



Research article

Dynamical analysis of a delayed pine wilt disease model under temperature conditions

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Abstract: Pine wilt disease represents a devastating forest pest with severe ecological risks. Biological control based on the natural enemy *Dastarcus helophoroides* has become a core management strategy. Most existing dynamical models mainly focus on a single time delay or the effects of natural enemies, and studies comprehensively incorporating the coupled interplay of temperature, interspecific relationships, and time delay are still limited. Motivated by this situation, we establish a three-dimensional model of delayed differential equations, which captures the tripartite interaction among pine wood nematodes, *Monochamus alternatus*, and *Dastarcus helophoroides*. The model combines logistic population growth, Holling type II functional response, and the Brière type II nonlinear temperature-dependent developmental function, and introduces parasitic time delay to reflect temperature-driven regulation of development and reproduction across all three species. Analytically, we prove the existence of positive equilibria and derive criteria for the local asymptotic stability of the model. Taking the parasitic time delay as the bifurcation parameter, we obtain the critical time delay threshold and the transversality condition for Hopf bifurcation. The multiple time scales method is applied to derive the normal form of Hopf bifurcation, which further determines the stability and bifurcation direction of the periodic orbits. Numerically, we perform systematic simulations to examine how key parameters shape the model's dynamical behavior. Simulation results indicate that as the time delay increases, attracting periodic solutions emerge under the tested parameter values and initial histories. The ecological insights and biological control implications derived from this work are model-based hypotheses that may serve as a reference for further studies on pine wilt disease.

Keywords: pine wilt disease; delay differential equation; Hopf bifurcation; stability; temperature effect

1. Introduction

Pine wilt disease is a devastating forest disease caused by pine wood nematodes. It spreads rapidly, with an extremely high mortality rate among infected pine trees. The pine wood nematode is an invasive species originating from North America. Driven by frequent human activities, it has gradually spread to China, Japan, South Korea, and other countries, bringing severe damage to local forest resources and ecological environments. Given its rapid transmission, high host mortality, and difficult control, more than 50 countries worldwide have designated it as a priority quarantine pest for prevention and management [1].

In particular, the sustained spread of pine wilt disease has posed persistent threats to China's native pine forests and forest ecological security. According to the 2025 pine wilt disease epidemic area announcement released by the National Forestry and Grassland Administration [2], pine wilt disease has successively spread to 18 provinces nationwide since its introduction into China. Figure 1 characterizes the spatial pattern of pine wilt disease across mainland China, with varying fill shades for each province visually representing differences in the number of county-level epidemic sites. Accordingly, the prevention and control of pine wilt disease is of great significance to forestry development.

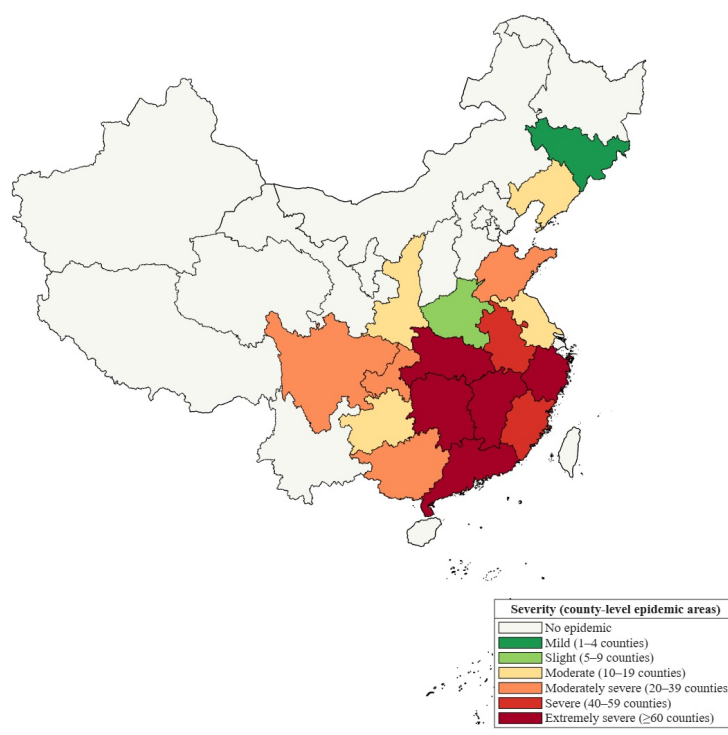


Figure 1. Provincial severity distribution of pine wilt disease in China, 2025. Note: The basemap used in this figure is the Multi-year Provincial Administrative Boundary Dataset of China from the Resource and Environment Science Data Registration and Publishing System. Full citation: Xu X L. Multi-year Provincial Administrative Boundary Dataset of China. Resource and Environment Science Data Registration and Publishing System (<http://www.resdc.cn/DOI>), 2023. DOI: 10.12078/2023010103.

Pine wilt disease spreads through two major channels: vector insects and human activities. Figure 2 illustrates the natural transmission process mediated by vector insects. First, vector-mediated transmission constitutes the primary natural spread route, with *Monochamus alternatus* (hereafter *M. alternatus*) as the principal vector. When adult pine sawyer beetles carrying pine wood nematodes feed on pine bark, juvenile nematodes invade healthy pine trees through feeding wounds and reproduce rapidly. Infected pine trees gradually decline and eventually die, and these dead hosts then become oviposition sites for *M. alternatus*. This cycle repeats in the following year, leading to continuous disease transmission [3]. Second, human-assisted transmission arises when forestry practitioners, lacking sufficient professional knowledge and biosecurity awareness, accidentally transport nematode-infected trees and their products into uninfected forest stands during forestry operations, resulting in human-mediated disease spread [4].

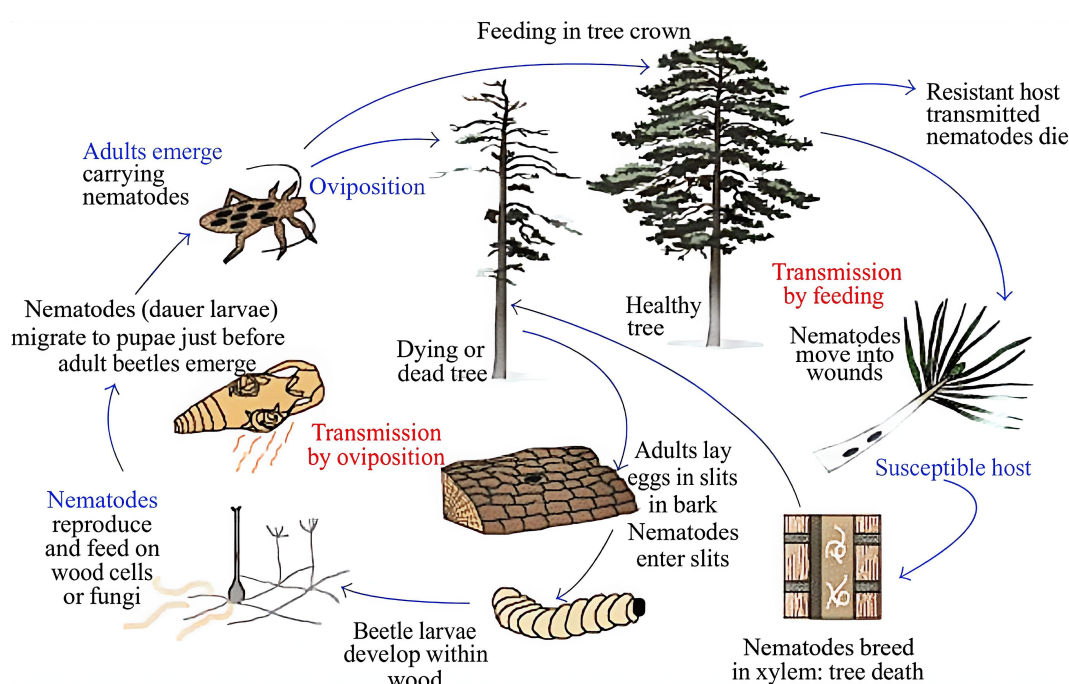


Figure 2. A schematic diagram illustrating the relationship between the pine wood nematode and its insect vector, *M. alternatus*. Note: This schematic diagram is reproduced with permission from Li and Ding (2025) [5].

In recent years, numerous researchers have conducted in-depth analyses of the pathogenic mechanisms, control strategies, and current status of pine wood nematode management, and have proposed scientifically sound and effective control recommendations. Although chemical control is an important method for managing pests and diseases—offering advantages such as rapid and efficient action, a broad spectrum of nematode control, and high controllability—its long-term use can easily induce resistance, kill natural enemies, and result in environmental residues [6]. Therefore, biological control, centered on the principles of using insects to control insects and using fungi to control insects, has become the core development direction for the integrated management of pine wood nematode disease due to its combination of environmental safety and long-term pest control efficacy. Numerous studies have indicated that *Dastarcus helophoroides* (hereafter *D. helophoroides*) can effectively reduce the popu-

lation density of *M. alternatus* in forests, thereby decreasing the risk of pine wood nematode disease transmission [7, 8]. *D. helophoroides* is one of the primary natural enemies of the pine sawyer beetle. Its larvae parasitize *M. alternatus*, reducing its population density, thereby decreasing the likelihood of pine wood nematode disease transmission and lowering the infection rate, which indirectly helps control the incidence of the disease.

Numerous studies both domestically and internationally have shown that temperature is a key factor influencing insect population dynamics [9]. Jikumaru and Togashi [10] reported that low temperatures shorten the lifespan of *M. alternatus*, reduce nematode transmission efficiency, delay the peak period of nematode transmission, and further lower the overall transmission rate, whereas Hou et al. [11] found that pine wood nematodes possess cold tolerance and can markedly improve their cold resistance via dehydration dormancy. Lee et al. [9] found that temperature exerts a marked influence on the lifespan and fecundity of *M. alternatus*, which allows researchers to predict population growth potential and evaluate disease outbreak risks. However, existing studies have primarily focused on the temperature response patterns of individual species, lacking detailed modeling and quantitative analysis of the temperature coupling effects among the pine wood nematode, *M. alternatus*, and *D. helophoroides*. Consequently, the combined regulatory effect of temperature on the population dynamics of the three species and its subsequent impact on disease transmission has not been fully clarified.

In mathematical modeling research on pine wilt disease, Li and Ding [5] established a delayed differential equation model for the pine wood nematode, *M. alternatus*, and *D. helophoroides*, focusing on the analysis of time-delay effects on model stability and periodic solutions, and proposed corresponding control recommendations based on these findings. Separately, Hou and Ding [12] constructed a reaction–diffusion predator–prey model with Holling type III functional response. Their analysis revealed that the joint action of memory diffusion and nonlocal effects may generate spatially inhomogeneous periodic population solutions. Yoshimura et al. [13] developed a static host–vector spatial model to quantify pine–beetle transmission patterns and test beetle removal interventions. Takasu et al. [14] established an integral–difference model to describe the invasion and expansion of pine wilt disease, and further analyzed model stability and transmission thresholds. In general, most existing models investigate influencing factors one at a time. Analyses that couple temperature with developmental delays to quantify interactions among pine sawyer beetles, parasitoids, and ambient temperature are comparatively less prevalent. Against this backdrop, our work integrates biological traits of pine wood nematodes, *M. alternatus*, and *D. helophoroides*, interspecific interactions, and temperature response patterns and builds a nonlinear dynamic model that unifies temperature responses, developmental delays, parasitism efficiency, and multispecies dynamics. We use nonlinear temperature functions to capture how temperature shapes growth and reproduction, and combine delay terms with parasitism interactions. The resulting model better reproduces real biological processes of pine wilt disease and offers theoretical foundations and modeling tools to support refined, site-specific forest disease management.

The structure of this paper is as follows: In Section 2, we construct a time-delay dynamic model of pine wilt disease under temperature conditions. In Section 3, we focus on the stability of the positive equilibria and the existence condition of Hopf bifurcation. In Section 4, the normal form of Hopf bifurcation is deduced by the multiple scales method, and the stability of the periodic solution is analyzed. In Section 5, the numerical simulation is carried out to verify the theoretical results. Finally, we give the conclusions in Section 6.

2. Mathematical modeling

According to the transmission mechanism of pine wilt disease, we establish a time-delay dynamic model for the prevention and control of pine wood nematode disease, which fully integrates temperature-dependent biological processes as a key driving factor:

$$\begin{cases} \frac{dM(t)}{dt} = r_1 M(t) - b_1 M^2(t) + \frac{a_1 M(t)N(t)}{1 + a_1 h_1 M(t)N(t)} + \frac{M(t)d_1 T(T - T_{m1}) \sqrt{T_{M1} - T}}{P_1}, \\ \frac{dN(t)}{dt} = r_2 N(t) - b_2 N^2(t) + \frac{a_1 M(t)N(t)}{1 + a_1 h_1 M(t)N(t)} - \frac{mP(t)N(t)}{1 + hmN(t)} \\ \quad + \frac{N(t)d_2 T(T - T_{m2}) \sqrt{T_{M2} - T}}{P_2}, \\ \frac{dP(t)}{dt} = r_3 P(t) - b_3 P^2(t) + \frac{mP(t - \tau)N(t - \tau)}{1 + hmN(t - \tau)} + \frac{P(t)d_3 T(T - T_{m3}) \sqrt{T_{M3} - T}}{P_3}, \end{cases} \quad (2.1)$$

where $M(t)$, $N(t)$, and $P(t)$ denote the population sizes of pine wood nematode, *M. alternatus*, and *D. helophoroides* at time t , respectively. All parameters in the model are positive real numbers, with detailed descriptions given in Table 1. Throughout this paper, time is measured in months; temperature in degrees Celsius ($^{\circ}\text{C}$); and the population abundances $M(t)$, $N(t)$, and $P(t)$ in units of 10^4 individuals. This scaling is adopted uniformly in all mathematical analysis, numerical simulations, and figures.

A further explanation of the model (2.1) is provided below:

(1) According to the logistic growth model, r represents the natural growth rate, which denotes the population growth rate under conditions of abundant resources, no competition, and no predators. However, in real-world environments, factors such as environmental carrying capacity and intraspecific competition introduce survival restriction factors; therefore, each population equation for M , N , and P includes a logistic growth term $r_i X(t) - b_i X^2(t)$, where $i = 1, 2, 3$ corresponds to $X = M, N, P$ in sequence.

(2) In the natural environment, the pine wood nematode and *M. alternatus* form a mutually beneficial symbiotic relationship. *M. alternatus* provides an effective route of transmission for the pine wood nematode: *M. alternatus* carries nematode-spreading larvae during eclosion, causing wounds by supplementary feeding, so that nematodes invade healthy pine trees; nematodes can cause pine trees to wither, thereby eliminating resin defenses, improving the feeding environment, and significantly increasing the survival rate of *M. alternatus* larvae. However, the promoting effect of the two is not infinite. When the population density of either species is very large, there will be a state of “resource saturation,” and their population densities converge to a steady level. The Holling type II functional response function can satisfy the conditions of two-way promotion and resource saturation at the same time; the expression is $\frac{a_1 M(t)N(t)}{1 + a_1 h_1 M(t)N(t)}$.

(3) *D. helophoroides* is one of the core natural enemies for the prevention and control of *M. alternatus*. Its adults can locate the pine trees damaged by *M. alternatus* larvae; lay eggs around the *M. alternatus* moth track; and invade the beetle galleries after hatching, parasitizing and feeding on *M. alternatus* larvae, pupae, and even newly emerged adults, eventually leading to the death of the host. The two form a typical host–parasitoid relationship. Field trapping and laboratory rearing ex-

periments have repeatedly verified that there is a significant time delay effect in the parasitic process of *D. helophoroides* on *M. alternatus*. We therefore introduce the time delay parameter τ , which represents the effective delay in the numerical response of the parasitoid population, with the pre-adult development of parasitoid offspring as its underlying biological mechanism.

This time delay results in distinct timing of effects on the host and parasitoid sides. On the host side, the model assumes that an *M. alternatus* individual attacked by *D. helophoroides* is removed from the effective vector population N at the moment of attack. This means that the individual ceases to contribute to nematode transmission from that moment onward, prior to its eventual death. Because nematode transmission relies on dispersing adult beetles that acquire the nematode at eclosion, this biological assumption gives rise to the instantaneous loss term. On the parasitoid side, the offspring produced by parasitism must complete their pre-adult development before emerging as adults and joining population P . The recruitment of adult parasitoids at time t therefore originates from parasitism events at time $t - \tau$, corresponding to the delayed recruitment term. Based on the Holling type II functional response, which describes the saturation of *D. helophoroides* parasitization efficiency with increasing *M. alternatus* density, the two corresponding terms are derived as: $-\frac{mP(t)N(t)}{1 + hmN(t)}$ and $\frac{mP(t - \tau)N(t - \tau)}{1 + hmN(t - \tau)}$.

(4) The Brière equation is a classical nonlinear model describing the relationship between biological developmental rate and temperature. It is widely used in insect ecology and other fields. Its basic form is:

$$V(T) = \begin{cases} a T (T - T_L) \sqrt{T_H - T}, & T_L \leq T \leq T_H, \\ 0, & \text{otherwise.} \end{cases} \quad (2.2)$$

$V(T)$ is the developmental rate at temperature T , a is a constant, and T_L and T_H are the lower developmental threshold temperature and the upper developmental threshold temperature, respectively [15].

Using this form, we introduce the effect of temperature on the developmental rate of the pine wood nematode, *M. alternatus*, and *D. helophoroides*. Therefore, each temperature-dependent term for M , N , and P takes the form $\frac{X(t)}{P_i} [d_i T (T - T_{mi}) \sqrt{T_{Mi} - T}]$, valid for $T_{mi} \leq T \leq T_{Mi}$, where $i = 1, 2, 3$ corresponds to $X = M, N, P$ in sequence.

Although the Brière function is originally defined as a developmental rate, the temperature-dependent term built from it enters model (2.1) as a contribution to the per-capita growth. This construction follows the common use of thermal performance curves (TPCs), which describe how temperature shapes many biological traits, including population growth, and for which the Brière model serves as a standard benchmark [16]; Brière-type equations have also been applied to growth processes beyond development [17]. The temperature-dependent term thus modulates the per-capita growth of species X with temperature; it is defined only for $T \in [T_{mi}, T_{Mi}]$ and is set to zero outside this range.

Table 1. Descriptions of variables and parameters in the model (2.1).

Symbol	Ecological description
r_1	Natural growth rate of pine wood nematode
r_2	Natural growth rate of <i>M. alternatus</i>
r_3	Natural growth rate of <i>D. helophoroides</i>
b_1	Survival restriction factor of pine wood nematode
b_2	Survival restriction factor of <i>M. alternatus</i>
b_3	Survival restriction factor of <i>D. helophoroides</i>
a_1	Contact efficiency between <i>M. alternatus</i> and pine wood nematode
h_1	Time required for <i>M. alternatus</i> to process a single pine tree
h	Time required for <i>D. helophoroides</i> to process <i>M. alternatus</i>
m	Parasitism efficiency of <i>D. helophoroides</i>
T	Ambient forest temperature
T_{m1}	Lower developmental threshold temperature for pine wood nematode eggs
T_{m2}	Lower developmental threshold temperature for <i>M. alternatus</i> eggs
T_{m3}	Lower developmental threshold temperature for <i>D. helophoroides</i> eggs
T_{M1}	Upper developmental threshold temperature for pine wood nematode eggs
T_{M2}	Upper developmental threshold temperature for <i>M. alternatus</i> eggs
T_{M3}	Upper developmental threshold temperature for <i>D. helophoroides</i> eggs
d_1	Scaling coefficient in the effect of temperature on pine wood nematode abundance
d_2	Scaling coefficient in the effect of temperature on <i>M. alternatus</i> abundance
d_3	Scaling coefficient in the effect of temperature on <i>D. helophoroides</i> abundance
P_1	Proportional coefficient of fecundity to total abundance of pine wood nematode
P_2	Proportional coefficient of fecundity to total abundance of <i>M. alternatus</i>
P_3	Proportional coefficient of fecundity to total abundance of <i>D. helophoroides</i>

3. Stability analysis

In this section, we will investigate the existence and stability of equilibria for the model (2.1). Let $H_i = \frac{1}{P_i} [d_i T (T - T_{mi}) \sqrt{T_{Mi} - T}]$, where the subscript $i = 1, 2, 3$ corresponds to the temperature-dependent term in the model (2.1) for populations M , N , and P , respectively. Model (2.1) has eight equilibria, listed as follows:

$$\begin{aligned}
 E_1 &= (0, 0, 0), & E_2 &= \left(0, 0, \frac{r_3 + H_3}{b_3}\right), & E_3 &= \left(0, \frac{r_2 + H_2}{b_2}, 0\right), & E_4 &= \left(\frac{r_1 + H_1}{b_1}, 0, 0\right), \\
 E_5 &= (0, N_5, P_5), & E_6 &= \left(\frac{r_1 + H_1}{b_1}, 0, \frac{r_3 + H_3}{b_3}\right), & E_7 &= (M_7, N_7, 0), & E_8 &= (M_8, N_8, P_8),
 \end{aligned}$$

where equilibrium E_6 takes an explicit analytical form, as the two surviving species grow independently and have no direct interspecific interactions. Equilibria E_5 and E_7 , corresponding to the systems (3.1) and (3.2), respectively, have no explicit analytical expressions; their positive coordinates are computed

numerically in Section 5.

$$\begin{cases} r_2 - b_2 N_5 - \frac{mP_5}{1 + hmN_5} + H_2 = 0, \\ r_3 - b_3 P_5 + \frac{mN_5}{1 + hmN_5} + H_3 = 0, \end{cases} \quad (3.1)$$

$$\begin{cases} r_1 - b_1 M_7 + \frac{a_1 N_7}{1 + a_1 h_1 M_7 N_7} + H_1 = 0, \\ r_2 - b_2 N_7 + \frac{a_1 M_7}{1 + a_1 h_1 M_7 N_7} + H_2 = 0. \end{cases} \quad (3.2)$$

For E_1 – E_4 , the linearization admits at least one positive eigenvalue in a direction in which an absent population can invade: $\lambda = r_1 + H_1$ (invasion of M) for E_1 and E_2 , $\lambda = r_1 + a_1(r_2 + H_2)/b_2 + H_1$ (invasion of M) for E_3 , and $\lambda = r_3 + H_3$ (invasion of P) for E_4 . Because the ambient temperature lies in the admissible developmental range, $H_i > 0$, and hence $r_i + H_i > 0$ ($i = 1, 2, 3$), E_1 – E_4 are therefore all unstable. For E_5 – E_7 , the same invasion argument applies, even though E_5 and E_7 lack closed-form coordinates. At E_5 , the M -component of the linearized system decouples and yields the positive eigenvalue $\lambda = r_1 + a_1 N_5 + H_1$, as $N_5 > 0$ (confirmed numerically in Section 5), and $H_1 > 0$. At E_6 , the N -component decouples and yields $\lambda = r_2 + H_2 + a_1(r_1 + H_1)/b_1 - m(r_3 + H_3)/b_3$, which is exactly the left-hand side of (H1) and is therefore positive under assumption (H1). At E_7 , the P -component decouples and yields the characteristic factor $g(\lambda) = \lambda - r_3 - H_3 - \frac{mN_7}{1 + hmN_7}e^{-\lambda\tau}$, for which $g(0) = -(r_3 + H_3) - \frac{mN_7}{1 + hmN_7} < 0$, $g'(\lambda) = 1 + \tau \frac{mN_7}{1 + hmN_7}e^{-\lambda\tau} > 0$, and $g(\lambda) \rightarrow +\infty$ as $\lambda \rightarrow +\infty$. By the intermediate value theorem, $g(\lambda)$ has at least a positive root, so E_7 is unstable. Thus, under (H1) and $H_i > 0$, all boundary equilibria E_1 – E_7 are analytically unstable. Ecologically, these states only describe partial species extinction, which cannot reflect the coexistence of all three populations in real forest ecosystems. For this reason, we focus our subsequent analysis on the equilibrium E_8 .

We can get the characteristic equation of the linearized model at E_8 as follows:

$$\begin{cases} r_1 - b_1 M_8 + \frac{a_1 N_8}{1 + a_1 h_1 M_8 N_8} + H_1 = 0, \\ r_2 - b_2 N_8 + \frac{a_1 M_8}{1 + a_1 h_1 M_8 N_8} - \frac{mP_8}{1 + hmN_8} + H_2 = 0, \\ r_3 - b_3 P_8 + \frac{mN_8}{1 + hmN_8} + H_3 = 0. \end{cases} \quad (3.3)$$

Considering the biological significance of the model (2.1), we require that the equilibrium E_8 is non-negative. Therefore, we make the following assumption:

$$(H1) \quad r_2 + H_2 + a_1 \frac{r_1 + H_1}{b_1} - \frac{m(r_3 + H_3)}{b_3} > 0.$$

Based on the above assumption, we present the following theorem.

Theorem 3.1. Under Assumption (H1), the model (2.1) admits at least one positive equilibrium (M_8, N_8, P_8) .

Proof. According to the third equation of (3.3), we derive the explicit expression of P_8 in terms of N_8 :

$$P_8(N_8) = \frac{1}{b_3} \left(r_3 + H_3 + \frac{mN_8}{1 + hmN_8} \right). \quad (3.4)$$

From the biological interpretation of each parameter, all parameters are positive. Hence, $P_8 > 0$ automatically holds as long as $N_8 > 0$. Then, the first equation of (3.3) can be rearranged as

$$AM_8^2 + BM_8 + C = 0, \quad (3.5)$$

where

$$\begin{cases} A = -a_1h_1b_1N_8, \\ B = a_1h_1N_8(r_1 + H_1) - b_1, \\ C = r_1 + H_1 + a_1N_8. \end{cases}$$

Note that the discriminant reads

$$\Delta = [a_1h_1N_8(r_1 + H_1) + b_1]^2 + 4a_1^2h_1b_1N_8^2 > 0.$$

This quadratic equation (3.5) possesses two real roots, x_1 and x_2 . Because $x_1x_2 = \frac{C}{A} < 0$, one root is positive, and the other is negative. We take the positive root as $M_8(N_8)$, whose explicit expression is

$$M_8(N_8) = \frac{-B - \sqrt{\Delta}}{2A}. \quad (3.6)$$

Substituting Eqs (3.4) and (3.6) into the second equation of (3.3), we derive

$$F(N_8) = r_2 + H_2 - b_2N_8 + \frac{a_1M_8(N_8)}{1 + a_1h_1M_8(N_8)N_8} - \frac{mP_8(N_8)}{1 + hmN_8}. \quad (3.7)$$

Obviously, $F(N_8)$ is continuous for all $N_8 > 0$.

As $N_8 \rightarrow 0^+$, we have $P_8(N_8) \rightarrow \frac{r_3 + H_3}{b_3}$ from the third equation of (3.3). The first equation of (3.3) degenerates to $r_1 - b_1M_8(N_8) + H_1 = 0$, which yields $M_8(N_8) \rightarrow \frac{r_1 + H_1}{b_1}$. Accordingly,

$$F(0^+) = r_2 + H_2 + a_1 \frac{r_1 + H_1}{b_1} - \frac{m(r_3 + H_3)}{b_3}. \quad (3.8)$$

Under Assumption (H1), we immediately get $F(0^+) > 0$. As $N_8 \rightarrow +\infty$, it follows that $\frac{mN_8}{1 + hmN_8} \rightarrow \frac{1}{h}$,

so $P_8(N_8) \rightarrow \frac{1}{b_3} \left(r_3 + H_3 + \frac{1}{h} \right)$, a finite positive constant. Meanwhile, $M_8(N_8)$ converges to a finite positive value, as the first equation of (3.3) simplifies to $r_1 + H_1 - b_1M_8 + \frac{1}{h_1M_8} = 0$, which admits a unique finite positive root. The dominant term of $F(N_8)$ is $-b_2N_8$; hence, $F(+\infty) \rightarrow -\infty$.

Because $F(N_8)$ is continuous on $(0, +\infty)$ with $F(0^+) > 0$, and $F(+\infty) \rightarrow -\infty$, the intermediate value theorem guarantees that there exists at least one $N_8 \in (0, +\infty)$ such that $F(N_8) = 0$. Consequently, the model (2.1) admits at least one positive equilibrium, (M_8, N_8, P_8) . $\square$

Remark 3.1. We note that the above argument ensures only the existence of a positive equilibrium. For the baseline parameter set in Section 5, the positive equilibrium is numerically unique.

Finally, we derive the characteristic equation of the linearized model (2.1) evaluated at E_8 as follows:

$$(A_1\lambda^2 + B_1\lambda + C_1)e^{-\lambda\tau} + \lambda^3 + A_2\lambda^2 + B_2\lambda + C_2 = 0, \quad (3.9)$$

where

$$\begin{aligned} A_1 &= -B_{33}, & A_2 &= -(A_{11} + A_{22} + A_{33}), \\ B_1 &= -A_{23}B_{32} + B_{33}(A_{22} + A_{11}), & B_2 &= A_{11}A_{22} + A_{22}A_{33} + A_{33}A_{11} - A_{12}A_{21}, \\ C_1 &= A_{11}A_{23}B_{32} - A_{11}A_{22}B_{33} + A_{12}A_{21}B_{33}, & C_2 &= -A_{11}A_{22}A_{33} + A_{12}A_{21}A_{33}, \end{aligned}$$

with

$$\begin{aligned} A_{11} &= r_1 - 2b_1M_8 + \frac{a_1N_8}{(1 + a_1h_1M_8N_8)^2} + H_1, & A_{12} &= \frac{a_1M_8}{(1 + a_1h_1M_8N_8)^2}, \\ A_{13} &= 0, & A_{21} &= \frac{a_1N_8}{(1 + a_1h_1M_8N_8)^2}, \\ A_{22} &= r_2 - 2b_2N_8 + \frac{a_1M_8}{(1 + a_1h_1M_8N_8)^2} - \frac{mP_8}{(1 + hmN_8)^2} + H_2, & A_{23} &= -\frac{mN_8}{1 + hmN_8}, \\ A_{31} &= 0, & A_{32} &= 0, \\ A_{33} &= r_3 - 2b_3P_8 + H_3, & B_{32} &= \frac{mP_8}{(1 + hmN_8)^2}, \\ B_{33} &= \frac{mN_8}{1 + hmN_8}. \end{aligned}$$

In particular, when $\tau = 0$, the characteristic equation (3.9) reduces to

$$\lambda^3 + (A_1 + A_2)\lambda^2 + (B_1 + B_2)\lambda + (C_1 + C_2) = 0. \quad (3.10)$$

To investigate the stability of the positive equilibrium E_8 when $\tau = 0$, we further introduce the following assumption:

$$(H2) \quad A_1 + A_2 > 0, \quad (A_1 + A_2)(B_1 + B_2) - (C_1 + C_2) > 0, \quad C_1 + C_2 > 0.$$

Then by the Routh–Hurwitz criterion for cubic polynomials, all roots of the characteristic equation (3.10) have negative real parts. Thus, we have the following lemma.

Lemma 3.1. For the model (2.1), if Assumptions (H1) and (H2) hold, then the positive equilibrium E_8 is locally asymptotically stable when $\tau = 0$. At this time, $\lambda = 0$ is not the root of the characteristic equation (3.10); in other words, the model (2.1) does not undergo the fixed-point bifurcation.

We next investigate the existence of Hopf bifurcations near the positive equilibrium E_8 for $\tau > 0$. Let $\lambda = i\omega$ with $\omega > 0$ denote a purely imaginary root of the characteristic equation (3.9). Substituting $\lambda = i\omega$ into Eq (3.9) and separating real and imaginary parts yields the following system:

$$\begin{cases} (C_1 - A_1\omega^2)\cos(\tau\omega) + B_1\omega\sin(\tau\omega) - A_2\omega^2 - C_2 = 0, \\ (C_1 - A_1\omega^2)\sin(\tau\omega) - B_1\omega\cos(\tau\omega) + \omega^3 - B_2\omega = 0. \end{cases} \quad (3.11)$$

It is concluded that:

$$\begin{cases} \sin(\tau\omega) = \frac{B_1\omega(A_2\omega^2 - C_2) + (C_1 - A_1\omega^2)(B_2\omega - \omega^3)}{B_1^2\omega^2 + (C_1 - A_1\omega^2)^2}, \\ \cos(\tau\omega) = \frac{(A_2\omega^2 - C_2)(C_1 - A_1\omega^2) - B_1\omega(B_2\omega - \omega^3)}{B_1^2\omega^2 + (C_1 - A_1\omega^2)^2}. \end{cases} \quad (3.12)$$

Letting $z = \omega^2$, we know that z satisfies the following:

$$f(z) = z^3 + Jz^2 + Kz + L = 0, \quad (3.13)$$

where

$$\begin{aligned} J &= A_2^2 - A_1^2 - 2B_2, \\ K &= B_2^2 + 2C_1A_1 - B_1^2 - 2A_2C_2, \\ L &= C_2^2 - C_1^2. \end{aligned}$$

Assume that Eq (3.13) has k ($k = 1, 2, 3$) positive roots, denoted by $z_1 < z_2 < z_3$. Substituting $\omega_k = \sqrt{z_k}$ ($k = 1, 2, 3$) into Eq (3.12), we first define the sine and cosine quantities at $\omega = \omega_k$:

$$\begin{cases} \Phi_k = \frac{B_1\omega_k(A_2\omega_k^2 - C_2) + (C_1 - A_1\omega_k^2)(B_2\omega_k - \omega_k^3)}{B_1^2\omega_k^2 + (C_1 - A_1\omega_k^2)^2}, \\ \Psi_k = \frac{(A_2\omega_k^2 - C_2)(C_1 - A_1\omega_k^2) - B_1\omega_k(B_2\omega_k - \omega_k^3)}{B_1^2\omega_k^2 + (C_1 - A_1\omega_k^2)^2}, \end{cases} \quad (3.14)$$

where Φ_k and Ψ_k correspond to the sine and cosine of the same phase angle and satisfy $\Phi_k^2 + \Psi_k^2 = 1$ whenever z_k is a root of Eq (3.13).

Accordingly, the sequence of critical delays can be expressed in a compact atan2 form as

$$\tau_k^{(j)} = \frac{1}{\omega_k} (\text{atan2}(\Phi_k, \Psi_k) + 2j\pi), \quad j = 0, 1, 2, \dots, k = 1, 2, 3, \dots \quad (3.15)$$

where the two-argument arctangent is taken in the range $[0, 2\pi)$; that is, 2π is added whenever $\text{atan2}(\Phi_k, \Psi_k)$ returns a negative value.

For each fixed positive root z_k of Eq (3.13), the sequence $\tau_k^{(j)}$ defined by Eq (3.15) is strictly increasing in j , so the smallest critical delay generated by z_k is $\tau_k^{(0)}$. Therefore, we obtain the following lemma.

Lemma 3.2. If $f'(z_k) \neq 0$ for some positive root z_k of (3.13), where $f'(z)$ denotes the derivative of $f(z)$ with respect to z and $z_k = \omega_k^2$, then we have the following transversality condition:

$$\begin{aligned} \text{Re} \left(\frac{d\lambda}{d\tau} \Big|_{\tau=\tau_k^{(j)}} \right)^{-1} &= \text{Re} \left(\frac{d\tau}{d\lambda} \Big|_{\tau=\tau_k^{(j)}} \right) \\ &= \frac{f'(z)}{(C_1 - A_1z)^2 + B_1^2z} \neq 0, \quad k = 1, 2, 3, j = 0, 1, 2, \dots \end{aligned}$$

After the above discussion, we arrive at the following conclusion.

Theorem 3.2. For the model (2.1), assume that Assumptions (H1) and (H2) hold. Then, the following statements hold:

(1) If Eq (3.13) admits no positive roots, the positive equilibrium E_8 of the model (2.1) is locally asymptotically stable for all $\tau \geq 0$.

(2) If Eq (3.13) possesses exactly one positive root z , the characteristic equation (3.9) has a unique pair of purely imaginary roots $\pm i\omega$ with $\omega = \sqrt{z}$. The equilibrium E_8 is locally asymptotically stable for $\tau \in [0, \tau_1^{(0)})$ and unstable for $\tau > \tau_1^{(0)}$. The equilibrium E_8 of the model (2.1) undergoes the Hopf bifurcation at $\tau = \tau_1^{(j)}$, $j = 0, 1, 2, \dots$.

(3) If Eq (3.13) has more than one positive root, each positive root z_k generates its own strictly increasing sequence of critical delays $\tau_k^{(j)}$, and by Lemma 3.2, the crossing direction at each critical value is determined by the sign of $f'(z_k)$. In this case, as τ passes through successive critical delays, characteristic roots enter or leave the right half-plane, so the local asymptotic stability of E_8 may switch accordingly; the precise switching pattern depends on the ordering of all the critical delays, which varies with the parameter values.

4. Normal form of Hopf bifurcation

In this section, we derive the normal form of Hopf bifurcation for the model (2.1) by using the multiple time scales method. In order to reflect the practical biological background of *D. helophoroides* parasitizing *M. alternatus*, we focus on the parasitic time delay τ and study its effects on population dynamics so as to provide a theoretical basis for the prevention and treatment of pine wilt disease. When $\tau = \tau_c$, where $\tau_c = \tau_k^{(j)}$ is given in Eq (3.15), the characteristic equation (3.9) has a pair of purely imaginary eigenvalues $\lambda = i\omega$, at which the model (2.1) undergoes Hopf bifurcation at the equilibrium $E_8 = (M_8, N_8, P_8)$. Therefore, we consider the time delay τ as the bifurcation parameter.

Let $\tau = \tau_c + \varepsilon\mu$, where τ_c is the critical value of Hopf bifurcation given in Eq (3.15), μ is the disturbance parameter, and ε is the dimensionless scaling parameter.

After shifting the equilibrium E_8 to the origin point and applying the time transformation $t \rightarrow t/\tau$, the model (2.1) can be rewritten by keeping terms up to the third order as follows:

$$\begin{aligned}
\frac{dM}{dt} = & \tau \left(-b_1 M^2 + \left(r_1 - 2b_1 M_8 + H_1 + \frac{a_1 N_8}{(1 + a_1 h_1 M_8 N_8)^2} \right) M + \frac{a_1 M_8}{(1 + a_1 h_1 M_8 N_8)^2} N \right. \\
& - \frac{a_1^2 h_1 N_8^2}{(1 + a_1 h_1 M_8 N_8)^3} M^2 - \frac{a_1^2 h_1 M_8^2}{(1 + a_1 h_1 M_8 N_8)^3} N^2 + \frac{a_1 (1 - a_1 h_1 M_8 N_8)}{(1 + a_1 h_1 M_8 N_8)^3} MN \\
& + \frac{a_1^3 h_1^2 N_8^3}{(1 + a_1 h_1 M_8 N_8)^4} M^3 + \frac{a_1^3 h_1^2 M_8^3}{(1 + a_1 h_1 M_8 N_8)^4} N^3 + \frac{a_1^3 h_1^2 M_8^2 N_8 - 2a_1^2 h_1 M_8}{(1 + a_1 h_1 M_8 N_8)^4} MN^2 \\
& \left. + \frac{a_1^3 h_1^2 M_8 N_8^2 - 2a_1^2 h_1 N_8}{(1 + a_1 h_1 M_8 N_8)^4} M^2 N \right), \\
\frac{dN}{dt} = & \tau \left(-\frac{m N_8}{1 + h m N_8} P - \frac{m}{(1 + h m N_8)^2} P N - \frac{a_1^2 h_1 N_8^2}{(1 + a_1 h_1 M_8 N_8)^3} M^2 \right. \\
& + \left(r_2 - 2b_2 N_8 + H_2 + \frac{a_1 M_8}{(1 + a_1 h_1 M_8 N_8)^2} - \frac{m P_8}{(1 + h m N_8)^2} \right) N \\
& + \frac{a_1 N_8}{(1 + a_1 h_1 M_8 N_8)^2} M + \left(\frac{h m^2 P_8}{(1 + h m N_8)^3} - \frac{a_1^2 h_1 M_8^2}{(1 + a_1 h_1 M_8 N_8)^3} - b_2 \right) N^2 \\
& \left. + \frac{a_1 (1 - a_1 h_1 M_8 N_8)}{(1 + a_1 h_1 M_8 N_8)^3} M N \right), \\
\frac{dP}{dt} = & \tau \left((r_3 - 2b_3 P_8 + H_3) P - b_3 P^2 + \frac{m N_8}{1 + h m N_8} P(t-1) + \frac{m P_8}{(1 + h m N_8)^2} N(t-1) \right. \\
& + \frac{m}{(1 + h m N_8)^2} P(t-1) N(t-1) - \frac{h m^2 P_8}{(1 + h m N_8)^3} N^2(t-1) \\
& \left. + \frac{h^2 m^3 P_8}{(1 + h m N_8)^4} N^3(t-1) - \frac{h m^2}{(1 + h m N_8)^3} N^2(t-1) P(t-1) \right).
\end{aligned} \tag{4.1}$$

We denote q as the eigenvector of the linearized model (2.1) corresponding to the eigenvalue $i\omega\tau$ and q^* as the normalized eigenvector of the adjoint linear operator corresponding to the eigenvalue $-i\omega\tau$, satisfying $\langle q^*, q \rangle = 1$. Next, through straightforward calculations, we obtain

$$q = \begin{pmatrix} q_1 \\ q_2 \\ q_3 \end{pmatrix} = \begin{pmatrix} 1 \\ \frac{\omega i - A_{11}}{A_{12}} \\ -\frac{A_{21}}{A_{23}} + \frac{(\omega i - A_{22})(\omega i - A_{11})}{A_{12} A_{23}} \end{pmatrix}, \tag{4.2}$$

$$q^* = d \begin{pmatrix} q_1^* \\ q_2^* \\ q_3^* \end{pmatrix} = d \begin{pmatrix} 1 \\ -\frac{\omega i + A_{11}}{A_{21}} \\ \left[\frac{(\omega i + A_{22})(\omega i + A_{11})}{A_{21} B_{32}} - \frac{A_{12}}{B_{32}} \right] e^{-\omega \tau i} \end{pmatrix}, \tag{4.3}$$

where

$$d = \frac{1}{q_1^* \bar{q}_1 + q_2^* \bar{q}_2 + q_3^* \bar{q}_3}.$$

We assume that the solution of Eq (4.1) is as follows:

$$X(t) = X(T_0, T_1, T_2, \dots) = \sum_{k=1}^{+\infty} \varepsilon^k X_k(T_0, T_1, T_2, \dots), \quad (4.4)$$

where $X(T_0, T_1, T_2, \dots) = (M(T_0, T_1, T_2, \dots), N(T_0, T_1, T_2, \dots), P(T_0, T_1, T_2, \dots))^T$,

$$X_k(T_0, T_1, T_2, \dots) = (M_k(T_0, T_1, T_2, \dots), N_k(T_0, T_1, T_2, \dots), P_k(T_0, T_1, T_2, \dots))^T.$$

The derivative with respect to t is converted to

$$\frac{d}{dt} = \frac{\partial}{\partial T_0} + \varepsilon \frac{\partial}{\partial T_1} + \varepsilon^2 \frac{\partial}{\partial T_2} + \dots = D_0 + \varepsilon D_1 + \varepsilon^2 D_2 + \dots,$$

where D_i is a differential operator, and

$$D_i = \frac{\partial}{\partial T_i} \quad (i = 0, 1, 2, \dots).$$

According to Eq (4.1), we can get:

$$\dot{X}(t) = \varepsilon D_0 X_1 + \varepsilon^2 D_1 X_1 + \varepsilon^3 D_2 X_1 + \varepsilon^2 D_0 X_2 + \varepsilon^3 D_1 X_2 + \varepsilon^3 D_0 X_3 + \dots. \quad (4.5)$$

We expand $X_k(T_0 - 1, \varepsilon(T_0 - 1), \varepsilon^2(T_0 - 1), \dots)$ around $X_k(T_0 - 1, T_1, T_2, \dots)$ using Taylor series expansion and obtain

$$X(t - 1) = \varepsilon X_{1,\tau_c} + \varepsilon^2 X_{2,\tau_c} + \varepsilon^3 X_{3,\tau_c} - \varepsilon^2 D_1 X_{1,\tau_c} - \varepsilon^3 D_2 X_{1,\tau_c} - \varepsilon^3 D_1 X_{2,\tau_c} + \dots, \quad (4.6)$$

where $X_{j,\tau_c} = X_j(T_0 - 1, T_1, T_2, \dots)$, $j = 1, 2, \dots$

As mentioned above, τ is the bifurcation parameter, and we write $\tau = \tau_c + \varepsilon\mu$. Define $Q_1 = 1 + a_1 h_1 M_8 N_8$, $Q_2 = 1 + h m N_8$. Substituting the above expressions into Eq (4.1) and comparing the coefficients of ε on both sides, we obtain the following result:

$$\begin{aligned} D_0 M_1 - \tau_c M_1 \left(r_1 - 2b_1 M_8 + H_1 + \frac{a_1 N_8}{Q_1^2} \right) - \tau_c \frac{a_1 M_8}{Q_1^2} N_1 &= 0, \\ D_0 N_1 - \tau_c N_1 \left(r_2 - 2b_2 N_8 + H_2 + \frac{a_1 M_8}{Q_1^2} - \frac{m P_8}{Q_2^2} \right) - \tau_c \frac{a_1 N_8}{Q_1^2} M_1 + \tau_c \frac{m N_8}{Q_2} P_1 &= 0, \\ D_0 P_1 - \tau_c P_1 (r_3 - 2b_3 P_8 + H_3) - \tau_c \frac{m N_8}{Q_2} P_{1,\tau_c} - \tau_c \frac{m P_8}{Q_2^2} N_{1,\tau_c} &= 0. \end{aligned} \quad (4.7)$$

The solution of Eq (4.7) has the following form:

$$X_1(T_1, T_2, T_3, \dots) = G(T_1, T_2, T_3, \dots) q e^{i\omega\tau_c T_0} + \bar{G}(T_1, T_2, T_3, \dots) \bar{q} e^{-i\omega\tau_c T_0}. \quad (4.8)$$

The expression corresponding to the coefficient of ε^2 is as follows:

$$\begin{aligned}
 & D_0 M_2 - \tau_c M_2 \left(r_1 - 2b_1 M_8 + H_1 + \frac{a_1 N_8}{Q_1^2} \right) - \tau_c \frac{a_1 M_8}{Q_1^2} N_2 \\
 &= -D_1 M_1 - \tau_c b_1 M_1^2 - \tau_c \frac{a_1^2 h_1 N_8^2}{Q_1^3} M_1^2 - \tau_c \frac{a_1^2 h_1 M_8^3}{Q_1^3} N_1^2 + \mu \frac{a_1 M_8}{Q_1^2} N_1 \\
 &+ \tau_c \frac{a_1 (1 - a_1 h_1 M_8 N_8)}{Q_1^3} M_1 N_1 + \mu M_1 \left(r_1 - 2b_1 M_8 + H_1 + \frac{a_1 N_8}{Q_1^2} \right), \\
 & D_0 N_2 - \tau_c N_2 \left(r_2 - 2b_2 N_8 + H_2 + \frac{a_1 M_8}{Q_1^2} - \frac{m P_8}{Q_2^2} \right) - \tau_c \frac{a_1 N_8}{Q_1^2} M_2 + \tau_c \frac{m N_8}{Q_2^2} P_2 \\
 &= -D_1 N_1 + \tau_c \left(\frac{h m^2 P_8}{Q_2^3} - \frac{a_1^2 h_1 M_8^2}{Q_1^3} - b_2 \right) N_1^2 - \tau_c \frac{a_1^2 h_1 N_8^2}{Q_1^3} M_1^2 - \tau_c \frac{m}{Q_2^2} P_1 N_1 \\
 &+ \tau_c \frac{a_1 (1 - a_1 h_1 M_8 N_8)}{Q_1^3} M_1 N_1 + \mu N_1 \left(r_2 - 2b_2 N_8 + H_2 + \frac{a_1 M_8}{Q_1^2} - \frac{m P_8}{Q_2^2} \right) \\
 &+ \mu \frac{a_1 N_8}{Q_1^2} M_1 - \mu \frac{m N_8}{Q_2^2} P_1, \\
 & D_0 P_2 - \tau_c P_2 (r_3 - 2b_3 P_8 + H_3) - \tau_c \frac{m N_8}{Q_2} P_{2,\tau_c} - \tau_c \frac{m P_8}{Q_2^2} N_{2,\tau_c} \\
 &= -D_1 P_1 - \tau_c \frac{m N_8}{Q_2} D_1 P_{1,\tau_c} - \tau_c \frac{m P_8}{Q_2^2} D_1 N_{1,\tau_c} - \tau_c \frac{h m^2 P_8}{Q_2^3} N_{1,\tau_c}^2 \\
 &+ \mu \frac{m N_8}{Q_2} P_{1,\tau_c} + \tau_c \frac{m}{Q_2^2} P_{1,\tau_c} N_{1,\tau_c} - \tau_c b_3 P_1^2 + \mu \frac{m P_8}{Q_2^2} N_{1,\tau_c} \\
 &+ \mu (r_3 - 2b_3 P_8 + H_3) P_1.
 \end{aligned} \tag{4.9}$$

Substituting Eq (4.8) into the right-hand side of Eq (4.9), the coefficient vector of $e^{i\omega\tau_c T_0}$ is denoted as m_1 . According to the solvability condition $\langle q^*, m_1 \rangle = 0$, the following expression is obtained:

$$\frac{\partial G}{\partial T_1} = \frac{V_1}{V_2} \mu G, \tag{4.10}$$

where

$$\begin{aligned}
 V_1 = & q_1 \left(r_1 - 2b_1 M_8 + H_1 + \frac{a_1 N_8}{Q_1^2} \right) + q_2 \frac{a_1 M_8}{Q_1^2} + \frac{\omega i - A_{11}}{A_{21}} \\
 & \times \left[q_2 \left(r_2 - 2b_2 N_8 + H_2 + \frac{a_1 M_8}{Q_1^2} - \frac{m P_8}{Q_2^2} \right) + q_1 \frac{a_1 N_8}{Q_1^2} - q_3 \frac{m N_8}{Q_2} \right] \\
 & + \left[\frac{(A_{22} - \omega i)(A_{11} - \omega i)}{A_{21} B_{32}} - \frac{A_{12}}{B_{32}} \right] e^{i\omega\tau} \times \left[q_3 (r_3 - 2b_3 P_8 + H_3) \right. \\
 & \left. + \frac{m N_8}{Q_2} q_3 e^{-i\omega\tau_c} + \frac{m P_8}{Q_2^2} q_2 e^{-i\omega\tau_c} \right], \\
 V_2 = & q_1 + \frac{\omega i - A_{11}}{A_{21}} q_2 + \left[\frac{(A_{22} - \omega i)(A_{11} - \omega i)}{A_{21} B_{32}} - \frac{A_{12}}{B_{32}} \right] e^{i\omega\tau} \\
 & \times \left(\tau_c \frac{m N_8}{Q_2} q_3 e^{-i\omega\tau_c} + \tau_c \frac{m P_8}{Q_2^2} q_2 e^{-i\omega\tau_c} + q_3 \right).
 \end{aligned}$$

Because μ is a perturbation parameter, we only consider its influence on the linear part. It has little effect on the higher order, so it can be ignored. Therefore, we ignore the part of the higher order containing μ . We assume that the solution of Eq (4.9) is as follows:

$$\begin{aligned}
 M_2 &= g_1 e^{2i\omega\tau_c T_0} G^2 + \overline{g_1} e^{-2i\omega\tau_c T_0} \overline{G}^2 + l_1 G \overline{G}, \\
 N_2 &= g_2 e^{2i\omega\tau_c T_0} G^2 + \overline{g_2} e^{-2i\omega\tau_c T_0} \overline{G}^2 + l_2 G \overline{G}, \\
 P_2 &= g_3 e^{2i\omega\tau_c T_0} G^2 + \overline{g_3} e^{-2i\omega\tau_c T_0} \overline{G}^2 + l_3 G \overline{G},
 \end{aligned} \tag{4.11}$$

where

$$\begin{aligned}
 \begin{pmatrix} g_1 \\ g_2 \\ g_3 \end{pmatrix} &= \begin{pmatrix} g_{11} & -\tau_c \frac{a_1 M_8}{Q_1^2} & 0 \\ -\tau_c \frac{a_1 N_8}{Q_1^2} & g_{22} & \tau_c \frac{m N_8}{Q_2} \\ 0 & -\tau_c \frac{m P_8}{Q_2^2} e^{-2i\omega\tau_c} & g_{33} \end{pmatrix}^{-1} \begin{pmatrix} g_{111} \\ g_{222} \\ g_{333} \end{pmatrix}, \\
 \begin{pmatrix} l_1 \\ l_2 \\ l_3 \end{pmatrix} &= \begin{pmatrix} l_{11} & -\tau_c \frac{a_1 M_8}{Q_1^2} & 0 \\ -\tau_c \frac{a_1 N_8}{Q_1^2} & l_{22} & \tau_c \frac{m N_8}{Q_2} \\ 0 & -\tau_c \frac{m P_8}{Q_2^2} & l_{33} \end{pmatrix}^{-1} \begin{pmatrix} l_{111} \\ l_{222} \\ l_{333} \end{pmatrix},
 \end{aligned}$$

with

$$\begin{aligned}
 g_{11} &= 2\omega\tau_c i - \tau_c \left(r_1 - 2b_1 M_8 + H_1 + \frac{a_1 N_8}{Q_1^2} \right), \\
 g_{22} &= 2\omega\tau_c i - \tau_c \left(r_2 - 2b_2 N_8 + H_2 + \frac{a_1 M_8}{Q_1^2} - \frac{m P_8}{Q_2^2} \right), \\
 g_{33} &= 2\omega\tau_c i - \tau_c (r_3 - 2b_3 P_8 + H_3) - \tau_c \frac{m N_8}{Q_2} e^{-2i\omega\tau_c}, \\
 l_{11} &= -\tau_c \left(r_1 - 2b_1 M_8 + H_1 + \frac{a_1 N_8}{Q_1^2} \right), \\
 l_{22} &= -\tau_c \left(r_2 - 2b_2 N_8 + H_2 + \frac{a_1 M_8}{Q_1^2} - \frac{m P_8}{Q_2^2} \right), \\
 l_{33} &= -\tau_c (r_3 - 2b_3 P_8 + H_3) - \tau_c \frac{m N_8}{Q_2},
 \end{aligned}$$

$$\begin{aligned}
 g_{111} &= -\tau_c q_1^2 \left(\frac{a_1^2 h_1 N_8^2}{Q_1^3} + b_1 \right) - \tau_c q_2^2 \frac{a_1^2 h_1 M_8^2}{Q_1^3} + \tau_c q_1 q_2 \frac{a_1 (1 - a_1 h_1 M_8 N_8)}{Q_1^3}, \\
 g_{222} &= \tau_c q_2^2 \left(\frac{h m^2 P_8}{Q_2^3} - \frac{a_1^2 h_1 M_8^2}{Q_1^3} - b_2 \right) - \tau_c q_1^2 \frac{a_1^2 h_1 N_8^2}{Q_1^3} - \tau_c q_2 q_3 \frac{m}{Q_2^2} + \tau_c q_1 q_2 \frac{a_1 (1 - a_1 h_1 M_8 N_8)}{Q_1^3}, \\
 g_{333} &= -\tau_c q_2^2 \frac{h m^2 P_8}{Q_2^3} e^{-2i\omega\tau_c} + \tau_c q_2 q_3 \frac{m}{Q_2^2} e^{-2i\omega\tau_c} - \tau_c b_3 q_3^2, \\
 l_{111} &= -2\tau_c q_1 \bar{q}_1 \left(b_1 + \frac{a_1^2 h_1 N_8^2}{Q_1^3} \right) - 2\tau_c q_2 \bar{q}_2 \frac{a_1^2 h_1 M_8^2}{Q_1^3} + \tau_c \frac{a_1 (1 - a_1 h_1 M_8 N_8)}{Q_1^3} (q_1 \bar{q}_2 + \bar{q}_1 q_2), \\
 l_{222} &= 2\tau_c q_2 \bar{q}_2 \left(\frac{h m^2 P_8}{Q_2^3} - \frac{a_1^2 h_1 M_8^2}{Q_1^3} - b_2 \right) - 2\tau_c q_1 \bar{q}_1 \frac{a_1^2 h_1 N_8^2}{Q_1^3} - \tau_c \frac{m}{Q_2^2} (q_2 \bar{q}_3 + q_3 \bar{q}_2) \\
 &\quad + \tau_c \frac{a_1 (1 - a_1 h_1 M_8 N_8)}{Q_1^3} (q_1 \bar{q}_2 + q_2 \bar{q}_1), \\
 l_{333} &= -2\tau_c q_2 \bar{q}_2 \frac{h m^2 P_8}{Q_2^3} + \tau_c \frac{m}{Q_2^2} (\bar{q}_2 q_3 + q_2 \bar{q}_3) - 2\tau_c b_3 q_3 \bar{q}_3.
 \end{aligned}$$

The expression corresponding to the coefficient of ε^3 is as follows:

$$\begin{aligned}
& D_0 M_3 - \tau_c M_3 \left(r_1 - 2b_1 M_8 + H_1 + \frac{a_1 N_8}{Q_1^2} \right) - \tau_c \frac{a_1 M_8}{Q_1^2} N_3 \\
&= \tau_c \frac{a_1^3 h_1^2 N_8^3}{Q_1^4} M_1^3 + \tau_c \frac{a_1^3 h_1^2 M_8^3}{Q_1^4} N_1^3 - 2b_1 \tau_c M_1 M_2 - 2\tau_c \cdot \frac{a_1^2 h_1 N_8^2}{Q_1^3} M_1 M_2 - 2\tau_c \frac{a_1^2 h_1 M_8^2}{Q_1^3} N_1 N_2 \\
&+ \mu M_2 \left(r_1 - 2b_1 M_8 + H_1 + \frac{a_1 N_8}{Q_1^2} \right) + \frac{\tau_c a_1 (1 - a_1 h_1 M_8 N_8)}{Q_1^3} (M_1 N_2 + M_2 N_1) + \mu \frac{a_1 M_8}{Q_1^2} N_2 \\
&+ \frac{\tau_c (a_1^3 h_1^2 M_8^2 N_8 - 2a_1^2 h_1 M_8)}{Q_1^4} M_1 N_1^2 + \frac{\tau_c (a_1^3 h_1^2 M_8 N_8^2 - 2a_1^2 h_1 N_8)}{Q_1^4} M_1^2 N_1 - D_1 M_2 - D_2 M_1 \\
&- \mu b_1 M_1^2 - \mu \frac{a_1^2 h_1 N_8^2}{Q_1^3} M_1^2 - \mu \frac{a_1^2 h_1 M_8^2}{Q_1^3} N_1^2 + \frac{\mu a_1 (1 - a_1 h_1 M_8 N_8)}{Q_1^3} M_1 N_1, \\
& D_0 N_3 - \tau_c N_3 \left(r_2 - 2b_2 N_8 + H_2 + \frac{a_1 M_8}{Q_1^2} - \frac{m P_8}{Q_2^2} \right) - \tau_c \frac{a_1 N_8}{Q_1^2} M_3 + \tau_c \frac{m N_8}{Q_2} P_3 \\
&= 2\tau_c \left(\frac{h m^2 P_8}{Q_2^3} - \frac{a_1^2 h_1 M_8^2}{Q_1^3} - b_2 \right) N_1 N_2 - 2\tau_c \frac{a_1^2 h_1 N_8^2}{Q_1^3} M_1 M_2 - \tau_c \frac{m}{Q_2^2} (P_1 N_2 + P_2 N_1) + \mu \frac{a_1 N_8}{Q_1^2} M_2 \\
&+ \tau_c \frac{a_1 (1 - a_1 h_1 M_8 N_8)}{Q_1^3} (M_1 N_2 + M_2 N_1) + \tau_c \frac{a_1^3 h_1^2 N_8^3}{Q_1^4} M_1^3 + \tau_c \frac{a_1^3 h_1^2 M_8^3}{Q_1^4} N_1^3 - D_1 N_2 - D_2 N_1 \\
&+ \tau_c \frac{a_1^3 h_1^2 M_8^2 N_8 - 2a_1^2 h_1 M_8}{Q_1^4} M_1 N_1^2 + \tau_c \frac{a_1^3 h_1^2 N_8^2 M_8 - 2a_1^2 h_1 N_8}{Q_1^4} M_1^2 N_1 - \mu \frac{a_1^2 h_1 N_8^2}{Q_1^3} M_1^2 \\
&- \tau_c \frac{h^2 m^3 P_8}{Q_2^4} N_1^3 + \tau_c \frac{h m^2}{Q_2^3} N_1^2 P_1 + \mu \left(r_2 - 2b_2 N_8 + H_2 + \frac{a_1 M_8}{Q_1^2} - \frac{m P_8}{Q_2^2} \right) N_2 - \mu \frac{m N_8}{Q_2} P_2 \\
&+ \mu \left(\frac{h m^2 P_8}{Q_2^3} - \frac{a_1^2 h_1 M_8^2}{Q_1^3} - b_2 \right) N_1^2 - \mu \frac{m}{Q_2^2} P_1 N_1 + \mu \frac{a_1 (1 - a_1 h_1 M_8 N_8)}{Q_1^3} M_1 N_1, \\
& D_0 P_3 - \tau_c P_3 (r_3 - 2b_3 P_8 + H_3) - \tau_c \frac{m N_8}{Q_2} P_{3,\tau_c} - \tau_c \frac{m P_8}{Q_2^2} N_{3,\tau_c} \\
&= -\tau_c \frac{m N_8}{Q_2} (D_2 P_{1,\tau_c} + D_1 P_{2,\tau_c}) - \tau_c \frac{m P_8}{Q_2^2} (D_2 N_{1,\tau_c} + D_1 N_{2,\tau_c}) + \tau_c \frac{h^2 m^3 P_8}{Q_2^4} N_{1,\tau_c}^3 - \mu b_3 P_1^2 \\
&- \tau_c \frac{h m^2 P_8}{Q_2^3} (2N_{1,\tau_c} N_{2,\tau_c} - 2N_{1,\tau_c} D_1 N_{1,\tau_c}) - \tau_c \frac{h m^2}{Q_2^3} N_{1,\tau_c}^2 P_{1,\tau_c} - 2\tau_c b_3 P_1 P_2 - D_2 P_1 - D_1 P_2 \\
&+ \tau_c \frac{m}{Q_2^2} [P_{1,\tau_c} (N_{2,\tau_c} - D_1 N_{1,\tau_c}) + N_{1,\tau_c} (P_{2,\tau_c} - D_1 P_{1,\tau_c})] + \mu (r_3 - 2b_3 P_8 + H_3) P_2 \\
&+ \mu \frac{m N_8}{Q_2} (P_{2,\tau_c} - D_1 P_{1,\tau_c}) + \mu \frac{m P_8}{Q_2^2} (N_{2,\tau_c} - D_1 N_{1,\tau_c}) - \mu \frac{h m^2 P_8}{Q_2^3} N_{1,\tau_c}^2 + \mu \frac{m}{Q_2^2} P_{1,\tau_c} N_{1,\tau_c}.
\end{aligned}
\tag{4.12}$$

Using the above equations, the coefficient vector of $e^{i\omega\tau_c T_0}$ is expressed as m_2 . According to the

solvability condition $\langle q^*, m_2 \rangle = 0$, the following expression can be obtained:

$$\frac{\partial G}{\partial T_2} = \frac{W_1}{W_2} \tau_c G^2 \bar{G}, \quad (4.13)$$

where

$$\begin{aligned} W_1 = & \bar{q}_1^* \left\{ 3 \frac{a_1^3 h_1^2 N_8^3}{Q_1^4} q_1^2 \bar{q}_1 + 3 \frac{a_1^3 h_1^2 M_8^3}{Q_1^4} q_2^2 \bar{q}_2 + \frac{a_1^3 h_1^2 M_8^2 N_8 - 2a_1^2 h_1 M_8}{Q_1^4} (2q_1 q_2 \bar{q}_2 + \bar{q}_1 q_2^2) \right. \\ & + \frac{a_1^3 h_1^2 M_8 N_8^2 - 2a_1^2 h_1 N_8}{Q_1^4} (2q_2 q_1 \bar{q}_1 + \bar{q}_2 q_1^2) - (2b_1 + 2 \frac{a_1^2 h_1 N_8^2}{Q_1^3}) (\bar{q}_1 g_1 + q_1 l_1) \\ & - 2 \frac{a_1^2 h_1 M_8^2}{Q_1^3} (\bar{q}_2 g_2 + q_2 l_2) + \frac{a_1 (1 - a_1 h_1 M_8 N_8)}{Q_1^3} (\bar{q}_1 g_2 + q_1 l_2 + \bar{q}_2 g_1 + q_2 l_1) \Big\} \\ & + \bar{q}_2^* \left\{ 2 \left(\frac{h m^2 P_8}{Q_2^3} - \frac{a_1^2 h_1 M_8^2}{Q_1^3} - b_2 \right) (\bar{q}_2 g_2 + q_2 l_2) - 2 \frac{a_1^2 h_1 N_8^2}{Q_1^3} (\bar{q}_1 g_1 + q_1 l_1) \right. \\ & - \frac{m}{Q_2^2} (\bar{q}_3 g_2 + q_3 l_2 + \bar{q}_2 g_3 + q_2 l_3) + \frac{a_1 (1 - a_1 h_1 M_8 N_8)}{Q_1^3} (\bar{q}_1 g_2 + q_1 l_2 + \bar{q}_2 g_1 + q_2 l_1) \\ & + 3 \frac{a_1^3 h_1^2 N_8^3}{Q_1^4} q_1^2 \bar{q}_1 + 3 \frac{a_1^3 h_1^2 M_8^3}{Q_1^4} q_2^2 \bar{q}_2 + \frac{a_1^3 h_1^2 M_8^2 N_8 - 2a_1^2 h_1 M_8}{Q_1^4} (2q_1 q_2 \bar{q}_2 + \bar{q}_1 q_2^2) \\ & + \frac{a_1^3 h_1^2 M_8 N_8^2 - 2a_1^2 h_1 N_8}{Q_1^4} (2q_2 q_1 \bar{q}_1 + \bar{q}_2 q_1^2) - 3 \frac{h^2 m^3 P_8}{Q_2^4} q_2^2 \bar{q}_2 + \frac{h m^2}{Q_2^3} (2q_3 q_2 \bar{q}_2 + \bar{q}_3 q_2^2) \Big\} \\ & + \bar{q}_3^* \left\{ - \frac{h m^2 P_8}{Q_2^3} (2q_2 l_2 e^{-i\omega\tau_c} + 2\bar{q}_2 g_2 e^{-i\omega\tau_c}) + 3 \frac{h^2 m^3 P_8}{Q_2^4} q_2^2 \bar{q}_2 - 2b_3 (\bar{q}_3 g_3 + q_3 l_3) \right. \\ & + \frac{m}{Q_2^2} (q_3 l_2 e^{-i\omega\tau_c} + \bar{q}_3 g_2 e^{-i\omega\tau_c} + q_2 l_3 e^{-i\omega\tau_c} + \bar{q}_2 g_3 e^{-i\omega\tau_c}) \\ & \left. - \frac{h m^2}{Q_2^3} (q_2^2 \bar{q}_3 e^{-i\omega\tau_c} + 2q_2 \bar{q}_2 q_3 e^{-i\omega\tau_c}) \right\}, \\ W_2 = & \bar{q}_1^* q_1 + \bar{q}_2^* q_2 + \bar{q}_3^* \left(\tau_c \frac{m N_8}{Q_2} q_3 e^{-i\omega\tau_c} + \tau_c \frac{m P_8}{Q_2^2} q_2 e^{-i\omega\tau_c} + q_3 \right), \end{aligned}$$

where q_c, q_c^* ($c = 1, 2, 3$) are given by Eqs (4.2) and (4.3), and g_c, l_c ($c = 1, 2, 3$) are determined by Eq (4.11).

Then, we obtain the normal form of the Hopf bifurcation for the model (2.1), truncated at the third order:

$$\dot{G} = \frac{V_1}{V_2} \mu G + \frac{W_1}{W_2} \tau_c G^2 \bar{G}, \quad (4.14)$$

where V_1, V_2 is given in Eq (4.10), and W_1, W_2 is given in Eq (4.13). Substituting $G = r e^{i\theta}$ into Eq (4.14), the normal form of the Hopf bifurcation in polar coordinates is obtained as follows:

$$\begin{cases} \dot{r} = \text{Re}(\frac{V_1}{V_2}) \mu r + \tau_c \text{Re}(\frac{W_1}{W_2}) r^3, \\ \dot{\theta} = \text{Im}(\frac{V_1}{V_2}) \mu + \tau_c \text{Im}(\frac{W_1}{W_2}) r^2. \end{cases} \quad (4.15)$$

According to the standard form of Hopf bifurcation in polar coordinates, we only need to consider the first equation in system (4.15). Thus, the following theorem holds.

Theorem 4.1. For system (4.15), if $\frac{\operatorname{Re}(\frac{V_1}{V_2})\mu}{\tau_c \operatorname{Re}(\frac{W_1}{W_2})} < 0$, then there exists a nontrivial fixed point $r =$

$\sqrt{-\frac{\operatorname{Re}(\frac{V_1}{V_2})\mu}{\tau_c \operatorname{Re}(\frac{W_1}{W_2})}}$, and the model (2.1) admits a periodic solution near the equilibrium E_8 .

(1) If $\operatorname{Re}(\frac{W_1}{W_2}) < 0$, the bifurcation is supercritical, and the periodic solution is orbitally stable; it exists for $\mu > 0$ (forward) when $\operatorname{Re}(\frac{V_1}{V_2}) > 0$, and for $\mu < 0$ (backward) when $\operatorname{Re}(\frac{V_1}{V_2}) < 0$.

(2) If $\operatorname{Re}(\frac{W_1}{W_2}) > 0$, the bifurcation is subcritical, and the periodic solution is unstable; it exists for $\mu < 0$ (backward) when $\operatorname{Re}(\frac{V_1}{V_2}) > 0$, and for $\mu > 0$ (forward) when $\operatorname{Re}(\frac{V_1}{V_2}) < 0$.

5. Numerical simulations

In order to verify the previous theoretical results, we carry out numerical simulations. Given that pine wilt disease has caused severe damage to forest ecosystems in China, we set model parameters mainly based on domestic field studies and official forestry statistics, with only a small number of parameters supplemented by international literature. All parameters are adjusted to match the actual ecological conditions of pine forests in China. On this basis, we calculate the positive equilibrium E_8 of the model (2.1). Then, we simulate the population dynamics of pine wood nematodes, *M. alternatus*, and *D. helophoroides* over time. Finally, we analyze the simulation results within the present modeling framework, explore the key factors influencing the control efficacy of pine wilt disease, and provide corresponding reference implications for disease prevention and management.

5.1. Determination of parameter values

In this subsection, we analyze real data from official databases and experimental parameters from related literature and derive the practically meaningful range of each parameter.

(1) The lower developmental threshold temperature T_{m1} and upper developmental threshold temperature T_{M1} for pine wood nematode eggs.

According to the technical introduction of pine wilt disease released by the Hunan Forestry Bureau [18], the developmental threshold temperature range of pine wood nematodes is 9.5–33 °C. Therefore, we set $T_{m1} = 9.5$ °C, $T_{M1} = 33$ °C.

(2) The lower developmental threshold temperature T_{m2} and upper developmental threshold temperature T_{M2} for *M. alternatus* eggs.

According to [19], the lower developmental temperature for the egg stage of *M. alternatus* is 14.3 ± 0.86 °C, and the upper developmental temperature is 35 °C. Therefore, we take the mean value of the minimum temperature as T_{m2} , namely $T_{m2} = 14.3$ °C, $T_{M2} = 35$ °C.

(3) The lower developmental threshold temperature T_{m3} and upper developmental threshold temperature T_{M3} for *D. helophoroides* eggs.

(a) According to [20], the lower developmental temperature for the egg stage of *D. helophoroides* is 12.8 ± 0.33 °C. Therefore, we take the mean value of the lower temperature as T_{m3} , namely $T_{m3} = 12.8$ °C.

(b) It can be seen from [21] that the upper developmental temperature for the egg stage of *D. helophoroides* ranges from 42 to 45 °C. We adopt 45 °C as this upper threshold.

(4) Time h required for *D. helophoroides* to process *M. alternatus*.

According to [22], we can know that the handling time of *D. helophoroides* on *M. alternatus* is 7–9 days. If the month is taken as the unit, the range of h is 0.23–0.3 months.

(5) Parasitism efficiency m of *D. helophoroides*.

According to [23], the observed parasitism rate of *D. helophoroides* in forests is 0.46, and the indoor parasitism rate is 0.92. Because parasitism performance varies with environmental conditions, we set the model parameter m to the range 0.46–0.92 month⁻¹.

(6) The scaling coefficients d_1 , d_2 , and d_3 characterize temperature effects on the abundances of pine wood nematodes, *M. alternatus*, and *D. helophoroides*. Each d_i carries the unit °C^{-5/2} month⁻¹, which is just what makes the Brière term $d_i T (T - T_{mi}) \sqrt{T_{Mi} - T}$ ($i = 1, 2, 3$) a developmental rate in month⁻¹.

(a) Scaling coefficient d_1 in the effect of temperature on pine wood nematode abundance.

It can be seen from [24] that Figure 3 below shows the effects of different temperatures on the hatching rates of two pine wood nematode strains, ZJ and YW4.

Combined with the parameter estimation results of different strains, it can be seen that the parameter d corresponding to pine wood nematode strain ZJ ranges from 0.000395 to 0.000657, and the parameter d corresponding to strain YW4 ranges from 0.000303 to 0.000483. Based on the estimation results of the two strains, the overall value range of parameter d_1 is determined to be 0.000303–0.000657. This interval covers the parameter variation range under strains with different virulence and provides reliable parameter boundaries for subsequent model sensitivity analysis and scenario simulation.

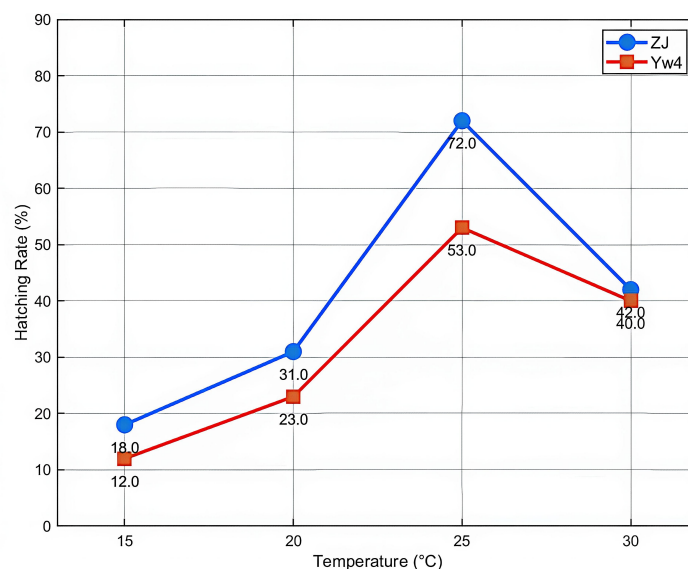


Figure 3. Effects of temperature on the egg hatching rate of two pine wood nematode strains, ZJ and YW4.

(b) Scaling coefficient d_2 in the effect of temperature on *M. alternatus* abundance. According to [19], the hatching rates of the eggs at 15, 20, 25, and 30 °C were 64 %, 78 %, 94 %, and 82 %, respectively.

The overall trend increased obviously as temperature rose, peaking at 25 °C before declining slightly. Similarly, we calculated the d value for each group and found that the range of d_2 is 0.00087–0.01364.

(c) Scaling coefficient d_3 in the effect of temperature on *D. helophoroides* abundance. According to [25], the hatching rate of *D. helophoroides* eggs at different temperatures is shown in Table 2 below:

Table 2. Hatching rates at different temperatures.

Temperature/°C	20	26	32
Hatching rate/%	62.14	57.22	55.07

Similarly, the d values of each group were calculated, and the range of d_3 was found to be 0.00028–0.00092.

(7) Proportional coefficients P_1 , P_2 , and P_3 between fecundity and total abundance of pine wood nematode, *M. alternatus*, and *D. helophoroides*, respectively. The factors P_i ($i = 1, 2, 3$) are dimensionless proportions.

$$\begin{aligned}
 \text{Egg production} &= \text{per-female fecundity} \times \text{number of female individuals} \\
 &= \text{per-female fecundity} \times \text{female proportion} \\
 &\quad \times \text{total population of male and female adults} \\
 &= \frac{1}{P} \times \text{total population of male and female adults}.
 \end{aligned}$$

(a) Proportional coefficient P_1 of fecundity to total abundance of pine wood nematode.

According to the introduction of pine wilt disease released by the Hunan Forestry Bureau [18], a single female pine wood nematode lays approximately 100 eggs. According to [26], the female-to-male ratio of pine wood nematodes in the field ranges from 0.93 to 2.20, so the range of P_1 is 0.0145–0.021.

(b) Proportional coefficient P_2 of fecundity to total abundance of *M. alternatus*.

It can be seen from [27] that the number of eggs laid by a single female *M. alternatus* is about 48–158, and egg production fluctuates under different environments. According to [28], the sex ratio of *M. alternatus* is $1/0.47 - 1/0.87$, so the range of P_2 is 0.011–0.042.

(c) Proportional coefficient P_3 of fecundity to total abundance of *D. helophoroides*.

According to [29], the number of eggs laid by a single female of *D. helophoroides* is about 33 to 419, and the ratio of female to male is close to 1–1, so the range of P_3 can be obtained as 0.0047–0.06.

(8) Time h_1 required for *M. alternatus* to process a single pine tree.

It can be seen from [30] that the time for *M. alternatus* to treat a single pine tree is 16–30 days. This process includes oviposition and nematode release in months; that is, the range of h_1 is 0.5–1 month.

(9) According to the parameter setting scheme provided in [5], we adopt a set of identical values from the original paper for the natural growth rates r_1 , r_2 , r_3 and survival restriction factors b_1 , b_2 , b_3 , whose admissible ranges $r_1 \in [0.68, 0.83]$, $r_2 \in [0.45, 0.59]$, $r_3 \in [0.59, 0.72]$, and $b_1, b_2, b_3 \in [2.23, 5.86]$ with $b_1 > b_2 > b_3$ are also given there. The rates r_i and b_i ($i = 1, 2, 3$) all carry the unit month⁻¹. For the contact efficiency a_1 between *M. alternatus* and pine wood nematodes, we set $a_1 = 0.298$ month⁻¹ on the basis of the relevant results in [30].

Based on the above analysis, we get the following parameters:

$$r_1 = 0.76 \text{ month}^{-1}, \quad r_2 = 0.52 \text{ month}^{-1}, \quad r_3 = 0.66 \text{ month}^{-1},$$

$$\begin{aligned}
b_1 &= 3.64 \text{ month}^{-1}, & b_2 &= 3.20 \text{ month}^{-1}, & b_3 &= 2.56 \text{ month}^{-1}, \\
T_{m1} &= 9.5^\circ\text{C}, & T_{m2} &= 14.3^\circ\text{C}, & T_{m3} &= 12.8^\circ\text{C}, & T &= 25^\circ\text{C}, \\
T_{M1} &= 33^\circ\text{C}, & T_{M2} &= 35^\circ\text{C}, & T_{M3} &= 45^\circ\text{C}, & a_1 &= 0.298 \text{ month}^{-1}, \\
P_1 &= 0.0145, & P_2 &= 0.0310, & P_3 &= 0.01170, & h_1 &= 0.60 \text{ month}, \\
d_1 &= 0.0003690^\circ\text{C}^{-5/2} \cdot \text{month}^{-1}, & d_2 &= 0.0008600^\circ\text{C}^{-5/2} \cdot \text{month}^{-1}, \\
d_3 &= 0.0007473^\circ\text{C}^{-5/2} \cdot \text{month}^{-1}, & m &= 0.76 \text{ month}^{-1}, & h &= 0.27 \text{ month}.
\end{aligned}$$

5.2. Simulation and verification

Under the above parameter values, the model (2.1) satisfies Assumptions (H1) and (H2): The left-hand side of (H1), $r_2 + H_2 + a_1(r_1 + H_1)/b_1 - m(r_3 + H_3)/b_3$, evaluates to approximately $0.27 > 0$, and at the equilibrium E_8 , one has $A_1 + A_2 = 117.216 > 0$, $(A_1 + A_2)(B_1 + B_2) - (C_1 + C_2) = 2.998 \times 10^5 > 0$ and $C_1 + C_2 = 346.9 > 0$, so the three inequalities of (H2) hold with a wide margin.

$$\begin{aligned}
E_1 &= (0.000000, 0.000000, 0.000000), & E_2 &= (0.000000, 0.000000, 34.289540), \\
E_3 &= (0.000000, 7.495988, 0.000000), & E_4 &= (7.871348, 0.000000, 0.000000), \\
E_5 &= (0.000000, 1.343101, 34.522216), & E_6 &= (7.871348, 0.000000, 34.289540), \\
E_7 &= (7.927655, 27.406409, 0.000000), & E_8 &= (7.903957, 0.911316, 34.517464).
\end{aligned}$$

The equilibria E_1 – E_7 are all unstable, and there exists a positive equilibrium E_8 . Substituting the baseline parameters into Eq (3.15), we obtain the critical time delay $\tau_c = 13.77$ months, which corresponds to the single positive root of Eq (3.13). According to Theorem 3.2, the positive equilibrium E_8 is locally asymptotically stable for $\tau \in [0, \tau_c)$ and unstable for $\tau > \tau_c$. To verify the above theoretical result, we perform numerical simulations under three representative delay settings: the delay-free case $\tau = 0$ and two delayed cases with $\tau = 7$ and $\tau = 13$ (all within the stable interval, in months). All simulations adopt the identical initial function $(M(\theta), N(\theta), P(\theta)) = (7, 0.5, 33)$ for $\theta \in [-\tau, 0]$, and the corresponding time trajectories are shown in Figure 4.

It can be seen that the equilibrium E_8 of the model (2.1) is locally asymptotically stable when the time delay does not exceed the critical value, and the model (2.1) can finally reach an ecological equilibrium state. Similar convergence is also observed when the simulations are repeated with other positive initial histories close to E_8 , such as $(M(\theta), N(\theta), P(\theta)) = (6, 1.5, 33)$ and $(9, 0.7, 36)$ for $\theta \in [-\tau, 0]$, which further supports the local stability result. When the time delay is small (such as $\tau = 0$), the model (2.1) can quickly restore balance and fluctuate slightly. As the time delay increases to $\tau = 7$, the model (2.1) begins to show an obvious oscillation adjustment process. When τ further increases to 13, close to the critical value $\tau_c = 13.77$ months, the oscillations decay much more slowly, indicating that the model is approaching the stability boundary. In contrast, although the pine wood nematode population fluctuates, its trajectory still converges, whereas that of *D. helophoroides* stays close to its equilibrium level throughout the simulations. It can be seen that *M. alternatus* is the most sensitive to the critical time delay. These results yield a practical implication: Shortening the high-population period of *M. alternatus* and appropriately timing *D. helophoroides* releases can weaken the adverse effect of the critical time delay via natural enemy suppression. Nevertheless, this model-derived inference requires field validation.

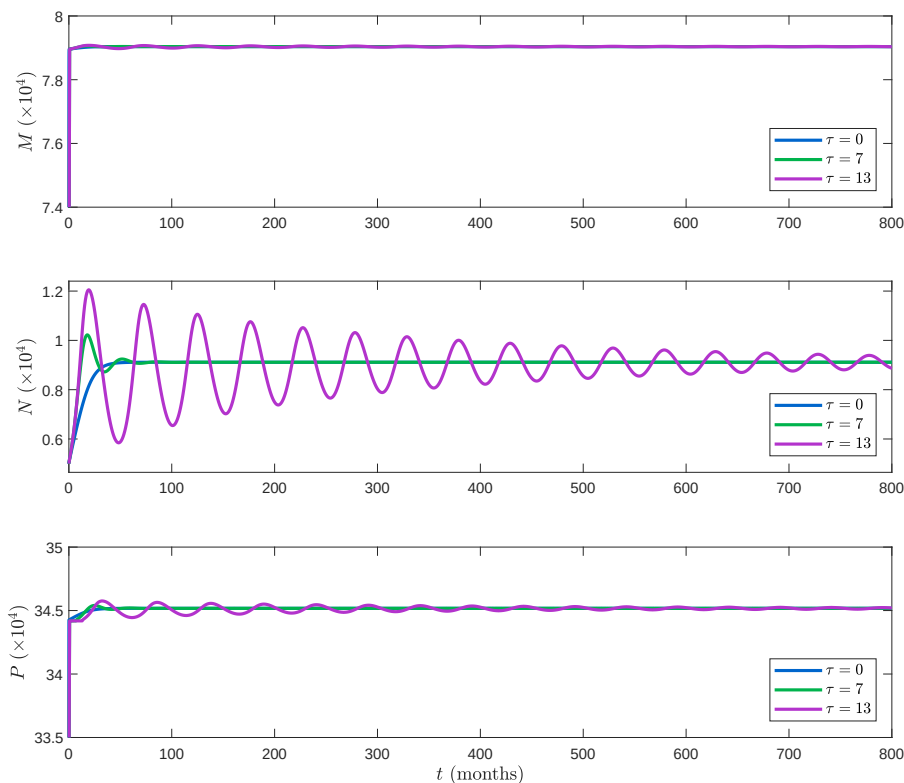


Figure 4. Local asymptotic stability of model (2.1) for $\tau = 0$, $\tau = 7$ and $\tau = 13$.

When $\tau > 0$, Eq (3.13) has a single positive root, which gives the critical delay $\tau_c = 13.77$. Substituting the baseline parameters into (4.10) and (4.13) gives $\text{Re}(V_1/V_2) = 0.0481 > 0$ and $\text{Re}(W_1/W_2) = -198.374 < 0$, so the cubic coefficient $\tau_c \text{Re}(W_1/W_2)$ is negative. By Theorem 4.1, the bifurcation is supercritical and the periodic solution is orbitally stable; because $\text{Re}(V_1/V_2) > 0$, it appears for $\tau > \tau_c$ (forward). For reference, the positive root of (3.13) is $z = 0.014722$, the Hopf frequency is $\omega = \sqrt{z} = 0.1213$, and the transversality condition $\text{Re}\left(\frac{d\tau}{d\lambda}\right) = \frac{f'(z)}{(C_1 - A_1 z)^2 + B_1^2 z} = 67.13 > 0$ holds, so E_8 loses stability as τ crosses τ_c .

When $\tau > \tau_c$, the positive equilibrium E_8 loses its local asymptotic stability. For parameter values falling in this regime, trajectories of the model (2.1) initiated close to E_8 will drift away from the unstable equilibrium and eventually settle onto the stable periodic orbits arising from the forward Hopf bifurcation. We present Figure 5 to exhibit the temporal evolution of solutions to the model (2.1) with $\tau = 14 > \tau_c = 13.77$ months, where the initial function is $(M(\theta), N(\theta), P(\theta)) = (8, 2, 35)$ for $\theta \in [-\tau, 0]$.

Consistent with our theoretical analysis results, this finding indicates that pine wood nematode population abundance fluctuates temporally; that is, pine wilt disease suffers periodic outbreaks. Due to the influence of season and other climatic factors on tree growth and population reproduction, many forest pests and diseases will erupt after a period of time, resulting in a significant increase in the difficulty of disease prevention and control.

To quantify the period of these oscillations, we count the peaks within the steady-state window $t \in [500, 1000]$ months; the average period is estimated at about 50 months; that is, under the baseline parameter set, the model (2.1) predicts that pine wilt disease breaks out roughly every four years. This

agrees well with the theoretical period $\frac{2\pi}{\omega} \approx 51.8$ ($\omega \approx 0.1213$) predicted at the Hopf bifurcation point by the auxiliary equation (3.13). The small difference lies within the resolution of the peak-counting procedure (about one period may be miscounted in a window of 500 months) and can also be attributed to the nonlinear frequency correction at finite oscillation amplitude beyond the bifurcation point.

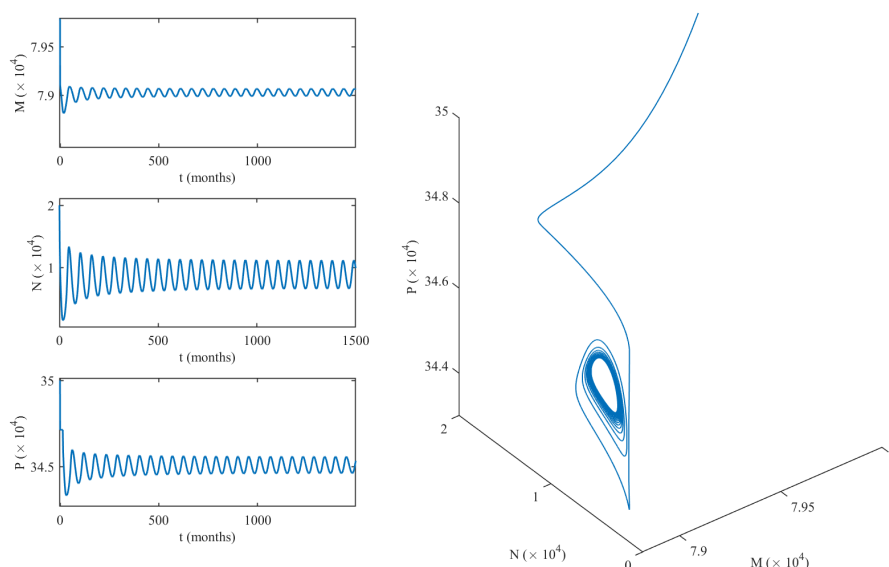


Figure 5. When $\tau = 14 > \tau_c$, the solutions of the model (2.1) exhibit attracting periodic oscillations around E_8 .

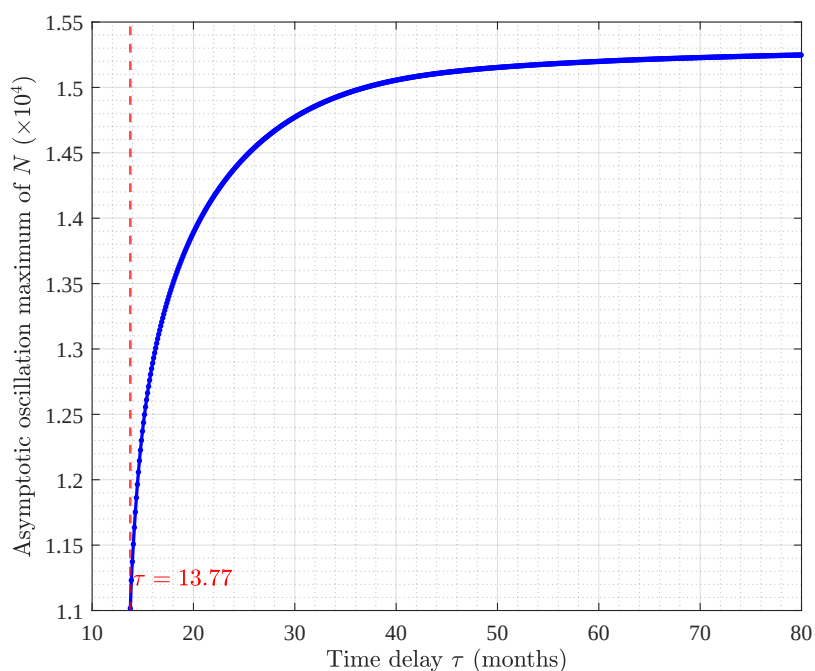


Figure 6. Asymptotic oscillation maximum of N against time delay τ .

Figure 6 shows how the asymptotic oscillation maximum of *M. alternatus* population changes with the parasitic time delay τ . The red dashed line marks the critical threshold $\tau_c = 13.77$ for Hopf bifurcation. When the delay is below this value, the positive equilibrium E_8 is locally asymptotically stable, and all three populations stay at a constant level without regular oscillations. Once τ exceeds 13.77 months, the model (2.1) undergoes a Hopf bifurcation, and the solutions approach attracting periodic oscillations. For τ ranging from 13.77 to 80 months, the asymptotic oscillation maximum of N rises steeply at first and then slowly levels off. This indicates that longer developmental delays of *D. helophoroides* larvae lead to larger population swings of *M. alternatus* and correspondingly raise the risk of large-scale pine wilt disease outbreaks. We emphasize that $\tau_c = 13.77$ months is a model-based warning line rather than a field measurement: Only when the effective response of *D. helophoroides* lags behind the increase of *M. alternatus* by more than about one year can delay-induced periodic outbreaks be triggered. In practice, the response of the parasitoid through parasitism and offspring development is generally much shorter than one year, so under routine biological control, the model stays on the stable side of this line, consistent with the observation that pine wilt disease can be kept under control by timely releases. Because the field delay is difficult to measure and varies with temperature and voltinism, this threshold should serve as a reference criterion for release management, and its calibration against field data deserves further study.

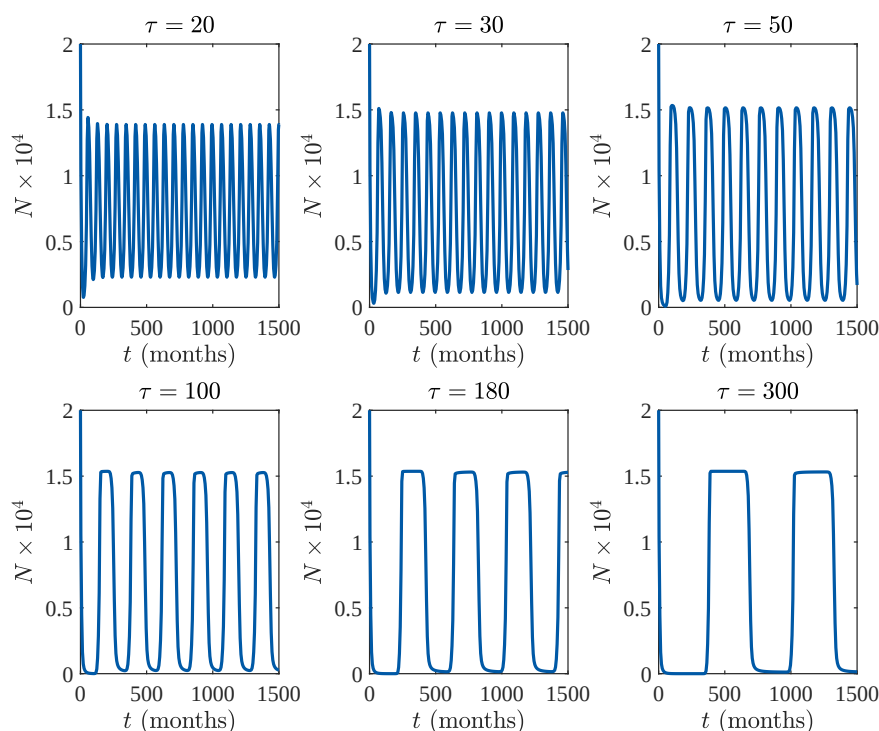


Figure 7. Fluctuation trajectories of *M. alternatus* population N under different parasitic time delays τ .

Furthermore, to intuitively demonstrate how the oscillation pattern shifts under different time delays, we take the vector beetle *M. alternatus* as an example and plot the fluctuation trajectories of its

population N for six values of τ , as presented in Figure 7. Simulations confirm that attracting periodic solutions exist for all tested delays. As τ increases from 20 to 300 months, oscillations persist across the entire range, and the waveform gradually shifts from smooth sinelike waves to steeper squarelike waves, and the oscillation maxima follow the increasing trend shown in Figure 6. The wide parameter range of sustained periodicity suggests that once the parasitic delay exceeds the critical value, outbreaks are likely to recur over successive years rather than die out after a single event, which makes pine wilt disease difficult to control in real forests. Such large delays are adopted here to illustrate the delay effect itself rather than to represent field conditions.

Having clarified how the oscillation amplitude shifts with varying time delay, we next examine the sensitivity of this critical bifurcation threshold (in months) to individual model parameters. For this analysis, we perturb one parameter at a time while holding all other quantities constant to quantify how minor parameter variations alter the timing of periodic outbreaks in the model (2.1). For all sensitivity analyses presented in this section, we verify that the positive equilibrium persists and that all assumptions required for the Hopf bifurcation analysis remain satisfied over the full parameter ranges shown in the figures.

We study the influence of the natural growth rate of the pine wood nematode, *M. alternatus*, and *D. helophoroides* on the critical time delay, as illustrated in Figure 8.

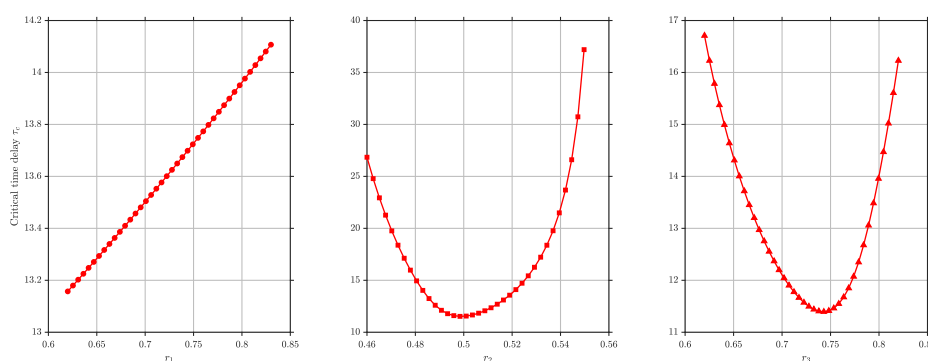


Figure 8. Variation of the critical time delay τ_c (in months) with respect to the natural growth rates r_1 , r_2 , and r_3 (month^{-1}).

As the natural growth rate of the pine wood nematode increases, the critical delay rises monotonically, whereas those of *M. alternatus* and *D. helophoroides* show a U-shaped pattern (in months), so the three species play rather different roles in delay-driven dynamics.

(a) The population growth of *D. helophoroides* is limited by the abundance of its host *M. alternatus*, and both insect populations are subject to their own density dependence. When r_2 , r_3 are too small, the population densities stay low, the fluctuations are weak, and the model (2.1) is relatively stable. When r_2 , r_3 are too large, the densities saturate under strong intraspecific competition. In the intermediate state, the critical time delay is relatively small, and outbreaks of the two populations become likely.

(b) The simulations point to a somewhat counterintuitive observation: Suppressing the pine wood nematode alone does not necessarily increase the critical delay. In the runs, a moderate nematode level is associated with a larger critical delay than an over-suppressed low nematode level, whereas regulation through the natural enemy appears to matter more for stability. We treat this as a hypothesis

suggested by one-at-a-time parameter variations rather than a settled conclusion, and its field relevance remains to be studied.

(c) The sensitivity analysis shows that the intrinsic growth rate r_1 of pine wood nematodes has the widest value range, which is consistent with its strong colonization ability and high reproductive potential as an invasive forest pest. In contrast, the value range of r_3 for *D. helophoroides* is relatively narrow, indicating that the population growth of the parasitoid is more sensitive to environmental constraints, and the model dynamics respond more strongly to perturbations in r_3 .

Next, we synthesize the influence of survival restriction factors of pine wood nematode, *M. alternatus*, and *D. helophoroides* on the critical time delay of the model (2.1) and find that all three show a significant U-shaped nonlinear relationship.

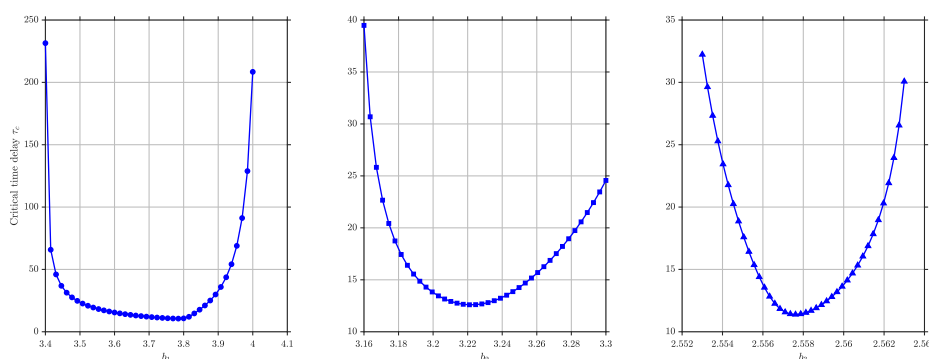


Figure 9. Variation of the critical time delay τ_c (in months) with respect to the survival restriction factors b_1 , b_2 , and b_3 (month^{-1}).

Figure 9 has the following biological significance:

(a) When the survival restriction factors of pine wood nematode, *M. alternatus*, and *D. helophoroides* take small values, environmental resources are relatively sufficient, and all three populations tend to grow explosively. When the factors take large values, resources are severely constrained, intraspecific competition intensifies, population fluctuations are significantly suppressed, and the model enters a more controllable state. In this parameter region, the effect of time delay on the model is negligible. From a dynamical perspective, this is the most favorable region. However, our model focuses on the dynamical mechanisms of the model, and does not address the specific field implementation approaches for real forest ecosystems.

(b) When the survival restriction factors b_1 and b_2 of pine wood nematode and *M. alternatus* take intermediate values, the critical time delay threshold of the model is comparatively low, making the model highly sensitive to delay perturbations. In this sense, this intermediate parameter range constitutes the high-risk regime of the model.

(c) It should be noted that within the U-shaped valley interval of the survival restriction factor for *D. helophoroides*, although the population has the potential for rapid expansion, the critical time delay drops to its minimum, resulting in extremely poor model stability. Under such conditions, even minor disturbances in parasitic time delay can easily trigger severe oscillations, causing large periodic fluctuations in the populations of both *D. helophoroides* and *M. alternatus*. This not only undermines the continuity of pest control but may also induce secondary pest outbreaks.

(d) From the scale characteristics of the three abscissas, the survival restriction factor b_3 of *D. helophoroides* has the narrowest variation range, indicating that its population dynamics are highly sensitive to environmental resources, and even small parameter changes can drive the model to switch between stable and unstable regions. In contrast, the valley bottom interval of pine wood nematode and *M. alternatus* is wide, making it difficult to achieve effective prevention and control through simple regulation.

Then, we draw the image of the influence of the handling time h of *D. helophoroides* on the critical time delay of the model (2.1) (see Figure 10).

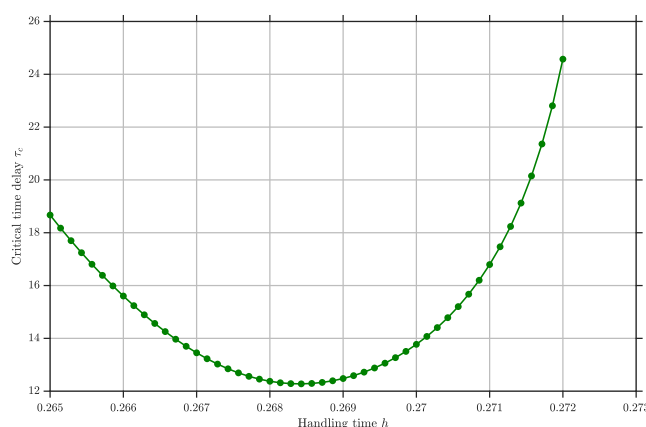


Figure 10. Variation of the critical time delay τ_c (in months) with the handling time h (in months).

When $h < 0.265$ months, the population renewal rate of *D. helophoroides* remains high, exerting stable and moderate suppression on *M. alternatus*, and periodic outbreaks of *M. alternatus* are unlikely to occur. When $h > 0.272$, *D. helophoroides* shows a weak response to population fluctuations of *M. alternatus*, and the time-delay effect is also negligible. Under these two scenarios, Hopf bifurcation is not prone to occur, and the model (2.1) tends to maintain local asymptotic stability.

When h lies between 0.265 and 0.272 months, the perturbation caused by time delay becomes prominent, the critical time delay appears, and Hopf bifurcation occurs in the model (2.1). The handling time of *D. helophoroides* imposes a pronounced U-shaped effect on the critical time delay of the model (2.1) within this very narrow interval, indicating that handling time is a highly sensitive factor affecting model stability. When h falls in the range of 0.268–0.269 months, the critical time delay of the model (2.1) reaches its lowest level, and minor parameter variations can easily trigger population oscillations. Notably, on the right segment with larger handling time values, the critical delay rises sharply, suggesting that a relatively longer handling time of *D. helophoroides* is instead conducive to model stability.

The handling time h turns out to be a highly sensitive parameter: In the simulations, strains whose handling time lies outside this narrow interval give a larger critical delay. This finding offers preliminary reference value for screening natural enemy strains. However, it is derived from single-parameter sensitivity analysis based on a single baseline calibration, and experimental validation is needed before it can be used to guide release management.

Finally, we explore the effect of temperature on the critical time delay, varying T in a small neighborhood of the baseline value 25°C ; the critical delay again exhibits a pronounced U-shaped pattern.

As shown in Figure 11, the critical time delay decreases rapidly with rising temperature, remains much shorter than at the two ends of the scanned range across the intermediate temperatures, and then rises rapidly again. This pattern reflects that temperature exerts a strong regulatory effect on the stability of the three-species interaction model (2.1).

When the temperature falls within the interval $24.9\text{--}25.15^{\circ}\text{C}$, the critical time delay reaches its minimum. This implies that if the forest temperature stays in this range, a slight increase in parasitic time delay can exceed the critical threshold and trigger periodic population oscillations of *M. alternatus* and *D. helophoroides*, making this temperature interval a high-risk window for pine wilt disease outbreaks. This pattern is distinct from the narrow U-shaped relationship between the handling time of *D. helophoroides* and the critical time delay. For handling time, the minimum critical delay occurs only within a very narrow parameter band, reflecting high local sensitivity. For temperature, by contrast, the high-risk range is relatively wider: Small temperature fluctuations within the optimal developmental range will not significantly elevate the critical delay, so the model (2.1) remains in a high-risk state and imposes sustained pressure on pest prevention and control.

In the low-temperature interval $24.8\text{--}24.9^{\circ}\text{C}$, the critical time delay drops rapidly from above 180 months to the minimum as temperature rises. This reveals that lower temperature substantially increases the critical time delay and significantly enhances the anti-interference capacity of the model (2.1). In the high-temperature interval $25.15\text{--}25.25^{\circ}\text{C}$, the critical time delay rebounds sharply from the minimum to above 120 months with increasing temperature, which implies that higher temperature can also improve model stability. This phenomenon demonstrates that the stability of the three-species interaction model (2.1) is enhanced when temperature deviates either below or above the optimal developmental range of the populations, and oscillations induced by time delay become correspondingly less likely to occur. This regularity provides a model-based reference for regions with different climatic backgrounds to develop targeted prevention and control measures tailored to local temperature conditions.

In terms of numerical magnitude, the critical time delay varies substantially across the studied temperature interval, with a total variation range far larger than those induced by individual biological parameters such as the intrinsic growth rate, survival restriction factor, and natural enemy handling time. This indicates that temperature is the core environmental factor driving stability switching in model (2.1), and its overall effect on population dynamics significantly outweighs the disturbance caused by any single biological parameter.

Note that this differs from the local sensitivity discussed earlier: Although handling time exhibits high local sensitivity near its optimal value (where the minimum critical delay is confined to a very narrow parameter band), temperature exerts a stronger global effect on the critical delay threshold. The critical time delay exists throughout the range of $24.8\text{--}25.25^{\circ}\text{C}$, which demonstrates that temperature variations consistently modulate the instability threshold of model (2.1). Importantly, Hopf bifurcation persists across the entire studied temperature range: Temperature variations only alter the magnitude of the critical time delay and thus the likelihood of model instability rather than eliminating the bifurcation phenomenon itself.

These relatively large critical time delay values (above 180 and 120 months, respectively) arise only in temperature ranges that deviate substantially from the species' optimal developmental range. Such

delay durations far exceed the insects' actual developmental period under field conditions, and they represent mathematical extrapolations of the model rather than biologically realistic scenarios.

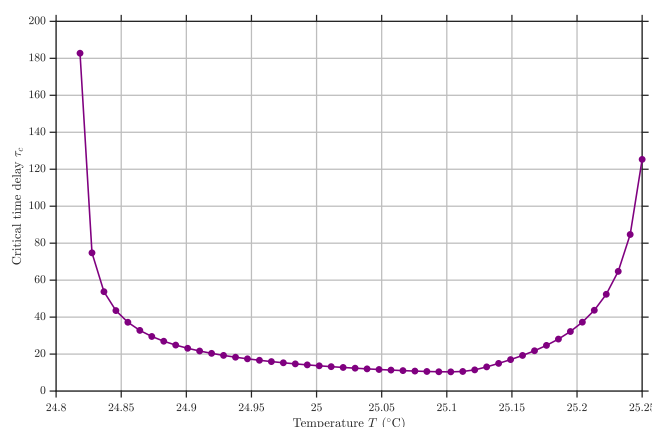


Figure 11. Variation of the critical time delay τ_c (in months) with the temperature T (°C).

From an application perspective, the model results indicate that temperature is the key driver of stability in model (2.1): The critical delay is shortest for temperatures around 25 °C, so this interval is a high-risk window for population oscillations in the model sense. In early spring and late autumn, when the temperature deviates from this suitable range, the model is more stable, lower pest pressure may favor the release and establishment of the natural enemy, and the overall regulatory effect of temperature is significantly stronger than that of biological factors such as handling time. These model-derived patterns may provide a reference for pest monitoring and for optimizing the timing of natural enemy release, although empirical validation is required before any field application.

6. Conclusions

In this work, we developed a delay differential model (2.1) for the pine wood nematode, *M. alternatus*, and *D. helophoroides*. We adopted logistic growth equations and Holling type II functions to describe the interspecific relationships and introduced the Brière function to characterize how temperature regulates species development and reproduction. Theoretical analyses were carried out to prove the existence of a positive equilibrium and to derive the Hopf bifurcation conditions with the parasitic delay as the bifurcation parameter, followed by numerical simulations to examine the parameter responses. In addition, for $\tau > \tau_c$, the numerical simulations suggest the existence of attracting periodic solutions over the tested range of delays and initial histories.

Our simulation results show that Hopf bifurcation occurs once the parasitic delay surpasses the critical value $\tau_c = 13.77$ months, leading to periodic population oscillations, which correspond to recurrent pine wilt disease outbreaks in the model. This critical value τ_c is relatively large, at approximately one year: As discussed in Figure 6, oscillations would require the development of the parasitoid offspring to last longer than this period, which is generally not the case under routine and timely releases, so the model (2.1) is expected to remain on the stable side in practice. The natural growth rates and the survival restriction factors both form U-shaped curves against the critical delay, and the critical delay

is smallest when these parameters take intermediate values. Temperature acts as the leading environmental factor behind the stability shifts of the model: In the simulations, the critical delay is shortest over 24.9–25.15 °C, which we therefore identify as a model-based high-risk window, whereas away from this interval, the critical delay is larger, and the model (2.1) is more stable.

Finally, we note several limitations of this study. The model assumes constant ambient temperature, a spatially homogeneous stand, and deterministic system dynamics, so seasonal temperature forcing, spatial heterogeneity, and stochastic effects are not included. Our work focuses on dynamical properties and stability analysis near the positive equilibrium, and this one-at-a-time framework serves to disentangle the individual influence of each biological factor. In the future, we plan to conduct a systematic global uncertainty and robustness analysis to quantify the joint effects of multiparameter variations on the critical delay and model stability.

In addition, most baseline parameters are taken from laboratory experiments in the literature with inherent uncertainty, and the model has not been validated against independent field data. Accordingly, the management implications proposed here are model-based research hypotheses, and empirical validation is required before their application to field management.

Use of AI tools declaration

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

Acknowledgments

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Conflict of interest

The authors declare there is no conflict of interest.

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