

RESEARCH PAPERS

Seasonal variance in P system models for metapopulations*Daniela Besozzi^{1**}, Paolo Cazzaniga², Dario Pescini² and Giancarlo Mauri²

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Abstract Metapopulations are ecological models describing the interactions and the behavior of populations living in fragmented habitats. In this paper, metapopulations are modelled by means of dynamical probabilistic P systems, where additional structural features have been defined (e.g., a weighted graph associated with the membrane structure and the reduction of maximal parallelism). In particular, we investigate the influence of stochastic and periodic resource feeding processes, owing to seasonal variance, on emergent metapopulation dynamics.

Keywords: P system, metapopulation, stochastic ecological model.

P systems, or membrane systems, were introduced by Gh. Păun as a class of unconventional computing devices of distributed, parallel and nondeterministic type, inspired by the compartmental structure and the functioning of living cells. The basic model consists of a membrane structure where multi-sets of objects evolve according to given evolution rules. Assuming an universal clock, a computation is obtained by letting all regions and all objects inside them be simultaneously processed, by using the rules in a nondeterministic and maximally parallel manner; the evolved objects are then communicated to the regions specified by the rules. A computing device is obtained, starting from an initial configuration, letting the system evolve as just described and collecting the output in a specified membrane or outside the system. We assume that the reader is familiar with P systems. A comprehensive overview of basic P systems and of other classes appeared in Ref. [2], an updated bibliography can be found in the P systems web page: <http://psystems.disco.unimib.it/>.

Recently, P systems have been applied in various research areas, ranging from biology to linguistics and to computer science (see, e.g., [3]). In this paper, membrane systems are used as modelling tools for metapopulations, which have been extensively investigated in ecology to analyze the behavior of interacting populations, with the aim of determining how a

fragmented habitat can influence local and global population dynamics. A metapopulation, or multipatch system, consists of local populations living in spatially separated habitat patches, and a dispersal pool, which is the place allowing the migration of individuals among different patches. In multi-patch systems, two principal classes of dynamics exist: the populations can locally interact inside a patch—according to the Lotka-Volterra equation^[4], while the dispersal of individuals among patches can affect the global behavior of the whole system^[5–8].

Other works in the area of membrane computing previously appeared with some applications to ecological or population systems. For instance, Lotka-Volterra dynamics were analyzed in [9, 10], while a tritrophic system consisting of herbivore-induced plant volatiles and carnivorous was modelled in the framework of ARMS^[11]. The main difference between this work and previous ones lies in the effective use of many regions to model an ecological system, thus really exploiting the advantages of the membrane structure. However, for modelling metapopulations the classical definition of membrane structure is not suitable, since it does not grasp all the peculiarities characterizing fragmented habitats and real landscapes. Hence, other features have to be added to the basic membrane structure in order to model the spatial and dimensional properties of a metapopulation.

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Moreover, we will also need to operate on the classical notion of maximal parallelism, by reducing the maximal consumption of objects.

In this paper we use the class of dynamical probabilistic P systems (DPPs)^[10,12], recently introduced for the analysis and simulation of the behavior of complex systems. DPPs are discrete and stochastic models, where probability values are associated with the rules, and these values change during the evolution according to the current state of the system. In [13] we have shown that DPPs represent a valid modelling method for the analysis of population systems living in fragmented habitats, where individuals can interact and where stochastic mechanisms also play a role in governing the local and global population behavior. Here we go on with the analysis of metapopulation models, by focusing on the effects of stochastic and periodic resource feeding, that is, we simulate the influence of seasonal variance over food availability.

The paper is structured as follows. In Section 1 we recall dynamical probabilistic P systems, that will be used to define the stochastic discrete model for metapopulations; we also review there the basic ecological characteristics of metapopulations. Then, we outline the necessity of some new features of membrane systems, and focus on the strategies for periodic and stochastic resource feeding, in Section 2 we propose our model for the study of metapopulations, and show the results obtained from stochastic simulations, concerning the role of seasons over resource availability, and the corresponding metapopulation emergent dynamics. Finally, we conclude with some final remarks.

1 P systems and metapopulations

In this section we provide the useful definitions

$$\tilde{p}_i(r) = \begin{cases} 0 & \text{if } \exists h \in H \text{ s.t. } M_i(a_h) < \alpha_h \\ k \cdot \prod_{h \in H} \frac{M_i(a_h)!}{\alpha_h! (M_i(a_h) - \alpha_h)!} & \text{if } M_i(a_h) \geq \alpha_h \forall h \in H \end{cases} \quad (1)$$

The normalized probability of rule r is then given by the expression $p_i(r) = \tilde{p}_i(r) / \sum_{r' \in R_i} \tilde{p}_i(r')$.

A configuration C_t of a DPP at a given step t , $t \geq 0$, consists of the multisets M_0, \dots, M_n occurring inside the membranes at step t . Starting from an initial configuration C_0 , the system evolves according to the given parameters, which consist of the rule constants and other values needed to simulate open systems (e.g., the values corresponding to resource

of dynamical probabilistic P systems (DPPs), and give a description of (the principal characteristics of) metapopulations.

1.1 Dynamical probabilistic P systems

For a complete definition of DPPs, as well as for examples of some simulated systems, we refer the interested reader to [10, 12, 14, 15]. Here we only briefly recall how DPPs work and some notes on the software simulators.

DPPs are a stochastic class of membrane systems where probability values, associated with the rules according to a prescribed strategy, vary during the evolution of the system (the approach used to evaluate the probability of a rule is very close to the strategy used by the stochastic simulation algorithm, introduced by Gillespie in [16, 17]). The probability value depends on both the constant associated with the rule and a combinatorial part that accounts for all the distinct interacting tuples of objects—expressed by the left-hand side of the rule—that are available in the multiset at any evolution step. The probability is evaluated as follows: let us denote by $V = \{a_1, \dots, a_l\}$ the alphabet of the system, M_i the multiset inside membrane i , $i = 0, \dots, n$, and $r: u \xrightarrow{k} (v, \text{tar})$ a rule in R_i , where $k \in \mathbb{R}^+$ is the constant associated with the rule and $\text{tar} \in \{\text{here}, \text{out}, \text{in}_1, \dots, \text{in}_n\}$. We also use the notations $u = a_1^{\alpha_1} \dots a_s^{\alpha_s}$, $\text{alph}(u) = \{a_1, \dots, a_s\}$ and $H = \{1, \dots, s\}$. To obtain the actual normalized probability p_i of applying r with respect to all other rules that are applicable in membrane i at the same step, we first need to evaluate the (non-normalized) pseudo-probability $\tilde{p}_i(r)$ of r :

feeding in the case of metapopulations). At each step of the evolution, a transition from the current configuration to the next one is obtained by simultaneously applying all applicable rules, and consuming all occurrences of the left-hand sides of the applied rules. We assume that the system evolves according to a universal clock, that is, all membranes and the application of all rules are synchronized. The applied rules are chosen according to the probability values dynamically assigned to them; the rules with the highest normalized probability values will be more frequently tossed.

In [13] we introduced a method which allows to maintain the maximal parallelism at the level of rule application, but to reduce it at the level of object consumption. This strategy is adopted in order to achieve a closer resemblance to biological systems, where it is unlikely that all system components are simultaneously subject to the same process.

To this aim, we add to each membrane the rules of the form $u \rightarrow (u, \text{here})$ (where u is the multiset over V occurring in the left-hand side of the rules in that membrane) which, whenever applied, will not affect the multiset currently present inside the membrane. We call these rules the mute rules. In this way, all occurrences of u appearing in the membrane multiset are actually processed because of the maximal application of rules, but, at the same time, some occurrences of u are also reproduced in the membrane multiset, thus reducing—or modulating *ad hoc*—the maximal parallelism at the level of object consumption.

Anyway, when adding mute rules to a membrane, we obviously do not want to change either the dynamical conditions determined (inside that membrane) by the constants associated with the other rules, or their respective mutual ratios. To achieve this, we choose to apply the following strategy to compute the constant of the added mute rules, as well as the new constants of their corresponding rules originally defined inside the membrane. Let $S = \{r_1: u \xrightarrow{k_1} (v_1, \text{tar}_1), r_2: u \xrightarrow{k_2} (v_2, \text{tar}_2), \dots, r_h: u \xrightarrow{k_h} (v_h, \text{tar}_h)\} \subseteq R_j$ be the maximal subset of rules appearing inside a membrane j and having the same left-hand side, with u, v_1, \dots, v_h multisets over V , $v_i \neq u$ for all $i = 1, \dots, h$, $h \geq 1$. Let us also define $K_S = \sum_{i=1}^h k_i$. Now, we add the mute rule $r_{h+1}: u \xrightarrow{k_{h+1}} u$ to the set S , and we call $S' = S \cup \{r_{h+1}\}$. Since we want to preserve in S' the relative dynamic determined by the rules initially present in S , we have to associate new constants with the rules in S' . So, let denote by k'_1, \dots, k'_h the new constants of rules r_1, \dots, r_h in S' , and let also be $K_{S'} = \sum_{i=1}^h k'_i$. It is easy to verify that, by choosing $k'_i = k_i / (1 + \rho)$ for all $i = 1, \dots, h$, and $k_{h+1} = \rho K_S / (1 + \rho)$, we obtain that:

(i) The mute rule r_{h+1} will be applied with a certain proportionality with respect to the rules in S ,

that is, for some arbitrarily fixed $\rho \in [0, \infty)$ the ratio $\rho = k_{h+1} / K_{S'}$ holds;

(ii) the addition of the mute rule r_{h+1} to the set S does not modify the underlying dynamics, that is, $K_S + k_{h+1} = K_{S'}$ still holds.

The simulation of DPPs can be performed by means of a dedicated program written in C language, which was initially developed for single processor machines (see details of the underlying algorithm in [10]). The simulator is also available for download from the P systems web page. Recently, another simulator of DPPs has been implemented using the Message Passing Interface (MPI) C libraries (<http://www-unix.mcs.anl.gov/mmpi/>). The MPI-based simulator allows to (1) spread the computation over a cluster of processors in order to achieve a higher scalability, (2) have a direct mapping of the communications among the membranes, and (3) speed up the computation. Some details on MPI implementation of DPPs can be found in [15].

1.2 Metapopulations

Since its introduction in [18], the concept of metapopulation (or multi-patch system) has been consistently applied to different population species living in both natural or artificial fragmented habitat landscapes, to the aim of determining how the habitat can influence the population dynamics. A metapopulation consists of local populations, living in spatially separated habitat patches (which can be characterized by different areas, quality or isolation), and a dispersal pool, which is the spatial place where individuals from a population spend some lifetime during the migration among patches. The dispersal of individuals is distance-dependent, it may reduce the local population growth and lead to an increase in extinction risk, which can be due also to environmental and demographical stochasticity. Thus, the persistence of populations is assumed to be balanced between local extinctions and the establishment of new populations in empty patches^[19].

In multi-patch systems it is possible to distinguish between two principal types of dynamics: on the one hand, the populations can locally interact inside a patch (according, e.g., to the Lotka-Volterra model of preys and predators); on the other hand, the dispersal of individuals can influence the global behavior of the whole system.

Several theoretical frameworks for metapopulation analysis have been defined up to now, remarking specific properties of multi-patch systems which are to be explicitly or implicitly considered (see [19, 20, 21] for further details). For instance, referring to the landscape, most theoretical models take care of the spatial structure, the local environmental quality, the patch area and the connectivity (isolation), in order to capture the effect of habitat fragmentation on species persistence. In fact, local conditions determine the growth and survival of populations inside patches, and high patch connectivity can decrease local extinction risk. Moreover, dispersal and colonization are distance-dependent elements which can account for the importance of real landscape structures. Referring to population interactions and dynamics, colonization can depend or not on the cooperation of migrating individuals. Models not accounting for within-patch dynamic—but only assuming whether a patch is occupied or not—usually consider local dynamics on a faster time scale with respect to the global dynamic, and also neglect the dependence of colonization and extinction rates on population sizes. Finally, regional stochasticity can account for “bad” or “good” years over the local environmental quality, which depends on, e. g., the weather conditions which affect sustenance resource availability and, once more, they can influence the growth and survival of populations.

2 A model for stochastic seasonality in metapopulations

In this section we provide an extension of the modelling framework for metapopulations initially proposed in [13] by means of DPPs.

We consider a membrane structure μ with degree $n + 1$ and depth 2, with the skin membrane labelled with 0 and the internal membranes labelled with numbers $1, \dots, n$. In what follows, we will refer without distinction to the skin membrane or dispersal pool, and to the internal membranes or regions or patches. For the modelling of a metapopulation, the membrane structure has to be intended as a set of spatially distributed regions, each one completed with a “dimension” value and a fixed “distance” with respect to all other regions. Since the membrane structure should have a precise spatial arrangement, we associate with the set of internal membranes an (undirected) weighted graph with node attributes. In this way, we can outline both the spatial distribution of patches and the relevant additional features associated

to them: the dimension of a patch is needed to define the density of the populations living inside the patch; the distance, or cost, is needed to define the dispersal rates inside the pool, as well as to identify the isolated patches. We remark that the cost among patches is not necessarily intended as a physical distance: it can also represent how stiff it is to move from one patch to another one due to the geographical morphology of the landscape, or to other general local conditions.

A formalization of this can be achieved by using a weighted undirected graph $G = (N_\Delta, E, w)$ where (1) N_Δ is the set of nodes and Δ is a set of attributes, such that with each node $x \in N_\Delta$ there is associated a value $a \in \Delta$, (2) $E \subseteq \{\{x, y\} \mid x, y \in N_\Delta, x \neq y\}$ is the set of (undirected) edges between nodes, (3) $w: E \rightarrow \mathbb{R}^+$ is the weight function associating a cost with each edge.

In the case of a membrane structure, the set of nodes N_Δ coincides with the set $\{m_1, \dots, m_n\}$ of internal membranes, the attribute of a patch represents the area of the patch, the edges characterize the connectivity among patches. When saying that a patch m_i is connected to—or can directly reach—patch m_j , we mean that individuals exiting from patch m_i will then be allowed to enter patch m_j after some time spent in the pool (and viceversa). The weight of the edge between patch m_i and patch m_j represents a cost to measure the effort that individuals have to face when moving from m_i to m_j , passing through the dispersal pool. Note that we consider the case of undirected graphs, though also directed graphs with two (differently weighted) edges between any couple of patches can be used, thus better characterizing the nature of the landscape.

The area of a patch m_i , $i = 1, \dots, n$, is a value $\sigma_i \in \mathbb{R}^+$. The area of the pool is implicitly assumed to be large enough to contain all patches and to allow the dispersal of individuals, that is, $\sigma_0 \gg \sum_{i=1}^n \sigma_i$.

Given the alphabet V of population species, the density of patch m_i , $i = 0, 1, \dots, n$, with respect to population species $X \in V$ is $\delta_X(m_i) = |X|_{m_i} / \sigma_i$, where $|X|_{m_i}$ denotes the number of individuals of species X inside patch m_i .

Given all the necessary prerequisites, we can now define the modelling framework for multi-patch

systems with DPPs^[13], extended with the use of different feeding strategies of a stochastic type. We consider a generic metapopulation consisting of n patches, a dispersal pool, and two population species. We also assume that the populations dynamic inside each patch follows the Lotka-Volterra model (see [10] for a previous description of preys-predators dynamic with DPPs). Hence, let

$$\Pi = (V, O, \mu, I, G, M_0, \dots, M_n, R_0, \dots, R_n)$$

be such that:

$V = \{A, A', X, Y, Y_1, \dots, Y_n\}$ consists of the symbol A for sustenance resources, X for the species of preys, Y for the species of predators. A' is used to simulate the stochastic feeding of resources, while Y_1, \dots, Y_n are used to denote which was the original patch of a predator before it migrated to the pool.

$O = \{X, Y\}$, $I = \{1, \dots, n\}$ are, respectively, the sets of symbols and region labels whose dynamics will be analyzed.

μ is a membrane structure consisting of n elementary membranes, m_1, \dots, m_n , and the skin membrane, m_0 .

G is the graph associated with the internal membranes, where we specify the set of area attributes for patches, $\Delta = \{\sigma_1, \dots, \sigma_n\}$, and the set of costs associated to the edges, $\Omega = \{w_{i,j} \mid \{m_i, m_j\} \in E, i, j = 1, \dots, n\}$;

$M_0 = \emptyset$ and $M_i = \{A'X^{p_i}Y^{q_i}\}$, for some $p_i, q_i \in \mathbb{N}$, $i = 1, \dots, n$, are the multisets initially present inside the regions.

For each $i = 1, \dots, n$, R_i contains the following rules:

$$\begin{aligned} r_{(feeding)}^i &: A' \xrightarrow{k_j^i} (A'A^\gamma, \text{here}), \gamma \in \mathbb{N} \\ r_{(Xgrowth)}^i &: AX \xrightarrow{k_{Xg}^i} (XX, \text{here}) \\ r_{(Ygrowth)}^i &: XY \xrightarrow{k_{Yg}^i} (YY, \text{here}) \\ r_{(Xdeath)}^i &: X \xrightarrow{k_{Xd}^i} (\lambda, \text{here}) \\ r_{(Ydeath)}^i &: Y \xrightarrow{k_{Yd}^i} (\lambda, \text{here}) \\ r_{(dispersal)}^i &: YY \xrightarrow{k_d^i} (Y, \text{here})(Y_i, \text{out}) \end{aligned}$$

and their corresponding mute rules:

$$r_1^i: AX \xrightarrow{k_1^i} (AX, \text{here})$$

$$\begin{aligned} r_2^i &: XY \xrightarrow{k_2^i} (XY, \text{here}) \\ r_3^i &: X \xrightarrow{k_3^i} (X, \text{here}) \\ r_4^i &: Y \xrightarrow{k_4^i} (Y, \text{here}) \\ r_5^i &: YY \xrightarrow{k_5^i} (YY, \text{here}) \end{aligned}$$

for some $k_f^i, k_{Xg}^i, k_{Yg}^i, k_{Xd}^i, k_{Yd}^i, k_d^i, k_1^i, \dots, k_5^i \in \mathbb{R}^+$, $i = 1, \dots, n$. Rule $r_{(feeding)}^i$ describes the feeding of sustenance resources, according to the current season of the seasonal variation cycle, as it will be described below. The available resources then allow the growth of preys by rule $r_{(Xgrowth)}^i$. Rule $r_{(Ygrowth)}^i$ governs the direct interactions among preys and predators, and the consequent growth of predators, while rule $r_{(dispersal)}^i$ describes the action of predators migrating from patch m_i into the dispersal pool. The use of the multiset YY in the left-hand side of this rule allows to account for the predator density inside the patch during the process of migration. Note that, when a predator Y exits patch m_i , it arrives in the pool denoted by Y_i : the subscript is needed in order to distinguish, inside the pool, among predators migrating from different patches, who then colonize (see rules $R_{(colonization)}^0$ in the set R_0) other patches. The colonization process takes care of the mutual distance between the originating patch m_i and the other patches connected to it. Rules $r_{(Xdeath)}^i, r_{(Ydeath)}^i$ describe the death of individuals for causes which do not depend on inter-species interactions. Finally, r_1^i, \dots, r_5^i are the mute rules allowing the non-maximal consumption of individuals.

R_0 contains the subsets of rules

$$\begin{aligned} R_{(colonization)}^0 &: \{Y_i \xrightarrow{k_{c,i,j}^0} (Y, \text{in}_j) \mid \{m_i, m_j\} \in E, i, j = 1, \dots, n\} \\ R_{(death)}^0 &: \{Y_i \xrightarrow{k_{d,i}^0} (\lambda, \text{here}) \mid i = 1, \dots, n\} \\ R_{(wandering)}^0 &: \{Y_i \xrightarrow{k_{w,i}^0} (Y_i, \text{here}) \mid i = 1, \dots, n\} \end{aligned}$$

for some $k_{c,i,j}^0, k_{d,i}^0, k_{w,i}^0 \in \mathbb{R}^+$, $i, j = 1, \dots, n$. The rules in the subset $R_{(colonization)}^0$ describe the process of colonization of patch m_j by predators Y_i which migrated from patch m_i . Note that, when entering a patch, a predator Y_i loses its subscript and is again denoted by Y . Rules in $R_{(wandering)}^0$ describe the life spent by predators inside the dispersal pool during the

migration (and also act as mute rules in the set R_0).

In [13] we considered a feeding process of a purely stochastic type: at each step of the evolution, a random number of objects A were created inside each patch to simulate the availability of resources. As an extension, in this paper we consider more general situations where the availability of resources can periodically vary according to seasonality. Our proposed framework could hence be used to model both natural landscapes, where different weather conditions or environmental quality can influence the breeding seasonality, and artificial landscapes where, e.g., populations can be constantly fed by humans.

Formally, we consider the feeding process as governed by a *cycle* of different *phases* (or seasons), each one characterized by an increasing, decreasing, stationary or fixed resource availability. Thus, let $Cycle = (P_1, \dots, P_\nu)$ be an ordered sequence (of length ν) of phases P_1, \dots, P_ν . A phase P_j is characterized by means of a resource trend and a sequence of $h_j \in \mathbb{N}$ evolution steps. The trend determines the feeding strategy that is used during the whole duration of the phase:

(i) Increasing trend (IT): at each step of phase P_j , $\gamma_j = (N_j + (l-1)\Delta_j) + \alpha$ copies of resource A are produced inside each patch, where $N_j \in \mathbb{N}$, $l = 1, \dots, h_j$, and α is randomly chosen in the set $[N'_j, N''_j]$, $N'_j, N''_j \in \mathbb{N}$.

(ii) Decreasing trend (DT): at each step of phase P_j , $\gamma_j = (N_j - (l-1)\Delta_j) + \alpha$ copies of resource A are produced inside each patch, where $N_j \in \mathbb{N}$, $l = 1, \dots, h_j$, and α is randomly chosen in the set $[N'_j, N''_j]$, $N'_j, N''_j \in \mathbb{N}$.

(iii) Stationary trend (ST): at each step of phase P_j , $\gamma_j = N_j + \alpha$ copies of resource A are produced inside each patch, where $N_j \in \mathbb{N}$, and α is randomly chosen in the set $[N'_j, N''_j]$, $N'_j, N''_j \in \mathbb{N}$.

(iv) Fixed trend (FT): at each step of phase P_j , $\gamma_j = N_j$ copies of A are produced inside each patch, where $N_j \in \mathbb{N}$.

In other words, during an increasing (decreasing) phase, the number γ_j of A 's produced inside each patch is given by the sum of two terms: a fixed feeding base N_j , which is increased (decreased) step

by step by a value Δ_j , and a stochastic part determined by the number α that is randomly chosen in a fixed set. The feeding base is used to characterize the current season, and the stochastic term is used to better describe random variations in natural habitats.

On the contrary, a stationary phase is characterized by a constant feeding base plus a stochastic term, while the fixed trend considers only a constant feeding where stochasticity plays no role (it will not be used in this paper).

A feeding cycle can be iterated several times during a simulation, to model how the breeding of populations can be seasonally controlled, and to find out the corresponding (emergent) dynamics of the metapopulation.

Finally, we describe how to evaluate the probabilities of some specific rules in order to let the dynamics of the system depend on the "geometrical" structure of the patches, the initial population multi-sets and the patch densities (thus implicitly considering also the patch areas).

On one side, the application of the rules $R^0_{(\text{colonization})}$ in the pool has to be affected by the cost of moving from the patch from which the individuals migrated to the patch that the individuals will colonize, in such a way that the higher the cost between two patches, the lower the probability for moving from one to the other. Thus, given a rule $r: Y_i \rightarrow (Y, \text{in}_j)$ in $R^0_{(\text{colonization})}$, and $w_{i,j}$ the cost associated with the edge $\{m_i, m_j\} \in E$, then the probability associated with rule r is $p(r) = 1/w_{i,j} \cdot \tilde{p}(r)$ (where $\tilde{p}(r)$ is given by Eq. 1).

On the other side, the rules inside the patches governing the growth and dispersal have to depend on the local populations densities:

For $r^i_{(X_{\text{growth}})}$ we define the probability $p(r^i_{(X_{\text{growth}})}) = (1/\sigma_i) k^i_{X_G} (|A|_{m_i} |X|_{m_i})$, meaning that the higher the number of preys inside the patch, the higher the competition for food resources among them, hence the lower their growth; for $r^i_{(Y_{\text{growth}})}$ we define the probability $p(r^i_{(Y_{\text{growth}})}) = (1/\sigma_i) k^i_{Y_G} (|X|_{m_i} |Y|_{m_i})$, meaning that the higher the number of preys, the higher the growth of predators—but if too many predators are present inside the patch, then

their growth is reduced; for $r_{(\text{dispersal})}^i$ we define the probability $p(r_{(\text{dispersal})}^i) = (1/\sigma_i)k_d^i(|Y|_{m_i}|Y-1|_{m_i})/2$, meaning that the higher the number of predators, the higher the probability that they will leave the patch in search of new colonizable patches for higher survival chances.

2.1 Simulation results of stochastic feeding strategies

In [13] we investigated some emergent metapopulation behaviors, such as the processes of migration and colonization, the role of mute rules and different level of parallel application of rules, the isolation of patches and the effect of different areas on the patch dynamics, etc. Here, we concentrate our attention on different strategies which can simulate the seasonal variance in resource availability.

In the following simulations we consider a membrane structure with four elementary membranes, m_1, \dots, m_4 , spatially arranged by means of a complete underlying undirected graph. The edge costs are $\omega_{1,2} = \omega_{3,4} = 10$, $\omega_{1,3} = \omega_{1,4} = \omega_{2,3} = \omega_{2,4} = 30$. The areas of patches m_1, \dots, m_4 are $\sigma_1 = 1$, $\sigma_2 = 0.35$, $\sigma_3 = 1.5$, $\sigma_4 = 2.5$, respectively. Hence, the membrane structure here describes a landscape with two couples of close patches (m_1 and m_2 , m_3 and m_4), which differ in area dimensions. The initial multisets are set to $p_i = q_i = 1000$, for all $i = 1, \dots, 4$.

The values fixed for the simulations are $k_{Xg}^i = 0.75$, $k_{Yg}^i = 0.075$; $k_{Xd}^i = 0.1$, $k_{Yd}^i = 7.5$, $k_d^i = 0.075$, $k_1^i = k_2^i = 0.25$, $k_3^i = 0.9$, $k_4^i = 2.5$, $k_5^i = 0.025$, for all $i = 1, \dots, 4$, while inside the pool they are $k_{c,i,j}^0 = 1$, $k_{d,i}^0 = 0.8$, $k_{w,i}^0 = 0.2$. All constants have been fixed according to the strategy explained in Section 1.1. All simulations have been performed with the MPI-based simulator of DPPs.

In order to show the difference between the metapopulation behaviors emerging from a pure stochastic feeding trend (as used in [13]) and from periodic feeding cycles, we have performed four simulations characterized by:

(i) A stochastic feeding with random interval equal to [150, 250];

(ii) a cycle of length 2, with P_1 of IT type, P_2 of DT type, $h_1 = h_2 = 50$ steps (thus one complete cycle is 100 steps long), $N_1 = N_2 = 50$, $\Delta_1 = \Delta_2 = 2$

and random intervals equal to [0, 200] for both phases;

(iii) a cycle of length 4, with P_1 of IT type, P_2 of ST type, P_3 of DT type, P_4 of ST type, $h_1 = \dots = h_4 = 100$ steps (thus one complete cycle is 400 steps long), bases equal to 50, $\Delta_1 = \Delta_3 = 1$ and random intervals equal to [0, 200] for all phases;

(iv) a cycle of length 8, with P_1 of IT type, P_2 of ST type, P_3 of IT type, P_4 of ST type, P_5 of DT type, P_6 of ST type, P_7 of DT type, P_8 of ST type, $h_1 = \dots = h_8 = 100$ steps (thus one complete cycle is 800 steps long), bases equal to 50, $\Delta_1 = \Delta_3 = \Delta_5 = \Delta_7 = 1$ and all random intervals equal to [0, 200].

Note that in these simulations we are considering a common feeding cycle for all patches, though other cases where (distant) patches can undergo different feeding processes—or similar cycles but with different lengths—could be easily simulated, too.

Due to space restrictions, we only report the behavior of populations X and Y inside patches 2 and 4, which are characterized by the smallest and the biggest area, respectively. In Fig. 1 we show the

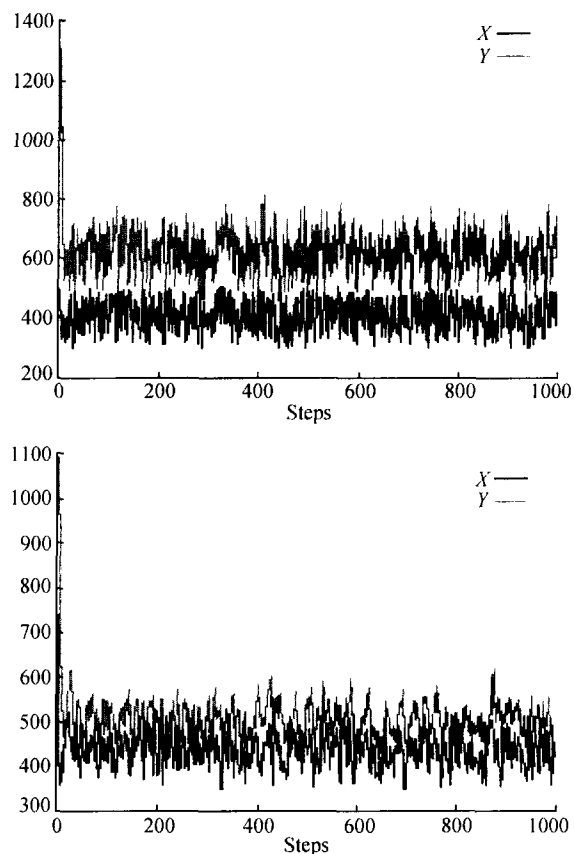


Fig. 1. Pure stochastic feeding strategy inside patch 2 (top) and 4 (bottom).

rapid oscillations in preys and predators multiplicities due to stochastic feeding and dispersal. The effect of the different areas is detectable from the average size and the fluctuations of populations inside the two patches.

In Fig. 2 we show, instead, how the behavior

of the populations changes when considering periodic feeding cycles of different length. Namely, the various feeding trends of the phases characterizing each cycle can be distinguished among each other patch, as well as the role played by the patch areas over the population size.

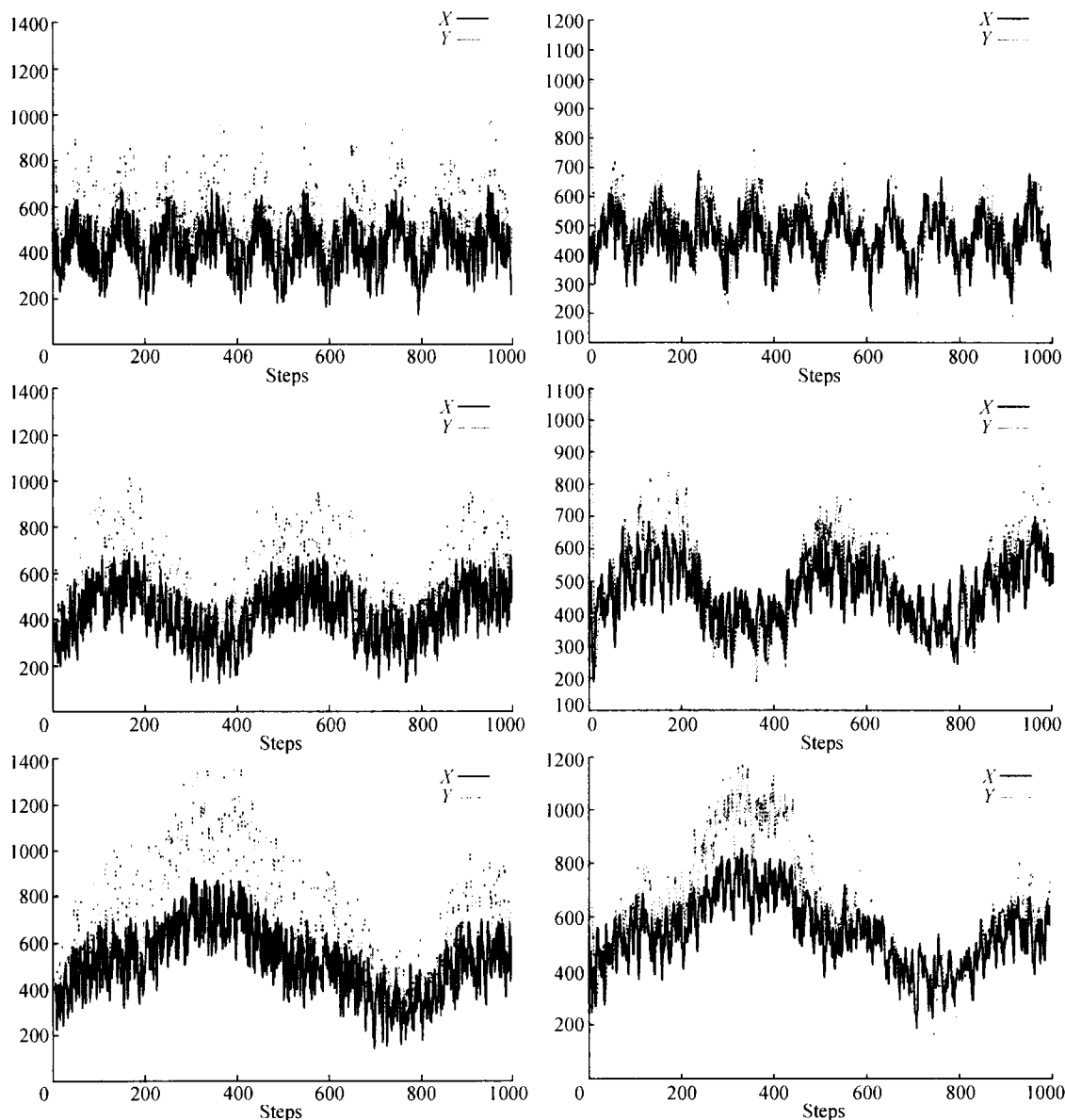


Fig. 2. Cycle of length 2 (top), cycle of length 4 (middle), cycle of length 8 (bottom) inside patch 2 (left column) and patch 4 (right column).

Finally, in Fig. 3 we represent the phase space of patch 4 for the stochastic feeding strategy (top) and for the feeding cycle of length 4 (bottom). Here it can be better seen how, in the first case, the population size varies in a small range of values, while in

the second case there is an effective large variation due to the seasonal differences in the availability of resources. This variation first influences the growth of preys and then, in a cascade of events, also affects the growth of predators and the dispersal.

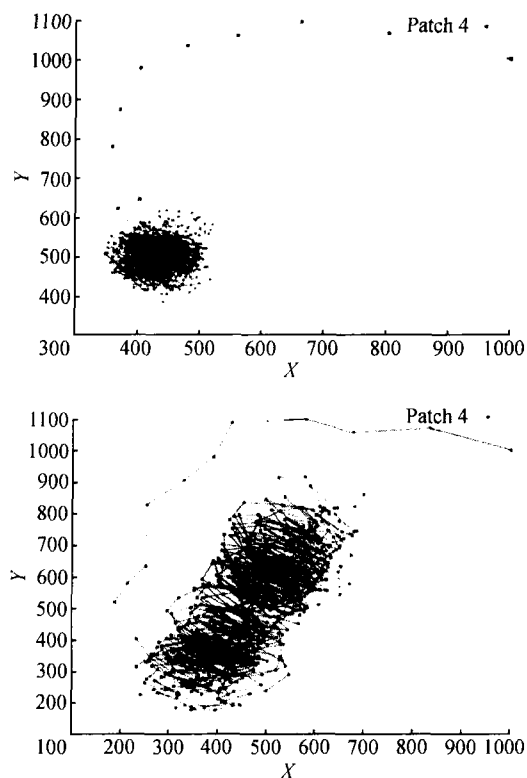


Fig. 3. Phase spaces of patch 4 with stochastic feeding (top) and with a feeding cycle of length 4 (bottom).

3 Final remarks

Dynamical probabilistic P systems were initially introduced with the aim of modelling the dynamics of biochemical and cellular systems. Nonetheless, their underlying structure and functioning are feasible also for the investigation of biological systems at a higher degree of complexity, such as ecological systems. As a particular case, we have considered metapopulation systems with 2-species predator-prey dynamics; a natural extension would be to consider ecological systems where either interaction of more species occur, or also different types of inter-species dynamics are defined.

In this paper, we have analyzed how periodic resource feeding strategies can influence metapopulation dynamics, by comparing systems where either increasing, decreasing, stationary or purely feeding stochastic phases are defined inside the patches. In particular, we have shown how the seasonal variance can transform the basic Lotka-Volterra dynamic inside each patch into a more complex dynamic, where the different phases of a feeding cycle can be identified.

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