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Dynamical behaviors determined by the Lyapunov function in competitive Lotka-Volterra systems

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Dynamical behaviors of the competitive Lotka-Volterra system even for 3 species are not fully understood. In this paper, we study this problem from the perspective of the Lyapunov function. We construct explicitly the Lyapunov function using three examples of the competitive Lotka-Volterra system for the whole state space: (1) the general 2-species case, (2) a 3-species model, and (3) the model of May-Leonard. The basins of attraction for these examples are demonstrated, including cases with bistability and cyclical behavior. The first two examples are the generalized gradient system, where the energy dissipation may not follow the gradient of the Lyapunov function. In addition, under a new type of stochastic interpretation, the Lyapunov function also leads to the Boltzmann-Gibbs distribution on the final steady state when multiplicative noise is added.

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I. INTRODUCTION

Ever since the Lotka-Volterra system was proposed [1], it has been applied in a variety of practical problems in physics [2], chemistry [3], and mathematical ecology [4]. Recently, the lattice Lotka-Volterra model has been studied to address the spontaneous formation of dynamical patterns [5], the stability for the competition of two defensive alliances [6], and the noise-guided evolution [7]. In chemical reactions, the reversible Lotka-Volterra system with the oscillatory dynamics has been reported [8,9]. In addition, in the stochastic Lotka-Volterra system, coexistence or extinction [10–12] and the stochastic resonance phenomenon [13] have been analyzed. Although those problems have been well modeled by the Lotka-Volterra-type system, the dynamical behaviors of the competitive Lotka-Volterra system have not been fully understood, even for the 3-species case [14–16].

To demonstrate the dynamical behaviors for the n-species competitive Lotka-Volterra system, Hirsch has proved that any trajectory will converge to an invariant surface, homeomorphic to the $(n-1)$-dimensional unit simplex in state space [17]. In the 3-species competitive case, following Hirsch's general result, Zeeman identified 33 stable equivalence classes, of which only the classes 26–31 can have limit cycles [14]. Then, Hofbauer and So conjectured that the number of limit cycles is at most two [18]. However, three limit cycles were constructed numerically in [19,20] and four in [15,16]. The number of limit cycles has proven to be finite without a heteroclinic polycycle [21]. Till now, however, the question of how many limit cycles can appear in Zeeman's six classes 26–31 remains open [15,16].

Energy-like functions can demonstrate the number of limit cycles by showing the basins of attraction, but no satisfactory treatment on their construction for the competitive Lotka-Volterra system has been given. Planck applied the Hamiltonian theory, however, to a limited parameter region [22]. The split Lyapunov function has been used [23], but it is not monotone along with all the trajectories in the state space. Besides, the conventional Lyapunov function has been constructed in the parameter region with one global stable equilibrium [24,25]. Since it is usually difficult to construct the Lyapunov function [26], this method has not been fully explored to study the competitive Lotka-Volterra system.

Thus, a major question is whether the Lyapunov function can be constructed for the competitive Lotka-Volterra system beyond the global stable equilibrium case. The answer is positive based on our work in this paper. We construct the Lyapunov function for three competitive Lotka-Volterra systems and analyze their dynamics in the state space. The first example is the general 2-species case [24], the second one is a 3-species system [24], and the third one is the model of May-Leonard [27]. The dynamics include cases with bistability and cyclical behavior.

Then another question is what dynamical insights the Lyapunov function can provide for physics. First, based on the Lyapunov function and the corresponding dynamical matrices constructed, we define the generalized gradient system, where the energy dissipation may not follow the gradient of the Lyapunov function. Similar behavior of trajectories has been observed in the reversible Lotka-Volterra system [8,9], and such system has also been reported in real physical situations [28]. Second, in stochastic sense when multiplicative noise is added, the Lyapunov function leads to the Boltzmann-Gibbs distribution under a new type of stochastic interpretation, which is called A-type integration [29]. Thus, the basins of attraction indicated by the Lyapunov function are the most probable states for the corresponding stochastic systems.

This paper is organized as follows. In Sec. II, we analyze dynamics of three competitive Lotka-Volterra systems with the Lyapunov function. In Sec. III, we define the generalized gradient system and discuss its physical implications. In Sec. IV, we have a discussion on the meaning of the Lyapunov function in stochastic sense. In Sec. V, we summarize our work. In the appendixes, we briefly review the definition of

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the Lyapunov function. We then show the construction of the Lyapunov function for the three examples, and give detailed calculations on other dynamical parts in our framework.

II. DYNAMICAL BEHAVIORS DETERMINED BY THE LYAPUNOV FUNCTION

The competitive Lotka-Volterra system for n species is given by the following ordinary differential equations:

Definition 1 (competitive Lotka-Volterra system).

$$\dot{x}_i = x_i\left(b_i - \sum_{j=1}^{n} a_{ij}x_j\right), \quad i = 1,\ldots,n, \tag{1}$$

where each x_i $(i = 1,\ldots,n)$ represents the population of one species and b_i, a_{ij} $(i = 1,\ldots,n;\ j = 1,\ldots,n)$ are constants depending on the environment. The state space of system (1) is represented by the nonnegative vectors $R^n_+ = \{(x_1,\ldots,x_n) \in R^n | x_i \geqslant 0, i = 1,\ldots,n\}$. When $b_i > 0, a_{ij} > 0$ $(i = 1,\ldots,n)$, it is the competitive Lotka-Volterra system.

A. The general 2-species case

Example 1. The general 2-species competitive Lotka-Volterra system is given by

$$\dot{x}_1 = x_1(b_1 - x_1 - \alpha x_2), \quad \dot{x}_2 = x_2(b_2 - \beta x_1 - x_2), \tag{2}$$

where b_1, b_2, α, β are nonnegative constants [24]. By setting $\dot{x}_1 = \dot{x}_2 = 0$, four nonnegative equilibriums are derived: (1) a positive one $E_{++} = (b_1 - \alpha b_2, b_2 - \beta b_1)/(1 - \alpha\beta)$ existing when $\alpha < b_1/b_2$, $\beta < b_2/b_1$ or $\alpha > b_1/b_2$, $\beta > b_2/b_1$; (2) $E_{+0} = (b_1,0)$; (3) $E_{0+} = (0,b_2)$; and (4) $E_{00} = (0,0)$. Here the subscript $+$ denotes that the population of the species is positive and the subscript 0 means the species dies out.

Based on the construction in the appendixes, the Lyapunov function of the system is

$$\phi = \frac{\beta}{2}x_1^2 + \frac{\alpha}{2}x_2^2 - \beta b_1 x_1 - \alpha b_2 x_2 + \alpha\beta x_1 x_2. \tag{3}$$

We observe from the Hessian matrix of the Lyapunov function at E_{++} that the dynamics can be classified into four different parameter regions. In detail, as $\frac{\partial^2\phi}{\partial x_1^2} = \beta$, $\frac{\partial^2\phi}{\partial x_2^2} = \alpha$, $\frac{\partial^2\phi}{\partial x_1 \partial x_2} = \frac{\partial^2\phi}{\partial x_2 \partial x_1} = \alpha\beta$, we find the determinant of the Hessian matrix:

$$\Delta \doteq \frac{\partial^2\phi}{\partial x_1^2}\frac{\partial^2\phi}{\partial x_2^2} - \left(\frac{\partial^2\phi}{\partial x_1 \partial x_2}\right)^2 = \alpha\beta(1 - \alpha\beta). \tag{4}$$

Thus, when E_{++} exists, the determinant of the Hessian matrix can be divided into two cases ($\Delta > 0$ and $\Delta < 0$). When E_{++} does not exist, we have the third case; the remaining one is the degenerate case. We then give detailed analysis on dynamics in each case:

(a) Stable coexistence case: $\alpha < b_1/b_2$, $\beta < b_2/b_1$.

$\Delta > 0$ and $\frac{\partial^2\phi}{\partial x_1^2} > 0$ indicate that E_{++} is a globally stable equilibrium with the minimum value of the Lyapunov function.

(b) Bistable case: $\alpha > b_1/b_2$, $\beta > b_2/b_1$.

$\Delta < 0$ indicates that E_{++} is a saddle point. As the system is bounded in the first quadrant, it has two stable equilibriums E_{+0} and E_{0+} on the boundary.

(c) One survival case: $\alpha < b_1/b_2$, $\beta > b_2/b_1$ or $\alpha > b_1/b_2$, $\beta < b_2/b_1$.

It has one globally stable equilibrium on an axis of coordinate, E_{+0} appears when $\alpha < b_1/b_2$, $\beta > b_2/b_1$ or E_{0+} appears when $\alpha > b_1/b_2$, $\beta < b_2/b_1$. We just show the case where the species x_1 survives in Fig. 1, i.e., when $\alpha < b_1/b_2$, $\beta > b_2/b_1$. The case where the species x_2 survives can be shown similarly.

(d) Degenerate case: $\alpha = b_1/b_2$, $\beta = b_2/b_1$.

The Lyapunov function has the minimum value along with the line: $\sqrt{b_1 b_2} - \sqrt{b_2/b_1}x_1 - \sqrt{b_1/b_2}x_2 = 0$ as in this case

$$\phi = \tfrac{1}{2}(\sqrt{b_1 b_2} - \sqrt{b_2/b_1}x_1 - \sqrt{b_1/b_2}x_2)^2 - b_1 b_2. \tag{5}$$

Each trajectory will converge to one of the points on the line, depending on the initial value.

Two remarks are made here:

(1) Our result on the dynamics of the system is consistent with the stability analysis near equilibriums [24]. Visualization with the landscape of the Lyapunov function (Fig. 1) also provides a clear observation on dynamics in each case above separately. Saddle-node bifurcation can be observed from this landscape. The bifurcation happens from the case (a) to the case (b) and the degenerate case (d) has the minimum value on a line.

(2) The Lyapunov function is constructed uniformly for the whole parameter space in this paper and thus can provide dynamics for any perturbation on the parameters. Zeeman used the Lyapunov function to prove that the stable nullcline classes coincide with the stable topological classes in this system [14]. However, we show here that the dynamics of the system can directly be determined by the Lyapunov function alone.

B. A 3-species model

Example 2. This 3-species competitive Lotka-Volterra system is given by [24]

$$\begin{aligned}
\dot{x}_1 &= x_1(1 - x_1 - \alpha x_2),\\
\dot{x}_2 &= x_2(1 - \beta x_1 - x_2 - \beta x_3),\\
\dot{x}_3 &= x_3(1 - \alpha x_2 - x_3),
\end{aligned} \tag{6}$$

where α,β are nonnegative coefficients. By setting $\dot{x}_1 = \dot{x}_2 = \dot{x}_3 = 0$, nonnegative equilibriums are derived: (1) a positive one $E_{+++} = (1 - \alpha, 1 - 2\beta, 1 - \alpha)/(1 - 2\alpha\beta)$ existing when $(1 - \alpha)/(1 - 2\alpha\beta) > 0$ and $(1 - 2\beta)/(1 - 2\alpha\beta) > 0$; (2) $E_{+0+} = (1,0,1)$; (3) $E_{0+0} = (0,1,0)$; and (4) $E_{000} = (0,0,0)$.

Based on the construction in the appendixes, the Lyapunov function is

$$\begin{aligned}
\phi = {}& \frac{\beta}{2}\left(x_1^2 + x_3^2\right) + \frac{\alpha}{2}x_2^2 + \alpha\beta(x_1 x_2 + x_2 x_3)\\
&- \beta(x_1 + x_3) - \alpha x_2.
\end{aligned} \tag{7}$$

With the Lyapunov function constructed globally on R^3_+, the classified stability analysis near equilibriums by [24] can now be unified. Besides, when $\alpha = 1$ and $\beta = 1/2$,

$$\phi = \tfrac{1}{4}[(x_1 + x_2 - 1)^2 + (x_2 + x_3 - 1)^2 - 2] \tag{8}$$

indicates that in the degenerate case the Lyapunov function of the system has the minimum value on the intersection of the surfaces $x_1 + x_2 - 1 = 0$ and $x_2 + x_3 - 1 = 0$.

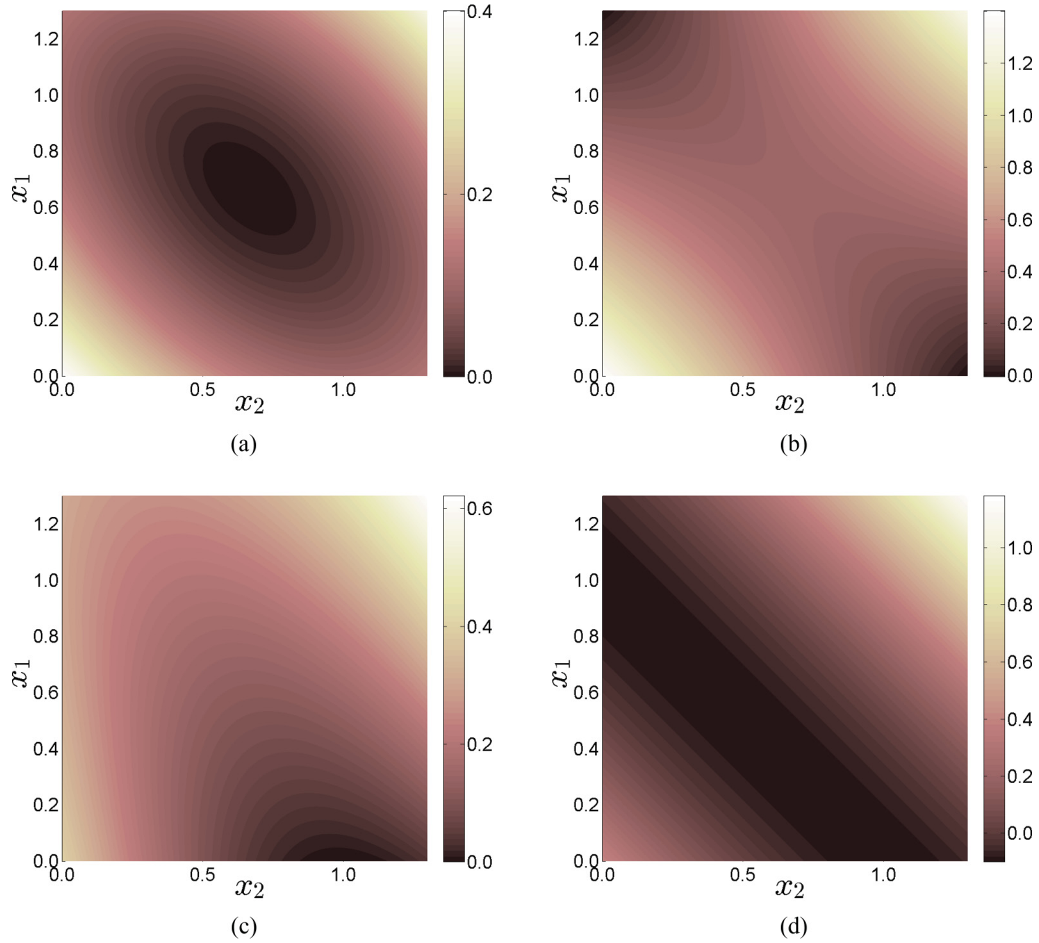

FIG. 1. (Color online) The Lyapunov function of example 1 for the various cases: (a) $\alpha = \beta = \frac{1}{2}$, $b_1 = b_2 = 1$: stable coexistence case, where E_{++} is a globally stable equilibrium; (b) $\alpha = \beta = 2$, $b_1 = b_2 = 2$: bistable case, where E_{++} is a saddle point and E_{+0}, E_{0+} are two stable equilibriums; (c) $\alpha = \frac{1}{2}$, $\beta = 2$, $b_1 = b_2 = 1$: one survival case, where E_{+0} is a globally stable equilibrium; and (d) $\alpha = \beta = b_1 = b_2 = 1$: degenerate case, where the Lyapunov function has the minimum value along with a line.

C. The model of May-Leonard

Example 3. May and Leonard studied a 3-species competitive Lotka-Volterra system [27]:

$$\begin{aligned} \dot{x}_1 &= x_1(1 - x_1 - \alpha x_2 - \beta x_3), \\ \dot{x}_2 &= x_2(1 - \beta x_1 - x_2 - \alpha x_3), \\ \dot{x}_3 &= x_3(1 - \alpha x_1 - \beta x_2 - x_3), \end{aligned} \tag{9}$$

where α,β are nonnegative coefficients. The possible equilibriums contain (1) (0,0,0); (2) three single-populations survive (1,0,0),(0,1,0),(0,0,1); (3) three two-population solutions of the form $\frac{(1-\alpha,1-\beta,0)}{1-\alpha\beta}$; and (4) a three-population survives $\frac{(1,1,1)}{1+\alpha+\beta}$.

For convenience, let us introduce some new variables: $\gamma = \alpha + \beta - 2$, $P = x_1 x_2 x_3$, and $O = x_1 + x_2 + x_3$. Then

$$\dot{P} = P[3(1 - O) - \gamma O] \tag{10}$$

and

$$\dot{O} = O(1 - O) - \gamma(x_1 x_2 + x_2 x_3 + x_3 x_1), \tag{11}$$

where $\dot{P}$ and $\dot{O}$ denote the Lie derivatives ($\dot{P} = \nabla P \cdot \dot{\mathbf{x}}$) of P and O, respectively.

Then the Lyapunov function is constructed in two parameter regions separately:

1. When $\gamma = 0$:

$$\phi = 3(x_1 + x_2 + x_3) - \ln(x_1 x_2 x_3). \tag{12}$$

Thus

$$\dot{\phi} = -\frac{\dot{P}}{P} + 3\dot{O} = -3(1 - O)^2 \leqslant 0. \tag{13}$$

$\dot{\phi} = 0$ only when $O - 1 = 0$, i.e., all the trajectories converge to the plane $O = 1$.

2. When $\gamma \neq 0$:

$$\phi = \gamma \frac{P}{O^3}, \tag{14}$$

and its Lie derivative

$$\dot{\phi} = \gamma \frac{\dot{P}O - 3\dot{O}P}{O^4} \leqslant 0. \tag{15}$$

$\dot{\phi} = 0$ can happen at a point on the line $x_1 = x_2 = x_3$ or in the set $(x_1,x_2,x_3)|P = 0$.

With the Lyapunov function constructed, we discuss the dynamics in the classified parameter space of the system here.

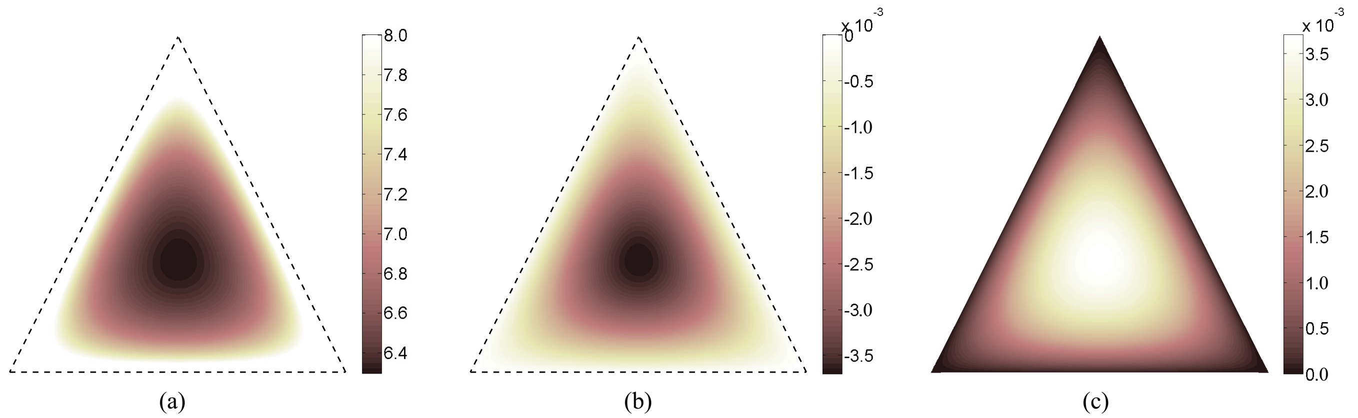

FIG. 2. (Color online) The Lyapunov function of example 3 on the plane $O = 1$. (a) When $\gamma = 0$, the limit set is the intersection of the hyperboloid that P equals a constant and the plane $O = 1$, where the system has Hamiltonian structure. (b) When $\gamma = -0.1 < 0$, the system has a global stable equilibrium on the line $x_1 = x_2 = x_3$. (c) When $\gamma = 0.1 > 0$, the limit set is $(x_1, x_2, x_3)|P = 0, O = 1$.

(a) When $\gamma = 0$:

As $\dot{\phi} = 0$ only on the plane $O = 1$, all the trajectories will converge to this plane. Besides, on this plane, the value of the Lyapunov function $\phi = 3 + \ln P$ will be a constant, and thus the value of P will be a constant for each trajectory. This means that the limit set for any initial point will be the intersection of the plane $O = 1$ and the hyperboloid that P equals to a constant, which is a cycle on the plane. Based on the calculations in the appendixes, the matrices S and T indicate that the system has Hamiltonian structure on the plane.

(b) When $\gamma < 0$:

As $\phi = \gamma \frac{P}{O^3}$ is nonpositive now, the minimum value of ϕ will not be zero if its initial value is not. Thus, in order to minimize the value of the Lyapunov function, all the trajectories will converge to one point on the line $x_1 = x_2 = x_3$. Therefore, this case has a global stable equilibrium.

(c) When $\gamma > 0$:

As $\phi = \gamma \frac{P}{O^3}$ is nonnegative now, the minimum value of ϕ will be zero. That is, all the trajectories will converge to the set $(x_1, x_2, x_3)|P = 0$. In the neighborhood of $P = 0$, the terms of order $x_1 x_2$, etc., in $\dot{O}$ asymptotically make a negligible contribution [27]. Thus $\dot{O} = O(1 - O)$ leads to $O \to 1$ in the end. Finally, the limit set in this case is the set $(x_1, x_2, x_3)|P = 0, O = 1$.

Two remarks are made here:

(1) Our result is consistent with that in [27]. Furthermore, we give a full description on dynamics for the whole state space with the Lyapunov function. The landscape of the Lyapunov function on the plane $O = 1$ (Fig. 2) gives a direct observation on dynamics: (1) When $\gamma = 0$, Fig. 2(a) shows that the system has Hamiltonian structure; (2) when $\gamma < 0$, Fig. 2(b) shows that the system has a global stable equilibrium; and (3) when $\gamma > 0$, Fig. 2(c) shows that the limit set of the system is $(x_1, x_2, x_3)|P = 0, O = 1$.

(2) Our construction is for the whole parameter space and we provide an explicit method to find this Lyapunov function compared to that in [30,31]. Besides, Chi studied the asymmetric May-Leonard system [32]. Our construction method here may be generalized to their system. Then the limit cycle problem for the 3-species competitive Lotka-Volterra system [14] can be solved.

III. GENERALIZED GRADIENT SYSTEM

In this section, we define the generalized gradient system, as a natural generalization to the typical gradient system. The major difference is that the descending path of a generalized gradient system may not follow the gradient of the Lyapunov function. This property is similar to the trajectories' behavior of the system in [8,9]. In other words, the gradient of the Lyapunov function is anisotropic. Such anisotropic system has been observed in real physical systems, such as Fourier's equation [28]. Given definition, we further show that the 2-species system (2) and the 3-species system (6) discussed above meet the definition, while the model of May-Leonard does not. We will also give a linear generalized gradient system.

First of all, we need to briefly introduce our dynamical framework. It was recently discovered during the study on the stability problem of a genetic switch [33,34] and has been found very useful in physics and biology [35,36]. The key result of the framework is a transformation from the n-dimensional smooth dynamical system

$$\dot{\mathbf{x}} = \mathbf{f}(\mathbf{x}) \tag{16}$$

to the vector differential equation

$$[S(\mathbf{x}) + T(\mathbf{x})]\dot{\mathbf{x}} = -\nabla\phi(\mathbf{x}). \tag{17}$$

Here ϕ is a scalar function, the Lyapunov function. The matrix S is a semipositive definite and symmetric matrix. T is an antisymmetric matrix.

Symmetrically, if $(S + T)$ is nonsingular, Eq. (17) can be rewritten as a reverse form

$$\dot{\mathbf{x}} = -[D(\mathbf{x}) + Q(\mathbf{x})]\nabla\phi(\mathbf{x}), \tag{18}$$

where D is a semipositive definite and symmetric matrix and Q is an antisymmetric matrix.

From a physical point of view, the Lyapunov function ϕ is a potential function [37]. The matrix S can be explained as a frictional force indicating dissipation of the potential function, and T as a Lorentz force. The symbol D is the diffusion matrix indicating the random driving force; therefore for deterministic systems, D is free to be chosen.

In this decomposition of the dynamical system, S can be considered as a gradient part and T as a rotational part. When $S = 0$, it is a conserved system with first integral. If T is a scalar matrix at the same time, it is a Hamiltonian system where the trajectory would be a contour along the landscape of the Lyapunov function. When $T = 0$, it is a generalized gradient system defined below. Thus both S and T can provide dynamical information for a given system.

Next, we define the generalized gradient system:

Definition 2 (generalized gradient system). A generalized gradient system on $\mathbb{R}^n$ is a dynamical system of the form

$$\dot{\mathbf{x}} = -D(\mathbf{x})\nabla\phi(\mathbf{x}), \tag{19}$$

where $\phi : \mathbb{R}^n \mapsto \mathbb{R}$ is a continuous differentiable scalar function and $D(\mathbf{x})$ is a semipositive definite and symmetric matrix.

By definition, when D is the product of a nonzero constant and the identity matrix, it degenerates to the classical gradient system [38].

A. The three competitive Lotka-Volterra systems

For the system (2), it is not a typical gradient system as the curl of the vector field $\nabla \times \dot{\mathbf{x}} = \alpha x_1 - \beta x_2 \neq 0$. We calculate the matrices:

$$S = \begin{pmatrix} \beta/x_1 & 0 \\ 0 & \alpha/x_2 \end{pmatrix}, \quad T = 0,$$

$$D = \begin{pmatrix} x_1/\beta & 0 \\ 0 & x_2/\alpha \end{pmatrix}, \quad Q = 0.$$

The matrix D being semipositive definite and symmetric and $T = 0$ indicate that the system (2) is a generalized gradient system with zero rotational part. Besides, S is singular only on the coordinate axis in this system. This means that the dissipation is infinite and thus the trajectory will stay on the axis once reaching it and finally approach the equilibrium $E_{+0} = (b_1,0)$ or $E_{0+} = (0,b_2)$.

For the system (6), the matrices are

$$S = \begin{pmatrix} \beta/x_1 & 0 & 0 \\ 0 & \alpha/x_2 & 0 \\ 0 & 0 & \beta/x_3 \end{pmatrix}, \quad T = 0,$$

$$D = \begin{pmatrix} x_1/\beta & 0 & 0 \\ 0 & x_2/\alpha & 0 \\ 0 & 0 & x_3/\beta \end{pmatrix}, \quad Q = 0.$$

As $T = 0$, the system does not have a trajectory contouring along the landscape of the Lyapunov function.

For the model of May-Leonard, it is not a generalized gradient system as the matrix $T \neq 0$. The detailed calculations are in the appendixes.

B. The linear cases

A linear autonomous dynamical system is given by the following ordinary differential equations:

$$\dot{\mathbf{x}} = F\mathbf{x}, \tag{20}$$

where $\mathbf{x} = (x_1, \ldots, x_n)$ with $x_1, \ldots, x_n$ the n Cartesian coordinates of the state space, $\dot{\mathbf{x}} = d\mathbf{x}/dt$, and F a constant matrix. To ensure the independence of all the state variables, we require the determinant of the F matrix to be finite: $\det(F) \neq 0$.

To illustrate the coherence and generality of the generalized gradient system in the linear cases, we first mention that a linear system (20) is a gradient system $\dot{\mathbf{x}} = -\nabla\phi$ if and only if its F matrix is symmetric:

(i) A gradient system $\dot{\mathbf{x}} = -\nabla\phi$ has $\partial\phi/\partial x_i = -\Sigma_{j=1}^n F_{ij}x_j$; then $\nabla \times \nabla\phi = 0$ leads to the F matrix being symmetric.

(ii) If a linear system (20) has a symmetric F matrix, then by setting $\partial\phi/\partial x_i = -\Sigma_{j=1}^n F_{ij}x_j$, the solution of ϕ exists, and we can rewrite (20) as $\dot{\mathbf{x}} = -\nabla\phi$.

But a linear system (20) can be a generalized gradient system when the F matrix is asymmetric. Such systems have nonzero curl; that is, $\nabla \times \dot{\mathbf{x}} \neq 0$. We give a 2-dimension linear generalized gradient system in the following.

Example 4. This example is given by [38]:

$$\begin{pmatrix} \dot{x}_1 \\ \dot{x}_2 \end{pmatrix} = \begin{pmatrix} 0 & 3 \\ 1 & -2 \end{pmatrix} \begin{pmatrix} x_1 \\ x_2 \end{pmatrix}. \tag{21}$$

We set a Lyapunov function to be $\phi = x_2^2 - x_1x_2$ as its Lie derivative

$$\dot{\phi} = -3x_2^2 - (x_1 - 2x_2)^2 \leqslant 0.$$

Then the system (21) can be rewritten as

$$\begin{pmatrix} \dot{x}_1 \\ \dot{x}_2 \end{pmatrix} = -\begin{pmatrix} 3 & 0 \\ 0 & 1 \end{pmatrix} \begin{pmatrix} \frac{\partial\phi}{\partial x_1} \\ \frac{\partial\phi}{\partial x_2} \end{pmatrix}. \tag{22}$$

Therefore, the original system (21) is a generalized gradient system by definition, but not a gradient system as its F matrix is asymmetric.

IV. DISCUSSION IN STOCHASTIC SENSE

In this section, we discuss in the stochastic sense the implications obtained from the Lyapunov function for the three competitive Lotka-Volterra systems. We consider the deterministic dynamical system added with a multiplicative noise:

$$\dot{\mathbf{x}} = \mathbf{f}(\mathbf{x}) + \zeta(\mathbf{x},t). \tag{23}$$

According to the recent explorations of stochastic differential equations, a generalized form of Eq. (17) is provided [34]:

$$[S(\mathbf{x}) + T(\mathbf{x})]\dot{\mathbf{x}} = -\nabla\phi(\mathbf{x}) + \xi(\mathbf{x},t). \tag{24}$$

The Lyapunov function ϕ leads to the Boltzmann-Gibbs distribution on the final steady state of the stochastic process under A-type stochastic calculus [29,34]:

$$\rho(\mathbf{x},t \to \infty) \propto \exp\left\{-\frac{\phi(\mathbf{x})}{\varepsilon}\right\}, \tag{25}$$

where ρ is the probability density function and ε measures the strength of the noise.

Therefore, the stable equilibriums of the deterministic system, for example, are locally most probable states for the corresponding stochastic process. This correspondence, however, cannot be kept when Itô or Stratonovich integration is applied. A numerical example demonstrates this exact correspondence between the deterministic dynamics and the steady state distribution under the A-type stochastic calculus [29]. What is more interesting is that a recent experiment on a one-dimensional Brownian particle near a wall subjected to gravitational and electrostatic forces suggested that the A-type integration is consistent with the experimental data [39], where Itô's and Stratonovich's fail.

For the bistable case of the 2-species competitive Lotka-Volterra system with a multiplicative noise, the Lyapunov function enables a straightforward calculation of the transition probability from one stable equilibrium to another (through the difference of the Lyapunov function between the stable equilibrium and the saddle point). For Itô or Stratonovich integrations, however, this is not direct and can even be impossible, because the original stable equilibriums do not correspond to the most probable states for the long-time sampling distribution [29].

When it comes to the model of May-Leonard, the system can have a cycle as its limit set when the parameter $\gamma > 0$. Thus, when added with a multiplicative noise, the system has a final distribution with cyclical most probable states indicated by the Lyapunov function. Besides, the calculations in the appendixes show that the matrix T does not equal to zero, which implies that the corresponding stochastic system is not detail balanced [29].

V. CONCLUSION

We have demonstrated that the Lyapunov function can be constructed in general 2-species and two 3-species competitive Lotka-Volterra systems. For each example, we have shown the basins of attraction for the whole state space by the Lyapunov function, including cases with bistability and cyclical behavior. Besides, we have noticed that the construction method used in the model of May-Leonard may be generalized to the asymmetric May-Leonard system. Thus our method can be helpful to solve the limit cycle problems in the general 3-species competitive Lotka-Volterra system.

We have defined the generalized gradient system and discussed its coherence and generality with the classical gradient system. Note that in the generalized gradient system, the trajectory may not follow the gradient of the Lyapunov function. Thus, our dynamical construction provides an explanation to the observation that "the descending path of a system does not follow the gradient of the free energy function" [8,9].

We have also demonstrated that the Lyapunov function leads to the Boltzmann-Gibbs distribution on the final steady state under A-type stochastic interpretation. Thus, for the bistable case of our model added with a multiplicative noise, the transition probability between two stable equilibriums can be calculated directly, which is useful in many applications.

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APPENDIX A: THE LYAPUNOV FUNCTION

The conventional Lyapunov function for a given dynamical system (16) is defined as follows:

Definition 3 (conventional Lyapunov function [38]). Let $L : \mathcal{O} \to \mathbb{R}$ be a C^1 function, where $\mathcal{O}$ is an open set in $\mathbb{R}^n$. L is a conventional Lyapunov function of the system (16) on $\mathcal{O}$ if

(1) for a specified equilibrium $\mathbf{x}^*$ in $\mathcal{O}$, $L(\mathbf{x}^*) = 0$ and $L(\mathbf{x}) > 0$ when $\mathbf{x} \neq \mathbf{x}^*$;

(2) $\dot{L}(\mathbf{x}) = \frac{dL}{dt}|_{\mathbf{x}} \leqslant 0$ for all $\mathbf{x} \in \mathcal{O}$.

LaSalle has extended the conventional Lyapunov function to include stable region by abandoning the positive definite requirement, but his generalization is too rough to lose stability information inside the stable region.

Definition 4 (LaSalle's Lyapunov function [40]). Let $L : \mathcal{O} \to \mathbb{R}$ be a C^1 function, where $\mathcal{O}$ is an open set in $\mathbb{R}^n$. Function L is a LaSalle's Lyapunov function of the system (16) on $\mathcal{O}$ if $\dot{L}(\mathbf{x}) = \frac{dL}{dt}|_{\mathbf{x}} \leqslant 0$ for all $\mathbf{x} \in \mathcal{O}$.

Following the Lyapunov function used in [34,37], here we give a more precise definition on the Lyapunov function:

Definition 5 (Lyapunov function). Let $\phi : \mathbb{R}^n \mapsto \mathbb{R}$ be a C^1 function. Function ϕ is a Lyapunov function of the system (16) if $\dot{\phi}(\mathbf{x}) = \frac{d\phi}{dt}|_{\mathbf{x}} \leqslant 0$ for all $\mathbf{x} \in \mathbb{R}^n$ and $\dot{\phi}(\mathbf{x}) = 0$ only when $\mathbf{x}$ belongs to the union of the ω-limit sets $\cup_{\mathbf{s}\in\mathbb{R}^n}\omega(\mathbf{s})$.

APPENDIX B: CONSTRUCTION OF THE LYAPUNOV FUNCTION

For the general 2-species competitive Lotka-Volterra system (2), the idea is as follows: Assume there is a Lyapunov function ϕ and its partial derivative is given by

$$\begin{pmatrix} \frac{\partial\phi}{\partial x_1} \\ \frac{\partial\phi}{\partial x_2} \end{pmatrix} \doteq -\begin{pmatrix} A_{11}(x_1,x_2) & A_{12}(x_1,x_2) \\ A_{21}(x_1,x_2) & A_{22}(x_1,x_2) \end{pmatrix} \begin{pmatrix} \dot{x}_1 \\ \dot{x}_2 \end{pmatrix},$$

where $A_{11}(x_1,x_2)$, $A_{12}(x_1,x_2)$, $A_{21}(x_1,x_2)$, $A_{22}(x_1,x_2)$ are undetermined coefficients. Our aim is to choose proper coefficients so that (1) $\nabla \times \nabla\phi = 0$ and (2) $\dot{\phi} \leqslant 0$, i.e., the Lie derivative of ϕ decreasing along with trajectories.

We discover that $A_{11}(x_1,x_2) = \beta/x_1$, $A_{12}(x_1,x_2) = 0$, $A_{21}(x_1,x_2) = 0$, $A_{22}(x_1,x_2) = \alpha/x_2$ is a proper setting. Thus we get

$$\frac{\partial\phi}{\partial x_1} = -\beta(b_1 - x_1 - \alpha x_2), \quad \frac{\partial\phi}{\partial x_2} = -\alpha(b_2 - \beta x_1 - x_2). \tag{B1}$$

With direct calculation, $\nabla \times \nabla\phi = 0$ and

$$\begin{aligned}\dot{\phi} &= \frac{\partial\phi}{\partial x_1}\dot{x}_1 + \frac{\partial\phi}{\partial x_2}\dot{x}_2 \\ &= -\beta x_1(b_1 - x_1 - \alpha x_2)^2 - \alpha x_2(b_2 - \beta x_1 - x_2)^2 \leqslant 0,\end{aligned}$$

as x_1 and x_2 are all nonnegative population species and β and α are all nonnegative constants. $\dot{\phi}(\mathbf{x}) = 0$ happens only at $\mathbf{x} \in \cup_{\mathbf{s}\in\mathbb{R}^2_+}\omega(\mathbf{s})$, where $\omega(\mathbf{s})$ denotes the ω-limit set [38]. Thus, we can get the Lyapunov function by integrating Eq. (B1).

Here we mention that the choice on the coefficients $A_{11}(x_1,x_2)$, $A_{12}(x_1,x_2)$, $A_{21}(x_1,x_2)$, $A_{22}(x_1,x_2)$ is not unique. Our choice is straightforward and meets the requirements.

For the 3-species model (6), the construction method is the same as that for the general 2-species competitive Lotka-Volterra system, because both are the generalized gradient system. We choose the corresponding undetermined matrix to be

$$\begin{pmatrix} \beta/x_1 & 0 & 0 \\ 0 & \alpha/x_2 & 0 \\ 0 & 0 & \beta/x_3 \end{pmatrix};$$

then

$$\begin{aligned} \frac{\partial\phi}{\partial x_1} &= -\beta(1 - x_1 - \alpha x_2), \\ \frac{\partial\phi}{\partial x_2} &= -\alpha(1 - \beta x_1 - x_2 - \beta x_3), \\ \frac{\partial\phi}{\partial x_3} &= -\beta(1 - \alpha x_2 - x_3). \end{aligned} \tag{B2}$$

Thus $\nabla \times \nabla\phi = 0$ and the Lie derivative of ϕ is

$$\begin{aligned} \dot\phi &= -\beta x_1(1 - x_1 - \alpha x_2)^2 - \alpha x_2(1 - \beta x_1 - x_2 - \beta x_3)^2 \\ &\quad - \beta x_3(1 - \alpha x_2 - x_3)^2 \leqslant 0, \end{aligned}$$

as x_1,x_2, and x_3 are all nonnegative population species and β and α are all nonnegative constants. $\dot\phi(\mathbf{x}) = 0$ happens only at $\mathbf{x} \in \cup_{\mathbf{s}\in\mathbb{R}_+^3} \omega(\mathbf{s})$. We can construct the Lyapunov function by integrating Eq. (B2).

For the model of May-Leonard, we find that this model is not the generalized gradient system, and thus the construction method above cannot be applied here. We give another method to construct the Lyapunov function in the following.

For convenience, let us again write the variables defined before: $\gamma = \alpha + \beta - 2$, $P = x_1x_2x_3$, and $O = x_1 + x_2 + x_3$. Then

$$\begin{aligned} \dot P &= \dot x_1 x_2 x_3 + x_1 \dot x_2 x_3 + x_1 x_2 \dot x_3 = P[3 - (1 + \alpha + \beta)O] \\ &= P[3 - (3 + \gamma)O] = P[3(1 - O) - \gamma O], \end{aligned}$$

and

$$\begin{aligned} \dot O &= \dot x_1 + \dot x_2 + \dot x_3 \\ &= O - \left[x_1^2 + x_2^2 + x_3^2 + (\alpha + \beta)(x_1x_2 + x_2x_3 + x_3x_1)\right] \\ &= O(1 - O) - \gamma(x_1x_2 + x_2x_3 + x_3x_1). \end{aligned}$$

Next, we construct the Lyapunov function in two different parameter regions: (i) $\gamma = 0$ and (ii) $\gamma \neq 0$.

(i) When $\gamma = 0$:

Noting that $\dot P = 3P(1 - O)$ and $\dot O = O(1 - O)$, thus

$$-\frac{\dot P}{P} + 3\dot O = -3(1 - O)^2 \leqslant 0. \tag{B3}$$

Therefore, if we can construct a function whose Lie derivative is $-\dot P/P + 3\dot O$, then it is a Lyapunov function. This can be done by simply integrating $-\dot P/P + 3\dot O$ and we get a Lyapunov function

$$\phi = 3O - \ln P = 3(x_1 + x_2 + x_3) - \ln(x_1x_2x_3). \tag{B4}$$

(ii) When $\gamma \neq 0$:Noting that $\dot O = O(1 - O) - \gamma(x_1x_2 + x_2x_3 + x_3x_1)$ and $\dot P = P[3(1 - O) - \gamma O]$, thus

$$\begin{aligned} &\gamma[\dot P O - 3\dot O P] \\ &\quad = \gamma[3PO(1 - O) - \gamma PO^2 - 3PO(1 - O) \\ &\qquad + 3\gamma P(x_1x_2 + x_2x_3 + x_3x_1)] \\ &\quad = -\gamma^2 P[O^2 - 3(x_1x_2 + x_2x_3 + x_3x_1)] \\ &\quad = -\gamma^2 P\left[x_1^2 + x_2^2 + x_3^2 - (x_1x_2 + x_2x_3 + x_3x_1)\right] \\ &\quad = -\frac{\gamma^2 P}{2}[(x_1 - x_2)^2 + (x_2 - x_3)^2 + (x_3 - x_1)^2] \leqslant 0. \end{aligned}$$

Therefore, we need to find a function whose Lie derivative is $\gamma[\dot P O - 3\dot O P]$. We notice that we can not integrate it directly; however, we find out that the function

$$\phi = \gamma\frac{P}{O^3} \tag{B5}$$

has the Lie derivative

$$\dot\phi = \gamma\frac{\dot P O - 3\dot O P}{O^4} \leqslant 0. \tag{B6}$$

Thus it is a Lyapunov function.

APPENDIX C: MATRICES S AND T FOR THE MODEL OF MAY-LEONARD

According to [37], if the Lyapunov function has been constructed for a system, the other dynamical parts can be obtained as

$$S = -\frac{\nabla\phi\cdot\mathbf{f}}{\mathbf{f}\cdot\mathbf{f}}I, \quad T = -\frac{\nabla\phi\times\mathbf{f}}{\mathbf{f}\cdot\mathbf{f}}. \tag{C1}$$

The corresponding explicit expression of the diffusion matrix D and the antisymmetric matrix Q can be provided as well:

$$D = -\left[\frac{\mathbf{f}\cdot\mathbf{f}}{\nabla\phi\cdot\mathbf{f}}I + \frac{(\nabla\phi\times\mathbf{f})^2}{(\nabla\phi\cdot\mathbf{f})(\nabla\phi\cdot\nabla\phi)}\right], \quad Q = \frac{\nabla\phi\times\mathbf{f}}{\nabla\phi\cdot\nabla\phi}. \tag{C2}$$

Then, we calculate S and T by Eq. (C1) for the model of the May-Leonard system. For convenience, let us list the Lyapunov functions again:

(i) When $\gamma = 0$:

$$\phi = 3O - \ln P = 3(x_1 + x_2 + x_3) - \ln(x_1x_2x_3).$$

(ii) When $\gamma \neq 0$:

$$\phi = \gamma\frac{P}{O^3} = \gamma\frac{x_1x_2x_3}{(x_1 + x_2 + x_3)^3}.$$

Then we do calculations separately for these two cases.

(i) When $\gamma = 0$:

As

$$\frac{\partial\phi}{\partial x_1} = \frac{3x_1 - 1}{x_1}, \quad \frac{\partial\phi}{\partial x_2} = \frac{3x_2 - 1}{x_2}, \quad \frac{\partial\phi}{\partial x_3} = \frac{3x_3 - 1}{x_3}, \tag{C3}$$

$$S = -\frac{\nabla\phi\cdot\mathbf{f}}{\mathbf{f}\cdot\mathbf{f}}I = \frac{3[1 - (x_1 + x_2 + x_3)]^2}{\dot x_1^2 + \dot x_2^2 + \dot x_3^2}I. \tag{C4}$$

Notice S is zero matrix on the plane $O = 1$, and thus the system is conserved.

As for T:

$$T = -\frac{\nabla\phi\times\mathbf{f}}{\mathbf{f}\cdot\mathbf{f}} = -\frac{\left(\frac{3x_i - 1}{x_i}\dot x_j - \frac{3x_j - 1}{x_j}\dot x_i\right)_{3\times3}}{\dot x_1^2 + \dot x_2^2 + \dot x_3^2}. \tag{C5}$$

Since T is antisymmetric, we just need to calculate the elements T_{12}, T_{13}, and T_{23} of the above 3×3 matrix. As we have proven all the trajectories will converge to the plane $O = 1$, we calculate the elements on the plane below. We first calculate T_{12}:

$$T_{12} = \frac{3x_1 - 1}{x_1}\dot{x}_2 - \frac{3x_2 - 1}{x_2}\dot{x}_1 = \frac{3x_1 - 1}{x_1}(1 - \beta x_1 - x_2 - \alpha x_3)x_2 - \frac{3x_2 - 1}{x_2}(1 - x_1 - \alpha x_2 - \beta x_3)x_1. \quad (C6)$$

We notice that $1 - \alpha = -(1 - \beta) = \frac{\beta - \alpha}{2}$ in the case of $\gamma = 0$. Thus we have

$$T_{12} = \frac{\beta - \alpha}{2}\left\{\frac{x_2}{x_1}[(x_1 - x_2) + (x_1 - x_3)](x_3 - x_1) + \frac{x_1}{x_2}[(x_2 - x_1) + (x_2 - x_3)](x_3 - x_2)\right\}. \quad (C7)$$

We calculate T_{13} and T_{23} similarly:

$$T_{13} = \frac{3x_1 - 1}{x_1}\dot{x}_3 - \frac{3x_3 - 1}{x_3}\dot{x}_1 = \frac{3x_1 - 1}{x_1}(1 - \alpha x_1 - \beta x_2 - x_3)x_3 - \frac{3x_3 - 1}{x_3}(1 - x_1 - \alpha x_2 - \beta x_3)x_1 = \frac{\beta - \alpha}{2}\left\{\frac{x_3}{x_1}[(x_1 - x_2) + (x_1 - x_3)](x_1 - x_2) + \frac{x_1}{x_3}[(x_3 - x_1) + (x_3 - x_2)](x_2 - x_3)\right\}. \quad (C8)$$

$$T_{23} = \frac{3x_2 - 1}{x_2}\dot{x}_3 - \frac{3x_3 - 1}{x_3}\dot{x}_2 = \frac{3x_2 - 1}{x_2}(1 - \alpha x_1 - \beta x_2 - x_3)x_3 - \frac{3x_3 - 1}{x_3}(1 - \beta x_1 - x_2 - \alpha x_3)x_2 = \frac{\beta - \alpha}{2}\left\{\frac{x_3}{x_2}[(x_2 - x_1) + (x_2 - x_3)](x_1 - x_2) + \frac{x_2}{x_3}[(x_3 - x_1) + (x_3 - x_2)](x_3 - x_1)\right\}. \quad (C9)$$

Thus we obtain each element of matrix T on the plane $O = 1$.

(ii) When $\gamma \neq 0$:

As

$$\frac{\partial \phi}{\partial x_1} = \gamma \frac{P}{O^4}[x_2 x_3(x_1 + x_2 + x_3) - 3x_1 x_2 x_3],$$
$$\frac{\partial \phi}{\partial x_2} = \gamma \frac{P}{O^4}[x_1 x_3(x_1 + x_2 + x_3) - 3x_1 x_2 x_3], \quad (C10)$$
$$\frac{\partial \phi}{\partial x_3} = \gamma \frac{P}{O^4}[x_1 x_2(x_1 + x_2 + x_3) - 3x_1 x_2 x_3],$$

$$S = -\frac{\nabla\phi \cdot \mathbf{f}}{\mathbf{f} \cdot \mathbf{f}} I = \frac{\frac{\gamma^2 P}{2O^4}[(x_1 - x_2)^2 + (x_2 - x_3)^2 + (x_3 - x_2)^2]}{\dot{x}_1^2 + \dot{x}_2^2 + \dot{x}_3^2} I. \quad (C11)$$

Since on the plane $O = 1$, S is not zero matrix except on the limit set $(x_1, x_2, x_3)|P = 0, O = 1$. Thus the system is dissipative except on the limit set.

As for T:

$$T = -\frac{\nabla\phi \times \mathbf{f}}{\mathbf{f} \cdot \mathbf{f}} = -\frac{\gamma \frac{P^2}{O^4}\left(\frac{O - 3x_i}{x_i}\dot{x}_j - \frac{O - 3x_j}{x_j}\dot{x}_i\right)_{3\times 3}}{\dot{x}_1^2 + \dot{x}_2^2 + \dot{x}_3^2}. \quad (C12)$$

Again, as all the trajectories will converge to the plane $O = 1$, we just calculate the elements of the above 3×3 matrix on the plane:

$$\widetilde{T}_{ij} = \frac{1 - 3x_i}{x_i}\dot{x}_j - \frac{1 - 3x_j}{x_j}\dot{x}_i. \quad (C13)$$

Here we use $\widetilde{T}_{ij}$ to denote the matrix elements so that they can be distinguished with the matrix elements T_{ij} in the case of $\gamma = 0$. Since $1 - \alpha = \frac{\beta - \alpha - \gamma}{2}$ and $1 - \beta = -\frac{\beta - \alpha + \gamma}{2}$ in the case of $\gamma \neq 0$, we get $\widetilde{T}_{12}$, $\widetilde{T}_{13}$, and $\widetilde{T}_{23}$ with similar calculations:

$$\widetilde{T}_{12} = \frac{x_1}{x_2}[(x_2 - x_1) + (x_2 - x_3)][(1 - \alpha)x_2 + (1 - \beta)x_3] - \frac{x_2}{x_1}[(x_1 - x_2) + (x_1 - x_3)][(1 - \alpha)x_3 + (1 - \beta)x_1]. \quad (C14)$$

$$\widetilde{T}_{13} = \frac{x_1}{x_3}[(x_3 - x_1) + (x_3 - x_2)][(1 - \alpha)x_2 + (1 - \beta)x_3] - \frac{x_3}{x_1}[(x_1 - x_2) + (x_1 - x_3)][(1 - \alpha)x_1 + (1 - \beta)x_2]. \quad (C15)$$

$$\widetilde{T}_{23} = \frac{x_2}{x_3}[(x_3 - x_1) + (x_3 - x_2)][(1 - \alpha)x_3 + (1 - \beta)x_1] - \frac{x_3}{x_2}[(x_2 - x_1) + (x_2 - x_3)][(1 - \alpha)x_1 + (1 - \beta)x_2]. \quad (C16)$$

Therefore, we obtain each element of the matrix T on the plane $O = 1$. On the limit set, T and S converge to zero in the same order.

In both cases, the matrix T does not equal zero. Therefore, the model of May-Leonard is not a generalized gradient system. Besides, this implies that the corresponding stochastic system added with a multiplicative noise is not detail balanced [34].

[1] A. Lotka, *Elements of Physical Biology* (Williams & Wilkins, Baltimore, 1925).

[2] J. Hofbauer and K. Sigmund, *Evolutionary Games and Population Dynamics* (Cambridge University Press, Cambridge, 1998).

[3] E. Di Cera, P. Phillipson, and J. Wyman, Proc. Natl. Acad. Sci. USA **85**, 5923 (1988).

[4] R. M. May, *Stability and Complexity in Model Ecosystems*, Vol. 6 (Princeton University Press, Princeton, 2001).

[5] A. Provata and G. A. Tsekouras, Phys. Rev. E **67**, 056602 (2003).

[6] M. Perc, A. Szolnoki, and G. Szabó, Phys. Rev. E **75**, 052102 (2007).
[7] M. Perc and A. Szolnoki, New J. Phys. **9**, 267 (2007).
[8] Y. Li, H. Qian, and Y. Yi, J. Chem. Phys. **129**, 154505 (2008).
[9] Y. Li, H. Qian, and Y. Yi, J. Dyn. Diff. Eqn. **22**, 491 (2010).
[10] T. Reichenbach, M. Mobilia, and E. Frey, Phys. Rev. E **74**, 051907 (2006).
[11] A. Dobrinevski and E. Frey, Phys. Rev. E **85**, 051903 (2012).
[12] G. Q. Cai and Y. K. Lin, Phys. Rev. E **70**, 041910 (2004).
[13] A. La Cognata, D. Valenti, A. A. Dubkov, and B. Spagnolo, Phys. Rev. E **82**, 011121 (2010).
[14] M. Zeeman, Dynam. Stabil. Syst. **8**, 189 (1993).
[15] M. Gyllenberg and P. Yan, Comput. Math. Appl. **58**, 649 (2009).
[16] Q. Wang, W. Huang, and B. Li, Appl. Math. Comput. **217**, 8856 (2011).
[17] M. Hirsch, Nonlinearity **1**, 51 (1999).
[18] J. Hofbauer and J. So, Appl. Math. Lett. **7**, 59 (1994).
[19] Z. Lu and Y. Luo, Comput. Math. Appl. **46**, 231 (2003).
[20] M. Gyllenberg, P. Yan, and Y. Wang, Appl. Math. Lett. **19**, 1 (2006).
[21] D. Xiao and W. Li, J. Differ. Equ. **164**, 1 (2000).
[22] M. Plank, J. Math. Phys. **36**, 3520 (1995).
[23] E. C. Zeeman and M. L. Zeeman, Trans. Am. Math. Soc. **355**, 713 (2003).
[24] Y. Takeuchi, *Global Dynamical Properties of Lotka-Volterra Systems* (World Scientific Publishing Company, Singapore, 1996).
[25] B. S. Goh, Am. Nat. **111**, 135 (1977).
[26] S. H. Strogatz, *Nonlinear Dynamics and Chaos: With Applications to Physics, Biology, Chemistry, and Engineering* (Perseus Books, Reading, 2000), p. 201.
[27] R. M. May and W. J. Leonard, SIAM J. Appl. Math. **29**, 243 (1975).
[28] N. de Koker, Phys. Rev. Lett. **103**, 125902 (2009).
[29] R.-S. Yuan and P. Ao, J. Stat. Mech. (2012) P07010.
[30] R. Robinson, *An Introduction to Dynamical Systems: Continuous and Discrete* (Pearson Prentice Hall, Upper Saddle River, NJ, 2004).
[31] J. Hofbauer, Nonlinear Anal. Theory Methods Appl. **5**, 1003 (1981).
[32] C. Chi, L. Wu, and S. Hsu, SIAM J. Appl. Math. **58**, 211 (1998).
[33] X. Zhu, L. Yin, L. Hood, and P. Ao, Funct. Integr. Genomics **4**, 188 (2004).
[34] P. Ao, J. Phys. A: Math. Gen. **37**, L25 (2004).
[35] P. Ao, Commun. Theor. Phys. **49**, 1073 (2008).
[36] P. Ao, J. Genet. Genomics **36**, 63 (2009).
[37] R.-S. Yuan, Y.-A. Ma, B. Yuan, and P. Ao, arXiv:1012.2721.
[38] M. W. Hirsch and S. Smale, *Differential Equations, Dynamical Systems, and Linear Algebra* (Academic Press, San Diego, 1974).
[39] G. Volpe, L. Helden, T. Brettschneider, J. Wehr, and C. Bechinger, Phys. Rev. Lett. **104**, 170602 (2010).
[40] J. P. LaSalle, *The Stability of Dynamical Systems* (Society for Industrial and Applied Mathematics, Philadelphia, 1976).