

3. Species Richness and Diversity

Beta Diversity

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2024-01-26

How do we compare diversity between sites?



These 3 sites could easily have the same α -diversity measure. Would that mean they're the same?

Are these two fynbos sites the same?

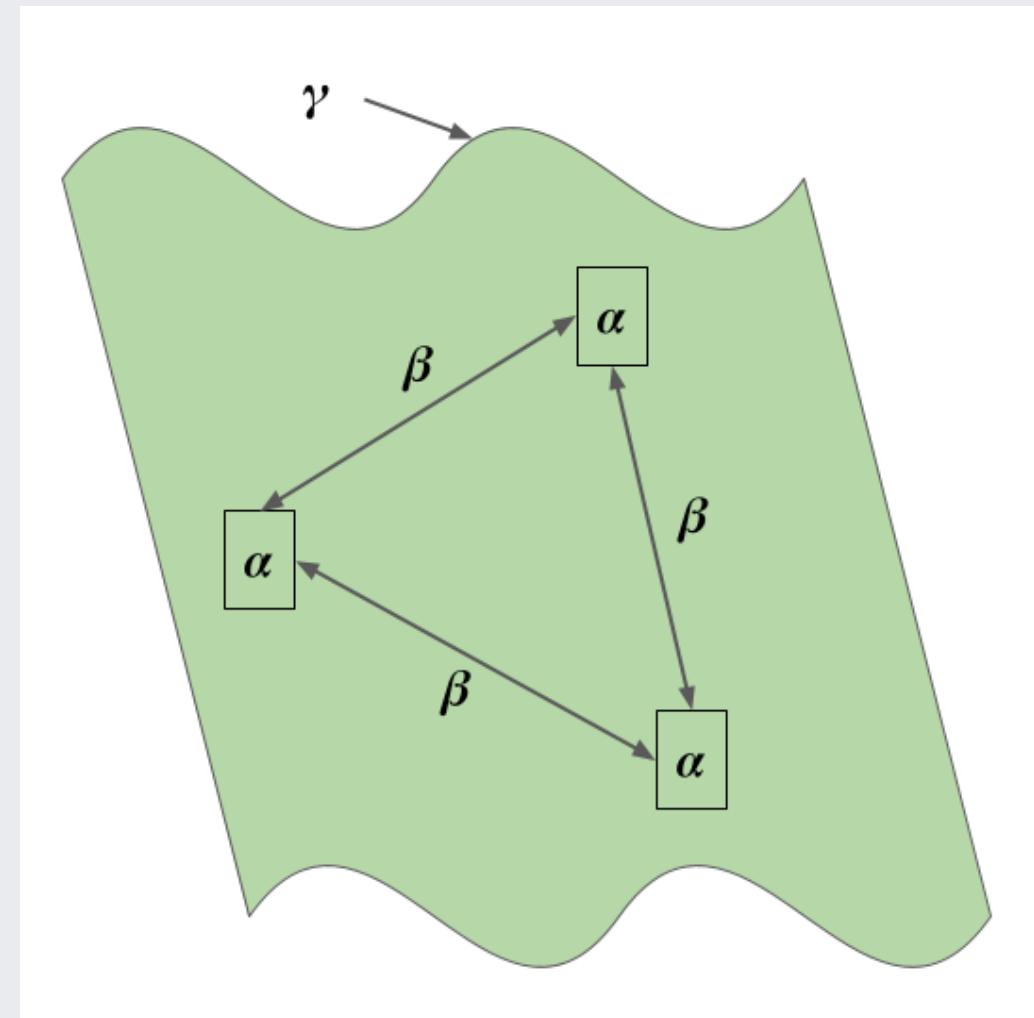


The components of diversity

Alpha (α) = mean species diversity/richness within local-scale sites, habitats or communities (often termed "point diversity")

Beta (β) = diversity/richness differences between sites or habitats (attributable to species "turnover" or "nestedness")

Gamma (γ) = total landscape species diversity/richness



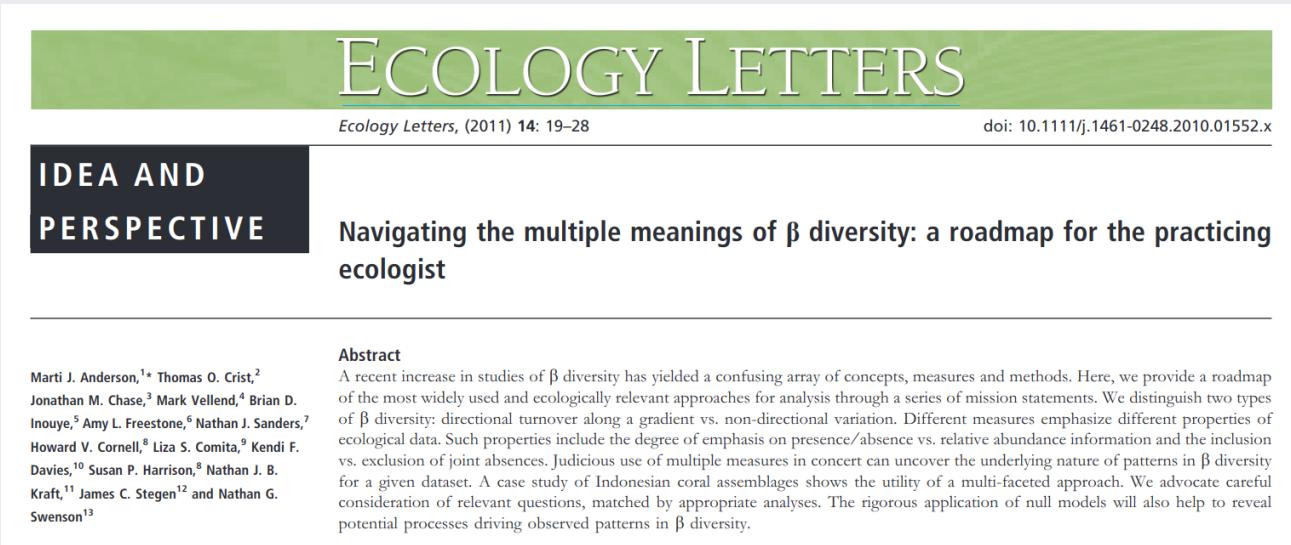
Whittaker (1972)

Three sample localities in a landscape.

WARNING!

β diversity can get a little complicated...

There's lots of methods, and opinions often differ among experts...¹



The image shows the cover of the journal 'Ecology Letters'. The title 'ECOLOGY LETTERS' is at the top in large white letters on a green background. Below it, the subtitle 'Ecology Letters, (2011) 14: 19–28' and the doi 'doi: 10.1111/j.1461-0248.2010.01552.x' are visible. A dark grey sidebar on the left contains the text 'IDEA AND PERSPECTIVE' in white. The main article title 'Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist' is centered below the sidebar. At the bottom left, author names are listed: Marti J. Anderson, Thomas O. Crist, Jonathan M. Chase, Mark Vellend, Brian D. Inouye, Amy L. Freestone, Nathan J. Sanders, Howard V. Cornell, Liza S. Comita, Kendi F. Davies, Susan P. Harrison, Nathan J. B. Kraft, James C. Stegen, and Nathan G. Swenson.

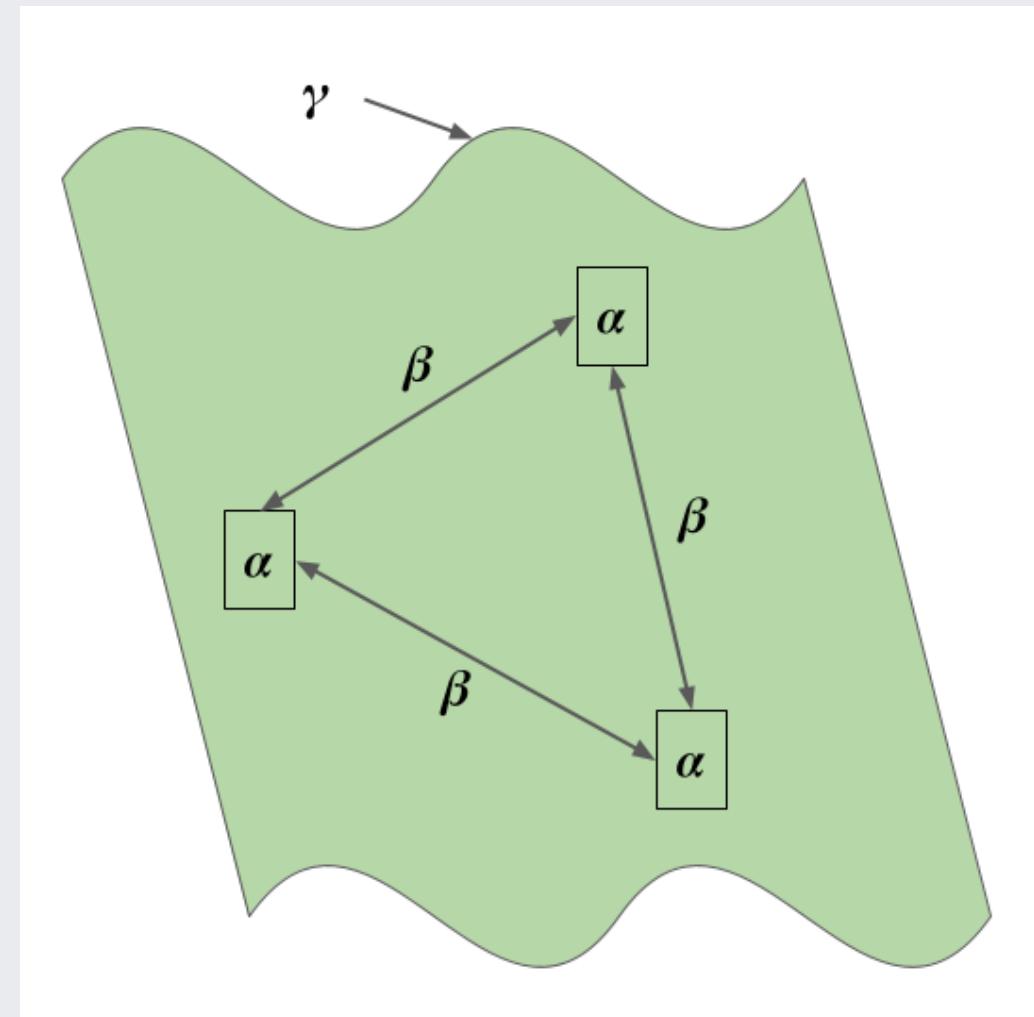
Abstract
A recent increase in studies of β diversity has yielded a confusing array of concepts, measures and methods. Here, we provide a roadmap of the most widely used and ecologically relevant approaches for analysis through a series of mission statements. We distinguish two types of β diversity: directional turnover along a gradient vs. non-directional variation. Different measures emphasize different properties of ecological data. Such properties include the degree of emphasis on presence/absence vs. relative abundance information and the inclusion vs. exclusion of joint absences. Judicious use of multiple measures in concert can uncover the underlying nature of patterns in β diversity for a given dataset. A case study of Indonesian coral assemblages shows the utility of a multi-faceted approach. We advocate careful consideration of relevant questions, matched by appropriate analyses. The rigorous application of null models will also help to reveal potential processes driving observed patterns in β diversity.

¹i.e. this is a highly active area of research...

Measuring β diversity

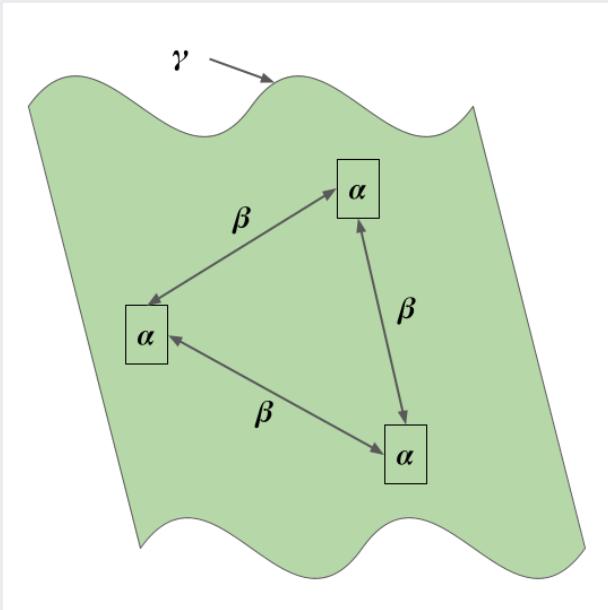
There are two major approaches:

- "*Classical*" diversity metrics, calculated directly from measures of regional (γ) and local (α) diversity through additive or multiplicative decomposition
- *Multivariate measures* that calculate distances (or dissimilarities) that represent the compositional resemblance between pairs of samples

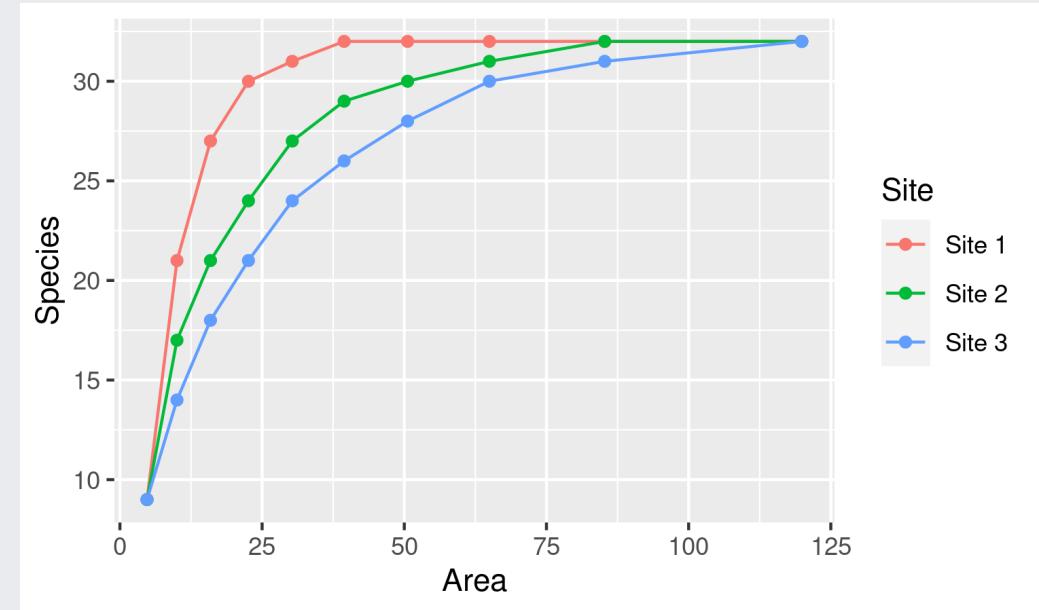


The two are related, and can even be the same thing in certain scenarios, but I'm not going to go there in this course...

The decomposition of "classical" diversity metrics...



Consider this in the context of the species-area relationship.



If γ is constant (32) across sites, then

- S1 = higher α , lower β (i.e. more homogeneous)
- S2 = intermediate α and β
- S3 = lower α , higher β (i.e. more heterogeneous)

Comparing floras...



Fynbos has moderate to high α and very high β , resulting in high γ

- ~9500 vascular plant species in the Cape Flora
- ~2200 native species on the Cape Peninsula alone

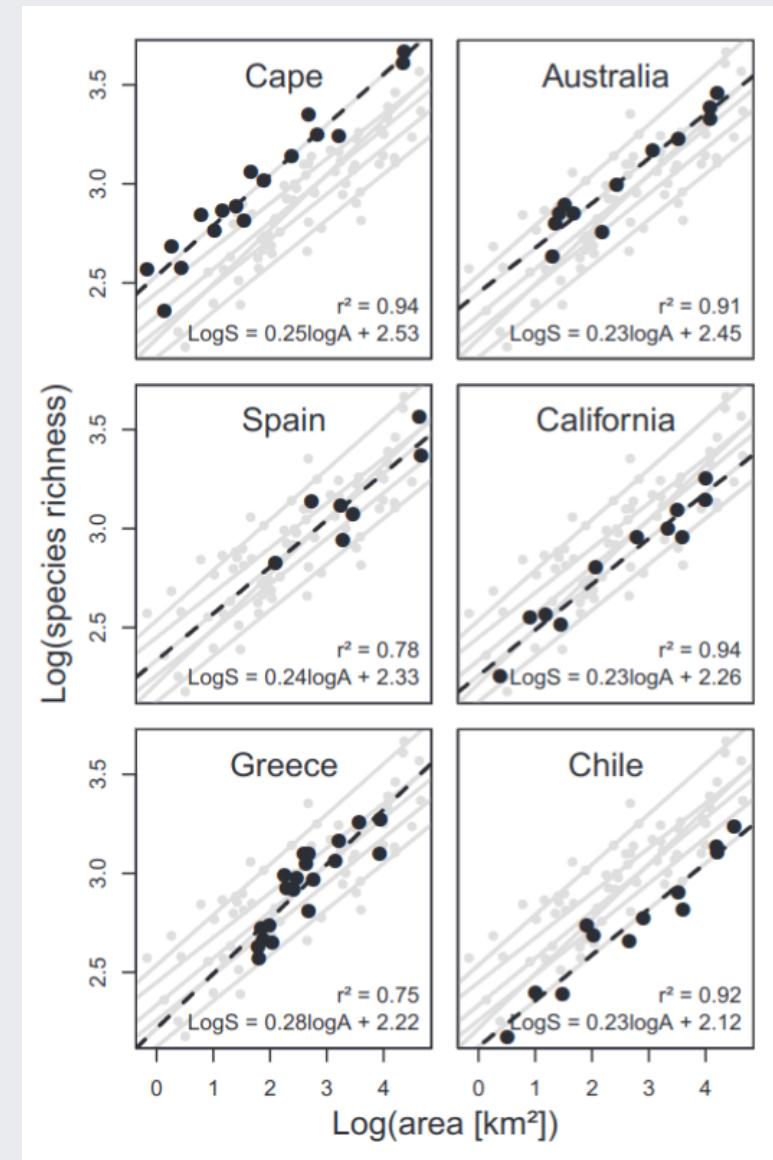


English meadows have very high α , but very low β , resulting in moderate to low γ

- only 1390 native species in the entire Great Britain and Ireland (~3 x the size of the CFR)

Comparing floras...

We often compare the diversity of different regions using species-area curves (usually on log-log axes so the curves are linear) - e.g. Cowling et al. 2015



The decomposition of "classical" diversity metrics...

The components of biodiversity are interrelated and, depending on your preference or application, can be expressed:

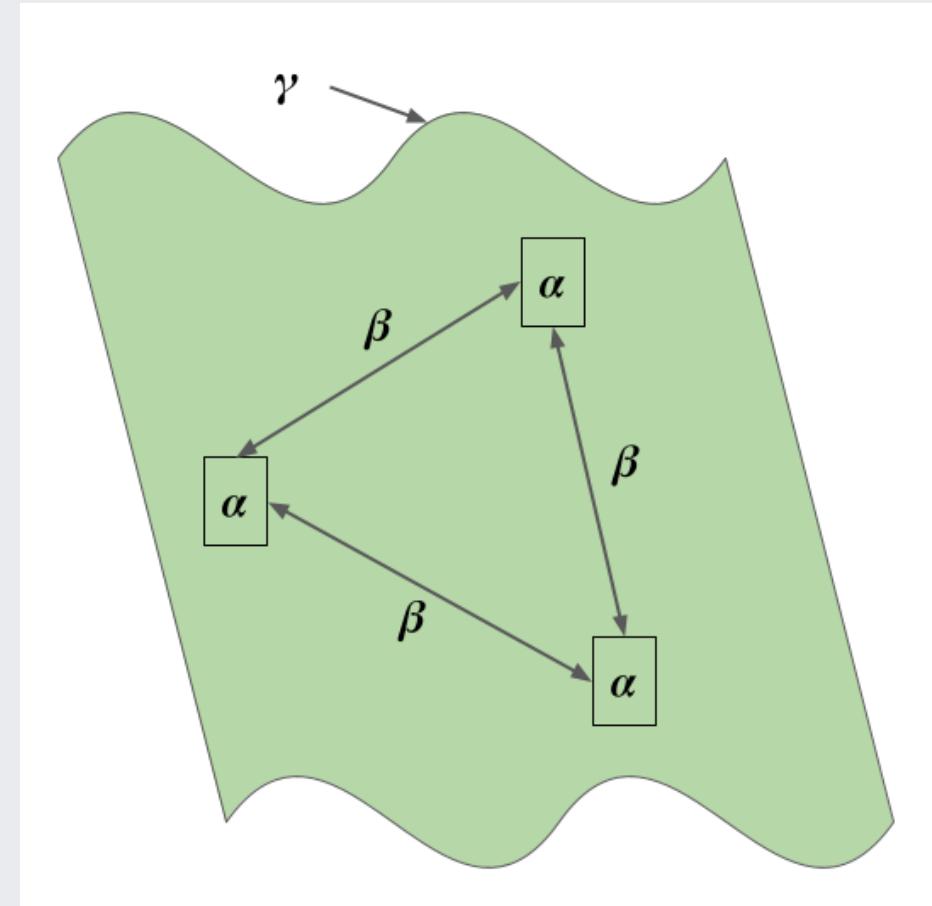
Multiplicatively (*sensu* Whittaker 1972):

$$\beta = \gamma/\alpha$$

Additively (*sensu* MacArthur et al. 1966, Lande 1996):

$$\beta = \gamma - \alpha$$

¹For reviews see Veech et al. 2002 and Anderson et al. 2011.



Multiplicative "classical" diversity

$$\beta = \gamma/\alpha \text{ (*sensu* Whittaker 1972)}$$

...expresses β diversity as the ratio of landscape (γ) to local (α) diversity (usually the mean of multiple local samples, i.e. $\bar{\alpha}$).

If most local (α) samples capture most of the landscape (γ) diversity, then β diversity (i.e. differences between sites or habitats) must be low, and vice versa.

Disadvantages:

- the ratio is unitless
- usually need to know landscape diversity (γ)

5	6	10
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9 samples

4	8	9
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15 species in total

6	8	7
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$$\bar{\alpha} = 7$$

$$\gamma = 15$$

$$\beta = \gamma/\bar{\alpha} = 15/7 = 2.143$$

Additive "classical" diversity

$$\beta = \gamma - \alpha \text{ (*sensu* MacArthur et al. 1966, Lande 1996)}$$

...expresses β diversity as the difference between landscape (γ) and local (α) diversity (again, usually the mean of multiple local samples, i.e. $\bar{\alpha}$).

If local (α) samples capture most of the landscape (γ) diversity, then β diversity (i.e. differences between sites or habitats) must be low, and vice versa.

Advantage:

- the difference is expressed as species (i.e. the average number of species missing from each local site)

Disadvantage: still usually need to know (γ)

5	6	10	9 samples
4	8	9	15 species in total
6	8	7	

$$\bar{\alpha} = 7$$

$$\gamma = 15$$

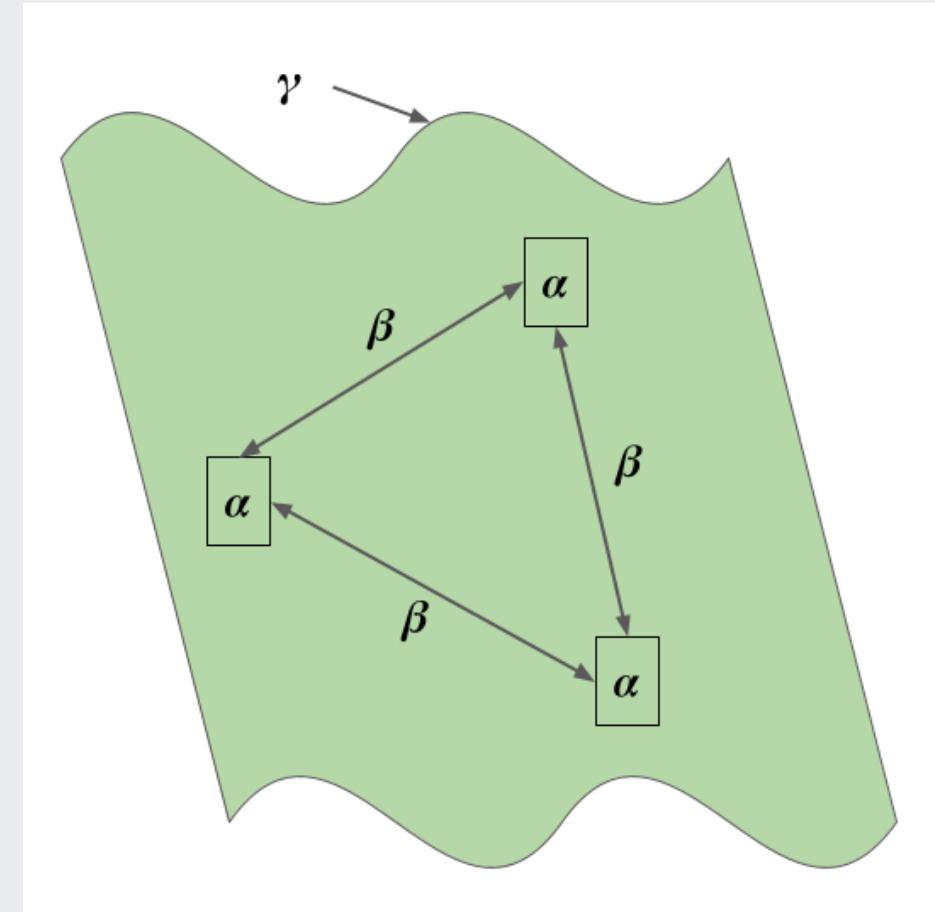
$$\beta = \gamma - \bar{\alpha} = 15 - 7 = 8$$

Multivariate measures of β diversity

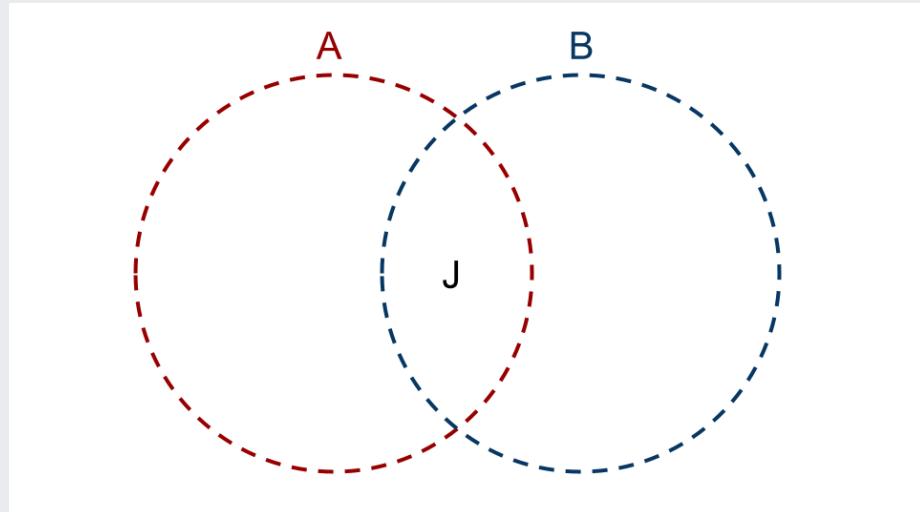
There are a large number of metrics that calculate the dissimilarity of pairs of samples based on the number of species that are shared between them or unique to each.

The metrics typically differ in whether they:

- are based on species presence/absence only, or also include abundance information
- include/exclude joint absence information
- account for differences in the α diversity of samples



Multivariate measures of β diversity



e.g. the same equation, $(A + B - 2 * J)/(A + B)$

where J is the shared quantity, and A and B are totals for each community

can be...

Sorenson's Dissimilarity Index

when based on species presence/absence only

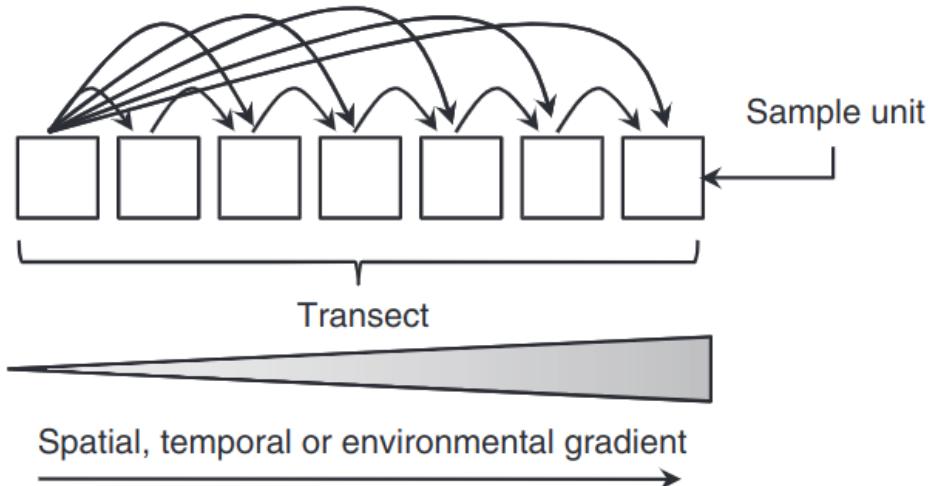
Bray-Curtis distance

when it includes abundance information

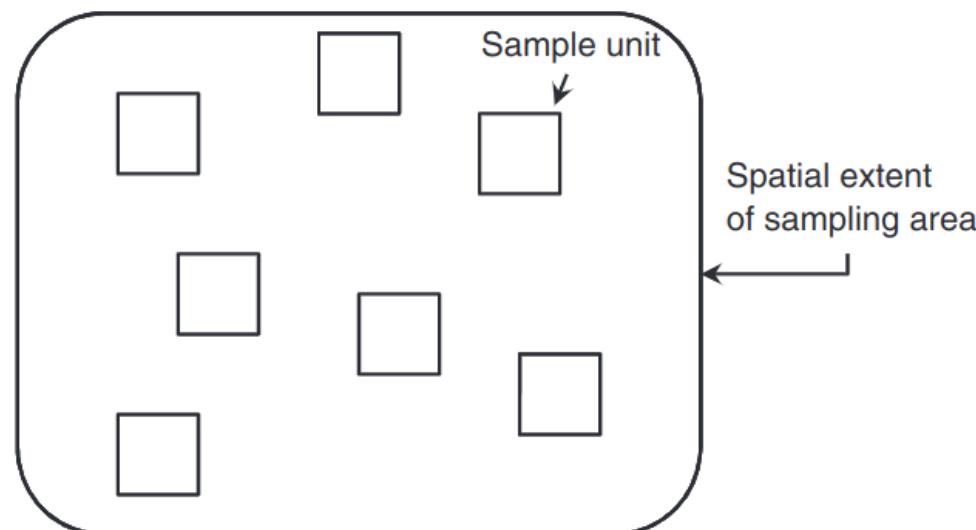
Values range from 0 (identical communities) to 1 (complete turnover).

Be careful. The indices are often inverted (i.e. similarity metrics) depending on the goals of the study.

(a) Directional turnover in community structure



(b) Variation in community structure (non-directional)

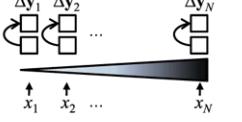
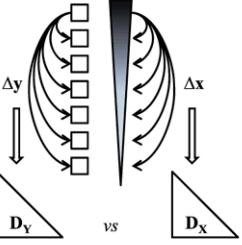
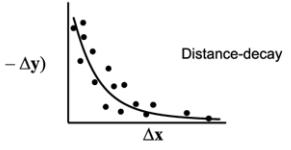
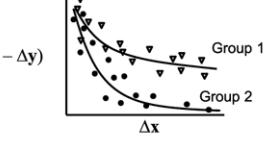
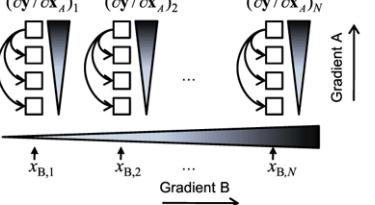


Turnover vs Variation

The application of β diversity can be largely split into:

- directional analyses, that explore *turnover* along spatial, temporal or environmental gradients, and
- non-directional analyses, that explore *variation* within or among groups.

figure from Anderson et al. 2011

Mission statement	Schematic representation	Analysis
T1. Measure turnover between two communities.		Calculate Δy (e.g., Jaccard or Sørensen).
T2. Model turnover between two communities along an environmental factor or gradient.		Linear or non-linear regression of Δy vs x .
T3. Model pair-wise dissimilarities in communities as a function of pair-wise spatial, temporal or environmental distances.		Linear or non-linear regression of Δy vs Δx . The Mantel test: test of the null hypothesis of no relationship between two distance matrices. Examine relationship at a series of distance classes: Mantel correlogram.
T4. Estimate the rate of turnover along a spatial, temporal or environmental gradient.		Linear or non-linear model of $(1 - \Delta y)$ vs Δx . Rate ($\partial y / \partial x$) is the estimated slope of a distance-decay model.
T5. Compare rates of turnover along one gradient for different groups of species or taxa.		Compare slope (and r^2) values obtained for two different groups ($\partial y / \partial x_1$) and ($\partial y / \partial x_2$).
T6. Model the rate of turnover along one gradient (A) across the levels of a factor or along a second gradient (B).		Linear or non-linear regression of $(\partial y / \partial x_A)$ vs x_B .

"Turnover" applications

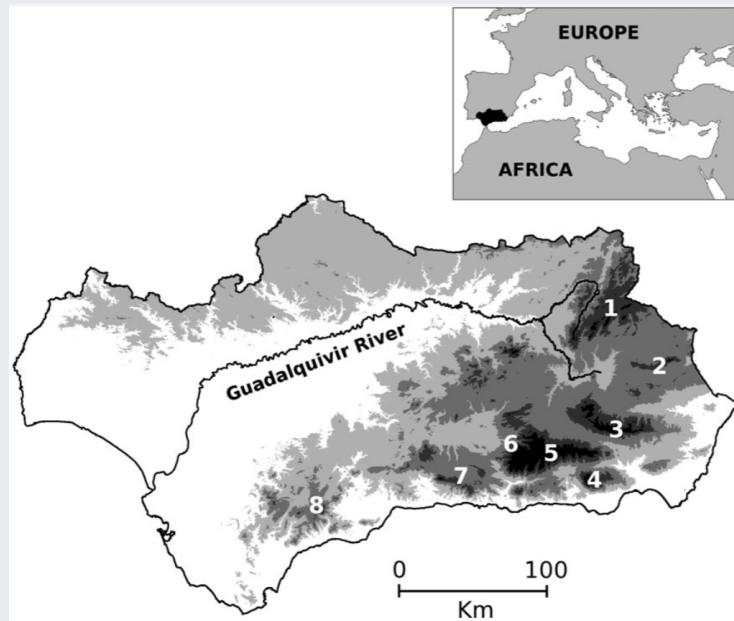
Typically explores change in community composition of one or more groups (e.g. taxa) along one or more gradients (e.g. distance, time, elevation, rainfall).

Δy = change in community composition

Δx = change in gradient

$\delta y / \delta x$ = rate of turnover along a gradient

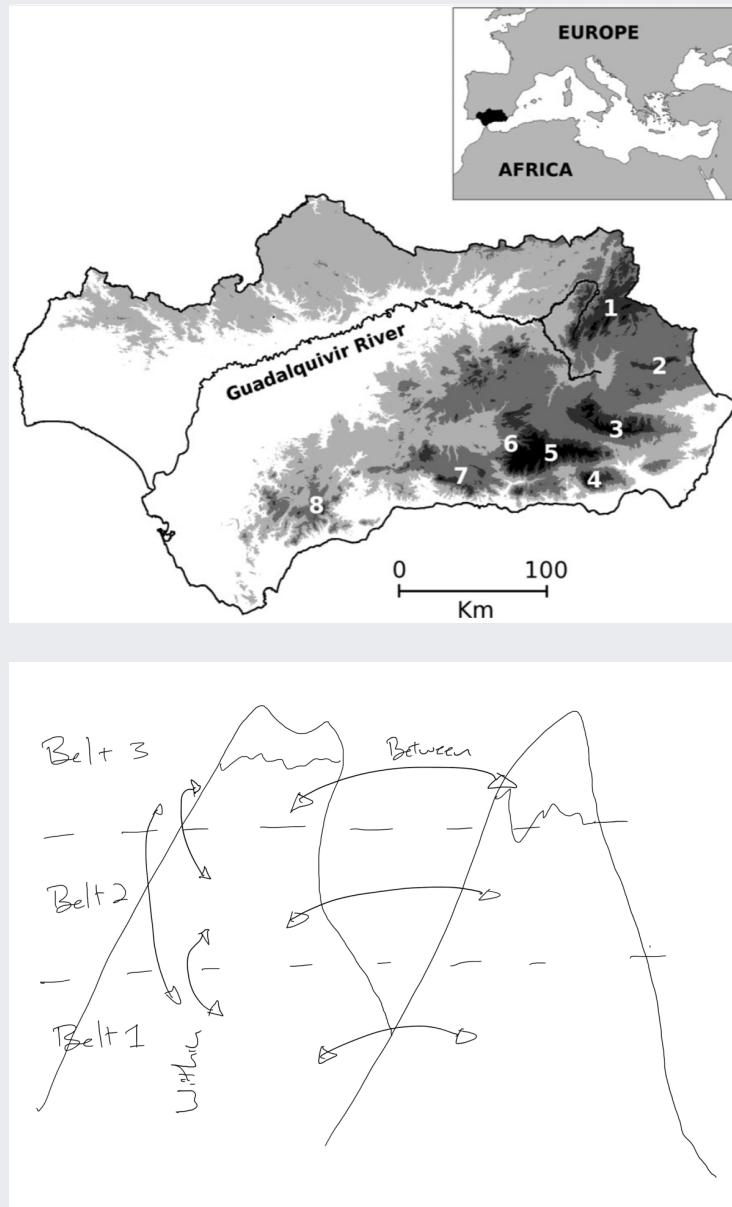
figure from Anderson et al. 2011



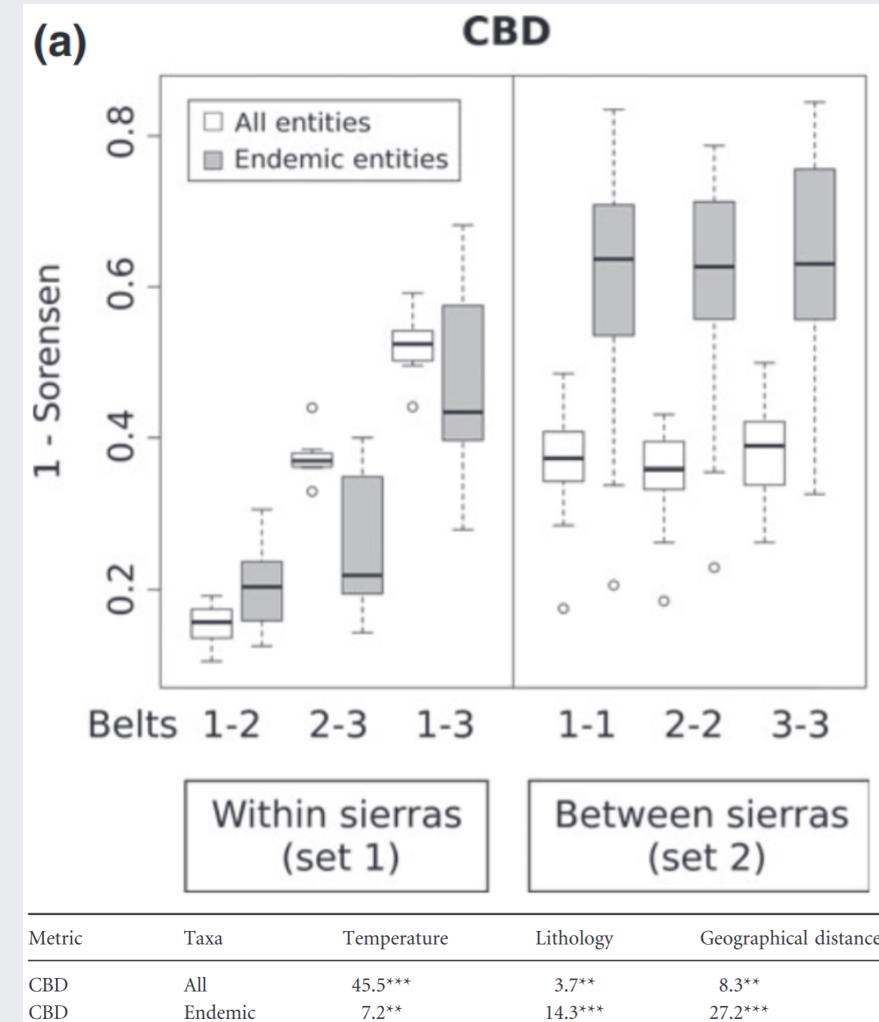
E.g. Floristic **turnover** with change in elevation vs between mountains (Molina-Venegas et al. 2015)



Eudicots of the Baetic mountains of Andalusia, Spain



E.g. Floristic ***turnover*** with change in elevation vs between mountains (Molina-Venegas et al. 2015)



VARIATION

Mission statement	Schematic representation	Analysis
V1. Measure variation among communities from a set of samples.	<p>Sampling area e.g., d_j Sample unit, y_i</p>	Calculate one or more of: β_W , β_{Add} , \bar{d}_{cen} or $\hat{\sigma}^2 = \frac{1}{(N-1)} \left(\sum_{i,j \neq i} d_{ij}^2 / N \right)$
V2. Explore relationships between community structure and factors or environmental variables.	<p>Unconstrained ordination PCO, MDS</p>	Visualise patterns in an ordination (e.g., PCO or MDS), Superimpose labels, bubbles, vectors, etc.
V3. Partition variation in community structure according to some factors or continuous (spatial/environmental) variables.	<p>Species data $Y \rightarrow D_Y \rightarrow G, H \rightarrow X$ Dissimilarity matrix Gower's centred matrix Predictor variable(s) or factors Projection matrix for the model $tr(G) = (N-1)\hat{\sigma}^2$</p>	Linear or non-linear RDA (Euclidean), CCA (chi-squared) or dbRDA (other measures). Explained: $tr(HG)$ Residual: $tr(I-H)G$ Total SS: $tr(G)$
For dbRDA, partitioning is done on Gower's centred matrix (G); for RDA, partitioning is done on the SSCP matrix of Y.		
V4. Compare variation either (a) among <i>a priori</i> groups or (b) along a continuous gradient.	<p>(a) $\bar{d}_{cen,1}, \bar{d}_{cen,2}, \bar{d}_{cen,3}$ etc. Group 1 Group 2 Group 3</p> <p>(b) $\hat{\sigma}_1^2, \hat{\sigma}_2^2, \dots, \hat{\sigma}_g^2$ x_1, x_2, \dots, x_g</p>	For (a), do a test for homogeneity of multivariate dispersions. More generally (for a or b), fit a linear or non-linear model of $\hat{\sigma}_\ell^2$ or $\bar{d}_{cen,\ell}$ vs x_ℓ ($\ell = 1, \dots, g$)
V5. Partition variation according to a series of hierarchical spatial (or temporal) scales.	<p>Locations Sites Areas Replicates</p>	Partition $\hat{\sigma}^2$ and estimate components of variation (based on dissimilarity of choice). Additive partitioning of β_{Add} in units of richness (α), or multiplicative partitioning of β_W .
V6. Compare components of variation or effect sizes across levels of another factor or for different groups of taxa (V7).	<p>Disturbed sites Undisturbed sites $\hat{\sigma}_{sites,D}^2, \hat{\sigma}_{areas,D}^2, \hat{\sigma}_{rep,D}^2$ $\hat{\sigma}_{sites,U}^2, \hat{\sigma}_{areas,U}^2, \hat{\sigma}_{rep,U}^2$</p>	Estimate sizes of components. Test for differences in sizes of components using separate-sample bootstraps on differences or on two-tailed pseudo-F values.

"Variation" applications

Typically explores the amount of variation in community composition among sample units across one or more groups (e.g. taxa), sometimes trying to partition the drivers of variation among factors (e.g. experimental treatments), spatial scales or environmental variables.

Δy = change in community composition

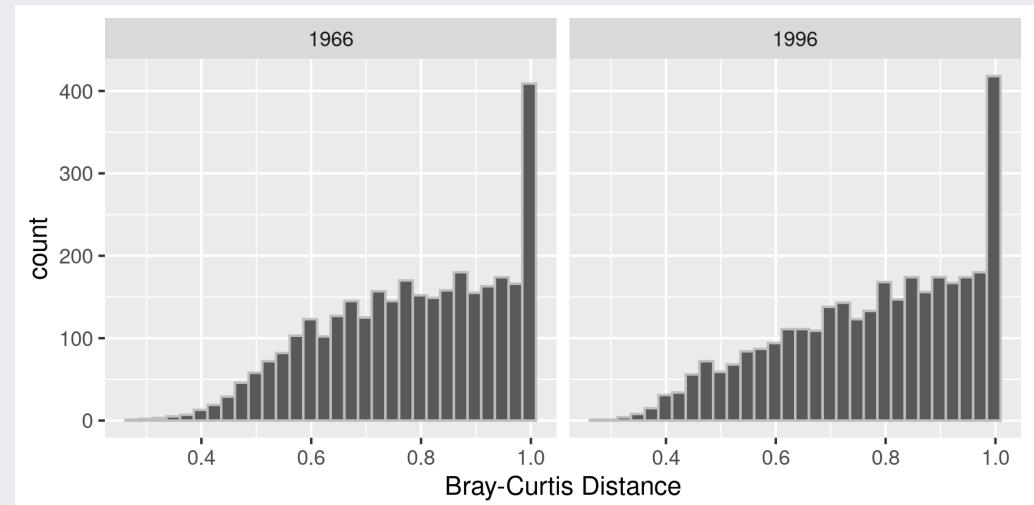
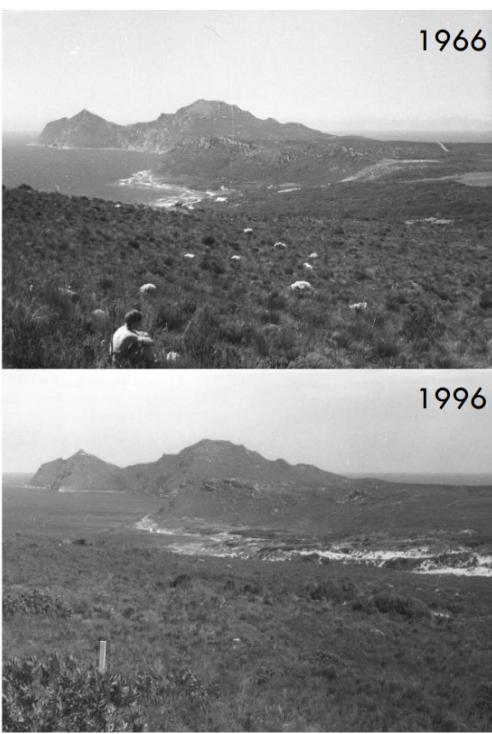
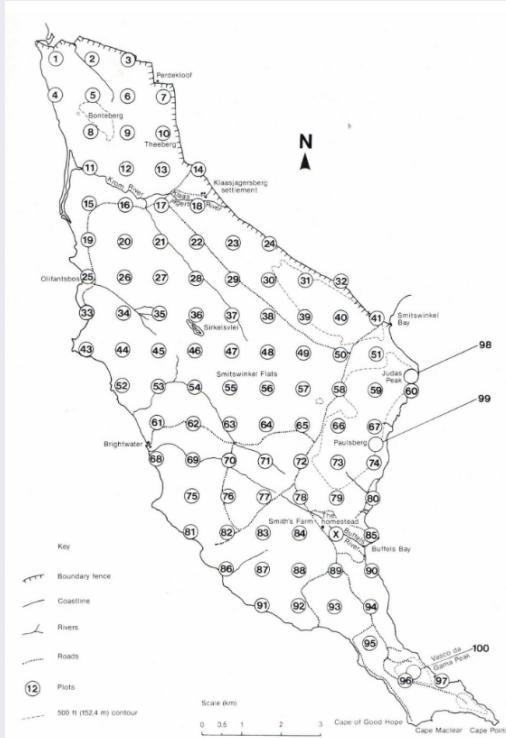
$\hat{\sigma}^2$ = variation in community structure among sample units

\bar{d}_{cen} = average distance-to-centroid of all sample units

figure from Anderson et al. 2011

"Variation" examples

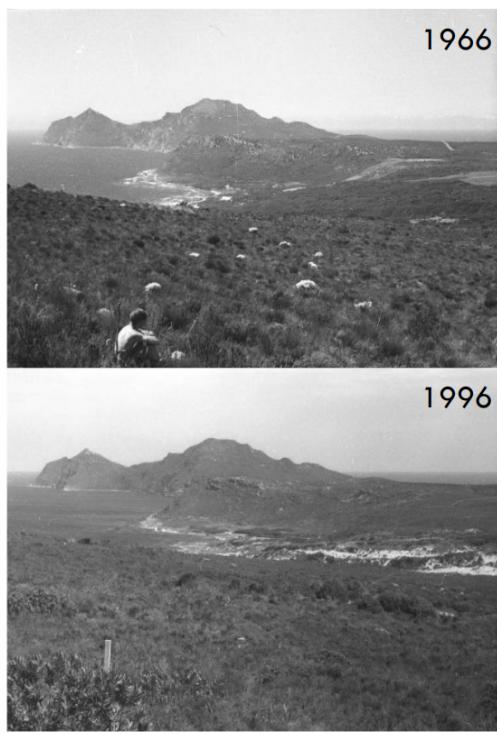
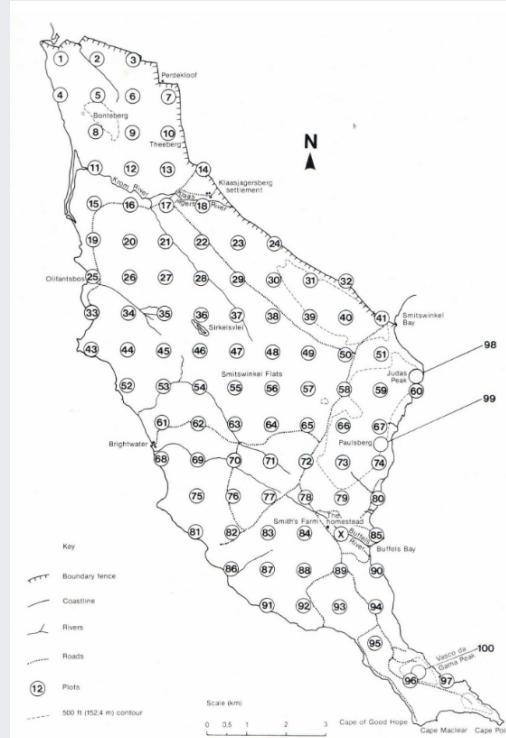
Exploring variation among samples from one or more surveys or datasets



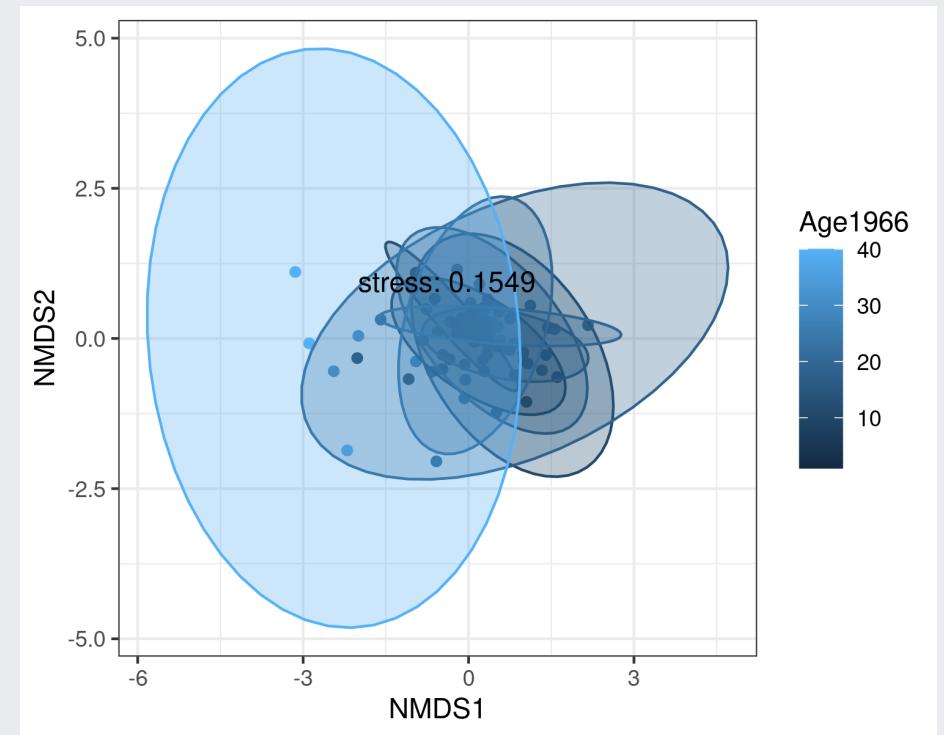
Average turnover between plots: 1966 = 0.784; 1996 = 0.780

"Variation" examples

Variation among communities in relation to an environmental variable



Data from Slingsby et al. 2017

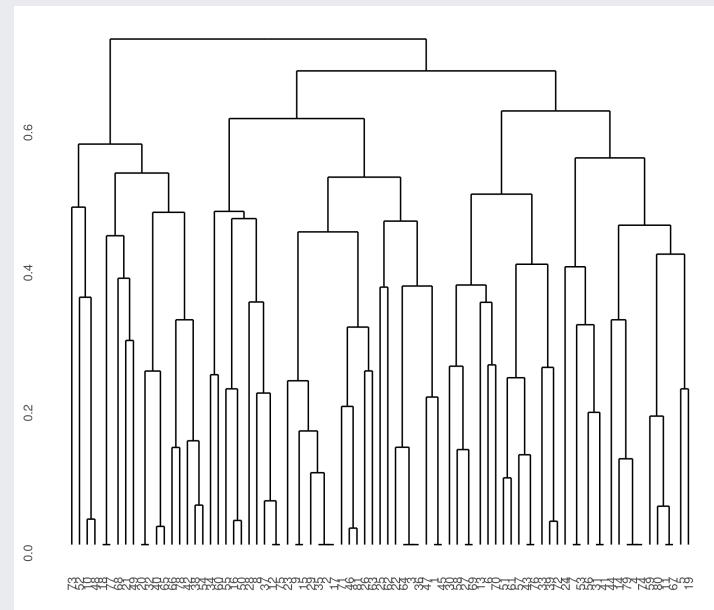


Community similarity in relation to age since last fire

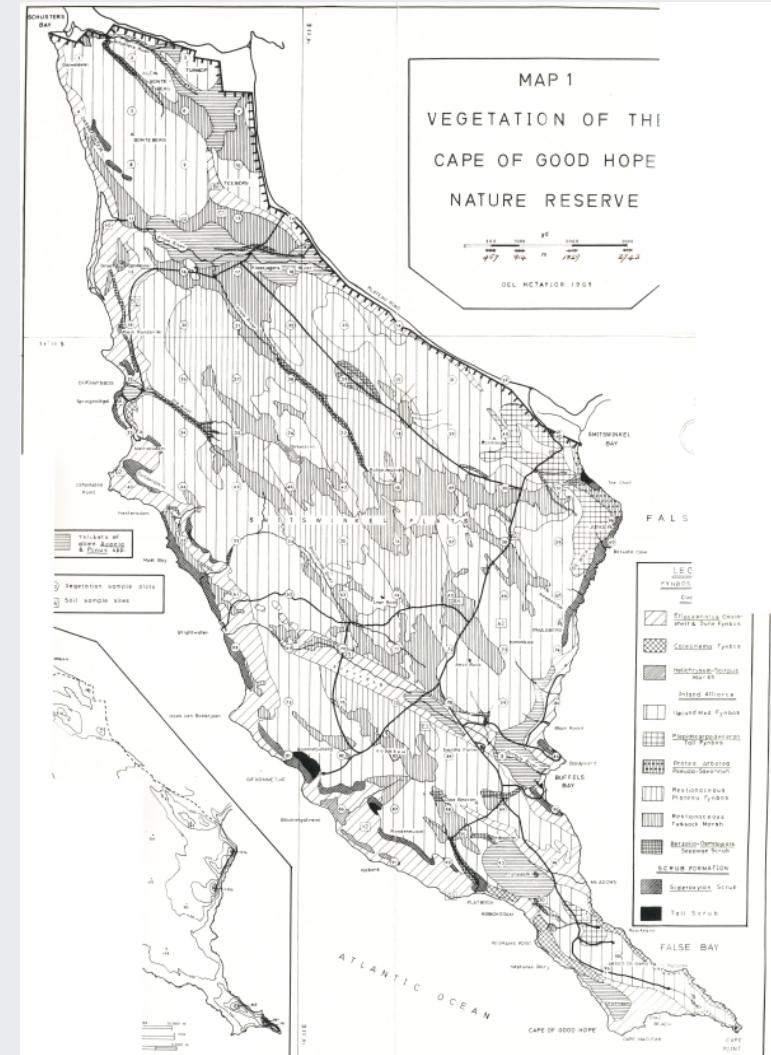
"Variation" examples

Grouping samples by compositional similarity

e.g. used to identify distinct vegetation communities



Data from Slingsby et al. 2017



Map from Taylor 1983

Take-home

There are many ways of measuring and analysing β diversity.

"Plurality in the concept of β diversity can yield important ecological insights when navigated well. By knowing the properties of the measures being used and applying more than one, the underlying ecological structures in the data generating patterns in β diversity can be revealed..." - Anderson et al. 2011

"This applies to most measures of diversity..." - Slingsby 2023

References

Anderson, M. J., T. O. Crist, J. M. Chase, et al. (2011). "Navigating the multiple meanings of beta-diversity: a roadmap for the practicing ecologist". En. In: *Ecology letters* 14.1, pp. 19-28. ISSN: 1461-023X, 1461-0248. DOI: 10.1111/j.1461-0248.2010.01552.x.

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Veech, J. A., K. S. Summerville, T. O. Crist, et al. (2002). "The additive partitioning of species diversity: recent revival of an old idea". En. In: *Oikos* 99.1, pp. 3-9. ISSN: 0030-1299, 1600-0706. DOI: 10.1034/j.1600-0706.2002.990101.x.

Thanks!

Slides created via the R packages:

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gadenbuie/xaringanthemer

The chakra comes from remark.js, **knitr**, and R Markdown.