Network impact on persistence in a finite population dynamic exchange model

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Context: Emergence of an alternative agriculture model in France from 10 years: Réseau Semences Paysannes

Characteristics:

- people involved in seed autonomy
- **seed exchanges among farmers** and seed multiplication activities
- interest in old varieties of crop species
- small but growing community

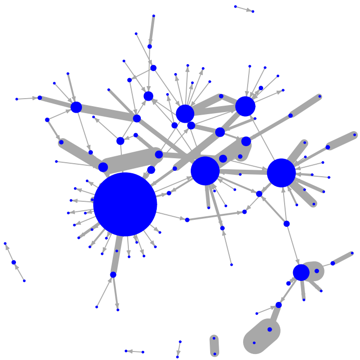
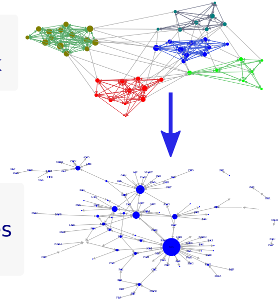


Figure : Seed exchange network among farmers involved in alternative agriculture

What are the properties of such system to maintain crop varieties?

Advice Network



Seed Exchanges network

Assumption

Seed exchange networks are nested within advice networks

Refine question

To what extent do the topological properties of the advice network influence the persistence of crop varieties?

Outline

Outline

Plan

Dynamic Model specifications: assumptions

- number of farms=nodes=patches (*n*) is fixed in time
- each patch has two possible states: presence or absence of the variety (no demography, drift, mutation, selection, migration and recombination).
- **Initial state**: every patch is occupied.

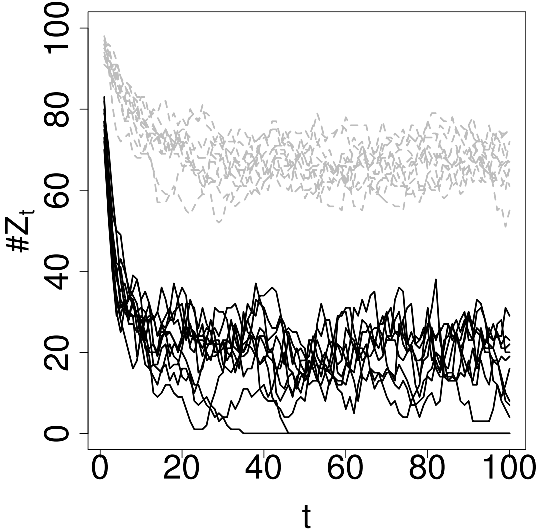
Temporal dynamic : 2 steps

- **extinction**: each occupied patches may be affected with probability *e*,
- **colonisation**: for empty patches with rate *c* from an occupied neighbour based on a **fixed network G**.

Remark

This model is similar to SIS (Susceptible Infected Susceptible) in epidemiology. Studied in Gilarranz& Bascompte (2012), Chakrabarti (2008)).

Assessing persistence under uncertainties



Equilibrium ?

- Model: $\{Z_t\}_{t\leq 0} \in \{0,1\}^N$: Markov chain with 2^N possible states.
- when N not too large (≤ 10), computing the transition matrix $M = E \cdot C$ (Day & Possingham (1995)).
- If $e > 0$, convergence of the chain toward its stationary distribution: a coffin state "total extinction":
- Extinction time:

$$T_0 = \inf\{t > 0, Z_t = 0\}\,,$$

$\mathbb{P}_z(T_0 < \infty) = 1$ for any initial state z .

Speed of convergence

$$\mathbb{P}_z(T_0 > t) = O(\lambda_{M,2}^t)\,,$$

where $\lambda_{M,2}$ is the second eigenvalue of M.

Quasi-equilibrium

- If $\mathbb{E}(T_0) >> nbgenerations \Rightarrow$ quasi-equilibrium.
- Z_t conditioned to $\{T_0 > t\}$ (non extinction) can converge toward a so-called quasi-stationary distribution
- If $\{Z_t\}_{t\geq 0}$ is irreducible and aperiodic ($\Leftrightarrow$ G has a unique connected component), existence and uniqueness of the quasi-stationary distribution (Darroch & Seneta, 1965).
- its transition matrix R is $2^n - 1 \times 2^n - 1$ obtained by deleting the first row and column of M.
- Convergence toward the quasi-stationary distribution is governed by $|\lambda_{R,2}|/\lambda_{R,1}$:

$$\sup_{z,z' \text{ transient states}} |\mathbb{P}_z(Z_t = z' | T_0 > t) - \alpha_{z'}| = O\left(\left(\frac{|\lambda_{R,2}|}{\lambda_{R,1}}\right)^t\right) . \quad (1)$$

- quasi-stationary distribution is met if $|\lambda_{R,2}|/\lambda_{R,1} << \lambda_{R,1}$.

quantities of interest/to be monitored

Our choice, study 100 generations to make the comparisons:

- Probability of persistence in 100 generations: $\mathbb{P}(T_0 > 100)$.
- Mean number of occupied patches at the 100th generation: $\mathbb{E}(\#Z_{100})$ or mean number of occupied patches at the 100th conditioned to non extinction $\mathbb{E}(\#Z_{100}|T_0 > 100)$.

Sensitivy Analysis

$$e,\ c,\ G \rightarrow \boxed{\text{Dynamic Model}} \rightarrow \mathbb{P}(T_0 > 100),\ \mathbb{E}(\#Z_{100})\,,$$

based on:

- exact computations when the number of patches ≤ 10,
- simulations otherwise, enhanced when necessary by particular or IS techniques.

Plan

Differences with deterministic models

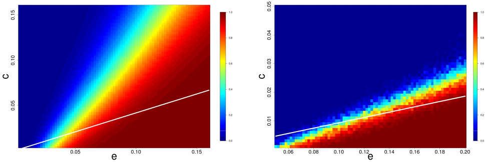


Figure : For fixed networks with 10 (lhs) and 100 patches (rhs), Probabilities of extinction in 100 generation with varying e and c.

White line corresponds to the threshold

$$e/c = \lambda_{G,1} .$$

(Hanski & Ovaskainen (2000); Sole & Bascompte (2006))

When dealing with a finite horizon in time and a finite population, ratio e/c is not sufficient.

Plan

In case of rare persistence

Algorithm 1

- **Initialisation:** N particles set at $Z_0^i = (1, \ldots, 1)$ for any $i = 1, \ldots, N$.
- **Iterations:** $t = 1, \ldots, 100$:
  - *Mutation:* Each particle evolves independently according to the Markov model (obtaining $\tilde{Z}_t^i$ from Z_{t-1}^i by simulation).
  - *Selection/Regeneration:* If $\tilde{Z}_t^i = 0$, then Z_t^i is randomly chosen among the surviving particles $\tilde{Z}_t^j \neq 0$. Otherwise $Z_t^i = \tilde{Z}_t^i$.
    Compute $\#E_t = \sum_{i=1}^N \mathbb{I}(\tilde{Z}_t^i = 0)/N$.

- Estimator of $\mathbb{P}(T_0 \leq 100)$: $\prod_{t=1}^{100} \#E_t$ (unbiased).
- Estimator of $\mathbb{E}(\#Z_{100} | T_0 > 100)$: $\sum_{i=1}^N Z_{100}^i / N$
- Sufficient number of particles N chosen to ensure that not all the particles die during a mutation step.

In case of rare extinction: Importance sampling

Algorithm 2

- **Initialisation:** $Z_0 = (1, \ldots, 1)$, a vector $(e_1^{IS}, \ldots, e_{100}^{IS})$ of twisted extinction rate chosen.
- **Iterations:** $t = 1, \ldots, 100$:
  - *Extinction* Extinction simulated with the corresponding twisted extinction rate e_t^{IS} and the ratio is computed as

    $$r_t = \left(\frac{e}{e_t^{IS}}\right)^{d_t} \cdot \left(\frac{1-e}{1-e_t^{IS}}\right)^{\#Z_{t-1}-d_t},$$

    with d_t number of extinction events which occur at generation t and $\#Z_{t-1} - d_t$ number of occupied patches which do not become extinct at generation t.
  - *Colonisation:* Colonisation is applied according to the model.

- N particles with ratio generated (can be done in parallel).
- Estimator of $\mathbb{P}(T_0 \leq 100)$: $\frac{1}{N}\sum_{i=1}^{N}\prod_{t=1}^{100} r_t^i \times \mathbb{I}(Z_{100}^i = 0)$
- Drawback: choice of $(e_1^{IS}, \ldots, e_{100}^{IS})$, better according to the variance if e_t^{IS} increases with t.

In case of rare extinction: Splitting technique with fixed success

Algorithm 3

- **Initialisation:** N particles set to $Z_0^i = (1, \ldots, 1)$ for any $i = 1, \ldots, N$. Choose the sequence of decreasing thresholds $S_1 \geq \ldots \geq S_p$ and the number of successes $n_{success}$. By convention, $S_{p+1} = 0$. Set the beginning level of trajectories $L_0^i = 0$ and starting state $Z_0^i = (1, \ldots, 1)$ for $i = 1, \ldots, n_{success}$.
- For each threshold S_m, $1 \leq m \leq p + 1$, set $s = 0$ and $k^m = 0$ and repeat until $s = n_{succes}$:
  - Do $k^m = k^m + 1$.
  - Choose uniformly $i \in \{1, \ldots, n_{success}\}$.
  - Simulate a trajectory from generation L_{m-1}^i at state Z_{m-1}^i: $(Z_t)_{L_{m-1}^i \leq t \leq 100}$.
  - If there exists t such that $Z_t \leq S_m$, do
    1. $s = s + 1$,
    2. $L_m^s = \inf\{t,\ Z_t \leq S_m\}$,
    3. $Z_m^s = Z_{L_m^s}$.

- Estimator of $\mathbb{P}(T_0 \leq 100)$: $\prod_{m=1}^{p+1} \frac{n_{succes}-1}{k^m-1}$
- Drawback: choice of $S_1, \ldots S_p$.

In case of rare extinction: Splitting technique with fixed success. Justification

$$\begin{aligned}\mathbb{P}(\#Z_{100}=0) &= \mathbb{P}(\exists t,\ \#Z_t=0)\\ &= \mathbb{P}(\exists t,\ \#Z_t\le S_1)\times\mathbb{P}(\exists t,\ \#Z_t\le S_2|\exists t,\ \#Z_t\le S_1)\\ &\quad\times\cdots\times\mathbb{P}(\exists t,\ \#Z_t=0|\exists t,\ \#Z_t\le S_p)\,,\end{aligned}$$

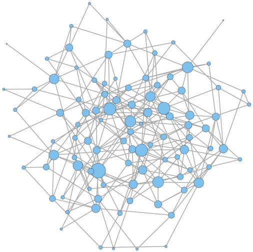
Extinction is split into intermediate less rare events (cross a level of number of a occupied patches).

Outline

Compare network topologies

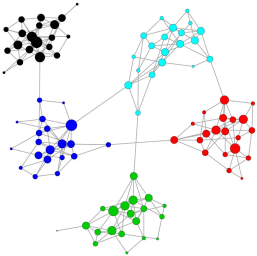
- Comparison of topologies for a fixed number of patches (difficulties to keep topological features when changing the number of patches).
- For a given number of edges/connections, simulations of graphs according to different models (different ways to distribute degrees):
  - Erdős-Rényi model (Erdős & Rényi, 1959),
  - Community model obtained thanks to Stochastic Block Models (Nowicki & Snijders, 2001),
  - Lattice model,
  - Preferential attachment model (Albert & Barabási, 2002).
- Following examples with 100 patches and 5% of possible edges (247 edges).

Random Graph: Erdős-Rényi model



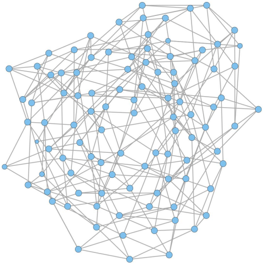
- Each pair of patches has the same probability to be linked by an edge.
- Independence of edges.

Community model



- Groups with the same intra and inter connection probabilities and same size.
- Stronger intra connection than inter connection.
- Conditionally to the groups of patches, independence of edges.

Lattice graphes



- Quasi-Homogeneity of degrees.
- May account for a spatially structured network.

Preferential attachment: Barabási-Albert

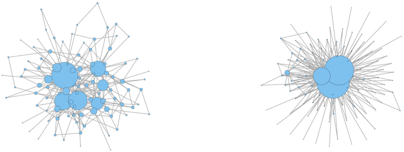


Figure : Preferential attachment networks with attachment power 1 and 3

- A sequentially constructed network.
- An incoming node is linked more likely to the most connected patches (rich get richer).
- $\mathbb{P}(\cdot \text{ linked to node } k) \propto \text{degree}(k)^{\text{pow}}$.

Outline

Plan

Sensitivity analysis

$$e,\ c,\ G \rightarrow \boxed{\text{Dynamic Model}} \rightarrow \mathbb{P}(T_0 > 100),\ \mathbb{E}(\#Z_{100}),$$

	10 patches	100 patches
e	$\{0.05,\ 0.10,\ 0.15\}$	$\{0.10,\ 0.20,\ 0.25\}$
c	$\{0.01,\ 0.05,\ 0.10\}$	$\{0.001,\ 0.005,\ 0.010\}$
d	$\{30\%,\ 50\%,\ 70\%\}$	$\{5\%,\ 10\%,\ 30\%\}$

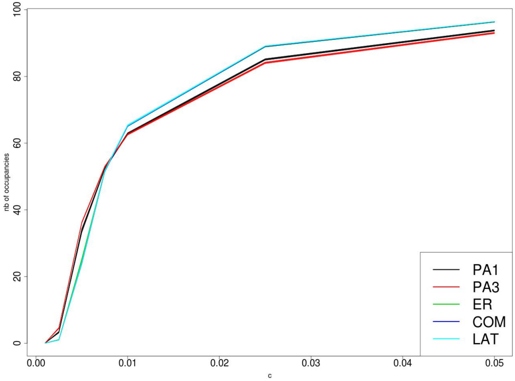
- d percentage of edges among $n(n-1)/2$ possible edges,
- G simulated with number of edges given by d and according to a chosen topology:
  - Erdős-Rényi,
  - Community (5 equal communities for $n = 100$, 2 equal communities for $n = 10$),
  - Lattice,
  - Preferential attachment (power 1),
  - Preferential attachment (power 3).
- ten replications for a chosen topology $\Rightarrow$ unique source of variability.

Sensitivity analysis

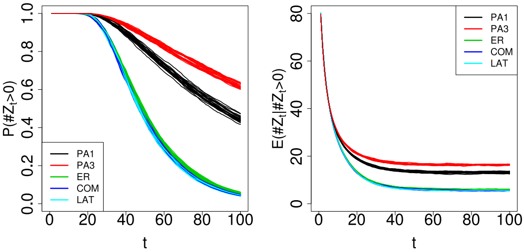
- Analysis of Variance with complete interactions to assess the significance of the parameters,
- main influent parameters are obviously e, c and d the density of G,
- network topology not always important, but can have a key impact for some settings of e, c, d especially when persistence is jeopardized.
- 2 main groups of networks leading to common behaviours
  1. Preferential attachment are more resistant if extinction is probable,
  2. Balanced networks (ER, COM, LAT) have a bigger number of occupancies ($\mathbb{E}(\#Z_{100})$ if extinction is unlikely,
- A network can be better for mean number of occupied patches and worse for the probability of persistence.

Inversion in the ranking of the topologies

As it was noticed in Gilarranz& Bascompte (2012)



An example of the crucial role of the topology in a particular setting



(a) (b)

Figure : (a) Probability of persistence and (b) mean number of occupied patches, in varying t generations (based on 20 replications of the network for a given topology) for $n = 100$, $c = 0.01$, $e = 0.25$ and $d = 30\%$. COM: community network, ER: Erdős-Rényi network, LAT: Lattice network, PA1: preferential attachment network with power 1, PA3: preferential attachment with power 3.

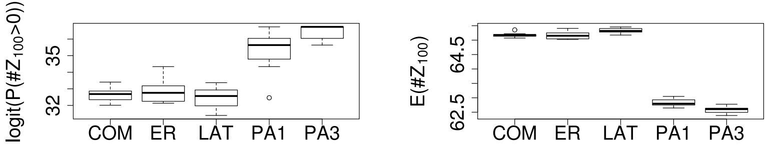
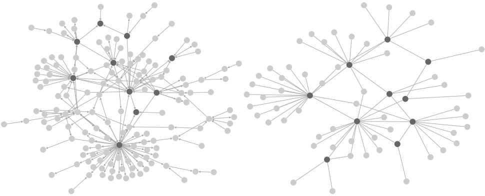


Figure : Boxplots of the probabilities of persistence over 100 generations and the number of occupied patches at generation 100 computed with 10 replications of each network topology. COM: community network, ER: Erdős-Rényi network, LAT: Lattice network, PA1: preferential attachment network with power 1, PA3: preferential attachment with power 3.

Plan

Survey from 1970 to 2005: Réseau Semences Paysannes



(a) (b)

Figure : (a) Summary network of bread wheat seed circulation among 152 farmers drawn from data collected based on 10 interviews covering a period from 1970 to 2005. (b) Subgraph of the reliable seed circulation events from 1970 to 2005 based on the 10 interviews and used to estimate $\hat{p}_{50}$. Interviewed people are in dark grey and mentioned people in light grey.

Scenarios and hypotheses

Networks with density fixed to $p_{50} = 0.21$ and $p_{500} = 0.021$ (constant number of connection)

- 1: random seed exchanges among few farmers (ER:50)
- 2: scale-free seed exchanges among few farmers (PA:50)
- 3: community-based seed exchanges among many farmers (COM:500), 10 groups of 50 farmers
- 4: random seed exchanges among many farmers (ER:500)
- 5: scale-free seed exchanges among many farmers (PA:500)

3 levels of event frequency (seed circulation) :

- low frequency $e = 0.1$,
- medium frequency $e = 0.5$,
- high frequency $e = 0.8$.

2 kinds of variety :

- popular $c = e$,
- rare $c = e/5$.

Results

Early networks,

	e	$\mathbb{P}(\#Z_{30} > 0)$	$\mathbb{E}(\#Z_{30})$
$e/c = 1$	0.1	$ER = PA = 1$	$ER \sim PA = 44$
	0.5	$ER = PA = 1$	$ER \gtrsim PA = 44$
	0.8	$ER = 0.9 > PA = 0.7$	$ER = 37 > PA = 25$
$e/c = 5$	0.1	$ER = PA = 1$	$PA \gtrsim ER = 25$
	0.5	$PA = 0.8 \gg ER = 0.3$	$PA = 13 \gg ER = 3$
	0.8	$PA = ER = 0$	$PA = ER = 0$

Final networks,

	e	$\mathbb{P}(\#Z_{30} > 0)$	$\mathbb{E}(\#Z_{30})$
$e/c = 1$	0.1	$PA = ER = COM = 1$	$ER \sim COM \gtrsim PA = 425$
	0.5	$PA = ER = COM = 1$	$ER \sim COM \gtrsim PA = 427$
	0.8	$PA \sim ER = COM = 1$	$ER \sim COM = 382 > PA = 314$
$e/c = 5$	0.1	$PA = ER = COM = 1$	$ER \sim COM \sim PA = 249$
	0.5	$ER \sim COM \sim PA = 1$	$PA = 193 \gg ER \gg COM = 40$
	0.8	$PA = 0.5 \gg ER = COM = 0$	$PA = 43 > ER = COM = 0$

Outline

- Stochastic context with a finite number of patches $\Rightarrow$ finite number of generations studied (chosen according to the application context).
- Differences with the deterministic approximation, notion of threshold questioned.
- "Extreme" situation studied thanks to improved algorithms.
- Most of the times, the role of the topology is not crucial except in cases with high uncertainties.
- Topologies with hubs / central patches are more resistant in case of a likely extinction.
- Community and ER topologies are quite close.

Questions and further works

- Estimation of parameters e, c, G sampling individuals of a network.
- Varying network over time...
- Several varieties of crop in the system (with interaction...)
- Refined study on the community topology.
  - different size of communities,
  - different activities,
  - hub in communities.

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