# Asymptotic properties of spatially hierarchical matrix population models

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# Biological context

- ☞ Conservation and management of natural populations
- ☞ understanding of the dynamic development of populations
  - Specific demographic parameters : recruitment, birth, growth or ageing, and mortality
  - Global indices : extinction probability or stock recovery rate. function of specific demographic parameters

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Question 1

Asymptotic properties of stock recovery rate

# Biological context : forestry example

☞ sustainable management

- an equilibrium between taking of trees and natural stock recovery
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monitoring of permanent sample plots ?

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Questions 2

monitoring of permanent sample plots ?

- useful for multi-species
- management costs must be as low as possible
- estimate with a given precision the stock recovery rate.
  - depending on sample size
    - sample size is random
    - depending spatial repartition of the species

# Contents

# Usher models I

- ☞ size-structured populations
- ☞ description of the evolution at discret time $t$
- ☞ Usher's hypotheses
  - Hypothesis of independence
  - Markov hypothesis
  - Usher hypothesis : during each time step, an individual can stay in the same class, move up a class, or die ; each individual may give birth to a number of offspring.
  - Hypothesis of stationarity : evolution of individuals between two time steps is independent of time.

# Usher models II

Let $\mathbf{E}(t)$, $E_i(t)$ for $i = 1, \dots, m$, the number of individuals in each class $i$ ;
Usher Model :

$$\mathbf{E}(t+1) = U\mathbf{E}(t)$$

where the Usher matrix U is equal to :

$$U = \begin{pmatrix} p_1 + f & f & \dots & f \\ q_2 & p_2 & & 0 \\ & \ddots & \ddots & \\ 0 & & q_m & p_m \end{pmatrix}.$$

$p_i \in ]0, 1[$, the probability for an individual to stay in stage $i$.
$q_{i+1} \in ]0, 1[$, the probability to move up from stage $i$ to $i+1$.
$f \in \mathbb{R}^+$, the average fecundity.

# Usher models III

Let $d = (d_1, \ldots, d_m)$ be the stage-distribution of the population
Let $\mathbf{X}$ describes the state of an individual at time $t$ and $t + 1$.
The following transition probabilities :

$$\begin{array}{rcl} \Pr[\mathbf{X} = (i,i)] & = & (1 - f^\star) p_i d_i \\ \Pr[\mathbf{X} = (i,i+1)] & = & (1 - f^\star) q_{i+1} d_i \\ \Pr[\mathbf{X} = (i,\dagger)] & = & (1 - f^\star)(1 - p_i - q_{i+1}) d_i \\ \Pr[\mathbf{X} = (0,1)] & = & f^\star = \frac{f}{1+f} \end{array}$$

defined the distribution $F_\theta$ of $\mathbf{X}$.

$$\begin{array}{rcl} L(x_1, \ldots, x_n; \theta) & = & \prod_{k=1}^{n} \sum_{i=1}^{m} (1 - f^\star) p_i d_i \mathbb{1}_{x_k = (i,i)} \\ & & + (1 - f^\star) q_{i+1} d_i \mathbb{1}_{x_k = (i,i+1)} \\ & & + (1 - f^\star)(1 - p_i - q_{i+1}) d_i \mathbb{1}_{x_k = (i,\dagger)} + f^\star \mathbb{1}_{x_k = (0,1)} \end{array}$$

# Stock Recovery $R$

- Let $T$ be the rotation time
- exploitable stock at time $t$, $S(t)$, is thus defined as the number of trees whose diameter is greater than the threshold

$R$ is defined as

$$S(T)/S(0)$$

$c$ the class of the smallest exploitable diameter :

$$\begin{aligned} S(t) &= \sum_{i=c}^{m} E_i(t) = \mathbf{C}'\mathbf{E}(t) \\ &= \mathbf{C}' U^t \mathbf{E}(0^+) \text{ with } \mathbf{E}(0^+) \text{ initial stand structure.} \end{aligned}$$

Then,

$$R = \frac{\mathbf{C}' U^T \mathbf{E}(0^+)}{\mathbf{C}'\mathbf{E}(0)}.$$

# Stock Recovery $R$, multi-specific case

if growth dynamics can be model using matrix population models, then dynamics between each species are independent.
Usher matrix for $K$ species is block diagonal,

$$U = \begin{pmatrix} U_1 & 0 & \dots & 0 \\ 0 & \ddots & 0 & 0 \\ \vdots & 0 & \ddots & 0 \\ 0 & 0 & 0 & U_K \end{pmatrix},$$

and stock recovery for $K$ species is equal to :

$$\begin{aligned} \mathbf{R} = (R_1, \dots, R_K) &= \left( \frac{\mathbf{C}_1' U_1^T \mathbf{E}_1(0^+)}{\mathbf{C}_1' \mathbf{E}_1(0)}, \dots, \frac{\mathbf{C}_K' U_K^T \mathbf{E}_1(0^+)}{\mathbf{C}_K' \mathbf{E}_K(0)} \right) \\ &= (\phi_1(\theta_1), \dots, \phi_K(\theta_K)) . \end{aligned}$$

# Stock recovery estimator

Let ML estimator $\hat{\theta}$ of $\theta$. Then, the ML estimator of stock recovery is :

$$\hat{R} = \frac{\mathbf{C}'\widehat{U}^T\mathbf{E}(0^+)}{\mathbf{C}'\mathbf{E}(0)} = \phi(\hat{\theta}) \tag{1}$$

where $\widehat{U}$ is the ML estimator of the Usher matrix :

$$\widehat{U} = \begin{pmatrix} \hat{p}_1 + \hat{f} & \hat{f} & \dots & \hat{f} \\ \hat{q}_2 & \hat{p}_2 & & 0 \\ & \ddots & \ddots & \\ 0 & & \hat{q}_m & \hat{p}_m \end{pmatrix}.$$

# Estimation precision of stock recovery

$\rho_k, k = 1, \ldots, K$ the desired precision at level $\alpha_k\%$.

$$\left(q_{1-\alpha_k/2} - q_{\alpha_k/2}\right) \frac{\sqrt{\mathbb{V}(\hat{R}_k)}}{\mathbb{E}(\hat{R}_k)} \leq \rho_k$$

$q_{.}$ are quantiles of order $1 - \alpha_k$ of $\mathcal{N}(0, 1)$.

But

$$\mathbb{E}(\hat{R}_1, \ldots, \hat{R}_K) = \mathbb{E}[\mathbb{E}(\hat{R}_1, \ldots, \hat{R}_K | N_1, \ldots, N_K)]$$

and

$$\begin{aligned} \mathbb{V}(\hat{R}_1, \ldots, \hat{R}_K) &= \mathbb{E}[\mathbb{V}(\hat{R}_1, \ldots, \hat{R}_K | N_1, \ldots, N_K)] \\ &\quad + \mathbb{V}[\mathbb{E}(\hat{R}_1, \ldots, \hat{R}_K | N_1, \ldots, N_K)]. \end{aligned}$$

# Results I : asymptotic cas, given $N = n$

Zetlaoui *et al.* (2006)

$$\sqrt{n}(\hat{\theta} - \theta) \xrightarrow{\mathcal{L}} \mathcal{N}(0, I(\theta)^{-1}) \tag{2}$$

## Proposition

*Let $\hat{R} = \phi(\hat{\theta})$ be the maximum likelihood estimator of $R = \phi(\theta)$ then*

1. *Asymptotic distribution*

$$\sqrt{n}(\hat{R} - R) \xrightarrow{\mathcal{L}} \mathcal{N}(0, \sigma_\theta^2)$$

2. *Bias of the estimator*

$$b_\theta = n\mathbb{E}(\hat{R} - R) \approx \frac{(\mathbf{E}(0^+)' \otimes \mathbf{C}')\mathbf{D}}{2\mathbf{C}'\mathbf{E}(0)}$$

3. *Asymptotic variance is equal to*

$$\sigma_\theta^2 = (D_\theta \phi)\, I(\theta)^{-1}\, (D_\theta \phi)'$$

# Spatially hierarchical matrix population models

Let $S$ be a spatial point pattern generated by a $K$-variate point process in a finite subset of $\mathbb{R}^2$.
Let $\mathbf{N}(S) = [N^{(1)}(S), \ldots, N^{(K)}(S)]$ be the count of events of each type in $S$.
Let $X_i^{(k)}, k = 1, \ldots, K$ and $i = 1, \ldots, N^{(k)}$ describes the state of an individual $i$ of the population $k$ at time $t$ and $t+1$. A hierarchical matrix population model is defined as follows :

$$\begin{aligned} F(\mathbf{X}^{(1)}, \ldots, \mathbf{X}^{(K)} | \mathbf{N}(S)) &= \prod_{k=1}^{K} \prod_{i=1}^{N^{(k)}(S)} F_{\theta_k}(X_i^{(k)}) \\ S &\sim \mathcal{MPP} \end{aligned}$$

# Results I

Hypothesis

$$\hat{R}_k | N^{(k)} \sim \mathcal{N}(r_k(N^{(k)}), \sigma_k^2(N^k)), \quad k = 1, \dots, K$$

## Proposition (Covariance approximation)

*The covariance between $\hat{R}_k$ and $\hat{R}_{k'}$, can be approximated by :*

$$\mathbb{C}\mathrm{ov}(\hat{R}_k, \hat{R}_{k'}) \approx b_k b_{k'} \frac{\mathbb{C}\mathrm{ov}(N^{(k)}, N^{(k')})}{2\,\mathbb{E}(N^{(k)})^2\,\mathbb{E}(N^{(k')})^2}$$

*where*

$$b_k = \frac{1}{2} \sum_{i=1}^{6m} \sum_{j=1}^{6m} [I^{-1}(\theta)]_{ij} \frac{\partial^2 \phi_k(\theta)}{\partial \theta_i \partial \theta_j}, \; k = 1, \dots, K.$$

# Results II

**Proposition (Bias approximation)**

$$\mathbb{E}(\hat{R} - R) \approx b_\theta \left[ \frac{1}{\mathbb{E}(N)} + \frac{\mathbb{V}(N)}{\mathbb{E}(N)^3} \right]$$

**Proposition (Variance approximation)**

$$\mathbb{V}(\hat{R}) \approx \sigma_\theta^2 \left[ \frac{1}{\mathbb{E}(N)} + \frac{\mathbb{V}(N)}{\mathbb{E}(N)^3} \right]$$

*where $\sigma_\theta^2$ is the asymptotic variance of $\hat{R}$.*

# Results III : Precision of the estimator

Let $\mathcal{A}(S, s)$ be the area of sampling.

Corollary (Case of an homogeneous point process)

$$\sigma_\theta^2 \left[ \frac{1}{S\lambda} + \frac{\mathbb{V}(N(S))}{(S\lambda)^3} \right] \leq \left( \frac{\rho \mathbb{E}(\hat{R})}{q_{1-\alpha}} \right)^2$$

*where $\lambda$ is the intensity of the point process.*

Corollary (Case of an inhomogeneous Poisson point process)

$$\sigma_\theta^2 \left[ \frac{1}{\mathbb{E}(N(S,s))} + \frac{1}{\mathbb{E}(N(S,s))^2} \right] \leq \left( \frac{\rho \mathbb{E}(\hat{R})}{q_{1-\alpha}} \right)^2$$

*with* $E(N(S,s)) = \int_{\mathcal{A}(S,s)} \lambda(x)dx$

# Application : Study site and species

- ☞ Study site : Paracou
  - rain forest in French Guiana
  - effects of logging damage on stock recovery
- ☞ Species
  - Eperua falcata : highly aggregated, located along bottomlands
  - Vouacapoua americana : clustered in large patches, located on the tops and slopes of hills
  - Oxandra asbeckii : located on the tops and slopes of hills.
- ☞ Altitude discriminant environmental factor, inhomogeneous Poisson process with intensity :

$$\lambda_k(x) = \exp[\alpha_{0k} + \alpha_{1k} h(x) + \alpha_{2k} h(x)^2]$$

# Application : monitoring permanent sample plots

- management cost

$$C(P,S,\mathbf{s}) = \underbrace{4aP\sqrt{S}}_{\text{delimitation cost}} + \underbrace{bPS}_{\text{inventory cost}} + \underbrace{d(\mathbf{s})/V}_{\text{moving cost}} \quad (3)$$

  - $V$ is moving speed : 5000 m $h^{-1}$,
  - $a$ is the linear delimitation cost : $7 \cdot 10^{-3}$ h $m^{-1}$,
  - $b$ is the surface inventory cost : $3.5 \cdot 10^{-3}$ h $m^{-2}$,
  - $d(s_1, \ldots, s_P)$ the length of a route joining the points $s_1, \ldots,$ $s_P$ : minimum spanning tree algorithm (kruskal)
- Estimation of stock recovery for multi-species at a given precision

# Monitoring permanent sample plots : a optimization under (spatial) constraints problem

$$\begin{cases} \underset{(P,S)}{\operatorname{argmin}} \ \underset{(s_1,\dots,s_P)}{\operatorname{argmin}} C(P, S_u, s_1, \dots, s_P) \\ \sigma_\theta^{(k)2} \left[ \frac{1}{\mathbb{E}[N^{(k)}(S,\mathsf{s})]} + \frac{1}{\mathbb{E}[N^{(k)}(S,\mathsf{s})]^2} \right] \leq \left( \frac{\rho_k \mathbb{E}(\hat{R}^{(k)})}{q_{1-\alpha_k}} \right)^2 , \quad k = 1, 2, 3 \end{cases}$$

- $\mathbb{E}[N^{(k)}(S,\mathsf{s})] = \sum_{i=1}^{P} \int_{\mathcal{A}(S,s_i)} \lambda_k(x) dx$
- $\lambda_k$ intensity of the inhomogeneous Poisson process for species $k$ :$\lambda_k(x) = \exp[\alpha_{0k} + \alpha_{1k} h(x) + \alpha_{2k} h(x)^2]$

# Simulated Annealing Algorithm

$1 \leq P \leq 50$

**Require:** $S_u0$, position0, $T_0$, $T_f$, NT {number of iteration at constant temperature}

$S_u \Leftarrow S_u0$ and position $\Leftarrow$ position0

$T \Leftarrow T_0$

**while** $T > T_f$ **do**

  **for** $i = 1$ to NT **do**

    [new position] $\Leftarrow$ Voisinconf($P$, position)

    new $S_u \Leftarrow$ RechercheSu( $S_u$, new position)

    dC $\leftarrow$ Cout(new $S_u$, new position) - Cout( $S_u$, position)

    **if** Acceptation(dC, $T$) **then**

      $S_u \Leftarrow$ new $S_u$ and position $\Leftarrow$ new position

    **end if**

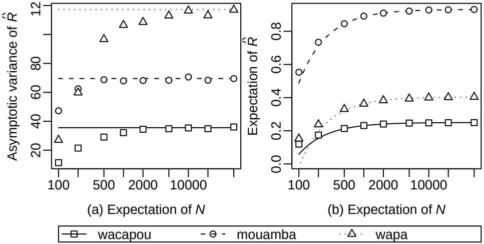
  **end for**

  $T \Leftarrow$Decrease($T$)

**end while**

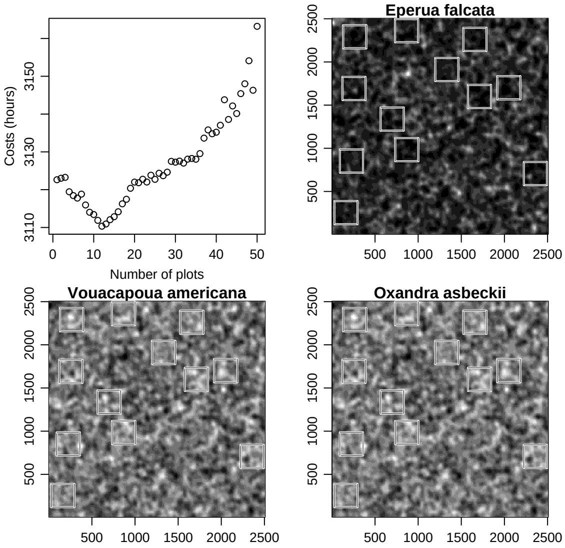
**return** $S_u$, position

# Results I




Hight asymptotic variance : $\rho_k = 50\%$

# Results II



Costs (hours)
3110
3130
3150
0
10
20
30
40
50
Number of plots
Eperua falcata
Vouacapoua americana
Oxandra asbeckii
500
1000
1500
2000
2500

# Conclusion

- About the method
  - using second-order Taylor expansions, we approximate expressions for the first two moments of the stock recovery estimator in a hierarchical context where sample size $N$ is random
  - stock recovery estimator was addressed in the multi-specific case
  - cost function is not autonomous from the spatial coordinates of plots, and the $K$ constraints are interrelated through plot locations
  - the reasoning could be extended to other matrix models, other predicted quantities, and other estimators
- About the results
  - sampling variability should not be disregarded in matrix modelling
  - statistical model that gives the distribution of observations were defined is a discrete distribution
  - generalize the present study to transition rate estimators based on continuous size.