

A unified index to measure ecological diversity and species rarity

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Several indices have been created to measure diversity, and the most frequently used are the Shannon-Wiener (H) and Simpson (D) indices along with the number of species (S) and evenness (E). Controversies about which index should be used are common in literature. However, a generalized entropy (Tsallis entropy) has the potential to solve part of these problems. Here we explore a family of diversity indices (S_q , where q is the Tsallis index) and evenness (E_q), based on Tsallis entropy that incorporates the most used indices. It approaches S when $q = 0$, H when $q \rightarrow 1$ and gives D when $q = 2$. In general, varying the value of the Tsallis index (q), S_q varies from emphasis on species richness ($q < 1$) to emphasis on dominance ($q > 1$). Similarly, E_q also works as a tool to investigate diversity. In particular, for a given community, its minimum value represents the maximum deviation from homogeneity ($E_q = 1$) for a particular q (herein named q^*). It is remarkable that our analysis indicates that q^* and its corresponding evenness, E_{q^*} , are negatively affected by S when using simulated data. They may represent an index related to species rarity. Furthermore, S_{q^*} (i.e. the value of S_q for a specific q^*) is positively affected by richness that is an important property of any diversity index. In general, our findings indicate that the indices H , D , S , S_{q^*} , E and E_{q^*} are only part of a whole set of possibilities. In addition, the ecological properties of E_{q^*} and S_{q^*} , proposed here for the first time, show promise in ecology.

Biodiversity has attracted the attention of ecologists and conservationists, particularly in the last two decades. This attention is mainly the result of recognizing the loss of diversity caused by extinctions (Wilson and Peter 1988) and implications for ecosystem functioning and stability (McCann 2002, Loreau et al. 2002). Because biodiversity is the sum total of all biotic variation from the level of genes to ecosystems, the challenge is to find an efficient way to express or to measure this complexity (Purvis and Hector 2000). The most common measures of biodiversity (or diversity) are the Shannon-Wiener index (H ; Shannon and Weaver 1949), which is derived from information theory, and the Simpson index (D ; Simpson 1949), which is interpreted from probability theory. Both have been widely used in the last fifty years and they are appealing because they summarize, in a single number, a partial description of species richness (S) and species evenness (E). Thus, they make simple comparisons of samples possible (Hubálek 2000).

Controversy over which index should be used exists in the literature, but some authors have suggested that D performs the best (Lande 1996, Mouillot and Leprêtre 1999, Keylock 2005). Interpreted individually, these indices are not sensitive in many ecosystems where habitats are impacted but community changes have been identified by other techniques (Hurlbert 1971, Lydy et al. 2000, Rochet

and Trenkel 2003). In addition, most indices that combine S and E lose information by reducing these two aspects to one (Purvis and Hector 2000).

An alternative, common application in ecology is the use of S as a proxy for diversity. S has become the most widely used diversity measure (Ricklefs and Schluter 1993, Gaston 1996, Stirling and Wilsey 2001) with some advantages being 1) it captures the essence of biodiversity because S is promptly associated with the presence of a variety of species, 2) its meaning is widely understood, 3) it is a measurable parameter, and 4) much data on S already exist (Gaston 1996). However, it does not give information about the dominant species (i.e. the most abundant species or the ones with the highest biomass) in a given site. A more complete understanding of diversity is attained only if aspects related to evenness, rarity and dominance are considered (Wilsey et al. 2005). In addition, comparisons of S of different communities can be problematic when the effects of abundance and sampling effort are not taken into account (Gotelli and Colwell 2001).

A good measure for the dominance is the Simpson index, which unfortunately is a poor indicator of richness. In contrast, the Shannon-Wiener index is an intermediate measure that attempts to account for both aspects of diversity. These notions reinforce that idea that biodiversity can never be fully captured by a single number (Purvis and

Hector 2000). As a solution, Jost (2006) proposed that comparisons between the diversity of different samples could be more effective by obtaining the diversity of each sample equivalent to a community composed of equally-common species for each index.

In the last few decades, some of the theoretical papers on diversity indices discussed unifying aspects. In particular, Hill (1973) proposed a family of diversity indices that may be interpreted as mean numbers of species. These numbers can be written in an entropic form, thus giving content based on the information theory to these indices (Patil and Taillie 1982, Jost 2006). A comparison of these entropic indices was made by Tothmeresz (1995) using artificial communities, and by Ricotta et al. (2004) using real communities (vegetation of serpentine soils). The Patil and Taillie's indices haven recently been intensely studied in the context of statistical physics (Tsallis 1988, Tsallis et al. 1998). Motivated by their studies, Keylock (2005) explored these families of indices in an ecological context. A critical discussion of these indices was made by Jost (2006).

In this paper we introduce a new index (S_q) to measure ecological diversity. It is based on Patil and Tallie's indices (also here referred to as Tsallis entropy) and the corresponding evenness. By using a large real dataset of varying diversity in tropical fish communities and simulated data, we stress that Tsallis entropy captures multiple aspects of biodiversity and provides a better perspective that goes beyond individual indices that are currently used in ecology. We also propose special diversity and evenness indices associated with Tsallis family that balance commonness and rareness, a practice still unemployed by ecologists. In addition, we show that a specific evenness index estimated using this approach is negatively affected by species richness, thus it can be seen as an index associated with species rarity. Finally, we consider potential ideas for exploring beta diversity based on Patil and Tallie's indices.

Diversity indices and Tsallis entropy

Shannon entropy was introduced in the 1940s (Shannon 1948, Shannon and Weaver 1949) and rapidly became widespread in many areas, including ecology (Margalef 1958). In the context of statistical physics, a definition of entropy that extends statistical mechanics to an important new set of inquiries has been explored. This definition gave insight into a very large number of physical systems. In particular, it has suitable applications in complex systems and is known as Tsallis entropy, given by

$$S_q = \frac{1 - \sum_{i=1}^W p_i^q}{q - 1}, \quad (1)$$

where W is the number of states, p_i is the probability of the state i , and q is a real parameter (the Tsallis index; Tsallis 1988, Tsallis et al. 1998). Note that S_q is a family of entropies and q indicates the degree of deviation from the usual Shannon entropy that corresponds to the limiting case $q \rightarrow 1$. Usually, q is considered non-negative in order to ensure that S_q is concave.

In modern times, Tsallis entropy has been extensively applied in several different branches of science, similarly to

what happened for Shannon entropy in the last few decades. The focus of the application of this entropy lies on those systems for which the usual Shannon entropy does not work properly (Gell-Mann and Tsallis 2004, Europhysics News 2005).

Before the use of S_q as entropy in statistical mechanics, it had a rich history. To our knowledge, Havrda and Charvat (1967) were the first to introduce an entropic form like S_q . Vajda (1968), following Havrda and Charvat, further studied this form, while Daroczy (1970) and Lindhard and Nielsen (1971) rediscovered it (without knowledge of their predecessors). Sharma and Mittal (1975) introduced a two-parameter form which reproduces both eq. (1) and Renyi entropy. Wehrl (1978) mentions the entropy (1), but quoted only Daroczy. Patil and Taillie (1982) defined the diversity index eq. (1) without mentioning the preceding ideas. Finally, Tsallis (1988) rediscovered this form, but also quoted none of the predecessors. After Tsallis' contribution, investigations based on eq. (1) suddenly increased (Tsallis 2008).

As a family of diversity indices, eq. (1) interpolates the well known Simpson ($q = 2$), $S_2 = 1 - \sum_{i=1}^W p_i^2$; and Shannon-Wiener indices ($q \rightarrow 1$), $S_1 = -\sum_{i=1}^W p_i \ln(p_i)$; however, the true relevance of S_q in ecology deserves further investigation. In general, each specific application of the entropy S_q requires the determination of a particular value of q . This is not an easy task, especially when dealing with statistical mechanical systems. As discussed above, a desirable measure of diversity has to take into account all the relevant aspects that characterize ecological systems, from richness to dominance of species. Along these lines, when the possible values of q are considered, S_q becomes a family of diversity indices because it accounts for the fundamental properties of, and embodies the usual diversity indices in a simple and unified way. For instance, besides incorporating H and D , the Tsallis entropy can be used as a measure of richness because when $q = 0$, $S_0 = S - 1$ because $S = W$ and $p_i^0 = 1$ for $p_i \neq 0$.

Data set characterization

To illustrate the usefulness of this idea, we applied this family of indices to an extensive and highly diverse fish dataset. These data were collected using electrofishing in stretches of 50 m (block net at the end of the section to capture stunned fish) over 15 min, in low order streams. Out of the 34 sampled streams, 11 are located in central-west Brazil, and 23 are located in south Brazil; all belong to the Paraná River basin (thus, sites were located in distinct latitudes within Brazil). Electrofishing was employed because it is considered the best method for sampling fish in streams, because it is less selective and reduces bias regarding fish richness relative to fish densities (Agostinho and Penczak 1995, Mazzoni and Lobón-Serviá 2000).

The family of indices was also applied to two kinds of simulated dataset: 1) communities based on the log-normal distribution, with S oscillating from 9 to 108 (the same richness of our fish communities); 2) communities rarefied from our richest, real fish communities. For each simulated dataset, p_i values were estimated after 1000 randomizations.

Mathematica software (Wolfram 1991) was used for simulations.

The family of diversity indices and q^*

In our first attempt to assess the possibility of using the Tsallis entropy and to discuss the properties of this family of indices, we selected three distinct fish assemblages with 18, 45, and 108 species. In the Whittaker plots (Fig. 1), the diversity of species follows a classical trend, varying with latitude (Hubbell 2001). It is of particular relevance that we caught 108 species in Cancela Stream in the central-west part of Brazil, in a 50 m long sampling site (i.e. one fourth of the total richness found in the Palaearctic biogeographic region; Matthews 1998). The other data were samples from Rochoso Stream (45 species), also in central-west Brazil, and Barra Grande Stream (18 species) in southern Brazil.

In Fig. 2, S_q is shown as a function of q for the data presented in Fig. 1. Two things deserve special attention in this diagram. For $q < 1$, S_q gives a measure of richness and for $q > 1$, S_q gives a measure of the dominant species. The Shannon-Wiener index ($q \rightarrow 1$) separates these regions and is characterized by richness and dominance. In fact, in this family of indices, H occupies an intermediate position because p_i^q gives relatively more weight to common species when $q > 1$ and more weight to rare species when $q < 1$. This tendency is consistent with higher weight given to dominance when D is used (i.e. when $q = 2$; Magurran 1988, Wilsey et al. 2005).

Consistent with what happens with S_q , it is possible to consider a family of evenness indices labeled by q (Keylock 2005). This family is constructed from eq. (1) in the form

$$E_q = \frac{S_q}{S_q^{\max}}, \quad (2)$$

where $S_q^{\max} = (1 - W^{1-q}) / (q - 1)$ is the maximum value of S_q when only the constraint $\sum_{i=1}^W p_i = 1$ is imposed. Hence,

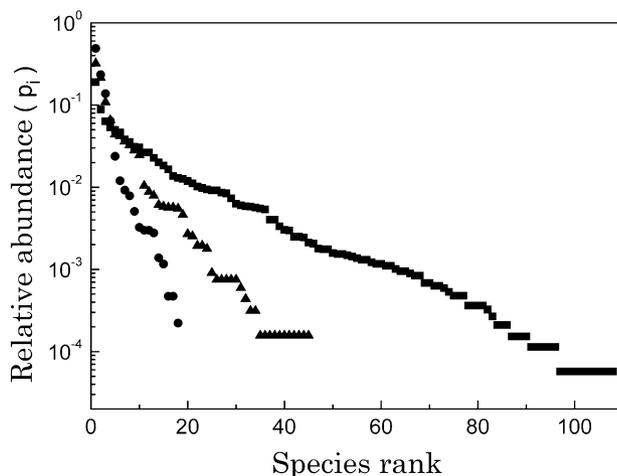


Figure 1. Whittaker plot for fish collected in three streams in Brazil. Cancela (squares; $S = 108$; $14^\circ 42'S$, $56^\circ 15'W$), Rochoso (triangles; $S = 45$; $17^\circ 50'S$, $48^\circ 31'W$) and Barra Grande (circles; $S = 18$; $25^\circ 30'S$, $53^\circ 07'W$) streams. Species are ranked according to their abundances.

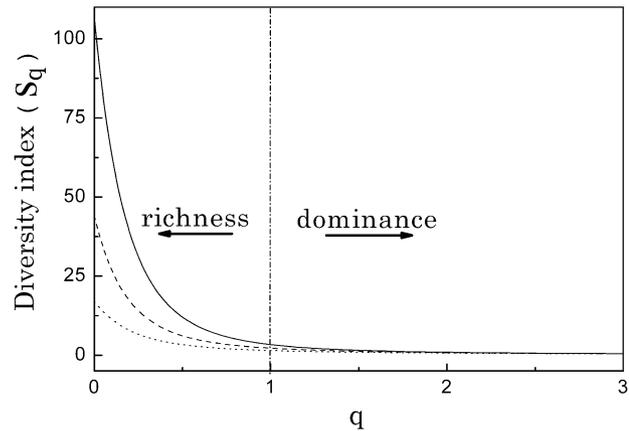


Figure 2. The diversity indices S_q versus q for three sites in Brazil (shown in Fig. 1). The region $q < 1$ emphasizes richness whereas the region $q > 1$ emphasizes species dominance (in this case, based on abundance). The limit $q \rightarrow 1$ leads to $S_1 = H$, i.e. the Shannon-Wiener index. Solid line: Cancela; dashed line: Rochoso; dotted line: Barra Grande.

the classical evenness connected to the Shannon-Wiener index ($q \rightarrow 1$) is only a particular case. Likewise, there may exist an evenness related to the Simpson index ($q = 2$), another to the richness ($q = 0$), and so on for other values of q . The evenness E_q is shown in Fig. 3 for a range of q for the three sites considered. The case $q = 0$ gives an evenness $E_0 = 1$ that is independent of relative abundances. On the other hand, the evenness index corresponding to the Simpson index E_2 reveals some contrasts among relative abundances, but is close to unity. The classical evenness $E_1 = E$ is clearly improved with respect to the two preceding cases because, among the three, it is the one that most deviates from the unity.

To obtain a still improved evenness E_q other values of q must be explored. From Fig. 3, it is clear that each family E_q contains a minimum value for each dataset. Thus, at the minimum value of E_q , a maximum contrast between S_q^{\max} and S_q occurs for a particular q (q^*). Then, q^* represents the position in the curve where relative differences among S_q and S_q^{\max} values are maximized. Another remarkable feature

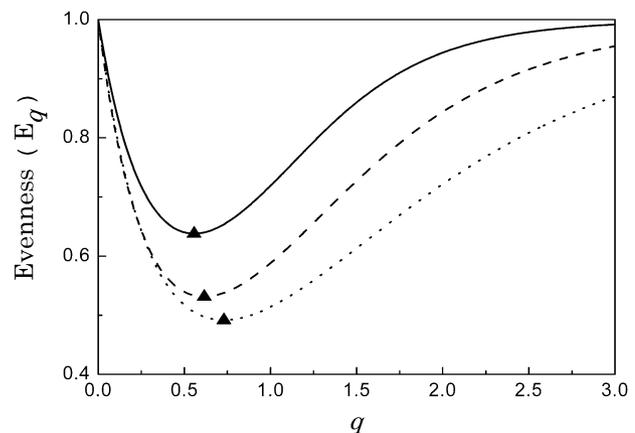


Figure 3. Evenness indices E_q versus q for the data of Fig. 1. E_q exhibits a minimum for $q = q^*$ (triangles). The values are $q^* \simeq 0.56$ (solid line; Cancela), $q^* \simeq 0.62$ (dashed line; Rochoso), and $q^* \simeq 0.73$ (dotted line; Barra Grande).

of Fig. 3 is the general trend that the value of q at the minimum of E_q ($q = q^*$) increases for decreasing number of species.

To further explore the properties of q^* , we used our entire fish dataset and the simulated log-normal dataset (with S oscillating from 9 to 108) to simulate our real communities. Both datasets showed a negative relationship between q^* and S (Fig. 4a), and the same was true when we plotted q^* against S that obtained after rarefying our richest fish sample (Fig. 4b). We noted that values of q^* basically remained between 0.56 and 1.12 for the real dataset, between 0.60 and 0.95 for the simulated log-normal dataset and between 0.56 and 0.81 for the rarefied dataset. Thus, indices close to this range (i.e. between S and H approximately) are the ones that best display the deviation from the maximum equitability ($E_q = 1.0$) of a given sample. This has a practical consequence: although D is unbiased and has a minimum standard deviation (Lande 1996, Moullot and Leprêtre 1999, Keylock 2005), theoretically any indices between S and H (i.e. any S_q for q between zero and one) better express the diversity of a biological community than alternate values.

The consistent pattern of decreasing q^* with S obtained with our real and simulated dataset deserves a biological or

ecological interpretation. Before offering an alternative, let us consider two important aspects: 1) increasing S in our log-normal simulated data (Fig. 4a) certainly means an addition of rare species (Tokeshi 1999); 2) similarly, when we move from more to less rarefied communities (Fig. 4b), the increase in species richness is a result of adding the less abundant (rare) species through the process of rarefaction. Because there was a clear tendency of q^* to decrease with increasing the number of rare species for both the simulated and rarefied communities, it is tempting to suggest that this index is sensitive to species rarity of a community. In fact, when using our entire fish dataset (Fig. 4a), it is clear that at similar, lower S values, q^* is highly variable (i.e. it varies independent of S). This indicates that it is much more affected by species relative abundances than by species richness per se. Thus, the decrease of q^* with S in our real dataset also indicates that this index is more affected by relative abundances than by species richness, indicating the presence of rare species.

Although E_{q^*} apparently increased with species richness (Fig. 3) by using our entire real dataset, we showed that this tendency was not maintained (Fig. 5). Thus, although q^* is highly affected by species richness, E_{q^*} was highly variable, especially at low values of S . However, it was apparently

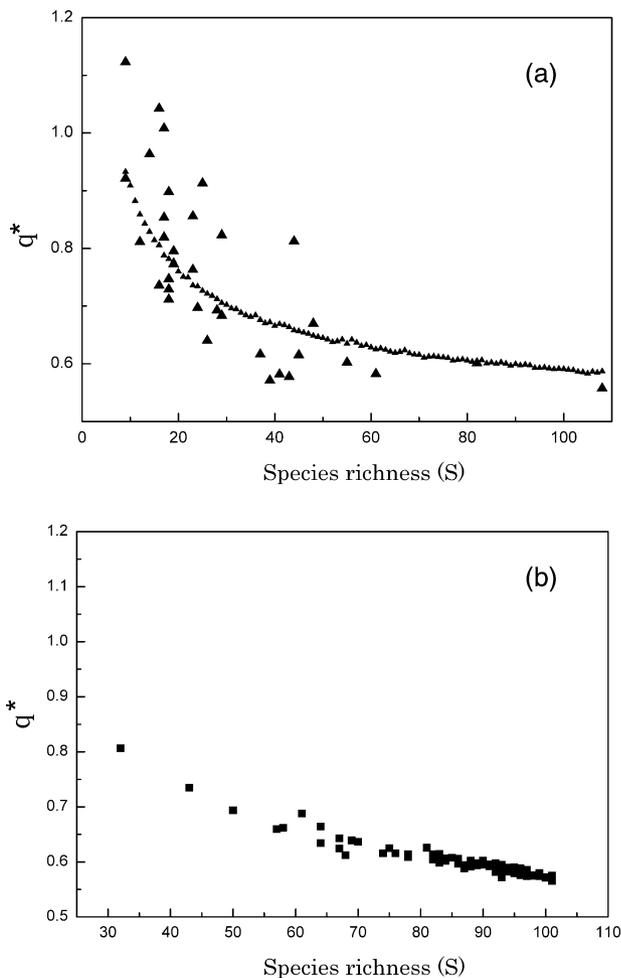


Figure 4. Values of q^* versus S for the entire dataset (large triangles) and log-normal communities (small triangles) (a) and for rarefaction of the richest fish community (b).

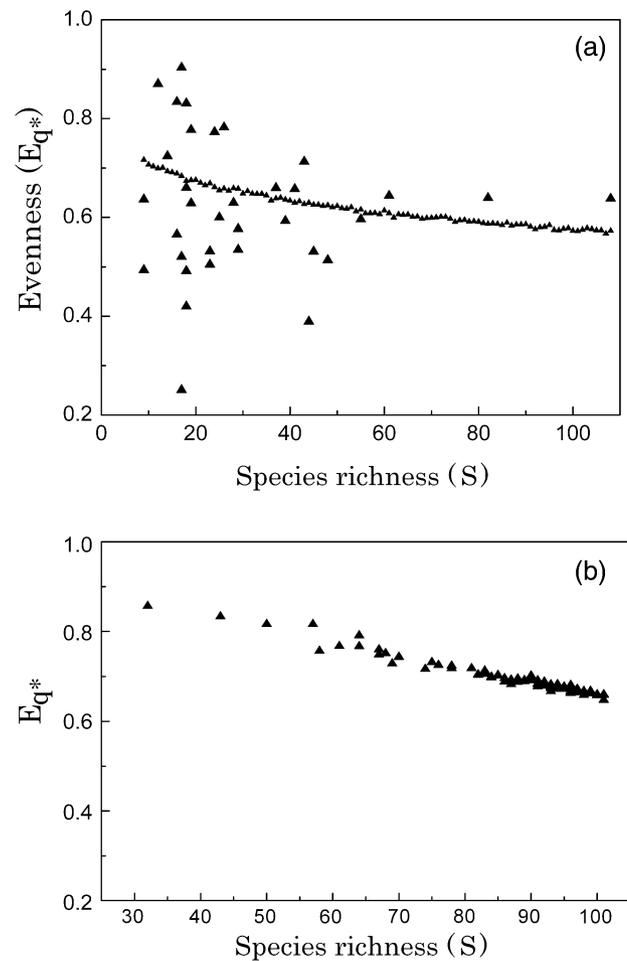


Figure 5. Values of E_{q^*} versus S for the entire dataset (large triangles) and log-normal communities (small triangles) (a) and for rarefaction of the richest fish community (b).

independent of the number of species when looking at the entire fish dataset. This suggests that this index is invariant, i.e. independent of species richness. A different picture emerged, though, when we used our simulated log-normal (Fig. 5a) and our rarefied (Fig. 5b) communities because a clear and constant decrease of E_{q^*} with increasing S was observed. Again it is tempting to suggest that E_{q^*} is related to species rarity. However, its different behavior when using real versus simulated data deserves further attention.

Regarding S_{q^*} , it was clear that this index was positively affected by S in both the real and simulated log-normal communities (Fig. 6). This is not a surprise because a significant positive relationship between S and H (an index whose value is reached when $q \rightarrow 1$) has been recorded (Hill 1973). However, this tendency deserves further investigation as conflicting results have been registered (Stirling and Wilsey 2001, Wilsey et al. 2005). It is also worth noting that despite being estimated through E_{q^*} via q^* , S_{q^*} was much more conservative than these two indices. In other words, although E_{q^*} and q^* varied conspicuously at low values of S (Fig. 4a, b), S_{q^*} consistently increased with S (Fig. 6).

Considering the emphasis on the deviation from the equitability and the positive relationship between S and S_{q^*} , the latter (i.e. values of S_q correspondent to q^*) also has a potential to be used as an alternative diversity index. We emphasize that this is an innovative index, differing from the others because it is based on E_{q^*} . So, this is an index that theoretically varies insofar as q and q^* vary from zero to infinity (in our samples, q^* assumes values from 0.56 to 1.12 and thus S_{q^*} assumes values from $S - 1$ ($q = 0$) and H ($q \rightarrow 1$)).

The comparisons of S_{q^*} with other traditional indices (namely Shannon and Simpson) indicated that, in general, they follow the same tendency of increasing with S , as shown in Fig. 6. For our fish communities, the values of Shannon-Wiener fluctuated from 0.71 to 3.37 (a factor of 4.7 times) and from 0.31 to 0.94 for the Simpson index (a factor of 3 times), whereas the S_{q^*} oscillated from 0.70 to 10.02 (a factor of 14.3 times) thus increasing the contrast among samples (Fig. 6). The same tendency was observed

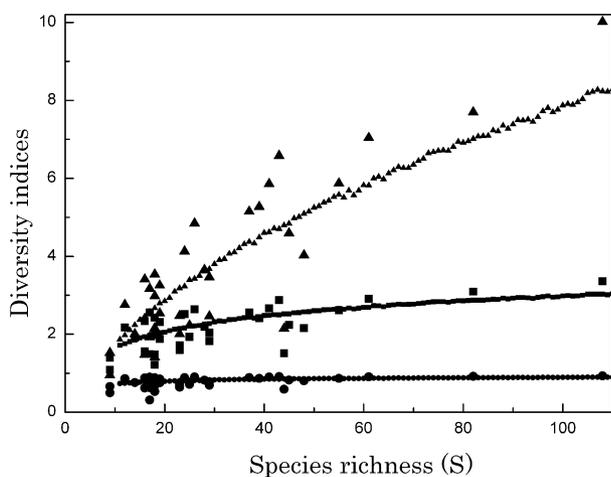


Figure 6. Values of S_{q^*} (triangles), H (squares) and D (circles) versus S for the entire dataset (large symbols) and log-normal communities (small symbols).

when we used our simulated dataset: 1.72 to 3.04 for Shannon-Wiener, 0.74 to 0.90 for Simpson, and 1.86 to 8.28 for S_{q^*} (Fig. 6). Thus, S_{q^*} may be used as an alternative index, especially when the contrast among communities is not apparent by other indices.

Further development

As pointed out in our work, S_q was used by others. However, in this work, we explored the meaning of a particular value of q (namely q^*). Before concluding, we would like to call attention to another possibility of exploring the concept of beta diversity using the general concept presented in this paper in tandem with alpha diversity measured via S_q , but for generic values of q . In the same manner as Shannon indices have been used to measure alpha diversity and the closely related Kullback-Leibler, relative information was employed for investigating beta diversity (Orloci 1969, Colwell and Futuyma 1971, Macchiato et al. 1992, Ricotta and Avena 2002, Ernoult et al. 2003, Cazelles 2004, Gorelick et al. 2004, Gorelick 2006, Ludovisi and Taticchi 2006). A generalized Kullback-Leibler relative entropy, related to eq. (1), may be used for an information-theoretical measure of beta diversity. The generalized Kullback-Leibler distance is given by Patil and Taillie (1982) and Tsallis (1998):

$$K_q(p, p') = \sum_{i=1}^W \frac{p_i}{1-q} \left[1 - \left(\frac{p_i}{p'_i} \right)^{q-1} \right], \quad (3)$$

where p_i and p'_i are probabilities to be compared. Notice that eq. (3) reduces to $-S_q$ if p'_i is absent, because $\sum_{i=1}^W p_i = 1$. Moreover, if $q = 0$, then $K_0(p, p') = 0$. If, on the other hand, $q \rightarrow 1$, the usual Kullback-Leibler distance (Kullback and Leibler 1961) is recovered. Finally, the distance connected with Simpson's measure is $K_2(p, p') = 1 - \sum_{i=1}^W \frac{p_i^2}{p'_i}$. These formulas may be helpful to investigate relevant aspects regarding beta diversity. For instance, the program recently started by Gorelick (2006) to extend Shannon's and Simpson's indices to simultaneously account for species richness and relative abundance may now be extended by considering a continuous family of q values.

Concluding remarks

In contrast to what occurs in statistical mechanics where a value of q has been attributed to every class of systems (Tsallis 2008), in ecology, S_q represents a family of indices labelled by q that expresses diversity in a broader way. Thus, S_q as a function of q is a quantitative and powerful measure of the enormous variation found in natural systems. This approach shows a solution for the multi-dimensional aspect of diversity which cannot be reduced to a single number. Indeed, biodiversity can be measured by a family of indices labelled by q that gives a special meaning to the quantity S_{q^*} in addition to the classical ones ($S_0 = S - 1$, $S_1 = H$, and $S_2 = D$). Curves produced by this approach could be used to compare samples in a

similar way that Whittaker plots are used by ecologists (Tokeshi 1999). However, usage of Tsallis entropy is beneficial: not only are the separate effects of S and E observed (as occur with Whittaker plots), but the combination of both S and E is also shown.

By analogy, evenness should be characterized by a class of numbers E_q , instead of a single value derived from Shannon information theory. In this family, E_{q^*} has a special role because it gives a measure of maximum contrast between S_q and S_q^{\max} and it apparently is a parameter associated with species rarity.

The idea of a family of diversity and evenness indices are not new in ecology; they were proposed earlier by others. However, their use in ecology is under-explored. The alternative index of diversity (S_{q^*}) and evenness (E_{q^*}) emerged from this family. They are associated with q^* , i.e. the value of q where the minimum E_q occurs, and thus they are unique for each sample. Most importantly, these indices have desirable ecological properties because S_{q^*} is positively related to S whereas q^* and E_{q^*} are negatively related to S , and positively affected by rarity (i.e. they are an indication of the importance that rare species have in a given community). S_{q^*} enhances the contrast between samples (i.e. increase the differences between minimum and maximum values of the index), when compared to Shannon-Wiener and Simpson indices. Therefore, these properties deserve further analyses using different real and simulated communities. In addition, the families of indices S_q and E_q should be investigated because their strength lies on their high probability of having wide applications by serving as unifying tools for several areas of inquiry, from ecology to statistical physics.

Acknowledgements – The authors are especially thankful to the Brazilian Council of Research (CNPq) for continuous funding through a Research Productivity Grant.

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