

The Role of Geography in Adaptive Radiation

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ABSTRACT: Although the importance of biogeography in the speciation process is well recognized, the fundamental role of geographic diversification during adaptive radiations has not been studied to determine its importance during the adaptive radiation process. We examined the relationship between lineage and regional diversification patterns in the South American rodent subfamily Sigmodontinae, one of the best candidates for an adaptive radiation in mammals, to propose a conceptual framework for geographic transitions during adaptive radiations. We reconstructed a time-calibrated phylogeny from four nuclear genes and one mitochondrial gene for 77% of sigmodontine diversity. Historical biogeography was reconstructed among 14 regions, for which we applied a sliding-window approach to estimate regional transition rates through time. We compared these rate patterns and measured whether regions consisted of species that were more phylogenetically related than expected by chance. Following the initial South American colonization around 7 million years ago, multiple expansions from northern regions correlated with a burst of speciation. Subsequently, both diversification and regional transition rates decreased overall and within the majority of regions. Despite high regional transition rates, nearly all regional assemblages were phylogenetically clustered, indicating that within-region diversification was common. We conclude that biogeographic complexity and partitioning played a profound role in the adaptive radiation of the South American Sigmodontinae (*Oryzomyia*), the degree to which is determined by the relative scales of spatial variation and dispersal abilities.

Keywords: adaptive radiation, dispersal, ecological opportunity, historical biogeography, Sigmodontinae, South America.

Adaptive radiation, as facilitated by ecological opportunity (exposure to novel niches by dispersal to new areas, extinction of competitors, or key innovations; Simpson 1953; Schluter 2000; Yoder et al. 2010), is characterized by an increase in speciation rates (Glor 2010). All speciation events, however, have a geographic component of spatial structuring (Losos and Glor 2003), and adaptive radiations are no exception. Despite its fundamental importance in the speciation process,

the role of geography in an adaptive radiation has received less attention than the roles of other patterns or processes of diversification, such as lineage and phenotypic diversification rates (e.g., Harmon et al. 2010; Mahler et al. 2010; Derryberry et al. 2011; Martin and Wainwright 2011). How clades diversify spatially is critical to the process of ecological opportunity, and the rates of dispersal can yield valuable insights into the process of diversification—especially for ecological opportunity mediated by colonization into novel areas.

Geographic barriers are important in insular adaptive radiations like the Caribbean anoles, among other organisms (e.g., Bennett and O’Grady 2013), and have facilitated partitioning of ecological space in parallel across islands (Mahler et al. 2013), but the significance of geographic barriers as a lineage rapidly multiplies remains poorly understood. We have even less understanding about the role of geographic barriers in continental radiations, where the contrast between hospitable and inhospitable habitats is far less discrete. Studies of the geography of diversification have focused on the causes of diversity gradients (e.g., the latitudinal diversity gradient; Wiens et al. 2006) or the frequencies of allopatric, parapatric, or sympatric speciation (Losos and Glor 2003; Pigot et al. 2010). Here we focus on the much less studied role of regional dispersals and subdivisions in adaptive radiations.

Geography could play several roles in adaptive radiations, either via the rates at which regions become occupied or if regionalization increases or decreases diversification rates. Our basic model for continental geographic contribution to an adaptive radiation is that following the initial colonization, subsequent dispersal among subregions within that continent (hereafter, “regions”) leads to allopatric speciation. Because these regions generally differ in their environments, transitions also promote adaptive divergence locally (Fine et al. 2014; Warren et al. 2014). Each new regional colonization within the continent might be thought of as an ecological opportunity event at a smaller scale (Stanley 1979), and we expect increased diversification rates associated with these later colonizations. We predict high initial transition rates as species disperse into the many new and underutilized regions and their associated niches. Over time, these regions and their

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niches fill up, and competitive exclusion slows diversification within and among regions (Schluter 2000). Moderate regional transitions relative to the age of the clade would lead to clades diversifying within regions, and we predict that species within regions would be more closely related to each other (i.e., more phylogenetically clustered) than to species in other regions. Thus, under this model (hereafter, the regionalization effect [RE] model), regional transition and speciation rates would be positively correlated (high at the beginning of a radiation and declining through time), and regional biotas would be phylogenetically clustered. The RE model is largely concordant with the ecological opportunity model (Schluter 2000; Harmon et al. 2003; Yoder et al. 2010; Schenk et al. 2013) but not identical because allopatric speciation plays an additional and important role in generating species diversity.

Geography can alternatively play an incidental role in adaptive radiation. Under such a process, cladogenesis will occur within and across regions at similar rates following colonization, and the transition rate among regions will not be correlated with lineage diversification rates. In addition, if the distributions of descendant species are not mediated by interactions with closely related species, the invasibility of new regions should remain constant. Because speciation would be driven entirely by adaptive divergence with spatial autocorrelation (Warren et al. 2014) but not directly related to colonization of new areas, the null model would predict no correlation between speciation and regional transition rates or regional transition rates and time (e.g., constant), and there would be no significant phylogenetic clustering.

A third alternative hypothesis would be that biogeographic barriers impede lineage diversification. Here niche space fills up within regions, but the radiation is constrained by between-region barriers (or by niche conservatism if the evolution of new habitat preferences is too slow to allow adaptation and expansion into new regional habitats). Geographic distance acts to impede regional diversification, with that effect decreasing over time as the increasing number of niches occupied within each region provides more opportunities for at least one lineage to find suitable habitats in other regions (i.e., barriers are broached more frequently as time passes). Such a radiation would proceed slowly at first, with both speciation and transition rates increasing over time as increasing phenotypic divergence of lineages increases the possibility of successful regional transitions. This model (hereafter, the geographic impedance [GI] model) predicts a positive correlation between speciation and transition rates but a pattern of increasing rates over time, and regions would exhibit phylogenetic overdispersion (due to both retention of basal lineages in the region of origin and recent, phylogenetically dispersed transitions in the recently colonized regions).

Figure 1 summarizes expectations of the three models. Under the RE model (fig. 1, gray line), transition rates increase sharply after colonization (fig. 1 shows only the postcoloniza-

tion history, so the gray line starts high) and decrease as regional niches become saturated. Speciation rates would follow the same pattern, creating a positive correlation with transition rates. Under the GI model (fig. 1, dashed line), both transition and speciation rates start slow and then increase, creating a positive correlation. If we observe such a radiation late in its history, we might observe a subsequent decrease in rates, creating a modal pattern (fig. 1, dotted line). These first three scenarios (but two models) are consistent with regional transitions playing an important role in an adaptive radiation. The null model, alternatively, predicts no trend in regional transitions (fig. 1, solid black line). This does not mean that geography plays no role in speciation but rather that regional transitions are not key determinants of changes in diversification rate. We also note that both ecological processes, such as competitive exclusion, and historical processes, such as allopatric speciation, can be strongly confounded in a scale-dependent fashion, as has been discussed elsewhere (Warren et al. 2014).

The South American sigmodontine rodents (superfamily Muroidea, family Cricetidae) have experienced ecological opportunity on a continental scale and are ideal for a study that explores the relationship between historical bio-

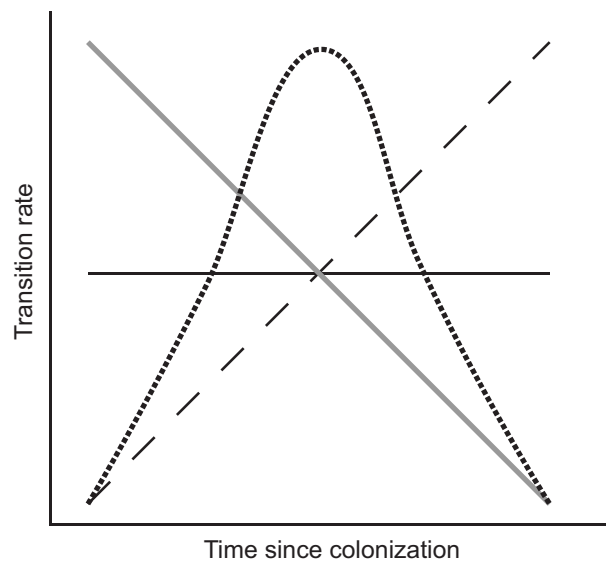


Figure 1: Predicted models of the role geography plays in an adaptive radiation. The gray line (regionalization effect model) indicates transition rates that are high as species diversify into the many new and underutilized biogeographic regions and their associated niches but that decline over time as these regions and niches become saturated. The dashed line (geographic impedance [GI] model) indicates early lineages diversifying within regions after colonization and only diversifying into different regions later in the radiation. The solid black line (null model) indicates no trend in transition rates over time. The dotted black line indicates a scenario that is compatible with the GI model: transition rates increase quickly at first but decline as biogeographic regions become saturated.

geography and ecological opportunity. The group originated in North America, and two to three lineages colonized South America (Schenk et al. 2013)—one of which subsequently became ecologically and geographically diverse (Smith and Patton 1999; Parada et al. 2013, 2015). The only other rodents inhabiting South America at that time were the generally much larger and less fecund caviomorph rodents (suborder Hystrichomorpha; Simpson 1980), which were unlikely to have filled the same niche as the sigmodontines. The diurnal squirrels (suborder Sciuromorpha) colonized South America several million years after the sigmodontines, following the completion of the Panamanian Isthmus, leaving open niches for predominantly nocturnal sigmodontines. By far the largest clade resulting from colonization is *Oryzomyia* (Steppan et al. 2004), containing 92% of sigmodontine species. Its rapid diversification after colonization (7.0–13.2 million years ago; Schenk et al. 2013) has been noted by several studies (D'Elia et al. 2006; Parada et al. 2013, 2015; Salazar-Bravo et al. 2013; Schenk et al. 2013) and is perhaps the most rapid geographically discrete diversification event in mammals.

Strong statistical support was identified in *Oryzomyia* for a rapid initial diversification rate (early burst), followed by a diversity-dependent decrease in diversification (Schenk et al. 2013; Parada et al. 2015) consistent with the ecological opportunity model that predicts that speciation rates will decrease over time as niches are filled (Schluter 2000; Phillimore and Price 2008). Indeed, *Oryzomyia* is the only one out of 28 continental colonizations by muroid rodents to satisfy the predictions of the ecological opportunity model (Schenk et al. 2013; Alhajeri et al. 2016). Alhajeri et al. (2016) identified an increased rate of diversification in relative tail length and elevation in *Oryzomyia*, and a multivariate value for limb appendage variation was identified as having early subclade diversification, providing additional evidence that species ecologically diversified early in the radiation. Therefore, the sigmodontines appear to be the best example of a continental adaptive radiation in muroids, both classically defined and supported by empirical results.

In this study, we applied phylogenetic approaches to quantify the how clades disperse across biogeographic barriers through time. We then combined these and additional approaches with the most comprehensive Sigmodontinae phylogeny to reconstruct the tempo and estimate the mode of their geographic history. We then tested the predictions of our three biogeographic models of diversification to determine the role of geography in an adaptive radiation.

Material and Methods

Sampling

We reanalyzed sequence data from the 291 sigmodontines (77.4% of species, representing the most completely sam-

pled Sigmodontinae phylogeny to date) and four Central American Tylomyinae from Steppan and Schenk (2017; table S1; tables S1, S2 are available online). Reducing the taxon sampling size from 904 to 295 species allowed us to sample parameter space more effectively during relaxed-clock dating. The in-group consisted of the core South American Sigmodontinae (*Oryzomyia*) and their sister group, the North and South American Sigmodontini and Ichthyomyini (Sigmodontalia, sensu Leite et al. 2014). Seven species were represented by two deeply divergent genotypes that were also spatially separated, which we interpret as cryptic, undescribed species. Additionally, we included unassigned accessions of *Rhipidomys*, *Thomasomys*, and *Zygodontomys* that also likely represent undescribed species. We used five commonly sequenced genes that resolve relationships among and within muroid families (Steppan and Schenk 2017). These included four nuclear loci—exon 11 of the breast cancer 1 (*BRCA1*) gene, exon 10 of the growth hormone receptor (*GHR*) gene, exon 1 of the interphotoreceptor retinoid binding protein (*IRBP*) gene, the single exon of the recombination activation gene 1 (*RAG1*) gene—and the most widely sequenced mitochondrial gene, cytochrome *b* (*cyt-b*).

Divergence Time Estimates

Divergence times were estimated with the uncorrelated log-normal rates model in BEAST version 1.8.0 on the CIPRES Science Gateway (Miller et al. 2010). We applied a starting tree that was pruned from a maximum likelihood estimation of Muroidea by Steppan and Schenk (2017) but searched alternative rearrangements of the tree during optimization (data available from the Dryad Digital Repository, <http://doi.org/10.5061/dryad.3mn2402> [Schenk and Steppan 2018]). We attempted to create partitions that explored coding and noncoding regions as well as codon structure, but these computationally expensive strategies would not complete in a reasonable amount of time. We therefore inferred the best partition by analyzing a partition-by-gene strategy optimized with PartitionFinder version 1.1.1 (Lanfear et al. 2012). Importantly, this captures the differences in the rate between and among mitochondrial and nuclear genes.

Five Sigmodontinae nodes were calibrated with ages estimated from fossil data to infer divergence times. The placements of all five calibrations were justified in a larger Muroidea phylogeny (Schenk et al. 2013; nodes 5–9 in their appendix 2) and included stem age divergences for *Sigmodon*, *Holochilus*, *Reithrodon*, *Necromys*, and *Auliscomys* applied as lognormal prior distributions identical to Schenk et al. (2013). Two independent BEAST analyses were run for 200 million generations, and the Markov chain Monte Carlo (MCMC) chain was sampled every 20,000 generations. Stationarity was determined in Tracer version 1.6 (Rambaut and Drummond 2005) by plotting the log-likelihood values across generations and by esti-

mating effective sample sizes for each parameter that exceeded 300. Convergence between the two independent analyses was determined in Tracer and AWTY (Wilgenbusch et al. 2004; Nylander et al. 2008). The first half of the chain was removed from each analysis as the burn-in, and we summarized our results with a 95% highest posterior density (HPD) tree in TreeAnnotator (Drummond and Rambaut 2007).

Historical Biogeography

How regions are defined is important analytically and can affect interpretations of the results. We divided our study area into 14 regions on the basis of geographic features (e.g., Andes, Isthmus of Panama), relatively abrupt changes in habitats, and previous regionalization studies (Udvardy 1975; Olson et al. 2001; Kreft and Jetz 2010; table S2). These regions were further corroborated by the codistribution of endemic sigmodontines by reference to sigmodontine phylogenetic studies (e.g., Smith and Patton 1999; Salazar-Bravo et al. 2013; fig. 2; table 1) and the distributions of all known species from the International Union for Conservation of Nature and Natural Resources (2014). Regions were circumscribed to qualitatively maximize the uniformity of habitats within and compactness as well as differences among them in habitat (e.g., alpine from tropical rain forests habitats). The number of regions applied in the study balanced both environmental uniformity within them (which increases as regions decrease in size) and computational complexity. Fewer regions would yield too few transitions for fine-scale analyses of diversification patterns, while more regions would become computationally intractable. Two regions were fully outside continental South America—the combined North and Central America area and the Galapagos Islands. Continental South America was divided into 12 regions, with the Andean region divided into four (regions 0–4 in fig. 2; table 1). Species ranges have likely shifted with respect to these regional boundaries because of climate and geologic changes through time, but these regions should be reasonable proxies for some codistribution patterns to the extent that they also represent sets of associated habitats.

Historical biogeographic reconstructions were estimated with statistical dispersal-vicariance analysis (S-DIVA; Yu et al. 2010) and Bayesian binary MCMC (BBM; Yu et al. 2012). S-DIVA is a modification of DIVA (Ronquist 1997), which is an event-based parsimony approach that applies a step matrix to infer transitions. Zero steps are assigned to vicariance and cladogenetic events, thus favoring these processes, and one step is assigned to dispersal and regional extinction events. S-DIVA expands on the DIVA approach by measuring uncertainty in both biogeographic events and phylogeny by estimating across multiple phylogenies. We estimated dispersals across 1,000 randomly chosen post-burn-in trees from the posterior distribution from the BEAST analysis in RASP version 2.1 (Yu et al. 2012).

The BBM analysis is a full hierarchical Bayesian approach that models transition rates across biogeographic regions. This complementary approach to S-DIVA assesses the robustness of our results given the differences in methodological assumptions to those of S-DIVA. Analyses were conducted in RASP (Yu et al. 2012). We applied a model comparable to the F81+ Γ model (Felsenstein 1981), which allows for uneven distributions across regions while accounting for differences in transition rates among regions. We ran 10 chains for 10,000 generations and randomly selected 1,000 trees from our posterior distribution of chronograms after applying a burn-in period of 200 generations. As in the S-DIVA analysis, we allowed a maximum of three areas to be reconstructed from current distributions of species.

The complexities of our biogeographic data precluded us from estimating transition rates with alternative approaches. Some tips were assigned multiple areas, which prevented us from estimating transitions with likelihood-based approaches. Applying 14 regions precluded the use of stochastic mapping as implemented in SIMMAP (Bollback 2006), maximum likelihood methods in Lagrange (Ree and Smith 2008), or Bayesian approaches in BioGeoBears (Matzke 2014). Applying the above methods would force us to combine half our regions, which would make less biological sense and convolute interpreting our results. Using S-DIVA and BBM, therefore, is a solution that allows us to apply 14 character states with polymorphic tips in an event-based historical biogeographic framework while accounting for uncertainty.

Estimating the Rates of Regional Transitions

We analyzed the number of dispersals across time to determine the pattern of regional transition rates after the Sigmodontinae lineage first colonized South America. We wrote a custom script in R (R Development Core Team 2005) to evenly divide the time since Sigmodontinae first colonized South America (root node of *Oryzomyia*) into 60 time units (= 215,646 years) and then manually summed the number of transitions in each unit. The numbers of transitions were standardized by the number of lineages at the beginning of their respective time slice, yielding a per-lineage transition rate. Transition rates were compared for both the S-DIVA and the BBM analyses.

Community Assemblage Approaches

We explored occurrence patterns in *Oryzomyia* using a community assemblage phylogenetic approach (Webb 2000; Webb et al. 2002). This approach was developed to determine whether communities contained species that were more or less phylogenetically related than expected by chance. More recently, this approach has been adapted to explore



Figure 2: Biogeographic regions of South America. 0 = high-elevation northern Andes; 1 = high-elevation central Andes; 2 = west-central Andean Altiplano; 3 = high-elevation southern Andes; 4 = Guianan savanna/Antilles island; 5 = Amazon forest and basin; 6 = Chaco/Pampas; 7 = Patagonian Highlands; 8 = Brazilian Highlands; 9 = Brazilian Atlantic forest; 10 = Central/North American; 11 = Chaco; 12 = Galapagos; 13 = west-central South American coastal.

Table 1: Biogeographic regions of Sigmodontinae

| Code | Region | No. species |
|------|-------------------------------------|-------------|
| 0 | High-elevation northern Andes | 24 |
| 1 | High-elevation central Andes | 73 |
| 2 | West-central Andean Altiplano | 14 |
| 3 | High-elevation southern Andes | 20 |
| 4 | Guianan savanna/Antilles island | 28 |
| 5 | Amazon forest and basin | 44 |
| 6 | Chaco/Pampas | 50 |
| 7 | Patagonian Highlands | 24 |
| 8 | Brazilian Highlands | 49 |
| 9 | Brazilian Atlantic forest | 40 |
| 10 | Central/North American | 35 |
| 11 | Chaco | 11 |
| 12 | Galapagos | 4 |
| 13 | West-central South American coastal | 10 |

Note: Codes correspond with the map in figure 2. The number of species is estimated from the number of species per region, in which a species could occur in multiple areas.

within-region diversification patterns (Price et al. 2014) to ask whether regional biotas, analogous to community composition, are composed of closely related species or drawn from a phylogenetically larger pool. The former category indicates that local diversification is common, while the latter category indicates that biotas are built from dispersal and structured by competitive exclusion and dispersal rates. Although this approach might suffer from not applying a fully sampled phylogeny, many of the unsampled species were from genus-level clades that occur mostly in identical biogeographic regions, and we consequently expect our sampling biases to favor less clustering.

We used mean pairwise distance (MPD) and mean nearest taxon distance (MNTD) to ask how closely related the average pair of species within a biogeographic region are. MPD calculates the average pairwise distance of branch lengths between all members of a biogeographic region and compares the observed values to a null distribution constructed from 5,000 randomizations of the assignment of regions to the tips on the chronogram. MNTD estimates the average patristic distance that separates one tip from its closest relative in the same region and, like the MPD analysis, compares observed MNTD values to those from 5,000 randomizations.

Analyses were conducted on our 95% HPD tree with the Picante version 1.6 library (Kembel et al. 2010) in R. We estimated the MPD and MNTD values and their associated standardized effect sizes (SES). SES compares MPD and MNTD estimates to expectations of null communities, which provide a measure for the difference between our observations and expectations given the phylogeny. The SES_{MPD} values are equivalent to negative net related index values; a high positive value indicates that regions are composed of distantly related species (phylogenetic overdispersion). Negative SES_{MPD}

and low P values indicate that species are more closely related within regions than what we would expect by chance (phylogenetic clustering). The SES_{MNTD} values are equivalent to the nearest taxon index. The MPD and MNTD approaches answer the same question; however, MPD values are more sensitive to patterns deeper in the tree, whereas MNTD values are more sensitive to patterns near the tips.

Lineage Diversification

A significant increase in the diversification rate of *Oryzomyia* was determined with three different methods by Schenk et al. (2013), who applied analyses across all of Muroidea. We therefore did not repeat these analyses. Instead, we estimated the diversification rate with the sliding-window analysis of Meredith et al. (2011) that we coded in R (Schenk 2017), with a 2-million-year sliding window. We also compared the empirical results to sliding-window analyses of 100 randomly simulated birth-death trees, with a speciation rate of 0.30 and an extinction rate of 0.01 that accounted for the effect of extinction (Schenk 2017). Speciation and extinction rates were empirically derived by fitting a birth-death model onto the phylogeny with the ape package (Paradis et al. 2004) in R, which accounted for expectations given a constant diversification rate.

In addition to identifying strong support for an increased speciation rate at the base of *Oryzomyia*, Schenk et al. (2013) identified a significant decrease in their net diversification rate with the Markov chain constant rates (MCCR) test (Pybus and Harvey 2000) that corrected for incomplete, biased sampling (Brock et al. 2011). We repeated those analyses to test for a significant decrease in the diversification rate given the considerable increase in our sampling from 72 *oryzomyialian* species. We applied the MCCR test that incorporated a parameter to account for incomplete and biased sampling (Brock et al. 2011).

To further examine diversification rates, we fit several diversification models onto our data and compared their fit with the Akaike information criterion (AIC) scores. We fit constant diversification rate pure-birth and birth-death models and compared them to the fit of the exponential and linear diversity-dependent models in the laser package (Rabosky 2006) in R. The two diversity-dependent models describe the initial increase in diversification rates and subsequent decrease that is consistent with expectations under the RE model.

The lineage diversification rates per region were visualized by lineage through time plots. We used the ape package in R to prune all clades that did not occur in a respective region and then estimated regional lineage through time plots. The few taxa that occurred in multiple regions were included in multiple plots of their respective regions. If par-

allel diversification drives diversity in adaptive radiations, we expect to find the signature of ecological opportunity within each region. To test this hypothesis, we fit four models onto regional phylogenies, which included constant rate birth-death and pure-birth models as well as linear and exponential diversity-dependent models. We assessed the fit of the four models with the laser package in R across the 95% HPD tree and 500 BEAST chronograms from the posterior distribution and used a difference in the AIC scores (>2) to select a best set of models. We repeated analyses across 100 randomly sampled chronograms with the TreePar version 3.3 package (Stadler 2011) in R, which allowed us to compare constant diversification rates to a diversity-dependent model that accounts for extinction.

To answer our primary question of whether regional transition rates (transitions between biogeographic regions/number of lineages/unit time) were correlated with lineage diversification rates (rate of new lineage accumulation/unit time), we explored the relationship between lineage diversification rates and regional transition rates with a linear model in R.

Results

Phylogeny and Divergence Time Estimates

Divergence time analyses effectively sampled parameters and estimates converged as evidenced by AWTY and Tracer parameter and tree evaluations. The most recent common ancestor (MRCA) of Sigmodontinae was estimated as 8.47–11.37 million years ago, and the colonization of South America (MRCA *Oryzomyia*) occurred by at least 6.49–7.96 million years ago (fig. 3; figs. S1, S2; figs. S1–S10 are available online). After the dispersal into South America, rapid diversification led to 12 major lineages within 1.2 million years. All of the 12 tribal-level clades (the seven named tribes plus five basal lineages that could be formally elevated to tribes) were monophyletic with strong support (>0.95 posterior probability; figs. 3, S1). Relationships among these 12 are generally poorly supported, but four more inclusive clades are strongly supported (Abrotrichini through *Juliomys*, Reithrodontini plus *Chinchillula*, Phyllotini plus *Delomys*, and Phyllotini through *Juliomys*), whereas the remaining six nodes receive support values from 0.31 to 0.75.

The morphologically defined Phyllotini (e.g., sensu Steppan 1995) was highly polyphyletic (fig. 3). Among genera previously assigned to Phyllotini, *Chinchillula* (chinchilla rat) was sister to Reithrodontini, and the Altiplano genera *Andinomys* (Andean mouse) and *Punomys* (Puna mouse) formed a clade sister to the phyllotines and the mostly Andean genera *Euneomys* (chinchilla mice), *Irenomys* (Chilean climbing mouse), and *Neotomys* (Andean swamp rat). Most other nodes were well supported (fig. S1), with uncertain relationships concentrated within larger genera, such as *Akodon* (grass mice),

Oecomys rats, *Oligoryzomys* (pygmy rice rats), *Phyllotis* (leaf-eared mice), and *Thomasomys* (oldfield mice).

Historical Biogeography

The region of greatest species diversity was the high elevations of the central Andes (table 1). Collectively, the high-elevation and high-latitude Andes (regions 0–3) accounted for 45% of the species sampled. Other regions of high diversity included the Chaco/Pampas (region 6; 50 species) and Brazilian Highlands (region 8; 49 species). The Galapagos Islands had the fewest species (region 12; four species), but on continental South America the west-central coastal region had the fewest (region 13; 10 species).

S-DIVA inferred 142 dispersal events (fig. S2). Early movement into South America involved the Brazilian Highlands region and the central Andes (regions 8 and 1, respectively). Lineages then quickly migrated southward during the rapid lineage diversification phase, spreading into the Amazon forest and basin, Patagonia, and west-central Andean Altiplano regions in one clade (regions 2, 5, and 7; *Oryzomyini* through *Reithrodontini*, *Nesoryzomys fernandinae* through *Chinchillula sahamae*), but they remained in the Andes in the other major clade (Phyllotini through *Thomasomyini*).

The BBM analysis also inferred numerous dispersals ($n = 188$; fig. 3), but transitions tended to occur closer to the tips. Basal divergences were reconstructed in the Brazilian Highlands and Brazilian Atlantic forest regions (regions 8 and 9), and then lineages quickly spread into the Amazon forest and basin, central Andean, Altiplano, Guyana savanna, and Chaco/Pampas regions (regions 1–6). The Phyllotini-*Thomasomyini* clade dispersed into the Brazilian Atlantic forest region but then quickly extended to the high-elevation central Andes. Reconstructing the specific sequence of events at the base of *Oryzomyia* is highly dependent on the branching sequence, for which there remains uncertainty. Dispersal back into North/Central America was inferred within *Oryzomyini* ancestral to *Oryzomys*, in which the lineage diversified and then dispersed back into two South American regions, the high-elevation northern Andes and Chaco (*Aegialomys*, *Melanomys*), and from the Chaco two lineages dispersed to the nearby Galapagos Islands (*Nesoryzomys* and *Aegialomys galapagoensis*). Similar results were inferred with S-DIVA for the origin of the Galapagos taxa but with a more widespread ancestor that inhabited the Galapagos and North/Central America. In addition, two clades (*Handleyomys*, *Transandinomys*) diversified in the adjacent regions of Central America and the Chaco with multiple transitions across the Isthmus of Panama.

Regarding major subclades, Akodontini first diversified in the east (Brazilian Highlands/Atlantic forest; regions 8, 9), *Oryzomyini* in the Guiana Highlands/Amazon basin (regions 4, 5), Abrotrichini in the southern Andes (region 3),

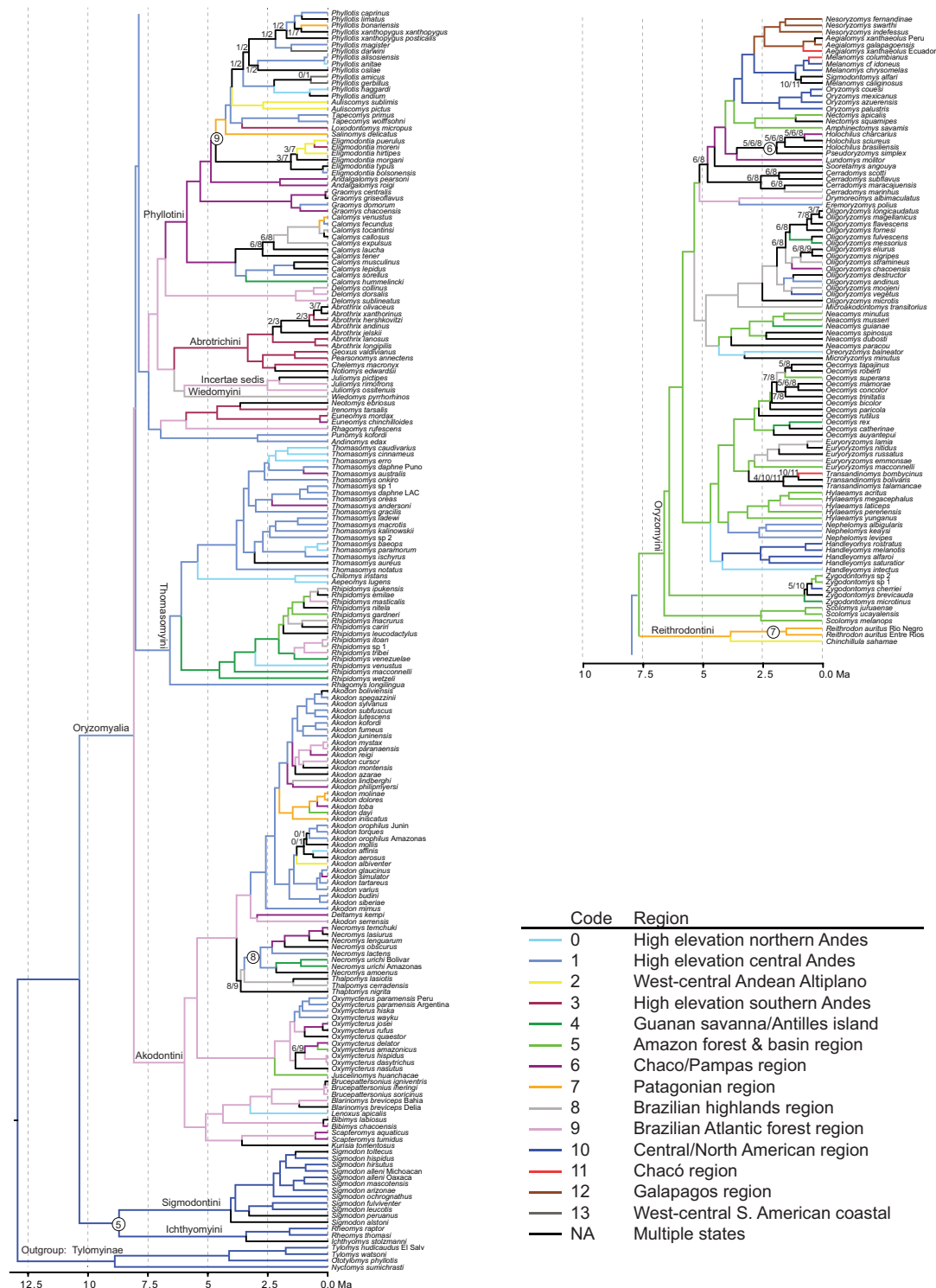


Figure 3: Regional transitions mapped onto a chronogram of Sigmodontinae and out-groups from BEAST analyses with five calibrated nodes assigned the same number in circles as they were in Schenk et al. (2013; nodes 5–9 in their appendix 2). Biogeographic states were estimated with the Bayesian binary Markov chain Monte Carlo analysis and represent the most likely states. When multiple states were inferred we colored the clades black, and the inferred state codes are indicated at nodes. Biogeographic codes correspond with those in figure 2 and table 1.

and Phyllotini in the lower-elevation Chaco/Pampas (region 6). Reconstruction of the ancestral *Thomasomyia* is less certain because of wide geographic dispersion among its basal lineages.

Estimating the Rate of Biogeographic Transitions

Transition rates in the Sigmodontinae dramatically increased after the oryzomyalian colonization of South America (fig. 4). After the initial peak, transition rates declined gradually toward the present (figs. 4, S3). Transition rates estimated with S-DIVA and BBM were qualitatively similar (figs. 3, S4). The BBM estimates tended to be slightly higher and toward the present (fig. S5).

Community Assemblage Approaches

The majority of the South American biogeographic regions were significantly clustered phylogenetically; species within

a region were more closely related than expected under random distributions. Ten of 14 regions in the MPD analysis and 13 of 14 regions in the MNTD analysis were inferred to have significant clustering (table 2). The only strong conflict between the MPD and MNTD estimates involved the high-elevation northern Andes region; the MPD analysis identified this region as significantly overdispersed, but the MNTD analysis identified it as significantly clustered. Non-significant values were identified in the high-elevation southern Andes region for both methods and the Guianan savanna/Antilles island region in MPD analyses.

Lineage Diversification

The sliding-window analysis estimated a dramatic increase in lineage diversification rates soon after the colonization of South America (figs. 4, S6, S4). The initial increase lasted approximately 1.5 million years and then declined, a pattern we could not attribute to high extinction rates (fig. S6). About

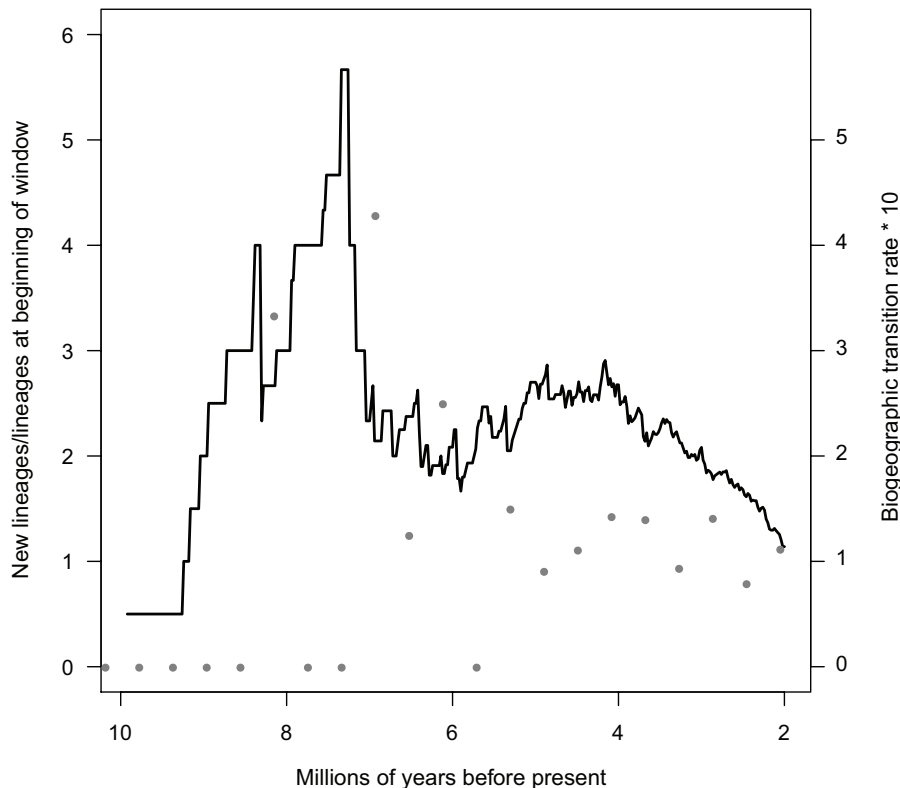


Figure 4: Sliding-window analysis of diversification rates plotted with regional transition rates across time. The sliding-window analysis illustrates the rate of lineage formation (black line) as a function of time since the colonization of South America on the left-hand Y-axis. The regional transitions are from statistical dispersal-vicariance analysis estimates, and the rate of dispersals across biogeographic regions (gray circles) is plotted against time since the South American colonization (plotted on the right-hand Y-axis). Note that we multiplied the regional transition rates by 10 to clearly illustrate the correlated rates. Figure S6 shows the results of the sliding-window analysis across simulated birth-death trees, including the regional transition rates for the last 2 million years that more clearly demonstrate the decrease in transitions toward the present (figs. S10, S5, S4).

Table 2: Results of the mean pairwise distance (MPD) and mean nearest taxon distance (MNTD) analysis

| Region | <i>N</i> | MPD | | | MNTD | | |
|-------------------------------------|----------|----------|----------|----------|-----------|----------|----------|
| | | MPD obs. | <i>Z</i> | <i>P</i> | MNTD obs. | <i>Z</i> | <i>P</i> |
| High-elevation northern Andes | 24 | 14.662 | -1.049 | .152 | 5.367 | -2.576 | .004 |
| High-elevation central Andes | 73 | 14.200 | -3.348 | .001 | 4.468 | -2.001 | .028 |
| West-central Andean Altiplano | 14 | 13.618 | -1.878 | .011 | 6.737 | -1.729 | .042 |
| High-elevation southern Andes | 20 | 11.978 | -4.414 | .001 | 2.775 | -5.078 | .001 |
| Guianan savanna/Antilles island | 28 | 14.024 | -2.114 | .008 | 5.291 | -2.483 | .007 |
| Amazon forest and basin | 44 | 13.171 | -4.485 | .001 | 4.573 | -2.884 | .002 |
| Chaco/Pampas | 50 | 13.980 | -3.127 | .001 | 3.418 | -4.790 | .001 |
| Patagonian Highlands | 24 | 14.148 | -1.781 | .020 | 4.088 | -3.757 | .001 |
| Brazilian Highlands | 49 | 13.620 | -3.845 | .001 | 4.367 | -3.079 | .001 |
| Brazilian Atlantic forest | 40 | 14.274 | -2.142 | .006 | 4.438 | -3.167 | .001 |
| Central/North American | 35 | 17.362 | 3.340 | .999 | 3.367 | -4.666 | .001 |
| Chaco | 11 | 13.249 | -1.958 | .008 | 5.103 | -2.950 | .002 |
| Galapagos | 4 | 4.096 | -5.344 | .001 | 3.622 | -3.550 | .001 |
| West-central South American coastal | 10 | 14.752 | -.556 | .328 | 7.083 | -1.827 | .033 |

Note: Negative *Z* values and low *P* values ($\leq .05$) indicate phylogenetic clustering. High *Z* and *P* values ($\geq .95$) indicate phylogenetic overdispersion. obs. = observed.

3 million years after the colonization of South America, the diversification of *Oryzomyia* becomes nearly constant. Similar patterns were identified with the corrected MCCR test that estimated a gamma statistic of -6.056 , which was determined to be significant after accounting for biased, unsampled diversity ($P < .001$), indicating an early burst of speciation followed by a cladewide decrease in diversification rates over time. Declining rates of lineage diversification were further identified in the model-fitting approach that evaluated four species diversification models. Based on the AIC scores, we determined that the linear diversity-dependent model fit the data much better than the exponential diversity-dependent model, which fit second best, and better than both constant rate models (table 3).

The lineages-through-time plots generated for the five most species-rich biogeographic regions exhibited an early steep slope, suggesting high net speciation rates early in the *Oryzomyia* lineages (fig. 5). The high-elevation central Andes region had a much higher diversification rate, with multiple increases at approximately 6, 3, and 1 million years ago. The Amazon forest and basin, Chaco/Pampas, and Brazilian Highlands regions all experienced very similar diversification rates. The Brazilian Atlantic forest region also had an early burst of diversification similar to that of the other four regions, but the rates decrease sharply at about 4 million years ago. All regions but the Galapagos showed a rapid diversification approximately 6–8 million years ago (fig. S7). The Central/North American region is the only one to have a constant rate of diversification (fig. S7). When all regions are analyzed together at the larger scale, a constant rate of diversification is identified despite individual regions displaying exponential curves.

The model-fitting approach that tested for the signature of ecological opportunity within regions determined that

diversity-dependent models (linear, linear with extinction, exponential, or a mix of the three) fit the data better than constant rate models in seven of the 13 regions (regions F, G, I–K, M, and N [the lack of species diversity in the Galapagos region precluded it from analyses]; table 4). These results held especially for the five most species-rich regions and other relatively species-richer regions (figs. 6, S8). Diversity-dependent models fit the remaining regional phylogenies in all cases but not more than 2 AIC units from the constant rate models (table 4).

In the *Oryzomyia* clade, high speciation rates were associated with high regional transition rates (fig. 7), and both rates decrease toward the present (fig. 4). The linear model approach identified a significant correlation in dispersal and speciation rates from both S-DIVA (fig. 4; $R^2 = 0.136$, $P = .004$; fig. 7) and BBM (fig. S4) estimates. Given that the reconstructions of ancestral distributions from S-DIVA and BBM were quite different, determining a significant linear relationship with lineage diversification rates in both analyses suggests that the results are robust to uncertainty in an-

Table 3: Results of lineage diversification model fitting on the Sigmodontinae chronogram that excluded out-groups (Tylomyinae)

| Model | Net diversification | |
|--------------------------------|---------------------|--------------|
| | rate | Δ AIC |
| Pure birth | .420 | 10.656 |
| Birth-death | .420 | 12.656 |
| Linear density dependence | .584 | 0 |
| Exponential density dependence | .704 | 9.063 |

Note: Net diversification rates (speciation – extinction) estimated from each model are included, as is the relative fit of each model from Δ AIC scores. AIC = Akaike information criterion.

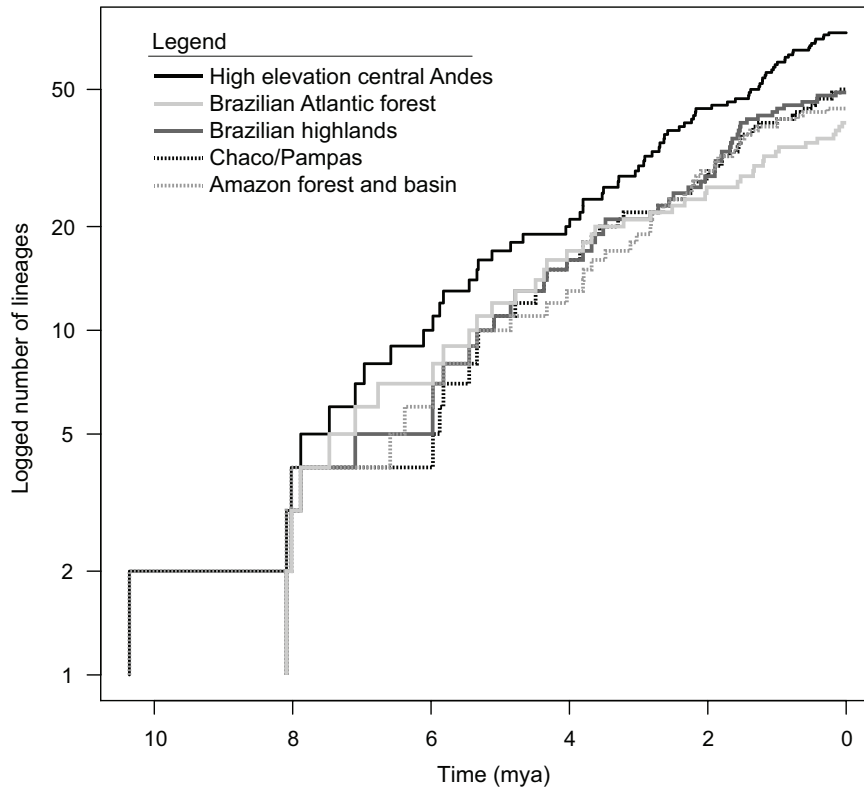


Figure 5: Lineage-through-time plots for the five most species-rich lineages. See figure S9 for all regions plotted separately.

cestral state estimations. Plotting regional transitions across a posterior distribution of chronograms further suggested robustness to phylogenetic uncertainty (fig. S9). We observed high variation in the relationship between geographic and lineage diversification rates when the *Oryzomyia* first begins to diversify and a possible lag in the estimated dates of transition rate pulses approximately 0.5 million years behind the early speciation rate pulses.

Discussion

Despite the notable advances in the study of ecological opportunity and adaptive radiation over the past two decades (Schluter 2000; Harmon et al. 2003; Gavrilets and Vose 2005; Rabosky and Lovette 2008; Alfaro et al. 2009; Gavrilets and Losos 2009; Parent and Crespi 2009; Harmon et al. 2010; Losos 2010), much remains to be learned about this process (Yoder et al. 2010). Our results indicate that the geographic partitioning of South America played an important role in the adaptive radiation of *Oryzomyia*. Our results corroborate the predictions of the RE model; regional transition and speciation rates were positively correlated (fig. 4), both rates rapidly increased after the initial colonization and decreased with time, and nearly all of the regions were phyloge-

netically clustered (table 2). Each of the other models was rejected by at least two lines of evidence.

Our results determined that geographic substructuring promotes species diversity during an adaptive radiation. Rapid speciation could be facilitated by relaxed selection, which allowed expansion into novel habitats with limited phenotypic adaptation (Yoder et al. 2010). Initial high speciation rates would then be driven by allopatric fragmentation of widespread ranges, which would then facilitate local adaptation and divergence in parallel. As species diverge among regions, further range expansions and regional transitions would occur into regions lacking direct competitors, fostering additional allopatric divergence. Indeed, regional allopatry and environmental variation could contribute to diversification in parallel (Warren et al. 2014). As niches within each region become saturated, competition would increase and the probability of successful colonizations would decrease, which is what we observed in the regional diversity-dependence results. Within-region diversification that leads to phylogenetic clustering might be quite common in groups that have adaptively radiated (Bennett and O’Grady 2013; Price et al. 2014). Diversity dependence that we identified within regions was mostly attributable to within-region diversification, but diversity was also attributed to regional colonization (fig. 3). The RE model predicts that transition rates decline in part be-

Table 4: Differences in Akaike information criterion (AIC) scores when comparing diversification models on regional phylogenies

| Region | PB | BD | DDL | DDX | DDL + μ |
|-----------------------------------|------|------|------|------|-------------|
| Central/North America | 0 | 1.90 | 1.89 | 1.88 | 14.43 |
| Chaco | 0 | 1.96 | 1.68 | 1.91 | 5.05 |
| West-central South American coast | 0 | 2.00 | .63 | .56 | 2.05 |
| High-elevation northern Andes | 1.61 | 3.61 | 0 | .96 | 2.08 |
| High-elevation central Andes | 2.37 | 4.37 | 0 | 1.15 | 1.79 |
| West-central Andean Altiplano | 4.54 | 6.54 | .02 | 0 | 2.12 |
| High-elevation southern Andes | 0 | 1.69 | 1.98 | 1.94 | .81 |
| Guinanan savanna/Antilles island | 6.23 | 8.23 | 0 | 4.66 | 1.98 |
| Amazon forest and basin | 5.46 | 7.46 | 0 | 4.78 | 4.53 |
| Chaco/Pampas | 2.72 | 4.72 | .17 | 0 | 2.91 |
| Patagonian Highlands | 1.90 | 3.90 | 1.85 | 0 | 2.47 |
| Brazilian Highlands | 6.25 | 8.25 | 0 | 1.69 | 2.59 |
| Brazilian Atlantic forest | 4.12 | 6.12 | 3.07 | 0 | 1.09 |

Note: Estimates represent averaged Δ AIC scores that were estimated across a randomly sampled posterior distribution of BEAST chronograms. Models were fitted in the laser and TreePar packages in R. Shown are pure-birth (PB), birth-death (BD), diversity-dependent linear (DDL), diversity-dependent exponential (DDX), and DDL plus extinction (μ) models.

cause the invasibility of regions decreases with completion, in contrast to the GI model where invasibility might actually increase through time and, with it, regional transitions. Our results suggest that diversity dependence is not reached by ecological divergence alone, as regional movement and establishment also contributed to niche saturation.

What Is the Role of Geography in Adaptive Radiation?

Studies, including classic examples of adaptive radiations, support Simpson's (1953) and later Schluter's (2000) predictions of the ecological opportunity process (see also Stanley 1979), including Hawaiian silverswords (Baldwin and Sanderson 1998), Hawaiian lobeliads (Givnish et al. 2009), Hawaiian *Drosophila* (O'Grady and DeSalle 2008), *Oryzomyia* (Schenk et al. 2013; Alhajeri et al. 2016; current study), and Malagasy vangas (Jönsson et al. 2012). Recent studies, however, have demonstrated that ecological opportunity following colonization does not always lead to adaptive radiation (Seehausen 2006; Harmon et al. 2010; Burbrink et al. 2012; Schenk et al. 2013; Liedtke et al. 2016), although the reason why is seldom known (but see Stroud and Losos 2016). Here we propose one general and testable hypothesis of why adaptive radiations do not occur after colonizations: a lack of distinct biogeographic regions or the inability (or lack of opportunity) to colonize them and diversify in parallel.

Geographic structure is an underappreciated but important component of adaptive radiations. In addition to the 10 patterns of adaptive radiation proposed by Gavrillets and Losos (2009), we propose that diversification into a geographically heterogeneous area containing multiple biogeographic regions and subsequent ecological diversification within them is an additional, but not a necessary, adaptive radiation pattern. Rapid, potentially even nonadaptive (Pigot et al. 2010;

Moen and Morlon 2014) expansion into multiple regions can catalyze simultaneous adaptive radiations, although not identical ones because of the ecological, size, and scale of biogeographic barrier differences among regions. Our results and those of insular adaptive radiations (Mahler et al. 2013) point to an underappreciated component general to adaptive radiations: biogeographic barriers isolate close relatives and allow diversification to occur in parallel, which generates greater species diversity than would be possible otherwise. Our best examples of adaptive radiations include groups that have diversified in parallel across biogeographic regions, such as Caribbean anoles (Mahler et al. 2013), Hawaiian silverswords (Baldwin and Sanderson 1998), and Hawaiian lobeliads (Givnish et al. 2009; Kisel and Barraclough 2010). Although diversification might not necessarily be deterministic (Losos 2010), these barriers allow for replicated radiations to occur (Mahler et al. 2013). The ocean provides a formidable barrier for terrestrial organisms to disperse across, and perhaps that is why most model systems of adaptive radiations are insular. This point might be especially important if the evolvability of the ancestral phenotype/genotype allows for diversification following ecological opportunity, as its descendants are likely to also inherit this propensity to radiate (Seehausen 2006; Flohr et al. 2013).

We propose that the total species diversity in an adaptive radiation is a product of the number of biogeographic regions and evolvability of the group given the group's dispersal ability (Phillimore et al. 2006), chance, and extinction rate (Stanley 1979). Diversification could occur in sympatry or allopatry (Losos and Ricklefs 2009), but the number of regions likely determines the number of species (Ayres and Clutton-Brock 1992). Dispersal is important; if species do not cross barriers, then diversification will not happen in parallel. Previous studies have determined that high annual dispersal predicted high

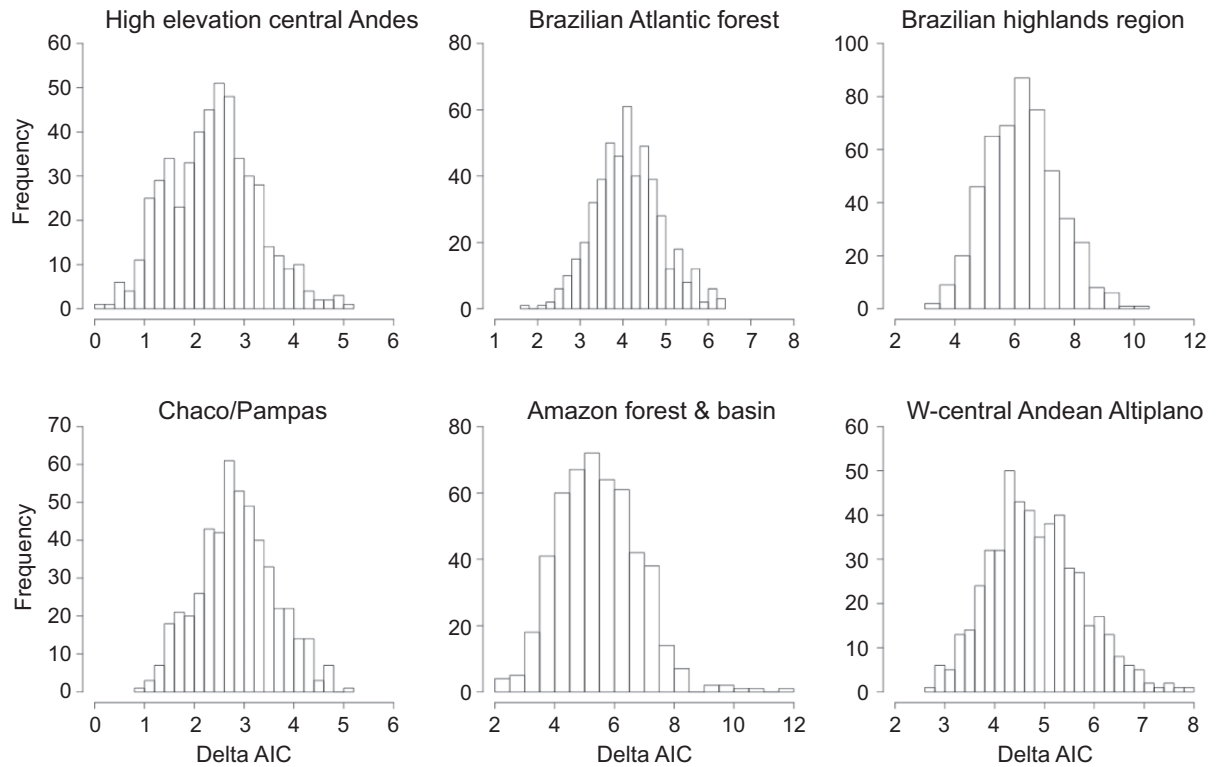


Figure 6: Differences in the Akaike information criterion scores comparing constant rate to diversity-dependent models for a subset of six diverse biogeographic regions across a posterior distribution of 500 trees. Negative values indicate that constant rate models fit the data better than diversity-dependent models, zero indicates equal support for both sets of models, and positive values indicate that diversity-dependent models better fit the data. Comparisons of all biogeographic regions (excluding the Galapagos Islands, which have too few taxa to analyze) can be found in figure S8. In each case, negative values lie outside the 95% credibility intervals.

diversification rates (Levin 2006; Phillimore et al. 2006). Our results, and those of others (Claramunt et al. 2012; Smith et al. 2014), suggest that it is not high dispersal but rather intermediate rates that correlate with high speciation rates. Genetic divergence should decrease as dispersal increases (Stanley 1979; Givnish et al. 2009; Beaudrot et al. 2014), inhibiting speciation, which explains why groups with greater dispersal abilities have lower species diversity (Kisel and Barraclough 2010; Smith et al. 2014). Ecological specialization within biogeographic regions could prevent successful colonization of new regions (Wiens and Donoghue 2004); thus, depending on the geographic and ecological framework, a positive feedback loop might promote ecological divergence within regions (Trevor et al. 2014). Schenk et al. (2013) showed that the order of dispersal is also important, as the lineage that first colonizes an unoccupied region will have greater diversity and a larger carrying capacity than a closely related lineage that colonizes the same region secondarily. Our results do not support this hypothesis at the intracontinental scale, as first colonizers are seldomly the most diverse (fig. 3).

The ability to detect the effect of regionalization on species diversity in an adaptive radiation is dependent on iden-

tifying meaningful biogeographic regions. Here we used endemism studies, codistribution of species, and physical structures to hypothesize biogeographic barriers. The barriers that best demarcate the ranges of sigmodontines likely would not describe distributions of all species (e.g., bats). The number of regions is also important to consider, as too few regions would underestimate transition rates and likely result in greater phylogenetic clustering. A clear and objective justification is therefore needed to define regions, which might be lineage specific.

Although dispersal into an underutilized area might be an important driver of diversification, the role of geography in adaptive radiations associated with key innovations or the extinction of competitors or predators is less clear. The African cichlids have a preexisting key innovation of the functional decoupling of the upper and the lower pharyngeal jaws (Seehausen 2006), and regional structuring and dispersal have played an important role in generating diversity (with notable within-lake diversification occurring). A similar pattern was observed in bill morphology following ecological opportunity in Malagasy vangas (Jönsson et al. 2012). Dispersal events might be confounded by the effects

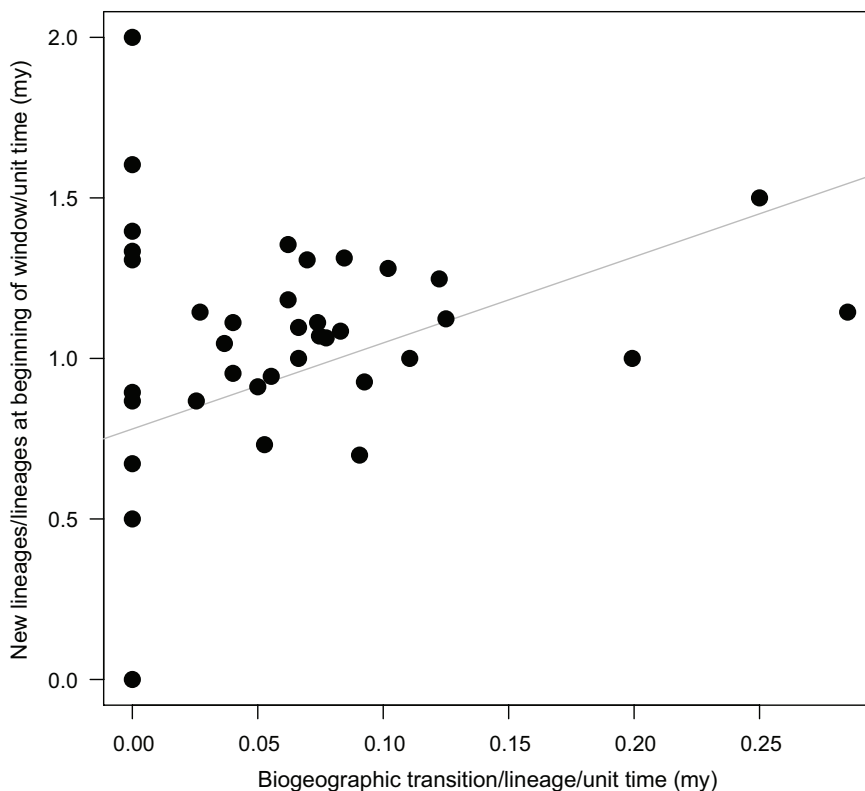


Figure 7: Linear relationship between geographic and species diversification rates ($R^2 = 0.136$, $P = .004$) demonstrating that, on average, high speciation rates are associated with high regional transition rates. Regional transition rates were estimated as the number of transitions per the number of lineages per unit of time (=215,646 years). Lineage transitions were estimated as the number of new lineages given the number of lineages per unit of time (=215,646 years).

of a key innovation, but clearly the two factors are important in determining the number of species in this system. Key innovations and dispersal events could also be linked, for example, if a key innovation allows descendant species to successfully establish into new areas (Moore and Donoghue 2007).

The RE model we present here might also explain the common pattern of a constant rate of diversification on continental radiations (Derryberry et al. 2011; Schweizer et al. 2014; Liedtke et al. 2016). Diversity dependence might not be observed at the continental scale if newer regions are sequentially colonized and species are able to diversify into them. If lineages experience diversity-dependent diversification, saturation will be a function of the number of biogeographic regions, not just time, therefore temporally delaying when diversification rates decrease. This pattern is evident in figure 4, which shows that following rapid diversification, lineage diversification rates decrease within regions but remain constant at the continental scale (fig. S7a).

The sliding window results suggest that two mechanisms make geography important in an adaptive radiation. We proposed that transitions into new regions create new local-

ized opportunities for diversification. But our results (fig. 4) indicate that the early primary peaks in the speciation rate preceded the bursts in transitions by approximately 0.5 million years, suggesting that another element of our model might be common: rapid and putatively adaptive divergence within a region increases the probability of successful among-region dispersal, either by expanding the niche space of the clade or by simply increasing the number of species available for dispersal. This pattern may also be caused by the ancestral reconstruction approach and where transitions are inferred to occur. For example, S-DIVA results tend to infer more widespread ancestral ranges at the base of the tree. This illustrates the difficulty of fully disentangling spatial variation and processes from population genetic ones.

Conclusion

The role of biogeographic barriers in isolating populations and generating species diversity is well established (Slatkin 1987; Capparella 1991; Claramunt et al. 2012). Our study is the first to directly examine how the process of dispersal and subsequent isolation across intracontinental barriers

can be an important driver of species diversification in continental adaptive radiations. Our findings support a model where parallel dispersal into adjacent regions followed by within-region diversification is an important determinant of the net diversification of an adaptive radiation. We conclude that transitions across biogeographic barriers are an important but underappreciated evolutionary force in adaptive radiations.

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Phyllotis darwini Waterhouse (1838; Sigmodontinae, Cricetidae) from Chile. Photo credit: Peter Meserve, © the Mammal Images Library of the American Society of Mammalogists.