

## Research

### Tracing the diversification history of a Neogene rodent invasion into South America

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We investigated spatial patterns of evolutionary relatedness and diversification rates to test hypotheses about the historical biogeographic processes underlying the radiation of Neotropical rats and mice (Sigmodontinae, ~400 species). A negative correlation between mean phylogenetic distance and diversification rates of rodent assemblages reveals a pattern of species co-occurrence in which assemblages of closely related species are also the fastest diversifying ones. Subregions of the Neotropics occupied by distantly related species that are on average more slowly diversifying include Central America, northern South America, and the Atlantic forest. In southern South America, recent species turnover appears to have been higher. Ancestral locations for the main tribes of sigmodontines were also estimated, suggesting eastern South America and the Amazonian lowlands were colonized before some central Andean regions, even though the latter are now centers of species richness for these rodents. Moreover, a past connection between the tropical Andes and the Atlantic Forest is suggested by our results, highlighting a role for a hypothetical arc connecting the two biomes, which would have impacted many other groups of organisms. Whether rapid, recent speciation in some regions is related to Quaternary climatic fluctuations and the young age of sigmodontines (~12.7 Ma crown age) or instead to intrinsic traits of these rodents remains an open question. If the former is true, we hypothesize that contrasting trends will characterize older Neotropical clades.

Keywords: diversification rate, evolutionary radiation, historical biogeography

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#### Introduction

Understanding the ecological and evolutionary processes that shape the large-scale formation of species assemblages is a fundamental goal of both ecologists and biogeographers (Wiens and Donoghue 2004). However, community ecology, macroecology, and historical biogeography examine spatial patterns of assemblages from different perspectives that often produce different interpretations from similar results (Cardillo 2011, Ricklefs and Jenkins 2011, Warren et al. 2014, Mazel et al.

2016). A complex scenario arises from the multiple processes that determine species distributions across space, including speciation, extinction, and species dispersal as fundamental macroevolutionary processes, mediated at the assemblage level by vicariant events, niche evolution, and ecological filtering and competition, among other factors (Webb et al. 2002, Wiens and Donoghue 2004, Fritz and Rahbek 2012). Understanding how these various processes contribute to any individual outcome necessarily involves the integration of both ecological and historical perspectives (Ricklefs 2004, Maestri et al. 2018a, Velasco and Pinto-Ledezma 2018).

The diverse historical, evolutionary, and ecological processes shaping clade colonization often leave behind different mechanistic signatures (Fritz and Rahbek 2012, Carlucci et al. 2017). For example, young clades with rapid rates of speciation are thought to produce assemblages comprised of closely related species, making them phylogenetically clustered (Cardillo 2011). Rapid speciation can accompany the colonization of new or ecologically ‘unoccupied’ environments (Lv et al. 2016, García-Navas et al. 2018) where gene flow is consequently limited among population isolates, driving allopatric or peripatric speciation (Wiens 2004). When ecological space in a region becomes saturated and rates of speciation and extinction equilibrate (Simpson 1953, but see the debate about diversity-dependent diversification – Harmon and Harrison 2015, Rabosky and Hurlbert 2015), local assemblages may become less phylogenetically clustered and more overdispersed (Cardillo 2011). Phylogenetic overdispersion can also result from multiple events of allopatric speciation of distantly related clades in the same region (Hardy and Senterre 2007, Warren et al. 2014).

It is reasonable to expect that the first clades to arrive in a region are more likely to have reached ecological saturation than later-arriving clades, so that species from early-arriving clades should be distributed randomly or be overdispersed (rather than phylogenetically clustered). During the course of a clade’s evolution and diversification, such relationships can vary (i.e. assemblages can dynamically change through time and be composed of closely related or distantly related species at different moments), impacting processes of local extinction, speciation, and dispersal across space and time.

We can infer histories of diversification and community assembly by comparing assemblage-level summaries of mean pairwise phylogenetic distance (MPD) versus mean per-species diversification rate (mDR; measured as the inverse of equal splits, Redding and Mooers 2006, Jetz et al. 2012) (Fig. 1). Considering this framework in the context of biogeographic diversification, areas occupied early in a group’s history are more likely to still be occupied today by species derived from early divergences, resulting in phylogenetic overdispersion of assemblages in those long-occupied areas. As ancestral species spread into new unoccupied geographical areas, their descendant lineages continue to proliferate, resulting in recently diversified species likely living in proximity, becoming phylogenetically clustered assemblages (scenario A in Fig. 1). If colonization of a new environment involves niche evolution, closely related species will likely share those traits needed to meet new environmental challenges (but only if trait conservatism exists, see Provete (2013) for a review of ecophylogenetics); this results in assemblage homogenization via environmental filtering (Webb et al. 2002) (Fig. 1A). We hypothesize that this first scenario is more likely in younger

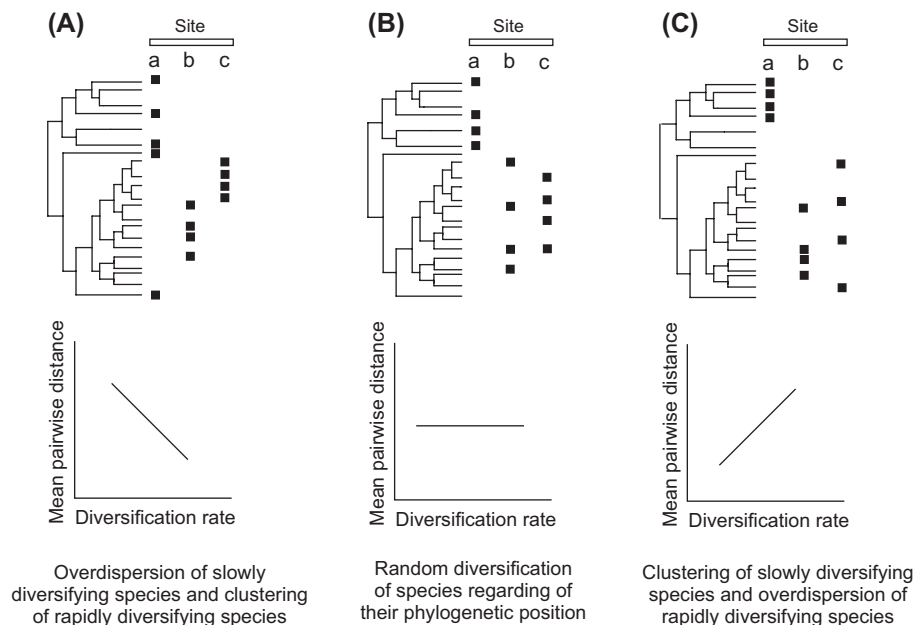


Figure 1. A theoretical framework for the relationship between mean pairwise distance and assemblage diversification rate (see main text for explanation). For brevity, the words ‘clustering’ and ‘overdispersion’ are used only to indicate the co-occurrence of closely related or of distantly related species, respectively. Scenario (A) is hypothesized to characterize younger radiations with faster speciation and dispersal rates, whereas scenarios (B) and (C) should characterize older clades.

clades that rapidly diversified through a region (Cardillo 2011, García-Navas et al. 2018). On the other hand, species co-occurrence may be unrelated to phylogenetic position (Fig. 1B) or even opposite to it, where species from early divergences compose assemblages of closely related species and recently diversified species compose assemblages of distantly related species (Fig. 1C). These last scenarios are more likely to appear only after long-term occupancy of a region, where competition and extinction become more important, eliminating recently diversified species occupying similar niches and leading to overdispersion (Hardy and Senterre 2007, Mazel et al. 2016).

The Neotropical region is one of the most biodiverse regions in the world (Schipper et al. 2008, Jenkins et al. 2013) and offers numerous evolutionary radiations to test these predictions. Sigmodontine rodents comprise the most diversified mammal group in the Neotropics, and their ~400 species and 12 tribe-level lineages have become widespread over the last 10 Ma (Parada et al. 2013, Vilela et al. 2014, Steppan and Schenk 2017). Sigmodontines arrived from North America before the closure of the Panamanian land-bridge (Reig 1981, Pardiñas and Tonni 1998, Pardiñas 1999) and currently reach their highest diversity in tropical montane regions of South America (Maestri and Patterson 2016). To date, understanding of the group's historical biogeography remains incomplete, especially regarding patterns of phylogenetic endemism, species diversification, and community assembly.

Here, we evaluate two main hypotheses advanced to explain sigmodontine routes of colonization and ancestral areas of diversification. The first was proposed more than 30 yr ago (Reig 1981, 1984, 1986) and has never been fully tested with comprehensive phylogenetic sampling. Reig (1986) postulated an Andean origin of Sigmodontinae and its major tribes (Oryzomyini [including Thomasomyini], Akodontini [including Abrotrichini], Phyllotini, and Sigmodontini), which later diversified elsewhere (e.g. Akodontini in eastern South America and Oryzomyini in the lowlands). Reig (1981, 1986) argued that the Andes were the area of original differentiation (AOD) for both the subfamily and the major tribes; AOD is not necessarily equivalent to an area of origin but rather where the main diversification events occurred.

However, developing understanding of distributions and phylogenetic relationships has led some to propose a different scenario, one including an origin outside the Andes for at least some of the main tribes (Smith and Patton 1999, Salazar-Bravo et al. 2013, Leite et al. 2014, Pardiñas et al. 2014, Parada et al. 2015). Notably, the origin of Akodontini would then be linked to eastern South America (D'Elia and Pardiñas 2015, Pardiñas et al. 2016). We generated predictions from each hypothesis (Table 1) to evaluate them.

In this study, we seek to integrate ideas from scenarios of evolutionary community assembly (Fig. 1) with the competing hypotheses regarding AODs of sigmodontine rodents (Table 1) to investigate factors underlying the sequence and timing of Neotropical diversification. We examined the relationships between pairwise phylogenetic distances (MPD) and diversification rates (mDR) to 1) investigate the possible imprints of diversification rates upon phylogenetic patterns of sigmodontine community assembly, and 2) evaluate evidence for where each tribe of sigmodontine rodents originally diversified. Ancestral biogeographic reconstruction and range estimation additionally help us trace the spatial evolutionary history of Neotropical rats and mice.

## Methods

### Rodent species data

Geographic range maps for 400 species of sigmodontine rodents were taken from IUCN (2008) and Patton et al. (2015). South American species each had their range maps updated in the recent compendium of Patton et al. (2015) by numerous taxonomic specialists, which were digitized for Maestri and Patterson (2016). The digitized range maps are available in the Dryad link accompanying this publication. Ranges for species from Central America were obtained from IUCN (2008). From the maps, the incidence of rodents was calculated in a grid of  $110 \times 110 \text{ km}^2$  ( $\sim 1^\circ \times 1^\circ$  at the equator) over the Neotropics, excluding islands (totaling 1758 grid cells). Species were considered present in a cell if at least 50% of a cell was included in its range. The incidence matrix and grid were constructed in R using the packages

Table 1. Predictions tested in this study, derived from the principal competing hypotheses about the historical biogeography of sigmodontine rodents.

Hypotheses	Proposed patterns and processes of diversification	Predictions	References
1	Areas of original differentiation for sigmodontines and their main tribes are along the Andes cordillera; species of each tribe subsequently dispersed to colonize other regions.	Early diversification areas will be found in the Andes; deepest nodes for the main tribes will be reconstructed in Andean bioregions; ancestral ranges will be reconstructed close to the Andes.	Reig 1981, 1986
2	Diversification is centered in regions outside the Andes, particularly in the lowlands; eastern regions were important centers of differentiation during sigmodontine evolution.	Early diversification areas will be found in northern lowlands and in eastern South America; deepest nodes for the main tribes will be placed in bioregions outside the Andes; ancestral ranges for some of the main tribes will be reconstructed outside the Andes.	Smith and Patton 1999, Salazar-Bravo et al. 2013, Leite et al. 2014, D'Elia and Pardiñas 2015

rgdal (Bivand et al. 2018), raster (Hijmans 2017), and letsR (Vilela and Villalobos 2015). Species richness was calculated by summing species incidences within the grid cell.

We used the phylogenetic hypothesis for 279 species of sigmodontines with DNA sequence data employed in Maestri et al. (2017). The fossil-calibrated molecular timetree was derived from a supermatrix alignment of 11 genes, including eight nuclear exons and three mitochondrial regions, culled from a broader study on all mammals (Upham et al. unpubl.). The root of the tree includes six species as outgroups, five Tylomyinae plus *Rattus norvegicus* (Maestri et al. 2017). The maximum clade consensus (MCC) tree was used to perform most analyses on this ‘DNA-only’ data set. For the biogeographic reconstructions, the geographic occurrence matrix and phylogeny were pruned to include only species found in both datasets, resulting in 260 species, including all major tribes, 90% of genera, and 65% of the ~400 species in Sigmodontinae (cf. Patton et al. 2015). Missing species in the biogeographic analyses were therefore evenly distributed across the sigmodontine phylogeny.

For the diversification rate analyses of Sigmodontinae, it was necessary to directly account for the full extant diversity in the phylogeny in order to avoid biasing the calculation of tip-level rates (Jetz et al. 2012). We calculated all diversification metrics using the ‘completed’ trees of 413 species from Maestri et al. (2017), which contrast to the ‘DNA-only’ trees described above by using genus- or tribe-level constraints to randomly add missing species across a posterior sample of trees (note: this method conserves the birth-death process of the sampled species by drawing new branch lengths from the same rate distribution; Thomas et al. (2013)). We used a sample of 100 completed trees to gather unbiased inferences about recent rates of diversification in sigmodontines.

### Phylogenetic metrics and analyses

We calculated mean pairwise distance (MPD) by taking the arithmetic mean of phylogenetic distances among all pairs of species in each assemblage (Webb et al. 2002), as calculated using the consensus tree from the DNA-only analyses. MPD has been used as a measure of phylogenetic relatedness (or divergence – Tucker et al. 2017), where low values indicate assemblages of more closely related species, and high values indicate the co-occurrence of more distantly related species (Cadotte et al. 2012).

For comparison, we also calculated the mean assemblage diversification rate (mDR) for each assemblage based on our sample of 100 completed sigmodontine trees. Per-species diversification rates (DR) were calculated as the reciprocal of the shared proportion of root-to-tip branch length, using the inverse of the equal-splits measure (sensu Jetz et al. 2012). The DR metric accounts for both shared branch lengths and number of nodes from root to tip per species (Redding and Mooers 2006, Jetz et al. 2012). The metric captures recent pure-birth diversification rates, which are similar to birth-death speciation rates when recent extinction has been minimal (Belmaker and Jetz 2015). DR is thus highly correlated

with the tip-level speciation rates obtained with BAMM, although computationally less demanding (Quintero and Jetz 2018, Rabosky et al. 2018). The harmonic mean of DR for all species occurring in an assemblage was used as a measure of assemblage diversification rate (here called ‘mDR’; see also Quintero and Jetz 2018). The harmonic, not arithmetic, mean is preferred where rates are averaged (Ferguson 1931). Each mDR value was the product of tree-wise calculations (per species harmonic mean of DR on 100 completed trees) and assemblage-wise calculations (per grid cell harmonic mean of species present in > 50% of the cell). While the completed trees were used in DR calculations, only the 260 species coded in our geographic matrix were used in the mDR calculations from those values. Because variance in relatedness metrics (i.e. mean root distances) are affected by richness (Fritz and Rahbek 2012), we used a randomization procedure to sample a maximum of 10 species from each assemblage and calculate assemblage mDR, repeating the procedure 10 000 times. Plotting mDR against richness revealed that 10 species is a highly conservative number that ensures absence of a richness effect – assemblage mDR variance starts to narrow at ~23 species per site. The average values of the 10 000 randomizations were used as mDR, and the standard deviation (SD) of the randomization was used to calculate mDR + SD and mDR – SD, to investigate the effect of richness on the calculations. Analyses were repeated with mDR, mDR + SD and mDR – SD. As the results were similar, and SD values were low (maximum SD was 0.067), we show in the text only mDR and relegate the analyses with + SD and – SD to the Supplementary material Appendix 1. MPD was calculated using the package picante (Kembel et al. 2010) and species DR using custom functions written in R (R Core Team).

The relationship between MPD and mDR was estimated using a generalized least squares (GLS) model including an exponential autocorrelation structure in the variance–covariance matrix. Spatial gradients may generate residual spatial autocorrelation that inflates the degrees of freedom in the model (Borcard and Legendre 2002), justifying the GLS approach. The correlation structure was constructed using latitude and longitude values for the centroid of each cell in the grid. This approach was used to minimize spatial autocorrelation in the residuals of the model (Diniz-Filho et al. 2003). Note that no phylogenetic correction is required in spatial analyses of mDR, as demonstrated by Quintero and Jetz (2018). Exponential autocorrelation was selected after fitting models using different spatial covariance structures, and selecting the best model using AICc (AICc weight = 0.67). Cells with four or fewer species were excluded from analyses to avoid spurious values. Package nlme (Pinheiro et al. 2017) was used to conduct the GLS in R.

### Biogeographical areas of differentiation

We assembled and coded biogeographic regions (bioregions) for sigmodontines using the Infomap Bioregions clustering algorithm (Rosvall and Bergstrom 2008, Edler et al. 2017). This routine inputs species range maps and grid cells to

calculate a bipartite network between species and grid cells, and to cluster the network into bioregions (Edler et al. 2017). We used the range maps of all 400 known sigmodontine species to generate the bioregions, using 1° as the grid cell size, and a minimum cell capacity of 1 species. Although we could have employed a generalized regional framework (Morrone 2014), sigmodontine distributions should reflect only those geological, geographic, biological, and climatological factors that were operational during their Neogene diversification, not those shaping other taxa with very different histories or ecologies. Eleven relevant bioregions were identified in the Neotropical region. A shapefile containing the bioregions for sigmodontines is available in the supplemental material. Analyses of variance were used to investigate differences in MPD and mDR among bioregions. Boxplots were used to represent variation in these metrics among bioregions.

Ancestral biogeographic distributions were reconstructed using these bioregions. We used biogeographical stochastic mapping (Dupin et al. 2017), under an equal rates of transition, through a dispersal–extinction–cladogenesis model (DEC) (Ree and Smith 2008) as implemented in the R package BioGeoBEARS (Matzke 2013). DEC calculates likelihood values for biogeographical states and ancestral areas of occupation. We choose DEC because it permits changes in states to occur along the branches of a phylogeny and more reliably captures anagenetic events than models incorporating the ‘jump’ parameter (Ree and Sanmartín 2018). Based on their range maps, each taxon was assigned to 1–3 bioregions (assigned where necessary by proportion of geographic range) to limit computation time, and a time-calibrated phylogeny (260 species) was used as explained above. A total of 47 species (18%) occurred in more than three bioregions, and the least occupied bioregion(s) of these were treated as unoccupied. We summarized the results by plotting the estimation of the highest-probability ancestral states under the globally optimal model.

### Ancestral range reconstruction

We use ancestral range reconstruction (rasc – Quintero et al. 2015) to infer the geographical location of the ancestors of the principal sigmodontine tribes. Rasc uses a Bayesian framework to infer ancestral range location based on species’ entire geographical ranges, without the distortion of a bioregion(s) or a single location being used in proxy (Quintero et al. 2015). The reconstructed ancestral ranges are also not restricted to a single or a set of bioregions but can be placed anywhere in space and produce complex shapes taking into account the uncertainty in the range estimates (Quintero et al. 2015). We ran rasc using 12 000 iterations, discarding the first 2000 as burn-in, to obtain posterior distributions of ancestral nodes. We use the package rasc in R (Quintero et al. 2015) to conduct the ancestral reconstruction, based on the range maps for each species and the phylogeny for sigmodontines as described earlier. The R package coda (Plummer et al. 2006) was used to summarize the MCMC results. Maps of ancestral ranges were plotted in R for the ancestral nodes of each

of the main tribes of sigmodontines, along with confidence intervals for the range estimates.

### Data deposition

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.8vt6s95>> (Maestri et al. 2018b).

## Results

### Evolutionary diversification

A spatially structured pattern of diversification rates is evident from the mapping of assemblage mDR (Fig. 2B). The lowest mDR values are found in Central America, northern South America, parts of Amazonia, and the Atlantic Forest. Highest values of mDR are found in southern and north-eastern South America. The evolutionary relatedness pattern shows that lower values of MPD (i.e. closer relationships among co-occurring species) are found in Amazonia and in southern South America, especially along the Pacific coast (Fig. 2C). The overall relationship between MPD and mDR is negative and significant, albeit non-descriptive (GLS:  $b \pm SE = -1.14 \pm 0.71$ ,  $t = -1.48$ ,  $p < 0.001$ , for all 1633 cells with richness  $> 4$ ;  $R^2 = 0.10$ ). Lower values of mDR are generally associated with higher MPD values, and vice versa (Fig. 3). This relationship is strengthened if the bioregion containing Amazonia is excluded (GLS:  $b \pm SE = -1.78 \pm 0.77$ ,  $t = -2.31$ ,  $p < 0.001$ ;  $R^2 = 0.21$ ) (Fig. 3); Amazonia has lower MPD values than expected from its mDR. The *Oryzomyini* root is close to older nodes in our phylogenetic hypothesis and its species predominate in Amazonia, generating a co-occurrence of closely related species there. The highest richness values are evident along the Andean chain, with a secondary peak in Atlantic Forest (Fig. 2A). Figure 2A includes an elevation map and visually documents the positive relationship between species richness and elevation for sigmodontines.

We delimited 11 biogeographical regions (Fig. 4) that showed significant differences between each other in values of mDR ( $R^2 = 0.46$ ;  $F = 140$ ;  $p < 0.001$ ) and MPD ( $R^2 = 0.64$ ;  $F = 292.6$ ;  $p < 0.001$ ). Lower values of mDR were found in the bioregions of Central America and northern South America (C, B, I, and J), low to intermediate values were found in Amazonia and eastern South America (A and D, respectively), and higher values of mDR were found in southern and western South America (F, H, G and E) (Fig. 4A). MPD values were higher in bioregions of Central America and northern South America (C, B, I and J) and lower in the remaining bioregions (Fig. 4B). A bioregion with an especially low MPD was A, which includes Amazonia.

Estimation of ancestral bioregions using DEC (Fig. 5) showed that northern South America (bioregion I), the Amazonian bioregion (A), and the eastern bioregion (D) were likely the first to be occupied during sigmodontine evolution. The putative ancestor of *Oryzomyini* was recovered

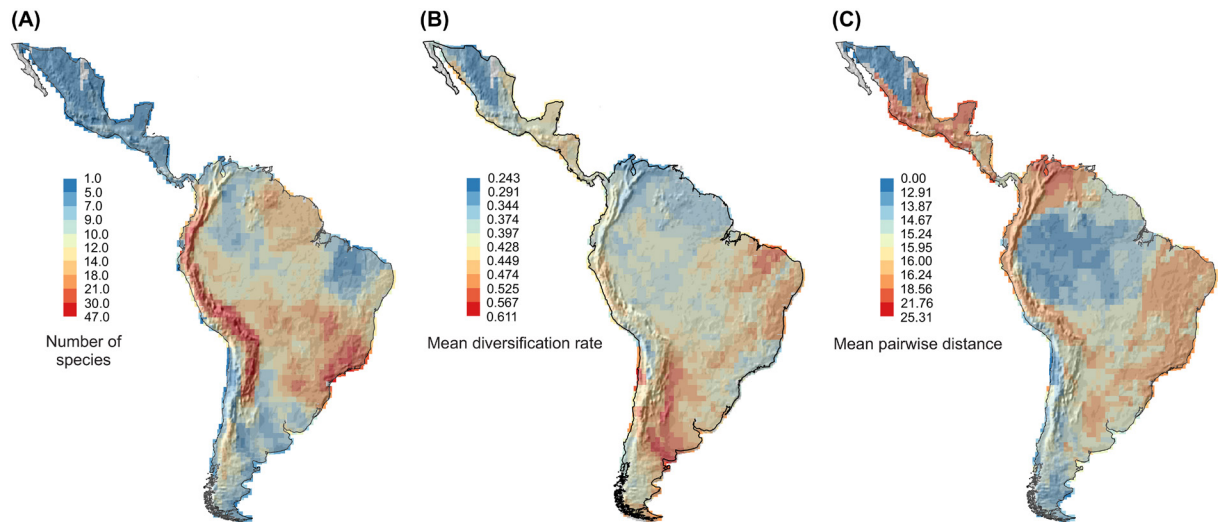


Figure 2. Maps of (A) species richness, (B) mean assemblage diversification rate and (C) mean pairwise distance. An elevation map is used as background. Maps are in Behrmann projection.

in bioregion A (containing the Amazon region and Guianan Shield), while the putative ancestor of South American tribes other than *Oryzomyini* was reconstructed to bioregion D (eastern South America). We also recovered the putative ancestor of *Akodontini* in bioregion D. The putative ancestors of *Thomasomyini* and *Phyllotini* were not localized in a single bioregion, and the probabilities of single reconstructed states were generally low. Exceptions were the putative ancestor of *Abrotrichini*, placed with high probability in bioregion E (Southern Cone), and the putative ancestor of the *Phyllotis + Eligmodontia* clade (*Phyllotini* excluding *Calomys*),

estimated with high probability in bioregion F (Central Andes plus Atacama).

### Ancestral range reconstruction

The geographical distributions of the ancestral nodes for the main tribes of sigmodontines are shown in Fig. 6. The estimated dispersal rates for sigmodontines, according to rase, revealed slightly greater latitudinal displacements (mean of 5.98 degrees<sup>2</sup>/Ma, SD = 1.68) than longitudinal displacements (mean of 3.48 degrees<sup>2</sup>/Ma, SD = 1.02). The average decimal latitude and longitude of the posterior distribution for all ancestors are shown in Supplementary material Appendix 2. Except for *Sigmodontini*, *Ichthyomyini*, and *Abrotrichini*, whose ancestors were reconstructed in Central America and in the far south of South America, respectively, the ancestral nodes leading to other tribes were reconstructed on or along the eastern margins of the Central Andes (Fig. 6). In terms of bioregions, the reconstructed ancestral ranges for the nodes leading to *Oryzomyini* and *Thomasomyini* both fall along the southern limit of bioregion A (containing Amazonia), the ancestor of *akodontines* includes bioregions A, D, F and H, the ancestor of *Phyllotini* falls within bioregions F and H, and the node leading to *Abrotrichini* falls unambiguously in bioregion E.

### Discussion

The inferences resulting from the diversification patterns were closely aligned with the biogeographical reconstructions for sigmodontine rodents, helping to consolidate a history of occupation in the Neotropical region that explains the phylogenetic patterns of species assembly found. Both are considered below in separate sections, after a short discussion of the arenas of diversification.

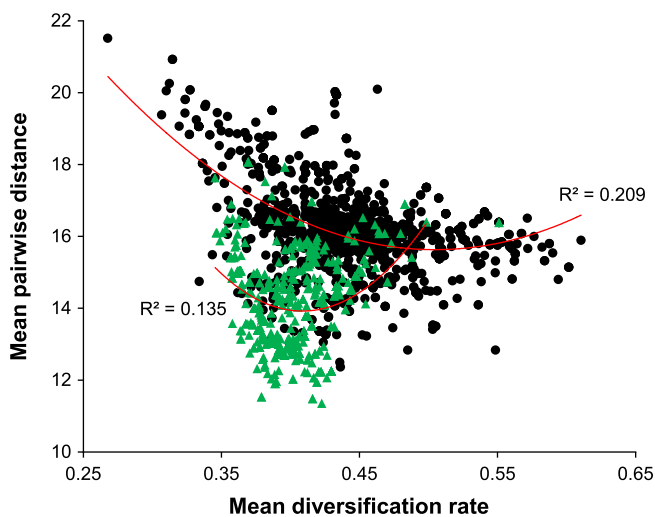


Figure 3. Scatterplot showing the relationship between mean assemblage diversification rate and mean pairwise distance over all grid cells. Green triangles identify the cells of the bioregion containing Amazonia. Black lines show the fitted quadratic regressions and associated  $R^2$  for the Amazonian bioregion vs other cells.

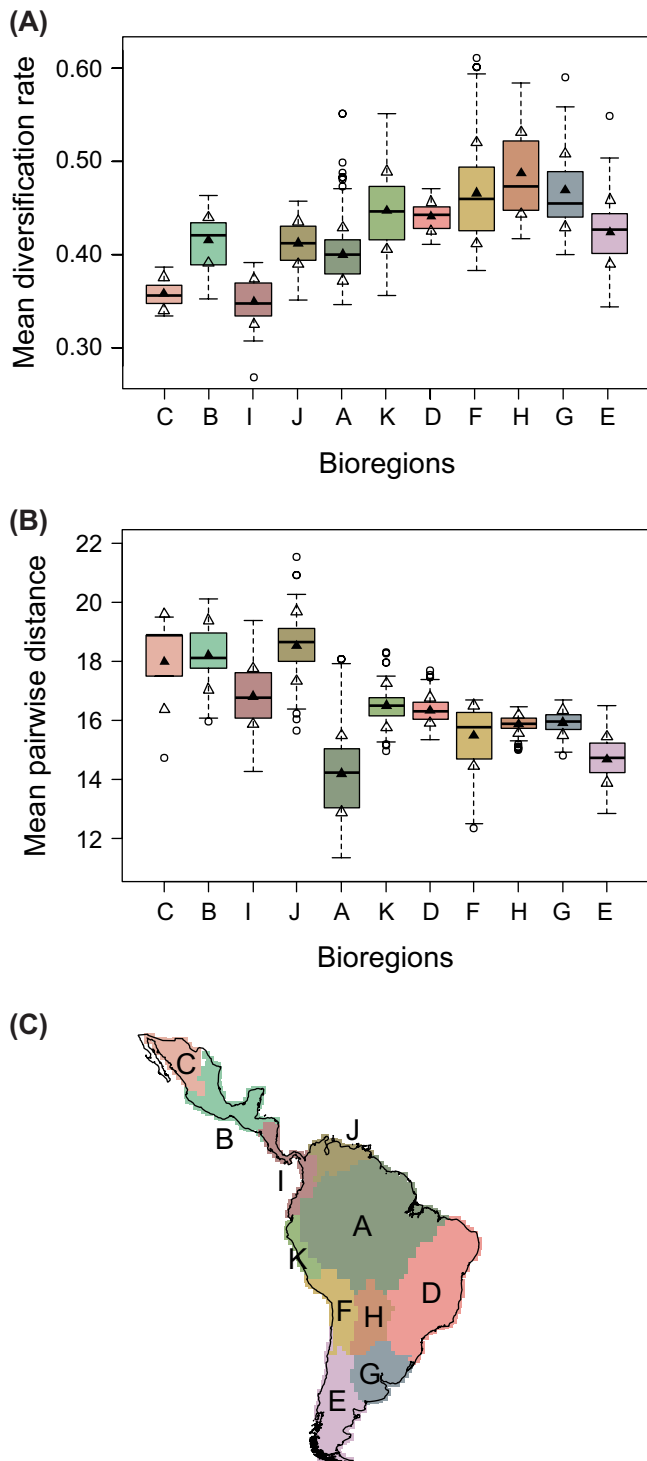


Figure 4. Boxplots representing variation in (A) mean assemblage diversification rate and (B) mean pairwise distance among bioregions (which are shown in (C)). Boxes represent the first and third quartiles, the median (bold line), and upper and lower limits. Open circles represent outliers. Solid triangles represent the average, and open triangles the standard deviations of values on each plot.

## Bioregions

The eleven biogeographical regions we identified for sigmodontines have parallels in biomes of Cabrera and Willink (1980), the regions of endemism of Cracraft (1985), the ecoregions of Olson et al. (2001) and the biogeographical regions of Morrone (2014). Two large bioregions were identified corresponding to the Amazon region (A) and eastern South America (D), including both interior and coastal Atlantic Forests, the Caatinga, and Cerrado biomes. Three bioregions (I, K, F) were identified along the cordillera from the northern to central Andes. Generally, boundaries of bioregions agree with regions of high species turnover of Sigmodontinae (Maestri and Patterson 2016). Because the bioregions were defined by the distributions of sigmodontines themselves, rather than other lineages evolving over different time-periods (Morrone 2014), their number and dimensions more closely reflect the particular history and ecology of sigmodontines over the Neogene.

## Sigmodontine diversification history

The co-occurrence of distantly related species that are in slowly diversifying lineages and of closely related species that are in more rapidly diversifying lineages matches the expectations from scenario A in Fig. 1. The recent and rapid nature of the sigmodontine diversification may underlie this pattern, as rapid speciation and/or slow extinction are predicted to generate co-occurrence of closely related species in continental regions (Cardillo 2011, Warren et al. 2014, García-Navas et al. 2018). However, the impressive diversity of sigmodontines permits a further prediction: that phylogenetic relatedness will also vary among assemblages within such radiations, and this variation can be negatively associated with the pace of diversification (Fig. 3). This pattern can be explained, first, by simple historical factors and sampling. When an initial speciation event occurs, the resulting species (say A and B) are sisters, but after additional speciation events (A gives rise to multiple daughter species, as does B), the initial pair become more distantly related relative to the entire tree. If A and B occur in the same assemblages, they generate co-occurrence of distantly related species from older nodes. As species successively multiply, rapid dispersal and high speciation rates lead to the in situ speciation of clades within geographic regions, which may result in the predicted clustering (Cardillo 2011). Historical events of initial colonization, faster speciation rates, and possibly environmental filtering can all contribute to explain the historical biogeography of young clades, such as sigmodontines.

Patterns of mDR are thus compatible with the tropical niche conservatism hypothesis (TNC; Wiens and Donoghue 2004, Hawkins et al. 2005, 2007), where early-diverging lineages would have long ago become adapted to areas initially occupied (in this case, tropical habitats), while recently diversified species would be phylogenetically clustered in

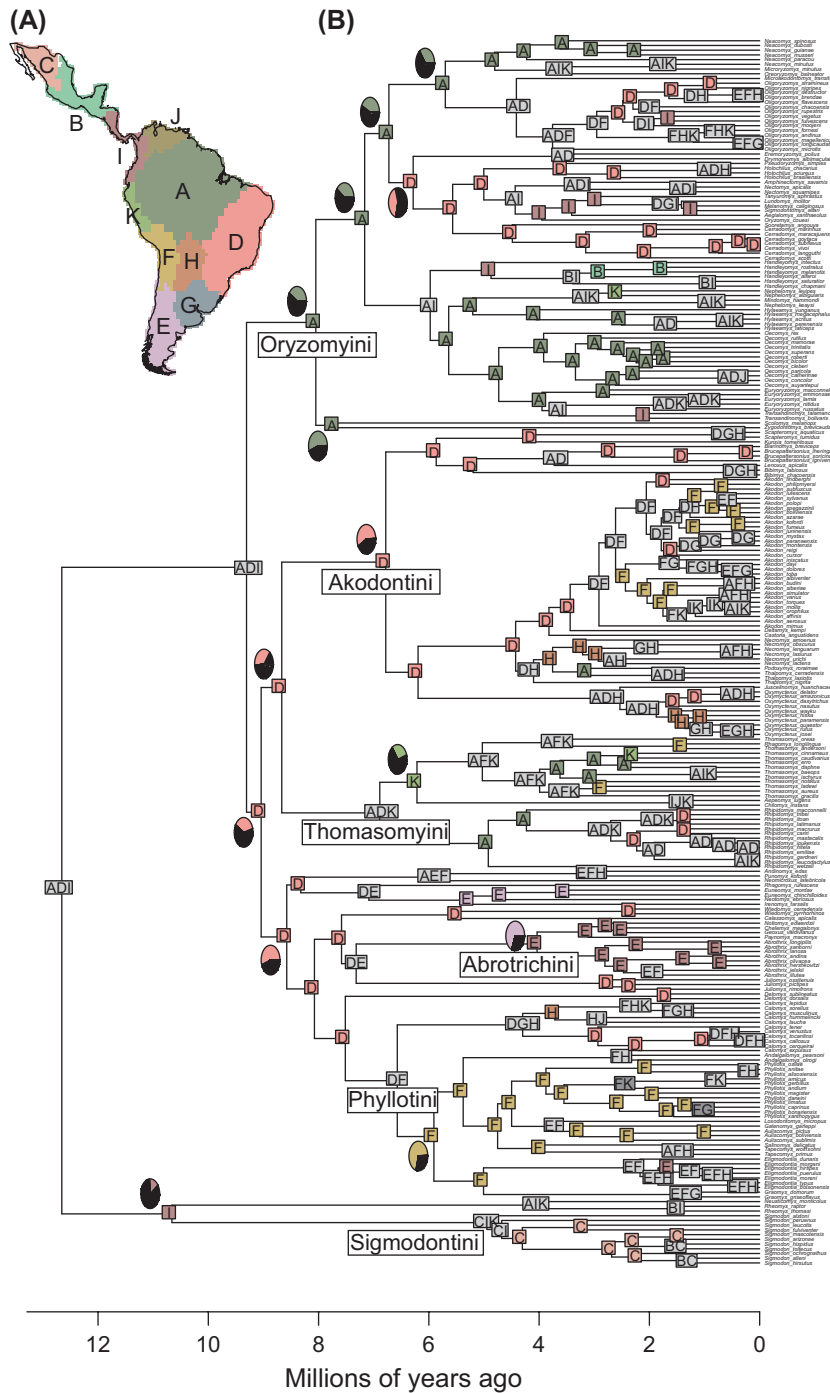


Figure 5. Biogeographical regions for sigmodontines in (A), constructed using Infomap Bioregions (Edler et al. 2017). Estimation of ancestral biogeographic ranges for sigmodontines (B) was based on a dispersal–extinction–cladogenesis (DEC) analysis. States at nodes represent the ancestral bioregion occupied immediately before speciation. Instantaneous states on the branches leading away from nodes were not plotted to avoid clutter. The relative probabilities of favored states were shown as pie charts for some nodes with single-reconstructed states due to space constraints.

newly occupied environments, such as temperate habitats at high latitudes or elevations (Fig. 1A). This pattern of TNC is evident in bird (Hawkins et al. 2007) and frog clades (Wiens et al. 2006). On the other hand, long-term occupancy of a geographic region provides more time for species

to accumulate in a region (e.g. clustering of early-diverging lineages in the same assemblage – Hardy and Senterre 2007), as well as for extinction to occur (Cardillo 2011), implying that niches may become filled or ‘saturated’ and thus lead to stronger competition and overdispersion among recently



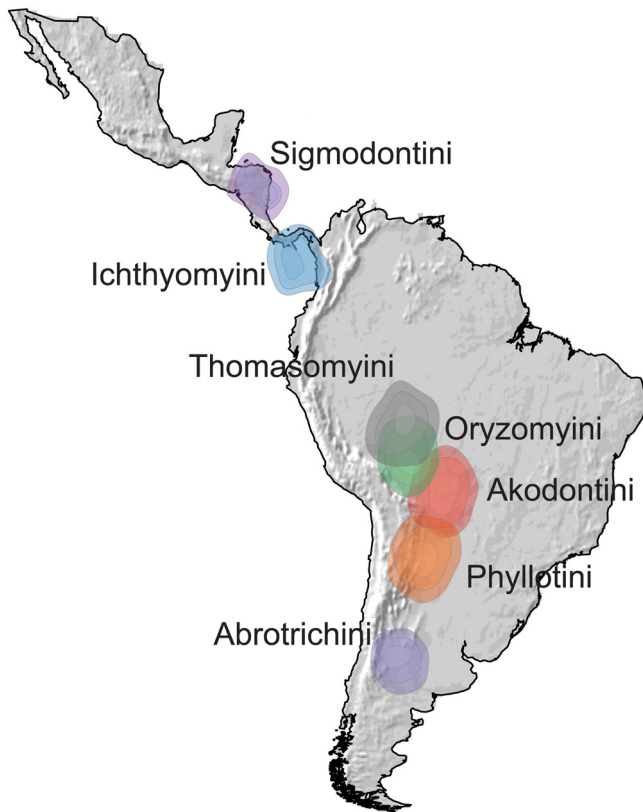


Figure 6. Ancestral range reconstruction using *rasc* for the ancestors of the main tribes of sigmodontines. The color intensity gradient denotes the 70, 80, and 90% highest confidence intervals for each estimation. An elevation map is used as background. Maps are in Behrmann projection.

diversified lineages (Hardy and Senterre 2007, Mazel et al. 2016). Such factors may contribute to patterns approximated by scenarios B or C in Fig. 1.

The pattern of sigmodontine colonization and diversification also reflects the historical contingences expected from a clade of small-bodied, narrow-ranging species colonizing the vastness of South America via a northern isthmus (Patterson 1999). Different tribes were able to colonize and subsequently diversify in different areas of South America, shaping the adaptive landscape for later-appearing lineages (Maestri and Patterson 2016). The Amazon region is now dominated by *Oryzomyini* rodents (Maestri and Patterson 2016), but this tribe did not give rise to other tribes, particularly those in the Southern Cone, nor were ancestors of *Oryzomyini* responsible for colonizing other regions (although select members of this lineage, e.g. *Oligoryzomys*, have proven highly successful in doing so and now occur throughout the Neotropics). Nevertheless, the low mDR values together with high MPD values in Central America and in the Atlantic forest suggest that these areas harbor assemblages of early diversifying and distantly related species, characterizing the low turnover in tropical areas (see also the low turnover in the Amazon region in Maestri and Patterson 2016) that may act as ‘museums’ of diversity. On the other hand, regions in the south

and associated with Caatinga habitats in northeastern South America seem to have been occupied later and experienced higher turnover (Maestri and Patterson 2016), resulting in more rapid diversification.

The explosive diversification of Sigmodontinae is well established (Fabre et al. 2012, Steppan and Schenk 2017), but this cannot be taken as evidence of an adaptive radiation. As others have extensively and emphatically argued, the ecological and adaptive components of a radiation must be investigated and related to those rates to conclude that a radiation is adaptive (Schluter 2000, Olson and Arroyo-Santos 2009, Losos 2010, Moen and Morlon 2014, Givnish 2015). Nonadaptive processes can also give rise to impressive radiations of species and high rates of diversification (Rundell and Price 2009, Alhajeri et al. 2016, Maestri et al. 2017). Nonadaptive and adaptive processes offer profoundly different interpretations for patterns of evolutionary radiation (Givnish 2015), but various authors, including (Schenk and Steppan 2018) with sigmodontines, continue to invoke adaptive radiation, despite detailed evidence to the contrary (Maestri et al. 2017).

### Sigmodontine biogeographical history

We found that the diversification patterns of sigmodontines described above matched closely their path of colonization since their arrival from North America, connecting phylogenetic patterns of community assembly (Fig. 2–4) with biogeographical history (Fig. 5, 6). The first regions to be colonized were Central America and northernmost South America (Fig. 5, 6). This is reflected in the basal dichotomy of Sigmodontini + Ichthyomyini (in Central America and northern South America) and *Oryzomyia* (remaining tribes and widespread) (Steppan et al. 2004). Afterwards, according to DEC, ancestral forms colonized the lowlands in Amazonia (forming the clustering of *Oryzomyini* species there – Fig. 2C, 5B), the central portions of South America and the forested Atlantic coast (Fig. 5). Only later were the Southern Cone of the continent and the Altiplano and Central Andes colonized. This pattern is in line with the mDR-MPD scenario (Fig. 2, 3) which suggests early diversification of distantly related species in Amazonia and most of the Atlantic forest.

However, *rasc* estimation suggests a complementary explanation for some tribes (Fig. 6). The putative ancestor of *Oryzomyini*, while in the Amazonian bioregion, was reconstructed near its southern limit, next to the Central Andes. Overlapping with it, the putative ancestor of *Akodontini* was also reconstructed close to the Central Andes, placed in the westernmost portion of the eastern bioregion (D). Ancestors of *Phyllotini*, *Abrotrichini*, and *Sigmodontini* were recovered by both DEC and *rasc* more or less in the same regions. The distinctive estimates of the two methods for *Oryzomyini* and *Akodontini* suggests that classification of bioregions can be inexact, as such regions are large and the precise location of ancestors might not be localized inside a given bioregion. *Rasc* suggests that areas adjoining the Central Andes were loci for the initial divergence of the main tribes, each subsequently

colonizing different subregions (see tribal richness patterns in Maestri and Patterson 2016). The juxtaposition of this analysis alongside the DEC model also reconciles incongruences between Reig's (1981, 1986) views and more recent evidence favoring lowland centers (Parada et al. 2015).

Nevertheless, rase estimated putative ancestors for the main tribes in different areas than those envisioned by Reig (1986). The Reig's AOD for Oryzomyini (which included Thomasomyini), for example, was in the northernmost areas of South America, whereas rase placed the ancestors of both Oryzomyini and Thomasomyini near the center of the continent (Fig. 6), adjacent to the Andes, with the main center of diversification in the Amazon bioregion (Fig. 5). This new scenario seems far more likely, given recent evidence that Lake Pebas would have made much of the Orinoco and Amazon basins uninhabitable during the earliest phase of sigmodontine colonization in South America (de Fátima Rossetti et al. 2005, Antonelli et al. 2009, Tejada-Lara et al. 2015, Antoine et al. 2016). Reig's AOD for Akodontini (which also included Abrotrichini) was at a latitude close to that estimated by rase, however Reig's (1986) lay closer to the Pacific coast, whereas rase estimated that the Akodontini ancestor lived to the east, corroborating with the DEC estimate in the eastern bioregion. This agrees closely with recent evidence supporting an important role of the lowlands and eastern South America in sigmodontine diversification (Smith and Patton 1999, Gonçalves et al. 2018), particularly for Akodontini and Phyllotini (Salazar-Bravo et al. 2013, Pardiñas et al. 2014, Parada et al. 2015).

Moreover, early diversification both in the tropical Andes and in the Atlantic forest suggests a historical connection between these two biomes. Arcs of seasonally dry climates (Prado and Gibbs 1993) may have supported forest that acted as corridors for the dispersal of many clades (see also Rangel et al. 2018). Disjunct sister taxa occupying the tropical Andes and Atlantic forest have been observed in sigmodontines (Percequillo et al. 2011a, b), hylid frogs (Faivovich et al. 2004) and parrots (Ribas et al. 2007). These arcs, extending from the tropical Andes and passing through northern Argentina and into the Atlantic forest of northeastern Brazil, were vegetated by seasonally dry forests during the Pleistocene (Prado and Gibbs 1993, see also Fig. 1 in Pennington et al. 2000 for a map with the distribution of seasonal dry forests). The age of the seasonal dry tropical forests may be as old as the Middle Eocene (Pennington et al. 2009). Our results suggest that this arc or other similar connection persisted throughout the Pliocene.

Importantly, the pattern of diversification and phylogenetic relatedness (Fig. 2, 4) suggests that the extant diversity along the Andes chain was not the product of a single colonization event, but resulted from multiple independent colonization events by members of ramifying clades. First, the northern Andes were initially colonized by the species that first arrived in South America, and their descendants thus stem from older nodes (Fig. 2B); this results in co-occurrence

of species from more distantly related lineages than in other parts of the Neotropics (higher MPD – Fig. 2C, 4B). Second, the central Andean regions (~ bioregions K and F) were colonized independently by members of each of the principal tribes (see the complementarity of tribal richness patterns in Maestri and Patterson 2016), which contributed to the co-occurrence of distantly related species (Fig. 2C). Third, the later colonization of the Southern and Western Andes was mainly accomplished by members of the Phyllotini and Abrotrichini, resulting in the co-occurrence there of more closely related species (low MPD, high mDR – Fig. 2, 4). Sigmodontine richness in the Andes (Fig. 2A) is therefore driven by the assembly of species hailing from both older and younger groups. Multiple events of independent colonization, together with the dynamic history and topographical complexity of the Andes, explain its exceptionally high diversity. A similar pattern holds for mammals at a global scale, where elevated richness is mainly associated with younger nodes (Hawkins et al. 2012) and can be expected for other taxonomic groups.

## Conclusions

We suggest that there may be general patterns of evolutionary relatedness in the course of lineage diversification, ones shared among contemporary radiations with similar biological characteristics (Fig. 1). Our investigation of this pattern using sigmodontine rodents confirms those predictions, and biogeographical history and community ecology (rapid and recent speciation within bioregions and/or environmental filtering on recent nodes) jointly explain much of the pattern. Currently, it is not possible to disentangle other processes of community assembly and speciation that may generate similar patterns. An interesting next step would be to simulate null expectations of diversification and assembly patterns using appropriate mechanistic models. Regardless, some early sigmodontine diversification in the Neotropical region is clearly linked to the lowlands and eastern South America, and a Pliocene-aged connection between the tropical Andes and the Atlantic forest would help explain the group's biogeographical history. Future investigations of community ecology of sigmodontine rodents at local to regional scales must consider these phylogenetic and historical biogeographic components of their modern patterns of spatial richness.

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Supplementary material (Appendix ECOG-04102 at <[www.ecogeography.org/appendix/ecog-04102](http://www.ecogeography.org/appendix/ecog-04102)>). Appendix 1–2.