Individual-based models of prairial ecosystems

ANR project MODECOL[*]

Working Paper

Fabien Campillo[†]
INRIA Méditerranée in Montpellier

Nicolas Champagnat[‡]
INRIA Méditerranée in Sophia Antipolis

Pierre Del Moral[§]
INRIA Bordeaux Sud-Ouest

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Abstract

Our goal is first to propose models of dynamics of a simplified grassland ecosystem, then to develop simulation techniques for these models and finally to establish their mathematical properties. The ecosystem is a community of individuals (ramets) linked by connections (rhizomes). This ecosystem relies on resources (nitrates) and can store a portion of these resources. We propose different individual-based models coupled with continuous models for the available resources and the stored resources, in this case the individual is the ramet; or the available resources only, in this case the individual is the ramet or the rhizome.

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[*] `http://ecobio.univ-rennes1.fr/modecol/fr/`

[†] `Fabien.Campillo@inria.fr`, INRIA/INRA UMR ASB - bât. 29, 2 place Pierre Viala 34060 Montpellier Cedex 01, France

[‡] `Nicolas.Champagnat@sophia.inria.fr`, 2004 route des Lucioles - BP 93, 06902 Sophia Antipolis Cedex, France

[§] `Pierre.Del_Moral@inria.fr`, Institut de Mathématiques de Bordeaux, Université Bordeaux I, 351, cours de la Libération, 33405 Talence cedex, France

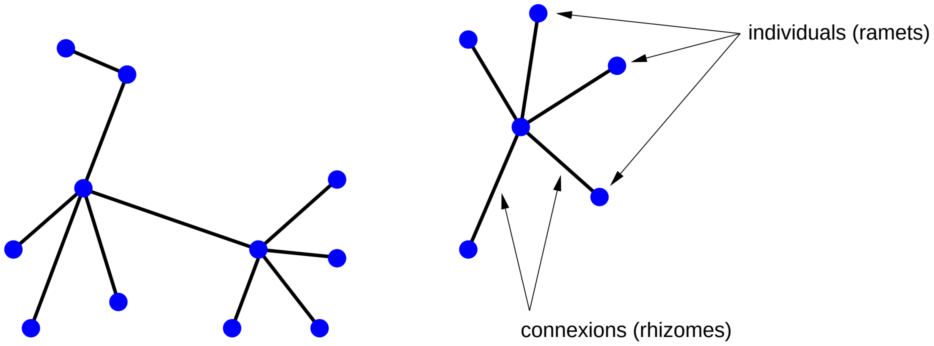

Figure 1: *We consider a population of individuals (ramets) connected by rhizomes. The term "individual" is not to be taken in the biological sense but in the sense of individual-basede modeling, here it represents a ramet.*

1 Introduction

Our goal is to describe, construct and analyze ecological individual-based models of population dynamics of prairial ecosystems, in the fashion of models already proposed in [**?**, **?**, **?**, **?**, **?**, **?**, **?**, **?**, **?**, **?**].

The specificities of prairial plants are the following:

- individuals are linked by rhizomes, thus forming a network;
- individuals may use information of other individuals of the network they belong to in order to choose their reproduction rate and the position of the new individuals they are going to produce;
- when the environmental conditions are good, resources may be stored and shared in rhizomes by the individuals in the network, for use when the environmental conditions are bad.

2 Three levels of modeling

We are going to describe three levels of modeling, more and more precise. The first one is deterministic and describes the dynamics of densities. The second one is stochastic and individually based, it describes the dynamics of each individuals. The last one is stochastic, it describes the dynamics of each individual and each connection between individuals. We try to give the motivation of our choices of parameters and give some simple examples.

In all the models, we are going to assume that individuals are located in a bounded domain $\mathcal{X}$ of $\mathbb{R}^d$ (typically, $d = 2$ for prairial dynamics).

2.1 First level: deterministic model

2.1.1 The model

The dynamics is describe by three nonnegative functions of time and space on $\mathbb{R}_+ \times \mathcal{X}$:

- the density of available resources $I(t, x)$;
- the density of individuals $n(t, x)$;
- the density of stored resources in rhizomes $R(t, x)$.

All these quantities are expressed in term of resources unit.

We consider the system of PDEs:

$$\partial_t n(t,x) = -n(t,x)\,\mu(t,x) + \int_{\mathcal{X}} n(t,y)\,\big[I(t,y)\,\lambda_I(t,y) + R(t,y)\,\lambda_R(t,y)\big] \times S(\nabla R(t,y), x-y)\,dy \tag{1a}$$

$$\partial_t I(t,x) = \sigma(x)\,\Delta I(t,x) + b(x)\cdot\nabla I(t,x) + n(t,x)\,\mu(t,x) - I(t,x)\,n(t,x)\,(\lambda_I(t,x) + \lambda_S(t,x)) \tag{1b}$$

$$\partial_t R(t,x) = -n(t,x)\,R(t,x)\,\lambda_R(t,x) + I(t,x)\,n(t,x)\,\lambda_S(t,x)\,. \tag{1c}$$

The boundary conditions are as follows: for all $x \in \mathcal{X}$, $I(0,x) = I_0(x)$, $n(0,x) = n_0(x)$, $R(0,x) = R_0(x)$ and for all $x \in \partial\mathcal{X}$, $\nabla I(t,x)\cdot n(x) = D(t,x)$, where $n(x)$ is the exterior normal to $\partial\mathcal{X}$ at x.

This system describe the dynamics of (I, n, R). The interpretation of the parameters are the following:

- $\sigma(x)$ is the diffusion coefficient of resources at $x \in \mathcal{X}$;
- $b(x)$ is the drift on the resources density representing the effects of the fields slope or of run-off (rain streaming);
- λ_I is the rate of birth of new individuals from non-stored ressources; a typical dependence on (t, x) of λ_I can be

$$\lambda_I(t,x) = \lambda_I(M_r I(t,x), M_{r'} R(t,x)). \tag{2}$$

- λ_R is the rate of birth of new individuals from stored ressources; typically,
$$\lambda_R(t,x) = \lambda_R(M_r I(t,x), M_{r'} R(t,x)). \tag{3}$$

- λ_S is the rate of storage of exterior resources in the network; typically,
$$\lambda_S(t,x) = \lambda_S(M_r I(t,x), M_{r'} R(t,x), M_{r''} n(t,x)). \tag{4}$$

- μ is the rate of death in the population; we assume that the biomass of dead individuals is instantaneously converted into exterior resources. Typically,
$$\mu(t,x) = \mu(M_r I(t,x), M_{r'} R(t,x), M_{r''} n(t,x)). \tag{5}$$

- $S(u,v)\,dv$ is the dispersal probability distribution: a birth from an individual at x occurs at position $y = x + V$, where V has the law $S(\nabla R(t,x), v)\,dv$;

- Let
$$M_r R(t,x) = \frac{1}{|B(x,r)|} \int_{B(x,r)} R(t,z)\,dz$$
where $B(x,r)$ is the ball centered at $x \in \mathcal{X}$ with radius $r > 0$; by convention, if $r = 0$, $M_r R(t,x) = R(t,x)$. Note that we assumed here a uniform dependence of the interactions in the ball. All the models described here can easily be extended to situations where the interactions decrease with distance, for example, by defining $M_r R(t,x) = \int_{B(x,r)} \alpha(z-x)\,R(t,z)\,dz$ for some nonnegative interaction kernel α of L^1 norm 1. Below, we restrict to the uniform interaction case for simplicity.

- $D(t,x)$ requires the outward (signed) flow of resources exiting (or entering) from the domain;

- $r, r', r'' \geq 0$ are fixed parameters.

The interpretation of this model is the following: individuals in the population can use environmental resources either for reproduction (with rate λ_I) or for storage in the network (with rate λ_S). Stored resources can also be used for reproduction when the environmental conditions are bad, with rate λ_R. Individuals may also dye with rate μ. Since every quantity is expressed in resources concentration units, we have the conservation law
$$\frac{d}{dt} \int_{\mathcal{X}} \big[I(t,x) + n(t,x) + R(t,x) \big]\,dx = \int_{\partial\mathcal{X}} D(t,x)\,dx. \tag{6}$$

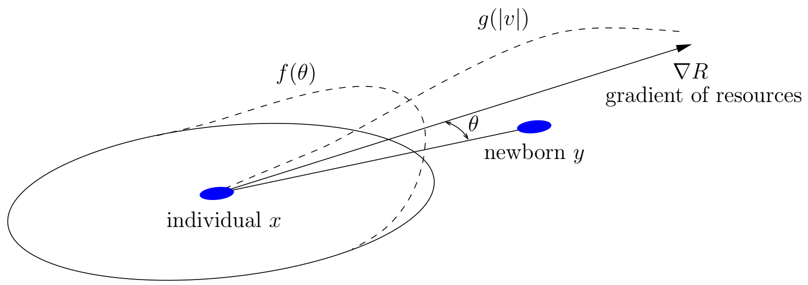

Figure 2: *Dispersal probability distribution: a birth from an individual at x occurs at position $y = x + V$, where V has the law $S(\nabla R(t,x), v)\,dv$ with S given by (7), f by (8), and g a lognormal pdf.*

The network structure of the model is contained in the quantity $R(t,x)$, which describes the density of stored resources. We also assume that the environmental information used by an individual at x for reproduction is summarized by the gradient $\nabla R(t,x)$ appearing in the jump distribution S. We assume that no other information about the network is needed to describe the population dynamics. We finally assume that birth and death rates may depend on the local resources available and on the quantity of resources available in the network in a neighborhood of the focal individual. Death rates may also depend on the local density of population. Note also that the increase or decrease of the resources densities I and R depends *locally* of the density of individuals $n(t,x)$.

2.1.2 An example

The typical parameters we have in mind are of the form:

- The dispersal probability distribution is of the form:

  $$S(u,v) = f((u,v))\, g(|v|)\,, \qquad (7)$$

  where (u,v) denotes the angle between u and v in $\mathbb{R}^3$, where f is a function representing the distribution of the angle between the "optimal" dispersal direction (the gradient of R) and the direction where the individual chooses to send the rhizome, and g represents the distribution of the distance of dispersal. For example

  $$f(\theta) = \frac{C}{1+\theta^2}\,, \quad \forall \theta \in [-\pi, \pi] \qquad (8)$$

and g is the density of a log-normal distribution of given parameters (cf. Figure 2).

- We may assume that the death rate has the form $\mu(a,b,c) = \mu_0 + \alpha\, c$, where μ_0 represents the death rate in the absence of competition, and α represents the local competition strength between individuals.
- For λ_I, λ_R and λ_S, we may assume the following form, which models the fact that birth and storage rates are bounded when I and R go to infinity:

  $$\begin{aligned} \lambda_I(t,x) &= \frac{c_1}{1 + c_2\, I(t,x)}\,, \\ \lambda_R(t,x) &= \frac{c_3}{1 + c_4\, R(t,x)}\,, \\ \lambda_S(t,x) &= \frac{c_5}{1 + c_6\, I(t,x)}\,. \end{aligned}$$

  With such functions, the individual birth rate from non-stored resources is c_1 when there are few resources available and c_1/c_2 when there are many resources (typically, c_1 is much smaller than c_1/c_2).

2.1.3 Mathematical comments

The local dependence of S on ∇R may cause well-posedness problems for the PDE we consider. Instead, the term $S(\nabla R(t,x), x-y)$ in (1) may be replaced by

$$S(M_\rho \nabla R(t,x), x-y)$$

or

$$S\left(\frac{5}{\rho^2}\int_{B(x,\rho)} (R(t,z) - R(t,x))\,(z-x)\,dz\ ,\ x-y\right), \tag{9}$$

where ρ is a positive constant parameter. The last possibility corresponds to a local estimation of the gradient of R. The constant $5/\rho^2$ comes from the fact that

$$\int_{B(x,\rho)} (R(t,z) - R(t,x))(z-x)\,dz \approx \int_{B(x,\rho)} (\nabla R(t,x)\cdot(z-x))\,(z-x)\,dz$$

and

$$\int_{B(0,\rho)} (a\cdot x)\,x\,dx = \frac{\rho^2}{5}\,a, \quad \forall a \in \mathbb{R}^2.$$

This model poses the following mathematical (analytical) questions:

- Existence and uniqueness for (1);
- Non explosion of the solution when time goes to infinity.

2.2 Second level: individual-based approximation of the first level

When the population size is small, the deterministic model (1) can differ drastically from individual stochastic dynamics. In this case, an individual-based version of the model must be constructed. Our first individual-based model is directly derived from the deterministic model (1), and thus is not based on an explicit network structure of the population. In Section 2.3, we propose another model with explicit network structure.

2.2.1 The model

The population density $n(t,x)$ will be replaced by an empirical measure of a finite population, whose dynamics mimics the one of (1a). We choose to keep the resources dynamics continuous and deterministic. This amounts to implicitly assume that the ecological time scale and resources dynamics time scale are separated.

In the previous model, the dependence of the resources dynamics on the density $n(t,x)$ is local. This poses a problem for the construction of the individual-based model. As done in [**?**], a way to solve this problem is to introduce a small parameter $\delta > 0$, which represents the range of resources absorption of a single individual. This amounts to replace the terms $n(t,x)$ in (1b) and (1c) by $M_\delta n(t,x)$ and to do the corresponding modifications in (1a). As suggested by the results of [**?**] (proved for a different model), choosing δ small and the number of individuals big should give a good approximation of the original deterministic dynamics. Note that this technical problem is inherent to the fact that we want to couple a deterministic density dynamics with a stochastic discrete one.

At each time t, the population is composed of a finite (stochastic) number N_t of individuals at spatial position $x_1, \dots, x_{N_t}$. It is convenient to represent the population state by the counting measure

$$\nu_t = \sum_{i=1}^{N_t} \delta_{x_i}.$$

The dynamics of the population is the following: each individual at position $x \in \mathcal{X}$ at time t

- dies at (infinitesimal) rate $M_\delta \mu(t,x)$;
- gives birth to a new individual from non-stored resources with rate $M_\delta(I\lambda_I)(t,x)$;
- gives birth to a new individual from stored resources with rate $M_\delta(R\lambda_R)(t,x)$;
- at a birth event from this individual, the position of the newborn is chosen as $x+z$, where z has law $S(\nabla R(t,x),z)\,dz$.

It is biologically reasonable that individuals absorb resources continuously during their lives, but for mathematical reasons, it is simpler to assume that death events induce instantaneous jumps in the local resources densities. This leads to the following dynamics for I and R, coupled with the discrete stochastic birth and death events: between death events,

$$\begin{aligned}\partial_t I(t,x) &= \sigma(x)\,\Delta I(t,x) + b(x)\cdot\nabla I(t,x)\\ &\qquad - I(t,x)\Big(\lambda_I(t,x)+\lambda_S(t,x)\Big)\,\frac{\nu_t(B(x,\delta)}{|B(x,\delta)|} \qquad \text{(10a)}\\ \partial_t R(t,x) &= \Big(I(t,x)\,\lambda_S(t,x) - R(t,x)\,\lambda_R(t,x)\Big)\,\frac{\nu_t(B(x,\delta)}{|B(x,\delta)|}\,. \qquad \text{(10b)}\end{aligned}$$

and at a death time t of an individual at position x,

$$I(t,y) = I(t^-,y) + \chi(y-x) \quad \text{and} \quad R(t,x) = R(t^-,x),$$

where $\chi \geq 0$ represents the spatial dispersion of ressources in the environment after the death of an individual. Note that one should have $\int \chi(x)\,dx = 1$ to be consistent with the definition of ν_t and the assumption of biomass conservation.

The biological justification of the parameters is the same as for the previous model. Note that the size of the population is controlled by the competitive pressure. More precisely, if

$$\mu(t,x) = \mu_0 + \alpha\,\frac{\nu_t(B(x,r''))}{|B(x,r'')|}$$

as in the example of Section 2.1.2, then $1/\alpha$ controls the size of the population (see Section 2.2.3 for more details).

2.2.2 Simulation of the IBM

The algorithmic simulation of individual-based process has several advantages:

- the discrete individual-based part of the model can be simulated exactly (of course, some error will come from the discretization of the PDEs (10)).
- it is easy to implement;
- it is quite efficient in the case of logistic competition (see the extensions below).

It is based on an acceptance-rejection procedure, where potential jump times are constructed using an upper bound of the total jump rate in the population.

The algorithmic description of the model mimics its mathematical construction as a stochastic differential equation driven by Poisson point processes.

Our construction is based on the following assumptions:

(A1) λ_I, λ_R, λ_S and μ are given by (2)–(5), where λ_I, λ_R and λ_S are upper bounded continuous functions, respectively by constants $\bar{\lambda}_I$, $\bar{\lambda}_R$, $\bar{\lambda}_S$, and $\mu(a,b,c) \leq \bar{\mu}_0 + \bar{\mu}_1 \, |B(0,r'')| \, c$ for some constants $\bar{\mu}_0$ and $\bar{\mu}_1$, i.e. $\mu(t,x) \leq \bar{\mu}_0 + \bar{\mu}_1 \, N_t$.

(A2) σ and b are uniformly Hölder-continuous in $\mathcal{X}$.

(A3) For a complete construction of the process, assumptions on the form of the jump measure $S(\cdot,\cdot)$ are needed, that we do not precise for the moment[1].

(A4) There exist positive constants C_1 and C_2 such that $\lambda_S(a,b,c) \leq C_1/(C_2 + c)$. We also assume that $r'' > \delta$.

A key property for the construction of the process is the computation of a priori bounds for I and R. An upper bound for I can be obtained by observing that the nonlinear terms in (10a) are negative and by applying the maximum principle[2]. Then, the time derivative of the maximum of $I(t,\cdot)$ should be controlled by $D(t,x)$.

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[1] To complete.

[2] This point requires a full justification, with analytical tools that don't know well. To be checked.

Using Assumption (A4) and the fact that $\nu_t(B(x,\delta)) \leq \nu_t(B(x,r''))$

$$\partial_t R(t,x) \leq \frac{C_1}{C_2 + \frac{\nu(B(x,\delta))}{|B(0,r'')|}} \frac{\nu(B(x,\delta))}{|B(0,\delta)|}$$

which is upper bounded by a constant $K > 0$. Therefore

$$\sup_{x\in\mathcal{X}} R(t,x) \leq \sup_{x\in\mathcal{X}} R_0(x) + K\,t$$

for all $t \geq 0$.

Let us describe the simulation algorithm on a finite time interval $[0,T]$. We introduce $\bar{I}$ (resp. $\bar{R}$) the upper bound for $\sup_{t\in[0,T],\ x\in\mathcal{X}} I(t,x)$ (resp. $\sup_{t\in[0,T],\ x\in\mathcal{X}} R(t,x)$) computed above.

Given an initial condition $(I_0(x), R_0(x), N_0, \mathbf{X}_0)$, where $\mathbf{X}_0 = (X_1, \ldots, X_{N_0})$ is the vector of initial positions,

1. Set $k = 0$ and $T_0 = 0$;

2. Assume $(I_k(x), R_k(x), N_k, \mathbf{X}_k, T_k)$ given, where $\mathbf{X}_k = (X_1^{(k)}, \ldots, X_{N_k}^{(k)}) \in \mathcal{X}^{N_k}$. It can be easily checked that

   $$C_k := N_k(\bar{\mu}_0 + \bar{\mu}_1 N_k + \bar{I}\,\bar{\lambda}_I + \bar{R}\,\bar{\lambda}_R)$$

   is an upper bound for the total jump rate in the population. Let $T_{k+1} = T_k + E_k$, where E_k is an exponential random variable of parameter C_k independent of all the previous random variables introduced in the algorithm.

3. Set $\nu_t = \sum_{i=1}^{N_k} \delta_{X_i^{(k)}}$ for all $t \in [T_k, T_{k+1}]$.

4. Solve with your favorite discretization technique the PDEs (10a) and (10b) on the time interval $[T_k, T_{k+1}]$ with initial conditions $I_k(x)$ and $R_k(x)$, respectively. Set $I_{k+1}(x) = I(T_{k+1}, x)$ and $R_{k+1}(x) = R(T_{k+1}, x)$.

5. Let θ_k be a random variable with uniform law on $[0, C_k/N_k]$ independent of all the previous random variable introduced in the algorithm. Choose an individual i among the N_k living individuals uniformly at random.

   (a) If $\theta_k \leq M_\delta \mu(T_{k+1}, X_i^{(k)}) =: \theta_1^{(k)}$, then the individual i dies at time T_{k+1}, i.e. $N_{k+1} = N_k - 1$, and $\mathbf{X}_{k+1}$ is the N_{k+1}-tuple equal to $\mathbf{X}_k$ without the i-th component.

(b) If $\theta_1^{(k)} < \theta \leq \theta_1^{(k)} + M_\delta(I\lambda_I)(T_{k+1}, X_i^{(k)}) =: \theta_2^{(k)}$, then the individual i gives birth to a new individual at time T_{k+1}, with position $X_{N_k+1}^{(k+1)} = X_i^{(k)} + Z$, where Z is a random variable of law $S(\nabla R(T_{k+1}, X_i^{(k)}), z)\,dz$, i.e. $N_{k+1} = N_k + 1$, and $\mathbf{X}_{k+1} = (\mathbf{X}_k, X_{N_k+1}^{(k+1)})$.

(c) If $\theta_2^{(k)} < \theta \leq \theta_2^{(k)} + M_\delta(R\lambda_R)(T_{k+1}, X_i^{(k)})$, then the individual i gives birth to a new individual at time T_{k+1}, with position $X_{N_k+1}^{(k+1)} = X_i^{(k)} + Z$, where Z is a random variable of law $S(\nabla R(T_{k+1}, X_i^{(k)}), z)\,dz$, i.e. $N_{k+1} = N_k + 1$, and $\mathbf{X}_{k+1} = (\mathbf{X}_k, X_{N_k+1}^{(k+1)})$.

(d) Otherwise, nothing happens, $N_{k+1} = N_k$ and $\mathbf{X}_{k+1} = \mathbf{X}_k$.

6. Set $k = k + 1$ and if $T_{k+1} < T$, go back to Step 2, otherwise, end.

This algorithm is the most general one. Several improvements are possible in practice.

- The upper bounds for I and R may be very bad, implying many inefficient rejections in the algorithm. This may be improved as follows: at the k-th step of the algorithm, set $\bar{I}_k$ (resp. $\bar{R}_k$) as the maximal value of $I(T_k, \cdot)$ (resp. $R(T_k, \cdot)$). Then replace $\bar{I}$ and $\bar{R}$ in step k of the algorithm by $\alpha\,\bar{I}_k$ and $\alpha\,\bar{R}_k$, respectively, for some fixed $\alpha > 1$ .Then, due to the Markov property for the IBM process, Step 4 may be replaced by the following:

    4. Solve with your favorite discretization technique the PDEs (10a) and (10b) on the time interval $[T_k, T_{k+1}]$ with initial conditions $I_k(x)$ and $R_k(x)$, respectively. If $\sup_{t\in[T_k,T_{k+1}]} \sup_{x\in\mathcal{X}} I(t, x) \leq \alpha\,\bar{I}_k$ and $\sup_{t\in[T_k,T_{k+1}]} \sup_{x\in\mathcal{X}} R(t, x) \leq \alpha\,\bar{R}_k$, go to Step 5. Otherwise, set T_{K+1} as the first time $s \geq T_k$ where there exists x such that $I(s, x) \geq \alpha\,\bar{I}_k$ or $R(s, x) \geq \alpha\,\bar{R}_k$, set $N_{k+1} = N_k$, $\mathbf{X}_{k+1} = \mathbf{X}_k$, $I_{k+1}(x) = I(T_{k+1}, x)$ and $R_{k+1}(x) = R(T_{k+1}, x)$, and go back to Step 2.

- In the logistic competition case, where

$$\mu(a, b, c) = \mu_0(a, b) + \mu_1(a, b)\,|B(0, r'')|\,c \tag{11}$$

  for functions μ_0 and μ_1 bounded by $\bar{\mu}_0$ and $\bar{\mu}_1$, respectively, the algorithm may be improved by replacing Step 5. (a) by the two following steps

5. (a) If $\theta \leq N_k \bar{\mu}_1 =: \theta_0^{(k)}$, let $j \in \{1, \dots, N_k\}$ be such that $(j-1)\bar{\mu}_1 < \theta_k \leq j\bar{\mu}_1$. Then, if

$$\theta_k - (j-1)\bar{\mu}_1 \leq \frac{1}{|B(0,\delta)|} \int_{B(X_i^{(k)},\delta)} \mu_1(T_{k+1}, y) \mathbf{1}_{\{|X_j^{(k)} - y| \leq r''\}} dy,$$

the individual i dies from competition with individual j at time T_{k+1}, i.e. $N_{k+1} = N_k - 1$, and $\mathbf{X}_{k+1}$ is the N_{k+1}-tuple equal to $\mathbf{X}_k$ without the i-th component.

5. (a') If $\theta_0^{(k)} < \theta_k \leq \theta_0^{(k)} + M_\delta \mu_0(T_{k+1}, X_i^{(k)}) =: \theta_1^{(k)}$, then the individual i dies from oldness at time T_{k+1}, i.e. $N_{k+1} = N_k - 1$, and $\mathbf{X}_{k+1}$ is the N_{k+1}-tuple equal to $\mathbf{X}_k$ without the i-th component.

This modification avoids to compute at each step of the algorithm the quantity $M_{r''}\nu_{T_{k+1}}(T_{k+1}, x)$, which is a sum over all the population, in order to compute $\mu(t,x)$ in Step 5. (a) of the general algorithm.

2.2.3 Mathematical questions

Several mathematical questions must be solved for such models.

- First, the general theory for individual-based models is well-developed in simpler situations, where the dynamics is not coupled with PDEs. The construction of the stochastic process, its uniqueness in law and the justification of the previous algorithm must be justified in this specific model. In particular, this requires good stability and regularizing properties for the PDEs (10), which are not immediate because of the nonlinearity. In particular, the maximum principle mentioned above must be carefully checked in this case. Moreover, the dependence of the individuals rates on ∇R will also cause problems. It would be certainly mathematically simpler to assume that the function S is of the form (9).

- Another important question is the consistency property with deterministic approximations: one should recover the PDE (1) with a correct large population and local interaction scaling of the parameters. Here again, the general tools for such questions are well-developed, but have never been used for individual-based models coupled with PDEs. The way to do such a scaling is the following: assume that the interaction in the death rate is of logistic type, as in (11), introduce a scaling parameter K for the size of the population (K is often referred to as the "system size" and is closely related to the notion of carrying capacity), and let the parameter α depend on K as $\alpha_K = \alpha/K$. Then, defining

$$\nu_t^K = \frac{1}{K}\nu_t = \frac{1}{K}\sum_{i=1}^{N_t} \delta_{x_i}$$

and assuming that ν_0^K converges in distribution for the weak topology to a deterministic measure on $\mathcal{X}$ admitting a density $\xi(x)\,dx$, then one expects the stochastic process ν^K to converge to the deterministic measure whose solution solves the non-local version of (1) with localization parameter $\delta > 0$. Next, it remains to prove the convergence of this solution to the solution of (1) when $\delta \to 0$ (see [**?**]).

2.3 Third level: explicit graph structure

We are now going to follow a different approach than previously, by constructing an network-explicit individual-based model of a prairial asexual population, and then try to describe the corresponding deterministic approximation in the limit of large population. This approach is interesting because it produces non-standard deterministic models that really describe the relevant microscopic structure.

For simplicity of the model and of the mathematical study, we are only going to model a single aspect of the network structure of prairial asexual ecosystems, namely the capacity to choose ones reproduction strategy using environmental information taken from the network. Our model will also include the possibility of rupture of rhizomes between individuals through time. It would be easy to model also the capacity of rhizomes to store environmental resources for use by individuals in the network.

2.3.1 The model

The system state will be describe by the following three dynamical parameters:

- A function $I(t, x)$ which will describe as above the resources available.
- A finite set of living individuals at time t, of (random) size N_t, and with (random) positions $x_1(t), \ldots, x_{N_t}(t)$. As above, it will be convenient to describe the *population state* by the counting measure

$$\nu_t = \sum_{i=1}^{N_t} \delta_{x_i(t)}.$$

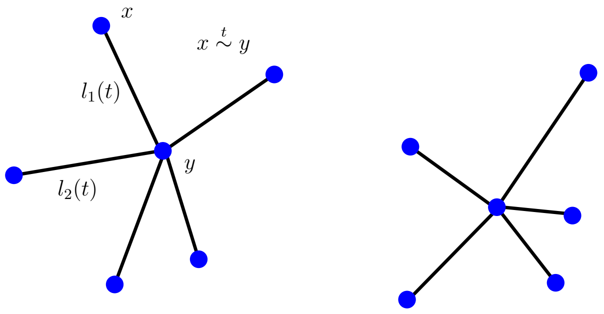

Figure 3: *At time* t *the population of ramets is defined by* $\nu_t = \sum_{i=1}^{N_t} \delta_{x_i(t)}$ *—* $x_i(t)$ *is the location of the* i*th ramet; the population of rhizome is defined by* $\eta_t = \sum_{j=1}^{R_t} \delta_{l_j(t)}$ *—* $l_j(t)$ *is the* j*th rhizome, i.e. an element of the set of unordered pairs with distinct elements in* $\{x_1(t), \ldots, x_{N_t}(t)\}$*. We note* $x \sim_t y$ *whenever there exists* j *such that* $l_j(t) = \{x, y\}$*.*

- A finite set of rhizomes linking pairs of individuals at time t, of (random) size R_t, and with (random) links $l_1(t), \ldots, l_{R_t}(t)$ in the set of unordered pair with distinct elements in $\{x_1, \ldots, x_{N_t}\}$. It will be convenient to describe the *network state* by the counting measure

$$\eta_t = \sum_{i=1}^{R_t} \delta_{l_i(t)}.$$

We will use the following notation:

- We write that $x \sim_t y$ if there exists $j \in \{1, \ldots, R_t\}$ such that $l_j(t) = \{x, y\}$.
- We write $x \in l$, where l is an unordered pair with distinct elements in $\mathcal{X}$, if x is one of the elements of l.
- For all $x \in \mathcal{X}$ and $t \geq 0$, we define

$$J(t, x) = \{i \in \{1, \ldots, N_t\} : x_i(t) \sim_t x\}.$$

The dynamics of the population and network states are as follows:

($e1$) An individual at position x at time t can give birth to a new individual at (infinitesimal) rate $M_\delta(I\lambda)(t, x)$, where $\lambda(t, x) = \lambda\left(M_r I(t, x), \frac{\nu_t(B(x,r'))}{|B(0,r'')|}\right)$.

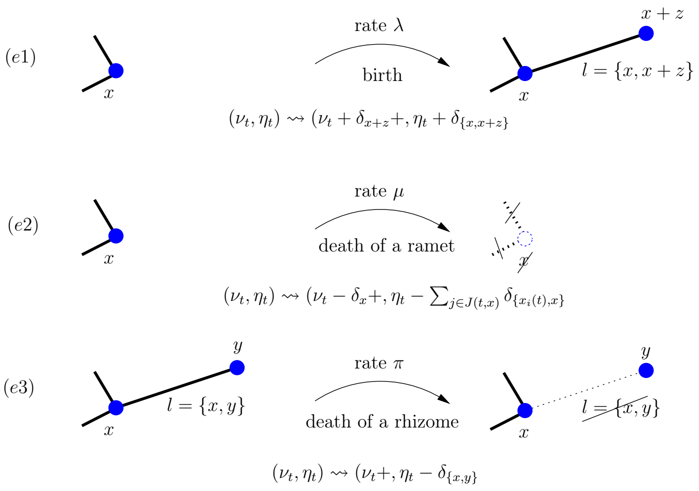

Figure 4: *The IBM gathers three type of discrete events: (e1) birth of a new ramet and of the corresponding rhizome; (e2) death of a ramet and of all the connected rhizome; (e3) death of a rhizome.*

The new individual appear at the position $x+z$ and the link $\{x,x+z\}$ is added to the network, where z has law

$$S\left(\frac{2}{|J(t,x)|}\sum_{i\in J(t,x)}(I(t,x_i(t))-I(t,x))\frac{x_i(t)-x}{|x_i(t)-x|^2}\;;\;x-y\right),$$

where S has already been defined in the other algorithms. The choice of the first variable in S is guided by the fact that it is an asymptotic estimator of $\nabla I(t,x)$ when the number of neighbors goes to infinity and with positions independent of each other. This event corresponds to the transition

$$(\nu_t,\eta_t) \quad \rightsquigarrow \quad \left(\nu_t+\delta_{x+z},\eta_t+\delta_{\{x,x+z\}}\right).$$

$(e2)$ An individual at position x at time t can die at rate $M_\delta\mu(t,x)$, where $\mu(t,x)=\mu\left(M_rI(t,x),\frac{\nu_t(B(x,r'))}{|B(0,r'')|}\right)$. In this case, all the rhizomes linked to this individual also disappear from the network. This event corresponds to the transition

$$(\nu_t,\eta_t) \quad \rightsquigarrow \quad \left(\nu_t-\delta_x,\eta_t-\sum_{i\in J(t,x)}\delta_{\{x_i(t),x\}}\right).$$

($e3$) A rhizome $\{x, y\}$ at time t may die at rate

$$\pi(t, x, y) = \pi(M_r I(t, x), M_r I(t, y), M_{r'} n(t, x), M_{r'} n(t, y)).$$

This event corresponds to the transition

$$(\nu_t, \eta_t) \quad \rightsquigarrow \quad \left(\nu_t, \eta_t - \delta_{\{x,y\}}\right).$$

Between to of these events, we assume that the resources satisfy a similar dynamics as in the previous model:

$$\partial_t I(t, x) = \sigma(x)\Delta I(t, x) + b(x) \cdot \nabla I(t, x) - I(t, x)\lambda(t, x)\frac{\nu_t(B(x, \delta)}{|B(x, \delta)|}, \qquad (12)$$

and at a death time t of an individual at position x,

$$I(t, y) = I(t^-, y) + \chi(y - x),$$

where χ has been defined in Section 2.2.1.

2.3.2 Simulation of the IBM

The algorithmic simulation of this model is very similar to the one already described in Section 2.2.2. Let us omit its description.

2.3.3 Mathematical questions

Here again, questions of construction, existence, uniqueness and justification of the discretization procedure may be asked. If we can prove this for Model 2, it should clearly also hold for this model.

More interestingly, the question of large population behavior of the model is interesting both from the mathematical and the modeling points of views. In particular, assuming a logistic death rate and doing the same scaling in K as in Section 2.2.3, introducing

$$\nu_t^K = \frac{1}{K}\sum_{i=1}^{N_t} \delta_{x_i(t)} \quad \text{and} \quad \eta_t^K = \frac{1}{K}\sum_{i=1}^{R_t} \delta_{l_i(t)},$$

what is the corresponding limit? We have the following

Conjecture 2.1 *Under sufficient regularity conditions of the coefficients and assuming that the initial distributions of* (ν_0^K, η_0^K) *converge suitably to the deterministic measures* $(\xi(x)\,dx, \zeta(x, y)\,d\lambda(x, y))$ *admitting densities* *w.r.t. Lebesgue's measures on* $\mathcal{X}$ *and* $\mathcal{X}^2/\mathrm{flip}$*, where* $\mathrm{flip}(x,y) = (y,x)$ *on* $\mathcal{X}^2$*, respectively. Then,* $(I^K(t,\cdot), \nu_t^K, \eta_t^K)$ *converges for the Skorohod topology in* $\mathbb{D}(\mathbb{R}_+, \mathcal{C}(\mathcal{X}) \times \mathcal{M}_+(\mathcal{X}) \times \mathcal{M}_+(\mathcal{X}^2/\mathrm{flip}))$ *to the deterministic function* $(I(t,x), \xi(t,x)\,dx, \zeta(t,x,y)\,d\lambda(x,y))$ *unique solution to the PDE*

$$\begin{aligned} \partial_t I(t,x) = \sigma(x)\,\Delta I(t,x) + b(x)\cdot\nabla I(t,x) - I(t,x)\,\lambda(t,x)\,M_\delta\xi(t,x) \\ + \int_{\mathcal{X}} \chi(x-z)\,\mu(t,z)\,M_\delta\xi(t,z)\,dz \end{aligned} \tag{13a}$$

$$\begin{aligned} \partial_t\xi(t,x) = \int_{\mathcal{X}} M_\delta(I\lambda)(t,z)\,S(\nabla I(t,z), x-z)\,\xi(t,z)\,dz \\ - \xi(t,x)\,M_\delta\mu(t,x) \end{aligned} \tag{13b}$$

$$\begin{aligned} \partial_t\zeta(t,x,y) = M_\delta(I\lambda)(t,x)\,S(\nabla I(t,x), y-x)\xi(t,x) \\ + M_\delta(I\lambda)(t,y)\,S(\nabla I(t,y), x-y)\,\xi(t,y) \\ - \pi(t,x,y)\,\zeta(t,x,y) - \frac{\int \mu(t,x)\zeta(t,x,z)\,dz}{\xi(t,x)}. \end{aligned} \tag{13c}$$

This result is suggested by the analysis of the generator of the individual-based model. However, due to the singularity of the corresponding limit, existing methods do not apply to such a situation and a careful mathematical study must be carried out.