Probabilistic models for (ecological) networks

Sophie Donnet. MIA Paris-Saclay, UMR INRAE - AgroParisTech, APPLIBUGS Meeting. Dec. 2021

Introduction

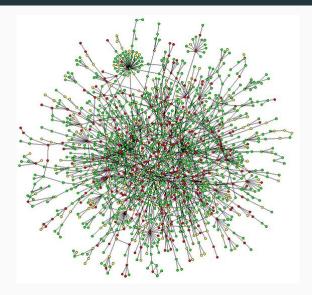
Descriptive statistics

Probabilistic models

Frequentist and Bayesian inference

Conclusion

Network data





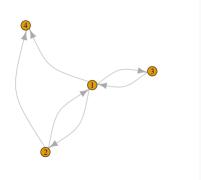
Networks can account for

- Ecological networks : Food web , Co-existence networks, Host-parasite interactions, Plant-pollinator interactions,
- Social networks
- Inventory datasets : who cultivates what?
- ...

A network

- nodes/vertices which represent individuals / species /ships which may interact or not,
- links/edges/connections which stand for an interaction between a pair of nodes / dyads.

For a directed relation: advice networks, foodwebs,

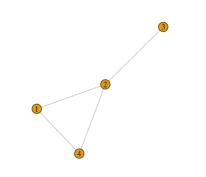






- *n* rows and *n* columns,
- non symmetric matrix

For a non-directed relation: co-occurrence, co-publication, ...

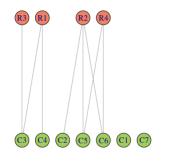


 $Y = \left(\begin{array}{rrrrr} 0 & 1 & 0 & 1 \\ 1 & 0 & 1 & 1 \\ 0 & 1 & 0 & 0 \\ 1 & 1 & 0 & 0 \end{array}\right)$

- *n* rows and *n* columns,
- symmetric matrix

In general, no self-loop

Two types of nodes : Plant-pollinators, farmer-crop species, clients-films on netflix



- n rows and m columns
- rectangular matrix

- Unraveling / describing / modeling the network topology.
- Discovering particular structure of interaction between some subsets of nodes.
- Understanding network heterogeneity.
- Not inferring the network !

Additional available data



- the network provided as:
 - an adjacency matrix (for simple network) or an incidence matrix (for bipartite network),
 - a list of pair of nodes / dyads which are linked.
- some additional covariates on nodes, dyads which can account for sampling effort.

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Some common features studied on networks

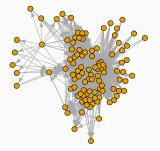
- Degree of a node: number of connexion for each node.
- Degree distribution can be viewed as a measure of heterogeneity,
- Nestedness: a network is said to be nested when its nodes that have the smallest degree, are connected to nodes with the highest degree, [Rodríguez-Gironés and Santamaría, 2006]
- Betweenness centrality: for a node, numbers of shortest paths between any pair of nodes passing through this node. [Freeman, 1978]
- Modularity: is a measure for a given partition of its tendency of favoring intra-connection over inter-connection. ⇒ Finding the best partition with respect to modularity criterion. [Clauset et al., 2008]

All this criterion shall be adapted to:

- directed network,
- bipartite network.

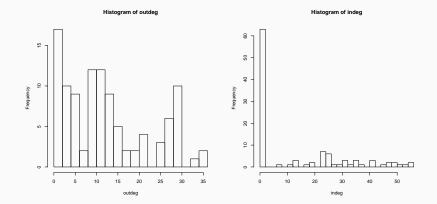
R packages: igraph, sna, vegan.

Example Chilean food web



- n = 106 species / nodes,
- density of edges: 12.1%.

[Kéfi et al., 2016]



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Probabilistic models The stochastic Block Model Latent block models Some possible extensions

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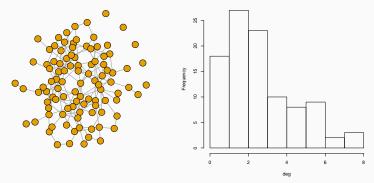
- Context: our matrix Y is the realization of a stochastic process.
- Aim: Propose a stochastic process is able to mimic heterogeneity in the connections.
- Advantage: benefit from the statistical tools (tests, model selection, etc...)

A first random graph model for network: null model

Erdős-Rényi (1959) Model for n nodes

$$\forall 1 \leq i, j \leq n, \quad Y_{ij} \stackrel{i.i.d.}{\sim} \mathcal{B}ern(p),$$

where $p \in [0, 1]$ a probability for a link to exist.



degree distribution

- Homogeneity of the connections
- Degree distribution too concentrated, no high degree nodes,
- All nodes are equivalent (no nestedness...),
- No modularity, no hubs

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[Nowicki and Snijders, 2001] Let (Y_{ij}) be an adjacency matrix

Latent variables

- The nodes i = 1, ..., n are partitionned into K clusters
- $Z_i = k$ if node *i* belongs to cluster (block) *k*
- Z_i independant variables

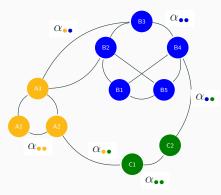
$$\mathbb{P}(Z_i=k)=\pi_k$$

Conditionally to $(Z_i)_{i=1,...,n}$...

 (Y_{ij}) independant and

$$Y_{ij}|Z_i, Z_j \sim \mathcal{B}ern(\alpha_{Z_i, Z_j}) \quad \Leftrightarrow \quad P(Y_{ij} = 1|Z_i = k, Z_j = \ell) = \alpha_{k\ell}$$

Stochastic Block Model : illustration



Parameters

Let n nodes divided into 3 clusters

• $\mathcal{K} = \{\bullet, \bullet, \bullet\}$ clusters

•
$$\pi_{\bullet} = \mathbb{P}(i \in \bullet), \ \bullet \in \mathcal{K}, i = 1, \dots, n$$

•
$$\alpha_{\bullet\bullet} = \mathbb{P}(i \leftrightarrow j | i \in \bullet, j \in \bullet)$$

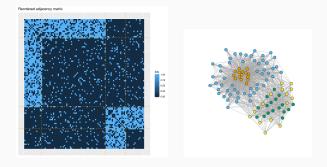
$$Z_i = \mathbf{1}_{\{i \in \bullet\}} \quad \sim^{\text{iid}} \mathcal{M}(1, \pi), \quad \forall \bullet \in \mathcal{K},$$
$$Y_{ij} \mid \{i \in \bullet, j \in \bullet\} \sim^{\text{ind}} \mathcal{B}(\alpha_{\bullet \bullet})$$

- Generative model : easy to simulate
- Very flexible
- Combination of modularity, nestedness, etc...

Networks with hubs generated by SBM

•
$$\pi = c(.15, .35, .15, .35)$$

• $\alpha = \begin{pmatrix} 0.80 & 0.80 & 0.20 & 0.20 \\ 0.80 & 0.20 & 0.20 & 0.20 \\ 0.20 & 0.20 & 0.80 & 0.80 \\ 0.20 & 0.20 & 0.80 & 0.20 \end{pmatrix}$

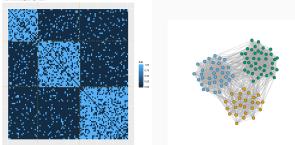


Community network generated by SBM

•
$$\pi = c(0.25, 0.35, 0.40)$$

• $\alpha = \begin{pmatrix} 0.80 & 0.20 & 0.20 \\ 0.20 & 0.80 & 0.20 \\ 0.20 & 0.20 & 0.80 \end{pmatrix}$

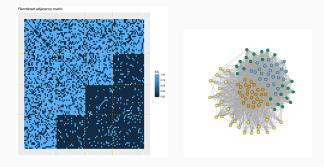
Reordered adjacency matrix



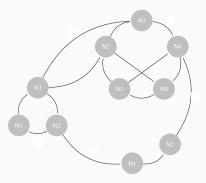
Nestedness generated by SBM

•
$$\pi = c(.15, .35, .15, .35)$$

• $\alpha = \begin{pmatrix} 0.80 & 0.80 & 0.80 & 0.80 \\ 0.80 & 0.80 & 0.80 & 0.20 \\ 0.20 & 0.80 & 0.20 & 0.80 \\ 0.80 & 0.20 & 0.20 & 0.20 \end{pmatrix}$



Statistical inference



Stochastic Block Model

Let n nodes divided into

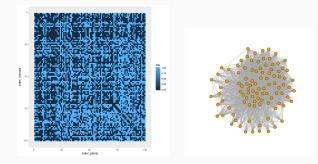
• $\mathcal{K} = \{\bullet, \bullet, \bullet\}$, card(\mathcal{K}) known

[Nowicki and Snijders, 2001], [Daudin et al., 2008]

R packages: blockmodels, sbm

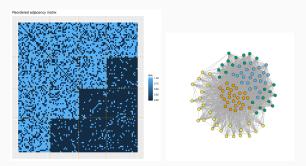
Statistical inference

From....



Statistical inference

... to



Statistician job

- Find the clusters
- Find the number of clusters
- Practical implementation
- Theoretical results

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Let Y_{ij} be a bi-partite network. Individuals in row and cols are not the same.

Latent variables : bi-clustering

- Nodes i = 1,..., n₁ partitionned into K₁ clusters, nodes j = 1,..., n₂ partitionned into K₂ clusters
 - $Z_i^1 = k$ if node *i* belongs to cluster (block) k $Z_j^2 = \ell$ if node *j* belongs to cluster (block) ℓ
- Z_i^1, Z_j^2 independent variables

$$\mathbb{P}(Z_i^1=k)=\pi_k^1, \quad \mathbb{P}(Z_j^2=\ell)=\pi_\ell^2$$

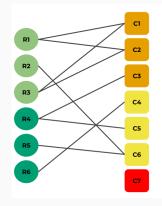
Conditionally to $(Z_i^1)_{i=1,\ldots,n_1}, (Z_j^2)_{j=1,\ldots,n_2}...$

 (Y_{ij}) independent and

$$Y_{ij}|Z_i^1, Z_j^2 \sim \mathcal{B}ern(\alpha_{Z_i^1, Z_i^2}) \quad \Leftrightarrow \quad \mathbb{P}(Y_{ij} = 1|Z_i^1 = k, Z_j^2 = \ell) = \alpha_{k\ell}$$

[Govaert and Nadif, 2008]

Latent Block Model : illustration



$$Z_i^R = \mathbf{1}_{\{i \in \bullet\}} \quad \sim^{\text{iid}} \mathcal{M}(1, \pi^R), \quad \forall \bullet \in \mathcal{Q}_R,$$
$$Z_j^C = \mathbf{1}_{\{j \in \bullet\}} \quad \sim^{\text{iid}} \mathcal{M}(1, \pi^C), \quad \forall \bullet \in \mathcal{Q}_C,$$
$$Y_{ij} \mid \{i \in \bullet, j \in \bullet\} \sim^{\text{ind}} \mathcal{B}ern(\alpha_{\bullet\bullet})$$

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Valued-edge networks

Values-edges networks

Information on edges can be something different from presence/absence. It can be:

- 1. a count of the number of observed interactions,
- 2. a quantity interpreted as the interaction strength,

Natural extensions of SBM and LBM

- 1. Poisson distribution: $Y_{ij} \mid \{i \in \bullet, j \in \bullet\} \sim^{ind} \mathcal{P}(\lambda_{\bullet \bullet}),$
- 2. Gaussian distribution: $Y_{ij} \mid \{i \in \bullet, j \in \bullet\} \sim^{\text{ind}} \mathcal{N}(\mu_{\bullet\bullet}, \sigma^2)$, [Mariadassou et al., 2010]
- 3. More generally,

$$Y_{ij} \mid \{i \in \bullet, j \in \bullet\} \sim^{\mathsf{ind}} \mathcal{F}(\theta_{\bullet \bullet})$$

Sometimes covariates are available. They may be on:

- nodes,
- edges,
- both.
- 1. They can be used a posteriori to explain blocks inferred by SBM.
- 2. Extension of the SBM which takes into account covariates. Blocks are structure of interaction which is not explained by covariates !

If covariates are sampling conditions, case 2 be may more interesting.

SBM with covariates

- As before : (*Y_{ij}*) be an adjacency matrix
- Let $x^{ij} \in \mathbb{R}^p$ denote covariates describing the pair (i, j)

Latent variables : as before

- The nodes *i* = 1, ..., *n* are partitioned into *K* clusters
- *Z_i* independent variables

$$\mathbb{P}(Z_i=k)=\pi_k$$

Conditionally to $(Z_i)_{i=1,...,n}$...

 (Y_{ij}) independent and

If K = 1: all the connection heterogeneity is explained by the covariates.

Multiplex networks

Several kind of interactions between nodes . For instance :

- Love and friendship
- Working relations and friendship
- In ecology : mutualistic and competition

Block model for multiplex networks

$$Y_{ij} \in \{0,1\}^Q = (Y^a_{ij},Y^b_{ij}), \, orall w \in \{0,1\}^2$$

$$\mathbb{P}(Y_{ij}^{a}, Y_{ij}^{b} = w | Z_{i} = k, Z_{j} = \ell) = \alpha_{k\ell}^{w}$$

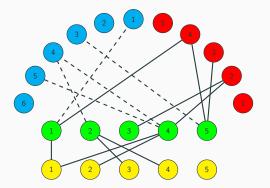
[Kéfi et al., 2016], [Barbillon et al., 2017]

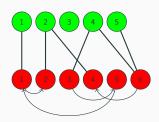
In R package: blockmodels when two relations are at stake.

Remark: a particular case of multiplex network is dynamic network, [Matias and Miele, 2017].

Multipartite networks

More than 2 types of nodes : Plant-pollinators, plant-ants interactions for instance





[Kéfi et al., 2016], [Bar-Hen et al., 0] In R package: GREMLINS and sbm

Descriptive statistics

Probabilistic models

Frequentist and Bayesian inference Statistical tasks and likelihood Frequentist inference Bayesian inference

Descriptive statistics

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Frequentist inference

Bayesian inference

- Selection of the number of clusters K for SBM or K_1, K_2 for LBM
- Estimation of the parameters π, θ for a given number of clusters
- Clustering $\hat{\boldsymbol{Z}}$

Complete likelihood (Y) et (Z)

$$\begin{aligned} \mathcal{Q}_{c}(\mathbf{Y}, \mathbf{Z}; \theta) &= p(\mathbf{Y} | \mathbf{Z}; \alpha) p(\mathbf{Z}; \pi) \\ &= \prod_{i,j} f_{\alpha_{Z_{i}, Z_{j}}}(Y_{ij}) \times \prod_{i} \pi_{Z_{i}} \\ &= \prod_{i,j} \alpha_{Z_{i}, Z_{j}}^{Y_{ij}} (1 - \alpha_{Z_{i}, Z_{j}})^{1 - Y_{ij}} \prod_{i} \pi_{Z_{i}} \end{aligned}$$

Marginal likelihood (Y)

$$\log \ell(\mathbf{Y}; \theta) = \log \sum_{\mathbf{Z} \in \boldsymbol{\mathcal{Z}}} \ell_c(\mathbf{Y}, \mathbf{Z}; \theta) \,. \tag{1}$$

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$$\log \ell(\mathbf{Y}; \theta) = \log \sum_{\mathbf{Z} \in \boldsymbol{\mathcal{Z}}} \ell_c(\mathbf{Y}, \mathbf{Z}; \theta).$$

Remark

 $\mathcal{Z} = \{1, \dots, K\}^n \Rightarrow$ when K and n increase, impossible to compute.

Standard tool to maximize the likelihood when latent variables involved : EM algorithm.

Standard EM

At iteration (t) :

• Step E: compute

$$Q(\theta|\theta^{(t-1)}) = \mathbb{E}_{\mathbf{Z}|\mathbf{Y},\theta^{(t-1)}}\left[\log \ell_c(\mathbf{Y},\mathbf{Z};\theta)\right]$$

• Step M:

$$\theta^{(t)} = \arg \max_{\theta} Q(\theta | \theta^{(t-1)})$$

- Step E requires the computation of
 ^E_{Z|Y,θ^(t-1)} [log ℓ_c(Y, Z; θ)]
- However, once conditioned by par Y, the Z are not independent anymore: complex distribution if K and n big.

Variational EM : maximization of a lower bound

Idea : replace the complicated distribution $p(\cdot | \mathbf{Y}; \theta) = [\mathbf{Z} | \mathbf{Y}, \theta]$ by a simpler one.

Let $\mathcal{R}_{\mathbf{Y},\tau}$ be any distribution on \mathbf{Z}

Central identity

$$\begin{aligned} \mathcal{I}_{\theta}(\mathcal{R}_{\mathbf{Y},\tau}) &= \log \ell(\mathbf{Y};\theta) - \mathsf{KL}[\mathcal{R}_{\mathbf{Y},\tau}, p(\cdot|\mathbf{Y};\theta)] &\leq \log \ell(\mathbf{Y};\theta) \\ &= \mathbb{E}_{\mathcal{R}_{\mathbf{Y},\tau}} \left[\log \ell_c(\mathbf{Y},\mathbf{Z};\theta) \right] - \sum_{\mathbf{Z}} \mathcal{R}_{\mathbf{Y},\tau}(\mathbf{Z}) \log \mathcal{R}_{\mathbf{Y},\tau}(\mathbf{Z}) \\ &= \mathbb{E}_{\mathcal{R}_{\mathbf{Y},\tau}} \left[\log \ell_c(\mathbf{Y},\mathbf{Z};\theta) \right] + \mathcal{H} \left(\mathcal{R}_{\mathbf{Y},\tau}(\mathbf{Z}) \right) \end{aligned}$$

Note that:

$$\mathcal{I}_{ heta}(\mathcal{R}_{\mathbf{Y}, au}) = \log \ell(\mathbf{Y}; heta) \Leftrightarrow \mathcal{R}_{\mathbf{Y}, au} = p(\cdot | \mathbf{Y}; heta)$$

- Maximization of log ℓ(Y; θ) w.r.t. θ replaced by maximization of the lower bound *I*_θ(*R*_{Y,τ}) w.r.t. τ and θ.
- Benefit : we choose $\mathcal{R}_{\mathbf{Y},\tau}$ such that the maximization calculus can be done explicitly
 - In our case: mean field approximation : neglect dependencies between the (Z_i)

$$P_{\mathcal{R}_{\mathbf{Y},\tau}}(Z_i=k)=\tau_{ik}$$

Algorithm

At iteration (t), given the current value $(\theta^{(t-1)}, \mathcal{R}_{\mathbf{Y}, \tau^{(t-1)}})$,

• Step 1 Maximization w.r.t. τ

$$\begin{split} \tau^{(t)} &= \arg \max_{\tau \in \mathcal{T}} \mathcal{I}_{\theta^{(t-1)}}(\mathcal{R}_{\mathbf{Y},\tau}) \\ &= \arg \min_{\tau \in \mathcal{T}} \mathsf{KL}[\mathcal{R}_{\mathbf{Y},\tau}, p(\cdot|\mathbf{Y}; \theta^{(t-1)})] \end{split}$$

• Step 2 Maximization w.r.t. $\boldsymbol{\theta}$

$$\begin{split} \theta^{(t)} &= \arg \max_{\theta} \mathcal{I}_{\theta}(\mathcal{R}_{\mathbf{Y},\tau^{(t)}}) \\ &= \arg \max_{\theta} \mathbb{E}_{\mathcal{R}_{\mathbf{Y},\tau^{(t)}}}\left[\log \ell_{c}(\mathbf{Y},\mathbf{Z};\theta)\right] \end{split}$$

- Really fast
- Strongly depend on the initial values

- Selection of the number of clusters K (or K₁, K₂ in the LBM)
- Integrated Classification Likelihood (ICL) [Biernacki et al., 2000]

$$ICL(\mathcal{M}_{\mathbf{K}}) = \log \ell_{c}(\mathbf{Y}, \hat{\mathbf{Z}}; \hat{\theta}_{\mathbf{K}}) - \operatorname{pen}(\mathcal{M}_{\mathbf{K}})$$
(2)

where

$$\hat{Z}_i = \underset{k \in \{1, \dots, K\}}{\arg \max} \hat{\tau}_{ik}.$$
(3)

Integrated Complete Likelihood (ICL)

$$ICL(\mathcal{M}_{\mathbf{K}}) = \mathbb{E}_{p(\cdot|\mathbf{Y},\hat{\theta}_{\mathbf{K}})}[\log \ell_{c}(\mathbf{Y},\hat{\mathbf{Z}};\hat{\theta}_{\mathbf{K}}) - \operatorname{pen}(\mathcal{M}_{\mathbf{K}})$$
(4)

Expression of the penalization

For SBM

$$pen_{\mathcal{M}} = \begin{cases} -\frac{1}{2} \left\{ (K-1)\log(n) + K^{2}\log(n^{2}-n) \right\} & \text{for directed network} \\ -\frac{1}{2} \left\{ \underbrace{(K-1)\log(n)}_{\text{Clust.}} + \frac{K(K+1)}{2}\log\left(\frac{n^{2}-n}{2}\right) \right\} & \text{for undirected network} \end{cases}$$

For LBM

$$pen_{\mathcal{M}} = -\frac{1}{2} \qquad \left\{ \underbrace{(K_1 - 1)\log(n_1) + (K_2 - 1)\log(n_2)}_{\text{Bi-Clust.}} + \underbrace{(K_1K_2)\log(n_1n_2)}_{\text{Connection}} \right\}$$

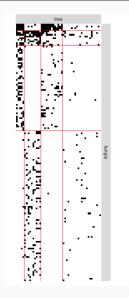
- its capacity to outline the clustering structure in networks
- Involves a trade-off between goodness of fit and model complexity
- ICL values : goodness of fit AND clustering sharpness.

Application : interactions Tree-fungi



- Fungi: Amphiporthe leiphaemia, Apiognomonia errabunda, Apiognomonia veneta, Armillaria cepistipes, Armillaria gallica,...
- Trees: Abies alba, Abies grandis, Abies nordmanniana, Large Maples (Acer platanoides, Acer pseudoplatanus), Small Maples

Application : reordered Tree-fungi



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$$(\pi_1, \ldots, \pi_K) \sim \mathcal{D}ir(a_1, \ldots, a_K)$$

 $\alpha_{kl} \sim \mathcal{B}eta(a_0, b_0)$

- Solution 1: any MCMC sampler
- Solution 2 : variational Bayes

[Latouche et al., 2012]

- Idea: approximate $p(\mathbf{Z}, \theta | \mathbf{Y})$ by a simpler one $q(\mathbf{Z}, \theta)$
- Approximating = Minimizing

$$D_{\mathsf{KL}}(q(\mathsf{Z}, heta), p(\mathsf{Z}, heta|\mathsf{Y})) = \mathsf{E}_q\left[\lograc{q(\mathsf{Z}, heta)}{p(\mathsf{Z}, heta|\mathsf{Y})}
ight]$$

$$D_{\mathsf{KL}}(q(\mathsf{Z},\theta), p(\mathsf{Z},\theta|\mathsf{Y})) = \\ \log \ell(\mathsf{Y}) - \left[\underbrace{\mathsf{E}_{q}[\log \ell(\mathsf{Y}|\mathsf{Z},\theta)p(\mathsf{Z}|\theta)\pi(\theta)] - \mathsf{E}_{q}[\log q(\mathsf{Z},\theta)]}_{\mathcal{F}(q)}\right]$$

- $\log \ell(\mathbf{Y})$ independent of q
- Minimizing the KL w.r. to q is equivalent to maximizing $\mathcal{F}(q)$ with respect to q

Choose a form for

$$q(\mathbf{Z}, \theta) = q_{\tau}(\mathbf{Z}) \; q_{\mathcal{D}ir}(\pi) q_{\mathcal{B}eta}(\alpha)$$

- Iteratively maximization in the various parameters
- Conjugacy helps to be able to explicitly maximize

- In presence of covariates, no more explicite maximization.
- Our solution
 - Build a pseudo posterior distribution using the Variational EM algorithm with estimation of the variance with Louis formula
 - Use this first posterior approximation to accelerate a sequential Monte Carlo sampler to get a sample from the true posterior
 - [Donnet and Robin, 2021]

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$\mathsf{SBM}/\mathsf{LBM}$

- generative models,
- flexible,
- comprehensive models which can be linked to a lot of classical descriptors.

- Time evolving networks Matias
- Multipartite, Multiplexe networks
- Multilevel networks (individuals and organizations) [Chabert-Liddell et al., 2021b]
- Collections of networks (on going work by CL)
- Link with robustness of ecological networks [Chabert-Liddell et al., 2021a]
- Missing data in the network [Tabouy et al., 2020]
- R-package sbm

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Conjecture

$$BIC(\mathcal{M}) = \log \ell(\mathbf{Y}; \hat{\theta}, \mathcal{M}) - \operatorname{pen}(\mathcal{M})$$

with the same penalty

Under this conjecture

$$ICL(\mathcal{M}) = BIC(\mathcal{M}) + \sum_{\mathbf{Z}} p(\mathbf{Z}|\mathbf{Y}; \hat{\theta}_{\mathbf{K}}) \log p(\mathbf{Z}|\mathbf{Y}; \hat{\theta}_{\mathbf{K}})$$
$$= BIC(\mathcal{M}) - \mathcal{H}(p(\cdot|\mathbf{Y}; \theta))$$

 As a consequence, because of the entropy, ICL will encourage clustering with well-separated groups

$$\widehat{ICL}(\mathcal{M}) = BIC(\mathcal{M}) + \sum_{\mathbf{Z}} \mathcal{R}_{\mathbf{Y}}(\mathbf{Z}, \widehat{\tau}) \log \mathcal{R}_{\mathbf{Y}, \widehat{\tau}}(\mathbf{Z}) - \mathsf{KL}[\mathcal{R}_{\mathbf{Y}, \widehat{\tau}}, p(\cdot | \mathbf{Y}; \widehat{\theta})].$$
⁶⁹

- Going trough the models and initiate VEM at the same time
- Bounds on $K : \{K_{\min}, \ldots, K_{\max}\}$

Stepwise procedure

Starting from K

- Split : if $K < K_{max}$
 - Maximize the likelihood (lower bound) of \mathcal{M}_{K+1}
 - *K* initializations of the VEM are proposed : split each cluster into 2 clusters
- Merge : If $K > K_{min}$
 - Maximize the likelihood (lower bound) of model $\mathcal{M}_{\mathcal{K}-1}$
 - $\frac{K(K-1)}{2}$ initializations of the VEM are proposed : merging all the possible pairs of clusters

- Identifiability and a first consistency result by [Celisse et al., 2012]
- Consistency of the posterior distribution of the latent variables [Mariadassou and Matias, 2015]
- Consistency and properties of the variational estimators [Bickel et al., 2013]