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Geographic Range Shifts Do Not Erase the Historic Signal of Speciation in Mammals

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Online enhancements: appendix tables, zip file.

ABSTRACT: Many evolutionary analyses assume that the positions of species geographic ranges are sufficiently phylogenetically conserved that current ranges reflect ancestral ranges and retain the historic signal of speciation. The validity of this assumption has been challenged, because there is evidence that ranges can shift rapidly and extensively. Here I test the assumption of range conservatism using simulations and empirical tests of phylogenetic signal in geographic positions of ranges within mammal orders, families, and genera. In most taxa, range positions show strong phylogenetic signal, quantified using Pagel's λ , Mantel tests, and a novel method to measure phylogenetic signal near the tips of a phylogeny. Taxa with highly labile range positions are exceptions to the general pattern and include very young groups such as *Sciurus* that may still be in the early, rapid-expansion phase of adaptive radiation. In two orders containing many species with large distributions (Artiodactyla and Carnivora), temporal patterns of range evolution are consistent with large instantaneous shifts in range position associated with allopatric speciation. In most other taxa, range evolution is better described by models that allow ranges to evolve along branches of the phylogeny. The results point to a common pattern of phylogenetically conserved ranges where the current position of species ranges reflects their position at the time of speciation, modified by gradual drift of range boundaries through time.

Keywords: phylogenetic signal, phylogenetic conservatism, geographic distributions.

Introduction

Since the nineteenth century, evolutionary biologists have debated the geographic mode of speciation. Although it is widely accepted that speciation in animals happens primarily by geographic subdivision of distributions, sympatric speciation is theoretically plausible (Gavrilets 2003; Bolnick and Fitzpatrick 2007; Feder et al. 2013), and much of the debate has focused on the prevalence of sympatric speciation. Comparative methods such as age-range cor-

relations are often used to infer the frequency of different geographic modes of speciation, based on the overlap of geographic ranges among species that diverged at different times. Such methods share the key assumption that range boundaries drift gradually following speciation, so that range differences between species accumulate in proportion to the time since divergence (Barracough et al. 1998; Barracough and Vogler 2000). Under this assumption, the relative positions of the range boundaries of recently diverged species retain the historic signal of the speciation mode, and this signal decays gradually with increasing divergence time. In addition to the geography of speciation, the assumption of gradual range drift is central to some other areas of biodiversity theory, including the tropical niche conservatism hypothesis for latitudinal diversity gradients (Wiens and Donoghue 2004). Gradual range drift is also the basic assumption that underlies the use of geographic variables in many phylogenetic comparative analyses (e.g., Cardillo et al. 2008; Lanfear et al. 2013; Bonier et al. 2014).

Although a gradual-drift model of range evolution has received support from a recent simulation study (Pigot et al. 2012), this assumption has also been strongly challenged, because there is clear evidence that species distributions can be highly dynamic. For example, in the space of just a few decades it has been possible to observe the distributions of many invasive species expand rapidly and those of many other species contract to a fraction of their former size. A number of different models of range evolution have been proposed (succinctly reviewed recently in de Moraes Weber et al. 2014 and more comprehensively in Jones et al. 2005 and Gaston 2003). An alternative to the gradual-drift model described above is a stochastic dynamic model in which ranges shift rapidly but unpredictably as each species tracks changes in its own preferred environmental conditions. Such a scenario is predicted by dynamic niche models (e.g., Rangel et al. 2007) and is supported by large and idiosyncratic postglacial range

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shifts in mammals (Graham et al. 1996). More deterministic scenarios of range movement have also been suggested. Under Willis's (1922) classic age and area model, a species range increases steadily through most of its evolutionary life span, before contracting rapidly as the species approaches extinction. Other models include stasis post-expansion, in which species attain their geographic ranges early in their history (Jablonski 1987; Liow and Stenseth 2007; de Moraes Weber et al. 2014), and an expansion-contraction model, in which range sizes reach their maxima somewhere midway in a species' life span (Carotenuto et al. 2010).

In this context, many authors have argued that species ranges are too dynamic to retain the historic signal of the speciation process, calling into question the power of range-overlap methods to recover the geographic mode of speciation (Berlocher and Feder 2002; Losos and Glor 2003; Fitzpatrick and Turelli 2006; Bolnick and Fitzpatrick 2007). On the other hand, when examined on a sufficiently large geographic and phylogenetic scale, range positions must retain some of the signal of history, for the simple reason that closely related groups of species often tend to be found in the same parts of the world (e.g., all species of the primate family Lemuridae are found in Madagascar, while all species of the family Galagonidae are found in tropical Africa). How can these apparently contradictory observations be reconciled?

The issue of whether species range boundaries drift gradually and nondirectionally following speciation can be rephrased as a question of whether there is significant phylogenetic signal in the geographic positions of species ranges. The gradual-drift process can be considered analogous to a Brownian motion (BM) process of trait evolution and leads to the expectation that the variance in a set of range positions is proportional to divergence times among species (Felsenstein 1985). This can be tested using standard approaches to quantifying phylogenetic signal in biological traits, even though the heritability in geographic ranges is of a different kind (Webb and Gaston 2003). In the four nongradual models described above, we would expect to find a low level of phylogenetic signal in species range positions using methods that assume an underlying BM process of change.

While there have been many analyses of range size heritability or phylogenetic signal in range size (e.g., Jablonski 1987; Freckleton et al. 2002; Hunt et al. 2005; Jones et al. 2005; Waldron 2007; Carotenuto et al. 2010; Machac et al. 2011; de Moraes Weber et al. 2014), very few studies have explored phylogenetic signal in the geographic positions of species ranges (but see Carotenuto et al. 2010; Machac et al. 2011). The extent to which it is reasonable to assume that range sizes and positions evolve independently is an issue to which I return in Discussion. The

aim of this article is to present a set of analyses that quantify the strength and variation in the phylogenetic signal in species range positions across the world's terrestrial mammals. To do this I use several approaches. First, I test for phylogenetic signal in the geographic coordinates of species range centroids and distribution limits. Second, I test for associations between geographic and phylogenetic distance matrices among species. Third, I test for rapid, recent range shifts using a novel method to quantify phylogenetic signal near the tips of a phylogeny. I then ask whether the patterns of phylogenetic signal in range positions that emerge from these tests show any predictable, systematic associations with features of phylogenies (size, age, and resolution) or geography (latitude, longitude, mean species range size, and overall range size) of clades. Fourth, I test the phylogenetic patterns in geographic range coordinates against several models of trait evolution, to examine the temporal patterns of range evolution. Finally, I use simulations of the process of geographic range evolution to show that the methods I use to test phylogenetic signal in range positions have good power to distinguish gradual from labile models of range evolution.

Methods

Mammal Phylogenetic and Geographic Data

My analyses are limited to nonmarine mammals. The phylogeny I use is the supertree of Bininda-Emonds et al. (2007), updated to the current mammal taxonomy by Fritz et al. (2009), which includes 5,020 species. Geographic distributions of 4,668 nonmarine species were obtained as shapefiles from the International Union for Conservation of Nature website (<http://www.iucnredlist.org/technical-documents/spatial-data#mammals>) and projected to a Behrmann equal-area projection. To characterize the geographic position of each species distribution, I recorded the latitude and longitude of the range centroid, the highest and lowest latitude of the range, and the easternmost and westernmost longitude of the range. Comparisons of longitude may suffer from problems associated with the discontinuity at $\pm 180^\circ$, but since the number of species with distributions approaching this longitude is comparatively small, I expect the influence on the results to be minimal. All analyses of shapefiles were done using functions in the R libraries *rgdal*, *sp*, *maptools*, and *rworldmap*.

Testing Phylogenetic Signal: Pagel's Lambda

Pagel's λ (Pagel 1999) is a branch-length transformation parameter, the maximum likelihood estimate of which is widely used as a quantitative measure of phylogenetic signal in evolving, continuously distributed traits. Freckleton

et al. (2002) showed that λ has good power to detect phylogenetic dependence of a trait in simulated phylogenies with more than 20 tips, but the power declines in smaller trees. I selected mammal taxa with at least 20 species at the levels of order ($n = 14$), family ($n = 40$), and genus ($n = 25$). Within each taxon, for each geographic position descriptor (latitude and longitude of range centroid and the four distribution limits), I calculated the maximum likelihood estimate of λ together with the probability that this estimate differs from a value of 1, as expected under a BM model of trait evolution. Estimates of λ and significance tests were done using the function “phylosig” in the R library phytools.

Testing Phylogenetic Signal: Mantel Tests

Mantel tests offer an alternative approach to quantifying phylogenetic signal, as they are based on matrices of distances among species rather than absolute values of geographic range coordinates. This means these tests are unaffected by the discontinuity in longitude. For each mammal taxon, I calculated pairwise great-circle distances among species geographic centroids. I then used Mantel tests to examine phylogenetic signal by testing for significant correlations between geographic and phylogenetic (patristic) distance matrices, with significance obtained by permuting the matrices 10,000 times. Great-circle distances were calculated using the function “earth.dist” in the R library fossil, and Mantel tests were done using the function “mantel” in the R library ecodist.

Testing Phylogenetic Signal at the Tips of Phylogenies

An important criticism of the use of present-day distributions to recover the speciation process is that the rate of postspeciation range movement may be rapid compared to the timescale on which phylogenetic divergences are typically measured. This would mean that range shifts erase the historic signal even between recently diverged sister species (Losos and Glor 2003). Conversely, there may be a postspeciation lag time before daughter species are able to adapt to new environments and expand their distributions. In such cases, recently diverged species may retain a similarity in their range positions, but at deeper levels in the phylogeny, the correlation between geographic and phylogenetic distances breaks down. For this reason, it is desirable to test phylogenetic signal near the tips of the phylogeny, but standard methods for quantifying phylogenetic signal, including λ and Mantel tests, are applied to the entire depth of the tree. I therefore used the fol-

lowing method to test for significant phylogenetic signal near the tips of a phylogeny.

The method defines phylogenetic signal as a tendency for geographic distances between the distributions of two sister species to be smaller than the geographic distance from either of these species to the next-closest relative. For each mammal taxon, I identified all phylogenetically independent triplet sets consisting of a pair of sister species and their nearest outgroup species. For each triplet a distance ratio was calculated, defined as the ingroup distance (great-circle distance between centroids of the ingroup species) divided by the outgroup distance (mean distance between each ingroup species and the outgroup species). Where terminal polytomies occurred (i.e., there were more than two ingroup species) and/or there were several outgroup species equally related to the ingroup, the distance ratio was calculated as the mean of all pairwise ingroup distances divided by the mean of all pairwise outgroup distances. Under the null hypothesis of no phylogenetic signal, the value of the distance ratio should be approximately 1. A value less than 1 is indicative of phylogenetic signal, while a value greater than 1 indicates that sister species are more geographically distant from one another than they are from their next-closest relative. The test statistic tip distance (TD) is the median of distance ratios across all triplet sets in the clade. The significance of TD is tested by comparison with a null distribution generated by shuffling geographic coordinate values across the tips of the phylogeny 1,000 times. The R code used to implement the calculation of TD and generate null models is presented as a zip file, available online.

Analyzing the Variation in Phylogenetic Signal Measures among Taxa

I then tested whether values of the three measures of phylogenetic signal vary systematically with features of the phylogenies (crown age, species richness, percent of nodes resolved compared to a fully bifurcating tree) or the geography of clades (mean range size of species, total clade range size, mean latitude of species range centroids, mean longitude of species range centroids). To do this I used Spearman rank correlations to test for associations between these seven variables and values of λ (for centroid latitude and centroid longitude), Mantel r , and TD, across taxa at each taxonomic level (order, family, genus).

Comparing Models of Range Evolution

Tests of phylogenetic signal allow us to conclude whether closely related species tend to be less geographically distant

than species drawn at random from the phylogeny but provide no information on temporal variation in the rate of range evolution. To do this I compared the phylogenetic patterns in species centroid coordinates to the patterns expected under alternative models of trait evolution, using the “fitContinuous” function in the R library Geiger. For each mammal taxon, I fitted five models.

Brownian motion. Ranges shift gradually, nondirectionally, and at a constant rate, so that variance in range positions across lineages increases with divergence time.

Ornstein-Uhlenbeck. Range shift is gradual and constant, but values are attracted back to a central position. This form of range evolution might be expected if ranges are associated strongly with environmental niches that are phylogenetically conserved.

Early burst. Range shift is most rapid early in the history of a clade’s radiation and subsequently slows. This might be the expectation under an adaptive radiation where new ecological opportunities are exploited most readily early in a clade’s history.

Speciational. Range evolution is associated most strongly with speciation events. This could be the case under predominantly allopatric speciation followed by gradual range movement during the lifetime of species. This could apply especially in a set of species with large ranges, where an allopatric speciation event results in an immediate large shift in range centroids of daughter species. I modeled speciational range evolution by constraining the value of the κ parameter in fitContinuous to be 0, which transforms all phylogenetic branches to an equal value of 1.

White noise. Under this model there is no phylogenetic pattern in the distribution of range position values. This could be the case if ranges move so rapidly that the signal of speciation is quickly erased.

I compared the fit of the five different models to the data for each mammal taxon using the corrected Akaike information criterion (AICc) and used the differences in AICc values to judge the relative suitability of the different models.

Simulation of Range Evolution

I simulated the evolution of geographic ranges to test the assumption that a BM process of gradual drift in the position of range boundaries leads to significant phylogenetic signal in present-day range positions, under the three methods of quantifying phylogenetic signal. The simulations begin by generating a random phylogeny under a pure-birth diversification process and then setting an ancestral range as a square defined by four boundary values (north, south, east, west). At the root node and at each bifurcation in the phylogeny, the range undergoes an al-

lopatric speciation event, in which it is divided either north/south or east/west (with equal probability), at a position between the two range boundaries drawn randomly from a uniform distribution. I simulated two models of range evolution. Under a BM model, the four boundaries of the range evolve independently along each branch of the phylogeny. The branch is divided into time steps, with the number of steps determined by specifying a grain size. At each step, the amount of shift in the position of each boundary is drawn randomly from a normal distribution with a mean of 0 and a standard deviation σ that determines the size of the possible shift. The only constraints on the drift of range boundaries are (1) opposite boundaries can meet but not cross (i.e., the north and east boundaries must retain values no lower than the south and west, respectively) and (2) no boundary can drift outside the limits of the predefined domain. If the two pairs of opposite boundaries simultaneously drift into contact, the lineage suffers extinction and its descendant species are pruned from the phylogeny at the completion of the simulation. Under a labile model, range boundaries do not evolve gradually along branches, but at each branch the entire ancestral range undergoes a shift to the north, south, east, or west, with equal probability. If the shift is to the north (e.g.), then the north and south boundaries of the range of the descendant node are drawn randomly from uniform distributions, bounded by the range boundaries of the ancestral node and the northern limit of the domain. Under the labile model, the same constraints apply and the same allopatric speciation process occurs as in the BM model. The R code used to write the simulations is presented in a zip file.

For each of the two range evolution models I carried out simulations of 1,000 replicates each, on trees with 20 and 50 tips, with rate parameter values of $\sigma = 0.35$ and $\sigma = 0.7$. I then applied Pagel’s λ to the y (latitudinal) centroids and range sizes, and Mantel tests and TD to the distances between centroids of the simulated ranges. The proportion of tests showing significant phylogenetic signal under the two models gives an estimate of the rate of type 1 and type 2 error in each of the three phylogenetic signal measures.

Results

Phylogenetic Signal in Range Positions

The majority of the nonmarine mammal orders, families, and genera with at least 20 species display significant phylogenetic signal in the geographic coordinates of their distributions. Eight of the 14 orders have values of λ significantly different from 0 for all of the geographic position descriptors (fig. 1; table A1; tables A1–A4 available online).

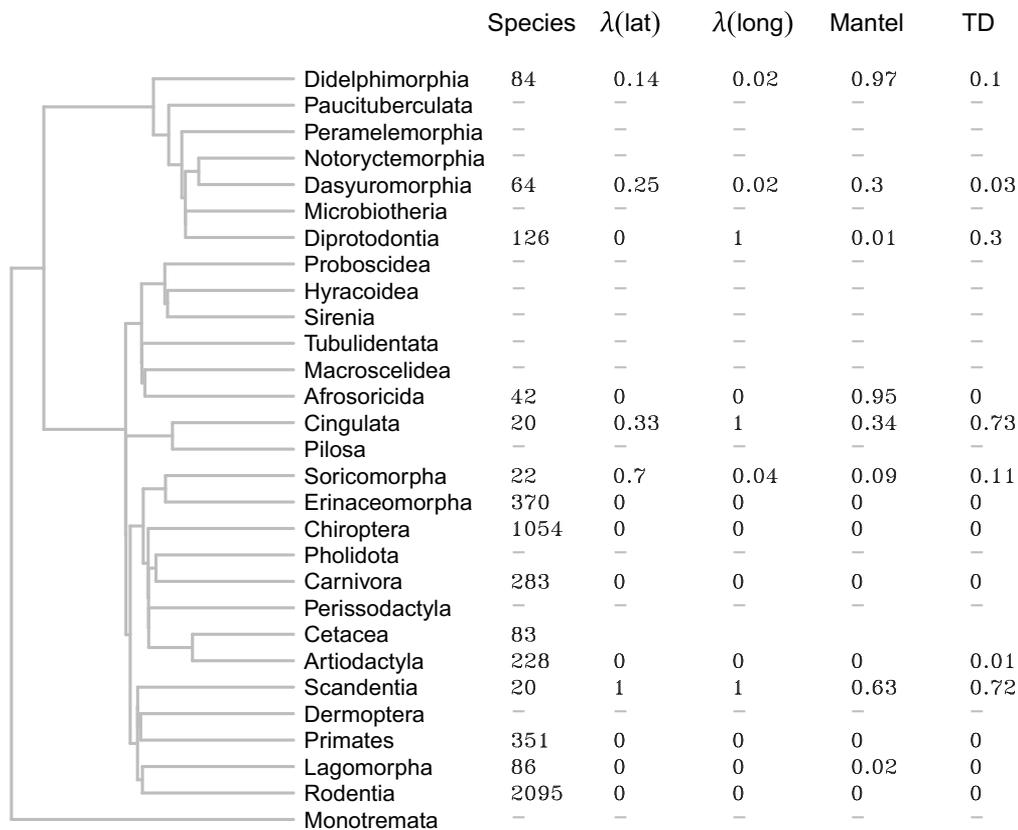


Figure 1: Order-level phylogeny of the mammals, with summary data for the phylogenetic signal in species ranges within each order. Columns to the right of the order names show species richness, P values of tests for phylogenetic signal in centroid latitudes ($\lambda(\text{lat})$) and centroid longitudes ($\lambda(\text{long})$) using Pagel's λ , and P values for phylogenetic signal in distances between range centroids using Mantel tests and tip distance (TD). Values are shown only for orders with at least 20 species.

Only two orders (Scandentia and Cingulata) do not show significant λ values for any of the position descriptors. At the family level, 12 out of 40 families have values of λ significantly different from 0 for all of the position descriptors (table A1), but only two families (Ctenomyidae and Dasypodidae) do not show significant λ values for any of the position descriptors. Of the 25 genera, three (*Lepus*, *Cryptotis*, and *Macaca*) have values of λ significantly different from 0 for all of the position descriptors, and three (*Ctenomys*, *Sciurus*, and *Neotoma*) do not show significant λ values for any of the position descriptors (table A1).

The results of the Mantel tests (fig. 1; table A2) show that distances between species range positions also show significant phylogenetic signal for the majority of orders (9 out of 14), families (25 out of 40), and genera (15 out of 25). Tests for phylogenetic signal at the tips of phylogenies (fig. 1; table A3) showed strong evidence that distances between sister species tend to be smaller than distances to the nearest outgroup species. Eight of the 14

orders had values of TD significantly lower than expected under the null model, while 23 out of 40 families had significantly low TD values and 14 out of 25 genera had significantly low TD values.

Patterns in Phylogenetic Signal of Range Positions across Taxa

Table 1 shows Spearman correlations between measures of phylogenetic signal and features of the phylogenies and geography of taxa. At the order level, there is a tendency for larger and older taxa to show stronger phylogenetic signal in the tests that utilize the entire tree depth (λ and Mantel tests). There is also some evidence (but inconsistent) that phylogenetic signal is associated with tree resolution and latitude.

Table 1: Spearman correlations between measures of phylogenetic signal in species ranges (Pagel's λ for centroid latitude and longitude, Mantel r and tip distance [TD] for centroid distances) and features of the phylogenies and geography of taxa

Taxonomic level and correlate	λ (centroid latitude)	λ (centroid longitude)	Mantel r	TD
	ρ	ρ	ρ	ρ
Order:				
Crown age	.53*	.69*	.68*	-.34
Species richness	.51*	.67*	.55*	-.32
Tree resolution	-.23	-.33	-.22	-.18
Range size (species mean)	-.3	-.03	-.11	-.38
Range size (clade total)	.17	.4	.32	-.64*
Centroid latitude	.07	.35	.24	-.52*
Centroid longitude	-.21	-.33	-.1	-.15
Family:				
Crown age	-.08	-.04	.03	.15
Species richness	-.04	.05	-.06	-.3
Tree resolution	-.23	-.47*	-.07	.32*
Range size (species mean)	-.36*	-.09	-.24	-.09
Range size (clade total)	-.2	-.02	-.08	-.31*
Centroid latitude	.02	.09	.07	-.24
Centroid longitude	-.14	-.17	-.03	.02
Genus:				
Crown age	.06	-.02	.21	.04
Species richness	-.09	.19	-.27	-.003
Tree resolution	-.09	-.39*	.02	.23
Range size (species mean)	-.17	-.28	.005	.1
Range size (clade total)	-.05	-.2	-.1	.15
Centroid latitude	.02	-.32	.08	.29
Centroid longitude	-.26	.08	-.16	-.17

* $P \leq .05$.

Models of Range Evolution

Comparisons of range evolution models for latitude and longitude of range centroids are shown in tables 2 and A4. At the order level (table 2), the data are most frequently consistent with an Ornstein-Uhlenbeck (OU), early-burst (EB), or white noise model. For no order does BM give the best fit, although in a few cases ΔAICc values are <2 , the conventional cutoff value for a significant difference. The speciation model provides the best fit for only one order for latitude (Artiodactyla) and one order for longitude (Carnivora). Among families and genera (table A4), the speciation model is clearly the poorest-fitting for the majority of taxa. The OU model is most frequently the best-fitting model, although in many cases the fit for BM, EB, or white noise is equal or only marginally inferior.

Simulation of Range Evolution

Simulations of range evolution using the two rate parameters $\sigma = 0.35$ and $\sigma = 0.7$ produced very similar results, so only results using $\sigma = 0.35$ are presented. The simu-

lations confirm that Pagel's λ and Mantel tests on range positions have good power to distinguish gradual from nongradual processes of range boundary movement. High proportions of simulations under a BM process returned significant values for λ and Mantel tests, particularly for 50-tip trees (fig. 2a, 2c), but low proportions of simulations under a labile process returned significant results (fig. 2b, 2d). The simulations also indicate that range position tends to show stronger phylogenetic signal than range size, with a substantial difference in the proportion of significant λ values under the BM simulations (fig. 1a). For TD, power is substantially lower, with only 28.6% and 56.2% (for 20-tip and 50-tip trees, respectively) of simulations under BM returning significant phylogenetic signal near the tips (fig. 2e). However, there is still a large difference between the false-negative rate (fig. 2e) and the false-positive rate (fig. 2f).

Figure 3 shows the association between pairwise distances among geographic centroids of simulated ranges and the degree of range overlap. The degree of overlap falls off rapidly with increasing centroid distance before leveling off, so that the association can be described ac-

Table 2: Range evolution model comparisons

Taxon	Centroid latitude					Centroid longitude				
	BM	OU	EB	WN	SP	BM	OU	EB	WN	SP
Rodentia	118.4	.0	.0	2,232.5	4,486.9	177.7	.0	.0	2,744.8	420.0
Lagomorpha	.8	.0	.0	50.2	189.5	12.2	.0	.0	37.4	37.7
Primates	27.4	.0	.0	285.3	423.7	15.4	.0	15.6	960.8	119.5
Scandentia	1.8	1.7	2.1	.0	165.4	18.1	2.9	2.9	.0	92.4
Artiodactyla	101.6	26.8	26.8	62.5	.0	50.4	.0	.0	97.0	252.0
Carnivora	81.8	.0	.0	35.3	150.9	63.6	13.7	13.7	66.7	.0
Chiroptera	176.1	.0	.0	310.8	2,390.4	14.8	.0	4.9	1,235.5	104.8
Soricomorpha	14.3	.0	.0	273.9	2,127.7	12.3	.0	14.3	241.2	2,103.2
Erinaceomorpha	4.1	1.8	1.8	.0	80.7	2.9	.2	.2	.0	45.0
Cingulata	2.4	.5	.5	.0	137.0	9.7	2.9	2.9	.0	143.4
Afrosoricida	4.8	.0	6.5	12.3	601.1	2.0	.0	4.3	36.5	549.1
Diprotodontia	8.8	.0	.0	44.7	12.9	76.0	2.0	3.0	.0	213.7
Dasyuromorphia	23.5	2.2	2.3	.0	25.0	13.5	1.0	1.0	.0	75.4
Didelphimorphia	7.4	1.2	1.2	.0	8.7	11.0	.0	3.9	3.1	172.2

Note: Values shown are $\Delta AICc$ for the fit of five models (BM = Brownian motion, OU = Ornstein-Uhlenbeck, EB = early burst, WN = white noise, SP = speciation) against the phylogenetic distributions of the latitude and longitude of species range centroids. For brevity, only the results for orders are shown here, arranged in descending order of species richness.

curately using segmented regression with two slopes and a breakpoint. Hence, relative range positions are closely reflective of range overlap but in a highly nonlinear fashion.

Discussion

The idea that present-day distributions of species reflect their distributions at the time of speciation, modified by gradual drift of range boundaries over time, is compelling because it permits inferences about the speciation process from spatial configurations of species ranges, together with estimated times of divergence (Lynch 1989; Chesser and Zink 1994; Barraclough et al. 1998). However, the validity of this assumption is caught between two conflicting observations. On the one hand, there is lots of evidence that ranges can be highly dynamic, rapidly erasing the historic signal of speciation; on the other is the broadly obvious observation that closely related groups of species tend to be found in the same parts of the world, which must reflect history. What is less obvious is whether strong phylogenetic signal in range positions exists only at the broadest geographic, phylogenetic, and temporal scales or only in a limited set of taxa. The results of this study suggest that neither of these is the case: strong phylogenetic signal in range positions exists in most mammal taxa and is found near the tips of phylogenies as well as through their entire depth. This is consistent with the view that range boundaries drift gradually following speciation (Lynch 1989; Chesser and Zink 1994; Barraclough et al. 1998; Pigot et al. 2012), an expectation that is confirmed by simulations of the range evolution process.

One explanation for phylogenetic signal in range positions is that it results from conservatism in environmental niches (perhaps due to constraints on adaptation to new environments) together with spatially autocorrelated environmental features. Under niche conservatism, we might expect close relatives to be geographically closer to one another than expected from the phylogeny (Losos 2008), which would give rise to values of Pagel's λ significantly greater than 1 or to temporal patterns of range evolution more consistent with an OU model than a BM model. However, in only one taxon (*Ctenomys*) are λ values significantly greater than 1. The OU model does provide the best fit for many taxa, although in many cases the AIC value is only marginally lower than BM or EB models, so that the OU process cannot necessarily be considered the best description of range evolution. The evidence (from these analyses) that range position conservatism is driven by niche conservatism is therefore equivocal, although there is a limit to what we can infer about environmental niches based on geographic position alone. An alternative, more parsimonious, explanation is that phylogenetic signal in range positions is the simple result of the historic legacy of speciation together with limitations on the dispersal of species away from their ancestral ranges, without the need to invoke any active processes maintaining niche conservatism. To properly distinguish these two hypotheses would require explicit tests using data on environmental niches, particularly since it has been argued that actively conserved environmental niches may produce a degree of phylogenetic signal consistent with BM evolution (Wiens et al. 2010).

Although phylogenetic signal in range positions is wide-

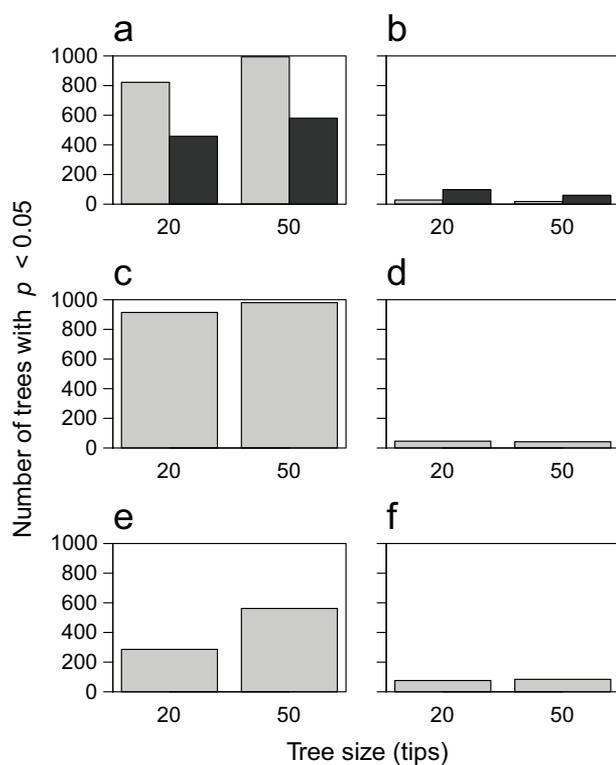


Figure 2: Proportions of 1,000 simulated phylogenies showing significant phylogenetic signal in geographic range position. The left column shows results for range evolution simulated under a Brownian motion model and the right column under a labile model (see text for details). Panels show phylogenetic signal in latitudinal centroids (gray bars) and range size (black bars) using Pagel's λ (a, b), phylogenetic signal in pairwise centroid distances using Mantel tests (c, d), and phylogenetic signal in centroid distances near the tips using tip distance (e, f). In each panel, results are shown for 20-tip and 50-tip phylogenies.

spread among mammal taxa, it is not universal. In particular, two orders—Scandentia (tree shrews) and Cingulata (armadillos)—show no phylogenetic signal in range positions under any of the three measures used (λ , Mantel tests, and TD). It is not clear whether these two taxa possess any distinct biological properties that dispose their species toward more labile geographic ranges, and it is possible that the lack of phylogenetic signal in these two groups simply reflects their low species richness compared to other orders. In general, it would seem fairly obvious that taxa with more species, a broader combined geographic extent, and deeper evolutionary origins should be more likely to show phylogenetic signal in species range positions. This is because in such taxa, species diversity is more likely to be the sum of multiple independent radiations in different regions. However, the correlations presented in table 2 provide only partial support for this

expectation. Crown age and species richness are associated positively with phylogenetic signal at the order level but not the family or genus levels, perhaps because orders are more likely to capture deep intercontinental divergences and multiple endemic radiations. For example, in primates the split between Catarrhini (Old World monkeys and apes) and Platyrrhini (New World monkeys) approximately 52 million years ago would probably contribute substantially to the phylogenetic signal in range positions within the Primate order, even if ranges within each hemisphere were highly dynamic.

A contrasting situation is found in some very recent radiations, notably, the genus *Sciurus* (tree squirrels), which shows highly labile range positions using λ and Mantel tests but significant signal near the tips of the phylogeny using TD. According to the phylogeny I have used, *Sciurus* began diversifying less than 5 million years ago (although Mercer and Roth 2003 give a slightly greater age of 8.6 ± 1.3 Mya for the *Sciurus* crown node) but in that short time managed to diversify into 27 species and occupy a large part of the New World and the Palearctic, implying rapid rates of speciation and geographic spread. This suggests that this group may still be in the early phase of an adaptive radiation, in which species are expanding rapidly into new ecogeographical space (Schluter 2000), thereby erasing the historic signal of speciation. However, the significant TD value for *Sciurus* (showing a signal of speciation close to the tips of the phylogeny) suggests there may be a postspeciation time lag before these rapid range shifts occur.

Perhaps the clearest pattern that emerges from the analyses of temporal patterns in range evolution is that the speciation model is the least well-supported across the mammal taxa. This is an unexpected result, given that allopatric subdivision is widely regarded as the primary speciation mode in mammals (Coyne and Orr 2004) and large shifts in range positions are expected to be associated with allopatric speciation events. However, the poor support for a speciation model of range evolution does not necessarily equate to poor support for allopatric speciation. Even under predominantly allopatric speciation, the extent to which a speciation model best describes the evolution of range positions would depend on the amount of instantaneous shift in range positions that occurs at speciation, relative to the amount that occurs gradually during the course of a species' lifetime. The instantaneous shift will necessarily be greatest in species with large ranges. In fact, the two mammal orders in which the speciation model did provide the best fit (Artiodactyla and Carnivora) are characterized by many species with very large distributions across mid- and high northern latitudes. An allopatric split in one of these distributions could result in an immediate separation of thousands of kilometers

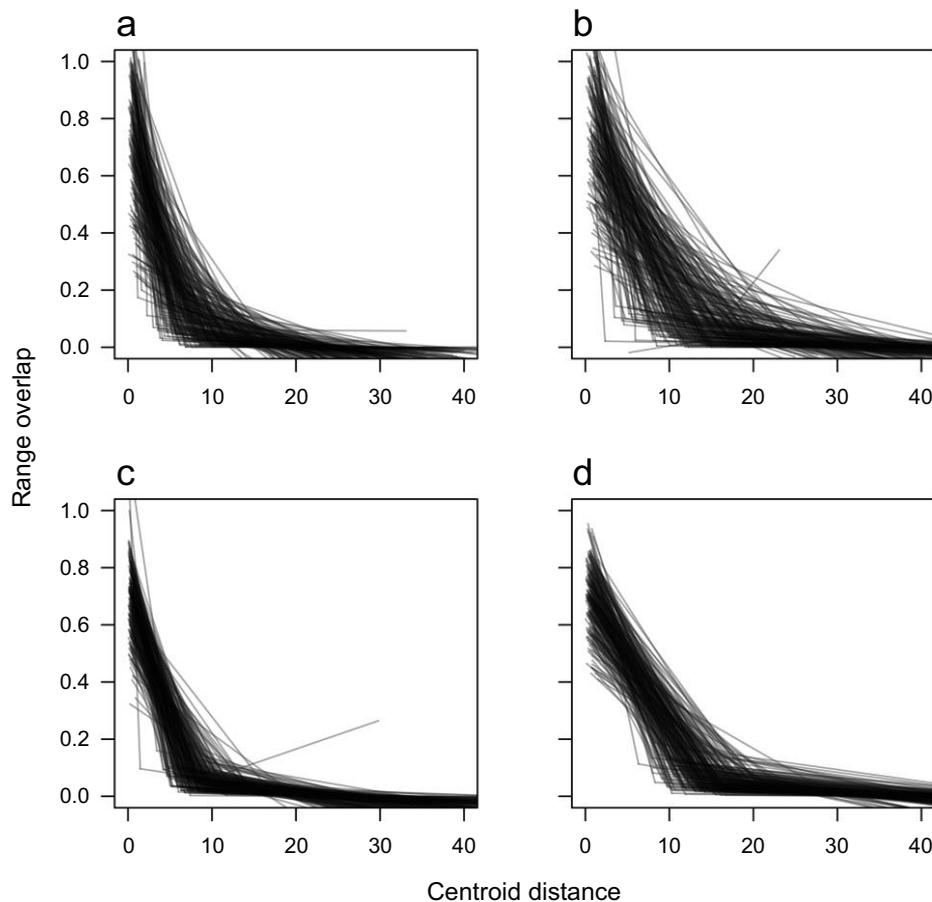


Figure 3: Associations between range centroid distances and range overlap among species within 250 simulated phylogenies. Slopes shown are from segmented regression with two slopes and one breakpoint. Range evolution is simulated under a Brownian motion model with $\sigma = 0.35$ (a, c) and $\sigma = 0.7$ (b, d); see text for details. Results are shown for 20-tip phylogenies (a, b) and 50-tip phylogenies (c, d).

between the range centroids of daughter species. In other taxa, the poor performance of the speciation model probably reflects the predominance of mammal species with small ranges (Jones et al. 2005), in which gradual drift of range boundaries is likely to contribute at least as much to range position shifts as allopatric speciation events.

In general, patterns of phylogenetic signal in the different geographic position descriptors (latitudinal and longitudinal centroids and range limits) are congruent within taxa. However, the cases in which range centroids and limits tell different stories might reflect particular biogeographic processes. For example, rapid but nondirectional range expansion during the radiation of a clade might result in range centroids maintaining phylogenetic signal but range limits being more labile. This is seen in a number of families and genera from across the mammal phylogeny. Likewise, differences in the patterns for latitudinal and longitudinal range centroids and limits could be revealing.

Given the ubiquity of strong environmental gradients across latitudes, we might expect niche conservatism to maintain phylogenetic signal in the latitudinal positions of species ranges while longitudinal positions may perhaps be more labile. If anything, the opposite is the case: there are more taxa for which longitudinal positions show phylogenetic signal but latitudinal positions do not; again, this includes taxa from across the mammal phylogeny. Perhaps this reflects the fact that environmental transitions across longitudes are often very abrupt, for example, those produced by the north-south mountain chains in North and South America and Australia.

To what extent does the phylogenetic signal in geographic range centroids and distribution limits simply reflect the heritability of geographic range sizes, for which there is considerable evidence in mammals (Freckleton et al. 2002; Jones et al. 2005; Carotenuto et al. 2010; Machac et al. 2011; de Moraes Weber et al. 2014), rather than the

independent evolution of range boundaries? From a purely geometric perspective, the simulations of range evolution point to a decoupling of range size and position, with range size tending to be more labile than range position. This is probably unsurprising if the movement of range boundaries is random, with no directional bias. From a biological perspective, heritability of range sizes is expected if range size is strongly linked to conserved biological traits such as body size (Gaston 2003; Jones et al. 2005) and if species typically fill their fundamental (i.e., their potential) distributions. On the other hand, heritability of range positions is more likely to be a result of historically contingent processes of speciation and limited dispersal. Even in bats, probably the mammal group with the greatest powers of dispersal, species frequently do not fill their potential distributions, at least until late in their evolutionary lifetimes (de Moraes Weber et al. 2014). To the extent that range size and position are influenced by different processes, therefore, they can probably be considered largely independent. Empirically, this conclusion is supported by the observation that range sizes of mammal genera remained relatively constant during the late Pleistocene and Holocene, despite large shifts in range positions in many cases (Hadly et al. 2009).

If the geographic positions of mammal distributions tend to be phylogenetically conserved, what are the implications for age-range correlations and other biogeographic analyses? In age-range correlations, speciation mode is inferred from the degree of overlap between species ranges, so strong phylogenetic signal in range position is relevant only if gradual drift in the positions of range centroids and distribution limits through time are correlated with gradual drift in the degree of range overlap. The simulations of range evolution suggest that this is broadly the case, with strong negative correlations between centroid distances and range overlap, although the association is highly nonlinear (fig. 3). Among pairs of species that are not widely separated, therefore, the distance between range centroids closely reflects the degree of range overlap, while for pairs of species that are geographically distant, range centroids do not reflect overlap closely. This suggests that age-range correlations may be useful in recovering the geographic mode of speciation across a restricted geographic area, but the value of this method may be more limited across very large geographic regions in which many species are widely separated from one another.

Finally, the existence of strong phylogenetic signal in range positions lends confidence in comparative analyses that involve inferring ancestral distributions (e.g., Cardillo et al. 2008; Lanfear et al. 2013; Bonier et al. 2014), because in many cases, these are based on the assumption of a BM process of range evolution. Phylogenetically conserved ranges also support one of the explicit assumptions of the

hypothesis of tropical niche conservatism (Wiens and Donoghue 2004). Under this hypothesis, latitudinal gradients in species richness have arisen as a consequence of the origins of many major taxa in tropical environments, combined with the relative rarity of migration into non-tropical environments. In general, conservatism in latitudinal positions of mammal ranges is supported by my results, although there are a number of taxa for which this is not the case. Perhaps these exceptions to the general pattern may prove useful in further testing of the predictions of the tropical niche conservatism hypothesis.

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