Brevia

Anthropogenic impacts weaken Bergmann's rule

Søren Faurby and Miguel B. Araújo

S. Faurby (soren.faurby@bioenv.gu.se) and M. B. Araújo, Depto de Biogeografía y Cambio Global, Museo Nacional de Ciencias Naturales, Consejo Superior de Investigaciones Científicas (CSIC), Madrid, Spain. Present address of SF: Dept of Biological and Environmental Sciences, Univ. of Gothenburg, Goteborg, Sweden. MBA also at: InBio/Centro de Investigação em Biodiversidade e Recursos Genéticos (CIBIO), Univ. de Évora, Largo dos Colegiais, Évora, Portugal, and Center for Macroecology, Evolution and Climate, Natural History Museum of Denmark, Univ. of Copenhagen, Copenhagen, Denmark.

Humans have modified species distributions in most of the world's natural ecosystems. Analyses of species distributions tend to ignore these modifications, potentially masking the signatures of natural processes on them. We examine the strength of a classic pattern in ecology – the body mass-latitudinal relationship, aka Bergmann's rule – for all mammal species worldwide using both contemporary and estimated natural distributions. We show that human modifications of mammal species distributions lead to substantially underestimating the strength of the Bergmann's rule. We speculate that other broad-scale ecological patterns might be similarly affected.

Bergmann's rule was described in the 19th century (Bergmann 1848). It states that animal body sizes of related organisms are larger at higher latitudes and has been heavily discussed both at the intra and interspecific level in the last 150 yr (Clauss et al. 2013). Most interspecific tests of the Bergmann's rule relied on contemporary distributions of species, which have been greatly modified by humans. The extent to which human activities have modified the natural patterns is the focus of our analysis.

We compared body mass-latitude relationships of mammal species when analyzed at the interspecific level using contemporary distributions (Schipper et al. 2008) versus estimated contemporary distributions in the absence of human modification (hereafter termed natural ranges). The latter were estimated considering information on historical ranges, the climatic conditions in their contemporary distributions, and fossil co-occurrence patterns; all were used to indirectly infer the climatic preferences for extinct species (Faurby and Svenning 2015). We found that anthropogenic extinctions and human modification of distributions substantially changed the body size distribution of mammals outside equatorial latitudes (Fig. 1). In both Southern and Northern Hemispheres, median body sizes across species were smaller for current ranges compared to natural ranges. These differences in body sizes between current and natural ranges were significantly larger at higher latitudes (adjusted $R^2 = 0.81$, $p = 5 \times 10^{-15}$ for southern latitudes between 0 and 40 degrees; adjusted $R^2 = 0.76$, $p < 2 \times 10^{-16}$ for northern latitudes between 0 and 60 degrees; Supplementary material Appendix 1, Fig. A3).

These differences lead to weakening of the expected gradient of increased body masses with latitude (normalized slope of linear regression of maximum latitude on $\log_{body\ size}$ 0.121 ± 0.013 for natural ranges and 0.011 ± 0.014 for contemporary ranges) across all mammals ($Z = 5.71$, $p = 6 \times 10^{-9}$). When accounting for phylogeny, the strength of the Bergmann's rule is also stronger using natural ranges than contemporary ranges (0.026 ± 0.004 vs 0.017 ± 0.004) ($Z = 1.47$, $p = 0.071$). Analyses were repeated for numerous smaller clades, generally showing comparable patterns to that of all species combined (Supplementary material Appendix 1, Table A1, A2). Among the 21 orders with at least 3 extant species, 16 had more pronounced latitudinal slopes when examining natural ranges, 2 had identical slopes, and 3 had less pronounced slopes when contemporary ranges were used. (This pattern is significant as the probability of observing only 3 (or fewer) decreases out of 19 differences is 2.2×10^{-3}.) None of the three orders with less pronounced slopes are meaningful exceptions to the overall pattern. Two of them have smaller numbers of species, thus, inherently, great uncertainties in slope estimates (Peramelemorphia has 19 extant species and Pholidota has 8 extant species), while the third order (Dirpotodontia) has slightly less pronounced slope with a phylogenetic regression for contemporary ranges but substantially more pronounced slope with a standard regression (Supplementary material Appendix 1, Table A2).

Based on analysis of natural distributions, it appears that the Bergmann's rule is stronger among families or orders with larger body sizes, and occurring at higher latitudes. Since anthropogenic range contractions are more intense for larger species this pattern is, however, not visible based on contemporary distributions (Supplementary material Appendix 1, Fig. A2). The pattern for latitude is weak and non-significant but the relationship between body size and strength of Bergmann's rule is significant based on natural distributions at both the order (adjusted $R^2 = 0.13$, $p = 0.045$) and family level (adjusted $R^2 = 0.05$, $p = 0.010$)
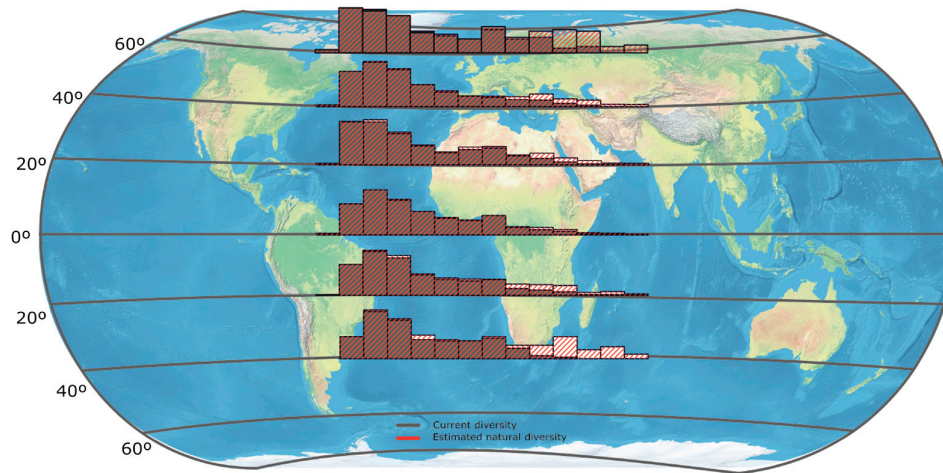
Figure 1. Log-transformed size distributions of mammals occurring at each latitudinal band based on contemporary ranges or estimated natural ranges. The x-axis shows log10 transformed body sizes binned into classes with a width of 0.5. The y-axis is not standardized between latitudes and the maximum diversity in a size class is 29 for 60°N, 141 for 40°N, 163 for 20°N, 301 at the equator, 196 for 20°S and 33 for 40°S. An alternative representation of the figure with more readable legends is shown in Supplementary material Appendix 1, Fig. A1.

but non-significant based on contemporary ones at both the ordinal (adjusted $R^2 = -0.05$, $p = 0.917$) and family level (adjusted $R^2 = -0.001$, $p = 0.817$).

Like with other 'rules' there are exceptions. For example, the South American fossorial tuco-tocus (Ctenomyidae) (Supplementary material Appendix 1, Table A1) have opposite trends of body size distribution, with species bodies increasing with decreasing latitude (Medina et al. 2007) – a pattern that remains unaltered with estimated natural ranges.

The full extent to which human modification of species ranges truncates estimated relationships between species ranges and other variables remains unknown. It is well known that species distributions are generally not in equilibrium with climate (Araújo and Pearson 2005), owing to historical climatic fingerprints (Araújo et al. 2008) and lags in colonization of poorly dispersing species (Svenning and Skov 2007). It is less frequently acknowledged that this lack of equilibrium can be increased by non-random spatial patterns of human driven extinctions (Channel and Lomolino 2000; but see Blackburn and Gaston 1998). The effect of all of these factors combined is bound to generate biases in macro-ecological analysis that rely on contemporary species distributions to make inferences of any kind, and human effects are likely pervasive (Faurby and Svenning 2015).

But why would Bergmann's rule be particularly affected? We propose that the recorded bias arises, at least partly, as a consequence of the spatial distribution of range contractions and extinctions beginning in the Late Pleistocene (Barnosky et al. 2004). In particular, two of the world's tropical regions (Sub-Saharan Africa and southeast Asia) have experienced very limited late Pleistocene extinctions whereas extinctions have been higher in all temperate regions (Sandom et al. 2014). If true, our analysis of the Bergmann's rule suggests that, at least for mammals, it should be very difficult to find a global biodiversity pattern based on contemporary distributions that can be analyzed without biases.

Supplementary material (Appendix ECOG-02287 at < www. ecography.org/appendix/ecog-02287 >). Appendix 1.

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