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ECOLOGICAL SOUNDING

The geography of body size – challenges of the interspecific approach

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ABSTRACT

Recent compilations of large-scale data bases on the geographical distributions and body sizes of animals, coupled with developments in spatial statistics, have led to renewed interest in the geographical distribution of animal body sizes and the interspecific version of Bergmann's rule. Standard practice seems to be an examination of mean body sizes within higher taxa on gridded maps, with little regard to species richness or phylogeny. However, because the frequency distribution of body sizes is typically highly skewed, average size within grid cells may differ significantly between species-rich and species-poor cells even when the median and modal sizes remain constant. Species richness influences body size patterns because species are not added to communities at random in relation to their size: areas of low diversity are characterized by a higher range of body sizes than is expected by chance. Finally, a consideration of phylogenetic structure within taxa is necessary to elucidate whether patterns in the geography of size result from turnover between or within intermediate taxonomic levels. We suggest that the highest and lowest quantiles of body size distribution be mapped in order to expose possible physiological or ecological limitations on body size.

Keywords

Bergmann's rule, body size, climate, community assembly, geographical variation, species richness, taxon replacement.

In 1847 Carl Bergmann proposed that smaller homeotherms should, in general, inhabit warmer areas than larger-bodied species. He reasoned that surface to volume ratios influenced animal sizes because larger ratios facilitate heat loss, whereas small ratios facilitate heat retention, and in similar-shaped animals larger individuals have lower ratios (Bergmann, 1847). The association between cold climates and large body size, subsequently termed Bergmann's rule, is probably the first and best-known ecogeographical generalization. Here we consider some current approaches to testing geographical patterns in body size, such as Bergmann's rule. We discuss how large-scale data bases of species distributions, body sizes and environmental variables enable us to examine some of the factors that affect size evolution and size-related community assembly.

Bergmann probably envisioned the mechanism linking body size with climate to act at several levels. He stated that: 'We are going to consider the distribution of smaller and larger homeotherms over the earth's surface ... in order to see how far the effects of our rule are suggested in this distribution' (Bergmann, 1847, p. 629; all quotes are from the translation in James, 1970). Thus he inferred that assemblages of homeotherms would be characterized by smaller body sizes in warmer areas. However, Bergmann probably thought that this hypothesis applied mostly to closely related species (especially congenerics) rather than to broader taxonomic groups: 'If there are genera in which the species differ only in size, the smaller species would demand a warmer climate' (Bergmann, 1847, p. 638). Bergmann also thought his rule should be strongest within species (p. 677): 'Is it not to be expected that races which should be more similar to each other in their organization than the species of a genus, should be more dependent on their size ratios in their distribution than the latter? This sounds obvious'. Thus Bergmann obviously thought his rule could apply at various levels: for all homeotherm species at some higher taxonomic level (e.g. species within families or orders), for species within genera, and for populations within species, although he probably stressed the second pattern more than the others.

Rensch (1938) and Mayr (1942, 1956) claimed that Bergmann's rule is a purely intraspecific phenomenon, and should be studied at that level. They reasoned that in Bergmann's era geographical

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variants were treated as different species, whereas under the new (at the time) taxonomy the very existence of a size cline proved that members of different populations were conspecifics. Recent meta-analyses have focused on testing the generality of Bergmann's rule, and finding attributes that distinguish between species that show latitudinal size clines and those that do not. Bergmann's rule was found to hold within the majority of endotherm species (Ashton *et al.*, 2000, Meiri & Dayan, 2003), although in ectotherm species, patterns seem more complex (e.g. Atkinson, 1994, Ashton, 2002, Ashton & Feldman, 2003). Attempts to find which species tend to show size clines, however, have found only weak and idiosyncratic correlates for this tendency (e.g. Ashton, 2004, Meiri *et al.*, 2004, 2007).

Lindsey (1966) was probably the first to quantify the body size patterns of species within higher taxa (families, orders and classes) at different latitudes. He showed that size frequency distributions of fishes and amphibians (but not of reptiles) tended to peak at higher body sizes in colder areas. Recent developments in spatial statistics, combined with compilations of large-scale climatic data, animal geographical distributions and body sizes enable rigorous assessment of the geographical distributions of body size. Here, instead of examining size patterns within species, each species is assigned a single body size, and the spatial distribution of sizes is studied in multispecies assemblages.

Testing for correlates of geographical variation in body size of species within higher taxa, however, presents several analytical challenges. Blackburn *et al.* (1999) advocated using species within higher taxa, arguing that studies that examine body sizes of large numbers of related species across a range of latitudes have the best chance of detecting a pattern. They reasoned that phylogenetically more restricted data sets (e.g. species within genera) can miss the true pattern because much of the size cline is expected to result from higher-taxon turnover (Blackburn *et al.*, 1999). This broad-scale approach has recently become popular in macroecology, with studies usually involving: (1) mapping the distributions of species in the focal taxon; (2) estimating species-specific body sizes; (3) averaging log-transformed body sizes within grid cells (equivalent to the log of the geometric mean of the raw data); and (4) regressing the averaged body sizes on latitude, temperature and other climatic variables to assess which factors influence size (Blackburn & Hawkins, 2004; Olalla-Tarraga *et al.*, 2006; Rodríguez *et al.*, 2006).

While such an approach is conceptually straightforward, we suggest that more emphasis should be given to issues such as size indices, species richness and the breadth of taxonomic/phylogenetic scope.

QUANTIFYING BODY MASS IN SPATIAL UNITS

First, we argue that using the arithmetic mean of the log-transformed masses as a measure of the body size of a grid cell reveals only part of the picture. Body size distributions are often right-skewed (Maurer *et al.*, 1992; Gardezi & da Silva, 1999; Greer, 2001). The tendency of assemblages to show modal size distributions and skewed size distributions probably depends to a large extent on the spatial and taxonomic scales of a particular study. However, species-poor cells can contain large animals, but are less modal than species-rich cells (e.g., Brown & Maurer, 1989; Brown & Nicoletto, 1991; Cardillo, 2002). Thus, species-poor cells will be characterized by larger mean body sizes, but similar modal size classes, than species-rich cells, the median showing an intermediate tendency (provided the distribution is right-skewed). Consider an extreme example with two grid cells: one with a 100 kg ostrich and nine 30 g passerines, the other with an ostrich and 100 such passerines. In the first cell the mean mass (using log-transformed data) would be 68 g, while the median and mode would be 30 g. Similarly, in the second cell the mean mass would be 33 g, but the median and mode, at 30 g, would be identical to those of the first cell. Thus, the mean tends substantially to overestimate other measures of central tendency where there are few small-bodied species, even when using log-transformed data. If, for example, the species-rich cell is tropical and the species-poor one more temperate, using means will show a positive association between size and latitude whereas the mode and median will show no such relationship. Thus, the biological conclusion will depend on the measure of central tendency one uses. Using the mean, for example, may lead to the conclusion that small species cannot tolerate low temperatures, despite the fact that some small species do occupy high latitudes, albeit in low numbers. We therefore suggest that the median body size or the modal size class within cells be used as size indices. If body size frequency distributions are not modal the median is preferable to the mode.

ACCOUNTING FOR THE EFFECTS OF SPECIES RICHNESS

We also believe that species richness should be taken into account when geographical variation in size of species within higher taxa is analysed. This is because species richness is often strongly correlated with the mean or median mass within a grid cell. Blackburn & Gaston (1996) showed that species richness was a better predictor of body mass than latitude in New World birds. Cardillo (2002) reasoned that this is because the size range within grid cells remains relatively stable through space, while species richness increases towards lower latitudes mainly by the addition of small species. Disregarding species richness makes the implicit assumption that, with respect to body size, species are added to assemblages/cells at random. Comparing the size of the largest species within a taxon across multiple geographical areas representing different temperature regimes, Makarieva *et al.* (2005) showed that the largest species within each of 24 taxa of poikilotherms tended to occur in warmer regions. However, their approach implicitly assumes that species are not added at random, but that both the largest and smallest members of a community that can live in an area will be present even in species-poor cells. We suggest that both assumptions are unlikely. Although the body mass range increases with increasing sample size (Marquet & Taper, 1998; Boback & Guyer, 2003; Meiri *et al.*, 2005), it probably increases faster than expected if species were simply added to assemblages at random (Figure 1):

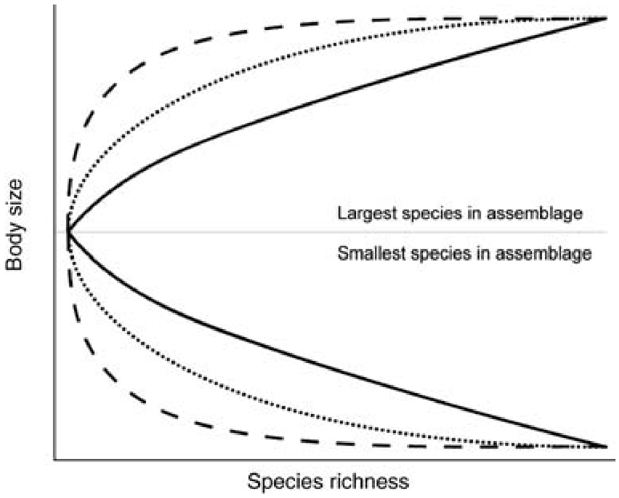

Figure 1 Body size as a function of species richness. The relationship between species richness and range in body size under three different assumptions of community assembly: random draw (solid line, Blackburn *et al.*, 1999); mostly modal-sized species added at high-richness cells (dotted line, Brown & Nicoletto, 1991; Cardillo, 2002); and entire size range present at very low richness (dashed line, Makarieva *et al.*, 2005).

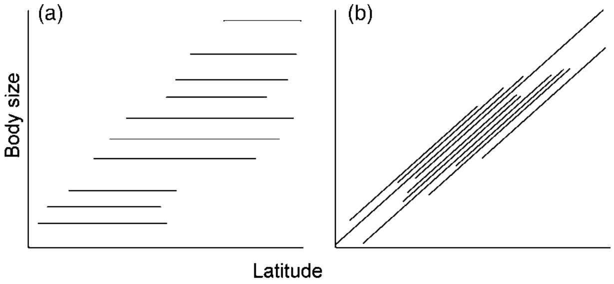

Figure 2 The relationship between body size and latitude. Each line represents the relationship between body size and latitude for species within a family (or other higher taxon). Body size increases with latitude could occur due to: (a) larger-bodied families occurring at higher latitudes; or (b) larger-bodied species within families occurring at higher latitudes.

the shape of the body size frequency distribution often changes from highly modal, usually peaking below the median of the mass spectrum, to more uniform as richness decreases (Brown & Nicoletto, 1991). Thus it is not that small species cannot inhabit colder regions, higher latitudes or regions of low species richness, but simply that there is a strong interaction between species richness and body size (Cardillo, 2002). Where species richness is low, the contribution of small-bodied species to the average body mass is small and since species richness is typically lower at high latitudes the average body mass of taxa at higher latitudes will tend to be high.

An interesting way to examine whether turnover is responsible for body size patterns can be to map separately the distribution of body size in the highest and lowest quantiles of the body size distribution. This will enable us to inspect whether, for example, very small animals do not inhabit the coldest area, suggesting some physiological limitation on body size. Similarly, the proportion of the largest and smallest species, relative to total species richness, could be examined to see if small species are underrepresented in cold areas or large species are underrepresented in warm ones. These approaches are rarely taken. A more sophisticated approach would attempt to quantify and map separately the degree to which the body size of an assemblage (or grid cell) is determined by shared evolutionary history or by ecology (e.g. Gittleman & Kot, 1990; Diniz-Filho *et al.*, 1998). Furthermore, if the ecological component is to be of value, then multiple measures of body size within a species should be taken across its range.

PHYLOGENETIC ISSUES

The latter approach draws attention to two additional problems associated with the study of species within higher taxa, both of which relate to taxonomy and phylogeny. First, if gridded data are used (with each grid cell contributing one data point), then it may be beneficial to examine patterns within more restricted taxa, rather than just treating all species in some higher taxon regardless of phylogeny. For example, if a class is being studied, then it will be worthwhile also to examine intra-ordinal, intra-familial and intra-generic patterns to see whether patterns remain similar across all scales (Fig. 2). If so, a common mechanism can be safely invoked. The class pattern may also be caused by turnover of lower taxa (Blackburn *et al.*, 1999), suggesting that variation in body size should be analysed at multiple taxonomic levels (Fig. 2). Alternatively, it could be a combination of the two.

The second problem with studying species within higher taxa is the question of how broad the taxonomic scope of the analyses should be. The finding that the mean size of European mammals, for example, increases from north to south (Rodríguez *et al.*, 2006) may be largely due to the absence of bats from northern latitudes. Whether this absence is due to their small size is not at all clear – it may just result from the relative scarcity of their insect prey in the cold parts of the year. It is likewise reasonable that the fact that bats as a group show the reverse to Bergmann's rule is because the large fruit bats (Megachiroptera) cannot inhabit higher latitudes because of food limitation, not because they are large. Thus body size patterns that are driven by taxon turnover may not be a result of selection on body size *per se*, but instead stem from selection on other natural-history attributes. Therefore, simply pooling all species of some higher taxon may not be very informative for inferring the environmental correlates of body size. An obvious solution to this problem would be to map the geographical distribution of body size with the data subdivided according to some life-history or ecological trait. For example, Rodríguez *et al.* (2006) examined the body size distribution of European mammals by splitting them into dietary groups. An alternative approach is to treat species, rather than grid cells, as the unit of analysis and perform a phylogenetic correction, with measures of the climate conditions experienced by each species (temperature, primary productivity, etc.) as the explanatory variable and body size as the response. Under Bergmann's rule we would expect shifts to colder regions to be accompanied by shifts towards larger size. While this method does not easily lend itself to mapping patterns of body size (Ruggiero & Hawkins, 2006), it has the advantage of being insensitive to species richness. It is also conservative in that every species is counted only once, at the centroid of its range, whereas with most grid-based analyses, each species contributes the same body size value to each cell in which is occurs. Thus, large ranged species may be overrepresented in grid-based analyses. Large range size also presents problems for species-level studies because it may not be appropriate to take a single value for body size and its possible environmental correlates, which may show considerable variation across space (Meiri *et al.*, 2007). Only extensive sampling from throughout the range and the assignment of different body size values for each cell can overcome this problem. Furthermore, this method will tend to portray species with very large ranges as occurring at low latitudes (e.g. the puma, *Felis concolor*, with a latitudinal range > 100° will be portrayed as roughly equatorial). We suggest that the most powerful studies will be those that used a combined approach of grid cell and species-level analyses.

CONCLUDING REMARKS

Mapping body sizes offers exciting opportunities for understanding the selective pressures behind size evolution and community assembly. We urge, however, that caution be practiced when interpreting the results of such analyses. A simple representation of spatial patterns in average body mass is not very informative. Species richness should be corrected for, body size ranges should be examined, and within-taxon patterns of turnover across multiple taxonomic or phylogenetic scales should be studied if we are to reach good understanding of the forces that drive spatial patterns of body size.

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BIOSKETCHES

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