

# Complex Dynamical Analysis of Two Prey-One Predator Model in a Patch Environment Utilizing Spectral Bound

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April 14, 2024

## Abstract

In this article, a two prey-one predator model in which prey and predator disperse simultaneously in a heterogeneous environment with  $n$  patches is proposed and analyzed. We prove that the solution of the system is positive and uniformly ultimately bounded. Meanwhile, we use the monotonic theory of spectral bounds to investigate the effect of the dispersal rate on population dynamics. To be precise, we discuss the stability behaviour for the trivial equilibrium and semitrivial equilibrium as well as the uniform persistence of the system. Furthermore, we prove the global asymptotic stability of the positive equilibrium by constructing a global Lyapunov function which applies the results from graph theory. Some numerical simulations are provided to show the effectiveness of the theoretical results.

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## Abstract

In this article, a two prey-one predator model in which prey and predator disperse simultaneously in a heterogeneous environment with  $n$  patches is proposed and analyzed. We prove that the solution of the system is positive and uniformly ultimately bounded. Meanwhile, we use the monotonic theory of spectral bounds to investigate the effect of the dispersal rate on population dynamics. To be precise, we discuss the stability behaviour for the trivial equilibrium and semitrivial equilibrium as well as the uniform persistence of the system. Furthermore, we prove the global asymptotic stability of the positive equilibrium by constructing a global Lyapunov function which applies the results from graph theory. Some numerical simulations are provided to show the effectiveness of the theoretical results.

*Keywords:* Patch model, Spectral bound, Graph theory, Global asymptotic stability

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## 1. Introduction

It is well known that the theoretical study of predator-prey systems in mathematical ecology has a long history, starting with the innovative work on prey and predator species by Lotka [6] in 1925 and Volterra [25] in 1926. Parrish and Saito [16] first proposed a simple mathematical model of the two prey-one predator system which better reflects the diversity of biological systems in nature. Much progress has ever been made in the study of the dynamics of three-dimensional models of two-prey and one-predator [9, 14], but the dispersal of species between patches has been not considered in those models. Although dispersal makes the models more complicated, there has been some progress in studying predator-prey models of dispersal in heterogeneous environments. For example, some scholars have studied predator-prey models with dispersal between two types of patches [5, 7, 17]. Certainly, others have also studied predator-prey models for dispersal in heterogeneous environments with multiple patches. Takeuchi [21] investigated the global dynamics of a single-species model of dispersal in

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heterogeneous environments with  $n$  patches. Shuai [8] developed the global dynamics of a two-dimensional predator-prey model where only the prey dispersed in heterogeneous environments with  $n$  patches. Since diffused predators play an important role in population regulation, Chen et al. [2] studied the global dynamics of a two-dimensional predator-prey model in a heterogeneous environment with  $n$  patches, where both predator and prey disperse simultaneously. Additionally, Lu et al. [12] used the basic reproduction number as a threshold value to establish the global dynamics of a three-dimensional predator-prey model with age structure, where all species disperse simultaneously in a heterogeneous environment with  $n$  patches.

Therefore, based on the above research results, we consider the following two prey-one predator model with a general functional response in a heterogeneous environment with  $n$  patches ( $n \geq 2$ ):

$$\begin{cases} u'_i = r_{1i}u_i \left(1 - \frac{u_i}{K_{1i}}\right) - g_i(u_i)w_i + \rho_u \sum_{j=1}^n (a_{ij}u_j - a_{ji}u_i), & i = 1, 2, \dots, n, \\ v'_i = r_{2i}v_i \left(1 - \frac{v_i}{K_{2i}}\right) - g_i(v_i)w_i + \rho_v \sum_{j=1}^n (a_{ij}v_j - a_{ji}v_i), & i = 1, 2, \dots, n, \\ w'_i = w_i (c_i (g_i(u_i) + g_i(v_i)) - d_i) + \rho_w \sum_{j=1}^n (a_{ij}w_j - a_{ji}w_i), & i = 1, 2, \dots, n, \end{cases} \quad (1.1)$$

where  $u_i$ ,  $v_i$  and  $w_i$  denote the population density of the three species  $u$ ,  $v$  and  $w$  in the  $i$ th patch, respectively;  $r_{1i}$ ,  $r_{2i}$ ,  $K_{1i}$ ,  $K_{2i} > 0$  are the growth rate and carrying capacity of the prey  $u$  and prey  $v$  in the  $i$ th patch, respectively;  $d_i$ ,  $c_i$  is the mortality rate and conversion rate of the predator  $w$  in the  $i$ th patch, respectively; the connectivity matrices  $A = (a_{ij})_{n \times n}$  describes the dispersal pattern between patches for prey and predators, where  $a_{ij} \geq 0$ ,  $i \neq j$ , represents rate of the prey and predators from patch  $j$  to patch  $i$ , and  $a_{jj} = -\sum_{i \neq j} a_{ij}$  is the total movement out from patch  $j$  of the prey and predators;  $\rho_u$ ,  $\rho_v$ ,  $\rho_w \geq 0$  represent the dispersal rates of the three species  $u$ ,  $v$  and  $w$ , respectively. Function  $g_i$  represents the functional response of predator in the  $i$ th patch and satisfies the following assumption.

(g) For  $1 \leq i \leq n$ ,  $g_i : \mathbb{R}_+ \rightarrow \mathbb{R}_+$  is continuous and strictly increasing and  $g_i(0) = 0$ . The flowchart of dispersal is shown in Figure 1

In contrast to the general two-dimensional predator-prey model, there are few scholars who research the two prey-one predator model, where both predator and prey disperse simultaneously in a heterogeneous environment with multiple patches. Due to the high dimensionality of the population model and the existence of migration terms, it is difficult to prove the global asymptotic stability of its equilibrium points. In this paper, based on the ideas of [2, 8], the stability behavior of the equilibria of system (1.1) is discussed by using monotonicity theory of spectral bounds and graph theory knowledge. For trivial equilibrium and semi-trivial equilibrium, we obtain the threshold parameters with respect to the dispersal rate  $\rho$  to determine the boundary between population persistence and extinction. Then the local asymptotic stability of the semitrivial equilibrium is proven based on these threshold parameters. Next, we ex-

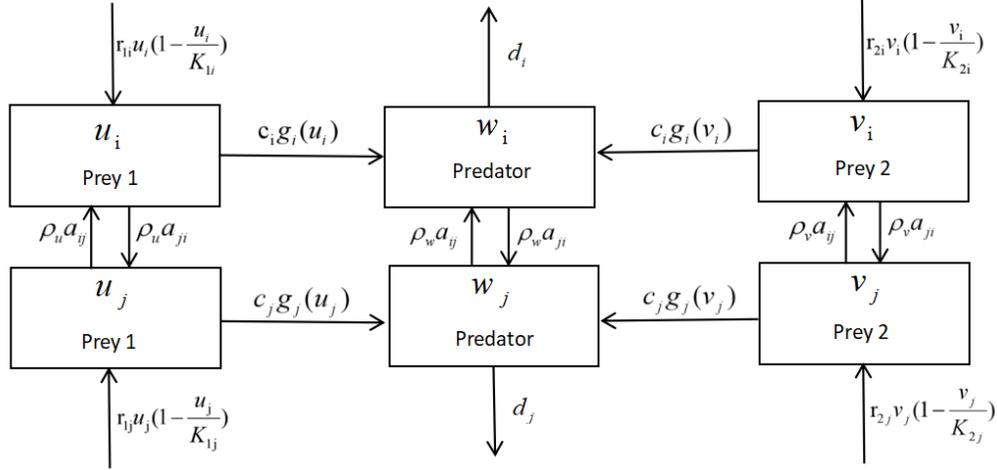


Figure 1: Flowchart of the dispersal process between patch  $i$  and  $j$

explore the global asymptotic stability of the semitrivial equilibrium by the comparison principle [18, 20] and the theory of asymptotically autonomous semiflows [22]. For most investigations on the global asymptotic stability of positive equilibrium, it is a classical method to establish a suitable Lyapunov function and utilize the LaSalle invariance principle [4, 11]. However, for the population model with migration terms, we use the results of graph theory [8] to construct the global Lyapunov function for large-scale coupled system from individual vertex system, and then prove the global asymptotic stability of positive equilibrium.

The paper is structured as follows. In Section 2, we provide essential preliminary knowledge to discuss the stability of equilibrium points. In Section 3, we demonstrate that the solution of system (1.1) is positive and uniformly ultimately bounded. In Section 4, we discuss the stable behavior of the trivial equilibrium and semitrivial equilibrium based on the monotonicity theory of spectral bounds with respect to the dispersal rate. In Section 5, we prove the uniform persistence of system (1.1) and the global asymptotic stability of the positive equilibrium. Some numerical examples and simulation results are provided in Section 6. Finally, the research results and relevant ecological explanations are summarized in Section 7.

## 2. Preliminaries

We shall briefly review the basic knowledge so as to facilitate the subsequent proofs.

Let  $A$  be an  $n \times n$  matrix and let  $\sigma(A)$  be the set of eigenvalues of  $A$ .  $A$  is called non-negative if  $a_{ij} \geq 0$  for all  $i, j = 1, 2, \dots, n$ .  $A$  is called essentially non-negative (Metzler matrix) if  $a_{ij} \geq 0$  for all  $i \neq j$ .  $A$  is called irreducible if there nonexistent a permutation matrix  $P$  such that  $PAP^T$  is the upper triangular matrix. Let  $s(A)$  be the spectral bound of  $A$ , i.e.,

$$s(A) = \max\{Re\lambda : \lambda \in \sigma(A)\}.$$

Let us now give the definition with respect to the graph theory and the uniform persistence.

**Definition 2.1.** (*Graph theory [8]*)

- (i) A directed graph  $\mathcal{G} = (V, E)$  contains a set  $V = \{1, 2, \dots, n\}$  of vertices and a set  $E$  of arcs  $(i, j)$  leading from initial vertex  $i$  to terminal vertex  $j$ .
- (ii) A digraph  $\mathcal{G}$  is strongly connected if for any pair of distinct vertices, there exists a directed path from one to the other.
- (iii) A weighted digraph  $(\mathcal{G}, A)$  is strongly connected if and only if the weight matrix  $A$  is irreducible.

**Definition 2.2.** [15] System (1.1) is said to be uniformly persistent if solution  $((u_i(t), v_i(t), w_i(t)))$  of it with initial condition  $(u_i(0), v_i(0), w_i(0)) \in \text{int}\mathbb{R}_+^{3n}$  satisfies the following conditions:

- (i)  $u_i(t) \geq 0, v_i(t) \geq 0, w_i(t) \geq 0$ , for  $\forall t \geq 0$ .
- (ii) There exists  $\varepsilon > 0$  such that  $\lim_{t \rightarrow \infty} \inf (u_i(t), v_i(t), w_i(t)) \geq \varepsilon$ .

Next, we state one useful theorem about spectral monotonicity.

**Theorem 2.1.** [2] Let  $A = (a_{ij})_{n \times n}$  be an irreducible essentially nonnegative matrix and let  $Q = \text{diag}(q_i)$  be a real diagonal matrix. Then the following results hold:

- (i) If  $s(A) < 0$ , then  $s(\rho A + Q)$  is strictly decreasing in  $\rho \in (0, \infty)$ . Moreover,

$$\lim_{\rho \rightarrow 0} s(\rho A + Q) = \max_{1 \leq i \leq n} \{q_i\} \quad \text{and} \quad \lim_{\rho \rightarrow \infty} s(\rho A + Q) = -\infty.$$

- (ii) If  $s(A) = 0$ , then  $s(\rho A + Q)$  is strictly decreasing provided that  $Q$  is not a multiple of  $I$ . Moreover,

$$\lim_{\rho \rightarrow 0} s(\rho A + Q) = \max_{1 \leq i \leq n} \{q_i\} \quad \text{and} \quad \lim_{\rho \rightarrow \infty} s(\rho A + Q) = \sum_{i=1}^n v_i q_i,$$

where  $v_i \in (0, 1)$  for each  $1 \leq i \leq n$  is determined by  $A$  and satisfies  $\sum_{i=1}^n v_i = 1$  (if  $A$  has each row sum equaling zero, then  $v$  is a left positive eigenvector of  $A$ ).

### 3. Uniform ultimate boundedness of positive solution

Throughout this section, we use the following notation. Let  $\mathbb{N}_n = \{1, 2, \dots, n\}$ ,  $(u(t), v(t), w(t)) = (u_1(t), \dots, u_n(t), v_1(t), \dots, v_n(t), w_1(t), \dots, w_n(t)) \in \mathbb{R}_+^{3n}$ , and  $A_0 = (u(0), v(0), w(0))$ . Moreover, we may assume that each component of  $A_0$  is nonnegative and the initial conditions are as follows:

$$\sum_{i=1}^n u_i(0) > 0, \quad \sum_{i=1}^n v_i(0) > 0, \quad \sum_{i=1}^n w_i(0) > 0. \quad (3.1)$$

System (1.1) with initial conditions  $A_0$  satisfies the standard existence and uniqueness theorem for ordinary differential equations [24]. Therefore, it follows that system (1.1) has a unique solution  $(u(t), v(t), w(t))$ .

From biological point of view, positivity implies the survival of the populations and uniform ultimate boundedness of the solution means that none of the interacting population grow abruptly for a long period of time. Therefore, it is necessary to illustrate that the solution of system (1.1) is positive and uniformly ultimately bounded.

**Theorem 3.1.** *For nonnegative initial conditions (3.1), system (1.1) has a unique positive solution  $(u(t), v(t), w(t))$  for all  $t > 0$ , and the solution is uniformly ultimately bounded.*

*Proof.* We first prove that  $u_i(t) > 0$  for  $t > 0$  and  $i \in \mathbb{N}_n$ . For convenience, we rewrite the first equation of system (1.1) as

$$u'_i(t) = u_i(t)p_i(t) + q_i(t), \quad i = 1, \dots, n, \quad (3.2)$$

where

$$\begin{aligned} p_i(t) &= \left( r_{1i} - \frac{r_{1i}u_i(t)}{K_{1i}} \right) - \frac{g_i(u_i(t))}{u_i(t)}w_i(t) - \rho_u \sum_{j=1}^n a_{ji}, \\ q_i(t) &= \rho_u \sum_{j=1}^n a_{ij}u_j(t). \end{aligned} \quad (3.3)$$

Let  $I_1 = \{i \in \mathbb{N}_n \mid u_i(0) > 0\}$  and  $I_2 = \mathbb{N}_n \setminus I_1$ . Since  $\sum_{i=1}^n u_i(0) > 0$ , we can know that  $I_1 \neq \emptyset$ . Consequently, there must exist  $i_0 \in I_1$ , from equation (3.2) with  $i = i_0$ , one can then derive

$$u'_{i_0}(t) = u_{i_0}(t) \left[ \left( r_{1i_0} - \frac{r_{1i_0}u_{i_0}(t)}{K_{1i_0}} \right) - \frac{g_{i_0}(u_{i_0}(t))}{u_{i_0}(t)}w_{i_0}(t) - \rho_u \sum_{j=1}^n a_{ji_0} \right] + \rho_u \sum_{j=1}^n a_{i_0j}u_j(t). \quad (3.4)$$

Applying (3.4) and the constant variation formula, we get

$$u_{i_0}(t) = u_{i_0}(0)e^{\int_0^t p_{i_0}(\zeta)d\zeta} + \int_0^t q_{i_0}(\zeta)e^{-\int_t^\zeta p_{i_0}(\xi)d\xi}d\zeta. \quad (3.5)$$

Noting  $u_{i_0}(0) > 0$ , we can obtain that  $u_{i_0}(t) > 0$  for  $t > 0$ . If  $I_2 = \emptyset$ , then the situation remains the same as discussed above. Suppose now that  $I_2 \neq \emptyset$ , which implies  $u_i(0) = 0$  for  $i \neq i_0$ ,  $i \in \mathbb{N}_n$ . Similarly, by (3.2) and the constant variation formula, we derive

$$u_i(t) = u_i(0)e^{\int_0^t p_i(\zeta)d\zeta} + \int_0^t q_i(\zeta)e^{-\int_t^\zeta p_i(\xi)d\xi}d\zeta. \quad (3.6)$$

Obviously, with the initial condition  $u_i(0) = 0$ , we only need to consider the sign of  $q_i(t)$ . Since

$A = (a_{ij})$  is irreducible, it is clear that there exists  $i_1 \in I_2$  such that  $a_{i_1 j} \neq 0$  for some  $j \in I_1$ . Therefore,  $q_{i_1}(t) > 0$  for  $t > 0$ . By substituting  $i = i_1$  into equation (3.6), we can conclude that  $u_{i_1}(t) > 0$  for  $t > 0$ . Let  $M_1 = I_1 \cup \{i_1\}$  and  $M_2 = I_2 \setminus \{i_1\}$ . If  $M_2 = \emptyset$ , then the situation remains the same as discussed above. However, if  $M_2 \neq \emptyset$ , we continue the process. After a finite number of steps, it is easy to see  $u_i(t) > 0$  for  $t > 0$  and  $i \in \mathbb{N}_n$ . We can use the similar way to obtain  $v_i(t) > 0$ ,  $w_i(t) > 0$  for  $t > 0$  and  $i \in \mathbb{N}_n$ .

We next prove the uniform ultimate boundedness of the positive solution  $((u(t), v(t), w(t)))$ . Denote  $u(t) = \sum_{i=1}^n u_i(t)$ , then we have

$$\frac{du(t)}{dt} = \sum_{i=1}^n r_{1i} u_i(t) \left(1 - \frac{u_i(t)}{K_{1i}}\right) - \sum_{i=1}^n g_i(u_i(t)) w_i(t).$$

Let  $r_1 = \max_{1 \leq i \leq n} \{r_{1i}\}$ ,  $r_2 = \max_{1 \leq i \leq n} \{r_{2i}\}$ ,  $\bar{r}_1 = \min_{1 \leq i \leq n} \{\frac{r_{1i}}{K_{1i}}\}$ ,  $\bar{r}_2 = \min_{1 \leq i \leq n} \{\frac{r_{2i}}{K_{2i}}\}$ . Then by the Cauchy-Schwartz inequality, we derive

$$\begin{aligned} \frac{du(t)}{dt} &\leq \sum_{i=1}^n r_{1i} u_i(t) - \sum_{i=1}^n \frac{r_{1i}}{K_{1i}} u_i^2(t) \\ &\leq \max_{1 \leq i \leq n} \{r_{1i}\} u(t) - \min_{1 \leq i \leq n} \left\{ \frac{r_{1i}}{K_{1i}} \right\} \sum_{i=1}^n u_i^2(t) \\ &\leq \max_{1 \leq i \leq n} \{r_{1i}\} u(t) - \min_{1 \leq i \leq n} \left\{ \frac{r_{1i}}{K_{1i}} \right\} \frac{u^2(t)}{n} \\ &= r_1 u(t) - \frac{\bar{r}_1 u^2(t)}{K_1 n} \\ &= r_1 u(t) \left(1 - \frac{u(t) \bar{r}_1}{n K_1 r_1}\right). \end{aligned}$$

Hence,  $\lim_{t \rightarrow \infty} \sup u(t) \leq n K_1 r_1 / \bar{r}_1$  is established. We can use the similar way to obtain  $\lim_{t \rightarrow \infty} \sup v(t) \leq n K_2 r_2 / \bar{r}_2$ . We further denote  $G(t) = \sum_{i=1}^n (c_i u_i(t) + c_i v_i(t) + w_i(t))$ , and let  $l = \max_{1 \leq i \leq n} \{2c_i r_{1i}, 2c_i r_{2i}\}$ ,  $h = \max_{1 \leq i \leq n} \{c_i\}$ ,  $d = \min_{1 \leq i \leq n} \{r_{1i}, r_{2i}, d_i\}$ . Then one can obtain

$$\begin{aligned} \frac{dG(t)}{dt} &= \sum_{i=1}^n \left[ c_i r_{1i} u_i \left(1 - \frac{u_i}{K_{1i}}\right) + c_i r_{2i} v_i \left(1 - \frac{v_i}{K_{2i}}\right) + c_i \rho_u \sum_{j=1}^n (a_{ij} u_j - a_{ji} u_i) \right. \\ &\quad \left. + c_i \rho_v \sum_{j=1}^n (a_{ij} v_j - a_{ji} v_i) - d_i w_i \right] \\ &\leq \sum_{i=1}^n \left[ 2c_i r_{1i} u_i + 2c_i r_{2i} v_i + c_i \rho_u \max_{1 \leq j \leq n} \{a_{ij}\} u(t) + c_i \rho_v \max_{1 \leq j \leq n} \{a_{ij}\} v(t) \right] \\ &\quad - \sum_{i=1}^n [c_i r_{1i} u_i + c_i r_{2i} v_i + d_i w_i] \end{aligned}$$

$$\leq \left( l + \sum_{i=1}^n h\rho_u \max_{1 \leq j \leq n} \{a_{ij}\} \right) u(t) + \left( l + \sum_{i=1}^n h\rho_v \max_{1 \leq j \leq n} \{a_{ij}\} \right) v(t) - dG(t).$$

Since  $\lim_{t \rightarrow \infty} \sup u(t) \leq nK_1 r_1 / \bar{r}_1$  and  $\lim_{t \rightarrow \infty} \sup v(t) \leq nK_2 r_2 / \bar{r}_2$ , we can conclude that for arbitrary  $\varepsilon > 0$ , there exists  $T = T(\varepsilon)$  such that the solutions  $u(t)$  and  $v(t)$  satisfy  $u(t) < nK_1 r_1 / \bar{r}_1 + \varepsilon$  and  $v(t) < nK_2 r_2 / \bar{r}_2 + \varepsilon$  for  $t \geq T$ . Hence, it follows that

$$\begin{aligned} & \limsup_{t \rightarrow \infty} G(t) \\ & \leq \frac{(l + \sum_{i=1}^n h\rho_u \max_{1 \leq j \leq n} \{a_{ij}\}) nK_1 r_1 \bar{r}_2 + (l + \sum_{i=1}^n h\rho_v \max_{1 \leq j \leq n} \{a_{ij}\}) nK_2 r_2 \bar{r}_1}{d\bar{r}_1 \bar{r}_2}. \end{aligned}$$

This completes the proof.  $\square$

Moreover, according to the above theorem, we can obtain the feasible domain of system (1.1) as follows:

$$\begin{aligned} \Gamma &= \left\{ (u(t), v(t), w(t)) \in \mathbb{R}_+^{3n} \mid G(t) \right. \\ & \leq \left. \frac{(l + \sum_{i=1}^n h\rho_u \max_{1 \leq j \leq n} \{a_{ij}\}) nK_1 r_1 \bar{r}_2 + (l + \sum_{i=1}^n h\rho_v \max_{1 \leq j \leq n} \{a_{ij}\}) nK_2 r_2 \bar{r}_1}{d\bar{r}_1 \bar{r}_2} \right\}. \end{aligned}$$

Further, we also have the following theorem.

**Theorem 3.2.** *For nonnegative initial conditions (3.1), system (1.1) is dissipative, that is, there exists  $M > 0$  such that each positive orbit  $(u(t), v(t), w(t))$  eventually enters the set  $\Gamma = \{(u(t), v(t), w(t)) \in \mathbb{R}_+^{3n} \mid G(t) = \sum_{i=1}^n (c_i u_i(t) + c_i v_i(t) + w_i(t)) \leq M\}$  and  $\Gamma$  is a positive invariant set with respect to system (1.1).*

#### 4. Trivial equilibrium and semitrivial equilibrium

In this section, we discuss the stability of the trivial equilibrium and semitrivial equilibrium.

We shall now start to prove the instability of the trivial equilibrium  $E_0$  using the monotonicity of spectral bounds with respect to the dispersal rate. The following theorem describes this result in detail.

**Theorem 4.1.** *Let  $A$  be an irreducible matrix, and denote  $(\alpha_1, \alpha_2, \dots, \alpha_n)^T$  as the positive eigenvector of  $A$  corresponding to eigenvalue 0 with  $\sum_{i=1}^n \alpha_i = 1$ . Then for any  $\rho_u > 0$ ,  $\rho_v > 0$ ,  $\rho_w > 0$ , system (1.1) admits a trivial equilibrium  $E_0 = (0, 0, \dots, 0)$ . And  $E_0$  is unstable for any  $\rho_w > 0$ .*

*Proof.* Linearizing (1.1) at  $E_0$ , the local stability of  $E_0$  is decided by the following eigenvalue

problem:

$$\begin{cases} \lambda\phi_i = r_{1i}\phi_i + \rho_u \sum_{j=1}^n (a_{ij}\phi_j - a_{ji}\phi_i), & i = 1, 2, \dots, n, \\ \lambda\psi_i = r_{2i}\psi_i + \rho_v \sum_{j=1}^n (a_{ij}\psi_j - a_{ji}\psi_i), & i = 1, 2, \dots, n, \\ \lambda\varphi_i = -d_i\varphi_i + \rho_w \sum_{j=1}^n (a_{ij}\varphi_j - a_{ji}\varphi_i), & i = 1, 2, \dots, n, \end{cases} \quad (4.1)$$

where  $(\phi, \psi, \varphi)$  with  $\phi = (\phi_1, \phi_2, \dots, \phi_n)^T$ ,  $\psi = (\psi_1, \psi_2, \dots, \psi_n)^T$  and  $\varphi = (\varphi_1, \varphi_2, \dots, \varphi_n)^T$  is an eigenvector of (4.1) corresponding to eigenvalue  $\lambda$ . Hence, we know that the local stability of  $E_0$  is determined by the sign of  $s(\rho_u A + \text{diag}(r_{1i}))$ ,  $s(\rho_v A + \text{diag}(r_{2i}))$  and  $s(\rho_w A - \text{diag}(d_i))$ .

Since  $A = (a_{ij})_{n \times n}$  is an essential nonnegative matrix and  $\sum_{i=1}^n a_{ij} = 0$ ,  $-A$  is a Laplacian matrix, it follows that the minimum eigenvalue of  $-A$  is 0. Therefore, we have  $s(A) = \max\{\text{Re}\lambda\} = 0$ . By Theorem 2.1, we can get

$$\begin{aligned} 0 &< \sum_{i=1}^n \alpha_i r_{1i} = \lim_{\rho \rightarrow \infty} s(\rho_u A + \text{diag}(r_{1i})) \leq s(\rho_u A + \text{diag}(r_{1i})), \\ 0 &< \sum_{i=1}^n \alpha_i r_{2i} = \lim_{\rho \rightarrow \infty} s(\rho_v A + \text{diag}(r_{2i})) \leq s(\rho_v A + \text{diag}(r_{2i})), \\ s(\rho_w A - \text{diag}(d_i)) &\leq \lim_{\rho \rightarrow 0} s(\rho_w A - \text{diag}(d_i)) = \max_{1 \leq i \leq n} \{-d_i\} < 0. \end{aligned}$$

Clearly,  $E_0$  is unstable for any  $\rho_w > 0$ . This proof is complete.  $\square$

Next, based on the comparison principle [18, 20] and the theory of asymptotically autonomous semiflows [22], we will prove the global asymptotic stability of the semitrivial equilibrium  $E_1$  by using new threshold parameters  $M$  and  $m$  in Theorem 4.2. Meanwhile, the theorem also highlights the impact of dispersal rates on population dynamics of system (1.1).

**Theorem 4.2.** *Let  $A$  be an irreducible matrix, and denote  $(\alpha_1, \alpha_2, \dots, \alpha_n)^T$  as the positive eigenvector of  $A$  corresponding to eigenvalue 0 with  $\sum_{i=1}^n \alpha_i = 1$ . Then for any  $\rho_u > 0$ ,  $\rho_v > 0$ ,  $\rho_w > 0$ , system (1.1) admits a semitrivial equilibrium  $E_1 = (u^*, v^*, 0)$  and satisfies*

$$\begin{cases} r_{1i}u_i^* \left(1 - \frac{u_i^*}{K_{1i}}\right) + \rho_u \sum_{j=1}^n (a_{ij}u_j^* - a_{ji}u_i^*) = 0, & i = 1, 2, \dots, n, \\ r_{2i}v_i^* \left(1 - \frac{v_i^*}{K_{2i}}\right) + \rho_v \sum_{j=1}^n (a_{ij}v_j^* - a_{ji}v_i^*) = 0, & i = 1, 2, \dots, n, \end{cases} \quad (4.2)$$

where  $u^* = (u_1^*, u_2^*, \dots, u_n^*)$ ,  $v^* = (v_1^*, v_2^*, \dots, v_n^*)$ ,  $u_i^* > 0$ ,  $v_i^* > 0$ . Let  $M = \max_{1 \leq i \leq n} \{c_i(g_i(u_i^*) + g_i(v_i^*)) - d_i\}$  and  $m = \sum_{i=1}^n \alpha_i (c_i(g_i(u_i^*) + g_i(v_i^*)) - d_i)$ . Then the following results hold:

- (i) If  $M < 0$ , then the equilibrium  $E_1$  is globally asymptotically stable in  $\mathbb{R}_+^{3n} - \{E_0\}$  for all  $\rho_w > 0$ .
- (ii) If  $m > 0$ , then the equilibrium  $E_1$  is unstable for all  $\rho_w > 0$ .

(iii) If  $m < 0 < M$ , then there exists a unique  $\rho_w^* > 0$  such that  $E_1$  is globally asymptotically stable in  $\mathbb{R}_+^{3n} - \{E_0\}$  for  $\rho_w > \rho_w^*$  while  $E_1$  is unstable for  $0 < \rho_w < \rho_w^*$ .

*Proof.* To start with, we prove the local asymptotic stability of  $E_1$ . Linearizing (1.1) at  $E_1$ , the local asymptotic stability of  $E_1$  is decided by the following eigenvalue problem:

$$\begin{cases} \lambda\phi_i = r_{1i}\phi_i \left(1 - \frac{2u_i^*}{K_{1i}}\right) - g_i(u_i^*)\varphi_i + \rho_u \sum_{j=1}^n (a_{ij}\phi_j - a_{ji}\phi_i), & i = 1, 2, \dots, n, \\ \lambda\psi_i = r_{2i}\psi_i \left(1 - \frac{2v_i^*}{K_{2i}}\right) - g_i(v_i^*)\varphi_i + \rho_v \sum_{j=1}^n (a_{ij}\psi_j - a_{ji}\psi_i), & i = 1, 2, \dots, n, \\ \lambda\varphi_i = \varphi_i [c_i (g_i(u_i^*) + g_i(v_i^*)) - d_i] + \rho_w \sum_{j=1}^n (a_{ij}\varphi_j - a_{ji}\varphi_i), & i = 1, 2, \dots, n, \end{cases} \quad (4.3)$$

where  $(\phi, \psi, \varphi)$  with  $\phi = (\phi_1, \phi_2, \dots, \phi_n)^T$ ,  $\psi = (\psi_1, \psi_2, \dots, \psi_n)^T$  and  $\varphi = (\varphi_1, \varphi_2, \dots, \varphi_n)^T$  is an eigenvector of (4.3) corresponding to eigenvalue  $\lambda$ . If  $Re\lambda < 0$  for any eigenvalue  $\lambda$  of (4.3), then  $E_1$  is locally asymptotically stable; if (4.3) has an eigenvalue  $\lambda$  such that  $Re\lambda > 0$ , then  $E_1$  is unstable. If  $\varphi = 0$ , then  $\lambda$  is an eigenvalue of

$$\begin{cases} \lambda\phi_i = r_{1i}\phi_i \left(1 - \frac{2u_i^*}{K_{1i}}\right) + \rho_u \sum_{j=1}^n (a_{ij}\phi_j - a_{ji}\phi_i), & i = 1, 2, \dots, n, \\ \lambda\psi_i = r_{2i}\psi_i \left(1 - \frac{2v_i^*}{K_{2i}}\right) + \rho_v \sum_{j=1}^n (a_{ij}\psi_j - a_{ji}\psi_i), & i = 1, 2, \dots, n, \end{cases} \quad (4.4)$$

i.e.,  $\lambda$  is an eigenvalue of  $\rho_u A + \text{diag}(r_{1i}(1 - 2u_i^*/K_{1i}))$  and  $\rho_v A + \text{diag}(r_{2i}(1 - 2v_i^*/K_{2i}))$ . By (4.2) and the Perron-Frobenius theorem [13], it follows that  $s(\rho_u A + \text{diag}(r_{1i}(1 - u_i^*/K_{1i}))) = 0$ ,  $s(\rho_v A + \text{diag}(r_{2i}(1 - v_i^*/K_{2i}))) = 0$ . Consequently, we have

$$\begin{cases} Re\lambda \leq s(\rho_u A + \text{diag}(r_{1i}(1 - 2u_i^*/K_{1i}))) < s(\rho_u A + \text{diag}(r_{1i}(1 - u_i^*/K_{1i}))) = 0, \\ Re\lambda \leq s(\rho_v A + \text{diag}(r_{2i}(1 - 2v_i^*/K_{2i}))) < s(\rho_v A + \text{diag}(r_{2i}(1 - v_i^*/K_{2i}))) = 0. \end{cases} \quad (4.5)$$

If  $\varphi \neq 0$ , then  $\lambda$  is an eigenvalue of

$$\lambda\varphi_i = \varphi_i [c_i (g_i(u_i^*) + g_i(v_i^*)) - d_i] + \rho_w \sum_{j=1}^n (a_{ij}\varphi_j - a_{ji}\varphi_i), \quad i = 1, 2, \dots, n,$$

i.e.,  $\lambda$  is an eigenvalue of  $\rho_w A + \text{diag}(c_i (g_i(u_i^*) + g_i(v_i^*)) - d_i)$ . Therefore, by Theorem 2.1, we can easily know that the local asymptotic stability of  $E_1$  is decided by the sign of  $s(\rho_w A + \text{diag}(c_i (g_i(u_i^*) + g_i(v_i^*)) - d_i))$ . Then the results on the local asymptotic stability of  $E_1$  in (i) – (iii) can be explained.

Further, we prove the global asymptotic stability of  $E_1$  when  $s(\rho_w A + \text{diag}(c_i (g_i(u_i^*) + g_i(v_i^*)) - d_i)) < 0$ . Assume that  $(u_1(0), u_2(0), \dots, u_n(0))$  is nontrivial. Let  $\hat{u}_i(t)$ ,  $1 \leq i \leq n$ , be

the solution of

$$\begin{cases} \hat{u}'_i = r_{1i}\hat{u}_i \left(1 - \frac{\hat{u}_i}{K_{1i}}\right) + \rho_u \sum_{j=1}^n (a_{ij}\hat{u}_j - a_{ji}\hat{u}_i), & i = 1, 2, \dots, n, \\ \hat{u}_i(0) = u_i(0), & i = 1, 2, \dots, n, \end{cases}$$

and  $\hat{v}_i(t)$ ,  $1 \leq i \leq n$ , be the solution of

$$\begin{cases} \hat{v}'_i = r_{2i}\hat{v}_i \left(1 - \frac{\hat{v}_i}{K_{2i}}\right) + \rho_v \sum_{j=1}^n (a_{ij}\hat{v}_j - a_{ji}\hat{v}_i), & i = 1, 2, \dots, n, \\ \hat{v}_i(0) = v_i(0), & i = 1, 2, \dots, n. \end{cases}$$

According to the comparison principle [18, 20], we have  $u_i(t) \leq \hat{u}_i(t)$ ,  $v_i(t) \leq \hat{v}_i(t)$  for all  $t \geq 0$  and  $1 \leq i \leq n$ . Noting [2, Theorem 5.1], we conclude  $\lim_{t \rightarrow \infty} \hat{u}_i(t) = u_i^*$ ,  $\lim_{t \rightarrow \infty} \hat{v}_i(t) = v_i^*$ , thus it can be seen  $\lim_{t \rightarrow \infty} \sup \hat{u}_i(t) = u_i^*$ ,  $\lim_{t \rightarrow \infty} \sup \hat{v}_i(t) = v_i^*$  for  $1 \leq i \leq n$ . Choose  $\varepsilon_0 > 0$  such that  $s(\rho_w A + \text{diag}(c_i(g_i(u_i^* + \varepsilon_0) + g_i(v_i^* + \varepsilon_0)) - d_i)) < 0$ . Then there exists  $T > 0$  such that  $u_i(t) \leq u_i^* + \varepsilon_0$ ,  $v_i(t) \leq v_i^* + \varepsilon_0$  for all  $t \geq T$ . By the third equation of system (1.1) and the monotonicity of  $g_i$ , we obtain

$$\begin{cases} w'_i \leq w_i (c_i (g_i(u_i^* + \varepsilon_0) + g_i(v_i^* + \varepsilon_0)) - d_i) + \rho_w \sum_{j=1}^n (a_{ij}w_j - a_{ji}w_i), & t \geq T, i = 1, 2, \dots, n, \\ w_i(T) \leq C\tilde{\alpha}_i, & t \geq T, i = 1, 2, \dots, n, \end{cases}$$

where  $(\tilde{\alpha}_1, \tilde{\alpha}_2, \dots, \tilde{\alpha}_n)$  is a positive principal eigenvector of  $\rho_w A + \text{diag}(c_i(g_i(u_i^* + \varepsilon_0) + g_i(v_i^* + \varepsilon_0)) - d_i)$  corresponding with eigenvalue  $s_0 := s(\rho_w A + \text{diag}(c_i(g_i(u_i^* + \varepsilon_0) + g_i(v_i^* + \varepsilon_0)) - d_i))$  and  $C > 0$  is large. Again by the comparison principle [18, 20], we can derive  $w_i(t) \leq \hat{w}_i(t)$  for all  $t \geq T$ , where  $\hat{w}_i$  is the solution of

$$\begin{cases} \hat{w}'_i = \hat{w}_i (c_i (g_i(u_i^* + \varepsilon_0) + g_i(v_i^* + \varepsilon_0)) - d_i) + \rho_w \sum_{j=1}^n (a_{ij}\hat{w}_j - a_{ji}\hat{w}_i), & t \geq T, i = 1, 2, \dots, n, \\ \hat{w}_i(T) = C\tilde{\alpha}_i, & t \geq T, i = 1, 2, \dots, n. \end{cases} \quad (4.6)$$

Then, it is easy to solve that the solution of (4.6) is  $\hat{w}_i(t) = C\tilde{\alpha}_i e^{s_0(t-T)}$ ,  $1 \leq i \leq n$ . Since  $s_0 < 0$ , we obtain that  $\lim_{t \rightarrow \infty} \hat{w}_i(t) = 0$ , which implies  $\lim_{t \rightarrow \infty} w_i(t) = 0$ . Finally, by the theory of asymptotically autonomous semiflows [22], we have  $\lim_{t \rightarrow \infty} u_i(t) = u_i^*$ ,  $\lim_{t \rightarrow \infty} v_i(t) = v_i^*$ ,  $1 \leq i \leq n$ . Therefore, we can illustrate that  $E_1$  is global asymptotically stable. This proof is complete.  $\square$

## 5. Positive equilibrium

In this section, we discuss the existence and stability of the positive equilibrium.

To start with, we aim to obtain the conditions for the existence of the positive equilibrium

by proving the uniform persistence of system (1.1). To achieve this, we need to discuss the stability of the trivial equilibrium  $E^0 = (0, 0)$ , semitrivial equilibrium  $E' = (u^*, 0)$ ,  $\hat{E} = (0, v^*)$ , and positive equilibrium  $\bar{E} = (u^*, v^*)$  of system (5.1). Similar to the proof of the stability of  $E_0$  and  $E_1$ , as shown in Theorem 4.1 and Theorem 4.2 in Section 4, we utilize the monotonicity of spectral bounds to analyze  $E^0$ ,  $E'$  and  $\hat{E}$ . It follows that  $E^0$ ,  $E'$  and  $\hat{E}$  are evidently unstable.

As shown in Lemma 5.1, we prove the global asymptotic stability of  $\bar{E} = (u^*, v^*)$  by constructing the Lyapunov function.

$$\begin{cases} u'_i = r_{1i}u_i \left(1 - \frac{u_i}{K_{1i}}\right) + \rho_u \sum_{j=1}^n (a_{ij}u_j - a_{ji}u_i), & i = 1, 2, \dots, n, \\ v'_i = r_{2i}v_i \left(1 - \frac{v_i}{K_{2i}}\right) + \rho_v \sum_{j=1}^n (a_{ij}v_j - a_{ji}v_i), & i = 1, 2, \dots, n. \end{cases} \quad (5.1)$$

**Lemma 5.1.** *Assume that the following assumptions hold.*

(i) *Dispersal matrix  $A = (a_{ij})_{n \times n}$  is irreducible.*

(ii) *There exists  $\sigma_j > 0$  such that  $\rho_u a_{ij} u_j^* = \sigma_j \rho_v a_{ij} v_j^*$ .*

*Then system (5.1) has a globally asymptotically stable positive equilibrium  $\bar{E}$  in  $\mathbb{R}_+^{2n}$ .*

*Proof.* Clearly, system (5.1) has at least one positive equilibrium [1, 20]. Let  $\bar{E} = (u^*, v^*) = (u_1^*, \dots, u_n^*, v_1^*, \dots, v_n^*)$ ,  $u_i^*, v_i^* > 0$  for  $1 \leq i \leq n$ , where  $u^*, v^*$  satisfy

$$0 = r_{1i} \left(1 - \frac{u_i^*}{K_{1i}}\right) + \rho_u \sum_{j=1}^n \left(a_{ij} \frac{u_j^*}{u_i^*} - a_{ji}\right), \quad i = 1, \dots, n, \quad (5.2)$$

$$0 = r_{2i} \left(1 - \frac{v_i^*}{K_{2i}}\right) + \rho_v \sum_{j=1}^n \left(a_{ij} \frac{v_j^*}{v_i^*} - a_{ji}\right), \quad i = 1, \dots, n. \quad (5.3)$$

Denote

$$V_i(u_i, v_i) = u_i - u_i^* - u_i^* \ln \frac{u_i}{u_i^*} + v_i - v_i^* - v_i^* \ln \frac{v_i}{v_i^*}. \quad (5.4)$$

It can be checked that  $V_i(u_i, v_i) > 0$  for all  $u_i, v_i \geq 0$  and  $V_i(u_i, v_i) = 0$  if and only if  $u_i = u_i^*$ ,  $v_i = v_i^*$ . Using (5.2) and (5.3), we can get

$$\begin{aligned} \dot{V}_i &= \frac{u'_i}{u_i} (u_i - u_i^*) + \frac{v'_i}{v_i} (v_i - v_i^*) \\ &= (u_i - u_i^*) \left[ r_{1i} \left(1 - \frac{u_i}{K_{1i}}\right) + \rho_u \sum_{j=1}^n \left(a_{ij} \frac{u_j}{u_i} - a_{ji}\right) \right] \\ &\quad + (v_i - v_i^*) \left[ r_{2i} \left(1 - \frac{v_i}{K_{2i}}\right) + \rho_v \sum_{j=1}^n \left(a_{ij} \frac{v_j}{v_i} - a_{ji}\right) \right] \\ &= (u_i - u_i^*) \left[ r_{1i} \left(1 - \frac{u_i}{K_{1i}}\right) - r_{1i} \left(1 - \frac{u_i^*}{K_{1i}}\right) + \rho_u \sum_{j=1}^n \left(a_{ij} \frac{u_j}{u_i} - a_{ji}\right) - \rho_u \sum_{j=1}^n \left(a_{ij} \frac{u_j^*}{u_i^*} - a_{ji}\right) \right] \end{aligned}$$

$$\begin{aligned}
& + (v_i - v_i^*) \left[ r_{2i} \left( 1 - \frac{v_i}{K_{2i}} \right) - r_{2i} \left( 1 - \frac{v_i^*}{K_{2i}} \right) + \rho_v \sum_{j=1}^n \left( a_{ij} \frac{v_j}{v_i} - a_{ji} \right) - \rho_v \sum_{j=1}^n \left( a_{ij} \frac{v_j^*}{v_i^*} - a_{ji} \right) \right] \\
& = (u_i - u_i^*) \left[ r_{1i} \left( 1 - \frac{u_i}{K_{1i}} \right) - r_{1i} \left( 1 - \frac{u_i^*}{K_{1i}} \right) \right] + (v_i - v_i^*) \left[ r_{2i} \left( 1 - \frac{v_i}{K_{2i}} \right) - r_{2i} \left( 1 - \frac{v_i^*}{K_{2i}} \right) \right] \\
& \quad + \rho_u \sum_{j=1}^n a_{ij} u_j^* \left( \frac{u_j}{u_j^*} - \frac{u_i}{u_i^*} - \frac{u_j u_i^*}{u_i u_j^*} + 1 \right) + \rho_v \sum_{j=1}^n a_{ij} v_j^* \left( \frac{v_j}{v_j^*} - \frac{v_i}{v_i^*} - \frac{v_j v_i^*}{v_i v_j^*} + 1 \right) \\
& = -\frac{r_{1i}}{K_{1i}} (u_i - u_i^*)^2 - \frac{r_{2i}}{K_{2i}} (v_i - v_i^*)^2 + \rho_u \sum_{j=1}^n a_{ij} u_j^* \left[ \left( \frac{u_j}{u_j^*} - \frac{u_i}{u_i^*} - \frac{u_j u_i^*}{u_i u_j^*} + 1 \right) + \frac{1}{\sigma_j} \left( \frac{v_j}{v_j^*} - \frac{v_i}{v_i^*} - \frac{v_j v_i^*}{v_i v_j^*} + 1 \right) \right] \\
& \leq \rho_u \sum_{j=1}^n a_{ij} u_j^* \left[ \left( \frac{u_j}{u_j^*} - \frac{u_i}{u_i^*} - \frac{u_j u_i^*}{u_i u_j^*} + 1 \right) + \frac{1}{\sigma_j} \left( \frac{v_j}{v_j^*} - \frac{v_i}{v_i^*} - \frac{v_j v_i^*}{v_i v_j^*} + 1 \right) \right].
\end{aligned}$$

For convenience, we let

$$\begin{aligned}
d_{ij} & = \rho_u a_{ij} u_j^*, \quad G_i(u_i, v_i) = -\frac{u_i}{u_i^*} + \ln \frac{u_i}{u_i^*} - \frac{1}{\sigma_j} \left( \frac{v_i}{v_i^*} + \ln \frac{v_i}{v_i^*} \right), \\
F_{ij}(u_i, u_j, v_i, v_j) & = \frac{u_j}{u_j^*} - \frac{u_i}{u_i^*} - \frac{u_j u_i^*}{u_j^* u_i} + 1 + \frac{1}{\sigma_j} \left( \frac{v_j}{v_j^*} - \frac{v_i}{v_i^*} - \frac{v_j v_i^*}{v_j^* v_i} + 1 \right).
\end{aligned}$$

Then this is straightforward:

$$\dot{V}_i(u_i, v_i) \leq \sum_{j=1}^n d_{ij} F_{ij}(u_i, u_j, v_i, v_j), \tag{5.5}$$

and since  $1 - a + \ln a \leq 0$  for  $a > 0$  with equality holding iff  $a = 1$ , one can obtain

$$\begin{aligned}
F_{ij}(u_i, u_j, v_i, v_j) & = G_i(u_i, v_i) - G_j(u_j, v_j) + 1 - \frac{u_j u_i^*}{u_j^* u_i} + \ln \frac{u_j u_i^*}{u_j^* u_i} \\
& \quad + \frac{1}{\sigma_j} \left( 1 - \frac{v_j v_i^*}{v_j^* v_i} + \ln \frac{v_j v_i^*}{v_j^* v_i} \right) \\
& \leq G_i(u_i, v_i) - G_j(u_j, v_j).
\end{aligned} \tag{5.6}$$

Thus,  $V_i$ ,  $F_{ij}$ ,  $G_i$  and  $d_{ij}$  satisfy the assumptions in [8, Theorem 3.1]. Denote  $\mathbb{T}_i$  be the set of all spanning trees  $\mathcal{T}$  of  $(\mathcal{G}, A)$ , rooted at vertex  $i$ , and  $w(\mathcal{T})$  be the weight of  $\mathcal{T}$ . If we let  $C_i = \sum_{\mathcal{T} \in \mathbb{T}_i} w(\mathcal{T})$  is the cofactor of the  $i$ -th diagonal element in the Laplacian matrix of the weighted digraph  $(\mathcal{G}, A)$ , then

$$V(u_1, \dots, u_n, v_1, \dots, v_n) = \sum_{i=1}^n C_i V_i(u_i, v_i)$$

as defined in [8, Theorem 3.1] is a Lyapunov function for (5.1). Namely,  $\dot{V} \leq 0$  for all

$$(u_1, \dots, u_n, v_1, \dots, v_n) \in \mathbb{R}_+^{2n}.$$

To show  $\bar{E}$  is globally asymptotically stable, we examine the largest compact invariant set of  $\{(u_1, \dots, u_n, v_1, \dots, v_n) \in \mathbb{R}_+^{2n} \mid \dot{V} = 0\}$ . Since  $(\mathcal{G}, A)$  is strongly connected, that is,  $\dot{V} = 0$  implies that  $-r_{1i}(u_i - u_i^*)^2/K_{1i} - r_{2i}(v_i - v_i^*)^2/K_{2i} = 0$  and  $d_{ij}F_{ij}(u_i, u_j, v_i, v_j) = 0$ . Further, from  $r_{1i}, r_{2i}, K_{1i}$ , and  $K_{2i}$  are positive constant, we have  $u_i = u_i^*$  and  $v_i = v_i^*$ . According to the irreducibility of the matrix  $A$ , there exists an arc from  $j$  to  $i$  in weight graph  $(\mathcal{G}, A)$ . Hence,  $d_{ij}F_{ij}(u_i, u_j, v_i, v_j) = 0$  indicates that  $u_i = u_j$  and  $v_i = v_j$ . Let  $l \neq k$  denote any vertex of  $(\mathcal{G}, A)$ , then by the strong connectivity of  $(\mathcal{G}, A)$ , there exists a directed path  $p$  from  $l$  to  $k$ . Applying the relation  $u_i = u_j$  and  $v_i = v_j$  to each arc  $(j, i)$  of  $p$ , we can obtain that  $u_l = u_k$  and  $v_l = v_k$ . As a consequence,  $\dot{V} = 0$  implies  $u_i = u_i^*$  and  $v_i = v_i^*$  for all  $i$ . This suggests that the largest compact invariant subset of  $\{(u_1, \dots, u_n, v_1, \dots, v_n) \in \mathbb{R}_+^{2n} \mid \dot{V} = 0\}$  is the singleton  $\{\bar{E}\}$ . By the LaSalle Invariance Principle [10],  $\bar{E}$  is globally asymptotically stable in  $\mathbb{R}_+^{2n}$ . The proof is now complete.  $\square$

In the subsequent analysis, we utilize persistence theory [3, 19, 23, 26, 27] to establish the uniform persistence of system (1.1). This enables us to deduce the existence of a positive equilibrium for system (1.1). We present this significant result in the following theorem.

**Theorem 5.1.** *If  $m > 0$  and there exists  $\sigma_j > 0$  such that  $\rho_u a_{ij} u_j^* = \sigma_j \rho_v a_{ij} v_j^*$ , then system (1.1) is uniformly persistent, that is, there exists  $\varepsilon > 0$  such that every solution  $\Phi_t(A_0) = (u(t), v(t), w(t))$  with  $A_0 = (u(0), v(0), w(0)) \in \mathbb{R}_+^{2n} \times \text{Int}\mathbb{R}_+^n$  satisfies*

$$\liminf_{t \rightarrow \infty} (w_i(t)) \geq \varepsilon, \quad i = 1, \dots, n.$$

Hence, system (1.1) has at least one positive equilibrium.

*Proof.* Let

$$X = \{(u_i, v_i, w_i) \mid u_i \geq 0, v_i \geq 0, w_i \geq 0\},$$

$$\tilde{X}_0 = \{w_i > 0, \quad i = 1, \dots, n\},$$

$$\partial\tilde{X}_0 = X \setminus \tilde{X}_0.$$

According to Lemma 3.1, it is easy to know that  $\tilde{X}_0$  is a positive invariant set and system (1.1) is dissipative. Define

$$M_\partial := \{A_0 \in \partial\tilde{X}_0 \mid \Phi_t(A_0) \in \partial\tilde{X}_0, \quad \forall t \geq 0\}.$$

We first claim that

$$M_\partial = \{A_0 \in X \mid w(t) = 0, \quad \forall t \geq 0\}.$$

Suppose on the contrary that there exists  $t_0 \geq 0$  such that  $w(t_0) > 0$ . We partition  $\{1, 2, \dots, n\}$  into two sets  $Z_1$  and  $Z_2$ , such that  $w_i(t_0) = 0, \forall i \in Z_1$ , and  $w_i(t_0) > 0, \forall i \in Z_2$ . If  $Z_1 = \emptyset$ , it

is not difficult to see that  $w_i(t) > 0$  for  $t_0 < t < t_0 + \varepsilon$ ,  $\forall i = 1, 2, \dots, n$ , given a enough small  $\varepsilon_0 > 0$ . On the other hand, if  $Z_1 \neq \emptyset$ , then for  $\forall i \in Z_1$ , we get

$$\begin{aligned}\dot{w}_i(t_0) &= w_i(t_0) (c_i (g_i (u_i(t_0)) + g_i (v_i(t_0)))) - d_i + \rho_w \sum_{j=1}^n (a_{ij} w_j(t) - a_{ji} w_i(t_0)) \\ &= \rho_w \sum_{j \in Z_2} a_{ij} w_j(t_0).\end{aligned}$$

Since  $A = (a_{ij})$  is irreducible, it is clearly that there exists  $i_0 \in Z_1$  such that  $a_{i_0 j} \neq 0$  for some  $j \in Z_2$ , which implies that  $\rho_w \sum_{j \in Z_2} a_{ij} w_j(t_0) > 0$ , i.e.  $\dot{w}_i(t_0) > 0$ . Therefore, there exists a enough small  $\varepsilon > 0$  such that  $w_i(t) > 0$  for  $t_0 < t < t_0 + \varepsilon$ ,  $\forall i \in Z_1 \cup Z_2$ . According to the above discussion, we can obtain that  $\Phi_t(A_0) \notin \partial \tilde{X}_0$  for  $t_0 < t < t_0 + \varepsilon$ , which contradicts with the definition of  $M_\partial$ , thus the above claim has been verified on  $M_\partial$ .

We next prove that for some constant  $\eta > 0$ , the solution  $\Phi_t(A_0)$  through  $A_0$  satisfies

$$\limsup_{t \rightarrow \infty} \max_{1 \leq i \leq n} \{w_i(t)\} > \eta. \quad (5.7)$$

Assume (5.7) is not true, then there must exist  $T > 0$  such that

$$0 < \max_{1 \leq i \leq n} \{w_i(t)\} \leq \eta, \quad \forall t \geq T.$$

Therefore, it is easy to see

$$\begin{aligned}\frac{du_i}{dt} &= r_{1i} u_i \left(1 - \frac{u_i}{K_{1i}}\right) - g_i(u_i) w_i + \rho_u \sum_{j=1}^n (a_{ij} u_j - a_{ji} u_i) \\ &\geq r_{1i} u_i \left(1 - \frac{u_i}{K_{2i}}\right) - g_i(u_i) \eta + \rho_u \sum_{j=1}^n (a_{ij} u_j - a_{ji} u_i), \\ \frac{dv_i}{dt} &= r_{2i} v_i \left(1 - \frac{v_i}{K_{2i}}\right) - g_i(v_i) w_i + \rho_v \sum_{j=1}^n (a_{ij} v_j - a_{ji} v_i) \\ &\geq r_{2i} v_i \left(1 - \frac{v_i}{K_{2i}}\right) - g_i(v_i) \eta + \rho_v \sum_{j=1}^n (a_{ij} v_j - a_{ji} v_i).\end{aligned}$$

Consider the following auxiliary equation

$$\begin{aligned}
\frac{d\bar{u}_i}{dt} &= r_{1i}\bar{u}_i \left(1 - \frac{\bar{u}_i}{K_{1i}}\right) - g_i(\bar{u}_i)\eta + \rho_u \sum_{j=1}^n (a_{ij}\bar{u}_j - a_{ji}\bar{u}_i), \\
(\bar{u}_1(T), \dots, \bar{u}_n(T)) &= (u_1(T), \dots, u_n(T)). \\
\frac{d\bar{v}_i}{dt} &= r_{2i}\bar{v}_i \left(1 - \frac{\bar{v}_i}{K_{2i}}\right) - g_i(\bar{v}_i)\eta + \rho_v \sum_{j=1}^n (a_{ij}\bar{v}_j - a_{ji}\bar{v}_i), \\
(\bar{v}_1(T), \dots, \bar{v}_n(T)) &= (v_1(T), \dots, v_n(T)).
\end{aligned} \tag{5.8}$$

Applying comparison principle [18, 20], we have  $u(t) \geq \bar{u}(t)$ ,  $v(t) \geq \bar{v}(t)$ ,  $\forall t \geq T$ , where  $\bar{u}(t) = (\bar{u}_1(t), \dots, \bar{u}_n(t))^T$ ,  $\bar{v}(t) = (\bar{v}_1(t), \dots, \bar{v}_n(t))^T$ . By Lemma 5.1, we also have that  $(u^*, v^*)^T(\eta)$  is globally asymptotically stable for (5.8) and  $u^*(0) = u^*$ ,  $v^*(0) = v^*$ . Then there exists a sufficiently small  $\delta$  with  $\delta = (\delta_1, \dots, \delta_n)^T \in \mathbb{R}_+^n$  and a sufficiently large  $T > 0$ , such that  $u^*(\eta) > u^* - \delta$ ,  $v^*(\eta) > v^* - \delta$ , and it follows that  $u(t) \geq u^*(\eta) \geq u^* - \delta$ ,  $v(t) \geq v^*(\eta) \geq v^* - \delta$  for all  $t \geq T + T_1$ . Hence, we obtain

$$\begin{aligned}
\frac{dw_i(t)}{dt} &= w_i(t) (c_i (g_i(u_i(t)) + g_i(v_i(t))) - d_i) + \rho_w \sum_{j=1}^n (a_{ij}w_j(t) - a_{ji}w_i(t)) \\
&\geq w_i(t) (c_i (g_i(u_i^* - \delta) + g_i(v_i^* - \delta)) - d_i) + \rho_w \sum_{j=1}^n (a_{ij}w_j(t) - a_{ji}w_i(t)).
\end{aligned}$$

Consider the following auxiliary system:

$$\frac{d\bar{w}_i(t)}{dt} = \bar{w}_i(t) (c_i (g_i(u_i^* - \delta) + g_i(v_i^* - \delta)) - d_i) + \rho_w \sum_{j=1}^n (a_{ij}\bar{w}_j(t) - a_{ji}\bar{w}_i(t)). \tag{5.9}$$

Using the Perron-Frobenius theory and  $m_0 > 0$ , it then follows that the matrix  $D$  has a positive eigenvalue  $s(D)$  with a positive eigenvector, where  $D$  is  $\rho_w A + \text{diag}(c_i (g_i(u_i^* - \delta) + g_i(v_i^* - \delta)) - d_i)$ . Besides, denote  $\bar{\alpha} = (\alpha_1, \dots, \alpha_n)^T$  be a positive eigenvector corresponding to  $s(D)$ , then the solution of system (5.9) is given by  $k\bar{\alpha}e^{s(D)t}$ . Again, using the comparison principle [18, 20], we can get

$$w_i(t) \geq k\bar{\alpha}e^{s(D)t}, \quad \forall t \geq T.$$

Then  $w_i(t) \rightarrow \infty$ ,  $i = 1, \dots, n$ , for  $t \rightarrow \infty$ , which results to a contradiction.

In the end, we will prove that system (1.1) is uniformly persistent in regard to  $(\tilde{X}_0, \partial\tilde{X}_0)$ . Note that  $(u^*, v^*)^T$  is globally asymptotically stable in  $\mathbb{R}_+^{2n} \setminus \{E^0, E', \hat{E}\}$  when  $\rho_u a_{ij} u_j^* = \rho_v a_{ij} v_j^*$ . By the above discussion, we obtain that  $E_0$ ,  $E_1$ ,  $(u^*, 0, 0)$  and  $(0, v^*, 0)$  are isolated invariant subsets in  $X$ . At the same time, we have  $W^s(E_0) \cap \tilde{X}_0 = \emptyset$ ,  $W^s(E_1) \cap \tilde{X}_0 = \emptyset$ ,  $W^s((u^*, 0, 0)) \cap \tilde{X}_0 = \emptyset$  and  $W^s((0, v^*, 0)) \cap \tilde{X}_0 = \emptyset$ . Here  $W^s(E_0)$ ,  $W^s(E_1)$ ,  $W^s((u^*, 0, 0))$  and  $W^s((0, v^*, 0))$

are stable set of  $E_0$ ,  $E_1$ ,  $(u^*, 0, 0)$  and  $(0, v^*, 0)$ , respectively. It is obvious that every orbit in  $M_\partial$  converges to one of four equilibria, which include  $(u^*, 0, 0)$ ,  $(0, v^*, 0)$ ,  $E_0$  and  $E_1$ . Moreover,  $(u^*, 0, 0)$ ,  $(0, v^*, 0)$ ,  $E_0$  and  $E_1$  are acyclic in  $M_\partial$ . By [3], we can infer that system (1.1) is uniformly persistent in regard to  $(\tilde{X}_0, \partial\tilde{X}_0)$ . According to [26], system (1.1) has at least one positive equilibrium  $(u^*, v^*, w^*) \in \tilde{X}_0$  with  $w^* \gg 0$ . We further assert that  $u^* \neq 0$ ,  $v^* \neq 0$ . Otherwise, if  $u^* = v^* = 0$ , by summing up the equilibrium equations for  $w$ , we have  $\sum_{i=1}^n -d_i w^* = 0$ . Consequently,  $w^* = 0$ , which leads to a contradiction. This proof is complete.  $\square$

We now focus on studying the global asymptotic stability of the positive equilibrium  $E_2$  under the assumption of a linear functional response for system (1.1). This allows us to rewrite the system (1.1) as follows:

$$\begin{cases} u'_i = r_{1i}u_i \left(1 - \frac{u_i}{K_{1i}}\right) - b_i u_i w_i + \rho_u \sum_{j=1}^n (a_{ij}u_j - a_{ji}u_i), & i = 1, 2, \dots, n, \\ v'_i = r_{2i}v_i \left(1 - \frac{v_i}{K_{2i}}\right) - b_i v_i w_i + \rho_v \sum_{j=1}^n (a_{ij}v_j - a_{ji}v_i), & i = 1, 2, \dots, n, \\ w'_i = w_i (c_i(b_i u_i + b_i v_i) - d_i) + \rho_w \sum_{j=1}^n (a_{ij}w_j - a_{ji}w_i), & i = 1, 2, \dots, n. \end{cases} \quad (5.10)$$

The result is shown in the following theorem.

**Theorem 5.2.** *Assume that the following assumptions hold.*

(i) *Dispersal matrix  $A = (a_{ij})_{n \times n}$  is irreducible;*

(ii)  *$m > 0$ ;*

(iii) *There exists  $\sigma_{1j}, \sigma_{2j} > 0$  such that  $\rho_u a_{ij} u_j^* = \sigma_{1j} \rho_v a_{ij} v_j^* = \frac{1}{c_i} \sigma_{2j} \rho_w a_{ij} w_j^*$ ;*

where  $m$  is given in Theorem 4.2 and  $g_i(u_i) = b_i u_i$ ,  $g_i(v_i) = b_i v_i$ . Then system (5.10) has a globally asymptotically stable positive equilibrium  $E_2$  in  $\Gamma$ .

*Proof.* By Theorem 5.1, we know that system (5.10) has at least one positive equilibrium. Let  $E_2 = (u^*, v^*, w^*) = (u_1^*, \dots, u_n^*, v_1^*, \dots, v_n^*, w_1^*, \dots, w_n^*)$ ,  $u_i^*, v_i^*, w_i^* > 0$  for  $1 \leq i \leq n$ , where  $u^*$ ,  $v^*$ ,  $w^*$  satisfy

$$0 = r_{1i} \left(1 - \frac{u_i^*}{K_{1i}}\right) - b_i w_i^* + \rho_u \sum_{j=1}^n \left(a_{ij} \frac{u_j^*}{u_i^*} - a_{ji}\right), \quad i = 1, \dots, n, \quad (5.11)$$

$$0 = r_{2i} \left(1 - \frac{v_i^*}{K_{2i}}\right) - b_i w_i^* + \rho_v \sum_{j=1}^n \left(a_{ij} \frac{v_j^*}{v_i^*} - a_{ji}\right), \quad i = 1, \dots, n, \quad (5.12)$$

$$0 = c_i (b_i u_i^* + b_i v_i^*) - d_i + \rho_w \sum_{j=1}^n \left(a_{ij} \frac{w_j^*}{w_i^*} - a_{ji}\right), \quad i = 1, 2, \dots, n. \quad (5.13)$$

Denote

$$V_i(u_i, v_i, w_i) = u_i - u_i^* - u_i^* \ln \frac{u_i}{u_i^*} + v_i - v_i^* - v_i^* \ln \frac{v_i}{v_i^*} + \frac{1}{c_i} (w_i - w_i^* - w_i^* \ln \frac{w_i}{w_i^*}). \quad (5.14)$$

It can be checked that  $V_i(u_i, v_i, w_i) \geq 0$  for all  $u_i, v_i, w_i > 0$  and  $V_i(u_i, v_i, w_i) = 0$  if and only if  $u_i = u_i^*, v_i = v_i^*, w_i = w_i^*$ . Using (5.11), (5.12) and (5.13). we can get

$$\begin{aligned} \dot{V}_i &= \frac{u_i'}{u_i} (u_i - u_i^*) + \frac{v_i'}{v_i} (v_i - v_i^*) + \frac{1}{c_i} \frac{w_i'}{w_i} (w_i - w_i^*) \\ &= (u_i - u_i^*) \left[ r_{1i} \left( 1 - \frac{u_i}{K_{1i}} \right) - b_i w_i + \rho_u \sum_{j=1}^n \left( a_{ij} \frac{u_j}{u_i} - a_{ji} \right) \right] \\ &\quad + (v_i - v_i^*) \left[ r_{2i} \left( 1 - \frac{v_i}{K_{2i}} \right) - b_i w_i + \rho_v \sum_{j=1}^n \left( a_{ij} \frac{v_j}{v_i} - a_{ji} \right) \right] \\ &\quad + \frac{1}{c_i} (w_i - w_i^*) \left[ c_i (b_i u_i + b_i v_i) - d_i + \rho_w \sum_{j=1}^n \left( a_{ij} \frac{w_j}{w_i} - a_{ji} \right) \right] \\ &= (u_i - u_i^*) \left[ r_{1i} \left( 1 - \frac{u_i}{K_{1i}} \right) - b_i w_i + \rho_u \sum_{j=1}^n \left( a_{ij} \frac{u_j}{u_i} - a_{ji} \right) - r_{1i} \left( 1 - \frac{u_i^*}{K_{1i}} \right) + b_i w_i^* \right. \\ &\quad \left. - \rho_u \sum_{j=1}^n \left( a_{ij} \frac{u_j^*}{u_i^*} - a_{ji} \right) \right] + (v_i - v_i^*) \left[ r_{2i} \left( 1 - \frac{v_i}{K_{2i}} \right) - b_i w_i + \rho_v \sum_{j=1}^n \left( a_{ij} \frac{v_j}{v_i} - a_{ji} \right) \right. \\ &\quad \left. - r_{2i} \left( 1 - \frac{v_i^*}{K_{2i}} \right) + b_i w_i^* - \rho_v \sum_{j=1}^n \left( a_{ij} \frac{v_j^*}{v_i^*} - a_{ji} \right) \right] + \frac{1}{c_i} (w_i - w_i^*) \left[ \rho_w \sum_{j=1}^n \left( a_{ij} \frac{w_j}{w_i} - a_{ji} \right) \right. \\ &\quad \left. + c_i (b_i u_i + b_i v_i) - d_i - c_i (b_i u_i^* + b_i v_i^*) + d_i - \rho_w \sum_{j=1}^n \left( a_{ij} \frac{w_j^*}{w_i^*} - a_{ji} \right) \right] \\ &= (u_i - u_i^*) \left[ r_{1i} \left( 1 - \frac{u_i}{K_{1i}} \right) - r_{1i} \left( 1 - \frac{u_i^*}{K_{1i}} \right) \right] + (v_i - v_i^*) \left[ r_{2i} \left( 1 - \frac{v_i}{K_{2i}} \right) - r_{2i} \left( 1 - \frac{v_i^*}{K_{2i}} \right) \right] \\ &\quad + \rho_u \sum_{j=1}^n a_{ij} u_j^* \left( \frac{u_j}{u_j^*} - \frac{u_i}{u_i^*} - \frac{u_j u_i^*}{u_i u_j^*} + 1 \right) + \rho_v \sum_{j=1}^n a_{ij} v_j^* \left( \frac{v_j}{v_j^*} - \frac{v_i}{v_i^*} - \frac{v_j v_i^*}{v_i v_j^*} + 1 \right) \\ &\quad + \frac{\rho_w}{c_i} \sum_{j=1}^n a_{ij} w_j^* \left( \frac{w_j}{w_j^*} - \frac{w_i}{w_i^*} - \frac{w_j w_i^*}{w_i w_j^*} + 1 \right) \\ &= -\frac{r_{1i}}{K_{1i}} (u_i - u_i^*)^2 - \frac{r_{2i}}{K_{2i}} (v_i - v_i^*)^2 + \rho_u \sum_{j=1}^n a_{ij} u_j^* \left[ \left( \frac{u_j}{u_j^*} - \frac{u_i}{u_i^*} - \frac{u_j u_i^*}{u_i u_j^*} + 1 \right) \right. \\ &\quad \left. + \frac{1}{\sigma_{1j}} \left( \frac{v_j}{v_j^*} - \frac{v_i}{v_i^*} - \frac{v_j v_i^*}{v_i v_j^*} + 1 \right) + \frac{1}{\sigma_{2j}} \left( \frac{w_j}{w_j^*} - \frac{w_i}{w_i^*} - \frac{w_j w_i^*}{w_i w_j^*} + 1 \right) \right]. \end{aligned}$$

For convenience, we let

$$d_{ij} = \rho_u a_{ij} u_j^*, \quad G_i(u_i, v_i, w_i) = -\frac{u_i}{u_i^*} + \ln \frac{u_i}{u_i^*} - \frac{1}{\sigma_{1j}} \left( \frac{v_i}{v_i^*} - \ln \frac{v_i}{v_i^*} \right) - \frac{1}{\sigma_{2j}} \left( \frac{w_i}{w_i^*} - \ln \frac{w_i}{w_i^*} \right),$$

$$F_{ij}(u_i, u_j, v_i, v_j, w_i, w_j) = \frac{u_j}{u_j^*} - \frac{u_i}{u_i^*} - \frac{u_j u_i^*}{u_j^* u_i} + 1 + \frac{1}{\sigma_{1j}} \left( \frac{v_j}{v_j^*} - \frac{v_i}{v_i^*} - \frac{v_j v_i^*}{v_j^* v_i} + 1 \right) + \frac{1}{\sigma_{2j}} \left( \frac{w_j}{w_j^*} - \frac{w_i}{w_i^*} - \frac{w_j w_i^*}{w_j^* w_i} + 1 \right).$$

Then one can get

$$\dot{V}_i(u_i, v_i, w_i) \leq \sum_{j=1}^n d_{ij} F_{ij}(u_i, u_j, v_i, v_j, w_i, w_j), \quad (5.15)$$

and since  $1 - a + \ln a \leq 0$  for  $a > 0$ , we have

$$\begin{aligned} F_{ij}(u_i, u_j, v_i, v_j, w_i, w_j) &= G_i(u_i, v_i, w_i) - G_j(u_j, v_j, w_j) + 1 - \frac{u_j u_i^*}{u_j^* u_i} + \ln \frac{u_j u_i^*}{u_j^* u_i} \\ &\quad + \frac{1}{\sigma_{1j}} \left( 1 - \frac{v_j v_i^*}{v_j^* v_i} + \ln \frac{v_j v_i^*}{v_j^* v_i} \right) + \frac{1}{\sigma_{2j}} \left( 1 - \frac{w_j w_i^*}{w_j^* w_i} + \ln \frac{w_j w_i^*}{w_j^* w_i} \right) \quad (5.16) \\ &\leq G_i(u_i, v_i, w_i) - G_j(u_j, v_j, w_j). \end{aligned}$$

We have proven that  $V_i$ ,  $F_{ij}$ ,  $G_i$  and  $d_{ij}$  satisfy the assumptions in [8, Theorem 3.1]. Therefore,

$$V(u_1, \dots, u_n, v_1, \dots, v_n, w_1, \dots, w_n) = \sum_{i=1}^n C_i V_i(u_i, v_i, w_i)$$

as defined in [8, Theorem 3.1] is a Lyapunov function for (5.10), where  $C_i$  is the same as defined in Lemma 5.1. Namely,  $\dot{V} \leq 0$  for all  $(u_1, \dots, u_n, v_1, \dots, v_n, w_1, \dots, w_n) \in \Gamma$ .

To show  $E_2$  is globally asymptotically stable, we examine the largest compact invariant set of  $\{(u_1, \dots, u_n, v_1, \dots, v_n, w_1, \dots, w_n) \in \Gamma \mid \dot{V} = 0\}$ . Through a discussion similar to Lemma 5.1, it is easy to see that  $\dot{V} = 0$  indicates that  $u_i = u_i^*$ ,  $v_i = v_i^*$  and  $w_i = w_i^*$  for all  $i$ . This implies that the largest compact invariant subset of  $\{(u_1, \dots, u_n, v_1, \dots, v_n, w_1, \dots, w_n) \in \Gamma \mid \dot{V} = 0\}$  is the singleton  $\{E_2\}$ . By the LaSalle Invariance Principle [10],  $E_2$  is globally asymptotically stable in  $\Gamma$ . This completes the proof.  $\square$

## 6. Numerical simulations

In this section, we provide some numerical simulations to prove the effectiveness of the theoretical results discussed in Sections 4 and 5. In order to make the simulation results more intuitive, we may assume that the functional response in system (1.1) is linear,  $n = 2$  and

$(a_{ij})_{2 \times 2} = \begin{pmatrix} -1 & 1 \\ 1 & -1 \end{pmatrix}$ . Then system (1.1) can be simplified into the following form.

$$\begin{cases} u'_1 = r_{11}u_1 \left(1 - \frac{u_1}{K_{11}}\right) - b_1u_1w_1 + \rho_u(u_2 - u_1), \\ u'_2 = r_{12}u_2 \left(1 - \frac{u_2}{K_{12}}\right) - b_2u_2w_2 + \rho_u(u_1 - u_2), \\ v'_1 = r_{21}v_1 \left(1 - \frac{v_1}{K_{21}}\right) - b_1v_1w_1 + \rho_v(v_2 - v_1), \\ v'_2 = r_{22}v_2 \left(1 - \frac{v_2}{K_{22}}\right) - b_2v_2w_2 + \rho_v(v_1 - v_2), \\ w'_1 = w_1 (c_1(b_1u_1 + b_1v_1) - d_1) + \rho_w(w_2 - w_1), \\ w'_2 = w_2 (c_2(b_2u_2 + b_2v_2) - d_2) + \rho_w(w_1 - w_2). \end{cases} \quad (6.1)$$

**Example 6.1.** Let us take the parameter values as follows:  $r_{11} = 0.2$ ,  $r_{12} = 0.1$ ,  $r_{21} = 0.1$ ,  $r_{22} = 0.15$ ,  $K_{11} = 10$ ,  $K_{12} = 11$ ,  $K_{21} = 12$ ,  $K_{22} = 13$ ,  $b_1 = 0.1$ ,  $b_2 = 0.05$ ,  $c_1 = 0.02$ ,  $c_2 = 0.05$ ,  $d_1 = 0.1$ ,  $d_2 = 0.1$ ,  $\rho_u = 0.01$ ,  $\rho_v = 0.01$ ,  $\rho_w = 0.02$ .

Based on the above parameter values, the semitrivial equilibrium of system (6.1) is determined as  $E_1 \approx (10.04, 10.91, 12.09, 12.94, 0, 0)$ . By computing, we have that  $M \approx -0.0404 < 0$ . Then condition (i) of Theorem 4.2 is satisfied. Analysis of Figure 2(a) and Figure 2(d) reveals that maintaining the other parameter values constant, any positive value  $\rho_w$  does not affect the stable behavior of  $E_1$ . In addition, as shown in Figure 2(c) and Figure 2(f), we can see that the solutions of system (6.1) all run to point  $E_1$  for any initial value. Consequently, combined with Figure 2(b), Figure 2(e), we can conclude that  $E_1$  is globally asymptotically stable for all  $\rho_w > 0$ .

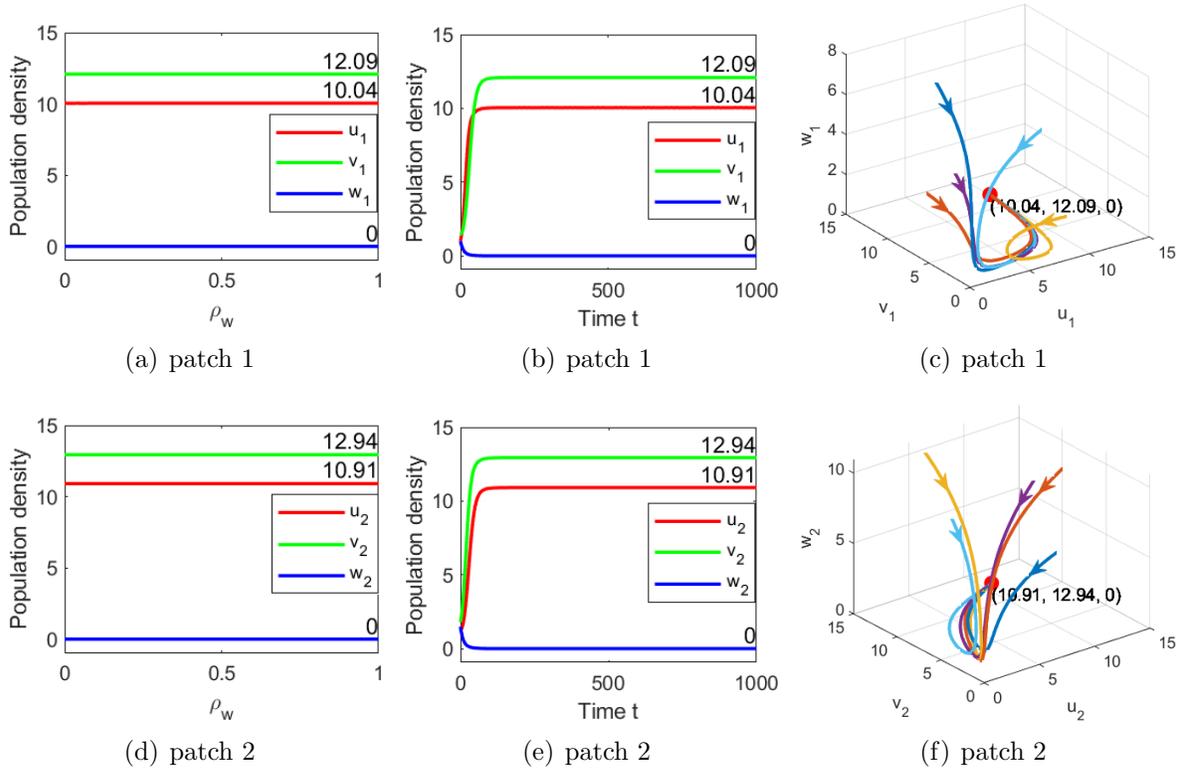


Figure 2: Stable behavior and Phase portrait of  $E_1$  with  $M < 0$

**Example 6.2.** We take the parameter values as follows:  $r_{11} = 0.2$ ,  $r_{12} = 0.1$ ,  $r_{21} = 0.1$ ,  $r_{22} = 0.15$ ,  $K_{11} = 10$ ,  $K_{12} = 11$ ,  $K_{21} = 12$ ,  $K_{22} = 13$ ,  $b_1 = 0.4$ ,  $b_2 = 0.1$ ,  $c_1 = 0.1$ ,  $c_2 = 0.2$ ,  $d_1 = 0.07$ ,  $d_2 = 0.06$ ,  $\rho_u = 0.01$ ,  $\rho_v = 0.01$ ,  $\rho_w = 0.02$ .

By computations we get that  $m \approx 0.6161 > 0$ , then the condition (i) of Theorem 4.2 is satisfied. As shown in Figure 3(a) and Figure 3(b), we can find that any solution curve of system (6.1) eventually runs towards  $\tilde{E} \approx (0.75, 0.41, 0.34, 3.16, 0.14, 1.05)$  and away from  $E_1 \approx (10.04, 10.91, 12.09, 12.94, 0, 0)$ . Hence, simulation results demonstrate that the semitrivial equilibrium  $E_1 \approx (10.04, 10.91, 12.09, 12.94, 0, 0)$  is unstable.

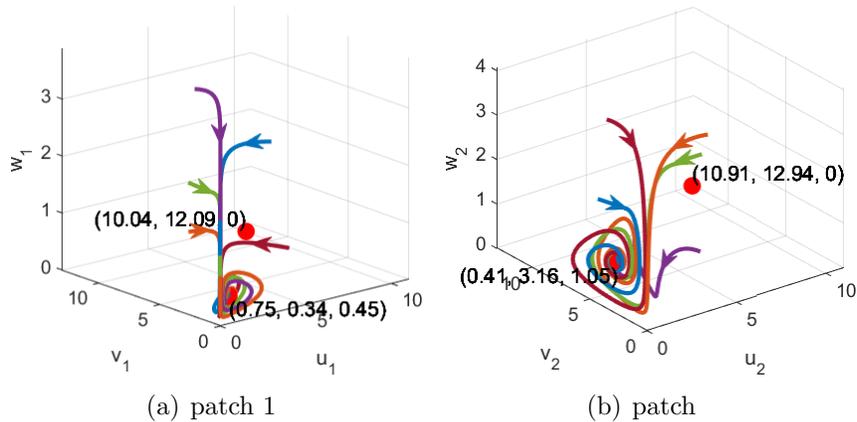


Figure 3: Unstable behavior of  $E_1$

**Example 6.3.** We set the parameters as:  $r_{11} = 0.2$ ,  $r_{12} = 0.1$ ,  $r_{21} = 0.1$ ,  $r_{22} = 0.15$ ,  $K_{11} = 10$ ,  $K_{12} = 11$ ,  $K_{21} = 12$ ,  $K_{22} = 13$ ,  $b_1 = 0.1$ ,  $b_2 = 0.06$ ,  $c_1 = 0.02$ ,  $c_2 = 0.05$ ,  $d_1 = 0.1$ ,  $d_2 = 0.05$ ,  $\rho_u = 0.01$ ,  $\rho_v = 0.01$ .

Based on the parameter values in Example 6.3, we numerically simulate the stable behavior of the semitrivial equilibrium  $E_1$  as the dispersal rate  $\rho_w$  varies. In Figure 4(a) and Figure 4(d), it is not difficult to observe that the three curves represented by  $u$ ,  $v$  and  $w$  tend to be stable when  $\rho_w > \rho_w^*$ . This indicates that the values of  $(u, v, w)$  become stable around the equilibrium point  $E_1 \approx (10.04, 10.91, 12.09, 12.94, 0, 0)$ . We may assume that  $\rho_w = 1$ , then  $m \approx -0.0171 < 0$ ,  $M \approx 0.0216 > 0$  satisfy the condition (iii) of Theorem 4.2. The stable behavior of  $E_1$  and phase portrait are presented in the Figure 4(b), Figure 4(e), Figure 4(c) and Figure 4(f), respectively. Hence, we can infer that  $E_1$  is unstable for  $0 < \rho_w < \rho_w^*$ , while  $E_1$  is globally asymptotically stable for  $\rho_w > \rho_w^*$ .

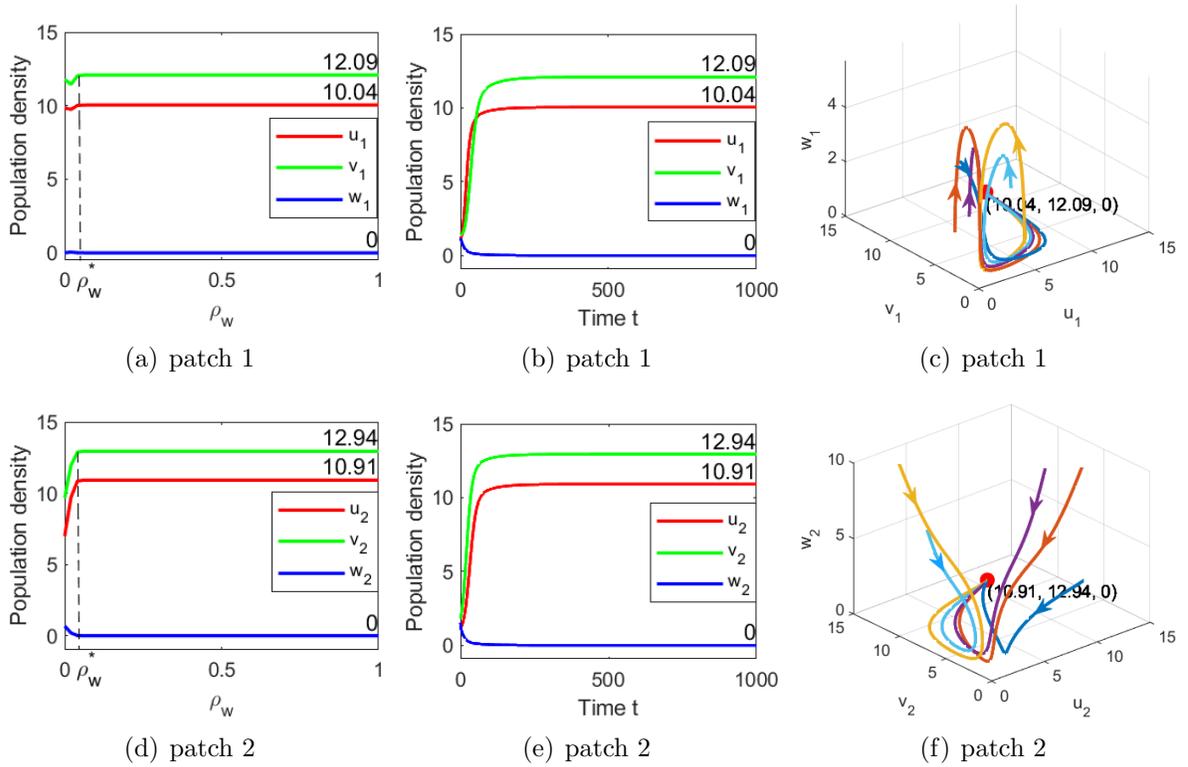


Figure 4: Stable behavior and Phase portrait of  $E_1$  with  $m < 0 < M$

**Example 6.4.** We set the parameter values as follows:  $r_{11} = 0.2$ ,  $r_{12} = 0.1$ ,  $r_{21} = 0.1$ ,  $r_{22} = 0.15$ ,  $K_{11} = 10$ ,  $K_{12} = 11$ ,  $K_{21} = 12$ ,  $K_{22} = 13$ ,  $b_1 = 0.4$ ,  $b_2 = 0.1$ ,  $c_1 = 0.15$ ,  $c_2 = 0.25$ ,  $d_1 = 0.05$ ,  $d_2 = 0.02$ ,  $\rho_u = 0.1$ ,  $\rho_v = 0.1$ ,  $\rho_w = 0.01$ .

It is easy to verify that  $m \approx 0.9334 > 0$  and there exists  $\sigma_j > 0$  such that  $\rho_u a_{ij} u_j^* \approx \sigma_j \rho_v a_{ij} v_j^*$ , then the conditions of Theorem 5.1 are satisfied. Thus we can illustrate the uniform persistence of system (6.1) and the existence of its positive equilibrium  $E_2 \approx (0.376, 0.388, 0.305,$

0.603, 0.489, 0.935), as shown in Figure 5(a) and Figure 5(b). In addition, we also find there exists  $\sigma_{1j}, \sigma_{2j} > 0$  such that  $\rho_u a_{ij} u_j^* \approx \sigma_{1j} \rho_v a_{ij} v_j^* \approx \frac{1}{c_i} \sigma_{2j} \rho_w a_{ij} w_j^*$ . Hence, the conditions of Theorem 5.2 are satisfied, which implies that  $E_2$  is globally asymptotically stable. The results are shown in Figure 5(c) and Figure 5(d).

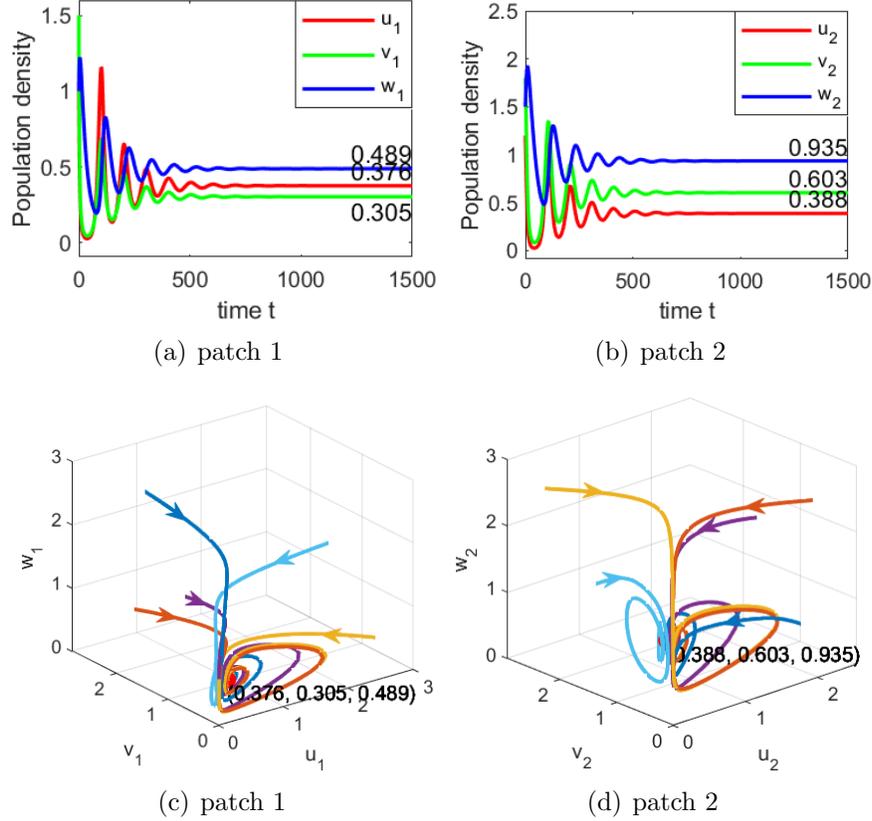


Figure 5: The positive equilibrium  $E_2$  of system (6.1) and stable behavior of  $E_2$

Next, we investigate the apparent competition relation between the prey  $u$  and  $v$  by observing the population density of the prey and predator with respect to changes in the prey growth rate.

**Example 6.5.** We may assume that  $r_1 = r_{11} = r_{12}$ ,  $r_2 = r_{21} = r_{22}$ ,  $K_{11} = 5$ ,  $K_{12} = 8$ ,  $K_{21} = 15$ ,  $K_{22} = 18$ ,  $b_1 = 0.4$ ,  $b_2 = 0.1$ ,  $c_1 = 0.1$ ,  $c_2 = 0.2$ ,  $d_1 = 0.07$ ,  $d_2 = 0.06$ ,  $\rho_u = 0.1$ ,  $\rho_v = 0.1$ ,  $\rho_w = 0.01$ .

Firstly, in Figure 6(a) and Figure 6(b), it is not difficult to observe that as the growth rate  $r$  of one prey increases, corresponding to an increase in its population density, the population density of the predator  $w$  also increases. This increase the risk of another prey being preyed upon, causing a decrease in its population density. Therefore, it can be explained that there is a negative interaction between the prey  $u$  and  $v$  with the predator  $w$  as the intermediary. This indicates the presence of an apparent competition relationship between the prey  $u$  and  $v$ .

Secondly, by rotating Figure 6(a) and Figure 6(b) at an angle, we obtain Figures 6(c) and Figure 6(d). It can be observed that the appropriate growth rates  $r_1$  and  $r_2$  can allow the prey  $u$ ,  $v$  and predator  $w$  to reach a coexistence state.

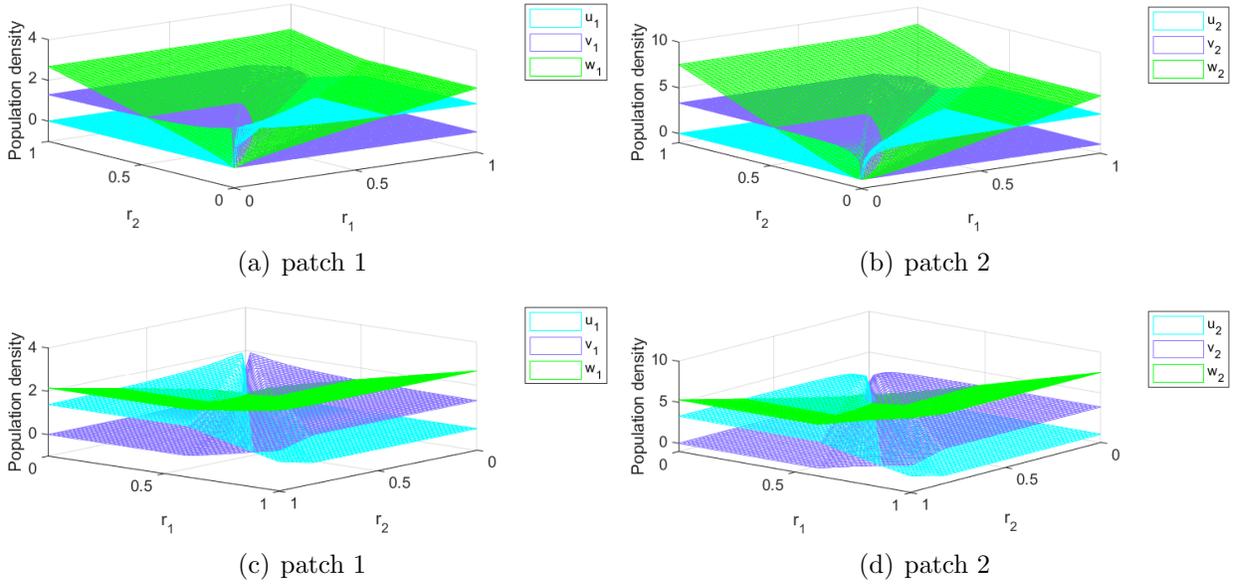


Figure 6: The apparent competition between prey  $u$  and  $v$

## 7. Conclusion

In this paper, a three-dimensional model in which two prey and one predator disperse simultaneously in a heterogeneous environment with multiple patches is proposed, and the stability of its equilibrium points is extensively studied.

We prove theoretically the positivity and uniform ultimate boundedness of the solution of system (1.1), and analyze the stability of the trivial equilibrium and semitrivial equilibrium by using threshold values. Under certain parameters constraint, we obtain sufficient conditions for the uniform persistence of the system, which shows that there exists at least one positive equilibrium in the model. Furthermore, we prove the global asymptotic stability of the positive equilibrium by constructing a global Lyapunov function and combining the method of graph theory. To be precise, it has been seen that the diffusion rate affects the persistence and extinction of the population, that is, the faster the diffusion rate, the worse the survival of the population, which plays an important role in maintaining the ecological balance. In addition, the two groups of prey in the model interact with each other through the shared predator, leading to a likelihood competition between them. The numerical simulations verified the validation of the theoretical results.

Certainly, our model can also be applied to various domains of epidemiological systems by constructing different growth rates and multiple functional responses. This is a direction we plan to explore in the future.

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