VOL. 180, NO. 2 THE AMERICAN NATURALIST AUGUST 2012

# The Imprint of Cenozoic Migrations and Evolutionary History on the Biogeographic Gradient of Body Size in New World Mammals

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*Submitted October 26, 2011; Accepted April 11, 2012; Electronically published June 20, 2012*

*Online enhancements:* appendix PDF. *Dryad data*: http://dx.doi.org/10.5061/dryad.95ct6q2c.

ABSTRACT: Ecology, evolution, and historical events all contribute to biogeographic patterns, but studies that integrate them are scarce. Here we focus on how biotic exchanges of mammals during the Late Cenozoic have contributed to current geographic body size patterns. We explore differences in the environmental correlates and phylogenetic patterning of body size between groups of mammals participating and not participating in past biotic exchanges. Both the association of body size with environmental predictors and its phylogenetic signal were stronger for groups that immigrated into North or South America than for indigenous groups. This pattern, which held when extinct clades were included in the analyses, can be interpreted on the basis of the length of time that clades have had to diversify and occupy niche space. Moreover, we identify a role for historical events, such as Cenozoic migrations, in configuring contemporary mammal body size patterns and illustrate where these influences have been strongest for New World mammals.

*Keywords:* body size, mammal, allochthonous, autochthonous, Great American Biotic Interchange, niche conservatism.

## Introduction

Body size patterns of mammals have been extensively studied in macroecology and macroevolution. One recurring theme has been to explain ecogeographic rules through comparative associations between body size and contemporary climatic conditions (Rodríguez et al. 2006, 2008; Diniz-Filho et al. 2009). A contrasting approach has been to investigate mammalian body size patterns from an evolutionary perspective to determine which models better explain body size evolution (Cooper and Purvis 2010), when maximum body sizes were reached (Smith et al. 2010; Raia et al. 2012*b*), or whether body size influences conservatism of climatic niches (Cooper et al. 2011).

Historical processes, such as past biotic exchanges or Pleistocene glaciations, have also been suggested as drivers for mammal body size patterns (Marquet and Cofré 1999; Blackburn and Hawkins 2004; Rodríguez et al. 2006). Accordingly, large-scale migratory movements of mammals in the Pliocene and Pleistocene, either between the American continents (i.e., the Great American Biotic Interchange [GABI]) or from Eurasia to the Americas (Marshall 1982; Webb and Barnosky 1989; Marquet and Cofré 1999; Woodburne et al. 2006; Cody et al. 2010), in which mainly large-sized clades were involved (Bowman et al. 2002), might be expected to have left an imprint on current mammal body size gradients. Additionally, the extinction of megamammals, which occurred during the late Pleistocene either as a result of climate change cycles or because of humans (Pushkina and Raia 2008; Cione et al. 2009), may also have influenced contemporary body size gradients. Nonetheless, the potential influence of nonindigenous clades or Pleistocene extinctions on the current geographical body size patterns of mammals is unknown.

Here we expand the assemblage-level analyses of Rodríguez et al. (2008) by explicitly considering evolutionary and historical factors related to the body size gradient of nonvolant mammals in the New World. To document the influence of historical migrations on body size gradients, we separately analyze body size patterns of allochthon and autochthon species (i.e., those belonging or not belonging, respectively, to genera arriving through Pliocene-Pleistocene biotic exchanges) and compare them with the overall gradient across all species. We investigate associations of the body size of the different groups (i.e., all species, autochthon species, and allochthon species) with ecological

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Am. Nat. 2012. Vol. 180, pp. 246–256.
DOI: 10.1086/666608

hypotheses for body size represented by a set of environmental predictors. To determine the extent to which body size patterns are influenced by phylogenetic autocorrelation, we use process-based phylogenetic metrics, such as Blomberg et al.'s (2003) *K*-statistic or Pagel's (1999) $\lambda$. We also use pattern-based metrics, such as Moran's *I* (Gittleman and Kot 1990), which allow us to assess the variation of phylogenetic signal at different phylogenetic distances. Because there may be other influences on spatial variation in the patterns of body size, we also account for spatial variation in body size that is unrelated to the ecological hypotheses. Finally, we compare extant and extinct latitudinal body size patterns and phylogenetic signal to determine whether late Pleistocene extinctions influenced contemporary mammalian body size gradients.

Marquet and Cofré (1999) identified the GABI as a key event in configuring the patterns in the statistical distribution of mammal body size in South America. Therefore, we expect to find a strong influence of allochthon clades on geographical body size patterns. We also hypothesize that evolutionary time must play a role in adaptation by clades to macroclimatic conditions through macroevolution, derived from the time-for-speciation effect (Stephen and Wiens 2003). It has been shown that, in more climatically stable areas, clades of different taxa find more opportunities to adapt, occupy different niches, and diversify (Weir and Schluter 2007; Carnaval et al. 2009; Davies et al. 2009; Hortal et al. 2011). In contrast, clades that evolved in climatically unstable areas (or, analogously, allochthon clades that have spent shorter periods of time in more recently colonized areas) would have less time to occupy the ecological niche space (e.g., Peterson 2011). In that case, macroclimate would act as a filter leading allochthon clades to occupy only the suitable climatic niches to which they were previously adapted (Hawkins et al. 2006, 2007). Based on the assumption that allochthons arrived in North America or South America more recently than autochthons and have thus had less time to diversify, we make two predictions. First, we predict a stronger signature of macroclimate on the body size of allochthon clades, simply because autochthon clades have had more time to adapt and fill different niches. Second, we predict stronger phylogenetic signal in the body size of allochthons than in the body size of autochthons, because niche conservatism might accompany strong phylogenetic signal for body size, which is correlated with many ecological and life-history traits. That prediction may also arise from the fact that allochthons are formed by the nonrandom subset of clades that participated in biotic exchanges; these clades are likely to have broadly similar dispersal ability (Phillimore et al. 2006), which has been linked to body size (Bowman et al. 2002).

If niche conservatism is stronger in allochthons, they should have settled in their preferred habitats by means of habitat tracking (Raia et al. 2012*a*). Because these habitats were widespread in the past but are no longer as common, we would expect allochthons to be unevenly distributed. In sum, if allochthon clade distributions are filtered by macroclimatic conditions, if they show strong phylogenetic signal for body size, and if they show some degree of niche conservatism, then their contemporary distributions should be related to the environmental conditions to which they were adapted before migration.

## Material and Methods

### *Data Collection*

Range maps for all New World nonvolant terrestrial mammal species were extracted from Schipper et al. (2008) and rasterized in a Behrmann equal-area 9,319-km$^2$ grid comprising 3,966 cells. After cross-comparison with the most recent mammal taxonomy (Wilson and Reeder 2005) and with species included in Bininda-Emonds et al.'s (2007, 2008) phylogeny, a total of 1,109 species were considered for analysis (available in Dryad: http://dx.doi.org/10.5061/dryad.95ct6q2c). Body mass (in grams) for each species was compiled from the PanTHERIA database (Jones et al. 2009). For 14 species (1.2% of all species) for which we could not find direct measures of size, we assigned the average mass of its genus. Body masses were $\log_{10}$ transformed for analysis.

Originations in a given continent or region consist of new evolutionary branches (autochthons) and new immigrants (allochthons); according to Webb and Barnosky (1989), the distinction between allochthons and autochthons in the New World's mammal fauna can usually be made with confidence for the relatively complete records of the late Cenozoic genera (Webb and Barnosky 1989; Woodburne et al. 2006). Thus, to investigate the influence of migrations on body size gradients, we divided our database into groups of species differentiated by the continent of origin of each genus (see http://dx.doi.org/10.5061/dryad.95ct6q2c). We identified 429 species belonging to 225 genera native to North America (NA-autochthons) and 322 species belonging to 145 genera native to South America (SA-autochthons). Also, allochthons in North America belong to one of two groups depending on whether they belong to genera that migrated from Eurasia in the Plio-Pleistocene (Eurasian-allochthons: 56 species, 17 genera) or from South America during the GABI (GABI-allochthons of NA: 19 species, 16 genera). Finally, most South American allochthons belong to genera native to North America that colonized South America during the GABI (GABI-allochthons of SA: 347 species, 124 genera). Although a handful of Eurasian genera also arrived in South America during this event, we did not analyze this group because of the small sample size (7 species in 3 genera).

Environmental variables were used to assess four hypotheses previously identified as probable but not mutually exclusive (e.g., Olson et al. 2009) explanations of geographic mammal body size patterns. (1) The heat conservation hypothesis, that larger endotherms abound in colder areas because of their lower surface-area-to-volume ratio and thus greater capability to preserve body heat (Bergmann 1847), was investigated using mean annual temperature (Bio 1 from WorldClim; Hijmans et al. 2005). (2) The resource availability hypothesis, that more productive environments lead to larger body sizes because resource availability sets a limit to the body size that an animal can reach (Rosenzweig 1968; Geist 1987), was explored using annual average net primary productivity (NPP), extracted from Imhoff et al. (2004; data available at http://sedac.ciesin.columbia.edu/es/hanpp.html; last accessed in March 2011). (3) The resistance to starvation hypothesis (or fasting endurance hypothesis), that larger animals are favored in less productive and more seasonal environments because they metabolize fat stores at lower weight-specific rates and thus cope with starvation better than do smaller animals (Calder 1984; Lindstedt and Boyce 1985; Cushman et al. 1993), was also assessed on the basis of NPP, but in this case predicted negative covariation with body size. (4) The habitat availability hypothesis, that the finer habitat zonation associated with stronger mesoscale climatic gradients in tropical mountains limits the occurrence of large species (Hawkins and Diniz-Filho 2006; Rodríguez et al. 2008), was assessed using range in elevation (data available at http://www.ngdc.noaa.gov/seg/cdroms/ged_iia/datasets/a13/fnoc.htm; accessed in January 2011) as our indicator of variation in mesoclimate (see Rodríguez et al. 2008 for details). All variables were rescaled and binned within each cell in our grid for analyses. We also computed the number of species in each cell and mapped species richness for each group of mammals (fig. S1, available online).

### *Environmental Correlates of Body Size*

The hypotheses linking body size to the environmental variables were evaluated with saturated multiple ordinary least squares (OLS) regression models of the observed mean log-transformed body sizes for each group (all species, autochthons, and Eurasian and GABI allochthons). Because the hypotheses are not mutually exclusive, the environmental variables linked to them are not orthogonal ($r_{\mathrm{TEMP\,vs.\,NPP}} = 0.615$, $r_{\mathrm{TEMP\,vs.\,RIE}} = 0.038$, and $r_{\mathrm{NPP\,vs.\,RIE}} = 0.179$ in the Nearctic and $r_{\mathrm{TEMP\,vs.\,NPP}} = 0.766$, $r_{\mathrm{TEMP\,vs.\,RIE}} = 0.558$, and $r_{\mathrm{NPP\,vs.\,RIE}} = 0.469$ in the Neotropics). To evaluate the influence of collinearity on the stability of the standardized regression coefficients, we computed both the condition number (CN) and the variance inflation factors (VIFs) of the models, assuming that values of VIF lower than 10 and a CN lower than 5 indicate that collinearity is not a major problem (see Olalla-Tárraga et al. 2009 for details). Analyses were performed separately for the Nearctic and Neotropics biogeographic regions (Cox 2001) because of their different evolutionary histories (Laurasia vs. Gondwana) and geographic patterns of mammal body size variation (Rodríguez et al. 2008).

Data in macroecology are spatially structured, so we expected strong spatial autocorrelation in both mean $\log_{10}$ body sizes and environmental predictors. The spatial structure in body size represents the pattern that we are trying to explain, although regression models that include only three environmental predictors are likely to result in spatially autocorrelated residual variation. This would impact statistical inference if we used significance tests for variable evaluation, but we circumvented this issue by focusing our interpretations on the regression coefficients of the OLS models, which are not biased by residual autocorrelation (Cressie 1993; Fortin and Dale 2005; Schabenberg and Gotway 2005). However, we also quantified spatial autocorrelation in model residuals to evaluate the extent to which the environmental variables (and their associated hypothesis) might underlie the observed body size patterns. For this, we generated sets of spatial filters describing the spatial variation in body size variables that are independent of the spatial variation already explained by the environmental predictors. We selected spatial filters for each response variable (i.e., the mean $\log_{10}$ body size of all species, GABI allochthons, Eurasian allochthons, and autochthons in both the Nearctic and the Neotropics) using the algorithm proposed by Griffith and Peres-Neto (2006). This method selects the set of eigenvectors that describe all of the variation in a given trait that is spatially autocorrelated above a certain threshold (residual Moran's $I \leq 0.05$ in this case). We first regressed body size against the set of spatial eigenvectors. Subsequently, the amount of variation in the trait that was spatially structured, as predicted by the set of eigenvectors, was regressed against the environmental predictors. We then used the residuals of this second regression as a predictor in OLS regressions for body size (in combination with environmental predictors) to account for the spatial structure of the trait that is independent from the spatial structure explained by environmental variables (for details, see table S1, fig. S2, both available online). We used Moran's $I$ spatial correlograms (data not shown) to confirm whether this approach removed the spatial autocorrelation of the residuals of our multiple-regression models at all distance classes.

Because relationships of mammal body size to temperature are nonlinear, with body size increasing as temperature falls below a threshold of 10.9°C in the Nearctic and 12.6°C in the Neotropics (Rodríguez et al. 2008), we investigated such relationships by fitting lowess regression lines. We visually inspected body size versus temperature scatterplots and reported only those for which nonlinearity was found (i.e., all species and allochthon species; fig. S3, available online). We recalculated OLS models below and above the temperature for which body size–temperature relationships shifted (~11°C; table S2, available online).

### *Phylogenetic Autocorrelation Analyses*

We used the best dates, species-level phylogenetic supertree from Bininda-Emonds et al. (2007, 2008) to compute amounts of phylogenetic signal in the cross-species variation of body sizes for all the species in our database and for the groups of autochthon and allochthon species and pruned the tree in each case to include the species involved in each analysis. Phylogenetic signal was first calculated using Pagel's (1999) $\lambda$, which varies from 0 (no phylogenetic signal) to 1 (compatible with Brownian motion [BM]). Likelihood ratios were used to test whether $\lambda$ was significantly different from 1.0 (Cooper et al. 2010). Because values of $\lambda$ that are >1.0 are not defined (Freckleton et al. 2002; Revell et al. 2008), the metric is unable to detect phylogenetic signal stronger than BM; we therefore also calculated Blomberg's $K$ statistic (Blomberg et al. 2003). $K$ ranges from 0 to $\infty$, with values <1.0 indicating low phylogenetic signal, values equal to 1.0 indicating BM, and values >1.0 indicating a stronger phylogenetic signal than the neutral expectation. The statistical significance of $K$ was tested through randomization of the data among species (to test $K = 0$) and through simulations of a character evolving under a BM model (to test $K = 1$; see Machac et al. 2011). For both Pagel's $\lambda$ and Blomberg's $K$, polytomies in the phylogeny were resolved randomly by zero-length branches. We used R, version 2.10.1 (R Development Core Team 2009), to compute both metrics. Finally, we inspected Moran's $I$ correlograms to explore the patterns of phylogenetic autocorrelation at different depths of the phylogeny (Machac et al. 2011; fig. S4, available online).

### *Pleistocene Megamammal Extinctions*

To determine the extent to which our results were affected by extinctions of large-sized mammals during the late Pleistocene, we repeated both biogeographical and phylogenetic analyses that included the extinct genera of megamammals (>44 kg) identified in Koch and Barnosky (2006). It was necessary to downscale the analyses to equate the better resolution of the data for extant species to that for extinct species. First, we compared the latitudinal patterns in body size of extant and extinct species for the groups of all mammals, autochthon mammals, and allochthon mammals (see details and results in fig. S5, available online). Second, we recalculated the phylogenetic signal metrics at the genus level for extant clades only and for extant plus extinct clades. To do this, we collapsed the phylogenies to the generic level and included extinct genera as sister clades of their closest relatives. The database and phylogenies generated for these analyses can be accessed through the Dryad data repository.

## Results

### *Geographical Patterns in Body Size*

The geographical patterns of body size of all species were virtually identical to those reported by Rodríguez et al. (2008), even though our database comprised fewer species (i.e., only those included in the Bininda-Emonds et al. 2007, 2008 supertree). In the Nearctic, a Bergmannian latitudinal gradient was found, whereas in the Neotropics, large-sized assemblages occurred mostly in tropical lowlands (fig. 1*A*). The body size gradient of autochthon species resembled that of all species in both the Nearctic ($r = 0.672$) and the Neotropics ($r = 0.651$; fig. 1*B*). Nonetheless, differences were observed in the northernmost Nearctic and in the Amazonian lowlands, where mean body sizes were smaller for autochthon species (fig. 1*B*). Also, assemblages of large-sized autochthons were found in Patagonia (fig. 1*B*); this is not a consequence of very few species occurring there, because more than 25 autochthons inhabit the region (fig. S1).

The spatial body size patterns of GABI allochthons were virtually identical to the pattern of all species in the Neotropics ($r = 0.946$) but were different from the pattern of other species in the Nearctic, where large mean body size values for GABI allochthons were uniformly distributed across the continent (fig. 1*C*). This reflects that Nearctic assemblages of GABI allochthons comprise no more than 5 large species that mostly inhabited temperate, boreal, and subarctic latitudes (fig. S1). On the other hand, Eurasian allochthons showed a pattern of large-sized assemblages in Canada and along the Rocky Mountains (fig. 1*D*). That pattern of large sizes in the north coincides with the latitudinal species-richness gradient of Eurasian allochthons, which reverses the classical latitudinal species-richness gradient (fig. S1). Large-sized assemblages of Eurasian allochthons were also found throughout Central and South America (fig. 1*D*), where a gradient of decreasing species richness southwards is particularly evident, from the relatively poor Central America (with up to 7 species) to the highly impoverished Patagonia (1 species; fig. S1).

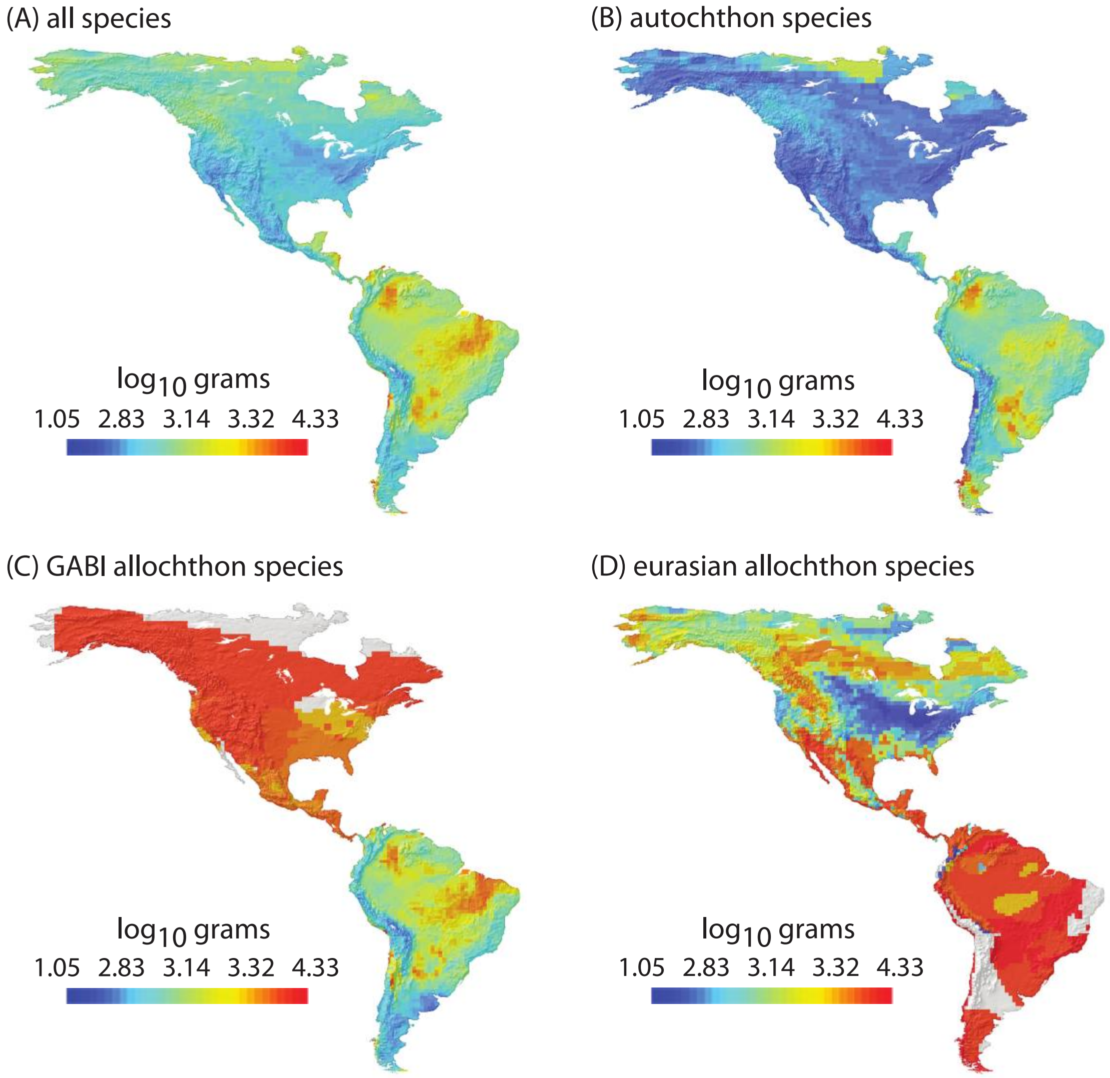

**Figure 1:** Geographical patterns of mean $\log_{10}$ body size for all species (*A*), autochthon species (*B*), Great American Biotic Interchange (GABI) allochthon species (*C*), and Eurasian allochthon species (*D*) in the New World. Maps of autochthons and allochthons were generated separately for North America and South America, because autochthon species in one continent will be considered allochthon species in the other.

In sum, Eurasian and GABI allochthons were differently distributed across the New World. Eurasian allochthons increased the mean body sizes of all species in northernmost North America, whereas GABI allochthons had mean body sizes that were smaller than those of South American autochthons in Patagonia and the Andes, which decreased the mean body sizes of all species in the Neotropics (fig. 2).

### *Environmental Correlates of Mean Body Size*

Our three-variable models accounted for over half of the variation in mean body size of all species in both the Nearctic ($R^2 = 0.546$) and the Neotropics ($R^2 = 0.503$; table 1). The inclusion in the models of spatial filters accounting for all residual spatial autocorrelation revealed meaningful amounts of spatially structured variation unrelated to our environmental predictors, which indicates that other spatially structured factors or processes influence broad-scale body size gradients across the New World (table S2; fig. S2). Also, the regression coefficients of OLS models were not affected by instability attributable to collinearity (all $\mathrm{CN} \leq 3.127$, $\mathrm{VIF} \leq 2.625$).

*The Nearctic.* Mean annual temperature was the primary

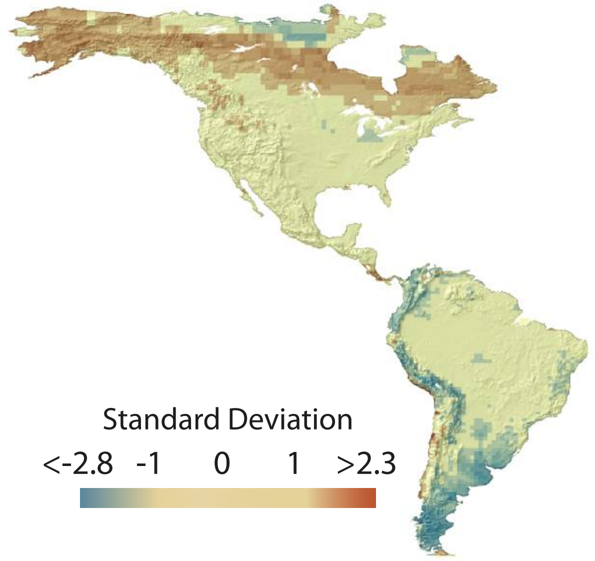

**Figure 2:** Standard deviation of the difference between the body size patterns of all species and those of autochthon species. Red colors indicate a positive contribution in body size attributable to allochthon clades. Blue colors indicate a negative contribution in body size attributable to allochthons. Although the presence of allochthons in the Nearctic influences the body size pattern with an increase in the average size of species in the northernmost regions, it contributes with a decrease in the average size of species in the southernmost regions of the Neotropics. A likely explanation for this reversed pattern must be related to differences among the migrants to both subcontinents and particularly in the radiation of small-sized rodents belonging to the family Muridae, which are allochthons in the Neotropics.

predictor in all models except for Eurasian allochthons, which was the only group showing positive regression coefficients for temperature (table 1). However, the relationships of body size of all species and Eurasian allochthons with temperature were nonlinear (fig. S3). Lowess regression identified temperature thresholds at which relationships with mammal body size shift from negative to positive (~11°C in both continents; see Rodríguez et al. 2008). Below the threshold, temperature became the main predictor for Eurasian allochthons body size as well and showed negative coefficients below the threshold and positive coefficients above it (fig. S3).

Productivity was the secondary predictor in all models, although it was the primary predictor for Eurasian allochthon body size when the whole range of temperatures was considered (table 1). Regression coefficients of productivity were negative in all cases (table 1), which suggests large mean body sizes in the less productive areas of the Nearctic. Range in elevation was the weakest predictor in all models of the Nearctic, with positive regression coefficients except for autochthons (table 1). However, it should be noted that the environmental model for autochthons was weaker than models for all species and for both groups of allochthons and explained less than one-fifth of the variation in body size (table 1).

*The Neotropics.* Mean annual temperature was the main predictor in environmental models for body size of all species and GABI allochthons and showed positive standardized coefficients for those groups (table 1). As in the Nearctic, relationships of temperature with mean body size of all species and allochthons were nonlinear (fig. S3), with negative regression coefficients below an 11°C temperature threshold (table S2). In the Neotropics, unlike in the Nearctic, autochthon body size was weakly associated with temperature and productivity, but it was more strongly linked with range in elevation (table 1). The negative coefficient of range in elevation indicates a trend of small autochthons in mountainous areas. In contrast, allochthon species body size was weakly but positively associated with range in elevation in the Neotropics (table 1). That association was stronger in cold areas of the Neotropics (i.e., those areas below the 11°C threshold), where elevation became the primary predictor of allochthon body size, with a positive regression coefficient (table S2). A positive association of allochthon body size with range in elevation was also observed in the Nearctic when temperature thresholds were taken into account (table S2). As in the Nearctic, environmental models were stronger for all species and GABI allochthons than for autochthons in the Neotropics, where less than one-quarter of the variation in autochthon body size was explained by the environmental predictors (table 1).

### *Phylogenetic Autocorrelation in Body Size*

Unsurprisingly, body size showed strong phylogenetic signal across all species and all subsets (table 2). Blomberg's $K$ statistic indicated stronger phylogenetic signal in body size than was expected under BM for allochthons ($K = 2.365$, $P[K = 1] = .001$). For all species of the New World, the phylogenetic signal was not significantly different from the BM expectation ($K = 1.067$, $P[K = 1] = .851$). Phylogenetic signal for autochthon species was somewhat weaker than expected under BM ($K = 0.805$, $P[K = 1] = .584$), although not significantly so according to both the $K$ and $\lambda$ statistics (table 2). These results suggest strong phylogenetic niche conservatism (PNC; sensu Losos 2008) for body size of allochthons, but little PNC (sensu Losos 2008) for autochthon species.

**Table 1:** Ordinary least squares environmental saturated models for mean $\log_{10}$ body mass for all species, autochthon species, and allochthon species from the Great American Biotic Interchange (GABI) and Eurasia in both the Nearctic and the Neotropics

| Region, group | No. species | Temperature | Net primary productivity | Range in elevation | $R^2$ |
|---|---|---|---|---|---|
| Nearctic: | | | | | |
| All species | 508 | **−.656** | −.124 | .006 | .546 |
| Autochthons | 429 | **−.338** | −.120 | −.103 | .186 |
| Eurasian allochthons | 56 | .314 | **−.472** | .191 | .211 |
| GABI allochthons | 19 | **−.455** | −.419 | .061 | .619 |
| Neotropics: | | | | | |
| All species | 669 | **.517** | .004 | −.274 | .503 |
| Autochthons | 322 | .054 | .094 | **−.395** | .233 |
| GABI allochthons | 347 | **.785** | −.147 | .051 | .425 |

Note: Boldface type indicates the primary predictor in each model. It is important to note that species that are considered autochthons in the Nearctic can be considered allochthons in the Neotropics and vice versa. In addition, the number of species belonging to genera that crossed to North America during the GABI that are currently present in the Nearctic are only a small proportion of all of the species that belong to such genera (19 of 113 species), and hence models for GABI allochthons in the Nearctic must be interpreted with care.

Phylogenetic signal at the species level was consistent with signal for the extant subsets of genera (table 2). Allochthon body size had higher phylogenetic signal than the body size of all extant genera and autochthon genera, although it was only marginally significantly different from BM ($K = 1.626$, $P[K = 1] = .078$). Incorporation of extinct genera of megamammals into the analyses increased the phylogenetic signal in all cases. However, the trend for higher body sizes of allochthons held for the extant plus extinct genera of allochthons, which was significantly different from BM according to the $K$ statistic ($K = 1.918$, $P[K = 1] = .010$) but was not according to the $\lambda$ statistic (table 2).

Phylogenetic autocorrelation patterns were very similar for all species and allochthon species across phylogenetic distances showing high Moran's $I$ values up to 150 Ma (fig. S4, available online). Autochthons had lower Moran's $I$ values, which decreased to levels near 0 at 100 Ma (fig. S4).

## Discussion

Biotic exchanges during the Plio-Pleistocene period have left a detectable imprint in the mammal body size patterns found in the Americas. The imprint is determined by a mixture of opposing signals provided by autochthon and allochthon species, which differ in their body size relationships with phylogeny and environmental variables. Other historical events, such as the megamammal Pleistocene extinctions, do not seem to change these findings.

### *Environmental Hypotheses Linked to Body Size*

Consistent with Rodríguez et al. (2008), support for ecological hypotheses differed between the Nearctic and the Neotropics. The heat conservation hypothesis is favored in the Nearctic, whereas a positive association with temperature in combination with the habitat availability hypothesis emerges as the main statistical explanation for body size patterns in the Neotropics. However, when the nonlinearities in the correlations of body size with temperature are accounted for, the explanations for body size coincide in both the Nearctic and the Neotropics (Rodríguez et al. 2008; table S2).

### *The Influence of Autochthons and Allochthons on Body Size Gradients*

The different evolutionary histories of the faunas of the two continents have also played a key role in determining the current body size gradient of New World mammals (Rodríguez et al. 2008) in two main ways. First, assemblages are composed of authochthonous and allochthonous species, whose influences over the body size of all species patterns are different in the Nearctic and the Neotropics (fig. 1). This difference is probably attributable to the asymmetry of the GABI (Woodburne et al. 2006), with significantly more genera crossing from north to south (124 genera) than from south to north (16 genera). Likewise, the large number of Eurasian genera in North America (18 genera) differs from the low number of such genera that reached South America (3 genera; see fig. S1). Furthermore, allochthons that moved into South America were particularly successful in colonizing the continent because of both competitive replacement (Webb 1976,

**Table 2:** Phylogenetic signal and phylogenetic autocorrelation metrics for mean $\log_{10}$ body size of all species, autochthons, and allochthons

| Group | *N* | Pagel's λ | LR λ | *P* | Blomberg's *K* | *P* (*K*=0) | *P* (*K*=1) |
|---|---|---|---|---|---|---|---|
| All: | | | | | | | |
| Extant species | 1,109 | .994 | 38.533 | .001 | 1.067 | .001 | .851 |
| Extant genera | 269 | .983 | 191.705 | .001 | .989 | .005 | .975 |
| Extant and extinct genera | 330 | 1.000 | <.001 | .999 | 1.521 | .005 | .143 |
| Autochthon: | | | | | | | |
| Extant species | 412 | .998 | .130 | .718 | .805 | .005 | .584 |
| Extant genera | 105 | .979 | .385 | .534 | .701 | .005 | .401 |
| Extant and extinct genera | 141 | 1.000 | .000 | 1.000 | 1.437 | .005 | .219 |
| Allochthons: | | | | | | | |
| Extant species | 697 | .992 | 40.375 | .000 | 2.365 | .001 | .001 |
| Extant genera | 164 | .974 | 5.103 | .024 | 1.626 | .005 | .078 |
| Extant and extinct genera | 189 | .996 | .290 | .590 | 1.918 | .005 | .010 |

Note: Phylogenetic signal and phylogenetic autocorrelation metrics are given as measured by Pagel's λ (1999) and Blombgerg's *K* (Blomberg et al. 2003). Metrics of phylogenetic signal are also shown for the phylogeny of each group collapsed to the generic level and for generic level phylogenies in which genera of extinct megafaunal mammals were included.

1985; Simpson 1980; but see Lessa and Fariña 1996) and Cenozoic climate changes, with the subsequent niche conservatism dynamics (Webb 1991; Marquet and Cofré 1999).

Second, authochthon and allochthon species have different associations between body size and environmental predictors (table 1). Autochthons have weaker associations and hence less pronounced spatial gradients in body size than do allochthons. These results suggest an influence of the time that clades have had available in which to adapt and diversify with respect to the extent to which they respond to current climatic conditions.

One of the most obvious effects of allochthon clades on the body size patterns of mammals in the New World is the fact that, although the average body size increases by over 1 standard deviation in the northernmost parts of the Nearctic, it decreases in cold regions of the southernmost Neotropics because of the presence of allochthons (fig. 2). This explains why the pattern for large-bodied assemblages of autochthon species in southernmost South America (fig. 1*B*) is not found for mammals overall (fig. 1*A*). This Bergmann-like pattern was not found in previous analyses of mammals (Rodríguez et al. 2008) or carnivores (Diniz-Filho et al. 2009), although it was found in analyses of birds (Ramirez et al. 2008). An example of taxa potentially responsible for this are the sigmodontine rodents, which radiated in North America in the Miocene before colonizing South America (Baskin 1986). This clade would have found suitable habitats in the coldest southernmost Neotropics, formerly inhabited by larger autochthon species, and might have induced a subsequent decrease in average body size in this area (fig. 2).

### *Phylogenetic Signal in Body Size of Autochthons and Allochthons*

The strong phylogenetic signal in mammalian body size is not a novel finding (e.g., Freckleton et al. 2002; Cooper and Purvis 2010), but the stronger signal in allochthons than in autochtons is. Although the evolution of body size in autochthons appears to be compatible with BM, allochthon body sizes are more similar among closely related species than is expected under BM (table 2), which suggests PNC sensu Losos (2008) for the latter group. This does not mean that size has evolved more slowly in allochthons than in autochthons; rather, it might indicate that allochthons have had less time to occupy a broader range of the niche space (i.e., diversifying body sizes). In addition, the strong phylogenetic signal in allochthon body size might partly reflect that clades that have participated in biotic exchanges are those with strong dispersal abilities (Davies et al. 2007; Raia et al. 2012*a*). It is possible that dispersal ability, which is associated with body size (Wolff 1999; Sutherland et al. 2000; Bowman et al. 2002), is the phylogenetically conserved trait, instead of body size, although we cannot explicitly test this.

Body size of allochthons consistently contains stronger phylogenetic signal than does body size of autochthons, even if extinct clades are incorporated to the analysis. At the generic level, only the body size of the extant plus extinct allochthon genera shows a phylogenetic signal that is significantly different from the BM expectation (*K* statistic; table 2). That the λ statistic for this group is not significantly different from BM might be attributable to the fact that inclusion of extinct large-sized clades generates a logical increase in the phylogenetic signal for all groups, which λ is not able to discriminate from BM, because the metric is not defined above 1.

### *Why Are Autochthons and Allochthons Different?*

Differences between autochthon and allochthon species in body size's phylogenetic signal and in its environmental correlates can be interpreted in terms of a straightforward mechanism that is based on recent results of Hortal et al. (2011) for European dung beetle faunas. Specifically, Hortal et al. (2011) found that more climatically stable areas promoted diversification and occupation of the niche space by these faunas during the Pleistocene, whereas in areas that experienced strong climatic shifts (i.e., the last glaciation), macroclimate and niche conservatism acted as filters that limited the number of species able to disperse to those areas and constrained where each one could survive. Similarly, we hypothesize that climatic stability would produce an equivalent effect on the amount of time available to each group to diversify. That is, assuming that autochthon clades have been present in either North America or South America for longer than allochthon clades, they have had more time to diversify and occupy a wider range of niche space, as predicted by the time-for-speciation effect (e.g., Stephens and Wiens 2003). In contrast, allochthons, which have colonized and diversified more recently, would be composed of mostly large-sized clades that are capable of long-distance migration because of higher dispersal abilities (e.g., Wolff 1999; Sutherland et al. 2000; Bowman et al. 2002). Arriving allochthons would not distribute uniformly across the continents but, rather, would remain in the most suitable habitats because of niche conservatism (Peterson et al 1999; Wiens and Donoghue 2005). Allochthons, similar to postglacial dispersers, would be conditioned by climatic filtering and previous adaptations (to climates in biogeographic regions where the groups originated) and would thus have a tendency to reproduce existing climatic gradients. Allochthon clades, filtered by macroclimate and selected by their dispersal abilities, would encompass a subset of species that show higher phylogenetic signal for body size, compared with autochthons.

An additional support for this mechanism is provided by the different biogeographic origin of allochthon species in North and South America. Allochthons that colonized the Nearctic from Eurasia since the late Pliocene were adapted to cold and temperate climates (Webb and Barnosky 1989) that were similar to the environments preferred by the largest autochthon species. In contrast, mammal genera that participated in the GABI and migrated to South America would have been adapted to warm open savanna settings before migration (Webb and Rancy 1996). Furthermore, richness patterns of allochthons show how species that belong to genera coming from Eurasia would have progressively colonized the Nearctic, with only a few species reaching the far south (fig. S1). The same colonization pattern is shown by GABI allochthons not being able to reach the northern Nearctic and by fewer species reaching the southernmost regions of South America (fig. S1).

### *The Role of Megafaunal Extinctions on Mammal Body Size Patterns*

Differential extinction, known to have primarily affected large species (e.g., Martin and Steadman 1999), could have played a role in determining body size patterns, especially for species in South America, which underwent the largest Late Pleistocene megamammal extinction event (Cione et al. 2009). Interestingly, we found that latitudinal patterns in body size of extinct megamammal species resemble those of extant mammal species whether all species are considered or only the autochthon and allochthon groups are considered (fig. S5). Our results indicate that, if we had spatial resolution for the distributions of extinct species that equaled what we have for extant ones, it is likely that contemporary body size gradients would be reinforced by the inclusion of extinct clades. This preliminary analysis suggests that mechanisms that operate on current body size patterns might have acted similarly on the body size patterns of extinct species. However, this issue deserves additional research.

### *Concluding Remarks*

We acknowledge that the spatial variation in mammal body size almost certainly also reflects other macroevolutionary processes, such as different centers of diversification. The spatial variation in body size that is unrelated to our environmental variables might be explained by such factors, although measuring them is difficult. Comprehensive data on centers of diversification and better resolution of the data on both mammalian extinctions and human distribution will provide a more complete picture of the influence of evolutionary history on contemporary patterns. For the time being, this work provides evidence of how late Cenozoic biotic exchanges have helped to configure the contemporary body size gradients of New World mammals.

## Acknowledgments

This study was sponsored by grants from the Ministry of Science and Innovation of Spain (FPI-fellowship BES-2007-16314 to I. M.-C. and grant CGL2010-22119 to

M.Á.R.). M.Á.O.-T. was supported by the European Commission (PHYLONICHE-FP7 Marie Curie Intra-European Fellowship for Career Development). We also thank the two anonymous reviewers for their helpful comments on the manuscript.

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Associate Editor: Dean C. Adams
Editor: Mark A. McPeek

# SUPPLEMENTARY MATERIAL

**Figure S1:** Geographical patterns of species richness.

**Table S1:** OLS environmental models including spatial variation independent from the spatial structure in body mass explained by environmental predictors.

**Figure S2:** Spatial filtering procedure.

**Figure S3:** Scatterplots of mean log10-body mass vs. temperature.

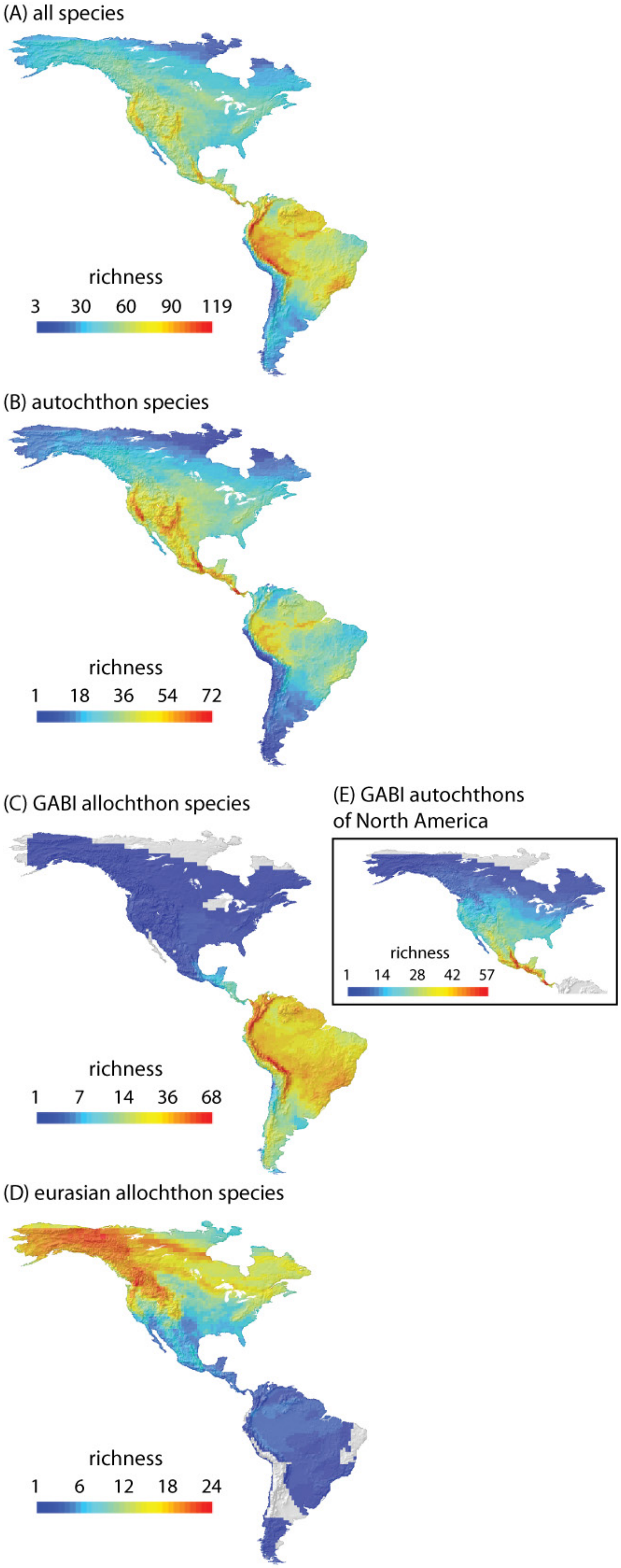
**Table S2:** OLS environmental models below and above temperature threshold.

**Figure S4:** Moran's *I* phylogenetic correlograms.

**Figure S5:** Comparison of extant vs. extinct patterns in body size.

## Species richness geographical patterns

**Figure S1.** Species richness geographical patterns of all species (A), autochthon species (B), allochthon species belonging to genera involved in the GABI (C), and species belonging to genera immigrating from Eurasia through Beringia (D). The inset illustrates the species richness of the North American distribution of the GABI allochthons in South America (E).


(A) all species
richness
3 30 60 90 119
(B) autochthon species
richness
1 18 36 54 72
(C) GABI allochthon species
richness
1 7 14 36 68
(E) GABI autochthons of North America
richness
1 14 28 42 57
(D) eurasian allochthon species
richness
1 6 12 18 24

## OLS environmental models including spatial variation independent from the spatial structure in body mass explained by environmental predictors

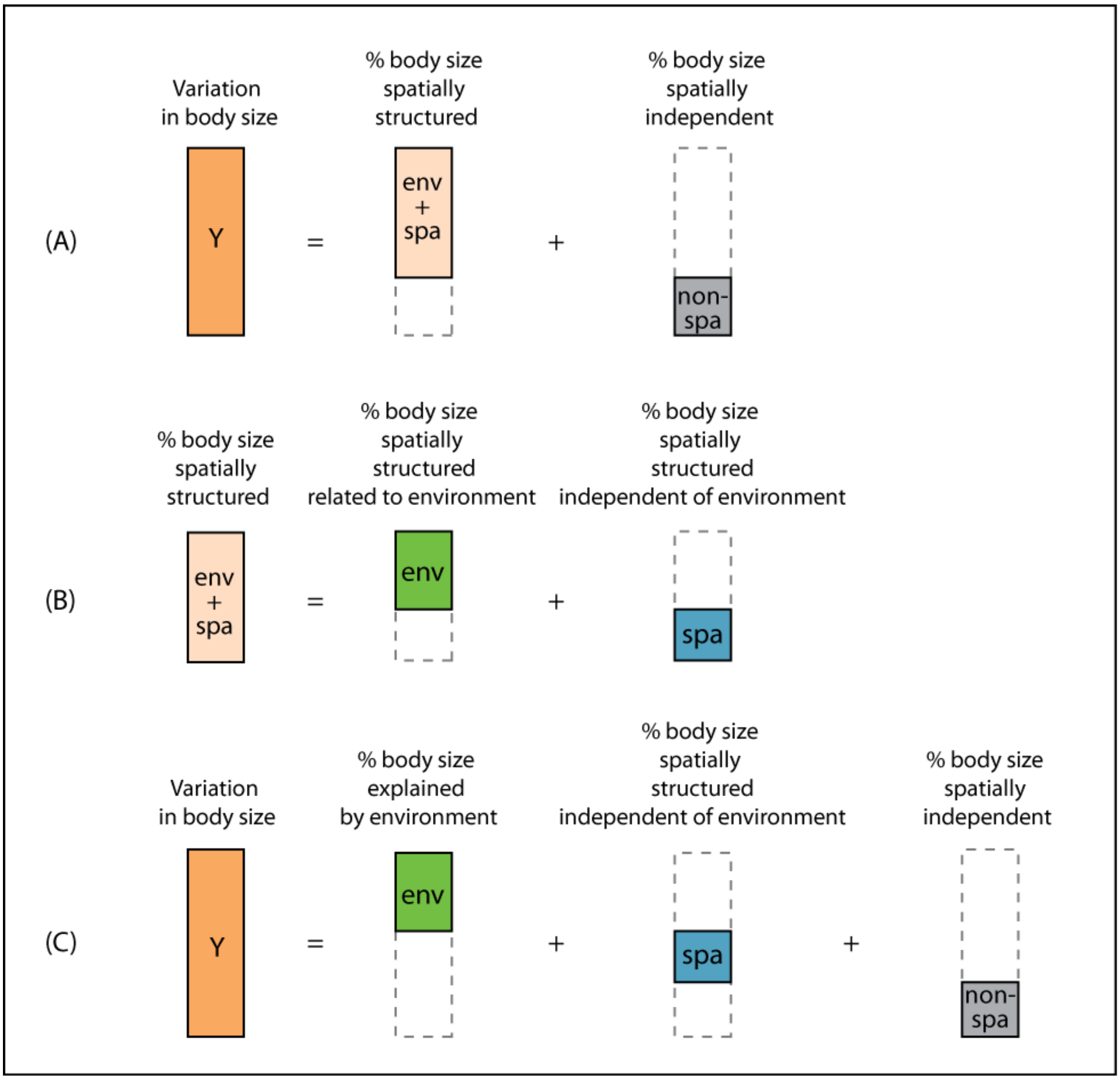
**Table S1.** Three-variable environmental OLS regressions for mean log10-body size including all its spatial autocorrelation in the set of predictors.

| Region | Group | n | TEMP | NPP | RIE | Independent spatial variation | R²env+spa | R²env | R²spa | R²non-spa |
|---|---|---|---|---|---|---|---|---|---|---|
| Nearctic | All species | 508 | -0.646 | -0.139 | 0.001 | 0.592 | 0.897 | 0.546 | 0.351 | 0.103 |
| | Autochthons | 429 | -0.325 | -0.134 | -0.113 | 0.753 | 0.754 | 0.186 | 0.568 | 0.246 |
| | Eurasian-allochthons | 56 | 0.335 | -0.477 | 0.183 | 0.785 | 0.827 | 0.211 | 0.616 | 0.173 |
| | GABI-allochthons | 19 | -0.462 | -0.412 | 0.062 | 0.534 | 0.904 | 0.619 | 0.285 | 0.096 |
| Neotropics | All | 669 | 0.508 | -0.012 | -0.300 | 0.628 | 0.898 | 0.503 | 0.394 | 0.102 |
| | Autochthons | 322 | 0.040 | 0.104 | -0.398 | 0.766 | 0.820 | 0.233 | 0.587 | 0.180 |
| | GABI-allochthons | 347 | 0.793 | -0.187 | 0.014 | 0.689 | 0.898 | 0.426 | 0.472 | 0.102 |

Note: The spatial structure of body size that is not accounted by mean annual temperature (TEMP), mean annual net primary productivity (NPP) and range in elevation (RIE), is included as an additional independent variable (Independent spatial variation) in the models. Residual spatial autocorrelation was eliminated in all cases (Moran's I $\leq 0.05$) and thus standardized regression coefficients can be compared with those from OLS models not including any spatial variables (Table 1). Partial regression indicating the amounts of variation in body size explained by the environmental variables ($R^2$env), the variation explained by other sources of spatial variation ($R^2$spa) and the variation which is not spatially structured ($R^2$non-spa) are also shown. The spatial variation variable has the highest standardized coefficients except for all species in the Nearctic and allochthon species in the Neotropics, indicating that the set of sources of spatial variation in body size not accounted by our predictors are of importance to explain body size spatial variation. Acknowledging that, both the rank and sign of the predictors from OLS models (Table 1) remain robust once spatial filters are included and residual spatial autocorrelation is removed.

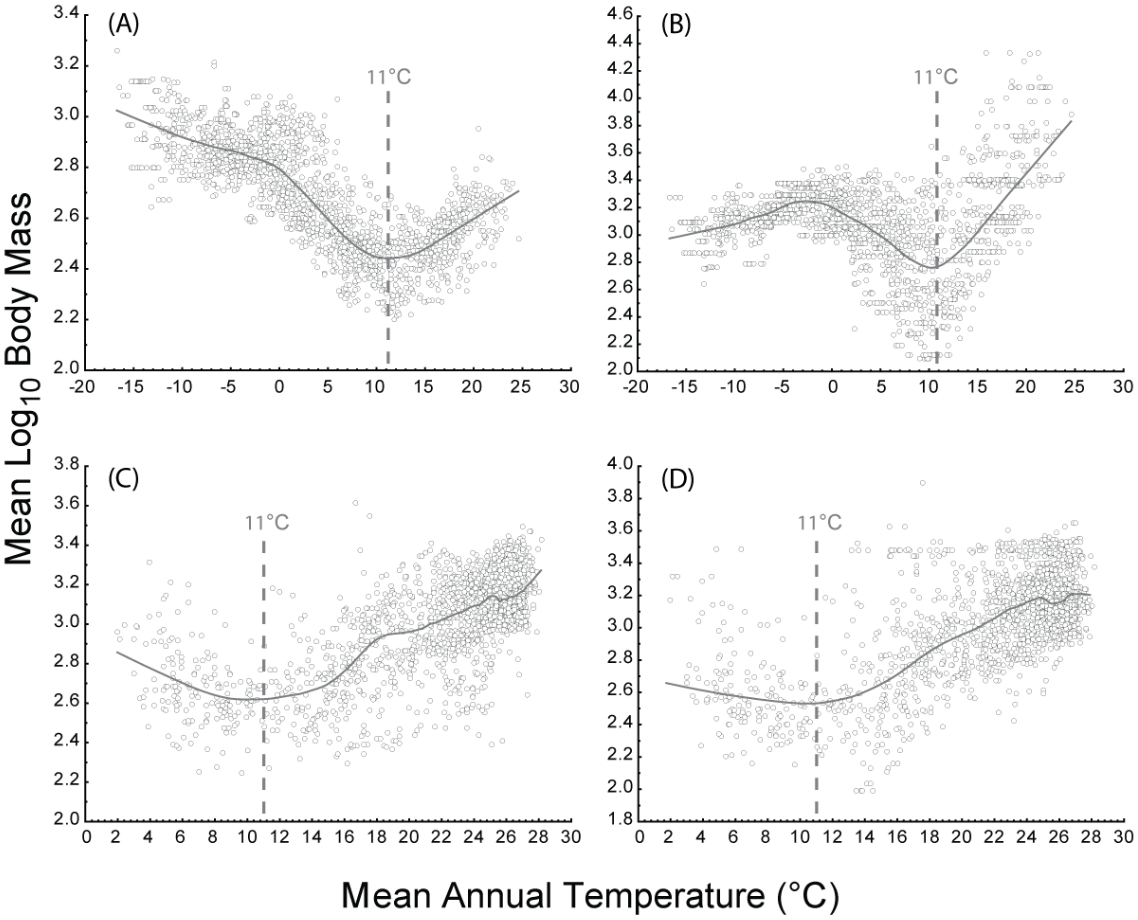
## Spatial filtering procedure

**Figure S2.** Spatial filtering procedure performed to include spatial structure independent of trait variation. First, spatial filters are selected for body size using the Griffith and Peres-Neto (2006) algorithm and used as predictors in a regression that yields the proportion of body size that is spatially autocorrelated (A). Second, that proportion of spatially autocorrelated body size is regressed against the environmental predictors to obtain the residuals, that is, the proportion of spatially structured body size independent of the environment (B). Those residuals are finally included as a predictor in the models (C).



### Scatterplots of mean log10-body mass vs. temperature

**Figure S3.** Scatterplots of mean log-10 body mass against mean annual temperature for all species (A) and Eurasian allochthons (B) in the Nearctic, and for all species (C) and GABI allochthons (D) in the Neotropics. Lowess regression fits were used to identify at what temperature the relationships with temperature shift. Shifts in relationships are found near 11°C and are proximal to the temperature thresholds identified by Rodríguez et al. (2008).



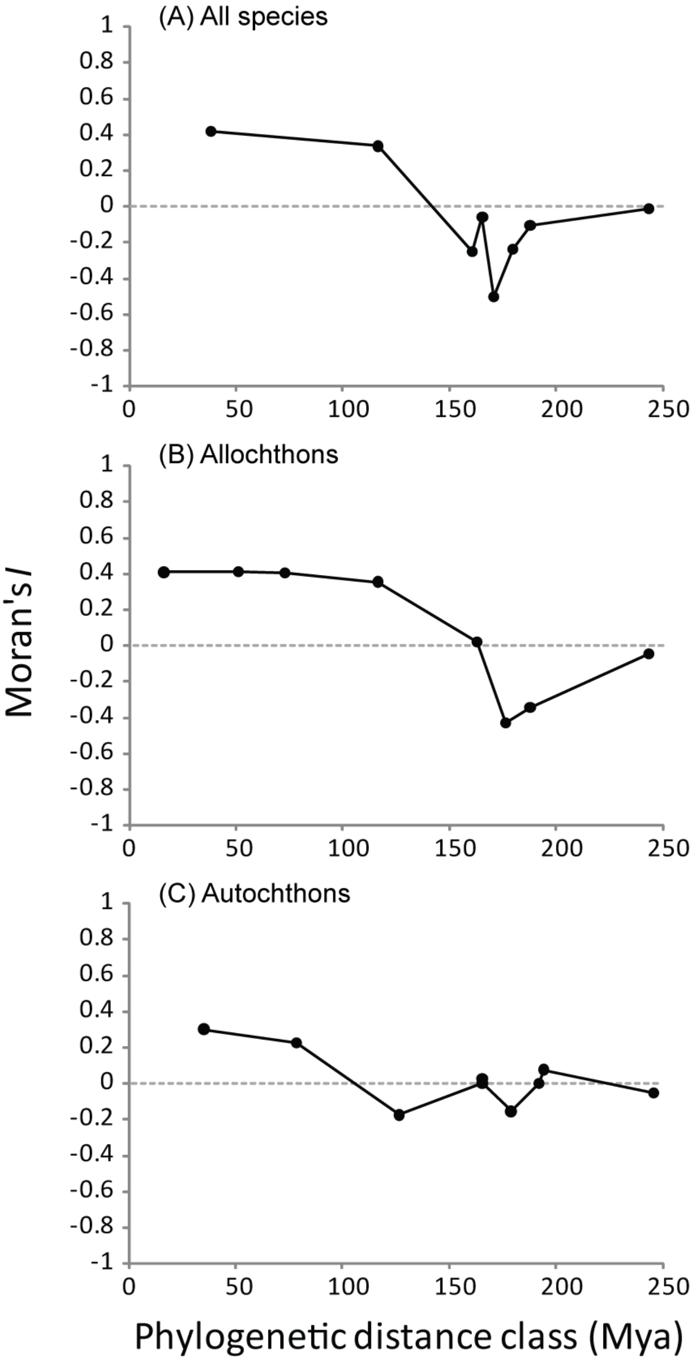
## OLS environmental models below and above temperature threshold

**Table S2.** OLS three-variable environmental models for body mass of all species and allochthon species using mean annual temperature (TEMP), mean annual net primary productivity (NPP) and range in elevation (RIE). Models are performed below and above temperature values where relationships with temperature shift as confirmed by lowess regressions (i.e. ~11°C, see Appendix 4). Models for allochthon species are only conducted for Eurasian allochthons in the Nearctic and GABI allochthons in the Neotropics. Bold regression coefficients indicate the primary predictor in each model.

| Region | Group | TEMP | NPP | RIE | $R^2$ |
|---|---|---|---|---|---|
| Nearctic | All species | | | | |
| | below 11°C | **-0.800** | 0.015 | 0.123 | 0.610 |
| | above 11°C | **0.578** | -0.190 | -0.380 | 0.442 |
| | Eurasian-allochthons | | | | |
| | below 11°C | **-0.340** | -0.130 | 0.276 | 0.253 |
| | above 11°C | **0.606** | -0.280 | 0.277 | 0.663 |
| Neotropics | All species | | | | |
| | below 11°C | **-0.360** | -0.130 | 0.069 | 0.157 |
| | above 11°C | **0.545** | -0.070 | -0.320 | 0.489 |
| | GABI-allochthons | | | | |
| | below 11°C | -0.330 | -0.150 | **0.345** | 0.293 |
| | above 11°C | **0.757** | -0.230 | -0.010 | 0.397 |

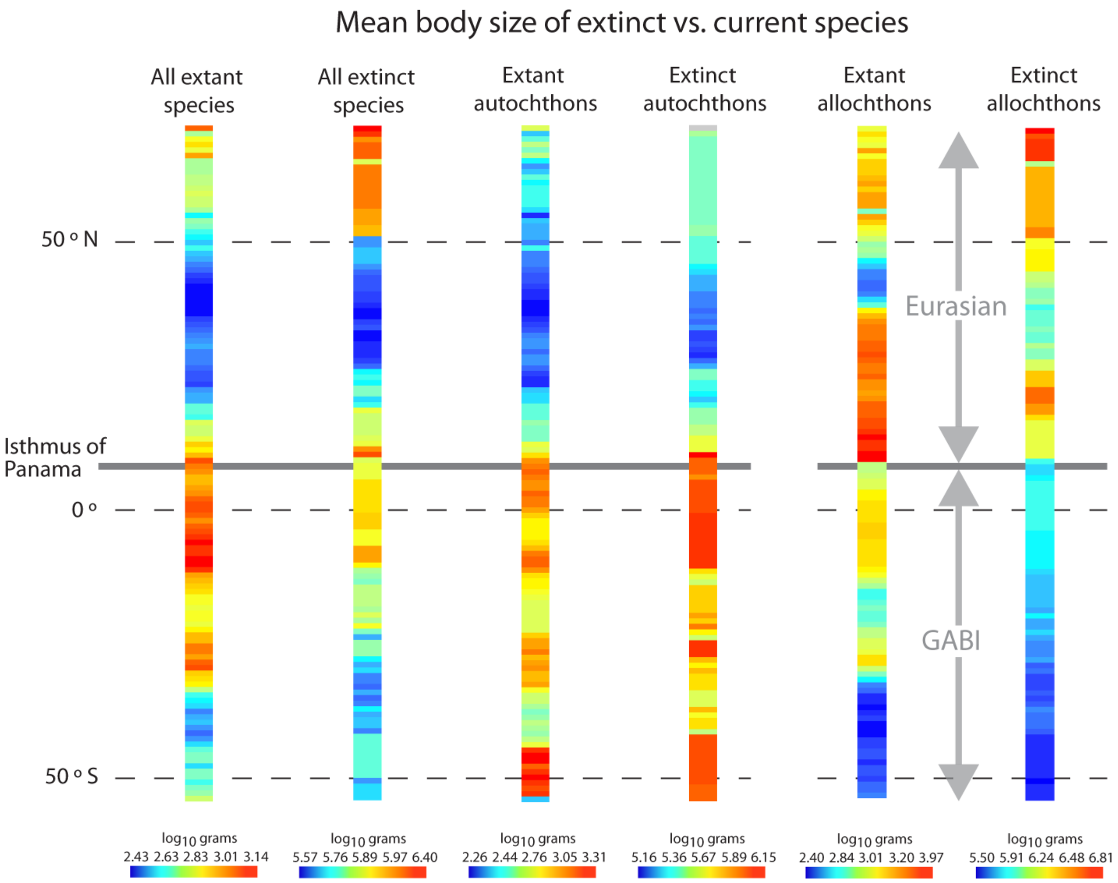
## Moran's *I* phylogenetic correlograms.

**Figure S4.** Moran's *I* correlograms showing phylogenetic autocorrelation in observed body size patterns for all species (A), allochthon species (B) and autochthon species (C). The distance intervals at which Moran's I values are calculated differs among groups since they are defined with equal number of pairs of species.



## Comparison of extant vs. extinct patterns in body size

**Figure S5.** Latitudinal patterns in mean $\log_{10}$-body size of extant and extinct mammals for all, autochthon and allochthon species. $\mathrm{Log}_{10}$-body size values were binned within 1° latitudinal bands for easier comparison to the maps in Figure 1. Species belonging to 61 genera of extinct mammals were included in the analyses based on the review by Koch & Barnosky (2006) on late Quaternary extinctions. Only Pleistocene megafaunal species and genera were considered (≥44 kg) since they are known to have selectively been driven extinct. Body size values were obtained from Smith et al. (2003), and for unspecific generic fossil records an average of the body sizes of the species within was used. Latitudinal geographic distribution of extinct species was reconstructed based on the fossil record of the selected species, assuming continuity in latitudinal distributions between maximum and minimum latitude for each species. This is because during the period for which we considered extinctions (i.e. Pleistocene), distribution of the clades underwent major latitudinal shifts. Fossil record data were downloaded from the Paleobiology Database (http://paleodb.org/ - url accessed 17 December 2011, using the following parameters: taxon name = Mammalia; time intervals = Early to Late Pleistocene; continents = North America and South America; include occurrences of extant or extinct taxa? = extinct only). Because of the low species richness of Eurasian allochthons in South America and of GABI allochthons in North America, comparison between extant and extinct allochthons was performed for Eurasian species in North America and for GABI species in South America. There is a general consistency in the latitudinal body size patterns of the extant and extinct groups of mammals. This is indicated by strong correlations of the latitudinal body size patterns of extant species with extant plus extinct species for all mammals ($r=0.952$), autochthons ($r=0.710$) and allochthons ($r=0.886$). Overall resemblance of extant-extinct patterns indicates that contemporary mammalian latitudinal patterns in body size are not strongly affected by the differential loss of large-bodied species; rather, current patterns would be reinforced by inclusion of extinctions. This is, however, a somewhat crude analysis, limited by the resolution of available data on extinct species. The database assembled to perform this analysis is available in the datadryad repository.



## Literature cited in figure S5

Koch, P. L. and A. D. Barnosky. 2006. Late Quaternary Extinctions: State of the Debate. Annual Reviews of Ecology, Evolution and Systematics 37:215–250.

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Smith, F. A., S. K. Lyons, S. K. Morgan Ernest, K. E. Jones, D. M. Kaufman, T. Dayan, P. A. Marquet, J. H. Brown, and J. P. Haskell. 2003. Body mass of late quaternary mammals. Ecology 84:3403.