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Effective numbers in the partitioning of biological diversity

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HIGHLIGHTS

- Partitioning (metacommunity) diversity into its alpha- and beta-component must be based on indices of apportionment of diversity.
- Beta-diversity equals the "number of effectively monomorphic communities".
- Differentiation effective numbers of communities exist but are not associated with beta-diversity.
- The dual perspective, where community membership of types is relevant, addresses important aspects of community ecology.
- Diversity can also be partitioned under the dual perspective.

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ABSTRACT

Admissible measures of diversity allow specification of the number of types (species, alleles, etc.) that are "effectively" involved in producing the diversity (the "diversity effective number", also referred to as "true diversity") of a community or population. In metacommunities, effective numbers additionally serve in partitioning the total diversity (symbolized by γ) into one component summarizing the diversity within communities (symbolized by α) and an independent component summarizing the differences between communities (symbolized by β). There is growing consensus that the β-component should be treated in terms of an effective number of "distinct" communities in the metacommunity. Yet, the notion of distinctness is shown in the present paper to remain conceptually ambiguous at least with respect to the diversity within the "distinct" communities.

To overcome this ambiguity and to provide the means for designing further desirable effective numbers, a new approach is taken that involves a generalized concept of effective number. The approach relies on first specifying the distributional characteristics of partitioning diversity among communities (among which are differentiation, where the same types tend to occur in the same communities, and apportionment, where different types tend to occur in different communities), then developing the indices which measure these characteristics, and finally inferring the effective numbers from these indices.

Major results: (1) The β-component reflects apportionment characteristics of metacommunity structure and is quantified by the "apportionment effective number" of communities (number of effectively monomorphic communities). Since differentiation between communities arises only as a side effect of apportionment, the common interpretation of the β-component in terms of differentiation is unwarranted. (2) Multiplicative as well as additive methods of partitioning the total type diversity (γ) involve apportionment effective numbers of communities that are based on different apportionment indices. (3) "Differentiation effective numbers" of communities exist but do not conform with the classical concept of partitioning total type diversity into components within and between communities. (4) Differentiation characteristics are measured as effective numbers of distinct types (rather than communities) from the dual perspective, in which the roles of type and community membership are exchanged. This is relevant e.g. in studies of endemism and competitive exclusion. (5) For Shannon-Wiener diversity, all of the differentiation and apportionment effective numbers are equal, with the exception of those representing additive partitioning. (6) Under either perspective, that is dual or non-dual, measures of compositional differentiation (as originally suggested for the assessment of β-diversity) do not figure in the partitioning of total diversity into components, since they do not build on the intrinsic concept of diversity.

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1. Introduction

One of the probably most frequently recurring topics in community ecology is concerned with the partitioning of total (species, genetic) diversity (i.e. γ-diversity) into components within and between communities (i.e. α- and β-diversity) and how to specify these components (for more recent reviews, see e.g. Jost, 2007; Jurasinski et al., 2009; Tuomisto; 2010). The reviews particularly highlight the various concepts and measures of β-diversity and suggest ways and terminology that helps to distinguish them from each other. It turns out in the reviews that in many if not most cases of dissent, there is no consistent relationship between the measures and the concepts they invoke. This applies in particular to the otherwise apparently broad consent that in the context of partitioning diversity, β-diversity should be specified in terms of an effective number of "distinct" communities.

The conceptual ambiguities probably trace back to the central idea behind almost every effort of partitioning of diversity, which Rao (1982), for example, referred to as the "apportionment of diversity between and within populations", where the "between" component is covered by the notion of β-diversity (here "populations" can be replaced by "communities"). Carrying this view to its extreme of complete apportionment, all "diversity" would occur between communities with the result that there is no diversity within the communities (communities are monomorphic). This includes the possibility that different communities share the same type and are thus not completely differentiated. Apparently, "distinctness" refers here to communities that are monomorphic for different types, so that for complete apportionment the effective number of distinct communities is directly related to the effective number of types in the metacommunity.

This simple consideration seems to confine the notion of β-diversity to equivalents of distinct monomorphic communities. Polymorphic communities, even when completely differentiated, would thus not be appropriate for the description of β-diversity. To illustrate the latter statement consider a species-rich assemblage of communities in which the number of species exceeds by far the number of communities under study (which applies to quite a number of taxa). In this situation it is impossible to have all communities consisting of a single species, so that by the apportionment concept of β diversity the number of effectively distinct communities is expected to be always small. This expectation would include the possibility that all communities are completely differentiated for their species compositions. The problem becomes the more relevant the more traits (especially genetic) are available that can detect cryptic species divergence, since this increases the diversity measures (see e.g. Richards et al., 2016). Similar considerations apply in a population genetic context as discussed by Jost (2008) with reference to highly polymorphic gene markers (which are currently in extensive use). This topic is referred to in more detail in the Concluding remarks.

This clearly is at variance with the common notion of β-diversity as a component that describes the contribution of variation between communities to the total diversity irrespective of the amount of variation within the communities. The validity of the common interpretation of β-diversity, and especially the interpretation as an effective number of "distinct" communities, could therefore be questioned. This asks for more elaboration of the underlying conceptual basis, allowing for the possibility that there are hitherto overlooked effective numbers that are relevant and desirable or are without substance in the partitioning of diversity.

To this end the present paper suggests taking a different approach towards the partitioning of diversity by starting with

- The identification of general structural characteristics of communities and metacommunities that are relevant for the partitioning of diversity (concentration and division approach),
- Then specifying indices (denoted by I) which quantify these characteristics, and
- Inferring effective numbers (denoted by N^e) from these indices in order to retain the structural characteristics assessed by the respective index.

By this it is intended to enhance the interpretation of the common components of diversity (α, β, γ) in terms of effective numbers, to demonstrate how the interpretation accords with or contradicts traditional as well as more recently advocated notions of partitioning diversity, and to enable development of new kinds of effective numbers that address frequent criticism of common methods. The indices relevant in the partitioning of diversity draw from those introduced in Gregorius (2010) and are modified (and the notation changed) to fit the present requirements. The indices rest on the pervasive requirement that the collective variation within communities (or α-diversity) should not exceed the total metacommunity variation (or γ-diversity) and become equal only if there are no differences between communities. This *principle of partitioning diversity* derives from the perception that mixing communities that differ in type composition should result in a gain of diversity (see e.g. Rao, 1982, p.29).

In the present paper the diversity aspect of variation (as detailed in Section 2.1) is focused on. In special cases this may include aspects of the decomposition of variances of type frequencies as treated e.g. by Legendre and De Cáceres (2013). This approach will however not be further pursued in the present paper, since its conceptual idea rests on quantitative rather than qualitative variables, the latter being the proper objects of diversity considerations.

In preparation of the results to be obtained, the following Section 2 is aimed at recalling the individual levels of diversity that determine the theme, defining the problems, and outlining approaches to solving the problems.

2. Preliminary remarks

2.1. Diversity and effective numbers

In ecology, the term diversity commonly refers to the assessment of the heterogeneity existing in a community with respect to a *qualitative* trait (species affiliation, genetic type). In its most elementary form, the assessment takes place by counting the number of trait states found in a community (for the specific use of the term 'trait" as well as further terms to be introduced in the following, see Table 1). This characterizes the intrinsic diversity concept. Its generalization to variable type frequencies or other representations (such as biomass of individuals of a type, or area occupied) rests on the evenness criterion. The criterion requires that whenever the difference in representation between two types decreases without changing the sum of their representations, the measure of diversity never decreases (Gregorius, 2010 with slightly different accentuation, the criterion is also known as the "principle of transfers"; for more details about the purport of this principle within the diversity concept, see Jost, 2009).

As a consequence, for given number of types, diversity attains its maximum only if all types are equally frequent. The evenness criterion thus implies that each measure of diversity can be evaluated as to the number of types that "effectively" give rise to the measure. This number, named the "diversity effective number of types", again obeys the evenness criterion and therefore is a measure of diversity. It is obtained by equating the actual diversity to the diversity obtained for an ideal situation, in which all types are equally frequent, and then solve the equation for the number