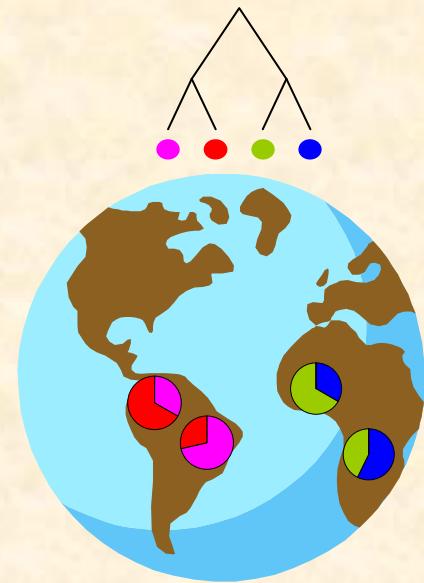
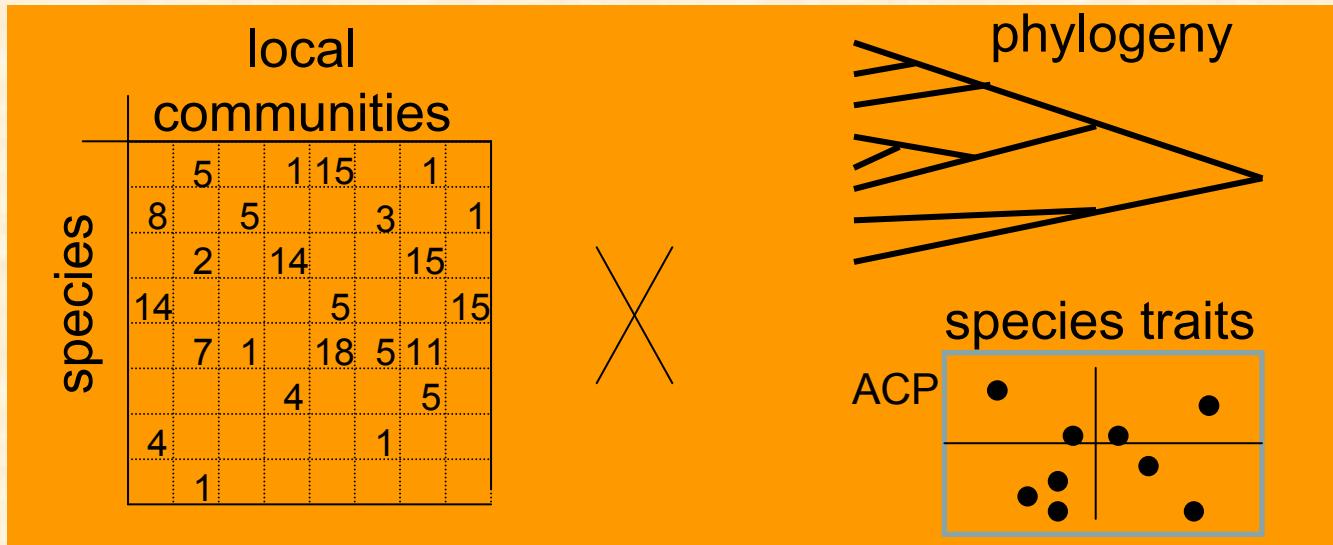


Structures fonctionnelle et phylogénétique des communautés - inférences sur les processus structurant

Olivier Hardy

Université Libre de Bruxelles



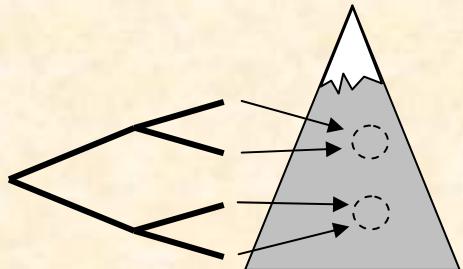
⇒ test d'hypothèses sur les mécanismes déterminant les assemblages d'espèces

Community phylogenetic structure

Example under environmental filtering (adaptation to altitude)

Phylogenetic clustering

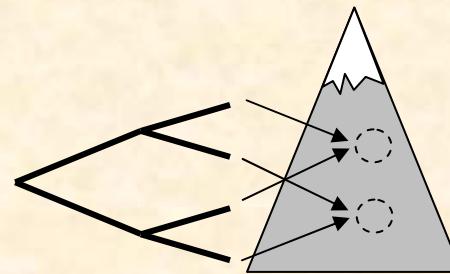
species within habitat **more** related than among habitats



habitat conservatism

Phylogenetic overdispersion

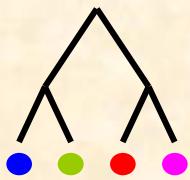
species within habitat **less** related than among habitats



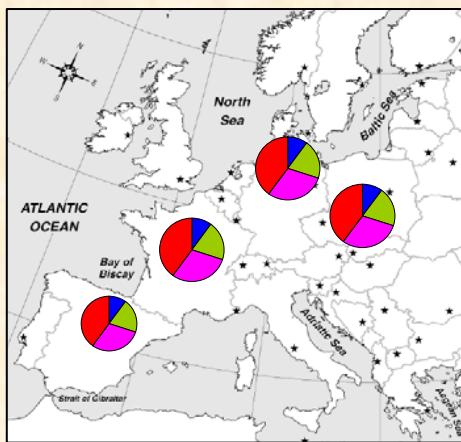
habitat convergence

e.g. *radiation of several clades in a set of new habitats*

Species turnover versus phylogenetic turnover

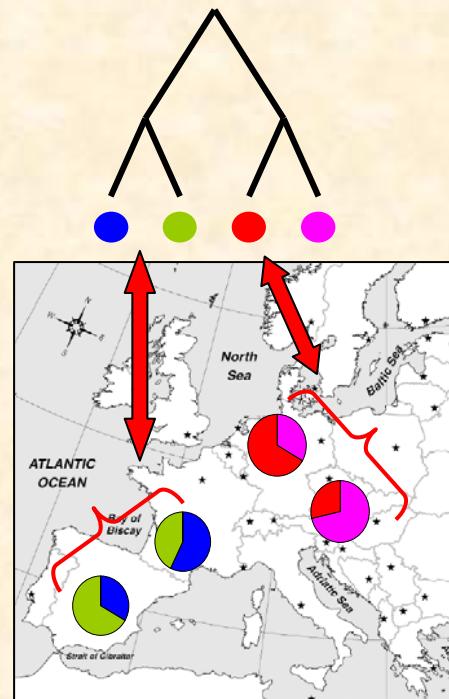


Phylogenetic tree
for 4 species

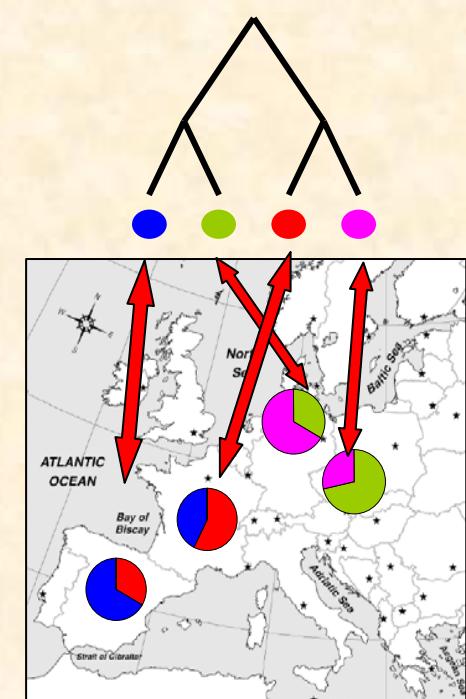


No species
turnover
&
No phylogenetic
turnover

Species turnover
but
No phylogenetic
turnover



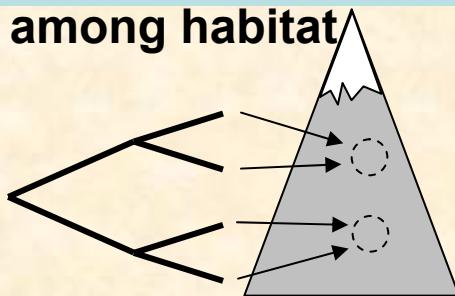
Species turnover
+
Phylogenetic
clustering
(attraction)



Species turnover
+
Phylogenetic
overdispersion
(evenness, repulsion)

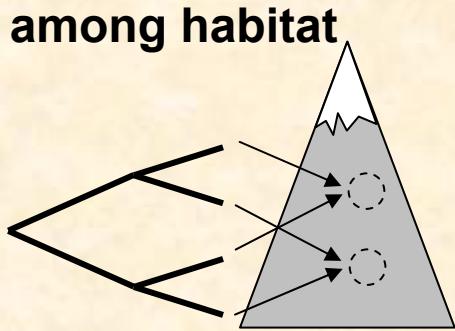
Phylogenetic turnover caused by ecological & evolutionary processes

Phylogenetic clustering



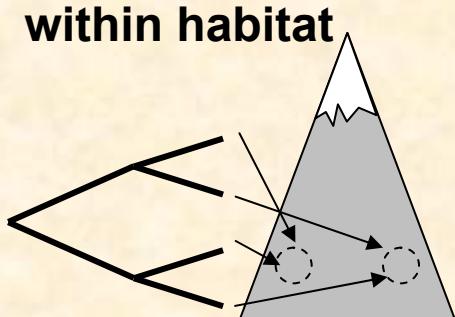
environmental filtering
adaptation to ≠ elevation
+
habitat conservatism

Phylogenetic overdispersion
(= evenness = repulsion)



environmental filtering
adaptation to ≠ elevation
+
habitat convergence
e.g. *radiation of several clades in a set of new habitats*

Phylogenetic overdispersion
(= evenness = repulsion)



competitive exclusion
+
niche conservatism
→ sister species cannot coexist because of niche overlap

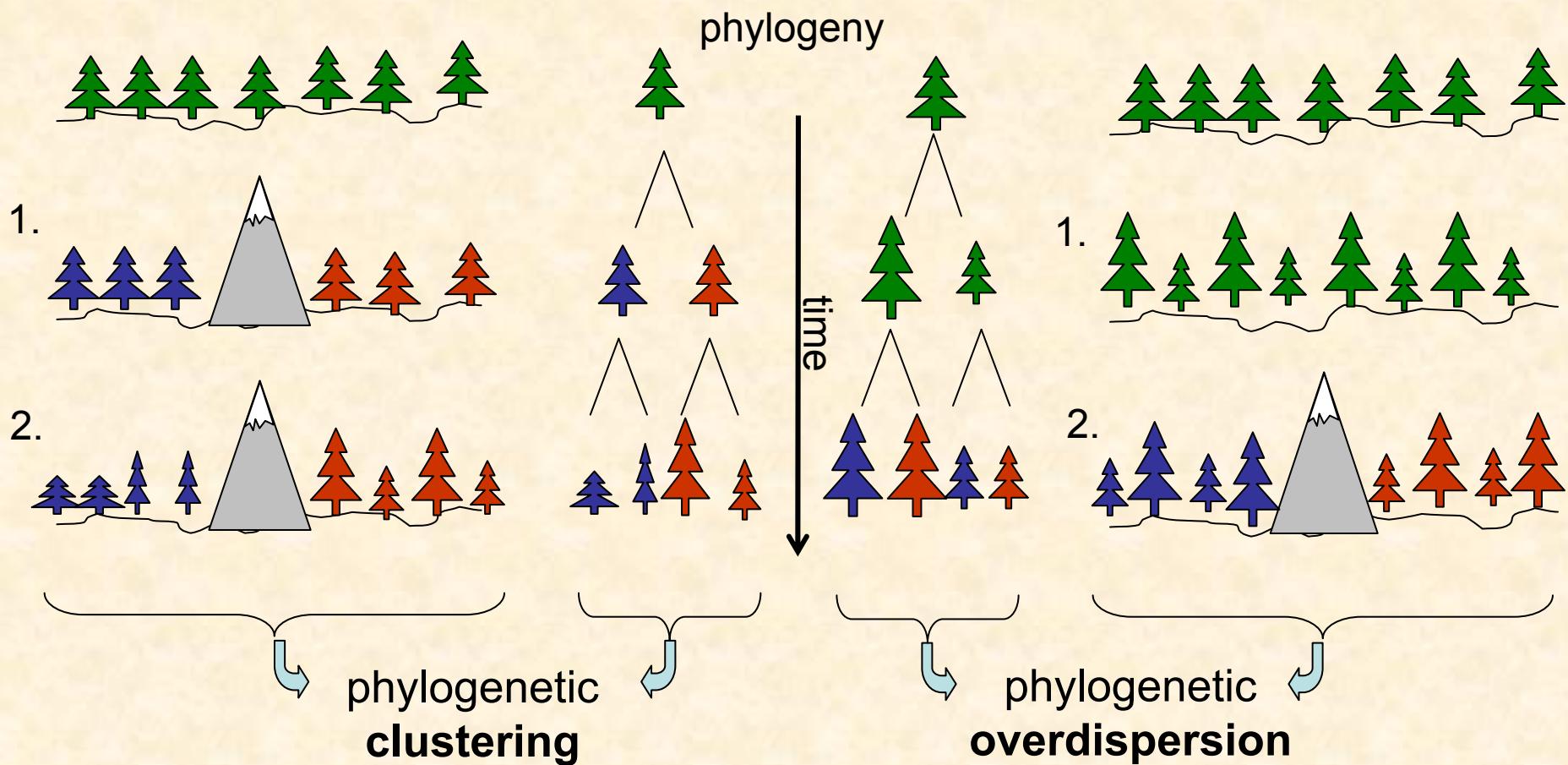
Phylogenetic turnover caused by biogeographic barrier

Scenario A:

1. barrier (allopatric speciation)
2. sympatric speciations

Scenario B:

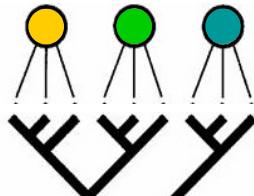
1. sympatric speciation
2. barrier (allopatric speciations)



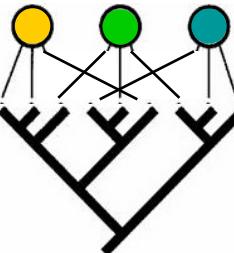
The link between Community assembly and Phylogeny: species Traits

C x P

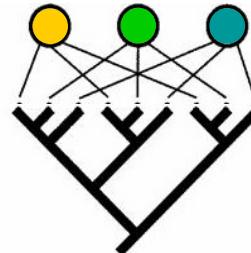
Phylogenetic clustering



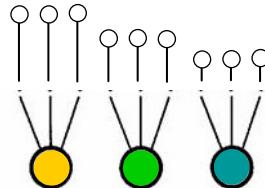
Random phylogenetic structure



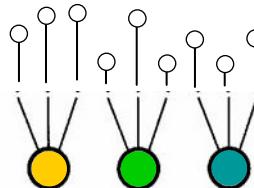
Phylogenetic overdispersion



T x P



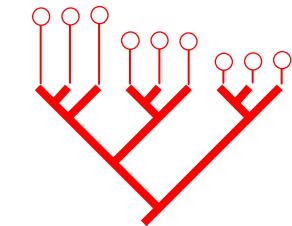
T x C Environmental filtering



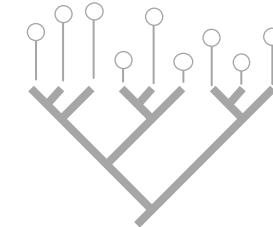
Random assembly
(neutrality)

Competitive exclusion

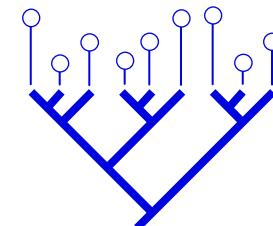
T x P



Trait conservatism



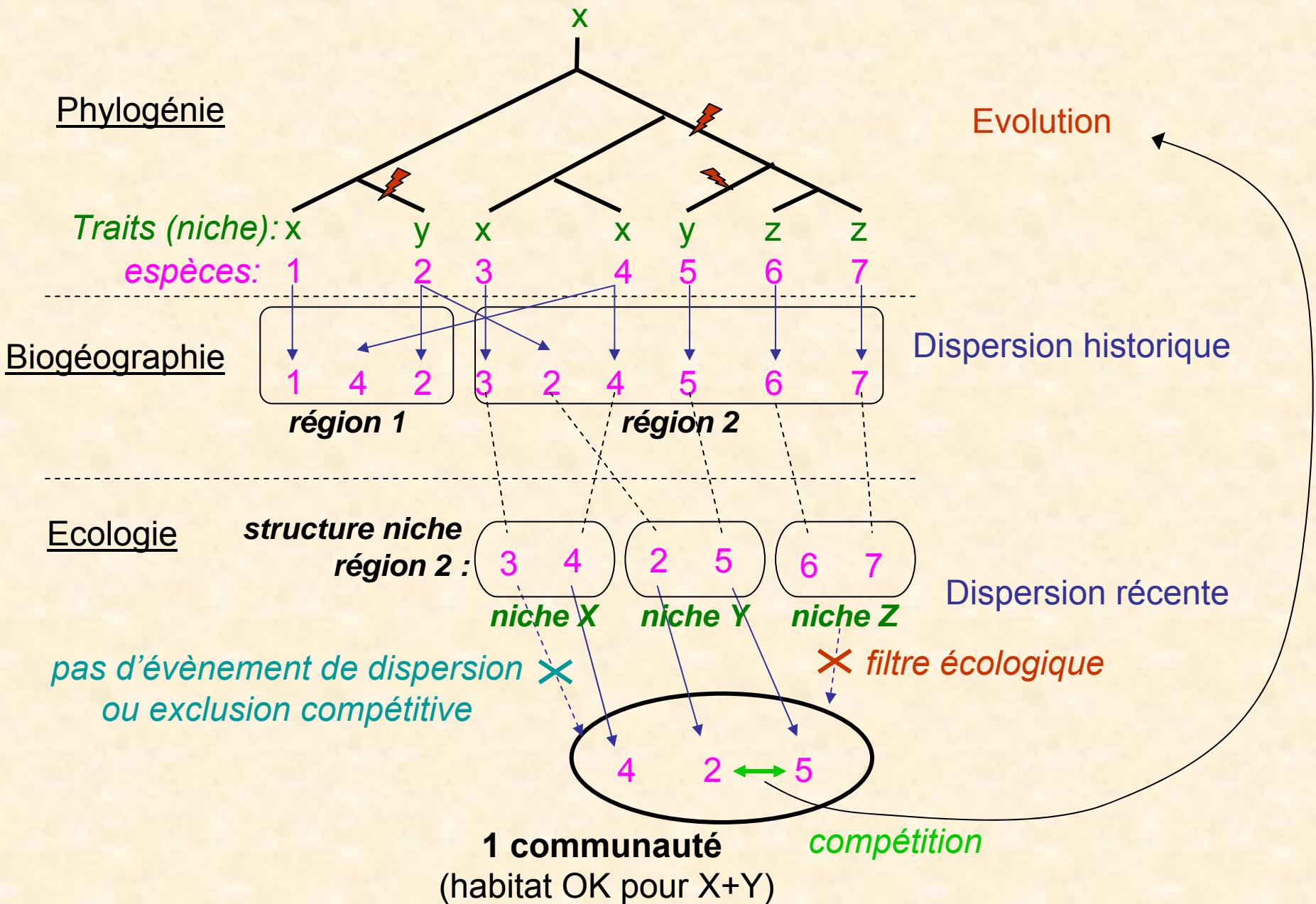
No phylogenetic signal



Trait convergence

Community phylogenetic structure depends on ecological and evolutionary processes

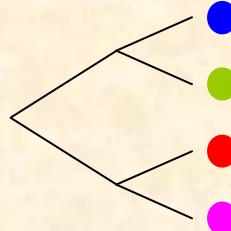
Intégration communautés – traits – écologie – biogéographie – évolution



How to quantify phylogenetic turnover from species incidence data ?

↳ many methods developed; here just one presented

1. From a phylogeny → phyletic distances between species



$$\delta_{kl}$$

●	0	1	2	2
●	1	0	2	2
●	2	2	0	1
●	2	2	1	0

→ divergence time
(molecular phylogeny)

→ (taxonomic level)

2. From community inventories → mean δ_{kl} between species

sampled

- within sites
- among sites

$$MPD_w = \bar{\delta}_{(2_species_from_same_site)}$$

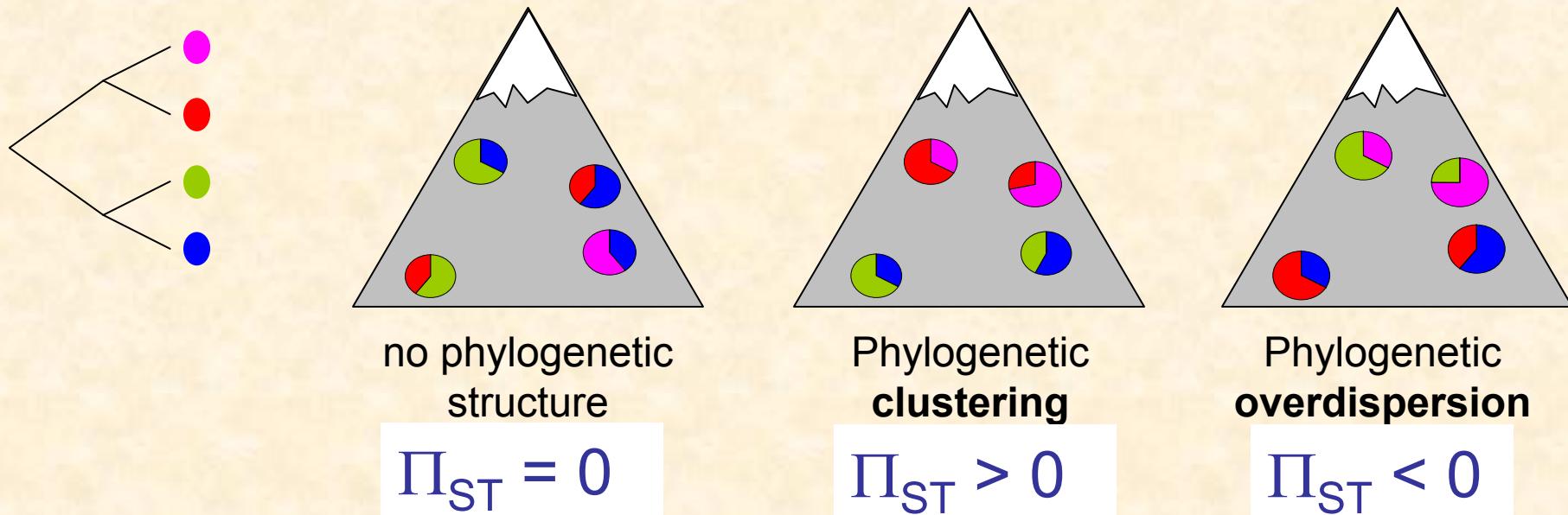
$$MPD_a = \bar{\delta}_{(2_species_from_different_sites)}$$

$$\rightarrow \Pi_{ST} = 1 - MPD_w / MPD_a$$

relative excess of relatedness between species co-occurring within a site (relative to species pairs sampled in distinct sites)

-> phylogenetic turnover

How to test phylogenetic turnover?



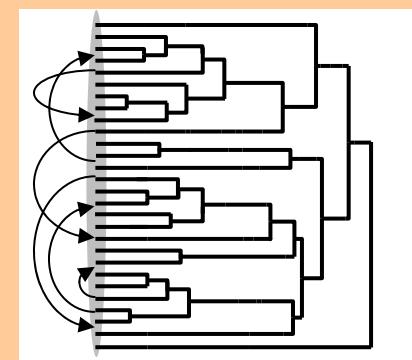
Testing $\Pi_{ST} \neq 0$

→ randomize phylogeny

→ assess distribution of Π_{ST} for 1000 permutations

→ P-value = % of Π_{ST} after permutation > or < Π_{ST} observed

(more elaborated randomization tests: Hardy 2008, J Ecol)



How to quantify species + phylogenetic turnover from species abundance data ? (using QE: quadratic entropy)

From a phylogeny → distances between species



$$\delta_{kl}$$

●	●	●	●
●	0	1	2
●	1	0	2
●	2	2	0
●	2	2	1

From community inventories:

> partition of QE = mean δ_{kl} between individuals

sampled

within sites

$$QE_w = \bar{\delta}_{(2_individuals_from_same_site)}$$

among sites

$$QE_a = \bar{\delta}_{(2_individuals_from_different_sites)}$$



$$P_{ST} = 1 - QE_w / QE_a$$

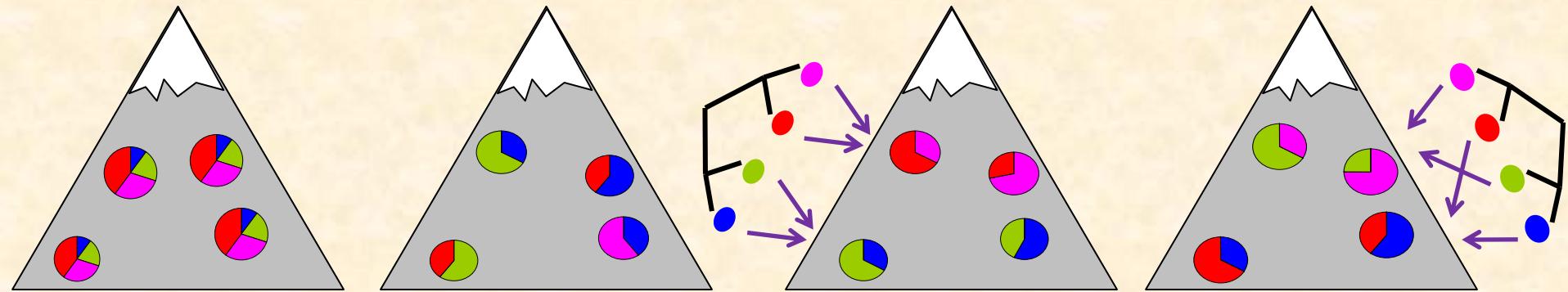
species + phylogenetic turnover

> partition of Simpson's D = probability of species non-identity btw individuals



$$I_{ST} = 1 - D_w / D_a$$

species turnover



No species turnover
&
No phylogenetic turnover

Species turnover
but
No phylogenetic turnover

Species turnover
+
Phylogenetic clustering

Species turnover
+
Phylogenetic overdispersion

$$P_{ST} = I_{ST} = 0$$

$$P_{ST} = I_{ST} > 0$$

$$P_{ST} > I_{ST} > 0$$

$$I_{ST} > P_{ST} > 0$$

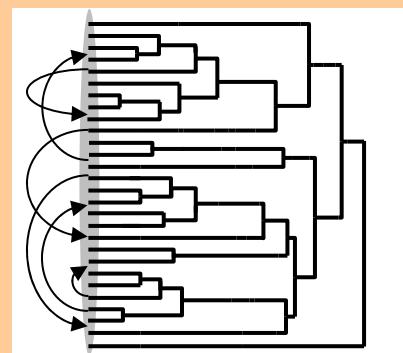
Testing $P_{ST} \leftrightarrow I_{ST}$

→ randomize phylogeny

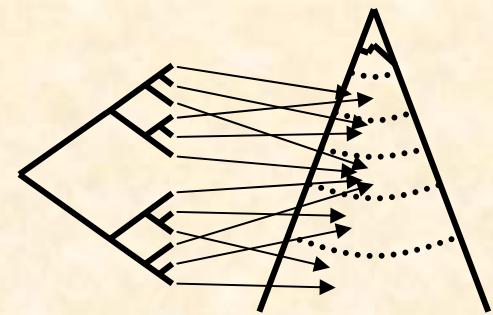
→ assess distribution of P_{ST} for 1000 permutations

→ P-value = % of P_{ST} after permutation > or < P_{ST} observed

(for more elaborated randomization tests: Hardy 2008, J Ecol)



Data exploration



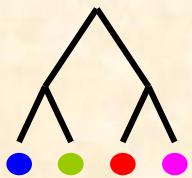
Pairwise analyses between pairs of local communities:

- compute P_{ST} or Π_{ST} for each pair
- check correlations between P_{ST} or Π_{ST} and {
geographic distance
ecological distance

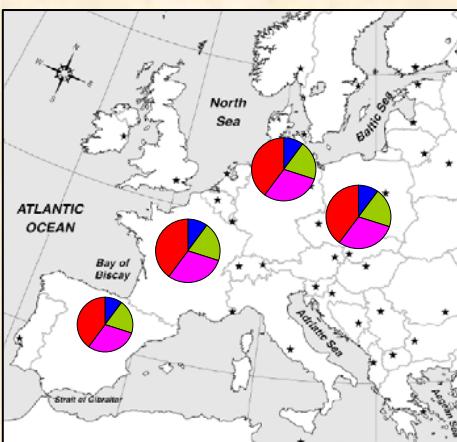
Case studies in tropical forest plant communities

1. Impact of **dispersal limitation versus ecological gradients** → species and phylogenetic turnover in Central African inselberg vegetation
2. Impact of **ecological gradients versus biogeography** → phylogenetic turnover along rainfall gradients in Western Ghats and Panama
3. Integrating **phylogeny** and **traits** → **phylogenetic versus functional** structures of rainforests from French Guiana
4. Phylogenetic **overdispersion** due to multiple recent radiations → forest communities from Reunion island
5. Phylogenetic structure at the scale of **inter-individual competition** → fine-scale spatial phylogenetic turnover in 50-ha plots

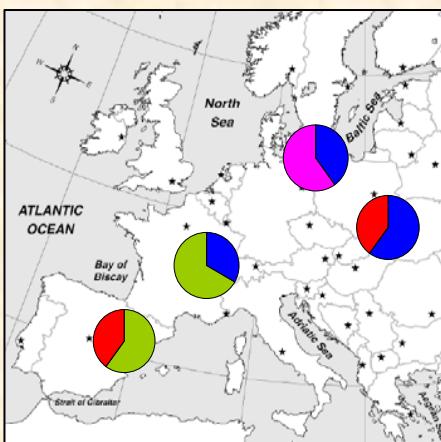
1. Impact of dispersal limitation vs ecological gradients on species turnover and phylogenetic turnover



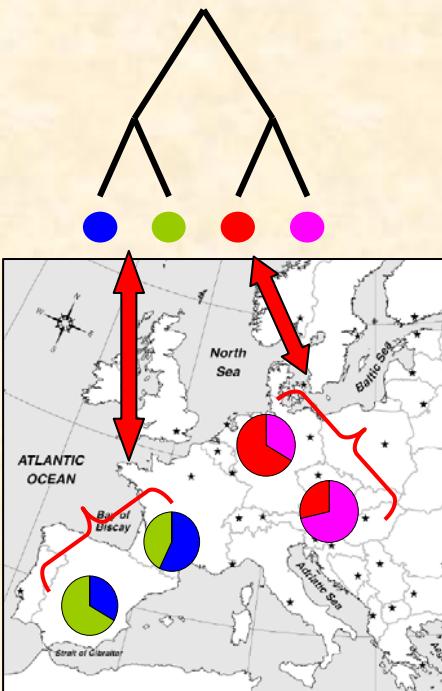
Phylogenetic tree
for 4 species



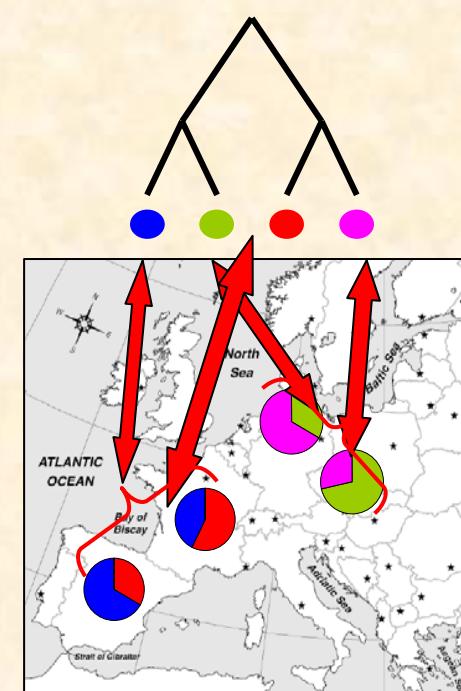
No species turnover
&
No phylo. turnover



Species turnover
but
No phylo. turnover



Species turnover
+
Phylo. clustering

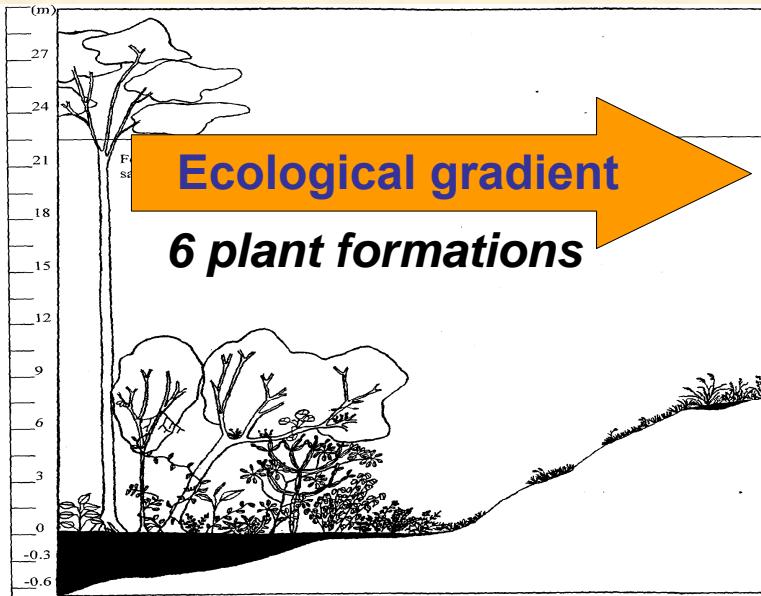


Species turnover
+
Phylo. overdisp.

Species turnover → Jaccard index of species similarity or I_{ST}

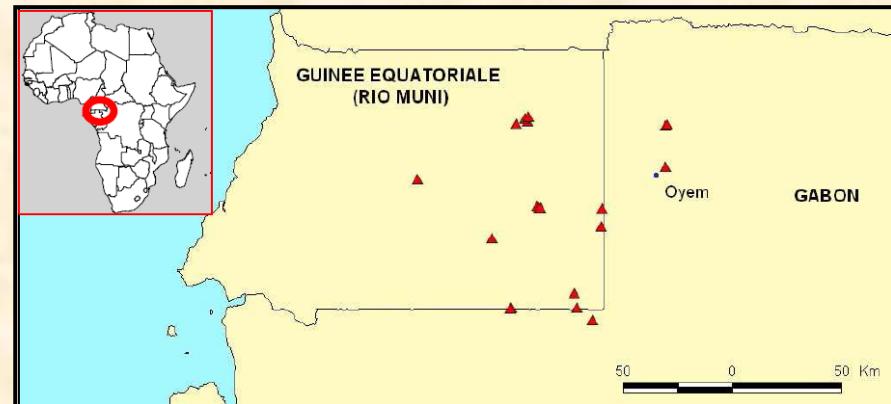
Phylogenetic turnover → Π_{ST} or P_{ST}

Inselberg vegetation in Equatorial Guinea



Geographical isolation

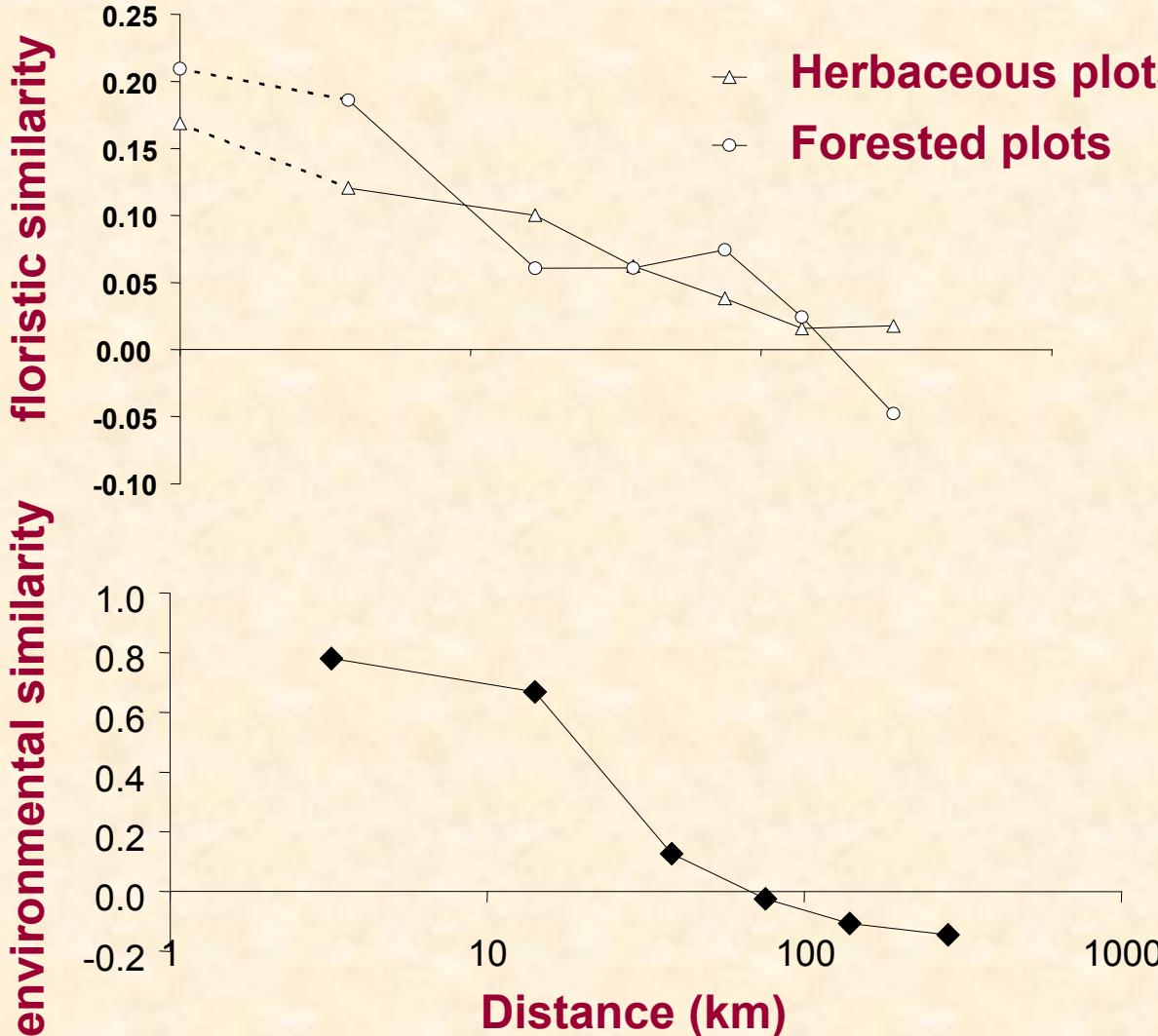
inselberg ↔ island



(ca. 300 floristic plots on 21 inselbergs)

Regional scale: subregional species pools

Spatial autocorrelation



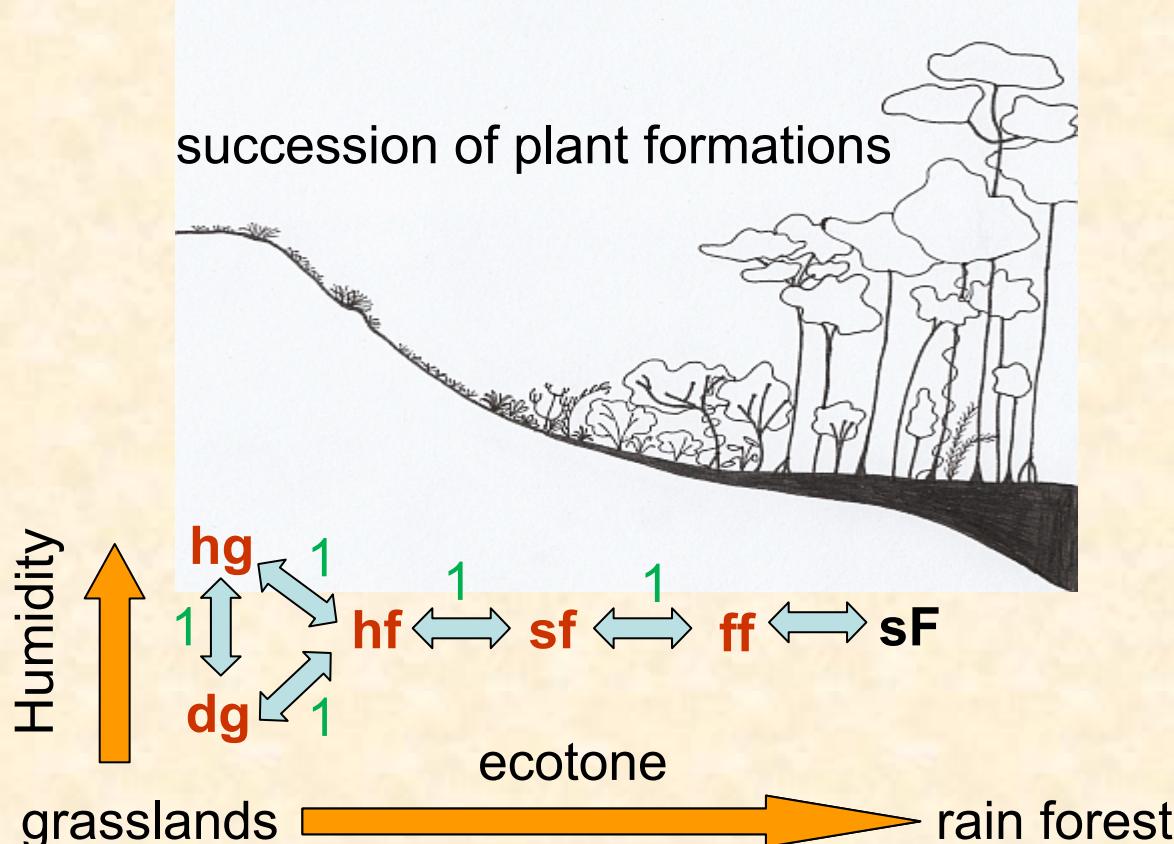
Species turnover due to:
Regional scale
deterministic factors
(climate...) ?
or
Dispersal limitation
(and/or colonization
history) ?

Parmentier *et al.* 2005
J Biogeography



Local scale: environmental constraints

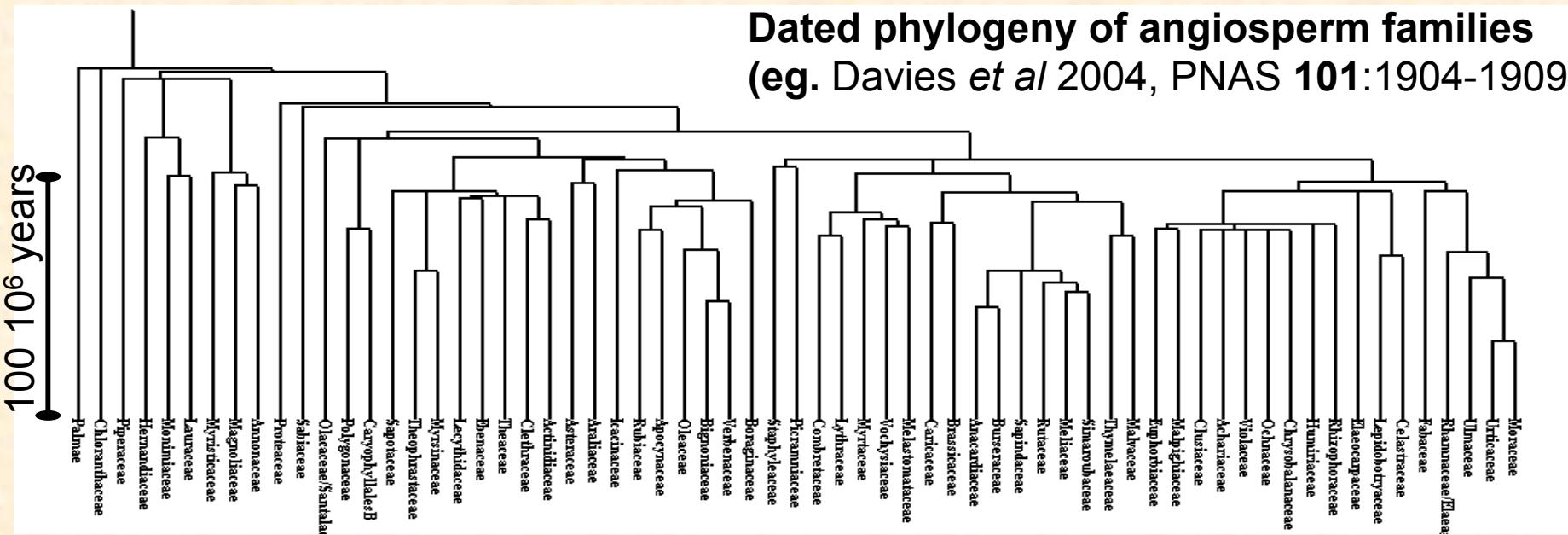
Ecotone : soil depth, luminosity, humidity...



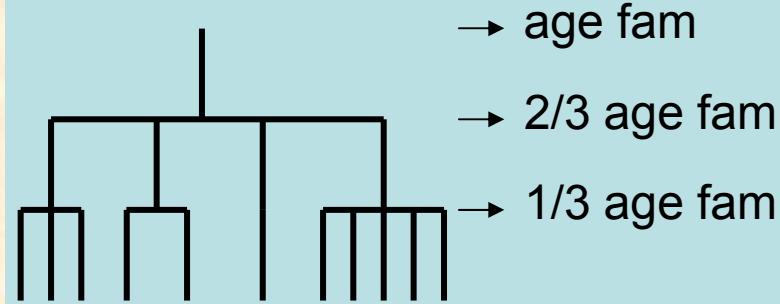
Ecological distance =
number of steps along the ecotone

Species phylogeny

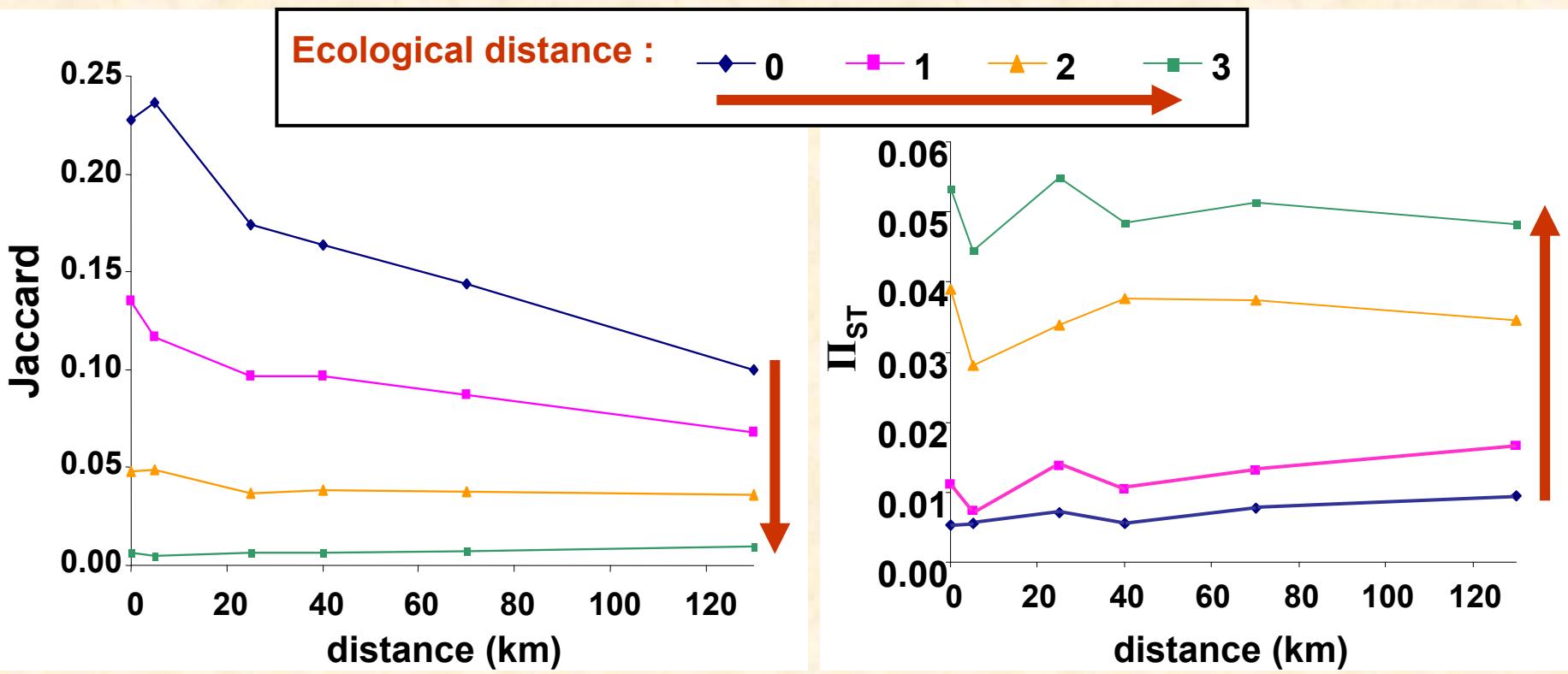
-> software Phylomatics (<http://www.phylodiversity.net/phylomatic/phylomatic.html>)
⇒ requires a list of species with their families (APG)



Within families, if no phylogeny available
→ polytomies of genera
→ polytomies of species
within genus



Species and phylogenetic turnover among inselbergs



Species turnover (J) depends on spatial distance + ecological gradient

Phylogenetic turnover (Π_{ST}) depends on ecological gradient only

Species turnover among inselbergs is probably due to dispersal limitation

Conclusion 1

At deep phylogenetic level (e.g. within angiosperms)

- phylogenetic clustering \Leftrightarrow ecological differentiation
 ~~$\not\Leftrightarrow$~~ dispersal limitation at regional scale
- ⇒ disantangle dispersal limitation *versus* ecological filtering

2. Impact of ecological gradients versus biogeography

Patterns of tree species phylogenetic turnover for 1ha (semi-)evergreen forest plots (DBH>10cm) on different continents

O Hardy, P Couteron, F Munoz, BR Ramesh, R Pélissier



data CTFS

Panama canal watershed

50 plots
Area 50km x 60km

Rainfall:

1500-3300mm

Elevation :

50-400m

data French Institute
Pondicherry

Western Ghats

50 plots
Area 50km x 200km

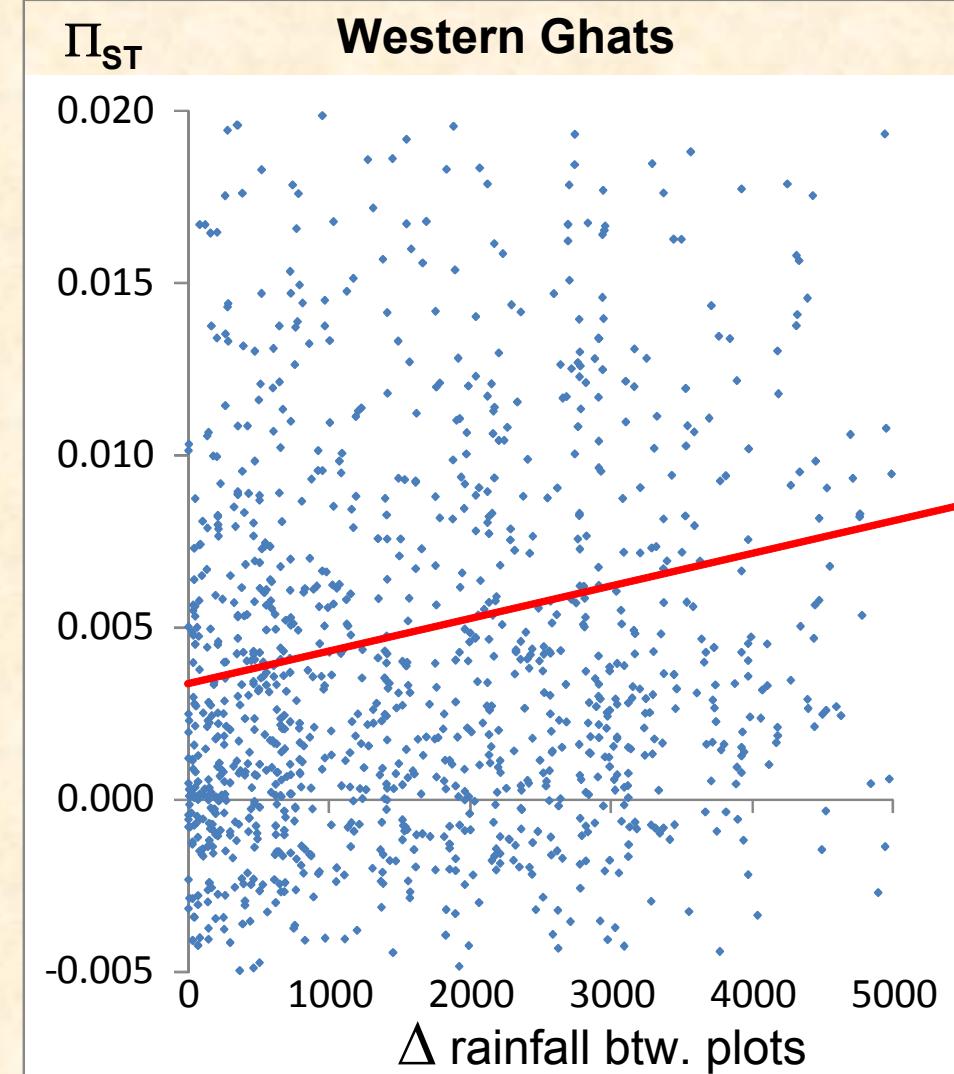
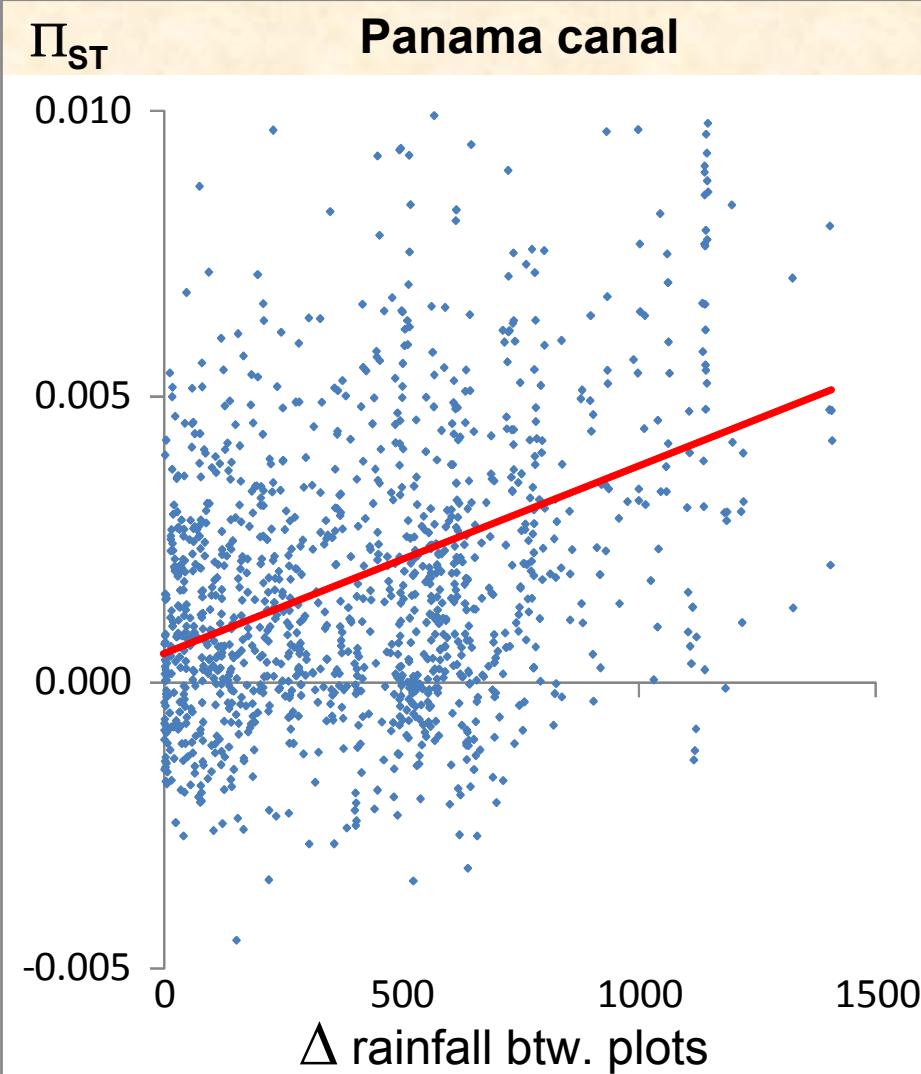
Rainfall:

1400-6000mm

Elevation:

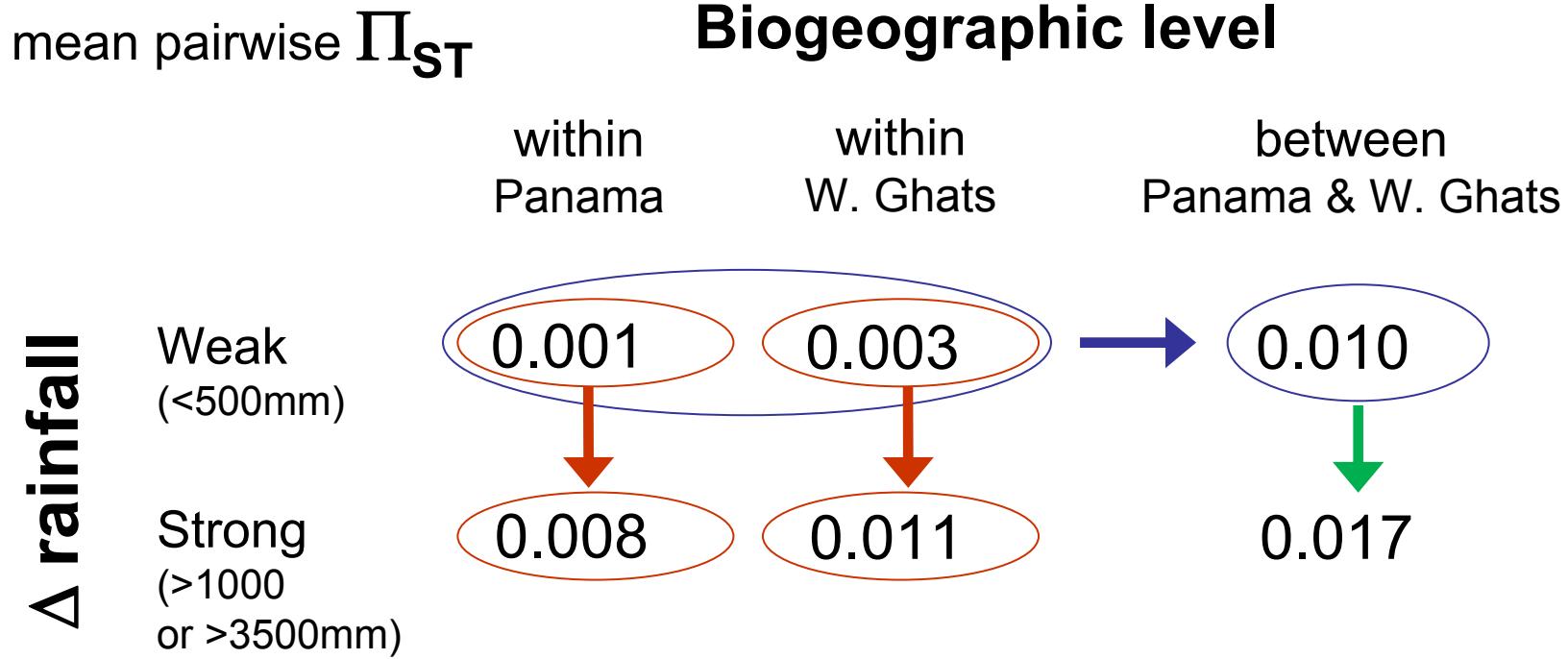
50-1050m

Phylogenetic turnover at regional scale



↳ Phylogenetic clustering within plots mostly explained by rainfall differences

Phylogenetic turnover impact of ecological gradients vs biogeography

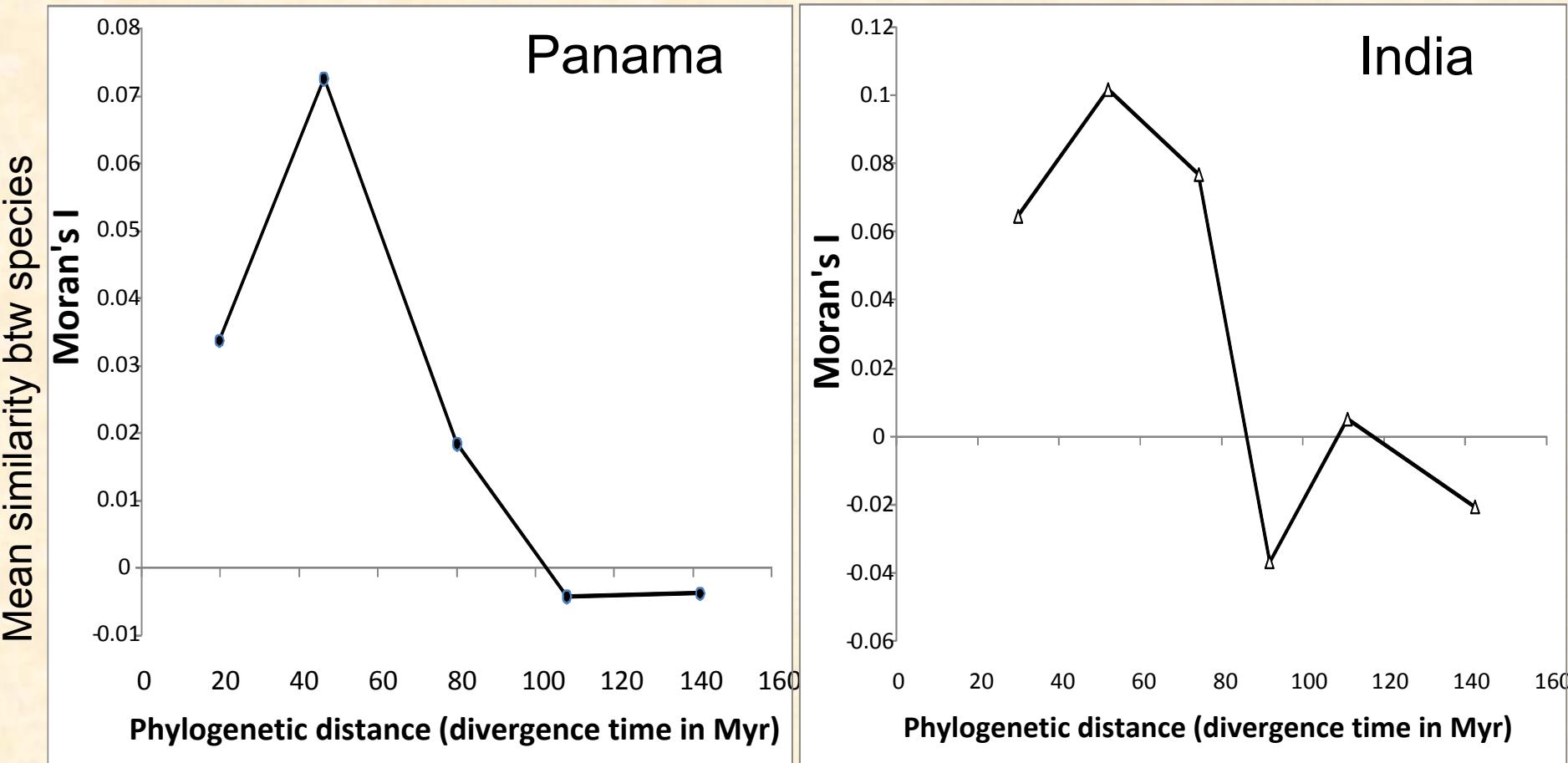


For forest tree communities, **at the scale of angiosperms**:

Impacts on Π_{ST} of { biogeography (inter-continental)
meso-climatic gradient } are comparable + seem cumulative

Is there a phylogenetic signal in species ‘adaptations’ towards the rainfall gradient?

Adaptation quantified by correlation between species abundance and rainfall/yr



Species having diverged <80 Myrs ago tend to share similar ‘adaptations’

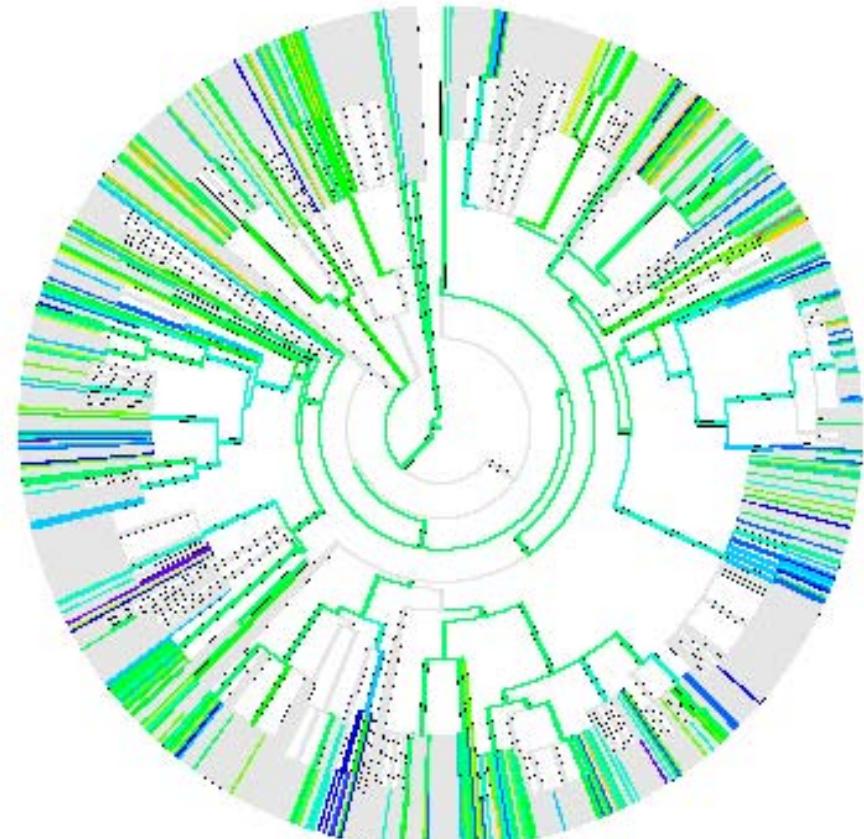
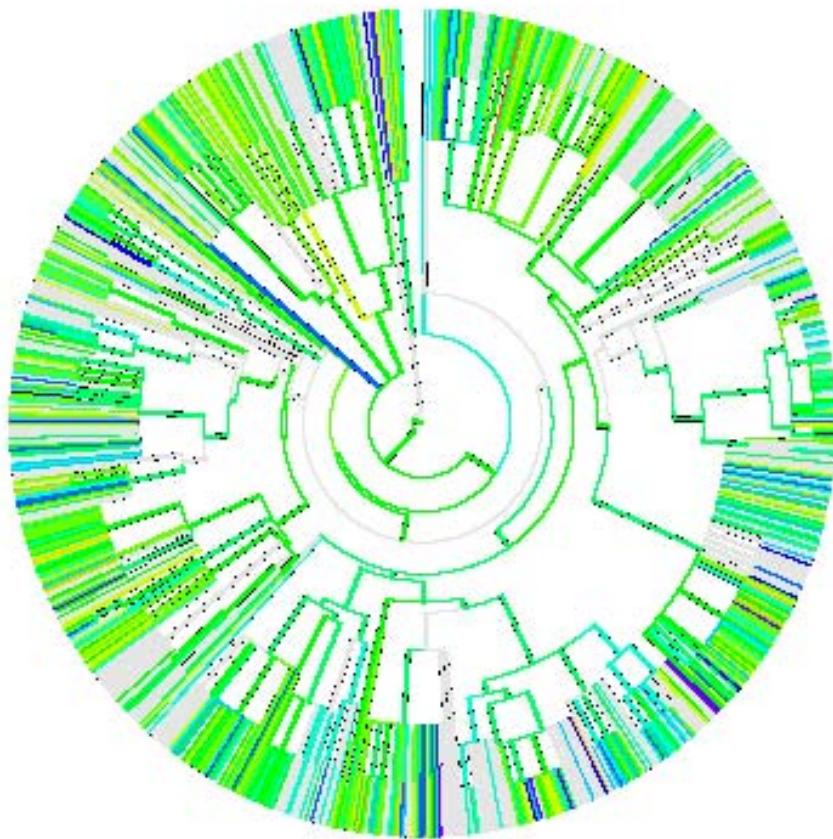
Reconstruction of ancestral niche along the phylogenies

 Mesquite software

Panama

India

No shared species but
many shared clades



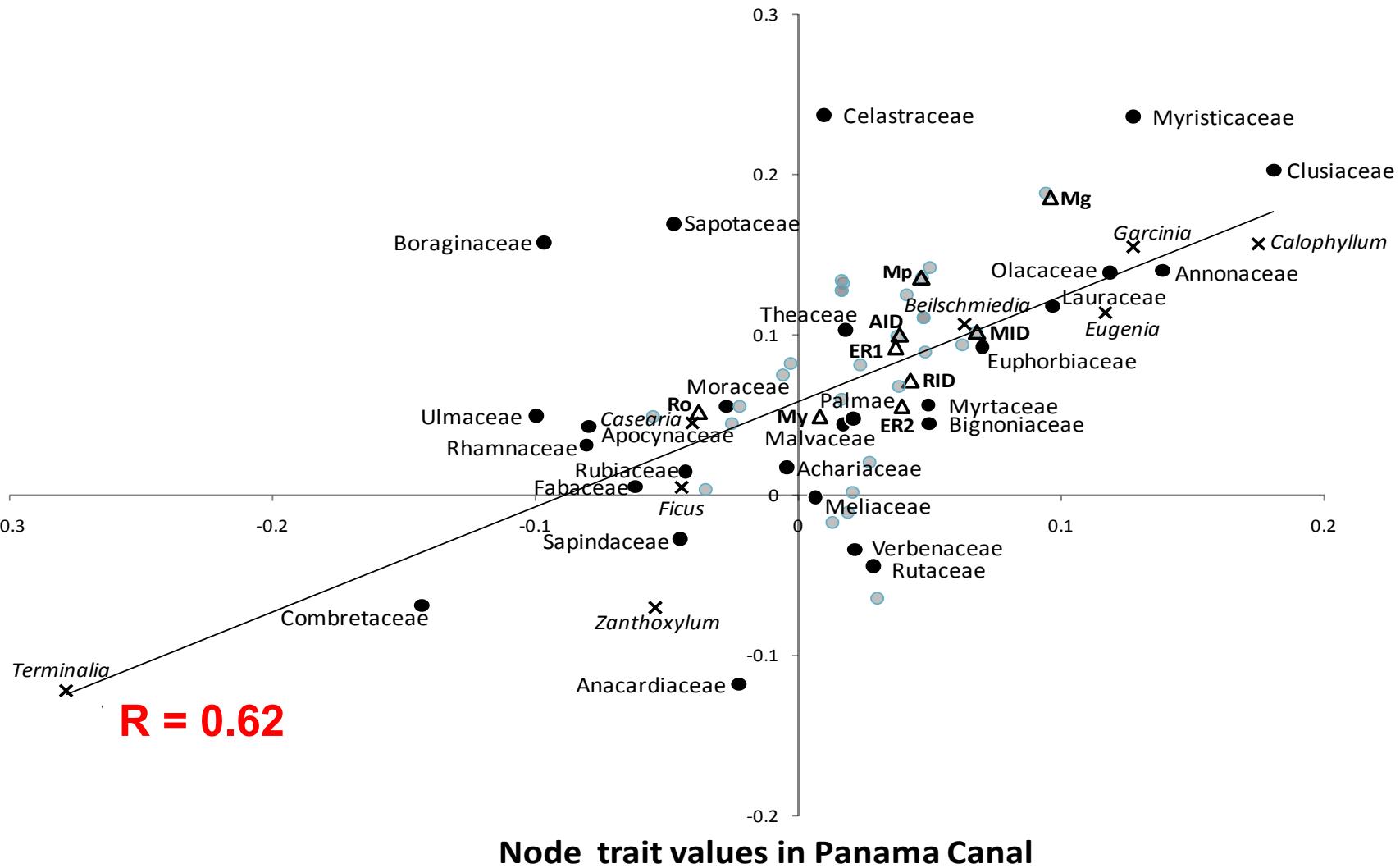
Moister



Drier

Inter-continental correlation of clade ‘adaptations’ with respect to rainfall gradient

Node trait values in Western Ghats



-> (pre)adaptations can persist over long evolutionary time (ca. 100 Myrs)

Conclusion 2

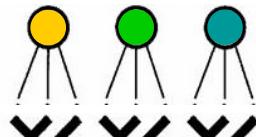
In rainforest tree communities, at deep phylogenetic level (e.g. within angiosperms):

- relative impacts of biogeography and meso-climatic gradients on phylogenetic clustering are comparable (on Π_{ST} metric)
- deep (worldwide) phylogenetic conservatism of climate adaptations

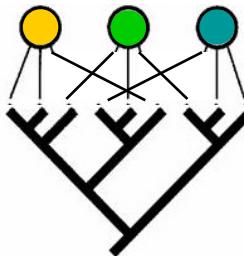
3. Integrating phylogeny and traits

C x P

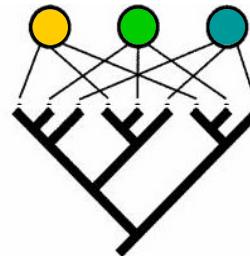
Phylogenetic clustering



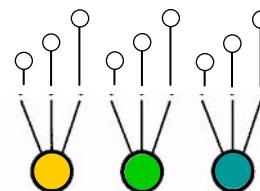
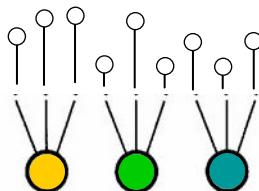
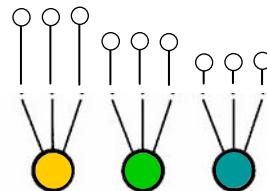
Random phylogenetic structure



Phylogenetic overdispersion



T x P



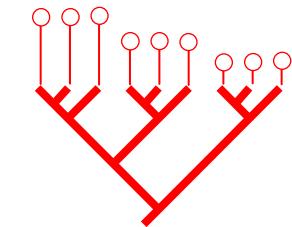
T x C

Environmental filtering

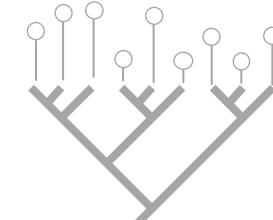
Random assembly (neutrality)

Competitive exclusion

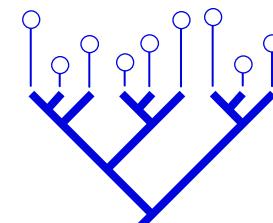
T x P



Trait conservatism



No phylogenetic signal



Trait convergence

Ideally, all levels should be taken into account

3. The BRIDGE project : phylogenetic and functional structures of rainforests from French Guiana

Jérôme Chave, Chris Baraloto, Kyle Dexter, Timothy Paine, Olivier Hardy, Vincent Savolainen



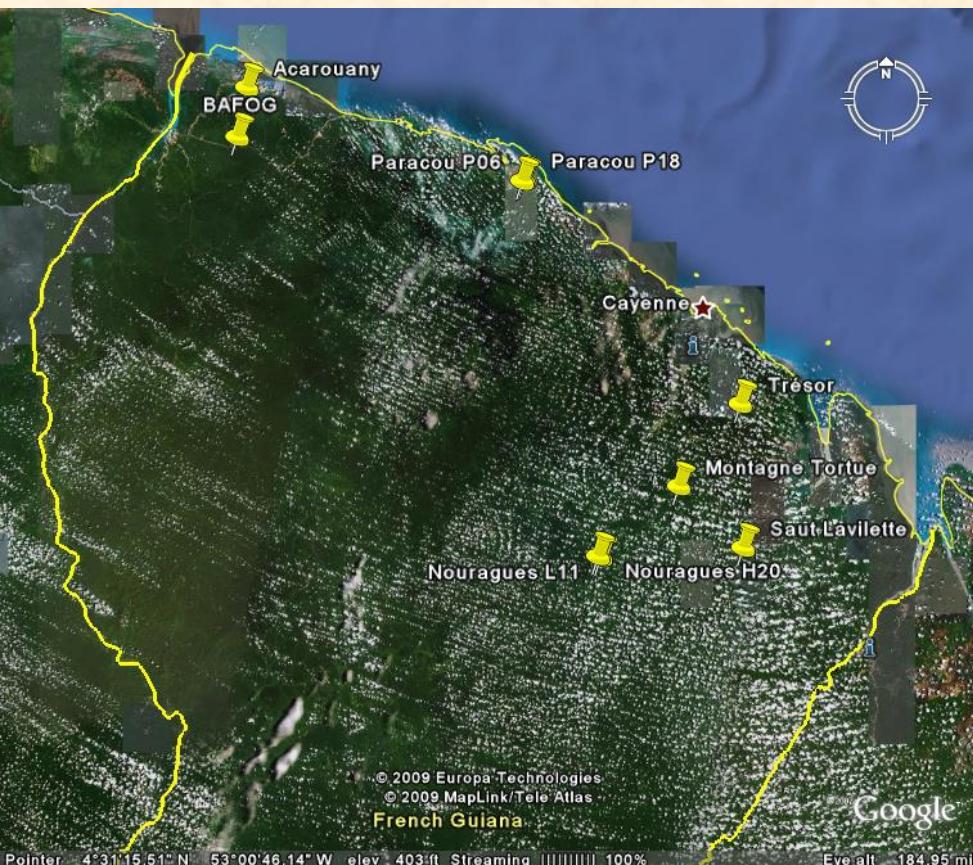
Guyane field teams (Jean-Yves Serein, Jean-Yves Goret, Elodie Courtois, Pierre-Alain Blandinières, Pascal Pétronelli, Mailyn Gonzalez, Odile Poncy, Julien Engel...)

Toulouse lab team (Celine Vicedos, Mailyn Gonzalez, Julien Vieu...)

Funding:
ANR (programme Biodiversité)
CNRS (programme AMAZONIE)
Génoscope
Région Guyane, DIREN, DRRT

BRIDGE Project: 9 one-ha plots sampled

Trees DBH > 10cm



Plot	# ind	# sp	Fisher's α
Bafog	576	153	67.4
Acarouany	442	147	75.3
Paracou 1	632	149	60.8
Paracou 2	478	151	74.6
Nouragues 1	544	196	108.2
Nouragues 2	507	177	95.6
Trésor-Kaw	418	156	89.2
Montagne Tortue	501	201	122.3
Saut Lavilette	582	208	114.8
TOTAL	4680	688	



Traits Measured

- Leaf toughness
- Leaf tissue density
- Leaf area
- Specific leaf area
- N content
- C:N ratio
- NH_4 proportion
- P content
- K content
- leaf ^{13}C
- Chlorophyll content

**Leaf
structure
traits**

- Sapwood density

- Trunk moisture

- Bark thickness

- Twig wood density

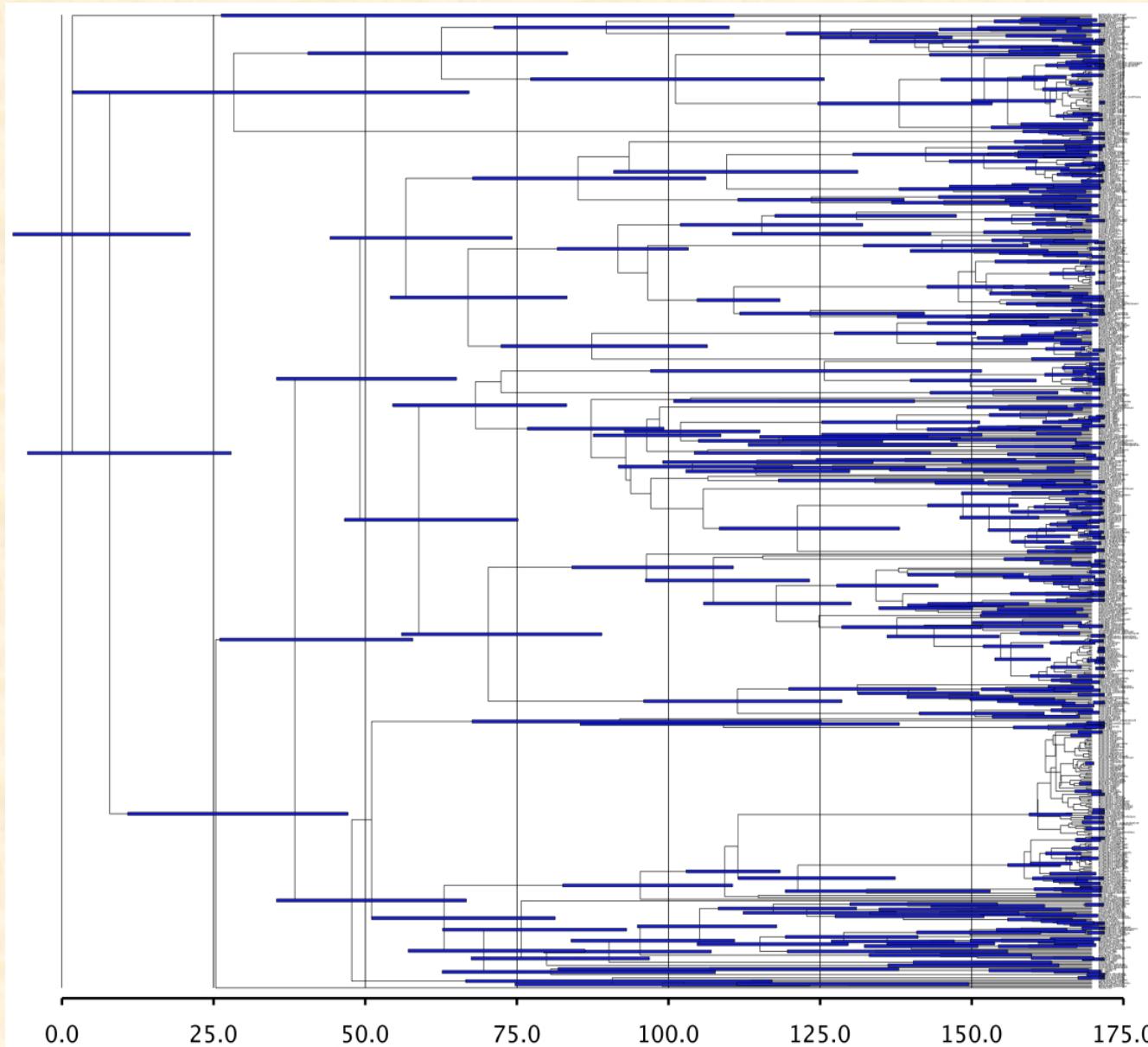
- Twig bark thickness

**Leaf
chemistry
traits**

**Trunk and
wood traits**

**Twig
traits**

**Phylogeny generated for >600 species (*rbcL* and *matK*)
+ temporal calibration using relaxed molecular clock**



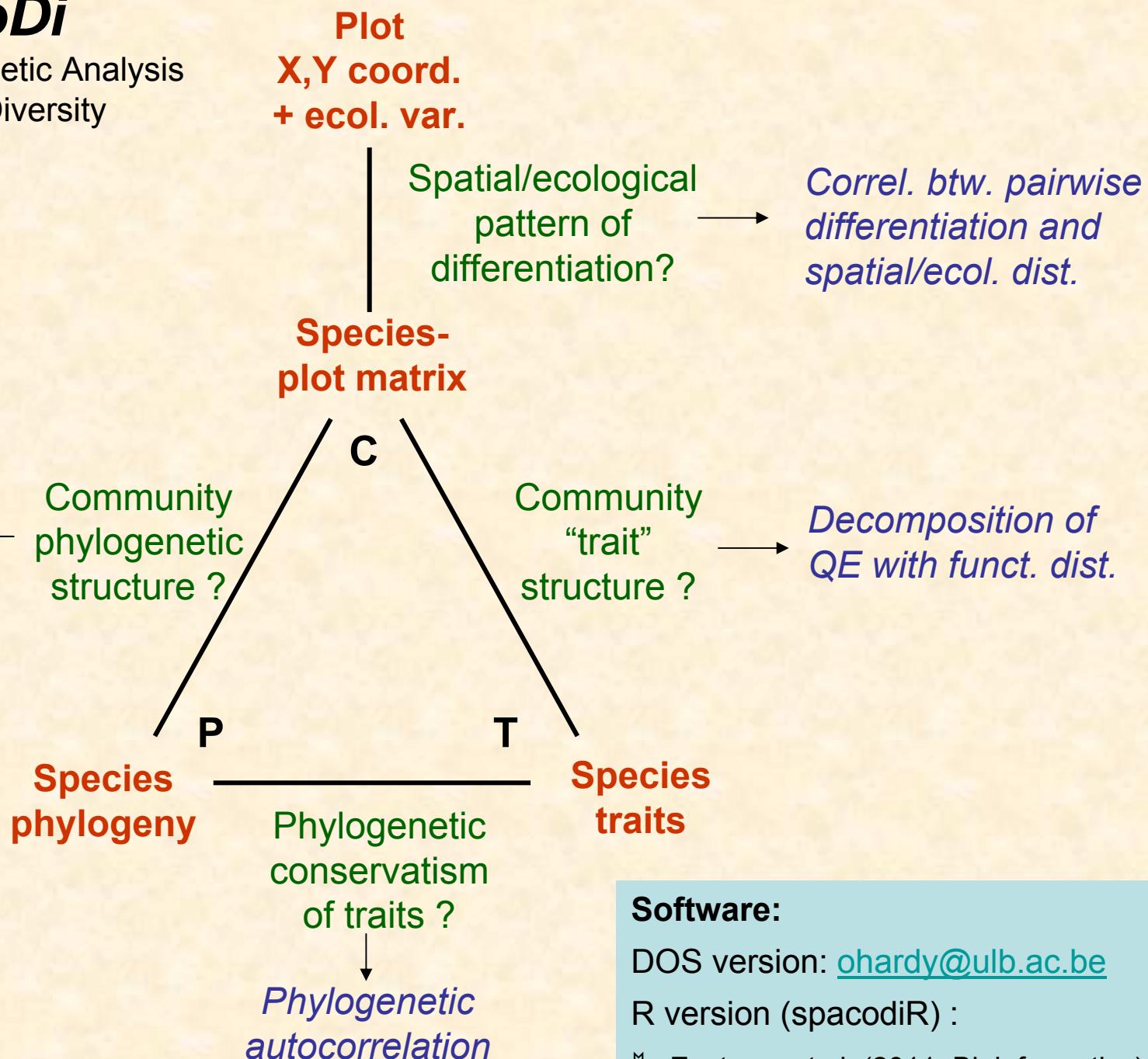
BEAST v1.53
Drummond and
Rambaut 2009

SPACoDi

Spatial and Phylogenetic Analysis
of Community Diversity

{
Data
Questions
Methods

Decomposition
of QE with phylo
distance
Whole or partial
phylogeny
random. tests



Comparing phylogenetic and functional community structures

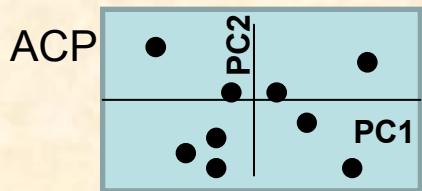
From a phylogeny



phylogenetic
or
functional

From species traits

distances between species



δ_{kl}

	0	1	2	3
0	0	1	2	3
1	1	0	2	2
2	2	2	0	1
3	3	2	1	0

From community inventories:

⇒ partition of QE = mean δ_{kl} between individuals

sampled
— within sites
— among sites

$$QE_w = \bar{\delta}_{(2_individuals_from_same_site)}$$

$$QE_a = \bar{\delta}_{(2_individuals_from_different_sites)}$$

→ $P_{ST} = 1 - QE_w / QE_a$

species + phylogenetic turnover

→ $T_{ST} = 1 - QE_w / QE_a$

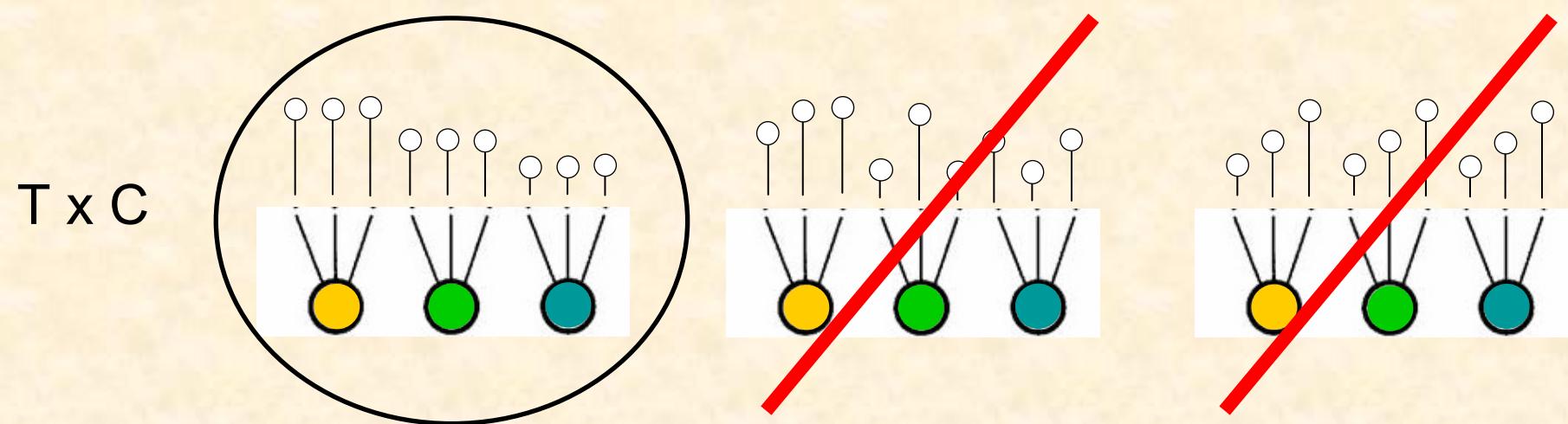
species + functional turnover

or

CxT : Functional structure of communities

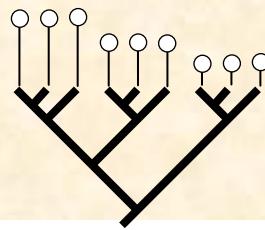
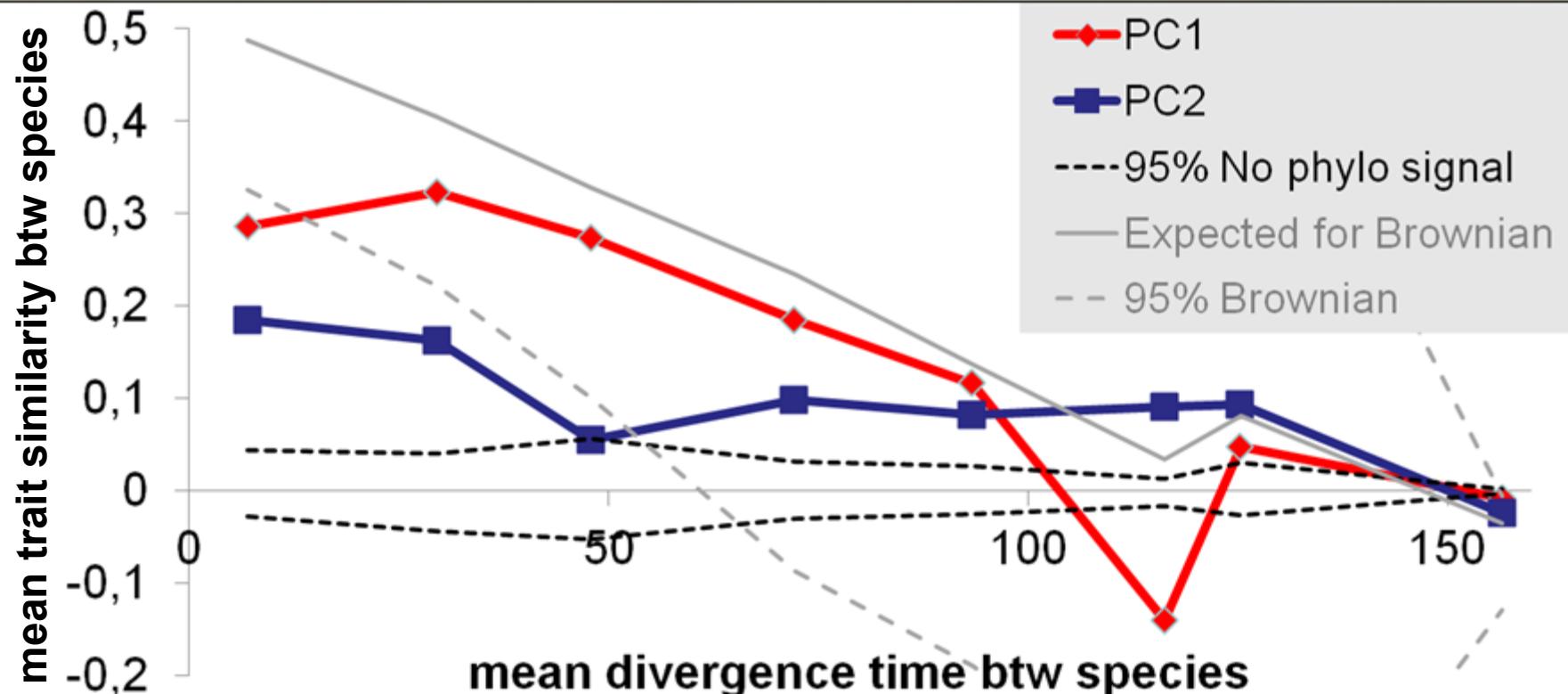
- $T_{ST} = 0.0313 > [0.0076, 0.0172]$ under H_0
- $\tau_{ST} = 0.0119 > [-0.0010, 0.0014]$ under H_0

→ **Functional clustering**

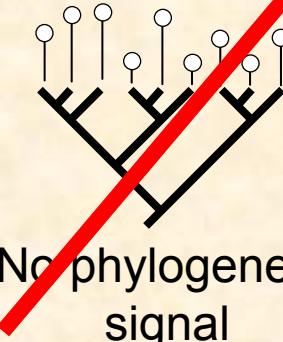


↳ interpretation: habitat filtering dominates

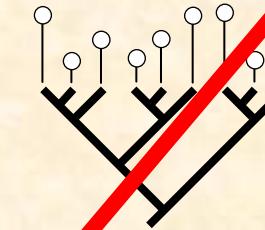
TxP : Phylogenetic structure of traits



T x P
Trait conservatism



No phylogenetic
signal



Trait convergence

PC1 conforms to Brownian motion model

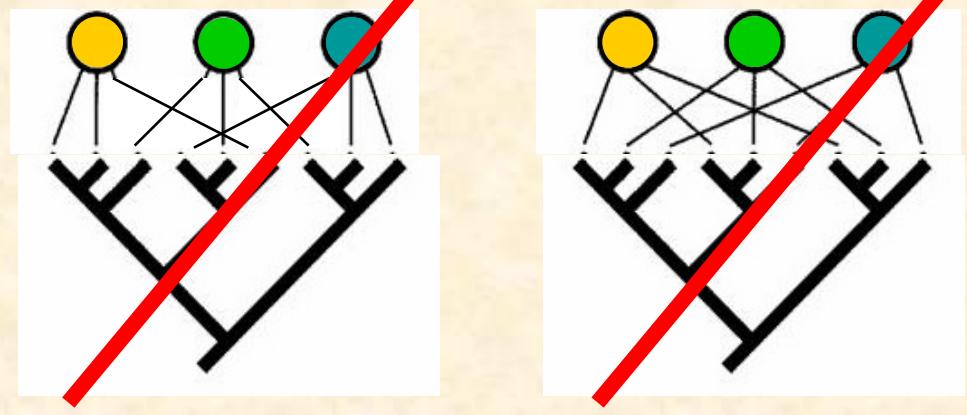
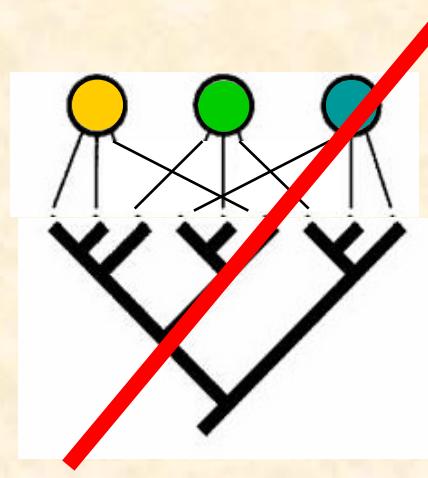
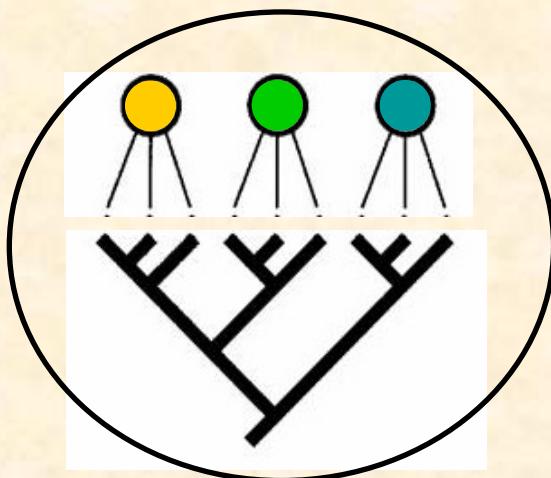
PC2 less conserved than Brownian (conform to Ornstein-Uhlenbeck model)

PxC : Phylogenetic structure of communities

- $P_{ST} = \mathbf{0.0246} > [0.0098, 0.0161]$ under Ho
- $\Pi_{ST} = \mathbf{0.0033} > [-0.0006, 0.0008]$ under Ho

→ Phylogenetic clustering

P x C

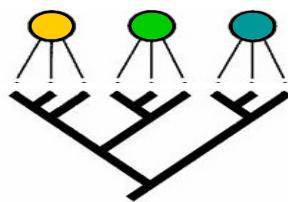


Conclusion 3

In continental tropical rainforests

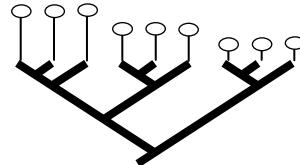
- trait conservatism seems to hold in general
- phylogenetic clustering reflects functional clustering due to environmental filtering

$C \times P$



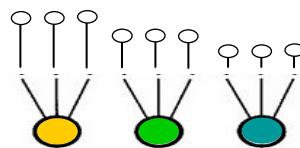
**Phylogenetic
clustering**
(at least at deep
phylogenetic level)

$T \times P$



Trait conservatism

$T \times C$



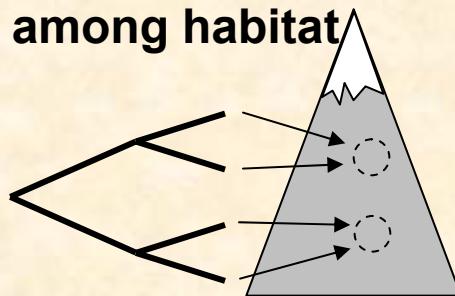
**Environmental
filtering**



Does phylogenetic overdispersion sometimes occur ?

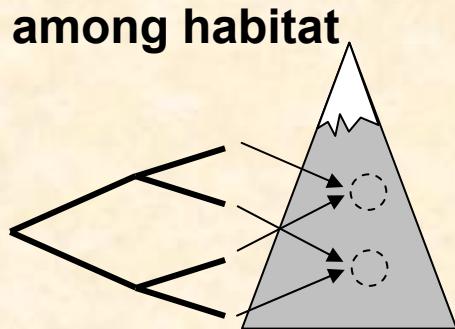
Phylogenetic clustering

↳ case studies 1, 2, 3



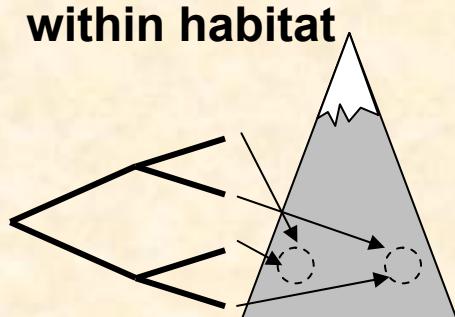
Phylogenetic overdispersion

↳ case study 4 ?



Phylogenetic overdispersion

↳ case study 5 ?



environmental filtering

adaptation to ≠ elevation
+

habitat conservatism

environmental filtering

adaptation to ≠ elevation
+

habitat convergence

e.g. *radiation of several clades
in a set of new habitats*

competitive exclusion

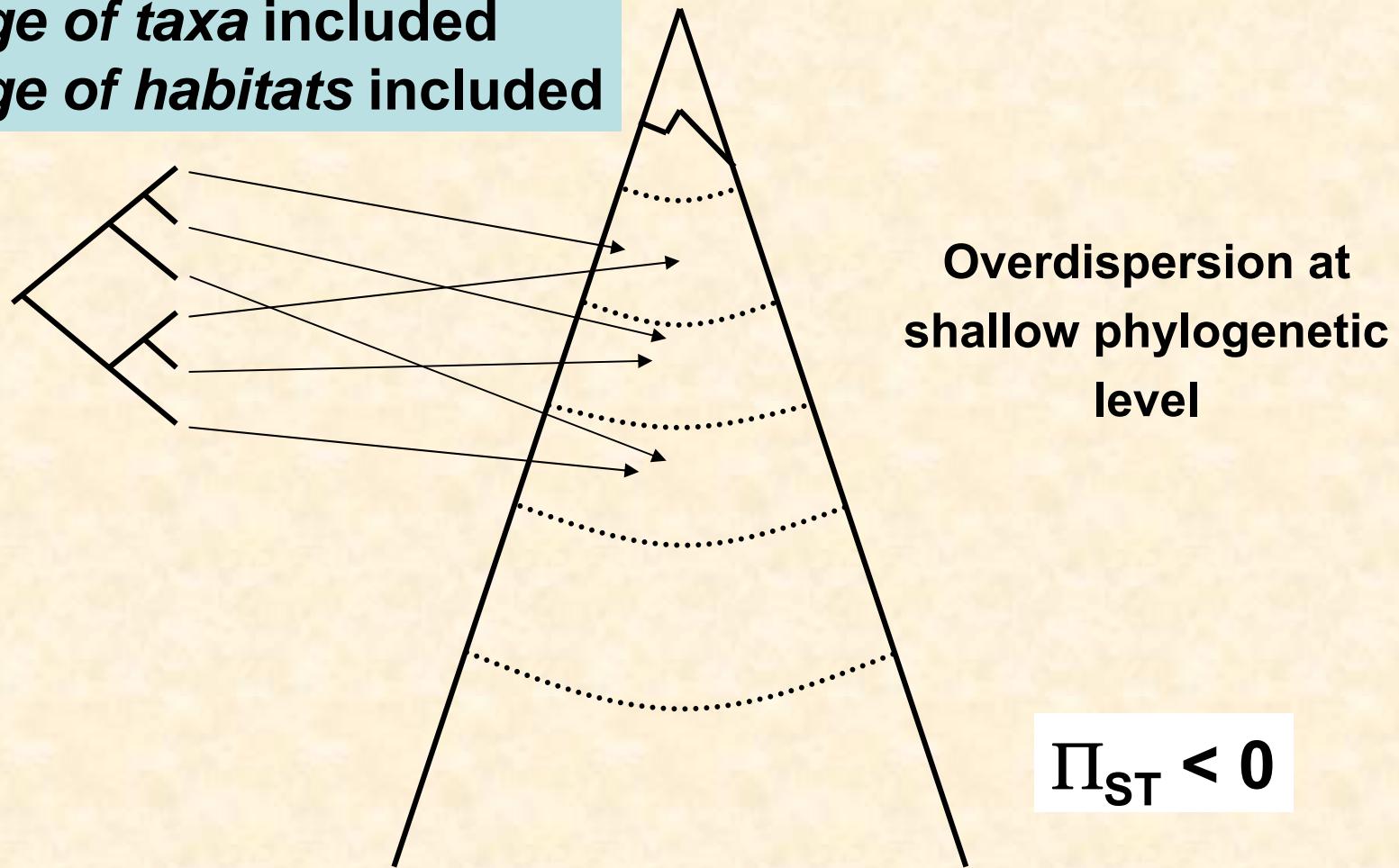
+

niche conservatism

→ sister species cannot coexist
because of niche overlap

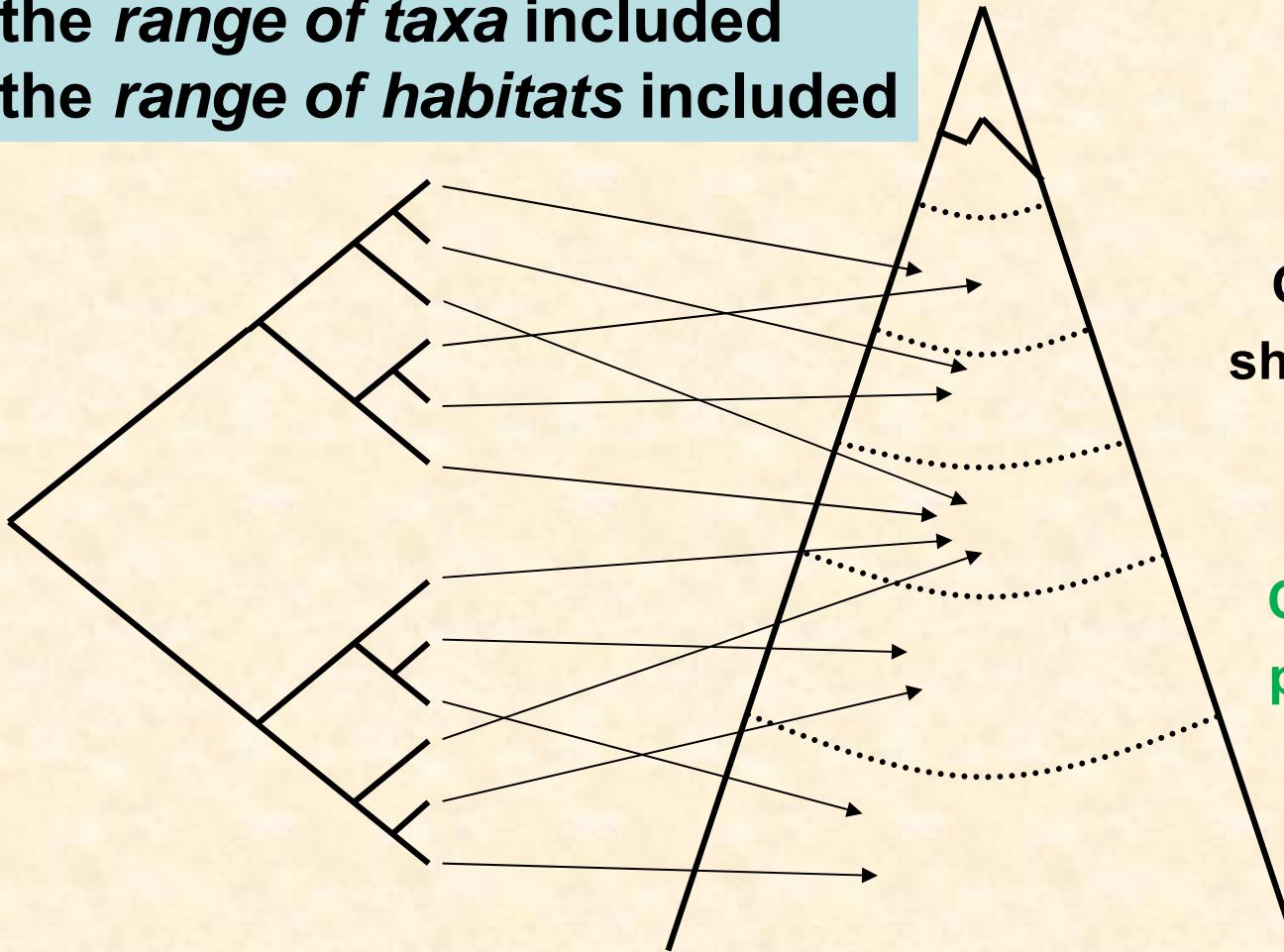
Phylogenetic clustering / overdispersion is relative to

{ the *range of taxa included*
the *range of habitats included*



Phylogenetic clustering / overdispersion is relative to

{ the *range of taxa included*
the *range of habitats included*



Overdispersion at
shallow phylogenetic
level

+

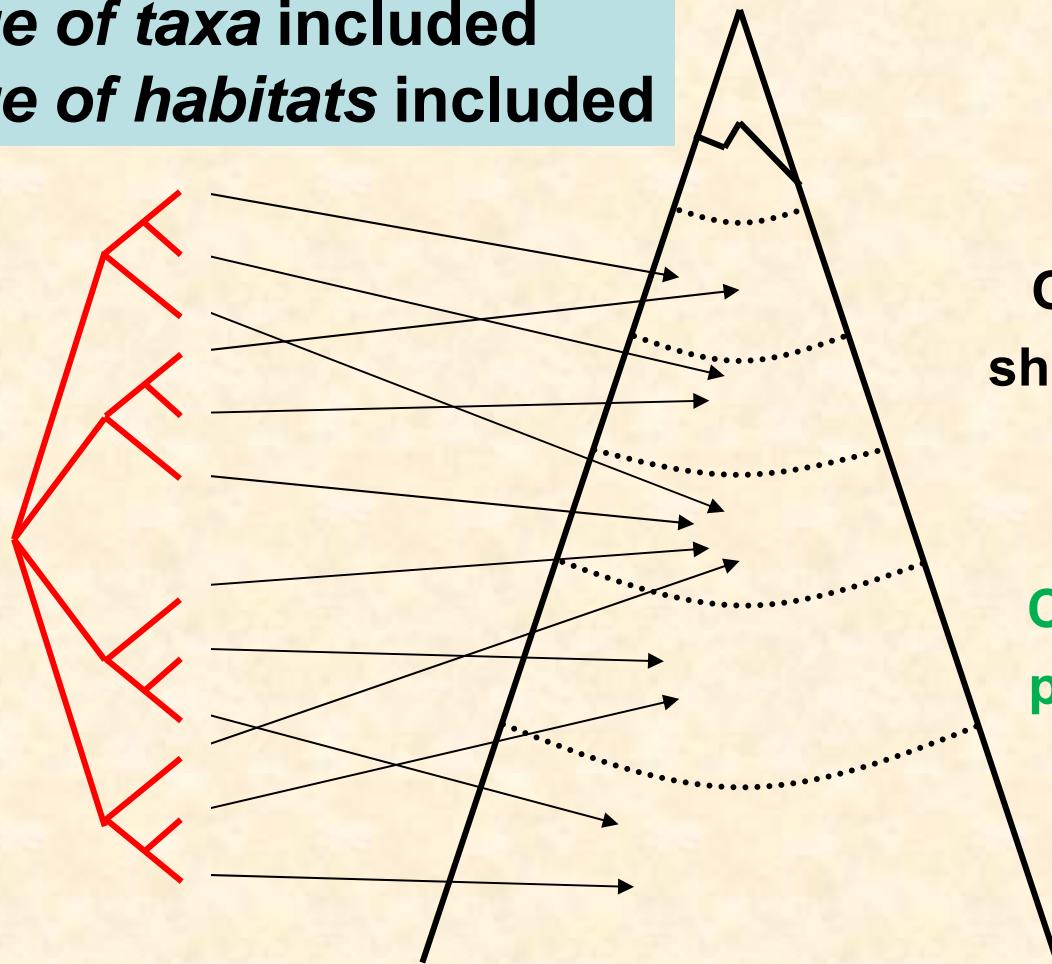
Clustering at deep
phylogenetic level

$$\Pi_{ST} > 0$$

How to test this pattern ?

Phylogenetic clustering / overdispersion is relative to

{ the *range of taxa included*
the *range of habitats included*



Overdispersion at
shallow phylogenetic
level

+

Clustering at deep
phylogenetic level

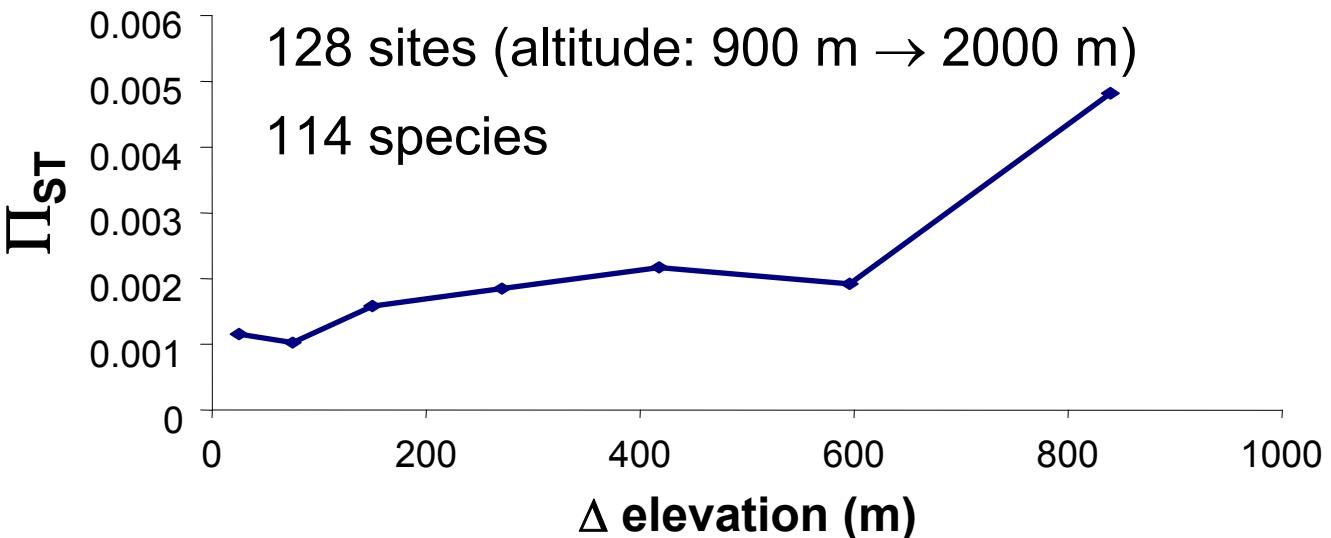
$$\Pi_{ST} < 0$$

How to test this pattern ?

👉 transform the phylogenetic tree to remove deep phylogenetic information

4. Phylogenetic structure under recent multiple radiations: Forest communities from Reunion island

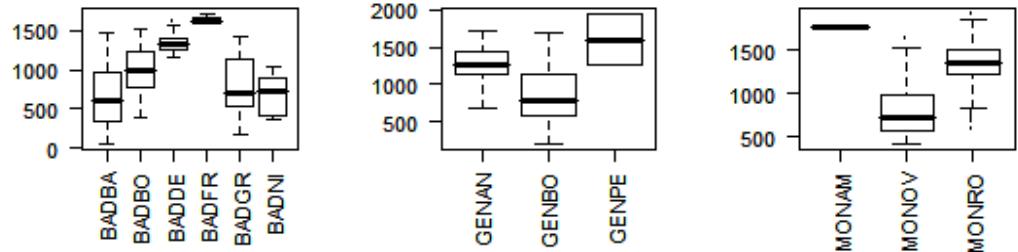
J. Eyraud, D. Stasberg, C. Thebaud, O. Hardy, J. Chave (unpublished)



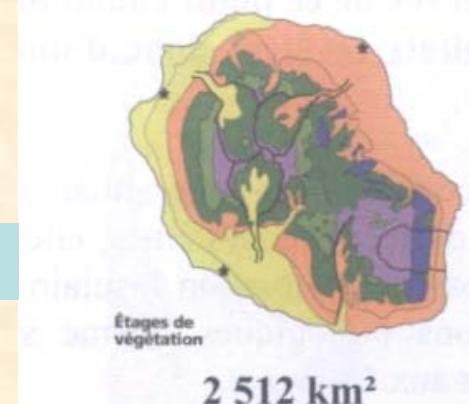
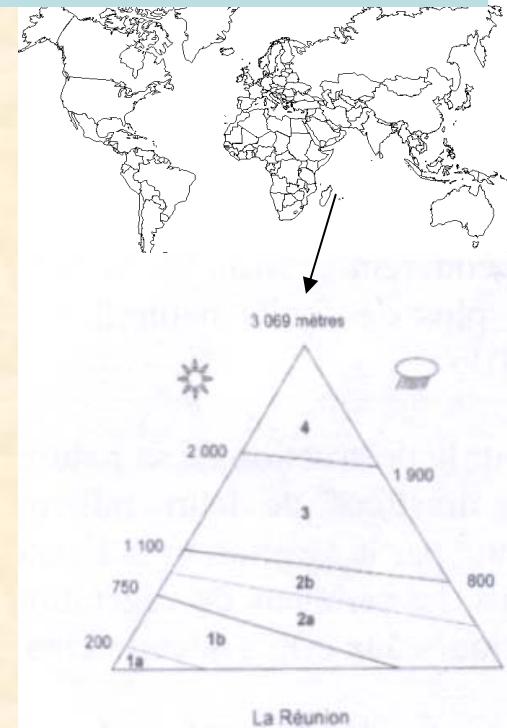
⇒ phylogenetic clustering ↑ with Δ elevation

However, 9 genera have diversified on the island
→ why no phylogenetic overdispersion ?

Elevation ranges of endemic species in 3 genera



PARADOX?



Phylogenetic turnover at different time depths

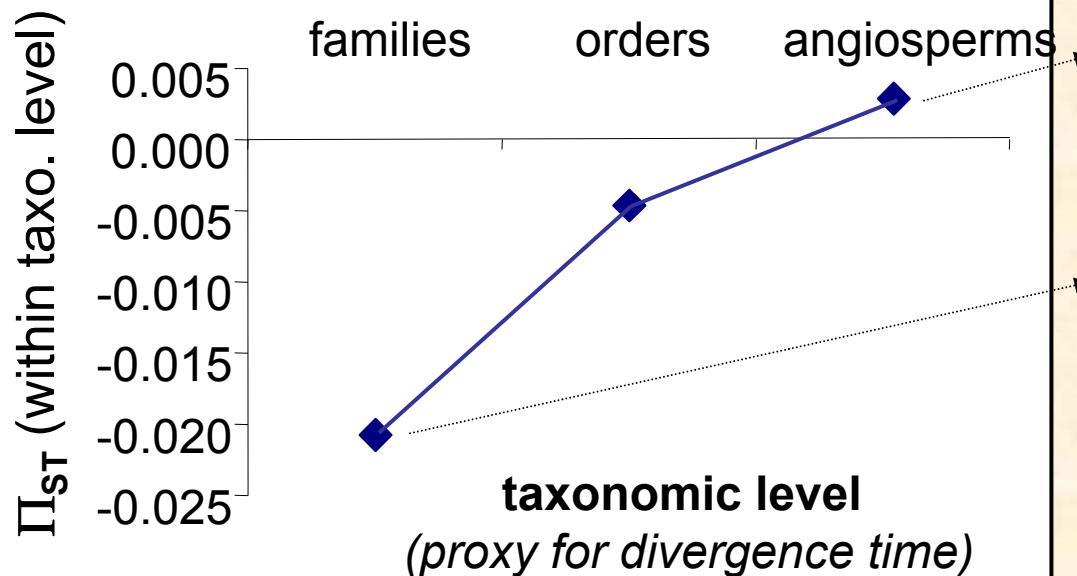
$MPD^{\delta < T}$ mean divergence time (δ) between species for $\delta < T$

→ compare pairs of species sampled *within* versus *among* sites :

$$\Pi_{ST}^T = 1 - MPD_w^{\delta < T} / MPD_a^{\delta < T}$$

→ characterize phylogenetic turnover at different time depths

Example: Reunion island



for all angiosperms

→ phylogenetic clustering

↳ overall habitat conservatism

within families

→ phylogenetic overdispersion

↳ diversification of several genera
(congeneric species do not co-occur)

Conclusion 4

At shallow phylogenetic levels (e.g. within a genus or a family)

- phylogenetic overdispersion may occur due to recent local diversification (e.g. on island)

⇒ impact of time depth detectable using $\Pi_{ST}^{\delta < T}$

Emerging patterns in the comparative analysis of phylogenetic community structure

S . M. VAMOSI,* S . B. HEARD,† J . C. VAMOSI* and C. O. WEBB‡

Molecular Ecology (2009) 18, 572–592

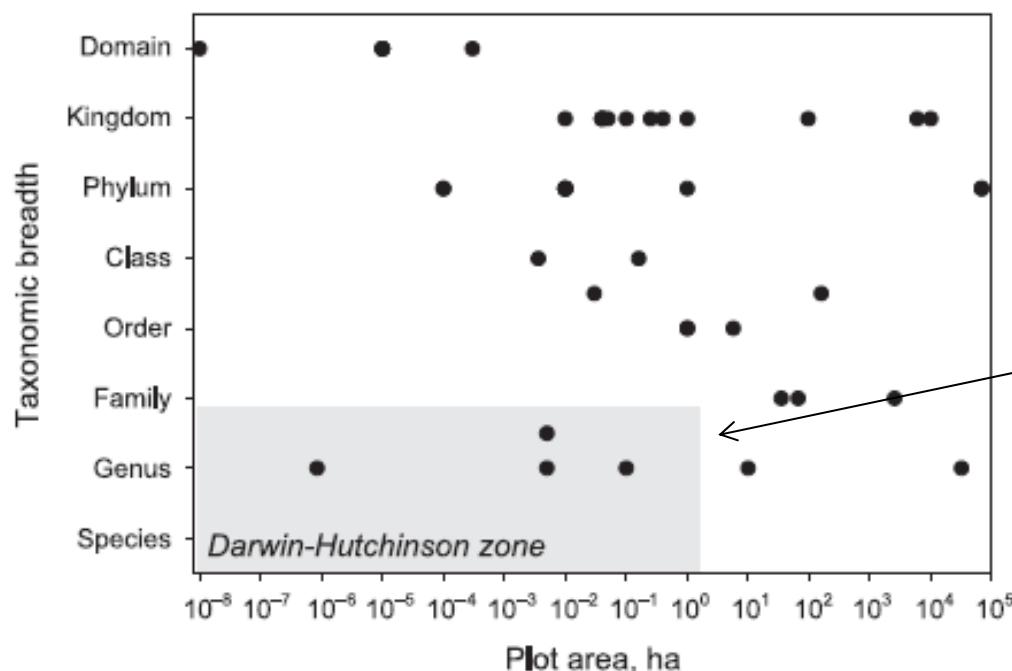


Fig. 4 Taxonomic and geographical scales of contemporary studies in phylogenetic community structure. The x-axis refers to the geographical extent of individual study plots, and the y-axis the highest taxonomic level considered in the study. The 'Darwin–Hutchinson zone' marks an approximate region of the plane for which we might be particularly interested in community phylogenetic structure: plots small enough for individuals to interact, and species closely enough related that competition is a plausible expectation (see Taxonomic and geographical scales for further discussion).

=> Phylogenetic clustering most often observed, but competitive exclusion may be important in the 'Darwin–Hutchinson zone'



Investigate patterns at:

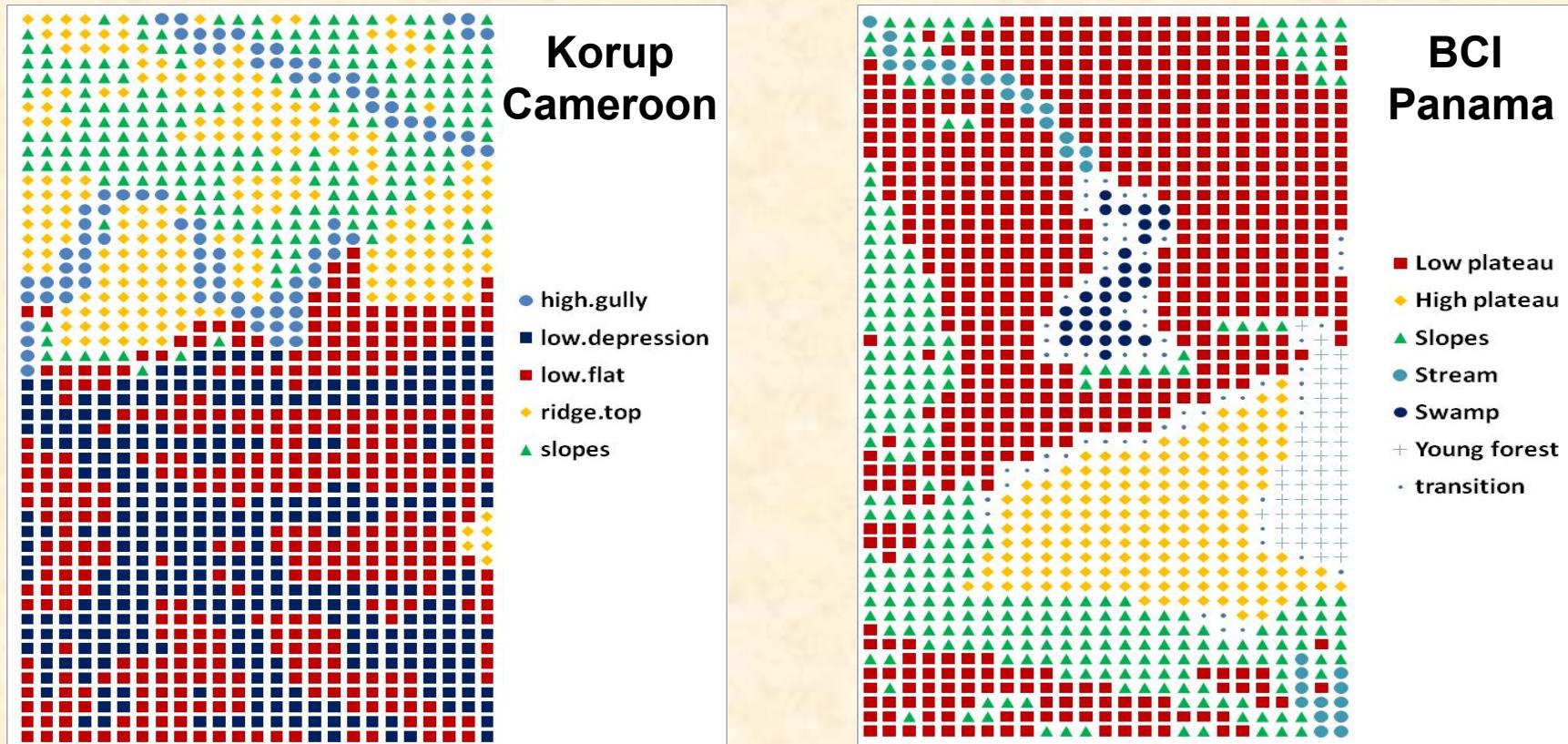
- scale of inter-individual competition
- shallow phylogenetic depth

5. Phylogenetic structure under **inter-individual competition** : fine-scale spatial phylogenetic turnover in 50-ha plots

O Hardy, I Parmentier, M Réjou-Méchain, J Duminil, M Kuzmina, DW Thomas, D Kenfack, GB Chuyong, J Kress, D Erickson (unpublished)

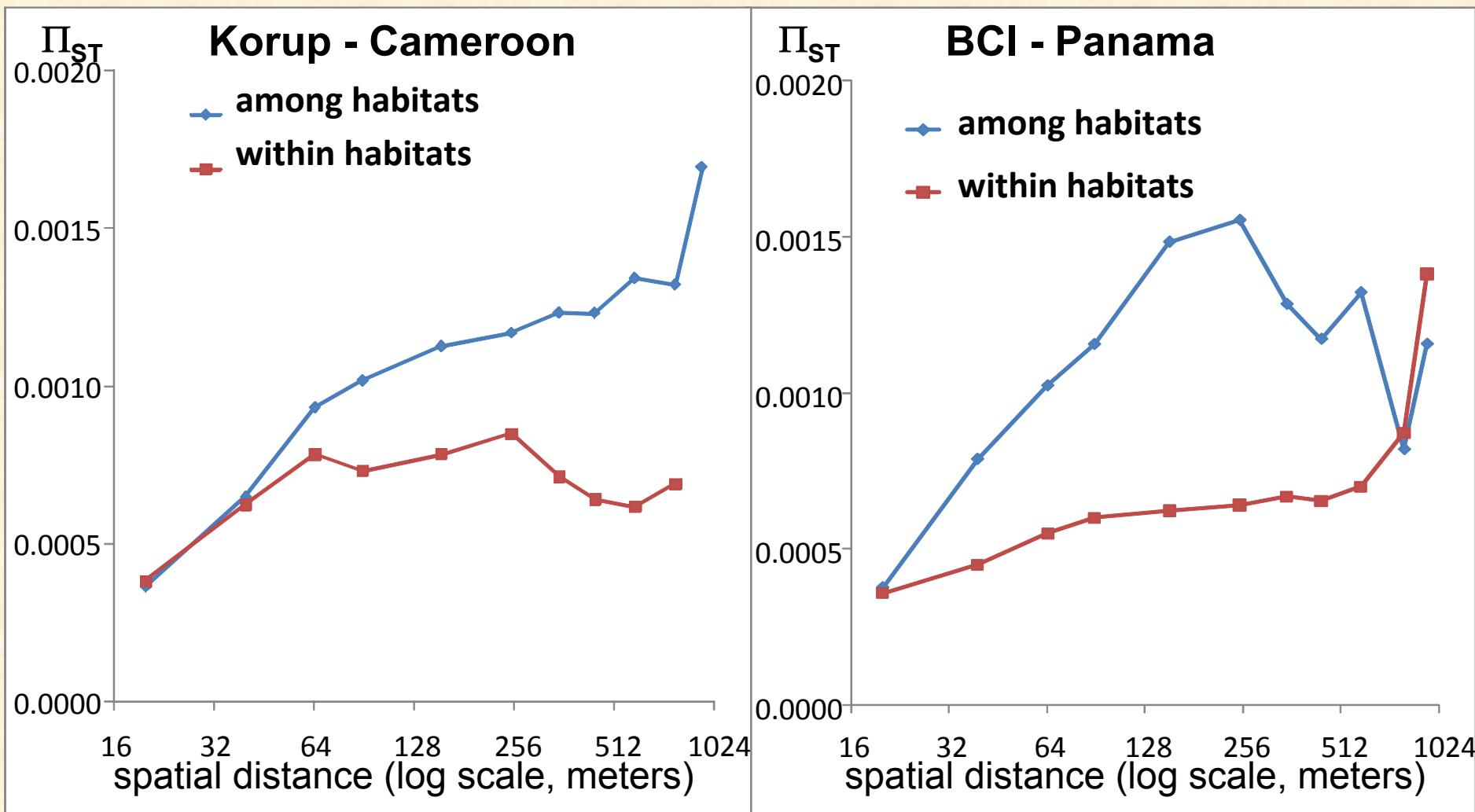
500m x 1000m evergreen forest plots (all stems DBH>1cm inventoried)

↳ subdivided into 20m x 20m subplots categorized into **5-6 habitats**



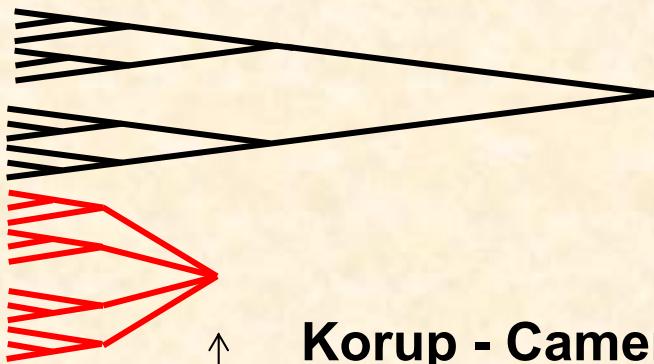
Molecular phylogenetic trees based on *rbcL* + *matK*

Phylogenetic turnover impact of spatial distance vs topographic habitat types



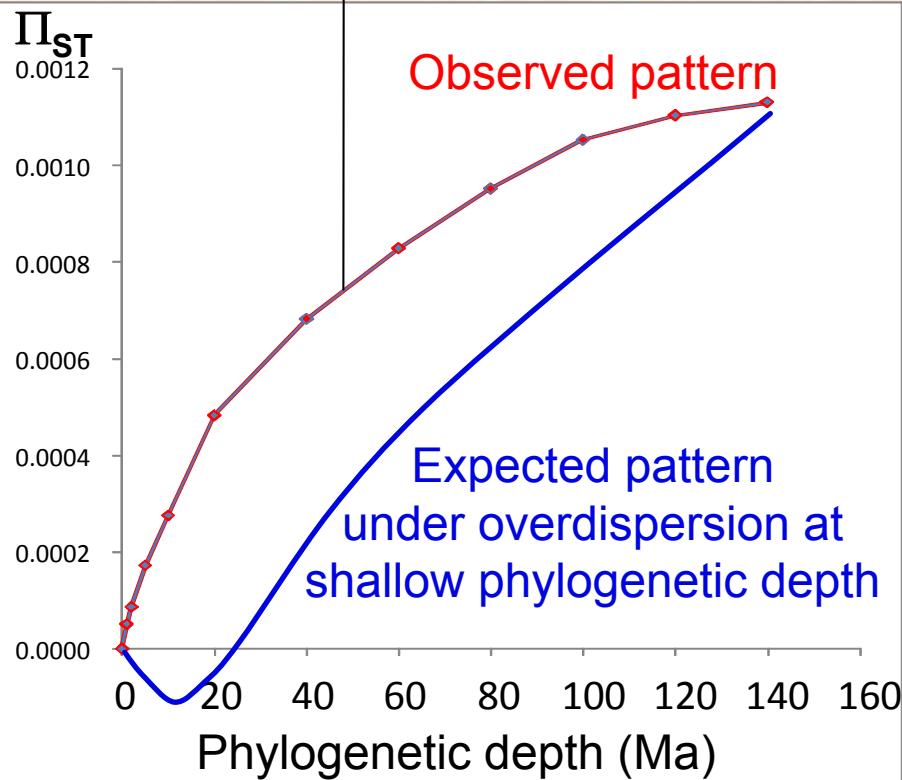
- 👉 Habitat categories explain part but not all the phylogenetic turnover
- 👉 Phylogenetic clustering ($\Pi_{ST}>0$) occurs at all scales (no overdispersion)

Phylogenetic turnover at shallow phylogenetic depth: Does phylogenetic overdispersion occur?

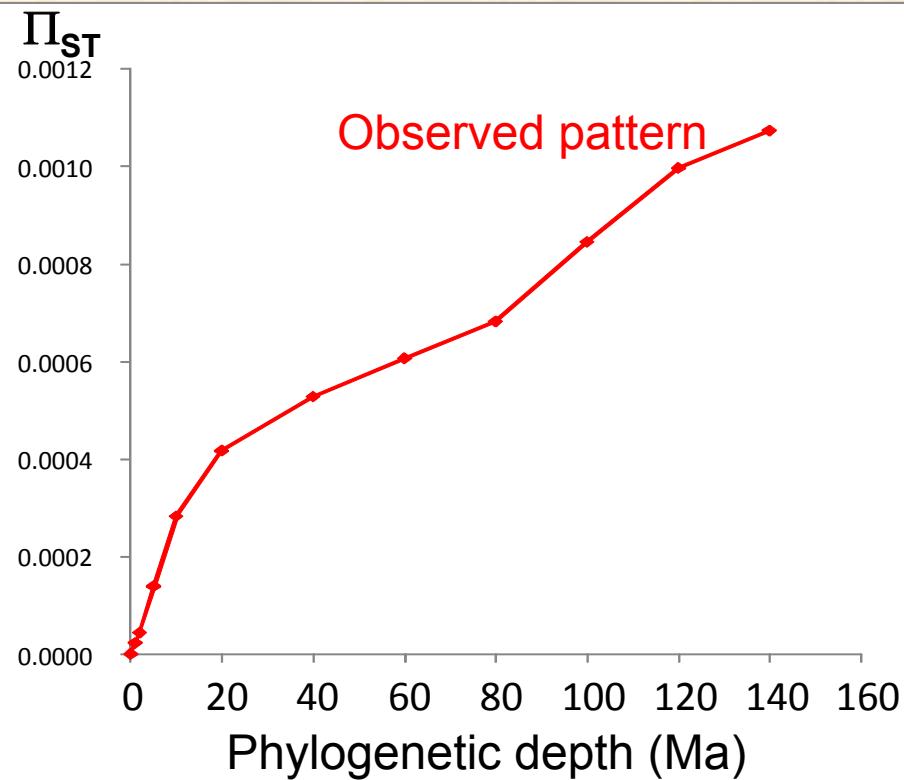


↗ no evidence of
phylogenetic overdispersion

Korup - Cameroon



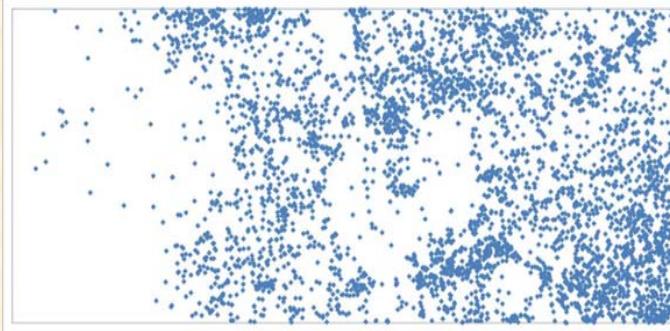
BCI - Panama



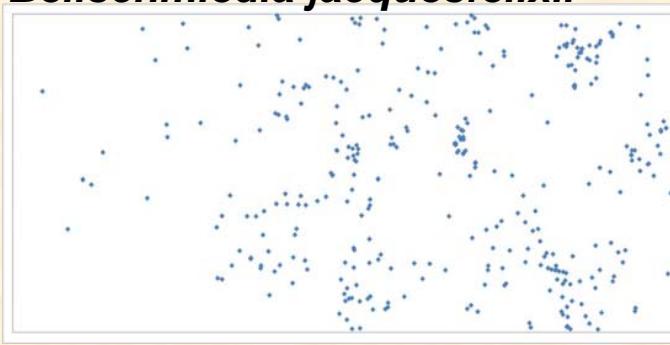
Does phylogenetic overdispersion occur at smaller scales?

↳ individual-based analyses

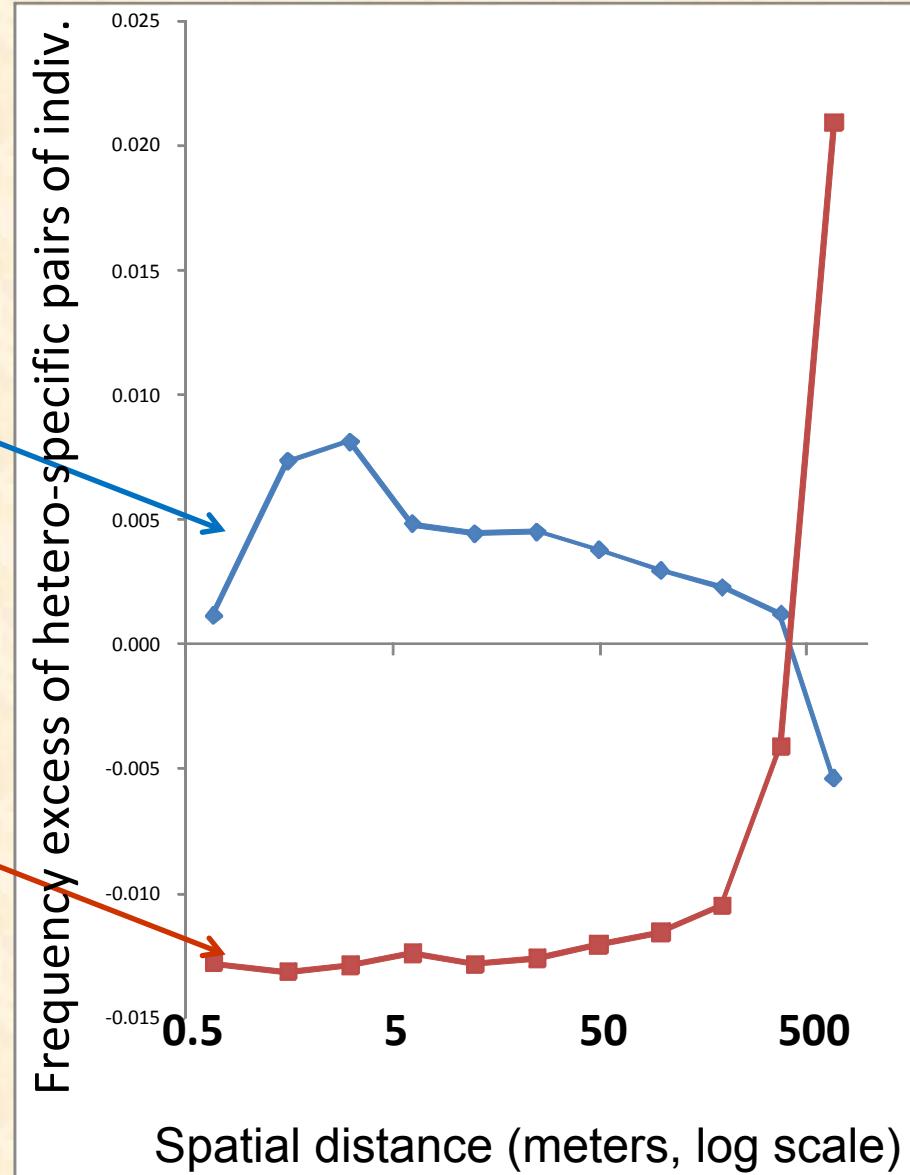
Cola cauliflora



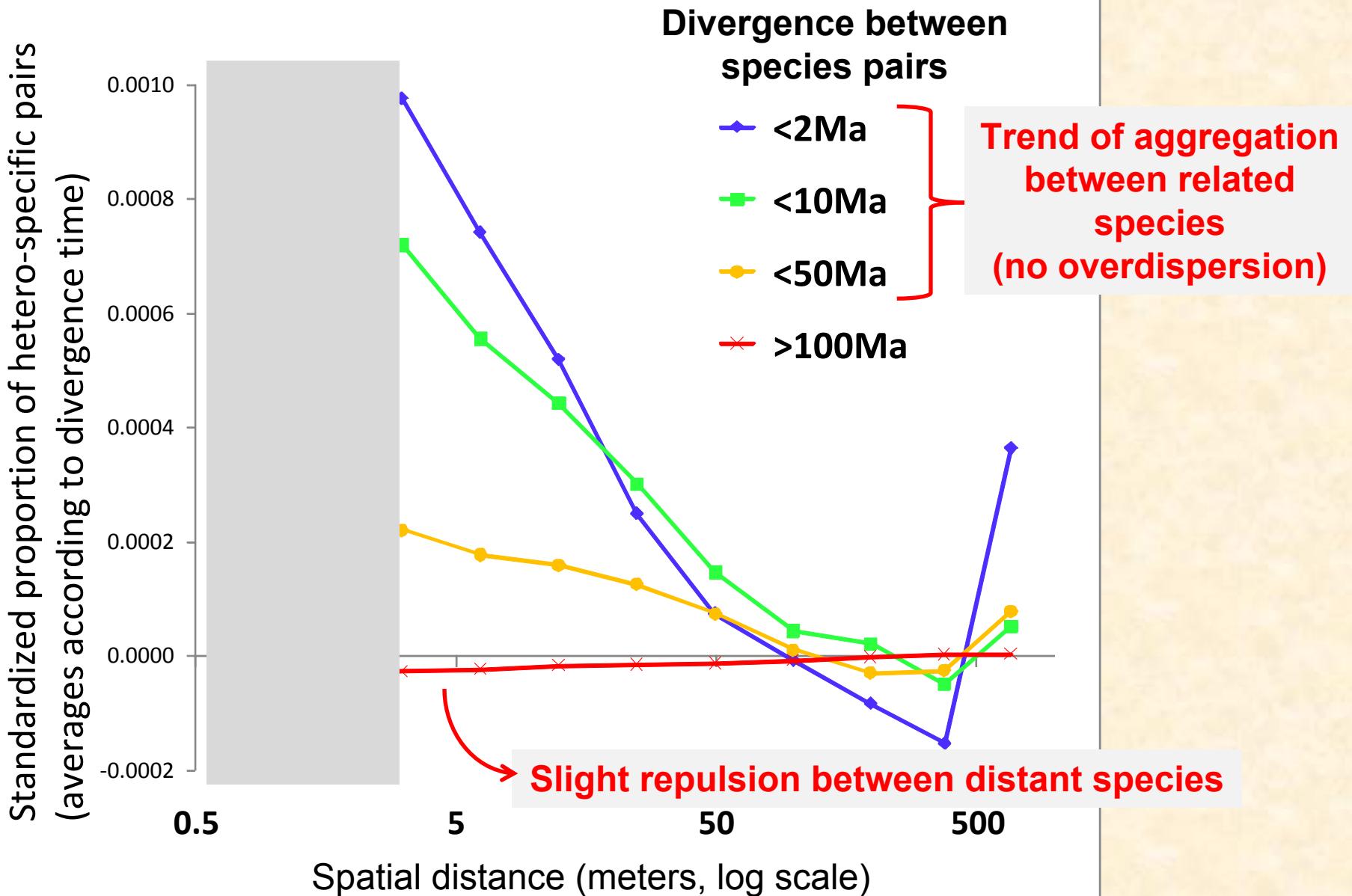
Beilschmiedia jacquesfelixii



Rinorea gabunensis



Korup - Cameroon



Korup - Cameroon

Repulsion between related species at <1m

Divergence between
species pairs

<2Ma

<10Ma

<50Ma

>100Ma

Trend of aggregation
between related
species
(no overdispersion)

Standardized proportion of hetero-specific pairs
(averages according to divergence time)

0.5

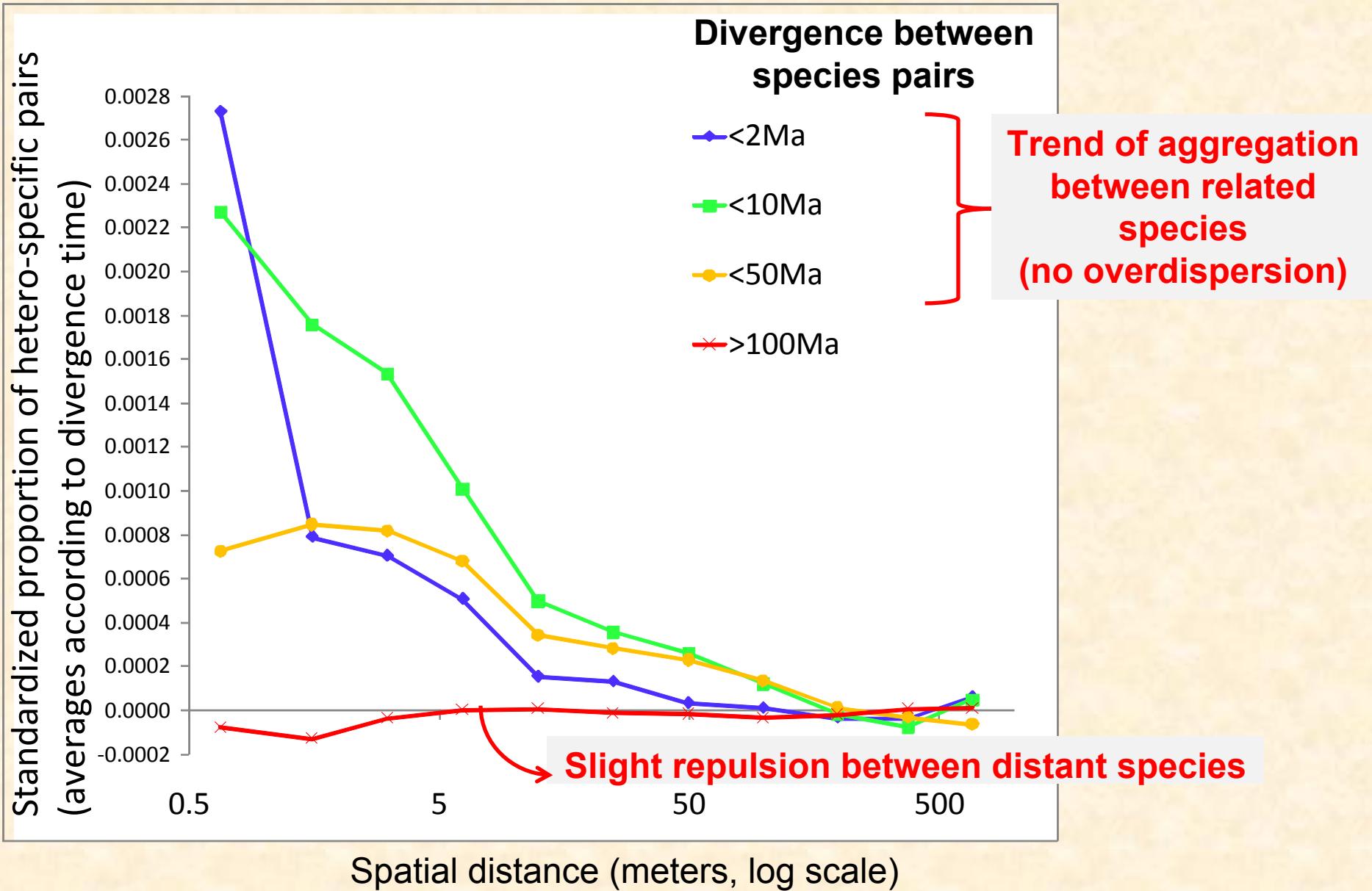
5

50

500

Spatial distance (meters, log scale)

Slight repulsion between distant species



Conclusion 5

In rainforest tree communities, **at a local scale**

- phylogenetic clustering due to topographic habitats
- no phylogenetic overdispersion due to competitive exclusion between related species, except may be at very short distance (<1m)

Perspective for modelling

- many metrics/methods used to characterize the phylogenetic or functional structures of communities
 - their interpretation in terms of biological processes essentially based on “verbal” arguments (lack of mathematical formality)
 - neutral processes can generate non-random patterns (Hardy 2008, J Ecol)
- ↳ must evaluate robustness and power (type I and II error rates) of methods against simulated data sets (cf. Münkemüller et al. 2012 Ecography)

From diversity indices to community assembly processes: a test with simulated data

T. Münkemüller, F. de Bello, C. N. Meynard, D. Gravel, S. Lavergne, D. Mouillot, N. Mouquet and W. Thuiller

Ecography 35: 468–480, 2012

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 - Belgian Fund for Scientific Research (FRS-FNRS)
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 - ANR

Thank you for your attention