Bayesian Modelling of Abundance Data in Ecology Using Joint Species Distribution Models

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Context: Joint species distribution models

Multi-species abundance data

Ecological context

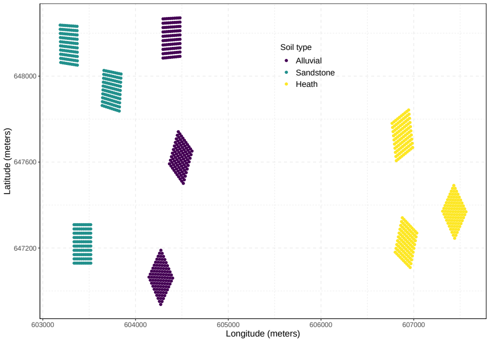
- **Goal** Describe and understand distribution of species within an ecosystem;
- **Mean** Counting individuals of all encountered species through surveys.

Statistical challenges

- Multivariate count data;
- Modelling dependencies:
  - Coming from spatial sampling;
  - Coming from species interactions.

Forest communities in Borneo

Figure 1: Data from Sellan et al. (2019).



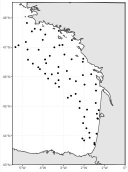
- 900 forest plots (20m × 20m) in Malaysia (Borneo island);
- All trees are counted are counted on all plots: 600 encountered species;

Ecological question

Do variations in plots communities is explained by the soil composition?

Invertebrate communities in the Bay of Biscay

Figure 2: Data from de Outrequin et al. (2025).

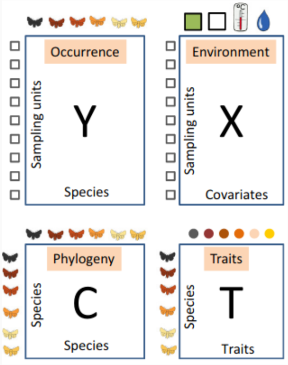


- 64 sites trawling sites across Bay of Biscay (EVOHE Project, 2019);
- Sampling made over different substrats, at different depth;
- 256 invertebrate species encountered.

What are the spatial patterns of species distributions. Are there some communities?

Joint species distribution data

Figure 3: Source: Ovaskainen and Abrego (2020)



- $\mathbf{Y}$ a $n \times p$ matrix with entries in $\mathbb{N}$;
- $\mathbf{X}$ a $n \times n_{\text{cov}}$ matrix of real values;
- $\mathbf{C}$ a $p \times p$ correlation matrix;
- $\mathbf{T}$ a $p \times n_{\text{trait}}$ matrix of real values;

A multivariate generalized linear mixed model approach

- Latent variable approach: modelling of joint distribution of $(\mathbf{Y}, \mathbf{Z})$.

  For $1 \leq i \leq n, 1 \leq j \leq p,\ Y_{i,j}|Z_{i,j} \overset{\text{ind}}{\sim} \mathcal{D}(\exp(Z_{i,j}), \phi)$. Observation model

- $\mathcal{D}$ is some distribution (Negative binomial, Poisson) with:
  - Expectation $\exp(Z_{i,j})$;
  - Dispersion parameter ϕ.

$$\mathbf{Z} \sim \mathcal{MN}(\mathbf{X}\boldsymbol{\beta}, \Sigma_{\text{Site}}, \Sigma_{\text{Species}}) \text{ . Latent variable}$$

- $\mathcal{MN}(\mathbf{X}\boldsymbol{\beta}, \Sigma_{\text{Site}}, \Sigma_{\text{Species}})$ is the *matrix normal* distribution with:
  - Expectation $\mathbf{X}\beta$ (a $n \times p$ matrix);
  - Covariance between rows Σ_{Site} (a $n \times n$ symmetric positive definite matrix);
  - Covariance between columns Σ_{Species} (a $p \times p$ SPD matrix);
- β is an **unknown** $n_{\text{cov}} \times p$ matrix: **response of species to environment**.

The matrix normal distribution

Definition

$\mathbf{M}$: $n \times p$ matrix, $\mathbf{U}$ (resp. $\mathbf{V}$): $n \times n$ (resp. $p \times p$) SPD matrix:

$$\mathbf{Z} \sim \mathcal{MN}(\mathbf{M}, \mathbf{U}, \mathbf{V}) \Leftrightarrow \text{vec}(\mathbf{Z}) \sim \mathcal{N}_{np \times np}(\text{vec}(\mathbf{M}), \mathbf{V} \otimes \mathbf{U}) \, .$$

Properties

- Separability hypothesis over covariances;
- If $\mathbf{Z} \sim \mathcal{MN}(M, \mathbf{U}, \mathbf{V})$, then $\mathbf{A}Z\mathbf{B}^\intercal + \mathbf{C} \sim \mathcal{MN}\left(\mathbf{AMB}^\intercal + \mathbf{C}, \mathbf{AUA}^\intercal, \mathbf{BVB}^\intercal\right)$;
    - Useful both for simulation and whitening;

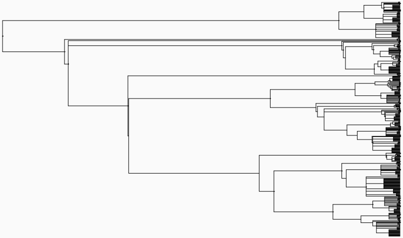
Modelling the fixed effects

Structuring the niches

- Suppose we have access to other data about species:
- Species traits in a matrix $\mathbf{T}$:

Species	Growth rate	Wood density	Max. Height
Strychnos borneensis	0.008	0.750	19.749
Dysoxylum indet	0.027	0.585	8.588
Memecylon indet	0.013	0.783	8.692
Cratoxylum cochinchinense	0.025	0.670	9.894
Sterculia stipulata	0.027	0.365	10.087

- Phylogeny, giving a correlation matrix $\mathbf{C}$:



Structuring the β matrix

- The matrix β stacks vector of responses to environment:
  - The environmental niches of species;
- Assume that:
  - The **traits** affect β (similar traits lead to similar niche);
  - Columns (species) of β are correlated because of **phylogeny**.

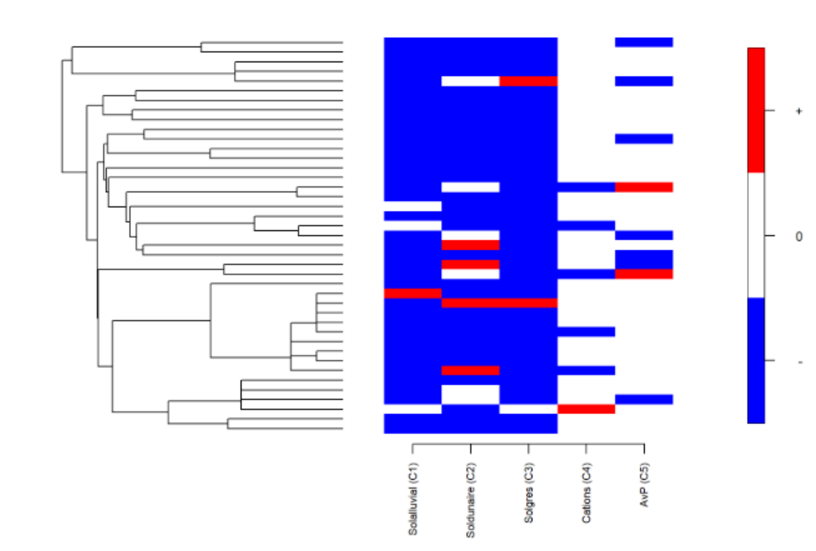
Formally, $\boldsymbol{\beta}$ is assumed to be a Matrix Normal random variable such that:

$$\boldsymbol{\beta} \sim \mathcal{MN}\left(\boldsymbol{\Gamma}\mathbf{T}^{\top}, \eta^2 \mathbf{I}_{n_{\text{cov}}}, \rho\mathbf{C} + (1-\rho)\mathbf{I}_p\right) .$$

- $\boldsymbol{\Gamma}$ is a $n_{\text{cov}} \times n_{\text{trait}}$ matrix structuring $\boldsymbol{\beta}$:
  - **Do the species niches are correlated to species traits?**
- $\mathbf{C}$ is the correlation matrix induced by the **phylogeny**;
- $0 \leq \rho \leq 1$ is the weight of **phylogeny** in the columns correlation of $\boldsymbol{\beta}$.

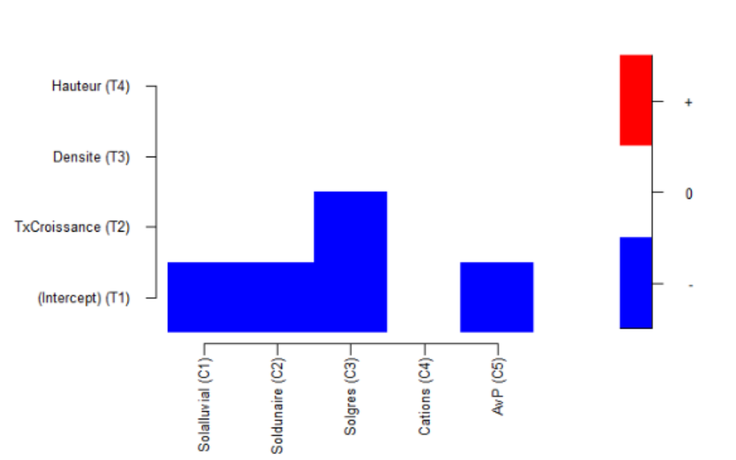
Illustration on trees of Borneo, estimation of β

Figure 4: Estimated sign for β, obtained with `Hmsc` package.



Impact of traits over niches

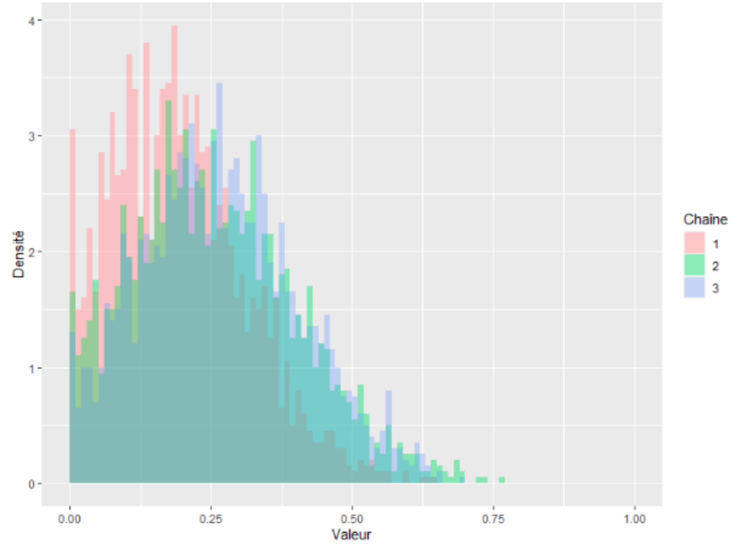
Figure 5: Estimated sign for Γ, obtained with `Hmsc` package.



- Higher growth rate correlates with low abundance and sandstone soil;

Influence of phylogeny on niche correlation?

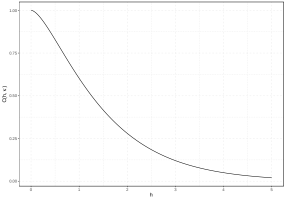
Figure 6: Posterior sampling of weights ρ of phylogeny.



Modelling two source of dependences

Modelling the dependences between sites

Figure 7: Matern covariance function for $\nu = 1, \sigma^2 = 1, \kappa = 1$



Model on spatial dependences (rowwise dependences)

- For two sites i and ℓ separated by a distance $h_{i,\ell}$, $(\Sigma_{\text{Site}})_{i,\ell} = C(h_{i,\ell}, \kappa)$ with:

$$C(h, \kappa) = \kappa h K_1(\kappa h)\,,$$

  with $K_1(\cdot)$ the modified Bessel function of second kind.
- Matern covariance with:
  - Fixed regularity $\nu = 1$ and marginal variance $\sigma^2 = 1$;
  - Unknown range parameter κ to estimate.

Modelling the dependences between species

Model on species dependences (colwise dependences)

- No "natural" structure induced by a "natural" distance;
- Need for a geometrical/statistical structure to avoid $p \times (p+1)/2$ free parameters;

Low rank structures on covariances

- Reducing number of parameters by assuming a low-rank structure

$$\Sigma_{\text{Species}} = \Lambda \Lambda^{\top},$$

  where Λ is a $p \times q$ matrix with $q \ll p$;
- Probabilistic PCA structure;
- Λ interpreted as species response to q unmeasured covariates;

Modelling the dependences between species (II)

Model on species dependences (colwise dependences)

- No "natural" structure induced by a "natural" distance;
- Need for a geometrical/statistical structure to avoid $p \times (p+1)/2$ free parameters;

Model on species dependences (colwise dependences)

- Modelling the precision matrix $\Omega = \Sigma_{\text{Species}}^{-1}$;
- Conditional independence property: For $1 \leq j, k \leq p$:

$$\Omega_{j,k} = 0 \Leftrightarrow \left(\mathbf{Z}_{\cdot,j} | \mathbf{Z}_{\cdot,-(j,k)}\right) \perp \left(\mathbf{Z}_{\cdot,k} | \mathbf{Z}_{\cdot,-(j,k)}\right) .$$

- Induces a graph between species: Draw an edge between species j and k iff $\omega_{j,k} = 0$;
- *Interpretation:* Ecological interaction network;

Bayesian Model considered (Invertebrate case, Rozier et al. 2026+)

$$Y_{i,j}|Z_{i,j} \overset{\text{ind}}{\sim} \mathcal{NB}(\exp(Z_{i,j}), \phi)\,, \qquad \text{Observation model}$$

$$\mathbf{Z} \sim \mathcal{MN}\left(\mathbf{X}\boldsymbol{\beta}, \Sigma(\kappa), \Omega^{-1}\right). \qquad \text{Latent variable}$$

Priors

$$\boldsymbol{\beta} \sim \mathcal{MN}(0, \mathbf{I}_{n_{\text{cov}}}, \mathbf{I}_p)$$

$$\phi \sim \log\mathcal{N}\left(m, s^2\right)$$

$$\kappa \sim \mathcal{G}\text{amma}(a, b)$$

$$\Omega \sim \text{Continuous spike and slab prior (CSS)}$$

- CSS comes from Wang (2015).

Bayesian priors for precision matrices

A frequentist reference: the graphical Lasso

Learning Ω

- We want to learn an interpretable graph;
- This suggest to have a sparse Ω;
- Natural approach: Penalizing matrices having few zeros.

- Let rows of $\mathbf{Z}$ be centered and independent *i.e.*

$$\mathbf{Z} \sim \mathcal{MN}\left(0, \mathbf{I}_n, \Omega^{-1}\right).$$

- The graphical Lasso learns Ω by maximizing:

$$\log\left(\det(\Omega)\right) - \mathsf{Tr}\left(\frac{1}{n}\mathbf{Z}^\intercal \mathbf{Z}\Omega\right) - \lambda\|\Omega\|_1, \ \|\Omega\|_1 = \sum_{1 \leq i,j \leq p} |\omega_{i,j}|.$$

- The λ penalty parameter is chosen using model selection criterion.
- Implemented for JSDM (Chiquet, Mariadassou, and Robin (2021)).

Bayesian graphical lasso

- Prior distribution[1] over Ω;

$$p(\Omega|\lambda) \propto \prod_{i<j} \mathcal{L}\mathsf{ap}(w_{i,j}|\lambda) \prod_{i=1}^{p} \mathcal{E}(w_{i,i}|\lambda) \mathbf{1}_{\mathbb{S}_+}(\Omega) \,.$$

- Leads to a Bayesian posterior proportional to graphical Lasso objective;
- Suitable for efficient Gibbs sampling (Wang (2012)).
- Does not lead to a straightforward rule about what is a “true” 0;

[1] $\mathcal{L}\mathsf{ap}(x|\lambda)$ and $\mathcal{E}(x|\lambda)$ are the p.d.f. of centered Laplace and exponential distributions with parameter λ, $\mathbb{S}_+$ is the set of SPD matrices.

Continuous spike and slab prior for precision matrix (I)

- Idea: Modelling[2] a 0 and non-0 regime;

$$
\begin{aligned}
p(\Omega|\theta) =& \mathsf{C}(\theta)^{-1} \times \\
& \left(\prod_{i<j} \Big(1-\pi)\mathcal{N}\Big(w_{i,j}|0, v_0^2\Big) + \pi\mathcal{N}\Big(w_{i,j}|0, v_1^2\Big)\Big) \right. \\
& \left. \times \prod_{i=1}^{p} \mathcal{E}(w_{i,i}|\lambda) \right) \times \mathbf{1}_{\mathbb{S}_+}(\Omega),
\end{aligned}
$$

where:

- π can be interpreted as a *a priori* probability of an edge to exist;
- v_0^2 and v_1^2 are *a priori* variances of $\omega_{i,j}$ under the 2 regimes ($v_0^2 \ll v_1^2$);
- $\theta = \{\pi, v_0^2, v_1^2, \lambda\}$.

[2] $\mathsf{C}(\cdot)$ is a normalizing constant.

Continuous spike and slab prior for precision matrix (II)

- Hierarchical version: Introduction of a latent binary matrix $\mathbf{G}$:

$$
\begin{aligned}
p(\mathbf{G}|\theta) \propto & \mathsf{C}(\mathbf{G},\theta) \times \prod_{i<j} \pi^{\mathbf{G}_{i,j}} (1-\pi)^{\mathbf{G}_{i,j}} \,, \\
p(\Omega|\theta,\mathbf{G}) = & \mathsf{C}(\mathbf{G},\theta)^{-1} \times \\
& \left(\prod_{i<j} \mathcal{N}\left(w_{i,j}|0, v^2_{\mathbf{G}_{i,j}}\right) \times \prod_{i=1}^{p} \mathcal{E}(w_{i,i}|\lambda) \right) \times \mathbf{1}_{\mathbb{S}_+}(\Omega) \,.
\end{aligned}
$$

- $\mathsf{C}(\mathbf{G},\theta)$ is an intractable normalizing term that cancels out in the joint distribution of $(\Omega,\mathbf{G})$;
- “The latent binary variables $\mathbf{G}$ can be viewed as edge-inclusion indicators” (Wang (2015)).

Other bayesian priors for sparse precision matrices

- Lots of methods:
  - Horseshoe prior (Li, Craig, and Bhadra (2019));
  - G-Wishart (Atay-Kayis and Massam (2005));
  - Sparsifying from the Cholesky decomposition (Mastrantonio, Di Loro, and Mingione (2025));
- Nice review with empirical comparisons (Vogels et al. (2024));
- Main challenges: interpretable prior with scalable posterior sampling.

Posterior sampling

Full model and target posterior distribution

Model's equations

$$
\begin{aligned}
Y_{i,j}|Z_{i,j} &\overset{\text{ind}}{\sim} \mathcal{NB}(\exp(Z_{i,j}), \phi)\,, \\
\mathbf{Z} &\sim \mathcal{MN}\left(\mathbf{X}\boldsymbol{\beta}, \Sigma(\kappa), \Omega^{-1}\right)\,, \\
\boldsymbol{\beta} &\sim \mathcal{MN}(0, \mathbf{I}_{n_{\text{cov}}}, \mathbf{I}_p)\,, \\
\phi &\sim \log\mathcal{N}\left(m, s^2\right)\,, \\
\kappa &\sim \mathcal{G}\text{amma}(a, b)\,, \\
p(\Omega|\theta, \mathbf{G}) &= \mathsf{C}(\mathbf{G}, \theta)^{-1}\left(\prod_{i<j} \mathcal{N}\left(w_{i,j}|0, v^2_{\mathbf{G}_{i,j}}\right) \times \prod_{i=1}^{p} \mathcal{E}(w_{i,i}|\lambda)\right)\mathbf{1}_{\mathbb{S}_+}(\Omega)\,, \\
p(\mathbf{G}|\theta) &\propto \mathsf{C}(\mathbf{G}, \theta) \times \prod_{i\leq j} \pi^{\mathbf{G}_{i,j}}(1-\pi)^{\mathbf{G}_{i,j}}
\end{aligned}
$$

$p(\mathbf{Z}, \boldsymbol{\beta}, \phi, \kappa, \Omega, \mathbf{G}|\mathbf{Y})$ Target posterior distribution

Gibbs approach

Table 2: Steps of the Gibbs algorithm

Conditional variable	**Sampling Method**
$\mathbf{Z}\vert\mathbf{Y},\boldsymbol{\beta},\kappa,\Omega$	MALA (rowwise)
$\boldsymbol{\beta}\vert\mathbf{Z},\kappa,\Omega$	Exact (gaussian)
$\phi\vert\mathbf{Y},\mathbf{Z}$	MALA
$\Omega\vert\mathbf{Z},\mathbf{G},\boldsymbol{\beta},\kappa$	Exact
$\mathbf{G}\vert\Omega$	Exact
$\kappa\vert\mathbf{Z},\boldsymbol{\beta},\Omega$	MALA

Gibbs sampling of $\Omega | \mathbf{Z}, \mathbf{G}, \boldsymbol{\beta}, \kappa$

- *Row whitening:* Compute $\tilde{\mathbf{Z}} = \mathbf{L}_\kappa^{-1}(\mathbf{Z} - \boldsymbol{\beta})$, where $\mathbf{L}_\kappa \mathbf{L}_\kappa^\intercal = \Sigma(\kappa)$;
- Consider $\mathbf{S} = \tilde{\mathbf{Z}}^\intercal \tilde{\mathbf{Z}}$;
- Sample new columns of Ω iteratively:
- To sample from the (say) last column conditionally to the $(p-1)$ other, partition:

$$\mathbf{S} = \begin{pmatrix} \mathbf{S}_{-p,-p} & \vec{s}_{-p,p} \\ \vec{s}_{-p,p}^\intercal & s_{p,p} \end{pmatrix}$$

- Set:

$$\Omega_{\text{new}} = \begin{pmatrix} \Omega_{-p,-p} & \vec{u} \\ \vec{u}^\intercal & v + \vec{u}^\intercal \Omega_{-p,-p} \vec{u} \end{pmatrix},$$

  where

$$v \sim \mathcal{G}\text{amma}\left(\frac{n}{2} + 1, \frac{s_{p,p} + \lambda}{2}\right),$$
$$\vec{u} \sim \mathcal{N}_{p-1}(-\mathbf{H}\vec{s}_{-p,p}, \mathbf{H}),$$

  where $\mathbf{H}$ is a matrix depending on $\mathbf{G}$ (easy to compute).
- Starting from a SPD matrix, it returns a SPD matrix.

Sampling of $\mathbf{G}|\Omega$

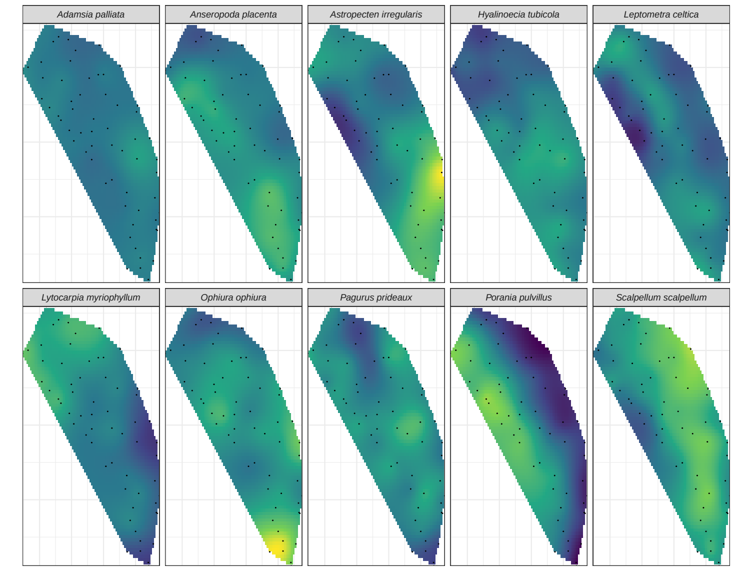
- Using the proposed hierarchical prior, conditional of $\mathbf{G}|\Omega$ sampling is straightforward.
- Sample independently for $1 \leq i < j \leq p$:

$$\mathbb{P}(\mathbf{G}_{i,j} = 1|\Omega) = \frac{\mathcal{N}\left(\omega_{i,j}|0, v_1^2\right)\pi}{\mathcal{N}(\omega_{i,j}|0, v_1^2)\pi + \mathcal{N}(\omega_{i,j}|0, v_0^2)(1-\pi)}.$$

Application to Bay of Biscay invertebrates

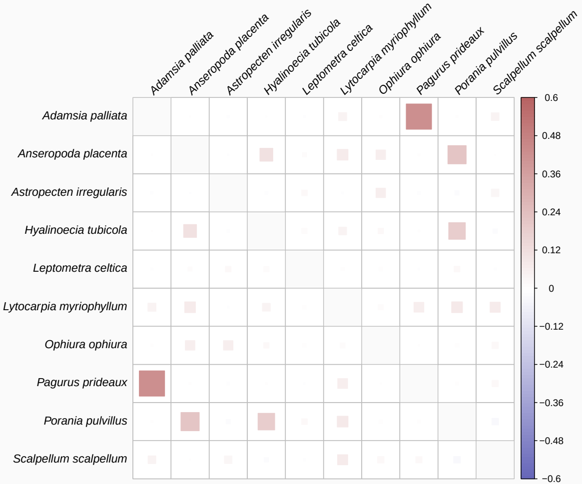
Estimation of the spatial field per species

Figure 8: Estimated spatial field for 10 species (posterior mean)



Estimation of the interaction network (partial correlation)

Figure 9: Estimated partial correlation matrix between species (posterior mean)



Estimation of $\mathbf{G}$

Figure 10: Posterior prob. of $\mathbf{G}_{i,j} = 1$

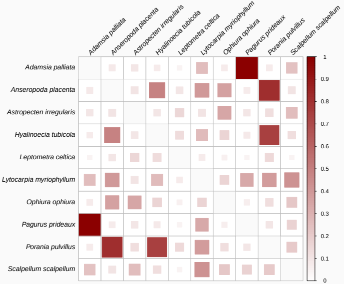
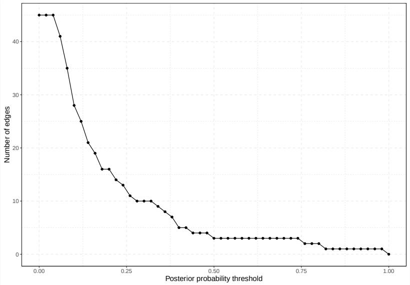
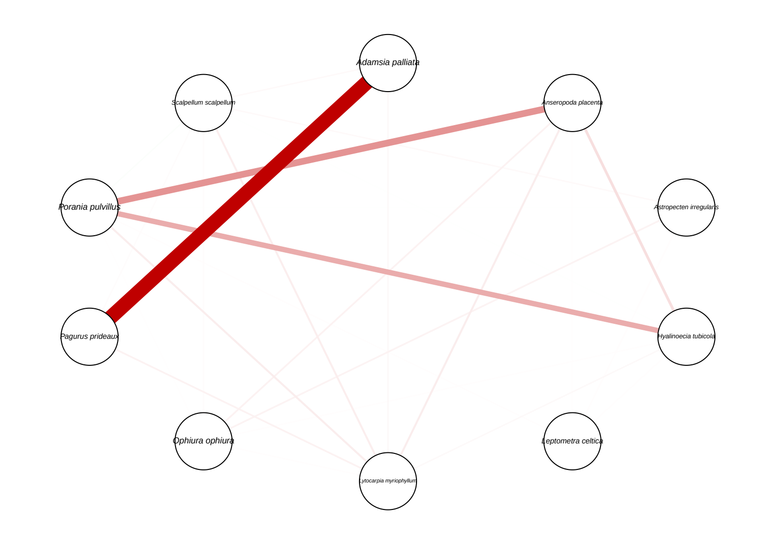


Figure 11: Number of edges depending on post. prob. threshold.



Estimated residual network

Figure 12: Estimated interaction network



Meet *Pagurus prideaux* and *Adamsa palliata*

Figure 13: Photo from Jim Greenfield flickr.com

Conclusions

- JSDM gathers classical statistical methods to analyze complex relations.
- Inference is a challenge, leading to various algorithms;
- Possibility of Exact Bayesian inference for network estimation using spatialized data;
- Estimation of two sources of dependence on a separable context;
- Works on n around hundreds, and p around dozens;
- For higher scalability (in n and p):
  - Need of appropriate sampler to not depend on Choleski decomposition;
  - Possibility to use approximate methods;

Perspectives

- Assess ecological pertinence on various different ecological data (trees, mosquitoes, invertebrate, fishes);
  - What are we looking at?
- Proposing some priors based on ecological assumptions;

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