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PATTERN RESILIENCE

Thematic Priority: New and Emerging Science and Technology
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Deliverable D2.1: Report on methods and tools for computing pattern dynamics. From Individual-Based-Models to Macroscopic descriptions.

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1 Introduction.

Interacting particle systems are useful models to understand a variety of effects in fields as diverse as condensed matter physics, chemical kinetics, population biology (where they are called individual based models) or sociology (agent based models) [1]. In many situations and under different external conditions, these systems exhibit non-trivial collective phenomena like order-disorder transitions, anomalous diffusion, critical phenomena, coarsening dynamics driven or not by curvature, or, in biological contexts, the clustering or, more generally, the formation of spatial patterns of organisms [2, 3, 4, 5, 6]. In the last case, it is obvious that the patterns are manifest and observable only at the level of the population, but are mediated at the level of the individual.

A natural framework to study these collective phenomena is the use of continuum fields like the chemical concentration, the magnetization field, or the density of organisms. A standard example of continuum descriptions is given by the Reaction-Diffusion (RD) systems that describe how the concentration of one or more substances distributed in space changes under the influence of two processes: local chemical reactions in which the substances are converted into each other, and diffusion which causes the substances to spread out in space. They exemplify the usefullness of macro-descriptions, since they are amenable of analytical study and, in fact, constitute a prototype for pattern formation studies, i.e., the formation of spatial structures. But any continuum description should retain the discreteness nature of the particle dynamics. Thus it is needed a mathematical linkage between the individual level where the dynamics proceeds, and the *macroscopic* description where the collective phenomena emerge.

The objective of this report is to present a short summary of the different levels of macroscopic descriptions, and of the mathematical tools that allow to properly build the above-mentioned bridge between the microscopic and macroscopic worlds. These are techniques developed in the framework of Non-Equilibrium Statistical Physics, and the most accurate description is given by stochastic partial differential equations (Langevin equations) where the noise term accounts for the discreteness of the particle system [7, 8, 9, 10, 11, 12]. The different levels of description are summarised in the next section. In the following ones we will exemply them with some of the case studies analysed in the PATRES project: bacteria dynamics in Section 5, savannas in Sec. 4, and a general system with two symmetric absorbing states in Section 6.

2 Different types of macro-evolution equations.

Different levels of macro-descriptions can be used when approximating a system of interacting particles. A non-exhaustive list, attending at the topology of interactions between individuals, is the following:

1. **Mean-field equations.**

   These are rate equations for the time evolution of a global quantity, like the total spin magnetization, the total population of species, or the global density of particles [15]. In general, it gives good estimates on well-mixed populations where every individual interacts with any other. If the original microscopic system is defined on a lattice, one says that the mean-field description is appropriate in a situation of complete graph or fully connected network.

   This is possibly the simplest approach, but lacks of essential ingredients of the dynamics. With mean-field descriptions, the spatial dependence of the system, its correlations and fluctuations are neglected.

2. **Pair approximation.**

   This is an approximation where one describes the system with a rate equation for the evolution of the global density of different types of particle-pairs of neighboring sites in the lattice. In this case, one accounts for nearest-neighbor correlations, but neglects the fluctuations. A useful example of this methodology, developed in the context of PATRES to study savanna dynamics, can be consulted in [16], and in section 4 of this report. Though the spatial dependence of the system is not fully described, one can have a good idea of it within this approximation [16], in particular the tendency of the particles to aggregate.

3. **Stochastic partial differential or spatial-dependent Langevin equations.**

   This is the most complete description in terms of a macroscopic field that one can obtain for a system of interacting agents [8, 7, 15, 9]. It is a stochastic partial differential equation for the evolution of a spatially extended field like the local density or magnetization. It is obvious that this description accounts for correlations and spatial dependence, but it also takes into account fluctuations via a noise term which is generally associated to the discreteness nature of the particle system. It is generally equivalent to the so-called

Fokker-Planck equations, which are evolution equations for the probability-density of the macroscopic field; and typically are, like the Fokker-Planck itself, and approximation for the so-called Master equations [8, 7]. We will concentrate on this kind of description in the section 6, using as an example a general system with two (symmetric) absorbing states.

This report summarises the development and the use of these methods in the project without going into the technical details. These details and more complete references are given in the hand book of the project (deliverable 4.2).

3 Deriving simplified individual-based models. SimExplorer software

These macro-evolution equations cannot be derived directly from complex models. For instance the Jeltsch model of savanna, which is the starting point of our work on the savanna case study, includes a large set of spatial cells, each one with two levels of ground with different properties, and on each cell different types of vegetation, each one with its specific dynamics. It includes also the impact of the rain regime and a specific model for the impact of fire. This model includes too many variables with heterogenous interacting processes to derive properly a master equation or a similar equation: the state space to consider is too large and heterogeneous, and we have no clue on how to make relevant approximations. This is the same for the model of bacteria, in which the size of the bacteria is taken into account, as well as the diffusion dynamics of the substrate. To derive these macro-evolution equations, the first step is to define a simplified individual-based model which approximates the complex one, as we did in the project in the case studies about savanna and bacteria.

In this first step, we define simpler individuals (i.e. for the savanna, the spatial cells are described with a single binary variable, or the bacteria are described as simple points in a continuous space), and simplified dynamics associated to these individuals. This work is done through a trial and error approach. The hypotheses on the simplified models are implemented, and then their behaviour is compared with the one of the initial big model, focusing on some important indicators. The hypotheses are revised accordingly. Often this process includes the identification of the best parameters for the simplified model, to fit the behaviour of the big model (as we did for the savanna model).

This process implies to make a lot of simulations with the intial big model and with its hypothetical simplifications. Often, this requires to develop as specific application to launch them, for instance with defined parameter variations and a defined number of replicas (when random processes take place in the model). Moreover, once the simplified model shows satisfactory properties with respect to the big model, it can be interesting to explore it independently from the big model. This is for instance what we did with the simplified IBM of bacteria, which shows transitions between uniform, regularly spaced microcolonies, and labyrinth like patterns. This implies also a lot of simulation experiments, with the objective to explore the possible dynamical behaviour of the model.

The objective of SimExplorer to facilitate this task of simulation experiments. This software tool, partly developed in the project, can be applied to any executable model, taking files as input and files as output. It offers facilities to define an experimental design on parameters (directly of the model or for generating the initial conditions), and organises the loop on the set of experiments with the different steps: generation of the model inputs, launching the model, treating the model results. The tool also aims at driving more attention on the definition and treatment of simulation experiments, which is an essential step in the global process of modelling. For instance, being able to reproduce exactly these experiments is an elementary scientific requirement which is not always so easy to fulfil, without an appropriate tool. Indeed, making such experiments generates many different files for each experiment. The versions of the model and of the experiments evolve rapidly.

SimExplorer provides an information system which keeps a memory of the performed experiments which are kept in a data base, potentially shared among different users through a server. This favours the reusability and sharing the codes of the different components used in simulation experiments (experimental designs, statitical treatments, generation of specific initial conditions, etc...). This tool is important to guarantee a level of quality in the practise of experiments on models.

Moreover, SimExplorer includes facilities for lauching experiments on PC clusters or computer grids, requiring a minimum investment from the user. Indeed, exploring a paramater space leads often to define a large number of simulation experiments, and it is much more efficient to launch these experiments in parallel on a cluster or a grid. This is the reason why the cluster bought by CNRS with the partial support of PATRES was important in the project. However, the practical use of a grid remains uneasy for non specialists, and a part of the new development on SimExplorer was to add software layers that make the operation

to launch the experiments in parallel on a grid as light as possible.

SimExplorer is a deliverable of the project, within workpackage 2. It is described in more details in one chapter of PATRES handbook. Moreover the information system is described in more details in (PAPER IS) and some complementary development about a datawarehouse for model results, using the Jeltsch model of Savanna as an example.

4 Pair approximation in discrete space: applications to savanna modelling

Savanna ecosystems are widespread and economically important and harbor considerable biodiversity. Despite extensive study, the mechanisms regulating savanna tree populations are not well understood. Recent empirical work suggests that both tree-tree competition and fire are key factors in semiarid to mesic savannas, but the potential for competition to structure savannas, particularly in interaction with fire, has received little theoretical attention. We develop a minimalistic and analytically tractable (in particular, we use it here to show how the pair approximation works) stochastic cellular automaton to study the individual and combined effects of these two factors on savannas. We find that while competition often substantially depresses tree density, fire generally has little effect but can drive tree extinction in extreme scenarios. When combined, competition and fire interact nonlinearly with strong negative consequences for tree density.

Moreover, our model is capable of generating the patterns of trees distribution that are found in savannas:a) regular, random or clumped at short distances; b) generally clumped at intermediate scales; and c) clumped to random at larger scales. This suggests that a small set of simple processes, as the one present in our model as we will see below, might account for much of the variation in spatial pattern among savannas. A key strength of our approach is that, by using mean-field and pair approximations, we can establish analytically the conditions under which the model's important qualitative behavior occurs.

The simple model we have built is focussed on tree dynamics, it is an extension of the well-known contact process which is implemented as a continuous-time, discrete-state Markov chain on a square lattice. it is based on the following fundamental processes (detail in [16]):

1. Death: at a constant rate a tree dies independently of the status of its neighbours.

2. There is seed dispersal to local (both to far and near) neighborhoods.

3. A seed that has landed in a given non-tree-occupied site can establish in that site if it survies both *competition with nearby adult trees* and *fire*. In other language: the probability of establishment is the product of the probabilities of the seed to survive competition and to survive fire.

We have considered in [16] two levels of description to this model: a mean-field approximation, and a pair approximation which accounts for the *spatial dependence* of the mean density. The mean-field approach consists in using the transition rules of the model to find an equation for the dynamics of the mean tree density of trees, $\rho[1]$. The pair approximation (the foucus in this section) considers two evolution equations: one for the mean tree density, and another one for the mean frequency of pairs, $\rho[ij]$, that gives the probability that a randomly selected site is in state i (1 or 0, i.e, tree o grass), and a randomly selected neighboring site is in state j. We have a closed system of equations of the type [16]:

$$\frac{d\rho[1]}{dt} = F_1(\rho[1], \rho[11]), \quad (1)$$

$$\frac{d\rho[11]}{dt} = F_2(\rho[1], \rho[11]). \quad (2)$$

For a given set of fire and competition parameters, $\rho[1]$ and $\rho[11]$ reach stationary values, and one can study, for example, the pair correlation statistic defined as $g = \frac{\rho[11]}{\rho[1]}$, which equations 1 for a random spatial disstribution, and with values greater and less than 1 indicating clustered and regular distributions, respectively. That is, studying g one can obtain much spatial information about the system.

A most relevant result of our model, obtained with the pair approximation and numerical studies, is the steady spatial distribution of trees in terms of the fire and competition parameters [16].

5 Pair approximation in continuous space: models of bacteria dynamics

Bacteria are ubiquituous in nature and are used in many industrial bioprocesses like in biological wastewater treatment. They grow preferentially attached to each others or to any submerged surface and form complex microscopic spatial structure broadly called biofilms. Advanced experimental observation tools like confocal microscopy and molecular biology revealed the complexity and diversity of

these spatial structures. There is an ongoing active research on how biofilms form and how these patterns affect the interactions between the individual cells and the dynamics of the community.

The formation of biofilms involves a complex interplay between cell proliferation, surface-associated motility, the production of extracellular macromolecules that form a structural matrix and bacteria detachment (for a review see Parsek et al. [23]). Individual-based models (IBMs) can be used to assess how these processes yield biofilm formation. We propose a novel spatially explicit IBM in which bacteria-surface associated motility is reduced by a self-produced extracellular substance [24]. This mechanism coupled to growth and detachment can yield a diversity of spatial patterns ranging from rounded-shaped isolated colonies, to pattern with interconnected microcolonies and labyrinth-like structures. We proposed a simplified version of the IBM with the following three processes:

- A bacterial cell in location x divides yielding a new cell in location x' with a probability (per unit of time) $B(x, x')$ given by:

$$B(x, x') = b_1 K\left(\frac{||x - x'||}{w_b}\right) \tag{3}$$

  where b_1 is a constant division probability and $K(||x - x'||/w_b)$ is a birth kernel that gives the probability that the newborn cell is located at a distance $x - x'$ from the mother cell.

- A bacterial cell in x detaches with a probability $D(x)$ that increases with the increase of local density of individuals such that:

$$D(x) = d_1 + d_2 \sum_i K\left(\frac{||x - x_i||}{w_d}\right) \tag{4}$$

  where d_1 and d_2 are respectively the density-independent and density-dependent detachment rates and $K(||x-x_i||/w_d)$ is an interaction kernel that measures how an individual i located in x_i affects the detachment rate of the individual in location x

- A bacterial cell in location x can move to another location x' with a probability (per unit of time) $M(x, x')$ that decreases with the increase of the local density of individuals such that:

$$M(x, x') = \left[m_1 - m_2 \sum_i K\left(\frac{||x - x_i||}{w_v}\right)\right] K\left(\frac{||x - x'||}{w_m}\right) \tag{5}$$

where m_1 and m_2 are respectively the density-independent and the density-dependent motility rates. The kernel $K(||x - x_i||/w_v)$ measures how an individual i located in x_i affects the motility probability of the focal individual in location x and $K(||x - x'||/w_m)$ is the motility kernel that gives the probability to move with a distance $x - x'$.

For simplicity we consider uniform kernels for birth, interaction and motility:

$$K\left(\frac{||x - x'||}{w}\right) = \begin{cases} 1/w & \text{if} \quad ||x - x'|| < w \\ 0 & \text{else} \end{cases} \tag{6}$$

The simplified IBM still allows to reproduce the main patterns (isolated colonies and labyrinth-like structure). In order to analyze the dynamics of this system we approximate the simplified IBM with a pair approximation approach also called moment model. The moment approximation model state variables are the average density of individuals N and the pair correlation function $C(\xi)$ giving the average density of pairs formed with two individuals separated with a (vectorial) distance ξ.

$$\frac{dN}{dt} = b_1 N - d_1 N - d_2 \int C(\xi) K\left(\frac{||\xi||}{w_d}\right) d\xi \tag{7}$$

Note that the motility is not involved in equation 7 as the motility of an individual from one position to another does not affect the total number of individuals. However, motility may affects the average number of individuals indirectly by modifying the spatial distribution of the individuals and consequently their detachment rates.

$$\frac{dC(\xi)}{dt} = \left(\frac{dC(\xi)}{dt}\right)_{division} + \left(\frac{dC(\xi)}{dt}\right)_{detachment} + \left(\frac{dC(\xi)}{dt}\right)_{motility} \tag{8}$$

The first term accounts for the net variation of $C(\xi)$ due to division events The second term accounts for the net variation of $C(\xi)$ due to detachment events. The third term accounts for the net variation of density of pairs at distance ξ.

The precise expressions of these terms are given in PATRES handbook. The moment model describes the determinitic dynamics of the average density of individuals N and the pair correlation function $C(\xi)$. The model is based on the average neighbourhood of the individuals and requires a closure expression that

expresses the triplet density function $T(\xi, \xi')$ in term of N and C. A common closure expression is given by:

$$T(\xi, \xi') = \frac{C(\xi)C(\xi')}{N} \tag{9}$$

The comparison of the moment model and the individual-based model simulations shows that the moment approach can capture the important features of the spatial pattern. For example patterns of immotile cells with forming colonies separated with a regular distance are well captured by the moment approach. In comparison to the individual-based model, the moment model is deterministic (no need to replicate the simulations)and involves a small number of aggregated variables that directly describe the spatial pattern (rather than describing the state of all the individuals as in the IBM) while still capturing the effect of local interaction as in the IBM. The moment model is therefore easier to analyse than the IBM enven if only by numerical methods.

Our results however point out some of the limitations of the moment approach in particular capturing the effect of stochastic fluctuations of the individuals neighbourhood as the moment model is based on the average neighbourhood. In certain situation these fluctuations can impact the dynamics of the system and this is not well captured by the moment approach.

6 Macroscopic description of systems with two symmetric absorbing states.

In this section we show the general methodology to go from the micro-dynamics towards a macroscopic description, using a particular example to guide our calculations. The example is rather general, and refers to spin or particle systems with two (symmetric) absorbing states [13]. This means that the system shows two states of total consensus (all spins up or all down) from which there is zero probability of exiting. Much of the interest in the study of these systems resides in the relevance of a sub-class of them, the so-called Voter-like models, which have been widely used to model, among others, species in competition [17], allele frequency in genetics [18], kinetics of heterogeneous catalysis [19], the dynamics of languages in competition [20] and opinion formation [21]. Voter-like models are spin or particle systems where the state of a particle in a lattice site evolves according to the density of states in its near neighbourhood. A detailed analysis of what follows can be consulted in [14].

The general model is defined as follows: Each site $\mathbf{r} = (r_1, .., r_d)$ of a d-dimensional square lattice is occupied by one particle with a spin that can assume either value 1 (up) or -1 (down). The dynamics consists of choosing, at each time step, a site $\mathbf{r}$ at random and flipping the spin at this site, $S_\mathbf{r}$, with a probability f. This flipping probability (also called, transition rate) is a function of the density of spins in the near neighborhood, $\psi_\mathbf{r} = \frac{1}{4}\sum_{\mathbf{r}'} S_{\mathbf{r}'}$; where the sum is over the 4 nearest-neighboring sites $\mathbf{r}'$ of site $\mathbf{r}$. I.e., we have $f(\psi_\mathbf{r})$.

We want to derive a Langevin equation for the field ϕ that represents the spin profile on the lattice. For this we consider a coarse-graining of the spins in the lattice and write a master equation for the resulting density field. Expanding this master equation (see details in [14]) one can obtain a Fokker-Planck equation for the probability distribution of the continuus density. Finally, this Fokker-Planck is equivalent to a langevin equation of the type:

$$\frac{\partial \phi(\mathbf{r},t)}{\partial t} = \left[1-\phi(\mathbf{r},t)\right] f(\psi_\mathbf{r}) - \left[1+\phi(\mathbf{r},t)\right] f(-\psi_\mathbf{r}) + \eta(\mathbf{r},t), \qquad (10)$$

where η is a Gaussian white noise with a very complex correlation function (see [14]).

Note that up to now our derivation is completely general, and the fact that the system has two absorbing states is only present in the condition for the flipping probability: $f(-1) = 0$, i.e., the transition rate must vanish when the spin is aligned with all of its neighboring spins. We can still go further and look for an approximation of Eq.(10) which, however, captures the behavior of a wide range of models. A closed equation for $\phi(\mathbf{r},t)$ can be obtained by expanding the flipping probabilities, $f(\psi_\mathbf{r})$. So that we finally obtain a Langevin equation for for $\phi(\mathbf{r},t)$

$$\begin{aligned} \frac{\partial \phi}{\partial t} &= (1-\phi^2)(a\phi - b\phi^3) \\ &+ \left[a + c + (d-2a-3b)\phi^2\right]\Delta\phi + \eta \end{aligned} \qquad (11)$$

(for the correlations of the noise term again consult [14]). And where the coefficients are given in terms of derivatives of the flipping probabilities:

$$c \equiv 2f|_0,\ a \equiv 2f'|_0 - c,\ d \equiv f''|_0 - a,\ b \equiv -\frac{f'''|_0}{3} + d. \qquad (12)$$

With this Langevin equation one can now study interesting phenomena like ordering dynamics, cluster formation or critical properties.

It is important to stress the significance of our result. We have derived from the microscopic dynamics, the Langevin equation for the density or magnetization field of general nonequilibrium spin systems with two symmetric absorbing states. In this equation the dependence of the different terms on the flipping probability is explicitly stated. This methodology allows one to predict the macroscopic behavior, such as critical properties and ordering dynamics, a priori, by simply knowing the derivatives of the transition rates. A large class of models in many different disciplines can be studied in this way. In particular recent advances have been obtained for language competition models [22].

7 Summary.

Most of physical, biological, chemical or social systems can be described as a finite number of individuals in interaction, in a more or less complex environment. This description is suitable for computer simulations (often called Individual-based models, or IBMs), but mathematical analysis, where the role of the different parameters can be better studied, is most of the time useless at this level. In particular, studying the viability or the resilience of the system at this level is impossible with current tools (see deliverable D3.1 and the handbook for more details about this). In addition, such systems often produce statistically robust patterns (collective behaviours) which define the relevant level of description. The use of IBM is thus only a means to access these collective behaviours and understand the process of their generation.

Then one has to resort to collective or macroscopic descriptions of the system, generally in terms of continuous fields like the density of particles. This implies a first simplification of the system where the individuals of the system have rough descriptions similar to the one of physical particles (although the dynamics of these simplified individuals can be of course very different from the one of physical particles). This first simplification step represents a lot of work through trial and errors, and many simulation tests of the simplified and initial models. SimExplorer (deliverable 2.2) is a tool which aims at facilitating this task, though a certain level of expertise and know-how will always be necessary at this stage.

Moreover proper macroscopic descriptions should be faithful enough to the simplified individuals dynamics, so that the discrete character of the system has to be properly *catched* in the continuous description. We have briefly summarised in this report the different levels of approximation of the macroscopic description. Using as examples some case studies of the PATRES project (savannas, bacteria,

or voter-like systems) we have given examples of the different macroscopic approximations: mean-field, pair approximation and Langevin equations. Certainly, the most accurate description is given in terms of spatial-dependent stochastic or Langevin equations, where there is a random function that accounts for the fact that the system has a finite number of particles. But mean-field or pair approximations may give sufficient information on the dynamics of the system.

Non-Equilibrium Statistical Mechanics provides the tools to cross the bridge between the micro and the macro world. Using particular examples we have shown some of the steps needed to cross this bridge. A large class of models in many different disciplines are taking advantadge of these tools to gain further insight.

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