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# The dynamics of *Wolbachia* spread in mosquito population under period-2 perturbation of environments

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## Abstract

A nonautonomous periodic discrete model is proposed to characterize the dynamics of *Wolbachia* spread in mosquito populations under period-2 environments, where the *Wolbachia* strain in the first environment is less competitive than the one in the second environment. By introducing the associated Poincaré map, the existence, exact number, and stability of periodic solutions and the long-term behavior of the discrete model are analyzed. Sufficient conditions are obtained to guarantee the bistable dynamics of the model: the model has exactly two periodic solutions, among which one is unstable, and the other is locally asymptotically stable. The origin, corresponding to the *Wolbachia* vanishment, of the model is locally asymptotically stable. Counting the exact number of periodic solutions of nonautonomous periodic discrete models is always challenging. In this paper, we provide three exclusive methods to prove the uniqueness of the periodic solutions, together with their stability analyses. Biologically, the unstable periodic solution serves as a threshold for *Wolbachia* invasion, and the stable periodic solution identifies where *Wolbachia* will be stabilized. Numerical simulations are provided to locate these two periodic solutions and analyze the parameter space to identify regions where periodic solutions emerge or disappear through bifurcations.

**Mathematics Subject Classification:** 39A05; 39A23; 39A30; 92B05

**Keywords:** *Wolbachia*; Release threshold; Periodic environment; Periodic solutions; Existence and stability

## 1 Introduction

The World Mosquito Program (WMP) is working with local communities in Asia, Latin America, and Oceania to reduce the transmission of mosquito-borne diseases like dengue, Zika, Chikungunya, and yellow fever. Using a tiny bacteria called *Wolbachia* discovered in 1924, WMP has released *Wolbachia* mosquitoes in more than 14 countries and has protected almost 11 million people [1] under the difficult situation (neither effective drugs nor safe vaccine) of dengue control. This satisfactory result owes to three mechanisms induced from *Wolbachia*.

The first mechanism is cytoplasmic incompatibility (CI for short), which causes eggs produced by the mating of infected males and uninfected females to fail to hatch, partially or completely [2]. To the end, the parameter $h$ with $h \in (0,1]$ is usually introduced to estimate the intensity of CI, that is, among the eggs produced from the incompatible mating, $h$ of them will not hatch, leaving $1-h$ of them survived from CI [3, 4]. The second mechanism is that Wolbachia is passed from generation to generation, usually with high fidelity, i.e., the proportion of infected offspring is higher than that of uninfected offspring from infected mothers. Let $\mu \in [0,1)$ be the maternal transmission leakage rate. Among all offspring produced from *Wolbachia*-infected females, $1-\mu$ of them are infected, and $\mu$ of them are uninfected. Thirdly, *Wolbachia* endows the host with the ability of pathogen blocking by inhibiting the replication of dengue viruses in mosquito tissues, such as fat bodies, ommatidia, midgut, salivary glands and brain [5–7]. Hence, dengue viruses will not be transmitted to humans during subsequent blood-feeding. However, *Wolbachia*-infected females usually undergo a fitness cost at a disadvantage compared to uninfected females on female mosquitoes' oviposition, longevity, and environmental adaptability [8–10]. Let $f \in [0,1]$ be the fitness cost of *Wolbachia*-infected females. That is, if the fitness of uninfected females is 1, then the fitness of *Wolbachia*-infected females is $1-f$.

Currently, releasing *Wolbachia* mosquitoes to suppress or replace wild vector mosquitoes has become a promising method to control mosquito and mosquito-borne diseases. As a hot research topic, the dynamics of *Wolbachia* spread in mosquito populations has attracted much attention, and various mathematical models have been established, see [11–21] to cite a few. This paper uses a time-switching discrete model to study the dynamics of *Wolbachia* spread in mosquito populations under period-2 perturbation. The first discrete model

$$x_{n+1} = \frac{(1-f)x_n}{hx_n^2-(f+h)x_n+1}, \quad n \in \mathbb{Z} \tag{1.1}$$

was established by Caspari and Watson in 1959 [11], where $x_n$ is the *Wolbachia* infection frequency at the $n$-th generation, $f$ and $h$ with $f<h$ are respectively the fitness cost and the CI intensity as introduced above, and $\mathbb{Z}=\{1,2,3,\ldots\}$ be the set of all positive integers. Let $x_n = x_n(1,x_1)$ be the solution of model (1.1) initiated from $x_1$. Model (1.1) generates the bistable dynamics: if $x_1 \in [0,f/h)$, then $x_n \to 0$ as $n \to +\infty$, and if $x_1 \in (f/h,1]$, then $x_n \to 1$ as $n \to +\infty$. Later, in 1978, based on the first discrete model and motivated by the phenomenon of imperfect maternal transmission of *Wolbachia* [12], Fine in [13] developed a similar but more general model

$$x_{n+1} = \frac{(1-\mu)(1-f)x_n}{hx_n^2-(f+h)x_n+1}, \quad n \in \mathbb{Z}. \tag{1.2}$$

In 2019, the authors in [16] offered a complete mathematical analysis of model (1.2) and obtained the following theorem.

**Theorem 1.1** ([16]) *Model* (1.2) *always admits the trivial equilibrium point* $x_0^*=0$, *which is locally asymptotically stable. By introducing*

$$\mu^* = \frac{(h-f)^2}{4h(1-f)}, \tag{1.3}$$

*model* (1.2) *has*

(1) *two nonzero equilibria*

$$x^* = \frac{h+f-\sqrt{(h-f)^2-4\mu h(1-f)}}{2h}, \; x^{**} = \frac{h+f+\sqrt{(h-f)^2-4\mu h(1-f)}}{2h} \tag{1.4}$$

*with* $0 < x^* < x^{**} < 1$ *when* $\mu \in [0,\mu^*)$, *among which* $x^*$ *is unstable, and* $x^{**}$ *is locally asymptotically stable. That is, if* $x_1 \in [0,x^*)$, *then* $x_n \to 0$ *as* $n \to \infty$, *whereas for* $x_1 \in (x^*,1]$, $x_n \to x^{**}$ *as* $n \to \infty$.

(2) *a nonzero equilibrium point*

$$\hat{x}^* = \frac{h+f}{2h},$$

*when* $\mu = \mu^*$, *and* $x_n \to 0$ *as* $n \to \infty$ *if* $x_1 < \hat{x}^*$, *whereas for* $x_1 > \hat{x}^*$, $x_n \to \hat{x}^*$ *as* $n \to \infty$.

(3) *the unique equilibrium solution* $x_0^* = 0$ *when* $\mu > \mu^*$, *which satisfies* $x_n \to 0$ *as* $n \to \infty$ *for any* $x_1 \in [0,1]$.

The bistable dynamics shown in Theorem 1.1(1) captures the infection frequency threshold $x^*$, which plays the most important role in field trials for the fate of *Wolbachia* invasion. Besides, the bifurcation value $\mu^*$ defined in (1.3) confirms that if the maternal leakage rate is larger than $\mu^*$, then *Wolbachia* invasion is impossible as Theorem 1.1(3) shown. Hence, Theorem 1.1 has offered all possible cases when *Wolbachia*-related parameters are independent of the external environmental conditions. However, the dynamical behavior of *Wolbachia* in mosquitoes changes in response to natural fluctuations in living conditions such as temperature and precipitation [22] and *Wolbachia*-related parameters are also highly related to the external environmental conditions [23–27]. For example, the authors in [25] found that *w*Mel-infected males and uninfected females produced complete CI without eggs hatching when reared at 26°C and almost complete CI when reared in 99% shaded barrels (23.2–29.6°C). Raising them in a 50% shaded barrel (23.7–35.3°C) caused a much weaker CI. Therefore, it is more realistic to extend model (1.2) to

$$x_{n+1} = \frac{(1-\mu_n)(1-f_n)x_n}{h_n x_n^2 - (f_n+h_n)x_n + 1}, \; n \in \mathbb{Z}, \tag{1.5}$$

that describes the parameters in the external environment of the *n*th generation mosquito in terms of $\mu_n, f_n, h_n$.

In the current study, we focus on the dynamics of *Wolbachia* spread in mosquito populations under the period-2 environments by assuming that

$$\mu_{n+2} = \mu_n, \; h_{n+2} = h_n, \; \text{and} \; f_{n+2} = f_n, \; n \in \mathbb{Z}, \tag{1.6}$$

and leaving the general case as our future study. Let $\mu_1$, $h_1$, and $f_1$ be respectively the maternal transmission leakage rate, the CI intensity, and the fitness cost of infected females in the first environment, followed by the second environment with $\mu_2$, $h_2$, and $f_2$. In such a situation, model (1.5) becomes a switching model

$$x_{n+1} = \begin{cases} \dfrac{(1-\mu_1)(1-f_1)x_n}{h_1x_n^2-(f_1+h_1)x_n+1}, & n = 2k+1, \\ \dfrac{(1-\mu_2)(1-f_2)x_n}{h_2x_n^2-(f_2+h_2)x_n+1}, & n = 2k+2, \end{cases} \tag{1.7}$$

where $k \in \mathbb{Z}(0) = \{0, 1, 2, \dots\}$ are all nonnegative integers.

When the environment condition undergoes a period-2 perturbation, the dynamics of *Wolbachia* spread in mosquito populations is dictated by model (1.7) instead of model (1.2). It is obvious that model (1.7) has the origin 0 as the unique equilibrium point. The dynamics shown in Theorem 1.1 for model (1.2) do not hold anymore for model (1.7).

To study the dynamics of model (1.7), without loss of generality, we assume that the *Wolbachia* strain in the first environment is less competitive than the one in the second environment, that is,

$$\mu_2 < \mu_1, f_2 < f_1 < h_1 < h_2, \tag{1.8}$$

which implies that the *Wolbachia* strain in the first environment has a larger maternal transmission leakage rate, higher fitness cost, and lower CI intensity. We define

$$\mu_1^* = \frac{(h_1-f_1)^2}{4h_1(1-f_1)}, \text{ and } \mu_2^* = \frac{(h_2-f_2)^2}{4h_2(1-f_2)}$$

as Theorem 1.1 suggested. Since only those *Wolbachia* strains with $\mu_1 < \mu_1^*$ and $\mu_2 < \mu_2^*$ would be considered a release candidate, we only treat this case in the current study and leave the other cases as our future work. Noticing that

$$\frac{\partial \mu^*}{\partial h} = \frac{(h-f)(h+f)}{4h^2(1-f)} > 0, \text{ and } \frac{\partial \mu^*}{\partial f} = \frac{-(h-f)(2-h-f)}{4h(1-f)^2} < 0,$$

we have the fact that $\mu^*$ is strictly monotonically increasing in $h$, and strictly monotonically decreasing in $f$. Therefore, with (1.8), we have

$$\mu_1^* = \frac{(h_1-f_1)^2}{4h_1(1-f_1)} \overset{f_2<f_1}{<} \frac{(h_1-f_2)^2}{4h_1(1-f_2)} \overset{h_1<h_2}{<} \frac{(h_2-f_2)^2}{4h_2(1-f_2)} = \mu_2^*.$$

These observations imply that if we let

$$\mu_1 < \mu_1^*, \tag{1.9}$$

then we must have $\mu_2 < \mu_2^*$ with (1.8) satisfied. The main result of this paper is as follows.

**Theorem 1.2** *Assume that* (1.8) *and* (1.9) *hold. Then the switching model* (1.7) *has exactly two* 2*-periodic solutions, among which the smaller one is unstable, and the bigger one is locally asymptotically stable. Furthermore, the origin of model* (1.7) *is locally asymptotically stable.*

The rest of the paper is organized as follows: Sect. 2 proves that model (1.7) has at least two 2-periodic solutions by exploring the qualitative property of the associated Poincaré map. We prove that model (1.7) has at most two 2-periodic solutions by way of contradiction in Sect. 3, with three exclusive methods dealing with different cases. Section 4 is devoted to the stability analysis stated in Theorem 1.2. The whole paper ends with a short discussion, especially focusing on the nonlinear dependence of the periodic solutions on model parameters.

## 2 Existence of at least two 2-periodic solutions

We begin with the local monotonicity of $x^*$ and $x^{**}$ defined in (1.4) with respect to $\mu, f$ and $h$. When $\mu \in [0, \mu^*)$, it is obvious that $x^*$ is strictly monotonically increasing in $\mu$, and $x^{**}$ is strictly monotonically decreasing in $\mu$. The larger the maternal transmission leakage, the larger the infection frequency threshold, and the smaller the level of *Wolbachia* fixation.

Regarding the monotonicity of $x^*$ and $x^{**}$ in $f$, we calculate

$$\frac{\partial x^*}{\partial f} = \frac{1 - \dfrac{-2(h-f) + 4\mu h}{2\sqrt{(h-f)^2 - 4\mu h(1-f)}}}{2h} = \frac{\sqrt{(h-f)^2 - 4\mu h(1-f)} - [2\mu h - (h-f)]}{2h\sqrt{(h-f)^2 - 4\mu h(1-f)}}.$$

Since $\mu < \mu^*$, one has

$$2\mu h - (h-f) < 2h\frac{(h-f)^2}{4h(1-f)} - (h-f) = \frac{h-f}{2(1-f)}(h+f-2) < 0, \tag{2.1}$$

which leads to $\dfrac{\partial x^*}{\partial f} > 0$. Similarly, we have

$$\frac{\partial x^{**}}{\partial f} = \frac{1 + \dfrac{-2(h-f) + 4\mu h}{2\sqrt{(h-f)^2 - 4\mu h(1-f)}}}{2h} = \frac{\sqrt{(h-f)^2 - 4\mu h(1-f)} - [(h-f) - 2\mu h]}{2h\sqrt{(h-f)^2 - 4\mu h(1-f)}}.$$

By (2.1), it is easy to get

$$\begin{aligned} &\sqrt{(h-f)^2 - 4\mu h(1-f)} < (h-f) - 2\mu h \\ &\text{iff } (h-f)^2 - 4\mu h(1-f) < (h-f)^2 - 4\mu h(h-f) + 4\mu^2 h^2 \\ &\text{iff } 4\mu h(h-1) < 4\mu^2 h^2 \\ &\text{iff } h - 1 < \mu h, \end{aligned}$$

with the last inequality always holding, which implies that $\dfrac{\partial x^{**}}{\partial f} < 0$. These observations claim that $x^*$ is strictly monotonically increasing in $f$, and $x^{**}$ is strictly monotonically decreasing in $f$.

On the monotonicity of $x^*$ and $x^{**}$ with respect to $h$, we get

$$\begin{aligned} \frac{\partial x^*}{\partial h} &= \frac{2h\left[1 - \dfrac{2(h-f) - 4\mu(1-f)}{2\sqrt{(h-f)^2 - 4\mu h(1-f)}}\right] - 2\left[h + f - \sqrt{(h-f)^2 - 4\mu h(1-f)}\right]}{4h^2} \\ &= \frac{-f(h-f) - 2\mu h(1-f) - f\sqrt{(h-f)^2 - 4\mu h(1-f)}}{2h^2\sqrt{(h-f)^2 - 4\mu h(1-f)}} < 0, \end{aligned}$$

and

$$\frac{\partial x^{**}}{\partial h} = \frac{2h\left[1 + \frac{2(h-f) - 4\mu(1-f)}{2\sqrt{(h-f)^2 - 4\mu h(1-f)}}\right] - 2\left[h + f + \sqrt{(h-f)^2 - 4\mu h(1-f)}\right]}{4h^2}$$

$$= \frac{f\left[(h-f) - \sqrt{(h-f)^2 - 4\mu h(1-f)}\right] + 2\mu h(1-f)}{2h^2\sqrt{(h-f)^2 - 4\mu h(1-f)}} > 0.$$

To sum up, we have the following results on the monotonicity of $\mu^*$, $x^*$, and $x^{**}$ with respect to $h$ and $f$.

**Lemma 2.1** *The threshold value $\mu^*$ is strictly monotonically increasing in h and strictly monotonically decreasing in f. When $\mu \in [0, \mu^*)$, the unstable equilibrium point $x^*$ is strictly monotonically increasing in both $\mu$ and f, and strictly monotonically decreasing in h. The stable equilibrium point $x^{**}$ is strictly monotonically decreasing in both $\mu$ and f and strictly monotonically increasing in h.*

Based on the assumption $\mu_1 < \mu_1^*$, the first equation in (1.7) becomes

$$\Delta x_n = -\frac{h_1 x_n (x_n - x_1^*)(x_n - x_1^{**})}{h_1 x_n^2 - (h_1 + f_1)x_n + 1}, \; n = 2k+1, \; k \in \mathbb{Z}(0), \tag{2.2}$$

where

$$x_1^* = \frac{h_1 + f_1 - \sqrt{(h_1 - f_1)^2 - 4\mu_1 h_1 (1 - f_1)}}{2h_1}, \; x_1^{**} = \frac{h_1 + f_1 + \sqrt{(h_1 - f_1)^2 - 4\mu_1 h_1 (1 - f_1)}}{2h_1}.$$

We also have $\mu_2 < \mu_2^*$. In this case, the second equation in (1.7) becomes

$$\Delta x_n = -\frac{h_2 x_n (x_n - x_2^*)(x_n - x_2^{**})}{h_2 x_n^2 - (h_2 + f_2)x_n + 1}, \quad n = 2k+2, \; k \in \mathbb{Z}(0), \tag{2.3}$$

where

$$x_2^* = \frac{h_2 + f_2 - \sqrt{(h_2 - f_2)^2 - 4\mu_2 h_2 (1 - f_2)}}{2h_2}, \; x_2^{**} = \frac{h_2 + f_2 + \sqrt{(h_2 - f_2)^2 - 4\mu_2 h_2 (1 - f_2)}}{2h_2}.$$

Using the monotonicity of $x^*$ and $x^{**}$ stated in Lemma 2.1, we get

$$x_2^* = x^*(\mu_2, f_2, h_2) \overset{\mu_2<\mu_1}{<} x^*(\mu_1, f_2, h_2) \overset{f_2<f_1}{<} x^*(\mu_1, f_1, h_2) \overset{h_2>h_1}{<} x^*(\mu_1, f_1, h_1) = x_1^*,$$

and

$$x_1^{**} = x^{**}(\mu_1, f_1, h_1) \overset{\mu_1>\mu_2}{<} x^{**}(\mu_2, f_1, h_1) \overset{f_1>f_2}{<} x^{**}(\mu_2, f_2, h_1) \overset{h_1<h_2}{<} x^{**}(\mu_2, f_2, h_2) = x_2^{**}.$$

Therefore, we can draw the conclusion that

$$x_2^* < x_1^* < x_1^{**} < x_2^{**}. \tag{2.4}$$

By exploring the qualitative property of the associated Poincaré map ($h(u)$ defined below), in the following lemma, we prove that model (1.7) has at least two 2-periodic solutions with (1.8) and (1.9) satisfied.

**Lemma 2.2** *Assume that* (1.8) *and* (1.9) *hold. Then model* (1.7) *has at least two* 2*-periodic solutions among which one initiates from* $(x_2^*, x_1^*)$ *and the other initiates from* $(x_1^{**}, x_2^{**})$.

*Proof* To unload the notation burden, we let

$$P_1(u) = (1-\mu_1)(1-f_1)u,\ Q_1(u) = h_1u^2 - (f_1+h_1)u + 1, \tag{2.5}$$

and

$$P_2(u) = (1-\mu_2)(1-f_2)u,\ Q_2(u) = h_2u^2 - (f_2+h_2)u + 1. \tag{2.6}$$

Then, for any $x_1 = u \in [0,1]$, it follows from (2.2) that

$$x_2 = \frac{P_1(u)}{Q_1(u)} := \bar{h}(u),\ \bar{h}(x_1^*) = x_1^*,\ \ \bar{h}(x_1^{**}) = x_1^{**},$$

and

$$\bar{h}(u) < u \text{ for } u \in (0, x_1^*) \cup (x_1^{**}, 1],\ \bar{h}(u) > u \text{ for } u \in (x_1^*, x_1^{**}). \tag{2.7}$$

To bridge, initiated from $x_2 = \bar{h}(u)$, it follows from (2.3) that

$$x_3 = \frac{P_2(\bar{h}(u))}{Q_2(\bar{h}(u))} := h(u),\ h(x_2^*) = x_2^*,\ h(x_2^{**}) = x_2^{**},$$

and

$$h(u) < \bar{h}(u) \text{ for } \bar{h}(u) \in (0, x_2^*) \cup (x_2^{**}, 1],\ h(u) > \bar{h}(u) \text{ for } \bar{h}(u) \in (x_2^*, x_2^{**}). \tag{2.8}$$

Combining (2.4), (2.7), and (2.8), we get

$$h(u) < u \text{ for } u \in (0, x_2^*] \cup [x_2^{**}, 1],\ h(u) > u \text{ for } u \in [x_1^*, x_1^{**}]. \tag{2.9}$$

Hence, the continuity of $h(u)$ and (2.9) guarantee that $h(u)$ has at least two fixed points initiated from $(x_2^*, x_1^*)$ and $(x_1^{**}, x_2^{**})$, respectively. This proves that model (1.7) has at least two 2-periodic solutions when both (1.8) and (1.9) hold. □

## 3 At most two 2-periodic solutions

It follows from Lemma 2.2 that there exist $u_1 \in (x_2^*, x_1^*)$ and $u_2 \in (x_1^{**}, x_2^{**})$, such that $h(u_1) = u_1$ and $h(u_2) = u_2$. That is, model (1.7) has two 2-periodic solutions. In this section, we prove that model (1.7) has no other 2-periodic solutions except the two 2-periodic

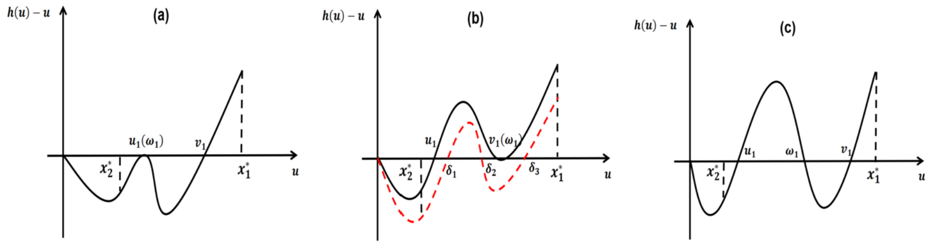

**Figure 1** Panel (a) and (b) show the situation that model (1.7) has two 2-periodic solutions initiated from $(x_2^*, x_1^*)$, corresponding to Case 1 and Case 2, respectively. Panel (c) corresponds to Case 3, under which model (1.7) has three 2-periodic solutions initiated from $(x_2^*, x_1^*)$

solutions initiated from $u_1$ and $u_2$, which can be guaranteed by the following qualitative property of $h(u)-u$:

$$h'(u_1) \geq 1,\ h'(u_2) \leq 1,\ h(u) < u \text{ for } u \in (0,u_1) \cup (u_2,1], \text{ and } h(u) > u \text{ for } u \in (u_1,u_2).$$

We will separately prove that the 2-periodic solutions initiated from $(x_2^*, x_1^*)$ or $(x_1^{**}, x_2^{**})$ are unique by contradiction. For the uniqueness of the 2-periodic solutions initiated from $(x_2^*, x_1^*)$, we assume by contradiction that there exists another 2-periodic solution $v_1 \in (x_2^*, x_1^*)$ with $v_1 > u_1$ such that

$$h(v_1) = v_1,\ h'(v_1) \geq 1,\ h(u) > u \text{ for } u \in (v_1, x_1^*).$$

Therefore, there must exist at least one $w_1 \in [u_1, v_1]$ such that

$$h(w_1) = w_1,\ h'(w_1) \leq 1,$$

and one of the following three cases holds:

Case 1: $w_1 = u_1,\ h'(u_1) = h'(w_1) = 1,\ h'(v_1) \geq 1;$

Case 2: $v_1 = w_1,\ h'(u_1) \geq 1,\ h'(v_1) = h'(w_1) = 1;$

Case 3: $w_1 \in (u_1, v_1),\ h'(u_1) \geq 1,\ h'(w_1) \leq 1,\ h'(v_1) \geq 1$

if model (1.7) has at most three 2-periodic solutions initiated from $(x_2^*, x_1^*)$. See Fig. 1 for an illustration.

Similarly, regarding the uniqueness of the 2-periodic solutions of model (1.7) initiated from $(x_1^{**}, x_2^{**})$, we assume by contradiction that there exists $v_2 \in (x_1^{**}, x_2^{**})$ with $v_2 < u_2$ satisfying

$$h(v_2) = v_2,\ h'(v_2) \leq 1,\ h(u) > u \text{ for } u \in (x_1^{**}, v_2),$$

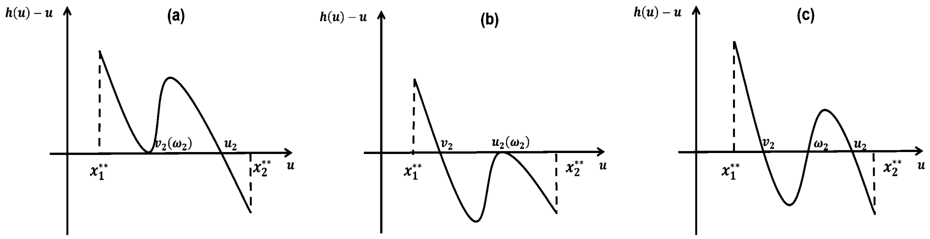

**Figure 2** Panel (a) and (b) show that model (1.7) has two 2-periodic solutions initiated from ($x_1^{**}$,$x_2^{**}$), corresponding to Case 4 and Case 5. Panel (c) shows Case 6 for which model (1.7) has three 2-periodic solutions initiated from ($x_1^{**}$,$x_2^{**}$)

then there must exist at least one $w_2 \in [v_2, u_2]$ such that

$$h(w_2) = w_2,\ h'(w_2) \geq 1.$$

Three cases should be considered.

Case 4: $w_2 = v_2,\ h'(v_2) = h'(w_2) = 1,\ h'(u_2) \leq 1.$

Case 5: $w_2 = u_2,\ h'(v_2) \leq 1,\ h'(u_2) = h'(w_2) = 1.$

Case 6: $w_2 \in (v_2, u_2),\ h'(v_2) \leq 1,\ h'(w_2) \geq 1,\ h'(u_2) \leq 1.$

See Fig. 2 for an illustration. We prove in the next two subsections that the above six cases are impossible, which guarantees that model (1.7) has at most two 2-periodic solutions.

### 3.1 Uniqueness of 2-periodic solutions initiated from ($x_2^*$, $x_1^*$)

We begin by excluding the possibility of Case 1 in the following lemma.

**Lemma 3.1** *If the assumptions in Theorem* 1.2 *hold, then Case* 1 *is impossible.*

*Proof* Since $\bar{h}(u) = P_1(u)/Q_1(u)$, where $P_1$ and $Q_1$ are defined in (2.5), we have

$$\begin{aligned}\frac{d\bar{h}(u)}{du} &= \frac{[P_1'(u) - Q_1'(u)\bar{h}(u)]\bar{h}(u)}{P_1(u)} \\ &= \frac{[(1-\mu_1)(1-f_1) - (2h_1 u - f_1 - h_1)\bar{h}(u)]\bar{h}(u)}{(1-\mu_1)(1-f_1)u}.\end{aligned} \tag{3.1}$$

Similarly, $h(u) = P_2(\bar{h}(u))/Q_2(\bar{h}(u))$ with $P_2$ and $Q_2$ defined in (2.6), we get

$$\begin{aligned}\frac{dh(u)}{d\bar{h}(u)} &= \frac{[P_2'(\bar{h}(u)) - Q_2'(\bar{h}(u))h(u)]h(u)}{P_2(\bar{h}(u))} \\ &= \frac{[(1-\mu_2)(1-f_2) - (2h_2\bar{h}(u) - f_2 - h_2)h(u)]h(u)}{(1-\mu_2)(1-f_2)\bar{h}(u)}.\end{aligned} \tag{3.2}$$

Combining (3.1) and (3.2), we achieve

$$h'(u)=\frac{h(u)}{u}\cdot\frac{(1-\mu_2)(1-f_2)-(2h_2\bar{h}(u)-f_2-h_2)h(u)}{(1-\mu_2)(1-f_2)}\\ \cdot\frac{(1-\mu_1)(1-f_1)-(2h_1u-f_1-h_1)\bar{h}(u)}{(1-\mu_1)(1-f_1)},\tag{3.3}$$

and at any point $\xi\in\{u_1,v_1,w_1\}$ with $h(\xi)=\xi$, one has

$$h'(\xi)=\frac{M(\xi)}{(1-\mu_2)(1-f_2)}\cdot\frac{N(\xi)}{(1-\mu_1)(1-f_1)},\tag{3.4}$$

where

$$M(\xi)=(1-\mu_2)(1-f_2)-(2h_2\bar{h}(\xi)-f_2-h_2)h(\xi),$$

and

$$N(\xi)=(1-\mu_1)(1-f_1)-(2h_1\xi-f_1-h_1)\bar{h}(\xi).$$

We further calculate $M(\xi)$ as

$$\begin{aligned}M(\xi)&=(1-\mu_2)(1-f_2)-(2h_2\bar{h}(\xi)-f_2-h_2)\xi\\&=\frac{(1-\mu_2)(1-f_2)Q_1(\xi)-2h_2\xi P_1(\xi)+(f_2+h_2)\xi Q_1(\xi)}{Q_1(\xi)}\\&=\frac{m_0+m_1\xi+m_2\xi^2+m_3\xi^3}{Q_1(\xi)},\end{aligned}$$

where

$$\begin{aligned}&m_0=(1-\mu_2)(1-f_2),\ m_1=-(1-\mu_2)(1-f_2)(f_1+h_1)+(f_2+h_2),\\&m_2=h_1(1-\mu_2)(1-f_2)-2h_2(1-\mu_1)(1-f_1)-(f_1+h_1)(f_2+h_2),\ m_3=h_1(f_2+h_2).\end{aligned}$$

Similarly, $N(\xi)$ can be specified as

$$N(\xi)=\frac{(1-\mu_1)(1-f_1)Q_1(\xi)-2h_1\xi P_1(\xi)+(f_1+h_1)P_1(\xi)}{Q_1(\xi)}=\frac{(1-\mu_1)(1-f_1)(1-h_1\xi^2)}{Q_1(\xi)}.$$

Revisiting (3.4) at $u=\xi$, we have $h'(\xi)\geq 1$ if and only if (iff) $M(\xi)N(\xi)-(1-\mu_2)(1-f_2)(1-\mu_1)(1-f_1)\geq 0$, or equivalently,

$$G(\xi)=g_0+g_1\xi+g_2\xi^2+g_3\xi^3+g_4\xi^4\geq 0.\tag{3.5}$$

And $h'(\xi)<1$ iff $G(\xi)<0$. In (3.5),

$$g_0=m_1+2(f_1+h_1)(1-\mu_2)(1-f_2)=(f_1+h_1)(1-\mu_2)(1-f_2)+(f_2+h_2)>0.$$

The coefficient $g_1$ satisfies

$$\begin{aligned} g_1 &= (m_2 - m_0h_1) - (1-\mu_2)(1-f_2)(2h_1 + (f_1+h_1)^2) \\ &= -2h_2(1-\mu_1)(1-f_1) - (f_1+h_1)(f_2+h_2) - (1-\mu_2)(1-f_2)(2h_1+(f_1+h_1)^2) < 0. \end{aligned}$$

The coefficient $g_2 = 3h_1(1-\mu_2)(1-f_2)(f_1+h_1) > 0$ and $g_3$ satisfy

$$\begin{aligned} g_3 &= -m_2h_1 - (1-\mu_2)(1-f_2)h_1^2 \\ &= h_1[-2h_1(1-\mu_2)(1-f_2) + 2h_2(1-\mu_1)(1-f_1) + (f_1+h_1)(f_2+h_2)]. \end{aligned}$$

The coefficient $g_4 = -h_1^2(f_2+h_2) < 0$.

Without confusion, we still write $G(u) = g_0 + g_1u + g_2u^2 + g_3u^3 + g_4u^4$. With the help of $G(u)$, we next prove $h'(v_1) < 1$ to get the contradiction to Case 1 with $h'(v_1) \geq 1$. We begin with $G''(u) = 2g_2 + 6g_3u + 12g_4u^2$. Direct computations lead to $G''(0) = 2g_2 > 0$ and

$$G''(\bar{x}) = 2g_2 + 6g_3\bar{x} + 12g_4\bar{x}^2 = 6h_2(1-\mu_1)(1-f_1)(f_1+h_1) > 0, \tag{3.6}$$

where $\bar{x}$ is introduced as

$$\bar{x} = \frac{h_1+f_1}{2h_1} \in (x_1^*, x_1^{**}) \tag{3.7}$$

to get around the difficulty in complex calculations.

It follows from (3.6) and $g_4 < 0$ that $G''(u) > 0$ for all $u \in [0, \bar{x}]$. This implies that

$$G'(u) = g_1 + 2g_2u + 3g_3u^2 + 4g_4u^3$$

with $G'(0) = g_1 < 0$ is strictly monotonically increasing in $u$ for any $u \in (0, \bar{x})$. We move on to the monotonicity of $G(u)$ at $(0, \bar{x})$. There are two situations to consider.

(i) If $G'(\bar{x}) \leq 0$, the above analysis implies that $G'(u) \leq 0$ for $u \in [0, \bar{x}]$. This means that $G(u)$ is strictly monotonically decreasing in $u$ for any $u \in (0, \bar{x})$. For Case 1, we have $h'(u_1) = 1$, which implies that $G(u_1) = 0$. Then, we must have $G(v_1) < 0$ since $v_1 > u_1$. That is, $h'(v_1) < 1$, which contradicts Case 1.

(ii) If $G'(\bar{x}) > 0$, then there exists a unique $\hat{u} \in (0, \bar{x})$ such that

$$G'(u) < 0 \text{ for } u \in (0, \hat{u}), \; G'(\hat{u}) = 0, \text{ and } G'(u) > 0 \text{ for } u \in (\hat{u}, \bar{x}).$$

That is, $G(u)$ is strictly monotonically decreasing in $u$ for any $u \in (0, \hat{u})$, and strictly monotonically increasing in $u$ for $u \in (\hat{u}, \bar{x})$. Next, we prove that $G(\bar{x}) < 0$. To proceed, we calculate

$$\begin{aligned} 16h_1^2G(\bar{x}) &= 16h_1^2(g_0 + g_1\bar{x} + g_2\bar{x}^2 + g_3\bar{x}^3 + g_4\bar{x}^4) \\ &= 4h_2(1-\mu_1)(1-f_1)(f_1+h_1)\left[(f_1+h_1)^2 - 4h_1\right] \\ &\quad + (f_2+h_2)\left[(f_1+h_1)^2 - 4h_1\right]^2 \end{aligned}$$

$$\begin{aligned} &= \left[(f_1+h_1)^2 - 4h_1\right]\Big\{4h_2(1-\mu_1)(1-f_1)(f_1+h_1) \\ &\quad + (f_2+h_2)[(f_1+h_1)^2 - 4h_1]\Big\}. \end{aligned}$$

By the definition of $\mu_1^*$, we get

$$[(f_1+h_1)^2 - 4h_1] = -4h_1(1-f_1)(1-\mu_1^*) < 0 \tag{3.8}$$

and reach

$$\begin{aligned} &4h_2(1-\mu_1)(1-f_1)(f_1+h_1) + (f_2+h_2)[(f_1+h_1)^2 - 4h_1] \\ &= 4(1-f_1)[h_2(1-\mu_1)(f_1+h_1) - h_1(1-\mu_1^*)(f_2+h_2)] \\ &> 4(1-f_1)(1-\mu_1^*)(h_2f_1 - h_1f_2) > 0 \end{aligned} \tag{3.9}$$

since $f_2 < f_1 < h_1 < h_2$. It follows from (3.8) and (3.9) that $G(\bar{x}) < 0$. With $G(0) = g_0 > 0$, by graphing the curve of $G(u)$ satisfying Case 1, we see that $u_1$ is the unique zero point of $G(u)$. Hence, $G(v_1) < 0$ since $v_1 > u_1$. Again, a contradiction to $h'(v_1) \geq 1$ in Case 1.

This excludes the possibility of Case 1 and completes the proof. ☐

However, this method is invalid in excluding the possibility of Case 2. The reason is that according to the property of $G(u)$, if $h'(v_1) = 1$, then at any 2-periodic solution initiated from $u_1 \in (0, v_1)$, we always get $h'(u_1) > 1$, failing to achieve a contradiction to Case 2. To overcome this, we use the perturbation technique by investigating the qualitative property of $h_k'(u)$ at any $u$ where $h_k(u) = h(u) - ku$ with $k - 1 > 0$ being small enough. The perturbation from $h(u) - u$ to $h(u) - ku$ generates three zero points of $h(u) - ku$ shown in Fig. 1(b)(the red dashed curve), denoted by $\delta_i$, $i = 1,2,3$ satisfying $u_1 < \delta_1 < \delta_2 < v_1 < \delta_3 < x_1^{**}$, and

$$h(\delta_i) = k\delta_i,\ i = 1,2,3, \text{ and } h'(\delta_1) \geq k,\ h'(\delta_2) \leq k,\ h'(\delta_3) \geq k. \tag{3.10}$$

**Lemma 3.2** *Assume that the assumptions in Theorem 1.2 hold. Then,* (3.10) *is impossible, and hence Case* 2 *is impossible.*

*Proof* We calculate $h'(\xi)$ with any 2-periodic solution initiated from $\xi \in \{\delta_1, \delta_2, \delta_3\}$ by (3.3), which yields

$$h'(\xi) = k \cdot \frac{M_k(\xi)}{(1-\mu_2)(1-f_2)} \cdot \frac{N_k(\xi)}{(1-\mu_1)(1-f_1)},$$

where

$$\begin{aligned} M_k(\xi) &= \frac{(1-\mu_2)(1-f_2)Q_1(\xi) - 2kh_2\xi P_1(\xi) + k\xi(f_2+h_2)Q_1(\xi)}{Q_1(\xi)} \\ &= \frac{\widetilde{m}_0 + \widetilde{m}_1\xi + \widetilde{m}_2\xi^2 + \widetilde{m}_3\xi^3}{Q_1(\xi)}, \end{aligned}$$

with

$$\begin{aligned}
&\widetilde{m}_0 = (1-\mu_2)(1-f_2) = m_0,\ \widetilde{m}_1 = -(1-\mu_2)(1-f_2)(f_1+h_1) + k(f_2+h_2),\\
&\widetilde{m}_2 = h_1(1-\mu_2)(1-f_2) - 2kh_2(1-\mu_1)(1-f_1) - k(f_1+h_1)(f_2+h_2),\\
&\widetilde{m}_3 = kh_1(f_2+h_2) = km_3,
\end{aligned}$$

and

$$N_k(\xi) = \frac{(1-\mu_1)(1-f_1)(1-h_1\xi^2)}{Q_1(\xi)}.$$

Similarly, we have $h'(\xi) \geq k$ iff $M_k(\xi)N_k(\xi) - (1-\mu_1)(1-f_1)(1-\mu_2)(1-f_2) \geq 0$, or equivalently,

$$G_k(\xi) = g_0(k) + g_1(k)\xi + g_2(k)\xi^2 + g_3(k)\xi^3 + g_4(k)\xi^4 \geq 0.$$

And $h'(\xi) < k$ iff $G_k(\xi) < 0$.

Again, we make use of the property of

$$G_k(u) = g_0(k) + g_1(k)u + g_2(k)u^2 + g_3(k)u^3 + g_4(k)u^4$$

for $u \in (0,\bar{x})$ to exclude the possibility of (3.10), i.e.,

$$G_k(\delta_1) \geq 0,\ G_k(\delta_2) \leq 0,\ G_k(\delta_3) \geq 0. \tag{3.11}$$

To begin with, we determine the signs of coefficients $g_i(k)$ for $G_k(u)$. It is easy to get

$$g_0(k) = \widetilde{m}_1 + 2(f_1+h_1)(1-\mu_2)(1-f_2) = (f_1+h_1)(1-\mu_2)(1-f_2) + k(f_2+h_2) > 0.$$

For the coefficient of $u$, one has

$$\begin{aligned}
g_1(k) &= \widetilde{m}_2 - \widetilde{m}_0 h_1 - (1-\mu_2)(1-f_2)(2h_1 + (f_1+h_1)^2)\\
&= -k[2h_2(1-\mu_1)(1-f_1) + (f_1+h_1)(f_2+h_2)]\\
&\quad - (1-\mu_2)(1-f_2)(2h_1 + (f_1+h_1)^2) < 0.
\end{aligned}$$

The parameter $g_2(k) \equiv g_2 > 0$, and

$$\begin{aligned}
g_3(k) &= -\widetilde{m}_2 h_1 - (1-\mu_2)(1-f_2)h_1^2\\
&= h_1 k[2h_2(1-\mu_1)(1-f_1) + (f_1+h_1)(f_2+h_2)] - 2h_1^2(1-\mu_2)(1-f_2).
\end{aligned}$$

The calculation of $g_4(k)$ yields that $g_4(k) = -h_1^2 k(f_2+h_2) < 0$.

Taking the second derivative of $G$ reaches

$$G_k''(u) = 2g_2(k) + 6g_3(k)u + 12g_4(k)u^2.$$

We claim that

$$G_k''(0) > 0,\ G_k''(\bar{x}) > 0, \tag{3.12}$$

where $\bar{x}$ is defined in (3.7). It is obvious that $G_k''(0) = 2g_2(k) > 0$. For $G_k''(\bar{x})$, we have

$$G_k''(\bar{x}) = 2g_2(k) + 6g_3(k)\bar{x} + 12g_4(k)\bar{x}^2 = 6kh_2(1-\mu_1)(1-f_1)(f_1+h_1) = kG''(\bar{x}) > 0.$$

It follows from (3.12) and the fact that $g_4(k) < 0$ that $G_k''(u) > 0$ for any $u \in [0,\bar{x}]$. In other words, the function $G_k'(u)$ is strictly monotonically increasing for $u$ lying in $(0,\bar{x})$. For more explorations on $G_k(u)$, we consider

$$G_k'(u) = g_1(k) + 2g_2(k)u + 3g_3(k)u^2 + 4g_4(k)u^3$$

with $G_k'(0) = g_1(k) < 0$ in two cases.

(i) If $G_k'(\bar{x}) \leq 0$, then $G_k'(u) \leq 0$ for any $u \in (0,\bar{x}]$. This contradicts the fact shown in (3.11) that $G_k(u)$ changes the monotonicity at least once.

(ii) If $G_k'(\bar{x}) > 0$, then there exists a unique $u_k^* \in (0,\bar{x})$ such that

$$G_k'(u) < 0,\ \text{for } u \in (0,u_k^*),\ \text{and } G_k'(u) > 0,\ \text{for } v \in (u_k^*,\bar{x}).$$

Therefore, $G_k(u)$ is strictly monotonically decreasing in $u$ for any $u \in (0,u_k^*)$ and strictly monotonically increasing in $u$ for any $u \in (u_k^*,\bar{x})$. Due to $G_k(0) = g_0(k) > 0$ and

$$\begin{aligned} 16h_1^2G_k(\bar{x}) &= 16h_1^2(g_0(k) + g_1(k)\bar{x} + g_2(k)\bar{x}^2 + g_3(k)\bar{x}^3 + g_4(k)\bar{x}^4) \\ &= 4h_2k(1-\mu_1)(1-f_1)(f_1+h_1)[(f_1+h_1)^2 - 4h_1] \\ &\quad + k(f_2+h_2)[(f_1+h_1)^2 - 4h_1]^2 \\ &= kG(\bar{x}) < 0, \end{aligned}$$

there exists a unique $\hat{u}_k \in (0,\bar{x})$ such that

$$G_k(u) > 0,\ \text{for } u \in (0,\hat{u}_k),\ \text{and } G_k(u) < 0,\ \text{for } u \in (\hat{u}_k,\bar{x}).$$

Therefore, if $G_k(\delta_1) \geq 0$ and $G_k(\delta_2) \leq 0$, then we must have $G_k(\delta_3) < 0$, a contradiction to (3.11).

Combining the above two cases, we have proved that (3.10), and hence Case 2 is impossible. The proof is complete. □

We end this subsection by excluding Case 3 from the following lemma.

**Lemma 3.3** *Assume that conditions in Theorem 1.2 hold. Then Case 3 is not possible.*

*Proof* It follows from the proof of Lemma (4.3) that either $G(u)$ is strictly monotonically decreasing in $u$ or $G(u)$ only changes its monotonicity once with $G(0) > 0$ and $G(\bar{x}) < 0$.

For the situation of Case 3, we have

$$G(u_1) \geq 0,\ G(w_1) \leq 0,\ \text{and}\ G(v_2) \geq 0,$$

which can not be held simultaneously, proving the lemma. □

With the qualitative property of $G(u)$, it is obvious that it is impossible that model (1.7) has more than three 2-periodic solutions initiated from $(x_2^*, x_1^*)$. To sum up, Lemma 3.1, Lemma 3.2, and Lemma 3.3 have completed the proof of the uniqueness of the 2-periodic solutions of model (1.7) initiated from $(x_2^*, x_1^*)$.

### 3.2 Uniqueness of 2-periodic solutions initiated from $(x_1^{**}, x_2^{**})$

The uniqueness of 2-periodic solutions for model (1.7) initiated from $(x_1^{**}, x_2^{**})$ can be proved in a much cleaner way as follows.

**Lemma 3.4** *Assume that conditions in Theorem 1.2 hold. Then Case* 4, *Case* 5, *and Case* 6 *are impossible.*

*Proof* We exclude the possibilities of Case 4, Case 5, and Case 6 by proving that $h'(\xi) < 1$ for any $\xi \in (x_1^{**}, x_2^{**})$ with $h(\xi) = \xi$. To the end, we define

$$F_1(x) = \frac{(1-\mu_1)(1-f_1)x}{h_1x^2 - (f_1+h_1)x + 1}, \text{ and } F_2(x) = \frac{(1-\mu_2)(1-f_2)x}{h_2x^2 - (f_2+h_2)x + 1}.$$

We first calculate

$$\begin{aligned}\frac{dF_n(x)}{dx} &= \frac{(1-\mu_n)(1-f_n)}{h_nx^2-(f_n+h_n)x+1} - \frac{(1-\mu_n)(1-f_n)[2h_nx-(f_n+h_n)]x}{[h_nx^2-(f_n+h_n)x+1]^2} \\ &= \frac{F_n(x)}{x} - \frac{[2h_nx-(f_n+h_n)]x}{h_nx^2-(f_n+h_n)x+1}\cdot\frac{F_n(x)}{x} \\ &= \frac{1-h_nx^2}{h_nx^2-(f_n+h_n)x+1}\cdot\frac{F_n(x)}{x},\ n=1,2. \end{aligned} \tag{3.13}$$

Then, for any $u \in (0,1)$, we get $h(u) = F_2(F_1(u))$ and

$$\begin{aligned}\frac{dh(u)}{du} &= \frac{dF_2(F_1(u))}{dF_1(u)}\cdot\frac{dF_1(u)}{du} \\ &= \frac{1-h_2F_1^2(u)}{h_2F_1^2(u)-(f_2+h_2)F_1(u)+1}\cdot\frac{1-h_1u^2}{h_1u^2-(f_1+h_1)u+1}\cdot\frac{F_2(F_1(u))}{u}. \end{aligned} \tag{3.14}$$

At the initial values $\xi \in \{u_2, v_2, w_2\}$ of 2-periodic solutions introduced in Cases 4, 5, and 6, we have

$$\frac{dh(\xi)}{d\xi} = \frac{1-h_2F_1^2(\xi)}{h_2F_1^2(\xi)-(f_2+h_2)F_1(\xi)+1}\cdot\frac{1-h_1\xi^2}{h_1\xi^2-(f_1+h_1)\xi+1}. \tag{3.15}$$

Direct computations yield that

$$\frac{1-h_1\xi^2}{h_1\xi^2-(f_1+h_1)\xi+1}<1 \text{ iff } \xi>\frac{h_1+f_1}{2h_1}, \tag{3.16}$$

and

$$\frac{1-h_2F_1^2(\xi)}{h_2F_1^2(\xi)-(f_2+h_2)F_1(\xi)+1}<1 \text{ iff } F_1(\xi)>\frac{h_2+f_2}{2h_2}. \tag{3.17}$$

The relation $\xi>\frac{h_1+f_1}{2h_1}$ in (3.16) holds since

$$\xi>x_1^{**}=\frac{h_1+f_1+\sqrt{(h_1-f_1)^2-4\mu_1h_1(1-f_1)}}{2h_1}>\frac{h_1+f_1}{2h_1},\ \xi\in\{u_2,v_2,w_2\}. \tag{3.18}$$

Similarly, it follows from (3.13) that $F_n(x)$ is strictly monotonically increasing in $x$, and hence (3.18) implies that for $\xi\in\{u_2,v_2,w_2\}$,

$$F_1(\xi)>F_1(x_1^{**})=x_1^{**}>\frac{h_1+f_1}{2h_1}>\frac{h_2+f_2}{2h_2}, \tag{3.19}$$

where the last inequality holds because $0<f_2<f_1<h_1<h_2<1$. Combining (3.15)–(3.19), we have

$$h'(\xi)<1,\ \text{for } \xi\in\{u_2,v_2,w_2\}.$$

A contradiction to $h'(v_2)=h'(w_2)=1$ in Case 4, a contradiction to $h'(u_2)=h'(w_2)=1$ in Case 5, and a contradiction to $h'(w_2)\geq 1$ in Case 6. This completes the proof. □

*Remark* 3.5 We should mention here that, if possible, we may prove the uniqueness of the 2-periodic solutions initiated from $(x_2^*,x_1^*)$ by proving that

$$h'(\xi)>1 \text{ for } \xi\in(x_2^*,x_1^*) \text{ satisfying } h(\xi)=\xi. \tag{3.20}$$

Since if (3.20) holds, then we get a contradiction to $h'(u_1)=h'(w_1)=1$ in Case 1, a contradiction to $h'(v_1)=h'(w_1)=1$ in Case 2, and a contradiction to $h'(w_1)\leq 1$ in Case 3. However, by carefully checking the proof of Lemma 3.4, we get

$$h'(\xi)=\frac{1-h_2F_1^2(\xi)}{h_2F_1^2(\xi)-(f_2+h_2)F_1(\xi)+1}\cdot\frac{1-h_1\xi^2}{h_1\xi^2-(f_1+h_1)\xi+1},\ \xi\in\{u_1,v_1,w_1\}.$$

Since $\xi\in(x_2^*,x_1^*)$, we have

$$\xi<x_1^*=\frac{h_1+f_1-\sqrt{(h_1-f_1)^2-4\mu_1h_1(1-f_1)}}{2h_1}<\frac{h_1+f_1}{2h_1},$$

and hence

$$\frac{1-h_1\xi^2}{h_1\xi^2-(f_1+h_1)\xi+1} > 1.$$

We can also estimate $F_1(\xi)$ as

$$F_1(\xi) < F_1(x_1^*) = x_1^* < \frac{h_1+f_1}{2h_1}.$$

However, the inequality

$$\frac{h_1+f_1}{2h_1} < \frac{h_2+f_2}{2h_2}$$

does not hold, which halts us to reach

$$\frac{1-h_2F_1^2(\xi)}{h_2F_1^2(\xi)-(f_2+h_2)F_1(\xi)+1} > 1,$$

and then fails to prove (3.20).

## 4 Stability analysis stated in Theorem 1.2

This section is devoted to the stability analysis of the equilibrium point $x_0^* = 0$, and the two 2-periodic solutions of model (1.7) when conditions stated in Theorem 1.2 are satisfied. We begin by calculating $h'(0)$ to determine the stability of the origin. It follows from (3.13) that

$$F_n'(0) = (1-\mu_n)(1-f_n),\ n = 1,2.$$

Together with $F_n(0) \equiv 0$ for $n = 1,2$, we get

$$h'(0) = F_2'(F_1(0))F_1'(0) = F_2'(0)F_1'(0) = (1-\mu_1)(1-f_1)(1-\mu_2)(1-f_2) < 1,$$

which guarantees the local asymptotical stability of $x_0^* = 0$.

Next, we move on to the stability analysis of the two 2-periodic solutions of model (1.7). As we have proved in Sects. 2 and 3, there exist $u_1$ and $u_2$ satisfying $0 < u_1 < u_2$ such that $h(u_1) = u_1$, $h(u_2) = u_2$,

$$h(u) < u,\ u \in (0,u_1) \cup (u_2,+\infty),$$

and

$$h(u) > u,\ u \in (u_1,u_2). \tag{4.1}$$

We claim that the 2-periodic solution $\{u_2, F_1(u_2), u_2, F_1(u_2), \ldots\}$ of model (1.7) attracts all solutions initiated from $u$ with $u \in (u_1,u_2) \cup (u_2,+\infty)$. In fact, it follows from (3.14) that $h(u)$ is strictly monotonically increasing in $u$ for any $u \in (0,1)$, which leads to

$$u_1 = h(u_1) < h(u) < h(u_2) = u_2, \; u \in (u_1, u_2).$$

Combining with (4.1), one has

$$h^2(u) > h(u), \; u \in (u_1, u_2),$$

and inductively, we have

$$u_1 < h^n(u) < u_2, \text{ and } h^{n+1}(u) > h^n(u), \; u \in (u_1, u_2), \; n = 2, 3, \ldots.$$

That is, the sequence $\{h^n(u)\}_{n=0}^{\infty}$ with $u \in (u_1, u_2)$ is strictly monotonically increasing and bounded, which implies that

$$\lim_{n\to\infty} h^n(u) = u^* \tag{4.2}$$

exists with $u^* \in (u_1, u_2]$. We must have $u^* = u_2$ because if (4.2) holds, then

$$h(u^*) = h(\lim_{n\to\infty} h^n(u)) = \lim_{n\to\infty} h^{n+1}(u) = u^*$$

holds, and $h$ has the unique fixed point $u_2$ lying in $(u_1, \infty)$. Until now, we have proved that

$$\lim_{n\to\infty} h^n(u) = u_2, \;\; u \in (u_1, u_2). \tag{4.3}$$

With the continuity of $F_1$, we have

$$\lim_{n\to\infty} F_1(h^n(u)) = F_1(\lim_{n\to\infty} h^n(u)) = F_1(u_2), \;\; u \in (u_1, u_2). \tag{4.4}$$

Combining with (4.3) and (4.4), we have proved that the 2-periodic solution

$$\{u_2, F_1(u_2), u_2, F_1(u_2), \ldots\}$$

of model (1.7) attracts all solutions initiated from $u$ with $u \in (u_1, u_2)$. Similarly, we can prove that all solutions initiated from $(u_2, +\infty)$ are also attracted by this 2-periodic solution by observing that for any $u \in (u_2, +\infty)$, $h(u) < u$ guarantees that the sequence $\{h^n(u)\}_{n=0}^{+\infty}$ is strictly monotonically decreasing and bounded.

Regarding the local stability of the 2-periodic solution $\{u_2, F_1(u_2), u_2, F_1(u_2), \ldots\}$, we first notice that (3.13) implies that $F_n(u)$ is strictly monotonically increasing in $u$ for any $u \in (0,1)$ and $n = 1, 2$. Together with $h(u) > u$ for $u \in (u_1, u_2)$ stated in (4.1), we get $F_1(h(u)) > F_1(u)$, and inductively we get

$$F_1(h^n(u)) > F_1(h^{n-1}(u)), \; n \in \mathbb{Z}, \; u \in (u_1, u_2).$$

That is, $\{F_1(h^n(u))\}_{n=0}^{\infty}$ is strictly monotonically increasing in $n$, bounded below by $F_1(u)$ and bounded above by $F_1(u_2)$ when $u \in (u_1, u_2)$. Together with the fact that $\{h^n(u)\}_{n=0}^{\infty}$ with

$u \in (u_1, u_2)$ is strictly monotonically increasing in $n$ and bounded, for any $\epsilon \in (0, u_2 - u_1)$, if we take $\delta$ such that $\delta < \epsilon$ and $F_1(u_2) - F_1(u_2 - \delta) < \epsilon$, then for any $u \in (u_2 - \delta, u_2)$, one has

$$x_n(1, u_2) - x_n(1, u) < \epsilon, \ n \in \mathbb{Z}.$$

Similarly, for any $\epsilon > 0$, if we take $\delta$ such that $\delta < \epsilon$ and $F_1(u_2 + \delta) - F_1(u_2) < \epsilon$, then for any $u \in (u_2, u_2 + \delta)$, we have

$$x_n(1, u) - x_n(1, u_2) < \epsilon, \ n \in \mathbb{Z}$$

because both $\{F_1(h^n(u))\}_{n=0}^{\infty}$ and $\{h^n(u)\}_{n=0}^{\infty}$ are strictly monotonically decreasing and bounded for $u \in (u_2, u_2 + \delta)$. This completes the proof of the stability of the 2-periodic solution initiated from $u_2$.

The instability of the 2-periodic solution initiated from $u_1$ is obvious since all solutions initiated from $(0, u_1) \cup (u_1, +\infty)$ will be repelled away. This completes the stability analysis stated in Theorem 1.2.

## 5 Discussion

Based on the autonomous difference equation model (1.2) and a complete mathematical analysis of model (1.2) in [16] (see Theorem 1.1), we introduce the nonautonomous difference equation model (1.5) to study the *Wolbachia* spread dynamics in mosquito populations under changing environment. Model (1.7) generates a bistable dynamics in a period-2 environment under condition (1.8) and (1.9) (see Theorem 1.2). That is, model (1.7) has exactly two 2-periodic solutions, among which the smaller one is unstable, and the bigger one is locally asymptotically stable. This result partially confirms the conjecture proposed in [20]. In Theorem 1.2, the unstable 2-periodic solution can be regarded as the introduction threshold of *Wolbachia* infection frequency for *Wolbachia* invasion, and the locally asymptotically stable 2-periodic solution is the one that the infection frequency will ultimately reach. Furthermore, the unique equilibrium point $x_0^* = 0$ of model (1.7) is locally asymptotically stable. We offer the following example to verify the results stated in Theorem 1.2.

*Example* 1 Take

$$f_1 = 0.2, \ h_1 = 0.85, \ f_2 = 0.15, \ h_2 = 0.9. \tag{5.1}$$

Then $\mu_1^* = 0.1553$ and $\mu_2^* = 0.1838$. If we take

$$\mu_1 = 0.1, \ \mu_2 = 0.05, \tag{5.2}$$

then all conditions in Theorem 1.2 are satisfied, and hence model

$$x_{n+1} = \begin{cases} \dfrac{0.9 \cdot 0.8 x_n}{0.85 x_n^2 - 1.05 x_n + 1}, & n = 2k + 1, \\ \dfrac{0.95 \cdot 0.85 x_n}{0.9 x_n^2 - 1.05 x_n + 1}, & n = 2k + 2, \end{cases} \quad k \in \mathbb{Z}(0) \tag{5.3}$$

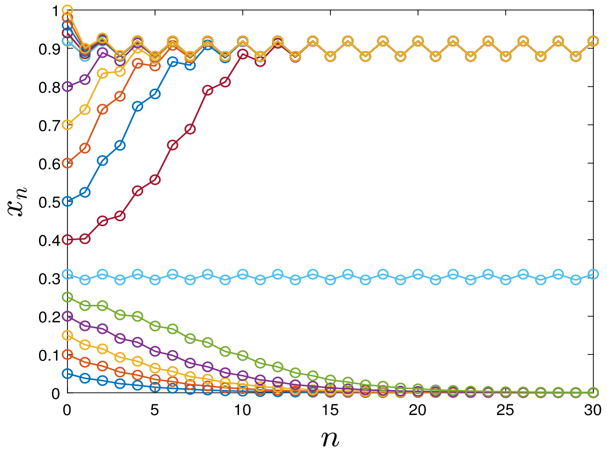

**Figure 3** Numerical verification of the bistable dynamics of model (5.3) shown in Theorem 1.2: the origin $x_0^* = 0$ of model (5.3) is locally asymptotically stable, together with an unstable 2-periodic solution and a locally asymptotically stable 2-periodic solution

has exactly two 2-periodic solutions. Our numerical calculations yield that the unstable 2-periodic solution initiates at approximately $u_1 \approx 0.3096705064533504$, and the stable 2-periodic solution initiates at approximately $u_2 \approx 0.91879$. Besides the two 2-periodic solutions, in Fig. 3, we plot five solutions initiated from $(0, u_1)$, which stay very close to the origin when $n$ exceeds 25. Five solutions initiated from $(u_1, u_2)$ and five solutions initiated from $(u_2, 1)$ are also plotted in Fig. 3, which are attracted by the 2-periodic solution initiated from $u_2$.

Biologically, the unstable 2-periodic solution in Theorem 1.2 serves as a threshold, as the unstable equilibrium point $x^*$ defined in (1.4) of model (1.2), for *Wolbachia* invasion: above which *Wolbachia* infection frequency will be eventually stabilized at the stable 2-periodic solution, and below which *Wolbachia* will be washed out. Hence, it is crucial to explore the dependence of the location of the unstable 2-periodic solution on the values of model parameters in (1.2) to estimate the threshold for *Wolbachia* invasion. Also, to identify where *Wolbachia* will be stabilized, we need to locate the position of the stable 2-periodic solution.

As stated in Example 1, we let $u_1$ and $u_2$ be the initial values of the unstable and stable periodic solution, respectively. When we take

$$h_1 = 0.85,\ f_2 = 0.15,\ h_2 = 0.9,\ \mu_1 = 0.1,\ \mu_2 = 0.05, \tag{5.4}$$

model (5.3) is specified as

$$x_{n+1} = \begin{cases} \dfrac{0.9 \cdot (1 - f_1)x_n}{0.85x_n^2 - (f_1 + 0.85)x_n + 1}, & n = 2k+1, \\ \dfrac{0.95 \cdot (1 - 0.15)x_n}{0.9x_n^2 - (0.15 + 0.9)x_n + 1}, & n = 2k+2, \end{cases} \quad k \in \mathbb{Z}(0). \tag{5.5}$$

To see the dependence of $u_1$ and $u_2$ on $f_1$, we solve model (5.5) to seek $u_1$ and $u_2$ with Matlab for different values of $f_1$. See Table 1 for details.

**Table 1** Seeking the starting points $u_1$ and $u_2$ of periodic solutions of model (5.5) with different values of $f_1$

| $f_1$ | 0 | 0.1 | 0.2 | 0.3 | 0.4 | 0.5 | 0.6 | 0.7 | 0.735013 |
|---|---|---|---|---|---|---|---|---|---|
| $u_1$ | 0.184034 | 0.244143 | 0.309670 | 0.381213 | 0.459647 | 0.546406 | 0.644443 | 0.764793 | 0.845014 |
| $u_2$ | 0.9207 | 0.92 | 0.9188 | 0.9173 | 0.9153 | 0.9115 | 0.9054 | 0.8865 | 0.845014 |

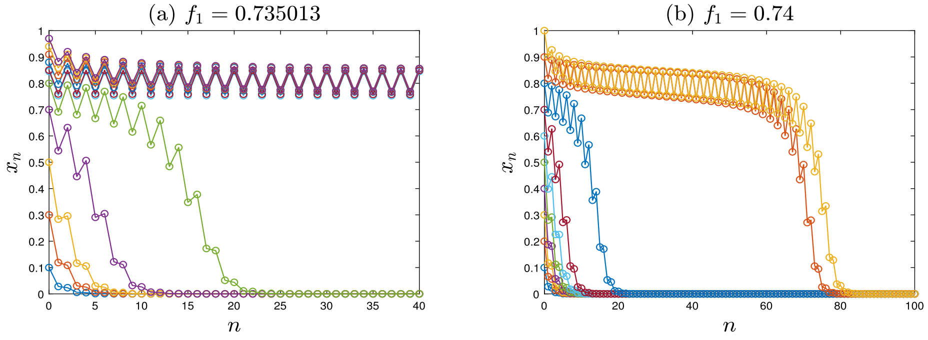

**Figure 4** Model (5.5) undergoes a bifurcation at $f_1 \approx 0.735013$. (a) When $f_1 = 0.735013$, model (5.5) has a unique 2-periodic solution, which is semi-stable. (b) When $f_1 = 0.74 > 0.735013$, the semi-stable 2-periodic solution disappears, and the origin is globally asymptotically stable

Furthermore, with $\mu_1 = 0.1$ and $h_1 = 0.85$ being fixed, we find that $\mu_1 < \mu_1^*$ if $f_1 \in [0, 0.3973) \cup (0.9627, 1)$ and $\mu_1 > \mu_1^*$ if $f_1 \in (0.3973, 0.9627)$. Hence, according to Table 1, the condition $\mu_1 < \mu_1^*$ in Theorem 1.2 is only sufficient, not necessary, to guarantee the existence of exactly two 2-periodic solutions of model (1.7).

When $f_1 = 0.735013$, our numerical simulations show that the two periodic solutions coalesce with $u_1 = u_2 \approx 0.845014$. Figure 4(a) plots five solutions initiated from $(0, 0.845014)$, all of which are close to the origin when $n$ exceeds 20, showing the locally asymptotical stability of the origin. The 2-periodic solution initiated from 0.845014 attracts all solutions starting from $(0.845014, 1)$, showing the stability of the 2-periodic solution from the right-hand side. If we increase $f_1$ to $f_1 = 0.74$, the 2-periodic solution disappears, and Fig. 4(b) manifests that the origin attracts all solutions initiated from $[0, 1]$.

To clearly show the bifurcation of model (5.5) with respect to $f_1$, we plot the location of $u_1$ and $u_2$ against $f_1$ in Fig. 5(a). The white region denotes the situation of two periodic solutions, and the yellow region denotes the case of no periodic solutions. The two areas overlap at the bifurcation point. Following the same procedure, we can numerically seek the bifurcation point of $h_1 \approx 0.087158$ when

$$f_1 = 0.2,\ \mu_1 = 0.1,\ f_2 = 0.15,\ h_2 = 0.9,\ \mu_2 = 0.05.$$

When $h_1 \in [0, 0.087158)$, model

$$x_{n+1} = \begin{cases} \dfrac{0.72x_n}{h_1 x_n^2 - (0.2 + h_1)x_n + 1}, & n = 2k+1, \\ \dfrac{0.95 \cdot 0.85x_n}{0.9x_n^2 - 1.05x_n + 1}, & n = 2k+2, \end{cases} \qquad k \in \mathbb{Z}(0), \tag{5.6}$$

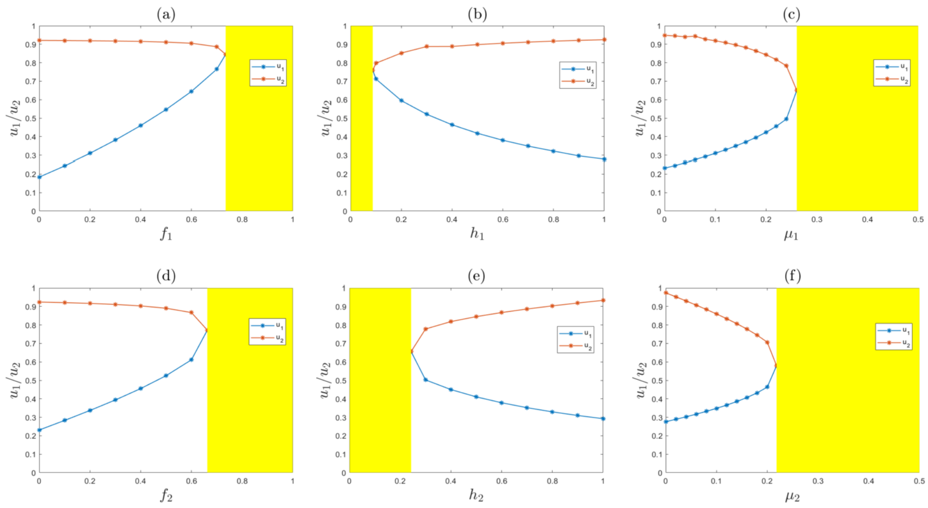

**Figure 5** The dependence of $u_1$ and $u_2$ on model parameters. (a) Model (5.5) undergoes a bifurcation at $f_1 \approx 0.735013$. (b) Model (5.6) undergoes a bifurcation at $h_1 \approx 0.087158$. (c) The bifurcation of $\mu_1 \approx 0.260601$ when taking $f_1 = 0.2$, $h_1 = 0.85$, $f_2 = 0.15$, $h_2 = 0.9$, $\mu_2 = 0.05$. (d) Take $f_1 = 0.2$, $h_1 = 0.85$, $\mu_1 = 0.1$, $h_2 = 0.9$, $\mu_2 = 0.05$, the bifurcation of $f_2 \approx 0.662721$. (e) The bifurcation of $h_2 \approx 0.243016$ if we take $f_1 = 0.2$, $h_1 = 0.85$, $\mu_1 = 0.1$, $f_2 = 0.15$, $\mu_2 = 0.05$. (f) Take $f_1 = 0.2$, $h_1 = 0.85$, $\mu_1 = 0.1$, $f_2 = 0.15$, $h_2 = 0.9$, the bifurcation of $\mu_2 \approx 0.218415$. The yellow areas in (a)-(f) represent cases where model (5.6) has no periodic solutions

has no 2-periodic solutions, and the origin is globally asymptotically stable. At $h_1 \approx 0.087158$, a unique 2-periodic solution starting from $u_1 = u_2 \approx 0.759034$. As the increase in $h_1$, $u_1$ decreases, and $u_2$ increases. See Fig. 5(b) for the location of $u_1$ and $u_2$ when $h_1 = 0.087158, 0.1, 0.2, 0.3, \ldots, 1$. For completeness, we plot the other four cases in Fig. 5(c)–(f). The above observations imply that the nonautonomous 2-period model (1.7) has at most two 2-periodic solutions. Aside from the cases where (1.8) does not hold, we defer the general cases with $T > 2$ in (1.6) to future research.

### Abbreviations

WMP, World Mosquito Program; CI, cytoplasmic incompatibility.

### Author contributions

All authors contributed equally to the writing of this paper. All authors read and approved the final manuscript.

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### Data availability

Not applicable.

## Declarations

### Competing interests

The authors declare no competing interests.

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