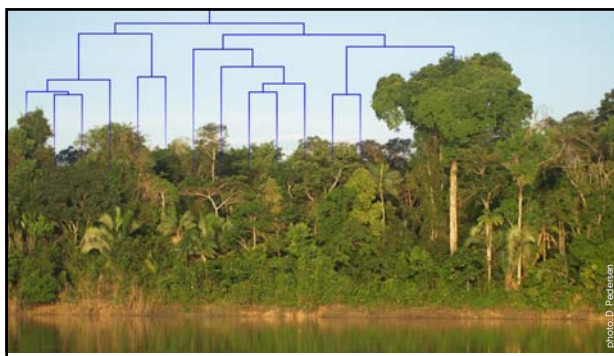




Integrating Phylogenetic Data in Ecological Analysis
Wolf L. Eiserhardt

Ecoinformatic approaches to understand ecological processes in a changing world
Summer School 16.-20.9.2013, Department of Bioscience, Aarhus University

Outline

- Why phylogenetic data in ecological analysis?
- Character evolution: basic principles
- Phylogenetic community ecology
- Phylogenetic data: practical issues
- Tutorial

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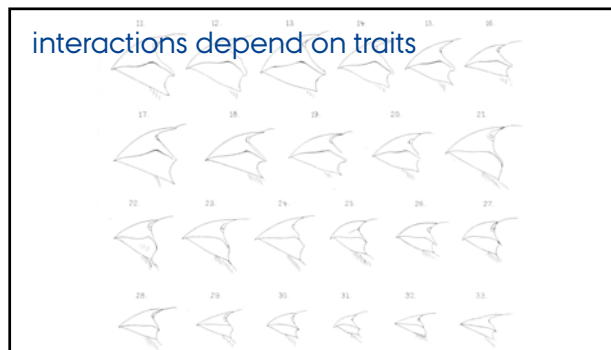
1. ecology = interactions



"It is interesting to contemplate an entangled bank, [...] and to reflect that these elaborately constructed forms, so different from each other, and dependent on each other in so complex a manner, have all been produced by laws acting around us."
Charles Darwin 1859, *On The Origin of Species*

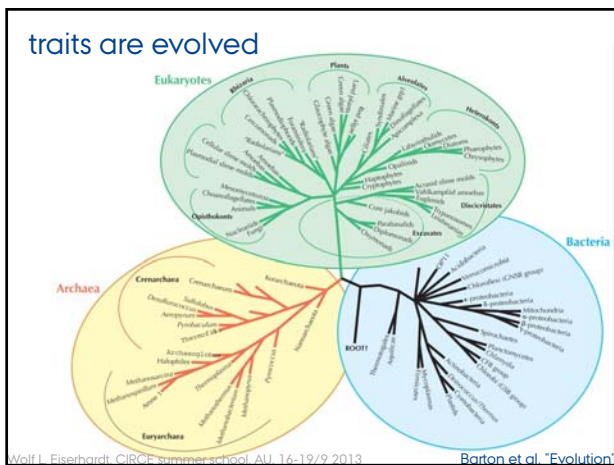
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interactions depend on traits



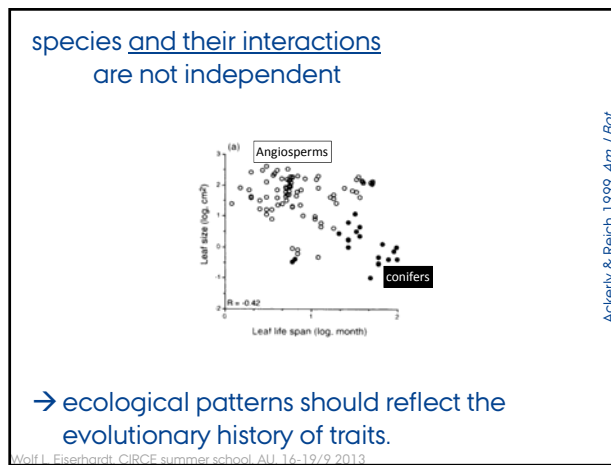
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traits are evolved



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species and their interactions are not independent

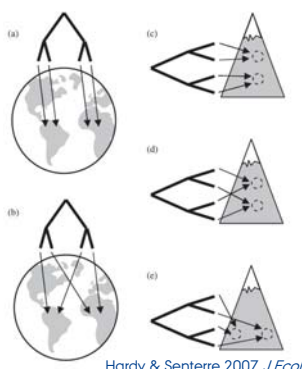


→ ecological patterns should reflect the evolutionary history of traits.

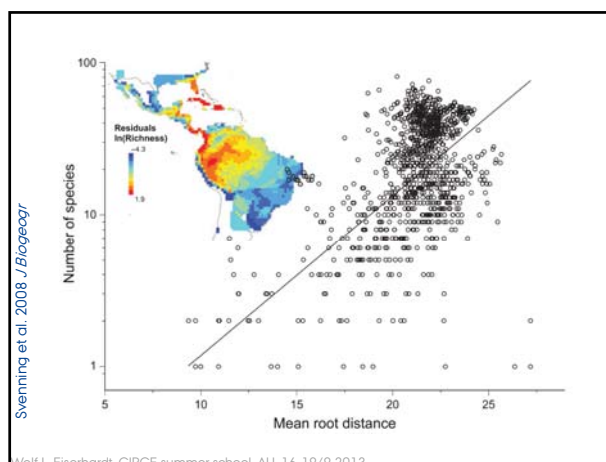
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Ackerly & Reich 1999 *Am. J. Bot.*

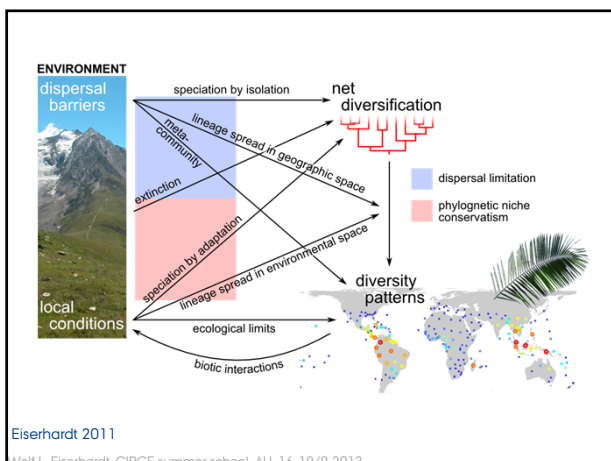
2. species pools ← lineage diversification



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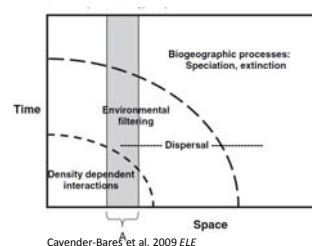


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community assembly: evolutionary history matters across scales



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ecology ↔ evolution

- adaptive speciation/radiation
- coevolution in trophic networks
- character displacement
- convergence
- ...



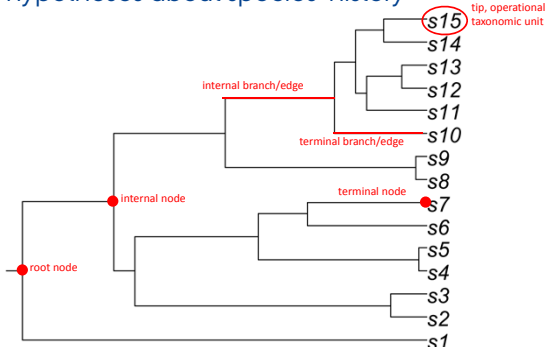
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Outline

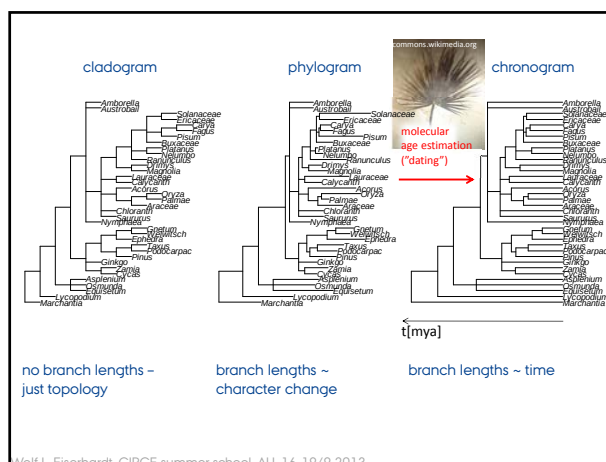
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phylogenetic trees: hypotheses about species' history

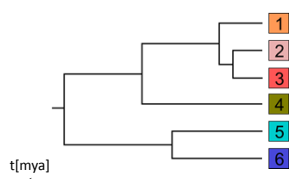


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phylogenetic signal



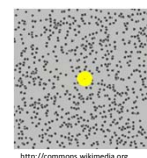
phenotypic similarity ~ time of joint evolution

"Phylogenetic signal [is the] tendency (pattern) for evolutionarily related organisms to resemble each other, with no implication as to the mechanism that might cause such resemblance (process)." Blomberg et al. 2003

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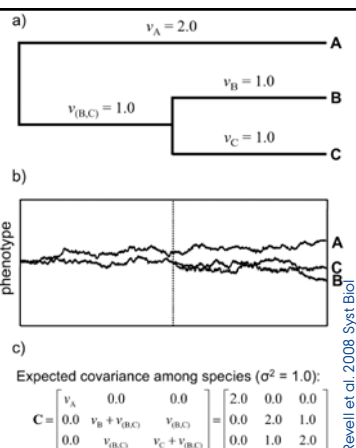
Brownian Motion

$$x_{t+1} = x_t + \mathcal{N}(0, \sigma^2)$$



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Brownian Motion



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Brownian Motion is often wrong.

Numerous alternative models

- Ornstein-Uhlenbeck (selective optima)
- ACDC
- density dependence
- punctuational
- trait-dependent (##SSE-models)
- ...

can be tested using e.g. GEIGER

(Harmon et al. 2008 *Bioinformatics*)

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Phylogenetic Signal (PS)

Quantitative statistic: How strong is the "tendency for related species to resemble each other"?

Blomberg's K: observed vs. BM

$$K = \text{observed} \frac{\text{MSE}_0}{\text{MSE}} / \text{expected} \frac{\text{MSE}_0}{\text{MSE}}$$

0 1 ∞
random BM early divergence,
trait values expectation later stasis - "Phylogen. Niche Conservatism"

(Blomberg, Garland & Ives 2008 *Evolution*)

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Phylogenetic Signal (PS)

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0 1 ∞
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trait values expectation later stasis - "Phylogen. Niche Conservatism"

(Blomberg, Garland & Ives 2008 *Evolution*)

Picante:
Kcalc
phyloSignal
multiPhyloSignal



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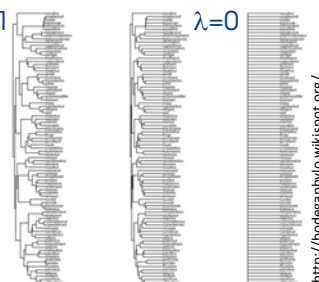
Phylogenetic Signal (PS)

Quantitative statistic: How strong is the "tendency for related species to resemble each other"?

$\lambda=1$ $\lambda=0$

Pagel's λ

GEIGER:
fitDiscrete
fitContinuous



<http://bioinformatics.wikimedia.org/>

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"As species of the same genus have usually ... some similarity in habits and constitution, and always in structure, the struggle will generally be more severe between species of the same genus."

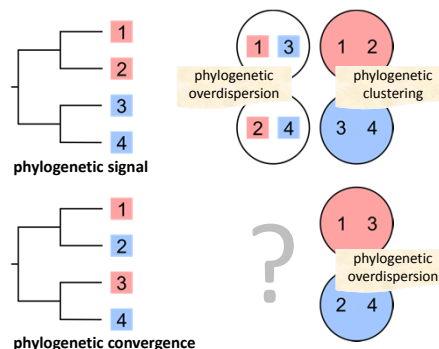
Darwin (1859) *On the Origin of Species*



Are co-occurring species more closely related (less closely related) than expected based on random assembly?

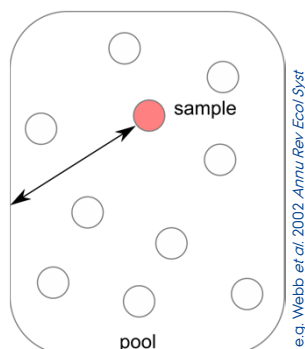
e.g. Webb et al. 2002 *Annu Rev Ecol Syst*

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1. quantifying phylogenetic relatedness
2. null model testing



e.g. Webb et al. 2002 Annu Rev Ecol Syst

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1. quantifying phylogenetic relatedness

- Faith's PD

→ "feature diversity"

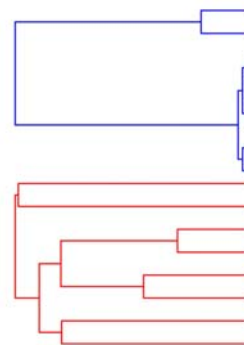
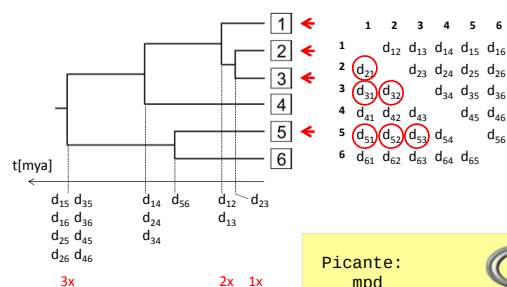
Picante:
pd

Figure: Swenson 2011 Am J Bot

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1. quantifying phylogenetic relatedness

- MPD

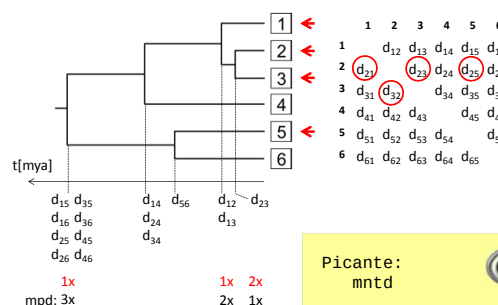
Picante:
mpd

Webb et al. 2002 Annu Rev Ecol Syst

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1. quantifying phylogenetic relatedness

- MNTD

Picante:
mntd

Webb et al. 2002 Annu Rev Ecol Syst

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1. quantifying phylogenetic relatedness

- PD

- MPD

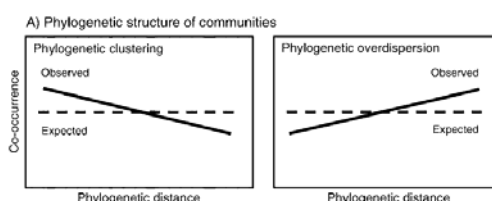
- MNTD

- PSV/PSR/PSE/PSC (Helmus et al. 2007 Am Nat)

- B_{ST}/Π_{ST} (Hardy & Senterre 2007 J Ecol
Hardy & Jost 2008 J Ecol)Picante:
psv
spacodiR:
spacodi.calc

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Alternatively: distance based measures



Hardy 2008 J Ecol for a comparison with the previous approach

Cavender-Bares et al. 2006 Ecology

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Which metric should I use?

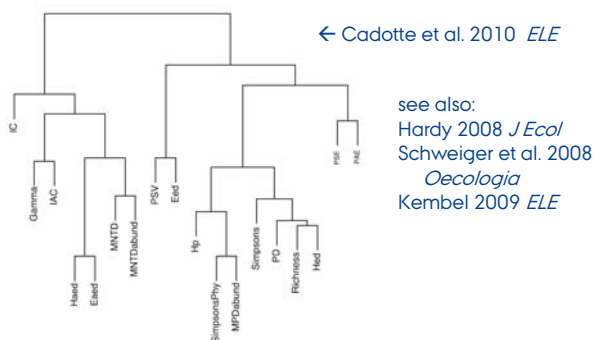


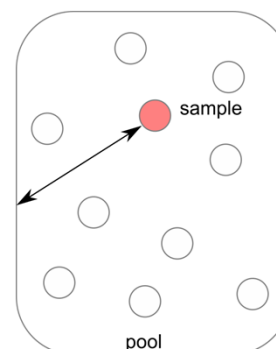
Figure 3 Hierarchically clustered Euclidean distances of the community ranking for 18 diversity metrics.

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1. quantifying phylogenetic relatedness
2. null model testing

Simulate community assembly *without* the process(es) of interest

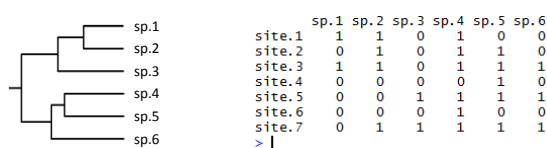
$$S_0 = S_{\text{obs}} \text{ (usually...)}$$



eq. Webb et al. 2002 *Annu. Rev. Ecol. Syst.* 33: 475-505

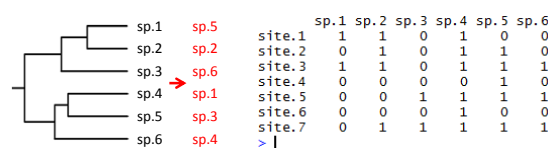
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eliminate all processes that have something to do with phylogeny



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eliminate all processes that have something to do with phylogeny



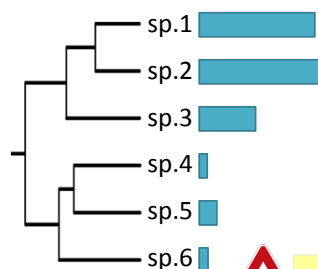
Picante: null.model = "taxa.labels"
spacodiR: resamp.1s

tree\$tip.label <- sample(tree\$tip.label)
colnames(dmat) <- rownames(dmat) <- sample(colnames(dmat))



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problem: abundance/occupancy PS



- 1) test for PS or APD $\neq 0$
(Hardy 2008 *J Ecol*)
- 2) abundance-corrected null model
(Hardy 2008 *J Ecol*)

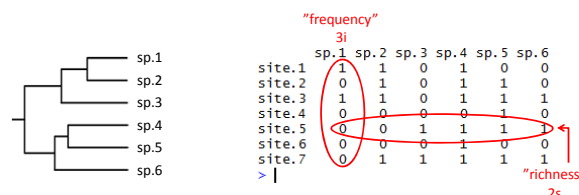


spacodiR:
resamp.1a



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randomizing the community matrix

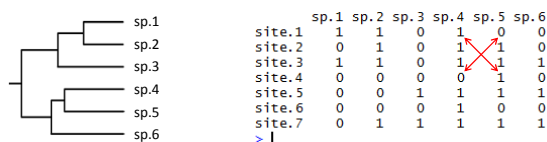


Picante: null.model = c("independentswap",
"trialswap")
spacodiR: resamp.2x, resamp.3x



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randomizing the community matrix



Picante: null.model = c("frequency", "richness")
 spacodiR: resamp.2s, resamp.3i



see Hardy 2008 *J Ecol* and Kembel 2009 *ELE*
 for a comparison of NULL models.

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Table 2. Constraints of the different null models on the structural features of data. Equivalences with previous works are given as footnotes

Null model (equivalence)	Constraints (structural features of data left unchanged after randomization)			
	Local species diversity per site	Among sites abundance distribution per species	Spatial autocorrelation of local abundances for each species	Phylogenetic distribution of global species abundances
1s ¹	X	X	X	
1p ²	X	X	X	
1a	X	X	X	(X) ³
2s ⁴	X			
2p ⁵	X			
2a ⁶	X	(X) ³		(X) ³
3i ⁷		X		X
3e ⁸	(X) ³	X		X
3t		X	X	X

¹Equivalent to 'null model 1' in Cavender-Bares *et al.* (2004).

²Equivalent to model '1' of function 'construct' in Phylocom 3.41 (Webb *et al.* 2007).

³Equivalent to model '1' of function 'construct' in Phylocom 3.41 (Webb *et al.* 2007), to the 'unconstrained null model' in Kembel & Hubbell (2006), and to 'null 1' in Helmus *et al.* (2007a).

⁴Equivalent to model '2' of function 'construct' in Phylocom 3.41 (Webb *et al.* 2007).

⁵Equivalent to 'null model 2' in Cavender-Bares *et al.* (2004), 'null model 1' in Cavender-Bares *et al.* (2006), and to 'null 1' in Helmus *et al.* (2007a).

⁶With presence/absence data, equivalent to model '3' of function 'construct' in Phylocom 3.41 (Webb *et al.* 2007), to the 'constrained null model' in Kembel & Hubbell (2006), to 'null model 3' in Cavender-Bares *et al.* (2004), to 'null model 2' in Cavender-Bares *et al.* (2006), and to 'null 3' in Helmus *et al.* (2007a).

⁷Only local species richness is left unchanged (the distribution of species abundances per site is affected).

⁸Only the number of sites where each species occurs is left unchanged (for each species, the distribution of abundances among sites is affected).

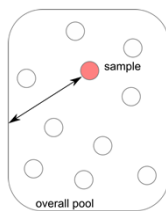
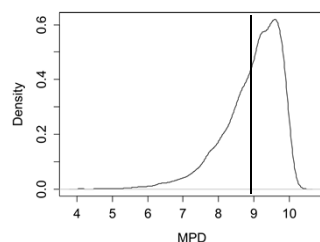
⁹Approximately true according to the criterion defining when species have similar enough abundances to be permuted.

¹⁰True only for presence/absence data.

Hardy 2008 *J Ecol*

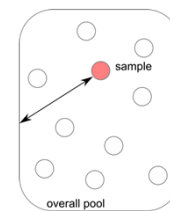
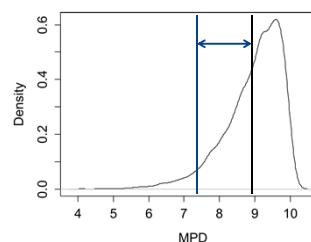
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deviation from the 0: standardized effect size



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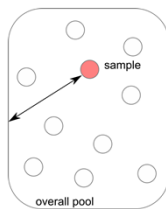
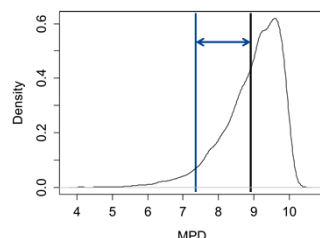
deviation from the 0: standardized effect size



$$SES = \frac{r_{obs} - \text{mean}(r_0)}{sd(r_0)}$$

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deviation from the 0: standardized effect size



$$NRI = -1 \times \frac{MPD_{obs} - \text{mean}(MPD_0)}{sd(MPD_0)}$$

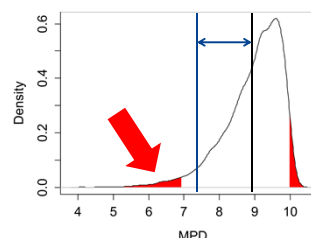
$$NTI = -1 \times \frac{MNTD_{obs} - \text{mean}(MNTD_0)}{sd(MNTD_0)}$$

Picante:
 ses.mpd
 ses.mntd



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significance??



ses.mpd/mntd		
mpd.obs.rank	mpd.obs.z	mpd.obs.p
3	-2.55445	0.003
671	0.439168	0.671
862	1.029289	0.862
981	1.952396	0.981
988	2.184158	0.988

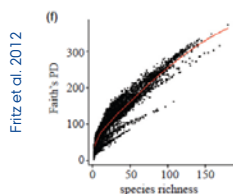
one-tailed test!

or: Z-score (e.g. $\alpha=0.05 \leftarrow |Z| > 1.96$)
 (assumes normal distribution)

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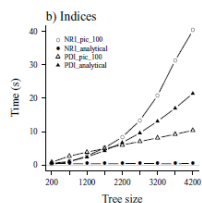
alternatives to null models?

empirical PD~SR



→ problematic if
effect ~ SR

analytical null



→ good, but with
assumptions

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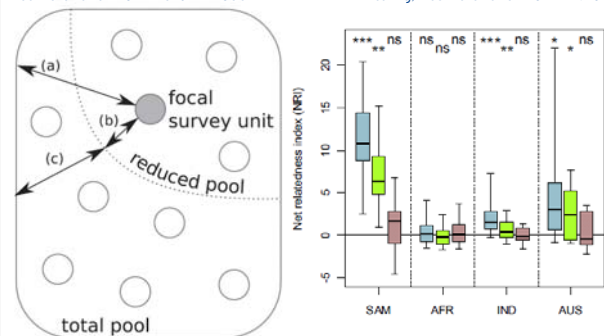
limitations of the "alpha-level": its ambiguous

Ecological mechanisms	Dependence	Representative studies
Density dependent mechanisms:		
Competition/limiting similarity	+	Singhby & Vohorn 2005, Kozak <i>et al.</i> 2005, Homer-Devine & Bohannan 2006, Davies <i>et al.</i> 2007, Helmus <i>et al.</i> 2007, Cahill & Webb 2007
Herbivore/Pathogen specificity	+	Fine <i>et al.</i> 2004, 2006, Fig. 4
Herbivore facilitated ecological sorting	+	Valiente-Banuet & Vendlé 2007
Facilitation of some plants	+	Sargent & Ackerly 2008
Pollinator-plant interactions	+	Cavender-Bares <i>et al.</i> 2004a, Kelly <i>et al.</i> 2008
Temporal niche dynamics	+	Webb 2000, Ackerly <i>et al.</i> 2004, Cavender-Bares <i>et al.</i> 2004a,b, Cavender-Bares <i>et al.</i> 2006, Vendlé & Proulx 2007, Kraft <i>et al.</i> 2007
Environmental filtering	+	Sargent & Ackerly 2008
Facilitation by mutualists	+	Sargent & Ackerly 2008
Plant-pollinator interactions	+	Hubbell 2001, Kembel & Hubbell 2006
Neutral processes	x	Lorente & Hodachka 2006, Cavender-Bares <i>et al.</i> 2006
Combinations of processes	x	Vamosi <i>et al.</i> 2008
Dispersal	?	Ricklefs 2004, Wiens & Donoghue 2004, Vamosi <i>et al.</i> 2008
Evolutionary/genetic mechanisms		
Biogeographic history	+	Johnson & Stinchcombe 2007
Allopatric speciation (depends on scale)	+	Schluter 2000, Grant & Grant 2006
Sympatric speciation	+	Cavender-Bares <i>et al.</i> 2004a, Kraft <i>et al.</i> 2007
Character displacement	+	Brooker 1996
Convergent evolution	+	Dobzhansky 1937, Mayr 1942, Loson 1990, Levin 2006, Grant & Grant 2008, Fig. 5
Mimicry	+	
Gene flow and local hybridization	+	

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Cavender-Bares *et al.* 2009 *Ecol Lett*

species pool scaling

Eiserhardt *et al.* 2012 *Bot J Linn Soc*Kissling, Eiserhardt *et al.* 2012 *PNAS*

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"Phylogenetic beta diversity" (Graham & Fine 2008 *Ecol Lett*)

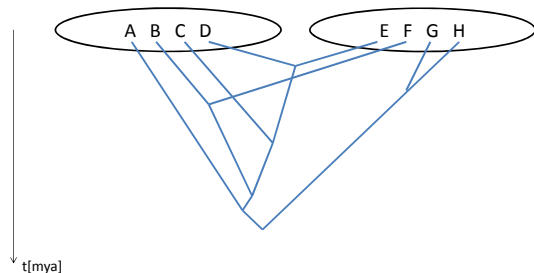
allows more specific hypothesis tests.



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"Phylogenetic beta diversity" (Graham & Fine 2008 *Ecol Lett*)

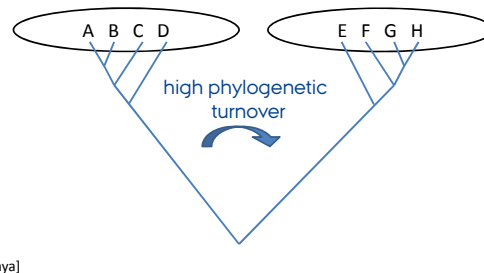
allows more specific hypothesis tests.



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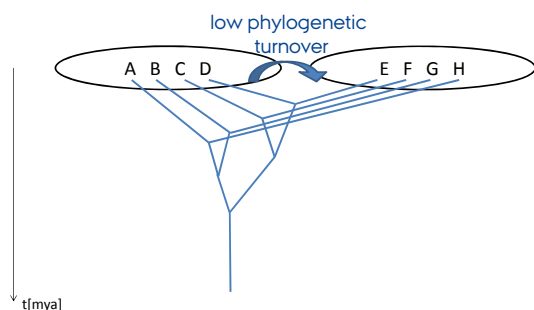
"Phylogenetic beta diversity" (Graham & Fine 2008 *Ecol Lett*)

allows more specific hypothesis tests.



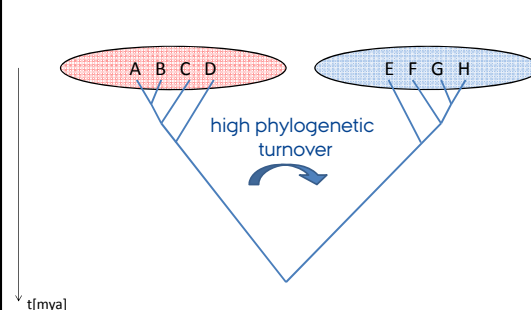
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"Phylogenetic beta diversity" (Graham & Fine 2008 *Ecol Lett*) allows more specific hypothesis tests.



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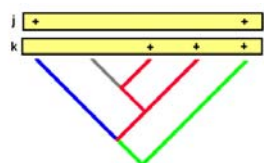
"Phylogenetic beta diversity" (Graham & Fine 2008 *Ecol Lett*) allows more specific hypothesis tests.



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branch-length based indices

- a: shared branch length
- b: independent branch lengths
- c: independent branch lengths



Faith et al. 2009

$$\text{phylosor} = \frac{a}{0.5 \cdot (2a + b + c)}$$

$$\text{unifrac} = \frac{b + c}{a + b + c}$$

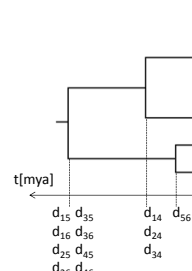
Picante:
phylosor
unifrac



phylosor: Bryant et al. 2008 *PNAS* 105, 11505-11511
unifrac: Lozupone & Knight 2005 *Appl Environ Microbiol* 71, 8228-8235
general: Faith et al. 2009 *Int J Mol Sci* 10, 4723-4741

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distance-based indices



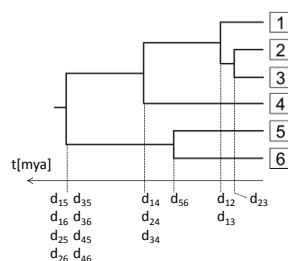
	1	2	3	4	5	6
1	0	d ₁₂	d ₁₃	d ₁₄	d ₁₅	d ₁₆
2		0	d ₂₃	d ₂₄	d ₂₅	d ₂₆
3			0	d ₃₄	d ₃₅	d ₃₆
4				0	d ₄₅	d ₄₆
5					0	d ₅₆
6						0

Picante:
comdist
comdistnt

Webb et al. (2008) in Carson & Schmitzer (eds.) *Tropical Forest Community Ecology*

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distance-based indices



	1	2	3	4	5	6
1	0	d ₁₂	d ₁₃	d ₁₄	d ₁₅	d ₁₆
2		0	d ₂₃	d ₂₄	d ₂₅	d ₂₆
3			0	d ₃₄	d ₃₅	d ₃₆
4				0	d ₄₅	d ₄₆
5					0	d ₅₆
6						0

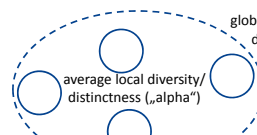
comdist: 6x 3x 1x 2x +0
comdistnt: 1x 1x +0

Picante:
comdist
comdistnt



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distance-based indices: diversity partitioning



$$\frac{\alpha - \gamma}{\gamma}$$

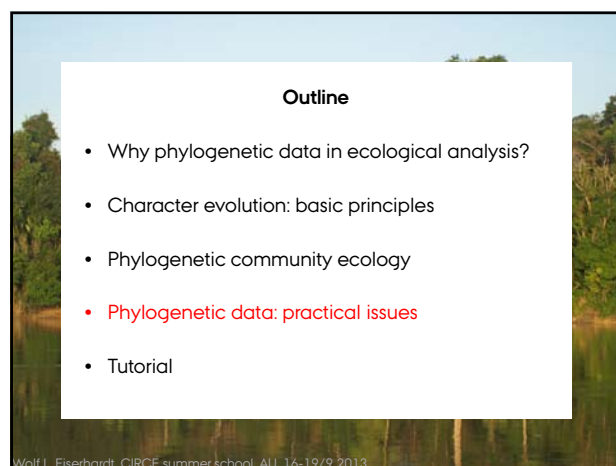
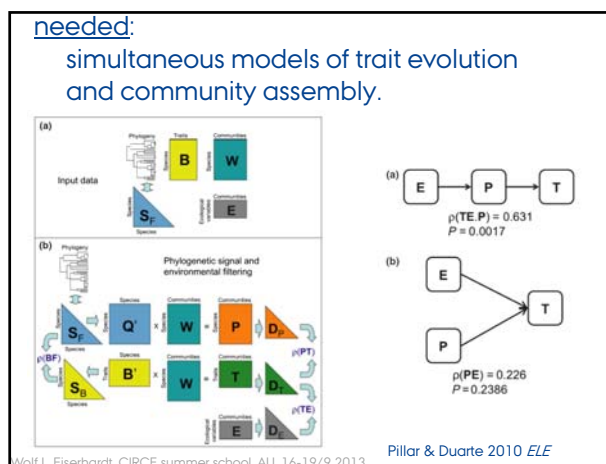
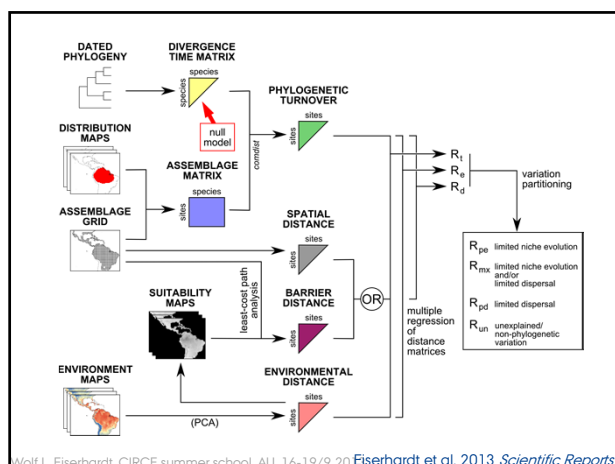
abundance: B_{ST} (Hardy & Jost 2008 *J Ecol*)

presence-absence: Π_{ST} (Hardy & Senterre 2007 *J Ecol*)

spacodiR:
spacodi.calc



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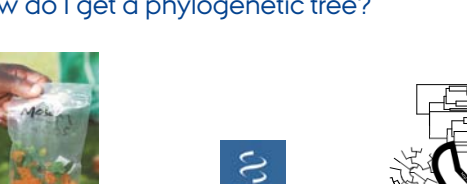
A background image showing a calm lake reflecting the surrounding green trees and a clear sky. The reflection is sharp and clear.

Outline

- Why phylogenetic data in ecological analysis?
- Character evolution: basic principles
- Phylogenetic community ecology
- **Phylogenetic data: practical issues**
- Tutorial

Wolf J. Eiserhardt: CIRCE summerschool, Aug. 14-19/9 2013

how do I get a phylogenetic tree?



The collage consists of several elements: a hand holding a clear plastic bag with orange fish inside; a blue square with the NCBI logo; two heatmaps showing genetic data with red and blue bars; and a thumbs-up gesture next to a phylogenetic tree diagram.

<http://acdb.co.za/>

NCBI

ecological sampling is bad for phylogenetics!

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normally there is no tree covering all your spp.

"backbone"

PF Stevens: <http://www.mobot.org/MOBOT/research/APweb/>



A Database of Phylogenetic Knowledge

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Submit

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People

Partnerships

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NSF Data Management

Data Access

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Welcome to TreeBASE

TreeBASE is a repository of phylogenetic information, specifically user-submitted phylogenetic trees and the data used to generate them. TreeBASE accepts all types of phylogenetic data (e.g., trees of species, trees of populations, trees of genes) representing all biotic taxa. Data in TreeBASE are exposed to the public if they are used in a publication that is in press or published in a peer-reviewed scientific journal, book, conference proceedings, or thesis. Data used in publications that are in preparation or in review can be submitted to TreeBASE but are only available to the authors, publication editors, or reviewers using a special access code. TreeBASE is produced and governed by the The Phyloinformatics Research Foundation, Inc.

Some recent additions:

- Underestimating taxa will underestimate molecular divergence dates: An example from the South American *Hydrobia* Liliaceae
September 05, 2013
- Mutational intensity and filtering by altitude shape the structure of Andean butterfly communities
September 03, 2013
- Phylogeny of Heteromyzinae: the largest lineage of Sarcophaga (Diptera: Sarcophagidae)
September 03, 2013
- Evolutionary relations of Hexanchiformes deep-sea sharks elucidated by whole mitochondrial genome sequencing
August 27, 2013
- Evolutionary diversification and characterization of the eubacterial gene family encoding OXA1 type II, an alternative isoprenoid biosynthetic enzyme
August 16, 2013
- Taxonomy of the Crematogaster degeneri species assemblage in the Malagasy region (Hymenoptera: Formicidae)
August 16, 2013
- Taxonomic revision of Eucritium and transfer of species to Aspergillus
August 16, 2013
- Molecular phylogenetic analyses identify *Alpina* differentiation and dynamic chromosome number changes as major forces for the evolution of the European endemic *Phytoneura* [Campanulaceae]
August 16, 2013

[illegible]

how do I get a phylogenetic tree?

manual adjustments („grafting“):

The diagram shows two phylogenetic trees. The top tree, in red, represents a clade with six tips labeled **gen1sp1** through **gen1sp6**. The bottom tree, in black, represents a larger clade with six tips labeled **gen1sp1** through **gen3sp6**. A yellow lightning bolt symbol points to the node where the red tree is being grafted onto the black tree. A horizontal arrow at the bottom points to the left and is labeled **t[mya]**, indicating time in millions of years ago.

how do I get a phylogenetic tree?

gen1sp1
gen1sp2
gen1sp3
gen1sp4
gen1sp5
gen1sp6

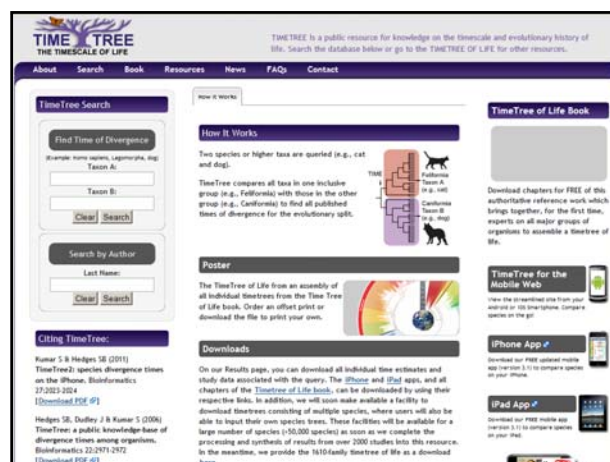
gen1sp5
gen1sp1
gen1sp2

gen2sp1
gen2sp2
gen3sp1
gen3sp2
gen3sp3
gen3sp4
gen3sp5
gen3sp6

← t[mya]

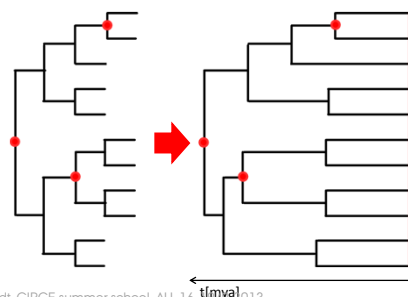
how do I assign missing divergence times?

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how do I assign missing divergence times?

BLADJ = BranLenGth Adjustment
in Phylocom (Webb et al. 2008 *Bioinformatics*)



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how do I assign missing divergence times?

BLADJ = BranLenGth Adjustment
in Phylocom (Webb et al. 2008 *Bioinformatics*)

- not model based
- doesn't handle uncertainty

→ randomize if you can.

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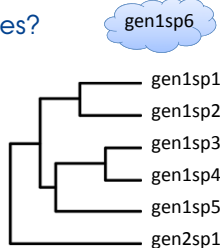
how do I assign missing species?

use taxonomy

1. random addition

- pick a branch
- $P(b_i) \sim \text{Length}(b_i)$
- pick a time on the branch.

Add multiple spp. in random order
Do it N times.



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how do I assign missing species?

use taxonomy

1. model-based addition

- model expected MPD for the taxon based on richness and age (e.g. Yule model)
- update divergence time matrix

cannot be represented as tree any more.

Eiserhardt et al. 2012 *Bot J Linn. Soc*

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how do I get a phylogenetic tree?

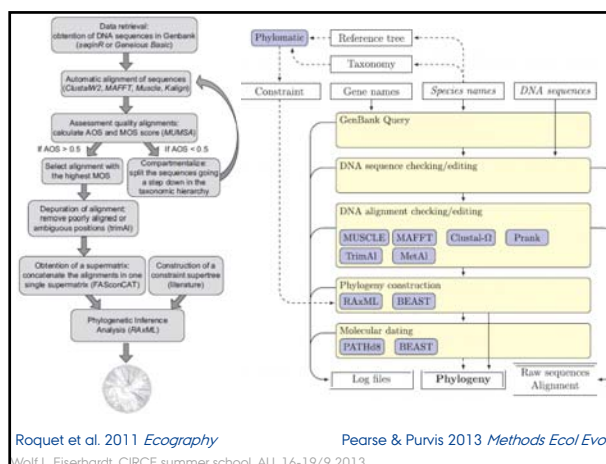
supertree services:

- phylomatic/phylotastic
- Beaulieu et al. 2012 *Ecology*

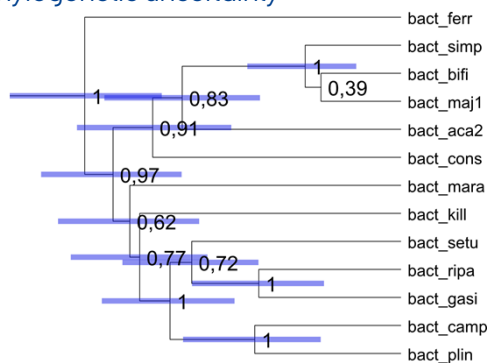
supermatrix services:

- Roquet et al. 2012 *Ecography*
- phyloGenerator
(Pearse & Purvis 2013 *Methods Ecol Evol*)

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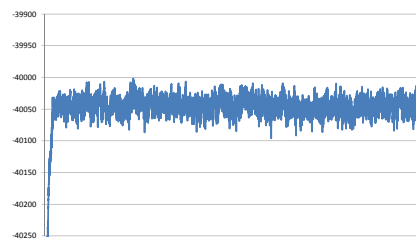


phylogenetic uncertainty



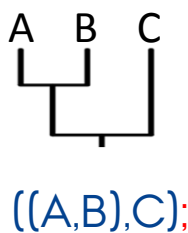
phylogenetic uncertainty

optimal: Bayesian phylogenetics
→ sample N trees from the Markov chain



structure and handling of tree files:

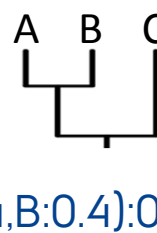
Newick (Phylip):



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structure and handling of tree files:

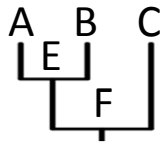
Newick (Phylip):



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structure and handling of tree files:

Newick (Phylip):

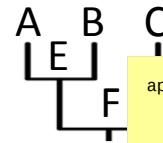


`((A:0.4,B:0.4)E:0.6,C:1)F;`

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structure and handling of tree files:

Newick (Phylip):



ape:
read.tree
write.tree



`((A:0.4,B:0.4)E:0.6,C:1)F;`

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```
#NEXUS
BEGIN TAXA;
  TAXLABELS spA spB spC;
END;

BEGIN DATA;
  DIMENSIONS ntax=4 nchar=15;
  FORMAT datatype=dna symbols="ACTG" missing=? gap=-;
  MATRIX
    spA atgctagctagctcg
    spB atgcta??tag-tag
    spC atgttagctag-tgg
  ;
END;

BEGIN TREES;
  LINK Taxa = Taxa;
  TRANSLATE
    1 spA,
    2 spB,
    3 spC;
  TREE tree1 = ((1,2),3);
END;
```

NEXUS



ape:
read.nexus
write.nexus



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```
#NEXUS
BEGIN TAXA;
  TAXLABELS spA spB spC;
END;

BEGIN DATA;
  DIMENSIONS ntax=4 nchar=15;
  FORMAT datatype=dna symbols="ACTG" missing=? gap=-;
  MATRIX
    spA atgctagctagctcg
    spB atgcta??tag-tag
    spC atgttagctag-tgg
  ;
END;

BEGIN TREES;
  LINK Taxa = Taxa;
  TRANSLATE
    1 spA,
    2 spB,
    3 spC;
  TREE tree1 = ((1,2),3);
END;
```

NEXUS



ape:
read.nexus
write.nexus



→ use other software (e.g. mesquiteproject.org)

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