



# Decoupled Patterns of Diversity and Disparity Characterize an Ecologically Specialized Lineage of Neotropical Cricetids

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## Abstract

A link between morphological diversity and species richness is often implied in several evolutionary concepts, but conflicting results hamper a more direct link between these variables. Using a morphologically and ecologically diverse clade of Neotropical cricetids, Akodontini, we (1) characterized the tribe's patterns of morphological disparity and lineage diversification, contrasting the two major clades; and (2) tested whether morphological disparity and rates of morphological evolution are associated with their lineage diversification patterns. We found no correlation between diversification rates and morphological patterns; instead, our results reveal a pattern of ecological and morphological diversification that is independent of cladogenetic events. We found higher rates of morphological evolution in lineages with longer independent evolutionary histories, leading to fewer, but more disparate and specialized species occupying the peripheral areas of the ecomorphospace and increasing the overall morphological diversity of the group.

**Keywords** Morphological evolution · Akodontini · Diversification · Cricetidae · Geometric morphometrics

## Introduction

Understanding the underlying patterns of morphological diversity is a major challenge in evolutionary biology, due to its potential interaction with lineage diversification dynamics, rates of morphological evolution, and ecological differentiation (Hopkins & Gerber, 2018; Schluter, 2000). Morphological diversity, or disparity (Foote, 1993a), can increase in events of speciation (Rabosky et al., 2013), where lineage divergence is accompanied by morphological differentiation. One of the processes that is usually linked to an association between diversity and disparity is described by the punctuated equilibrium theory (Eldredge & Gould, 1972; but see Hopkins & Lidgard, 2012; Pennell et al.,

2014a), where morphological change would be concentrated in cladogenetic events. An increase in morphological diversity can also occur in adaptive radiations, where lineage diversification is accompanied by phenotypic and ecological differentiation (Gillespie et al., 2020; Schluter, 2000). On the other hand, phenotypic and taxonomic diversity may not be related: in non-adaptive radiations, when species diversify without a clear association with ecological and morphological differentiation (Gittenberger, 1991; Rundell & Price, 2009); and in cryptic speciation, where speciation events are not accompanied by morphological distinction (Cerca et al., 2020).

Extinction rates can also influence patterns of morphological disparity: high extinction rates, whether they happen selectively or not, can increase the disparity of recent clades if they result in the survival of species that are morphologically distinct from each other (Hopkins, 2013). Although these scenarios are not mutually exclusive—present-day disparity can arise as a combination of factors (Foote, 1993a; Hopkins & Gerber, 2018)—the different mechanisms that may give rise to distinct patterns of morphological diversity can be tested by comparing speciation/extinction rates with morphological disparity (Adams et al., 2009; Alhajeri & Stepan, 2018; Lee et al., 2016; Rabosky & Adams, 2012; Rabosky et al., 2013). Furthermore, morphological patterns

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can be investigated in the light of the estimation of rates of morphological evolution (Gingerich, 2001; Hansen et al., 2022 and references therein).

Due to their species richness, high rates of diversification, and morphological diversity (Fabre et al., 2012; Upham et al., 2019), rodents constitute an excellent group for studies on diversification. However, rodents also present cryptic speciation (*e.g.* Bastos et al., 2011; Suárez-Villota et al., 2018; Ojeda et al., 2021; Brito et al., 2022), and recent studies found a decoupled pattern between morphological disparity and diversification rates for several clades (Alhajeri & Steppan, 2018; Maestri et al., 2017; Rowe et al., 2011). Alhajeri and Steppan (2018) explicitly tested the relationship between lineage diversity and morphological disparity across muroid rodents—describing a decoupled pattern of these variables, while Rowe et al. (2011) found little ecomorphological divergence combined with higher diversification rates among *Rattus*. Maestri et al. (2017) detected significantly higher morphological evolutionary rates in insectivorous species of sigmodontine rodents, but, in general, species diversification in these rodents is not related to phenotypic specialization. While studies of major radiations offer useful insights on diversification patterns, testing the relationship between mechanisms at smaller phylogenetic and temporal scales might more clearly identify determinant processes (Foote, 1993a; Ricklefs, 2005, 2006). Furthermore, the evolutionary patterns observed in different taxonomic levels may be distinct (Michaud et al., 2022), justifying and requiring explorations of such patterns in less inclusive clades, even when more inclusive clades have been widely studied.

Sigmodontine rodents are the most diversified group of mammals in South America (D'Elía & Pardiñas, 2015a; Patterson, 2020), where they inhabit practically all terrestrial biomes (Maestri & Patterson, 2016). The tribe Akodontini is the second-most diverse clade within Sigmodontinae, numbering 16 genera and 89 species, of which 46% belong to the speciose genus *Akodon* (D'Elía & Pardiñas, 2015b; Mammal Diversity Database, 2022). The tribe is endemic to South America (Maestri et al., 2019) and highly diverse in life history, including fossorial species such as *Blarinomys* and the woolly giant rat *Kunsia*, swamp rats such as *Scapteromys*, and cursorial and scansorial generalists such as species of *Akodon* and *Necomys* (D'Elía & Pardiñas, 2015b). Akodontini includes a number of insectivorous species, a trophic strategy derived several times independently accompanied by clear morphological and functional adaptations that expand the occupation of morphological space (Maestri et al., 2016a; Missagia et al., 2019, 2021).

The diversity in adaptive types of Akodontini appears to be reflected in skull morphology (Hershkovitz, 1966; Maestri et al., 2022; Missagia et al., 2021), and a recent investigation also pointed to their high morphological disparity

(Maestri et al., 2022). Their diversity patterns makes them a good model to test the association between different macroevolutionary processes, because the tribe consists of two major clades with contrasting patterns of morphological and lineage diversity: one of the clades has fewer species (15 species; Mammal Diversity Database, 2022) and greater ecological and functional diversity (D'Elía & Pardiñas, 2015b; Maestri et al., 2017, 2022; Missagia & Perini, 2018; Missagia et al., 2021; Reig, 1987), whereas the other has 76 species (Mammal Diversity Database, 2022) with most of them numbering as cryptic species of *Akodon*. Here, we estimated and compared diversification rates, morphological evolutionary rates, and disparity, in order to understand how these factors interact when promoting heterogeneous diversification in this diverse tribe. We (1) characterized the tribe's patterns of morphological disparity and lineage diversification, contrasting the two major clades; and (2) tested whether morphological disparity and rates of morphological evolution are associated with their lineage diversification patterns.

## Material and Methods

### Data Collection

Ventral (745 specimens) and lateral views (606 specimens) of skulls and lateral views of mandibles (645 specimens) of 59 species of Akodontini rodents (66% of species and 94% of recognized genera) were photographed using an Olympus Tough TG-4 16MP digital camera, keeping a standardised orientation, plane, and distance from the camera to the specimens (see Online Resource 1 for voucher list). We followed the taxonomic arrangement of Patton et al. (2015) and Pardiñas et al. (2017), and whenever possible, specimens were chosen in order to encompass sexual and geographic variation for each species. The landmarks were chosen to represent the general shape of the skull and mandible in order to preserve their biological significance, represent functionally relevant structures, and include points that were recognizable enough to be scored with minimal error among specimens (see repeatability measurements below) (Zelditch et al., 2012). The landmarks of each view of the skull (ventral and lateral; Online Resource 2) and of the mandible were digitised using TpsDig2.30 software (Rohlf, 2015). We evaluated the error associated with landmark digitization through the equation of Arnqvist & Martensson (1998), originally proposed to measure the repeatability of linear measurements but discussed in Fruciano (2016) as a repeatability measure for landmark digitization using the mean squares of Procrustes ANOVA. Landmarks were marked one day apart on replicated photos of ten individuals belonging to different Akodontini genera for each view. We calculated whether variation among repeated measures

is large compared to the variation among individuals. The closer this repeatability measurement gets to one, the smaller the variation among repeated measures of the same subjects, which are reflective of measurement error (Arnqvist & Martensson, 1998; Fruciano, 2016). Repeatability was above 97% for all views (Online Resource 3). Landmarks in some images that could not be marked due to skull damage were estimated with the ‘estimate.missing’ function using the thin-plate spline method (‘TPS’) in the package *geomorph* v. 4.0.4 (Adams et al., 2016) in R v. 4.2.0 (R Core Team, 2022). As the majority of landmarks in ventral view represent mirrored points, we partitioned shape variation of this view into components of symmetric shape (Cardini, 2016), and the superimposed coordinates for the symmetric component were used in subsequent analyses of shape variation.

For the phylogenetic comparative analyses, we considered the Sigmodontinae chronogram obtained from the supplementary material of Maestri et al. (2017). This molecular tree was selected because it was the most comprehensive time-calibrated phylogeny available at the time our study was initiated, including all taxa for which we had morphological samples. The molecular data used to infer this tree was a preliminary version of the mammalian phylogeny published by Upham et al. (2019). The complete tree contained additional 226 taxa, which were pruned with the function ‘drop.tip’ in the package *ape* v. 5.6–2 to retain only the Akodontini taxa for which morphological data were sampled.

### PCA and Phylomorphospace

The landmarks were superimposed with a generalised Procrustes analysis (GPA) to remove the effects of scale, position, and orientation. The mean Procrustes coordinates and the natural logarithm of the centroid size of each skull and mandible view were calculated for each species. The resulting GPA coordinates were submitted to a principal component analysis using the ‘gm.prcomp’ function of *geomorph* to extract the scores for each principal component.

After confirming that the ln-transformed centroid sizes obtained from both cranial views and from the mandible were significantly, positively correlated (Online Resource 4), we summarized size as the mean of the three estimates. A total of four datasets were considered independently in subsequent analyses—skull lateral shape, skull ventral shape, mandible shape, and size. For exploratory visualization of the morphological disparity associated with shape, we plotted the Akodontini phylogeny in the morphospace of the first two principal components with the function ‘phylomorphospace’ of the R package *phytools* v. 1.2–0 (Revell, 2012). Tips and branches were colored according to their estimated phenotypic rates.

### Phylogenetic Signal

We calculated the phylogenetic signal in each of the four datasets using the K-statistic and its multivariate generalization K-multi (Adams, 2014a; Blomberg et al., 2003), considering 1000 permutations to assess the significance of the results ( $\alpha=0.05$ ).

### Allometry and Morphological Disparity

The allometry on shape was evaluated by phylogenetic Procrustes regressions with the ‘procD.pgls’ function, assuming a Brownian Motion (BM) model of evolution (Adams, 2014b). Significance was assessed after 1000 permutations ( $\alpha=0.05$ ).

We compared the differences in disparity (*i.e.* Procrustes variances, Zelditch et al., 2012) between the two main clades of Akodontini (clade A—comprising the genera *Scaptomys*, *Kunsia*, *Blarinomys*, *Brucepattersonius*, *Lenoxus*, and *Bibimys*; clade B—*Akodon*, *Castoria*, *Deltamys*, *Necromys*, *Thalpomys*, *Thaptomys*, *Podoxymys*, *Juscelinomys*, and *Oxymycterus*) with the function ‘morphol.disparity’ in *geomorph*. These analyses considered the model object resulting from allometry analyses, therefore comparing shape variation after accounting for size differences. We also performed this analysis for the size dataset alone. Significance was assessed with 1000 permutations ( $\alpha=0.05$ ). We also obtained partial disparities (Foote, 1993b) of each shape dataset in the form of Procrustes variances for each species with the function ‘morphol.disparity’ in *geomorph*. To further characterize the patterns of morphological disparity across the phylogeny, we obtained the clade-wise disparities with the function ‘disparity’ in *geiger* v. 2.0.10 (Pennell et al., 2014b), calculated as the average squared Euclidean distance among all pairs of taxa descended from a given node.

### Morphological Evolutionary Rates

For morphological evolutionary rates’ analyses, we restricted the dataset to the set of PCs representing  $\geq 90\%$  of the variance for each shape data—the first eight PCs for all datasets. This approach was taken to avoid a large number of among-PCs correlation parameters, leading to overly complex, time-consuming analyses.

Branch-specific morphological rates for each species were estimated with RevBayes 1.1 (Höhna et al., 2016) with a relaxed Brownian Motion (BM) model. This model considers that rates vary following a constant rate BM most of the time, but allow for a few rate shifts to be observed across the branches of the tree, *i.e.* a random local clock (Eastman et al., 2011). This provides a more conservative

approach to modelling branch rate variation than allowing all branches to have independent rates (*e.g.* Castiglione et al., 2018). This approach is possibly more accurate too, since rates show phylogenetic signal as traits do (Sakamoto & Venditti, 2018). To shape datasets, we applied a multivariate version of this model that also considers correlations among variables (here, the PCs). These correlations, if not modelled, may lead to incorrect estimations when dealing with multivariate data (Adams et al., 2017). For multivariate datasets the BM model was assumed since a multivariate relaxed Ornstein–Uhlenbeck (OU) model is not currently available in RevBayes. Markov chain Monte Carlo analyses were conducted with two independent runs (50,000 for size and 400,000 for shape datasets, sampling every 100 and 400 steps, respectively), discarding the first 10% as burn-in. Convergence and mixing were inspected in Tracer 1.7 (Rambaut et al., 2018) with trace plots and an effective sample size > 200 for each parameter.

For the univariate dataset (size), we performed model selection using Bayes factors (Kass & Raftery, 1995). For that, marginal likelihoods were estimated with stepping-stone sampling analyses comparing BM and OU models. Two independent runs were conducted, with 50 steps of 1000 generations each, sampling at every 1000. An initial burn-in of 10,000 generations was applied. Reliability was assessed inspecting the consistency in estimates of marginal likelihoods between the two runs. A univariate relaxed BM version was selected for size data, with this model being strongly favored relative to the relaxed OU ( $2 \cdot \log$  Bayes Factor = 8.7, Kass & Raftery, 1995). These analyses used modified versions of the scripts available in the page of the aforementioned software, with default prior configurations, except for the expected number of rate shifts.

In order to estimate the best number of rate shifts to be used as prior information for the RevBayes analyses, we performed a data-driven rate-shift analysis with the R package *PhylogeneticEM* (Bastide et al., 2018), considering a scalar OU model for the multivariate shape datasets, which accounts for the possible interdependence among traits, whereas a simple OU model was considered for the univariate size dataset. Although the use of OU models here creates a mismatch with RevBayes estimation of branch rates using BM, *PhylogeneticEM* inferences were only applied heuristically to obtain a reasonable estimate of the purported number of rate shifts in our datasets. To the best of our knowledge, a multivariate method for automatically detecting the number of rate shifts across branches (and not time) using BM was not available, excepting for the variable rates model implemented in BayesTraits (Venditti et al., 2011). Still, simulations have shown that this model sometimes overestimates rate variation on individual branches, inflating the number of rate shifts (Chira & Thomas, 2016). Preliminary runs suggest this may be the case for our datasets (analyses

not shown). Therefore, this approach was not pursued further in this study.

The estimated rates were compared between clades A and B with regressions using the ‘procD.pgls’ function in *geomorph*. For shape rates, we included size rates as covariates, applying a type I (*i.e.* sequential) sum of squares, therefore comparing between-clade rate variation that is unrelated to size differences. Significance was assessed after 1000 permutations ( $\alpha = 0.05$ ).

## Diversification Rates

Speciation and extinction rates were estimated with BAMM 2.5.0 (Rabosky et al., 2013; Rabosky, 2014; Online Resource 5). Priors were obtained with the R package *BAMMtools* v. 2.1.10 (Rabosky et al., 2014). We conducted two runs, with 4 chains and 10,000,000 generations each, sampling every 5000. A burn-in of 25% was applied and convergence was assessed with R package *coda* (Plummer et al., 2006), with the same criteria used for RevBayes analyses. We accounted for the incomplete taxonomic sampling by providing sample probabilities for genera (according to species recognized by the Mammal Diversity Database, 2022), and summarized our results, obtaining tip speciation and extinction rates with *BAMMtools*. Speciation and extinction rate differences between clades A and B, and between the genus *Akodont* and other akodontines were evaluated using regressions with the ‘procD.pgls’ function in *geomorph*. Significance was assessed after 1000 permutations ( $\alpha = 0.05$ ).

## Correlation Between Diversification Rates and Phenotypic Variables

In order to test if speciation and extinction rates could have been influenced by morphological variation in shape disparity, size or rates of evolution, we applied the Structured Rate Permutations on Phylogenies (STRAPP) method (Rabosky & Huang, 2016), using the *BAMMtools* function ‘traitDependentBAMM’. This method uses a state-dependent model of diversification which requires repeated associations between diversification rates and the variables under comparison beyond the null expectancy obtained by structured permutations (Rabosky & Huang, 2016). Significance was assessed with a two-tailed test, after 1000 permutations ( $\alpha = 0.05$ ). A Holm correction for multiple comparisons was applied to p-values using the *stats* function ‘p.adjust’.

Additionally, we used Phylogenetic Generalised Least-Square (PGLS) regressions to test if partial disparities and rates of morphological and size evolution could be predicted by speciation and extinction rates. We also evaluated if partial disparities and morphological evolutionary rates were associated in each shape dataset. The variables were standardized into z-scores to enhance interpretability (Mundry,

2014), and the analyses were conducted using the ‘procD.pgls’ function in *geomorph*. Significance was assessed after 1000 permutations ( $\alpha=0.05$ ), and a Holm correction for multiple comparisons was applied to p-values.

The R, RevBayes and BAMM codes and data for reproducing all analyses are available at <https://github.com/rmissagia/diversification-Akodontini>.

## Results

### PCA, Phylomorphospace and Morphological Evolutionary Rates

The distribution of species in the morphospace for each shape dataset is depicted in Figs. 1, 2 and 3.

The first component of the ventral view of the skull encompasses 30.2% of the overall variance and, in line with the lateral view, shows differences in rostral length and width of the zygomatic plate, with long rostra and narrow zygomatic plates on the negative end and short rostra and broad zygomatic plates on the positive end (Fig. 1). The second PC comprises 27.5% of the variation and is related to anteroposterior shortening of the skull and dorsoventral enlargement of the braincase towards positive values.

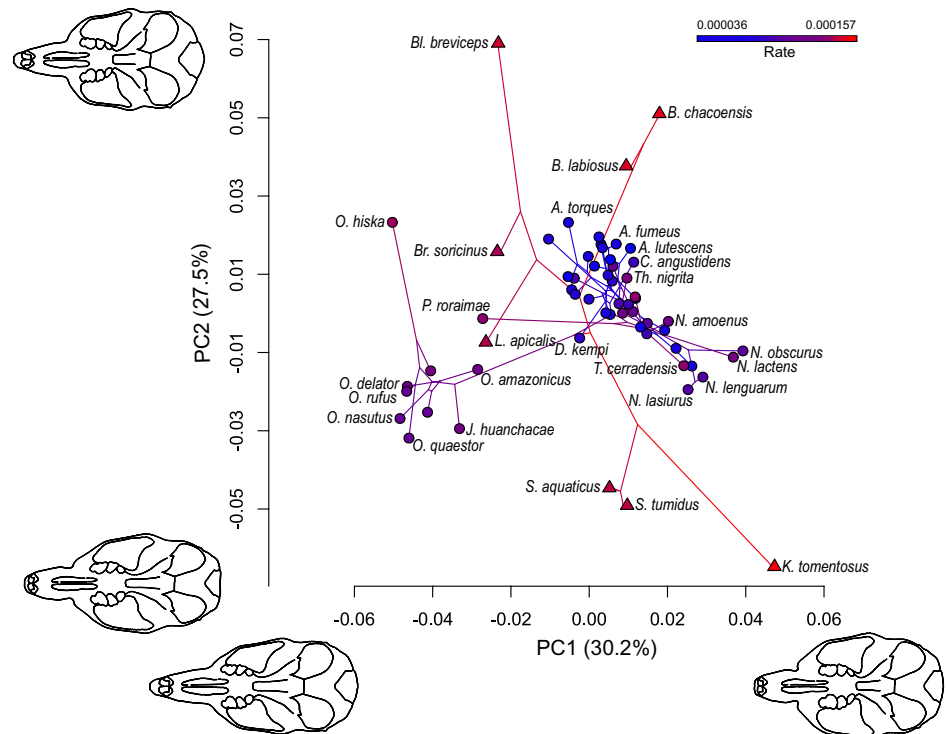
For the lateral view of the skull, the first principal component (PC) accounts for 52.4% of total variation, and is

mainly related to shape differences of the rostrum and zygomatic plate, with shorter rostra and wider zygomatic plates towards more negative values and longer rostra and narrower zygomatic plates towards more positive values (Fig. 1). The second PC, accounting for 13.9% of the variation, is related to differences on the dorsoventral height of the braincase and point of insertion of the zygomatic plate, with higher braincases and anteriorly displaced zygomatic plates towards negative values and lower braincases and posteriorly displaced zygomatic plates towards more positive values (Fig. 2).

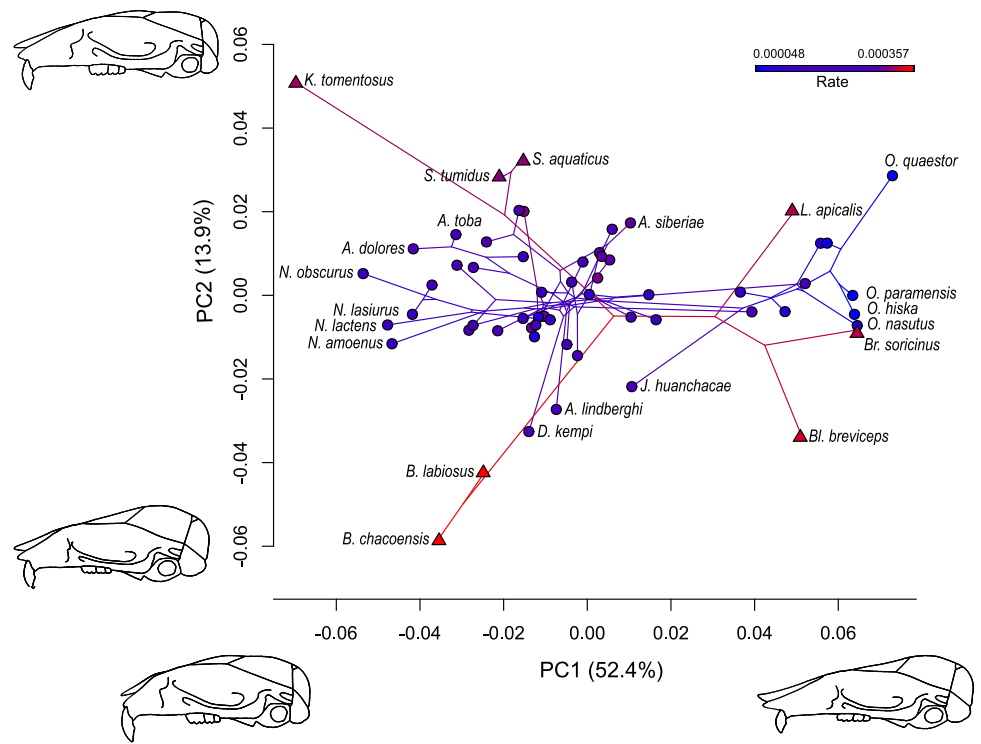
In the PCA results for the shape of the mandible (lateral view), the first PC accounts for 43.6% of the total variation, and PC2 for 18.2%. The first component shows a general compression of the dorsoventral axis combined with an anteroposterior elongation of the mandible, and a posterior displacement of the masseteric ridge towards higher values, while the second PC is related, in addition to differences in the position of the masseteric ridge that is closer to the first molar alveolus towards more negative values, to changes in the procumbency of the incisor, being more procumbent in species with more positive values; and to an anterior displacement of the angular process, also toward more positive values (Fig. 3).

The distribution of species in the morphospace shows that clade A species are usually more dispersed in all shape datasets (Figs. 1, 2, 3). Clade A is also associated with higher morphological evolutionary rates than clade

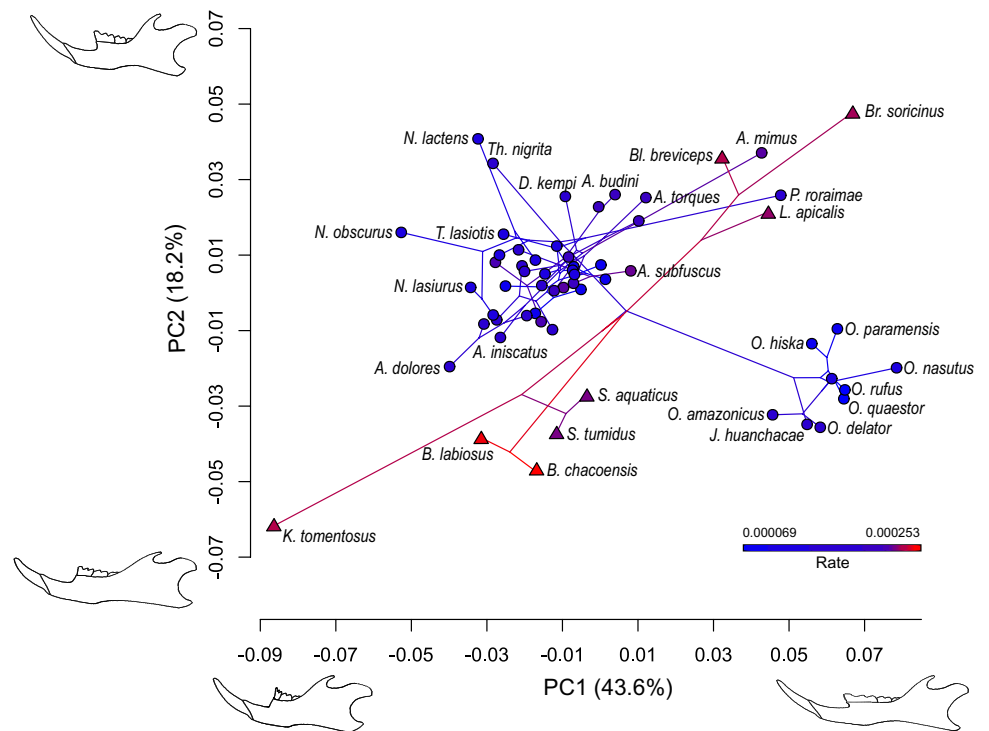
**Fig. 1** Phylomorphospace of the ventral view of the skull, depicting the first two principal components, their associated variance, and outlines of extreme morphologies on each axis. Nodes and branches colored according to morphological evolutionary rates. Triangles indicate species of clade A, and circles of clade B. Not all species names are exhibited, for clarity (Color figure online)



**Fig. 2** Phylomorphospace of the lateral view of the skull, depicting the first two principal components, their associated variance, and outlines of extreme morphologies on each axis. Nodes and branches colored according to morphological evolutionary rates. Triangles indicate species of clade A, and circles of clade B. Not all species names are exhibited, for clarity (Color figure online)



**Fig. 3** Phylomorphospace of the lateral view of the mandible, depicting the first two principal components, their associated variance, and outlines of extreme morphologies on each axis. Nodes and branches colored according to morphological evolutionary rates. Triangles indicate species of clade A, and circles of clade B. Not all species names are exhibited, for clarity (Color figure online)



B in all analyses (Figs. 1, 2, 3), and these differences were found to be statistically significant even after accounting for differences in clade size (Table 1, Online Resource 6). For skull shape in lateral view, rates among taxa in clade

A are more heterogeneous, if compared with the same clade in other datasets, with *Bibimys* showing the highest rates and *Scapteromys* the lowest (Figs. 1 and 4, Online Resource 5). Clade B shows relatively uniform rates for

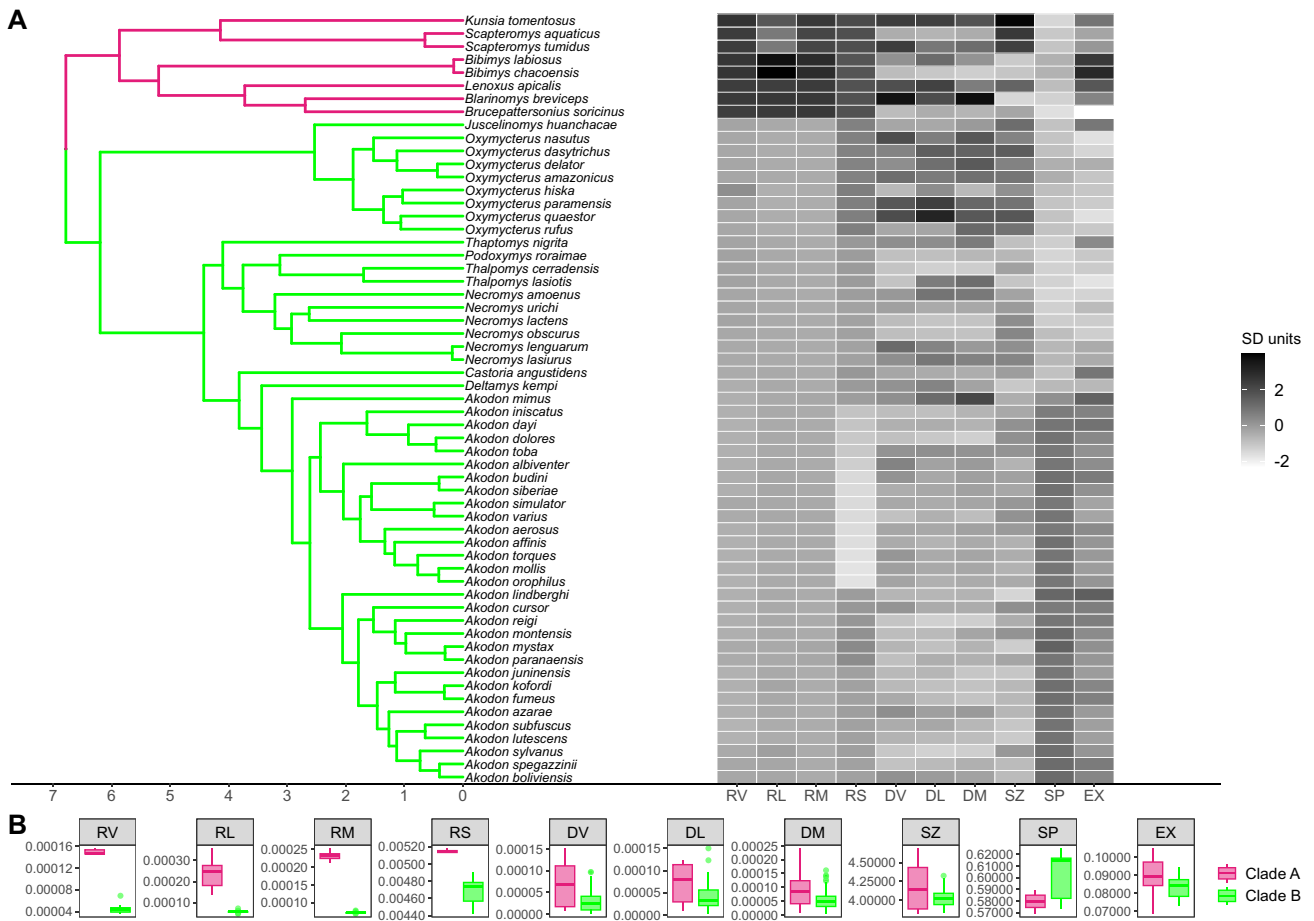
**Table 1** Summary of the disparity, morphological evolutionary rates and phylogenetic signal for the four datasets

Dataset	Proc. var. Clade A	Proc. var. Clade B	Pairwise abs. dist	Phylo. sig. (Kmult)	Avg. rate Clade A	Avg. rate Clade B	F-statistic (rates)
Skull ventral	0.00250	0.00150	0.00100*	0.68570*	0.00015	0.00004	179.05756*
Skull lateral	0.00360	0.00230	0.00130*	0.61280*	0.00024	0.00006	51.49009*
Mandible	0.00520	0.00260	0.00260*	0.64880*	0.00023	0.00007	993.50763*
Size	0.11120	0.01340	0.09780*	1.28800*	0.00515	0.00471	24.31284*

Proc. Var. procrustes variance, Pairwise abs. dist pairwise absolute distances between clades, Phylo. sig. phylogenetic signal, Avg. rates average rates

F-statistics for regressions performed with 'procD.pgls.'

Significant results are marked with \*



**Fig. 4** **A** Chronogram of Akodontini and heatmap with associated values (Z-scores), and **B** boxplots summarizing the absolute values for the variables investigated for clade A (pink) and clade B (green). RV morphological evolutionary rates of the ventral view of the skull, RL morphological evolutionary rates of the lateral view of the skull, RM morphological evolutionary rates of the lateral view of the man-

dible, RS morphological evolutionary rates of centroid size (in logarithmic scale), DV partial disparities of the ventral view of the skull, DL partial disparities of the lateral view of the skull, DM partial disparities of the lateral view of the mandible, SZ centroid size (in logarithmic scale), SP lineage speciation rates, EX lineage extinction rates. Time scale in millions of years ago (Color figure online)

cranial and mandibular shape (Figs. 1–4). For size, on the other hand, there is a gradual pattern of rate variation, with *Juscelinomys* plus *Oxymycterus* being associated with the highest rates and *Akodon* with the lowest (Fig. 4, Online Resource 5).

### Morphological Disparity and Phylogenetic Signal

The PGLS regression of shape on log of centroid size was significant for the shape datasets of the lateral views of the skull and mandible, indicating shape allometry of the group, but not for the ventral view of the skull (Online Resource 7). Clade A showed higher disparity than Clade B, with this difference being statistically significant (Fig. 4, Table 1).

Results of node disparity analyses indicated that most of the cranial, mandibular and size disparity is concentrated towards the root of the phylogeny and is much higher among lineages of clade A, whereas those of clade B showed lower morphological diversity (Fig. 5, Online Resource 8). The phylogenetic signal was statistically significant for all four datasets (Table 1).

For the ventral view of the skull, most of the disparity is related to the root node of clade A, followed by the node uniting *Bibimys* and *Lenoxus* + *Blarinomys* + *Brucepattersonius*, and, to a lesser degree, the node of clade *Blarinomys* + *Brucepattersonius* (Fig. 5A). Regarding the lateral view of the skull, the root of clade A and the node uniting *Bibimys* and a clade composed of *Lenoxus*, *Blarinomys* and *Brucepattersonius* also account for most of the disparity (Fig. 5B). Another node accounting for a noticeable amount of the total disparity was that uniting of *Thalpomys* and *Podoxymys* (Fig. 5B). The nodes responsible for most of the mandibular disparity are the same as those reported for the ventral view of the skull plus that of *Scapteromys* + *Kunsia* (Fig. 5C). Size disparity is mostly associated with a single node, the root of clade A, with all other nodes showing considerably less morphological diversity (Fig. 5D).

Aligned with the results above, partial disparities were in general greater for taxa of clade A than clade B (Fig. 4, Online Resource 5). Nevertheless, some notable exceptions to this pattern are evident, such as higher partial disparities for *Oxymycterus quaestor* (skull, lateral view) and *Akodon mimus* (mandible), or lower disparity for *Scapteromys aquaticus*, *Brucepattersonius soricinus* and *Bibimys chacoensis* (all three shape datasets, Fig. 4, Online Resource 5).

### Diversification Rates

The diversification analysis performed with *BAMM* indicates a gradual pattern, with the null model (*i.e.* with no rate shifts) receiving a much higher support than the

alternatives (Online Resources 9 and 10), although the 95% credible set also includes a solution with one rate-shift associated with the genus *Akodon* (or the genus excluding *A. mimus* in the other *BAMM* run), but these rate-shift configurations were associated with a much lower posterior probability (< 3%). Tip speciation rates for *Akodon* were slightly higher than those of remaining akodontines (Fig. 4, Online Resource 5 and 11), and this difference was statistically significant (Table 2). Differences between the extinction rates of *Akodon* vs. all other akodontines and differences in speciation or extinction rates between clades A and B were not significant (Table 2, Online Resource 11).

### Correlation Between Diversification Rates and Phenotypic Variables

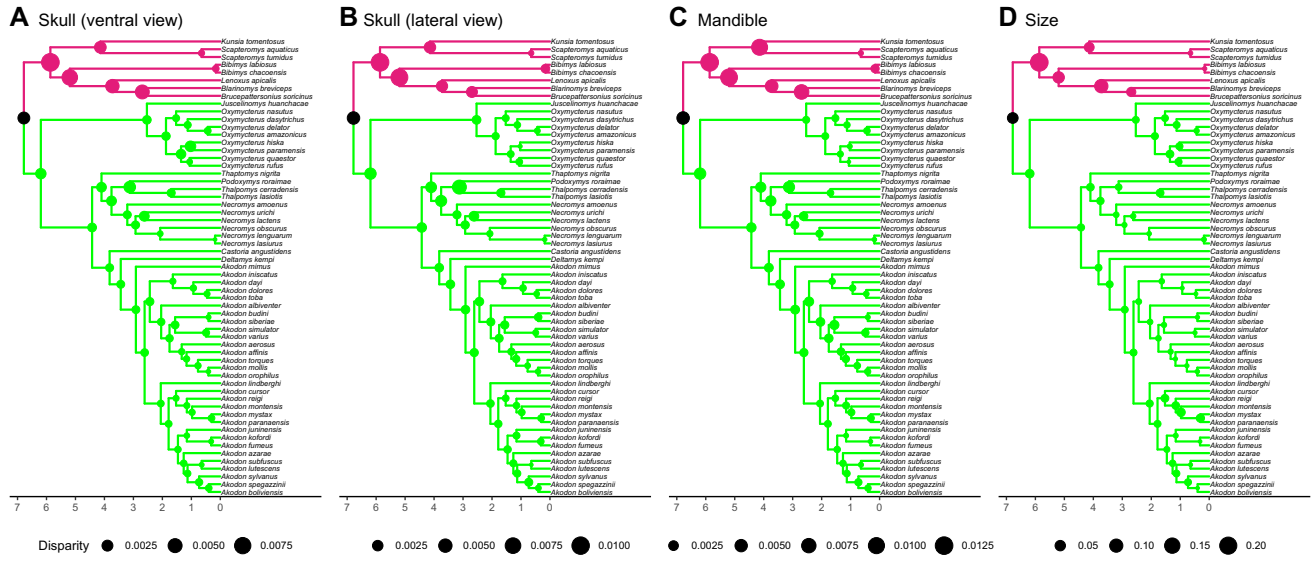
The results of both STRAPP (Table 3) and PGLS (Fig. 6, Table 4, Online Resource 12) indicated that none of the tested correlations were significant, suggesting that diversification rates and phenotypic patterns were decoupled during the evolution of akodontine rodents.

### Discussion

In this study, we used tip values of speciation, extinction, disparity and morphological evolutionary rates to describe the diversification patterns in one of the most diverse groups of Neotropical rodents, uncovering a decoupled dynamic between morphological disparity and species diversification. The diversification of Akodontini resulted in two main lineages that contrast in species richness, indicating heterogeneous speciation-extinction dynamics, which in turn is inversely related to their disparity patterns.

Several studies explicitly tested the relationship between lineage diversification and phenotypic disparity, with results ranging from an association between rates of diversification and morphological evolution (Rabosky et al., 2013; Cooney & Thomas, 2021), to its absence (Adams et al., 2009; Alhajeri & Stepan, 2018; Lee et al., 2016; Rabosky & Adams, 2012; Slater et al., 2010). While most studies consider only living species (Adams et al., 2009; Alhajeri & Stepan, 2018; Burbrink et al., 2012; Lee et al., 2016; Slater et al., 2010; Zelditch et al., 2015), the inclusion of fossils allows inferring patterns including extinction mechanisms (Foote, 1993a; Hopkins, 2013). In general, these studies are not directly comparable because they use different methodologies and proxies to address morphological diversity and species diversity (Cooney & Thomas, 2021). The present study aimed to contribute to our knowledge of this subject by evaluating the association between estimates of speciation/extinction, rates of morphological evolution and partial





**Fig. 5** Node disparity values, with node size displayed proportional to disparity. **A** Skull, in ventral view; **B** skull, in lateral view; **C** mandible, in lateral view; **D** size (natural logarithm of the centroid size).

Clade A colored with pink and Clade B with green. Time scale in millions of years ago (Color figure online)

**Table 2** Summary of the speciation and extinction rates for clades A and B, and for *Akodon* and other (non-*Akodon*) akodontines

Rate	Avg. rate Clade A	Avg. rate Clade B	F-statistic (rates) Clade A × Clade B	Avg. rate <i>Akodon</i>	Avg. rate other	F-statistic (rates) <i>Akodon</i> × other
Speciation	0.57970	0.60195	0.55044	0.61668	0.58056	66.35381*
Extinction	0.08964	0.08346	1.50430	0.08678	0.08172	2.10412

F-statistics for regressions performed with 'procD.pgls'

Avg. rates average rates

Significant results are marked with \*

**Table 3** Results of STRAPP correlation tests for the two MCMC runs performed in BAMM. Correlations were not significant

Phenotype	Rate	Avg. cor. 1	p-value 1	p-adj. 1	Avg. cor. 2	p-value 2	p-adj. 2
Skull ventral rates	Speciation	-0.04341	0.98400	1.00000	-0.05596	0.98000	1.00000
Skull lateral rates	Speciation	0.00523	0.97200	1.00000	0.00173	0.97900	1.00000
Mandible rates	Speciation	0.00562	0.97700	1.00000	0.00078	0.98000	1.00000
Size rates	Speciation	-0.04599	0.97600	1.00000	-0.03174	0.98700	1.00000
Skull ventral disparity	Speciation	-0.01793	0.98100	1.00000	-0.01643	0.97800	1.00000
Skull lateral disparity	Speciation	-0.03354	0.97900	1.00000	-0.02860	0.97300	1.00000
Mandible disparity	Speciation	-0.02903	0.96900	1.00000	-0.02728	0.97500	1.00000
Size	Speciation	-0.03400	0.98300	1.00000	-0.02982	0.98100	1.00000
Skull ventral rates	Extinction	-0.02326	0.97300	1.00000	-0.01636	0.98000	1.00000
Skull lateral rates	Extinction	0.01483	0.97600	1.00000	0.01649	0.97500	1.00000
Mandible rates	Extinction	0.00999	0.97000	1.00000	0.01353	0.95900	1.00000
Size rates	Extinction	-0.00397	0.98600	1.00000	-0.02029	0.98000	1.00000
Skull ventral disparity	Extinction	-0.01161	0.98100	1.00000	-0.00883	0.98600	1.00000
Skull lateral disparity	Extinction	-0.01754	0.97100	1.00000	-0.00633	0.96000	1.00000
Mandible disparity	Extinction	-0.01673	0.97800	1.00000	-0.00748	0.96700	1.00000
Size	Extinction	-0.01149	0.97300	1.00000	-0.01899	0.97000	1.00000

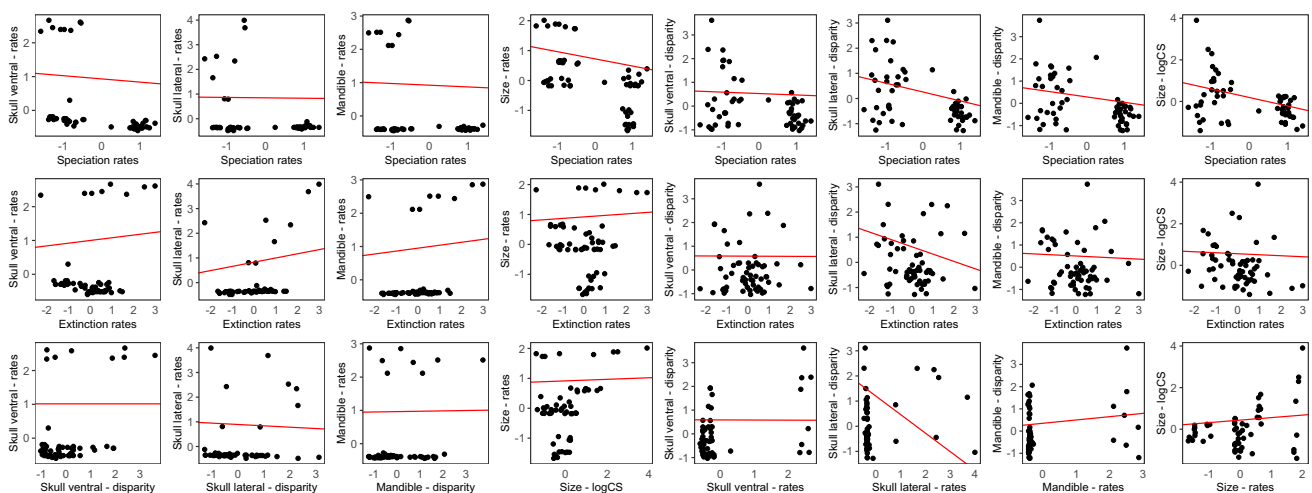
Avg. cor average correlation, p-adj. adjusted p-value, with Holm correction for multiple comparisons

disparities for each species, contrary to most of the previous studies, which considered clade estimates (e.g. Adams et al., 2009; Rabosky & Adams, 2012; Rabosky et al., 2013; Zelditch et al., 2015; Lee et al., 2016; Alhajeri & Steppan, 2018) or tip values, but investigated this association for a smaller number of proxies (e.g. Rabosky et al., 2014; Michaud et al., 2018, 2022; Cooney & Thomas, 2021). Furthermore, the patterns of diversity and disparity are idiosyncratic for each clade, so that conclusions are difficult to extrapolate to other groups; that is, patterns found at broad macroevolutionary scales may not translate to less inclusive clades, and vice versa (Cooney & Thomas, 2021). However, the possible mechanisms can be interpretable for the clade in question.

Alhajeri and Steppan (2018) found a similar pattern for Akodontini in their more comprehensive analysis of Muroidea, with the clade comprising *Kunsia*, *Scapteromys*, *Lenoxus* and *Brucepattersonius* exhibiting higher disparity and lower diversification values in opposition to lower disparity and higher diversification for the clade including *Akodon*, *Thaptomys*, *Deltamys* and *Necromys*. They attributed this pattern to the different ages of lineages affecting the time for accumulation of morphological variation, with older clades showing higher disparities, and younger clades presenting high diversity coupled with low disparity, but this pattern may arise in four different ways. First, it could be due to different rates of morphological evolution (Hopkins, 2016), causing clade A species to become more distinct from one another in the same time interval as clade B, which, in turn, experienced lower rates. Second, it could reflect equivalent rates of morphological evolution between lineages, but over different time periods (Alhajeri & Steppan, 2018; Erwin, 2007); this seems unlikely given the highly

similar divergence times of clade A and clade B, that is, approximately 6 million years according to the dated tree of Maestri et al. (2017). The third option is that only part of the evolutionary history of clade A is visible, which might include additional species that went extinct during that time interval. These species would fill the morphospace, lessening the disparity of extant species and comprising part of a morphological continuum (Ciampaglio et al., 2001; Foote, 1997; Hopkins, 2013; Sidlauskas, 2008). A final scenario to be considered is the one that arises in response to higher speciation rates accompanied by morphological stasis in clade B (Foote, 1993a).

The above-mentioned scenarios are not mutually exclusive, and our results suggest that multiple factors may be involved. Considering the dated tree (Maestri et al., 2017), the species and genera in clade A present higher rates of morphological diversification (Figs. 1, 2, 3, and 4) and had more time of independent evolution to diverge phenotypically than most species of clade B. Alternatively, the genus *Akodon*, which accounts for 55% of species of clade B, presents higher diversification rates and occupies more central areas of the morphospace. *Akodon* is one of the most speciose genera of Sigmodontinae with 42 species (Mammal Diversity Database, 2022), and presents cryptic species complexes (Astúa et al., 2015; Geise et al., 2001; Gonçalves et al., 2007; Pardiñas et al., 2015). Our results agree with previous findings of higher diversification rates for the genus (Parada et al., 2015; Reis et al., 2018), which fit the pattern of younger lineages having less of the morphological disparity documented in older groups (Alhajeri & Steppan, 2018; Collar et al., 2005; Erwin, 2007; Rowe et al., 2011). Besides, several ecological and life history factors not considered here



**Fig. 6** Graphical summary of the regression models evaluate with PGLS analyses considering diversification (speciation and extinction) and phenotypic (disparity, size and evolutionary rates) variables

as Z-scores. The regression lines with the intercepts and slopes are depicted in red (Color figure online)

**Table 4** Results of PGLS regression models

PGLS models	Intercept	Slope	F-statistic	Effect size	p-value	p-adj
Skull ventral rates × speciation rates	0.93243	−0.09549	0.70123	0.28708	0.40900	1.00000
Skull lateral rates × speciation rates	0.84749	−0.01562	0.01421	−1.27749	0.88700	1.00000
Mandible rates × speciation rates	0.92274	−0.05232	0.22595	−0.35361	0.64700	1.00000
Size rates × speciation rates	0.72226	−0.23808	4.26426	1.73252	0.03600*	0.82800
Skull ventral disparity × speciation rates	0.52938	−0.06034	0.01855	−1.30686	0.88600	1.00000
Skull lateral disparity × speciation rates	0.25662	−0.35282	0.54329	0.16003	0.46900	1.00000
Mandible disparity × speciation rates	0.28745	−0.24027	0.35420	−0.07125	0.54500	1.00000
Size × speciation rates	0.19225	−0.41057	2.67570	1.23903	0.11100	1.00000
Skull ventral rates × extinction rates	1.00012	0.07954	2.06989	1.00614	0.16500	1.00000
Skull lateral rates × extinction rates	0.82863	0.17030	8.00353	2.15904	0.00900*	0.21600
Mandible rates × extinction rates	0.95141	0.08784	2.76278	1.20589	0.12000	1.00000
Size rates × extinction rates	0.91930	0.04978	0.72989	0.40839	0.36000	1.00000
Skull ventral disparity × extinction rates	0.58245	−0.00386	0.00031	−2.08398	0.98400	1.00000
Skull lateral disparity × extinction rates	0.61802	−0.29086	1.56120	0.85211	0.19600	1.00000
Mandible disparity × extinction rates	0.50490	−0.04743	0.05706	−0.98161	0.81300	1.00000
Size × extinction rates	0.55748	−0.04778	0.14420	−0.49581	0.68600	1.00000
Skull ventral rates × skull ventral disparity	1.01546	−0.00035	0.00010	−2.12685	0.98900	1.00000
Skull lateral rates × skull lateral disparity	0.89177	−0.05462	2.38707	1.20291	0.10000	1.00000
Mandible rates × mandible disparity	0.96263	0.01109	0.09463	−0.72614	0.76300	1.00000
Size rates × size	0.91455	0.02595	0.17777	−0.49889	0.69200	1.00000
Skull ventral disparity × skull ventral rates	0.58702	−0.00522	0.00010	−2.28725	0.99200	1.00000
Skull lateral disparity × skull lateral rates	1.19629	−0.73588	2.38707	1.15066	0.10800	1.00000
Mandible disparity × mandible rates	0.35116	0.14947	0.09463	−0.72989	0.75700	1.00000
Size × size rates	0.43712	0.11980	0.17777	−0.41112	0.67300	1.00000

*p-adj.* adjusted p – value, with Holm correction for multiple comparisons

Significant results are marked with \*

may also be correlated with both patterns of lineage disparity and diversification of clade B—such as biogeographical history and geological events (Maestri et al., 2017, 2019). *Akodon* is widely distributed in different biomes of South America (Geise et al., 2001; Gonçalves et al., 2007; Maestri et al., 2019), and at least part of its diversification seems to be related to differences in climatic niches (Reis et al., 2018).

The differential extinction scenario (*i.e.* third scenario) seems unlikely according to our results, as we found no differences in extinction rates between the two main lineages. However, this possibility cannot be ruled out considering the ongoing discussion about what can be inferred about past diversification processes from extant timetrees alone, including the caveats of estimating extinction rates from molecular phylogenies in the absence of fossil data (Louca & Pennell, 2021; Rabosky, 2010), and the identifiability of alternative speciation and extinction parameters (Louca & Pennell, 2020, but see Morlon et al., 2022). Unfortunately, most fossil records of akodontines correspond to living species (Pardiñas et al., 2002) and the few records of certainly extinct species are difficult to place phylogenetically, owing

to the fragmentary state of the material (Pardiñas et al., 2002), limiting their use in assessing this scenario.

In Akodontini, speciation and extinction rates do not substantially vary through time or between clades and are mostly decoupled from morphological evolutionary rates or disparity, a pattern that is not uncommon (Bromham et al., 2002; Adams et al., 2009; Hopkins, 2013; Zelditch et al., 2015; Alhajeri & Stepan, 2018; but see Rabosky et al., 2013). Our results also suggest the absence of significant association of partial disparities and tip morphological rates of evolution, although both are significantly larger in clade A (Fig. 4), indicating that those metrics cannot be taken as proxies for one another (Adams et al., 2009; Alhajeri & Stepan, 2018; Michaud et al., 2018). Despite apparent differences (Fig. 4), the non-significance between the variables of diversification versus morphological diversity is probably due to their clustered distribution in the phylogeny (Fig. 4), with clade A concentrating high values of disparity and clade B lower values, together with higher speciation values in *Akodon*. This means that we have insufficient independent points to test correlation. Felsenstein (1985) described this

scenario as a reason for including evolutionary history in comparative analyses.

Clade A apparently achieved high levels of morphological specialization that seem to accompany corresponding ecological diversity, since this group accounts for most of the specialised dietary and locomotory habits found in the tribe (Hershkovitz, 1966; Maestri et al., 2016a, 2017; Missagia et al., 2019, 2021). Stable isotope analysis retrieves this clade as the one with the greatest trophic niche diversity (Missagia et al., 2019), including species that feed mainly on C4 plants (e.g. *Kunsia tomentosus* and *Bibimys labiosus*) as well as specialist insectivores (e.g. *Blarinomys breviceps*, *Lenoxus apicalis*, and *Brucepattersonius soricinus*). Trophic diversity may explain the morphological disparity of the clade, considering that the principal shape changes identified here involve functional characteristics of the masticatory complex (see Samuels, 2009; Maestri et al., 2016a; Missagia et al., 2021). In addition to the ecologically specialized species of clade A, the genus *Oxymycterus* of specialized insectivores of clade B (Missagia et al., 2021) also shows high rates of morphological disparity (Fig. 4). The mode of locomotion and substrate utilization can also affect cranial morphology (Agrawal, 1967; Camargo et al., 2019), although they are generally better reflected in postcranial features (Samuels & van Valkenburgh, 2008; Tavares et al., 2021). Locomotion and substrate use may have affected the morphological evolution of some akodontines like *Blarinomys*, which has a unique skull morphology that combines characteristics related to both insectivory and fossoriality (Geise et al., 2008; Missagia & Perini, 2018), and presents some of the higher partial disparities and rates of morphological evolution (Fig. 4). *Kunsia tomentosus* is also described as semifossorial (Bezerra & Pardiñas, 2016; Hershkovitz, 1966; Maestri et al., 2017), and some of the demands imposed by excavation, aided by use of the incisors, may explain the distinctiveness of its skull among akodontines (Agrawal, 1967; Stein, 2000). Other studies that proposed to describe the morphological variation of vertebrate skulls, and whether and how it is linked to ecological aspects, found similar patterns, with ecologically specialised species occupying extreme points in the morphospace and increasing the overall morphological diversity (e.g. Claude et al., 2004; Stayton, 2005; Samuels, 2009; Jones et al., 2015; Arbour et al., 2019; Zelditch et al., 2020. Felice et al., 2021), showing this is a common result of ecological specialization on morphological diversification.

Morphological variation appears as a result of several patterns, including ecological and functional adaptations, phylogenetic relationships, and also size (Foote, 1997; Hopkins & Gerber, 2018). Clade A is more heterogeneous in size (Fig. 5D), which may explain part of its morphological disparity considering the positive allometry for the group as a whole. Maestri et al. (2017) found larger sizes driven by

herbivorous diet and semifossorial or semi-aquatic habits for a more comprehensive sample of sigmodontine rodents that included *Kunsia* and *Scapteromys*, an herbivorous semifossorial and insectivorous semi-aquatic species, respectively, also included in our sample. These two species increase the size range of Akodontini and contribute to the size heterogeneity of clade A, with *Kunsia* reaching up to 600 g (Bezerra & Pardiñas, 2016) as opposed to the smaller sizes of *Blarinomys*, *Bibimys*, and *Brucepattersonius* (approximately 30 g; Maestri et al., 2016b). In clade B, most species cluster around smaller sizes (approximately 30 g; Maestri et al., 2016b), with the exception of some *Oxymycterus* species that can reach 80 g (Maestri et al., 2016b). Increase in size can permit access to different resources (Price, 1983), and larger species of rodents can be more ecologically derived (Renaud et al., 2007). Despite being context-dependent, a recent study in Australia found evidence of greater risks of extinction in larger rodents (Roycroft et al., 2021), and, although not yet tested for Neotropical cricetids, it indicates the possibility of differential diversification dynamics related to body size and evolutionary rates. Body size may, in turn, interact with the historical processes and environmental gradients involved in diversification (Maestri et al., 2016b).

The skull of vertebrates may be viewed as a morphological structure that accumulates variation in response to ecological adaptations for being essential in interactions with the external environment (Novacek, 1993), which is one of the reasons it is used so often in studies of morphological disparity (e.g. Jones et al., 2015; Arbour et al., 2019; Bardua et al., 2019; Felice et al., 2021). However, the skull may instead fit a “one-to-many” pattern, where similar morphologies can serve distinct ecological functions, which can have different impacts on lineage diversification (Maestri et al., 2017; Zelditch et al., 2020). This can lead to a pattern of little morphological differentiation, even in scenarios where diversification could be triggered by ecological opportunity (Maestri et al., 2017; Rundell & Price, 2009). However, the greater disparity in ecologically specialised species of clade A is obvious. Regardless of whether small clades have fewer species due to higher rates of extinction or lower rates of diversification, there are indications that these clades may be pushed to the periphery of an evolutionary radiation in morphospace or even in geographic space (Ricklefs, 2005). This peripheral occupation may be related to their persistence for longer periods that could lead to morphological and ecological distinction (Ricklefs, 2005). The low climatic niche diversification rate found by Reis et al., (2018) for most species in clade A indicates some degree of habitat specialization that may have allowed these species to persist in particular environments for longer time periods.

The diversification dynamics of Akodontini can be summarized as a contrast between the two main lineages, with one of the clades showing high rates of morphological

disparity combined with low diversity, while the other presents higher diversity and lower morphological disparity. This pattern can be obscured by more comprehensive studies, which underscores the difficulty of establishing more general patterns for mammals or vertebrates in general. Our results help to elucidate the patterns of morphological diversification of a diverse group of Neotropical rodents, adding to the evidence of the possible lack of connection between morphological evolution and diversification in some groups.

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## Declarations

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

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