# Climate history, human impacts and global body size of Carnivora (Mammalia: Eutheria) at multiple evolutionary scales

ORIGINAL ARTICLE

José Alexandre Felizola Diniz-Filho[1]*, Miguel Ángel Rodríguez[2], Luis Mauricio Bini[1], Miguel Ángel Olalla-Tarraga[3], Marcel Cardillo[3,4], João Carlos Nabout[5], Joaquín Hortal[3] and Bradford A. Hawkins[6]

[1]Departamento de Ecologia, Instituto de Ciências Biológicas, Universidade Federal de Goiás, Goiania, GO, Brazil, [2]Departamento de Ecología, Universidad de Alcalá, Alcalá de Henares, Madrid, Spain, [3]NERC Centre for Population Biology/Division of Biology, Imperial College at Silwood Park, Ascot, UK, [4]Centre for Macroevolution and Macroecology, School of Biology, Australian National University, Canberra, ACT, Australia, [5]Programa de Pós-Graduação em Ciências Ambientais, CIAMB, UFG, Goiânia, GO, Brazil and [6]Department of Ecology and Evolution, University of California, Irvine, CA, USA

## ABSTRACT

**Aim** One of the longest recognized patterns in macroecology, Bergmann's rule, describes the tendency for homeothermic animals to have larger body sizes in cooler climates than their phylogenetic relatives in warmer climates. Here we provide an integrative process-based explanation for Bergmann's rule at the global scale for the mammal order Carnivora.

**Location** Global.

**Methods** Our database comprises the body sizes of 209 species of extant terrestrial Carnivora, which were analysed using phylogenetic autocorrelation and phylogenetic eigenvector regression. The interspecific variation in body size was partitioned into phylogenetic (P) and specific (S) components, and mean P- and S-components across species were correlated with environmental variables and human occupation both globally and for regions glaciated or not during the last Ice Age.

**Results** Three-quarters of the variation in body size can be explained by phylogenetic relationships among species, and the geographical pattern of mean values of the P-component is the opposite of the pattern predicted by Bergmann's rule. Partial regression revealed that at least 43% of global variation in the mean phylogenetic component is explained by current environmental factors. In contrast, the mean S-component of body size shows large positive deviations from ancestors across the Holarctic, and negative deviations in southern South America, the Sahara Desert, and tropical Asia. There is a moderately strong relationship between the human footprint and body size in glaciated regions, explaining 19% of the variance of the mean P-component. The relationship with the human footprint and the P-component is much weaker in the rest of the world, and there is no relationship between human footprint and S-component in any region.

**Main conclusions** Bergmannian clines are stronger at higher latitudes in the Northern Hemisphere because of the continuous alternation of glacial–interglacial cycles throughout the late Pliocene and Pleistocene, which generated increased species turnover, differential colonization and more intense adaptive processes soon after glaciated areas became exposed. Our analyses provide a unified explanation for an adaptive Bergmann's rule within species and for an interspecific trend towards larger body sizes in assemblages resulting from historical changes in climate and contemporary human impacts.

*Correspondence: José Alexandre Felizola Diniz-Filho, Departamento de Ecologia, Instituto de Ciências Biológicas, Universidade Federal de Goiás, Cx.P. 131, 74001-970 Goiania, GO, Brazil.
E-mail: diniz@icb.ufg.br

*Journal of Biogeography*

## INTRODUCTION

The integration of ecology and evolutionary biology within the macroecology research programme (Brown, 1995; Gaston & Blackburn, 2000; Blackburn & Gaston, 2003) is shedding new light on patterns known since the 19th century, especially those related to 'latitudinal' diversity gradients and ecogeographical and evolutionary rules such as Bergmann's rule (Gaston *et al.*, 2008). Bergmann's rule states that, within groups of phylogenetically related homeothermic animals, organisms living in colder climates are generally larger than those living in warmer climates. Many recent papers have discussed the ecological and evolutionary mechanisms that may explain this pattern, both at intraspecific (i.e. across populations) and at interspecific (i.e. across multispecies assemblages) levels (Partridge & Coyne, 1997; Blackburn *et al.*, 1999; Ashton *et al.*, 2000; Freckleton *et al.*, 2003; Meiri & Dayan, 2003; Meiri *et al.*, 2004, 2007; Rodríguez *et al.*, 2006, 2008; Olalla-Tárraga & Rodríguez, 2007; Pincheira-Donoso *et al.*, 2008; Olson *et al.*, 2009).

A common view is that Bergmannian patterns can be generated by adaptive processes operating in a strict Darwinian sense, so that, within populations of species that inhabit cooler environments, large-bodied individuals are favoured owing to their lower surface area-to-volume ratios and, hence, their higher body-heat retention (heat conservation hypothesis), and/or because they metabolize fat stores at lower weight-specific rates and thus may cope better with resource shortages (resource availability hypothesis; e.g. Rodríguez *et al.*, 2006; but see Guillaumet *et al.*, 2008). Thus, assuming that these selective processes drive body size variation within species, interspecific Bergmannian clines would arise because assemblages in cold areas would tend to be composed of large-bodied individuals of each species, and/or of larger species generated by adaptive processes creating new large-bodied taxa in the cooler parts of ancestral species ranges (see also Davies *et al.*, 2007, for potential mechanisms, including biotic interactions). In the latter case, Bergmannian patterns would be associated with positive deviations (increases) from ancestral body sizes expressed independently in different species inhabiting a region.

On the other hand, geographical patterns of body size variation at the interspecific or assembly level (*sensu* Gaston *et al.*, 2008; see also Blackburn & Hawkins, 2004) could also be generated by other processes directly shaping the body size frequency distributions (BSFDs) of assemblages (Blackburn & Hawkins, 2004; Diniz-Filho, 2004; Smith *et al.*, 2004; Olalla-Tárraga *et al.*, 2006; Diniz-Filho *et al.*, 2007; Olalla-Tárraga & Rodríguez, 2007; Ramirez *et al.*, 2008; Rodríguez *et al.*, 2008), in addition to the classical adaptive processes at the population level described above. Under this view, assemblage-level body size patterns could arise from 'species sorting' mechanisms, including selective extinctions and/or contractions or expansions of species geographical ranges.

Species sorting processes may also explain Cope's rule, that is, the trend towards increasing body size within a lineage through evolutionary time (see Alroy, 1998; Demetrius, 2000).

For example, in the cool and less stable climates of the Northern Hemisphere, the adaptive advantages of large body size have potentially triggered the evolution of hypercarnivory (i.e. dietary specialization in which diet is composed of at least 70% flesh; see Van Valkenburgh, 1999, 2007). However, this increase in body size may also lead to high extinction rates and species turnover, which could explain the right-skewed BSFD observed in carnivoran faunas in North America (e.g. Smith *et al.*, 2004; Van Valkenburgh *et al.*, 2004). Thus, this process may shift the BSFD independently of intraspecific adaptive responses to climate, and would be better viewed as cladogenetic mechanisms creating assemblage patterns that result from a life-history threshold related to resource use. Moreover, higher extinction rates biased towards large-bodied species would generate lower mean body sizes for assemblages in the Northern Hemisphere and hence give rise to inverse Bergmannian patterns (see Hunt & Roy, 2006). That is, these mechanisms predict an inverse outcome to that generated by the selective pressures that past climates may have exerted on the body sizes of individual species.

Finally, recent human impacts may also have disrupted the BSFD of faunas by shifting geographical ranges and eliminating some species, especially large-bodied ones, from local assemblages. Therefore, human impact should be considered as an additional explanation for broad-scale patterns in body size. Indeed, recent analyses suggest that extinction risks are predicted by an interaction between intrinsic biological traits and exposure to external effects (such as human occupation; Cardillo *et al.*, 2004, 2005). Large-bodied mammal species (i.e. those with body masses larger than 3 kg) tend to have relatively higher extinction risks owing to their life-history traits, which means that human impacts can alter the BSFD at an assemblage level in a similar way to changes driven by macroevolutionary processes (i.e. they may increase the extinction rates of large-bodied species and generate a right-skewed BSFD). These assemblage-level patterns would be a consequence of the reduction and fragmentation of species geographical ranges that have increased extinction rates at local or regional spatial scales. We might expect to find a disturbed BSFD in highly impacted regions as a result of the selective loss of large-bodied species, especially on the east coast of North America and in Europe (Sanderson *et al.*, 2002; Haberl *et al.*, 2004).

Here we investigate the extent to which these multiple processes can be integrated to explain global geographical patterns in body size of the eutherian mammalian order Carnivora. Specifically, we use phylogenetic comparative methods to decouple geographical variation in species body sizes into within-species and macroevolutionary (interspecific) components that can be explained by recent and past adaptations to environmental conditions, macroevolutionary trends, and patterns generated by modern human impacts. Carnivora are an ideal group for macroecological and macroevolutionary analyses, as their geographical distributions and phylogenetic relationships are well known (Bininda-Emonds *et al.*, 1999; Johnson *et al.*, 2006), and they show large

variation in body sizes and life-history traits (Gittleman, 1985, 1986; Webster *et al.*, 2004; Friscia *et al.*, 2007). Furthermore, they have been extensively studied for intraspecific Bergmannian patterns (Meiri *et al.*, 2004, 2007, 2009) and for macroevolutionary trends in body size (Kelt & Brown, 1998; Van Valkenburgh *et al.*, 2004). Finally, because of their relatively large body size, life-history characteristics and ecological specialization, Carnivora usually have high extinction rates (Werdelin & Lewis, 2005; Leonard, 2007) and may be particularly sensitive to recent human impacts (Cardillo *et al.*, 2004), being thus an important group for biodiversity conservation.

## MATERIALS AND METHODS

### Body size data

Our database comprises the 209 species of extant terrestrial Carnivora that are native to either continental regions (Australia was excluded) or the islands of Baffin, Tierra del Fuego, Great Britain and Sumatra, which we consider large enough and close enough to mainlands that macroecological and macroevolutionary patterns are not affected by island effects (see Meiri *et al.*, 2005) (for a list of all study species see Appendix S1 in Supporting Information). The body size of each species was measured as its $\log_{10}$-transformed mean body mass (in grams) as provided in Meiri *et al.* (2005) and Smith *et al.* (2003). Because we are primarily interested in broad-scale comparative patterns, we did not differentiate between males and females, although some species are sexually dimorphic. Species geographical ranges (extents of occurrence) were obtained from a global database of mammal distributions (Sechrest, 2003; Grenyer *et al.*, 2006), and the presence/absence of each species was mapped onto an equal-area grid (Behrmann global projection) comprising 12,580 cells of $96.5 \times 96.5$ km each (i.e. of about one-degree resolution), which constituted the grain size of our study.

Following the standard approach for analyses of body size at the assemblage level (see Blackburn & Hawkins, 2004; Olalla-Tárraga *et al.*, 2006; Diniz-Filho *et al.*, 2007; Olalla-Tárraga & Rodríguez, 2007; Ramirez *et al.*, 2008; Rodríguez *et al.*, 2008), we generated the variable 'mean body size' by averaging the ($\log_{10}$-transformed) body sizes of the species present in each grid cell. This variable, partitioned into its phylogenetic and specific components (see below), constituted the basis of our interspecific (assemblage) analysis of the spatial variation of body size at the global extent (see Fig. 1). Results from analyses based on medians and means of untransformed body masses are similar because body size is log-normally distributed.

### Environmental predictors

Initially, five environmental variables were generated for each cell in the grid: (1) mean annual temperature (TEMP); (2) annual precipitation (PREC); (3) annual actual evapotranspiration (AET, following Ahn & Tateishi's, 1994, formulation);

(4) the global vegetation index (GVI – an indicator of standing plant biomass obtained from radiometer data from the NOAA polar-orbiting environmental satellites and related to the density and greenness of the plant canopy, total standing biomass, green leaf-area index and percentage vegetation cover); and (5) range in elevation (RELEV – the difference between maximum and minimum elevations within each grid cell, reflecting mesoscale climatic gradients). Details and data sources for these environmental variables are given by Rodríguez *et al.* (2005, 2006, 2008) and Olalla-Tárraga & Rodríguez (2007). These variables can be explicitly linked to hypotheses (see Rodríguez *et al.*, 2006, 2008) previously developed to explain associations between climate and body size, including heat conservation (TEMP), heat dissipation (PREC and AET), resource availability (GVI), and habitat availability (RELEV). However, a principal components analysis on these variables revealed that they could be reduced to two main dimensions, based on the broken-stick distribution of eigenvalues (Jackson, 1993). Because most ecological interpretations for Bergmann's rule are related to temperature (Rodríguez *et al.*, 2006, 2008), we used TEMP and RELEV to express the main directions of variation in the data (see Table S1 in Appendix S2).

To examine anthropogenic-driven disruptions of geographical ranges that may also have affected body size frequency distributions at the assemblage scale (see Cardillo *et al.*, 2004, 2005), we included human footprint (HUMANS) as an explanatory variable. This variable consisted of cell averages of the biome-normalized footprint values generated by Sanderson *et al.* (2002) at 1-km resolution by combining global records of population density, land use, transport access (roads, rivers, etc.) and electrical power infrastructure (data available at http://www.ciesin.columbia.edu/wild_areas/; accessed October 2008).

We hypothesized that mean body size gradients would be stronger in the Northern Hemisphere because of greater climatic instability throughout the late Pliocene and Pleistocene (e.g. Araújo *et al.*, 2008). Thus, we partitioned the global dataset according to the stability of temperatures since the Last Glacial Maximum (LGM), which we calculated as the difference between current mean annual temperatures and those of 21,000 years ago as estimated by the ECHAM3 palaeoclimatic model (see Araújo *et al.*, 2008; Braconnot *et al.*, 2007; and http://pmip.lsce.ipsl.fr). Before temperature stability was calculated, original palaeo-temperature data were downscaled to the 96.5-km resolution used herein using a mean-mobile technique to generate a continuous downscaled temperature surface from the centroids of the original surface, ensuring that the main geographical trends in temperature were retained in the downscaled data. Temperature stability was subjected to a *K*-means non-hierarchical clustering (Legendre & Legendre, 1998) that generated a two-cluster solution encapsulating both the dramatic environmental changes experienced in the north since the LGM ($n = 2249$ cells) and the relatively greater climatic stability of the rest of the world ($n = 10,324$ cells). For simplicity, we refer to these groups of cells found by *K*-means clustering as GLACIATED and NON-GLACIATED regions.
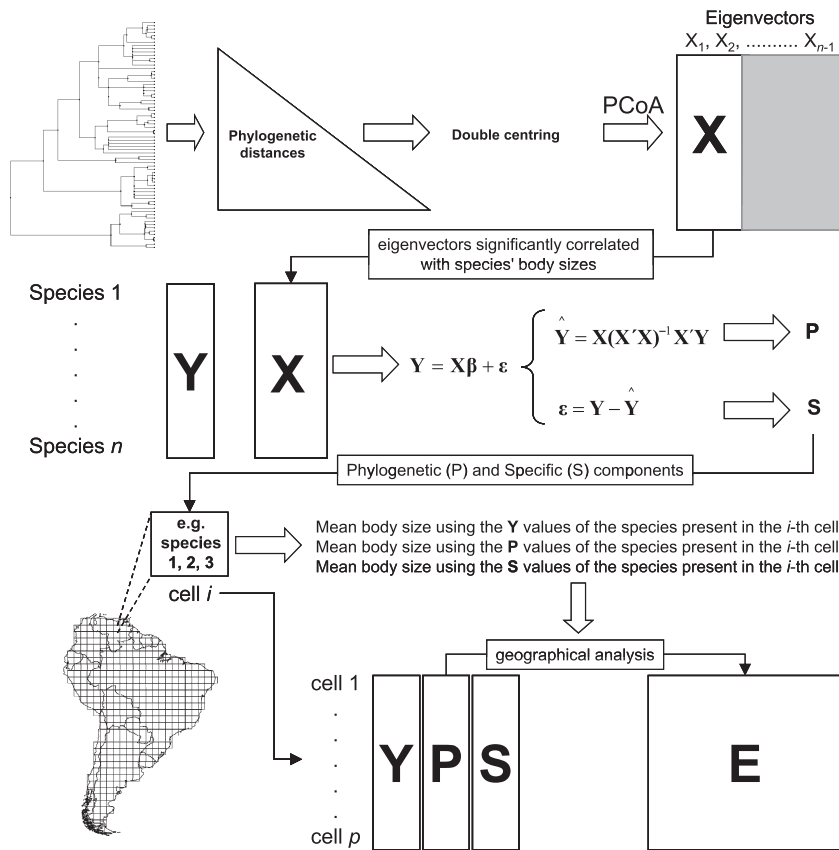
**Figure 1** Representation of the approach used to map body size components of 209 species of Carnivora. The first part of the figure shows the procedures involved in the phylogenetic eigenvector regression (PVR): (1) back-transform the phylogeny into a phylogenetic distance matrix; and (2) double-centre this matrix and compute a principal coordinates analysis (PCoA). The transition between the first and second parts illustrates how the eigenvectors were selected. The second part shows how phylogenetic (**P**) and specific (**S**) components were estimated: (1) run a multiple linear regression between body size (matrix **Y**) and the selected eigenvectors (**X**); and (2) save the estimated values and residuals, as they represent the phylogenetic (**P**) and specific (**S**) components, respectively. These values (in addition to original body size) are used to estimate means per cell. Then, as indicated in the last part, the vectors containing different components of body size are regressed against environmental factors (**E**) in an explicit spatial context.

Finally, we divided the 209 species into two body size classes, distinguishing species weighing less or more than 3 kg, a size-threshold above which extinction risk has been predicted to increase sharply owing to intrinsic and extrinsic factors (Cardillo *et al.*, 2005). We calculated for each cell in our global grid the species richness of large-bodied (> 3 kg) and small-bodied (< 3 kg) species and correlated the richness patterns with the human footprint.

## Phylogenetic comparative analyses

Phylogenetic patterns in species body sizes were initially evaluated using Moran's *I* coefficients (Gittleman & Kot, 1990; Gittleman *et al.*, 1996; Diniz-Filho, 2001; Pavoine *et al.*, 2008), given by

$$I = \left(\frac{n}{S}\right) \left[ \frac{\sum_i \sum_j (y_i - \bar{y})(y_j - \bar{y}) \, w_{ij}}{\sum_i (y_i - \bar{y})^2} \right],$$

where $n$ is the number of species, $y_i$ and $y_j$ are body size values for species i and j, $\bar{y}$ is the average body size across all species

and $w_{ij}$ is an element of the matrix **W**. In matrix **W**, $w_{ij}$ elements are equal to 1 for all i, j species pairs within a given phylogenetic distance interval, and to 0 otherwise. $S$ indicates the number of pairs of species connected in the **W** matrix. The value expected under the null hypothesis of the absence of a phylogenetic autocorrelation is $-1/(n-1)$, and the statistical significance can be established under a normal approximation (Legendre & Legendre, 1998) or using randomization (Manly, 1998). High positive Moran's *I* coefficients indicate that species separated by a given distance in the phylogeny are similar for the trait under study, whereas high negative values indicate that species pairs are dissimilar. Moran's *I* coefficients were calculated for eight distance classes, connecting in the matrix **W** pairs of species situated at increasing intervals of *c.* 5 Myr. Thus, a series of Moran's *I* coefficients is obtained, which when plotted against phylogenetic distances generates a correlogram. The **W** matrices were obtained by deconstructing a pairwise patristic distance matrix derived from the Carnivora supertree (Bininda-Emonds *et al.*, 1999). Although other phylogenies for some particular groups of Carnivora are available (e.g. Johnson

*et al.*, 2006), we use the Bininda-Emonds *et al.* (1999) supertree because it provides a complete phylogeny of species. Moreover, incorporating these new phylogenies would require creating a new supertree, which is beyond the scope of this paper. We believe that the effects of any inaccuracies in this supertree on our results are minimal. Indeed, recent phylogenetic autocorrelation analyses of body size variation based on the new molecular phylogeny of felids (Johnson *et al.*, 2006) and the supertree (Bininda-Emonds *et al.*, 1999) gave almost identical results (Diniz-Filho & Nabout, 2009).

Once phylogenetic patterns in body size are described using phylogenetic autocorrelation (Moran's *I*), it is possible to use linear models to partition the total variation (T) of a trait (i.e. body size in this case) into (1) a phylogenetic component (P), which expresses the expected species trait values if current values are entirely determined by the value in all species weighted by their phylogenetic relationships, and (2) a unique, or specific, component (S), which expresses deviations from the phylogenetic expectation arising from measurement error and the independent evolution of each species after speciation events (see Cheverud *et al.*, 1985; Gittleman & Kot, 1990; Gittleman & Luh, 1992; Fig. 1). Although the interpretation of evolutionary mechanisms underlying these two components remains controversial (see Westoby *et al.*, 1995; Desdevises *et al.*, 2003), they can be useful for disentangling patterns shared by all species in a clade (the P-component) and independent patterns of each species (the S-component). Moreover, any correlation between the S-components of different traits is a good estimate of the 'input' correlation (*sensu* Martins & Garland, 1991), which is the correlation between simultaneous changes of two traits at each time-step of a phylogeny. This is indeed the correlation estimated by all phylogenetic comparative methods, including Felsenstein's (1985) independent contrasts method (see Martins *et al.*, 2002, and Diniz-Filho & Tôrres, 2002, for a comparative evaluation of the statistical performance of different methods in estimating this parameter under alternative evolutionary models).

The partitioning of T into P- and S-components can be done using a range of statistical techniques, including autoregressive models (Cheverud *et al.*, 1985; Gittleman & Kot, 1990) or mixed models (Lynch, 1991). Here we use phylogenetic eigenvector regression (PVR) (Diniz-Filho *et al.*, 1998), which uses a principal coordinates analysis (PCoA) (see Legendre & Legendre, 1998) to describe the phylogenetic structure among taxa by a set of eigenvectors (**X**) extracted from a matrix of pairwise phylogenetic distances among species (Fig. 1). Formally, the response variable **Y** (body size) is regressed against the phylogenetic structure following the model

$$\mathbf{Y} = \mathbf{X}\boldsymbol{\beta} + \boldsymbol{\varepsilon},$$

where **X** is the matrix with eigenvectors and $\boldsymbol{\beta}$ are the regression coefficients of each eigenvector on **Y**, so that $\mathbf{X}\boldsymbol{\beta}$ corresponds to the P-component (the **Y**-values estimated by the PVR model) and the model residuals $\boldsymbol{\varepsilon}$ correspond to the S-component. The coefficient of determination ($R^2$) of this linear model measures the amount of variation in body size explained by the phylogeny (phylogenetic inertia, or signal; Diniz-Filho *et al.*, 1998, 2007; see also Freckleton *et al.*, 2002). Finally, a phylogenetic correlogram was used to test the assumption that phylogenetic effects were not present in the model residuals, as suggested by Gittleman & Kot (1990).

PVR is part of a family of eigenvector-based techniques whose main purpose is to describe spatial (Borcard & Legendre, 2002; Griffith, 2003; Borcard *et al.*, 2004; Diniz-Filho & Bini, 2005; Griffith & Peres-Neto, 2006) or phylogenetic (Diniz-Filho *et al.*, 1998; Desdevises *et al.*, 2003) patterns. In terms of phylogenetic distances, each eigenvector numerically expresses groups of species that are similar at distinct phylogenetic levels, and the first eigenvectors tend to describe variation among deeper nodes of the phylogeny. Successive increases in the number of eigenvectors tend to better approximate the relationship among species, and this can be evaluated by a matrix correlation between the original phylogenetic distances and pairwise distances in the reduced eigenvector space. The advantage of this approach, however, is that the phylogenetic relationships are now expressed by a set of eigenvectors (and not as pairwise distances) that can be used directly in any form of linear or non-linear model (e.g. see Legendre *et al.*, 2005, for a similar reasoning in community ecology).

We performed the PCoA by extracting eigenvalues and eigenvectors from the double-centred (see Legendre & Legendre, 1998; Desdevises *et al.*, 2003) phylogenetic distance matrix derived from the Carnivora supertree (Bininda-Emonds *et al.*, 1999). We used for further modelling those eigenvectors with significant correlations ($P < 0.01$) with species body sizes (Griffith, 2003; see Table S2 in Appendix S2). The values estimated by a multiple regression analysis of body size against these eigenvectors represent the vector with the phylogenetic components (P), whereas the residuals of this regression model give the vector with the specific components (S) (see Fig. 1).

The interpretation of the S-component as reflecting unique components of species variation independently of trait values in other species is analogous to evaluating the departure of trait values in each species from its ancestral states. This was explicitly verified by correlating the S-component with the size change index (SCI) of Webster *et al.* (2004) for 117 species common to both studies. This index was derived by modelling ancestral body sizes across the Carnivora phylogeny and by directly comparing evolution from the most recent common ancestor (MRCA) and extant species. Moreover, published measures of the intraspecific form of Bergmann's rule for 42 species (i.e. the correlations between body size and latitude provided in Meiri *et al.*, 2004, 2007) were correlated with the S-component values of PVR that we obtained for these species. [Note that Meiri *et al.* (2004, 2007) used latitude to approximate Bergmann's rule, and this may be problematic when dealing with regions in which latitude is not a good surrogate for temperature. Even so, this may be a reasonable general proxy for intraspecific Bergmann gradients in the group.]

Based on the phylogeny, we also computed the age of the root from each species to its MRCA with other living species, and calculated a mean age for each cell. We randomized species MRCA values to generate a null distribution of these values within each cell, and then analysed the deviation between observed and null MRCA values, to establish if, on average, species in a given cell are younger than expected by a random association of species (see Greve *et al.*, 2008).

## Geographical analyses

As for the case of mean body size, we also calculated the mean values of P and S in each cell (Diniz-Filho *et al.*, 2007; see also Fig. 1), and regressed each of these new variables against the set of environmental predictors (TEMP, RELEV and human footprint). Because relationships of both mean P- and mean S-values with TEMP were curvilinear at the global scale, we introduced a squared term of TEMP in the global models.

We also partitioned the effects of these environmental predictors and human footprint on body size components (i.e. mean P and mean S) using a series of partial regressions based on the adjusted $R^2$ (Legendre & Legendre, 1998). The relative strengths of the predictor variables were assessed according to their mean standardized regression coefficient in the full models. These coefficients were generated as weighted averages (we used the Akaike weight index as the weighting variable; see Burnham & Anderson, 2002) of the coefficients of all possible models that can be obtained with the analysed predictors. This procedure tends to avoid problems in finding minimum adequate models because of high levels of uncertainty in predictor choice (Diniz-Filho *et al.*, 2008). Because of the large number of cells, even within regions, it is difficult to deal with statistical inaccuracies caused by spatial autocorrelation in the analysis of environmental drivers of body size patterns. Although problems due to autocorrelation in establishing Type I errors are well known (Legendre & Legendre, 1998), unbiased estimates of regression coefficients are obtained at very large sample sizes, and thus the relative importance of predictors can be safely established by ordinary least squares (OLS), especially when uncertainty is reduced by using model averaging (see Diniz-Filho *et al.*, 2008; see also Hawkins *et al.*, 2007).

All geographical analyses were performed for the global data and for data divided into GLACIATED and NON-GLACIATED regions. All analyses were performed in SAM 3.0 (Rangel *et al.*, 2006), freely available at http://www.ecoevol.ufg.br/sam.

## RESULTS

### Phylogenetic patterns in body size

The Moran's I correlogram for species body sizes shows that closely related species are very similar ($I = 0.988$), and this similarity tends to decrease with time, stabilizing after *c.* 20 Myr (Fig. 2). Thus, there is a strong phylogenetic signal in the data, and a large proportion of the variation in Carnivora body size ($R^2 = 78.2\%$) can be explained by the PVR model.
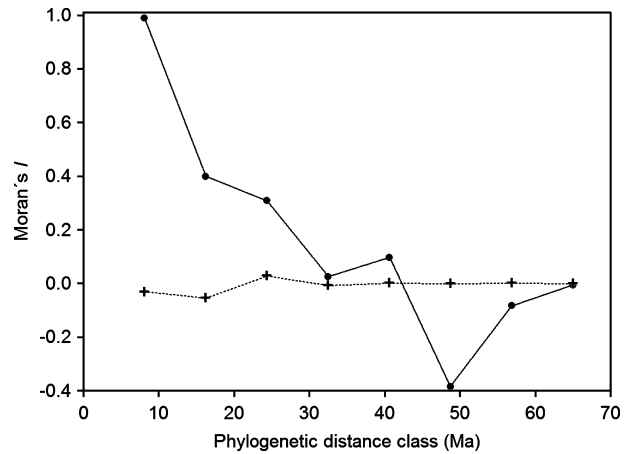


**Figure 2** Phylogenetic correlograms built with Moran's I coefficients for the body size of 209 Carnivora species (solid circles) based on Bininda-Emonds *et al.*'s (1999) supertree and for the residuals of the phylogenetic eigenvector regression (PVR) model (crosses).

The phylogenetic structure was expressed by 21 eigenvectors extracted from the phylogenetic distances that are significantly correlated with body size (see Table S2 in Appendix S2). The pairwise similarity between species in this reduced dimensional space formed by the 21 eigenvectors was strongly correlated ($r = 0.992$) with the original phylogenetic distances, so there was almost no loss of phylogenetic information during the eigenanalysis.

The residual variation of the PVR constitutes the specific (S) component and expresses the amount of body size evolution that cannot be predicted by phylogenetic relationships, plus measurement error of species traits. More importantly, Moran's I coefficients for the S-component were not statistically significant and, therefore, this component can be interpreted as phylogenetically independent body size variation among species (Fig. 2).

The interpretation of the S-component as indicating unique species variation independently of other species is supported by the high correlation between S-component values and the size change index generated by Webster *et al.* (2004) for 117 species ($r = 0.76$; $P \ll 0.001$; Fig. 3). Confirming the findings of Freckleton *et al.* (2003), there was no significant relationship between the published intraspecific Bergmann's rule strengths for 42 species (Meiri *et al.*, 2004, 2007) and species body size values (T variation; $r = 0.23$; $P = 0.135$; Fig. 4a). However, there was a low but statistically significant correlation between S-component values and the intraspecific Bergmann's rule ($r = 0.30$; $P = 0.047$; Fig. 4b). This indicates that intraspecific geographical variation in body size consistent with Bergmann's rule tends to emerge when a species deviates significantly from its ancestral body size.

### Geographical patterns in mean body size

Maps for mean body size (Fig. 5a) and its mean P-component (Fig. 5b) are very similar across the world, and the correlation
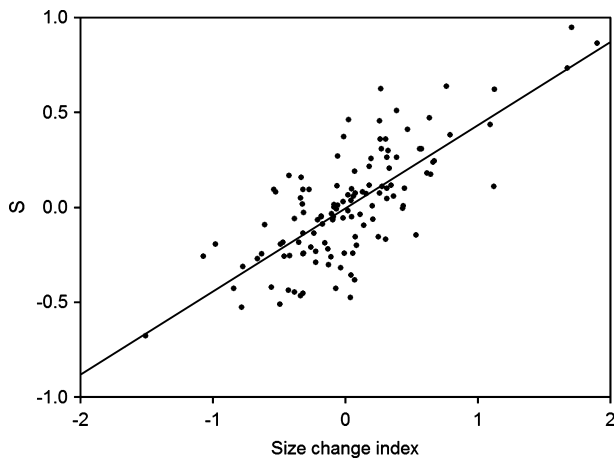
**Figure 3** Correlation between S (from phylogenetic eigenvector regression) and Webster *et al.*'s (2004) size change index (SCI), for 117 species of Carnivora common to this study and Webster *et al.*'s (2004) ($r = 0.76$; $P < 0.001$).

between the two variables is very high ($r = 0.902$), which was expected given the strong phylogenetic signal detected by PVR and Moran's *I* coefficients. On average, large-bodied species tend to occur in the tropics, and smaller species in temperate regions (see Fig. 5a). Partial regressions revealed that *c.* 43% of the global variation in the mean phylogenetic component is explained by the combination of current environmental factors, with high positive standardized regression coefficients for both temperature (including a squared term) and range in elevation, a surrogate for mesoscale climatic gradients (Table 1).

In contrast, the mean S-component of body size (Fig. 5c) shows large positive deviations from ancestors across the Holarctic and in northern sub-Saharan Africa, and negative deviations in southern South America, the Sahara Desert, and tropical Asia. In addition, although the explanatory power of the environmental model for this component is relatively low at the global scale (*c.* 13%), the coefficient for temperature is negative (Table 1), as expected under climatically driven adaptive processes generating Bergmannian gradients within lineages (Diniz-Filho *et al.*, 2007).

The patterns differed when glaciated and non-glaciated regions were analysed separately. The proportion of the variance in the mean S-component explained by our environmental predictors was 39% in the glaciated regions but only 5% in non-glaciated regions, with the highest regression coefficients corresponding to temperature and having a negative sign in both cases (Table 1). The comparison of mean MRCA values between glaciated and non-glaciated areas (Fig. 6) shows that, in glaciated regions, species tend to be younger than expected by chance, as would be expected if there had been more faunal turnover.

The influence of climate independent of human effects in the phylogenetic (mean P) component is much lower in glaciated (6%) than in non-glaciated (31%) areas, and this component is positively related to temperature in both regions
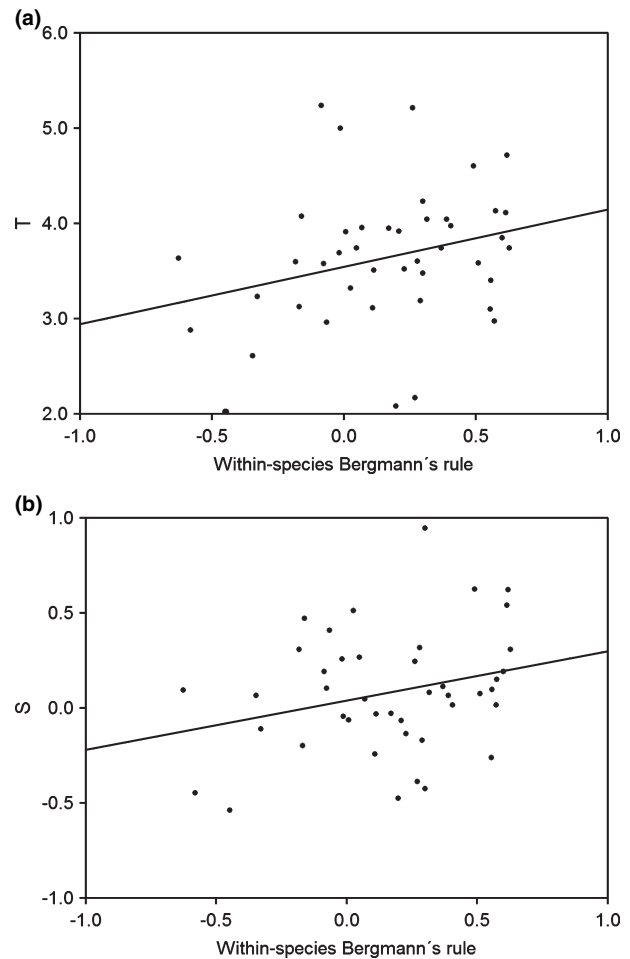


**Figure 4** Relationships between within-species Bergmann's rule (*r* from Meiri *et al.*, 2004) and (a) total variation (T) and (b) specific (S) components from phylogenetic eigenvector regression (PVR), for 42 species of Carnivora common to this study and Meiri *et al.*'s (2004). The correlation with the T-component is not significant ($r = 0.23$; $P = 0.135$), but that with the S-component is ($r = 0.30$; $P = 0.047$).

(see Table 1). This can be interpreted as indicating stronger environmentally driven selection of lineages in areas unaffected by glaciation. However, it should also be noted that the regression coefficients of the model for the phylogenetic component reveal a stronger and negative impact of human footprint in glaciated regions (see Table 1), which may have influenced our ability to identify the signal left by environmental selection on the lineages. Indeed, partial regressions suggest that this may well be the case, as they showed that shared effects between human footprint and climate described nearly half (20%) of the total variance explained by the model (46%). This is consistent with the strong correlation between temperature and the human footprint ($r = 0.787$ in glaciated regions, as compared with a much lower correlation in non-glaciated areas: $r = 0.158$), and it may explain why temperature, being negatively correlated with the mean phylogenetic component in glaciated areas ($r = -0.457$), had a positive
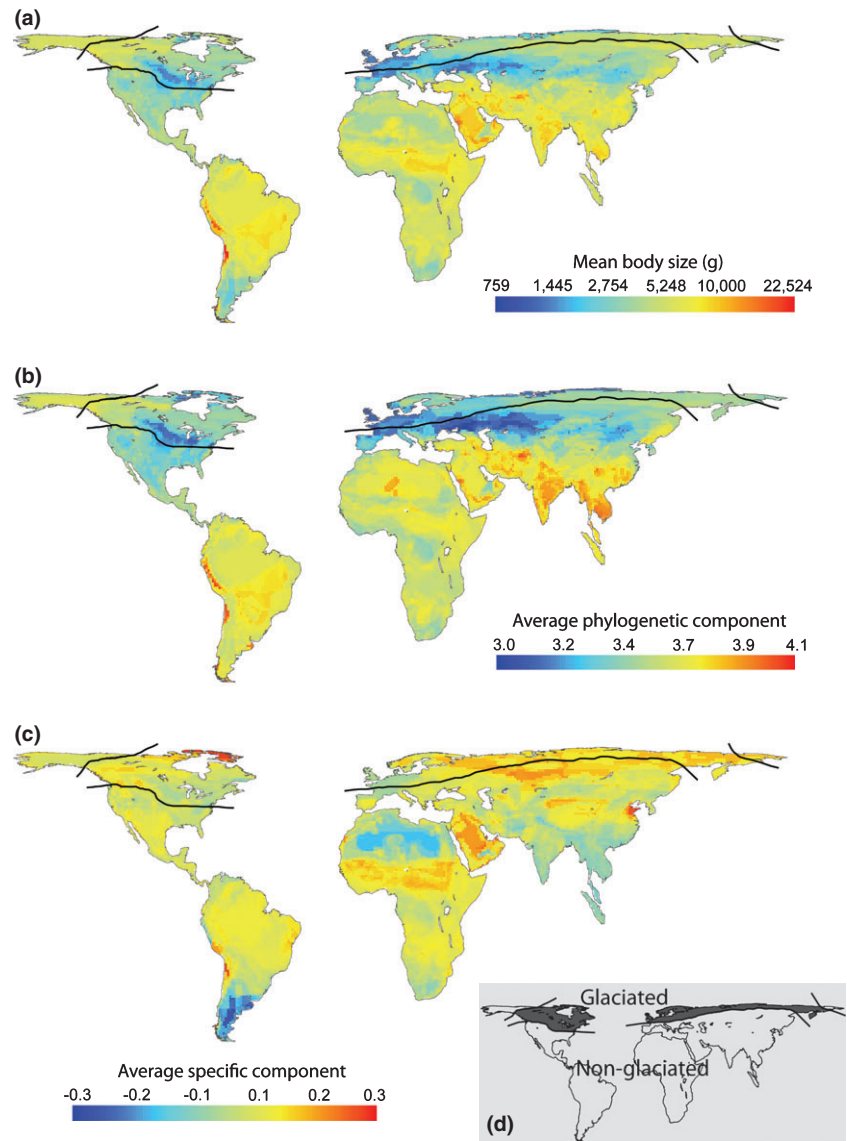
**Figure 5** Geographical patterns of (a) mean body size and its (b) phylogenetic and (c) specific (S) components for the 209 extant species of terrestrial Carnivora native to continental regions or the large islands of Baffin, Tierra del Fuego, Great Britain and Sumatra. The insert (d) shows the glaciated and non-glaciated regions considered in the analyses.

coefficient in the multiple regression. Moreover, these results are consistent with temperature-driven selective processes of the lineages giving rise to Bergmannian patterns in the glaciated areas.

Although most of the variation of the mean P-component in glaciated areas is explained by independent and overlapping effects of the human footprint and climate, the effects of the human footprint on this component are much weaker in the rest of the world, as is the relationship of the human footprint and the S-component, regardless of the area (Table 1). A deconstructive approach of species richness provides a better visualization of the relationship between body size patterns and human occupation. Species richness for Carnivora weighing less or more than 3 kg is positively correlated with the human footprint both globally ($r = 0.276$ and $0.191$, respectively) and non-glaciated areas ($r = 0.225$ and $0.198$). However, for glaciated regions, although the human footprint is more strongly positively correlated with the richness of small

species ($r = 0.552$), the correlation with the richness of larger species is negative ($r = -0.223$). This suggests that dense human occupation in previously glaciated areas promotes the presence of small-bodied species while it limits the presence of larger species (Fig. 7).

## DISCUSSION

### Global geographical patterns in assemblages

As found in many studies, across-lineage body size variation in terrestrial Carnivora is strongly phylogenetically conserved (Gittleman *et al.*, 1996; Diniz-Filho & Tôrres, 2002; Freckleton & Jetz, 2009). Consequently, maps of mean body size and mean P-component are quite similar, showing that, on average, large-bodied assemblages occur in the tropics and small-bodied assemblages occupy temperate regions (see Fig. 5). Although a recent study by Olson *et al.* (2009)

**Table 1** Adjusted coefficients of determination of climatic variables and human footprint (HUMANS) predicting values of phylogenetic (P) and specific (S) components from phylogenetic eigenvector regression (PVR) analysis for 209 Carnivora species, and partition of their independent and overlapped effects by partial regression, for global data and for glaciated and unglaciated regions. Climatic variables used were mean annual temperature (TEMP) and range in elevation (RELEV), given as the difference between maximum and minimum elevations within each grid cell and reflecting mesoscale climatic gradients.

| Dataset | Component | $R^2$ | Partial $R^2$ | | | Standardized regression coefficients | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | Climate | Shared (Climate + HUMANS) | HUMANS | TEMP | TEMP$^2$ | RELEV | HUMANS |
| Global | P | 0.435 | 0.434 | −0.019 | 0.020 | 0.191 | 0.499 | 0.37 | −0.162 |
| | S | 0.127 | 0.116 | 0.004 | 0.007 | −0.646 | 0.414 | −0.14 | 0.100 |
| Glaciated | P | 0.455 | 0.059 | 0.203 | 0.193 | 0.172 | – | 0.247 | −0.712 |
| | S | 0.386 | 0.137 | 0.249 | 0.000 | −0.615 | – | −0.011 | −0.025 |
| Unglaciated | P | 0.308 | 0.307 | −0.025 | 0.026 | 0.599 | – | 0.341 | −0.167 |
| | S | 0.046 | 0.045 | −0.005 | 0.006 | −0.203 | – | −0.188 | 0.076 |
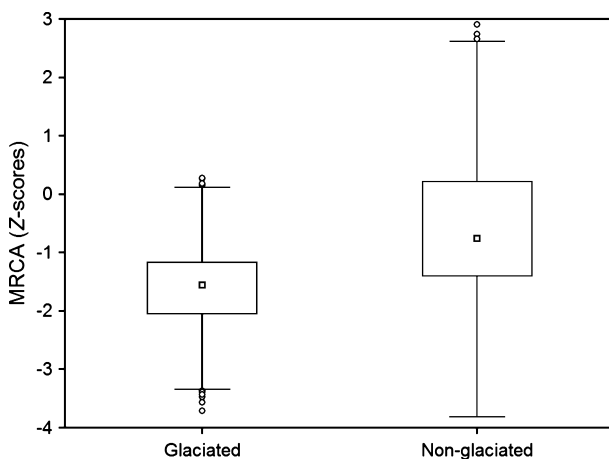


**Figure 6** Box-plot of most recent common ancestor (MRCA) values derived from the Carnivora supertree, expressed as *Z*-deviations from a null distribution within cells of glaciated ($n$ = 2256 cells) and non-glaciated ($n$ = 10,324 cells) regions of the world (see Fig. 5).

supported Bergmann's rule for birds globally, our findings on Carnivora body size variation are counter to Bergmann's rule. This inverted pattern was also observed for non-volant New World mammals by Rodríguez *et al.* (2008). This is certainly the main pattern emerging from our analyses. We also found a strong phylogenetic basis for BSFD changes at the faunal level, in agreement with the proposition that temperature-driven Bergmannian trends may occur within cold regions but not across the entire globe (Rodríguez *et al.*, 2006; see also Blackburn & Hawkins, 2004). As described below, understanding these global patterns thus requires integrating arguments involving adaptation to past and recent climates, selective species extinctions, and variable species turnover rates in different parts of the world.

A potential explanation for this inverse pattern uses the logic of the macroevolutionary models developed to explain the evolution of body size for North American species, which have been based on a life-history threshold that results in high extinction rates in large-bodied species (generating a higher relative diversification rate in small-bodied species; Van Valkenburgh *et al.*, 2004; see also Carbone *et al.*, 1999; Carbone & Gittleman, 2002). We can hypothesize that trends towards larger body sizes related to Bergmannian adaptation to cooler environments (expressed in the S-component) and the evolution of hypercarnivory have generated a higher turnover of species and higher taxa through time in these climatically unstable northern areas (Alroy, 1998; Kelt & Brown,1998; see also Fig. 5). Because both a higher turnover of large-bodied species and greater diversification rates of small-bodied species would tend to generate lower mean body sizes across assemblages, they can explain the smaller average body size of the species pools in colder regions, and, hence, converse Bergmann trends at the global scale. This interpretation is supported by the comparison of mean MRCA values of glaciated and non-glaciated areas (see Fig. 6), which shows that species tend to be younger in glaciated regions than expected by chance: this is consistent with there having been more faunal turnover.

Within colder regions, long-term adaptation to changing (generally cooling) environments and niche conservatism may have initially triggered the evolution of past larger body sizes in ancestral species, with other taxa subsequently diversifying from them. Under a niche conservatism model (see Wiens & Donoghue, 2004; Diniz-Filho *et al.*, 2007; Losos, 2008), these new taxa would have continued being large-bodied. That is, contemporary mean body size patterns can be interpreted both as a consequence of adaptive changes tracking climatic events in the past and, to a large extent, as a consequence of phylogenetic inertia in body size and niche conservatism after past adaptation (Diniz-Filho & Bini, 2008). If this occurred during the progressive cooling of the late Cenozoic and the Pleistocene in the northern parts of the world, it would have generated a gradient of selective advantage for large body sizes, thus establishing a potential link between Cope's and Bergmann's rules (Hunt & Roy, 2006).

Despite the fact that no relationship was found between the P-component and the human footprint (see below), it is important to note that the footprint reflects current patterns of interference on faunal patterns and not historical ones. Past
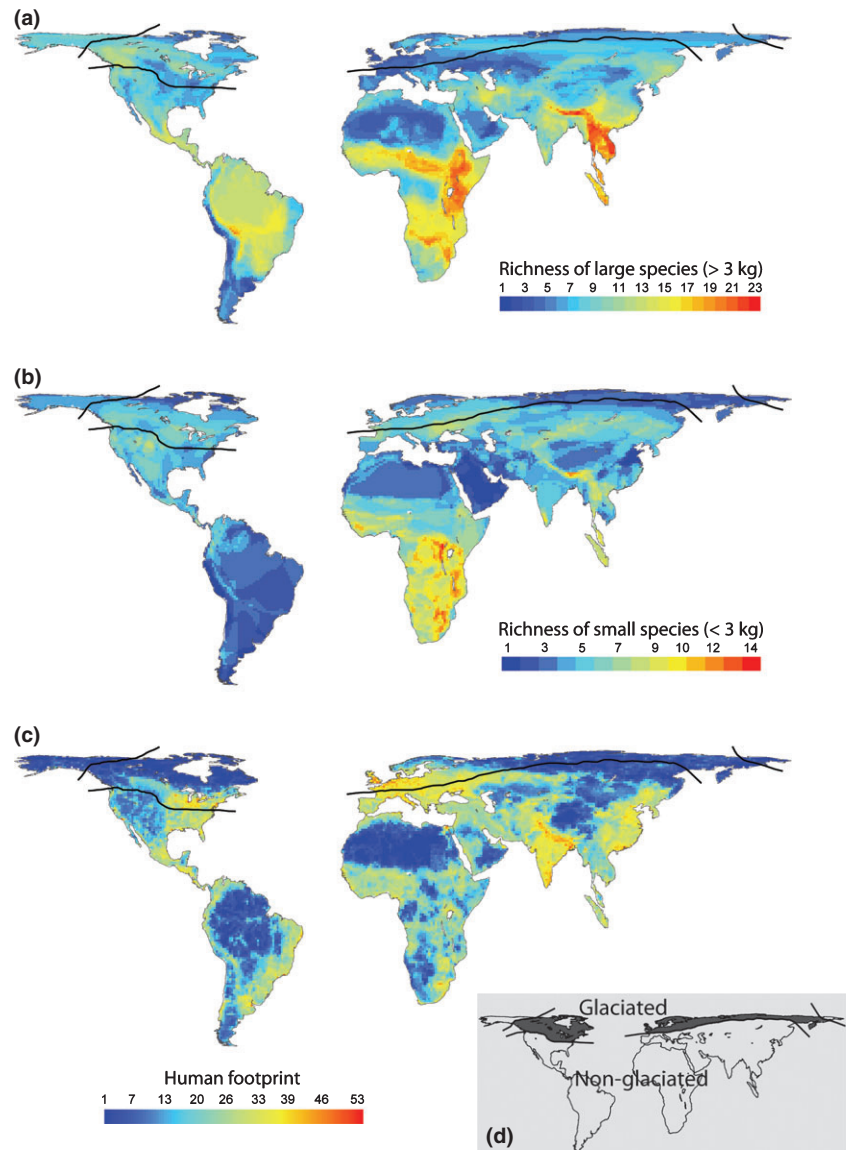
**Figure 7** Spatial patterns of species richness of (a) large-bodied carnivore species (> 3 kg; $n = 108$ species), (b) small-bodied carnivore species (< 3 kg; $n = 101$ species), and (c) the human footprint. The insert (d) shows the glaciated and non-glaciated regions considered in the analyses.

megafaunal extinctions may have been more intense in northern parts of the world, in Europe and North America (as well as in Australia), but there is evidence for anthropogenically driven extinction events in the Pleistocene mammal megafauna in different regions of the world (Martin, 1984; Alroy, 2001; Lyons *et al.*, 2004; but see de Vivo & Carmignotto, 2004). Furthermore, the persistence of large mammals in Africa and southern Asia suggests a weaker effect of human-caused Pleistocene extinctions in these regions, usually attributed to a longer co-existence of humans and these faunas (Nieto *et al.*, 2005; Leonard, 2007). The survival of these large mammals has often been explained either as a result of a long co-evolutionary history with humans and the consequent development of anti-predatory behaviour (Martin, 1984), or by modification in vegetation cover (increases of open savanna) in response to climate change during the Holocene (Cristoffer & Peres, 2003; de Vivo & Carmignotto, 2004). Whether or not these explanations hold remains to be seen,

but, if large-bodied animals have experienced lower levels of Pleistocene extinction in the tropics, this purely historical event could explain in part why both mean body size and its P-component increase towards warmer areas, although this would not necessarily explain the large differences in the observed MRCA values (which are better explained by the previously described faunal turnover and macroevolutionary patterns).

On the other hand, the map for the mean S-component of body size differs substantially from the patterns found globally for both mean body size and the mean P-component. This component expresses the average amount of anagenetic evolution of body size independently of ancestral values (see Fig. 3). The explanatory power of the environmental model for this component is relatively low at the global scale, reinforcing the overall conclusions of Meiri *et al.* (2004) that Carnivora do not provide strong evidence for Bergmann's rule. Even so, it is important to note that, globally, the regression coefficient for

temperature is negative and relatively high (Table 1), indicating that in colder regions species tend to be larger than expected by phylogenetic expectations (i.e. they have positive S-components, indicating an increase with respect to ancestral species). This can be expected under adaptive processes generating Bergmannian gradients within lineages. However, the pattern is not globally consistent because in cooler regions of southern South America species are smaller than expected based on the body size of their ancestors.

## Contrasting glaciated and non-glaciated regions

The comparison between glaciated and non-glaciated regions revealed interesting patterns that could not be perceived in the global analysis. For the P-component, most of the variation in glaciated regions is explained by the human footprint and its overlap with climate, so that cooler regions with less dense human occupation still harbour Carnivora assemblages with larger mean body sizes (see below). In contrast, the P-component for the non-glaciated regions, which cover most of the world, follows the inverse Bergmannian pattern observed at the global scale, which can be interpreted as reflecting less faunal turnover in these areas, as previously discussed.

Although global patterns in body size do not follow Bergmann's rule, and adaptation detected at this scale for the S-component is relatively weak, if we focus on the cooler regions of the world (see Fig. 5c) and, particularly, on the glaciated regions, the rule does apply in an adaptive sense, and the S-component increases northwards and is negatively correlated with temperature. Indeed, 39% of the variation in the mean S-component is explained by the environmental variables in glaciated regions, against < 5% in the non-glaciated ones. In both areas, but especially in the glaciated north, the data indicate that, within each species, average deviations from ancestral body sizes are negatively associated with temperature, and thus can be interpreted as an adaptive process generating intraspecific Bergmannian gradients. Coupled with the correlation between the S-component and the independently measured intraspecific Bergmann's rule strengths (see Fig. 4), this supports an adaptive interpretation for these gradients, although the overall amount of explanation with respect to total body size variation is relatively small.

## Recent human impacts

Multiple mechanisms can affect the BSFD across geographical and taxonomic scales. However, an important aspect of our analysis for the glaciated regions is that it suggests a strong effect of the human footprint on body size, explaining independently almost 20% of the variance of the mean P-component (Table 1). The effect of the human footprint on the P-component is much less important in the rest of the world, as is the association between the human footprint and the S-component, regardless of the area. This would be expected if human effects were causing a phylogenetically autocorrelated pattern of extinctions, probably as a result of

phylogenetic patterns in ecological and life-history traits that are related to extinction risk (see Purvis *et al.*, 2000).

Human impacts affect assemblage patterns by disrupting the BSFD but not the unique (S) component of species body size, thus creating more asymmetry in the statistical distribution of body sizes. Biased extinctions of large-bodied species caused by humans happened recently in both Europe and North America (Leonard, 2007), and have begun to impoverish the fauna in many parts of the world. Carnivores may be particularly sensitive to human impacts (Cardillo *et al.*, 2004) because of their life-history traits, and this sensitivity will be greater in large-bodied species owing to allometric scaling of these traits (Cardillo *et al.*, 2006). More specifically, it has been found that intrinsic factors predict greater extinction risk in species weighing more than 3 kg, and, above this size, susceptibility to both intrinsic and external threats (such as those caused by human occupation) increases sharply. The non-additive effects of intrinsic and extrinsic factors are also supported by our analyses for previously glaciated areas, as we found that, although intense human occupation is positively associated with the richness of Carnivora species weighing < 3 kg, it is negatively associated with that of larger species (see Fig. 7).

## CONCLUSIONS

Our analyses indicate that global patterns in body size must be understood as resulting from a geographically structured combination of evolutionary processes operating across multiple spatio-temporal scales. The relationship between environmental predictors and the phylogenetic expectation of body size suggests a connection between Bergmann's and Cope's rules, driving body size evolution. Recent human impacts were detected at the assemblage level mainly for temperate North America and Europe, and thus our analyses indicate that humans can modify the BSFD of entire faunas rapidly within ecological time-scales through anthropogenic extinction events. How the extirpation of large-bodied species in faunas with little or no ecological redundancy (owing to the low number of species) will affect food-webs and ecosystem functioning remains a speculative issue, but it is undoubtedly a theme that deserves further attention. On the other hand, adaptive processes within species, related to climatic variation, could also be detected for the northern part of the world. Thus, the multiple explanations for global body size gradients in Carnivora, based on human impacts and climate changes, highlight the need for a broad understanding of evolutionary mechanisms acting at different scales and of their association with biogeographical dynamics and contingencies in the history of the Earth.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** List of the 209 species of Carnivora analysed in this study, with values of their log-transformed mean body mass.

**Appendix S2** Results from principal components analysis of environmental variables (Table S1) and details of phylogenetic eigenvector regression (PVR) of body size against 21 eigenvectors extracted from phylogenetic distances among the 209 species (Table S2).

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## BIOSKETCH

**José Alexandre Felizola Diniz-Filho** is Professor of Animal Ecology and Evolution in the Departamento de Biologia Geral of the Universidade Federal de Goiás, Brazil, and is a 1A Productivity Researcher of the Brazilian Council for Scientific Development and Technology (CNPq). His main research interests are the evolutionary aspects of macroecological theory and the application of spatial statistical methods in macroecology, evolutionary biology, population biology and conservation. He is currently an editor of *Global Ecology and Biogeography*.

Author contributions: J.A.F.D.-F., M.A.R. and B. H. conceived the ideas; M.C., M.A. R. and J.H. processed and organized the data; L.M.B., M.A.O.-T. and J.C.N. conducted different steps of the analyses; and J.A.F.D.-F. led the writing, which received significant inputs from all other authors.

Editor: Brett Riddle