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(Citation)
Nonlinear Analysis: Real World Applications,14(4):1845-1853

(Issue Date)
2013-08

(Resource Type)
journal article

(Version)
Accepted Manuscript

Lotka-Volterra system and KCC theory: Differential geometric structure of competitions and predations

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Abstract

We consider the differential geometric structure of competitions and predations in the sense of the Lotka-Volterra system based on KCC theory. For this, we visualise the relationship between the Jacobi stability and the linear stability as a single diagram. We find the following. (I) Ecological interactions such as competition and predation can be described by the deviation curvature. In this case, the sign of the deviation curvature depends on the type of interaction, which reflects the equilibrium point type. (II) The geometric quantities in KCC theory can be expressed in terms of the mean and Gaussian curvatures of the potential surface. In this particular case, the deviation curvature can be interpreted as the Willmore energy density of the potential surface. (III) When the equations of the system have nonsymmetric structure for the species (e.g. a predation system), each species also has nonsymmetric geometric structure in the nonequilibrium region, but symmetric structure around the equilibrium point. These findings suggest that KCC theory is useful to establish the geometrisation of ecological interactions.

Keywords: Lotka-Volterra system, KCC theory, Competitions, Predations, Jacobi stability, Curvatures

1. Introduction

The geometrisation of nature has been the subject of theoretical interest. This includes the use of geometric concepts and techniques in the natural

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sciences, such as the general theory of relativity in physics (e.g. [1]). In biology, the geometrisation of nature is also of scientific and practical interest. For example, the theory of Kosambi-Cartan-Chen (KCC theory: the geometric theory of the stability of dynamic systems [2, 3, 4]) has been applied to several biological problems, such as production in the Volterra method [5, 6], the Volterra-Hamilton system [7, 8, 9], Tyson's model for the cell division cycle [10] and the robustness of biological systems [11].

The general theory of relativity is well known to geometrise the interaction between masses. Can we also geometrise competitions and predations, i.e. the interaction between living things? The main purpose of this paper is to consider the differential geometric structure of the Lotka-Volterra system based on KCC theory. We are concerned with (I) the nature of the competitions (intraspecific vs. interspecific) and (II) predations between the prey and the predator. Even though these are the typical ecological interactions described by the Lotka-Volterra system, few geometric studies have investigated these concrete cases.

The structure of this paper is as follows. In Section 2, we give a brief review of KCC theory. It has been applied to various nonlinear dynamic systems (e.g. [12, 13, 14, 15, 16, 17]) because it clarifies their intrinsic properties using differential geometric concepts such as "connections" and "curvatures". In Section 3, we consider the geometric structure of the competitions and predations described by the Lotka-Volterra system. In this analysis, we use the equation for the differential geometric quantities in terms of the Jacobian matrix of the linearised system. Based on this result, we discuss the ecological meaning of the geometric expression for the interactions between living things in Section 4. This will give new insights into the effect of the curvatures of the potential surface on the stability of the system. We also discuss the nonequilibrium case and the bifurcations in KCC theory. Section 5 is devoted to the conclusions.

2. Brief review of KCC theory and Jacobi stability

In this section, we give a brief review of KCC theory and Jacobi stability based on previous papers [7, 15]. Throughout this paper, Einstein's summation convention is used.

Let M be a real smooth n-dimensional manifold, and (TM, π, M) be its tangent bundle, where $\pi : TM \to M$ is a projection from the total space TM to the base manifold M. A point $x \in M$ has local coordinates (x^i), where

$i = 1, \dots, n$. The local chart of a point in TM is denoted by $(x^i, \dot{x}^i)$, where t is time (regarded as an absolute invariant) and $\dot{x}^i = dx/dt$.

Let us consider the path equation

$$\ddot{x}^i + g^i(x, \dot{x}) = 0, \tag{1}$$

where $g^i(x, \dot{x})$ is a smooth function. The trajectory $x^i(t)$ of the system (1) is changed to nearby trajectories according to $\overline{x}^i = x^i + u^i \delta\tau$, where u^i is a vector field and $\delta\tau$ is a small parameter. In this case, Eq. (1) becomes the variational equation for the limit $\delta\tau \to 0$:

$$\ddot{u}^i + \frac{\partial g^i}{\partial x^j} u^j + \frac{\partial g^i}{\partial \dot{x}^j} \dot{u}^j = 0. \tag{2}$$

The covariant form of (2) is given by

$$\frac{D^2 u^i}{Dt^2} = P^i_j u^j, \tag{3}$$

where $D(\cdots)/Dt$ is a covariant differential defined by

$$\frac{Du^i}{Dt} = \frac{du^i}{dt} + N^i_j u^j, \tag{4}$$

N^i_j is a coefficient of the nonlinear connection

$$N^i_j = \frac{1}{2} \frac{\partial g^i}{\partial \dot{x}^j}, \tag{5}$$

P^i_j is the deviation curvature tensor

$$P^i_j = -\frac{\partial g^i}{\partial x^j} + \frac{\partial N^i_j}{\partial x^k} \dot{x}^k - G^i_{jk} g^k + N^i_k N^k_j, \tag{6}$$

and G^i_{jk} is a Finsler (Berwald) connection

$$G^i_{jk} = \frac{\partial N^i_j}{\partial \dot{x}^k}. \tag{7}$$

The first term of (6): $\partial g^i / \partial x^j$ is the curvature when all the coefficients of connections become zero. In this paper, we tentatively call it the zero-connection curvature

$$Z^i_j = \frac{\partial g^i}{\partial x^j}. \tag{8}$$

As we will see in Section 4.2, the zero-connection curvature corresponds to the Gaussian curvature of the potential surface.

The deviation curvature tensor P^i_j gives the stability of whole trajectories via the following theorem [5]: *The trajectories of the system (1) are Jacobi stable if and only if the real parts of the eigenvalues of P^i_j are strictly negative everywhere, and Jacobi unstable otherwise.* In particular, the trajectories of the one-dimensional system are Jacobi stable when $P^1_1 \leq 0$, and Jacobi unstable when $P^1_1 > 0$.

3. Differential geometric quantities for competitions and predations

In this section, we derive the deviation curvature for competitions and predations in the sense of the Lotka-Volterra system. In previous studies, a linear stability analysis has often been applied to the Lotka-Volterra system. Linear stability analysis is the theory of local stability around a point on the tangent space, which means that the behaviour of the nonlinear dynamic systems is described by the tangent bundle. In this case, the equation (1) is a first-order differential equation with respect to $\dot{x}^i$, and the Jacobi stability equation (2) is reduced to an equation in a linear stability theory (e.g. [17]). Therefore, the Jacobi stability gives a more global stability than the linear stability (see also [13, 14]).

In linear stability analysis, the Jacobian matrix of the linearised system plays an important role. To clarify the relationship between the Jacobi stability and the linear stability in a linearised system, we express the geometric quantities of KCC theory in terms of the Jacobian matrix of the linearised system (see also [11, 18]).

3.1. Differential geometric quantities in terms of the Jacobian matrix

We consider a vector field described by

$$\dot{x}^i = f^i(x), \tag{9}$$

where $i = 1, 2, \ldots, n$ and f^i denote a given function. This can be approximated by a linear system around an equilibrium point x^i_0 using the relation $x^i = x^i_0 + \xi^i$, where ξ^i is a small quantity. That is,

$$\dot{\xi}^i = J^i_j(x_0)\xi^j, \tag{10}$$

where $J^i_j(x_0)$ is the Jacobian matrix of f^i.

In this paper, we consider the two-dimensional case ($i = 1, 2$):

$$\dot{\xi} = J(x_0)\xi, \tag{11}$$

where

$$\xi = \begin{pmatrix} \xi^1 \\ \xi^2 \end{pmatrix}, \tag{12}$$

$$J(x_0^i) = J = \begin{pmatrix} \partial_1 f^1(x_0) & \partial_2 f^1(x_0) \\ \partial_1 f^2(x_0) & \partial_2 f^2(x_0) \end{pmatrix}, \tag{13}$$

and $\partial_i = \partial(\cdots)/\partial x^i$. The simultaneous differential equation (11) can be rewritten as a second-order ordinary differential equation. When we consider the coordinate system $(\xi^i, \dot{\xi}^i)$, we have the following equation for $i = 1$:

$$\ddot{\xi}^1 - tr[J]\dot{\xi}^1 + det[J]\xi^1 = 0. \tag{14}$$

This is a particular case of (1) for $g^1 = -tr[J]\dot{\xi}^1 + det[J]\xi^1$. Therefore, Eqs. (5), (8) and (6) give the nonlinear connection, the zero-connection curvature and the deviation curvature of the linearised system, respectively:

$$N = -\frac{1}{2}tr[J], \tag{15}$$

$$Z = det[J], \tag{16}$$

$$P = \frac{1}{4}\{(tr[J])^2 - 4det[J]\} = N^2 - Z, \tag{17}$$

where $N^1_1 = N$, $Z^1_1 = Z$ and $P^1_1 = P$ (we use the same abbreviation throughout this paper). From Eq. (7), the Finsler connection vanishes in this linearised system (the nonvanishing case will be shown in Section 4.3). Now, Eqs. (15), (16) and (17) show that the geometric quantities of the linearised system can be easily calculated when the Jacobian matrix of the system is obtained. Eq. (17) has already been derived in previous papers (e.g. [11, 18]). In the next section, we derive the differential geometric quantities describing competitions and predations from these equations.

3.2. Lotka-Volterra competition system

As an example of (9), we consider the Lotka-Volterra competition system for two-species: $x^1 = x$ and $x^2 = y$. The standard form of the system is given by (e.g. [19])

$$\dot{x} = r_1 x(1 - \frac{x + a_1 y}{k_1}), \tag{18}$$

$$\dot{y} = r_2 y(1 - \frac{y + a_2 x}{k_2}), \tag{19}$$

where r_i is the natural growth rate, k_i is the carrying capacity and a_i is the competition coefficient. These parameters are all positive.

This system can be approximated by a linear system around an equilibrium point (x_0, y_0). From (13), the Jacobian matrix of the system is

$$J = \begin{pmatrix} r_1 - 2(r_1/k_1)x_0 - a_1(r_1/k_1)y_0 & -a_1(r_1/k_1)x_0 \\ -a_2(r_2/k_2)y_0 & r_2 - 2(r_2/k_2)y_0 - a_2(r_2/k_2)x_0 \end{pmatrix}. \tag{20}$$

Next, we consider the deviation curvature in two cases: 1) two species coexist and 2) only one species survives. Because the standard form for the competition does not allow extinction of the two species except for under the trivial condition, we ignore this case.

In the case when the two species coexist, i.e. $x_0 \neq 0$ and $y_0 \neq 0$, we have $k_1 = x_0 + a_1 y_0$ and $k_2 = y_0 + a_2 x_0$. Therefore, (20) becomes

$$J = \begin{pmatrix} A_1 & a_1 A_1 \\ a_2 A_2 & A_2 \end{pmatrix}, \tag{21}$$

where $A_1 = -r_1 x_0/k_1$ and $A_2 = -r_2 y_0/k_2$. From (15) and (16), the nonlinear connection and the zero-connection curvature are given by $N = -(A_1 + A_2)/2$ and $Z = (1 - a_1 a_2)A_1 A_2$, respectively. Then, from (17), the deviation curvature for the two species coexisting is

$$P = \frac{1}{4}\left\{(A_1 - A_2)^2 + 4a_1 a_2 A_1 A_2\right\}. \tag{22}$$

We discuss the ecological meaning of (22) in Section 4.1.

In the case when only x survives, i.e. $x_0 = k_1$ and $y_0 = 0$, (20) becomes

$$J = \left(\begin{array}{cc} -r_1 & -a_1 r_1 \\ 0 & C \end{array} \right), \tag{23}$$

where $C = r_2(1 - a_2 k_1/k_2)$. In this case, since $N = -(C - r_1)/2$ and $Z = -r_1 C$, the deviation curvature for only x surviving is

$$P = \frac{1}{4}(C - r_1)^2 + r_1 C. \tag{24}$$

For the Jacobi matrix to be stable, P should be negative or zero. This requires at least $C \leq 0$, i.e. $k_2 - a_2 k_1 \leq 0$. This condition also guarantees linear stability, as the zero isoclines method indicates (e.g. [19]).

3.3. Lotka-Volterra predation system

We consider the Lotka-Volterra predation system for the prey $x^1 = x$ and predator $x^2 = y$. The standard form of the system is given by (e.g. [19, 20])

$$\dot{x} = rx - axy, \tag{25}$$

$$\dot{y} = bxy - cy, \tag{26}$$

where r is the natural growth rate of the prey, a and b are coefficients of predation and c is the natural death rate of the predator. These parameters are all positive.

This system can be approximated by a linear system around an equilibrium point (x_0, y_0). From (13), the Jacobian matrix of the system is

$$J = \left(\begin{array}{cc} r - ay_0 & -ax_0 \\ by_0 & bx_0 - c \end{array} \right). \tag{27}$$

Next, we consider the deviation curvature in two cases: 1) the two species coexist and 2) extinction. Because the standard form of the predation does not include the case of only x or y surviving, we ignore this case.

In the case when the two species coexist, i.e. $x_0 \neq 0$ and $y_0 \neq 0$, we have $x_0 = c/b$ and $y_0 = r/a$. Therefore, (27) becomes

$$J = \left(\begin{array}{cc} 0 & -ac/b \\ br/a & 0 \end{array} \right). \tag{28}$$

From (15) and (16), the nonlinear connection and the zero-connection curvature are given by $N = 0$ and $Z = cr$. Then, from (17), the deviation curvature of coexistence is

$$P = -cr. \tag{29}$$

We discuss the ecological meaning of (29) in Section 4.1.

In the case of extinction, i.e. $x_0 = y_0 = 0$, (27) becomes

$$J = \begin{pmatrix} r & 0 \\ 0 & -c \end{pmatrix}. \tag{30}$$

In this case, since $N = -(r-c)/2$ and $Z = -cr$, the deviation curvature of extinction is

$$P = \frac{1}{4}(r-c)^2 + rc. \tag{31}$$

This is always positive, i.e. the extinction state is the Jacobi unstable.

4. Discussion

4.1. Geometric structure of competitions and predations: Jacobi stability and linear stability

In this paper, we have considered the geometric meaning of competition and predation based on KCC theory. In the case of the two species coexisting, the deviation curvatures of competition and predation were given by

$$P = \frac{1}{4}\{(A_1 - A_2)^2 + 4a_1a_2A_1A_2\} > 0, \tag{32}$$

$$P = -cr < 0, \tag{33}$$

where $A_1 = -r_1x_0/k_1$ and $A_2 = -r_2y_0/k_2$. These equations show that the deviation curvature of the competition and predation are always positive and negative, respectively. That is, the competition and the predation have essentially distinct geometric structures.

The ecological meaning of this result can be understood if we return to the equations for the geometric quantities in terms of the Jacobian matrix, which were derived in Section 3.1:

$$N = -\frac{1}{2}tr[J], \tag{34}$$

$$Z = det[J], \tag{35}$$

$$P = \frac{1}{4}\{(tr[J])^2 - 4det[J]\}. \tag{36}$$

As indicted in Section 2, the left term of Eq. (36) is related to the Jacobi stability, i.e.

$$\begin{cases} \text{Jacobi stable for } P \leq 0, \\ \text{Jacobi unstable for } P > 0. \end{cases} \tag{37}$$

On the other hand, the right term of Eq. (36) is related to the linear stability. Let $\triangle$ be a discriminant of the characteristic polynomial of J: $\triangle = (tr[J])^2 - 4det[J]$. In this case, the classification of an equilibrium point as shown on a single diagram such as Fig. 1(a) is well known (e.g. [21]). From (34) and (35), this diagram gives the relationship between the Jacobi stability and the linear stability, as shown in Fig. 1(b). Fig.1(b) shows that the deviation curvature corresponds to the discriminant, i.e. the Jacobi stability distinguishes the node-saddle system and the spiral-centre system, as pointed out by Sabău [11, 18]. Fig. 1(b), however, also shows that the linear stability is related to the nonlinear connection but not to the deviation curvature. That is, the system is

$$\begin{cases} \text{linear stable for } N > 0, \\ \text{linear unstable for } N < 0. \end{cases} \tag{38}$$

The coexistence of predation systems often results in periodic variations in populations (e.g. [22, 23]). This corresponds to the spirals in the linear stability theory, so the deviation curvature of the predations should be negative at least. This agrees with Eq. (33). On the other hand, the coexistence state of the competition system is not periodic, i.e. no nodes exist. Therefore, the deviation curvature of the competition should be positive at least, in agreement with Eq. (32).

The zero-connection curvature of the competitions derived in Section 3.2 ($Z = (1 - a_1 a_2)A_1 A_2$) allows geometric interpretation of the intra- and inter-species competition as follows. When the interspecific competition is more intense than the intraspecific competition, i.e. $a_1 a_2 > 1$, we have negative Z.

However, when the intraspecific competition is more intense, i.e. $a_1 a_2 < 1$, we have positive Z. Because $P > 0$ and $N > 0$ in the competition system, the latter case ($Z > 0$) is Jacobi unstable and in the linear stable region of Fig. 1(b), i.e. the stable nodes. The former case ($Z < 0$) is in the Jacobi unstable region, i.e. the saddle points. These results show that the sign of geometric quantities in KCC theory can describe the type of the ecological interactions.

4.2. Geometric structure of potential surface and stability

As indicated in the previous section, Eqs. (34), (35) and (36) are useful for analysing the geometric structure of the ecological system. The left-hand sides of these equations are geometric quantities, but the right hand sides are not. To fully geometrise the ecosystem, we must try to express these equations as purely geometric relations. For this, we introduce the concept of a potential surface. Because ecological systems have often been analysed using the Lyapunov function, the results of this discussion are expected to show how the geometric restriction of the potential surface affects the stability of the ecological system.

We define the potential $V = V(x^i)$ for the vector field in Eq. (9) as

$$\dot{x}^i = f^i(x) = -\partial_i V(x). \tag{39}$$

In the two-dimensional case, the necessary and sufficient condition for the existence of the potential $V = V(x^1, x^2)$ is $\partial_2 f^1 = \partial_1 f^2$. In this case, the Jacobian matrix (13) becomes

$$J = \begin{pmatrix} -\partial_1\partial_1 V & -\partial_2\partial_1 V \\ -\partial_1\partial_2 V & -\partial_2\partial_2 V \end{pmatrix}. \tag{40}$$

Therefore, $tr[J]$ and $det[J]$ correspond to the mean curvature H and Gaussian curvature K of the potential surface, respectively.

$$tr[J] = -(\partial_1\partial_1 V + \partial_2\partial_2 V) = -2H, \tag{41}$$

$$det[J] = (\partial_1\partial_1 V)(\partial_2\partial_2 V) - (\partial_1\partial_2 V)^2 = K. \tag{42}$$

Eqs. (34), (35) and (36) can therefore be expressed as purely geometric relations:

$$N = H, \tag{43}$$

$$Z = K, \tag{44}$$

$$P = H^2 - K. \tag{45}$$

Eqs. (43) and (44) show the geometric quantities of KCC theory: N and Z correspond to H and K in classic differential geometry, respectively. As Fig. 1 indicates, the classification of the equilibrium points is determined by N and Z. On the other hand, H and K are fundamental quantities that characterise the surface. Therefore, this correspondence describes the effect of the geometric restrictions on the stability of the system.

What is the meaning of the remaining equation (45)? When the potential surface is a smooth closed surface embedded in three-dimensional space, we can define the Willmore energy W as [24, 25]:

$$W = \int_V (H^2 - K) dA, \tag{46}$$

where dA is the area form of V. In this case, Eqs. (45) and (46) show that the deviation curvature of KCC theory corresponds to a kind of Willmore energy density per unit area.

When the potential surface is minimal, i.e. $H = 0$, we have $P = -K$. This shows that the sign of the deviation curvature (i.e. Jacobi stable or unstable) depends on the Gaussian curvature. Moreover, if we can define the Willmore energy, the integration of the deviation curvature is expressed only by the topological invariant, following the Gauss-Bonnet theorem. For example, this is the case of a velocity potential surface with zero vortex [26]. In this case, Okubo-Weiss's Q-value Q corresponds to the deviation curvature P, since the Q-value is defined as the negative Gaussian curvature: $Q = -K$ [27]. In fact, Okubo-Weiss's Q-value has been interpreted as the stability of the trajectory of Lagrangian particles immersed in a velocity field [28, 29].

Eq. (40) means that the eigenvalues of the Jacobi matrix are the principal curvature of the potential surface. Since the principal curvature in ordinary differential geometry is expressed in terms of real numbers, we assume a condition for the eigenvalues to be real numbers: $H^2 - K \geq 0$. From (45), this means that $P \geq 0$. In this case, the application of (44) and (45) to Fig.

1 gives the following correspondence:

(1) $P > 0$,
  (1-1) $K > 0$ (elliptic) $\longleftrightarrow$ nodes,
  (1-2) $K < 0$ (hyperbolic) $\longleftrightarrow$ saddle,
  (1-3) $K = 0$ (parabolic) $\longleftrightarrow$ non-isolated fixed points,

(2) $P = 0 \longleftrightarrow$ degenerate nodes.

These correspondences show that the deviation curvature P and the Gaussian curvature K are related to the type of equilibrium point. On the other hand, Eqs. (38) and (43) show that the mean curvature H is related to the stability of the equilibrium point: the system is stable for $H > 0$ and unstable for $H < 0$.

We now discuss the effect of the geometric restriction on the stability. The Hartman-Grobman theorem (e.g. [21]) states that *the local phase portrait near a hyperbolic equilibrium point is topologically equivalent to the phase portrait of the linearisation; in particular, the stability type of the equilibrium point is faithfully captured by the linearisation.* When the equilibrium point is hyperbolic, the Gaussian curvature of the potential surface is negative, so Eq. (45) shows that the deviation curvature is always positive, i.e. the system is always Jacobi unstable. According to the theorem, this is captured by the linearisation. For example, when the potential surface is the minimal surface ($H = 0$ and $K < 0$), the stability type of the equilibrium point is captured by the linearisation. However, if the equilibrium point is non-hyperbolic, the Gaussian curvature is more than zero, so the sign of the deviation curvature (i.e. the Jacobi stability) is not uniquely determined. For example, when the potential surface is elliptic ($K > 0$), the stability type cannot be uniquely determined.

4.3. Nonequilibrium case of predations and competitions

In this paper, we have studied small perturbations at the equilibrium point. However, KCC theory can treat small perturbations at any point. In this section, we discuss the deviation curvature in the nonequilibrium case for the predation and the competition systems.

First, we consider the predation system. To use Eq. (6) based on Eq. (1), we rewrite Eqs. (25) and (26) as the equation for the predator $y = x^2$ by vanishing $x = x^1$:

$$\ddot{y} + \gamma = 0, \tag{47}$$

with

$$\gamma = -\frac{\dot{y}^2}{y} + (ay - r)\dot{y} + acy^2 - cry, \tag{48}$$

where $\gamma = g^2$. To derive this equation, we assume that $y \neq 0$, so the following case is that of coexistence. From (5), (7) and (8), we have $N_2^2 = (1/2)\partial\gamma/\partial\dot{y} = -\dot{y}/y + (ay - r)/2$, $G_{22}^2 = -1/y$ and $Z_2^2 = \dot{y}^2/y^2 + a\dot{y} + 2acy - cr$. Therefore, from (6), the deviation curvature of the predator in the nonequilibrium case can be obtained:

$$P_2^2 = -\frac{a}{2}\dot{y} - acy + \frac{a^2}{4}\left(y - \frac{r}{a}\right)^2. \tag{49}$$

This is derived from the equation for the predator (47). In a similar fashion, we can derive the deviation curvature of the prey in the nonequilibrium case:

$$P_1^1 = \frac{b}{2}\dot{x} - brx + \frac{b^2}{4}\left(x - \frac{c}{b}\right)^2. \tag{50}$$

The comparison between Eq. (49) and Eq. (50) shows that the predator and prey have distinct geometric structure in the nonequilibrium case because the original equations (25) and (26) are not symmetric for the predator and prey. However, the predator and prey in the equilibrium case ($y = y_0 = r/a$ and $x = x_0 = c/b$) have the same geometric structure, $P_1^1 = P_2^2 = -cr$, in agreement with Eq. (29). This implies that the equilibrium point can be interpreted as the point in which the two deviation curvatures become equal, although the original equations have a nonsymmetric variable structure. In other words, the nonsymmetric structure inherent in the system develops over the geometric structure in the nonequilibrium region. As noted in Sections 4.1 and 4.2, the geometric structure of the dynamic system is related to the stability of the system, which means that the system has a different stability structure for each species in the nonequilibrium region.

Next, we consider the competition system (18) and (19). In a similar fashion to that described above, we can obtain the deviation curvature of the competition in the nonequilibrium case:

$$
\begin{aligned}
P_1^1 = &\left(-\frac{1}{2k_1} + \frac{1}{a_1 k_2} - \frac{a_2}{2k_2}\right)\dot{x} + \left(\frac{1}{4k_1^2} + \frac{1}{a_1 k_1 k_2} - \frac{3a_2}{2k_1 k_2} + \frac{a_2^2}{4k_2^2}\right) x^2 \\
&+ \left(\frac{1}{2k_1} - \frac{1}{a_1 k_2} + \frac{a_2}{2k_2}\right) x + \frac{1}{4},
\end{aligned} \tag{51}
$$

where we assume that $x \neq 0$. Moreover, we assume that $r_1 = r_2 = 1$ because the natural growth rate is not related to the stability analysis. The deviation curvature for species y has the same structure because the original equations (18) and (19) are symmetric for x and y. When the two species coexist $x = x_0 = (k_1 - a_1 k_2)/(1 - a_1 a_2)$, in agreement with Eq. (22). When only x survives, $x = x_0 = k_1$, in agreement with Eq. (24). These results mean that nonlinear analysis gives the same result as linear analysis around the equilibrium point.

4.4. Extended predation system: bifurcations and KCC theory

The stability according to linear theory plays an important role in bifurcation theory. How is the Jacobi stability of KCC theory related to bifurcation theory? Here we consider a simple example.

To consider bifurcation, we modify Eqs. (25) and (26) as

$$
\dot{x} = rx\left(1 - \frac{x}{k}\right) - \frac{axy}{1 + hx}, \tag{52}
$$

$$
\dot{y} = \frac{bxy}{1 + hx} - cy, \tag{53}
$$

where the new parameter k is the carrying capacity of the prey, and h is the saturation of the predation rate. When $b > ch$, the equilibrium population of the coexistence case is $(x_0, y_0) = (c/(b - ch), (r/a)(1 - x_0/k)(1 + hx_0))$. According to linear stability analysis, the critical point is $x_C = (1/2)(k - 1/h)$, and the system is linearly stable for $x_0 > x_C$ and linearly unstable for $x_0 < x_C$.

We reconsider this bifurcation from the viewpoint of KCC theory. The Jacobian matrix of Eqs. (52) and (53) is

$$
J = \begin{pmatrix} \dfrac{2rhx_0}{k(1 + hx_0)}(x_C - x_0) & \dfrac{-ax_0}{1 + hx_0} \\ \dfrac{by_0}{(1 + hx_0)^2} & 0 \end{pmatrix}. \tag{54}
$$

From (15), (16) and (17), we have

$$N = -\frac{rhx_0}{k(1+hx_0)}(x_C - x_0), \tag{55}$$

$$Z = \frac{abx_0y_0}{(1+hx_0)^3}, \tag{56}$$

$$P = N^2 - Z. \tag{57}$$

Eq. (55) shows that the sign of the nonlinear connection is changed due to the bifurcation. However, Eq. (57) shows that the bifurcation does not affect the sign of the deviation curvature. In KCC theory, the sign of the deviation curvature has been of considerable concern because this is related to the Jacobi stability. However, this result means that sign of the other geometric quantities such as N and Z should receive attention because it is expected to be related to the bifurcations. For example, Fig. 1 implies that the nonlinear connection is related to bifurcations such as the Hopf type, and the zero-connection curvature is related to bifurcations such as the saddle-node type. As a subject of future study, it would be interesting to consider how differential geometric structures are related to the type of bifurcation.

5. Conclusions

Our main conclusions are as follows.

1. The geometric quantities of KCC theory can be expressed in terms of the Jacobian matrix of the linearised system. This clarifies the relationship between the Jacobi stability and the linear stability, as shown in Fig. 1.
2. The competitions and predictions described by Lotka-Volterra system show a distinct geometric structure. This reflects the type of equilibrium point in the sense of the ecology.
3. When the potential of a dynamic system can be defined, the nonlinear connection and the zero-connection curvature correspond to the mean and Gaussian curvature of the potential surface, respectively. In this case, the deviation curvature is a function of only one geometric concept: the curvature. This means that the geometric structure of the potential surface restricts not only the linear stability but also the Jacobi stability.

4. When the equations of the system have nonsymmetric structures for the species (e.g. the predation system), each species also has nonsymmetric geometric quantities in the nonequilibrium region, but symmetric quantities around the equilibrium point. This means that KCC theory is useful for considering the development of the nonsymmetric system.
5. In KCC theory, the deviation curvature has been of considerable concern. However, as the extended predation system implies, other geometric quantities such as the nonlinear connection and the zero-connection curvature are also important because they may be related to bifurcation theory.

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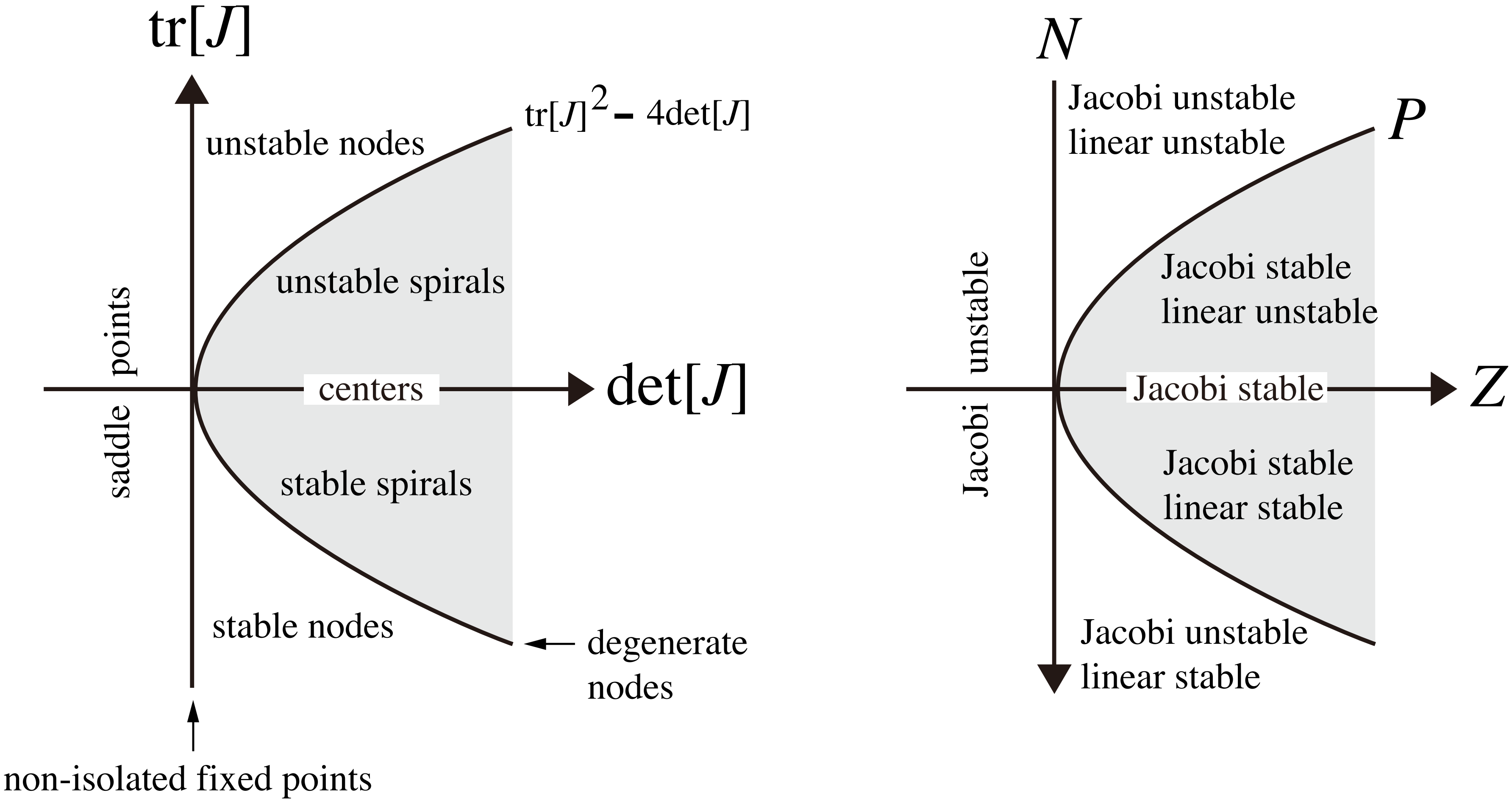
Figure captions

Fig. 1. Type and stability of the equilibrium points. (a) The well known diagram expressed in terms of the Jacobian J. (b). The corresponding diagram expressed in terms of the geometrical quantities of the KCC theory. Note that the N-axis is reversed because N is given by negative $Tr[J]$.


tr[J]
tr[J]^2 – 4det[J]
unstable nodes
unstable spirals
saddle points
centers
det[J]
stable spirals
stable nodes
degenerate nodes
non-isolated fixed points
N
Jacobi unstable
linear unstable
P
Jacobi stable
linear unstable
Jacobi unstable
Jacobi stable
Z
Jacobi stable
linear stable
Jacobi unstable
linear stable

(a) (b)