Body Size and the Species-Area Relationship Parameters

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2005

Introduction

Biodiversity conservation is a major scientific issue today. Understanding how biodiversity is distributed across Earth and how it is related with ecosystems processes is of great concern in order to predict its likely response to global environmental change and to identify the most effective schemes for conservation and sustainable use. Some spatial patterns as the species area relationship have been described, although understanding why these patterns appear is still not clear.

Body size is a critical feature when studying processes of energy uptake and use by organisms. It may affect behavioural patterns at several levels (feeding, reproduction strategies, space use, etc.). However, studies about body size relationships usually follow an allometric methodology in which other differences besides body size are neglected. This approach can be misleading, especially because the statistical method used, the linear regression which tends to face deviations from the calculated equation as “measurement errors”. In fact, these deviations should be seen as an expression of the differences between organisms due to their unique evolutionary histories.

The DEB theory suggests a different approach to the study of body size scaling relationships, considering three levels of body size scaling relations.
At the primary level the parameters that are related with the physical design of the organism scale with volumetric length. Then, at the secondary level, scaling relationships for eco-physiological processes, which can be described as functions of primary parameters and state variables, are derived from the scaling relations defined at the prior level. Finally the tertiary scaling relationships are related to processes belonging to the population level and how individual characters may influence macro-ecological patterns. Body size could be inversely related with population abundance, because maximum ingestion rate and maintenance costs

are directly related with body size and environmental resources are limited, therefore a population of more demanding organisms would have a smaller effective than a population of less demanding organisms.

However, predictions made at this level are weaker than the ones made at the first two levels, because at this stage there are much more variables influencing the processes, for example, the interactions between the individuals.

Energy requirements can explain how population density decreases with body size (Jetz et al., 2004). Greater energy availability is assumed to enable a greater support of biomass in an area. In turn, this enables more individual organisms to coexist, and thus more species at abundances that allow the maintenance of viable populations. The result is an increase in species richness with energy availability, more usable energy should allow for a greater subdivision of energy into more distinct niches (Gaston, 2000).

In other words because all aerobic eukaryotes utilize the same basic biochemical pathways– glycolysis and the tricarboxylic acid cycle – their metabolism is fundamentally very similar. Consequently, variation in metabolic rate among individuals and species of eukaryotes is due primarily to two factors: body size, which affects the rate of uptake and distribution of resources, and temperature, which affects the kinetics of biochemical reactions. (Brown et al., 2002) Body size will affect organisms' physiology (secondary scaling relationships) and ultimately populations' dynamics (tertiary scaling relationships).

One of the few relationships that have reached the status of a law in ecology is the species-area relationship or SAR (Brown & Lomolino, 1998). It states that the number of species S in a sampling area of size A, is given by the following power law,

$$S = c\, A^{z}$$

where c is a constant that depends on the taxonomic group and the region being studied and z is a constant that depends on the sampling regime and scale (Rosenzweig, 1995).

It has been hypothesized that z depend on other variables as well, such as latitude/biome and taxon (Preston 1962, Connor and MCCoy, 1979).

Although this issue has been strongly discussed there is not still an agreement about the real meaning of these parameters and how they are affected by the referred variables. There is no doubt, nevertheless, about the importance of the estimation of species-area curve parameters in biogeography and conservation biology. The SAR has provided a basis for identifying biodiversity hotspots (Myers et al., 2000) and forecasted biodiversity loss as a function of habitat fragmentation (Adler, 2004).

The purpose of this essay is to discuss how SAR parameters may be explained by body size and organisms energetic needs (here represented by thermal behavior).

Methods

We worked with a database composed by more than 100 entries (see Appendix 1). The values of the parameters *c* and *z* were obtained in two ways: directly from the literature or estimated from the graphics presented in the articles.

The arthropods were associated with a small body size and the chordates with a large one, reptiles and arthropods represented the ectotherms and birds and mammals the endotherms.

We also tested for differences between parameters values of different latitudinal levels for all the taxa and for specific taxa: insects, mammals, birds and reptiles. We considered 4 zones on each hemisphere: [0º, 20º], [20º, 40º], [40º, 60º] and >60º.

Results

According to results *z* values for arthropods (small bodied organisms) and chordates (large bodied organisms) are significantly different (Fig.1). However these differences were not noticed when the groups were subdivided in lower taxa (Fig.2). *Z* values for endotherms and ectotherms were not significantly different (Fig.3). However, the only difference between these two groups and the later ones is that ectotherms comprise arthropods plus reptiles and endotherms, chordates minus reptiles. So, we decided to analyse if the reptiles alone were significantly different from each of the groups in which they were included (large body organisms and ectotherms). Results indicate that *z* values for reptiles are not significantly different from the values for other chordates, but are different from the values of the other ectotherms. Results for these analyses are presented in Table 1.

All the tests for *c* values did not result in significant differences between the analyzed groups (Table 1).

There were not found any differences in *z* and *c* values with respect to latitudinal zones, when all the taxa were considered. Analyses with isolated taxa indicated differences between some pairs, for insects and birds (both parameters) and reptiles (just for *c*). (Table 2)

Table 1 – T-tests and One-way ANOVA results for the effect of body size and energetic needs on z and c parameters (* - p<0.05)

Z value			
	t	df	
Arthropods vs. Chordates	-2.61035*	98	
Endotherms vs. Ectotherms	-1.74084	98	
Reptiles vs. Other chordates[1]	-0.929189	72	
Reptiles vs. Other ectotherms[2]	-2.47576*	30	
	MS	df	F
Lower taxa[3]	0.039426	4	2.3633
C value			
	t	df	
Arthropods vs. Chordates	-0.574372	86	
Endotherms vs. Ectotherms	-1.55581	86	
	MS	df	F
Lower taxa[3]	0.62425	4	2.0573

1 – Other chordates: Birds and mammals

2 – Other ectotherms: Arthropods

3 – Lower taxa: Insects, Other arthropods, Reptiles, Birds and Mammals

Table 2 – One-way ANOVA results for the effect of latitude[1] on z and c parameters (* - p<0.05)

Z value			
	MS	df	F
All taxa	0.029490	6	1.6880
Insects	0.069123	3	9.20860*
[0º, 20º S] s.d. [0º, 20º N]			
[0º, 20º S] s.d. [20º N, 40º N]			
[40º N, 60º N] s.d. [0º, 20º N]			
[40º N, 60º N] s.d. [20º N, 40º N]			
Reptiles	0.001761	2	0.18139
Birds	0.054011	6	3.4149*
[0º, 20º S] s.d. [20º N, 40º N]			
Mammals	0.016253	4	1.33544
C value			
	MS	df	F
All taxa	0.029490	6	1.6880
Insects	1.169021	4	6.41795
[40º S, 20º S] s.d. [20º S, 0º]			
[40º S, 20º S] s.d. [20º N, 40º N]			
[40º N, 60º N] s.d. [20º N, 40º N]			
Reptiles	0.428495	2	12.38448
[20º S, 40º S] s.d. [20º N, 40º N]			
Birds	0.79676	5	3.4582
[40º N, 60º N] s.d. [0º, 20º S]			
[40º N, 60º N] s.d. [0º, 20º N]			
[40º N, 60º N] s.d. [20º N, 40º N]			
Mammals	0.149063	3	0.36167

1 – Latitude Classes (for both hemispheres) : [0º, 20º], [20º,40º],[40º,60º], >60º

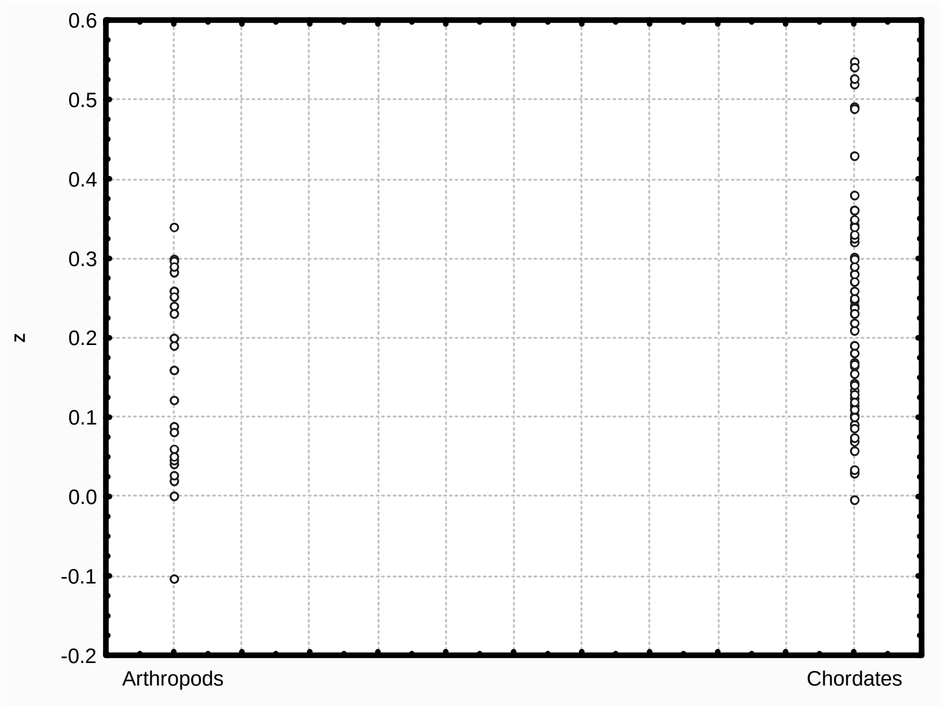

Fig. 1 – z values for arthropods and chordates.

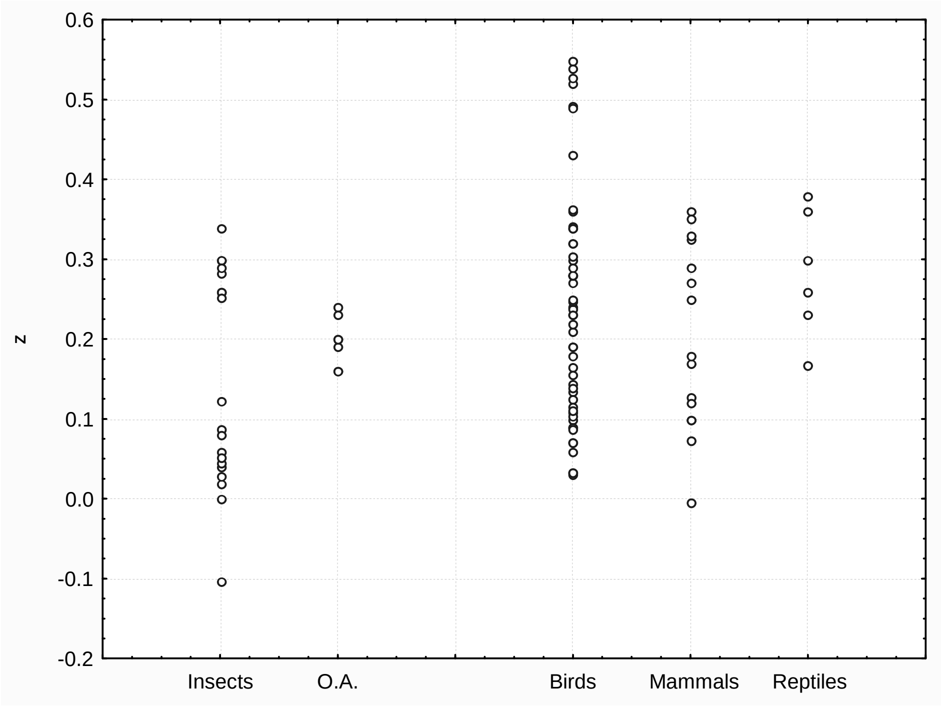

Fig.2 – z values for lower taxa of arthropods and chordates.

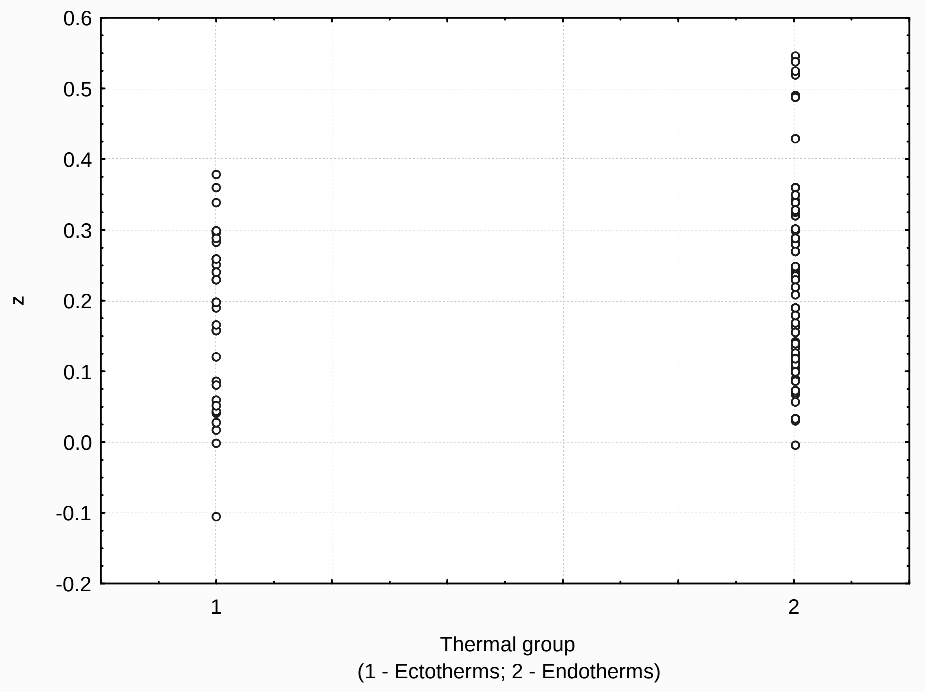

Fig.3 – z values for ectotherms and endotherms.

Discussion

Results from these preliminary analyses suggest that body size is indeed an important variable when studying patterns and processes that involve organisms and their environment.

Small bodied organisms had, in general, lower *z* values than large bodied ones. Thermal behaviour did not seem to influence the value of *z*. These results were also reflected in the analysis that tested reptiles versus the other chordates and the other ectotherms.

Although the variability of *z* values is quite large for both groups, arthropods and chordates, the average value is higher for chordates. This is probably due to the fact that small organisms have smaller home ranges, needing less area to survive. This means that after a certain value for area the number of new species that will appear as a result of its increase will be progressively smaller. The pattern for larger species will be identical, with the difference that the minimum critical area is much bigger, so the increase of species with the increase of area will be more pronounced, resulting in higher values for *z*.

There were not found any differences in relation to *c* values. This is a scaling parameter, groups that have more species will be expected to have species area curves “higher represented” in a graph, for this reason, we were predicting greater *c* values for arthropods due to their small body size, which would permit higher species abundance and consequently higher number of species.

There were found some differences in both parameters for different latitude zones for some taxa. However, these differences do not seem to follow any pattern and probably are, in most cases, a consequence of the low sample size for each of the latitudinal zones.

We expected to find lower values for z towards the equator, since the latitudinal zones would become more "energetic" leading to smaller home ranges and this would fade the effect of an increasing area. On the other hand we expected higher values for c towards the equator, since more "energetic" zones would be able to support more species.

We were aware that the information in this database was not the ideal one to test the effect of body size and energy requirements. On the one hand because the information was not discriminated enough, arthropods and chordates are groups extremely diverse and this confers too much variability to the data. On the other hand the number of entries for each group was not balanced, there was a bias toward birds.

Besides that, in order to have samples with a reasonable size, we had to join information collected in different types of habitat and in different sized places (islands, continental regions, continents, etc.)

We still believe that body size should be considered when studying the factors that affect species-area relationship parameters. It would have been preferable to work with a database that had information referent to lower taxonomic levels, allowing to test between more similar organisms, for example it would be interesting to test between species of different orders of mammals or even species from families, of the same order, according to their body size. A complementary analysis would be to test organisms from different taxa but with similar body sizes.

Nonetheless it is important to have in mind that, the dynamics of biodiversity patterns, could not be explained by simple mechanisms. There is a multitude biotic and abiotic factors, that act, and interact, leading to a great complexity and heterogeneity of communities.

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APPENDIX 1

Source	Taxon	Sub-taxon	Therm.	Lat.	C	Z
Douglas and Lake 1993	Arthropods	Insects	1	-2	-0.5	0.683
Wilson 1961	Arthropods	Insects	1	-1	0.8	0.000
Wilson 1961	Arthropods	Insects	1	-1	0.9	0.041
Wilson 1961	Arthropods	Insects	1	-1	1.0	0.019
Wilson 1961	Arthropods	Insects	1	-1	0.9	0.045
Wilson 1961	Arthropods	Insects	1	-1	1.1	0.028
Wilson 1961	Arthropods	Insects	1	-1	1.2	0.052
Wilson 1961	Arthropods	Insects	1	-1	1.3	0.123
Wilson 1961	Arthropods	Insects	1	-1	1.4	0.081
Wilson 1961	Arthropods	Insects	1	-1	1.5	0.088
Wilson 1961	Arthropods	Insects	1	-1	0.0	0.298
Moroe 1948	Arthropods	Insects	1	1	0.8	0.260
Scott 1986	Arthropods	Insects	1	1	0.9	0.260
Darlington 1943	Arthropods	Insects	1	1		0.340
Davies and Smith 1997	Arthropods	Insects	1	1	1.1	1.060
Koh et al.2002	Arthropods	Insects	1	1	1.1	0.290
Morrison 1998	Arthropods	Insects	1	1		0.060
Fattorini 2002	Arthropods	Insects	1	2	0.5	0.252
Goldstein 1975	Arthropods	Insects	1	2	1.9	0.300
Goldstein 1975	Arthropods	Insects	1	2	2.1	0.283
Magura 2001	Arthropods	Insects	1	3	1.2	-0.103
Southwood 1984 and Birks 1980	Arthropods	Insects	1	3	-0.1	0.890
Rodriguez 1991	Arthropods	Oniscidea	1	2	0.6	0.240
Taiti and Ferrara 1989	Arthropods	Oniscidea	1	3	1.2	0.160
Sfenthourakis 1996	Arthropods	Terrestrial art.	1		1.0	0.230
Sfenthourakis 1996	Arthropods	Terrestrial art.	1		1.0	0.200
Sfenthourakis 1996	Arthropods	Terrestrial art.	1		1.0	0.160
Sfenthourakis 1996	Arthropods	Terrestrial art.	1	2	1.0	0.200
Sfenthourakis 1996	Arthropods	Terrestrial art.	1	2	1.0	0.190
Matter et al. 2002	Chordates	Birds	2	-3		0.180
Matter et al. 2002	Chordates	Birds	2	-3		0.190
Nores 1995	Chordates	Birds	2	-2	0.1	0.362
Cody 1975	Chordates	Birds	2	-2	1.5	0.116
Cody 1975	Chordates	Birds	2	-2	1.7	0.143
Hamilton et al. 1964	Chordates	Birds	2	-1		0.280
Hamilton et al. 1964	Chordates	Birds	2	-1		0.303
Diamond 1973	Chordates	Birds	2	-1	1.1	0.220
Preston 1962	Chordates	Birds	2	-1	1.2	0.290
Preston 1962	Chordates	Birds	2	-1	0.8	0.280
Adler 1992	Chordates	Birds	2	-1	-0.4	0.540
Rahbeck, per.com.	Chordates	Birds	2	-1	0.3	0.430
Rahbeck, per.com.	Chordates	Birds	2	-1	1.1	0.320
Rahbeck, per.com.	Chordates	Birds	2	-1	1.5	0.230
Rahbeck, per.com.	Chordates	Birds	2	-1	1.6	0.270
Slud 1976	Chordates	Birds	2		1.6	0.660
Williamson 1981	Chordates	Birds	2			0.300
Peterson et al. 2000	Chordates	Birds	2	1	1.2	0.248
Hamilton and Armstrong 1965	Chordates	Birds	2	1		0.489
Hamilton et al. 1964	Chordates	Birds	2	1		0.237
Koh et al.2002	Chordates	Birds	2	1	1.5	0.250
Matter et al. 2002	Chordates	Birds	2	1		0.210
Preston 1962	Chordates	Birds	2	1	0.8	0.240
Vuilleumier and Simberloff 1980	Chordates	Birds	2	1	0.5	0.340

Vuilleumier and Simberloff 1980	Chordates	Birds	2	1	0.3	0.340
Wright 1981	Chordates	Birds	2	1	0.8	0.230
Brown 1978	Chordates	Birds	2	2	0.4	0.165
Blake 1986	Chordates	Birds	2	2	1.8	0.058
Blake 1986	Chordates	Birds	2	2	1.5	0.190
Blake 1986	Chordates	Birds	2	2	1.1	0.070
Blake 1986	Chordates	Birds	2	2	1.2	0.100
Blake 1986	Chordates	Birds	2	2	1.1	0.033
Blake 1986	Chordates	Birds	2	2	1.0	0.030
Blake 1986	Chordates	Birds	2	2	0.9	0.034
Bolger et al. 1991	Chordates	Birds	2	2	0.9	0.134
Bolger et al. 1991	Chordates	Birds	2	2	1.0	0.361
Kratter 1992	Chordates	Birds	2	2	1.0	0.156
Kratter 1992	Chordates	Birds	2	2	0.9	0.109
Kratter 1992	Chordates	Birds	2	2	1.0	0.280
Selmi et al. 2002	Chordates	Birds	2	2	1.0	0.070
Wilson 1985	Chordates	Birds	2	2	1.3	0.341
Cody 1975	Chordates	Birds	2	2	1.6	0.125
Reed 1981	Chordates	Birds	2	3	1.2	0.320
Gaston 2000	Chordates	Birds	2	3	1.6	0.280
Gaston 2000	Chordates	Birds	2	3	1.7	0.110
Hissley et al. 1998	Chordates	Birds	2	3	2.2	0.548
Hissley et al. 1998	Chordates	Birds	2	3	2.1	0.526
Hissley et al. 1998	Chordates	Birds	2	3	2.0	0.492
Lennon et al. 2002	Chordates	Birds	2	3	1.6	0.140
Storch 2003	Chordates	Birds	2	3		0.090
Storch 2003	Chordates	Birds	2	3		0.090
Storch 2003	Chordates	Birds	2	3		0.087
Storch 2003	Chordates	Birds	2	3		0.103
Haila et al. 1983	Chordates	Birds	2	4	1.5	0.520
Wilcox 1978	Chordates	Insects	1	-2	1.0	0.260
Wilcox 1978	Chordates	Insects	1	-2	1.3	0.360
Fox 1982	Chordates	Mammals	2	-2	1.0	0.360
Heaney 1984	Chordates	Mammals	2	-1	0.7	0.250
Cowlishaw 1999	Chordates	Mammals	2	-1		0.270
Cowlishaw 1999	Chordates	Mammals	2	-1		0.180
Mares and Ojeda 1982	Chordates	Mammals	2	-1	1.1	0.930
Heaney 1984	Chordates	Mammals	2	1	1.6	0.100
Brashares et al. 2001	Chordates	Mammals	2	1	1.2	0.074
Brashares et al. 2001	Chordates	Mammals	2	1	0.2	0.290
Brashares et al. 2001	Chordates	Mammals	2	1	1.5	-0.004
Dueser and Brown 1980	Chordates	Mammals	2	1	1.7	0.640
Lawlor 1986	Chordates	Mammals	2	1	-0.1	0.330
Lawlor 1998	Chordates	Mammals	2	2	0.6	0.128
Mcdonald and Brown 1991	Chordates	Mammals	2	2	0.1	0.326
Newmark 1986	Chordates	Mammals	2	2	1.3	0.120
Rosenblatt et al. 1999	Chordates	Mammals	2	2	1.1	0.100
Lawlor 1986	Chordates	Mammals	2	2	0.1	0.170
Matter et al. 2002	Chordates	Mammals	2	4		0.350
Wright 1981	Chordates	Reptiles	1	1	0.3	0.300
Case 1975	Chordates	Reptiles	1	2	0.4	0.166
Wilcox 1978	Chordates	Reptiles	1	2	0.4	0.230
Mylonas and Valakos 1990	Chordates	Reptiles	1	2	0.1	0.380

Legend:

Therm. (Thermal behaviour): 1 – Ectotherms; 2 – Endotherms;

Lat. (latitudinal classes): 1 -[0º, 20º], 2 - [20º,40º], 3 - [40º,60º],4 - >60º, negative values are referent to southern hemisphere zones

Z values in grey were considered as outliers and were not used in the analysis.