Biodiversity measures and the role of species similarity

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Quantifying diversity

- Richness: How many species?

Species	Site 1	Site 2	Site 3
	1	1	10000
	1	10	1
	1	10	1
	10	1	1

- All sites have 4 species – how do we distinguish them?

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- All sites have 4 species – how do we distinguish them?
- *Answer:* Include relative contribution of a species to the community

- Diversity captures richness, eveness and dominance

Hill numbers and the spectrum of view points

- Let p_i be the relative abundance of the ith species. $\mathbf{p}=(p_1, p_{2\ldots} p_s)$. The diversity of order q of the community is exp (Rényi entropy):

$$ {}^{q}D(p) = \begin{cases} \left(\sum_{i=1}^{S} p_i^q \right)^{1/(1-q)} & \text{if } q \neq 1, \infty \\ 1/(p_1^{p_1} p_2^{p_2} \cdots p_S^{p_S}) & \text{if } q = 1 \\ 1/\max_{1 \le i \le S} p_i & \text{if } q = \infty \end{cases} $$

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Jost (2006) Oikos

Why take the exponential of entropy?

- Consider a continent of 1 million equally abundant species. A meteorite hits the continent wiping out 50% of the species. What happens to diversity?

- *Expected answer:* Diversity drops by 50%

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Jost (2006) Oikos

Why take the exponential of entropy?

- Consider a continent of 1 million equally abundant species. A meteorite hits the continent wiping out 50% of the species. What happens to diversity?

- *Expected answer:* Diversity drops by 50%
- BUT… Shannon entropy – drops by just 5%!
- Entropies are not effective numbers, Hill numbers are.

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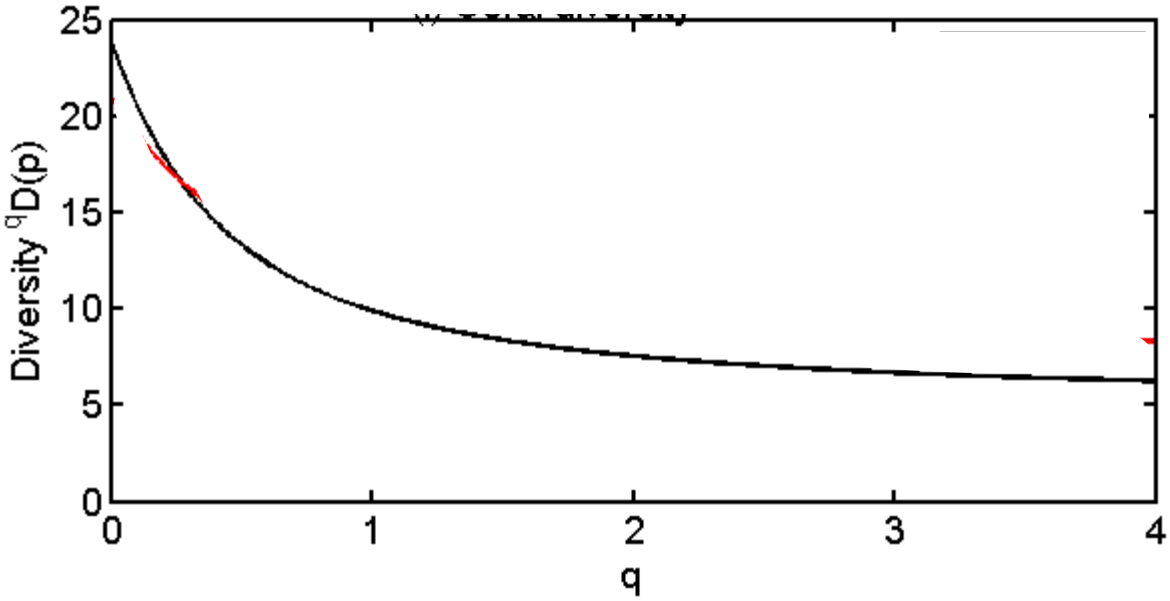
What is the role of q? Diversity profile



‘view point parameter’

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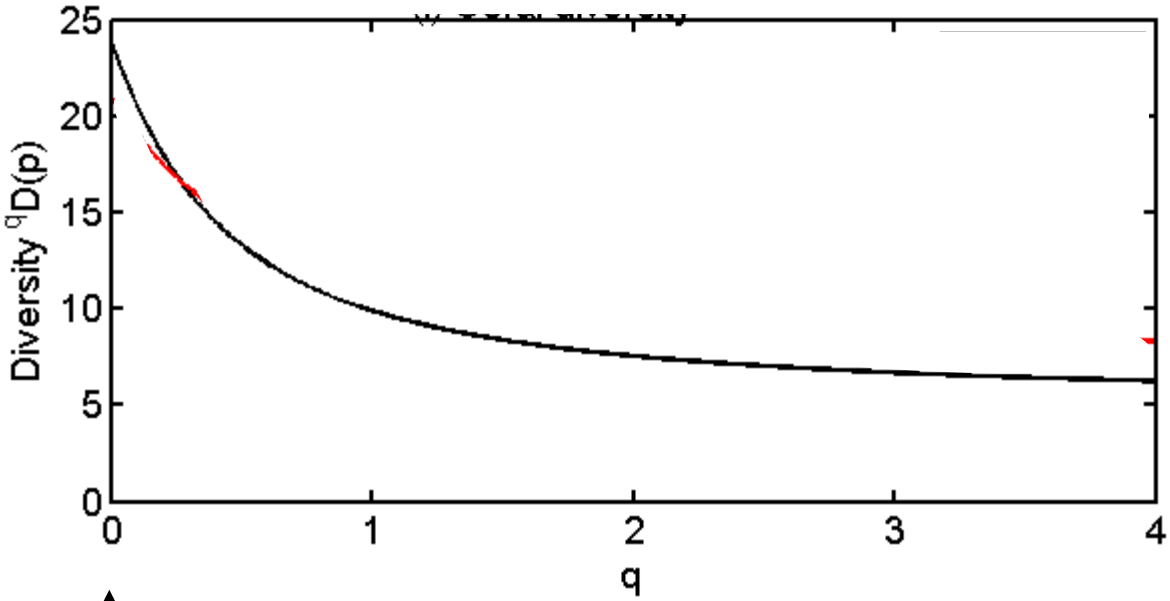

‘view point parameter’

q=0, species richness

rare species are important

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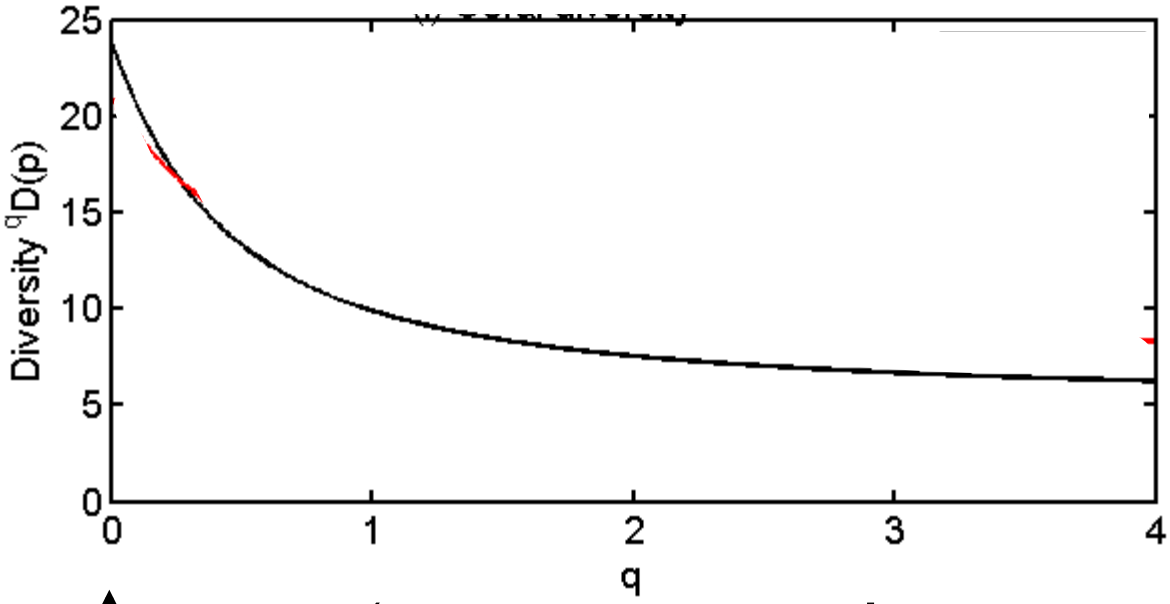

'view point parameter'

q=0, species richness
rare species are important

q=infinity, 1/Berger-Parker
rare species are unimportant

'Importance of evenness'

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What are some of the limitations of Hill numbers

- "…associated with the idea of diversity is the concept of 'distance' i.e. some measure of the dissimilarity of the resources in question"

OECD Handbook on biodiversity valuation: A guide for policy makers

- "A community of ten species of barnacle should clearly be less diverse than a community of ten very different species"

The essence of a point made by E.C. Pielou, Ecological Diversity

- There is not always a good notion of what constitutes a species e.g. microbial communities

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Leinster and Cobbold (2012) Ecology

Including species similarity

model of community

Similarity data, **Z** Abundance data, **p**

S × S matrix (S = number of species)
Z_{ij} = similarity between ith and jth species

$$0 \leq Z_{i,j} \leq 1$$

totally dissimilar ← 0 ≤ $Z_{i,j}$ ≤ 1 → *identical*

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Example

This model assumes that distinct species are totally dissimilar

$$\mathbf{Z} = \begin{pmatrix} 1 & 0 & \cdots & 0 \\ 0 & 1 & \ddots & \vdots \\ \vdots & \ddots & \ddots & 0 \\ 0 & \cdots & 0 & 1 \end{pmatrix}$$

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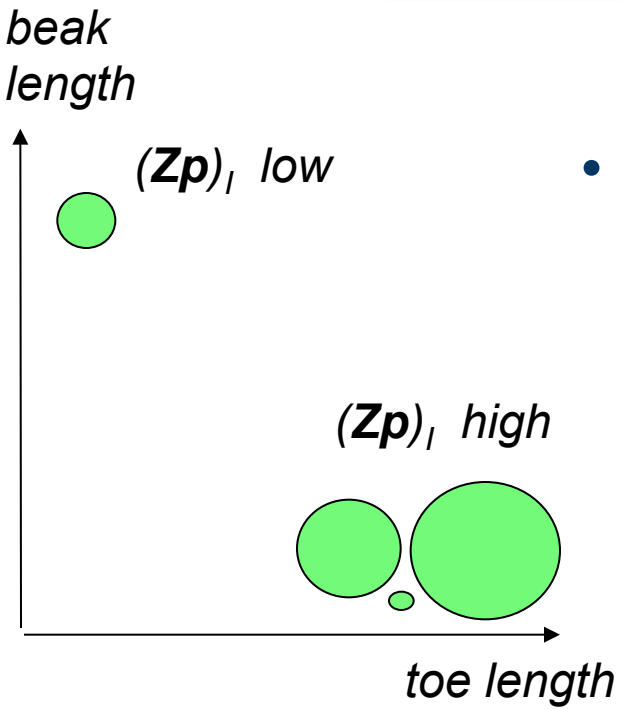
Similarity-sensitive diversity measures



- The ordinariness of the *i*-th species is

$$(Zp)_i = \sum_{j=1}^{S} Z_{ij} p_j$$

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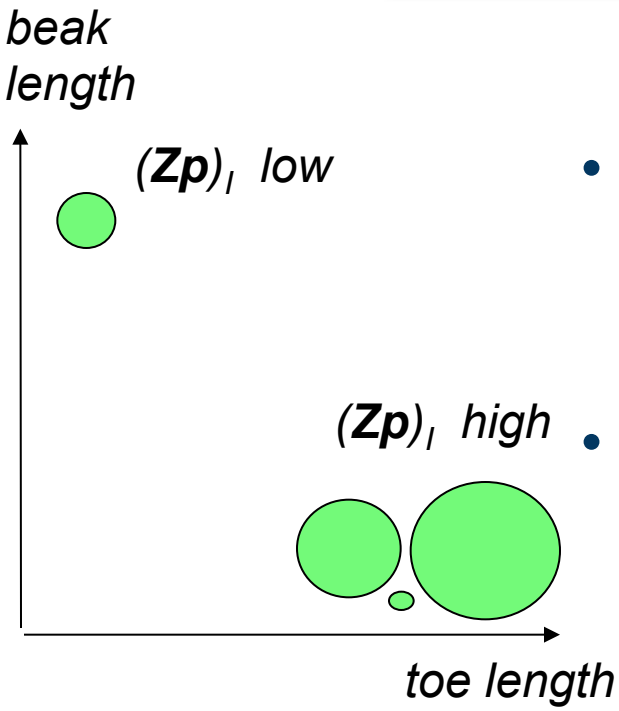

- The ordinariness of the *i*-th species is

$$(Zp)_i = \sum_{j=1}^{S} Z_{ij} p_j$$

- Average ordinariness of an individual within the community

$$\sum_{i=1}^{S} p_i (Zp)_i$$

which measures lack of diversity.

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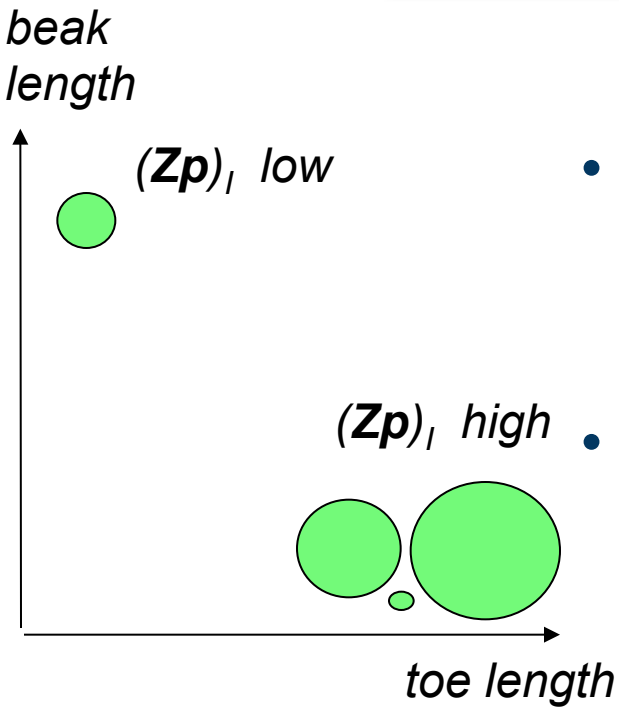
Similarity-sensitive diversity measures



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- So one measure of diversity is

$$1 \Big/ \sum_{i=1}^{S} p_i (Zp)_i$$

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Spectrum of view points: general q

- Generalised weighted power mean of $x=(x_1 \ldots x_S)$ has the form

$$\left(\sum_{i=1}^{S} p_i x_i^{\,q-1} \right)^{1/(q-1)}$$

- So the generalised power mean of ordinariness is

$$\left(\sum_{i=1}^{S} p_i (Zp)_i^{q-1} \right)^{1/(q-1)}$$

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- Diversity of order q is 1/ generalised power mean

$$^{q}D^{\mathbf{Z}}(\mathbf{p}) = \left(\sum_{i:p_i>0} p_i (Z\mathbf{p})_i^{q-1} \right)^{\frac{1}{1-q}}$$

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Example: Butterfly data in the Ecuadorian rainforest

Abundance data of Charaxinae Butterflies at a rainforest site in Ecuador

Species	Canopy	Understorey
Prepona laertes	15	0
Archaeoprepona demophon	14	37
Zaretis itys	25	11
Memphis arachne	89	23
Memphis offa	21	3
Memphis xenocles	32	8

Taxonomic similarity matrix

$$Z_{ij} = \begin{cases} 0 & \text{if of different genera} \\ 0.5 & \text{if different but congeneric} \\ 1 & \text{if i = j,} \end{cases}$$

Data from DeVries et al (1997)

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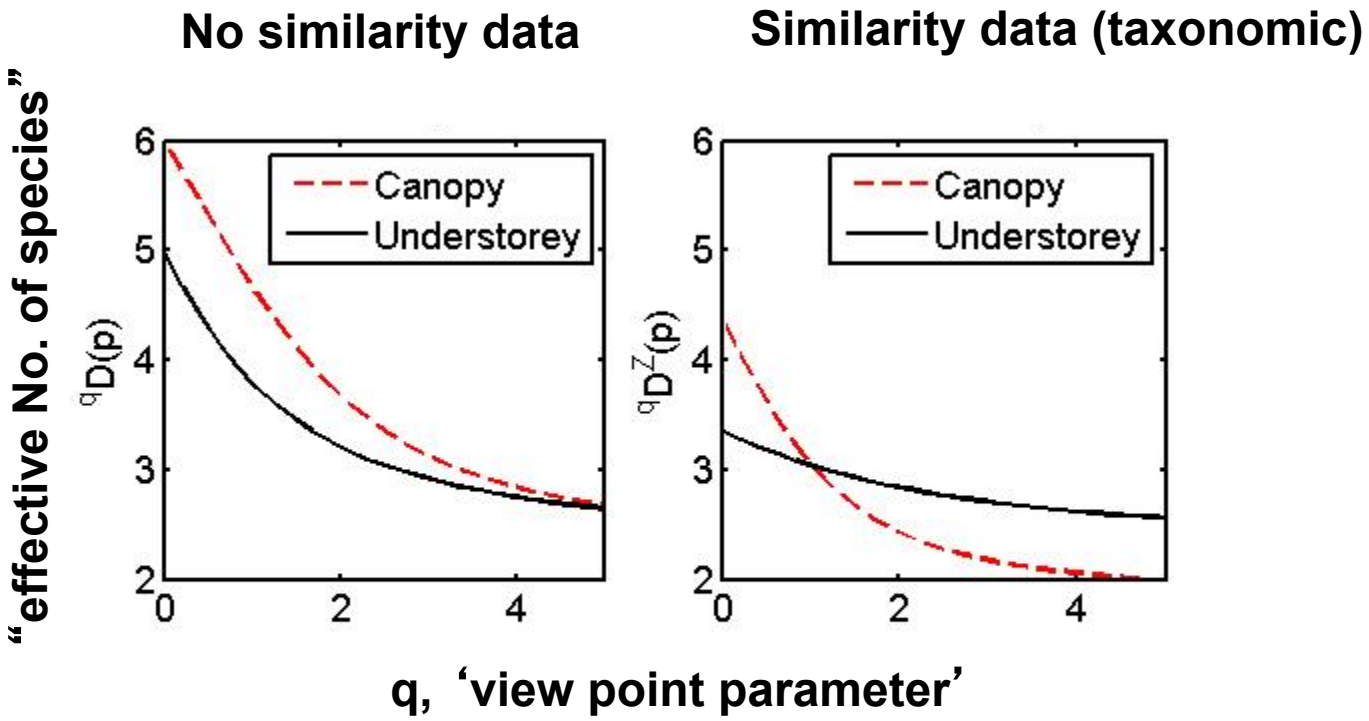
Butterfly data in the Ecuadorian rainforest



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Comparing sites:

	Site 1	…	Site k	….	Ecosystem
Species 1			p_1		g_1
Species 2			p_2		g_2
Species 3			p_3		g_3
Species 4			p_4		g_4
…			…		…
Species S			p_S		g_S

- *How does diversity of site k contribute to the ecosystem diversity?*
- *Is site k typical or distinct in some way?*

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Reeve et al http://arxiv.org/abs/1404.6520

Average ordinariness of site j from the ecosystem point of view

- The ordinariness of the *i*-th species in the *ecosystem*

$$(Zg)_i = \sum_{j=1}^{S} Z_{ij} g_j$$

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- Generalised power mean of ordinariness of species in site k when viewed from the ecosystem perspective:

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- Renyi's cross entropy

$$(1-q)^{-1} \ln \left(\sum_{i=1}^{S} p_i (Zg)_i^{q-1} \right)$$

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"Cross diversity" – exp (cross entropy)

- Which site/s has highest cross diversity?

Species	Site 1	Site 2	Site 3	Ecosystem (my back garden)
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Relationship between entropy and cross entropy

- For Z=I and q=1

Relative entropy=Cross entropy – Entropy

$$(1-q)^{-1}\ln\left(\sum_{i=1}^{S} p_i (Zp/Zg)_i^{q-1}\right) = (1-q)^{-1}\ln\left(\sum_{i=1}^{S} p_i (Zg)_i^{q-1}\right) - (1-q)^{-1}\ln\left(\sum_{i=1}^{S} p_i (Zp)_i^{q-1}\right)$$

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- This does not hold for general q and Z, but does relative entropy tell us something about diversity?

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Relative entropy and ordinariness

- The ordinariness of the *i*-th species at *site j* compared to the ordinariness of the *i*-th species in the *ecosystem*

$$(Zp / Zg)_i = \sum_{j=1}^{S} Z_{ij} p_j \Big/ \sum_{j=1}^{S} Z_{ij} g_j$$

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- *Averaging relative ordinariness* weighted by relative abundance of species i at site j

$$\left(\sum_{i=1}^{S} p_i (Zp/Zg)_i^{q-1} \right)^{1/(q-1)}$$

- Relative diversity = 1/ Av relative ordinariness

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Summary

- Generalised entropy allows us to consider evenness and dominance

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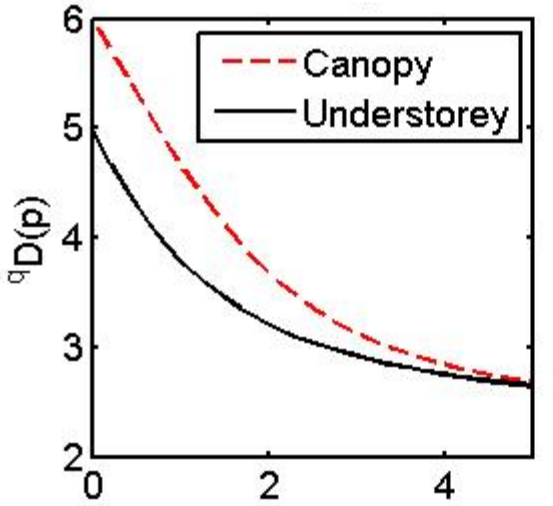

- Similarity sensitive diversity – functional diversity, genetic diversity etc
- Cross entropy allows us to consider sites containing “rarity”
- Relative entropy allows to consider “distinctness” of sites

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Acknowledgements to….

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University of Glasgow

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University of Glasgow

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Microbe communities: notion of a species is problematic

- Expected similarity between a randomly chosen pair of individuals:

$$1/{}^{2}D^{Z}(p) = \mu_2$$

- Now consider q>2 (whole number). Given q individuals of species $i_1, i_2 \ldots, i_q$ *then a measure of group similarity is:*

$$Z_{i_1 i_2} Z_{i_1 i_3} \cdots Z_{i_1 i_q}$$

- *Let μ_q be the expected similarity of a randomly chosen group of q individuals (sampled with replacement). Then*

$${}^{q}D^{Z}(p) = \mu_q^{1/(1-q)}$$

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Properties of diversity of order q

Elementary properties:

1. If two species are **nearly identical**, then merging them into one leaves the diversity nearly unchanged.
2. Diversity is unchanged by adding a new species of abundance 0
3. The order we list species in does not change diversity.

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Properties of diversity of order q

Partitioning properties:

4. It is an **effective number**: diversity of a community of S equally abundant, totally dissimilar species is S.

5. **Replication**: If *m* islands of equal size each have diversity *d*, and species on different islands are totally dissimilar, the the diversity of the whole is *md*

6. **Modularity:** If the *m* islands have different sizes and diversities (species on different islands totally dissimilar), the diversity of the whole is determined by the sizes and diversities of the islands

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Properties of diversity of order q

Similarity properties:

7. *Monotonicity*: increasing species similarity decreases diversity
8. *Naïve model*: ignoring species similarity increases diversity.
9. *Range:* The diversity of a community of S species is between 1 and S