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Diversity measurement of benthic diatom taxocoenoses based on information theory (H') using genus-to-species ratio

Mediciones de diversidad en taxocenosis de diatomeas bentónicas con base en la teoría de la información (H') utilizando la razón género-especie

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ABSTRACT

Background. Within any given taxocenosis of benthic diatoms (BDT), the distribution of the taxa relative abundances renders them as very abundant, common, uncommon, and rare taxa. This structure is considered when estimating species diversity using Shannon's index (H') based on information theory. Thus, because this distribution also occurs within the taxonomic hierarchy of BDT, i.e., genera with a high number of species-infraspecies (SS) or species singletons, estimating species diversity (H') using the genus/SS ratio instead of relative abundances, represents an alternative measure of diversity but resorting to a much smaller data matrix. Hence, the diversity index designated $H'_{G/SS}$ is proposed here. **Objective.** In this essay, we sought to gather evidence that combining information on the genus-level taxa and their included SS provides a reliable estimation of taxonomic diversity for BDT. Hence, we tested the hypothesis that the estimated $H'_{G/SS}$ for the floristic of BDT in a particular locality would be as high as the highest value using diatom relative abundances. **Method.** To test the above, floristic and species diversity (H') data from several studies of BDT along Mexican shores were analyzed quantitatively under the premise that diversity estimates based on relative abundances of species (H') or the $H'_{G/SS}$ index would be equivalent. **Results.** Statistical tests supported our hypothesis showing no significant differences between the original values of H' and those using $H'_{G/SS}$. **Conclusions.** This diversity estimation using $H'_{G/SS}$ for BDT represents a reliable, quicker, and more comprehensive approach and another parameter that can be used for further conservationist, ecological, and biogeographical purposes.

Keywords: Diversity estimate; Ecological indices; Ecological parameters; Floristics; H'

RESUMEN

Antecedentes. En cualquier taxocenosis de diatomeas bentónicas (TDB), según la distribución de sus abundancias relativas, los taxa se clasifican como muy abundantes, abundantes, comunes, poco comunes, y raros. Esta estructura es la base del cálculo de diversidad de especies mediante el índice de diversidad de Shannon (H') con base en la teoría de la información. Así, dado que dicha distribución ocurre igualmente dentro de la jerarquía taxonómica de TDB, i.e., géneros con muy abundantes o abundantes especies o infraespecies (SS), o que contienen una sola SS, el estimar (H') mediante la razón género/SS en vez de abundancias relativas, representa una medida alternativa de diversidad, empero recurriendo a una matriz de datos mucho más pequeña. De acuerdo con esto, se propone aquí el índice de diversidad designado $H'_{G/SS}$. **Objetivo.** En este ensayo se buscó reunir evidencias de que la combinación de información a nivel de género y las SS que incluyen, proporciona una estimación confiable de diversidad taxonómica para TDB. Así, se contrastó la hipótesis de que los valores calculados de $H'_{G/SS}$ para la florística de TDB en una localidad en particular serían tan altos como el valor máximo calculado utilizando las abundancias relativas. **Método.** Para contrastar la hipótesis se analizaron cuantitativamente datos floristicos y de diversidad de especies (H') de diversos estudios de TDB conducidos en litorales Mexicanos, bajo la premisa de que los cálculos de diversidad hechos, tanto con abundancias relativas (H') o con el índice $H'_{G/SS}$ serían equivalentes. **Resultados.** Las pruebas estadísticas apoyan nuestra hipótesis mostrando que no había diferencias significativas entre los valores originales de H' y los de $H'_{G/SS}$. **Conclusiones.** Esta forma de estimar diversidad en TDB representa una aproximación confiable, más rápida y comprensiva, así como un parámetro adicional para ser utilizado con fines de conservación, ecológicos y biogeográficos.

Palabras clave: Florística; H', Índices ecológicos; Medición de diversidad; Parámetros ecológicos

INTRODUCTION

After constructing reliable floristics of benthic diatom taxocoenoses (BDT) and estimating the relative or proportional abundances (inventories) of the recorded taxa at species and infraspecific levels, for any given locality, the data can be used for estimating ecological parameters that better describe the assemblages by incorporating the numerical proportions of said taxa into a desired algorithm. Said ecological studies are to be based on analyses of classical parameters that can reflect undisturbed environments or reflect various types of impact (Magurran, 1998). Thus, unlike species richness alone, analysis of species diversity depicts a structure in benthic diatom assemblages based on composition, relative abundance, diversity, equitability, and dominance, which can be used to assess environmental conditions in protected areas (Siqueiros-Beltrones *et al.*, 2017). Notwithstanding, floristics still constitutes the primary basis to achieve it, inasmuch it constitutes the main reference for the occurrence of indicator species in a given locality that help to infer appropriate conditions for their presence.

Ecological diversity measurements based on information theory, e.g., Shannon's H' condense the relative abundances of individuals of all the taxa accounted for in the inspected samples that generally exhibit a distribution that can be summarized into very abundant, abundant, common, uncommon, and rare taxa. Then, these are used to estimate parameters of the taxocenoses that lead to ecological interpretation. However, the numerical distribution of abundances across species-infraspecies also occurs within the taxonomic hierarchy of benthic diatom assemblages or taxocoenoses (BDT), i.e., genera that are very diverse or contain a high number of species-infraspecies (SS) or that have only one SS (singletons), with many other genera being represented by various numbers of species in between (common and uncommon), as shown in figure 1 using data from Revillagigedo Archipelago (Siqueiros-Beltrones *et al.*, 2021).

Indeed, this approximation should work for very distinct BDT, for example, those from harsh or extreme environments, or allow to compare the calculated $H'_{G/SS}$ index values from related, albeit particular life forms, i.e., other taxonomical groups with similar assemblage structures such as macroalgae taxocoenoses. An overall value of H' usually represents an average for several samples that exhibit extreme values due to the patchy distribution of benthic diatoms, where the highest values are associated with the highest species richness. Likewise, diversity estimates based on relative abundances or the genus/SS ratio are expected to be equivalent, since, as stated above, they exhibit the same distribution, i.e., individuals within species and SS within genera. Thus, the working hypothesis states that the estimated value of $H'_{G/SS}$ for a given locality would be equivalent and as high as the highest value computed for H' using relative abundances of the diatom taxa.

MATERIAL AND METHODS

Floristic and quantitative data from several published BDT studies were extracted, expressly those of genus and species richness and the corresponding values of diversity (H'). For BDT, the following studies were used: Siqueiros-Beltrones (1998), Siqueiros-Beltrones *et al.* (2004), Siqueiros-Beltrones *et al.* (2017), Siqueiros-Beltrones *et al.* (2019), Siqueiros-Beltrones & Sánchez-Castrejón (1999), Siqueiros-Beltrones & Hernández-Almeida (2006), Martínez *et al.* (2021), , López-Fuerte & Siqueiros-Beltrones (2006), Hernández-Almeida & Siqueiros-Beltrones (2008), Hernández-Almeida (2009), Hernández-Almeida & Siqueiros-Beltrones (2012), for BDT from harsh environments López-Fuerte *et al.* (2020) and Siqueiros-Beltrones (1990) and, for macroalgae assemblages Serviere-Zaragoza *et al.* (2003) and Serviere-Zaragoza *et al.* (2007). Ten of the main diatom genera present in most floristic studies were also compared between these localities in search of any trend.

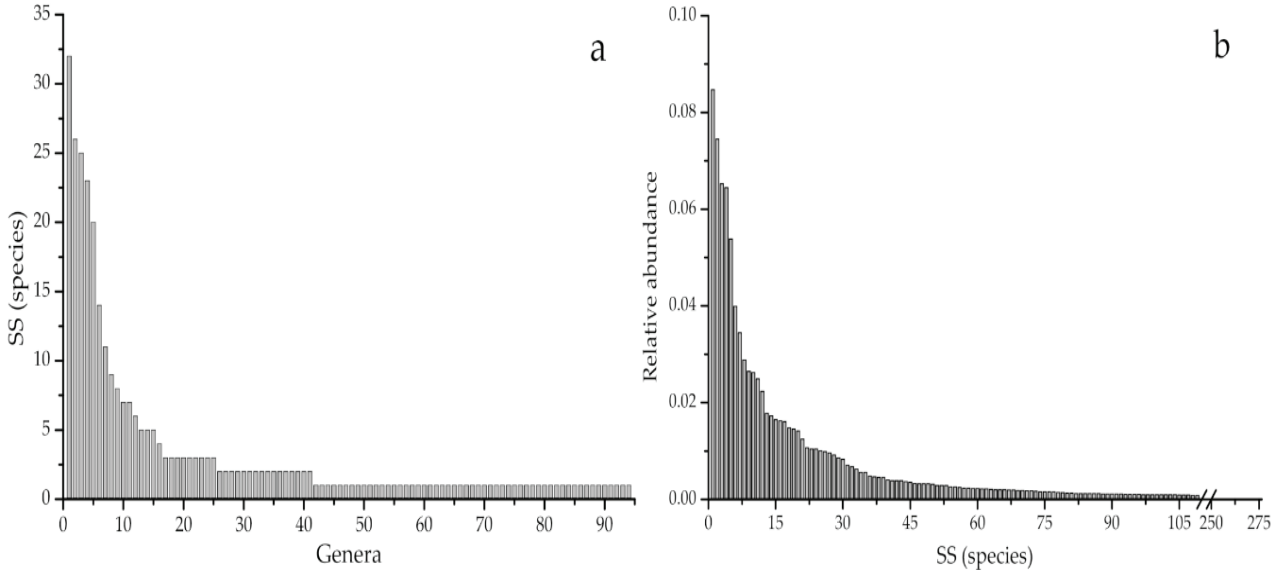

Figure 1. a) Distribution of SS per genus in BDT of Revillagigedo Archipelago, b) distribution of relative abundance per SS in BDT of Revillagigedo Archipelago. SS=species or infraspecies.

The quantitative data were analyzed to estimate taxonomic diversity (G/SS) using the information theory-based diversity index H' in its derivation for $H'_{G/SS}$ and other diversity indices (J', λ) and to observe if the computed values reflect the structure of diatom assemblages that were obtained based on both their relative abundances (Formula 1) and derived genus-to-species (Formula 2).

$$H'_{\left(\frac{n}{N}\right)} = -\sum_{i}^{n} p_i log_2 p_i$$

The quantity p_i is the proportion of individuals found in the *i*th species among the total number of individuals on the sample.

$$H'_{\left(\frac{G}{SS}\right)} = -\sum_{i}^{n} \left(\frac{G}{SS}\right) log_2 \left(\frac{G}{SS}\right)$$

The quantity *G/SS* is the proportion of species found in the *i*th genus among the total number of species on the sample.

To test that this approximation is valid for other taxonomical groups, data derived from studies on two macroalgae taxocoenoses were also used to compare the calculated $H'_{G/SS}$ index values from related, albeit distinct life forms, with a similar assemblage structure. To test if our estimated values of taxonomic diversity using G/SS were equivalent to those using relative abundance, we performed a Mann-Whitney test with $\alpha = 0.01$ (SPSS 26 software).

RESULTS

The marked variation in the number of taxa can be noted (Table 1), both for the SS (45 – 395) level as for the genus (G) level (19 – 103) for the various localities considered, ranging from harsh (extreme) subtropical environments (lowest SS and G) to highly productive environments in tropical and temperate latitudes (higher SS and G). The BDT in these studies conforms to the promised structure according to the distribution of the SS among the present genera. These may be either similarly numerous or entirely different in the various taxocoenoses, thus showing no particular trend in their occurrences. Also, no trend was observed in the ten main diatom genera in the analyzed floristic studies from these localities.

Overall, $H'_{G/SS}$ estimated values (Table 2) were similarly high or higher (3.65 – 5.65 bits/taxon) than those maximum calculated in the correspondent study using the relative abundance of the SS (3.2 – 5.9 bits/taxon). The above indicates a more homogeneous distribution of the SS among the genera in the taxocoenoses than the relative abundances among the SS, as confirmed by the overall high values (0.81 – 0.91) of equitability ($J'_{G/SS}$) and lowest values of (Simpson's) dominance ($Ds_{[G/SS]}$). Although the estimated values of $H'_{G/SS}$ for the surveyed studies were as high as the highest value computed using relative abundances of the benthic diatom taxa (Table 2), the median value does not show a statistical difference (Mann-Whitney U=49 n_1=14 n_2=12, z=-1.3, p = 0.19 two-tailed) thus backing the posed hypothesis. The computed values for indices measuring the other components of the diversity of the analyzed BDT agree with said values.

The proportion of genus singletons (PGS) ranged from 41% (BM) to 59% (CGPhy) in productive environments and 63% (LP) in harsh ones (Table 2). Interestingly, in productive environments, CGPhy got the higher PGS that corresponds with the highest $H'_{G/SS}$ (5.65 bits/taxon), in contrast with AR and BM taxocoenoses that got more genera and SS; however, a lower PGS. From a different perspective, most taxocoenoses exhibited over 50% proportion of genus singletons. This was the case in both studies of macroalgae, for which the diversity ($H'_{G/SS}$) values were among the highest.

Table 1. Number of genera (G) and species-infraspecies (SS) for epiphytic diatoms and number of SS for the main ten genera in the taxocoenoses from: central region Gulf of California (CGC), epiphytes on *Phyllodyction* (CGPh); Revillagigedo Archipelago (AR); Gulf of California mouth: Caimancito (BGc), BGp (phaeophytes), BGr (rhodophytes); Balandra lagoon (Bal); W coast of the Baja California Peninsula: BCS (WBS); Guerrero Negro lagoon (LGN); Bahia Magdalena (BM); Laguna Figueroa (LF); La Poza (LP). A) *Achnanthes*; B) *Amphora*; C) *Caloneis*; D) *Cocconeis*; E) *Diploneis*; F) *Grammatophora*; G) *Lyrella*; H) *Mastogloia*; I) *Navicula*; J) *Nitzschia*. * represent harsh environments.

	CGC	AR	WBS	BGc	BGp	BGr	LGN	CGPh	BM	Bal	LF*	LP*
SS	328	395	322	278	317	234	232	244	306	230	67	45
G	94	103	83	79	85	74	78	86	79	49	31	19
A)	14	5	12	11	13	3	3	7	9	14	2	1
B)	32	23	31	23	31	19	22	17	30	27	6	8
C)	2	14	5	2	2	2	4	2	4	1	0	0
D)	26	27	34	23	28	22	13	12	13	9	2	2
E)	20	20	25	9	8	4	10	15	13	12	4	1
F)	7	15	4	1	3	1	1	5	1	1	0	0
G)	11	4	3	10	6	5	21	4	9	6	0	0
H)	8	56	2	26	31	20	5	3	17	6	2	1
I)	25	23	24	23	20	16	18	13	29	39	7	7
J)	23	25	25	22	30	22	5	25	28	27	9	9
SS /10 G	168	203	165	150	172	114	102	103	153	132	32	29

DISCUSSION

Several assays concerning the use of information theory and its interpretation of the estimated values of diversity, through computation of H' based on relative abundances of taxa, have been published. These have focused on establishing the proper way of adapting this non-ecological algorithm as a valuable biodiversity measurement (Washington, 1984; Siqueiros-Beltrones, 1998; Siqueiros-Beltrones & Sánchez-Castrejón, 1999; Siqueiros-Beltrones, 2005; Hernández-Almeida, 2008). The actual meaning of the computed values of H' is questioned as to whether they directly measure species diversity or other properties of the data such as information, uncertainty, entropy, order, or stability, thus requiring further processing (Hernández-Almeida, 2008) and analysis of their intrinsic paradoxical interpretations that lead to the proposal of changing the measuring units from bits/ind. to bits/taxon (Siqueiros-Beltrones, 2005).

The hypothesis that the estimated value of $H'_{G/SS}$ for a particular locality would be as high as the highest value computed using relative abundances of the diatom taxa was supported by the calculated values and the correspondent values of the other structural components of the BDT, such as dominance and equitability. This may be interpreted as the presence of many SS taxa, or high species/genus richness, that corresponds with a high variety of taxa at the genus level, thus giving a better sense of taxonomic diversity that takes into consideration both number or genera and the proportion of SS for each genus. Although this should be implied by estimating H' using relative abundances of species that demand extra effort, it is only related to the species level.

Much earlier, McIntire & Overton (1971) estimated diversity using H' and relative abundances for the genera (generic diversity) with a different approach and obtained much higher values and averages of H' at the species level. On the other hand, our observations agree with the second part of the hypothesis, i.e., that diversity estimates based either on relative abundances or the taxonomic diversity index were to be equivalent. This also matches with the distribution patterns of G/SS and species relative abundances in both approaches (Fig. 1).

The fact that most taxocoenoses exhibited over 50% of the genera with a single SS that may be represented by one or many individuals is challenging to interpret. In general, except for the taxocoenoses from harsh environments, the more proportion of genus singletons there are, the higher $H'_{G/SS}$ seems to be. This may be associated with the equitability component (J'), which is displaced to the "rare" taxa side of the typical distribution, where the many singletons influence (both types of) H'max values and usually the computed values of (both types of) H'. Namely, many genus singletons have a higher impact on the $H'_{G/SS}$ estimate, increasing the uncertainty in the identity of a randomly collected specimen when the more diverse genera do not have extreme values of SS. The same behavior can be perceived when calculating species diversity based on relative abundances.

Thus, in this study, in the algorithm $H'_{G/SS} = -\Sigma pi \log_2 pi$, the notation G/SS = pi, i.e., the probability for any given genus being represented by the collected SS, or that, given a certain number of SS, the expected number of genera to be represented.

The relation between genus richness, the proportion of genus singletons (PGS), and genera without a disproportionate number of SS determines the highest taxonomic diversity values, as seen with the macroalgae taxocoenoses. Although this approach generally allows the relative abundances and use of a sample size to be omitted, it renders a better correspondence between floristics and its generic distribution within a certain taxocoenosis. Moreover, the better representation of a genus allows, as with a species, to make inferences on the environmental conditions favoring it or its adaptability when exhibiting an ubiquitous distribution. Further ideas leading to plausible hypotheses should include examining the more efficient approach, either taxo-

Table 2. Estimated taxonomic diversity ($H'_{G/SS}$) for epiphytic diatoms: Gulf of California central region (CGC), on Phyllodyction (CGPhy), Revillagigedo Archipelago (AR); Gulf of California mouth: Caimancito (BGc), phaeophytes (BGp), rhodophytes (BGr); Balandra lagoon (Bal); W coast of the Baja California Peninsula: BCS (WBS), Guerrero Negro lagoon (LGN), Bahia Magdalena (BM), Laguna Figueroa (LF), La Poza (LP). Macroalgae taxocoenoses: Revillagigedo Archipelago (RAm); W coast of BCS (WBSm). * represent harsh environments.

Index	CGC	CGPhy	AR	BGC	BGp	BGr	Bal	LGN	WBS	BM	LF*	LP*	RAm	WBSm
$H'_{G/SS}$	5.48	5.65	5.47	5.30	5.30	5.35	4.55	5.44	5.30	5.44	4.53	3.65	6.42	5.46
H'c	4.8	NC	5.2	4.9	4.6	4.4	4.5	5.9	5.4	5.5	4.2	3.2	NC	4.85
$H'_{maxG/SS}$	6.55	6.43	6.69	6.3	6.41	6.28	5.62	6.23	6.37	6.32	4.95	4.25	6.72	5.7
$J'_{G/SS}$	0.84	0.88	0.82	0.84	0.83	0.85	0.81	0.87	0.83	0.86	0.91	0.86	0.95	0.958
$Ds_{G/SS}$	0.04	0.03	0.04	0.04	0.04	0.04	0.07	0.03	0.04	0.03	0.04	0.09	0.009	0.015
Gn	94	86	103	79	85	78	49	75	83	80	31	19	106	52
S	319	245	386	275	317	234	230	233	322	326	68	45	192	79
G_{singl}	53	51	53	43	42	43	23	35	42	33	17	12	66	39
PGS %	56	59	52	54	49	55	47	47	51	41	55	63	62	75

$H'_{G/SS}$= taxonomic diversity calculated with the genus-to-species ratio; H'c= original maximum value for H' in each study, $H_{maxG/SS} = (\log_2 Gn)$; $J'=H'/H'_{max}$; $Ds_{G/SS}$= Simpson's dominance calculated with the genus-to-species ratio; Gn= genus richness; S= species richness; G_{singl}= number of genus singletons; PGS % = Percentage of genus singletons; NC= no computed value.

nomic or ecological diversity, using information theory or combined. Notwithstanding, the relevance of taxonomic issues such as classification, determination, and identification of benthic diatoms in marine environments will be adequately complemented if the structure of BDT is compared. Hence, this taxonomic diversity estimation for BDT represents a quicker, more comprehensive, and reliable approach, and with it, another parameter of interest is added that can be used for further conservationist, biogeographical, and ecological purposes.

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