ECOLOGICAL SOUNDING

Macroecology and the hierarchical expansion of evolutionary theory

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ABSTRACT

The constraint envelope describing the relationship between geographical range size and body size has usually been explained by a minimum viable population size model, furnishing a strong argument for species selection if geographical range size turns out to be 'heritable'. Recent papers have questioned this assumption of nonzero geographical range heritability at a phylogenetic level, meaning that the logic that constraint envelopes provide support for higher-level selection fails. However, I believe that analysis of constraint envelopes can still furnish insights for the hierarchical expansion of evolutionary theory because the fitness furnished by variation in body size, which is frequently measured as a highly 'heritable' trait at the species level, can be partitioned into anagenetic and cladogenetic components. The constraint envelope furnishes an explicit mechanism for large-body biased extinction rates influencing the distribution of body size. More importantly, it is possible to envisage a scenario in which anagenetic trends driving an increase in body size in higher latitudes within species (Bergmann's rule) are counteracted by available habitat area or continental edges constraining overall species distribution in these higher latitudes, increasing the probability of extinction. Under this combined model, faunas at higher latitudes and under habitat constraints may reach equilibrium points between these opposing hierarchical adaptive forces at smaller body size than faunas with less intense higher-level constraints and will tend to be more right-skewed.

Keywords
Bergmann's rule, body size evolution, constraint envelope, extinction, geographical range size, latitudinal trends, macroecology, macroevolution, minimum viable populations, species selection.

Species selection is usually defined as the differential reproduction or extinction of species caused by heritable differences in the fitness of species-level traits, and it is a basic argument for the validity of the hierarchical expansion of evolutionary theory (Gould, 2002). Most of the debate is centred on theoretical arguments about the plausibility of these higher-level mechanisms and the definition of species-level traits, without clear and definitive empirical tests (Grantham, 1995; Webb & Gaston, 2003).

Brown & Maurer (1987, 1989) proposed that the macroecological relationship between geographical range size and body size is defined by a constraint envelope in the bivariate space (Fig. 1), which set up the conditions for a species selection process. The lower-right bound of this envelope is a probabilistic ('fuzzy') line above which species have a low probability of extinction (see Brown, 1995 and Gaston & Blackburn, 2000; for details). Because large-bodied species require more individual

energy, they are forced to live in low local ecological densities and, consequently, minimum viable populations must occupy large geographical extents [Kelt & Van Vuren (2001) recently found support for this model at a population level, by analysing patterns of home range ecology and macroecology]. Large-bodied species that are constrained to small ranges will have higher probabilities of extinction, thus creating a nonrandom distribution of species in the bivariate space. On the other hand, small-bodied species (below the modal size of around 100 g for mammals) require resources of high energetic concentration and so must also increase their geographical ranges by living on habitat-specific patches that may be widely distributed in space (although they could still maintain minimum local populations even within small patches) (Maurer, 1999). By this logic then, this envelope will appear only for assemblages of organisms with large variability in body size across species and for which
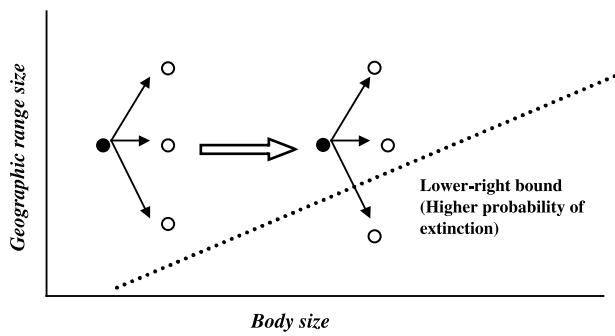
Figure 1 Bivariate macroecological space formed by geographical range size and body size, showing body size evolution between ancestral (black circles) and their descendants (open circles) species, linked by small arrows (speciation) toward larger body sizes under a zero heritability range size pattern. Along the *X*-axis, ancestor and descendent are relatively similar, but along the *Y*-axis different values could be found in the descendants. However, the descendants of large-bodied ancestral species have a higher probability of extinction because they can be driven to below the lower boundary of the constraint envelope. So, under certain circumstances, an increase in body size by Bergmann's rule within species may be counteracted by opposite trends at higher hierarchical levels, while extinction probability is smaller if speciation or intraspecific trends reduce body size.

constraints to increase local densities are strong, which in turn depends on different life history and demographic parameters (see Blackburn & Gaston, 2001; Maurer & Taper, 2002).

Grantham (1995) pointed out that, under this model, the fitness of a species largely depends on geographical range size and, assuming that range is heritable, that this envelope constraint space and the associated minimum viable model proposed by Brown & Maurer (1987, 1989) to explain it, furnishes a strong argument for species selection. However, he also pointed out that '… if range turns out not to be heritable, then this example cannot be considered species selection'. In this context, Webb & Gaston (2003) recently tested the 'heritability' of geographical range size and questioned the results obtained by Jablonski (1987), one of the primary papers supporting higher-level selection (see also Lee & Doughty, 2003). Webb & Gaston (2003) showed that geographical range size is not 'heritable' and that variation in this trait is better explained by 'the history of the place' and not by intrinsic biological traits (see also Brown *et al.*, 1996). This is expected if range size is viewed as being driven by interactions between organismic traits and the environment (Hawkins & Diniz-Filho, 2002; Webb & Gaston, 2003), and indeed many previous papers have shown that both geographical range size and other life history and demographic traits are not strongly structured across phylogenies and are very labile (Gaston & Blackburn, 1997; Diniz-Filho & Tôrres, 2002; see also Freckleton *et al.*, 2002 for a recent review). Thus, species selection processes cannot explain or drive evolution of geographical ranges or their statistical distribution across species within a clade.

Yet, despite Grantham's (1995) claims, I believe that Brown & Maurer's (1987, 1989) original model still furnishes insights and

empirical validation of the hierarchical expansion of evolutionary theory, in terms of how the evolution of body size in the macroecological space is driven. This is because the fitness furnished by variation in body size, which is frequently measured as a highly 'heritable' trait at species level, could be partitioned into two (or more) hierarchical components (see below). In this way, we must assume a less restrictive definition of species selection, which can act on aggregate (and not only on emergent) traits, such as body size (Lloyd & Gould, 1993; Simons, 2002; see Grantham, 1995 for definitions).

The evolution of body size in macroecological space, starting from any initial value, will track a clear pathway (Fig. 1), as follows. Because body size is highly 'heritable' at the species level, species will change relatively slowly across the *X*-axis of the bivariate space, most frequently toward larger body size values, by different mechanisms (for reviews see Maurer *et al.*, 1992; Jablonski, 1996; Kelt & Brown, 1998; Maurer, 1998, 1999). On the other hand, following Webb & Gaston (2003), a low phylogenetic heritability of geographical range sizes implies that the newly formed species, although quite close to its ancestor along the *X*-axis, may be 'anywhere' along the *Y*-axis (geographical range size). However, independently of the factors that drive the evolution of body size, any changes increasing body size will lead, in principle, to higher probabilities of extinction because the minimum geographical range size necessary to avoid stochastic extinction will be gradually larger (Fig. 1). Note that these extinction processes may occur independently of the higher Darwinian fitness provided by a large body size of the individual organisms within a species, and that this effect furnishes an explicit mechanism for the large-body biased extinction rates simulated by Maurer *et al.* (1992). Also, these evolutionary dynamics will lead to the well known negative correlation between body size and net diversification rate (speciation minus extinction), at least for mammals and birds (Dial & Marzluff, 1988; Maurer, 1999; but see Owens *et al.*, 1999). Most importantly, irrespective of whether body mass evolution is due to directional, broad-scale trends acting at clade level by niche shifts and active drive (Alroy, 1998), or by individual Darwinian competitive advantages within species increasing body size values of the entire species (by aggregation) (e.g. Smith *et al.*, 1995), any processes increasing body size will be continuously counteracted by increasing probability of extinction (species level processes) due to geographical range collapse caused by eventual habitat shifts. So, even under a low or zero geographical range size heritability, evolution of body size in macroecological space is constrained by minimum geographical range size and, consequently, also subjected to species level processes (Marquet & Taper, 1998).

Indeed, as pointed out by Vrba (1989), the crucial test for species selection is whether it can oppose selection at the lower (hierarchical) level. So, it would be necessary to imagine a scenario for opposite trends in body size evolution through macroecological space, within and among species. Perhaps combining constraint envelope analyses and Bergmann's rule into the same framework would provide an explicit test of this scenario with opposite adaptive forces. After a long debate, some recent papers are once again finding support for Bergmann's rule (see Ashton

et al., 2000; Freckleton *et al.*, 2003; Meiri & Dayan, 2003), which claims that endothermic species living in cooler climates (usually higher latitudes) tend to be larger than their relatives in warmer climates. Despite many studies attempting to identify the mechanisms controlling this geographical pattern, all explanatory models within species are based on different physiological and ecological processes related to the advantages provided by individual adaptations to cold environments, within species (Meiri & Dayan, 2003). Thus, larger individuals are favoured at higher latitudes and, by aggregation, this may drive evolution towards larger body sizes within these species and, eventually, even among closely related species by sequential speciation events. It follows that, in this case, micro- and macro-evolutionary mechanisms would be coupled and an increase in the average body size of species should be expected for faunas at higher latitudes (although the total range of variation in species body sizes may be undetermined, due to long term historical events of colonization by clades with different initial body sizes). But this will occur only by assuming that species evolving toward larger body sizes will be able to expand their geographical ranges and avoid extinction.

What if the available habitat area, or even continental edges, constrain overall species distribution in these higher latitudes, in such a way that maximum geographical range tends to be smaller than the minimum viable range size? According to Brown & Maurer's (1987, 1989) model, the new species at these higher latitudes are more prone to extinction than their counterparts in lower latitudes, or than small-bodied species, independently of the high fitness of the individuals that compose these populations. Thus, the distribution of body sizes at the faunal assemblage level would be determined by an equilibrium between opposing adaptive forces at the two hierarchical levels (Fig. 2), and faunas at higher latitudes under habitat and geographical constraints may reach an equilibrium point at a smaller average body size than faunas not subjected to these constraints. Because many clades with different initial body sizes are simultaneously found in the region and since small-bodied species are less sensitive to these opposing forces (and could achieve viable populations and avoid extinction even with small geographical ranges), body size of faunas at higher latitudes and under geographical constraints would be not only smaller on average for each clade, but also more right skewed (see Fig. 2 and Maurer *et al.*, 1992; Marquet & Cofre, 1999).

Of course, because of the many confounding effects, an empirical test of this complex scenario would be a difficult task. It would be necessary to find a geographical region where habitat area for a large taxonomic assemblage is constrained at higher latitudes, compared to other regions, and to obtain body size data showing Bergmann's rule within species (taking into account that these effects are more difficult to detect in small-bodied species, due to habitat specialization or small geographical range sizes — see Freckleton *et al.*, 2003). For example, it would be possible to compare parameters (means, ranges, skew and slopes of body size against latitude) of both intraspecific and interspecific body size variation in North and South American mammals, since continent shapes show opposite geometric constraints and body size distribution varies among them in many
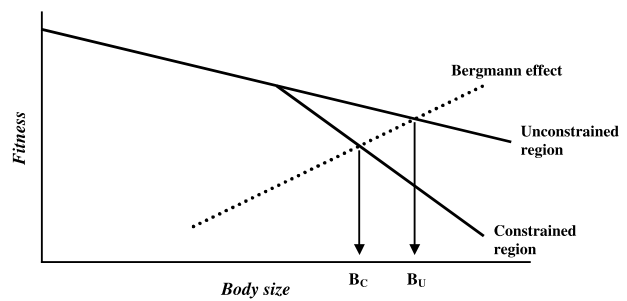

Figure 2 Fitness functions of body size at higher latitudes, in which intraspecific body size tends to increase under Bergmann's rule (dashed line), while the species level process (extinction under the constraint envelope — solid lines) tends to decrease it. If there are geographical or habitat constraints in the region, above a given critical body size the species will not be able to persist given minimum viable population model constraints and so equilibrium values between processes at distinct hierarchical levels will be smaller for habitat- or geographically-constrained (B_C) than for unconstrained (B_U) regions. The constraint envelope determines the slope of the geographically unconstrained fitness function. Because historical colonization processes influence the overall range of body sizes (clades) present in a region, these distinct equilibrium points for large-bodied species should increase extinction bias in geographically constrained regions and so the body size distribution for the entire fauna will tend to be more right-skewed (see Maurer *et al.*, 1992).

ways (see Mourelle & Ezcurra, 1997; Marquet & Cofre, 1999; Bakker & Kelt, 2000). But it would also be necessary to take into account the complex history of colonization by different clades (e.g. the Great American Biotic Interchange — see Lessa & Valkenburg, 1997) and phylogenetic effects (perhaps using pairwise comparisons for clades currently living in opposite continental extremes), the palaeoclimatic changes determining past adaptations within species living in different habitats, scaling and sampling bias, and recent anthropogenic effects, in an explicit spatial context. Another confounding factor is that, in some instances, intraspecific adaptations toward smaller body sizes may also be associated with a reduction in area (e.g. in islands), by a mechanism involving decreasing energetic requirements to allow higher local population densities and avoid extinction (Lomolino, 1985; Marquet & Taper, 1998). After keeping constant all these confounding factors, the model presented here predicts that extinction rates should be higher for large-bodied species living at higher latitudes and for which habitat and geographical constraints exist, even if the intraspecific Bergmann's rule drives evolution toward large body sizes in these regions (an effect that would be comparatively inferred by examination of species in the same clade, but living in geographically or habitat unconstrained regions). Despite difficulties, if such a scenario could be even tentatively measured, it would be theoretically possible to partition the fitness of body size into different hierarchical components. This would fulfil recent calls for more theoretical emphasis and consilience of the macroecological research programme (Brown, 1999; Maurer, 2000), furnishing a research agenda for years to come.

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BIOSKETCH

José Alexandre Felizola Diniz-Filho is interested in statistical methods applied to macroecology and evolutionary biology. Current projects involve the application of spatial autocorrelation analysis and phylogenetic comparative methods to understand ecological processes associated with latitudinal gradients in species richness and to establish priority areas for conservation.