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Abstract. In this article, Functional Structural Plant growth Models (FSPMs) with stochastic organogenesis are described in the framework of Jump Markov Models. A Bayesian approach is adopted to estimate uncertain ecophysiological parameters. In particular, two estimation procedures are detailed: the Rao-Blackwellized Particle Filter and the Convolution Particle Filter. These methods are then applied and compared throughout a particular FSPM: the GreenLab model with stochastic organogenesis.
Keywords: Functional Structural Plant growth Model, Jump Markov Model, Rao-Blackwallised Particle Filter, Convolution Particle filter.

1 Introduction

Functional-Structural Plant growth Models (FSPMs) aim at describing the structural development of individual plants in interaction with their ecophysiological functioning, see Sievänen *et al.* [1]. The complexity of the biological phenomena involved when modeling such sophisticated systems has sometimes led to the development of very heavy simulation models, capitalizing an important amount of biological knowledge but very difficult to calibrate on experimental data. This is often due to a large number of uncertain parameters that cannot be measured directly and should (therefore) be estimated by inverse methods. However, recent efforts have been made to implement some FSPMs in the framework of dynamic systems, both in the deterministic case (Cournède *et al.*[2]) and also when organogenesis (structural development) is stochastic (Kang *et al.*[3]). Estimation methods of the Generalized Least Squares type were devised [4] to estimate the functional parameters. Even if (potentially) such methods could lead the modeler to a good model fitting, statistical inference based on these fitting results is rather limited. This is due to simplistic assumptions in the structure of the covariance matrix of the error model (heteroscedastic but diagonal in Cournède *et al.* [4]), even more when the underlying organogenesis is stochastic. In such a context,

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the objective of this paper is to propose a new mathematical formalism of FSPMs with stochastic organogenesis based on Jump Markov Models (Andrieu *et al.*[5]) and to adapt Bayesian estimation methods to this framework, namely Rao-Blackwell Particle Filtering (RBPF, Doucet *et al.*[6]) and Convolution Particle Filter (CPF, Campillo and Rossi[7]). In Section 2, we recall the definition of Jump Markov Models and the principles of the above-cited filtering techniques. Then, in Section 3, we show how functional-structural models with stochastic organogenesis can be described in this framework, and in Section 4, we apply and compare the two aforementioned Bayesian methods in a particular plant growth model of this kind (GreenLab with stochastic organogenesis, Kang *et al.*[3]). Finally, the obtained results and some possible generalizations are discussed.

2 Bayesian parameter estimation for Jump Markov Models

We introduce here the necessary mathematical notations. Random vectors are denoted by capital letters and their realizations by the same letter in a lower-case format. Let Z be a generic random vector. For notational simplicity, if Z admits a probability density (with respect to the Lebesgue measure), it is denoted by $p(z)$, and if Z is discrete, its probability function is denoted by $P(z)$. We typically use this convention for vectors Z_n of a generic stochastic process $\{Z_n\}_{n\in\mathbb{N}}$.

Let us consider a discrete dynamic system characterized by a hidden state sequence $\{X_n\}_{n\in\mathbb{N}}$ and an observed state sequence $\{Y_n\}_{n\in\mathbb{N}}$, which are defined on a common probability space $(\Omega, \mathcal{F}, \mathbb{P})$. We assume that they take values respectively in $(\mathcal{X}, \mathcal{B}(\mathcal{X}))$ and $(\mathcal{Y}, \mathcal{B}(\mathcal{Y}))$ ($\mathcal{B}$ stands for Borel). In the context of our application we restrict our attention to the case that $\mathcal{X}, \mathcal{Y}$ are Euclidean subsets, even if the results could be extended to Polish spaces as well. The aforementioned processes are both dependent on a third state sequence $(C_n)_{n\in\mathbb{N}}$ with values in a discrete state space $\mathcal{C}$ and are both affected by noise.

2.1 Jump Markov Model

Now, we give a formal definition of the class of models that we consider.

Definition 1. Let $\{C_n\}_{n\in\mathbb{N}}$ be a (generally non-homogeneous) Markov chain with values in a discrete state space $\mathcal{C}$, initial probabilities $P(c_0)$ and transition probabilities $P(c_{n+1}|c_n)$. A **Jump Markov Model** (JMM) is a dynamic system characterized by the following state equations :

$$\begin{cases} X_0 \sim p(x_0) \\ X_{n+1} = f_{n+1}(X_n, C_{n+1}, W_{n+1}, \Theta), & n \geq 0, \\ Y_n = g_n(X_n, C_n, \Theta) + V_n, & n \geq 0, \end{cases} \tag{1}$$

where f_n, g_n are Borel functions, $\{V_n\}_{n\geq 0}$ (measurement noise) and $\{W_n\}_{n\geq 0}$ (process noise) are mutually independent sequences of i.i.d. random vectors, and Θ is a parameter vector with values in $\mathcal{P} \subset \mathbb{R}^{dim(\Theta)}$. In addition, the process $\{C_n\}_{n\in\mathbb{N}}$ is independent of both the state noise and of the measurement noise.

Our objective is to estimate the parameter vector Θ from observations $(Y_0, \ldots, Y_n) \stackrel{\text{def}}{=} Y_{0:n}$, where n corresponds to the observation length. For this purpose, we propose a Bayesian approach. Θ is considered as a random vector and is incorporated into the hidden state vector. If Θ_n denotes the vector of parameters at step n, then, for all n, $\Theta_n = \Theta_{n+1}$ since Θ_n is constant. The corresponding augmented state vector is denoted by $X_n^a = (X_n, \Theta_n)$ ($\mathcal{X}^a = \mathcal{X} \times \mathcal{P}$ denotes the associated state space).

2.2 Bayesian methods

The following methods aim at giving an estimate $\hat{p}(x_n^a|y_{0:n})$ of $p(x_n^a|y_{0:n})$. The augmented hidden state vector X_n^a will be estimated by a minimum mean squared error estimator $\hat{x}_n^a$:

$$\hat{x}_n^a = E[X_n^a|Y_{0:n}] \approx \int_{\mathcal{X}^a} x_n^a \hat{p}(x_n^a|y_{0:n})\lambda(dx_n^a) \tag{2}$$

where λ denotes the Lebesgue measure on $\mathbb{R}^{dim(\mathcal{X}^a)}$. Two particle filtering based methods are briefly introduced (see the corresponding references for more details): Rao-Blackwellized Particle Filtering (RBPF, Doucet *et al.*[6]) and Convolution Particle Filter (CPF, Campillo and Rossi[7]).

• **Rao-Blackwellized Particle Filtering**: this method is a classical one in the framework of JMM and has already been extensively applied (see Andrieu *et al.*[5]). It is based on the following decomposition:

$$p(x_n^a|y_{0:n}) = \sum_{c_{0:n}\in\mathcal{C}^{n+1}} p(x_n^a|c_{0:n}, y_{0:n})P(c_{0:n}|y_{0:n}).$$

Therefore, the estimation of $p(x_n^a|y_{0:n})$ can be separated into two steps: i) approximate $P(c_{0:n}|y_{0:n})$ thanks to a Particle Filtering approach (see Doucet *et al.*[6]) and ii) approximate $p(x_n^a|c_{0:n}, y_{0:n})$ by a Gaussian probability density function with one step of an Unscented Kalman Filter (UKF, see Julier and Uhlmann[8]). After the n-th step of the procedure, we have a set of M particles $\{(\tilde{c}_n^{(i)}, \tilde{x}_n^{a\,(i)}, \Sigma_n^{x(i)})\ i = 1, \ldots, M\}$ where $\Sigma_n^{x(i)}$ is the covariance matrix associated to the state vector $\tilde{x}_n^{a\,(i)}$. Let us denote by $\tilde{w}_n^{(i)}$ the weight of the i-th particle at step n. The algorithm associated to the RBPF method is thus the following (x_0 and Σ_0^x are supposedly known initial conditions):

- Initialization:
  - Sample $\tilde{c}_0^{(i)} \sim P(c_0)$, $i = 1, \ldots, M$

  - Set the predicted state vector as x_0 and the associated covariance matrix as Σ_0^x for each particle i, $i = 1, \ldots, M$
  - Compute the predicted observation $\tilde{y}_0^{(i)}$ and the corrected predicted state vector $\tilde{x}_0^{a\,(i)}$ and their corresponding covariance matrices $\Sigma_0^{y\,(i)}$ and $\Sigma_0^{x\,(i)}$ with one step of UKF, $i = 1, \ldots, M$
  - Set $\tilde{w}_0^{(i)} \sim \mathcal{N}(y_0; \tilde{y}_0{}^{(i)}, \tilde{\Sigma}_0^{y\,(i)})$, $i = 1, \ldots, M$
- Iteration (we have a set of particles $\{(\tilde{c}_{n-1}^{(i)}, \tilde{x}_{n-1}^{a}{}^{(i)}, \Sigma_{n-1}^{x}{}^{(i)}), i = 1, \ldots, M\}$) :
  - Sample $\tilde{c}_n^{(i)} \sim P(c_n|\tilde{c}_{n-1}^{(i)})$, $i = 1, \ldots, M$
  - Compute the predicted observation $\tilde{y}_{n|n-1}^{(i)}$ and the corrected predicted state vector $\tilde{x}_n^{a\,(i)}$ and their corresponding covariance matrices $\Sigma_{n|n-1}^{y}{}^{(i)}$ and $\Sigma_n^{x\,(i)}$ with one step of UKF, $i = 1, \ldots, M$
  - Set $\tilde{w}_n^{(i)} \sim \tilde{w}_{n-1}^{(i)} \mathcal{N}(y_n; \tilde{y}_{n|n-1}^{a}{}^{(i)}, \tilde{\Sigma}_{n|n-1}^{y}{}^{(i)})$, $i = 1, \ldots, M$
  - Resampling (if needed)

$\mathcal{N}(y_n; \tilde{y}_{n|n-1}^{a}{}^{(i)}, \tilde{\Sigma}_{n|n-1}^{y}{}^{(i)})$ denotes the probability density function associated to a Gaussian law $\mathcal{N}(\tilde{y}_{n|n-1}^{a}{}^{(i)}, \tilde{\Sigma}_{n|n-1}^{y}{}^{(i)})$ with y_n as input. At the end of the n-th step, the estimate $\hat{p}(x_n^a|y_{1:n})$ is given by:

$$\hat{p}(x_n^a|y_{0:n}) = \sum_{i=1}^{M} \tilde{w}_n^{(i)} \mathcal{N}(x_n^a; \tilde{x}_n^{a\,(i)}, \tilde{\Sigma}_n^{x\,(i)}).$$

• **Convolution Particle Filter**: this method relies on a convolution kernel approximation technique. At the n-th step, the estimate $\hat{p}(x_n^a|y_{1:n})$ is built from a set of M particles $\{(\tilde{c}_n^{(i)}, \tilde{x}_n^{a\,(i)}, \tilde{y}_{n^-}^{(i)}), i = 1, \ldots, M\}$ and the corresponding set of weights $\{\tilde{w}_n^{(i)}, i = 1, \ldots, M\}$. Let us denote by $K_{h_M}^C$, $K_{h_M}^{X^a}$ and $K_{h_M}^Y$ the Parzen-Rozenblatt kernels associated respectively to C_n, X_n^a and Y_n. $h_M > 0$ is the bandwidth parameter. Therefore, the procedure works as follows:

- Initialization:
  - Sample $\tilde{c}_{0^-}^{(i)} \sim P(c_0)$, $i = 1, \ldots, M$
  - Sample $\tilde{x}_{0^-}^{a}{}^{(i)} \sim p(x_0^a|c_0)$, $i = 1, \ldots, M$
  - Sample $\tilde{y}_{0^-}^{(i)} \sim p(y_0|\tilde{c}_{0^-}^{(i)}, \tilde{x}_{0^-}^{a}{}^{(i)})$, $i = 1, \ldots, M$
  - Set $\tilde{w}_0^{(i)} \sim K_{h_M}^Y(y_0 - \tilde{y}_{0^-}^{(i)})$, $i = 1, \ldots, M$
  - Set $\hat{p}(c_0, x_0^a|y_0) = \sum_{i=1}^{M} \tilde{w}_0^{(i)} K_{h_M}^C(c_0 - \tilde{c}_{0^-}^{(i)}) K_{h_M}^X(x_0^a - \tilde{x}_{0^-}^{(i)})$
  - Sample $(\tilde{c}_0{}^{(i)}, \tilde{x}_0^{a(i)}) \sim \hat{p}(c_0, x_0^a|y_0)$
- Iteration (we have a set of particles $\{(\tilde{c}_{n-1}^{(i)}, \tilde{x}_{n-1}^{a}{}^{(i)}, \tilde{y}_{n-1}^{(i)}), i = 1, \ldots, M\}$) :
  - Sample $\tilde{c}_{n^-}^{(i)} \sim P(c_n|\tilde{c}_{n-1}^{(i)})$, $i = 1, \ldots, M$
  - Sample $\tilde{x}_{n^-}^{a}{}^{(i)} \sim p(x_n^a|\tilde{c}_{n^-}^{(i)}, \tilde{x}_{n-1}^{a}{}^{(i)})$, $i = 1, \ldots, M$
  - Sample $\tilde{y}_{n^-}^{(i)} \sim p(y_n|\tilde{c}_{n^-}^{(i)}, \tilde{x}_{n^-}^{a}{}^{(i)})$, $i = 1, \ldots, M$

– Set $\tilde{w}_n^{(i)} \sim K_{h_M}^Y(y_n - \tilde{y}_{n^-}^{(i)})$, $i = 1, \ldots, M$
– Set $\hat{p}(c_n, x_n^a | y_{0:n}) = \sum_{i=1}^{M} \tilde{w}_n^{(i)} K_{h_M}^C(c_n - \tilde{c}_{n^-}^{(i)}) K_{h_M}^X(x_n^a - \tilde{x}_{n^-}^{(i)})$
– Sample $(\tilde{c}_n{}^{(i)}, \tilde{x}_n^{a\,(i)}) \sim \hat{p}(c_n, x_n^a | y_{0:n})$

At the end of the n-th step, the estimate $\hat{p}(x_n^a | y_{0:n})$ is given by:

$$\hat{p}(x_n^a | y_{0:n}) = \sum_{i=1}^{M} \tilde{w}_n^{(i)} K_{h_M}^X(x_n^a - \tilde{x}_{n^-}^{(i)}).$$

3 FSPMs with Stochastic Organogenesis as Jump Markov Models

The aim of this section is to set a suitable statistical model allowing the estimation of functional parameters (denoted by Θ) in functional-structural plant model with stochastic organogenesis (for example, the GreenLab 2 model of Kang *et al.*[3]). For the sake of clarity, we only consider here models with immediate expansion and we suppose that leaves are only active for one step (this model applies to most temperate trees). We assume that the organogenesis parameters are already determined by using a symbolic approach (see Loi *et al.*[9])

3.1 Description of the model

Plants can be seen as discrete dynamic systems. At each time step, two processes shall be considered: organogenesis, corresponding to structural development, and biophysical functioning, corresponding to the production of biomass and its allocation among organs. The organogenesis is the creation of new organs by buds. Let us denote by T_{obs} the time when the plant is observed, $\mathcal{B}$ the set of symbols representing the different botanical types of buds and $\mathcal{O}$ the set of all types of other organs composing plant structure (leaves, internodes, fruits ...), potentially grouped into categories. For all $n \in \{1, \ldots, T_{obs}\}$, let N_n^a be either the number of active leaves at step n if $a \in \mathcal{B}$ or the number of organs of type a created at step n if $a \in \mathcal{O}$. $N_n = (\ldots, N_n^b, \ldots, N_{n-1}^o, \ldots)_{b \in \mathcal{B}, o \in \mathcal{O}}$ is called the organogenesis vector at step n. By convention, N_0 denotes the vector whose components are all equal to zero except the one corresponding to the seed which is equal to 1 (N_0 is thus known). In this article, we consider plant models in which $(N_n)_{n \in \mathbb{N}}$ is a Galton-Watson multitype branching process (see Loi and Cournède[10], the transition probabilities are supposed known in the sequel).

The biomass contained in the seed is represented by Q_0 (supposed known). For $n \geq 1$, Q_n is the biomass produced at step n by photosynthesis and it is determined by the production equation:

$$Q_n = \Phi(Q_{n-1}, N_{n-1}, E_n, \Theta)(1 + W_n) \qquad n \geq 1 \tag{3}$$

where E_n is the environmental input (generally global radiations) and Θ a vector of endogenous parameters to estimate. The process $\{W_n\}_{n\in\mathbb{N}}$ refers to the process noise modelling the uncertainties arising from the biomass production and it is assumed to be a white gaussian noise with $W_n \sim N(0, J_n)$. When dealing with the GreenLab growth model, the production equation is :

$$Q_n = E_n \mu S_p \left(1 - exp\left(-\frac{k_b N_{n-1}^l P_l}{e\sum_{o\in\mathcal{O}} N_{n-1}^o P_o} Q_{n-1}\right)\right)(1+W_n)$$

where $l \in \mathcal{O}$ is representing leaves. The vector of parameters Θ contains μ, S_p and P_o with $o \in \mathcal{O}\setminus\{l\}$. The parameter P_l is fixed to avoid identifiability issues and k_b and e are botanical parameters supposed known.

The biomass Q_n is then fully distributed to organs which appeared at step n. The amount of biomass allocated to an organ of type $o \in \mathcal{O}$ at step n depends not only from its type o but also from the vector N_n (the biomass is distributed by taking into account the number of all organs competing for it). It is denoted by $Al_n^o(Q_n, N_n, \Theta)$. Since the organs of the plants consume biomass only once, the mass M_n^o of an organ o appeared at step n is then given by:

$$M_n^o = Al_n^o(Q_n, N_n, \Theta).$$

In the GreenLab model, the allocation function is given by :

$$M_n^o = Al_n^o(Q_n, N_n, \Theta) = \frac{P_o}{\sum_{o\in\mathcal{O}} N_n^o P_o} Q_n.$$

3.2 Associated Jump Markov Model

The vector of endogenous parameters Θ is generally unknown. In order to estimate it, the previous model of plant growth is formulated as a JMM. By doing so, the Bayesian methods of Section 2.2 can be used. Let us first describe the observations of the system. At a given growth step T_{obs}, the plant is cut up and a number of organs are weighted. Let $\bar{M}_n^o$ be the mean of all weighted organs of type o created at step n. The observation sequence of vectors $\{Y_n\}_{n\in\mathbb{N}}$ is thus defined as follows:

$$Y_n = \left(\ldots, \bar{M}_n^o, \ldots\right)_{o\in\mathcal{O}} + V_n, \qquad n \geq 1.$$

The process $\{V_n\}_{n\in\mathbb{N}}$ refers to the measurement noise and it is assumed to be a white gaussian noise independent from $\{W_n\}_{n\in\mathbb{N}}$ with $V_n \sim N(0, R_n)$.

We prove hereafter that FSPMs with stochastic organogenesis can be described by a JMM. The biomass created by photosynthesis is chosen as state variable. Therefore, $X_n = Q_n$ for $n \geq 0$. Given that $M_n^o = Al_n^o(Q_n, N_n, \Theta)$,

$(\ldots, \bar{M}_n^o, \ldots)_{o\in\mathcal{O}}$ can be rewritten as a function g_n with Q_n, N_n and Θ as inputs. The observation equation becomes:

$$Y_n = g_n(Q_n, N_n, \Theta) + V_n = g_n(X_n, N_n, \Theta) + V_n, \qquad n \geq 1. \tag{4}$$

Let C_n be the random vector defined as follows:

$$\begin{cases} C_0 = (0, N_0), \\ C_n = (N_{n-1}, N_n), \qquad \forall n \geq 1. \end{cases}$$

Given that $(N_n)_{n\in\mathbb{N}}$ is a multitype branching process, $(C_n)_{n\in\mathbb{N}}$ is a Markov chain whose transition probabilities $P(c_{n+1}|c_n)$ are entirely determined by the ones of $(N_n)_{n\in\mathbb{N}}$. Since N_0 is known, the initial state C_0 is fixed and is equal to $(0, N_0)$. Therefore, the dynamic system associated to FSPMs can be written as follows:

$$\begin{cases} X_0 = Q_0, \\ X_{n+1} = \Phi(X_n, C_{n+1}, E_{n+1}, \Theta)(1 + W_{n+1}), & n \geq 1, \\ Y_n = g_n(Q_n, C_n, \Theta) + V_n, & n \geq 0. \end{cases} \tag{5}$$

Therefore, according to Definition 1, the previous system is a JMM.

4 Analysis and comparision of the statistical methods

In this section, the Bayesian methods are applied to a specific FSPM (the GreenLab model with stochastic organogenesis) and then compared. The objective is to estimate the vector of parameters $\Theta = (\mu, S_p, \ldots, P^o, \ldots)_{o\in\mathcal{O}\setminus\{l\}}$ by using simulated data. We assume that the parameters of the process and measurement noises are known. The observation time is $T_{obs} = 28$.

Both methods give good results in estimating the parameters (see Table 1). The parameters μ and S_p are slightly biased due the limited number of observations.

Parameters	True value	CPF estimation	RBPF estimation
μ	3.40×10^{-3}	3.44×10^{-3}	3.53×10^{-3}
S_p	70	65.79	63.80
P^p	0.3	0.2971	0.2988
P^{i1}	3	2.9981	3.0273
P^{i2}	2	1.9992	2.0401

Table 1. Estimation results. The superscripts p, $i1$ and $i2$ are types of organs and stand for petiols, internode of type 1 and internode of type 2.

Both methods are also pretty good at estimating the biomass created at each step (*i.e.* the hidden state, see Figure 1). They are also convergent and robust if the number of particles is sufficient (at least 200 for RBPF and 5000 for CPF). As far as convergence time is concerned, their behaviour is

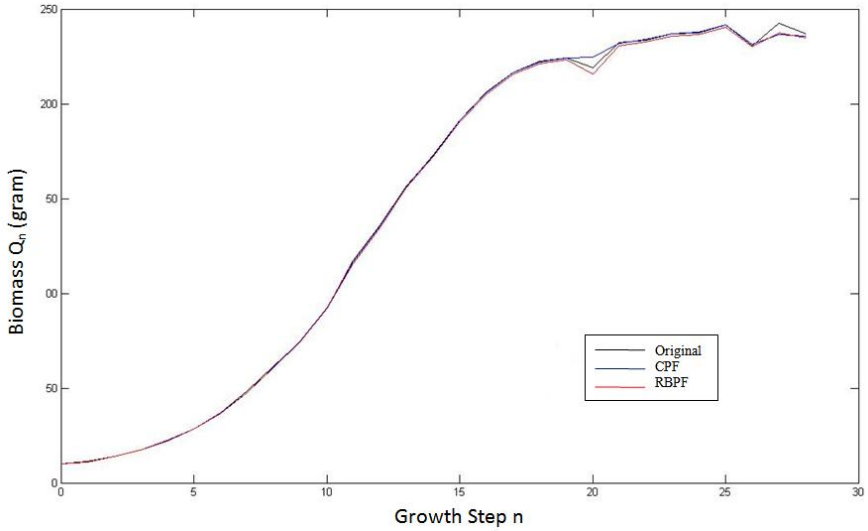

Fig. 1. Estimation of the biomass created at each step.

quite different. The CPF method is a particle filtering method. Since a great number of particles is required to have convergence, a step of the algorithm can last long. This is not the case for RBPF because fewer particles are needed and a step of UKF is quick. However, CPF needs fewer iterations of the entire algorithm (*i.e.* from step 0 to T_{obs}) than RBPF to get convergence. Finally, by taking into account these two points, it appears that CPF is slightly faster than RBPF. CPF can also be applied to a wider class of models since the hypotheses needed to use the method are quite loosed contrary to RBPF which needs the model to be conditionally Gaussian given the process $\{C_n\}_{n\in\mathbb{N}}$.

5 Conclusion

We proposed a JMM framework for FSPM with stochastic organogenesis where the expansion is immediate and the leaves are active only for one step. The theoretical extension to the general case is simple and only necessitates to modify the hidden state vector by incorporating the created biomass from the previous steps. This framework enables the use of Bayesian methods (CPF and RBPF) to estimate the endogenous parameters. Both methods are quite effective. CPF appears to be slightly better because it runs faster and can be applied to a wider class of models. Since the estimation of the hidden states is good, these methods can also be used to determine confidence intervals for the estimated parameters (using bootstrap or the distributions given by the particle weights).

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