How to partition diversity

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Abstract

Partitioning ecosystem biodiversity exposes the variability in sub-community species composition. This can be considered in terms of their diversities in isolation, their contribution to ecosystem diversity, their distinctiveness, the turnover between them, or the number of unique sub-communities present. Partitioning biodiversity should allow us to measure all of these and thereby enable us to systematically compare the diversity of the sub-communities of an ecosystem. It must also do so not only in terms of species diversity, but in a general way that accounts for any kind of similarity among individuals or species, whether phylogenetic, genetic, taxonomic, or functional.

We propose a new partitioning that emerges naturally from recent similarity-sensitive gamma diversity measures and established results in information theory. Our new family of measures provides powerful tools that account for any type of similarity among individuals while identifying the ecosystem’s true underlying sub-community structure and dynamics.

1. Introduction

Diversity is a ubiquitous feature of biological systems from the scale of the molecule to the rainforest. Its accurate assessment is fundamental to such contrasting problems as selecting the most efficacious vaccines, selecting the best sires for breeding, or deciding which ecosystem should be prioritised for conservation. However, despite diversity’s fundamental importance to such areas of the life sciences, there has been great difficulty in agreeing a common approach to quantifying and interpreting it.

In recent years significant movement towards a unified approach has seen agreement that this should be rooted in the idea of the numbers equivalent of existing diversity measures (Ellison, 2010), also known as the effective number (of species or other biologically meaningful unit), which postulates that the diversity of $S$ equally abundant species is $S$. At the core of effective number measures of diversity are the Hill numbers (Hill, 1973; Routledge, 1979) (Table 1). These are derived from Rényi’s generalisations (Rényi, 1961) of Shannon entropy (Shannon, 1948), and are a weighted power mean of order $q - 1$, averaging across the relative abundances of species $i$ (denoted by $p_i$) and weighted by $p = (p_1, ..., p_S)$. 

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Table 1. Basic formulae

| Name                        | Formula                                                                 |
|-----------------------------|-------------------------------------------------------------------------|
| Power mean of order $r$ of $x$ weighted by $u$ | $M_r(u, x) = \begin{cases} \left[\sum_{i=1}^{n} u_i x_i^r\right]^{1/r} & r \neq 0^* \\ \prod_{i=1}^{n} x_i^{u_i} & r = 0^+ \end{cases}$ |
| Hill numbers                | $qD(p) = M_{q-1}(p, p)^{-1}$                                           |
| Similarity-sensitive diversity | $qD^Z(p) = M_{q-1}(p, Zp)^{-1}$                                          |
|                            | $[qD(p) = qD^I(p)]$                                                     |

*This formulation of the power means assumes that $u_i > 0$ for all $i$.  
†At $r = 0$, $1/r$ is undefined, but the corresponding expression arises naturally in the limit.

The importance attached to species abundance is reflected in the viewpoint parameter $q$, which lies between 0 and $\infty$. At $q = 0$, species richness only detects presence/absence, giving equal significance to rare species and common ones; at $q = \infty$, on the other hand, Berger and Parker’s diversity measure (Berger & Parker, 1970) depends only on the most abundant species, neglecting all of the other less abundant species entirely; Shannon entropy (Shannon, 1948) and Simpson diversity (Simpson, 1949) lie in between (at $q = 1$ and $q = 2$, respectively). Jost has recently pushed for the adoption of effective numbers for gamma (total) diversity (Jost, 2006), for alpha (within) and for beta (between) sub-community diversity (Jost, 2007), showing that this produces an intuitive and coherent family of diversity measures. However, it is also clear that measures of diversity should not just depend on the relative abundance of species, but also the similarity and differences between species. This is perhaps most evident when measuring functional diversity, when unrelated species can play similar functional roles in an ecosystem, but it is also important, for instance, for comparisons of diversity between species in the same genus versus those in different families, or for measuring diversity amongst individuals with differing amounts of shared phylogenetic history.

Addressing this challenge, Leinster and Cobbold (Leinster & Cobbold, 2012) generalised Hill’s approach to develop just such a measure (Table 1, Similarity-sensitive diversity). Species similarity is encapsulated in the similarity matrix $Z$, which is the identity matrix, $I$, in the naïve-similarity case where all species are viewed as completely distinct from one another (giving the Hill numbers), but otherwise each entry $Z_{ij}$ represents the similarity (from 0 to 1) between species $i$ and $j$. This elegantly encapsulates any notion of similarity or distance between species (whether functional, taxonomic, genetic or other), while still having an effective number interpretation (that is, the effective number of distinct entities), and reducing to the original effective number formulation when all species are distinct. The approach is sufficiently general to incorporate existing partial generalisations of diversity which include distance, such as that for phylogenetic similarity (Chao, Chiu, & Jost, 2010).

1.1 Current beta diversity measures

Despite emerging agreement on using numbers equivalents for handling diversity, general approaches to measuring beta diversity remain a problem (Chao, Chiu, & Hsieh, 2012; Ellison, 2010; Jost, 2007; Tuomisto, 2010a; 2010b). A beta diversity measure needs to address two related issues (Whittaker, 1972): 1. How many distinct sub-communities does the ecosystem naturally divide into, what is their composition, and how diverse are they individually (Whittaker, 1960)? and
2. Given an ecosystem divided into sub-communities, what is the turnover in (species, functional, phylogenetic, etc.) diversity between them (Jaccard, 1912)? The former is primarily concerned with how many distinct sub-communities exist in principle (and what they are like); the latter with how quickly species composition varies across a specific, selected set of sub-communities such as along a spatial gradient or a time series. Only the former is usually considered to be an effective number.

Numbers equivalent approaches to measuring beta diversity, as well as gamma and alpha, have existed for many years (Whittaker, 1960; 1972), and are increasingly widely accepted (Ellison, 2010). They have focussed on satisfying either a simple multiplicative relationship between the components of diversity (\(\alpha \times \beta = \gamma\)) (Baselga, 2010; Jost, 2007; Tuomisto, 2010a; Veech & Crist, 2010) – although this suggestion dates back much further (Whittaker, 1960) – or occasionally an additive relationship (\(\alpha + \beta^+ = \gamma\)) (Veech & Crist, 2010; Veech, Summerville, Crist, & Gering, 2002), where alpha is consistently (if vaguely) defined as some type of average (Jost, 2007) of sub-community diversities. The advantages of multiplicative beta centre around independence of alpha and beta diversity in determining gamma (Wilson & Shmida, 1984), although multiple definitions of independence often make this unclear (Chao et al., 2012; Veech & Crist, 2010). Tuomisto (Tuomisto, 2010a) reviewed many of these proposals for beta diversity, and these have subsequently been extended in the context of specific similarity-sensitive beta diversity proposals (Chiu & Chao, 2014; Chiu, Jost, & Chao, 2014), but, beyond agreement on the importance of the mathematical relationship between alpha, beta and gamma, no consensus has been reached on which is the best partitioning of diversity.

However, Hill’s effective number formulation (Hill, 1973), and Leinster and Cobbold’s similarity-sensitive generalisation of it (Leinster & Cobbold, 2012), are both based on Rényi’s generalised entropies (Rényi, 1961). Given the power and generality of this entropy-based approach, a natural next step is to use Rényi’s notion of relative entropy to derive a measure of the diversity of a sub-community relative to the ecosystem as a whole. These measures coincide with existing beta diversity measures in degenerate cases (Jost, 2007). This is all proved in Appendix A. Moreover, they answer the questions and satisfies all of the requirements we believe to be important for partitioning schemes. These are mostly taken from the existing literature, including that relative diversities are effective numbers “that enable us to speak naturally” (Hill, 1973), and satisfy the replication principle (Chakravarty & Eichhorn, 1991; Hill, 1973), as well as other more specific properties that we detail below. We leave the explanation of relative entropy and its role in deriving a partitioning of diversity for now, and instead we focus here on providing the reader with an intuitive understanding of these new formulae and their properties.

2. Identifying the underlying structure of an ecosystem

Wilson and Shmida (Wilson & Shmida, 1984) propose that alpha and beta diversities should be independent to ensure “useful application of a measure to systems with different alpha diversity”; Jost (Jost, 2007) agrees, constraining their measurement by (a) requiring that “a given number should denote the same amount of diversity or uncertainty, whether it comes from the alpha component, the beta component, or the gamma component”, and (b) generalising the definition of alpha diversity itself to “some type of average” of sub-community diversities. He then clarifies independence as (c) “alpha is logically and mathematically unrelated to [beta]” (Jost, 2010). These are his first three properties of “intuitive alpha and beta”, and we believe they form an excellent starting point for a family of diversity measures. However, we will offer a reinterpretation of his fifth requirement that alpha is never greater than gamma, not least because we reject his fourth requirement that gamma is entirely determined by alpha and beta.

Instead, we believe that it is more important that any mathematical relationship should emerge from and reflect fundamental and practical requirements – namely, the ability to identify the sites of
particular interest within an ecosystem, in terms of taxonomic, phylogenetic or functional distinctiveness relative to the rest of the ecosystem; in terms of overall contribution to ecosystem diversity; or in terms of which sub-communities are the most diverse in their own right.

In this paper, we propose such sub-community measures and demonstrate that they can be combined to provide the ecosystem level descriptors we believe are important: How many distinct sub-communities are there in the ecosystem (a kind of beta diversity)? What is the turnover in species composition between the sub-communities we have identified (again, a kind of beta diversity)? What is the overall diversity of the ecosystem (gamma diversity)? And what is the average diversity of its sub-communities (alpha diversity)? However, we argue that it is from the sub-community decomposition itself that we extract the most useful information.

2.1 A sub-community focus for alpha, beta and gamma diversity

The critical composition to be made is therefore not that of alpha and beta to make gamma, but rather that of sub-community alpha, beta and gamma diversities to make ecosystem alpha, beta and gamma diversities. We therefore focus on sub-community alpha, beta and gamma diversities (Table 2, Sub-community), and form the ecosystem diversities (Table 2, Ecosystem) as weighted power means of the corresponding sub-community components.

Table 2. Ecosystem alpha, beta and gamma diversities, and their sub-community components.

| Diversity measure | Sub-community | Ecosystem† |
|-------------------|---------------|------------|
| Alpha             | $q\alpha_j^Z = M_{q-1}(P_j, ZP_j)^{-1}$ | $q\bar{A}^Z = M_{1-q}(w, q\alpha_j^Z | j \in \{1⋯N\})$ |
|                   | Diversity of sub-community j as a sub-community | Naïve-community ecosystem diversity |
|                   | $q\alpha_j^Z = M_{q-1}(P_j, ZP_j)^{-1}$ | $q\bar{A}^Z = M_{1-q}(w, q\alpha_j^Z | j \in \{1⋯N\})$ |
|                   | $= qD^Z(P_j) = w_j \times q\alpha_j^Z$ | Average sub-community diversity |
|                   | Diversity of sub-community j in isolation | |
| Beta              | $q\beta_j^Z = M_{q-1}(P_j, ZP_j/Zp)^{\dagger}$ | $q\bar{B}^Z = M_{1-q}(w, q\beta_j^Z | j \in \{1⋯N\})$ |
|                   | Distinctiveness of sub-community j within ecosystem | Average distinctiveness of sub-communities |
|                   | $q\beta_j^Z = M_{q-1}(P_j, ZP_j/Zp*) = \frac{q\beta_j^Z}{w_j}$ | $q\bar{B}^Z = M_{1-q}(w, q\beta_j^Z | j \in \{1⋯N\})$ |
|                   | Number of distinct sub-communities like j in ecosystem | Effective number of distinct sub-communities in ecosystem |
| Gamma*            | $q\gamma_j^Z = M_{q-1}(P_j, Zp)^{-1}$ | $q\bar{G}^Z = M_{1-q}(w, q\gamma_j^Z | j \in \{1⋯N\})$ |
|                   | Diversity of sub-community j from perspective of ecosystem | Diversity of ecosystem in isolation |

*Where we use diversity as a descriptor in the body of this table, we are referring to the effective number of species.
†Ecosystem alpha, beta and gamma diversities are all power means weighted by relative size of the individual sub-community diversities. ‡All vector division is element-wise. †Where all sub-communities are assumed to be distinct.
*Since we assume that $\sum_i p_i = 1$, we do not need to consider normalisation of $p, \gamma_j$ or $G$.
We adopt the following notation. Consider an ecosystem where the vector \( p = (p_1, ..., p_S) \) contains the relative abundance of the \( S \) species. The ecosystem is divided into \( N \) sub-communities, and \( P \) is the matrix of their relative abundances. The abundance of species \( i \) in sub-community \( j \) relative to the total ecosystem is \( p_{ij} \), so the raw relative abundances of the species in sub-community \( j \) are \( P_j = (p_{1j}, ..., p_{Sj}) \). These form a generalised probability distribution (where \( \sum_i p_{ij} \leq 1 \)), and this sub-community constitutes a fraction \( \sum_i p_{ij} = w_j \) of the total ecosystem abundance (so \( \sum_j w_j = 1 \)). It follows that \( p = \sum_j P_j \), and we also denote the normalised relative abundances in sub-community \( j \) in isolation as \( \tilde{P}_j = P_j/w_j \) (so \( \sum_i \tilde{P}_{ij} = 1 \)). Correspondingly we define both raw and normalised alpha and beta diversities. There is no need for a normalised gamma diversity, since we are only considering the case where the ecosystem is complete, and so \( \sum_i p_i = 1 \).

Since we believe that any diversity measure that neglects similarity between individuals cannot meaningfully represent the diversity of a population, ecosystem gamma diversity (Table 2, Ecosystem Gamma Diversity, \( G \)) must be equal to the similarity-sensitive diversity of the ecosystem (Table 1, Similarity-sensitive Diversity). Furthermore, we can decompose this into terms for each sub-community (\( y_j \)), which are conditionally independent of all of the other sub-community compositions. The ecosystem gamma diversity is then the power mean of order \( l - q \) of the sub-community gamma diversities weighted by the sub-community sizes.

Like gamma diversity, ecosystem beta diversity can be broken down into sub-community components. The raw sub-community beta diversity (\( \beta_j \), Table 2, Sub-community Beta) is the distinctiveness of the sub-community relative to the ecosystem, and can also approximate the turnover rate between the sub-communities in the ecosystem – it lies between 0 and 1, where the value is 0 if and only if the sub-community is empty, increasing numbers indicate increasing novelty of the sub-community, and 1 indicates that the sub-community is completely distinct from the rest of the ecosystem. The normalised sub-community beta diversity (\( \bar{\beta}_j \)), on the other hand, is the number of distinct communities like the sub-community necessary to make the whole ecosystem. The raw ecosystem beta diversity (\( B \), Ecosystem Beta), the \( l - q \) power mean of the sub-community diversities, is then the average distinctiveness of each community or an approximation to the average turnover between communities; and the normalised ecosystem beta diversity (\( \bar{B} \)) is the average number of distinct communities necessary to make the ecosystem (the effective number of distinct communities). In the naïve-community case, where all sub-communities are distinct, \( \bar{B} \) reduces to \( qD_w \) (Tuomisto, 2010a). These formulae to calculate normalised ecosystem beta diversity satisfy Jost’s first three requirements of an intuitive beta diversity measure and satisfy \( \bar{B} \geq 1 \) in the naïve-similarity case that he considers (where all species are distinct, so \( Z = I \)). The latter can be interpreted as answering Jost’s fifth requirement that alpha is never greater than gamma. See Appendix A for proofs.

Sub-community alpha diversity in turn is simply the similarity-sensitive diversity of the sub-community (Table 2, Sub-community Alpha). We can generate two alpha diversities for each sub-community, a raw and a normalised one. The normalised sub-community alpha diversity (\( \tilde{\alpha}_j \)) is simply the sub-community’s diversity in isolation; the raw sub-community alpha diversity (\( \alpha_j \)) is its diversity as a sub-community, and can be viewed as delivering a naïve-community estimate of the ecosystem gamma diversity from one sub-community. Normalised ecosystem alpha diversity (\( \tilde{A} \), Ecosystem Alpha) is therefore the \( l - q \) power mean of the normalised sub-community diversities, which reduces to Tuomisto’s \( c_I \) in the naïve-similarity case (where all species are distinct). Raw ecosystem alpha diversity (\( A \)), is an estimate of the naïve-community ecosystem gamma diversity, and acts as an upper bound on the true ecosystem gamma diversity, \( G \). This allows us to constrain \( G \) without any knowledge of the relationship between, or indeed the species present in the sub-communities.
These individual quantities allow us to identify sub-communities with high inherent diversity ($\alpha_i$ and $\alpha_j$), high distinctiveness relative to the ecosystem ($\beta_j$ and $\beta_j$), and strong influence on ecosystem diversity ($\gamma_j$). Ecosystem gamma diversity ($G$) and normalised sub-community alpha diversity ($\bar{\alpha}_j$) are simply our usual notions of diversity for an undivided group, while the other ecosystem and sub-community diversity measures in Table 2 are novel. See Appendix A for further details.

Our new definitions of sub-community alpha, beta and gamma diversities satisfy existing intuitive requirements as well as allowing for species similarity, and furthermore they relate to key concepts in information theory – such as communication inefficiencies when substituting the whole ecosystem for one of its sub-communities.

2.2 New properties of new measures

New properties that we consider to be extremely important also arise from these new diversity measures:

1. Normalised ecosystem alpha, beta and gamma diversities ($\bar{A}$, $\bar{B}$ and $G$) are invariant under shattering of the sub-communities;

2. All sub-community alpha, beta and gamma diversities ($\alpha_i$, $\bar{\alpha}_j$, $\beta_j$ and $\gamma_j$) are conditionally independent and therefore invariant to differences in partitioning of the rest of the ecosystem;

3. All sub-community alpha, beta and gamma diversities can therefore be directly compared within an ecosystem to determine the relative merits of different sub-communities.

2.2.1 Invariance under shattering

To understand shattering, imagine a simple, idealised ecosystem with 4 genuine sub-communities (Figure 1, left), for example sub-communities defined by geographical features or local abiotic conditions, which have species in common. Additionally, each sub-community is assumed to be well-mixed so if we geographically split a sub-community (Figure 1, right) the relative abundances of species in the new sub-communities would be the same as their parent sub-community.

![Figure 1](image-url). An idealised ecosystem with four true sub-communities, which have been identified correctly (left) and incorrectly (right).
Suppose this ecosystem has a beta diversity of $\mathcal{B} = b$. As the sub-communities have species in common and are therefore not completely distinct, $b < 4$ (since $b$ is an effective number). If, in our field study of the ecosystem, we correctly identify 4 geographically distinct sub-communities (Figure 1, labelled as regions), then our diversity analysis should tell us that there are effectively $b$ distinct sub-communities. However, what happens if we incorrectly partition the ecosystem? Imagine that we think some geographical feature meaningfully divides two of the sub-communities, but that this turns out to be ecologically irrelevant (Figure 1, right). Since drawing lines that do not cross sub-community boundaries creates no genuinely new sub-communities, we claim that there must still be effectively $b$ sub-communities. We refer to this as invariance under shattering — that breaking down the sub-communities into smaller but identical parts must not affect beta diversity.

Our new normalised ecosystem beta diversity measure ($\mathcal{B}$) satisfies the requirement that it is invariant under shattering, in contrast to Jost’s simple multiplicative beta diversity (Jost, 2007), and most of the other beta diversity measures listed by Tuomisto including the simplest naïve-community beta diversity, $qD_\omega$ (Tuomisto, 2010a).

Our normalised ecosystem alpha diversity ($\bar{A}$) is also invariant under shattering. Other ecosystem alpha diversities can also be invariant under shattering (e.g. Tuomisto’s $\alpha_t$ and “true alpha diversity” $\alpha_d$, which are actually both just $\bar{A}$ in the naïve-similarity case). However, the manner of averaging suggested by Jost (Jost, 2007) (Tuomisto’s $\alpha_R$), where ecosystem alpha diversity depends on $1/\sum w_i^q$, means that in this case diversity would vary as sub-communities are broken up.

Any sensible definition of ecosystem gamma diversity (e.g. $G$) must also be invariant under shattering, since otherwise an arbitrary rearrangement of sub-communities might change gamma, and by definition gamma diversity does not depend on any specific decomposition into sub-communities.

Our raw ecosystem alpha and beta diversity measures are not invariant under shattering, but this would not be desirable, since $A$, the naïve-community estimate of ecosystem gamma diversity, should increase when smaller (shattered) communities are created with the same diversity, and $B$, the average distinctiveness of the sub-communities, should decrease as they are shattered into identical pieces.

### 2.2.2 Individual sub-community diversities do not depend on the distributions or boundaries of other sub-communities

In order to be meaningful, the contributions of individual sub-communities to ecosystem alpha, beta and gamma diversities should be conditionally independent of each other — i.e. they should only depend on the composition of the other sub-communities through the total ecosystem species composition. Without this condition, the perceived importance of one sub-community would be affected by arbitrary rearrangements of other sub-community boundaries, despite these involving no gain or loss in individuals or species to the ecosystem as a whole, making any assessment of sub-community diversity arbitrary. That conditional independence is satisfied is evident from inspection of the formulae for sub-community diversities (Table 2), because they do not contain any terms for the relative abundances of the other sub-communities. The contribution from any given sub-community to any ecosystem-level measure of alpha, beta and gamma diversity is therefore invariant with respect to the division of the rest of the ecosystem into sub-communities.

This property is not satisfied by many established diversity measures, except for sub-community alpha diversities, since they are universally accepted as the diversities of the sub-communities in isolation, and the decomposition of Jost’s multiplicative beta (Jost, 2007) when $q = 1$, which is actually just the same as $\bar{\beta}_j$ in the naïve-similarity case.

### 2.2.3 Sub-community diversity diversity comparisons
Our new formulation provides measures of alpha, beta and gamma diversity at the sub-community level that are conditionally independent from each other, and that are invariant to changes in the partitioning of the rest of the ecosystem. This allows us to make direct, consistent comparisons between sub-communities that allow us to determine their relative merits in the context of the ecosystem as a whole.

3. Conclusions

We have developed measures of ecosystem alpha and beta diversity, extending Leinster and Cobbold’s similarity-sensitive gamma diversity measure (Leinster & Cobbold, 2012), and decomposed these diversity measures into their alpha, beta and gamma components at the sub-community level. We have shown that these measures satisfy the desired properties of previous definitions of biodiversity at the ecosystem level, while rejecting the well-established, but ultimately unhelpful, simple mathematical relationship between ecosystem alpha, beta and gamma.

We have also proposed new properties for diversity measures that are strongly desirable in order to meaningfully compare sub-communities. We have shown that our new measures satisfy these properties, while many existing measures do not. These properties are: 1. Invariance under shattering, which requires that biologically irrelevant divisions of sub-communities into smaller units does not affect measurements of normalised ecosystem alpha, beta or gamma diversity; 2. Independence and invariance of sub-community diversity measures to differences in composition and partitioning of the rest of the ecosystem, indicating that the diversity of a sub-community and its contribution to ecosystem diversity depend only on the composition of the sub-community itself and the ecosystem as a whole; and, arising from these properties, 3. The ability to directly compare sub-communities in terms of their absolute (alpha) diversity, their (beta) distinctiveness relative to the ecosystem as a whole, and their (gamma) influence on ecosystem gamma diversity.

In summary, we have proposed new measures of alpha and beta diversity, sensitive to species similarity, that emerge naturally from recent similarity-sensitive gamma diversity measures. Our key advance is the decomposition of all three of these diversity measures into components reflecting the distinctiveness of each sub-community within the ecosystem, and their relative contributions to total ecosystem diversity. These provide powerful tools to reveal biologically important sub-communities within an ecosystem, to assess the spatial and temporal variation in diversity, and thereby to identify the ecosystem’s true underlying sub-community structure and dynamics.

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Appendix A
Mathematical proofs and simple examples

Here we prove the mathematical assertions made in the main text, along with some further statements that clarify the meanings of our measures. We also illustrate their behaviour with some simple hypothetical examples.

Conventions We follow the notation of the main text. When not indicated otherwise, the variable \( i \) ranges over species 1, \( \ldots \), \( S \) and the variable \( j \) over sub-communities 1, \( \ldots \), \( N \). We assume that none of the sub-communities is empty, so that \( w_j > 0 \) for all \( j \).

When the values of \( q \) and \( Z \) are clear, we usually abbreviate \( q^\alpha Z_j, q^A Z_j \), etc., as \( \alpha_j, A_j \) etc. We write \( \alpha = (\alpha_1, \ldots, \alpha_N) \), and similarly for \( \bar{\alpha}, \beta, \bar{\beta} \) and \( \gamma \).

For vectors \( u = (u_1, \ldots, u_n) \) and \( v = (v_1, \ldots, v_n) \), we write \( u / v \) for the vector \( (u_1/v_1, \ldots, u_n/v_n) \), and similarly \( 1/v = (1/v_1, \ldots, 1/v_n) \). Also, we write \( u \leq v \) if \( u_k \leq v_k \) for all \( k \in \{1, \ldots, n\} \).

Power means Given a probability distribution \( u = (u_1, \ldots, u_n) \) (that is, a vector of nonnegative reals summing to 1) and another vector \( x = (x_1, \ldots, x_n) \) of nonnegative reals, the power means \( M_r(u, x) \) are defined as in Table 1 of the main text, for all real \( r \). But it is also useful to define them for \( r = \pm \infty \), which is done as follows:

\[
M_{-\infty}(u, x) = \min_{i: u_i > 0} x_i, \quad M_{\infty}(u, x) = \max_{i: u_i > 0} x_i.
\]

These are, respectively, the limits of \( M_r(u, x) \) as \( r \to \pm \infty \).

We use some further facts about power means. They are increasing in their second arguments: if \( x \leq y \) then \( M_r(u, x) \leq M_r(u, y) \) for all \( r \) and \( u \). More substantially, \( M_r \) is also increasing in \( r \); that is, if \( r \leq s \) then \( M_r(u, x) \leq M_s(u, x) \) for all \( u \) and \( x \).

All these facts are classical, and proofs can be found in texts such as Hardy, Littlewood and Pólya, Inequalities, Cambridge University Press, 1952.

A1 Proofs

A1.1 Upper and lower bounds

Here we establish the range of possible values taken by our measures.

We will use the fact that the measures \( q^D Z \) of Leinster & Cobbold (2012) always take values between 1 and \( S \), for a community of \( S \) species. In particular, this is true of the Hill numbers \( q^D = q^D^f \).
**Alpha-diversities**  
By the observations just made, \(1 \leq \alpha_j \leq S\) for all \(j\), and so \(1 \leq A \leq S\).

It follows that \(1/w_j \leq \alpha_j \leq S/w_j\) for all \(j\). Hence

\[
M_{1-q}(w,1/w) \leq A \leq M_{1-q}(w,S/w),
\]

or equivalently

\[
qD(w) \leq A \leq S \cdot qD(w).
\]

Hence \(1 \leq A \leq NS\).

**Beta-diversities**  
First, fix \(j\). We have

\[
\beta_j = M_{q}^{\frac{1}{q}} \left( \frac{P_j}{Zp} \right).
\]

Since \(M_{q}^{\frac{1}{q}}\) is increasing in \(q\),

\[
\beta_j \leq M_{\infty} \left( \frac{P_j}{Zp} \right) = \max_{i:P_{ij} > 0} \left( \frac{ZP_{j}}{Zp} \right)_i.
\]

Now

\[
p = \sum_{j'} P_{j'} \geq P_{j} = w_j \overline{P}_j,
\]

so \(Zp \geq w_j Z\overline{P}_j\). This gives the upper bound \(\beta_j \leq 1/w_j\).

For a lower bound, certainly \(\beta_j > 0\). In the naïve-similarity case \(Z = I\), more can be said:

\[
\beta_j^I \geq M_{-1} \left( \frac{P_j}{P_{j} \cdot \overline{P}_j} \right) = \left( \sum_{i:P_{ij} > 0} p_i \right)^{-1} \geq \left( \sum_{i=1}^S p_i \right)^{-1} = 1,
\]

giving \(\beta_j^I \geq 1\).

We can deduce bounds for \(\overline{B}\). For an arbitrary \(Z\),

\[
\overline{B} \leq M_{1-q}(w,1/w) = qD(w) \leq N.
\]

Also \(\overline{B} > 0\), and in the naïve-similarity case, \(\overline{B} \geq 1\).

Turning now from the normalised to the raw measures, we have \(\beta_j = w_j \beta_j^I\), so \(0 < \beta_j \leq 1\) and \(0 < B \leq 1\). In the naïve case, \(w_j \leq \beta_j^I \leq 1\), giving \(\min_j w_j \leq B \leq 1\).
**Gamma-diversities**  By definition,

$$\gamma_j = M_{q-1}(\overline{P_j}, Zp)^{-1}. $$

Again we use the fact that $M_r$ is increasing in $r$. On the one hand, this gives

$$\gamma_j \geq M_\infty(\overline{P_j}, Zp)^{-1} = \frac{1}{\max_i p_{ij} > 0 (Zp)_i}. $$

But $(Zp)_i = \sum_{i'} Z_{ii'} p_{i'} \leq 1$ for all $i$, since every entry of $Z$ is $\leq 1$. Hence $\gamma_j \geq 1$.

On the other hand,

$$\gamma_j \leq M^{-1}(\overline{P_j}, Zp)^{-1} = \sum_{i : P_{ij} > 0} \frac{P_{ij}}{(Zp)_i}. $$

Now $(Zp)_i \geq p_i \geq P_{ij}$ (on the assumption that $Z_{ii} = 1$), so

$$\sum_{i : P_{ij} > 0} \frac{P_{ij}}{(Zp)_i} \leq \sum_i \frac{1}{w_j} = S \frac{1}{w_j}, $$

giving $\gamma_j \leq S/w_j$.

Finally, $1 \leq G \leq S$, since $G = qD^Z(p)$.

**Effective numbers**  We have shown that $\overline{A} \leq S$, $\overline{B} \leq N$ and $G \leq S$. These are, respectively, effective numbers of distinct species, sub-communities and species.

**Comparison between alpha- and gamma-diversities**  Fix $j$. We have $p \geq P_j$, so $Zp \geq ZP_j$, and so

$$M_{q-1}(\overline{P_j}, Zp) \geq M_{q-1}(\overline{P_j}, ZP_j).$$

Taking reciprocals on both sides gives $\alpha_j \geq \gamma_j$. This holds for all $j$, so $A \geq G$.

**Monotonicity in $q$**  Because the power means $M_r$ are increasing in both $r$ and their second arguments, each of $\alpha_j$, $A$, $\overline{\sigma}_j$, $\overline{A}$, $\gamma_j$ and $G$ is decreasing in $q$. Moreover, $\beta_j$ and $\overline{\beta}_j$ are increasing in $q$.

However, $B$ and $\overline{B}$ are in general neither increasing nor decreasing in $q$. For example, take $P = (0.1 0.2)$ and $Z = I$; then plotting $B$ and $\overline{B}$ against $q$ shows that neither is monotone.
A1.2 Invariance under shattering

Here we prove that the ecosystem diversities \( \overline{A} \) and \( \overline{B} \) are invariant under shattering (as of course is \( G \)).

It suffices to prove that \( \overline{A} \) and \( \overline{B} \) are unchanged when we split a single well-mixed sub-community into two. Suppose that we split the last sub-community in proportions \( t \) and \( 1 - t \), where \( 0 < t < 1 \). Thus, the new relative abundance matrix \( P' \) is the \( S \times (N + 1) \) matrix given by

\[
P'_{j} = \begin{cases} 
P_{j} & \text{if } j < N \\
tP_{N} & \text{if } j = N \\
(1 - t)P_{N} & \text{if } j = N + 1. 
\end{cases}
\]

Let us write \( w', \alpha' \), etc., for the analogues of \( w, \alpha \), etc., in the newly-divided ecosystem. Then \( p' = p \),

\[
w' = (w_1, \ldots, w_{N-1}, tw_N, (1-t)w_N), \quad \overline{P}'_{j} = \begin{cases} 
\overline{P}_{j} & \text{if } j < N \\
\frac{p_{j}}{p_{N}} & \text{if } j = N \\
(1-t)\overline{P}_{N} & \text{if } j = N + 1.
\end{cases}
\]

Now

\[
\overline{\alpha}'_{j} = \begin{cases} 
\overline{\alpha}_{j} & \text{if } j < N \\
\overline{\alpha}_{N} & \text{if } j \geq N
\end{cases}
\]

(that is to say, the normalised alpha-diversity of a sub-community of the new ecosystem is the same as that of its parent in the old ecosystem). Hence

\[
\overline{A}' = M_{1-q}\left((w_1, \ldots, w_{N-1}, tw_N, (1-t)w_N), (\overline{\alpha}_1, \ldots, \overline{\alpha}_{N-1}, \overline{\alpha}_N, \overline{\alpha}_N)\right)
\]

\[
= M_{1-q}(w, x) = \overline{A}
\]

where the second equality is by an elementary property of power means. Similarly,

\[
\overline{B}' = \frac{p_{j}}{p_{N}} \quad \text{if } j < N
\]

\[
\overline{B}' = \overline{B} \quad \text{by the same argument as for the alpha-diversities.}
\]

The raw ecosystem diversities \( A \) and \( B \) are not invariant under shattering. For an example, see Section A2.3 below.

A1.3 Replication

Consider a region divided into \( m \) equal-sized ecosystems, each of which is further divided into \( N \) sub-communities. The \( m \) ecosystems are identical in every way (the same sub-community divisions, the same species similarities, and the same relative abundances) except that each uses a fresh set of species, and species in different ecosystems are completely dissimilar. Our
region is divided into $mN$ sub-communities. Proposition A11 of (Leinster & Cobbold, 2012) shows that the diversity of the region is $m$ times the diversity of any one of its constituent ecosystems. What about the various alpha-, beta- and gamma-diversities?

Let us use starred notation ($P^*, \alpha^*_j, Z^*, \ldots$) for the region and, as usual, unstarred notation ($P, \alpha, Z, \ldots$) for the ecosystem. Then

$$P^* = \begin{pmatrix} \frac{1}{m} P & 0 & \cdots & 0 \\ 0 & \frac{1}{m} P & \cdots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \cdots & \frac{1}{m} P \end{pmatrix}, \quad Z^* = \begin{pmatrix} Z & 0 & \cdots & 0 \\ 0 & Z & \cdots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \cdots & Z \end{pmatrix}$$

(where both right-hand sides are block sums). Elementary calculations then give:

$$A^* = mA, \quad \overline{A}^* = \overline{A}, \quad B^* = B, \quad \overline{B}^* = m\overline{B}, \quad G^* = mG.$$

A1.4 Independence

Assume that we are using the na"ive-similarity model. We showed in Section A1.1 that $1 \leq \overline{A} \leq S$ and $1 \leq \overline{B} \leq N$. Here we show that $\overline{A}$ and $\overline{B}$ are independent in the sense of Jost (2010), at least for $q > 0$. This means that being told the value of the alpha-diversity $\overline{A}$ gives no certain information about the value of the beta-diversity $\overline{B}$, and vice versa. This is true even if we also know $q, N$ and $S$.

In precise terms, the assertion is that for all real numbers $a$ and $b$ such that $1 \leq a \leq S$ and $1 \leq b \leq N$, and all $q > 0$, there exists an $S$-species ecosystem, divided into $N$ sub-communities, such that $\overline{A} = a$ and $\overline{B} = b$.

One way of constructing such a system is as follows. For probability distributions $r = (r_1, \ldots, r_S)$, the diversity $qD(r)$ is continuous in $r$ (since $q \neq 0$), and has maximum value $S$ and minimum value 1. Hence we may choose an $r$ such that $qD(r) = a$. Similarly, we may choose $w = (w_1, \ldots, w_N)$ such that $qD(w) = b$.

Now consider an ecosystem made up of $N$ sub-communities of relative sizes $w_1, \ldots, w_N$, with no shared species, where each sub-community contains $S$ species in proportions $r_1, \ldots, r_S$. Thus, there are $NS$ species in all. The diversity of each sub-community is $qD(r) = a$; that is, $\sigma_j = a$ for all $j$. Hence $\overline{A} = a$. Moreover, the results of Section A2.4 below imply that $\overline{B} = qD(w) = b$, as required.

A1.5 Jost’s measures

Operating within the na"ive-similarity model $Z = I$, Jost (2007) defines ecosystem alpha-, beta- and gamma-diversities, all depending on a parameter $q$. His gamma-diversity is the same as our $G$; it is simply the ecosystem
Hill number. His alpha- and beta-diversities are most closely analogous to our $\overline{A}$ and $\overline{B}$, so we denote them here by $\overline{A}_{\text{Jost}}$ and $\overline{B}_{\text{Jost}}$. They are defined by

$$\overline{A}_{\text{Jost}} = M_{1-q}(w^{(q)}, \overline{\alpha}), \quad \overline{B}_{\text{Jost}} = G/\overline{A}_{\text{Jost}},$$

where $w_j^{(q)} = w_j^q / \sum_{j'} w_{j'}^q$.

**Comparison with our measures** Since $\overline{A} = M_{1-q}(w, \overline{\alpha})$, usually $\overline{A}_{\text{Jost}} \neq \overline{A}$. But since $w^{(1)} = w$, we do have $\overline{A}_{\text{Jost}} = \overline{A}$ when $q = 1$. Moreover, it is shown in Section A2.6 below that when $q = 1$ in the naïve-similarity model, $\overline{B} = G/\overline{A}$; so then, $\overline{B}_{\text{Jost}} = \overline{B}$ too.

Hence when $q = 1$, under the naïve-similarity model, our $\overline{A}$, $\overline{B}$ and $G$ reproduce Jost’s alpha-, beta- and gamma-diversities.

For $q \neq 1$, if the sub-communities are of equal size ($w = (1/N, \ldots, 1/N)$) or of equal diversity ($\overline{\alpha}_1 = \cdots = \overline{\alpha}_N$) then $\overline{A}_{\text{Jost}} = \overline{A}$, but even so, $\overline{B}_{\text{Jost}} 
eq \overline{B}$.

**Failure of invariance under shattering** Jost’s measures are not invariant under shattering (unless $q = 1$, in which case they coincide with ours). For example, take an ecosystem consisting of two equal-sized sub-communities with respective diversities $d_1$ and $d_2$, where $d_1 \neq d_2$. Then

$$\overline{A}_{\text{Jost}} = M_{1-q}((1/2, 1/2)^{(q)}, (d_1, d_2)) = ((1/2) d_1^{1-q} + (1/2) d_2^{1-q})^{1/(1-q)}$$

($q \neq 1$). Now split the second sub-community (which we suppose to be well-mixed) into two equal-sized parts. In this newly-divided ecosystem,

$$\overline{A}_{\text{Jost}} = M_{1-q}((1/2, 1/4, 1/4)^{(q)}, (d_1, d_2, d_2)) = \left(\frac{(1/2)^q d_1 + 2(1/4)^q d_2}{(1/2)^q + 2(1/4)^q}\right)^{1/(1-q)}$$

($q \neq 1$). Unless $q = 1$, the new and old values of $\overline{A}_{\text{Jost}}$ are not equal. And since $G$ is unchanged, the new and old values of $\overline{B}_{\text{Jost}} = G/\overline{A}_{\text{Jost}}$ are not equal either. Hence neither $\overline{A}_{\text{Jost}}$ nor $\overline{B}_{\text{Jost}}$ is invariant under shattering, except when $q = 1$.

**A2 Examples**

Most of the hypothetical examples that follow are extreme cases, intended to shed light on the measures that we have defined.

**A2.1 Ecosystem is single sub-community**

First suppose that our ecosystem is divided into a single sub-community, that is, not divided at all. Then $N = 1$, $P_1 = P_1 = p$, $w = (1)$, and

$$\alpha_1 = A = \overline{\alpha}_1 = \overline{A} = {}^qD^Z(p), \quad \beta_1 = B = \overline{B}_1 = \overline{B} = 1, \quad \gamma_1 = G = {}^qD^Z(p).$$
A2.2 Sub-Communities are species

At the other extreme, suppose that the sub-communities are exactly the species. Thus, \( S = N \), \( P \) is the diagonal matrix with entries \( p_1, \ldots, p_S \), \( \mathbf{w} = \mathbf{p} \), \( \mathbf{Z} \mathbf{P} = \mathbf{Z} \), and in particular, \( (\mathbf{Z} \mathbf{P})_j = 1 \) (assuming that every species has a self-similarity of 1). Straightforward computations show, for instance, that

\[
A = qD(\mathbf{p}), \quad \overline{A} = 1, \quad \overline{B} = qD(\mathbf{p}), \quad G = qDZ(\mathbf{p}).
\]

(Note that \( A \) is the naïve diversity \( qD(\mathbf{p}) \), not \( qDZ(\mathbf{p}) \).)

A2.3 Well-mixed ecosystem

Take an arbitrary ecosystem, with relative abundance vector \( \mathbf{p} = (p_1, \ldots, p_S) \) and similarity matrix \( \mathbf{Z} \). Assume that our ecosystem is well-mixed. Then no matter how we divide it geographically into sub-communities, all those sub-communities will have the same species distribution.

Mathematically, choose any \( N \geq 1 \) and any \( \mathbf{w} = (w_1, \ldots, w_N) \) such that \( w_j > 0 \) and \( \sum w_j = 1 \). Put \( P_{ij} = p_i w_j \). Then \( \mathbf{P} = (P_{ij}) \) is the relative abundance matrix for our ecosystem divided into sub-communities of sizes \( w_1, \ldots, w_N \). We have \( \overline{\mathbf{P}} = \mathbf{p} \) for all \( j \), and:

\[
\alpha_j = \frac{qDZ(\mathbf{p})}{w_j}, \quad \overline{\alpha}_j = qDZ(\mathbf{p}), \quad A = qDZ(\mathbf{p}) \cdot qD(\mathbf{w}),
\]

\[
\beta_j = w_j, \quad \overline{\beta}_j = 1, \quad B = M_{1-q}(\mathbf{w}, \mathbf{w}), \quad G = qDZ(\mathbf{p}),
\]

Note that \( \overline{\mathbf{A}} \), \( \overline{\mathbf{B}} \) and \( G \) are independent of \( \mathbf{w} \). This is a special case of invariance under shattering. But \( A \) and \( B \) clearly do depend on \( \mathbf{w} \), so they are not invariant under shattering.

A2.4 Naïve-community model

Suppose that the \( N \) different sub-communities of our ecosystem have no species in common, and that, moreover, species in different sub-communities are always completely dissimilar to one another.

Let us say that the first sub-community contains species \( 1, \ldots, S_1 \), the second contains species \( S_1+1, \ldots, S_1+S_2 \), and so on. Then \( S_1+\cdots+S_N = S \),

\[
\mathbf{P}_{ij} = (\underbrace{0, \ldots, 0}_{S_1+\cdots+S_{j-1}}, r_{1j}, \ldots, r_{S_{j}j}, \underbrace{0, \ldots, 0}_{S_{j+1}+\cdots+S_N}),
\]

and

\[
\mathbf{p} = (r_{11}, \ldots, r_{1S_1}, \ldots, r_{N1}, \ldots, r_{NS_N}).
\]
Write $\overline{r_{ij}}$ for the normalisation of $r_{ij}$ (that is, $\overline{r_{ij}} = r_{ij}/w_j$); then

$$
\overline{P_{ij}} = (0, \ldots, 0, \overline{r_{ij}}, \ldots, \overline{r_{S_jS_j}}, 0, \ldots, 0).
$$

The similarity matrix $Z$ decomposes as a block sum

$$
Z = \begin{pmatrix}
Z^1 & 0 \\
0 & Z^2 \\
& & \ddots \\
& & & Z^N
\end{pmatrix}
$$

where $Z^j$ is an $S_j \times S_j$ matrix. Write $d_j = qDZ^j(\overline{r_{ij}})$; this is the diversity of the $j$th sub-community considered in isolation. Simple calculations show that the alpha-diversities are:

$$
\alpha_j = d_j/w_j, \quad A = M_{1-q}(w, d/w) = \left( \sum_j w_j^q d_j^{1-q} \right)^{1/(1-q)},
$$

$$
\overline{\alpha}_j = d_j, \quad \overline{A} = M_{1-q}(w, d).
$$

The beta-diversities are:

$$
\beta_j = 1, \quad B = 1,
$$

$$
\overline{\beta}_j = 1/w_j, \quad \overline{B} = qD(w).
$$

These are all the maximum possible values (as computed in Section A1.1), reflecting the fact that the sub-communities have nothing in common. Finally, the gamma-diversities are:

$$
\gamma_j = d_j/w_j, \quad G = M_{1-q}(w, d/w) = \left( \sum_j w_j^q d_j^{1-q} \right)^{1/(1-q)},
$$

the last of which is precisely the modularity formula proved in Proposition A10 of (Leinster & Cobbold, 2012).

In this case, atypically, $G = AB$.

### A2.5 Sub-Communities consisting of only rare species

This example illustrates the difference in meanings of $\gamma_j$ and $\beta_j$. It concerns only the sub-community measures, not the ecosystem measures.

For simplicity, let us assume we are working in the naïve-similarity model $Z = I$. Suppose that the first two sub-communities consist entirely of very rare species whose relative abundance in the whole ecosystem is $10^{-9}$. The first sub-community consists of just one such species, but the second consists of $10^3$ such species in equal proportions.
The sub-community gamma-diversities are $\gamma_1 = \gamma_2 = 10^9$ (for all $q$). This high value reflects the fact that each individual in either of these sub-communities contributes a great deal to the ecosystem diversity. It is unaffected by whether the sub-community consists of one or a thousand different species.

On the other hand, $\overline{\beta}_1 = 10^9 > \overline{\beta}_2 = 10^6$. The single-species sub-community has larger beta-diversity, because its relative abundance distribution is less like that of the whole ecosystem than the multi-species sub-community’s is.

### A2.6 Naïve-similarity model

The formulas for our measures do not simplify dramatically in the special case of the naïve-similarity model $Z = I$. However, we note in passing that we recover two of the quantities described in Tuomisto’s survey of beta-diversities (Tuomisto, 2010a). First, $\overline{A}$ is the same as the quantity that Tuomisto denotes by $\alpha_t$, the ‘t’ standing for ‘turnover’. Second, when there are no shared species between sub-communities, the calculations in Section A2.4 tell us that $\overline{B} = qD(w)$, which is what Tuomisto denotes by $qD_w$.

We now explore some further special cases that help to explain the meanings of our measures.

**Naïve-similarity model with $q = 0$** For a vector $v = (v_1, \ldots, v_n)$, write $\#v$ for the number of indices $i$ such that $v_i \neq 0$. Then the naïve diversities for $q = 0$ are as follows:

\[
\alpha_j = \frac{\#P_{j}}{w_j}, \quad A = \sum_j \frac{\#P_{j}}{w_j}, \quad \overline{\alpha}_j = \frac{\#P_{j}}{\#P_j}, \quad \overline{A} = \sum_j \frac{w_j \cdot \#P_{j}}{w_j}.
\]

\[
\beta_j = \frac{w_j}{\sum_{i: P_{ij} > 0} p_i}, \quad B = \sum_j \frac{w_j^2}{\sum_{i: P_{ij} > 0} p_i}, \quad \overline{\beta}_j = \frac{1}{\sum_{i: P_{ij} > 0} p_i}, \quad \overline{B} = \sum_j \frac{w_j}{\sum_{i: P_{ij} > 0} p_i},
\]

\[
\gamma_j = \frac{\sum_{i: P_{ij} > 0} P_{ij}}{p_i}, \quad G = \#p.
\]

For instance, $\overline{A}$ is simply the average number of species present in a sub-community, weighted according to sub-community size. The normalised sub-community beta-diversity $\overline{\beta}_j$ is highest when the sub-community consists exclusively of species that are rare in the ecosystem, but decreases sharply if it contains even one individual of a common species.
**Naïve-similarity model with** $q = 1$ Here we have:

$$
\alpha_j = \prod_i P_{ij}^{P_{ij}}, \quad A = \prod_{i,j} P_{ij}^{P_{ij}}, \quad \varpi_j = \prod_i P_{ij}^{-P_{ij}}, \quad \overline{A} = \prod_{i,j} P_{ij}^{-P_{ij}},
$$

$$
\gamma_j = \prod_i p_{ij}^{P_{ij}}, \quad G = \prod_i p_{ij}^{-P_{ij}},
$$

$$
\beta_j = \gamma_j / \alpha_j, \quad B = G / A, \quad \overline{\beta}_j = \gamma_j / \varpi_j, \quad \overline{B} = G / \overline{A}.
$$

Here we have multiplicative relationships $G = \overline{A} \overline{B} = AB$, and our measures $\overline{A}$ and $\overline{B}$ coincide with Jost’s alpha- and beta-diversities.

**Naïve-similarity model with** $q = \infty$ Diversities of order $\infty$ reflect the influence of the most common species. We have:

$$
\alpha_j = \frac{1}{\max_{i: P_{ij} > 0} P_{ij}}, \quad A = \frac{1}{\max_{i,j: P_{ij} > 0} P_{ij}}, \quad \varpi_j = \frac{1}{\max_{i: P_{ij} > 0} P_{ij}}, \quad \overline{A} = \frac{1}{\max_{i,j: P_{ij} > 0} P_{ij}},
$$

$$
\beta_j = \frac{\max_{i: P_{ij} > 0} P_{ij}}{p_i}, \quad B = \min_j \max_{i: P_{ij} > 0} P_{ij}, \quad \overline{\gamma}_j = \max_{i: P_{ij} > 0} P_{ij}, \quad \overline{B} = \min_j \max_{i: P_{ij} > 0} p_i
$$

$$
\gamma_j = \frac{1}{\max_{i: P_{ij} > 0} p_i}, \quad G = \frac{1}{\max_{i: P_{ij} > 0} p_i}.
$$

So, for instance, $\beta_j$ is high if there is at least one species that lives almost nowhere in the ecosystem outside the $j$th sub-community. This conforms with the intuitive idea that $\beta_j$ is high if the $j$th sub-community is in some sense unusual relative to the ecosystem. The ecosystem measure $B$ is high if every sub-community is home to at least one such specialist species.