Range Size Heritability in Carnivora Is Driven by Geographic Constraints

Antonin Machac,[1,2,*] Jan Zrzavý,[1] and David Storch[2]

1. Department of Zoology, Faculty of Science, University of South Bohemia, Branisovska 31, 370 05, Ceske Budejovice, Czech Republic; and Department of Statistics and Probability, University of Economics, nam. W. Churchilla 4, 130 67, Praha 3, Czech Republic;   2. Center for Theoretical Study, Charles University and Academy of Sciences of the Czech Republic, Jilska 1, 110 00, Praha 1, Czech Republic; and Department of Ecology, Faculty of Sciences, Charles University, Vinicna 7, 128 44, Praha 2, Czech Republic

ABSTRACT: Range size heritability refers to an intriguing pattern where closely related species occupy geographic ranges of similar extent. Its existence may indicate selection on traits emergent only at the species level, with interesting consequences for evolutionary processes. We explore whether range size heritability may be attributable to the fact that range size is largely driven by the size of geographic domains (i.e., continents, biomes, areas given by species' climatic tolerance) that tend to be similar in phylogenetically related species. Using a well-resolved phylogeny of carnivorans, we show that range sizes are indeed constrained by geographic domains and that the phylogenetic signal in range sizes diminishes if the domain sizes are accounted for. Moreover, more detailed delimitation of species' geographic domain leads to a weaker signal in range size heritability, indicating the importance of definition of the null model against which the pattern is tested. Our findings do not reject the hypothesis of range size heritability but rather unravel its underlying mechanisms. Additional analyses imply that evolutionary conservatism in niche breadth delimits the species' geographic domain, which in turn shapes the species' range size. Range size heritability patterns thus emerge as a consequence of this interplay between evolutionary and geographic constraints.

Keywords: macroecology, species selection, biogeography, eigenvector, generalized least squares (GLS).

Introduction

During the last 2 decades, range size heritability has been a subject of vigorous and sometimes controversial debates. The term "range size heritability" refers to a tendency of closely related species to retain more similar range sizes than distinct species do (Jablonski 1987). The appeal of range size heritability for biologists resides in its association with the species selection concept (Ricklefs and

* Corresponding author; e-mail: a.machac@email.cz.

Latham 1992; Grantham 1995). Species selection is an outcome of heritable differences in speciation and extinction rates among phylogenetic lineages. It is widely accepted that differential speciation and extinction owing to purely emergent traits (collective properties of individuals within a species; e.g., geographic range size, sex ratio, intraspecific variability) has to be due to the species selection. However, for any selection process, heritability of the selected traits is a necessary prerequisite. Convincing evidence for range size heritability might therefore highlight the species selection as one of the central evolutionary processes (Gould and Lloyd 1999; Webb and Gaston 2003; Jablonski 2008; Rabosky and McCune 2010).

Tempted by this outlook for crucial findings, numerous studies have examined and variously documented (Jablonski 1987; Taylor and Gotelli 1994), refuted (Diniz-Filho and Torres 2002; Webb and Gaston 2003), and reaffirmed (Hunt et al. 2005; Jones et al. 2005) range size heritability via a spectrum of methods ranging from sister-species pair comparison and phylogenetic autocorrelation to the construction of explicit models of range size evolution (see reviews by Gaston 2003; Waldron 2007). As recent discussions illustrate (Hunt et al. 2005; Webb and Gaston 2005), distinct methods may lead to different outcomes even when applied to the same data set. The ambiguous conclusions prove the range size heritability to be a difficult conundrum. This is not only due to the methodological pitfalls but also to presumably varied patterns among different taxonomic groups (Jones et al. 2005).

Despite the lack of compelling evidence for the pattern itself, many underlying mechanisms have been hypothesized and tested. For instance, phylogenetically conserved life-history traits such as niche breadth, physiological tolerance, dispersal ability, and functional group membership may eventually lead to range size heritability (Mouillot and Gaston 2009). Surprisingly, only rarely have geographic constraints such as spatial limits of continents or

biomes been appraised (Bohning-Gaese et al. 2006; Freckleton and Jetz 2009).

Spatial structure is an inherent component of biogeographic data and is routinely considered when analyzing patterns in diversity or abundance (Legendre et al. 2002; Blackburn 2004; Rangel et al. 2006). It naturally affects range sizes as well. As Brown et al. (1996, p. 607) highlighted in their keystone work, we need to consider "how geographic ranges are distributed on and constrained by the spherical geometry and basic geography of the earth." A number of studies have documented that species occupying biogeographic provinces of vast spatial extent tend to have larger range sizes (Pagel et al. 1991; Smith et al. 1994; Gaston et al. 1998; Fortes and Absalao 2004). This means that we cannot make reliable conclusions about range size heritability without controlling for spatiogeographic constraints. However, only several studies so far have addressed simultaneously the evolutionary and geographic constituents of range sizes. Specifically, Freckleton and Jetz (2009) designed an integrated framework that allowed simultaneous evaluation of phylogenetic and spatial components of life-history traits. Having detected spatial signal in range sizes, the authors outlined that range size variation may be driven by where species live rather than by evolutionary history. However, Bohning-Gaese et al. (2006) did not discover any substantial correlation when examining the relation between range sizes of 26 bird species and the area of corresponding ecoregions and biomes. These surprising conclusions are balanced by the findings of Mouillot and Gaston (2009) that imply spatial autocorrelation in an extensive data set of 1,136 bird species (the autocorrelation is therein manifested as a positive relationship between mutual overlap and similarity in size of sister species' geographic ranges).

In our study, we thoroughly explore the impact of geographic constraints on carnivoran range sizes. As delimitation of specific geographic constraints might be contentious, we assess the constraints for several levels of geographic resolution (i.e., edges of continents, biomes, and climate envelopes). Subsequently, we contrast the effects of geographic and phylogenetic constraints on range size variation. We evaluate the stability of phylogenetic signal in range sizes after the correction for geographic constraints, and explore possible causes of the revealed patterns.

Material and Methods

We have employed a complex statistical approach to investigate the effect of geographic constraints/domains on range size heritability. Herein, we describe the foundations of the methodological framework we adopted; a detailed technical description of the analyses and statistical pro-

cedures is given in appendix A in the online edition of the *American Naturalist.*

Overview

We assume that if range size is determined by the size of a respective geographic domain, these two variables should correlate with each other. Moreover, if the range size heritability (i.e., the phylogenetic signal in range size) is entirely due to the size of geographic domains, the residuals from the regression of range size on the domain size should have no phylogenetic signal. This represents the first relatively simple approach to testing the effects of geographic domains on range size.

For a detailed examination of the role of geographic and evolutionary constraints (i.e., the role of variously delimited geographic domains vs. the role of phylogeny), we performed a decomposition of range size variation. However, rather than exploring factors underlying species' range sizes, we explored factors responsible for range size similarity. This means that we examined whether the similarity of species in terms of their range sizes is attributable to (*a*) species' phylogenetic relatedness, (*b*) similarity in the geographic location of species' ranges, and (*c*) similarity of the size of species' geographic domains (regardless of physical distances between individual domains). We proceeded using the following steps:

We constructed similarity matrices between all pairs of species based on (*a*) patristic distances derived from branch lengths of carnivoran phylogeny, (*b*) physical distances between midpoints of species' geographic ranges, and (*c*) differences between the areas of species' geographic domains (see below). Subsequently, we processed these similarity matrices by means of the phylogenetic/spatial eigenvector filtering (or PVR[1]) and the phylogenetic/spatial generalized least squares (GLS).

The PVR procedure, based on metric multidimensional scaling, transformed each of the distance matrices into a series of mutually independent variables, forming either "phylogenetic filters" (Diniz-Filho and Torres 2002; Carrascal et al. 2008) or "spatial filters" (Diniz-Filho and Bini 2005). We regressed species' actual range sizes against the set of spatial filters representing distances of range midpoints as well as the differences among the areas of each species' geographic domain. Subsequently, we explored the residuals from these regressions for range size heritability,

---

[1] Throughout the text, we use the abbreviation PVR to indicate eigenvector filtering. The abbreviation itself stands for phylogenetic eigenvector regression (termed "eigenvector filtering" by some authors). Since PVR is not restricted to only phylogenetic applications and produces eigenvector filters, we feel that the term "eigenvector filtering" is more appropriate for our purposes than "phylogenetic eigenvector regression." For brevity, however, we refer to eigenvector filtering by means of the widely known abbreviation PVR.

that is, heritability after controlling for geographic position, and for the size of geographic domains. (In addition, see the appendix section "Eigenvector Filtering (PVR) and the Generalized Least Squares (GLS) Framework" for a discussion of the PVR inference and its drawbacks; Freckleton et al. 2011.)

The GLS procedure, as proposed by Freckleton and Jetz (2009), modifies the method of phylogenetically independent contrasts to evaluate the phylogenetic and spatial component of trait variance. To infer the role of spatial effects (characterized by the distance matrices described above) with respect to range size, parameter Φ was estimated. Value of the Φ parameter ranges from 0 to 1. A zero value of Φ indicates that the range sizes are independent of the ranges' spatial distances, whereas when $\Phi = 1$, the variation in species' range sizes is attributable to space only.

Finally, the role of spatial and phylogenetic effects was contrasted. In the case of the PVR, we performed variation partitioning by means of a standard multiple regression using the sets of filters as independent variables and the actual range size as a dependent variable. We tested the effect of individual variables (i.e., the sets of filters derived from similarity/distance matrices), controlling for the remaining effects, and also explored their common effect. This enabled us to evaluate the role of phylogeny when accounting for the effect of similarity in geographic domain areas or similarity in range location, and vice versa. In the case of the GLS, we fitted an additional parameter λ to the range size data simultaneously with Φ. The λ parameter transformed the variance-covariance matrix derived from the carnivoran phylogeny so that phylogenetically correlated variation as well as independent variation in range sizes was allowed for. Consequently, the relative roles of spatial effects, phylogenetic effects, and effects independent of both space and phylogeny could be assessed. Below, we provide details of all the calculations.

Geographic Ranges of Carnivora

Since carnivorans are among the most studied taxa in range size heritability studies (Diniz-Filho and Torres 2002; Jones et al. 2005; Freckleton and Jetz 2009), we opted for them as our model as well. Thus, our results will be comparable with findings of the previous studies. Our data set comprised 231 species of terrestrial carnivorans (i.e., excluding Pinnipedia: Otariidae + Odobenidae + Phocidae). Maps of their geographic ranges were gathered from Pechlakova (2006) and IUCN (2010). Whenever possible, the original extent of ranges (i.e., not the extent recently reduced by humans) was reconstructed. After digitalization of the maps in ArcView GIS (ver. 3.2, Environmental Sys-

tems Research Institute, Redlands, CA), the range sizes were calculated.

Assembling the Phylogeny

We constructed an updated phylogeny of carnivorans with particular attention to recent studies (Bardeleben et al. 2005; Lindblad-Toh et al. 2005; Fulton and Strobeck 2006; Gaubert and Cordeiro-Estrela 2006; Koepfli et al. 2006, 2007; Arnason et al. 2007; Gaubert and Begg 2007; Krause et al. 2008; Patou et al. 2009). To construct a supertree, the topology of partial phylogenies was coded using the matrix representation with parsimony method (Baum 1992; Ragan 1992; for its phylogenetic applications see, e.g., Bininda-Emonds et al. 1999; Liu et al. 2001). The phylogenetic data sets were analyzed by NONA software (ver. 2.0; Goloboff 1999).

We employed published information on dates of carnivoran diversification events (Johnson et al. 2006; Koepfli et al. 2008; Patou et al. 2008; Sato et al. 2009; and studies cited above) to calibrate the branch lengths of our supertree. Diversification estimates for nodes with no dating available were calculated in Phylocom v4.0 through the BLADJ algorithm, which minimizes the variance in branch lengths within the constraints of dated nodes, as described in Webb et al. (2008).

Delimiting Geographic Constraints

Our baseline assumption stems from the obvious notions that every range size is restrained by the area of corresponding geographic domain (e.g., continent or biome; see below) and that range sizes within geographic domains of similar sizes also tend to be similar. However, we need to address the fundamental question of how to define the geographic domains. Since any particular definition would be inevitably disputable as we do not know all the factors shaping range sizes of individual species, we decided to use three different levels of spatial/geographic scale and to contrast subsequent outcomes. For this reason we use three distinct domain definitions (i.e., three levels of "geographic resolution"), differing in the amount of information used for the delimitation of domains: (*a*) continental domains, (*b*) biome domains, and (*c*) climate envelopes.

Continental geographic domains were represented by the four distinct continents, that is, Africa, North and South America, and Eurasia. Island areas (British Isles, Borneo, Greenland, etc.) were affiliated with their adjacent continents.

Biome domains were represented by 14 biomes distinguished by Olson et al. (2001). The area of individual biomes was considered for each continent separately; within the continents, however, all the discrete areas of

individual biomes were merged. Each of the acquired areas represented a biome domain (e.g., all the temperate grasslands of North America). If a species occurred in several biomes within a given continent, the total area of all biomes where the species occurred was taken as its biome domain.

The most precise description of geographic domains was acquired by means of climate envelopes (Guisan and Zimmermann 2000). Climate envelopes were inferred for each individual species with respect to annual mean temperature, annual precipitation, and NDVI (normalized difference vegetation index, an estimate of environmental productivity based on spectral properties of vegetation) within its geographic range. The original climate data sets (Hijmans et al. 2005; Tucker et al. 2005) were resampled to a 50 × 50-km spatial resolution, which is close to the recommended threshold of 1°–2° for species distribution data (Hurlbert and Jetz 2007). Climate envelope was delimited as an area within which none of the above-mentioned environmental variables exceeded minimum or maximum values reached within the actual species' range.

We need to explain what the climate envelopes represent from the conceptual viewpoint. As Soberon and Nakamura (2009) illustrate, climate envelopes lie somewhere between the species' realized and fundamental niches. The envelopes do not incorporate biotic interactions (food webs, competition, etc.) and consider climate tolerances only. Thus, they approximate a species' fundamental niche. However, the climate tolerances are inferred from species' geographic distributions which, ipso facto, represent the realized niche. Consequently, the area of a climate envelope extends beyond the area of a species' realized niche but does not reach the area corresponding to the fundamental niche. Unlike more advanced techniques of niche modeling, the envelope-based approach is computationally efficient and straightforward to interpret (Guisan and Thuiller 2005). Its performance has been shown to be slightly worse but still satisfactory in comparison with more sophisticated methods based on regression trees, multivariate distances, or maximum entropy (Kadmon et al. 2003; Elith et al. 2006).

Whenever the species occupied several isolated geographic domains on different continents (e.g., America and Eurasia in the case of *Mustela erminea*), the area of each domain was considered separately. We presume that the area of isolated subranges is constrained by the corresponding domains independently and not by their sum across different continents. Therefore, we handled these isolated subranges as individual data points within our analyses. There were in fact only seven such cases in our data set (*Canis lupus, Gulo gulo, Mustela erminea, Mustela nivalis, Panthera pardus, Ursus arctos, Vulpes vulpes*).

We need to explicitly notify the readers that information on geographic domains was inferred from the species' geographic ranges. As a consequence, the more information inferred from the species' geographic distribution we used for a delimitation of its domain, the closer the domain was to the species' actual geographic range. Considering this inevitable circularity associated with domain definition, we a priori expect the effect of geographic domains on range size to increase with the geographic resolution (continents, biomes, climate envelopes) at which the domain was defined.

Constructing Similarity Matrices

We prepared three matrices of similarity between species' ranges: (1) matrix of phylogenetic distances between species, (2) matrix of distances between locations of species ranges, and (3) matrix of differences in areas of geographic domains, which were delimited as explained above.

Phylogenetic relatedness was represented by patristic distances among individual species. The distances were derived from the branch lengths of our carnivoran phylogeny (see above).

To create a distance matrix of range locations, we computed mutual physical distances among range midpoints (i.e., the average from maximum and minimum range extents in east-west and north-south directions). This measure was employed by previous studies (Freckleton and Jetz 2009) and allows us to compare the obtained results.

The distances between areas of species' geographic domains were calculated in two ways. Both of the distances increase with the dissimilarity of geographic domains' areas, regardless of ranges' mutual physical distance:

$$\text{distance 1 (A, B)} = \log \frac{S(B)}{S(A)}, \tag{1}$$

$$\text{distance 2 (A, B)} = \log [S(B) - S(A)], \tag{2}$$

where distance (A, B) is the distance between ranges A and B, and $S(A)$, $S(B)$ are areas of geographic domains for species A and B, respectively, so that $S(A) < S(B)$. We calculated the distances distance 1 and distance 2 for each of the three geographic resolutions (i.e., continents, biomes, and climate envelopes). Subsequently, the distance matrices were processed by the PVR and the GLS (as described above and in "Eigenvector Filtering (PVR) and the Generalized Least Squares (GLS) Framework").

Assessing Range Size Heritability

The range size heritability was assessed by means of Blomberg's K (Blomberg et al. 2003), Pagel's λ (Freckleton et al. 2002), and Moran's I (Gittleman and Kot 1990; Legendre et al. 2002; Jones et al. 2005). We favor Moran's I
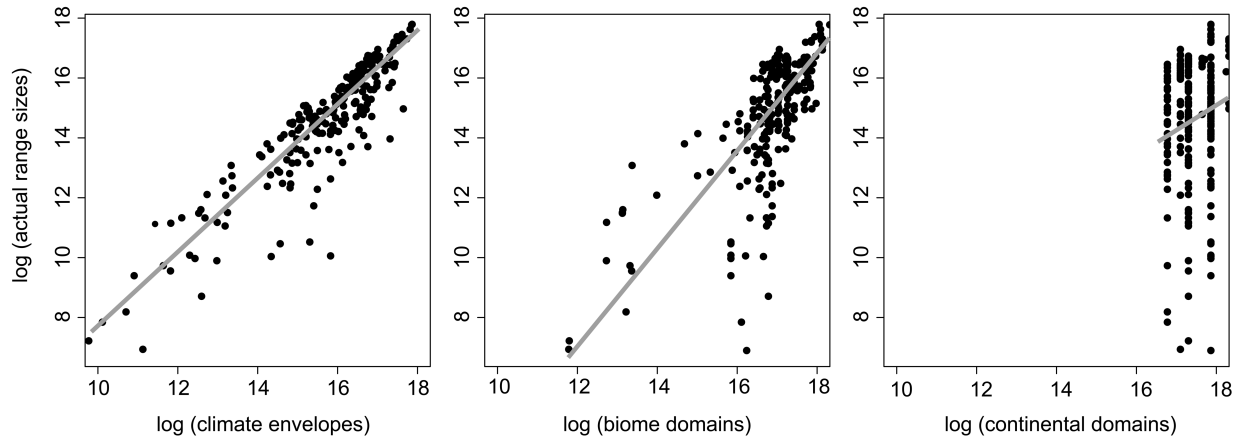
Figure 1: The correlation between actual range sizes and areas of geographic domains. The domains were defined as continents, biomes, and climate envelopes.

as a measure of range size heritability not only due to its compatibility with spatial statistics framework but also because it provides an option to evaluate the heritability for different patristic distance classes (i.e., varying depths of phylogeny). This is critical because range size heritability patterns have been documented to vary among different taxonomic levels (Jones et al. 2005). Consequently, antagonistic patterns at different levels can obscure one another when the analysis of phylogenetic signal is conducted across the whole phylogeny at once (appendix section "Analyses of Phylogenetic Signal"). Therefore, we preferably interpret the values of Moran's *I* calculated for different depths of phylogeny separately. Values of Moran's *I* vary from −1 to +1. Positive values indicate that range sizes of taxa at a particular phylogenetic level (or within a particular patristic distance class) are more similar than would be expected by chance; negative values of Moran's *I* indicate that range sizes are more different. The alternative measures of range size heritability (Blomberg's *K*, Pagel's λ) are provided and discussed in appendix section "Analyses of Phylogenetic Signal."

All the measures of heritability were inferred for the actual range sizes and afterwards recalculated with the data controlled for the geographic constraints, as explained above. The calculations were conducted in the R 2.8 environment (R Development Core Team 2009; packages ape, geiger, picante, and spdep; Paradis et al. 2004; Bivand et al. 2008; Harmon et al. 2008; Kembel et al. 2010).

Contrasting the Role of Geographic and Phylogenetic Constraints

We employed two disparate methodical frameworks, the PVR and the GLS, to compare the role of phylogenetic and spatial effects on carnivorans' range sizes. In the case of the PVR, once the geographic constraints and the phylogenetic relatedness were expressed in a format convenient for statistical analyses, that is, spatial/phylogenetic filters ("Eigenvector Filtering (PVR) and the Generalized Least Squares (GLS) Framework"), we conducted the variation partitioning. Consequently, we assessed whether geographic constraints, phylogenetic relatedness, or other factors not involved in our analyses are accountable for the major fraction of range size variation and, ultimately, for range size heritability.

In the case of GLS, the estimates of parameters Φ and λ were inferred via a likelihood optimization whereby the likelihood function was maximized jointly over both of the parameters. Subsequently, parameters λ' $(= [1 - \Phi] \times \lambda)$ and γ $(= 1 - [\lambda' + \Phi])$ were derived. The parameters are defined so that $\lambda' + \Phi + \gamma = 1$. Thus, their values can be interpreted as proportional contributions of phylogenetic effects (λ'), spatial effects (Φ), and effects independent of both space and phylogeny (γ) to the range size variation (Freckleton and Jetz 2009). All the analyses were performed in R 2.8 (R Development Core Team 2009), employing a code kindly provided by R. P. Freckleton.

Factors beyond the Geographic Domains: Niche Breadth and Shared Physical Barriers

For a proper understanding of geographic constraints on range size, we need to explore the processes that determine the area of species' geographic domains. We investigated two alternative scenarios: (*a*) If closely related species of carnivorans were generally sympatric, their range sizes would be constrained by identical geographic barriers; for example, the coastline of a particular sea or a mountain
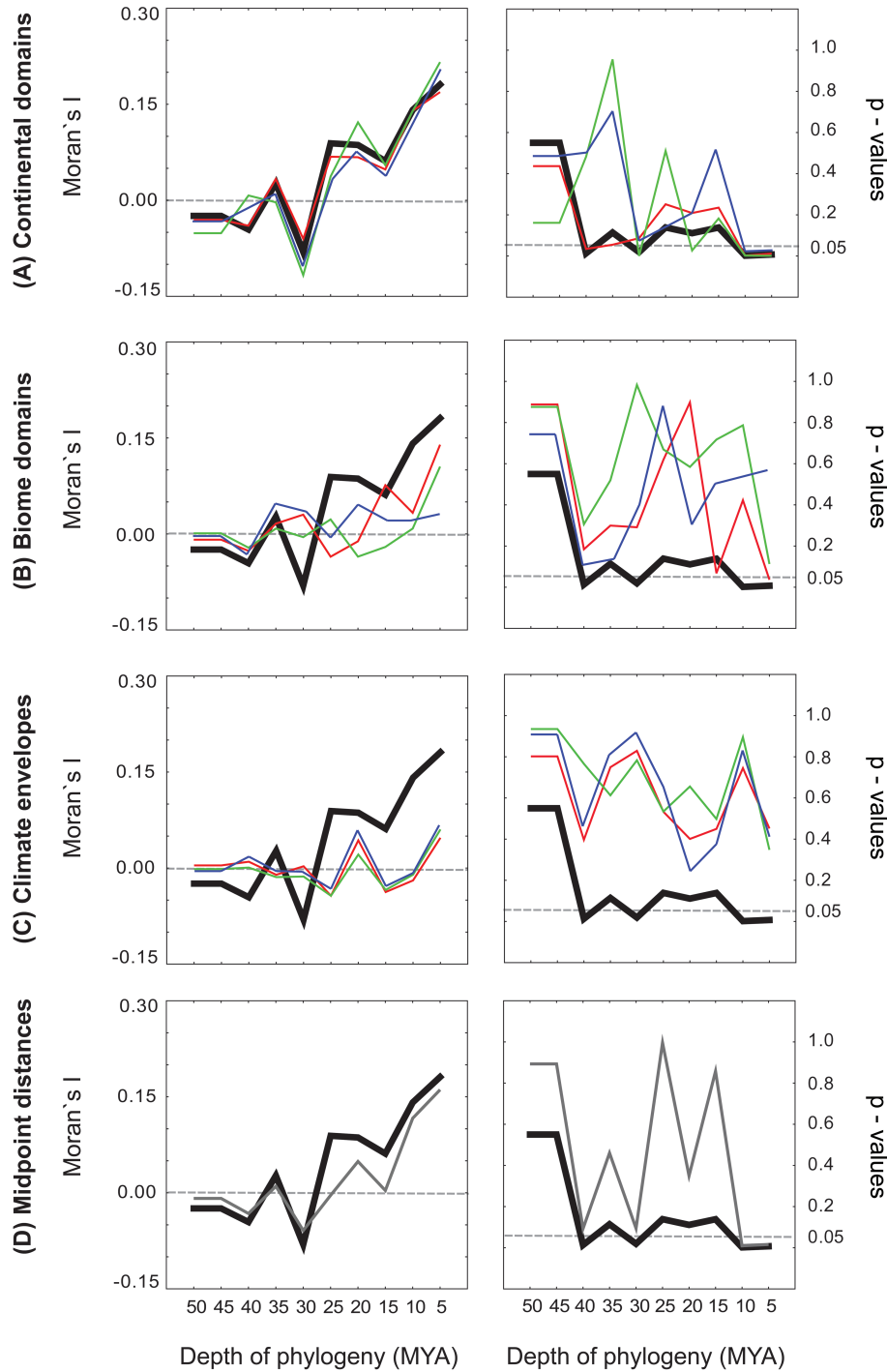
Figure 2: Range size heritability patterns calculated for 5-million-year distance classes. The figure provides values of Moran's *I* as well as their significance (i.e., *P* values). Heritability in actual range sizes (*thick black line*) is contrasted with heritability after accounting for the areas of geographic domains (*red lines*), two area-derived distances (*blue lines* = distance 1; *green lines* = distance 2), and range midpoint distances (*gray lines*; see text for details). The effect of continental domains (*A*) or midpoint distances (*D*) on range size heritability is rather marginal as the actual heritability does not differ from heritability after the geographic constraints are accounted for (i.e., the black line is congruent with the red, blue, and green lines). In contrast, excluding the effects of biome domains (*B*) or climate envelopes (*C*) leads to a significant suppression of the range size heritability pattern.

Table 1: Partitioning of the range size variation by means of eigenvector filtering (=eigenvector regression, or PVR)

Phylogeny	Overlap	Geography	Type of geographic constraint
.012	.243	.581	Climate envelopes
.015	.240	.584	Distance 1 (climate envelopes)
.009	.246	.569	Distance 2 (climate envelopes)
.080	.175	.322	Biomes
.038	.217	.467	Distance 1 (biomes)
.045	.210	.453	Distance 2 (biomes)
.249	.006	.006	Continents
.123	.132	.012	Distance 1 (continents)
.190	.065	.029	Distance 2 (continents)
.212	.043	.050	Midpoint distances

Note: Values refer to the amount of variance in range sizes (R^2) explained by phylogeny, geographic constraints, and their mutual overlap. Each row of the table represents an independent variation partitioning procedure. While phylogeny was expressed identically during each variation partitioning procedure, geographic constraints were expressed differently in each case (climate envelopes, biomes, continents, etc.). All the effects of geographic constraints as well as of the phylogeny were highly significant ($P < .001$).

range. The range size heritability would thus emerge as a consequence of shared physical barriers, or phylogenetic signal in geographic position of ranges. (*b*) However, absence of phylogenetic signal in ranges' geographic position would indicate that some other mechanisms are responsible for the range size heritability being driven by geographic constraints. For instance, shared biological traits such as niche breadth or physiological tolerances could underlie the size of geographic domains and, ultimately, range size heritability patterns.

To compare the plausibility of these two hypotheses, we compared the phylogenetic signal in carnivorans' niche breadth and range geographic position. Ecological niche was represented by temperature, precipitation, and environmental productivity (Hijmans et al. 2005; Tucker et al. 2005; see above); these variables generally govern species distribution and diversity and correspond to major axes of ecological niche differentiation in vertebrates (e.g., Currie 1991; Gittleman 1996; Rahbek and Graves 2001). The geographic range of each species was split into 50 × 50-km grid cells, and the standard deviation of individual climate variables across these grid cells was used as a proxy for the species' niche breadth. Since the values of climate variables appeared to be highly skewed, we log transformed them before the standard deviation was calculated.

The geographic position of individual ranges was represented by coordinates of ranges' geographic centroid and distant vertices (i.e., coordinates of the southernmost, northernmost, westernmost, and easternmost vertex). To combine the coordinates into a single variable, a principal components analysis, as implemented in Canoco for Windows 4.5 (ter Braak and Smilauer 2002), was employed. Species were ordinated with respect to the geographic co-

ordinates of their ranges, and the species' scores along the first ordination axis were subjected to phylogenetic signal examination. In addition, we tested for phylogenetic signal in physical distances among range midpoints (i.e., whether the mutual distances between range midpoints correspond with phylogeny). The midpoint distance matrix was transformed into an eigenvector through the PVR (see above), and the acquired eigenvector was examined for phylogenetic signal.

The phylogenetic signal examination was conducted by means of three distinct metrics, Blomberg's K, Pagel's λ, and Moran's I, in R 2.8 (R Development Core Team. 2009; packages ape, geiger, picante, spdep; Gittleman and Kot 1990; Freckleton et al. 2002; Blomberg et al. 2003; Paradis et al. 2004; Bivand et al. 2008; Harmon et al. 2008; Kembel et al. 2010; see also Cubo et al. 2005 and Machac et al. 2010 for alternative methods of phylogenetic signal testing). Significance of the K values was estimated through both randomization (trait values were rearranged along the tips of phylogeny; H_0: $K = 0$) and simulation (evolution of the traits was simulated under the Brownian motion model; H_0: $K = 1$) employing 999 iterations. Values of Pagel's λ were also tested against two distinct hypotheses, absence of a phylogenetic signal (H_0: $\lambda = 0$) and presence of a phylogenetic signal consistent with the Brownian motion model (H_0: $\lambda = 1$), by means of likelihood ratio tests. Finally, significance of Moran's I (H_0: $I = 0$) was estimated via randomizations conducted in a manner similar to that in the case of Blomberg's K.

Comparing the phylogenetic signal in each of the selected dimensions of niche breadth (temperature, precipitation, and NDVI tolerance) and ranges' geographic position, we can infer processes responsible for the range size

Table 2: Proportional contributions of the spatial effects (Φ), the phylogenetic effects (λ′), and effects independent of both space and phylogeny (γ) to range size variation, as estimated through generalized least squares analysis

	Maximum likelihood values			Proportional contributions		
	λ	Φ	Log likelihood	λ′	Φ	γ
Distance 1 (climate envelopes)	.329	.779	−335.947	.073	.779	.148
Distance 2 (climate envelopes)	.990	.969	−443.243	.031	.969	.000
Distance 1 (biomes)	.012	.864	−440.025	.002	.864	.134
Distance 2 (biomes)	.000	.858	−442.144	.000	.858	.142
Distance 1 (continents)	.499	.097	−505.227	.451	.097	.452
Distance 2 (continents)	.515	.086	−503.839	.471	.086	.443
Midpoint distances	.725	.271	−505.227	.529	.271	.200

Note: The sum of the proportional contributions Φ, λ′, and γ always equals 1. The proportional contributions were derived from the maximum likelihood values of parameters Φ and λ jointly fitted to the range size data.

heritability patterns. If range size heritability patterns emerge despite the lack of phylogenetic signal in ranges' geographic position, we can infer that niche breadth rather than shared physical barriers is accountable for the range size heritability pattern, and vice versa.

Results

The impact of the area of geographic domain (defined at three resolution levels: continents, biomes, and climate envelopes) on species' range size was assessed by means of linear regression. Naturally, the firmest relationship was detected between the actual range sizes and areas of climate envelopes ($F = 1,109$, df $= 236$, $P < .001$, $R^2 = 0.824$), followed by biome domains ($F = 235$, df $= 236$, $P < .001$, $R^2 = 0.497$) and then by continental domains (nonsignificant relationship: $F = 3.765$, df $= 236$, $P = .054$, $R^2 = 0.012$; fig. 1).

Range size heritability was assessed for the actual range sizes. Values of Moran's I calculated for 5-million-year distance classes unraveled a significant positive range size heritability at lower levels of phylogeny (5 million years ago [mya]: $I = 0.181$, $P = .007$; 10 mya: $I = 0.141$, $P = .002$), whereas distantly related taxa demonstrated negative range size correlation (30 mya: $I = -0.081$, $P = .019$; 40 mya: $I = -0.046$, $P = .013$; fig. 2).

Furthermore, we inspected the range size heritability after accounting for the geographic constraints (i.e., areas of continents, biomes, climate envelopes, and midpoint distances). The patterns of range size heritability were noticeably suppressed after the areas of climate envelopes (fig. 2*C*; table A1) and biomes (fig. 2*B*; table A1) were accounted for. However, excluding the effects of continental domains (fig. 2*A*; table A1) and midpoint distances (fig. 2*D*; table A1) left the heritability patterns rather un-

changed (as illustrated in fig. 2 and thoroughly discussed in appendix section "Analyses of Phylogenetic Signal").

The PVR-based variation partitioning as well as the GLS-based parameters Φ, λ′, and γ yielded outcomes equivalent to those of the phylogenetic signal analyses (previous paragraph). As tables 1 and 2 indicate, when defined as climate envelopes ($R^2 \approx 0.80$; $\Phi \approx 0.80$, $\lambda' \approx 0.05$) or biomes ($R^2 \approx 0.50$; $\Phi \approx 0.85$, $\lambda' \approx 0$), the geographic constraints appeared to be the dominant driver of range size variation. In contrast, when the constraints were described as midpoint distances ($R^2 = 0.09$; $\Phi = 0.27$, $\lambda' = 0.53$) and continental domains ($R^2 \approx 0.10$; $\Phi \approx 0.10$, $\lambda' \approx 0.45$), a reverse outcome was achieved, and phylogeny outweighed the spatial effects.

Taken together, our results indicate that the more comprehensive the description of geographic constraints is, the more they affect the range sizes. When a detailed definition of geographic domains is employed, the phylogenetic component of range sizes appears rather marginal (tables 1, 2). Thus, stability of the range size heritability pattern (fig. 2) is vastly affected by the amount of information we consider when defining the geographic constraints on range size.

To identify the most appropriate level of geographic resolution (concerning the constraints), we employed geographic information system tools to calculate average size of ranges of species occurring within each of the 10,000-km^2 grid cells covering the globe. The acquired figure (fig. 3) indicates, for instance, that all the grid cells within equatorial Africa accommodate ranges of a consistent size; this size apparently reflects the extent of African rain forests. Similarly, ranges spreading through Saharan desert, Namibian desert, or Indo-Malaysian rain forests reach generally identical sizes (fig. 3). These patterns imply that carnivoran range sizes are predominantly constrained by
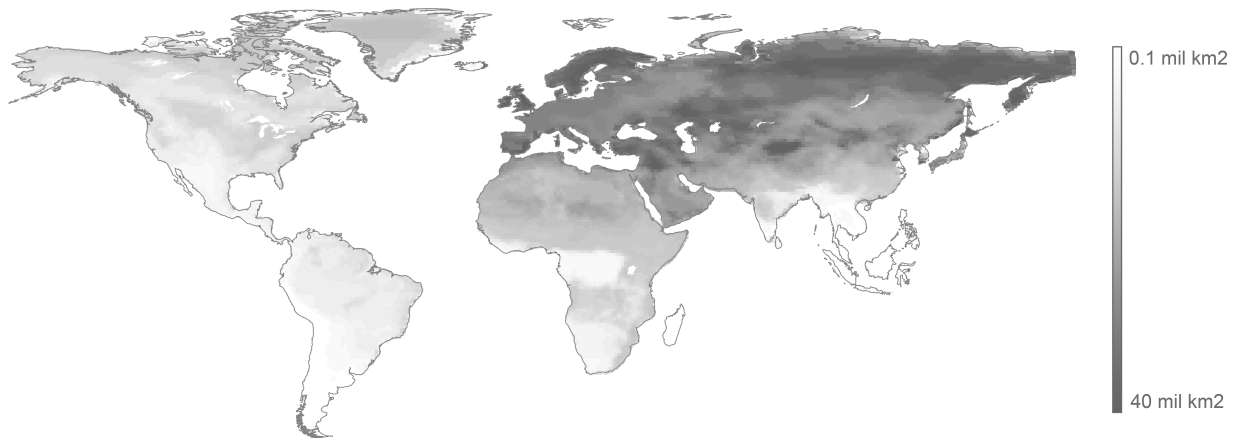
Figure 3: Average size of geographic ranges within 10,000-km^2 grid cells covering the globe. The pattern of carnivorans' distribution is largely congruent with the outline of major biomes, which particularly applies in Indo-Malaysia, Africa, and Eurasia.

the edges of biomes, which represent the most convenient level of geographic resolution for further reasoning.

Additional analyses of phylogenetic signal indicated that the ranges of carnivorans are positioned over the Earth's surface randomly with regard to phylogeny (table 3). Even closely related species might occupy distant geographic regions. In contrast, carnivorans' niche breadth (characterized by proxies for species' temperature, precipitation, and NDVI tolerances) yielded a notable phylogenetic signal. All of the metrics (table 3) consistently demonstrate that the species' temperature, precipitation, and NDVI tolerances are not arranged randomly across the phylogeny but reflect it to a certain extent. Whether this reflection may be considered as niche conservatism was verified via the simulations of trait evolution. The results illustrate that the proxies for temperature ($K = 1.996$, $P = .022$) and precipitation ($K = 1.912$, $P = .023$) tolerance significantly diverge from their values as expected under Brownian motion (i.e., $K = 1$); hence, we can consider them phylogenetically conserved (sensu Losos 2008). Although the NDVI tolerances proved significantly phylogenetically dependent ($K = 1.712$, $P(K = 0) = .001$), they are not phylogenetically conserved (sensu Losos 2008), as their phylogenetic dependence is not higher than expected under the Brownian motion model ($P[K = 1] = .057$).

Discussion

Biogeographic patterns are produced by a complex interaction among numerous factors whereby limits of continents, montane systems, and other physical barriers represent a crucial agent. Though their influence has been widely acknowledged, physical barriers appear rather dif-

ficult to grasp, and appropriate spatial analyses still represent a challenging issue. Herein, we aimed to verify and assess the effect of geographic constraints on range size heritability patterns. Employing two advanced methods for analysis of phylogenetically and spatially structured data (PVR, GLS), we infer that edges of biomes are largely responsible for the observed patterns of range size heritability. Furthermore, we propose a mechanism whereby range size heritability patterns emerge due to interplay between geographic and phylogenetic constraints. Phylogenetically conserved physiological tolerances appear to shape the extent of geographic domains that, subsequently, underlie species' range size.

So far, spatial constraints have only rarely been considered when studying range sizes and their heritability. Employing midpoint distances, Freckleton and Jetz (2009) documented spatial signal in range sizes of artiodactyls, carnivorans, and primates. Their study provides an insightful impetus for exploration of the spatial constraints on range sizes; however, the description of ranges' spatial arrangement by means of their midpoint distances is potentially imprecise. For instance, the midpoint distances of north-south orientation generally traverse a number of climate zones, whereas east-west distances do not; thus, the distances convey different biological information depending on their direction. Therefore, instead of using physical distances among ranges' midpoints, we decided to utilize the distances reflecting dissimilarity of geographic domains areas. The geographic domain approach promisingly avoids the pitfalls of midpoint distances; however, it is also inherently associated with circularity as the domains are derived from the species' geographic distributions (see "Material and Methods"). The domain-based

Table 3: Phylogenetic signal in niche breadth and range geographic position as evaluated by Blomberg's *K*, Pagel's λ, and Moran's *I*

	Blomberg's *K*	*P* (*K* = 0)	*P* (*K* = 1)	Moran's *I*	*P* (*I* = 0)	Pagel's λ	*P* (λ = 1)	*P* (λ = 0)
Niche breadth:								
Log(temperature) SD	1.996	.001	.022	.856	.007	.997	.994	.001
Log(precipitation) SD	1.912	.001	.023	.823	.011	.997	.994	.001
Log(NDVI) SD	1.712	.001	.057	.695	.036	.996	.990	.001
Geographic position:								
Midpoint distances	.005	.005	.001	.015	.059	.073	.001	.001
Geographic coordinates	.001	.998	.001	.003	.989	.689	.023	.047

Note: *P* values are indicated along with the null hypothesis tested. In sum, the geographic position of ranges proved virtually no phylogenetic dependence ($K \approx 0, I \approx 0, \lambda < 1$). The phylogenetic dependence in the case of normalized difference vegetation index (NDVI) tolerance was consistent with the expectations under the Brownian motion model of trait evolution ($K \approx 1, \lambda \approx 1$). Phylogenetic conservatism was detected in the case of temperature and precipitation tolerances ($K > 1, P[K = 1] < .025$), as their values were significantly more similar than expected under Brownian motion.

approach revealed a noticeable spatial signal in carnivoran range sizes.

Unlike Mouillot and Gaston (2009), we used Moran's *I* rather than sister-species pair comparison to examine range size heritability. Hence, we could utilize all of the information conveyed by a phylogenetic tree (i.e., not only by sister species) and also explore heritability patterns above the species level (fig. 2). This is particularly important as heritability patterns have been documented to vary among taxonomic levels (Jones et al. 2005; appendix section "Analyses of Phylogenetic Signal"). Despite employing a different methodical approach than Mouillot and Gaston (2009), we arrive at the same conclusion that range sizes are considerably spatially dependent.

Our finding that biome domains are largely responsible for the carnivoran range sizes contrasts with conclusions of Bohning-Gaese et al. (2006) based on 26 bird species. It is possible that range sizes of birds and carnivorans are constrained differently, but also that the group of 26 *Sylvia* warblers studied by Bohning-Gaese et al. (2006) was rather atypical due to the specifics of their life history. Since our conclusions are founded on a data set of 231 carnivorans, they are liable to be plausible and of more general relevance.

The outcomes of our analyses provide different conclusions for different levels of domains' delimitation (i.e., continents, biomes, and climate envelopes). When the geographic constraints of continental domains or range midpoint distances are considered, phylogeny appears as the major agent responsible for the range size variation. In contrast, detailed description of geographic constraints in terms of biomes and climate envelopes proves phylogeny to be of only marginal importance, so that the geographic constraints underlie the range sizes over and above the effects of phylogeny. This situation is in fact fairly characteristic. The finding that the obtained results depend on how the model is constructed (i.e., the effect of geographic

domains depending on the geographic resolution in our case) has been recognized since the early 1970's in the context of community assembly rules and their null models (Wilson 1995; Stone et al. 1996; Gotelli 2001). It has turned out that there is no "correct" null model, only models differing in the amount of information used for their construction. If considerable prior information about the system is used for the construction of the model (i.e., delimitation of biomes or climate envelopes in our case), the model usually proves plausible, but it is a simple consequence of the fact that the pattern is already somehow contained in the model, a situation sometimes called "the narcissus effect" (Gotelli 2001). From this point of view, it makes no sense to ask whether range size heritability can be attributed to the geographic constraints but rather how precise definition of the constraints is necessary for a concise description of the range size patterns (see fig. 3). In this light, our conclusion that the more comprehensive the definition of geographic domain, the greater its effect on range size in comparison to phylogeny, is not particularly surprising.

In fact, our findings do not reject the effect of phylogeny on range size but rather imply the mechanisms underlying the range size heritability patterns. We have shown that heritability is largely driven by the extent of biomes; however, this extent appears to be determined by phylogeny because related species share temperature and precipitation tolerances (table 3) as well as habitat and environmental preferences (Peterson et al. 1999; Diniz-Filho et al. 2010). Thus, bound by common evolutionary history, related species are limited in their distribution by similar geographic constraints. As these constraints represent a more proximate factor shaping species' ranges, they account for more of the range size variation than phylogeny does. Thus, the range size heritability patterns presumably emerge as a consequence of this interplay between evolutionary and geographic constraints.

Since the biome domains account for approximately 50% of the range size variation ($R^2 \approx 0.50$, $\Phi \approx 0.85$; tables 1, 2), they appear to be the major single factor responsible for range size heritability patterns, at least in carnivorans. The other proposed mechanisms of range size heritability (dispersal ability, physiological tolerances, functional group membership; Mouillot and Gaston 2009) are either subcategories of geographic constraints or phenomena of rather marginal importance. Since geographic position of carnivoran ranges exhibits no phylogenetic pattern (table 3; Cox and Moore 2005), range size heritability is not underlain by shared physical barriers (i.e., related species being limited by identical rivers, mountain ranges, or coastline), as even geographically distant species occupy ranges of similar extent (table 3). With respect to our results, phylogenetically conserved niche breadth, which determines the size of geographic domains, appears to be the crucial driver of range size heritability. Nonetheless, we note as a caveat that we comply with the general practice and interpret high phylogenetic signal in niche breadth (table 3) as evidence for niche conservatism (Blomberg et al. 2003; Swenson and Enquist 2007), although some studies have challenged such interpretation (e.g., Revell et al. 2008).

Our findings imply that despite being emergent only at the species level, geographic range size is associated with individual-level traits (i.e., physiological tolerance and niche breadth). Therefore, we conclude that the range size heritability phenomenon does not necessarily enforce the species selection concept as range size heritability can be directly linked to the natural selection that operates on the level of individuals.

Literature Cited

Arnason, U., A. Gullberg, A. Janke, and M. Kullberg. 2007. Mitogenomic analyses of caniform relationships. Molecular Phylogenetics and Evolution 45:863–874.

Bardeleben, C., R. L. Moore, and R. K. Wayne. 2005. A molecular phylogeny of the Canidae based on six nuclear loci. Molecular Phylogenetics and Evolution 37:815–831.

Baum, B. R. 1992. Combining trees as a way of combining data sets for phylogenetic inference and the desirability of combining gene trees. Taxon 41:3–10.

Bininda-Emonds, O. R. P., J. L. Gittleman, and A. Purvis. 1999. Building large trees by combining phylogenetic information: a complete phylogeny of the extant Carnivora (Mammalia). Biological Reviews 74:143–175.

Bivand, R., L. Anselin, R. Assuncao, and O. Berke. 2008. Spatial dependence: weighting schemes, statistics and models. R package, version 0.4-21. http://cran.r-project.org/web/packages/spdep/index.html.

Blackburn, T. M. 2004. Method in macroecology. Basic and Applied Ecology 5:401–412.

Blomberg, S. P., T. Garland Jr., and A. R. Ives. 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. Evolution 57:717–745.

Bohning-Gaese, K., T. Caprano, K. van Ewijk, and M. Veith. 2006. Range size: disentangling current traits and phylogenetic and biogeographic factors. American Naturalist 167:555–567.

Brown, J. H., G. C. Stevens, and D. M. Kaufman. 1996. The geographic range: size, shape, boundaries, and internal structure. Annual Review of Ecology and Systematics 27:597–623.

Carrascal, L. M., J. Seoane, D. Palomino, and V. Polo. 2008. Explanations for bird species range size: ecological correlates and phylogenetic effects in the Canary Islands. Journal of Biogeography 35:2061–2073.

Cox, C. B., and P. B. Moore. 2005. Biogeography: an ecological and evolutionary approach. Blackwell, Malden.

Cubo, J., F. Ponton, M. Laurin, E. de Margerie, and J. Castanet. 2005. Phylogenetic signal in bone microstructure of sauropsids. Systematic Biology 54:562–574.

Currie, D. J. 1991. Energy and large-scale patterns of animal-species and plant-species richness. American Naturalist 137:27–49.

Diniz-Filho, J. A., and L. M. Bini. 2005. Modelling geographical patterns in species richness using eigenvector-based spatial filters. Global Ecology and Biogeography 14:177–185.

Diniz-Filho, J. A., and N. M. Torres. 2002. Phylogenetic comparative methods and the geographic range size–body size relationship in New World terrestrial carnivora. Evolutionary Ecology 16:351–367.

Diniz-Filho, J. A. F., L. C. Terrible, M. J. R. da Cruz, and L. C. G. Vieira. 2010. Hidden patterns of phylogenetic non-stationarity overwhelm comparative analyses of niche conservatism and divergence. Global Ecology and Biogeography 19: 916–926.

Elith, J., C. H. Graham, R. P. Anderson, M. Dudik, S. Ferrier, A. Guisan, R. J. Hijmans, et al. 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29:129–151.

Fortes, R. R., and R. S. Absalao. 2004. The applicability of Rapoport's rule to the marine molluscs of the Americas. Journal of Biogeography 31:1909–1916.

Freckleton, R. P., and W. Jetz. 2009. Space versus phylogeny: disentangling phylogenetic and spatial signals in comparative data. Proceedings of the Royal Society B: Biological Sciences 276:21–30.

Freckleton, R. P., P. H. Harvey, and M. Pagel. 2002. Phylogenetic analysis and comparative data: a test and review of evidence. American Naturalist 160:712–726.

Freckleton, R. P., N. Cooper, and W. Jetz. 2011. Comparative methods

as a statistical fix: the dangers of ignoring evolution. American Naturalist (forthcoming).

Fulton, T. L., and C. Strobeck. 2006. Molecular phylogeny of the Arctoidea (Carnivora): effect of missing data on supertree and supermatrix analyses of multiple gene data sets. Molecular Phylogenetics and Evolution 41:165–181.

Gaston, K. J. 2003. The structure and dynamics of geographic ranges. Oxford University Press, Oxford.

Gaston, K. J., T. M. Blackburn, and J. I. Spicer. 1998. Rapoport's rule: time for an epitaph? Trends in Ecology & Evolution 13:70–74.

Gaubert, P., and C. M. Begg. 2007. Re-assessed molecular phylogeny and evolutionary scenario within genets (Carnivora, Viverridae, Genettinae). Molecular Phylogenetics and Evolution 44:920–927.

Gaubert, P., and P. Cordeiro-Estrela. 2006. Phylogenetic systematics and tempo of evolution of the Viverrinae (Mammalia, Carnivora, Viverridae) within feliformians: implications for faunal exchanges between Asia and Africa. Molecular Phylogenetics and Evolution 41:266–278.

Gittleman, J. L. 1996. Carnivore behavior, ecology, and evolution. Cornell University Press, Ithaca, NY.

Gittleman, J. L., and M. Kot. 1990. Adaptation: statistics and a null model for estimating phylogenetic effects. Systematic Zoology 39:227–241.

Goloboff, P. A. 1999. NONA. Version 2.0 (software and manual). Fundación e Instituto Miguel Lillo, Tucumán, Argentina.

Gotelli, N. J. 2001. Research frontiers in null model analysis. Global Ecology and Biogeography 10:337–343.

Gould, S. J., and E. A. Lloyd. 1999. Individuality and adaptation across levels of selection: how shall we name and generalize the unit of Darwinism? Proceedings of the National Academy of Sciences of the USA 96:11904–11909.

Grantham, T. A. 1995. Hierarchical approaches to macroevolution: recent work on species selection and the effect hypothesis. Annual Review of Ecology and Systematics 26:301–321.

Guisan, A., and W. Thuiller. 2005. Predicting species distribution: offering more than simple habitat models. Ecology Letters 8:993–1009.

Guisan, A., and N. E. Zimmermann. 2000. Predictive habitat distribution models in ecology. Ecological Modelling 135:147–186.

Harmon, L. J., J. T. Weir, C. D. Brock, R. E. Glor, and W. Challenger. 2008. GEIGER: investigating evolutionary radiations. Bioinformatics 24:129–131.

Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25:1965–1978.

Hunt, G., K. Roy, and D. Jablonski. 2005. Species-level heritability reaffirmed: a comment on "On the heritability of geographic range sizes." American Naturalist 166:129–135.

Hurlbert, A. H., and W. Jetz. 2007. Species richness, hotspots, and the scale dependence of range maps in ecology and conservation. Proceedings of the National Academy of Sciences of the USA 104:13384–13389.

IUCN (International Union for Conservation of Nature). 2010. The IUCN Red List of Threatened Species. http://www.iucnredlist.org.

Jablonski, D. 1987. Heritability at the species level: analysis of geographic ranges of cretaceous mollusks. Science 238:360–363.

———. 2008. Species selection: theory and data. Annual Review of Ecology, Evolution, and Systematics 39:501–524.

Johnson, W. E., E. Eizirik, J. Pecon-Slattery, W. J. Murphy, A. An-

tunes, E. Teeling, and S. J. O'Brien. 2006. The Late Miocene radiation of modern Felidae: a genetic assessment. Science 311:73–77.

Jones, K. E., W. Sechrest, and J. L. Gittleman. 2005. Age and area revisited: identifying global patterns and implications for conservation. Pages 141–165 *in* A. Purvis, J. L. Gittleman, and T. Brooks, eds. Phylogeny and conservation. Cambridge University Press, Cambridge.

Kadmon, R., O. Farber, and A. Danin. 2003. A systematic analysis of factors affecting the performance of climatic envelope models. Ecological Applications 13:853–867.

Kembel, S. W., P. D. Cowan, M. R. Helmus, W. K. Cornwell, H. Morlon, D. D. Ackerly, S. P. Blomberg, and C. O. Webb. 2010. Picante: R tools for integrating phylogenies and ecology. Bioinformatics 26:1463–1464.

Koepfli, K. P., S. M. Jenks, E. Eizirik, T. Zahirpour, B. Van Valkenburgh, and R. K. Wayne. 2006. Molecular systematics of the Hyaenidae: relationships of a relictual lineage resolved by a molecular supermatrix. Molecular Phylogenetics and Evolution 38:603–620.

Koepfli, K. P., M. E. Gompper, E. Eizirik, C. C. Ho, L. Linden, J. E. Maldonado, and R. K. Wayne. 2007. Phylogeny of the Procyonidae (Mammalia: Carnivora): molecules, morphology and the Great American Interchange. Molecular Phylogenetics and Evolution 43:1076–1095.

Koepfli, K. P., K. A. Deere, G. J. Slater, C. Begg, K. Begg, L. Grassman, M. Lucherini, G. Veron, and R. K. Wayne. 2008. Multigene phylogeny of the Mustelidae: resolving relationships, tempo and biogeographic history of a mammalian adaptive radiation. BMC Biology 6, http://www.biomedcentral.com/1741-7007/6/10.

Krause, J., T. Unger, A. Nocon, A. S. Malaspinas, S. O. Kolokotronis, M. Stiller, L. Soibelzon, et al. 2008. Mitochondrial genomes reveal an explosive radiation of extinct and extant bears near the Miocene-Pliocene boundary. BMC Evolutionary Biology 8, http://www.biomedcentral.com/1471-2148/8/220.

Legendre, P., M. R. T. Dale, M. J. Fortin, J. Gurevitch, M. Hohn, and D. Myers. 2002. The consequences of spatial structure for the design and analysis of ecological field surveys. Ecography 25:601–615.

Lindblad-Toh, K., C. M. Wade, T. S. Mikkelsen, E. K. Karlsson, D. B. Jaffe, M. Kamal, M. Clamp, et al. 2005. Genome sequence, comparative analysis and haplotype structure of the domestic dog. Nature 438:803–819.

Liu, F. G. R., M. M. Miyamoto, N. P. Freire, P. Q. Ong, M. R. Tennant, T. S. Young, and K. F. Gugel. 2001. Molecular and morphological supertrees for eutherien (placental) mammals. Science 291:1786–1789.

Losos, J. B. 2008. Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. Ecology Letters 11:995–1003.

Machac, A., M. Janda, R. R. Dunn, and N. J. Sanders. 2010. Elevational gradients in phylogenetic structure of ant communities reveal the interplay of biotic and abiotic constraints on diversity. Ecography (forthcoming), doi:10.1111/j.1600-0587.2010.06629.x.

Mouillot, D., and K. Gaston. 2009. Spatial overlap enhances geographic range size conservatism. Ecography 32:671–675.

Olson, D. M., E. Dinerstein, E. D. Wikramanayake, N. D. Burgess, G. V. N. Powell, E. C. Underwood, J. A. D'Amico, et al. 2001. Terrestrial ecoregions of the worlds: a new map of life on Earth. BioScience 51:933–938.

Pagel, M. D., R. M. May, and A. R. Collie. 1991. Ecological aspects

of the geographical distribution and diversity of mammalian species. American Naturalist 137:791–815.

Paradis, E., J. Claude, and K. Strimmer. 2004. APE: analyses of phylogenetics and evolution in R language. Bioinformatics 20:289–290.

Patou, M. L., R. Debruyne, A. P. Jennings, A. Zubaid, J. J. Rovie-Ryan, and G. Veron. 2008. Phylogenetic relationships of the Asian palm civets (Hemigalinae & Paradoxurinae, Viverridae, Carnivora). Molecular Phylogenetics and Evolution 47:883–892.

Patou, M. L., P. A. McLenachan, C. G. Morley, A. Couloux, A. P. Jennings, and G. Veron. 2009. Molecular phylogeny of the Herpestidae (Mammalia, Carnivora) with a special emphasis on the Asian *Herpestes*. Molecular Phylogenetics and Evolution 53:69–80.

Pechlakova, E. 2006. Macroecology of the Carnivora: patterns in the geographic ranges with respect to phylogeny. MSc thesis. University of South Bohemia, Ceske Budejovice.

Peterson, A. T., J. Soberon, and V. Sanchez-Cordero. 1999. Conservatism of ecological niches in evolutionary time. Science 285:1265–1267.

Rabosky, D. L., and A. R. McCune. 2010. Reinventing species selection with molecular phylogenies. Trends in Ecology & Evolution 25:68–74.

Ragan, M. A. 1992. Phylogenetic inference based on matrix representation of trees. Molecular Phylogenetics and Evolution 1:53–58.

Rahbek, C., and G. R. Graves. 2001. Multiscale assessment of patterns of avian species richness. Proceedings of the National Academy of Sciences of the USA 98:4534–4539.

Rangel, T., J. A. F. Diniz-Filho, and L. M. Bini. 2006. Towards an integrated computational tool for spatial analysis in macroecology and biogeography. Global Ecology and Biogeography 15:321–327.

R Development Core Team. 2009. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Revell, L. J., L. J. Harmon, and D. C. Collar. 2008. Phylogenetic signal, evolutionary process, and rate. Systematic Biology 57:591–601.

Ricklefs, R. E., and R. E. Latham. 1992. Intercontinental correlation of geographical ranges suggests stasis in ecological traits of relict genera of temperate perennial herbs. American Naturalist 139:1305–1321.

Sato, J. J., M. Wolsan, S. Minami, T. Hosoda, M. H. Sinaga, K.

Hiyama, Y. Yamaguchi, and H. Suzuki. 2009. Deciphering and dating the red panda's ancestry and early adaptive radiation of Musteloidea. Molecular Phylogenetics and Evolution 53:907–922.

Smith, F. D. M., R. M. May, and P. H. Harvey. 1994. Geographical ranges of Australian mammals. Journal of Animal Ecology 63:441–450.

Soberon, J., and M. Nakamura. 2009. Niches and distributional areas: concepts, methods, and assumptions. Proceedings of the National Academy of Sciences of the USA 106:19644–19650.

Stone, L., T. Dayan, and D. Simberloff. 1996. Community-wide assembly patterns unmasked: the importance of species' differing geographical ranges. American Naturalist 148:997–1015.

Swenson, N. G., and B. J. Enquist. 2007. Ecological and evolutionary determinants of a key plant functional trait: wood density and its community-wide variation across latitude and elevation. American Journal of Botany 94:451–459.

Taylor, C. M., and N. J. Gotelli. 1994. The macroecology of *Cyprinella*: correlates of phylogeny, body size, and geographical range. American Naturalist 144:549–569.

ter Braak, C. J. F., and P. Smilauer 2002. CANOCO 4.5 reference manual and CanoDraw for Windows. User's guide to CANOCO for Windows: software for canonical community ordination. Microcomputer Power, Ithaca, NY.

Tucker, C. J., J. E. Pinzon, M. E. Brown, D. A. Slayback, E. W. Pak, R. Mahoney, E. F. Vermote, and N. El Saleous. 2005. An extended AVHRR 8-km NDVI dataset compatible with MODIS and SPOT vegetation NDVI data. International Journal of Remote Sensing 26:4485–4498.

Waldron, A. 2007. Null models of geographic range size evolution reaffirm its heritability. American Naturalist 170:221–231.

Webb, C. O., D. D. Ackerly, and S. W. Kembel. 2008. Phylocom: software for the analysis of phylogenetic community structure and trait evolution. Bioinformatics 24:2098–2100.

Webb, T. J., and K. J. Gaston. 2003. On the heritability of geographic range sizes. American Naturalist 161:553–566.

———. 2005. Heritability of geographic range sizes revisited: a reply to Hunt et al. American Naturalist 1646:136–143.

Wilson, J. B. 1995. Null models for assembly rules: the Jack Horner effect is more insidious than the narcissus effect. Oikos 72:139–144.