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Letter to the Editor

An allometric tragedy of the commons: Response to the article "Evaluation of models capacity to predict size spectra parameters in ecosystems under stress"



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To address the anthropogenic effects on species assemblages, an explicitly multivariate approach is surely needed. The sense of community as superorganism embraces the concept of a huge amount of living species cohabiting to keep their independent ecological processes, hence to maintain ecosystem functioning and preserve ecosystem services. Being this kind of functioning often hard to define precisely, allometry provides for sure the needed multivariate way to visualise main changes in abundance, size and biomass of this huge amount of cohabiting species. However, although it is undisputed that most processes depend on size, such scaling relations must be addressed in an accurate way. Unfortunately, it did not happen properly in the article by Dos Santos et al. (2017), printed this August on *Ecological Indicators*. Here, we have to explain briefly why.

One century ago, modern community ecology was launched by two American botanists. One of them, Frederic E. Clements, claimed in 1916 (and later in 1936) that a plant community can be seen as a kind of superorganism where species combine their forces in synergy; the other one, Henry A. Gleason, proposed on his hand that plant species in a community share no common function but act independently for their individual success (Gleason, 1926). Who was right? Actually both. As a matter of fact, their ideas still apply to most communities and with trait ecology we can see how events might accumulate and drive together the size-structuring of single populations within species assemblages. Allometry synthesizes such contrasting perspectives.

Body mass (hereafter, M) is recognized since decades as a key driver of the food-web structure of species assemblages, as many explorations revealed strong size-structures in both aquatic and terrestrial communities (Blanchard et al., 2017; Boudreau and Dickie, 1992; Zurlini et al., 1983), although effects of spatiotemporal changes in the numerical abundance (hereafter, N) as co-driver remain relatively underexplored. Most studies (Belgrano et al., 2002; Jennings et al., 2007; Hildrew et al., 2007; Olden et al., 2007) used either the regression slopes of (log-summed) biomass–size spectra (a function of the bin centres on a log(M)-scale indicating how biomass changes with increasing M-bins) or the mass–abundance linear regression slopes (a line fitted in the log–log space in terms of predicted N-values for given values of M). Fewer studies (Reuman and Cohen, 2005; Reuman et al., 2008) focused on the deviations from allometric regression models, as a relationship between M, N, and species diversity is often affected by changes in energy flow (McClain, 2004). Even less studies (Martinez et al., 1999; Mulder and Mancinelli, 2017) addressed the influence of different observation efforts, sampling intensities and protocols on these models.

Biomass–size spectra are therefore widely used in aquatic ecology, for instance to assess the cascading effects of overfishing, whilst the classic mass–abundance approach (a typical first-degree equation in autecological investigations) has been applied to synecology much later (e.g., Brown and Gillooly, 2003; Cohen et al., 2003; Mulder et al., 2005; Long et al., 2006). Hence, there is a long tradition of authors proposing studies dealing with effect of different functional types on resources quality and the trait-induced cascading effects on ecosystem functioning. In comparable ways, some authors proposed allometry as a perfect tool for exploring effects of food-web properties on stability (Cohen et al., 2009; Jennings and Mackinson, 2003; Mulder et al., 2005, 2006; Pope et al., 2006; Sechi et al., 2015). In the latter case, allometric indicators were claimed to be superior to previous indicators as slopes and intercepts can translate into effective energetic keys to clarify mechanisms of ecosystem functioning (Mulder et al., 2011, 2013). Common aim was to stimulate ecologists to link theoretical and empirical studies of food-web structure with landscape ecology.

Such a characterization makes it possible to visualise in a log-log space the environmental effects of changing individual forces and total biodiversity on the structure of food webs. Act in fact the populations independently from each other (Gleason's view) or synergetically with each other (Clements' view)? Let us briefly focus on basic forms of biodiversity. Alpha (α) diversity is the species diversity in local landscapes (here, number of nodes). Beta (β) diversity is the taxonomical change among those landscapes (here, changes in N and M for each node). Technically, allometric slopes and intercepts are suitable to compare the (α , β) diversities with each other as soon the same taxonomic resolution is kept across the data set (empirical evidence in Sechi et al., 2015 and their online data repository). A stable biomass distribution, like in the case of isometry, would then result in a kind of steady state, comparable to the latter synergy (climax) of Clements.

Aside all questions that have been raised by proposing challenging perspectives on ecological processes and ecosystem services and despite the debate that arose, we were surprised that in a recent paper by Dos Santos et al. (2017), largely based on a merely qualitative inspection of a scarce set of studies, it was assumed that suggested common denominators of both biomass–size spectrum as mass–abundance linear regression will provide the *same* environmental signal on externally-driven size-structuring of food webs, regardless of any discretinization of M-bins and chosen resolution of nodes and sites. We strongly believe that it is wrong to build up an integrated data set with both functions together (Fig. 1) and will adress allometric implications from both an ecological as a statistical point of view.

Perhaps this appears only a subtle semantic difference, but already too many different terms refer to the same parameters. Biomass-size spectra and mass-abundance regressions are not the same. That is, it appears that the distinction between the few models investigated by Dos Santos et al. (2017) and the continuously growing Big Data "Commons" is that from the latter, much newer challenges emerge, related with e.g., scale-dependent forecasting power of models. It remains obviously impossible to cite even the majority of relevant works, but aside a clear description of the kind of performed literature search, claims of missing evidence derived from a scarce selection of articles must be avoided. In our day of easily-recovering real data from simple scanning of printed figures, data must be organized and reanalyzed in the same way to avoid any artefact or bias. Along so many investigated studies with fully downloadable gradients of increasing environmental stress, differently sized-structures can then come into play



Fig. 1. Biomass–size spectra and mass–abundance regression slopes differ one unit (a), hence as site–specific investigations show a mass–abundance slope statistically undistinguishable from -3/4 (c), the vaste majority of biomass–size spectra have a positive slope (see Mulder and Mancinelli for data and examples). Only in the case of isometry (b), detected once at functional level (right part of this composite figure, above the theoretical argument, b, below the empirical evidence, d), the biomass–size spectrum will have no slope (horizontal line, b), but a costant elevation. Single plots are redrawn from Long et al. (2006) and Sechi et al. (2015) and modified with permission.

and take actual prominence (Mulder and Elser, 2009; Peñuelas and Sardans, 2009). Only in this way the true nature of allometric relationships will unravel changes with external drivers like nutrient availability (Mulder et al., 2011, 2013, 2015; Mancinelli and Mulder, 2015; Ott et al., 2014a,b), with evident effects on supporting, provisioning and regulating ecosystem services.

Is such a theory novel? Dos Santos et al. (2017) acknowledge that their idea is embedded in current ecology research without providing additional value, for instance by an exhaustive metareview to show to what extent allometry incorporates size-structuring forces from ongoing processes in the environment, from acidification and eutrophication up to global warming and land-use intensification. Obviously we welcome that the authors make a plea for the (undisputed) validity in stress ecology of allometric metrics, i.e. slopes, intercepts and variability, but we are concerned by their limited literature survey, a kind of evidence that may not allow to state that "unclear how response to stress varies across models and in comparison to data". It is out of our scope to propose here in our day of Big Data, Internet of Things, eScience and Machine Learning how a metareview should be done (although we regret that any mention of the possibly used keywords is missing), but we identified severe caveats that must be addressed if we ever wish to use such metrics as ecological indicators.

Dos Santos et al. (2017) correctly address the three main components of allometric models, the allometric slope, the allometric intercept, and the variance (or departure ε) of the model. However, the authors switch too easily between biomass–size spectra and mass–abundance regressions (as shown in their Fig. 3), because the take-home message of a biomass–size spectrum and a mass–abundance slope is conceptually very different (first

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