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Complex Balanced Equilibria of Weakly Reversible Poly-PL Kinetic Systems and Evolutionary Games

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Abstract

This study is concerned with chemical reaction networks endowed with poly-PL kinetics, that is, the positive linear combination of power law kinetic systems. We discovered that complex balanced equilibria exist for weakly reversible poly-PL kinetics with zero kinetic reactant deficiency. The result is then applied to evolutionary games with replicator dynamics such that the polynomial payoff functions lead to polynomial kinetic systems, a subset of poly-PL kinetic systems. In particular, sufficient conditions to admit a zero kinetic reactant deficiency were derived for games with nonlinear payoff functions and poly-PL kinetics, allowing the application of the main result.

1 Introduction

This paper studies positive linear combinations of power law kinetic systems, which we call poly-PL kinetics and denote with PYK. A subset of PYK consisting of polynomial kinetics (denoted by POK) occurs in chemical kinetic system (CKS) realizations of evolutionary

games with replicator dynamics as proposed by Veloz et al. [39]. The main results of the paper are in two areas:

1. Theorems 3 and 4 establish the existence and parametrization of complex balanced equilibria for weakly reversible poly-PL kinetic system with zero kinetic reactant deficiency (see Section 3 for a precise definition). They extend corresponding results on power law systems ([38], Theorem 6).
2. The applicability of Theorem 3 to symmetric population games in evolutionary game theory (EGT) using the Veloz et al. approach is assessed, with the following main findings:
   - A correction to a claim of Veloz et al. is provided.
   - The class of symmetric matrix games, i.e. those with linear payoff functions, lie outside the scope of Theorem 3.
   - A sufficient condition for the application of Theorem 3 to symmetric population games with nonlinear payoff functions (also called "playing the field" games) is provided in Theorem 5.

Games under evolutionary game theory (EGT) model situations that tell how groups change their strategy over time based on payoff functions, interpreted for example in biology as fitness or reproductive success. EGT has transcended its biological origins, finding applicability in other scientific fields, including several subdisciplines of chemistry: biochemistry ([34], [4], prebiotic chemistry [40], physical chemistry [26] and medical chemistry [31].

In an evolutionary game, a player can have different roles according to assigned probabilities. If a player can have more than one role, then the game is called an asymmetric game, otherwise a symmetric game. According to Cressman and Tao [9], symmetric games with finitely many pure strategies $\{e_1, e_2, ..., e_m\}$ are called (symmetric) population games if the payoff function $\pi(e_i, x)$ is a continuous function of x. Population games are called matrix games if the payoff function is linear in x and "playing the field" games otherwise.

The replicator equation is the most widely used model for game dynamics in evolutionary game theory [25]. Veloz et al. [39] proposed the realization, i.e. construction of a dynamically equivalent ODE system, as a chemical kinetic system. For games with poly-

nomial (or more generally, poly-PL) fitness functions, this approach leads to polynomial (poly-PL) kinetics, which are studied in this paper.

The paper is organized as follows: Section 2 collects the fundamentals of chemical reaction networks and kinetic systems required for the later sections. Section 3 contains the first two main results of the paper: Theorem 3 states that for weakly reversible poly-PL systems with zero kinetic reactant deficiency, complex balanced equilibria exist. The parametrization of the set of equilibria and some uniqueness properties are described in Theorem 4. The realization of a symmetric population game with replicator dynamics introduced by Veloz et al. [39] is discussed in Section 4, including a correction of one of their claims and the derivation of a simple CRN representation for systems with positive payoff functions. In the same section, it is shown that for symmetric matrix games, a different approach is needed, since these games in general have non-zero kinetic reactant deficiency. Section 5 focuses on "playing the field" games, i.e., those with nonlinear payoff functions, and derives a sufficient condition for such games with poly-PL payoff functions to have zero kinetic reactant deficiency, allowing the application of Theorem 3. Conclusions and an outlook constitute Section 6. Tables of acronyms and frequently used symbols are provided in Appendix A.

2 Fundamentals of chemical reaction networks and kinetic systems

This section introduces reaction networks and their associated kinetics systems. One can look at [2, 1, 3, 37] for details of the concepts presented here. A **chemical reaction network (CRN)** is a digraph $(\mathscr{C},\mathscr{R})$ where each vertex has positive degree and stoichiometry, i.e., there is a finite set $\mathscr{S}$ (whose elements are called **species**) such that $\mathscr{C}$ is a subset of $\mathbb{R}^{\mathscr{S}}_{\geq}$. Each vertex is called a **complex** and its coordinates in $\mathbb{R}^{\mathscr{S}}_{\geq}$ are called **stoichiometric coefficients**. Hence, it can be identified as a linear combination of species. The arcs are called **reactions**. We denote this nonempty finite collection of reactions as $\mathscr{R}(\subset \mathscr{C}\times\mathscr{C})$. We implicitly assume the sets are numbered and let

$$\mathscr{S}=\{X_1,X_2,...,X_m\},\quad \mathscr{C}=\{C_1,C_2,...,C_n\},\text{ and }\quad \mathscr{R}=\{R_1,R_2,...,R_r\} \tag{2.1}$$

where m, $\mathcal{N}$, and r are their respective cardinalities. Thus, $\mathbb{R}^{\mathscr{S}}_{\geq}\cong\mathbb{R}^{m}_{\geq}$. Consider the reaction

$$\alpha X_1+\beta X_2\to\gamma X_3, \tag{2.2}$$

where X_1, X_2 and X_3 are the species. $\alpha X_1+\beta X_2$ and γX_3 are the complexes. In particular, $\alpha X_1+\beta X_2$ is called the **reactant** (or **source**) **complex** and γX_3 the **product complex**. The stoichiometric coefficients are the nonnegative coefficients α, β and γ. Under mass action kinetics (MAK), the rate at which the reaction occurs is given by the monomial

$$\mathbf{K} = kX_1^{\alpha}X_2^{\beta} \tag{2.3}$$

with rate constant $k > 0$. We can generalize this by considering power-law kinetics where the reaction rate is

$$\mathbf{K} = kX_1^{a}X_2^{b}, \tag{2.4}$$

such that a and b can be any real number. We call a and b as kinetic orders. Within a network involving additional species and reactions, the above reaction contributes to the dynamics of the species concentrations as

$$\dot{X} = \begin{bmatrix} \dot{X}_1 \\ \dot{X}_2 \\ \dot{X}_3 \\ \vdots \end{bmatrix} = kX_1^{a}X_2^{b} \begin{pmatrix} -\alpha \\ -\beta \\ \gamma \\ \vdots \end{pmatrix} + \dots \tag{2.5}$$

Consider our running example with chemical reaction network (CRN) and rates of reactions given below.

$$\begin{array}{c} A \underset{k_{21}}{\overset{k_{12}}{\leftrightarrow}} B \\ 2A+B \underset{k_{43}}{\overset{k_{34}}{\leftrightarrow}} A+2B \end{array}$$

In this example, we have $m = 2$ (species), $n = 4$ (complexes), $n_r = 4$ (reactant complexes) and $r = 4$ (reactions). We can write

$\mathscr{S} = \{A, B\}$

$\mathscr{C} = \{C_1 = A, C_2 = B, C_3 = 2A + B, C_4 = A + 2B\}$

$\mathscr{C} = \{R_1, R_2, R_3, R_4\}$

where

$R_1 : A \to B$

$R_2 : B \to A$

$R_3 : 2A + B \to A + 2B$

$R_4 : A + 2B \to 2A + B.$

The **linkage classes** of a CRN are the subnetworks of a reaction graph where for any complexes C_i, C_j of the subnetwork, there is path between them. Thus, the number of linkage classes, denoted as l, of our running example is two ($l = 2$).

$$\mathscr{L}_1 = \{R_1, R_2\}$$
$$\mathscr{L}_2 = \{R_3, R_4\}$$

The linkage class is said to be a **strong linkage class** if there is a directed path from C_i to C_j and vice versa for any complexes C_i, C_j of the subnetwork. Considering the running example, both subnetworks are strong linkage classes which implies that the number sl of strong linkage classes is 2. Moreover, **terminal strong linkage classes**, the number of which is denoted as t, are strong linkage classes where there are no edges (reactions) from a complex in the subnetwork to a complex outside the subnetwork. In the example, $t = 2$. The terminal strong linkage classes can be of two kinds: cycles (not necessarily simple) and singletons (which we call "terminal points").

We can now define important CRN classes. A CRN is **weakly reversible** if $sl = l$, i.e. every linkage class is a strong linkage class. A CRN is **t-minimal** if $t = l$. Note that our example is both weakly reversible and t-minimal. Let n_r be the number of reactant complexes of a CRN. Then $n - n_r$ is the number of terminal points. A CRN is called **cycle-terminal** if and only if $n - n_r = 0$, i.e., each complex is a reactant complex. It is called **point-terminal** if and only if $n - n_r = t$ and **point- and cycle-terminal** if $n - n_r < t$.

The dynamical system of the CRN of our running example can be written as

$$\dot{x} = \begin{bmatrix} \dot{A} \\ \dot{B} \end{bmatrix} = \begin{array}{c} \begin{matrix} R_1 & R_2 & R_3 & R_4 \end{matrix} \\ \begin{bmatrix} -1 & 1 & -1 & 1 \\ 1 & -1 & 1 & -1 \end{bmatrix} \end{array} \begin{bmatrix} k_{12}A^{f_{11}} \\ k_{21}B^{f_{21}} \\ k_{34}A^{f_{31}}B^{f_{32}} \\ k_{43}A^{f_{41}}B^{f_{42}} \end{bmatrix} = NK(x). \tag{2.6}$$

$\mathcal{N}$ is called the stoichiometric matrix and $K(x)$ is called the **kinetic vector (or chemical kinetics)**. The pairing of $(\mathcal{N}, K)$ is called a **chemical kinetic system** (CKS). In the general case, we can define a **chemical kinetics** as an assignment to each reaction $j \in \mathcal{R}$ of a rate function K_j satisfying the positivity condition, that is, for each reaction $j : y \to y', K_j(c) > 0$ if and only if $\operatorname{supp} y \subset \operatorname{supp} c$. The ODE system above is under **power law kinetics** which have the form

$$K_i(x) = k_i \Pi_{j=1}^{m} x^{F_{ij}} \quad \forall i \in \{1, 2, ..., r\} \tag{2.7}$$

with $k_i \in \mathbb{R}_>$ and $F_{ij} \in \mathbb{R}$. Power law kinetics is defined by an $r \times m$ matrix $F = [F_{ij}]$, called the **kinetic order matrix**, and vector $k \in \mathbb{R}^r$, called the **rate vector**. A particular example of power law kinetics is the well-known mass action kinetics where the kinetic order matrix consists of stoichiometric coefficients of the reactants. In the running example, we assume power law kinetics so that the kinetic order matrix is

$$F = \begin{array}{c} \begin{matrix} A & B \end{matrix} \\ \begin{bmatrix} f_{11} & 0 \\ 0 & f_{21} \\ f_{31} & f_{32} \\ f_{41} & f_{42} \end{bmatrix} \end{array} \begin{matrix} R_1 \\ R_2 \\ R_3 \\ R_4 \end{matrix}, \tag{2.8}$$

where $f_{ij} \in \mathbb{R}$. Another special class of power law kinetics is the **power law reactant-determined kinetics** (PL-RDK) where reactions with the same reactant complex have identical kinetic orders. In this paper, we are more interested in a kinetic vector composed of non-negative linear combinations of power law functions. See Section 3.

We further decompose the stoichiometric matrix $\mathcal{N}$. Writing the stoichiometric complexes as column vectors of the (molecularity) matrix Y, we have

$$Y = \begin{array}{c} \begin{matrix} C_1 & C_2 & C_3 & C_4 \end{matrix} \\ \begin{bmatrix} 1 & 0 & 2 & 1 \\ 0 & 1 & 1 & 2 \end{bmatrix} \end{array} \begin{matrix} A \\ B \end{matrix}. \tag{2.9}$$

Considering the digraph of our CRN, the incidence matrix

$$(I_a)_{(i,j)} = \begin{cases} -1, \text{if } i \text{ is the reactant complex of reaction } j \in \mathscr{R}, \\ 1, \text{if } i \text{ is the product complex of reaction } j \in \mathscr{R}, \\ 0, \text{otherwise} \end{cases} \tag{2.10}$$

will be

$$I_a = \begin{array}{c} \begin{matrix} R_1 & R_2 & R_3 & R_4 \end{matrix} \\ \begin{bmatrix} -1 & 1 & 0 & 0 \\ 1 & -1 & 0 & 0 \\ 0 & 0 & -1 & 1 \\ 0 & 0 & 1 & -1 \end{bmatrix} \end{array} \begin{matrix} C_1 \\ C_2 \\ C_3 \\ C_4 \end{matrix}. \tag{2.11}$$

Note that stoichiometric matrix $N = YI_a$. Hence, the stoichiometric map $N : \mathbb{R}^r \to \mathbb{R}^m$ is defined as the composition $Y \circ I_a$. The linear subspace of $\mathbb{R}^m$ defined by $\operatorname{Im} N$ is called the **stoichiometric subspace**, denoted as S. Let $s = \dim S$. The **deficiency** δ is defined as $\delta = n - l - s$. According to Shinar and Feinberg [35], this non-negative integer is essentially a measure of the linear dependency of the network's reactions. In the running

example, the deficiency of the network is 2. It is an important parameter in CRNT in establishing claims regarding the existence, multiplicity, finiteness and parametrization of the **set of positive steady states**, defined as $E_+(\mathscr{N}, K) = \{x \in \mathbb{R}^m_> | NK(X) = 0\}$.

Furthermore, considering the linkage class of the network, we can write $N = [N_1, N_2, \cdots, N_l]$ and $K(X) = [K_1(X), K_2(X), \cdots, K_l(X)]^\top$ in block forms where l is the number of linkage class. Let s_i be the dimension of the image of N_i and n_i be the number of complexes in linkage class $\mathscr{L}_i$. We can define the **linkage class deficiency** of $\mathscr{L}_i$ as $\delta_i = n_i - 1 - s_i$ and the **set of positive steady states for linkage class** $\mathscr{L}_i$ as $E_+(\mathscr{L}_i, K) = \{x \in \mathbb{R}^m_> | N_i K_i(X) = 0\}$.

In [22], Horn and Jackson introduced a subset of E_+ called the set of complex balanced of equilibria denoted as Z_+. It is defined as

$$Z_+(\mathscr{N}, K) = \left\{x \in \mathbb{R}^m_+ \middle| I_a \cdot K(x) = 0\right\} =\subseteq E_+(\mathscr{N}, K). \tag{2.12}$$

In other words, a positive vector c in $\mathbb{R}^m$ is called **complex balanced** (CB) if $K(c)$ is contained in $\ker I_a$. A chemical kinetic system is called **complex balanced** if it has a complex balanced equilibrium. We can also say that a kinetic system is complex-balanced at a state (i.e. a species composition) if for each complex, formation and degradation are at equilibrium. In studying complex balanced equilibria of a chemical kinetic system, the k-Laplacian matrix and related results are important. The **k-Laplacian matrix** of a CRN is an $n \times n$ matrix such that

$$(A_k)_{ij} = \begin{cases} k_{ji}, \text{if } i \neq j, \\ -\sum_{x=1}^n k_{jx}, \text{if } i = j. \end{cases} \tag{2.13}$$

where k_{ji} is the label (often called the rate constant) associated to the reaction from C_j to C_i. We state an important result below. For $t \in \mathbb{N}$, $\overline{1,t} := \{1, 2, ..., t\}$.

Theorem 1 (Structure Theorem of the Laplacian Kernel [14])**.** *Let $(\mathscr{C}, \mathscr{R}, k)$ be a labeled directed graph with $k : \mathscr{R} \to \mathbb{R}$. Let $\mathscr{C}'' = \mathscr{C} \setminus \cup_{k=1}^t \mathscr{C}^k$. Let A_k be the Laplacian matrix. Denote by A_k'' the submatrix of A_k with rows and columns corresponding to V''. Then there exists a basis $y_1, y_2, ..., y_t \in \mathbb{R}^n_{\geq 0}$ in $\ker A_k$ such that $supp(y_k) = \mathscr{C}_k \quad \forall k \in \overline{1,t}$ (i.e., $k \in \{1, 2, ..., t\}$).*

Regarding the relationship between weak reversible networks and complex balanced equilibria of kinetics, we recall a well-known result:

Proposition 1. *(Horn [21]) If a chemical kinetic system has a complex balanced steady state, then the underlying CRN is weakly reversible.*

A proof can also be found in [2].

3 Complex balanced equilibria for a class of weakly reversible PYK systems

Poly-PL kinetics (PYK) are kinetic systems consisting of non-negative linear combinations of power law functions. This set contains the set PLK of power law kinetics as "mono-PL kinetics with coefficient 1". Like PLK, the definition domain of PYK is the positive orthant $\mathbb{R}^m_>$. However, for subsets, this may be extended to the whole non-negative orthant $\mathbb{R}^m_\geq$. Clearly, PYK and PLK generate the same sets of SFRFs, the power law dynamical systems (or GMA systems in BST terminology).

3.1 Properties of complex factorizable poly-PL kinetics

After setting the standard ordering of species $X_1, ..., X_m$, we have the following definition:

Definition 1. A kinetics $K : \mathbb{R}^m_> \to \mathbb{R}^r$ is a **poly-PL kinetics** if

$$K_i(x) = k_i(a_{i,1}x^{F_{i,1}} + ... + a_{i,j}x^{F_{i,j}}) \quad \forall i \in \overline{1,r} \tag{3.1}$$

written in lexicographic order with $k_i \in \mathbb{R}_>$, $a_{i,j} \in \mathbb{R}_\leq$, $F_{i,j} \in \mathbb{R}^m$ and $j \in \overline{1,h_i}$ (where h_i is the number of terms in reaction i). Power-law kinetics is defined by $r \times m$ matrices $F_{i,k} = [F_{ij}]$, called the **kinetic order matrices**, vectors $k = [k_i], a_{i,\cdot} \in \mathbb{R}^r_>$, called the **rate vector** and **poly-rate vectors**, respectively.

We first recall some terminology from [15]:

Definition 2. A rate constant-interaction map decomposable (RID) kinetics is a kinetics, such that for each reaction r, the coordinate function $K_r : \Omega \to \mathbb{R}$ can be written in the form $K_r(x) = k_r I_{K;r}(x)$, with a positive real number k_r (called a rate constant) and $\Omega \in \mathbb{R}^m$. We call the map $I_K : \Omega \to \mathbb{R}^{\mathscr{R}}$ defined by $I_{K;r}$ as the interaction map and the set of kinetics RIDK.

Nearly all the kinetics studied in CRNT belong to RIDK. Recently however, G. Craciun et al. [8] have introduced variable k systems, where the rates may vary between an upper

and lower bound. Furthermore, there are kinetics sets such as the weakly monotonic kinetics studied by [36] or the span surjective kinetics introduced by Arceo et al. [1] which do not explicitly require constant rates. The fractal kinetics studied primarily by physical chemists, e.g. Brouers [7] have rate values given by a function of exponential type. In view of this, we introduce the above set explicitly.

We are particularly interested in the following subset of RIDK:

Definition 3. A set $\mathscr{K} \subset RIDK$ is said to be of type RID kinetics with interaction parameter maps if there is a family of maps $\{p_K : \mathscr{R} \to \mathbb{R}^{m_1} \times \cdots \times \mathbb{R}^{m_k} | K \in \mathscr{K}\}$ such that

i. $p_K(r) = p_K(r') \Rightarrow I_K(X)_r = I_K(X)_{r'}$ for all $x \in \Omega$ and

ii. $p_K = p_{K'} \Rightarrow I_K(X) = I_{K'}(X)$ for all $x \in \Omega$.

We denote the union of the sets of RIP kinetics with interaction parameter maps as RIPK.

Example 1. *PLK with the family of kinetic order matrices, i.e.* $p_K(r) = F_r$ *(kinetic order row vector or interaction), is the primary example. Since* $I_K(x) = x^F$*, the properties i) and ii) are straightforward.*

Clearly, a poly-PL kinetics is rate constant-interaction decomposable, i.e. an element of RIDK. For each positive integer h, the set PYK_h consists of all poly-PL kinetics with h positive terms. Clearly, the set $\{\text{PYK}_h | h > 0\}$ forms a countable covering of PYK. Note that any poly-PL kinetics with at most h positive terms, say h', can be represented in PYK by replacing any positive term $a_j M_j$ with the sum of $(h - h' + 1)$ copies of $1/(h - h' + 1)a_j M_j$. Clearly, this representation is not unique.

Proposition 1. PYK_h *posseses an interaction parameters map, i.e. is an element of RIPK.*

Proof. For each reaction r_i and each of the monomials of K_{r_i}, we form the kinetic order vector (as for PLK systems). These kinetic order vectors are lexicographically written and we denote the corresponding monomials as $M_{i,1}$, $M_{i,2}$, ..., $M_{i,h}$. We denote the coefficient of $M_{i,j}$ as $a_{i,j}$ and its kinetic order vector as $F_{ij} = \begin{bmatrix} f_{ij1} & \cdots & f_{ijm} \end{bmatrix}$. For each fixed j, $1 \leq j \leq h$, the matrix F_{ij} defines a PLK kinetics on $\mathscr{N}$, which we denote by

K_j. Our interaction parameters map lists the kinetic order vectors in lexicographic order and then the coefficients also in lexicographical order. This map would be $p_K : R \to R^m \times \cdots \times R^m \times R^h$. The dimension of the codomain is $p = h(m+1)$. ■

In the following, we consider **complex factorizable PYK systems**, i.e. reactions branching from a reactant all have the same interaction map

$$\psi_i(x) = a_{i,1}x^{F_{i,1}} + ... + a_{i,j}x^{F_{i,j}} \quad \forall i \in \overline{1, n_r}. \tag{3.2}$$

Clearly, a reactant complex y is a CF-node for K iff it is a CF-node for K_j for each j and the coefficients $a_{i,j}$ coincide for all reactions in its reaction set and for each j. Moreover, we extend the definition of PL-RDK kinetics [3] to poly-PL kinetics.

Definition 4. A poly-PL kinetic system has **reactant-determined kinetics** if for any two reactions a, b with identical reactant complexes, the corresponding columns of kinetic orders for each F_κ are identical, i.e., $(F_\kappa)_{ai} = (F_\kappa)_{bi}$ for $i = 1, ..., m$.

We also note that the PYK systems with reactant-determined kinetics are precisely the complex factorizable ones.

Remark 1. If $(\mathscr{N}, K)$ is a PYK systems with reactant-determined kinetics then it can be shown that $Z_+(\mathscr{N}, K) = \{x \in \mathbb{R}^m_> | A_k \cdot \psi_K(x) = 0\}$.

Theorem 2. *Let $(\mathscr{N}, K)$ be a weakly reversible complex factorizable PYK system with linkage classes $\mathscr{L}_1$, $\mathscr{L}_2$, ..., and $\mathscr{L}_l$. Then $Z_+(\mathscr{N}, K) = \bigcap Z_+(\mathscr{L}_i, K)$ for each linkage class $\mathscr{L}_i$.*

Proof: Suppose $\mathscr{N}$ is weakly reversible. Consider A_k and $\psi(x)$ in block forms:

$$A_k = \begin{bmatrix} A_{k,1} & & 0 \\ & \ddots & \\ 0 & & A_{k,l} \end{bmatrix} \text{ and } \psi(x) = \begin{bmatrix} (\psi_1)(x) \\ \vdots \\ (\psi_l)(x) \end{bmatrix} \tag{3.3}$$

where $A_{k,i}$ and $\psi_i(x)$ correspond to linkage class $\mathscr{L}^i$. Thus,

$$\operatorname{Im} A_k = \operatorname{Im} A_{k,1} \oplus \operatorname{Im} A_{k,2} \oplus \ldots \oplus \operatorname{Im} A_{k,l} \tag{3.4}$$

Recall the definition of $Z_+(\mathscr{N}, K) = \left\{x \in \mathbb{R}^m_+ \middle| A_k \cdot \psi(x) = 0\right\}$ and $Z_+(\mathscr{L}_i, K) = \left\{x \in \mathbb{R}^m_+ \middle| A_{k,i} \cdot \psi(x) = 0\right\}$. Clearly, $A_k \cdot \psi(x) \in \operatorname{Im} A_k$ and $A_{k,i} \cdot \psi(x) \in \operatorname{Im} A_{k,i}$. Hence, Equation 3.4 concludes the proof. ■

For each kinetic order matrix F_κ ($\forall\kappa \in \overline{1,h}$), we define the $m \times n$ matrix $\widetilde{Y}_\kappa$ defined as:

$$(\widetilde{Y}_\kappa)_{ij} = \begin{cases} (F_\kappa)_{ri}, & \text{if j is a reactant complex of reaction r} \\ 0, & \text{otherwise} \end{cases}$$

Definition 5. The $m \times n_r$ **poly T-matrix** T_κ ($\forall\kappa \in \overline{1,h}$) is the truncated $\widetilde{Y}_\kappa$ where the non-reactant columns are deleted. Define the $n_r \times l$ matrix $L = [e_1, e_2, ..., e_l]$ where e^i is a characteristic vector for linkage class $\mathscr{L}^i$. The block matrix $\widehat{T}_\kappa \in \mathbb{R}^{(m+l)\times n_r}$ ($\forall\kappa \in \overline{1,h}$) is defined as

$$\widehat{T}_\kappa = \begin{bmatrix} T_\kappa \\ L^\top \end{bmatrix}. \tag{3.5}$$

Definition 6. The block matrix $\widehat{T} \in \mathbb{R}^{h\cdot(m+l)\times h\cdot n_r}$ is defined as

$$\widehat{T} = \begin{bmatrix} \widehat{T}_1 & & 0 \\ & \ddots & \\ 0 & & \widehat{T}_h \end{bmatrix} \tag{3.6}$$

Definition 7. Let $\mathscr{N}$ be a network with n_r reactant complexes and K a poly-PL kinetics with poly T-matrices T_1, ..., T_h. If $\widehat{q} = \text{rank}(\widehat{T})$, then the **kinetic reactant deficiency** $\widehat{\delta}$ is defined as

$$\widehat{\delta} = h \cdot n_r - \widehat{q}. \tag{3.7}$$

As a consequence of Rank-Nullity Theorem and Definition 7, we have the following result.

Proposition 2. *Let $(\mathscr{N}, K)$ a poly-PL kinetic system with poly T-matrices T_1, ..., T_h and kinetic reactant deficiency $\widehat{\delta}$. Then*

$$\widehat{\delta} = \dim\ker(\widehat{T}). \tag{3.8}$$

3.2 A zero reactant deficiency theorem for weakly reversible PYK systems

Definition 8. The set PY-TIK consists of all complex factorizable poly-PL kinetics with zero kinetic reactant deficiency.

3.2.1 Proof of the Zero Reactant Deficiency Theorem for PY-TIK

We can now state and prove one of the main results of the paper:

Theorem 3. *Let $(\mathscr{N}, K)$ be a PY-TIK systems, that is, $(\mathscr{N}, K)$ has a complex factorizable kinetics and $\widehat{\delta} = 0$. Then $\mathscr{N}$ is weakly reversible if and only if $Z_+(\mathscr{N}, K) \neq \emptyset$.*

Proof. The converse is Proposition 1. For the forward direction, consider a weakly reversible network $\mathscr{N}$. Then, every linkage class is a terminal strong linkage class which means $t_i = 1 = \dim \ker A_{k,i}$ for all $\mathscr{L}_i$. If $Z_+(\mathscr{L}_i, K) \neq \emptyset$ for each linkage class, thus by Theorem 2, $Z_+(\mathscr{N}, K) \neq \emptyset$. Hence, with no loss of generality, we assume a single linkage class network $\mathscr{N}$.

It is important to note that $\psi(x) = \psi_1(x) + \psi_2(x) + \ldots + \psi_h(x)$ where $\psi_i(x) = a_1 x^{F_{i,1}} + ... + a_h x^{F_{i,h}}$ for each $i \in \overline{1,n}$.

Let T_1, ..., T_h be the poly T-matrices. Take $\psi_1(x)$. By Theorem 1, we can find a $y \in \mathbb{R}^n_>$ such that $\ker A_k = \operatorname{span} y$. Because $\psi_1 \in \mathbb{R}^n_\geq$ for all $x \in \mathbb{R}^m_>$, finding a solution to the equation $A_k\psi_1(x) = 0$ is equivalent to finding some $\gamma \in \mathbb{R}_>$ and $x \in \mathbb{R}^m_>$ such that $\gamma y = \psi_1(x)$. Taking the logarithm of $\gamma y = \psi_1(x)$ coordinate-wise yields $\log(\gamma)\mathbf{1} + \log(y) = T_1^\top \log(x) + \log(a)$, where $\mathbf{1}$ is the vector in $\mathbb{R}^n$ whose coordinates are all equal to 1. Hence, $A_k\psi_1(x) = 0$ if and only if there exists $\gamma \in \mathbb{R}_>$ such that

$$\log(y) - \log(a) = \widehat{T}_1^\top \cdot \begin{bmatrix} \log(x) \\ -\log(\gamma) \end{bmatrix}. \tag{3.9}$$

Since $\dim(\ker(\widehat{T}_1)) = 0$, $\widehat{T}_1{}^\top$ has full range, $\log(y) - \log(a) \in \operatorname{Im} \widehat{T}_1{}^\top$. Because log and $-\log$ are bijective, we can find $x \in \mathbb{R}^m_>$ such that $A_k\psi_1(x) = 0$.

Fix $x^* \in \mathbb{R}^m_>$ such that $A_k\psi_1(x^*) = 0$. Take $\psi_i(x)$ for any $i \in \overline{1,h}$ where the associated poly T-matrix is T_i. Since $\dim(\ker(\widehat{T}_i)) = 0$, $\widehat{T}_i{}^\top$ has full range. Hence, we can find $\log(y) - \log(a)$ and $\log(\gamma)$ such that

$$\log(y) - \log(a) = \widehat{T}_i^\top \cdot \begin{bmatrix} \log(x^*) \\ -\log(\gamma) \end{bmatrix} \tag{3.10}$$

where $\gamma \in \mathbb{R}_>$ and $y \in \mathbb{R}^n_>$. Thus, we have $\log(\gamma)\mathbf{1} + \log(y) = T_i^\top \log(x^*) + \log a$, where $\mathbf{1}$ is the vector in $\mathbb{R}^n$ whose coordinates are all equal to 1. Since log is bijective, reversing the logarithm to the equation yields $\gamma y = \psi_i(x^*)$ which is, by Theorem 1 ($\ker A_k = \operatorname{span} y$), equivalent to $A_k\psi_i(x^*) = 0$. Therefore

$A_k\psi_1(x^*) + A_k\psi_2(x^*) + \cdots + A_k\psi_h(x^*) = A_k(\psi_1(x^*) + \psi_2(x^*) + \cdots + \psi_h(x^*)) = A_k\psi(x^*) = 0.$

Hence, $Z_+(\mathscr{N}, K) \neq \emptyset$.

■

Example 2. *Consider the CRN of the running example in Section 2. Suppose the kinetics is*

$$K(X) = \begin{bmatrix} A^{0.2}B^{1.1} + A^2B^3 + A^{3.1}B^{0.01} \\ A^{0.2}B^{-1} + A^2B^{-3.1} + A^{2.1}B^{-3.1} \\ A^2B^1 + A^1B^2 + A^{-1}B^{-1} \\ A^{0.2}B^2 + A^{0.1}B^{4.1} \end{bmatrix} \begin{matrix} R_1 \\ R_2 \\ R_3 \\ R_4 \end{matrix} . \tag{3.11}$$

The kinetics can be written as

$$K(X) = \begin{bmatrix} A^{0.2}B^{1.1} + A^2B^3 + A^{3.1}B^{0.01} \\ A^{0.2}B^{-1} + A^2B^{-3.1} + A^{2.1}B^{-3.1} \\ A^2B^1 + A^1B^2 + A^{-1}B^{-1} \\ A^{0.2}B^2 + 0.5A^{0.1}B^{4.1} + 0.5A^{0.1}B^{4.1} \end{bmatrix} \begin{matrix} R_1 \\ R_2 \\ R_3 \\ R_4 \end{matrix} . \tag{3.12}$$

Thus, the kinetic order matrices are

$$F_1 = \begin{matrix} \\ R_1 \\ R_2 \\ R_3 \\ R_4 \end{matrix} \begin{matrix} A \\ \begin{bmatrix} 0.2 \\ 0.2 \\ 2 \\ 0.2 \end{bmatrix} \end{matrix} \begin{matrix} B \\ \begin{bmatrix} 1.1 \\ -1 \\ 1 \\ 2 \end{bmatrix} \end{matrix} , \; F_2 = \begin{matrix} \\ R_1 \\ R_2 \\ R_3 \\ R_4 \end{matrix} \begin{matrix} A \\ \begin{bmatrix} 2 \\ 2 \\ 1 \\ 0.1 \end{bmatrix} \end{matrix} \begin{matrix} B \\ \begin{bmatrix} 3 \\ -3.1 \\ 2 \\ 4.1 \end{bmatrix} \end{matrix} \quad \textit{and} \tag{3.13}$$

$$F_3 = \begin{matrix} \\ R_1 \\ R_2 \\ R_3 \\ R_4 \end{matrix} \begin{matrix} A \\ \begin{bmatrix} 3.1 \\ 2.1 \\ -1 \\ 0.1 \end{bmatrix} \end{matrix} \begin{matrix} B \\ \begin{bmatrix} 0.01 \\ -3.1 \\ -1 \\ 4.1 \end{bmatrix} \end{matrix} \tag{3.14}$$

with the rate vector and the poly-rate vectors

$$k = \begin{bmatrix} 1 \\ 1 \\ 1 \\ 1 \end{bmatrix} , \; a_1 = \begin{bmatrix} 1 \\ 1 \\ 1 \\ 1 \end{bmatrix} , \; a_2 = \begin{bmatrix} 1 \\ 1 \\ 1 \\ 0.5 \end{bmatrix} \textit{ and } a_3 = \begin{bmatrix} 1 \\ 1 \\ 1 \\ 0.5 \end{bmatrix}. \tag{3.15}$$

For all $\kappa \in \{1, 2, 3\}$, the poly T-matrix $T_\kappa = F_\kappa^\top$. One can compute that the block matrices $\widehat{T}_\kappa$ and $\widehat{T}$ have maximal rank. Hence, $\widehat{\delta} = 0$. Since the network of the running example is weakly reversible, we have a complex balanced equilibria for this chemical kinetic system by Theorem 3.

3.2.2 Structure of the set of complex balanced equilibria for PY-TIK system

For the structure of Z_+, we use techniques in [5]. To make claims similar to Boros' Proposition 4.3 and its consequences [5], we have the following definition.

Definition 9. Consider an arbitrary poly T-matrix T_κ. The k^{th} **kinetic reactant flux subspace** $\widetilde{S}_\kappa$ is the linear space generated by the product of $T_\kappa I_a$. For $q \in \mathbb{R}^m_{\geq}$, the set $(q + \widetilde{S}_\kappa) \cap \mathbb{R}^m_{\geq}$ is called the k^{th} **kinetic reactant flux class**. A k^{th} kinetic reactant flux class Q_κ is said to be positive if $Q_\kappa \cap \mathbb{R}^m_{>} \neq \emptyset$.

Proposition 3. *Let $(\mathscr{N}, K)$ a poly-PL kinetic system with poly T-matrices T_1, ..., T_h and $\widehat{\delta} = 0$. Consider an arbitrary poly T-matrix T_κ. Let $P_1 : \mathbb{R}^m \times \mathbb{R}^l \to \mathbb{R}^m$ be the first projection map, i.e., $Pr_1(v) = v^1$ for $v = \begin{bmatrix} v^1 \\ v^2 \end{bmatrix} \in \mathbb{R}^m \times \mathbb{R}^l$. Then $P_1|_{\ker \widehat{T}^\top_\kappa}$ is a bijection between $\ker \widehat{T}^\top_\kappa$ and $(\widetilde{S}_\kappa)^\perp$ where $(\widetilde{S}_\kappa)$ is the space generated by $T_\kappa I_a$.*

Proof. Consider an arbitrary poly T-matrix T_κ. We show that $P_1|_{\ker \widehat{T}^\top_\kappa}$ is both surjective and injective. Let $w \in (\widetilde{S}_\kappa)^\perp$. Since $\mathscr{N}$ is weakly reversible, each column of $T_\kappa(I_a)$ corresponds to a reaction (i, j) in such a way that the corresponding column is $(T_\kappa)_{\cdot,j} - (T_\kappa)_{\cdot,i}$. Thus, we have

$$\langle (T_\kappa)_{\cdot,j} - (T_\kappa)_{\cdot,i}, w \rangle = 0, \quad \forall (i,j) \in \mathscr{R}. \tag{3.16}$$

It follows $\langle (T_\kappa)_{\cdot,j}, w \rangle = \langle (T_\kappa)_{\cdot,i}, w \rangle$. Thus, we can use similar argument presented in the proof of Proposition 12 in [37] showing the surjectivity and injectivity of $P_1|_{\ker \widehat{T}^\top_\kappa}$. ■

The bijection in Proposition 3 will be the key for Corollaries 1 and 2.

Corollary 1. *Let $(\mathscr{N}, K)$ a poly-PL kinetic system with poly T-matrices T_1, ..., T_h and $\widehat{\delta} = 0$. Consider an arbitrary poly T-matrix T_κ. Fix $w \in (\widetilde{S}_\kappa)^\perp$ and $x^* \in \mathbb{R}^m_{>}$ such that there exists $\gamma^* \in \mathbb{R}^l_+$ with $\widehat{T}^\top_\kappa \begin{bmatrix} \log(x^*) \\ -\log(\gamma^*) \end{bmatrix} = w$. Then for $x \in \mathbb{R}^m_{>}$, the following are equivalent:*

(i) There exists $\gamma \in \mathbb{R}^l_{>}$ such that $\widehat{T}^\top_\kappa \begin{bmatrix} \log(x) \\ -\log(\gamma) \end{bmatrix} = w$.

(ii) The vector $\log(x) - \log(x^*) \in (\widetilde{S}_\kappa)^\perp$.

Proof. The equivalence is an immediate consequence of Proposition 3. ■

Corollary 2. *Let $(\mathscr{N}, K)$ a poly-PL kinetic system with poly T-matrices T_1, ..., T_h and $\widehat{\delta} = 0$. Consider an arbitrary poly T-matrix T_κ. Fix $w \in (\widetilde{S}_\kappa)^\perp$. Then for all $q \in \mathbb{R}^m_>$, there exists $(x, \gamma) \in \mathbb{R}^m_> \times \mathbb{R}^l_>$ such that $x \in (q + \widetilde{S}_R)$ and $\widehat{T}_\kappa^\top \begin{bmatrix} \log(x) \\ -\log(\gamma) \end{bmatrix} = w$.*

Proof. The statement is an immediate consequence of Corollary 1 and Lemma 3.3 of [5]. ■

We can now state and prove the main result of this subsection.

Theorem 4. *Let $(\mathscr{N}, K)$ a weakly reversible poly-PL kinetic system with poly T-matrices T_1, ..., T_h and $\widehat{\delta} = 0$. Consider an arbitrary poly T-matrix T_k.*

(i) if $Z_+(\mathscr{N}, K) \neq \emptyset$ and $x^* \in Z_+(\mathscr{N}, K)$ then

$$Z_+(\mathscr{N}, K) = \left\{ x \in \mathbb{R}^m_\geq \middle| \log(x) - \log(x^*) \in (\widetilde{S}_k)^\perp \right\}.$$

(ii) if $Z_+(\mathscr{N}, K) \neq \emptyset$ then $|Z_+(\mathscr{N}, K) \cap Q_k| = 1$ for each positive kinetic reactant flux class Q_k.

Proof. Suppose $Z_+(\mathscr{N}, K) \neq \emptyset$ and fix $x^* \in Z_+(\mathscr{N}, K)$. By Theorem 2, $x^* \in Z_+(\mathscr{L}_i, K)$ for all $i \in 1, 2, .., l$. Consider an arbitrary poly T-matrix T_κ. Each T_κ and incidence matrix I_a can be written in block forms (using the linkage class partition):

$$T_\kappa = \begin{bmatrix} T_{\kappa,1} & T_{\kappa,2} & \cdots & T_{\kappa,l} \end{bmatrix} \text{ and } I_a = \begin{bmatrix} I_{a,1} & & 0 \\ & \ddots & \\ 0 & & I_{a,l} \end{bmatrix}. \tag{3.17}$$

Define $\widetilde{S}_{\kappa,i}$ as the image of the matrix $T_{\kappa,i} I_{a,i}$ where $T_{\kappa,i}$, $I_{a,i}$ correspond to the poly T-matrix and incidence matrix of the linkage class $\mathscr{L}_i$.

Thus, by Corollary 1 and Equation 3.9, we have

$$Z_+(\mathscr{L}_i, K) = \left\{ x \in \mathbb{R}^m_\geq \middle| \log(x) - \log(x^*) \in (\widetilde{S}_{\kappa,i})^\perp \right\} \tag{3.18}$$

for each linkage class $\mathscr{L}_i$.

Since $\widetilde{S}_\kappa^\perp = (\sum \widetilde{S}_{\kappa,i})^\perp = \cap \widetilde{S}_{\kappa,i}^\perp$, the set

$$\left\{ x \in \mathbb{R}^m_> \middle| \log(x) - \log(x^*) \in (\widetilde{S}_\kappa)^\perp \right\} = \cap \left\{ x \in \mathbb{R}^m_> \middle| \log(x) - \log(x^*) \in \widetilde{S}_{\kappa,i}^\perp \right\}. \tag{3.19}$$

Thus, from Theorem 2, $Z_+(\mathscr{N}, K) = \left\{ x \in \mathbb{R}^m_\geq \middle| \log(x) - \log(x^*) \in (\widetilde{S}_\kappa)^\perp \right\}$. The last statement follows from Corollary 2. ■

4 CKS representations of poly-PL replicator systems

An important motivation for our study of poly-PL kinetics derived from the work of Veloz et al. [39] which proposed the representation of evolutionary games with replicator dynamics as chemical kinetic systems. In this framework, evolutionary games with polynomial payoff functions lead to polynomial kinetic systems. The consideration of the superset of poly-PL kinetics, i.e. of real exponents instead of just non-negative integers, came from the observation that "sums of power law functions" occurred in power law approximations of some carbon cycle models which we analyzed with CRNT methods. In this section, we first review the proposed CKS representation of a replicator system (RS), correct an erroneous claim in the paper and then present a simple dynamically equivalent representation to which, in the case of poly-PL replicator systems, the main result (Theorem 3) for PY-TIK can be applied.

Veloz et al's proposal is the following: "Note that the replicator equation implies a reaction network: it can be written as $\dot{x}_k = x_k(f_k(x) - \phi(x))$, where x_k is the proportion of players using strategy k, $f_k(x)$ is their fitness and $\phi(x) = \sum_{i=1}^{n} x_i f_i(x)$ the average fitness of the population (dilution flow in chemical reactions) represented by $x = (x_1, ..., x_n)$. The reaction network consists of decay reactions of the form $x_k \to \emptyset$ due to the dilution term $-x_k\phi(x)$. The production term $x_k f_k(x)$ implies catalytic reactions of the form $x_k + i_1 + \cdots + i_m \to 2x_k + i_1 + \cdots + i_m$, where $i_1, ..., i_m$ are those species that are necessary for k to replicate, i.e., $f(x)$ is these species have positive concentrations in x."

4.1 Correction of a claim in the Veloz et al.paper

The approach of Veloz et al. **assumes** that the CKS representation is valid. It is valid if and only if the functions $x_i f_i$ and $x_i\phi$ are kinetic functions, for $i = 1, ..., m$. This implies that they are all positive for positive x. They claim that there will be species (the catalysts) that ensure replication, which can happen only if those functions are positive. This "biological argument" - replication happening implies positive kinetics - works only under mass action kinetics when the stoichiometric coefficients determine the kinetic function. In the general setting, e.g. for polynomial kinetics, it begs the question of valid representation because the kinetics is determined by the fitness or payoff functions, and not by the stoichiometric coefficients. To show that the claim - that the functions described are kinetic functions - in general is not correct, we provide a family

of counterexamples through the following proposition:

Proposition 4. *Let* $f(x) = \sum a_j M_j(x)$, $j = 1, ..., h$, $h > 1$, *with* $M_j(x) = \prod x_i^{f_{j,i}}$, $i = 1, ..., m$. *Let* $a_j > 0$ *for* $j = 1, ..., h-1$ *and* $a_h < 0$. *Suppose further that there is an* i' *such for each* j, $f_{j,i'} > f_{h,i'}$. *Then* $f(1, ..., 1, x_i', 1, ..., 1) < 0$ *for sufficiently small positive* $x_{i'}$. *An analogous result holds for "*$\leq$*" and "sufficiently large".*

Proof. Note that $M_j(x) > 0$ for all $x > 0$. Now,

$$f(x) = \sum a_j M_j(x) < 0 \Leftrightarrow \sum_{1,...,h-1} a_j M_j(x)/M_h(x) < |a_h|.$$

If we set $a = \max_{1,...,h-1} a_j$, then $\sum_{1,...,h-1} a_j M_j(x)/M_h(x) \leq a(h-1) \sum M_j(x)/M_h(x)$, so that it suffices to show that the $RHS < |a_h|$ to show the claim. Since $M_j(x)/M_h(x) = \prod x_i^{f_{j,i}-f_{h,i}}$, this is the same as $\sum_j \prod_i x_i^{f_{j,i}-f_{h,i}}$ less than the constant $|ah|/a(h-1)$. By assumption, the exponents are all positive. We set $x_i = 1$, $i \neq i'$, so that to show is $\sum_j x_{i'}^{f_{j,i'}-f_{h,i'}} < |ah|/a(h-1)$. Each summand $\to 0$ when $x_{i'} \to 0$, which proves the claim. ■

Example 3. *The EGT model of multiple myeloma in Pacheco et al. [32] has the payoff functions* $f_1(x) = x_2 + bx_3$, $f_2(x) = x_1 - dx_3$, $f_3(x) = bx_1$ *(with* $b, d > 0$, $x_1 + x_2 + x_3 = 1$*). For* $f_2(x)$, $h = 2$ *and* x_1 *has* $f_{1,1} = 1$ *and* $f_{2,1} = 0$, *so that the Proposition is applicable. Hence the EGT with replicator dynamics cannot be represented as a CKS in the sense of Veloz et al. Moreover, it is easy to see that* $f_2(x) < 0$ *for the case wherein* $x = (0, 0, 1)$ *or more generally, whenever* $d > \frac{x_1}{x_3}$.

The following restricted claim is however correct:

Proposition 5. *If a replicator system has continuous payoff functions which are positively bounded from below, then* $x_i f_i$ *and* $x_i \phi$ *are kinetic functions, and hence, the systems has a CKS representation.*

The Proposition follows from the following Lemma:

Lemma 1. *(Payoff function transformation) If a replicator system has continuous payoff functions, then these can be adjusted to be positive, with the same set of replicator equations.*

Proof. We conduct the adjustment in two cases.

Case 1. Each payoff function is bounded from below, say by b_k. Let $B = \min b_k$. Set the new payoff function $\widehat{f_k} := f_k - (B-1)$. It follows that $\widehat{f_k}(x) > 0$ for all nonnegative x.

Case 2. If a payoff function is not bounded from below, it nevertheless takes on a minimum on the compact set $x_1 + \ldots + x_m = 1$. This can be taken as b_k, and the same inequalities hold for the adapted function, though now restricted to the above compact set.

For the new payoff functions, we obtain the following replicator equations: $\frac{dx_k}{dt} = x_k(\widehat{f_k}(x) - \widehat{\phi}(x))$ with $\widehat{f_k} := f_k - (B-1)$ and $\widehat{\phi} = \sum x_i(f_i - (B-1)) = \sum x_i f_i - (B-1)$. Case 1 provides the proof of the previous proposition. ■

4.2 A weakly reversible CKS representation of a poly-PL replicator system

When considering power law replicator system, one usually takes the positive orthant $\mathbb{R}^{\mathscr{S}}_{>}$ as the definition domain Ω of the PYK kinetics to accommodate negative exponents. If one excludes such exponents, one could extend the definition domain to include zero coordinates. This consideration is relevant for the application to replicator systems, since the definition domain of he latter is the simplex $x_1 + ... + x_m \leq 1$ and some steady states have zero coordinates. This extension of the definition domain however may reduce the set of PYK available as kinetics as the following example shows:

Example 4. *Set $\mathscr{S} = \{X_1, X_2\}$. The CRN is simply: $X_1 \to X_2$ with function $K(X_1, X_2) = 2X_1X_2$. This is not a kinetics if one allows $X_2 = 0$, since $X_1 > 0$ fulfills* $\operatorname{supp} y \subset \operatorname{supp} X$ *but $K(X_1, X_2) = 0$. In this case, the PYK function must not only have nonnegative exponents but also at least one term with only X_1 as factor.*

However, taking the positive orthant as definition domain is not really a restriction for the analysis using CKS since the main results from CRNT that could be used concern positive equilibria.

Clearly, if each payoff function $f_i(x)$ of a replicator system in m variables $x_1, ..., x_m$ is a positive linear combination of power laws, then the functions $x_i f_i(x)$, $x_i\phi(x)$ are PYK kinetics on the replicator network: $0 \leftarrow x_i \to 2x_i$ formulated by Veloz et al. This network is dynamically equivalent to the reversible, non-branching and zero deficiency network

$x_i \leftrightarrow 2x_i$. Note that since the network is weakly reversible and have kinetic reactant deficiency = 0, Theorem 3 concludes the existence of (at least one) positive steady state. To get dynamic equivalence, all rate constants are set equal to 1.

4.3 Two basic properties of positive equilibria of replicator systems

In the following Proposition, we document two basic facts about positive equilibria of the replicator equation, for which we did not find an appropriate reference in the literature.

Proposition 6. *Let x^* be a positive equilibrium of the replicator equation $\frac{dx_i}{dt} = x_i f_i(x) - x_i\phi(x)$ with $f_i(x) > 0$ for $x \in \mathbb{R}^m_>$. Then*

(i) $\sum x_i^* = 1$, i.e. x^* lies on the simplex $x_1 + x_2 + \cdots x_m = 1$ and

(ii) $f_i(x^*) = \phi(x^*)$ for all i.

Proof. (i) Summing the equations $0 = x_i^* f_i(x^*) - x_i^*\phi(x^*)$, we obtain $0 = \sum x_i^* f_i(x^*) - x_i^*\phi(x^*) = \phi(x^*) - \sum x_i^*\phi(x^*) = \phi(x^*)(1 - \sum x_i^*) \Rightarrow (1 - \sum x_i^*) = 0$ since $\phi(x^*) > 0$. (ii) follows immediately from $x_i^* > 0$. ■

Remark 2. It follows from Theorem 3 for PY-TIK that a poly-PL replicator system with zero kinetic reactant deficiency has a positive equilibrium on the simplex.

4.4 The case of symmetric matrix games

One of the most studied games in EGT is the symmetric matrix game. In this game, each player is given a finite set of m pure strategies $\{e_1, e_2, ..., e_m\}$. The $m \times m$ payoff matrix strategy game is given by $A = [a_{ij}]$ where a_{ij} is the payoff to e_i played against strategy e_j. One can think of a number n_i of individuals using strategy e_i from the large population $n = \sum_{i=1}^m n_i$. In a population state $x = (x_1, x_2, ..., x_m)$ from the simplex $\Delta^m = \left\{(x_1, x_2, ..., x_m)\middle|\sum_{j=1}^m x_j = 1\right\}$ the value $x_i = \frac{n_i}{n}$, defines the proportion of the population using strategy e_i at time t.

The fitness or payoff function associated with strategy e_i when the composition of the population is $x \in \Delta^m$ is given by the linear equation

$$f_i(x) = \sum_{j=1}^m a_{ij}x_j \tag{4.1}$$

and the average fitness of an individual chosen at random is given by the equation

$$\phi = \sum_{j=1}^{m} x_j f_j(x). \tag{4.2}$$

When the different strategies are played against each other, the selection dynamics are described by the replicator equations

$$\dot{x_i} = x_i(f_i(x) - \phi), \quad i = 1, 2, \cdots, m. \tag{4.3}$$

It is however, relatively easy to see, that with the exception of a few trivial cases, the CKS representation of a symmetric matrix game discussed above, does not have zero kinetic reactant deficiency. The following example illustrates this for a 2×2 symmetric matrix game.

Example 5. *Given the fitness functions (payoff functions) in two variables:*

$$f_1(x) = a_{11}x_1 + a_{12}x_2, \quad f_2(x) = a_{21}x_1 + a_{22}x_2 \tag{4.4}$$

equivalently we have

$$f_1(x) = a_{11}x_1^1x_2^0 + a_{12}x_1^0x_2^1, \quad f_2(x) = a_{21}x_1^1x_2^0 + a_{22}x_1^0x_2^1. \tag{4.5}$$

Note that $\phi(x) = a_{11}x_1^2x_2^0 + a_{12}x_1^1x_2^1 + a_{21}x_1^1x_2^1 + a_{22}x_1^0x_2^2$. *Consequently, we have four* 4×4 *poly-*$\widehat{T}$ *matrices (columns indexed by the reactant complexes* $x_1, 2x_1, x_2, 2x_2$*). Computing* $NK(x)$ *and* $\widehat{T}_1$*, we have*

$$NK(x) = \begin{bmatrix} 1 & -1 & 0 & 0 \\ 0 & 0 & 1 & -1 \end{bmatrix} \begin{bmatrix} x_1f_1(x) \\ x_1\phi(x) \\ x_2f_2(x) \\ x_2\phi(x) \end{bmatrix}, \quad \widehat{T}_1 = \begin{bmatrix} 2 & 3 & 1 & 2 \\ 0 & 0 & 1 & 1 \\ 1 & 1 & 0 & 0 \\ 0 & 0 & 1 & 1 \end{bmatrix}. \tag{4.6}$$

If we set a linear relation of the 4 columns of each poly-$\widehat{T}$ *matrix, we have* α, $-\alpha$, β *and* $-\beta$ *as coefficients respectively. On* $\widehat{T}_1$*, we obtain* $2\alpha - 3\alpha + \beta - 2\beta = 0$. *Hence,* $-\alpha = \beta$. *With this,* $\widehat{T}_1$ *matrix has a rank less than 4. Thus, the kinetic reactant deficiency* $\widehat{\delta} \neq 0$.

Thus, the overall kinetic reactant deficiency is also nonzero. A similar argument holds in general for $m \times m$ *symmetric matrix games.*

Since symmetric matrix games do not fall under the scope of Theorem 3, we use alternative approaches for their CRNT-based analysis. In [16], we employ two methods to

represent them as mass action systems: the "communication species" method introduced in the same paper of [39] and the analysis of systems dynamically equivalent to the canonical realization of their replicator equation given by the Hars-Toth Criterion [20].

5 Sufficient conditions for PY-TIK replicator systems

Symmetric population games are games where the fitness or payoff functions are arbitrary continuous functions of the strategies. The symmetric matrix games form the proper subset of population games with linear payoff functions. The subset with nonlinear payoff functions are called "playing the field games" [9]. A well-known example of a "playing the field" game is the habitat game [9]. While different game dynamics models are used with population games, the replicator equation remains the most widely used one. Thus, poly-PL replicator systems with zero kinetic reactant deficiency belong to the set of "playing the field" symmetric population games.

In this section, we will identify a class of poly-PL replicator systems which have zero kinetic reactant deficiency. We only illustrate the sufficient condition defining the class and formulate the Theorem characterizing it in the following. The complete proofs can be found in [27]. We also indicate the class of symmetric population games to which the sufficient condition may be applicable.

5.1 Formulation of the sufficient condition

We consider first the simplest form, a replicator system in two variables x_1 and x_2 and a mono-PL, i.e. a power law with positive coefficient.

The payoff functions can be written as: $f_1(x) = a_1 x_1^{f_{11}} x_2^{f_{12}}$ and $f_2(x) = b_1 x_1^{g_{11}} x_2^{g_{12}}$.

Then $\phi(x) = a_1 x_1^{f_{11}+1} x_2^{f_{12}} + b_1 x_1^{g_{11}} x_2^{g_{12}+1}$. Consequently, $h = 2$ and the two (4×4) poly-$\widehat{T}$ matrices are (columns indexed by the reactant complexes $x_1, 2x_1, x_2$ and $2x_2$):

$$\widehat{T}_1 = \begin{bmatrix} f_{11}+1 & f_{11}+2 & g_{11} & f_{11}+1 \\ f_{12} & f_{12} & g_{12}+1 & f_{12}+1 \\ 1 & 1 & 0 & 0 \\ 0 & 0 & 1 & 1 \end{bmatrix} \quad \widehat{T}_2 = \begin{bmatrix} f_{11}+1 & g_{11}+1 & g_{11} & g_{11} \\ f_{12} & g_{12}+1 & g_{12}+1 & g_{12}+2 \\ 1 & 1 & 0 & 0 \\ 0 & 0 & 1 & 1 \end{bmatrix}.$$

If we set a linear relation of the 4 columns of $\widehat{T}_1$ with the coefficients α, β, γ and σ, we obtain immediately $\beta = -\alpha$ and $\sigma = -\gamma$. Further computations result in: $\alpha =$

$\gamma(g_{11} - f_{11} - 1)$ and $\gamma(g_{12} - f_{12}) = 0$. Hence if $g_{12} \neq f_{12}$, then $\gamma = 0$. This implies that α, β and σ are also zero. Hence $\widehat{T}_1$ has maximal rank equal to 4, and $\widehat{\delta}_1 = 0$. Similarly, one obtains, using $\widehat{T}_2$, that if $g_{11} \neq f_{11}$, then $\widehat{\delta}_2 = 0$. Combining the two results, then the RS has a positive equilibrium (necessarily complex balanced).

Now, using the similar process, if we set the payoff functions of 3-variable replicator system are mono-PL, i.e. of the form

$$f_1(x) = a_1 x_1^{f_{11}} x_2^{f_{12}} x_3^{f_{13}}; \qquad f_2(x) = b_1 x_1^{g_{11}} x_2^{g_{12}} x_3^{g_{13}}; \qquad f_3(x) = c_1 x_1^{p_{11}} x_2^{p_{12}} x_3^{p_{13}}$$

then $f_{11} \neq g_{11} = p_{11}$, $g_{12} \neq f_{12} = p_{12}$ and $p_{13} \neq f_{13} = g_{13}$, then the replicator system has a positive equilibrium (necessarily complex balanced).

Fixing the payoff functions as mono-PL but generalizing the number of variables in replicator systems, we obtain the following proposition:

Proposition 7. *($m \geq 2$ variables , mono-PL) If the payoff functions of m-variable replicator system are mono-PL, i.e. of the form*

$$f_p(x) = a_{p1} \prod_{j=1}^{m} x_j^{g_{1j}^p} \text{ where } 2 \leq p \leq m \tag{5.1}$$

then for each j, the sets $G^j = \{g_{1j}^p | 1 \leq p \leq m; p \neq j\}$ for $1 \leq j \leq m$ are singleton $\{g^j\}$ such that $g^j \neq g_{1j}^j$ for $1 \leq j \leq m$ then the replicator system has a positive equilibrium (necessarily complex balanced).

The proof of Proposition 7 can be found in [27]. At this point, we will try to increase the number of terms of the payoff functions denoted by h'. We now consider replicator systems in 2 variables x_1 and x_2 with 2 terms in the form

$$f_1(x) = a_1 x_1^{f_{11}} x_2^{f_{12}} + a_2 x_1^{f_{21}} x_2^{f_{22}} \qquad f_2(x) = b_1 x_1^{g_{11}} x_2^{g_{12}} + b_2 x_1^{g_{21}} x_2^{g_{22}} \tag{5.2}$$

Then,

$$\phi(x) = a_1 x_1^{f_{11}+1} x_2^{f_{12}} + a_2 x_1^{f_{21}+1} x_2^{f_{22}} + b_1 x_1^{g_{11}} x_2^{g_{12}+1} + b_2 x_1^{g_{21}} x_2^{g_{22}+1}. \tag{5.3}$$

Consequently, we have four 4×4 poly-$\widehat{T}$ matrices are (columns indexed by the reactant complexes $x_1, 2x_1, x_2, 2x_2$):

$$\widehat{T}_1 = \begin{bmatrix} f_{11}+1 & f_{11}+2 & g_{11} & f_{11}+1 \\ f_{12} & f_{12} & g_{12}+1 & f_{12}+1 \\ 1 & 1 & 0 & 0 \\ 0 & 0 & 1 & 1 \end{bmatrix} \quad \widehat{T}_2 = \begin{bmatrix} f_{11}+1 & g_{11}+1 & g_{11} & g_{11} \\ f_{12} & g_{12}+1 & g_{12}+1 & g_{12}+2 \\ 1 & 1 & 0 & 0 \\ 0 & 0 & 1 & 1 \end{bmatrix}$$

$$\widehat{T}_3 = \begin{bmatrix} f_{21}+1 & f_{21}+2 & g_{21} & f_{21}+1 \\ f_{22} & f_{22} & g_{22}+1 & f_{22}+1 \\ 1 & 1 & 0 & 0 \\ 0 & 0 & 1 & 1 \end{bmatrix} \quad \widehat{T}_4 = \begin{bmatrix} f_{21}+1 & g_{21}+1 & g_{21} & g_{21} \\ f_{22} & g_{22}+1 & g_{22}+1 & g_{22}+2 \\ 1 & 1 & 0 & 0 \\ 0 & 0 & 1 & 1 \end{bmatrix}$$

If we set a linear relation of the 4 columns of each poly-$\widehat{T}$ matrix, we obtain $\alpha, -\alpha, \beta$ and $-\beta$ respectively. We obtain:

$$\begin{gathered} \alpha_1 = \beta_1(g_{11} - f_{11} - 1) \\ \beta_1(g_{12} - f_{12}) = 0 \\ \alpha_2(f_{11} - g_{11}) = 0 \\ \beta_2 = \alpha_2(f_{12} - g_{12} - 1) \\ \alpha_3 = \beta_3(g_{21} - f_{21} - 1) \\ \beta_3(g_{22} - f_{22}) = 0 \\ \alpha_4(f_{21} - g_{21}) = 0 \\ \beta_4 = \alpha_4(f_{22} - g_{22} - 1) \end{gathered} \tag{5.4}$$

If we set $f_{11} \neq g_{11}$, $f_{12} \neq g_{12}$, $f_{21} \neq g_{21}$ and $f_{22} \neq g_{22}$ then $\alpha_i = \beta_i = 0$ where $1 \leq i \leq 4$.

With this, each poly-$\widehat{T}$ matrix has a maximal rank equal to 4. Hence, each kinetic reactant deficiency $\widehat{\delta} = 0$. Therefore, the replicator system has a positive equilibrium (necessarily complex balanced).

For the case that the replicator systems have 2 variables and the payoff functions have h' terms, we have the following proposition:

Proposition 8. *(2 variables , h' terms) If the payoff functions of a 2-variable replicator system are of the form*

$$f_1(x) = a_1 x_1^{f_{11}} x_2^{f_{12}} + \ldots + a_k x_1^{f_{k1}} x_2^{f_{x2}} \tag{5.5}$$

$$f_2(x) = b_1 x_1^{g_{11}} x_2^{g_{12}} + \ldots + b_k x_1^{g_{k1}} x_2^{g_{k2}} \tag{5.6}$$

then $f_{j1} \neq g_{j1}$ and $f_{j2} \neq g_{j2}$ where $1 \leq j \leq k$ imply that the replicator system has a positive (complex balanced) equilibrium.

For the proof of the previous proposition and succeeding theorem, see [27]. As a result of the two previous propositions, we arrived at the following theorem that reflects the general case.

Theorem 5. *(m variables , h' terms) If the payoff functions of m-variable replicator system with h' terms are of the form*

$$f_p(x) = \sum_{i=1}^{h'} \left(a_{pi} \prod_{j=1}^{m} x_j^{g_{ij}^p} \right) \quad where \quad 1 \leq p \leq m \tag{5.7}$$

then for each j, the sets $G^{ij} = \{g_{ij}^p | 1 \leq p \leq m; p \neq j\}$ for $1 \leq j \leq m$ where $1 \leq i \leq h'$ are singleton $\{g^{ij}\}$ such that $g^{ij} \neq g_{ij}^j$ for $1 \leq j \leq m$ where $1 \leq i \leq h'$ then the replicator system has a positive equilibrium (necessarily complex balanced).

Remark 3. Note that the previous theorem also covers the case when the payoff functions do not have the same number of terms. One simply uses the same "trick" of replacing the last term of the shorter function with $(k - k' + 1)$ copies of $\frac{1}{k-k'+1}$ of that term.

5.2 Applicability to symmetric population games

Among the "playing the field" games, i.e. those with non-linear payoff functions, multi-player games frequently lead to polynomial payoff functions [17]. Such evolutionary games hence are the most likely candidates for examples which satisfy the sufficient condition. In future work, we will study the properties of population games with zero kinetic reactant deficiency and hope to identify examples for the sufficient condition in the EGT literature.

6 Conclusions and outlook

We introduced the poly-PL chemical kinetic systems to be the positive linear combinations of power law kinetic systems. We then derived a sufficient and necessary condition for chemical reaction networks with this type of kinetics to admit a complex balanced equilibrium. That is, we found out that weakly reversible reaction networks possess a complex balanced equilibrium iff it has zero kinetic reactant deficiency. This result extends the result of Talabis et al. [38] to a more general kinetic system, e.g., Poly-PL kinetic systems (PYK). A parametrization and uniqueness properties of this set of equilibria are also shown.

In the aim of applying Theorem 3 to evolutionary games, we considered the symmetric population games with the replicator equation model studied by Veloz et al. [39]. A correction to their work was discussed in this paper. While those with linear payoff

functions lie outside the scope of main result, a sufficient condition for population games with nonlinear payoff functions to have a zero kinetic reactant deficiency, was formulated.

In the future, we would like to continue analyzing the complex equilibrium exhibited by weakly reversible poly-PL kinetic systems, for instance, the stability of such equilibrium. As mentioned, population games with zero kinetic reactant deficiency will also be explored.

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A Nomenclature

We have list some of the acronyms and symbols mentioned in the paper.

Meaning	Symbol
deficiency of a CRN	δ
incidence matrix of a CRN	I_a
$k-$ Laplacian matrix	A_k
factor map of a kinetics K	ψ_K
kinetics of a CRN	K
interaction map	I_K
molecularity map/matrix of complexes	Y
kinetic order matrix	F
set of positive equilibria of a system	$E_+(\mathscr{N}, K)$
set of complex balanced equilibria of a system	$Z_+(\mathscr{N}, K)$
poly T-matrix	T_κ
augmented T matrix	$\widehat{T}_\kappa$
kinetic reactant deficiency	$\widehat{\delta}$
κ^{th} kinetic reactant flux subspace	$\widetilde{S}_\kappa$
κ^{th} kinetic reactant flux class	Q_κ

Abbreviation	Meaning
CB	complex balanced
CKS	chemical kinetic system
CRN	chemical reaction network
EGT	evolutionary game theory
PL-RDK	power-law reactant-determined kinetics
PL-RLK	reactant set linear independent kinetics
PLK	power-law kinetics
PYK	poly-PL kinetics
PY-TIK	complex factorizable poly-PL kinetics with $\widehat{\delta} = 0$
RIDK	rate constant-interaction map decomposable kinetics
RS	replicator systems
SFRF	species formation rate function