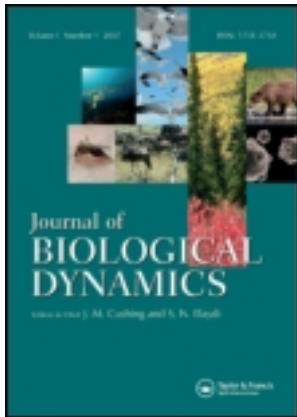


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Permanence induced by life-cycle resonances: the periodical cicada problem

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Periodical cicadas are known for their unusually long life cycle for insects and their prime periodicity of either 13 or 17 years. One of the explanations for the prime periodicity is that the prime periods are selected to prevent cicadas from resonating with predators with submultiple periods. This paper considers this hypothesis by investigating a population model for periodical predator and prey. The study shows that if the periods of the two periodical species are not coprime, then the predator cannot resist the invasion of the prey. On the other hand, if the periods are coprime, then the predator can resist the invasion of the prey. It is also shown that if the periods are not coprime, then the life-cycle resonance can induce a permanent system, in which no cohorts are missing in both populations. On the other hand, if the periods are coprime, then the system cannot be permanent.

Keywords: Leslie matrix; Lotka–Volterra equation; semelparity; heteroclinic cycle; permanence

AMS Subject Classification: 34C05; 34C14; 37N25; 92B05; 92D25

1. Introduction

‘An insect population is said to be *periodical* if the life cycle has a fixed length of k years ($k > 1$) and if the adults do not appear every year but only every k th year’ [2]. Periodical cicadas (*Magicalicada* spp.), inhabiting the Eastern United States, are examples of periodical insects. Nymphs of periodical cicadas spend underground for precisely 17 years in the North and 13 years in the South before emerging from the ground. Adult individuals spend the last few weeks of their life aboveground to mate, lay eggs and die (see [12,27,28,33] for the details).

In addition to the perfect periodicity, the prime periodicity is an intriguing characteristic of periodical cicadas. Seventeen and 13 are prime numbers. There are two dominant hypotheses explaining this prime periodicity. The first hypothesis is due to a hypothetical predator (or parasitoid). Lloyd and Dybas [28] suggest that parasitoids may have played a role in evolution of periodical cicadas from protoperiodicities to prime periodicities to escape from parasitoids with

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submultiple periods of dormancy. Also in [11], the advantage of prime periodicities to escape from natural enemies with cycles is suggested (see also [29]). Based on this idea, Webb [32] constructed mathematical models and gave a numerical example that predators with 2- or 3-year cycles eliminate nonprime number periodical cicadas (see also Davydova [8] for an analogous hypothesis proposing that prime periodicities are selected to escape from competition with short-living periodical cicadas). The second hypothesis was proposed by Cox and Carlton [3,4]. They argue that prime periodicities are selected to avoid coemergence and hybridization with periodical cicadas with different periods since the hybridization disrupts their perfect periodicities and produces stragglers, which are eliminated by predators or by reduced mating opportunities. This idea is advanced by Yoshimura [34] and is illustrated by numerical experiments in [31,35]. However, as pointed out by Lehmann-Ziebarth *et al.* [26], ‘a difficulty of this explanation is that prime-period phenotypes might in fact be more likely to hybridize; if, for example, 12- and 13-year phenotypes co-occur, they will emerge together at least within 156 years, while 12- and 14-year phenotypes will never emerge together if they initially emerge 1 year apart’. The hybridization hypothesis only takes into account certain cohorts initially coemerging.

A similar weak point can be seen in a mathematical model in [32]. The model assumes that

- (S1) the predator dynamics is independent of the cicada dynamics;
- (S2) periodical cicadas initially emerge when periodically oscillating predators are abundant (i.e. only certain cohorts of periodical cicadas are considered).

Although these assumptions contribute to simplifying model equations, we might obtain a different outcome if the assumptions are relaxed. If (S2) is not assumed, then periodical cicadas could never emerge when predators are abundant. For instance, consider a 12-year periodical cicada and a periodically oscillating predator with a 2-year period. If the cicada initially avoids a year when the predator is abundant, then the cicada will never emerge in the abundant years. But the emergence in the abundant years is inevitable for prime number periodical cicadas. Therefore, nonprime number periodical cicadas could have an advantage. If both (S1) and (S2) are not assumed, we cannot simply conclude that nonprime number periodical cicadas are selected for since a phase shift of predators might occur in response to the periodical cicada dynamics. The aim of this paper is to examine this aspect of the predator-resonance hypothesis by using a mathematical model without assuming (S1) and (S2) and to show that the mechanism proposed in [11,28] does not work to explain the advantage of prime number periodical cicadas.

For this purpose, we need to assume that there exists a predator (or parasitoid) whose influence to periodical cicadas is periodic. In order to emphasize the essential point of the mechanism proposed in [11,28], we assume a simple hypothetical predator with periodic influence to periodical cicadas. More precisely, we assume a hypothetical predator (or parasitoid) that is periodical in the sense of Bulmer [2] and attacks only cicadas aboveground. This hypothetical predator produces periodic predation pressure on periodical cicadas. It is unlikely that such a predator exists and it is unclear that such a predator has existed. But if such a hypothetical predator cannot explain the advantage of prime number periodical cicadas, then we see that a new mechanism that is not involved in the mechanism proposed in [11,28] is necessary.

The following is the outline of how we derive the conclusion that prime periodicities are not advantageous even under periodic predation pressure. In Section 2, we construct an age-structured model for dynamically interacting prey and predator without assuming (S1) and (S2). The predator-prey model is described by a discrete-time coupled Leslie matrix model. Since the prey corresponds to periodical cicadas, the prey is assumed to be semelparous. Furthermore, the prey is assumed to be periodical if it is isolated from its hypothetical predator. This means that prey’s perfect periodicity is maintained by some mechanism that is not due to the hypothetical predator. For instance, satiation of predators (such as birds) and severe inter-class competition can maintain prey’s perfect periodicity (e.g. see [2,18]). As mentioned above, the hypothetical predator

is also assumed to be periodical. This also means that predator’s perfect periodicity is maintained by some mechanism that is not due to its prey. Furthermore, the predator is assumed to be semelparous since if non-semelparous periodical species is unlikely [23]. In Section 3, the discrete-time model is reduced to a certain Lotka–Volterra differential equation, which will be studied in the subsequent sections. Section 4 provides a mathematical condition ensuring that both the predator and the prey are periodical in terms of Lotka–Volterra equations. Section 5 provides some miscellaneous things that are necessary and helpful in the subsequent sections. Sections 6 and 7 evaluate the advantage of prime number periodical cicadas. For this evaluation, we consider the invasibility of the periodical prey to the environment with the hypothetical periodical predator. Furthermore, we study the dynamics after successful prey invasion. Section 6 focuses on the asynchronous case where the life-cycle durations of the prey and the predator, say n_1 and n_2 , are coprime, i.e. the greatest common divisor of n_1 and n_2 is 1. In this case, it is shown that the periodical predator can resist the invasion of the periodical prey (see Theorem 6.2). Furthermore, it is shown that the predator–prey system is never permanent (see Theorem 6.3). Section 7 considers the case where n_1 and n_2 are not coprime. In this case, it is shown that, with the help of a well-timed cohort of itself, the periodical prey can always invade the system with the periodical predator (see Theorem 7.1). To illustrate the fate after the invasion, we focus on the case $n_1 = n_2 = 2$, and observe interesting phenomena due to life-cycle resonances. Especially, we find that permanence of predator–prey systems is induced by life-cycle resonances (see Theorems 7.14 and 7.15). The last section includes concluding remarks. Some mathematically technical parts are contained in the appendices.

2. Model

In this section, we construct an age-structured predator–prey model to study the dynamic interaction between a periodical cicada species and its hypothetical predator (or parasitoid). We assume that the prey consists of $n_1 \geq 1$ discrete age-classes and the predator consists of $n_2 \geq 1$ discrete age-classes. Let $\mathbf{u} = (u_1, u_2, \dots, u_{n_1})^T$ and $\mathbf{v} = (v_1, v_2, \dots, v_{n_2})^T$ be the population vectors for the prey and the predator, respectively. Then u_i (resp. v_i) denotes the population density of the prey (resp. predator) of age i . For convenience, let $n := n_1 + n_2$. We construct a dynamical system on the n -dimensional nonnegative cone $\mathbb{R}_+^n := \{\mathbf{z} = (z_1, z_2, \dots, z_n)^T \in \mathbb{R}^n : z_1 \geq 0, z_2 \geq 0, \dots, z_n \geq 0\}$.

The time evolution of the population vectors follows the system of difference equations:

$$\begin{aligned} \mathbf{u}(t + 1) &= L_{n_1}[\sigma_1, \sigma_2, \dots, \sigma_{n_1}]\mathbf{u}(t), \\ \mathbf{v}(t + 1) &= L_{n_2}[\tau_1, \tau_2, \dots, \tau_{n_2}]\mathbf{v}(t), \end{aligned} \tag{1}$$

where

$$L_i[l_1, l_2, \dots, l_i] := \begin{pmatrix} 0 & 0 & \dots & 0 & l_i \\ l_1 & 0 & \dots & 0 & 0 \\ 0 & l_2 & \dots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \dots & l_{i-1} & 0 \end{pmatrix}.$$

The matrix L_i is a special case of the Leslie matrix. $\sigma_i, i \in \{1, 2, \dots, n_1 - 1\}$ (resp. $\tau_i, i \in \{1, 2, \dots, n_2 - 1\}$) denotes the survival probability of age-class i of the prey (resp. predator). σ_{n_1} (resp. τ_{n_2}) denotes the fertility of the prey (resp. predator). The sign pattern of the first row of L_i reflects the assumption of semelparity.

To include the interplay between the prey and the predator, the vital rates σ_i and τ_i are assumed to be the functions defined by

$$\sigma_i := \sigma_i((B_{11}\mathbf{u})_i + (B_{12}\mathbf{v})_i) \quad \text{and} \quad \tau_i := \tau_i((B_{21}\mathbf{u})_i + (B_{22}\mathbf{v})_i),$$

where each B_{ij} is a constant matrix with an appropriate size and a vector with a subscript, say i , denotes the i th component of the vector (e.g. $(B_{11}\mathbf{u})_i$ denotes the i th component of the vector $B_{11}\mathbf{u}$). B_{ij} may include a negative entry. For convenience, define

$$B = (b_{ij}) := \begin{pmatrix} B_{11} & B_{12} \\ B_{21} & B_{22} \end{pmatrix}.$$

This matrix determines the age-specific species-interaction between the prey and the predator. The diagonal and the off-diagonal blocks determine types of intra- and inter-specific interactions, respectively. The diagonal and the off-diagonal entries of B_{ii} determine types of conspecific intra- and inter-class interactions, respectively. To remove the ambiguity, we assume that

(H1) σ_i and τ_i are increasing functions.

Then B_{12} is nonpositive and B_{21} is nonnegative since the first species is a prey and the second species is a predator. This paper considers more special predator-prey interaction: two species meet only after they mature. Such an interaction is realized if the prey is a cicada and the predator is a parasitoid whose adult individuals attack adult cicadas (or cicada eggs) aboveground (note that σ_{n_1} can be interpreted as a product of fertility of adult cicadas and survival probability of cicada eggs if timing of census is just after egg hatching). The interaction can be expressed by assuming that both B_{12} and B_{21} have unique nonzero entries $b_{n_1 n} < 0$ and $b_{m_1} > 0$, respectively. $b_{n_1 n} < 0$ implies that σ_{n_1} is reduced by the predator of age n_2 . $b_{m_1} > 0$ implies that τ_{n_2} is enhanced by the prey of age n_1 . It is further assumed that all interactions within a species are competitive, i.e. all entries of B_{11} and B_{22} are negative. The assumptions on B are summarized as follows:

(H2)

$$B_{11} < 0, \quad B_{22} < 0, \quad B_{12} = \begin{pmatrix} 0 & \cdots & 0 & 0 \\ \vdots & & \vdots & \vdots \\ 0 & \cdots & 0 & 0 \\ 0 & \cdots & 0 & - \end{pmatrix} \quad \text{and} \quad B_{21} = \begin{pmatrix} 0 & \cdots & 0 & 0 \\ \vdots & & \vdots & \vdots \\ 0 & \cdots & 0 & 0 \\ 0 & \cdots & 0 & + \end{pmatrix}.$$

The basic reproduction number of the prey is

$$\mathcal{R}_0^1 := \sigma_1(0)\sigma_2(0) \cdots \sigma_{n_1}(0).$$

This number represents the expected number of offspring that a single prey individual reproduces per lifetime when all density-dependent effects are ignored [5,7]. Similarly, the basic reproduction number of the predator is

$$\mathcal{R}_0^2 := \tau_1(0)\tau_2(0) \cdots \tau_{n_2}(0).$$

In this paper, it is assumed that

(H3) $\mathcal{R}_0^1 > 1$ and $\mathcal{R}_0^2 > 1$.

This assumption implies that two species can persist when they are isolated from each other (see [25]). The reason why these inequalities are assumed is the following. Periodical cicadas are unreliable resources for a predator aboveground since they are not available between emergence years. Hence it is unlikely that the hypothetical predator attacking cicadas aboveground utilizes periodical cicadas as an essential resource. Therefore, we assume that the predator does not perfectly rely on the prey and mainly relies on some other resources that are not explicitly expressed in Equation (1). This assumption leads to the inequality $\mathcal{R}_0^2 > 1$, i.e. the predator is *self-supporting*. Furthermore, since we are not interested in the case where the prey is always eliminated from the system, it is assumed that the prey is also self-supporting, i.e. $\mathcal{R}_0^1 > 1$.

3. Lotka–Volterra equations for semelparous populations

In this section, following the procedure given in [22], we derive a Lotka–Volterra differential equation from Equation (1) (see also [10]). To this end, we need to assume that

(H4) $\sigma_1, \sigma_2, \dots, \sigma_{n_1}$ and $\tau_1, \tau_2, \dots, \tau_{n_2}$ are continuously differentiable;

(H5)

$$\begin{aligned} \sigma_i(0) > 0 \quad \text{and} \quad \left. \frac{1}{\sigma_i(0)} \frac{d\sigma_i(x)}{dx} \right|_{x=0} &= 1 \quad \text{for all } i \in \{1, 2, \dots, n_1\}, \\ \tau_j(0) > 0 \quad \text{and} \quad \left. \frac{1}{\tau_j(0)} \frac{d\tau_j(x)}{dx} \right|_{x=0} &= 1 \quad \text{for all } j \in \{1, 2, \dots, n_2\}. \end{aligned}$$

The assumption (H5) is introduced to normalize the functions σ_i and τ_i . For instance, $\sigma_i(x) = \sigma_i^0 \exp(x)$ and $\tau_i(x) = \tau_i^0 \exp(x)$ with positive constants $\sigma_i^0 > 0$ and $\tau_i^0 > 0$ satisfy (H4) and (H5) in addition to (H1).

Let m be the least common multiple of n_1 and n_2 . Then within m time steps the prey and the predator experience m/n_1 and m/n_2 generations, respectively. Hence, $(\mathcal{R}_0^1)^{m/n_1}$ (resp. $(\mathcal{R}_0^2)^{m/n_2}$) denotes the expected number of descendants of a single prey (resp. predator) individual after m time steps when all density-dependent effects are ignored. Let $s_1, s_2 \in \mathbb{R}$ be numbers satisfying

$$\frac{m}{s_1 n_1} \log \mathcal{R}_0^1 = \frac{m}{s_2 n_2} \log \mathcal{R}_0^2 > 0.$$

Note that such numbers are not unique but exist. By (H3), both s_1 and s_2 are positive. Define h by $h := (m/s_1 n_1) \log \mathcal{R}_0^1$. By definition, $h = 0$ if $\mathcal{R}_0^1 = \mathcal{R}_0^2 = 1$. Let $\lambda_i := \sqrt[n_i]{\mathcal{R}_0^i} = e^{s_i h/m}$, $i = 1, 2$. Then λ_1 and λ_2 are eigenvalues of the nonnegative irreducible matrices

$$L_{n_1}[\sigma_1(0), \sigma_2(0), \dots, \sigma_{n_1}(0)] \quad \text{and} \quad L_{n_2}[\tau_1(0), \tau_2(0), \dots, \tau_{n_2}(0)],$$

respectively. Let $\mathbf{d}_1 = (d_1, d_2, \dots, d_{n_1})^T > \mathbf{0}$ and $\mathbf{d}_2 = (d_{n_1+1}, d_{n_1+2}, \dots, d_{n_1+n_2})^T > \mathbf{0}$ be right eigenvectors associated with λ_1 and λ_2 , respectively. By the Perron–Frobenius theorem, we can choose positive \mathbf{d}_1 and \mathbf{d}_2 . We normalize them by assuming $d_1 + d_2 + \dots + d_{n_1} = 1$ and $d_{n_1+1} + d_{n_1+2} + \dots + d_{n_1+n_2} = 1$. Define

$$D_1 := \begin{pmatrix} d_1 & 0 & \dots & 0 \\ 0 & d_2 & \dots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \dots & d_{n_1} \end{pmatrix} \quad \text{and} \quad D_2 := \begin{pmatrix} d_{n_1+1} & 0 & \dots & 0 \\ 0 & d_{n_1+2} & \dots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \dots & d_{n_1+n_2} \end{pmatrix}.$$

We rescale Equation (1) with the new vectors $\mathbf{x} = (1/h)D_1^{-1}\mathbf{u}$ and $\mathbf{y} = (1/h)D_2^{-1}\mathbf{v}$. Then Equation (1) can be rewritten as follows:

$$\begin{aligned} \mathbf{x}(t+1) = e^{s_1 h/m} L_{n_1} &\left[\frac{\sigma_1(h\{(B_{11}D_1\mathbf{x}(t))_1 + (B_{12}D_2\mathbf{y}(t))_1\})}{\sigma_1(0)}, \right. \\ &\frac{\sigma_2(h\{(B_{11}D_1\mathbf{x}(t))_2 + (B_{12}D_2\mathbf{y}(t))_2\})}{\sigma_2(0)}, \\ &\left. \dots, \frac{\sigma_{n_1}(h\{(B_{11}D_1\mathbf{x}(t))_{n_1} + (B_{12}D_2\mathbf{y}(t))_{n_1}\})}{\sigma_{n_1}(0)} \right] \mathbf{x}(t), \end{aligned} \tag{2}$$

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$$\mathbf{y}(t + 1) = e^{s_2 h/m} L_{n_2} \left[\begin{array}{c} \frac{\tau_1(h\{(B_{21}D_1\mathbf{x}(t))_1 + (B_{22}D_2\mathbf{y}(t))_1\})}{\tau_1(0)}, \\ \frac{\tau_2(h\{(B_{21}D_1\mathbf{x}(t))_2 + (B_{22}D_2\mathbf{y}(t))_2\})}{\tau_2(0)}, \\ \dots, \frac{\tau_{n_2}(h\{(B_{21}D_1\mathbf{x}(t))_{n_2} + (B_{22}D_2\mathbf{y}(t))_{n_2}\})}{\tau_{n_2}(0)} \end{array} \right] \mathbf{y}(t).$$

Note that $\mathbf{x}(t + 1) \rightarrow L_{n_1}[1, 1, \dots, 1]\mathbf{x}(t)$ and $\mathbf{y}(t + 1) \rightarrow L_{n_2}[1, 1, \dots, 1]\mathbf{y}(t)$ as $h \rightarrow 0$. Because of the cyclicity of L_{n_1} and L_{n_2} , we have the following equation:

$$\begin{aligned} x_i(t + m) &= x_i(t) e^{s_1 h} \prod_{j=0}^{m-1} \frac{\sigma_{j+i}(h\{(B_{11}D_1\mathbf{x}(t + j))_{j+i} + (B_{12}D_2\mathbf{y}(t + j))_{j+i}\})}{\sigma_{j+i}(0)}, \\ i &= 1, 2, \dots, n_1, \\ y_i(t + m) &= y_i(t) e^{s_2 h} \prod_{j=0}^{m-1} \frac{\tau_{j+i}(h\{(B_{21}D_1\mathbf{x}(t + j))_{j+i} + (B_{22}D_2\mathbf{y}(t + j))_{j+i}\})}{\tau_{j+i}(0)}, \\ i &= 1, 2, \dots, n_2, \end{aligned} \tag{3}$$

where the additions in the subscripts in the first and the second equations are understood modulo n_1 and n_2 , respectively. Then, by L'Hôpital's rule, as $h \rightarrow 0$

$$\begin{aligned} \frac{x_i(t + m) - x_i(t)}{h} &\rightarrow x_i(t) \left(s_1 + \sum_{j=0}^{m-1} (B_{11}D_1P_1^j\mathbf{x}(t))_{j+i} + \sum_{j=0}^{m-1} (B_{12}D_2P_2^j\mathbf{y}(t))_{j+i} \right), \\ \frac{y_i(t + m) - y_i(t)}{h} &\rightarrow y_i(t) \left(s_2 + \sum_{j=0}^{m-1} (B_{21}D_1P_1^j\mathbf{x}(t))_{j+i} + \sum_{j=0}^{m-1} (B_{22}D_2P_2^j\mathbf{y}(t))_{j+i} \right), \end{aligned}$$

where $P_1 := L_{n_1}[1, 1, \dots, 1]$, $P_2 := L_{n_2}[1, 1, \dots, 1]$ and the additions in the subscripts in the first and the second equations are understood modulo n_1 and n_2 , respectively. Hence, formally, from the map (1) we obtain:

$$\begin{aligned} \dot{x}_i &= x_i(s_1 + (A_{11}\mathbf{x})_i + (A_{12}\mathbf{y})_i), \quad i = 1, 2, \dots, n_1, \\ \dot{y}_i &= y_i(s_2 + (A_{21}\mathbf{x})_i + (A_{22}\mathbf{y})_i), \quad i = 1, 2, \dots, n_2, \end{aligned} \tag{4}$$

where the matrix A_{ij} is the (i, j) -block of the partitioned interaction matrix

$$A = (a_{ij}) = \begin{pmatrix} A_{11} & A_{12} \\ A_{21} & A_{22} \end{pmatrix}$$

given by

$$A = K + P^{-1}KP + (P^{-1})^2K P^2 + \dots + (P^{-1})^{m-1}K P^{m-1}, \tag{5}$$

where $K = BD$,

$$P = \begin{pmatrix} P_1 & 0 \\ 0 & P_2 \end{pmatrix} \quad \text{and} \quad D = \begin{pmatrix} D_1 & 0 \\ 0 & D_2 \end{pmatrix}.$$

Note that P_1 and P_2 are permutation matrices corresponding to cyclic permutations. By (H2), A_{11} and A_{22} are negative, A_{12} is nonpositive and A_{21} is nonnegative. Moreover A_{12} and A_{21} are nonzero

since B_{12} and B_{21} are nonzero. Since the diagonal blocks of P correspond to cyclic permutations, the diagonal blocks of A are circulant. Therefore, for convenience, we write

$$A_{11} = \begin{pmatrix} -c_1 & -c_2 & \cdots & -c_{n_1} \\ -c_{n_1} & -c_1 & \cdots & -c_{n_1-1} \\ \vdots & \vdots & \ddots & \vdots \\ -c_2 & -c_3 & \cdots & -c_1 \end{pmatrix},$$

$$A_{22} = \begin{pmatrix} -c_{n_1+1} & -c_{n_1+2} & \cdots & -c_{n_1+n_2} \\ -c_{n_1+n_2} & -c_{n_1+1} & \cdots & -c_{n_1+n_2-1} \\ \vdots & \vdots & \ddots & \vdots \\ -c_{n_1+2} & -c_{n_1+3} & \cdots & -c_{n_1+1} \end{pmatrix},$$

where $c_1, c_2, \dots, c_{n_1+n_2} = c_n$ are positive.

For convenience, let

$$\mathbf{z} = (z_1, z_2, \dots, z_n)^T = (x_1, x_2, \dots, x_{n_1}, y_1, y_2, \dots, y_{n_2})^T.$$

Define $\text{supp}(\mathbf{z}) = \{i: z_i > 0\}$. The right-hand side of Equation (3) can be seen as a map of $\mathbf{z}(t)$. Denote the map by \mathfrak{G} . The following lemma shows that the equilibrium points of the map $\mathbf{z} \mapsto \mathfrak{G}(\mathbf{z})$ are inherited by Equation (4) with Equation (5).

LEMMA 3.1 *Let $\mathbf{z}^* \in \mathbb{R}_+^n$ be an isolated equilibrium point of Equation (4) with Equation (5). Then there exist a constant $h_1 > 0$, a neighbourhood $U \subset \mathbb{R}_+^n$ of \mathbf{z}^* and a unique continuous function $\zeta: [0, h_1] \rightarrow U$ such that $\zeta(h)$ is an equilibrium point of the map $\mathbf{z} \mapsto \mathfrak{G}(\mathbf{z})$, $\text{supp}(\zeta(h)) = \text{supp}(\mathbf{z}^*)$ for $h \in [0, h_1]$ and $\zeta(0) = \mathbf{z}^*$.*

Proof Suppose that \mathbf{z}^* is a positive equilibrium point of Equation (4) with Equation (5). Then \mathbf{z}^* satisfies

$$\mathbf{r} + A\mathbf{z}^* = \mathbf{0},$$

where

$$\mathbf{r} = (\underbrace{s_1, s_1, \dots, s_1}_{n_1}, \underbrace{s_2, s_2, \dots, s_2}_{n_2})^T.$$

Since \mathbf{z}^* is isolated, $\det A \neq 0$. Let $\mathbf{z}(t)$ be a solution of Equation (2) with $\mathbf{z}(0) = \mathbf{z}$. Define $\mathbf{f}: \mathbb{R}_+^n \times \mathbb{R} \rightarrow \mathbb{R}^{n_1}$ and $\mathbf{g}: \mathbb{R}_+^n \times \mathbb{R} \rightarrow \mathbb{R}^{n_2}$ by

$$f_i(\mathbf{z}, h) := \begin{cases} \frac{1}{h} \left\{ e^{s_1 h} \prod_{j=0}^{m-1} \frac{\sigma_{j+i}(h\{(B_{11}D_1\mathbf{x}(t+j))_{j+i} + (B_{12}D_2\mathbf{y}(t+j))_{j+i}\})}{\sigma_{j+i}(0)} - 1 \right\}, & h \neq 0, \\ s_1 + (A_{11}\mathbf{x})_i + (A_{12}\mathbf{y})_i, & h = 0 \end{cases}$$

and

$$g_i(\mathbf{z}, h) := \begin{cases} \frac{1}{h} \left\{ e^{s_2 h} \prod_{j=0}^{m-1} \frac{\tau_{j+i}(h\{(B_{21}D_1\mathbf{x}(t+j))_{j+i} + (B_{22}D_2\mathbf{y}(t+j))_{j+i}\})}{\tau_{j+i}(0)} - 1 \right\}, & h \neq 0, \\ s_2 + (A_{21}\mathbf{x})_i + (A_{22}\mathbf{y})_i, & h = 0. \end{cases}$$

Define $\mathbf{G}: \mathbb{R}_+^n \times \mathbb{R} \rightarrow \mathbb{R}^n$ by $\mathbf{G} = (G_1, G_2, \dots, G_n)^T := (f_1, f_2, \dots, f_{n_1}, g_1, g_2, \dots, g_{n_2})^T$. It is clear that $\mathbf{G}(\mathbf{z}^*, 0) = \mathbf{0}$ and \mathbf{G} is continuous. We see that a positive $\zeta \in \mathbb{R}_+^n$ satisfying $\mathbf{G}(\zeta, h) = \mathbf{0}$

with $h > 0$ is a positive equilibrium point of the map $\mathbf{z} \mapsto \mathfrak{G}(\mathbf{z})$. Furthermore, we see that for each $i, j \in \{1, 2, \dots, n\}$, $\partial G_i / \partial z_j$ is continuous and

$$\left. \frac{\partial G_i}{\partial z_j} \right|_{\mathbf{z}=\mathbf{z}^*, h=0} = a_{ij}.$$

Since $\det A \neq 0$, the Jacobi matrix $(\partial G_i / \partial z_j)|_{\mathbf{z}=\mathbf{z}^*, h=0}$ is nonsingular. By the implicit function theorem, the desired function ζ exists.

Suppose that \mathbf{z}^* is not positive. Then \mathbf{z}^* is a positive equilibrium point of some subsystem of Equation (4) with Equation (5). Hence, if we repeat the above argument for the subsystem, then we can construct the desired function ζ . We omit the detail. ■

Suppose that $\mathbf{z}^* \in \mathbb{R}_+^n$ is an isolated equilibrium point of Equation (4) with Equation (5) satisfying $\mathbf{z}^* = P^l \mathbf{z}^*$ and $\mathbf{z}^* \neq P^j \mathbf{z}^*$, $0 < j < l$. By Lemma 3.1, the map $\mathbf{z} \mapsto \mathfrak{G}(\mathbf{z})$ has an equilibrium point $\zeta(h)$ that $\zeta(h) \rightarrow \mathbf{z}^*$ as $h \rightarrow 0$ and $\text{supp}(\zeta(h)) = \text{supp}(\mathbf{z}^*)$. Since the map (2) approaches $\mathbf{z}(t+1) = P\mathbf{z}(t)$ as $h \rightarrow 0$, $\zeta(h)$ is an l -periodic point of Equation (2). Therefore, \mathbf{z}^* corresponds to an l -periodic point of Equation (1).

The prey (resp. predator) has potentially n_1 (resp. n_2) reproductively isolated cohorts, and each of them is represented by one of the components of \mathbf{x} (resp. \mathbf{y}). If the unit of time of Equation (1) is a year, each component of \mathbf{x} (resp. \mathbf{y}) corresponds to the population density of a year-class of the prey (resp. predator).

Finally, we prove that Equation (5) remains unchanged even if we interchange the variables x_1, x_2, \dots, x_{n_1} and y_1, y_2, \dots, y_{n_2} according to the permutation matrix P (cf. [10, Lemma 2.1]).

LEMMA 3.2 *If $\mathbf{z}(t)$ is a solution of Equation (4) with Equation (5), then $P\mathbf{z}(t)$ is also a solution of the same equation.*

Proof Since P and A commute (i.e. $AP = PA$), we have $A_{11}P_1 = P_1A_{11}$, $A_{12}P_2 = P_1A_{12}$, $A_{21}P_1 = P_2A_{21}$ and $A_{22}P_2 = P_2A_{22}$. This property leads to

$$\begin{aligned} (P_1\dot{\mathbf{x}})_i &= \dot{x}_{i-1} = x_{i-1}(s_1 + (A_{11}\mathbf{x})_{i-1} + (A_{12}\mathbf{y})_{i-1}) \\ &= (P_1\mathbf{x})_i(s_1 + (P_1A_{11}\mathbf{x})_i + (P_1A_{12}\mathbf{y})_i) \\ &= (P_1\mathbf{x})_i(s_1 + (A_{11}P_1\mathbf{x})_i + (A_{12}P_2\mathbf{y})_i), \quad i = 1, 2, \dots, n_1, \end{aligned}$$

where the subtractions of the subscripts are understood modulo n_1 . Similarly, we can show that

$$(P_2\dot{\mathbf{y}})_i = (P_2\mathbf{y})_i(s_2 + (A_{21}P_1\mathbf{x})_i + (A_{22}P_2\mathbf{y})_i), \quad i = 1, 2, \dots, n_2.$$

This shows that $P\mathbf{z}(t)$ is a solution of Equation (4) with Equation (5). ■

4. Perfect periodicity

In this section, we introduce the assumption ensuring that both the prey and the predator are periodic, i.e. their population dynamics have perfect periodicities. Mathematically, we are interested in the case where both the subsystems $\mathbf{u} = \mathbf{0}$ and $\mathbf{v} = \mathbf{0}$ of Equation (1) have stable periodic orbits

with the following sign pattern:

$$\begin{pmatrix} + \\ 0 \\ \vdots \\ 0 \end{pmatrix} \rightarrow \begin{pmatrix} 0 \\ + \\ \vdots \\ 0 \end{pmatrix} \rightarrow \dots \rightarrow \begin{pmatrix} 0 \\ 0 \\ \vdots \\ + \end{pmatrix} \rightarrow \begin{pmatrix} + \\ 0 \\ \vdots \\ 0 \end{pmatrix}.$$

By (H2) and (H3), each axis of Equation (4) with Equation (5) has a unique nonzero equilibrium point. Let $F_i, i = 1, 2, \dots, n_1$ (resp. $F^j, j = 1, 2, \dots, n_2$), be the unique nonzero equilibrium point on the x_i -axis (resp. y_j -axis). Then we have $F_{i+1} = PF_i$ and $F^{j+1} = PF^j$, where the subscript and the superscript are counted modulo n_1 and n_2 , respectively. This shows that F_i and F^j are the desired equilibrium points of Equation (4) if they are stable in the respective subsystems. The stability conditions for F_i and F^j are given as follows:

LEMMA 4.1 *Each $F_i, i = 1, 2, \dots, n_1$, is asymptotically stable in the subsystem $\mathbf{y} = \mathbf{0}$ if and only if $c_1 < c_l$ for all $l \in \{2, 3, \dots, n_1\}$. Each $F^j, j = 1, 2, \dots, n_2$, is asymptotically stable in the subsystem $\mathbf{x} = \mathbf{0}$ if and only if $c_{n_1+1} < c_{n_1+l}$ for all $l \in \{2, 3, \dots, n_2\}$.*

Proof In the subsystem $\mathbf{y} = \mathbf{0}$, Equation (4) is reduced to

$$\dot{x}_i = x_i(s_1 + (A_{11}\mathbf{x})_i), \quad i = 1, 2, \dots, n_1, \tag{6}$$

where A_{11} is a circulant matrix as mentioned above. The subsystem has the equilibrium point $\tilde{F}_1 = (s_1/c_1, 0, \dots, 0)^T$, which corresponds to F_1 of the full system. The Jacobi matrix of Equation (6) evaluated at \tilde{F}_1 has the eigenvalues

$$-s_1, s_1 \left(1 - \frac{c_2}{c_1}\right), s_1 \left(1 - \frac{c_3}{c_1}\right), \dots, s_1 \left(1 - \frac{c_{n_1}}{c_1}\right).$$

Hence \tilde{F}_1 is asymptotically stable if $c_1 < c_l$ for all $l \in \{2, \dots, n_1\}$. Conversely, suppose that $c_1 \geq c_l$ for some $l \in \{2, \dots, n_1\}$. If $c_1 > c_l$, then one of the eigenvalues shown above is positive, and hence \tilde{F}_1 is unstable. Suppose $c_1 = c_l$. Then the subsystem of Equation (6) composed of x_1 and x_l is given by

$$\begin{aligned} \dot{x}_1 &= x_1(s_1 - c_1x_1 - c_1x_l), \\ \dot{x}_l &= x_l(s_1 - c_{2-l}x_1 - c_1x_l), \end{aligned} \tag{7}$$

where $2 - l$ is understood modulo n_1 . If $c_1 = c_{2-l}$, then Equation (7) has a segment of equilibrium points connecting $(s_1/c_1, 0)^T$ and $(0, s_1/c_1)^T$. Hence \tilde{F}_1 is not an asymptotically stable equilibrium point of Equation (6). If $c_1 > c_{2-l}$, then one of the eigenvalues shown above is positive, and hence \tilde{F}_1 is unstable. If $c_1 < c_{2-l}$, then we can show that $(0, s_1/c_1)^T$ is an unstable equilibrium point of Equation (7). In fact, the instability is shown as follows. Define

$$\Omega := \{(x_1, x_l)^T \in \mathbb{R}_+^2 : s_1 - c_1x_1 - c_1x_l > 0, s_1 - c_{2-l}x_1 - c_1x_l < 0\}.$$

Then Ω is forward invariant under Equation (7) and any neighbourhood of $(0, s_1/c_1)^T$ intersects with Ω . Every solution in Ω is monotone (i.e. $\dot{x}_1 > 0, \dot{x}_l < 0$) and converges to $(s_1/c_1, 0)^T$. Hence $(0, s_1/c_1)^T$ is an unstable equilibrium point of Equation (7). This means that \tilde{F}_l is an unstable equilibrium point of Equation (6). Consequently, by Lemma 3.2, \tilde{F}_1 is also an unstable equilibrium point of Equation (6). Furthermore, by Lemma 3.2, we can conclude that every \tilde{F}_i ,

$i = 1, 2, \dots, n_1$, is an asymptotically stable equilibrium point of Equation (6) if and only if $c_1 < c_l$ for all $l \in \{2, 3, \dots, n_1\}$. The same argument applies to the stability problem of F^j . ■

Therefore, we need to assume that

(H6) $c_1 < c_i$ for all $i \in \{2, 3, \dots, n_1\}$ and $c_{n_1+1} < c_{n_1+i}$ for all $i \in \{2, 3, \dots, n_2\}$.

There are two ecological mechanisms stabilizing perfect periodicity. Hoppenstead and Keller [18] showed that the combination of predator satiation and resource limitation stabilizes perfect periodicity (see also [1,2,24,29]). Bulmer [2] showed that severe inter-class competition stabilizes perfect periodicity and predation reinforces the tendency (e.g. see also [6,9,24]). Appendix 1 shows that (H6) can be realized when inter-class competition is severe. However, note that, as shown in [24], inter-class competition can be apparently severe if we take account of the effect of predators with a certain functional response (e.g. birds for periodical cicadas).

5. Preliminaries

In this section, we provide some miscellaneous things that are necessary and helpful in the subsequent sections.

The model equation that we examine in this paper is the Lotka–Volterra equation (4) that possesses the interaction matrix (5) and satisfies the assumptions (H2), (H3) and (H6). For convenience, the model is simply denoted by Equation (4)_H.

Define $\text{int}\mathbb{R}_+^n := \{\mathbf{z} \in \mathbb{R}_+^n : z_1 > 0, z_2 > 0, \dots, z_n > 0\}$, $\text{bd}\mathbb{R}_+^n := \{\mathbf{z} \in \mathbb{R}_+^n : z_1 z_2 \cdots z_n = 0\}$. Let $\omega(\mathbf{z})$ be the ω -limit set of $\mathbf{z} \in \mathbb{R}_+^n$. For a subset $S \subset \mathbb{R}_+^n$, define $\omega(S) := \bigcup_{\mathbf{z} \in S} \omega(\mathbf{z})$. As defined above, $\mathbf{z} = (x_1, x_2, \dots, x_{n_1}, y_1, y_2, \dots, y_{n_2})^T$ and $\text{supp}(\mathbf{z}) := \{i : z_i > 0\}$. We identify z_i with x_i if $i \in \{1, 2, \dots, n_1\}$ and z_i with y_{i-n_1} if $i \in \{n_1 + 1, n_1 + 2, \dots, n_1 + n_2\}$.

DEFINITION 5.1 (a) *The prey is said to be able to invade $F^j, j = 1, 2, \dots, n_2$, if there exists an index $i \in \{1, 2, \dots, n_1\}$ such that*

$$\left. \frac{\dot{x}_i}{x_i} \right|_{F^j} > 0.$$

(b) *The predator is said to be able to invade $F_i, i = 1, 2, \dots, n_1$, if there exists an index $j \in \{1, 2, \dots, n_2\}$ such that*

$$\left. \frac{\dot{y}_j}{y_j} \right|_{F_i} > 0.$$

By Lemma 3.2, the prey can invade all F^1, F^2, \dots, F^{n_2} if and only if the prey can invade one of them. Similarly, the predator can invade all F_1, F_2, \dots, F_{n_1} if and only if the predator can invade one of them. By (H6), $F^j, j = 1, 2, \dots, n_2$, of Equation (4)_H is asymptotically stable if $\dot{x}_i/x_i|_{F^j} < 0$ for all $i \in \{1, 2, \dots, n_1\}$. Similarly, $F_i, i = 1, 2, \dots, n_1$, of Equation (4)_H is asymptotically stable if $\dot{y}_j/y_j|_{F_i} < 0$ for all $j \in \{1, 2, \dots, n_2\}$. However, since $s_2 > 0$ and A_{21} is nonnegative, $\dot{y}_j/y_j|_{F_i} > 0$ holds for all $j \in \{1, 2, \dots, n_2\}$. Therefore, the predator can always invade $F_i, i = 1, 2, \dots, n_1$.

The dissipativity defined below ensures that the forward orbits of Equation (4) are eventually bounded both below and above by constants independent of initial conditions.

DEFINITION 5.2 *Equation (4) is said to be dissipative if there exist constants $\delta_1, \delta_2 \in \mathbb{R}$ such that*

$$\delta_1 < \liminf_{t \rightarrow \infty} z_i(t) \leq \limsup_{t \rightarrow \infty} z_i(t) < \delta_2, \quad i = 1, 2, \dots, n$$

for all $\mathbf{z}(0) \in \mathbb{R}_+^n$.

LEMMA 5.3 Equation (4)_H is dissipative.

Proof It is known that Equation (4) is dissipative if A is a B-matrix, i.e. for all $\mathbf{z} \geq \mathbf{0}$ with $\mathbf{z} \neq \mathbf{0}$ there exists an i such that $z_i > 0$ and $(A\mathbf{z})_i < 0$ (see [16, Theorem 15.2.4]). Let $\mathbf{z} \geq \mathbf{0}$ with $\mathbf{z} \neq \mathbf{0}$. Suppose that there exists an $i \in \{1, 2, \dots, n_1\}$ such that $z_i > 0$. Then $(A\mathbf{z})_i \leq (A_{11}\mathbf{x})_i < 0$. Suppose that $z_i = 0$ for all $i \in \{1, 2, \dots, n_1\}$. Then for $i \in \{n_1 + 1, n_1 + 2, \dots, n_1 + n_2\}$, $z_i > 0$ and $(A\mathbf{z})_i = (A_{22}\mathbf{y})_{i-n_1} < 0$. Hence A is a B-matrix. ■

As shown above, the predator can always invade $F_i, i = 1, 2, \dots, n_1$. We can further show that the predator can establish itself after invasion.

LEMMA 5.4 Let $\mathbf{z}(t)$ be a solution of Equation (4)_H. Then there exists a positive constant δ such that

$$\liminf_{t \rightarrow \infty} (y_1(t) + y_2(t) + \dots + y_{n_2}(t)) > \delta > 0$$

for all $\mathbf{z}(0) \in \mathbb{R}_+^n$ with $y_1(0) + y_2(0) + \dots + y_{n_2}(0) > 0$.

Proof Using a theorem of average Liapunov functions, we shall prove this lemma. Let $S = \{\mathbf{z} \in \mathbb{R}_+^n : y_1 + y_2 + \dots + y_{n_2} = 0\}$. Since Equation (4)_H is dissipative, a theorem of average Liapunov functions [19, Theorem 2.5] ensures that the conclusion of the lemma follows if there exists a continuously differentiable function $V : \mathbb{R}_+^n \rightarrow \mathbb{R}_+$ such that

- (i) $V(\mathbf{z}) = 0$ if and only if $\mathbf{z} \in S$;
- (ii) there exists a continuous function $\psi : \mathbb{R}_+^n \rightarrow \mathbb{R}$ such that $\dot{V}(\mathbf{z}) \geq V(\mathbf{z})\psi(\mathbf{z})$ for all $\mathbf{z} \in \mathbb{R}_+^n$;
- (iii) for any $\mathbf{z}(0) \in \overline{\omega(S)}$ there exists a $T > 0$ satisfying

$$\int_0^T \psi(\mathbf{z}(t)) dt > 0.$$

Here, $\overline{\omega(S)}$ is the closure of $\omega(S)$.

Define $V : \mathbb{R}_+^n \rightarrow \mathbb{R}_+$ by $V(\mathbf{z}) = y_1 + y_2 + \dots + y_{n_2}$. Then V is continuously differentiable and satisfies (i). The time-derivative of V along a solution of Equation (4)_H satisfies $\dot{V}(\mathbf{z}) \geq V(\mathbf{z})\psi(\mathbf{z})$ for the continuous function $\psi(\mathbf{z}) = \min_{i=1}^{n_2} \{s_2 + (A_{21}\mathbf{x})_i + (A_{22}\mathbf{y})_i\}$. Since $\psi(\mathbf{z}) = \min_{i=1}^{n_2} \{s_2 + (A_{21}\mathbf{x})_i\} > 0$ for $\mathbf{z} \in S$, (iii) is also satisfied. This completes the proof. ■

The following lemma shows that if the two species are isolated, then the predator has the largest total population density at $F^j, j \in \{1, 2, \dots, n_2\}$. Clearly, the similar conclusion holds for the prey species.

LEMMA 5.5 Let $\mathbf{z}^* = (x_1^*, x_2^*, \dots, x_{n_1}^*, y_1^*, y_2^*, \dots, y_{n_2}^*)^T \in \mathbb{R}_+^n$ be an equilibrium point of Equation (4)_H with $\mathbf{x}^* = \mathbf{0}$. Then

$$y_1^* + y_2^* + \dots + y_{n_2}^* \leq \frac{s_2}{c_{n_1+1}}$$

with equality only when $\mathbf{z}^* = F^j$ for $j \in \{1, 2, \dots, n_2\}$.

Proof The equality clearly holds if $\mathbf{z}^* = F^j$ for $j \in \{1, 2, \dots, n_2\}$. Suppose that $\mathbf{z}^* \neq F^j$ for all $j \in \{1, 2, \dots, n_2\}$. If $\mathbf{y}^* = \mathbf{0}$, then the strict inequality clearly holds. If $\mathbf{y}^* \neq \mathbf{0}$, then $s_2 - (A_{22}\mathbf{y}^*)_i = 0$ holds for $i \in \text{supp}(\mathbf{y}^*)$. By (H6), we have $s_2 - c_{n_1+1}(y_1^* + y_2^* + \dots + y_{n_2}^*) > s_2 - (A_{22}\mathbf{y}^*)_i = 0$. This completes the proof. ■

The permanence defined below ensures that two species coexist and none of them have missing cohorts.

DEFINITION 5.6 Equation (4) is said to be permanent if there exist positive constants δ_1 and δ_2 such that

$$0 < \delta_1 < \liminf_{t \rightarrow \infty} z_i(t) \leq \limsup_{t \rightarrow \infty} z_i(t) < \delta_2, \quad i = 1, 2, \dots, n$$

for all $z(0) \in \text{int}\mathbb{R}_+^n$.

Let $\mathfrak{M} := \{z \in \mathbb{R}_+^n : x_1 = x_2 = \dots = x_{n_1} \text{ and } y_1 = y_2 = \dots = y_{n_2}\}$. In [22], it is shown that \mathfrak{M} is forward invariant under Equation (4)_H. Furthermore, it is shown that the dynamics on \mathfrak{M} obeys the two-dimensional Lotka–Volterra predator–prey equation

$$\begin{aligned} \dot{|x|} &= |x|(s_1 + \bar{a}_{11}|x| + \bar{a}_{12}|y|), \\ \dot{|y|} &= |y|(s_2 + \bar{a}_{21}|x| + \bar{a}_{22}|y|), \end{aligned} \tag{8}$$

where $|x| = x_1 + x_2 + \dots + x_{n_1}$, $|y| = y_1 + y_2 + \dots + y_{n_2}$ and the coefficients \bar{a}_{11} , \bar{a}_{12} , \bar{a}_{21} and \bar{a}_{22} are defined by

$$\begin{aligned} \bar{a}_{11} &:= \frac{\sum_{i=1}^{n_1} \sum_{j=1}^{n_1} a_{ij}}{n_1^2} = -\frac{\sum_{i=1}^{n_1} c_i}{n_1}, \\ \bar{a}_{12} &:= \frac{\sum_{i=1}^{n_1} \sum_{j=n_1+1}^{n_1+n_2} a_{ij}}{n_1 n_2}, \\ \bar{a}_{21} &:= \frac{\sum_{i=n_1+1}^{n_1+n_2} \sum_{j=1}^{n_1} a_{ij}}{n_1 n_2}, \\ \bar{a}_{22} &:= \frac{\sum_{i=n_1+1}^{n_1+n_2} \sum_{j=n_1+1}^{n_1+n_2} a_{ij}}{n_2^2} = -\frac{\sum_{i=1}^{n_2} c_{n_1+i}}{n_2}. \end{aligned}$$

By (H2), $\bar{a}_{11} < 0$, $\bar{a}_{12} < 0$, $\bar{a}_{21} > 0$, $\bar{a}_{22} < 0$ hold. It is known that if Equation (8) has a positive equilibrium, it is globally asymptotically stable in $\text{int}\mathbb{R}_+^2$ (see Lemma A.1).

6. Asynchronous life cycles

In this section, we consider the case where n_1 and n_2 are coprime, i.e. the greatest common divisor of n_1 and n_2 is 1. In this case, the least common multiple of n_1 and n_2 is $m = n_1 n_2$, and we can prove the following lemma.

LEMMA 6.1 Consider the interaction matrix A of Equation (4)_H. If n_1 and n_2 are coprime, then $A_{12} = -\alpha E$ and $A_{21} = \beta E$ hold for

$$\alpha := -\sum_{i=1}^{n_1} \sum_{j=n_1+1}^{n_1+n_2} k_{ij} > 0, \quad \beta := \sum_{i=n_1+1}^{n_1+n_2} \sum_{j=1}^{n_1} k_{ij} > 0$$

and

$$E := \begin{pmatrix} 1 & \dots & 1 \\ \vdots & & \vdots \\ 1 & \dots & 1 \end{pmatrix}. \tag{9}$$

Proof Let γ_1 and γ_2 be the cyclic permutations

$$\begin{pmatrix} 1 & 2 & \dots & n_1 \\ 2 & 3 & \dots & 1 \end{pmatrix} \quad \text{and} \quad \begin{pmatrix} n_1 + 1 & n_1 + 2 & \dots & n_1 + n_2 \\ n_1 + 2 & n_1 + 3 & \dots & n_1 + 1 \end{pmatrix},$$

respectively. By Equation (5), for $i \in \{1, 2, \dots, n_1\}$ and $j \in \{n_1 + 1, n_1 + 2, \dots, n_1 + n_2\}$

$$a_{ij} = \sum_{l=0}^{m-1} k_{\gamma_1^l(i), \gamma_2^l(j)}.$$

It is known that if n_1 and n_2 are coprime, then $\{n_2, 2n_2, \dots, n_1 n_2\}$ is a complete system of incongruent residues (mod n_1) (e.g. see [13, Theorem 56]). Using this result, we can show that

$$\begin{aligned} a_{ij} &= \sum_{l=0}^{n_2-1} (k_{\gamma_1^{l+n_2}(i), \gamma_2^{l+n_2}(j)} + k_{\gamma_1^{l+2n_2}(i), \gamma_2^{l+2n_2}(j)} + \dots + k_{\gamma_1^{l+n_1 n_2}(i), \gamma_2^{l+n_1 n_2}(j)}) \\ &= \sum_{l=0}^{n_2-1} (k_{\gamma_1^l(1), \gamma_2^l(j)} + k_{\gamma_1^l(2), \gamma_2^l(j)} + \dots + k_{\gamma_1^l(n_1), \gamma_2^l(j)}) \\ &= \sum_{l_1=1}^{n_1} \sum_{l_2=n_1+1}^{n_1+n_2} k_{l_1 l_2}. \end{aligned}$$

Since all entries of A_{12} are identical, we have $A_{12} = (\sum_{l_1=1}^{n_1} \sum_{l_2=n_1+1}^{n_1+n_2} k_{l_1 l_2})E$. Similarly, we can show that $A_{21} = \sum_{l_1=n_1+1}^{n_1+n_2} \sum_{l_2=1}^{n_1} k_{l_1 l_2} E$. By (H2), α and β are positive. ■

By the simple structure of A , we can obtain the following theorem.

THEOREM 6.2 Consider Equation (4)_H with coprime n_1 and n_2 . Then the prey can invade F^j , $j \in \{1, 2, \dots, n_2\}$, if and only if $s_1 - s_2 \alpha / c_{n_1+1} > 0$.

Proof By Lemma 3.2, it is sufficient to show that the prey can invade F^1 if and only if $s_1 - s_2 \alpha / c_{n_1+1} > 0$. The conclusion follows since

$$\left. \frac{\dot{x}_i}{x_i} \right|_{F^1} = s_1 - \alpha \frac{s_2}{c_{n_1+1}}$$

for any $i \in \{1, 2, \dots, n_1\}$. ■

This theorem implies that if n_1 and n_2 are coprime, then there is a possibility that the predator can resist the invasion of the prey. This contrasts with the case where n_1 and n_2 are not coprime (see Theorem 7.1). The following theorem shows what happens after the invasion of the prey.

THEOREM 6.3 Suppose that n_1 and n_2 are coprime and $s_1 - s_2 \alpha / c_{n_1+1} > 0$.

(a) Let $\mathbf{z}(t)$ be a solution of Equation (4)_H. Then there exists a constant $\delta > 0$ such that

$$\liminf_{t \rightarrow \infty} (x_1(t) + x_2(t) + \dots + x_{n_1}(t)) > \delta > 0$$

for all $\mathbf{z}(0) \in \mathbb{R}_+^n$ with $x_1(0) + x_2(0) + \dots + x_{n_1}(0) > 0$;

(b) For any $i \in \{1, 2, \dots, n_1\}$ and $j \in \{1, 2, \dots, n_2\}$, Equation (4)_H has an equilibrium point F_i^j with $\text{supp}(F_i^j) = \{i, n_1 + j\}$ and F_i^j is asymptotically stable.

Proof (a) This case immediately follows from Theorem A.3 (see Appendix 3). In fact, by Lemma 5.3, system (4) is dissipative and, by Lemma 5.5, $s_1 - \alpha(y_1^* + y_2^* + \dots + y_{n_2}^*) \geq s_1 - \alpha s_2 / c_{n+1} > 0$ holds for all equilibrium points \mathbf{z}^* with $\mathbf{x}^* = \mathbf{0}$.

(b) Let $i \in \{1, 2, \dots, n_1\}$ and $j \in \{1, 2, \dots, n_2\}$. On the face spanned by the x_i - and the y_j -axes, system (4) is reduced to the two-dimensional Lotka–Volterra predator–prey equation:

$$\begin{aligned} \dot{x}_i &= x_i(s_1 - c_1 x - \alpha y_j), \\ \dot{y}_j &= y_j(s_2 + \beta x - c_{1+n_1} y_j). \end{aligned}$$

By Lemma A.1, this subsystem has a positive equilibrium point $(x_i^*, y_j^*)^T$, which corresponds to F_i^j of the full system. The Jacobi matrix of the above subsystem evaluated at $(x_i^*, y_j^*)^T$ is

$$\begin{pmatrix} -c_1 x_i^* & -\alpha x_i^* \\ \beta y_j^* & -c_{1+n_1} y_j^* \end{pmatrix}.$$

This Jacobi matrix is stable. Furthermore, we can show that

$$\left. \frac{\dot{x}_{i'}}{x_{i'}} \right|_{F_i^j} < s_1 - c_1 x_i^* - \alpha y_j^* = 0 \quad \text{and} \quad \left. \frac{\dot{y}_{i'}}{y_{i'}} \right|_{F_i^j} < s_2 + \beta x_i^* - c_{n_1+1} y_j^* = 0$$

hold for any $i' \neq i$ and $j' \neq j$. Here we used (H6). Therefore, the Jacobi matrix of Equation (4)_H evaluated at F_i^j is stable. ■

Theorem 6.3(a) with Lemma 5.4 shows that after the invasion of the prey, the prey establishes itself and coexists with the predator. Therefore, as long as n_1 and n_2 are coprime, we do not observe the phenomenon that an invader density is severely reduced after successful invasion due to an invasion-induced phase shift of predators (see [21,30] for an analogous phenomenon). This phenomenon is observed if n_1 and n_2 are not coprime (see Theorem 7.15). Since $F_i^j = P^m F_i^j$ and $F_i^j \neq P^j F_i^j, 0 < j < m$, the equilibrium F_i^j corresponds to an m -cycle of Equation (1). Since along the m -cycle the adults of the prey (resp. predator) appear only every n_1 th (resp. n_2 th) time-step, Theorem 6.3(b) shows that perfect periodicities of the prey and the predator are preserved after the prey invasion. Theorem 6.3(b) also shows that Equation (4)_H with coprime n_1 and n_2 is never permanent. In the next section, we see that Equation (4)_H can be permanent if n_1 and n_2 are not coprime.

7. Synchronous life cycles

In this section, we consider the case where n_1 and n_2 are not coprime, i.e. the greatest common divisor of n_1 and n_2 is not 1. The first result is applicable to any numbers n_1 and n_2 as long as they are not coprime.

THEOREM 7.1 *Consider Equation (4)_H with non-coprime n_1 and n_2 . Then the prey can always invade $F^j, j \in \{1, 2, \dots, n_2\}$.*

Proof By Lemma 3.2, it is sufficient to show that the prey can invade F^{n_2} . We shall show that $\dot{x}_1/x_1|_{F^{n_2}} > 0$.

Let γ_1 and γ_2 be the permutations defined in the proof of Lemma 6.1. By Equation (5),

$$a_{1n} = \sum_{l=0}^{m-1} k_{\gamma_1^l(1), \gamma_2^l(n)}.$$

Note that $n = n_1 + n_2$. Let m_0 be the greatest common divisor of n_1 and n_2 . Since n_1 and n_2 are not coprime, $m_0 \geq 2$ holds and hence $n_1 \geq 2$ and $n_2 \geq 2$. Let $n_1 = m_0 m_1$ and $n_2 = m_0 m_2$. Then m_1 and m_2 are coprime and the least common multiple of n_1 and n_2 is $m = m_0 m_1 m_2$. It is known that if m_1 and m_2 are coprime, then $\{m_2, 2m_2, \dots, m_1 m_2\}$ is a complete system of incongruent residues (mod m_1) (e.g. see [13, Theorem 56]). Using this result, we can show that

$$\begin{aligned} a_{1n} &= \sum_{l=0}^{n_2-1} (k_{\gamma_1^{l+n_2}(1), \gamma_2^{l+n_2}(n)} + k_{\gamma_1^{l+2n_2}(1), \gamma_2^{l+2n_2}(n)} + \dots + k_{\gamma_1^{l+m_1 n_2}(1), \gamma_2^{l+m_1 n_2}(n)}) \\ &= \sum_{l=0}^{n_2-1} (k_{\gamma_1^{l+m_2 m_0}(1), \gamma_2^l(n)} + k_{\gamma_1^{l+2m_2 m_0}(1), \gamma_2^l(n)} + \dots + k_{\gamma_1^{l+m_1 m_2 m_0}(1), \gamma_2^l(n)}) \\ &= \sum_{l=0}^{n_2-1} (k_{\gamma_1^{l+m_0}(1), \gamma_2^l(n)} + k_{\gamma_1^{l+2m_0}(1), \gamma_2^l(n)} + \dots + k_{\gamma_1^{l+m_1 m_0}(1), \gamma_2^l(n)}) \\ &= k_{\gamma_1^{m_0}(1), n} + k_{\gamma_1^{2m_0}(1), n} + \dots + k_{\gamma_1^{m_1 m_0}(1), n}. \end{aligned} \tag{10}$$

In the last step, we used the fact that only the last column of B_{12} is nonzero. It is known that the congruence $\xi x \equiv \eta \pmod{n_1}$ is soluble in integer x if and only if the greatest common divisor of ξ and n_1 divides η (e.g. see [13, Theorem 57]). Hence the congruence $m_0 x \equiv n_1 - 1 \pmod{n_1}$ is not soluble in integer x since m_0 cannot divide $m_0 m_1 - 1$. That is, $\gamma_1^{x m_0}(1) \neq n_1$ for all integers x . This shows that the sum in Equation (10) does not include $k_{n_1 n}$. Consequently, $a_{1n} = 0$ since every entry of B_{12} except $b_{n_1 n}$ is zero (see (H2)).

Let $y_{n_2}^*$ be the y_{n_2} -coordinate of F^{n_2} . Then we have

$$\left. \frac{\dot{x}_1}{x_1} \right|_{F^{n_2}} = s_1 + a_{1n} y_{n_2}^* = s_1 > 0.$$

This completes the proof. ■

This theorem shows that, independent of the parameters, there exists a well-timed prey-cohort that can initially increase its population density. In the rest of this section, by investigating the global dynamics of Equation (4)_H, we consider the fate of the system after the prey invasion. Since it is hard to obtain a general result concerning the global dynamics of Equation (4)_H, we focus on the specific case $n_1 = n_2 = 2$. In this case, the age-specific interaction matrix A is constructed as follows. Since $n_1 = n_2 = 2$, the permutation matrix P is

$$P = \begin{pmatrix} 0 & 1 & 0 & 0 \\ 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 \\ 0 & 0 & 1 & 0 \end{pmatrix}.$$

We see that $\sqrt{\sigma_1(0)\sigma_2(0)}$ and $\sqrt{\tau_1(0)\tau_2(0)}$ are the dominant eigenvalues of $L_{n_1}[\sigma_1(0), \sigma_2(0)]$ and $L_{n_2}[\tau_1(0), \tau_2(0)]$, respectively. The following vectors are positive right eigenvectors associated

of $\dot{x}_1/x_1|_{F^1} = \dot{x}_2/x_2|_{F^2}$:

$$\frac{\dot{x}_1}{x_1} \Big|_{F^1} = \frac{\dot{x}_2}{x_2} \Big|_{F^2} = s_1 - \frac{\alpha}{c_3} s_2 \begin{cases} > 0 \text{ (I)}, \\ < 0 \text{ (II)}. \end{cases}$$

In case (I), all prey-cohorts can invade both F^1 and F^2 , but in case (II), the prey-cohort x_1 (resp. x_2) cannot invade F^1 (resp. F^2).

7.1. Equilibria

The origin $\mathbf{0}$ is a trivial equilibrium point. As mentioned in Section 4, each axis has a unique positive equilibrium point. Since $s_1 > 0$ and $c_1 < c_2$ are assumed, the face $y_1 = y_2 = 0$ has a unique positive equilibrium point

$$F_{12} := \left(\frac{s_1}{c_1 + c_2}, \frac{s_1}{c_1 + c_2}, 0, 0 \right)^T.$$

Similarly, since $s_2 > 0$ and $c_3 < c_4$, the face $x_1 = x_2 = 0$ has a unique positive equilibrium point

$$F^{12} := \left(0, 0, \frac{s_2}{c_3 + c_4}, \frac{s_2}{c_3 + c_4} \right)^T.$$

Since the prey x_1 and the predator y_2 (resp. the prey x_2 and the predator y_1) do not interact, the face $x_2 = y_1 = 0$ (resp. $x_1 = y_2 = 0$) has a unique positive equilibrium point

$$F_1^2 := \left(\frac{s_1}{c_1}, 0, 0, \frac{s_2}{c_3} \right)^T \quad \left(\text{resp. } F_2^1 := \left(0, \frac{s_1}{c_1}, \frac{s_2}{c_3}, 0 \right)^T \right).$$

Note that $\mathbf{0}, F_1, F_2, F^1, F^2, F_{12}, F^{12}, F_1^2, F_2^1$ always uniquely exist. Equation (4)_H is reduced to a Lotka–Volterra predator–prey system on the faces $x_1 = y_1 = 0$ and $x_2 = y_2 = 0$. Therefore, the face $x_2 = y_2 = 0$ (resp. $x_1 = y_1 = 0$) has a positive equilibrium point

$$F_1^1 := \left(\frac{c_3 s_1 - \alpha s_2}{\alpha \beta + c_1 c_3}, 0, \frac{\beta s_1 + c_1 s_2}{\alpha \beta + c_1 c_3}, 0 \right)^T \quad \left(\text{resp. } F_2^2 := \left(0, \frac{c_3 s_1 - \alpha s_2}{\alpha \beta + c_1 c_3}, 0, \frac{\beta s_1 + c_1 s_2}{\alpha \beta + c_1 c_3} \right)^T \right)$$

if and only if (I) is satisfied, and F_1^1 (resp. F_2^2) is a unique positive equilibrium point of the face $x_2 = y_2 = 0$ (resp. $x_1 = y_1 = 0$) (see Lemma A.1).

The regions (I) and (II) are further subdivided into four regions as shown in Tables 1 and 2, respectively.

Let F_1^{12} (resp. F_2^{12}) be a positive equilibrium point of the face $x_2 = 0$ (resp. $x_1 = 0$). Then the following proposition holds.

PROPOSITION 7.2 F_1^{12} and F_2^{12} uniquely exist if (I-i), (I-ii), (II-ii) or (II-iii) holds. F_1^{12} and F_2^{12} do not exist if (I-iii), (I-iv), (II-i) or (II-iv) holds.

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Table 1. Definition of the parameter regions (I-i), (I-ii), (I-iii) and (I-iv).

	(I-i)	(I-ii)	(I-iii)	(I-iv)
$\frac{\dot{x}_1}{x_1} \Big _{F_1} = \frac{\dot{x}_2}{x_2} \Big _{F_2} = s_1 - \frac{\alpha}{c_3} s_2$	+	+	+	+
$\frac{\dot{x}_1}{x_1} \Big _{F_2} = \frac{\dot{x}_2}{x_2} \Big _{F_1} = \frac{\{\alpha\beta - (c_2 - c_1)c_3\}s_1 + \alpha c_2 s_2}{c_1 c_3 + \alpha\beta}$	-	+	-	+
$\frac{\dot{y}_1}{y_1} \Big _{F_1} = \frac{\dot{y}_2}{y_2} \Big _{F_2} = \frac{\beta}{c_1} s_1 - \frac{c_4 - c_3}{c_3} s_2$	-	-	+	+

Table 2. Definition of the parameter regions (II-i), (II-ii), (II-iii) and (II-iv).

	(II-i)	(II-ii)	(II-iii)	(II-iv)
$\frac{\dot{x}_1}{x_1} \Big _{F_1} = \frac{\dot{x}_2}{x_2} \Big _{F_2} = s_1 - \frac{\alpha}{c_3} s_2$	-	-	-	-
$\frac{\dot{x}_1}{x_1} \Big _{F_{12}} = \frac{\dot{x}_2}{x_2} \Big _{F_{12}} = s_1 - \frac{\alpha}{c_3 + c_4} s_2$	-	+	-	+
$\frac{\dot{y}_1}{y_1} \Big _{F_1} = \frac{\dot{y}_2}{y_2} \Big _{F_2} = \frac{\beta}{c_1} s_1 - \frac{c_4 - c_3}{c_3} s_2$	-	-	+	+

Proof By Lemma 3.2, the faces $x_1 = 0$ and $x_2 = 0$ have the same dynamics. Hence, we focus on the face $x_1 = 0$. Let $F_2^{12} = (0, x_2^*, y_1^*, y_2^*)^T$. Then it satisfies

$$\begin{aligned} s_1 - c_1 x_2^* - \alpha y_2^* &= 0, \\ s_2 - c_3 y_1^* - c_4 y_2^* &= 0, \\ s_2 + \beta x_2^* - c_4 y_1^* - c_3 y_2^* &= 0. \end{aligned} \tag{12}$$

Since $c_4 > c_3$ holds, the second and the third equations of (12) give

$$\begin{aligned} y_1^* &= \frac{s_2(c_4 - c_3) + \beta c_4 x_2^*}{c_4^2 - c_3^2}, \\ y_2^* &= \frac{s_2(c_4 - c_3) - \beta c_3 x_2^*}{c_4^2 - c_3^2}. \end{aligned}$$

Removing y_2^* from the first equation of (12), we obtain

$$\{\alpha\beta c_3 - c_1(c_4^2 - c_3^2)\}x_2^* = -(c_4^2 - c_3^2) \frac{\dot{x}_1}{x_1} \Big|_{F_{12}}.$$

Note that $\alpha\beta c_3 - c_1(c_4^2 - c_3^2) < 0$ (resp. $\alpha\beta c_3 - c_1(c_4^2 - c_3^2) > 0$) if $\dot{x}_1/x_1|_{F_{12}} > 0$ and $\dot{y}_1/y_1|_{F_1} < 0$ (resp. $\dot{x}_1/x_1|_{F_{12}} < 0$ and $\dot{y}_1/y_1|_{F_1} > 0$). Hence, we see that if (I-i), (I-ii), (II-ii) or (II-iii) holds, then $\alpha\beta c_3 - c_1(c_4^2 - c_3^2) \neq 0$. Note that (I) implies $x_1/x_1|_{F_{12}} > 0$.

Suppose $\alpha\beta c_3 - c_1(c_4^2 - c_3^2) = 0$. Then $\dot{x}_1/x_1|_{F_{12}} = 0$ must hold for the existence of F_2^{12} . However, if (I) is satisfied, then $\dot{x}_1/x_1|_{F_{12}} > 0$, and if one of (II-i), (II-ii), (II-iii) and (II-iv) is satisfied, then $\dot{x}_1/x_1|_{F_{12}} \neq 0$. This implies that F_2^{12} does not exist if one of (I), (II-i), (II-ii), (II-iii) and (II-iv) is satisfied,

Suppose $\alpha\beta c_3 - c_1(c_4^2 - c_3^2) \neq 0$. Then Equation (12) has a unique solution

$$\begin{aligned} x_2^* &= \frac{-(c_4^2 - c_3^2)}{\alpha\beta c_3 - c_1(c_4^2 - c_3^2)} \frac{\dot{x}_1}{x_1} \Big|_{F_{12}}, \\ y_1^* &= \frac{1}{\alpha\beta c_3 - c_1(c_4^2 - c_3^2)} \left\{ -\beta(c_3 + c_4) \frac{\dot{x}_1}{x_1} \Big|_{F_{12}} + c_1 c_3 \frac{\dot{y}_1}{y_1} \Big|_{F_1^2} \right\}, \\ y_2^* &= \frac{c_1 c_3}{\alpha\beta c_3 - c_1(c_4^2 - c_3^2)} \frac{\dot{y}_1}{y_1} \Big|_{F_1^2}. \end{aligned}$$

From these equations, we see that x_2^* , y_1^* and y_2^* are positive if (I-i), (I-ii), (II-ii) or (II-iii) holds. Finally, we see that either x_2^* or y_2^* is negative if (I-iii), (I-iv), (II-i) or (II-iv) holds. ■

Let F_{12}^1 (resp. F_{12}^2) be a positive equilibrium point of the face $y_2 = 0$ (resp. $y_1 = 0$). Then the following proposition holds.

PROPOSITION 7.3 F_{12}^1 and F_{12}^2 uniquely exist if (I-i) or (I-iii) holds. F_{12}^1 and F_{12}^2 do not exist if (I-ii), (I-iv) or (II) holds.

Proof By Lemma 3.2, the faces $y_1 = 0$ and $y_2 = 0$ have the same dynamics. Hence we focus on the face $y_1 = 0$. Let $F_{12}^2 = (x_1^*, x_2^*, 0, y_2^*)^T$. Then it satisfies

$$\begin{aligned} s_1 - c_1 x_1^* - c_2 x_2^* &= 0, \\ s_1 - c_2 x_1^* - c_1 x_2^* - \alpha y_2^* &= 0, \\ s_2 + \beta x_2^* - c_3 y_2^* &= 0. \end{aligned} \tag{13}$$

Since $c_2 > c_1$ holds, the first and the second equations of (13) give

$$\begin{aligned} x_1^* &= \frac{s_1(c_2 - c_1) - \alpha c_2 y_2^*}{c_2^2 - c_1^2}, \\ x_2^* &= \frac{s_1(c_2 - c_1) + \alpha c_1 y_2^*}{c_2^2 - c_1^2}. \end{aligned}$$

Removing x_2^* from the third equation of (13), we obtain

$$\{\alpha\beta c_1 - (c_2^2 - c_1^2)c_3\}y_2^* = -(c_2 - c_1)\{\beta s_1 + (c_1 + c_2)s_2\} < 0.$$

Hence if $\alpha\beta c_1 - (c_2^2 - c_1^2)c_3 \geq 0$, then Equation (13) has no positive solutions. If $\alpha\beta c_1 - (c_2^2 - c_1^2)c_3 < 0$, then Equation (13) has a unique solution

$$\begin{aligned} x_1^* &= \frac{\{\alpha\beta - (c_2 - c_1)c_3\}s_1 + \alpha c_2 s_2}{\alpha\beta c_1 - (c_2^2 - c_1^2)c_3} \left(= \frac{c_1 c_3 + \alpha\beta}{\alpha\beta c_1 - (c_2^2 - c_1^2)c_3} \frac{\dot{x}_1}{x_1} \Big|_{F_2^2} \right), \\ x_2^* &= \frac{-(c_2 - c_1)c_3 s_1 - \alpha c_1 s_2}{\alpha\beta c_1 - (c_2^2 - c_1^2)c_3} > 0, \\ y_2^* &= \frac{-(c_2 - c_1)\{\beta s_1 + (c_1 + c_2)s_2\}}{\alpha\beta c_1 - (c_2^2 - c_1^2)c_3} > 0. \end{aligned}$$

From these observations, we see that F_{12}^2 exists if (I-i) or (I-iii) holds since $\dot{x}_1/x_1|_{F_2^2} < 0$ implies $\alpha\beta c_1 - (c_2^2 - c_1^2)c_3 < 0$. In fact, if $\dot{x}_1/x_1|_{F_2^2} < 0$ holds, then $\alpha\beta - (c_2 - c_1)c_3 < 0$ holds, and the

assumption $c_2 > c_1$ leads to $\alpha\beta c_1 - (c_2^2 - c_1^2)c_3 < 0$. If (I-ii) or (I-iv) holds (i.e. $\dot{x}_1/x_1|_{F_2^2} > 0$), then $\{\alpha\beta - (c_2 - c_1)c_3\}s_1 + \alpha c_2 s_2 > 0$ and hence F_{12}^2 does not exist. Furthermore (II) implies $\{\alpha\beta - (c_2 - c_1)c_3\}s_1 + \alpha c_2 s_2 > 0$. Hence F_{12}^2 does not exist if (II) holds. ■

Let F_{12}^{12} be a positive equilibrium point of the full system. Then the following proposition holds.

PROPOSITION 7.4 F_{12}^{12} is always unique. F_{12}^{12} exist if and only if $\dot{x}_1/x_1|_{F^{12}} = \dot{x}_2/x_2|_{F^{12}} > 0$.

Proof Since $\det A = \alpha^2\beta^2 + 2\alpha\beta(c_1c_3 + c_2c_4) + (c_1^2 - c_2^2)(c_3^2 - c_4^2) > 0$, F_{12}^{12} is always unique. As mentioned in Section 5, the dynamics of Equation (4)_H on the forward invariant set \mathfrak{M} obeys Equation (8). Hence if Equation (8) has a positive equilibrium point, then F_{12}^{12} exists. Conversely, if F_{12}^{12} exists, then $F_{12}^{12} \in \mathfrak{M}$. Otherwise, by Lemma 3.2, there exist multiple positive equilibrium points. Equation (8) has a positive equilibrium point if and only if $\dot{x}_1/x_1|_{F^{12}} = \dot{x}_2/x_2|_{F^{12}} > 0$ (see Lemma A.1). ■

7.2. Stability of the equilibria

The origin $\mathbf{0}$ is clearly unstable and hyperbolic since $s_1 > 0$ and $s_2 > 0$. Stability conditions of the other equilibria are given below.

PROPOSITION 7.5 F_1 and F_2 are always unstable and hyperbolic.

Proof By Lemma 3.2, F_1 and F_2 have the same stability. Hence we focus on the stability of F_1 . The Jacobi matrix evaluated at F_1 is given by

$$J(F_1) = \begin{pmatrix} -s_1 & \bullet & \bullet & \bullet \\ 0 & -\frac{c_2 - c_1}{c_1}s_1 & 0 & 0 \\ 0 & 0 & \frac{\beta}{c_1}s_1 + s_2 & 0 \\ 0 & 0 & 0 & s_2 \end{pmatrix},$$

where \bullet denotes an arbitrary number. Hence F_1 is unstable and hyperbolic. ■

PROPOSITION 7.6 F^1 and F^2 are always unstable. F^1 and F^2 are hyperbolic if (I) or (II) holds.

Proof By Lemma 3.2, F^1 and F^2 have the same stability. Hence we focus on the stability of F^1 . The Jacobi matrix evaluated at F^1 is given by

$$J(F^1) = \begin{pmatrix} \dot{x}_1/x_1|_{F^1} & 0 & 0 & 0 \\ 0 & s_1 & 0 & 0 \\ \bullet & \bullet & -s_2 & \bullet \\ 0 & 0 & 0 & -\frac{c_4 - c_3}{c_3}s_2 \end{pmatrix},$$

where \bullet denotes an arbitrary number. Hence F^1 is always unstable, and if $\dot{x}_1/x_1|_{F^1} \neq 0$, then F^1 is hyperbolic. ■

PROPOSITION 7.7 F_{12} is always unstable and hyperbolic.

Proof Let $F_{12} = (x_1^*, x_2^*, 0, 0)^T$. Then the Jacobi matrix evaluated at F_{12} is given by

$$J(F_{12}) = \begin{pmatrix} -c_1x_1^* & -c_2x_1^* & \bullet & \bullet \\ -c_2x_2^* & -c_1x_2^* & \bullet & \bullet \\ 0 & 0 & \dot{y}_1/y_1|_{F_{12}} & 0 \\ 0 & 0 & 0 & \dot{y}_2/y_2|_{F_{12}} \end{pmatrix},$$

where \bullet denotes an arbitrary number. Since $c_2 > c_1$, the upper left 2×2 submatrix of $J(F_{12})$ is hyperbolic. Moreover,

$$\frac{\dot{y}_1}{y_1} \Big|_{F_{12}} = \frac{\dot{y}_2}{y_2} \Big|_{F_{12}} = \frac{\beta}{c_1 + c_2} s_1 + s_2 > 0. \tag{14}$$

Hence F_{12} is hyperbolic and unstable. ■

PROPOSITION 7.8 F^{12} is always unstable. F^{12} is hyperbolic if (I), (II-i), (II-ii), (II-iii) or (II-iv) holds.

Proof Let $F^{12} = (0, 0, y_1^*, y_2^*)^T$. Then the Jacobi matrix evaluated at F^{12} is given by

$$J(F^{12}) = \begin{pmatrix} \dot{x}_1/x_1|_{F^{12}} & 0 & 0 & 0 \\ 0 & \dot{x}_2/x_2|_{F^{12}} & 0 & 0 \\ \bullet & \bullet & -c_3y_1^* & -c_4y_1^* \\ \bullet & \bullet & -c_4y_2^* & -c_3y_2^* \end{pmatrix},$$

where \bullet denotes an arbitrary number. Since $c_4 > c_3$, the lower right 2×2 submatrix of $J(F^{12})$ is hyperbolic. Hence F^{12} is hyperbolic if and only if $\dot{x}_1/x_1|_{F^{12}} = \dot{x}_2/x_2|_{F^{12}} \neq 0$. Since

$$\frac{\dot{x}_1}{x_1} \Big|_{F^1} = \frac{\dot{x}_2}{x_2} \Big|_{F^2} < \frac{\dot{x}_1}{x_1} \Big|_{F^{12}} = \frac{\dot{x}_2}{x_2} \Big|_{F^{12}}, \tag{15}$$

F^{12} is hyperbolic if (I), (II-i), (II-ii), (II-iii) or (II-iv) holds. $J(F^{12})$ is unstable since its lower right 2×2 submatrix is unstable. ■

PROPOSITION 7.9 F_1^1 and F_2^2 are asymptotically stable if (I-i) or (I-iii) holds. F_1^1 and F_2^2 are unstable if (I-ii) or (I-iv) holds. F_1^1 and F_2^2 are hyperbolic if (I-i), (I-ii), (I-iii) or (I-iv) holds.

Proof By Lemma 3.2 F_1^1 and F_2^2 have the same stability. Hence we focus on the stability of F_1^1 . Let $F_1^1 = (x_1^*, 0, y_1^*, 0)^T$. Then the Jacobi matrix evaluated at F_1^1 is given by

$$J(F_1^1) = \begin{pmatrix} -c_1x_1^* & \bullet & -\alpha x_1^* & \bullet \\ 0 & \dot{x}_2/x_2|_{F_1^1} & 0 & 0 \\ \beta y_1^* & \bullet & -c_3y_1^* & \bullet \\ 0 & 0 & 0 & \dot{y}_2/y_2|_{F_1^1} \end{pmatrix},$$

where \bullet denotes an arbitrary number. The principal 2×2 submatrix of $J(F_1^1)$ corresponding to x_1 and y_1 is stable. Moreover,

$$\frac{\dot{y}_2}{y_2} \Big|_{F_1^1} = s_2 - c_4y_1^* < s_2 + \beta x_1^* - c_3y_1^* = 0. \tag{16}$$

Hence F_1^1 is hyperbolic if and only if $\dot{x}_2/x_2|_{F_1^1} \neq 0$. Furthermore, F_1^1 is stable (resp. unstable) if $\dot{x}_2/x_2|_{F_1^1} < 0$ (resp. $\dot{x}_2/x_2|_{F_1^1} > 0$). ■

PROPOSITION 7.10 F_1^2 and F_2^1 are asymptotically stable if (I-i), (I-ii), (II-i) or (II-ii) holds. F_1^2 and F_2^1 are unstable if (I-iii), (I-iv), (II-iii) or (II-iv) holds. F_1^2 and F_2^1 are hyperbolic if (I-i), (I-ii), (I-iii), (I-iv), (II-i), (II-ii), (II-iii) or (II-iv) holds.

Proof By Lemma 3.2, F_1^2 and F_2^1 have the same stability. Hence we focus on the stability of F_1^2 . Let $F_1^2 = (x_1^*, 0, 0, y_2^*)^T$. Then the Jacobi matrix evaluated at F_1^2 is given by

$$J(F_1^2) = \begin{pmatrix} -c_1 x_1^* & \bullet & \bullet & 0 \\ 0 & \dot{x}_2/x_2|_{F_1^2} & 0 & 0 \\ 0 & 0 & \dot{y}_1/y_1|_{F_1^2} & 0 \\ 0 & \bullet & \bullet & -c_3 y_2^* \end{pmatrix},$$

where \bullet denotes an arbitrary number. Since

$$\left. \frac{\dot{x}_2}{x_2} \right|_{F_1^2} = -\frac{c_2 - c_1}{c_1} s_1 - \frac{\alpha}{c_3} s_2 < 0, \tag{17}$$

F_1^2 is hyperbolic if and only if $\dot{y}_1/y_1|_{F_1^2} \neq 0$. Furthermore, F_1^2 is stable (resp. unstable) if $\dot{y}_1/y_1|_{F_1^2} < 0$ (resp. $\dot{y}_1/y_1|_{F_1^2} > 0$). ■

PROPOSITION 7.11 F_1^{12} and F_2^{12} are unstable if (I-i), (I-ii) or (II-ii) holds.

Proof By Lemma 3.2, F_1^{12} and F_2^{12} have the same stability. Hence, we focus on the stability of F_2^{12} . Let $F_2^{12} = (0, x_2^*, y_1^*, y_2^*)^T$. Then the Jacobi matrix evaluated at F_2^{12} is given by

$$J(F_2^{12}) = \begin{pmatrix} \dot{x}_1/x_1|_{F_2^{12}} & 0 & 0 & 0 \\ \bullet & -c_1 x_2^* & 0 & -\alpha x_2^* \\ \bullet & 0 & -c_3 y_1^* & -c_4 y_1^* \\ \bullet & \beta y_2^* & -c_4 y_2^* & -c_3 y_2^* \end{pmatrix},$$

where \bullet denotes an arbitrary number. Let $\tilde{J}(F_2^{12})$ be the lower right 3×3 submatrix of $J(F_2^{12})$. Then $\tilde{J}(F_2^{12})$ is stable if and only if

$$\begin{aligned} \text{tr } \tilde{J}(F_2^{12}) &= -c_1 x_2^* - c_3 (y_1^* + y_2^*) < 0, \\ \det \tilde{J}(F_2^{12}) &= -\{\alpha \beta c_3 - c_1 (c_4^2 - c_3^2)\} x_2^* y_1^* y_2^* < 0, \\ \tilde{M}(F_2^{12}) \text{tr } \tilde{J}(F_2^{12}) - \det \tilde{J}(F_2^{12}) &= -c_1 \{c_1 c_3 y_1^* + (c_1 c_3 + \alpha \beta) y_2^*\} x_2^{*2} \\ &\quad - c_3 \{c_1 c_3 (y_1^* + y_2^*)^2 + \alpha \beta y_2^{*2}\} x_2^* \\ &\quad + c_3 (c_4^2 - c_3^2) y_1^* y_2^* (y_1^* + y_2^*) < 0, \end{aligned}$$

where $\tilde{M}(F_2^{12})$ is the sum of the three 2×2 principal minors of $\tilde{J}(F_2^{12})$. If (I-i), (I-ii) or (II-ii) holds, then

$$\left. \frac{\dot{x}_1}{x_1} \right|_{F_2^{12}} = s_1 - \frac{\alpha}{c_3 + c_4} s_2 > 0$$

and

$$\left. \frac{\dot{y}_1}{y_1} \right|_{F_2^{12}} = \frac{\beta}{c_1} s_1 - \frac{c_4 - c_3}{c_3} s_2 < 0.$$

Note that $\dot{x}_1/x_1|_{F_2^{12}} > \dot{x}_1/x_1|_{F_1^2}$. These inequalities lead to

$$\alpha \beta c_3 - c_1 (c_4^2 - c_3^2) < 0.$$

Hence $\det \tilde{J}(F_2^{12}) > 0$, which implies that $\tilde{J}(F_2^{12})$ and $J(F_2^{12})$ are unstable. ■

Note that $\dot{x}_2/x_2|_{F_1^{12}} = \dot{x}_1/x_1|_{F_1^{12}} < 0$ always holds. In fact, by the second and the third equations of (12), we have $y_2^* - y_1^* = -\beta x_2^*/(c_4 - c_3) < 0$, which shows that

$$\frac{\dot{x}_1}{x_1} \Big|_{F_1^{12}} = s_1 - c_2 x_2^* - \alpha y_1^* = (c_1 - c_2)x_2^* + \alpha(y_2^* - y_1^*) < 0,$$

where the first equation of (12) is used. F_1^{12} and F_2^{12} can be both stabilized and destabilized if (II-iii) holds. For instance, $\tilde{J}(F_2^{12})$ is stable if $(s_1, s_2, c_1, c_2, c_3, c_4, \alpha, \beta) = (1, 1, 1, 2, 1, 2, 6.5, 1.1)$ and is unstable if $(s_1, s_2, c_1, c_2, c_3, c_4, \alpha, \beta) = (1, 1, 1, 2, 1, 2, 1, 6.5, 1.25)$. In this unstable case, a numerical simulation with the initial condition $(x_1(0), x_2(0), y_1(0), y_2(0)) = (0, 0.8, 1.4, 0.6)$ produces a limit cycle. Furthermore, if $(s_1, s_2, c_1, c_2, c_3, c_4, \alpha, \beta) = (1, 1, 1, 2, 1, 2, 1, 6.5, 1.3)$, then $\tilde{J}(F_2^{12})$ is unstable and a heteroclinic orbit from F_2^1 to F^2 can be observed numerically.

PROPOSITION 7.12 F_{12}^1 and F_{12}^2 are unstable if (I-i) or (I-iii) holds.

Proof By Lemma 3.2, F_{12}^1 and F_{12}^2 have the same stability. Hence we focus on the stability of F_{12}^1 . Let $F_{12}^1 = (x_1^*, x_2^*, y_1^*, 0)^T$. Then the Jacobi matrix evaluated at F_{12}^1 is given by

$$J(F_{12}^1) = \begin{pmatrix} -c_1 x_1^* & -c_2 x_1^* & -\alpha x_1^* & \bullet \\ -c_2 x_2^* & -c_1 x_2^* & 0 & \bullet \\ \beta y_1^* & 0 & -c_3 y_1^* & \bullet \\ 0 & 0 & 0 & \dot{y}_2/y_2|_{F_{12}^1} \end{pmatrix}.$$

Let $\tilde{J}(F_{12}^1)$ be the upper left 3×3 submatrix of $J(F_{12}^1)$. Then $\tilde{J}(F_{12}^1)$ is stable if and only if $\text{tr} \tilde{J}(F_{12}^1) < 0$ and $\det \tilde{J}(F_{12}^1) < 0$ and $\tilde{M}(F_{12}^1) \text{tr} \tilde{J}(F_{12}^1) - \det \tilde{J}(F_{12}^1) < 0$, where $\tilde{M}(F_{12}^1)$ is the sum of the three 2×2 principal minors of $\tilde{J}(F_{12}^1)$. However,

$$\det \tilde{J}(F_{12}^1) = -\{\alpha\beta c_1 - (c_2^2 - c_1^2)c_3\}x_1^*x_2^*y_1^* > 0$$

if (I-i) or (I-iii) holds. In fact, if (I-i) or (I-iii) holds, then $\alpha\beta - (c_2 - c_1)c_3 < 0$ holds, and the assumption $c_2 > c_1$ leads to $\alpha\beta c_1 - (c_2^2 - c_1^2)c_3 < 0$. Hence $J(F_{12}^1)$ is unstable if (I-i) or (I-iii) holds. ■

PROPOSITION 7.13 F_{12}^{12} is always unstable.

Proof Let $J(F_{12}^{12})$ be the Jacobi matrix evaluated at $F_{12}^{12} = (x_1^*, x_2^*, y_1^*, y_2^*)^T$. Then the characteristic polynomial $|J(F_{12}^{12}) - \lambda I|$ is

$$\begin{aligned} &[\lambda^2 + \{(c_1 + c_2)x_1^* + (c_3 + c_4)y_1^*\}\lambda + (c_1 + c_2)(c_3 + c_4)x_1^*y_1^* + \alpha\beta x_1^*y_1^*] \\ &\times [\lambda^2 - \{(c_2 - c_1)x_1^* + (c_4 - c_3)y_1^*\}\lambda + (c_2 - c_1)(c_4 - c_3)x_1^*y_1^* + \alpha\beta x_1^*y_1^*], \end{aligned}$$

where we used the fact that $x_1^* = x_2^*$ and $y_1^* = y_2^*$. Note that $F_{12}^{12} \in \mathfrak{M}$. Since $(c_2 - c_1)x_1^* + (c_4 - c_3)y_1^* > 0$, $J(F_{12}^{12})$ has an eigenvalue with a positive real part. Hence F_{12}^{12} is always unstable. ■

The above results are summarized in Table 3. In cases (I-i), (I-ii), (I-iii), (II-i) and (II-ii), the system always has an asymptotically stable boundary equilibrium point where both species have a missing cohort. Hence, in such cases, the system is not permanent.

Table 3. The sets of asymptotically stable equilibria.

	(I)	(II)
(i)	$\{F_1^1, F_2^2, F_2^1, F_1^2\}$	$\{F_1^2, F_2^1\}$
(ii)	$\{F_2^1, F_1^2\}$	$\{F_1^2, F_2^1\}$
(iii)	$\{F_1^1, F_2^2\}$	$\{F_1^{12}, F_2^{12}\}$ or \emptyset
(iv)	\emptyset	\emptyset

7.3. Nonequilibrium dynamics

In this subsection, we are interested in the global dynamics of (4)_H with $n_1 = n_2 = 2$. In cases (I-i), (I-ii), (I-iii), (II-i) and (II-ii), the system always has an asymptotically stable boundary equilibrium point where both species have a missing cohort (see Table 3). In contrast to these cases, we can show that all cohorts can coexist in cases (I-iv) and (II-iv).

THEOREM 7.14 *If (I-iv) holds, then Equation (4)_H with $n_1 = n_2 = 2$ has a heteroclinic cycle*

$$\Gamma_1 : F_1^1 \rightarrow F_2^1 \rightarrow F_2^2 \rightarrow F_1^2 \rightarrow F_1^1.$$

(a) Γ_1 is asymptotically stable if

$$\begin{aligned} &\beta c_3 \{ \alpha \beta - (c_2 - c_1)(c_3 + c_4) \} s_1^2 + 2 \alpha \beta (c_2 c_3 - c_1 c_4) s_1 s_2 \\ &+ \alpha c_1 \{ \alpha \beta - (c_1 + c_2)(c_4 - c_3) \} s_2^2 < 0. \end{aligned} \tag{18}$$

(b) *If the reversed inequality is satisfied, then the system is permanent.*

Proof In order to show that Γ_1 exists, we examine the dynamics on $\text{bd}\mathbb{R}_+^4$.

First, we construct a connecting orbit from F_2^1 to F_2^2 (see Figure 1(a)). Consider the dynamics on the face $x_1 = 0$. Let $\tilde{x}_1 = 0, \tilde{x}_2 > 0, \tilde{y}_1 > 0, \tilde{y}_2 > 0$. Since Equation (4)_H is dissipative, $\omega(\tilde{\mathbf{z}})$ is nonempty and compact. In case (I-iv), the face $x_1 = 0$ has no positive equilibrium points (see Proposition 7.2). It is known that if the Lotka–Volterra equation (A3) has no positive equilibrium points, then every ω -limit set is contained in $\text{bd}\mathbb{R}_+^n$ [16, Theorem 5.2.1]. Therefore,

$$\omega(\tilde{\mathbf{z}}) \subset \{ \mathbf{z} \in \mathbb{R}_+^4 : x_1 = 0, x_2 y_1 y_2 = 0 \}.$$

Furthermore, since the origin is repelling and the system is dissipative, there exist $\delta_1 > 0$ and $\delta_2 > 0$ such that

$$\omega(\tilde{\mathbf{z}}) \subset \{ \mathbf{z} \in \mathbb{R}_+^4 : x_1 = 0, x_2 y_1 y_2 = 0, \delta_1 < x_2 + y_1 + y_2 < \delta_2 \} =: S.$$

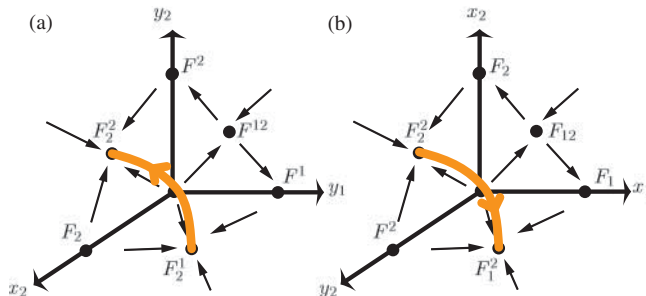


Figure 1. Phase portraits of the faces $x_1 = 0$ and $y_1 = 0$ for case (I-iv).

By the dynamical property of two-dimensional Lotka–Volterra equations (see Lemmas A.1 and A.2), we can draw the phase portrait on S as shown in Figure 1(a), and we see that $\omega(S) = \{F_2, F^1, F^2, F^{12}, F_2^1, F_2^2\}$. In the following, we show that $\omega(\tilde{\mathbf{z}}) = \{F_2^2\}$. Let $\hat{\mathbf{z}} \in \omega(\tilde{\mathbf{z}})$. Hence $\hat{\mathbf{z}} \in S$. Suppose that $\hat{\mathbf{z}}$ is not an equilibrium point. From Figure 1(a), we see that $\hat{\mathbf{z}}$ is attracted by an equilibrium point in S . Since S has no hetero/homoclinic cycles connecting equilibria, for small $\epsilon > 0$ and large $t_0 > 0$, we cannot construct an (ϵ, t_0) -chain in S connecting $\hat{\mathbf{z}}$ and itself (see Appendix 4 for the definition of an (ϵ, t_0) -chain). Since every ω -limit set of a dissipative system is internally chain transitive (see Theorem A.4), $\hat{\mathbf{z}} \notin \omega(\tilde{\mathbf{z}})$. Therefore, every element of $\omega(\tilde{\mathbf{z}})$ is an equilibrium point. Since $F_2, F^1, F^2, F^{12}, F_2^1$ and F_2^2 are isolated from each other, the internal chain transitivity of $\omega(\tilde{\mathbf{z}})$ implies that $\omega(\tilde{\mathbf{z}})$ is a singleton. Therefore, the forward orbit of $\tilde{\mathbf{z}}$ converges to an equilibrium point in $\omega(S)$. We see that $F_2, F^1, F^2, F^{12}, F_2^1$ and F_2^2 are hyperbolic and $\dot{y}_1/y_1|_{F_2^2} < 0, \dot{y}_2/y_2|_{F_2^2} > 0$ and $\dot{x}_2/x_2|_{F^{12}} > 0$ (see Equations (15) and (16)). By the stable manifold theorem, only F_2^2 has a stable manifold intersecting with a positive point of the face $x_1 = 0$. Hence we can conclude that $\omega(\tilde{\mathbf{z}}) = \{F_2^2\}$. Since F_2^1 has an unstable manifold intersecting with a positive point of the face $x_1 = 0$, there exists a connecting orbit from F_2^1 to F_2^2 .

Next, we construct a connecting orbit from F_2^2 to F_1^2 (see Figure 1(b)). Consider the dynamics on the face $y_1 = 0$. Let $\tilde{x}_1 > 0, \tilde{x}_2 > 0, \tilde{y}_1 = 0, \tilde{y}_2 > 0$. Since the subsystem $y_1 = 0$ has no positive equilibrium points (see Proposition 7.3), similarly to the above, there exist $\delta'_1 > 0$ and $\delta'_2 > 0$ such that

$$\omega(\tilde{\mathbf{z}}) \subset \{\mathbf{z} \in \mathbb{R}_+^4 : y_1 = 0, x_1x_2y_2 = 0, \delta'_1 < x_1 + x_2 + y_2 < \delta'_2\} =: S'.$$

The phase portrait on S' is shown in Figure 1(b). We see that $\omega(S') = \{F_1, F_2, F^2, F_{12}, F_1^1, F_2^2\}$. Similarly to the above, using the internal chain transitivity of $\omega(\tilde{\mathbf{z}})$, we can show that $\omega(\tilde{\mathbf{z}}) = \{F_1^2\}$. In fact, S' has no hetero/homoclinic cycles connecting equilibria, $F_1, F_2, F^2, F_{12}, F_1^1$ and F_2^2 are hyperbolic and $\dot{x}_2/x_2|_{F_1^2} < 0, \dot{x}_1/x_1|_{F_2^2} > 0$ and $\dot{y}_2/y_2|_{F_{12}} > 0$ hold (see Equations (14) and (17)). Furthermore, $\dot{x}_1/x_1|_{F_2^2} > 0$ shows that there exists a connecting orbit from F_2^2 to F_1^2 .

Since there exists a connecting orbit $F_2^1 \rightarrow F_2^2 \rightarrow F_1^2$, Lemma 3.2 shows that there also exists a connecting orbit $F_1^2 \rightarrow F_1^1 \rightarrow F_2^1$. Hence Γ_1 exists.

(a) Using the result in [15] (see also [16, Chapter 17]), we shall show that Γ_1 is asymptotically stable. We can make a characteristic matrix \mathcal{C}_1 of Γ_1 as follows:

$$\mathcal{C}_1 = \begin{pmatrix} \dot{x}_1/x_1|_{F_2^2} & \dot{x}_2/x_2|_{F_2^2} & \dot{y}_1/y_1|_{F_2^2} & \dot{y}_2/y_2|_{F_2^2} \\ \dot{x}_1/x_1|_{F_1^1} & \dot{x}_2/x_2|_{F_1^1} & \dot{y}_1/y_1|_{F_1^1} & \dot{y}_2/y_2|_{F_1^1} \\ \dot{x}_1/x_1|_{F_1^2} & \dot{x}_2/x_2|_{F_1^2} & \dot{y}_1/y_1|_{F_1^2} & \dot{y}_2/y_2|_{F_1^2} \\ \dot{x}_1/x_1|_{F_2^1} & \dot{x}_2/x_2|_{F_2^1} & \dot{y}_1/y_1|_{F_2^1} & \dot{y}_2/y_2|_{F_2^1} \end{pmatrix},$$

whose sign pattern is

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

Since each row and each column contain exactly one negative entry and one positive entry, the cycle Γ_1 is said to be *planer* in [15]. By [15, Corollary 2], the planer heteroclinic cycle Γ_1 is asymptotically stable if it is asymptotically stable within $\text{bd}\mathbb{R}_+^4$ and the product of the positive entries of \mathcal{C}_1 is less than the product of the negative entries of \mathcal{C}_1 in absolute value, i.e.

$$\frac{\dot{x}_2}{x_2} \Big|_{F_1^1} \times \frac{\dot{y}_2}{y_2} \Big|_{F_2^1} \times \frac{\dot{x}_1}{x_1} \Big|_{F_2^2} \times \frac{\dot{y}_1}{y_1} \Big|_{F_1^2} < \frac{\dot{y}_2}{y_2} \Big|_{F_1^1} \times \frac{\dot{x}_1}{x_1} \Big|_{F_2^1} \times \frac{\dot{y}_1}{y_1} \Big|_{F_2^2} \times \frac{\dot{x}_2}{x_2} \Big|_{F_1^2}.$$

By Lemma 3.2, this inequality is equivalent to

$$\frac{\dot{x}_2}{x_2} \Big|_{F_1^1} \times \frac{\dot{y}_1}{y_1} \Big|_{F_1^2} < \frac{\dot{y}_2}{y_2} \Big|_{F_1^1} \times \frac{\dot{x}_2}{x_2} \Big|_{F_1^2} \tag{19}$$

or

$$\frac{\{\alpha\beta - (c_2 - c_1)c_3\}s_1 + \alpha c_2 s_2}{c_1 c_3 + \alpha\beta} \left(\frac{\beta}{c_1} s_1 - \frac{c_4 - c_3}{c_3} s_2 \right) < \left(s_2 - c_4 \frac{\beta s_1 + c_1 s_2}{\alpha\beta + c_1 c_3} \right) \left(-\frac{c_2 - c_1}{c_1} s_1 - \frac{\alpha}{c_3} s_2 \right).$$

We see that this inequality is equivalent to Equation (18). The asymptotical stability of Γ_1 within $\text{bd}\mathbb{R}_+^4$ is proved in Appendix 5.

(b) It is known that the Lotka–Volterra equation (A3) is permanent if there exists a positive vector $\mathbf{p} = (p_1, p_2, \dots, p_n)^T > 0$ such that

$$\mathbf{p}^T(\mathbf{r} + A\mathbf{z}) > 0 \tag{20}$$

for all equilibrium points $\mathbf{z} \in \text{bd}\mathbb{R}_+^n$ (e.g. see [20] and [16, Exercise 13.6.3]). Our system has the following equilibrium points on $\text{bd}\mathbb{R}_+^4$:

$$\mathbf{0}, F_1, F_2, F^1, F^2, F_{12}, F^{12}, F_1^1, F_2^2, F_1^2, F_2^1.$$

Let $p_1 = p_2$ and $p_3 = p_4$. Then, by Lemma 3.2, our system is permanent if there exist $p_1 > 0$ and $p_3 > 0$ such that

$$\mathbf{0} : 2p_1 s_1 + 2p_3 s_2 > 0, \tag{21a}$$

$$F_1 : p_1(s_1 - c_2 x_1^*) + p_3(s_2 + \beta x_1^*) + p_3 s_2 > 0, \tag{21b}$$

$$F^1 : p_1(s_1 - \alpha y_1^*) + p_1 s_1 + p_3(s_2 - c_4 y_1^*) > 0, \tag{21c}$$

$$F_{12} : p_3(s_2 + \beta \hat{x}_1) + p_3(s_2 + \beta \hat{x}_2) > 0, \tag{21d}$$

$$F^{12} : p_1(s_1 - \alpha \hat{y}_1) + p_1(s_1 - \alpha \hat{y}_2) > 0, \tag{21e}$$

$$F_1^1 : p_1(s_1 - c_2 \tilde{x}_1) + p_3(s_2 - c_4 \tilde{y}_1) > 0, \tag{21f}$$

$$F_1^2 : p_1(s_1 - c_2 \bar{x}_1 - \alpha \bar{y}_2) + p_3(s_2 + \beta \bar{x}_1 - c_4 \bar{y}_2) > 0, \tag{21g}$$

where $F_1 = (x_1^*, 0, 0, 0)^T$, $F^1 = (0, 0, y_1^*, 0)^T$, $F_{12} = (\hat{x}_1, \hat{x}_2, 0, 0)^T$, $F^{12} = (0, 0, \hat{y}_1, \hat{y}_2)^T$, $F_1^1 = (\tilde{x}_1, 0, \tilde{y}_1, 0)^T$ and $F_1^2 = (\bar{x}_1, 0, 0, \bar{y}_2)^T$. It is clear that Equations (21a) and (21d) hold. Equation (21e) holds under the assumption (I-iv). Since $y_1^* < \tilde{y}_1$ and $s_1 - \alpha y_1^* > 0$, Equation (21f) implies Equation (21c). Furthermore, since $x_1^* = \bar{x}_1$, Equation (21g) implies Equation (21b). Therefore, it is sufficient to check Equations (21f) and (21g). Equations (21f) and (21g) can be expressed by

$$\begin{pmatrix} \dot{x}_2/x_2|_{F_1^1} & \dot{y}_2/y_2|_{F_1^1} \\ \dot{x}_2/x_2|_{F_1^2} & \dot{y}_1/y_1|_{F_1^2} \end{pmatrix} \begin{pmatrix} p_1 \\ p_3 \end{pmatrix} > \begin{pmatrix} 0 \\ 0 \end{pmatrix}.$$

This is fulfilled for some $p_1 > 0$ and $p_3 > 0$ if the reserved inequality of Equation (19) is fulfilled. ■

THEOREM 7.15 *If (II-iv) holds, then Equation (4)_H with $n_1 = n_2 = 2$ has a heteroclinic cycle*

$$\Gamma_2 : F^1 \rightarrow F_2^1 \rightarrow F^2 \rightarrow F_1^2 \rightarrow F^1.$$

(a) Γ_2 is asymptotically stable if

$$2\beta c_3 s_1 - \{\alpha\beta + (c_1 + c_2)(c_4 - c_3)\}s_2 < 0. \tag{22}$$

(b) *If the reversed inequality is satisfied, then the system is permanent.*

Proof By the same argument as in the proof of Theorem 7.14, we can show that there exists a connecting orbit from F_2^1 to F^2 . The phase portrait of the face $x_1 = 0$ is shown in Figure 2(a). Since x_1 and y_2 do not interact, the face $x_2 = y_1 = 0$ has a connecting orbit from F^2 to F_1^2 . The phase portrait of the face $x_2 = y_1 = 0$ is shown in Figure 2(b). Since there exists a connecting orbit $F_2^1 \rightarrow F^2 \rightarrow F_1^2$, Lemma 3.2 shows that there also exists a connecting orbit $F_1^2 \rightarrow F^1 \rightarrow F_2^1$. Hence Γ_2 exists.

(a) Using the result in [15] (see also [16, Chapter 17]), we shall show that Γ_2 is asymptotically stable. We can make a characteristic matrix \mathfrak{C}_2 of Γ_2 as follows:

$$\mathfrak{C}_2 = \begin{pmatrix} \dot{y}_2/y_2|_{F_2^1} & \dot{y}_1/y_1|_{F_2^1} & \dot{x}_2/x_2|_{F_2^1} & \dot{x}_1/x_1|_{F_2^1} \\ \dot{y}_2/y_2|_{F_1^2} & \dot{y}_1/y_1|_{F_1^2} & \dot{x}_2/x_2|_{F_1^2} & \dot{x}_1/x_1|_{F_1^2} \\ \dot{y}_2/y_2|_{F^1} & \dot{y}_1/y_1|_{F^1} & \dot{x}_2/x_2|_{F^1} & \dot{x}_1/x_1|_{F^1} \\ \dot{y}_2/y_2|_{F^2} & \dot{y}_1/y_1|_{F^2} & \dot{x}_2/x_2|_{F^2} & \dot{x}_1/x_1|_{F^2} \end{pmatrix},$$

whose sign pattern is

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

Since each row and each column contains exactly one positive entry, the cycle Γ_2 is said to be simple (but not planer) in [15]. By [15, Corollary 1], the simple heteroclinic cycle Γ_2 is asymptotically stable if it is asymptotically stable within $\text{bd}\mathbb{R}_+^4$, $\det \mathfrak{C}_2 \neq 0$ and at least one leading principal minor of \mathfrak{C}_2 is negative. By the sign pattern of \mathfrak{C}_2 , the 1×1 , 2×2 , 3×3 leading principal minors are positive. If we note that some entries of \mathfrak{C}_2 are identical, we have

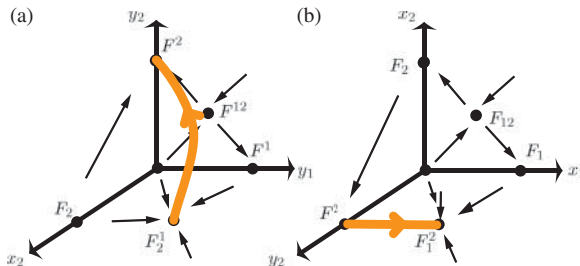


Figure 2. Phase portraits of the faces $x_1 = 0$ and $y_1 = 0$ for case (II-iv).

$$\det \mathcal{C}_2 = \left\{ \left(-\frac{\dot{x}_1}{x_1} \Big|_{F^1} + \frac{\dot{x}_2}{x_2} \Big|_{F^1} \right) \frac{\dot{y}_1}{y_1} \Big|_{F_1^2} + \frac{\dot{x}_2}{x_2} \Big|_{F_1^2} \frac{\dot{y}_2}{y_2} \Big|_{F^1} \right\} \\ \times \left\{ \left(\frac{\dot{x}_1}{x_1} \Big|_{F^1} + \frac{\dot{x}_2}{x_2} \Big|_{F^1} \right) \frac{\dot{y}_1}{y_1} \Big|_{F_1^2} - \frac{\dot{x}_2}{x_2} \Big|_{F_1^2} \frac{\dot{y}_2}{y_2} \Big|_{F^1} \right\}.$$

Since the first factor of the above equation is positive, $\det \mathcal{C}_2 < 0$ if and only if

$$\left(\frac{\dot{x}_1}{x_1} \Big|_{F^1} + \frac{\dot{x}_2}{x_2} \Big|_{F^1} \right) \frac{\dot{y}_1}{y_1} \Big|_{F_1^2} - \frac{\dot{x}_2}{x_2} \Big|_{F_1^2} \frac{\dot{y}_2}{y_2} \Big|_{F^1} < 0 \tag{23}$$

or

$$\left(2s_1 - \frac{\alpha}{c_3}s_2 \right) \left(\frac{\beta}{c_1}s_1 - \frac{c_4 - c_3}{c_3}s_2 \right) - \left(-\frac{c_2 - c_1}{c_1}s_1 - \frac{\alpha}{c_3}s_2 \right) \left(-\frac{c_4 - c_3}{c_3}s_2 \right) < 0,$$

which is equivalent to Equation (22). See Appendix 5 for the asymptotical stability of Γ_2 within $\text{bd}\mathbb{R}_+^4$.

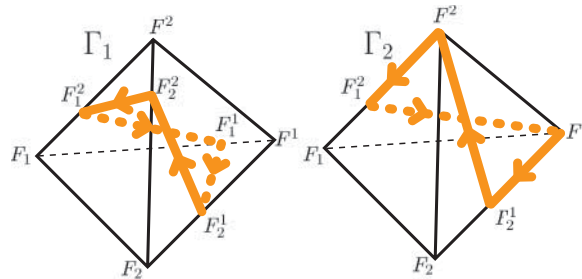


Figure 3. The behaviour of the heteroclinic cycles Γ_1 and Γ_2 .

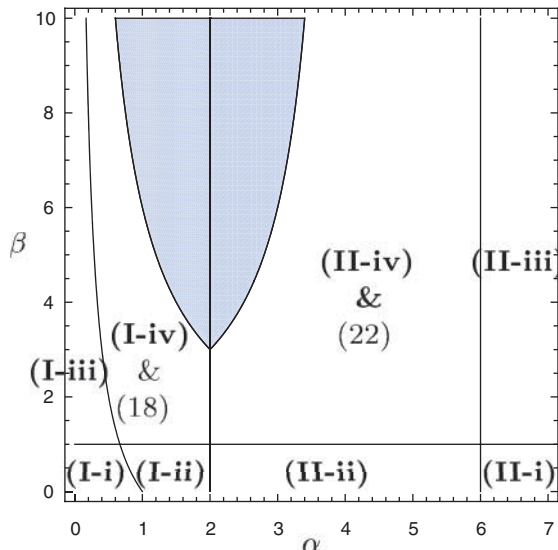


Figure 4. The (α, β) parameter plane. The other parameters are $s_1 = s_2 = 1, c_1 = 1, c_2 = 2, c_3 = 2, c_4 = 4$. In the hatched region, Equation (4) is permanent.

(b) We use the same method as in the proof of Theorem 7.14. Our system has the following equilibrium points on $\text{bd}\mathbb{R}_+^4$:

$$\mathbf{0}, F_1, F_2, F^1, F^2, F_{12}, F^{12}, F_1^2, F_2^1.$$

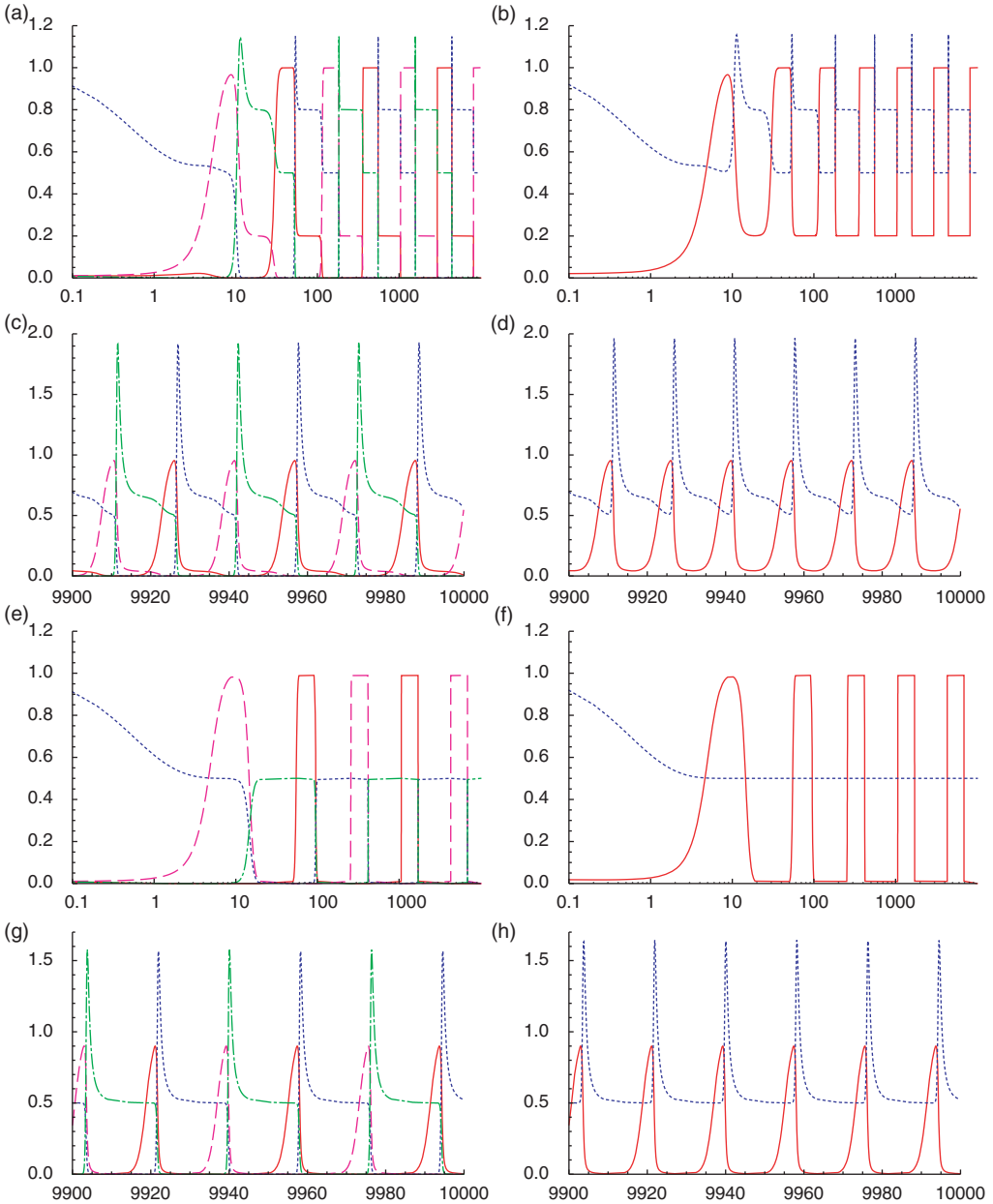


Figure 5. Numerical experiments of cases (I-iv) or (II-iv). In (a), (c), (e) and (g), the solid, the dashed, the dotted and the dot-dashed lines denote $x_1(t)$, $x_2(t)$, $y_1(t)$ and $y_2(t)$, respectively. In (b), (d), (f) and (h), the solid and the dotted lines denote $x_1(t) + x_2(t)$, respectively. The horizontal axes of (a), (b), (e) and (f) are scaled logarithmically. In (a) and (b), the solution converges to the heteroclinic cycle Γ_1 . In (e) and (f), the solution converges to the heteroclinic cycle Γ_2 . In (c), (d), (g) and (h), the solutions converge to periodic orbits. The parameters are chosen from the (α, β) parameter plane shown in Figure 4: $(\alpha, \beta) = (1, 3)$ for (a) and (b); $(\alpha, \beta) = (1.5, 8)$ for (c) and (d); $(\alpha, \beta) = (4, 2)$ for (e) and (f); $(\alpha, \beta) = (2.5, 9)$ for (g) and (h). The initial conditions are fixed at $(x_1(0), x_2(0), y_1(0), y_2(0)) = (0.01, 0.01, 1, 0.01)$.

Let $p_1 = p_2$ and $p_3 = p_4$. Then, by Lemma 3.2, our system is permanent if there exist $p_1 > 0$ and $p_3 > 0$ such that

$$\mathbf{0} : 2p_1s_1 + 2p_3s_2 > 0, \tag{24a}$$

$$F_1 : p_1(s_1 - c_2x_1^*) + p_3(s_2 + \beta x_1^*) + p_3s_2 > 0, \tag{24b}$$

$$F^1 : p_1(s_1 - \alpha y_1^*) + p_1s_1 + p_3(s_2 - c_4y_1^*) > 0, \tag{24c}$$

$$F_{12} : p_3(s_2 + \beta \hat{x}_1) + p_3(s_2 + \beta \hat{x}_2) > 0, \tag{24d}$$

$$F^{12} : p_1(s_1 - \alpha \hat{y}_1) + p_1(s_1 - \alpha \hat{y}_2) > 0, \tag{24e}$$

$$F_1^2 : p_1(s_1 - c_2\bar{x}_1 - \alpha\bar{y}_2) + p_3(s_2 + \beta\bar{x}_1 - c_4\bar{y}_2) > 0, \tag{24f}$$

where $F_1 = (x_1^*, 0, 0, 0)^T$, $F^1 = (0, 0, y_1^*, 0)^T$, $F_{12} = (\hat{x}_1, \hat{x}_2, 0, 0)^T$, $F^{12} = (0, 0, \hat{y}_1, \hat{y}_2)^T$ and $F_1^2 = (\bar{x}_1, 0, 0, \bar{y}_2)^T$. It is clear that Equations (24a) and (24d) hold. Equation (24e) holds under the assumption (II-iv). Furthermore, since $x_1^* = \bar{x}_1$, Equation (24f) implies Equation (24b). Therefore, it is sufficient to check Equations (24c) and (24f). Equations (24c) and (24f) can be expressed by

$$\begin{pmatrix} \dot{x}_1/x_1|_{F^1} + \dot{x}_2/x_2|_{F^1} & \dot{y}_2/y_2|_{F^1} \\ \dot{x}_2/x_2|_{F^2} & \dot{y}_1/y_1|_{F^2} \end{pmatrix} \begin{pmatrix} p_1 \\ p_3 \end{pmatrix} > \begin{pmatrix} 0 \\ 0 \end{pmatrix}.$$

Hence, the above inequality is fulfilled for some $p_1 > 0$ and $p_3 > 0$ if the reserved inequality of Equation (23) is fulfilled. ■

The behaviours of Γ_1 and Γ_2 are illustrated in Figure 3. Although Γ_1 approaches neither F^1 nor F^2 , Γ_2 approaches both of them. This implies that along Γ_2 the total population density of the prey approaches zero intermittently. Figure 4 shows the (α, β) parameter plane, in which the region satisfying Equation (18) or Equation (22) can be found. Numerical experiments of cases (I-iv) or (II-iv) are shown in Figure 5.

8. Concluding remark

Our aim was to provide mathematical evidences that prime periodicities are not advantageous for periodical cicadas even under periodic predation pressure. For this purpose, we studied an age-structured predator–prey model. Both prey and predator are assumed to be periodical in the sense of Bulmer [2]. The periods of the prey and the predator are denoted by n_1 and n_2 , respectively. We found that the dynamics of our age-structured model strongly depends on whether n_1 and n_2 are coprime. Theorem 6.2 shows that the periodical predator can resist the invasion of the periodical prey if n_1 and n_2 are coprime. On the other hand, Theorem 7.1 shows that if n_1 and n_2 are not coprime, then, with the help of a well-timed cohort of itself, the periodical prey can always invade the system with the periodical predator. This suggests that periodical predation pressure is deleterious to prime number periodical cicadas since their prime number periods are coprime with any shorter periods. Theorems 6.3, 7.14 and 7.15 show the outcome after the invasion of the periodical prey under periodic predation pressure. Theorem 6.3 shows that if n_1 and n_2 are coprime, then perfect periodicities are preserved in both populations even if the two species coexist. However, Theorems 7.14 and 7.15 show that if $n_1 = n_2 = 2$ (hence n_1 and n_2 are not coprime), then perfect periodicities can disappear and all cohorts can coexist.

Analogous behaviours to those observed in Theorem 7.15 are found by Kirlinger [21], who studied a four-dimensional Lotka–Volterra equation for two predator–prey pairs linked by inter-specific competition between the preys. In this system, she found an attractive heteroclinic cycle

$F_1 \rightarrow F_1^1 \rightarrow F_2 \rightarrow F_2^2 \rightarrow F_1$, which corresponds to Γ_2 if the role of prey and predators are exchanged. A sufficient condition for permanence is also provided. However, since predators are not self-supporting and interspecific competition between predators are absent in her system, we cannot simply apply her results to our Lotka–Volterra equation. Mylius and Diekmann [30] also found analogous behaviours in their three-dimensional discrete-time model for competition between annual and biennial populations. They assumed that the annual population in isolation has a stable 2-cycle. Under the assumption, they observed an attractive heteroclinic cycle connecting the 2-cycle of annuals. Due to this heteroclinic connection, successful invasion of a single cohort of biennials is inevitably followed by its extinction and re-establishment of the resident. They call this phenomenon resident strikes back. Furthermore, if the heteroclinic cycle is attractive in the full system, simultaneous invasion of two cohorts of biennials leads to repetition of invasion and extinction of biennials. Along Γ_2 in our system, we observe the similar behaviour.

Our model did not deal with an important respect considered by Webb [32]. In [32], instead of presuming that predators are periodical in the sense of Bulmer [2], he assumed that predators have fixed lengths of life cycles and have quasi-cycles, i.e. cycles that are damped. Under these assumption, he demonstrated that sustained oscillation appears if the damped oscillation of predators is periodically perturbed to mimic the periodical emergence of periodical cicadas. It is not clear whether such a resonance is still preserved even if quasi-cyclic predators dynamically interact with periodical cicadas. It is a future work to relax the assumption of perfect periodicities for predators.

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Appendix 1. Severe inter-class competition

In this appendix, we show that (H6) can be realized when inter-class competition is severe in each population.

Since the Lotka–Volterra equation (4) with Equation (5) is derived by taking the limit $h \rightarrow 0$, which implies $\mathcal{R}_0^1 \rightarrow 1$, it is reasonable to assume that the parameters satisfy the constraint $\sigma_1(0)\sigma_2(0) \cdots \sigma_{n_1}(0) = 1$. Then we note that the following equations hold:

$$\begin{aligned} \frac{d_2}{d_1} &= \sigma_1(0), \\ \frac{d_3}{d_1} &= \sigma_1(0)\sigma_2(0), \\ &\vdots \\ \frac{d_{n_1}}{d_1} &= \sigma_1(0)\sigma_2(0) \cdots \sigma_{n_1-1}(0). \end{aligned}$$

Define $\rho_l, l \in \{1, 2, \dots, n_1 - 1\}$, by

$$\begin{aligned} \rho_l &:= \frac{c_{1-l}}{c_1} = \frac{k_{1,1-l} + k_{2,2-l} + \cdots + k_{m,m-l}}{k_{11} + k_{22} + \cdots + k_{mm}} \\ &= \frac{(m/n_1)(k_{1+l,1} + k_{2+l,2} + \cdots + k_{n_1+l,n_1})}{(m/n_1)(k_{11} + k_{22} + \cdots + k_{n_1 n_1})} \\ &= \frac{b_{1+l,1}d_1 + b_{2+l,2}d_2 + \cdots + b_{n_1+l,n_1}d_{n_1}}{b_{11}d_1 + b_{22}d_2 + \cdots + b_{n_1 n_1}d_{n_1}} \\ &= \frac{b_{1+l,1} + b_{2+l,2}\sigma_1(0) + \cdots + b_{n_1+l,n_1}\sigma_1(0)\sigma_2(0) \cdots \sigma_{n_1-1}(0)}{b_{11} + b_{22}\sigma_1(0) + \cdots + b_{n_1 n_1}\sigma_1(0)\sigma_2(0) \cdots \sigma_{n_1-1}(0)}, \end{aligned}$$

where all subscripts are counted modulo n_1 and k_{ij} is the (i, j) -entry of $K = BD$. The denominator of ρ_l involves the intra-class competition coefficients b_{ii} of the prey while the numerator involves the inter-class competition coefficients $b_{ij}, i \neq j$, of the prey. The ratio ρ_l is introduced by Cushing [6] to measure the intensity of inter-class competition relative to the intensity of intra-class competition in a semelparous population. The ratio ρ_l measures the total effect that each

class i has on the survival (or reproduction) of the conspecific class $i + l \pmod{n_1}$. Since the condition that $c_l < c_i$ for all $l \in \{2, 3, \dots, n_1\}$ is equivalent to the condition that $\rho_l > 1$ for all $l \in \{1, 2, \dots, n_1 - 1\}$, F_i is stabilized in the subsystem $\mathbf{y} = \mathbf{0}$ if there is severe inter-class competition in the prey population. Similarly, we can show that F^j is stabilized in the subsystem $\mathbf{x} = \mathbf{0}$ if there is severe inter-class competition in the predator population.

Appendix 2. Two-dimensional Lotka–Volterra equations

In this appendix, we review some known results on two-dimensional Lotka–Volterra equations. Consider the following two-dimensional Lotka–Volterra predator–prey system:

$$\begin{aligned} \dot{x} &= x(s_1 - c_1x - \alpha y), \\ \dot{y} &= y(s_2 + \beta x - c_3y), \end{aligned} \tag{A1}$$

where $s_1, s_2, c_1, c_3, \alpha$ and β are positive. Then the following lemma holds.

LEMMA A.1 Consider Equation (A1).

- (a) If $s_1/\alpha > s_2/c_3$ holds, then there exists a positive equilibrium point that is globally asymptotically stable in $\{(x, y)^T \in \mathbb{R}^2 : x > 0, y > 0\}$.
- (b) If $s_1/\alpha \leq s_2/c_3$ holds, then there exist no positive equilibrium points and the boundary equilibrium point $(0, s_2/c_3)^T$ is globally asymptotically stable in $\{(x, y)^T \in \mathbb{R}^2 : x \geq 0, y > 0\}$.

Proof Equation (A1) has a positive equilibrium point if and only if

$$\begin{aligned} s_1 - c_1x^* - \alpha y^* &= 0, \\ s_2 + \beta x^* - c_3y^* &= 0 \end{aligned}$$

has a positive solution $(x^*, y^*)^T$. Hence Equation (A1) has a positive equilibrium point if and only if $s_1/\alpha > s_2/c_3$.

- (a) Suppose that $s_1/\alpha > s_2/c_3$ holds. Let $\Omega_1 := \{(x, y) \in \mathbb{R}^2 : x > 0, y > 0\}$ and define $V_1 : \Omega_1 \rightarrow \mathbb{R}$ by

$$V_1(x, y) := \beta(x^* \log x - x) + \alpha(y^* \log y - y).$$

Then the time-derivative of V_1 along a solution of Equation (A1) is

$$\dot{V}_1(x, y) = c_1\beta(x - x^*)^2 + c_3\alpha(y - y^*)^2.$$

This is positive for all $(x, y)^T \in \Omega_1$ with $(x, y)^T \neq (x^*, y^*)^T$. This implies that $(x^*, y^*)^T$ is globally asymptotically stable in Ω_1 .

- (b) Suppose that $s_1/\alpha \leq s_2/c_3$ holds. Let $\Omega_2 := \{(x, y) \in \mathbb{R}^2 : x \geq 0, y > 0\}$ and define $V_2 : \Omega_2 \rightarrow \mathbb{R}$ by

$$V_2(x, y) := -\beta x + \alpha \left(\frac{s_2}{c_3} \log y - y \right).$$

Then the time-derivative of V_2 along a solution of Equation (A1) is

$$\dot{V}_2(x, y) = c_1\beta x^2 + c_3\alpha \left(y - \frac{s_2}{c_3} \right)^2 - \beta x \left(s_1 - \alpha \frac{s_2}{c_3} \right).$$

This is positive for all $(x, y)^T \in \Omega_2$ with $(x, y)^T \neq (0, s_2/c_3)^T$. This implies that $(0, s_2/c_3)^T$ is globally asymptotically stable in Ω_2 . ■

Consider the following two-dimensional Lotka–Volterra competitive system:

$$\begin{aligned} \dot{x}_1 &= x_1(s_1 - c_1x_1 - c_2x_2), \\ \dot{x}_2 &= x_2(s_1 - c_2x_1 - c_1x_2), \end{aligned} \tag{A2}$$

where s_1, c_1 and c_2 are positive and $c_1 < c_2$ is assumed. Then the following lemma holds.

LEMMA A.2 Equation (A2) has a positive equilibrium point. Let $(x_1(t), x_2(t))$ be a solution of Equation (A2). Then

- (a) $(x_1(t), x_2(t)) \rightarrow (s_1/c_1, 0)$ as $t \rightarrow \infty$ if $x_1(0) > x_2(0) > 0$;
- (b) $(x_1(t), x_2(t)) \rightarrow (0, s_1/c_1)$ as $t \rightarrow \infty$ if $x_2(0) > x_1(0) > 0$;
- (c) $(x_1(t), x_2(t)) \rightarrow (s_1/(c_1 + c_2), s_1/(c_1 + c_2))$ as $t \rightarrow \infty$ if $x_2(0) = x_1(0) > 0$.

Proof It is easy to see that Equation (A2) has a positive equilibrium point

$$F_{12} := \left(\frac{s_1}{c_1 + c_2}, \frac{s_1}{c_1 + c_2} \right)^T.$$

Let $\mathfrak{M} := \{(x_1, x_2)^T \in \mathbb{R}_+^2 : x_1 = x_2\}$. Then \mathfrak{M} is forward invariant since

$$\frac{d}{dt} \begin{pmatrix} x_1 \\ x_2 \end{pmatrix} = \begin{pmatrix} x_1 \\ x_2 \end{pmatrix} (c_2 - c_1)(x_1 - x_2).$$

holds. If $(x_1, x_2)^T \in \mathfrak{M}$, then

$$\dot{x}_1 + \dot{x}_2 = (x_1 + x_2) \left\{ s_1 - \frac{c_1 + c_2}{2}(x_1 + x_2) \right\}$$

holds. Hence the dynamics on the line \mathfrak{M} obeys the logistic equation. The statement (c) is an immediate consequence of this observation.

Finally consider cases (a) and (b). We see that Equation (A2) is a competitive system in the sense that

$$\frac{\partial \dot{x}_1}{\partial x_2} \leq 0 \quad \text{and} \quad \frac{\partial \dot{x}_2}{\partial x_1} \leq 0$$

for all $(x_1, x_2)^T \in \mathbb{R}_+^2$. It is known that every solution of a competitive system converges an equilibrium point if the system is dissipative (e.g. see [16, Section 3.4]). By Lemma 5.3, Equation (A2) is dissipative. Hence every solution of Equation (A2) converges to an equilibrium point. By uniqueness of solutions, any orbit cannot cross the line \mathfrak{M} . Furthermore, we see that F_{12} is a saddle hyperbolic equilibrium point and the stable manifold of F_{12} is contained in \mathfrak{M} . By the stable manifold theorem, any orbit outside of \mathfrak{M} cannot converge to F_{12} . Since the origin $\mathbf{0}$ is a source, any nonzero orbit cannot converge to $\mathbf{0}$. From this observation, the statements (a) and (b) follow. ■

Appendix 3. Lotka–Volterra equations with some special structure

In this appendix, we derive a useful theorem for the Lotka–Volterra equation

$$\dot{z}_i = z_i(r_i + (A\mathbf{z})_i), \quad i = 1, 2, \dots, n, \tag{A3}$$

where $A = (a_{ij})$, $a_{ij} \in \mathbb{R}$ and $r_i \in \mathbb{R}$. We decompose n species into $N \geq 1$ groups. Let $n_1, n_2, \dots, n_N \geq 1$ and $n_1 + n_2 + \dots + n_N = n$. Define I_1, I_2, \dots, I_N by

$$\begin{aligned} I_1 &= \{1, 2, \dots, n_1\}, \\ I_2 &= \{n_1 + 1, n_1 + 2, \dots, n_1 + n_2\}, \\ &\vdots \\ I_N &= \{n_1 + n_2 + \dots + n_{N-1} + 1, n_1 + n_2 + \dots + n_{N-1} + 2, \dots, n\}. \end{aligned}$$

Define the reduced population vector $\mathbf{Z}(\mathbf{z}) = (Z_1(\mathbf{z}), Z_2(\mathbf{z}), \dots, Z_N(\mathbf{z}))^T$ by

$$Z_i(\mathbf{z}) := \sum_{j \in I_i} z_j, \quad i = 1, 2, \dots, N.$$

According to the index sets I_1, I_2, \dots, I_N , we decompose the interaction matrix A into N^2 blocks as follows:

$$A = \begin{pmatrix} A_{11} & \cdots & A_{1N} \\ \vdots & & \vdots \\ A_{N1} & \cdots & A_{NN} \end{pmatrix},$$

where A_{ij} is an $n_i \times n_j$ matrix. We assume that the interaction matrix A and the intrinsic growth rate r_i satisfy the following assumptions:

- For each $i, j \in \{1, 2, \dots, N\}$ with $i \neq j$, there exists a constant $\bar{a}_{ij} \in \mathbb{R}$ such that $A_{ij} = \bar{a}_{ij}E$, where E is defined by Equation (9);
- For each $i \in \{1, 2, \dots, N\}$, there exists a constant $s_i \in \mathbb{R}$ such that $r_j = s_i$ for all $j \in I_i$.

Define $N \times N$ matrix $\bar{A} := (\bar{a}_{ij})$. Under these assumptions we obtain the following theorem.

THEOREM A.3 *Let $\mathbf{z}(t)$ be a solution of Equation (A3). Suppose that Equation (A3) is dissipative. If there exists an $i \in \{1, 2, \dots, N\}$ such that $s_i + (\bar{A}\hat{\mathbf{z}})_i > 0$ for each equilibrium point $\hat{\mathbf{z}}$ of Equation (A3) with $Z_i(\hat{\mathbf{z}}) = 0$, then there exists a constant $\delta > 0$ such that $\liminf_{t \rightarrow \infty} Z_i(\mathbf{z}(t)) > \delta$ for all $\mathbf{z}(0) \in \mathbb{R}_+^n$ with $Z_i(\mathbf{z}(0)) > 0$.*

Proof The proof is almost parallel to the one for [17, Lemma 4.4].

Let $S = \{\mathbf{z} \in \mathbb{R}_+^n : Z_i(\mathbf{z}) = 0\}$. Since Equation (A3) is dissipative, a theorem of average Liapunov functions [19, Theorem 2.5] ensures that the conclusion of the theorem follows if there exists a continuously differentiable function $V : \mathbb{R}_+^n \rightarrow \mathbb{R}_+$ such that

- (i) $V(\mathbf{z}) = 0$ if and only if $\mathbf{z} \in S$;
- (ii) there exists a continuous function $\psi : \mathbb{R}_+^n \rightarrow \mathbb{R}$ such that $\dot{V}(\mathbf{z}) \geq V(\mathbf{z})\psi(\mathbf{z})$ for all $\mathbf{z} \in \mathbb{R}_+^n$;
- (iii) for any $\mathbf{z} \in \overline{\omega(S)}$ there exists a $T > 0$ satisfying

$$\int_0^T \psi(\mathbf{z}(t)) dt > 0, \tag{A4}$$

where $\mathbf{z}(t)$ is a solution of Equation (A3) with $\mathbf{z}(0) = \mathbf{z}$ and $\overline{\omega(S)}$ is the closure of $\omega(S)$.

Define $V : \mathbb{R}_+^n \rightarrow \mathbb{R}_+$ by $V(\mathbf{z}) = Z_i(\mathbf{z})$. Then V is continuously differentiable and satisfies (i). The time-derivative of V along a solution of Equation (A3) satisfies $\dot{V}(\mathbf{z}) \geq V(\mathbf{z})\psi(\mathbf{z})$ for the continuous function $\psi(\mathbf{z}) = \min_{j \in I_i} \{s_j + (A\mathbf{z})_j\}$. Hence the condition (ii) is satisfied. Note that $\psi(\mathbf{z}) = s_i + (\bar{A}\mathbf{z})_i$ if $Z_i(\mathbf{z}) = 0$. Let us check the condition (iii). We first claim that if Equation (A4) holds for every $\mathbf{z} \in \omega(\mathbf{y})$, then Equation (A4) also holds for the solution starting at \mathbf{y} . For $h > 0$ and $T > 0$, define

$$U(h, T) := \left\{ \mathbf{z} \in \mathbb{R}_+^n : \int_0^T s_i + (\bar{A}\mathbf{z}(t))_i dt > h \right\}.$$

Then $U(h, T)$ is open in \mathbb{R}_+^n . Let $\mathbf{y} \in S$ and $\mathbf{y}(t)$ be a solution with $\mathbf{y}(0) = \mathbf{y}$. Suppose that Equation A4 holds for every $\mathbf{z} \in \omega(\mathbf{y})$. 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 $\bar{h} > 0$ and $T_1, T_2, \dots, T_m > 0$ such that

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

Note that $U(h_1, T) \supset U(h_2, T)$ if $h_1 \leq h_2$. Since W is a neighbourhood 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 $t_1, t_2, \dots, t_l \in \{T_1, T_2, \dots, T_m\}$, the following inequality holds:

$$\int_0^{t_0} s_i + (\bar{A}\mathbf{z}(t))_i dt + \bar{h}l > 0.$$

This implies that the integral of Equation (A4) for \mathbf{y} becomes positive at $t = \sum_{j=0}^l t_j$.

Let $k(\mathbf{z})$ be the number of positive components of \mathbf{z} . By induction on k , we show that Equation (A4) holds for all $\mathbf{z} \in S$. If $k(\mathbf{z}) = 0$ (thus $\mathbf{z} = \mathbf{0}$), then Equation (A4) holds since $s_i > 0$. Suppose that Equation (A4) holds if $0 \leq k(\mathbf{z}) \leq m - 1$. Let $\mathbf{z} \in S$ with $k(\mathbf{z}) = m$. Then (I): $0 \leq k(\mathbf{y}) \leq m - 1$ holds for every $\mathbf{y} \in \omega(\mathbf{z})$ or (II): there exists a point $\mathbf{y} \in \omega(\mathbf{z})$ with $k(\mathbf{y}) = m$. In case (I), the induction hypothesis and the claim proved above yields Equation (A4). In case (II), the averaging property of solutions of Equation (A3) implies that there exists a sequence $T_j \rightarrow \infty$ and an equilibrium point $\hat{\mathbf{z}} \in S$ such that

$$\lim_{j \rightarrow \infty} \frac{1}{T_j} \int_0^{T_j} \mathbf{z}(t) dt = \hat{\mathbf{z}}$$

(e.g. see [16, Theorem 5.2.3]). Therefore, by assumption,

$$\frac{1}{T_j} \int_0^{T_j} s_i + (\bar{A}\mathbf{z}(t))_i dt > 0$$

holds for j sufficiently large. This implies that Equation (A4) holds. ■

Appendix 4. Internally chain transitive set

Let X be a metric space with metric d and $\phi : \mathbb{R}_+ \times X \rightarrow X$, $t \geq 0$, be a continuous semiflow. A nonempty invariant set $M \subset X$ for ϕ (i.e. $\phi(t, M) = M$, $t \geq 0$) is said to be internally chain transitive if for any $a, b \in M$ and any $\epsilon > 0$,

$t_0 > 0$, there is a finite sequence $\{x_1 = a, x_2, \dots, x_{m-1}, x_m = b; t_1, \dots, t_{m-1}\}$ with $x_i \in M$ and $t_i \geq t_0$, $1 \leq i \leq m - 1$, such that $d(\phi(t_i, x_i), x_{i+1}) < \epsilon$ for all $1 \leq i \leq m - 1$. The sequence $\{x_1, x_2, \dots, x_m; t_1, \dots, t_{m-1}\}$ is called an (ϵ, t_0) -chain in M connecting a and b .

THEOREM A.4 [14, Lemma 2.1'] *The ω -limit set of any precompact orbit is internally chain transitive.*

Appendix 5. Asymptotical stability of Γ_1 and Γ_2 with in $\text{bd}\mathbb{R}_+^4$

In this section, we show that the heteroclinic cycles Γ_1 and Γ_2 are asymptotically stable within $\text{bd}\mathbb{R}_+^4$. Before the proofs, we introduce useful notation. Let $d(\mathbf{z}_1, \mathbf{z}_2)$ be the Euclidean metric between $\mathbf{z}_1, \mathbf{z}_2 \in \mathbb{R}_+^n$. For $\mathbf{z} \in \mathbb{R}_+^n$ and $\epsilon > 0$, define $B_\epsilon(\mathbf{z}) = \{\mathbf{z}' \in \mathbb{R}_+^n : d(\mathbf{z}', \mathbf{z}) < \epsilon\}$ and $S_\epsilon(\mathbf{z}) = \{\mathbf{z}' \in \mathbb{R}_+^n : d(\mathbf{z}, \mathbf{z}') = \epsilon\}$. For $\mathbf{z} \in \mathbb{R}_+^n$ and $M \subset \mathbb{R}_+^n$, define $d(\mathbf{z}, M) = \inf\{d(\mathbf{z}, \mathbf{z}') : \mathbf{z}' \in M\}$. For $M \subset \mathbb{R}_+^n$ and $\epsilon > 0$, define $B_\epsilon(M) = \{\mathbf{z} \in \mathbb{R}_+^n : d(\mathbf{z}, M) < \epsilon\}$ and $S_\epsilon(M) = \{\mathbf{z} \in \mathbb{R}_+^n : d(\mathbf{z}, M) = \epsilon\}$. Let ϕ be the flow associated with our differential equation.

LEMMA A.5 *If (I-iv) holds, then Γ_1 is asymptotically stable within $\text{bd}\mathbb{R}_+^4$.*

Proof It is clear that Γ_1 is attractive within $\text{bd}\mathbb{R}_+^4$. Therefore, it is sufficient to show that it is stable. Suppose that Γ_1 is not stable within $\text{bd}\mathbb{R}_+^4$. Then there exist an $\epsilon > 0$ and sequences $\{\mathbf{z}_j\}$ with $\mathbf{z}_j \in \text{bd}\mathbb{R}_+^4 \setminus \Gamma_1$ and $\{t_j\}$ with $t_j \geq 0$ such that $d(\mathbf{z}_j, \Gamma_1) \rightarrow 0$ as $j \rightarrow \infty$ and

$$\phi(t_j, \mathbf{z}_j) \in S_\epsilon(\Gamma_1) \cap \text{bd}\mathbb{R}_+^4 \tag{A5}$$

for all j . We shall obtain a contradiction.

Consider the case where $H_1 := \{\mathbf{z} \in \mathbb{R}_+^4 : x_1 = 0\}$ includes infinitely many \mathbf{z}_j . Since Γ_1 is compact, there exist $\mathbf{z}^* \in \Gamma_1$ and a subsequence of $\{\mathbf{z}_j\}$, again denoted by $\{\mathbf{z}_j\}$, such that $\mathbf{z}_j \in H_1 \setminus \Gamma_1$ and $\mathbf{z}_j \rightarrow \mathbf{z}^*$. If $\mathbf{z}^* = F_2^2$, then Equation (A5) does not hold since F_2^2 is stable within H_1 . If $\mathbf{z}^* \in \Gamma_1 \setminus \{F_2^1, F_2^2\}$, then by continuous dependence on initial conditions, there exist a neighbourhood U_1 of \mathbf{z}^* such that $\phi(t, U_1 \cap H_1)$ eventually enters a small neighbourhood of the stable equilibrium point F_2^2 without leaving $B_\epsilon(\Gamma_1)$. Hence Equation (A5) does not hold. Finally, suppose $\mathbf{z}^* = F_2^1$ (see Figure A1). Since F_2^1 is hyperbolic, there exists a small $\eta > 0$ such that F_2^1 is the maximal invariant set in $B_\eta(F_2^1)$ and $B_\eta(F_2^1) \cap H_1$ and the unstable manifold of F_2^1 have a unique intersection. Let \mathbf{q} be the unique intersection. Since F_2^1 is the maximal invariant set in $B_\eta(F_2^1)$, for all $j \geq 0$ sufficiently large there exists a sequence $\{\bar{t}_j\}$ with $\bar{t}_j \geq 0$ such that

$$\phi(\bar{t}_j, \mathbf{z}_j) \in S_\eta(F_2^1) \cap H_1 \quad \text{and} \quad \phi(t, \mathbf{z}_j) \in B_\eta(F_2^1) \cap H_1$$

for all $t \in [0, \bar{t}_j)$. Since $S_\eta(F_2^1) \cap H_1$ is compact, a subsequence of $\phi(\bar{t}_j, \mathbf{z}_j)$ converges to a point $\mathbf{q}' \in S_\eta(F_2^1) \cap H_1$. Suppose $\mathbf{p}' \neq \mathbf{p}$. Then the backward orbit of \mathbf{p}' cannot stay in $B_\eta(F_2^1)$ since F_2^1 is the maximum invariant set in $B_\eta(F_2^1)$ and \mathbf{p} is a unique intersection between $B_\eta(F_2^1) \cap H_1$ and the unstable manifold of F_2^1 . Hence there exists a $\hat{t} > 0$ such that $\phi(-\hat{t}, \mathbf{q}') \notin B_\eta(F_2^1)$. By continuous dependence on initial conditions, there exists a neighbourhood U_2 of \mathbf{q}' such that $\mathbf{q} \notin U_2$ and $F_2^1 \notin \phi([-\hat{t}, 0], U_2)$. This is a contradiction to the fact that $\phi(\bar{t}_j, \mathbf{z}_j) \rightarrow \mathbf{q}'$ and $\mathbf{z}_j \rightarrow F_2^1$ as $j \rightarrow \infty$. Hence $\mathbf{q} = \mathbf{q}'$. Since $\mathbf{q} \in \Gamma_1$, $\mathbf{q} \neq F_2^2$ and $\mathbf{q} \neq F_2^1$ hold, the above argument shows that Equation (A5) does not hold.

Since the faces $x_2 = 0, y_1 = 0$ and $y_2 = 0$ have properties similar to the face $x_1 = 0$, the above argument is applicable to these faces and the stability of Γ_1 follows. ■

Since the proof of the following lemma is almost the same as the above proof, we omit it.

LEMMA A.6 *If (II-iv) holds, then Γ_2 is asymptotically stable within $\text{bd}\mathbb{R}_+^4$.*

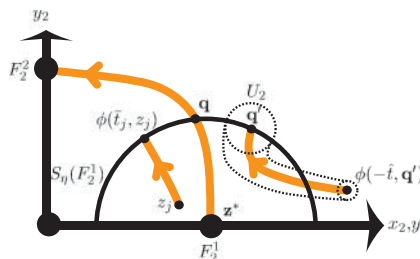


Figure A1. Cartoon for Lemma A.5.