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A Markovian individual-based model for terrestrial plant dynamics

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Abstract. *We propose an individual-based models (IBM) of a terrestrial plant systems. Each individual plant is explicitly represented as well as the basic mechanisms acting on each individual: natural birth and death, dispersion, death due to competition. The resulting model is a Markovian model of branching particles with diffusion. We describe the model and the associated Monte Carlo procedure. We study the asymptotic properties of this model in a large population setup.*

The development of individual-based models (IBM) in theoretical ecology has been studied in the past. The first attempts of this approach began in the 1930s. Since two decades, resurgence in this field has happened due to the development of computers. There have been mathematical developments of these models in the last ten years. The objective of this study is to propose a computational and mathematical framework for IBM of ecosystems, such as, terrestrial plant systems.

1 The model

We consider a family of individuals that live in a set of the from $\mathcal{X} = \mathcal{D} \times \mathbb{R}^d$ where $\mathcal{D}$ is a compact domain of $\mathbb{R}^n$. The state $x = (p, r) \in \mathcal{X}$ of an individual represents its position p in the physical space $\mathcal{D}$ and a mark r that could represent its size or its maturation age.

It is convenient to represent an individual at point $x \in \mathcal{X}$ by the Dirac measure δ_x;

hence the population at time t will be:

$$\nu_t(\mathrm{d}x) = \sum_{i=1}^{N_t} \delta_{x_t^i}(\mathrm{d}x) \tag{1}$$

where the sum is over all individuals alive at time t and N_t is the size of the population at time t. $(\nu_t)_{t\geq 0}$ is a $\mathcal{M}$-valued process the set of finite point measure on $\mathcal{X}$ ($\mathcal{M}_+(\mathcal{X})$ will be the set of finite positive measures on $\mathcal{X}$).

Considering the state $\nu = \sum_{i=1}^{N} \delta_{x^i}$ of the family at a given time, an individual in state $x \in \nu$ will be subject to 3 types of *punctual* events occurring at specific rates:

Intrinsic death: This individual disappears at a rate $\lambda^{\mathrm{d}}(x)$ which may depend on its state. This death is called “intrinsic” as it does not depend on the state of all the population ν. It represents the “natural death” as opposed to “competition death”.

Competition death: This individual disappears at a rate $\lambda^{\mathrm{c}}(x,\nu)$ which may depend on its state x and on the states of all the population. We suppose that $\lambda^{\mathrm{c}}(x,\nu)$ is of the form:

$$\lambda^{\mathrm{c}}(x,\nu) = \sum_{y\in\nu} u(x,y) = \int_{\mathcal{X}} u(x,y)\,\nu(\mathrm{d}y)\,. \tag{2}$$

Birth and dispersion: This individual gives birth to a new individual at a rate $\lambda^{\mathrm{b}}(x)$ which may depend on its state. The state $y \in \mathcal{X}$ of the new individual will be determined by a given dispersion kernel $D(x, \mathrm{d}y)$.

The population is also subject to a *continuous* mechanisms:

Displacement: Over time, the mark component of each individual i evolves in the state space $\mathbb{R}^d$ in interaction with the evolution of all other individuals according to the following system of stochastic differential equations (SDE):

$$\mathrm{d}\begin{pmatrix} p_t^i \\ r_t^i \end{pmatrix} = \begin{pmatrix} 0 \\ \tilde g(x_t^i,\nu_t) \end{pmatrix}\,\mathrm{d}t + \begin{pmatrix} 0 \\ \tilde\sigma(x_t^i,\nu_t) \end{pmatrix}\,\mathrm{d}\mathbf{B}_t^i \tag{3}$$

where $(\mathbf{B}_t^i)_{t\geq 0}$ are independent standard Brownian motions. To simplify the notation, Equation (3) will be represented as:

$$\mathrm{d}x_t^i = g(x_t^i,\nu_t)\,\mathrm{d}t + \sigma(x_t^i,\nu_t)\,\mathrm{d}\mathbf{B}_t^i\,. \tag{4}$$

Let $a(x,\nu) \stackrel{\text{def}}{=} \sigma(x,\nu)\,\sigma^*(x,\nu)$. We define the associated flow operator:

$$\nu_t = F(t,s;\nu_s) \tag{5}$$

defined for all $s \leq t$ between two successive punctual events (i.e. between two successive jump of the population size).

We suppose that these four mechanisms and the dispersion mechanism are mutually independent. Between punctual events of birth and death, the size of the population remains unchanged as well as the position of the individuals, and their marks evolve according to (4).

2 Monte Carlo simulation

We suppose that there exists positive real numbers $\lambda^{\mathrm{b}}_{\max}$, $\lambda^{\mathrm{d}}_{\max}$ and $u_{\max}$ such that: $\lambda^{\mathrm{b}}(x) \leq \lambda^{\mathrm{b}}_{\max}$, $\lambda^{\mathrm{d}}(x) \leq \lambda^{\mathrm{d}}_{\max}$, $u(x,y) \leq u_{\max}$. Hence $\lambda^{\mathrm{c}}(x,\nu) \leq u_{\max}\,\langle \nu, 1\rangle$.

At the scale of the population, the maximum rate of events (birth, natural death, death by competition) is bounded by: $\bar\lambda \stackrel{\mathrm{def}}{=} \bar\lambda^{\mathrm{d}} + \bar\lambda^{\mathrm{b}} + \bar\lambda^{\mathrm{c}}$ with $\bar\lambda^{\mathrm{b}} \stackrel{\mathrm{def}}{=} \lambda^{\mathrm{b}}_{\max}\,N$, $\bar\lambda^{\mathrm{d}} \stackrel{\mathrm{def}}{=} \lambda^{\mathrm{d}}_{\max}\,N$, $\bar\lambda^{\mathrm{c}} \stackrel{\mathrm{def}}{=} u_{\max}\,N^2$.

Iteration $\nu_{T_{k-1}} \to \nu_{T_k}$:

(*i*) Let $N = \langle \nu_{T_{k-1}}, 1\rangle$ be the population size.

(*ii*) Computation of the global rate $\bar\lambda \stackrel{\mathrm{def}}{=} \bar\lambda^{\mathrm{d}} + \bar\lambda^{\mathrm{b}} + \bar\lambda^{\mathrm{c}}$.

(*iii*) Simulation of the next event instant: $T_k = T_{k-1} + S_k$, with $S_k \sim \mathrm{Exp}(\bar\lambda)$.

(*iv*) Computation of the system evolution: $\nu_{T_k^-} = F(T_k, T_{k-1}, \nu_{T_{k-1}})$. In practice, the system is simulated with an Euler discretization scheme.

(*v*) Chose x at random uniformly in $\nu_{T_k^-}$; chose at random the nature of the next event according the probability values $(\bar\lambda^{\mathrm{b}}/\bar\lambda, \bar\lambda^{\mathrm{d}}/\bar\lambda, \bar\lambda^{\mathrm{c}}/\bar\lambda)$:

- birth:

$$\nu_{T_k} = \begin{cases} \nu_{T_k^-} + \delta_{x'} & \text{with probability } \frac{\lambda^{\mathrm{b}}(x)}{\lambda^{\mathrm{b}}_{\max}} \qquad \text{where } x' \sim D(x, \mathrm{d}z) \\ \nu_{T_k^-} & \text{with probability } 1 - \frac{\lambda^{\mathrm{b}}(x)}{\lambda^{\mathrm{b}}_{\max}} \end{cases}$$

- natural death:

$$\nu_{T_k} = \begin{cases} \nu_{T_k^-} - \delta_{x} & \text{with probability } \frac{\lambda^{\mathrm{d}}(x)}{\lambda^{\mathrm{d}}_{\max}} \\ \nu_{T_k^-} & \text{with probability } 1 - \frac{\lambda^{\mathrm{d}}(x)}{\lambda^{\mathrm{d}}_{\max}} \end{cases}$$

- competition death: chose y at random uniformly in $\nu_{T_k^-}$ and let

$$\nu_{T_k} = \begin{cases} \nu_{T_k^-} - \delta_{x} & \text{with probability } \frac{u(x,y)}{u_{\max}} \\ \nu_{T_k^-} & \text{with probability } 1 - \frac{u(x,y)}{u_{\max}} \end{cases}$$

□

3 Markov representation of the process $(\nu_t)_{t\geq 0}$

3.1 Identification of the infinitesimal generator

We introduce the following set $\mathcal{D}$ of test functions $\Phi : \mathcal{M} \mapsto \mathbb{R}$ of the form:

$$\Phi(\nu) = F(\langle \nu, f\rangle)$$

for any function $f : \mathcal{X} \mapsto \mathbb{R}$ and $F : \mathbb{R} \mapsto \mathbb{R}$ twice continuously differentiable, bounded with bounded derivatives.

For any $\Phi = (F, f) \in \mathcal{D}$, $\Phi(\nu_t) = F(\langle \nu_t, f \rangle)$ satisfies:

$$\Phi(\nu_t) = \Phi(\nu_0) + \int_0^t \mathcal{L}\Phi(\nu_s)\,\mathrm{d}s + M_{\Phi,t}(\nu) \tag{6}$$

where the infinitesimal generator $\mathcal{L} = \mathcal{L}^{\mathrm{d}} + \mathcal{L}^{\mathrm{b}} + \mathcal{L}^{\mathrm{c}} + \mathcal{L}^{\mathrm{g}}$ and the martingale term $M_{\Phi,t}(\nu) = \mathbf{M}^{\mathrm{d}}_{\Phi,t}(\nu) + \mathbf{M}^{\mathrm{b}}_{\Phi,t}(\nu) + \mathbf{M}^{\mathrm{c}}_{\Phi,t}(\nu) + \mathbf{M}^{\mathrm{g}}_{\Phi,t}(\nu)$ (corresponding respectively to natural death, birth, death by competition and growth respectively) can be explicitly described.

4 Large population limit

Let k be the initial population size, i.e. $k = \langle \nu_0, 1 \rangle$, and replace u by u^k, g by g^k and σ by σ^k suppose that:

$$k\,u^k(x,y) \to \bar{u}(x,y)\,, \qquad g^k(x, k\,\mu) \to \bar{g}(x,\mu)\,, \qquad \sigma^k(x, k\,\mu) \to \bar{\sigma}(x,\mu)\,.$$

Let $(\nu_t^k)_{0\leq t\leq T}$ be the Markov process defined in the previous section with initial population size k. We define:

$$\mu_t^k \stackrel{\mathrm{def}}{=} \frac{1}{k}\,\nu_t^k\,.$$

In this section we study the asymptotic property of the law of the process $(\mu_t^k)_{0\leq t\leq T}$ on the space $\mathbb{D}([0,T], \mathcal{M}_+(\mathcal{X}))$ of *c‡dl‡g* functions from $[0,T]$ with values in $\mathcal{M}_+(\mathcal{X})$.

$(\mu^k)_{k\in\mathbb{N}}$ converges in law to a deterministic process $\mu \in \mathbb{C}([0,T], \mathcal{M}_+(\mathcal{X}))$, characterized by

$$\langle \xi_t, f \rangle = \langle \xi_0, f \rangle + \int_0^t \bar{\ell} f(\xi_s)\,\mathrm{d}s \tag{7}$$

where

$$\begin{aligned}\bar{\ell} f(\xi) = \int_{\mathcal{X}} \Big\{ &- \lambda^{\mathrm{d}}(x)\, f(x) + \lambda^{\mathrm{b}}(x)\,\big[\textstyle\int_{\mathcal{X}} f(x+z)\,\bar{D}(z)\,\mathrm{d}z\big] \\ &- \big[\textstyle\int_{\mathcal{X}} \bar{u}(x,y)\;\xi(\mathrm{d}y)\big]\, f(x) + \big[\nabla f(x)\cdot \bar{g}(x,\xi) + \tfrac{1}{2}\,\tfrac{\partial^2 f}{\partial x_\ell\,\partial x_{\ell'}}\,\bar{a}_{\ell\ell'}(x,\xi)\big]\Big\}\;\xi(\mathrm{d}x)\,.\end{aligned}$$

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