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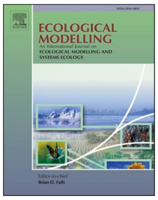

Decomposition of Whittaker’s gamma diversity: a novel way combining entropies and divergences

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ABSTRACT

Accurate, standardized, and comparable methods for estimating biodiversity are crucial in ecology to properly assess and monitor the health of communities. Special cases of generalized entropy are commonly used to estimate alpha diversity. The related concept of generalized divergence can be used to estimate the beta diversity. Using cross entropy notion, we propose a modular decomposition of gamma diversity by using entropy and divergence functions. We prove that if alpha is Shannon entropy and beta is Kullback-Liebler divergence, the classical Whittaker’s gamma diversity is mathematically decomposed via our proposed *local gamma* index. To show the ecological application of this index and its generalization we compute the local gamma of several orders using a real large biological dataset. The index is discussed in detail for two limit cases, one where the contribution of rare species is the highest and one where richness and evenness are balanced. The index defines a gradient from communities that are dominated by a few common species toward samples shared among several uncommon ones. Our findings support divergence-based measures as practical estimators of beta diversity. Also, the framework here proposed, based on entropy, divergences and cross-entropies, allows us to compute the classic gamma diversity while providing components that are independent, comparable, self-reliant and point-wise distributed.

1. Introduction

Biodiversity is ubiquitously considered an existing property of an ecosystem. Commonly it is associated to resilience to environmental changes as well as a source of ecosystem services (Irob et al., 2023; Le Provost et al., 2023; Luck et al., 2003; Mori et al., 2013). Biodiversity can be connected to the heterogeneity of a habitat (Rainey & Travisano, 1998) and it is usually associated with broader concepts such as balance, interactions, and wilderness (Mace et al., 2012). Biodiversity can be measured in several ways, such as for example the presence of indicative species (Carignan & Villard, 2002) but the most common methods consider diversity as descriptor of a community in terms of both, number of species and their relative contributions (Hamilton, 2005). The first attempt to define such quantity simply related the number of organisms to the number of species (Margalef, 1951). These attempts quickly shifted toward the use of the distributions of the individuals among the species (Sherwin & Prat i Fornells, 2019). After several independent developments, reviewed by Thukral (2017), and a more robust development of the information theory (Rényi, 1961; Shannon, 1948) the research in this field was boosted by the creation of a direct link between informational entropy and species diversity (Hill, 1973). The work of Hill is based on the generalization of the information index defined by Rényi and known as Rényi entropy (Rényi, 1961).

There are in fact infinitely many Rényi entropies defined along an order gradient (Hill, 1973) but some coincide or are connected to already defined diversity indices. In fact, along the order gradient the entropy values are differently influenced by rare species (Supplementary Fig. S1). Negative orders are more influenced by rare species than positive, and when the order is zero rare and common species influence the outcome equally. The utility of working on several orders when computing alpha entropies depends on the fact that at every order, different properties of a distribution emerge (Roswell et al., 2021) . In theory, even negative orders might prove useful. For example, evaluating diversity on ecological data measured using alternative variables (i.e., biomass and abundance) could suffer severe discrepancies due to the mismatch between the most numerous and the most massive taxa (Hatton et al., 2021; Vascotto et al., 2024a). Moreover, organisms can massively aggregate in space and decrease the diversity at local scale

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(Veech et al., 2003). Giving less weight to the most common taxa (decreasing the order q) could represent a way to exclude these effects if needed. However, usage of negative order diversity is limited by the practical issues with sampling of rare species (Tuomisto, 2017).

All previous considerations refer to the concept of diversity at a given site, also known as alpha diversity (Whittaker, 1972). The idea behind this definition is that within a given area, a certain diversity can be found at each site, and several alpha-diversities, one for each site can then be calculated. At the same time, the entire area could have been considered as a single site and a single diversity could be calculated. This total quantity is called gamma diversity (Whittaker, 1972). The difference between these two quantities corresponds to beta diversity. Beta-diversity could be related to alpha and gamma by the following relationships:

$$H_{\beta\ (heterogeneity)} = H_{\gamma(global\ \ entropy)} - H_{\alpha(site\ \ entropy)} \tag{1}$$

The assumption for gamma is that it represents the diversity of the total community, and thus when considering for example the richness index it corresponds to the number of all the species in the dataset (Tuomisto, 2017). Instead, since we approaching the decomposition from the information theoretical perspective the alpha in the formula corresponds the mean diversity of the samples in the dataset (Marcon et al., 2014), it is nonetheless important to underline that other methods to calculate alpha have been proposed (Jost, 2007; Tuomisto, 2017)

Beta diversity can correspond to the concept of the effective number of communities (Jost, 2007) or to the species turnover (Tuomisto, 2010b) or the total variation of the dataset (Legendre & De Cáceres, 2013). For beta it would we desirable being independent computationally from alpha and gamma (Ellison, 2010) and also being independent statistically from alpha, making gamma the derived quantity (Ellison, 2010; Jost, 2007). Among the cited methods the one proposed by Legendre & De Cáceres (2013) based on distances from average composition of the community has the property of producing a beta independent both computationally and statistically from alpha and gamma. The beta as variance of the community in fact does not need alpha and gamma to be calculated in advance. The framework proposed by (Legendre & De Cáceres, 2013) offer an additional advantage, in fact similarly as for alpha, also beta can be calculated independently for every community and only in a second moment the total value of beta for the dataset is computed (Agnetta et al., 2025). While calculating beta diversity independently from alpha and gamma is a step forward, the link to the Whittaker's framework is somehow missing and it is not clear which alpha and gamma diversity should connect to this beta diversity *via* Equation 1. The beta calculated as variance in fact is not expressed in unit of information (nats) as alpha or gamma and thus cannot be used directly in the formula. Instead, the linking concept between informational entropy and diversity (Hill, 1973) and few pioneering works (Huckeba et al., 2023; Ludovisi & Taticchi, 2006) suggested us to apply a different definition of beta diversity to mediate a new promising connection between alpha and gamma diversity. In fact, another direct way to calculate beta exists and offers several advantages.

In the context of information theory Rényi proposed the concept of informational divergence. The divergence quantifies the difference between two distributions in terms of information, and it can be generalized for infinite orders as well (Supplementary Fig. S1). Similarly to the Rènyi entropies also for the divergences it has been shown that they exist also for negative orders (Esposito et al., 2021; van Erven & Harremoës, 2012). In the negative spectrum the entropy shape reverses from concave to convex, for divergence the reversal is of the same type but contrary (from convex to concave). The beta diversity as *index of uniqueness* of a site (Legendre & De Cáceres, 2013) is the lowest when the site is like the pooled community. On the contrary, for negative order divergences, the closest a community is to the pooled the higher is its divergence value.

The use of entropies and divergences of the same order as estimators of Whittaker's alpha and beta diversity allows a sum to obtain the gamma diversity (Equation 1). The sum of Rènyi entropy and divergence of order one (Shannon and Kullback-Liebler) is appealing because it produces a third information concept, the cross-entropy, rarely applied in ecological data (but see Ricotta & Avena, 2003). In fact, as for the variance method proposed by Legendre and De Cáceres also using divergences a beta diversity value for each site can be computed, allowing us to calculate alpha and beta diversity independently and site by site. Thus, another way to compute gamma diversity should be possible, by summing all the entropy and divergences pairwise and then computing the average. We should obtain not only the correct gamma diversity as the mean, but also, the distribution of this quantity site by site that we propose to call Whittaker's *local gamma* diversity (Fig. 1). The local gamma diversities should be equal to the cross entropy between the local and the mean community. This indicates that, for each site, alpha, beta, and local gamma can be computed independently.

Our goal in this study is to illustrate the exact decomposition of Whittaker's gamma diversity in a real and large ecological dataset by calculating alpha, beta and local gamma components of order one and zero. The behavior of the novel concept of local gamma diversity will be discussed and the behavior of its components (alpha and beta) will be explored. Our aim is to show that entropy, divergence, and cross-entropy constitute the ideal operative framework to compute alpha, beta and gamma. Also, we want to show that this index produces a gradient from common/poor toward rich/unique communities.

2. Material and methods

2.1. Local gamma definition

The alpha diversity index H (Rényi entropy) is defined for a community P and an order q:

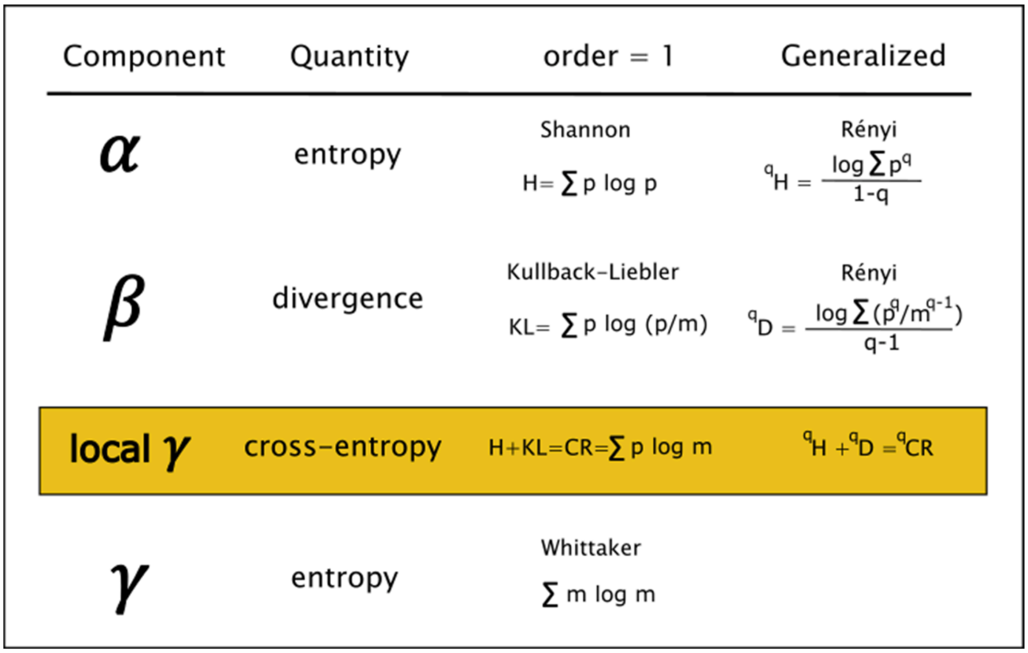
$$^{q}H(P) = \frac{1}{1-q}\log\left(\sum_{i=1}^{n} p_i^q\right) \tag{2}$$

With $0 < q < \infty$ and $q \neq 1$, and where p_i correspond to the proportions of abundance or biomass of a i th species of the community (Table 1). This formula corresponds when $q = 1$ to the Shannon entropy $-\left(\sum_{i=1}^{n} p_i \log p_i\right)$. When the order is $q = 0$ it corresponds to the $\log N$, with N as the number of species and when $q \to \infty$ it corresponds to $-\log\left(\max p_i\right)$ which is also known as min-entropy (Espinoza & Smith, 2013). Hill extended the dominion of the function to $-\infty < q < \infty$ and $q \neq 1$. When $q \to -\infty$ the corresponding diversity is equal to $-\log(1/(\min p_i))$ (Hill, 1973).

The beta diversity index D (Rényi divergence) is defined for two communities (P, M) and an order q:

$$^{q}D(P \parallel M) = \frac{1}{q-1}\log\left(\sum_{i=1}^{n} \frac{p_i^q}{m_i^{q-1}}\right) \tag{3}$$

With $0 < q < \infty$ and $q \neq 1$, and where p_i and m_i correspond to the proportional contribution of a species of the two communities. This formula corresponds when $q = 1$ to the Kullback-Leibler divergence (Kullback & Leibler, 1951; van Erven & Harremoës, 2012), that is: $\sum_{i=1}^{n} p_i \log(p_i/m_i)$. When the order is $q = 0$ it corresponds to the $\log M[P > 0]$, and when $q \to \infty$ it corresponds to $\log\left(\max(p_i/m_i)\right)$ which is also known as worst-case regret (van Erven & Harremoës, 2012). Moreover, other beta diversities can be found along with the gradient of the orders. For example, when $q = 0.5$ the divergence corresponds to a linear transformation of the Hellinger distance (van Erven & Harremoës, 2012) and which has been already proposed and used as beta diversity by Legendre & De Cáceres (2013). Divergences are asymmetric and are not distances because $^{q}D(P \parallel M) \neq {}^{q}D(M \parallel P)$ apart from the special case $q = 0.5$: in this specific case the Hellinger distance is in fact both a distance and a divergence. For the negative spectrum the terms p_i and m_i



Component	Quantity	order = 1	Generalized
α	entropy	Shannon $H = \sum p \log p$	Rényi $^{q}H = \frac{\log \sum p^{q}}{1-q}$
β	divergence	Kullback–Liebler $KL = \sum p \log (p/m)$	Rényi $^{q}D = \frac{\log \sum (p^{q}/m^{q-1})}{q-1}$
local γ	cross–entropy	$H+KL=CR=\sum p \log m$	$^{q}H + {}^{q}D = {}^{q}CR$
γ	entropy	Whittaker $\sum m \log m$	

Fig. 1. Concepts used in this study. The first column indicates the ecological component. The second column indicates the theoretical information quantity used to characterize each ecological component. The third column reports the equation when the order q is one. The last column reports the generalization formula for each component. The yellow line represents the novel index developed here.

Table 1
List of terms used in the manuscript and their related concept.

Term
Site: Unique location identified by a row in a dataset
Species: Unique taxon identified by a column in a dataset
Community biomass: Vector row of biomass of species sampled in one site
Community: Proportions of the community biomass
Pooled community: average community across group of sites
Rank: position of a species in the decreasing proportions of the pooled community from all sites
Rare species: species with high rank
Common species: species with low rank
Alpha: Diversity within one community in one site
Beta: Diversity between one community and the pooled community of all sites
Gamma: Diversity within the pooled community of all sites
Entropy: Theoretical information quantity linked to alpha diversity
Divergence: Theoretical information quantity linked to beta diversity
Cross-entropy: Theoretical information quantity linked to gamma diversity

get reversed by the negative exponents which means that when $q \to -\infty$ the entropy corresponds to $\log(\max(m_i/p_i))$.

In ecology cross-entropy can be used as loss function in machine learning algorithm (Vascotto et al., 2024b) or as minimization term in common species distribution models (Elith et al., 2011). The cross-entropy index CR corresponds to (Appendix, proof A):

$$CR(P, M) = -\sum_{i=1}^{n} p_i \log m_i \tag{4}$$

With p_i and m_i corresponding to the contribution of the i^{th} term in the two distributions P and M.

If M corresponds to the mean community $\overline{M}$ pooled from several sites s, it can be proven that average cross-entropy corresponds to the "classic" Whittaker's gamma diversity (Appendix, proof B).

$$\frac{\sum_{j=1}^{s} CR(P_j, \overline{M})}{s} = {}^{1}H(\overline{M}) \tag{5}$$

Thus because of the relation between entropy, divergence, and cross-entropy it can be proven also that (Appendix, proof C) when $q = 1$

$$\frac{\sum_{j=1}^{s}\sum_{i=1}^{n} p_{ji} \log \frac{p_{ji}}{\overline{m}_i}}{s} = -\sum_{i=1}^{n} \overline{m}_i \log \overline{m}_i + \frac{\sum_{j=1}^{s}\sum_{i=1}^{n} p_{ji} \log p_{ji}}{s} \tag{6}$$

With $\overline{m}$ corresponding to the mean community. Equation 6 corresponds to: $H_\beta = H_\gamma - H_\alpha$

2.2. *Testing local gamma calculation on a large ecological dataset*

To calculate alpha, beta, and local gamma diversity, we used data collected by the MEDITS survey program (Spedicato et al., 2019) from 1999 to 2021 in the GSA 16 (Strait of Sicily). Biomass (Kg Km $^{-2}$) of species in each haul (site) was divided by total biomass of the site to have the proportions contribution of species. The dataset was composed of 2251 sites and a total of 558 species.

For each species in the dataset, we assigned a rank value, which corresponds to the position of the species in the ordered pooled community. A rank of one indicates that the species was the most common in the dataset, meaning that it had the highest proportional contribution in the average community. Using this notion, we applied a cumulative sum over the average community to identify the species contributing for the

90% of the biomass. These species have been labelled “top 90°”. Finally, recognizing the non-parametric nature of the rank values we computed for each site its median rank value meant to indicate whether the sites were characterized by common or rare species.

For each site of the data set we computed the entropy, divergence, and local gamma. To observe the order effect on diversity patterns, we computed alpha and beta entropies of every site for all orders between 0 and 2.4 (step = 0.1) (Fig. 2). We chose this range because it covers many of the known ecological indexes that correspond to special cases along with the order gradient. To verify if decomposition was exact the mean local gamma entropy of the sites was compared to the classic Whittaker’s gamma for order one.

To observe the ordering of the sites at order one we picked all the sites in the 5° and 95° percentile of each three indexes (Fig. 2). We inspected visually the properties of these sites computing the pooled community which corresponds to the community average of the sites selected. These averages were then compared to the overall mean community both in terms of proportions and ranks.

To observe the properties at order zero we plotted the richness of top 90° species of all sites against the divergence at order zero and modeled the relation using a gam function (Zuur, 2012). Also, we plotted the median rank of all sites against the local gamma of order zero and modeled the relation using a gam function. Finally, we evaluated the index consistency across all the orders computed by calculating and plotting the pairwise Pearson R^2 on two heatmaps.

Additionally, to observe the effect of under sampling we randomly rarefied the dataset 100 times at 10 different under sampling levels where we removed 50% of the dataset each time. For each dataset alpha, beta and local gamma of order one has been computed. Also to observe the effect of a fixed level of random under sampling across the order gradient we computed the three diversity components at different order using randomly chosen 10% of the sites 100 times. Finally, to observe the effect of taxonomic incompleteness we randomly merged species into newly generated synthetic species. The procedure of merging has been randomly repeated 100 times at 8 different levels of merging where we reduced the number of species 50% at each time. For each dataset alpha beta and local gamma of order one has been computed.

3. Results

3.1. Local gamma order one

At order one the Whittaker’s gamma entropy for the biomass dataset was 4.23 (Supplementary Fig.. S2). This value was obtained for all the four methods selected: as Shannon entropy of the mean community, as the sum of the mean Shannon entropy with the mean Kullback-Liebler divergence, as the mean of the pairwise sum of all Shannon entropies with all Kullback-Liebler divergences (local gamma) and as the mean cross entropy.

The samples with highest alpha entropies (95°) defined a community with a heavier tail compared to the overall average community (Supplementary Fig.. S3 A). Conversely samples with the lowest alpha

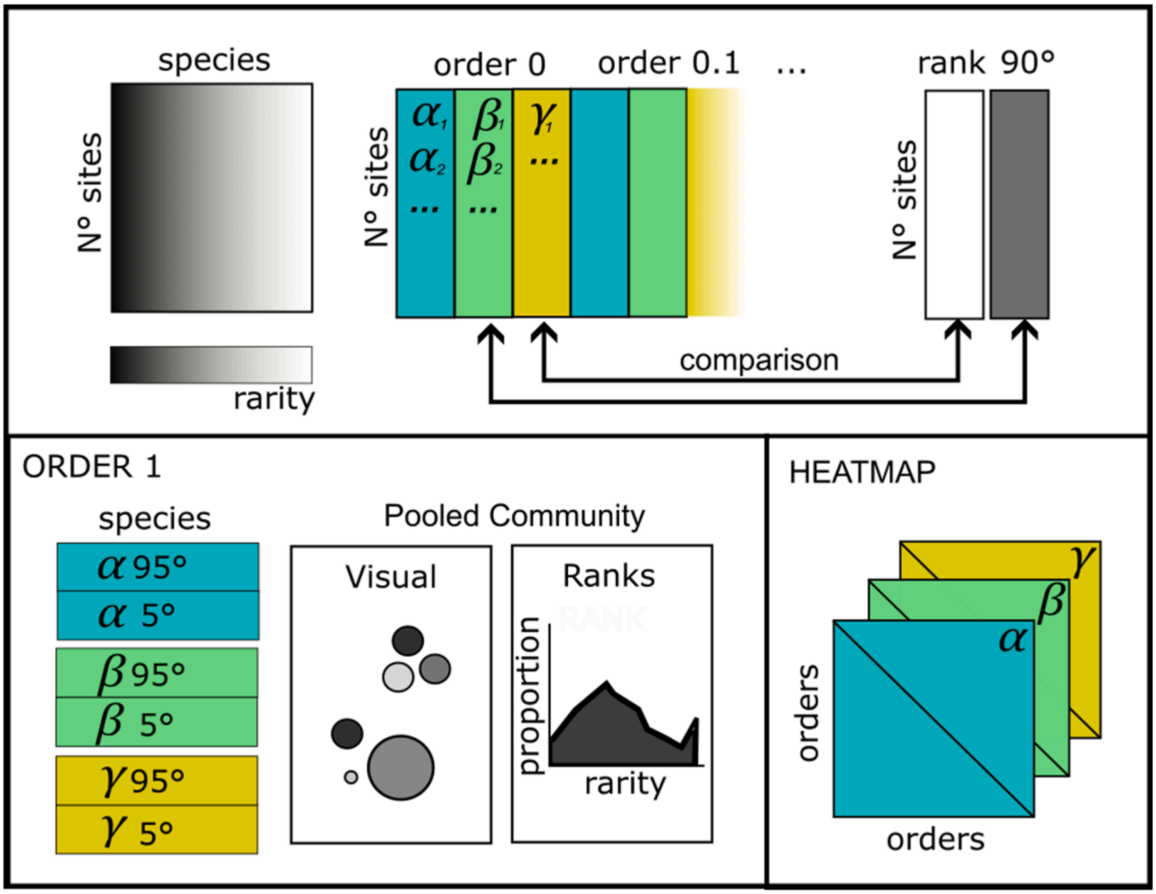


Fig. 2. Visual depiction of the main steps taken in the analysis of the MEDITS data. On the upper panel on the left a depiction of the dataset of sites and species is presented. The grays’ shadow represents the rarity of each species. At the center, a depiction of the results is presented. For each site, several indexes have been calculated. For each order the corresponding alpha beta and gamma are showed with distinctive colors (cyan, green, and yellow respectively). On the right a depiction of the two additional indexes calculated to help the interpretation is shown (median rank for site and number of top 90° species). On the bottom left panel, the selected subgroups of sites characterized by high or low indexes values is presented with the depiction of the associated analysis. On the bottom right panel, the square correlation heatmaps of the three indexes calculated for several orders is presented.

entropy were dominated by a few species. Two species dominated the pooled community of the low alpha samples (5°), the 3rd and the 16th most common. Visually, this can be appreciated in Fig. 3. There, for the low alpha samples the few circles of varying color ranges define much of the community.

The samples with the lowest beta entropies (beta 5° Supplementary Fig.. S3 A) did not present spikes as the alpha 5°, gamma 5° or beta 95° nor had a heavy tail as for alpha 95° and gamma 95° thus were the most similar among the six cases to the overall average community. Instead, the 95° percentile was characterized by samples strongly deviating from the overall average community. As in the case of the alpha, the peaks of the 16th species determined the results together with the presence of more rare species which made the tail of the distribution heavier in this case. Visually, this can be appreciated in Fig. 3. There, for the high beta the dark circles are mostly absent.

Finally, for the local gamma we observe two distinct patterns. For the 95° percentiles the tail is even heavier than the alpha case, and several rare species contribute strongly to the community in these samples (gamma 95° Supplementary Fig.. S3 A). Instead, for the 5° the samples are dominated only by the first three most common species. Visually, this can be appreciated in Fig. 3, there for the low gamma the few dark circles dominate the community.

3.2. *Local gamma order zero*

The alpha at order zero corresponds to the logarithm of the number of species. This index is straightforward in its interpretation thus we only use it to color the scatterplots present is Fig. 3. The richness of the top 90° species was negatively correlated with the divergence at order 0 (Fig. 3). This indicates that as the sites contained fewer common species the beta diversity increased. This can be seen also from the histograms in Supplementary Fig. (S3 B) in fact the divergence of order zero was selecting for its lowest values the samples having the largest number possible of common species as shown by the darker colors and the high percentage of presence of these species in the sites.

When comparing the median rank of the sites with their corresponding local gamma diversity of order zero we observed a significative positive correlation among the two (Fig. 3). High values of gamma diversity select sites with high median rank thus where several rare species were found. Conversely, the lowest the gamma the higher the presence of common species. The same results can be observed also in the histograms in Supplementary Fig. (S3 B).

3.3. *Patterns in entropy and divergence*

Alpha entropies patterns appear consistent when the entropy is higher than one (Fig. 3 C). Orders higher than one were mildly correlated to the near zero order entropies as we can see transition bands in yellow and red. Similarly, divergences (Fig. 3 C) appeared consistent when evaluated at orders higher than one. As before, as we got closer to zero the patterns changed quickly. The area appearing mostly blue in the upper right part of the diagram was narrower in the divergence case. This indicates that the divergences pattern changed more quickly compared to the alpha entropies. The correspondence between classic gamma and local gamma is limited to order 1 (Supplementary Fig. S4).

4. Discussion

The additive framework proposed by Whittaker finds a perfect application in the use of Equation 6. The most important aspect of the use of this equation is that there is no need to compute alpha or gamma entropy in advance to produce the beta. The second important aspect is that the beta component is completely independent from the alpha (Marcon et al., 2014). It is true that we could calculate the gamma entropy from the mean community and then for each site subtract from gamma the local alpha. This seems the only approach proposed so far (Jost, 2007) even when generalizations of entropy are proposed (Chao et al., 2012, 2019) but what is lacking in this approach is a direct way to compute a point-wise beta diversity independently of alpha and gamma.

Our approach allows us to calculate beta values independently of alpha while remaining consistent with the additive framework proposed by Whittaker (Equation 1). The additional advantage of calculating alpha and beta independently is that by summing these values point-wise, we obtain a new quantity that we refer to as *local gamma*. When the order is one, the average of the *local gamma* entropies is in fact the gamma entropy calculated in the classical Whittaker framework (Equation 1) as the entropy of the mean community.

Then the formula defining our beta diversity (Equation 6) reads as such: *the mean divergence corresponds to the difference between the entropy of the mean community and the mean of the single site entropies* $E(D) = H(E) - E(H)$. This formulation responds to an intuition about the property beta diversity should have from Rao & Nayak (1985), being similar in its formulation to the definition of variance. The agreement we found between the local gamma and the cross entropy (proof B) underlines the goodness of our approach and leads to some practical considerations. It is known that cross-entropy is limited by the reference distribution (Thierrin et al., 2022), which explains the limits of the curve values in the diagram of Supplementary Fig. S1. This property of boundedness could be used in ecological studies to estimate in advance whether a community has a high gamma diversity at a given location without having to calculate the distribution of all gamma diversities. Despite this promising potential the application to real-world data is subject to important limitations. Species distribution usually follows heavily tailed distribution (Alroy, 2015) thus the sparsity of the rarest species introduces uncertainty in the calculation of the diversity indexes. In literature it has been observed a bias in the computation of alpha diversity connected to the sampling effort (Chao et al., 2014; Willis, 2019). But we expect the beta component to be the most affected since it has been described as prone to numerical under-sampling (Schroeder & Jenkins, 2018). We observed a positive relation of local gamma with the increase of the dataset size (Supplementary Fig. S5). This is due to the beta components while for the alpha reducing the sampling effort only decreased the confidence around the mean. Nonetheless, until the 10% samples limit the uncertainty due to under-sampling was lower than the variability due to the order change (Supplementary Fig. S6). The resilience of the indexes to random under-sampling does not guarantee that severe temporal or spatial biases could be overtaken. The beta component can be interpreted as an indicator of the equivalent number of communities (Jost, 2007), thus removing completely a portion of the metacommunity variability would certainly decrease the value of both beta and gamma. The bias introduced by the taxonomic incompleteness occurs when part of the species cannot be identified (Beck & Schwanghart, 2010) and it is less predictable in its effects. Alternative specimens' organization, for example following the functional organization of the community has the potential to overcome such limitations (Stewart et al., 2023). We observed a negative relation of local gamma with an increased random merging of taxa (Supplementary Fig. S7). This trend was much stronger than the variability of each random sampling underlying once more the crucial role played by consistent and fine resolution taxonomic knowledge in the construction of biological datasets. Summarizing, the local gamma is susceptible to both under-sampling and taxonomic incompleteness bias with the beta component being the main source of error.

The perfect symmetry in computability, between alpha, beta, and gamma, holds unfortunately only for order one where the alpha diversity corresponds to the Shannon index and the divergence to the Kullback-Liebler. Marcon et al. (2014) proposed a generalization of beta that included equation 6, but for the remaining orders their beta entropy was not independent from the alpha component. Then in our case, for the rest of the order spectrum we can compute the gamma diversity from alpha and beta components, but the average value will not correspond to the Whittaker's gamma of the corresponding order, nor to any

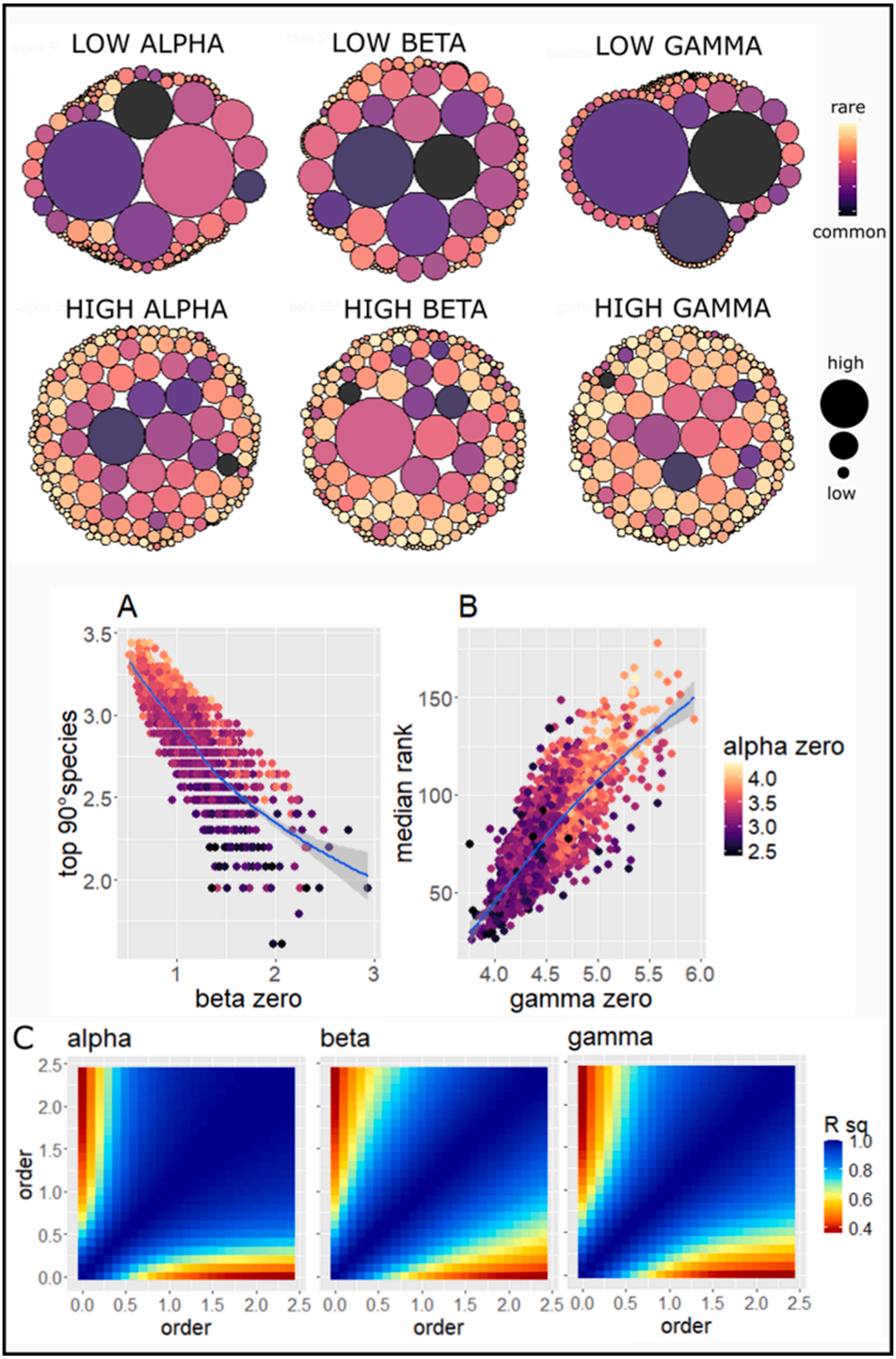


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Fig. 3. In the upper part the six cases of selected sites subgroups (alpha 5°, beta 5°, gamma 5°, alpha 95°, beta 95°, gamma 95°). Each circle of each of the six diagrams represents a species of the pooled subgroups sites. The color of each circle represents the rank of the species in the complete dataset while its dimension represents the average proportion of a species inside the selected sites subgroups. In the middle panel A shows the relation between divergence at order zero and richness of top 90° species (log scale). Each point represents a site. The colors of each point indicate the alpha diversity at order zero, thus the number of species at site. In the middle panel B shows the relation between the local gamma at order zero and the median rank of the sites. Each point represents a site. The colors of each point indicate the alpha diversity at order zero, thus the number of species at site. In the lower panel C, the heatmaps of the R squared matrix of the entropies and divergences computed on the MEDITS biomass dataset. The colors of each pixel represent the Pearson rˆ2 between the site's diversities calculated at the corresponding orders. The indices were computed for all orders between 0 and 2.4 separated by 0.1.

cross-entropy generalizations we found proposed so far (Andreieva & Shvai, 2020; Ding et al., 2024; Thierrin et al., 2022). So, except order one, our gamma diversity and the *local gamma* are computable only starting from the entropy and divergence. A desirable property for the decomposition of diversity is that gamma is completely determined by alpha and beta (Jost, 2007). Using an analogy from analysis of variance, the alpha represents the within-group variance and beta should represent the between-group variance (Anderson et al., 2006). The classic Whittaker gamma is calculated over the centroid and should represent the total variance. As we consider only some characteristics of the centroid, i.e. only the richness if the order is zero, we are making ourselves blind about the distribution of species across sites and thus about the between group variance. Then the value that should represent the total variance, the gamma, does not match anymore with the sum of the within (alpha) and between (beta) components. Thus, in face of a mismatch like the one we face we encourage to find an alternative definition for gamma. Here gamma is defined as the sum of the alpha and beta which also corresponds to the alpha of the mean community when the order is equal to one. For the rest of the cases gamma remains the sum of the two components but we miss a direct way to calculate it. We chose to work with arithmetic means and the additive properties of alpha and beta since we used Rényi entropies and a theoretical informational framework (Jost, 2007) but this choice could have been too strict a limitation. The concept of generalized means has been used in the context of diversity decomposition already (Tuomisto, 2010a). It is possible that the mismatch between entropy, divergence and cross entropy is due to this missing element.

As we saw, the application of equation 6 produced the correct value gamma diversity, moreover this equation allows to decompose the gamma site by site (Supplementary Fig. S2). The new index is a composition of alpha and beta, so its interpretation depends on these two. A low value in *local gamma* indicates sites where the community is dominated by one or few taxa (low alpha) which are also common in the dataset (low beta). This pattern can be observed in our results: for example, the five lowest *local gamma* diversity sites correspond to two sites where *Galeus melastomus* dominated (75% of the community) and three sites where *Trachurus trachurus* dominated (90% of the community). Both taxa were indeed common being the first and third most common species in the dataset. On the contrary, the highest gamma values correspond to those sites where there is present a rich community (high alpha) made of uncommon taxa (high beta). In our results the five highest gamma diversity sites corresponded to sites where the most important contribution came from taxa that were indeed not common in our dataset *Centracanthus cirrus* (130th), *Turritella communis* (145th), *Psammechinus microtuberculatus* (188th), *Pteromylaeus bovinus* (128th) and *Venus nux* (161th).

As we saw, low alpha diversity does not guarantee that the dominating species are common or rare. Instead, low beta indicates sites close to the average community but says nothing about the distribution of the species in the site. The local gamma by putting the two concepts together, selects the samples dominated by few common species for low values, while it selects rich communities of many rare species for high values. Finally, our decomposition framework allows us to compare the contribution of alpha and beta to the classic Whittaker gamma. In our case the diversity across samples, the beta (1.0-5.7 nats), varied more than inside samples, alpha (0.2-3.3 nats). The two ranges can be compared since they come in the same unit of measure, the natural units of information (nats). From the perspective of effective number analysis (Jost, 2007) we could say that there are more effective communities than species.

When the order reaches zero the distribution of the species contribution does not matter. Thus, the divergence of order zero corresponds to the logarithm of the *partial* sum of the mean community. The crucial term here is *partial,* if in the site of interest all species are at least present then the partial sum corresponds to one and its logarithm to zero. Thus, the highest values of divergence at order zero correspond to the cases where few rare species are present while the common taxa are completely missing. Drawing parallelism, the divergence at order zero is acting as an asymmetric nestedness index from the average community. As there are several rare species for each common one the divergence of order is skewed toward the loss of the common species. In fact, we are not sure exactly which rare species is present in a sample of high divergence, but we are sure the common species are missing. Again, the logic of the two components explains the behavior of gamma in Fig. 3, the index selects for samples with several species (high alpha) belonging only to the pool of the rarest taxa (high beta). Using the alpha, beta, and local gamma of order zero would be useful for all those cases when the proportions among the species are uncertain, such as for example in abundance data or metabarcoding reads.

In both cases alpha and beta divergences produce differences in spatial patterns when considered at different orders. At every order, different properties of a distribution emerge (Roswell et al., 2021) so it becomes apparent that to study an ecological dataset it is necessary to apply more than one index to observe the several patterns hidden in it. The heatmaps presented in Fig. 3 C show us that all entropies above 1 are strongly correlated with each other, and that positive and near zero entropies do not coincide. A similar pattern can be observed for the divergences. Our results show that when selecting multiple indices, it is more informative to select them from both the near zero and strongly positive spectrum. For example, if you select Simpson and Shannon (Francé et al., 2021), the results could be redundant. A similar redundancy should result if you select only a few close orders as estimators for beta diversity. The framework we propose, based on information entropies and divergences, allows us to compute alpha and beta diversities of arbitrary order. Consequently, it is also possible to obtain local gamma values of arbitrary order (Fig. 3C, right heatmap). At least for order = 1, our approach based on entropy, divergences and cross entropies is certainly the most correct, as Whittaker's framework remains intact and the alpha, beta and gamma divergences are all independently computable for each site.

5. Conclusions

The partitioning of diversity into alpha and beta components finds the ideal tools in the corresponding concepts of entropy and divergence. The independence of the two and the possibility to compute them site by site allows the emergence of a new type of diversity index, the local gamma. This way of linking alpha and beta diversity is a novelty in applied ecology. Local gamma sets a gradient from samples dominated by a few common species toward samples shared among several uncommon species. Entropy and divergence, come in comparable units of measures and exactly decompose gamma diversity when Shannon entropy and Kullback-Liebler divergence are used.

Entropy and divergence are both generalized functions, which means that infinite orders can be used in the calculation of both. For entropy and consequently also for alpha diversity, decreasing order makes rare species count more. In the case of divergences and consequently beta diversity, decreasing order makes losses in common species count more. For local gamma decreasing the order makes losses in common species in favor of several rare species count more.

CRediT authorship contribution statement

Ivano Vascotto: Writing – original draft, Methodology, Formal analysis, Conceptualization. **Davide Agnetta:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare no conflicts of interest.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2025.111317.

Appendix

Proof A: The first part of the proof shows that the sum of Shannon entropy and Kullback-Liebler divergence corresponds to the cross-entropy. Consider an n-species community characterized by relative biomasses vector $P = (p_1, p_2, \ldots p_n)$ such that $0 \leq p_i \leq 1$ and $\sum_{i=1}^{n} p_i = 1$. Also consider a second n-species community characterized by relative biomasses vector $M = (m_1, m_2, \ldots m_n)$ such that $0 \leq m_i \leq 1$ and $\sum_{i=1}^{n} m_i = 1$. The Shannon entropy ${}^1H(P)$ of P is $-\sum_{i=1}^{n} p_i \log p_i$ while the Kullback-Liebler divergence ${}^1D(P \parallel M)$ between P and M is $\sum_{i=1}^{n} p_i \log\left(\frac{p_i}{m_i}\right)$. The cross entropy $CR(P, M)$ between P and M is:

$$CR(P, M) = {}^1H(P) + {}^1D(P \parallel M) = -\sum_{i=1}^{n} p_i \log p_i + \sum_{i=1}^{n} p_i \log\left(\frac{p_i}{m_i}\right) \tag{A1}$$

$$CR(P, M) = -\sum_{i=1}^{n} p_i \log p_i + \sum_{i=1}^{n} p_i \log p_i - \sum_{i=1}^{n} p_i \log m_i = -\sum_{i=1}^{n} p_i \log m_i \tag{A2}$$

Proof B: The second part of the proof shows that the average cross-entropy L_{Y} between the local communities and the mean community corresponds to the Whittaker's gamma H_γ (Shannon entropy of the mean community). Consider an s-sites matrix S composed by s vectors P_j with $P_j = \left(p_{j1}, p_{j2}, \ldots p_{jn}\right)$ such that $0 \leq p_{ji} \leq 1$ and $\sum_{i=1}^{n} p_{ji} = 1$. Each of the vector community P_j has the same probability $1/s$. Also consider the mean community $\overline{M} = (\overline{m}_1, \overline{m}_2, \ldots \overline{m}_n)$ such that $\overline{m}_i = \frac{\left(\sum_{j=1}^{s} p_{ji}\right)}{s}$.

The mean cross entropy L_{Y} from the mean community corresponds to:

$$L_{\mathrm{Y}} = \frac{\sum_{j=1}^{s} CR\left(P_j, \overline{M}\right)}{s} = \frac{-\sum_{j=1}^{s} \sum_{i=1}^{n} p_{ji} \log \overline{m}_i}{s} \tag{B1}$$

Where p_{ji} is the contribution of the i^{th} species in the j^{th}community and $\overline{m}_i$ is the contribution of the same species in the mean community. The order of the upper summation can be inverted; this corresponds to sum over columns before rows in the matrix S:

$$L_{\mathrm{Y}} = \frac{-\sum_{i=1}^{n} \sum_{j=1}^{s} p_{ji} \log \overline{m}_i}{s} \tag{B2}$$

Since in the inner sum $\log \overline{m}_i$ does not depend on j it can be moved outside the sum and multiply then:

$$L_{\mathrm{Y}} = \frac{-\sum_{i=1}^{n} \log \overline{m}_i \sum_{j=1}^{s} p_{ji}}{s} \tag{B3}$$

Since in the outside multiplier also does not depend on j or i it can be moved inside the sum then:

$$L_{\mathrm{Y}} = -\sum_{i=1}^{n} \log \overline{m}_i \frac{\sum_{j=1}^{s} p_{ji}}{s} \tag{B4}$$

Since we defined $\overline{m}_i = \frac{\left(\sum_{j=1}^{s} p_{ji}\right)}{s}$ the equation corresponds to:

$$L_{Y} = -\sum_{i=1}^{n} \log\overline{m}_i\overline{m}_i = -\sum_{i=1}^{n} \overline{m}_i\log\overline{m}_i = {}^{1}H(\overline{M}) = H_{\gamma} \tag{B5}$$

Proof C The third part of the proof shows that the mean divergence H_β corresponds to the difference between the entropy of the mean community H_γ and the mean of the community entropies H_α. In proof A we proved that.

$$CR(P,M) = {}^{1}H(P) + {}^{1}D(P \parallel M) \tag{C1}$$

Then in proof B we showed that:

$$L_{Y} = \frac{\sum_{j=1}^{s} CR\left(P_j, \overline{M}\right)}{s} = {}^{1}H(\overline{M}) = H_{\gamma} \tag{C2}$$

Consider an s-sites matrix S composed by s vectors P_j with $P_j = \left(p_{j1}, p_{j2}, \ldots p_{jn}\right)$ such that $0 \leq p_{ji} \leq 1$ and $\sum_{i=1}^{n} p_{ji} = 1$. Also consider the mean community $\overline{M} = (\overline{m}_1, \overline{m}_2, \ldots \overline{m}_n)$ such that $\overline{m}_i = \frac{\left(\sum_{j=1}^{s} p_{ji}\right)}{s}$. Consider the Shannon entropy of each P_j is ${}^{1}H\left(P_j\right) = -\sum_{i=1}^{n} p_{ji}\log p_{ji}$ and the Kullback-Liebler divergence ${}^{1}D$ between P_j and $\overline{M}$ is ${}^{1}D\left(P_j \| \overline{M}\right) = \sum_{i=1}^{n} p_{ji}\log\left(\frac{p_{ji}}{\overline{m}_i}\right)$. Given that the alpha diversity H_α is the mean of the entropy across the communities $\frac{\sum_{j=1}^{s} {}^{1}H\left(P_j\right)}{s}$ and that the beta diversity H_β is the mean divergence $\frac{\sum_{j=1}^{s} {}^{1}D\left(P_j \| \overline{M}\right)}{s}$. Then gamma diversity H_γ

$$H_{\gamma} = {}^{1}H(\overline{M}) = \frac{\sum_{j=1}^{s} CR\left(P_j, \overline{M}\right)}{s} = \frac{\sum_{j=1}^{s}\left({}^{1}H\left(P_j\right) + {}^{1}D\left(P_j \| \overline{M}\right)\right)}{s} \tag{C3}$$

Which distributing the quotient to the sums corresponds to:

$${}^{1}H(\overline{M}) = \frac{\sum_{j=1}^{s} {}^{1}H\left(P_j\right)}{s} + \frac{\sum_{j=1}^{s} {}^{1}D\left(P_j \| \overline{M}\right)}{s} \tag{C4}$$

$$-\sum_{i=1}^{n} \overline{m}_i\log\overline{m}_i = \frac{\sum_{j=1}^{s}\sum_{i=1}^{n} p_{ji}\log p_{ji}}{s} + \frac{\sum_{j=1}^{s}\sum_{i=1}^{n} p_{ji}\log\frac{p_{ji}}{\overline{m}_i}}{s} \tag{C5}$$

$$\frac{\sum_{j=1}^{s}\sum_{i=1}^{n} p_{ji}\log\frac{p_{ji}}{\overline{m}_i}}{s} = -\sum_{i=1}^{n} \overline{m}_i\log\overline{m}_i + \frac{\sum_{j=1}^{s}\sum_{i=1}^{n} p_{ji}\log p_{ji}}{s} \tag{C6}$$

$$H_{\beta} = H_{\gamma} - H_{\alpha} \tag{C7}$$

Data availability

https://data.jrc.ec.europa.eu/dataset/ (Data is available to the public from the Joint Research Centre Data Catalogue)

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