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An individual-based model for clonal plant dynamics[1]

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Abstract. *We propose an IBM for clonal plant dynamics, focusing on the effects of the network structure of the plants on the reproductive strategy of ramets. After some numerical tests we propose a large population approximation as an advection-diffusion PDE for population densities.*

1 The model

Individual-based models are in constant development in computational ecology. These models aim to represent the dynamics of populations, they explicitly describe each individual as well as each mechanism acting on these individuals. Here we consider a model for a clonal plant: At time t it is represented as a set of nodes (ramets) that may be connected by links (rhizomes or stolons), see Figure 1. The state of the nodes is described by:

$$\nu_t = \sum_{i=1}^{N_t} \delta_{x_t^i}\,, \quad x_t^i \in \mathcal{D} \stackrel{\text{def}}{=} [x^{(1)}_{\text{min}}, x^{(1)}_{\text{max}}] \times [x^{(2)}_{\text{min}}, x^{(2)}_{\text{max}}]$$

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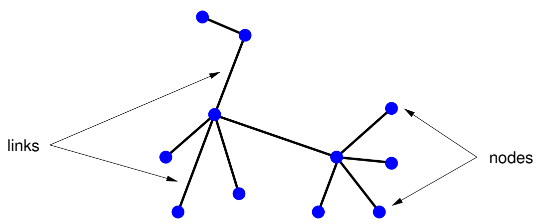

Figure 1: *The plant is represented as a set of nodes connected by links. The nodes can be seen as ramets and the links as rhizomes.*

where x_t^i is position of the ith node and N_t total number of nodes. For any node at position x we define the set of indices of the nodes connected to x: $J(t,x) = \{i = 1 \cdots N_t\,;\, x \text{ and } x_t^i \text{ are connected}\}$. The plant evolves in a resource landscape. At each time t, this resource is represented by $\mathbf{r}(t,x) \in [0, \mathbf{r}_{\text{max}}]$ the available resources at position $x \in \mathcal{D}$. The nodes accessing high levels of resources $\mathbf{r}(t,x)$ are more likely to give birth to new nodes.

Birth and death rates. Each node of ν_t in position x may disappear at a rate $\mu(t,x)$ and give birth to a new node at a rate $\lambda(t,x)$. These rates are *per capita rates*. Death and birth rates at population level are respectively: $\bar\lambda_t = \sum_{i=1}^{N_t} \lambda(t,x_t^i)$ and $\bar\mu_t = \sum_{i=1}^{N_t} \mu(t,x_t^i)$. The global event rate is $\kappa_t = \bar\mu_t + \bar\lambda_t$.

When a node is added to the population, it is always linked with the mother node, and the set of connections $J(t,x_t^i)$ corresponding to the mother node and the new node are modified accordingly. In addition, when a node x is removed from population, all connections to x are suppressed from all the sets $J(t,x_t^i)$.

Dispersion kernel. A node at position x at time t gives birth to a new node at position $y = x + v$ according to the following p.d.f.:

$$D_{t,x}(v) = f(\|\mathbf{d}_{t,x}\|,\ (\mathbf{d}_{t,x}, v))\, g(\|v\|) \tag{1}$$

where $(\mathbf{d}_{t,x}, v)$ is the angle between a preferred direction of reference $\mathbf{d}_{t,x}$ and the direction of the new shoot v, $f(a,\theta)$ is a p.d.f. on $[-\pi,\pi)$ for all $a \geq 0$; and $g(\|v\|)$ is the p.d.f. on the length $\|v\|$ of the connection.

For the preferred direction of reference $\mathbf{d}_{t,x}$, we need to account for the fact that the ramet can "perceive" the resource map from the connections with other ramets, for example because of resource translocations. A possible choice is $\mathbf{d}_{t,x} = \frac{1}{|J(t,x)|} \sum_{i\in J(t,x)} \frac{\mathbf{r}(t,x_t^i)-\mathbf{r}(t,x)}{|x_t^i - x|^2}\,[x_t^i - x]$, i.e. an approximation of the resource gradient based on the values of $\mathbf{r}(t,x)$ at x and at the connected nodes.

Interactions between nodes and resources. The natural way to model resource concentration is as a density function $\mathbf{r}(t,x)$ over the domain $\mathcal{D}$. Coupling (discrete) individual dynamics with resource density dynamics is a non-standard problem which requires a choice. We propose the following model:

$$\partial_t\,\mathbf{r} = \mathrm{div}\big(\mathbf{a}\,\nabla\mathbf{r}\big) + \mathbf{b}\cdot\nabla\mathbf{r} - \mathbf{r}\,\alpha\,\textstyle\sum_{i=1}^{N_t}\Gamma_{x_t^i} \tag{2}$$

with $\mathbf{r}(0,x)=\mathbf{r}_0(x)$ and $\Gamma_y(x)=\exp\big(-\frac{1}{2\,\sigma_{\mathbf{r}}^2}\,|x-y|^2\big)$.

2 Numerical approximation of the IBM

Starting from the state $\nu_{T_{k-1}} = \sum_{i=1\cdots N_{T_{k-1}}}\delta_{x^i_{T_{k-1}}}$ at last event time T_{k-1}, we first sample the time of the next event (birth or death): $T_k = T_{k-1}+S$ with $S\sim\mathrm{Exp}(\bar\lambda_{T_{k-1}}+\bar\mu_{T_{k-1}})$. The next event:

- is a birth with probability $\frac{\bar\lambda_{T_{k-1}}}{\bar\lambda_{T_{k-1}}+\bar\mu_{T_{k-1}}}$. Then sample $\hat\imath$ according to $\{\lambda(T_{k-1},x^i_{T_{k-1}})/\bar\lambda_{T_{k-1}}\,;\, i=1\cdots N_{T_{k-1}}\}$ and v according to the p.d.f. $D_{T_{k-1},x^{\hat\imath}_{T_{k-1}}}(v)$, finally let: $\nu_{T_k}=\nu_{T_{k-1}}+\delta_{(x^{\hat\imath}_{T_{k-1}}+v)}$;
- is a death with probability $\frac{\bar\mu_{T_{k-1}}}{\bar\lambda_{T_{k-1}}+\bar\mu_{T_{k-1}}}$. Then sample $\hat\imath$ according to $\{\mu(T_{k-1},x^i_{T_{k-1}})/\bar\mu_{T_{k-1}}\,;\, i=1\cdots N_{T_{k-1}}\}$, let: $\nu_{T_k}=\nu_{T_{k-1}}-\delta_{x^{\hat\imath}_{T_{k-1}}}$;

then update the sets of connections $J(T_k,x)$ accordingly. In parallel, we should numerically integrate the PDE (2).

The proposed model can account for conventional phalanx or guerrilla dynamics. More specifically, in (1): if the p.d.f. $f(a,\theta)$ of the shoot angle has a small (resp. large) variance and if the p.d.f. $g(\|v\|)$ favors large (resp. small) lengths, then the model will present the characteristics of a guerrilla (resp. phalanx) plant (see Figure 2).

3 Large population approximation of the IBM

The more relevant scaling within the context of phalanx-type clonal plants is the space-scaling and acceleration of births and deaths which leads to a reaction-diffusion PDE for population densities (see [2] for other possible scalings). In this case, the PDE approximation of the IBM takes the following form: denoting by $u(t,x)$ the population density at time t and position x in $\mathcal{D}$,

$$\begin{aligned}
\partial_t u &= \beta\,\Delta(\gamma\,u) + (\lambda-\mu)\,u - \mathrm{div}(\gamma\,F(x,\nabla\mathbf{r})\,u)\,,\\
\partial_t\mathbf{r} &= \nabla(\mathbf{a}\,\mathbf{r}) + \mathbf{b}\cdot\nabla\mathbf{r} - \delta\,\mathbf{r}\,u\,,\\
u(t,x) &= \mathbf{r}(t,x) = 0, \qquad\qquad \forall x\in\partial\mathcal{D}.
\end{aligned}$$

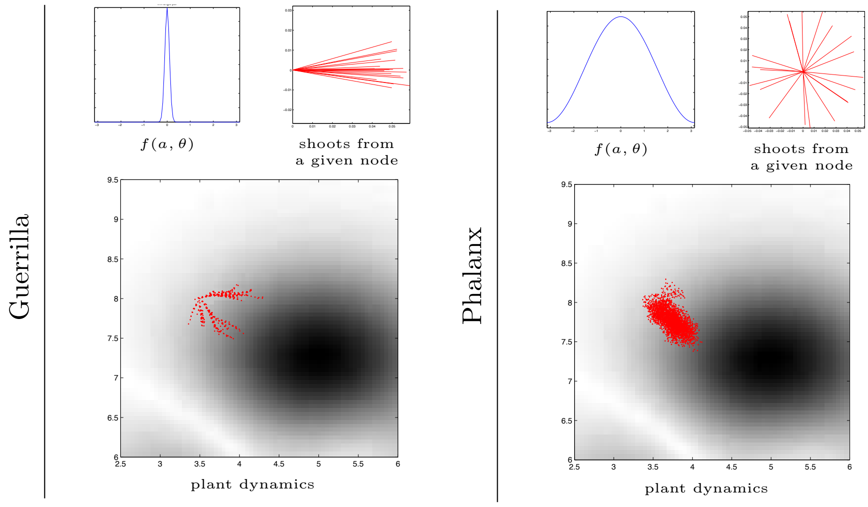

Figure 2: *If the shoot angle p.d.f. $f(a,\theta)$ has a large variance (resp. small variance) and if the p.d.f. $g(\|v\|)$ favors small lengths (resp. large lengths), then the model will present the characteristics of a phalanx growth strategy (resp. guerrilla growth strategy).*

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