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Species Coexistence and Extinction Resulting from Higher-order Lotka-Volterra Two-Faction Competition

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Abstract— **It is known that the effect of species' density on species' growth is non-additive in real ecological systems. This challenges the conventional Lotka-Volterra model, where the interactions are always pairwise and their effects are additive. To address this challenge, we introduce HOIs (Higher-Order Interactions) and are able to capture, for example, the indirect effect of one species on a second one correlating to a third species. Towards this end, we propose a purely cooperative higher-order Lotka-Volterra model and a higher-order Lotka-Volterra two-faction competition model. By utilizing the theory of monotone systems, we provide stability conditions for both models. The stability analysis further shows that small HOIs usually promote the coexistence of all species, while the extinction of some species is usually caused by a huge difference among the higher-order competitive terms. Finally, illustrative numerical examples are provided to highlight our contributions.**

Index Terms— **Higher-order Interactions, Lotka-Volterra model, Stability analysis**

I. Introduction

The Lotka-Volterra model is one of the most fundamental and widely adopted population models in mathematical biology and ecology, originating from Lotka [1] and Volterra [2]. An early analysis of the 2-species Lotka-Volterra model was conducted by [3]. Then, the stability results of the multi-species cooperative model (see Chapter 4 and Definition 16 [4]) were derived by [5], while [6] studied the stability of a generalized multi-species model with both competition and mutualism. Abundant book or textbook contributions [4], [7], [8] provide a detailed and comprehensive introduction to the conventional Lotka-Volterra models and their stability results. However, all these conventional models treat the species *pair* as a fundamental unit and only capture *pairwise* interactions, whose effects on the species' growth are additive.

Prompted by studies in ecology, such pairwise interaction and its purely additive setting are shown to be insufficient to represent real complex ecological systems, supported, for example, by [9]. In the recent study [10], *HOIs* (Higher-order Interactions) are introduced to represent non-additive effects and further incorporate the empirical evidence, e.g. the one showing HOIs play a significant role in natural plant communities. Followed by this idea, [11] introduced HOIs into the Lotka–Volterra competition and then demonstrated, by using empirical data and simulations, that HOIs appear under almost all assumptions and help to improve the accuracy of model predictions. Despite the advantages brought by HOIs, the model becomes mathematically more challenging to analyze. In order to understand what role HOIs play in influencing the species' coexistence, [12], utilizing the higher-order Lotka-Volterra model, studies the aforementioned problem through simulations. Even more recently, in [13], numerical simulations with techniques from statistical physics are used to estimate the HOIs' influence on species coexistence. The results of the existence and stability of equilibria in the higher-order Lotka-Volterra model by rigorous mathematical proof are still largely missing, mainly because the higher-order system is highly nonlinear.

Alongside developments regarding the stability of the conventional Lotka-Volterra model, there is a long history concerning monotone systems' theory [14], [15], which is a useful tool whenever the system is cooperative or its Jacobian can be permuted into an irreducible Metzler matrix. Very recently, monotone systems' theory has been applied to study the bi-virus competition model [16], whereas the tri-virus competition model is shown not to be a monotone system [17]. In [18], an abstract system of two-subcommunity competition is studied, but the main results are restricted to the positive equilibrium and not applicable to the higher-order system. Furthermore, a generalization of cooperativity is introduced and further analyzed in [19]. All these tools serve as a good foundation to study a higher-order Lotka-Volterra model.

The contributions of this paper are summarized as follows: first, inspired by [11] and taking cooperation (mutualism) into account, we propose a purely cooperative higher-order Lotka-Volterra model and a higher-order Lotka-Volterra two-faction competition model. Second, by using the theory of monotone systems and the properties of an irreducible Metzler matrix, we provide stability conditions for each equilibrium. Our analytical results mathematically confirm some theoretical expectations in [12], [13], which were achieved either via simulations or by adopting some approximation. The results of the existence of the equilibria are obtained via perturbation theory under the condition that the higher-order interaction is small. Finally, we provide numerical examples to highlight our theoretical results.

Notation: Throughout this paper, whenever $a, b \in \mathbb{R}^n$, we

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use the notation $a \geq (\leq) b$ to denote that $a_i \geq (\leq) b_i$, for all $i = 1, \ldots, n$; $a > (<) b$ to denote that $a_i > (<) b_i$, for all $i = 1, \ldots, n$. For simplicity, the equilibrium point denotes both the point itself and the vector constructed from the point.

II. Cooperative Lotka-Volterra Model

Inspired by [11], we consider a higher-order cooperative Lotka-Volterra model for n species:

$$\dot{x_i} = r_i x_i \left(1 - a_{ii} x_i + \sum_{j \neq i} a_{ij} x_j - b_{iii} x_i^2 + \sum_{j,k \in Q} b_{ijk} x_j x_k \right) = r_i x_i L_i(x), \tag{1}$$

where for the given focal species i, $Q = \{j, k \,|\, (j,k) \neq (i,i)\}$, x_i denotes the density of species i; r_i is the per-capita intrinsic rate of increase of the focal species; a_{ij} is the first-order coefficient, denoting j's additive influence on i, and b_{ijk} is the second-order (higher-order) coefficient, denoting j and k's joint non-additive influence on i, or alternatively j's influence on i correlated with a co-occurring third species k. Since we consider here cooperative systems, which represent the symbiosis among several species, it is natural to assume that the inter-specific interaction is non-negative. We further assume that the intra-specific interaction is non-positive, which is interpreted as competition within the species. Thus, all parameters in (1) are non-negative. If all parameters in the model are assumed to be real, then the model is a generalized higher-order Lotka-Volterra model. Throughout the section, we assume $A = [a_{ij}]$ is irreducible such that $G(A)$ is strongly connected.

Remark 1: From the perspective of network science, if we ignore higher-order terms, then (1) is a model on a graph. One can construct the digraph and label all the species as nodes in the digraph. Then, one links node j to i with the weight a_{ij}. If we further consider higher-order terms, the model is then based on a hypergraph. Simply speaking, a hypergraph is a higher-order network where one hyperedge can have multiple tails and heads. In our model (1), we have the last term for three-body interactions. For example, b_{ijk} denotes j and k's joint influence on i. So one can create a hyperedge with the weight b_{ijk}, where j and k are the heads and i is the tail. For a more detailed explanation of the concept of a hypergraph and the dynamical systems on it, interested readers may refer to [20]. For the definition of a directed hyperedge, one may refer to [21].

Now we give some properties of the dynamical system (1).

Theorem 1: The system given by (1) is an irreducible monotone system in $\mathbb{R}^n_+$. Furthermore, if the system has an open and bounded positively invariant set $\mathcal{T} = \{x | \mathbf{0}_n < x < \mathbf{E}\}$, where $\mathbf{E} \in \mathbb{R}^n$, and if the model has a finite number of equilibria in the closure of $\mathcal{T}$, then the set of initial conditions in $\mathcal{T}$, such that the model does not converge to an equilibrium, is a set of Lebesgue measure zero.

Proof: Firstly, we calculate the Jacobian, which has components

$$\frac{\partial \dot{x}_i}{\partial x_i} = r_i L_i + r_i x_i (-a_{ii} - 2b_{iii} x_i + \sum_{k \neq i} b_{iik} x_k + \sum_{k \neq i} b_{iki} x_k), \tag{2}$$

$$\frac{\partial \dot{x}_i}{\partial x_j} = r_i x_i (a_{ij} + \sum_{k \neq i} b_{ijk} x_k + \sum_{k \neq i} b_{ikj} x_k). \tag{3}$$

We observe that the Jacobian is always an irreducible Metzler matrix (Definition 10.1 [8]). This ensures that (1) is an irreducible monotone system. Under the condition that the equilibrium set is finite and the system domain is bounded, by Lemma 2.3 of [16], the proof is completed. ■

Remark 2: Since the Jacobian of the system is an irreducible Metzler matrix, the system is indeed a cooperative system (see Chapter 4 and Definition 16 [4]). Theorem 1 requires that the positively invariant set of the system is open and bounded. One can easily check that the system is lower-bounded. Thus, this condition only requires that all solutions of the system have a supremum $\mathbf{E}$. It is worthwhile to mention that the system is not always upper-bounded and solutions may diverge to infinity due to the cooperation terms. Moreover, to derive the equilibrium set and to see whether it is finite, one only needs to check whether the equation set of $L_i = 0$ (which is a set of quadratic equations with multiple variables) for $i \leq n$ has a finite number of solutions. If we set all $a_{ij} = 0$ for $i \neq j$ and $b_{ijk} = 0$ for $j, k \in Q$, it is straightforward to check that the equilibrium set is finite. Also note that this parameter setting can only be used to check whether there is a particular choice such that the equation has a finite number of solutions. Since this algebraic question is different from the analysis of a system, it doesn't break the assumption that A is irreducible. According to Theorem B.1 and Corollary B.2 in [16], since there exists a particular choice of parameters such that the equation has a finite number of solutions, if the parameters are generic and do not lie on a certain algebraic set of measure zero, then the equilibrium set is finite. Since divergence to infinity is not natural in reality, we focus on the case when the system is upper-bounded throughout this paper. According to the definition of an irreducible monotone system, if there exists a positive equilibrium X^*, then $\{x | \mathbf{0} < x < X^*\}$ is positively invariant.

Before we introduce further results, We recall that an irreducible Metzler matrix has the following property.

Lemma 1 (Theorem 10.14 in [8]): If M is an irreducible Metzler matrix, then M is a Hurwitz matrix if and only if there is a vector $x > \mathbf{0}$ that satisfies $Mx < \mathbf{0}$.

Throughout this paper, we say that the species is a winner when it takes some positive value in the corresponding equilibrium or is a loser when it takes the zero value. We use the set S to denote the set of agents of the winner faction. A boundary equilibrium X^* is an equilibrium where $x_i \neq 0$ for some $i \in S$ with non-empty S and $x_j = 0$ for the rest.

Theorem 2: Consider system (1), then the following hold:

a) the origin is always an equilibrium and is unstable;
b) a boundary equilibrium, if it exists, is always unstable;

c) if an all-species-coexistence equilibrium point $X^* = (x_1^*, x_2^*, \cdots, x_n^*) \in \mathcal{T}$ exists, and if the second-order cooperative coefficients b_{ijk} $(j, k \in Q)$ are sufficiently small such that $(\mathbf{J}_{(X^*)} X^*) < \mathbf{0}$ with $\mathbf{J}_{(X^*)}$ the Jacobian of the system (1) at X^*, then X^* is locally stable.

Proof: For statement a), it is straightforward to see that $\mathbf{0}_n$ is always a solution of $r_i x_i L_i = 0$. For the equilibrium point $\mathbf{0}_n$, the corresponding Jacobian matrix is $\mathbf{J}_{(\mathbf{0}_n)} = \mathsf{diag}((r_1, \cdots, r_n)^\top)$. Since $r_i > 0$, the equilibrium point $\mathbf{0}_n$ is unstable.

Next, we prove statement b). By assumption, let (1) have a boundary equilibrium of $m < n$ winners. Consequently, the densities of the rest $n - m$ species are zero. Without loss of generality, we write the boundary equilibrium as $(x_1^*, x_2^*, \cdots, x_m^*, 0, 0, \cdots, 0) = (X_m^*, \mathbf{0}_{n-m})$. Note that any other boundary equilibrium can be written in the previous form by index permutation. The corresponding Jacobian matrix of a boundary equilibrium is $\mathbf{J}_{(X_m^*, \mathbf{0}_{n-m})} = \begin{pmatrix} M & \Omega \\ \mathbf{0}_{(n-m)\times m} & D \end{pmatrix}$, where M is an irreducible Metzler matrix, D is a diagonal matrix, with its diagonal entry $D_i = r_i(1 + \sum_{j\in S} a_{ij}x_j + \sum_{j,k\in S} b_{ijk}x_j x_k) > 0$, where S includes all the species of the winner faction. Hence, all boundary equilibrium points are unstable.

Finally, we investigate statement c). For the equilibrium point $X^* = (x_1^*, x_2^*, \cdots, x_n^*)$, the corresponding Jacobian matrix $\mathbf{J}_{(X^*)}$ is an irreducible Metzler matrix. Moreover, we see that:

$$
\begin{aligned}
&(\mathbf{J}_{(X^*)} X^*)_i = r_i x_i^* L_i(x^*) \\
&+ r_i x_i^* \left(-a_{ii}x_i^* - 2b_{iii}x_i^{*2} + \sum_{k\neq i} b_{iik}x_i^* x_k^* + \sum_{k\neq i} b_{iki}x_i^* x_k^* \right) \\
&+ \sum_{j\neq i} r_i x_i^* \left(a_{ij}x_j^* + \sum_{k\neq i} b_{ijk}x_j^* x_k^* + \sum_{k\neq j} b_{ikj}x_k^* x_j^* \right).
\end{aligned}
$$

Recalling (1) and plugging $r_i x_i^* L_i(x^*) = 0$ in the equation above, one can get $(\mathbf{J}_{(X^*)} X^*)_i = -r_i x_i^* + r_i x_i^*(-b_{iii}x_i^{*2} + \sum_{j,k\in Q} b_{ijk}x_j^* x_k^*)$. It follows that once there is equilibrium point $X^* = (x_1^*, x_2^*, \cdots, x_n^*) \in \mathcal{T}$, and if b_{ijk} $(i, j \in Q)$ is sufficiently small, then $(\mathbf{J}_{(X^*)} X^*)_i < 0$. Thus, the Jacobian is Hurwitz and furthermore, the equilibrium point $X^* = (x_1^*, x_2^*, \cdots, x_n^*)$ is stable by Lemma 1. ■

Now that we have described the dynamics of a single-faction model, we are ready to look into the two-faction model.

III. Higher-order Two-faction-competition Lotka-Volterra Model

Consider the case where two factions of species (or agents), denoted by $x \in \mathbb{R}^m$ and $y \in \mathbb{R}^n$ respectively, compete with each other but the agents inside the camp cooperate with each other. The corresponding model reads as:

$$
\begin{aligned}
\dot{x}_i &= r_i x_i \Big(1 - a_{ii}x_i + \sum_{j\neq i, j\in\mathbb{I}_m} a_{ij}x_j - \sum_{j\in\mathbb{I}_n} b_{ij}y_j \\
&\quad - c_{iii}x_i^2 + \sum_{j,k\in Q, j,k\in\mathbb{I}_m} c_{ijk}x_j x_k - \sum_{j,k\in\mathbb{I}_n} d_{ijk}y_j y_k \Big) \\
&= r_i x_i L_i(x, y), \qquad i \in \mathbb{I}_m,
\end{aligned}
\tag{4}
$$

$$
\begin{aligned}
\dot{y}_i &= \hat{r}_i y_i \Big(1 - \hat{a}_{ii}y_i + \sum_{j\neq i, j\in\mathbb{I}_n} \hat{a}_{ij}y_j - \sum_{j\in\mathbb{I}_m} \hat{b}_{ij}x_j \\
&\quad - \hat{c}_{iii}y_i^2 + \sum_{j,k\in Q, j,k\in\mathbb{I}_n} \hat{c}_{ijk}y_j y_k - \sum_{j,k\in\mathbb{I}_m} \hat{d}_{ijk}x_j x_k \Big) \\
&= \hat{r}_i y_i \hat{L}_i(x, y), \qquad i \in \mathbb{I}_n,
\end{aligned}
\tag{5}
$$

where $\mathbb{I}_m = \{1, 2, \cdots, m\}$, $\mathbb{I}_n = \{1, 2, \cdots, n\}$, and m, n are the total number of species in each faction respectively; $a_{ij}, b_{ij}, \hat{a}_{ij}, \hat{b}_{ij}$ are the first-order coefficients and $c_{ijk}, d_{ijk}, \hat{c}_{ijk}, \hat{d}_{ijk}$ are the higher-order coefficients. As for the modeling setup, we assume that all the parameters are non-negative so that all the intra-faction interaction is non-negative except the non-positive self-competition of one agent (species) with itself, while the inter-faction interaction is non-positive. We further assume that there is no multi-body interaction, where head agents are from different factions, i.e., there are no crossed terms $x_i y_j$. The modeling setting of the two factions is similar to that of bi-virus in epidemics [22]. We further assume throughout the section that the matrix $\begin{pmatrix} (a_{ij})_{m\times m} & (b_{ij})_{m\times n} \\ (\hat{b}_{ij})_{n\times m} & (\hat{a}_{ij})_{n\times n} \end{pmatrix}$ is irreducible. In general, the model described by (1) can be regarded as a special case of (4)-(5), where one faction is empty. For simplicity, throughout this paper, we call x the first faction and y the second. Define the notation $z = (x^\top, y^\top)^\top$ and z_0 denote the initial condition.

Theorem 3: The system (4)-(5) is an irreducible monotone system in $\mathbb{R}_+^{n+m}$.

Proof: Firstly, one can check that the Jacobian of (4)-(5) is of the form $\mathbf{J} = \begin{pmatrix} M_1 & T_1 \\ T_2 & M_2 \end{pmatrix}$, where M_1, M_2 are irreducible Metzler matrices, and T_1, T_2 are non-positive matrices (it is irreducible as long as $z > \mathbf{0}_{n+m}$). It follows that $\mathbf{J}$ can be permuted into an irreducible Metzler matrix $\tilde{\mathbf{J}} = \begin{pmatrix} M_1 & -T_1 \\ -T_2 & M_2 \end{pmatrix}$ via the matrix $P = \begin{pmatrix} I_m & \mathbf{0}_{m\times n} \\ \mathbf{0}_{n\times n} & -I_n \end{pmatrix}$, so the system (4)-(5) is irreducible monotone. ■

Remark 3: Theorem 3 tells us, in particular, that the Jacobian of the two-faction competition model can be permuted into an irreducible Metzler matrix. However, if one would deal with competition among more than two factions, the permutation may be no longer possible. For example, if we consider 3 factions, the structure of the Jacobian with 3 factions is analog to the case of Theorem 1 in [17]. A permutation is not possible for the same reason in [17]. In addition, the two-faction system may still diverge to infinity because of the cooperation terms.

In the following Theorems 4-8, we list all the possible equilibria of the model and study their stability.

Theorem 4: Consider the system (4)-(5), the origin is always an equilibrium and is unstable.

Proof: One can check that the zero vector is always a solution of the equation set ($r_i x_i L_i = 0$ and $\hat{r}_j y_j \hat{L}_j = 0$, $i \in \mathbb{I}_m, j \in \mathbb{I}_n$). Since the corresponding Jacobian matrix is $\mathbf{J}_{(\mathbf{0}_{m+n})} = \mathsf{diag}((r_1, \cdots, r_m, \hat{r}_1, \cdots, \hat{r}_n)^\top)$, clearly the equilibrium point $\mathbf{0}_{m+n}$ is unstable. ■

Theorem 5: Consider the system (4)-(5), and assume that a one-faction-wins-all boundary equilibrium $(X^*, \mathbf{0}_n) = (x_1^*, x_2^*, \cdots, x_m^*, 0, 0, \cdots, 0)$ or $(\mathbf{0}_m, Y^*) = (0, 0, \cdots, 0, y_1^*, y_2^*, \cdots, y_n^*)$ exists. Either equilibrium is locally stable whenever the coefficients of the first-order $(b_{ij}, \hat{b}_{ij} \,|\, i \neq j)$ and second-order $(d_{ijk}, \hat{d}_{ijk} \,|\, j, k \in Q)$ competitive terms from the loser faction are sufficiently large such that $D_i = \hat{r}_i(1 - \sum_{j\in S} \hat{b}_{ij} x_j^* - \sum_{j,k\in S} \hat{d}_{ijk} x_j^* x_k^*) < 0, \quad i \in \mathbb{I}_n$, and X^* or Y^* is a stable all-species-coexistence equilibrium point of the sub-cooperative-system from the winner faction when ignoring the loser faction.

Proof: Without loss of generality, we first investigate the case when the first faction is the winner. The equilibrium is then $(x_1^*, x_2^*, \cdots, x_m^*, 0, 0, \cdots, 0) = (X^*, \mathbf{0}_n)$. By plugging the equilibrium into the Jacobian, we obtain that $\mathbf{J}_{(X^*, \mathbf{0}_n)} = \begin{pmatrix} M & \Omega \\ \mathbf{0}_{n\times m} & D \end{pmatrix}$, where M is an irreducible Metzler matrix and represents the Jacobian of the sub-cooperative-system from the winner faction on an all-species-coexistence equilibrium point, D is a diagonal matrix, and its diagonal entry reads $D_i = \hat{r}_i(1 - \sum_{j\in S} \hat{b}_{ij} x_j^* - \sum_{j,k\in S} \hat{d}_{ijk} x_j^* x_k^*), \quad i \in \mathbb{I}_n$. Since the Jacobian is an upper-triangular block matrix, we know that the Jacobian is Hurwitz when all $D_i < 0, i \in \mathbb{I}_n$ and the matrix M is Hurwitz, which further implies that the coefficients of the first- and second-order competitive terms from the loser faction are sufficiently large and $(x_1^*, x_2^*, \cdots, x_m^*)$ is a stable all-species-coexistence equilibrium point of the sub-cooperative-system from the winner faction when ignoring the loser faction. We recall that the second condition is satisfied when the cooperative HOIs terms are sufficiently small for the winners. The proof, for the case when the second faction is the winner, is exactly the same and thus omitted here. ■

We then consider the following Lemma.

Lemma 2 (Corollary 3.2 and Proposition 3.5 [18]): Consider the system (4)-(5), if $(x_1^*, x_2^*, \cdots, x_m^*, 0, 0, \cdots, 0)$ and $(0, 0, \cdots, 0, y_1^*, y_2^*, \cdots, y_n^*)$ both exist and are both unstable, then there exists a positive all-species-coexistence equilibrium $(\tilde{x}_1^*, \tilde{x}_2^*, \cdots, \tilde{x}_m^*, \tilde{y}_1^*, \tilde{y}_2^*, \cdots, \tilde{y}_n^*)$ with $\tilde{x}_i^* \leq x_i^*, \tilde{y}_i^* \leq y_i^*$ for arbitrary i, and $\{z | \mathbf{0}_{(n+m)\times 1} \leq z \leq (x_1^*, x_2^*, \cdots, x_m^*, y_1^*, y_2^*, \cdots, y_n^*)^\top\}$ is a bounded positively invariant set.

The stability of a positive all-species-coexistence equilibrium can be checked by the following Theorem.

Theorem 6: Consider the system (4)-(5), if the all-species-coexistence equilibrium $(x_1^*, x_2^*, \cdots, x_m^*, y_1^*, y_2^*, \cdots, y_n^*)$ exists, then it is locally stable when the coefficients of all the first-order competitive terms $(b_{ij}, \hat{b}_{ij}, i \neq j)$ and all the second-order terms except the self-influence term $(c_{ijk}, d_{ijk}, \hat{c}_{ijk}, \hat{d}_{ijk}, j, k \in Q)$ are sufficiently small such that $\left(P\mathbf{J}_{(X^*,Y^*)}P\begin{pmatrix} X^* \\ Y^* \end{pmatrix}\right)_i < 0$ holds.

Proof: We know that the Jacobian $\mathbf{J}$ of the model (4)-(5) can be permutated into an irreducible Metzler matrix $\tilde{\mathbf{J}}$. Thus, $\mathbf{J}$ and $\tilde{\mathbf{J}}$ have the same eigenvalues. Therefore, $\mathbf{J}$ is Hurwitz if $\tilde{\mathbf{J}}$ is Hurwitz. Letting $Z^* = (X^*, Y^*)^\top$, we have

$$
\begin{aligned}
&\left(\tilde{\mathbf{J}}_{(X^*,Y^*)}\begin{pmatrix} X^* \\ Y^* \end{pmatrix}\right)_i = r_i x_i^* L_i(z^*) \\
&+ r_i x_i^* \Big(- a_{ii} x_i^* - 2c_{iii} x_i^{*2} + \sum_{k\neq i} c_{iik} x_i^* x_k^* + \sum_{k\neq i} c_{iki} x_i^* x_k^* \Big) \\
&\quad + \sum_{j\neq i} r_i x_i^* \Big(a_{ij} x_k^* + \sum_{k\neq i} c_{ijk} x_j^* x_k^* + \sum_{k\neq i} c_{ikj} x_j^* x_k^* \Big) \\
&\quad + \sum_{j\neq i} r_i x_i^* \Big(b_{ij} y_j^* + \sum_{k\in\mathbb{I}_n} d_{ijk} y_j^* y_k^* + \sum_{k\in\mathbb{I}_n} d_{ikj} y_j^* y_k^* \Big) \\
&= -r_i x_i^* + r_i x_i^* \Big(- c_{iii} x_i^{*2} + \sum_{j,k\in Q} c_{ijk} x_j^* x_k^* \\
&+ 3 \sum_{j,k\in Q} d_{ijk} y_j^* y_k^* + 2 \sum_{j\neq i} b_{ij} y_j^* \Big), \quad i \in \mathbb{I}_m.
\end{aligned}
$$

On the other hand, for $i = j + m, j \in \mathbb{I}_n$, $\left(\tilde{\mathbf{J}}_{(X^*,Y^*)}\begin{pmatrix} X^* \\ Y^* \end{pmatrix}\right)_i = -\hat{r}_i y_i^* + \hat{r}_i y_i^* \Big(- \hat{c}_{iii} y_i^{*2} + \sum_{j,k\in Q} \hat{c}_{ijk} y_j^* y_k^* + 3 \sum_{j,k\in Q} \hat{d}_{ijk} x_j^* x_k^* + 2 \sum_{j\neq i} \hat{b}_{ij} x_j^* \Big)$.

According to Lemma 1, $\tilde{\mathbf{J}}$ is Hurwitz if $b_{ij}, c_{ijk}, d_{ijk}, \hat{b}_{ij}, \hat{c}_{ijk}, \hat{d}_{ijk}$ are sufficiently small such that $\left(\tilde{\mathbf{J}}_{(X^*,Y^*)}\begin{pmatrix} X^* \\ Y^* \end{pmatrix}\right)_i < 0$ for all i. ■

Remark 4: In [5] (Theorem 3 and (A8) in Appendix) and [18] (Theorem 3.8), a sufficient condition for the global stability of a positive equilibrium (all-species-coexistence equilibrium) for the abstract system $\dot{N}_i = N_i F_i (N_1, N_2, \ldots, N_m), \quad i = 1, 2, \ldots, m$ was provided by Lyapunov theory [5] or monotone system theory [18]. Since both systems proposed in our paper can be written in such a form, the results in [5] are also valid for our models. However, Theorem 3.8 [18] can not apply to our system because HOIs break the condition 3.2. The results in [5], [18] miss the possibility of bistability and what kind of role the HOIs play in the species' coexistence. Our paper fills this gap.

Theorem 7: Consider the system (4)-(5), the boundary equilibrium $(x_1^*, \ldots, x_l^*, \mathbf{0}_{m-l}, \mathbf{0}_n), l < m$ or $(\mathbf{0}_m, y_1^*, \ldots, y_p^*, \mathbf{0}_{n-p}), p < n$, if it exists, is unstable.

Proof: We firstly investigate the first case $(x_1^*, \ldots, x_l^*, \mathbf{0}_{m-l}, \mathbf{0}_n), l < m$. The corresponding Jacobian matrix is $\mathbf{J}_{(X^*,0,\cdots,0)} = \begin{pmatrix} M & \Omega \\ \mathbf{0}_{(m+n-l)\times l} & D \end{pmatrix}$, where M is an irreducible Metzler matrix and represents the Jacobian of the sub-cooperative-system from the winner faction on a boundary equilibrium point, and D is a diagonal matrix. We know from Theorem 1, that M is unstable and thus the equilibrium $(x_1^*, \ldots, x_l^*, \mathbf{0}_{m-l}, \mathbf{0}_n), l < m$ is unstable. The proof, for the second case, is exactly analogous. ■

Remark 5: Theorem 7 shows that any equilibrium where the winners are a strict subset of a single faction, is unstable because any of those equilibria can be permuted into the equilibrium $(x_1^*, \dots, x_l^*, \mathbf{0}_{m-l}, \mathbf{0}_n), l < m$ or $(\mathbf{0}_m, y_1^*, \dots, y_l^*, \mathbf{0}_{n-l}), p < n$ by index permutation.

Theorem 8: Consider the system (4)-(5), the boundary equilibrium $M^* = (x_1^*, \cdots, x_a^*, \mathbf{0}_{m-a}, y_1^*, \cdots, y_b^*, \mathbf{0}_{n-b})$, if it exists, is locally stable when the coefficients of the first- ($b_{ij}, \hat{b}_{ij}, i \neq j$) and second-order competitive terms ($d_{ijk}, \hat{d}_{ijk}, j, k \in Q$) of the losers are sufficiently large, such that $1 + \sum_{j\in S} a_{ij}x_j^* - \sum_{j\in S} b_{ij}y_j^* + \sum_{j,k\in S} c_{ijk}x_j^* x_k^* - \sum_{j,k\in S} d_{ijk}y_j^* y_k^* < 0$ and $1 + \sum_{j\in S} \hat{a}_{ij}y_j^* - \sum_{j\in S} \hat{b}_{ij}x_j^* + \sum_{j,k\in S} \hat{c}_{ijk}y_j^* y_k^* - \sum_{j,k\in S} \hat{d}_{ijk}x_j^* x_k^* < 0$, and $(x_1^*, \cdots, x_a^*, y_1^*, \cdots, y_b^*)$ is a stable all-species-coexistence equilibrium point of the sub-system of the winners when ignoring the loser agents.

Proof: Firstly, we perform index permutation, and M^* can be permuted as $N^* = (x_1^*, \cdots, x_a^*, y_1^*, \cdots, y_b^*, \mathbf{0}_{m-a}, \mathbf{0}_{n-b})$. The corresponding Jacobian matrix after the index permutation is $\mathbf{J}_{N^*} = \begin{pmatrix} M & \Omega \\ \mathbf{0}_{(m+n-a-b)\times(a+b)} & D \end{pmatrix}$, where M is an irreducible Metzler matrix and represents the Jacobian of the sub-system of all winners on an all-species-coexistence equilibrium point, D is a diagonal matrix, with entries

$$D_i = r_i L_i(z^*) = r_i(1 + \sum_{j\in S} a_{ij}x_j^* - \sum_{j\in S} b_{ij}y_j^* + \sum_{j,k\in S} c_{ijk}x_j^* x_k^* - \sum_{j,k\in S} d_{ijk}y_j^* y_k^*);$$

if i denotes the loser agent in the first faction. Otherwise, if i denotes the loser agent in the second faction, D_i takes a similar form. In order to have all negative eigenvalues, the first- and second-order cooperative terms of the losers must be sufficiently small, so that all $D_i < 0$, and $(x_1^*, \cdots, x_a^*, y_1^*, \cdots, y_b^*)$ must be a stable all-species-coexistence equilibrium point of the sub-system of the winners when ignoring the loser agents so that M is Hurwitz. ■

Remark 6: Theorem 8 further implies that any equilibrium, where the winners are in the different camps, but not all of them, is stable under the same condition as Theorem 8 because any of those equilibria can be permuted into the equilibrium M^* or N^* by index permutation,

Remark 7: We are now able to provide a strategy different from [5], [18] to obtain sufficient conditions for the global stability of the positive equilibrium. If all the boundary equilibria are unstable, under the assumption that the system is upper-bounded, then there exists a positively invariant set $\mathcal{T} = \{x | \mathbf{0}_n < x < \mathbf{E}\}$. For example, the lemma 2 is a typical case. According to the Lemma 2.3 of [16], the solution converges to the positive equilibrium for almost all initial conditions in $\mathcal{T}$ and a generic choice of parameters, since the generic choice of parameters will ensure that there is a finite number of positive equilibria, because there is a particular choice of parameters which yields a finite number of solutions.

In summary, one can conclude that the small HOIs will usually promote all-species coexistence, while large differences among higher-order competitive terms usually result in the extinction of some of the species. These results coincide with the expectations in [13].

Now, it still remains unknown under which conditions an equilibrium other than the origin exists. Generally, it is challenging to give a comprehensive analysis that guarantees the existence of the equilibrium, because it is difficult to solve the multi-variable square equation set ($r_i x_i L_i = 0$ and $\hat{r}_j y_j \hat{L}_j = 0$, $i \in \mathbb{I}_m, j \in \mathbb{I}_n$). However, we are still able to give the result under a special case when the second-order interaction terms are sufficiently small so that regular perturbation theory can be applied. Let us now consider $0 < \epsilon \ll 1$ and the perturbed system:

$$\dot{x}_i = r_i x_i \big(1 - a_{ii}x_i + \sum_{j\neq i} a_{ij}x_j - \sum_{j\neq i} b_{ij}y_j - \epsilon c_{iii}x_i^2 + \sum_{j,k\in Q} \epsilon c_{ijk}x_j x_k - \sum_{j,k\in Q} \epsilon d_{ijk}y_j y_k\big), i \in \mathbb{I}_m, \quad (6)$$

$$\dot{y}_i = \hat{r}_i y_i \big(1 - \hat{a}_{ii}y_i + \sum_{j\neq i} \hat{a}_{ij}y_j - \sum_{j\neq i} \hat{b}_{ij}x_j - \epsilon \hat{c}_{iii}y_i^2 + \epsilon \sum_{j,k\in Q} \hat{c}_{ijk}y_j y_k - \epsilon \sum_{j,k\in Q} \hat{d}_{ijk}x_j x_k\big), i \in \mathbb{I}_n. \quad (7)$$

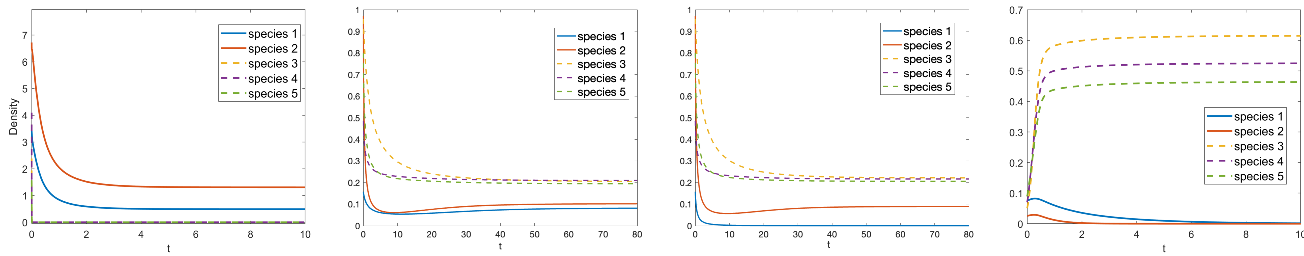
The system when all $\epsilon = 0$ is called an unperturbed system. The unperturbed system (6)-(7) with $\epsilon = 0$ corresponds to the conventional Lotka-Volterra model on a graph, which is well-introduced in, e.g., [4], [7], and from which we know when (6)-(7) with $\epsilon = 0$ has a hyperbolic equilibrium and whether it is stable.

Theorem 9: Consider the perturbed system (6)-(7). If the unperturbed system (6)-(7) with $\epsilon = 0$ has a hyperbolic equilibrium point $z^* = (x^*, y^*)$, then the perturbed system (6)-(7) also has a hyperbolic equilibrium point $\tilde{z}^*$ in the vicinity of the hyperbolic equilibrium point z^*.Furthermore, if z^* is locally stable, then $\tilde{z}^*$ is locally stable. Otherwise, if z^* is unstable, then $\tilde{z}^*$ is unstable.

Proof: We compactly write the state variable as $z = (x, y)^\top$. The unperturbed system can be represented as $\dot{z} = g(z)$ and the perturbed system as $\dot{z} = G(z, \epsilon)$, with $G(z, 0) = g(z)$. Let z^* be an equilibrium of the unperturbed system. By definition of the equilibrium point, $G(z^*, 0) = 0$ and $\frac{\partial G}{\partial x}(z^*, 0) = \frac{\partial g}{\partial z}(z^*)$. Due to the hyperbolicity of z^*, $\frac{\partial G}{\partial z}(z^*, 0) = \frac{\partial g}{\partial z}(z^*)$ has a nonvanishing determinant. By the implicit function theorem, there is a unique equilibrium in the neighborhood of z^* for sufficiently small ϵ. This equilibrium is also hyperbolic because of the continuous dependence of the eigenvalues of $\frac{\partial G}{\partial z}$ on ϵ. Thus, the local stability of the equilibrium persists. ■

IV. Numerical Example

In this section, we use some numerical examples to illustrate our analytical results in section 3. For the simulation setup, we randomly pick all the parameters from the set $[0, 10]$. Furthermore, the initial condition is randomly chosen from $[0, 10]$. We assume a total of 5 species, 2 in one faction and 3 in the other. Figures 1a-1c include all the possible results we can observe and are three typical examples for each case. Figure 1a is in line with Theorem 5, while Figure 1b corresponds to Theorem 6. Similarly, Figure 1c reflects the analytical results of Theorem 8. Since all other equilibria



(a) (b) (c) (d)

Fig. 1: (a) Only one faction wins and all members in the faction are the winners. (b) All species coexist. (c) Species from different factions win but some species die out. (d) From a different initial condition but the same parameters with (a), the solution converges to the different one-faction-wins-all boundary equilibrium. That is, bistability is reflected in an interchange of the winner faction.

are unstable, we don't observe that the solution converges to them from in simulation scenarios. From figure 1a and 1d, we confirm the bistability properties of the two-faction system. Furthermore, to highlight the influence of HOIs, the system parameters and initial conditions are the same in simulations 1b and 1c except that we change d_{1jk} to $5d_{1jk}$, respectively. As we increase the d_{1jk}, according to the Theorem 8, the first faction dies out, which is indeed in line with the simulation results. This shows that our theory can also be seen as a manipulation strategy to adjust the winner species. Since HOIs usually denote the indirect interaction in ecology, HOIs are potentially more suitable to adjust than pairwise direct interaction. Finally, from simulations, we observe that large self-competition terms $(a_{ii}, \hat{a}_{ii}, c_{iii}, \hat{c}_{iii})$ will improve the chance that the system doesn't diverge to infinity, which seems only related to the system's parameters.

V. Conclusion and Discussion

This paper proposes two higher-order Lotka-Volterra models. The first model is a fully cooperative model, while the second describes a competition between two factions. We have listed all the possible equilibria for these models. By applying the theory of monotone systems and exploiting the properties of an irreducible Metzler matrix, we have provided sufficient conditions for their stability and discovered the influence of HOIs on species' coexistence. In the end, we use simulations to highlight our analytical contributions. Future research directions that stem from our findings include the study of the general higher-order Lotka-Volterra model among more than 2 factions. The main challenge is that the Jacobian may no longer be permutated into an irreducible Metzler matrix, therefore new techniques are to be developed to address such a more general case.

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