipitation of Warmest Quarter	0.257	0.846
BIO19	Precipitation of Coldest Quarter	0.185	0.615

contributed to their geographic isolation (Werneck et al. 2011). Species of the genus *Galea* principally occupy open areas, with *G. leucoblephara* principally occupying the Chaco region of Argentina, Paraguay, and Bolivia, and the Monte region in Argentina; *G. musteloides* is principally distributed in the Puna region, in Bolivia and Peru; *G. spixii* has its greatest distribution in Brazil, restricted to Caatinga vegetation. As such, the current distribution patterns of the genus *Galea* in open areas could reflect the dynamics of SDTF retraction and expansion over time. The strong tendency for *Galea* species to inhabit arid and semiarid regions, and the difficulty they experience in crossing humid and closed vegetation areas apparently contributed to their reproductive isolation. As a result of the temporal dynamics of open vegetation areas, various sister species, and even populations of the same species associated with open areas, demonstrate disjunct distributions, such as the crab-eating fox *Cerdocyon thous* (Martinez et al. 2013), the bare-faced ibis *Phimosus infuscatus* (Matamala et al. 2012), and the pit viper *Crotalus durissus* (Ingenloff and Peterson 2015). Similar patterns of disjunct distributions have been observed with *C. aperea*, with a clear preference for open areas (with the Amazon forests being the principal barrier to connectivity between its populations). As such, there is a tendency among the Caviidae for phylogenetic niche conservatism, reflecting the fact that phylogenetically close lineages demonstrate greater similarity in their climatic niches than more distant species. The tendency to conserve niche characteristics arises, according to Wiens (2004), from the incapacity of those species to adapt to new environmental conditions, and climatic barriers will therefore have a fundamental role in their diversification (Pyron and Burbrink 2013). New dating techniques for divergence have demonstrated that diversification among the Caviidae has coincided with periods of climate change (for example: Benner et al. 2002; Darling et al. 2004; Zhang et al. 2006; Nascimento et al. 2013). As the group has a clear preference for dry climates, the recurrent dynamics of forest expansion and retraction could have driven

the diversification of members of the Caviidae lineage by means of geographic and/or climatic isolation.

Processes that result in the interruption of gene flow between populations will facilitate speciation (Colley and Fischer 2013). Our results indicate the existence of a similarity in the climatic niches of most species of the Caviidae family and indicated their clear preference for open vegetation areas. Our results highlight that the niche differentiation of the species is driven by a neutral process of evolution, leading to the existence of an ecological divergence proportional to the time of separation of the species. The evidence that neutral evolution promoted Caviidae diversification can explain their slow diversification when compared to other families of the same lineage, such as species of the families Ctenomyidae (63 species in the past 19 Myr) or Echimyidae (91 species in the past 27 Myr) (Patton et al. 2015; Álvarez et al. 2017; IUCN 2017). The empirical data presented here demonstrate the contribution of phylogenetic niche conservatism to the processes of diversification on a continental scale.

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