



Relating measures of compositional differentiation among communities to conceptual models of migration and selection



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ABSTRACT

Selection and migration are the major deterministic forces that control adaptational processes of differentiation among communities. With the aim of distinguishing between their effects on metacommunity structure, compositional differentiation in metacommunities is viewed from dual perspectives: between communities for their distributions of the types (CDT, the common perspective) and between types for the distribution of their community membership (TDC). A measure of dispersion and four measures that fulfill the basic characteristics of differentiation (maximality for complete difference and minimality in the absence of differences) from both perspectives are introduced and compared. Conceptual modeling of selection and migration (the latter distinguished for its control by descent and type) yields relationships between the values of the measures that, when not fulfilled, lead to rejection of the model. Major results are: measures of dispersion that are not measures of differentiation cannot distinguish between the two perspectives; the commonly held view that type-independent migration homogenizes communities with respect to type distributions is invalid, though it does homogenize types for their community membership; after type-independent migration, differentiation among communities with respect to the source communities of their members bounds differentiation for any other trait; the effects of migration on CDT and TDC cannot always be realized by selection, and vice versa; effective proportions of migration can be obtained from measures of compositional differentiation and number of communities. The last result is based on the general concept of effective variables applied to conceptual models.

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1. Introduction

In a general sense, the term community refers to a set of interacting entities ranging from functional species (ecological community) to conspecific, interbreeding individuals (reproduction community or population). In population genetics and ecology, the analysis of differences in the composition of communities usually aims at the detection of factors that affect community stability. The stability of individual communities is thought to benefit from their organization into a (functional) metacommunity, which acts as a reservoir of adaptive variants that can be exchanged via migration among the communities. The primary determinants of community stability are thus migration between communities and

selection within communities, the latter in a general sense that includes interaction among community members. Since selection and migration alter the composition of communities relative to each other, the proper framework for differentiation studies in stability analysis is the metacommunity. Mutation is of less concern in this respect, since it is not likely to distinguish between individuals and communities, does not become effective within adaptationally relevant time spans, and therefore is first of all involved in shaping the overall genetic diversity in the metacommunity rather than non-random differences between communities.

From this perspective, interpretation of observed differences in trait distribution between the communities of a metacommunity chiefly involves assessment of the contributions of selection and migration as adaptationally relevant deterministic factors on the one hand and purely random events on the other (for an ecologically oriented review see e.g. Hillebrand et al., 2008; for an attempt to cover both ecological and reproduction communities with emphasis on migration see Economo and Keitt, 2008). The standard procedure of assessment is to test the (null-)hypothesis

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of pure randomness with the help of permutation analysis. Rejection of the hypothesis is followed by model-supported reasoning of the potential contributions of each of the two deterministic factors.

First and foremost, the measurement of differences between two communities quantifies differences in the frequencies of the types (alleles, genotypes, species) they contain. This can be addressed as their compositional difference. To become measures of compositional differentiation among two or more communities, difference measures are required at a minimum to be bounded and to reach the upper bound only if communities share no types and are thus completely distinct (*distinctness criterion*). Yet in both ecology and population genetics, it is common practice to instead rely on approaches that invoke either diversity measures or probabilities of gene identity that violate this criterion.

In ecology, the concept of β -diversity (Whittaker, 1960) has several representations that address differences between species communities in terms of the total diversity of the metacommunity (or γ -diversity) and some kind of average diversity within communities (or α -diversity; see Jost, 2007, or Gregorius, 2010). In essence, this concept relies on the idea that total diversity (γ) can be partitioned into independent components of diversity within (α) and between (β) communities (see Jost, 2007 for a more rigorous treatment).

The widely used population genetic analogue of this partitioning is based on allelic diversities and quantified using the measure F_{ST} and its relatives (for an overview see Charlesworth, 1998). These measures were initially derived in terms of probabilities of gene identity (Nei, 1973). Yet, due to their normalizations, F_{ST} and relatives are not measures of compositional differentiation, since they assume their maximum value of 1 only for monomorphic (genetically fixed) populations (see e.g. Wright, 1978, p. 82; Gregorius and Roberds, 1986; Hedrick, 2005; Jost, 2008) rather than for populations that do not share alleles. However, in analogy to the ecological approach of partitioning total diversity into its within- and between-population components, it was shown by Jost (2008) that probabilities of gene identity can be used to arrive at a measure D that meets the distinctness criterion of a compositional differentiation measure.

Much of the appeal of F_{ST} and relatives as well as Jost's measure D is due to the fact that probabilities of gene identity can be readily used to analyze and characterize specific models of genetic drift combined with migration and mutation (see e.g. Rousset, 2004 or Jost, 2008). Computation of these measures from data obtained from collections of populations allows indirect estimation of important model parameters (such as the expected number of migrants per generation). Usually, these estimates cannot be obtained directly, which makes their relevance critically depend on the validity of the model. If testing were performed, rejection of the model (if experimentally feasible) would in fact imply that the parametrization of the model is inappropriate or that even other evolutionary forces involving selection are acting, thus invalidating the indirect estimates of the model parameters. The issue of indirect estimation will be taken up in more detail.

In order to establish useful relationships between measures of compositional differentiation and models of the adaptational processes that take place in metacommunities, two basic perspectives are helpful (Gregorius, 2009): (a) Organisms become differentially adapted to community habitats, where habitat characteristics determine the types that are allowed to thrive and by this may cause communities to become differentiated for types, and (b) organisms show differential disposition to stay in or migrate to special habitats, with the result that types are differentiated for the communities in which they dwell after migration or dispersal. This implies that differences and differentiation should be viewed from dual perspectives: (a) communities differ for their trait (type) distributions (CDT) or (b) trait states (types) differ for their community

memberships (TDC) (see glossary of terms in Appendix G). The absence of differences from one perspective implies their absence from the other perspective. At the other extreme, complete differentiation among communities for their trait distributions (CDT) is equivalent to specialization of each type to a single community (which may contain more than one type), while complete differentiation among types for community memberships (TDC) is equivalent to monomorphy of types in each community (more than one of which may be fixed for the same trait). It is interesting that F_{ST} and its relatives can be consistently regarded as measures of diversity-oriented differentiation among types (TDC), which is the antithesis of its usual interpretation as differentiation among populations (CDT) (Gregorius, 2010).

As a rule, forces that generate CDT and forces generating TDC can be expected to act together in shaping the distribution of types over communities, though to different degrees. Probably in the majority of plants, it is unlikely that particular phenotypic or genetic traits have direct effects on where their seed and pollen are dispersed (though indirect effects may result from preferences of animal vectors). In plants with wind-dispersed seeds, for example, the locations at which seed is found after dispersal can be expected to depend on where it was produced rather than on special traits of the parents or the seed itself. Consequently, CDT is suspected to be stronger than TDC for most plant traits. On the other hand, mobile organisms and particularly many animals are able to choose their locations of residence according to special preferences. TDC may therefore exceed CDT in these organisms.

The present paper explores the above aspects of difference and differentiation in metacommunities, with emphasis on ways to measure differentiation. For two reasons, the conceptual focus lies on the compositional approach to the measurement of differentiation (see Appendix G). One is that because the compositional approach is not based on diversity measurement, it avoids the ongoing debate on how to partition diversity so that it measures differentiation (for a recent demonstration see Chao et al., 2012). The other is our aim to directly relate models of adaptational processes to their primary effects on the composition of metacommunities. Recalling elementary characteristics of the major adaptational processes and presenting them as conceptual models, i.e., as formalizations of the semantic foundation of these processes, we demonstrate their effects on compositional differentiation under both the CDT and the TDC perspectives. The usage of conceptual models allows us to infer general relationships between model parameters, especially those relating to migration, and the compositional differentiation measures. It is pointed out that these relationships should be understood to yield effective values of the parameters rather than indirect estimates (see Appendix G).

2. Measures of difference between communities

Any characterization of differences between communities records the frequencies of the states of a trait of interest, however complex, among the members of each community. The compositional approach refers to the conception of community differences in its most straightforward form as differences in type frequencies among communities. To avoid unnecessary specialization and restriction of conclusions, the following considerations are based on differences of untransformed frequencies. Applying the notation in Table 1, this focuses on the sum of frequency differences between communities for each type, i.e. $\sum_t |P(T=t|C=x) - P(T=t|C=y)|$, where x and y represent two communities and the summation index t specifies summation over all types. One-half of this sum specifies the classical distance measure between two communities that assumes a value of 1 exactly if two communities share no types (i.e., are completely differentiated; see e.g. Whittaker, 1960,

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