



Effects and biological consequences of the predator-mediated apparent competition I: ODE models

Yuan Lou¹ · Weirun Tao² · Zhi-An Wang³

Received: 5 July 2024 / Revised: 4 June 2025 / Accepted: 2 August 2025

© The Author(s) 2025

Abstract

Predator-mediated apparent competition is an indirect negative interaction between two prey species mediated by a shared predator, which can lead to changes in population dynamics, competition outcomes and community structures. This paper is devoted to investigating the effects and biological consequences of the predator-mediated apparent competition based on a two prey species (one is native and the other is invasive) and one predator model with Holling type I and II functional responses. Through the analytical results and case studies alongside numerical simulations, we find that the initial mass of the invasive prey species, capture rates of prey species, and the predator mortality rate are all important factors determining the success/failure of invasions and the species coexistence/extinction. The global dynamics can be completely classified for the Holling type I functional response, but can only be partially determined for the Holling type II functional response. For the Holling type I functional response, we find that whether the invasive prey species can successfully invade to induce the predator-mediated apparent competition is entirely determined by the capture rates of prey species. For the Holling type II functional response, the dynamics are more complicated. First, if two prey species have the same ecological characteristics, then the initial mass of the invasive prey species is the key factor determining the success/failure of the invasion and hence the effect of the predator-mediated apparent competition. Whereas if two prey species have different ecological characteristics, say different capture rates, then the success of the invasion no longer depends on the initial mass of the invasive prey species, but on the capture rates. In all cases, if the invasion

✉ Zhi-An Wang
mawza@polyu.edu.hk

Yuan Lou
yuanlou@sjtu.edu.cn

Weirun Tao
taoweiruncn@163.com

¹ School of Mathematical Sciences, Shanghai Jiao Tong University, Shanghai 200240, China

² School of Mathematics, Southeast University, Nanjing 211189, China

³ Department of Applied Mathematics, The Hong Kong Polytechnic University, Hung Hom, Kowloon, Hong Kong

succeeds, then the predator-mediated apparent competition's effectiveness essentially depends on the predator mortality rate. Precisely we show that the native prey species will die out (resp. persist) if the predator has a low (resp. moderate) mortality rate, while the predator will go extinct if it has a large mortality rate. Our study reveals that predator-mediated apparent competition is a complicated ecological process, and its effects and biological consequences depend upon many possible factors.

Keywords Apparent competition · Invasion · Functional response · Global stability · Coexistence and extinction

Mathematics Subject Classification 34D05 · 34D23 · 92-10 · 92D25

1 Introduction

Predation is a primary determinant of the structure and function of ecological systems for maintaining biological diversity and balance (cf. Holt and Polis 1997; Schmitz 2007). This sounds like a paradoxical statement, as predators kill and consume prey, therefore seeming to cause death, not life. Indeed by doing so, predators may keep other species (like damaging pests) in check and ensure that a multitude of species occupying a variety of environmental niches can survive and thrive. For instance, without the regulation of predators, prey populations may reproduce beyond the carrying capacity of their environments, decimating the populations of smaller animals, plants, and coral reefs. As these species decline, additional organisms that rely on their presence will also decline, resulting in a domino effect that can ultimately push populations and habitats beyond the threshold of recovery. Predators can impact the ecosystem in enormously different ways, and hence gaining a comprehensive understanding of the role of predators in ecosystems is a daunting task. Nevertheless, theoretical models alongside analysis can play an important part in interpreting observed patterns/phenomena and making qualitative predictions, and in particular could pinpoint which processes, interactions, or parameter values are responsible for observed behaviors. Competition occurs at the same trophic level, while predation happens between different trophic levels. Though competition and predation can be intertwined directly or indirectly, these two ecological processes are often investigated separately in the existing research.

For the modeling of direct interspecific competition, the population growth rate of each species is described by a first-order differential equation

$$\frac{dN_i}{dt} = F_i(N_1, N_2, \dots, N_i, \dots).$$

The species i and j are competing if $\frac{\partial F_i}{\partial N_j}, \frac{\partial F_j}{\partial N_i} < 0$ at equilibrium (cf. May 2001). Indirect interactions between two organisms are mediated or transmitted by a third one. In particular, there is a special indirect negative interaction, called “apparent competition” (cf. Holt 1977; Holt and Bonsall 2017), that happens between victim species mediated through the action of one or more species of shared natural enemies (e.g., predators, herbivores, omnivores, parasitoids, and pathogens). The apparent competition is usu-

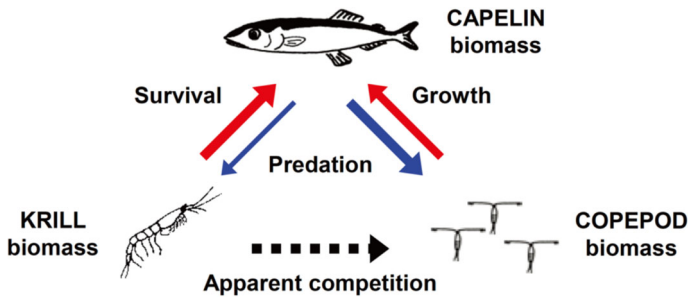


Fig. 1 Apparent competition between krill and copepods mediated by capelin in the Barents sea. The arrow width is approximately proportional to the strength of the effect size. Bottom-up effects are shown in red, and top-down in blue. (cf. (Stige et al. 2018, Fig. 1))

ally denoted by $(-, -)$, which means a reciprocal negative interaction between each pair of victim species in the presence of a shared natural enemy. Moreover, there are also other types of enemy-mediated indirect interactions, including apparent mutualism $(+, +)$, apparent predation $(+, -)$, apparent commensalism $(+, 0)$ and apparent amensalism $(-, 0)$ (cf. Chailleux et al. 2014; Chaneton and Bonsall 2000; Holt and Bonsall 2017 and references therein).

In the predator-prey system with one predator and one prey, the specialist predator cannot generally take the prey to extinction as the predators usually starve to death before they can find the last prey. However, if fueled by a secondary prey species, the predator may take the native prey species to a lower level. This process is called the predator-mediated apparent competition introduced by Holt (1977) where a species indirectly and negatively affects another species that shares the same predator by influencing predator abundance or biomass. Hereafter, we shall refer this secondary prey species as an invasive prey species for convenience. It has long been recognized as a widespread phenomenon observed in many ecological communities (cf. Chaneton and Bonsall 2000; DeCesare et al. 2010). In the experiment of Karban et al. (1994), releases of Willamette mites alone, or releases of predatory mites alone, failed to reduce populations of the damaging Pacific spider mite. However, when both herbivorous Willamette mites and predatory mites were released together, populations of Pacific mites were reduced. In Stige et al. (2018), apparent competition between krill and copepods mediated by capelin in the Barents Sea (see a schematic representation in Fig. 1) was employed to advocate that a krill invasion could affect copepod biomass negatively and result in the decrease of copepod biomass. This process involves both bottom-up and top-down effects, where the bottom-up effect influences communities from lower to higher trophic levels of the food web, and the top-down effect is vice versa. However, apparent competition may be difficult to detect or measure due to its indirect nature and the potential for concurrent exploitative competition or other community effects Stige et al. (2018).

It was pointed out in Holt and Bonsall (2017) that the idea that species can engage in apparent competition by sharing a predator has a venerable history in ecology (cf. Williamson 1957 and (Lotka 1925, pp. 94-95)). The mathematical model describing predator-mediated apparent competition was first introduced by Holt (1977), and

can be written as the following general form for a single predator species feeding on multiple prey (see also Holt and Bonsall 2017):

$$\begin{cases} \frac{du_i}{dt} = F_i(\vec{u}, w) = u_i [g_i(u_i) - f_i(\vec{u})w], \\ \frac{dw}{dt} = G(\vec{u}, w) = wF(\vec{u}), \end{cases} \quad (1.1)$$

where w and u_i are densities of the predator and prey species i , the arrow over u denotes a vector of prey abundances, F_i is the total growth rate of prey species i and G is the growth rate of the predator. In the first equation of (1.1), $g_i(u_i)$ is the inherent per capita growth rate of the prey i in the absence of the predator, $f_i(\vec{u})$ is the functional response of the predator to prey species i and the quantity $f_i(\vec{u})w$ is the per capita rate of mortality from predation experienced by prey species i . The right-hand side of the second equation of (1.1) states that the per capita growth rate $F(\vec{u})$ of the predator depends on prey availability. Focusing on the predator-mediated apparent competition (i.e., indirect interaction), it is assumed in (1.1) that direct interspecific competition among prey species is negligible.

Though the importance of the predator-mediated apparent competition has been extensively discussed in the biological literature (see Chaneton and Bonsall 2000; Stige et al. 2018; Karban et al. 1994; DeCesare et al. 2010 and references therein), mathematical studies on this topic are much less numerous than those for the classical predator-prey or direct competition systems (e.g. see Robert 2003; Cosner 2014; Kang and Wedekin 2013; Murdoch et al. 2013; Ni 2011; Ryan and Cantrell 2015; Sapoukhina et al. 2003; Wang et al. 2016 and references therein). Existing literature on two competing prey - one predator temporal (ODE) models has explored various scenarios. Numerical investigations in Caswell (1978) and Abrams (1999) revealed cyclic or chaotic dynamics under frequency-dependent and saturated functional responses with prey interactions, respectively. The periodic pattern was shown to exist in a two prey-one predator fast-slow dynamical system with switches of feeding between two prey species by the geometric singular perturbation method in Piltz et al. (2017). Elementary analyses in Vance (1978) gave the conditions for the existence of equilibria for frequency-dependent and Holling type I functional responses and numerically show that the predator's presence makes competitive coexistence possible. For the Holling type I functional response, Hsu (1981) characterized equilibrium stability, while Mimura and Kan-on (1986) analytically studied spatial segregation patterns by adding random diffusions to the ODE system. We note all prior works incorporated direct competition between two prey species and relied predominantly on numerical exploration, except for the limited analytical treatments in Hsu (1981), Mimura and Kan-on (1986), Piltz et al. (2017). This paper shifts focus to the indirect competition between two prey species mediated by a shared predator. To emphasize the predation-driven indirect interactions between two prey species while enhancing analytical tractability, we exclude direct prey-prey competition to streamline model complexity. Building on equation (1.1), we thus formulate the following predator-mediated apparent competition model featuring two prey species and one shared

predator:

$$\begin{cases} u_t = u(1 - u/K_1) - wf_1(u), & t > 0, \\ v_t = v(1 - v/K_2) - wf_2(v), & t > 0, \\ w_t = w(\beta_1 f_1(u) + \beta_2 f_2(v) - \theta), & t > 0, \\ (u, v, w)(0) = (u_0, v_0, w_0), \end{cases} \quad (1.2)$$

where $u(t)$, $v(t)$ and $w(t)$ represent the densities of the native prey species, the invasive prey species, and the shared predator species at time t , respectively. The initial data u_0, v_0, w_0 are assumed to be positive. The function f_i ($i = 1, 2$) and parameters have the following biological interpretations:

- f_i , $i = 1, 2$, - functional responses;
- K_i , $i = 1, 2$, - carrying capacities for the prey species;
- β_i , $i = 1, 2$, - trophic efficiency (conversion rates);
- θ - mortality rate of the predator.

All the parameters shown above are positive. For definiteness, we consider two types of functional responses:

$$f_i(s) = \alpha_i s, \quad i = 1, 2, \text{ (Holling type I),} \quad (1.3)$$

$$f_i(s) = \frac{\gamma_i s}{1 + \gamma_i h_i s}, \quad i = 1, 2, \text{ (Holling type II),} \quad (1.4)$$

where α_i and γ_i , $i = 1, 2$, denote the capture rates (i.e., the rates at which prey species are captured), and $h_i > 0$, $i = 1, 2$, represents the handling time.

Using rigorous analyses and quantitative computations, we investigate how system parameters and initial conditions influence the effectiveness of predator-mediated apparent competition. Since the predator-mediated apparent competition involves an introduction (or invasion) of the secondary prey species which is also a food supply to the shared predator, the invasion may not be successful and consequently, the predator-mediated apparent competition will not take effect in the long run. Therefore the first aim of this paper is to investigate

- A1.** Under what conditions, the invasive prey species can successfully invade to promote the predator-mediated apparent competition?

If the invasive prey species invades successfully and supplies additional food to the predator, then the native prey species will be under more intensive predation pressure, possibly resulting in a population decrease or even extinction. Hence the second aim of this paper is to address

- A2.** Whether the predator-mediated apparent competition could reduce the biomass of the native prey species or even cause the native species to go extinct? If so, what conditions are required, and which processes are the main determinants?

In this paper, we shall apply rigorous analysis along with numerical simulations to explore the above two questions. First we can fully characterize the global dynamics of (1.2) with the Holling type I functional response, proving that no non-constant patterns can emerge (see Theorem 2.1). In contrast, the Holling type II functional response can

induce complex dynamics and emergent patterns. To the best of our knowledge, both our analytical and numerical findings are new, as the Holling type II functional response has not been analyzed in the literature for two prey - one predator systems. This work not only serves as a meaningful extension of existing results but also uncovers a rich landscape of dynamics such as periodic oscillations or bistability phenomenon, which are absent in the Holling type I functional response. These insights highlight the critical role of functional response forms in shaping ecological system behavior, offering new perspectives for theoretical ecology and mathematical modeling. More critically, we perform detailed qualitative and quantitative analyses to pinpoint that capture rates of prey species, the predator mortality rate and the initial mass of the invasive prey species are all possible key factors governing the effects and outcomes of predator-mediated apparent competition in regulating native prey abundance, depending on the functional responses and ecological traits of prey species as summarized in Section 4. Our results provide mechanistic insights into how predator functional responses and ecological traits of species collectively determine the success of invasive prey introduction as a tool for native prey control.

The rest of this paper is organized as follows. In Sec. 2, we state our main mathematical results on the global stability of the system (1.2) with (1.3) and (1.4), and the relevant proofs are given in Appendix A. In Sec. 3, we focus on the case of the Holling type II functional response and conduct case studies to pinpoint the main factors determining the effects and biological consequences of the predator-mediated apparent competition. In Sec. 4, we summarize our main findings and discuss several open questions.

2 Global stability results

This section outlines our primary mathematical findings. We first introduce some notation used throughout the paper and then proceed to state the main results. Let

$$\begin{aligned} L_i &:= \beta_i f_i(K_i), \quad \lambda_i := \frac{1}{\gamma_i h_i}, \quad i = 1, 2, \\ L &:= L_1 + L_2, \quad \theta_0 := \max \left\{ \left(1 - \frac{\alpha_1}{\alpha_2}\right) L_1, \left(1 - \frac{\alpha_2}{\alpha_1}\right) L_2 \right\}. \end{aligned}$$

We denote the equilibrium of (1.2) by $E_s = (u_s, v_s, w_s)$, which includes the extinction equilibrium, predator-free equilibrium, semi-coexistence equilibrium and coexistence equilibrium listed in Table 1, where the coexistence equilibrium $E_* = (u_*, v_*, w_*)$ is obtained by solving (1.2) for $u, v, w > 0$. To differentiate coexistence equilibria for different functional responses, we utilize the notation

$$E_* = \begin{cases} P_*, & \text{if (1.3) holds,} \\ Q_*, & \text{if (1.4) holds.} \end{cases}$$

Moreover, in the case of the Holling type I functional response (1.3), the coexistence equilibrium P_* is uniquely given by

$$P_* = \left(\frac{K_1 [(\alpha_2 - \alpha_1)L_2 + \alpha_1\theta]}{\alpha_1 L_1 + \alpha_2 L_2}, \frac{K_2 [(\alpha_1 - \alpha_2)L_1 + \alpha_2\theta]}{\alpha_1 L_1 + \alpha_2 L_2}, \frac{L - \theta}{\alpha_1 L_1 + \alpha_2 L_2} \right),$$

while in the case of the Holling type II functional response (1.4), the coexistence equilibrium Q_* may not exist, may exist and be unique, or may exist but not be unique (see Remark 2.1).

Remark 2.1 For the system (1.2) with the Holling type II functional response (1.4), it is difficult to find the necessary and sufficient conditions for the existence of Q_* for general system parameters. Note that $0 < \theta < L$ is a necessary but not sufficient condition for the existence of Q_* . Indeed, the necessity is apparent since it is easy to see that $u_* < K_1$, $v_* < K_2$, and thus

$$\theta = \beta_1 f_1(u_*) + \beta_2 f_2(v_*) < \beta_1 f_1(K_1) + \beta_2 f_2(K_2) = L,$$

where we have used the fact that $f_i(s)$, $i = 1, 2$, strictly increases with respect to $s > 0$. However, if

$$\theta = \frac{3}{5}, \quad K_1 = 2, \quad K_2 = 3, \quad \text{and} \quad \beta_i = \gamma_i = h_i = 1, \quad i = 1, 2,$$

then the system (1.2) with (1.4) has no coexistence equilibria though $0 < \theta < L = \frac{17}{12}$.

Clearly we have $L_1, L_2, L > 0$, $0 \leq \theta_0 < L$ and $\theta_0 = 0$ if and only if $\alpha_1 = \alpha_2$. For the global stability of equilibria of systems (1.2), it is easy to find that the equilibria E_0, E_u, E_v are saddles for $\theta > 0$, and E_{uv} is also a saddle for $\theta \in (0, L)$ (see Lemma 3.1). Therefore, we will focus on analyzing the global stability of the equilibrium E_{uv} for $\theta \geq L$, and the semi-coexistence/coexistence equilibria for $\theta < L$. Now we can state our main results.

Theorem 2.1 (Global stability for Holling type I). *Let $f_1(u)$ and $f_2(v)$ be given by (1.3). Then the following global stability results hold for (1.2).*

- (i) *If $\alpha_1 < \alpha_2$ (resp. $\alpha_1 > \alpha_2$) and $\theta \in (0, \theta_0]$, then the semi-coexistence equilibrium P_1 (resp. P_2) is globally asymptotically stable.*
- (ii) *If $\theta \in (\theta_0, L)$, then the unique coexistence equilibrium $P_* = (u_*, v_*, w_*)$ of (1.2) is globally asymptotically stable.*
- (iii) *If $\theta \geq L$, then the equilibrium E_{uv} is globally asymptotically stable.*

Theorem 2.2 (Global stability for Holling type II). *Let $f_1(u)$ and $f_2(v)$ be given by (1.4). Then the following global stability results hold for (1.2).*

- (i) *Let $\theta \in (0, L_1)$. Then the semi-coexistence equilibrium Q_1 is globally asymptotically stable if*

$$(K_1, K_2) \in \Lambda_1 := \left\{ (K_1, K_2) \mid K_1 \leq \lambda_1 + u_{Q_1}, \frac{K_2}{f_2(K_2)} \leq w_{Q_1} \right\}, \quad (2.1)$$

Table 1 Equilibria of the system (1.2) with (1.3) or (1.4)

Type of equilibria	Expression of equilibria	Necessary and sufficient condition
Extinction equilibria	$E_0 = (0, 0, 0)$	$\theta > 0$
Predator-free equilibria	$E_u = (K_1, 0, 0), E_v = (0, K_2, 0), E_{uv} = (K_1, K_2, 0)$	$\theta > 0$
Semi-coexistence equilibria	(1.3) $P_1 = (u_{P_1}, 0, w_{P_1}) = \left(\frac{\theta}{\alpha_1 \beta_1}, 0, \frac{L_1 - \theta}{\alpha_1 L_1}\right)$	$0 < \theta < L_1$
	$P_2 = (0, v_{P_2}, w_{P_2}) = \left(0, \frac{\theta}{\alpha_2 \beta_2}, \frac{L_2 - \theta}{\alpha_2 L_2}\right)$	$0 < \theta < L_2$
	(1.4) $Q_1 = (u_{Q_1}, 0, w_{Q_1}) = \left(0, \frac{\theta}{(\beta_1 - h_1 \theta) \gamma_1}, 0, \frac{\beta_1 (L_1 - \theta)}{\gamma_1 f_1(K_1) (\beta_1 - h_1 \theta)^2}\right)$	$0 < \theta < L_1$
	$Q_2 = (0, v_{Q_2}, w_{Q_2}) = \left(0, \frac{\theta}{(\beta_2 - h_2 \theta) \gamma_2}, \frac{\beta_2 (L_2 - \theta)}{\gamma_2 f_2(K_2) (\beta_2 - h_2 \theta)^2}\right)$	$0 < \theta < L_2$
	(1.3) P_*	$\theta_0 < \theta < L$
Coexistence equilibria	(1.4) Q_*	Unclear (see Remark 2.1)

Table 2 Global stability of equilibria of the system (1.2) with (1.3)

	$\theta \in (0, \theta_0]$	$\theta \in (\theta_0, L)$	$\theta \in [L, \infty)$
$\alpha_1 > \alpha_2$	P_2 is GAS	P_* is GAS	E_{uv} is GAS
$\alpha_1 < \alpha_2$	P_1 is GAS	P_* is GAS	E_{uv} is GAS
$\alpha_1 = \alpha_2$ ($\iff \theta_0 = 0$)		P_* is GAS	E_{uv} is GAS

Note: Here the notations “GAS” and “ $\iff$ ” denote “globally asymptotically stable” and “if and only if”, respectively

Table 3 Global stability of equilibria of the system (1.2) with (1.4)

$i \in \{1, 2\}$	$\theta \in (0, L_i)$	$\theta \in [L_i, L)$	$\theta \in [L, \infty)$
$(K_1, K_2) \in \Lambda_i$	Q_i is GAS	Unclear	E_{uv} is GAS
$(K_1, K_2) \in \Lambda_*$	Q_* is GAS	Q_* is GAS	E_{uv} is GAS
$(K_1, K_2) \notin \Lambda_1 \cup \Lambda_2 \cup \Lambda_*$	Unclear	Unclear	E_{uv} is GAS

Note: Here the notation “GAS” has the same interpretation as in Table 2

where “=” in $\frac{K_2}{f_2(K_2)} \leq w_{Q_1}$ holds only in the case of $v_0 \leq K_2$.

(ii) Let $\theta \in (0, L_2)$. Then the semi-coexistence equilibrium Q_2 is globally asymptotically stable if

$$(K_1, K_2) \in \Lambda_2 := \left\{ (K_1, K_2) \mid K_2 \leq \lambda_2 + v_{Q_2}, \frac{K_1}{f_1(K_1)} \leq w_{Q_2} \right\}, \quad (2.2)$$

where “=” in $\frac{K_1}{f_1(K_1)} \leq w_{Q_2}$ holds only in the case of $u_0 \leq K_1$.

(iii) Let $\theta \in (0, L)$ and coexistence equilibrium $Q_* = (u_*, v_*, w_*)$ exist. Then Q_* is globally asymptotically stable if

$$(K_1, K_2) \in \Lambda_* := \left\{ (K_1, K_2) \mid K_1 \leq \lambda_1 + u_*, K_2 \leq \lambda_2 + v_* \right\}. \quad (2.3)$$

(iv) Let $\theta \geq L$. Then the equilibrium E_{uv} is globally asymptotically stable.

Remark 2.2 We note that the sets Λ_1 , Λ_2 and Λ_* given in (2.1)–(2.3) are mutually disjoint. See Appendix B for the detailed proof.

Remark 2.3 In view of Theorem 2.1, the global stability of the system (1.2) with Holling type I functional response (1.3) can be completely classified, as summarized in Table 2. However, for the Holling type II functional response (1.4), there are some gaps (see Table 3) left in the global stability for $0 < \theta < L$.

Theorem 2.1 and Theorem 2.2 will be proved by the Lyapunov function method along with LaSalle’s invariant principle. The proofs are given in Appendix A.

3 Numerical simulations and biological implications

From Table 2, we see that the global stability of solutions to (1.2) with (1.3) has been completely classified and there are no gaps left for the global stability of solutions. In contrast, there are some parameter gaps in which the global dynamics of (1.2) with (1.4) remain unknown (see Table 3). In the following, we shall numerically explore the global dynamics of (1.2) with (1.4) in these gaps. It is well known that one predator and one prey models with Holling type II functional response may have stable time-periodic solutions (cf. Cheng 1981). Therefore we anticipate that periodic solutions may arise from the system (1.2) with the Holling type II functional response. We shall also investigate the effect of the predator-mediated apparent competition on the population dynamics.

The associated Jacobian matrix of the system (1.2) at an equilibrium $E_s = (u_s, v_s, w_s)$ is

$$\begin{aligned} \mathcal{J}(E_s) &= \begin{pmatrix} 1 - \frac{2u_s}{K_1} - w_s f'_1(u_s) & 0 & -f_1(u_s) \\ 0 & 1 - \frac{2v_s}{K_2} - w_s f'_2(v_s) & -f_2(v_s) \\ \beta_1 w_s f'_1(u_s) & \beta_2 w_s f'_2(v_s) & \beta_1 f_1(u_s) + \beta_2 f_2(v_s) - \theta \end{pmatrix} \\ &=: \begin{pmatrix} J_{11} & 0 & J_{13} \\ 0 & J_{22} & J_{23} \\ J_{31} & J_{32} & J_{33} \end{pmatrix}. \end{aligned}$$

We denote the three eigenvalues of $\mathcal{J}(E_s)$ by ρ_1 , ρ_- and ρ_+ , which are the roots of

$$\rho^3 + a_2 \rho^2 + a_1 \rho + a_0 = 0, \quad (3.1)$$

where $a_i = a_i(E_s)$, $i = 0, 1, 2$, are given by

$$\begin{cases} a_0 := J_{11}J_{22}J_{33} - J_{11}J_{23}J_{32} - J_{13}J_{22}J_{31}, \\ a_1 := J_{11}J_{22} + J_{11}J_{33} + J_{22}J_{33} - J_{13}J_{31} - J_{23}J_{32}, \\ a_2 := -(J_{11} + J_{22} + J_{33}). \end{cases}$$

It follows from the Routh-Hurwitz criterion (cf. (Murray 2002, Appendix B)) that all roots of (3.1) have negative real parts if and only if

$$a_0, a_1, a_2 > 0 \quad \text{and} \quad a_1 a_2 - a_0 > 0.$$

Next, we use the above results to study the stability of all equilibria. First from Theorem 2.2 (iv) it follows that E_{uv} is globally asymptotically stable for $\theta \geq L$. The following results can also be easily obtained.

Lemma 3.1 *The equilibria E_0 , E_u , E_v are saddles for any $\theta > 0$. The equilibrium E_{uv} is a saddle for $\theta \in (0, L)$, while E_{uv} is globally asymptotically stable for $\theta \geq L$.*

Proof With simple calculations, one can easily find that the eigenvalues of $\mathcal{J}$ at the four equilibria E_0 , E_u , E_v , E_{uv} are

$$\begin{cases} \rho_1 = -\theta, & \rho_{\pm} = 1, & \text{if } E_s = E_0, \\ \rho_1 = L_1 - \theta, & \rho_{\pm} = \pm 1, & \text{if } E_s = E_u, \\ \rho_1 = L_2 - \theta, & \rho_{\pm} = \pm 1, & \text{if } E_s = E_v, \\ \rho_1 = L - \theta, & \rho_{\pm} = -1, & \text{if } E_s = E_{uv}, \end{cases}$$

which completes the proof. $\square$

We next investigate the stability of the semi-coexistence equilibria Q_1 , Q_2 , and coexistence equilibrium Q_* . It turns out that the stability analysis for these equilibria of (1.2) with Holling type II functional response (1.4) is too complicated for explicit stability/instability conditions. For clarity and definiteness, we assume that the handling time for the two prey species is the same by simply letting $h_1 = h_2 = 1$. By (1.4), it holds that

$$f_i(s) = \frac{s}{\frac{1}{\gamma_i} + s} =: \frac{s}{\lambda_i + s}, \quad s \geq 0, \quad i = 1, 2. \quad (3.2)$$

In what follows, we shall use (3.2) instead of (1.4) as the Holling type II functional response to undertake case studies along with numerical simulations. As illustrated in (Holt and Bonsall 2017, Figure 1), predator-mediated apparent competition among two prey species may be symmetric or asymmetric. Hence we shall distinguish these two scenarios in our subsequent analysis.

- **Symmetric apparent competition:** The two prey species have the same ecological characteristics, namely they are different phenotypes of the same species. In this case, we will consider

$$K_i = K, \quad \beta_i = \beta, \quad \gamma_i = \gamma, \quad h_i = h, \quad i = 1, 2,$$

where K , β , γ and h are positive constants.

- **Asymmetric apparent competition:** The prey species have different ecological characteristics. Such prey species may be dissimilar in many ways, such as the carrying capacity, trophic efficiency, the rate of being captured by the predator (i.e., capture rate), and so on. In this case, we may assume that the two prey species have different values for one parameter and the same values for other parameters.

3.1 Symmetric apparent competition

For definiteness and simplicity of computations, without loss of generality, we take

$$K_1 = K_2 = 3 \quad \text{and} \quad \beta_1 = \beta_2 = \lambda_1 = \lambda_2 = 1. \quad (3.3)$$

We deduce from (3.3) that $L_1 = L_2 = \frac{3}{4}$ and $L = \frac{3}{2}$. In addition to the equilibria E_0 , E_u , E_v and E_{uv} of (1.2) which exist for any $\theta > 0$, there are two semi-coexistence

equilibria

$$\begin{cases} Q_1 = \left(\frac{\theta}{1-\theta}, 0, \frac{3-4\theta}{3(1-\theta)^2} \right), \\ Q_2 = \left(0, \frac{\theta}{1-\theta}, \frac{3-4\theta}{3(1-\theta)^2} \right), \end{cases} \quad \text{if } \theta \in \left(0, \frac{3}{4} \right). \quad (3.4)$$

With tedious but elementary calculations, one can find that there is no coexistence equilibrium if $\theta \geq \frac{3}{2}$, a unique coexistence equilibrium Q_*^0 exists if $\theta \in (0, \frac{2}{3}] \cup [1, \frac{3}{2})$ and three coexistence equilibria Q_*^i ($i = 0, 1, 2$) exist if $\theta \in (\frac{2}{3}, 1)$, where

$$\begin{cases} Q_*^0 := \left(\frac{\theta}{2-\theta}, \frac{\theta}{2-\theta}, \frac{4(3-2\theta)}{3(2-\theta)^2} \right), \\ Q_*^1 := \left(1 + 2\sqrt{\frac{1-\theta}{2-\theta}}, 1 - 2\sqrt{\frac{1-\theta}{2-\theta}}, \frac{4}{3(2-\theta)} \right), \\ Q_*^2 := \left(1 - 2\sqrt{\frac{1-\theta}{2-\theta}}, 1 + 2\sqrt{\frac{1-\theta}{2-\theta}}, \frac{4}{3(2-\theta)} \right). \end{cases} \quad (3.5)$$

Remark 3.1 In addition to the global stability result for E_{uv} stated in Lemma 3.1, we can also apply Theorem 2.2 (iii) to see that Q_*^0 is globally asymptotically stable for $\theta \in [\frac{4}{3}, \frac{3}{2})$ since $u_* = v_* = \frac{\theta}{2-\theta} \geq 2 = K_i - \lambda_i$ ($i = 1, 2$).

In view of Lemma 3.1 and Remark 3.1, it remains to consider the stabilities of semi-coexistence and coexistence equilibria for $\theta \in (0, \frac{3}{2})$. We begin with the local stability of the semi-coexistence equilibria Q_1 and Q_2 for $\theta \in (0, \frac{3}{4})$.

Lemma 3.2 Let (3.3) hold and $\theta \in (0, \frac{3}{4})$. Then Q_i ($i = 1, 2$) has the following properties.

- If $\theta \in \{\frac{1}{2}, \frac{2}{3}\}$, then Q_i ($i = 1, 2$) is marginally stable, where $\rho_1 = -\frac{1}{3}$, $\rho_{\pm} = \pm \frac{i}{\sqrt{6}}$ if $\theta = \frac{1}{2}$, and $\rho_1 = 0$, $\rho_{\pm} = \frac{-2 \pm \sqrt{2}i}{9}$ if $\theta = \frac{2}{3}$.
- If $\theta \in (0, \frac{1}{2})$, then Q_i is a saddle-focus, where $\rho_1 < 0$, and $\rho_{\pm}$ are a pair of complex-conjugate eigenvalues with $\text{Re}(\rho_{\pm}) > 0$ and $\text{Im}(\rho_{\pm}) \neq 0$.
- If $\theta \in (\frac{1}{2}, \frac{2}{3})$, then Q_i is a stable focus-node, where $\rho_1 < 0$, and $\rho_{\pm}$ are a pair of complex-conjugate eigenvalues with $\text{Re}(\rho_{\pm}) < 0$ and $\text{Im}(\rho_{\pm}) \neq 0$.
- If $\theta \in (\frac{2}{3}, \theta_1)$, then Q_i is a saddle-focus, where $\rho_1 > 0$, and $\rho_{\pm}$ are a pair of complex-conjugate eigenvalues with $\text{Re}(\rho_{\pm}) < 0$ and $\text{Im}(\rho_{\pm}) \neq 0$.
- If $\theta \in [\theta_1, \frac{3}{4})$, then Q_i is a saddle with $\rho_1 > 0$ and $\rho_{\pm} < 0$.

Here, $\theta_1 \approx 0.6793$ is the unique real root of the equation $16\theta^3 - 37\theta^2 + 31\theta - 9 = 0$ for $\theta \in (0, \frac{3}{4})$.

Proof We omit the proofs for brevity as they are elementary. □

We next give the local stability of the coexistence equilibria.

Lemma 3.3 Let (3.3) hold and $\theta \in (0, \frac{3}{2})$. Then Q_*^0 has the following properties.

- If $\theta = 1$, then Q_*^0 is marginally stable with $\rho_1 = 0$ and $\rho_{\pm} = \pm \frac{i}{\sqrt{3}}$.

- If $\theta \in (0, 1)$, then $\rho_1 > 0$, and $\rho_{\pm}$ are a pair of complex-conjugate eigenvalues with $\operatorname{Re}(\rho_{\pm}) > 0$ and $\operatorname{Im}(\rho_{\pm}) \neq 0$. Therefore, Q_*^0 is an unstable focus-node.
- If $\theta \in (1, \frac{3}{4})$, then $\rho_1 < 0$, and $\rho_{\pm}$ are a pair of complex-conjugate eigenvalues with $\operatorname{Re}(\rho_{\pm}) < 0$ and $\operatorname{Im}(\rho_{\pm}) \neq 0$. As a result, Q_*^0 is a stable focus-node.
- If $\theta \in [\frac{3}{4}, \frac{2}{3})$, then Q_*^0 is globally asymptotically stable.

Proof The proofs of the first two conclusions are omitted for brevity since they are standard and elementary. The third conclusion is a direct consequence of Theorem 2.2 (iii), see Remark 3.1. $\square$

With some tedious calculations, we also obtain the following result.

Lemma 3.4 *Let (3.3) hold and $\theta \in (\frac{2}{3}, 1)$. Then $\rho_1 < 0$, and $\rho_{\pm}$ are a pair of complex-conjugate eigenvalues with $\operatorname{Re}(\rho_{\pm}) < 0$ and $\operatorname{Im}(\rho_{\pm}) \neq 0$. Hence Q_*^1 and Q_*^2 are stable focus-nodes.*

With the stability results given in Lemmas 3.1–3.4, we summarize the stability/instability properties of all equilibria in Table 4. The bifurcation diagrams of these equilibria are shown in Fig. 2. The results in Table 4 imply that if the predator mortality rate θ is sufficiently large ($\theta \geq \frac{3}{2}$), then the predator will die out and the two prey species coexist (i.e., E_{uv} is globally asymptotically stable). If θ is suitably large (i.e., $\theta \in [\frac{4}{3}, \frac{3}{2})$), then the predator will coexist with the two prey species (i.e., Q_*^0 is globally asymptotically stable). However, if θ is not large (i.e., $0 < \theta < \frac{4}{3}$), the global dynamics largely remain unknown and different outcomes are expected from the local dynamics shown in Table 4. We shall use numerical simulations to foresee the possible global dynamics for $0 < \theta < \frac{4}{3}$ and quantify the population size in the next subsection, and discuss the underlying biological implications. Our numerical simulations and biological discussion will focus on the questions A1 and A2 given in the Introduction. Therefore, we consider two classes of initial data. The first class of initial data is set as a perturbation of the invasive species free equilibrium $Q_1 = (u_{Q_1}, 0, w_{Q_1})$ while keeping u_{Q_1} and w_{Q_1} unchanged, namely $(u_0, v_0, w_0) = (u_{Q_1}, R, w_{Q_1})$ with $R > 0$ being a constant. The numerical results for such initial data can address the effect of the invasion of the invasive prey species on the dynamics of the native prey species, and further investigate under what conditions the native prey species is reduced in its population size or annihilated. The second class of initial data is set as a perturbation of the coexistence equilibrium Q_* , for which the numerical results can address the robustness of coexistence in the predator-mediated apparent competition.

Numerical simulations and implications. The numerical simulations for $\theta \in (0, \frac{4}{3})$ will be divided into three parts: $\theta \in (0, \frac{1}{2})$, $\theta \in [\frac{1}{2}, \frac{3}{4})$ and $\theta \in [\frac{3}{4}, \frac{4}{3})$, and in each part we take an arbitrary value of θ to conduct the numerical simulations.

Part 1: $\theta \in (0, \frac{1}{2})$. We take $\theta = \frac{1}{4} \in (0, \frac{1}{2})$ and focus on the semi-coexistence equilibrium $Q_1 = (\frac{1}{3}, 0, \frac{32}{27})$ given by (3.4) which is unstable (see Table 4). The initial value is set as $(u_0, v_0, w_0) = (\frac{1}{3}, R, \frac{32}{27})$ with $R > 0$ denoting the initial mass of invasive prey species v . The numerical results for different values of R are plotted in Fig. 3, where we find three different typical outcomes showing that whether the invasion is successful depends on the initial biomass of invasive prey species v if the

Table 4 The stability of equilibria of system (1.2) with (3.3)

Equilibria	θ	$(0, \frac{1}{2})$	$\frac{1}{2}$	$(\frac{1}{2}, \frac{2}{3})$	$\frac{2}{3}$	$(\frac{2}{3}, \theta_1)$	$[\theta_1, \frac{3}{4})$	$[\frac{3}{4}, 1)$	1	$(1, \frac{4}{3})$	$[\frac{4}{3}, \frac{3}{2})$	$[\frac{3}{2}, \infty)$
E_0, E_H, E_v		Saddle	Saddle	Saddle	Saddle	Saddle	Saddle	Saddle	Saddle	Saddle	Saddle	Saddle
E_{uv}		Saddle	Saddle	Saddle	Saddle	Saddle	Saddle	Saddle	Saddle	Saddle	Saddle	GAS
Q_1, Q_2		SF	MS	S-FN	MS	SF	Saddle	/	/	/	/	/
Q_*^0		U-FN	U-FN	U-FN	U-FN	U-FN	U-FN	U-FN	MS	S-FN	GAS	/
Q_*^1, Q_*^2		/	/	/	/	S-FN	S-FN	S-FN	/	/	/	/

Note: The abbreviations “MS”, “SF”, “S-FN”, and “U-FN” stand for “marginally stable”, “saddle-focus”, “stable focus node”, and “unstable focus node”, respectively. The notation “GAS” has the same interpretation as in Table 2. The notation “/” denotes “equilibria do not exist” and $\theta_1 \approx 0.6793$ is given in Lemma 3.1

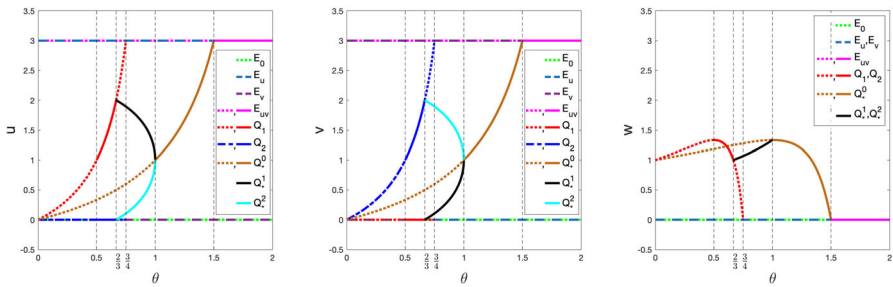


Fig. 2 Bifurcation diagrams of system (1.2) with (3.3) versus θ . The solid curves denote linearly stable equilibria, and other types of curves represent unstable equilibria

mortality rate of the predator is suitably small. Specifically, we have the following observations.

- (i) If the initial mass v_0 of the invasive prey species is small (e.g. $v_0 = R = 0.1$), then the invasive prey species fails to invade and dies out while the native prey species coexists with the predator periodically (i.e., the solution asymptotically develops into a periodic solution $(u_1^*(t), 0, w_1^*(t))$ with period $T_1 = 23.8942$; see Fig. 3(a).
- (ii) If the initial mass v_0 of the invasive prey species is medial (e.g. $v_0 = R = 0.5$), the invasive species v invades successfully and finally coexists with the native prey species u and the predator w periodically (i.e., the solution asymptotically develops into a periodic solution $(u_2^*(t), v_2^*(t), w_2^*(t))$ with period $T_2 = 33.3879$), but the biomass of the native prey species u is reduced due to the increase of the predator's biomass, where

$$\begin{cases} \frac{1}{T_1} \int_0^{T_1} u_1^*(t) dt = \bar{u} = 0.5098 > 0.3225 = \frac{1}{T_2} \int_0^{T_2} u_2^*(t) dt, \\ \frac{1}{T_1} \int_0^{T_1} w_1^*(t) dt = \bar{w} = 1.3625 < 2.1233 = \frac{1}{T_2} \int_0^{T_2} w_2^*(t) dt, \end{cases}$$

as shown in Fig. 3(b).

- (iii) If the initial mass v_0 of the invasive prey species is large (e.g. $v_0 = R = 1$), the invasive species v not only invades successfully but also wipes out the native prey species via the predator-mediated apparent competition (i.e., the solution asymptotically develops into a periodic solution $(0, v_3^*(t), w_3^*(t))$ with period $T_3 = 23.8933$); see Fig. 3(c).

The above observations indicate that whether the invasive prey species can invade successfully to trigger the predator-mediated apparent competition essentially depends on the size of the initial biomass of the invasive prey species. Small initial biomass will lead to failed invasions and does not change the existing population dynamics. However, if the invasive prey species has a suitably large initial biomass, then the invasion will be successful and the predator-mediated apparent competition will take effect, resulting in the decrease or even extinction of the native prey species. To reduce the biomass of a certain species (like pests), it is suitable to employ the strategy of

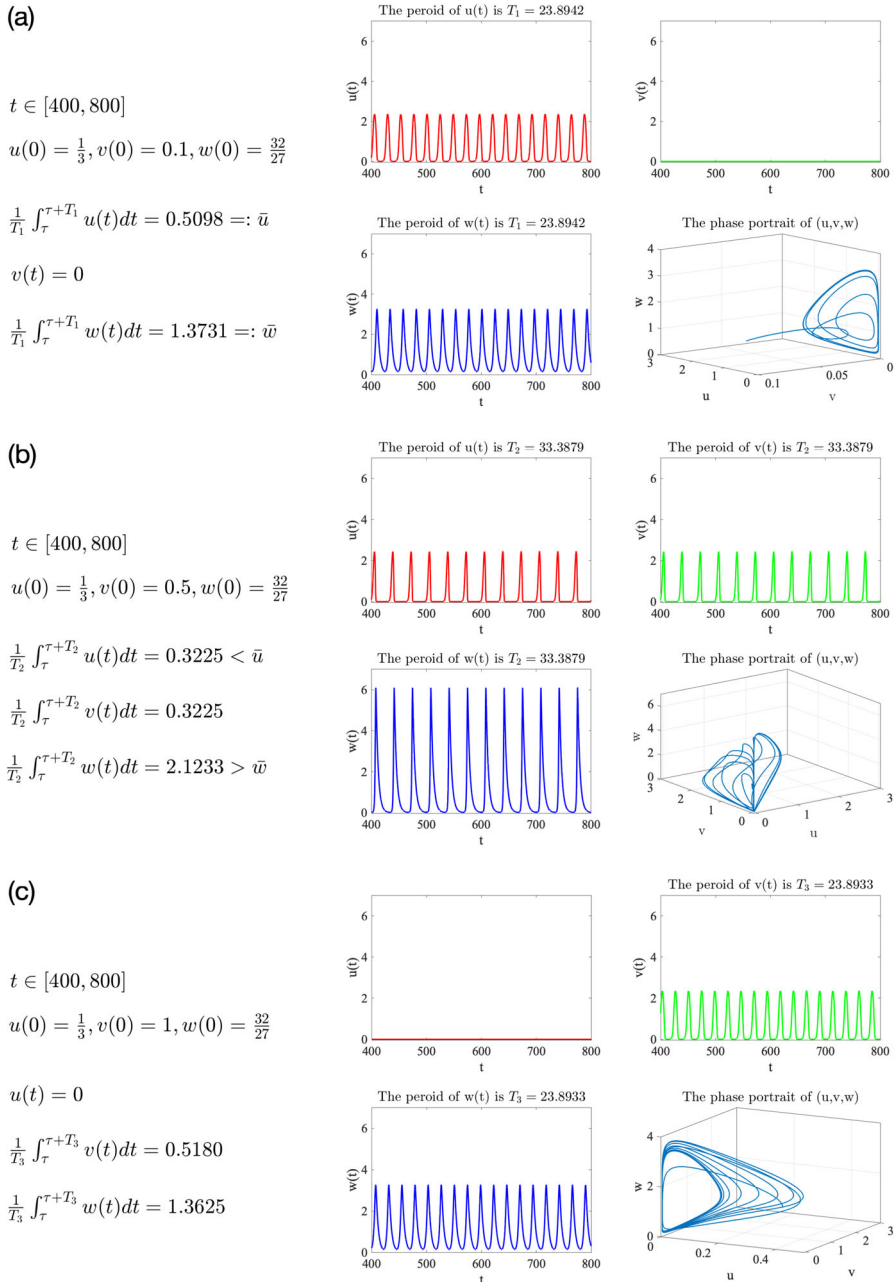


Fig. 3 Asymptotic dynamics of the system (1.2) with (1.4) under the parameter setting (3.3) and $\theta = \frac{1}{4}$. The initial data are taken as : (a) $(\frac{1}{3}, 0.1, \frac{32}{27})$; (b) $(\frac{1}{3}, 0.5, \frac{32}{27})$; (c) $(\frac{1}{3}, 1, \frac{32}{27})$

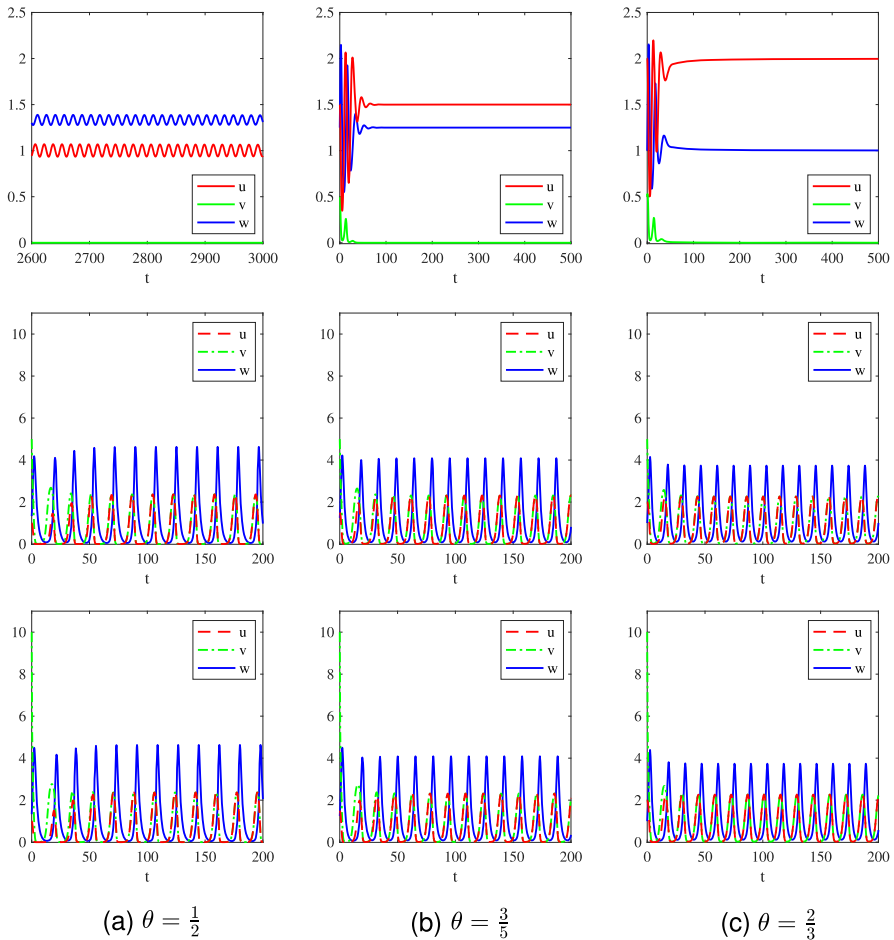


Fig. 4 Long-time dynamics of the system (1.2) with (1.4), (3.3), and different values of $\theta \in \left\{\frac{1}{2}, \frac{3}{5}, \frac{2}{3}\right\}$. The initial data are taken as $(u_0, v_0, w_0) = Q_1 + (0, R, 0)$, where $Q_1 = (1, 0, \frac{4}{3})$ in (a), $Q_1 = (\frac{3}{2}, 0, \frac{5}{4})$ in (b), and $Q_1 = (2, 0, 1)$ in (c); $R = 0.5$ in the first row, $R = 5$ in the second row, and $R = 10$ in the third row

predator-mediated apparent competition by introducing a new (invasive) species with appropriate initial biomass.

Part 2: $\theta \in [\frac{1}{2}, \frac{3}{4})$. In this case, we first consider the following three values for θ :

$$\theta \in \left\{\frac{1}{2}, \frac{3}{5}, \frac{2}{3}\right\},$$

and corresponding numerical simulations are plotted in Fig. 4. We observe similar behaviors to those for $\theta \in (0, \frac{1}{2})$ shown in Fig. 3, where the invasive species v will fail to invade if its initial mass is small as illustrated in the first row of Fig. 4. However, with a large initial mass, the invasive prey species can invade successfully as shown in

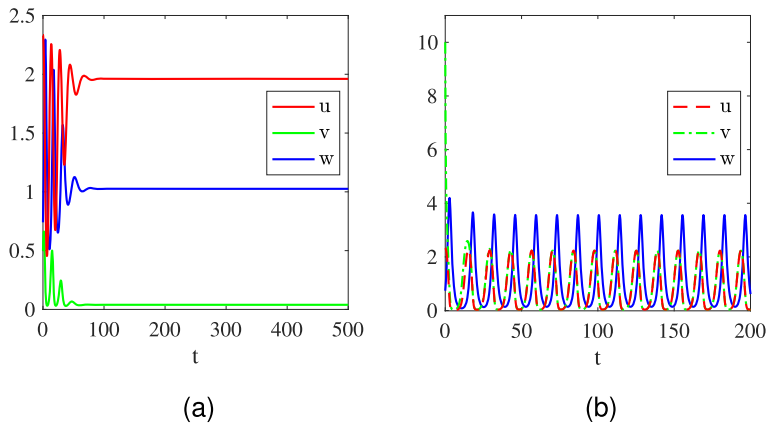


Fig. 5 Long-time dynamics of the system (1.2) with (1.4) and parameters given in (3.3) for $\theta = \frac{7}{10}$. The initial data are taken as $(u_0, v_0, w_0) = Q_1 + (0, R, 0)$, where $Q_1 = (\frac{7}{3}, 0, \frac{20}{27})$, $R = 0.5$ for (a) and $R = 10$ for (b)

the second row of Fig. 4, but cannot annihilate the native prey species via the predator-mediated apparent competition. This is perhaps because the predator mortality rate θ is too large to annihilate the native species even if the invasive species can boost the food supply of the predator. This result alongside the numerical simulations shown in Fig. 3 implies that whether the native prey species will be driven to extinction via the predator-mediated apparent competition depends not only on the initial mass of the invasive species but also on the mortality rate of the predator. Further increasing the value of θ to be $\theta = \frac{7}{10} \in (\theta_1, \frac{3}{4})$, at which $Q_1 = (\frac{7}{3}, 0, \frac{20}{27})$, we find from the numerical simulations shown in Fig. 5(a) that the invasion is successful albeit small initial population abundance of the invasive species (in comparison with those in the first row of Fig. 4). Mathematically this is because Q_1 is a saddle and any small perturbation of Q_1 will result in instability. With a large predator mortality rate, the invasive species (even with a large initial mass) cannot drive the native species to extinction (see Fig. 5(b)), similar to other large values of θ shown in the second and third rows of Fig. 4. This implies that if the predator has a large mortality rate, it can not drive the native prey species to extinction even if its food supply is boosted by the invasive prey species.

Concerning the questions raised in A1, the above numerical results pinpointed two key factors determining successful invasion of the invasive prey species: the initial invasive mass v_0 and mortality rate θ of the predator. Specifically, for a fixed mortality rate θ not large, increasing the initial invasive mass v_0 can lead to a successful invasion. If the mortality rate θ is large, then the predator will go extinct and the mass of the native prey species will not be affected though the invasion is successful. Conversely, for a fixed initial invasive mass that is not too small, the larger mortality rate of the predator will be beneficial to the success of the invasion. Moreover, the population abundance of the native prey species will be reduced by the predator-mediated apparent competition as shown in Fig. 3. Another interesting finding in our numerical simulations is that the asymptotic profiles of the native and invasive prey species coincide as long as the

Table 5 Quantitative properties of $(u_R^*, v_R^*, w_R^*)(t)$ for $R = 0.5, 5, 10$

R	0.5	5	10
Period T_R	/	15.3714	15.3714
$\bar{u} = \frac{1}{T_R} \int_0^{T_R} u_R^*(t) dt$	$\frac{3}{2}$	0.6277	0.6275
$\bar{v} = \frac{1}{T_R} \int_0^{T_R} v_R^*(t) dt$	0	0.6277	0.6275
$\bar{w} = \frac{1}{T_R} \int_0^{T_R} w_R^*(t) dt$	$\frac{5}{4}$	1.5866	1.5844

Remark: Here the notation “/” means “this is not a non-constant periodic case”

non-trivial periodic coexistence state appears (see Fig. 3 to Fig. 5). This result is not yet understood and deserves further investigation.

Next, we explore how the population abundance of native prey species changes with respect to the initial invasive mass. To this end, we take the numerical results shown in Fig. 4(b) as an example. Denote the three solutions shown in Fig. 4(b) by $(u_R^*, v_R^*, w_R^*)(t)$ for $\theta = \frac{3}{5}$ and $R = 0.5, 5, 10$. Then $(u_R^*, v_R^*, w_R^*)(t) |_{R=0.5} \equiv Q_1 = (\frac{3}{2}, 0, \frac{5}{4})$ for all $t > 0$, and $(u_R^*, v_R^*, w_R^*)(t)$ are periodic solutions with period T_R for $R = 5, 10$. Quantitative estimates of the total population in a period for $R = 0.5, 5, 10$ are summarized in Table 5. We see from these results that the total mass of the native prey species decreases with respect to the initial mass of the invasive prey species, as expected.

We proceed to examine whether the constant coexistence/positive solution is stable. To this end, we shall investigate the stability/instability of Q_0^* which exists if $\theta < \frac{3}{2}$. The results of Theorem 2.2 show that Q_0^* is globally asymptotically stable if $\theta \in [\frac{4}{3}, \frac{3}{2})$. This indicates that if the mortality rate of the predator is appropriately large, then coexistence will persist as long as the invasion is successful. However, this is no longer the case if the mortality rate of the predator is suitably small, as shown in Fig. 6 where we see that any small negative (resp. positive) perturbation of one prey species density may lead to the extinction or abundance decrease of this species (resp. the other one). This indicates that the constant coexistence solution is not robust against (small) perturbations.

Part 3: $\theta \in [\frac{3}{4}, \frac{4}{3})$. In view of Table 4, both coexistence equilibria Q_*^1 and Q_*^2 are stable for $\theta \in [\frac{3}{4}, 1)$, that is the system (1.2) generates bistable dynamics as illustrated in Fig. 7 for $\theta = 0.8$, where

$$Q_*^1 = \left(1 + \sqrt{\frac{2}{3}}, 1 - \sqrt{\frac{2}{3}}, \frac{10}{9}\right), \quad Q_*^2 = \left(1 - \sqrt{\frac{2}{3}}, 1 + \sqrt{\frac{2}{3}}, \frac{10}{9}\right).$$

With an initial value (u_0, v_0, w_0) which is “closer” to Q_*^1 than Q_*^2 , the corresponding numerical results shown in Fig. 7(a) demonstrate that the solution converges to Q_*^1 , while Fig. 7(b) illustrates the convergence of solutions to Q_*^2 when the initial value is closer to Q_*^2 . We wonder if a non-constant solution may develop if the initial value is not close to either of these two stable equilibria. Hence, we choose an initial value $(u_0, v_0, w_0) = (1.2, 0.5, 1)$ neither close to Q_*^1 nor to Q_*^2 ; the corresponding numeri-

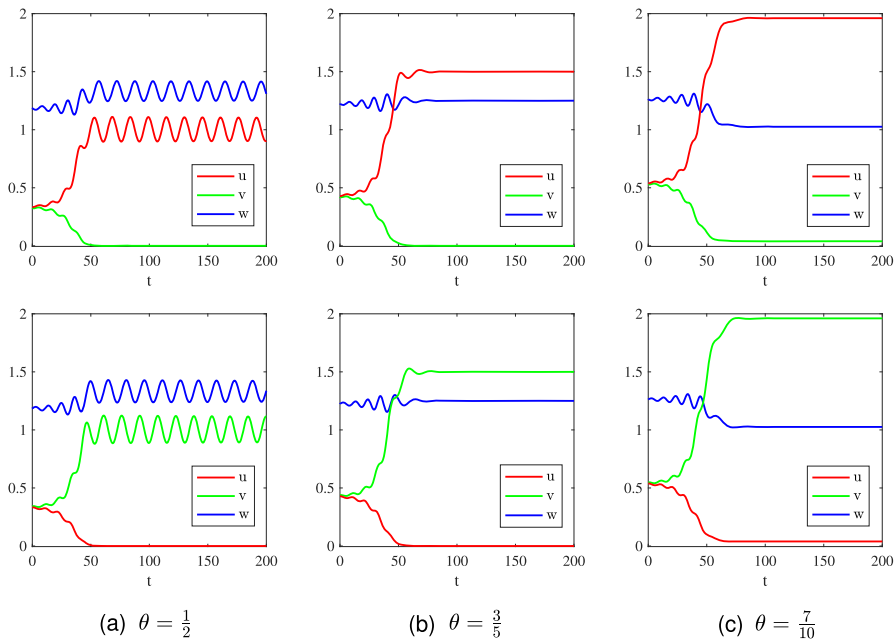


Fig. 6 Long-time dynamics of the system (1.2) with (1.4) and parameters given in (3.3) for $\theta \in \left\{\frac{1}{2}, \frac{3}{5}, \frac{7}{10}\right\}$. The initial data are taken as $(u_0, v_0, w_0) = Q_*^0 + (0, R, 0)$, where $R = -0.01$ for the first row and $R = 0.01$ for the second row, and Q_*^0 is given by (3.5): (a) $(\frac{1}{3}, \frac{1}{3}, \frac{32}{27})$; (b) $(\frac{3}{7}, \frac{3}{7}, \frac{60}{49})$; (c) $(\frac{7}{13}, \frac{7}{13}, \frac{640}{507})$

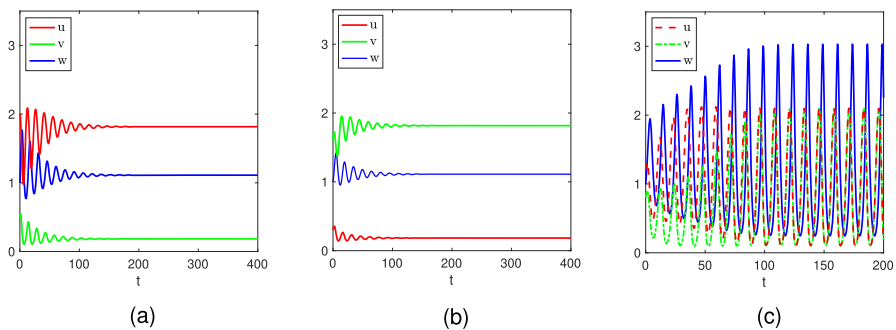


Fig. 7 Long-time dynamics of the system (1.2) with (1.4) under the parameter setting (3.3) and $\theta = 0.8$. The initial data are taken as (u_0, v_0, w_0) : (a) $(2, 0.5, 1)$; (b) $(0.3, 1.6, 1)$; (c) $(1.2, 0.8, 1)$

cal result shown in Fig. 7(c) demonstrates that the periodic solution will develop. But how to rigorously prove the existence of periodic solutions remains an interesting open question.

In applications, the invasive prey species may be used as a biological control agent to regulate the population size of the native prey species if they are harmful (like pests). The ideal situation is that a small number of invasive prey species can achieve this goal. The above linear stability analysis alongside numerical simulations indicates

that this is unfeasible if two prey species are ecologically identical (i.e., the symmetric case). However, this is achievable when two prey species are ecologically different (i.e., asymmetric case) as to be shown in the next subsection.

3.2 Asymmetric apparent competition

For simplicity, we first rescale the system (1.2) with (1.4). To this end, we set

$$\tilde{u} = \frac{u}{K_1}, \quad \tilde{v} = \frac{v}{K_2}, \quad \tilde{w} = w, \quad (\tilde{\gamma}_i, \tilde{h}_i, \tilde{\beta}_i) = (\gamma_i, h_i K_i, \beta_i K_i), \quad i = 1, 2. \quad (3.6)$$

Substituting the above rescalings into (1.2) with (1.4) and dropping the tildes for brevity, we obtain the following rescaled system

$$\begin{cases} u_t = u(1-u) - w \frac{\gamma_1 u}{1+\gamma_1 h_1 u}, & t > 0, \\ v_t = v(1-v) - w \frac{\gamma_2 v}{1+\gamma_2 h_2 v}, & t > 0, \\ w_t = w \left(\beta_1 \frac{\gamma_1 u}{1+\gamma_1 h_1 u} + \beta_2 \frac{\gamma_2 v}{1+\gamma_2 h_2 v} - \theta \right), & t > 0, \\ (u, v, w)(0) = (u_0, v_0, w_0). \end{cases} \quad (3.7)$$

The rescaled system (3.7), which can be viewed as a special case of (3.6) with $K_1 = K_2 = 1$, has three types of parameters: capture rates γ_i , handling times h_i and conversion rates β_i , where $i = 1, 2$. In the following, we shall focus on the case where the two prey species have different capture rates (i.e., $\gamma_1 \neq \gamma_2$), and by assuming $h_1 = h_2$, $\beta_1 = \beta_2$, we can study the effects of predator-mediated apparent competition with different capture rates. For definiteness, we set without loss of generality

$$h_i = 1, \quad \beta_i = b > 0 \quad \text{and} \quad 0 < \gamma_2 < \gamma_1 = 1. \quad (3.8)$$

The biological meaning of parameter values set in (3.8) is that the two prey species u and v have the same handling times and conversion rates but vary in capture rates, while the predator prefers to hunt the native prey species u ($\gamma_1 > \gamma_2$). Clearly the rescaled system (3.7) with (3.8) has four predator-free equilibria

$$E_0 = (0, 0, 0), \quad E_u = (1, 0, 0), \quad E_v = (0, 1, 0), \quad E_{uv} = (1, 1, 0), \quad \text{if } \theta > 0,$$

two semi-coexistence equilibria

$$\begin{cases} Q_1 = (u_{Q_1}, 0, w_{Q_1}) = \left(\frac{\theta}{b-\theta}, 0, \frac{b(b-2\theta)}{(b-\theta)^2} \right), & \text{if } \theta \in (0, L_1), \\ Q_2 = (0, v_{Q_2}, w_{Q_2}) = \left(0, \frac{\theta}{\gamma_2(b-\theta)}, \frac{b(b\gamma_2-(1+\gamma_2)\theta)}{\gamma_2^2(b-\theta)^2} \right), & \text{if } \theta \in (0, L_2), \end{cases}$$

and a unique coexistence equilibrium (see Lemma C.3 in Appendix C for detailed reasons)

$$Q_* = (u_*, v_*, w_*), \quad \text{if } \theta \in (\Theta_1, L), \quad (3.9)$$

where

$$\begin{cases} L_1 = \frac{b}{2} > L_2 = \frac{b\gamma_2}{1+\gamma_2}, \quad L = L_1 + L_2 < b, \\ \Theta_1 = \varphi_1(\gamma_2)b \in (0, L_2), \quad \varphi_1(\gamma_2) := \frac{\sqrt{(1-\gamma_2)(3\gamma_2+1)} - (1-\gamma_2)(2\gamma_2+1)}{2\gamma_2^2}. \end{cases} \quad (3.10)$$

For $b > 0$ and $\gamma_2 \in (0, 1)$, it holds that

$$\begin{cases} \varphi_1''(\gamma_2) < 0, \quad \varphi_1'(\frac{2}{3}) = 0, \quad \lim_{\gamma_2 \rightarrow 0} \varphi_1(\gamma_2) = \lim_{\gamma_2 \rightarrow 1} \varphi_1(\gamma_2) = 0, \\ 0 < \Theta_1 \leq b\varphi_1(\frac{2}{3}) = \frac{b}{4}, \text{ and } \Theta_1 \text{ attains its maximum } \frac{b}{4} \text{ if and only if } \gamma_2 = \frac{2}{3}. \end{cases}$$

This implies that Θ_1 is non-monotone in γ_2 , i.e., it is a convex function maximized at $\gamma_2 = \frac{2}{3}$.

Remark 3.2 Applying Theorem 2.2 (iii)-(iv) with $K_1 = K_2 = 1$ to system (3.7)-(3.8), we can easily find that Q_* is globally asymptotically stable for $\theta \in (\Theta_1, L)$, and $E_{uv} = (1, 1, 0)$ is globally asymptotically stable for $\theta \geq L$. Since $\frac{1+\gamma_1 h_1}{2} = 2 > \lim_{\theta \rightarrow \Theta_1} w_{Q_2} = 1$ for $b > 0$ and $\gamma_2 \in (0, 1)$, the results in Theorem 2.2(ii) with $K_1 = K_2 = 1$ are inapplicable to assert the global stability of Q_2 for $\theta \in (0, \Theta_1]$. However, this can be shown in the following lemma.

Lemma 3.5 *The semi-coexistence equilibrium Q_2 of the rescaled system (3.7) with (3.8) is globally asymptotically stable if $\theta \in (0, \Theta_1]$.*

Proof Let $\theta \in (0, \Theta_1]$. Then (3.10) implies $0 < \theta < \frac{b\gamma_2}{1+\gamma_2} < \frac{b}{2}$. For $t > 0$, let

$$\mathcal{E}(t; Q_2) = bu + (b - \theta) \left(v - v_{Q_2} - v_{Q_2} \ln \frac{v}{v_{Q_2}} \right) + \left(w - w_{Q_2} - w_{Q_2} \ln \frac{w}{w_{Q_2}} \right).$$

Then by similar arguments as in the proofs of Lemma A.2 and Lemma A.5, we have $\mathcal{E}(t; Q_2) > 0$ for all $(u, v, w) \neq Q_2$, and

$$\begin{aligned} \mathcal{E}'(t; Q_2) &= b \left(1 - u - \frac{w}{1+u} \right) u + (b - \theta) \left(1 - v - \frac{\gamma_2 w}{1 + \gamma_2 v} \right) (v - v_{Q_2}) \\ &\quad + \left(\frac{b\gamma_2 v}{\gamma_2 v + 1} + \frac{bu}{u + 1} - \theta \right) (w - w_{Q_2}) \\ &= -(b - \theta) \frac{(1 - \gamma_2 + \gamma_2(v + v_{Q_2}))}{\gamma_2 v + 1} (v - v_{Q_2})^2 - \frac{bu^3}{u + 1} + \frac{bu\varphi_2(\theta)}{\gamma_2^2(u + 1)(b - \theta)^2} \\ &< -(b - \theta) \frac{\gamma_2(v + v_{Q_2})}{\gamma_2 v + 1} (v - v_{Q_2})^2 - \frac{bu^3}{u + 1}, \end{aligned}$$

where we have used $\gamma_2 \in (0, 1)$ and the fact that the quadratic function

$$\begin{aligned} \varphi_2(\theta) &:= \gamma_2^2 \theta^2 + b \left(-2\gamma_2^2 + \gamma_2 + 1 \right) \theta + b^2(\gamma_2 - 1)\gamma_2 \\ &= \gamma_2^2 \left[\theta + \Theta_1 + b \left(\frac{1 + \gamma_2}{\gamma_2^2} - 2 \right) \right] (\theta - \Theta_1) \end{aligned} \quad (3.11)$$

Table 6 Global stability of (3.7) with (3.8)

θ	$(0, \Theta_1]$	(Θ_1, L)	$[L, \infty)$
Global stability	Q_2 is GAS	Q_* is GAS	E_{uv} is GAS

Note: The notation “GAS” has the same interpretation as in Table 2. The parameter Θ_1 is given in (3.10)

is nonpositive for $\theta \in (0, \Theta_1]$ in the last inequality. Finally, similar arguments based on the Lyapunov function method and LaSalle’s invariant principle as in the proof of Lemma A.2 complete the proof. $\square$

With Remark 3.2 and Lemma 3.5, we summarize the global stability results in Table 6 for the rescaled system (3.7) with (3.8).

Under the parameter setting (3.8), the capture rate of the invasive prey species v is smaller than the native prey species u , namely $0 < \gamma_2 < \gamma_1 = 1$. According to the results shown in Table 6 for any $\theta > 0$, we can derive the following biological implications.

- (i) If $\theta \in (0, \Theta_1]$ (i.e., the predator has a low mortality rate), the global stability of Q_2 implies that the invasive prey species can invade successfully regardless of its initial population size and wipe out the native prey species via the predator-mediated apparent competition.
- (ii) If $\theta \in (\Theta_1, L)$ (i.e., the predator has a moderate mortality rate), then the global stability of Q_* indicates that moderate predator mortality allows the native prey species to survive and to coexist with the invasive prey species and the predator.
- (iii) If $\theta \geq L$, the global stability of E_{uv} entails that the poor physical condition of the predator (i.e., the predator has a large mortality rate) will result in the extinction of the predator even though the invasive prey species can boost the food supply to the predator.

The above results indicate that if the predator has a hunting preference for the native species (i.e., larger capture rate of the native prey species), then the invasive prey species can always invade successfully regardless of its initial population size. Furthermore, whether or not the native prey species can be eradicated through the predator-mediated apparent competition essentially depends upon the mortality rate of the predator (i.e., low predator mortality rate will result in the extinction of the native prey species while a moderate or large mortality rate will allow the native prey species to persist). In the general parameter set in which $0 < \gamma_2 < \gamma_1$, the case $0 < \gamma_2 < \gamma_1 = 1$ is only a special situation where we can completely classify the global stability of solutions as given in Table 6. For other parameter regimes contained in the set $0 < \gamma_2 < \gamma_1$, we can perform the linear stability analysis to obtain local stability results and employ the Lyapunov function method alongside LaSalle’s invariant principle to obtain the global stability results in partial parameter regimes, but a complete classification of global stability can not be established. Indeed, in some parameter regimes, periodic solutions may exist (see Fig. 8), and hence the global stability in the whole parameter domain is impossible. Nevertheless, the biological phenomena observed from our numerical simulations (not shown here for brevity) are essentially similar to the case $0 < \gamma_2 < \gamma_1 = 1$: the invasive prey species will

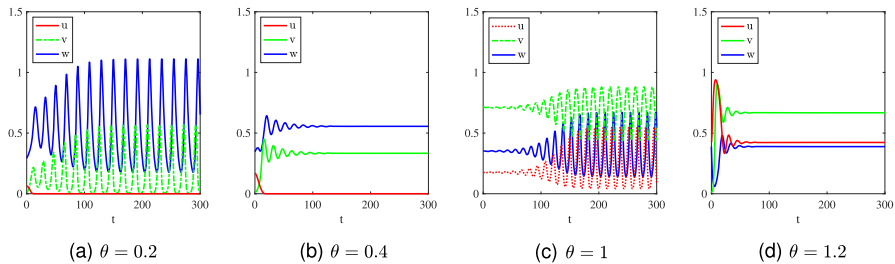


Fig. 8 Long-time dynamics of the rescaled system (3.7) with $h_i = \beta_i = 1$ ($i = 1, 2$), $(\gamma_1, \gamma_2) = (4, 2)$ and $\theta = 0.2, 0.4, 1, 1.2$. The initial data are taken as $(u_0, v_0, w_0) = Q_1 + (0, 0.01, 0)$ in (a)–(b), $(u_0, v_0, w_0) = Q_* + (0, 0.01, 0)$ in (c), and $(u_0, v_0, w_0) = (u_*, 0.01, w_*)$ in (d)

always invade successfully regardless of its initial population abundance and can even wipe out the native prey species through the predator-mediated apparent competition if the mortality rate of the predator is low, while the native prey species can persist and coexist with the predator and invasive prey species if the mortality rate of the predator is moderate, where the difference from the case $0 < \gamma_2 < \gamma_1 = 1$ is that the coexistence state may be periodic or constant as shown in Fig. 8.

If we assume $0 < \gamma_1 < \gamma_2 = 1$ (i.e., the capture rate of the native prey species is smaller than that of the invasive prey species), then the results in Table 6 hold by swapping Q_1 with Q_2 . This means that if the predator has a hunting preference for the invasive prey species, then a successful invasion depends heavily on the predator mortality rate (precisely, the invasion will fail for $\theta \in (0, \Theta_1]$ while succeeding for $\theta > \Theta_1$). Even if the invasion is successful, the invasive prey species is unable to wipe out the native prey species through predator-mediated apparent competition, regardless of its initial population abundance. These interesting results have significant value in applications. For instance, if we were to control the population abundance of some harmful species (like pests) by their natural enemies, we can introduce a small amount of secondary (invasive) prey species that are less preferred by their natural enemies based on the principle of predator-mediated apparent competition.

4 Summary and discussion

Predator-mediated apparent competition is an indirect and negative interaction between two prey species mediated by a shared predator. As stressed in Stige et al. (2018), quantifying such indirect effects is methodologically challenging but important for understanding ecosystem function. To study the effects of predator-mediated apparent competition on population dynamics, in this paper, we propose to consider system (1.2) by viewing u as a native prey species and v as an invasive prey species, both of which share one predator w . We find conditions for the local and global stability of the equilibria of system (1.2) with Holling type I and II functional responses in Section 2, and employ numerical simulations to demonstrate the possible population dynamics and biological consequences due to the predator-mediated apparent competition in Section 3.

In summary, we find that if two prey species employ the Holling type I functional responses, whether the invasion is successful and hence promotes the predator-mediated apparent competition is entirely determined by their capture rates (i.e., the rates being captured by the predator). In contrast, the dynamics with the Holling type II functional responses are more complicated. First, if two prey species have the same ecological characteristics, then the initial mass of the invasive prey species is the key factor determining the success of the invasion and hence the promotion of the predator-mediated apparent competition. Whereas if two prey species have different ecological characteristics, say different capture rates without loss of generality, then the success of the invasion (i.e., the promotion of the predator-mediated apparent competition) no longer depends on the initial mass of the invasive prey species, but on the capture rates. In all cases, if the invasion succeeds, whether the native prey species can be annihilated via predator-mediated apparent competition essentially depends on the predator mortality rate (i.e., the low predator mortality rate will result in the extinction of the native prey species). These intriguing findings not only fully address the questions posed in **A1** and **A2** of Section 1 but also offer actionable insights for decision-makers when introducing alien species into ecological systems to maintain ecological balance and biodiversity.

Our present work not only pinpoints key factors promoting predator-mediated apparent competition but also shows the significant effects of predator-mediated apparent competition on the structure and stability of ecological systems. Therefore, a comprehensive understanding of the mechanism underlying dynamics of this indirect interaction is imperative. This paper only takes a (first) step forward in this direction and many interesting questions remain open.

- We consider the same functional response for both prey species, either Holling type I or Holling type II. In reality, the functional response for two prey species may be different, such as Holling type I for the native prey species and Holling type II for the invasive one, or vice versa. Then we anticipate that the dynamics might be different from those obtained in this paper. This deserves to be clarified in a future work.
- The model considered in this paper does not include spatial structure, such as random diffusion and/or directed movement (e.g. prey-taxis cf. Kareiva and Odell 1987), which are indispensable factors to make the model more realistic. This raises a natural question: what are the dynamics of the predator-mediated apparent competition with spatial structure and whether the spatial movement of species will bring significantly different effects? These interesting questions can serve as a roadmap to study spatial effects on the population dynamics of predator-mediated apparent competition and hence provide insights into the understanding of complex dynamics of ecological systems. We shall explore this question in the future.
- In the model, the direct (i.e., interference) competition of two prey species is not considered. If we include the direct competition in the model, the complexity of both qualitative and quantitative analysis will be considerably increased. However, it is still very interesting to explore how the direct competition and indirect interaction (i.e., predator-mediated apparent competition) between the two prey species jointly affect the population dynamics.

Appendix A. Proof of the global stability

In this appendix, we aim to prove the global stability of the equilibria of the system (1.2). As mentioned earlier, we will primarily focus on proving the global stability of the equilibrium E_{uv} for $\theta \geq L$ and semi-coexistence/coexistence equilibria for $0 < \theta < L$. Before proceeding with the stability analysis, we first establish the global well-posedness of the system (1.2) by proving the following result.

Lemma A.1 *Let $(u_0, v_0, w_0) \in \mathbb{R}_+^3$, and let $f_1(u)$ and $f_2(v)$ be given by (1.3) or (1.4). Then the system (1.2) admits a unique nonnegative solution, which is bounded for $t > 0$. Moreover, the solution satisfies*

$$\sup_{t \geq 0} u(t) \leq M_1, \quad \sup_{t \geq 0} v(t) \leq M_2, \quad \sup_{t \geq 0} w(t) \leq M_3, \quad (\text{A1})$$

and

$$\limsup_{t \rightarrow \infty} u(t) \leq K_1, \quad \limsup_{t \rightarrow \infty} v(t) \leq K_2, \quad \limsup_{t \rightarrow \infty} w(t) \leq \frac{(1+\theta)^2}{4\theta} (\beta_1 K_1 + \beta_2 K_2), \quad (\text{A2})$$

where the constants M_i , $i = 1, 2, 3$, are given by

$$\begin{cases} M_1 := \max \{u_0, K_1\}, & M_2 := \max \{v_0, K_2\}, \\ M_3 := \max \left\{ \beta_1 u_0 + \beta_2 v_0 + w_0, \frac{(1+\theta)^2}{4\theta} (\beta_1 K_1 + \beta_2 K_2) \right\}. \end{cases}$$

Proof Since the vector field, defined by the terms on the right-hand side of the system (1.2), is smooth in $\mathbb{R}_+^3$, the existence theory of ordinary differential equations (cf. (Logemann and Ryan 2014, Theorem 4.18)) guarantees that the system (1.2) admits a unique maximal solution with a maximal time $T_{\max} \in (0, \infty]$. By the first equation of (1.2), we have

$$u(t) = u_0 e^{\int_0^t \left(1 - \frac{u(s)}{K_1} - \frac{w(s)f_1(s)}{u(s)}\right) ds} \geq 0 \quad \text{for all } t \in (0, T_{\max}).$$

We can similarly obtain $v(t), w(t) \geq 0$ for all $t \in (0, T_{\max})$. Then the first equation of (1.2) shows that $u_t \leq u(1 - u/K_1)$, which along with the comparison principle gives $u(t) \leq \max \{u_0, K_1\} = M_1$ for all $t \in (0, T_{\max})$. Similarly, it holds that $v(t) \leq \max \{v_0, K_2\} = M_2$ for all $t \in (0, T_{\max})$. Let $z(t) := \beta_1 u(t) + \beta_2 v(t) + w(t)$, then we have from (1.2) and Young's inequality that

$$\begin{aligned} z_t &= \beta_1 u \left(1 - \frac{u}{K_1}\right) + \beta_2 v \left(1 - \frac{v}{K_2}\right) - \theta (z - \beta_1 u - \beta_2 v) \\ &= -\theta z + \beta_1 \left((1+\theta)u - \frac{u^2}{K_1}\right) + \beta_2 \left((1+\theta)v - \frac{v^2}{K_2}\right) \\ &\leq -\theta z + \frac{(1+\theta)^2}{4} (\beta_1 K_1 + \beta_2 K_2) \quad \text{for all } t \in (0, T_{\max}). \end{aligned}$$

By the comparison principle, we get $w(t) \leq z(t) \leq M_3 = \max\{\beta_1 u_0 + \beta_2 v_0 + w_0, \frac{(1+\theta)^2}{4\theta} (\beta_1 K_1 + \beta_2 K_2)\}$ for all $t \in (0, T_{max})$. Therefore the solution is bounded and hence $T_{max} = \infty$. Given the above analysis, (A1) and (A2) follow immediately. The proof is completed. $\square$

Now we consider the global stability of the equilibria of the system (1.2). Before proceeding, for $t > 0$ and a given equilibrium $E_s = (u_s, v_s, w_s)$, we let

$$\mathcal{E}(t; E_s) := \Gamma_1 \left(u - u_s - u_s \ln \frac{u}{u_s} \right) + \Gamma_2 \left(v - v_s - v_s \ln \frac{v}{v_s} \right) + \left(w - w_s - w_s \ln \frac{w}{w_s} \right), \quad (\text{A3})$$

where the constants Γ_1 and Γ_2 are given by

$$\Gamma_i := \begin{cases} \frac{\beta_i f_i(u_s)}{\alpha_i u_s} = \beta_i, & \text{if (1.3) holds,} \\ \frac{\beta_i f_i(u_s)}{\gamma_i u_s} = \frac{\beta_i}{1 + \gamma_i h_i u_s}, & \text{if (1.4) holds,} \end{cases} \quad i = 1, 2. \quad (\text{A4})$$

Then we prove the global stability of the equilibria.

A.1. Global stability for $\theta \geq L$

The first result asserts that the equilibrium E_{uv} is globally asymptotically stable if $\theta \geq L$.

Lemma A.2 *Let $\theta \geq L$, and let $f_1(u)$ and $f_2(v)$ be given by (1.3) or (1.4). Then the equilibrium E_{uv} is globally asymptotically stable.*

Proof We first recall that $u, v, w \geq 0$ for all $t \geq 0$. Let $E_s = E_{uv} = (K_1, K_2, 0)$ in (A3) and (A4). Then

$$\mathcal{E}(t; E_{uv}) = \Gamma_1 \left(u - K_1 - K_1 \ln \frac{u}{K_1} \right) + \Gamma_2 \left(v - K_2 - K_2 \ln \frac{v}{K_2} \right) + w,$$

and

$$\begin{aligned} \mathcal{E}'(t; E_{uv}) = & \Gamma_1 \left(1 - \frac{u}{K_1} - \frac{w f_1(u)}{u} \right) (u - K_1) + \Gamma_2 \left(1 - \frac{v}{K_2} - \frac{w f_2(v)}{v} \right) (v - K_2) \\ & + w (\beta_1 f_1(u) + \beta_2 f_2(v) - \theta). \end{aligned} \quad (\text{A5})$$

We claim that

$$\begin{cases} \mathcal{E}(t; E_{uv}) > 0 \text{ for all } (u, v, w) \neq E_{uv}, \\ \mathcal{E}'(t; E_{uv}) \leq 0, \text{ where “} = \text{” holds if and only if } (u, v, w) = E_{uv}. \end{cases} \quad (\text{A6})$$

Indeed, for any given $c_0 > 0$, the function $\phi_1(s) := s - c_0 - c_0 \ln \frac{s}{c_0}$ for $s > 0$ satisfies $\phi_1'(s) = 1 - \frac{c_0}{s}$ and $\phi_1''(s) = \frac{c_0}{s^2} > 0$, which implies that $\phi_1(s) \geq \phi_1(c_0) = 0$

and $\phi_1(s) = 0$ if and only if $s = c_0$. Therefore, the first conclusion in (A6) follows. Moreover, if (1.3) holds, then (A4) gives $\Gamma_1 = \beta_1$ and $\beta_1 (f_1(u) - f_1(K_1)) = \Gamma_1 \frac{f_1(u)}{u} (u - K_1)$. If (1.4) holds, then (A4) gives $\Gamma_1 = \frac{\beta_1}{1 + \gamma_1 h_1 K_1}$ and

$$\beta_1 (f_1(u) - f_1(K_1)) = \frac{\gamma_1 \beta_1 (u - K_1)}{(1 + \gamma_1 h_1 K_1)(1 + \gamma_1 h_1 u)} = \Gamma_1 \frac{f_1(u)}{u} (u - K_1). \quad (\text{A7})$$

Similarly, we have

$$\beta_2 (f_2(v) - f_2(K_2)) = \Gamma_2 \frac{f_2(v)}{v} (v - K_2). \quad (\text{A8})$$

Using (1.3), (1.4), (A3), (A7), (A8) and $\theta \geq L$, we have

$$\begin{aligned} w (\beta_1 f_1(u) + \beta_2 f_2(v) - \theta) &\leq \beta_1 w (f_1(u) - f_1(K_1)) + \beta_2 w (f_2(v) - f_2(K_2)) \\ &= \Gamma_1 \frac{w f_1(u)}{u} (u - K_1) + \Gamma_2 \frac{w f_2(v)}{v} (v - K_2), \end{aligned}$$

which along with (A5) yields

$$\mathcal{E}'(t; E_{uv}) \leq -\frac{\Gamma_1}{K_1} (u - K_1)^2 - \frac{\Gamma_2}{K_2} (v - K_2)^2.$$

The above inequality indicates that $\mathcal{E}'(t; E_{uv}) \leq 0$, where “=” holds in the case of $(u, v) = (K_1, K_2)$. Note that if $(u, v) = (K_1, K_2)$, the first equation of (1.2) becomes $0 = w f_1(K_1)$, which implies $w = 0$ due to $f_1(K_1) > 0$. Therefore, $\mathcal{E}'(t; E_{uv}) < 0$ if $(u, v, w) \neq E_{uv}$. Clearly, (A5) implies $\mathcal{E}'(t; E_{uv}) = 0$ for $(u, v, w) = E_{uv}$. Hence (A6) is proved. With (A6) and LaSalle’s invariant principle (cf. (LaSalle 1960, Theorem 3)), the proof is completed. $\square$

In what follows we assume $\theta \in (0, L)$ and consider two types of functional responses separately.

A.2. Global stability for $\theta \in (0, L)$ and Holling type I (1.3)

We next show that the unique coexistence equilibrium P_* is globally asymptotically stable as long as it exists.

Lemma A.3 (Global stability of P_*). *Let (1.3) hold and $\theta \in (\theta_0, L)$. Then the unique coexistence equilibrium $P_* = (u_*, v_*, w_*)$ of (1.2) is globally asymptotically stable.*

Proof Let $E_s = P_* = (u_*, v_*, w_*)$ in (A3) and (A4). Then (A4) implies $\Gamma_i = \beta_i$, $i = 1, 2$. Using (1.2), (1.3), (A3), (A4) and the fact that

$$\theta = \beta_1 f_1(u_*) + \beta_2 f_2(v_*) = \alpha_1 \beta_1 u_* + \alpha_2 \beta_2 v_*, \quad 1 = \frac{u_*}{K_1} + \alpha_1 w_* = \frac{v_*}{K_2} + \alpha_2 w_*,$$

we have

$$\begin{aligned}\mathcal{E}'(t; P_*) &= \beta_1 \left(1 - \frac{u}{K_1} - \alpha_1 w\right) (u - u_*) + \beta_2 \left(1 - \frac{v}{K_2} - \alpha_2 w\right) (v - v_*) \\ &\quad + (\alpha_1 \beta_1 u + \alpha_2 \beta_2 v - \theta)(w - w_*) \\ &= \beta_1 \left(1 - \frac{u}{K_1} - \alpha_1 w_*\right) (u - u_*) + \beta_2 \left(1 - \frac{v}{K_2} - \alpha_2 w_*\right) (v - v_*) \\ &= -\frac{\beta_1}{K_1} (u - u_*)^2 - \frac{\beta_2}{K_2} (v - v_*)^2.\end{aligned}$$

Hence $\mathcal{E}'(t; P_*) \leq 0$, where “=” possibly holds in the case of $(u, v) = (u_*, v_*)$. Note that if $(u, v) = (u_*, v_*)$, then $w = w_*$ since the system (1.2) admits the unique coexistence equilibrium P_* for $\theta \in (\theta_0, L)$. Therefore, $\mathcal{E}'(t; P_*) < 0$ if $(u, v, w) \neq E_{uv}$. If $(u, v, w) = P_*$, then (A3) obviously shows that $\mathcal{E}(t; P_*) = 0$ for all $t > 0$, which implies that $\mathcal{E}'(t; P_*) = 0$ for all $t > 0$. We obtain

$$\mathcal{E}'(t; E_{uv}) \leq 0, \text{ where “=” holds if and only if } (u, v, w) = E_{uv}.$$

Moreover, the same arguments as in the proof of Lemma A.2 yield that $\mathcal{E}(t; P_*) > 0$ for $(u, v, w) \neq P_*$. Then the proof is completed by an application of LaSalle’s invariant principle. $\square$

Note that $\theta_0 = 0$ if and only if $\alpha_1 = \alpha_2$. If $\alpha_1 = \alpha_2$, then Lemma A.2 and Lemma A.3 imply that for any $\theta > 0$, either E_{uv} or P_* is globally asymptotically stable. We next consider the case $\alpha_1 \neq \alpha_2$, which implies $\theta_0 > 0$. Then in view of Table 1, the semi-coexistence equilibria P_1 and P_2 exist for $\theta \in (0, \theta_0]$ since $0 < \theta_0 < \min\{L_1, L_2\}$. The following result gives the global stability of P_1 and P_2 .

Lemma A.4 (Global stability of P_1 and P_2). *Let (1.3) hold, $\alpha_2 > \alpha_1$ (resp. $\alpha_1 > \alpha_2$) and $\theta \in (0, \theta_0]$. Then the semi-coexistence equilibrium P_1 (resp. P_2) of (1.2) is globally asymptotically stable.*

Proof Without loss of generality, we only prove the global stability for $P_1 = (u_{P_1}, 0, w_{P_1}) = (\frac{\theta}{\alpha_1 \beta_1}, 0, \frac{L_1 - \theta}{\alpha_1 L_1})$ in the case of $\alpha_2 > \alpha_1$, and the proof for P_2 in the case of $\alpha_1 > \alpha_2$ is similar. Let $E_s = P_1$ in (A3) and (A4), then (A4) implies $\Gamma_i = \beta_i, i = 1, 2$. Clearly, $0 < \theta_0 = (1 - \frac{\alpha_1}{\alpha_2})L_1 < L_1$, and hence

$$\alpha_2 w_{P_1} = \frac{\alpha_2}{\alpha_1} \left(1 - \frac{\theta}{L_1}\right) \geq \frac{\alpha_2}{\alpha_1} \left(1 - \frac{\theta_0}{L_1}\right) = 1,$$

which alongside (1.2), (1.3), $\theta = \alpha_1 \beta_1 u_{P_1}$ and $\alpha_1 w_{P_1} = 1 - \frac{u_{P_1}}{K_1}$ implies that

$$\begin{aligned}\mathcal{E}'(t; P_1) &= \beta_1 \left(1 - \frac{u}{K_1} - \alpha_1 w\right) (u - u_{P_1}) + \beta_2 \left(1 - \frac{v}{K_2} - \alpha_2 w\right) v \\ &\quad + (\beta_1 f_1(u) + \beta_2 f_2(v) - \theta) (w - w_{P_1}) \\ &= \beta_1 \left(1 - \frac{u}{K_1} - \alpha_1 w_{P_1}\right) (u - u_{P_1}) + \beta_2 \left(1 - \frac{v}{K_2} - \alpha_2 w_{P_1}\right) v \\ &\leq -\frac{\beta_1}{K_1} (u - u_{P_1})^2 - \frac{\beta_2}{K_2} v^2.\end{aligned}$$

The rest of the proof is similar to that of Lemma A.2, and we omit it for brevity. $\square$

A.3. Global stability for $\theta \in (0, L)$ and Holling type II (1.4)

We now consider the case of Holling type II (1.4). We first give the global stability of semi-coexistence equilibria Q_1 and Q_2 .

Lemma A.5 (Global stability of Q_1 and Q_2). *Let (1.4) hold and $\theta \in (0, L_1)$ (resp. $\theta \in (0, L_2)$). Then the semi-coexistence equilibrium Q_1 (resp. Q_2) of (1.2) is globally asymptotically stable if (2.1) (resp. (2.2)) holds.*

Proof Without loss of generality, we only prove the global stability for $Q_1 = (u_{Q_1}, 0, w_{Q_1})$, and the case for Q_2 can be proved similarly. Let $E_s = Q_1 = (u_{Q_1}, 0, w_{Q_1})$ in (A3) and (A4). Then (A4) implies

$$\Gamma_1 = \frac{\beta_1}{1 + \gamma_1 h_1 u_{Q_1}} \quad \text{and} \quad \Gamma_2 = \beta_2 \quad (\text{A9})$$

If $v_0 \leq K_2$, then (A1) implies $v(t) \leq K_2$ for all $t \geq 0$. This along with (2.1) and the fact $\frac{f_2(s)}{s}$ decreases for $s \geq 0$ indicates that $\frac{w_{Q_1} f_2(v)}{v} \geq \frac{w_{Q_1} f_2(K_2)}{K_2} \geq 1$ for all $t \geq 0$. Similarly, if $v_0 > K_2$, then (2.1) implies $\frac{K_2}{f_2(K_2)} < w_{Q_1}$. Hence (A2) yields $T_1 > 0$ such that $\frac{w_{Q_1} f_2(v)}{v} > 1$ for all $t \geq T_1$. Therefore, for $v_0 \geq 0$, it holds that

$$\frac{w_{Q_1} f_2(v)}{v} \geq 1 \quad \text{for all } t \geq T_1. \quad (\text{A10})$$

Using $\theta = \beta_1 f_1(u_{Q_1})$, (1.4), (A9) and (A10), we have

$$\beta_1 f_1(u) - \theta = \beta_1 (f_1(u) - f_1(u_{Q_1})) = \beta_1 \frac{\gamma_1 (u - u_{Q_1})}{(1 + \gamma_1 h_1 u)(1 + \gamma_1 h_1 u_{Q_1})} = \Gamma_1 \frac{f_1(u)}{u} (u - u_{Q_1}).$$

Consequently,

$$\begin{aligned}
 \mathcal{E}'(t; Q_1) &= \Gamma_1 \left(1 - \frac{u}{K_1} - \frac{wf_1(u)}{u} \right) (u - u_{Q_1}) + \beta_2 \left(1 - \frac{v}{K_2} - \frac{wf_2(v)}{v} \right) v \\
 &\quad + (\beta_1 f_1(u) + \beta_2 f_2(v) - \theta) (w - w_{Q_1}) \\
 &= \Gamma_1 \left(1 - \frac{u}{K_1} - \frac{wQ_1 f_1(u)}{u} \right) (u - u_{Q_1}) + \beta_2 \left(1 - \frac{v}{K_2} - \frac{wQ_1 f_2(v)}{v} \right) v \\
 &= -\frac{\Gamma_1 h_1 \gamma_1 (\lambda_1 + u_{Q_1} - K_1 + u)}{K_1 (1 + h_1 \gamma_1 u)} (u - u_{Q_1})^2 - \frac{\beta_2}{K_2} v^2 + \beta_2 \left(1 - \frac{wQ_1 f_2(v)}{v} \right) v \\
 &\leq -\frac{\Gamma_1 h_1}{K_1} f_1(u) (u - u_{Q_1})^2 - \frac{\beta_2}{K_2} v^2 \quad \text{for all } t \geq T_1.
 \end{aligned}$$

Then the global stability of Q_1 follows from the Lyapunov function method and LaSalle's invariant principle, similar as in the proof of Lemma A.2. $\square$

We next prove the global stability of the coexistence equilibrium Q_* .

Lemma 4.1 (Global stability of Q_*). *Let (1.4) hold, $\theta \in (0, L)$ and Q_* be a coexistence equilibrium of (1.2). Then Q_* is globally asymptotically stable if (2.3) holds.*

Proof Let $E_s = Q_* = (u_*, v_*, w_*)$ in (A3) and (A4). Then (A4) gives

$$\Gamma_1 = \frac{\beta_1}{1 + \gamma_1 h_1 u_*}, \quad \Gamma_2 = \frac{\beta_2}{1 + \gamma_2 h_2 v_*}.$$

Using (1.2), (1.3) and $\theta = \beta_1 f_1(u_*) + \beta_2 f_2(v_*)$, we obtain

$$\begin{aligned}
 \mathcal{E}'(t; Q_*) &= \Gamma_1 \left(1 - \frac{u}{K_1} - \frac{wf_1(u)}{u} \right) (u - u_*) + \Gamma_2 \left(1 - \frac{v}{K_2} - \frac{wf_2(v)}{v} \right) (v - v_*) \\
 &\quad + \beta_1 (f_1(u) - f_1(u_*)) (w - w_*) + \beta_2 (f_2(v) - f_2(v_*)) (w - w_*). \quad (\text{A11})
 \end{aligned}$$

Similar as in driving (A7) and (A8), we have

$$\beta_1 (f_1(u) - f_1(u_*)) = \Gamma_1 \frac{f_1(u)}{u} (u - u_*) \quad \text{and} \quad \beta_2 (f_2(v) - f_2(v_*)) = \Gamma_2 \frac{f_2(v)}{v} (v - v_*). \quad (\text{A12})$$

Substituting (A12) into (A11) and using $w_* = \frac{u_*}{f_1(u_*)} (1 - \frac{u_*}{K_1}) = \frac{v_*}{f_2(v_*)} (1 - \frac{v_*}{K_2})$ yields

$$\begin{aligned}
 \mathcal{E}'(t; Q_*) &= \Gamma_1 \left(1 - \frac{u}{K_1} - \frac{w_* f_1(u)}{u} \right) (u - u_*) + \Gamma_2 \left(1 - \frac{v}{K_2} - \frac{w_* f_2(v)}{v} \right) (v - v_*) \\
 &= -\frac{\Gamma_1 h_1 \gamma_1 (\lambda_1 + u_* - K_1 + u)}{K_1 (1 + h_1 \gamma_1 u)} (u - u_*)^2 - \frac{\Gamma_2 h_2 \gamma_2 (\lambda_2 + v_* - K_2 + v)}{K_2 (1 + h_2 \gamma_2 v)} (v - v_*)^2 \\
 &\leq -\frac{\Gamma_1 h_1}{K_1} f_1(u) (u - u_*)^2 - \frac{\Gamma_2 h_2}{K_2} f_2(v) (v - v_*)^2.
 \end{aligned}$$

Similar arguments with the Lyapunov function method alongside LaSalle's invariant principle as above complete the proof. $\square$

Proof of Theorem 2.1. In view of Lemmas A.2, A.3 and A.4, Theorem 2.1 is proved. $\square$

Proof of Theorem 2.2. With the results from Lemmas A.2, A.5 and 4.1, Theorem 2.2 is obtained. $\square$

Appendix B. Proof for Remark 2.2

This appendix is dedicated to proving the conclusion stated in Remark 2.2.

Proof for Remark 2.2 We first prove

$$\Lambda_1 \cap \Lambda_2 = \emptyset. \quad (\text{B1})$$

Note that w_{Q_1} strictly increases with respect to $K_1 > 0$ since

$$\frac{dw_{Q_1}}{dK_1} = \frac{u_{Q_1}^2}{f_1(u_{Q_1})K_1^2} = \frac{\beta_1 u_{Q_1}^2}{\theta K_1^2} > 0.$$

Let $(K_1, K_2) \in \Lambda_1$. If $\gamma_1 \geq \gamma_2$, then the first condition in Λ_1 implies that

$$w_{Q_1} \leq w_{Q_1}|_{K_1=\lambda_1+u_{Q_1}} = \frac{1}{\gamma_1} \leq \frac{1}{\gamma_2} < \frac{1+\gamma_2 h_2 K_2}{\gamma_2} = \frac{K_2}{f_2(K_2)},$$

which contradicts $(K_1, K_2) \in \Lambda_1$. Therefore, $\Lambda_1 = \emptyset$ in the case of $\gamma_1 \geq \gamma_2$. Similarly one can show that $\Lambda_2 = \emptyset$ in the case of $\gamma_1 \leq \gamma_2$. The claim (B1) is proved.

Without loss of generality, we next assume $\gamma_1 \geq \gamma_2$, then $\Lambda_1 = \emptyset$. It remains to prove that

$$\Lambda_2 \cap \Lambda_* = \emptyset. \quad (\text{B2})$$

Assuming that there exists a pair $(K_1, K_2) \in \Lambda_2 \cap \Lambda_*$, we shall derive a contradiction. Using

$$\theta = \beta_2 f_2(v_{Q_2}) = \beta_1 f_1(u_*) + \beta_2 f_2(v_*),$$

and the fact that $f_i(s)$ and $\frac{s}{f_i(s)}$ ($i = 1, 2$) strictly increase with respect to $s \geq 0$, we have

$$v_* < v_{Q_2} < K_2 \quad \text{and} \quad w_* = \frac{u_*}{f_1(u_*)} \left(1 - \frac{u_*}{K_1}\right) < \frac{u_*}{f_1(u_*)} < \frac{K_1}{f_1(K_1)}. \quad (\text{B3})$$

By the second condition in Λ_2 and (B3), we have $w_* < w_{Q_2}$, which means that

$$w_* = \varphi_0(v_*) < \varphi_0(v_{Q_2}) = w_{Q_2}, \quad (\text{B4})$$

where

$$\begin{aligned} \varphi_0(s) &:= \frac{s}{f_2(s)} \left(1 - \frac{s}{K_2}\right) = \frac{(K_2 - s)(1 + h_2 \gamma_2 s)}{K_2 \gamma_2} \\ &= -\frac{h_2}{K_2} \left(s - \frac{K_2 - \lambda_2}{2}\right)^2 + \frac{h_2(K_2 - \lambda_2)^2}{4K_2} + \frac{1}{\gamma_2}, \quad s \in [0, K_2]. \end{aligned} \quad (\text{B5})$$

The combination of the first equation of (B3), (B4) and (B5) implies that

$$v_* < \frac{K_2 - \lambda_2}{2} \quad \text{and} \quad v_* + v_{Q_2} < K_2 - \lambda_2. \quad (\text{B6})$$

Starting from the first condition in Λ_2 , the second condition in Λ_* , and the second inequality in (B6), we obtain $2K_2 < 2\lambda_2 + v_* + v_{Q_2} < 2\lambda_2 + K_2 - \lambda_2$, which simplifies to $K_2 \leq \lambda_2$. Therefore, the first inequality in (B6) indicates $v_* \leq 0$ which is absurd. This proves (B2) and hence proves that Λ_1 , Λ_2 and Λ_* are mutually disjoint. $\square$

Appendix C.

This appendix is devoted to proving that the rescaled system (3.7) with (3.8) has at most one coexistence equilibrium $Q_* = (u_*, v_*, w_*)$ (see (3.9)), which exists if and only if $\theta \in (\Theta_1, L)$, where Θ_1 and L are given by (3.10). Remark 2.1 implies $\theta \in (0, L)$ is a necessary condition for the existence of Q_* . Therefore, we shall consider $\theta \in (0, L)$ below. Within this appendix, we shall use the notations defined in (3.10). For clarity, we also introduce the following notations.

- For $\gamma_2 \in (0, 1)$, $b > 0$ and $\theta \in (0, L)$, let

$$v_M := \frac{\theta}{\gamma_2(b - \theta)} \quad (\text{C1})$$

be a positive constant (note that (3.10) implies $\theta < b$), then v_M strictly increases in $\theta \in (0, L)$ and

$$v_M \begin{cases} < 1, & \text{if } \theta \in (0, L_2), \\ \geq 1, & \text{if } \theta \in [L_2, L). \end{cases} \quad (\text{C2})$$

- It is straightforward to check that either of the equations

$$\begin{cases} 8s^3 + 7s^2 - 8s + 1 = 0, \\ 24s^3 - 13s^2 - 6s + 3 = 0, \end{cases} \quad s \in \mathbb{R},$$

has two positive (real) roots and one negative (real) root. Denote the two positive roots of the first equation by η_1 and η_3 with $\eta_1 < \eta_3$, and the largest root of the second equation by η_4 . Let $\eta_2 = \frac{4\sqrt{7}-7}{9}$. Then

$$(\eta_1, \eta_2, \eta_3, \eta_4) \approx (0.1471, 0.3981, 0.5429, 0.6195).$$

- For $b > 0$, define the functions

$$\xi_1(\gamma_2) := \frac{b(4\gamma_2^2 - 5\gamma_2 + 1)}{1 - 3\gamma_2}, \quad \gamma_2 \in (\eta_1, \frac{1}{4}) \cup (\eta_3, 1),$$

$$\xi_2(\gamma_2) := \frac{b}{3}(4 - \gamma_2 - \sqrt{\gamma_2^2 + \gamma_2 + 1}), \quad \gamma_2 \in (\eta_2, 1).$$

It holds that $\xi_1(\gamma_2)$ strictly decreases in each connected domain with $\xi_1(\gamma_2) \in (0, L)$,

$$\lim_{\gamma_2 \rightarrow \eta_1} \xi_1(\gamma_2) = \lim_{\gamma_2 \rightarrow \eta_3} \xi_1(\gamma_2) = L \quad \text{and} \quad \lim_{\gamma_2 \rightarrow \frac{1}{4}} \xi_1(\gamma_2) = \lim_{\gamma_2 \rightarrow 1} \xi_1(\gamma_2) = 0.$$

The function $\xi_2(\gamma_2)$ strictly decreases in $(\eta_2, 1)$ with $\xi_2(\gamma_2) \in (m_b, L)$,

$$\lim_{\gamma_2 \rightarrow \eta_2} \xi_2(\gamma_2) = L \quad \text{and} \quad \lim_{\gamma_2 \rightarrow 1} \xi_2(\gamma_2) = m_b,$$

where $m_b := (1 - \frac{1}{\sqrt{3}})b$. Moreover, for $\gamma_2 \in (\eta_3, 1)$,

$$\begin{cases} \xi_1(\gamma_2) > \xi_2(\gamma_2), & \text{if } \gamma_2 \in (\eta_3, \eta_4), \\ \xi_1(\eta_4) = \xi_2(\eta_4) \approx 0.6550, \\ \xi_1(\gamma_2) < \xi_2(\gamma_2), & \text{if } \gamma_2 \in (\eta_4, 1). \end{cases}$$

The graphs of three functions $\frac{\xi_1(\gamma_2)}{b}$, $\frac{\xi_2(\gamma_2)}{b}$ and $\frac{L}{b} = \frac{1+3\gamma_2}{2(1+\gamma_2)}$ are shown in Fig. 9(a)

- For $b > 0$, $\gamma_2 \in (0, 1)$ and $0 < \theta < L$, let

$$G(s) := \sum_{k=0}^4 D_k s^k, \quad s \geq 0, \quad (\text{C3})$$

where the coefficients are given by

$$\begin{cases} D_4 = \gamma_2^3(2b - \theta)^2, \\ D_3 = \gamma_2^2(2b - \theta)(2b(2 - \gamma_2) - \theta(3 - \gamma_2)), \\ D_2 = (\gamma_2 - 1)\gamma_2(b^2(3\gamma_2 - 5) - 2b\theta(\gamma_2 - 4) - 3\theta^2), \\ D_1 = b^2(4\gamma_2^2 - 5\gamma_2 + 1) - 2b\theta(2\gamma_2^2 - 4\gamma_2 + 1) + \theta^2(1 - 3\gamma_2), \\ D_0 = b^2(\gamma_2 - 1) - 2b\theta(\gamma_2 - 1) - \theta^2. \end{cases} \quad (\text{C4})$$

By elementary analysis (omitted for brevity), we have the following result concerning the signs of the coefficients given in (C4).

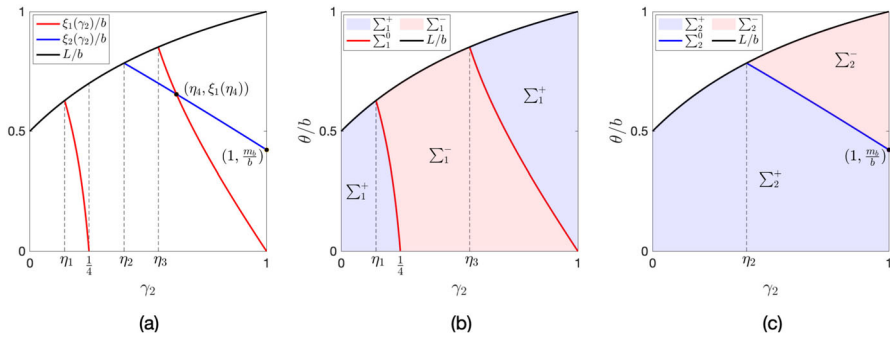


Fig. 9 The graphs of three functions $\frac{\xi_1(\gamma_2)}{b}$, $\frac{\xi_2(\gamma_2)}{b}$ and $\frac{L}{b}$ versus $\gamma_2 \in (0, 1)$ are shown in (a). The signs of D_1 and D_2 in the γ_2 - θ/b plane within $(\gamma_2, \theta) \in (0, 1) \times (0, L)$ are shown in (b) and (c), respectively

Proposition C.1 Let $b > 0$, $\gamma_2 \in (0, 1)$ and $\theta \in (0, L)$. Then $D_4, D_3 > 0$, $D_0 < 0$, and

$$D_1 \begin{cases} < 0, & \text{if } (\gamma_2, \theta) \in \Sigma_1^- := (\eta_1, \frac{1}{4}] \times (\xi_1, L) \cup (\frac{1}{4}, \eta_3] \times (0, L) \cup (\eta_3, 1) \times (0, \xi_1), \\ = 0, & \text{if } (\gamma_2, \theta) \in \Sigma_1^0 := (\eta_1, \frac{1}{4}) \times \{\xi_1(\gamma_2)\} \cup (\eta_3, 1) \times \{\xi_1(\gamma_2)\}, \\ > 0, & \text{if } (\gamma_2, \theta) \in \Sigma_1^+ := (0, \eta_1] \times (0, L) \cup (\eta_1, \frac{1}{4}) \times (0, \xi_1) \cup (\eta_3, 1) \times (\xi_1, L), \end{cases}$$

and

$$D_2 \begin{cases} < 0, & \text{if } (\gamma_2, \theta) \in \Sigma_2^- := (\eta_2, 1) \times (\xi_2, L), \\ = 0, & \text{if } (\gamma_2, \theta) \in \Sigma_2^0 := (\eta_2, 1) \times \{\xi_2(\gamma_2)\}, \\ > 0, & \text{if } (\gamma_2, \theta) \in \Sigma_2^+ := (0, \eta_2] \times (0, L) \cup (\eta_2, 1) \times (0, \xi_2). \end{cases}$$

Proposition C.1 provides a geometric illustration for the signs of D_1 and D_2 in the γ_2 - θ/b plane within $(\gamma_2, \theta) \in (0, 1) \times (0, L)$, as shown in Fig. 9(b)-(c). Based on Proposition C.1, we get the following results with tedious but elementary calculations.

Proposition C.2 Let $b > 0$, $\gamma_2 \in (0, 1)$ and $\theta \in (0, L)$. Then the function $G(s)$ defined by (C3) has exactly one real root in $(0, +\infty)$.

We can now prove the main result of this appendix.

Lemma C.3 The rescaled system (3.7) with (3.8) has a unique coexistence equilibrium $Q_* = (u_*, v_*, w_*)$ if and only if $\theta \in (\Theta_1, L)$. Moreover,

$$u_* = \frac{\gamma_2 v_*(b - \theta)(v_M - v_*)}{\gamma_2 v_*(2b - \theta) + b - \theta}, \quad w_* = (1 - v_*) \left(v_* + \frac{1}{\gamma_2} \right),$$

and $v_* \in (0, \min\{1, v_M\})$ satisfies $G(v_*) = 0$, where the positive constant v_M and the function G are given by (C1) and (C3), respectively.

Proof Clearly, it follows from (C3) and Proposition C.1 that $G(0) = D_0 < 0$, which alongside Proposition C.2 implies that the rescaled system (3.7) with (3.8) has a unique

coexistence equilibrium $Q_* = (u_*, v_*, w_*)$ if and only if $G(\min\{1, v_M\}) > 0$. If $\theta \in [L_2, L)$, then (C2) implies $G(\min\{1, v_M\}) = G(1) = 2b\gamma_2(\gamma_2 + 1)^2(L - \theta) > 0$. If $\theta \in (0, L_2)$, then

$$G(\min\{1, v_M\}) = G(v_M) = \frac{b^4\varphi_2(\theta)}{\gamma_2(b - \theta)^4},$$

where $\varphi_2(\theta)$ is given by (3.11), and $\varphi_2(\theta) > 0$ if and only if $\theta > \Theta_1$. The proof is completed. $\square$

Acknowledgements The authors are grateful to the anonymous reviewer for the careful reading, insightful comments and grammatical corrections, which greatly helped us improve the precision and exposition of this article. The research of Y. Lou is partially supported by the NSF of China (No. 12261160366 and No. 12250710674). The research of W. Tao is partially supported by PolyU Postdoc Matching Fund Scheme Project ID P0030816/B-Q75G, 1-W15F and 1-YXBT, and the NSF of China (No. 12201082). The research of Z.-A. Wang was partially supported by the NSFC/RGC Joint Research Scheme sponsored by the Research Grants Council of Hong Kong and the National Natural Science Foundation of China (Project No. N_PolyU509/22), and PolyU Postdoc Matching Fund Scheme Project ID P0034904 (Primary Work Programme W15F).

Funding Open access funding provided by The Hong Kong Polytechnic University

Data Availability The authors declare that the manuscript has no associated data.

Declaration

Conflict of interest The authors have no conflicts of interest to declare that are relevant to the content of this article.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

References

- Abrams PA (1999) Is predator-mediated coexistence possible in unstable systems? *Ecology* 80(2):608–621
- Robert S (2003) Cantrell and Chris Cosner. Spatial ecology via reaction-diffusion equations. John Wiley & Sons Ltd, Chichester
- Caswell H (1978) Predator-mediated coexistence: a nonequilibrium model. *Amer Nat* 112(983):127–154
- Chailloux A, Mohl EK, Alves MT, Messelink GJ, Desneux N (2014) Natural enemy-mediated indirect interactions among prey species: potential for enhancing biocontrol services in agroecosystems. *Pest Manag Sci* 70(12):1769–1779
- Chaneton EJ, Bonsall MB (2000) Enemy-mediated apparent competition: empirical patterns and the evidence. *Oikos* 88(2):380–394
- Cheng K-S (1981) Uniqueness of a limit cycle for a predator-prey system. *SIAM J Math Anal* 12(4):541–548
- Cosner C (2014) Reaction-diffusion-advection models for the effects and evolution of dispersal. *Discrete Contin Dyn Syst* 34(5):1701–1745

- DeCesare NJ, Hebblewhite M, Robinson HS, Musiani M (2010) Endangered, apparently: the role of apparent competition in endangered species conservation. *Anim Conser* 13(4):353–362
- Holt RD (1977) Predation, apparent competition, and the structure of prey communities. *Theor Popul Biol* 12(2):197–229
- Holt RD, Bonsall MB (2017) Apparent competition. *Annu Rev Ecol Evol Syst* 48(1):447–471
- Holt RD, Polis GA (1997) A theoretical framework for intraguild predation. *Amer Nat* 149(4):745–764
- Hsu S-B (1981) Predator-mediated coexistence and extinction. *Math Biosci* 54(3):231–248
- Kang Y, Wedekin L (2013) Dynamics of a intraguild predation model with generalist or specialist predator. *J Math Biol* 67(5):1227–1259
- Karban R, Hougén-Eitzmann D, English-Loeb G (1994) Predator-mediated apparent competition between two herbivores that feed on grapevines. *Oecologia* 97(4):508–511
- Kareiva P, Odell G (1987) Swarms of predators exhibit “preytaxis” if individual predators use area-restricted search. *Amer Natur* 130(2):233–270
- LaSalle JP (1960) Some extensions of Liapunov’s second method. *IRE Trans CT-7*:520–527
- Logemann H, Ryan EP (2014) Ordinary differential equations: Analysis, qualitative theory and control. Springer, London
- Lotka AJ (1925) Elements of physical biology. Williams & Wilkins, Baltimore
- May RM (2001) Stability and Complexity in Model Ecosystems. Princeton University Press, Princeton, second edition
- Mimura M, Kan-on Y (1986) Predation-mediated coexistence and segregation structures. in studies in mathematics and its applications. Elsevier 18:129–155
- Murdoch WW, Briggs CJ, Nisbet RM (2013) Consumer-Resource Dynamics (MPB-36). Princeton University Press, Princeton
- Murray JD (2002) Mathematical Biology I: An introduction, volume 17 of Interdisciplinary Applied Mathematics. Springer-Verlag, New York, third edition, (2002)
- Ni W-M (2011) The mathematics of diffusion. SIAM, (2011)
- Piltz SH, Veerman F, Maini PK, Porter MA (2017) A predator-2 prey fast-slow dynamical system for rapid predator evolution. *SIAM J Appl Dyn Syst* 16(1):54–90
- Ryan D, Cantrell RS (2015) Avoidance behavior in intraguild predation communities: a cross-diffusion model. *Discrete Contin Dyn Syst* 35(4):1641
- Sapoukhina N, Tyutyunov Y, Arditi R (2003) The role of prey taxis in biological control: a spatial theoretical model. *Amer Nat* 162(1):61–76
- Schmitz OJ (2007) Predator diversity and trophic interactions. *Ecology* 88(10):2415–2426
- Stige LC, Kvile KØ, Bogstad B, Langangen Ø (2018) Predator-prey interactions cause apparent competition between marine zooplankton groups. *Ecology* 99(3):632–641
- Vance RR (1978) Predation and resource partitioning in one predator - two prey model communities. *Amer Nat* 112(987):797–813
- Wang X, Zanette L, Zou X (2016) Modelling the fear effect in predator-prey interactions. *J Math Biol* 73(5):1179–1204
- Williamson MH (1957) An elementary theory of interspecific competition. *Nature* 180(4583):422–425