

The phylogenetic structure of tree communities: insights from small inventory plots of tropical forests on different continents

O.J. HARDY¹, J. EYRAUD², S. KOUOB¹, I. PARMENTIER¹, B.R. RAMESH³, B. SENTERRE¹

¹Université Libre de Bruxelles, Belgium

²Université de La Réunion, Réunion – France

³French Institute of Pondichery, India

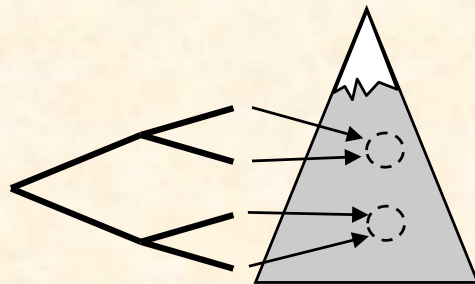
Impact of ecological gradients on **< species turnover
phylogenetic structure**
among communities of angiosperms

Community phylogenetic structure

Example under environmental filtering (adaptation to altitude)

Phylogenetic clustering

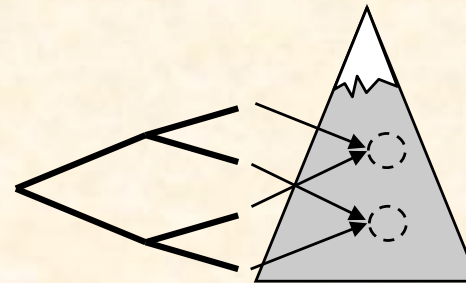
species within habitat **more** related than among habitats



habitat conservatism

Phylogenetic overdispersion

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



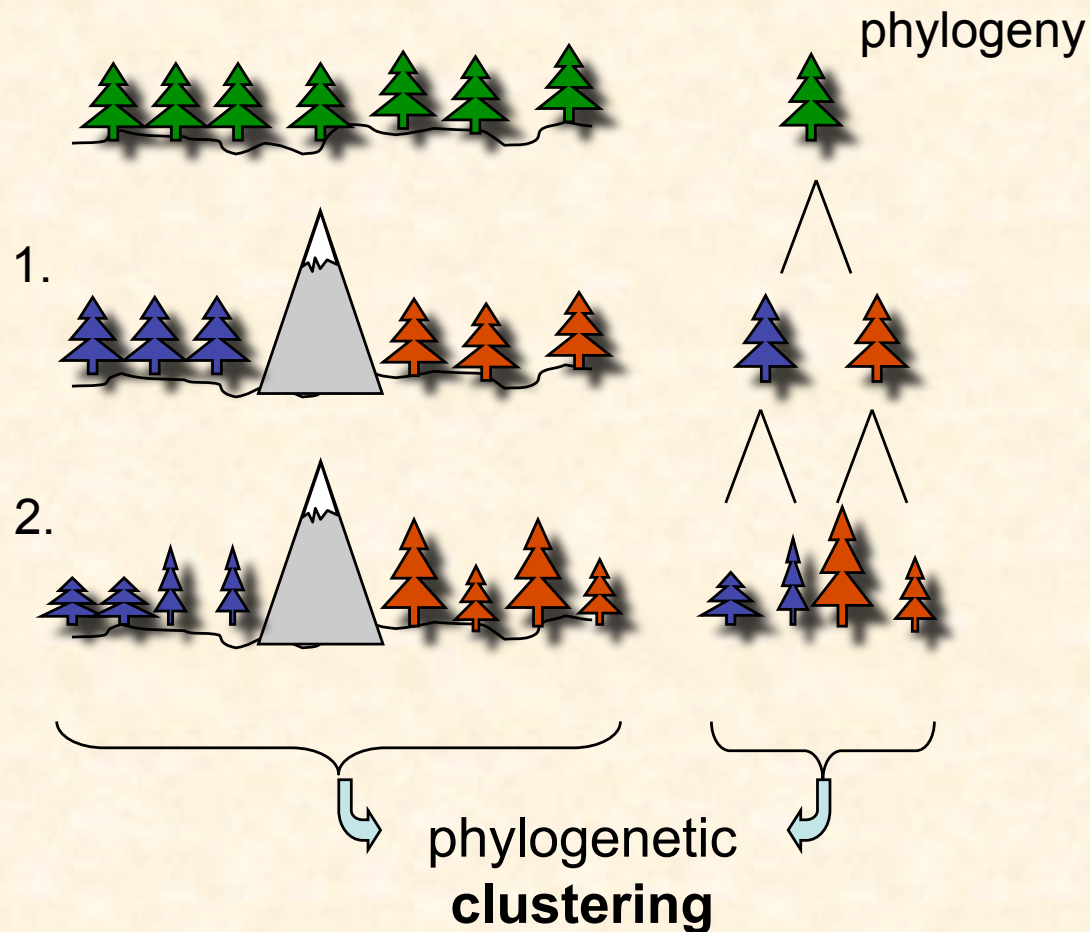
habitat convergence

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

Community phylogenetic structure can also be *caused by biogeographic barrier*

e.g. scenario:

1. barrier (allopatric speciation)
2. sympatric speciations



How to measure community phylogenetic structuring ?

1. From a species phylogeny → phyletic distances between species



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

sampled: / within sites

$$\Delta_w = \overline{\delta}_{(2_species_from_same_site)}$$

/ among sites

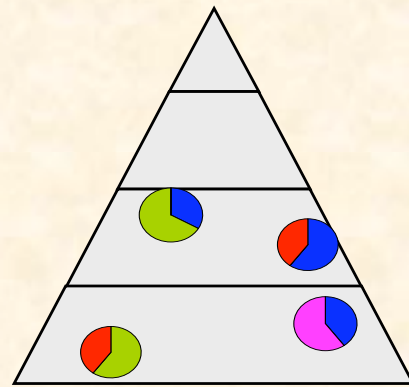
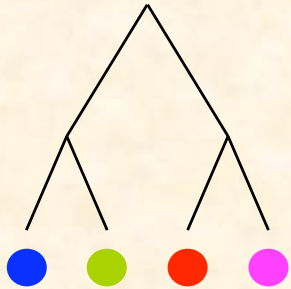
$$\Delta_a = \overline{\delta}_{(2_species_from_different_sites)}$$

$$\rightarrow \Pi_{ST} = \frac{\Delta_a - \Delta_w}{\Delta_a}$$

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

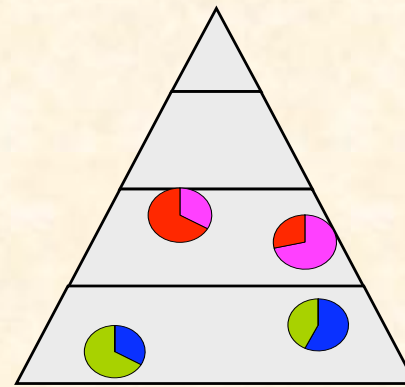
NB: Species abundances can also be taken into account
(cf. Hardy & Senterre 2007, J. Ecol. **95**: 493–506)

How to test community phylogenetic structuring ?



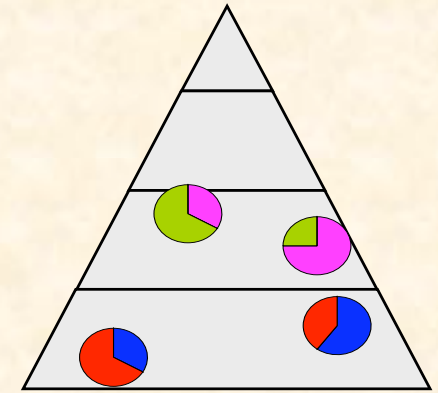
no phylogenetic
structure

$$\Pi_{ST} = 0$$



Phylogenetic
clustering

$$\Pi_{ST} > 0$$

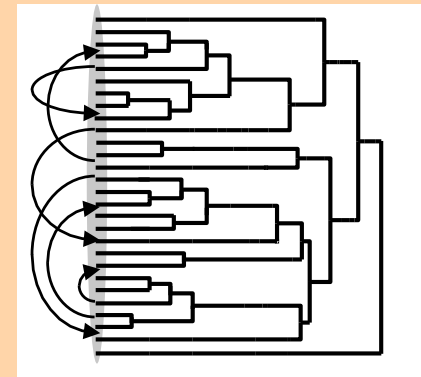


Phylogenetic
overdispersion

$$\Pi_{ST} < 0$$

Testing $P_{ST} \neq 0$

- **randomize phylogeny**
- assess distribution of Π_{ST} for 1000 permutations
- P-value



Patterns of species turnover (Jaccard index) and phylogenetic structure (Π_{ST})
for 1ha evergreen forest plots (DBH>10cm) at a regional scale
on different continents



Panama canal

50 plots

Rainfall:
1500-3300mm

Altitude:
50-400m

Monte Alen NP
(Equatorial Guinea)
28 plots

Rainfall:
 $\cong 2000\text{mm}$

Altitude:
20-1200m

Dja NP
(Cameroon)
70 plots

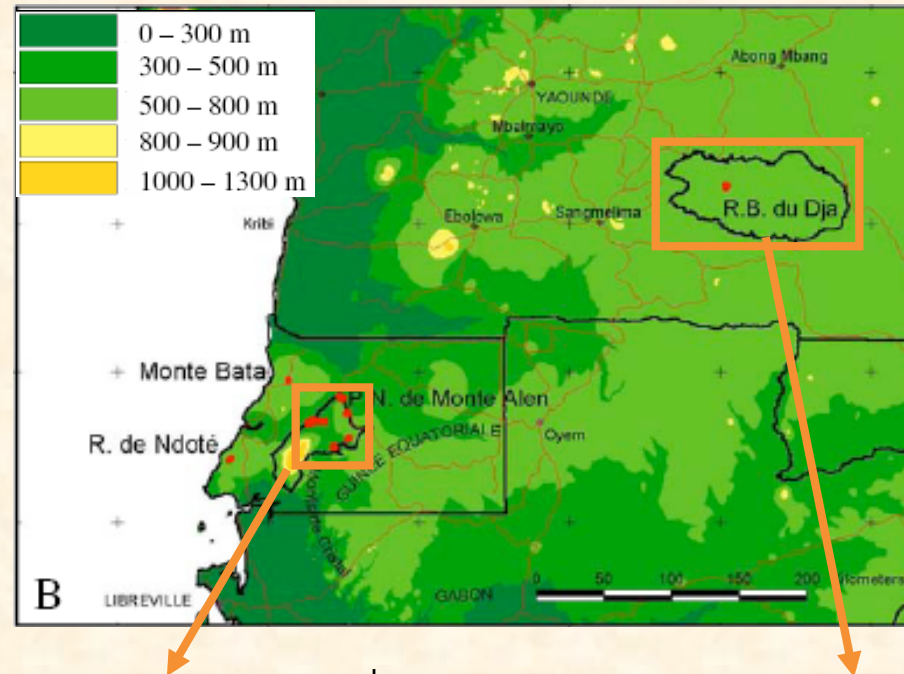
Rainfall:
 $\cong 1500\text{mm}$

Altitude:
400-600m

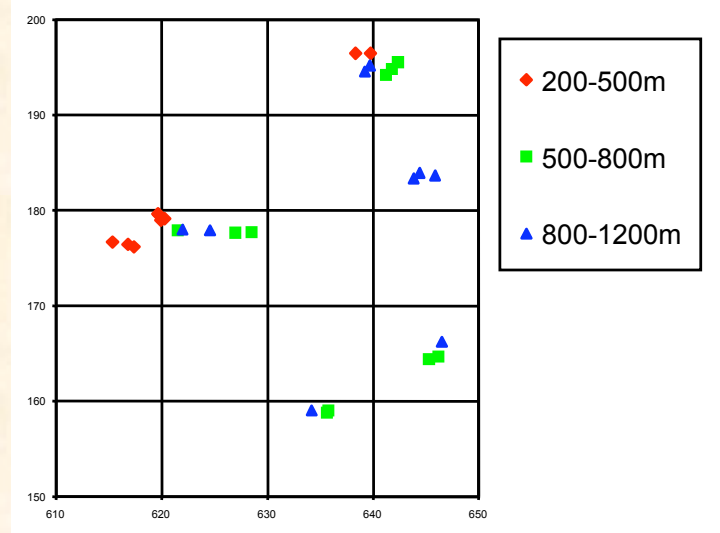
Western Ghats
(India)
50 plots

Rainfall:
1400-6000mm
Altitude:
500-800m

Plots in central Africa:

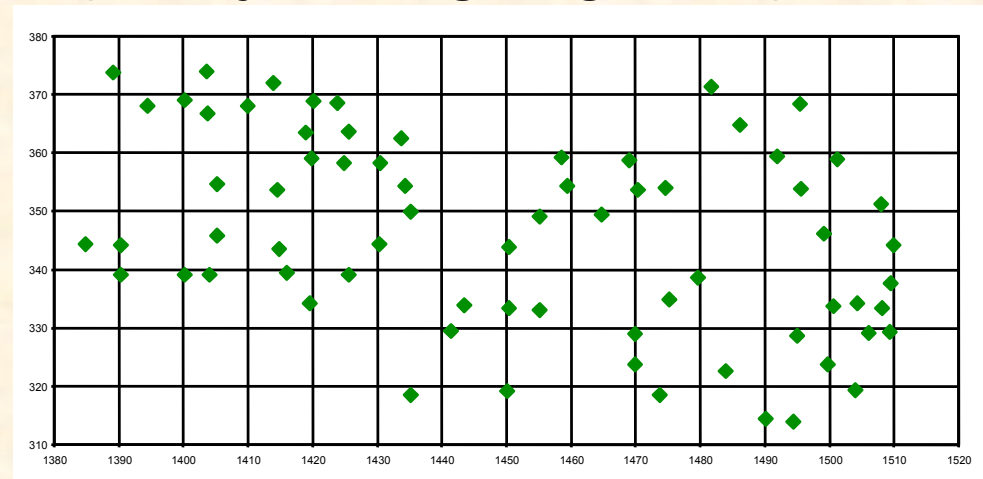


Monte Alen NP: sampling of mature forest plots along **altitudinal gradients**



data from **B. SENTERRE**

Dja NP: systematic sampling of mature '*tierra firme*' 1ha forest plots (no major ecological gradient)

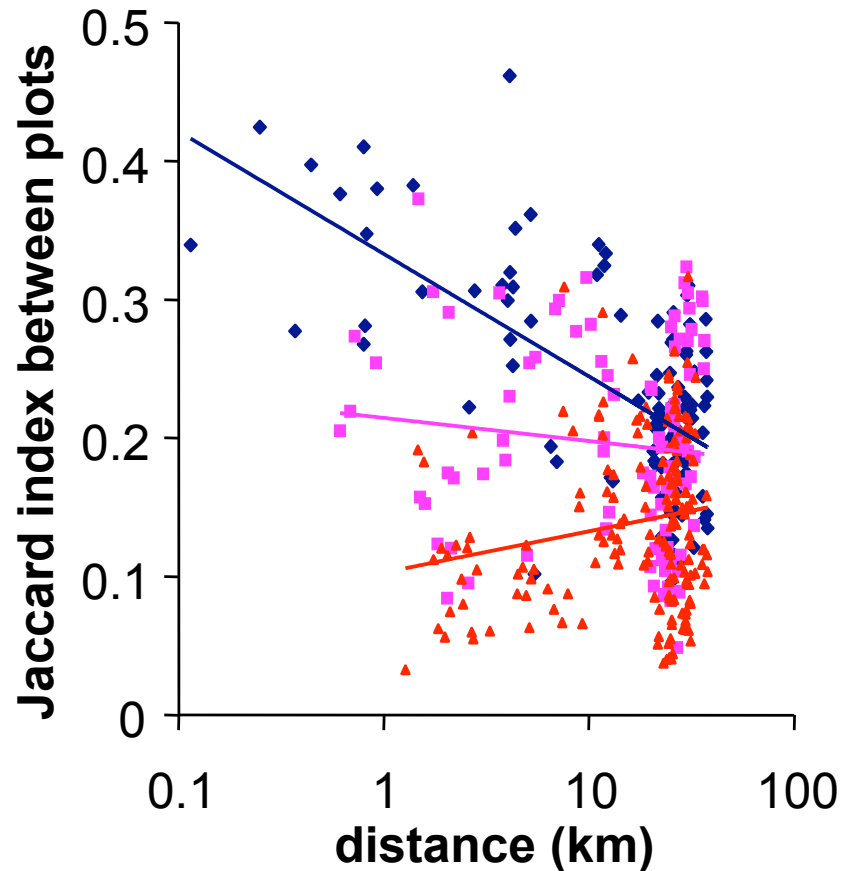


data from **S. KOUOB**

Monte Alen NP

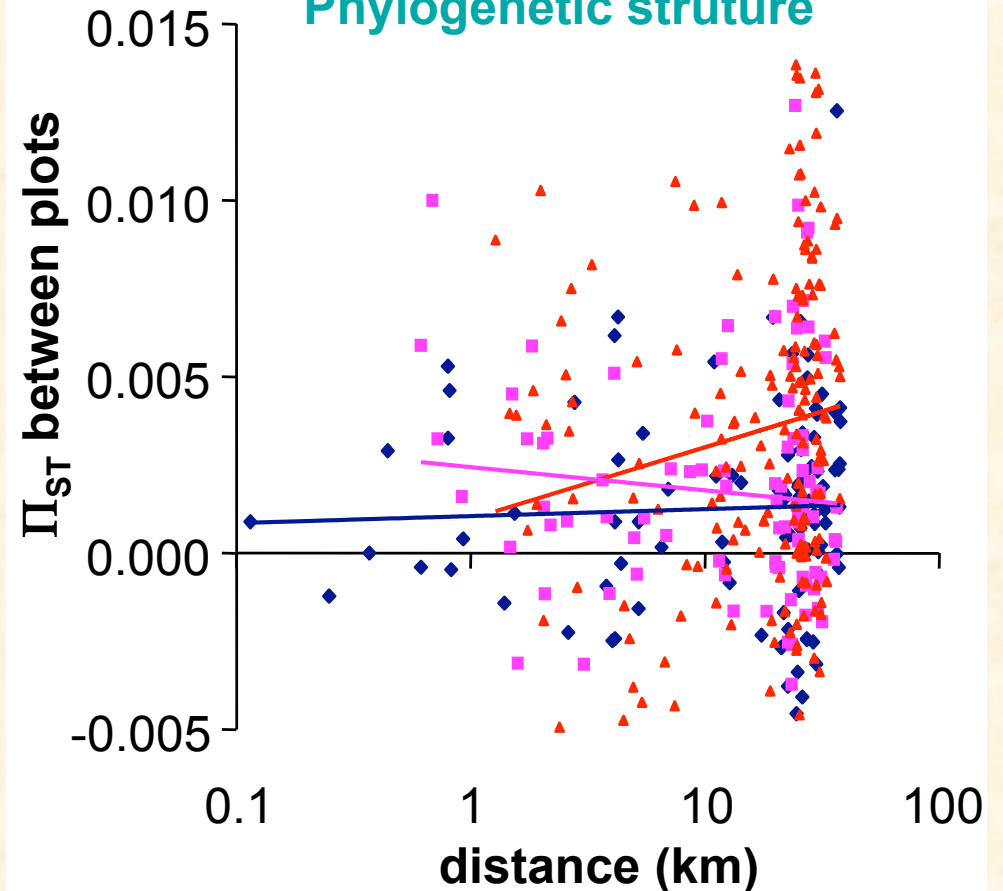
△ altitude btw. plots : ◆ <150m ■ 150-300m ▲ >300m

Species turnover



Impact of
spatial distance + elevation gradient

Phylogenetic structure

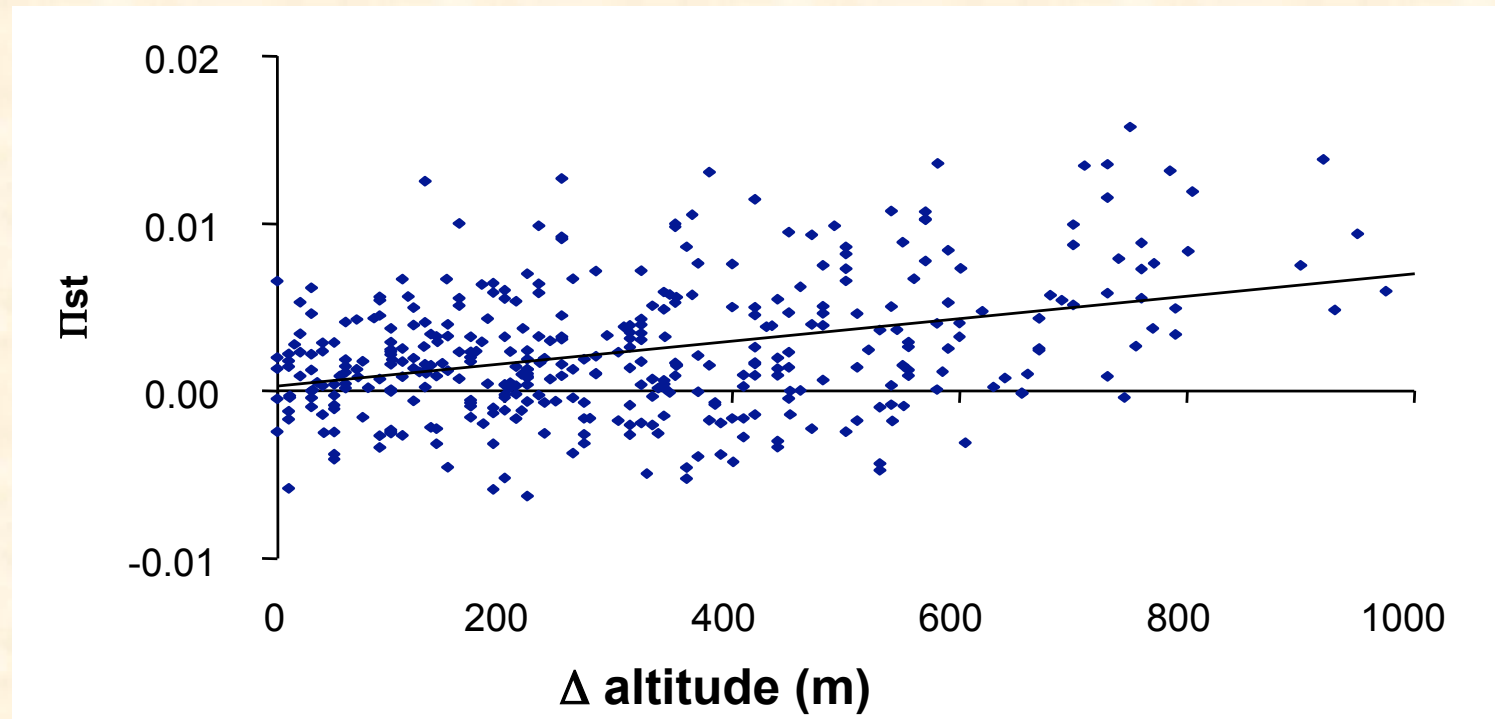


Impact of
elevation gradient only

Monte Alen NP

Pearson's correlation coefficient:

| | J | Π_{ST} |
|--------------------|-------|------------|
| $\ln(\text{dist})$ | -0.24 | 0.09 |
| Δ altitude | -0.52 | 0.37 |

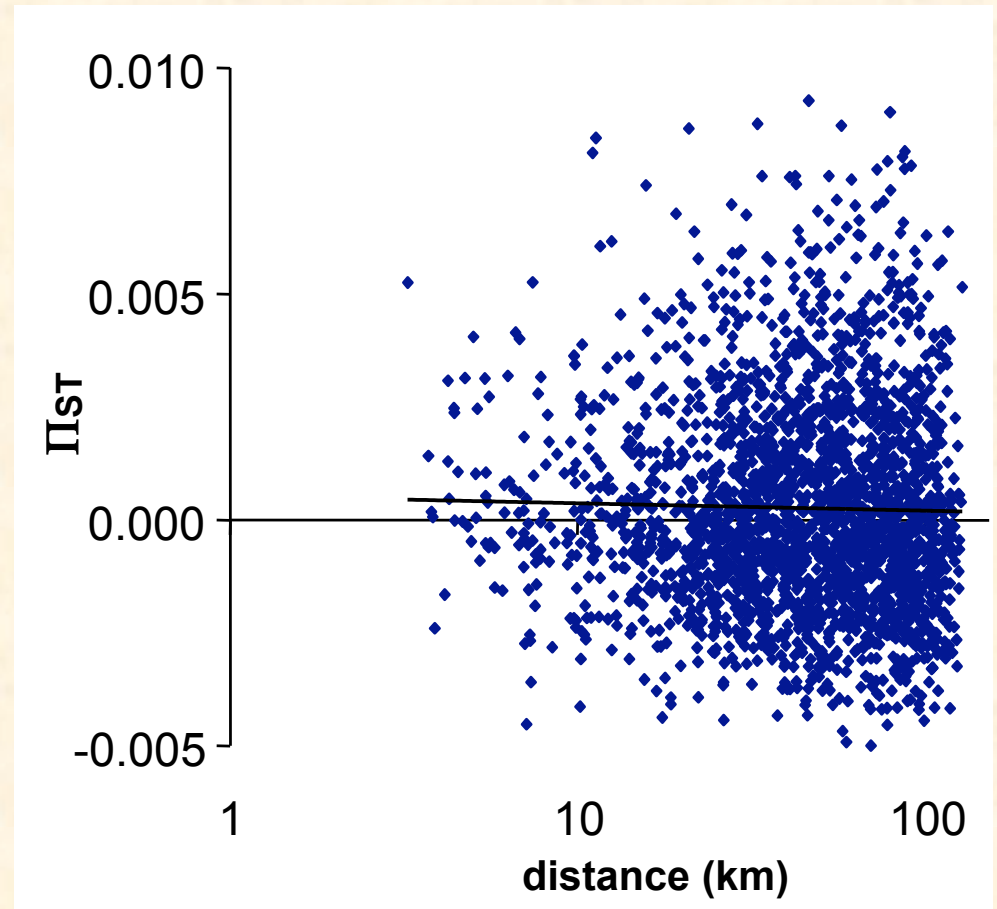
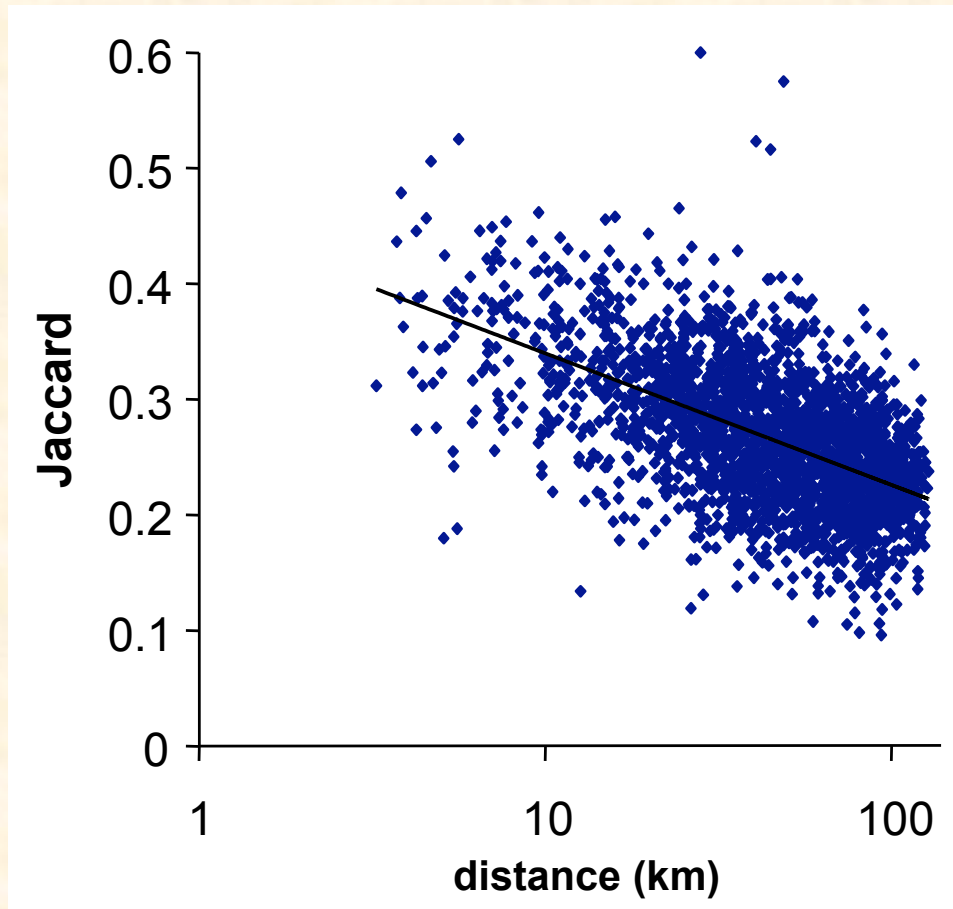


Species turnover (J) depends on spatial distance + ecological gradient

Phylogenetic structure (Π_{ST}) depends on ecological gradient

⇒ distinguish stochastic and deterministic processes
(dispersal limitation versus ecological filtering)

Dja NP

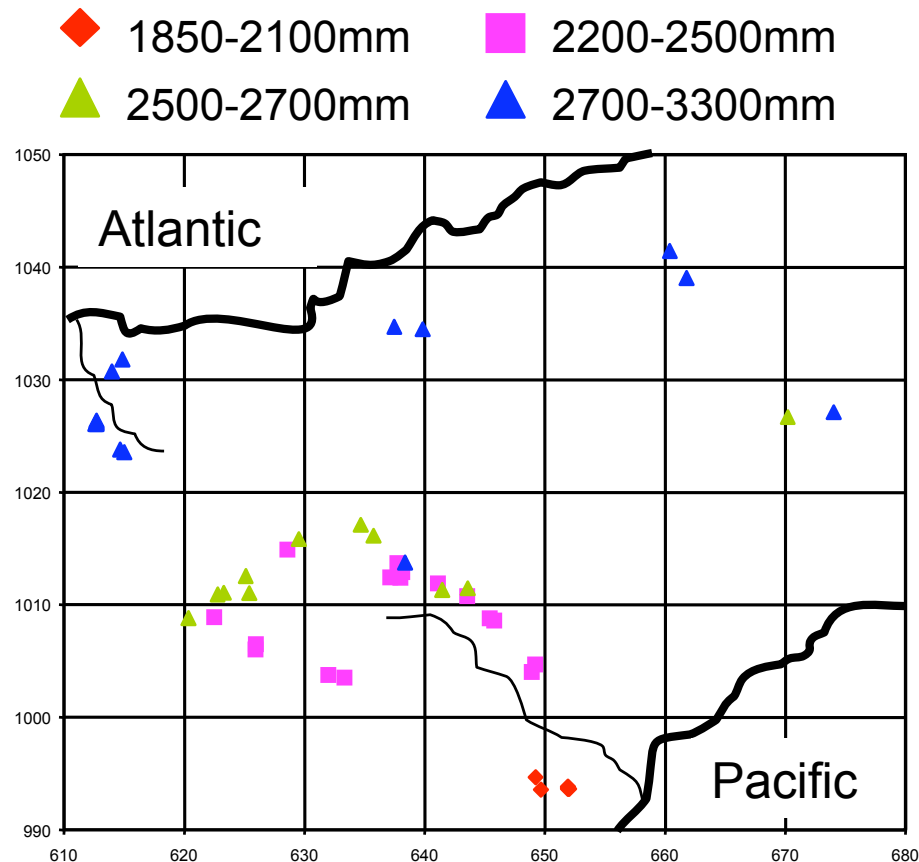


No major ecological gradient

Species turnover (J) depends on spatial distance

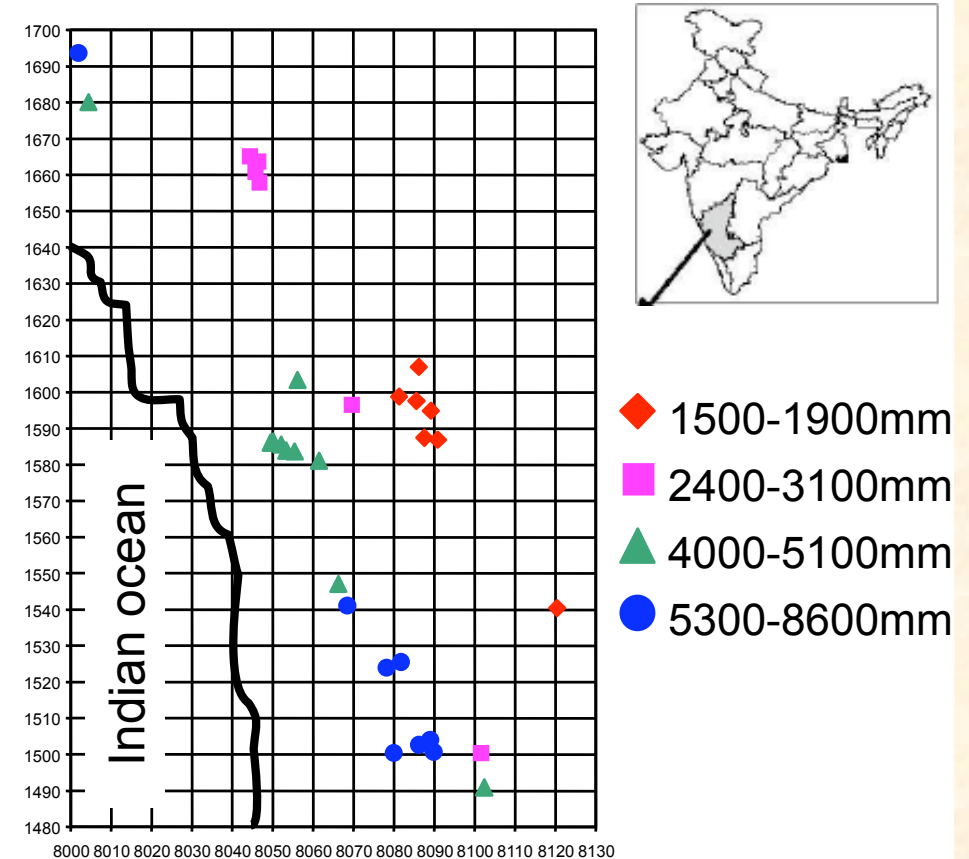
No phylogenetic structure ($\Pi_{ST} \approx 0$)

Panama canal area: rainfall gradient (1850 – 3300 mm)



data from **CTFS**

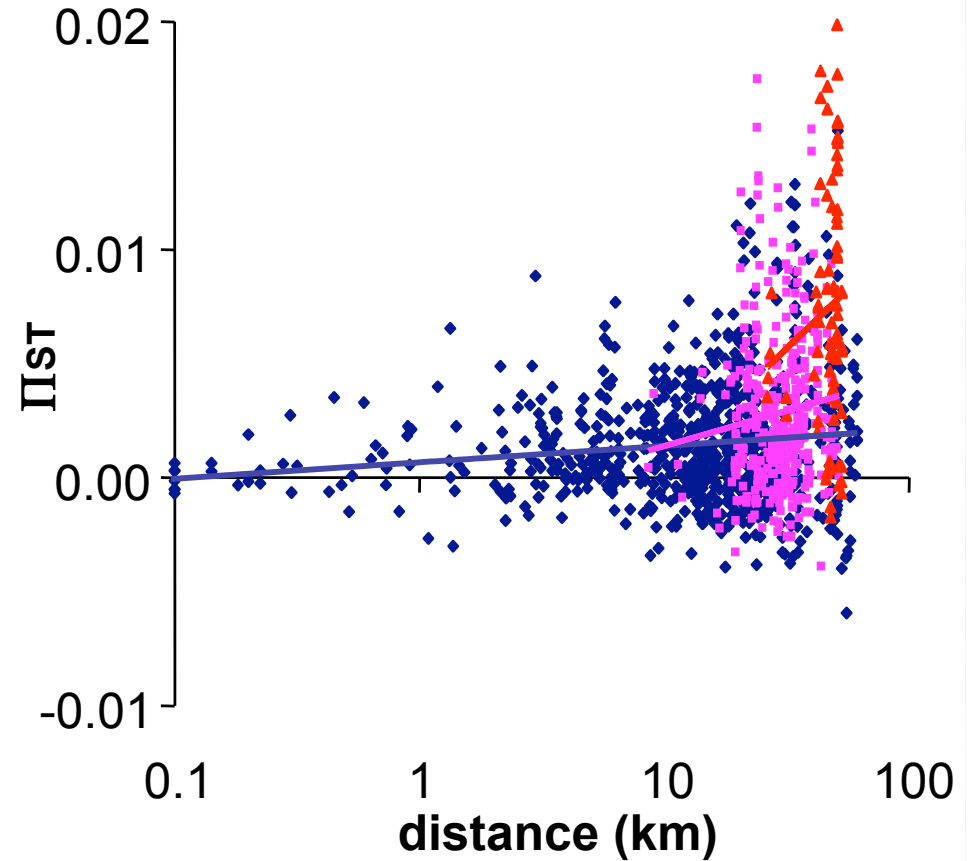
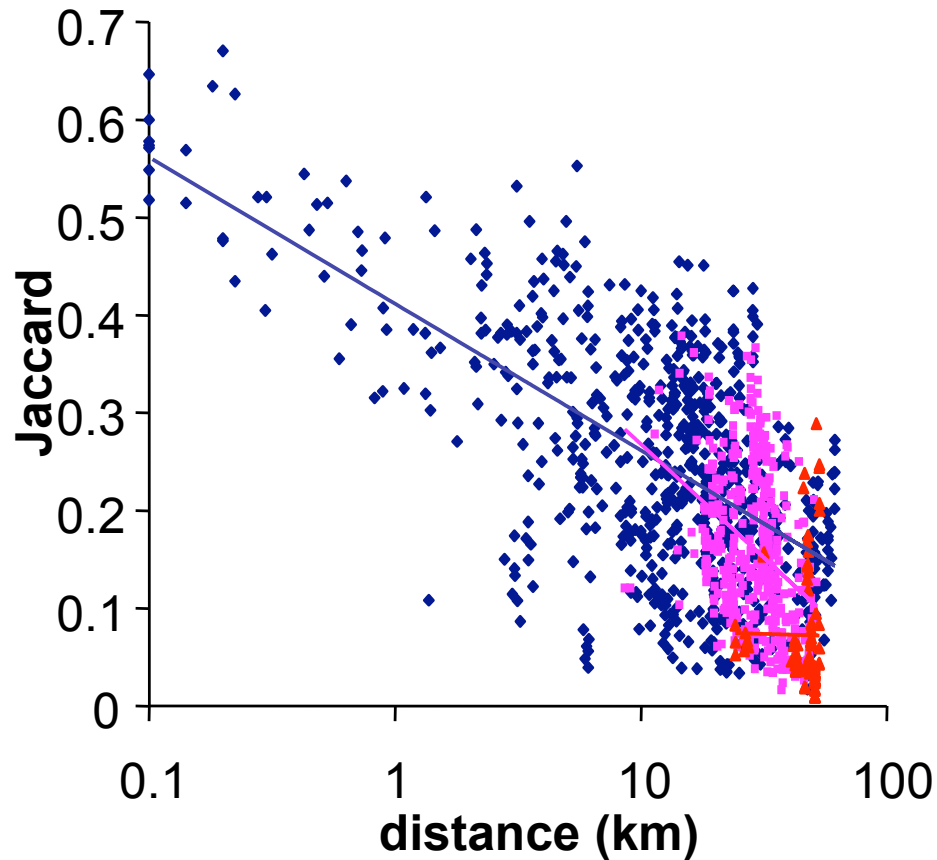
Western Ghats: rainfall gradient (1500 – 8600 mm)



data from **B.R. RAMESH**

Panama canal area

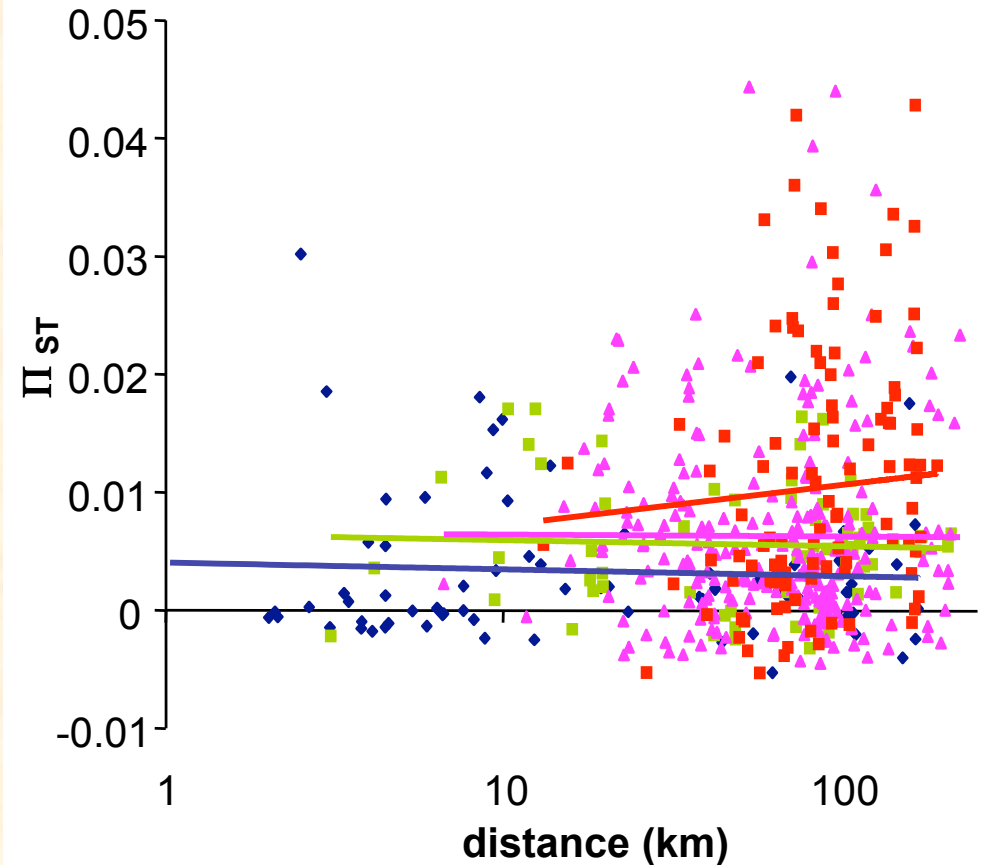
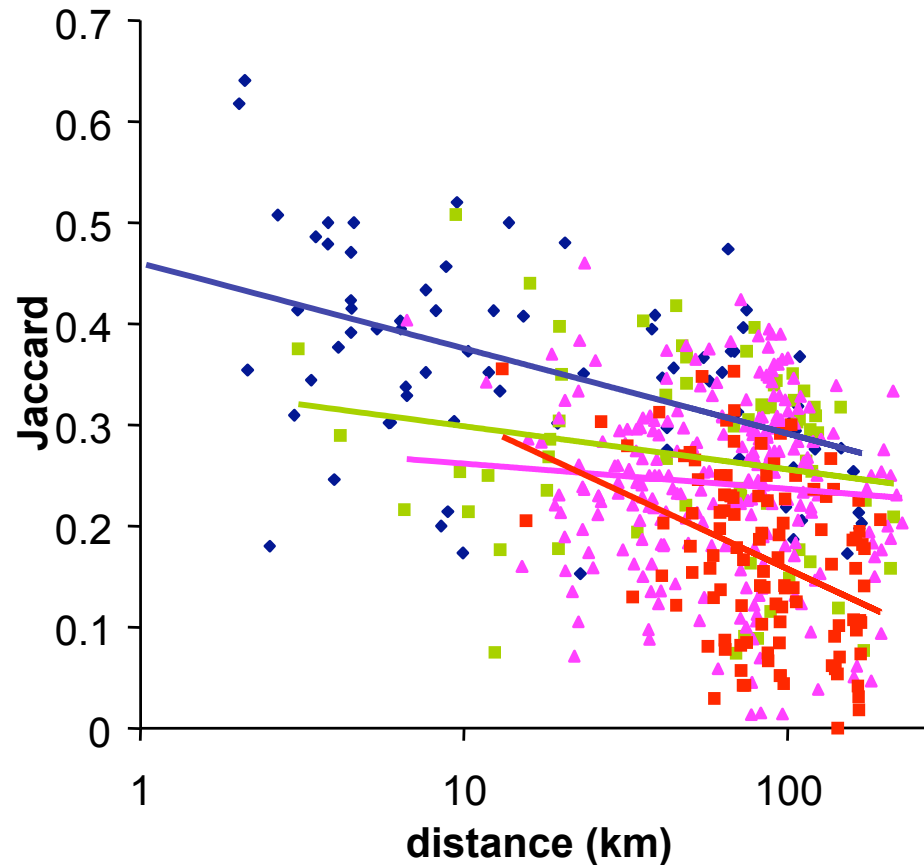
Δ rainfall btw. plots : ◆ <500mm ■ 500-1000mm ▲ 1000-2100mm



| <u>Pearson's correlation coefficient:</u> | J | Π _{st} |
|---|-------|-----------------|
| ln(dist) | -0.67 | 0.23 |
| Δ rainfall | -0.54 | 0.43 |

Western Ghats

Δ rainfall btw. plots : ◆ <500mm ■ 500-1000mm ▲ 1000-3500mm ■ 3500-6000mm



Pearson's correlation coefficient:

ln(dist)

-0.45

Π_{st}

0.14

Δ rainfall

-0.53

0.31

Ecological gradients versus biogeography

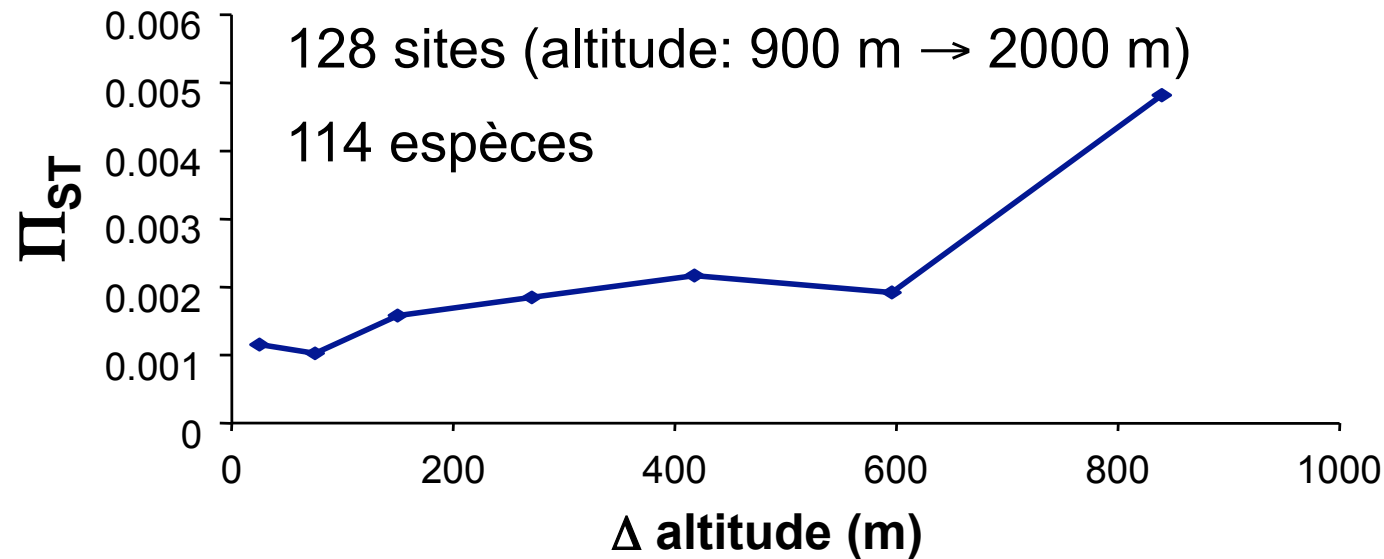
| mean Π_{ST} | | <u>regional scale</u> | | <u>intercontinental scale</u> |
|-------------------------------------|---------------------------|-----------------------|-----------------|-------------------------------|
| | | within Panama | within W. Ghats | between Panama & W. Ghats |
| Δ rainfall | Weak (<500mm) | 0.001 | 0.003 | 0.010 |
| | Strong (>1000 or >3500mm) | 0.008 | 0.011 | 0.017 |

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

Impacts on Π_{ST} of { biogeography (inter-continental)
steep ecological gradient } are comparable

Forest communities from Reunion island

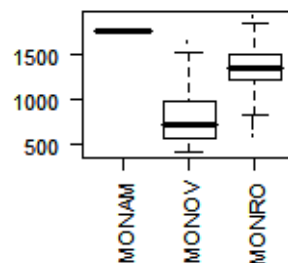
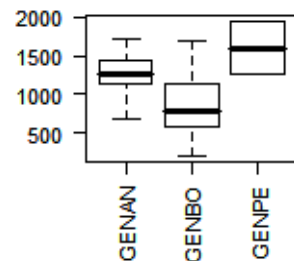
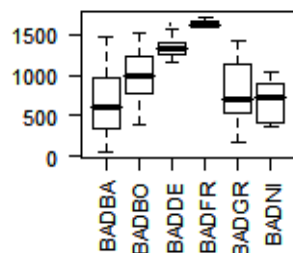
data analyzed by J. EYRAUD



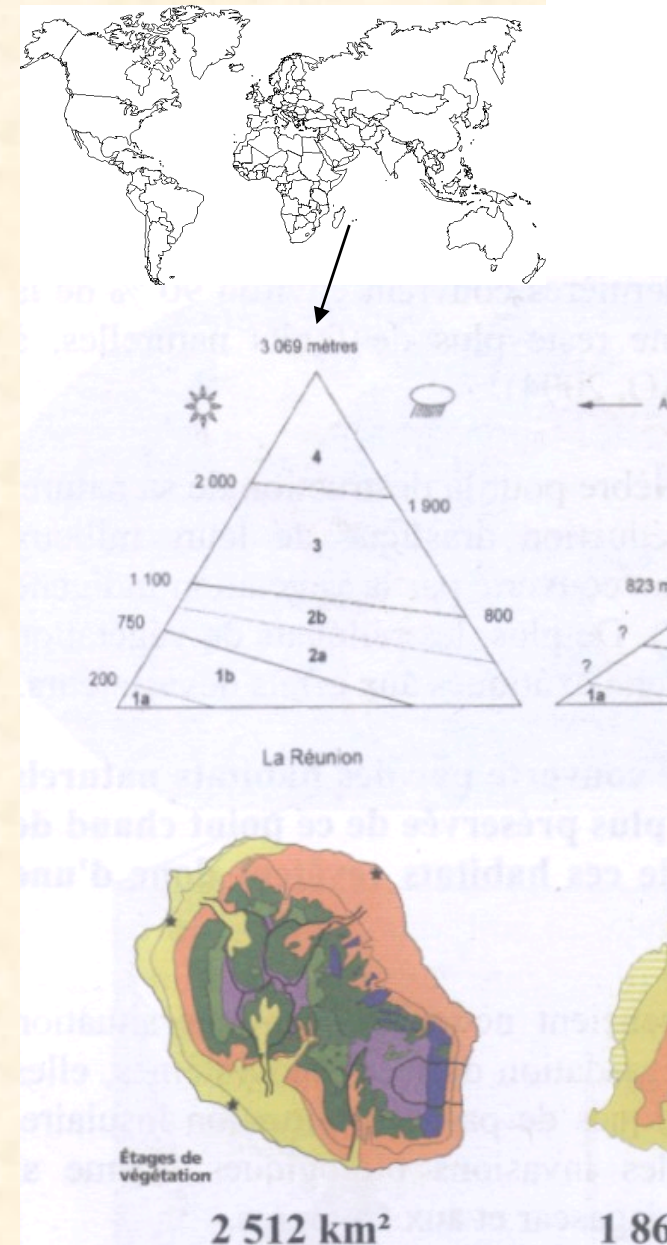
⇒ phylogenetic clustering ↑ with Δ altitude

However, 9 genera have diversified on the island
→ phylogenetic overdispersion is expected

Altitude ranges of endemic species in 3 genera



PARADOX?



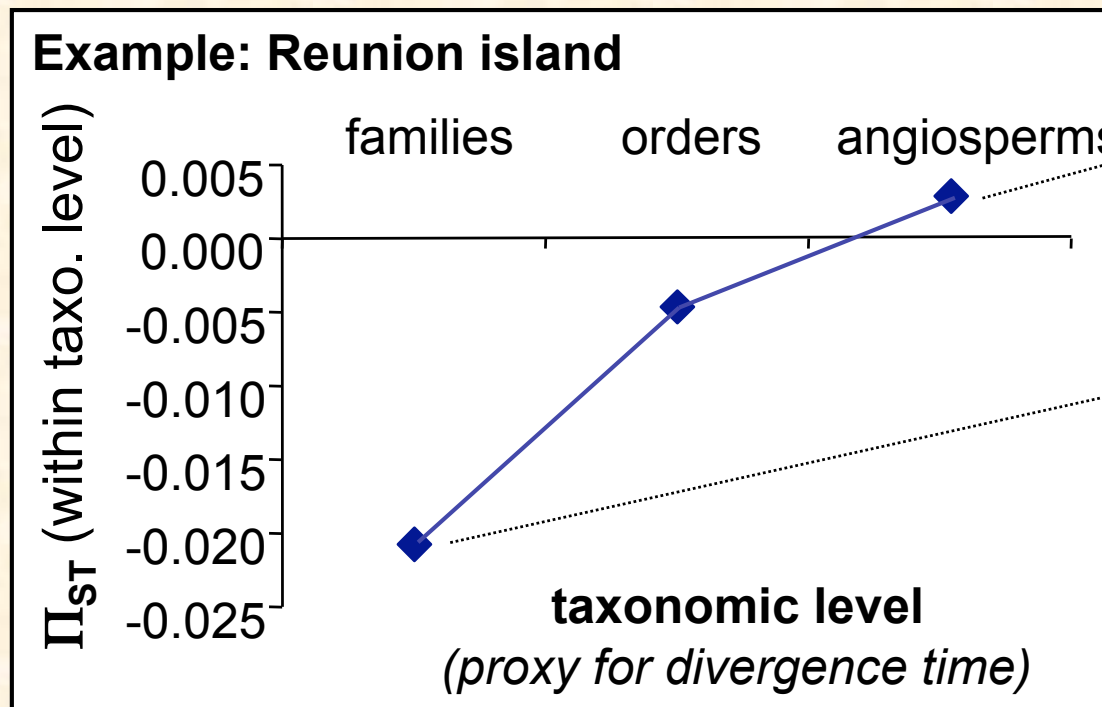
Phylogenetic structure at different time depths

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

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

$$\Pi_{ST}^T = \frac{\Delta_a^{\delta < T} - \Delta_w^{\delta < T}}{\Delta_a^{\delta < T}}$$

→ characterize phylogenetic structure at different time depths



for all angiosperms

→ phylogenetic **clustering**

↪ overall habitat conservatism

within families

→ phylogenetic **overdispersion**

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

Conclusions

- At deep phylogenetic levels (e.g. within angiosperms)
 - ↳ phylogenetic clustering \Leftrightarrow ecological differentiation
 - ~~↳ dispersal limitation at regional scale~~

⇒ distinguish dispersal limitation *versus* ecological filtering

↳ impact biogeographic barriers \approx impact ecological gradients

- 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 $\Pi_{ST}^{\delta < T}$

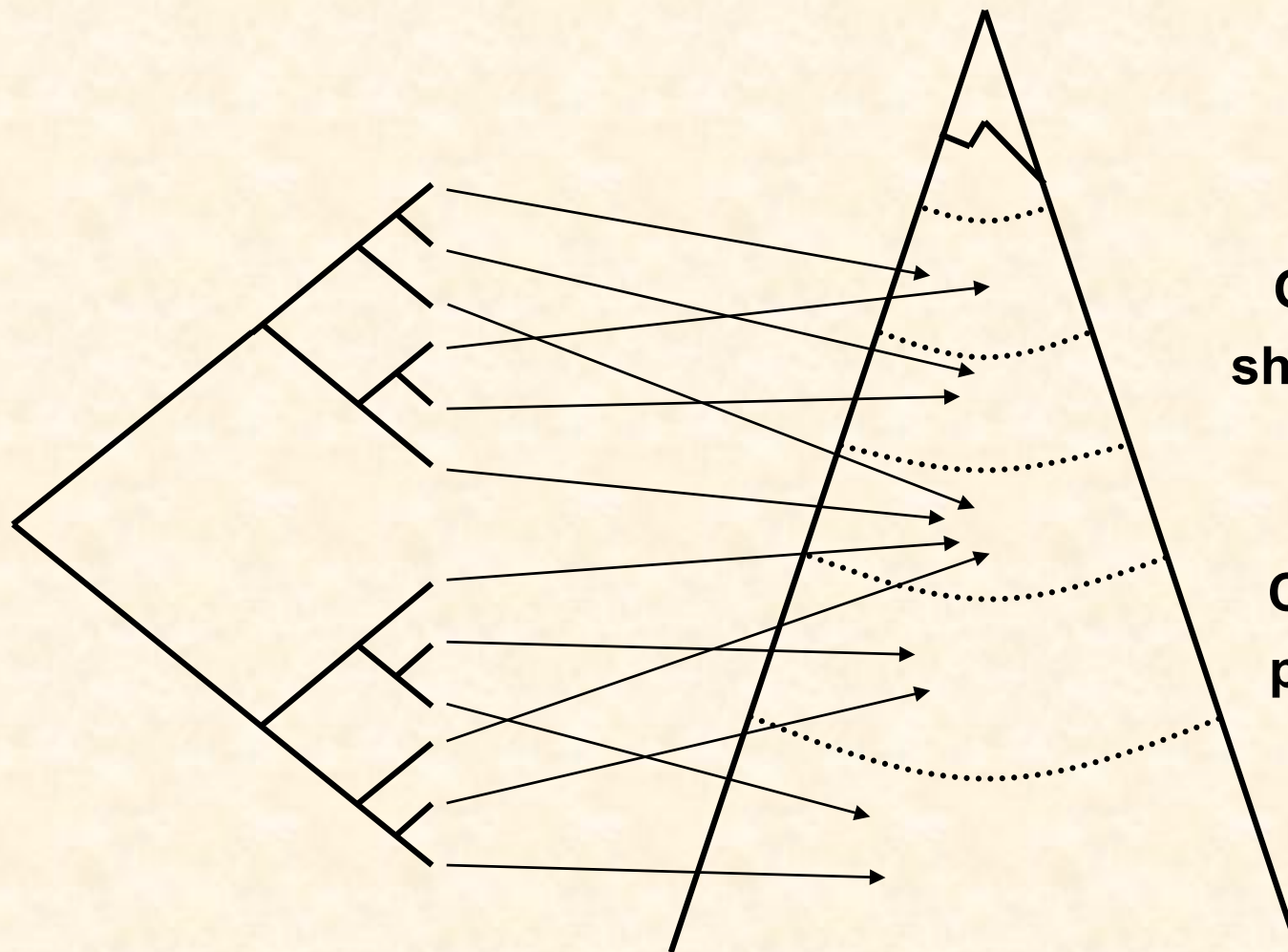
Perspectives

Compare Π_{ST} using inter-species

- phylogenetic** distances (δ = divergence time btw species)
- phenotypic** distances (δ = euclidean dist. btw species for traits)

⇒ traits should better explain ecological filtering (higher Π_{ST} signal)

Thanks for your attention



**Overdispersion at
shallow phylogenetic
level
+
Clustering at deep
phylogenetic level**