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# A metaworld: metastability in metacommunities

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# Some points which will be addressed

- 1 Motivations
- 2 Communities, Metapopulations & Metacommunities
- 3 Metastable state and quasi-stationary distribution
- 4 Mean field approximation
- 5 Some results on the role of the geometry of the connections
- 6 Conclusion

# Community Structure of Tropical Rainforests



# Bats and rabbies in French Guiana

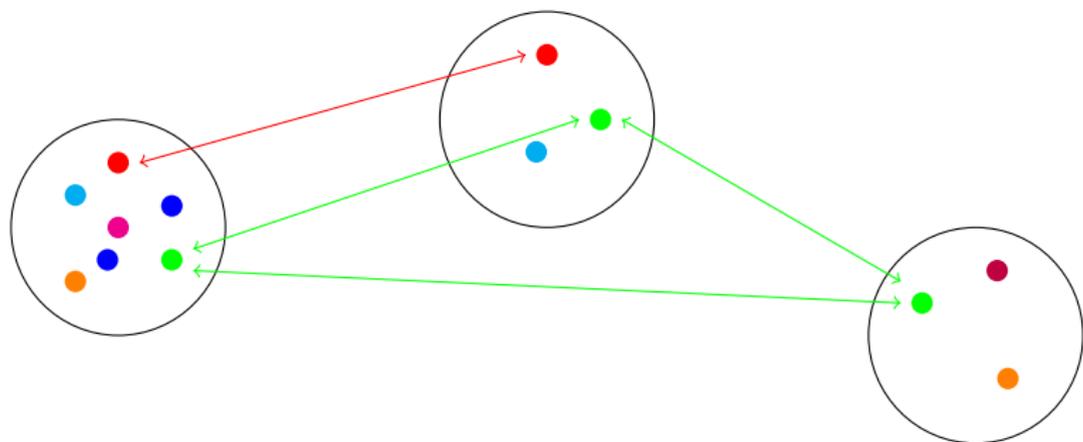


- bats live in caves
- males and females are distinguished (different dispersal)
- they can be healthy or infected
- a cave is a patch: island model
- dispersal between caves distance dependent, by males

# What is a metacommunity?

Definition (Leibold & *al.*, Ecology Letters, 2004)

A metacommunity is a set of communities located at some sites, or patches, connected by dispersal.



## Modeling

- species interact within one patch
- species disperse along a graph connecting patches

# Which questions to address?

Context: longstanding question in ecology (Clements (1936), Gleason (1926), Hubbel (2001))

What is the role of local adaptation and dispersal in shaping communities?

- here: which is the role of the shape of dispersal networks?

## ⇒ Geometry of networks

The within patches processes having been selected, what is the impact of the structures of dispersal graphs on the outcome of the model

- the quasi-stationary distribution
- the bifurcations (or phase transitions)

## • Simplification

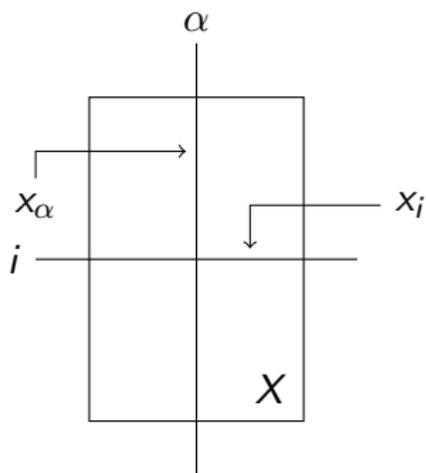
Is it possible to exhibit relevant results with simplifications like mean field approximation?

# Modeling metacommunities as reaction-diffusion processes on graphs

## Formalisation

space	discrete (patches)
time	continuous
state	binary matrix
reaction	intra-patch dynamics one reaction process per patch
diffusion	between patches dispersal one dispersal graph per species

# State of the metacommunity



# The model: a times continuous Marckov Chain

## Master equation ( $2^{np} \times 2^{np}$ )

$$\mathbb{P}(X^{t+dt} = x) = \sum_{x'} \underbrace{\mathbb{P}(X^{t+dt} = x | X^t = x')}_{\text{one event}} \times \mathbb{P}(X^t = x')$$

an event: **reaction** (within patch interaction) or **diffusion** (between patches dispersal)

## Reaction phase ( $2^p \times 2^p$ )

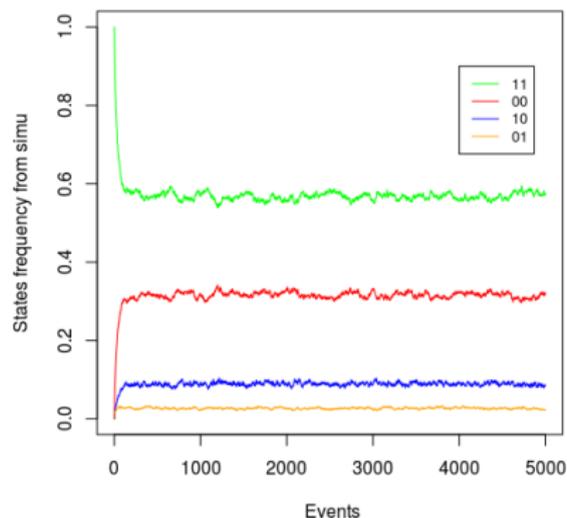
$$\mathbb{P}(X_i^{t+dt} = x | X_i^t = x') = \begin{cases} R_{i,xx'} dt & \text{if } x \subsetneq x' \\ 1 - \sum_{x \subsetneq x'} R_{i,xx'} dt & \text{if } x = x' \end{cases}$$

## Dispersal phase ( $2^n \times 2^n$ )

For each species  $\alpha$ , dispersal along an edge of a weighted graph

$$\mathbb{P}(A_\alpha^{t+dt} = a | A_\alpha^t = a') = \begin{cases} D_{\alpha,aa'} dt & \text{if } a' \subsetneq a \\ 1 - \sum_{a' \subsetneq a} D_{\alpha,aa'} dt & \text{if } a = a' \end{cases}$$

# Simulations ...



Erdős-Renyi random graph ; 50 nodes; edge density = 0.2 ; reaction as predator-prey ; dispersal 0.2 & 0.8

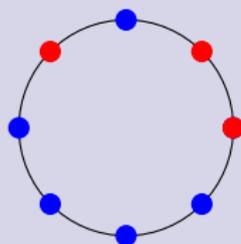
# Metastability or quasi-stationary distribution

heuristically ...

For a Markov chain with an absorbing state:

- the asymptotic state (or equilibrium) is the absorbing state
- however the chain can wander during a very long (not infinite) time over an **observed** subset of non absorbing states

Contact Process



Metastable state

$$\rho_t = \frac{1}{n} \sum_i x_i^t$$

# Some notions (here in discrete time)

## Killing time

$$T_0 = \inf \{t \in \mathbb{R} : x^t = x_\infty\}$$

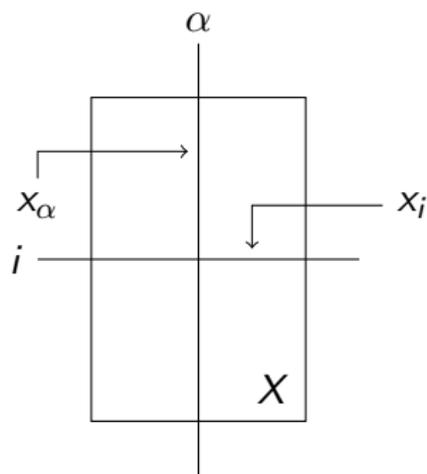
## Conditionally Invariant Distribution

$$P = \begin{pmatrix} 1 & a \\ \mathbf{0} & P^* \end{pmatrix} \quad \begin{pmatrix} 0 \\ u^* \end{pmatrix} \xrightarrow{P^t} \begin{pmatrix} 1 - \rho^t \\ \rho^t u^* \end{pmatrix} \quad \text{if } P^* u = \rho u^*$$

## Quasi-stationary distribution

$$u^* \quad \text{s.t.} \quad P^* u^* = \rho u^*, \quad \mathbb{E}(T_0) = \frac{1}{1 - \rho}$$

# Computational Complexity



## Computational Complexity

- Dynamics of a metacommunity is modeled as a Markov Chain on a state space  $\Omega$  with  $|\Omega| = 2^{np}$
- the size of matrix  $P$  is  $2^{np} \times 2^{np}$

## Pollet's contribution (discrete time too)

### Block diagonal form of transition matrix

$$P = \begin{pmatrix} 1 & A_{11} & \dots & A_{1q} \\ 0 & P_1 & \ddots & \vdots \\ \vdots & \ddots & \ddots & A_{q-1,q} \\ 0 & \dots & \dots & P_q \end{pmatrix}$$

$\implies$  to compute quasi-stationary distribution, it suffices to compute largest eigenvalues of matrices  $P_k$  (circulation classes).

### An observation

There is a one to one correspondence between circulation classes and subsets of species.

# Still some limits from computation complexity

## Size of circulation classes

If  $p = 2$ , there are 4 blocks, of size respectively

$S$	size
00	1
01	$2^n - 1$
10	$2^n - 1$
11	$(2^n - 1)^2$

## block sizes for $n = 10$

$1 \times 1$	$1 \times 511$	$1 \times 511$	$1 \times 1\,046\,529$
<b>0</b>	$511 \times 511$	$511 \times 511$	$511 \times 1\,046\,529$
<b>0</b>	<b>0</b>	$511 \times 511$	$511 \times 1\,046\,529$
<b>0</b>	<b>0</b>	<b>0</b>	$1\,046\,529 \times 1\,046\,529$

# Mean-Field approximation: mean degree

(back to continuous time)

with words ...

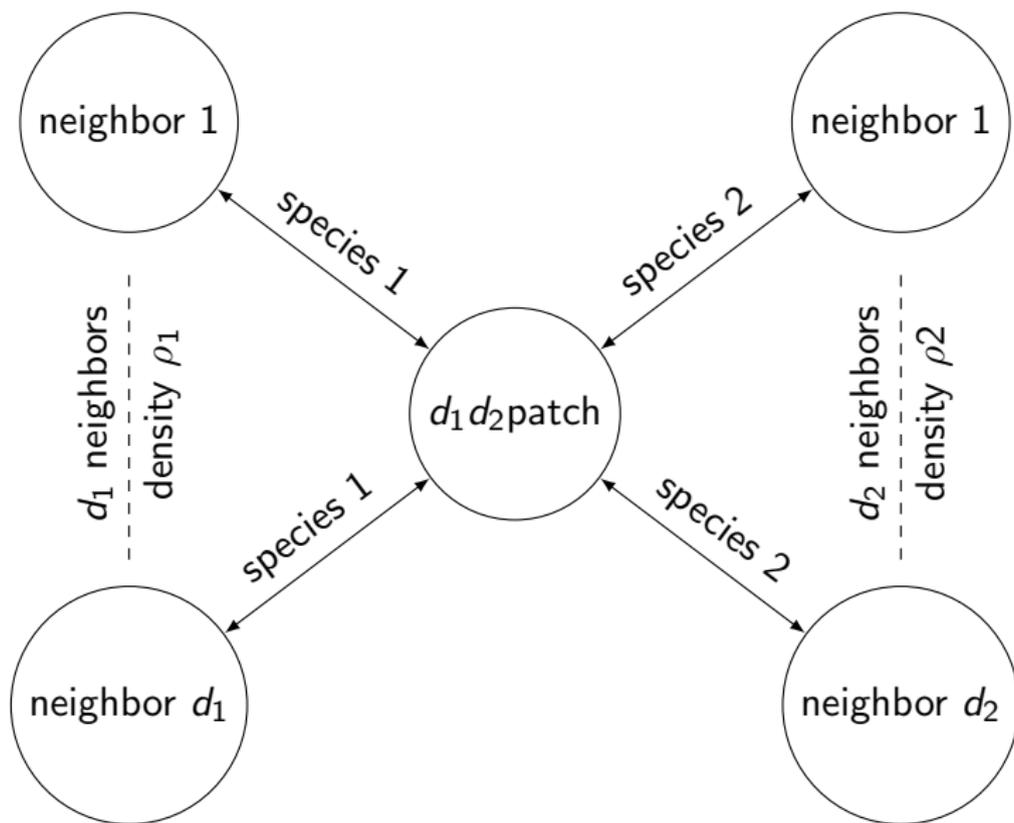
Each species  $\alpha$  in site  $i$  "sees"  $z_{\alpha i}$  neighbor patches occupied or not by species  $\alpha$  with **global probability**

$$\rho_{\alpha}^t = \frac{1}{n} \sum_i X_{i\alpha}^t$$

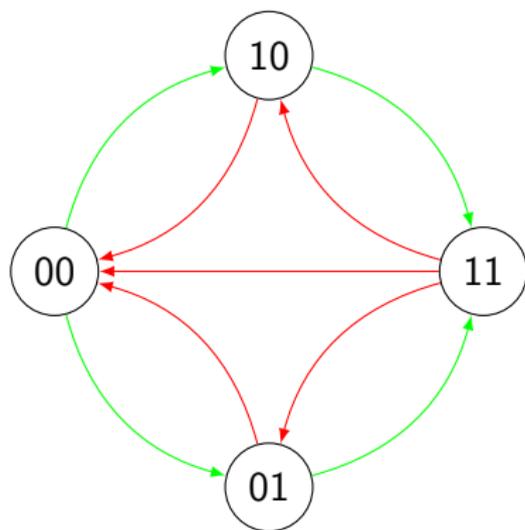
with equations ...

$$\begin{cases} \mathbb{P}(X_{i\alpha}^{t+dt} = 1 \mid X_{i\alpha}^t = 1) = 1 \\ \mathbb{P}(X_{i\alpha}^{t+dt} = 1 \mid X_{i\alpha}^t = 0) = c d_{\alpha i} \rho_{\alpha} dt \end{cases}$$

# Mean-Field approximation: with degree distribution (1/2)



# Mean-Field approximation: with degree distribution (2/2)



state at time $t + dt$	event ( $01 \rightarrow \dots$ )	rate
11	reaction	$R_{01,11} dt$
00	dispersal of species 2	$d_2 c_2 \rho_2^t dt$
01	no reaction	$1 - R_{00,01} d_1 t$
01	no dispersal of species 1	$1 - d_1 c_1 \rho_1^t dt$

# The role of space: graph families

## Geometry of networks

The within patches processes having been selected, what is the impact of the structures of dispersal graphs on the outcome of the model

- the quasi-stationary distribution
- the bifurcations (or phase transitions)

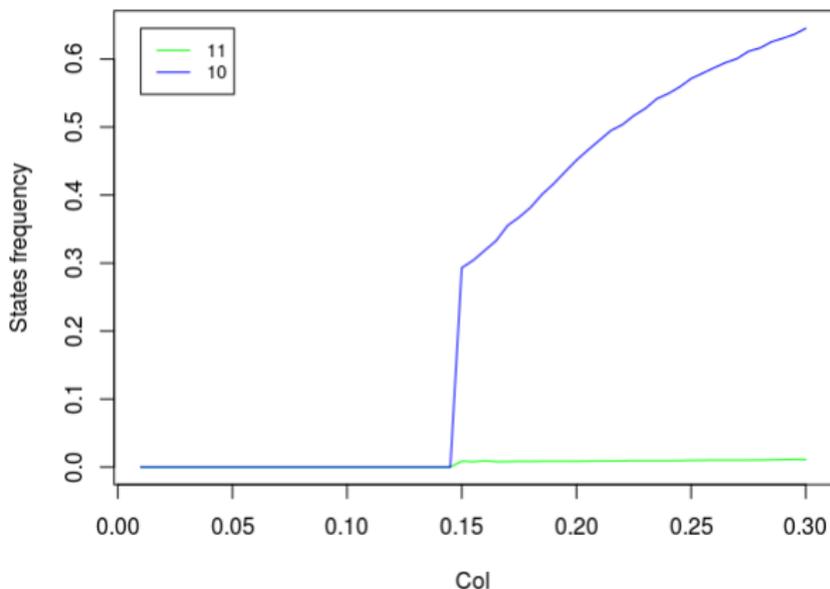
## Graph families

- a graph with  $n$  nodes can have  $2^{\frac{n(n-1)}{2}}$  edge patterns
- $\implies$  a simplification with the notion of *graph family*
- which is a rule to build a graph (with random)

## Exemples

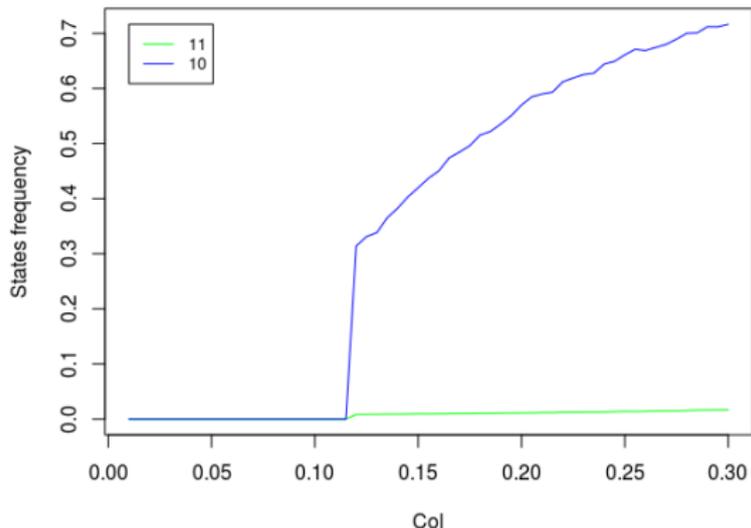
- Erdős-Rényi random graph with degree probability  $p$
- Geometric random graph
- Star graph

# Grid or a lattice



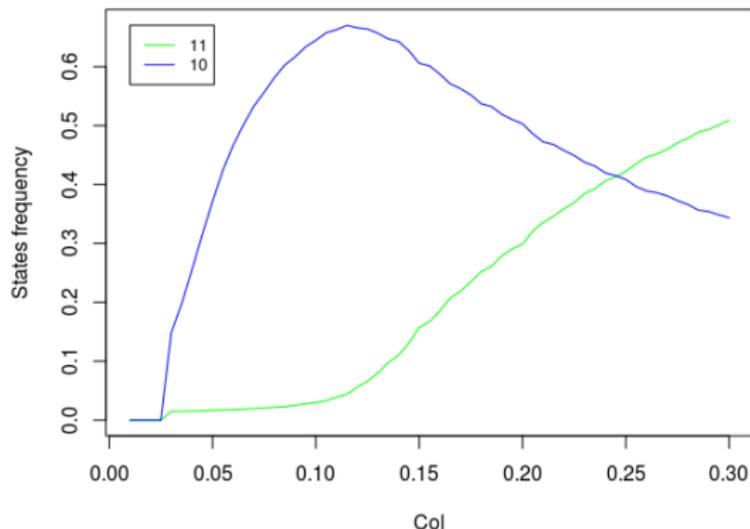
A host/parasite system (one colonization rate) ; the dispersal graph is a square grid of size  $7 \times 7$ ; healthy host in blue ; infected host in green.

# Geometric Random Graph



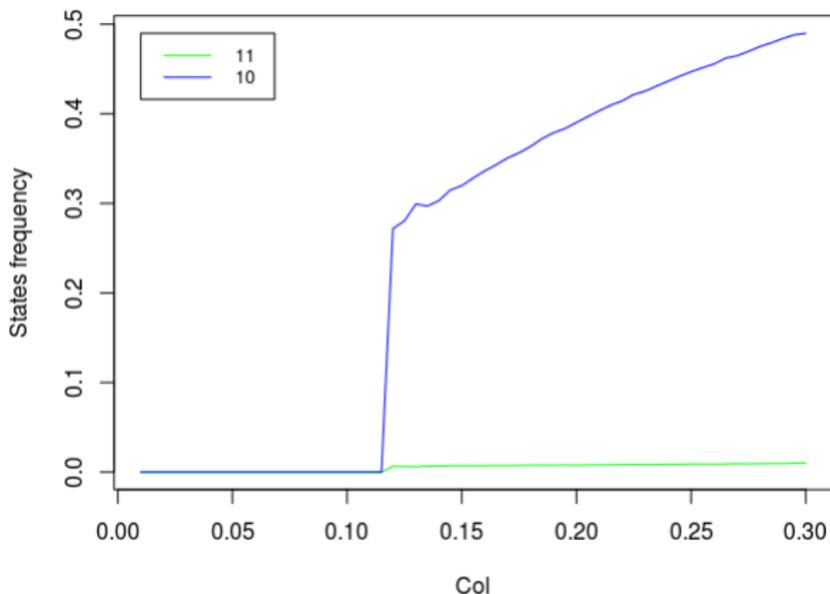
A host/parasite system (one colonization rate) ; the dispersal graph is a Geometric Random Graph ; **50 nodes** ; healthy host in blue ; infected host in green.

# Geometric Random Graph



A host/parasite system (one colonization rate) ; the dispersal graph is a Geometric Random Graph ; **100 nodes** ; healthy host in blue ; infected host in green.

# A star



A host/parasite system (one colonization rate) ; the dispersal graph is a star ; 50 nodes ; healthy host in blue ; infected host in green.

# Conclusions & perspectives

## Methods

- Some work remains to be done on mean-field approximation
- can be extended to pair approximation, Bethe, Kikuchi, ...

## Ecological models

The model is versatile: can be tuned with some work to be relevant in different situations:

- trophic web
- epidemiology (compartment models as mean field)
- biogeography (dispersal and competition between trees)

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ceba



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