A metaworld: metastability in metacommunities

Alain Franc, Nathalie Peyrard

A metaworld: metastability in metacommunities

A. Franc & N. Peyrard

INRA BioGeCo & MIAT

October 17th, 2017

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

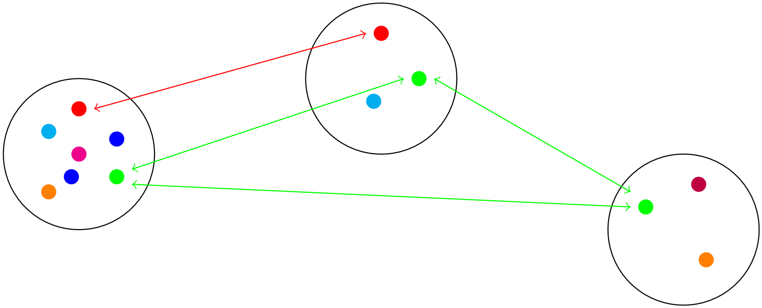
Bats and rabbies in French Guiana

- 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?

$\Rightarrow$ 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

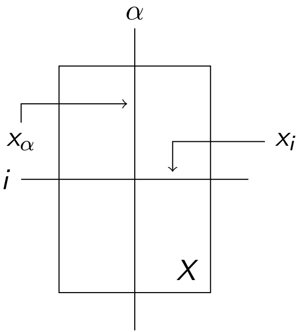
Is it possible to exhibit relevant results with simplifications like mean field approximation?

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 ($2^{np} \times 2^{np}$)

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

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

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

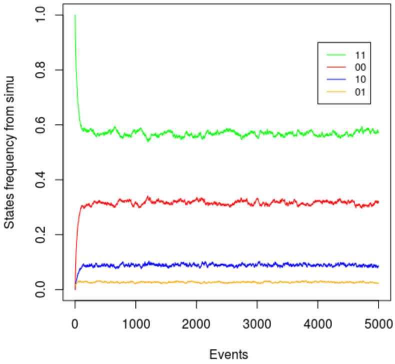
$$\mathbb{P}(X_i^{t+dt} = x \,|\, X_i^t = x') = \begin{cases} R_{i,xx'}\,dt & \text{if} \quad x \subsetneq x' \\ 1 - \sum_{x \subsetneq x'} R_{i,xx'}\,dt & \text{if} \quad x = x' \end{cases}$$

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

For each species α, dispersal along an edge of a weighted graph

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

Simulations ...



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

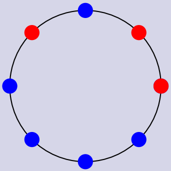
Metastability or quasi-stationary distribution

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

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

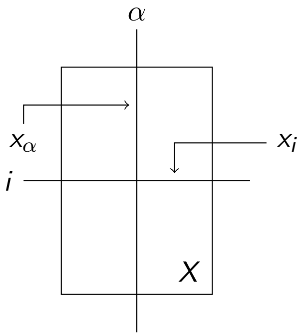
Conditionally Invariant Distribution

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

Quasi-stationary distribution

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

Computational Complexity



Computational Complexity

- Dynamics of a metacommunity is modeled as a Markov Chain on a state space Ω 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

$$P = \begin{pmatrix} 1 & A_{11} & \dots & A_1 q \\ 0 & P_1 & \ddots & \vdots \\ \vdots & \ddots & \ddots & A_{q-1,q} \\ 0 & \dots & \dots & P_q \end{pmatrix}$$

$\Longrightarrow$ 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	$(2^n - 1)^2$

bock sizes for $n = 10$

1×1	1×511	1×511	$1 \times 1\,046\,529$
$\mathbf{0}$	511×511	511×511	$511 \times 1\,046\,529$
$\mathbf{0}$	$\mathbf{0}$	511×511	$511 \times 1\,046\,529$
$\mathbf{0}$	$\mathbf{0}$	$\mathbf{0}$	$1\,046\,529 \times 1\,046\,529$

Mean-Field approximation: mean degree

(back to continuous time)

with words ...

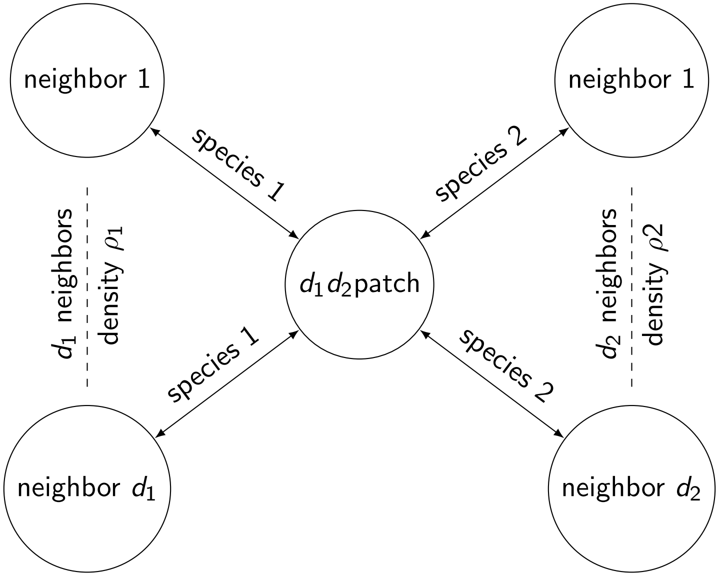
Each species α in site i "sees" $z_{\alpha i}$ neighbor patches occupied or not by species α with global probability

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

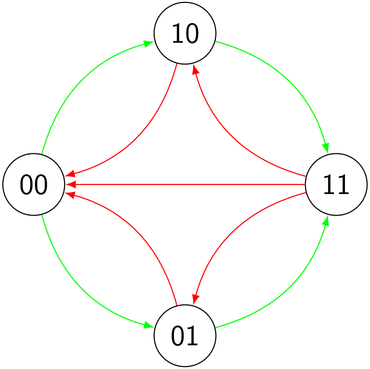
with equations ...

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

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



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



state at time $t + dt$	event $(01 \to \dots)$	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)

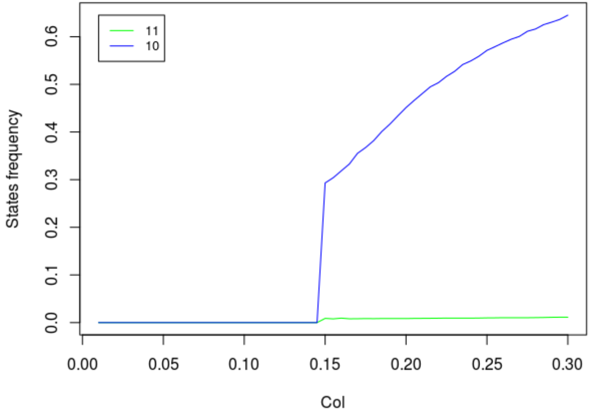
Graph families

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

Exemples

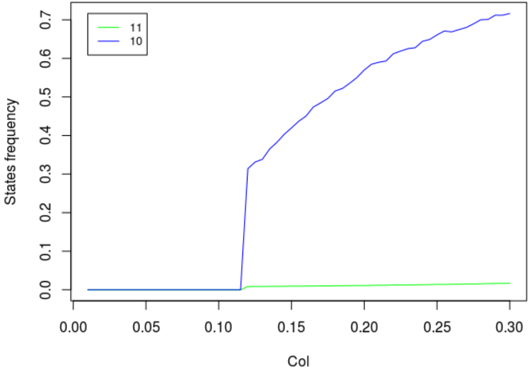
- Erdös-Rényi random graph with degree probability p
- Geometric random graph
- Star graph

Grid or a lattice



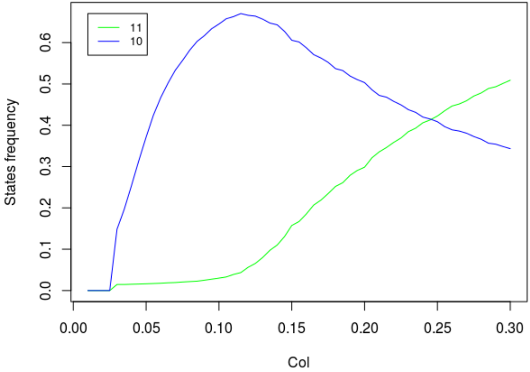
A host/parasite system (one colonization rate) ; the dispersal graph is a square grid of size 7×7; healthy host in blue ; infected host in green.

Geometric Random Graph



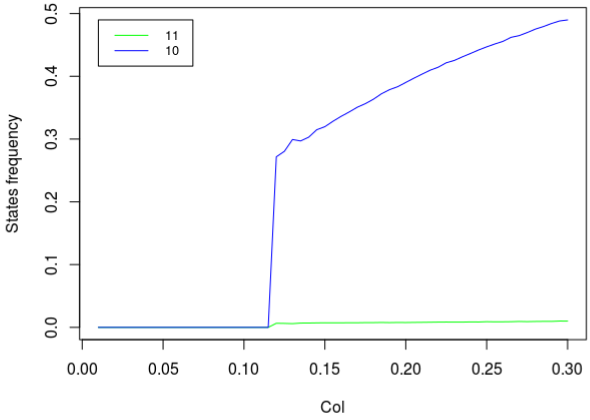
A host/parasite system (one colonization rate) ; the dispersal graph is a Geometric Random Graph ; 50 nodes ; healthy host in blue ; infected host in green.

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 (compartiment models as mean field)
- biogeography (dispersal and competition between trees)

Acknowlegements

- Labex CEBA (Centre d'Etde sur la Biodiversité Amazonienne)
- Programme *microbiome*

- Anne Lavergne & Benoit de Thoisy, Institut Pasteur de Cayenne