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# Qualitative permanence of Lotka–Volterra equations

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**Abstract** In this paper, we consider permanence of Lotka–Volterra equations. We investigate the sign structure of the interaction matrix that guarantees the permanence of a Lotka–Volterra equation whenever it has a positive equilibrium point. An interaction matrix with this property is said to be qualitatively permanent. Our results provide both necessary and sufficient conditions for qualitative permanence.

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## 1 Introduction

One of the important challenges in ecology is to develop a theory which predicts the stability of an ecosystem when its community structure is given. In this paper, to tackle this problem, we study the well-known Lotka–Volterra system:

$$\dot{x}_i = x_i(r_i + \sum_{j=1}^{n} a_{ij}x_j), \quad i = 1, 2, \ldots, n, \tag{1.1}$$

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where $x_i$ denotes the population density of species $i$. The parameter $r_i$ denotes the intrinsic growth rate of species $i$ and the matrix $A$ composed of $a_{ij}$ determines the community structure (the matrix $A$ is called the *interaction matrix*). One of the important assumptions in Lotka-Volterra systems is that the functional responses are linear. This assumption is relaxed in many ecological models to include non-linear functional responses such as Holling type II functional responses. Although such a relaxation provides a system with an important stabilization mechanism (e.g., see [17,18]), the linear functional response has an advantage in developing a general theory applicable to systems of large and complex networks. This paper focuses on the ecological system with simple functional responses and explores large and complex ecological networks.

The theory of VL-stable (or dissipative) matrices is one of the important theories for understanding the global dynamics of Lotka–Volterra equations (e.g., see [4,14, 23,24]). A square matrix $A$ is said to be *VL-stable* if there exists a positive diagonal matrix $D > 0$ such that the symmetric matrix $DA + A^\top D$ is negative definite, i.e., if there exist positive numbers $d_i$ such that

$$\sum_i \sum_j d_i a_{ij} x_i x_j < 0$$

for all $\mathbf{x} \neq \mathbf{0}$. The theory of VL-stable matrices shows that if $A$ is VL-stable, then for every $r_i \in \mathbb{R}$ system (1.1) has a globally asymptotically stable equilibrium point $\widehat{\mathbf{x}}$, i.e., $\widehat{\mathbf{x}}$ is stable in $\mathbb{R}^n_+$ and attracts all solutions with the initial conditions $\mathbf{x}(0) \in \mathbb{R}^n_+$ satisfying $x_i(0) > 0$ for all $i \in \operatorname{supp}(\widehat{\mathbf{x}})$. Here $\mathbb{R}^n_+ = \{\mathbf{x} \in \mathbb{R}^n : x_i \geq 0\}$ and $\operatorname{supp}(\mathbf{x}) = \{i : x_i > 0\}$. If (1.1) has an interior equilibrium point $\widehat{\mathbf{x}}$, then $\widehat{\mathbf{x}}$ is the globally asymptotically stable equilibrium point. A matrix $A$ is said to be *qualitatively VL-stable* if every matrix with the same sign pattern is VL-stable. The application of qualitative stability concepts to ecology goes back to May [15]. A necessary and sufficient condition for qualitative VL-stability is given as follows [4,14]:

$$\begin{aligned}
&\text{(i) } a_{ii} < 0,\\
&\text{(ii) } a_{ij}a_{ji} \leq 0,\\
&\text{(iii) there are no cycles of length} \geq 3 \text{ (i.e., } a_{i_1i_2}a_{i_2i_3}\cdots a_{i_ki_1} = 0 \text{ for all}\\
&\qquad \text{pairwise distinct } i_1, i_2, \ldots, i_k \text{ with } k \geq 3).
\end{aligned} \tag{1.2}$$

Therefore, under this qualitative condition, all species coexist at a globally asymptotically stable equilibrium point as long as the positive equilibrium point exists. A typical example covered by (1.2) is an $n$ species food chain.

Although the theory of VL-stable matrices provides a sufficient condition for global stability of the Lotka–Volterra equations, it has been recognized that the global stability is a rather strong concept for species coexistence. In fact, we often observe species coexistence in the Lotka–Volterra equation even if it does not have a globally asymptotically stable positive equilibrium point. This implies that species coexistence is possible under a wider class of community structures than that predicted by the theory of VL-stable matrices. Therefore, in this paper, instead of global stability we consider permanence of (1.1). The definition of permanence is given as follows: (1.1) is said to be *permanent* if there exists a positive constant $\delta > 0$ such that

$$\delta \le \liminf_{t\to\infty} x_i(t) \le \limsup_{t\to\infty} x_i(t) \le \frac{1}{\delta}, \quad i = 1, 2, \ldots, n$$

for all solutions $\mathbf{x}(t)$ with $\mathbf{x}(0) > 0$ ($x_i(0) > 0$ for all $i$). It is obvious that system (1.1) is permanent if the positive equilibrium point is globally asymptotically stable. Conversely, even if the positive equilibrium point is unstable, (1.1) can be permanent. Permanent systems could exhibit every possible type of coexistence dynamics.

In the next section, to emphasize the influence of the community structure on permanence, we define qualitative permanence. Then we list our main results on qualitative permanence of (1.1). These results include both necessary and sufficient conditions for qualitative permanence. The necessary condition provides a community structure with which system (1.1) is not permanent even if it has a positive equilibrium point, and the sufficient condition provides a community structure with which system (1.1) is permanent as long as it has a positive equilibrium point. All proofs are given in the subsequent sections: Sects. 5–7. In Sect. 3, we provide some ecological interpretation of our mathematical results. In Sect. 4, we define the reduced systems of (1.1) and introduce a theorem on average Liapunov functions. They are used in the proofs of our main results. The final section includes concluding remarks.

## 2 Qualitative permanence

It is known that a positive equilibrium point is necessary for (1.1) to be permanent (see Theorem 13.5.1 of [4]). If system (1.1) does not have a positive equilibrium point, then the omega-limit set $\omega(\mathbf{x})$ of every $\mathbf{x} \in \mathbb{R}^n_+$ is contained in the boundary of $\mathbb{R}^n_+$ (see Theorem 5.2.1 of [4]). Suppose that system (1.1) has a positive equilibrium point, which is given as a positive root $\mathbf{x}^* > 0$ of the following equations:

$$r_i + \sum_{j=1}^{n} a_{ij} x_j^* = 0, \quad i = 1, 2, \ldots, n.$$

Substituting this equation into (1.1) and removing the parameters $r_i$, we obtain

$$\dot{x}_i = x_i \sum_{j=1}^{n} a_{ij}(x_j - x_j^*), \quad i = 1, 2, \ldots, n. \tag{2.1}$$

Conversely, consider (2.1) with $\mathbf{x}^* > 0$. It is obvious that $\mathbf{x}^*$ is a positive equilibrium point of (2.1), and for any pair $A = (a_{ij})$ and $\mathbf{x}^*$ the vector $\mathbf{r} \in \mathbb{R}^n$ is uniquely determined by $r_i + \sum_{j=1}^{n} a_{ij} x_j^* = 0$, $i = 1, 2, \ldots, n$. So, (2.1) represents any Lotka–Volterra system of the form (1.1) admitting a positive equilibrium point.

Let $Q_A$ be the set of the matrices $\widetilde{A} = (\widetilde{a}_{ij})$ with the same sign pattern as $A = (a_{ij})$, i.e., $\operatorname{sgn}\widetilde{a}_{ij} = \operatorname{sgn} a_{ij}$ for all $i$, $j$. Then qualitative permanence is defined as follows:

**Definition 2.1** (Qualitative permanence). An $n \times n$ matrix $A = (a_{ij})$ is said to be qualitatively permanent if

$$\dot{x}_i = x_i \sum_{j=1}^{n} \widetilde{a}_{ij}(x_j - x_j^*), \quad i = 1, 2, \ldots, n$$

is permanent for every $\widetilde{A} \in Q_A$ and every $\mathbf{x}^* > \mathbf{0}$.

Note that qualitative permanence is a property of square matrices. An $n \times n$ matrix $A$ is qualitatively permanent if and only if

$$\dot{x}_i = x_i(r_i + \sum_{j=1}^{n} \widetilde{a}_{ij} x_j), \quad i = 1, 2, \ldots, n$$

is permanent for every $\widetilde{A} \in Q_A$ and $\mathbf{r} \in \mathbb{R}^n$ satisfying $\mathbf{r} + \widetilde{A}\mathbf{x}^* = \mathbf{0}$ for some $\mathbf{x}^* > \mathbf{0}$. Hence, if $A$ is qualitatively permanent, then system (1.1) is permanent as long as it has a positive equilibrium point.

We start with a simple necessary condition for qualitative permanence.

**Proposition 2.2** *If a matrix $A = (a_{ij})$ is qualitatively permanent, then $a_{ii} \le 0$ for all $i$, and $a_{ii} < 0$ for at least one $i$.*

The proof of this proposition is given in Sect. 5. In the following we restrict to the "generic" (and realistic) case that all diagonal entries of $A$ are negative. Then we obtain strong necessary conditions for qualitative permanence as follows.

**Theorem 2.3** *Suppose that $a_{ii} < 0$ for all $i$. If a matrix $A = (a_{ij})$ is qualitatively permanent, then*

(C1) *all cycles of length $\ge 2$ are nonpositive (i.e., $a_{i_1 i_2} a_{i_2 i_3} \cdots a_{i_k i_1} \le 0$ for all pairwise distinct $i_1, i_2, \ldots, i_k$, $k \ge 2$),*

(C2) *every negative cycle $a_{i_1 i_2} a_{i_2 i_3} \ldots a_{i_k i_1} < 0$ contains a unique negative $a_{ij}$.*

The condition (C1) follows from a necessary condition for permanence of (1.1) in terms of the sign of the determinant of the interaction matrix. The condition (C2) is obtained by constructing an attractive heteroclinic cycle contained in the boundary of $\mathbb{R}^n_+$. The proof of this theorem is given in section 5.

We believe that (C1) and (C2) already characterize qualitative permanence.

**Conjecture 2.4** *Suppose that $a_{ii} < 0$ for all $i$ and that conditions* (C1) *and* (C2) *hold. Then the matrix $A = (a_{ij})$ is qualitatively permanent.*

In the following we provide some partial results in this direction. Note that the conditions (C1) and (C2) are much weaker than the characterization (1.2) of qualitative VL–stability. This provides many sign patterns for the interaction matrix $A$ that guarantee permanence without global stability of the interior equilibrium, and hence lead to more interesting dynamics such as a stable limit cycle or chaos. Some explicit sign patterns are listed in Sects. 3 and 8.

The following theorem provides a sufficient condition for permanence for certain generalizations of food chains.

**Theorem 2.5** *Suppose that $A$ has the following sign pattern:*

$$\begin{pmatrix} \bullet & \bullet & \cdots & \bullet & \bullet \\ \oplus & \bullet & \cdots & \bullet & \bullet \\ 0 & \oplus & \cdots & \bullet & \bullet \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & \oplus & \bullet \end{pmatrix}, \tag{2.2}$$

*where $\bullet$ denotes an arbitrary sign and $\oplus$ denotes either $0$ or $+$. Then system (1.1) is permanent if $-A$ is a P-matrix and there exists a positive equilibrium point.*

Note that if $-A$ is a P-matrix, then all diagonal entries of $A$ are negative (the definition of P-matrices is given in Definition 6.1). The proof of this theorem is given in Sect. 6.

Since every (nonzero) cycle of $A$ with the sign pattern (2.2) consists of a single $\bullet$ sign and several $\oplus$ signs, the sign pattern (2.2) satisfies the condition (C2). Therefore, by Theorems 2.3 and 2.5 (and Lemma 6.2), we obtain the following theorem, which provides a sufficient condition for qualitative permanence.

**Theorem 2.6** *Suppose that $a_{ii} < 0$ for all $i$ and $A$ has the sign pattern (2.2). Then $A$ is qualitatively permanent if (C1) holds.*

In low dimensional cases (i.e., $n \leq 3$), the necessary condition (C1)–(C2) given in Theorem 2.3 becomes a sufficient condition.

**Theorem 2.7** *Suppose that $a_{ii} < 0$ for all $i$ and $n \leq 3$. Then an $n \times n$ matrix $A$ is qualitatively permanent if and only if the conditions (C1) and (C2) hold.*

## 3 Ecological interpretations

In this section, we consider ecological interpretations of our results.

In Theorem 2.3, we provide two necessary conditions (C1) and (C2) for qualitative permanence which we believe to be also sufficient. (C1) includes the condition that $a_{ij}a_{ji} \leq 0$ for all $i \neq j$. This means that all pairwise interactions are of predator–prey type or degenerate ($a_{ij}a_{ji} = 0$). Indeed, strong mutualist interaction can lead to unbounded orbits, whereas strong competition may lead to competitive exclusion in form of bistability, both of which are incompatible with permanence. (C2) says that each nonzero cycle $a_{i_1i_2}a_{i_2i_3}\cdots a_{i_ki_1}$ contains precisely one negative element. The reason is that an even number of negative entries would again enable a form of bistability whereas an odd number (of at least three) allows for a repressilator-like system that can lead to an attractive heteroclinic cycle on the boundary (e.g., see [19]).

Theorem 2.7 shows that the conditions (C1) and (C2) are necessary and sufficient for qualitative permanence if $n \leq 3$. If $n = 1$ or 2, the result is clear. Consider the case $n = 3$. In this case, every matrix satisfying (C1) and (C2) belongs to at least one of the following five sign patterns (up to permutation):

$$B_1 = \begin{pmatrix} - & \ominus & \ominus \\ \oplus & - & \ominus \\ 0 & \oplus & - \end{pmatrix}, \quad B_2 = \begin{pmatrix} - & 0 & \ominus \\ \oplus & - & \ominus \\ \oplus & \oplus & - \end{pmatrix}, \quad B_3 = \begin{pmatrix} - & \ominus & \ominus \\ \oplus & - & 0 \\ \oplus & \oplus & - \end{pmatrix},$$
$$B_4 = \begin{pmatrix} - & 0 & 0 \\ \oplus & - & \ominus \\ \ominus & \oplus & - \end{pmatrix}, \quad B_5 = \begin{pmatrix} - & \ominus & 0 \\ \oplus & - & 0 \\ \ominus & \oplus & - \end{pmatrix},$$

where $\ominus$ denotes either 0 or $-$. Although the matrices $B_4$ and $B_5$ do not have a nonzero cycle of length 3 (and thus they are reducible), the matrices $B_1$, $B_2$ and $B_3$ could have a negative cycle of length 3, i.e., $a_{13}a_{32}a_{21} < 0$ (note that this cycle can destabilize the matrices). $B_1$, $B_2$ and $B_3$ are limit cases of the following tri-trophic food web with omnivory:

$$B = \begin{pmatrix} - & - & - \\ + & - & - \\ + & + & - \end{pmatrix}.$$

This matrix includes two nonzero cycles of length 3: $a_{13}a_{32}a_{21} < 0$ and $a_{12}a_{23}a_{31} > 0$. The latter cycle is not allowed for qualitative permanence. In fact, the matrices $B_1$, $B_2$ and $B_3$ do not have this cycle. If the latter cycle exists, strong competition may lead to competitive exclusion in form of bistability as mentioned above. Species 2 and 3 are indeed competing for a common resource, species 1.

Our results are robust against a small perturbation of the parameters $r_i$ and $a_{ij}$. If (1.1) satisfying some sufficient condition given in this paper has a positive equilibrium point, then, by definition, it is permanent. Furthermore, it is still permanent even if we replace the zero entries of $A$ by nonzero entries close to 0. For example, consider system (1.1) with $B_1$ as an interaction matrix, and suppose that this system has a positive equilibrium point. Then this system is still permanent even if we replace the (3, 1)-entry of the interaction matrix by $\epsilon$ whose absolute value is sufficiently small ($\epsilon$ is also allowed to be negative). Since the same conclusion also holds for other matrices, a comparison of $B_1$, $B_2$ and $B_3$ with $B$ shows that the positive cycle $a_{12}a_{23}a_{31} > 0$ must be very small for the application of our results. As mentioned above, competitive exclusion can follow from large $a_{12}a_{23}a_{31}$. More generally, suppose the $n$-trophic food web with species $i$ feeding on species $i-1$, $i = 2, \ldots, n$ and species 1 at the bottom. If species $n$ (top-predator) also feeds on species 1, the food web has two long cycles, $a_{1k}a_{k,k-1} \ldots a_{21} = - + \cdots +$ and $a_{12} \ldots a_{k-1,k}a_{k1} = - \cdots - +$. Although the former cycle satisfies (C1) and (C2), the latter cycle is not allowed for qualitative permanence, then it could lead to extinction of species due to competitive exclusion or heteroclinic cycles observed in a repressilator-like system (note that both cycles can destabilize the matrix). To avoid this extinction, the food web must have a pattern to reduce the latter cycle. This means that if a food web has such a cycle due to omnivory, then some top down effect in the path through several trophic levels, or the bottom up effect directly from the bottom to the top trophic level must be small. However, it is not clear how small must the absolute value of such a cycle be to allow for permanence (but see [4] for a classification of permanence of (1.1) with $n \leq 3$).

## 4 Preliminaries

In this section, we define a reduced system of (1.1) and develop a method for proving our theorems.

### 4.1 Reduced systems

A reduced system of (1.1) is introduced to obtain useful information about the equilibrium points of (1.1) and their external eigenvalues. The same technique is utilized by Kirlinger [9] in a three predator one prey system. Before the definition of a reduced system of (1.1), we introduce some notation. Define $I = \{1, 2, \ldots, n\}$ (This notation is used throughout this paper). Let $J = \{i_1, i_2, \ldots, i_k\} \subset I$ and $J \neq \emptyset, I$. Let $A_{11}$ (resp. $A_{22}$) be the principal submatrix of $A$ with respect to $J$ (resp. $I \backslash J$). Let $A_{12}$ (resp. $A_{21}$) be the submatrix of $A$ with $a_{ij}, i \in J, j \in I \backslash J$ (resp. $a_{ij}, i \in I \backslash J, j \in J$). Then, by renumbering the indices, $A$ is transformed to

$$\begin{pmatrix} A_{11} & A_{12} \\ A_{21} & A_{22} \end{pmatrix}.$$

Similarly we define $\mathbf{r}_1$ (respectively, $\mathbf{r}_2$) by the vector composed of $r_i, i \in J$ (respectively, $r_i, i \in I \backslash J$). If $A_{22}$ is nonsingular, we can define the reduced system of (1.1) with respect to $J$ as follows.

**Definition 4.1** If $A_{22}$ is nonsingular, then the following system is called the reduced system of (1.1) with respect to $J$:

$$\dot{x}_i = x_i(r_i^J + \sum_{j \in J} a_{ij}^J x_j), \quad i \in J,$$

where $r_i^J$ and $a_{ij}^J$ are defined by

$$\mathbf{r}^J = \begin{pmatrix} r_{i_1}^J \\ r_{i_2}^J \\ \vdots \\ r_{i_k}^J \end{pmatrix} := \mathbf{r}_1 - A_{12} A_{22}^{-1} \mathbf{r}_2,$$

$$A^J = \begin{pmatrix} a_{i_1 i_1}^J & a_{i_1 i_2}^J & \cdots & a_{i_1 i_k}^J \\ a_{i_2 i_1}^J & a_{i_2 i_2}^J & \cdots & a_{i_2 i_k}^J \\ \vdots & \vdots & \ddots & \vdots \\ a_{i_k i_1}^J & a_{i_k i_2}^J & \cdots & a_{i_k i_k}^J \end{pmatrix} := A_{11} - A_{12} A_{22}^{-1} A_{21}.$$

The reduced system is denoted by (1.1)$^J$. If $J = I \backslash \{k\}$, then $r_i^J$ and $a_{ij}^J$, $i, j \in J$, are given by $r_i^J = r_i - a_{ik} r_k / a_{kk}$ and $a_{ij}^J = a_{ij} - a_{ik} a_{kj} / a_{kk}$.

The matrix $A^J$ is often called the Schur complement of $A_{22}$ in $A$, and Schur's identity says that $\det A_{22} \det A^J = \det A$.

The following lemma is useful for checking the feasibility of the reduced systems.

**Lemma 4.2** *Let $k \in J$. Suppose that $A_{22}$ is nonsingular. Then the reduced system* (1.1)$^{J \backslash \{k\}}$ *is defined if $a_{kk}^J \neq 0$.*

*Proof* It is straightforward to show $a_{kk}^J = \det A'_{22} / \det A_{22}$, where $A'_{22}$ is the principal submatrix of $A$ with respect to $(I \backslash J) \cup \{k\}$. (This is a special case of Schur's identity) The assumption implies $\det A'_{22} \neq 0$.

The equilibrium points of the reduced system (1.1)$^J$ are closely related to those of (1.1).

**Lemma 4.3** *For $\widehat{\mathbf{x}} \in \mathbb{R}^n$, let $\widehat{\mathbf{x}}_1$ and $\widehat{\mathbf{x}}_2$ be the vectors composed of $\widehat{x}_i$, $i \in J$, and $\widehat{x}_i$, $i \in I \backslash J$, respectively. Suppose that $A_{22}$ is nonsingular.*

(a) *If $\widehat{\mathbf{x}}_1 \geq \mathbf{0}$ is an equilibrium point of the reduced system* (1.1)$^J$ *and $\widehat{\mathbf{x}}_2 = -A_{22}^{-1}(\mathbf{r}_2 + A_{21}\widehat{\mathbf{x}}_1) \geq \mathbf{0}$, then $\widehat{\mathbf{x}} \geq \mathbf{0}$ is an equilibrium point of* (1.1).
(b) *If $\widehat{\mathbf{x}} \geq \mathbf{0}$ is an equilibrium point of* (1.1) *satisfying $\widehat{\mathbf{x}}_2 > \mathbf{0}$, then $\widehat{\mathbf{x}}_1 \geq \mathbf{0}$ is an equilibrium point of the reduced system* (1.1)$^J$. *Furthermore, for any $i \in J$ with $\widehat{x}_i = 0$, $r_i^J + (A^J \widehat{\mathbf{x}}_1)_i$ is the external eigenvalue of* (1.1) *evaluated at $\widehat{\mathbf{x}}$ with respect to the $x_i$-direction.*

*Proof* Consider case (a). By assumption, $\widehat{\mathbf{x}}_1$ and $\widehat{\mathbf{x}}_2$ satisfy

$$\widehat{x}_i (r_i^J + (A^J \widehat{\mathbf{x}}_1)_i) = 0, \quad i \in J, \tag{4.1}$$

$$\mathbf{r}_2 + A_{21}\widehat{\mathbf{x}}_1 + A_{22}\widehat{\mathbf{x}}_2 = \mathbf{0}. \tag{4.2}$$

Substitution of $\widehat{\mathbf{x}}_2 = -A_{22}^{-1}(\mathbf{r}_2 + A_{21}\widehat{\mathbf{x}}_1)$ into the first equation yields

$$\widehat{x}_i (r_i + (A_{11}\widehat{\mathbf{x}}_1)_i + (A_{12}\widehat{\mathbf{x}}_2)_i) = 0, \quad i \in J. \tag{4.3}$$

Hence, by (4.2) and (4.3), we see that $\widehat{\mathbf{x}}$ is a nonnegative equilibrium point of (1.1).

Consider case (b). Every equilibrium point $\widehat{\mathbf{x}}$ of (1.1) with $\widehat{\mathbf{x}}_2 > 0$ satisfies (4.2) and (4.3). Equation (4.2) leads to $\widehat{\mathbf{x}}_2 = -A_{22}^{-1}(\mathbf{r}_2 + A_{21}\widehat{\mathbf{x}}_1)$ and its substitution into (4.3) yields (4.1), which is the equilibrium equation for the reduced system (1.1)$^J$.

For $i \in J$, we have

$$\begin{aligned} r_i^J + (A^J \widehat{\mathbf{x}}_1)_i &= (\mathbf{r}_1 - A_{12}A_{22}^{-1}\mathbf{r}_2)_i + ((A_{11} - A_{12}A_{22}^{-1}A_{21})\widehat{\mathbf{x}}_1)_i \\ &= r_i + (A\widehat{\mathbf{x}})_i, \end{aligned}$$

where (4.2) is used. This implies that if $\widehat{x}_i = 0$, then $r_i^J + (A^J \widehat{\mathbf{x}}_1)_i$ denotes the external eigenvalue of (1.1) evaluated at $\widehat{\mathbf{x}}$ with respect to the $x_i$-direction.

### 4.2 Average Liapunov functions

One of the powerful tools for proving permanence of (1.1) is an average Liapunov function. The function $P(\mathbf{x}) = x_1^{p_1} x_2^{p_2} \cdots x_n^{p_n}$ is often used as an average Liapunov function to show that the boundary of $\mathbb{R}^n_+$ is repelling (see [4]). However, in this paper, we adopt the function $P(\mathbf{x}) = x_i$, $i \in I$, as an average Liapunov function to show that the face $S_i = \{\mathbf{x} \in \mathbb{R}^n_+ : x_i = 0\}$ is repelling. More precisely, by using this function, we show that, in a given compact forward invariant set $X \subset \mathbb{R}^n_+$, there exists a compact *absorbing set* $X' \subset X \backslash S_i$ *for* $X \backslash S_i$ (i.e., $X'$ is forward invariant and for every $\mathbf{x} \in X \backslash S_i$ the semi-orbit $\gamma^+(\mathbf{x})$ satisfies $\gamma^+(\mathbf{x}) \cap X' \neq \emptyset$). By the combination of some known results (e.g., see Corollary 2.3 of [7] and Theorem 2.5 of [5]), we can obtain the following lemma.

**Lemma 4.4** *Suppose that* $X \subset \mathbb{R}^n_+$ *is a compact forward invariant set. If there exists an* $i \in I$ *such that*

$$r_i + (A\widehat{\mathbf{x}})_i > 0$$

*for all equilibrium points* $\widehat{\mathbf{x}} \in S_i \cap X$*, then there exists a compact absorbing set* $X' \subset X \backslash S_i$ *for* $X \backslash S_i$.

*Proof* Let $S = S_i \cap X$ and define $P : X \to \mathbb{R}_+$ by $P(\mathbf{x}) = x_i$. The theory of average Liapunov functions [4,7,8] ensures that the conclusion of the lemma follows if

(a): $P(\mathbf{x}) = 0$ if and only if $\mathbf{x} \in S$,
(b): For every $\mathbf{x} \in S$

$$\sup_{T>0} \int_0^T r_i + (A\mathbf{x}(t))_i dt > 0, \tag{4.4}$$

where $\mathbf{x}(t)$ is a solution of (1.1) with $\mathbf{x}(0) = \mathbf{x}$.

The condition (a) is obviously satisfied. Let us check the condition (b). We first claim that if (4.4) holds for every $\mathbf{x} \in \omega(\mathbf{y})$ ($\omega(\mathbf{y})$ is the omega-limit set of $\mathbf{y}$), then (4.4) also holds for the solution starting at $\mathbf{y}$. For $h > 0$ and $T > 0$, define

$$U(h, T) = \{\mathbf{x} \in X : \int_0^T r_i + (A\mathbf{x}(t))_i dt > h\}.$$

Then $U(h, T)$ is open. Let $\mathbf{y} \in S$ and $\mathbf{y}(t)$ be a solution with $\mathbf{y}(0) = \mathbf{y}$. Suppose that (4.4) holds for every $\mathbf{x} \in \omega(\mathbf{y})$. Then the sets $U(h, T)$, $h > 0$, $T > 0$, form an open cover of $\omega(\mathbf{y})$. Since $\omega(\mathbf{y})$ is compact, there exist $\overline{h} > 0$ and $T_1, T_2, \ldots, T_m > 0$ such that

$$\omega(\mathbf{y}) \subset \cup_{i=1}^m U(\overline{h}, T_i) =: W.$$

Note that $U(h_2, T) \supset U(h_1, T)$ if $h_1 \leq h_2$. Since $W$ is a neighborhood of $\omega(\mathbf{y})$, there exists a $t_0 \geq 0$ such that $\mathbf{y}(t) \in W$ for all $t \geq t_0$. Therefore, for some $t_1, t_2, \ldots, t_l \in \{T_1, T_2, \ldots, T_m\}$, the following inequality holds

$$\int_0^{t_0} r_i + (A\mathbf{y}(t))_i dt + \bar{h} \sum_{j=1}^{l} t_j > 0.$$

This implies that the integral of (4.4) for $\mathbf{y}$ becomes positive at $t = \sum_{j=0}^{l} t_j$.

Let $k(\mathbf{x})$ be the number of positive components of $\mathbf{x}$. By induction on $k$, we show that (4.4) holds for all $\mathbf{x} \in S$. If $k(\mathbf{x}) = 0$ (thus $\mathbf{x} = \mathbf{0}$ and $S$ contains the origin), then (4.4) holds since $r_i > 0$. Suppose that (4.4) holds if $0 \leq k(\mathbf{x}) \leq m - 1$. Let $\mathbf{x} \in S$ with $k(\mathbf{x}) = m$. Then (i): $0 \leq k(\mathbf{y}) \leq m - 1$ holds for every $\mathbf{y} \in \omega(\mathbf{x})$ or (ii): there exists a point $\mathbf{y} \in \omega(\mathbf{x})$ with $k(\mathbf{y}) = m$. In case (i), the induction hypothesis and the claim proved above yields (4.4). In case (ii), the averaging property of solutions of (1.1) implies that there exists a sequence $s_j \to \infty$ and an equilibrium point $\widehat{\mathbf{x}} \in S$ such that

$$\lim_{j \to \infty} \frac{1}{s_j} \int_0^{s_j} \mathbf{x}(t) dt = \widehat{\mathbf{x}}$$

(e.g., see Theorem 5.2.3 of [4] and Lemma 2.4 of [5]). Therefore, by assumption,

$$\frac{1}{s_j} \int_0^{s_j} r_i + (A\mathbf{x}(t))_i dt > 0$$

holds for $j$ sufficiently large. This implies that (4.4) holds.

## 5 Proof of Proposition 2.2 and Theorem 2.3

In this section, we prove the necessary conditions for qualitative permanence: Proposition 2.2 and Theorem 2.3. Proposition 2.2 and condition (C1) follow from known necessary conditions for permanence of (1.1) (see Lemmas 5.1 and 5.2). On the other hand, the condition (C2) is obtained by constructing an attractive heteroclinic cycle located in the boundary of $\mathbb{R}^n_+$ (see Lemma 5.4).

First, we list two lemmas utilized to obtain Proposition 2.2 and condition (C1).

**Lemma 5.1** (Theorem 13.5.2 of [4]). *If system* (1.1) *is permanent with interior equilibrium* $\mathbf{x}^*$, *then* (*a*) $\sum a_{ii} x_i^* < 0$ *and* (*b*) $\det(-A) > 0$.

**Lemma 5.2** *Suppose that* $a_{ii} < 0$ *for all* $i$. *If* $\det(-\widetilde{A}) > 0$ *for every* $\widetilde{A} \in Q_A$, *then* (C1) *holds.*

*Proof* Let $A$ be an $n \times n$ matrix. Then, by assumption, we have

$$\det(-\widetilde{A}) = (-1)^n \sum_{\sigma \in \mathcal{S}_n} (\operatorname{sgn} \sigma)\widetilde{a}_{1\sigma(1)}\widetilde{a}_{2\sigma(2)} \cdots \widetilde{a}_{n\sigma(n)} > 0.$$

where $\mathcal{S}_n$ is the set of all permutations of $\{1, 2, \ldots, n\}$. Let $\tau$ be a cyclic permutation $(i_1\ i_2\ \ldots\ i_k)$ of length $k \geq 2$. Then sgn $\tau = k - 1$. Suppose that the cycle $a_{i_1 i_2} a_{i_2 i_3} \ldots a_{i_k i_1}$ is positive. Choose $\widetilde{a}_{ij}$ as follows:

$$\begin{aligned} \widetilde{a}_{ii} &= -1, \quad i \in I \backslash \{i_1, i_2, \ldots, i_k\} \\ \widetilde{a}_{ii} &= -\epsilon, \quad i \in \{i_1, i_2, \ldots, i_k\} \\ \widetilde{a}_{ij} &= \epsilon, \qquad i, j \in I,\ j \neq \tau(i),\ i \neq j. \end{aligned}$$

Then

$$\begin{aligned} \det(-\widetilde{A}) = &-\widetilde{a}_{i_1 i_2}\widetilde{a}_{i_2 i_3} \cdots \widetilde{a}_{i_k i_1} \\ &+ (-1)^n \sum_{\sigma \neq \tau,\ \sigma \in \mathcal{S}_n} (\operatorname{sgn} \sigma)\widetilde{a}_{1\sigma(1)}\widetilde{a}_{2\sigma(2)} \cdots \widetilde{a}_{n\sigma(n)}, \end{aligned}$$

where the first term does not contain any $\epsilon$, but each term in the summation contains at least one $\epsilon$. If $\epsilon$ is sufficiently small, then $\det(-\widetilde{A})$ becomes negative. This is a contradiction, thus any cycle of length $\geq 2$ is nonpositive.

Lemma 5.2 is essentially Theorem 3.1 in [16]. For convenience we included a proof here. Now Part (a) of Lemma 5.1 immediately implies Proposition 2.2 while condition (C1) follows by combining Part (b) of Lemma 5.1 with Lemma 5.2.

In order to construct an attractive heteroclinic cycle, we define a specific matrix. For $n \geq 3$, define a matrix $D(\alpha_1, \alpha_2, \ldots, \alpha_n)$ by

$$D(\alpha_1, \alpha_2, \ldots, \alpha_n) = \begin{pmatrix} -1 & 0 & \cdots & 0 & \alpha_1 \\ \alpha_2 & -1 & \cdots & 0 & 0 \\ \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & \cdots & \alpha_n & -1 \end{pmatrix}.$$

Note that this matrix has a cycle $\alpha_1 \alpha_2 \cdots \alpha_n$. The matrix $D(\alpha_1, \alpha_2, \ldots, \alpha_n)$ has the following property.

**Lemma 5.3** *Let* $\mathbf{s} = (r_1, r_2, \ldots, r_{n-\mu})^\top$, $B = D(\alpha_1, \alpha_2, \ldots, \alpha_{n-\mu})$ *be an* $(n-\mu)$*-dimensional vector and an* $(n-\mu) \times (n-\mu)$ *matrix. Then the* $n$*-dimensional vector* $\mathbf{r} = (r_1 - \mu\alpha_1, r_2, \ldots, r_{n-\mu}, 1, \ldots, 1)^\top$ *and the* $n \times n$ *matrix* $A = D(\alpha_1, \alpha_2, \ldots, \alpha_{n-\mu}, 1, \ldots, 1)$ *satisfy* $\mathbf{s} = \mathbf{r}^{\{1,2,\ldots,n-\mu\}}$ *and* $B = A^{\{1,2,\ldots,n-\mu\}}$.

*Proof* This lemma follows from the definition of the reduced systems (see Definition 4.1).

Let $J = \{1, 2, \ldots, n - \mu\}$. Let $\mathbf{r}_i$ and $A_{ij}$, $i, j \in \{1, 2\}$, be the same as in Definition 4.1. Then they are given as follows:

$$\mathbf{r}_1 = (r_1 - \mu\alpha_1, r_2, \ldots, r_{n-\mu})^\top, \quad \mathbf{r}_2 = (1, 1, \ldots, 1)^\top,$$

$$A_{11} = \begin{pmatrix} -1 & 0 & \cdots & 0 & 0 \\ \alpha_2 & -1 & \cdots & 0 & 0 \\ \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & \cdots & \alpha_{n-\mu} & -1 \end{pmatrix}, \quad A_{12} = \begin{pmatrix} 0 & \cdots & 0 & \alpha_1 \\ 0 & \cdots & 0 & 0 \\ \vdots & & \vdots & \vdots \\ 0 & \cdots & 0 & 0 \end{pmatrix},$$

$$A_{21} = \begin{pmatrix} 0 & \cdots & 0 & 1 \\ 0 & \cdots & 0 & 0 \\ \vdots & & \vdots & \vdots \\ 0 & \cdots & 0 & 0 \end{pmatrix}, \quad A_{22} = \begin{pmatrix} -1 & 0 & \cdots & 0 & 0 \\ 1 & -1 & \cdots & 0 & 0 \\ \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & \cdots & 1 & -1 \end{pmatrix}.$$

Since the inverse of $A_{22}$ is given by

$$A_{22}^{-1} = \begin{pmatrix} -1 & 0 & \cdots & 0 \\ -1 & -1 & \cdots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ -1 & -1 & \cdots & -1 \end{pmatrix},$$

it is clear that $\mathbf{r}^J = \mathbf{r}_1 - A_{12}A_{22}^{-1}\mathbf{r}_2 = (r_1, r_2, \ldots, r_{n-\mu})^\top$ and $A^J = A_{11} - A_{12}A_{22}^{-1}A_{21} = D(\alpha_1, \alpha_2, \ldots, \alpha_{n-\mu})$ hold.

The important point of this lemma is that the positive entries in the matrix $A$ are removed in the reduction process.

The following lemma provides an example of a matrix $A$ leading to an attractive heteroclinic cycle contained in the boundary of $\mathbb{R}^n_+$. The system is related to the repressilator [19]. In the statement of the lemma and its proof, $F_J$, $J \subset I$, denotes the equilibrium point $\mathbf{x}$ of (1.1) satisfying $x_i > 0$ for all $i \in J$ and $x_i = 0$ for all $i \in I \backslash J$.

**Lemma 5.4** *Let $m$ be an odd integer with $3 \le m \le n$, and let $J^- = \{i_1, i_2, \ldots, i_m\}$ be a subset of $I$ with $i_1 < i_2 < \cdots < i_m$. Define $\mu_{i_1}, \mu_{i_2}, \ldots, \mu_{i_m}$ and $J^+$ as follows:*

$$\begin{aligned} \mu_{i_1} &= n - i_m + i_1 - 1, \\ \mu_{i_j} &= i_j - i_{j-1} - 1, \quad j = 2, 3, \ldots, m, \\ J^+ &= I \backslash J^-. \end{aligned}$$

*Suppose that*

$$r_i = \begin{cases} 1 + \mu_i c & i \in J^- \\ 1 & i \in J^+, \end{cases} \qquad \alpha_i = \begin{cases} -c & i \in J^- \\ 1 & i \in J^+, \end{cases}$$

*where* $c > 1$. *Then* (1.1) *with* $A = D(\alpha_1, \alpha_2, \ldots, \alpha_n)$ *has a heteroclinic cycle* $\Gamma$ : $F_{I_1} \to F_{I_2} \to \cdots \to F_{I_m} \to F_{I_1}$, *where*

$$\begin{aligned} I_1 &= \{i_1, i_3, i_5, \ldots, i_{m-2}\} \cup J^+ \\ I_2 &= \{i_3, i_5, i_7, \ldots, i_m\} \cup J^+ \\ &\vdots \\ I_m &= \{i_{m-1}, i_1, i_3, \ldots, i_{m-4}\} \cup J^+. \end{aligned}$$

*This heteroclinic cycle is attractive if* $c > (m+1)/(m-1)$.

*Proof* We shall employ Theorem 1(b) of [3] to prove this theorem (see also Theorem 17.5.1(b) of [4]).

First we consider the existence of the equilibrium points $F_{I_1}, F_{I_2}, \ldots, F_{I_m}$. By Lemma 5.3, $\mathbf{r}^{J^-} = (1, 1, \ldots, 1)^\top$ and $A^{J^-} = D(-c, -c, \ldots, -c)$ hold. It is straightforward to show that the reduced system $(1.1)^{J^-}$ has the equilibrium points

$$F_{\{i_1, i_3, i_5, \ldots, i_{m-2}\}}, F_{\{i_3, i_5, i_7, \ldots, i_m\}}, \ldots, F_{\{i_{m-1}, i_1, i_3, \ldots, i_{m-4}\}}.$$

By Lemma 4.3(a), we shall show that $F_{I_1}, F_{I_2}, \ldots, F_{I_m}$ are equilibrium points of (1.1). Let $\mathbf{r}_2$ be the vector composed of $r_i$, $i \in J^+$ and $A_{21}$ and $A_{22}$ be the submatrices of $A$ with respect to the indices $i \in J^+$, $j \in J^-$ and $i, j \in J^+$, respectively. Then $\mathbf{r}_2$ is a positive vector and $A_{21}$ is a nonnegative matrix. Furthermore, we see that $-A_{22}$ is a nonsingular M-matrix (all off-diagonal entries of $-A_{22}$ are nonpositive and all principal minors of $-A_{22}$ are positive). By the M-matrix theory, we can show that $-A_{22}^{-1} \geq 0$ (e.g., see Chap. 6 of [1]). Additionally, the sign pattern of $-A_{22}$ implies that all diagonal entries of $-A_{22}$ are positive, all diagonal entries of $-A_{22}^{-1}$ are positive. Hence, $-A_{22}^{-1}\mathbf{r}_2$ is positive, and thus $-A_{22}^{-1}(\mathbf{r}_2 + A_{21}\mathbf{x}_1)$ is positive for all $\mathbf{x}_1 \in \mathbb{R}_+^m$. Consequently, by Lemma 4.3(a), system (1.1) has the equilibrium points $F_{I_1}, F_{I_2}, \ldots, F_{I_m}$.

Let us consider the existence of the heteroclinic orbit $\Gamma_1$ connecting $F_{I_m}$ and $F_{I_1}$. Since the heteroclinic orbit $\Gamma_1$ is contained in the face $S_{i_m} := \{\mathbf{x} \in \mathbb{R}_+^n : x_{i_m} = 0\}$, we consider the dynamics of (1.1) on $S_{i_m}$. On the face $S_{i_m}$, system (1.1) is reduced to the $(n-1)$-dimensional Lotka–Volterra system with the interaction matrix $D(\alpha_1, \ldots, \alpha_{i_m - 1}, 0, \alpha_{i_m + 2}, \ldots, \alpha_n)$. Note that this matrix satisfies the qualitative VL-stability criterion (1.2). By the VL-stability theory (e.g., see Sect. 15.3 of [4] and [23,24]), this subsystem has an equilibrium point $\mathbf{p}$ which is globally asymptotically stable in the sense that every solution $\mathbf{x}(t)$ with $\mathbf{x}(0) \in \mathbb{R}_+^{n-1}$ and $x_i(0) > 0$ for all $i \in \mathrm{supp}(\mathbf{p})$ converges to $\mathbf{p}$. Since the Jacobi matrix evaluated at $F_{I_1}$ has a single positive eigenvalue corresponding to the $x_{i_m}$-direction and $n-1$ negative eigenvalues (see Table 1), $F_{I_1}$ is asymptotically stable within $S_{i_m}$. Thus $\mathbf{p} = F_{I_1}$. Similarly, we can show that the Jacobi matrix evaluated at $F_{I_m}$ has a single positive eigenvalue corresponding to the $x_{i_{m-2}}$-direction and $n-1$ negative eigenvalues. Therefore, by the unstable manifold theorem, we can construct a heteroclinic orbit connecting $F_{I_m}$ and $F_{I_1}$. By the similar argument, we can also construct the heteroclinic orbits $\Gamma_i$, $i = 2, \ldots, m$, connecting $F_{I_{i-1}}$ and $F_{I_i}$. Therefore, the heteroclinic cycle $\Gamma$ exists.

**Table 1** The eigenvalues of $F_{I_1}$

| $x_{i_1}$ | $x_{i_1+1}$ | $\cdots$ | $x_{i_2-1}$ | $x_{i_2}$ | $x_{i_2+1}$ | $\cdots$ | $x_{i_3-1}$ | $\cdots$ | $x_{i_m}$ | $x_{i_m+1}$ | $\cdots$ | $x_{i_1-1}$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| $-1$ | $-2$ | $\cdots$ | $-\mu_{i_2}-1$ | $1-c$ | $-1$ | $\cdots$ | $-\mu_{i_3}$ | | $1$ | $-1$ | $\cdots$ | $-\mu_{i_1}$ |

It is obvious that a small neighborhood of $\Gamma$ within the boundary of $\mathbb{R}^n_+$ is contained in $\cup_{i\in J^-} S_i$. The dynamics in $\cup_{i\in J^-} S_i$ implies that the heteroclinic cycle $\Gamma$ is asymptotically stable within the boundary of $\mathbb{R}^n_+$.

By Theorem 1(b) of [3], we see that the attractivity of this heteroclinic cycle is determined by the eigenvalues of the Jacobi matrix of (1.1) evaluated at the $m$ equilibrium points. In our case, it is sufficient to show that the sum of the external eigenvalues at each $F_{I_i}$ is negative, then the heteroclinic cycle becomes attractive. Let us focus on $F_{I_1}$. There are $(m+1)/2$ external and $n-m+(m-1)/2$ internal eigenvalues associated with $F_{I_1}$. $(m-1)/2$ of the external eigenvalues are $1-c<0$ and the remaining one, which corresponds to the $x_{i_m}$-direction, is 1. Since every equilibrium in the heteroclinic cycle has similar eigenvalues, the heteroclinic cycle is attractive if

$$\frac{m-1}{2}(1-c)+1<0$$

$$1-c<-\frac{2}{m-1}$$

$$c>1+\frac{2}{m-1}=\frac{m+1}{m-1}.$$

*Proof of Theorem 2.3* By Lemmas 5.1 and 5.2, it is clear that the condition (C1) is necessary for qualitative permanence.

Consider the condition (C2). Let $\mathbf{r}$ and $A$ be the same as in Lemma 5.4. Then system (1.1) has an attractive heteroclinic cycle on the boundary of $\mathbb{R}^n_+$ if $c$ is large. Furthermore, since the reduced system $(1.1)^{J^-}$ has a positive equilibrium point

$$\left(\frac{1}{1+c},\frac{1}{1+c},\ldots,\frac{1}{1+c}\right),$$

Lemma 4.3(a) shows that system (1.1) also has a positive equilibrium point. Therefore, the matrix $A$ is not permanent. It is straightforward to show that this result still holds even if we slightly perturb the matrix $A$ (e.g., we replace the zero entries of $A$ by $\epsilon\approx 0$) since our proof of Lemma 5.4 is robust against a small perturbation to the parameters. This implies that an $n\times n$ matrix with a negative cycle of length $n$ is not qualitatively permanent if the cycle contains multiple negative entries.

Finally consider the case where an $n\times n$ matrix $A$ contains a shorter negative cycle of length $k<n$ that consists of multiple negative entries. It is clear that system (1.1) with the following matrix $A$ can have an attractive heteroclinic cycle on the boundary of $\mathbb{R}^n_+$:

$$A = \begin{pmatrix} B & 0 & \cdots & 0 \\ 0 & -1 & \cdots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \cdots & -1 \end{pmatrix},$$

where $B$ is a $k \times k$ matrix with a negative cycle of length $k$ that consists of multiple negative entries. Similarly to the above, this result is robust against a small perturbation to the parameters. Hence every matrix with a negative cycle containing multiple negative entries is not qualitatively permanent. This completes the proof. □

## 6 Proof of Theorem 2.5

In this section, we prove Theorem 2.5. Before its proof, we introduce some useful lemmas utilized in the proof. The lemmas are closely related to the concept of P-matrices, which is defined as follows:

**Definition 6.1** (P-matrix) A matrix $A$ is said to be a P-matrix if all its principal minors are positive. A matrix $A$ is said to be a qualitative P-matrix if every $\widetilde{A} \in Q_A$ is a P-matrix.

A qualitative P-matrix is characterized as follows.

**Lemma 6.2** (Theorem 3.1 of [16] and Exercise 15.5.5 of [4]). *A matrix $-A$ is a qualitative P-matrix if and only if $a_{ii} < 0$ for all $i$ and* (C1) *holds.*

When we apply Lemma 4.4 to (1.1), we have to construct a compact forward invariant set $X$. By the following lemma, the existence of such a compact set is ensured.

**Lemma 6.3** (c.f. Theorem 15.2.1 and Exercise 15.4.3 of [4]). *If $-A$ is a P-matrix, then there exists a compact absorbing set $X \subset \mathbb{R}^n_+$ for $\mathbb{R}^n_+$.*

The equilibrium point $\widehat{\mathbf{x}}$ of (1.1) is said to be *saturated* if $r_i + (A\widehat{\mathbf{x}})_i \leq 0$ whenever $\widehat{x_i} = 0$. A positive equilibrium point is necessarily saturated. By definition, if $\widehat{\mathbf{x}}$ is not saturated (*unsaturated*), then there exists an $i \in I$ such that $\widehat{x_i} = 0$ and $r_i + (A\widehat{\mathbf{x}})_i > 0$. The following lemma shows that, under the condition that $-A$ is a P-matrix, all boundary equilibrium points are unsaturated if (1.1) has a positive equilibrium point.

**Lemma 6.4** (Theorem 15.4.5 [4]). *System* (1.1) *has a unique saturated equilibrium point for every $\mathbf{r} \in \mathbb{R}^n_+$ if and only if $-A$ is a P-matrix.*

Now we are ready to prove Theorem 2.5. We use a sequential method to prove permanence, similar to [10–13].

*Proof of Theorem 2.5* By Lemma 6.3, system (1.1) has a compact absorbing set $X \subset \mathbb{R}^n_+$ for $\mathbb{R}^n_+$. Therefore, we focus on the orbits in $X$.

Hereafter, we shall show that there exists a sequence $i_1, i_2, \ldots, i_n$ such that each $\cup_{j=1}^k S_{i_j}$, $k = 1, 2, \ldots, n$, is repelling. Let $J = I \backslash \{i_1, i_2, \ldots, i_{k-1}\}$ and $J \neq \emptyset, I$. For the induction hypothesis, we suppose that there exists a compact absorbing set

$X_{I\backslash J} \subset X\backslash \cup_{i\in I\backslash J} S_i$ for $X\backslash \cup_{i\in I\backslash J} S_i$, and the matrix $A^J$ has the same sign pattern as (2.2) (note that $A_{22}$, which is the principal submatrix of $A$ with respect to $I\backslash J$, is nonsingular since $-A$ is a P-matrix). Then system (1.1) has a boundary equilibrium point $\widehat{\mathbf{x}}$ such that $\widehat{x}_i > 0$ for $i \in I\backslash J$ and $\widehat{x}_i = 0$ for $i \in J$ since the subsystem of (1.1) on $\cap_{i\in J} S_i$ is permanent (e.g., see Theorem 13.5.1 of [4]). By Lemma 6.4, $\widehat{\mathbf{x}}$ is unsaturated, i.e., $r_i^J = r_i + (A\widehat{\mathbf{x}})_i > 0$ holds for some $i \in J$. Choose an $i_k$ such that $r_{i_k}^J > 0$ and $r_i^J \leq 0$ for all $i \in J$ with $i > i_k$. Since $\widehat{\mathbf{x}}$ is a unique equilibrium point located in $\cap_{i\in J} S_i \cap X_{I\backslash J}$, Lemma 4.4 with $r_{i_k}^J > 0$ implies that the subsystem of (1.1) on $\cap_{i\in J\backslash\{i_k\}} S_i$ is permanent. Therefore, the subsystem has a positive equilibrium point, i.e., system (1.1) has an equilibrium point $\check{\mathbf{x}}$ satisfying $\check{x}_i > 0$ for $i \in (I\backslash J) \cup \{i_k\}$ and $\check{x}_i = 0$ for $i \in J\backslash\{i_k\}$. By the relationship of equilibrium points between (1.1) and $(1.1)^J$, we obtain $r_{i_k}^J + a_{i_k i_k}^J \check{x}_{i_k} = 0$. This implies $a_{i_k i_k}^J < 0$.

We claim that each equilibrium point $\overline{\mathbf{x}}$ of system (1.1) on $X_{I\backslash J} \cap S_{i_k}$ satisfies $\overline{x}_i = 0$ for all $i \in J$ with $i > i_k$. Suppose not. Then, by Lemma 4.3, the reduced system $(1.1)^J$ has an equilibrium point $\overline{\mathbf{x}}_1$ such that $\overline{x}_i > 0$ for some $i \in J$ with $i > i_k$. Since all elements below the sub-diagonal of $A^J$ are zero and $\overline{x}_{i_k} = 0$, the equilibrium equation

$$\overline{x}_i (r_i^J + (A^J \overline{\mathbf{x}}_1)_i) = 0, \quad i \in J \tag{6.1}$$

still holds even if we replace all $\overline{x}_i, i \in J, i \leq i_k$, by zero. Therefore, we can construct a vector $\overline{\mathbf{x}}$ such that

$$\begin{aligned} \overline{x}_i &= 0, \qquad i \in J, \quad i \leq i_k \\ \overline{x}_i &\geq 0, \qquad i \in J, \quad i > i_k \end{aligned}$$

and both (6.1) and

$$r_i + (A\overline{\mathbf{x}})_i = 0, \quad i \in I\backslash J$$

are satisfied. Note that $\overline{\mathbf{x}}$ is an equilibrium point of (1.1). Since both $\overline{\mathbf{x}}$ and $\widehat{\mathbf{x}}$ are saturated equilibrium points in the subsystem composed of species $i \in \operatorname{supp}(\overline{\mathbf{x}})$, we have a contradiction to Lemma 6.4. This completes the proof of the claim.

By the sign patterns of $\overline{\mathbf{x}}$ and $A^J$,

$$r_{i_k}^J + \sum_{j\in J} a_{i_k j}^J \overline{x}_j = r_{i_k}^J > 0$$

holds for every equilibrium point $\overline{\mathbf{x}} \in X_{I\backslash J} \cap S_{i_k}$. Therefore, Lemma 4.4 implies that $S_{i_k}$ is repelling in $X_{I\backslash J}$, thus $\cup_{j=1}^k S_{i_j}$ is repelling. By Lemma 4.2 and $a_{i_k i_k}^J < 0$, the reduced system $(1.1)^{J\backslash\{i_k\}}$ can be defined and the matrix $A^{J\backslash\{i_k\}}$ has the same sign pattern as (2.2).

Similarly to the above, if we choose $i_1 \in I$ such $r_{i_1} > 0$ and $r_i \leq 0$ for all $i > i_1$, then we can show that $S_{i_1}$ is repelling. This completes the proof. □

## 7 Proof of Theorem 2.7

*Proof of Theorem 2.7* It follows from Theorem 2.3 that the conditions (C1) and (C2) are necessary for qualitative permanence.

Let us consider the sufficiency. It is obvious that an $n \times n$ matrix $A$ with $n \le 2$ is qualitatively permanent if (C1) holds. Indeed such a matrix satisfies the sufficient condition given in Theorem 2.6.

Let us consider the case $n = 3$. By listing all the sign patterns satisfying (C1) and (C2), we see that such sign patterns are categorized into at least one of $B_1, B_2, \dots, B_5$ listed in Sect. 3 (up to permutation). Therefore, in order to prove the theorem, we shall show that every sign pattern $B_i$, $i = 1, 2, \dots, 5$, is qualitatively permanent.

By Theorem 2.6, the sign pattern $B_1$ is qualitatively permanent. To show that the remaining sign patterns are qualitatively permanent, we construct a sequence $i_1, i_2, i_3$ such that $S_{i_1}$, $S_{i_1} \cup S_{i_2}$ and $S_{i_1} \cup S_{i_2} \cup S_{i_3}$ are repelling. This is the same method used in the proof of Theorem 2.6.

First, we shall show that $S_1$ is repelling in all cases. On the face $S_1$, there are at most four equilibrium points, which have the following sign patterns:

$$\mathbf{p}_0 = \begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix}, \quad \mathbf{p}_1 = \begin{pmatrix} 0 \\ + \\ + \end{pmatrix}, \quad \mathbf{p}_2 = \begin{pmatrix} 0 \\ + \\ 0 \end{pmatrix}, \quad \mathbf{p}_3 = \begin{pmatrix} 0 \\ 0 \\ + \end{pmatrix}.$$

Since the first rows of all $B_i$ are nonnegative, the existence of a positive equilibrium point implies $r_1 > 0$. Therefore, the origin $\mathbf{p}_0$ is unstable in the $x_1$-direction. Furthermore, since every boundary equilibrium point is unsaturated, $r_1 + (A\mathbf{p}_1)_1 > 0$ holds. The inequalities $r_1 + (A\mathbf{p}_2)_1 > 0$ and $r_1 + (A\mathbf{p}_3)_1 > 0$ can be shown as follows. Let $\mathbf{x}^*$ be a positive equilibrium point. Then $\mathbf{r} + A\mathbf{x}^* = 0$ holds. Let $\mathbf{p}_2 = (0, y, 0)^\top$ and $\mathbf{p}_3 = (0, 0, z)^\top$. Then $y$ and $z$ satisfy

$$\begin{aligned} r_2 + (A\mathbf{p}_2)_2 &= -(A\mathbf{x}^*)_2 + a_{22} y = 0, \\ r_3 + (A\mathbf{p}_3)_3 &= -(A\mathbf{x}^*)_3 + a_{33} z = 0. \end{aligned}$$

Thus $y = (A\mathbf{x}^*)_2 / a_{22}$ and $z = (A\mathbf{x}^*)_3 / a_{33}$. By these equalities, we have

$$\begin{aligned} r_1 + (A\mathbf{p}_2)_1 &= -(A\mathbf{x}^*)_1 + a_{12} y \\ &= -(A\mathbf{x}^*)_1 + a_{12} (A\mathbf{x}^*)_2 / a_{22} \\ &= (-a_{11} + \frac{a_{12} a_{21}}{a_{22}}) x_1^* + (-a_{13} + \frac{a_{12} a_{23}}{a_{22}}) x_3^*, \\ r_1 + (A\mathbf{p}_3)_1 &= -(A\mathbf{x}^*)_1 + a_{13} z \\ &= -(A\mathbf{x}^*)_1 + a_{13} (A\mathbf{x}^*)_3 / a_{33} \\ &= (-a_{11} + \frac{a_{13} a_{31}}{a_{33}}) x_1^* + (-a_{12} + \frac{a_{13} a_{32}}{a_{33}}) x_2^*. \end{aligned}$$

It follows from the sign patterns of $B_2, \dots, B_5$ that these two numbers are positive. Therefore, $S_1$ is repelling (i.e., $i_1 = 1$).

We can choose $i_2$ and $i_3$ as follows. Since $r_1 > 0$, the $x_1$-axis always has an equilibrium point $(+, 0, 0)$. Since this equilibrium point is unsaturated and every equilibrium point on the interior of $S_2$ and $S_3$ are also unsaturated, at least one of $S_2$ and $S_3$ are repelling in $\mathbb{R}^3_+ \backslash S_1$. The interior of the remaining face $S_i$ contains one equilibrium point, which is unsaturated. Therefore, the sequence 1, 2, 3 or 1, 3, 2 completes the proof. □

## 8 Concluding remarks

In this paper, we have investigated permanence of Lotka–Volterra equations from a qualitative, structural point of view. When does the structure of a community, i.e., the signs of the interaction matrix, guarantee permanence of the system, assuming only the existence of an interior equilibrium? Theorem 2.3 provides two necessary conditions (C1) and (C2) for such qualitative permanence which we believe to be also sufficient. Theorem 2.7 proved that they are necessary and sufficient if $n \leq 3$. This theorem is proved by listing all possible sign patterns satisfying (C1) an (C2) and examining qualitative permanence of each pattern. Unfortunately, if $n = 4$, the possible sign patterns satisfying (C1) and (C2) are categorized into 60 maximal sign patterns (up to permutation). It remains open to question whether (C1) and (C2) are sufficient for qualitative permanence if $n \geq 4$ (see Conjecture 2.4; Theorem 2.6).

Let us compare the conditions (C1) and (C2) with the ones for qualitative VL-stability. By definition, the concept of qualitative permanence is weaker than that of qualitative VL-stability. Indeed, the class of qualitative VL-stability is a proper subset of the class of qualitative permanence. For example, consider the following sign pattern:

$$B_1' = \begin{pmatrix} - & - & - \\ + & - & - \\ 0 & + & - \end{pmatrix}.$$

Since $B_1'$ is a special case of $B_1$, $B_1'$ is qualitatively permanent. However, it is not qualitatively VL-stable since it has a cycle of length 3, i.e., $a_{13}a_{32}a_{21} < 0$. This cycle can destabilize the matrix $B_1'$. In fact, since qualitative VL-stability is equivalent to qualitative stability (or sign stability) under the assumption $a_{ii} < 0$ for all $i$ (e.g., see [14,22]), we can choose the parameters $r_i$ and $a_{ij}$ leading to a permanent system with an unstable positive equilibrium point (note that the Jacobi matrix evaluated at a positive equilibrium point $\mathbf{x}^*$ is given by $(x_i^* a_{ij})$). Note that $B_1'$ gives a special case of a system with intra-guild predation, which is known as a system with oscillatory dynamics [6].

We can expect that interaction strengths in food webs of real ecosystems have patterns. For example, we can expect that the effect of an insect feeding on a tree is very small, but the converse is very large [21]. In fact, an increasing number of studies find a pattern in food webs of real ecosystems. For example, de Ruiter et al. [2] found that the effect of a predator on its prey is relatively large at lower trophic level, while the effect of a prey on its predator is relatively large at higher trophic level. Furthermore, Neutel et al. [20] found the pattern that a long cycle comprises relatively weak links. These studies examine patterns for stability of steady state in ecosystems (thus the patterns are observed in community matrices, which correspond to the Jacobi matrices evaluated at a positive equilibrium point, constructed from data of real ecosystems). As the stability theory does, our results of qualitative permanence would provide a pattern that we expect to be ubiquitous in real ecosystems.

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