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Winnerless competition principle and prediction of the transient dynamics in a Lotka–Volterra model

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Predicting the evolution of multispecies ecological systems is an intriguing problem. A sufficiently complex model with the necessary predicting power requires solutions that are structurally stable. Small variations of the system parameters should not qualitatively perturb its solutions. When one is interested in just asymptotic results of evolution (as time goes to infinity), then the problem has a straightforward mathematical image involving simple attractors (fixed points or limit cycles) of a dynamical system. However, for an accurate prediction of evolution, the analysis of transient solutions is critical. In this paper, in the framework of the traditional Lotka–Volterra model (generalized in some sense), we show that the transient solution representing multispecies sequential competition can be reproducible and predictable with high probability. © *2008 American Institute of Physics*. [DOI: 10.1063/1.2991108]

Evolution of an ecological system with many participants, who compete with each other, is usually a very complex process. In the transient period of evolution, which is mostly relevant for prediction purposes, some species prevail temporarily over others, thus, supporting the biodiversity of the food web. Such sequential switching between momentary winners is often characterized by irregular timing. Therefore it is impossible to predict this transient winnerless competition for a long time in complete detail. However, as we show in the framework of the traditional Lotka–Volterra (LVM) model for ecology, the main characteristic of the competitive process, i.e., temporal order of the prevalent species, can be predicted. This prediction is possible due to a compact continuum of transient trajectories in the phase space of the LVM. The behavior of these trajectories, except at early stages, is independent of the initial conditions, hence it is robust.

I. INTRODUCTION

Ecologists have been using dynamical principles to design their models and experiments since the days of Lotka, Volterra, and Gause. Nowadays, the methods of nonlinear dynamics have become the main tool for the analysis of evolution of ecological systems. Traditionally, ecological theory is mostly interested in the asymptotic states of limit sets of the food web and their stability (see, for example, Refs. 1 and 2). However, in complex ecological models, competition often does not lead to simple attractors (equilibrium or limit cycle), instead it demonstrates chaotic pulsations[3–6] or long and complex transients before reaching a limit set. In particular, great interest in transient ecological dynamics has emerged in the last 10 years.[5,7–10] Generally speaking, winners in such multispecies competition cannot be predictable since, due to dynamical interactions, different species become temporary winners in different time intervals. The sequential switching from one group of the predominant species (metastable state) to another depends on the interaction with the environment: different environmental conditions lead to different temporal sequences (transients). This is called transient winnerless competition (TWLC).[12–16] According to TWLC dynamics lifetimes (temporal duration) of the metastable states are a random value. Nevertheless the order of the sequential switching from one winner to another can be reproducible.

It is important to emphasize that competition without a winner is a widely known phenomenon in systems that involve three interacting agents that satisfy a relationship similar to the voting paradox or the popular game rock-paper-scissor. Such interactions lead to nontransitive competition or cyclic behavior. The mathematical image of it is a stable heteroclinic cycle. For ecological systems with nontransitive competition the critical point is the spatial structurization of the certain communities. In particular, recent experiments with three populations of *Escherichia coli*[11] showed that nontransitivity and spatial structurization are both necessary for the evolution of restrain in the biofilms.

In this paper we consider the transitive (or transient) competition in complex ecological systems with many interacting species. The prediction of the evolution is possible if two conditions are satisfied: (i) the dynamical model of the ecological network is structurally stable, and (ii) the transient solution corresponding to the evolutionary process loses its dependence on the initial conditions in a short period of time. We suppose that the generalized Lotka–Volterra model is valid for the description of the evolution of N competitive species and we show based on Refs. 17 and 18 that it is possible to make some predictions about food web evolution.

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The noise determines the "exit time" from a saddle vicinity, i.e., the metastable set. In Ref. 19 the authors have proposed a theoretical description of reproducible transient dynamics based on the interaction of competitive agents (species). The mathematical image of such transient evolution, in many situations, is a stable heteroclinic channel (SHC), i.e., a set of trajectories in the vicinity of a heteroclinic skeleton that consists of saddles (metastable sets) and an unstable manifold that connects their surroundings. For the generalized multidimensional Lotka–Volterra model in Ref. 19 it has been proved that the topology and sequence of the metastable sets of a SHC does not depend on small changes in parameters. The SHC is a structurally stable object. Such reproducibility means that a prediction of transient competitive dynamics is possible.

In a more general (pluralistic) case, metastable sets have a multidimensional unstable manifold. For such cases the trajectories manifest a prescribed sequence of switchings only in the presence of noise. The mathematical image of a corresponding sequence is a generalized heteroclinic channel (GHC). In this paper we present the first results about the predictability of the competitive transients for the generalized Lotka–Volterra model in the case when saddles have multidimensional unstable manifolds.

II. GENERALIZED LOTKA–VOLTERRA MODEL (GLVM): TRANSIENT COMPETITION

We are going to investigate a transient multispecies competition in the framework of the following form of GLVM:

$$\frac{da_i}{dt} = a_i\left[\sigma_i(\mathbf{E}) + \eta_i(t) - \sum_j^n \rho_{ij} a_j\right]. \tag{1}$$

Here each $a_i(t) \geqslant 0$ represents an instantaneous density of the ith species, $\rho_{ij} \geqslant 0$ is the interaction strength between species i and j, $\sigma_i(\mathbf{E})$ is the growth rate for species i that depends on the environmental parameter $\mathbf{E}$ (σ_i/ρ_{ii} is the overall carrying capacity of species i in the absence of the other species); η_i is environmental noise. The product $a_i[\sigma_i(\mathbf{E})+\eta_i(t)]$ determines the interaction of the species i with the environment. We will consider a nonsymmetrical species interaction, $\rho_{ij} \neq \rho_{ji}$. The role of nonsymmetry for the stability of food webs has been considered in Ref. 20. Here we also assume complex interactions as in Refs. 21 and 22.

The phase space of the system (1) is bounded by the manifolds $\{a_i = 0\}$, which are included in the phase space.

Let us focus on the region in the control parameter space, where, in the absence of noise, all nontrivial equilibria (fixed points) $a_i^0 = \sigma_i/\rho_{ii} > 0$, $a_j^0 = 0$, $j \neq i$, on the a_i-axis are saddles. In this region long multispecies transients (i.e., biodiversity) may exist. The necessary conditions for these are the following: for each increment i, i.e., the eigenvalues of the matrix of the linearized at the equilibrium $(0\cdots 0\sigma_i 0 \cdots 0)$, there is at least one positive: $\sigma_j - \rho_{ji}\sigma_i > 0$.

Each saddle has one or m dimensional unstable separatrix (manifold), $m < N-2$. The unstable separatrix connects the previous saddle with the next one (or the saddle with a stable equilibrium). For multispecies competition, the existence of heteroclinic sequences (that consist of saddles and heteroclinic trajectories connecting them) in the phase space is a structurally stable and a very general phenomenon.

From the theoretical point of view, the prediction of the species evolution in some ecological niche means the analysis of the transient trajectories that represent the competition inside this niche in the phase space of the model. Thus, the goal of our paper is to answer the following question: What are the conditions of the parameters of Eq. (1) that guarantee the reproducibility of such transients. The reproducibility of the transient behavior implies that the system, in a neighborhood of a transient trajectory, mostly forgets the initial conditions. Reproducibility, together with the structural stability of the transients, makes the prediction possible. Such prediction, however, cannot be deterministic. First, since we consider the multidimensional unstable saddle manifold case, the next saddle cannot be uniquely determined, and second, even in the case of one-dimensional unstable separatrices the time that the system spends in the vicinity of the saddle ("exit time") is a random variable. The expected exit value, τ_e, is estimated in Refs. 23 and 24 (provided that an initial point is chosen on the stable manifold) as

$$\tau_e = \frac{1}{\lambda} \ln\left(\frac{1}{|\eta|}\right), \tag{2}$$

where λ is a maximal positive eigenvalue of the matrix of the linearized system at the saddle equilibriums, and $|\eta|$ is a level of noise. In Ref. 19, we analyzed the mathematical image of the transients generated by one-dimensional unstable manifolds which is a stable heteroclinic channel (SHC). Here we analyze more realistic cases with two- and three-dimensional unstable saddle manifolds. The dynamics of transients in these cases are more complex and become similar to SHC in the presence of noise. We name the mathematical image of such transient dynamics the generalized heteroclinic channel (GHC).

Predictability of the transitive competition means that it is possible to predict the sequential order of the temporal winners in the real evolutionary process. Note that it is impossible to predict the temporal characteristics of such sequence. To connect the robust transient solution generated by the dynamical model with the real ecological process we have to know the connectivity matrix. In principle, such matrix can be calculated based on the experimental data (see Sec. VI). If the growth rates are fixed, then the numbers of unstable directions of the metastable states are determined by the elements of the connectivity matrix. Since the time that the system spends in the vicinity of the saddles is not predictable due to the presence of noise [see Eq. (2)], the exact time scale of the ecological evolution cannot be determined in the framework of the discussed model and needs a probabilistic description. Our modeling confines the uncertainty to the switching times, and leaves the sequential order of the species predictable.

III. GENERALIZED HETEROCLINIC CHANNEL (GHC)

In Ref. 19 a definition of SHC was presented. A SHC is a tube consisting of pieces of trajectories that travel from a small neighborhood of one saddle point to another, and a finite collection of these saddle equilibria is ordered in a prescribed way. From the neighborhood of the saddle equilibria, each trajectory follows the unstable one-dimensional separatrix until it reaches the neighborhood of the next saddle. To get a SHC one must impose conditions on the saddle: each of them must be dissipative and have a one-dimensional unstable manifold. The occurrence of a SHC in a system is a structurally stable event, which means that it persists being subjected to an action of a small noise. The motion in a SHC can be described as a sequence of switching among saddle equilibria.

For multidimensional unstable manifolds the trajectories arriving into a neighborhood of a saddle have multiple choices by following any direction in the multidimensional unstable manifold. Nevertheless, the direction corresponding to the maximal positive eigenvalue of the linearized system at the equilibrium point is preferable. The preference becomes feasible if the system is subjected to the action of a small noise, such that the probability of getting closer to one of the exit points corresponding to the strongest unstable manifold is higher. Therefore, by adjusting the parameters of a system, one may organize a sequence of saddles joined by one-dimensional strongly unstable manifolds. If this behavior is achieved, we say that the system has a GHC.

Let us give mathematical definitions without considering noise.

A. Stable heteroclinic sequence for saddles with multidimensional unstable manifolds

Here we deal with a system of ordinary differential equations,

$$\dot{x} = X(x), \quad x \in \mathfrak{R}^d, \tag{3}$$

where the vector field X is C^2-smooth. We assume that the system (3) has N equilibria $Q_1, Q_2, \ldots, Q_N$, such that each Q_i is a hyperbolic point of saddle-type with one-dimensional strongly unstable manifold $W^u_{Q_i}$, that consists of Q_i and two "separatrices," the connected components of $W^u_{Q_i} \setminus Q_i$ which we denote by Γ_i^+ and Γ_i^-. This manifold corresponds to the maximal positive eigenvalue of the linearized at Q_i system (3). We assume also that

$$\Gamma_i^+ \subset W^s_{Q_{i+1}}, \tag{4}$$

the stable manifold of Q_{i+1}.

Definition 1: The set $\Gamma := \cup_{i=1}^N Q_i \cup_{i=1}^{N-1} \Gamma_i^+$ is called the heteroclinic sequence (HS). Denote by $\lambda_1^{(i)}, \ldots, \lambda_d^{(i)}$ the eigenvalues of the matrix $\mathcal{D}X|_{Q_i}$. By the assumption above, at least one of the eigenvalues is positive. Without loss of generality one can assume that they are ordered in such a way that

$$\lambda_1^{(i)} > \cdots \geqslant \mathrm{Re}\,\lambda_{m_i}^{(i)} > 0 > \mathrm{Re}\,\lambda_{m_i+1}^{(i)} \geqslant \geqslant \cdots \geqslant \mathrm{Re}\,\lambda_d^{(i)}. \tag{5}$$

The number

$$\nu_i = \frac{-\mathrm{Re}\,\lambda_{m_i+1}^{(i)}}{\lambda_1^{(i)}}$$

is called the saddle value.

Definition 2: The heteroclinic sequence Γ is called the stable heteroclinic sequence (SHS) if

$$\nu_i > 1, \quad i = 1, \ldots, N.$$

For $m_i=1$ this definition coincides with the definition of SHS in Ref. 13. If $m_i=1$, the conditions imply stability of Γ, in the sense that every trajectory, started at a point in a vicinity of Q_1, remains in a neighborhood of Γ until it comes to a neighborhood of Q_N. In fact, the motion along this trajectory can be treated as a sequence of switchings between the equilibria Q_i, $i=1,2,\ldots,N$. If $m_i > 1$, then some amount of stability remains to be feasible if we subject the system (3) to the action of a small noise, see below.

We conjecture: if a system (3) has a SHS, then being subjected to the influence of small noise, it will manifest the occurrence of GHC. For the system (1), the conjecture is confirmed numerically as shown below.

Of course, the condition $\Gamma_i^+ \subset W^s_{Q_{i+1}}$ indicates the fact that the system (3) is not structurally stable and can only be realized either for exceptional values of parameters or for systems of a special form. As an example of such a system one may consider the model (1) that under some conditions on its parameters will generate GHC.

IV. SHS IN GLVM IN THE ABSENCE OF NOISE

Selection of saddles. We are dealing now with the system (1) in the absence of noise. We look for the conditions under which the system has a SHS consisting of saddles $\mathbf{S}_k = (0,\ldots,0,\sigma_{i_k},0,\ldots,0)$ linked by heteroclinic trajectories, $k=1,\ldots,N \leqslant n$. The saddles $\mathbf{S}_k$ have the following increments (eigenvalues of the linearized system at $\mathbf{S}_k$): $\sigma_j - \rho_{j i_k}\sigma_{i_k}$, $j \neq i_k$, and $-\sigma_{i_k}$.[13]

The saddles $\mathbf{S}_k = (0,\ldots,0,\sigma_{i_k},0,\ldots,0)$, $k=2,\ldots,N$ are selected in such a way that: there are $m_{i_k}-1$ positive eigenvalues, $m_{i_k} > 1$, one of them is maximal, and the rest, are negative. Then the following inequalities are verified:

$$\sigma_{i_{k+1}} - \rho_{i_{k+1} i_k}\sigma_{i_k} > \sigma_{i^{(2)}_{k+1}} - \rho_{i^{(2)}_{k+1} i_k}\sigma_{i_k} > \cdots > \sigma_{\beta_{k+1}} - \rho_{\beta_{k+1} i_k}\sigma_{i_k} > 0, \tag{6}$$

where $\beta_{k+1} = i_{k+1}^{m_{i_k}-1}$, and the other eigenvalues are negative.

Heteroclinic connections. To assure that there is a heteroclinic orbit $\Gamma_{i_{k-1} i_k}$ joining $\mathbf{S}_{k-1}$ and $\mathbf{S}_k$, the following condition has to be satisfied:

$$1 - \rho_{i_{k-1} i_k}\rho_{i_k i_{k-1}} \neq 0. \tag{7}$$

This orbit belongs to the plane $P_{i_{k-1} i_k} = \cap_{j \neq i_{k-1}, i_k}^n \{a_j = 0\}$, where the point $\mathbf{S}_k$ has a one-dimensional strongly unstable direction (determined by i_{k+1}). This fact can be shown in the same way as for the one-dimensional unstable direction.[13] Indeed, the restriction of Eq. (1) on the plane $P_{i_{k-1} i_k}$ has the form that is independent of the dimension of the unstable manifold.

Leading directions. Under the following conditions:

$$-\sigma_{i_k} < \sigma_{i_{k-1}} - \rho_{i_{k-1}i_k}\sigma_{i_k} < 0 \tag{8}$$

and

$$\sigma_i - \rho_{ii_k}\sigma_{i_k} < \sigma_{i_{k-1}} - \rho_{i_{k-1}i_k}\sigma_{i_k}, \tag{9}$$

the separatrix $\Gamma_{i_{k-1}i_k}$ comes to $\mathbf{S}_k$ following a leading direction, transversal to the a_{i_k}-axis on the plane $P_{i_{k-1}i_k}$, where we use the same arguments given in Ref. 13.

Dissipativity of saddles. The saddle value

$$\nu_{i_k} = \frac{\rho_{i_{k-1}i_k}\sigma_{i_k} - \sigma_{i_{k-1}}}{\sigma_{i_{k+1}} - \rho_{i_{k+1}i_k}\sigma_{i_k}}, \tag{10}$$

is defined for every saddle $\mathbf{S}_k$. We assume that

$$\nu_{i_k} > 1, \quad k=1,\dots,N. \tag{11}$$

It means that every saddle $\mathbf{S}_k$ is "dissipative."

It was shown in Ref. 13 that if $m_{i_k}=1$ for every k, i.e., if all saddles have one-dimensional unstable manifolds, then under the conditions above, the SHS consisting of the saddles $\mathbf{S}_k$ and joining the separatrices $\Gamma_{i_{k-1}i_k}$ is stable in the following sense: if one chooses a positive initial condition in a small neighborhood of $\mathbf{S}_0$, the trajectory going through it will follow the sequence $\{\Gamma_{i_{k-1}i_k}\}$, staying in a small vicinity of them until it comes to a neighborhood of the last saddle $\mathbf{S}_N$.

We show below that under these conditions the system (1) admits a GHC, for $m_{i_k}=2,3$ which corresponds to saddles with two- or three-dimensional unstable manifolds.

V. RESULTS

In this section we impose conditions on the system (1) to satisfy the assumptions of Sec. III, and we confirm the existence of a GHC.

A. Occurrence of a GHC with two-dimensional unstable manifolds

For the model (1), we reformulate the conditions stated in Sec. III to obtain the two-dimensional case.

Selection of saddles. In Sec. III the saddles $\mathbf{S}_k=(0,\dots,0,\sigma_{i_k},0,\dots,0)$, $k=2,\dots,m$, belonging to a SHS, are selected in such a way that there are two positive eigenvalues with one of then being maximal, such that

$$\sigma_{i_{k+1}} - \rho_{i_{k+1}i_k}\sigma_{i_k} > \sigma_{i^{(2)}_{k+1}} - \rho_{i^{(2)}_{k+1}i_k}\sigma_{i_k} > 0, \qquad i^{(2)}_{k+1} \neq \{i_{k-1},i_k,i_{k+1}\}, \tag{12}$$

and the other eigenvalues are negative,

$$\sigma_i - \rho_{ii_k}\sigma_{i_k} < 0, \tag{13}$$

$1 \leq i \leq n$, $i \neq \{i_k, i_{k+1}, i^{(2)}_{k+1}\}$.

Thus, all points $\mathbf{S}_k$, $2 \leq k \leq N$ are saddles with two-dimensional unstable manifolds. And since there is only one maximal eigenvalue, corresponding to the i_{k+1} direction, there is a preference of the system to evolve in that direction, with or without, the influence of a small noise.

To simplify our calculations we impose the following conditions on the parameters:

$$\frac{\sigma_{i_{k-1}}}{\sigma_{i_k}} + 1 > \rho_{i_{k-1}i_k} > \frac{\sigma_{i_{k-1}}}{\sigma_{i_k}}, \tag{14}$$

$$\frac{\sigma_{i_{k+1}}}{\sigma_{i_k}} > \rho_{i_{k+1}i_k} > \frac{\sigma_{i_{k+1}}}{\sigma_{i_k}} - 1, \tag{15}$$

$$\frac{\sigma_{i^{(2)}_{k+1}}}{\sigma_{i_k}} > \rho_{i^{(2)}_{k+1}i_k} > \frac{\sigma_{i^{(2)}_{k+1}}}{\sigma_{i_k}} - \frac{\sigma_{i_{k+1}}}{\sigma_{i_k}} + \rho_{i_{k+1}i_k}, \quad i^{(2)}_{k+1} \neq \{i_{k-1},i_k,i_{k+1}\}, \tag{16}$$

$$\rho_{ii_k} > \rho_{i_{k-1}i_k} + \frac{\sigma_i - \sigma_{i_{k-1}}}{\sigma_{i_k}}, \tag{17}$$

$1 \leq i \leq n$, $i \neq \{i_{k-1}, i_k, i_{k+1}, i^{(2)}_{k+1}\}$.

Therefore, for the simulation procedure, the following values are appropriate:

$$\rho_{i_{k-1}i_k} = \frac{\sigma_{i_{k-1}}}{\sigma_{i_k}} + 0.51, \tag{18}$$

$$\rho_{i_{k+1}i_k} = \frac{\sigma_{i_{k+1}}}{\sigma_{i_k}} - 0.5 \tag{19}$$

and having set the value for Eq. (19), we have

$$\rho_{i^{(2)}_{k+1}i_k} = \frac{\sigma_{i^{(2)}_{k+1}}}{\sigma_{i_k}} - 0.25, \quad i^{(2)}_{k+1} \neq i_{k+1}, \tag{20}$$

$$\rho_{ii_k} = \rho_{i_{k-1}i_k} + \frac{\sigma_i - \sigma_{i_{k-1}}}{\sigma_{i_k}} + 2, \tag{21}$$

for $1 \leq i \leq n$, $i \neq \{i_{k-1}, i_k, i_{k+1}, i^{(2)}_{k+1}\}$.

We have checked that the conditions (14)–(17) imply the conditions of Sec. III (see the Appendix).

Ten sets of 100 simulations of the dynamics of GLVM were performed, where the integration was performed using the Milstein integration scheme,[25] with $n=25$ and $N=8$, and multiplicative noise level of $5\cdot 10^{-4}$. The growth rates σ_i were set to be random numbers taken uniformly from the interval (5, 10) and kept for each set of 100 simulations with a variation smaller than $\pm 10^{-4}$. Initial conditions for $a_i(t)$ were set randomly but uniformly from (0, 0.001), except for $a_0(0)$, that was set to be equal to $\sigma_0 - 0.01$. An illustrative example is shown in Fig. 1.

In Fig. 2 we present the statistics of several runs as displayed in Fig. 1. We observed in this first run, that the occurrence of the whole sequence is of 54% and its median is 66.5, which seemed to be very low. We noted the cases when the sequence would not appear, then a new experiment was carried out, with the same exact parameters, but with the additional condition that $i^{(2)}_{k+2} \neq i^{(2)}_{k+1}$ (see Fig. 3), which means that there will not be trajectories belonging to the unstable manifolds of $\mathbf{S}_{k+1}$ and $\mathbf{S}_{k+2}$ that go to the same equilibrium,

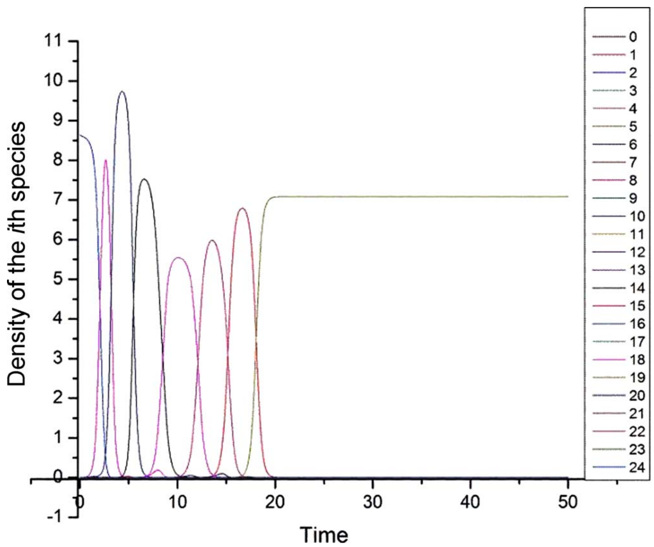

FIG. 1. (Color online) Illustrative example of a single run for a total of 25 variables and eight saddles connected following the sequence 2, 4, 6, 14, 18, 22, 1,5. It is a sequence of partially reproducible states (compare to Ref. 6).

even though we also noticed that when $i^{(2)}_{k+1}=i^{(2)}_{k+2}$, it does not necessarily mean that the sequence will not appear.

In Fig. 4 we observe that the occurrence of the whole sequence is of 81.1% and its median is 95. The results improved by 27.1% and the median went very close to 100. We believe that this is because the condition $i^{(2)}_{k+1}=i^{(2)}_{k+2}$ causes such an influence that the system will evolve to equilibria different from the ones in the expected sequence. Eventually it gets back to a last portion of the expected sequence, and by avoiding this condition, there is a minor probability for that kind of deviation to happen.

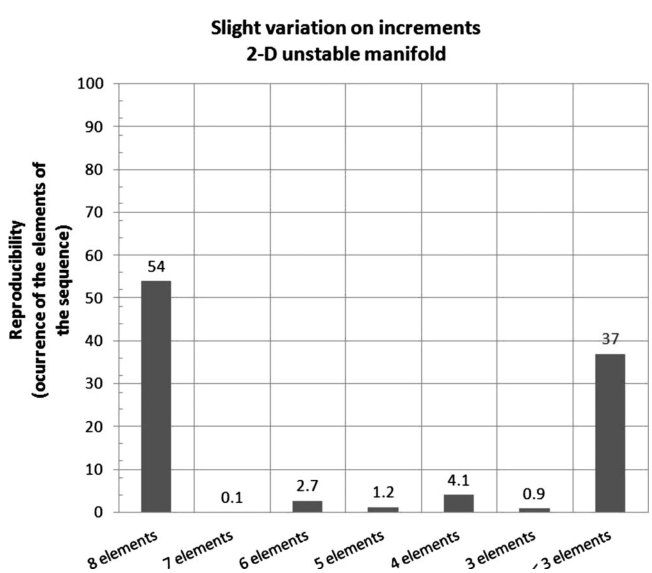

FIG. 2. Reproducibility level with two-dimensional unstable manifolds. Here it is represented by the average of the ten trials with 100 runs each. The distribution is bimodal meaning that the system may recover the whole sequence (occurrence of the eight elements) or just go through the last few steps of the sequence.

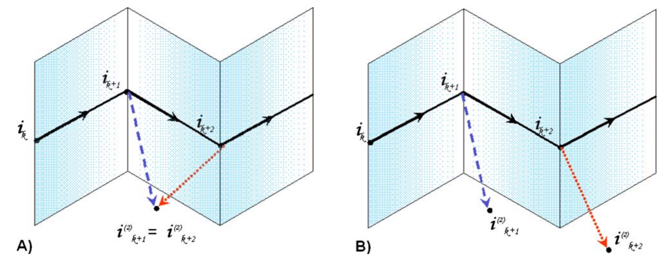

FIG. 3. (Color online) (a) There are heteroclinic trajectories joining the saddles $\mathbf{S}_{k+1}$ and $\mathbf{S}_{k+2}$ and another (the same) equilibrium. (b) There are no trajectories belonging to the unstable manifolds of $\mathbf{S}_{k+1}$ and $\mathbf{S}_{k+2}$ that go to the same equilibrium.

B. Occurrence of a GHC with three-dimensional unstable manifolds

For the model (1), we reformulate the conditions described in Sec. III to have the three-dimensional case.

Selection of saddles. We refer to Sec. III, where it was shown that the saddles $\mathbf{S}_k=(0,\ldots,0,\sigma_{i_k},0,\ldots,0)$, $k=2,\ldots,m$, belonging to a SHS are selected in such a way that there are three positive eigenvalues instead of two, one of which is maximal. Provided that, in addition to Eq. (12) we have

$$\begin{aligned}&\sigma_{i_{k+1}}-\rho_{i_{k+1}i_k}\sigma_{i_k}>\sigma_{i^{(3)}_{k+1}}-\rho_{i^{(3)}_{k+1}i_k}\sigma_{i_k}>0,\\ &i^{(3)}_{k+1}\neq\{i_{k-1},i_k,i_{k+1},i^{(2)}_{k+1}\},\end{aligned}\tag{22}$$

and the other eigenvalues are negative

$$\sigma_i-\rho_{ii_k}\sigma_{i_k}<0,\tag{23}$$

$1\leqslant i\leqslant n$, $i\neq\{i_k,i_{k+1},i^{(2)}_{k+1},i^{(3)}_{k+1}\}$.

Thus, all points $\mathbf{S}_k$, $2\leqslant k\leqslant N$ are saddles with three-dimensional unstable manifolds. And again, since there is

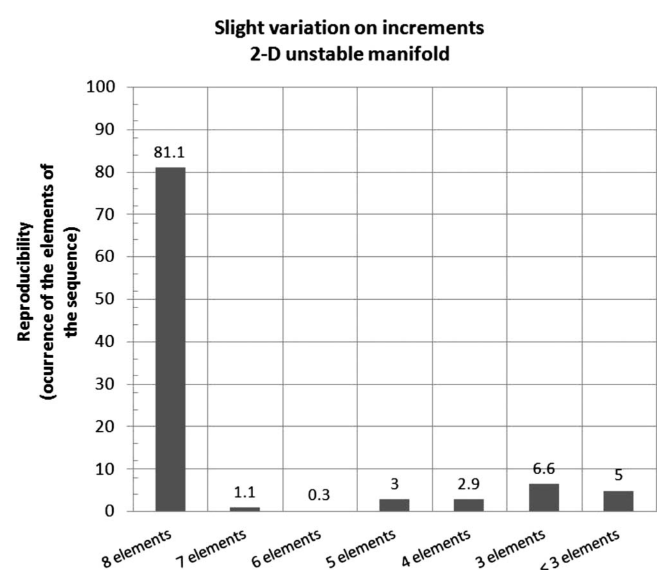

FIG. 4. Reproducibility level with two-dimensional unstable manifolds by avoiding manifold collision as shown in Fig. 3. The reproducibility level increases notably by introducing a repulsion mechanism in the matrix construction with the additional condition: $i^{(2)}_{k+2}\neq i^{(2)}_{k+1}$. Again, it is represented the average of the ten trials with 100 runs each. The distribution is bimodal in the same sense as Fig. 2.

only one maximal eigenvalue, corresponding to the i_{k+1} direction, there is a preference of the system to evolve in that direction that is well manifested under the influence of a small noise.

In the same way as for the two-dimensional case, we impose the following conditions on the parameters of the system (1): it can be verified in the same way as for the two-dimensional case that these conditions imply the fact that all saddles in the sequence have the three-dimensional unstable manifolds,

$$\frac{\sigma_{i_{k-1}}}{\sigma_{i_k}} + 1 > \rho_{i_{k-1}i_k} > \frac{\sigma_{i_{k-1}}}{\sigma_{i_k}}, \tag{24}$$

$$\frac{\sigma_{i_{k+1}}}{\sigma_{i_k}} > \rho_{i_{k+1}i_k} > \frac{\sigma_{i_{k+1}}}{\sigma_{i_k}} - 1, \tag{25}$$

$$\begin{gathered}\frac{\sigma_{i^{(2)}_{k+1}}}{\sigma_{i_k}} > \rho_{i^{(2)}_{k+1}i_k} > \frac{\sigma_{i^{(2)}_{k+1}}}{\sigma_{i_k}} - \frac{\sigma_{i_{k+1}}}{\sigma_{i_k}} + \rho_{i_{k+1}i_k},\\ i^{(2)}_{k+1} \neq \{i_{k-1}, i_k, i_{k+1}\},\end{gathered} \tag{26}$$

$$\begin{gathered}\frac{\sigma_{i^{(3)}_{k+1}}}{\sigma_{i_k}} > \rho_{i^{(3)}_{k+1}i_k} > \frac{\sigma_{i^{(3)}_{k+1}}}{\sigma_{i_k}} - \frac{\sigma_{i_{k+1}}}{\sigma_{i_k}} + \rho_{i_{k+1}i_k},\\ i^{(3)}_{k+1} \neq \{i_{k-1}, i_k, i_{k+1}, i^{(2)}_{k+1}\},\end{gathered} \tag{27}$$

$$\rho_{ii_k} > \rho_{i_{k-1}i_k} + \frac{\sigma_i - \sigma_{i_{k-1}}}{\sigma_{i_k}}, \tag{28}$$

$1 \leqslant i \leqslant n$, $i \neq \{i_{k-1}, i_k, i_{k+1}, i^{(2)}_{k+1}, i^{(3)}_{k+1}\}$.

Therefore, for the simulation procedure, the next values are appropriate,

$$\rho_{i_{k-1}i_k} = \frac{\sigma_{i_{k-1}}}{\sigma_{i_k}} + 0.51, \tag{29}$$

$$\rho_{i_{k+1}i_k} = \frac{\sigma_{i_{k+1}}}{\sigma_{i_k}} - 0.5 \tag{30}$$

and having set the value for Eq. (30), we have

$$\rho_{i^{(2)}_{k+1}i_k} = \frac{\sigma_{i^{(2)}_{k+1}}}{\sigma_{i_k}} - 0.25, \quad i^{(2)}_{k+1} \neq \{i_{k-1}, i_k, i_{k+1}\}, \tag{31}$$

$$\rho_{i^{(3)}_{k+1}i_k} = \frac{\sigma_{i^{(3)}_{k+1}}}{\sigma_{i_k}} - 0.25, \quad i^{(3)}_{k+1} \neq \{i_{k-1}, i_k, i_{k+1}, i^{(2)}_{k+1}\}, \tag{32}$$

$$\rho_{ii_k} = \rho_{i_{k-1}i_k} + \frac{\sigma_i - \sigma_{i_{k-1}}}{\sigma_{i_k}} + 2, \tag{33}$$

for $1 \leqslant i \leqslant n$, $i \neq \{i_{k-1}, i_k, i_{k+1}, i^{(2)}_{k+1}, i^{(3)}_{k+1}\}$.

To verify the reproducibility of the GHC with three-dimensional unstable manifolds, we performed an experiment with ten sets of 100 simulations each. There, we used

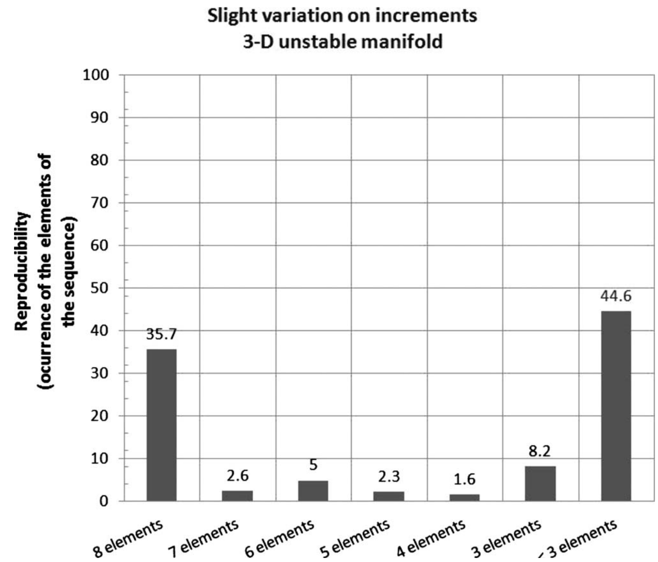

FIG. 5. Reproducibility level with three-dimensional unstable manifolds. Here it represented the average of the ten trials with 100 runs each. The distribution is bimodal meaning that the system may recover the whole sequence (occurrence of the eight elements) or just go through the last few steps of the sequence.

the same parameters as for the two-dimensional unstable manifold case. Figure 5 displays the obtained results.

We observe that we obtained 35.7% of reproducibility with median 42.5. With the previous experience of the two-dimensional case, and with similar observations, we carried out a new experiment with the same exact parameters but with the additional condition: $[i^{(2)}_{k+2}, i^{(3)}_{k+2}] \neq [i^{(2)}_{k+1}, i^{(3)}_{k+1}]$ (see Fig. 6), with the purpose of avoiding the behavior when the system evolves to equilibria different from the ones in the expected sequence. And again, the results improved remarkably as seen in Fig. 7.

Here we observe that we obtained 74.2% of reproducibility with median 93. The results improved in 38.5%, and again, the median went very close to 100. Similar observations to the two-dimensional case are made.

So, the main result of the article is that the reproducibility occurs with a high probability in spite of the multidimensionality of the saddle manifolds in heteroclinic sequences.

We obtain the following observation. When choosing the nonmaximal positive eigenvalues, the additional restrictions $i^{(2)}_{k+2} \neq i^{(2)}_{k+1}$ for the two-dimensional case (see Fig. 3), and $[i^{(2)}_{k+2}, i^{(3)}_{k+2}] \neq [i^{(2)}_{k+1}, i^{(3)}_{k+1}]$ for the three-dimensional case (see Fig. 6), are not necessary for the sequence to appear, but they improve the probability of occurrence of the expected sequence remarkably.

As we can see, the probability to observe the full sequence is much higher in the last case. Currently, we do not have an explanation for this fact.

VI. DISCUSSION

In the last decade, theoretical ecologists have envisioned a new role for the transient solutions of models of the ecological system.[5,7–10] Transient dynamics plays an even more important role, than the simple attractors, such as stable

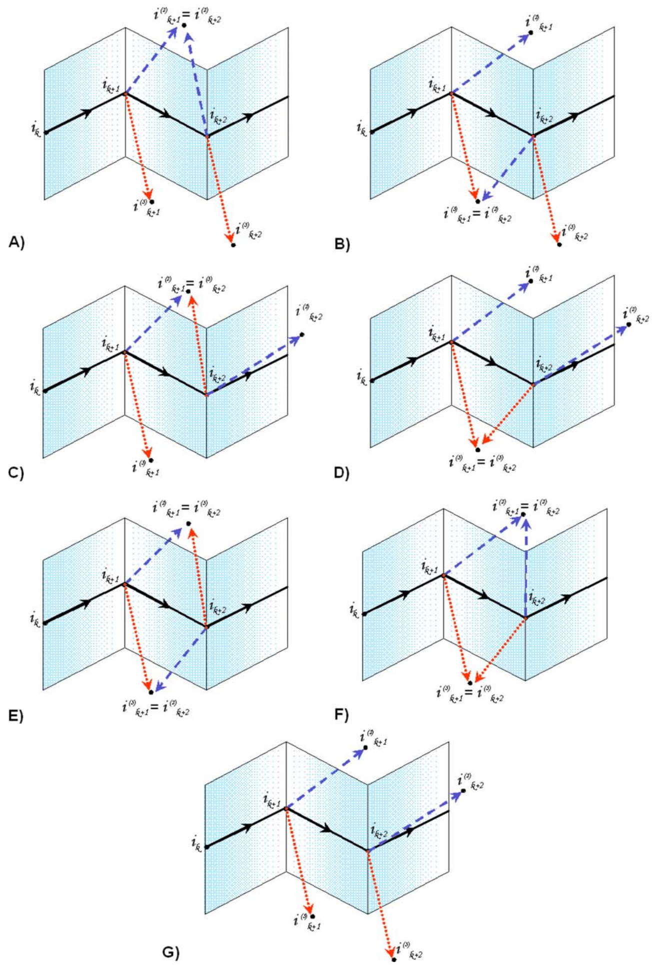

FIG. 6. (Color online) For the three-dimensional case, A–F correspond to the situation of Fig. 3(a), and G corresponds to Fig. 3(b).

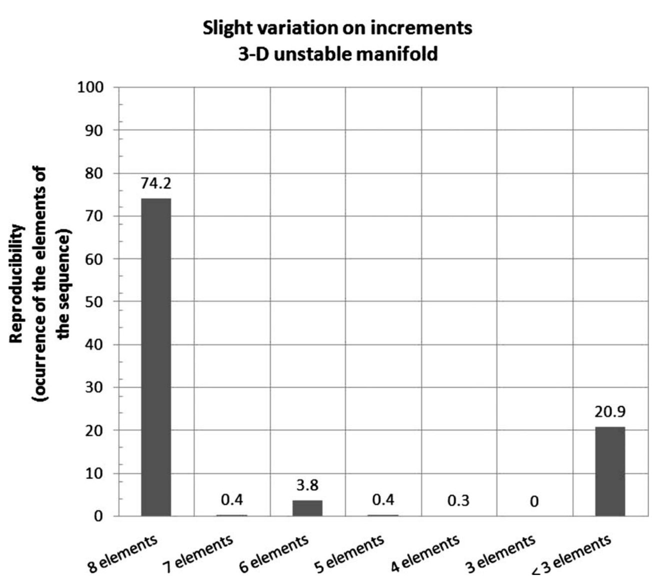

FIG. 7. Reproducibility level with three-dimensional unstable manifolds by avoiding manifold collisions as shown in Fig. 6. The reproducibility level increases notably by introducing a repulsion mechanism in the matrix construction with the additional condition: $[i^{(2)}_{k+2}, i^{(3)}_{k+2}] \neq [i^{(2)}_{k+1}, i^{(3)}_{k+1}]$. Again, it is represented by the average of the ten trials with 100 runs each. The distribution is bimodal in the same sense as Fig. 5.

steady state solution (fixed points) and limit cycles, for the understanding and predicting of natural ecological processes. There are at least two reasons for this: (i) the stable solutions do not necessarily exist in a multidimensional system with realistic values of control parameters, and (ii) if such solutions exist, the basin of their attraction in the phase space could be not large enough to keep the system in the vicinity of the stable solution in the presence of environmental perturbations. Thus, the transients (solutions that precede the simple attractors or substitute them) are key objects that we have to analyze to understand natural ecological systems.

It is important to emphasize that many kinds of dynamical phenomena (like winnerless competition and stable transient), which would be nongeneric in an arbitrary complex dynamical system, can become generic when constrained by specific variables. For GLVM, such specificity is in the positive value of the variables. It is also worth mentioning that the Lotka–Volterra model in a high dimensional space may display different types of dynamical behavior as Milnor or fragile attractors.[31] The conditions analyzed here were set to form stable heteroclinic channels. However, it is likely that within this complex system and for another set of parameters one can find Milnor or fragile attractors. It is an interesting problem for the future to investigate the conditions for their existence and compare them to the SHCs.

In this paper, we have analyzed a new dynamical object that exists in the phase space of the multidimensional generalized Lotka–Volterra model of n competitive species. The GHC is in some sense an image of predictable ecological transients. GHC is a set with a complex structure that can exist in two forms: a) dissipative sticky set, i.e., heteroclinic chain that ends in the simple attractor, and b) strange heteroclinic attractor.[17] Both forms of GHC are characterized by specific chaotic patterns with ordered switching between temporal winners and irregular temporal duration of the "winner's time." The observed phenomenon—stable complex transients (or chaotic heteroclinic attractor)—can be a dynamical origin of the sequential coexistence of the food webs that is associated with stability and persistence in complex ecosystems.[20]

The food web, as a network of dynamical systems, is not just a dynamical system with a high-dimensional phase space. It is also equipped with a canonical set of observables—the states of the individual nodes of the network and network motifs.[26–29]

It has been recently observed in a unique long-term experiment with a plankton community that the population dynamics was characterized by positive Lyapunov exponents.[30] It would be interesting to check, based on these data, not a prediction of the time evolution of the different species, which can be fundamentally impossible,[30] but to check the reproducibility just to the order of the prevalent species in the evolutionary sequence.

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APPENDIX: INEQUALITIES FOR THE SIMULATION PROCEDURE

From Eq. (13), we take $i=i_{k-1}$ and Eq. (8) and we have

$$\sigma_{i_{k-1}} - \rho_{i_{k-1}i_k}\sigma_{i_k} < 0 < \sigma_{i_{k-1}} + \sigma_{i_k} - \rho_{i_{k-1}i_k}\sigma_{i_k},$$

$$\sigma_{i_{k-1}} < \rho_{i_{k-1}i_k}\sigma_{i_k} < \sigma_{i_{k-1}} + \sigma_{i_k}, \tag{A1}$$

$$\frac{\sigma_{i_{k-1}}}{\sigma_{i_k}} < \rho_{i_{k-1}i_k} < \frac{\sigma_{i_{k-1}}}{\sigma_{i_k}} + 1.$$

We assume $\nu_{i_k} > 1$, $k=1,\ldots,N$, i.e., the saddles are dissipative. Then $\lambda_k > 1$ is satisfied, and then

$$\nu_{i_k} = \frac{\rho_{i_{k-1}i_k} - \sigma_{i_{k-1}}}{\sigma_{i_{k+1}} - \rho_{i_{k+1}i_k}\sigma_{i_k}} > 1, \tag{A2}$$

and from Eqs. (A2) and (12), we have

$$\rho_{i_{k-1}i_k}\sigma_{i_k} - \sigma_{i_{k-1}} > \sigma_{i_{k+1}} - \rho_{i_{k+1}i_k}\sigma_{i_k} > \sigma_{i^{(2)}_{k+1}} - \rho_{i^{(2)}_{k+1}i_k}\sigma_{i_k},$$

$$\rho_{i_{k-1}i_k}\sigma_{i_k} > \sigma_{i_{k-1}} + \sigma_{i_{k+1}} - \rho_{i_{k+1}i_k}\sigma_{i_k} > \sigma_{i_{k-1}} + \sigma_{i^{(2)}_{k+1}} - \rho_{i^{(2)}_{k+1}i_k}\sigma_{i_k}, \tag{A3}$$

$$\rho_{i_{k-1}i_k} > -\rho_{i_{k+1}i_k} + \frac{\sigma_{i_{k-1}}}{\sigma_{i_k}} + \frac{\sigma_{i_{k+1}}}{\sigma_{i_k}} > -\rho_{i^{(2)}_{k+1}i_k}\sigma_{i_k} + \frac{\sigma_{i_{k-1}}}{\sigma_{i_k}} + \frac{\sigma_{i^{(2)}_{k+1}}}{\sigma_{i_k}}.$$

From Eq. (A3), the next pair of inequalities hold,

$$\rho_{i_{k+1}i_k} > -\rho_{i_{k-1}i_k} + \frac{\sigma_{i_{k-1}}}{\sigma_{i_k}} + \frac{\sigma_{i_{k+1}}}{\sigma_{i_k}},$$

$$\rho_{i^{(2)}_{k+1}i_k} > -\rho_{i_{k-1}i_k} + \frac{\sigma_{i_{k-1}}}{\sigma_{i_k}} + \frac{\sigma_{i^{(2)}_{k+1}}}{\sigma_{i_k}}$$

and we can rewrite Eq. (A2) as follows:

$$-\rho_{i_{k-1}i_k} > -\frac{\sigma_{i_{k-1}}}{\sigma_{i_k}} - 1,$$

and combined we have the following:

$$\rho_{i_{k+1}i_k} > \frac{\sigma_{i_{k+1}}}{\sigma_{i_k}} - 1 \tag{A4}$$

and

$$\rho_{i^{(2)}_{k+1}i_k} > \frac{\sigma_{i^{(2)}_{k+1}}}{\sigma_{i_k}} - 1,$$

but we have $\rho_{i_{k+1}i_k} - \sigma_{i_{k+1}}/\sigma_{i_k} > -1$ from Eq. (A4), then the last inequality becomes

$$\rho_{i^{(2)}_{k+1}i_k} > \frac{\sigma_{i^{(2)}_{k+1}}}{\sigma_{i_k}} - \frac{\sigma_{i_{k+1}}}{\sigma_{i_k}} + \rho_{i_{k+1}i_k}. \tag{A5}$$

From Eq. (12) we have $\sigma_{i_{k+1}}/\sigma_{i_k} > \rho_{i_{k+1}i_k}$. With Eq. (A4) we obtain

$$\frac{\sigma_{i_{k+1}}}{\sigma_{i_k}} > \rho_{i_{k+1}i_k} > \frac{\sigma_{i_{k+1}}}{\sigma_{i_k}} - 1. \tag{A6}$$

Just as well, from Eq. (12) we have $\sigma_{i^{(2)}_{k+1}}/\sigma_{i_k} > \rho_{i^{(2)}_{k+1}i_k}$. With Eq. (A5), we obtain

$$\frac{\sigma_{i^{(2)}_{k+1}}}{\sigma_{i_k}} > \rho_{i^{(2)}_{k+1}i_k} > \frac{\sigma_{i^{(2)}_{k+1}}}{\sigma_{i_k}} - \frac{\sigma_{i_{k+1}}}{\sigma_{i_k}} + \rho_{i_{k+1}i_k}. \tag{A7}$$

And the condition (9) can be reinstated as follows:

$$\rho_{ii_k} > \rho_{i_{k-1}i_k} + \frac{\sigma_i - \sigma_{i_{k-1}}}{\sigma_{i_k}}, \tag{A8}$$

$$1 \leq i \leq n, \quad i \neq \{i_{k-1}, i_k, i_{k+1}, i^{(2)}_{k+1}\}.$$

So, the inequalities to consider for our simulation procedure satisfy Eqs. (A1) and (A6)–(A8),

$$\frac{\sigma_{i^{(2)}_{k+1}}}{\sigma_{i_k}} > \rho_{i^{(2)}_{k+1}i_k} > \frac{\sigma_{i^{(2)}_{k+1}}}{\sigma_{i_k}} - \frac{\sigma_{i_{k+1}}}{\sigma_{i_k}} + \rho_{i_{k+1}i_k}, \quad i^{(2)}_{k+1} \neq \{i_{k-1}, i_k, i_{k+1}\}, \tag{A9}$$

$$\rho_{ii_k} > \rho_{i_{k-1}i_k} + \frac{\sigma_i - \sigma_{i_{k-1}}}{\sigma_{i_k}}, \quad 1 \leq i \leq n, \quad i \neq \{i_{k-1}, i_k, i_{k+1}, i^{(2)}_{k+1}\}.$$

Therefore, for the simulation procedure, the next values are appropriate,

$$\rho_{i_{k-1}i_k} = \frac{\sigma_{i_{k-1}}}{\sigma_{i_k}} + 0.51, \tag{A10}$$

$$\rho_{i_{k+1}i_k} = \frac{\sigma_{i_{k+1}}}{\sigma_{i_k}} - 0.5 \tag{A11}$$

and having set the value for Eq. (A11), we have

$$\rho_{i^{(2)}_{k+1}i_k} = \frac{\sigma_{i^{(2)}_{k+1}}}{\sigma_{i_k}} - 0.25, \quad i^{(2)}_{k+1} \neq i_{k+1}, \tag{A12}$$

$$\rho_{ii_k} = \rho_{i_{k-1}i_k} + \frac{\sigma_i - \sigma_{i_{k-1}}}{\sigma_{i_k}} + 2, \tag{A13}$$

for $1 \leq i \leq n$, $i \neq \{i_{k-1}, i_k, i_{k+1}, i^{(2)}_{k+1}\}$.

[1] V. Bastolla, M. Lassig, S. C. Manrubia, and A. Valleriani, J. Theor. Biol. **235**, 521 (2005).
[2] M. Toro and J. Aracil, Syst. Dyn. Rev. **4**, 56 (2006).
[3] J. M. Cushing, R. F. Costantino, R. A. Desharnais, and B. Dennis, "An inordinate fondness for beetles," Foreword to *Chaos in Ecology* (Academic, New York, 2002).
[4] A. Hastings and T. Powell, Ecology **72**, 896 (1991).
[5] A. Hastings and K. Higgins, Science **263**, 1133 (1994).
[6] J. Huisman and F. J. Weissing, Am. Nat. **157**, 488 (2001).
[7] A. Hastings, Trends Ecol. Evol. **19**, 39 (2004).
[8] J. L. Green, A. Hastings, P. Arzberger, F. J. Ayala, K. L. Cottingham, K. Cuddington, F. Davis, J. A. Dunne, M.-J. Fortin, L. Gerber, and M. Neubert, BioScience **55**, 501 (2005).
[9] A. Hastings, Ecol. Lett. **4**, 215 (2001).
[10] X. Chen and J. E. Cohen, Proc. R. Soc. London, Ser. B **268**, 869 (2001).
[11] F. Prado and B. Kerr, Evaluation **62**, 538 (2008).
[12] P. Ashwin and M. Timme, Nature (London) **436**, 36 (2005).
[13] V. S. Afraimovich, V. P. Zhigulin, and M. I. Rabinovich, Chaos **14**, 1123 (2004).

[14]M. Rabinovich, A. Volkovskii, P. Lecanda, R. Huerta, H. D. I. Abarbanel, and G. Laurent, Phys. Rev. Lett. **87**, 068102 (2001).
[15]M. I. Rabinovich, R. Huerta, and P. Varona, Phys. Rev. Lett. **96**, 014101 (2006).
[16]M. Rabinovich, R. Huerta, and G. Laurent, Science **321**, 48 (2008).
[17]P. Varona, M. I. Rabinovich, A. I. Selverston, and Y. I. Arshavsky, Chaos **12**, 672 (2002).
[18]R. Huerta and M. Rabinovich, Phys. Rev. Lett. **93**, 238104 (2004).
[19]M. I. Rabinovich, R. Huerta, P. Varona, and V. S. Afraimovich, PLOS Comput. Biol. **4**, e1000072 (2008).
[20]N. Rooney, K. McCann, G. Gellner, and J. C. Moore, Nature (London) **442**, 265 (2006).
[21]V. A. A. Jansen and G. D. Kokkoris, Ecol. Lett. **6**, 498 (2003).
[22]I. D. Rozdilsky and L. Stone, Ecol. Lett. **4**, 397 (2001).
[23]Y. Kifer, Isr. J. Math. **40**, 74 (1981).
[24]E. Stone and P. Holmes, SIAM J. Appl. Math. **50**, 726 (1990).
[25]B. K. Oksendal, *Stochastic Differential Equations: An Introduction with Applications*, 4th ed. (Springer, New York, 2003).
[26]J. Camacho, D. B. Stouffer, and L. A. N. Amaral, J. Theor. Biol. **246**, 260 (2007).
[27]R. Milo, S. Shen-Orr, S. Itzkovitz, N. Kashtan, D. Chklovskii, and U. Alon, Science **298**, 824 (2002).
[28]S. R. Proulx, D. E. L. Promislow, and P. C. Phillips, Trends Ecol. Evol. **20**, 345 (2005).
[29]S. Allesina and M. Pascual, Theor Ecol **1**, 55 (2008).
[30]E. Beninca, J. Huisman, R. Heerkloss, K. D. Johnk, P. Branco, E. H. Van Nes, M. Scheffer, and S. P. Ellner, Nature (London) **451**, 822 (2008).
[31]K. Kaneko, Phys. Rev. E **66**, 055201 (2002).