Classifying measures of biological variation

– Phenotypic variation is the raw material on which selection acts –
The heritability of this variation decides on
the evolutionarily adaptive significance of the selection process

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Trait variation is determined by the genetic units (genotypes, populations, species)
and by the environmental conditions that participate in trait expression

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Discrete patterns of variation form when
modifying effects of the environment are small (narrow norms of reaction)
and differences between genetic units become more distinct (high heritability)

Patterns of variation are therefore basically characterized by
▷ the overall dispersion or spread of the trait
▷ the diversity in terms of the number of distinguishable clusters of trait states

Perception of variation means perception of differences. Measures of difference should therefore guide attempts to classify measures of variation.

Difference measures

Dispersion

Diversity

Differentiation

Partitioning of variation

- division of variation among communities
- partitioning of total diversity into components within and between communities
- identity probabilities

Duality of differentiation

Difference measures

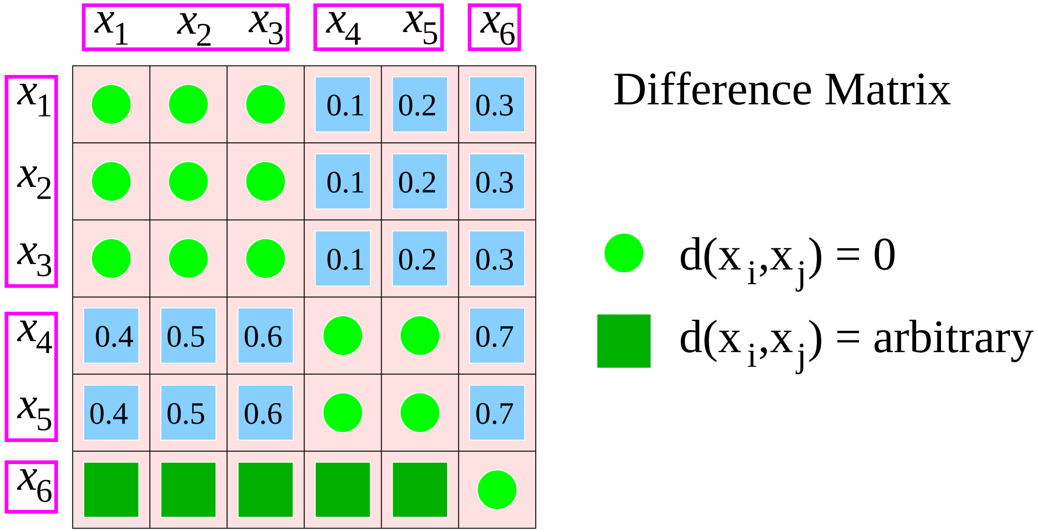
Difference measures

Criteria: (a) $d(x, y) \geq 0$

(b) $d(x, x) = 0$

(c) $d(x, y) = 0$ implies $d(x, z) = d(y, z)$ for all z

$d(x, y) = 0$ implies $d(y, x) = 0$ by criterion (c); $d(x, y)$ is not required to be symmetric*.



* think of behavioral differences that are not reciprocal, for example

Difference measures

The primary partition $\rightarrow$

Let $\sim$ be a relation defined by $x \sim y$ if $d(x, y) = 0$.

- $\sim$ is reflexive, symmetric, and transitive; it is an equivalence relation
- The equivalence classes establish a partition of the community named the primary partition generated by the difference measure d
- The primary partition represents a trait with states (types) specified by the classes of the partition.

Difference measures

- Bounded difference measures are called dissimilarity measures; maximum difference is identified with complete distinctness.
  - ▷ Dissimilarity measures that assume only two values (usually zero and one) are called discrete metrics. The term binary difference measure is preferred if the upper bound can assume any positive but fixed value (the "contrast").
    Qualitative traits can be characterized by discrete metrics.

Dispersion

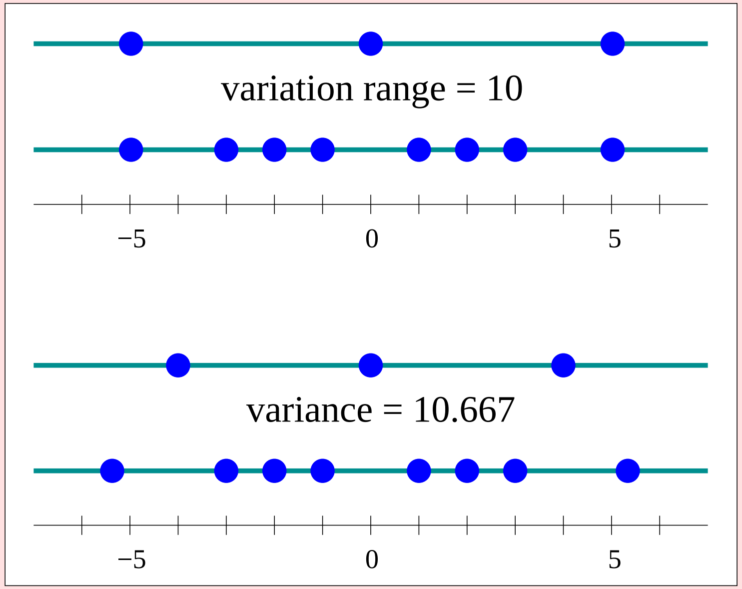
Dispersion

Objective: Assess the extent to which community members differ from each other.

- Dispersion measures provide the appropriate means;
  - ▷ they are non-negative functions of type frequencies and type differences and are zero only if all differences are zero;
  - ▷ they do not decrease as differences increase.
  - ▷ they increase strictly with increasing upper bounds of binary differences.
- Dispersion effective difference
  - ▷ equals the upper bound (contrast) of a binary difference measure that, given the observed type frequencies, generates the same dispersion as the observed dispersion.

Dispersion

- Maximum differences and various kinds of average differences among community members are typical examples of dispersion measures. Numbers of types (or equivalence classes) do not explicitly enter the measurement of dispersion.



The classics are $\max_{i,j} d_{i,j}$ and $\sum_{i,j} p_i \cdot p_j \cdot d_{i,j}$

The dispersion effective differences are
$\max_{i,j} d_{i,j}$ and $\sum_{i,j} p_i \cdot p_j \cdot d_{i,j} / (1 - \sum_i p_i^2)$

Dispersion

Effective numbers?

- Types are provided by the classes of the primary partition generated by the difference measure. This justifies consideration of numbers of types in dispersion studies.
- The range over which community members vary can be viewed to be spanned by the types specified through the primary partition; it is therefore meaningful under certain conditions to require that dispersion should increase with number of types.
- To enable unambiguous counting of types, unit differences between them (binary differences) and equal frequencies must be realized. Under this premise
  - ▷ dispersion is required to strictly increase with number of types for each binary difference measure (the "number-characteristic" of dispersion measures).

Dispersion

- Determination of an effective number of types requires definition of ideal communities,
  (a) which realize all dispersion values occurring among the (non-ideal) communities under consideration,
  (b) in which the differences between types do not vary (binary differences),
  (c) in which all types are equally frequent, and
  (d) in which the measure of dispersion strictly increases with the number of types.

$\Rightarrow$ The effective number results from equating an observed dispersion with the dispersion of an ideal community with specified binary difference measure and solving for the number of types in the latter. Since the number refers to dispersion characteristics it is termed dispersion effective number of types.

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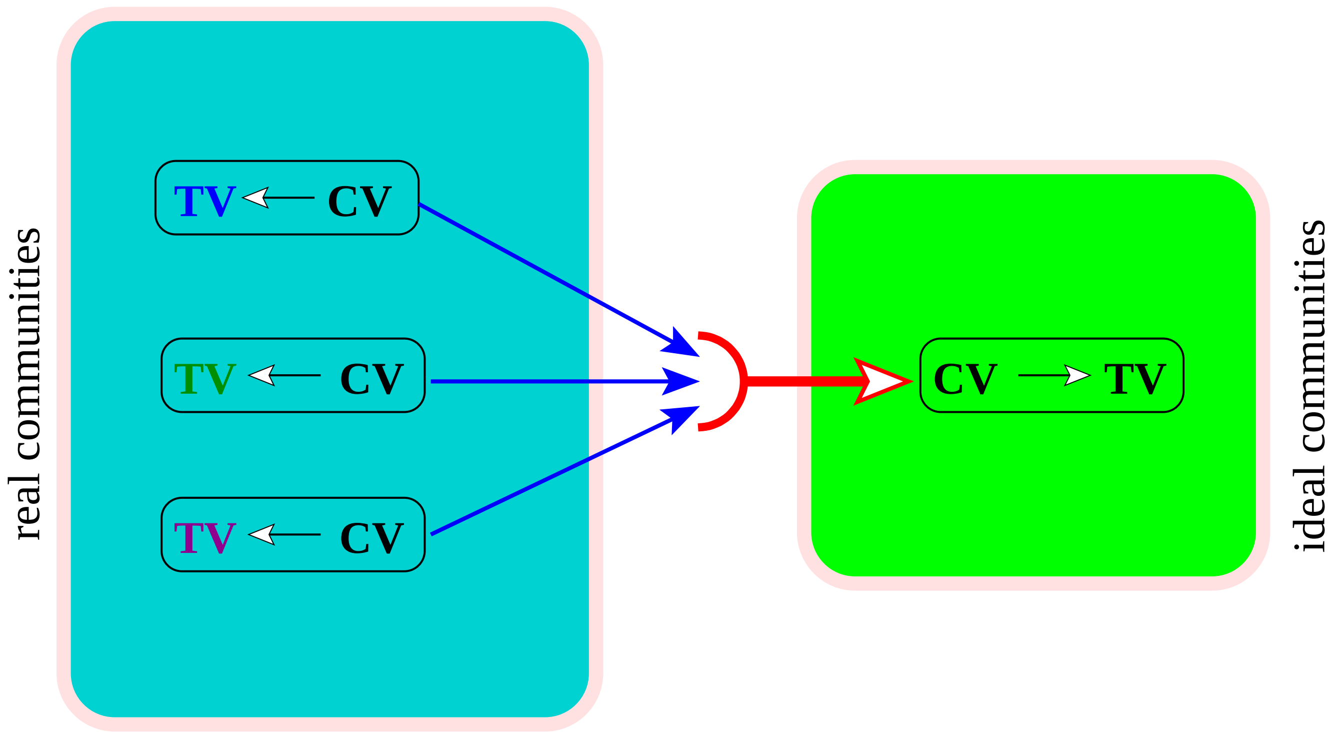
Dispersion

The concept of effective variables



CV = characteristic variable of a community (dispersion, diversity)
TV = target variable of a community (number of types)

Dispersion

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- ▷ **The dispersion effective number of types depends on the chosen binary difference measure: the number decreases strictly with increasing upper bound (contrast) of the binary difference.**

Dispersion

- Replacement of dissimilarities by their complements, i.e. similarities, converts measures of dispersion into measures of concentration.
  - ▷ The procedure leading to the definition of the dispersion effective number applies identically to similarities and thus to the definition of the concentration effective number.

Dispersion

Examples

dissimilarity measure $0 \leq d_{i,j} \leq 1$, similarity measure $s_{i,j} = 1 - d_{i,j}$
$p_i :=$ type frequencies, $n :=$ number of types

- **dispersion measure** $\bar{d} := \sum_{i,j} p_i \cdot p_j \cdot d_{i,j}$

  For complete dissimilarity $\bar{d}_{ideal} = 1 - n^{-1} \Rightarrow$ **dispersion effective number*** $= (1 - \bar{d})^{-1}$

- **concentration measure** ${}^aC := \left(\sum_i p_i \cdot \left(\sum_j s_{i,j} \cdot p_j \right)^{a-1} \right)^{\frac{1}{a-1}}$ $(0 \leq a \neq 1)$

  For complete dissimilarity ${}^aC_{ideal} = n^{-1} \Rightarrow$ **concentration effective number**** $= {}^aC^{-1}$

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* Ricotta & Szeidl, 2009, doi:10.1016/j.tpb.2009.10.001
** Leinster & Cobbold, 2012, doi:10.1890/10-2402.1

Dispersion

Examples

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- An effective number does not exist for the following measures of dispersion, since they do not fulfill requirement (d) $\rightarrow$

  ▷ $\max_{i,j} d_{i,j}$

  ▷ $\sum_i p_i \cdot \left(\sum_{j:j\neq i} p_j \cdot d_{i,j}/(1-p_i)\right)$

  ▷ $\sum_{i\neq j} p_i \cdot p_j \cdot d_{i,j}/(1-\sum_i p_i^2)$

Dispersion

Summary

- ♣ Measures of dispersion summarize differences between objects without explicit reference to numbers of types.
- ♣ Numbers of types enter the assessment of dispersion via the primary partition.
- ♣ Effective numbers of types are defined only for dispersion measures that increase strictly with number of types when applied to binary differences and equally frequent types.
- ♣ Not all dispersion measures have effective numbers.

Diversity

Diversity

Objective: Determine the variability of a community on the basis of its number of types (the intrinsic diversity concept).

- Counting types is unambiguous in the ideal situation of equal differences and equal representations among types $\Rightarrow$ uniform distribution of the primary partition generated by a discrete metric.

  - ▷ In this ideal situation, measures of diversity are non-negative and strictly increasing functions of the number of classes in the primary partition.

  - ▷ Non-uniform distributions: measures of diversity become non-negative functions of sets of positive values (representations) summing to one; variable representations of types are provided for by fulfillment of the evenness criterion*.

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* diversity never decreases as the difference in representation between two types decreases while the sum of their representations remains the same – measures of evenness characterize the *form of frequency profiles*, they are not measures of variation

Diversity

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▷ Types (classes of partitions) are represented by non-negative numbers that can specify e.g. ⋄ the number of community members showing a type, ⋄ the area occupied by carriers of a type, ⋄ the total biomass of the carriers of a type, ⋄ the average similarity of a type to all community members*. All of these enter the measurement of diversity after normalization by their sums.

▷ An effective number of types can be determined following the procedure described for dispersion measures and applying the same specification of ideal communities (substituting dispersion by diversity). This results in a diversity effective number of types. Diversity effective numbers are diversity measures.

* termed "relative abundance of species similar to the i-th", $\sum_j s_{ij} \cdot p_j$, in Leinster & Cobbold, 2012, doi:10.1890/10-2402.1

Diversity

Examples

$p_i :=$ relative representation of the i-th type (only $p_i > 0$ considered)

diversity measure	diversity effective number	
$1 - \sum_i p_i^a$, $a > 1$	$\left(\sum_i p_i^a\right)^{\frac{1}{1-a}}$	(Rényi diversity* of order a)
$\sum_i p_i^a$, $0 \leq a < 1$	$\left(\sum_i p_i^a\right)^{\frac{1}{1-a}}$	"
$-\sum_i p_i \cdot \log p_i$	$\prod_i p_i^{-p_i}$	(Rényi diversity of order $a = 1$)

* also called Hill numbers; Hill gave credit to Rényi

Diversity

- Variable differences – Adherence to the intrinsic diversity concept entails relating differences to partitions ⇒ combination of the classes of the primary partition forms hierarchically organized higher order partitions referring to higher orders of difference.
  - ▷ Higher order partitions typically result from application of clustering methods to the difference measure under consideration.
  - ▷ Each clustering level gives rise to a partition the diversity of which can be determined. Clustering levels can be considered as levels of resolution*.
  - ▷ Plotting the diversity of each partition against its corresponding clustering level, one obtains diversity portraits in the form of decreasing step functions.

* with higher resolution going along with finer partitions

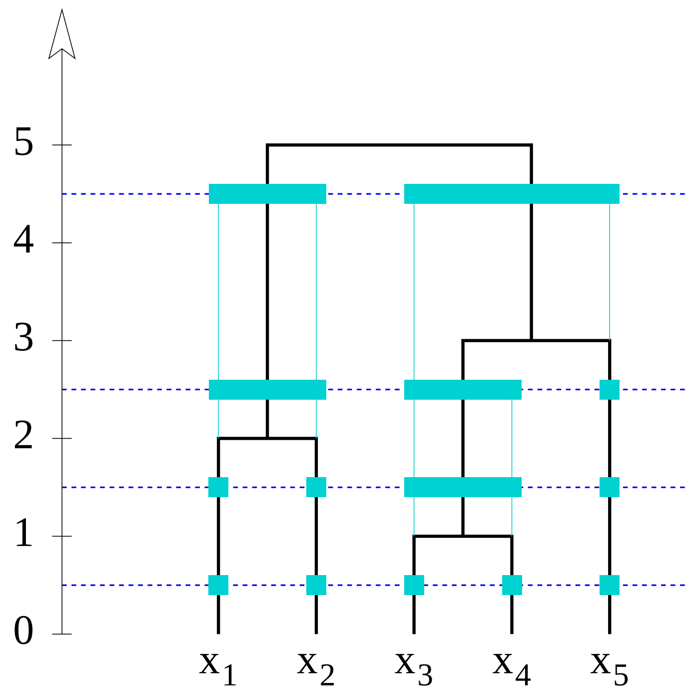
Diversity

Example

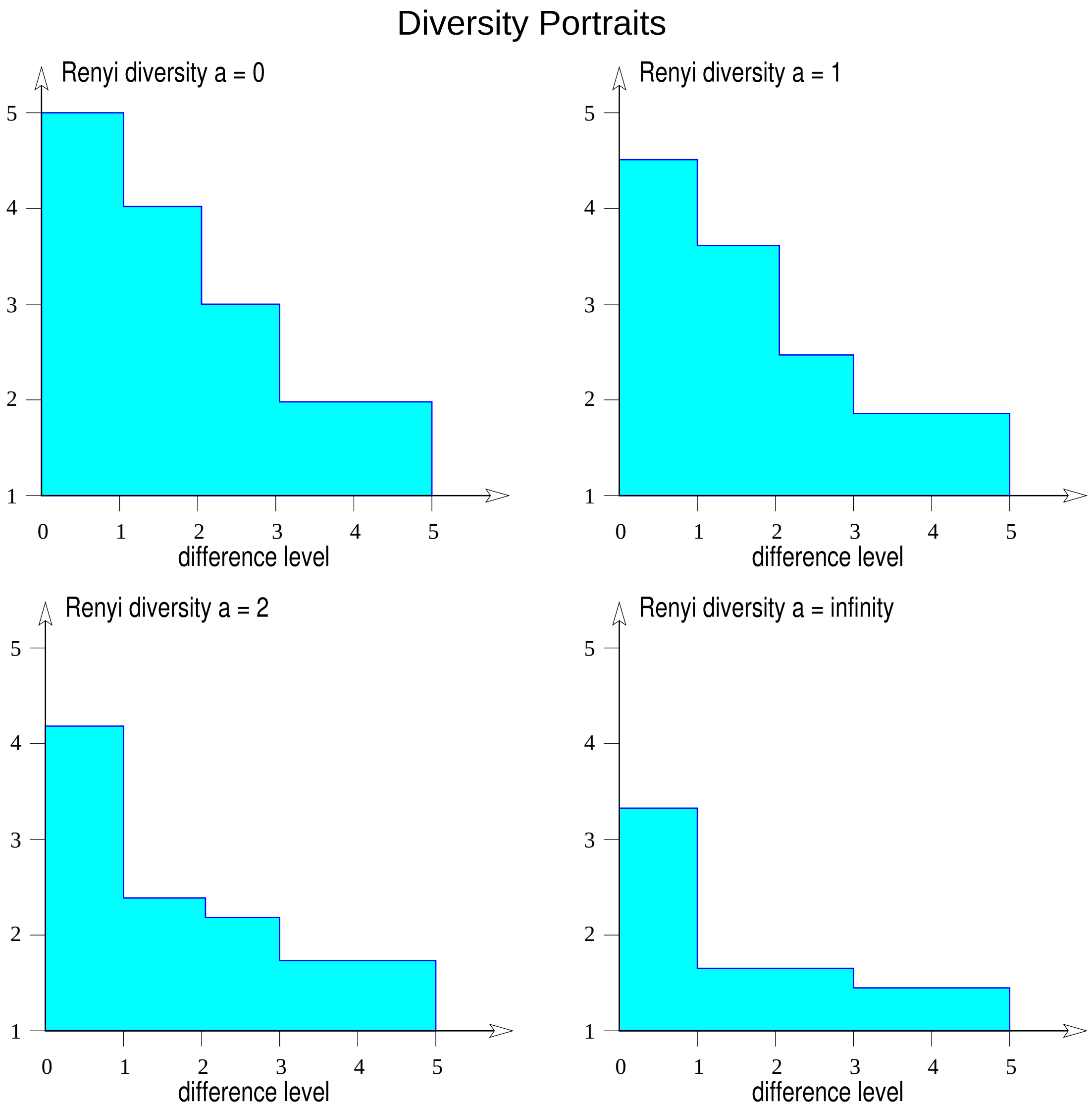
G-clustering of five types yielding three hierarchically organized higher order partitions in addition to the primary partition.

differences

types	x_1	x_2	x_3	x_4	x_5	freq
x_1	0	2	5	4	4	10
x_2	2	0	4	4	5	20
x_3	5	4	0	1	3	30
x_4	4	4	1	0	2	30
x_5	4	5	3	2	0	10



Diversity



Diversity Portraits
Renyi diversity a = 0
Renyi diversity a = 1
Renyi diversity a = 2
Renyi diversity a = infinity
1
2
3
4
5
0
1
2
3
4
5
difference level

Diversity

Conceptual problem: Considering the classes of a partition as distinct types is questionable since levels of distinctness among classes may vary and since the intrinsic diversity concept is built on qualitative traits and thus on equally distinct types.

Instead of partitioning variation into classes it may be meaningful to consider variable differences and frequencies as part of the type representation (such as the average similarity of a type to all community members). However, this awaits conceptual substantiation.

Diversity

Connecting diversity to dispersion –

The number-characteristic of dispersion measures can be extended to require that the evenness criterion is realized for binary difference measures. Such dispersion measures are termed diversity-compatible.

Example: $\left[\sum_i p_i \cdot \left(\sum_j d_{ij} \cdot p_j\right)^a\right]^{1/a}$ for $a \leq 3$ and $a \neq 0$.

For binary difference measure with contrast d: $d \cdot [\sum_i p_i \cdot (1 - p_i)^a]^{1/a}$

Diversity

Summary

♣ The intrinsic diversity concept rests on discretizable and countable units of perception. The units combine to form a partition of the community.

♣ Variable frequencies are taken into account by the evenness criterion.

♣ Variable differences can be considered via hierarchically organized partitions that relate to difference levels.
Yet, variable distinctness between the classes of partitions raises a conceptual problem.

♣ Diversity effective numbers link general diversity measures to the intrinsic diversity concept.

♣ The conceptual connection between diversity effective numbers and dispersion effective numbers is provided by diversity-compatible dispersions.

Differentiation

Differentiation

Objective: Determine the dissimilarity among the communities that make up a metacommunity.

- Differentiation involves two tiers of difference, ⋄ differences between individual members of the metacommunity and ⋄ differences between communities. Both enter the assessment of differentiation in terms of dissimilarities.

Differentiation

- There are at least two ways of conceiving metacommunity differentiation,
  - ◇ as dispersive differentiation, where the focus is on the dispersion among communities, and
  - ◇ as complementary differentiation, where the focus is on the unshared (complementary) contributions of each community to the metacommunity.

▷ To become a differentiation measure of a metacommunity, it is required that the respective measure

(i) is bounded and assumes its maximum only if all communities are mutually completely dissimilar, and

(ii) does not decrease with increasing trait resolution.*

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* Let d and d' be two difference measures defined on the same community, and let T and T' be the two traits generated by the difference measures. Then difference d' (and thus trait T') represents an increased resolution of difference d (and thus of trait T), if for any two members μ_1 and μ_2 of the community $d'(\mu_1, \mu_2) \geq d(\mu_1, \mu_2)$ with strict inequality for at least one pair of members.

Differentiation

- Minimum differentiation – Basically, the dissimilarity between two communities can be assessed by the amount of change required in the trait distribution of one community to match the trait distribution of the other.
  - ▷ Changes consist of a frequency shift between types weighted by their dissimilarities. Given a quantification of frequency shifts, minimization of changes leads to a unique measure of differentiation.

Differentiation

Example

For discrete metrics and a metacommunity consisting of two communities, a measure of minimum differentiation used in many fields is

$$\frac{1}{2}\sum_i |p_i - q_i|$$

where p_i is the relative representation of the i-th class of the primary partition of the metacommunity in one community, and q_i is the analogous representation in the other community.

Differentiation

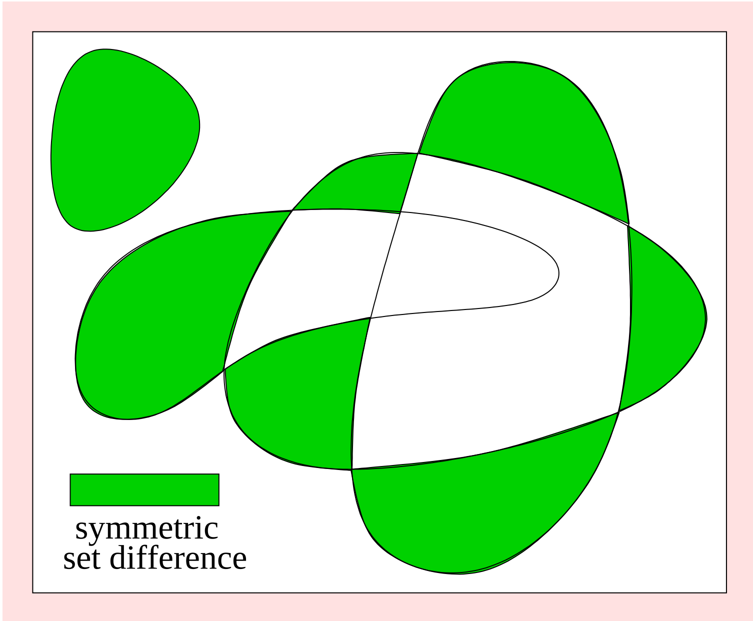
- **Multiple communities – Metacommunity differentiation must reflect the dissimilarities between its constituent communities.**

▷ Among the various approaches, the complementarity approach relies on the symmetric (multiple) set difference. The set difference summarizes the uniqueness of each community for its trait distribution. The corresponding measure becomes

$$\Delta_{SD} = \sum_x P(C = x) \cdot \Delta(C = x, C \neq x).$$

In this expression $P(C = x)$ denotes the relative representation of community x, and

$$\Delta(C = x, C \neq x)$$



denotes the differentiation of community x from the remainder $(C \neq x)$ of the metacommunity. In particular, $\Delta(C = x, C \neq x)$ may quantify the minimum amount of change required in the trait distribution of community x to match the trait distribution in the remainder.

Differentiation

- **Differentiation levels – Consider the primary partition and the higher order partitions obtainable from application of an appropriate clustering method to the metacommunity** → partitions correspond to difference levels obtained from the clustering method → type distributions within communities result from intersection of the partition classes with the communities.
  - ▷ **For each partition the differentiation of the metacommunity can be determined.***
  - ▷ **The differentiation measure quantifies the degree to which the partition separates the communities.**
  - ▷ **Plotting the differentiation obtained for each partition against its corresponding difference levels, one obtains a differentiation portrait******.**

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* where the differentiation measure can be based on the discrete metric associated with the partition, or it can be chosen to consider variable differences via the minimum differentiation created by the partition
** corresponding to the diversity portrait

Differentiation

Summary

♣ Differentiation measures quantify dissimilarities between communities with respect to type frequencies and type differences. They reach a maximum only for complete distinctness among communities.

♣ For metacommunities consisting of multiple communities, differentiation can be conceived of in two ways: ⋄ dispersion between communities and ⋄ uniqueness of communities.

♣ For variable differences between types, differentiation can be considered at various levels of difference.

♣ Effective numbers and diversities are not at issue in the above concept of differentiation.*

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* to emphasize the fact that only differences in type frequencies between communities are considered, the term compositional differentiation is occasionally used in this context.

Partitioning of variation

Partitioning of variation

Objective: Determine degrees to which the total variation in a metacommunity is divided (partitioned) among the communities.

Principles of partitioning

(i) specify tendencies of individuals of the same type to occur in the same community (concentration principle) versus

(ii) tendencies of individuals of different type to occur in different communities (division principle).

▷ Complete concentration is reached if communities are completely differentiated (share no types).

▷ Complete division is reached if each community consists of one type (monomorphism, fixation).

▷ The absence of any of the two tendencies indicates identity in type composition among the communities (absence of differentiation).

Partitioning of variation

Implications of the concentration principle for diversity →

- With increasing concentration, communities share ever fewer individuals of the same type and finally become completely distinct for their type distributions.
- Keeping the marginal distributions of types and community membership constant during this process, one expects both the average number of types per community and the number of type-community combinations to decrease with increasing concentration.

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Partitioning of variation

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- According to common perceptions, merging differentiated communities into a metacommunity should result in an excess of diversity over the diversity within communities. Only identity in composition among the communities (absence of differentiation) results in zero excess.
  - ▷ Conceptually consistent measures of diversity within communities are well-defined for the generalized notion of diversity measures.*
  - ▷ In community-ecology, the symbols γ and α are used for metacommunity-diversity and diversity within communities ($\alpha \leq \gamma$); a third component, termed β-diversity is addressed as “diversity between communities”, but is not directly associated with differentiation between communities.

- Measures of concentration of type-diversity to communities are termed measures of diversity-oriented differentiation.

* Gregorius, 2014, doi:10.5194/we-14-51-2014

Partitioning of variation

Examples

Two kinds of measures of concentration of type-diversity to communities (diversity-oriented measures of differentiation)

$$D_m := \frac{v_T - v_{T|C}}{v_{TC} - v_{T|C}} \quad \text{and} \quad D'_m := \frac{1 - v_{T|C}/v_T}{1 - v_{T|C}/v_{TC}}$$

where $v_T :=$ metacommunity diversity (for trait T, γ-diversity),
$v_{T|C} :=$ trait diversity within communities (α-diversity),
$v_{TC} :=$ joint diversity of trait and community membership.

When applied to Rényi-diversities for equal community sizes (in which case $v_{TC} = v_{T|C} \cdot v_T$), D'_m becomes Jost's* D, and D_m becomes Jost's** generalization of the "turnover rate per sample".

* Jost, 2008, doi:10.1111/j.1365-294X.2008.03887.x, eq. 10
** Jost, 2007, doi: 10.1890/06-1736.1, eq. 25

Partitioning of variation

Implications of the division principle for diversity (apportionment) $\rightarrow$

- With increasing division of type variation among communities the number of different types decreases in each community until each community is dominated by a single type.
  - ▷ Measures of apportionment of diversity therefore focus on the diversity within communities.

Partitioning of variation

Examples

Two kinds of measures of division (apportionment) of type diversity among communities*

$$F_p = \frac{v_T - v_{T|C}}{v_T - v_{min}} \quad \text{and} \quad F_p' = \frac{F_p}{v_{T|C}^e} = \frac{(v_T^e / v_{T|C}^e) - 1}{v_T^e - 1}$$

v_T^e := diversity effective number of v_T

$v_{T|C}^e$:= diversity effective number of $v_{T|C}$ (effective number of types within communities)

v_{min} := value of the diversity measure v for monomorphism (equals 1 for the diversity-effective numbers v^e)

* Gregorius, 2010, doi:10.3390/d2030370

Partitioning of variation

In community ecology:

- More recently β-diversity is agreed to be specified as an effective number of communities based on their type distributions.
  - ▷ Reference to β-diversity as an effective number of "distinct" communities is questionable.
  - ▷ The apportionment principle as quantified by F_p and F'_p provides more direct access, with effective numbers of communities resulting as $v_T^e / v_{T|C}^e$ and $v_T^e - v_{T|C}^e + 1$, respectively. These reflect the common multiplicative and additive versions of β-diversity.
  - ▷ β-diversity thus presents itself as an "apportionment effective number of communities" or more explicitely as a number of effectively monomorphic communities.*

* Gregorius, 2016, doi:10.1016/j.jtbi.2016.08.037

Partitioning of variation

In population genetics:

The most common measure of genetic diversity is Simpson's index $v = 1 - \sum_i p_i^2$ with diversity effective number $v^e = 1/\sum_i p_i^2$, where p_i equals the relative frequency of the i-th allele or some more complex genetic type.

For p_{ij} := frequency of the i-th genetic type in the j-th population ($\sum_i p_{ij} = 1$), p_i := frequency of the i-th genetic type in the metapopulation, c_j := relative size of the j-th population, one obtains $v_T = 1 - \sum_i p_i^2$, $v_{T|C} = \sum_j c_j \cdot (1 - \sum_i p_{ij}^2)$.

▷ In this case, either for F_p applied to Simpson's index, or F'_p applied to the effective number of the index, one obtains

$$G_{ST} = \frac{\sum_j c_j \cdot \sum_i p_{ij}^2 - \sum_i p_i^2}{1 - \sum_i p_i^2}$$

⇒ G_{ST} measures apportionment of genetic diversity but not differentiation.

Partitioning of variation

Combined apportionment and differentiation* $\rightarrow$

- Differentiation or apportionment
  - ▷ No distinction is made between concentration and division tendencies towards the extreme where either complete concentration (differentiation) or complete division (monomorphism) is reached:

$$F_p^* = \frac{F_p}{\tilde{F}_p} \qquad F_p'^* = \frac{F_p'}{\tilde{F}_p'}$$

where $\tilde{F}_p = [v_{TC} - v_{T|C}]/[v_{TC} - v_{min}]$ and $\tilde{F}_p' = [v^e_{TC} - v^e_{T|C}]/[v^e_{T|C}(v^e_{TC} - 1)]$

Population genetics: Applying $F_p'^*$ to the "effective number of alleles" $1/\sum_i p_i^2$ as measure of diversity yields the measure G'_{ST} of PW Hedrick (Evolution, 59(8); 1633-1638, 2005). >>>>

* Gregorius, 2016, doi:10.1016/j.jtbi.2016.08.037

Partitioning of variation

$>>>>$

- Differentiation and apportionment
  - ▷ Both tendencies, concentration and division, are realized simultaneously, with the extreme reached for both complete concentration (differentiation) and complete division (monomorphism):

$$F_p^\circ = \frac{v_T - v_{T|C}}{v_{TC} - v_{min}} \qquad F_p'^\circ = F_p^\circ \cdot \frac{v_{TC}}{v_T}$$

Partitioning of variation

Identity probabilities

- One of the most frequently taken approaches to partitioning variation uses probabilities of sampling two individuals of identical or different type. G_{ST} is one example. Measures of diversity are not explicitly involved.
  - ▷ Applying explicit sampling within and between communities with P_T, P_W and P_B as probabilities of sampling individuals of different type in the metacommunity, within communities, and between communities, one arrives at

$$G_{ST} = \frac{P_T - P_W}{P_T} \quad \text{and} \quad D_{ST} = \frac{P_T - P_W}{P_T - P_W + 1 - P_B}$$

    as measures of apportionment and differentiation, respectively.
  - ▷ G_{ST} and D_{ST} can be used to assess the share that division and concentration tendencies have in the partitioning of variation:

    $G_{ST} > D_{ST}$ if division tendencies outperform concentration tendencies.

Partitioning of variation

- When differences between types vary, partitioning of variation is possible, provided the differences are dissimilarities (bounded from above by 1), and the matrix of dissimilarities is conditionally negative definite. (Gregorius, 2014, doi:10.1007/s12080-014-0220-1)

  ▷ Under this premise, the previous probabilities of sampling explicitely within and between communities are replaced by their corresponding average dissimilarities: $P_T \to E_T$ (average dissimilarity in the metacommunity), $P_W \to E_W$ (average dissimilarity within communities), and $P_B \to E_B$ (average dissimilarity between communities)

$$G_{ST}^{\circ} = \frac{E_T - E_W}{E_T} \quad \text{and} \quad D_{ST}^{\circ} = \frac{E_T - E_W}{E_T - E_W + 1 - E_B}$$

  are the corresponding measures of apportionment and differentiation, respectively. The interpretations in terms of division and concentration tendencies remain the same.

Summary

- ♣ Partitioning of diversity chiefly follows two principles of distributing type variation over communities: (a) concentration of carriers of the same type in the same community (differentiation), and (b) division of different types between communities (apportionment); combinations of these principles are yet poorly studied.
- ♣ Partitioning in the common sense of division of variation among communities cannot be used for an assessment of differentiation between them (confusing apportionment with differentiation).
- ♣ Measures of β-diversity rely on the division principle. When expressed as effective numbers of communities, they address the number of effectively monomorphic rather than the number of effectively distinct communities.
- ♣ Partitioning of identity probabilities obtained from explicit sampling within and between communities allow ranking of division and concentration tendencies on the basis of measures of apportionment and differentiation.

The dual perspective of variation

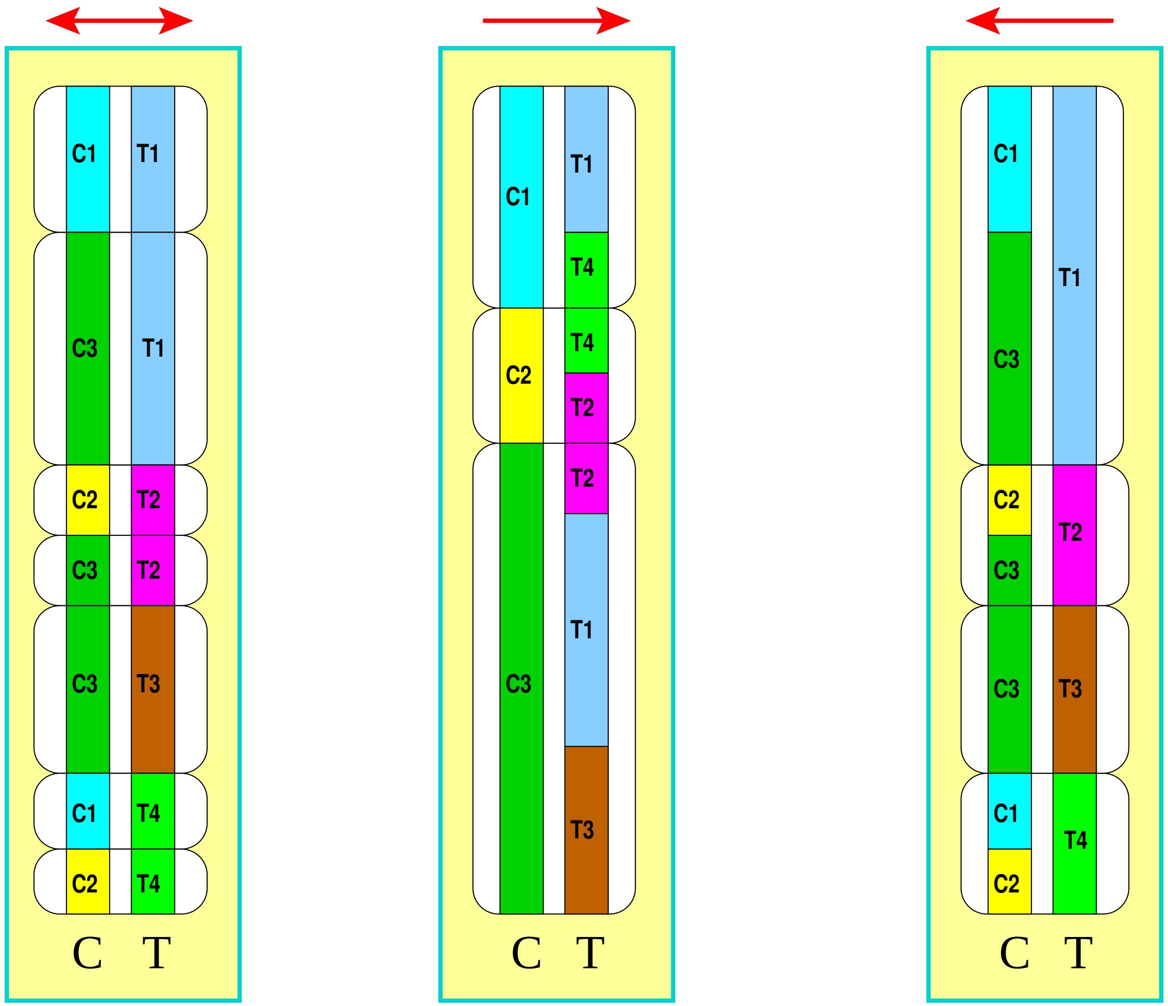
The dual perspective of variation

Perspective: Just as communities may differ for the trait states of their members (CDT) may trait states differ for the community membership of their carriers (TDC).

▷ TDC is the dual perspective of CDT and vice versa.

⇒ TDC is relevant e.g. in studies on the adaptational versatility of genotypes or species (e.g. specialists vs. generalists, habitat selection):
CDT = communities determine on which type to accept,
TDC = types determine in which community to settle.

The dual perspective of variation



joint distribution of trait state and community membership

communities differentiated for trait states (CDT)

trait states differentiated for community memberships (TDC)

The dual perspective of variation

- **All of the above considerations on (compositional) differentiation and partitioning of variation can be applied to TDC by swapping trait state (type) with community membership. In particular, the concentration and division principle now read (i) members of the same community tend to show the same type versus (ii) members from different communities tend to differ in type.**

  ▷ While under CDT, communities are completely differentiated when each type occurs in only one community,
  under TDC, types are completely differentiated when each community is monomorphic.

  Conversely,

  ▷ While under CDT, communities are monomorphic when different types do not occur in the same community,
  under TDC, each type is confined to a single community when communities are completely differentiated.

The dual perspective of variation

- Even though what appears as differentiation under CDT appears as apportionment under TDC and vice versa, measuring differentiation under the CDT perspective cannot be equated to measuring apportionment under the TDC perspective and vice versa.

The dual perspective of variation still awaits awareness in community ecology and population genetics