

Update: A non-parametric method for the measurement of size diversity, with emphasis on data standardization. The measurement of the size evenness

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Abstract

A method for the measurement of the size diversity based on the classical Shannon–Wiener expression was proposed as a proxy of the shape of the size distribution. The summatory of probabilities of a discrete variable (such as species relative abundances) in the original Shannon–Wiener expression was substituted by an integral of the probability density function of a continuous variable (such as body size). Here, we propose an update of this method by including the measurement of the size e-evenness, just dividing the exponential of the size diversity by its possible maximum for a given size range. Assuming a domain of the size range of $(0, \infty)$, for a given logarithmic mean (m_{\ln}) and a logarithmic standard deviation (σ_{\ln}), the distribution with the highest diversity is the Log-Normal. The size e-evenness ranges between 0 and 1 because of the division by the maximum exponential diversity. Size e-evenness is useful to discriminate whether variations in size diversity are due to changes in the shape of the size distribution or caused by differences in size dispersion.

Quintana et al. (2008) proposed a nonparametric method for the measurement of the size diversity as a proxy of the shape of the size distribution. Size diversity is computed on the basis of the Shannon–Wiener diversity expression (Pielou 1969) and adapted for continuous variables, such as size. The use of the size diversity for the analysis of the shape of a size distribution has several advantages (Quintana et al. 2008): (1) it integrates sizes of individuals and a size-density in the same way that Shannon–Wiener species diversity integrates the number of species and their relative abundance; (2) after data standardization, samples measured with different units, such as length, weight or volume, are comparable; and (3) its meaning is easy to interpret, since the concept of diversity is well established (Hurlbert 1971): a high size diversity means a wide size range and/or similar proportions of the different sizes along the size distribution. For the size

diversity measurement the summatory of probabilities of discrete variables of the classical Shannon–Wiener expression (such as species relative abundances), is substituted by an integral involving the probability density function of the size (X) of the individuals ($p_X(x)$) and takes the form

$$\mu_2(X) = - \int_0^{+\infty} p_X(x) \log_2 p_X(x) dx,$$

when based on the base 2 logarithm. A more conventional form, using natural logarithms is

$$\mu(X) = - \int_0^{+\infty} p_X(x) \ln p_X(x) dx, \quad (1)$$

such that $\mu(X) = \ln(2) \mu_2(X)$ as pointed out in Quintana et al. (2008). The probability density function (pdf) of the size of the individuals X is estimated by a non-parametric kernel local evaluation of $p_X(x)$, applicable to any type of size distribution. Data are previously standardized by means of the division of each size value by the geometric mean of the size distribution. Then, the density of $Y = \ln X$ is estimated using standard kernel techniques. Standardization dividing by the geometric mean is equivalent to centering

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the distribution of Y to have 0 mean. The estimated pdf of X is obtained as $p_X(x) = 1/x p_Y(y)$, where the factor $1/x$ corresponds to the derivative of the transformation $y = \ln x$.

For discrete variables, such as species composition, a value of evenness can be obtained, ranging between 0 and 1, just dividing species diversity by the maximum diversity that can be achieved with the same number of species (Pielou 1969; Magurran 1988). Species evenness shows how similar are the relative abundances of species involved. This cannot be discriminated using only diversity values, since diversity integrates both number of species and proportionality among them.

We investigate how to obtain the evenness for a continuous variable such as body size. For a continuous size distribution, with no defined upper and lower limit, the distribution with the highest diversity is the Log-Normal (e.g., Park and Bera 2009). Thus, we obtain the size evenness of a size distribution by comparing its size diversity (obtained by the above described non parametric kernel approach) with that of a Log-Normal distribution with the same logarithmic mean and standard deviation. Because negative values of size diversity are feasible, meaning low values of size diversity, the size evenness will not range between 0 and 1. We propose the use of an e-evenness, as the quotient of the exponential of diversities to avoid this problem. We also provide an R routine for the computation of size diversity and size e-evenness.

Materials and procedures

For a discrete probability function, such as the relative abundance of the different species in a community, the evenness is calculated simply by dividing the Shannon diversity value by $\log_2 S$, where S is the number of species. The $\log_2 S$ is the maximum diversity possible with S species, and represents the diversity of a distribution of S species when all species are equiprobable (Pielou 1969; Magurran 1988). For continuous variables, such as size, the maximum possible diversity is not so trivial. If the size range is finite, as is the case when there is an upper and lower threshold in the sampling procedure, the unconditional maximum diversity is achieved by a uniform function, which has to satisfy

$$\int_{\min}^{\max} p_X(x) dx = 1.$$

In this case, the evenness of the size distribution is

$$\text{evenness} = \frac{\mu_2}{\log_2 R_S} = \frac{\mu}{\ln R_S}, \tag{2}$$

where μ_2 and μ are the size diversities and R_S is the size range.

However, there are difficulties in the estimation of the minimum and maximum threshold, unless there is a clear limit of the counting or sampling device (i.e., when organisms are filtered by several mesh sizes, so that meshes define both the upper and the lower limit). If size limits are not determined by the methodological procedure, size range estimation will strongly

depend on the variability in the estimation of the minimum and the maximum sizes. Usually, the biggest or the smallest organisms in a size distribution are scarce, and this makes the estimation of the size range very variable and uncertain.

Another way to assess the maximum diversity in a continuous distribution is to assume that there are no limits to the size distribution. In this case, we need to find which distribution achieves the highest diversity, also satisfying that

$$\int_0^{\infty} p_X(x) dx = 1.$$

For a given logarithmic mean (m_{\ln}) and a logarithmic standard deviation (σ_{\ln}), the distribution with the highest diversity is the Log-Normal. That Log-Normal distribution is the maximum entropy or maximum diversity distribution, subject to a given mean value and variance, is well known and derived from the general information theory (e.g., Kullback 1968). Specific derivations of the general form of maximum entropy distributions can be found in Zellner and Highfield (1988) and Golan et al. (1996). Park and Bera (2009) report the result for the Log-Normal distribution.

The size diversity of a Log-Normal distribution is (see Quintana et al. 2008)

$$\mu(\text{LN}) = \ln(2) \mu_2(\text{LN}) = \left[\frac{1}{2} + \ln \left(\sqrt{2\pi} \sigma_{\ln} \right) + m_{\ln} \right], \tag{3}$$

where m_{\ln} and σ_{\ln} are the logarithmic mean and standard deviation of the Log-Normal distribution. When the Log-Normal variable (LN) is standardized dividing by the geometric mean, $m_{\ln} = 0$, or approximately so when using estimates of the geometric mean. The traditional form of defining the evenness would lead to

$$J_{\mu}(X) = \frac{\mu(X)}{\mu(\text{LN})}, \tag{4}$$

or equivalently using μ_2 . However, negative values of $\mu(X)$ are feasible, meaning low values of size diversity. In fact, the integrand in Eq. 1 can take positive values when $p_X(x)$ take values larger than 1, thus producing negative diversity values. Figure 1 shows three pdf's: the dashed line corresponds to a log-normal pdf which μ is null; the full line is a log-normal pdf with negative diversity as corresponds to a pdf more peaky than that represented by the dashed line. The third represented pdf (dotted line) is the kernel estimation of a simulated sample from the full line pdf.

To avoid the problem of negative values in Eq. 4 we propose to use the e-evenness (J_e), defined as

$$J_e(X) = \frac{\exp(\mu(X))}{\exp(\mu(\text{LN}))} = \frac{2^{\mu_2(X)}}{2^{\mu_2(\text{LN})}}, \quad 0 \leq J_e(X) \leq 1. \tag{5}$$

Regarding the standardization, it should be taken into account that, to define an evenness function, i.e., the ratio

of a diversity of a given pdf over the log-normal diversity, the two pdf's must have the equal logarithmic variance. The diversity of a log-normal pdf is given in Eq. 3, which is larger than any diversity corresponding to a pdf with logarithmic mean equal to m_{ln} and logarithmic variance equal to σ_{ln}^2 . When the comparison is done using a kernel estimate of the pdf, these parameters should be those of the kernel estimated pdf. When using a standardization of data dividing by the geometric mean of the data $m_{ln} \approx 0$, but not exactly equal to 0 due to kernel estimation. Similarly, σ_{ln}^2 must be that corresponding to the kernel estimation of the pdf, which is not equal to the logarithmic variance estimated from the data but only an approximation. Then, e-evenness

function using the log-variance of the standardized data can be larger than that of the corresponding Log-Normal distribution. However, this seldom occurs.

Assessment

After data standardization ($m_{ln} \approx 0$), Eq. 5 can be written as

$$\mu(X) = \frac{1}{2} + \ln(J_e(X)) + \ln(\sqrt{2\pi} \sigma_{ln}). \tag{6}$$

According to this Eq. 6, we can use $\ln(J_e(X))$ and $\ln(\sigma_{ln})$ in a variation partitioning procedure to discriminate whether variations in size diversity of natural samples are due to changes in the logarithmic standard deviation, σ_{ln} , or in the shape of the pdf which is quantified by the e-evenness $J_e(X)$.

We computed the size e-evenness for several contrasting size distributions: the phytoplankton of some oligohaline and meso-euhaline coastal lagoons and marshes (Baix Ter wetlands); the zooplankton of meso-euhaline coastal saltmarshes (Empordà wetlands); the hypobenthic macroinvertebrates of the same saltmarshes; and the epibenthic macrofauna, including invertebrates and amphibians, of a temporary pond (platja d'Espolla). All these ecosystems are located in Girona (NE Spain). Details on sampling procedure, body size estimations, species composition and ecological characteristics of waterbodies sampled are found in López-Flores et al. (2006) for phytoplankton data, Brucet et al. (2005) for zooplankton data, Gascón et al. (2005) for hypobenthic macroinvertebrates and Boix et al. (2004) for epibenthic macrofauna. Some descriptives of all these size distributions are listed in Table 1.

We compared the size diversity with the size e-evenness (J_e) and the standard deviation of sizes (σ_{ln}) in all these data sets. To make sizes data comparable, we use standardized sizes, that is, after the division of each size value by the geometric mean of the size distribution. For the comparison of the relative contribution of the e-evenness and the logarithmic standard deviation we used a variation partitioning procedure (Borcard et al. 1992; Legendre and Legendre 1998),

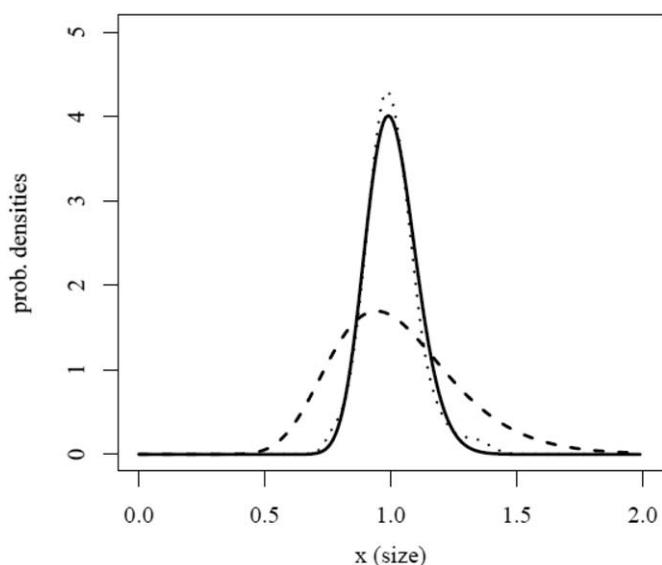


Fig. 1. Example of a negative size diversity. Full line: pdf of LN ($m_{ln} = 0, \sigma_{ln} = 0.1$), $\mu(X) = -0.884$. Dashed line: pdf of LN ($m_{ln} = 0, \sigma_{ln} = 0.242$) and null diversity; LN densities with σ_{ln} less than $\exp((-0.5)/2\pi) = 0.242$ have negative diversity and they appear more peaky than the dashed line. Dotted line: kernel density estimation of a simulated 500-sample from LN ($m_{ln} = 0, \sigma_{ln} = 0.1$) (full line).

Table 1. Mean and standard deviation values (in brackets) of some descriptives of the size distributions used.

Dataset	Phytoplankton in oligohaline coastal ecosystems	Phytoplankton in meso-euhaline coastal ecosystems	Zooplankton in meso-euhaline coastal saltmarshes	Hypobenthic macro-invertebrates in meso-euhaline coastal saltmarshes	Epibenthic macrofauna in a temporary karstic pond
	# Samples	36	80	528	15
# Sizes measured	3295 (1764)	5000(1669)	128(23.86)	670(376)	270(75.70)
Size units	μm^3 Biovolume	μm^3 Biovolume	μg Dry Weight	μg Dry Weight	mg Dry Weight
Body size geometric mean	1.916 (2.023)	37.03 (71.79)	3.051 (58.19)	0.693 (0.648)	0.0126 (0.0077)
Body size σ_{ln}	2.324 (0.258)	0.968 (0.417)	1.215(0.604)	1.782 (0.402)	1.036 (0.367)
$J_e(X)$	0.906 (0.050)	0.820 (0.134)	0.720 (0.110)	0.791 (0.069)	0.611 (0.101)
$\mu_2(X)$	3.146 (0.116)	1.622 (0.480)	1.837 (0.777)	2.528 (0.387)	1.363 (0.638)
$\mu(X)$	2.181 (0.081)	1.125 (0.333)	1.273 (0.538)	1.796 (0.276)	0.945 (0.443)

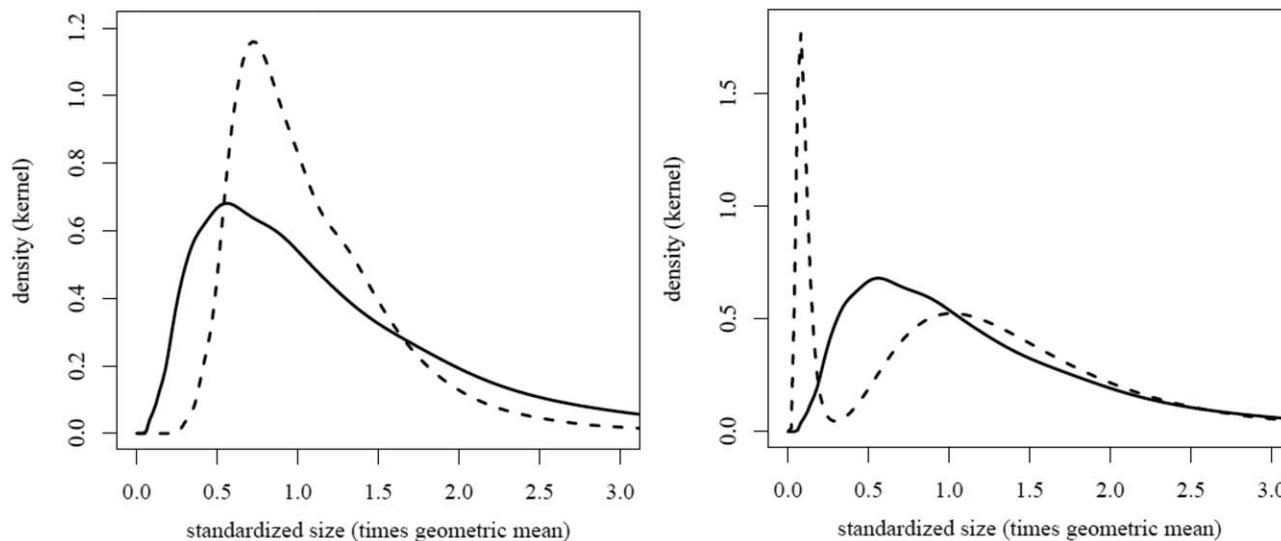


Fig. 2. Probability density functions for standardized size data sets, estimated using kernel technique on the log-scale. Left panel shows densities with similar e-evenness and different diversity: full line, a sample with $\mu(X) = 1.07$, $J_e(X) = 0.98$; dashed line, a sample with $\mu(X) = 0.55$, $J_e(X) = 0.97$. Both are phytoplankton samples in a meso-euhaline coastal ecosystem. Right panel shows densities with similar diversity but different e-evenness. Full line is the same full line distribution found in left panel; dashed line is an epibenthic macrofauna sample in a temporary karstic pond ($\mu(X) = 1.05$, $J_e(X) = 0.50$).

using the “hier.part” package (Oksanen et al. 2009) of the R language (R Development Core Team 2008). According to Eq. 6, we compared the % of variance of the size diversity (response variables) explained by $\ln(J_e(X))$ (as a proxy of the shape of the size distribution) or by $\ln(\sigma_{\ln})$ (as a proxy of the size range). Size diversity was mostly related to variation of $\ln(\sigma_{\ln})$ in all the data sets analyzed (78–88%), suggesting that increases in size diversity are mainly caused by the increase of size variability. However, e-evenness contribution can also be significant, varying between 11% and 24%, indicating that some variability in size diversity can be caused by the equalization of the relative abundances of the different sizes.

The e-evenness, $J_e(X)$, can be interpreted as a measure of goodness of fit of the standardized data ($m_{\ln}=0$) to a log-normal distribution with σ_{\ln} estimated from the data. However, for similar values of $J_e(X)$, the values of $\mu(X)$ can differ substantially depending on the values of $\ln(\sigma_{\ln})$, as shown in Eq. 6. Figure 2, shows examples of pdf’s, estimated using the kernel techniques described in Quintana et al. (2008). They correspond to some samples of the data sets (standardized) used in Table 1. Left panel shows pdf’s of two cases, which have a similar $J_e(X)$ (0.98, 0.97) but quite different diversities (1.07, 0.55 respectively). Both pdf’s fit well to a log-normal pdf’s ($J_e(X) \approx 1$, but their σ_{\ln} differ, as can be observed looking at the upper tail of the pdf’s. Right panel of Fig. 2 shows a reverse case. These data sets present similar diversities (1.07, 1.05 respectively) but their shape quantified by $J_e(X)$ (0.98, 0.50) differ, thus pointing out that the full line size distribution fits quite well a log-normal distribution but the dashed line one does not so.

Discussion

Size diversity has been applied in the analysis of size-based organization of communities, including effects of predation on prey size distribution (Compte et al. 2010, 2011, 2012; Rudolf 2012; Ye et al. 2013; Quintana et al. 2015; Sorf et al. 2015; Tavşanoğlu et al. 2015), responses to environmental biotic or abiotic gradients at local or global scale (Badosa et al. 2007; Gascón et al. 2009; Ruhí et al. 2009; Brucet et al. 2010; Schartau et al. 2010; Emmrich et al. 2011; Arranz et al. 2015; Benejam et al. 2015) and seasonal dynamics or successional patterns after disturbances (Brucet et al. 2006; Paredes and Montecino 2011). Size-based approaches have also been used for the establishment of the ecological status in aquatic ecosystems (Gallardo et al. 2011; Basset et al. 2012).

Both variability and regularity of data distribution contribute to size diversity as described in Eq. 6. The e-evenness term accounts for regularity, thus showing whether increases in size diversity are due to increase of variability or not. This cannot be discriminated when using only diversity values. Furthermore, e-evenness values range between 0 and 1 similarly to standard evenness. This is especially useful in ecological status monitoring, where a reference value is needed, from which the different thresholds of ecological status are derived (Birk et al. 2012; Kail et al. 2012). Examples in Fig. 2 illustrate the usefulness of the e-evenness. Size distributions with the same shape but different dispersion differ in $\mu(X)$ but not in $J_e(X)$ (left panel), while those with similar $\mu(X)$ but different $J_e(X)$ differ mainly in their shape (right panel). The fact that the dashed pdf in right panel has low e-evenness points out that its bimodal shape is not close to a Log-Normal distribution.

Table 2. Maximum, minimum, median, mean and quartiles of diversity ($\mu(X)$) and e-evenness ($J_e(X)$) for a phytoplankton sample belonging to the phytoplankton in meso-euhaline coastal ecosystems data set (351 size values; total abundance 12992) after bootstrap resampling. The size distribution was replicated 100 times by a multinomial simulation of counts.

	$\mu(X)$	$J_e(X)$
Min.	1.078	0.4420
1st Qu.	1.098	0.4469
Median	1.104	0.4489
Mean	1.105	0.4486
3rd Qu.	1.114	0.4507
Max.	1.130	0.4533

At this point, it is convenient to recall the underlying assumptions in the procedures for estimating both diversity and e-evenness. The parameters of the size distribution (m_{ln} , σ_{ln}) have to be estimated from the available sample. Consequently, uncertainty on these parameters depends on the size of the sample. The pdf of the log-transformed variable is estimated using a kernel technique. The kernel has been assumed normal and its bandwidth has been estimated taking into account the available sample. Afterward, the integral in Eq. 1 is computed using Monte Carlo. This means that there are many sources of uncertainty in the estimation of both diversity and e-evenness. To show the estimation variability of $\mu(X)$ and $J_e(X)$, a bootstrap experiment has been conducted (Davison and Hinkley 1997). We have chosen a real sample of sizes of the phytoplankton in meso-euhaline coastal ecosystems data set. It consists of 351 data-points with their corresponding abundances (summing up 12992). From this data set, 100 re-samples have been obtained. For each of these re-samples $\mu(X)$ and $J_e(X)$ have been computed. Table 2 shows the bootstrap quantiles of $\mu(X)$ and $J_e(X)$. It can be concluded that, for this kind of data sets, both $\mu(X)$ and $J_e(X)$ are estimated with a moderate uncertainty. In both $\mu(X)$ and $J_e(X)$, there are two significant digits.

A program for the computation of the size diversity and the size e-evenness is available for free in the web site of the Research Team on Limnology of Mediterranean Lagoons and Wetlands of the University of Girona. A tutorial explaining how to proceed is also available.

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