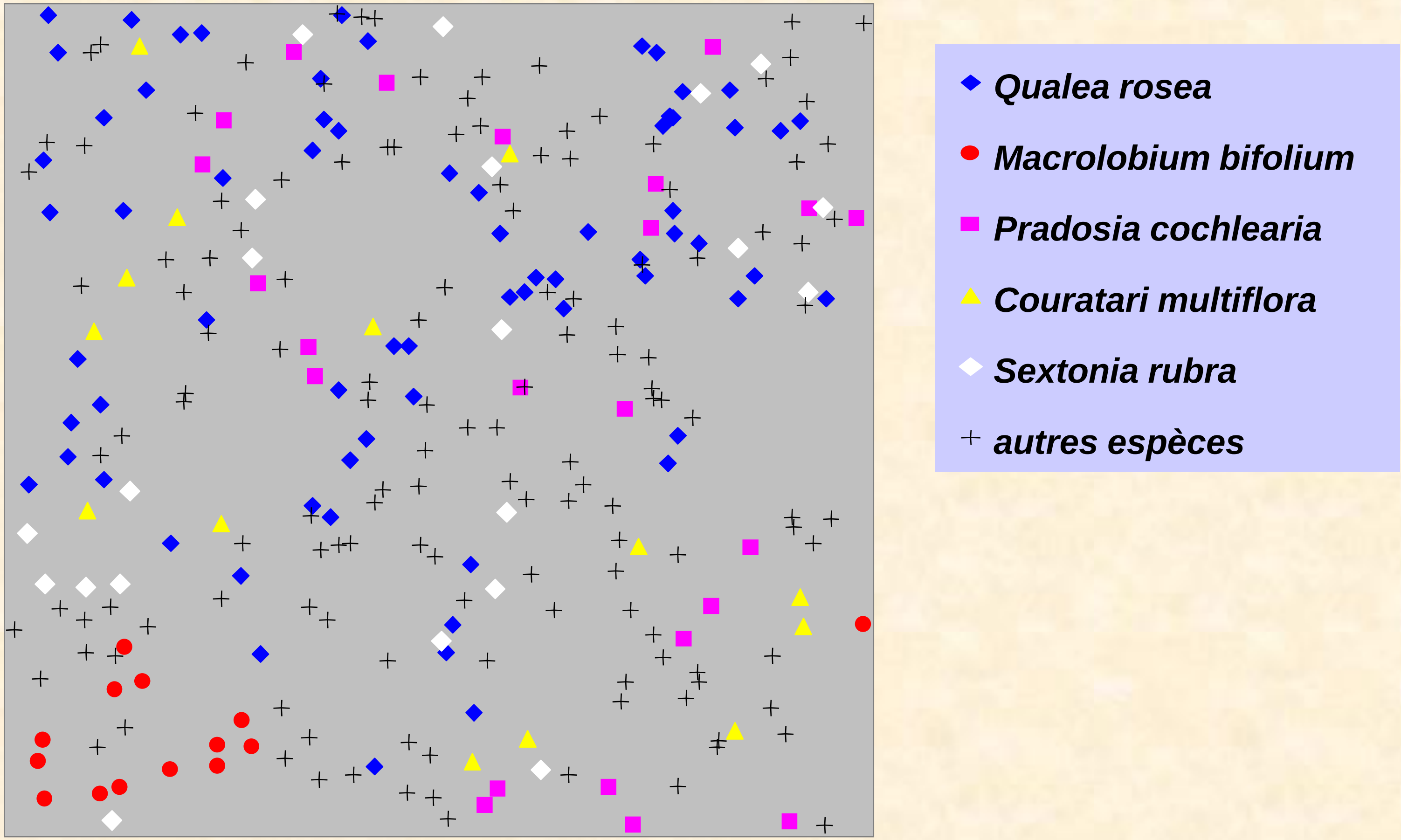
Distribution spatiale des individus et modèles neutres / de niches

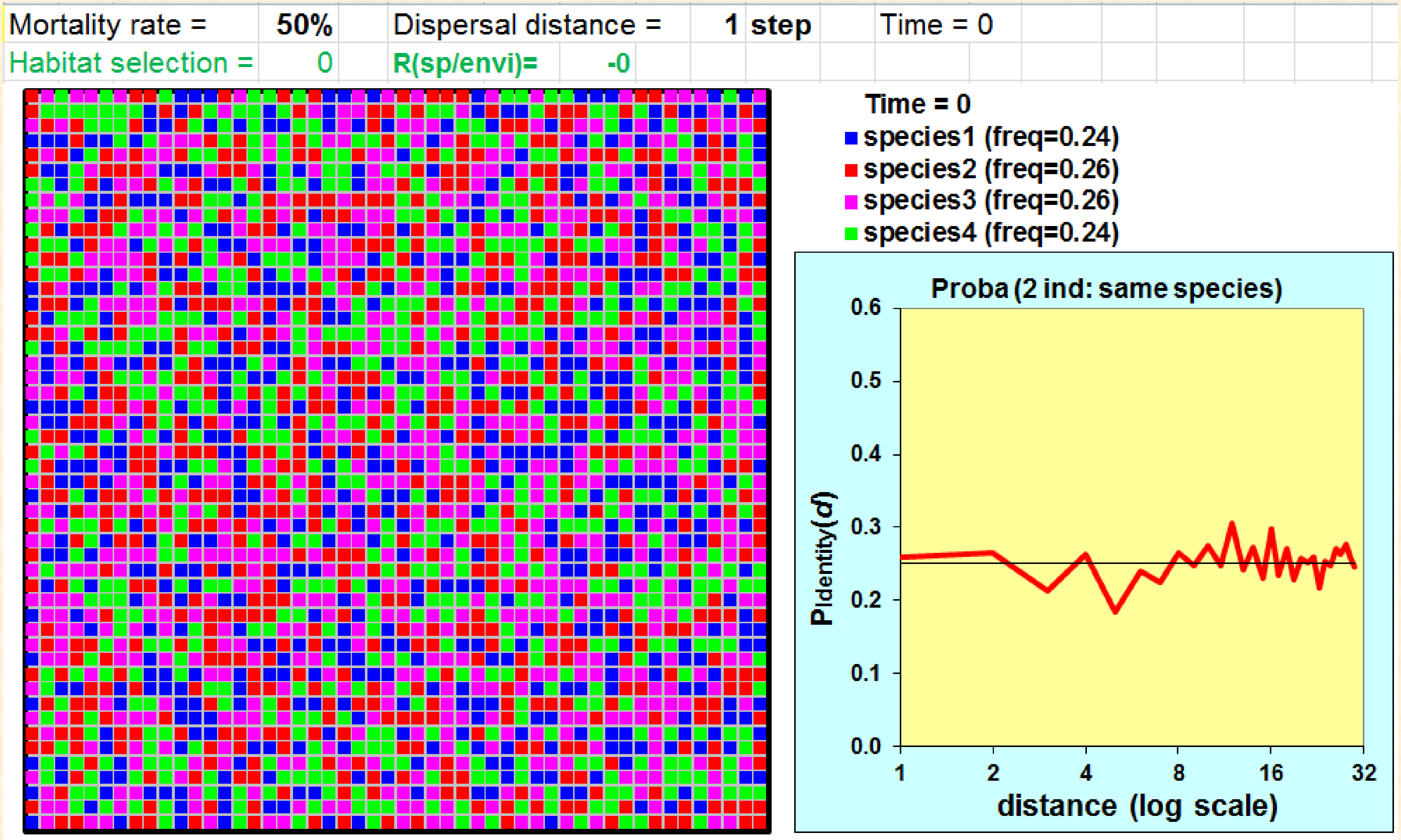
Distribution de 5 espèces d'arbres dans une parcelle de 25 ha (Guyane française)



Ces distributions spatiales reflètent-elles

- **l'effet de l'hétérogénéité des conditions du milieux ? -> niche**
- **une dispersion limitée des espèces ? -> neutre**

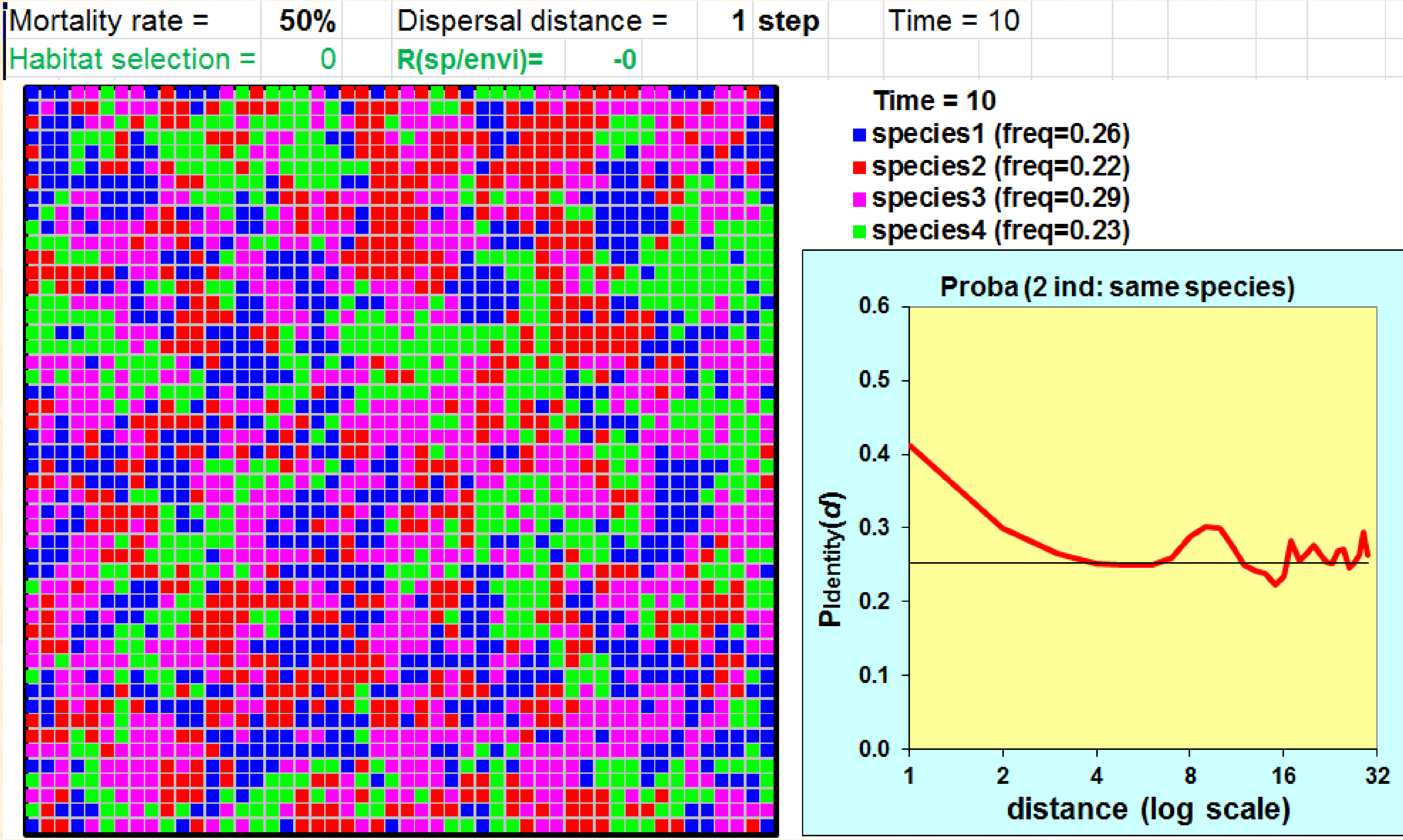
Simulateur (4 espèces sur une grille de 50x50) : état initial



Mortality rate =	**50%**	Dispersal distance =	**1**	**step**	Time = 0
Habitat selection =	0	**R(sp/envi)=**	**-0**		

Time = 0
- 🟦 species1 (freq=0.24)
- 🟥 species2 (freq=0.26)
- 🟪 species3 (freq=0.26)
- 🟩 species4 (freq=0.24)

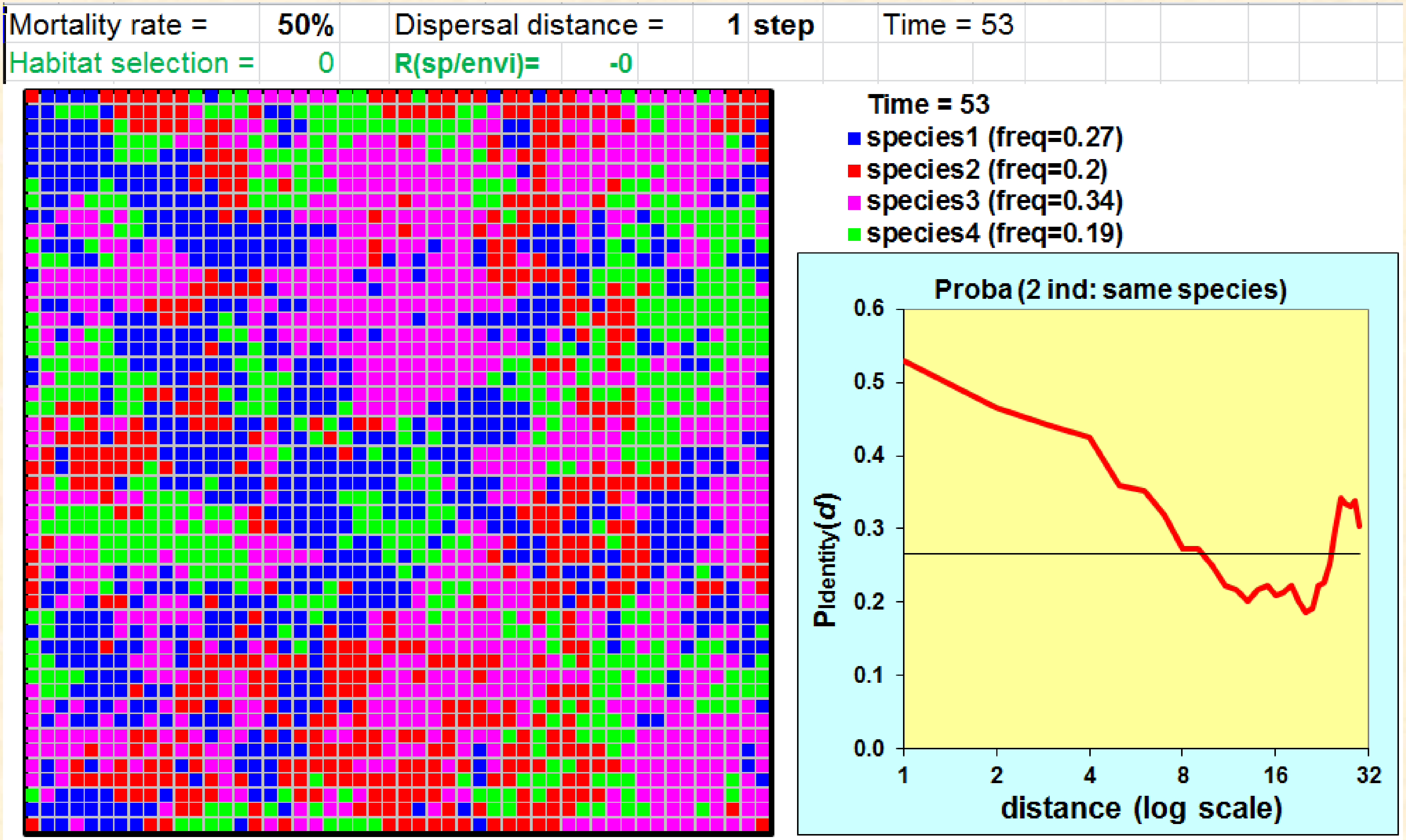
Neutre + dispersion très limitée (10 pas de temps)



Mortality rate = **50%**
Dispersal distance = **1 step**
Time = 10
Habitat selection = 0
R(sp/envi)= -0

Time = 10
- 🟦 **species1 (freq=0.26)**
- 🟥 **species2 (freq=0.22)**
- 🟪 **species3 (freq=0.29)**
- 🟩 **species4 (freq=0.23)**

Neutre + dispersion très limitée (50 pas de temps)



Mortality rate = **50%** Dispersal distance = **1 step** Time = 53

Habitat selection = 0 **R(sp/envi)= -0**

Time = 53

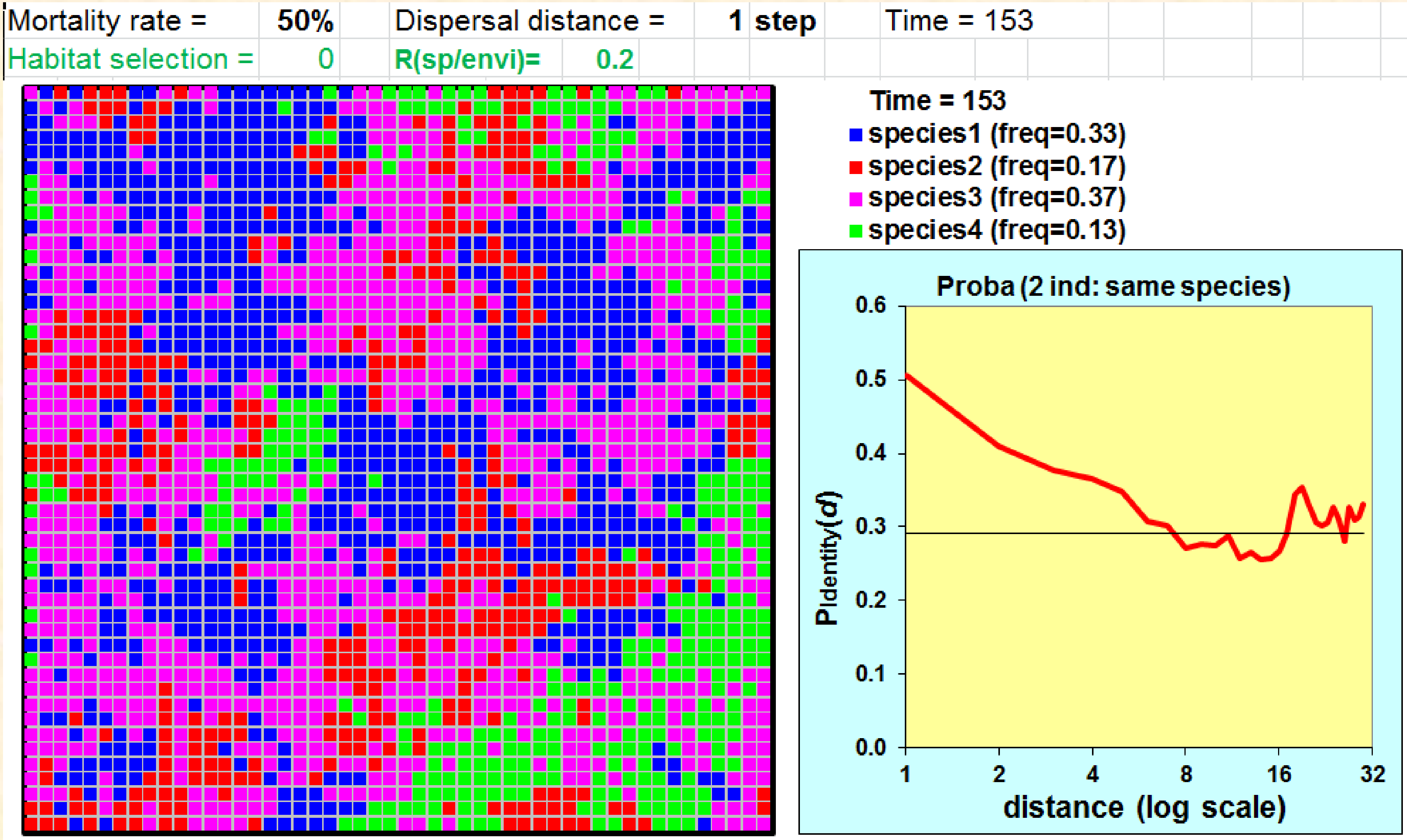
🟦 species1 (freq=0.27)

🟥 species2 (freq=0.2)

🟪 species3 (freq=0.34)

🟩 species4 (freq=0.19)

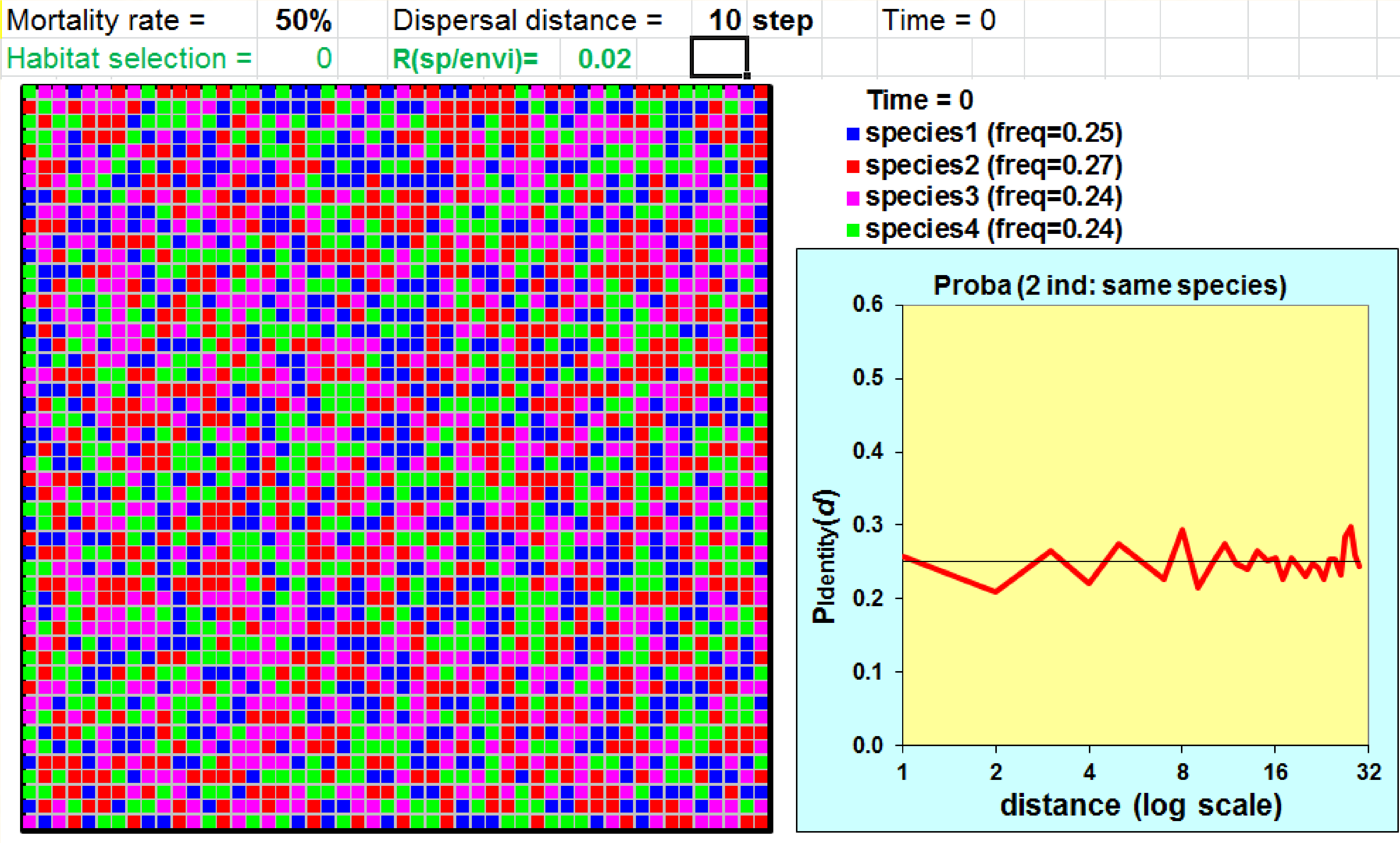
Neutre + dispersion très limitée (150 pas de temps)



Mortality rate =	50%	Dispersal distance =	1 step	Time = 153
Habitat selection =	0	R(sp/envi)=	0.2	

Time = 153
- 🟦 species1 (freq=0.33)
- 🟥 species2 (freq=0.17)
- 🟪 species3 (freq=0.37)
- 🟩 species4 (freq=0.13)

Neutre + dispersion étendue (10 pas de temps)



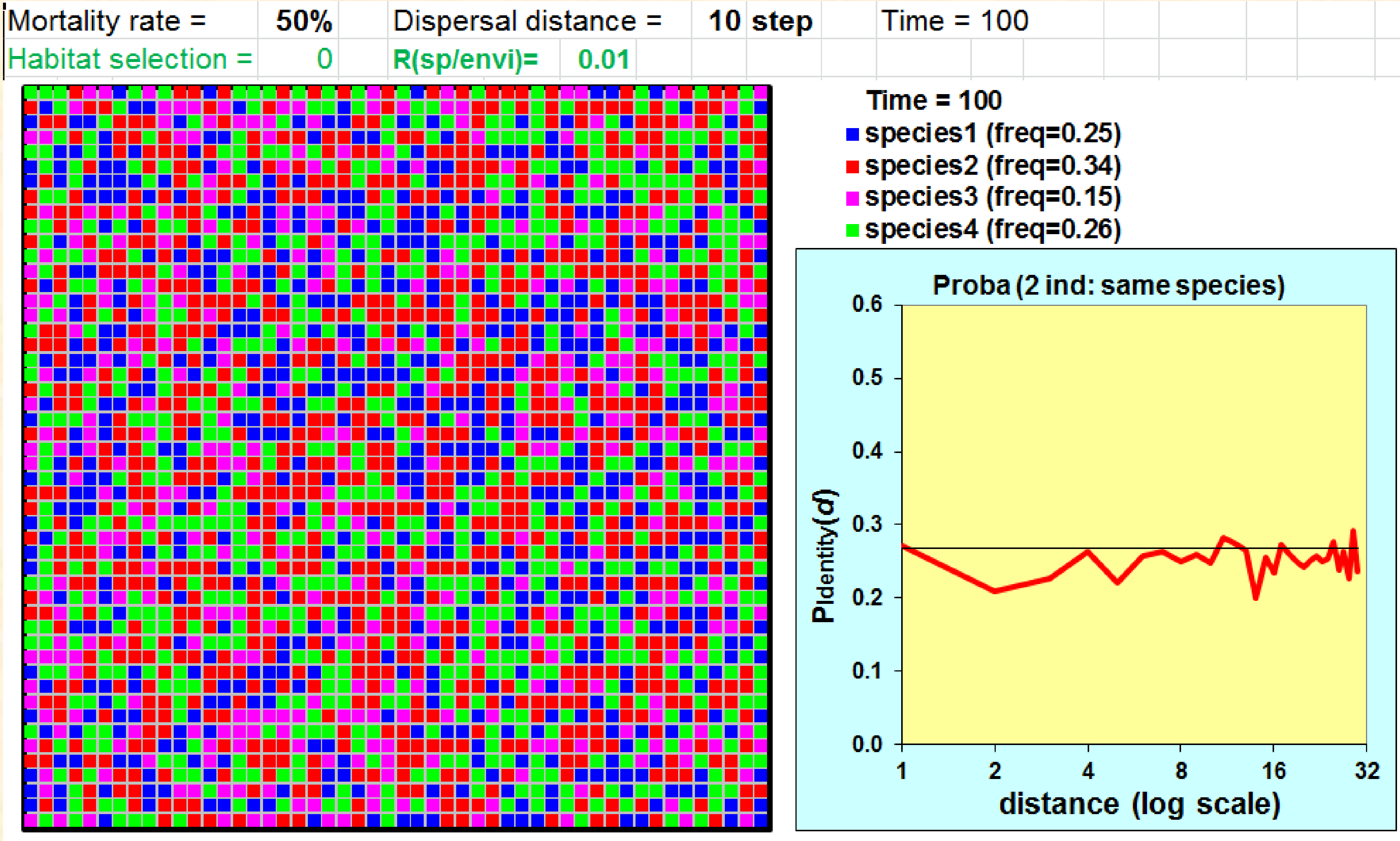
Mortality rate = **50%** Dispersal distance = **10 step** Time = 0

Habitat selection = 0 R(sp/envi)= 0.02

Time = 0

- 🟦 **species1 (freq=0.25)**
- 🟥 **species2 (freq=0.27)**
- 🟪 **species3 (freq=0.24)**
- 🟩 **species4 (freq=0.24)**

Neutre + dispersion étendue (100 pas de temps)



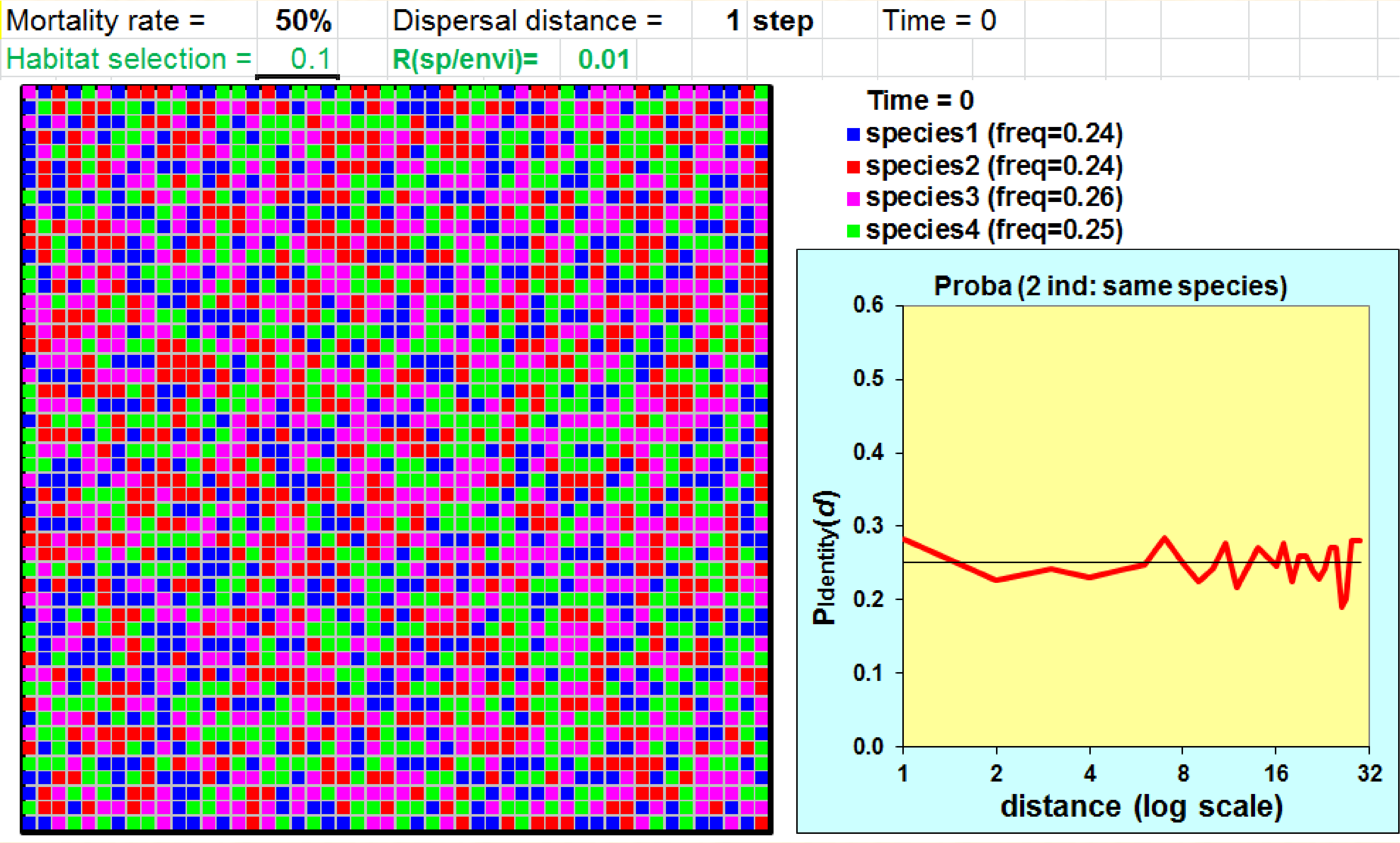
Mortality rate = **50%** Dispersal distance = **10 step** Time = 100

Habitat selection = 0 **R(sp/envi)= 0.01**

Time = 100

- 🟦 **species1 (freq=0.25)**
- 🟥 **species2 (freq=0.34)**
- 🟪 **species3 (freq=0.15)**
- 🟩 **species4 (freq=0.26)**

Filtre environnemental sur gradient ecol + dispersion très limitée (état initial)

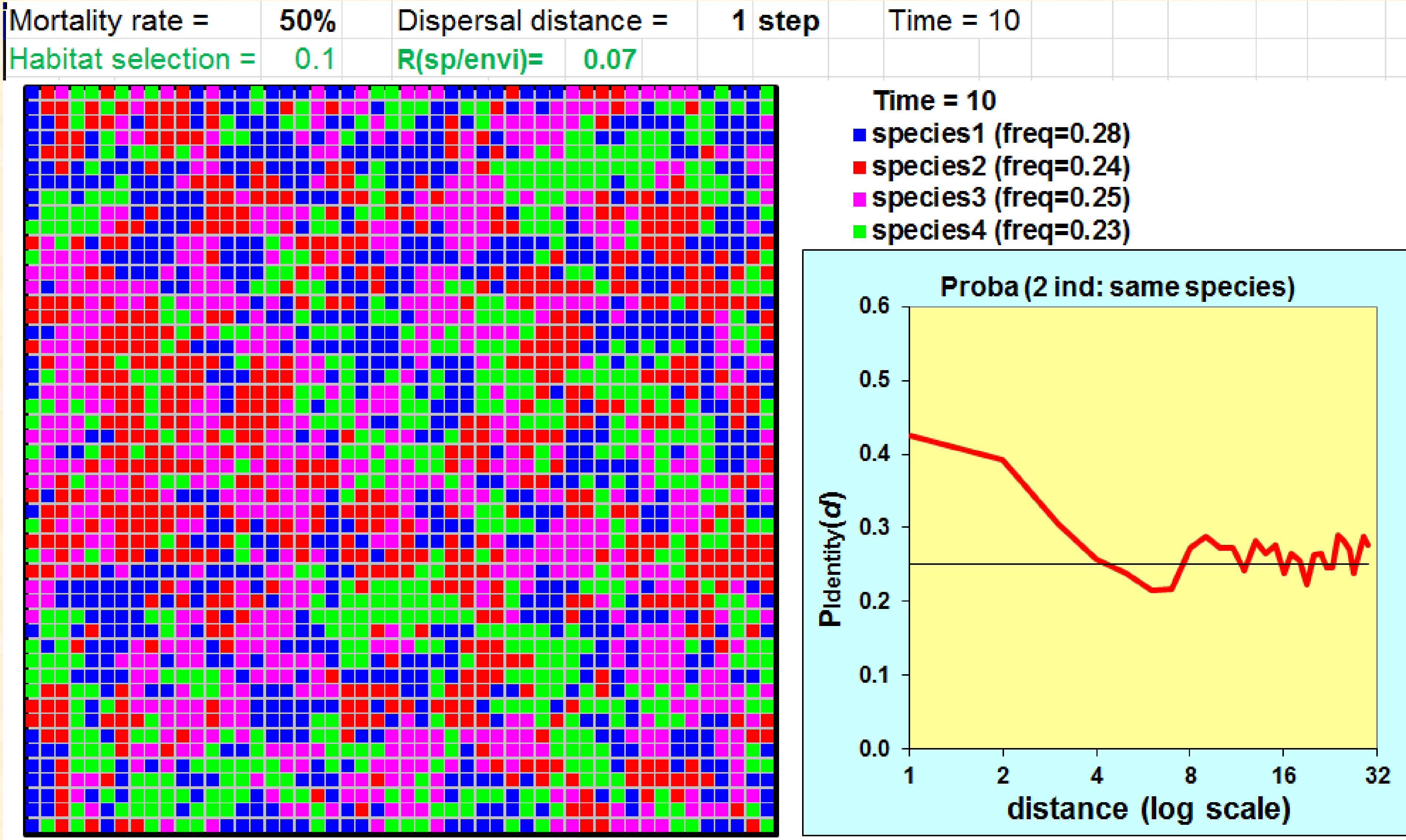


Mortality rate =	**50%**	Dispersal distance =	**1 step**	Time = 0
Habitat selection =	0.1	**R(sp/envi)=**	**0.01**	

Time = 0

- 🟦 **species1 (freq=0.24)**
- 🟥 **species2 (freq=0.24)**
- 🟪 **species3 (freq=0.26)**
- 🟩 **species4 (freq=0.25)**

Filtre environnemental sur gradient ecol + dispersion très limitée (10 pas de temps)

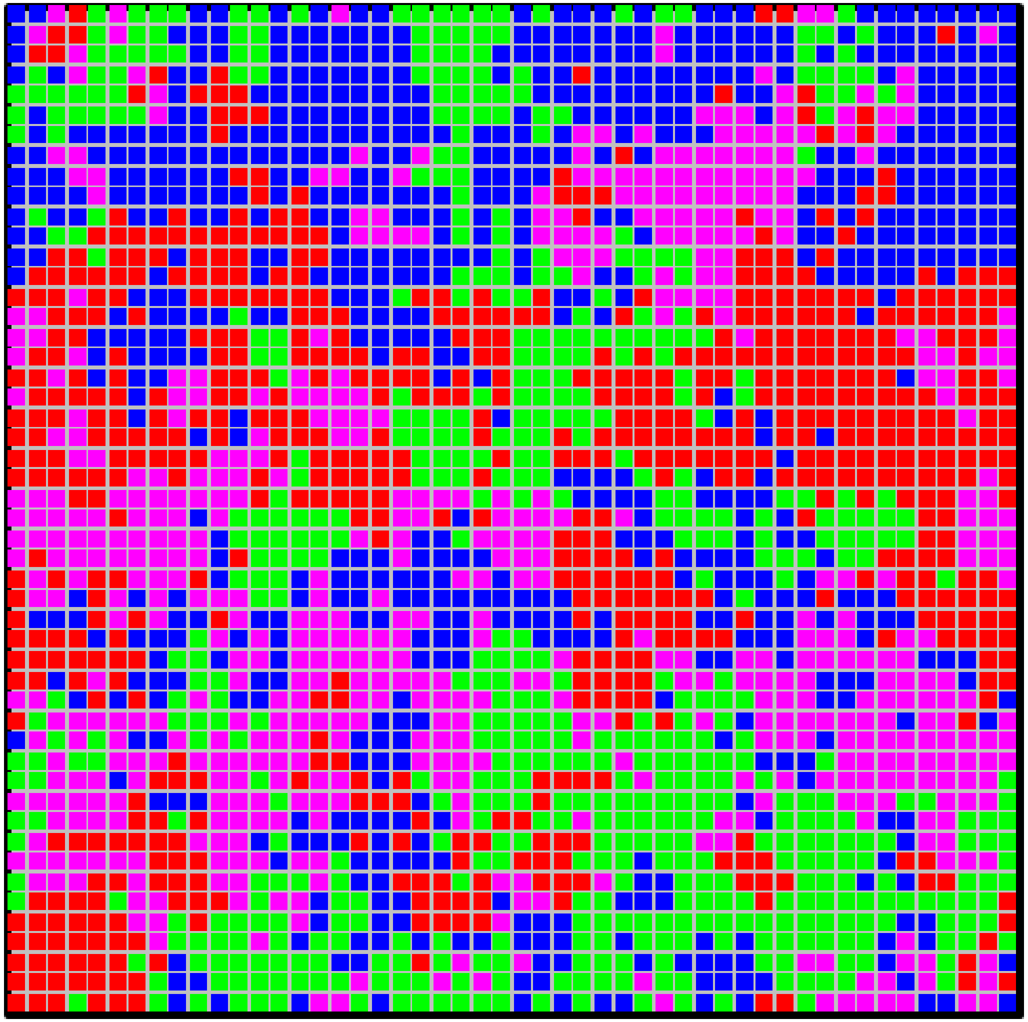


Mortality rate =	50%	Dispersal distance =	1 step	Time = 10
Habitat selection =	0.1	R(sp/envi)=	0.07	

Time = 10
- 🟦 species1 (freq=0.28)
- 🟥 species2 (freq=0.24)
- 🟪 species3 (freq=0.25)
- 🟩 species4 (freq=0.23)

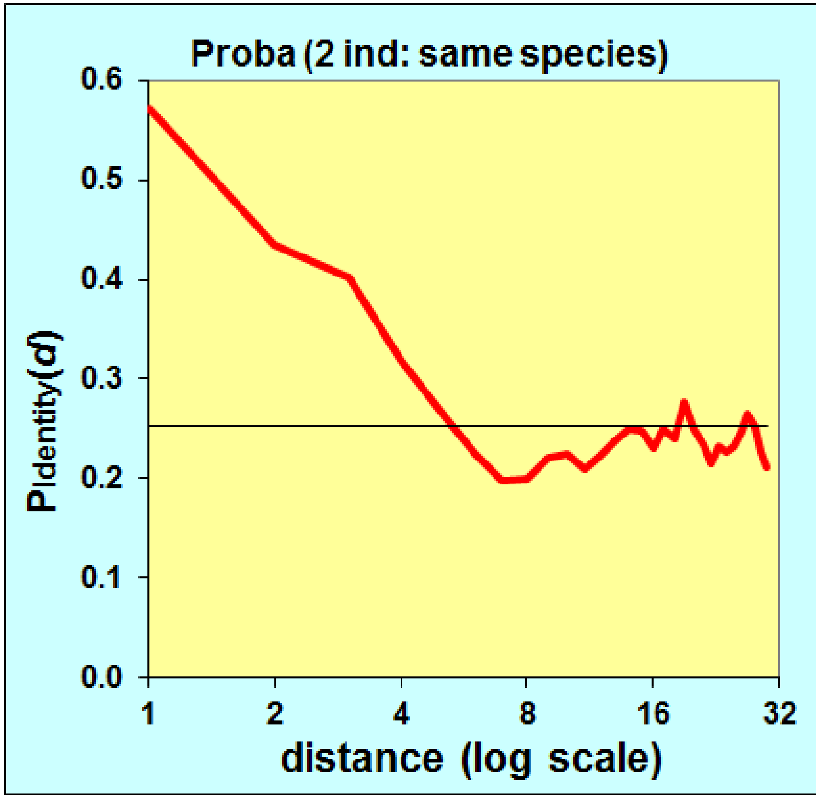
Filtre environnemental sur gradient ecol + dispersion très limitée (50 pas de temps)

Mortality rate =	**50%**	Dispersal distance =	**1 step**	Time = 50
Habitat selection =	0.1	**R(sp/envi)=**	**0.29**	

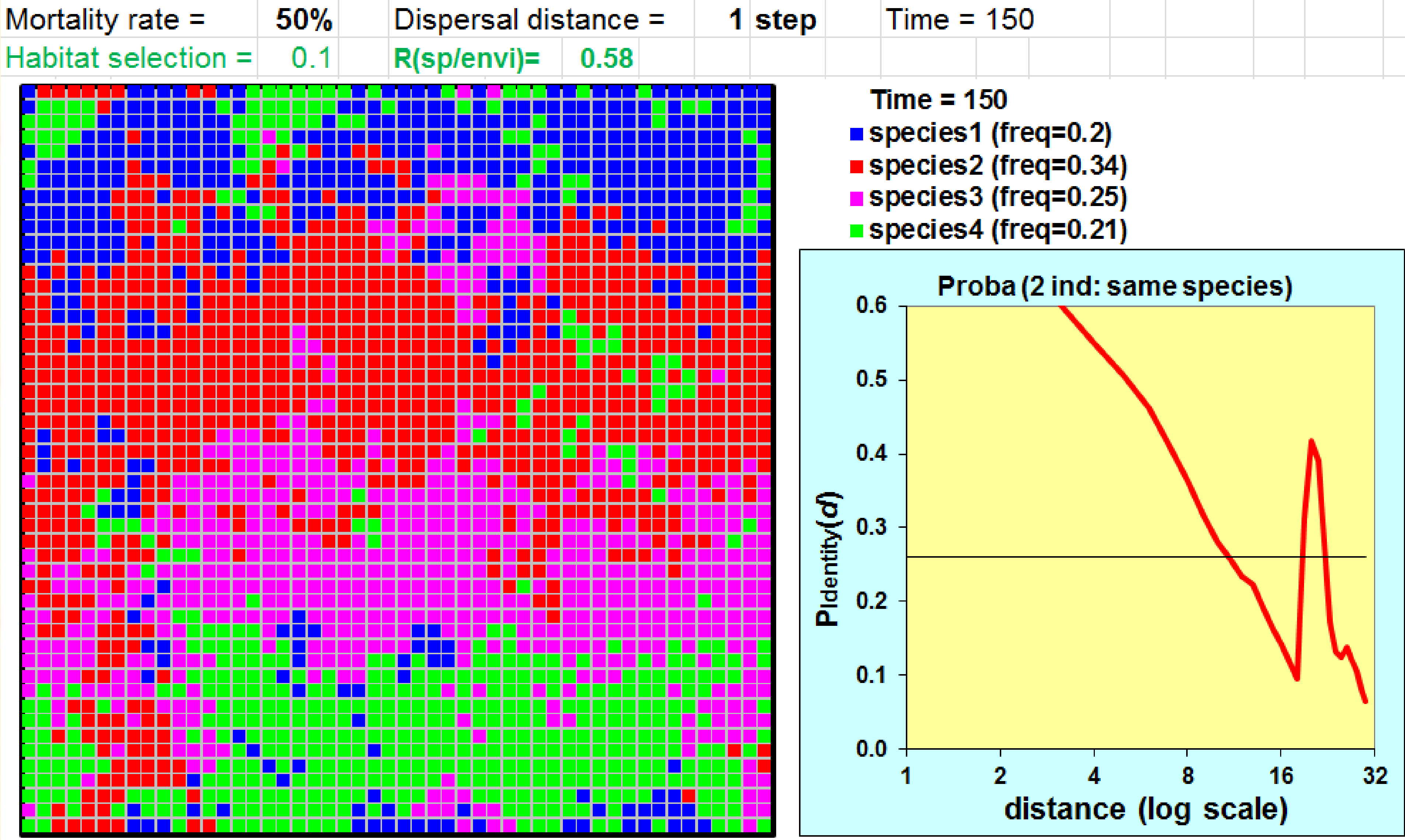


Time = 50

- 🟦 **species1 (freq=0.28)**
- 🟥 **species2 (freq=0.26)**
- 🟪 **species3 (freq=0.23)**
- 🟩 **species4 (freq=0.23)**



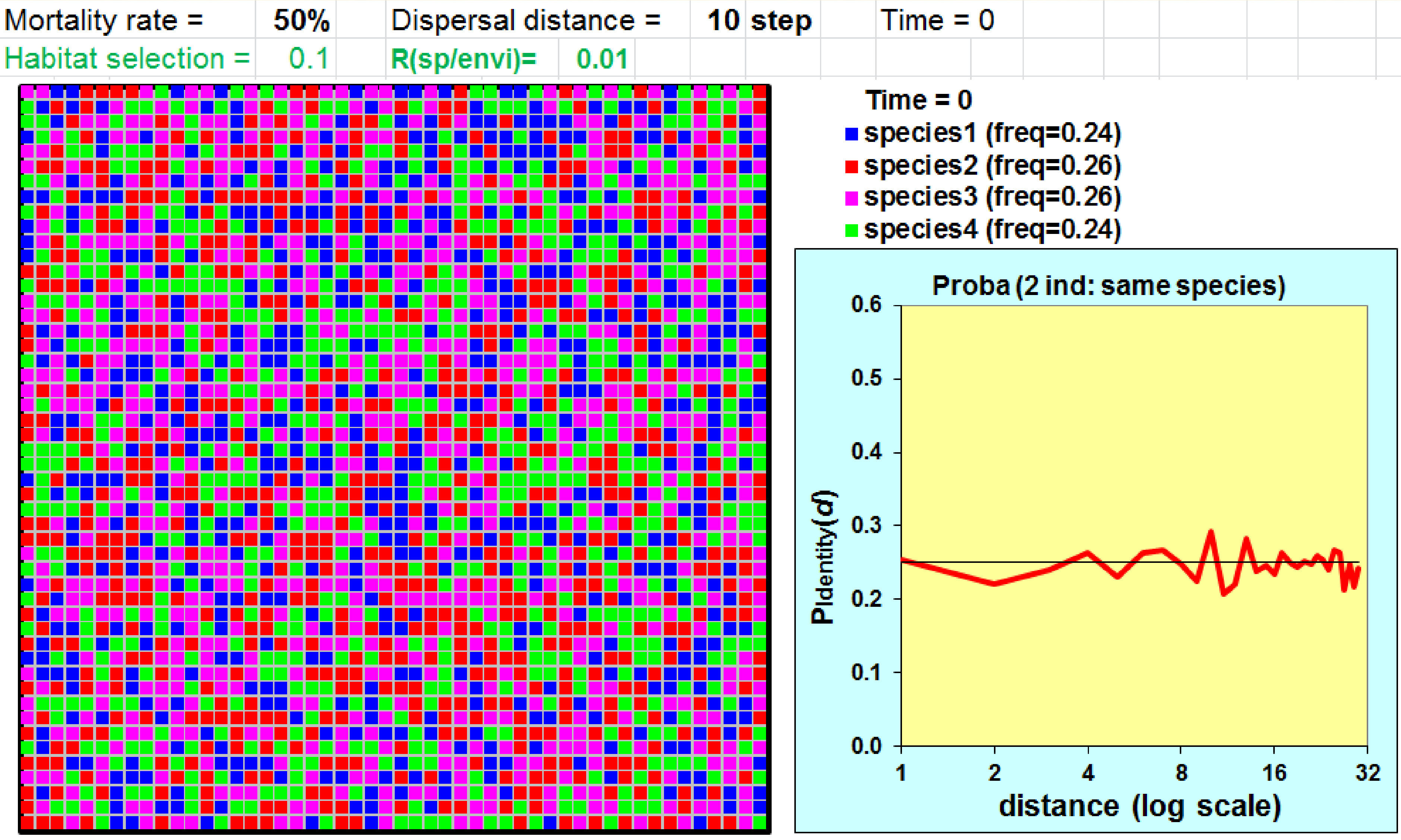
Filtre environnemental sur gradient ecol + dispersion très limitée (150 pas de temps)



Mortality rate =	50%	Dispersal distance =	1 step	Time = 150
Habitat selection =	0.1	R(sp/envi)=	0.58	

Time = 150
🟦 species1 (freq=0.2)
🟥 species2 (freq=0.34)
🟪 species3 (freq=0.25)
🟩 species4 (freq=0.21)

Filtre environnemental sur gradient ecol + dispersion étendue (état initial)



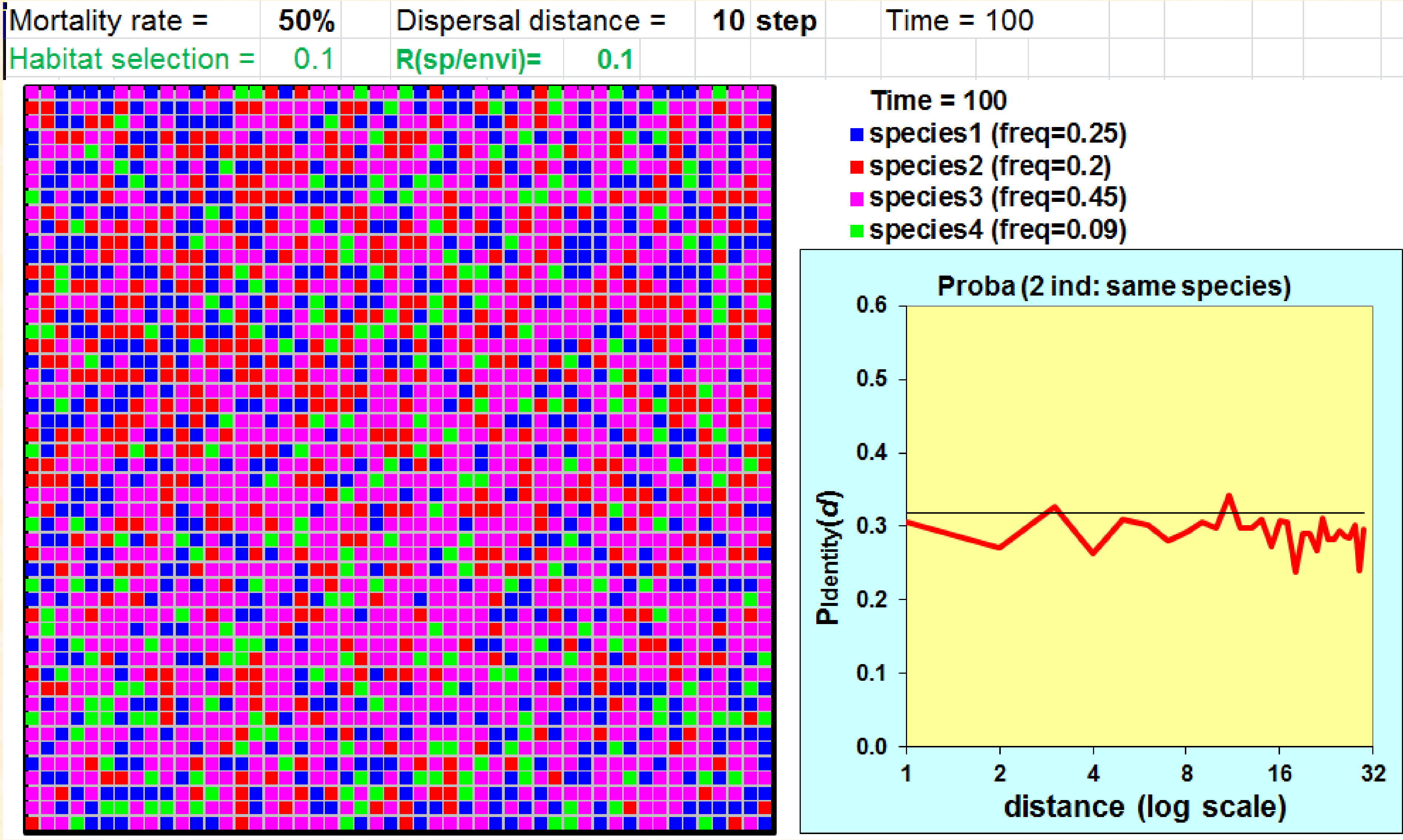
Mortality rate = **50%** Dispersal distance = **10 step** Time = 0

Habitat selection = 0.1 **R(sp/envi)= 0.01**

Time = 0

- 🟦 **species1 (freq=0.24)**
- 🟥 **species2 (freq=0.26)**
- 🟪 **species3 (freq=0.26)**
- 🟩 **species4 (freq=0.24)**

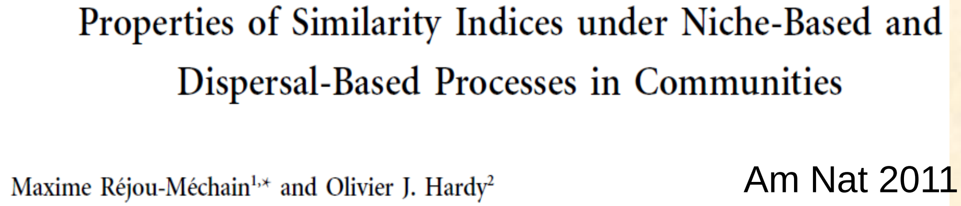
Filtre environnemental sur gradient ecol + dispersion étendue (100 pas de temps)



Mortality rate =	50%	Dispersal distance =	10 step	Time = 100
Habitat selection =	0.1	R(sp/envi)=	0.1	

Time = 100

- 🟦 species1 (freq=0.25)
- 🟥 species2 (freq=0.2)
- 🟪 species3 (freq=0.45)
- 🟩 species4 (freq=0.09)

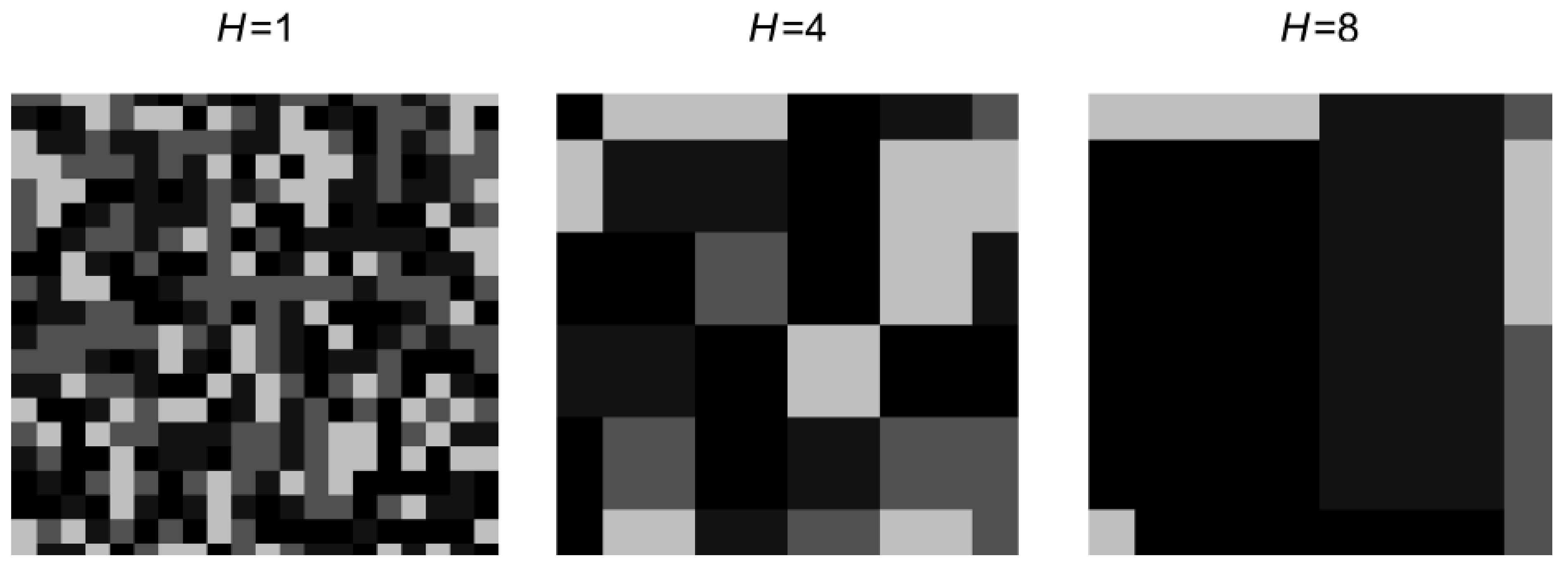


Properties of Similarity Indices under Niche-Based and Dispersal-Based Processes in Communities

Maxime Réjou-Méchain[1,*] and Olivier J. Hardy[2]

Am Nat 2011

Grid of local communities each with N=100
4 habitats at different heterog. grain (H)
0.001 immigration from constant source
20-500 species, log-series distrib.
Dispersal=expon. (mean dist δ=0.5, 1.5, ..)
Neutral or selection (1 optimal hab/sp)



Measures of species turnover in space using pairwise (dis)similarity indices btw comm.

$$\text{Sorensen} = \frac{2a}{2a+b+c}$$

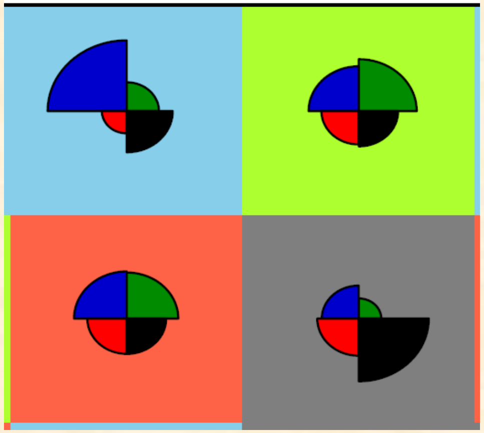
$$F = \sum_s p_{is} p_{js}$$

within vs between hab if selection

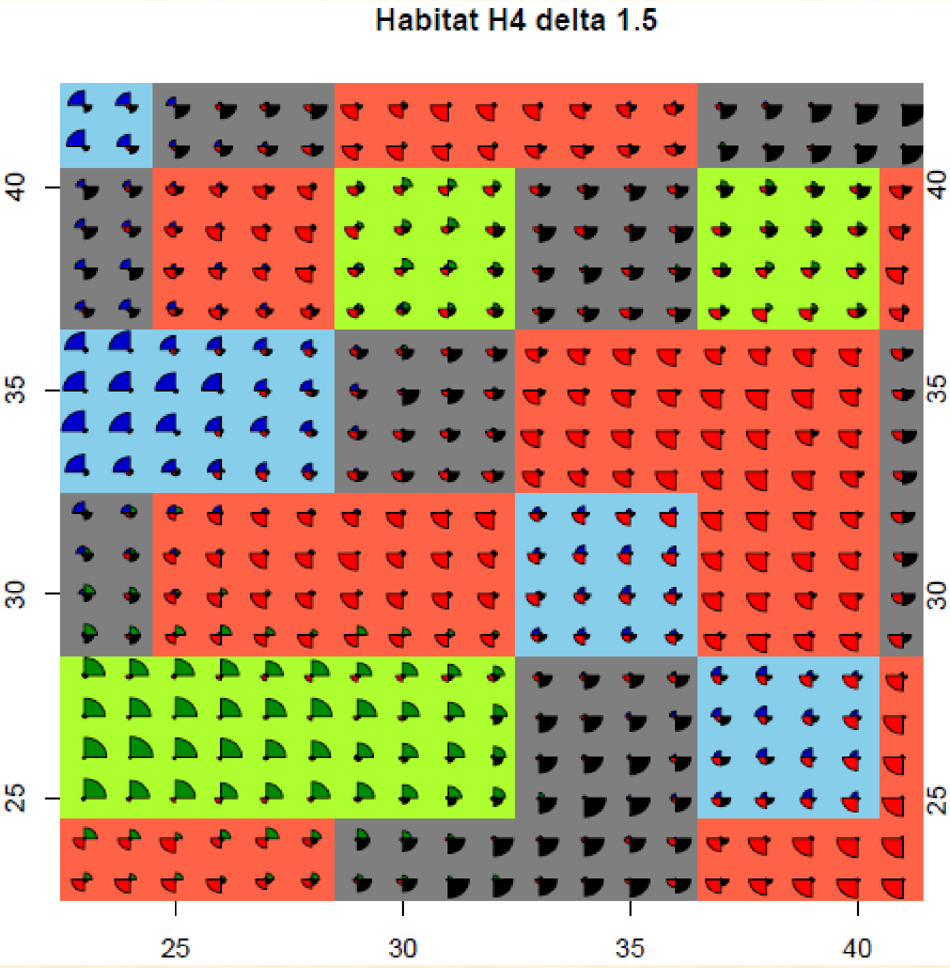
$$\text{Morisita-Horn} = \frac{\sum_s p_{is} p_{js}}{\left(\sum_s p_{is}^2 + \sum_s p_{js}^2\right)/2}$$

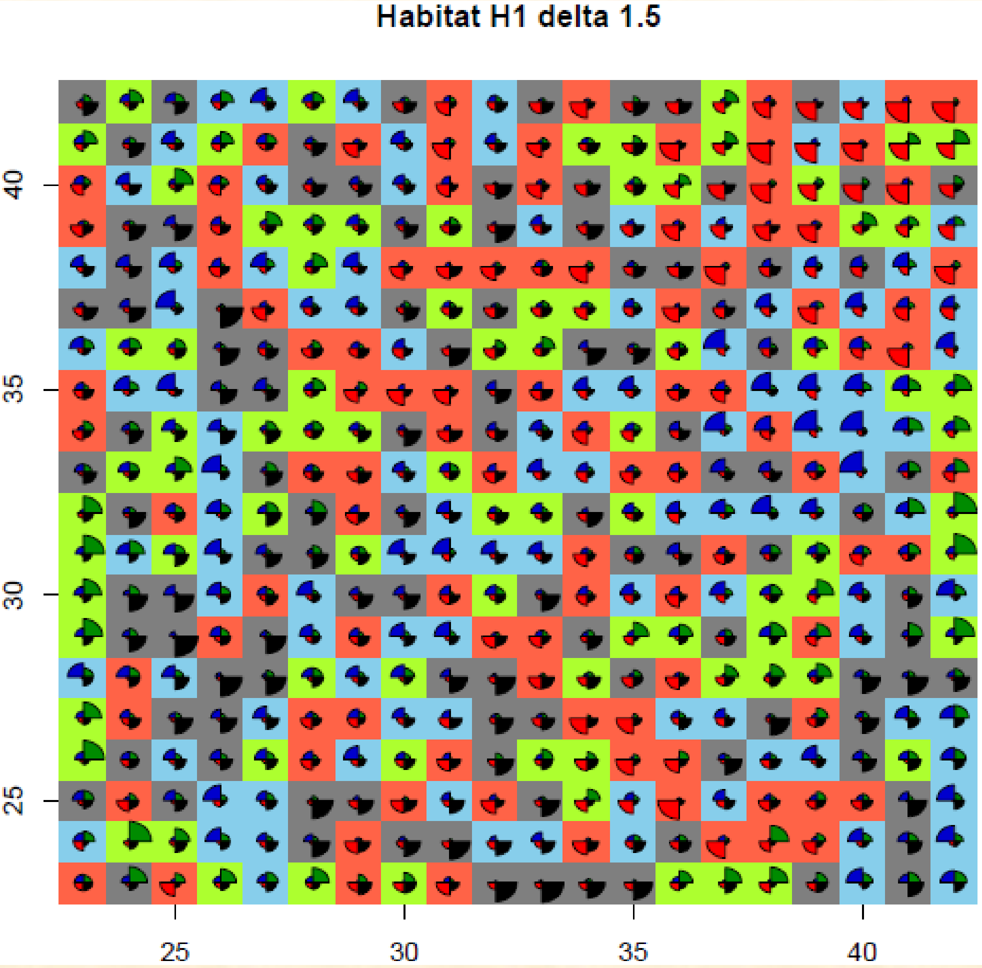
$$I_{ST} = 1 - \frac{1 - \left(\sum_s p_{is}^2 + \sum_s p_{js}^2\right)/2}{1 - \left(\sum_s p_{is} p_{js}\right)}$$

Selection (*s*=0.3) : efficiency of selection



Mean dispersal distance = 1.5 grid units





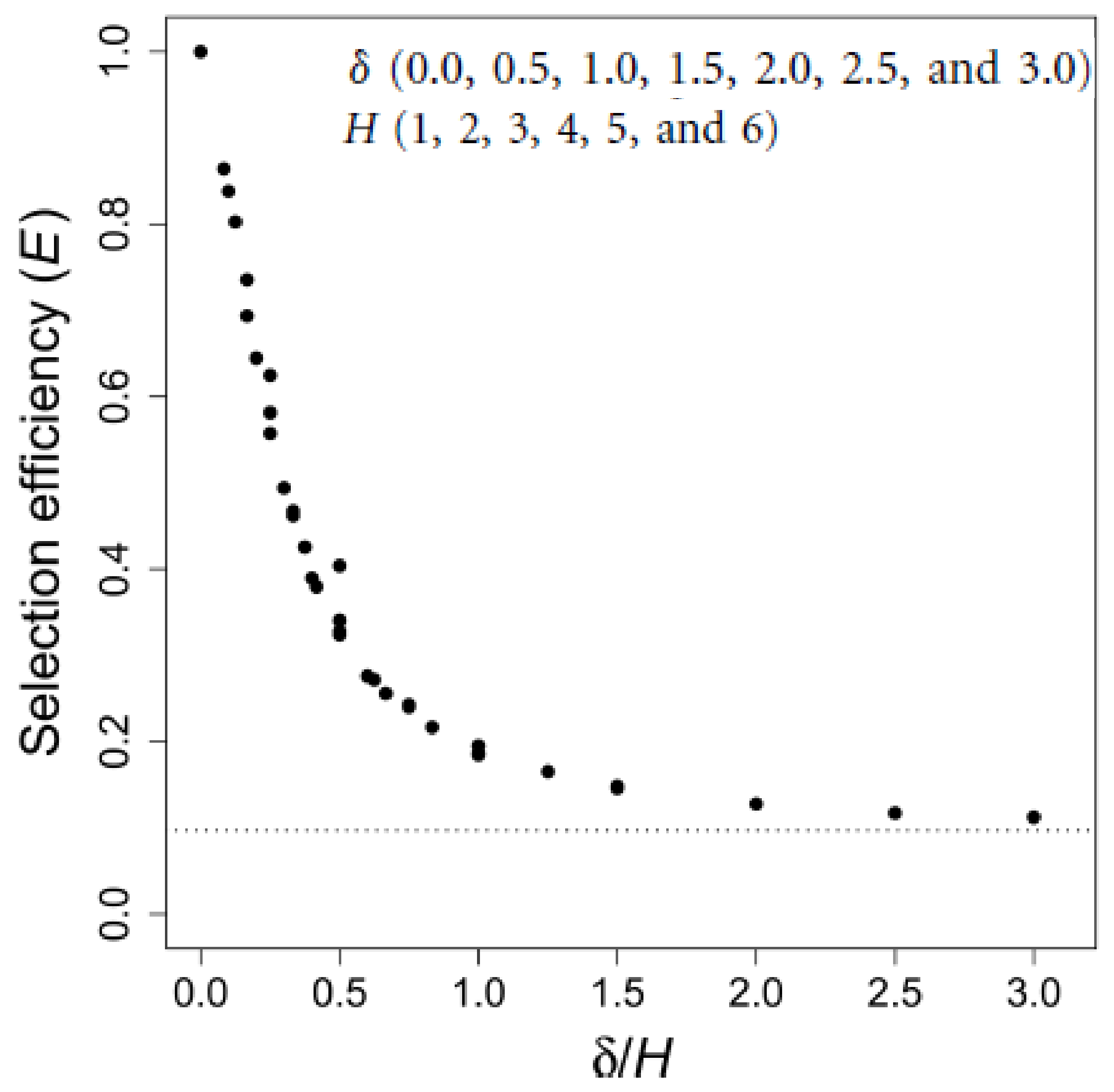
Selection : efficiency of selection

according to ratio dispersal distance / grain environm heterog

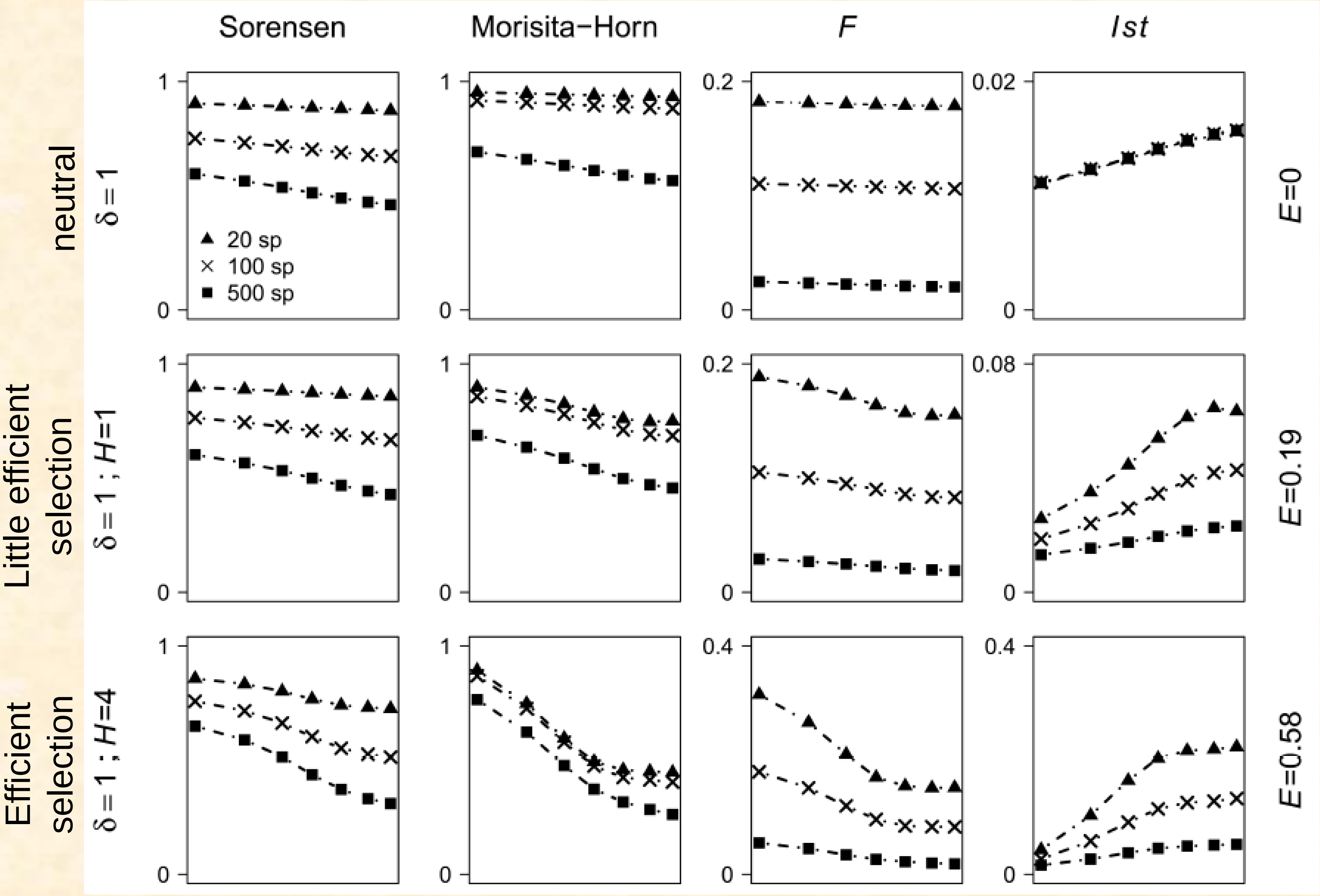
$$E = \frac{P_o - P_e}{1 - P_e}$$

Po = observed freq. of ind. in their optimal habitat

Pe = expected freq. of ind. in their optimal habitat under random distribution



Species turnover: effect of neutral/selection + species richness on different indices

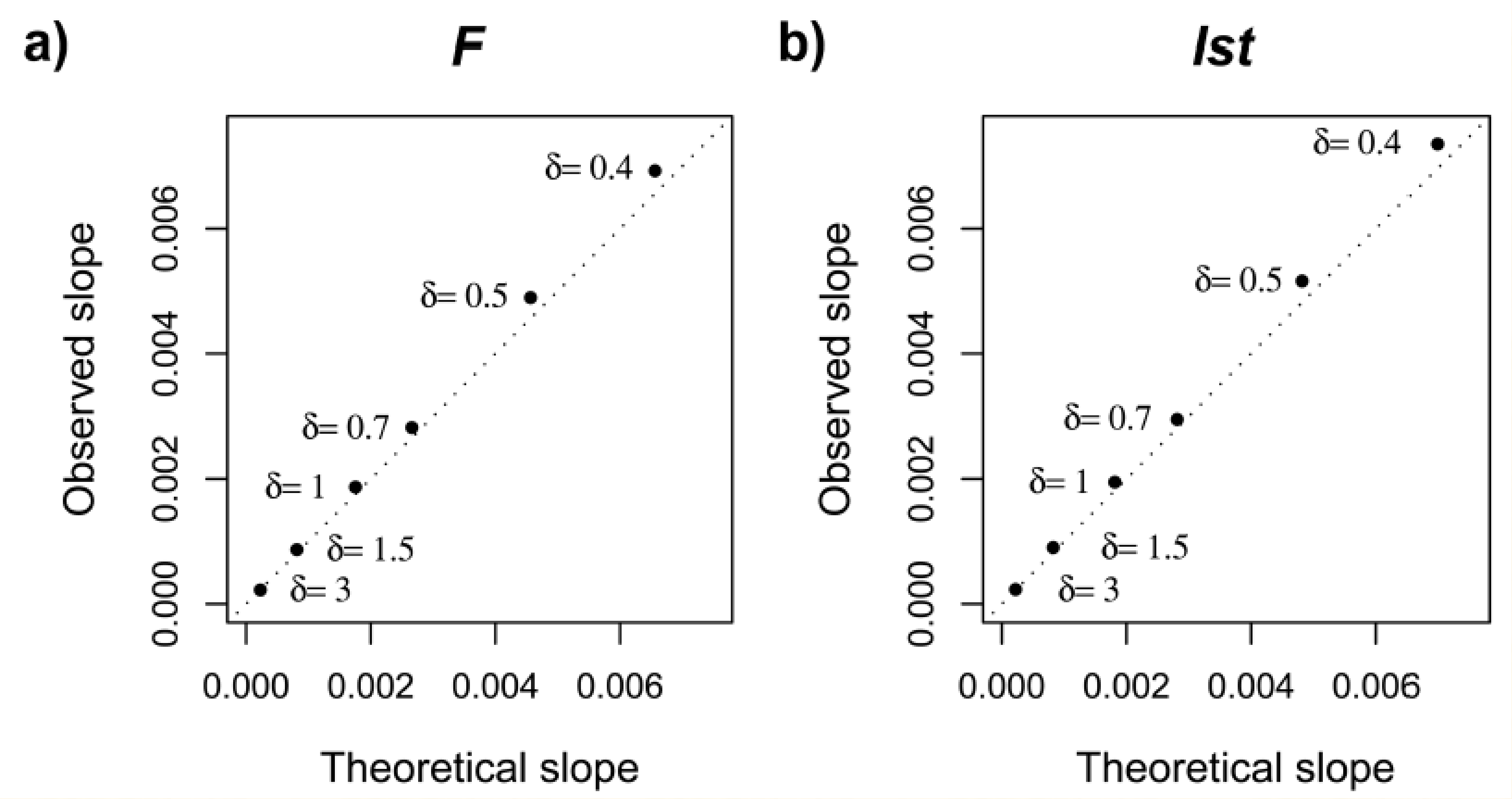


Geographical distance (log scale)

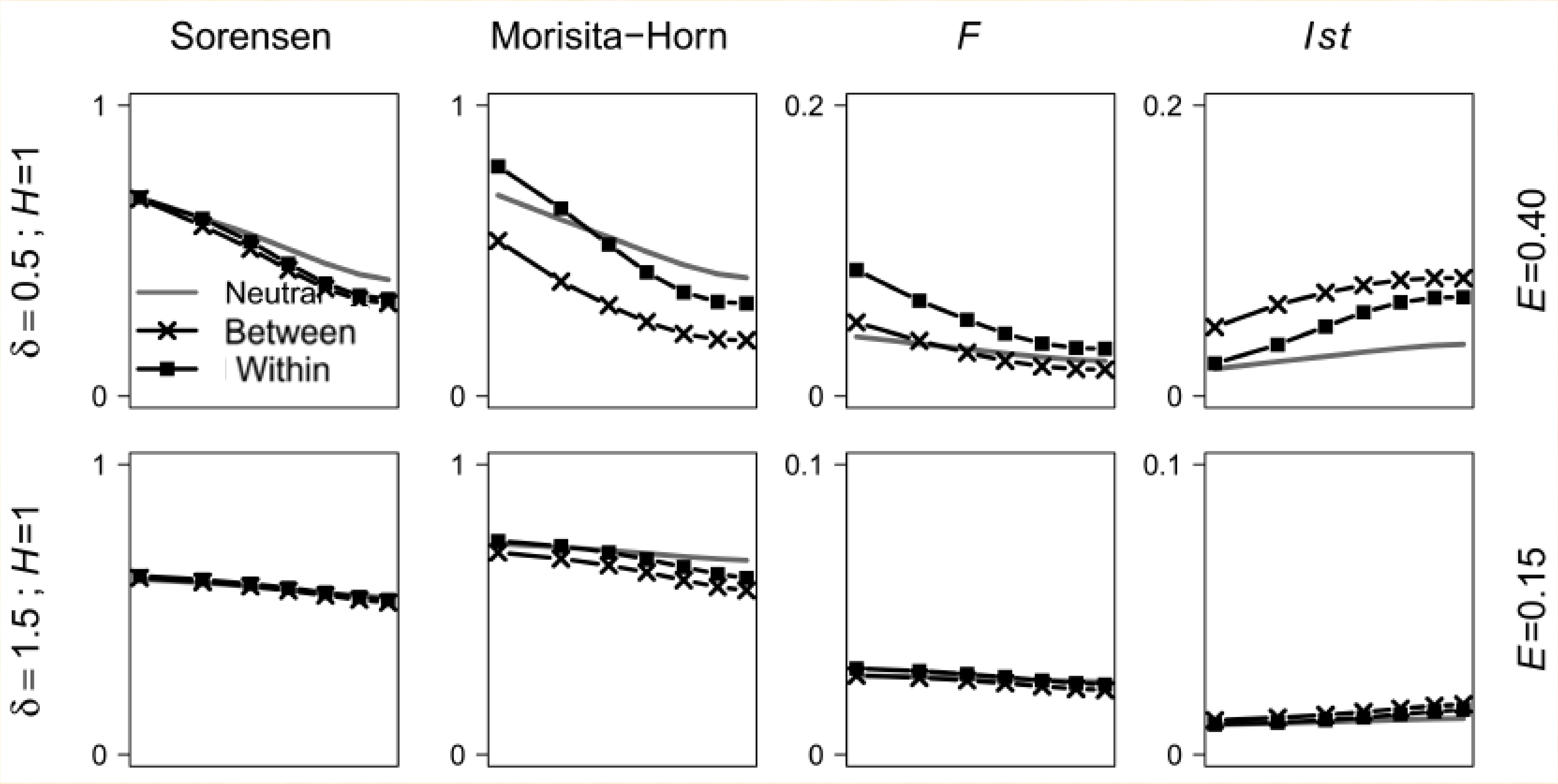
Neutral case: verification of isolation by distance prediction

Slope $Ist/(1-Ist)$ on ln(dist) = $(2\pi D\sigma^2)^{-1}$

Rousset 1997



Species turnover within versus between habitat types under selection



Efficient selection

Little efficient selection

Geographical distance (log scale)

Modèle de communauté neutre (Hubbell 2001)
-> toutes les espèces sont équivalentes;
la notion d'espèce se réduit à une étiquette héritable

Modélisation d'une communauté neutre
+ capacités de dispersion limitées dans l'espace:

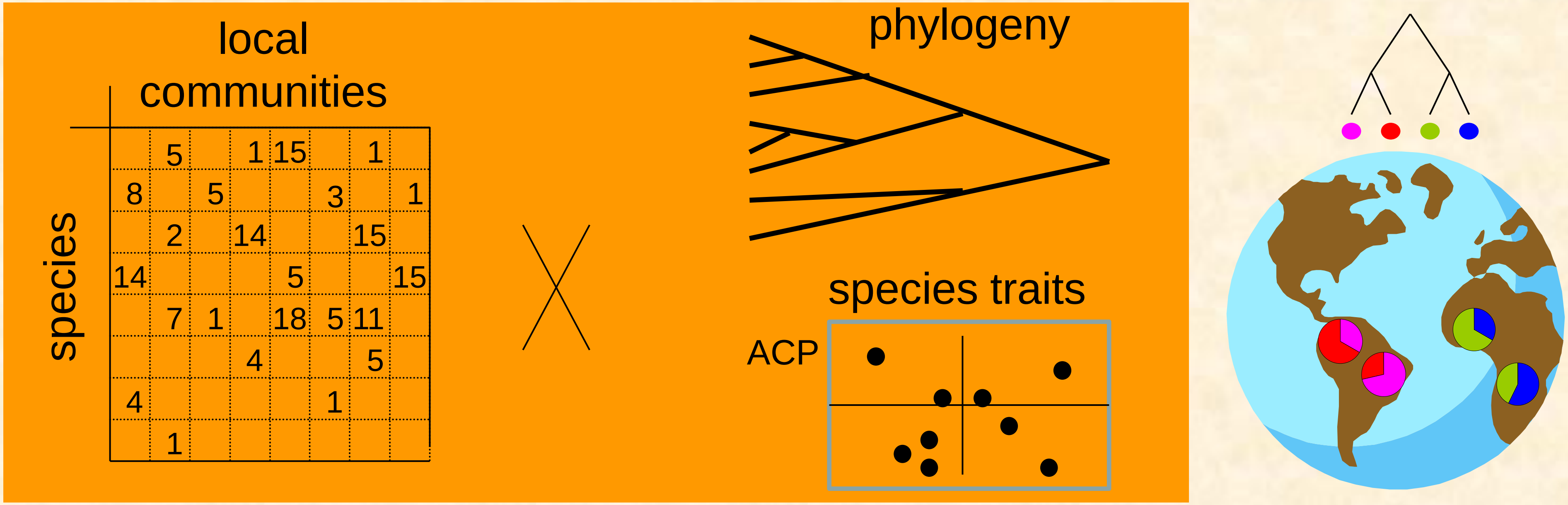
-> des espèces peuvent coexister longtemps malgré l'absence de différenciation de niche

-> des structures spatiales apparaissent
⇘ effet confondant avec l'impact d'une hétérogénéité du milieu

Modélisation avec différenciation de niche:
-> la dispersion limitée peut accroître la réponse des espèces à l'hétérogénéité du milieu

Evolutionary aspects of community assembly

Insights on species assembly rules from the phylogenetic and functional structure of tropical plant communities



	5		1	15		1	
8		5			3		1
	2		14			15	
14				5			15
	7	1		18	5	11	
			4			5	
4					1		
	1						

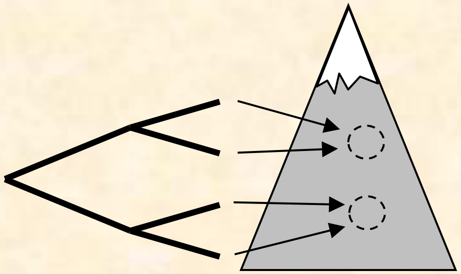
⇒ test hypotheses on mechanisms determining species assembly

Community phylogenetic structure

Example under environmental filtering
(adaptation to altitude)

Phylogenetic **clustering**

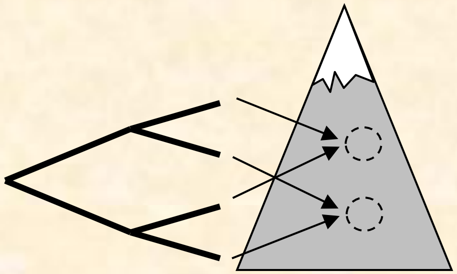
species within habitat **more** related than among habitats



habitat conservatism

Phylogenetic **overdispersion**

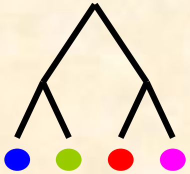
species within habitat **less** related than among habitats



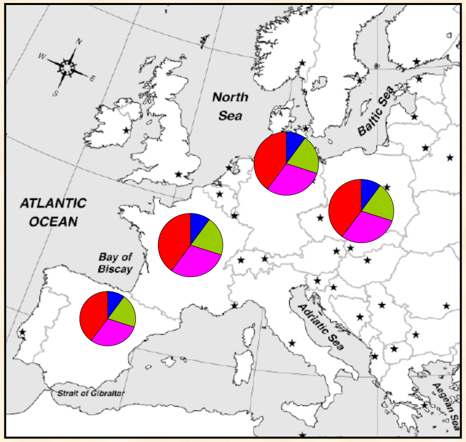
habitat convergence

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

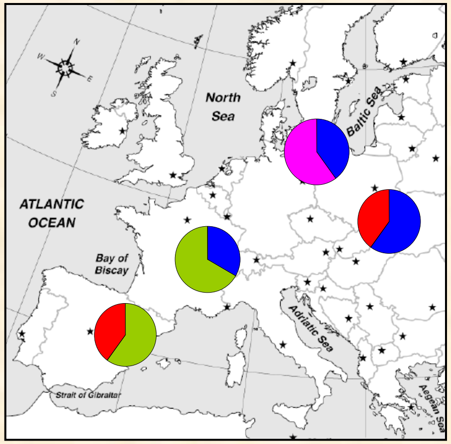
Species turnover *versus* phylogenetic turnover



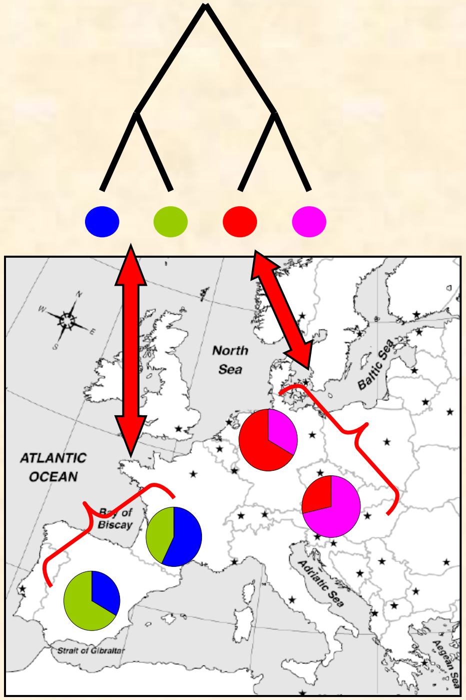
Phylogenetic tree
for 4 species



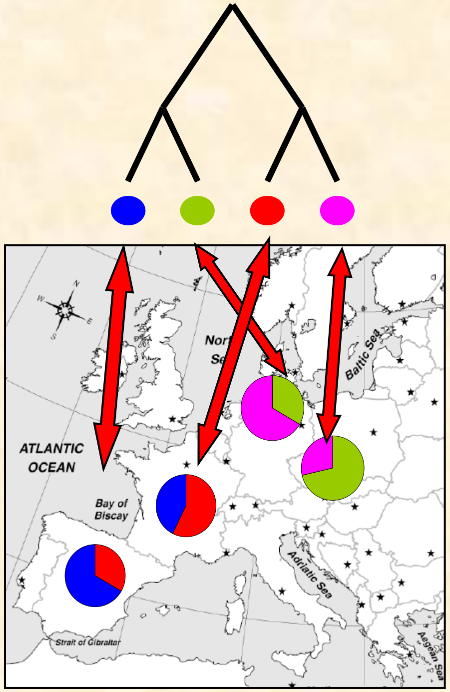
**No species
turnover
&
No phylogenetic
turnover**



**Species turnover
but
No phylogenetic
turnover**



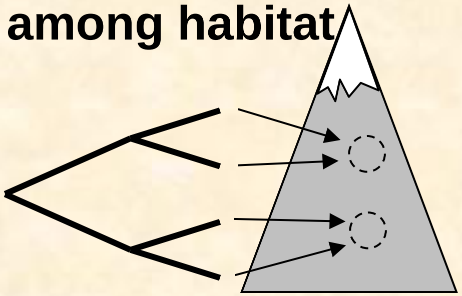
**Species turnover
+
Phylogenetic
clustering**
(attraction)



**Species turnover
+
Phylogenetic
overdispersion**
(eveness, repulsion)

Phylogenetic turnover caused by ecological & evolutionary processes

Phylogenetic clustering



environmental filtering

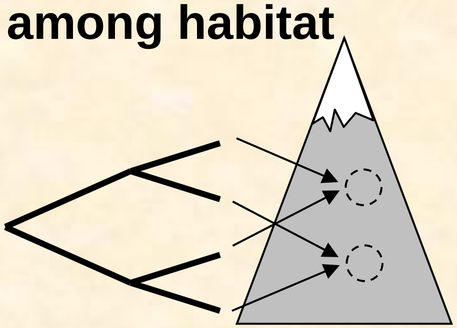
adaptation to ≠ elevation

+

habitat conservatism

Phylogenetic overdispersion

(= evenness = repulsion)



environmental filtering

adaptation to ≠ elevation

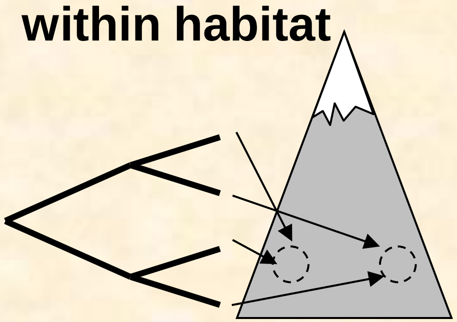
+

habitat convergence

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

Phylogenetic overdispersion

(= evenness = repulsion)



competitive exclusion

+

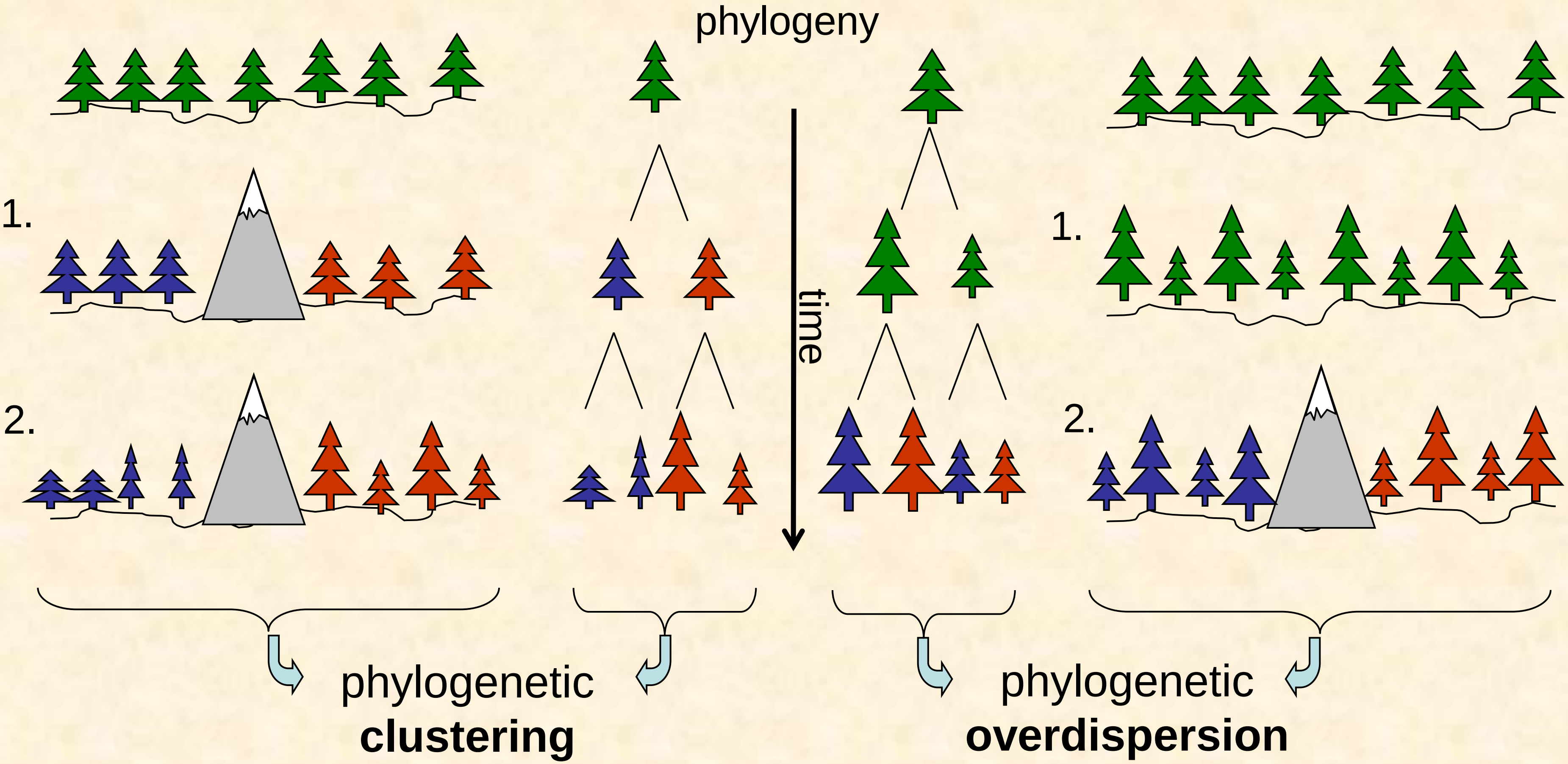
niche conservatism

→ sister species cannot coexist because of niche overlap ('limiting similarity' principle)

Phylogenetic turnover caused by biogeographic barrier

Scenario A:
1. barrier (allopatric speciation)
2. sympatric speciations

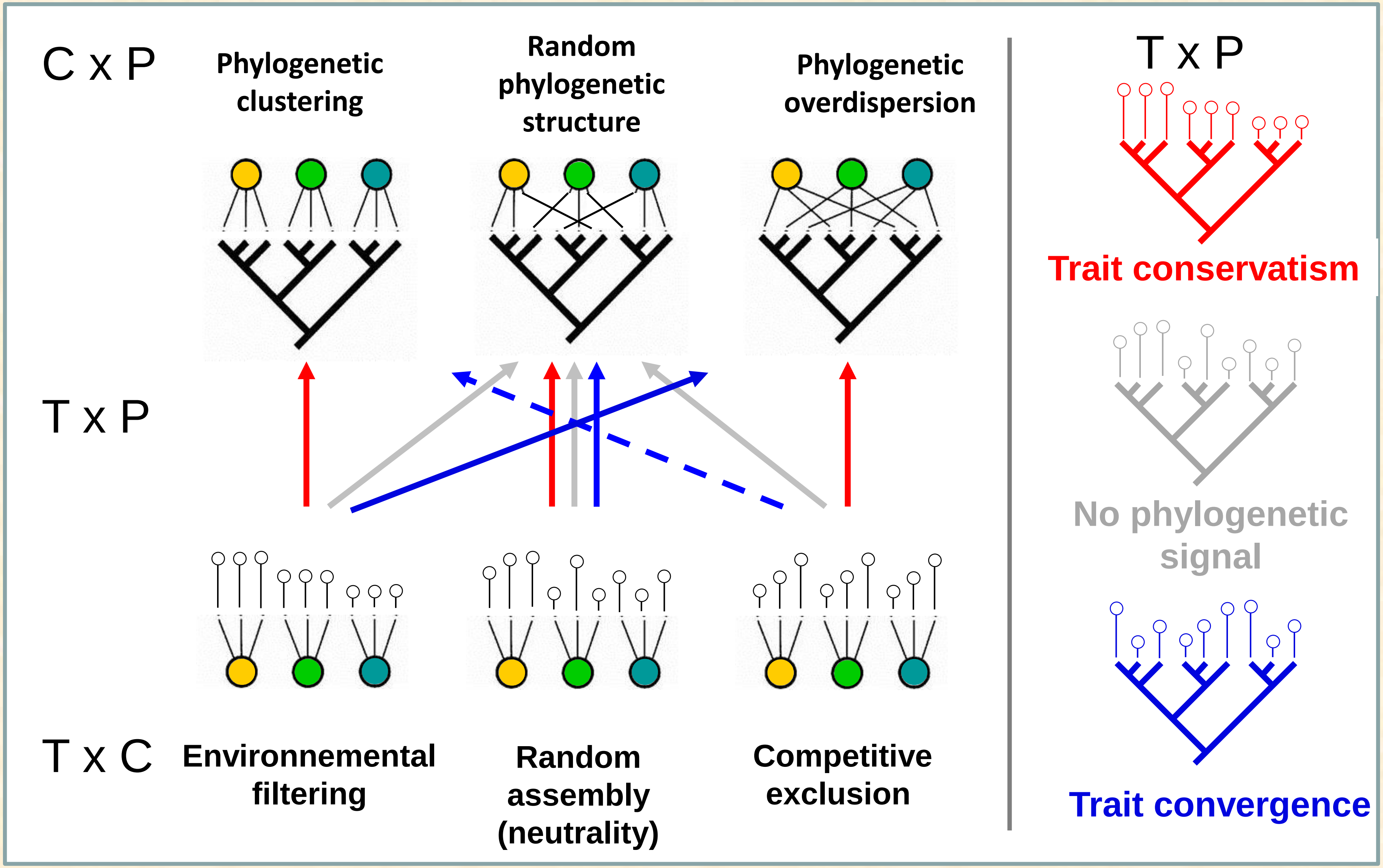
Scenario B:
1. sympatric speciation
2. barrier (allopatric speciations)



phylogenetic **clustering**

phylogenetic **overdispersion**

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

Environnemental filtering

Random assembly (neutrality)

Competitive exclusion

T x P

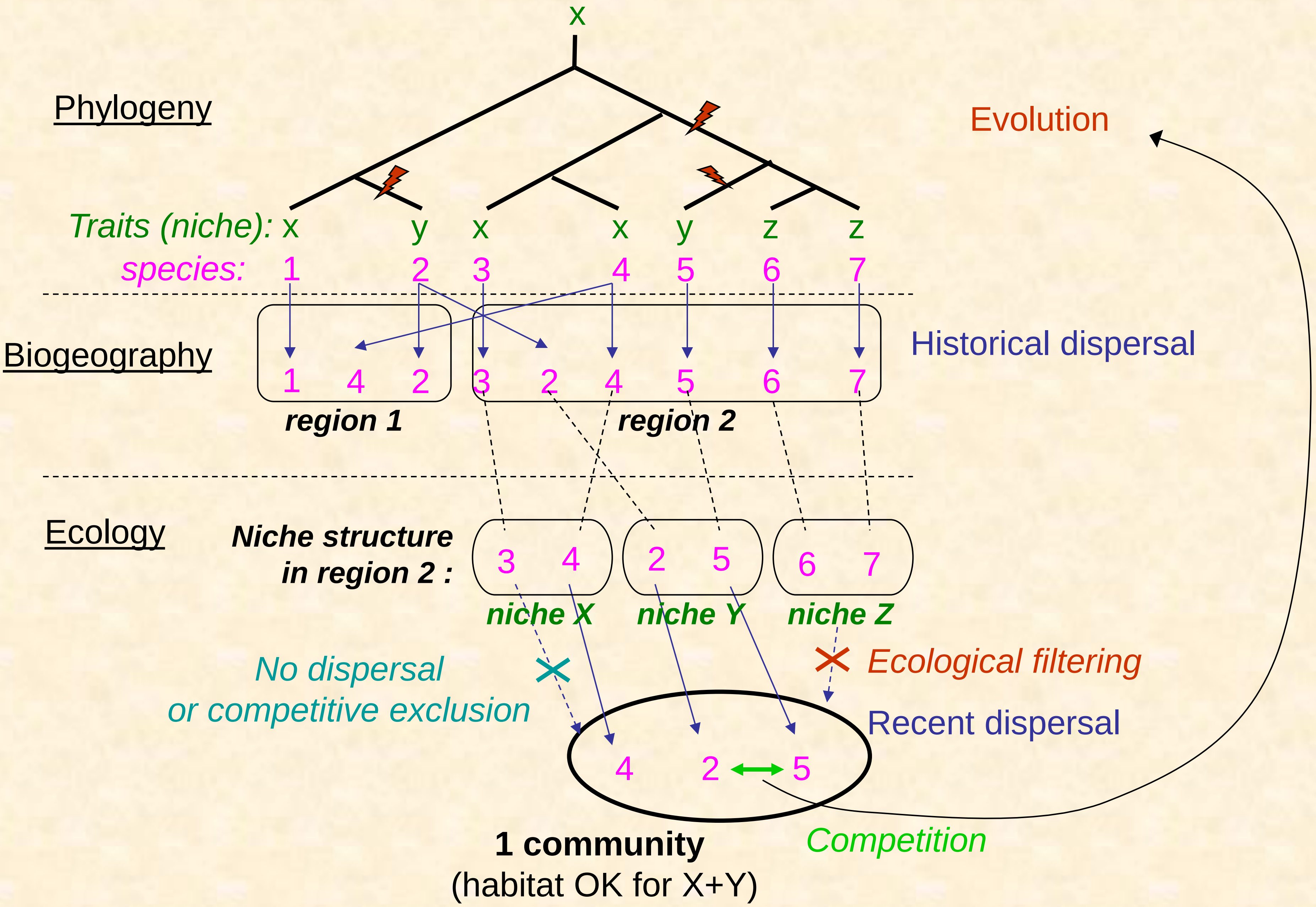
Trait conservatism

No phylogenetic signal

Trait convergence

Community phylogenetic structure depends on ecological and evolutionary processes

Integration communities – traits – ecology – biogeography – evolution



Phylogeny

Evolution

Traits (niche):

species:

Biogeography

Historical dispersal

region 1

region 2

Ecology

Niche structure in region 2 :

niche X ***niche Y*** ***niche Z***

No dispersal or competitive exclusion

Ecological filtering

Recent dispersal

Competition

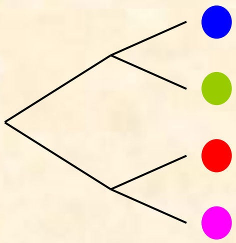
1 community

(habitat OK for X+Y)

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

$$MPD_w = \bar{\delta}_{(2\_species\_from\_same\_site)}$$

among sites

$$MPD_a = \bar{\delta}_{(2\_species\_from\_different\_sites)}$$

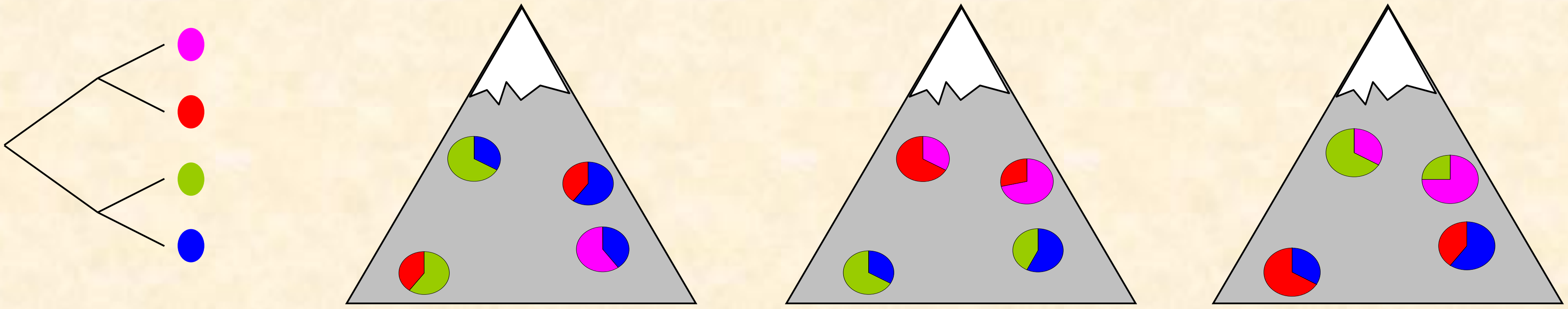
$$\rightarrow \quad \Pi_{ST} = 1 - MPD_w / MPD_a$$

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

Hardy & Senterre 2007 (J. Ecol. 95: 493–506)
Hardy & Jost 2008 (J. Ecol. 96: 849–852)

-> phylogenetic turnover

How to test phylogenetic turnover?



no phylogenetic structure

$\Pi_{ST} = 0$

Phylogenetic **clustering**

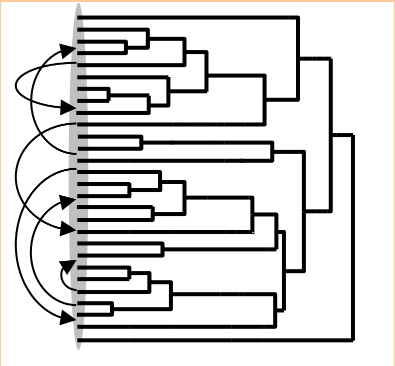
$\Pi_{ST} > 0$

Phylogenetic **overdispersion**

$\Pi_{ST} < 0$

Testing Π_{ST} <> 0

→ **randomize phylogeny** ⟶

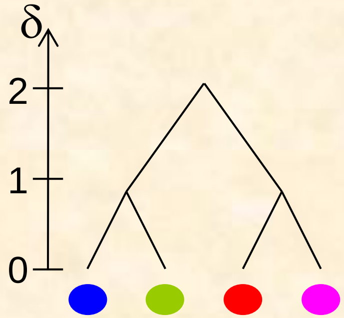


→ assess distribution of Π_{ST} for 1000 permutations

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

More elaborated randomization tests: Hardy 2008 (J Ecol 96: 914–926)

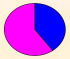
Exemple of computation of pairwise Π_{ST} for simple cases

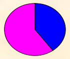


$$MPD_{\mathrm{w}} = \bar{\delta}_{(2 \neq species\_from\_same\_site)}$$

$$MPD_{\mathrm{a}} = \bar{\delta}_{(2 \neq species\_from\_different\_sites)}$$

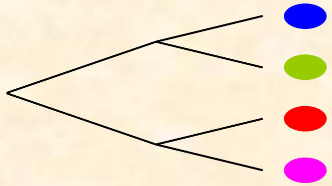
$$\Pi_{ST} = 1 - MPD_{\mathrm{w}} / MPD_{\mathrm{a}}$$

	MPD_w	1	2
MPD_w	MPD_a		
2		5/3	3/2
1		2	5/3
5/3=1.67		5/3	5/3

Π_{ST}		
	1-(3/2)/(5/3)=0.1	1-2/(3/2)=-0.33
	1-1/2=0.5	1-(3/2)/(5/3)=0.1
	1-(4/3)/(5/3)=0.2	1-(11/6)/(5/3)=-0.1

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

From a phylogeny → distances between species



$$\delta_{kl}$$

	🔵	🟢	🔴	🟣
🔵	0	1	2	2
🟢	1	0	2	2
🔴	2	2	0	1
🟣	2	2	1	0

From community inventories:

> **partition of QE** = mean δ_{kl} between <u>individuals</u>

(Hardy & Senterre 2007,

sampled

<u>w</u>ithin sites $QE_w = \bar{\delta}_{(2\_individuals\_from\_same\_site)}$

<u>a</u>mong sites $QE_a = \bar{\delta}_{(2\_individuals\_from\_different\_sites)}$

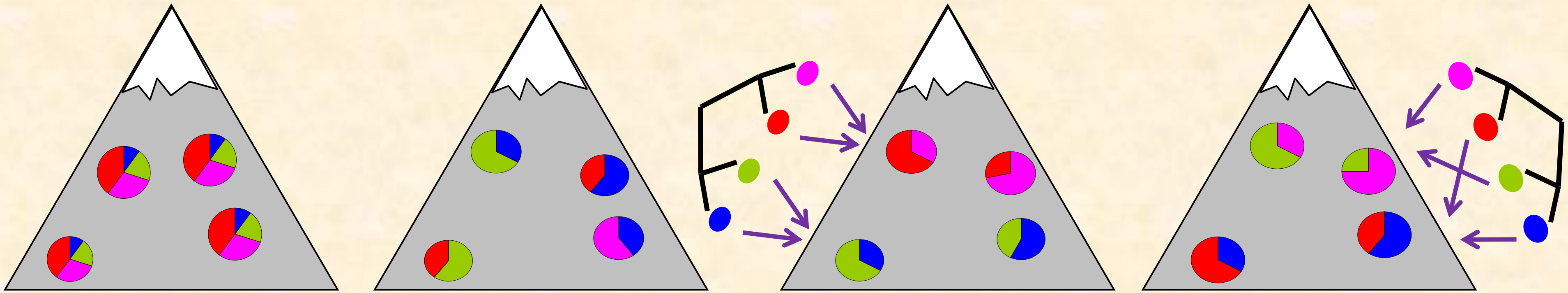
→ $P_{ST} = 1 - QE_w / QE_a$ **species + phylogenetic turnover**

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

→ $I_{ST} = 1 - D_w / D_a$ **species turnover**

> **partition of QE'** = mean δ_{kl} between <u>individuals</u> *of distinct species*

→ $B_{ST} = 1 - QE'_w / QE'_a \approx P_{ST} - I_{ST}$ **phylogenetic turnover**



No species turnover
&
No phylogenetic
turnover

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

Species turnover
but
No phylogenetic
turnover

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

Species turnover
+
Phylogenetic
clustering

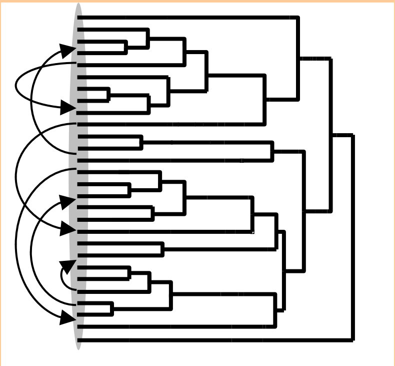
$P_{ST} > I_{ST} > 0$
$B_{ST} > 0$

Species turnover
+
Phylogenetic
overdispersion

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

Testing $P_{ST} <> I_{ST}$ or $B_{ST} <> 0$

→ **randomize phylogeny**



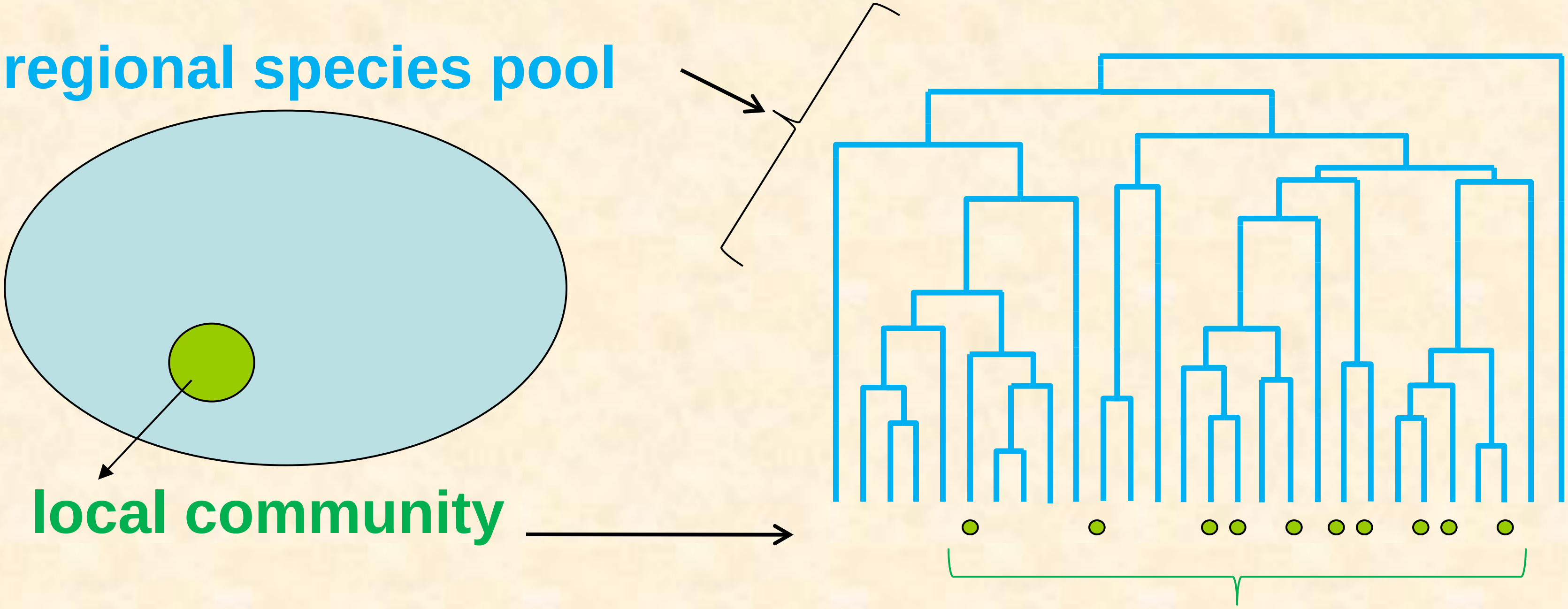
→ assess distribution of P_{ST} for 1000 permutations

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

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

Community phylogenetic structure – the “species pool” approach (NRI, NTI indices)

C. Webb’s approach (Webb 2000, Webb et al. 2002):



regional species pool

local community

Phylogenetic clustering

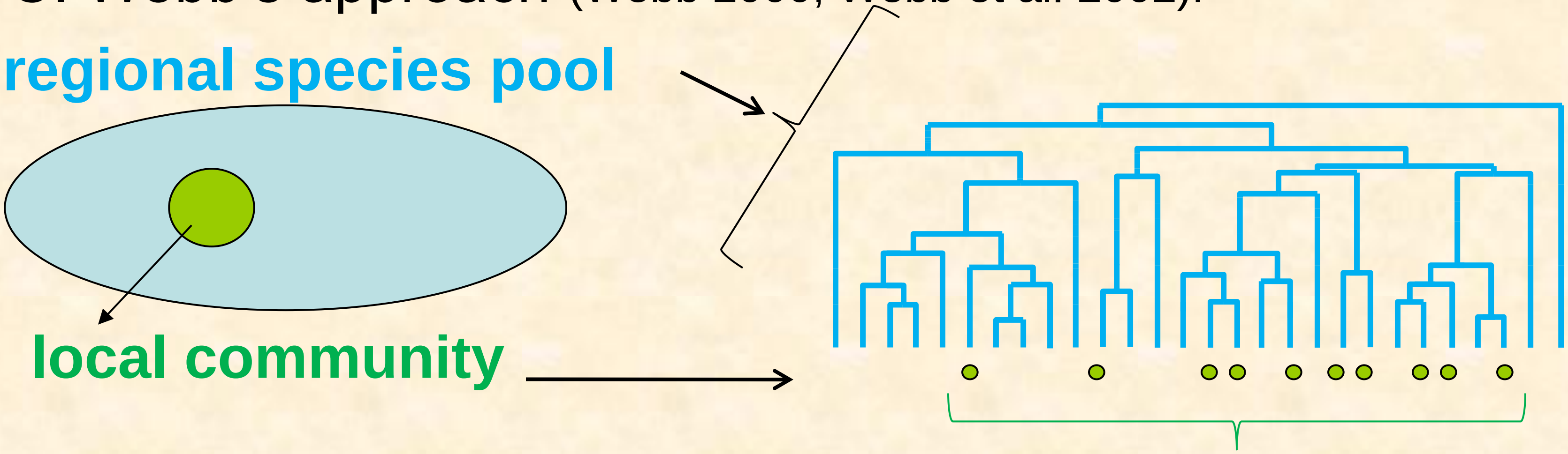
Are species in the local community more / less related than random species from the regional pool?

→

Compare the mean phylogenetic distance (MPD) within local community with distribution of MPD for ‘random’ communities generated by a null model

Community phylogenetic structure – the "species pool" approach (NRI, NTI indices)

C. Webb's approach (Webb 2000, Webb et al. 2002):



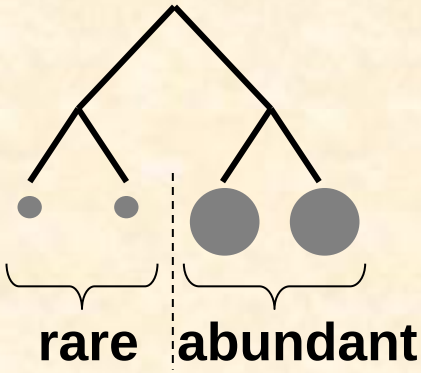
Phylogenetic clustering

Net Relatedness Index: $$NRI = -\frac{MPDw - mean(MPDrandomized)}{SD(MPDrandomized)}$$

Randomization: different null models are possible, most often it consists in random sampling from the species pool or in random permutations of the species across the phylogeny (both are equivalent when applied on a single local community).

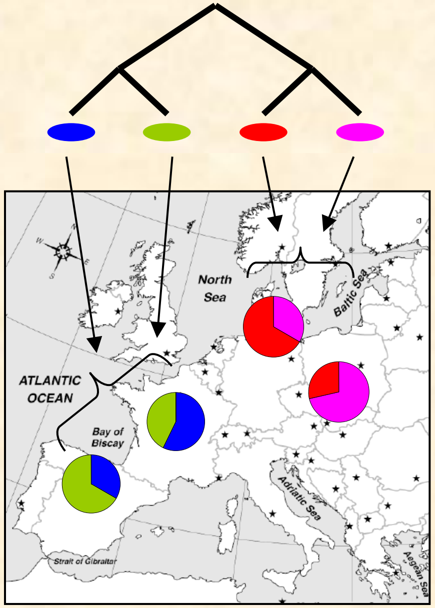
2 aspects of community phylogenetic structure (CPS)

species abundance CPS

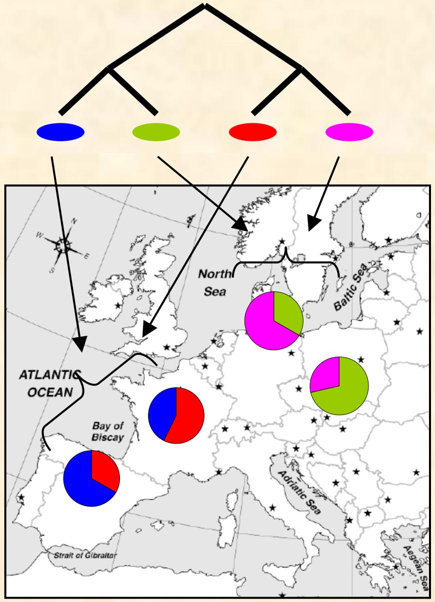


phylogenetic clustering

spatial CPS = **phylogenetic turnover**



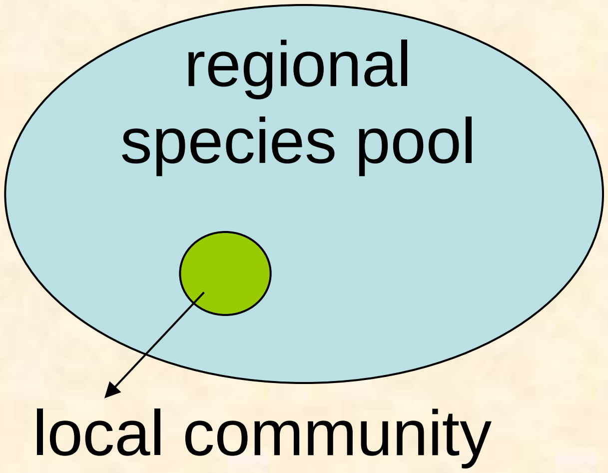
phylogenetic clustering



phylogenetic overdispersion

2 ways of investigating CPS

Species pool based


regional species pool

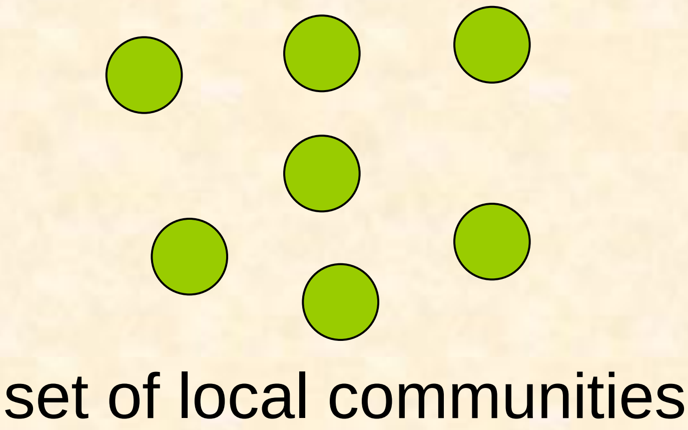
local community

Are species in the local community more / less related than random species from the regional pool?

Difficulties:

- How to delimit a species pool?
- How to account for differences in species abundances?
- How to distinguish species abundance from spatial CPS?

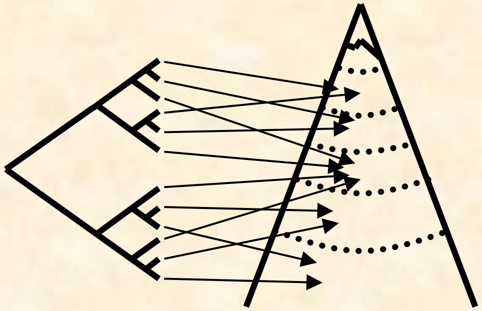
Sample based


set of local communities

Are species within local communities more / less related than species from distinct local communities?

- Describe only spatial CPS (phylogenetic turnover).
- Pattern specific for a given sample of local communities.
- Pairwise measures to regress on explanatarory variables

Data exploration



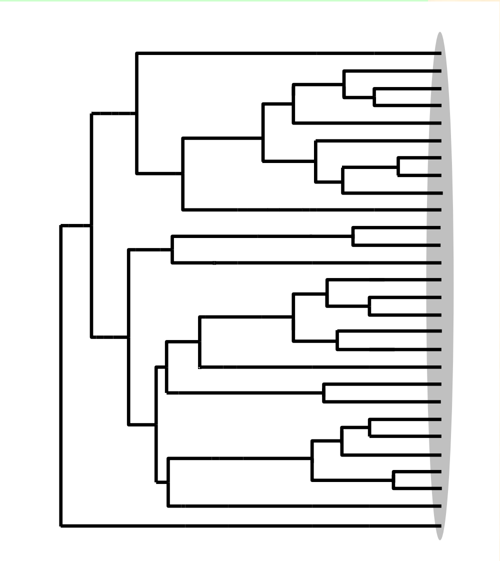
1. Pairwise analyses (between plots):

→ compute P_{ST} or Π_{ST} for each pair of plots

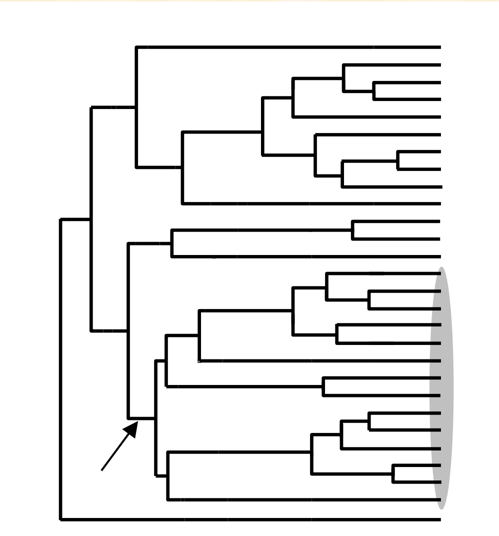
→ check correlations between P_{ST} or Π_{ST} and { geographic distance
ecological distance

2. Partial tests

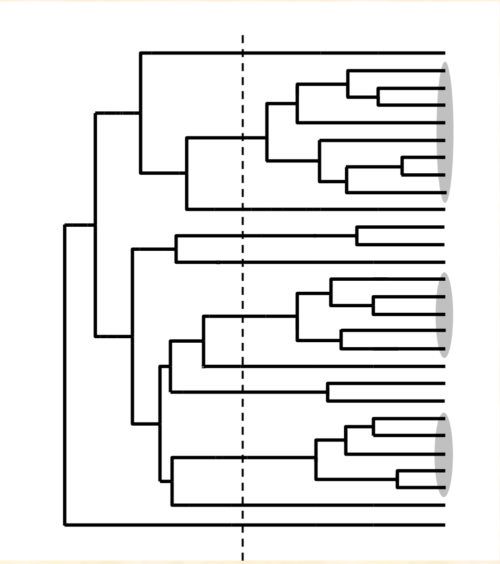
→ randomize only some parts of the phylogenetic tree



Complete randomization



Randomiz. within one clade



Randomiz. within clades younger than age threshold

Case studies in tropical forest plant communities

1. Impact of **dispersal limitation *versus* ecological gradients** → species and phylogenetic turnover in Central African inselberg vegetation

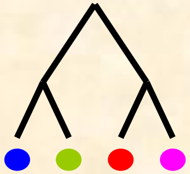
2. Impact of **ecological gradients *versus* biogeography** → phylogenetic turnover along rainfall gradients in Western Ghats and Panama

3. Integrating **phylogeny** and **traits** → **phylogenetic *versus* functional** structures of rainforests from French Guiana

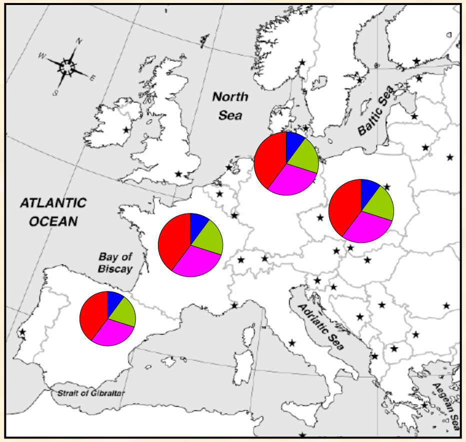
4. Phylogenetic **overdispersion** due to multiple recent radiations → forest communities from Reunion island

5. Phylogenetic structure at the scale of **inter-individual competition** → fine-scale spatial phylogenetic turnover in 50-ha plots

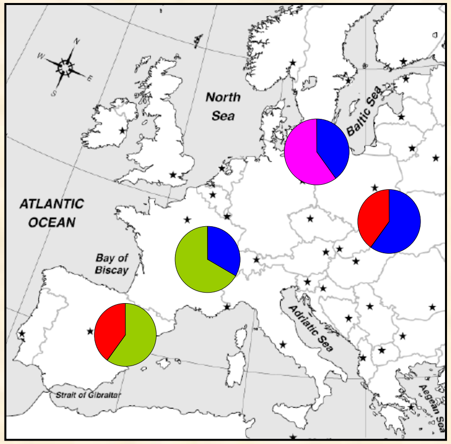
1. Impact of dispersal limitation vs ecological gradients on species turnover and phylogenetic turnover



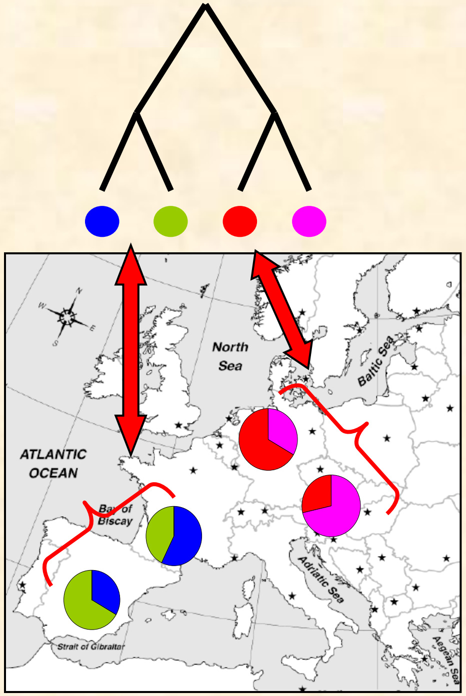
Phylogenetic tree
for 4 species



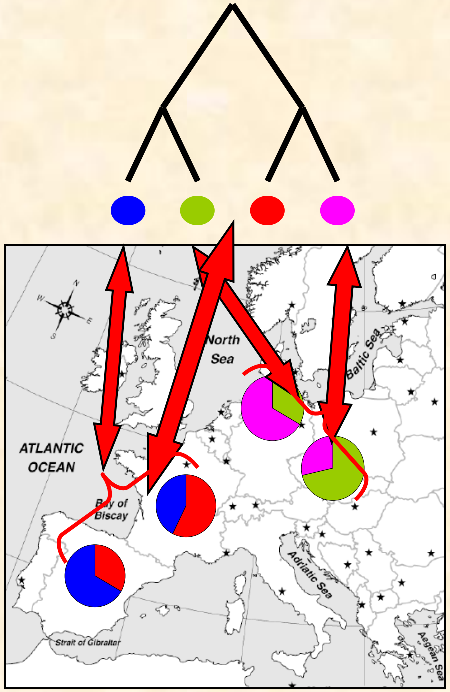
No species turnover
&
No phylo. turnover



Species turnover
but
No phylo. turnover



Species turnover
+
Phylo. clustering

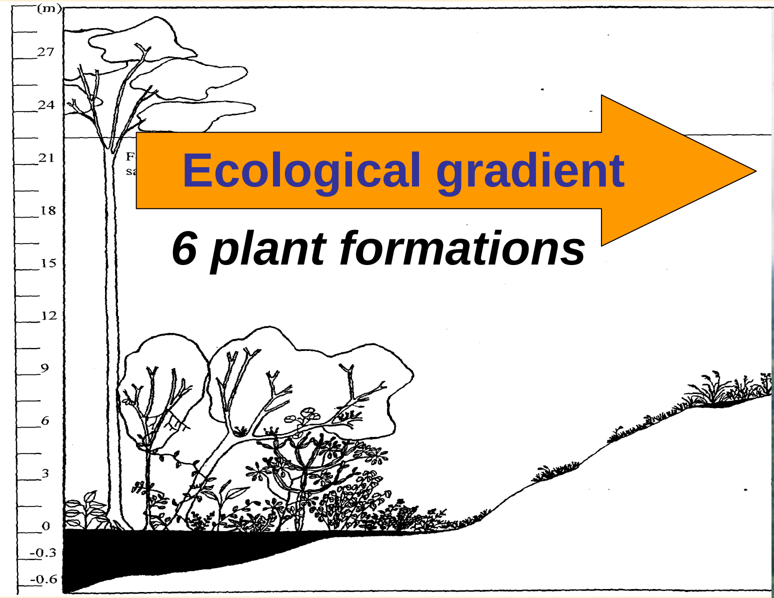


Species turnover
+
Phylo. overdisp.

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

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

Inselberg vegetation in Equatorial Guinea

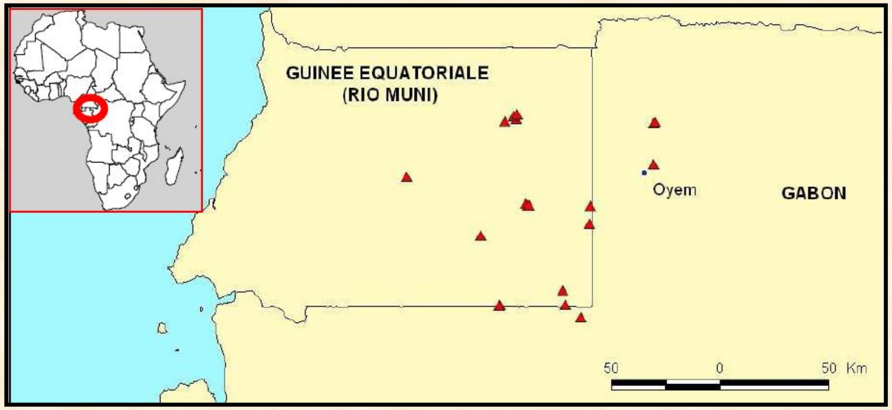


Ecological gradient

6 plant formations

Geographical isolation

inselberg ⇔ island

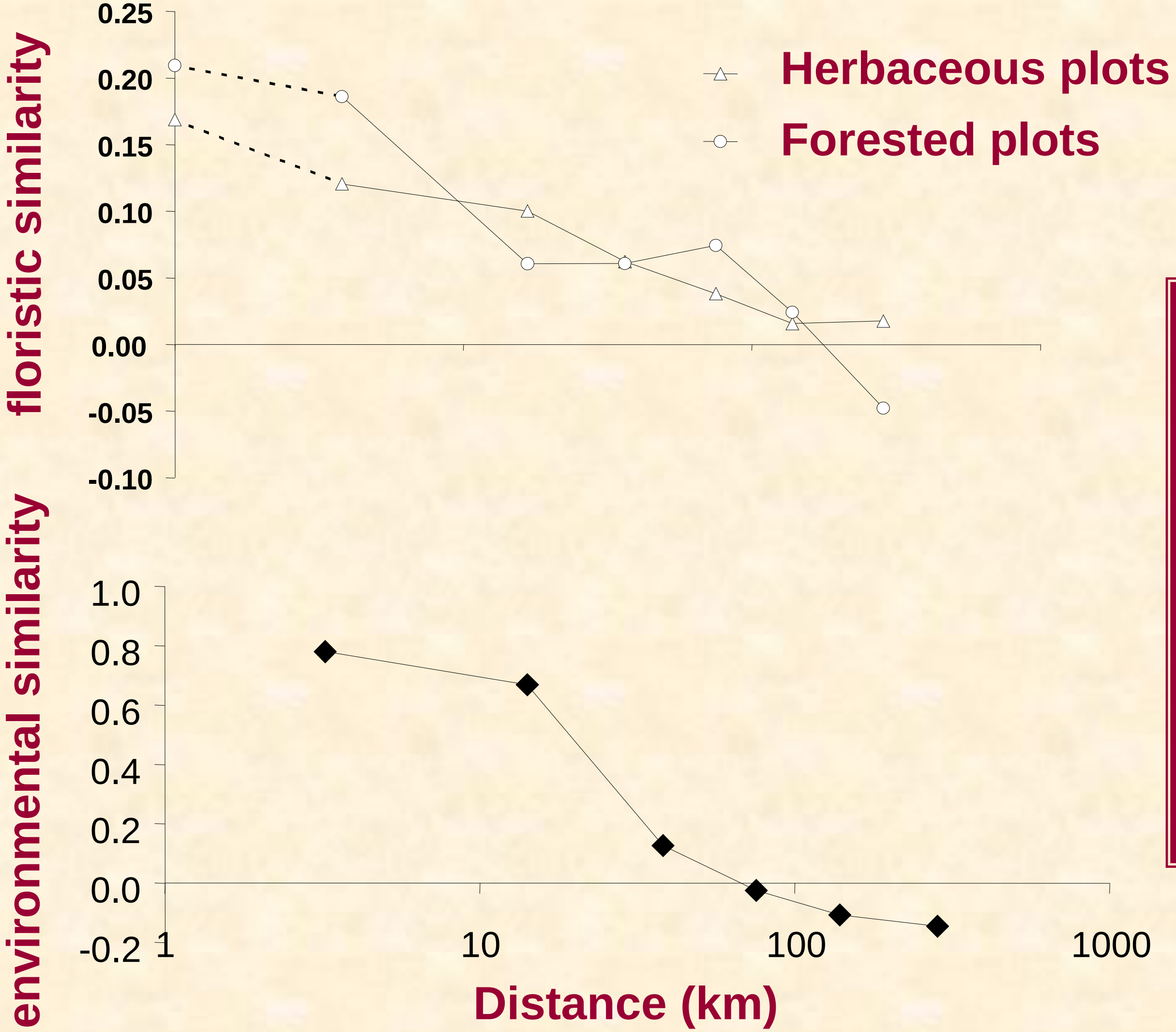


(ca. 300 floristic plots on 21 inselbergs)

Parmentier & Hardy 2009 (Ecography 32: 613-622)

Regional scale: subregional species pools

Spatial autocorrelation



Species turnover due to:

Regional scale deterministic factors (climate…) ?

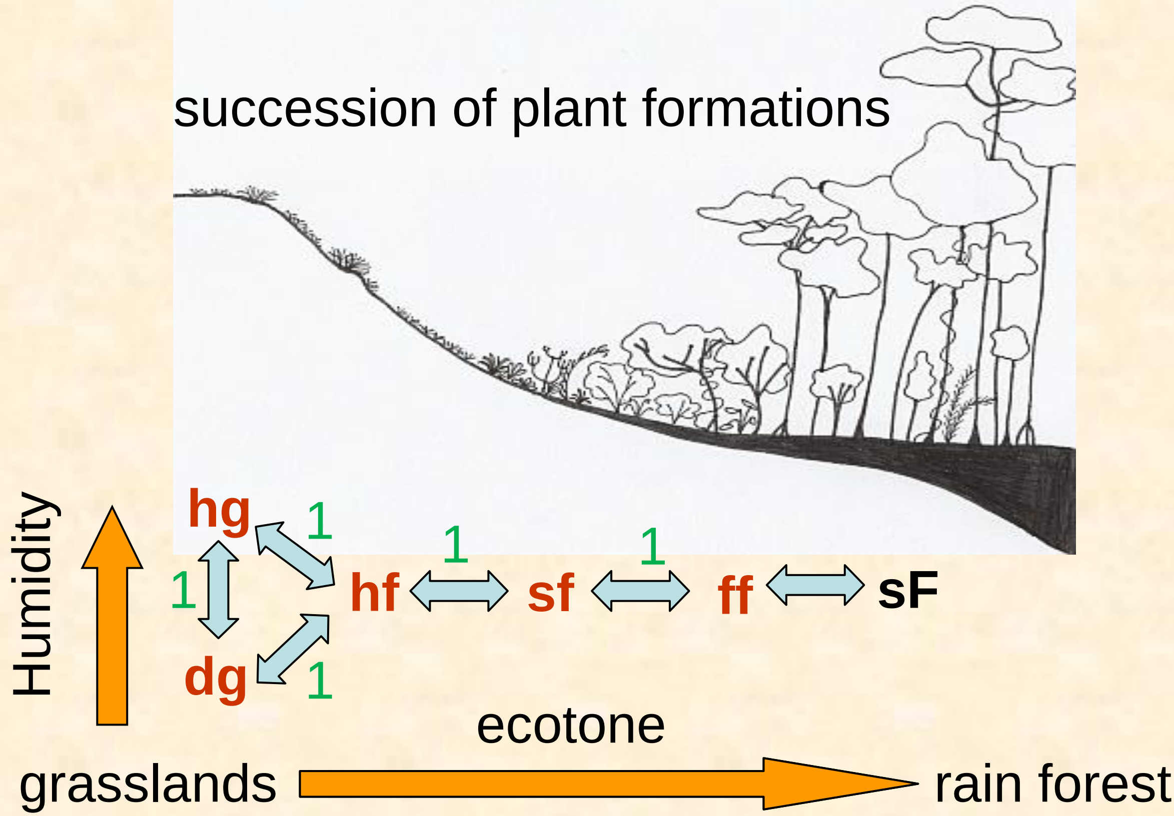
or

Dispersal limitation (and/or colonization history) ?

Parmentier *et al.* 2005
J Biogeography

Local scale: environmental constraints

Ecotone : soil depth, luminosity, humidity…

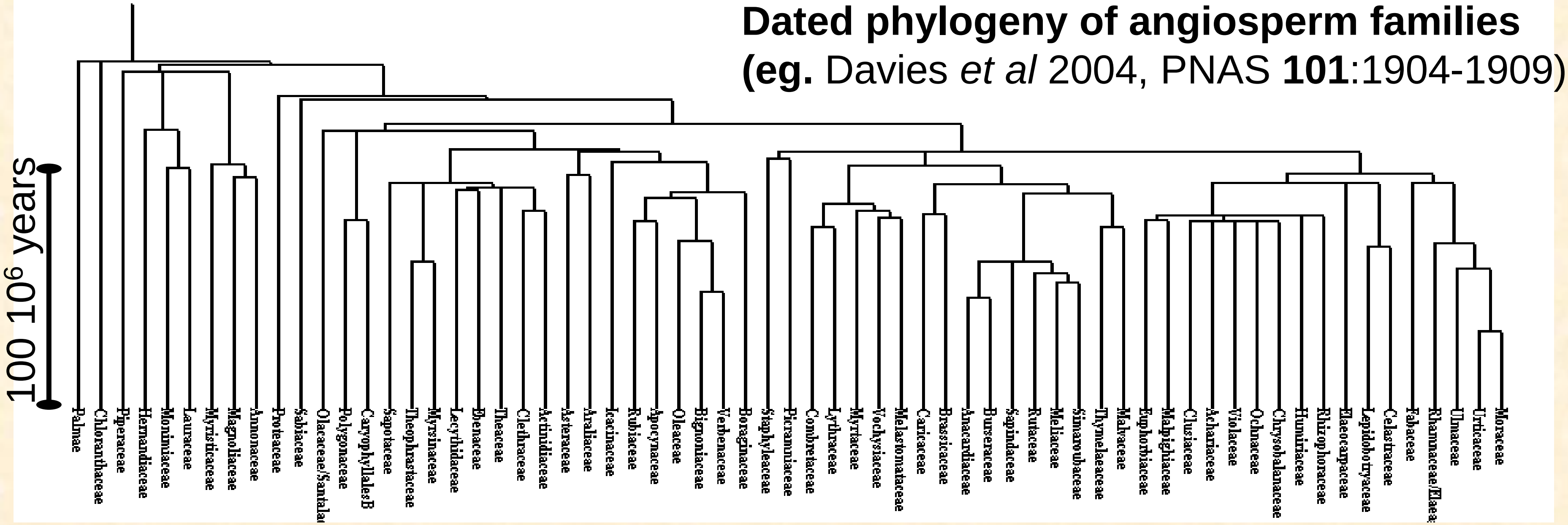

succession of plant formations

Ecological distance =
number of steps along the ecotone

Species phylogeny

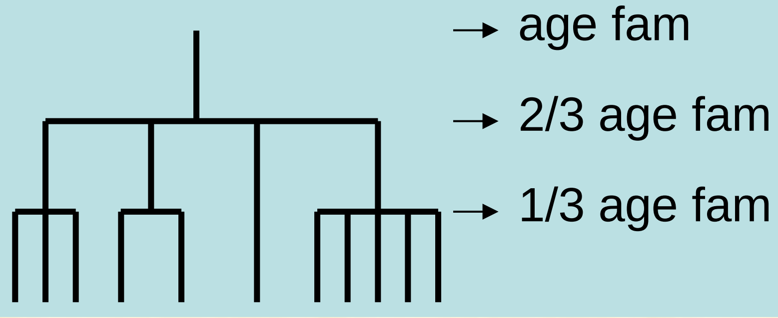
-> software Phylomatics (http://www.phylodiversity.net/phylomatic/phylomatic.html)

⇒ requires a list of species with their families (APG)

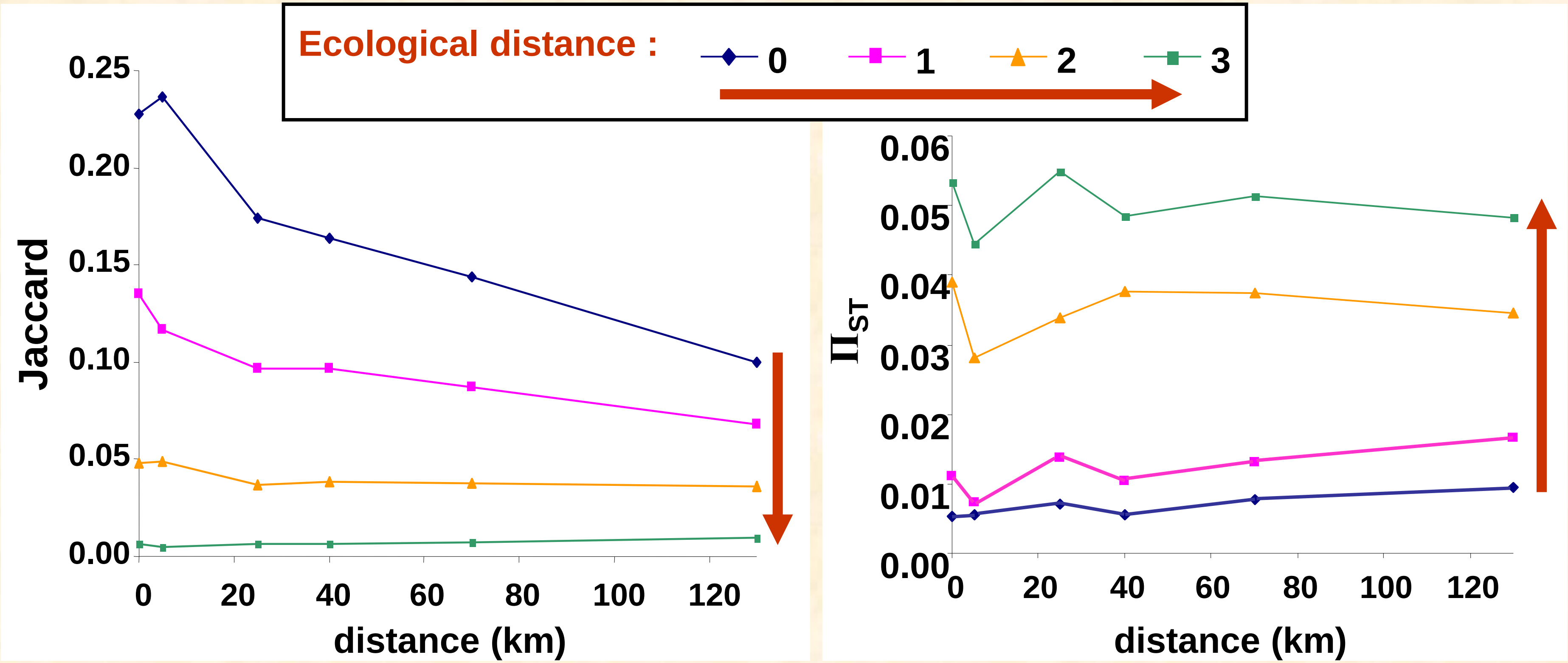


Dated phylogeny of angiosperm families
(eg. Davies *et al* 2004, PNAS **101**:1904-1909)

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 ⇔ ecological differentiation
  $\not\Leftrightarrow$ dispersal limitation at regional scale

⇨ disentangle dispersal limitation *versus* ecological filtering

Parmentier & Hardy 2009 (Ecography 32: 613-622)

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 of 1ha
Area 50km x 60km

Rainfall:
1500-3300mm
Elevation :
50-400m

data **French Institute Pondicherry**

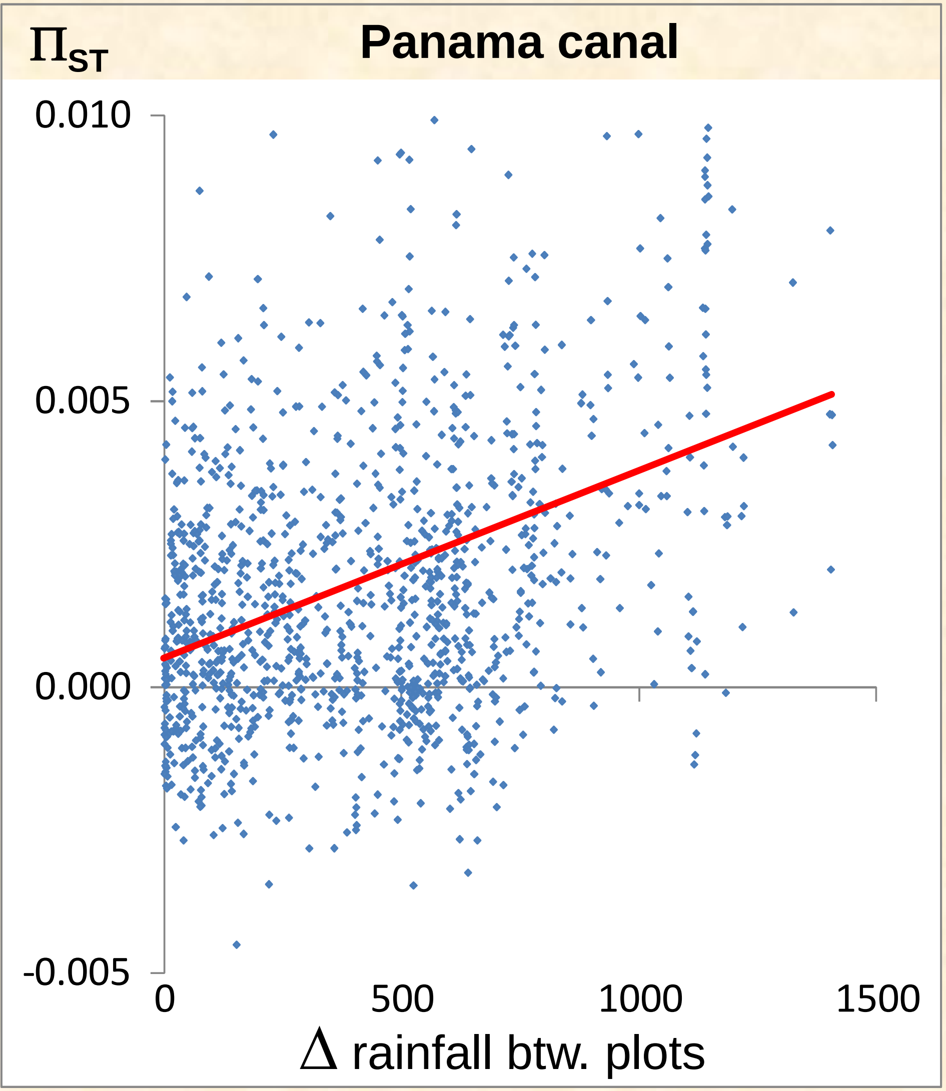
Western Ghats

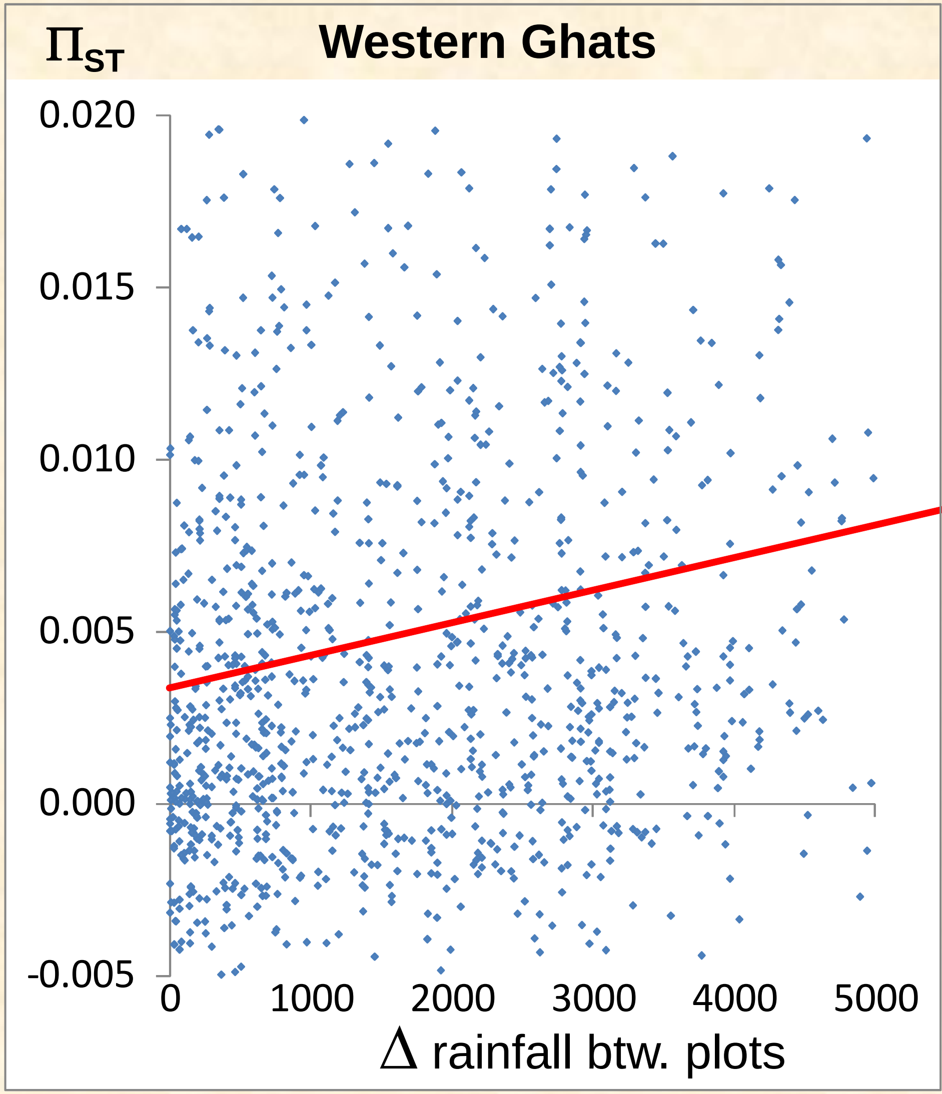
50 plots of 1ha
Area 50km x 200km

Rainfall:
1400-6000mm
Elevation:
50-1050m

Hardy et al. 2012 (Glob. Ecol. Biogeogr. 21:1007–1016)

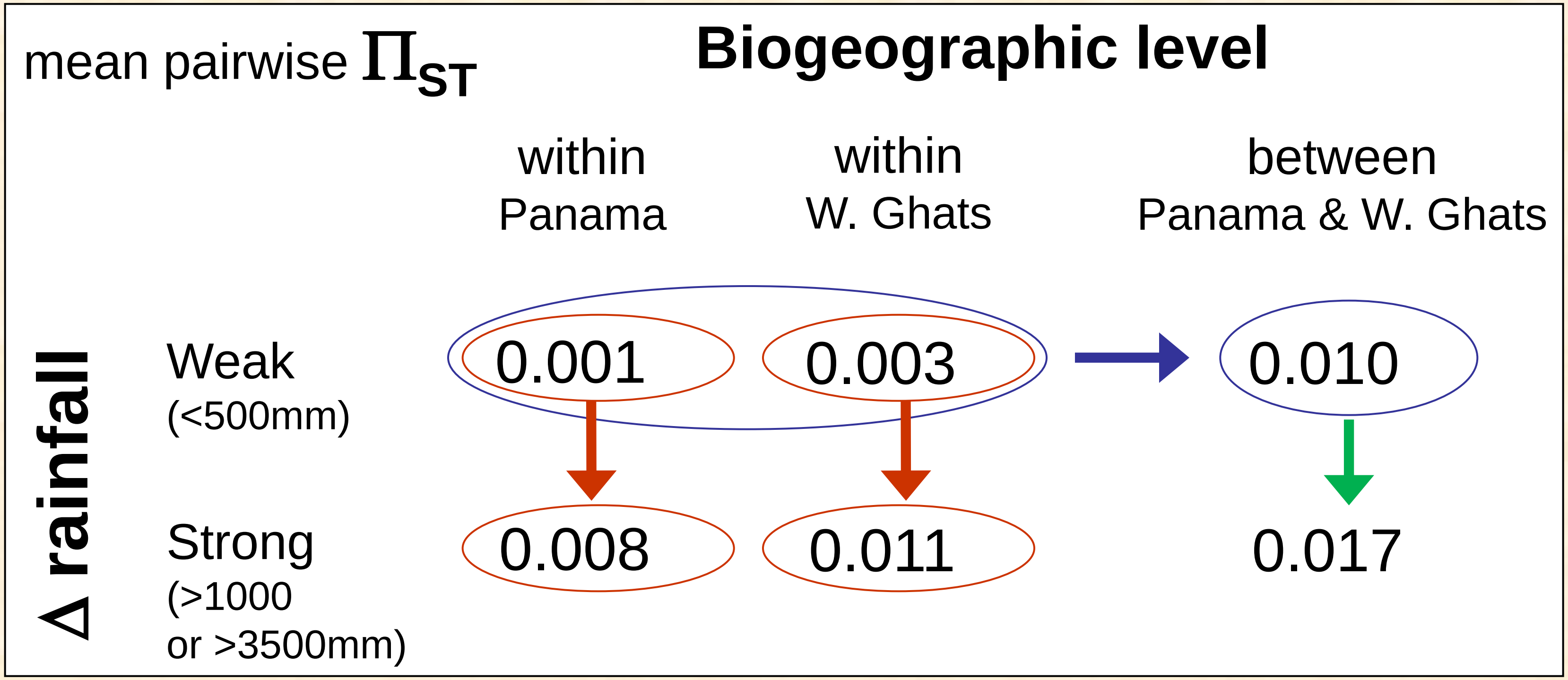
Phylogenetic turnover at regional scale





➯ Phylogenetic clustering within plots mostly explained by rainfall differences

Phylogenetic turnover
impact of ecological gradients vs biogeography



mean pairwise Π_{ST}

Biogeographic level

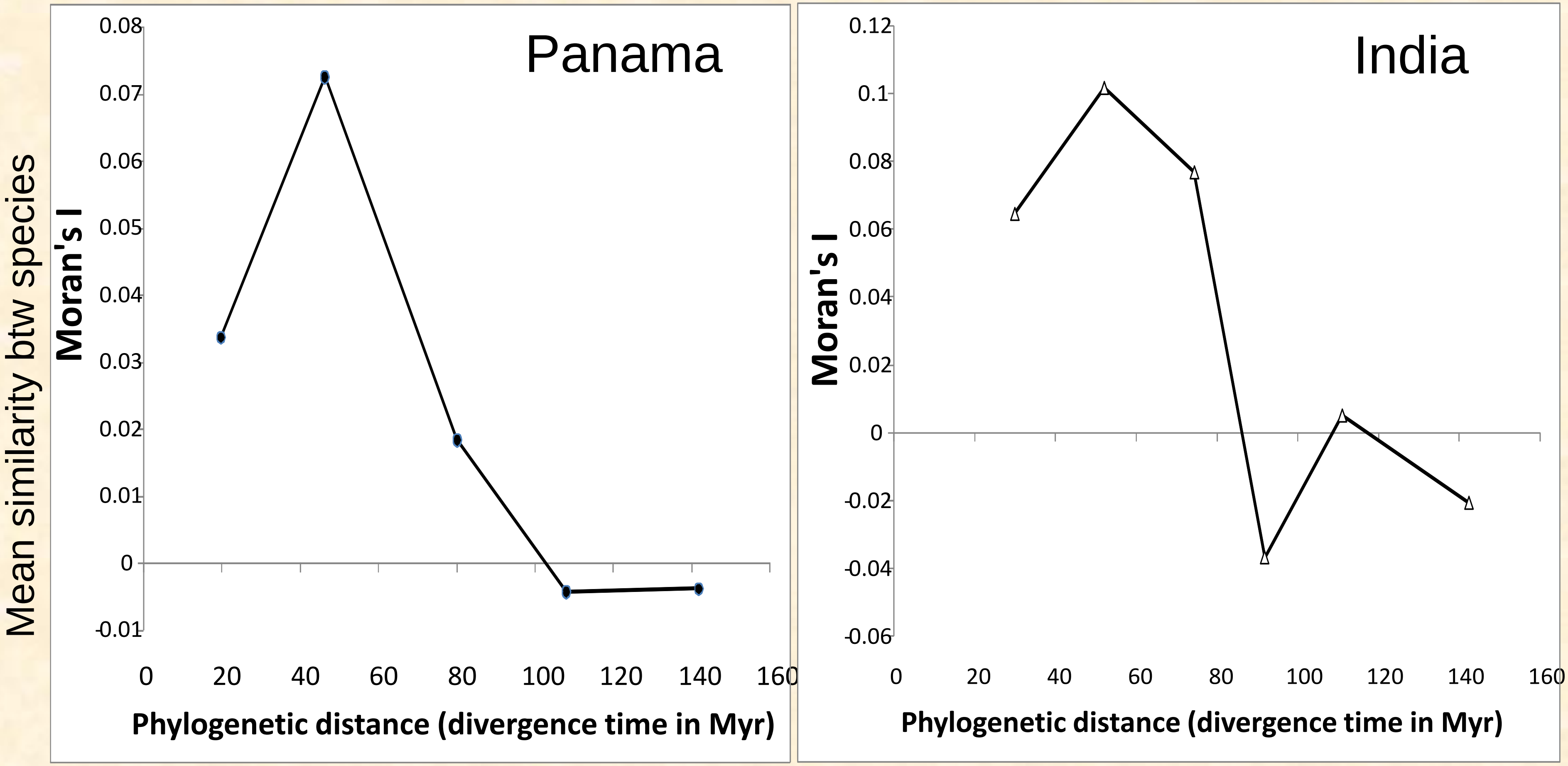
Δ rainfall	within Panama	within W. Ghats	between Panama & W. Ghats
Weak (<500mm)	0.001	0.003	→ 0.010
Strong (>1000 or >3500mm)	0.008	0.011	0.017

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

Impacts on Π_{ST} of {biogeography (inter-continental) / 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'

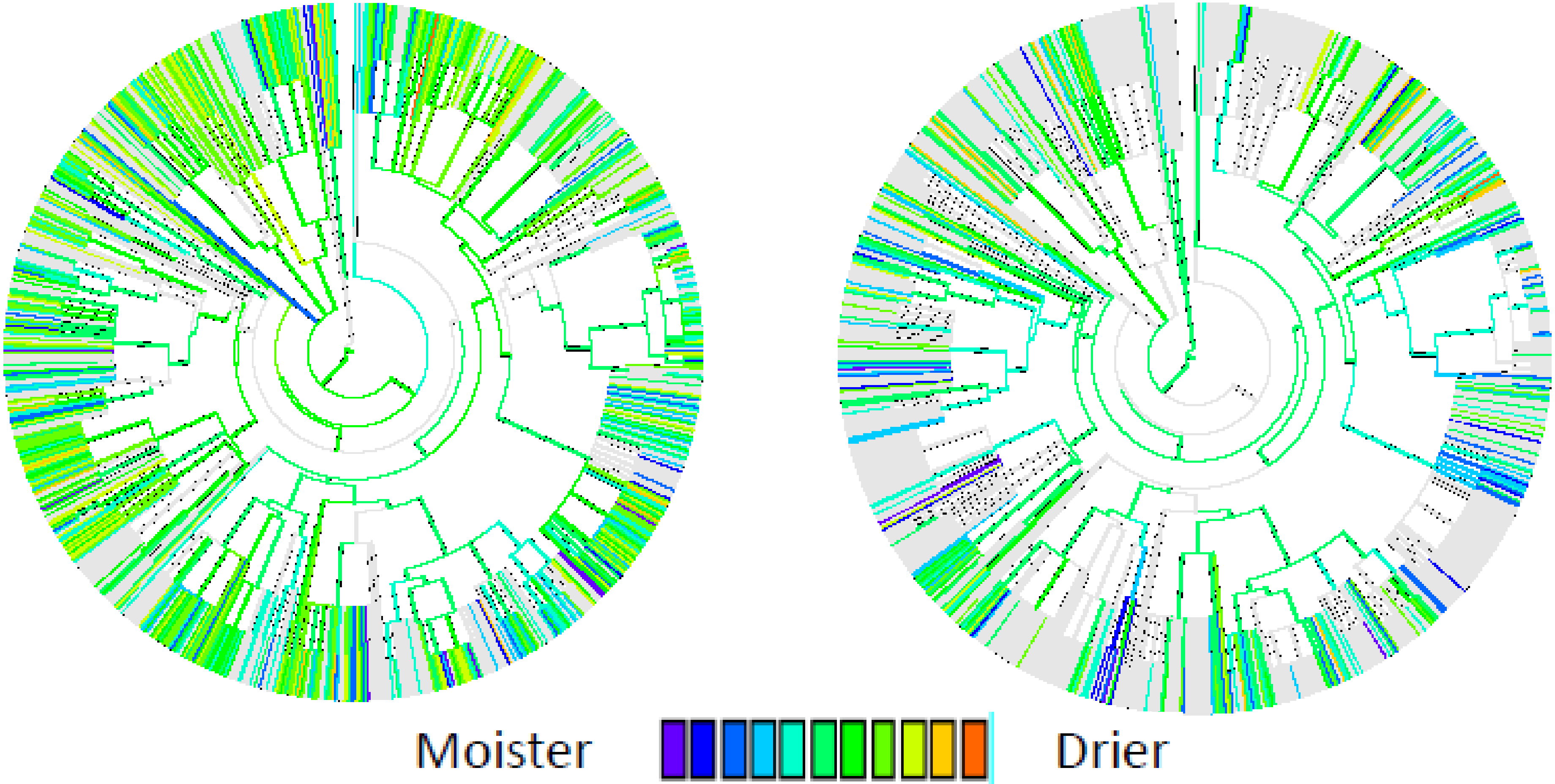
Reconstruction of ancestral niche along the phylogenies

- Mesquite software

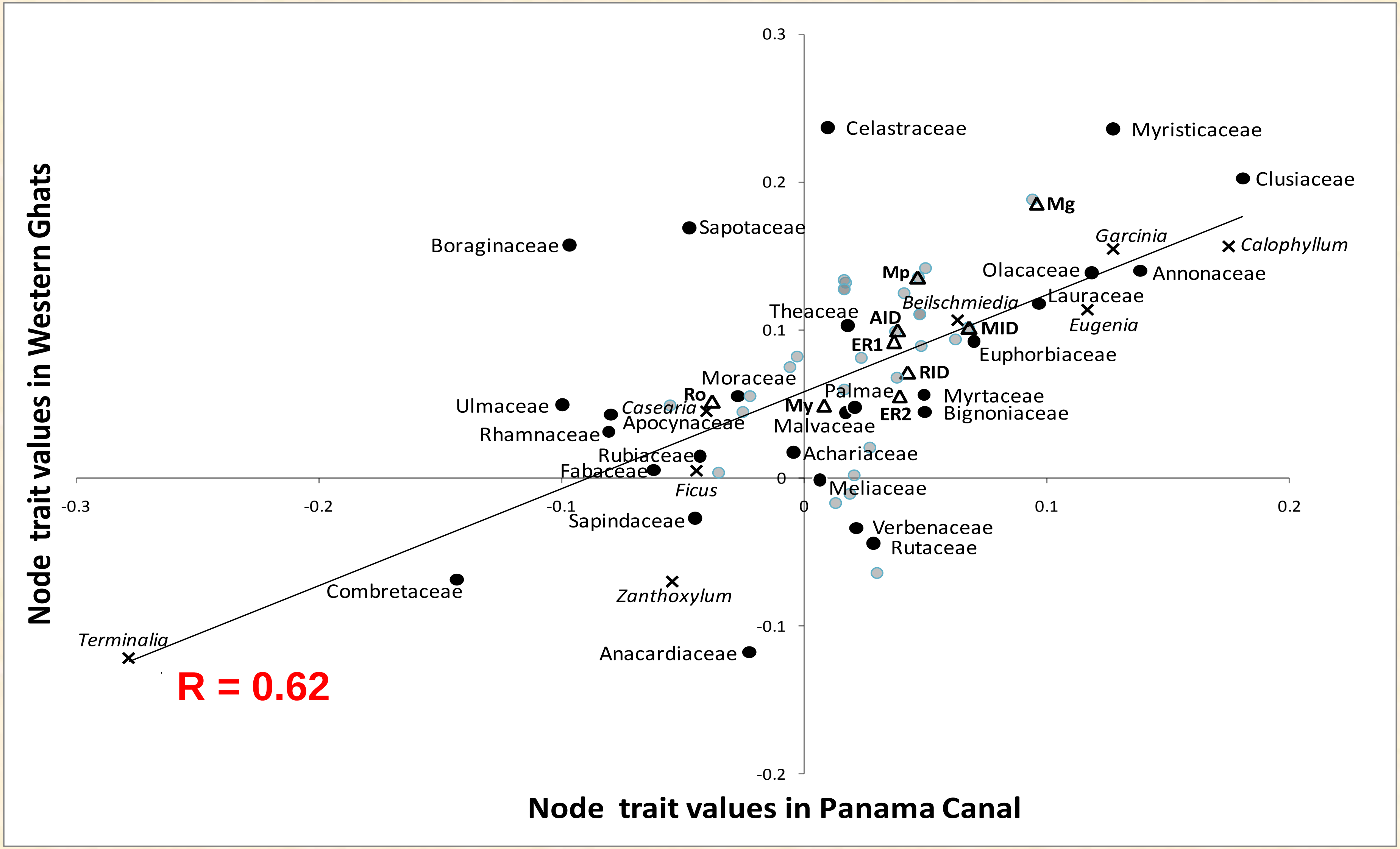
Panama

India

No shared species but
many shared clades



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



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

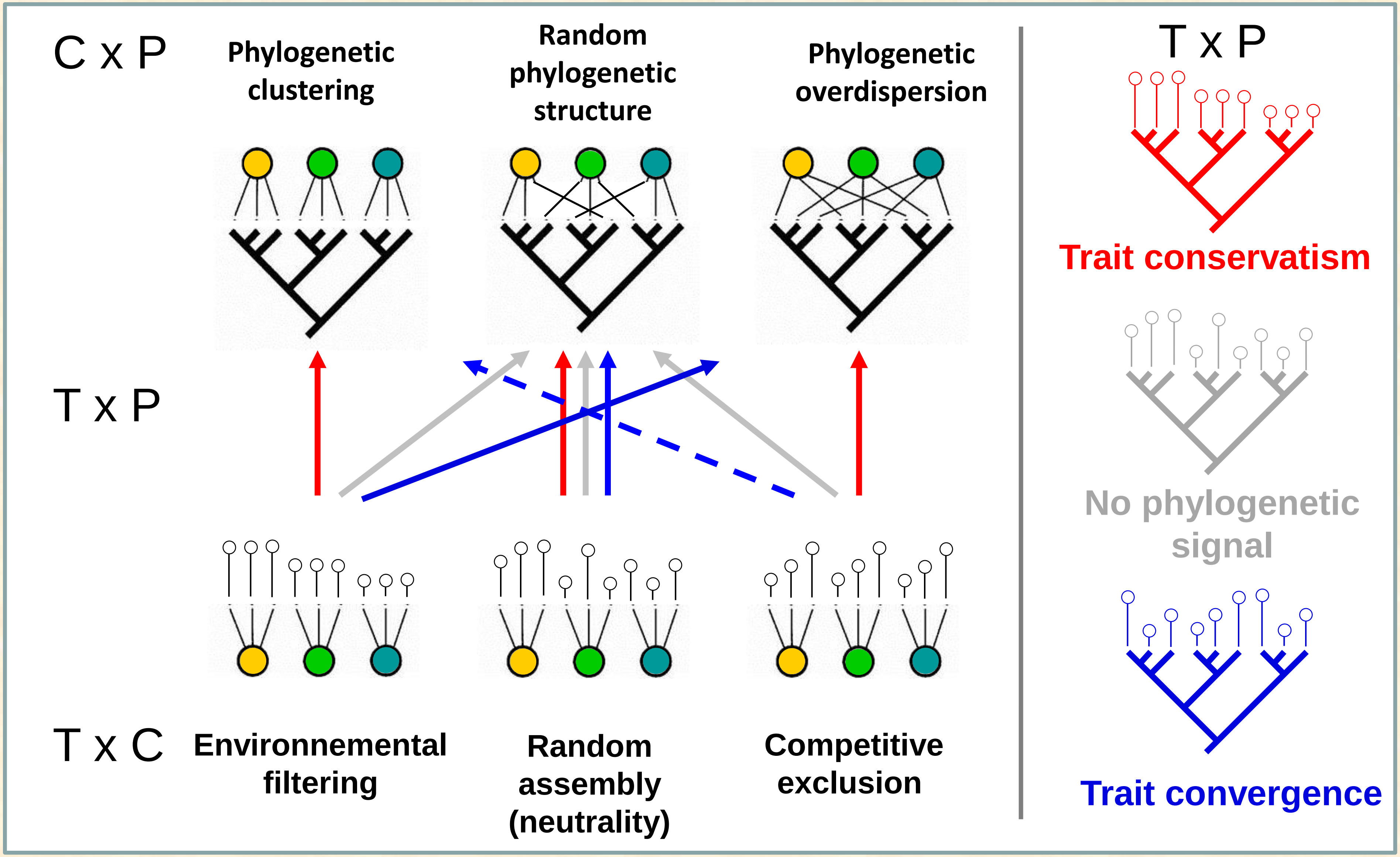
Conclusion 2

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

Hardy et al. 2012 (Glob. Ecol. Biogeogr. 21:1007–1016)

3. Integrating **phylogeny** and **traits**



Ideally, all levels should be taken into account

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

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

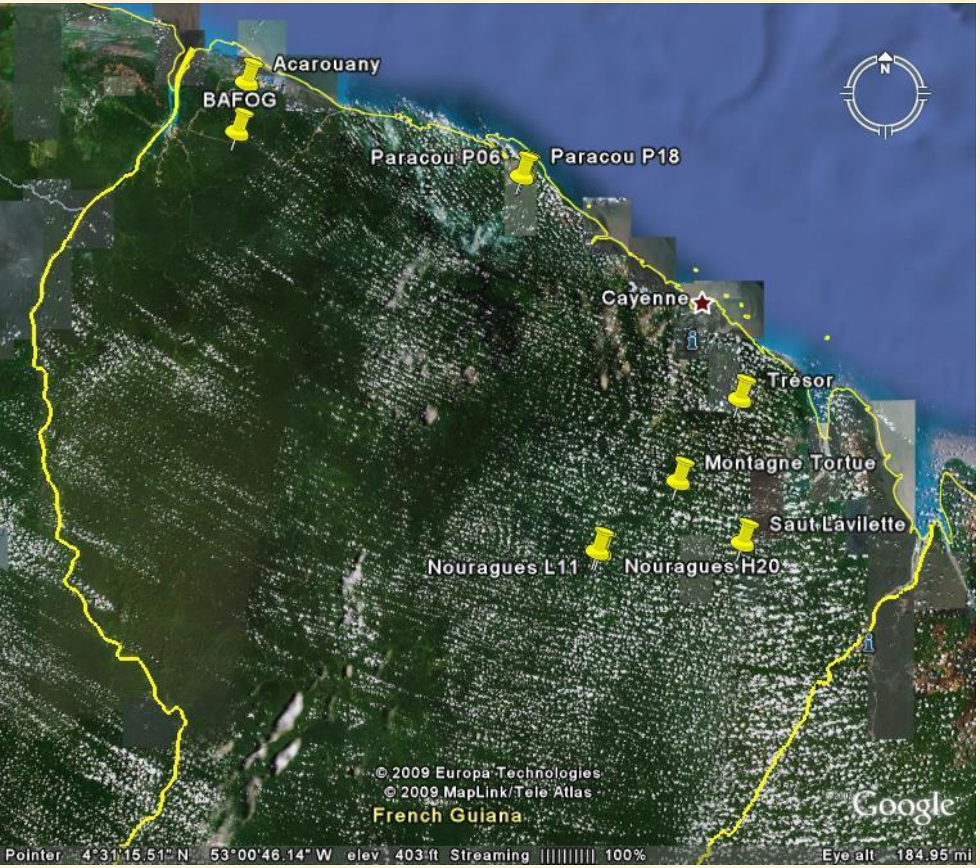
Guyane field teams (Jean-Yves Serein, Jean-Yves Goret, Elodie Courtois, Pierre-Alain Blandinières, Pascal Pétronelli, Mailyn Gonzalez, Odile Poncy, Julien Engel...)

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**	

Baraloto et al. (2012, Journal of Ecology 100:690-701)

Traits Measured

Leaf structure traits

- Leaf toughness
- Leaf tissue density
- Leaf area
- Specific leaf area

Leaf chemistry traits

- N content
- C:N ratio
- NH_4 proportion
- P content
- K content
- leaf ^{13}C
- Chlorophyll content

Trunk and wood traits

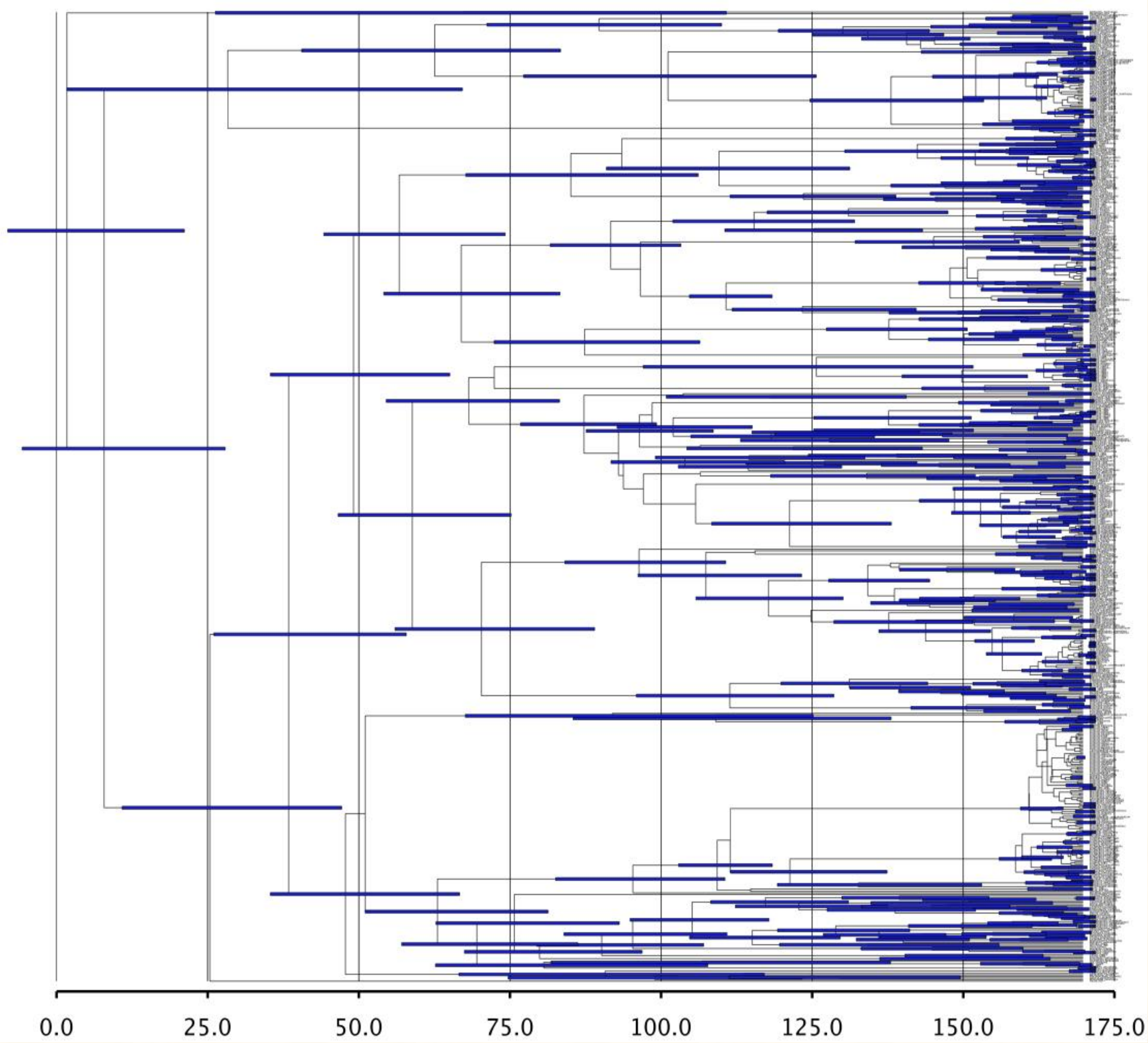
- Sapwood density
- Trunk moisture
- Bark thickness

Twig traits

- Twig wood density
- Twig bark thickness

Phylogeny generated for >600 species (*rbcL* and *matK*)

+ temporal calibration using relaxed molecular clock

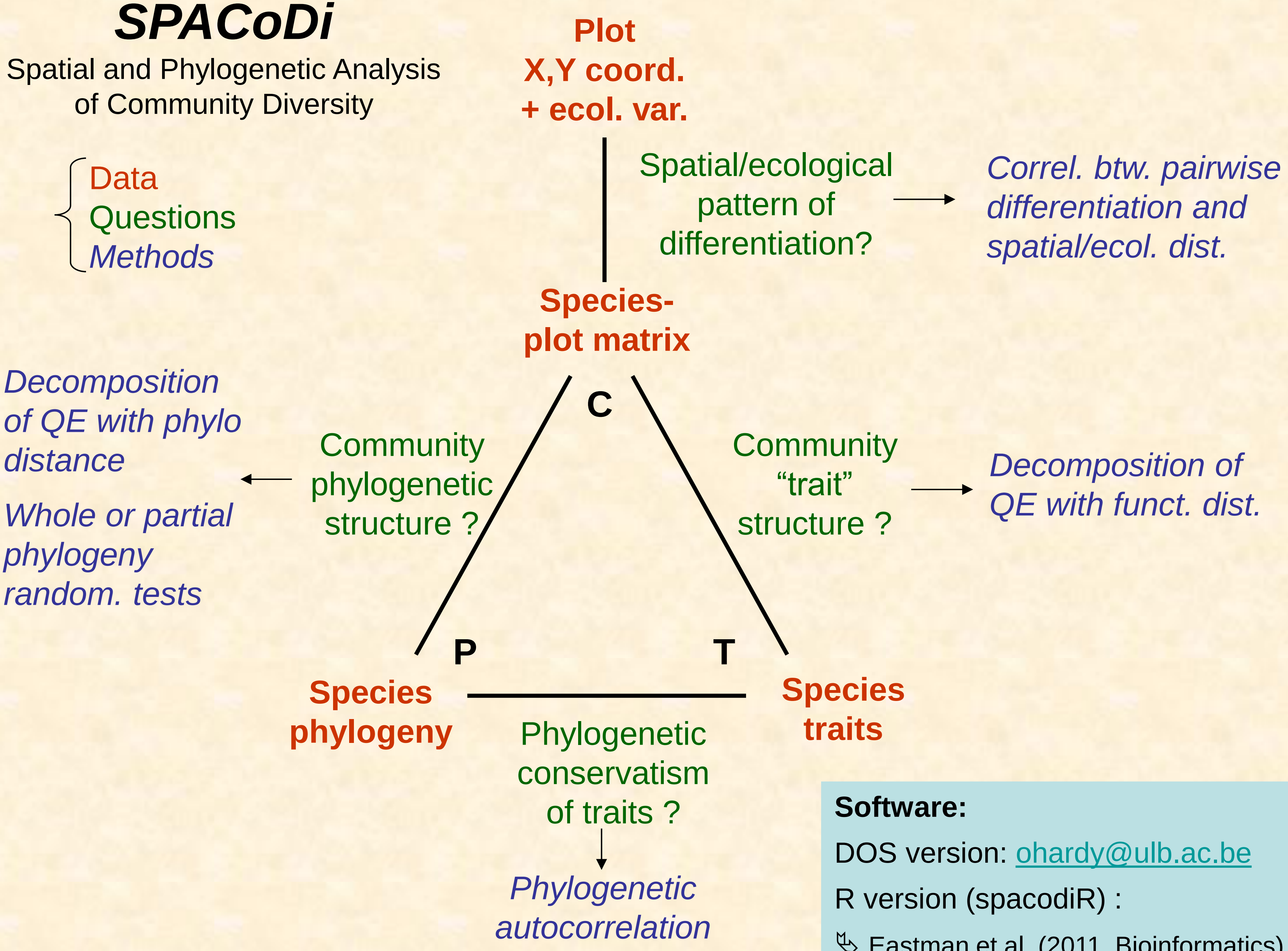


BEAST v1.53
Drummond and
Rambaut 2009

SPACoDi

Spatial and Phylogenetic Analysis
of Community Diversity

Data
Questions
Methods



Plot
X,Y coord.
+ ecol. var.

Spatial/ecological pattern of differentiation? → *Correl. btw. pairwise differentiation and spatial/ecol. dist.*

Species-
plot matrix

C

Decomposition of QE with phylo distance

Whole or partial phylogeny random. tests

← Community phylogenetic structure ?

Community “trait” structure ? → *Decomposition of QE with funct. dist.*

P

T

Species phylogeny

Species traits

Phylogenetic conservatism of traits ?

↓

Phylogenetic autocorrelation

Software:

DOS version: ohardy@ulb.ac.be

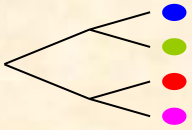
R version (spacodiR) :

➥ Eastman et al. (2011, Bioinformatics)

Comparing phylogenetic and functional community structures

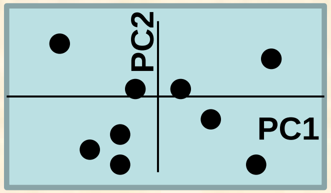
From a phylogeny

or



From species traits

ACP



phylogenetic
or
functional
distances between species

δ_{kl}

	🔵	🟢	🔴	🟣
🔵	0	1	2	3
🟢	1	0	2	2
🔴	2	2	0	1
🟣	3	2	1	0

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

or

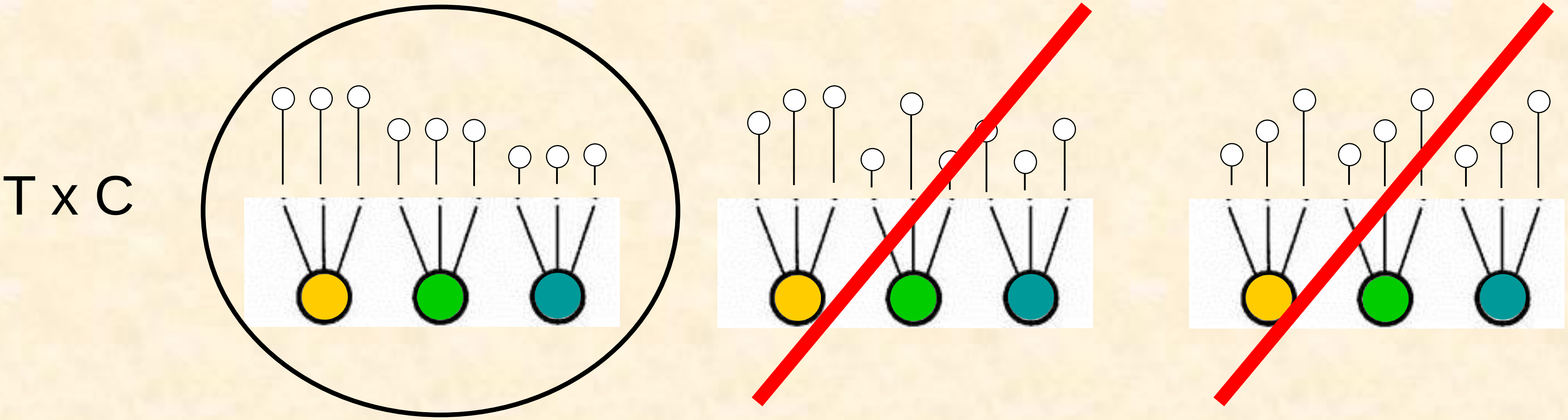
➡ $$T_{ST} = 1 - QE_w / QE_a$$

species + functional turnover

CxT : Functional structure of communities

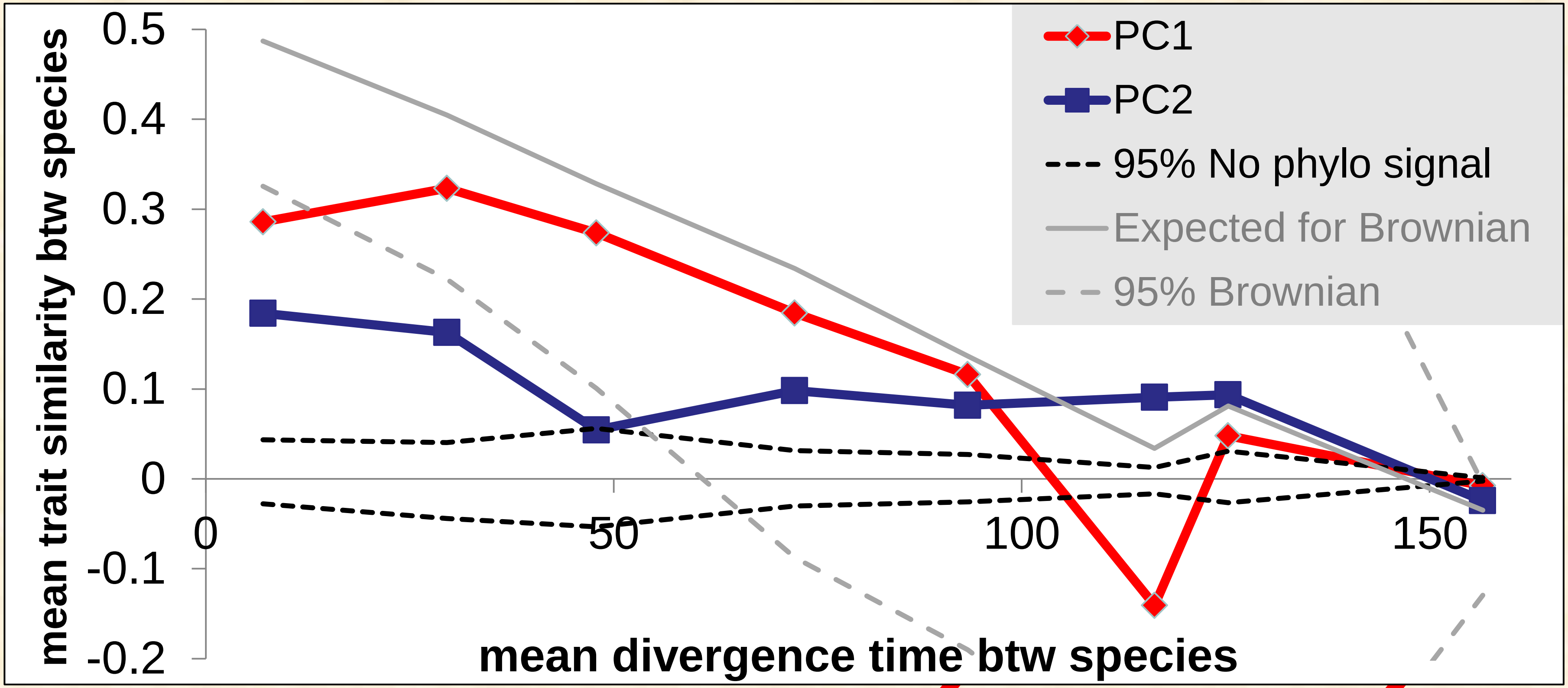
- T_{ST} = **0.0313** **>** [0.0076, 0.0172] under Ho
- τ_{ST} = **0.0119** **>** [-0.0010, 0.0014] under Ho

→ Functional clustering

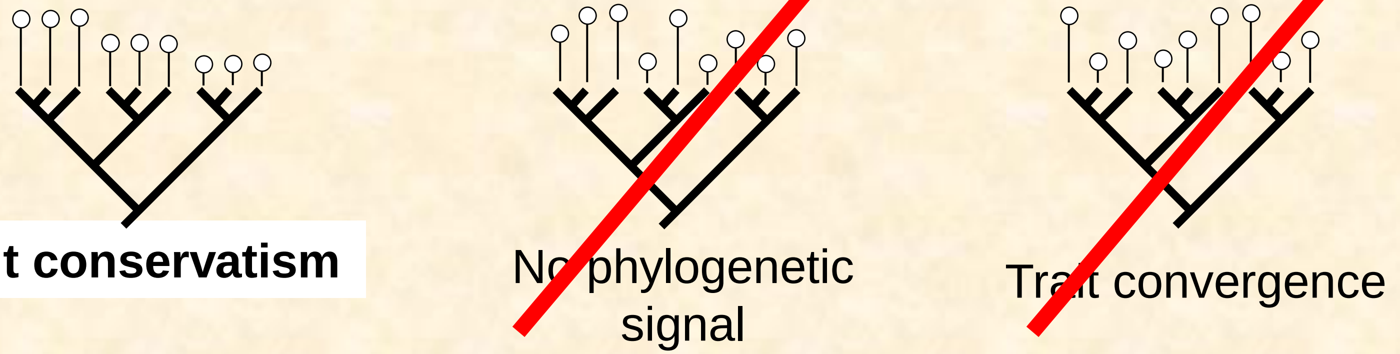


➥ **interpretation: habitat filtering dominates**

TxP : Phylogenetic structure of traits



T x P



PC1 conforms to Brownian motion model

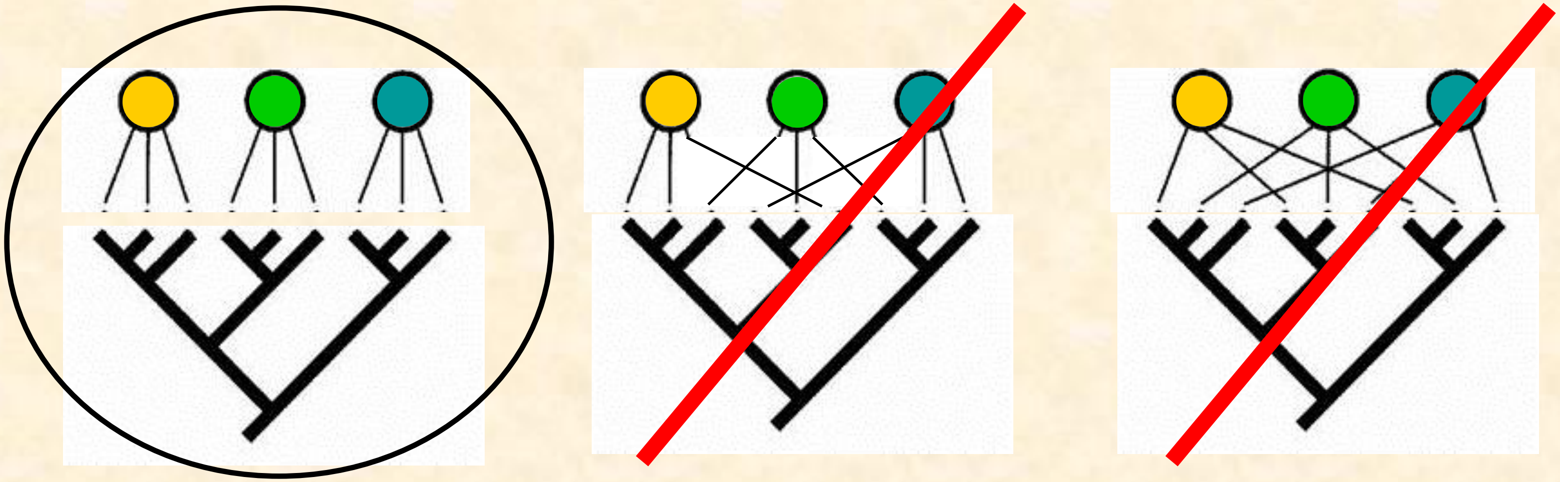
PC2 less conserved than Brownian (conform to Ornstein-Uhlenbeck model)

PxC : Phylogenetic structure of communities

- P_{ST} = **0.0246** **>** [0.0098, 0.0161] under Ho
- Π_{ST} = **0.0033** **>** [-0.0006, 0.0008] under Ho

→ **Phylogenetic clustering**

P x C



Phylogenetic clustering

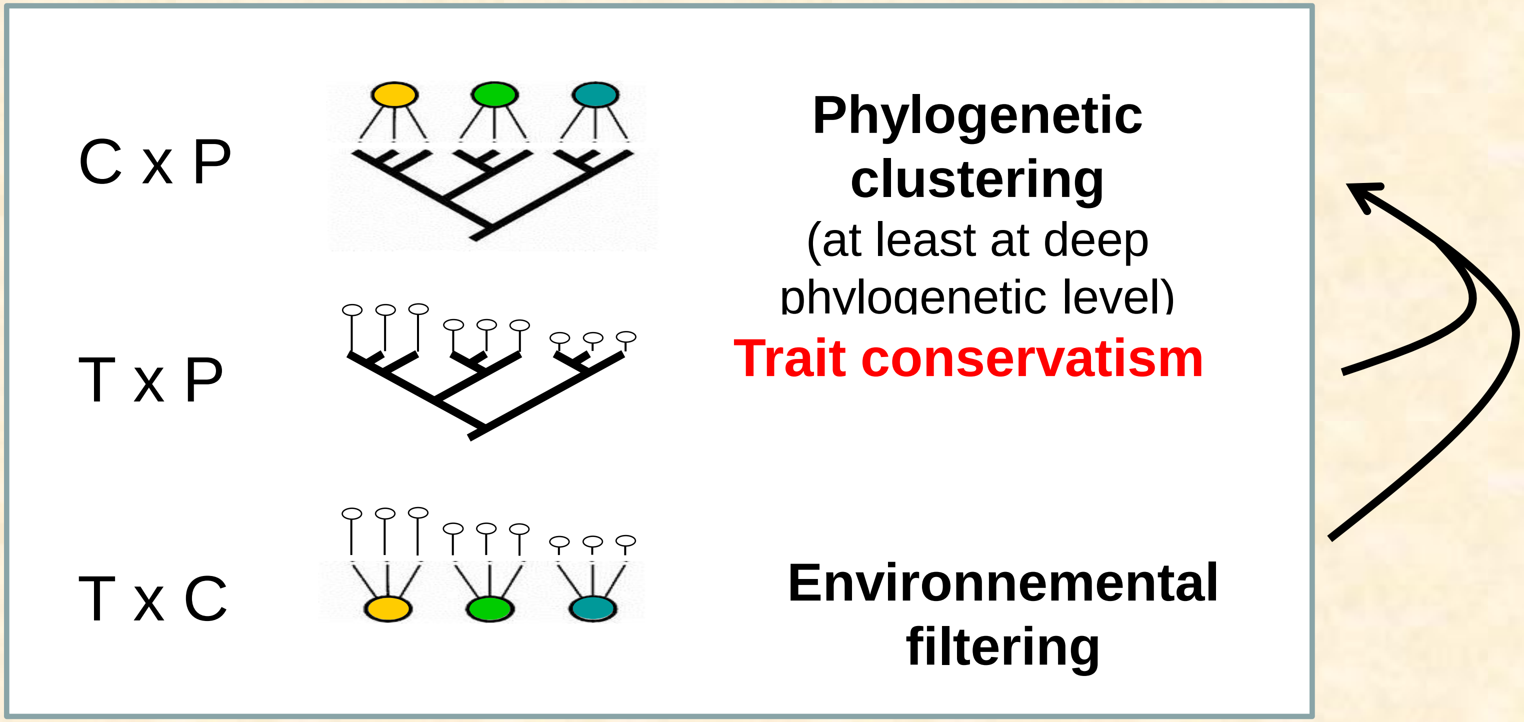
Random phylogenetic structure

Phylogenetic overdispersion

Conclusion 3

In continental tropical rainforests

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



C x P

Phylogenetic clustering
(at least at deep phylogenetic level)

T x P

Trait conservatism

T x C

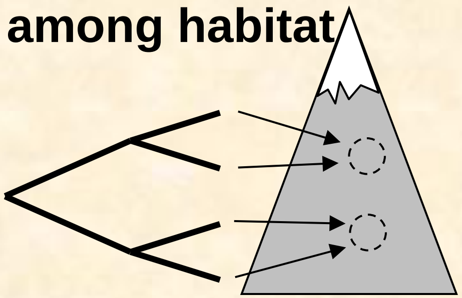
Environnemental filtering

Baraloto et al. (2012, *Journal of Ecology* 100:690-701)

Does phylogenetic overdispersion sometimes occur ?

Phylogenetic clustering

➾ case studies 1, 2, 3



environmental filtering

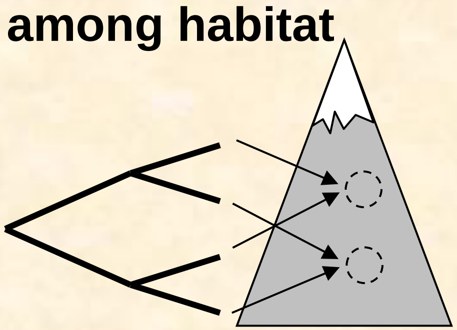
adaptation to ≠ elevation

+

habitat conservatism

Phylogenetic overdispersion

➾ case study 4 ?



environmental filtering

adaptation to ≠ elevation

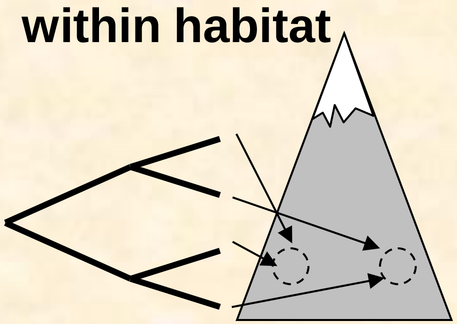
+

habitat convergence

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

Phylogenetic overdispersion

➾ case study 5 ?



competitive exclusion

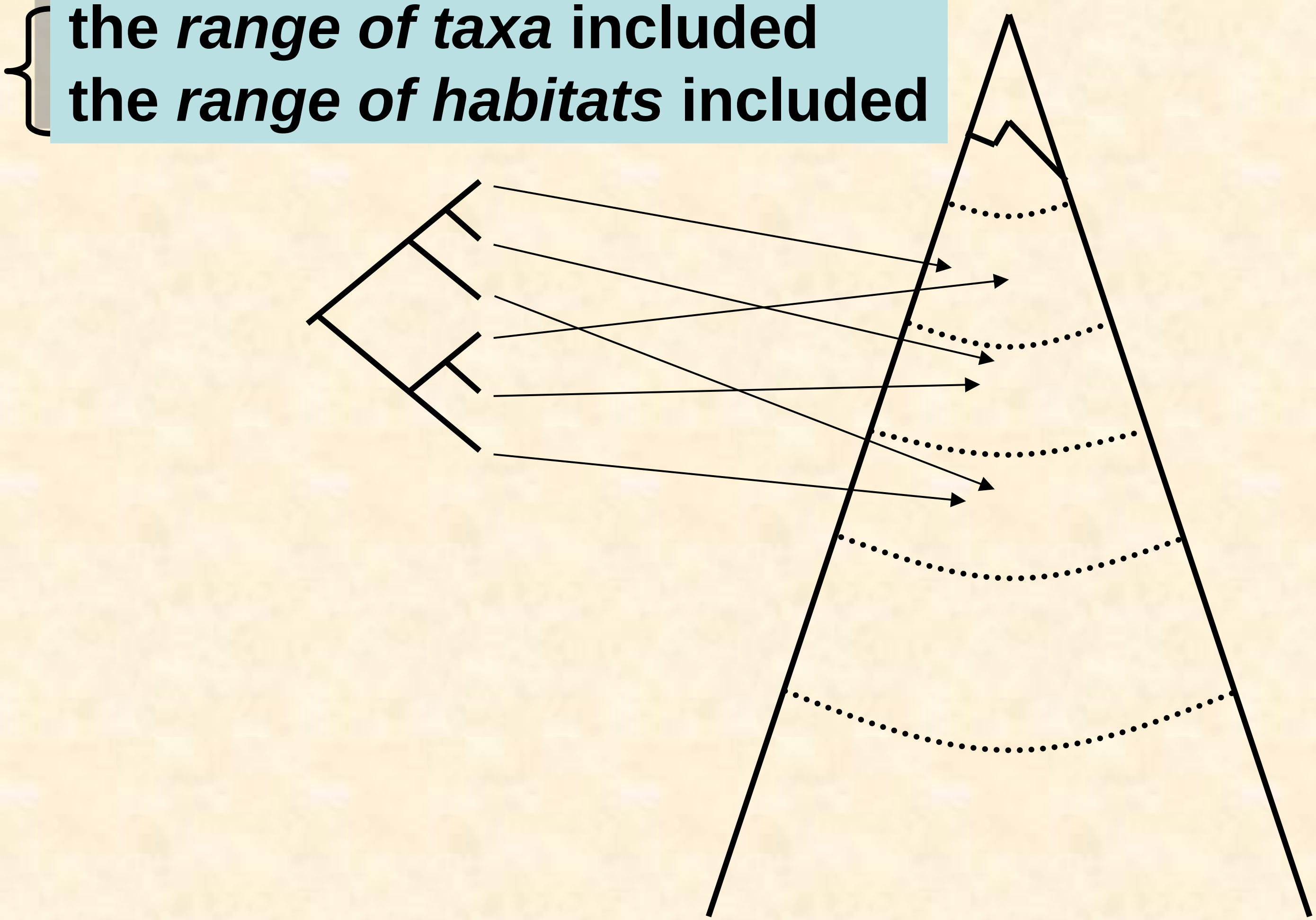
+

niche conservatism

→ sister species cannot coexist because of niche overlap

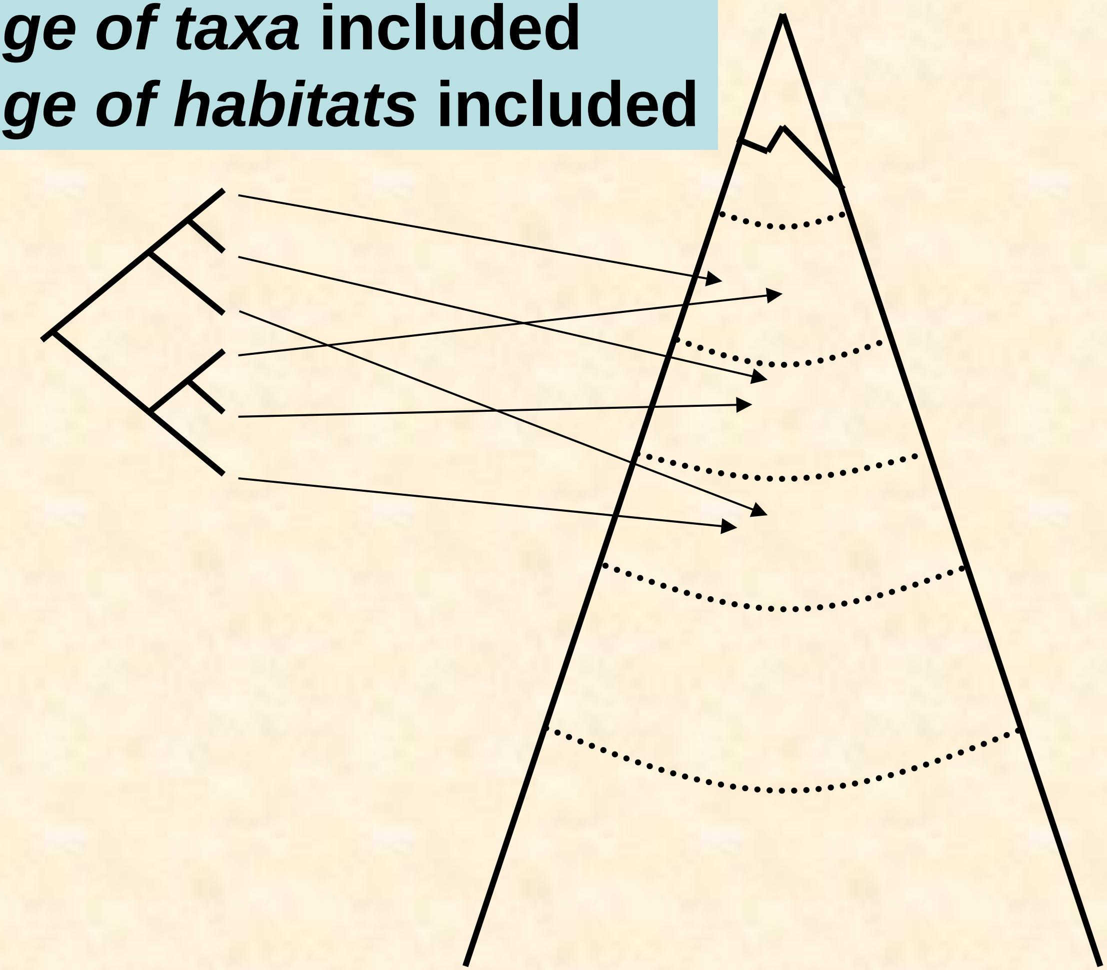
Phylogenetic clustering / overdispersion is <u>relative</u> to

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

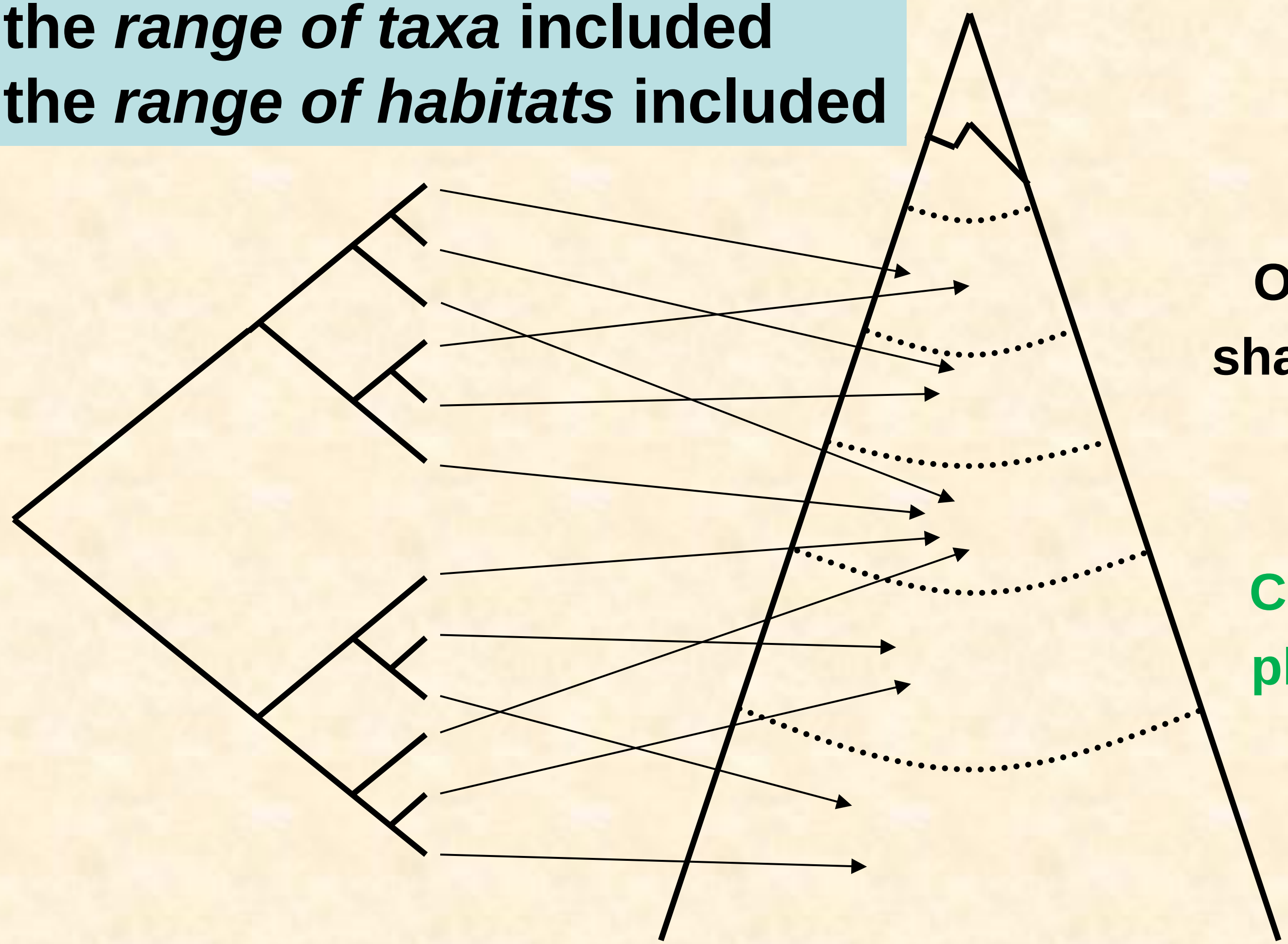


Overdispersion

$\Pi_{ST} < 0$

Phylogenetic clustering / overdispersion is relative to

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



Overdispersion at shallow phylogenetic level

+

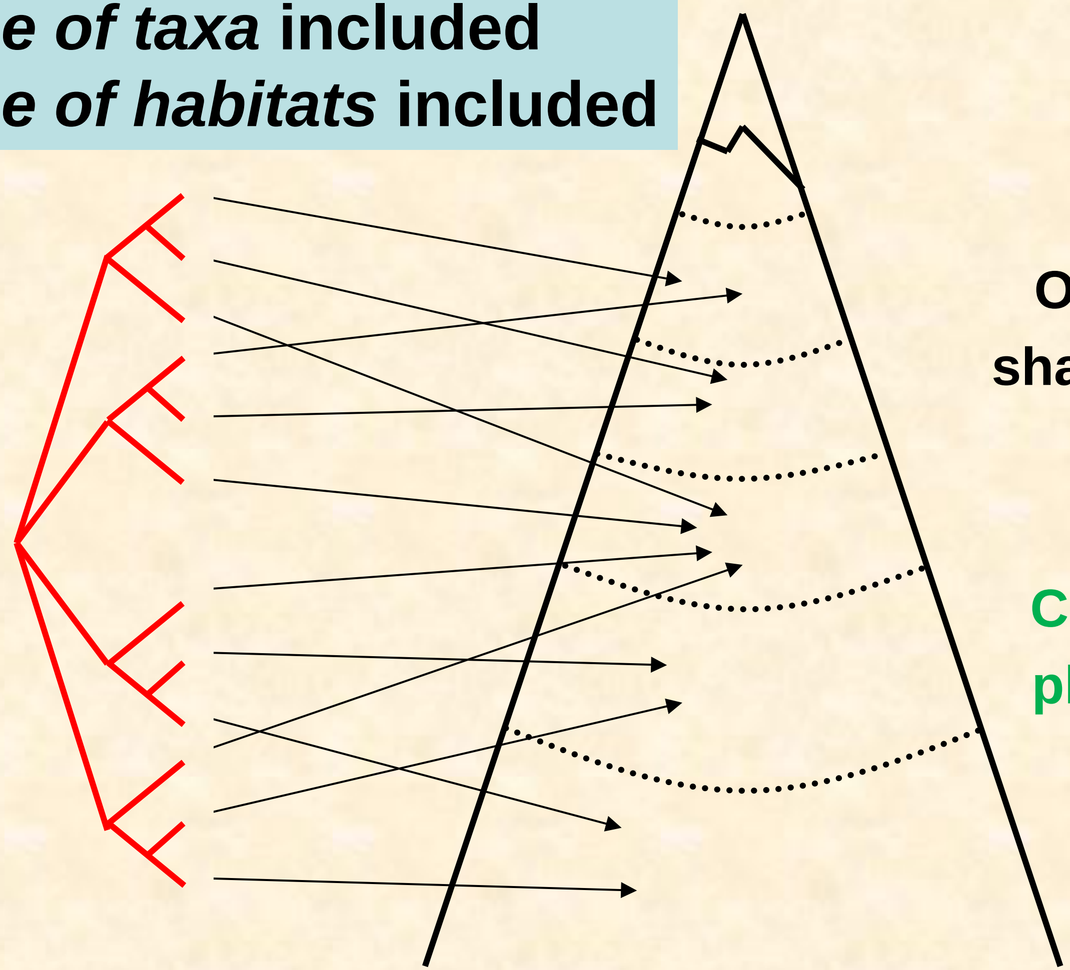
Clustering at deep phylogenetic level

$\Pi_{ST} > 0$

How to test this pattern ?

Phylogenetic clustering / overdispersion is <u>relative</u> to

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



Overdispersion at shallow phylogenetic level

+

Clustering at deep phylogenetic level

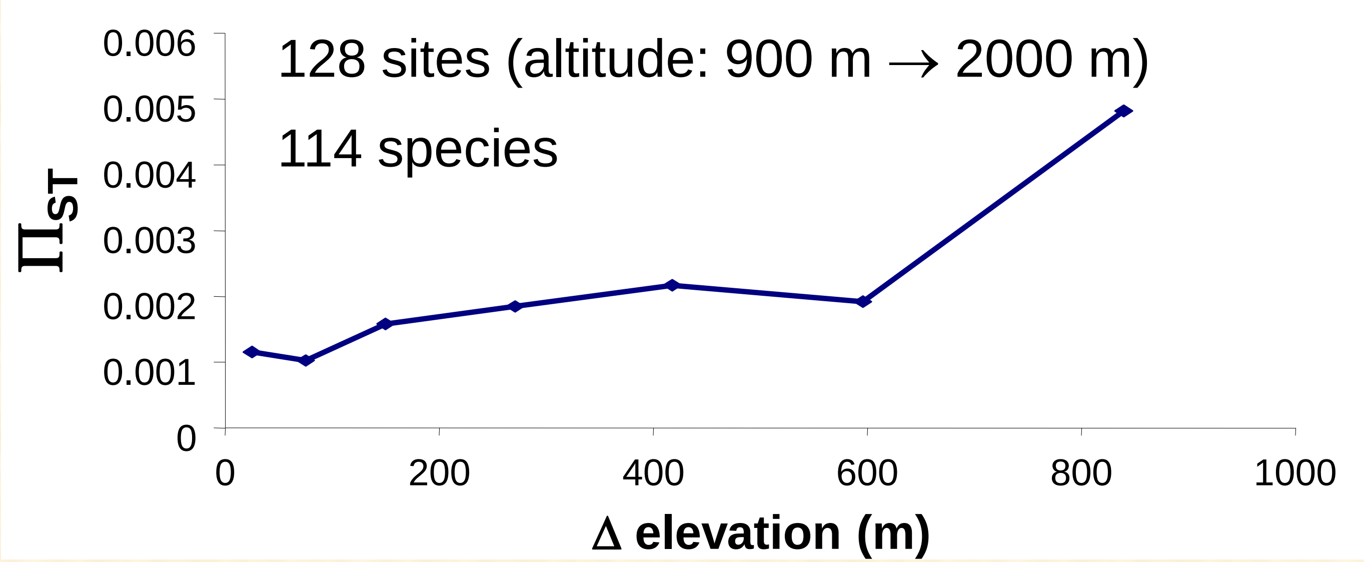
$\Pi_{ST} < 0$

How to test this pattern ?

➯ transform the phylogenetic tree to remove deep phylogenetic information

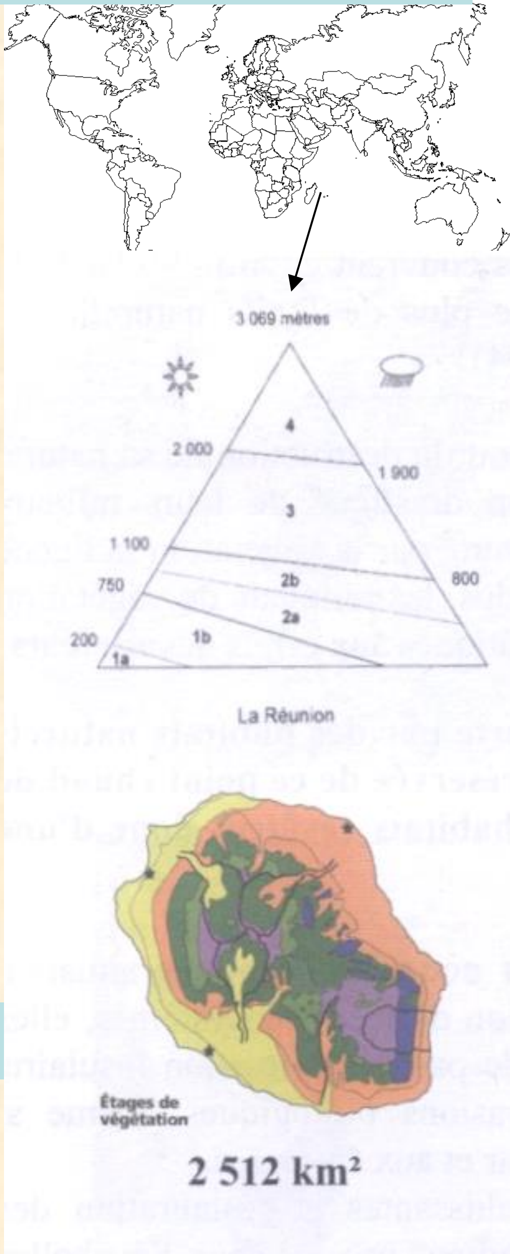
4. Phylogenetic structure under recent multiple radiations: Forest communities from Reunion island

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



128 sites (altitude: 900 m → 2000 m)

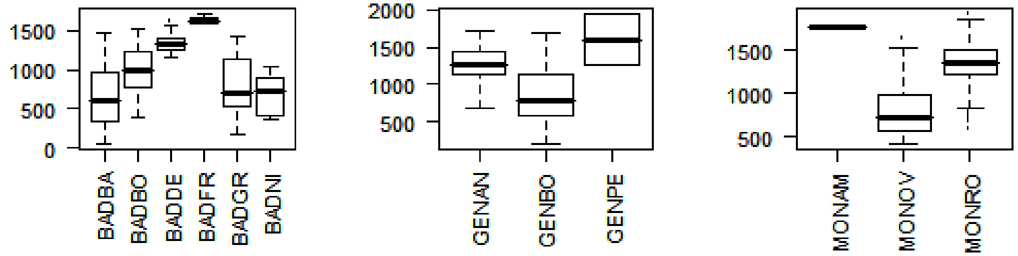
114 species



⇨ 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

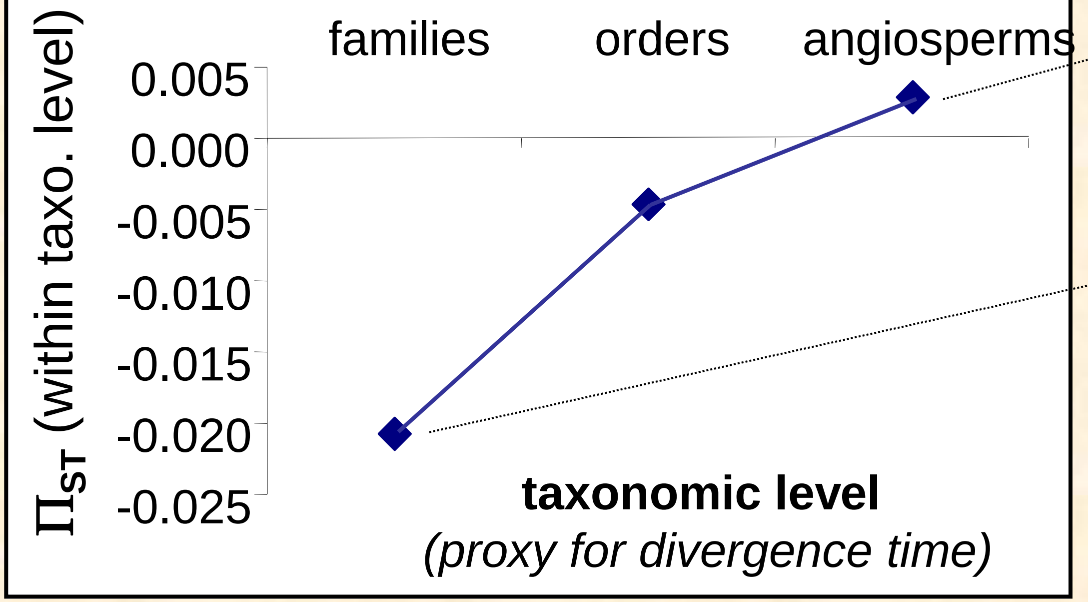
$MPD^{\delta<T}$ mean divergence time (δ) between species for $\delta < T$

→ 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 $\Pi_{\mathrm{ST}}^{\delta<T}$

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**

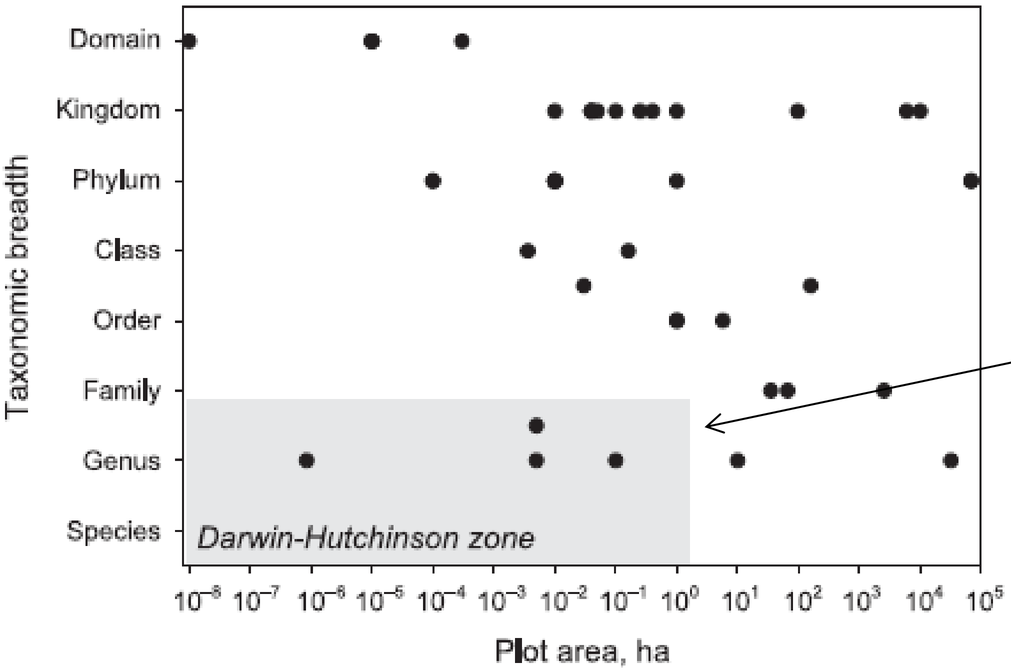


Fig. 4 Taxonomic and geographical scales of contemporary studies in phylogenetic community structure. The *x*-axis refers to the geographical extent of individual study plots, and the *y*-axis the highest taxonomic level considered in the study. The 'Darwin–Hutchinson zone' marks an approximate region 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

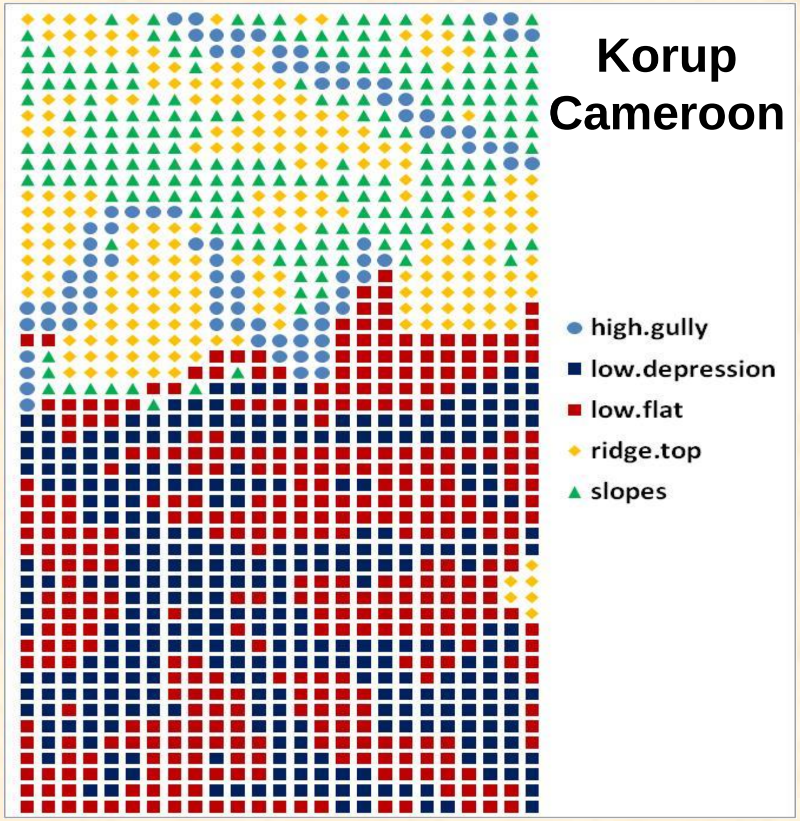
- shallow phylogenetic depth

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

500m x 1000m evergreen forest plot (330 000 stems DBH>1cm inventoried)

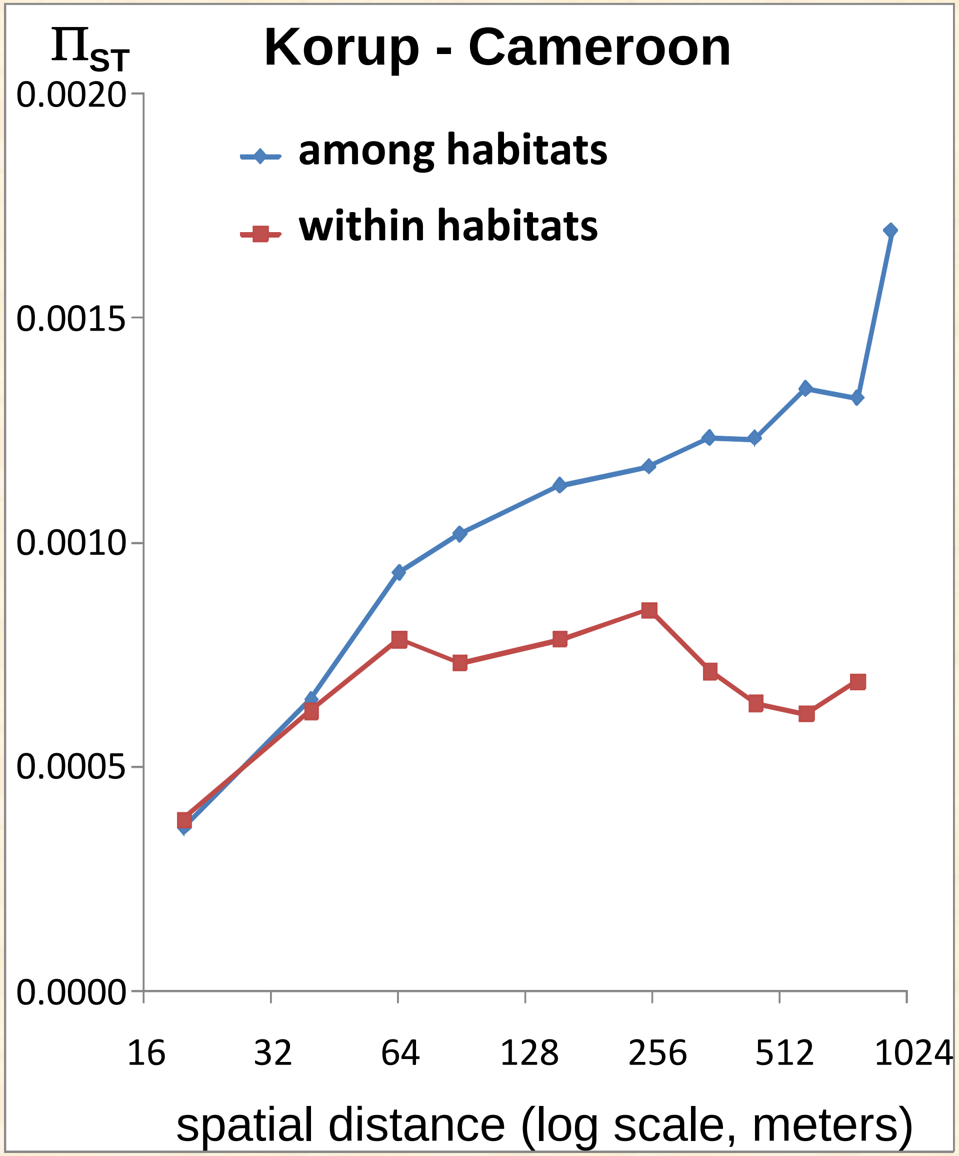
⇰ subdivided into 20m x 20m subplots categorized into **5 habitats**



Molecular phylogenetic trees based on *rbcL* + *matK*
(for 272 species represented by >50 individuals and making 97% of all stems of 494 species)

Parmentier et al. (2014, Journal of Ecology 102:1008–1016)

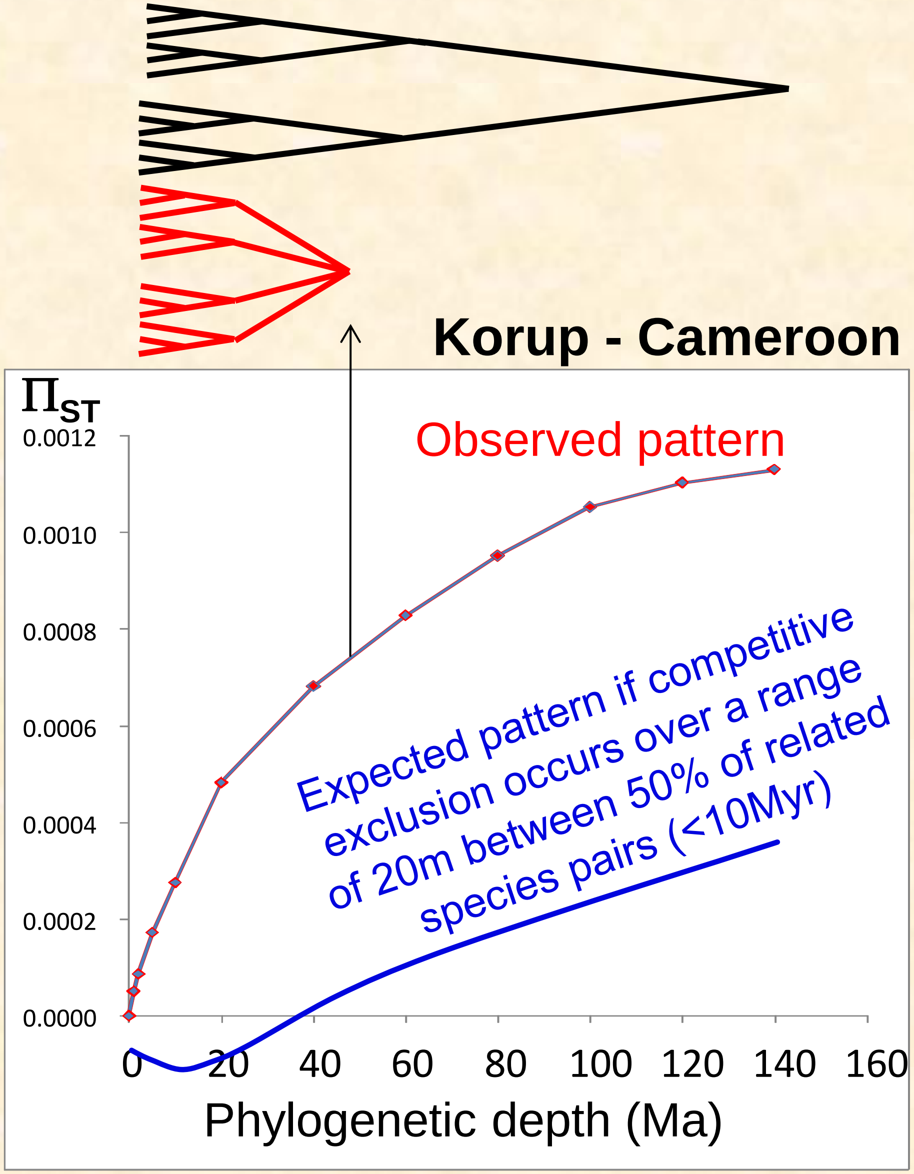
Phylogenetic turnover:
impact of spatial distance vs topographic habitat types



Habitat categories explain part but not all the phylogenetic turnover

Phylogenetic clustering (Π_{ST}>0) occurs at all scales (no overdispersion)

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



Korup - Cameroon

Observed pattern

Expected pattern if competitive exclusion occurs over a range of 20m between 50% of related species pairs (<10Myr)

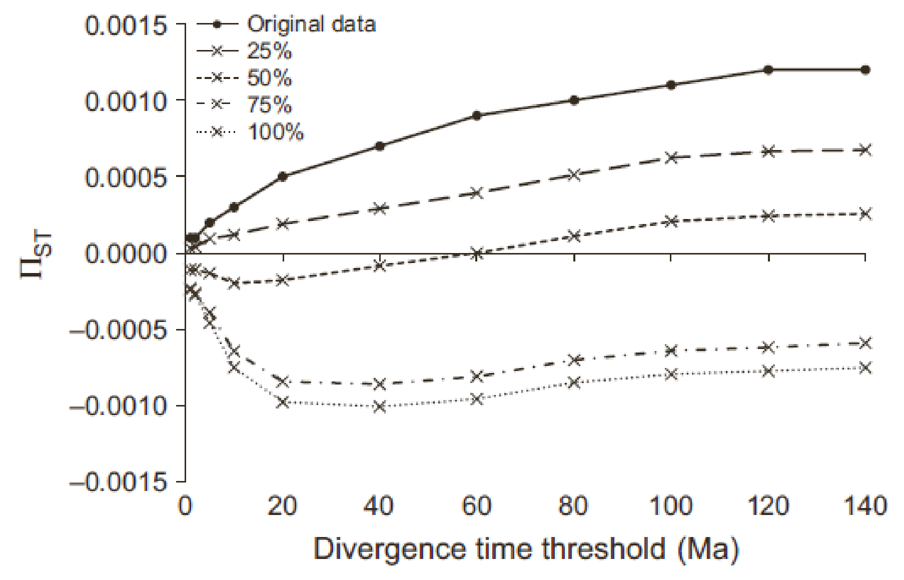


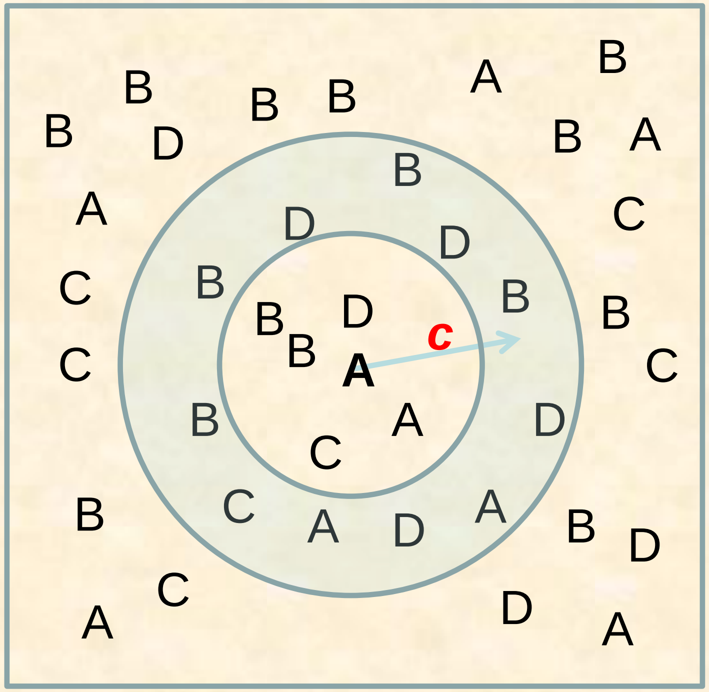
Fig. 4. Overall signal of phylogenetic turnover among quadrats (mean Π_{ST}, solid line) depending on phylogenetic depth (in Ma). To eliminate signal occurring above a given phylogenetic depth, the mean Π_{ST} is computed using truncated phylogenetic trees (see Fig. 1) for a range of divergence time thresholds. Simulated data help compare the observed pattern (i.e. original data) with a situation where competitive exclusion would have occurred between closely related species over a distance range of 20 meters (dashed lines) for 25% to 100% of the species pairs having diverged <10 Ma ago.

↳ no evidence of phylogenetic overdispersion

Does phylogenetic overdispersion occur at smaller scales?

➯ individual-based analyses

Computing a ‘co-occurrence excess’ of hetero-specific pairs



$\varepsilon_{A,i}$ =1 if ind i belongs to species A, otherwise 0

$\omega_{i,j,c}$ =1 if distance i-j belongs to interval c, otherwise 0

$$f_{A,B,c} = \frac{\sum_{i,j} \varepsilon_{A,i}\varepsilon_{B,j}\omega_{i,j,c}}{\sum_{i,j} \varepsilon_{A,i}\omega_{i,j,c}(1-\varepsilon_{A,j})} - \frac{\sum_i \varepsilon_{B,i}}{\sum_i (1-\varepsilon_{A,i})}$$

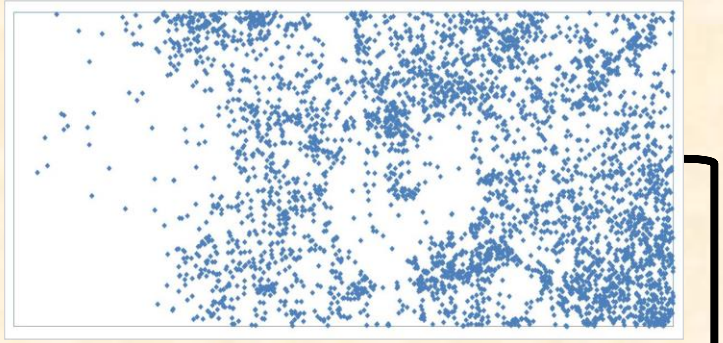
frequency of B at distance c from A (excluding A)

frequency of B in the plot (excluding A)

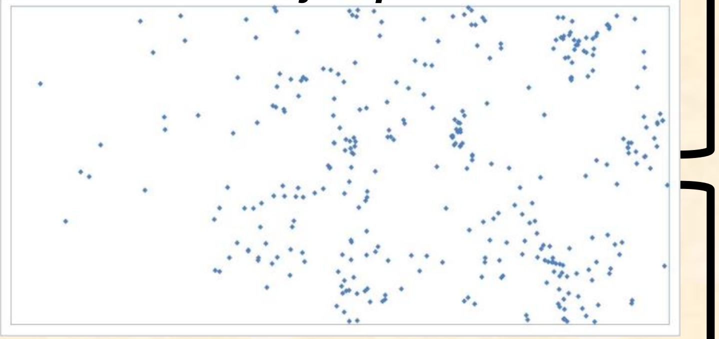
Does phylogenetic overdispersion occur at smaller scales?

↳ individual-based analyses

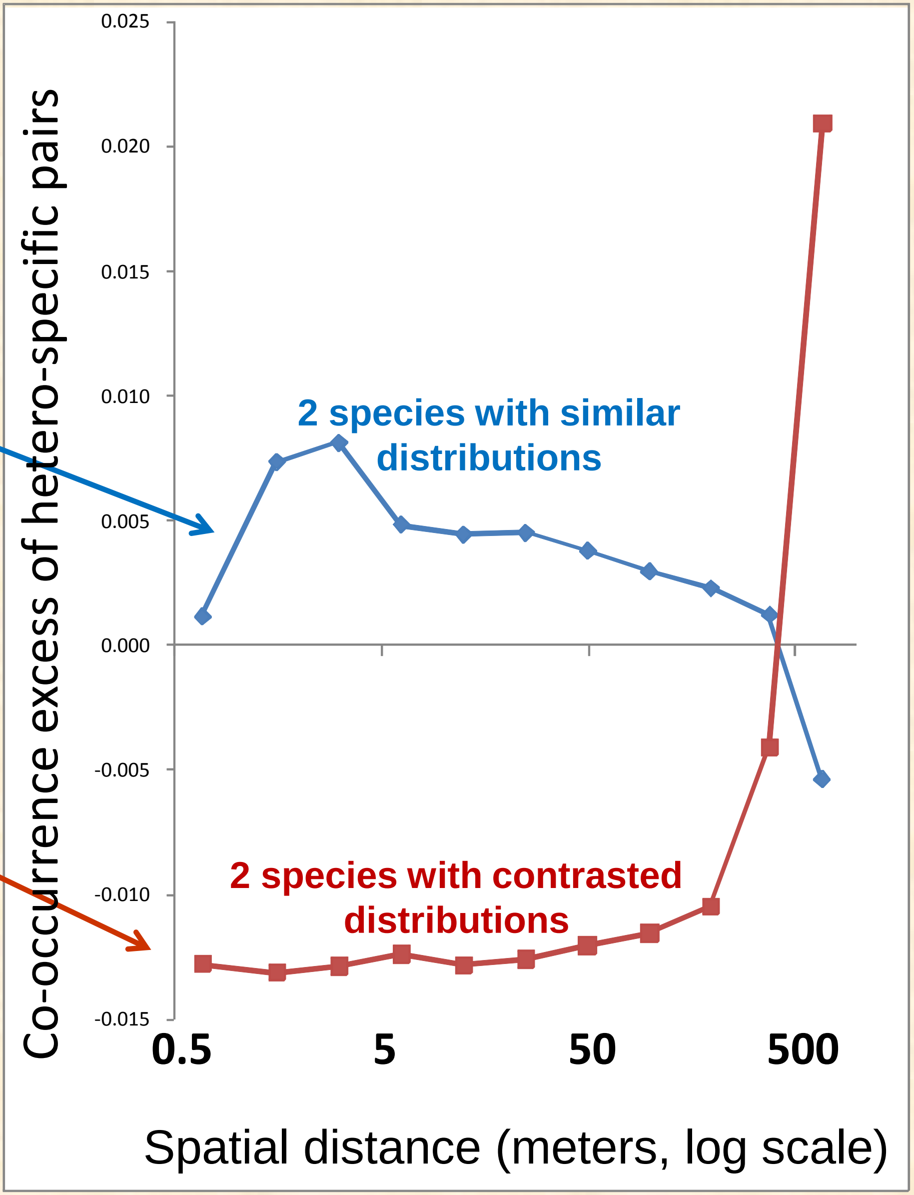
Cola cauliflora



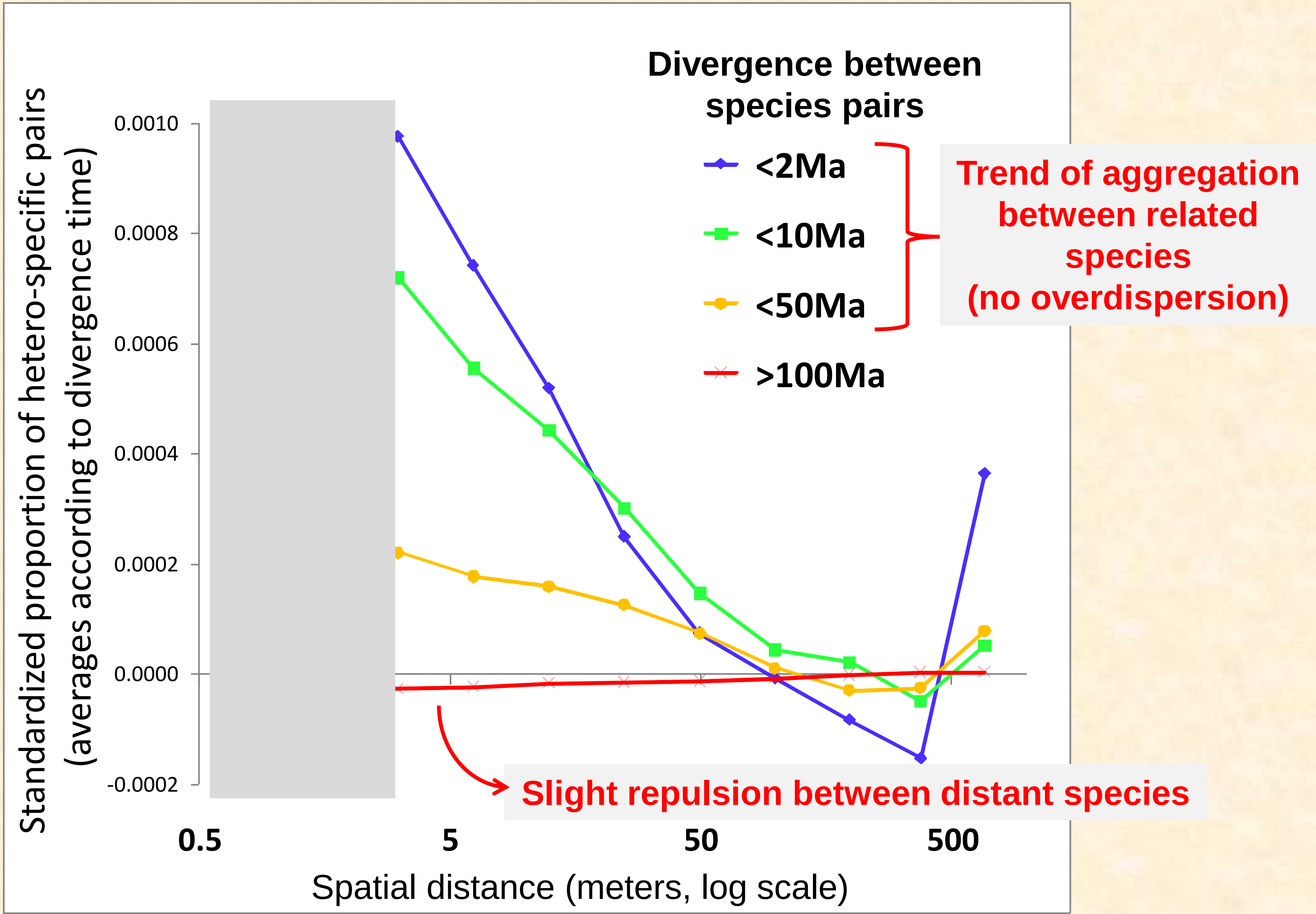
Beilschmiedia jacquesfelixii



Rinorea gabunensis



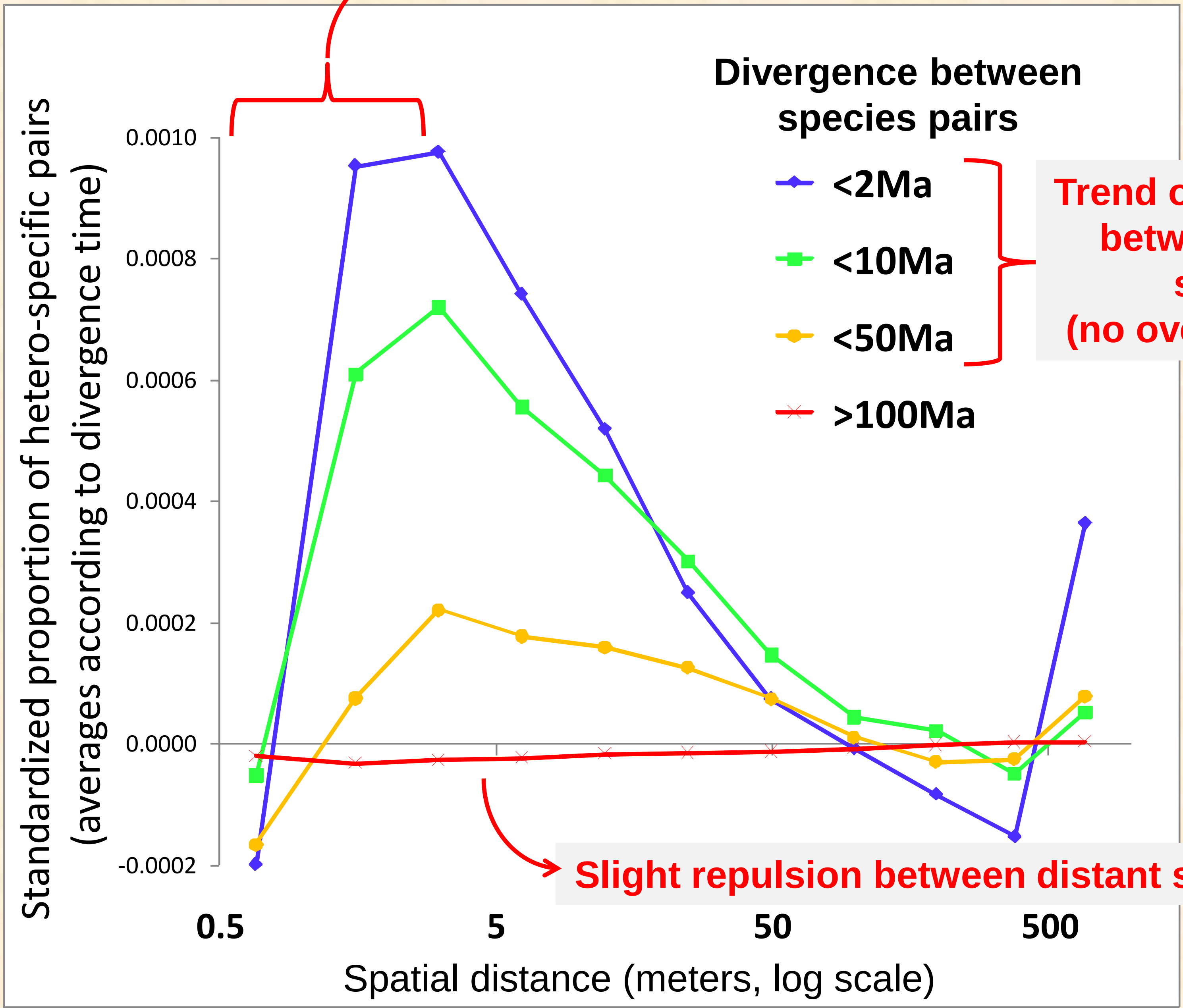
Korup - Cameroon



Trend of aggregation between related species (no overdispersion)

Slight repulsion between distant species

Korup - Cameroon



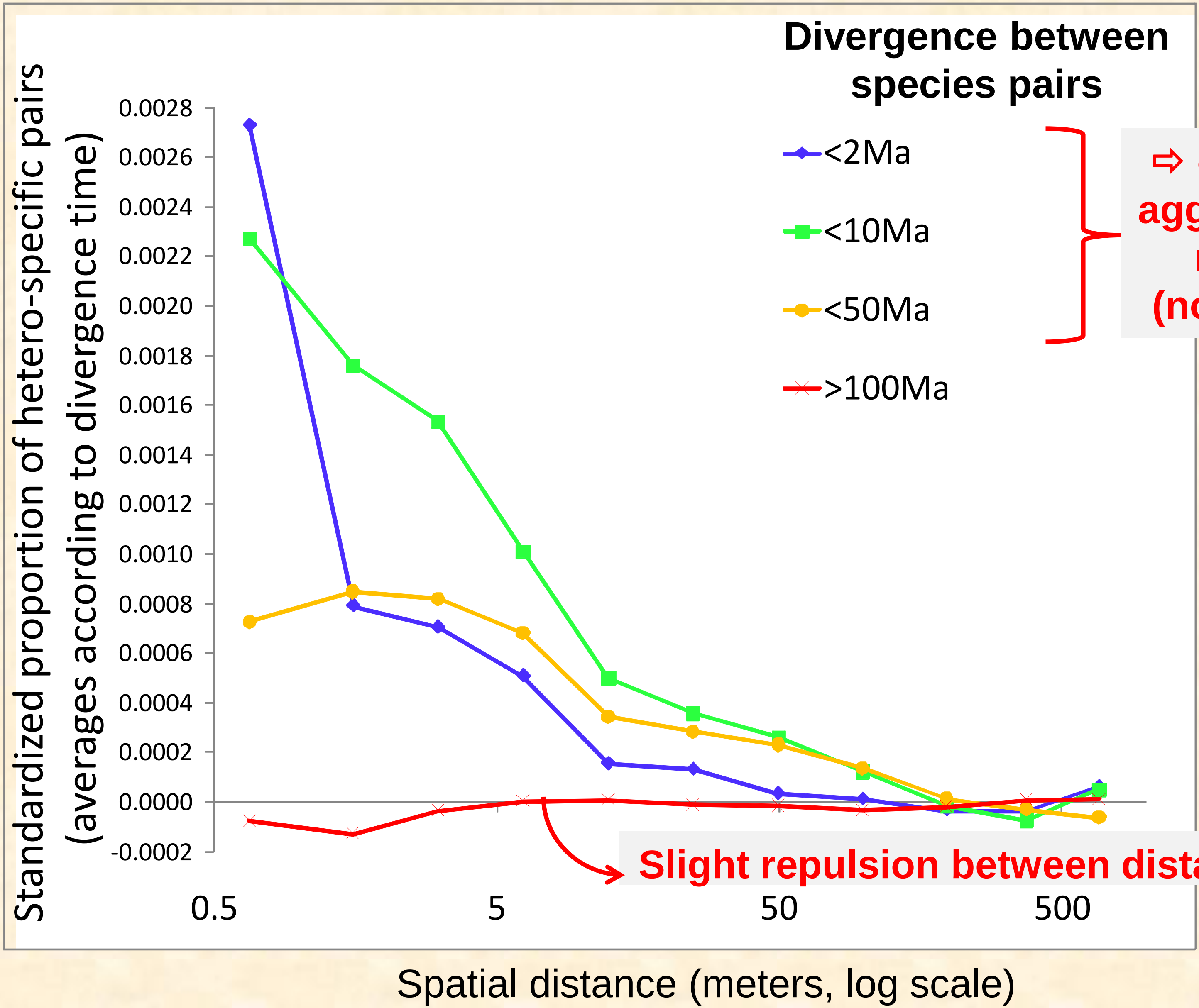
Repulsion between related species at <1m

Trend of aggregation between related species
(no overdispersion)

Slight repulsion between distant species

BCI - Panama

⇨ does not confirm repulsion between related species at <1m



⇨ confirms trend of aggregation between related species (no overdispersion)

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. Munkemuller 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

Testing the phylogenetic structure of local communities: which null model is adequate?

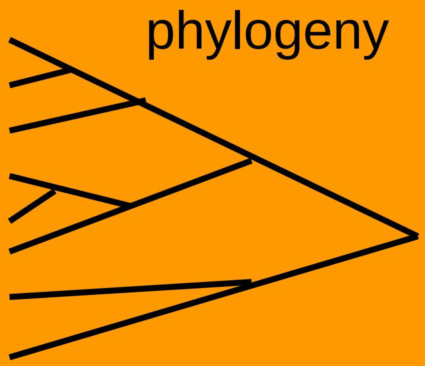
Hardy 2008 (J Ecol 96: 914–926)

local communities

species

	5		1	15		1	
8		5			3		1
	2		14			15	
14				5			15
	7	1		18	5	11	
			4			5	
4					1		
	1						

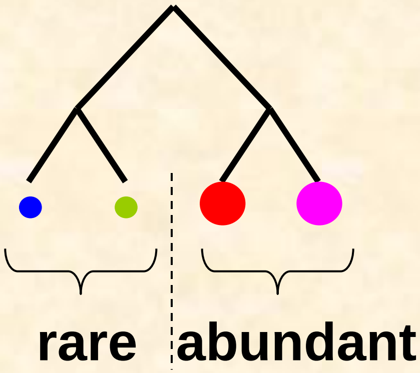
×



⇒ evaluation of Type I error rates for various combinations of metrics and data randomization schemes (null models)

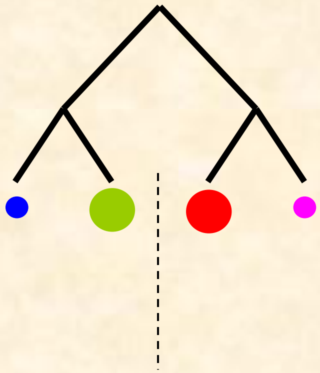
2 types of community phylogenetic structure (CPS)

species abundance CPS



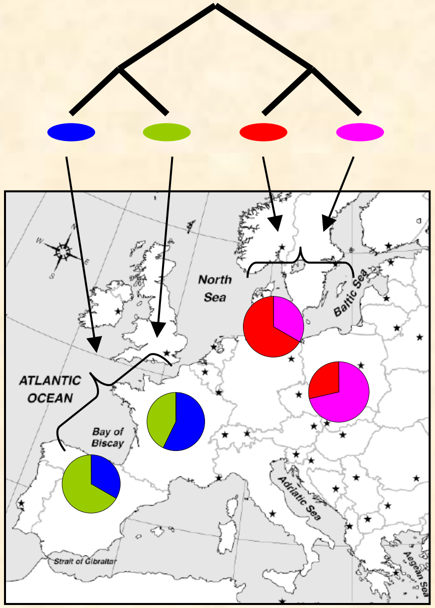
rare **abundant**

phylogenetic clustering

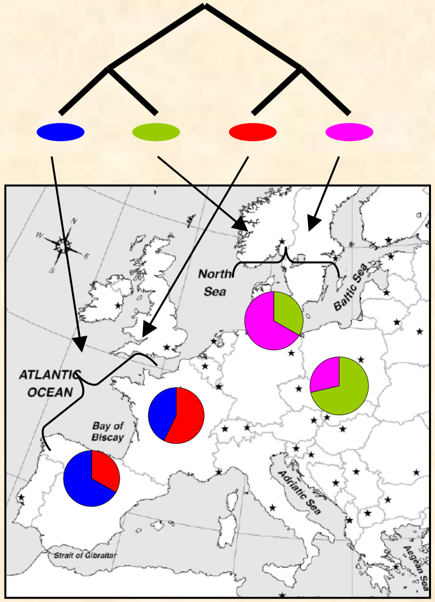


phylogenetic overdispersion

spatial CPS



phylogenetic clustering

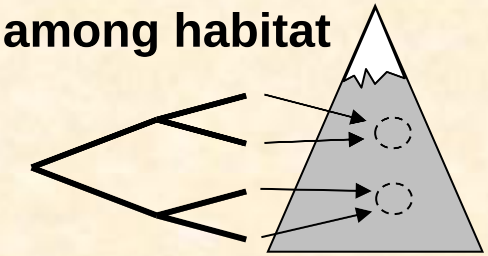


phylogenetic overdispersion (or **evenness**)

CPS caused by ecological & evolutionary processes

Phylogenetic clustering

among habitat



environmental filtering

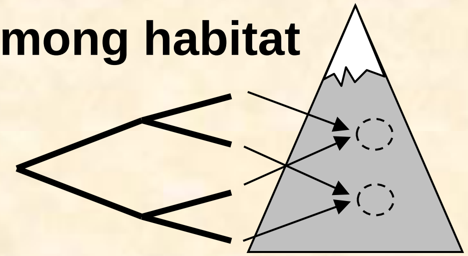
adaptation to altitude

+

habitat conservatism

Phylogenetic overdispersion (or evenness)

among habitat



environmental filtering

adaptation to altitude

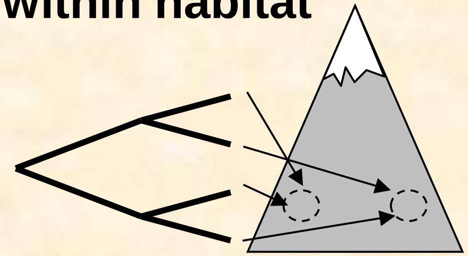
+

habitat convergence

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

Phylogenetic overdispersion (or evenness)

within habitat



competitive exclusion

+

niche conservatism

→ sister species cannot coexist
because of niche overlap

---

test of spatial CPS ⇔ test of community neutrality

(if biogeographic effects can be neglected)

How to characterize spatial CPS?

1- <u>Metric</u> to quantify the signal

based on
- **species presence/absence**
- **species abundances**

2- Adequate randomization procedure (<u>null model</u>)

↳ generates artificial datasets devoid of CPS

↳ distribution of metric under Ho

↳ test if observed value significantly different

randomization of
- **phylogenetic tree**
- **species-plot matrix**

CPS metrics

Using species **presence/absence**

☞ ***MPD***: mean phylogenetic distance
between species within a site

Webb 2000, Am Nat

variants: $\boldsymbol{mMPD_w}$ mean *MPD* over a set of sites

☞ $\Pi_{\mathbf{ST}} = (mMPD_a - mMPD_w) \,/\, mMPD_a$

Hardy 2007, J Ecol

relative increase of *MPD* for species
sampled **among sites *versus* within sites**

Using species **relative abundances**

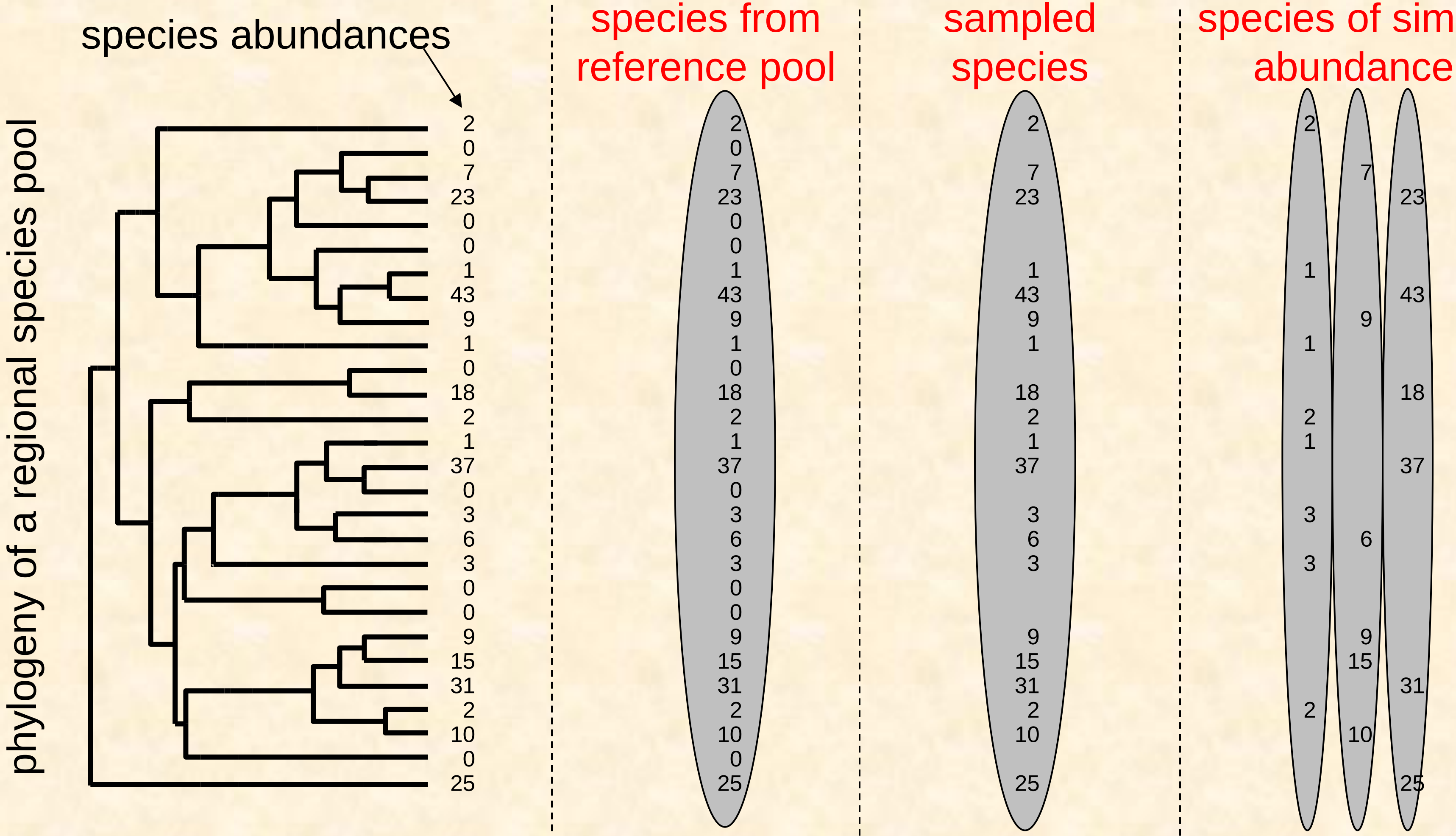
☞ $\boldsymbol{B}_{\mathbf{ST}}$: analogue of $\Pi_{\mathbf{ST}}$ $(\cong \boldsymbol{P}_{\mathbf{ST}} - \boldsymbol{I}_{\mathbf{ST}})$

Hardy 2007, J Ecol

Null models

randomizing the **phylogenetic tree** -> 3 null models

Randomization of tips of phylogenetic tree for:



	species from reference pool	sampled species	species of similar abundance
Null models:	**1r**	**1s**	**1a**
Constrains:	**no**	**sp occurrence**	**sp abundance**

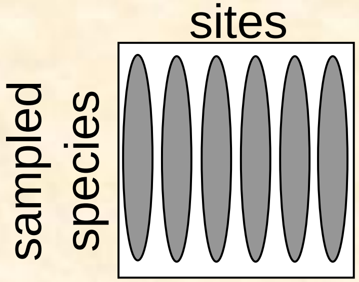
Null models

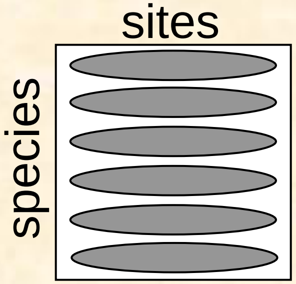
randomizing the **species – sites matrix** -> 6 null models

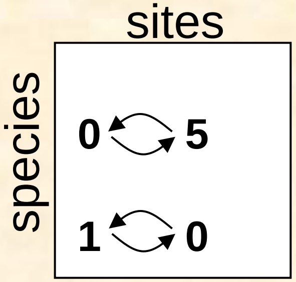
independent shuffling of local abundances within species or site

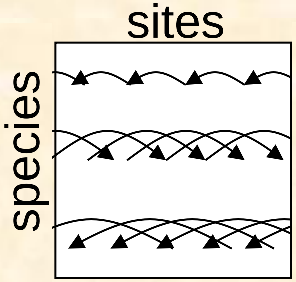
Swap algorithm

toroidal translation of local species abundances









Null models: 2s **3i** **3x** **3t**

Constrains :

local diversity

abundance distribution for each species

local sp richness

spatial autocorrelation

All null models (NM) destroy the spatial CPS

but other structural features of the original data set can be affected

e.g. **spatial autocorrelation of species distribution**

→ maintained under phylogenetic tree randomization (NM 1)

→ generally broken under species-site matrix randomization (NM 2 or 3)

e.g. **abundance CPS**

→ broken under phylogenetic tree randomization (except NM 1a)

→ maintained under NM 3

⇘ impact on the ‘validity’ of tests ?

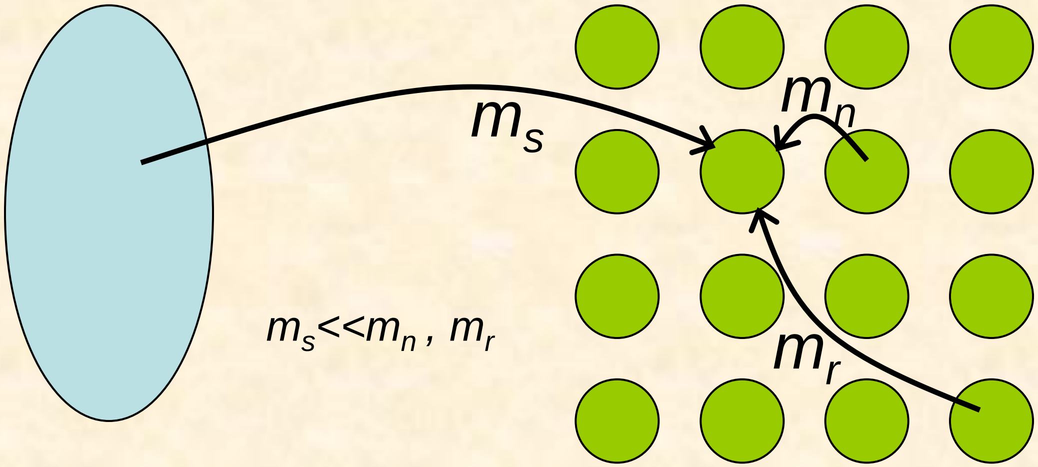
(1 test = combination of 1 metric and 1 null model)

A ‘locally neutral’ subdivided community model

☞ **structure devoid of spatial CPS**

constant **source community**
(≈ regional pool)

focal community =
set of connected
sub-communities



Species dispersal
immigration from:
m_s source community
m_n adjacent sub-comm.
m_r random sub-comm.

S **species with f_s relative abundances**
(CPS possible)

N **sub-communities containing n_i individuals**

⇘ species assembly within focal community results from:
- species **dispersal**
- **drift** (demographic stochasticity per species)

⇒ **neutral assembly**

Simulation analysis

10 metrics X 9 null models = 90 types of test

↳ applied on 'locally neutral' community model

↳ **simulation** of 10x10 sub-communities

→ migrants from source community (m_s=0.001, 227 tree sp from BCI)

variable parameters:

1- sp **abundance CPS**: - **realistic** (as on BCI)
- **random** (BCI sp abund. shuffled)
- **highly clustered** (Fabaceae sp over-abundant)

2- species **dispersal**: - **random** (m_r=0.1 m_n=0)
- **limited to neighbors** (m_r=0 m_n=0.1)
- **hierarchical** (4 subsets with m_{within}=0.1, m_{among}=0.01)

3- sub-community **sizes**: - **constant** (n_i = 100 individuals)
- **variable** (n_i = 40 or 160 individuals)

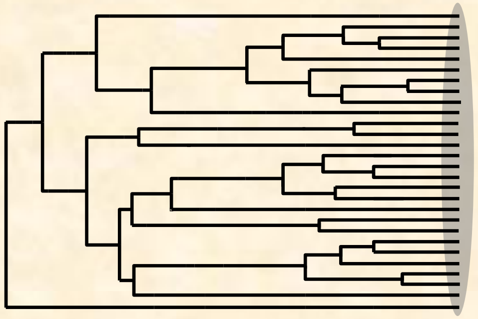
↳ **18 parameter sets**

Tests on 1000 data sets →

25 significant clustering
25 significant overdispersion

expected under H_0 for α=0.05

Null model 1s:
Phylogenetic tree randomization of sampled species



data sets showing significant spatial phylogenetic clustering / overdispersion over 1000 replicates (25 expected)

	Species abundances:		
	P Random	Realistic	**P Clustered**
mMPDw	**21 / 33**	**0 / 81**	**997 / 0**
Π_{ST}	**23 / 22**	**34 / 27**	**121 / 25**

Test :

'exact'

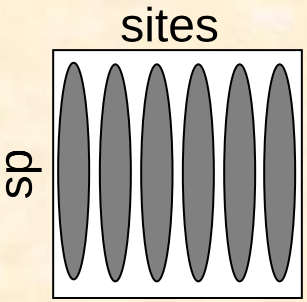
moderately biased

very liberal

⇒ Randomizing phylogenetic tree always OK if
species abundances are phylogenetically random

⇒ *mMPD* (or *NRI*) highly dependent on the phylogenetic structure of species abundances => problem when interpreting the test

Null model 2s: *independent shuffling of local abundances within species*



data sets showing significant spatial phylogenetic clustering/overdispersion over 1000 replicates (25 expected)

	Species abundances:		
	P Random	**BCI**	**P Clustered**
mMPD	**337 / 366**	**48 / 782**	**1000 / 0**
Π_{ST}	**8 / 5**	**7 / 6**	**50 / 4**

Test :

‘exact’

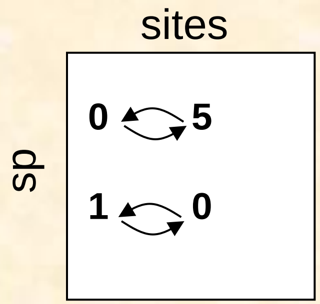
moderately biased

very liberal

⇒ Most troublesome null model !

Null model 3x:

SWAP algorithm



data sets showing significant spatial phylogenetic clustering/overdispersion over 1000 replicates (25 expected)

	Species abundances:			
	P Random	P Random	**BCI**	**P Clust**
	Dispersal			
	random	***limited***	*random*	*random*
mMPD	**25 / 20**	**68 / 61**	**26 / 27**	**17 / 41**
Π_{ST}	**25 / 20**	**68 / 61**	**26 / 27**	**17 / 41**

⇒ Much “better” null model

⇒ Still **somewhat liberal under limited dispersal**

Overall performances (type I error rate) over 18 simulation parameter sets

	Null model								
Metric	**1s**	**1r**	**1a**	**2s**	**2r**	**2x**	**3i**	**3x**	**3t**
mMNTD	🟥	🟥	🟪	🟥	🟥	🟥	🟥	🟥	🟥
mMPD	🟥	🟥	🟪	🟥	🟥	🟥	🟥	🟥	🟥
D^{P}_{w} = *Rao*	🟥	🟥	🟪	🟥	🟥	🟥	🟥	🟥	🟥
Π_{ST}	🟥	🟥	🟩	🟥	🟥	🟥	🟥	🟥	🟥
B_{ST}	🟪	🟪	🟩	🟪	🟪	🟥	🟪	🟥	🟪

Test :

‘exact’

moderately biased

very liberal

⇒ **Null model 1a** (randomization of phylogenetic tree constrained by species abundances) performs best

⇒ **Metrics B_{ST} more robust**

Hardy 2008 (J Ecol 96: 914–926)

Summary

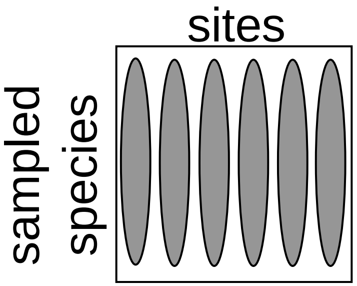
Most metric X null model combinations

→ test with inconsistent Type I error rate (often liberal tests)

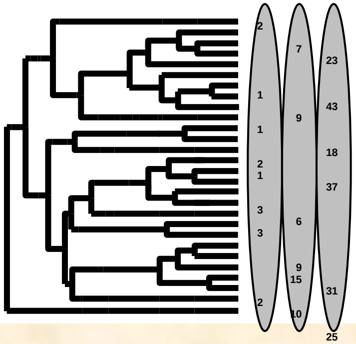
⇒ inadequate to assess if a community is locally neutral

Problems arises

- under phylogenetically non-random sp abundances
- under spatially limited dispersal and/or variable sample sizes



Null model 2r is the **least reliable**



Null model 1a is the **most reliable**

(but rarely used in published studies)

Summary

MPD → particularly **sensitive**

↳ does not distinguish **spatial CPS** from **sp abund CPS**

Π_{ST} (and $\boldsymbol{B}_{ST}$) → more **robust**

↳ focus on **spatial CPS**

Guidelines

Test overall species abundance CPS

↳ if test significant ⇒ use null model 1a (maintains species abundance CPS)

↳ if test not significant ⇒ use null model 1s (more degrees of freedom)

Simulateur d’assemblage de communautés avec traits et phylogénie

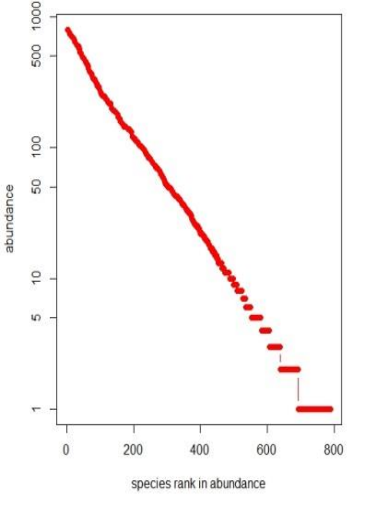
Gilles Dauby

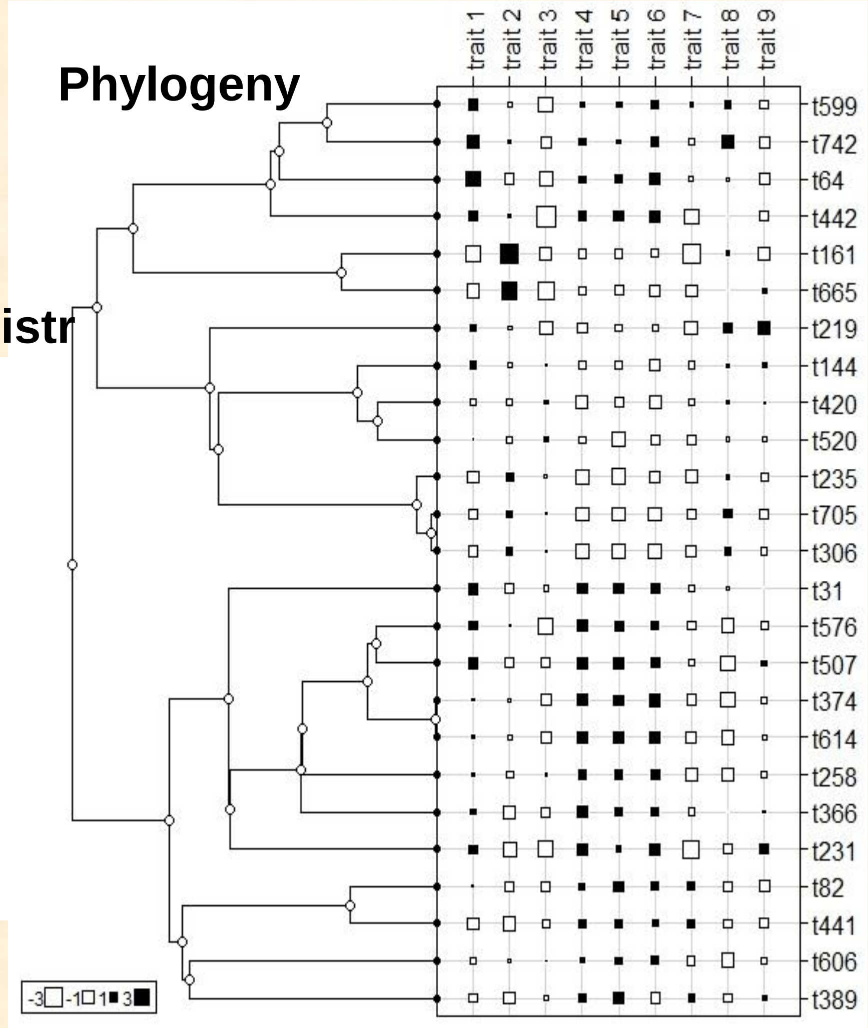
Meta-communauté

Trait evolution

Phylogeny

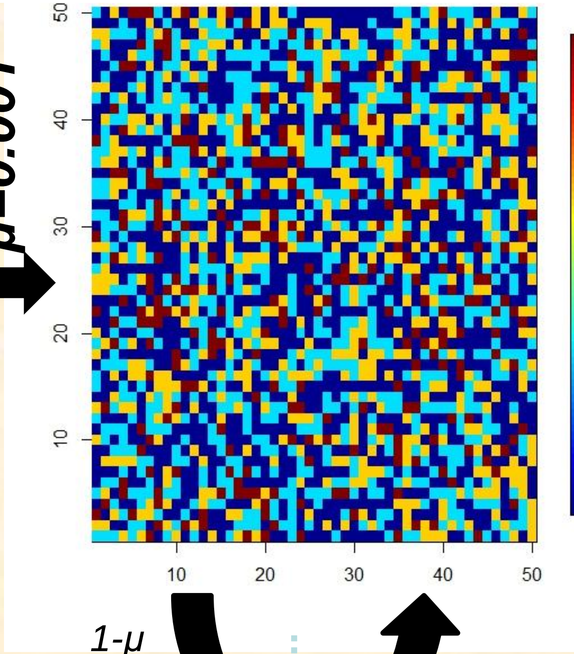
Species abund distr
(log-series)



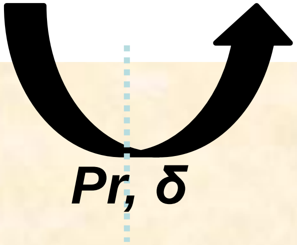


μ=0.001

Communauté locale

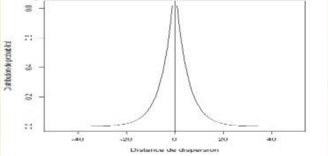


1-μ



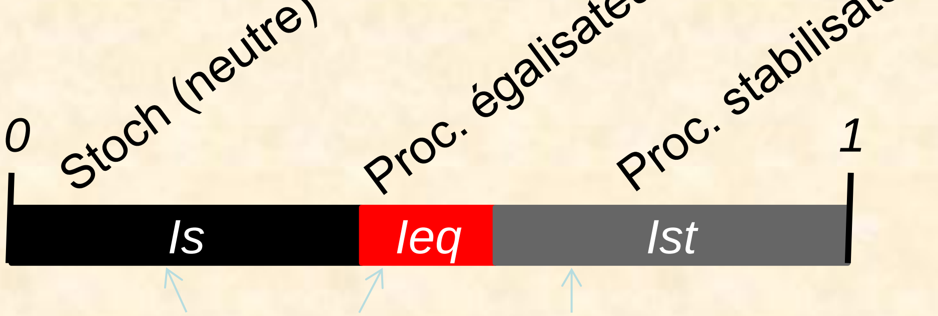
Pr, δ

Dispersion limitée (δ



Simulateur d'assemblage de communautés

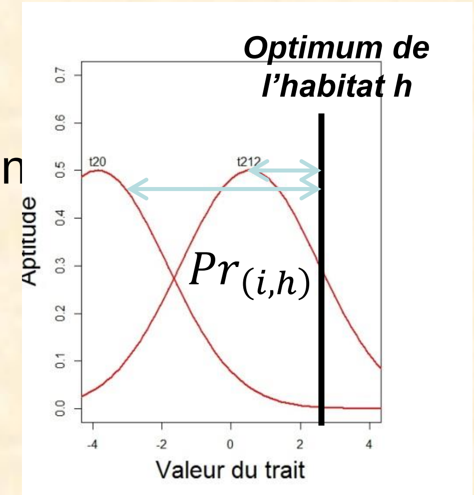
Proba recrutement:



$$Pr = I_S + I_{eq}\,.\,Pr_{eq} + I_{st}.\,Pr_{st}$$

Processus égalisateurs
(capacité compétitive selon filtre environ

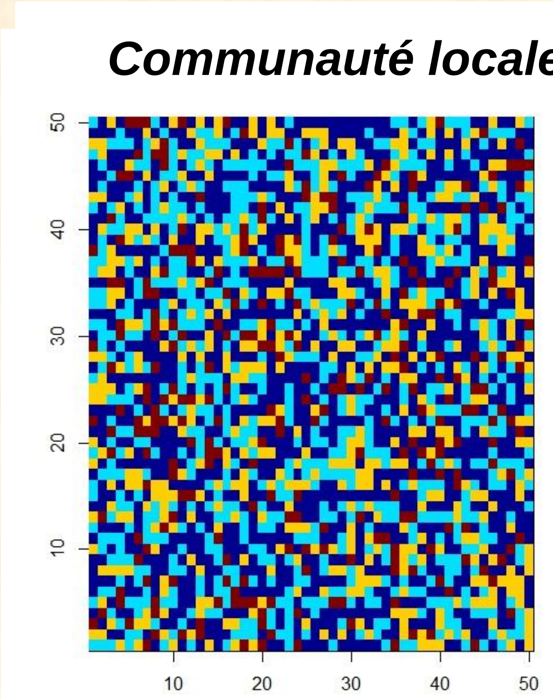
$$Pr_{eq(i,h)} = \sum_j f_j\, min\left(1, \frac{Pr_{(i,h)}}{Pr_{(j\ h)}}\right)$$

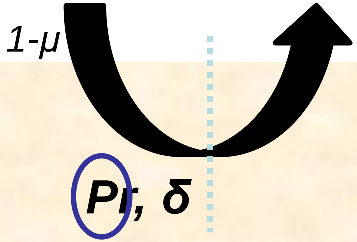


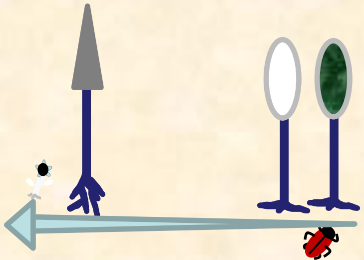
Processus stabilisateurs
(complémentarité de niche - limiting similarity)

$$Pr_{st(i)} = \sum_j \frac{\overline{d_{i,j}}}{d_{max}}$$

Distance fonctionnelle moyenne







Simulateur d’assemblage de communautés

Analyses implémentées

Structure fonctionnelle		Structure phylogénétique
Indices *Ust, Taust*	***Indices intra-sites/inter-sites (diversité beta standardisé)*** Hardy O.J. & Senterre B. 2007 J.Ecol.; Jost & Hardy 2008 J.Ecol.	Indices *Bst, ∏st*
Indices *mMFD, mMNTD*	***Moyennes d’indices intra-sites (diversité alpha)*** Vamosi S.M. *et al.* 2009 Mol.Ecol.; Hardy O.J. 2008 J.Ecol.	Indices *mMPD, mMNTD*
Indices *MFD, MNTD , NRI, NTI*	***Indices intra-sites (diversité alpha)*** Kembel S. 2009 Ecol.Let.; Hardy O.J. 2008 J.Ecol.	Indices *MPD, MNTD, NRI, NTI*
Etendus, écart-type des valeurs de traits	***Indices intra-sites (diversité alpha)*** Cornwell W.K. & Ackerly D. 2009 Ecol.Mono.	/
Indices *Ust, Taust, …*	***Corrélation entre indices de Beta diversité s.l. et distance spatiale (décomposée en intra et inter-habitats)*** Parmentier I. & Hardy O.J. 2009 Ecography; .Swenson N. *et al.* 2011 Proc.R.B.Soc.	Indices *Bst, ∏st, Pst, COMDIST, …*

Simulateur d'assemblage de communautés

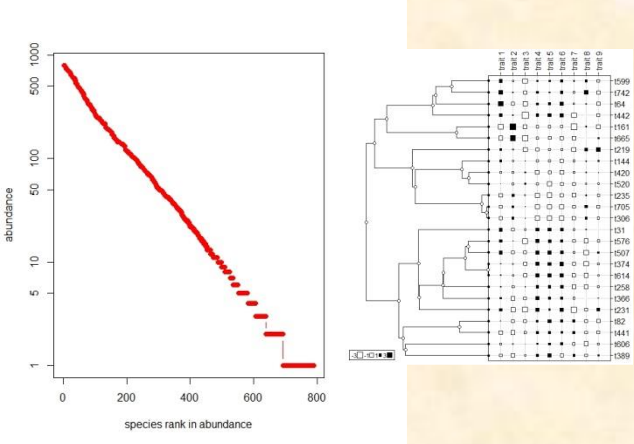
9 traits
- 3 impliqués dans proc. égalisateurs
- 3 impliqués dans proc. stabilisateurs
- 3 "neutres"

Hétérogénéité environnementale

- Grain de l'habitat
- Nombre d'habitat

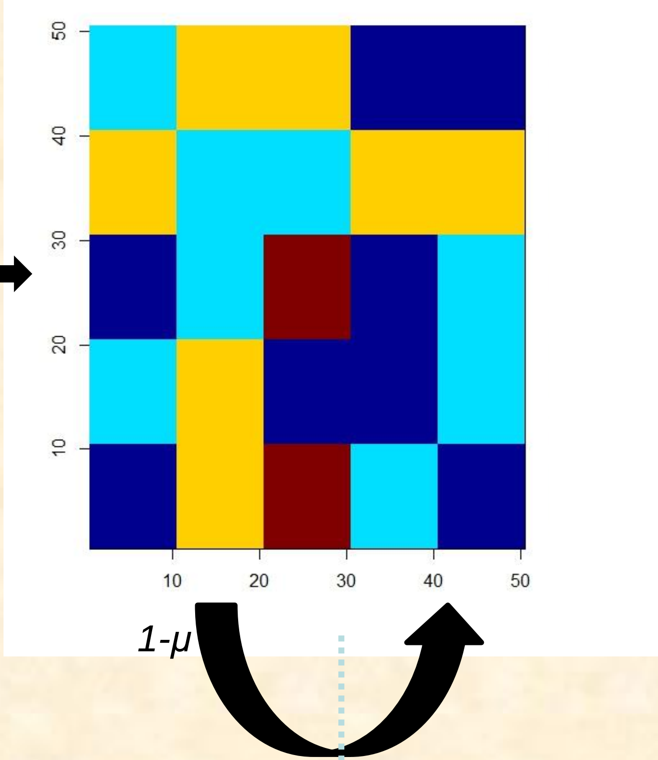
Meta-communauté

NS, Ntraits



μ

Communauté locale



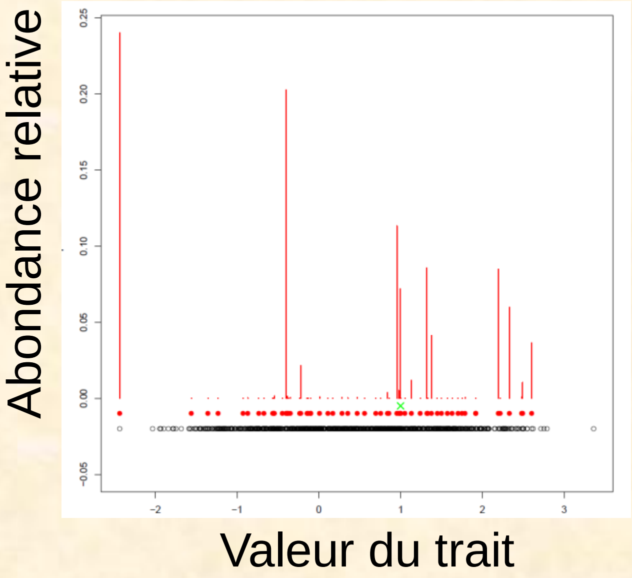
1-μ

Pr, δ

Quelques résultats

1 habitat homogène

Assemblage → Processus stabilisateurs

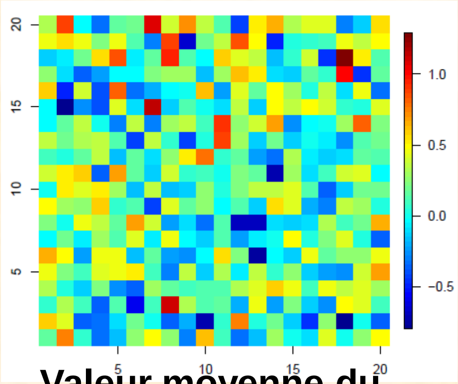


→ Dispersion des traits impliquées

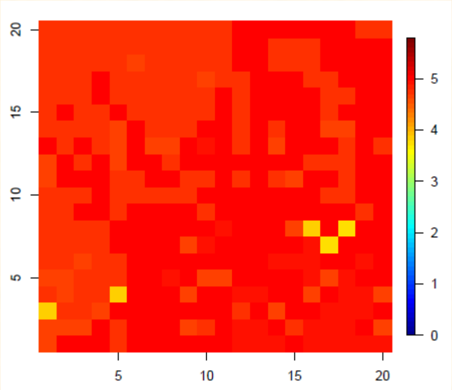
Structure fonctionnelle

→ Surdispersion fonctionnelle (métriques **combinant les 9 traits)** détectée pour 80 à 100% des simulations (*p-value* <0.05)

→ Parfois surdispersion détectée pour les **traits neutres** (jusqu'à 30%)



Valeur moyenne du trait intra-plot



Etendue du trait intra-plot

Structure phylogénétique

Indices *Bst, ∏st*
→ Détection d'une surdispersion dans >70% des cas

Indices *mMPD, mMNTD*
→ *Pas détecté*

Quelques résultats

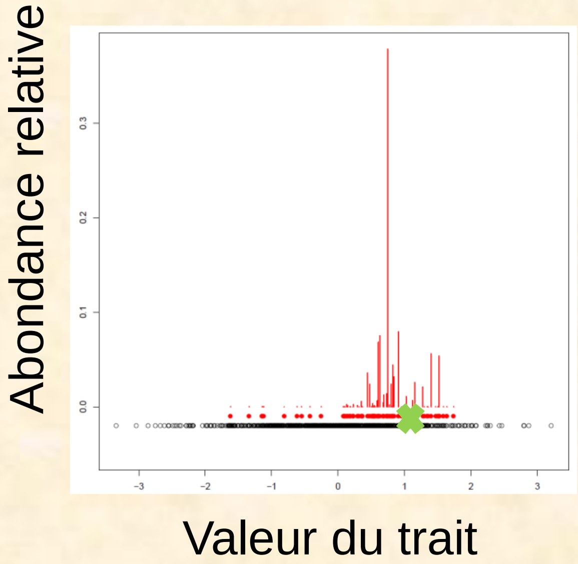
1 habitat homogène

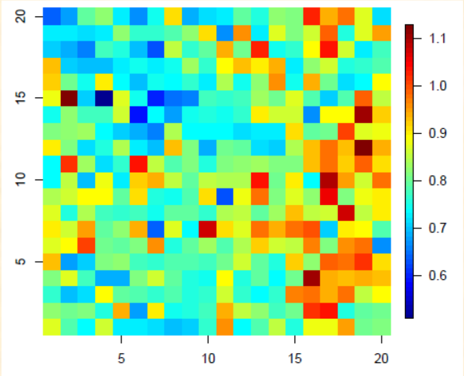
Assemblage
→ Processus égalisateurs

Structure fonctionnelle

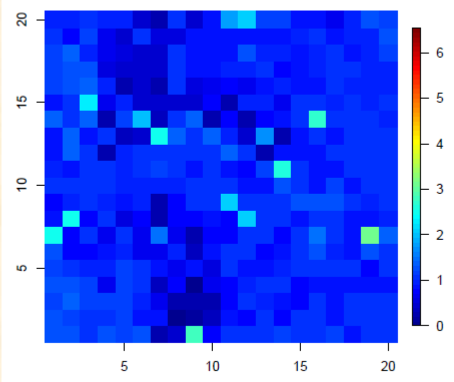
Indices *mMFD, mMNTD*
→ Détection d'une agrégation phylogénétique
→ Indices biaisés par la ***structure phylogénétique des abondances***

Indices *Ust, Taust*
→ Insensible à la structure phylogénétique des abondances





Valeur moyenne du trait intra-plot



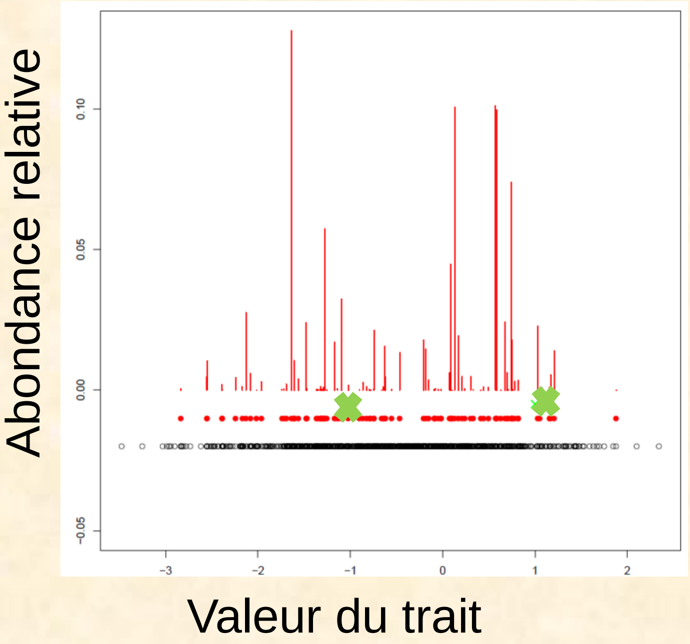
Etendue du trait intra-plot

→ Correction en utilisant un **modèle nul contraignant les permutations dans des intervalles d'abondances**

Quelques résultats

2 habitats
Grain d'habitat =5

Assemblage
→ Processus égalisateurs



Structure fonctionnelle

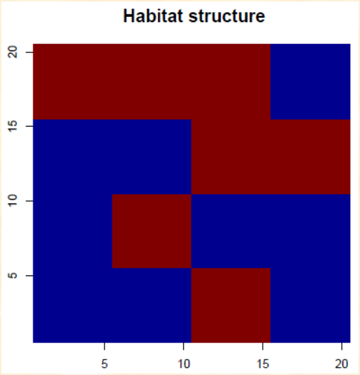
→ Effet fort du filtrage environnemental

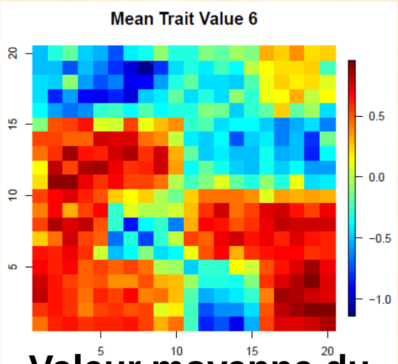
→ Agrégation fonctionnelle (métriques **combinant les 9 traits)** détecté pour >80% des simulations (*p-value* <0.05)

→ Parfois agrégation détectée pour les **traits neutres** (jusqu'à 30%)

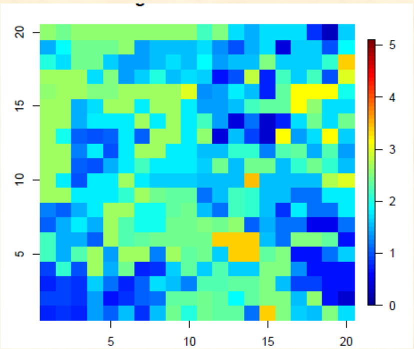
Structure phylogénétique

→ Détection d'une agrégation phylogénétique dans >60% des cas





Valeur moyenne du trait intra-plot

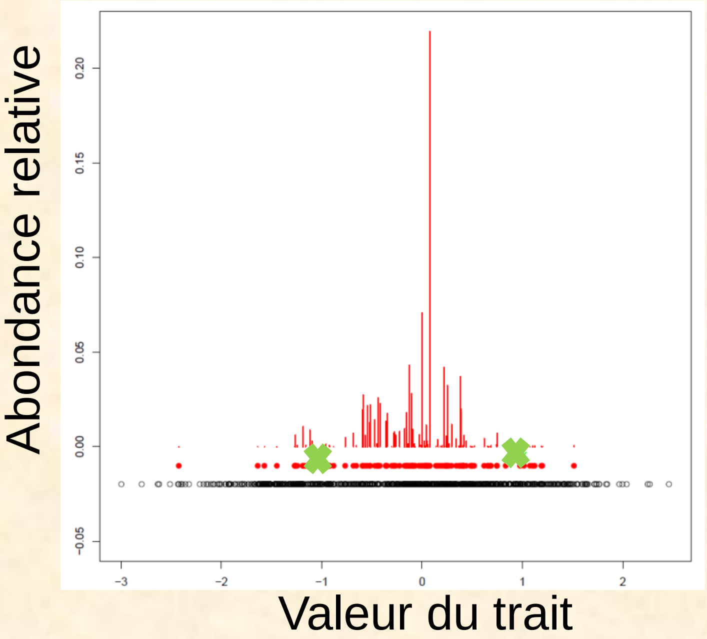


Etendue du trait intra-plot

Quelques résultats

2 habitats
Grain d'habitat =2

Assemblage
→ Processus égalisateurs



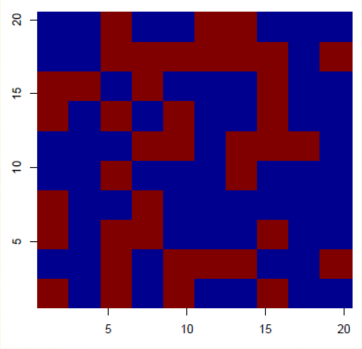
Structure fonctionnelle

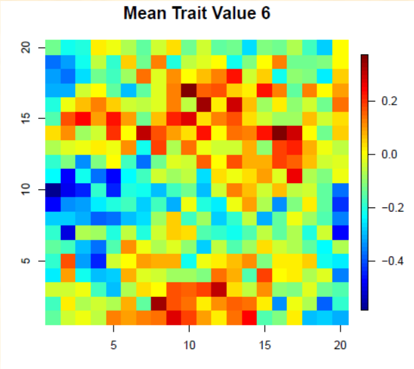
Grain de l'habitat + petit
→ Espèces généralistes avantagées

→ Indices *Ust, Taust* détectent une agrégation pour les 3 traits impliqués dans les processus pour + de 70% des cas

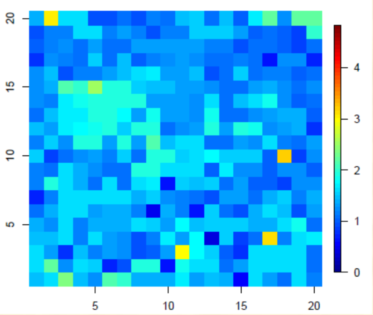
Structure phylogénétique

→ Pas de structuration phylogénétique détectée





Valeur moyenne du trait intra-plot

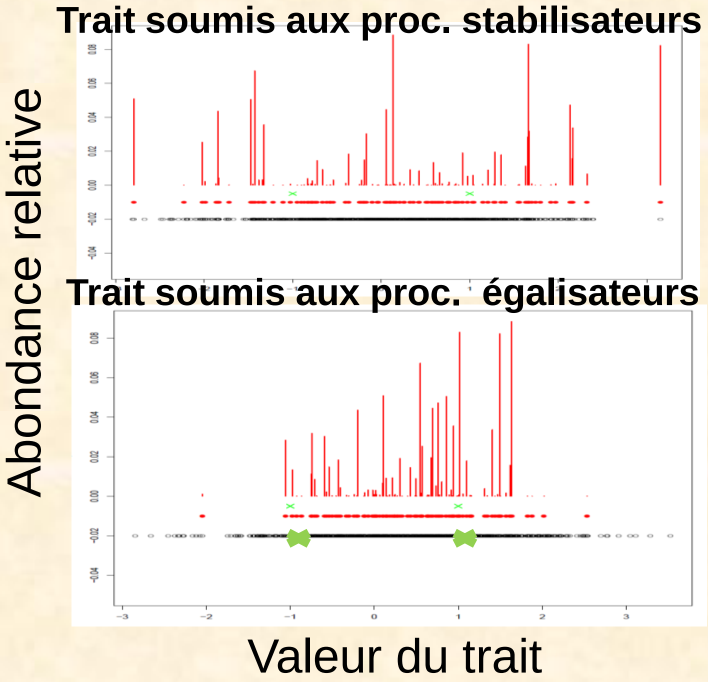


Etendue du trait intra-plot

Quelques résultats

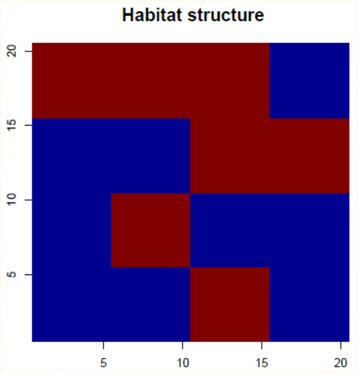
2 habitats
Grain d'habitat =5

Assemblage
→Stoc+Equal
+Stabil



Trait soumis aux proc. stabilisateurs

Trait soumis aux proc. égalisateurs



Structure fonctionnelle

→ Surdispersion bien détectée pour les traits stabilisateurs

→ Agrégation bien détectée pour les traits égalisateurs

Structure phylogénétique

Indices *Pst, PIst*
→ Structure (surdispersion/agrégation) détectée dans seulement 15 à 20% des simulations → **Compensation entre les processus**

Should assembly processes be inferred from alpha or beta (phylo/functional) diversity patterns?

Alpha (phylo)diversity: MPDw or QEw (+...)

Beta (phylo)diversity: P_{ST} or B_{ST} (+...)

Phylogenetic clustering usually interpreted as the impact of “environmental filtering” (EF)

However, EF is ubiquitous (fishes do not occur in meadows, mosquitoes do not occur in oceans,...)
-> hence, is the question “does EF occur in a particular local community” relevant?
I don’t think so, EF always occur.

The relevant question is probably: considering two (or a set of) local communities, “does differential EF among species explain different species assemblages”?
⇘ this question refers to beta diversity

-> the major focus found in the current literature about phylogenetic/functional community structuring is given to “alpha” diversity where clustering/overdispersion tests rely on the problematic notion of “species pool”. My impression is that more focus should be devoted to beta diversity patterns.

Thank you for your attention