

4. Functional and Phylogenetic Diversity

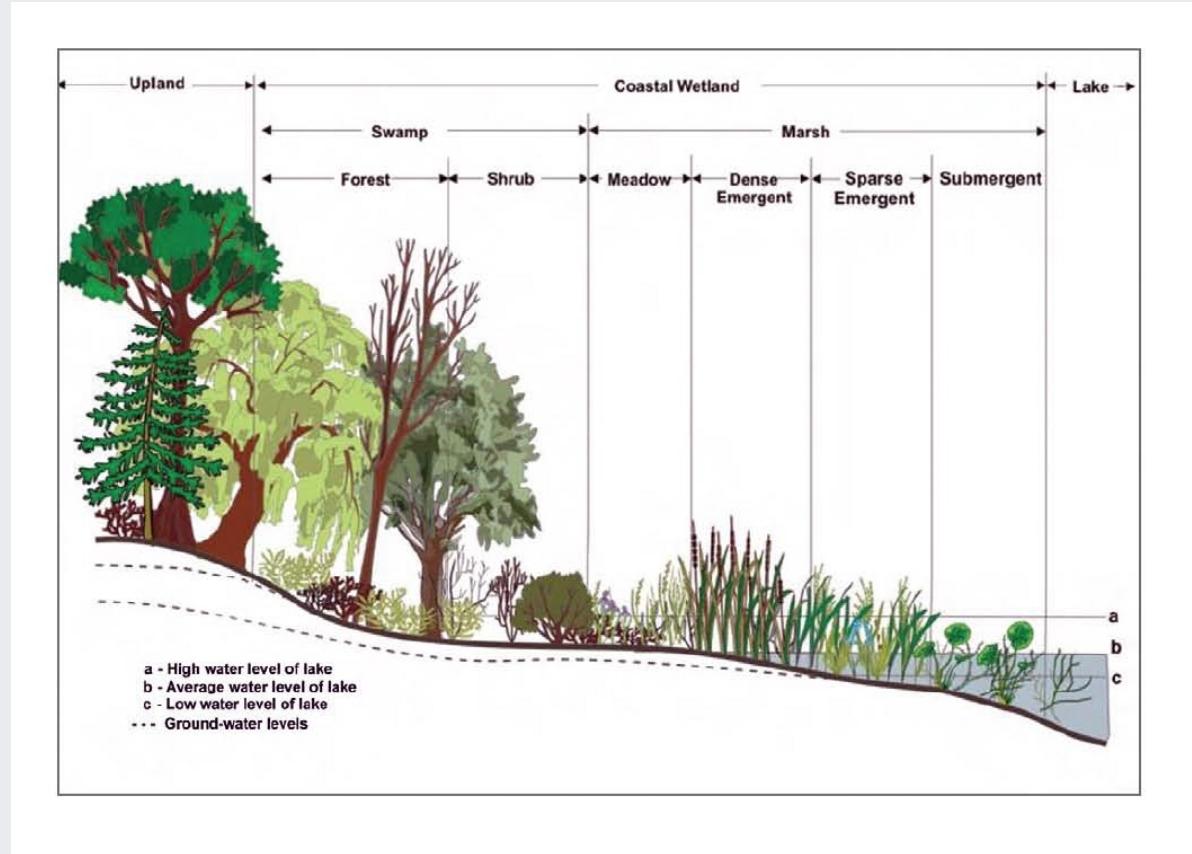
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Are simple metrics of the number of species and individuals enough?



There's a lot of diversity in the form of species



Often associated with the environments in which they occur...

There's a lot of diversity in the form of species



...and they have various effects on the environment, such as creating habitat for other species...

Drawbacks of looking at species diversity only?

- What is a species? There are many definitions! Species are *hypotheses*!
- Are all species equal?
 - Would you consider 2 *Erica* species to be equivalent to an *Erica* and a *Protea* or cacao and coffee?
- Species counts don't tell you about:
 - the identity of species or the similarities or differences between them
 - the functioning of species or communities
 - the origins and maintenance of diversity (evolution, ecology and biogeography)



Measuring functional and phylogenetic diversity

Representing differences in the functional form and evolutionary history of species

Many measurement approaches!



Measuring functional and phylogenetic diversity

Oldest and simplest measures are based on **discrete** predefined categories:

- **functional groups** (growth form, etc)
- **taxonomic rank** (genera, families, etc¹)

Simply assign your species to the categories (e.g. trees, shrubs, grasses, etc if you're working with plant functional groups) and calculate your diversity metrics as you would for species.



¹Species diversity is just a discrete measure of phylogenetic diversity where the taxonomic rank is "species"...

Drawbacks of discrete measures

Similar to issues with species diversity...

Taxonomic ranks

- What is a genus or family?
- Are all genera or families equal?
- Taxonomic ranks are mostly pragmatic categories that help us identify taxa based on shared characters...

Functional groups

- How are they defined?
 - Qualitative (expert opinion), e.g. tree, shrub,...?
 - Quantitative (analysis of measured traits)?

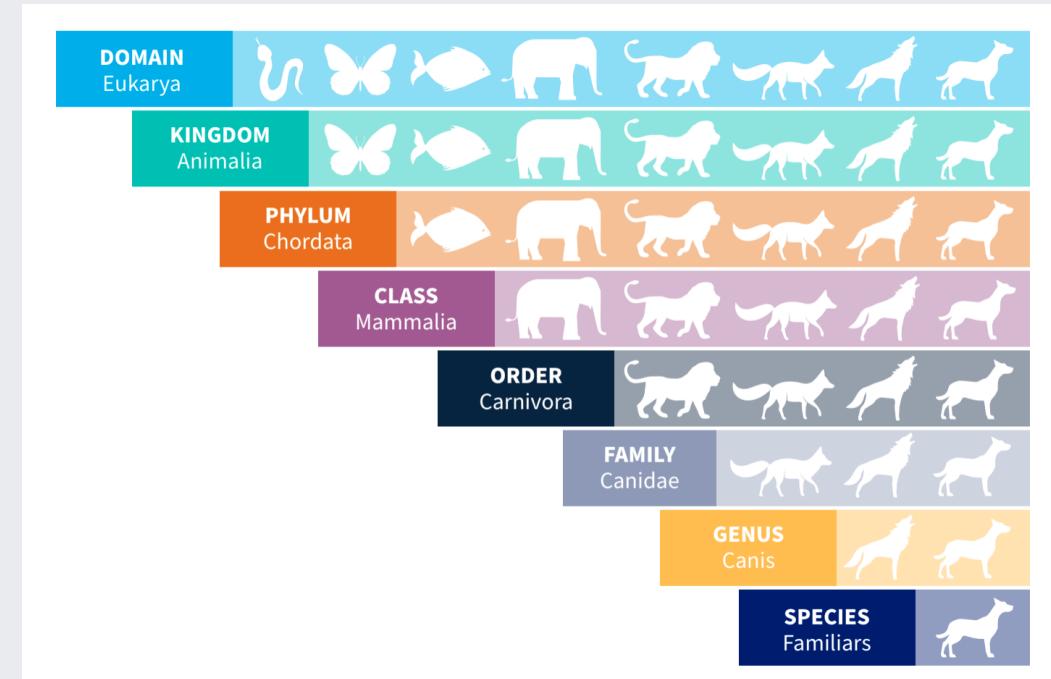
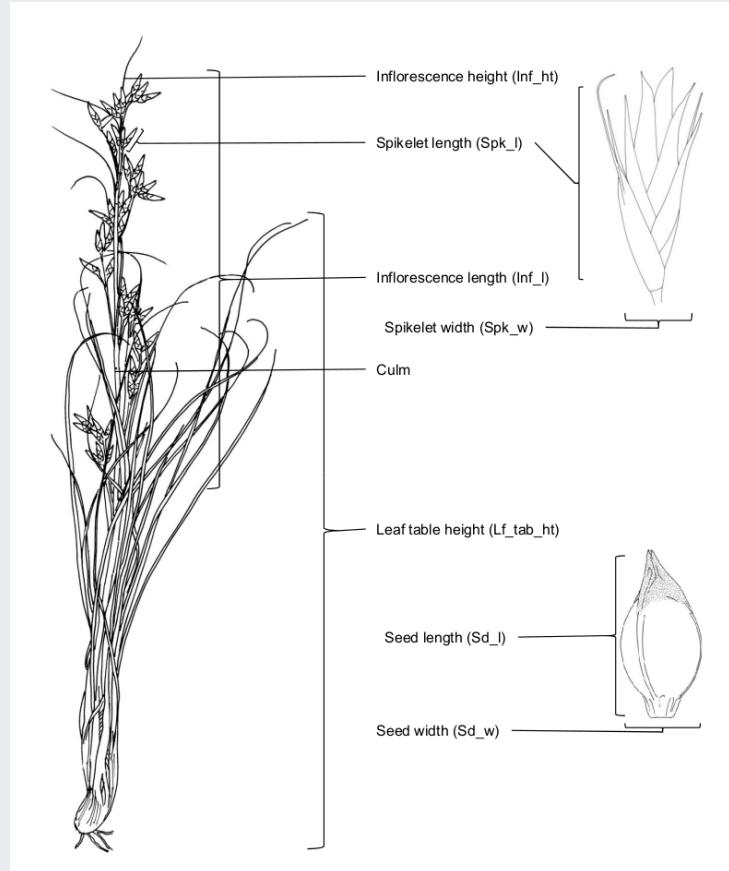


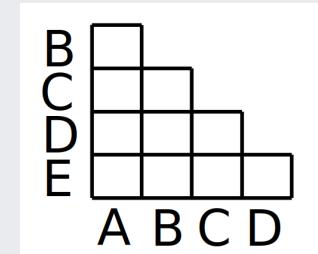
Image from <https://www.poolparty.biz/taxonomy-management-101>

Defining functional groups quantitatively

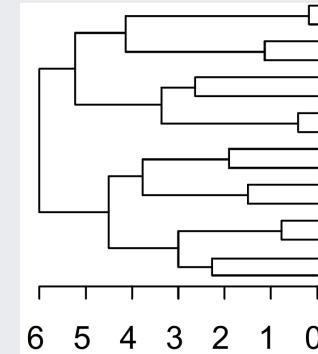
1) Measure traits of the species under study



2) Calculate functional distances between species



3) Cluster species based on distances



4) Define groups based on similarity (depth in tree) or desired number of groups

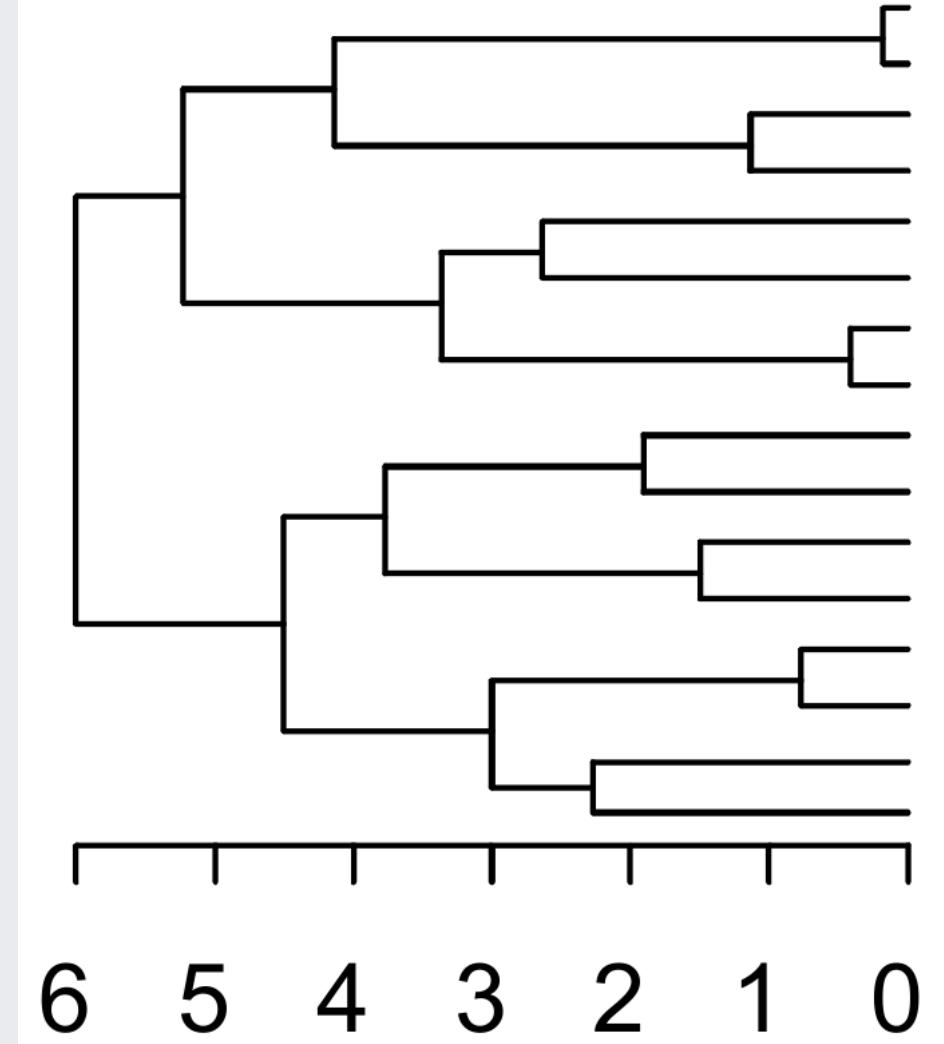
...but wait a second?

There's a lot of useful information in the data and analyses used to define functional groups quantitatively!

Continuous measures of functional diversity

Rather than lose that information by defining discrete groups and counting them, we can use the unique information directly!

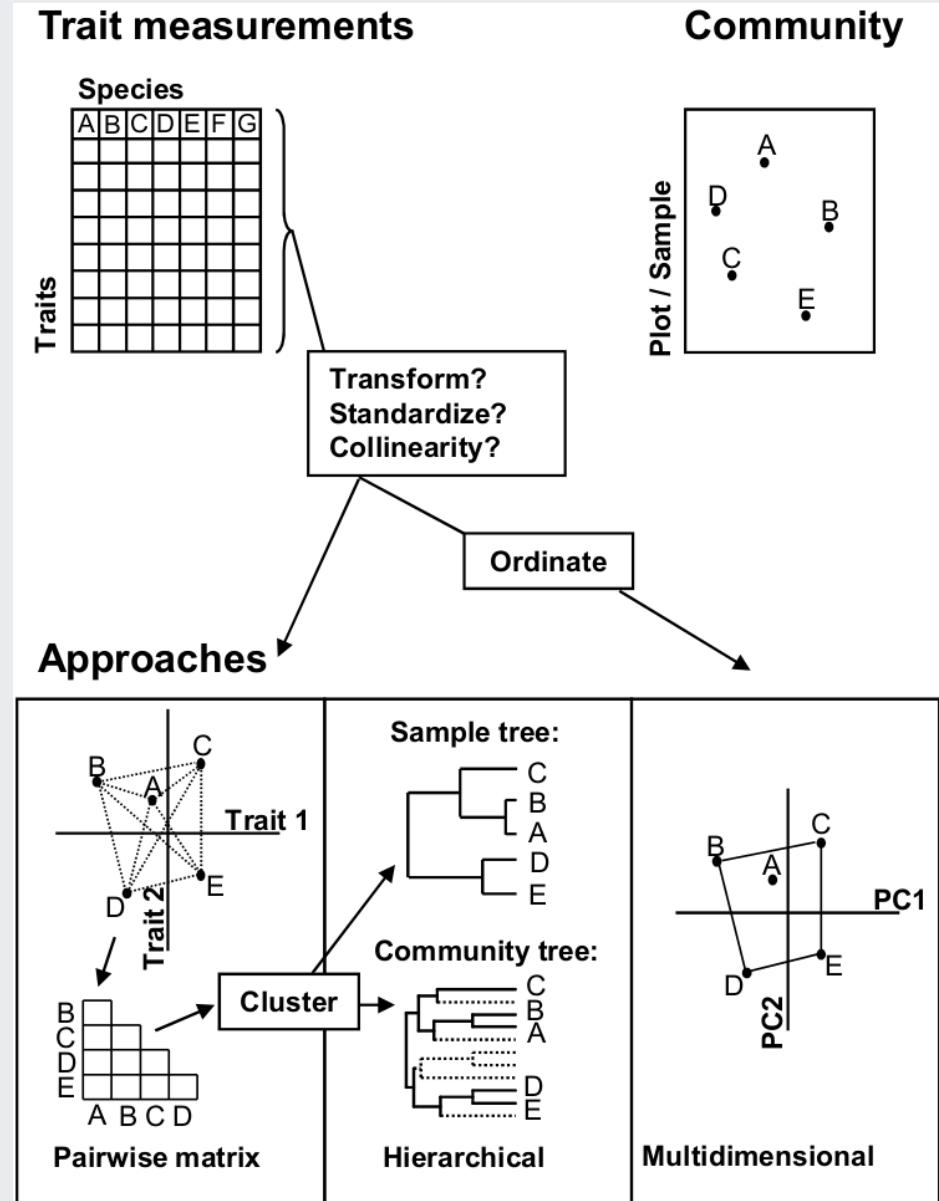
E.g. functional diversity can be calculated as the *sum of the branch length* joining all species in the sample (Petchey and Gaston 2002)



Continuous measures of functional diversity

There are 3 major approaches to calculating **continuous** metrics of functional diversity:

- *Pairwise distances* - e.g. mean or sum of the pairwise distances between all species in a sample (Walker et al. 1999)
- *Hierarchical clustering* - e.g. sum of the branch length joining all species in the sample (Petchey and Gaston 2002)
- *Multidimensional ordination* - e.g. the area or volume of encompassed by the set of species in an ordination of trait space - 2 or more dimensions - (Villeger et al. 2008)

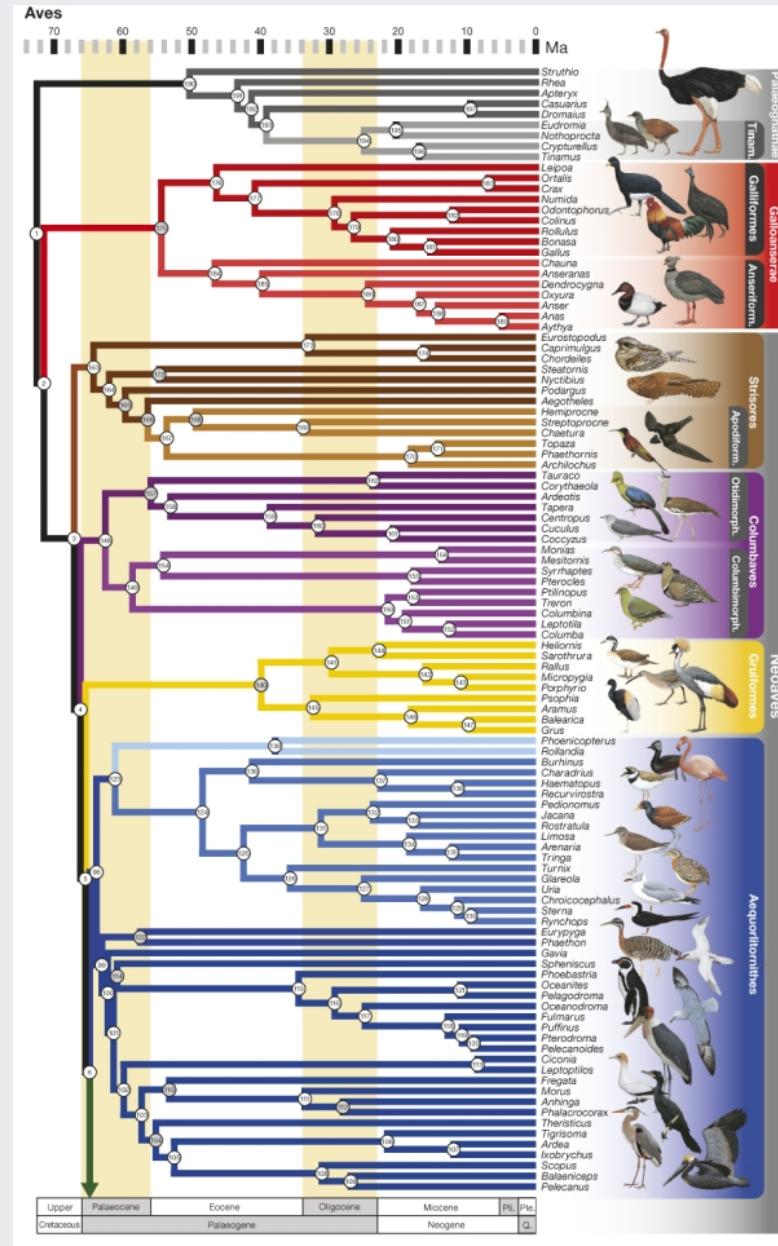


Phylogenetic diversity

A **molecular phylogeny** (or "phylogenetic tree") represents the relationships between species based on similarity of their DNA.

Branch lengths are usually time-calibrated based on a molecular clock (rate of mutation through time) to represent time (or evolutionary history).

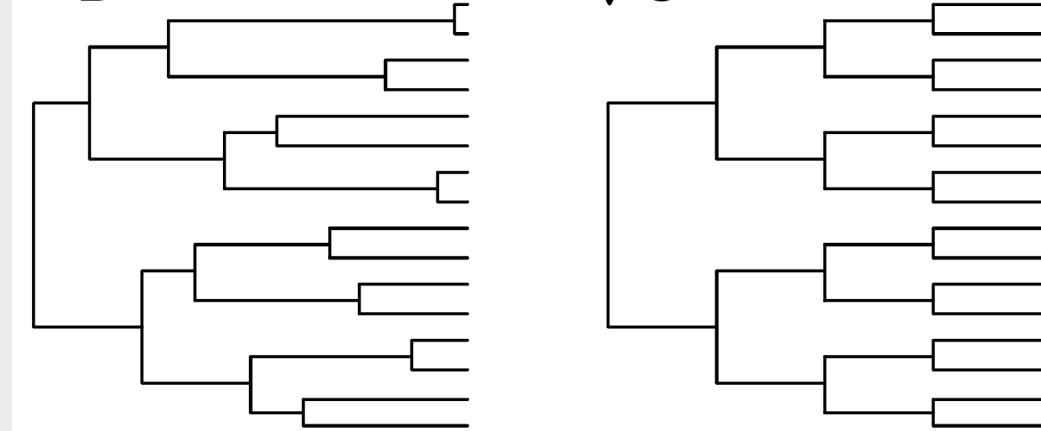
Phylogenetic distance is often considered a more complete or integrated measure of the functional similarity of species, because it avoids subjectivity in the selection of traits measured...



Continuous measures of phylogenetic diversity

Similar approaches used for phylogenetic diversity.

- *Pairwise distances* - e.g. mean pairwise distances (branch lengths) between all species in a sample or minimum nearest taxon distance (Webb et al. 2002)
- *Phylogenetic trees* - e.g. sum of the branches joining all species (Faith 1991)
 - can also use the taxonomic hierarchy instead of a phylogeny, but this suffers from the subjectivity of taxonomic ranks
- No *multidimensional ordination* methods for phylogenetic diversity



Molecular phylogeny vs taxonomic hierarchy

The sum of the branch lengths of a phylogeny linking species in a sample represents the *sum total independent evolutionary history* in that sample.

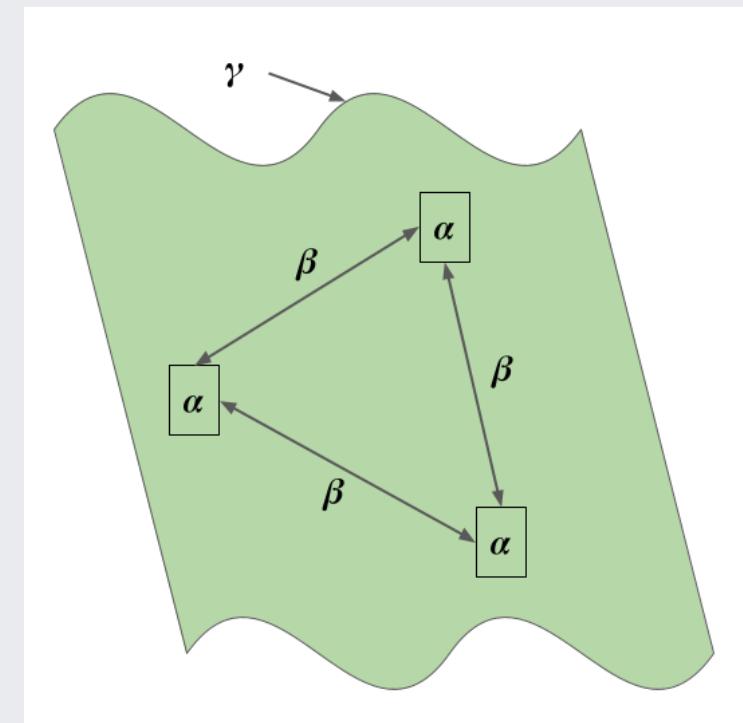
The taxonomic hierarchy (Order, Family, Genus etc) is far less objective.

- That said, phylogenies aren't perfect, and there are many sources of error - molecular regions sampled, methods used, etc.

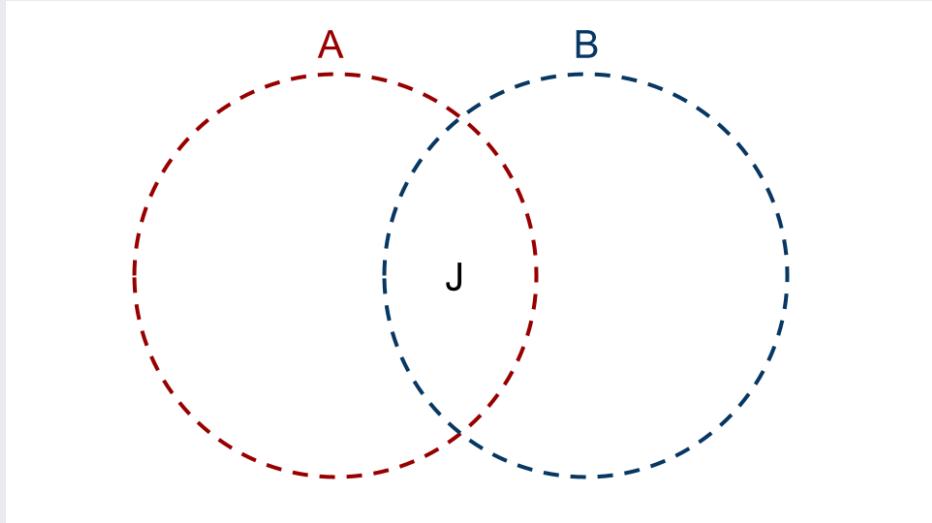
What about the other components of functional and phylogenetic diversity?

We've only covered measures of α (or γ) diversity.

Similar methods as for species diversity can be applied to discrete and continuous measures of functional and phylogenetic β diversity...



Functional or phylogenetic beta 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 used for...

Discrete measures

when based on *counts of functional groups or taxonomic ranks* instead of species

Continuous measures

when based on **branch length** (e.g. PhyloSor - Bryant et al. 2008)

So what?

How does being able to measure functional or phylogenetic diversity help us?

"Phylogenetic regionalization"

Defining phytoregions based on turnover of phylogenetic diversity in the (woody) flora of southern Africa.

These kinds of novel analyses can reveal areas of novel evolutionary history that were previously not recognised!

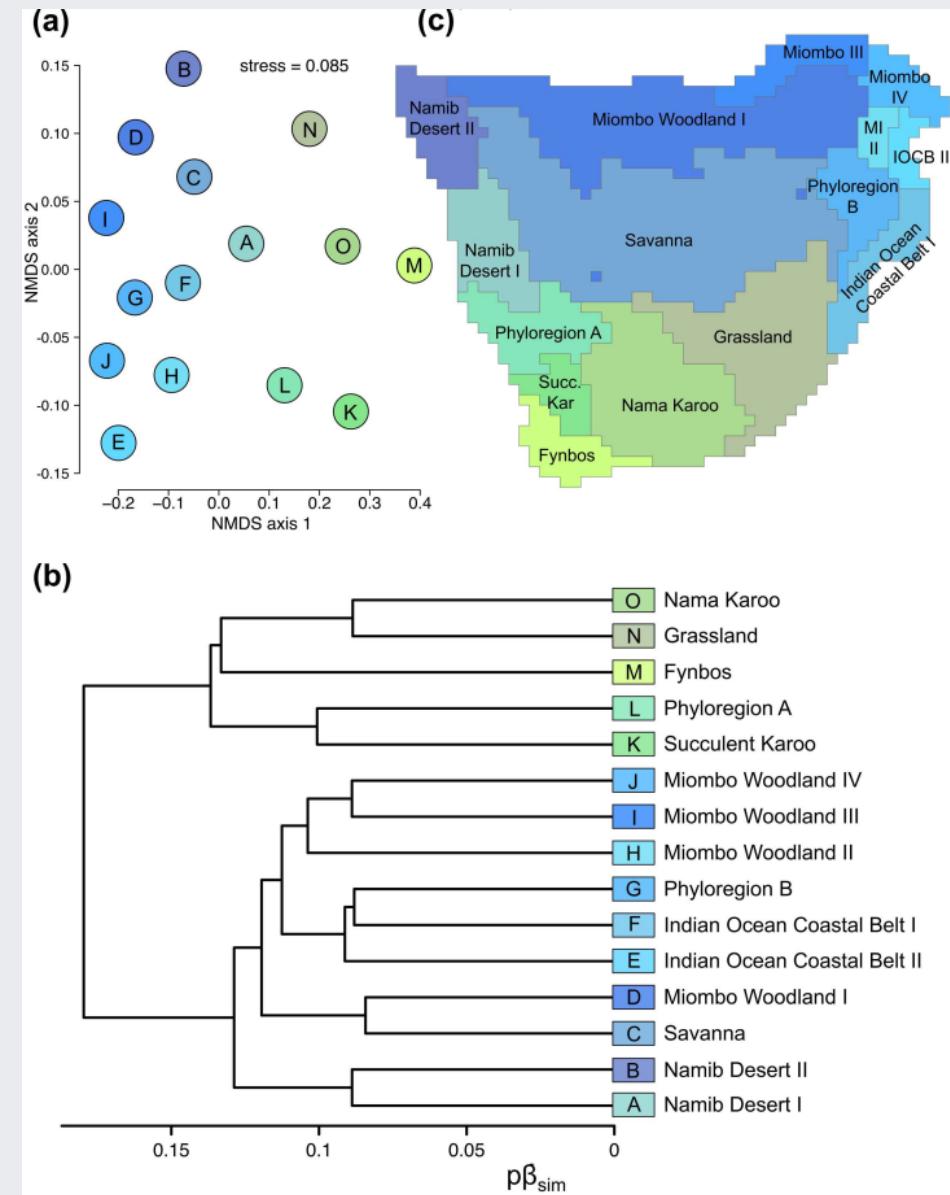


figure from Daru et al. 2016

Deciphering the determinants of community assembly

Don't worry about the scary figure... This is the focus of the next two lectures...

But first, it would be useful if you knew more about...

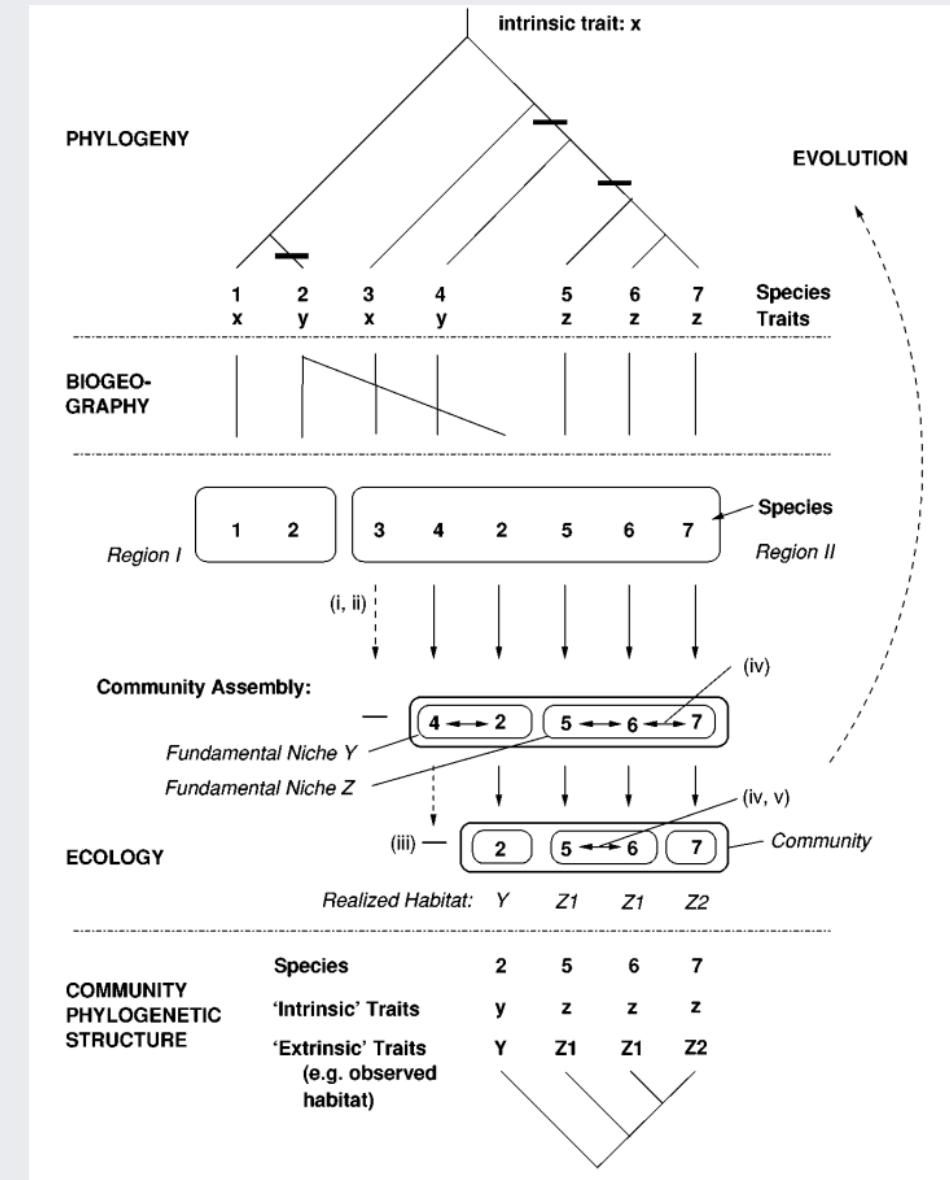


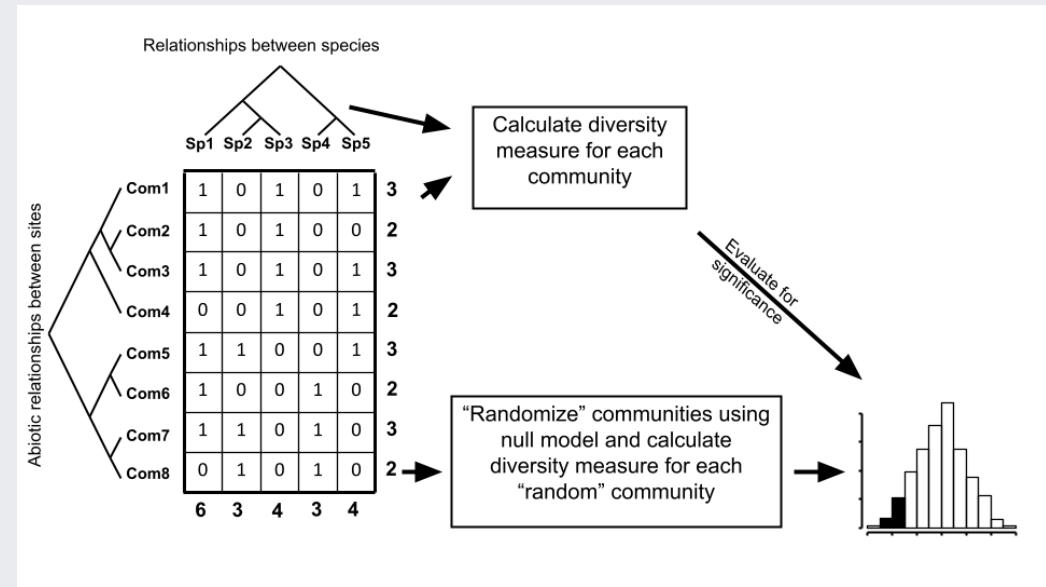
figure from Webb et al. 2002

Null models...

We often explore the drivers behind the patterns of diversity we see by contrasting different measures of diversity and/or comparing them to the patterns we would expect to see in the absence of that driver.

One commonly used method for generating the expected patterns is *null models*...

Null models can be used to "randomize" properties of interest in the data. Typically we generate a large number of "randomized" datasets (e.g. 999) and explore where the observed data rank with respect to the null datasets.



We can address questions like:

- Are species in communities more closely (or distantly) related than we'd expect?
- Are species in communities more functionally similar (or dissimilar) than we'd expect?

And infer processes from these patterns.

figure from Slingsby 2011, PhD

A note on "randomize"...

I put it in inverted commas, because nothing is ever truly random. Also because random is almost never a reasonable null expectation.
I would never expect anything in biology to be completely random, and to do so seems silly.

Null models...

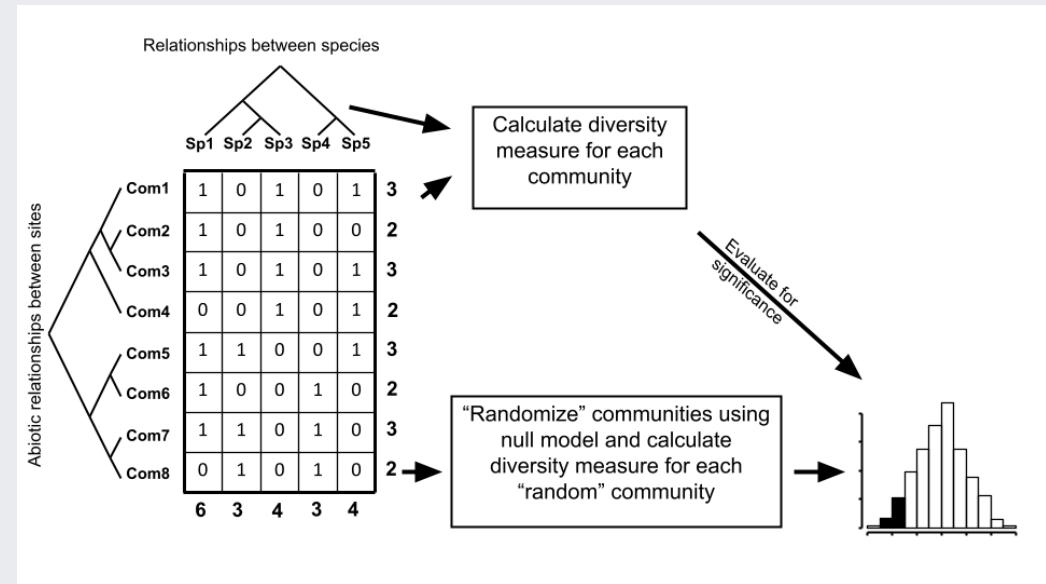
Null models "randomize" properties of interest in the data, serving as a "null expectation" for comparison to your actual data.

There are a number of ways of doing this, but the key is to only randomize the property of interest and keep everything else the same.

Properties include (*inter alia*):

- functional or phylogenetic relationships
- abiotic (or spatial) relationships among sites
- number of species in communities (row sums)
- number of occurrences (or abundances) of species across all communities (column sums)

You have to think very carefully about what properties are affected when applying null models!



You also need to think carefully about how you sample your communities and how you structure them in your null model (e.g. grouping and analyzing sites separately by region or doing one global analysis, etc).

See Gotelli and Graves 1996 for more detail.

figure from Slingsby 2011, PhD

Take-home

There's a lot more to diversity than simple counts of species.

Functional and phylogenetic diversity allow us to explore more intricate questions around the ecology, evolution and function of assemblages.

Null models can be useful for exploring the factors that determine the assembly of communities.

References

- Gotelli, N. J. and R. K. Colwell (2001). "Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness". In: *Ecology letters* 4.4, pp. 379-391. ISSN: 1461-023X, 1461-0248. DOI: 10.1046/j.1461-0248.2001.00230.x.
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- Whittaker, R. H. (1972). "Evolution and measurement of species diversity". En. In: *Taxon* 21.2-3, pp. 213-251. ISSN: 0040-0262, 1996-8175. DOI: 10.2307/1218190.

Thanks!

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