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Research article

The effect of migration on transmission of *Wolbachia* in *Nilaparvata lugens*

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Abstract: Brown planthopper *Nilaparvata lugens*, which can transmit rice ragged stunt virus, is a serious and damaging pest to rice plants. Rice plants can protect themselves from the associated diseases of *N.lugens* by either suppressing or replacing *N.lugens* by releasing *N.lugens* infected by a special strain of *Wolbachia wStri*. The long-distance migration habit of *N.lugens* is one of the important precursors leading up to the large-scale occurrence of *N.lugens*. To study the effect of migration on the transmission of *Wolbachia* in *N.lugens*, a *Wolbachia* spreading dynamics model with migration of *N.lugens* between two patches is put forward. The existence and local stability conditions of equilibrium points of the system and its subsystems are obtained. Moreover, the effects of migration on the dynamic properties and the control of *N.lugens* are analyzed; the results show that the system can exhibit a bistable phenomenon, and the migration can change the stability of equilibrium infected with *wStri* from stable to unstable. The quantitative control methods for the migration of the insect *N.lugens* are proposed, which provide a theoretical guidance for future field experiments. Lastly, we use the Markov chain Monte Carlo (MCMC) method to estimate the parameters of the wild *N.lugens* migration model based on limited observational data; the numerical simulation results show that migration can increase the quantity of *N.lugens*, which is consistent with the relevant experimental results.

Keywords: *Wolbachia*; *Nilaparvata lugens*; Migration; stability; mathematical modeling

1. Introduction

Brown planthopper *Nilaparvata lugens* (Stål) (Hereinafter referred to as *N.lugens*) is a monophagous insect species, which causes irreversible damage to rice mainly by either piercing or sucking the phloem juice of rice and transmitting Rice Ragged Stunt Viruses (RRSV) [1]; the frequent occurrence of *N.lugens* seriously affects food security worldwide. A number of studies have been performed to develop technology that controls agricultural pests by utilizing *Wolbachia* [2–10]. Researchers have identified an endosymbiotic *Wolbachia* strain, *wStri*, from a small planthopper *Laodelphax striatellus* (Fallén) that induces cytoplasmic incompatible (CI) phenotypes in its host [3–5]. CI is a phenomenon of either embryo death or offspring sterility when the male insects infected with *Wolbachia* mate with females that are either uninfected or infected with a different strain of *Wolbachia* [5–10]. A study from 2020 reported that *Wolbachia wStri* can cause cytoplasmic incompatibility in *N.lugens* and can significantly inhibit the infection and transmission of rice ragged stunt viruses (RRSV) in a laboratory environment [2]. This is a breakthrough achievement in the development of a control mechanism of rice planthopper by applying endosymbiotic bacteria. The artificial cultivation of the *N.lugens* line showed the required characteristics of either population replacement or population suppression in the laboratory.

Because *N.lugens* is a rice pest with the habit of long-distance migration [11], and the total number of migrating *N.lugens* is often in the hundreds of millions, they have a huge impact on the agricultural ecosystem. Over the years, the migration rule of *N.lugens* in China has been discovered mainly through modern monitoring technology and international cooperation research: under suitable conditions, *N.lugens* migrate from the southern rice area in spring, then fly northward alongside monsoons to the Huaibei rice area, and migrate back to the south in autumn [12–17]. The whole migration process spans across a large area in a large amount of time, which is one of the main causes for the large-scale *N.lugens* disaster. The existing dynamics models of *N.lugens* generally based the population migration on the diffusion mode between two patches [18–21]. In 2019, Vattikuti et al. established linear and nonlinear differential equation models in which the growth rate of *N.lugens* is described as a function of temperature, and further estimated the bioclimatological threshold under the influence of temperature [19]. Additionally, Thuy et al. proposed an ordinary differential equation model of *N.lugens* where they rapidly disperse in two patches with a stage structure [20]. In 2022, Nguyen et al. constructed a herbivore (*N.lugens*) -host plant (rice) model of *N.lugens* dispersal between two adjacent patches, and studied the effect of monsoons on the interaction between *N.lugens* and rice [21]. However, the seasonality of *N.lugens* migration was not fully reflected in the aforementioned models, and more importantly, these models did not consider the spread of *Wolbachia* in *N.lugens*. Although we previously studied the transmission of *Wolbachia* in *N.lugens* [5, 6], we did not consider their migration.

In addition, there are some literatures that use the reaction diffusion equation model to study the transmission dynamics of *Wolbachia* in a mosquito population [22–25]. Ref. [22, 23] studied the spreading dynamics of *Wolbachia* in mosquitoes that activate and diffuse within a relatively isolated and limited region. The diffusion problem of mosquitoes within a free boundary region was also discussed in Ref. [24]. Liu et al. proposed a coupled model to evaluate the efficiency of *Wolbachia* on a mosquito control [25]. However, the conception of the migration of *N.lugens* is different from that of the mosquitoes diffusion. The main characteristics of *N.lugens* migration are seasonality and the simultaneously uniform tropism (i.e., *N.lugens* migration in one direction is influenced by the unidirectional carrier air flow. In this case, the small random diffusion effect in other directions is negligible, where the carrier air flow is a southeast wind in summer and a northeast wind in autumn [26]). Therefore, *N.lugens* migration can not be studied simply by a research method based on diffusion behavior. In this article, we define a migration coefficient based on the population proportion to construct a *Wolbachia* transmission model that reflects the *N.lugens* migration. Through in-depth research on the basic dynamic characteristics of the model, we will analyze how to limit the control effect of *Wolbachia* during their migration on brown planthoppers.

This paper is organized as follows. In Section 2, the *Wolbachia* spreading dynamic model with the migration of *N.lugens* is introduced. In Sections 3 and 4, we analyze the existence and stability of equilibria for the main model. The global stabilities of three subsystems are studied in Section 5. Then, we provide numerical simulations for the stability of equilibria in Section 6. A discussion for the impact of migration on the dynamic properties of the system and the control effects of *N.lugens* are included in section 7. Finally, we give our conclusions in section 8.

2. Model

2.1. A general diffusion model with two patches

In order to establish the migration model of *N.lugens*, we give the following assumptions:

- Based on the data of the insect trap catches under lights and the data of field surveys of insects in Ref. [11], we assume that *N.lugens* migrates between two areas, where area 1 is referred to as the main source area of the northward migrants of *N.lugens*, and area 2 is referred to as the main destination area of the northward migrants of *N.lugens*.
- *N.lugens* infected with *wStri* is only released in area 1.
- *N.lugens* mainly migrates northward from area 1 to area 2 in the spring, and it mainly migrates southward from area 2 to area 1 in the autumn.

Let $I^{(i)}(t)$ and $U^{(i)}(t)$ represent the number of the *wStri*-infected *N.lugens* and the uninfected *N.lugens* in time t in the area i, respectively. Moreover, the total number of *N.lugens* within area 1 and area 2 are denoted as $N^{(i)} = I^{(i)}(t) + U^{(i)}(t)$, respectively, $i = 1, 2$.

When population migration is not considered, the *N.lugens* population only interacts within each patch. Thus, based on the modeling method in [5, 6], it is easy to obtain the following interaction dynamic model of the *N.lugens* population in each patch:

$$\begin{cases} \frac{\mathrm{d}I^{(1)}(t)}{\mathrm{d}t} = bI^{(1)}(t) - d_1 I^{(1)}(t)N^{(1)}(t), \\ \frac{\mathrm{d}U^{(1)}(t)}{\mathrm{d}t} = bU^{(1)}(t)\frac{(1-\xi)I^{(1)}(t)}{N^{(1)}(t)} + bU^{(1)}(t)\frac{U^{(1)}(t)}{N^{(1)}(t)} - d_2 U^{(1)}(t)N^{(1)}(t), \\ \frac{\mathrm{d}U^{(2)}(t)}{\mathrm{d}t} = bU^{(2)}(t) - d_2 U^{(2)}(t)N^{(2)}(t), \end{cases} \tag{2.1}$$

where *N.lugens* infected with *wStri* has a perfect maternal transmission characteristic, and *wStri* can induce higher CI levels for the uninfected *N.lugens* female [2, 5] and the CI intensity of the male *N.lugens* infected with *wStri* I_M against the uninfected female *N.lugens* U_F be $\xi \in (0, 1)$. According to a two-sex model (1) in Ref [6], b denotes the half natural birth rate of *N.lugens*. Note that *N.lugens* infected with *wLug* is not considered here. d_1 and d_2 denote the decay rate constants of the individuals infected with *wStri* and the uninfected, respectively.

When population migration is taken into the aforementioned system (2.1), it is transfered to the following general discrete diffusion system (2.2):

$$\begin{cases} \frac{\mathrm{d}I^{(1)}(t)}{\mathrm{d}t} = & bI^{(1)}(t) - d_1 I^{(1)}(t)N^{(1)}(t) - n_{12}I^{(1)}(t) + n_{21}I^{(2)}(t), \\ \frac{\mathrm{d}U^{(1)}(t)}{\mathrm{d}t} = & bU^{(1)}(t)\frac{(1-\xi)I^{(1)}(t)}{N^{(1)}(t)} + bU^{(1)}(t)\frac{U^{(1)}(t)}{N^{(1)}(t)} - d_2U^{(1)}(t)N^{(1)}(t) - m_{12}U^{(1)}(t) + m_{21}U^{(2)}(t), \\ \frac{\mathrm{d}I^{(2)}(t)}{\mathrm{d}t} = & bI^{(2)} - d_1 I^{(2)}(t)N^{(2)}(t) + n_{12}I^{(1)}(t) - n_{21}I^{(2)}(t), \\ \frac{\mathrm{d}U^{(2)}(t)}{\mathrm{d}t} = & bU^{(2)}(t)\frac{(1-\xi)I^{(2)}(t)}{N^{(2)}(t)} + bU^{(2)}(t)\frac{U^{(2)}(t)}{N^{(2)}(t)} - d_2U^{(2)}(t)N^{(2)}(t) + m_{12}U^{(1)}(t) - m_{21}U^{(2)}(t), \end{cases} \tag{2.2}$$

where n_{ij} and m_{ij} stand for the average migration rate of the *wStri*-infected *N.lugens* and the uninfected *N.lugens* from area i to area j, respectively, where $i, j = 1, 2$. It must be specified that all parameters of model (2.2) have positive values. Notice that the average migration rates of *N.lugens* are all constant, and system (2.2) can not fully reflect the characteristics of *N.lugens* migration affected by a monsoon. Thus, we need to develop a *N.lugens* migration model that better reflects the effects of the season.

2.2. Migration model

The diffusion coefficient is generally related to population density of the two patches. Many predator-prey models with diffusion assume that the diffusion coefficient is a linear function of the diffused species density; some of these models assume that only one species has this dispersal property [27], while others assume that there is a dispersal effect in only one monsoon direction [21]. The system we consider is markedly different from these models. First, two *N.lugens* species do not display a predator-prey relationship. Second, *N.lugens* migration is different from population diffusion, in which the directions of migration are different at different seasons. Simply considering *N.lugens* migration in one direction does not reflect the bidirectional characteristics of migration. Moreover, the migration coefficient is not a linear function of the population density of the initial source area because the linear function can not reflect the phased one-way migration phenomenon. Therefore, it is key to construct a migration coefficient of *N.lugens* which can reflect the influence of the season.

Since the migration of *N.lugens* is influenced by the season, its migration coefficient should reflect the seasonal factor. In the spring, *N.lugens* migrates northward due to a southeast wind from area 1 to area 2. At this time, the number of *N.lugens* in area 1 is much greater than in area 2. When *N.lugens* begins to migrate back due to a northeast wind from the northern rice area 2 to the southern rice area 1 in autumn, the number of *N.lugens* in area 2 is much greater than in area 1. We use the ratio $\frac{N^{(i)}}{N^{(j)}}$, which represent the number of *N.lugens* in two areas as a diffusion coefficient, to accurately reflect the seasonal migration characteristics of *N.lugens* $(i, j = 1, 2)$. We call this coefficient the ratio dependent migration coefficient. Substituting n_{ij} and m_{ij} with $\frac{N^{(i)}}{N^{(j)}}$ in system (2.2), we obtain the following migration system (2.3):

$$\begin{cases} \frac{\mathrm{d}I^{(1)}(t)}{\mathrm{d}t} = & bI^{(1)}(t) - d_1 I^{(1)}(t)N^{(1)}(t) - \frac{b_{12}N^{(1)}(t)}{N^{(2)}(t)}I^{(1)}(t) + \frac{a_{21}N^{(2)}(t)}{N^{(1)}(t)}I^{(2)}(t), \\ \frac{\mathrm{d}U^{(1)}(t)}{\mathrm{d}t} = & bU^{(1)}(t)\frac{(1-\xi)I^{(1)}(t)}{N^{(1)}(t)} + bU^{(1)}(t)\frac{U^{(1)}(t)}{N^{(1)}(t)} - d_2U^{(1)}(t)N^{(1)}(t) - \frac{\bar{b}_{12}N^{(1)}(t)}{N^{(2)}(t)}U^{(1)}(t) + \frac{\bar{a}_{21}N^{(2)}(t)}{N^{(1)}(t)}U^{(2)}(t), \\ \frac{\mathrm{d}I^{(2)}(t)}{\mathrm{d}t} = & bI^{(2)}(t) - d_1 I^{(2)}(t)N^{(2)}(t) + \frac{a_{12}N^{(1)}(t)}{N^{(2)}(t)}I^{(1)}(t) - \frac{b_{21}N^{(2)}(t)}{N^{(1)}(t)}I^{(2)}(t), \\ \frac{\mathrm{d}U^{(2)}(t)}{\mathrm{d}t} = & bU^{(2)}(t)\frac{(1-\xi)I^{(2)}(t)}{N^{(2)}(t)} + bU^{(2)}(t)\frac{U^{(2)}(t)}{N^{(2)}(t)} - d_2U^{(2)}(t)N^{(2)}(t) + \frac{\bar{a}_{12}N^{(1)}(t)}{N^{(2)}(t)}U^{(1)}(t) - \frac{\bar{b}_{21}N^{(2)}(t)}{N^{(1)}(t)}U^{(2)}(t), \end{cases} \tag{2.3}$$

with the initial value

$$I^{(1)}(0) > 0, U^{(1)}(0) \geq 0, I^{(2)}(0) \geq 0, U^{(2)}(0) \geq 0, \tag{2.4}$$

where a_{12} (a_{21}) and $\bar{a}_{12}$ ($\bar{a}_{21}$) denote the successful landing rate of the *wStri*-infected *N.lugens* and the uninfected *N.lugens* after a long-distance northward (or southward) migration, respectively, and b_{12} (b_{21}) and $\bar{b}_{12}$ ($\bar{b}_{21}$) denote the successful take-off rate of the *wStri*-infected *N.lugens* and the uninfected *N.lugens* as northward (or southward) migration, respectively. a_{12}, $\bar{a}_{12}$, a_{21}, $\bar{a}_{21}$, b_{12}, $\bar{b}_{12}$, b_{21}, $\bar{b}_{21} \in [0, 1]$. Clearly, the successful take-off rate is more than the successful landing rate (i.e., $b_{12} > a_{12}, b_{21} > a_{21}, \bar{b}_{12} > \bar{a}_{12}$ and $\bar{b}_{21} > \bar{a}_{21}$). We will analyze the dynamics of system (2.3) with the initial value condition (2.4) under the aforementioned basic restriction conditions.

System (2.3) can be regarded as the phased migration model in the first and second half of the year. In the spring, the number of *N.lugens* in area 1 is much greater than in area 2. The major part of the last two expressions reflecting the migration in the first two equations of system (2.3) is the minus term, and the major part of the last two expressions reflecting the migration in the last two equations of system (2.3) is the plus term, which reveals the reality that there is a significant northward migration of *N.lugens* in spring, but not an obvious return to the south. On the contrary, the number of *N.lugens* in area 2 is much greater than in area 1 in autumn; this shows that *N.lugens* has a significant southward migration, but not an obvious northward migration. It essentially reflects the bidirectional property of *N.lugens* migration. Additionally, system (2.3) also reflects a simultaneously uniform tropism. Therefore, except for the migration coefficient being a function of population density, it is multiplied by the population density of the corresponding type of *N.lugens*, which reflects that the simultaneous uniform tropism effect increases when the population density increases during the same season.

Denote the right function of system (2.3) by $\mathbf{F}(I^{(1)}, U^{(1)}, I^{(2)}, U^{(2)}) = (f_1, f_2, f_3, f_4)^T$. Since

$$\lim_{(I^{(1)},U^{(1)},I^{(2)},U^{(2)})\to(0,0,0,0)}\mathbf{F}(I^{(1)}, U^{(1)}, I^{(2)}, U^{(2)}) = \mathbf{0},$$

the right-hand side function f_i of system (2.3) can be continuously extended to the origin $(0, 0, 0, 0)$ by $f_i(0, 0, 0, 0) = 0$ $(i = 1, 2, 3, 4)$. Thus, system (2.3) is well-defined in the following region:

$$R^4_+ = \{(I^{(1)}, U^{(1)}, I^{(2)}, U^{(2)}) : I^{(1)} \geq 0, U^{(1)} \geq 0, I^{(2)} \geq 0, U^{(2)} \geq 0\}.$$

3. The nonnegativity and boundedness of solutions for system (2.3)

In this section, we will analyze the nonnegativity and boundedness of solutions for system (2.3).

Theorem 1. *Suppose that* $(I^{(1)}(t), U^{(1)}(t), I^{(2)}(t), U^{(2)}(t))$ *is any solution of system (2.3) with the initial condition (2.4). Then, it is nonnegative and bounded.*

Proof. **Nonnegativity**. When $I^{(1)} = 0$, $U^{(1)} \geq 0$, $I^{(2)} \geq 0$ and $U^{(2)} \geq 0$, we have the following:

$$f_1(0, U^{(1)}, I^{(2)}, U^{(2)}) = \frac{a_{21}N^{(2)}I^{(2)}}{U^{(1)}} \geq 0.$$

Moreover, when $I^{(1)} \geq 0$, $U^{(1)} = 0$, $I^{(2)} \geq 0$ and $U^{(2)} \geq 0$, we have the following:

$$f_2(I^{(1)}, 0, I^{(2)}, U^{(2)}) = \frac{\bar{a}_{21}N^{(2)}U^{(2)}}{I^{(1)}} \geq 0.$$

Similarly, when $I^{(1)} \geq 0$, $U^{(1)} \geq 0$, $I^{(2)} = 0$ and $U^{(2)} \geq 0$, we have the following:

$$f_3(I^{(1)}, U^{(1)}, 0, U^{(2)}) = \frac{a_{12}N^{(1)}I^{(1)}}{U^{(2)}} \geq 0,$$

when $I^{(1)} \geq 0$, $U^{(1)} \geq 0$, $I^{(2)} \geq 0$ and $U^{(2)} = 0$, we have

$$f_4(I^{(1)}, U^{(1)}, I^{(2)}, 0) = \frac{\bar{a}_{12} N^{(1)} U^{(1)}}{I^{(2)}} \geq 0.$$

According to proposition B.7 in [28], it follows that

$$(I^{(1)}(t), U^{(1)}(t), I^{(2)}(t), U^{(2)}(t)) \in R_+^4, t \geq 0.$$

Thus, the solution of system (2.3) with the initial condition (2.4) is nonnegative.

Boundedness. Let $W(t) = I^{(1)}(t) + U^{(1)}(t) + I^{(2)}(t) + U^{(2)}(t)$. From the nonnegativity of solution which has been proven, and the basic constraints of parameters $b_{12} > a_{12}, b_{21} > a_{21}, \bar{b}_{12} > \bar{a}_{12}$ and $\bar{b}_{21} > \bar{a}_{21}$, we have the following:

$$\begin{aligned}\frac{\mathrm{d}W(t)}{\mathrm{d}t} \leq & bI^{(1)} - d_1 {I^{(1)}}^2 + b(1-\xi)U^{(1)} + bU^{(1)} - d_2 {U^{(1)}}^2 \\ & + bI^{(2)} - d_1 {I^{(2)}}^2 + b(1-\xi)U^{(2)} + bU^{(2)} - d_2 {U^{(2)}}^2.\end{aligned}$$

Then, we have the following:

$$\begin{aligned}\frac{\mathrm{d}W}{\mathrm{d}t} + bW \leq & 2bI^{(1)} - d_1 {I^{(1)}}^2 + b(3-\xi)U^{(1)} - d_2 {U^{(1)}}^2 \\ & + 2bI^{(2)} - d_1 {I^{(2)}}^2 + b(3-\xi)U^{(2)} + bU^{(2)} - d_2 {U^{(2)}}^2.\end{aligned}$$

Therefore, we obtain the following:

$$\begin{aligned}\frac{\mathrm{d}W}{\mathrm{d}t} + bW \leq & -d_1\Big(\Big(I^{(1)} - \frac{b}{d_1}\Big)^2 - \frac{b^2}{d_1^2}\Big) \\ & - d_2\Big(\Big(U^{(1)} - \frac{b(3-\xi)}{2d_2}\Big)^2 - \frac{b^2(3-\xi)^2}{4d_2^2}\Big) \\ & - d_1\Big(\Big(I^{(2)} - \frac{b}{d_1}\Big)^2 - \frac{b^2}{d_1^2}\Big) \\ & - d_2\Big(\Big(U^{(2)} - \frac{b(3-\xi)}{2d_2}\Big)^2 - \frac{b^2(3-\xi)^2}{4d_2^2}\Big) \\ \leq & \frac{2b^2}{d_1} + \frac{b^2(3-\xi)^2}{2d_2^2} \triangleq L,\end{aligned}$$

namely, $\frac{\mathrm{d}W}{\mathrm{d}t} + bW \leq L$.

It follows from the differential inequality theory that $0 \leq W(t) \leq \frac{L}{b}(1 - e^{-bt}) + W(0)e^{-bt}$. Therefore, we get $0 \leq W(t) \leq L/b$ as $t \to +\infty$.

Consequently the solution $(I^{(1)}(t), U^{(1)}(t), I^{(2)}(t), U^{(2)}(t))$ starting from region R_4^+ is restricted to the following region:

$$\Lambda = \{(I^{(1)}, U^{(1)}, I^{(2)}, U^{(2)}) \in R_4^+ : 0 \leq I^{(1)}(t) + U^{(1)}(t) + I^{(2)}(t) + U^{(2)}(t) \leq \frac{L}{b}\},$$

where $L = \frac{2b^2}{d_1} + \frac{b^2(3-\xi)^2}{2d_2^2}$. □

The aforementioned region Λ is the positive invariant set with respect to system (2.3). The nonnegative solution for system (2.3) shows that the population density of *N.lugens* can not be negative, and the boundedness of the solution for system (2.3) indicates that the population density of *N.lugens* in the wild can not increase indefinitely, which are consistent with reality.

4. The existence and the stability of equilibria

4.1. The existence of equilibria

Now we discuss the existence of equilibria of system (2.3). It is easy to see that system (2.3) always has a trivial equilibrium point $E_0(0,0,0,0)$. In addition, system (2.3) may exist as equilibrium infected with *wStri* $E_1(\bar{I}^{(1)},0,\bar{I}^{(2)},0)$, the uninfected equilibrium $E_2(0,\hat{U}^{(1)},0,\hat{U}^{(2)})$ and the positive equilibrium $E_3(\tilde{I}^{(1)},\tilde{U}^{(1)},\tilde{I}^{(2)},\tilde{U}^{(2)})$.

1). The existence analysis of the equilibrium infected with *wStri* E_1. Equilibrium $E_1(\bar{I}^{(1)},0,\bar{I}^{(2)},0)$ should satisfy the following algebraic equations:

$$\begin{cases} b\bar{I}^{(1)} - d_1(\bar{I}^{(1)})^2 - \frac{b_{12}(\bar{I}^{(1)})^2}{\bar{I}^{(2)}} + \frac{a_{21}(\bar{I}^{(2)})^2}{\bar{I}^{(1)}} = 0, \\ b\bar{I}^{(2)} - d_1(\bar{I}^{(2)})^2 + \frac{a_{12}(\bar{I}^{(1)})^2}{\bar{I}^{(2)}} - \frac{b_{21}(\bar{I}^{(2)})^2}{\bar{I}^{(1)}} = 0, \end{cases}$$

where $\bar{I}^{(i)} > 0$, $i = 1, 2$. Simplifying the above equations gives two equivalent equations:

$$\begin{cases} b - d_1\bar{I}^{(1)} - \frac{b_{12}\bar{I}^{(1)}}{\bar{I}^{(2)}} + \frac{a_{21}(\bar{I}^{(2)})^2}{(\bar{I}^{(1)})^2} = 0, \\ b - d_1\bar{I}^{(2)} + \frac{a_{12}(\bar{I}^{(1)})^2}{(\bar{I}^{(2)})^2} - \frac{b_{21}\bar{I}^{(2)}}{\bar{I}^{(1)}} = 0. \end{cases} \tag{4.1}$$

Transferring the terms $-d_1\bar{I}^{(1)}$ and $-d_1\bar{I}^{(2)}$ to the right-hand side of (4.1) and dividing the first equation with the second equation, we obtain the following:

$$\frac{b - b_{12}\frac{\bar{I}^{(1)}}{\bar{I}^{(2)}} + a_{21}\frac{(\bar{I}^{(2)})^2}{(\bar{I}^{(1)})^2}}{b + a_{12}\frac{(\bar{I}^{(1)})^2}{(\bar{I}^{(2)})^2} - b_{21}\frac{\bar{I}^{(2)}}{\bar{I}^{(1)}}} = \frac{\bar{I}^{(1)}}{\bar{I}^{(2)}}. \tag{4.2}$$

Let $\frac{\bar{I}^{(1)}}{\bar{I}^{(2)}} = p$. By substituting it into formula (4.2), we obtain the following:

$$\frac{b - b_{12}p + a_{21}\frac{1}{p^2}}{b + a_{12}p^2 - b_{21}\frac{1}{p}} = p. \tag{4.3}$$

Simplifying and rearranging formula (4.3) produces a polynomial equation with respect to p:

$$a_{12}p^5 + (b + b_{12})p^3 - (b + b_{21})p^2 - a_{21} = 0. \tag{4.4}$$

Since a_{12}, $b+b_{12}$, $b+b_{21}$ and a_{21} are greater than 0, by ignoring those terms with the zero coefficient, the number of times of the coefficient signs changes for Eq (4.4) is 1. According to Descartes' Rule of Signs, we assert that Eq (4.4) has only one positive real root, which is denoted as c_1. As for either the remaining complex roots or the non-positive real roots, if they exist, they do not meet the requirements.

Thus, by substituting $\frac{\bar{I}^{(1)}}{\bar{I}^{(2)}} = c_1$ into Eq (4.1), and noticing that $\bar{I}^{(1)} = c_1\bar{I}^{(2)}$, we have

$$\begin{cases} \bar{I}^{(1)} = \frac{1}{d_1c_1^2}(a_{21} + bc_1^2 - b_{12}c_1^3), \\ \bar{I}^{(2)} = \frac{1}{d_1c_1^3}(a_{21} + bc_1^2 - b_{12}c_1^3), \end{cases} \tag{4.5}$$

or

$$\begin{cases} \bar{I}^{(1)} = \frac{1}{d_1}(a_{12}c_1^3 + bc_1 - b_{21}), \\ \bar{I}^{(2)} = \frac{1}{d_1c_1}(a_{12}c_1^3 + bc_1 - b_{21}). \end{cases} \tag{4.6}$$

Note that $\bar{I}^{(1)}$ in formula (4.5) is equivalent to that of formula (4.6), and so is also $\bar{I}^{(2)}$. Therefore, we obtain the existence of equilibrium E_1 as follows.

Theorem 2. *If $a_{21} + bc_1^2 - b_{12}c_1^3 > 0$ or $a_{12}c_1^3 + bc_1 - b_{21} > 0$, then system (2.3) exists as one equilibrium infected with wS tri $E_1(\bar{I}^{(1)}, 0, \bar{I}^{(2)}, 0)$, where $\bar{I}^{(1)}$ and $\bar{I}^{(2)}$ are shown in formula (4.5) or (4.6), and c_1 is the positive real root of Eq (4.4).*

2). The existence analysis of equilibrium $E_2(0, \hat{U}^{(1)}, 0, \hat{U}^{(2)})$. Similarly, equilibrium E_2 should satisfy the following equations:

$$\begin{cases} b\hat{U}^{(1)} - d_2(\hat{U}^{(1)})^2 - \bar{b}_{12}\frac{(\hat{U}^{(1)})^2}{\hat{U}^{(2)}} + \bar{a}_{21}\frac{(\hat{U}^{(2)})^2}{\hat{U}^{(1)}} = 0, \\ b\hat{U}^{(2)} - d_2(\hat{U}^{(2)})^2 + \bar{a}_{12}\frac{(\hat{U}^{(1)})^2}{\hat{U}^{(2)}} - \bar{b}_{21}\frac{(\hat{U}^{(2)})^2}{\hat{U}^{(1)}} = 0, \end{cases}$$

where $\hat{U}^{(i)} > 0$, $i = 1, 2$.

Simplifying the equation above, we obtain that

$$\begin{cases} b - d_2\hat{U}^{(1)} - \bar{b}_{12}\frac{\hat{U}^{(1)}}{\hat{U}^{(2)}} + \bar{a}_{21}\frac{(\hat{U}^{(2)})^2}{(\hat{U}^{(1)})^2} = 0, \\ b - d_2\hat{U}^{(2)} + \bar{a}_{12}\frac{(\hat{U}^{(1)})^2}{(\hat{U}^{(2)})^2} - \bar{b}_{21}\frac{\hat{U}^{(2)}}{\hat{U}^{(1)}} = 0, \end{cases} \tag{4.7}$$

Thus, we get

$$\frac{b - \bar{b}_{12}\frac{\hat{U}^{(1)}}{\hat{U}^{(2)}} + \bar{a}_{21}\frac{(\hat{U}^{(2)})^2}{(\hat{U}^{(1)})^2}}{b + \bar{a}_{12}\frac{(\hat{U}^{(1)})^2}{(\hat{U}^{(2)})^2} - \bar{b}_{21}\frac{\hat{U}^{(2)}}{\hat{U}^{(1)}}} = \frac{\hat{U}^{(1)}}{\hat{U}^{(2)}}.$$

Let $\frac{\hat{U}^{(1)}}{\hat{U}^{(2)}} = q$. By substituting it into the formula above, the following polynomial equation can be easily obtained via simple algebraic operation:

$$\bar{a}_{12}q^5 + (b + \bar{b}_{12})q^3 - (b + \bar{b}_{21})q^2 - \bar{a}_{21} = 0. \tag{4.8}$$

Because of $\bar{a}_{12}$, $b + \bar{b}_{12}$,$b + \bar{b}_{21}$ and $\bar{a}_{21}$ are all greater than 0, it follows from Descartes' Rule of Signs that Eq (4.8) has only a positive real root, which is denoted as c_2. As for either the remaining complex roots or non-positive real roots, if they exist, they do not meet the requirements.

Substituting $\frac{\hat{U}^{(1)}}{\hat{U}^{(2)}}$ with c_2 in formula (4.7), we have

$$\begin{cases} \hat{U}^{(1)} = \frac{1}{d_2c_2^2}(\bar{a}_{21} + bc_2^2 - \bar{b}_{12}c_2^3), \\ \hat{U}^{(2)} = \frac{1}{d_2c_2^3}(\bar{a}_{21} + bc_2^2 - \bar{b}_{12}c_2^3). \end{cases} \tag{4.9}$$

or

$$\begin{cases}\hat{U}^{(1)} = \frac{1}{d_2}(\bar{a}_{12}c_2^3 + bc_2 - \bar{b}_{21}),\\ \hat{U}^{(2)} = \frac{1}{d_2 c_2}(\bar{a}_{12}c_2^3 + bc_2 - \bar{b}_{21}),\end{cases} \tag{4.10}$$

It is easy to see that formulas (4.9) and (4.10) are actually equivalent from the calculation process above. Thus, we obtain the existence result of equilibrium E_2 as follows.

Theorem 3. *If* $\bar{a}_{21} + bc_2^2 - \bar{b}_{12}c_2^3 > 0$ *or* $\bar{a}_{12}c_2^3 + bc_2 - \bar{b}_{21} > 0$, *then system (2.3) has an uninfected equilibrium* $E_2(0, \hat{U}^{(1)}, 0, \hat{U}^{(2)})$, *where* $\hat{U}^{(1)}$ *and* $\hat{U}^{(2)}$ *are shown in formula (4.9) or (4.10), and* c_2 *satisfies Eq (4.8).*

4.2. The stability of equilibrium

In this subsection, we discuss the stability of equilibrium for system (2.3). For the sake of convenience, let symbols $E(I^{(1)}, U^{(1)}, I^{(2)}, U^{(2)})$ be any equilibrium of system (2.3), and let $J_E = (f_{ij})_{4\times 4}$ be the Jacobi matrix corresponding system (2.3) at equilibrium E, where

$$\begin{aligned}
f_{11} =& b - d_1N^{(1)} - d_1I^{(1)} - \frac{b_{12}(I^{(1)} + N^{(1)})}{N^{(2)}} - \frac{a_{21}N^{(2)}I^{(2)}}{(N^{(1)})^2};\\
f_{12} =& - d_1I^{(1)} - \frac{b_{12}I^{(1)}}{N^{(2)}} - \frac{a_{21}N^{(2)}I^{(2)}}{(N^{(1)})^2};\\
f_{13} =& \frac{b_{12}N^{(1)}I^{(1)}}{(N^{(2)})^2} + \frac{a_{21}(I^{(2)} + N^{(2)})}{N^{(1)}};\\
f_{14} =& \frac{b_{12}N^{(1)}I^{(1)}}{(N^{(2)})^2} + \frac{a_{21}I^{(2)}}{N^{(1)}};\\
f_{21} =& b(1-\xi)U^{(1)}\frac{N^{(1)} - I^{(1)}}{(N^{(1)})^2} - \frac{b(U^{(1)})^2}{(N^{(1)})^2} - d_2U^{(1)} - \frac{\bar{b}_{12}U^{(1)}}{N^{(2)}} - \frac{\bar{a}_{21}N^{(2)}U^{(2)}}{(N^{(1)})^2};\\
f_{22} =& b(1-\xi)I^{(1)}\frac{N^{(1)} - U^{(1)}}{(N^{(1)})^2} + b\frac{2U^{(1)}N^{(1)} - (U^{(1)})^2}{(N^{(1)})^2} - d_2U^{(1)}\\
& - d_2N^{(1)} - \frac{\bar{b}_{12}(U^{(1)} + N^{(1)})}{N^{(2)}} - \frac{\bar{a}_{21}N^{(2)}U^{(2)}}{(N^{(1)})^2};\\
f_{23} =& \frac{\bar{b}_{12}N^{(1)}U^{(1)}}{(N^{(2)})^2} + \frac{\bar{a}_{21}U^{(2)}}{N^{(1)}};\\
f_{24} =& \frac{\bar{b}_{12}N^{(1)}U^{(1)}}{(N^{(2)})^2} + \frac{\bar{a}_{21}(U^{(2)} + N^{(2)})}{N^{(1)}};\\
f_{31} =& \frac{a_{12}(I^{(1)} + N^{(1)})}{N^{(2)}} + \frac{b_{21}N^{(2)}I^{(2)}}{(N^{(1)})^2};\\
f_{32} =& \frac{a_{12}I^{(1)}}{N^{(2)}} + \frac{b_{21}N^{(2)}I^{(2)}}{(N^{(1)})^2};\\
f_{33} =& b - d_1N^{(2)} - d_1I^{(2)} - \frac{a_{12}N^{(1)}I^{(1)}}{(N^{(2)})^2} - \frac{b_{21}(I^{(2)} + N^{(2)})}{N^{(1)}};\\
f_{34} =& - d_1I^{(2)} - \frac{a_{12}N^{(1)}I^{(1)}}{(N^{(2)})^2} - \frac{b_{21}I^{(2)}}{N^{(1)}};
\end{aligned}$$

$$\begin{aligned}
f_{41} =& \frac{\bar{a}_{12}U^{(1)}}{N^{(2)}} + \frac{\bar{b}_{21}N^{(2)}U^{(2)}}{(N^{(1)})^2};\\
f_{42} =& \frac{\bar{a}_{12}(N^{(1)} + U^{(1)})}{N^{(2)}} + \frac{\bar{b}_{21}N^{(2)}U^{(2)}}{(N^{(1)})^2};\\
f_{43} =& b(1-\xi)U^{(2)}\frac{N^{(2)} - I^{(2)}}{(N^{(2)})^2} - b\frac{(U^{(2)})^2}{(N^{(2)})^2} - d_2U^{(2)} - \frac{\bar{a}_{12}N^{(1)}U^{(1)}}{(N^{(2)})^2} - \frac{\bar{b}_{21}U^{(2)}}{N^{(1)}};\\
f_{44} =& b(1-\xi)I^{(2)}\frac{N^{(2)} - U^{(2)}}{(N^{(2)})^2} + b\frac{2U^{(2)}N^{(2)} - (U^{(2)})^2}{(N^{(2)})^2} - d_2N^{(2)} - d_2U^{(2)}\\
&- \frac{\bar{a}_{12}N^{(1)}U^{(1)}}{(N^{(2)})^2} - \frac{\bar{b}_{21}(U^{(2)} + N^{(2)})}{N^{(1)}}.
\end{aligned}$$

First, we consider the stability of system (2.3) at equilibrium E_1. The Jacobi matrix J_{E_1} of the corresponding linearized system of system (2.3) at equilibrium E_1 is as follows:

$$\begin{pmatrix}
-b - \frac{3a_{21}}{c_1^2} & -\frac{2a_{21}}{c_1^2} - b & b_{12}c_1^2 + \frac{2a_{21}}{c_1} & b_{12}c_1^2 + \frac{a_{21}}{c_1}\\
0 & b(1-\xi) - \bar{b}_{12}c_1 - d_2\bar{I}^{(1)} & 0 & \frac{\bar{a}_{21}}{c_1}\\
2a_{12}c_1 + \frac{b_{21}}{c_1^2} & a_{12}c_1 + \frac{b_{21}}{c_1^2} & -3a_{12}c_1^2 - b & -2a_{12}c_1^2 - b\\
0 & \bar{a}_{12}c_1 & 0 & b(1-\xi) - \frac{\bar{b}_{21}}{c_1} - d_2\bar{I}^{(2)}
\end{pmatrix}.$$

Thus, the characteristic equation of J_{E_1} is as follows:

$$(\lambda^2 + A_1\lambda + A_2)(\lambda^2 + A_3\lambda + A_4) = 0, \tag{4.11}$$

where

$$\begin{aligned}
A_1 =& -2b(1-\xi) + d_2\bar{I}^{(1)} + d_2\bar{I}^{(2)} + \bar{b}_{12}c_1 + \frac{\bar{b}_{21}}{c_1};\\
A_2 =& \big(-b(1-\xi) + \bar{b}_{12}c_1 + d_2\bar{I}^{(1)}\big)\Big(-b(1-\xi) + \frac{\bar{b}_{21}}{c_1} + d_2\bar{I}^{(2)}\Big) - \bar{a}_{12}\bar{a}_{21};\\
A_3 =& 2b + \frac{3a_{21}}{c_1^2} + 3a_{12}c_1^2;\\
A_4 =& \Big(b + \frac{3\bar{a}_{21}}{c_1^2}\Big)(b + 3a_{12}c_1^2) - \Big(b_{12}c_1^2 + \frac{2a_{21}}{c_1}\Big)\Big(2a_{12}c_1 + \frac{b_{21}}{c_1^2}\Big).
\end{aligned}$$

Since $A_3 > 0$, to make all the roots of the characteristic equation (4.11) have the negative real part, the following condition (H1) must be satisfied:
(H1) $A_1 > 0, A_2 > 0$ and $A_4 > 0$.

Therefore, we have the stability result of system (2.3) at equilibrium E_1 as follows:

Theorem 4. *Suppose that the condition (H1) holds; then, the equilibrium infected with wStri $E_1(\bar{I}^{(1)}, 0, \bar{I}^{(2)}, 0)$ of system (2.3) is locally asymptotically stable.*

Then, we consider the stability of equilibrium $E_2(0, \hat{U}^{(1)}, 0, \hat{U}^{(2)})$ of system (2.3). The Jacobi matrix

J_{E_2} of the corresponding linear system of system (2.3) at E_2 is as follows:

$$\begin{pmatrix} b - d_1\hat{U}^{(1)} - b_{12}c_2 & 0 & \frac{a_{21}}{c_2} & 0 \\ -b(1+\xi) - \frac{2\bar{a}_{21}}{c_2^2} & -b - \frac{3\bar{a}_{21}}{c_2^2} & \bar{b}_{12}c_2^2 + \frac{\bar{a}_{21}}{c_2} & \bar{b}_{12}c_2^2 + \frac{2\bar{a}_{21}}{c_2} \\ a_{12}c_2 & 0 & b - d_1\hat{U}^{(2)} - \frac{b_{21}}{c_2} & 0 \\ \bar{a}_{12}c_2 + \frac{\bar{b}_{21}}{c_2^2} & 2\bar{a}_{12}c_2 + \frac{\bar{b}_{21}}{c_2^2} & -b(1+\xi) - 2\bar{a}_{12}c_2^2 & -b - 3\bar{a}_{12}c_2^2 \end{pmatrix}.$$

Therefore, the characteristic equation of J_{E_2} is as follows:

$$(\lambda^2 + B_1\lambda + B_2)(\lambda^2 + B_3\lambda + B_4) = 0, \tag{4.12}$$

where

$$\begin{aligned} B_1 &= -2b + d_1\hat{U}^{(1)} + d_1\hat{U}^{(2)} + b_{12}c_2 + \frac{b_{21}}{c_2}; \\ B_2 &= (-b + d_1\hat{U}^{(1)} + b_{12}c_2)\Big(-b + d_1\hat{U}^{(2)} + \frac{b_{21}}{c_2}\Big) - a_{12}a_{21}; \\ B_3 &= 2b + \frac{3\bar{a}_{21}}{c_2^2} + 3\bar{a}_{12}c_2^2; \\ B_4 &= \Big(b + \frac{3\bar{a}_{21}}{c_2^2}\Big)(b + 3\bar{a}_{12}c_2^2) - \Big(\bar{b}_{12}c_2^2 + \frac{2\bar{a}_{21}}{c_2}\Big)\Big(2\bar{a}_{12}c_2 + \frac{\bar{b}_{21}}{c_2^2}\Big). \end{aligned}$$

Due to $B_3 > 0$, the following condition (H2) must be satisfied to make all the roots of the characteristic equation of J_{E_2} have a negative real part:
(H2) $B_1 > 0, B_2 > 0$ and $B_4 > 0$.

Therefore, we have the following the stability result of equilibrium E_2.

Theorem 5. *Suppose that the condition (H2) holds; then, the uninfected equilibrium* $E_2(0, \hat{U}^{(1)}, 0, \hat{U}^{(2)})$ *of system (2.3) is locally asymptotically stable.*

The existence of system (2.3) at the positive equilibrium will be analyzed by a numerical simulation method in Section 6. The existence and stability of E_1 indicates that *wStri* can fully invade the wild population even though there exists migration, while the existence and stability of the positive equilibrium E_3 suggest that migration may lead to an incomplete invasion of *wStri*; however, the existence and stability of E_2 suggest that migration may lead to a failure of the control method based on *Wolbachia*.

5. The global stability of the degenerated system for system (2.3)

5.1. The subsystem without N.lugens migration

N.lugens is a wing dimorphic insect with long and short wings. The long-winged morph has a migration habit, which allows them to escape adverse habitats and track changing resources [29]. The short-winged morph lacks a long distance migration ability, though its strong fecundity is conducive to the rapid proliferation of the population. Therefore, in order to theoretically reveal the interaction of the unmigrated *N.lugens* population, we need to study the interaction of the subsystem without migration.

When *N.lugens* migration is not considered, system (2.3) is degenerated into the following system (5.1):

$$\begin{cases} \frac{\mathrm{d}I^{(1)}(t)}{\mathrm{d}t} = bI^{(1)}(t) - d_1 I^{(1)}(t)N^{(1)}(t), \\ \frac{\mathrm{d}U^{(1)}(t)}{\mathrm{d}t} = bU^{(1)}(t)\frac{(1-\xi)I^{(1)}(t)}{N^{(1)}(t)} + bU^{(1)}(t)\frac{U^{(1)}(t)}{N^{(1)}(t)} - d_2 U^{(1)}(t)N^{(1)}(t), \\ \frac{\mathrm{d}I^{(2)}(t)}{\mathrm{d}t} = bI^{(2)}(t) - d_1 I^{(2)}(t)N^{(2)}(t), \\ \frac{\mathrm{d}U^{(2)}(t)}{\mathrm{d}t} = bU^{(2)}(t)\frac{(1-\xi)I^{(2)}(t)}{N^{(2)}(t)} + bU^{(2)}(t)\frac{U^{(2)}(t)}{N^{(2)}(t)} - d_2 U^{(2)}(t)N^{(2)}(t). \end{cases} \tag{5.1}$$

Since the first two equations are independent of the second two equations in system (5.1), we study the following system of the interaction between *Wolbachia* and *N.lugens* when *N.lugens* infected with *wStri* is only released in area 1:

$$\begin{cases} \frac{\mathrm{d}I^{(1)}(t)}{\mathrm{d}t} = bI^{(1)}(t) - d_1 I^{(1)}(t)N^{(1)}(t), \\ \frac{\mathrm{d}U^{(1)}(t)}{\mathrm{d}t} = bU^{(1)}(t)\frac{(1-\xi)I^{(1)}(t)}{N^{(1)}(t)} + bU^{(1)}(t)\frac{U^{(1)}(t)}{N^{(1)}(t)} - d_2 U^{(1)}(t)N^{(1)}(t). \end{cases} \tag{5.2}$$

Obviously, system (5.2) always has equilibria $E_{00}(0,0)$, $E_{10}(\frac{b}{d_1},0)$ and $E_{01}(0,\frac{b}{d_2})$. A straightforward calculation shows that system (5.2) has a unique positive equilibrium $E_{11}(\check{I}^{(1)},\check{U}^{(1)})$ if and only if $0 < 1 - \frac{d_2}{d_1} < \xi$ is true, where

$$\begin{cases} \check{I}^{(1)} = \frac{b}{d_1\xi}(1 - \frac{d_2}{d_1}), \\ \check{U}^{(1)} = \frac{b}{d_1}\Big(1 - \frac{1}{\xi}(1 - \frac{d_2}{d_1})\Big). \end{cases} \tag{5.3}$$

By a direct calculation, the Jacobi matrix $J_{E_{00}}$ corresponding to system (5.2) at the E_{00} is as follows:

$$\begin{pmatrix} b & 0 \\ 0 & b \end{pmatrix}.$$

The Jacobi matrix $J_{E_{10}}$ and $J_{E_{01}}$ corresponding to system (5.2) at the E_{10} and E_{01} are

$$\begin{pmatrix} -b & -b \\ 0 & b(1-\xi) - \frac{bd_2}{d_1} \end{pmatrix},$$

and

$$\begin{pmatrix} b(1 - \frac{d_1}{d_2}) & 0 \\ -b(1+\xi) & -b \end{pmatrix},$$

respectively. Moreover, the Jacobi matrix of system (5.2) corresponding to E_{11} is as follows:

$$J_{E_{11}} = \begin{pmatrix} -d\check{I}^{(1)} & -d\check{I}^{(1)} \\ -\frac{\xi d_1^2}{b}\check{U}^{(1)} - d_2\check{U}^{(1)} & -\frac{\xi d_1^2}{b}(\check{I}^{(1)})^2 + b - d_2\frac{b}{d_1} - d_2\check{U}^{(1)} \end{pmatrix},$$

and its determinant $\det J_{E_{11}} < 0$ from the existence condition of E_{11}. Therefore, the stability results of those equilibria for system (5.2) are obtained as follows:

Lemma 1. *$E_{00}(0,0)$ is always unstable. $E_{10}(\frac{b}{d_1},0)$ is locally asymptotically stable if $1 - \xi < \frac{d_2}{d_1}$. $E_{01}(0,\frac{b}{d_2})$ is locally asymptotically stable if $d_2 < d_1$. $E_{11}(\check{I}^{(1)},\check{U}^{(1)})$ is always unstable if it exists.*

Theorem 6. *If $\frac{d_2}{d_1} > 2 - \xi$, then, equilibrium infected with wStri E_{10} of system (5.2) is globally asymptotically stable in region $\{(I^{(1)},U^{(1)}) : I^{(1)} > 0, U^{(1)} \geq 0\}$.*

Proof. Let $(I^{(1)}(t), U^{(1)}(t))$ be the trajectory of system (5.2) with the initial value $(I_0^{(1)}, U_0^{(1)})$. It follows from $\frac{d_2}{d_1} > 2 - \xi$ that $\frac{d_2}{d_1} > 1$ and $\frac{d_2}{d_1} > 1 - \xi$; therefore, the unstability of $E_{01}(0, \frac{b}{d_2})$, the nonexistence of the positive equilibrium E_{11} and the local asymptotic stability of $E_{10}(\frac{b}{d_1}, 0)$ are obtained, where E_{10} is a saddle point and its stable manifold is $U^{(1)}$-axis.

If $I_0^{(1)} > 0$ and $U_0^{(1)} = 0$, then for any $t > 0$, $U^{(1)}(t) = 0$ and $\frac{dI^{(1)}(t)}{dt} = bI^{(1)} - d_1(I^{(1)})^2$. Therefore, the system's trajectories will tend to E_{10}.

If $I_0^{(1)} > 0$ and $U_0^{(1)} > 0$, then we have $I^{(1)}(t) > 0$ and $U^{(1)}(t) > 0$ for all $t > 0$. To apply the Poincaré's method of tangential curves [30], we introduce the following function:

$$H(t) = \ln\Big((I^{(1)}(t))^{\frac{1}{\alpha_1}}(U^{(1)}(t))^{-\frac{1}{\alpha_2}}\Big),$$

where $\alpha_1 > 0$, $\alpha_2 > 0$ and $\frac{\alpha_1}{\alpha_2} = \frac{d_1}{d_2}$. Taking the derivative of $H(t)$ with respect to the solution to system (5.2), we have the following:

$$\begin{aligned} \frac{dH}{dt}\Big|_{(5.2)} &= \frac{1}{\alpha_1 I^{(1)}(t)}\frac{dI^{(1)}(t)}{dt} - \frac{1}{\alpha_2 U^{(1)}(t)}\frac{dU^{(1)}(t)}{dt} \\ &= \frac{b}{\alpha_1} - \frac{d_1}{\alpha_1}N^{(1)} - \frac{b(1-\xi)I^{(1)}}{\alpha_2 N^{(1)}} - \frac{bU^{(1)}}{\alpha_2 N^{(1)}} + \frac{d_2}{\alpha_2}N^{(1)} \\ &= \frac{b}{\alpha_1} - \frac{b(1-\xi)I^{(1)}}{\alpha_2 N^{(1)}} - \frac{bU^{(1)}}{\alpha_2 N^{(1)}} \\ &\geq \frac{b}{\alpha_1} - \frac{b(1-\xi)}{\alpha_2} - \frac{b}{\alpha_2} \\ &= \frac{b}{\alpha_1}\Big(1 - \frac{d_1}{d_2}(2-\xi)\Big) > 0. \end{aligned}$$

Hence, $H(t)$ strictly increases with respect to t, and it follows that system (5.2) does not have any nontrivial periodic solution in region $\{(I^{(1)}, U^{(1)}) : I^{(1)} > 0, U^{(1)} \geq 0\}$. Thus, the system's trajectories from the initial value $I_0^{(1)} > 0$ and $U_0^{(1)} > 0$ will be attracted to E_{10}.

Therefore, E_{10} is globally asymptotically stable in region $\{(I^{(1)}, U^{(1)}) : I^{(1)} > 0, U^{(1)} \geq 0\}$. □

For example, the parameters are taken as $b = 0.45$, $d_1 = 0.1$, $d_2 = 0.2$ and $\xi = 0.675$ because of $1 - \frac{d_1}{d_2}(2-\xi) = 0.3375 > 0$, and the condition of Theorem 6 is satisfied. Thus, the equilibrium infected with *wStri* $E_{10} = (4.5, 0)$ is globally asymptotically stable. In such case, there exists no positive equilibrium, and the uninfected equilibrium $E_{01} = (0, 2.25)$ is a saddle point of system (5.2), whose stable manifold is $U^{(1)}$-axis. The numerical verification of Theorem 6 is shown in Figure 1.

At the end of this subsection, we provide the existence and stability of equilibria for system (5.1). There are always three equilibria $E_0^w(0,0,0,0)$, $E_1^w(b/d_1, 0, b/d_1, 0)$, $E_2^w(0, b/d_2, 0, b/d_2)$, and there exists a positive equilibrium $E_3^w(\check{I}^{(1)}, \check{U}^{(1)}, \check{I}^{(2)}, \check{U}^{(2)})$ if and only if the condition $1 - \xi < \frac{d_2}{d_1} < 1$ holds. For the stability of system (5.1), we have the following conclusion.

Theorem 7. *$E_0^w(0,0,0,0)$ is always unstable. E_1^w is locally asymptotically stable if $1 - \xi < \frac{d_2}{d_1}$. E_2^w is locally asymptotically stable if $d_2 < d_1$. E_3^w is always unstable if it exists. In addition, E_1^w and E_2^w are both locally asymptotically stable if $1 - \xi < \frac{d_2}{d_1} < 1$.*

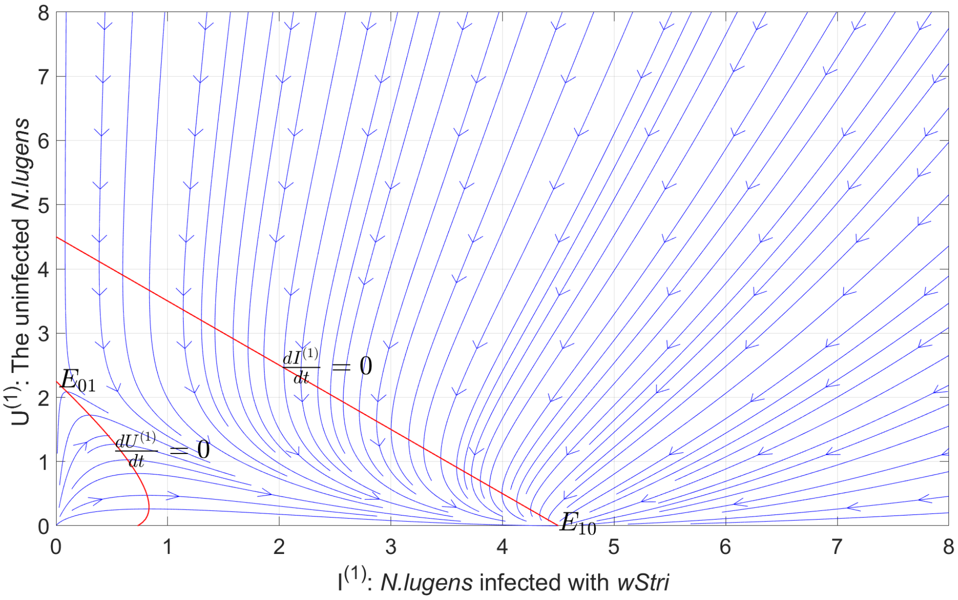


Figure 1. The global asymptotic stability of equilibrium infected with *wStri* E_{10} for system (5.2). The parameters $b = 0.45, \xi = 0.675, d_1 = 0.1$ and $d_2 = 0.2$, the two red lines represent the horizontal and vertical isocline, respectively.

5.2. *The wild N.lugens migration model*

In this subsection, we study the migration dynamics of wild *N.lugens* with the long-winged morph (i.e., subsystem without *N.lugens* infected with *wStri* in system (2.3)) as follows:

$$\begin{cases} \frac{dU^{(1)}}{dt} = bU^{(1)} - d_2(U^{(1)})^2 - \frac{\bar{b}_{12}U^{(1)}}{U^{(2)}}U^{(1)} + \frac{\bar{a}_{21}U^{(2)}}{U^{(1)}}U^{(2)}, \\ \frac{dU^{(2)}}{dt} = bU^{(2)} - d_2(U^{(2)})^2 + \frac{\bar{a}_{12}U^{(1)}}{U^{(2)}}U^{(1)} - \frac{\bar{b}_{21}U^{(2)}}{U^{(1)}}U^{(2)}. \end{cases} \tag{5.4}$$

System (5.4) reflects the southward and northward migration dynamic of the wild *N.lugens*. Denote the right hand function of system (5.4) by $(g_1, g_2)^T$, and $g_i (i = 1, 2)$ can be continuously extended to the origin $(0, 0)$ by the supplementary definition $g_1(U^{(1)}, 0) = bU^{(1)} - d_2(U^{(1)})^2$, $g_1(0, U^{(2)}) = 0$, $g_2(U^{(1)}, 0) = 0$, $g_2(0, U^{(2)}) = bU^{(2)} - d_2(U^{(2)})^2$, $g_1(0, 0) = g_1(0, 0) = 0$.

The interior $\{(U^{(1)}, U^{(2)}) : U^{(1)} > 0, U^{(2)} > 0\}$ of the first quadrant for $U^{(1)}U^{(2)}$-plane is the positive invariant set of system (5.4), and its trajectory starting from this region is eventually bounded. It is easy to see that system (5.4) has a trivial equilibrium $E_{20}(0, 0)$, which is unstable by a direct calculation. Furthermore, if $\bar{a}_{21} + bc_2^2 - \bar{b}_{12}c_2^3 > 0$, then there exists only a positive equilibrium $E_{21}(\hat{U}^{(1)}, \hat{U}^{(2)})$, where c_2 is the positive real root of equation (4.8), and $\hat{U}^{(1)}$ and $\hat{U}^{(2)}$ are the same as (4.9).

By a direct calculation, it is not hard to know that the trivial equilibrium $E_{20}(0, 0)$ is always unstable. We provide the global stability results for the positive equilibrium E_{21} as follows. The Jacobi matrix corresponding to system (5.4) at E_{21} is

$$\begin{pmatrix} -b - \frac{3\bar{a}_{21}}{c_2^2} & \bar{b}_{12}c_2^2 + \frac{2\bar{a}_{21}}{c_2} \\ 2\bar{a}_{12}c_2 + \frac{\bar{b}_{21}}{c_2^2} & -b - 3\bar{a}_{12}c_2^2 \end{pmatrix},$$

and its characteristic equation is

$$\lambda^2 + B_3\lambda + B_4 = 0,$$

where B_3 and B_4 are consistent with that of Eq (4.12). Therefore, we have the following result of the local stability for the positive equilibrium,

Lemma 2. *If $B_4 > 0$, then the positive equilibrium $E_{21}(\hat{U}^{(1)}, \hat{U}^{(2)})$ of system (5.4) is locally asymptotically stable.*

In fact, the positive equilibrium E_{21} is not only locally asymptotically stable, but also globally asymptotically stable.

Theorem 8. *If $B_4 > 0$, then the positive equilibrium $E_{21}(\hat{U}^{(1)}, \hat{U}^{(2)})$ of system (5.4) is globally asymptotically stable in the region $\{(U^{(1)}, U^{(2)}) : U^{(1)} > 0, U^{(2)} > 0\}$.*

Proof. We only need to show that system (5.4) does not have any nontrivial periodic solution in $\{(U^{(1)}, U^{(2)}) : U^{(1)} > 0, U^{(2)} > 0\}$. According to Dulac's criteria (see, e.g., Theorem 2, Section 3.9 of Ref. [31]), we choose the Dulac function $B(U^{(1)}, U^{(2)}) = \frac{1}{U^{(1)}U^{(2)}}$, where the divergence of the vector field (g_1B, g_2B) satisfies the following:

$$\begin{aligned}\nabla \cdot (g_1B, g_2B) &= \frac{\partial(g_1B)}{\partial U^{(1)}} + \frac{\partial(g_2B)}{\partial U^{(2)}}\\ &= -\frac{d_2}{U^{(2)}} - \frac{\bar{b}_{12}}{(U^{(2)})^2} - \frac{2\bar{a}_{21}U^{(2)}}{(U^{(1)})^3} - \frac{d_2}{U^{(1)}} - \frac{2\bar{a}_{12}U^{(1)}}{(U^{(2)})^3} - \frac{\bar{b}_{21}}{(U^{(1)})^2} < 0\end{aligned}$$

for any $(U^{(1)}, U^{(2)}) \in \{(U^{(1)}, U^{(2)}) : U^{(1)} > 0, U^{(2)} > 0\}$. Thus, system (5.4) does not exist as a closed orbit in the interior of the first quadrant of the $U^{(1)}U^{(2)}$-plane. In addition, the condition $B_4 > 0$ implies that E_{21} is locally asymptotically stable, and there exists no other equilibrium in the interior of the first quadrant for system (5.4). Therefore, the positive equilibrium $E_{21}(\hat{U}^{(1)}, \hat{U}^{(2)})$ is globally asymptotically stable in the region $\{(U^{(1)}, U^{(2)}) : U^{(1)} > 0, U^{(2)} > 0\}$. □

We choose the parameters $b = 0.5$, $d_2 = 0.2$, $\xi = 0.675$, $\bar{b}_{12} = 0.75$, $\bar{b}_{21} = 0.85$, $\bar{a}_{12} = 0.7$ and $\bar{a}_{21} = 0.8$; then, we have $c_2 = 1.0405$, $\hat{U}^{(1)} = 2.2933$ and $\hat{U}^{(2)} = 2.2041$. Furthermore, we get $B_4 = 2.3761 > 0$. It follows from Theorem 8 that the positive equilibrium $E_{21} = (2.2933, 2.2041)$ is globally asymptotically stable, and the numerical simulation results as shown in Figure 2.

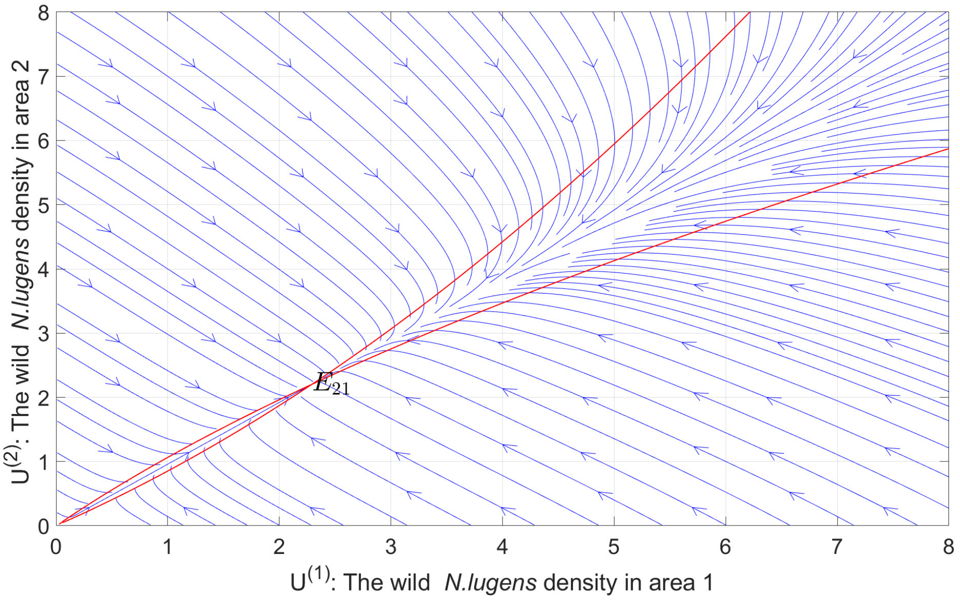


Figure 2. The global asymptotic stability of the positive equilibrium E_{21} for system (5.4). The parameters $b = 0.5$, $d_2 = 0.2$, $\xi = 0.675$, $\bar{b}_{12} = 0.75$, $\bar{b}_{21} = 0.85$, $\bar{a}_{12} = 0.7$ and $\bar{a}_{21} = 0.8$, the two red lines represent the horizontal and vertical isocline, respectively.

5.3. The migration model of N.lugens infected with wStri

In this subsection, we will analyze the migration dynamics of *N.lugens* infected with *wStri* with long-winged morph (i.e., subsystem without the uninfected *N.lugens* in system (2.3)) as follows:

$$\begin{cases} \frac{\mathrm{d}I^{(1)}}{\mathrm{d}t} = bI^{(1)} - d_1(I^{(1)})^2 - \frac{b_{12}I^{(1)}}{I^{(2)}}I^{(1)} + \frac{a_{21}I^{(2)}}{I^{(1)}}I^{(2)}, \\ \frac{\mathrm{d}I^{(2)}}{\mathrm{d}t} = bI^{(2)} - d_1(I^{(2)})^2 + \frac{a_{12}I^{(1)}}{I^{(2)}}I^{(1)} - \frac{b_{21}I^{(2)}}{I^{(1)}}I^{(2)}. \end{cases} \tag{5.5}$$

System (5.5) reveals the *wStri*-infected *N.lugens* migration dynamic after *Wolbachia wStri* completely invades the wild *N.lugens*. The study of system (5.5) is mainly aimed at proposing the artificial control measures for the *wStri*-infected *N.lugens*.

Similar to system (5.4), the first quadrant of the $I^{(1)}I^{(2)}$-plane is the positive invariant set of system (5.5). If $a_{21} + bc_1^2 - b_{12}c_1^3 > 0$ holds, then system (5.5) only has a positive equilibrium $E_{31}(\bar{I}^{(1)}, \bar{I}^{(2)})$, where c_1 is the positive real root of (4.4), and $\bar{I}^{(1)}$ and $\bar{I}^{(2)}$ are consistent with that of formula (4.5) or (4.6).

The Jacobi matrix corresponding to system (5.5) at E_{31} is as follows:

$$\begin{pmatrix} -b - \frac{3a_{21}}{c_1^2} & b_{12}c_1^2 + \frac{2a_{21}}{c_1} \\ 2a_{12}c_1 + \frac{b_{21}}{c_1^2} & -b - 3a_{12}c_1^2 \end{pmatrix}.$$

Its characteristic equation is as follows:

$$\lambda^2 + A_3\lambda + A_4 = 0,$$

where A_3 and A_4 are completely consistent with that of Eq (4.11).

Lemma 3. *If* $A_4 > 0$*, then the positive equilibrium* $E_{31}(\bar{I}^{(1)}, \bar{I}^{(2)})$ *of system (5.5) is locally asymptotically stable.*

Theorem 9. *If* $A_4 > 0$*, then the positive equilibrium* $E_{31}(\bar{I}^{(1)}, \bar{I}^{(2)})$ *of system (5.5) is globally asymptotically stable in the region* $\{(I^{(1)}, I^{(2)}) : I^{(1)} > 0, I^{(2)} > 0\}$.

Proof. We only need to show that there exists no closed orbit in the interior of the first quadrant of the $I^{(1)}I^{(2)}$-plane for system (5.5). Let $(h_1, h_2)^T$ be the right hand function of system (5.5). Similar to the proof of Theorem 8, to apply Dulac's criteria (see, e.g., Theorem 2, Section 3.9 of Ref. [31]), we take the Dulac function $D(I^{(1)}, I^{(2)}) = \frac{1}{I^{(1)}I^{(2)}}$, for any $I^{(1)} > 0$ and $I^{(2)} > 0$, the divergence of the vector field (h_1D, h_2D) is equal to the following:

$$\begin{aligned}\nabla \cdot (h_1D, h_2D) &= \frac{\partial(h_1D)}{\partial I^{(1)}} + \frac{\partial(h_2D)}{\partial I^{(2)}}\\ &= -\frac{d_1}{I^{(2)}} - \frac{b_{12}}{(I^{(2)})^2} - \frac{2a_{21}I^{(2)}}{(I^{(1)})^3} - \frac{d_1}{I^{(1)}} - \frac{2a_{12}I^{(1)}}{(I^{(2)})^3} - \frac{b_{21}}{(I^{(1)})^2} < 0.\end{aligned}$$

According to the Dulac criterion, system (5.5) has no closed orbit in the interior of the first quadrant of the $I^{(1)}I^{(2)}$-plane. Furthermore, it follows from $A_4 > 0$ that the positive equilibrium E_{31} is locally asymptotically stable. Additionally, there is no other equilibrium in the interior of the first quadrant. Therefore, $E_{31}(\bar{I}^{(1)}, \bar{I}^{(2)})$ is globally asymptotically stable in the region $\{(I^{(1)}, I^{(2)}) : I^{(1)} > 0, I^{(2)} > 0\}$. □

For example, taking the parameters $b = 0.6$, $\xi = 0.675$, $d_1 = 0.1$, $b_{12} = 0.6$, $b_{21} = 0.85$, $a_{12} = 0.5$ and $a_{21} = 0.7$, we get $c_1 = 1.1106$, $\bar{I}^{(1)} = 5.0121$ and $\bar{I}^{(2)} = 4.5131$; then, we have $A_4 = 2.0410 > 0$. Hence, the positive equilibrium $E_{31} = (5.0121, 4.5131)$ is globally asymptotically stable from Theorem 9. The numerical simulation results are shown in Figure 3.

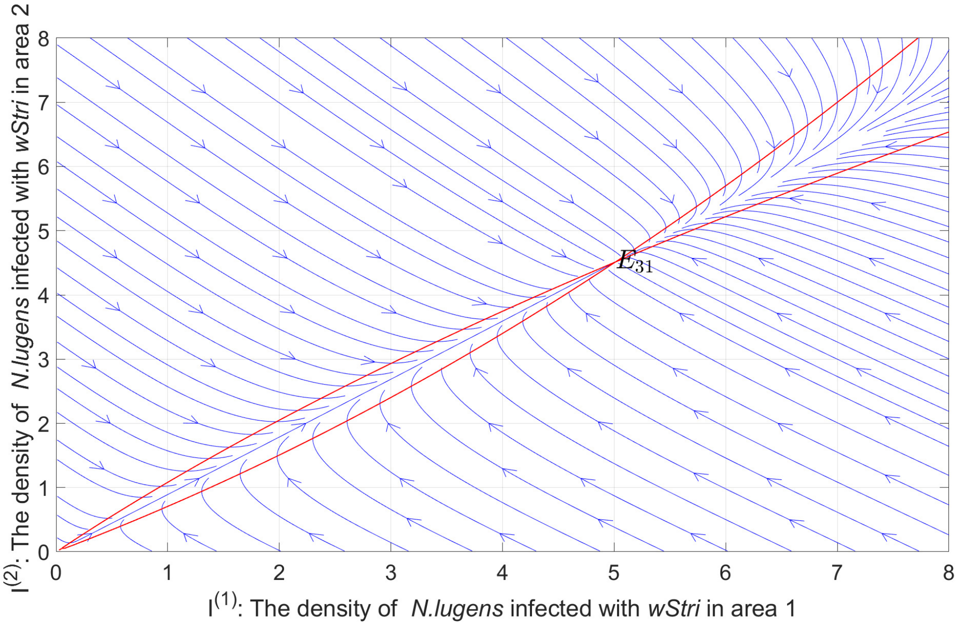


Figure 3. The global asymptotic stability of the positive equilibrium E_{31} for system (5.5). The parameters $b = 0.6$, $\xi = 0.675$, $d_1 = 0.1$, $b_{12} = 0.6$, $b_{21} = 0.85$, $a_{12} = 0.5$ and $a_{21} = 0.7$, the two red lines represent the horizontal and vertical isocline, respectively.

The result of Theorem 2, 4 and 9 indicate that although *N.lugens* infected with *wStri* are only released in area 1, they can coexist in both area 1 and area 2 after *wStri* completely invades the wild population.

6. Numerical simulation

We need to estimate some biological parameters of *N.lugens* for a numerical simulation, such as b, d_1, d_2 and ξ, which can systematically reflect the biological characteristics of the *N.lugens* population dynamics and development, and are often used for population dynamics monitoring, prediction and bioassay [32]. *N.lugens* has different natural birth rates in the different rice varieties, ranging from $(0.1 \pm 0.016, 0.6)$ [32–34]. However, if *N.lugens* is not affected by any adverse factors, its birth rates should be high, and even close to 1. The natural mortality of *N.lugens* is not only associated with artificial factors such as insecticide, but also with the meteorological conditions such as rainfall and temperature. Its daily mortality rates are approximately 3% to 5%, and can reach 10% to 30% in case of severe weather [35,36]. Therefore, the natural mortality rates of wild *N.lugens* are within the ranges of $(0.03, 0.3)$.

The experimental data in Ref. [2] indicated that the lifespan of female *N.lugens* infected with *wStri* was not shorter than that of the uninfected female *N.lugens*, and there was no significant difference in male survivorship among those two *N.lugens* types. Thus, we consider that the mortality rate of *N.lugens* infected with *wStri* has roughly the same range of values as that of the uninfected *N.lugens*. In addition, the CI intensity is $\xi = 0.675$ by [2].

When the *N.lugens* population migrates northward and returns southward, atmospheric circulation and the weather exert a direct influence on its takeoff and landing. In September, the peak of *N.lugens* infestation appears in the southern rice area under the influence of a low pressure circulation. It is easy to obtain the daily cumulative numbers of *N.lugens* infestation by using the data of the insect trap catches under lights. However, there is no literature reports on the successful landing rate and takeoff rate of *N.lugens* after its northward migration.

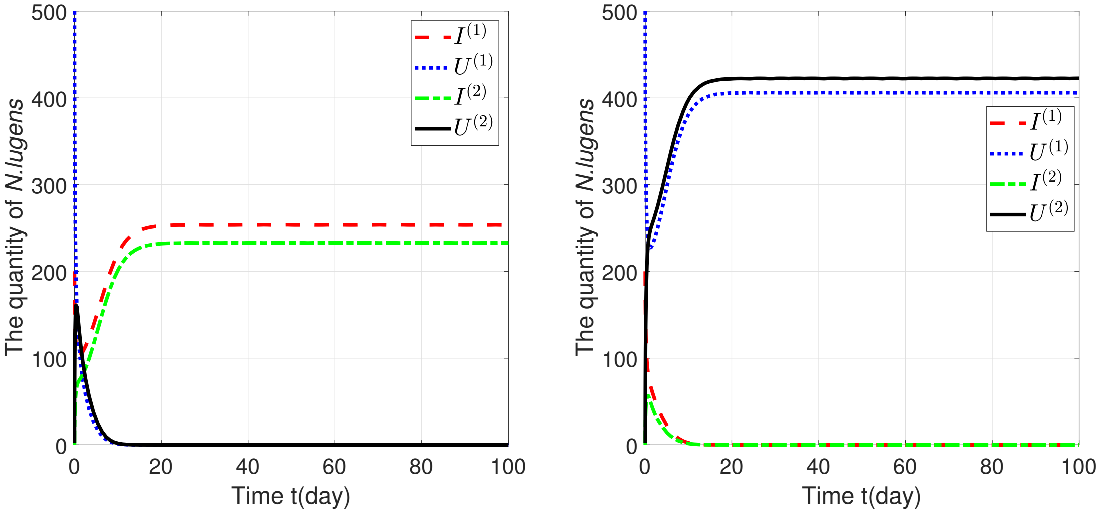
The above biological and migration parameters of *N.lugens* are summarized in Table 1.

6.1. Verifying the existences and stabilities of two boundary equilibria of system (2.3)

We take parameters $b = 0.54$, $d_1 = 0.0015$, $d_2 = 0.0032$, $\xi = 0.675$, $a_{12} = 0.4222$, $a_{21} = 0.5453$, $\bar{a}_{12} = 0.543$, $\bar{a}_{21} = 0.4317$, $b_{12} = 0.568$, $b_{21} = 0.754$, $\bar{b}_{12} = 0.68$ and $\bar{b}_{21} = 0.64$. By solving equation (4.4), we obtain $c_1 = 1.0896$. Furthermore, we have $E_1 = (253.6439, 0, 232.7944, 0)$, $A_1 = 2.5339 > 0$, $A_2 = 1.3586 > 0$ and $A_4 = 1.3144 > 0$. Therefore, from Theorem 4, equilibrium infected *wStri* E_1 is locally asymptotically stable, and the numerical simulation is shown in Figure 4(a). When parameters are taken as $b = 0.6438$, $d_1 = 0.0025$, $d_2 = 0.0011$, $\xi = 0.675$, $a_{12} = 0.4$, $a_{21} = 0.5$, $\bar{a}_{12} = 0.54$, $\bar{a}_{21} = 0.42$, $b_{12} = 0.56$, $b_{21} = 0.75$, $\bar{b}_{12} = 0.68$ and $\bar{b}_{21} = 0.65$, we obtain that $c_2 = 0.9602$, and $E_2 = (0, 405.7542, 0, 422.5527)$. In such a case we have $B_1 = 2.1020 > 0$, $B_2 = 0.8842 > 0$ and $B_4 = 1.681 > 0$. Thus, the condition of Theorem 5 is met, the uninfected equilibrium E_2 is locally asymptotically stable, and the numerical simulation result is shown in Figure 4(b).

Table 1. The biological and migration parameters of *N.lugens*.

Para.	Definition	Value	Reference
b	The half birth rate of *N.lugens*	$(0.1, 1)$	[32–34]
h_{NLT}	Mean hatching rate per the uninfected *N.lugens* female when NLS males mated with NLT females (day^{-1})	32.5%	[2]
ξ	The CI intensity of I_M against U_F: $1 - h_{NLT}$	0.675	[2]
d_1	The decay of *N.lugens* infected with *wStri*	$(0, 0.3)$	[2, 35, 36]
d_2	The decay of the uninfected *N.lugens*	$(0, 0.3)$	[35, 36]
$b_{12}, \bar{b}_{12}$	The successful take-off rates of I and U during northward migration	$[0, 1]$	
$b_{21}, \bar{b}_{21}$	The successful take-off rates of I and U during southward migration	$[0, 1]$	
$a_{12}, \bar{a}_{12}$	The successful landing rates of I and U during northward migration	$[0, 1]$	
$a_{21}, \bar{a}_{21}$	The successful landing rates of I and U during southward migration	$[0, 1]$	



(a)

(b)

Figure 4. The stabilities of equilibria E_1 and E_2 for system (2.3). The initial value $(I_0^{(1)}, U_0^{(1)}, I_0^{(2)}, U_0^{(2)},) = (200, 500, 0, 2)$. (a) The stability of equilibrium E_1. (b) The stability of equilibrium E_2.

6.2. *Existence of the positive equilibrium*

Now, we numerically analyze the existence of the positive equilibrium E_3 of system (2.3). For simplicity of presentation, we still use the notation $J_{E_3} = (f_{ij})_{4\times4}$ to represent the Jacobian matrix of system (2.3) at $E_3 = (\tilde{I}^{(1)}, \tilde{U}^{(1)}, \tilde{I}^{(2)}, \tilde{U}^{(2)})$, whose characteristic equation is $\lambda^4 - C_1\lambda^3 + C_2\lambda^2 - C_3\lambda + C_4 = 0$. When the parameters are taken as $b = 0.6438$, $d_1 = 0.0025$, $d_2 = 0.0031$, $\xi = 0.675$, $a_{12} = 0.1$, $a_{21} = 0.34$, $\bar{a}_{12} = 0.1593$, $\bar{a}_{21} = 0.4317$, $b_{12} = 0.32$, $b_{21} = 0.64$, $\bar{b}_{12} = 0.2316$ and $\bar{b}_{21} = 0.5639$. System (2.3) has a positive equilibrium $E_3 = (29.4676, 139.75, 21.9651, 108.2649)$ and

$$J_{E_3} = \begin{pmatrix} -0.3751 & -0.1800 & 0.3999 & 0.1382 \\ -1.1907 & -1.0892 & 0.5991 & 0.9314 \\ 0.2165 & 0.0866 & -0.3417 & -0.1674 \\ 0.4486 & 0.6556 & -1.2189 & -1.1248 \end{pmatrix}.$$

The characteristic equation is $\lambda^4 + 2.9308\lambda^3 + 1.7108\lambda^2 + 0.2311\lambda - 0.0172 = 0$, which has characteristic roots $\lambda_1 = -2.2036$, $\lambda_3 = -0.4414$, $\lambda_4 = -0.3382$ and $\lambda_2 = 0.0524$. Therefore, the positive equilibrium E_3 is unstable.

6.3. *Bistable phenomena*

Further numerical simulation results indicate that system (2.3) can appear as a bistable phenomenon. For example, we take the parameters $b = 0.55$, $d_1 = 0.2$, $d_2 = 0.1$, $\xi = 0.675$, $a_{12} = 0.75$, $a_{21} = 0.8$, $\bar{a}_{12} = 0.6$, $\bar{a}_{21} = 0.8$, $b_{12} = 0.88$, $b_{21} = 0.93$, $\bar{b}_{12} = 0.85$ and $\bar{b}_{21} = 0.98$. By numerically solving equations (4.4) and (4.8), we get $c_1 = 1.0189$ and $c_2 = 1.0691$. Therefore, system (2.3) exists as an equilibrium infected *wStri* $E_1 = (2.1193, 0, 2.0799, 0)$. In addition, it is easy to obtain that $A_1 = 1.8903 > 0$, $A_2 = 0.4112 > 0$ and $A_4 = 2.2373 > 0$. From Theorem 4, it follows that E_1 is locally asmyptotically stable. On the other hand, system (2.3) also has an uninfected equilibrium $E_2 = (0, 3.4119, 0, 3.1913)$. Furthermore, we can obtain $B_1 = 2.0313 > 0$, $B_2 = 0.4283 > 0$ and $B_4 = 1.6263 > 0$. Thus, from Theorem 5, we know that E_2 is also locally asmyptotically stable. Therefore, system (2.3) appears as a bistable phenomenon. By randomly generating the initial values for numerical verification of 10 groups, we obtain the $I^{(1)} - U^{(1)} - I^{(2)}$-diagram for system (2.3), as shown in Figure 5. It is apparent from Figure 5 that system (2.3) has two stable equilibria.

7. Discussion

7.1. *Impact of migration on dynamical properties of system*

When *N.lugens* migration is not considered, system (5.1) reflects the population evolution of the *wStri*-infected *N.lugens* and the wild *N.lugens*. From Theorem 7, we know that equilibrium infected with *wStri* E_1^w or the uninfected equilibrium E_2^w are asymptotically stable under certain conditions, and E_1^w and E_2^w are simultaneously locally asymptotically stable as $1 - \xi < \frac{d_2}{d_1} < 1$. This indicates that system (5.1) can exhibit a bistable phenomenon. In addition, the positive equilibrium of system (5.1) is always unstable, which shows that without considering migration, the two types of *N.lugens* must eventually not coexist in each patch. On the other hand, when migration is considered, system (2.3) reflects population evolution with *N.lugens* migrating in both patches. According to numerical simulation results from Subsection 6.2, we know that there exists a positive equilibrium for system

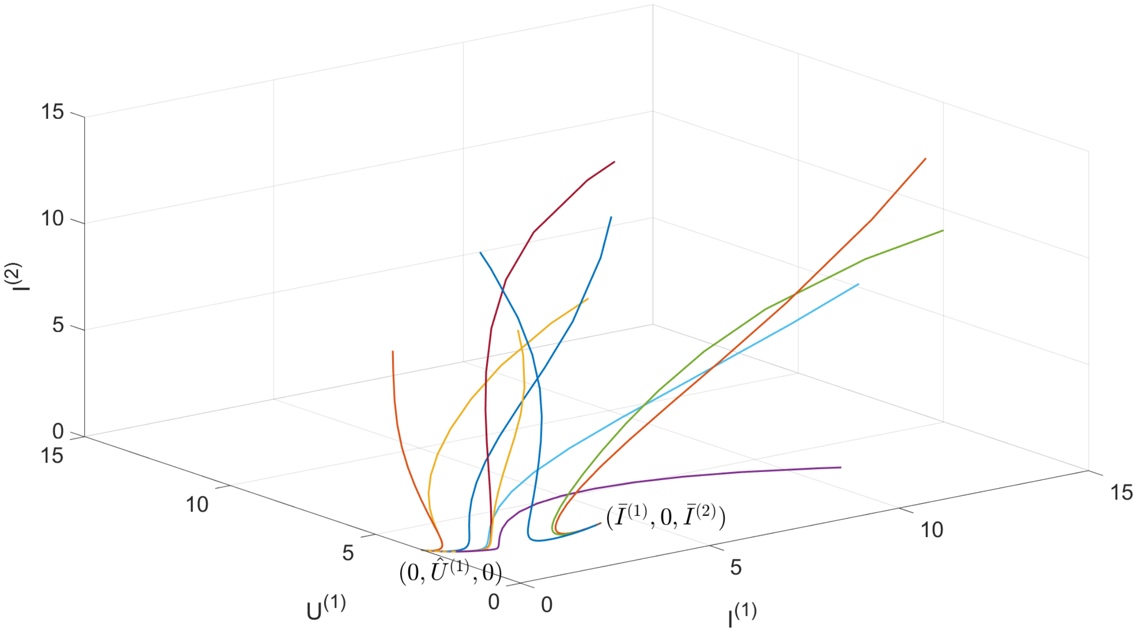


Figure 5. The bistability of the equilibrium with infected *wStri* E_1 and the uninfected equilibrium E_2 of system (2.3). The initial values are randomly generated.

(2.3) under certain conditions. Moreover, from subsection 6.3, we know that system (2.3) can exhibit bistable phenomenon.

We further qualitatively summarize the impact of migration parameters on equilibria of system (2.3). According to Theorems 2 and 4, we know that either decreasing the successful landing rate $\bar{a}_{ij}$ or increasing the take-off rate $\bar{b}_{ij}$ of the uninfected *N.lugens* is beneficial to the existence and stability of equilibrium infected with *wStri* E_1. Additionally, from Theorem 3 and Theorem 5, we know that either decreasing the successful landing rate a_{ij} or increasing the take-off rate b_{ij} of *N.lugens* infected *wStri* is conducive to the existence and stability of the uninfected equilibrium E_2. We will further analyze the controllable migration parameters threshold value for the existence and stability of each equilibrium in Subsection 7.3.

To numerically verifying the above theoretical results, we investigate the effect of migration coefficient $\bar{a}_{12}$ on the stability of the equilibrium infected with *wStri* E_1. The parameters are taken as $b = 0.6438$, $d_1 = 0.0025$, $d_2 = 0.0081$, $\xi = 0.675$, $a_{12} = 0.3$, $a_{21} = 0.2$, $\bar{a}_{21} = 0.82$, $b_{12} = 0.76$, $b_{21} = 0.55$, $\bar{b}_{12} = 0.28$, and $\bar{b}_{21} = 0.15$. Without considering migration, we have $1 - \xi = 0.325 < \frac{d_2}{d_1} = 3.24$ and $d_2 > d_1$. It follows from Theorem 7 that E_1^w is locally asymptotically stable, and E_2^w and E_3^w are not stable for system (5.1). When migration is considered, we find that increasing the migration parameter $\bar{a}_{12}$ to a threshold value 0.75, equilibrium E_1 of system (2.3) is not stable, and E_2 is locally asymptotically stable, as shown in Figure 6. The numerical simulations show that when migration is not considered, equilibrium infected with *wStri* E_1^w is stable; with the increase of migration coefficient $\bar{a}_{ij}$, the stability of E_1^w can be changed from stable to unstable, which may lead E_2^w to be stable.

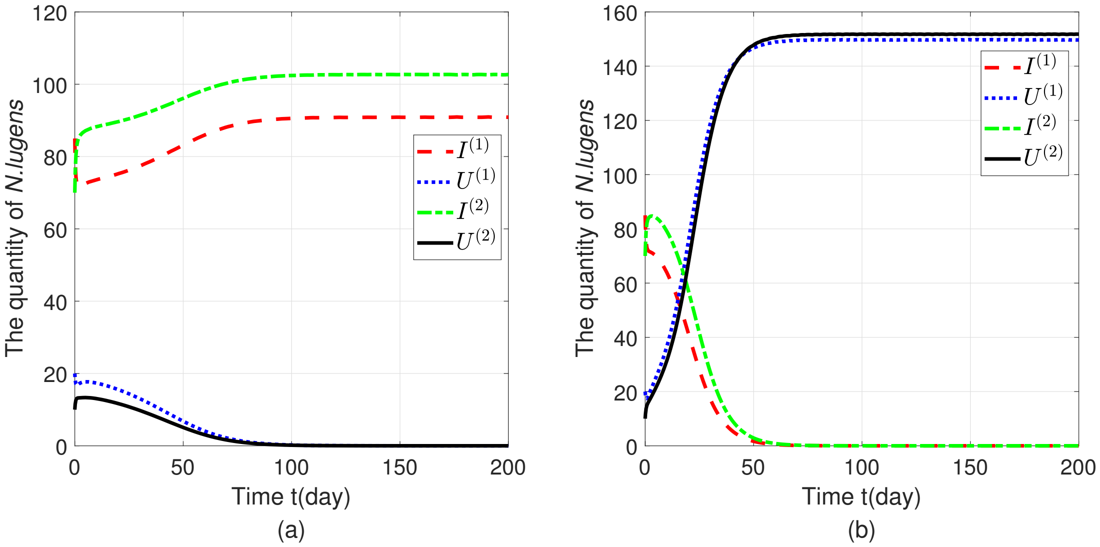


Figure 6. Impact of migration coefficient on stability of equilibrium infected with *wStri*. The initial value $(I_0^{(1)}, U_0^{(1)}, I_0^{(2)}, U_0^{(2)}) = (85, 20, 70, 10)$, where $\bar{a}_{12} = 0.6 < 0.75$ in figure (a), and $\bar{a}_{12} = 0.76 > 0.75$ in figure (b).

7.2. *Impact of migration on control effects of N.lugens using Wolbachia*

First, the influence of migration on the control effect of the wild *N.lugens* will be numerically analyzed by comparing the control degree of the wild *N.lugens*:

$$e(t) = \frac{U_0^{(1)} + U_0^{(2)} - U^{(1)}(t) - U^{(2)}(t)}{U_0^{(1)} + U_0^{(2)}} \times 100\%.$$

Notice that the control degree of the wild *N.lugens* at migration refers to the total control degree of both patches, where the concept of the control degree is consistent with that of the wild *N.lugens* introduced in Ref. [6]. The control degree curves are plotted in Figure 7 after computing from system (2.3) (with migration) and system (5.1) (without migration). Here, Figure 7(b) illustrates that when migration is considered, all of the *N.lugens* infected with *wStri* are only released in area 1, namely the initial value $(I_0^{(1)}, U_0^{(1)}, I_0^{(2)}, U_0^{(2)}) = (230, 530, 0, 20)$. When migration is not considered, the *wStri*-infected *N.lugens* is simultaneously released in two areas in proportion to the numbers of the uninfected *N.lugens* in both areas, so the initial value $(I_0^{(1)}, U_0^{(1)}, I_0^{(2)}, U_0^{(2)}) = (222, 530, 8, 20)$. Numerical simulation results show that the control degree of the wild *N.lugens* with migration may be smaller than that without migration, which indicates that migration may lead to a decrease of the control effect of the wild *N.lugens*, which is consistent with the general understanding.

It is generally believed that effective control is achieved when the control degree reaches 95% [6]. The dotted lines in Figure 7 show that the goal of effective control is not achieved under migration. Therefore, in the presence of migration, the original strategy (i.e., quantity and timing of release) for releasing *N.lugens* infected with *wStri* may not achieve the goal of either complete or even effective control of the wild *N.lugens*.

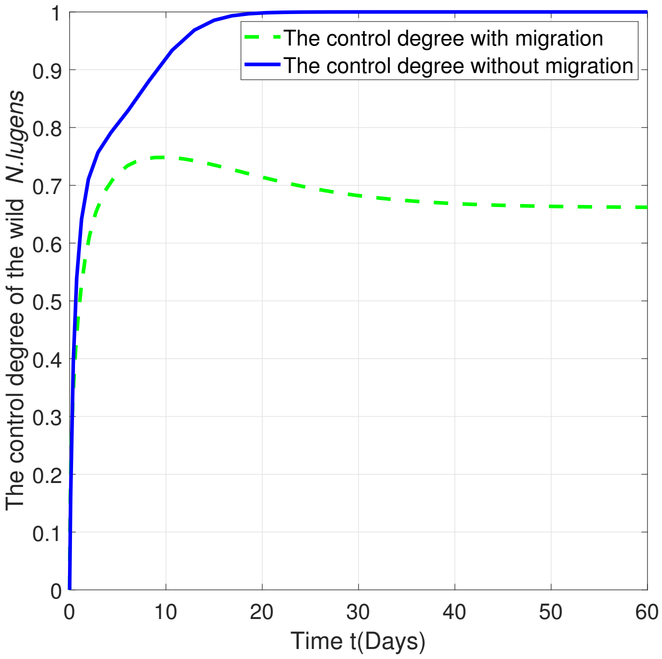


Figure 7. The control degree of the wild *N.lugens*. The biological parameters $b = 0.5, d_1 = 0.0025, d_2 = 0.0031, \xi = 0.675$. Migration parameters are $a_{12} = 0.05, a_{21} = 0.63, \bar{a}_{12} = 0.4573, \bar{a}_{21} = 0.4317, b_{12} = 0.4716, b_{21} = 0.7554, \bar{b}_{12} = 0.6674$, and $\bar{b}_{21} = 0.6439$. $(I_0^{(1)}, U_0^{(1)}, I_0^{(2)}, U_0^{(2)}) = (230, 530, 0, 20)$ when without considering migration, while $(I_0^{(1)}, U_0^{(1)}, I_0^{(2)}, U_0^{(2)}) = (222, 530, 8, 20)$ when with considering migration.

Notice that the optimal state for controlling *N.lugens* using *Wolbachia* is stability of E_1. Next, we numerically analyze the effect of migration on this state. Taking $\bar{a}_{12}$ as an example, we fix $b = 0.6438$, $d_1 = 0.0025$, $d_2 = 0.0031$, $\xi = 0.675$, $a_{12} = 0.1222$, $a_{21} = 0.5453$, $\bar{a}_{21} = 0.4317$, $b_{12} = 0.4716$, $b_{21} = 0.7554$, $\bar{b}_{12} = 0.6867$ and $\bar{b}_{21} = 0.6439$. Here, we consider the birth rate of *N.lugens* in natural conditions, which is greater than that of *N.lugens* in resistant rice. Selecting $\bar{a}_{12} = 0.15, 0.25, 0.35, 0.45$ and 0.55, respectively, the control degree curves under the different migration parameters $\bar{a}_{12}$ are plotted in Figure 8(a). Similarly, we analyze the influences of the successful landing rate $\bar{a}_{21}$ of a southward migration on the control degree of the wild *N.lugens* in both patches. Figure 8(b) shows the control degree curves of the wild *N.lugens* within 60 days under the different values of $\bar{a}_{21}$. Although the stability of E_1 makes the control degree of the wild *N.lugens* close to 1 in a long time, it is not hard to find that increasing the successful landing rate $\bar{a}_{ij}$ of the wild *N.lugens* can decrease its control degree within a finite time.

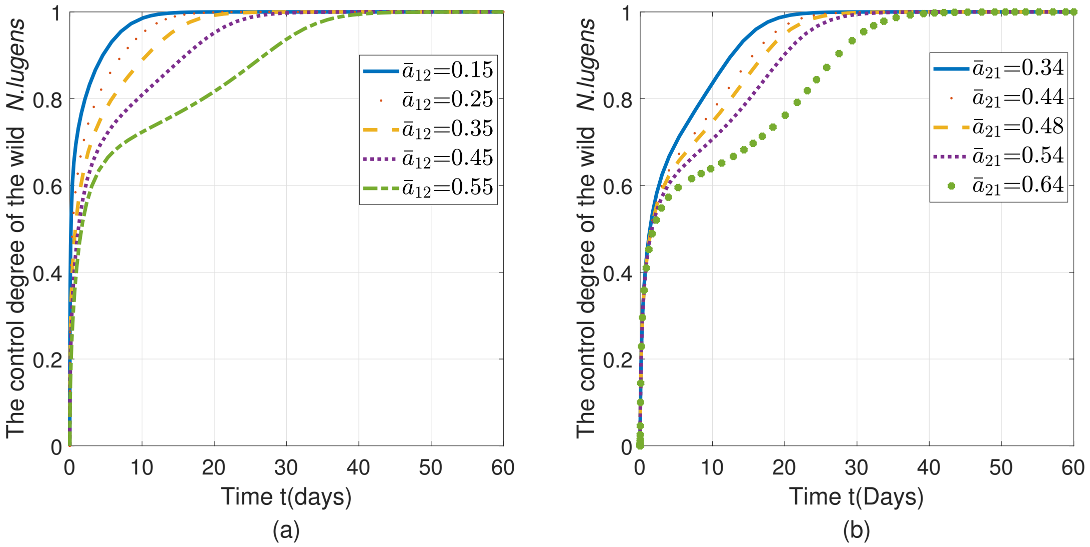
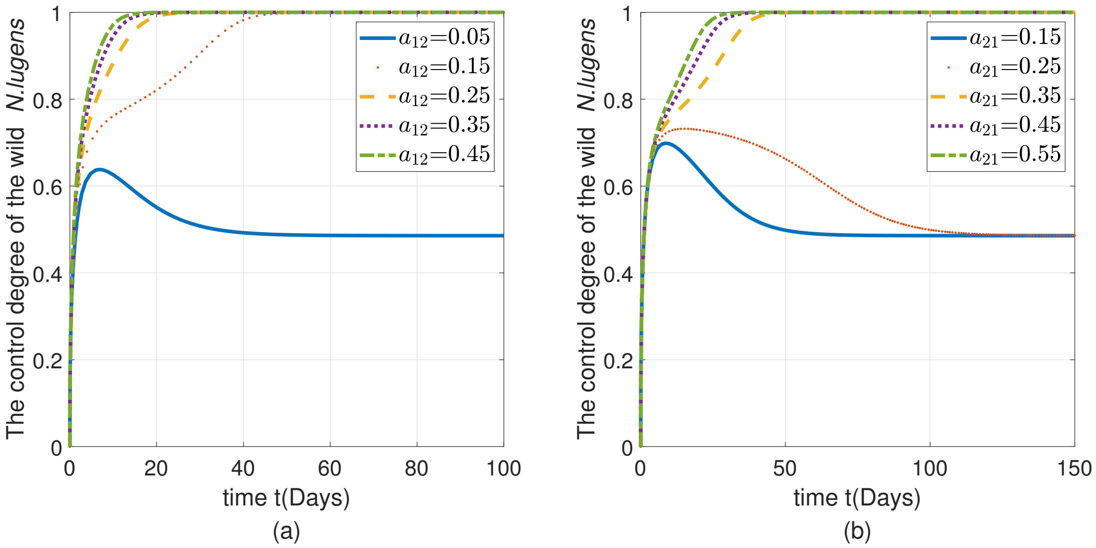


Figure 8. The influence of migration on the optimal control effect. The initial condition $(I_0^{(1)}, U_0^{(1)}, I_0^{(2)}, U_0^{(2)}) = (230, 530, 0, 2)$. The insect biological parameters are $b = 0.6438$, $d_1 = 0.0025$, $d_2 = 0.0031$, $\xi = 0.675$. (a) The effect of $\bar{a}_{12}$ on the control degree. $a_{12} = 0.1222$, $a_{21} = 0.5453$, $\bar{a}_{21} = 0.4317$, $b_{12} = 0.4716$, $b_{12} = 0.7554$, $\bar{b}_{12} = 0.6867$ and $\bar{b}_{21} = 0.6439$. (b) The effect of $\bar{a}_{21}$ on the control degree. The parameters $a_{12} = 0.1, a_{21} = 0.34, b_{12} = 0.32, b_{21} = 0.64, \bar{a}_{12} = 0.1593, \bar{b}_{12} = 0.2316$, and $\bar{b}_{21} = 0.6639$.

7.3. Measures to reduce the impact of migration on the control of N.lugens

A worthy question is how to take the effective measures to reduce the impact of migration on the control of wild *N.lugens*. The take-off rate of *N.lugens* is not easily controlled in practice, while the successful landing rate for *N.lugens* migration can be controlled through the relevant interference measures. Therefore, the successful landing rates of the two types of *N.lugens* are the controllable migration parameters. Next, we shall obtain the control measures by comparing the control degree of the wild *N.lugens* under the different successful landing rate values. First, the impact of the successful landing rate $\bar{a}_{ij}$ on the control degree have been calculated in subsection 7.2. From the numerical simulation results, we find that decreasing the successful landing rate of the wild *N.lugens* can improve its control effects. In future field trials, we can take measures to reduce the landing of the wild *N.lugens* in destination area and source area to improve the control effects of the wild *N.lugens*, such as spraying pesticides during their flight by unmanned aerial vehicle.

Second, by the similar numerical simulation method, the total control degree of the wild *N.lugens* in those two areas can be calculated under the different landing rates a_{12} and a_{21} of *N.lugens* infected with *wStri*. The control degree curves of the wild *N.lugens* are given in Figure 9(a) and (b). The numerical simulation results indicate that the control degree of the wild *N.lugens* increases when the successful landing rate of the northward or southward migration of *N.lugens* infected with *wStri* appropriately increases. Therefore, increasing the landing rate of *N.lugens* infected with *wStri* can improve the control degree of the wild *N.lugens*. Although it is not possible to directly increase the landing rate of *N.lugens* infected with *wStri*, we can achieve the same effect by releasing them in area 1 in autumn or in area 2 in summer. The numerical simulations demonstrate that this measure is feasible.

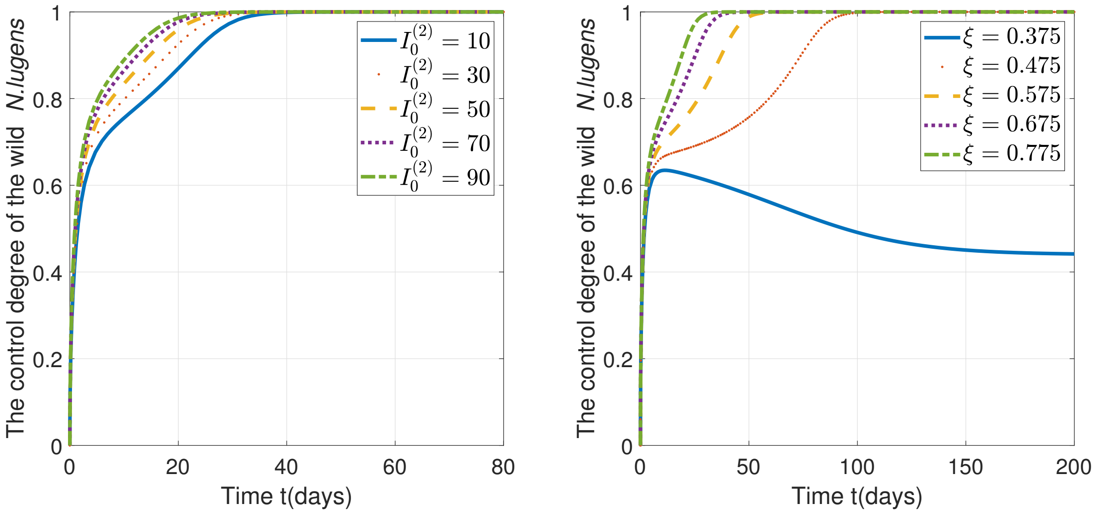


(a)

(b)

Figure 9. Effect of the successful landing rate of *N.lugens* infected with *wStri* on the control degree of the wild *N.lugens*. The biological parameters of insect are taken as $b = 0.6438, d_1 = 0.0025, d_2 = 0.0031$, $\xi = 0.675$, the initial values $(I_0^{(1)}, U_0^{(1)}, I_0^{(2)}, U_0^{(2)}) = (230, 530, 0, 2)$. (a) Effect of a_{12} on the control of the wild *N.lugens*. The control parameters $a_{21} = 0.2322, \bar{a}_{12} = 0.4593, \bar{a}_{21} = 0.4317, b_{12} = 0.4716, b_{21} = 0.7554, \bar{b}_{12} = 0.6867$ and $\bar{b}_{21} = 0.6439$. (b) Effect of a_{21} on the control of the wild *N.lugens*. The control parameters $a_{12} = 0.1222, \bar{a}_{12} = 0.4593, \bar{a}_{21} = 0.4317, b_{12} = 0.4716, b_{21} = 0.7554, \bar{b}_{12} = 0.6867$ and $\bar{a}_{21} = 0.6439$.

Moreover, we study the impacts of the initial release quantity and the CI intensity of the *wStri*-infected *N.lugens* on the control degree of wild *N.lugens*. Under the parameters $b = 0.6438$, $d_2 = 0.0031$, $d_1 = 0.0025$, $\xi = 0.675$, $a_{12} = 0.1222$, $a_{21} = 0.5453$, $\bar{a}_{12} = 0.54$, $\bar{a}_{21} = 0.4317$, $b_{12} = 0.4716$, $b_{21} = 0.7554$, $\bar{b}_{12} = 0.6867$ and $\bar{b}_{21} = 0.6439$, the control degree curves of the wild *N.lugens* with respect to the different initial release quantity of the *wStri*-infected *N.lugens* are shown in Figure 10(a). The numerical simulation shows that increasing the initial release quantity of *N.lugens* infected with *wStri* can effectively improve the control degree of the wild *N.lugens*. Similarly, when the CI intensity is selected as $\xi = 0.375, 0.475, 0.575, 0.675$ and $\xi = 0.775$, respectively, and the remaining parameters are the same as that of Figure 10(a). The control degree curves of the wild *N.lugens* with respect to the different CI intensity are given in Figure 10(b). The numerical simulation results show that an increase of the CI intensity is beneficial to improve the control degree of the wild *N.lugens*. Therefore, to effectively control the wild *N.lugens*, the release measures can be taken in area 2 to improve the initial release quantity of the *wStri*-infected *N.lugens* with the higher CI intensity.



(a)

(b)

Figure 10. The control degree of the wild *N.lugens*. (a) Effect of the initial release quantity of *N.lugens* infected with *wStri* on the control of the wild *N.lugens*. The initial value $(I_0^{(1)}, U_0^{(1)}, I_0^{(2)}, U_0^{(2)}) = (230, 530, I_0^{(2)}, 2)$, and $\xi = 0.675$. (b) Effect of the CI intensity of *wStri* on the control of the wild *N.lugens*. The initial value $(I_0^{(1)}, U_0^{(1)}), I_0^{(2)}, U_0^{(2)}) = (230, 530, 0, 2)$.

Previously, we found relevant control measures for migration by using numerical calculation method, namely reducing the landing rate $\bar{a}_{ij}$ or increasing the landing rate a_{ij}. However, the lower limit of $\bar{a}_{ij}$ reduction and the upper limit of a_{ij} increase need to be determined theoretically. According to Theorem 2, we can take measures such as increasing the release quantity of *wStri* in area 1 such that the successful landing rate a_{21} of the southward migration of *N.lugens* infected with *wStri* is greater than the threshold value $b_{12}c_1^3 - bc_1^2$, or the successful landing rate a_{12} of the northward migration of *N.lugens* infected with *wStri* is greater than the threshold value $\frac{1}{c_1^3}(b_{21} - bc_1)$ in area 2. Further, according to stability conditions of E_1, in order to ensure local asymptotic stability of E_1, the control measures we take should meet the following three conditions $d_2\bar{I}^{(1)} + d_2\bar{I}^{(2)} + \bar{b}_{12}c_1 + \frac{\bar{b}_{21}}{c_1} > 2b(1-\xi)$, $(-b(1-\xi) + \bar{b}_{12}c_1 + d_2\bar{I}^{(1)})(-b(1-\xi) + \frac{\bar{b}_{21}}{c_1} + d_2\bar{I}^{(2)}) > \bar{a}_{12}\bar{a}_{21}$ and $(b + \frac{3\bar{a}_{21}}{c_1^2})(b + 3a_{12}c_1^2) > (b_{12}c_1^2 + \frac{2a_{21}}{c_1})(2a_{12}c_1 + \frac{b_{21}}{c_1^2})$. Therefore, the wild *N.lugens* can be completely eliminated by initially releasing a certain quantity of *N.lugens* infected with *wStri*, thereby achieving the ideal control state for the wild *N.lugens* in two areas.

From the existence conditions of the uninfected equilibrium E_2 in system (2.3), as long as the artificial control measures taken in area 2 ensure that the successful landing rate $\bar{a}_{12}$ of the wild *N.lugens* migrating northward does not exceed the threshold value $\frac{1}{c_2^3}(\bar{b}_{21} - bc_2)$, or those taken in area 1 ensure that the successful landing rate $\bar{a}_{12}$ of the wild *N.lugens* migrating southward does not exceed the threshold value $\bar{b}_{12}c_2^3 - bc_2^2$, we can make system (2.3) not have equilibrium E_2. Even if the equilibrium

E_2 exists, we can still take the control measures, such as increasing the landing rate a_{ij} of *N.lugens* infected with *wStri* in destination area to make the inequality $(-b+d_1\hat{U}^{(1)}+b_{12}c_2)(-b+d_1\hat{U}^{(2)}+\frac{b_{21}}{c_2}) < a_{12}a_{21}$ holds, making equilibrium E_2 to be unstable.

7.4. *Migration strengthens the N.lugens population*

The wild *N.lugens* migration model (5.4) has two important applications. First, the global asymptotic stability of the positive equilibrium for model (5.4) indicates that the wild *N.lugens* can survive in both areas long term in the process of south-north migration. Therefore, a successful migration can lead to the rapid development and smooth propagation of *N.lugens* after adapting to long-distance migration into a new habitat [37]. Second, it can be used to simulate the phenomenon of migration strengthening the *N.lugens* population. In order to know the relationship between migration and population reproduction, Shen and Cheng conducted the experiment of pair breeding on Shanyou 63 hybrid rice by using *N.lugens* to be emigrated in Guilin and *N.lugens* moving in An'qing [38]. The results showed that the amount of eggs laid and the reproductivity of *N.lugens* have significantly improved after a long distance migration.

The take-off rate data and the landing rate data of *N.lugens* are not found, based on the total labeled data of rice planthopper in Xiangxiang, Qidong, Linli and Guiyang observation sites in Hunan Province of China from September 1, 2021 to September 30, 2021 (data from Hunan Provincial plant protection and inspection station), we first estimate the parameters of model (5.4). Notice that the statistical data have a strong randomness. By using the Markov Chain Monte Carlo (MCMC) method to estimate the parameters and the initial value $(b, d_2, \bar{b}_{12}, \bar{a}_{21}, \bar{a}_{12}, \bar{b}_{21}, U_0^{(1)})$ in system (5.4), we obtain the estimation values $b = 0.6438, d_2 = 0.0031, \bar{b}_{12} = 0.2316, \bar{a}_{21} = 0.4317, \bar{a}_{12} = 0.4593, \bar{b}_{21} = 0.3639$, and $U_0^{(1)} = 130.0119$. We provide additional details about the estimation process in Appendix. In order to numerically verify that migration strengthens the *N.lugens* population, by substituting the estimated parameters into system (5.4), we get that the positive equilibrium $(\hat{U}^{(1)}, \hat{U}^{(2)}) = (260.8292, 252.3654)$ and $B_4 = 2.4616 > 0$. Thus, from Theorem 8, the positive equilibrium is globally asymptotically stable. Therefore, the total number of *N.lugens* eventually approaches $\hat{U}^{(1)}+\hat{U}^{(2)} = 513.1945$. In addition, when there is no migration of *N.lugens*, the wild *N.lugens* population only interacts in their respective area; then, system (5.4) is further reduced to $\frac{\mathrm{d}U^{(1)}}{\mathrm{d}t} = bU^{(1)} - d_2(U^{(1)})^2$ and $\frac{\mathrm{d}U^{(2)}}{\mathrm{d}t} = bU^{(2)} - d_2(U^{(2)})^2$. It is easy to show that the number of *N.lugens* in south-north areas eventually approaches $\frac{2b}{d_2} = 415.3548$. Therefore, we have $\hat{U}^{(1)} + \hat{U}^{(2)} > \frac{2b}{d_2}$. This numerical simulation result shows that the number of wild *N.lugens* after migration is more than that of *N.lugens* without migration, as shown in Figure 11. The main experimental result of Ref. [38] is verified.

8. Conclusions

According to the release methods of *N.lugens* infected with *wStri* proposed in our previous work [6], the wild *N.lugens* in a paddy field or an area can be effectively controlled. However, *N.lugens* is an agricultural pest with a long distance migration habits. The *Wolbachia* spreading dynamic model, which takes the migration of *N.lugens* into account, can better reflect the reality in future field experiments; additionally, it is beneficial to understand how migration affects the control effect of *Wolbachia* to provide theoretical guidance for a accurate control of *N.lugens* and reduction of the risk of *N.lugens* occurrence.

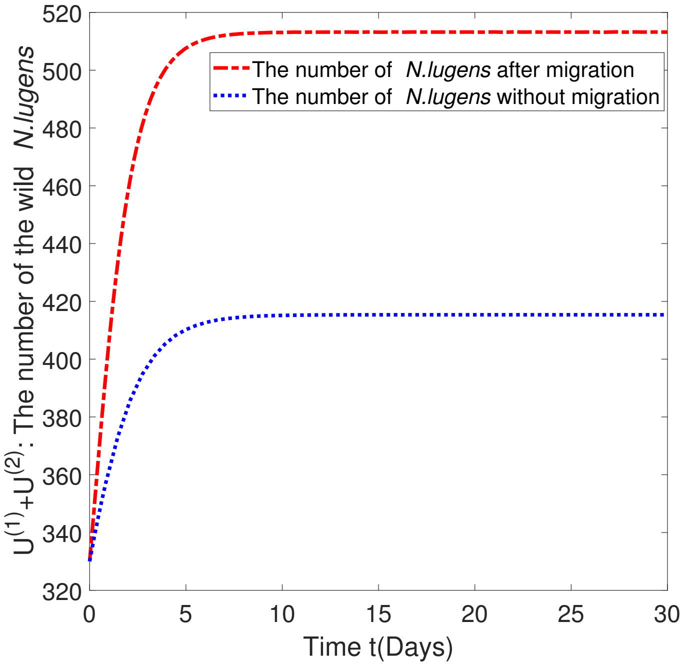


Figure 11. The influence of migration on the reproduction of *N.lugens*. The parameters are estimated as $b = 0.6438, d_2 = 0.0031, \bar{a}_{12} = 0.4593, \bar{a}_{21} = 0.4317, \bar{b}_{12} = 0.2316, \bar{b}_{21} = 0.3639$ by the way of MCMC. The initial value $(U_0^{(1)}, U_0^{(2)}) = (130.0119, 200)$. The blue dotted line shows the number of the wild *N.lugens* without migration, while the red dotted line shows the number of the wild *N.lugens* after migration.

The northern and southern rice areas were abstracted into two discrete patches. Based on the proposed population density proportional dependent migration coefficient, the discrete migration model reflecting the spread of *Wolbachia* in *N.lugens* is established.

The analysis results of equilibria show that the equilibrium infected with *wStri* and the uninfected equilibrium may be locally asymptotically stable under certain conditions. Based on numerical simulation, there may exist a positive equilibrium for system (2.3). From analyzing the subsystem without migration, we know that the positive equilibrium is always unstable and the subsystem can exhibit a bistable phenomenon.

The long-distance migration can increase the difficulty of controlling wild *N.lugens*. Numerical simulations results indicate that as the successful landing rate of the wild *N.lugens* increases, the equilibrium infected with *wStri* can change from stable state to unstable state, which may cause E_2 to be stable. Moreover, as the successful landing rate of the wild *N.lugens* decreases, the control degree of *N.lugens* increases, while the control degree of *N.lugens* increases as the successful landing rate of *N.lugens* infected with *wStri* increases. Additionally, some specific measures affecting the landing rate of *N.lugens* have also been suggested.

The global asymptotic stability of the positive equilibrium for the subsystem of the wild *N.lugens* migration shows that successful migration can lead to rapid development and smooth propagation of *N.lugens* after long distance migration. Further numerical simulation results suggested that the quantity of *N.lugens* population is increased after long distance migration, which is consistent with the experimental results found within literature [38].

Use of AI tools declaration

The authors declare they have not used Artificial Intelligence (AI) tools in the creation of this article.

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Conflict of interest

The authors declare there is no conflict of interest.

Appendix: Parameter estimation process based on MCMC

Since the observed data are the total labeled data of rice planthopper in four observation sites, which can be viewed as the number of wild *N.lugens* in area 1 to a certain extent. In order to use the MCMC method in Bayes statistical computation to estimate the six parameters and the initial value for model (5.4), let X_i and $Y = (y_1, y_2, \cdots, y_{30})^T$ be the real data for wild *N.lugens* and the observed data, respectively. Because these statistics approximately reflect the Hunan Province labeling data for wild *N.lugens* in September, rather than the real number of wild *N.lugens* for area 1, there is strong randomness for these statistics, so we assume that the observed data statistic is a Poisson process. Therefore, given day i, under the condition that the real number of wild *N.lugens* is x_i, the probability of the statistical data y_i is

$$P(Y_i = y_i | X_i = x_i) = \frac{x_i^{y_i}}{y_i!} e^{-x_i},$$

and the observed data each day is independent.

We use Metropolis-Hastings algorithm in MCMC to estimate parameters for model (5.4). Since *N.lugens* returns to the south from September, we assume that the initial value of wild *N.lugens* in area 2 is $U_0^{(2)} = 200$. Let the likelihood function be $L(Y|\theta)$, where $\theta = (b, d_2, \bar{b}_{12}, \bar{a}_{21}, \bar{a}_{12}, \bar{b}_{21}, U_0^{(1)}) \in \Theta$. In order to determine the posterior distribution, the seven parameters are nonnegative constant due to a practical problem is considered, we select non-informative prior distribution, and assuming the prior distribution is $p(\theta) \propto$ constant. Thus, the posterior distribution is

$$\begin{aligned} p(\theta|Y) &\propto L(Y|\theta) p(\theta) \\ &\propto \Pi_{i=1}^{30} p(y_i | x_i(\theta)) \\ &\propto \Pi_{i=1}^{30} \frac{x_i^{y_i}}{y_i!} e^{-x_i}. \end{aligned}$$

From the initial value $(b, d_2, \bar{b}_{12}, \bar{a}_{21}, \bar{a}_{12}, \bar{b}_{21}, U_0^{(1)}) = (0.5, 0.2, 0.06, 0.4, 0.5, 0.05, y_1)$, we choose a zero-centered uniform distribution as the proposed distribution, and a random walk Metropolis sampler is taken to produce the posterior distribution $p(\theta|Y)$ as stationary distribution of Markov chains [39,40], and implementing the following algorithm to generate random numbers (Markov chain):

1 Given the initial vector value $\theta^{(0)} = (b, d_2, \bar{b}_{12}, \bar{a}_{21}, \bar{a}_{12}, \bar{b}_{21}, U_0^{(1)})$;
2 Given the initial time $i = 0$;
3 Circulation
  - Sampling θ' from the proposed distribution $g(\cdot|\theta_i)$;
  - Extracting a random number u from the uniform distribution $U(0, 1)$;
  - If $u \leq \min\left\{1, \frac{p(\theta'|Y)}{p(\theta|Y)}\right\}$, then $\theta^{(i+1)} = \theta'$, else $\theta^{(i+1)} = \theta^{(i)}$.
  - $i = i + 1$;
  - After a burn-in period, store $\theta^{(i+1)}$ after a cycle of each s times.

4 Breaking circulation when i is sufficiently large.

Here, we cycle MCMC 10000 times, and take the burn-in period as 2000, and calculate the average value of the parameters of the last 8000 times, and get the estimated values of the seven parameters as follows: $b = 0.6438, d_2 = 0.0031, \bar{b}_{12} = 0.2316, \bar{a}_{21} = 0.4317, \bar{a}_{12} = 0.4593, \bar{b}_{21} = 0.3639$, and $U_0^{(1)} = 130.0119$.

References

1. P. Q. Cabauatan, R. C. Cabunagan, I.-R. Choi, *Rice viruses transmitted by the brown planthopper* Nilaparvata lugens *Stål*, International Rice Research Institute: Los Baños, Philippines, 2009.

2. J. Gong, Y. Li, T. Li, Y. Liang, L. Hu, D. Zhang, et al., Stable introduction of plant-virus-inhibiting *Wolbachia* into planthoppers for rice protection, *Curr. Biol.*, **30** (2020), 4837–4845.e5. https://doi.org/10.1016/j.cub.2020.09.033

3. K.-J. Zhang, W.-C. Zhu, X. Rong, Y. L. Ding, J. Liu, D. S. Chen, et al., The complete mitochondrial genomes of two rice planthoppers, *Nilaparvata lugens* and *Laodelphax striatellus*: conserved genome rearrangement in Delphacidae and discovery of new characteristics of atp8 and tRNA genes, *BMC Genom.*, **14** (2013), 417. https://doi.org/10.1186/1471-2164-14-417

4. H. Noda, Y. Koizumi, Q. Zhang, K. Ding, Infection density of *Wolbachia* and incompatibility level intwo planthopper species, *Laodelphax striatellus* and *Sogatella furcifera*, *Insect Biochem. Mol. Biol.*, **31** (2001), 727–737. https://doi.org/10.1016/S0965-1748(00)00180-6

5. Z. Liu, T. Zhou, *Wolbachia* spreading dynamics in *Nilaparvata lugens* with two strains, *Nonlinear Anal. RWA*, **62** (2021), 103361. https://doi.org/10.1016/j.nonrwa.2021.103361

6. Z. Liu, T. Chen, T. Zhou, Analysis of impulse release of *Wolbachia* to control *Nilaparvata lugens*, *Commun. Nonlinear SCI.*, **116** (2023), 106842. https://doi.org/10.1016/j.cnsns.2022.106842

7. J. H. Yen, A. R. Barr, New hypothesis of the cause of cytoplasmic incompatibility in Culex pipiens L., *Nature*, **232** (1971), 657–658. https://doi.org/10.1038/232657a0

8. D. P. LePage, J. A. Metcalf, S. R. Bordenstein, J. On, J. I. Perlmutter, J. D. SHropshire, et al., Prophage WO genes recapitulate and enhance *Wolbachi*a-induced cytoplasmic incompatibility, *Nature*, **543** (2017), 243–247. https://doi.org/10.1038/nature21391

9. Z. Xi, C. Khoo, S. Dobson, *Wolbachia* establishment and invasion in an *Aedes aegypti* laboratory population, *Science*, **310** (2005), 326–328. https://doi.org/10.1126/science.1117607
10. M. Turelli, A. Hoffmann, Rapid spread of an inherited incompatibility factor in *California Drosophila*, *Nature*, **353** (1991), 440–442. https://doi.org/10.1038/353440a0
11. Y. Bao, B. Zhai, X. Cheng, Numerical simulation of the migration parameters of the Brown Planthopper, *Nilaparvata lugens* (stål), *Acta. Ecologica. Sinica.*, **25** (2005), 1107–1114.
12. X. Cheng, R. Chen, X. Xi, L. Yang, Z. Zhu, J. Wu, et al., Study on the migrations of brown planthopper Nilaparvata lugens, *Acta Entomol. Sinica*, **22** (1979), 1–21.
13. X. Cheng, X. Zhang, J. Cheng, Radar observation of brown planthopper migration in eastern China in autumn, *J. Nanjing Agric. Univ.*, **17** (1994), 24–32.
14. Y. Wang, G. Hu, M. Xie, Air flow analysis of migratory paths of the white back planthopper and rice brown planthopper in China, *J. Plant Protec.*, **9** (1982), 73–82.
15. G. Hu, Q. Tang, Distribution and harm of brown planthopper in China, *Chinese J. Appl. Entomol.*, **34** (1997), 50–51,61.
16. J. Kennedy, Turning point in the study of insect migration, *Nature*, **189** (1961), 785–791. https://doi.org/10.1038/189785a0
17. T. Southwood, Migration of terrestrial arthropods in relation to habitat, *Biol. Rev.*, **37** (1962), 171–214. https://doi.org/10.1111/j.1469-185X.1962.tb01609.x
18. K. E. Khor, T. H. Chua, A rigorous population model for the brown planthopper, *Nilaparvata lugens* (Stål) (Homoptera: Delphacidae), *Res. Popul. Ecol.*, **28** (1986), 103–116. https://doi.org/10.1007/BF02515540
19. J. Vattikuti, V. Sailaja, Y. Prasad, P. M. Chiutkar, G. R. Rao, A. P. Padmakumari, et al., Temperature driven development of the rice brown planthopper, *Nilaparvata lugens*, *J. Agrometeor.*, **21** (2019), 131–140. https://doi.org/10.54386/jam.v21i2.221
20. N. Thuy, N. Doanh, T. Oanh, Effects of fast dispersal and stage structured on predator-prey dynamics: A case study of brown plant hopper ecological system, *J. Agrometeor.*, **17** (2019), 29–56.
21. A. Nguyen, D. Do, H. Nguyen, T. Nguyen, Stability analysis and Hopf bifurcation of a brown planthopper-rice model under the effect of monsoon, *Ecol. Model.*, **468** (2022), 109942. https://doi.org/10.1016/j.ecolmodel.2022.109942
22. M. Huang, M. Tang, J. Yu, *Wolbachia* infection dynamics by reaction-diffusion equations, *Sci. China Math.*, **58** (2015), 77–96. h ttps://doi.org/10.1007/s11425-014-4934-8
23. M. Huang, J. Yu, L. Hu, B. Zheng, Qualitative analysis for a *Wolbachia* infection model with diffusion, *Sci. China Math.*, **59** (2016), 1249–1266. https://doi.org/10.1007/s11425-016-5149-y
24. Y. Liu, Z. Guo, M. E. Smaily, L. Wang, A *wolbachia* infection model with free boundary, *J. Biol. Dynam.*, **14** (2020), 515–542. https://doi.org/10.1080/17513758.2020.1784474
25. Y. Liu, F. Jiao, L. Hu, Modeling mosquito population control by a coupled system, *J. Math. Anal. Appl.*, **506** (2022), 125671. https://doi.org/10.1016/j.jmaa.2021.125671
26. T. Hou, Causes of meteorological environment influencing on migration of rice planthopper, *J. Nat. Disaster*, **12** (2003), 142–148.

27. R. Mchich, P. Auger, J. C. Poggiale, Effect of predator density dependent dispersal of prey on stability of a predator–prey system, *Math. Biosci.*, **206** (2007), 343–356. https://doi.org/10.1016/j.mbs.2005.11.005
28. H. Smith, P. Waltman, *The Theory of the Chemostat*, Cambridge University Press, 1995.
29. H. Xu, J. Xue, B. Lu, X. Zhang, J. Zhuo, S. He, et al., Two insulin receptors determine alternative wing morphs in planthoppers, *Nature*, **519** (2015), 7544. https://doi.org/10.1038/nature14286
30. Z. Zhang, T. Ding, W. Huang, Z. Dong, *Qualitative theory of differential equations*, (Translations of Mathematical Monographs, 101), Providence, RI : American Mathematical Soc., 2006.
31. L. Perko, *Differential Equations and Dynamical Systems*, Springer, Berlin, 2001. https://doi.org/10.1007/978-1-4613-0003-8
32. X. Zheng, M. Zhao, S. He, X. Li, F. Yang, G. Wu, Effects of five different rice varieties on the life history and population dynamics of the brown planthopper, *Nilaparvata lugens* in central China, *Chin. J. Appl. Entomol.*, **57** (2020), 142–152.
33. S. He, N. Xiao, X. Zheng, M. Zhao, The life history parameters and population dynamics of brown planthopper *Nilaparvata lugens* feeding on different rice varieties in central China, *J. Plant Protection*, **48** (2021), 357–366. 10.13802/j.cnki.zwbhxb.2021.2020072
34. S. Ding, Z. Zeng, F. Yan, J. Wei, The development and life table parameters of *Nilaparvata lugens* (stål) feeding on nine rice varieties, *Acta Phytophylacica Sinica*, **39** (2012), 334–340.
35. V. Nguyen, H. Huynh, T. Vo, A. Drogoul, On weather affecting to brown plant hopper invasion using an agent-based model, *In: Proceedings of the International Conference on Management of Emergent Digital EcoSystems, MEDES*, (2011), 150–157. https://doi.org/10.1145/2077489.2077517
36. C. Phan, H. Huynh, A. Drogoul, An agent-based approach to the simulation of brown plant hopper(BPH) invasions in the mekong delta, *IEEE Rivf International Conference on Computing and Communication Technologies*, (2010). https://doi.org/10.1109/RIVF.2010.5633134
37. B. Lavie, U. Ritte, The relation between dispersal behavior and reproductive fitness inthe flour beetle tribolium castaneum, *Genome*, **20** (1978), 589–595. https://doi.org/10.1139/g78-068
38. L. Shen, X. Cheng, The effect of migration on reproduction of *Nilaparvata lugens* (stål), *J. Nanjing Agric. Univ.*, **21** (1998), 32–35.
39. N. Metropolis, M. Rosenbluth, M. Rosenbluth, A. Teller, E. Teller, Equations of state calculations by fast computing machines, *J. Chem. Phys.*, **21** (1953), 1087–1092. https://doi.org/10.1063/1.1699114
40. W. Hastings, Monte Carlo sampling methods using Markov chains and their applications, *Biometrika*, **57** (1970), 97–109. https://doi.org/10.1093/biomet/57.1.97

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