

Alpha Diversity – Distance-Based

SESYNC

1 February 2017

Functional Diversity (FD) via Petchey & Gaston

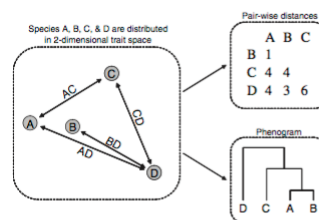
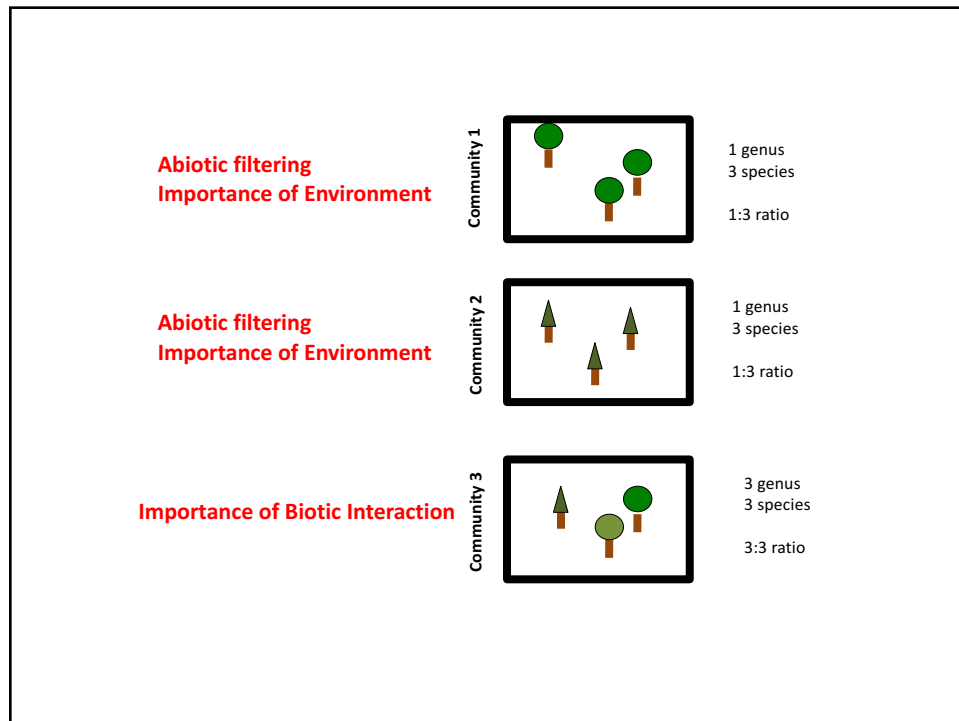


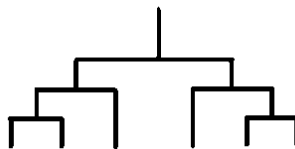
Figure 2 Measuring functional diversity is a problem of how to measure the amount of variation represented by a set of points in multivariate space, for example, species A, B, C and D in the left-most dashed box. The arrows between the species (shaded circles) represent four of the six pair-wise distances. All six pair-wise distances are given in the matrix in the upper-right dashed box. Pair-wise distances are used directly by some measures of functional diversity (Table 1). The phenogram in the lower-right dashed box is a hierarchical description of the distances between species. Some measures of functional diversity work directly on this phenogram (Table 1). In these examples, the distance metric (i.e. Euclidean, Manhattan and Jaccard) is arbitrary, as is the clustering method (e.g. average linkage and minimum linkage) that produced the phenogram.



Beyond genus:species

- Solution for genus:species = Use phylogenetic trees to estimate the relatedness of coexisting species
 - This solution was first proposed by Cam Webb (Webb 2000 American Naturalist)

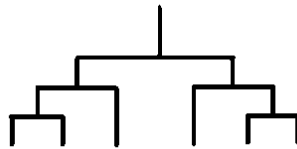
Phylogeny



Community Assembly and Species Co-Existence

- Cam Webb's solution proposed to use a phylogenetic tree to estimate the relatedness of species in a community rather than using the traditional genus : species ratio approach

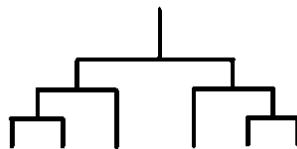
Phylogeny



Community Assembly and Species Co-Existence

- To do this first one must first generate a phylogeny that represents all possible species that could potentially exist in a community (i.e. a *community phylogeny*).
- We also need data on species in communities

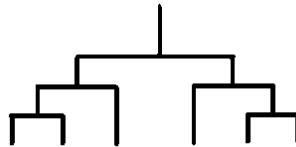
Phylogeny



Community Assembly and Species Co-Existence

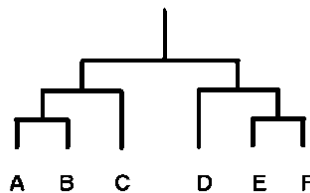
- In the next slides I will show you the example from Webb (2000) where he provides a cartoon of: 1) a community phylogeny; 2) a phylogenetic distance matrix; 3) a calculation of MPD and NRI and 4) a calculation of MNTD and NTI

Phylogeny



Community Phylogeny

Phylogeny



Community 1: A, B, C, D

Community 2: A, B, E, F

Nodal distances:

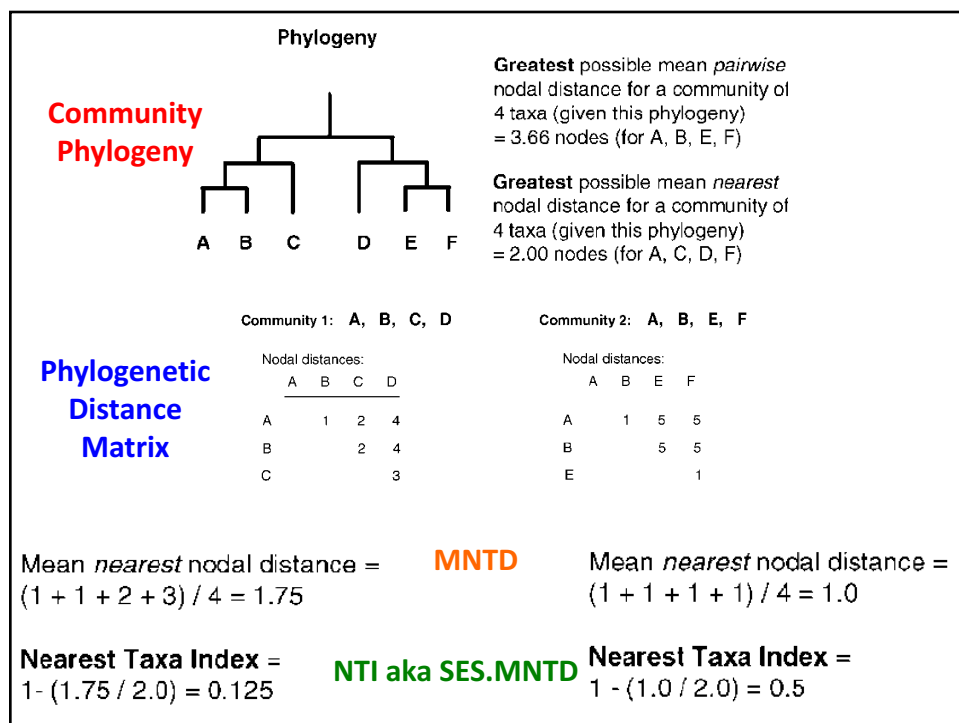
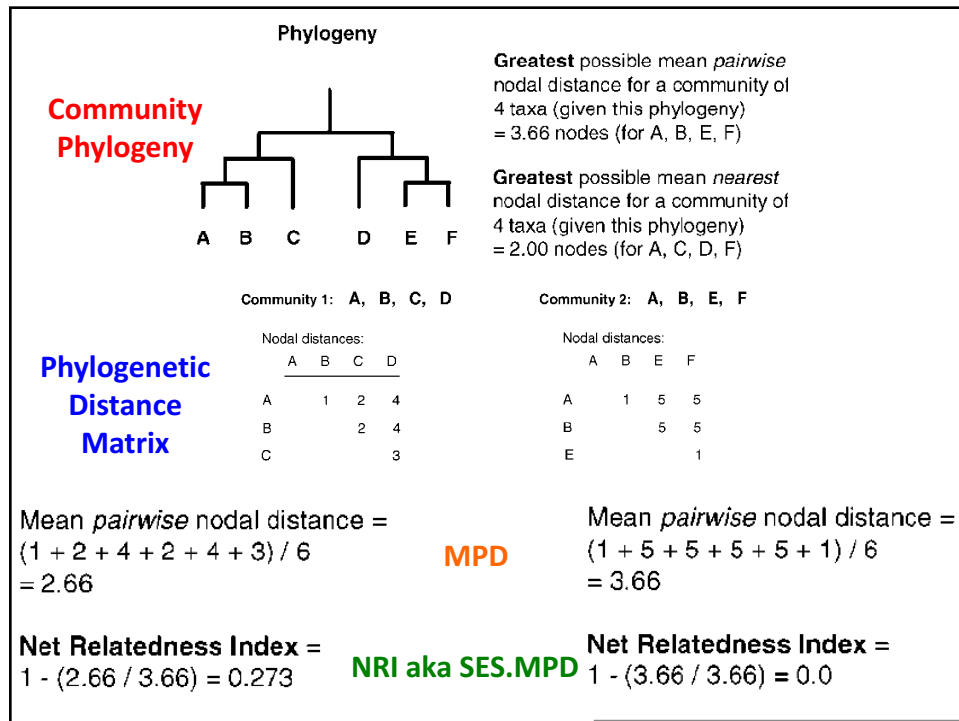
	A	B	C	D
A		1	2	4
B			2	4
C				3

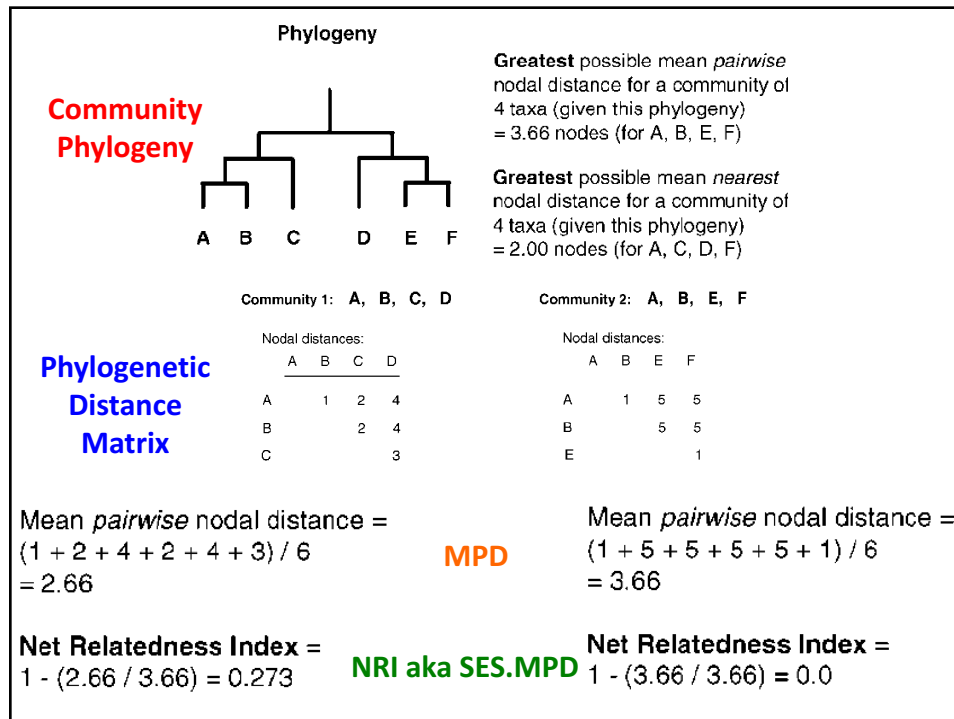
cophenetic(phylo)

**Phylogenetic
Distance
Matrix**

Nodal distances:

	A	B	E	F
A		1	5	5
B			5	5
E				1





Community Assembly and Species Co-Existence

- The approach by Webb (2000) and a review article by Webb et al. (Annual Reviews Ecol Syst 2002) sparked major interest in what is now termed 'community phylogenetics'
- This literature was running in parallel with a functional diversity literature often using the exact same distance matrix-based metrics (pairwise and nearest neighbor)

Main Phylogenetic Diversity Indices

phylogenetic distance matrix instead of a trait distance matrix. The pairwise metric that Webb [28] developed is still the most widely used metric and is called the mean pairwise distance (*mpd*).

$$mpd = \frac{\sum_i^n \sum_j^n \delta_{i,j}}{n}, \text{ where } i \neq j$$

Where there are n species in the community or sample, δ is the phylogenetic distance matrix, and $\delta_{i,j}$ is the phylogenetic distance between species i and j . Because this metric calculates all pairwise distances in a community or sample it is often considered to be a 'basal' metric of PD. That is, this metric and all other pairwise metrics capture the overall phylogenetic dissimilarity of the taxa in a sample and do not detect finer scale phylogenetic patterns. We will discuss this in more detail in the next subsection on

Community 1: A, B, C, D

Nodal distances:				
	A	B	C	D
A		1	2	4
B			2	4
C				3

Community 2: A, B, E, F

Nodal distances:				
	A	B	E	F
A		1	5	5
B			5	5
E				1

Main Phylogenetic Diversity Indices

closely related. In such instances the abundance weighted *mpa* value would be much higher or much lower, respectively, than the un-weighted *mpd* value.

The abundance weighted *mpd*, which I will call *mpd.a*, can be formalized as follows:

$$mpd.a = \frac{\sum_i^n \sum_j^n \delta_{i,j} f_i f_j}{\sum_i^n \sum_j^n f_i f_j}, \text{ where } i \neq j$$

The variables in the *mpd.a* equation are the same as those in the *mpd* equation with the addition of the abundances of species denoted with the variable f for frequency. The *mpd.a* metric was 'invented' and became more widely used towards the end of the first decade of this millennium. However, it should be pointed out that Rao had published a very similar metric nearly three decades earlier [68]. The Rao metric was designed as a general dissimilarity metric utilizing a distance matrix between taxa and has been applied to both phylogenetic and trait based investigations. The primary difference between the Rao metric for within community diversity and the *mpd.a* calculation is that species i can equal species j . In simple terms, this means that a mean of the lower triangle of a community phylogenetic distance matrix is calculated using the diagonal elements.

Main Phylogenetic Diversity Indices

$$Rao's D_{alpha} = \frac{\sum_i \sum_j \delta_{i,j} f_i f_j}{\sum_i \sum_j f_i f_j}$$

While the inclusion of zeros in the Rao calculation, indicating the distance from an individual species to itself, is conceptually important we will see below that the *mpd.a* and *Rao's D_{alpha}* metrics are monotonic and therefore will give the same rankings of PD when comparing communities in your community data matrix. In other words, conceptually it might matter, but it will not matter for your results.

In the spirit of consistency we will proceed with a simple calculation of *mpd.a* in R while understanding that this concept, and essentially the same metric, was invented by Rao [68]. The calculation of *mpd.a* is slightly more difficult because we must weight the mean of the phylogenetic distances separating all species in a community by the product of their abundances. We will eschew the calculation of the metric for a single community

Main Phylogenetic Diversity Indices

implemented in the literature. The first metric I will cover was produced by Hardy and Senterre [69] where they translated commonly used metrics from population genetics, such as F_{st} , into the realm of community phylogenetics. Specifically, Hardy and Senterre proposed that phylogenetic diversity, D , within a community k can be calculated as:

$$D_k = \sum_i^n \sum_j^n \delta_{i,j} f_{ik} f_{jk}$$

Where the variables are the same as the above equations aside from using a subscript of ik to specify the abundance of species i in community k and not another community. This clause becomes important when Hardy and Senterre [69] extend their mathematical treatment to the partitioning of gamma phylogenetic diversity into the within and between community components. We can see that this metric should be highly correlated with both the Rao and *mpd.a* metrics and is a natural phylogenetic extension of the Shannon Diversity index [69]. We can also see that this metric could be simply calculated using the above code for *mpd.a* that we have written replacing the weighted mean by summing the product of the community phylogenetic distance matrix and abundance products.

Main Phylogenetic Diversity Indices

$$mntd = \frac{\sum_i^n \min \delta_{i,j}}{n}, \text{ where } i \neq j$$

Where there are n species in the community, $\delta_{i,j}$ is the phylogenetic distance between species i and species j , and $\min \delta_{i,j}$ is the minimum phylogenetic distance between species i and all other species in the community (i.e. the nearest neighbor distance). As in the *mpd* calculation, the distance from one species to itself is not considered. If we consider the structure of a community phylogenetic distance matrix it quickly becomes clear how to calculate *mntd*. In particular, for each row (i.e. species) in the matrix we

Community 1: A, B, C, D

Nodal distances:				
A	B	C	D	
A	1	2	4	
B		2	4	
C			3	

Community 2: A, B, E, F

Nodal distances:				
A	B	E	F	
A	1	5	5	
B		5	5	
E			1	

Main Phylogenetic Diversity Indices

$$mntd.a = \frac{\sum_i^n \min \delta_{i,j} f_i}{n}, \text{ where } i \neq j$$

Where we have added the variable f_i to indicate the abundance of species i in the community. In order to calculate this new metric we can see that we simply need to weight the mean by abundance of each species represented as rows in the community phylogenetic distance matrix. In other words, we must quantify the product of the abundance of a species with the minimum value found in the row in the community phylogenetic distance matrix for that species and take an average across all species. This can be accomplished with the following function.

Main Phylogenetic Diversity Indices

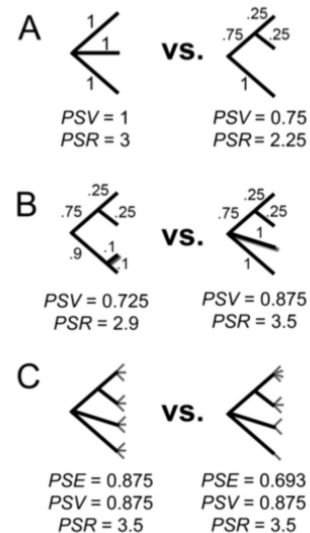
- Helmus metrics

VOL. 169, NO. 3 THE AMERICAN NATURALIST MARCH 2007

E-ARTICLE

Phylogenetic Measures of Biodiversity

Matthew R. Helmus,^{1,*} Thomas J. Bland,^{1,†} Christopher K. Williams,^{2,‡} and Anthony R. Ives^{1,§}



Main Phylogenetic Diversity Indices

- Phylogenetic Species Variability (PSV) – Helmus et al. 2007 Am. Nat.
- For ultrametric phylogenies = 2 times MPD (pres/abs weighted)

Main Phylogenetic Diversity Indices

- Phylogenetic Species
Evenness(PSE) – Helmus et al.
2007 Am. Nat.
- Scales with the abundance-
weighted version of MPD

Main Phylogenetic Diversity Indices

- Phylogenetic Species Richness
(PSR) – Helmus et al. 2007 Am.
Nat.
- MPD multiplied by species
richness

Awash in metrics!!!!

- Comparison of different metrics (Vellend et al. 2011 in Biological diversity: frontiers in measurement and assessment)

CHAPTER 14

Measuring phylogenetic biodiversity

Mark Vellend, William K. Cornwell, Karen Magnuson-Ford,
and Arne Ø. Mooers

Table 14.3 Correlations among sums of type I metrics, as well as species richness (*SR*) and phylogenetic diversity (*PD*), for 10 000 simulated species sets selected from a pure birth phylogenetic tree. Short forms correspond to those in Table 14.1.

<i>TD</i>	0.92							
<i>SO</i>	0.95	0.91						
<i>WSO</i>	0.94	0.92	0.98					
<i>PE</i>	0.93	0.83	0.91	0.87				
<i>SEH</i>	0.95	0.96	0.94	0.95	0.86			
<i>SEH_fair</i>	0.97	0.96	0.95	0.95	0.87	1.00		
<i>OSS</i>	0.73	0.91	0.76	0.79	0.62	0.88	0.87	
<i>PD</i>	0.87	0.90	0.85	0.86	0.78	0.94	0.94	0.87
	<i>SR</i>	<i>TD</i>	<i>SO</i>	<i>WSO</i>	<i>PE</i>	<i>SEH</i>	<i>SEH_fair</i>	<i>OSS</i>

Metrics somewhat unique to
functional diversity

Functional (alpha) Diversity

- In many ways the development of functional diversity measures has been the same as phylogenetic diversity measures
- Indeed many metrics were borrowed from one field or the other or even designed for both functional and phylogenetic at the same time

Functional (alpha) Diversity

- Similar to as phylogenetic diversity there are 3 general classes of functional diversity metrics
 - FD (same as PD, but with trait phylogeny)
 - Pairwise metrics
 - Nearest Neighbor metrics
 - Additional types exist that don't fall neatly into one of these categories
- But there are others that incorporate ranges and 'functional groups'
- The speed at which metrics are published for FD is incredible and outpaces the production of new PD metrics. So there are MANY to consider

Why not just phylogeny?

- Many phylogenetic diversity studies are simply using the phylogeny as a proxy for functional similarity.
- So why not just measure functional diversity directly?
 - Go measure some traits (presumably the 'right' traits)

Now that we have traits ... what do we do?

- Most functional trait analyses of communities require you to quantify the similarity of species
 - Can be done using a simple Euclidean distance
 - Can be done using Euclidean distance AND a clustering algorithm to make a dendrogram

Now that we have traits ... what do we do?

- Most functional trait analyses of communities require you to quantify the similarity of species
 - Can be done using a simple Euclidean distance
 - Can be done using Euclidean distance AND a clustering algorithm to make a dendrogram
- An important consideration!
 - Often we measure say 6 traits (4 from LES, 1 from WES and 1 from SES)
 - So the Euclidean distance is biased by the leaf economics spectrum
 - In my opinion reducing data redundancy via a PCA is essential prior to calculating a similarities

Raw Distance Matrices vs Dendrograms

- Distance matrices are often preferred because there is no distortion of the data like there might be when using a clustering algorithm.
 - Also argued that traits aren't hierarchically clustered or ordered

Raw Distance Matrices vs Dendrograms

- Distance matrices are often preferred because there is no distortion of the data like there might be when using a clustering algorithm.
 - Also argued that traits aren't hierarchically clustered or ordered while a phylogenetic tree is (not sure I totally 'buy' this argument)
- Some prefer dendrograms because they cluster into groups.
 - Functional groups may be a useful concept or application and fine scale variation may not be important
- Further many use dendrograms simply because the metrics developed can only use dendrograms.

Raw Distance Matrices vs Dendrograms

- In many cases you can get a different 'answer' from these two approaches
- So justifying them is important
- More and more you see papers with distance matrices and not dendrograms

Functional (alpha) Diversity

- Pairwise metrics
- The most commonly used metrics are a simple pairwise distance between all individuals or species in a plot (same as MPD)
 - These have a LONG history of use dating back to at least the 1970's with limiting similarity research
- These can accept dendrograms or raw trait distance matrices

Functional (alpha) Diversity

- Nearest Neighbor metrics
- The most commonly is the mean nearest neighbor distance (same as MNND or MNTD)
 - Again these have a long history dating to the 1970's
- Alternative methods examine the *st dev* of the nearest neighbor distances (how equally spaced are species in 'trait space')
- Accept dendrograms or raw trait distance matrices

Functional (alpha) Diversity

- Descriptive stats of trait distributions
- Range ('trait volume' in multiple dimensions)
- Variance
- Skew
- Kurtosis
- Does not use dendrogram
- Can use abundance but it can do strange things to these metrics

Functional (alpha) Diversity

- Functional group richness statistics
- Binning species into functional groups based on trait similarity
- Counting up groups
- Needs a trait dendrogram and can use abundance

Laliberte & Legendre

- Many of the previous analyses are now in the R package “FD”
- Laliberte & Legendre 2010 Ecology formalized many of these and refined some

Ecology, 91(1), 2010, pp. 299–305
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A distance-based framework for measuring functional diversity from multiple traits

ETIENNE LALIBERTÉ^{1,3} AND PIERRE LEGENDRE²

Laliberte & Legendre

Ecology, 91(1), 2010, pp. 299–305
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A distance-based framework for measuring functional diversity from multiple traits

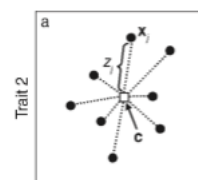
ETIENNE LALIBERTÉ^{1,3} AND PIERRE LEGENDRE²

- The first is functional dispersion
- This is essentially a pairwise distance measure

computed as

$$FDis = \frac{\sum a_j z_j}{\sum a_j}$$

where a_j is the abundance of species j and z_j is the distance of species j to the weighted centroid c .

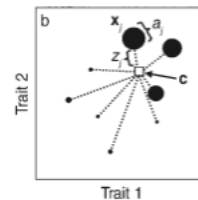


Centroid

$$c = [c_i] = \frac{\sum x_i}{n}$$

Functional dispersion

$$FDis = \frac{\sum z_i}{n}$$



Centroid

$$c = [c_i] = \frac{\sum a_j x_j}{\sum a_j}$$

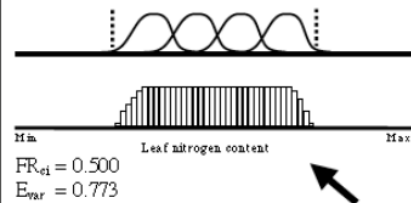
Functional dispersion

$$FDis = \frac{\sum a_j z_j}{\sum a_j}$$

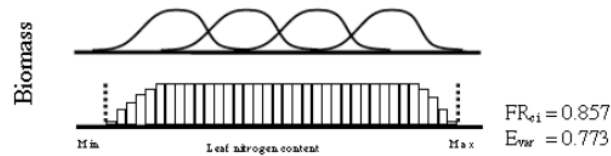
Laliberte & Legendre

- Functional richness = range

(A1) Lower functional richness



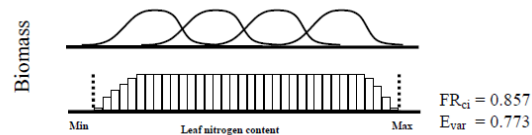
(B) High functional evenness and functional richness



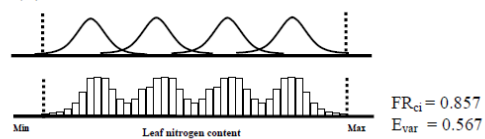
Laliberte & Legendre

- Functional evenness = overlaps of trait distributions weighted by abundances

(B) High functional evenness and functional richness

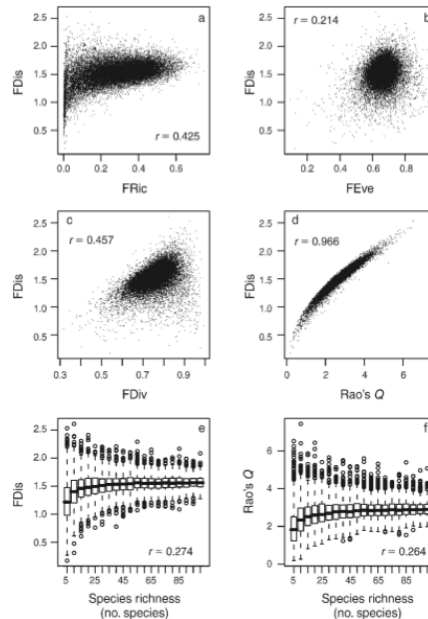


(C) Lower functional evenness



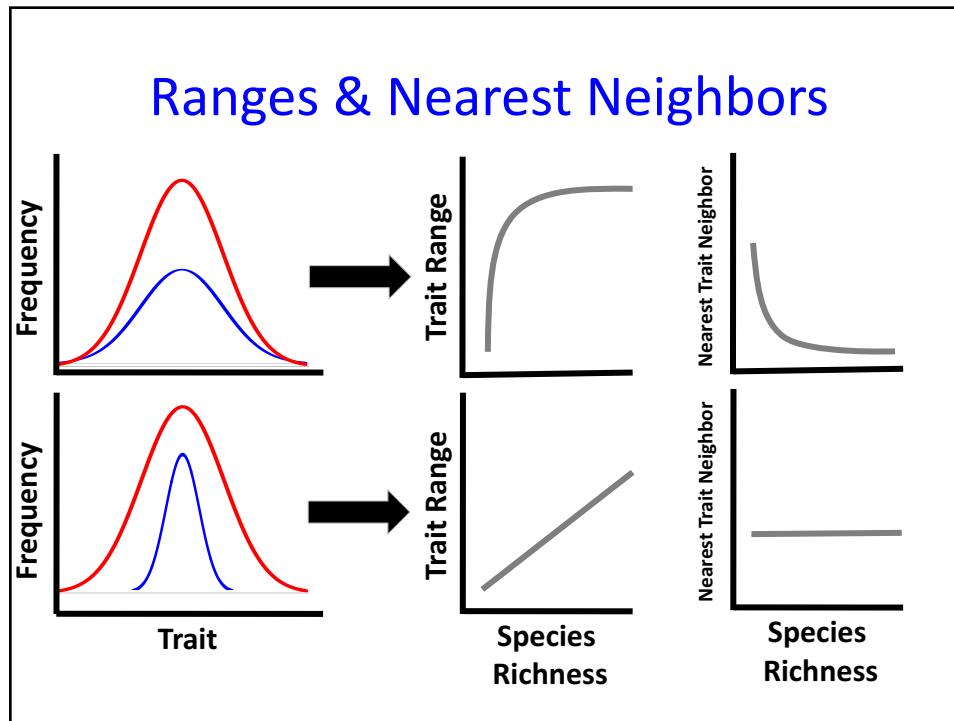
Laliberte & Legendre

- Relationships between the metrics in L & L



Combining Metrics

- In many cases multiple metrics are utilized in the same study to investigate multiple dimensions of functional diversity



Ranges & Nearest Neighbors

- Ricklefs & O'Rourke 1975 in Evolution

- Wing morphological 'volume' and nearest neighbor distance

- Prediction

- Limiting similarity should increase volume in tropics and maintain nearest neighbor distances across latitude
 - Supported in this paper

ASPECT DIVERSITY IN MOTHS:
A TEMPERATE-TROPICAL COMPARISON¹
ROBERT E. RICKLEFS AND KEVIN O'ROURKE
Department of Biology, University of Pennsylvania, Philadelphia, PA. 19174
Received March 3, 1974

Ranges & Nearest Neighbors

- Ricklefs & O'Rourke 1975 in Evolution
- Ricklefs 2009 American Naturalist
 - Revisits 1975 paper with more data and finds original conclusions not supported
 - Nearest neighbor distances decrease in the tropics

ASPECT DIVERSITY IN MOTHS:
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Notes and Comments
Aspect Diversity in Moths Revisited
Robert E. Ricklefs²
Department of Biology, University of Missouri, St. Louis, Missouri 63121
Submitted July 14, 2009; Accepted October 1, 2009; Electronically published January 26, 2009
Online enhancement: appendix.

Examples of functional diversity studies in forest plots – Kraft et al. 2008 Science

Functional Traits and Niche-Based Tree Community Assembly in an Amazonian Forest

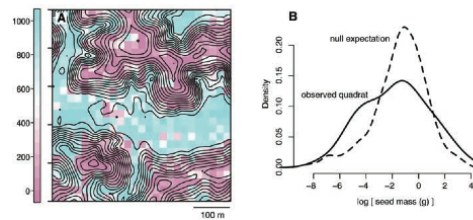
Nathan J. B. Kraft,¹ Renato Valencia,² David D. Ackerly¹

Examples of functional diversity studies in forest plots – Kraft et al. 2008

- Functional traits collected in Yasuni, Ecuador Forest Dynamics Plot
- Are co-occurring species non-random with respect to their traits?

Functional Traits and Niche-Based Tree Community Assembly in an Amazonian Forest

Nathan J. B. Kraft,¹ Renato Valencia,² David D. Ackerly¹

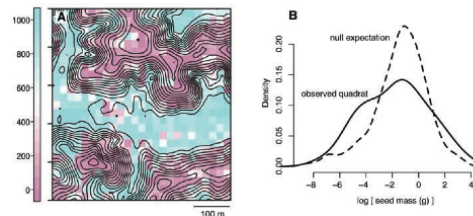


Examples of functional diversity studies in forest plots – Kraft et al. 2008

- Analytical methods:
 - Moments of trait distribution
 - Range
 - NN
 - Null model

Functional Traits and Niche-Based Tree Community Assembly in an Amazonian Forest

Nathan J. B. Kraft,¹ Renato Valencia,² David D. Ackerly¹



Examples of functional diversity studies in forest plots – Kraft et al. 2008

- Results:
 - Many traits are non-random in the quadrats

Functional Traits and Niche-Based Tree Community Assembly in an Amazonian Forest

Nathan J. B. Kraft,¹ Renato Valencia,² David D. Ackerly¹

Table 1. Trait coverage, an example of the ecological significance of each trait, and Wilcoxon signed-rank test of plot-wide null model results. The mean test was two-tailed; all other tests were one-tailed. n.s., not significant; NN, nearest neighbor.

Trait	Species sampled (% of plot stems)	Strategy correlation	Mean	Range	SD of NN distance	Kurtosis	Variance
SLA	1088 (99.9%)	Leaf economics-resource capture (29)	n.s.	<0.0001	0.012	0.007	<0.0001
Leaf nitrogen concentration	559 (90.5%)	Leaf economics-resource capture (29)	n.s.	0.0001	<0.0001	0.604	<0.0001
Leaf size	1084 (99.8%)	Disturbance and nutrient stress strategy (7)	n.s.	<0.0001	<0.0001	<0.0001	<0.0001
Seed mass	321 (58%)	Regeneration strategy (9)	n.s.	0.825	0.761	0.014	0.186
Wood density	265 (29%)	Allocation to growth versus strength/pathogen resistance (19)	n.s.	0.998	0.913	0.233	0.533
Maximum dbh	1123 (100%)	Light capture strategy (30)	n.s.	<0.0001	<0.0001	0.011	<0.0001

OTHER Functional Diversity Frontiers – Neighborhood Models

- Does the functional (or phylogenetic) composition around an individual influence it's growth and survival rates?

ECOLOGY LETTERS

Ecology Letters, (2010) 13: 1503–1514 doi: 10.1111/j.1461-0248.2010.01541.x

LETTER

Trait similarity, shared ancestry and the structure of neighbourhood interactions in a subtropical wet forest: implications for community assembly

Maria Uriarte,^{1,*} Nathan J. B. Kraft,¹ Robin L. Chazdon,¹ Lisa S. Comita,¹ W. John Kress,¹ David Erickson,² Jimena Perez-Montalva,³ Jess K. Zimmerman² and Jill Thompson^{1,4}

Abstract

The phylogenetic structure and distribution of functional traits in a community can provide insights into community assembly processes. However, these insights are sensitive to the spatial scale of analysis. Here, we use spatially explicit, neighbourhood models of tree growth and survival for 19 tree species, a highly resolved molecular phylogeny and information on eight functional traits to quantify the relative efficacy of functional similarity and shared ancestry in describing the effects of spatial interactions between tree

ECOLOGY LETTERS

Ecology Letters, (2011) doi: 10.1111/j.1461-0248.2011.01705.x

LETTER

Phylogenetic density dependence and environmental filtering predict seedling mortality in a tropical forest

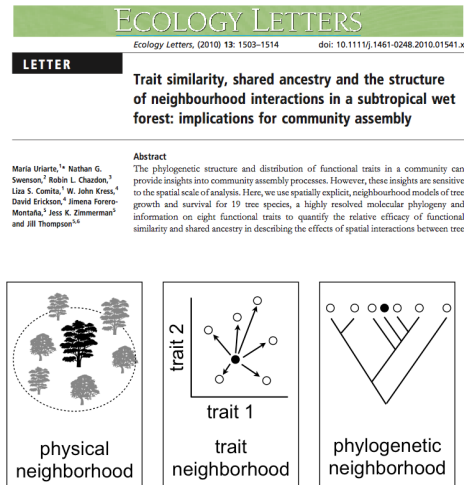
C. E. Timothy Paine,^{1,*} Natalia Norden,^{1,2} Jordana Chao,¹ Pierre-Michel Forget,³ Claire Perennet,⁴ Kate G. Suttle¹ and Christopher Baraloto^{1,2}

Abstract

Negative density dependence (NDD) and environmental filtering (EF) shape community assembly, but their relative importance is poorly understood. Recent studies have shown that seedling's mortality risk is positively related to the phylogenetic relatedness of neighbours. However, natural enemies, whose depredations often cause NDD, respond to functional traits of hosts rather than phylogenetic relatedness *per se*. To understand the roles of NDD and EF in community assembly, we assessed the effects on seedling mortality of functional similarity, phylogenetic relatedness and stem density of neighbouring seedlings and adults in a species-rich montane forest. Mortality risks increased for common species when their functional traits deviated substantially

OTHER Functional Diversity Frontiers – Neighborhood Models

- Is the deviation of an individual's growth or survival rate from that expected for the species linked to the functional (or phylogenetic) 'neighborhood'?



OTHER Functional Diversity Frontiers – Mapping Function on Continental Scales

Ecology, 91(8), 2010, pp. 2234–2241
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Plant geography upon the basis of functional traits: an example from eastern North American trees

NATHAN G. SWENSON^{1,3} AND MICHAEL D. WEISER²

¹Department of Plant Biology, Michigan State University, East Lansing, Michigan 48824 USA

²Department of Biology, North Carolina State University, Raleigh, North Carolina 27695 USA

- Can we map the distribution and diversity of plant function on continental scales?

OTHER Functional Diversity Frontiers – Mapping Function on Continental Scales

- ~18,000 forest inventory plots in the USA
- Compiled a trait database for species

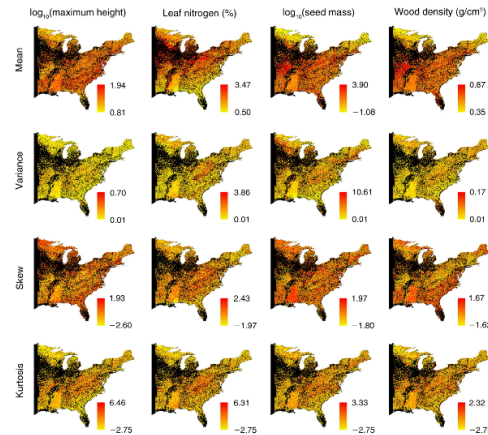
Ecology, 91(2), 2010, pp. 2234–2241
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Plant geography upon the basis of functional traits:
an example from eastern North American trees

NATHAN G. SWENSON^{1,2} AND MICHAEL D. WEISER²

¹Department of Plant Biology, Michigan State University, East Lansing, Michigan 48824 USA

²Department of Biology, North Carolina State University, Raleigh, North Carolina 27695 USA



OTHER Functional Diversity Frontiers – Mapping Function on Continental Scales

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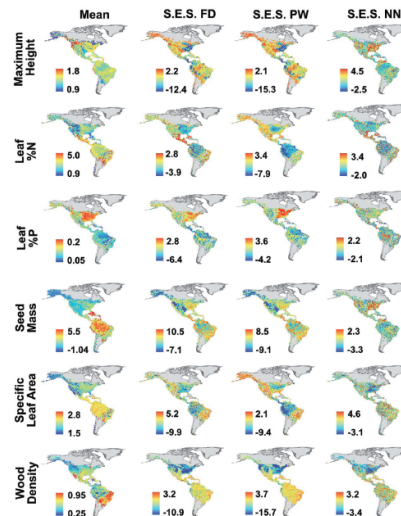
The biogeography and filtering of woody plant functional diversity in North and South America

Nathan G. Swenson^{1*}, Brian J. Enquist^{2,3,4}, Jason Pither⁵, Andrew J. Kerkhoff⁶,
Brad Boyle², Michael D. Weiser⁷, James J. Elser⁸, William E. Fagan⁹,
Jimena Forero-Montaña¹⁰, Nikolaos Fyllas¹¹, Nathan J. B. Kraft¹²,
Jeffrey K. Lake¹, Angela T. Moles¹³, Sandra Patiño¹⁴, Oliver L. Phillips¹¹,
Charles A. Price¹⁵, Peter B. Reich¹⁶, Carlos A. Quesada¹¹, James C. Stegen⁷,
Renato Valencia¹⁷, Ian J. Wright¹⁸, S. Joseph Wright¹⁹, Sandy Andelman³,
Peter M. Jørgensen²⁰, Thomas E. Lacher Jr²¹, Abel Monteagudo²²,
M. Percy Núñez-Vargas²³, Rodolfo Vasquez-Martinez²² and
Kristen M. Nolting¹

- What is the distribution and diversity of plant function across latitude?

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- Functional trait diversity is generally higher than expected in the tropics given their species richness, but the patterns are not simple



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- Over 5,000,000 geo-referenced specimens used
- Largest trait databases compiled to date for a study
- FD, PW, NN in each grid cell of unique species names and a null model

