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Statistical inference for density dependent Markovian forestry models

Abstract

A stochastic forestry model with a density-dependence structure is studied. The population evolves in discrete-time through stage-structured processes, in a way that its temporal evolution is described by a stochastic Markov chain. For adequate scalings of the transition rates, it is shown to converge to the deterministic matrix model, known as the Usher model, as a parameter n, interpreted as the population size roughly speaking, becomes large. From the perspective of the analysis of forestry data and predict the forestry population evolution, this approximation result may serve as a key tool for exploring the asymptotic properties of standard inference methods such as maximum likelihood estimation. We state preliminary statistical results in this context. Eventually, relation of the model to the available data of a tropical rain forest in French Guiana is investigated and numerical applications are carried out.

Keywords. Population dynamics; matrix model; Markov chain; density dependence; large population approximation; maximum likelihood estimation.

1 Introduction

Models of population dynamics are an important tool in many ecological studies. They are used to mimic the future evolution of the population. Among the discrete-time models, matrix model are often used to study the dynamics of structured populations (either age-structured or size-structured populations). They also permit to simplify the dynamics of a population into its basic components: recruitment or birth, growth or ageing, and mortality. Matrix models have been widely used in ecology to deal with invasive species [18, 29], population viability [5, 3, 26, 28, 15], or the management of the harvested populations [13, 7, 16].

The most general matrix model was proposed by [21], and allows any transition from one stage to another. The Usher model [31, 32] is a size-structured population model and restricts the possible transitions: during on time step, an individual either stays alive in the same stage, moves up to

the next stage, or dies. It is often used in forestry because it is well adapted to the dynamics of a forest stand and it permits to simulate quickly and in a synthetic way large areas of forest [14]. This model is particularly adapted to deal with forest management [27, 8, 33, 4, 7, 19], economic potential of forests [25, 6], or biodiversity assessment [8, 25, 17, 24, 23]. The Leslie model [22] describes a population grouped by age, and is a special case of the Usher model: during each time step, an individual can only move up a class or die.

Matrix models describe the dynamics of a population by the effectif vector which components are the number of individuals in each class. These models were at first deterministic. Demography stochasticity, consisting on describe the population dynamics by Markov chains, was used above all to deal with small-size populations, to model for instance the probability of extinction [5, 20, 26]. However some recent population modelling efforts have employed this type of modelisation [12, 9, 11, 1, 30].

In this paper we focuse on a generalized Usher model where individual evolutions are assumed to be dependent of the running density. This model take into account the tree interactions due to competition effects into individual dynamicsAt any time, recruitment, growth and mortality in each state class depend on the overall density. Assuming a large population of tree, the properties of the mathematical model are investigated and preliminaries statistical questions are tackled. Beyond the stochastic modelling, the main goal is to establish large population limit results (law of large number and limit central theorem) for the effective Markov chain describing the forest dynamics. This is a classical approach for the statistical analysis in population dynamics and its applications.

The paper is organized as follows. In section 1 a Markov chain with density-dependence in individual dynamics is introduced for modeling the temporal evolution of a forest stand. A short description giving an insight into how the dynamics is driven. In average, the evolution of the Markov chain verifies the deterministic relation given by the Usher model. A short probabilistic study is also given describing the long-term behavior of the Markov chain. The main part of this work is concerned by the section 3. Considering a Markov chain indexed by a positive natural n, representing approximatively the initial size of the population, limit results when n tends to infinity are established. These results provide maximum likelihood estimators that are consistent in a large population framework in section 4.

2 The markovian forestry model

2.1 The population dynamics

The population is grouped into I stages. Its evolution is described in discrete time by the random vector $N(t) = (N_i(t))_{i=1\ldots I}$, where $N_i(t)$ is the number of individuals in stage i at time t. The sequence $(N(t))_{t\in\mathbb{N}}$ takes its values

in $\mathbb{N}^I$ and is adapted with respect to the filtration $\mathcal{F} = (\mathcal{F}_t)_{t\in\mathbb{N}}$ defined by : $\mathcal{F}_t = \sigma\left(\cup_{s\leq t}\sigma(N(s))\right)$. Between time t and $t+1$ an individual either stays in the same class, or grows up to the next stage, or dies (see Fig. 1). Then the model is written by:

$$N_i(t+1) = F_{i\,i}(t) + F_{i-1\,i}(t) \tag{1}$$

where $F_{i\,j}(t)$ is the flow of individuals from the stage i to the stage j between time t et $t+1$, with convention $F_{0\,1}(t) = R_t$ where R_t being the number of birth. We denote also $F_{i\,\dagger}(t)$ the number of individuals from the stage i which die between the time t and $t+1$. Flow law conditionally to $N(t)$ is a multinomial law, and number of birth follows a Poisson's law:

$$\begin{aligned}(F_{i\,i}(t), F_{i\,i+1}(t), F_{i\,\dagger}(t)) &\sim \mathcal{M}\left(N_i(t), p_i(N(t)), q_i(N(t)), m_i(N(t))\right)\\ R_t &\sim \mathcal{P}(\sum_{i=1}^{I} f_i(N(t))N_i(t))\end{aligned}$$

where $p_i(N(t))$ is the transition rate for an individual in stage i which stays in the same stage, $q_i(N(t))$ the transition rate for an individual which grows up to the next stage, and $m_i(N(t))$ the death rate. Those parameters verify the stochastic relation:

$$p_i(N(t)) + q_i(N(t)) + m_i(N(t)) = 1 \tag{2}$$

Furthermore $f_i(N(t))$ denotes the fecundity of stage i.

With those assumptions, the average evolution of effective vector is given by the equation

$$\mathbb{E}(N(t+1)|N(t)) = U(N(t))N(t) \tag{3}$$

where U is a matrix of size $I \times I$, called "Usher" matrix. Its elements are

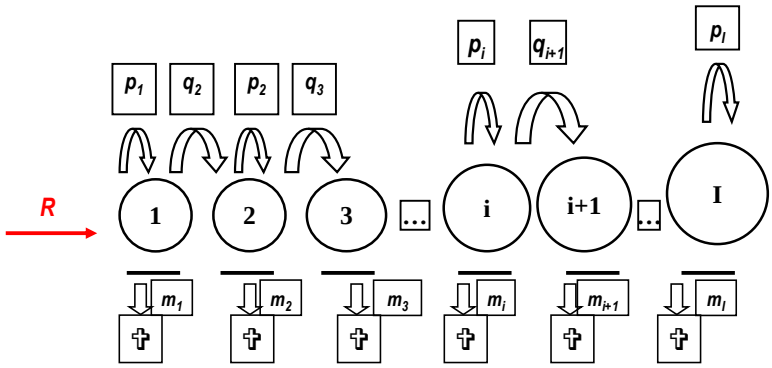

Figure 1: Flow diagram of the Usher model

the transition parameters, that is $U(N(t)) = P(N(t)) + \mathbf{R}(N(t))$ where:

$$P(N(t)) = \begin{pmatrix} p_1(N(t)) & 0 & \cdots & 0 \\ q_1(N(t)) & p_2(N(t)) & & \vdots \\ & \ddots & \ddots & 0 \\ 0 & & q_{I-1}(N(t)) & p_I(N(t)) \end{pmatrix}$$

$$\mathbf{R}(N(t)) = \begin{pmatrix} f_1(N(t)) & \cdots & f_I(N(t)) \\ 0 & \cdots & 0 \\ \vdots & & \vdots \\ 0 & \cdots & 0 \end{pmatrix}$$

Example 1 (On modelling the density-dependence) Density dependence can take an infinity of shapes, but the most commonly found (see [9]) are the Berverton-Holt dependence:

$$v(N) = \frac{c}{b + N \cdot \mathbf{a}}$$

and the Ricker (or exponential) dependence:

$$v(N) = c \exp(-bN \cdot \mathbf{a}) \tag{4}$$

where v is any of the vital rates, c and b are constant parameters, a is a constant positive vector of $\mathbb{R}^I$, and dot denotes the scalar product in $\mathbb{R}^I$. For instance, $\mathbf{a}$ can be the unit vector $(1, 1, ..., 1)$, so that $N \cdot \mathbf{a}$ is the total number of individuals at time t. In forestry applications, $\mathbf{a}$ is often taken as the vector whose ith element is the average basal area of an individual in stage i. The quantity $N \cdot \mathbf{a}$ then represents the cumulative basal area of the population. Exploratory analyses showed us that the exponential density-dependence better suited the experimental data at Paracou than the Beverton-Holt dependence. In what follows, we shall thus focus on the exponential dependence given by equation (4).

Nevertheless, this representation not assures the probability condition given by equation (2). For this reason, we propose the following model where each vital rate has his own density-dependence, that is to say:

$$\begin{aligned} p_i(N) &= (1-\gamma_i)\frac{\mu_i e^{\xi_i N \cdot \mathbf{a}}}{\mu_i e^{\xi N \cdot a} + \nu_i e^{-\kappa_i N \cdot \mathbf{a}}} \quad (i = 1, \ldots, I) \\ q_i(N) &= (1-\gamma_i)\frac{\nu_i e^{-\kappa_i N \cdot \mathbf{a}}}{\mu_i e^{\xi_i N \cdot \mathbf{a}} + \nu_i e^{-\kappa_i N \cdot \mathbf{a}}} \quad (i = 1, \ldots, I-1) \\ f(N) &= \alpha e^{-\beta N \cdot \mathbf{a}} \end{aligned} \tag{5}$$

Especially, p_i increases with $N \cdot \mathbf{a}$ and tends to a constant $1-\gamma_i$ at infinity, while q_i decreases toward zero. Here survival rate is constant, equal to $1-\gamma_i$,

and not depends on the density. With this simplification, the mortality rate represents the natural death. To take into account competition in mortality, we propose the following shape for death rate:

$$m_i(N) = \eta_i + \delta_i(1 - e^{-\lambda_i N \cdot \mathbf{a}}) \tag{6}$$

with $\eta_i + \delta_i < 1$. The death rate is the sum of natural mortality, η_i, and mortality due to competition. Also, when $N \cdot \mathbf{a}$ tends to infinity, the death rate increases toward $\eta_i + \delta_i$.

2.2 Markov chain description

The sequence $(N(t))_{t\in\mathbb{N}}$ that verifies equation (1) is a markov chain in $\mathbb{N}^I$ with initial law μ_0 and transition probability denoted Π, defined, for all $m = (m_1, \ldots, m_I)$ and $n = (n_1, \ldots, n_I)$ of $\mathbb{N}^I$, by :

$$\Pi\left((m_1, \ldots, m_I), (n_1, \ldots, n_I)\right) = \prod_{i=1}^{I} \Pi_i(m, n_i)$$

where $\Pi_i(m, n_i) = \mathbb{P}\left(N_i(t+1) = n_i | N(t) = m\right)$ is, for $i \geq 2$, the convolution of two binomial distributions, that is:

$$\Pi_i(m, n_i) = \begin{cases} \displaystyle\sum_{k=n_i-\min(m_{i-1},n_i)}^{\min(m_i,n_i)} B^1_{ik}(p, m, n) B^2_{ik}(q, m, n), & \text{if } n_i \leq m_i + m_{i-1} \\ 0 & \text{else} \end{cases}$$

and, for $i = 1$, the convolution of a binomial and a Poisson distribution:

$$\Pi_1(m, n_1) = \sum_{k=0}^{\min(m_1,n_1)} B^1_{1k}(p, m, n) D_k(f, m, n)$$

where:

$$\begin{cases} B^1_{ik}(p, m, n) &= C^k_{m_i} p_i(m)^k (1 - p_i(m))^{m_i - k} & \text{for } i = 1, \ldots, I \\ B^2_{ik}(q, m, n) &= C^{n_i-k}_{m_{i-1}} q_{i-1}(m)^{n_i-k} (1 - q_{i-1}(m))^{m_{i-1}-n_i+k} & \text{for } i = 2, \ldots, I \\ D_k(f, m, n) &= \dfrac{\left(\sum_{j=1}^{I} f_j(m) m_j\right)^{n_1-k}}{(n_1 - k)!} e^{-\sum_{j=1}^{I} f_j(m) m_j} & \end{cases}$$

2.3 Limiting behavior in long time asymptotics

We now state a limit result for the forestry markov chain, as time goes to infinity.

Proposition 1 *Considering the markov chain $(N_t)_{t>0}$ introduced in definition 1, we have, whatever the intitial state N_0, that (N_t) tends to 0 in distribution as t tends to infinity.*

The details of the proof is given in Appendix A. This ergodicity result shows that the time of population extinction is almost surely finite, though it may be very long in practice. In situation of long-lasting dynamics, as a tropical forest, the long-term behavior can be refined by studying *quasi-stationnarity measures*.

3 Large population limit

3.1 Renormalization

We consider a sequence $\{(N^{(n)}(t))_{t\in\mathbb{N}}; n \geq 1\}$ of Usher markov chain. For $n \geq 1$, the markov chain $(N^{(n)}(t))_{t\in\mathbb{N}}$ starting from $N^{(n)}(0)$, proportionnal to n and with the modifications on transition rates

$$v^{(n)}(N^{(n)}(t)) = v(\frac{N^{(n)}(t)}{n}) \tag{7}$$

where v verifies one of equations (5).

Remark 1 (On the meaning of the renormalization) With this renormalization, the competition term of any vital rate is function of the density. The definition of the competition then not depends of the plot area where the population lives.

Let consider a Usher markov chain starting from $N^{(n)}(0)$ during time T, $(N^{(n)}(0), \ldots, N^{(n)}(T))$. If the population size increases, the term $N^{(n)}(t)/n$ increases, and $p^{(n)}(N^{(n)}(t))$ increases while $q^{(n)}(N^{(n)}(t))$ decreases.

Let now $\widetilde{N}^n = \dfrac{N^n}{n}$ and $T \in \mathbb{N}^*$. Then $\widetilde{N}^n(T)$ verifies the following equation:

$$\widetilde{N}^n(T) = \widetilde{N}^n_0 + \sum_{s=0}^{T-1} F(\widetilde{N}^n(s)) + M^n(T) \tag{8}$$

where:

- F is the function defined for all $x = (x_i)_{i=1,\ldots,I}$ in $\mathbb{R}^I$ by:

$$F(x) = U(x)x - x$$

- the series $\left(\sum_{s=0}^{t-1} F(\widetilde{N}^n(s)), t \geq 1\right)$ is $\mathcal{F}^n$-predictable
- $M^n = (M^n(t), t \in \mathbb{N})$ is a $\mathcal{F}^n$-martingale, defined for all $t \geq 1$ by:

$$\begin{aligned} M^n(t) &= \sum_{s=0}^{t-1} \left[\widetilde{N}^n(s+1) - \mathbb{E}\left(\widetilde{N}^n(s+1)|\mathcal{F}_s^n\right)\right] \\ &= \sum_{s=0}^{t-1} \left[\widetilde{N}^n(s+1) - U\left(\widetilde{N}^n(s)\right)\widetilde{N}^n(s)\right] \end{aligned}$$

  and $M^n(0) = 0$.

3.2 The Law of Large Numbers

We want to show that $\widetilde{N}^n(T)$ tends, when n tends to infinity and almost surely, towards the deterministic vector y_T in $\mathbb{R}^I$ which verifies the following equation:

$$y_T = y_0 + \sum_{s=0}^{T-1} F(y_s) \tag{9}$$

This proof is particularly based on the convergence to zero of the martingale $M^n(t)$ when n tends to infinity and almost surely.

The convergence of $\widetilde{N}^n(T)$ is ensured under the following assumptions:

$(\mathcal{H}_1)$ f_i is a bounded function for all $i = 1, \ldots, I$.

$(\mathcal{H}_2)$ $\lim_{n\to\infty} \widetilde{N}^n(0) = y_0$ in L^1 and almost surely.

$(\mathcal{H}_3)$ For each compact $\mathcal{K}$ of $\mathbb{R}^I$, there is a constant $C_\mathcal{K}$ such that

$$\|F(x) - F(y)\|_1 \leq C_\mathcal{K} \|x - \ y\|_1$$

Remark 2 The assumption $(\mathcal{H}_3)$ can be substituted by the following assumption

$(\mathcal{H}_3')$ For each compact $\mathcal{K}$ of $\mathbb{R}^I$, there is a constant $C'_\mathcal{K}$ such that

$$\|U(x) - U(y)\|_1 \leq C_\mathcal{K} \|x - \ y\|_1$$

because of the relation

$$\|F(x) - F(y)\|_1 \leq \|U(y)\|_1 \|x - y\|_1 + \|U(x) - U(y)\|_1 \|x\|_1$$

Then, the following theorem is a limit theorem on the sequence $(\widetilde{N}_t^n)$ when n tends to infinity:

Theorem 3.1 *Let assumptions* $(\mathcal{H}_1)$, $(\mathcal{H}_2)$ *and* $(\mathcal{H}_3)$ *hold. Then:*

$$\lim_{n\to\infty} \sup_{t\leq T} \|\widetilde{N}^n(t) - y_t\|_1 = 0 \quad \textit{in } L^1$$

where y_t *is the unique solution of the equation (9).*

■

3.3 The Central Limit Theorem

Let $X^n(t) = \sqrt{n}(\widetilde{N}^n(t) - y_t)$. From the equations (8) and (9), we deduce that:

$$X^n(T) \quad = \quad X^n(0) + \sqrt{n}\sum_{t=0}^{T-1}\Big[F(\widetilde{N}^n(t)) - F(y_t)\Big] + \sqrt{n}M^n(T)$$

We want to show that $X^n(T)$ converges to the random vector X_T defined by the equation:

$$X_T = X_0 + \sum_{t=0}^{T-1} d_{y_t}F.X_t + M_T \tag{10}$$

where M_T is a centered random vector.

The convergence of $X^n(T)$ is ensured under assumption $(\mathcal{H}_1)$ and the following assumptions:

$(\mathcal{H}''_2)$ $\lim_{n\to+\infty} X^n(0) = X_0$

$(\mathcal{H}''_3)$ F is in class C^1

Theorem 3.2 *Let assumptions* $(\mathcal{H}_1)$, $(\mathcal{H}''_2)$ *and* $(\mathcal{H}''_3)$ *hold. Then:*

$$\lim_{n\to\infty} \sup_{t\leq T} \|X^n(t) - X_t\|_1 = 0 \quad \textit{in } L^1$$

where X_t *verifies the equation (10).*

4 Statistical applications

4.1 The likelihood function

Let $T > 0$ and $n \in \mathbb{N}^\star$. We suppose that the transitions parameters p_i, q_i and f_i for $i = 1, \ldots, I$ are entirely determined by a parameter θ taking values in a set $\Theta \subset \mathbb{R}^d$, with $d \geq 1$. The likelihood is:

$$\mathcal{L}_T^{(n)}(\theta) = \prod_{t=0}^{T-1}\prod_{i=1}^{I} \Pi_{\theta,i}^{(n)}\left(N^n(t), N^n(t+1)\right)$$

where, for all $m = (m_1, \ldots, m_I)$ and $l = (l_1, \ldots, l_I)$

$$\Pi_{\theta,i}^{(n)}(m, l_i) = \begin{cases} \displaystyle\sum_{k=l_i-\min(m_{i-1},l_i)}^{\min(m_i,l_i)} B_{\theta,ik}^{1\,(n)}(m,l) B_{\theta,ik}^{2\,(n)}(m,l), & \text{if } l_i \leq m_i + m_{i-1} \\ 0 & \text{else} \end{cases}$$

and, for $i = 1$, the convolution of a binomial and a Poisson distributions:

$$\Pi_{\theta,1}^{(n)}(m, l_1) = \sum_{k=0}^{\min(m_1,l_1)} B_{\theta,ik}^{1\,(n)}(m,l) D_{\theta,k}^{(n)}(m,l)$$

with:

$$\begin{cases} B_{\theta,ik}^{1\,(n)}(m,l) &= C_{m_i}^k p_{\theta,i}^n(m)^k (1 - p_{\theta,i}^n(m))^{m_i-k} & \text{for } i = 1, \ldots, I \\ B_{\theta,ik}^{2\,(n)}(m,l) &= C_{m_{i-1}}^{l_i-k} q_{\theta,i-1}^n(m)^{l_i-k} (1 - q_{\theta,i-1}^n(m))^{m_{i-1}-l_i+k} & \text{for } i = 2, \ldots, I \\ D_{\theta,k}^{(n)}(m,l) &= \dfrac{\left(\sum_{j=1}^I f_{\theta,j}^n(m) m_j\right)^{l_1-k}}{(l_1-k)!} e^{-\sum_{j=1}^I f_{\theta,j}^n(m) m_j} \end{cases}$$

Let $l_T^n(\theta) = \log[\mathcal{L}_T^{(n)}(\theta)]$.

4.2 The MLE consistency

Consider the ML estimator for $T > 0$ and $n \in \mathbb{N}^*$:

$$\hat{\theta}_n = \arg\max_{\theta \in \Theta} l_T^{(n)}(\theta).$$

Model identifiability

Let assume that the map $\theta \in \Theta \mapsto v_\theta$ is injective for any vital rate v.

Then, we want to show that for any $(\theta, \theta^*) \in \Theta^2$:

$$\frac{1}{n}[l_T^{(n)}(\theta) - l_T^{(n)}(\theta^*)] \xrightarrow[n\to\infty]{\mathbb{P}_{\theta^*}} K(\theta, \theta^*)$$

where $K(\theta, \theta^*) = 0$ iff $\theta = \theta^*$.

Proof: For n enough large,

$$\begin{aligned} B_{\theta,ik}^{1\,(n)}(N^n(t), N^n(t+1)) &\sim C_{ny_{t,i}}^k p_{\theta,i}(y_t)^k (1 - p_{\theta,i}(y_t))^{ny_{t,i}-k} \\ &\sim \frac{(ny_{t,i})^k}{k!} \left(\frac{p_{\theta,i}(y_t)}{1 - p_{\theta,i}(y_t)}\right)^k (1 - p_{\theta,i}(y_t))^{ny_{t,i}} \\ &\sim K_{\theta,i}^1(t,k)(ny_{t,i})^k (1 - p_{\theta,i}(y_t))^{ny_{t,i}} \end{aligned}$$

with $K^1_{\theta,i}(t,k) = \frac{1}{k!}\left(\frac{p_{\theta,i}(y_t)}{1-p_{\theta,i}(y_t)}\right)^k$. In the same way:

$$B^{2\,(n)}_{\theta,ik}(N^n(t), N^n(t+1)) \quad \sim \quad K^2_{\theta,i}(t,k)\tilde{B}^{2\,(n)}_{\theta,ik}(t)$$

with

$$\begin{aligned}
\tilde{B}^{2\,(n)}_{\theta,ik}(t) &= \frac{1}{(ny_{t+1,i}-k)!}\left(\frac{q_{\theta,i-1}(y_t)}{1-q_{\theta,i-1}(y_t)}\right)^{ny_{t+1,i}} (ny_{t,i-1})^{ny_{t+1,i}-k}(1-q_{\theta,i-1}(y_t))^{n(y_{t,i-1}-y_{t+1,i})} \\
K^2_{\theta,i}(t,k) &= \left(\frac{1-q_{\theta,i-1}(y_t)}{q_{\theta,i-1}(y_t)}\right)^k (1-q_{\theta,i-1}(y_t))^k
\end{aligned}$$

4.2.1 MLE asymptotic normality

Fisher Information

For all θ, the fisher information matrix is given by:

$$I(\theta) = \mathbb{E}[\nabla_\theta l_T(\theta)]^2$$

where $\nabla_\theta F$ is the gradient vector of F in θ.

We have:

$$\begin{cases}
\nabla_\theta B^1_{\theta,ik} &= \nabla_\theta p_{\theta,i}\dfrac{k-m_i p_{\theta,i}}{p_{\theta,i}(1-p_{\theta,i})}B^1_{\theta,ik} & \text{for } i=1,\dots,I \\
\nabla_\theta B^2_{\theta,ik} &= \nabla_\theta q_{\theta,i}\dfrac{(li-k)-m_{i-1}q_{\theta,i-1}}{q_{\theta,i}(1-q_{\theta,i})}B^2_{\theta,ik} & \text{for } i=2,\dots,I \\
\nabla_\theta D_{\theta,k} &= \displaystyle\sum_{j=1}^{I}\nabla_\theta f_{\theta,j} m_j\left(\frac{n_1-k}{\sum_{j=1}^I f_{\theta,j}(m)m_j}-1\right)D_{\theta,k}
\end{cases}$$

Then, for $i=2,\dots,I$:

$$\nabla_\theta \Pi_{\theta,t\,i} = \sum_{k=l_i-\min(m_{i-1},l_i)}^{\min(m_i,l_i)} B^1_{\theta,ik}B^2_{\theta,ik}\left[\nabla_\theta p_{\theta,i}\frac{k-m_i p_{\theta,i}}{p_{\theta,i}(1-p_{\theta,i})}+\nabla_\theta q_{\theta,i}\frac{(li-k)-m_{i-1}q_{\theta,i-1}}{q_{\theta,i}(1-q_{\theta,i})}\right]$$

and for $i=1$:

$$\nabla_\theta \Pi_{\theta,1} = \sum_{k=0}^{\min(m_1,l_1)} B^1_{\theta,1k}D_{\theta,k}\left[\nabla_\theta p_{\theta,1}\frac{k-m_1 p_{\theta,1}}{p_{\theta,1}(1-p_{\theta,1})}+\sum_{j=1}^{I}\nabla_\theta f_{\theta,j}m_j\left(\frac{n_1-k}{\sum_{j=1}^I f_{\theta,j}(m)m_j}-1\right)\right]$$

Appendices

A Proof of proposition 1

The markov chain $(N(t))_{t\in\mathbb{N}}$ is not an irreducible chain, the stage of extinction of the population $\{0_I\}$ being an absorbing stage. Nevertheless, under

hypothesis of "immigration", we can establish a convergence of the process to the stage $\{0_I\}$ with an exponential rate.

Let V the application of $\mathbb{N}^I$ in $[1;+\infty[$, defined for all $N=(N_i)_{i=1,\dots,I}$ by: $V(N)=\sum_{i=1}^{I} N_i$. The drift function at time t related to the function V, ΔV_t, is defined by the relation:

$$\begin{aligned}\Delta V_t &= \mathbb{E}(V(N(t+1))|N(t)) - V(N(t)) \\ &= \sum_{i=1}^{I} \left[\mathbb{E}(N_i(t+1)|N_t) - N_i(t)\right]\end{aligned}$$

From equation (3) given the evolution of the effective vector in mean, we deduce the expression of the drift function:

$$\begin{aligned}\Delta V_t &= \sum_{i=1}^{I} f_i(N(t))N_i(t) - \left[\sum_{i=1}^{I-1}\left[1-p_i(N(t))-q_i(N(t))\right]N_i(t) + \left[1-p_I(N(t))\right]N_I(t)\right] \\ &= \sum_{i=1}^{I}\left[f_i(N(t)) - m_i(N(t))\right]N_i(t)\end{aligned}$$

Denote strictly positive real β defined by $\beta = \inf_{i=1,\dots,I} m_i(N)$ and suppose that it exists constant $c>0$ such

$$\sup_{i=1,\dots,I} f_i(N)\|N\|_1 \leq c$$

Then

$$\Delta V(N) \leq -\beta V(N) + c$$

Let now define the markov chain $\overline{N}$ by:

$$\overline{N} = N + L$$

where L takes values in $\mathbb{R}^I$, and is equal to $L=(l,0,\dots,0)$ with: $l \sim \mathcal{P}(\lambda)$, $\lambda>0$. The markov chain $\overline{N}$ is irreducible, recurrent. Its drift function expresses itself as:

$$\Delta V(\overline{N}) = \Delta V(N) + \Delta V(L)$$

which verifies:

$$\begin{aligned}\Delta V(\overline{N}) &\leq -\beta V(N) + c + \lambda - V(L) \\ &\leq -\beta' V(\overline{N}) + c'\end{aligned}$$

with β' and $c' > 0$.

B Proof of proposition 3.1

We first show the following proposition:

Proposition B.1 *Let assumptions* $(\mathcal{H}_1)$ *and* $(\mathcal{H}_2)$ *hold. Then, for all* t*:*

1. $\dfrac{\widetilde{N}^n(t)}{n} \xrightarrow{n\to\infty} 0$ *in* L^1.
2. $\widetilde{N}^n(t)$ *is square integrable.*
3. $\mathbb{V}(\widetilde{N}^n(t+1)|\mathcal{F}_t^n) \xrightarrow{n\to\infty} 0$ *in* L^1.

Proof:

1. As $\widetilde{N}^n(0)$ tends to y_0 in L^1, $\widetilde{N}^n(0)$ verifies the property. Now, the equation (1) of the model can be also written like this:

$$N_i^n(t+1) = N_i^n(t) + F_{i-1\,i}^n(t) - (F_{i\,i+1}^n(t) + F_{i\,\dagger}^n(t))$$

Therefore by summing we obtain:

$$\|N^n(t+1)\|_1 = \|N^n(t)\|_1 + R^n(t) - M^n(t)$$

where $M^n(t) = \sum_{i=1}^I F_{i\,\dagger}^n(t))$ is the total number of dead trees between t and $t+1$. We deduce the inequality

$$\|N^n(t+1)\|_1 \leq R^n(t) + \|N^n(t)\|_1 \tag{11}$$

implying

$$\begin{aligned}\mathbb{E}\left(\frac{\|\widetilde{N}^n(t+1)\|_1}{n}\right) &\leq \mathbb{E}\left(\frac{R^n(t)}{n^2}\right) + \mathbb{E}\left(\frac{\|\widetilde{N}^n(t)\|_1}{n}\right) \\ &\leq \frac{1}{n}\sum_{i=1}^I \mathbb{E}(f_{\theta,i}(\widetilde{N}^n(t))\widetilde{N}_i^n(t)) + \mathbb{E}\left(\frac{\|\widetilde{N}^n(t)\|_1}{n}\right)\end{aligned}$$

Now, by the assumption $(\mathcal{H}_1)$, it exists a real $A > 0$ such as:

$$\mathbb{E}\left(\frac{\|\widetilde{N}^n(t+1)\|_1}{n}\right) \leq (1+A)\,\mathbb{E}\left(\frac{\|\widetilde{N}^n(t)\|_1}{n}\right)$$

as if to this relation for $t = 0, \ldots, T$:

$$\mathbb{E}\left(\frac{\|\widetilde{N}^n(t)\|_1}{n}\right) \leq (2+A)^t\,\mathbb{E}\left(\frac{\|\widetilde{N}^n(0)\|_1}{n}\right)$$

Then, as $\dfrac{\|\widetilde{N}^n(0)\|_1}{n}$ tends to zero in L^1, we deduce that $\dfrac{\|\widetilde{N}^n(t)\|_1}{n}$ tends also to zero in L^1

2. From the equation (11), we deduce that:

$$\begin{aligned}\mathbb{E}(\|\widetilde{N}^n(t+1)\|_1^2) &\leq \mathbb{E}\left(\frac{R^n(t)^2}{n^2}\right) + 4\mathbb{E}\left(\frac{R^n(t)}{n}\|\widetilde{N}^n(t)\|_1\right) + 4\,\mathbb{E}\left(\|\widetilde{N}^n(t)\|_1^2\right) \\ &\leq \sum_{i=1}^{I} \mathbb{E}(f_{\theta,i}(\widetilde{N}^n(t))\widetilde{N}_i^n(t))\ldots \\ &\leq \left(2+\frac{A}{n}\right)^2 \mathbb{E}(\|\widetilde{N}^n(t)\|_1^2) + \frac{A}{n}\mathbb{E}(\|\widetilde{N}^n(t)\|_1)\end{aligned}$$

As $\widetilde{N}^n(0)$ is square integrable, we prove by recurrence that $\widetilde{N}^n(t)$ is also like this for all t.

3. Now, $\mathbb{V}(\widetilde{N}^n(t)|\mathcal{F}_t^n) = \dfrac{1}{n^2}V^n(t)$, and the expression of $V^n(t)$ is given by the equation (**??**). As $p_{\theta,i}^n(N^n(t)) + q_{\theta,i}^n(N^n(t)) \leq 1$ for all n and t, and as $\dfrac{\widetilde{N}^n(t)}{n}$ tends to zero in L^1, therefore $\mathbb{V}(\widetilde{N}^n(t)|\mathcal{F}_t^n)$ tends to zero in L^1. ∎

Lemma 1 *Let assumptions* $(\mathcal{H}_1)$ *and* $(\mathcal{H}_2)$ *hold. Then:*

$$\lim_{n\to\infty} \sup_{t\leq T} \|M^n(t)\|_1 = 0 \qquad \textit{in } L^2 \textit{ and almost surely}$$

Proof

Step 1. We prove the convergence of $\sup_{t\leq T}\|M^n(t)\|_1$ in L^2.

- First, we verify that $M^n(t)$ is square integrable. Indeed :

$$\begin{aligned}\mathbb{E}\left(\|M^n(t)\|_1{}^2\right) &\leq \sum_{s=0}^{t-1} \mathbb{E}\left[\|\widetilde{N}^n(s+1) - \mathbb{E}\left(\widetilde{N}^n(s+1)|\mathcal{F}_s^n\right)\|_1{}^2\right] \\ &\leq 2\sum_{s=0}^{t-1} \mathbb{E}\left[\|\widetilde{N}^n(s+1)\|_1{}^2\right]\end{aligned}$$

  We conclude by the proposition B.1.

- Let $M_i^n(t)$ the ith composant of $M^n(t)$, for $i = 1,\ldots,I$. The series $M_i^n(t)$ is in L^2 and:

$$\begin{aligned}\mathbb{E}[M_i^n(t)^2] &= \mathbb{E}[(M_i^n(t) - M_i^n(0))^2] \\ &= \mathbb{E}\left[\left(\sum_{s=0}^{t-1}(M_i^n(s+1) - M_i^n(s))\right)^2\right]\end{aligned}$$

As $M_i^n(t)$ is a martingale, we deduce that:

$$\begin{aligned}\mathbb{E}[M_i^n(t)^2] &= \mathbb{E}\left[\sum_{s=0}^{t-1}(M_i^n(s+1)-M_i^n(s))^2\right] \\ &= \sum_{s=0}^{t-1}\mathbb{E}[\mathbb{V}(\widetilde{N}_i^n(s+1)|\mathcal{F}_s^n)]\end{aligned}$$

By the proposition B.1 we deduce that $M_i^n(t)$ converges to zero in L^2.

- Now, from the Doob's inequality:

$$\begin{aligned}\mathbb{E}[(\sup_{t\leq T}\|M^n(t)\|_1)^2] &\leq 4E[\|M^n(T)\|_1^2] \\ &\leq 4\mathbb{E}\left[\left(\sum_{i=1}^{I}|M_i^n(T)|\right)^2\right] \\ &\leq 4\sum_{i=1}^{I}\mathbb{E}[M_i^n(T)^2]\end{aligned}$$

Then, we deduce that $\sup_{t\leq T}\|M^n(t)\|_1$ tends to zero in L^2.

Step 2. [as convergence] Let $M_*^n = \sup_{t\leq T}\|M^n(t)\|_1$. M_*^n converges to zero in L^2 so in probability. Then, by the Borel-Cantelli's lemma, it exists an under-series of $(M_*^n)_n$ which converges to zero almost surely. We have to show that $(M_*^n)_n$ is a Cauchy series almost surely.(...)

■

Proof of theorem 3.1: First, as the sequence $(\widetilde{N}^n(t))$, for $t=0,\ldots,T$, are bounded in L^1, it exists a compact $\mathcal{K}$ in $\left(\mathbb{R}^I, \|.\|_{L^1((\mu_0,\Pi),\|.\|_1)}\right)$ which contains $\{y_0,\ldots,y_T\}$ and $\{\widetilde{N}^n(0),\ldots,\widetilde{N}^n(T)\}$ for all n, where:

$$\|f\|_{L^1(\mu,\|.\|_1)} = \int \|f\|_1 \mathrm{d}\mu$$

for all measurable function f with values in $\mathbb{R}^I$.

On the other hand, for all $t\leq T$ and in L^1:

$$\begin{aligned}\|\widetilde{N}^n(t)-y_t\|_1 &= \|\widetilde{N}^n(0)-y_0+M^n(t)+\sum_{s=0}^{t-1}\Big(F(\widetilde{N}^n(s)-F(y_s)\Big)\|_1 \\ &\leq \|\widetilde{N}^n(0)-y_0\|_1+\|M^n(t)\|_1+\sum_{s=0}^{t-1}\|F(\widetilde{N}^n(s))-F(y_s)\|_1 \\ &\leq \|\widetilde{N}^n(0)-y_0\|_1+\|M^n(t)\|_1+\sum_{s=0}^{t-1}C_{\mathcal{K}}\|\widetilde{N}^n(s)-y_s\|_1\end{aligned}$$

By Gronwall's inequality this implies that:

$$\|\widetilde{N}^n(t) - y_t\|_1 \leq \left(\|\widetilde{N}^n(0) - y_0\|_1 + \|M^n(t)\|_1\right) e^{C_{\mathcal{K}} t}$$

Then, taking the supremum on t, we obtain:

$$\sup_{t\leq T} \|\widetilde{N}^n(t) - y_t\|_1 \leq \left(\|\widetilde{N}^n(0) - y_0\|_1 + \sup_{t\leq T} \|M^n(t)\|_1\right) e^{C_{\mathcal{K}} T}$$

The first term in the brackets converges to 0 in L^1 by assumption, and the second term by the lemma 1. The exponential function is moreover independent of n. This completes the proof of the theorem. ∎

C Proof of theorem 3.2

Let $\Gamma(t)$ defined , for $i = 2, \ldots, I$, by:

$$\begin{aligned} \Gamma_{ii}(t) &= y_{t,i} p_i(y_t)[1 - p_i(y_t)] + y_{t,i-1} q_{i-1}(y_t)[1 - q_{i-1}(y_t)] \\ \Gamma_{i-1i}(t) &= \Gamma^t_{ii-1} = -y_{t,i-1} p_{i-1}(y_t) q_{i-1}(y_t) \\ \Gamma_{11}(t) &= y_{t,1} p_1(y_t)[1 - p_1(y_t)] + \sum_{i=1}^{I} f_i(y_t) y_{t,i} \end{aligned} \tag{12}$$

Proposition C.1 *Let assumptions $(\mathcal{H}_1)$, $(\mathcal{H}_2)$ and $(\mathcal{H}'_3)$ hold. Then, for all t*

$$n\mathbb{V}(\widetilde{N}^n(t+1)|\mathcal{F}^n_t) \xrightarrow{n\to\infty} \Gamma(t) \qquad \textit{in probability}$$

Proof The proposition is a straight result from the theorem 3.1 and from the continuity of U. ∎

Lemma 2 *It exists a real c such as for all $t = 1, \ldots, T$*

$$\mathbb{E}(\|X_n(t)\|_1) < c$$

Proof Let $t = 1, \ldots, T$. The random vector $X^n(t)$ verifies

$$X^n(t) = X^n(0) + \sqrt{n} \sum_{s=0}^{t-1} \left[F(\widetilde{N}^n(s)) - F(y_s)\right] + \sqrt{n} M^n(t)$$

Step 1. From the definition of the function F

$$\begin{aligned} F(\widetilde{N}^n(s)) - F(y_s) &= \left[U(\widetilde{N}^n(s))\widetilde{N}^n(s) - U(y_s) y_s\right] + [y_s - \widetilde{N}^n(s)] \\ &= \left[U(\widetilde{N}^n(s)) - U(y_s)\right] \widetilde{N}^n(s) + (1 - U(y_s))[y_s - \widetilde{N}^n(s)] \end{aligned}$$

Then, from the assumption $(\mathcal{H}_3^{'})$

$$\sqrt{n}\|F(\widetilde{N}^n(s)) - F(y_s)\| \leq \left[C_{\mathcal{K}}^{'}\widetilde{N}^n(s) + (1 - U(y_s))\right] \|X^n(s)\|$$

Step 2. As the same as the step 1 of the proof of the lemma 1,

$$\mathbb{E}[\|M_n(t)\|_1^2] \leq \sum_{i=1}^{I}\sum_{s=0}^{t-1}\mathbb{E}[\mathbb{V}(\widetilde{N}_i^n(s+1)|\mathcal{F}_s^n)]$$

Then

$$(\sqrt{n}\mathbb{E}[\|M_n(t)\|_1])^2 \leq \sum_{i=1}^{I}\sum_{s=0}^{t-1} n\mathbb{E}[\mathbb{V}(\widetilde{N}_i^n(s+1)|\mathcal{F}_s^n)]$$

By the proposition C.1, $\sqrt{n}\mathbb{E}[\|M_n(t)\|_1]$ is bounded.

Step 3. Hypothesis $(\mathcal{H}''_2)$ unsures that it exists a real c_0 such that $\mathbb{E}(\|X_n(0)\|) < c_0$. By a recurrence we deduce the lemma.

Lemma 3 *Let assumptions $(\mathcal{H}_1)$, $(\mathcal{H}_2)$ and $(\mathcal{H}_3^{'})$ hold. Then:*

$$\sqrt{n}M^n(T) \xrightarrow{n\to\infty} \mathcal{N}(0,\Gamma) \qquad \textit{in law}$$

where $\Gamma = \sum_{t=0}^{T-1}\Gamma(t)$.

Proof Let Φ_n the characteristic function of $\sqrt{n}M_n(T)$ and $\overline{N}^n(t) = \sqrt{n}\left[\widetilde{N}^n(t) - \mathbb{E}(\widetilde{N}^n(t)|\mathcal{F}_{t-1}^n)\right]$ for $t = 1,\ldots,T$. For all $\lambda \in \mathbb{R}^I$

$$\begin{aligned}
\Phi_n(\lambda) &= \mathbb{E}\left[\exp i\langle\lambda, \sqrt{n}M_n(T)\rangle\sqrt{n}\right] \\
&= \prod_{t=0}^{T-1}\mathbb{E}\left[\exp i\langle\lambda, \overline{N}^n(t)\rangle\sqrt{n}\right] \\
&= \prod_{t=0}^{T-1}\left[1 - \frac{1}{2}{}^t\lambda\mathbb{V}(\overline{N}^n(t))\lambda + \circ\left(\mathbb{V}(\overline{N}^n(t))\right)\right] \\
&= \exp[-\frac{1}{2}\sum_{t=0}^{T-1}{}^t\lambda\mathbb{V}(\overline{N}^n(t))\lambda]
\end{aligned}$$

From the proposition C.1 we deduce that

$$\Phi_n(\lambda) \xrightarrow{n\to\infty} \exp[-\frac{1}{2}{}^t\lambda\Gamma\lambda]$$

■

Proof of theorem 3.2: The Taylor's development of F gives:

$$\begin{aligned}
\sqrt{n}\left(F(\widetilde{N}^n(t)) - F(y_t)\right) &= \sqrt{n}d_{y_t}F.(\widetilde{N}^n(t) - y_t) + O(\sqrt{n}\|\widetilde{N}^n(t) - y_t\|_1^2) \\
&= d_{y_t}F.X^n(t) + O(\|\widetilde{N}^n(t) - y_t\|_1)X^n(t)
\end{aligned}$$

Then for all $t \geq 1$

$$X^n(t) \quad = \quad X_0^n + \sum_{s=0}^{t-1} \Big(d_{y_s} F.X^n(s) + O(\|\widetilde{N}^n(s) - y_t\|_1) X^n(s) \Big) + \sqrt{n} M^n(t)$$

and

$$X^n(t) - X_t = (X_0^n - X_0) + \sum_{s=0}^{t-1} d_{y_s} F.(X^n(s) - X_s) + (\sqrt{n} M^n(t) - M_t) + \epsilon_n(t)$$

where X_t verifies the equation (10) and $\epsilon_n(t) = \sum_{s=0}^{t-1} O(\|\widetilde{N}^n(s) - y_t\|_1) X^n(s)$.

As the same as the proof of the theorem 3.1, we deduce by Gronwall inequality that

$$\sup_{t \leq T} \|X^n(t) - X_t\|_1 \leq (\|X_0^n - X_0\|_1 + \sup_{t \leq T} \|\sqrt{n} M^n(t) - M_t\|_1) e^{C_F T} + \sup_{t \leq T} \|\epsilon_n(t)\|_1$$

where $C_F = \|dF\|_\infty$.

The first term in the brackets converges to 0 in L^1 by assumption and the second term by the lemma 3. By theorem 3.1 and lemma 2 we deduce the convergence of $\sup_{t \leq T} \|\epsilon_n(t)\|_1$ toward to zero. The exponential function being independent of n this completes the proof of the theorem. ■

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