Open Access

Web Ecology

Partitioning of diversity: the "within communities" component

H.-R. Gregorius

Institut für Populations- und ökologische Genetik, Am Pfingstanger 58, 37075 Göttingen, Germany

Abteilung Forstgenetik und Forstpflanzenzüchtung, Büsgenweg 2, 37077 Göttingen, Germany

Correspondence to: H.-R. Gregorius (gregorius@ipoeg.de)

Abstract. It is routinely understood that the total diversity within a metacommunity (γ-diversity) can be partitioned into one component summarizing the diversity within communities (α-diversity) and a second component representing the contribution of diversity (or differences) between communities (β-diversity). The underlying thought is that merging differentiated communities should raise the total diversity above the average level of diversity within the communities. The crucial point in this partitioning criterion is set by the notion of "diversity within communities" (DWC) and its relation to the total diversity. The common approach to summarizing DWC is in terms of averages. Yet there are many different ways to average diversity, and not all of these averages stay below the total diversity for every measure of diversity, corrupting the partitioning criterion. This raises the question of whether conceptual properties of diversity measures exist, the fulfillment of which implies that all measures of DWC obey the partitioning criterion. It is shown that the straightforward generalization of the plain counting of types (richness) leads to a generic diversity measure that has the desired properties and, together with its effective numbers, fulfills the partitioning criterion for virtually all of the relevant diversity measures in use. It turns out that the classical focus on DWC (α) and its complement (β as derived from α and γ) in the partitioning of total diversity captures only the apportionment perspective of the distribution of trait diversity over communities (which implies monomorphism within communities at the extreme). The other perspective, differentiation, cannot be assessed appropriately unless an additional level of diversity is introduced that accounts for differences between communities (such as the joint "type-community diversity"). Indices of apportionment I_A (among which is G_{ST} and specially normalized versions of β) and differentiation I_D are inferred, and it is demonstrated that conclusions derived from I_A depend considerably on the measure of diversity to which it is applied, and that in most cases an assessment of the distribution of diversity over communities requires additional computation of I_D.

1 Introduction

There seems to be general agreement that a diversity measure is a real-valued continuous function defined on a frequency simplex, is invariant towards permutations of the frequency components, and meets the *evenness criterion* or condition (see MacArthur, 1965; Hill, 1973, p. 429, bottom of right column; Patil and Taillie, 1982, p. 551, top of right column; Jost, 2009; Gregorius, 2010; and many more). The evenness criterion expresses the idea that diversity increases as the dis-

tribution of types becomes more even[1], and it implies that the diversity measure assumes a unique minimum value that is realized for frequency vectors with one component equal to 1 and all others equal to 0 (monomorphism), and that for even (uniform) distributions the measure increases strictly with the number of types represented in the distribution (for

---

[1]The evenness criterion states that diversity increases strictly as the difference in representation (frequency) between two types decreases while the sum of their representations remains the same. If types are recorded without reference to their representation, then diversity increases strictly with the number of types.

more implications of the evenness criterion see Patil and Tail-lie, 1982; Gregorius, 2010). Moreover, with this specification, each diversity measure is related to its plain notion, i.e., the number of types (frequently termed "richness"), via the concept of effective number (which will be returned to later on in more detail).

Another essential – though rarely explicitly stated – criterion relates to how assemblages of differentiated communities affect the diversity of the total assemblage. The criterion reflects the pervasive perception that merging differentiated communities ought to increase the total diversity in relation to the diversity realized in the individual communities (see, for example, Lewontin, 1972, or Gadagkar, 1989). While this need not apply to each individual community, it must still apply to the less diverse communities (think about merging a monomorphic community with a highly polymorphic one). This perception in turn gave rise to various attempts to partition the total diversity into a component that summarizes the diversities of the individual communities (akin to "α-diversity" in ecology) and a component that is commonly addressed as "diversity" between communities (akin to "β-diversity"). Herewith, the latter wording is unfortunate in that it refers to differences between communities rather than to the "diversity" of any specified collection of objects (a reminder that is already implicit in the paper of Whittaker, 1960, p. 320; also see Ricotta, 2005, paragraph following Eq. 1). Due to the conceptual structure of the present paper, however, it is not necessary to join into the ongoing discussion of the notion of β-diversity (Tuomisto, 2010, addresses this discussion in the title of her paper as the "diversity of beta diversities").

The notion of "diversity within communities" (abbreviated DWC in the following) is probably the most central and crucial facet of the partitioning concept, since its numerical specification is required as a reference for the "gain" in total diversity due to differences between communities. The requirement that the total diversity exceeds the DWC (however it is summarized), with equality only in the absence of differentiation between them, will be termed the partitioning criterion. Note that this criterion always applies when the measure of DWC is replaced by the minimum of the individual community diversities.

Usually, the DWC is summarized by some kind of average over the diversities within the individual communities that satisfies the partitioning criterion. In many cases, several averages are suitable (and many are not; see, for example, the arguments given in Jost, 2007, and Gregorius, 2010) and it may require additional demands on the diversity measure to yield a unique specification of the DWC. These demands of course depend on the purpose of the analysis, which subjects the notion of DWC and thus the concept of diversity partitioning to some equivocality. In every sense, the evenness criterion and the partitioning criterion are innate to the concept of diversity, which raises the question of whether these criteria already guarantee the existence of generally legitimate measures of DWC (preferably in the form of averages). In this case, the possibility that diversity can be partitioned would indeed be implicit in the concept of diversity, and this could in turn aid in the design of more targeted indices relating to the distribution of diversity over communities.

In view of the large number of diversity measures, many of which are highly complex and difficult to interpret, the present paper will focus on the generic idea of these measures (i.e., the plain notion of number of types) and make an attempt to consistently develop this idea further until it covers virtually all of the relevant measures in use. By doing this, the focus is set on legitimate specifications of the concept of DWC as mentioned above. The results of the analysis are used to clarify and extend established and more recent methods of quantifying the shares that diversity within, and differences between, communities has in the total diversity of a metacommunity.

2   Generalizing the plain notion of diversity

The assessment of diversity by simply counting numbers of types (plain notion) becomes ambiguous if types are not equally represented or if their representations are given different weights in the evaluation of diversity. Representation of types may encompass the frequency of individuals, their biomass, area occupied, etc., and these quantities enter into the assessment of diversity as relative quantities p_i for the ith type with $\sum_i p_i = 1$. Weights given to representations p can be viewed as non-negative functions $\omega(p)$ that specify the contribution of each type's representation to the overall diversity. For example, up to a certain threshold, rare species or alleles can be argued to contribute more to the adaptability of communities under varying environments and by this receive higher weight in the diversity assessment. Yet, at the extreme, where a type is not represented in a community ($p = 0$), it cannot in any sense contribute to its diversity and is therefore commonly characterized by $\omega(0) = 0$ (for an exception see the function with superscript 4 in Table 1). In fact, the ways in which $\omega(p)$'s can be specified is virtually unlimited, as are the ecological models that generate them. This should be recalled in view of the fact that the vast majority of diversity studies rely on a vanishingly small number of diversity indices – the significance of which for the studies' aims is rarely argued.

With this notation, the plain notion of diversity presents itself via the specification $\omega(p) = 1$ for all positive p's and by taking the sum $\sum_i \omega(p_i)$ over types. Hence, continuing this notion, a direct approach to the assessment of diversity consists in summing the weights of the types' representations, i.e., building the generic representation $\eta := \sum_i \omega(p_i)$ of diversity. This sum, in turn, may require further transformation in order to enable the design of indices that allow for special kinds of interpretation. Such interpretations may refer to the "effective" number of types or to the saturation

Table 1. Examples of strictly concave weight functions $\omega(p)$ together with their respective generic diversities η and strictly increasing transformations τ that make $\tau(\eta)$ into diversity effective numbers; $p_i :=$ relative representation of the ith type (only $p_i > 0$ considered).

Weight function $\omega(p)$	Generic diversity $\eta = \sum_i \omega(p_i)$	Effective number $\tau(\eta)$
$\omega(p) = 1$ for $p > 0$, $\omega(0) = 0$	plain notion (richness)	η
$p \cdot (1 - p^{a-1})$, $1 < a$	$1 - \sum_i p_i^a$ [1]	$(1 - \eta)^{\frac{1}{1-a}}$ [2]
p^a, $0 < a < 1$	$\sum_i p_i^a$	$\eta^{\frac{1}{1-a}}$ [2]
$p \cdot (p^{a-1} - 1)$, $0 \neq a < 1$	$\sum_i p_i^a - 1$	$(\eta + 1)^{\frac{1}{1-a}}$ [2]
$-p \cdot \log_a p$, $0 < a \neq 1$	$-\sum_i p_i \cdot \log_a p_i$ [3]	a^η [2]
$p \cdot (1 - p)^a$, $0 < a \leq 1$	$\sum_i p_i \cdot (1 - p_i)^a$	$1/\left(1 - \eta^{\frac{1}{a}}\right)$
$p \cdot \cos(p \cdot \frac{\pi}{2})$	$\sum_i p_i \cdot \cos(p_i \cdot \frac{\pi}{2})$	$\frac{\pi}{2} / \arccos \eta$
$(1 - p)^a$, $0 < a < 1$ [4]	$\sum_i (1 - p_i)^a$	$f^{-1}(\eta)$ with [5] $f(x) = x^{1-a}(x - 1)^a$

[1] for $a = 2$, known as the Simpson index; [2] also called Hill numbers or Rényi diversity (Hill, 1973; Rényi, 1961); [3] known as Shannon–Wiener index or entropy; [4] the requirement $\omega(0) = 0$ for weight functions is not met, yet ω is strictly concave, which guarantees that η is a measure of diversity; [5] for x equally frequent types $\eta = x \cdot (1 - (1/x))^a = x^{1-a}(x - 1)^a = f(x)$, where $f(x)$ is a strictly increasing function for $x \geq 1$, so that the inverse f^{-1} exists as a strictly increasing transformation of η.

of a community with diversity. While the former example refers to an essentially unbounded transformation (number of types), the latter example requires an upper bound for the transformation (where the upper bound is reached if all members differ in type). Denoting the transformations by τ, the pursued generalization of the plain notion of diversity obtains the form $\tau(\eta)$, where $\eta = \sum_i \omega(p_i)$ and τ is a non-negative and strictly monotonic function.

2.1 Implications of the evenness and partitioning criterion

As the first step, the functions ω and τ must be specified such that the two criteria (evenness and partitioning) of diversity measures are realized for $\tau(\sum_i \omega(p_i))$. The monotonicity of τ implies that any direction of change in the generic representation $\eta = \sum_i \omega(p_i)$ is preserved or inverted under τ, depending on whether τ is an increasing or decreasing function. Hence, validity of the criteria is primarily determined by η and thus by the structure of ω. Setting $r(p) = \omega(p)/p$ for positive p and imposing the assumptions that $r(p)$ decreases strictly with increasing p, Patil and Taillie (1982) referred to η as a measure of diversity that mirrors the "average rarity" of types. The "standard diversity indices" of Jost (2007, p. 2429) also follow the generic representation for a special case.

It is proven in Appendix A that η obeys the evenness criterion if $\omega(p)$ is a strictly concave function of p. Patil and Taillie (1982) arrived at a similar statement in their Theorem 4.3, though without explicit proof. Since weight functions should be allowed to take on variable forms, including the discontinuities that can occur under threshold conditions, the present proof proceeds from the most comprehen-

sive definition of concavity. The relation to the concept of average rarity is obtained by the observation that, by the evenness criterion, measures of diversity increase strictly with the number n of types in an even distribution. In such distributions, $\eta = n \cdot \omega(1/n) = r(1/n)$ therefore increases with n (decreases with increasing $1/n$), which makes it meaningful to require that this tendency extend from $1/n$ to all proportions p. The function $r(p)$ would then decrease strictly with increasing p. Hence η is referred to here as a measure of average rarity, even though in averages the weights given to measurements are generally independent of the latter.

To check the partitioning criterion, consider an assemblage of communities, for which p_{ij} denotes the frequency of the ith type in the jth community and c_j denotes the frequency (relative size) of the jth community in the assemblage (the metacommunity). Then $p_i := \sum_j c_j \cdot p_{ij}$ is the frequency of the ith type in the metacommunity, $\eta_j := \sum_i \omega(p_{ij})$ is the η-measure within the jth community, and $\hat{\eta} = \sum_i \omega(p_i)$ is the η-measure of the total metacommunity.

Concavity of $\omega(p)$ now implies $\omega(p_i) = \omega(\sum_j c_j \cdot p_{ij}) \geq \sum_j c_j \cdot \omega(p_{ij})$ and therefore $\hat{\eta} \geq \sum_i \sum_j c_j \cdot \omega(p_{ij}) = \sum_j c_j \cdot \sum_i \omega(p_{ij}) = \sum_j c_j \cdot \eta_j$, with equality holding only if, for each i, the p_{ij}'s are equal for all j. Herein, $\bar{\eta} := \sum_j c_j \cdot \eta_j$ is the (linear) average of the η-measures within the individual communities. It thus turns out that the total η-measure $\hat{\eta}$ of the metacommunity exceeds the average η-measure $\bar{\eta}$ within communities, and that both become equal only if there is no differentiation between the communities (Patil and Taillie, 1982, arrived at a similar result in their Chapter 8.3 and Theorem 5.2).

This demonstrates that the average $\bar{\eta}$ quantifies the notion of DWC in compliance with the partitioning criterion. Thus, fulfillment of the evenness condition via strict concavity

of $\omega(p)$ implies fulfillment of the partitioning criterion for the η-measure. Strict concavity of $\omega(p)$ thus makes the generic representation η a measure of diversity (consult Table 1 for a selection of strictly concave weight functions ω and their generic diversities η).

Obviously, application of the transformation τ to the generic diversity η does not affect the validity of the evenness criterion if the transformation is a strictly increasing function of η. Validity of the partitioning criterion is also guaranteed, even though the measure of DWC may now appear as a non-linear average. In fact, $\tau(\bar{\eta})$ is placed between the maximum and the minimum of the $\tau(\eta_j)$'s (the diversities within the individual communities), and $\bar{\eta} \leq \hat{\eta}$ implies $\tau(\bar{\eta}) \leq \tau(\hat{\eta})$ with equality only in the absence of differentiation. Therefore $\tau(\eta)$ satisfies the partitioning criterion, and the non-linear average $\tau(\bar{\eta})$ of the diversities $\tau(\eta_j)$ within the individual communities provides an appropriate measure of the DWC. In summary, $\tau(\eta)$ *becomes a measure of diversity if ω is a strictly concave function of p and τ is a strictly increasing function of η; under these conditions $\tau(\bar{\eta})$ is a legitimate measure of DWC for $\tau(\eta)$.* By "legitimate" it is meant that $\tau(\bar{\eta})$ meets the partitioning criterion.

While $\tau(\bar{\eta})$ is usually an average of non-linear type, it is also possible to obtain a linear average that suffices the partitioning criterion, when τ is additionally required to be (not necessarily strictly) concave. This follows directly from $\sum_j c_j \cdot \tau(\eta_j) \leq \tau(\sum_j c_j \cdot \eta_j) \leq \tau(\hat{\eta})$, with equality between the left and right end of the chain of inequalities only in the absence of differentiation. Hence, the "linear" average $\overline{\tau(\eta)} := \sum_j c_j \cdot \tau(\eta_j)$ again constitutes a legitimate measure of the DWC for the diversity measure $\tau(\eta)$, provided τ is a strictly increasing and concave function.

It should be noticed at this point that additional averages other than the above "linear" average $\bar{\eta}$ also comply with the partitioning criterion for η. One example is the generalized mean for a function g that is strictly increasing and concave (or strictly decreasing and convex). For such functions, the generalized g-mean implies $g^{-1}\left(\sum_j c_j \cdot g(\eta_j)\right) \leq \sum_j c_j \cdot \eta_j = \bar{\eta}$. Hence, $g^{-1}\left(\sum_j c_j \cdot g(\eta_j)\right)$ is a (non-linear) average that is smaller than the total diversity with equality only in the absence of differentiation. It is thus a legitimate measure of DWC. A summary of the properties of the generic diversity obtained so far is provided in Table 2.

2.2 Homogeneity, the opposite of diversity

The significance of the transformation τ is not just confined to production of versions of diversity measures that promote interpretation of the generic diversity. Even if the generic representation does not meet the conditions of a diversity measure, it can in certain cases be transformed into such a measure. An apparent example is provided by weight functions ω that are strictly convex and therefore give rise to generic representations η that are not diversity measures. Yet applying a strictly decreasing transformation τ to η turns $\tau(\eta)$ into

a diversity measure. This follows directly from the fact that all of the above inequalities involving η for strictly concave weight functions are simply reversed by convexity, so that application of a strictly decreasing transformation restores the initial inequalities that guarantee fulfillment of the evenness and partitioning criterion for $\tau(\eta)$ as well as legitimacy of $\tau(\bar{\eta})$ as a measure of DWC for $\tau(\eta)$.

This example points to the possibility to conceive the plain notion of diversity as a plain notion of homogeneity by simply reverting the line of sight: the fewer types in a community, the higher its homogeneity. η would then turn into a measure of homogeneity by requiring that the weight functions ω be strictly convex functions of p. As was mentioned above, under this condition, all of the above inequalities obtained for concave weight functions are reversed, and the notion of homogeneity is confirmed to be simply the opposite of diversity. This includes the notion of "homogeneity within communities", the measure $\bar{\eta}$ of which must now exceed the total metacommunity homogeneity $\hat{\eta}$ with equality only in the absence of differentiation. Strictly decreasing transformations provide the means for converting measures of homogeneity into measures of diversity and vice versa.

3 The diversity effective number of types

To relate any measure of diversity to the plain notion of diversity, i.e., the number of types present in a community, it is common practice to draw on comparisons with ideal communities in which all types are equally frequent (MacArthur, 1965). In such communities the number of types is unambiguously defined. It is thus consistent to specify an "effective number" of types of a non-ideal community via the number of types in an ideal community that show the same diversity measure as in the community under observation. More generally, the effective number of a measure of diversity is a strictly increasing transformation of that measure with the special feature that, for each even distribution of types, it equals the number of types represented in that distribution (for the general concept of effective number see Gregorius, 1991; the problem of definiteness of the effective number is considered in Appendix B).

In an ideal community with n types, the generic diversity equals $\eta = n \cdot \omega(1/n)$. Setting $r(p) = \omega(p)/p$ for positive p, this becomes $\eta = r(1/n)$, and the effective number of a community equals the value of n for which its generic diversity equals $r(1/n)$. The equation $\eta = r(1/n)$ is uniquely solvable for n if n is allowed to be any real number $x \geq 1$ and if r is strictly monotonic so that its inverse r^{-1} exists. As was argued above and in Appendix B, $r(1/n)$ being a strictly increasing function of n by the evenness criterion, it is indeed appropriate to assume that $r(p)$ is a strictly decreasing function across the whole range of positive proportions p. The diversity effective number τ_e of the generic diversity η then turns out to be $\tau_e(\eta) = 1/r^{-1}(\eta)$

Table 2. Summary of properties of the generic diversity $\eta = \sum_i \omega(p_i)$.

– The generic representation η becomes a diversity measure (satisfies the evenness and the partitioning criterion) if the weight function ω is strictly concave on the unit interval. The evenness criterion implies that $r(p) = \omega(p)/p$ decreases strictly with decreasing numbers of types in even distributions, which supports the assumption that $r(p)$ decreases strictly with increasing p.
– A method of quantifying the notion of "diversity within communities" (DWC) that suffices the partitioning criterion is provided for the diversity measure η by the linear average $\bar{\eta}$ of the diversities within the individual communities. This makes the diversity measure η a strictly concave function on the frequency simplex. Replacement of the linear average by certain generalized means yields further legitimate measures of DWC.
– Under strictly increasing transformations τ, the generic diversity η retains its properties of a diversity measure, and $\tau(\bar{\eta})$ is a (non-linear) average of the transformed diversities within the individual communities that is a legitimate measure of DWC for the diversity measure $\tau(\eta)$. If the transformation is concave in addition, the linear average of the transformed diversities within the individual communities is a legitimate measure of DWC for $\tau(\eta)$.

Effective numbers
– Effective numbers exist for all measures of diversity, and they again are measures of diversity. An effective number of the generic diversity η (having strictly concave $\omega(p)$) can always be obtained as $1/r^{-1}(\eta)$ provided $r(p) = \omega(p)/p$ decreases strictly with increasing p.
– The effective number of a strictly monotonic transformation of η can be specified such that it is the same as the effective number of η (scaling invariance of the effective number).
– For the effective number of the diversity measure η, a legitimate measure of DWC is provided by the (non-linear) average $1/r^{-1}(\bar{\eta})$ given that $r(p) = \omega(p)/p$ decreases strictly with increasing p.

(also compare Patil and Taillie, 1982, Eq. 3.2). Since $\tau_e(x) = 1/r^{-1}(x)$ is a strictly increasing function of x, τ_e is a special case of a strictly increasing transformation, which was shown above to always guarantee that the effective number $\tau_e(\eta) = 1/r^{-1}(\eta)$ is a diversity measure with a measure of DWC given by $\tau_e(\bar{\eta}) = 1/r^{-1}(\bar{\eta})$.

The transformations of the generic diversities listed in Table 1 are chosen such that they yield effective numbers, and the generic diversities themselves are based on strictly decreasing functions r. The Rényi diversities in this list have measures of DWC that are non-linear averages known as power means or Hölder means. For $a \neq 1$, these means have the form $\tau_e(\bar{\eta}) = \left(\sum_j c_j \eta_j^{1-a} \right)^{\frac{1}{1-a}}$ (Gregorius, 2010). The transformations τ_e applied to the generic diversities η to arrive at Rényi diversities (as given in Table 1) are easily proven to be convex rather than concave functions of η. Linear averages of the transformed diversities within the individual communities are therefore not legitimate measures of DWC, as has been recognized by several authors, probably starting with the paper of Gadagkar (1989).

One of the reasons why Rényi diversities have been attracting increasing interest recently can be seen in its characteristic of realizing the replication principle. This is closely related to β-diversity in that, for this family of diversity, measures $\tau_e(\hat{\eta})/\tau_e(\bar{\eta})$ equal the (diversity) effective number of communities for complete differentiation and equal diversities in all communities (in the more common version of the replication principle, community sizes are assumed to be equal, yet this is not necessary for Rényi diversities; see Gregorius, 2010). Clearly, this principle is meaningful only for

diversity effective numbers. The last three examples in Table 1 are, however, included to show that not all diversity effective numbers obey the replication principle. This is motivated by the fact that, as was mentioned above, the number of ecologically relevant specifications of weight functions ω and the resulting generic representations of diversity is virtually unlimited and should therefore not be restricted to measures the effective numbers of which follow the replication principle.

Another characteristic of the effective number is that it can be specified such that it is "scaling invariant". By this it is understood that the effective number of a strictly monotonic transformation of η is the same as the effective number of η. This is easily checked by letting g be a strictly monotonic transformation (which therefore is invertible), and considering that, for an ideal community with n evenly distributed types, one obtains $g(\eta) = g(r(\frac{1}{n}))$. Given that r is invertible, and successively applying g^{-1} and r^{-1} to this equality, one obtains $\frac{1}{n} = r^{-1}(\eta)$. The effective number of $g(\eta)$ thus again equals $1/r^{-1}(\eta)$, i.e., $\tau_e(g(\eta)) = \tau_e(\eta)$. Hence, though $g(\eta)$ need not be a diversity measure (since g is allowed to be either an increasing or a decreasing function of η), its effective number meets the criteria for a diversity measure via the strictly increasing transformation $1/r^{-1}(\eta)$. The above results on the effective numbers of generic diversities are summarized in Table 2.

Many situations are conceivable where *knowledge of both the diversity and its corresponding effective number* is desirable. A simple example is provided by Simpson's index $\frac{N}{N-1} \cdot (1 - \sum_i p_i^2)$ of diversity (Simpson, 1949), which is a very widely used special version of the generic diversity

(with $\omega(p) = \frac{N}{N-1} \cdot (1-p) \cdot p$). In this version (which Simpson referred to as an unbiased estimate), the index equals the probability of sampling without replacement in a community of size N two individuals that differ in type. The probability and thus the index reach their maximum value of 1 only if all community members differ from each other. This case describes a state of complete saturation of a community with diversity. Hence, Simpson's index measures the degree to which a community is saturated with diversity, but it provides no information on the number of types involved. This number is obtained by transforming the index into its well-known effective number $1/\sum_i p_i^2$ (note the absence of N). The example demonstrates that *one can only obtain an idea about the number of types involved in producing the original measure after the originally considered measure of diversity is transformed into its effective number*.

4 Concluding remarks

The above demonstrations show that acceptance of two basic characteristics of diversity measures – fulfillment of the evenness criterion and the generic representation – implies a generally and consistently applicable realization of the notion of DWC together with specifications of legitimate measures of DWC. By this, validity of the principles of partitioning diversity into components within and between communities is guaranteed, and no additional requirements such as concavity of the diversity measure on the frequency simplex are needed (as in Patil and Taillie, 1982, p. 552).

4.1 Quantifying the distribution of diversity within and between communities

Legitimate measures of DWC provide the basis for essentially all methods that quantify the distribution of diversity within and between communities. In ecology, DWC is usually addressed as α-diversity and is mostly measured by any of the specifications of $\tau(\bar{\eta})$. In this context, the total diversity $\tau(\hat{\eta})$ is termed γ-diversity, and either $\tau(\hat{\eta}) - \tau(\bar{\eta})$ or $\tau(\hat{\eta})/\tau(\bar{\eta})$ are conceived of as assessments of β-diversity (for a discussion of the relations between the two versions of β-diversity see Ricotta, 2005). As it comes to the design of indices that indicate the extent to which diversity is distributed over communities, two basic perspectives have to be distinguished that describe (a) tendencies of members of the same community to hold the same trait state (the apportionment perspective) vs. (b) tendencies of members of different communities to hold different trait states (the differentiation perspective; see Whittaker, 1972, or Gregorius, 2009).

Apparently, complete apportionment of type diversity to communities is reached if all communities are monomorphic and thus have minimum diversity. This is characteristic of the apportionment perspective as is realized in indices such as the classic G_{ST} used in population genetics. Denoting the minimum value of $\tau(\eta)$ by $\tau(\eta)_{min}$, *indices of apportionment*

(including G_{ST}) are typically of the form

$$I_A := \frac{\tau(\hat{\eta}) - \tau(\bar{\eta})}{\tau(\hat{\eta}) - \tau(\eta)_{min}}, \qquad (1)$$

which involves both the additive and multiplicative versions of β-diversity and which vary between 0 (absence of differentiation) and 1 (monomorphism within all communities) as required. *The index measures the proportion of the excess of total type diversity over the minimum value of the diversity measure that is due to the apportionment (allocation) of types to communities.* I_A becomes G_{ST} for $\omega(p) = p \cdot (1-p)$ and for τ equal to the identity mapping (so that $\tau(\eta)_{min} = \eta_{min} = 0$ and η equals the Simpson index; see Table 1).

The corresponding characteristic of the differentiation perspective identifies complete differentiation as a state where membership of different communities implies difference in type. Complete differentiation can be realized for monomorphic as well as polymorphic communities. Indices of diversity-based differentiation were developed only recently by Jost (2006) (termed $1 - S$) and Jost (2008) (termed D), the latter of which has since attracted considerable attention in population genetics.
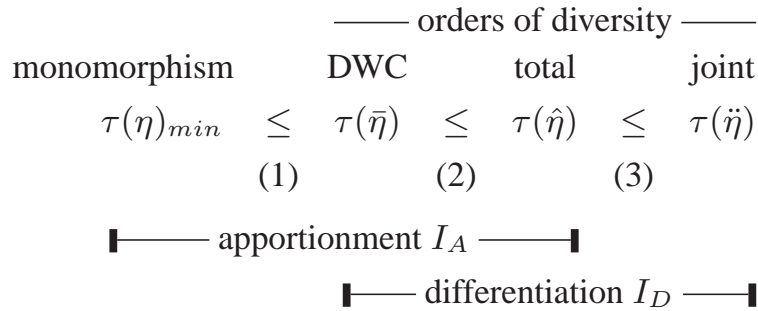
Under both perspectives, a lack of any tendencies in the distribution of diversity over communities is defined by the absence of differentiation. Since the absence or presence of differentiation is determined by the difference between DWC and total diversity, knowledge of DWC is essential from both perspectives. Yet knowledge of DWC and total type diversity is not sufficient for the determination of degrees of differentiation, since neither of the two nor any combination of them can indicate the situation of complete differentiation.

Measures of differentiation that solely refer to the distribution of diversity over communities require a third order of diversity called the *joint diversity* of the metacommunity (Gregorius, 2010). In the measurement of joint diversity, each individual is characterized jointly by its type (trait state) and community membership. Joint diversity $\tau(\ddot{\eta})$, say, then results from application of $\tau(\eta)$ to the joint distribution of type and community membership. Using the above notation, the generic joint diversity reads $\ddot{\eta} = \sum_{ij} \omega(c_j \cdot p_{ij})$. The relationship to differentiation is provided by the inequality $\tau(\ddot{\eta}) \geq \tau(\hat{\eta})$, with equality only for complete differentiation (follows from the evenness criterion; see Gregorius (2010). Using this relationship, Jost's approaches turn out to belong to the class of diversity-based *indices of differentiation* that are typically of the form

$$I_D := \frac{\tau(\hat{\eta}) - \tau(\bar{\eta})}{\tau(\ddot{\eta}) - \tau(\bar{\eta})}, \qquad (2)$$

which vary between 0 (absence of differentiation) and 1 (complete differentiation) as required. When applied to Rényi diversities with equal community sizes, I_D equals the $1 - S$ of Jost (2006) and more generally the D_m of Gregorius (2010). For effective numbers, multiplication of I_D by

Table 3. Relations between the three orders of diversity (DWC, total, joint), the ranges of diversity orders covered by the apportionment and differentiation perspective and their indices I_A and I_D, and effects on diversity associated with the transitions between diversity orders.

$$\text{——— orders of diversity ———}$$

monomorphism		DWC		total		joint
$\tau(\eta)_{min}$	$\leq$	$\tau(\bar{\eta})$	$\leq$	$\tau(\hat{\eta})$	$\leq$	$\tau(\ddot{\eta})$
		(1)		(2)		(3)

$$\vdash\!\!\!—— \text{apportionment } I_A ——\!\!\!\dashv$$

$$\vdash\!\!\!—— \text{differentiation } I_D ——\!\!\!\dashv$$

(1) Deviation of DWC from monomorphism, (2) gain in total type diversity as against DWC due to differentiation, and (3) deficiency of total type diversity as against complete differentiation (distance to complete differentiation).

$\tau_e(\ddot{\eta})/\tau_e(\hat{\eta})$ yields the D'_m of Gregorius (2010), which implies the D of Jost (2008) when applied to Rényi diversities of order 2 and equal community sizes.

For an illustration of the range of diversity orders covered by the apportionment and differentiation perspective and their indices I_A and I_D, see Table 3. From this it becomes more evident that in particular *the index I_D measures the proportion of the excess in joint type-community diversity over DWC that is due to the distribution (division) of types between communities*.

In all of these indices of the distribution of diversity over communities, DWC is the only quantity that is not by itself a measure of diversity in that it is not based on the distribution of a particular trait in a particular collection of objects. Its consistent specification provides the reference for the absence of differentiation in a diversity context, and thus it defines the starting point for any attempt at partitioning diversity into components within and between communities. The second component, the "diversity between communities", again does not refer to the diversity of any collection of objects and is seen to not be simply described by the complement of DWC with respect to the total type diversity.

4.2 Apportionment and differentiation are not complementary perspectives

Indeed, in the two perspectives, the notion of differentiation refers to different and non-complementary characteristics. While in the apportionment perspective differentiation aspects are *implicitly* involved in creating an excess of total type diversity over DWC, these aspects determine the differentiation perspective *explicitly*. The latter even prompts consideration of an additional order of diversity, the joint diversity.

This difference in focus suggests that the concept of partitioning diversity should be distinguished into two approaches, one (the classical view) focusing on the share that

DWC has in the total type diversity (apportionment), and the other focusing on the distribution of total type diversity between communities (differentiation). That these approaches are not just complementary can be demonstrated in various ways with the help of the indices I_A and I_D. The interpretation of I_D values is fairly straightforward in that it reflects differences between communities without any pronounced effect of the diversity within the communities. The index of apportionment I_A, however, is more intricate due to its implicit involvement of differentiation aspects and its special dependence on DWC as an indicator of monomorphism within communities. Therefore, in Appendix C, some relevant characteristics of I_A are pointed out that underline the differences between the apportionment and differentiation perspective and demonstrate the effects of the kind of diversity measure applied.

Probably most interesting is the observation that, for generic diversities based on the weight function $\omega(p) = p \cdot (1 - p^{a-1})$ with $a > 1$ (which yield Rényi diversities as effective numbers; see Table 1), I_A may become arbitrarily small simply as the result of high diversity effective numbers within the communities and irrespective of the degree of differentiation. This holds for all parameters $a > 1$, and it generalizes earlier results obtained for the Simpson index (in which case $I_A = G_{ST}$; see Hedrick, 1999; Gregorius et al., 2007). Viewing apportionment as a process that eventually leads to monomorphism within communities, one could argue that high DWC indeed indicates low degrees of apportionment, so that small I_A values make sense in this case. The fact that, irrespective of the degree of differentiation, high polymorphism within communities may reduce I_A to levels that could equally be reached by small degrees of polymorphism combined with little differentiation among communities, however, suggests additional consideration of I_D.

The picture becomes even more involved as one considers the weight function $\omega(p) = p^a$ for positive parameters $a < 1$ (which again yield Rényi diversities as effective numbers;

see Table 1). It is shown in Appendix C that, for generic diversities, I_A may now attain all values between 0 and 1 for arbitrarily large effective numbers of types within the communities. Again, additional consideration of I_D is thus required in order to distinguish between effects of apportionment and differentiation. Moreover, these examples demonstrate clearly that the assessment of degrees of apportionment decisively depends on the measure of diversity that enters into the index I_A.

On the other hand, when generic diversities are replaced by their effective numbers in the computation of I_A, a property shows up that is consistent across all diversity measures but that frequently does not apply to I_A when it is determined for generic diversities. Diversity effective numbers cause I_A to approach a value of 1 arbitrarily closely when imposing an upper bound to the average effective number of types within communities and letting the total effective number of types increase indefinitely (see Appendix C). This reflects a relative view of apportionment, where communities appear to be the more homogeneous, the smaller the diversity within communities is as compared with the total diversity in the meta-community. The assessment of the degree of apportionment of type diversity to communities therefore critically depends on whether it is based on generic diversities or on their diversity effective numbers. Moreover, as the above examples show, as a rule it is impossible to conclude from the degree of apportionment of trait diversity to communities the extent to which this is due to differentiation without explicitly computing the degree of differentiation.

Appendix A: Concavity and evenness

Lemma: let g be a real-valued function defined on a closed interval with left and right extremity 0 and c, respectively. If g is (not necessarily strictly) concave, then $f(x) := g(x) + g(c - x)$ increases (not necessarily strictly) as x approaches $c/2$ from above or below.

Proof: consider $f(x') - f(x) = g(x') - g(x) + g(c - x') - g(c - x)$ with all arguments in the interval of definition. Concavity of g implies that $[g(x') - g(x)]/[x' - x]$ is monotonically non-increasing in x' for fixed x and $x' \neq x$ (non-increasing slope). For $x < x' \leq c/2$, and therefore $x' \leq c - x'$, one thus obtains $[g(x') - g(x)]/[x' - x] \geq [g(c - x') - g(x)]/[c - x' - x]$, or $[g(x') - g(x)] \geq [g(c - x') - g(x)] \cdot [x' - x]/[c - x' - x]$. By the same means, since $x \leq c - x$, $[g(c - x') - g(x)]/[c - x' - x] \geq [g(c - x') - g(c - x)]/[x - x']$ or $[g(c - x') - g(c - x)] \geq [g(c - x') - g(x)] \cdot [x - x']/[c - x' - x]$. Hence,

$$f(x') - f(x) \geq [g(c - x') - g(x)] \cdot \frac{x' - x}{c - x' - x} +$$
$$+ [g(c - x') - g(x)] \cdot \frac{x - x'}{c - x' - x} = 0.$$

Since $f(x) = f(c - x)$, it follows analogously that for $c/2 \leq x' < x$, $f(x') \geq f(x)$: QED.

Proposition: if $\omega(p)$ is concave, then $\sum_i \omega(p_i)$ fulfills the evenness condition.

Proof: let $p_i + p_j = c$, and set $p = p_i$, $p_j = c - p$ and $g(p) = \omega(p)$. Then the above lemma implies that $\omega(p_i) + \omega(p_j)$ and thus $\sum_k \omega(p_k)$ increases as $|p_i - p_j|$ decreases while $p_i + p_j = c$: QED. Also compare the pertaining results of Patil and Taillie (1982, p. 551).

Note: $\omega(p)$ is concave, for example, if $r(p) = \omega(p)/p$ is a decreasing and concave function of $p > 0$.

Appendix B: Definiteness of the effective number

The problem of definiteness lies in the requirement that, for each non-ideal system, there exists an ideal system with identical value of the characteristic variable (i.e., the diversity measure; see Gregorius, 1991). Ideal systems, i.e., even distributions, do not realize all admissible values of the characteristic variable. In a strict sense, the unique relationship between the diversity effective number and the diversity measure therefore exists only for even distributions, where the diversity measure uniquely corresponds to the number of types, and where the evenness criterion implies that the diversity measure increases strictly with the number of types in an even distribution. One therefore requires an extension of the effective number, such that it is defined for all diversity values and is a strictly increasing function of these.

One way to achieve this goal consists in linear interpolation between the values realized for even distributions (polygonal line). If v_n is the diversity of an even distribution with n types for a given measure v of diversity, then, for any value v' of v with $v_n < v' < v_{n+1}$, its effective number lies between n and $n + 1$. For the polygonal interpolation, the effective number τ_e would thus attain the form $\tau_e(v') = n + (v' - v_n)/(v_{n+1} - v_n)$.

The more common alternative, however, is based on the condition that v_n can be considered as a function $\tilde{v}$ of n in which n can be replaced by any real number $x \geq 1$, so that $\tilde{v} = \tilde{v}(x)$ is a strictly increasing function of x with $\tilde{v}(n) = v_n$. This condition is realized for most of the common measures of diversity. In the case of the generic diversity η, an even distribution with n types yields $\eta = v_n = r(1/n)$, whereby the evenness condition $r(1/n)$ is a strictly increasing function of n (strictly decreasing function of $1/n$). Hence, replacing $1/n$ by arbitrary positive proportions p, $r(p) = \omega(p)/p$ is required to strictly decrease with increasing p. The function $\tilde{v}(x)$ thus obtains the representation $r(1/x)$ for $x \geq 1$.

Inversion of $\tilde{v}$ (i.e., $\tilde{v}^{-1}(v)$) then yields the effective number $\tau_e(v)$ corresponding to the diversity v, where in particular $\tau_e(v_n) = \tilde{v}^{-1}(v_n) = n$. For the generic diversity, this implies $\tau_e(\eta) = 1/r^{-1}(\eta)$. Since $\tau_e = \tilde{v}^{-1}$ is a strictly increasing function of the values of the diversity measure v, validity of the evenness criterion and the partitioning criterion for v is transferred to $\tilde{v}^{-1}(v)$, with the result that the effective number $\tau_e(v) = \tilde{v}^{-1}(v)$ again is a measure of diversity. This proves that, *for each measure of diversity, there exists at least one diversity effective number that is again a measure of diversity.*

Appendix C: Properties of I_A

When determined for the generic diversities η, the index of apportionment $I_A = (\hat{\eta} - \bar{\eta})/(\hat{\eta} - \eta_{\min})$ can be analyzed in more detail with the help of the effective numbers $\tau_e(\eta)$ of the generic diversities. For weight function $\omega(p) = p \cdot (1 - p^{a-1})$ with $a > 1$ (that yield Rényi diversities as effective number of the pertaining generic diversity), for example, one has (see Table 1) $\tau_e(\eta) = (1 - \eta)^{\frac{1}{1-a}}$ and thus $\eta = 1 - \tau_e(\eta)^{1-a}$. Since $\eta_{\min} = 0$, one obtains

$$I_A = \frac{\hat{\eta} - \bar{\eta}}{\hat{\eta}} = \frac{\tau_e(\bar{\eta})^{1-a} - \tau_e(\hat{\eta})^{1-a}}{1 - \tau_e(\hat{\eta})^{1-a}} =$$
$$= \frac{\tau_e(\hat{\eta})^{a-1} - \tau_e(\bar{\eta})^{a-1}}{\tau_e(\bar{\eta})^{a-1} \cdot (\tau_e(\hat{\eta})^{a-1} - 1)} \leq \frac{1}{\tau_e(\bar{\eta})^{a-1}}.$$

The expression after the third equality sign is obtained by multiplication of numerator and denominator by $\tau_e(\bar{\eta})^{a-1} \cdot \tau_e(\hat{\eta})^{a-1}$; the inequality follows from $\tau_e(\bar{\eta}) \geq 1$. Hence, I_A tends to zero as the average effective numbers of types in the communities tends to infinity. This statement does not depend on the degree of differentiation between communities, and it should be considered as a special property of this family of generic diversities.

For the weight function $\omega(p) = p^a$ with $0 \neq a < 1$ (which also yields Rényi diversities), one has (see Table 1) $\tau_e(\eta) = \eta^{\frac{1}{1-a}}$ and thus $\eta = \tau_e(\eta)^{1-a}$. Since now $\eta_{\min} = 1$, one obtains

$$I_A = \frac{\hat{\eta} - \bar{\eta}}{\hat{\eta} - 1} = \frac{\tau_e(\hat{\eta})^{1-a} - \tau_e(\bar{\eta})^{1-a}}{\tau_e(\hat{\eta})^{1-a} - 1}.$$

Consider the special case where $\tau_e(\hat{\eta}) = c \cdot \tau_e(\bar{\eta})$ with constant $c > 1$. Then

$$I_A = \frac{\tau_e(\bar{\eta})^{1-a} \cdot (c^{1-a} - 1)}{(c \cdot \tau_e(\bar{\eta}))^{1-a} - 1} = \frac{c^{1-a} - 1}{c^{1-a} - \tau_e(\bar{\eta})^{a-1}},$$

and this converges to $1 - c^{a-1}$ as $\tau_e(\bar{\eta})$ tends to infinity. Hence, contrasting with the case $a > 1$, for $a < 1$ the index I_A does not tend to zero as $\tau_e(\bar{\eta})$ tends to infinity but can rather realize all values between 0 and 1 depending on c.

On the other hand, when I_A is computed for effective numbers, $\tau_e(\eta)_{\min} = 1$ and

$$I_A = \frac{\tau_e(\hat{\eta}) - \tau_e(\bar{\eta})}{\tau_e(\hat{\eta}) - 1} = 1 - \frac{\tau_e(\bar{\eta}) - 1}{\tau_e(\hat{\eta}) - 1}.$$

As becomes immediately clear from this representation, irrespective of the size of the average effective number $\tau_e(\bar{\eta})$ of types within the communities, I_A may approach 1 arbitrarily closely when imposing an upper bound to $\tau_e(\bar{\eta})$ and letting the total effective number $\tau_e(\hat{\eta})$ increase indefinitely. This can be realized, for example, by ever-increasing the number of communities that show about the same diversities and are strongly differentiated. Yet, in the above example, where I_A is determined for generic diversities, the effective numbers of which are Rényi diversities with parameter $a > 1$, such situations cannot occur.

References

Gadagkar, R.: An undesirable property of Hill's diversity index N2, Oecologia, 80, 140–141, 1989.

Gregorius, H.-R.: On the concept of effective number, Theor. Popul. Biol., 40, 269–283, 1991.

Gregorius, H.-R.: Distribution of variation over communities, Theor. Biosci., 128, 179–189, 2009.

Gregorius, H.-R.: Linking diversity and differentiation, Diversity, 2, 370–394, 2010.

Gregorius, H.-R., Degen, B., and König, A.: Problems in the analysis of genetic differentiation among populations – a case study in *Quercus robur*, Silvae Genet., 56, 190–199, 2007.

Hedrick, P. W.: Perspective: highly variable loci and their interpretation in evolution and conservation, Evolution, 53, 313–318, 1999.

Hill, M. O.: Diversity and evenness: a unifying notation and its consequences, Ecology, 54, 427–432, 1973.

Jost, L.: Entropy and diversity, OIKOS, 113, 363–375, 2006.

Jost, L.: Partitioning diversity into independent alpha and beta components, Ecology, 88, 2427–2439, 2007.

Jost, L.: GST and its relatives do not measure differentiation, Mol. Ecol., 17, 4015–4026, 2008.

Jost, L.: Mismeasuring biological diversity: Response to Hoffmann and Hoffmann (2008), Ecol. Econ., 68, 925–928, 2009.

Lewontin, R. C.: The apportionment of human diversity, Evol. Biol., 6, 381–398, 1972.

MacArthur, R. H.: Patterns of species diversity, Biol. Rev., 40, 510–533, 1965.

Patil, G. P. and Taillie, C.: Diversity as a concept and its measurement, J. Am. Stat. Assoc., 77, 548–567, 1982.

Rényi, A.: On measures of information and entropy. Proceedings of the 4th Berkeley Symposium on Mathematics, Statistics and Probability 1960, 547–561, 1961.

Ricotta, C.: On hierarchical diversity decomposition, J. Veg. Sci., 16, 223–226, 2005.

Simpson, E. H.: Measurement of diversity, Nature, 163, 688, 1949.

Tuomisto, H.: A diversity of beta diversities: straightening up a concept gone awry. Part 1. Defining beta diversity as a function of alpha and gamma diversity, Ecography, 33, 2–22, 2010.

Whittaker, R. H.: Vegetation of the Siskiyou Mountains, Oregon and California, Ecol. Monogr., 30, 279–338, 1960.

Whittaker, R. H.: Evolution and measurement of species diversity, Taxon, 21, 213–251, 1972.