

Complex dynamics in plant-pollinator-parasite interactions: facultative versus obligate behaviors and novel bifurcations

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Abstract

Understanding the dynamics of plant-pollinator interactions is crucial for maintaining ecosystem stability and biodiversity. In this paper, we formulate a novel tripartite plant-pollinator-parasite model that incorporates the influence of parasites on mutualistic relationships. Our model consists of the plant-pollinator subsystem, which exhibits equilibrium dynamics with up to four bistable states; the pollinator-parasite subsystem, where stability is significantly affected by pollinator density and growth rate; and the complete system combining all three species. We perform comprehensive mathematical and bifurcation analyses on both the subsystems and the full system. We have many interesting findings, including that (1) plant-pollinator-parasite interactions are dependent on the properties of plants and pollinators (i.e., facultative or obligate interactions). For example, systems with facultative pollinators are more likely to exhibit multistability and periodic oscillations, thereby enhancing resilience, whereas scenarios with obligate pollinators are more likely to lead to system collapse. (2) Critical parameters such as parasite mortality and conversion rates can drive complex behaviors, including supercritical and subcritical Hopf bifurcations, saddle-node bifurcations, chaos, and heteroclinic orbits. Notably, we introduce three new concepts-the left bow, right bow, and wave bow phenomena-to characterize variations in oscillation amplitude resulting from parameter bifurcations. These important results provide theoretical guidance for

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ecological management strategies aimed at enhancing ecosystem resilience and stability by considering the complex interactions among plants, pollinators, and parasites.

Keywords Plant-pollinator system · Parasitism · Oscillations · Homoclinic loop · Multistability

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1 Introduction

The mutualistic relationship between plants and pollinators is fundamental to ecosystem stability and biodiversity. Pollinators-including bees, butterflies, and bats-facilitate plant reproduction by providing essential pollination services, while plants supply vital resources such as nectar and pollen to sustain pollinator populations. Globally, approximately 87.5% of flowering plants rely on animal-mediated pollination (Kumar and Khan 2023; Wright et al. 2013). Among these pollinators, bees are particularly crucial, responsible for pollinating 75% to 80% of the world's major crop species, including fruits, nuts, and certain vegetables (Alemberhe and Gebremeskel 2016; Johannsmeier and Mostert 2001). The economic value of these pollination services is immense, estimated to range from \$235 to \$577 billion annually (Potts et al. 2016). Given the critical importance of this mutualism in both ecological and agricultural contexts, substantial research has focused on understanding the dynamics of plant-pollinator interactions and the factors involved (Funamoto 2019; Heithaus 1974; Mitchell et al. 2009).

Dynamic models have become indispensable tools for studying plant-pollinator mutualisms. These models offers a rigorous framework for quantifying species interactions, predicting outcomes under various ecological scenarios, and exploring the long-term stability of these systems in response to environmental changes. Early mathematical models often involved simplified two-species systems, frequently using variations of the Lotka-Volterra differential equation model to explore the basic relationship between pollinator abundance and plant reproductive success (Fishman and Hadany 2010; Hale and Valdovinos 2021; Holland and DeAngelis 2010). As research progressed, these models were expanded to incorporate additional complexities (Oña and Lachmann 2011; Valdovinos and Marsland 2021; Fort and Mungan 2015; Wang 2019), such as pollinator specialization (Benadi et al. 2012; Revilla and Křivan 2018), population structure (Encinas-Viso et al. 2014; Lampo et al. 2024; Yahaya et al. 2024), and spatial distribution (Huang et al. 2017; Sánchez-Garduño and Breña-Medina 2011; Wang et al. 2015). These enhancements have significantly improved the models' ability to predict the complex behaviors observed in natural ecosystems, capturing phenomena like multistability and periodic oscillations (Glaum and Kessler 2017; Hale et al. 2022; Lv et al. 2024; Revilla and Encinas-Viso 2015) and providing critical insights into how plant-pollinator systems may respond to environmental pressures (Devi and Mishra 2020; Feng et al. 2024).

Plant-pollinator interactions are subjected to multiple ecological pressures, including climate change (Forrest 2015; Gérard et al. 2020; Settele et al. 2016; Zamora-Gutierrez et al. 2021), herbivores (Gómez 2003; Lucas-Barbosa et al. 2011), and parasites (Dunn et al. 2008; Krishnan and Borges 2014). For instance, climate change can lead to mismatches between plant flowering periods and pollinator activity, reducing pollination efficiency and altering the dynamic equilibrium of ecosystems (Hegland et al. 2009). Herbivores indirectly affect pollinators by reducing plant resources, diminishing the attractiveness of plants to pollinators (Strauss et al. 2002). Pollinators themselves face threats from predators and parasites, which can significantly reduce their numbers and limit pollinators and among plants influences the distribution of resources and reproductive success (Irwin et al. 2010; Rojas-Nossa et al. 2016; Ashman and Arceo-Gómez 2013; Crone and Rapp 2014; Iwasa and Satake 2004; Satake and Iwasa 2002).

Dynamic models have been extensively employed to study the impacts of these ecological pressures on plant-pollinator systems (Benadi et al. 2013; Lampo et al. 2024; Kawata and Takimoto 2023; Tachiki et al. 2010; Truitt et al. 2019). For example, adaptive mutualistic Lotka-Volterra models have demonstrated how environmental stress can trigger asynchronous species collapses in pollinator communities (Terpstra et al. 2024). Hybrid dynamical models have assessed how climate-driven phenological mismatches affect plant population dynamics, especially in short-lived species (Fagan et al. 2014). Other studies have investigated conditions under which pollination mutualisms persist despite disruptive influences like nectar robbers (Wang 2013; Wang et al. 2012; Wang and Wu 2013; Wang et al. 2012). Stable coexistence in plant-pollinator-herbivore communities has been shown to require a balance between the strengths of pollination and herbivory (Yacine and Loeuille 2022). Additional analyses of plant-pollinator-herbivore systems have identified conditions for species coexistence, extinction, and the emergence of limit cycles through bifurcation analysis (Chen et al. 2020; Castellanos and Sánchez-Garduño 2019). Collectively, these studies provide critical insights into the response mechanisms of plant-pollinator systems under ecological stress.

Despite these advances, the impacts of parasites-particularly pollinator parasites such as Varroa mites-remain underexplored. Parasites are a significant ecological pressure, exerting complex effects on plant-pollinator systems (Genersch 2010; Guzmán-Novoa et al. 2010; Van Dooremalen et al. 2012). Varroa mites weaken pollinators by compromising their immune systems and transmitting deadly pathogens, leading to sharp declines in pollinator populations and affecting pollination services (Chen et al. 2021; Martin et al. 2012; Rosenkranz et al. 2010). Infestations have caused a 30% to 50% decline in global honeybee populations, severely disrupting pollination networks essential for both crops and wild plants (Doeke et al. 2015; Goulson et al. 2015). In the United States alone, losses of bee colonies due to Varroa mites and associated viruses exceed 40% annually, posing a serious threat to agricultural sustainability (Kulhanek et al. 2017).

Given the profound impact that parasites can have on pollinator populations and, by extension, on plant-pollinator interactions, it is crucial to thoroughly understand the dynamics of parasitism within these systems. Dynamic models have proven invaluable for quantifying the long-term effects of parasite infestations on pollinator population dynamics and identifying factors that could lead to ecosystem collapse (Britton and Jane White 2021; Chen et al. 2023; DeGrandi-Hoffman and Curry 2004; Martin 1998;

Ratti et al. 2017; Vetharaniam and Barlow 2006). Previous studies have shown that Varroa mites can destabilize honeybee populations, leading to tipping points where colonies collapse (Kang et al. 2016). Incorporating factors like time lags in brood development and mite migration between patches has revealed complex outcomes, such as destabilization or stabilization of colonies depending on specific conditions (Messan et al. 2017, 2021). However, a significant gap remains in understanding how these effects feedback into plant dynamics. To fully grasp the broader ecological consequences of parasitism in plant-pollinator systems, further research integrating both pollinator and plant dynamics is needed. Addressing this gap is the central focus of this study.

This paper is organized as follows. In Sect. 2, we introduce a novel tripartite plantpollinator-parasite model that integrates the influence of parasites on mutualistic relationships. Section 3 offers a comprehensive analysis of the boundary subsystems, examining dissipation, the existence and global stability of equilibria, and identifying bistability. In Sect. 4, we explore the full plant-pollinator-parasite system, detailing the mechanisms by which parasites impact plant-pollinator interactions. Section 5 extends the theoretical insights through numerical bifurcation analysis, investigating the effects of critical biological parameters, such as parasitism rate and natural pollination rate, on system dynamics. Finally, Sect. 6 concludes the paper with a summary and potential avenues for future research.

2 Model derivation

In this study, we investigate the effects of parasitism on plant-pollinator interactions by developing a mathematical model that captures the dynamics among three critical components: plants (P), pollinators (A), and parasites (M). Building upon the two-dimensional plant-pollinator model proposed by Hale et al. (2022), we extend the framework to include the influence of parasites, thereby providing a more comprehensive understanding of these complex ecological relationships.

(1) *Plant dynamics.* Under ideal conditions, the plant population grows at an intrinsic rate b_P . Natural pollination mechanisms, such as self-pollination and wind pollination, result in a proportion f of successful pollination events. The overall reproductive success is further determined by the likelihood of seed formation g. As the population density increases, intraspecific competition for limited resources induces a natural decline in the plant population, modeled by a density-dependent factor s_P , along with a baseline mortality rate d_P . Pollinators enhance the pollination process by providing an additional pollination rate $\Psi(S_P)$, which is directly linked to the benefits S_P that plants gain from these services. The dynamics of the plant population are

therefore captured by the following differential equation:

$$\frac{dP}{dt} = \underbrace{b_P}_{\text{intrinsic growth rate}} \left(\underbrace{f}_{\text{natural pollination}} + \underbrace{\Psi(S_P)}_{\text{pollination by pollinators}} \right) \underbrace{g}_{\text{reproductive success}} P$$

$$\frac{s_P P^2}{\text{density-dependent limitation}} - \frac{d_P P}{\text{plant mortality}}.$$

(2) Pollinator dynamics. The pollinator population grows at a rate b_A , but this growth is constrained by factors such as nest size, represented by the density-dependent factor s_A , and is subject to a natural mortality rate d_A . Pollinators benefit from consuming plant rewards, which correspond to the total benefit that plants receive from pollination services. These rewards are converted into new individuals through birth and maturation with an efficiency ϵ . However, the introduction of parasites disrupts this mutualistic interaction by increasing pollinator mortality, modeled as $\Phi(A, M)$. The dynamics of the pollinator population are thus described by:

$$\frac{dA}{dt} = \underbrace{b_A A}_{\text{pollinator birth rate}} + \underbrace{\epsilon S_P}_{\text{conversion of rewards to offspring}} - \underbrace{s_A A^2}_{\text{density-dependent limitation}}$$

$$-\underbrace{d_A A}_{\text{pollinator mortality}} -\underbrace{\Phi(A, M)}_{\text{mortality from parasitism}}$$

(3) *Parasite dynamics*. Parasites exploit the energy and nutrients that pollinators obtain from plants, converting these resources into new individuals with an efficiency k. The parasite population also faces natural mortality at a rate d_M . The dynamics of the parasite population are given by:

$$\frac{dM}{dt} = \underbrace{k\Phi(A, M)}_{\text{parasite reproduction}} - \underbrace{d_M M}_{\text{parasite mortality}}$$

To accurately represent the interactions between these species, we define specific functional responses:

- *Plant benefits from pollination.* Following Hale et al. (2022), we assume that the benefits S_P that plants gain from pollination services follow a Holling Type II functional response:

$$S_P(P,A) = \frac{aAP}{1+ahP},$$

where a is the attack rate (the rate at which pollinators visit plants) and h is the handling time (the time a pollinator spends on each plant). This formulation reflects how the benefits saturate as plant density increases.

 Proportion of pollination by pollinators. The proportion of pollination performed by pollinators is positively correlated with the plant benefit rate, modeled as:

$$\Psi(S_P) = \frac{\phi S_P}{1 + S_P}$$

where ϕ represents the maximum proportion of pollination achievable by pollinators when the benefit rate saturates.

 Parasitic interactions. Following Kang et al. (2016), we model the parasitic interactions between parasites and pollinators using a Holling Type I functional response:

$$\Phi(A, M) = \beta A M,$$

where β is the parasitism rate.

Integrating these components, we arrive at the following set of three-dimensional differential equations that capture the complex dynamics of the plant-pollinatorparasite system:

$$\frac{dP}{dt} = \underbrace{b_P}_{\text{intrinsic growth rate}} \left(\underbrace{f}_{\text{natural pollination}} + \underbrace{\phi \frac{aAP}{1 + ahP + aAP}}_{\text{pollination by pollinators}} \right)_{\text{reproductive success}} P$$

$$- \underbrace{s_P P^2}_{\text{density-dependent limitation}} - \underbrace{d_P P}_{\text{density-dependent limitation}}, \\ \frac{dA}{dt} = \underbrace{b_A A}_{\text{pollinator birth rate}} + \underbrace{\epsilon \frac{aAP}{1 + ahP}}_{\text{conversion of rewards to offspring}} - \underbrace{s_A A^2}_{\text{density-dependent limitation}}, \\ \frac{dM}{dt} = \underbrace{k\beta AM}_{\text{parasite reproduction}} - \underbrace{d_M M}_{\text{parasite mortality}}. \\ \end{aligned}$$

This system (1) follows the traditional host-parasite modeling framework, accounting for non-lethal parasitism effects (Anderson 1978; Anderson and May 1981; Kang et al. 2016). Notably, if the pollinator population A goes extinct, the parasite population M will inevitably decline to extinction as well, highlighting the dependence of parasites on their hosts.

Mutualistic relationships between plants and pollinators can vary from obligate to facultative dependencies. To capture this variability, we define:

$$r_P := b_P fg - d_P$$
 and $r_A := b_A - d_A$.

(1)

here r_P and r_A represent the net growth rates of plants and pollinators, respectively, in the absence of mutualistic interactions. If $r_i < 0$ for i = A, P, then species i is an obligate mutualist, unable to persist without its partner. Conversely, if $r_i > 0$, species i is a facultative mutualist, capable of surviving independently.

Examples of mutualism types. A well-known obligate mutualism is observed between the yucca plant (*Yucca* spp.) and the yucca moth (*Tegeticula* spp.), where both species rely exclusively on each other for reproduction (Pellmyr and Huth 1994). In contrast, the fig tree (*Ficus* spp.) and fig wasp (Agaonidae family) exhibit a facultative-obligate mutualism; while fig wasps are entirely dependent on fig trees for reproduction, fig trees can also be pollinated by other agents (Jousselin et al. 2003). Similarly, the senita cactus (*Pachycereus schottii*) and the senita moth (Upiga virescens) demonstrate a relationship where the cactus is an obligate mutualist, but the moth is a facultative mutualist (Holland and Fleming 1999). Finally, the common milkweed (*Asclepias syriaca*) and its various generalist pollinators, such as bees and butterflies, represent a facultative mutualism, with both the plant and pollinators having multiple partners and not exclusively dependent on each other (Kephart 1983).

Considering these diverse mutualism types is essential for deriving general conclusions; therefore, in this paper, we incorporate all four types of mutualistic relationships into our model. By integrating these varied forms of mutualism, our primary objective is to investigate how parasitism influences plant-pollinator dynamics across different dependency scenarios, thereby enhancing our understanding of the mechanisms that underpin ecosystem resilience and stability.

3 Analysis of the partial system

3.1 Dynamics without parasites

To understand the foundational interactions between plant and pollinator populations, we begin by examining the system in the absence of parasites. Under this scenario, system (1) simplifies to the following two-dimensional model:

$$\frac{dP}{dt} = P \left[b_P \left(f + \phi \frac{aAP}{1 + ahP + aAP} \right) g - s_P P - d_P \right],$$

$$\frac{dA}{dt} = A \left(b_A + \epsilon \frac{aP}{1 + ahP} - s_A A - d_A \right).$$
(2)

Lemma 1 (Boundedness and invariance) For system (2) with initial conditions in the compact set

$$\mathbb{C}_1 = \left\{ (P, A) \in \mathbb{R}^2_+ : 0 \le P \le \frac{b_P \phi g + r_P}{s_P}, 0 \le A \le \frac{\frac{\epsilon}{h} + r_A}{s_A} \right\},\$$

the solutions remain within \mathbb{C}_1 for all future times.

Remark Since P(t) and A(t) represent the population densities of plants and pollinators, respectively, they must remain non-negative over time. Lemma 1 confirms the positive invariance of system (2), ensuring that solution trajectories stay within the biologically meaningful domain. For a detailed proof, refer to Appendix A.

Theorem 1 (Global dynamics) *The solutions of system* (2) *converge towards locally asymptotically stable equilibria. When there is a unique locally asymptotically stable equilibrium, it is globally asymptotically stable. The threshold conditions for the existence and stability of these equilibria are detailed as follows:*

- (1) Extinction equilibrium: There exists an extinction equilibrium at $E_0 = (0, 0)$. It is locally asymptotically stable if $\max\{r_P, r_A\} < 0$; otherwise, if $\max\{r_P, r_A\} > 0$, E_0 is unstable.
- (2) Pollinator-only equilibrium: When $r_A > 0$, a pollinator-only equilibrium $E_{0A} = (0, \frac{r_A}{s_A})$ is present. E_{0A} is locally asymptotically stable if $r_P < 0$; otherwise, if $r_P > 0$, E_{0A} is unstable.
- (3) Plant-only equilibrium: When $r_P > 0$, a plant-only equilibrium $E_{P0} = (\frac{r_P}{s_P}, 0)$ exists. E_{P0} is locally asymptotically stable if $r_A < -\frac{\epsilon a r_P}{s_P + a h r_P}$; otherwise, if $r_A > -\frac{\epsilon a r_P}{s_P + a h r_P}$, E_{P0} is unstable.
- (4) Coexistence equilibrium: The system can exhibit a maximum of three coexistence equilibria, as illustrated in Fig. 1. Specifically, if $r_P > 0$ and $r_A > 0$, the system exhibits either one or three coexistence equilibria. If $r_P < 0$ and $r_A > 0$, the system features either none or two coexistence equilibria. If $r_P > 0$ and $r_A < 0$, the system can potentially possess zero, one, two, or up to three coexistence equilibria. If $r_P < 0$ and $r_A < 0$, the system can host either zero, one, or at most two coexistence equilibria. We denote the coexistence equilibria as $E_i^* = (P_i^*, A_i^*)$, where i = 1, 2, 3, and they are ordered as $P_1^* < P_2^* < P_3^*$ whenever they are present. The stability of these coexistence equilibria can be summarized as follows: (1) if there is a unique coexistence equilibria E_i^* , $i = 1, 2, E_1^*$ is unstable, while E_2^* is locally asymptotically stable; (3) for the case of three coexistence equilibria, E_1^* and E_3^* are locally asymptotically stable, while E_2^* is unstable. (4) Notably, when two equilibria merge, the dimensions of both the stable and center-stable manifolds of the equilibrium are equal to 1.

Proof An equilibrium of the system (2) should satisfy

$$0 = P\left[b_P\left(f + \phi \frac{aAP}{1 + ahP + aAP}\right)g - s_PP - d_P\right] := \psi_1(P, A),$$

$$0 = A\left(b_A + \epsilon \frac{aP}{1 + ahP} - s_AA - d_A\right) := \psi_2(P, A).$$

Simple calculation shows that the system (2) always has an extinction equilibrium $E_0 = (0, 0)$. If $r_P := b_P fg - d_P > 0$, the system (2) has a plant-only equilibrium $E_{P0} = (\frac{r_P}{s_P}, 0)$, and if $r_A := b_A - d_A > 0$, the system (2) has a pollinator-only



Fig. 2 Schematic of real positive roots for cubic polynomial $\rho_2(P)$ and the subsystem (2) with $r_P > 0$

equilibrium $E_{0A} = (0, \frac{r_A}{s_A})$. Assume that $E^* = (P^*, A^*)$ is a coexistence equilibrium of the system (2). Solving $\psi_2(P^*, A^*) = 0$, we obtain

$$A^* = \frac{1}{s_A} \left(r_A + \epsilon \frac{aP^*}{1 + ahP^*} \right). \tag{3}$$

Substituting (3) into $\psi_1(P^*, A^*) = 0$ gives

$$\rho_1(P^*) := \frac{P^*}{s_A(1+ahP^*)^2 + ar_A(1+ahP^*)P^* + \epsilon a^2(P^*)^2} \cdot \rho_2(P^*) = 0,$$

where

$$\rho_2(P) = -a^2 s_P \left(\epsilon + h(r_A + hs_A)\right) P^3 + a[a(g\phi b_P + r_P)(\epsilon + hr_A) + hs_A(ahr_P - 2s_P) - r_A s_P]P^2 + (ag\phi b_P r_A + ar_A r_P + 2ahr_P s_A - s_A s_P) P + s_A r_P.$$

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It is evident, from the properties of cubic equations, that when $r_P > 0$, the equation $\rho_2(P) = 0$ may exhibit either one or three positive real roots, as illustrated in Fig. 2a and b. Conversely, in the case where $r_P < 0$, the equation $\rho_2(P) = 0$ may have either zero or two positive real roots, as depicted in Fig. 3a and b. With respect to the expression (3) for the component A^* , we can identify the existence of coexistence equilibria into the following four scenarios:

- (i) Case $r_P > 0$ and $r_A > 0$. The Eq. (3) clearly indicates that $A^* > 0$. Therefore, the system (2) may exhibit either one or three coexistence equilibria, as illustrated in Fig. 2a and b.
- (ii) Case $r_P > 0$ and $r_A < 0$. The system (2) can potentially have zero, one, two, or at most three coexistence equilibria. To elaborate: when $\rho_2(P) = 0$ has a single positive real root P_1^* , the system (2) lacks a coexistence equilibrium if $A(P_1^*) < 0$ (Fig. 2c). Conversely, if $A(P_1^*) > 0$, the system (2) has a unique coexistence equilibrium (Fig. 2d). When $\rho_2(P) = 0$ has three positive real roots $P_1^* < P_2^* < P_3^*$, the system (2) does not have a coexistence equilibrium if $A(P_3^*) < 0$ (Fig. 2e). However, if $A(P_2^*)A(P_3^*) < 0$, the system (2) features a unique coexistence equilibrium (Fig. 2f). In the event that $A(P_1^*)A(P_2^*) < 0$, the system (2) features two coexistence equilibria (Fig. 2g). Finally, if $A(P_1^*) > 0$, the system (2) hosts three coexistence equilibria, as presented in Fig. 2h.
- (iii) Case $r_P < 0$ and $r_A > 0$. In this scenario, the system (2) may either lack a coexistence equilibrium or exhibit two coexistence equilibria, as depicted in Fig. 3a and b.
- (iv) Case $r_P < 0$ and $r_A < 0$. In this scenario, the system (2) could potentially have zero, one or two coexistence equilibria. If $\rho_2(P) = 0$ has no positive real roots, the system (2) does not possess a coexistence equilibrium (Fig. 3c). If the function $\rho_2(P) = 0$ has two positive real roots $P_1^* < P_2^*$, the system (2) lacks a coexistence equilibrium if $A(P_2^*) < 0$ (Fig. 3d). However, the system (2) has a unique coexistence equilibrium if $A(P_1^*) A(P_2^*) < 0$ (Fig. 3e). When $A(P_1^*) > 0$, the system (2) features two coexistence equilibria, as illustrated in Fig. 3f.

Next, we verify the stability of the boundary and coexistence equilibria.

(1) *Stability of the extinction equilibrium* E_0 . Since the Jacobian matrix of the system (2) evaluated at $E_0 = (0, 0)$ is given by

$$J(E_0) = \begin{bmatrix} r_P & 0\\ 0 & r_A \end{bmatrix},$$

it follows that $\lambda_1 = r_P$ and $\lambda_2 = r_A$. That is, the extinction equilibrium E_0 is locally asymptotically stable if max{ r_P, r_A } < 0; while if max{ r_P, r_A } > 0, E_0 is unstable.

(2) *Stability of the plant-only equilibrium* E_{P0} . Evaluating the Jacobian matrix at E_{P0} , we obtain

$$J(E_{P0}) = \begin{bmatrix} -r_P & \frac{b_P \phi gar_P^2}{s_P(s_P + ahr_P)} \\ 0 & r_A + \frac{\epsilon ar_P}{s_P + ahr_P} \end{bmatrix}.$$



Fig. 3 Schematic of real positive roots for cubic polynomial $\rho_2(P)$ and the subsystem (2) with $r_P < 0$

The corresponding eigenvalues are given by

$$\lambda_1 = -r_P, \ \lambda_2 = r_A + \frac{\epsilon a r_P}{s_P + a h r_P}$$

Therefore, the plant-only equilibrium E_{P0} is locally asymptotically stable if $r_A <$ $-\frac{\epsilon a r_P}{s_P+ahr_P}$; while if $r_A > -\frac{\epsilon a r_P}{s_P+ahr_P}$, the plant-only equilibrium E_{P0} is unstable. (3) *Stability of the pollinator-only equilibrium* E_{0A} . The Jacobian matrix at E_{0A} can

be shown as

$$J(E_{0A}) = \begin{bmatrix} r_P & 0\\ \frac{r_A}{s_A} \in a & -r_A \end{bmatrix}.$$

Therefore, we have $\lambda_1 = r_P$ and $\lambda_2 = -r_A$. That is, the pollinator-only equilibrium E_{0A} is locally asymptotically stable if $r_P < 0$; while it is unstable if $r_P > 0.$

(4) Stability of the coexistence equilibrium. Let $E^* = (P^*, A^*)$ be a potential coexistence equilibrium. The Jacobian matrix of the system (2) evaluated at $E^* = (P^*, A^*)$ is

$$J(E^*) = \begin{bmatrix} \frac{b_P \phi g a A^* P^*}{(1+ahP^*+aA^*P^*)^2} - s_P P^* & b_P \phi g a \frac{(P^*)^2 (1+ahP^*)}{(1+ahP^*+aA^*P^*)^2} \\ \frac{\epsilon a A^*}{(1+ahP^*)^2} & -s_A A^* \end{bmatrix}.$$

The corresponding characteristic equation is given by

$$\lambda^{2} - \left[\frac{b_{P}\phi gaA^{*}P^{*}}{(1+ahP^{*}+aA^{*}P^{*})^{2}} - s_{P}P^{*} - s_{A}A^{*}\right]\lambda + \det(J(E^{*})) = 0,$$

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where

$$\det(J(E^*)) = -\left[\frac{b_P \phi g a A^* P^*}{(1+ahP^*+aA^*P^*)^2} - s_P P^*\right] s_A A^*$$
$$-\frac{b_P \phi g a (P^*)^2 (1+ahP^*)}{(1+ahP^*+aA^*P^*)^2} \frac{\epsilon a A^*}{(1+ahP^*)^2}.$$

Since $E^* = (P^*, A^*)$ is a coexistence equilibrium of the system (2), the implicit function theorem combined with $\psi_2(P^*, A^*) = 0$ implies that there is a continuous differentiable function

$$A(P) = \frac{1}{s_A} \left(r_A + \epsilon \frac{aP}{1 + ahP} \right) \tag{4}$$

such that $A(P^*) = 0$ and

$$\left. \frac{dA(P)}{dP} \right|_{P=P^*} = -\frac{\frac{\partial \psi_2(P,A)}{\partial P}}{\frac{\partial \psi_2(P,A)}{\partial A}} \right|_{P=P^*}.$$

Substituting Eq. (4) into $\psi_1(P, A)$, we obtain that

$$\psi_1(P, A(P)) = \rho_1(P).$$
 (5)

Taking the derivative of Eq. (5) with respect to P, we get that

$$\left[\frac{\partial\psi_1(P, A(P))}{\partial A}\frac{dA(P)}{dP} + \frac{\partial\psi_1(P, A(P))}{\partial P}\right]\Big|_{P=P^*} = \frac{d\rho_1(P)}{dP}\Big|_{P=P^*}$$

Therefore we have

$$\frac{d\rho_1(P)}{dP}\Big|_{P=P^*} \frac{\partial\psi_2(P,A)}{\partial A}\Big|_{P=P^*} = -\frac{\partial\psi_1(P,A(P))}{\partial A} \frac{\partial\psi_2(P,A)}{\partial P}\Big|_{P=P^*} + \frac{\partial\psi_1(P,A(P))}{\partial P}\Big|_{P=P^*} \frac{\partial\psi_2(P,A)}{\partial A}\Big|_{P=P^*} = \det(J(E^*)).$$

It follows that

$$\det(J(E^*)) = \frac{d\rho_1(P)}{dP} \bigg|_{P=P^*} \frac{\partial \psi_2(P, A)}{\partial A} \bigg|_{P=P^*} = -\frac{s_A A^* P^*}{s_A (1+ahP^*)^2 + ar_A (1+ahP^*)P^* + \epsilon a^2 (P^*)^2} \cdot \rho_1'(P^*).$$
(6)

By the characteristic Eq. (6) we know that the eigenvalues satisfy

$$\lambda_1(E^*) + \lambda_2(E^*) = -\frac{b_P \phi g a A^* P^*}{(1 + ah P^* + aA^* P^*)^2} + s_P P^* + s_A A^*$$

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and

$$\lambda_1(E^*)\lambda_2(E^*) = \det(J(E^*))$$

= $-\frac{s_A A^* P^*}{s_A(1+ahP^*)^2 + ar_A(1+ahP^*)P^* + \epsilon a^2(P^*)^2} \cdot \rho_1'(P^*).$

Now we will divide the analysis into two cases:

(*i*)
$$r_P > 0$$
, and (*ii*) $r_P < 0$.

Case $r_P > 0$. Given the equation

$$b_P\left(f + \phi \frac{aA^*P^*}{1 + ahP^* + aA^*P^*}\right)g - s_PP^* - d_P = 0,$$

it can be inferred that

$$\lambda_1(E^*) + \lambda_2(E^*) = \frac{b_P \phi g a A^* P^*}{(1 + ah P^* + aA^* P^*)^2} - s_P P^* - s_A A^*$$
$$< \frac{b_P \phi g a A^* P^*}{1 + ah P^* + aA^* P^*} - s_P P^* - s_A A^*$$
$$= -r_P - s_A A^* < 0.$$

Therefore, the local stability of a coexistence equilibrium is entirely determined by the slope of the cubic equation $\rho_2(P)$ at that equilibrium. Specifically: (i) If a unique coexistence equilibrium E_1^* exists, then the product $\lambda_1(E_1^*)\lambda_2(E_1^*)$ is positive, indicating the local asymptotic stability of E_1^* . (ii) In the presence of two coexistence equilibria, namely E_1^* and E_2^* , we observe that $\lambda_1(E_1^*)\lambda_2(E_1^*)$ is negative, while $\lambda_1(E_2^*)\lambda_2(E_2^*)$ is positive. This signifies that E_1^* is unstable, while E_2^* is locally asymptotically stable. Notably, when E_1^* and E_2^* coincide (i.e., $E_1^* = E_2^*$), we have $\lambda_1(E_1^*)\lambda_2(E_1^*) = 0$, and both the stable and center-stable manifold dimensions are equal to 1. (iii) In the case of three coexistence equilibria, denoted as E_i^* , i = 1, 2, 3, we find that $\lambda_1(E_i^*)\lambda_2(E_i^*)$ is positive for i = 1, 3 and negative for $\lambda_1(E_2^*)\lambda_2(E_2^*)$. Therefore, E_1^* and E_3^* are locally asymptotically stable, whereas E_2^* is unstable. Particularly, when E_1^* and E_2^* merge ($E_1^* = E_2^*$), we again have $\lambda_1(E_1^*)\lambda_2(E_1^*) = 0$, with both stable and center-stable manifold dimensions of stable and center-stable manifold are both equal to 1. Likewise, when E_2^* and E_3^* merge, we obtain $\lambda_1(E_2^*)\lambda_2(E_2^*) = 0$, and the dimensions of stable and center-stable manifolds are both equal to 1.

Case $r_P < 0$. In the case where a unique coexistence equilibrium E_1^* exists, we can establish that $\lambda_1(E_1^*) + \lambda_2(E_1^*) < 0$. Suppose otherwise. If $\lambda_1(E_1^*)\lambda_2(E_1^*) > 0$, it would imply that $\lambda_1(E_1^*)$ and $\lambda_2(E_1^*)$ are both greater than zero, which contradicts the boundlessness of the system. Therefore, we conclude that $\lambda_1(E_1^*) + \lambda_2(E_1^*) < 0$. In the case where the system has two coexistence equilibria E_1^* and E_2^* , we can deduce the instability of E_1^* from the fact that $\lambda_1(E_1^*)\lambda_2(E_1^*) < 0$. Using a similar line of reasoning as in the case of a unique coexistence equilibrium, we can directly ascertain that $\lambda_1(E_2^*) + \lambda_2(E_2^*) < 0$, signifying the local asymptotic stability of E_2^* .



Fig. 4 Pairwise phase diagrams demonstrate global stability of equilibrium states for the subsystem (2). a Global stability of the coexistence equilibrium E_1^* ; b Global stability of the extinction equilibrium E_0 ; c Global stability of the pollinator-only equilibrium E_{0A} ; d Global stability of the plant-only equilibrium E_{P0} . The corresponding parameter values are detailed in Table 1

Particularly, when $E_1^* = E_2^*$, we find that $\lambda_1(E_1^*)\lambda_2(E_1^*) = 0$, and the stable and center-stable manifold dimensions are both equal to 1.

Based on the discussion in cases where $r_P > 0$ and $r_P < 0$, the stability of these coexistence equilibria can be summarized as follows: (i) If there is a unique coexistence equilibrium E_1^* , it is locally asymptotically stable. (ii) In the case of two coexistence equilibria, E_1^* is unstable, while E_2^* is locally asymptotically stable. (iii) When there are three coexistence equilibria, E_1^* and E_3^* are locally asymptotically stable, while E_2^* is unstable. (iv) Notably, when two equilibria merge, the dimensions of both the stable and center-stable manifolds of the equilibria are equal to 1.

Straightforward calculations reveal that

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$$\frac{\partial \psi_1(P,A)}{\partial A} = \frac{b_P \phi g a P^2 (1+ahP)}{(1+ahP+aAP)^2} > 0$$

and

$$\frac{\partial \psi_2(P, A)}{\partial P} = \frac{\epsilon a A}{(1 + ahP)^2} > 0.$$

Hence, the system (2) is cooperative. Given the dissipative property of the system, it follows that (see Theorem 2.2 in Ref. Smith 1995), for any initial values (P(0), A(0)) $\in \mathbb{R}^2_+$, the solution to the system (2) converges to an equilibrium.



Fig. 5 Pairwise phase diagrams demonstrate bistability of equilibrium states for the subsystem (2). **a** Bistability between the low-level coexistence equilibrium E_1^* and the high-level coexistence equilibrium E_3^* ; **b** Bistability between the extinction equilibrium E_0 and the high-level coexistence equilibrium E_2^* ; **c** Bistability between the pollinator equilibrium E_{0A} and the high-level coexistence equilibrium E_2^* ; **d** Bistability between the plant equilibrium E_{P0} and the high-level coexistence equilibrium E_2^* ; **d** Bistability between the plant equilibrium E_{P0} and the high-level coexistence equilibrium E_2^* ; **d** Bistability between the plant equilibrium E_{P1} and the high-level coexistence equilibrium E_2^* ; **d** Bistability between the plant equilibrium E_{P1} and the high-level coexistence equilibrium E_2^* ; **d** Bistability between the plant equilibrium E_{P1} and the high-level coexistence equilibrium E_2^* ; **d** Bistability between the plant equilibrium E_{P1} and the high-level coexistence equilibrium E_2^* ; **d** Bistability between the plant equilibrium E_{P1} and the high-level coexistence equilibrium E_2^* ; **d** Bistability between the plant equilibrium E_1 and the high-level coexistence equilibrium E_2^* ; **d** Bistability between the plant equilibrium E_1 and the high-level coexistence equilibrium E_2^* ; **d** Bistability between the plant equilibrium E_2 and the high-level coexistence equilibrium E_2^* ; **d** Bistability between the plant equilibrium E_2 and the high-level coexistence equilibrium E_2 and the high-level coexistence equilibrium E_2^* ; **d** Bistability between the plant equilibrium E_2 and the high-level coexistence equilibrium E_2^* ; **d** Bistability between the plant equilibrium E_2^* ; **d** Bis

Para	Fig. <mark>4</mark> a	Fig. 4b	Fig. 4c	Fig. 4d	Fig. <mark>5</mark> a	Fig. <mark>5</mark> b	Fig. 5c	Fig. 5d	Unit
f	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	Unitless
ϕ	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	Unitless
g	1	1	1	1	1	1	1	1	Unitless
b_A	1	0.2	1	0.2	1.2	1	1	1	t^{-1}
b_P	1	0.5	0.5	1.55	1.45	1	1	1	t^{-1}
SP	0.15	0.05	0.05	0.05	0.61	0.05	0.05	0.15	P^{-2}
а	0.8	0.8	0.8	0.8	0.2	0.8	0.6	0.7	$P^{-1}t^{-1}$
h	1	1	1	1	1	1	1	1	t
ϵ	1	2	2	2	1	2	1	2	Unitless
s_A	0.15	0.15	0.15	0.15	2	0.15	0.15	0.11	$A^{-2}t^{-1}$
d_A	0.7	0.5	0.5	1.8	1.1	1.5	0.7	2	t^{-1}
d_P	0.2	0.75	0.75	0.75	0.67	0.75	0.75	0.4	t^{-1}

 Table 1
 Simulation parameters for the plant-pollinator subsystem (2), mainly sourced from Hale et al. (2022)

Remark Theorem 1 illuminates the global dynamics of the plant-pollinator system (2), providing theoretical validation for some of the numerical findings reported by Hale et al. (2022). Several key insights emerge from this analysis:

- (1) *The plant-pollinator system* (2) *inherently exhibits equilibrium dynamics*, meaning that the population sizes of both plants and pollinators eventually stabilize over time.
- (2) In scenarios where a unique locally stable equilibrium exists, the system achieves global asymptotic stability. Specifically: when both plants and pollinators are facultative species, the system maintains coexistence and, if the coexistence equilibrium is unique, it achieves global asymptotic stability (Fig. 4a). When no coexistence equilibrium exists, the following global asymptotic stability conditions apply:
 - (i) *Extinction equilibrium* (E_0) : Globally asymptotically stable when both plants and pollinators are obligate mutualists, unable to survive without each other (Fig. 4b).
 - (ii) *Pollinator-only equilibrium* (E_{0A}) : Globally asymptotically stable when plants are obligate mutualists but pollinators are facultative, allowing pollinators to persist independently (Fig. 4c).
 - (iii) *Plant-only equilibrium* (E_{P0}) : Globally asymptotically stable when plants are facultative and pollinators are obligate mutualists, enabling plants to survive without pollinators (Fig. 4d).
- (3) *The system can exhibit four types of bistability*, depending on the mutualistic dependencies of the species involved:
 - (i) *Facultative plants and pollinators:* Bistability may occur between a low-level coexistence equilibrium E_1^* and a high-level coexistence equilibrium E_3^* (Fig. 5a).
 - (ii) *Obligate plants and pollinators:* Bistability can be observed between the extinction equilibrium E_0 and a high-level coexistence equilibrium, indicating that the system may either collapse or thrive based on initial conditions (Fig. 5b).
 - (iii) *Facultative pollinators and obligate plants:* Bistability may emerge between the pollinator-only equilibrium E_{0A} and a high-level coexistence equilibrium E_2^* , suggesting that pollinators can either exist alone or coexist with plants under certain conditions (Fig. 5c).
 - (iv) Facultative plants and obligate pollinators: The system may exhibit bistability between the plant-only equilibrium E_{P0} and a high-level coexistence equilibrium E_2^* (Fig. 5d), or between a low-level coexistence equilibrium E_1^* and a high-level coexistence equilibrium E_3^* . This indicates that plants can survive independently, or the system can transition between multiple coexistence states, depending on initial populations and parameters.

These findings highlight the complex interplay between plant and pollinator populations and underscore the importance of mutualistic dependencies in determining the system's long-term behavior. The existence of multiple equilibria and types of bistability emphasizes that small changes in initial conditions or parameters can lead to vastly different outcomes, ranging from species extinction to stable coexistence.

3.2 Dynamics without plants

To further understand the interactions within our tripartite system, we examine the dynamics between pollinators and parasites in the absence of plants. This scenario isolates the direct effects of parasitism on pollinator populations without the mitigating influence of plant resources. Such an analysis is crucial for identifying the conditions under which pollinator populations can persist or collapse solely due to parasitic pressures, providing insights into the resilience of pollinators when plant dynamics are not a limiting factor. Under these conditions, model (1) reduces to the following two-dimensional system:

$$\frac{dA}{dt} = A \left(r_A - s_A A - \beta M \right),$$

$$\frac{dM}{dt} = M \left(k\beta A - d_M \right).$$
(7)

Lemma 2 (Boundedness and invariance) *The solutions of system* (7), *with initial conditions in the compact set*

$$\mathbb{C}_{2} = \left\{ (A, M) \in \mathbb{R}^{2}_{+} : 0 \le A \le \frac{r_{A}}{s_{A}}, 0 \le A + \frac{1}{k}M \le \frac{(r_{A} + d_{M})^{2}}{4s_{A}d_{M}} \right\},\$$

remain there for all forward time.

Proof The proof proceeds similarly to that of Lemma 1 and ensures that the trajectories of system (7) remain non-negative and bounded within the biologically relevant domain \mathbb{C}_2 . For brevity, we omit the detailed steps here.

Theorem 2 (Global dynamics) *The pollinator-parasite system described by* (7) *exhibits an extinction equilibrium* $E_0 = (0, 0)$ *, and potentially accommodates a pollinator-only equilibrium* $E_{A0} = (\frac{r_A}{s_A}, 0)$ as well as a coexistence equilibrium

$$E^* = (A^*, M^*) = \left(\frac{d_M}{k\beta}, \frac{1}{\beta}\left(r_A - \frac{s_A d_M}{k\beta}\right)\right).$$

The global dynamics of these equilibria are determined by the following conditions:

- (i) The extinction equilibrium $E_0 = (0, 0)$ is globally asymptotically stable if $r_A < 0$; otherwise, if $r_A > 0$, $E_0 = (0, 0)$ is unstable.
- (ii) In the case where $r_A > 0$, system (7) has a pollinator-only equilibrium $E_{A0} = (\frac{r_A}{s_A}, 0)$. Specifically, E_{A0} is globally asymptotically stable if $r_A < \frac{s_A d_M}{\beta k}$, and it is unstable if $r_A > \frac{s_A d_M}{\beta k}$.
- (iii) For $r_A > \frac{s_A d_M}{\beta k}$, system (7) admits a unique coexistence equilibrium $E^* = (A^*, M^*)$ that is globally asymptotically stable.

Proof An equilibrium of system (7) is characterized by

$$0 = A (r_A - s_A A - \beta M) := \psi_3(A, M), 0 = M (k\beta A - d_M) := \psi_4(A, M).$$

Simple calculations reveal that system (7) always has an extinction equilibrium $E_0 = (0, 0)$. If $r_A > 0$, the system (7) features a pollinator-only equilibrium $E_{A0} = (\frac{r_A}{s_A}, 0)$; while if $r_A > \frac{s_A d_M}{\beta k}$, the system (7) exhibits a unique coexistence equilibrium $E^* = (A^*, M^*)$.

In the following, we study the global stability of these equilibria.

(i) Global stability of the extinction equilibrium E_0 . By directly computing the eigenvalues of the system (7) at $E_0 = (0, 0)$, we find that $\lambda_1 = r_A$ and $\lambda_2 = -d_M < 0$. Therefore, the extinction equilibrium E_0 is locally asymptotically stable if $r_A < 0$ and unstable if $r_A > 0$. Since E_0 is the unique equilibrium of the system (7) when $r_A < 0$, the Pioncare-Bendixson theorem (Hale 2009) implies that all solutions of the system (7) converge to the extinction equilibrium E_0 , i.e., the extinction equilibrium E_0 is globally asymptotically stable if $r_A < 0$.

(ii) Global stability of the parasite-free equilibrium E_{A0} . Simple calculations reveal that the system (7) has two eigenvalues, denoted as $\lambda_1 = -r_A < 0$ and $\lambda_2 = -d_M + \frac{k\beta r_A}{s_A}$ at the parasite-free equilibrium E_{A0} . Therefore, E_{A0} is locally asymptotically stable if $r_A < \frac{s_A d_M}{\beta k}$ and unstable if $r_A > \frac{s_A d_M}{\beta k}$. Since in the case $r_A < \frac{s_A d_M}{\beta k}$ the extinction equilibrium E_0 is unstable and the system (7) has no coexistence equilibria, thus all solutions of the system (7) converge to the parasite-free equilibrium E_{A0} , i.e., E_{A0} is globally asymptotically stable if $r_A < \frac{s_A d_M}{\beta k}$.

(iii) Global stability of the coexistence equilibrium E*. Define a Lyapunov function

$$\mathbf{V}(A, M) = \int_{1}^{A} \frac{u-1}{u} du + \frac{1}{k} \int_{1}^{M} \frac{u-1}{u} du.$$

By calculating the derivative of the function V(A, M), we obtain

$$\begin{aligned} \frac{d\mathbf{V}}{dt}\Big|_{E^*} &= (A - A^*)(r_A - s_A A - \beta M) + \frac{1}{k}(M - M^*)(k\beta A - d_M) \\ &= (A - A^*)\left[r_A - s_A(A - A^*) - s_A A^* - \beta(M - M^*) - \beta M^*\right] \\ &+ \frac{1}{k}(M - M^*)\left(k\beta(A - A^*) + k\beta A^* - d_M\right) \\ &= -s_A(A - A^*)^2. \end{aligned}$$

Therefore, $\frac{d\mathbf{V}}{dt} < 0$ strictly for $\forall A, M \in \mathbb{R}^2_+$ except the fixed point (A^*, M^*) where $\frac{d\mathbf{V}}{dt} = 0$. Thus, the coexistence equilibrium E^* is globally asymptotically stable whenever it exists.

Remark Theorem 2 reveals that the pollinator-parasite subsystem exhibits straightforward equilibrium dynamics. Specifically:



Fig. 6 One-parameter bifurcation for the system (2) with the following parameter values: $d_A = 0.2$, k = 0.01, $\beta = 0.005$, $d_M = 0.1$, $s_A = 0.0001$, while varying $rA = b_A - d_A$ within the range of (-0.2, 0.5). Sink and saddle points are graphically represented by blue and green lines, respectively. The data for this analysis is sourced from Kang et al. (2016) (color figure online)

- *Extinction region*: When pollinators are obligate mutualists, both pollinator and parasite populations inevitably collapse to extinction (see Extinction Region, Fig. 6). This outcome occurs because the pollinators cannot sustain themselves without mutualistic interactions, leading to a lack of hosts for the parasites.
- (2) Pollinator region: In cases where pollinators are facultative but possess a limited net growth rate, the pollinator population can maintain itself but cannot support the parasite population, resulting in parasite extinction (see Pollinator Region, Fig. 6). The insufficient net growth rate of pollinators limits their population density, making it unfavorable for parasite persistence.
- (3) Coexistence region: When the net growth rate of pollinators is sufficiently high, both pollinators and parasites can coexist at stable population levels (see Coexistence Region, Fig. 6). The elevated net growth rate leads to higher pollinator densities, which enhance parasite transmission rates and reduce the likelihood of parasite extinction during the early stages of an outbreak (Graystock et al. 2016).

This analysis underscores the critical role of the pollinator's net growth rate in determining the fate of both populations. Higher pollinator densities create favorable conditions for parasite survival and proliferation by providing ample hosts for infection. Consequently, regulating the net growth rate or density of pollinators emerges as a vital strategy for managing parasite prevalence within pollinator communities.

4 Analysis of the full system

Building upon the analyses of the subsystems (2) and (7), we now focus on the comprehensive plant-pollinator-parasite model (1). Our investigation reveals that the full system can exhibit up to seven boundary equilibria. In the following, we provide a concise summary of the existence and stability conditions for these equilibria.

Theorem 3 (Boundary dynamics)

- (1) Extinction equilibrium: An extinction equilibrium $E_{000} = (0, 0, 0)$ always exists. E_{000} is locally asymptotically stable if $\max\{r_P, r_A\} < 0$; otherwise, if $\max\{r_P, r_A\} > 0$, E_{000} is unstable.
- (2) **Plant-only equilibrium:** A plant-only equilibrium $E_{P00} = (\frac{r_P}{s_P}, 0, 0)$ exists when $r_P > 0$. If $r_A < -\frac{\epsilon a r_P}{s_P + a h r_P}$, E_{P00} is locally asymptotically stable; otherwise, if $r_A > -\frac{\epsilon a r_P}{s_P + a h r_P}$, E_{P00} is unstable.
- (3) Pollinator-only equilibrium: A pollinator-only equilibrium $E_{0A0} = (0, \frac{r_A}{s_A}, 0)$ exists when $r_A > 0$. If $\max\{r_P, r_A - \frac{s_A d_M}{\beta k}\} < 0$, E_{0A0} is locally asymptotically stable; otherwise, if $\max\{r_P, r_A - \frac{s_A d_M}{\beta k}\} > 0$, E_{0A0} is unstable.
- (4) **Plant-pollinator equilibrium:** The system can exhibit up to three boundary equilibria on the P-A plane. Specifically, if $r_P > 0$ and $r_A > 0$, the system exhibits either one or three plant-pollinator equilibria. If $r_P < 0$ and $r_A > 0$, the system features either zero or two plant-pollinator equilibria. If $r_P > 0$ and $r_A < 0$, the system can have zero, one, two, or up to three plant-pollinator equilibria. If $r_P > 0$ and $r_A < 0$, the system can have zero, one, two, or up to three plant-pollinator equilibria. If $r_P > 0$ and $r_A < 0$, the system can host either zero, one, or at most two plant-pollinator equilibria. We denote the plant-pollinator equilibria as $E_{PA0}^i = (\bar{P}_i, \bar{A}_i, 0)$, where i = 1, 2, 3, and they are ordered such that $\bar{P}_1 < \bar{P}_2 < \bar{P}_3$ whenever they exist. The stability of these plant-pollinator equilibria is as follows: (i) When $\bar{A}_i < \frac{d_M}{k\beta}$, the plant-pollinator equilibria with odd labels (i.e., E_{PA0}^1 and E_{PA0}^3) are locally asymptotically stable; while the plant-pollinator equilibrium with an even label (i.e., E_{PA0}^2) is unstable. (ii) When $\bar{A}_i > \frac{d_M}{k\beta}$, the plant-pollinator equilibria are unstable.
- (5) **Pollinator-parasite equilibrium:** When $r_A > \frac{s_A d_M}{\beta k}$, the system admits a unique pollinator-parasite equilibrium $E_{0AM} = (0, \hat{A}, \hat{M})$. If $r_P < 0$, E_{0AM} is locally asymptotically stable, while if $r_P > 0$, E_{0AM} is unstable.

Proof The existence of boundary equilibria for the system (1) is a direct result of Theorems 1 and 2. Next, we study of the local stability associated with these boundary equilibria.

(1) Stability of the extinction equilibrium $E_{000} = (0, 0, 0)$. Since the Jacobian matrix of the system (1) evaluated at E_{000} is given by

$$J(E_{000}) = \begin{bmatrix} r_P & 0 & 0\\ 0 & r_A & 0\\ 0 & 0 & -d_M \end{bmatrix},$$

it follows that $\lambda_1 = r_P$, $\lambda_2 = r_A$ and $\lambda_3 = -d_M < 0$. That is, the extinction equilibrium E_{000} is locally asymptotically stable if max{ r_P, r_A } < 0; otherwise, if max{ r_P, r_A } > 0, E_{000} is unstable.

(2) *Stability of the plant-only equilibrium* E_{P00} . Evaluating the Jacobian matrix at E_{P00} , we obtain

$$J(E_{P00}) = \begin{bmatrix} -r_P & \frac{b_P \phi gar_P^2}{s_P (s_P + ahr_P)} & 0\\ 0 & r_A + \frac{\epsilon ar_P}{s_P + ahr_P} & 0\\ 0 & 0 & -d_M \end{bmatrix},$$

The corresponding eigenvalues are given by

$$\lambda_1 = -r_P < 0, \lambda_2 = r_A + \frac{\epsilon a r_P}{s_P + a h r_P}, \lambda_3 = -d_M < 0.$$

Therefore, the plant-only equilibrium E_{P00} is locally asymptotically stable if $r_A < -\frac{\epsilon a r_P}{s_P + a h r_P}$; while if $r_A > -\frac{\epsilon a r_P}{s_P + a h r_P}$, the plant-only equilibrium E_{P00} is unstable. (3) *Stability of the pollinator-only equilibrium* E_{0A0} . The Jacobian matrix at E_{0A0} can be shown as

$$J(E_{0A0}) = \begin{bmatrix} r_P & 0 & 0\\ \frac{r_A}{s_A} \epsilon a & -r_A & -\beta \frac{r_A}{s_A}\\ 0 & 0 & -d_M + k\beta \frac{r_A}{s_A} \end{bmatrix},$$

$$\lambda_1 = r_P, \lambda_2 = -r_A < 0, \lambda_3 = -d_M + k\beta \frac{r_A}{s_A}.$$

That is, the pollinator-only equilibrium E_{0A0} is locally asymptotically stable if $\max\{r_P, r_A - \frac{s_A d_M}{\beta k}\} < 0$; while it is unstable if $\max\{r_P, r_A - \frac{s_A d_M}{\beta k}\} > 0$.

(4) Stability of the plant-pollinator equilibrium. Let $E_{PA0}^i = (\bar{P}_i, \bar{A}_i, 0), i = 1, 2, 3$ be the potential plant-pollinator equilibria with order $\bar{P}_1 < \bar{P}_2 < \bar{P}_3$. The Jacobian matrix of the system (1) evaluated at E_{PA0}^i is

$$J(E_{PA0}^{i}) = \begin{bmatrix} -s_{P}\bar{P}_{i} + \frac{b_{P}\phi ga\bar{A}_{i}\bar{P}_{i}}{(1+ah\bar{P}_{i}+a\bar{A}_{i}\bar{P}_{i})^{2}} & b_{P}\phi ga\frac{(\bar{P}_{i})^{2}(1+ah\bar{P}_{i})}{(1+ah\bar{P}_{i}+a\bar{A}_{i}\bar{P}_{i})^{2}} & 0\\ \frac{\epsilon a\bar{A}_{i}}{(1+ah\bar{P}_{i})^{2}} & -s_{A}\bar{A}_{i} & -\beta\bar{A}_{i}\\ 0 & 0 & -d_{M}+k\beta\bar{A}_{i} \end{bmatrix}.$$

The corresponding characteristic equation is given by

$$\begin{aligned} \left(\lambda + d_M - k\beta \bar{A}_i\right) \left[\lambda^2 - \left(\frac{b_P \phi g a \bar{A}_i \bar{P}_i}{(1 + ah \bar{P}_i + a\bar{A}_i \bar{P}_i)^2} - s_P \bar{P}_i - s_A \bar{A}_i\right) \lambda \\ + \det(J_{PA}(E_{PA0}^i)) \right] &= 0, \end{aligned}$$

where

$$\det(J(E_{PA0}^{i})) = -\left[\frac{b_{P}\phi gaA_{i}P_{i}}{(1+ah\bar{P}_{i}+a\bar{A}_{i}\bar{P}_{i})^{2}} - s_{P}\bar{P}_{i}\right]s_{A}\bar{A}_{i}$$
$$-\frac{b_{P}\phi ga(\bar{P}_{i})^{2}(1+ah\bar{P}_{i})}{(1+ah\bar{P}_{i}+a\bar{A}_{i}\bar{P}_{i})^{2}}\frac{\epsilon a\bar{A}_{i}}{(1+ah\bar{P}_{i})^{2}}.$$

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We now consider the stability of $E_{PA0}^{i} = (\bar{P}_{i}, \bar{A}_{i}, 0)$ in two cases: (*i*) $\bar{A}_{i} > \frac{d_{M}}{k\beta}$ and (ii) $\bar{A}_{i} < \frac{d_{M}}{k\beta}$. In case (i), the positivity of $\lambda_{1} = -d_{M} + k\beta\bar{A}_{i} > 0$ implies that the plant-pollinator equilibrium $E_{PA0}^{i} = (\bar{P}_{i}, \bar{A}_{i}, 0)$ is always unstable. For case (ii), the subsequent analysis aligns with the stability of the coexistence equilibrium in the subsystem (2) (refer to Theorem 1 for proof), and therefore, it is omitted here.

(5) Stability of the pollinator-parasite equilibrium $E_{0AM} = (0, \hat{A}, \hat{M})$. The Jacobian matrix of the system (1) evaluated at $E_{0AM} = (0, \hat{A}, \hat{M})$ is

$$J(E_{0AM}) = \begin{bmatrix} r_P & 0 & 0\\ \epsilon a \hat{A} & -s_A \hat{A} & -\beta \hat{A}\\ 0 & k\beta \hat{M} & 0 \end{bmatrix}.$$

The corresponding characteristic equation is given by

$$(\lambda - r_P)\left(\lambda^2 + s_A\hat{A}\lambda + k\beta^2\hat{A}\hat{M}\right) = 0.$$

It follows that $\lambda_1 = r_P$, $\lambda_2 + \lambda_3 = -s_A \hat{A} < 0$ and $\lambda_2 \lambda_3 = k\beta^2 \hat{A} \hat{M} > 0$. Therefore, the pollinator-parasite equilibrium $E_{0AM} = (0, \hat{A}, \hat{M})$ is locally asymptotically stable if $r_P < 0$; otherwise, if $r_P > 0$, $E_{0AM} = (0, \hat{A}, \hat{M})$ is unstable. This completes the proof of Theorem 3.

Remark Theorem 3 reveals that the boundary dynamics of the full plant-pollinatorparasite system share both similarities with and differences from those of the plantpollinator and pollinator-parasite subsystems:

(1) Similarities:

- (i) Local stability of the extinction equilibrium: When both plants and pollinators are obligate mutualists, the extinction equilibrium is locally stable. This stability arises from their strong interdependence; the collapse of one population leads to the collapse of the other, resulting in system-wide extinction if either species declines below a critical threshold.
- (ii) Local stability of the plant-only equilibrium: When plants are facultative mutualists and the pollinator's birth rate is significantly lower than its mortality rate, the plant-only equilibrium is locally stable. In this scenario, plants can sustain their populations through alternative mechanisms such as self-pollination or interactions with other pollinator species, without relying exclusively on the pollinators modeled.

(2) Differences:

(i) Influence of pollinator density on the plant-pollinator equilibrium: In the full system, the stability of the plant-pollinator equilibrium is significantly affected by pollinator density. Specifically, low pollinator densities can stabilize the equilibrium, whereas high pollinator densities can destabilize it. Elevated pollinator densities provide abundant hosts and resources for parasites, facilitating their growth and undermining the stability of the plant-pollinator interaction.

- (ii) Local stability of the pollinator-only equilibrium: The pollinator-only equilibrium is locally stable when plants are obligate mutualists, pollinators are facultative, and the pollinator's net growth rate is not excessively high. Pollinators can persist by utilizing alternative plant species for sustenance. However, if the pollinator's net growth rate is too high, it can lead to rapid increases in pollinator density, creating favorable conditions for parasite survival and thereby destabilizing the pollinator-only equilibrium.
- (iii) Local stability of the pollinator-parasite equilibrium: Stability of the pollinatorparasite equilibrium requires both a sufficiently high net growth rate of pollinators and obligate plant-pollinator relationships. A high pollinator growth rate leads to dense pollinator populations, fostering optimal conditions for parasite survival due to increased resource availability. However, if plants are facultative mutualists, their ability to persist without exclusive dependence on pollinators can disrupt this equilibrium, as changes in plant populations affect pollinator dynamics and, consequently, parasite persistence.

These observations highlight that while certain stability conditions from the subsystems carry over to the full system, the inclusion of parasites introduces new dynamics-particularly related to pollinator density and mutualistic dependencies-that can significantly alter the system's stability landscape.

To investigate the coexistence dynamics of the system (1), let $E^* = (P^*, A^*, M^*)$ represent any coexistence equilibrium. The Jacobian matrix evaluated at E^* is given by

$$J(E^*) = \begin{bmatrix} -s_P P^* + \frac{b_P \phi g a A^* P^*}{(1+ah P^*+aA^* P^*)^2} & b_P \phi g a \frac{(P^*)^2 (1+ah P^*)}{(1+ah P^*+aA^* P^*)^2} & 0\\ \frac{\epsilon a A^*}{(1+ah P^*)^2} & -s_A A^* & -\beta A^*\\ 0 & k\beta M^* & 0 \end{bmatrix}.$$

The corresponding characteristic equation is expressed as

$$\lambda^3 + c_2\lambda^2 + c_1\lambda - \det(J(E^*)) = 0,$$

where

$$c_{2} = s_{P}P^{*} - \frac{b_{P}\phi gaA^{*}P^{*}}{(1 + ahP^{*} + aA^{*}P^{*})^{2}} + s_{A}A^{*},$$

$$c_{1} = -\frac{\epsilon b_{P}\phi ga^{2}(P^{*})^{2}A^{*}}{(1 + ahP^{*} + aA^{*}P^{*})^{2}(1 + ahP^{*})}$$

$$+ s_{A}A^{*}\left[s_{P}P^{*} - \frac{b_{P}\phi gaA^{*}P^{*}}{(1 + ahP^{*} + aA^{*}P^{*})^{2}}\right] + k\beta^{2}A^{*}M^{*},$$

$$c_{0} = -\det(J(E^{*})) = \left[s_{P}P^{*} - \frac{b_{P}\phi gaA^{*}P^{*}}{(1 + ahP^{*} + aA^{*}P^{*})^{2}}\right]k\beta^{2}A^{*}M^{*}.$$

Let $\mathcal{R}_0 = \min\{c_2, c_1c_2 - c_0\}$, we can derive the following results regarding the existence and local stability of coexistence equilibrium of the system (1).



Theorem 4 (Coexistence dynamics) The system can exhibit zero, one $(E_2^* = (P_2^*, A^*, M_2^*))$, or up to two coexistence equilibria

$$E_{i}^{*} = \left(P_{i}^{*}, A^{*}, M_{i}^{*}\right) = \left(P_{i}^{*}, \frac{d_{M}}{k\beta}, \frac{1}{\beta}\left(r_{A} + \epsilon \frac{aP_{i}^{*}}{1 + ahP_{i}^{*}} - \frac{s_{A}d_{M}}{k\beta}\right)\right), \ i = 1, 2,$$

as depicted in Fig. 7, where

$$\begin{split} P_1^* &= \frac{1}{2as_P\left(d_M + \beta hk\right)} [agb_P\left(d_M(f + \phi) + \beta fhk\right) - ad_P\left(d_M + \beta hk\right) - \beta ks_P \\ &- \sqrt{[agb_P\left(d_M(f + \phi) + \beta fhk\right) - ad_P\left(d_M + \beta hk\right) - \beta ks_P]^2 + 4as_P\left(d_M + \beta hk\right)k\beta r_P]}, \\ P_2^* &= \frac{1}{2as_P\left(d_M + \beta hk\right)} [agb_P\left(d_M(f + \phi) + \beta fhk\right) - ad_P\left(d_M + \beta hk\right) - \beta ks_P \\ &+ \sqrt{[agb_P\left(d_M(f + \phi) + \beta fhk\right) - ad_P\left(d_M + \beta hk\right) - \beta ks_P]^2 + 4as_P\left(d_M + \beta hk\right)k\beta r_P]}. \end{split}$$

Specifically, if $r_P > 0$ and $r_A > \frac{s_A d_M}{k\beta}$, the system admits a unique coexistence equilibrium. If $r_P > 0$ and $r_A < \frac{s_A d_M}{k\beta}$, the system exhibits either zero or one coexistence equilibrium. If $r_P < 0$ and $r_A > \frac{s_A d_M}{k\beta}$, the system features either zero or two coexistence equilibria. If $r_P < 0$ and $r_A < \frac{s_A d_M}{k\beta}$, the system can potentially possess zero, one, or up to two coexistence equilibria. Assume that the coexistence equilibria are ordered as $P_1^* < P_2^*$ whenever they are present. The local stability of these potential equilibria is outlined as follows:

- (i) In the case of a unique coexistence equilibrium E_2^* , it is locally asymptotically stable if $\mathcal{R}_0 > 0$, and unstable if $\mathcal{R}_0 < 0$.
- (ii) In the case of two coexistence equilibria E_1^* and E_2^* , E_1^* is always unstable, and the stability of E_2^* depends on the sign of \mathcal{R}_0 : E_2^* is locally asymptotically stable if $\mathcal{R}_0 > 0$, and unstable if $\mathcal{R}_0 < 0$.

Proof Define

$$\psi_{5}(P, A, M) = P \left[b_{P} \left(f + \phi \frac{aAP}{1 + ahP + aAP} \right) g - s_{P}P - d_{P} \right],$$

$$\psi_{6}(P, A, M) = A \left(b_{A} + \epsilon \frac{aP}{1 + ahP} - s_{A}A - d_{A} - \beta M \right),$$

$$\psi_{7}(P, A, M) = M \left(k\beta A - d_{M} \right).$$

An interior equilibrium, denoted as $E^* = (P^*, A^*, M^*)$, of the system (1) satisfies the conditions $\psi_i(P^*, A^*, M^*) = 0$ for i = 5, 6, 7. Solving for $\psi_7(P^*, A^*, M^*) = 0$ yields the relationship

$$A^* = \frac{d_M}{k\beta}.$$
(8)

Substituting (8) into $\psi_5(P^*, A^*, M^*) = 0$ and $\psi_6(P^*, A^*, M^*) = 0$, we obtain

$$M^* = \frac{1}{\beta} \left(r_A + \epsilon \frac{aP^*}{1 + ahP^*} - \frac{s_A d_M}{k\beta} \right) \tag{9}$$

and

$$0 = \frac{P^* \times \rho_4(P^*)}{k(1 + ahP^*)\beta + ad_MP^*} := \rho_3(P^*),$$

where

$$\rho_4(P) = -as_P (d_M + \beta hk) P^2 + [agb_P (d_M (f + \phi) + \beta f hk) -ad_P (d_M + \beta hk) - \beta ks_P]P + k\beta r_P.$$

Considering the characteristics of quadratic equations, when $r_P > 0$, the equation $\rho_4(P) = 0$ exhibits a unique positive real root, as illustrated in Fig. 8a. In cases where $r_P < 0$, the equation $\rho_4(P) = 0$ may exhibit either zero or two positive real roots, as depicted in Fig. 8d–e. These observations, coupled with the sign of M^* in Eq. (9), yield the following conclusion:

- (i) Case $r_P > 0$ and $r_A > \frac{s_A d_M}{k\beta}$. Equation (9) clearly indicates that $M^* > 0$. In this scenario, the system (1) exhibits a unique coexistence equilibrium $E_2^* = (P_2^*, A^*, M_2^*)$, as illustrated in Fig. 8a.
- (ii) Case $r_P > 0$ and $r_A < \frac{s_A d_M}{k\beta}$. The system (1) can potentially have zero or one coexistence equilibrium. When $\rho_4(P) = 0$ has a single positive real root P_2^* , the system (1) lacks a coexistence equilibrium if $M(P_2^*) < 0$ (Fig. 8b). Conversely, if $M(P_2^*) > 0$, the system (1) has a unique coexistence equilibrium $E_2^* = (P_2^*, A^*, M_2^*)$, see Fig. 8c.
- (iii) Case $r_P < 0$ and $r_A > \frac{s_A d_M}{k\beta}$. In this scenario, the system (1) may either lack a coexistence equilibrium or exhibit two coexistence equilibria $E_1^* = (P_1^*, A^*, M_1^*)$ and $E_2^* = (P_2^*, A^*, M_2^*)$, as depicted in Fig. 8d and e.
- (iv) Case $r_P < 0$ and $r_A < \frac{s_A d_M}{k\beta}$. The system (1) could potentially have zero, one or two coexistence equilibria. If $\rho_4(P) = 0$ has two positive real roots P_1^* and P_2^* ,



Fig. 8 Schematic of real positive roots for cubic polynomial $\rho_4(P)$

the system (1) lacks a coexistence equilibrium if $M(P_2^*) < 0$ (Fig. 8f). However, the system (1) has a unique coexistence equilibrium $E_2^* = (P_2^*, A^*, M_2^*)$ if $M(P_1^*)M(P_2^*) < 0$ (Fig. 8g). When $M(P_1^*) > 0$, the system (1) features two coexistence equilibria $E_1^* = (P_1^*, A^*, M_1^*)$ and $E_2^* = (P_2^*, A^*, M_2^*)$, as illustrated in Fig. 8h.

For any coexistence equilibrium $E^* = (P^*, A^*, M^*)$, we can derive the relationship

$$\lambda_1(E^*)\lambda_2(E^*)\lambda_3(E^*) = \det(J(E^*)) = k\beta^2 A^* M^* \rho'_3(P^*)$$
$$= \frac{k\beta^2 A^* M^* P^*}{k(1+ahP^*)\beta + ad_M P^*} \times \rho'_4(P^*).$$

Therefore, we have the following two cases:

- (i) In the case that the system (1) has a unique coexistence equilibrium $E_2^* = (P_2^*, A^*, M_2^*)$, we have $\rho'_4(P_2^*) < 0$ and thus $\lambda_1(E_2^*)\lambda_2(E_2^*)\lambda_3(E_2^*) < 0$. If $\min\{c_2, c_1c_2 - c_0\} > 0$, then the Routh-Hurwitz criterion shows that $\max\{\Re\lambda_1(E^*), \Re\lambda_2(E^*), \Re\lambda_3(E^*)\} < 0$, i.e., E_2^* is locally asymptotically stable; otherwise, if $\min\{c_2, c_1c_2 - c_0\} < 0$, we can deduce from the Routh-Hurwitz criterion that $\max\{\Re\lambda_1(E^*), \Re\lambda_2(E^*), \Re\lambda_2(E^*), \Re\lambda_3(E^*)\} > 0$, i.e., E_2^* is unstable.
- (ii) In the case that the system (1) has two coexistence equilibria $E_1^* = (P_1^*, A^*, M_1^*)$ and $E_2^* = (P_2^*, A^*, M_2^*)$, since $\rho'_4(P_1^*) > 0$, we obtain max{ $\Re\lambda_1(E^*), \Re\lambda_2(E^*), \Re\lambda_3(E^*)$ } > 0 and the coexistence equilibrium E_1^* is unstable. The stability of E_2^* is the same as in case (i) and is not repeated here.

This completes the proof of Theorem 4.

Remark Theorem 4 precisely delineates the conditions for the existence and stability of coexistence equilibria in the full plant-pollinator-parasite system, offering significant biological insights:



Fig. 9 Bifurcation diagram of the system (1) with varying β . a1 $d_A = 0.1$, f = 0.16; a2 $d_A = 1.1$, f = 0.16; a3 $d_A = 0.1$, f = 0.228; a4 $d_A = 1.1$, f = 0.228. Blue and green dotted lines indicate sink and saddle, respectively. \mathbf{H}_1^s , \mathbf{H}_2^s denote supercritical bifurcations, while \mathbf{H}_1^c , \mathbf{H}_2^c and \mathbf{H}_3^c indicate subcritical bifurcations. LP represents the limit point bifurcation. The equilibria E_{000} in cases (a1, a2, and a4), E_{P00} , E_{0A0} , as well as E_{0AM} in case a3, are always unstable and are not shown for clarity (the same applies to subsequent figures) (color figure online)

(1) Plant and pollinator traits determine the number of coexistence equilibria:

- (i) When the plant population is obligate-meaning it cannot survive without its mutualistic partner, the system (1) can sustain up to two coexistence equilibria (see red regions in Fig. 7). This multiplicity arises because the obligate nature of the plant increases the system's dependency on the pollinator, allowing for multiple equilibrium states under varying conditions.
- (ii) Conversely, if the plant population is facultative and can survive independently of the pollinator, the system (1) is limited to at most one coexistence equilibrium. Specifically, when the plant is facultative and the pollinator's net growth rate is high, the system (1) exhibits a unique coexistence equilibrium (see blue regions in Fig. 7). This scenario suggests that facultative plants, coupled with robust pollinator populations, tend to stabilize the system in a single coexistence state.
- (2) Plant population density influences the stability of coexistence equilibria.
 - (i) In cases where the system (1) supports two coexistence equilibria, the stability of these equilibria is partly determined by their associated plant population densities.



Fig. 10 Pairwise phase diagram of the system (1) with $d_A = 0.1$ and f = 0.16

- (ii) The coexistence equilibrium with a lower plant population density is always unstable. This instability is due to insufficient plant resources to support both pollinator and parasite populations effectively, making the system sensitive to perturbations at low plant densities.
- (iii) In contrast, the coexistence equilibrium with a higher plant population density may be stable or become unstable through bifurcation mechanisms (see, for instance, Fig. 9). A higher plant density provides more resources, potentially stabilizing the interactions among plants, pollinators, and parasites. However, changes in system parameters-such as increased parasitism rates or altered growth rates-can lead to bifurcations that destabilize this equilibrium, resulting in complex dynamics like oscillations or chaotic behavior.

5 Numerical simulations

Mathematical analysis of the boundary systems-specifically the plant-pollinator and pollinator-parasite interactions-reveals that these subsystems exhibit only equilibrium dynamics. However, when considering the full plant-pollinator-parasite system, a rich variety of dynamic behaviors emerges, including bistability, tristability, supercritical and subcritical Hopf bifurcations, limit point bifurcations, chaotic dynamics, and heteroclinic orbits. To delve deeper into the mechanisms driving these complex dynamics, we perform numerical bifurcation analyses by systematically varying the biological parameters in system (1). Our baseline parameter values are set as follows: $b_P = 3.25$, $b_A = 1$, $\epsilon = 1$, a = 2, h = 0.01, $s_P = 0.61$, $d_P = 0.74$, $s_A = 2$, g = 0.61, $d_P = 0.74$, $s_A = 2$, g = 0.61, $d_P = 0.74$, $s_A = 2$, g = 0.61, $d_P = 0.74$, $s_A = 2$, g = 0.61, $d_P = 0.74$, $s_A = 2$, g = 0.61, $d_P = 0.74$, $s_A = 2$, g = 0.61, $d_P = 0.74$, $s_A = 2$, g = 0.61, $d_P = 0.74$, $s_A = 0.61$, $d_P = 0.61$,



Fig. 11 Time series of the system (1) with $d_A = 0.1$ and f = 0.16: **a** Stable coexistence equilibrium; **b** Stable pollinator-parasite equilibrium; **c** Stable periodic solution. Red, blue, and black lines represent *P*, *A*, and *M*, respectively (color figure online)



1, $\phi = 0.64$, k = 1, $d_A = 0.1$, f = 0.16, $\beta = 1.2$ and $d_M = 0.5$. These values are partially adapted from Hale et al. (2022) and partially chosen to illustrate a range of possible dynamic behaviors. Any modifications to these parameters are specified in the figure captions accompanying the simulations.

5.1 Impact of parasitism rate

We begin by examining how variations in the parasitism rate β influence the dynamics of the system under different mutualistic scenarios. Specifically, we consider four cases based on the mutualistic dependencies of plants and pollinators: (i) plants obligate, pollinators facultative; (ii) both plants and pollinators obligate; (iii) both plants and pollinators facultative; and (iv) plants facultative, pollinators obligate.



Fig. 13 Pairwise phase diagram of the system (1) with $d_A = 0.1$ and f = 0.288

In the first scenario, where plants are obligate and pollinators are facultative, increasing the parasitism rate induces five types of bistability, two supercritical Hopf bifurcations, and one limit point bifurcation, potentially destabilizing the system at intermediate parasitism levels (Fig. 9a1). At very low parasitism rates, the system exhibits bistability between the pollinator-only equilibrium and the plant-pollinator equilibrium (Fig. 10a). A slight increase in parasitism rate shifts the bistability to occur between the pollinator-only equilibrium and the plant-pollinator-parasite coexistence equilibrium (Fig. 10b). Further increases in the parasitism rate trigger a supercritical Hopf bifurcation, leading to a nontrivial periodic solution that sequentially coexist in bistable states with the pollinator-only equilibrium (Fig. 10c) and later with the pollinator-parasite equilibrium (Fig. 10d). As the parasitism rate continues to rise, a second supercritical Hopf bifurcation occurs, destabilizing the periodic solution and leading to bistability between the pollinator-parasite equilibrium and the coexistence equilibrium (Fig. 10e). At sufficiently high parasitism rates, the system undergoes a limit point bifurcation, stabilizing into the pollinator-parasite equilibrium (Fig. 10f).

Increasing the parasitism rate reduces both the plant and pollinator components in the coexistence equilibrium, while the parasite component initially increases and then decreases (Fig. 11a). Simulations indicate that these outcomes occur consistently, whether plants and pollinators are facultative or obligate. In the pollinator-parasite equilibrium, the pollinator component decreases, and the parasite component first increases before declining (Fig. 11b). Furthermore, as the parasitism rate increases, the amplitude of the periodic solution initially grows, then diminishes, and finally vanishes (Fig. 11c). This bifurcation phenomenon, known as the *bubble phenomenon*, has been observed in studies of infectious disease dynamics (Liu et al. 2015) and social insect behavior (Feng et al. 2021).



Fig. 14 Bifurcation diagram of the system (1) with varying β and fixed parameters $d_A = 0.1$ and f = 0.228. The blue and green dotted lines indicate stable and unstable equilibria, respectively. The blue and green solid dots represent stable and unstable equilibria, respectively. The blue vertical solid line and the black solid line indicate the amplitude of the stable periodic solution, while the green vertical solid line and the red solid line represent the amplitude of the unstable periodic solution. The stable and unstable periodic solutions collide at the point **Is** (color figure online)



Fig. 15 Pairwise phase diagram of the system (1) with $d_A = 1.1$ and f = 0.288

In the scenario where both plants and pollinators are obligate, increasing the parasitism rate induces two types of bistability, a subcritical Hopf bifurcation, and a limit point bifurcation (Fig. 9a2). At low parasitism rates, the system exhibits bistability between the extinction equilibrium and the plant-pollinator equilibrium (Fig. 12a). As the parasitism rate increases to intermediate levels, the system transitions to bistability between the extinction equilibrium and the coexistence equilibrium (Fig. 12b). When the parasitism rate crosses the subcritical Hopf bifurcation point, the coexistence equilibrium destabilizes, leaving the extinction equilibrium as the only stable



Fig. 16 Bifurcation diagram of the system (1) with varying d_M . **a1** $d_A = 0.1$, f = 0.16; **a2** $d_A = 1.1$, f = 0.16; **a3** $d_A = 0.1$, f = 0.228; **a4** $d_A = 1.1$, f = 0.228. The blue and green dotted lines indicate sink and saddle, respectively. \mathbf{H}_1^s , \mathbf{H}_2^s denote supercritical bifurcations, while \mathbf{H}_1^c indicates a subcritical bifurcation. **LP** represents the limit point bifurcation (color figure online)

state. During this transition, the solution temporarily tracks an unstable periodic orbit before converging to the extinction equilibrium (Fig. 12c). At higher parasitism rates, the unstable periodic solution disappears, and the solution directly converges to the extinction equilibrium (Fig. 12d).

In the scenario where both plants and pollinators are facultative, increasing the parasitism rate induces both subcritical and supercritical Hopf bifurcations, with intermediate parasitism levels leading to either bistability or oscillations (Fig. 9a3). At very low parasitism rates, the system exhibits stable coexistence between plants and pollinators (Fig. 13a). As the parasitism rate rises, the system initially maintains a single stable coexistence equilibrium (Fig. 13b), which then transitions to bistability between the coexistence equilibrium and a nontrivial periodic solution (Fig. 13c). Further increases in the parasitism rate lead to a subcritical Hopf bifurcation, destabilizing the coexistence equilibrium, while the stable periodic solution remains until a supercritical Hopf bifurcation occurs (Fig. 13d). After this, the system stabilizes into a single stable coexistence equilibrium (Fig. 13e). Unlike in the obligate plant and facultative pollinator scenario, the amplitude of the periodic solution does not start increasing from zero. To explore this behavior, phase diagram simulations are conducted. The results show that as the parasitism rate crosses the subcritical bifurcation from the right, an unstable periodic solution emerges with increasing amplitude (Fig. 14, green vertical solid line and red solid line), while the amplitude of the stable periodic solution generated by the supercritical Hopf bifurcation decreases (Fig. 14, blue vertical solid line and black solid line). At point **Is**, the unstable and stable periodic solutions collide and disappear.

In the scenario where plants are facultative and pollinators are obligate (Fig. 9a4), increasing the parasitism rate leads to two types of bistability and three subcritical bifurcations. At very low parasitism rates, the system shows bistability between the plant-only equilibrium and the plant-pollinator equilibrium (Fig. 15a). As the parasitism rate increases, this transitions to bistability between the plant-only and coexistence equilibria (Fig. 15b). The first subcritical Hopf bifurcation destabilizes the coexistence equilibrium, leaving the plant-only equilibrium as the sole stable state (Fig. 15c). Further increases in parasitism trigger a second subcritical Hopf bifurcation, reintroducing bistability between the coexistence and plant-only equilibria (Fig. 15d). A third subcritical Hopf bifurcation at even higher parasitism levels destabilizes the coexistence equilibrium again, leaving the plant-only equilibrium as the only stable state (Fig. 15e).

5.2 Impact of parasite mortality

When plants are obligate mutualists and pollinators are facultative, varying the parasite mortality generates four distinct bistable states, two supercritical Hopf bifurcations, and one limit point bifurcation (Fig. 16a1). At low parasite mortality, the system stabilizes at a unique pollinator-parasite equilibrium (Fig. 17a). As the parasite mortality rate increases slightly, a limit point bifurcation occurs, introducing bistability between the pollinator-parasite equilibrium and a coexistence equilibrium involving all three species (Fig. 17b). Further increases in parasite mortality trigger a supercritical Hopf bifurcation, causing the coexistence equilibrium to lose stability and give rise to a stable periodic solution, which coexists in bistability with the pollinator-parasite equilibrium (Fig. 17c). As mortality continues to rise, the periodic solution vanishes, and the system reverts to a single stable pollinator-parasite equilibrium (Fig. 17d). A second supercritical Hopf bifurcation then creates bistability between the periodic solution and the pollinator-parasite equilibrium (Fig. 17e). As the system passes through this bifurcation, the periodic solution collapses, and bistability emerges between the coexistence equilibrium and the pollinator-only state (Fig. 17f). At high parasite mortality, the system shifts to bistability between the plant-pollinator and pollinator-only equilibria (Fig. 17g).

As parasite mortality increases, pollinator density rises and parasite density declines in the pollinator-parasite equilibrium (Fig. 18a). In the coexistence equilibrium, both plant and pollinator densities increase, while parasite density peaks at intermediate mortality rates (Fig. 18b). As the parasite mortality crosses the first Hopf bifurcation from the left, the amplitude of the periodic solution increases gradually before abruptly disappearing (Figs. 16a1 and 18c), a behavior we have named the *left-bow phenomenon*. Similarly, when the parasite mortality crosses the second Hopf bifurcation from the right, the amplitude of the periodic solution again gradually increases before vanishing (Figs. 16a1 and 18d), which we have named the *right-bow phenomenon*.



Fig. 17 Pairwise phase diagram of the system (1) with $d_A = 0.1$ and f = 0.16

In the scenario where both plants and pollinators are obligate (Fig. 16a2), very low parasite mortality leads to the collapse of the entire system (Fig. 19a). As parasite mortality increases to moderate levels, a limit point bifurcation occurs, followed by a subcritical Hopf bifurcation, resulting in bistability between the coexistence equilibrium and the extinction equilibrium (Fig. 19b). At higher parasite mortality rates, the system transitions to bistability between the plant-pollinator equilibrium and the extinction equilibrium (Fig. 19c). A similar dynamic is observed in the scenario where plants are facultative and pollinators are obligate (Fig. 16a4). At low parasite mortality, only the plant survives, while both pollinators and parasites collapse (Fig. 20a). As the parasite mortality increases to moderate levels, a subcritical Hopf bifurcation arises, leading to bistability between the coexistence equilibrium (Fig. 20b). At higher parasite mortality rates, the system exhibits bistability between the plant-only equilibrium (Fig. 20b). At higher parasite mortality rates, the system exhibits bistability between the plant-only equilibrium (Fig. 20c).

In the scenario where both plants and pollinators are facultative (Fig. 16a3), low parasite mortality leads to a stable coexistence of plants, pollinators, and parasites at



Fig. 18 Time series of the system (1) with $d_A = 0.1$ and f = 0.16: **a** Stable pollinator-parasite equilibrium; **b** Stable coexistence equilibrium; **c**-**d** Stable periodic solution. Red, blue, and black lines represent *P*, *A*, and *M*, respectively (color figure online)

constant population levels (Fig. 21a). As parasite mortality increases moderately, the system experiences a bubble phenomenon, characterized by two supercritical bifurcations. A periodic solution emerges between these bifurcations (Fig. 21b), with its amplitude initially increasing from zero, then gradually decreasing, and eventually disappearing. Further increases in parasite mortality restore the coexistence equilibrium as the sole stable state (Fig. 21c). When parasite mortality becomes sufficiently high, the system stabilizes at the plant-pollinator equilibrium (Fig. 21d).

5.3 Impact of conversion rate

In the scenario where plants are obligate and pollinators are facultative (Fig. 22a1), a low conversion rate results in bistability between the pollinator-parasite equilibrium and the coexistence equilibrium (Fig. 23a). At intermediate conversion rates, a supercritical Hopf bifurcation induces the left-bow phenomenon, resulting in bistability between the pollinator-parasite equilibrium and the periodic solution (Fig. 23b). As the conversion rate continues to increase, the system deterministically converges to the pollinator-parasite equilibrium (Fig. 23c). Notably, in this case, increasing the conversion rate does not affect the levels of the plant and pollinator components in the amplitude of the periodic solution (Figs. 24b and c). In contrast, if pollinators are obligate (Fig. 22a2), the system deterministically converges to the extinction equilibrium, regardless of changes in the conversion rate.



Fig. 19 Pairwise phase diagram of the system (1) with $d_A = 1.1$ and f = 0.16

In the scenario where both plants and pollinators are facultative (Fig. 22a3), a low conversion rate leads to the stable coexistence of plants, pollinators, and parasites (Figs. 25a and 26a). As the conversion rate increases, the system undergoes a supercritical Hopf bifurcation, destabilizing the coexistence equilibrium and giving rise to an oscillation. The bifurcation diagram reveals that the amplitude of the oscillation is not monotonic, but instead exhibits a wave-like pattern, which we have termed the wave-bow phenomenon. Phase portraits indicate that the wave-bow phenomenon is driven by complex periodic solutions and chaotic behavior. As the conversion rate crosses the supercritical Hopf bifurcation, the system sequentially transitions through a single-peaked periodic solution (Figs. 25b and 26b), a four-peaked periodic solution (Figs. 25c and 26c), and an eight-peaked periodic solution (Figs. 25d and 26d), eventually leading to chaos (Figs. 25e and 26e). With further increases in the conversion rate, the system passes through a sixteen-peaked periodic solution (Figs. 25f and 26f), an eight-peaked periodic solution (Figs. 25g and 26g), chaos (Figs. 25h and 26h), a four-peaked periodic solution (Figs. 25i and 26i), chaos (Figs. 25j and 26j), and a two-peaked periodic solution (Figs. 25k and 26k), ultimately converging to a single-peaked periodic solution (Figs. 251 and 261).

In the scenario where plants are facultative and pollinators are obligate (Fig. 22a4), a low conversion rate leads the system to converge to the plant-only equilibrium (Fig. 27a). As the conversion rate increases, the system transitions to a bistable state between the plant-only equilibrium and the plant-pollinator equilibrium (Fig. 27b). With further increases in the conversion rate, the system becomes bistable between the plant-only equilibrium and the coexistence equilibrium (Fig. 27c). When the conversion rate becomes sufficiently large, the system undergoes a subcritical Hopf bifurcation and deterministically converges to the plant-only equilibrium (Fig. 27d).

5.4 Impact of plant growth rate

In the scenario with facultative pollinators, a low plant growth rate leads to obligate mutualism for the plants (Fig. 28a1, red region). At sufficiently low plant growth rates, the system converges to the pollinator-parasite equilibrium (Fig. 29a). As the plant growth rate increases, the system undergoes a limit point bifurcation, resulting in bistability between the pollinator-parasite equilibrium and the coexistence equilibrium (Fig. 29b). With a further increase in the plant growth rate, a supercritical Hopf bifur-



Fig. 20 Pairwise phase diagram of the system (1) with $d_A = 1.1$ and f = 0.228

cation occurs, destabilizing the coexistence equilibrium, leading to bistability between the pollinator-parasite equilibrium and the non-trivial periodic solution (Fig. 29c). At sufficiently high plant growth rates, the plants transition from obligate to facultative mutualism, and the system reaches a state of coexistence between plants, pollinators, and parasites in periodic oscillations (Fig. 28a1, green region; Fig. 29d). Additionally, as the plant growth rate increases, the plant and parasite components in the coexistence equilibrium rise, while the pollinator levels remain unchanged. Meanwhile, the amplitude of the periodic solution gradually increases (Fig. 30b and c).

In the scenario where both the pollinators and plants are obligate (Fig. 28a2, red region), the system undergoes collapse at low plant growth rates (Fig. 31a). As the plant growth rate increases slightly, the plants shift to a facultative relationship (Fig. 28a2, green region), and the system converges to the plant-only equilibrium (Fig. 31b). With further increases in the plant growth rate, the system briefly tracks the plant-only equilibrium and the high-density plant-pollinator equilibrium before stabilizing at the low-density plant-pollinator equilibrium (Fig. 31c). When the plant growth rate becomes sufficiently high, the system generates a stable periodic solution characterized by a heteroclinic orbit connecting the plant-only equilibrium and the plant-pollinator equilibrium (Fig. 31d).

5.5 Impact of remaining parameters

In addition to the parameters previously discussed, we conduct bifurcation analyses on the remaining parameters of the system. Our findings reveal that the impact of these parameters on plant-pollinator-parasite interactions depends significantly on whether the plants and pollinators are facultative or obligate mutualists. The detailed results are summarized in Tables 2 and 3, and are briefly outlined below:

1. Variations in the pollination ratios provided by pollinators can lead to two types of bistability and induce both a supercritical Hopf bifurcation and a limit point bifurcation. Higher ratios may result in system instability. In the scenario where plants are obligate and pollinators are facultative (Fig. 32a1), low pollination ratios result in coexistence between pollinators and parasites, while intermediate ratios produce a limit point bifurcation, yielding bistability between the pollinator-parasite equilibrium and the coexistence equilibrium. When the pollination ratio is sufficiently high, a supercritical Hopf bifurcation occurs, leading to bistability between the pollinator-



parasite equilibrium and the nontrivial periodic solution. In the scenario where both plants and pollinators are facultative (Fig. 32a3), low pollination ratios allow stable coexistence of plants, pollinators, and parasites, whereas higher ratios lead to a supercritical Hopf bifurcation, causing periodic coexistence. For obligate pollinators, if the plants are also obligate, the system collapses (Fig. 32a2); however, if the plants are facultative (Fig. 32a4), the system converges to the plant-only equilibrium.

2. Variations in plant density dependence can lead to six types of bistability, one instance of tristability, and trigger a supercritical Hopf bifurcation, a subcritical Hopf bifurcation, and a limit point bifurcation. In the scenario where plants are obligate and pollinators are facultative (Fig. 33a1), low plant density dependence results in bistability between the pollinator-parasite equilibrium and the coexistence equilibrium. As plant density dependence increases, the system sequentially undergoes: (1) tristability among the pollinator-parasite equilibrium, the coexistence equilibrium, and the periodic solution; (2) bistability between the pollinator-parasite equilibrium and the periodic solution; (3) bistability between the pollinator-parasite equilibrium and the coexistence equilibrium. Sufficiently high plant density dependence causes the system to converge to the pollinator-parasite equilibrium. When both plants and pollinators are obligate (Fig. 33a2), low plant density dependence leads to bistability between the extinction equilibrium and the coexistence equilibrium, while high plant density dependence causes system collapse. In the scenario where both plants and pollinators are facultative (Fig. 33a3), low plant density dependence allows stable coexistence of plants, pollinators, and parasites at constant levels; intermediate values lead to bistability between the coexistence equilibrium and the periodic solution, followed by the periodic oscillation; high plant density dependence causes the system to converge to the coexistence equilibrium. When plants are facultative and pollinators are obligate (Fig. 33a4), low plant density dependence results in bistability between the plant-only



Fig. 22 Bifurcation diagram of the system (1) with varying ϵ . **a1** $d_A = 0.1$, f = 0.16; **a2** $d_A = 1.1$, f = 0.16; **a3** $d_A = 0.1$, f = 0.228; **a4** $d_A = 1.1$, f = 0.228. The blue and green dotted lines indicate sink and saddle, respectively. **H**^s₁ and **H**^c₁ denote supercritical and subcritical bifurcations, respectively. **LP** represents the limit point bifurcation (color figure online)



Fig. 23 Pairwise phase diagram of the system (1) with $d_A = 0.1$ and f = 0.16

equilibrium and the coexistence equilibrium, while high plant density dependence leads to the survival of plants only, with extinction of pollinators and parasites.

3. Variations in pollinator density dependence can lead to seven types of bistability, as well as a supercritical Hopf bifurcation and a subcritical Hopf bifurcation. In the scenario where plants are obligate and pollinators are facultative (Fig. 34a1), low pollinator density dependence results in a stable pollinator-parasite equilibrium. As the density dependence increases, the system sequentially exhibits bistability between the pollinator-parasite equilibrium and the periodic solution, then between the pollinator-only equilibrium and the coexistence equilibrium. Sufficiently high density dependence



Fig. 24 Time series of the system (1) with $d_A = 0.1$ and f = 0.16: **a** Stable coexistence equilibrium; **b**-**c** Stable periodic solution. Red, blue, and black lines represent *P*, *A*, and *M*, respectively (color figure online)



Fig. 25 Pairwise phase diagram of the system (1) with $d_A = 0.1$ and f = 0.228. In Fig. 25e, h, and j, the maximum Lyapunov exponents are 0.01044, 0.01049, and 0.01017, respectively

causes the system to converge to the pollinator-only equilibrium. When both plants and pollinators are obligate (Fig. 34a2), the system collapses. In the case where both plants and pollinators are facultative (Fig. 34a)), low pollinator density dependence leads to the periodic oscillation; intermediate values result in a stable coexistence equilibrium, followed by bistability between the coexistence equilibrium and the lowdensity plant-pollinator equilibrium, and then between high-density and low-density plant-pollinator equilibria. High density dependence causes the system to converge to the low-density plant-pollinator equilibrium. In the scenario where plants are facultative and pollinators are obligate (Fig. 34a4), low pollinator density dependence results in the stable plant-only equilibrium; intermediate values lead to bistability between the coexistence equilibrium and the plant-only equilibrium, and between the high-density plant-pollinator equilibrium and the plant-only equilibrium. High density dependence ultimately leads to the stable plant-only equilibrium.

4. Variations in the per-plant attack rate on rewards can lead to five types of bistability, one instance of tristability, and can induce a supercritical Hopf bifurcation, a subcritical Hopf bifurcation, and a limit point bifurcation. In the scenario where plants are obligate and pollinators are facultative (Fig. 35a1), a low attack rate stabilizes the pollinator-parasite equilibrium. As the attack rate increases, the system sequentially exhibits: (1) bistability between the pollinator-parasite equilibrium and the coexistence equilibrium; (2) bistability between the pollinator-parasite equilibrium and the periodic solution; (3) tristability among the pollinator-parasite equilibrium, the coexistence equilibrium, and the periodic solution. A sufficiently high attack rate leads to bistability between the coexistence equilibrium and the pollinator-parasite equilibrium. In the scenario where both plants and pollinators are obligate (Fig. 35a2), a low attack rate causes system collapse, while a high attack rate results in bistability between the coexistence equilibrium and the extinction equilibrium. When both plants and pollinators are facultative (Fig. 35a3), low and high attack rates cause the system to converge to the coexistence equilibrium. Intermediate attack rates sequentially lead to: (1) the periodic oscillation; (2) bistability between the periodic solution and the coexistence equilibrium. In the scenario where plants are facultative and pollinators are obligate (Fig. 35a4), a low attack rate stabilizes the plant-only equilibrium, while a high attack rate leads to bistability between the plant-only equilibrium and the coexistence equilibrium.

5. Variations in the handling time on rewards can lead to four types of bistability, a supercritical Hopf bifurcation, a subcritical Hopf bifurcation, and a limit point bifurcation. In the scenario where plants are obligate and pollinators are facultative (Fig. 36a1), low handling times result in bistability between the pollinator-parasite equilibrium and the periodic solution, while intermediate handling times lead to bistability between the pollinator-parasite equilibrium and the coexistence equilibrium; sufficiently large handling times stabilize the pollinator-parasite equilibrium. When both plants and pollinators are obligate (Fig. 36a2), the system collapses. In the case where both plants and pollinators are facultative (Fig. 36a3), low handling times lead to the periodic oscillation, whereas high handling times cause the system to converge to the coexistence equilibrium. For facultative plants with obligate pollinators (Fig. 36a4), low handling times stabilize the plant-only equilibrium; intermediate handling times sequentially lead to bistability between the plant-only equilibrium and the



Fig. 26 Time series of the system (1) with $d_A = 0.1$ and f = 0.228. The red shaded region highlights a cycle (color figure online)

coexistence equilibrium, and coexistence between the high-density plant-pollinator equilibrium and the plant-only equilibrium. High handling times ultimately stabilize the plant-only equilibrium.

6. Variations in the parasite reproduction rate can lead to seven types of bistability, three subcritical Hopf bifurcations, two supercritical bifurcations, and one limit point bifurcation. In the scenario where plants are obligate and pollinators are facultative (Fig. 37a1), low parasite reproduction rates result in the stable plant-pollinator equilibrium. As the parasite reproduction rate increases, the system sequentially transitions through: (1) the stable coexistence equilibrium; (2) the periodic oscillation; (3) bistability between the periodic solution and the pollinator-parasite equilibrium; (4) bistability between the coexistence equilibrium and the pollinator-parasite equilibrium. Sufficiently high parasite reproduction rates stabilize the pollinator-parasite



equilibrium. When both plants and pollinators are obligate (Fig. 37a2), low parasite reproduction rates lead to bistability between the plant-pollinator equilibrium and the extinction equilibrium, while intermediate rates result in bistability between the coexistence equilibrium and the extinction equilibrium; high parasite reproduction rates cause the system to collapse. In the scenario where both plants and pollinators are facultative (Fig. 37a3), low parasite reproduction rates cause the system to converge to the plant-pollinator equilibrium. Intermediate parasite reproduction rates sequentially lead to: (1) the stable coexistence equilibrium; (2) bistability between the coexistence equilibrium and the periodic solution; (3) the periodic oscillation. Sufficiently high parasite reproduction rates result in stable coexistence of plants, pollinators, and parasites. When plants are facultative and pollinators are obligate (Fig. 37a4), low parasite reproduction rates lead to bistability between the plant-pollinator equilibrium and the plant-only equilibrium. Intermediate parasite reproduction rates sequentially lead to: bistability between the coexistence equilibrium and the plant-only equilibrium; the stable plant-only equilibrium; and bistability between the coexistence equilibrium and the plant-only equilibrium again. High parasite reproduction rates result in the stable plant-only equilibrium.

7. Variations in the natural pollination ratio can lead to three types of bistability, as well as one supercritical bifurcation and one limit point bifurcation. In the scenario where pollinators are facultative (Fig. 38a1), low natural pollination ratios result in the stable pollinator-parasite equilibrium. Intermediate values sequentially lead to bistability between the coexistence equilibrium and the pollinator-parasite equilibrium, followed by bistability between the periodic solution and the pollinator-parasite equilibrium. Sufficiently high natural pollination ratios cause plants, pollinators, and parasites to persist in periodic oscillations. When pollinators are obligate (Fig. 38a2), low natural pollination ratios lead to system collapse. Intermediate values result in the



Fig. 28 Bifurcation diagram of the system (1) with varying b_P . **a1** $d_A = 0.1$; **a2** $d_A = 1.1$. The blue and green dotted lines indicate sink and saddle, respectively. \mathbf{H}_1^s denotes a supercritical bifurcation. LP represents the limit point bifurcation. In the red region, $r_P < 0$; in the green region, $r_P > 0$ (color figure online)

stable plant-only equilibrium, then the stable low-density plant-pollinator equilibrium, and eventually bistability between the low-density plant-pollinator equilibrium and the periodic solution. High natural pollination proportions lead to periodic oscillations.

8. Variations in the reproduction success rate can cause two types of bistability, one supercritical bifurcation, and one limit point bifurcation. With facultative pollinators (Fig. 39a1), low reproduction success rates stabilize the pollinator-parasite equilibrium. Intermediate rates lead to bistability between the coexistence equilibrium and the pollinator-parasite equilibrium, followed by the stable coexistence equilibrium. High reproduction success rates result in periodic oscillations among plants, pollinators, and parasites. In the obligate pollinator scenario (Fig. 39a2), low reproduction success rates cause system collapse. Intermediate rates sequentially stabilize the plant-only equilibrium and the low-density plant-pollinator equilibrium, followed by bistability between this equilibrium and the periodic solution. High reproduction success rates rates rates sequentially stabilize the plant-only equilibrium and the periodic solution. High reproduction success rates rates rates rates solution.

9. Variations in the plant mortality rate can lead to three types of bistability, one supercritical bifurcation, and one limit point bifurcation. For facultative pollinators (Fig. 40a1), low plant mortality rates result in periodic oscillations. Intermediate rates lead to bistability between the periodic solution and the pollinator-parasite equilibrium, then to bistability between the coexistence equilibrium and the pollinator-parasite equilibrium. High plant mortality rates cause plant extinction, with pollinators and parasites surviving at stable densities. When pollinators are obligate (Fig. 40a2), low plant mortality rates produce periodic oscillations. Intermediate rates stabilize the plant-pollinator equilibrium and then the plant-only equilibrium. High mortality rates lead to system collapse.

10. Variations in the pollinator birth rate can induce four types of bistability and one supercritical bifurcation. In the facultative plant scenario (Fig. 41a1), low birth rates stabilize the plant-only equilibrium. Intermediate rates sequentially stabilize the plant-pollinator equilibrium, lead to bistability between this equilibrium and the periodic solution, and then cause periodic oscillations. High birth rates result in constant-level coexistence. With obligate pollinators (Fig. 41a2), low birth rates cause system



collapse. Intermediate rates stabilize the pollinator-only equilibrium and then lead to bistability between this equilibrium and the periodic solution, followed by bistability between the periodic solution and the pollinator-parasite equilibrium. High birth rates result in bistability between the coexistence equilibrium and the pollinator-parasite equilibrium.

11. Variations in the pollinator mortality rate can lead to three types of bistability. For facultative plants (Fig. 42a1), low mortality rates cause periodic oscillations. Intermediate rates lead to bistability between the periodic solution and the plantpollinator equilibrium, eventually stabilizing the plant-pollinator equilibrium. High mortality rates stabilize the plant-only equilibrium. In the obligate pollinator scenario (Fig. 42a2), low mortality rates result in bistability between the periodic solution and the pollinator-parasite equilibrium. Intermediate rates lead to bistability between the periodic solution and the pollinator-only equilibrium, followed by stabilization of the pollinator-only equilibrium. High mortality rates cause system collapse.

6 Conclusion

The mutualistic interactions between plants and pollinators are fundamental to ecosystem stability and biodiversity. While extensive research has explored the dynamics of plant-pollinator interactions and their ecological impacts, the role of parasites within these systems remains underexplored. This study addresses this gap by constructing and analyzing a tripartite plant-pollinator-parasite system, systematically revealing how parasites can significantly alter the stability and dynamic behavior of plantpollinator interactions through complex feedback mechanisms. Our work extends the modeling framework proposed by Hale et al. (2022), providing new perspectives for a



Fig. 30 Time series of the system (1) with $d_A = 0.1$. **a** Stable coexistence equilibrium; **b–c** Stable periodic solution. Red, blue, and black lines represent *P*, *A*, and *M*, respectively (color figure online)

comprehensive understanding of the complexities inherent in plant-pollinator-parasite interactions. Notably, we introduce three novel concepts-the *left bow phenomenon*, *right bow phenomenon*, and *wave bow phenomenon*-to characterize the amplitude variations of oscillations induced by parameter bifurcations, thereby complementing the existing *bubble phenomenon*. These concepts are broadly applicable for characterizing parameter-induced bifurcations in ecological models.

The theoretical analysis encompasses the global dynamics of the plant-pollinator subsystem and the pollinator-parasite subsystem, as well as the local dynamics of the complete plant-pollinator-parasite system. The plant-pollinator subsystem exhibits only equilibrium dynamics, indicating the absence of cycles or chaos. Specifically, when there is a unique local equilibrium, it is globally asymptotically stable. Additionally, this subsystem may display four types of bistability, depending on whether plants and pollinators are obligate or facultative mutualists. This finding not only corroborates the numerical results of Hale et al. (2022) but also elucidates how plant and pollinator populations can remain stable or exhibit multistability under different ecological conditions. Similarly, the pollinator-parasite subsystem demonstrates equilibrium dynamics. Our results indicate that when pollinators are facultative and their intrinsic growth rates are limited, parasites become extinct due to unfavorable host conditions. Conversely, when the intrinsic growth rates of pollinators are sufficiently high, pollinators and parasites can coexist. This outcome underscores the critical role of pollinator population density in maintaining parasite dynamics and reflects the significant impact of pollinator growth rates on system stability.

In the complete plant-pollinator-parasite system, a detailed analysis of boundary dynamics reveals both similarities and differences compared to the subsystems. Similarities include the local stability conditions for plant-only and extinction equilibria. Differences emerge in the influence of pollinator density on the stability of the plant-pollinator equilibrium and the stability conditions for pollinator-only and pollinator-parasite equilibria. Furthermore, the existence and stability conditions of coexistence equilibria are elucidated, significantly influenced by the characteristics of plants and pollinators-such as whether plants are specialists and the intrinsic growth rates of pollinators. By integrating boundary dynamics analysis with coexistence equilibrium analysis, we demonstrate that parasites can induce multistability and complex dynamic behaviors throughout the system via intricate feedback mechanisms.

Table 2 Impact of parameters	ϕ , s_P , s_A , a , h and k on plant-pollinato	or-parasite dynamics	
Case	Varying parameter	Steady state	Figures
${}^{*}r_{A} > 0, r_{P} < 0$	¢	$E_{0AM} \xrightarrow{\text{LP}} \begin{cases} E_2^* & \text{H}_1^{\text{s}} \\ E_{0AM} & \end{cases} \\ E_{0AM} & E_{0AM} \end{cases}$	Fig. 32a1
	ds	$\begin{cases} E_2^* \\ E_{0AM}^* \end{pmatrix} \xrightarrow{\left\{ \begin{array}{cc} E_2^* \\ \text{Cycle} \end{array} \right\}} \begin{cases} \text{Cycle} \\ \text{Cycle} \end{array} \xrightarrow{\left \begin{array}{cc} H_1^* \\ E_{0AM} \end{array} \right } \begin{cases} \text{Cycle} \\ E_{0AM} \end{array} \xrightarrow{\left \begin{array}{cc} E_2^* \\ E_{0AM} \end{array} \right } \\ \hline \end{array} \xrightarrow{\left \begin{array}{cc} E_{0AM} \end{array} \right } \end{cases} \xrightarrow{\left \begin{array}{cc} E_2^* \\ E_{0AM} \end{array} \right } \end{cases}$	Fig. 33al
	<i>s</i> .A	$E_{0AM} \rightarrow \begin{cases} \text{Cycle} & \rightarrow \end{cases} \begin{cases} \text{Cycle} & \frac{\text{H}_{3}^{*}}{E_{0A0}} & \rightarrow \end{cases} \begin{cases} E_{2}^{*} & \rightarrow E_{0A0} \end{cases} \end{cases}$	Fig. 34a1
	a	$E_{0AM} \xrightarrow{\text{LP}} \left\{ \begin{array}{ccc} E_2^* & \text{H}_3^* \\ E_0^* & \xrightarrow{\text{H}_3^*} \end{array} \right\} \left[\begin{array}{ccc} \text{Cycle} & \text{H}_1^* \\ E_{0AM} & \xrightarrow{\text{Cycle}} \end{array} \right] \left\{ \begin{array}{ccc} E_2^* \\ E_{0AM} & \xrightarrow{\text{Cycle}} \end{array} \right\} \left[\begin{array}{ccc} E_2^* \\ E_{0AM} & \xrightarrow{\text{Cycle}} \end{array} \right]$	Fig. 35al
	ų	$\begin{cases} Cycle & \frac{H_1^s}{\longrightarrow} \begin{cases} E_2^* & \frac{LP}{B0AM} \end{cases} \\ E_{0AM} & & \\ \end{cases} \end{cases} \xrightarrow{E_{0AM}} \end{cases}$	Fig. 36a1
	ķ	$E_{PA0}^{2} \to E_{2}^{*} \xrightarrow{\mathrm{H}_{3}^{*}} \mathrm{Cycle} \to \begin{cases} \mathrm{Cycle} & \frac{\mathrm{H}_{5}^{*}}{E_{0AM}} \end{cases} \begin{cases} E_{2}^{*} & \frac{\mathrm{LP}}{E_{0AM}} \\ E_{0AM} & & \end{cases} \end{cases}$	Fig. 37a1
$r_A < 0, r_P < 0$	φ	$E_{000} \xrightarrow{\text{LP}} E_{000}$	Fig. 32 a2
	s_P	$\begin{cases} E_2^* & \text{H}_1^{\text{r}}, \text{LP} \\ E_{000} & E_{000} \end{cases}$	Fig. 33 a2
	$_{SA}$	E_{000}	Fig. 34a2
	a	$E_{000} \xrightarrow{\text{LP, H}_{C}} \begin{cases} E_{2}^{*} \\ E_{000} \end{cases}$	Fig. 35 a2
	ų	E_{000}	Fig. 36a2
	ķ	$\begin{cases} E_{PA0}^{2} & \rightarrow \end{cases} \begin{cases} E_{PA0}^{2} & H_{1}^{c}, LP \\ E_{000} & \rightarrow \end{cases} E_{000} \end{cases} \xrightarrow{H_{0}^{c}, LP} E_{000} \end{cases}$	Fig. 37a2

Case	Varying parameter	Steady state	Figures
$r_A > 0, r_P > 0$	φ	$E_2^* \xrightarrow{\mathrm{H}_1^s} \mathrm{Cycle}$	Fig. 32a3
	SP	$E_2^* ightarrow \left\{ egin{matrix} E_2^* & H_1^c \ C_2 & H_2^c \ Cycle & H_2^s \ Cycle & H_2^s \ \end{array} ight.$	Fig. 33a3
	SA	$\operatorname{Cycle} \stackrel{\operatorname{H}^{\circ}_{1}}{\longrightarrow} E_{2}^{\ast} \rightarrow \begin{cases} E_{2}^{\ast} \\ E_{PA0} \\ E_{PA0} \end{cases} \rightarrow \begin{cases} E_{PA0}^{3} \\ E_{PA0} \\ E_{PA0} \\ \end{cases} \rightarrow E_{PA0}^{1} \end{cases}$	Fig. 34a3
	a	$E_2^* \xrightarrow{\mathrm{H}_2^*} \mathrm{Cycle} \xrightarrow{\mathrm{H}_2^*} \left\{ \begin{array}{c} \mathrm{Cycle} \\ E_2^* \end{array} \rightarrow E_2^* \end{array} \right.$	Fig. 35a3
	ų	$\operatorname{Cycle} \xrightarrow{\operatorname{H}_1^s} E_2^*$	Fig. 36a3
	K	$E_{PA0}^2 ightarrow E_2^* ightarrow \begin{cases} Cycle & H_1^c \\ E_3^c & \longrightarrow \end{cases} Cycle & \stackrel{H_1^s}{\longrightarrow} E_2^* \end{cases}$	Fig. 37a3
$r_A < 0, r_P > 0$	φ	E_{P00}	Fig. 32a4
	s_P	$\begin{cases} E_2^* & \operatorname{H}_1^{c} \\ E_{P00} & E_{P00} \end{cases}$	Fig. 33a4
	SA	$E_{P00} \xrightarrow{\mathrm{H}_{1}^{c}} \left\{ E_{2}^{*} \rightarrow \left\{ E_{P00}^{2} \rightarrow \left\{ E_{P00}^{2} \rightarrow E_{P00} \right\} \right\} \right\}$	Fig. 34a4
	a	$E_{P00} \xrightarrow{\mathrm{H}_{\mathrm{C}}^{\mathrm{c}}} \left\{ E_{2}^{\mathrm{s}} \left\{ E_{P00}^{\mathrm{s}} \right\} \right\}$	Fig. 35a4
	h	$E_{P00} \xrightarrow{\mathrm{H}^{c}_{1}} \left\{ E_{2}^{E} \left\{ E_{P00}^{2} \rightarrow \left\{ E_{P00}^{2} \rightarrow E_{P00} \rightarrow E_{P00} \right\} \right\}$	Fig. 36a4
	k	$ \begin{cases} E_{PA0}^2 & \longrightarrow \\ E_{P00} & \rightarrow \\ \end{cases} \begin{cases} E_{P00}^* & \xrightarrow{H_1^c} E_{P00} \xrightarrow{H_2^c} \\ E_{P00} & \xrightarrow{H_2^c} \\ \end{array} \end{cases} \begin{cases} E_2^* & \xrightarrow{H_3^c} E_{P00} \\ \end{array} \end{cases} $	Fig. 37a4



Through bifurcation analyses, we reveal the complex dynamic behaviors of the plant-pollinator-parasite system under various biological scenarios. When pollinators are facultative, the system exhibits richer dynamical phenomena, including multiple bistable and tristable states, supercritical and subcritical Hopf bifurcations, saddle-node bifurcations, chaos, and complex periodic solutions. These dynamics indicate greater system resilience and the ability to maintain various stable states or periodic oscillations within specific parameter ranges. In contrast, when pollinators are obligate, the system is more prone to collapse. Notably, we introduce and define three novel dynamic phenomena: the *left bow phenomenon, right bow phenomenon*, and *wave bow phenomenon*. These concepts describe variations in oscillation amplitudes resulting from parameter bifurcations, complementing the existing *bubble phenomenon*. Specifically:

- Left Bow Phenomenon: Variations in parasite mortality rates induce a gradual increase in the amplitude of oscillations before an abrupt disappearance as the parameter crosses a bifurcation point from the left.
- *Right Bow Phenomenon:* Similar to the left bow, but the amplitude gradually increases as the parameter crosses the bifurcation point from the right.
- Wave Bow Phenomenon: Alterations in the conversion rate between parasite states trigger fluctuations in oscillation amplitudes, transitioning from unimodal to multimodal periodic solutions, followed by chaotic states, and reverting to multimodal and single-peaked periodic solutions. This mechanism highlights the system's high sensitivity to changes in the conversion rate.

Additionally, variations in plant birth rates lead to the formation of heteroclinic orbits, facilitating transitions between different equilibrium states and demonstrating complex orbital connections within the system. Comprehensive bifurcation analyses of all

key biological parameters-including pollination ratios, pollinator mortality rates, and density dependence coefficients-reveal that these parameters influence the system's dynamic behavior through various bifurcation mechanisms. The interactions among these parameters determine whether the system remains stable, exhibits periodic oscillations, or transitions into chaotic regimes. Collectively, these findings provide a robust theoretical framework for understanding the intricate dynamics of plant-pollinatorparasite systems. They emphasize the necessity of considering multiple interacting parameters and nonlinear phenomena in ecological management strategies to enhance ecosystem stability and resilience.

However, this study identifies several limitations that warrant further exploration:

- Limited Interaction Scope: The model focuses solely on the basic interactions between plants, pollinators, and parasites, neglecting other key interactions such as competition and predation. For instance, competition among plant species or predatory behavior among pollinators could significantly influence system dynamics (Tilman 1982). Future research should incorporate a broader range of interactions to better capture the complexity of real ecological systems (Hastings 2013).
- Parameter Uncertainty: Some parameters are based on assumptions or literature values, introducing uncertainty when applying them to real ecosystems where parameters may vary significantly. Empirical research is needed to obtain more accurate estimates and improve model predictions.
- Spatial Homogeneity Assumption: The study uses a non-spatial model, overlooking the role of spatial heterogeneity and migration. Including spatial factors-such as migration rates or spatial distribution models-could provide valuable insights into the effects of spatial structure on multistability and oscillations (Cantrell and Cosner 2004).
- Environmental Factors: Environmental variables like climate change and habitat fragmentation are not fully considered. Future studies should integrate these factors to assess their overall impact on the dynamics of plant-pollinator-parasite systems, offering a more comprehensive understanding of external environmental pressures on ecosystem stability.

In conclusion, this study significantly enhances our understanding of how parasites influence plant-pollinator interactions, unveiling complex dynamics that have critical implications for ecosystem management and conservation. By advancing our understanding of these intricate relationships, we lay the groundwork for future research that can inform strategies to preserve biodiversity and ecosystem functionality in the face of environmental change.

7 Appendix

A Proof of Lemma 1

Proof Considering the system (2), we observe that $P'|_{P=0} = 0, A'|_{A=0} = 0$. By invoking Theorem A.4 in Ref. (Thieme 2018), we conclude that the system (2) is positively invariant within the region $(P(t), A(t)) \in \mathbb{R}^2_+$. By simplifying the differential

CaseVarying parameterSteady state $r_A > 0$ f E_{0AM} $\frac{1}{E} \begin{bmatrix} E_{2}^{*} \\ E_{0AM} \end{bmatrix} \begin{bmatrix} Cycle \\ E_{0AM} \end{bmatrix} \begin{bmatrix} E_{2}^{*} \\ E_{0AM} \end{bmatrix} \begin{bmatrix} Cycle \\ E_{0AM} \end{bmatrix} \begin{bmatrix} E_{2}^{*} \\ E_{0AM} \end{bmatrix} \begin{bmatrix} E_{0AM} \\ E_{0AM} \end{bmatrix} \begin{bmatrix} E_{2}^{*} \\ E_{0AM} \end{bmatrix} \begin{bmatrix} E_{2}^{*} \\ E_{2}^{*} \\ E_{2}^{*} \\ E_{2}^{*} \end{bmatrix} \begin{bmatrix} E_{2}^{*} \\ E_{2}^{*} \\ E_{2}^{*} \\ E_{2}^{*} \end{bmatrix} \begin{bmatrix} E_{2}^{*} \\ E_{2}^{*} \\ E_{2}^{*} \\ E_{2}^{*} \end{bmatrix} \begin{bmatrix} E_{2}^{*} \\ E_{2}^{*} \\ E_{2}^{*} \\ E_{2}^{*} \\ E_{2}^{*} \end{bmatrix} \begin{bmatrix} E_{2}^{*} \\ E_{2}^{*} \\ E_{2}^{*} \\ E_{2}^{*} \end{bmatrix} \begin{bmatrix} E_{2}^{*} \\ E_{2}^{*} \\ E_{2}^{*} \\ E_{2}^{*} \end{bmatrix} \begin{bmatrix} E_{2}^{*} \\ E_{2}^{*} \\ E_{2}^{*} \\ E_{2}^{*} \end{bmatrix} \begin{bmatrix} E_{2}^{*} \\ E_{2}^{*} \\ E_{2}^{*} \\ E_{2}^{*} \end{bmatrix} \begin{bmatrix} E_{2}^{*} \\ E_{2}^{*} \\ E_{2}^{*} \\ E_{2}^{*} \end{bmatrix} \begin{bmatrix} E_{2}^{*} \\ E_{2}^{*} \\ E_{2}^{*} \\ E_{2}^{*} \\ E_{2}^{*} \\ E_{2}^{*} \end{bmatrix} \begin{bmatrix} E_{2}^{*} \\ E$	Table 3 Impact of parameter.others fixed, causes the system	s f, g, dp , b_A and d_A on plant-pollinaton n to transition from one stable state $E_1^{\#}$ to	-parasite dynamics. The notation $E_1^{\pm} \xrightarrow{LP} E_2^{\pm}$ indicates that varying one parameter, wh another stable state E_2^{\pm} via a limit point bifurcation	nile keeping
$\begin{aligned} r_A > 0 \qquad f \qquad E_{0AM} \stackrel{LP}{\longrightarrow} \left\{ \begin{array}{lll} E_{0AM}^* & \stackrel{LP}{\longrightarrow} \left\{ \begin{array}{ll} E_{0AM}^* & \stackrel{LP}{\longrightarrow} \left\{ \begin{array}{lll} E_{0AM}^* & \stackrel{LP}{\longrightarrow} \left\{ \begin{array}{ll} E_{0A}^* & \stackrel{LP}{\longrightarrow} \left\{ \begin{array}{ll} E_{0A}^* & \stackrel{LP}{\longrightarrow} \left\{ \begin{array}{ll} E_{0A}^* & \stackrel{LP}{\longrightarrow} \left\{ \left\{ \begin{array}{ll} E_{0A}^* & \stackrel{LP}{\longrightarrow} \left\{ \left\{ \begin{array}{ll} E_{0A}^* & \stackrel{LP}{\longrightarrow} \left\{ \left\{ \left\{ \begin{array}{ll} E_{0A}^* & \stackrel{LP}{\longrightarrow} \left\{ \left\{ \left\{ \right\{ E_{0A}^* & \stackrel{LP}{\longrightarrow} \left\{ \left\{ \left\{ \right\{ E_{0A}^* & \stackrel{LP}{\longrightarrow} \left\{ \left\{ \left\{ \left\{ \left\{ E_{0A}^* & \stackrel{LP}{\longrightarrow} \left\{ \left\{ E_{0A}^* & \stackrel{LP}{\longrightarrow} \left\{ E_{0A}^* & \stackrel{LP}{\longrightarrow} \left\{ E_{0A}^* & \stackrel{LP}{\oplus$	Case	Varying parameter	Steady state	Figures
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	$r_A > 0$	ſ	$E_{0AM} \xrightarrow{\text{LP}} \left\{ \begin{array}{cc} E_{2}^{*} & H_{1}^{s} \\ E_{0AM} & \longrightarrow \end{array} \right\} \left\{ \begin{array}{cc} \text{Cycle} & r_{P=0} \\ E_{0AM} & \longrightarrow \end{array} \right\} Cycle$	Fig. 38a1
$\begin{array}{llllllllllllllllllllllllllllllllllll$		00	$E_{0AM} \xrightarrow{\text{LP}} \begin{cases} E_2^* & \xrightarrow{r_P=0} E_2^* \xrightarrow{H_1^s} \text{Cycle} \\ E_{0AM} & \xrightarrow{r_P=0} E_2^* \xrightarrow{H_2^s} \text{Cycle} \end{cases}$	Fig. 39a1
$r_{A} < 0 \qquad f \qquad E_{000} \xrightarrow{IP} r_{P=0} \to E_{PA0} \rightarrow E_{PA0} \rightarrow \begin{bmatrix} Cycle \\ E_{PA0}^{1} \rightarrow Cycle \\ E_{PA0}^{1} \rightarrow Cycle \\ dp \qquad E_{000} \xrightarrow{rP=0} E_{P00} \rightarrow E_{PA0} \rightarrow \begin{bmatrix} Cycle \\ E_{PA0}^{1} \rightarrow Cycle \\ E_{PA0}^{1} \rightarrow E_{PA0} \rightarrow E_{P00} \rightarrow E_{000} \\ E_{PA0} \rightarrow E_{PA0} \rightarrow E_{P00} \rightarrow E_{000} \\ E_{PA0} \rightarrow E_{PA0} \rightarrow E_{P00} \rightarrow E_{000} \\ dA \qquad Cycle \rightarrow \begin{bmatrix} E_{PA0} & \Delta E_{PA0} \rightarrow E_{P00} \rightarrow E_{000} \\ Cycle & \Delta E_{PA0} \rightarrow E_{PA0} \rightarrow E_{P00} \rightarrow E_{P00} \\ E_{PA0} \rightarrow E_{PA0} \rightarrow E_{P00} \rightarrow E_{P00} \\ E_{PA0} \rightarrow E_{PA0} \rightarrow E_{P00} \rightarrow E_{P00} \\ E_{PA0} \rightarrow E_{P00} \rightarrow E_{P00} \rightarrow E_{P00} \\ E_{PA0} \rightarrow E_{PA0} \rightarrow E_{P00} \rightarrow E_{P0} \rightarrow E_{P00} \rightarrow E_{P0} \rightarrow E_{P0} \rightarrow E_{P0} \rightarrow E_{P0} \rightarrow E_{P0} \rightarrow E_$		d_P	$Cycle \xrightarrow{r_P=0} \begin{cases} Cycle & H_1^s \\ E_{0AM} & \end{pmatrix} \begin{cases} E_2^* & \xrightarrow{LP} \\ E_{0AM} & \end{pmatrix} \xrightarrow{E_{0AM}} $	Fig. 40a1
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	$r_A < 0$	f	$E_{000} \xrightarrow{\text{LP}, r_{P=0}} E_{P00} \to E_{PA0}^{1} \to \begin{cases} \text{Cycle} \\ E_{PA0}^{1} \end{cases} \to \text{Cycle} \end{cases}$	Fig. 38 a2
$\begin{array}{cccc} dp & & \\ r_P > 0 & & b_A & \\ r_P > 0 & & b_A & \\ r_P > 0 & & b_A & \\ & & \\ cycle \rightarrow \begin{cases} E_{PA0}^{1} \rightarrow E_{PA0} \rightarrow E_{P00} \rightarrow E_{000} \rightarrow E_{00} \rightarrow E_{00}$		50	$E_{000} \xrightarrow{r_P=0} E_{P00} \rightarrow E_{PA0}^1 \rightarrow \begin{cases} Cycle \\ E_{PA0}^1 \end{pmatrix} \rightarrow Cycle $	Fig. 39 a2
$r_{P} > 0 \qquad b_{A} \qquad E_{P00} \xrightarrow{r_{A}=0} E_{PA0} \rightarrow \begin{cases} E_{PA0}^{1} \rightarrow Cycle \xrightarrow{H_{2}^{1}} E_{2}^{*} \\ Cycle \rightarrow E_{PA0} \rightarrow Cycle \xrightarrow{H_{2}^{1}} E_{2}^{*} \end{cases}$ $d_{A} \qquad Cycle \rightarrow \begin{cases} Cycle \rightarrow E_{PA0}^{1} \rightarrow E_{PA0} \xrightarrow{r_{A}=0} E_{P00} \\ E_{PA0} \rightarrow E_{PA0} \rightarrow E_{PA0} \rightarrow E_{PA0} \rightarrow E_{PA0} \end{cases}$ $d_{A} \qquad Cycle \rightarrow \begin{cases} Cycle \rightarrow E_{PA0} \rightarrow E_{PA0} \xrightarrow{H_{2}^{1}} E_{2}^{*} \\ E_{0A0} \rightarrow E_{0A0} \rightarrow$		d_P	$ ext{Cycle} ightarrow \begin{cases} ext{Cycle} & \ \ \ \ \ \ \ \ \ \ \ \ \ \ \ \ \ \ $	Fig. 40a2
$d_A \qquad Cycle \rightarrow \begin{cases} Cycle \ = & F_{PA0} \ E_{PA0} \ \to & F_{PA0} \ E_{PA0} \ \to & F_{PA0} \ E_{PA0} \ \to & F_{PA0} \end{cases}$ $r_P < 0 \qquad b_A \qquad E_{000} \ \frac{r_A = 0}{2} \ E_{0A0} \rightarrow \begin{cases} Cycle \ = & F_{PA0} \ E_{0A0} \ \to & F_{PA0} \ E_{0AM} \ \to & F_{0A0} \ E_{0AM} \ \to & F_{0A0} \ E_{0AM} \ E_{0AM} \ E_{0AM} \ \to & F_{0A0} \ E_{0AM} \ E_{0AM} \ \to & F_{0A0} \ E_{0AM} \ E_{0AM} \ E_{0AM} \ \to & F_{0A0} \ E_{0AM} \ E_{0AM} \ \to & F_{0A0} \ E_{0AM} \ \to & F_{0A0} \ E_{0AM} \ E_{0AM} \ \to & F_{0A0} \ E_{0AM} \ E_{0AM} \ E_{0AM} \ E_{0AM} \ \to & F_{0A0} \ E_{0AM} \ E_{0AM} \ E_{0AM} \ \to & F_{0AM} \ E_{0AM} \ E_{0AM} \ \to & F_{0AM} \ E_{0AM} \ E_{0AM} \ E_{0AM} \ \to & F_{0AM} \ E_{0AM} \ E_{0AM} \ E_{0AM} \ \to & F_{0AM} \ E_{0AM} \ E_{0AM} \ \to & F_{0AM} \ E_{0AM} \ E_{0AM} \ E_{0AM} \ \to & F_{0AM} \ E_{0AM} \ E_{0AM} \ E_{0AM} \ \to & F_{0AM} \ E_{0AM} \ E_{0AM} \ \to & F_{0AM} \ E_{0AM} \ E_{0AM} \ E_{0AM} \ \to & F_{0AM} \ E_{0AM} \ E_{0$	$r_P > 0$	b_A	$E_{P00} \xrightarrow{r_A=0} E_{PA0}^1 \rightarrow \begin{cases} E_{PA0}^1 \\ Cycle \end{cases} \rightarrow Cycle \xrightarrow{H_1^s} E_2^* \end{cases}$	Fig. 41a1
$r_{P} < 0 \qquad b_{A} \qquad E_{000} \xrightarrow{r_{A}=0} E_{0A0} \rightarrow \begin{cases} Cycle & \rightarrow \\ E_{0A0} & \rightarrow \end{cases} \begin{cases} Cycle & \rightarrow \\ E_{0A0} & \rightarrow \end{cases} \begin{cases} E_{0A0} & \rightarrow \\ E_{0A$		d_A	$\text{Cycle} \rightarrow \begin{cases} \text{Cycle} \\ E_{PA0} \\ E_{PA0} \end{cases} \xrightarrow{r_A = 0} E_{P00} \end{cases}$	Fig. 42a1
$d_A \qquad \begin{cases} Cycle \ \to \ E_{0AB} \ \to \ \to \ \to \ \to \ \ \to \ \ \to \ \to \ \to \ $	$r_P < 0$	b_A	$E_{000} \xrightarrow{r_A = 0} E_{0A0} \rightarrow \begin{cases} Cycle \\ E_{0A0} \end{cases} \begin{cases} Cycle \\ E_{0AM} \end{cases} \begin{cases} E_2^* \\ E_{0AM} \end{cases}$	Fig. 41a2
		d_A	$\begin{cases} Cycle \\ E_{0AM} \\ \end{bmatrix} \begin{cases} Cycle \\ E_{0A0} \\ \end{bmatrix} E_{0A0} \xrightarrow{r_A=0} E_{000} \end{cases}$	Fig. 42a2

$$\begin{aligned} \frac{dP}{dt} &= P\left[b_P\left(f + \phi \frac{aAP}{1 + ahP + aAP}\right)g - s_PP - d_P\right] \\ &\leq P\left[b_Pg\left(f + \phi\right) - s_PP - d_P\right] \\ &= P\left[b_Pg\left(f + \phi\right) - d_P\right]\left(1 - \frac{P}{\frac{b_Pg(f + \phi) - d_P}{s_P}}\right), \end{aligned}$$

which implies

$$\limsup_{t \to +\infty} P(t) \le \frac{b_P g(f + \phi) - d_P}{s_P}.$$

Similarly, we obtain

$$\limsup_{t \to +\infty} A(t) \le \frac{b_A + \frac{\epsilon}{h} - d_A}{s_A}.$$

This concludes the proof of Lemma 1.

B Supplementary bifurcation diagrams

See Figs. 32, 33, 34, 35, 36, 37, 38, 39, 40, 41, 42.



Fig. 32 Bifurcation diagram of the system (1) with varying ϕ . **a1** $d_A = 0.1$, f = 0.16; **a2** $d_A = 1.1$, f = 0.16; **a3** $d_A = 0.1$, f = 0.228; **a4** $d_A = 1.1$, f = 0.228. The blue and green dotted lines indicate sink and saddle, respectively. **H**₁^s denotes a supercritical bifurcation, while **LP** represents the limit point bifurcation (color figure online)



Fig. 33 Bifurcation diagram of the system (1) with varying s_P . **a1** $d_A = 0.1$, f = 0.16; **a2** Case $d_A = 1.1$, f = 0.16; **a3** $d_A = 0.1$, f = 0.228; **a4** $d_A = 1.1$, f = 0.228. The blue and green dotted lines indicate sink and saddle, respectively. **H**^S₁ and **H**^C₁ denote supercritical and subcritical bifurcations, respectively. **LP** represents the limit point bifurcation (color figure online)



Fig. 34 Bifurcation diagram of the system (1) with varying s_A . **a1** $d_A = 0.1$, f = 0.16; **a2** $d_A = 1.1$, f = 0.16; **a3** $d_A = 0.1$, f = 0.228; **a4** $d_A = 1.1$, f = 0.228. The blue and green dotted lines indicate sink and saddle, respectively. **H**^s₁ and **H**^c₁ denote supercritical and subcritical bifurcations, respectively. **LP** represents the limit point bifurcation (color figure online)



Fig. 35 Bifurcation diagram of the system (1) with varying *a*. **a1** $d_A = 0.1$, f = 0.16; **a2** $d_A = 1.1$, f = 0.16; **a3** $d_A = 0.1$, f = 0.228; (a4) $d_A = 1.1$, f = 0.228. The blue and green dotted lines indicate sink and saddle, respectively. **H**^S₁ and **H**^C₁ denote supercritical and subcritical bifurcations, respectively. **LP** represents the limit point bifurcation (color figure online)



Fig. 36 Bifurcation diagram of the system (1) with varying *h*. **a1** $d_A = 0.1$, f = 0.16; **a2** $d_A = 1.1$, f = 0.16; **a3** $d_A = 0.1$, f = 0.228; **a4** $d_A = 1.1$, f = 0.228. The blue and green dotted lines indicate sink and saddle, respectively. **H**^s₁ and **H**^c₁ denote supercritical and subcritical bifurcations, respectively. **LP** represents the limit point bifurcation (color figure online)



Fig. 37 Bifurcation diagram of the system (1) with varying k. **a1** $d_A = 0.1$, f = 0.16; **a2** $d_A = 1.1$, f = 0.16; **a3** $d_A = 0.1$, f = 0.228; **a4** $d_A = 1.1$, f = 0.228. **H**^S₁ and **H**^C₁ denote supercritical and subcritical bifurcations, respectively. **LP** represents the limit point bifurcation



Fig. 38 Bifurcation diagram of the system (1) with varying f. **a1** $d_A = 0.1$; **a2** $d_A = 1.1$. The blue and green dotted lines indicate sink and saddle, respectively. \mathbf{H}_1^s denotes a supercritical bifurcation. LP represents the limit point bifurcation. In the red region, $r_P < 0$; in the green region, $r_P > 0$ (color figure online)



Fig. 39 Bifurcation diagram of the system (1) with varying g. **a1** $d_A = 0.1$; **a2** $d_A = 1.1$. The blue and green dotted lines indicate sink and saddle, respectively. **H**_1^s denotes a supercritical bifurcation. **LP** represents the limit point bifurcation. In the red region, $r_P < 0$; in the green region, $r_P > 0$ (color figure online)



Fig. 40 Bifurcation diagram of the system (1) with varying d_P . **a1** $d_A = 0.1$; **a2** $d_A = 1.1$. The blue and green dotted lines indicate sink and saddle, respectively. **H**_1^s denotes a supercritical bifurcation. **LP** represents the limit point bifurcation. In the red region, $r_P < 0$; in the green region, $r_P > 0$ (color figure online)



Fig. 41 Bifurcation diagram of the system (1) with varying b_A . **a1** f = 0.228; **a2** f = 0.16. The blue and green dotted lines indicate sink and saddle, respectively. **H**^S₁ denotes a supercritical bifurcation. In the red region, $r_A < 0$; in the green region, $r_A > 0$ (color figure online)



Fig. 42 Bifurcation diagram of the system (1) with varying d_A . **a1** f = 0.228; **a2** f = 0.16. The blue and green dotted lines indicate sink and saddle, respectively. In the red region, $r_A < 0$; in the green region, $r_A > 0$ (color figure online)

Data availability This manuscript does not include any direct data although most parameter values and units were obtained from the literature.

Declarations

Conflict of interest The authors declare that they have no Conflict of interest.

Ethical approval This study did not involve any experiments with human participants or animals.

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