

Science is a search for patterns but there are few cross-habitat patterns in ecology. We propose key questions following the findings of consistent scaling of abundance versus body mass from bacteria to earthworms and whales, based on an almost forgotten study of soils and a well-known one from the open ocean.

Sheldon and coauthors [1] have been widely acknowledged for their pioneering work on the size spectrum, originally sampled in open oceans and later extended to lakes. Research on the empirical size spectrum across aquatic and terrestrial realms has since grown and influenced community and food web ecology, development of global and local scale modeling of systems, and indicators for environmental management [2]. Probably because of the historical origins, size spectrum studies are still more common in aquatic ecosystems than in terrestrial ones, despite some notable exceptions [3,4]. However, they actually began in the soil rather than in the sea. An earlier and little-known description of the relationship between numerical abundance and body size was discovered 30 years before the seminal work of Sheldon *et al.* Here, we tell the story of the biomass equivalence rule, according to which there is no general trend of increasing or decreasing biomass per equal log body-size bins throughout the size range from small to large creatures. In a less precise way, this may be expressed as approximately equal biomasses contained in equal log body-size bins, as revealed by M.S. Ghilarov – a Russian soil zoologist and ecologist who made the discovery back in 1944 [5]. We also show how remarkably similar the patterns are found by Ghilarov and independently by Sheldon *et al.* Finally, we outline outstanding questions that could be tackled by integrative studies of aquatic and

---

## Forum

### Uniting Discoveries of Abundance-Size Distributions from Soils and Seas

Leonard V. Polishchuk<sup>1,3,\*</sup> and Julia L. Blanchard<sup>2,3,\*</sup>

terrestrial ecosystems using a size spectrum approach.

The war autumn of 1943, Moscow, Russia (then the Soviet Union). A young man (31 years old) submitted a paper to the *Reports of the Academy of Sciences of the USSR*, a prestigious Russian journal, although not widely available internationally. The paper was brief, just 2.5 printed pages in total, and contained a single – and impressive – plot, which suggested a strong linear relationship between log numerical abundance and log body size for the most common soil organisms, in the range from bacteria to earthworms [5]. The author Ghilarov stated that: ‘The biomass of soil organisms of different natural body-size groups is approximately of the same order of magnitude: the product of the number of organisms belonging to a given body-size group times their linear size cubed varies very little’ [5]. No statistical justification of this statement was provided, however. For one reason or another, Ghilarov’s original insight about biomass equivalence has been forgotten and lost; however, it would be revived, and a proper statistical treatment performed, only much later [6,7]. Ghilarov’s paper was well ahead of its time. In soil ecology, it has long been viewed as an early piece of evidence documenting the negative correlation between numbers and size. Furthermore, in a more general, cross-habitat context involving soils and seas, it can be seen as an early example of size spectrum analysis where the sign and the slope of the relationship both matter.

Here, we have rearranged Ghilarov’s [5] plot as the numerical abundance versus body-mass spectrum. Figure 1A shows that numerical abundance is inversely proportional to body mass, with the exponent of mass being  $-0.97 \pm 0.07$ . In terms of biomass, this implies that there is no general trend, either increasing or decreasing, in the biomass of the main

body-size groups of soil organisms. This does not mean that the biomasses are equal; in fact, they are not, although the variability does not show any monotonic trend (Figure 1B). In addition, the groups span approximately equal intervals on a log body-size scale; for example, log-transformed body-size ranges of myriapods, collembolans (springtails), and potworms (Enchytraeidae) are 0.30, 0.27, and 0.30, respectively [measured in terms of  $\sigma$  for species body-size distributions (see [7] for details)]. This ultimately justifies the above formulation of the biomass equivalence rule.

The biomass equivalence rule was independently rediscovered by Sheldon *et al.* [1] for a different array of organisms living in a distinct environment – the pelagic open ocean. If presented in a way similar to that for Ghilarov, the data of Sheldon *et al.* show a remarkably similar pattern (Figure 1C,D). The body-mass exponent here,  $-1.04 \pm 0.04$ , is also close to  $-1$ , implying no monotonic trend in biomass in the range from bacteria to whales. In addition, the main pelagic groups considered by Sheldon *et al.* occupy approximately equal intervals on a logarithmic body-size scale. The striking agreement between Ghilarov and Sheldon *et al.* reinvigorates at least three outstanding questions in ecology.

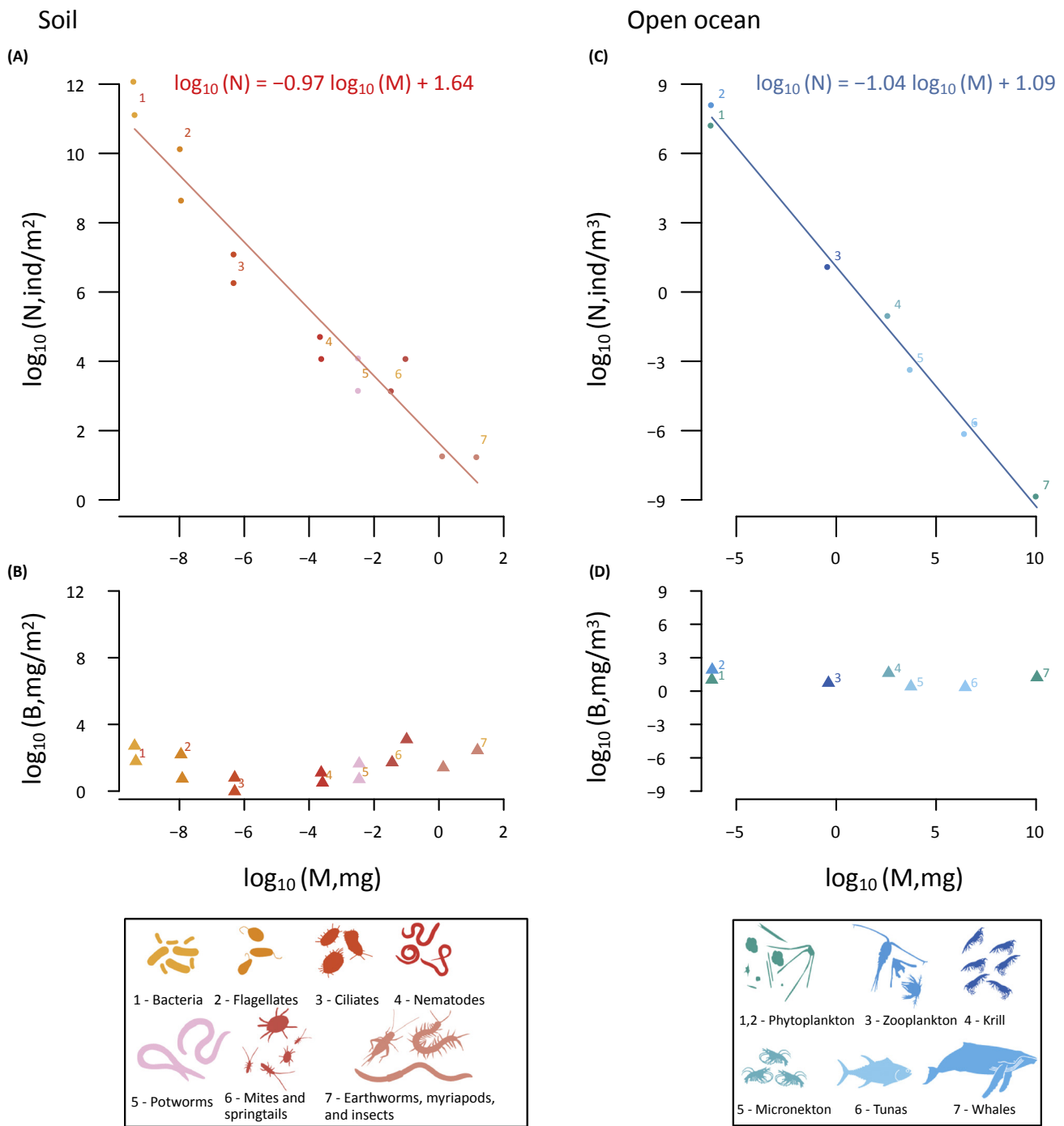
### What Are the Mechanisms That Give Rise to This Universal Pattern?

The consistency of size spectra both for land and sea suggests that the pattern is universal; hence, it should be associated with rather general mechanisms and processes [8]. A range of mechanisms has been studied that could give rise to this pattern including metabolic theory which explains the  $-1$  slope of size spectra (numerical abundance vs body mass) through the size-structured transfer of energy and consumer–prey interactions along a simple trophic chain [9,10].

Although size-structured predation fits well in pelagic ecosystems, it may not apply to soils because many soil invertebrates, such as those representing Ghilarov’s size groups (earthworms, millipedes among myriapods, some insect larvae, springtails, potworms, and nematodes; Figure 1A,B), are largely or entirely detritivorous and thus do not comprise a direct trophic chain. However, more detailed dynamic size spectrum theory explicitly incorporates species and size-structured networks interactions without each size class needing to consume the one directly below it [2]. Moreover, other mechanisms may be at play such as habitat structure or the assembly of power laws of multiple species [11]. Whether a single general mechanism or some set of mechanisms and processes acting in combination is driving this universal pattern needs to be addressed to advance our understanding, given the cross-habitat scope of the pattern.

### At Which Scales Does Biomass Equivalence Apply?

While apparently universal in terms of milieu, the biomass equivalence rule has the limits of applicability with respect to scale. Here, both on land and in the sea biomass equivalence arises on large, macroecological spatial scales. The Ghilarov data originate from several continents (Europe, Asia, and North America) and climatic zones, and the Sheldon data come from the vast areas of the equatorial Pacific and the Antarctic. Whether or not this pattern holds in local ecosystems such as a small patch of land, a pond, or a lake remains an open question; in general, the answer seems to be ‘no’. Biomass equivalence occurs predominantly on large spatial scales but it remains unclear where the boundary lies between the large and the small. To answer this question, we need to determine the relationship between the slope of size spectra and the



Trends in Ecology & Evolution

**Figure 1. Size Spectra in Soils and Seas Demonstrate Biomass Equivalence.** The relationships between numerical abundance  $N$  and biomass  $B$  versus body mass  $M$  of body-size or taxonomic groups for soil (A, B) and open ocean pelagic (C, D) organisms based on data of Ghilarov [5] and Sheldon *et al.* [1], respectively. The  $\log_{10}(N) - \log_{10}(M)$  relationships are highly significant ( $r^2$  is 0.94 and 0.99 for A and C, respectively;  $P < 0.001$  in both cases). The  $\log_{10}(B)$  is calculated as the sum of  $\log_{10}(N)$  and  $\log_{10}(M)$  and presented here by way of illustration. The scale of the y axis in panels B and D is made the same as the scale of the y axis in panels A and C, respectively, to visualize the variation in biomass as compared with the variation in numerical abundance; the former is smaller than the latter. For panels A and B, the

(Figure legend continued on the bottom of the next page.)

magnitude of scale. We envision that the slope would vary widely at small scales (it may be even positive [12]) and converges to  $-1$  at sufficiently large scales. The relationship will contribute to better understanding of the fundamental aspects of size spectra, making it possible to operationally define spatial scales where biomass equivalence normally applies. Additionally, on larger scales, inclusion of size into estimates of biomass could complement recent efforts to census the biomass distribution of all life on Earth [13].

### How Can Size Spectra Inform Environmental Management on Land and Sea?

Theoretical size spectra are often used as a benchmark to compare them with the observed spectra, and the shift is interpreted as being due to anthropogenic pressures [14]. We suggest that this approach will provide more reliable information on human impact when size spectra are examined on a large spatial scale. Moreover, the above knowledge of the appropriate spatial scale could assist in the use of ongoing monitoring programmes for comparing perturbed and unperturbed size spectra. Empirical size spectrum analyses of soils are already

being used to monitor impacts of human activities [3,4]. We suggest that development of dynamic size spectrum models in terrestrial systems, while appropriately accounting for different body-size groups as shown in the Ghilarov example, could help to yield new knowledge of the combined impacts of agriculture intensity and other drivers such as climate change. The understanding that land and sea size spectra have more in common than previously thought should open new avenues of integrative research into fundamental and applied aspects of size spectra.

### Acknowledgments

L.V.P. was supported by the Russian Foundation for Basic Research (grant 18-04-01143). J.L.B. acknowledges Australian Research Council (Discovery Grant DP170104240 'Rewiring Marine Food Webs'). Both authors thank Ilya Kopnin for digitizing M.S. Ghilarov's original figure and Kira Askaroff for illustrations.

<sup>1</sup>Department of General Ecology, Biological Faculty, M.V. Lomonosov Moscow State University, Moscow, 119991, Russia

<sup>2</sup>Institute for Marine and Antarctic Studies and Centre for Marine Socioecology, University of Tasmania, 20 Castray Esplanade, Hobart, TAS 7001, Australia

<sup>3</sup>These authors have contributed equally to this article

\*Correspondence:

leonard\_polishchuk@hotmail.com (L.V. Polishchuk) and

julia.blanchard@utas.edu.au (Blanchard).

<https://doi.org/10.1016/j.tree.2018.10.007>

### References

- Sheldon, R.W. *et al.* (1972) The size distribution of particles in the ocean. *Limnol. Oceanogr.* 17, 327–340
- Blanchard, J.L. *et al.* (2017) From bacteria to whales: using functional size spectra to model marine ecosystems. *Trends Ecol. Evol.* 32, 174–186
- Mulder, C. and Elser, J.J. (2009) Soil acidity, ecological stoichiometry and allometric scaling in grassland food webs. *Glob. Change Biol.* 15, 2730–2738
- Turnbull, M.S. *et al.* (2014) Weighing in: size spectra as a standard tool in soil community analyses. *Soil Biol. Biochem.* 68, 366–372
- Ghilarov, M.S. (1944) Correlation between size and number of soil animals. *Dokl. Akad. Nauk* 43, 283–285
- Tseitlin, V.B. (1986) *Energetics of Deep-Sea Pelagic Communities*, Nauka
- Polishchuk, L.V. (2018) M.S. Ghilarov's principle, or biomass equivalence rule, as one of conservation laws in ecology. *Zh. Obshch. Biol.* 79, 183–200
- Connolly, S.R. *et al.* (2017) Process, mechanism, and modeling in macroecology. *Trends Ecol. Evol.* 32, 835–844
- Brown, J.H. and Gillooly, J.F. (2003) Ecological food webs: high-quality data facilitate theoretical unification. *Proc. Natl. Acad. Sci. U. S. A.* 100, 1467–1468
- Jennings, S. and Mackinson, S. (2003) Abundance–body mass relationships in size-structured food webs. *Ecol. Lett.* 6, 971–974
- Rinaldo, A. *et al.* (2002) Cross-scale ecological dynamics and microbial size spectra in marine ecosystems. *Proc. Biol. Sci.* 269, 2051–2059
- Trebilco, R. *et al.* (2016) The paradox of inverted biomass pyramids in kelp forest fish communities. *Proc. R. Soc. B* 283, 20160816
- Bar-On, Y.M. *et al.* (2018) The biomass distribution on Earth. *Proc. Natl. Acad. Sci. U. S. A.* 115, 6506–6511
- Jennings, S. and Blanchard, J.L. (2004) Fish abundance with no fishing: predictions based on macroecological theory. *J. Anim. Ecol.* 73, 632–642

data were taken from Ghilarov's figure, a single one in the paper, which was digitized using the program ImagePro. The original figure depicts the numerical abundance versus body length of the groups; the former was used directly while the latter was transformed to body mass using a mass–length relationship from Tseitlin [6]. Here, as well as in the original data, each group is represented by a pair of points to characterise the variability within the group. The abundance and biomass refer to the 0 to ~25-cm soil layer. For panels C and D, the data were taken from Figure 12 in Sheldon *et al.* [1], which was digitised. The original figure shows the biomass versus body-size range of the groups where body size is expressed as equivalent spherical diameter. The mean diameter found from the body-size range was transformed into body volume and body mass, given the body density of 1 g/cm<sup>3</sup>; numerical abundance was calculated as the ratio of the biomass over body mass of the groups. Note that the figure of Sheldon *et al.* presents data for the equatorial Pacific and the Antarctic separately; here we combine them in one plot. Data points 2, 4, and 7 refer to the Antarctic, and 1, 3, 5, and 6 to the Pacific.