

# Chaos in Low-Dimensional Lotka-Volterra Models of Competition

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## Abstract

The occurrence of chaos in basic Lotka-Volterra models of four competing species is studied. A brute force numerical search conditioned on the largest Lyapunov exponent indicates that chaos occurs in a narrow region of parameter space but, is robust to perturbations. The dynamics of the attractor are studied using symbolic dynamics, and the question of self-organized critical behavior (scale-invariance) of the solution is considered.

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Originally derived by Volterra in 1926 to describe the interaction between a predator species and a prey species and independently by Lotka in 1920 to describe a chemical reaction, the general Lotka-Volterra model can be used to model a variety of different types of systems in ecology, biology, chemistry, physics, etc. Imposing additional conditions on this general class leads to models for competitive species in which each species or agent competes for a finite set of resources. In 1976 S. Smale showed that for five or more species any asymptotic dynamic behavior is possible. However, chaotic solutions are not possible in competitive Lotka-Volterra for one, two or three species. In this paper, we examine the possibility of chaos in solutions of four species competitive Lotka-Volterra. An example of such a system which exhibits chaotic behavior is given which, to our knowledge, is the first such example in which each of the four species has its own distinct growth rate. The attractor dimension, Lyapunov exponents and symbolic dynamics of the attractor are studied. Using a parameter to represent the intra-species coupling, we also examine one route to chaos for this system. Finally, the question of self-organized critical behavior or scale-invariance of the solution is considered.

## I. INTRODUCTION

The Lotka-Volterra model [1, 2] is widely used to study the dynamics of interacting species in ecology and elsewhere [3]. We consider here the simplest form of such a system in which  $N$  species (or agents) with population  $x_i$  for  $i = 1$  to  $N$  compete for a finite set of resources according to

$$\frac{dx_i}{dt} = r_i x_i \left( 1 - \sum_{j=1}^N a_{ij} x_j \right) \quad (1)$$

with parameters  $r_i$  and  $a_{ij}$  satisfying

$$r_i > 0, \quad (2a)$$

$$a_{ij} \geq 0 \quad (2b)$$

Here the  $r_i$  represents the growth rate of species  $i$ , and  $a_{ij}$  represents the extent to which species  $j$  competes for resources used by species  $i$ . For a wide class of models [4], Eq.

(1) can also be viewed as the first approximation in a Taylor-series expansion, and under conditions (2a) and (2b) the approximation has the highly desirable feature that solutions are asymptotically bounded within  $0 \leq x_i \leq 1$ .

Without loss of generality, we can reduce the parameters  $r_i$  and  $a_{ij}$  as follows. By measuring the population of each species in units of its carrying capacity (as measured in the absence of the other species), the self-interaction terms  $a_{ii}$  can be set to 1. By measuring time in units of the inverse growth rate of species 1, the growth rate of species 1 can be set to 1.

For five or more species, i.e.  $N \geq 5$ , Smale [5] demonstrated that any asymptotic dynamic behavior is possible. In contrast, under conditions (2a) and (2b) a theorem of Hirsch [6] reduces the asymptotic dynamics of Eq. (1) to a closed invariant, attracting  $N - 1$  dimensional cell. Thus, for three or fewer species, i.e.  $N \leq 3$ , the possible asymptotic dynamics are significantly reduced; in particular, via the Poincare-Bendixson theorem [7], no chaotic solutions are possible. Hence models with exactly four species, i.e.  $N = 4$ , are the simplest examples where chaotic behavior is possible.

Using a brute-force random numerical search, we explored the 15-dimensional parameter space of competitive four-species ecologies, i.e. Eq. (1) with  $N = 4$ , for chaotic solutions. While such solutions appear to be relatively rare in this vast parameter space, parameter values such as

$$r_i = \begin{bmatrix} 1 \\ 0.72 \\ 1.53 \\ 1.27 \end{bmatrix} \quad a_{ij} = \begin{bmatrix} 1 & 1.09 & 1.52 & 0 \\ 0 & 1 & 0.44 & 1.36 \\ 2.33 & 0 & 1 & 0.47 \\ 1.21 & 0.51 & 0.35 & 1 \end{bmatrix} \quad (3)$$

can be found which appear to produce chaotic solutions and furthermore appear to be rather robust to perturbations. The case above represents an attempt to maximize the largest Lyapunov exponent relative to the geometric mean of the growth rates  $(r_1 r_2 r_3 r_4)^{1/4}$ , subject to the constraint that none of the variables  $x_i$  fall below 0.001. The corresponding largest Lyapunov exponent is  $\lambda_1 \cong 0.0203$ , and the sum of all the exponents is  $\sum \lambda_i \cong -1.2834$ , implying a predictability horizon on the order of 50 growth times of a typical species. Also, note that this (3) choice of parameters does not have all  $r_i$  equal, and thus goes beyond the sub-class of systems studied by Arneodo et al. [8].

## II. PRELIMINARY ANALYSIS

### A. Summary of lower-dimensional dynamics

For the single species case, i.e.  $N = 1$ , Eq. (1) reduces to the Verhulst equation [9],

$$dx/dt = x(1 - x)$$

and solutions for all initial conditions  $0 < x(0)$  are asymptotic, as  $t \rightarrow \infty$ , to the stable equilibrium at  $x = 1$ .

In the two-species case, i.e.  $N = 2$ , there is a co-existing equilibrium at the fixed point

$$x_1 = (1 - a_{12})/(1 - a_{12}a_{21})$$

$$x_2 = (1 - a_{21})/(1 - a_{12}a_{21})$$

If both  $a_{12}$  and  $a_{21}$  are less than 1 the fixed point is stable and all initial conditions asymptotically approach not only the closed invariant, attracting one-dimensional cell but also the fixed point. If either  $a_{12}$  or  $a_{21}$  is greater than 1, the fixed point is a saddle point and all initial conditions (other than the fixed point) asymptotically approach the closed invariant, attracting one dimensional cell (which is the unstable manifold of the fixed point) and flow, by the principle of competitive exclusion [10], toward the boundary with one species approaching extinction.

For three species, if condition (2b) is relaxed, for appropriate choices of  $a_{ij}$  chaotic solutions of Eq. (1) are possible [11]. However, under the competition hypothesis (2b) the presence of a closed invariant, attracting two-dimensional cell implies, by the Poincare-Bendixson theorem, that the only asymptotic dynamics are fixed points, periodic orbits [12, 13] (or no periodic orbits [14]), or limit cycles [15]; for example with  $r_1 = r_2 = r_3 = 1$ ,  $a_{12} = a_{23} = a_{31} = \alpha$ ,  $a_{13} = a_{21} = a_{32} = \beta$  and  $\alpha + \beta = 2$ .

In the case of four species, Arneodo et al. [8] have demonstrated chaotic solutions with parameter values satisfying conditions (2a) and (2b). Their approach was to use the transformation described by Coste et al. [16], to embed their chaotic three-dimensional system [11] into a four-dimensional system, choosing the embedding appropriately to ensure conditions (2a) and (2b). While this method does result in a four-species system with chaotic orbits, many questions remain open. In particular, as a result of Coste's transformation, all the exhibited systems are forced to satisfy the symmetry  $r_1 = r_2 = r_3 = r_4$ .

## B. Equilibria and Eigenvalues

For the remainder of the paper we consider the four-species case described in Eq. (3). There are  $2^N = 16$  equilibrium points (each of the  $N$  species can be present or extinct), and the one corresponding to coexistence of all species can be calculated from

$$\sum_{j=1}^N a_{ij}x_j = 1$$

resulting in

$$\bar{x}_i \cong \begin{bmatrix} 0.3013 \\ 0.4586 \\ 0.1307 \\ 0.3557 \end{bmatrix} \quad (4)$$

This fixed point has an index-2 spiral saddle whose Jacobian matrix

$$\frac{\partial \dot{x}_i}{\partial x_j} = -a_{ij}r_i x_i$$

has eigenvalues  $0.0414 \pm 0.1903i$ ,  $-0.3342$ , and  $-1.0319$ .

Among the remaining 15 fixed points, six have one of their  $x_i$  values negative and hence cannot be reached by a trajectory that starts with all  $x_i$  positive. The remaining nine all lie on the boundary of the domain of non-negative populations (i.e.  $x_i \geq 0$  for all  $i$ ). One, with  $x_3 = 0$ , is an index-1 spiral saddle, seven are saddle points, and the origin  $x_1 = x_2 = x_3 = x_4 = 0$  is a repellor.

## C. A Homoclinic Orbit

The stable and unstable manifolds originating from the coexisting equilibrium point (4) appear to intersect tangentially, resulting in a homoclinic connection which is shown in Fig. 1 projected onto the  $x_1x_2$  plane. Given the non-generic nature of a tangential intersection, it is difficult to verify these numerics. In the bifurcation analysis discuss in section III, as the parameter  $s$  is varied, the homoclinic tangency appears to occur when the equilibrium point (which moves with  $s$ ) lies on the attractor (at  $s \cong 1.0001$ ). There also appear to be other homoclinic connections at much higher values of  $s$ . The eigenvalues of the equilibrium satisfy the Shilnikov condition [17] for the existence of chaos.

#### D. Chaotic Attractor

Figure 2 shows that the attractor projected onto  $x_1x_2x_3$  space is nearly two-dimensional with a folded-band structure reminiscent of the Rössler attractor [18], and Fig. 3 shows a portion of the time series of the four variables. The trajectory on the attractor comes very close (a Euclidean distance of  $< 1 \times 10^{-4}$ ) to the coexisting equilibrium point (4) and the homoclinic connection shown in Fig. 1.

The Lyapunov exponents [19, 20] for this orbit are 0.0203, 0,  $-0.2748$ , and  $-1.0289$ , which implies a Kaplan-Yorke dimension [21] of  $D_{KY} = 2.074$ . The correlation dimension of Grassberger and Procaccia [22] was estimated using the extrapolation method of Sprott and Rowlands [23] with the result  $D_2 = 2.066 \pm 0.086$ , in good agreement with the Kaplan-Yorke dimension.

For the parameters in Eq. (3), the only attractor for initial conditions  $x_i(0) > 0$  is the one in Fig. 2, and thus its basin of attraction is the entire domain of strictly positive populations (i.e.  $x_i > 0$  for all  $i$ ). However, some initial conditions cause  $x_3$  to become very small for a long time before approaching the chaotic attractor, which in a real ecology would likely result in the permanent extinction of that species (and the suppression of chaos). Once on the attractor, the value of  $x_3$  never falls below 0.0019.

#### E. Symbolic Dynamics

To better understand the dynamics of this system, we break the phase space ( $x_i \geq 0$ ) into  $2^4 = 16$  chambers corresponding to regions where  $x_i$  is increasing/decreasing and track which transitions are observed. Using 0 to denote an increasing value, 1 to denote a decreasing value, and taking  $x_1$  as the least significant bit and  $x_4$  as the most significant bit we can order the 16 chambers and label them from A to P (see table I).

Two chambers, namely chamber (A), which contains the origin, and chamber (P), the unbounded chamber containing the point at infinity, have all orbits exiting and thus not appear in any of the transitions observed on the attractor. The remaining 14 chambers can be broken into two categories: 8 of which have either three species increasing and one species decreasing (e.g. B, C, etc.) or three species decreasing and one species increasing (e.g. H, L, etc.) and 6 of which have two species increasing and two species decreasing (e.g. D, F,

etc.). There are a total of  $8 \times 3 = 24$  transitions possible from the former chambers and  $6 \times 4 = 24$  transitions from the later giving a total of 48 possible transitions.

Numerically the trajectory on the attractor only visits 12 of the 16 chambers and undergoes 20 of the possible 48 transitions.

Since the Lotka-Volterra vectorfield is quadratic and the boundaries of the chambers lie in a three-dimensional affine space, it is possible to determine analytically where in phase space various chamber transitions occur (as well as study how these transitions change with the bifurcation analysis discussed in section III). This, as well as a study of higher-order transition sequences, are under current investigation.

### III. ROUTES TO CHAOS

The routes to chaos were examined by introducing a bifurcation parameter  $s$  that multiplies the off-diagonal elements of the  $a_{ij}$  matrix in Eq. (1). This parameter can be viewed as a measure of species coupling since  $s = 0$  decouples the equations into a nonlinear system of  $N$  independent Verhulst equations which are asymptotic to  $x_i = 1$  for all  $i$ . For  $s = 1$ , the chaotic solution described in Section IID is obtained. On the other hand, as  $s \rightarrow \infty$  competition becomes increasingly severe and all but the species with the highest growth rate ( $i = 3$ ) die. Figure 5 shows a bifurcation diagram for successive maxima of  $x_1$  for increasing  $s$  over the range  $0.8 < s < 1.4$  and the corresponding largest Lyapunov exponent.

The coexisting equilibrium first becomes unstable through a Hopf bifurcation at  $s \cong 0.8185$ , producing a limit cycle that undergoes successive period doublings into chaos. The chaos persists except for numerous periodic windows until about  $s \cong 1.216$ , where an inverse period-doubling cascade begins. Meanwhile, the equilibrium point with only  $x_1 = x_2 = 0$  becomes stable at  $s \cong 1.0794$ , and its basin of attraction grows until it touches the limit cycle in a boundary crisis at  $s \cong 1.302$  where species 1 and 2 die. The bifurcation diagram exhibits hysteresis in that once  $s$  is increased to the point where  $x_1$  and  $x_2$  approach zero, the trajectory remains at that stable equilibrium until  $s$  is lowered below 1.0794, whereupon it reproduces the behavior in Fig. 5.

#### IV. SELF-ORGANIZED CRITICALITY

One curious feature of the model is that it exhibits a power-law variation of various quantities, implying scale-invariance as would characterize self-organized criticality [24]. For example, consider the volatility defined as

$$v(t) = \left( \frac{\sum \dot{x}_i(t)}{\sum x_i(t)} \right)^2$$

Here  $\sum x_i(t)$  is the total biomass (or stock market average in a financial model). The volatility is large when the biomass is rapidly changing, and small otherwise. A plot of the probability distribution function  $dP(v)/dv$  versus  $v$  in Fig. 6 shows a range of several decades of  $v$  over which the slope on a log-log scale is nearly constant at a value of about  $-0.77$ . Other quantities such as the power spectral density also show a power law, although typically over a more narrow range.

#### V. SUMMARY AND CONCLUSIONS

The results presented here represent a case study of chaos in a simple Lotka-Volterra model of four species competing for a common fixed resource. Chaotic solutions are relatively rare in the vast parameter space of possible species characteristics. For example, choosing the growth rates  $r_i$  and the off-diagonal terms of the competition matrix  $a_{ij}$  randomly from an exponential distribution with mean 1.0, produces chaotic solutions (as evidenced by a Lyapunov exponent greater than 0.001) in only about one in a hundred thousand cases for  $N = 4$ . Most solutions result in the death of one or more species, reducing the dimension to a value where chaos is not possible, or more rarely, a coexisting static equilibrium or stable limit cycle, perhaps after a period of transient chaos. For  $N > 4$ , the probability of finding a chaotic solution by randomly guessing is smaller still.

Thus if we are to believe that solutions of the type shown here are relevant to natural systems, such as in ecology or finance, there must be a more efficient mechanism for evolving such solutions out of the myriad of possibilities. There are no lack of candidates. It may be that such chaotic solutions arise naturally as a result of evolution in which species are constantly changing their characteristics [25]. The numerical method used to find and optimize the solution presented here is one possibility. It involves a variant of simulated annealing, in which the parameter space is sampled randomly, but each time a solution is found with a



Lyapunov exponent larger than one previously found, the search is centered on a Gaussian neighborhood of that point, and the neighborhood size is slowly decreased. Once a chaotic solution is found, it is relatively robust to perturbations of modest size as Fig. 5 attests.

Although this method works satisfactorily for  $N = 4$ , it does not scale very well to the high  $N$  values typical of natural systems. Instead, it is possible to employ a deterministic rule, in which species adapt by selectively lowering those matrix elements that threaten their extinction whenever their population drops below some threshold, while at the same time raising all the other values to represent adaptive learning of the surviving species. This method has been used to produce chaotic systems with  $N$  as large as 400. A characteristic of these systems is that they exhibit coexistence with weakly chaotic dynamics. Interesting questions about such systems include whether self-organized criticality is common and whether the networks evolve toward one that is scale-free in the sense that the connection strengths have a power-law distribution. These issues are under study and will be the subject of future publications.

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## Figures

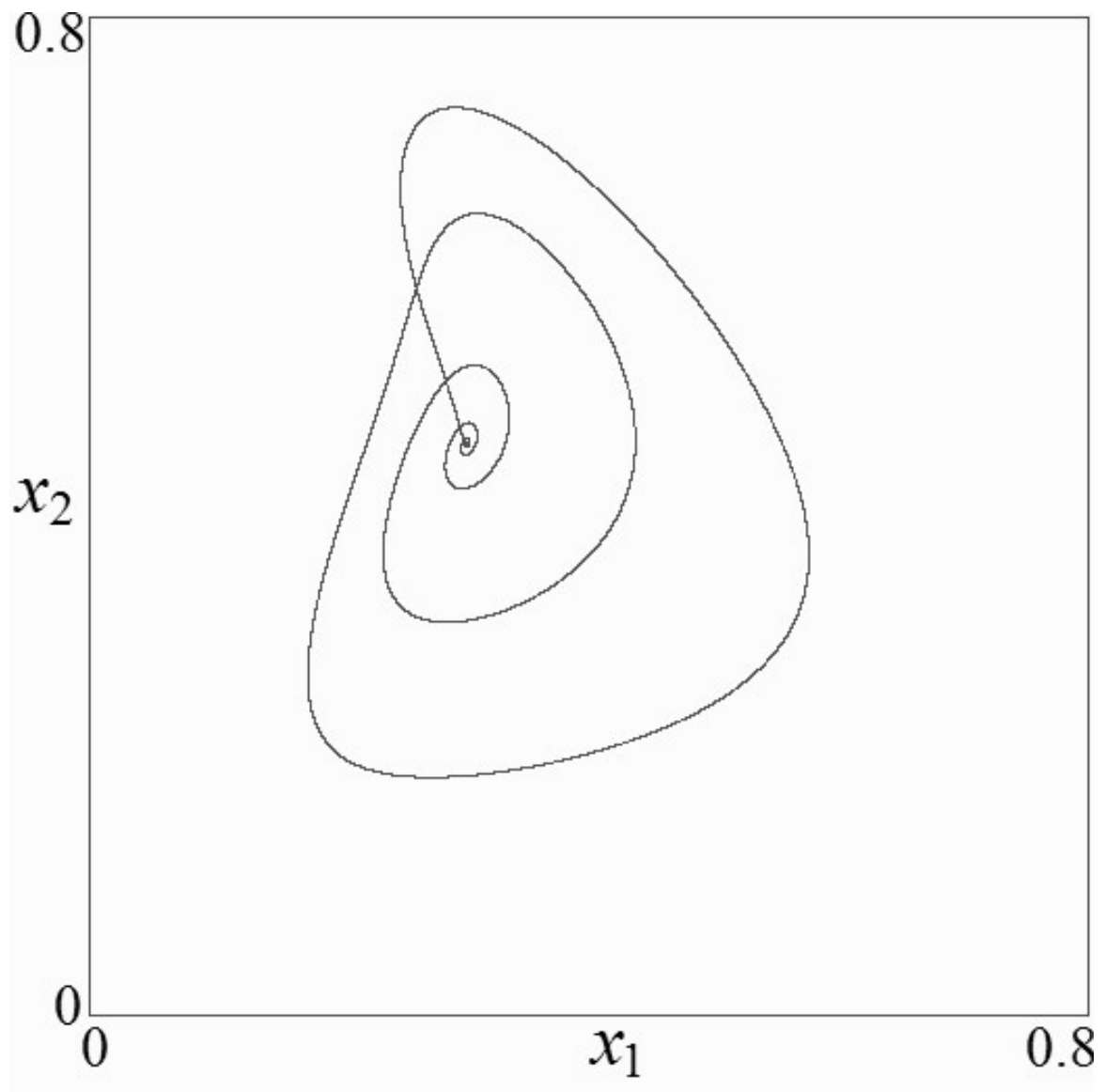


FIG. 1: Homoclinic connection projected onto the  $x_1x_2$  plane.

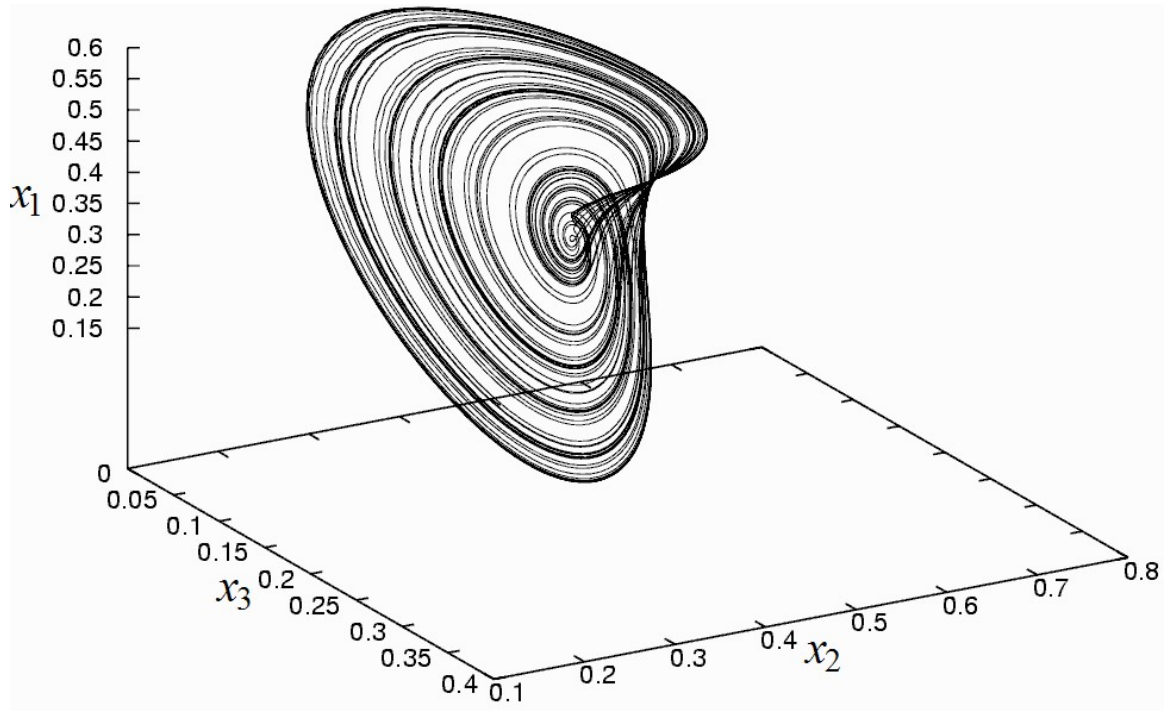


FIG. 2: Attractor projected onto  $x_1x_2x_3$  space.

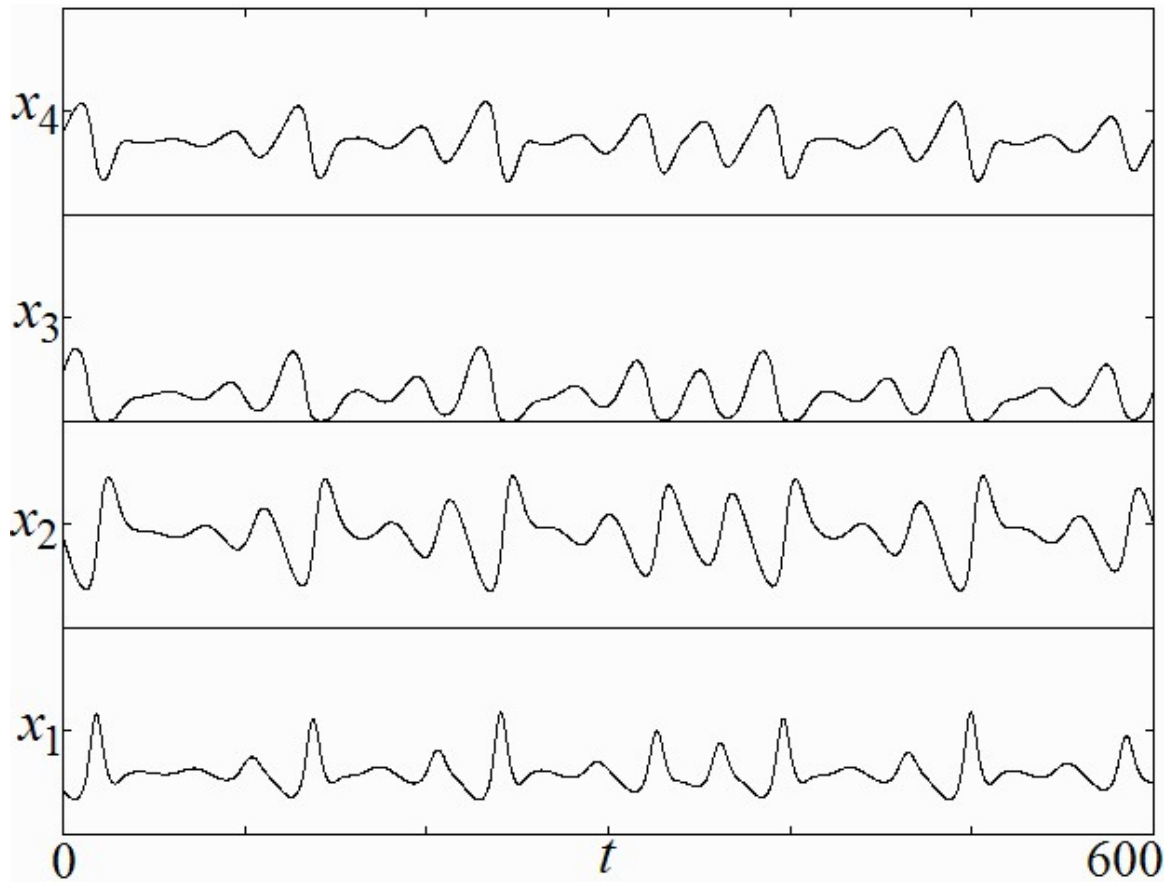


FIG. 3: Time series for each species (vertical scale is 0 to 1).

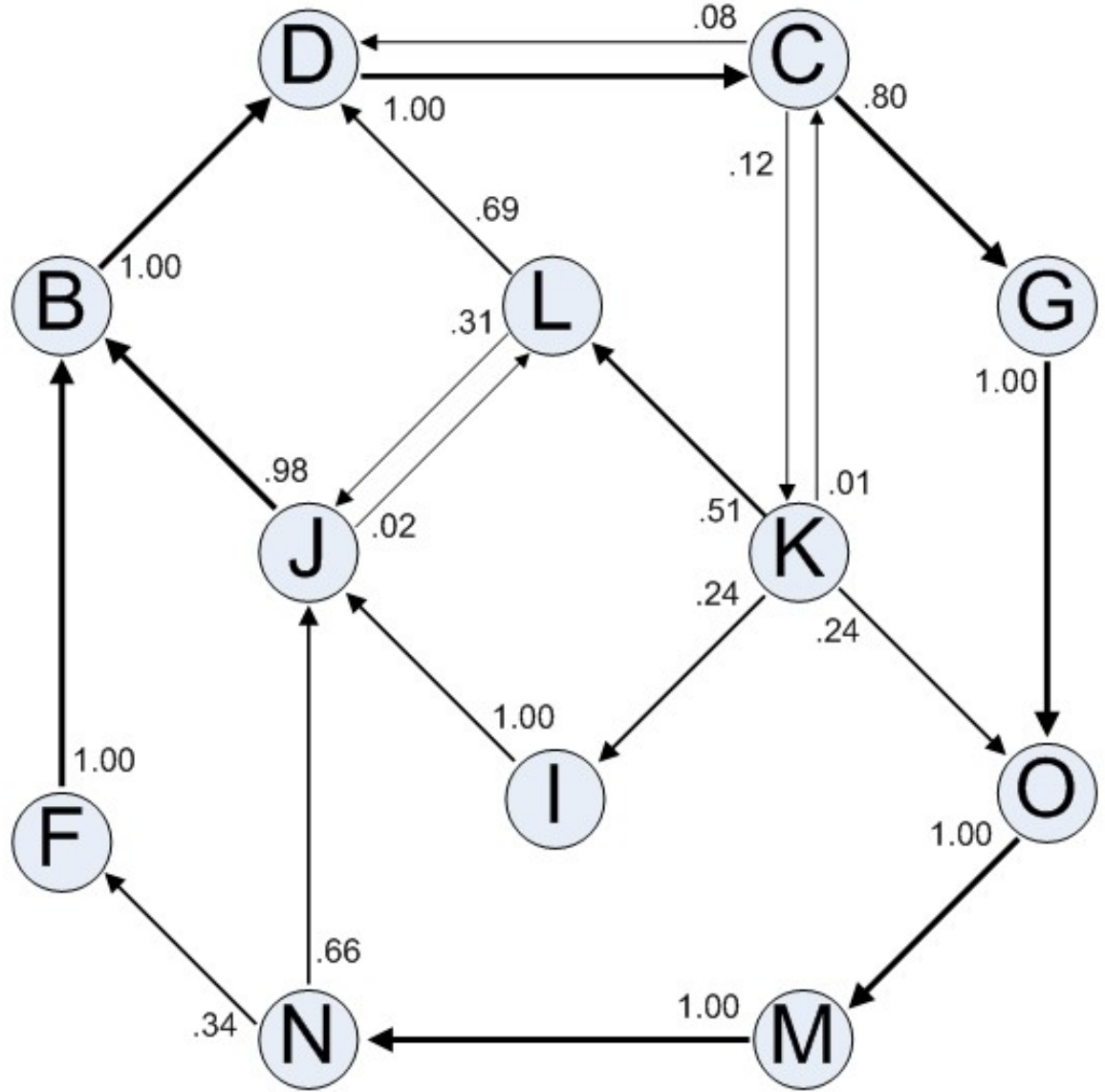


FIG. 4: Graph of symbolic dynamics of the attractor. The observed probability of the transitions are also indicated.

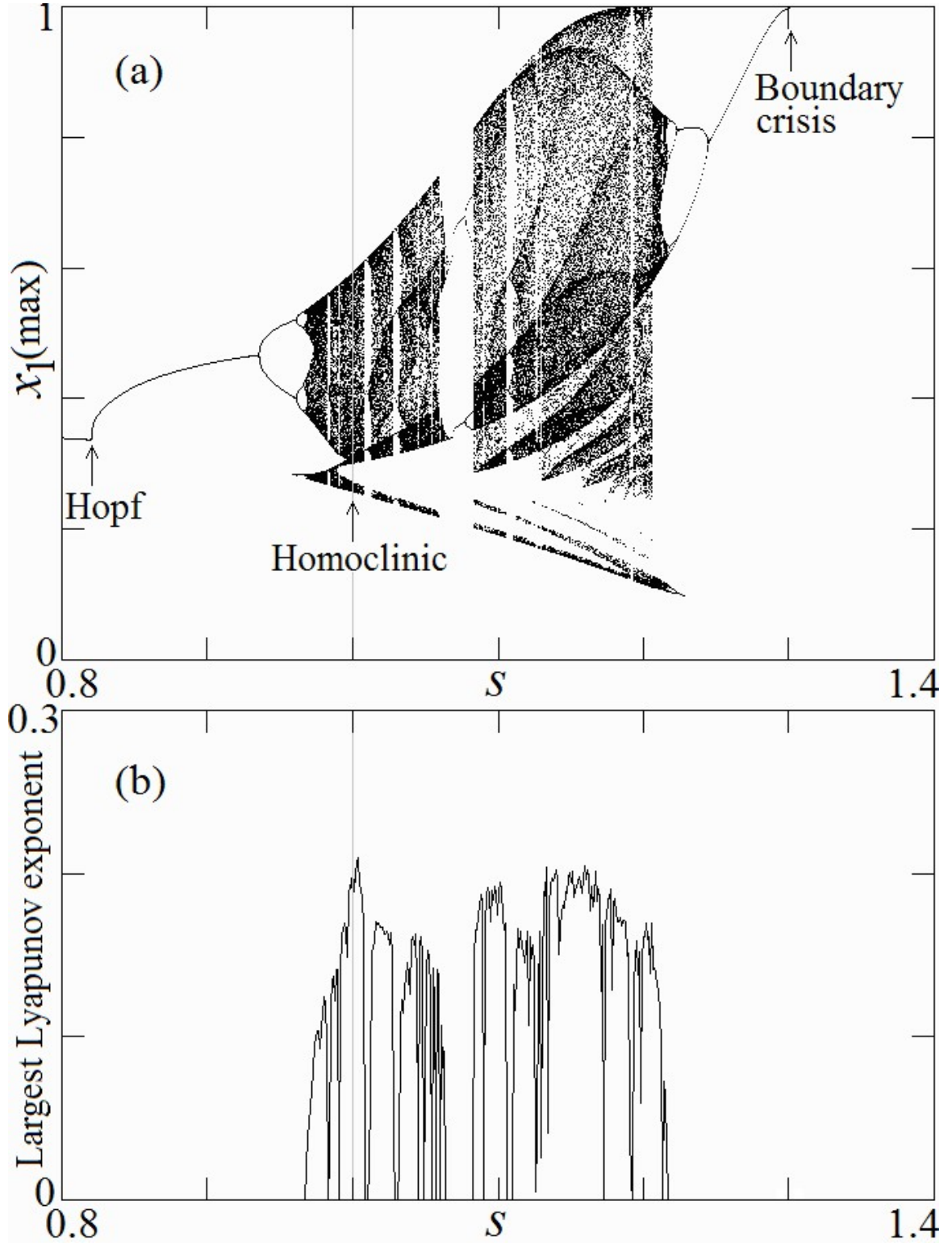


FIG. 5: (a) Bifurcation diagram showing successive maxima of  $x_1$  as the coupling  $s$  is increased and (b) the corresponding largest Lyapunov exponent.



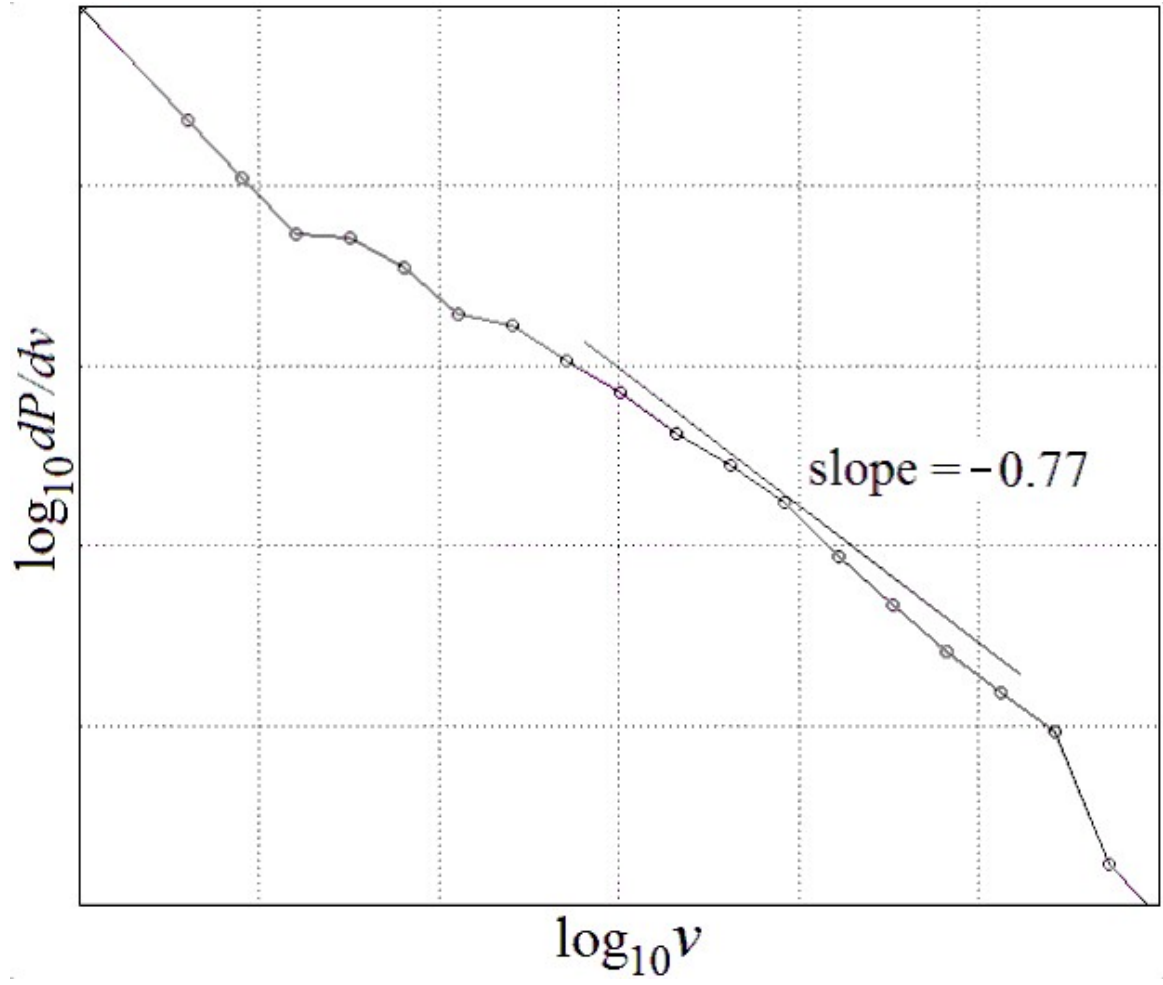


FIG. 6: Probability distribution function of volatility showing a power-law scaling (arbitrary scales).

## Tables

symbol	$\dot{x}_1$	$\dot{x}_2$	$\dot{x}_3$	$\dot{x}_4$
A	+	+	+	+
B	-	+	+	+
C	+	-	+	+
D	-	-	+	+
E	+	+	-	+
$\vdots$	$\vdots$	$\vdots$	$\vdots$	$\vdots$
N	-	+	-	-
O	+	-	-	-
P	-	-	-	-

TABLE I: Labeling scheme for chambers.