Journal of Mathematical Biology (2026) 93:11
https://doi.org/10.1007/s00285-026-02427-w

Mathematical Biology

Discrete-time exploitative competition model of different stage-specific predators

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Received: 1 December 2025 / Revised: 31 May 2026 / Accepted: 11 June 2026

Abstract

We consider a discrete-time competition model between native and alien predator populations for a common prey. The model is described by a system of three recurrence relations governing their population dynamics, with a generic density-dependent effect for prey and a generic predation factor. In our model, the native and alien predators prey on different stages of the common prey: juvenile-specific and adult-specific predators. In this paper, we focus on the invadability of native prey-predator system to an alien predator and investigate which stage-specific alien predator could be more successful in invading the native system with a different stage-specific native predator. Our mathematical results demonstrate that the prey-predator system with an adult-specific native predator is more vulnerable to the juvenile-specific alien predator invasion compared to the native system with a juvenile-specific native predator. To illustrate the general result more clearly, we present some detailed results on a specific model with a Beverton-Holt type of density-dependent effect and a Nicholson-Bailey type of predation factor, which effectively demonstrates such the dependence of vulnerability to an alien predator invasion on the stage-specific predation.

Keywords Prey-predator system · Exploitative competition · Stage-specific predation · Discrete-time model · Beverton-Holt model · Nicholson-Bailey model

Mathematics Subject Classification 92B99 · 92D25 · 92D40 · 39A60 · 37N25

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1 Introduction

Extinction and speciation processes have significantly impacted the biodiversity in nature (Johnson et al. 2017). Today, various human activities are causing unprecedented changes in biodiversity, primarily due to climate change, environmental degradation, and invasive species. These factors pose numerous challenges to ecosystem conservation (Sala et al. 2000; Chaudhary et al. 2021; Kubelka et al. 2022; Lopez et al. 2022; Le Hen et al. 2023). Among these, biological invasions are the primary and observable cause of biodiversity change, threatening the persistence of native species (Lockwood et al. 2013; Bellard et al. 2016; Turbelin et al. 2017; Seebens et al. 2018; King et al. 2021; Poland et al. 2021; Siddiqui et al. 2021; Wainright et al. 2021; Wilson et al. 2012; Haubrock et al. 2022a; Lopez et al. 2022; Ziska 2022; Wauters et al. 2023, and reference therein). can lead to the extinction of native species (Cambray 2003; Gherardi et al. 2011; Haubrock et al. 2021, 2022a, b; Le Hen et al. 2023).

As discussed in Abrams (2022), the competitive relationship between different populations is determined by the detail of ecological factors that cause mutually negative reactions to each population's growth. Consequently, the actual competitive interspecific reaction is characterized by these ecological details. This principle applies not only to competitive relationships but also to other interspecific relationships. The pioneering period witnessed the development of theoretical and mathematical theories on the population dynamics of interacting species. These theories, which primarily focus on the subsequent influences of interactions with other species, are still evolving today. Among the most traditional theories, the Lotka-Volterra system stands out (for instance, see the historical overviews in (Kingsland 1995; Bacaër 2011)).

One of the simplest forms of competitive interaction is exploitative competition, which arises when different consumers utilize a shared resource. This mutual negative influence is indirectly induced by the consumption of the common resource (Case 2000; Gotelli 2001; Odum and Barrett 2005; Abrams 2022; Seno 2022). For instance, two predator species preying on a common prey can be considered to be under a typical exploitative competition for the prey (Preisser and Elkinton 2008; Wignall et al. 2020; Case and Tarwater 2023; Page and Williams 2023).

The simplest modeling of exploitative competition dynamics typically involves more than one predator (parasitoids or, more broadly, consumers) and a common prey (host or resource). Numerous studies have explored mathematical models for such exploitative competition dynamics involving two predators or parasitoids and one prey or host. The most widely used mathematical modeling for the population dynamics of interacting species is of the Lotka-Volterra type, utilizing a system of differential equations. It is also the case regarding exploitative competition dynamics (refer to (Abrams 2022)). Discrete-time modeling, which employs a system of difference equations, that is, recurrence relations, has been applied less frequently to the population dynamics of interacting species compared to continuous time modeling. Previous research has shown that discrete-time models can exhibit complexities in their dynamical nature, even with simple nonlinearity (May 1974; Martelli 1992; Kaplan and Glass 1995; Allen 2007; Robinson 2012; Mickens 2015; Frisman et al. 2021a, b; Seno 2022; Elaydi and Cushing 2025).

One of the most popular extensions in modeling such prey-predator dynamics is to introduce a population structure in either the prey or predator population, based on factors like age, size, or stage. This approach has been widely used in research (Metz and Diekmann 1986; Cushing 1994, 1998; Cola et al. 1998; Hassell 2000; Liu et al. 2002; Kooi and Kelpin 2003; Murdoch et al. 2003; Buffoni and Pasquali 2007; Briggs et al. 2010; Iannelli and Milner 2017; Inaba 2017; Seno 2022). One of the ecologically intriguing aspects of such structured prey-predator population dynamics is the predation on a specific stage within the structured prey population. This predation can be categorized as *stage-specific* (stage-dependent) in general, *age-specific* if it depends on the age of the prey, or *size-specific* if it depends on the size of the prey. As in many other mathematical studies on prey-predator dynamics, the stage-specific predation was introduced in a continuous-time model with differential equations. In the model, the prey population is classified into juvenile and adult subpopulations as a simple modeling approach. Alternatively, it can follow a distribution of age, size, or physiological state to characterize the heterogeneity of the prey population. (for instance, (Smith and Mead 1974; Gurtin and Levine 1979; Levine 1981; Cushing and Saleem 1982; Saleem 1984; McNair 1987; Saleem et al. 1987; Hastings 1983; Hassell 2000; Murdoch et al. 2003; Cui and Takeuchi 2006; Falconi 2006; Misra et al. 2013; Feng et al. 2014)).

While there are numerous works on discrete-time models with recurrence relations about prey-predator or host-parasitoid population dynamics (for instance, (May and Hassell 1981; Hassell and Pacala 1257; Mills and Getz 1996; Tang and Chen 2002; Abbott and Dwyer 2007; Jang 2007; Çelik and Duman 2009; Asheghi 2014; Livadiotis et al. 2015; Marcinko and Kot 2020)), the stage-specific predation or parasitism itself has been the focus of only a few works with discrete-time models (May et al. 1981; Hastings 1984; Murdoch et al. 2003; Hackett-Jones et al. 2009; Weide et al. 2019; Hassell 2000; Jia et al. 2024). These previous works primarily focused on the role of stage-specific or age-specific predation in the stability of the prey-predator system. They explored how such specific predation could destabilize or stabilize the system, impacting the persistence of the composed species. This is because a particular type of predation can become a driving or suppressing force for the system's oscillatory state. We have not found any previous work that presents a mathematical model relating stage-specific predation to the success of an alien invasion in a native prey-predator system. We intend to discuss this topic in this paper.

In this paper, we will delve into the invadability of native prey-predator systems to alien predators, particularly considering the stage-specificity of both native and alien predators. We will examine a generic discrete-time prey-predator model with two distinct stage-specific predators and investigate the likelihood of an alien predator's invasion in the native prey-predator system. These native and alien predators are assumed to be specialists, preying on the same prey within a habitat region where the native predator resides, leading to exploitative competition for the common prey. As mentioned earlier, our focus will be on understanding how the stage at which the predator takes its prey could be linked to the invasion's success or failure, and we will explore the resistance of the native prey-predator system against the alien predator's invasion.

With mathematical results from our model, we will demonstrate that the invadability of a native prey-predator system significantly depends on the stage-specificity of predation for both native and alien predators. To provide a more comprehensive understanding of how invadability relates to the stage-specific predation of native and alien predators, we will present further detailed analytical and numerical results for a specific model with a given density-dependent effect function and predation term.

2 Modeling

2.1 Assumptions

To construct a population dynamics model that considers the invadability of a native prey-predator system to an alien predator invasion, we assume the following:

- Population dynamics for each of native and alien predators is generationally non-overlapping: Adult predators die out after their own reproduction season.
- Predator species $\mathrm{P^J}$ and $\mathrm{P^A}$ are specialists, that is, each predator's reproduction relies only on the predation for a specific prey species H, and the predator population goes extinct if the prey population does.
- Two predator species, $\mathrm{P^J}$ and $\mathrm{P^A}$, prey on juvenile and adult stages of a common prey H, respectively.
- The predation season for each predator species is over a sufficiently narrow window of time, so that there is no overlapping period between predation seasons for two predator species $\mathrm{P^J}$ and $\mathrm{P^A}$.
- No other interaction than the indirect exploitative competition about the common prey is assumed between predator species $\mathrm{P^J}$ and $\mathrm{P^A}$.
- Prey and predators produce their offspring only in respective reproduction seasons of every year (i.e., within every unit time step).
- The prey reproduction undergoes an intraspecific negative density-dependent effect. It is determined by the adult prey density at the reproduction season.
- Only the adult prey which successfully escapes from the predation can contribute to the reproduction.
- Prey and predators become adults in a year (i.e., within unit time step).

When two specialist predator species, $\mathrm{P^J}$ and $\mathrm{P^A}$, use the same prey, H, inhabiting a region, the predation by $\mathrm{P^J}$ reduces the juvenile prey population size. Consequently, the subsequent adult prey population size which is the prey available for the predator $\mathrm{P^A}$ is also reduced. The predation by $\mathrm{P^A}$ reduces the adult prey population size, leading to a decrease in the number of offspring produced by the adults who successfully escape the predation. Consequently, the number of juvenile prey available for the predator $\mathrm{P^J}$ diminishes. In this way, the two predator species, $\mathrm{P^J}$ and $\mathrm{P^A}$, exhibit an indirect interspecific reaction of exploitative competition, with distinct *stage-specific* predations for the common prey H. As we will describe in the next section, one of two predator species is designated as the native predator, while the other is introduced as the alien predator that invades the native system of the native predator and their prey H.

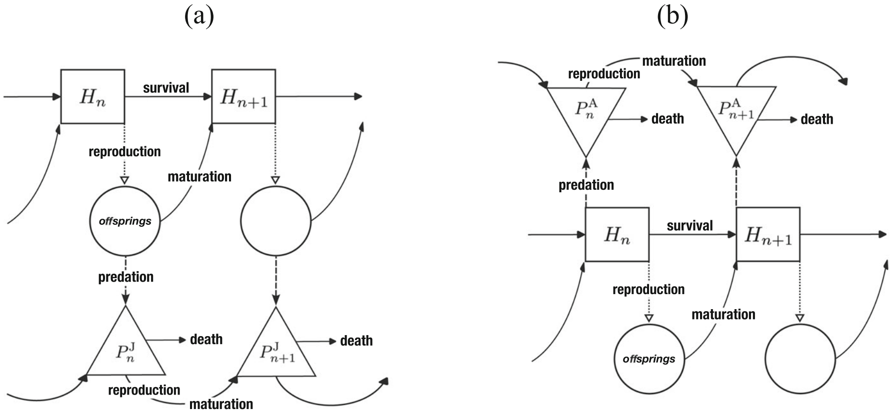

Fig. 1 Schematic illustration of interspecific relation in the native prey-predator system of (a) Model J; (b) Model A

A native system of prey and its specialized predator can be observed in various instances. For instance, a plant and its insect herbivore form such an interspecific relationship (Crawley 1989; Abbott and Dwyer 2007; Preisser and Elkinton 2008; Myers and Sarfraz 2017; Wilson et al. 2012; Jones et al. 2022). As another examples of such relationships, there are some host-parasitoid systems as mentioned in May and Hassell (1981); May et al. (1981); Hackett-Jones et al. (2009); Weide et al. (2019); Jia et al. (2024).

These assumptions made in this section exclude any additional complexity in prey-predator population dynamics. That is, they are intended to construct the simplest framework of mathematical models governing population dynamics, even though some are idealized for mathematical simplification. Nevertheless, they are the least complex to construct a reasonable basic mathematical model to discuss our theoretical problem. It is natural that modification of some assumptions would lead to more complex mathematical models. However, such modifications should be based on a reason to consider a specific aspect of prey-predator population dynamics.

2.2 Models J and A

To discuss the invadability of native prey-predator system to an alien predator invasion according to the difference in the stage-specific predation, we consider two models with distinct scenarios about an alien predator invasion of a native prey-predator system (Fig. 1):

Model J The native prey-predator system of $(\mathrm{H}, \mathrm{P}^{\mathrm{J}})$ undergoes the invasion of alien predator P^{J}.

Model A The native prey-predator system of $(\mathrm{H}, \mathrm{P}^{\mathrm{A}})$ undergoes the invasion of alien predator P^{A}.

2.3 Prey population dynamics without predation

We consider here the prey population dynamics governed by the following recurrence relation with an intraspecific density-dependent effect when there is no predator:

$$H_{n+1} = \sigma H_n + F(H_n)H_n, \tag{1}$$

where H_n denotes the adult prey population size at the beginning of its reproduction season in the n th year. The function F of H_n is the per capita growth rate of prey population, which gives the expected number of offsprings successfully becoming reproductive adults in the next reproduction season. The function F includes not only the density-dependent effect on the offspring production but also the survivability of offspring until its maturation. Parameter $\sigma \in [0, 1)$ represents the survival probability for the adult prey until the next reproduction season. In other words, it signifies the proportion σ of H_n that are expected to survive and participate in the reproduction of the next season. Therefore, the expected life span of adult prey after their first reproduction is calculated as $\sigma/(1-\sigma)$.

In our modeling, we assume the following mathematical features for the prey's per capita growth rate F:

- ▷ $F(0) = r_0 > 1 - \sigma$;
- ▷ $F(H) \to 0$ as $H \to \infty$;
- ▷ $F(H)$ is monotonically decreasing and positive for $H \geq 0$;
- ▷ $F(H)$ is differentiable twice for $H > 0$;
- ▷ $F'(H) \to F'(+0) := -\nu \in (-\infty, 0)$ as $H \to +0$;
- ▷ There exists a unique positive K such that $F(K) = 1 - \sigma$;
- ▷ $F(H)H$ is monotonically increasing for $H \in (0, K)$.

Parameter r_0 means the prey's intrinsic growth rate, that is the supremum of the expected number of offsprings produced per adult prey. From these features, the density-dependent effect is negative for the reproduction. The seventh feature of F, which is specific, will turn out to be essential for the mathematical results obtained from the analysis on our model. However, there is still a large family of functions for F that satisfy all the above features. A similar general setup of the per capita growth rate for a mathematical modeling is used in Jang (2007); Jang and Yu (2012).

From the above features of function F, we can easily find that the prey population dynamics (1) has the following nature, for example, by a proof making use of cobwebbing method (for instance, see (Allen 2007; Robinson 2012; Seno 2022; Elaydi and Cushing 2025)):

Lemma 1 *The prey population dynamics* (1) *generates a monotonic positive sequence* $\{H_n\}$ *from any initial value* $H_0 \in (0, K)$*, and it converges to* $K > 0$ *as* $n \to \infty$.

As a supplementary result, if $r_0 \leq 1 - \sigma$, the positive sequence $\{H_n\}$ is monotonically decreasing toward zero: $H_n \to 0$ as $n \to \infty$. Then the prey population necessarily goes extinct, and thus the prey-predator system itself cannot be established owing to the lack of prey persistence by itself. This is the reason why we take the first assumption given in the above: $r_0 > 1 - \sigma$, which is a necessary condition for the persistence of native prey-predator system.

In an ecological context, the equilibrium size K can be considered the *carrying capacity* for the prey population. Thus, for the ecological reasonability, we hereafter assume the initial value H_0 not beyond it: $H_0 \in (0, K]$. Then we have $H_n \in (0, K]$ for any $n \geq 0$ because of Lemma 1. From this modeling, it is the supremum of prey population size: $\sup_{\{H_n\}} H_n = K$ regardless of if the predator exists or not.

One of classic choices of F that satisfies the above features is given as

$$F(H) = \frac{r_0}{1 + H/\beta}, \tag{2}$$

where β is a positive parameter representing the strength of density-dependent effect on the prey reproduction. With the function F of (2), the carrying capacity K is given as

$$K = \beta\Big(\frac{r_0}{1-\sigma} - 1\Big) \tag{3}$$

with $r_0 > 1 - \sigma$. The prey population dynamics model by (1) and (2) with $\sigma = 0$ is is commonly referred to as the *Beverton-Holt model* (Beverton and Holt 1957; Hassell 1975). In a mathematical context, the Beverton-Holt model for a single population dynamics corresponds to the population growth governed by a well-known *logistic equation* in continuous time modeling, expressed as a single ordinary differential equation. The mathematical correspondence between these two models can be analytically demonstrated (for instance, see (Bohner and Warth 2007; Seno 2022; Elaydi and Cushing 2025)).

2.4 Native prey-predator system

Following the assumption about different stage-specific predations of two predator species P^{J} and P^{A} in Sect. 2.1, we shall consider the following systems of native prey-predator dynamics for Models J and A, respectively (see Fig. 1):

$$\text{Model J} \begin{cases} H_{n+1} = \sigma H_n + \Pi_{\mathrm{J}}(P_n^{\mathrm{J}}) F(H_n) H_n; \\ P_{n+1}^{\mathrm{J}} = \rho_{\mathrm{J}}\big\{1 - \Pi_{\mathrm{J}}(P_n^{\mathrm{J}})\big\} F(H_n) H_n; \end{cases} \tag{4}$$

$$\text{Model A} \begin{cases} H_{n+1} = \sigma \Pi_{\mathrm{A}}(P_n^{\mathrm{A}}) H_n + F\big(\Pi_{\mathrm{A}}(P_n^{\mathrm{A}}) H_n\big) \Pi_{\mathrm{A}}(P_n^{\mathrm{A}}) H_n; \\ P_{n+1}^{\mathrm{A}} = \rho_{\mathrm{A}}\big\{1 - \Pi_{\mathrm{A}}(P_n^{\mathrm{A}})\big\} H_n, \end{cases} \tag{5}$$

where P_n^{J} and P_n^{A} are the adult predator population sizes concerning the predation for the juvenile and adult prey stages at the n th year, respectively.

The factors Π_{J} and Π_{A} denote the probabilities of successful escape of the juvenile and adult prey from the predators P^{J} and P^{A}, respectively. Thus the value of $\Pi_\bullet$ is in $[0, 1)$, and $\Pi_\bullet = 1$ only when there is no predator. While the probability $\Pi_\bullet$

could depend in general on both densities of prey and predator, we assume here that it depends only on the predator density as denoted in (4) and (5). In this paper, we assume that the function $\Pi_\bullet(P)$ of P satisfies the following mathematical features:

- ▷ $\Pi_\bullet(0) = 1$;
- ▷ $\Pi_\bullet(P) \to 0$ as $P \to \infty$;
- ▷ $\Pi_\bullet(P) \in [0, 1)$ is monotonically decreasing, convex, and positive for $P \geq 0$;
- ▷ $\Pi_\bullet(P)$ is differentiable twice for $P > 0$;
- ▷ $\Pi'_\bullet(P) \to \Pi'_\bullet(+0) := -a_\bullet \in (-\infty, 0)$ as $P \to +0$;
- ▷ $\Pi''_\bullet(P) \to \Pi''_\bullet(+0) := b_\bullet \in (0, \infty)$ as $P \to +0$.

From these features, $\Pi_\bullet$ is a smooth curve in terms of $P \geq 0$ and especially it has the finite slope and curvature at $P = 0$.

For Model A, the product $\Pi_\mathrm{A} H_n$ means the expected population size of adult prey which successfully escape from the predation by predator P^A in the n th year. Only those adult prey of $\Pi_\mathrm{A} H_n$ can contribute to the prey reproduction, and subsequently, the density-dependent effect on the reproduction is determined by them. In a similar way, Åström et al. (1996) discussed the significance of the order of density-dependent effects for the single species discrete-time population dynamics model in a general context.

Positive parameters ρ_J and ρ_A denote the predator's reproduction rates per unit population size of prey taken by predators P^J and P^A, respectively. In this modeling, the per capita growth rate of predator population is proportional to the amount of prey taken by a predator. It gives the simplest *numerical response* of predator population growth (Solomon 1949; Abrams 2022; Seno 2022).

Functional response, representing the dependence of the net predation rate per predator on the prey population size, is determined here by the dependence of the total amount of prey taken by a predator individual at each predation season on the prey population size (see (Mills and Getz 1996)). Thus, for the population dynamics governed by (4) and (5), it can be defined as the mean amounts of prey taken by a predator individual at the predation season of every year. Consequently, it is proportional to the juvenile prey population size $F(H_n)H_n$ for predator P^J, and to the adult prey population size H_n for predator P^A, respectively. Therefore, the net predation rate per predator is proportional to the targeted prey population size in our model. Hence, it can be regarded as the functional response of Holling Type I ((Holling 1959a, b); also see (Abrams 2022; Seno 2022)).

The modeling of (4) and (5) for Models J and A follows the same idea as that mentioned in May and Hassell (1981); May et al. (1981) for the host-parasitoid population dynamics, where the order of parasitism and density-dependent effect on the host population is taken into account. However, May and Hassell (1981) did not investigate the models therein, but only gave the idea, and instead they investigated a model corresponding to

$$\begin{cases} H_{n+1} = F(H_n)\Pi(P_n)H_n; \\ P_{n+1} = \rho\bigl\{1 - \Pi(P_n)\bigr\}H_n. \end{cases} \tag{6}$$

This model may be called a generic expression of *Thompson-Nicholson-Bailey model* (Thompson 1929; Nicholson 1933, 1935; Hassell 1978; Getz and Mills 1996; Mills and Getz 1996; Lane et al. 1999). With the same general setup for F as ours, and $\Pi(P) = \mathrm{e}^{-aP}$, Jang and Yu (2012) mathematically investigated the model (6) with respect to the stability of equilibria, and further considered a pest control problem therein with a modified model.

Our models (4) and (5) with $\sigma = 0$ correspond to *Model 2* and *Model 3* of generic form, respectively, in May et al. (1981). They made some biological arguments just by some numerics of those models with

$$F(H) = r_0 \exp\Big(-\frac{H}{r_0 \nu}\Big) \tag{7}$$

and

$$\Pi_\bullet(P) = \Big(1 + \frac{a_\bullet P}{k_\bullet}\Big)^{-k_\bullet}. \tag{8}$$

The prey population dynamics governed by (1) and (7) with $\sigma = 0$ is what is called *Ricker model* or *Ricker-Moran model* (Moran 1950; Ricker 1954; MacFadyen 1963; May and Oster 1976). Note that the function (7) with $r_0 > e$ (Napier's constant) does not satisfy the last (seventh) assumption for F given in Sect. 2.3, because $F(H)H$ is monotonically decreasing for $H \in (r_0\nu, K)$ with $K = r_0\nu \log r_0$. While some of our mathematical results in this paper may be extendable for $r_0 > e$, we do not argue such applicability anymore in this paper but leave it as an open problem related to this work.

The formula (8) of $\Pi_\bullet$ was proposed as a part of the modeling about host-parasitoid population dynamics in May (1978), based on the zero term of the negative binomial distribution with positive characteristic parameter $k_\bullet$. Mathematically at the limit $k \to \infty$, the function (8) leads to

$$\Pi_\bullet(P) = \mathrm{e}^{-a_\bullet P}. \tag{9}$$

The function $\Pi_\bullet$ of (9) satisfies the mathematical features given in the above. This is the simplest modeling for $\Pi_\bullet$, where the Poisson process is assumed for the encounter and successful predation between them. Such a modeling with the Poisson process follows the same idea as well-known *Nicholson-Bailey model* originally about host-parasitoid population dynamics (Nicholson 1933, 1935; Bailey et al. 1962; Hastings 1984; Royama 1992; Murdoch et al. 2003; Allen 2007; Seno 2022; Elaydi and Cushing 2025). On the relation of (8) to (9), we can find further mathematical arguments in Livadiotis et al. (2015) and references therein.

Similarly, Weide et al. (2019) used the same idea to construct those two models (4) and (5) with $\sigma = 0$ as the prey-predator population dynamics models with the density-dependent effect function (2) and the probability of successful escape from predation

$$\Pi_\bullet = \Pi_\bullet(H, P) = \exp\Big(-\frac{a_\bullet P}{1 + c_\bullet H}\Big). \tag{10}$$

The modeling of $\Pi_\bullet = \Pi_\bullet(H, P)$ given by (10) can be regarded as the functional response of Holling Type II, differently from ours in this paper. However, as shown in the later section about the results for our specific model with (2) and (9), the dynamical nature of our model appears qualitatively very similar to that of their model with mathematically little significant difference.

On the other hand, there are some other reasonable modelings to explicitly introduce the juvenile and adult prey subpopulations as Hastings (1984); Castillo and Velasco-Hernández (2003); Liz and Pilarczyk (2012) did. For the native prey-predator systems of our Model J and A, we may show them with such a modeling as follows:

$$\text{Model J}\begin{cases} \mathcal{Y}_n &= F(H_n)H_n;\\ H_{n+1} &= \sigma H_n + \gamma\Pi_\mathrm{J}(P_n^\mathrm{J})\mathcal{Y}_n;\\ P_{n+1}^\mathrm{J} &= \rho_\mathrm{J}\big\{1 - \Pi_\mathrm{J}(P_n^\mathrm{J})\big\}\mathcal{Y}_n; \end{cases} \tag{11}$$

$$\text{Model A}\begin{cases} \mathcal{Y}_n &= F\big(\Pi_\mathrm{A}(P_n^\mathrm{A})H_n\big)\Pi_\mathrm{A}(P_n^\mathrm{A})H_n;\\ H_{n+1} &= \sigma\Pi_\mathrm{A}(P_n^\mathrm{A})H_n + \gamma\mathcal{Y}_n;\\ P_{n+1}^\mathrm{A} &= \rho_\mathrm{A}\big\{1 - \Pi_\mathrm{A}(P_n^\mathrm{A})\big\}H_n, \end{cases} \tag{12}$$

where $\mathcal{Y}_n$ is the juvenile prey population size produced by the reproductive adult prey at the n th year, matching our assumptions and modelings described in the above. Positive parameter γ less than one denotes the survival probability of juvenile prey to become mature. Remark that H_n denotes here the adult prey population size at the beginning of the predation season for adult-specific predator P^A, where the predation season for P^A is assumed to be before the reproduction season for the prey. The systems (11) and (12) are mathematically equivalent to (4) and (5), respectively. While the expression of (11) and (12) would be meaningful for the modification to take account of the other ecological factors, for example, a stage-specific fatal disease/pesticide or harvesting, we are going to focus on our models given as (4) and (5) in this paper.

2.5 Prey-predator system with alien predator invasion

With an alien predator invasion, the system transfers to one prey and two predator population dynamics governed by the following three recurrence relations commonly for Models J and A:

$$\begin{cases} H_{n+1} &= \sigma\Pi_\mathrm{A}(P_n^\mathrm{A})H_n + \Pi_\mathrm{J}(P_n^\mathrm{J})F\big(\Pi_\mathrm{A}(P_n^\mathrm{A})H_n\big)\Pi_\mathrm{A}(P_n^\mathrm{A})H_n;\\ P_{n+1}^\mathrm{J} &= \rho_\mathrm{J}\big\{1 - \Pi_\mathrm{J}(P_n^\mathrm{J})\big\}F\big(\Pi_\mathrm{A}(P_n^\mathrm{A})H_n\big)\Pi_\mathrm{A}(P_n^\mathrm{A})H_n;\\ P_{n+1}^\mathrm{A} &= \rho_\mathrm{A}\big\{1 - \Pi_\mathrm{A}(P_n^\mathrm{A})\big\}H_n. \end{cases} \tag{13}$$

From the nature of the sequence $\{H_n\}$ with no predator and $H_0 \in (0, K)$ as shown by Lemma 1 in Sect. 2.3, we have the following mathematical feature of the sequence $\{H_n\}$ generated by every system of (4), (5), and (13):

Lemma 2 *With respect to every system of* (4)*,* (5)*, and* (13)*, the sequence* $\{H_n\}$ *with* $H_0 \in (0, K)$ *satisfies that* $H_n \in (0, K)$ *for all* $n \geq 0$*, and the sequence* $\{P_n^\bullet\}$ *with* $P_0^\bullet > 0$ *satisfies that* $P_n^\bullet > 0$ *for all* $n \geq 0$.

On the other hand, May and Hassell (1981) considered a model of one host and two parasitoids population dynamics governed by

$$\begin{cases} H_{n+1} = \Pi_{\mathrm{Q}}(Q_n)\Pi_{\mathrm{P}}(P_n)F(H_n)H_n; \\ P_{n+1} = \rho_{\mathrm{P}}\bigl\{1 - \Pi_{\mathrm{P}}(P_n)\bigr\}H_n. \\ Q_{n+1} = \rho_{\mathrm{Q}}\bigl\{1 - \Pi_{\mathrm{Q}}(Q_n)\bigr\}\Pi_{\mathrm{P}}(P_n)H_n, \end{cases} \tag{14}$$

where P and Q are parasitoids competing for a common host H. This model cannot belong to ours by (13) even with $\sigma = 0$. They assume that the parasitoid P uses the larvae, while Q does the pupae. Jia et al. (2024) analytically investigated the model (14) with F of (7) and $\Pi_\bullet$ of (9). Remark that, in a precise sense, their H_n in (14) could be regarded as the population size of larvae just before the parasitism season for parasitoid P, differently from our H_n in (4) and (5). Moreover, the density-dependent effect introduced by $F(H_n)$ with the larvae density before the parasitism acts on the larvae population as its survivability before the parasitism seasons, differently from our F acting on the fertility.

2.6 Basic predator replacement number

The *net replacement rate* or *net reproduction rate* is defined in ecology as the expected number of mature females produced by a mature female over its lifetime (for instance, see (Begon et al. 1996; Case 2000; Gotelli 2001; Seno 2022)). When it is less than one, the population size eventually decreases. This definition has an obvious correspondence to what is called *basic reproduction number* for the epidemic dynamics, which is defined as the expected number of new cases of infection caused by an infective individual in a population consisting of susceptible contacts only (for a modern review about the definition, the translation, and the practical application of basic reproduction number for the epidemic dynamics, see (Delamater et al. 2019)).

Making use of a similar mathematical concept with the definition of basic reproduction number, we shall define here the *basic predator replacement number* for predators $\mathrm{P^J}$ and $\mathrm{P^A}$, respectively. For our discrete-time population dynamics given by (4) and (5), respectively, the basic predator replacement rate is defined as *the supremum for the number of adult predators produced by a single adult predator at a reproduction season* (Seno 2025), since the reproductive predator is assumed to die out after every reproduction season.

Firstly for the native prey-predator system (4) of Model J, the (average) number of adult predators produced by a single adult predator of P^{J} at the n th year is given by

$$\frac{\rho_{\mathrm{J}}\bigl\{1-\Pi_{\mathrm{J}}(P_n^{\mathrm{J}})\bigr\}F(H_n)H_n}{P_n^{\mathrm{J}}}. \tag{15}$$

We may call (15) the *effective predator replacement number* for predator P^{J} at the n th year, which depends on the population sizes H_n and P_n^{J}. The basic predator replacement number can be defined by the supremum for the effective predator replacement number as well as the definition of basic reproduction number in relation to the *effective reproduction number* about the epidemic dynamics (Seno 2022).

Therefore we shall define the basic replacement number for predator P^{J} by

$$\mathscr{R}_0^{\mathrm{J}} := \sup_{\{H,P\}} \frac{\rho_{\mathrm{J}}\bigl\{1-\Pi_{\mathrm{J}}(P)\bigr\}F(H)H}{P} = \rho_{\mathrm{J}}(1-\sigma)K \sup_{P} \frac{1-\Pi_{\mathrm{J}}(P)}{P}, \tag{16}$$

since the prey population size cannot exceed its carrying capacity K given by (3), that is, $\sup_{\{H_n\}} H_n = K$ as shown in Sect. 2.3. Besides, since $F(H)H$ is monotonically increasing in terms of $H \in (0, K)$ with $F(K) = 1-\sigma$, we have $\sup_{H} F(H)H = F(K)K = (1-\sigma)K$. Moreover, we can easily prove that

$$\sup_{P}\frac{1-\Pi_{\mathrm{J}}(P)}{P} = \lim_{P\to+0}\frac{1-\Pi_{\mathrm{J}}(P)}{P} = -\lim_{P\to+0}\frac{\Pi_{\mathrm{J}}(P)-\Pi_{\mathrm{J}}(0)}{P} = -\Pi_{\mathrm{J}}'(+0) = a_{\mathrm{J}} \tag{17}$$

for $P > 0$, because $\{1-\Pi_{\mathrm{J}}(P)\}/P$ is monotonically decreasing for $P > 0$ from the mathematical features of Π_{J} given in Sect. 2.4. Lastly from (16), we have the expression of the basic replacement number for predator P^{J}:

$$\mathscr{R}_0^{\mathrm{J}} := \rho_{\mathrm{J}} a_{\mathrm{J}}(1-\sigma)K. \tag{18}$$

In the same way, we can obtain the expression of the basic replacement number for predator P^{A} in the native prey-predator system (5) of Model A:

$$\mathscr{R}_0^{\mathrm{A}} := \rho_{\mathrm{A}} a_{\mathrm{A}} K. \tag{19}$$

In the following part, we are going to show that the basic predator replacement numbers $\mathscr{R}_0^{\mathrm{J}}$ and $\mathscr{R}_0^{\mathrm{A}}$ determine the stability of the predator extinction equilibria $E_{+0}^{\mathrm{J}}(H_*, P_*^{\mathrm{J}}) = (K, 0)$ and $E_{+0}^{\mathrm{A}}(H_*, P_*^{\mathrm{A}}) = (K, 0)$ with respect to the native prey-predator systems of Models J and A, respectively.

We can easily find its eigenvalues, $F'(K)K + 1$ and $\mathscr{R}_0^{\bullet}$, of the Jacobi matrix for the predator extinction equilibrium $E_{+0}^{\bullet}$. The former eigenvalue $F'(K)K + 1$ is in $(0, 1)$, because $F'(K)K + 1 = \{F(H)H\}'\big|_{H=K} + \sigma > 0$ and $F'(K) < 0$ from the mathematical features of F as given in Sect. 2.3. Hence, we find the following result:

Lemma 3 *The predator extinction equilibrium* $E^{\bullet}_{+0}$ *is*

$$\begin{cases} \textit{locally asymptotically stable if } \mathscr{R}_0^{\bullet} < 1; \\ \textit{unstable if } \mathscr{R}_0^{\bullet} > 1 \end{cases}$$

with respect to the native prey-predator systems of Models J and A, respectively.

This lemma gives the condition for the persistence of the native prey-predator system, that is, the persistence of native predator before an alien predator invasion: The native prey-predator system is persistent if $\mathscr{R}_0^{\bullet} > 1$, and only if $\mathscr{R}_0^{\bullet} \geq 1$.

Next, as for the system (13) with the native and alien predators, we can consider the predator extinction equilibrium $E^*_{+00}(H_*, P^{\mathrm{J}}_*, P^{\mathrm{A}}_*) = (K, 0, 0)$. Its Jacobi matrix has the eigenvalues $F'(K)K + 1 \in (0, 1)$, $\mathscr{R}_0^{\mathrm{J}}$, and $\mathscr{R}_0^{\mathrm{A}}$. Therefore, we get the following result on the local stability of E^*_{+00}:

Lemma 4 *The predator extinction equilibrium* E^*_{+00} *is*

$$\begin{cases} \textit{locally asymptotically stable if } \max\left\{\mathscr{R}_0^{\mathrm{J}}, \mathscr{R}_0^{\mathrm{A}}\right\} < 1; \\ \textit{unstable if } \max\left\{\mathscr{R}_0^{\mathrm{J}}, \mathscr{R}_0^{\mathrm{A}}\right\} > 1 \end{cases}$$

with respect to the system with native and alien predators.

Taking account of these results in Lemmas 3 and 4, we can prove the following result on the condition for the predator's extinction and persistence (Appendix A):

Theorem 1 *The predator* $\mathrm{P}^{\bullet}$ *with* $\mathscr{R}_0^{\bullet} \leq 1$ *goes extinct for the systems* (4)*,* (5)*, and* (13)*. For the native prey-predator systems* (4) *and* (5)*, the native predator* $\mathrm{P}^{\bullet}$ *persists with the prey if* $\mathscr{R}_0^{\bullet} > 1$.

This result suggests that the basic predator replacement number $\mathscr{R}_0^{\bullet}$ can serve as an index for the establishment of a native prey-predator system. Note that the former result in Theorem 1 indicates the global stability of the predator extinction equilibrium.

For the population dynamics given by (13) with the native and alien predators, Theorem 1 leads to the following feature on the persistence of native and alien predators:

Corollary 1 *For the system* (13)*, if* $\mathscr{R}_0^{\diamondsuit} > 1 \geq \mathscr{R}_0^{\blacklozenge}$ *for predators* $\mathrm{P}^{\diamondsuit}$ *and* $\mathrm{P}^{\blacklozenge}$*, then the predator* $\mathrm{P}^{\diamondsuit}$ *persists with the prey, while the predator* $\mathrm{P}^{\blacklozenge}$ *goes extinct.*

The result of Corollary 1 matches Lemma 4. Remark that, when $\mathscr{R}_0^{\mathrm{J}} > 1$ and $\mathscr{R}_0^{\mathrm{A}} > 1$ for the system (13) after the alien predator invasion, one of two predator species may go extinct due to the effect of exploitative competition between them, while the extinction of both predator populations does not occur from Lemma 4.

3 Coexistent equilibrium for native prey-predator system

For the existence of coexistent equilibrium $E^\bullet_{++}(H_*, P^\bullet_*)$ with $P^\bullet_* > 0$ about the native prey-predator systems (4) and (5), respectively, we can find the following result (Appendix B):

Theorem 2 *For the native prey-predator system, the coexistent equilibrium* $E^\bullet_{++}(H_*, P^\bullet_*)$ *uniquely exists if and only if* $\mathscr{R}^\bullet_0 > 1$. *The equilibria are determined as* $(H_*, P^{\mathrm{J}}_*) = \big(F^{-1}\big(\frac{1-\sigma}{\Pi^*_{\mathrm{J}}}\big), \Pi_{\mathrm{J}}^{-1}(\Pi^*_{\mathrm{J}})\big)$ *for* E^{J}_{++}, *and* $(H_*, P^{\mathrm{A}}_*) = \big(\frac{1}{\Pi^*_{\mathrm{A}}}F^{-1}\big(\frac{1}{\Pi^*_{\mathrm{A}}} - \sigma\big), \Pi_{\mathrm{A}}^{-1}(\Pi^*_{\mathrm{A}})\big)$ *for* E^{A}_{++} *with the inverse functions* F^{-1} *and* $\Pi_\bullet^{-1}$ *of* F *and* $\Pi_\bullet$, *where* Π^*_{J} *and* Π^*_{A} *are the unique root of equation* $\Phi_{\mathrm{J}}(x) = 0$ *in* $(\frac{1-\sigma}{r_0}, 1)$ *and that of* $\Phi_{\mathrm{A}}(x) = 0$ *in* $(\frac{1}{r_0+\sigma}, 1)$ *respectively with*

$$\begin{aligned} \Phi_{\mathrm{J}}(x) &:= \Pi_{\mathrm{J}}^{-1}(x) - \rho_{\mathrm{J}}(1-\sigma)\Big(\frac{1}{x} - 1\Big)F^{-1}\big(\tfrac{1-\sigma}{x}\big);\\ \Phi_{\mathrm{A}}(x) &:= \Pi_{\mathrm{A}}^{-1}(x) - \rho_{\mathrm{A}}\Big(\frac{1}{x} - 1\Big)F^{-1}\big(\tfrac{1}{x} - \sigma\big). \end{aligned} \tag{20}$$

Otherwise, if $\mathscr{R}^\bullet_0 \leq 1$, *no coexistent equilibrium* $E^\bullet_{++}$ *exists.*

From Theorems 1 and 2, we can get also the following result:

Corollary 2 *For the native prey-predator system, the predator extinction equilibrium* $E^\bullet_{+0}$ *is unstable when the coexistent equilibrium* $E^\bullet_{++}$ *exists.*

Further, we can prove the following result on the local stability of the coexistent equilibrium $E^\bullet_{++}$ (Appendix C):

Theorem 3 *When the coexistent equilibrium* $E^\bullet_{++}$ *exists for the native prey-predator system, it is locally asymptotically stable if*

$$-\frac{\Pi'_{\mathrm{J}}\big(\Pi_{\mathrm{J}}^{-1}(\Pi^*_{\mathrm{J}})\big)\Pi_{\mathrm{J}}^{-1}(\Pi^*_{\mathrm{J}})}{1-\Pi^*_{\mathrm{J}}}\Big\{F'\big(F^{-1}(\tfrac{1-\sigma}{\Pi^*_{\mathrm{J}}})\big)F^{-1}(\tfrac{1-\sigma}{\Pi^*_{\mathrm{J}}}) + \frac{1-\sigma}{\Pi^*_{\mathrm{J}}} + \sigma\Big\} < 1 \tag{21}$$

for E^{J}_{++}, *and*

$$-\frac{\Pi'_{\mathrm{A}}\big(\Pi_{\mathrm{A}}^{-1}(\Pi^*_{\mathrm{A}})\big)\Pi_{\mathrm{A}}^{-1}(\Pi^*_{\mathrm{A}})}{1-\Pi^*_{\mathrm{A}}}\Big\{F'\big(F^{-1}(\tfrac{1}{\Pi^*_{\mathrm{A}}} - \sigma)\big)F^{-1}(\tfrac{1}{\Pi^*_{\mathrm{A}}} - \sigma) + \frac{1}{\Pi^*_{\mathrm{A}}}\Big\} < 1 \tag{22}$$

for E^{A}_{++}, *where* $\Pi^*_\bullet$ *is defined in Theorem 2. The equilibria* E^{J}_{++} *and* E^{A}_{++} *are unstable if the inverse inequalities of* (21) *and* (22) *are satisfied, respectively.*

The significance of Theorem 3 is indicated by the following result to evidence the necessary existence of a parameter region where the condition (21) for E^{J}_{++}, or (22) for E^{A}_{++} holds (Appendix D):

Corollary 3 *For $\mathscr{R}_0^\bullet = 1 + \epsilon$ with $0 < \epsilon \ll 1$, the coexistent equilibrium $E_{++}^\bullet$ for the native prey-predator system exists, and it is locally asymptotically stable.*

Theorem 1 and the results presented in this section suggest that if the basic predator replacement number $\mathscr{R}_0^\bullet$ of native predator is greater than one, the population dynamics may converge towards a coexistent equilibrium state. Alternatively, it may converge towards a sustained oscillatory state with persistent prey and predator populations. The nature of such a coexistent state depends on the specific details of the density-dependent functions governing prey growth rate and predation rate.

4 Bifurcation of equilibria for native prey-predator system

From Lemma 3, the stability of predator extinction equilibrium $E_{+0}^\bullet$ changes at $\mathscr{R}_0^\bullet = 1$. For $\mathscr{R}_0^\bullet > 1$, it is unstable where one of the eigenvalues for the predator extinction equilibrium is less than one and the other greater than one. Then, from Corollary 3 and the proof in Appendix D, the locally asymptotically stable coexistent equilibrium $E_{++}^\bullet$ arises for $\mathscr{R}_0^\bullet > 1$ in a neighborhood of $\mathscr{R}_0^\bullet = 1$, satisfying that $E_{++}^\bullet \to E_{+0}^\bullet$ as $\mathscr{R}_0^\bullet \to 1 + 0$. Hence, the bifurcation at $\mathscr{R}_0^\bullet = 1$ is of what is called *transcritical bifurcation* (Allen 2007; Seno 2022; Elaydi and Cushing 2025).

The local stability of $E_{++}^\bullet$ is determined by the eigenvalues of Jacobi matrix $\mathcal{J}_{++}^\bullet$ for $E_{++}^\bullet$, which are the roots of characteristic equation $Q_\bullet(\lambda) := \lambda^2 - (\operatorname{tr} \mathcal{J}_{++}^\bullet)\lambda + \det \mathcal{J}_{++}^\bullet = 0$. In Appendix C, we have shown that the conditions $\operatorname{tr} \mathcal{J}_{++}^\bullet < 1 + \det \mathcal{J}_{++}^\bullet$ is satisfied when the coexistent equilibrium $E_{++}^\bullet$ exists. This means that $Q_\bullet(1) = 1 - \operatorname{tr} \mathcal{J}_{++}^\bullet + \det \mathcal{J}_{++}^\bullet > 0$ and $Q_\bullet(-1) = 1 + \operatorname{tr} \mathcal{J}_{++}^\bullet + \det \mathcal{J}_{++}^\bullet > 0$ because of $\operatorname{tr} \mathcal{J}_{++}^\bullet > 0$ and $\det \mathcal{J}_{++}^\bullet > 0$ when the coexistence equilibrium $E_{++}^\bullet$ exists. Therefore, the characteristic equation $Q_\bullet(\lambda) = 0$ never has the root 1 or -1. Hence, at the bifurcation condition with which the stability of coexistent equilibrium $E_{++}^\bullet$ changes, the eigenvalues contain not either of the critical value 1 or -1, but the imaginary value with the absolute value 1.

As a result, the instability of the coexistent equilibrium $E_{++}^\bullet$ follows what is called *Neimark-Sacker bifurcation* (Allen 2007; Seydel 2010; Seno 2022; Elaydi and Cushing 2025). Thus, at least with a condition sufficient near the bifurcation when the coexistent equilibrium $E_{++}^\bullet$ is unstable, the system behaves a quasi-periodic manner, on which we will show a numerical example later in Fig. 4 of Sect. 6. For some other specific discrete-time prey-predator or host-parasitoid models similar and different to ours, the Neimark-Sacker bifurcation was observed and investigated (Tang and Chen 2002; Asheghi 2014; Weide et al. 2019; Bešo et al. 2020; Din et al. 2020; Marcinko and Kot 2020; Jia et al. 2024).

5 Alien predator invasion of equilibrium native prey-predator system

5.1 Model J: Alien predator P^{A} invasion

For the alien predator P^{A} invasion according to Model J, we are going to consider here the local stability of the equilibrium $E^*_{++0}(H_*, P^{\mathrm{J}}_*, 0) = \bigl(F^{-1}\bigl(\frac{1-\sigma}{\Pi^*_{\mathrm{J}}}\bigr), \Pi_{\mathrm{J}}^{-1}(\Pi^*_{\mathrm{J}}), 0\bigr)$ for the system (13), where Π^*_{J} is determined as the unique root in $(\frac{1-\sigma}{r_0}, 1)$ of equation $\Phi_{\mathrm{J}}(x) = 0$ given by (20) in Theorem 2. If E^*_{++0} is asymptotically stable, the alien predator P^{A} invasion can be regarded as unsuccessful, and then the system asymptotically approaches the equilibrium E^*_{++0} with the declining population size of alien predator P^{A}, provided that the native prey-predator system (4) of Model J stayed at the asymptotically stable equilibrium E^{J}_{++} before the alien predator P^{A} invasion. Otherwise, if E^*_{++0} is unstable, the alien predator P^{A} invasion can be regarded as successful, and it can increase its density at least in the early period after its invasion.

This line of reasoning could be broadly referred to as the *invasibility criterion* (Chesson 2000). However, there is a general possibility that the successful invasion of an alien predator population could result in its extinction in the long run dynamics. The system might approach a state where the alien predator population is extinct, which is different from the original state of the native prey and predator system before the invasion. In the context of dynamical system theory, this could occur when there are multiple asymptotically stable states for the native prey-predator system. Alternatively, the native prey-predator system might be at a stably oscillatory state before the invasion. Even if the alien predator population temporarily increases after the invasion, its extinction may occur in the long run.

Now we suppose the existence of the equilibrium E^*_{++0}, that is, the existence of the equilibrium E^{J}_{++} for the native prey-predator system (4) of Model J. Thus, the condition $\mathscr{R}^{\mathrm{J}}_0 > 1$ is supposed here to hold from Theorem 2. We can easily find the eigenvalues of Jacobi matrix $\mathcal{J}_3(E^*_{++0})$, which are given as those of $\mathcal{J}^{\mathrm{J}}_{++}$ and the other one, $\lambda^{\mathrm{J}}_* := \rho_{\mathrm{A}} a_{\mathrm{A}} H_* = \frac{\mathscr{R}^{\mathrm{A}}_0}{K} F^{-1}\bigl(\frac{1-\sigma}{\Pi^*_{\mathrm{J}}}\bigr) > 0$. Hence, we can obtain the following result on the local stability of equilibrium E^*_{++0} for the system (13) for Model J according to the invasion of alien predator P^{A}:

Theorem 4 *Provided that the equilibrium E^{J}_{++} for the native prey-predator system* (4) *of Model J is asymptotically stable, the equilibrium E^*_{++0} for the system* (13) *is locally asymptotically stable if*

$$\mathscr{R}^{\mathrm{A}}_0 < \frac{K}{F^{-1}\bigl(\frac{1-\sigma}{\Pi^*_{\mathrm{J}}}\bigr)}. \tag{23}$$

In contrast, it is unstable if the inverse inequality of (23) *is satisfied.*

The right side of (23) is determined only by the native prey-predator system of Model J, while the left side characterizes the alien predator P^{A}.

Note that the right side of (23) is greater than one, because $\frac{1-\sigma}{\Pi^*_{\mathrm{J}}} \in (1-\sigma, r_0)$ for $\Pi^*_{\mathrm{J}} \in (\frac{1-\sigma}{r_0}, 1)$, and thus $F^{-1}\bigl(\frac{1-\sigma}{\Pi^*_{\mathrm{J}}}\bigr) \in \bigl(F^{-1}(r_0), F^{-1}(1-\sigma)\bigr) = (0, K)$ due to the decreasing monotonicity of F^{-1}. Hence, the result of Theorem 4 clearly demonstrates that the alien predator P^{A} can successfully invade the equilibrium native prey-predator system of Model J only with its basic replacement number beyond a critical value greater than one, which is given by the right side of (23).

Moreover, we can obtain the following secondary result from Theorem 4 (Appendix E):

Corollary 4 *Provided that the equilibrium E^{J}_{++} for the native prey-predator system* (4) *of Model J is asymptotically stable, the equilibrium E^{*}_{++0} for the system* (13) *is locally asymptotically stable if $\mathscr{R}^{\mathrm{A}}_0 < \mathscr{R}^{\mathrm{J}}_0$ when*

$$a_{\mathrm{J}}\Pi_{\mathrm{J}}^{-1}\Bigl(\frac{1-\sigma}{F\bigl(\frac{K}{\mathscr{R}^{\mathrm{J}}_0}\bigr)}\Bigr) < \frac{F\bigl(\frac{K}{\mathscr{R}^{\mathrm{J}}_0}\bigr)}{1-\sigma} - 1. \tag{24}$$

Further, when the condition (24) *is satisfied, the equilibrium E^{*}_{++0} may be locally asymptotically stable even if $\mathscr{R}^{\mathrm{A}}_0 > \mathscr{R}^{\mathrm{J}}_0$. In contrast, when the inverse inequality of* (24) *is satisfied, the equilibrium E^{*}_{++0} is unstable if $\mathscr{R}^{\mathrm{A}}_0 \geq \mathscr{R}^{\mathrm{J}}_0$.*

Note that the condition (24) depends only on the native prey-predator system of Model J. This result demonstrates that, if the condition (24) holds for the native prey-predator system at the locally asymptotically stable equilibrium E^{J}_{++} in Model J, the alien predator P^{A} invasion is successful only if it has the basic replacement number $\mathscr{R}^{\mathrm{A}}_0$ sufficiently greater than that of the native predator $\mathscr{R}^{\mathrm{J}}_0$. Even if $\mathscr{R}^{\mathrm{A}}_0 > \mathscr{R}^{\mathrm{J}}_0$, the invasion may fail. In contrast, if the inverse inequality of (24) holds, the invasion of alien predator P^{A} is successful if $\mathscr{R}^{\mathrm{A}}_0 \geq \mathscr{R}^{\mathrm{J}}_0$. Then, the invasion may be successful even if $\mathscr{R}^{\mathrm{A}}_0 < \mathscr{R}^{\mathrm{J}}_0$. For our analysis on a specific model in the later section, we will apply the result of Corollary 4, and find a distinct nature about the model.

In general, even if the equilibrium E^{*}_{++0} is unstable, we cannot determine the definitive consequence on the success or failure of alien predator P^{A} invasion of the native prey-predator system (4). This is because the native prey-predator system could be at an oscillatory stationary state before the alien predator P^{A} invasion, as seen later in Figs. 3 and 4 of Sect. 6 with numerical examples about specific models of (4) and (5) using (2) and (9). This means that even when the equilibrium E^{*}_{++0} is unstable, the alien predator P^{A} invasion could fail and the system would return to an oscillatory stationary state of the native prey-predator system with the extinction of alien predator P^{A}. In such a case, it should be supposed a priori that the native prey-predator system stably stays at an oscillatory state before the alien predator P^{A} invasion. In contrast, if the native prey-predator system stays at the asymptotically stable equilibrium E^{J}_{++} before the alien predator P^{A} invasion, the local stability of E^{*}_{++0} leads to the failure of invasion, and the system returns to E^{J}_{++} for the native prey-predator system with prey H and predator P^{J}.

5.2 Model A: Alien predator P^{J} invasion

As in the previous section, we suppose that the condition $\mathscr{R}_0^{\mathrm{A}} > 1$ is satisfied for the existence of the equilibrium $E_{+0+}^*(H_*, 0, P_*^{\mathrm{A}}) = \bigl(\frac{1}{\Pi_{\mathrm{A}}^*}F^{-1}\bigl(\frac{1}{\Pi_{\mathrm{A}}^*}-\sigma\bigr), 0, \Pi_{\mathrm{A}}^{-1}(\Pi_{\mathrm{A}}^*)\bigr)$, that is, for the existence of the equilibrium E_{++}^{A} for the native prey-predator system of Model A, where Π_{A}^* is determined as the unique root in $(\frac{1}{r_0+\sigma}, 1)$ of equation $\Phi_{\mathrm{A}}(x) = 0$ given by (20) in Theorem 2.

We can easily find the eigenvalues of Jacobi matrix $\mathcal{J}_3(E_{+0+}^*)$, which are given as those of E_{++}^{A} and the other one, $\lambda_*^{\mathrm{A}} := \rho_{\mathrm{J}} a_{\mathrm{J}} F\bigl(\Pi_{\mathrm{A}}^* H_*\bigr)\Pi_{\mathrm{A}}^* H_* = \frac{\mathscr{R}_0^{\mathrm{J}}}{(1-\sigma)K}\bigl(\frac{1}{\Pi_{\mathrm{A}}^*} - \sigma\bigr)F^{-1}\bigl(\frac{1}{\Pi_{\mathrm{A}}^*}-\sigma\bigr) > 0$. Then, correspondingly to Theorem 4, we can obtain the following result on the local stability of equilibrium E_{+0+}^* according to the system (13) for Model A with the invasion of alien predator P^{J}:

Theorem 5 *Provided that the equilibrium E_{++}^{A} for the native prey-predator system (5) of Model A is asymptotically stable, the equilibrium E_{+0+}^* for the system (13) is locally asymptotically stable if*

$$\mathscr{R}_0^{\mathrm{J}} < \frac{(1-\sigma)K}{\bigl(\frac{1}{\Pi_{\mathrm{A}}^*}-\sigma\bigr)F^{-1}\bigl(\frac{1}{\Pi_{\mathrm{A}}^*}-\sigma\bigr)}. \tag{25}$$

In contrast, it is unstable if the inverse inequality of (25) is satisfied.

The right side of (25) is determined only by the native prey-predator system of Model A, while the left side characterizes the alien predator P^{J}.

The right side of (25) is greater than one. This is because its denominator is monotonically decreasing in terms of $\frac{1}{\Pi_{\mathrm{A}}^*} \in (1, r_0+\sigma)$, and thus it is in $(0, (1-\sigma)K)$. Actually, according to $(x-\sigma)F^{-1}(x-\sigma) = F\bigl(F^{-1}(x-\sigma)\bigr)F^{-1}(x-\sigma)$, it is monotonically decreasing in terms of $x > 1$ due to the decreasing monotonicity of $F^{-1}(x)$ and the increasing monotonicity of $F(x)x$ for $x > 1$ from the features of F given in Sect. 2.3. The result of Theorem 5 demonstrates that the alien predator P^{J} can successfully invade the equilibrium native prey-predator system of Model A only with its basic replacement number beyond a critical value greater than one, which is given by he right side of (25).

Now, we can derive the following significant corollary from Theorem 5 (Appendix F):

Corollary 5 *Provided that the equilibrium E_{++}^{A} for the native prey-predator system (5) of Model A is asymptotically stable, the equilibrium E_{+0+}^* for the system (13) is unstable if $\mathscr{R}_0^{\mathrm{J}} \geq \mathscr{R}_0^{\mathrm{A}}$.*

This result demonstrates that if the alien predator's basic replacement number $\mathscr{R}_0^{\mathrm{J}}$ is not less than $\mathscr{R}_0^{\mathrm{A}}$ of the native predator, its invasion is necessarily successful. Inversely, the alien predator P^{J} invasion could fail and lead to its extinction only if its basic replacement number $\mathscr{R}_0^{\mathrm{J}}$ sufficiently smaller than $\mathscr{R}_0^{\mathrm{A}}$ of the native predator. In the subsequent section about a specific model, we will clearly see the significance of Corollary 5.

As mentioned in the previous section, even if E^*_{+0+} is unstable, we could not determine the definitive outcome of the alien predator P^{J} invasion of the native prey-predator system (5). This is because the native prey-predator system could be at a stably oscillatory state instead of the equilibrium E^*_{+0+} before the invasion.

6 Beverton-Holt+Nicholson-Bailey model

In this section, we show some more detail results on the following specific model of the system (13) using (2) and (9) with $\sigma = 0$:

$$\begin{cases} H_{n+1} = \mathrm{e}^{-a_{\mathrm{J}} P_n^{\mathrm{J}}} \dfrac{r_0}{1+\mathrm{e}^{-a_{\mathrm{A}} P_n^{\mathrm{A}}} H_n/\beta} \mathrm{e}^{-a_{\mathrm{A}} P_n^{\mathrm{A}}} H_n; \\ P_{n+1}^{\mathrm{J}} = \rho_{\mathrm{J}}\big(1-\mathrm{e}^{-a_{\mathrm{J}} P_n^{\mathrm{J}}}\big) \dfrac{r_0}{1+\mathrm{e}^{-a_{\mathrm{A}} P_n^{\mathrm{A}}} H_n/\beta} \mathrm{e}^{-a_{\mathrm{A}} P_n^{\mathrm{A}}} H_n; \\ P_{n+1}^{\mathrm{A}} = \rho_{\mathrm{A}}\big(1-\mathrm{e}^{-a_{\mathrm{A}} P_n^{\mathrm{A}}}\big) H_n. \end{cases} \tag{26}$$

This model can be considered a discrete-time prey-predator model that combines the Beverton-Holt model and the Nicholson-Bailey model for two predator populations and their shared prey population. The carrying capacity for the prey population is given as $K = \beta(r_0 - 1)$, given by (3) with $\sigma = 0$ in Sect. 2.3.

With the transformations of variables and parameters $h_n := \frac{H_n}{\beta}$; $p_n^{\mathrm{J}} := a_{\mathrm{J}} P_n^{\mathrm{J}}$; $p_n^{\mathrm{A}} := a_{\mathrm{A}} P_n^{\mathrm{A}}$; $\alpha_{\mathrm{J}} := \rho_{\mathrm{J}} a_{\mathrm{J}} \beta$; $\alpha_{\mathrm{A}} := \rho_{\mathrm{A}} a_{\mathrm{A}} \beta$, the system (26) becomes the following mathematically equivalent non-dimensionalized one:

$$\begin{cases} h_{n+1} = \mathrm{e}^{-p_n^{\mathrm{J}}} \dfrac{r_0}{1+\mathrm{e}^{-p_n^{\mathrm{A}}} h_n} \mathrm{e}^{-p_n^{\mathrm{A}}} h_n; \\ p_{n+1}^{\mathrm{J}} = \alpha_{\mathrm{J}}\big(1-\mathrm{e}^{-p_n^{\mathrm{J}}}\big) \dfrac{r_0}{1+\mathrm{e}^{-p_n^{\mathrm{A}}} h_n} \mathrm{e}^{-p_n^{\mathrm{A}}} h_n; \\ p_{n+1}^{\mathrm{A}} = \alpha_{\mathrm{A}}\big(1-\mathrm{e}^{-p_n^{\mathrm{A}}}\big) h_n. \end{cases} \tag{27}$$

According to this non-dimensionalized system, we have the following native prey-predator systems of Models J and A, respectively:

$$\text{Model J} \begin{cases} h_{n+1} = \mathrm{e}^{-p_n^{\mathrm{J}}} \dfrac{r_0}{1+h_n} h_n; \\ p_{n+1}^{\mathrm{J}} = \alpha_{\mathrm{J}}\big(1-\mathrm{e}^{-p_n^{\mathrm{J}}}\big) \dfrac{r_0}{1+h_n} h_n; \end{cases} \tag{28}$$

$$\text{Model A} \begin{cases} h_{n+1} = \dfrac{r_0}{1+\mathrm{e}^{-p_n^{\mathrm{A}}} h_n} \mathrm{e}^{-p_n^{\mathrm{A}}} h_n; \\ p_{n+1}^{\mathrm{A}} = \alpha_{\mathrm{A}}\big(1-\mathrm{e}^{-p_n^{\mathrm{A}}}\big) h_n. \end{cases} \tag{29}$$

The carrying capacity K for the prey population is non-dimensionalized to the supremum for h_n given as $\kappa := r_0 - 1$ too. Then, the basic replacement numbers for predators P^{J} and P^{A} are expressed as $\mathscr{R}_0^{\mathrm{J}} = \alpha_{\mathrm{J}}\kappa$ and $\mathscr{R}_0^{\mathrm{A}} = \alpha_{\mathrm{A}}\kappa$, respectively. Further, according to these non-dimensionalized systems, we have $F(h) = \frac{r_0}{1+h}$; $F^{-1}(v) = \frac{r_0}{v} - 1$; $\Pi_\bullet(p) = \mathrm{e}^{-p}$; $\Pi_\bullet^{-1}(w) = -\log w$.

The native prey-predator systems (28) and (29) for Models J and A correspond to the models considered in Weide et al. (2019) where F and $\Pi_\bullet$ are given by (2) and (10) with $c_\bullet = 0$, respectively. Additionally, the native prey-predator system (28) is mathematically equivalent to *Model 3* in Marcinko and Kot (2020). Hence, some of our results in the following sections concerning systems (28) and (29) can be considered analogous to those obtained by them, whereas we present our results here in our manner because we independently derive and describe them in a specific context related to the basic predator replacement number $\mathscr{R}_0^\bullet$.

6.1 Dynamical equivalence between native prey-predator systems with $\sigma = 0$

With the variable transformation $X_n = F(H_n)H_n$, the generic native prey-predator system (4) of Model J with $\sigma = 0$ can be mathematically transformed to

$$\begin{cases} X_{n+1} = F\big(\Pi_{\mathrm{J}}(P_n^{\mathrm{J}})X_n\big)\Pi_{\mathrm{J}}(P_n^{\mathrm{J}})X_n; \\ P_{n+1}^{\mathrm{J}} = \rho_{\mathrm{J}}\big\{1 - \Pi_{\mathrm{J}}(P_n^{\mathrm{J}})\big\}X_n. \end{cases} \tag{30}$$

The system (30) could have the structure mathematically equivalent to the native prey-predator system (5) of Model A with $\sigma = 0$. The transformation $X_n = F(H_n)H_n$ gives a one-to-one relation between H_n to X_n, since $F(H)H$ is monotonically increasing for $H > 0$ as assumed in Sect. 2.3. In a mathematically more precise sense, the transformation $X_n = F(H_n)H_n$ is a bijective map from $[0, K)$ to $[0, K)$.

From these arguments on the relation of the native prey-predator system (4) of Model J to (5) of Model A with $\sigma = 0$ through the transformation $X_n = F(H_n)H_n$, we can get the following result:

Lemma 5 *The generic native prey-predator systems* (4) *and* (5) *of Models J and A with* $\sigma = 0$ *have mathematically equivalent nature about the population dynamics.*

In other words, the solutions for the native prey-predator systems (4) and (5) of Models J and A with $\sigma = 0$ can be considered qualitatively equivalent. In the subsequent sections, we will demonstrate this qualitative dynamical equivalence in their population dynamics. Weide et al. (2019) also discussed a similar result regarding the qualitative correspondence of dynamical nature for their models (4) and (5) with $\sigma = 0$, F and $\Pi_\bullet$ given by (2) and (10).

6.2 Coexistent state for the native prey-predator system

From Theorem 2, we can get the following result on the existence of coexistent equilibrium $E^{\bullet}_{++}$ for the native prey-predator systems (28) and (29) of Models J and A:

Corollary 6 *For the native prey-predator systems* (28) *and* (29) *of Models J and A, the coexistent equilibrium* $E^{\bullet}_{++}$ *uniquely exists if and only if* $\mathscr{R}^{\bullet}_0 > 1$*. The equilibrium values is determined as* $E^{\mathrm{J}}_{++}(h^*, p^{\mathrm{J}}_*) = (r_0 x^{\mathrm{J}}_* - 1, -\log x^{\mathrm{J}}_*)$ *and* $E^{\mathrm{A}}_{++}(h^*, p^{\mathrm{A}}_*) = \big(r_0 - \frac{1}{x^{\mathrm{A}}_*}, -\log x^{\mathrm{A}}_*\big)$*, respectively with the unique root* $x^{\bullet}_* \in (\frac{1}{r_0}, 1)$ *of equation*

$$\Phi_{\bullet}(x) := \mathscr{R}^{\bullet}_0\Big(1 - \frac{1}{x}\Big)\Big(x - \frac{1}{r_0}\Big) - \Big(1 - \frac{1}{r_0}\Big)\log x = 0. \tag{31}$$

As long as the stability of the coexistence equilibrium $E^{\bullet}_{++}$ for the native prey-predator system is considered, its existence must be assumed. This implies that $\mathscr{R}^{\bullet}_0 > 1$ for the native prey-predator system, as per Theorem 2 and Corollary 6. Subsequently, following Theorem 3, we can derive the result on the local stability of the coexistence equilibria E^{J}_{++} and E^{A}_{++} for the native prey-predator systems (28) and (29) of Models J and A, respectively (Appendix G):

Corollary 7 *For the native prey-predator systems* (28) *and* (29) *of Models J and A, respectively, the coexistent equilibrium* $E^{\bullet}_{++}$ *exists, and it is locally asymptotically stable if one of the following conditions is satisfied:*

- ▹ $r_0 \in (1, 2\,]$ *and* $\mathscr{R}^{\bullet}_0 \in (1, r_0]$*;*
- ▹ $r_0 \in (1, 2\,]$ *and* $\mathscr{R}^{\bullet}_0 > r_0$ *with* $\Phi_{\bullet}(x^{\bullet}_-) < 0$*;*
- ▹ $r_0 > 2$ *and* $\mathscr{R}^{\bullet}_0 \in \big(1, 4(1 - \frac{1}{r_0})\big)$*;*
- ▹ $r_0 > 2$ *and* $\mathscr{R}^{\bullet}_0 \geq 4(1 - \frac{1}{r_0})$ *with* $\Phi_{\bullet}(x^{\bullet}_-) < 0$*;*
- ▹ $r_0 > 2$ *and* $\mathscr{R}^{\bullet}_0 \in \big[4(1 - \frac{1}{r_0}), r_0\big)$ *with* $\Phi_{\bullet}(x^{\bullet}_+) > 0$*,*

where

$$x^{\bullet}_{\pm} := \frac{\alpha_{\bullet}}{2}\left(1 \pm \sqrt{1 - \frac{4}{\alpha_{\bullet} r_0}}\right) = \frac{\mathscr{R}^{\bullet}_0}{2(r_0 - 1)}\left\{1 \pm \sqrt{1 - \frac{4}{\mathscr{R}^{\bullet}_0}\Big(1 - \frac{1}{r_0}\Big)}\right\}. \tag{32}$$

In a specific case where $\alpha_{\bullet} = \frac{4}{r_0}$, we have $x^{\bullet}_- = x^{\bullet}_+ = \frac{2}{r_0}$ and $\Phi_{\bullet}(x^{\bullet}_{\pm}) = \Phi_{\bullet}\big(\frac{2}{r_0}\big) = \big(1 - \frac{1}{r_0}\big)\big(\frac{4}{r_0} - 2 - \log\frac{2}{r_0}\big)$ for $r_0 \neq 2$, while $\Phi_{\bullet}(x^{\bullet}_{\pm}) = \Phi_{\bullet}(1) = 0$ for $\alpha_{\bullet} = 2$ with $r_0 = 2$. The case of $(r_0, \alpha_{\bullet}) = (2, 2)$, that is, $(r_0, \mathscr{R}^{\bullet}_0) = (2, 2)$ satisfies the first condition of Corollary 7. Hence, the coexistent equilibrium $E^{\bullet}_{++}$ is locally asymptotically stable in the case.

Making use of the conditions given in Corollary 7, we can get the $(\alpha_{\bullet}, r_0)$-dependence of the local stability of equilibria feasible for the native prey-predator system as shown in Fig. 2. Note that, as shown by Corollary 3 in Sect. 3, there certainly exists a region of $(\alpha_{\bullet}, r_0)$ with which the equilibrium $E^{\bullet}_{++}$ is locally asymptotically stable, while it is unstable for sufficiently large $\alpha_{\bullet}$ or r_0 to lead to an oscillatory state for the system.

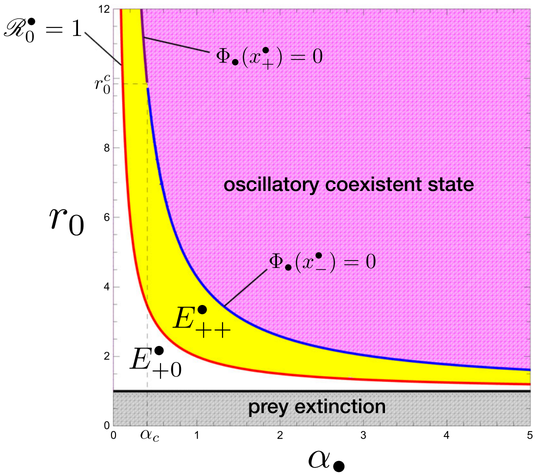

Fig. 2 $(\alpha_\bullet, r_0)$-dependence of the local stability of feasible equilibria for the native prey-predator system (28) and (29), obtained from Corollary 7. $r_0^c \approx 9.84311$; $\alpha_c = \frac{4}{r_0} \approx 0.406376$, where r_0^c is the root of equation $\frac{4}{r_0} - 2 - \log\frac{2}{r_0} = 0$ for $r_0 > 1$

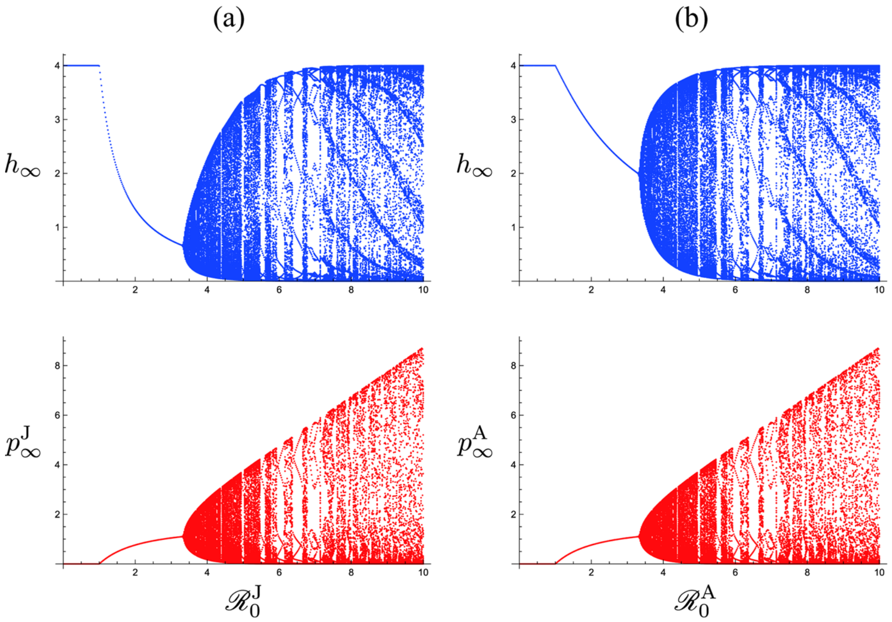

Fig. 3 Numerically drawn bifurcation diagrams for the native prey-predator systems (a) (28) of Model J; (b) (29) of Model A, respectively, where $\alpha_\bullet = \mathscr{R}_0^\bullet/\kappa = \mathscr{R}_0^\bullet/(r_0 - 1)$ commonly with $r_0 = 5.0$

6.3 Bifurcation of equilibria for the native prey-predator system

As argued in Sect. 4, there are complex conjugate eigenvalues with the absolute value 1 at the bifurcation condition according to the stability of coexistent equilibrium $E_{++}^\bullet$. Therefore, the bifurcation of the solution to make the coexistent equilibrium unstable must be of Neimark-Sacker type.

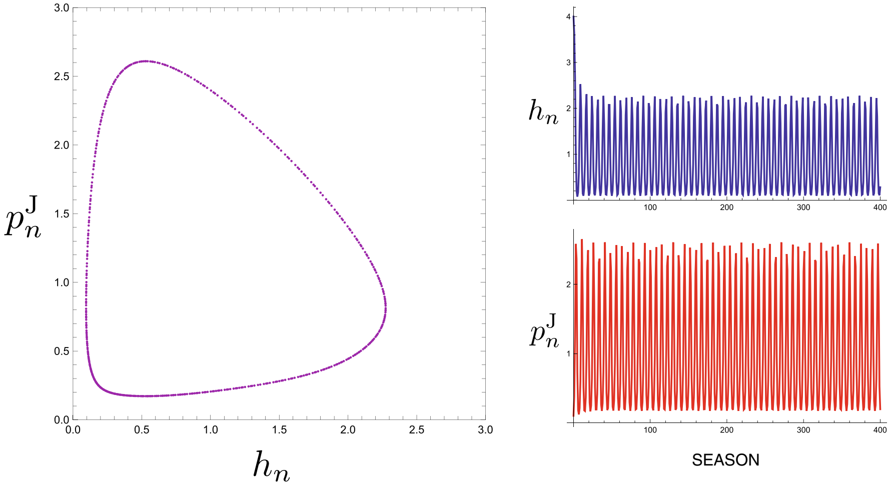

Fig. 4 Numerical example of the temporal variation (right) and the attractor in phase space (left) for the native prey-predator system (28) of Model J with $r_0 = 5.0$, $\alpha_{\mathrm{J}} = 1.0$, and $\mathscr{R}_0^{\mathrm{J}} = 4.0$. The initial condition for the temporal variation (right) is $(h_0, p_0^{\mathrm{J}}) = (4.0, 0.1)$

Actually, as clearly seen from the numerically drawn bifurcation diagrams in Fig. 3 for the native prey-predator systems (28) and (29), the system has a potential nature to approach an oscillatory stationary state when the coexistent equilibrium $E_{++}^{\bullet}$ is unstable. Indeed, the numerical example of Fig. 4 about the temporal variation and trajectory of h_n and p_n^{J} for (28) indicates a quasi-periodic variation typically for such a Neimark-Sacker type of bifurcation. It shows the attractor (ω-limit set) belongs to a closed curve in the phase plane, which might be a periodic cycle or alternatively a dense set on it (also refer to numerics of the temporal variation in Figs. 10 and 11).

Correspondingly, Marcinko and Kot (2020) explored the nature of Neimark-Sacker bifurcation and other mathematical features for their *Model 3* which is mathematically equivalent to our native prey-predator system (28) of Model J. The dynamical characteristics of our native prey-predator systems (28) and (29) are qualitatively similar to those of the models in Weide et al. (2019), where F and $\Pi_\bullet$ are given by (2) and (10), respectively. Furthermore, as discussed in Sect. 4 with respect to our generic native prey-predator systems (4) and (5), Din et al. (2020) provided a mathematically precise analysis of the transcritical and Neimark-Sacker bifurcations for one of the models in Weide et al. (2019), which includes our native prey-predator system (29) of Model A. Apart from the mathematical details of bifurcation and attracting states, the numerically drawn bifurcation diagrams in Fig. 3 effectively illustrate the dynamical equivalence between the native prey-predator systems of Models J and A, as stated in Lemma 5 of Sect. 6.1 concerning the generic native prey-predator systems (4) and (5) with $\sigma = 0$. Nevertheless, we refrain from delving deeper into these mathematical features for our native prey-predator system as it deviates from the focus of this paper.

6.4 Alien predator invasion of equilibrium native prey-predator system

From Theorem 4 in Sect. 5.1, we can obtain the following result on the local stability of equilibrium $E^{*}_{++0}(h^{*}, p^{\mathrm{J}}_{*}, p^{\mathrm{A}}_{*}) = (r_0 x^{\mathrm{J}}_{*} - 1, -\log x^{\mathrm{J}}_{*}, 0)$ for the system (27) with $x^{\mathrm{J}}_{*} \in (\frac{1}{r_0}, 1)$, where x^{J}_{*} is determined as the root of equation (31) in Corollary 6. (Appendix H):

Corollary 8 *Provided that the equilibrium E^{J}_{++} for the native prey-predator system (28) of Model J is asymptotically stable, the equilibrium E^{*}_{++0} for the system (27) is locally asymptotically stable if one of the following two conditions is satisfied:*

- ▷ $\mathscr{R}^{\mathrm{A}}_0 \leq \mathscr{R}^{\mathrm{J}}_0$;
- ▷ $\Phi_{\mathrm{J}}\big((1 - \frac{1}{r_0})\frac{1}{\mathscr{R}^{\mathrm{A}}_0} + \frac{1}{r_0}\big) < 0$ *with* $\mathscr{R}^{\mathrm{A}}_0 \in \big(\mathscr{R}^{\mathrm{J}}_0, \frac{r_0 - 1}{\log r_0}\mathscr{R}^{\mathrm{J}}_0\big)$.

In contrast, it is unstable if one of the following two conditions is satisfied:

- ▷ $\Phi_{\mathrm{J}}\big((1 - \frac{1}{r_0})\frac{1}{\mathscr{R}^{\mathrm{A}}_0} + \frac{1}{r_0}\big) > 0$ *with* $\mathscr{R}^{\mathrm{A}}_0 \in \big(\mathscr{R}^{\mathrm{J}}_0, \frac{r_0 - 1}{\log r_0}\mathscr{R}^{\mathrm{J}}_0\big)$;
- ▷ $\mathscr{R}^{\mathrm{A}}_0 \geq \frac{r_0 - 1}{\log r_0}\mathscr{R}^{\mathrm{J}}_0$.

From Corollary 8, the alien predator P^{A} invasion of the native prey-predator system (28) at the coexistent equilibrium E^{J}_{++} is successful only if the alien predator P^{A} has its basic replacement number greater than that of the native predator P^{J}: $\mathscr{R}^{\mathrm{A}}_0 > \mathscr{R}^{\mathrm{J}}_0$. Even if $\mathscr{R}^{\mathrm{A}}_0 > \mathscr{R}^{\mathrm{J}}_0$, it could fail. This result matches Corollary 4 in Sect. 5.1. Actually the condition (24) in Corollary 4 now becomes

$$F\Big(\frac{K}{\mathscr{R}^{\mathrm{J}}_0}\Big) - 1 - \log F\Big(\frac{K}{\mathscr{R}^{\mathrm{J}}_0}\Big) > 0 \tag{33}$$

with $F\big(\frac{K}{\mathscr{R}^{\mathrm{J}}_0}\big) > 1$ according to the system (27) of Model J. Since $x - 1 - \log x$ is positive for $x > 1$, the condition (33), that is, (24) holds now. While the condition (33) holds regardless of the detail of the function F, it essentially depends on the function $\Pi_{\bullet}$ given by (9).

In the same way, we can obtain the following result on the local stability of $E^{*}_{+0+}(h^{*}, p^{\mathrm{J}}_{*}, p^{\mathrm{A}}_{*}) = (r_0 x^{\mathrm{A}}_{*} - 1, 0, -\log x^{\mathrm{A}}_{*})$ with $x^{\mathrm{A}}_{*} \in (\frac{1}{r_0}, 1)$ for the system (27) of Model A concerning the alien predator P^{J} invasion, where x^{A}_{*} is determined as the root of equation (31) in Corollary 6 (Appendix H):

Corollary 9 *Provided that the equilibrium E^{A}_{++} for the native prey-predator system (29) of Model A is asymptotically stable, the equilibrium E^{*}_{+0+} for the system (27) is locally asymptotically stable if one of the following two conditions is satisfied:*

- ▷ $\mathscr{R}^{\mathrm{J}}_0 \leq \max\{\frac{r_0 - 1}{r_0 \log r_0}\mathscr{R}^{\mathrm{A}}_0, 1\}$;
- ▷ $\Phi_{\mathrm{A}}\big(\{r_0(1 - \frac{1}{\mathscr{R}^{\mathrm{J}}_0}) + \frac{1}{\mathscr{R}^{\mathrm{J}}_0}\}^{-1}\big) < 0$ *with* $\mathscr{R}^{\mathrm{J}}_0 \in \big(\max\{\frac{r_0 - 1}{r_0 \log r_0}\mathscr{R}^{\mathrm{A}}_0, 1\}, \mathscr{R}^{\mathrm{A}}_0\big)$.

In contrast, it is unstable if one of the following two conditions is satisfied:

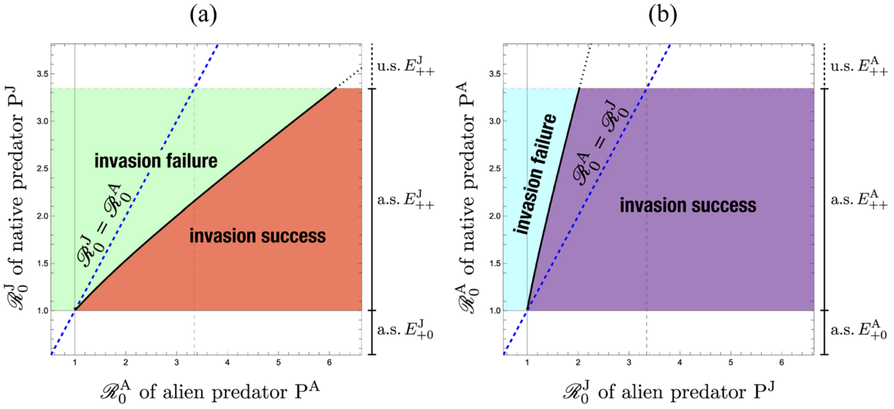

Fig. 5 $(\mathscr{R}_0^{\mathrm{J}}, \mathscr{R}_0^{\mathrm{A}})$-dependence of the success/failure of alien predator invasion at the coexistent equilibrium of native prey-predator system (a) (28) for Model J; (b) (29) for Model A. Numerically drawn parameter region by the conditions given in Corollaries 8 and 9 for $r_0 = 5.0$. The coexistent equilibrium of native prey-predator system $E_{++}^{\bullet}$ is locally asymptotically stable for the filled region. For the ranges a.s. $E_{+0}^{\bullet}$ and a.s. $E_{++}^{\bullet}$ in terms of $\mathscr{R}_0^{\bullet}$ about the native predator $E_{+0}^{\bullet}$ and $E_{++}^{\bullet}$ are locally asymptotically stable, respectively, while they are unstable for those indicated as u.s. $E_{++}^{\bullet}$. The upper bound for the local stability of $E_{++}^{\bullet}$ is numerically obtained from the condition given in Corollary 7. The lower bound is given by $\mathscr{R}_0^{\bullet} = 1$. The solid black boundary is given by $\Phi_{\mathrm{J}}\big((1-\frac{1}{r_0})\frac{1}{\mathscr{R}_0^{\mathrm{A}}}+\frac{1}{r_0}\big) = 0$ in (a), and $\Phi_{\mathrm{A}}\big(\{r_0(1-\frac{1}{\mathscr{R}_0^{\mathrm{J}}})+\frac{1}{\mathscr{R}_0^{\mathrm{J}}}\}^{-1}\big) = 0$ in (b). Note that, from Theorem 1, the predator population goes extinct with $\mathscr{R}_0^{\bullet} \le 1$. The upper blank region of u.s. $E_{++}^{\bullet}$ corresponds to an oscillatory coexistent state for the native predator system

- ▷ $\Phi_{\mathrm{A}}\big(\{r_0(1-\frac{1}{\mathscr{R}_0^{\mathrm{J}}})+\frac{1}{\mathscr{R}_0^{\mathrm{J}}}\}^{-1}\big) > 0$ *with* $\mathscr{R}_0^{\mathrm{J}} \in \big(\max\{\frac{r_0-1}{r_0 \log r_0}\mathscr{R}_0^{\mathrm{A}}, 1\}, \mathscr{R}_0^{\mathrm{A}}\big)$;
- ▷ $\mathscr{R}_0^{\mathrm{J}} \ge \mathscr{R}_0^{\mathrm{A}}$.

From Corollary 9, the alien predator $\mathrm{P^J}$ invasion of the native prey-predator system at the coexistent equilibrium E_{++}^{A} is successful if $\mathscr{R}_0^{\mathrm{J}} > \mathscr{R}_0^{\mathrm{A}}$. Moreover, even if $\mathscr{R}_0^{\mathrm{J}} \le \mathscr{R}_0^{\mathrm{A}}$, it could be successful. This result matches Corollary 5 in Sect. 5.2.

As discussed in Sect. 5, even if the equilibrium E_{++0}^{*} or E_{+0+}^{*} is unstable, we cannot definitively determine the success or failure of alien predator $\mathrm{P^A}$ or $\mathrm{P^J}$ invasion for Models J and A, respectively. As illustrated in Figs. 2, 3, and 4, the native prey-predator system may not be at the equilibrium state but rather at a stably oscillatory state before an alien predator invasion. Consequently, even if the equilibrium E_{++0}^{*} or E_{+0+}^{*} is unstable, the alien predator $\mathrm{P^A}$ or $\mathrm{P^J}$ invasion fails in Models J and A, respectively, when the system returns to a stably oscillatory state of the native prey-predator system with the extinction of alien predator. In such a scenario, it could be assumed a priori that the native prey-predator system stably stays at an oscillatory state before the alien predator invasion.

6.5 Invadability of native prey-predator system

As discussed in the previous sections on the local stability of equilibria, E^*_{++0} for Model J and E^*_{+0+} for Model A, the instability indicates the invadability of native prey-predator system to the alien predator, provided that the native prey-predator system stays at the asymptotically stable equilibrium with the persistent native prey and predator before the alien predator invasion.

Figure 5 illustrates the numerically demonstrated $(\mathscr{R}_0^{\mathrm{J}}, \mathscr{R}_0^{\mathrm{A}})$-dependence of the success of alien predator invasion at the coexistent equilibrium of native prey-predator system for Models J and A, respectively, based on the conditions given in Corollaries 8 and 9. The alien predator $\mathrm{P}^{\bullet}$ invasion is successful only when its basic replacement number $\mathscr{R}_0^{\bullet}$ is sufficiently large.

From Corollaries 8 and 9, as already mentioned in the previous sections and as clearly seen in Fig. 5, we can find the following feature about the success of alien predator invasion for Models J and A:

Corollary 10 *Provided that the native prey-predator system stays at the asymptotically stable coexistent equilibrium before the alien predator invasion, the alien predator* P^{J} *with* $\mathscr{R}_0^{\mathrm{J}} \geq \mathscr{R}_0^{\mathrm{A}}$ *successfully invades the native prey-predator system of Model A, while the alien predator* P^{A} *with* $\mathscr{R}_0^{\mathrm{A}} > \mathscr{R}_0^{\mathrm{J}}$ *may fail to invade the native prey-predator system of Model J.*

This result demonstrates that the alien predator P^{A} invasion of the native prey-predator system in Model J is harder to succeed than that of alien predator P^{J} of the native prey-predator system in Model A. Notably, when $\mathscr{R}_0^{\mathrm{J}} = \mathscr{R}_0^{\mathrm{A}}$ for predators P^{J} and P^{A}, the alien predator P^{J} invasion of the native prey-predator system in Model A is successful, while the alien predator P^{A} invasion of the native prey-predator system in Model J fails. See numerical illustrations in Fig. 6.

Therefore, we can conclude that, provided that the native prey-predator system stays at the asymptotically stable equilibrium with persistent native prey and predator before the alien predator invasion, *the native prey-predator system of Model J is less vulnerable to the alien predator invasion than that of Model A.* In the other context, *the juvenile-specific predator is more successful in the invasion than the adult-specific alien predator.*

Figure 7 shows the result blending numerical calculations for Models J and A in Fig. 5. It illustratively shows a region for the parameter values $(\mathscr{R}_0^{\mathrm{J}}, \mathscr{R}_0^{\mathrm{A}})$ such that both of equilibria E^*_{++0} and E^*_{+0+} are unstable, which is labeled with $\langle \mathrm{s}, \mathrm{s} \rangle$ there. For such values $(\mathscr{R}_0^{\mathrm{J}}, \mathscr{R}_0^{\mathrm{A}})$, the alien predator invasion is successful, and two predator species may come to coexist after the alien predator invasion in both Models J and A. As demonstrated by Corollary 10 and illustrated by Fig. 7, such a coexistence of native and alien predators appears only for values $(\mathscr{R}_0^{\mathrm{J}}, \mathscr{R}_0^{\mathrm{A}})$ such that $\mathscr{R}_0^{\mathrm{A}} > \mathscr{R}_0^{\mathrm{J}} > 1$.

Supplementarily with respect to the coexistence of native and alien predators, we can find the following result too (Appendix I):

Lemma 6 *A coexistent equilibrium* $E^*_{+++}(h^{**}, p^{\mathrm{J}}_{**}, p^{\mathrm{A}}_{**})$ *with* $p^{\mathrm{J}}_{**} > 0$ *and* $p^{\mathrm{A}}_{**} > 0$ *for the system* (27) *exists only if* $\mathscr{R}_0^{\mathrm{A}} > \mathscr{R}_0^{\mathrm{J}} > 1$. *If* $\mathscr{R}_0^{\mathrm{J}} \geq \mathscr{R}_0^{\mathrm{A}}$, *it does not exist.*

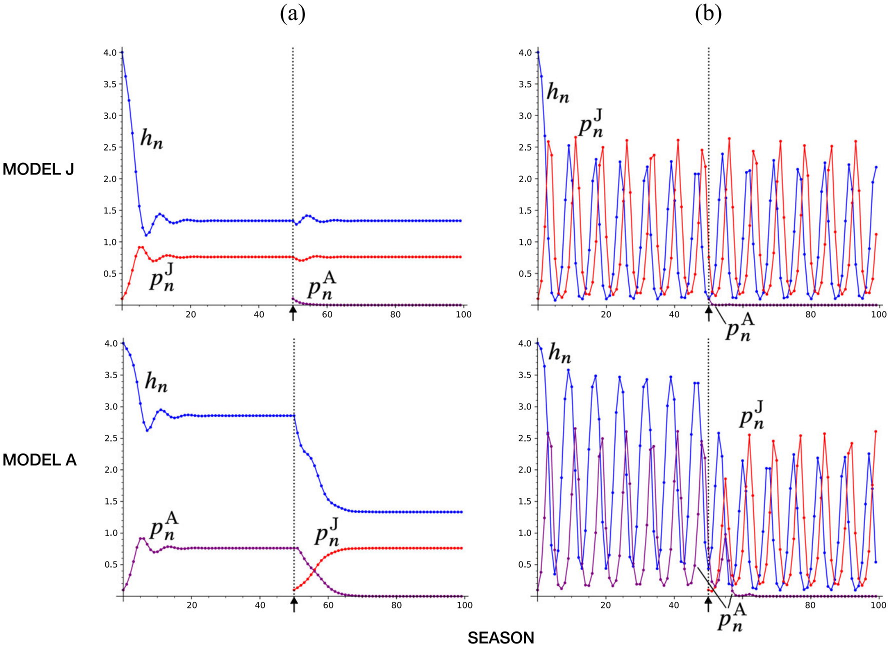

Fig. 6 Temporal variations of population sizes for Model J and Model A with $\mathscr{R}_0^J = \mathscr{R}_0^A$. Numerically drawn from $n = 0$ to $n = 100$ with (a) $\mathscr{R}_0^J = \mathscr{R}_0^A = 2.0$ ($\alpha_J = \alpha_A = 0.5$); (b) $\mathscr{R}_0^J = \mathscr{R}_0^A = 4.0$ ($\alpha_J = \alpha_A = 1.0$). Commonly $r_0 = 5.0$. The alien predator $P^\bullet$ invades the native prey-predator system at $n = 50$ (as indicated by the upward arrow in the figure). The initial condition for the native prey and predator populations is given as $(h_0, p_0^\bullet) = (4.0, 0.1)$, and the alien predator population size $p_{50}^\bullet = 0.1$ at the season of its invasion. The native prey-predator system tends to reach a coexistent state before the invasion of alien predator at $n = 50$. In Model J, the invasion of the alien predator P^A fails, leading to its extinction for $n > 50$. In Model A, the invasion of the alien predator P^J is successful, resulting in the establishment of coexistence between the prey and the alien predator. However, the native predator population p_n^A goes extinct for $n > 50$ due to the exploitative competition with the alien predator P^J

Remind that, from Theorem 1 and Corollary 1, no coexistent equilibrium exists if $\mathscr{R}_0^J \leq 1$ or $\mathscr{R}_0^A \leq 1$.

While we have not obtained further analytical result on the success or failure of alien predator invasion at the stably oscillatory state of native prey-predator system, we can obtain numerical results, as illustrated in Fig. 8. We observe a clear correspondence between the numerical results and the analytical results presented in Fig. 5, which were derived from Corollaries 8 and 9 about the success/failure of alien predator invasion at the coexistent equilibrium of native prey-predator system.

The same as the result of Corollary 10, the alien predator P^A invasion in Model J is less successful than that of alien predator P^J in Model A even when the native prey-predator system stays at a stably oscillatory state before the invasion (see Figure 6(b)). Thus, the numerical result suggests that, regardless of the stationary state the native prey-predator system stays at, *the native prey-predator system of Model J is less vulnerable to the alien predator invasion than that of Model A*. Moreover, *the juvenile-*

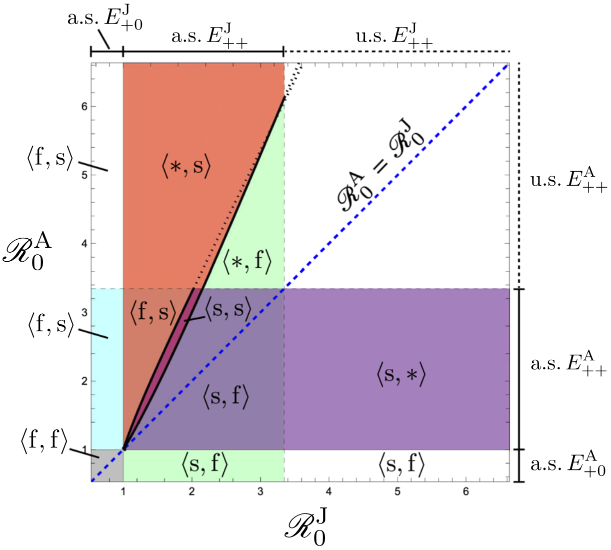

Fig. 7 ($\mathscr{R}_0^{\rm J}$, $\mathscr{R}_0^{\rm A}$)-dependence of the success/failure of alien predator invasion at the equilibrium of native prey-predator systems (28) and (29) in Models J and A. Numerically drawn by the conditions given in Corollaries 8 and 9 for $r_0 = 5.0$, merging those numerical results in Fig. 5. The solid black boundaries are the same as those in Fig. 5. The regions $\langle \bullet, \mathrm{s} \rangle$ and $\langle \mathrm{s}, \bullet \rangle$ are respectively for the success of predator $\mathrm{P}^{\rm A}$ invasion in Model J and for that of predator $\mathrm{P}^{\rm J}$ in Model A. In the same way, the regions $\langle \bullet, \mathrm{f} \rangle$ and $\langle \mathrm{f}, \bullet \rangle$ are for the failure of invasion. As for the regions $\langle \bullet, * \rangle$ and $\langle *, \bullet \rangle$, we do not have any analytical result on the success/failure of alien predators $\mathrm{P}^{\rm A}$ and $\mathrm{P}^{\rm J}$ invasion respectively in Models J and A, because they correspond to the oscillatory state for the native prey-predator system. The right upper blank region corresponds to the oscillatory state for the native prey-predator system in both Models J and A. For the left bottom region of $\langle \mathrm{f}, \mathrm{f} \rangle$, both predators go extinct

specific alien predator is more successful in the invasion than the adult-specific alien predator.

As evident from Figs. 7 and 8, the coexistence between native and alien predators is feasible only within a relatively narrow region of ($\mathscr{R}_0^{\rm J}$, $\mathscr{R}_0^{\rm A}$), where $\mathscr{R}_0^{\rm A} > \mathscr{R}_0^{\rm J} > 1$. Therefore, it is highly probable that the success of alien predator invasion leads to the extinction of native predator due to competitive exclusion, regardless of what state the native prey-predator system stays at before the invasion (see Fig. 6).

Hackett-Jones et al. (2009) developed and examined a mathematical model that incorporated the parasitism windows (i.e., timings). Their study focused on the coexistence of two parasitoids on a shared host. They demonstrated that the window widths and locations, determined by the host life cycle, play a crucial role in determining the coexistence of two parasitoids. This coexistence necessitates a delicate balance between parasitoid fecundity and survival (see also (Briggs et al. 1993; Hood et al. 2021)). In a similar context, the coexistence of native and alien predators in our model appears to require a balance between predators' fertilities, represented by the basic predator replacement rates $\mathscr{R}_0^{\bullet}$. If one predator's fertility much exceeds the other predator's, it reduces the prey population for the latter to a large extent, and at the same time, it reduces the prey population size for its own next generation. This is a negative

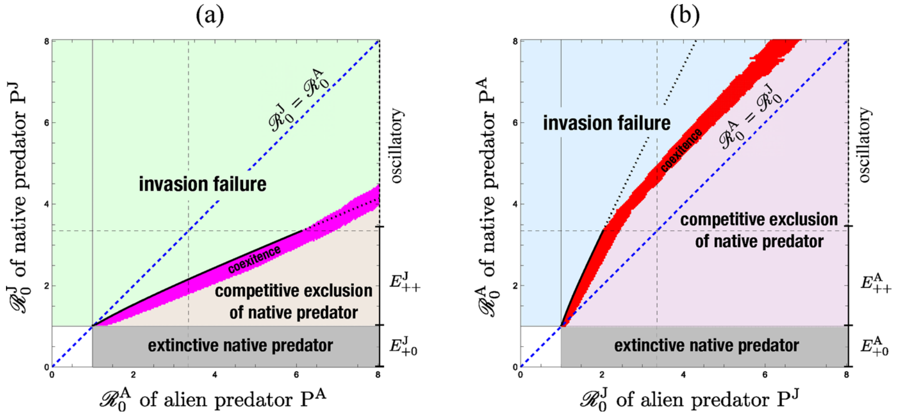

Fig. 8 $(\mathscr{R}^{\mathrm{J}}_0, \mathscr{R}^{\mathrm{A}}_0)$-dependence of the final state after the alien predator invasion for (a) Model J; (b) Model A. Numerically estimated with the temporal variation of population sizes generated by the system (27) for $r_0 = 5.0$. Boundaries of the region for the coexistence is jagged due to a numerical issue for the oscillatory state. The solid black boundary is the same as that in Figs. 5 and 7. The failure of alien predator invasion makes the system approach a state of native prey-predator system with the extinction of alien predator. The success of alien predator invasion makes the system transfer to a state with persistent native and alien predators, or alternatively with the extinction of native predator which is the consequence of competition or the lack of persistence of native predator. For the bottom region of extinctive native predator, the native predator is going extinct even without alien predator invasion, while the alien predator can persist with the native prey after its invasion. For the left bottom blank region, both predator species cannot persist but go extinct

feedback to the predator reproduction by its own predation, as known well in ecology (see some detailed discussion in (Chesson 2000)). Excessive fertility of one predator can prevent the coexistence of the other predator, leading to competitive exclusion.

On the other hand, based on numerical results of Fig. 8, we can observe from Fig. 9 that there exists a region of $(\mathscr{R}^{\mathrm{J}}_0, \mathscr{R}^{\mathrm{A}}_0)$ where the alien predator invasion fails for both Models J and A. It is labeled with $\langle \mathrm{f}, \mathrm{f} \rangle$ in the upper part of the figure. It is the scenario that the native prey-predator system is resistant to the alien predator invasion, regardless of which stages of prey are preyed on by the native and alien predators, respectively.

Mathematically, it indicates the existence of a bistability of the equilibrium E^*_{++0} and another oscillatory state for the system (27). In this situation, E^*_{+0+} is unstable, and the system approaches a stably oscillatory state of the native prey-predator system (29) for Model A while it returns to the equilibrium of the native prey-predator system (28) for Model J. This occurs because the region $\langle \mathrm{f}, \mathrm{f} \rangle$ in Fig. 9 contains such $(\mathscr{R}^{\mathrm{J}}_0, \mathscr{R}^{\mathrm{A}}_0)$. Additionally, there exists another bistability of two stably oscillatory states for the system (27). In this case, the system approaches one stably oscillatory state of the native prey-predator system (29) for Model A, while it approaches another stably oscillatory state of the native prey-predator system (28) for Model J. Furthermore, for a region in $\langle \mathrm{f}, \mathrm{s} \rangle$ or $\langle \mathrm{s}, \mathrm{f} \rangle$ of $(\mathscr{R}^{\mathrm{J}}_0, \mathscr{R}^{\mathrm{A}}_0)$, we also find a case where there exists a bistability of a coexistent state of native and alien predators, and a coexistent state of native prey-predator system with the extinction of the alien predator.

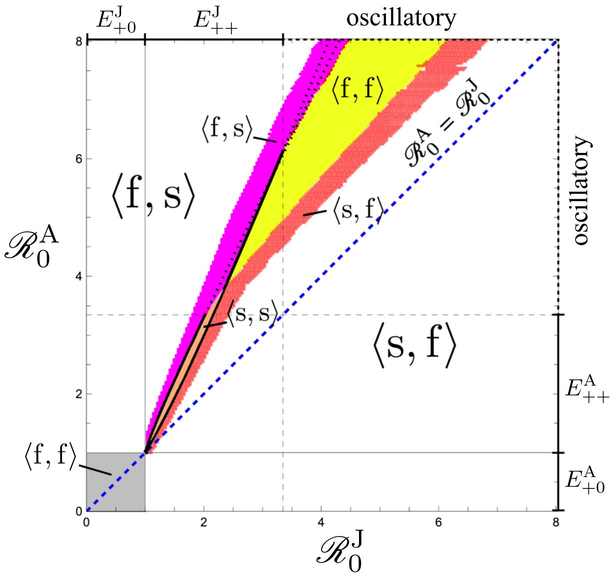

Fig. 9 ($\mathscr{R}_0^{\mathrm{J}}$, $\mathscr{R}_0^{\mathrm{A}}$)-dependence of the consequence of the alien predator invasion. Numerically estimated with the temporal variation of population sizes generated by the system (27) for $r_0 = 5.0$, merging those numerical results in Fig. 8. Symbols to denote the regions are the same as those in Fig. 7

6.6 Phase transition by alien predator invasion

As discussed in the previous section, the successful invasion of an alien predator is highly likely to lead to the extinction of native predator due to competitive exclusion. Consequently, the newly established system of native prey and alien predator could be at a phase different from the original native prey-predator system, potentially at an oscillatory state from the equilibrium or vice versa. Figures 10 and 11 provide numerical examples of such phase transitions resulting from the successful invasion of alien predator.

According to Model J, as depicted in Fig. 8(a) the successful invasion of alien predator P^{A} with the competitive exclusion of native predator P^{J} can cause a state transition from the equilibrium E^{J}_{++} for the native prey-predator system (28) to the equilibrium E^{A}_{++} for the native prey-predator system (29), as shown in Fig. 10(c). It can also cause a state transition from E^{J}_{++} to a stably oscillatory state for (29), as shown in Fig. 10(d), or alternatively a state transition from one stably oscillatory state for (28) to another stably oscillatory state for (29). However, it is worth noting that no phase transition is observed from a stably oscillatory state for (28) to the equilibrium E^{A}_{++} for (29).

On the other hand, according to Model A, as shown in Fig. 8(b), the successful invasion of alien predator P^{J} with the competitive exclusion of native predator P^{A} can cause a state transition from the equilibrium E^{A}_{++} to the equilibrium E^{J}_{++}, from E^{A}_{++} to a stably oscillatory state for (28), from one stably oscillatory state for (29) to another stably oscillatory state for (28), and from a stably oscillatory state for (29) to

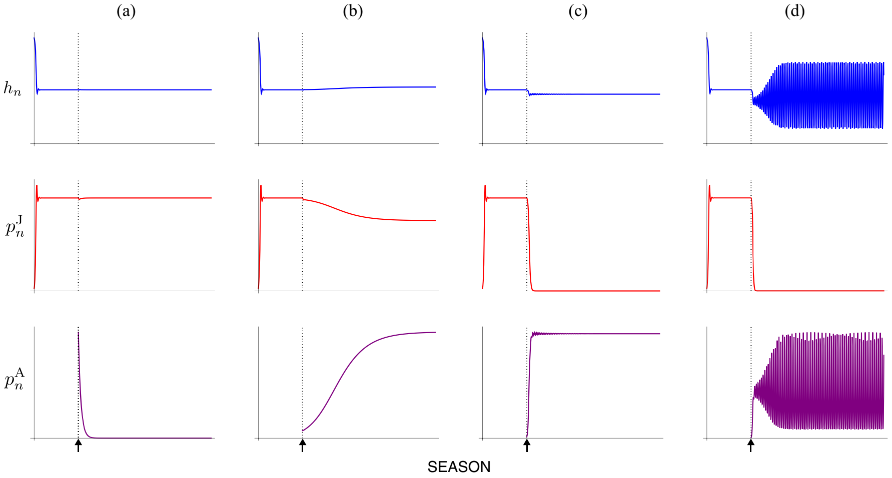

Fig. 10 Patterns in the temporal variation of population sizes for the system (27) with the alien predator $\mathrm{P^A}$ invasion of the native prey-predator system (28) at the equilibrium state E_{++}^{J} for Model J. Numerically drawn from $n = 0$ to $n = 800$ with (a) $\mathscr{R}_0^{\mathrm{A}} = 1.8$ ($\alpha_{\mathrm{A}} = 0.9$); (b) $\mathscr{R}_0^{\mathrm{A}} = 2.0$ ($\alpha_{\mathrm{A}} = 1.0$); (c) $\mathscr{R}_0^{\mathrm{A}} = 3.0$ ($\alpha_{\mathrm{A}} = 1.5$); (d) $\mathscr{R}_0^{\mathrm{A}} = 3.6$ ($\alpha_{\mathrm{A}} = 1.8$); and commonly $r_0 = 3.0$; $\alpha_{\mathrm{J}} = 0.8$; $\mathscr{R}_0^{\mathrm{J}} = 1.6$. The alien predator $\mathrm{P^A}$ invades the native prey-predator system at $n = 200$ (as indicated by the upward arrow in the figure). The initial condition is given as $(h_0, p_0^{\mathrm{J}}) = (2.0, 0.01)$, and the alien predator population size $p_{200}^{\mathrm{A}} = 0.01$

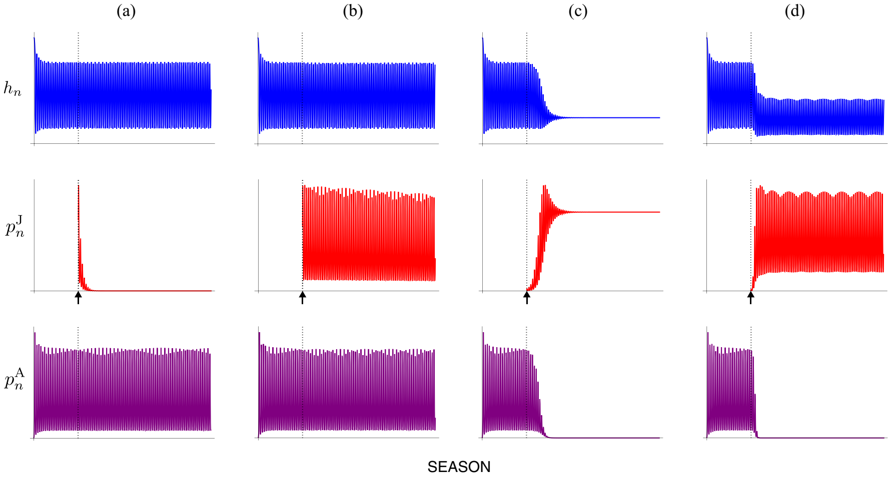

Fig. 11 Patterns in the temporal variation of population sizes for the system (27) with the alien predator $\mathrm{P^J}$ invasion of the native prey-predator system (29) at a stably oscillatory state for Model A. Numerically drawn from $n = 0$ to $n = 800$ with (a) $\mathscr{R}_0^{\mathrm{J}} = 2.4$ ($\alpha_{\mathrm{J}} = 1.2$); (b) $\mathscr{R}_0^{\mathrm{J}} = 2.6$ ($\alpha_{\mathrm{J}} = 1.3$); (c) $\mathscr{R}_0^{\mathrm{J}} = 2.8$ ($\alpha_{\mathrm{J}} = 1.4$); (d) $\mathscr{R}_0^{\mathrm{J}} = 3.4$ ($\alpha_{\mathrm{J}} = 1.7$); and commonly $r_0 = 3.0$; $\alpha_{\mathrm{A}} = 1.8$; $\mathscr{R}_0^{\mathrm{A}} = 3.6$. The alien predator $\mathrm{P^J}$ invades the native prey-predator system at $n = 200$ (as indicated by the upward arrow in the figure). The initial condition is given as $(h_0, p_0^{\mathrm{A}}) = (2.0, 0.01)$, and the alien predator population size $p_{200}^{\mathrm{J}} = 0.01$

the equilibrium E^{J}_{++}, as illustrated by Figs. 11(c) and (d). Notably, Model A includes a case where the successful invasion of alien predator P^{J} leads to a transition from a stably oscillatory state to the equilibrium state, whereas Model J does not have such a case for the successful invasion of any alien predator P^{A}.

In an ecological context, an oscillatory state of prey-predator system can make it vulnerable to the demographic stochasticity, such as severe climate conditions, injudicious human activities, etc. From an ecological perspective, the system at an oscillatory state would be considered less permanent in long-term run. In Model A, the successful invasion of alien predator P^{J} could transfer the system to a steady state with greater permanence. However, in Model J, the successful invasion of alien predator P^{A} could not induce such a state transition. Instead it could result in the system transitioning to an oscillatory state with reduced permanence.

7 Concluding remarks

Most predations can be categorized as stage-specific, with the range of prey stages preyed upon by each predator varying, as discussed in Godfray et al. (1994). From a perspective on the transition of a prey-predator system due to species invasion and extinction, a system with a stage-specific native predator could be invaded by an alien predator that preys on the same prey stage as the native does. In this paper, we did not consider such an alien predator invasion, but instead focused on how the stage-specific predation could be related to the invadability of the native prey-predator system or the success of the alien predator's invasion.

With a generic discrete-time model and its specific model, we investigated the invadability of a native prey-predator system with a stage-specific native predator to a different stage-specific alien predator invasion. Our mathematical results suggest that the prey-predator system with an adult-specific native predator would be more vulnerable to an alien predator invasion compared to that with a juvenile-specific native predator. The juvenile-specific predator could more successfully invade the native prey-predator system with adult-specific native predator, while the adult-specific predator would more likely fail to invade the system with juvenile-specific native predator.

Further we found that the success of a juvenile-specific alien predator invasion could stabilize the population dynamics of prey-predator system, while the success of an adult-specific alien predator invasion could not. Since the destabilization that induces an oscillatory state of the system could increase the system's vulnerability to demographic stochasticity, posing a risk of species extinction, the success of an adult-specific alien predator invasion would lead to a reduction of system permanence. In other words, the prey-predator system with adult-specific native predators would be less permanent in the long term, making it susceptible to demographic stochasticity or potentially transitioning to another prey-predator system after the extinction of the native predator and the successful invasion of juvenile-specific alien predators.

From a biological pest control perspective, the introduction of an operational alien predator would suggest that the predator's specificity in targeting the prey stage it consumes plays a crucial role in successful pest control, as also indicated by the work of Hood et al. (2021). While the introduction of an operational alien predator seems successful, it may fail to eliminate the (native) pest predator. This could lead to an oscillatory variation in the pest population size, resulting in repeated pest outbreaks. For successful pest control to suppress the pest population, it is necessary to control the predation feature of the introduced predator. Discrete-time population dynamics models have been extensively studied in the context of biological pest control problems (for instance, (Mills and Getz 1996; Lane et al. 1999; Tang and Cheke 2008; Jang and Yu 2012; Lee et al. 2022; Singh and Emerick 2022; Ackleh et al. 2023; Wu et al. 2023)).

Focusing on the vulnerability of native prey-predator systems to an alien predator invasion, we did not delve deeper into the mathematical analysis of the coexistent state between native and alien predators. In fact, it would require rigorous logical steps to obtain an analytical result regarding the existence and stability of such a coexistent state. This is true even for the coexistent equilibrium of the Beverton-Holt+Nicholson-Bailey model (26). Nevertheless, as shown by certain numerical results, the coexistence of native and alien predators is possible under specific conditions. In such cases, the coexistent state either reaches an equilibrium or undergoes a sustained oscillation.

As discussed in various works, the discrete-time prey-predator population dynamics model can exhibit complexity in the behavior of solutions and the occurrence of bifurcations. Ours demonstrated such features too. However, our mathematical assumptions for the generic model provide a straightforward setup for the growth of prey and predator population and the interspecific reaction between them. In this sense, we considered the generic and simplest model, as far as we are aware, and could not find any other work with a similar focus.

Since our mathematical results are on a generic discrete-time model of prey-predator system, they are applicable to a family of specific mathematical models about the prey-predator or host-parasitoid population dynamics. Notably, our generic model accommodates models involving different types of predation terms, allowing the native and alien predators to exhibit varying predation behaviors. It is evident that the distinct characteristics of density-dependent effect functions and predation terms can lead to different population dynamics. However, our results on the generic model can be applied to a range of prey-predator population dynamics models. We hope that our results in this paper provide valuable insights and inspiration for further theoretical exploration of ecological problems about the stability of prey-predator or host-parasitoid system.

Acknowledgements The authors greatly appreciate the valuable comments from anonymous referees to finalize the manuscript. The author HS was supported in part by JSPS KAKENHI Grant Number 22K03430.

Author Contributions Conceptualization: HS. Numerical simulation: HS, AG. Mathematical analysis: HS. Visualization: HS. Writing preliminary draft: HS, AG. Writing manuscript, review & editing: HS.

Funding Not applicable.

Availability of data and materials Not applicable.

Code availability Not applicable.

Declarations

Conflict of interest The authors state that there are no conflicts of interest.

Ethics approval Not applicable.

Consent to participate The authors agree to participate in this research project.

Consent for publication The authors approve publication of manuscript in a present form.

Appendix A Proof of Theorem 1

Consider the prey population dynamics in the native prey-predator system. From Lemma 2, the prey population size H_n is always less than the carrying capacity K. Thus, according to the native prey-predator system (4) of Model J, we have

$$\begin{aligned} P^{\mathrm{J}}_{n+1} &= \rho_{\mathrm{J}}\bigl\{1-\Pi_{\mathrm{J}}(P^{\mathrm{J}}_n)\bigr\}F(H_n)H_n \\ &< \rho_{\mathrm{J}}\bigl\{1-\Pi_{\mathrm{J}}(P^{\mathrm{J}}_n)\bigr\}F(K)K = \rho_{\mathrm{J}}(1-\sigma)K\bigl\{1-\Pi_{\mathrm{J}}(P^{\mathrm{J}}_n)\bigr\} \end{aligned} \tag{A1}$$

for any $n > 0$ and $H_n > 0$, since the right side of the recurrence relation for P^{J} is monotonically increasing in terms of H_n from the features of F given in Section 2.3.

Now let us consider the sequence $\{\widetilde{P}_n\}$ generated by the following recurrence relation with $\widetilde{P}_0 = P^{\mathrm{J}}_0 > 0$:

$$\widetilde{P}_{n+1} = f(\widetilde{P}_n) := \rho_{\mathrm{J}}(1-\sigma)K\bigl\{1-\Pi_{\mathrm{J}}(\widetilde{P}_n)\bigr\}. \tag{A2}$$

From the features of Π_{J} given in Section 2.4, the function $f(P)$ is differentiable, monotonically increasing, concave, and positive in terms of $P > 0$. In addition, it satisfies that $f(0) = 0$, $f(P) \to \rho_{\mathrm{J}}(1-\sigma)K$ as $P \to \infty$, and $\frac{f(P)-f(0)}{P} \to \rho_{\mathrm{J}}a_{\mathrm{J}}(1-\sigma)K = \mathscr{R}^{\mathrm{J}}_0 > 0$ as $P \to +0$. Hence, we can easily find that $f(P) < P$ for any $P > 0$ if and only if $\mathscr{R}^{\mathrm{J}}_0 \le 1$. Therefore, if $\mathscr{R}^{\mathrm{J}}_0 \le 1$, then the recurrence relation (A2) with $\widetilde{P}_0 > 0$ generates the sequence $\{\widetilde{P}_n\}$ such that $\widetilde{P}_{n+1} < \widetilde{P}_n$ and $\widetilde{P}_n > 0$ for any $n > 0$. Then, the Monotone Sequence Theorem demonstrates that $\widetilde{P}_n \to 0$ as $n \to \infty$ if $\mathscr{R}^{\mathrm{J}}_0 \le 1$. As a result, the inequality (A1) implies that $P^{\mathrm{J}}_n \to 0$ as $n \to \infty$ if $\mathscr{R}^{\mathrm{J}}_0 \le 1$. These arguments may be regarded as following what is called the comparison method (for instance, see (Elaydi and Cushing 2025)).

Similarly, according to the native prey-predator system (5) of Model A, we have

$$P_{n+1}^{\mathrm{A}} = \rho_{\mathrm{A}}\big\{1 - \Pi_{\mathrm{A}}(P_n^{\mathrm{A}})\big\}H_n < \rho_{\mathrm{A}}K\big\{1 - \Pi_{\mathrm{A}}(P_n^{\mathrm{A}})\big\}$$

for any $n > 0$ and $H_n > 0$, as well as that of Model J. Then, using the same arguments, we can determine that $P_n^{\mathrm{A}} \to 0$ as $n \to \infty$ if $\mathscr{R}_0^{\mathrm{A}} \le 1$. Consequently, these results demonstrate the *global stability* of the predator extinction equilibrium $E_{+0}^{\bullet}$ for the native prey-predator system when $\mathscr{R}_0^{\bullet} \le 1$.

As for the system (13) with native and alien predators, the right side of predator population dynamics of P^{A} is mathematically equivalent to the right side of predator population dynamics in the native prey-predator system (5), while that of P^{J} is necessarily less than the right side of predator population dynamics in the native prey-predator system (4). Therefore, the above arguments are applicable even for (13). Consequently, these arguments demonstrates the former result in Theorem 1. The latter result in Theorem 1 follows from the instability of the predator extinction equilibrium for the native prey-predator system, as shown in Lemma 3.

Appendix B Proof of Theorem 2

The coexistent equilibrium $E_{++}^{\mathrm{J}}(H_*, P_*^{\mathrm{J}})$ for the native prey-predator system (4) of Model J satisfies the following equations derived from the recurrence relations of (4):

$$\begin{cases} \sigma + \Pi_{\mathrm{J}}(P_*^{\mathrm{J}})F(H_*) = 1; \\ P_*^{\mathrm{J}} = \rho_{\mathrm{J}}\big\{1 - \Pi_{\mathrm{J}}(P_*^{\mathrm{J}})\big\}F(H_*)H_*. \end{cases} \tag{B3}$$

Let $\Pi_{\mathrm{J}}^* := \Pi_{\mathrm{J}}(P_*^{\mathrm{J}})$. From the former equation of (B3), if $E_{++}^{\mathrm{J}}(H_*, P_*^{\mathrm{J}})$ exists, then $F(H_*) = \frac{1-\sigma}{\Pi_{\mathrm{J}}^*} > 1 - \sigma$ because $\Pi_{\mathrm{J}}(P_*^{\mathrm{J}}) < 1$ for $P_*^{\mathrm{J}} > 0$ from the definition of Π_{J} given in Sect. 2.4. Thus, from the features of F given in Section 2.3, it is necessary that $F(0) = r_0 > \frac{1-\sigma}{\Pi_{\mathrm{J}}^*}$, since there is no $x > 0$ such that $F(x) = \frac{1-\sigma}{\Pi_{\mathrm{J}}^*}$ if $r_0 \le \frac{1-\sigma}{\Pi_{\mathrm{J}}^*}$. Therefore, if $E_{++}^{\mathrm{J}}(H_*, P_*^{\mathrm{J}})$ exists, then $\Pi_{\mathrm{J}}^* > \frac{1-\sigma}{r_0}$ with $r_0 > 1 - \sigma$. Moreover, for $\Pi_{\mathrm{J}}^* > \frac{1-\sigma}{r_0}$, the former equation of (B3) uniquely determines $H_* \in (0, K)$ because $F(H_*) = \frac{1-\sigma}{\Pi_{\mathrm{J}}^*} > 1-\sigma = F(K)$ with the monotonically decreasing function F. From these arguments, note that the coexistent equilibrium E_{++}^{J} cannot exist if $r_0 \le 1 - \sigma$.

The equations (B3) can be formally rewritten as

$$\begin{cases} H_* = F^{-1}\big(\frac{1-\sigma}{\Pi_{\mathrm{J}}^*}\big); \\ \Pi_{\mathrm{J}}^{-1}(\Pi_{\mathrm{J}}^*) = \rho_{\mathrm{J}}(1-\sigma)\Big(\dfrac{1}{\Pi_{\mathrm{J}}^*} - 1\Big)F^{-1}\big(\frac{1}{\Pi_{\mathrm{J}}^*}\big) \end{cases} \tag{B4}$$

with $r_0 > 1 - \sigma$, where F^{-1} and Π_{J}^{-1} are the inverse functions of F and Π_{J}, respectively. They can be well-defined from the features of F and Π_{J} given in Sect. 2.3 and 2.4. Note that $\Pi_{\mathrm{J}}^{-1}(x) \in (0, \infty)$ for $x \in (0, 1)$, and $F^{-1}(x) \in (0, \infty)$ for $x \in (0, r_0)$.

If the latter equation of (B4) in terms of Π_*^{J} has a positive root such that $\Pi_{\mathrm{J}}^* > \frac{1-\sigma}{r_0}$, then we have a positive value of $H_* < K$ from the former equation of (B4).

Now let us consider the existence of a root Π_{J}^* in $(\frac{1-\sigma}{r_0}, 1)$ about the latter equation of (B4), that is, the equation $\Phi_{\mathrm{J}}(x) = 0$ given by (20) for Model J. The function $\Phi_{\mathrm{J}}(x)$ is continuous in $[\frac{1-\sigma}{r_0}, 1]$ and differentiable in $(\frac{1-\sigma}{r_0}, 1)$ from the differentiability of Π_{J} and F in $(\frac{1-\sigma}{r_0}, 1)$, where their derivatives are negative. From the above arguments, if the equation $\Phi_{\mathrm{J}}(x) = 0$ has a root in $(\frac{1-\sigma}{r_0}, 1)$, then there exists an equilibrium as E_{++}^{J} for the native prey-predator system of Model J, while there exists no equilibrium E_{++}^{J} if the equation $\Phi_{\mathrm{J}}(x) = 0$ has no root in $(\frac{1-\sigma}{r_0}, 1)$.

We have

$$\begin{aligned}
\Phi_{\mathrm{J}}\big(\tfrac{1-\sigma}{r_0}\big) &= \Pi_{\mathrm{J}}^{-1}\big(\tfrac{1-\sigma}{r_0}\big) - \rho_{\mathrm{J}}(r_0 - 1 + \sigma)F^{-1}(r_0) = \Pi_{\mathrm{J}}^{-1}\big(\tfrac{1-\sigma}{r_0}\big) > 0;\\
\Phi_{\mathrm{J}}(1) &= \Pi_{\mathrm{J}}^{-1}(1) - \rho_{\mathrm{J}}(1-\sigma)(1-1)F^{-1}(1-\sigma) = 0,
\end{aligned}$$

since $\Pi_{\mathrm{J}}^{-1}(1) = 0$ and $F^{-1}(r_0) = 0$ from the features of F and Π_{J} given in Sect. 2.3 and 2.4. Further, with respect to the derivative

$$\Phi_{\mathrm{J}}'(x) = \frac{1}{\Pi_{\mathrm{J}}'\big(\Pi_{\mathrm{J}}^{-1}(x)\big)} + \rho_{\mathrm{J}}\frac{1-\sigma}{x^2}F^{-1}\big(\tfrac{1-\sigma}{x}\big) + \rho_{\mathrm{J}}\frac{(1-\sigma)^2}{x^2}\Big(\frac{1}{x} - 1\Big)\frac{1}{F'\big(F^{-1}\big(\frac{1-\sigma}{x}\big)\big)}, \tag{B5}$$

we find that

$$\begin{aligned}
&\Phi_{\mathrm{J}}'(x) \to \Phi_{\mathrm{J}}'\big(\tfrac{1-\sigma}{r_0} + 0\big) := \frac{1}{\Pi_{\mathrm{J}}'\big(\Pi_{\mathrm{J}}^{-1}\big(\frac{1-\sigma}{r_0}\big)\big)} - \rho_{\mathrm{J}}\Big(\frac{r_0}{1-\sigma} - 1\Big)r_0^2\frac{1}{\nu} < 0 \quad \text{as } x \to \tfrac{1}{r_0} + 0;\\
&\Phi_{\mathrm{J}}'(x) \to \Phi_{\mathrm{J}}'(1{-}0) := \frac{1}{-a_{\mathrm{J}}} + \rho_{\mathrm{J}}(1-\sigma)F^{-1}(1-\sigma) = -\frac{1}{a_{\mathrm{J}}} + \rho_{\mathrm{J}}(1-\sigma)K = \frac{\mathscr{R}_0^{\mathrm{J}} - 1}{a_{\mathrm{J}}}\\
&\hspace{28em}\text{as } x \to 1 - 0
\end{aligned}$$

again from the features of F and Π_{J} given in Sect. 2.3 and 2.4. Note that we have $F(K) = 1 - \sigma$ for a $K > 0$, and thus $F^{-1}(1-\sigma) = K$.

From the features of $\Phi_{\mathrm{J}}(x)$ in $[\frac{1-\sigma}{r_0}, 1]$, if $\Phi_{\mathrm{J}}'(1{-}0) > 0$, that is, if $\mathscr{R}_0^{\mathrm{J}} > 1$, then $\Phi_{\mathrm{J}}(x) < 0$ for $x \in (1-\epsilon, 1)$ with a sufficiently small positive ϵ because of $\Phi_{\mathrm{J}}(1) = 0$. Hence, if $\mathscr{R}_0^{\mathrm{J}} > 1$, then the equation $\Phi_{\mathrm{J}}(x) = 0$ has a root in $(\frac{1-\sigma}{r_0}, 1)$, from the Intermediate Value Theorem with $\Phi_{\mathrm{J}}(\frac{1-\sigma}{r_0}) > 0$. Inversely, if the equation $\Phi_{\mathrm{J}}(x) = 0$ has no root in $(\frac{1-\sigma}{r_0}, 1)$, then it is necessary that $\Phi_{\mathrm{J}}'(1{-}0) \le 0$, that is, $\mathscr{R}_0^{\mathrm{J}} \le 1$. From these arguments, we obtain the following lemma:

Lemma 7 *For the native prey-predator system* (4) *of Model J, the coexistent equilibrium* $E_{++}^{\mathrm{J}}(H_*, P_*^{\mathrm{J}})$ *exists if* $\mathscr{R}_0^{\mathrm{J}} > 1$. *Inversely, it does not exist only if* $\mathscr{R}_0^{\mathrm{J}} \le 1$.

Next, supposing that exists a root $x = \Pi_{\mathrm{J}}^* \in (\frac{1-\sigma}{r_0}, 1)$ for the equation $\Phi_{\mathrm{J}}(x) = 0$, we can prove the following lemma:

Lemma 8 *If there exists a root* $x = \Pi_{\mathrm{J}}^* \in (\frac{1-\sigma}{r_0}, 1)$ *for the equation* $\Phi_{\mathrm{J}}(x) = 0$*, it holds that* $\Phi_{\mathrm{J}}'(\Pi_{\mathrm{J}}^*) < 0$.

Proof From (B5), we can derive

$$\Phi_{\mathrm{J}}'(\Pi_{\mathrm{J}}^*) = \frac{1}{\Pi_{\mathrm{J}}'(P_*^{\mathrm{J}})} + \frac{\rho_{\mathrm{J}}}{1-\sigma}\{F(H_*)\}^2 H_* + \frac{\rho_{\mathrm{J}}}{1-\sigma}\{F(H_*) - 1 + \sigma\}\{F(H_*)\}^2 \frac{1}{F'(H_*)} \tag{B6}$$

$$< \frac{1}{\Pi_{\mathrm{J}}'(P_*^{\mathrm{J}})} + \frac{\rho_{\mathrm{J}}}{1-\sigma}\{F(H_*)\}^2 H_* - \frac{\rho_{\mathrm{J}}}{1-\sigma}\{F(H_*) - 1 + \sigma\}\{F(H_*)\}^2 \frac{H_*}{F(H_*)} \tag{B7}$$

$$= -\frac{P_*^{\mathrm{J}}}{\Pi_{\mathrm{J}}'(P_*^{\mathrm{J}})} \cdot \frac{d}{dP}\left\{\log \frac{1 - \Pi_{\mathrm{J}}(P)}{P}\right\}\bigg|_{P=P_*^{\mathrm{J}}} < 0, \tag{B8}$$

where we used the relations $\Pi_{\mathrm{J}}^{-1}(\Pi_{\mathrm{J}}^*) = P_*^{\mathrm{J}}$, $F(H_*) = \frac{1-\sigma}{\Pi_{\mathrm{J}}^*}$, and $F^{-1}(\frac{1-\sigma}{\Pi_{\mathrm{J}}^*}) = H_*$ from their definitions by (B3) and (B4). The inequality (B7) to bound $\Phi_{\mathrm{J}}'(\Pi_{\mathrm{J}}^*)$ from above is because of the increasing monotonicity of $F(H)H$ given in Section 2.3: Since the derivative of $F(H)H$ is positive, that is, since $F'(H)H + F(H) > 0$ in $(0, K)$, we have

$$\frac{1}{F'(H)} < -\frac{H}{F(H)} \tag{B9}$$

for $H \in (0, K)$, where $F'(H)$ is negative for $H > 0$ from its decreasing monotonicity given in Sect. 2.3. The inequality (B8) to show the negativeness is because of $\Pi_{\mathrm{J}}'(P_*^{\mathrm{J}}) < 0$ and the decreasing monotonicity of $\{1 - \Pi_{\mathrm{J}}(P)\}/P$ for $P > 0$ as already mentioned in Section 2.6. As a result, Lemma 8 is proved. □

Since $\Phi_{\mathrm{J}}(\frac{1-\sigma}{r_0}) > 0$, $\Phi_{\mathrm{J}}(1) = 0$, and $\Phi_{\mathrm{J}}'(\frac{1-\sigma}{r_0} + 0) < 0$ for the continuous function $\Phi_{\mathrm{J}}(x)$ in $[\frac{1-\sigma}{r_0}, 1]$, if the equation $\Phi_{\mathrm{J}}(x) = 0$ would have more than one roots in $(\frac{1-\sigma}{r_0}, 1)$, the derivative Φ_{J}' must be positive for one of them. This is contradictory to Lemma 8. Hence, we now find the following lemma:

Lemma 9 *If there exists a root* $x = \Pi_{\mathrm{J}}^* \in (\frac{1-\sigma}{r_0}, 1)$ *for the equation* $\Phi_{\mathrm{J}}(x) = 0$*, it is unique in* $(\frac{1-\sigma}{r_0}, 1)$.

Further, from those arguments for Lemma 7, if the equation $\Phi_{\mathrm{J}}(x) = 0$ has a root in $(\frac{1-\sigma}{r_0}, 1)$ for $\mathscr{R}_0^{\mathrm{J}} < 1$, then there must be more than one roots, because of the continuity of $\Phi_{\mathrm{J}}(x)$ in $[\frac{1-\sigma}{r_0}, 1]$ with $\Phi_{\mathrm{J}}'(1-0) < 0$. This is contradictory to Lemma 9. As a result, the equation $\Phi_{\mathrm{J}}(x) = 0$ has no root in $(\frac{1-\sigma}{r_0}, 1)$ if $\mathscr{R}_0^{\mathrm{J}} < 1$.

For the special case where $\mathscr{R}_0^{\mathrm{J}} = 1$, we have $\Phi_{\mathrm{J}}'(1-0) = 0$. Then, from the second derivative of Φ_{J}:

$$\Phi_{\mathrm{J}}''(x) = -\frac{\Pi_{\mathrm{J}}''\big(\Pi_{\mathrm{J}}^{-1}(x)\big)}{\big\{\Pi_{\mathrm{J}}'\big(\Pi_{\mathrm{J}}^{-1}(x)\big)\big\}^3} - \rho_{\mathrm{J}}(1-\sigma)\frac{2}{x^3}F^{-1}\big(\tfrac{1-\sigma}{x}\big)$$

$$+\rho_{\mathrm{J}}(1-\sigma)^2\Big[\Big(-\frac{3}{x^4}+\frac{1}{x^3}\Big)\frac{1}{F'\big(F^{-1}\big(\frac{1-\sigma}{x}\big)\big)}$$
$$+\Big(\frac{1}{x}-1\Big)\frac{1-\sigma}{x^4}\frac{F''\big(F^{-1}\big(\frac{1-\sigma}{x}\big)\big)}{\big\{F'\big(F^{-1}\big(\frac{1-\sigma}{x}\big)\big)\big\}^3}\Big],$$

we find that

$$\Phi_{\mathrm{J}}''(x)\to\Phi_{\mathrm{J}}''(1-0)=\frac{b_{\mathrm{J}}}{a_{\mathrm{J}}^3}-2\rho_{\mathrm{J}}(1-\sigma)\Big\{K+\frac{1-\sigma}{F'(K)}\Big\}$$

as $x\to 1-0$, where we used $\Pi_{\mathrm{J}}^{-1}(1)=0$, $\Pi_{\mathrm{J}}'(x)\to\Pi_{\mathrm{J}}'(+0)=-a_{\mathrm{J}}\in(-\infty,0)$ and $\Pi_{\mathrm{J}}''(x)\to\Pi_{\mathrm{J}}''(+0)=b_{\mathrm{J}}\in(0,\infty)$ as $x\to +0$, from the features of $\Pi_\bullet$ given in Section 2.4. Now, from (B9), we can find that

$$K+\frac{1-\sigma}{F'(K)}=(1-\sigma)\Big\{\frac{K}{F(K)}+\frac{1}{F'(K)}\Big\}=(1-\sigma)\lim_{H\to K-0}\Big[\frac{H}{F(H)}+\frac{1}{F'(H)}\Big]\le 0,$$

where we used $F(K)=1-\sigma$. Thus, we get the result that $\Phi_{\mathrm{J}}''(x)\to\Phi_{\mathrm{J}}''(1-0)>0$ as $x\to 1-0$. This result shows that, if $\Phi_{\mathrm{J}}'(1-0)=0$, then $\Phi_{\mathrm{J}}'(x)<0$ for $x<1$ in the neighborhood of 1. That is, if $\Phi_{\mathrm{J}}'(1-0)=0$, then $\Phi_{\mathrm{J}}(x)$ is monotonically decreasing for $x<1$ in the neighborhood of 1. Hence, from $\Phi_{\mathrm{J}}(1)=0$, we have $\Phi_{\mathrm{J}}(x)>0$ for $x<1$ in the neighborhood of 1 when $\Phi_{\mathrm{J}}'(1-0)=0$. Lastly, from the same arguments to prove Lemma 9, we can find that there is no root for the equation $\Phi_{\mathrm{J}}(x)=0$ in $(\frac{1-\sigma}{r_0},1)$ if $\mathscr{R}_0^{\mathrm{J}}=1$.

These arguments lead to the following result:

Lemma 10 *If* $\mathscr{R}_0^{\mathrm{J}}\le 1$, *the equation* $\Phi_{\mathrm{J}}(x)=0$ *has no root in* $(\frac{1}{r_0},1)$.

Finally, from Lemmas 7, 9, and 10, we obtain the result of Theorem 2 with respect to Model J.

With respect to the coexistent equilibrium $E_{++}^{\mathrm{A}}(H_*,P_*^{\mathrm{A}})$ for the native prey-predator system (5) of Model A, we have

$$\begin{cases}\big[\sigma+F\big(\Pi_{\mathrm{A}}(P_*^{\mathrm{A}})H_*\big)\big]\Pi_{\mathrm{A}}(P_*^{\mathrm{A}})=1;\\ P_*^{\mathrm{A}}=\rho_{\mathrm{A}}\big\{1-\Pi_{\mathrm{A}}(P_*^{\mathrm{A}})\big\}H_*,\end{cases}\tag{B10}$$

and thus, correspondingly to (B4),

$$\begin{cases}H_*=\dfrac{1}{\Pi_{\mathrm{A}}^*}F^{-1}\big(\frac{1}{\Pi_{\mathrm{A}}^*}-\sigma\big);\\ \Pi_{\mathrm{A}}^{-1}(\Pi_{\mathrm{A}}^*)=\rho_{\mathrm{A}}\Big(\dfrac{1}{\Pi_{\mathrm{A}}^*}-1\Big)F^{-1}\big(\frac{1}{\Pi_{\mathrm{A}}^*}-\sigma\big)\end{cases}\tag{B11}$$

with $\Pi_{\mathrm{A}}^*:=\Pi_{\mathrm{A}}(P_*^{\mathrm{A}})$ and the inverse function Π_{A}^{-1} of Π_{A}.

From the former equation of (B10), if $E_{++}^{\mathrm{A}}(H_*,P_*^{\mathrm{A}})$ exists, then $F\big(\Pi_{\mathrm{A}}^*H_*\big)=\frac{1}{\Pi_{\mathrm{A}}^*}-\sigma>1-\sigma$ and $F\big(\Pi_{\mathrm{A}}^*H_*\big)>F\big(\Pi_{\mathrm{A}}^*K\big)$ because $\Pi_{\mathrm{A}}(P_*^{\mathrm{A}})<1$ for $P_*^{\mathrm{A}}>0$ and

$H_* \in (0, K)$ from Lemma 2. We can easily find it necessary holds that $F\big(\Pi_\mathrm{A}^* K\big) < \frac{1}{\Pi_\mathrm{A}^*} - \sigma$, that is, $(\Pi_\mathrm{A}^* K) F\big(\Pi_\mathrm{A}^* K\big) < K - \sigma(\Pi_\mathrm{A}^* K)$ for $\Pi_\mathrm{A}^* \in (0, 1)$, making use of the assumption that $F(x)x$ is monotonically increasing for $x \in (0, K)$ as given in Sect. 2.3. Hence, for $\Pi_\mathrm{A}^* \in (0, 1)$, the former equation of (B10) determines $H_* \in (0, K)$. Thus, if $E_{++}^\mathrm{A}(H_*, P_*^\mathrm{A})$ exists, it holds that $F(0) = r_0 > \frac{1}{\Pi_\mathrm{A}^*} - \sigma$, since there is no $x > 0$ such that $F(x) = \frac{1}{\Pi_\mathrm{A}^*} - \sigma$ if $r_0 \le \frac{1}{\Pi_\mathrm{A}^*} - \sigma$. Therefore, if $E_{++}^\mathrm{A}(H_*, P_*^\mathrm{A})$ exists, then $\Pi_\mathrm{A}^* > \frac{1}{r_0+\sigma}$.

Now let us consider the existence of a root Π_A^* in $(\frac{1}{r_0+\sigma}, 1)$ about the latter equation of (B11), that is, the equation $\Phi_\mathrm{A}(x) = 0$ given by (20) for Model A. The function $\Phi_\mathrm{A}(x)$ is continuous in $[\frac{1}{r_0+\sigma}, 1]$ and differentiable in $(\frac{1}{r_0+\sigma}, 1)$ from the differentiability of Π_A and F in $(\frac{1}{r_0+\sigma}, 1)$, where their derivatives are negative. From the above arguments, if the equation $\Phi_\mathrm{A}(x) = 0$ has a root in $(\frac{1}{r_0+\sigma}, 1)$, then there exists an equilibrium as E_{++}^A for the native prey-predator system of Model J, while there exists no equilibrium E_{++}^A if the equation $\Phi_\mathrm{A}(x) = 0$ has no root in $(\frac{1}{r_0+\sigma}, 1)$.

Following the same steps as for E_{++}^J in the above, we can subsequently prove the corresponding lemmas:

Lemma 11 *For the native prey-predator system (5) of Model A, the coexistent equilibrium $E_{++}^\mathrm{A}(H_*, P_*^\mathrm{A})$ exists if $\mathscr{R}_0^\mathrm{A} > 1$. Inversely, it does not exist only if $\mathscr{R}_0^\mathrm{A} \le 1$.*

Lemma 12 *If there exists a root $x = \Pi_\mathrm{A}^* \in (\frac{1}{r_0+\sigma}, 1)$ for the equation $\Phi_\mathrm{A}(x) = 0$, it holds that*

$$\Phi_\mathrm{A}'(\Pi_\mathrm{A}^*) = \frac{1}{\Pi_\mathrm{A}'(P_*^\mathrm{A})} + \rho_\mathrm{A}\frac{H_*}{\Pi_\mathrm{A}^*} + \rho_\mathrm{A}\frac{1}{\{\Pi_\mathrm{A}^*\}^2}\Big(\frac{1}{\Pi_\mathrm{A}^*} - 1\Big)\frac{1}{F'(\Pi_\mathrm{A}^* H_*)} < 0. \qquad \text{(B12)}$$

Lemma 13 *If there exists a root $x = \Pi_\mathrm{A}^* \in (\frac{1}{r_0+\sigma}, 1)$ for the equation $\Phi_\mathrm{A}(x) = 0$, it is unique in $(\frac{1}{r_0+\sigma}, 1)$.*

Lemma 14 *If $\mathscr{R}_0^\mathrm{A} \le 1$, the equation $\Phi_\mathrm{A}(x) = 0$ has no root in $(\frac{1}{r_0+\sigma}, 1)$.*

Finally, based on Lemmas 11, 13, and 14, we derive the result of Theorem 2 for Model A. To establish the local stability of the coexistent equilibrium $E_{++}^\bullet$, we will later utilize the negativeness of (B6) and (B12), as presented in Lemmas 8 and 12.

Now, for the convenience of the later arguments regarding the stability of equilibria, we present the following nature of function $\Phi_\bullet$, which was found in this appendix based on those arguments:

Lemma 15 *When $\mathscr{R}_0^\bullet > 1$, $\Phi_\mathrm{J}(x) > 0$ for $x \in \big(\frac{1-\sigma}{r_0}, \Pi_\mathrm{J}^*\big)$ and $\Phi_\mathrm{A}(x) > 0$ for $x \in \big(\frac{1}{r_0+\sigma}, \Pi_\mathrm{A}^*\big)$, while $\Phi_\bullet(x) < 0$ for $x \in \big(\Pi_\bullet^*, 1\big)$, satisfying that $\Phi_\bullet\big(\Pi_\bullet^*\big) = 0$ and $\Phi_\bullet(1) = 0$.*

Appendix C Proof of Theorem 3

About the Jacobi matrix $\mathcal{J}_2(E^{\mathrm{J}}_{++}) = \mathcal{J}^{\mathrm{J}}_{++}$ for the coexistent equilibrium $E^{\mathrm{J}}_{++}(H_*, P^{\mathrm{J}}_*)$ with respect to the native prey-predator system (4) of Model J, we obtain

$$\begin{aligned}
\operatorname{tr}\mathcal{J}^{\mathrm{J}}_{++} &= \Pi_{\mathrm{J}}(P^{\mathrm{J}}_*)F'(H_*)H_* + 1 - \rho_{\mathrm{J}}\Pi'_{\mathrm{J}}(P^{\mathrm{J}}_*)F(H_*)H_*\\
&= \Pi_{\mathrm{J}}(P^{\mathrm{J}}_*)\tfrac{d}{dH}\{F(H)H\}\big|_{H=H_*} + \sigma - \rho_{\mathrm{J}}\Pi'_{\mathrm{J}}(P^{\mathrm{J}}_*)F(H_*)H_* > 0;\\
\det\mathcal{J}^{\mathrm{J}}_{++} &= -\rho_{\mathrm{J}}\Pi'_{\mathrm{J}}(P^{\mathrm{J}}_*)F(H_*)H_*\big[F'(H_*)H_* + 1 + \big\{1 - \Pi_{\mathrm{J}}(P^{\mathrm{J}}_*)\big\}F(H_*)\big]\\
&= -\rho_{\mathrm{J}}\Pi'_{\mathrm{J}}(P^{\mathrm{J}}_*)F(H_*)H_*\big[\tfrac{d}{dH}\{F(H)H\}\big|_{H=H_*} + \sigma\big] > 0,
\end{aligned}\tag{C13}$$

where we used the equations of (B3) in Appendix B, the decreasing monotonicity of $F(H)$ and $\Pi_{\mathrm{J}}(P)$, and the increasing monotonicity of $F(H)H$ for $H > 0$ and $P > 0$, as given in Sect. 2.3 and 2.4.

Here we shall apply the Jury stability criterion (Jury stability test) which gives the best possible sufficient condition such that the equation $\lambda^2 + c_1\lambda + c_2 = 0$ with real coefficients c_1 and c_2 has only roots of absolute value less than one: $c_2^2 < 1$ and $c_1^2 < (1 + c_2)^2$ (for instance, see (Allen 2007; Ledder 2013; Seno 2022; Elaydi and Cushing 2025)). Making use of this condition with $c_1 = -\operatorname{tr}\mathcal{J}^{\mathrm{J}}_{++}$ and $c_2 = \det\mathcal{J}^{\mathrm{J}}_{++}$, we find that the eigenvalues for $\mathcal{J}^{\mathrm{J}}_{++}$ have the absolute value less than one if $\det\mathcal{J}^{\mathrm{J}}_{++} < 1$ and $\operatorname{tr}\mathcal{J}^{\mathrm{J}}_{++} < 1 + \det\mathcal{J}^{\mathrm{J}}_{++}$, since $\operatorname{tr}\mathcal{J}^{\mathrm{J}}_{++} > 0$ and $\det\mathcal{J}^{\mathrm{J}}_{++} > 0$ as shown above. If $\det\mathcal{J}^{\mathrm{J}}_{++} > 1$ or $\operatorname{tr}\mathcal{J}^{\mathrm{J}}_{++} > 1 + \det\mathcal{J}^{\mathrm{J}}_{++}$, then the matrix $\mathcal{J}^{\mathrm{J}}_{++}$ as an eigenvalue with the absolute value greater than one.

From the above expressions of $\operatorname{tr}\mathcal{J}^{\mathrm{J}}_{++}$ and $\det\mathcal{J}^{\mathrm{J}}_{++}$, the condition $\operatorname{tr}\mathcal{J}^{\mathrm{J}}_{++} < 1 + \det\mathcal{J}^{\mathrm{J}}_{++}$ is equivalent to

$$\frac{1}{\Pi'_{\mathrm{J}}(P^{\mathrm{J}}_*)} - \rho_{\mathrm{J}}\frac{F(H_*)}{\Pi_{\mathrm{J}}(P^{\mathrm{J}}_*)F'(H_*)}\big\{1 - \sigma - F'(H_*)H_* - F(H_*)\big\} < 0.\tag{C14}$$

The left side of (C14) can be rewritten as

$$\begin{aligned}
&\frac{1}{\Pi'_{\mathrm{J}}(P^{\mathrm{J}}_*)} + \rho_{\mathrm{J}}\frac{F(H_*)}{\Pi_{\mathrm{J}}(P^{\mathrm{J}}_*)}H_* + \rho_{\mathrm{J}}\{F(H_*) - 1 + \sigma\}\frac{F(H_*)}{\Pi_{\mathrm{J}}(P^{\mathrm{J}}_*)}\frac{1}{F'(H_*)}\\
&= \frac{1}{\Pi'_{\mathrm{J}}(P^{\mathrm{J}}_*)} + \frac{\rho_{\mathrm{J}}}{1-\sigma}\{F(H_*)\}^2H_* + \frac{\rho_{\mathrm{J}}}{1-\sigma}\{F(H_*) - 1 + \sigma\}\{F(H_*)\}^2\frac{1}{F'(H_*)}\\
&= \Phi'_{\mathrm{J}}(\Pi^*_{\mathrm{J}})
\end{aligned}$$

with $\Pi_{\mathrm{J}}(P^{\mathrm{J}}_*)F(H_*) = 1 - \sigma$ and $\Phi'_{\mathrm{J}}(\Pi^*_{\mathrm{J}})$ defined by (B6) in Appendix B. Since $\Phi'_{\mathrm{J}}(\Pi^*_{\mathrm{J}}) < 0$ shown by Lemma 8 in Appendix B, the condition (C14) holds for the coexistent equilibrium E^{J}_{++}. Thus, the condition $\operatorname{tr}\mathcal{J}^{\mathrm{J}}_{++} < 1 + \det\mathcal{J}^{\mathrm{J}}_{++}$ necessarily holds for the coexistent equilibrium E^{J}_{++}.

Consequently, if $\det\mathcal{J}^{\mathrm{J}}_{++} < 1$, the coexistent equilibrium E^{J}_{++} is locally asymptotically stable, and otherwise, if $\det\mathcal{J}^{\mathrm{J}}_{++} > 1$, it is unstable. We note that $\det\mathcal{J}^{\mathrm{J}}_{++} < 1$ can be expressed as (21) in terms of $\Pi^*_{\mathrm{J}} := \Pi_{\mathrm{J}}(P^{\mathrm{J}}_*)$, which can be derived with $P^{\mathrm{J}}_* = \Pi_{\mathrm{J}}^{-1}(\Pi^*_{\mathrm{J}})$, (B3), and (B4).

With respect to the native prey-predator system (5) of Model A, we can derive

$$\begin{aligned}\operatorname{tr}\mathcal{J}^{\mathrm{A}}_{++} &= \Pi_{\mathrm{A}}(P^{\mathrm{A}}_*)\tfrac{d}{dH}\{F(H)H\}\big|_{H=\Pi_{\mathrm{A}}(P^{\mathrm{A}}_*)H_*} + \sigma\Pi_{\mathrm{A}}(P^{\mathrm{A}}_*) - \rho_{\mathrm{A}}\Pi'_{\mathrm{A}}(P^{\mathrm{A}}_*)H_* > 0;\\ \det\mathcal{J}^{\mathrm{A}}_{++} &= -\rho_{\mathrm{A}}\Pi'_{\mathrm{A}}(P^{\mathrm{A}}_*)H_*\big[\tfrac{d}{dH}\{F(H)H\}\big|_{H=\Pi_{\mathrm{A}}(P^{\mathrm{A}}_*)H_*} + \sigma\big] > 0\end{aligned} \tag{C15}$$

for the Jacobi matrix $\mathcal{J}_2(E^{\mathrm{A}}_{++}) = \mathcal{J}^{\mathrm{A}}_{++}$ concerning the coexistent equilibrium $E^{\mathrm{A}}_{++}(H_*, P^{\mathrm{A}}_*)$. Then, the condition $\operatorname{tr}\mathcal{J}^{\mathrm{A}}_{++} < 1 + \det\mathcal{J}^{\mathrm{A}}_{++}$ can be expressed as

$$\frac{1}{\Pi'_{\mathrm{A}}(P^{\mathrm{A}}_*)} - \rho_{\mathrm{A}}\frac{1}{\{\Pi_{\mathrm{A}}(P^{\mathrm{A}}_*)\}^2 F'(\Pi_{\mathrm{A}}(P^{\mathrm{A}}_*)H_*)} \times \big\{1 - \sigma - F'(\Pi_{\mathrm{A}}(P^{\mathrm{A}}_*)H_*)P^{\mathrm{A}}_* H_* - F(\Pi_{\mathrm{A}}(P^{\mathrm{A}}_*)H_*)\big\} < 0. \tag{C16}$$

In the same way as we did for Model J, we can prove that the left side of (C16) is equivalent to $\Phi'_{\mathrm{A}}(\Pi^*_{\mathrm{A}})$ defined by (B12) in Appendix B. Since $\Phi'_{\mathrm{A}}(\Pi^*_{\mathrm{A}}) < 0$ shown by Lemma 12 in Appendix B, the condition (C16) holds for the coexistent equilibrium E^{A}_{++}. Hence, the condition $\operatorname{tr}\mathcal{J}^{\mathrm{A}}_{++} < 1 + \det\mathcal{J}^{\mathrm{A}}_{++}$ holds for the coexistent equilibrium E^{A}_{++}. Therefore, with respect to the coexistent equilibrium E^{A}_{++}, if $\det\mathcal{J}^{\mathrm{A}}_{++} < 1$, it is locally asymptotically stable, and otherwise, if $\det\mathcal{J}^{\mathrm{A}}_{++} > 1$, it is unstable. Then, as well as $\det\mathcal{J}^{\mathrm{J}}_{++} < 1$, we note that $\det\mathcal{J}^{\mathrm{A}}_{++} < 1$ can be expressed as (22) in terms of $\Pi^*_{\mathrm{A}} := \Pi_{\mathrm{A}}(P^{\mathrm{A}}_*)$, which can be derived with $P^{\mathrm{A}}_* = \Pi^{-1}_{\mathrm{A}}(\Pi^*_{\mathrm{A}})$, (B10), and (B11).

Appendix D Proof of Corollary 3

Now let $\Pi^*_\bullet = 1 - \varepsilon$ with $0 < \varepsilon \ll 1$. By the Taylor expansion around $\Pi^*_\bullet = 1$, the left side of (21) becomes

$$\begin{aligned}&-\frac{-\varepsilon + \mathrm{o}(\varepsilon)}{\varepsilon}\left[1 - \sigma + F'(K)K + \left\{2 + \frac{F''(K)K}{F'(K)}\right\}\varepsilon + \mathrm{o}(\varepsilon) + \sigma\right]\\ &\qquad = 1 + F'(K)K - \frac{\mathrm{o}(\varepsilon)}{\varepsilon}\{1 + F'(K)K\} + \left\{2 + \frac{F''(K)K}{F'(K)}\right\}\varepsilon + \mathrm{o}(\varepsilon).\end{aligned}$$

We note that $1 + F'(K)K \in (0, 1)$ as already shown in Section 2.6. Therefore, we now find that the left side of (21) becomes positive and less than one for $\Pi^*_{\mathrm{J}} = 1 - \varepsilon$ with $0 < \varepsilon \ll 1$. In the same way, we can prove that the left side of (22) becomes positive and less than one for $\Pi^*_{\mathrm{A}} = 1 - \varepsilon$ with $0 < \varepsilon \ll 1$.

The value $\Pi^*_\bullet$ is continuous in terms of $\rho_\bullet$ and embedded parameters in functions F and $\Pi_\bullet$. Thus, we can regard $\Pi^*_\bullet$ as a function continuously depending on the value of $\mathscr{R}^\bullet_0$. Hence, from the arguments in Appendix B for the proof of Theorem 2, we note that $\Pi^*_\bullet \to 1$ as $\mathscr{R}^\bullet_0 \to 1$, which implies that $\Pi^*_\bullet = 1 - \epsilon + \mathrm{o}(\epsilon)$ for $\mathscr{R}^\bullet_0 = 1 + \epsilon$ with $0 < \epsilon \ll 1$. Consequently, from the arguments in this appendix, we conclude that the condition (21) holds for $\mathscr{R}^{\mathrm{J}}_0 = 1 + \epsilon$ with $0 < \epsilon \ll 1$, and so does the condition (22) for $\mathscr{R}^{\mathrm{A}}_0 = 1 + \epsilon$ with $0 < \epsilon \ll 1$.

Appendix E Proof of Corollary 4

From (20) of Theorem 2, the value Π_{J}^* about the equilibrium E_{++}^{J} for the native prey-predator system (4) of Model J satisfies the equation $\Phi_{\mathrm{J}}\big(\Pi_{\mathrm{J}}^*\big) = 0$. It can be rewritten as

$$\mathscr{R}_0^{\mathrm{J}} = g_{\mathrm{J}}\big(\Pi_{\mathrm{J}}^*\big) \cdot \frac{K}{F^{-1}\big(\frac{1-\sigma}{\Pi_{\mathrm{J}}^*}\big)} \tag{E17}$$

with $g_{\mathrm{J}}(x) := a_{\mathrm{J}}\Pi_{\mathrm{J}}^{-1}(x)/(1/x - 1)$ that is continuous and positive for $x \in (0, 1)$. Then, we can rewrite the condition (23) as

$$\mathscr{R}_0^{\mathrm{A}} < \frac{\mathscr{R}_0^{\mathrm{J}}}{g_{\mathrm{J}}\big(\Pi_{\mathrm{J}}^*\big)}. \tag{E18}$$

When $g_{\mathrm{J}}\big(\Pi_{\mathrm{J}}^*\big) \leq 1$, the condition (E18) is satisfied if $\mathscr{R}_0^{\mathrm{A}} < \mathscr{R}_0^{\mathrm{J}}$, because the right side of (E18) is then equal to or greater than $\mathscr{R}_0^{\mathrm{J}}$. When $g_{\mathrm{J}}\big(\Pi_{\mathrm{J}}^*\big) < 1$, the inverse inequality of (E18) is not necessarily satisfied even if $\mathscr{R}_0^{\mathrm{A}} > \mathscr{R}_0^{\mathrm{J}}$. The invasion success of alien predator P^{A} requires its basic replacement number $\mathscr{R}_0^{\mathrm{A}}$ sufficiently larger than $\mathscr{R}_0^{\mathrm{J}}$. In contrast, when $g_{\mathrm{J}}\big(\Pi_{\mathrm{J}}^*\big) > 1$, the right side of (E18) is smaller than $\mathscr{R}_0^{\mathrm{J}}$. Therefore, the alien predator P^{A} invasion is successful if $\mathscr{R}_0^{\mathrm{A}} \geq \mathscr{R}_0^{\mathrm{J}}$, while it fails only if $\mathscr{R}_0^{\mathrm{A}} < \mathscr{R}_0^{\mathrm{J}}$.

Now, from (E17), the condition $g_{\mathrm{J}}\big(\Pi_{\mathrm{J}}^*\big) < 1$ is equivalent to $\mathscr{R}_0^{\mathrm{J}} < K/F^{-1}\big(\frac{1-\sigma}{\Pi_{\mathrm{J}}^*}\big)$, which leads to

$$\Pi_{\mathrm{J}}^* < \frac{1-\sigma}{F\big(\frac{K}{\mathscr{R}_0^{\mathrm{J}}}\big)}. \tag{E19}$$

We have $\mathscr{R}_0^{\mathrm{J}} > 1$ from Theorem 2, provided that the equilibrium E_{++}^{J} for the native prey-predator system (4) of Model J is asymptotically stable. Then, $\frac{K}{\mathscr{R}_0^{\mathrm{J}}} < K$, which implies that $F\big(\frac{K}{\mathscr{R}_0^{\mathrm{J}}}\big) > F(K) = 1$, because of the decreasing monotonicity of F. Therefore, since the right side of (E19) is less than $1-\sigma$, we find from Lemma 15 in Appendix B that the condition (E19) is equivalent to $\Phi_{\mathrm{J}}\big(\frac{1-\sigma}{F(K/\mathscr{R}_0^{\mathrm{J}})}\big) < 0$, which leads to the condition (24) in Corollary 4. Following the same arguments, we can find that the inverse inequality of (24) is equivalent to $g_{\mathrm{J}}\big(\Pi_{\mathrm{J}}^*\big) > 1$. These arguments complete the proof of Corollary 4.

Appendix F Proof of Corollary 5

From (20) of Theorem 2, the value Π_{A}^* about the equilibrium E_{++}^{A} for the native prey-predator system (5) of Model A satisfies the equation $\Phi_{\mathrm{A}}\big(\Pi_{\mathrm{A}}^*\big) = 0$, which can be rewritten as

$$\mathscr{R}_0^{\mathrm{A}} = g_{\mathrm{A}}(\Pi_{\mathrm{A}}^*) \cdot \frac{(1-\sigma)K}{\left(\frac{1}{\Pi_{\mathrm{A}}^*} - \sigma\right)F^{-1}\left(\frac{1}{\Pi_{\mathrm{A}}^*} - \sigma\right)}$$

with

$$g_{\mathrm{A}}(x) := \frac{a_{\mathrm{A}}\Pi_{\mathrm{A}}^{-1}(x)}{1-\sigma} \cdot \frac{1-\sigma x}{1-x}$$

for $x \in (0, 1)$. Then, we can rewrite the inverse inequality of (25) as follows:

$$g_{\mathrm{A}}(\Pi_{\mathrm{A}}^*)\mathscr{R}_0^{\mathrm{J}} > \mathscr{R}_0^{\mathrm{A}}, \tag{F20}$$

From Theorem 5, if the condition (F20) is satisfied, the equilibrium E_{+0+}^* for the system (13) is unstable, so that the alien predator P^{J} invasion of the native prey-predator system (5) in Model A is successful, provided that the equilibrium E_{++}^{A} is asymptotically stable

From the features of Π_{A} given in Section 2.4, $g_{\mathrm{A}}(x)$ is continuous and differentiable for $x \in (0, 1)$. Furthermore, also making use of the convexity of $\Pi_{\mathrm{A}}^{-1}(x)$ for $x \in (0, 1]$, we can easily prove that $g_{\mathrm{A}}(x)$ is monotonically decreasing in terms of $x \in (0, 1)$, and $\lim_{x \to 1-0} g_{\mathrm{A}}(x) = 1$. Consequently, the monotonically decreasing function $g_{\mathrm{A}}(x)$ satisfies that $g_{\mathrm{A}}(x) > 1$ for $x \in (0, 1)$.

This result demonstrates that the left side of (F20) is necessarily greater than $\mathscr{R}_0^{\mathrm{J}}$ for $\Pi_{\mathrm{A}}^* \in (0, 1)$ about the equilibrium E_{++}^{A} for the native prey-predator system (5) of Model A. Therefore, if $\mathscr{R}_0^{\mathrm{J}} \geq \mathscr{R}_0^{\mathrm{A}}$, the condition (F20) is satisfied. Further, even if $\mathscr{R}_0^{\mathrm{J}} < \mathscr{R}_0^{\mathrm{A}}$, the condition (F20) may be satisfied. These arguments complete the proof of Corollary 5.

Appendix G Proof of Corollary 7

First, we present the following corollary derived from Theorem 3 according to the native prey-predator systems (28) and (29), which is useful in the subsequent arguments:

Corollary 11 *When the coexistent equilibrium $E_{++}^{\bullet}$ exists for the native prey-predator system defined by* (28) *and* (29), *it is locally asymptotically stable if*

$$\psi(x_*^{\bullet}) := (x_*^{\bullet})^2 - \alpha_{\bullet} x_*^{\bullet} + \frac{\alpha_{\bullet}}{r_0} > 0 \tag{G21}$$

with $x_*^{\bullet} = \Pi_{\bullet}^* = \Pi_{\bullet}(p_*^{\bullet}) = \mathrm{e}^{-p_*^{\bullet}}$ as defined in Corollary 6. If $\psi(x_*^{\bullet}) < 0$, it is unstable.

The function $\psi(x)$ is quadratic, and its discriminant is negative if and only if $\alpha_{\bullet} < \frac{4}{r_0}$, that is, $\mathscr{R}_0^{\bullet} < 4(1 - \frac{1}{r_0})$. Thus, if $\mathscr{R}_0^{\bullet} < 4(1 - \frac{1}{r_0})$, the inequality $\psi(x_*^{\bullet}) > 0$

is always satisfied. The condition $\mathscr{R}_0^\bullet < 4(1-\frac{1}{r_0})$ can be satisfied only if $r_0 > \frac{4}{3}$ when $E_{++}^\bullet$ exists, taking account of the existence condition of $E_{++}^\bullet$ in Corollary 6, $\mathscr{R}_0^\bullet > 1$. Then we can now get the following sufficient condition according to the local stability of $E_{++}^\bullet$:

Lemma 16 *For the native prey-predator systems* (28) *and* (29) *of Models J and A, respectively, if* $r_0 > \frac{4}{3}$ *and* $\mathscr{R}_0^\bullet \in \big(1, 4(1-\frac{1}{r_0})\big)$*, then the coexistent equilibrium* $E_{++}^\bullet$ *exists, and it is locally asymptotically stable.*

The discriminant of $\psi(x)$ is non-negative if and only if $\mathscr{R}_0^\bullet \geq 4(1-\frac{1}{r_0})$. Hence, let us consider now the case where the equilibrium $E_{++}^\bullet$ exists and the following condition is satisfied: $\mathscr{R}_0^\bullet \geq 4\big(1-\frac{1}{r_0}\big)$ and $\mathscr{R}_0^\bullet > 1$, which can be equivalently expressed as

$$\begin{cases} \mathscr{R}_0^\bullet > 1 & \text{for} \quad r_0 \in (1, \frac{4}{3}\,]; \\ \mathscr{R}_0^\bullet \geq 4\Big(1-\dfrac{1}{r_0}\Big) & \text{for} \quad r_0 > \frac{4}{3}. \end{cases} \tag{G22}$$

When the condition (G22) is satisfied, the inequality $\psi(x_*^\bullet) > 0$ is satisfied if and only if $x_*^\bullet < x_-^\bullet$ or $x_*^\bullet > x_+^\bullet$, where $x_\pm^\bullet$ are the zeros for $\psi(x)$, that is, the roots of equation $\psi(x) = 0$, satisfying that $x_+^\bullet \geq x_-^\bullet > 0$ as given by (32).

Now, from Lemma 15 in Appendix B, we have $\Phi_\bullet(x) > 0$ for $x \in (0, x_*^\bullet)$; $\Phi_\bullet(x_*^\bullet) = 0$; $\Phi_\bullet(x) < 0$ for $x \in (x_*^\bullet, 1)$; $\Phi_\bullet(1) = 0$ and $\Phi_\bullet(x) > 0$ for $x \in (1, \infty)$ when the equilibrium $E_{++}^\bullet$ exists with $x_*^\bullet \in (\frac{1}{r_0}, 1)$. Thus, firstly, the condition $x_*^\bullet < x_-^\bullet$ is satisfied if and only if $\Phi_\bullet(x_-^\bullet) < 0$ or $x_-^\bullet \geq 1$. The condition $x_-^\bullet \geq 1$ holds if and only if $\psi(1) = 1 - \frac{\mathscr{R}_0^\bullet}{r_0} \geq 0$ and $\psi'(1) = 2 - \frac{\mathscr{R}_0^\bullet}{r_0 - 1} \leq 0$. Then, taking account of the condition (G22), we find the following result:

Lemma 17 *For the native prey-predator systems* (28) *and* (29) *of Models J and A, respectively, if* $r_0 \in (1, \frac{4}{3}\,]$ *and* $\mathscr{R}_0^\bullet \in (1, r_0\,]$*, or if* $r_0 \in (\frac{4}{3}, 2\,]$ *and* $\mathscr{R}_0^\bullet \in [\,4(1-\frac{1}{r_0}), r_0\,]$*, then the coexistent equilibrium* $E_{++}^\bullet$ *exists and it is locally asymptotically stable.*

In the same way taking account of the condition (G22), we find that $x_-^\bullet < 1$ if $\mathscr{R}_0^\bullet > r_0$, or if $r_0 > 2$ and $\mathscr{R}_0^\bullet \in \big[\,4(1-\frac{1}{r_0}), r_0\big)$. Therefore, we get the following result:

Lemma 18 *For the native prey-predator systems* (28) *and* (29) *of Models J and A, respectively, if* $\Phi_\bullet(x_-^\bullet) < 0$ *with* $\mathscr{R}_0^\bullet > r_0$*, or with* $r_0 > 2$ *and* $\mathscr{R}_0^\bullet \in \big[\,4(1-\frac{1}{r_0}), r_0\big)$*, then the coexistent equilibrium* $E_{++}^\bullet$ *exists and it is locally asymptotically stable.*

Next, the condition $x_*^\bullet > x_+^\bullet$ is satisfied if and only if $\Phi_\bullet(x_+^\bullet) > 0$ and $x_+^\bullet < 1$. The condition $x_+^\bullet < 1$ holds if and only if $\psi(1) > 0$ and $\psi'(1) > 0$. Then, we can find that the condition $x_+^\bullet < 1$ with (G22) is satisfied if and only if $r_0 > 2$ and $\mathscr{R}_0^\bullet \in \big[\,4(1-\frac{1}{r_0}), r_0\big)$. Therefore, we get the following result:

Lemma 19 *For the native prey-predator systems* (28) *and* (29) *of Models J and A, respectively, if* $\Phi_\bullet(x_+^\bullet) > 0$ *with* $r_0 > 2$ *and* $\mathscr{R}_0^\bullet \in \big[\,4(1-\frac{1}{r_0}), r_0\big)$*, then the coexistent equilibrium* $E_{++}^\bullet$ *exists and it is locally asymptotically stable.*

Finally, Lemmas 16–19 leads to Corollary 7.

Appendix H Proof of Corollaries 8 and 9

Provided that the equilibrium E^{J}_{++} for the native prey-predator system (28) of Model J is asymptotically stable, Theorem 4 in Sect. 5.1 gives the condition (23) about the local stability of E^{*}_{++0} for the system (27), which now becomes

$$x^{\mathrm{J}}_{*} < \frac{1}{r_0}\Big(1 + \frac{1}{\alpha_{\mathrm{A}}}\Big) = \Big(1 - \frac{1}{r_0}\Big)\frac{1}{\mathscr{R}^{\mathrm{A}}_0} + \frac{1}{r_0}. \tag{H23}$$

Since $x^{\mathrm{J}}_{*} \in (\frac{1}{r_0}, 1)$ as shown in Corollary 6, the condition (H23) holds if the right side of (H23) is greater than or equal to one, that is, if $\mathscr{R}^{\mathrm{A}}_0 \leq 1$. Thus, we find the following result on the local stability of E^{*}_{++0}:

Lemma 20 *Provided that the equilibrium E^{J}_{++} is asymptotically stable, the equilibrium E^{*}_{++0} is locally asymptotically stable if $\mathscr{R}^{\mathrm{A}}_0 \leq 1$.*

This result matches Theorem 1 and Corollary 1. Since the existence of E^{J}_{++} requires $\mathscr{R}^{\mathrm{J}}_0 > 1$ from Theorem 2, the condition in Lemma 20 is satisfied only if $\mathscr{R}^{\mathrm{A}}_0 < \mathscr{R}^{\mathrm{J}}_0$, that is, $\alpha_{\mathrm{A}} < \alpha_{\mathrm{J}}$.

For $\mathscr{R}^{\mathrm{A}}_0 > 1$, the right side of (H23) is greater than $\frac{1}{r_0}$ and less than one. Now, from Lemma 15 in Appendix B, the condition (H23) is equivalent to

$$\Phi_{\mathrm{J}}\big(\tfrac{1}{r_0}(1 + \tfrac{1}{\alpha_{\mathrm{A}}})\big) = \Big(1 - \frac{1}{r_0}\Big)\Bigg[\frac{\mathscr{R}^{\mathrm{J}}_0}{\mathscr{R}^{\mathrm{A}}_0}\Bigg\{1 - \frac{1}{\frac{1}{r_0}(1 + \frac{1}{\alpha_{\mathrm{A}}})}\Bigg\} + \log\frac{1}{\frac{1}{r_0}(1 + \frac{1}{\alpha_{\mathrm{A}}})}\Bigg] < 0 \tag{H24}$$

with Φ_{J} defined by (31). When $\mathscr{R}^{\mathrm{A}}_0 > 1$, the condition (H23) holds if and only if the condition (H24) is satisfied. It can be easily found that the function $\zeta_1(x) := a(1 - x) + \log x$ with $a \geq 1$ is negative for any $x > 1$. Hence, the condition (H24) holds if $\frac{\mathscr{R}^{\mathrm{J}}_0}{\mathscr{R}^{\mathrm{A}}_0} \geq 1$ when $\frac{1}{r_0}(1+\frac{1}{\alpha_{\mathrm{A}}}) < 1$, that is, if $\mathscr{R}^{\mathrm{J}}_0 \geq \mathscr{R}^{\mathrm{A}}_0$ when $\mathscr{R}^{\mathrm{A}}_0 > 1$. Therefore, we have the following result:

Lemma 21 *Provided that the equilibrium E^{J}_{++} is asymptotically stable, the equilibrium E^{*}_{++0} is locally asymptotically stable if $\mathscr{R}^{\mathrm{J}}_0 \geq \mathscr{R}^{\mathrm{A}}_0 > 1$.*

In contrast, $\zeta_1(x)$ with $a < 1$ is positive in $(1, x_s)$ and negative in (x_s, ∞) with a certain $x_s > 1$ such that $\zeta_1(x_s) = 0$. Thus, if $\zeta_1(r_0) \geq 0$ with $a < 1$ and $r_0 > 1$, then we have $\zeta_1(x) > 0$ for any $x \in (1, r_0)$. Therefore, if $\frac{\mathscr{R}^{\mathrm{J}}_0}{\mathscr{R}^{\mathrm{A}}_0} < 1$ and $\frac{\mathscr{R}^{\mathrm{J}}_0}{\mathscr{R}^{\mathrm{A}}_0}(1-r_0)+\log r_0 \geq 0$, that is, $\frac{\mathscr{R}^{\mathrm{J}}_0}{\mathscr{R}^{\mathrm{A}}_0} \leq \frac{\log r_0}{r_0-1}$, the inverse inequality of (H24) holds. The inverse inequality of (H23) is equivalent to the inverse inequality of (H24) with $\frac{1}{r_0}(1 + \frac{1}{\alpha_{\mathrm{A}}}) < 1$, that is, with $\mathscr{R}^{\mathrm{A}}_0 > 1$. As a result, we have the following result:

Lemma 22 *Provided that the equilibrium E^{J}_{++} is asymptotically stable, the equilibrium E^{*}_{++0} is unstable if $\mathscr{R}^{\mathrm{A}}_0 \geq \frac{r_0-1}{\log r_0}\mathscr{R}^{\mathrm{J}}_0$.*

Note that $\frac{r_0-1}{\log r_0} > 1$ for $r_0 > 1$, and we have $\mathscr{R}_0^{\mathrm{J}} > 1$ from Theorem 2 as long as the equilibrium E_{++}^{J} exists. At the end, we have the following result too:

Lemma 23 *Provided that the equilibrium E_{++}^{J} is asymptotically stable, when $\mathscr{R}_0^{\mathrm{A}} \in \big(\mathscr{R}_0^{\mathrm{J}}, \frac{r_0-1}{\log r_0}\mathscr{R}_0^{\mathrm{J}}\big)$, the equilibrium E_{++0}^* is locally asymptotically stable if the condition* (H24) *holds, while it is unstable if the inverse inequality of* (H24) *holds.*

Finally, from Corollary 6 and Lemmas 20–23, we can obtain the result of Corollary 8 about Model J.

To prove Corollary 9 about Model A, we can apply some arguments modifying those above for Corollary 8. Provided that the equilibrium E_{++}^{A} for the native prey-predator system (29) of Model A is asymptotically stable, Theorem 5 in Sect. 5.2 gives the following condition (25) for the local stability of E_{++0}^* about the system (27):

$$\frac{1}{x_*^{\mathrm{A}}} > r_0 - \frac{1}{\alpha_{\mathrm{J}}} = r_0\Big(1 - \frac{1}{\mathscr{R}_0^{\mathrm{J}}}\Big) + \frac{1}{\mathscr{R}_0^{\mathrm{J}}}. \tag{H25}$$

Since $x_*^{\mathrm{A}} \in (\frac{1}{r_0}, 1)$ for the existence of E_{++}^{A} from Corollary 6, the condition (H25) is satisfied if the right side of (H25) is less than or equal to one, that is, if $\mathscr{R}_0^{\mathrm{J}} \le 1$. Thus we have found a sufficient condition for the local stability of E_{+0+}^*:

Lemma 24 *Provided that the equilibrium E_{++}^{A} is asymptotically stable, the equilibrium E_{+0+}^* is locally asymptotically stable if $\mathscr{R}_0^{\mathrm{J}} \le 1$.*

This result matches Theorem 1 and Corollary 1. Since the existence of E_{++}^{A} requires to have $\mathscr{R}_0^{\mathrm{A}} > 1$ from Theorem 2, the condition in Lemma 24 is satisfied only if $\mathscr{R}_0^{\mathrm{J}} < \mathscr{R}_0^{\mathrm{A}}$, that is, $\alpha_{\mathrm{J}} < \alpha_{\mathrm{A}}$.

When $\mathscr{R}_0^{\mathrm{J}} > 1$, the right side of (H25) is in $(1, r_0)$, and the condition (H25) can be rewritten as

$$x_*^{\mathrm{A}} < \frac{1}{r_0 - 1/\alpha_{\mathrm{J}}} = \Big\{ r_0\Big(1 - \frac{1}{\mathscr{R}_0^{\mathrm{J}}}\Big) + \frac{1}{\mathscr{R}_0^{\mathrm{J}}}\Big\}^{-1} \in (\tfrac{1}{r_0}, 1).$$

Then, from Lemma 15 in Appendix B, the condition (H25) is satisfied if and only if

$$\Phi_{\mathrm{A}}\big(\tfrac{1}{r_0-1/\alpha_{\mathrm{J}}}\big) = \Big(1 - \frac{1}{r_0}\Big)\Big[\frac{\mathscr{R}_0^{\mathrm{A}}}{\mathscr{R}_0^{\mathrm{J}}}\Big(\frac{1}{r_0 - 1/\alpha_{\mathrm{J}}} - 1\Big) - \log\frac{1}{r_0 - 1/\alpha_{\mathrm{J}}}\Big] < 0 \tag{H26}$$

with Φ_{A} defined by (31).

It can be easily found that the function $\zeta_2(x) := -\zeta_1(x) = a(x-1) - \log x$ with $a \le 1$ is positive for any $x \in (0, 1)$. Hence, the inverse inequality of (H26) necessarily holds if $\frac{\mathscr{R}_0^{\mathrm{A}}}{\mathscr{R}_0^{\mathrm{J}}} \le 1$ when $\frac{1}{r_0-1/\alpha_{\mathrm{J}}} \in (\frac{1}{r_0}, 1)$, that is, if $\mathscr{R}_0^{\mathrm{A}} \le \mathscr{R}_0^{\mathrm{J}}$ when $\mathscr{R}_0^{\mathrm{J}} > 1$. Note that we have $\mathscr{R}_0^{\mathrm{A}} > 1$ from Theorem 2 as long as the equilibrium E_{++}^{A} exists. Therefore, we have the following result:

Lemma 25 *Provided that the equilibrium* E^{A}_{++} *is asymptotically stable, the equilibrium* E^{*}_{+0+} *is unstable if* $\mathscr{R}^{\mathrm{J}}_{0} \geq \mathscr{R}^{\mathrm{A}}_{0} > 1$.

In contrast, $\zeta_2(x)$ with $a > 1$ is positive in $(0, x_s) \subset (0, \frac{1}{a})$ and negative in $(x_s, 1)$ with a certain $x_s \in (0, \frac{1}{a})$ such that $\zeta_2(x_s) = 0$. Thus, if $\zeta_2(\frac{1}{r_0}) \leq 0$ with $a > 1$ and $r_0 > 1$, then we have $\zeta_2(x) < 0$ for any $x \in (\frac{1}{r_0}, 1)$. Therefore, if $\frac{\mathscr{R}^{\mathrm{A}}_{0}}{\mathscr{R}^{\mathrm{J}}_{0}} > 1$ and $\frac{\mathscr{R}^{\mathrm{A}}_{0}}{\mathscr{R}^{\mathrm{J}}_{0}}\big(\frac{1}{r_0} - 1\big) - \log\frac{1}{r_0} \leq 0$, that is, $\frac{\mathscr{R}^{\mathrm{A}}_{0}}{\mathscr{R}^{\mathrm{J}}_{0}} \geq \frac{r_0 \log r_0}{r_0 - 1}$, the condition (H26) holds. Now we find the following result:

Lemma 26 *Provided that the equilibrium* E^{A}_{++} *is asymptotically stable, the equilibrium* E^{*}_{+0+} *is locally asymptotically stable if* $\mathscr{R}^{\mathrm{J}}_{0} \in \big(1, \frac{r_0 - 1}{r_0 \log r_0}\mathscr{R}^{\mathrm{A}}_{0}\big]$ *with* $\frac{r_0 - 1}{r_0 \log r_0}\mathscr{R}^{\mathrm{A}}_{0} > 1$.

Note that $\frac{r_0 - 1}{r_0 \log r_0} < 1$ for $r_0 > 1$. Further remark that when $\frac{r_0 - 1}{r_0 \log r_0}\mathscr{R}^{\mathrm{A}}_{0} \leq 1$, the above arguments necessarily lead to the condition that $\mathscr{R}^{\mathrm{J}}_{0} \leq 1$, and it is the case of Lemma 24. Lastly we find the following results when $\mathscr{R}^{\mathrm{J}}_{0} > 1$, taking account of the above arguments for Lemma 26:

Lemma 27 *Provided that the equilibrium* E^{A}_{++} *is asymptotically stable, when* $\mathscr{R}^{\mathrm{J}}_{0} \in \big(\max\{\frac{r_0 - 1}{r_0 \log r_0}\mathscr{R}^{\mathrm{A}}_{0}, 1\}, \mathscr{R}^{\mathrm{A}}_{0}\big)$, *the equilibrium* E^{*}_{+0+} *is locally asymptotically stable if the condition* (H26) *holds, while it is unstable if the inverse inequality of* (H26) *holds.*

In conclusion, from Corollary 6 and Lemmas 24–27, we can obtain Corollary 9.

Appendix I Proof of Lemma 6

If exists a coexistent equilibrium $E^{*}_{+++}(h^{**}, p^{\mathrm{J}}_{**}, p^{\mathrm{A}}_{**})$ with $p^{\mathrm{J}}_{**} > 0$ and $p^{\mathrm{A}}_{**} > 0$ for the system (27), we have the following parallel equations to determine E^{*}_{+++}:

$$h^{**} = r_0 x^{\mathrm{J}}_{**} - \frac{1}{x^{\mathrm{A}}_{**}}; \quad h^{**} = \frac{1}{\alpha_{\mathrm{J}}}\,\Psi(x^{\mathrm{J}}_{**}); \quad h^{**} = \frac{1}{\alpha_{\mathrm{A}}}\,\Psi\big(\tfrac{1}{x^{\mathrm{A}}_{**}}\big), \tag{I27}$$

where $x^{\mathrm{J}}_{**} := \mathrm{e}^{-p^{\mathrm{J}}_{**}}$, $x^{\mathrm{A}}_{**} := \mathrm{e}^{-p^{\mathrm{A}}_{**}}$, and $\Psi(x) := -\frac{x \log x}{1 - x}$, which is continuous, monotonically increasing, and concave for $x > 0$ with $\Psi(x) \to 0$ as $x \to +0$, $\Psi(x) \to 1$ as $x \to 1$, and $\Psi(x) \to \infty$ as $x \to \infty$.

From Theorem 1 and Corollary 1, it is necessary for the existence of E^{*}_{+++} that $\mathscr{R}^{\mathrm{J}}_{0} > 1$ and $\mathscr{R}^{\mathrm{A}}_{0} > 1$. The second and third equations of (I27) lead to the equality $\frac{1}{\alpha_{\mathrm{J}}}\Psi(x^{\mathrm{J}}_{**}) = \frac{1}{\alpha_{\mathrm{A}}}\Psi(\frac{1}{x^{\mathrm{A}}_{**}})$ which must be satisfied for the existence of E^{*}_{+++}. Since $x^{\mathrm{J}}_{**} < 1$ and $\frac{1}{x^{\mathrm{A}}_{**}} > 1$ for E^{*}_{+++}, we have $\Psi(x^{\mathrm{J}}_{**}) < 1 < \Psi(\frac{1}{x^{\mathrm{A}}_{**}})$ from the above-mentioned features of function Ψ. Therefore, there exists a pair $(x^{\mathrm{J}}, x^{\mathrm{A}}) \in (0, 1) \times (0, 1)$ to satisfy the equation $\frac{1}{\alpha_{\mathrm{J}}}\Psi(x^{\mathrm{J}}) = \frac{1}{\alpha_{\mathrm{A}}}\Psi(\frac{1}{x^{\mathrm{A}}})$ only if $\frac{1}{\alpha_{\mathrm{J}}} > \frac{1}{\alpha_{\mathrm{A}}}$, that is, only if $\mathscr{R}^{\mathrm{A}}_{0} > \mathscr{R}^{\mathrm{J}}_{0}$. These arguments prove Lemma 6.

References

Abbott KC, Dwyer G (2007) Food limitation and insect outbreaks: complex dynamics in plant-herbivore models. J Anim Ecol 76(5):1004–1014. https://doi.org/10.1111/j.1365-2656.2007.01263.x

Abrams PA (2022) Competition Theory in Ecology. Oxford Series in Ecology and Evolution Oxford University Press Oxford UK. https://doi.org/10.1093/oso/9780192895523.001.0001

Ackleh AS, Jahangir J, Veprauskas A (2023) The interplay between multiple control mechanisms in a host-parasitoid system: a discrete-time stage-structured modelling approach. J Biol Dyn 17(1):2241483. https://doi.org/10.1080/17513758.2023.2241483

Allen L (2007) An Introduction to Mathematical Biology. Pearson Prentice Hall, Upper Saddle River, NJ

Asheghi R (2014) Bifurcations and dynamics of a discrete predator-prey system. J Biol Dyn 8(1):161–186. https://doi.org/10.1080/17513758.2014.927596

Åström M, Lundberg P, Lundberg S (1996) Population dynamics with sequential density-dependencies. Oikos 75:174–181. https://doi.org/10.2307/3546241

Bacaër N (2011) A Short History of Mathematical Population Dynamics. Springer London UK. https://doi.org/10.1007/978-0-85729-115-8

Bailey VA, Nicholson AJ, Williams EJ (1962) Interaction between hosts and parasites when some host individuals are more difficult to find than others. J Theor Biol 3(1):1–8. https://doi.org/10.1016/S0022-5193(62)80002-2

Begon M, Mortimer M, Thompson DJ (1996) Population Ecology: A Unified Study of Animals and Plants, Third Edition. Blackwell Science, Oxford https://doi.org/10.1002/9781444313765

Bešo E, Kalabušić S, Mujić N, Pilav E (2020) Stability of a certain class of a host-parasitoid models with a spatial refuge effect. J Biol Dyn 14(1):1–31. https://doi.org/10.1080/17513758.2019.1692916

Bellard C, Cassey P, Blackburn TM (2016) Alien species as a driver of recent extinctions. Biol Let 12(2):20150623. https://doi.org/10.1098/rsbl.2015.0623

Beverton RJH, Holt SJ (1957) On the dynamics of exploited fish population. Fish Invest Lond 19:1–533

Bohner M, Warth H (2007) The Beverton-Holt dynamic equation. Appl Anal 86(8):1007–15. https://doi.org/10.1080/00036810701474140

Briggs J, Dabbs K, Holm M, Lubben J, Rebarber R, Tenhumberg B, Riser-Espinoza D (2010) Structured population dynamics: An introduction to integral modeling. Math Mag 83(4):243–257. https://doi.org/10.4169/002557010X521778

Briggs CJ, Nisbet RM, Murdoch WW (1993) Coexistence of competing parasitoid species on a host with a variable life cycle. Theor Popul Biol 44(3):341–73. https://doi.org/10.1006/tpbi.1993.1032

Buffoni G, Pasquali S (2007) Structured population dynamics: continuous size and discontinuous stage structures. J Math Biol 54(4):555–595. https://doi.org/10.1007/s00285-006-0058-2

Cambray JA (2003) Impact on indigenous species biodiversity caused by the globalisation of alien recreational freshwater fisheries. Hydrobiologia 500(1):217–230. https://doi.org/10.1023/A:1024648719995

Case SB, Tarwater CE (2023) Exploitation competition between seed predators and dispersers introduced to Hawaiian forests. Ecology 104(6):e4038. https://doi.org/10.1002/ecy.4038

Case TJ (2000) An Illustrated Guide to Theoretical Ecology. Oxford University Press, New York

Castillo D, Velasco-Hernández JX (2003) Coexistence in a competitive parasitoid-host system. J Theor Biol 221(1):61–77. https://doi.org/10.1006/jtbi.2003.3171

Çelik C, Duman O (2009) Allee effect in a discrete-time predator-prey system. Chaos Solitons & Fractals 40(4):1956–1962. https://doi.org/10.1016/j.chaos.2007.09.077

Chaudhary C, Richardson AJ, Schoeman DS, Costello MJ (2021) Global warming is causing a more pronounced dip in marine species richness around the equator. Proc Natl Acad Sci 118(15):e2015094118. https://doi.org/10.1073/pnas.2015094118

Chesson P (2000) Mechanisms of maintenance of species diversity. Annu Rev Ecol Syst 31(1):343–366. https://doi.org/10.1146/annurev.ecolsys.31.1.343

Crawley MJ (1989) Insect herbivores and plant population dynamics. Annu Rev Entomol 34(1):531–562. https://doi.org/10.1146/annurev.en.34.010189.002531

Cui JA, Takeuchi Y (2006) A predator-prey system with a stage structure for the prey. Math Comput Model 44(11–12):1126–1132. https://doi.org/10.1016/j.mcm.2006.04.001

Cushing JM (1994) Structured Population Dynamics. In: Levin SA (ed.) Frontiers in Mathematical Biology, Lecture Notes in Biomathematics Vol. 100, Springer, Berlin, Heidelberg, pp. 280–295 https://doi.org/10.1007/978-3-642-50124-1_17

Cushing JM (1998) An Introduction to Structured Population Dynamics. CBMS-NSF Regional Conference Series in Applied Mathematics Society for Industrial and Applied Mathematics Philadelphia doi 10(1137/1):9781611970005

Cushing JM, Saleem M (1982) A predator prey model with age structure. J Math Biol 14(2):231–250. https://doi.org/10.1007/BF01832847

Delamater PL, Street EJ, Leslie TF, Yang Y, Jacobsen KH (2019) Complexity of the basic reproduction number (R_0). Emerg Infect Dis 25(1):1–4. https://doi.org/10.3201/eid2501.17190

Cola D, Gilioli G, Baumgärtner G, J (1998) Mathematical models for age-structured population dynamics: an overview. In: Baumgartner J, Brandmayr P, Manly BFJ (eds). CRC Press, pp 45–62. https://doi.org/10.1201/9780429333422-5 (**Population and Community Ecology for Insect Management and Conservation**)

Din Q, Saleem N, Shabbir MS (2020) A class of discrete predator-prey interaction with bifurcation analysis and chaos control. Mathematical Modelling of Natural Phenomena 15:60. https://doi.org/10.1051/mmnp/2020042

Elaydi SN, Cushing JM (2025) Discrete Mathematical Models in Population Biology: Ecological, Epidemic, and Evolutionary Dynamics. Springer Nature Switzerland AG. https://doi.org/10.1007/978-3-031-64795-6

Falconi M (2006) The effect of the prey age structure on a predator-prey system. Scientiae Mathematicae Japonicae Online e-2006: 691–699

Feng W, Cowen MT, Lu X (2014) Coexistence and asymptotic stability in stage-structured predator-prey models. Mathematical Biosciences & Engineering 11(4):823–839. https://doi.org/10.3934/mbe.2014.11.823

Frisman EY, Zhdanova OL, Kulakov MP, Neverova GP, Revutskaya OL (2021) Mathematical modeling of population dynamics based on recurrent equations: results and prospects. Part I. Biol Bull Russ Acad Sci 48:1–5. https://doi.org/10.1134/S1062359021010064

Frisman EY, Zhdanova OL, Kulakov MP, Neverova GP, Revutskaya OL (2021) Mathematical modeling of population dynamics based on recurrent equations: Results and prospects. Part II. Biol Bull Russ Acad Sci 48:239–250. https://doi.org/10.1134/S1062359021030055

Getz WM, Mills NJ (1996) Host-parasitoid coexistence and egg-limited encounter rates. Am Nat 148(2):333–347. https://doi.org/10.1086/285928

Gherardi F, Britton JR, Mavuti KM, Pacini N, Grey J, Tricarico E, Harper DM (2011) A review of allodiversity in Lake Naivasha, Kenya: Developing conservation actions to protect East African lakes from the negative impacts of alien species. Biol Cons 144(11):2585–2596. https://doi.org/10.1016/j.biocon.2011.07.020

Godfray HC, Hassell MP, Holt RD (1994) The population dynamic consequences of phenological asynchrony between parasitoids and their hosts. J Anim Ecol 63(1):1–10. https://doi.org/10.2307/5577

Gotelli NJ (2001) A Primer of Ecology, 3rd edn. Sinauer Associates Incorporated, Massachusetts

Gurtin ME, Levine DS (1979) On predator-prey interactions with predation dependent on age of prey. Math Biosci 47(3–4):207–219. https://doi.org/10.1016/0025-5564(79)90038-5

Hackett-Jones E, Cobbold C, White A (2009) Coexistence of multiple parasitoids on a single host due to differences in parasitoid phenology. Thyroid Res 2(1):19–31. https://doi.org/10.1007/s12080-008-0025-1

Hassell MP (1975) Density-dependence in single-species populations. J Anim Ecol 44(1):283–295. https://doi.org/10.2307/3863

Hassell MP (1978) The Dynamics of Arthropod Predator-Prey Systems. Monographs in Population Biology 13, Princeton University Press, Princeton

Hassell MP (2000) The Spatial and Temporal Dynamics of Host-Parasitoid Interactions. Oxford University Press Oxford. https://doi.org/10.1093/oso/9780198540892.001.0001

Hassell MP, Pacala SW (1990) Heterogeneity and the dynamics of host–parasitoid interactions. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences 330(1257): 203–220 https://doi.org/10.1098/rstb.1990.0193

Hastings A (1983) Age-dependent predation is not a simple process. I. Continuous time models. Theoretical Population Biology 23(3): 347–362 https://doi.org/10.1016/0040-5809(83)90023-0

Hastings A (1984) Age-dependent predation is not a simple process. II. Wolves, ungulates, and a discrete-time model for predation on juveniles with a stabilizing tail. Theoretical Population Biology 26(2): 271–282 https://doi.org/10.1016/0040-5809(84)90033-9

Haubrock PJ, Ahmed DA, Cuthbert RN, Stubbington R, Domisch S, Marquez JR, Beidas A, Amatulli G, Kiesel J, Shen LQ, Soto I, Angeler DG, DG, Bonada N, Cañedo-Argüelles M, Csabai Z, Datry T, de Eyto E, Dohet A, Drohan E, England J, Feio MJ, Forio MAE, Goethals P, Graf W, Heino J, Hudgins EJ, Jähnig SC, Johnson RK, Larrañaga A, Leitner P, L'Hoste L, Lizee M-H, Maire A, Rasmussen JJ, Schäfer RB, Schmidt-Kloiber A, Vannevel R, Várbíró G, Wiberg-Larsen P, Haase P, (2022) Invasion impacts and dynamics of a European-wide introduced species. Glob Change Biol 28(15):4620–4632. https://doi.org/10.1111/gcb.16207

Haubrock PJ, Bernery C, Cuthbert RN, Liu C, Kourantidou M, Leroy B, Turbelin AJ, Kramer AM, Verbrugge LN, Diagne C, Courchamp F (2022) Knowledge gaps in economic costs of invasive alien fish worldwide. Sci Total Environ 803:149875. https://doi.org/10.1016/j.scitotenv.2021.149875

Haubrock PJ, Pilotto F, Innocenti G, Cianfanelli S, Haase P (2021) Two centuries for an almost complete community turnover from native to non-native species in a riverine ecosystem. Glob Change Biol 27(3):606–623. https://doi.org/10.1111/gcb.15442

Holling C (1959) The components of predation as revealed by a study of small mammals predation of the European pine sawfly. Canad Ent 91(5):292–320. https://doi.org/10.4039/Ent91293-5

Holling C (1959) Some characteristics of simple type of predation and parasitism. Canad Ent 91(7):385–398. https://doi.org/10.4039/Ent91385-7

Hood GR, Blankinship D, Doellman MM, Feder JL (2021) Temporal resource partitioning mitigates interspecific competition and promotes coexistence among insect parasites. Biol Rev 96(5):1969–1988. https://doi.org/10.1111/brv.12735

Iannelli M, Milner F (2017) The Basic Approach to Age-Structured Population Dynamics: Models. Lecture Notes on Mathematical Modelling in the Life Sciences Springer Dordrecht Methods and Numerics. https://doi.org/10.1007/978-94-024-1146-1

Inaba H (2017) Age-Structured Population Dynamics in Demography and Epidemiology. Springer Singapore. https://doi.org/10.1007/978-981-10-0188-8

Jang SJ (2007) Allee effects in a discrete-time host-parasitoid model with stage structure in the host. Discrete and Continuous Dynamical Systems-B 8(1):145–159. https://doi.org/10.3934/dcdsb.2007.8.145

Jang SR, Yu JL (2012) Discrete-time host-parasitoid models with pest control. J Biol Dyn 6(2):718–739. https://doi.org/10.1080/17513758.2012.700074

Jia L, Roh Y, Piao G, Jung IH (2024) Dynamic complexities in competing parasitoid species on a shared host. International Journal of Bifurcation and Chaos 34(02):2450014. https://doi.org/10.1142/S0218127424500147

Johnson CN, Balmford A, Brook BW, Buettel JC, Galetti M, Guangchun L, Wilmshurst JM (2017) Biodiversity losses and conservation responses in the Anthropocene. Science 356(6335):270–275. https://doi.org/10.1126/science.aam9317

Jones LC, Rafter MA, Walter GH (2022) Host interaction mechanisms in herbivorous insects - life cycles, host specialization and speciation. Biol J Lin Soc 137(1):1–4. https://doi.org/10.1093/biolinnean/blac070

Kaplan D, Glass L (1995) Understanding Nonlinear Dynamics. Textbooks in Mathematical Sciences Springer-Verlag New York. https://doi.org/10.1007/978-1-4612-0823-5

King NG, Wilmes SB, Smyth D, Tinker J, Robins PE, Thorpe J, Jones L, Malham SK (2021) Climate change accelerates range expansion of the invasive non-native species, the Pacific oyster. Crassostrea gigas ICES J Mar Sci 78(1):70–81. https://doi.org/10.1093/icesjms/fsaa189

Kingsland SE (1995) Modeling Nature, 2nd edn. The University of Chicago Press, Chicago

Kubelka V, Sandercock BK, Székely T, Freckleton RP (2022) Animal migration to northern latitudes: environmental changes and increasing threats. Trends in Ecology & Evolution 37(1):30–41

Kooi BW, Kelpin FD (2003) Physiologically structured population dynamics: a modeling perspective. Comments on Theoretical Biology 8(2–3):125–168

Lane SD, Mills NJ, Getz WM (1999) The effects of parasitoid fecundity and host taxon on the biological control of insect pests: the relationship between theory and data. Ecological Entomology 24(2):181–190. https://doi.org/10.1046/j.1365-2311.1999.00182.x

Le Hen G, Balzani P, Haase P, Kouba A, Liu C, Nagelkerke LA, Theissen N, Renault D, Soto I, Haubrock PJ (2023) Alien species and climate change drive shifts in a riverine fish community and trait compositions over 35 years. Sci Total Environ 867:161486. https://doi.org/10.1016/j.scitotenv.2023.161486

Ledder G (2013) Mathematics for the Life Sciences. Calculus, Modeling, Probability, and Dynamical Systems. Springer, https://doi.org/10.1007/978-1-4614-7276-6

Lee S, Han CY, Kim M, Kang Y (2022) Optimal control of a discrete-time plant-herbivore/pest model with bistability in fluctuating environments. Math Biosci Eng 19(5):5075–5103. https://doi.org/10.3934/mbe.2022237

Levine DS (1981) On the stability of a predator-prey system with egg-eating predators. Math Biosci 56(1–2):27–46. https://doi.org/10.1016/0025-5564(81)90026-2

Liu S, Chen L, Agarwal R (2002) Recent progress on stage-structured population dynamics. Math Comput Model 36(11–13):1319–1360. https://doi.org/10.1016/S0895-7177(02)00279-0

Livadiotis G, Assas L, Dennis B, Elaydi S, Kwessi E (2015) A discrete-time host-parasitoid model with an Allee effect. J Biol Dyn 9(1):34–51. https://doi.org/10.1080/17513758.2014.982219

Liz E, Pilarczyk P (2012) Global dynamics in a stage-structured discrete-time population model with harvesting. J Theor Biol 297:148–165. https://doi.org/10.1016/j.jtbi.2011.12.012

Lockwood JL, Hoopes MF, Marchetti MP (2013) Invasion Ecology, 2nd edn. John Wiley & Sons, Chichester UK

Lopez BE, Allen JM, Dukes JS, Lenoir J, Vilà M, Blumenthal DM, Beaury EM, Fusco EJ, Laginhas BB, Morelli TL, O'Neill MW, Sorte CJB, Maceda-Veiga A, Whitlock R, Bradley BA (2022) Global environmental changes more frequently offset than intensify detrimental effects of biological invasions. Proc Natl Acad Sci 119(22):e2117389119. https://doi.org/10.1073/pnas.2117389119

MacFadyen A (1963) Animal Ecology: Aims and Methods. Sir Isaac Pitman & Sons, London

Marcinko K, Kot M (2020) A comparative analysis of host-parasitoid models with density dependence preceding parasitism. J Biol Dyn 14(1):479–514. https://doi.org/10.1080/17513758.2020.1783005

Martelli M (1992) Discrete Dynamical Systems and Chaos, First Edition. CRC Press LLC, https://doi.org/10.1002/9781118032879

May RM (1974) Stability and Complexity in Model Ecosystems. Princeton University Press, Princeton, NJ

May RM (1978) Host-parasitoid systems in patchy environments: a phenomenological model. J Anim Ecol 47(3):833–844. https://doi.org/10.2307/3674

May RM, Hassell MP (1981) The dynamics of multiparasitoid-host interactions. Am Nat 117(3):234–261. https://doi.org/10.1086/283704

May RM, Hassell MP, Anderson RM, Tonkyn DW (1981) Density dependence in host-parasitoid models. J Anim Ecol 50(3):855–865. https://doi.org/10.2307/4142

May RM, Oster GF (1976) Bifurcations and dynamic complexity in simple ecological models. Am Nat 110(974):573–599. https://doi.org/10.1086/283092

McNair JN (1987) A reconciliation of simple and complex models of age-dependent predation. Theor Popul Biol 32(3):383–392. https://doi.org/10.1016/0040-5809(87)90056-6

Metz JA, Diekmann O (eds) (1986) The Dynamics of Physiologically Structured Populations, vol 68. Lecture Notes in Biomathematics, Springer, Berlin, Heidelberg

Mickens RE (2015) Difference Equations: Theory, Applications and Advanced Topics, Third Edition. Monographs and Research Notes in Mathematics. CRC Press, Boca Raton, FL,

Mills NJ, Getz WM (1996) Modelling the biological control of insect pests: a review of host-parasitoid models. Ecol Model 92(2–3):121–143. https://doi.org/10.1016/0304-3800(95)00177-8

Misra OP, Sinha P, Singh C (2013) Stability and bifurcation analysis of a prey-predator model with age based predation. Appl Math Model 37(9):6519–6529. https://doi.org/10.1016/j.apm.2013.01.036

Moran PA (1950) Some remarks on animal population dynamics. Biometrics 6(3):250–258. https://doi.org/10.2307/3001822

Murdoch WW, Briggs CJ, Nisbet RM (2003) Consumer-Resource Dynamics. Monographs in Population Biology 36, Princeton University Press, Princeton NJ

Myers JH, Sarfraz RM (2017) Impacts of insect herbivores on plant populations. Annu Rev Entomol 62(1):207–230. https://doi.org/10.1146/annurev-ento-010715-023826

Nicholson AJ (1933) Supplement: the balance of animal populations. J Anim Ecol 2(1):131–178. https://doi.org/10.2307/954

Nicholson AJ (1935) Bailey VA (1935) The balance of animal populations. Part I Proc Zool Soc Lond 3:551–598. https://doi.org/10.1111/j.1096-3642.1935.tb01680.x

Odum EP, Barrett GW (2005) Fundamentals of Ecology, 5th edn. Thomson Brooks/Cole, Belmont CA

Page ML, Williams NM (2023) Evidence of exploitative competition between honey bees and native bees in two California landscapes. J Anim Ecol 92(9):1802–1814. https://doi.org/10.1111/1365-2656.13973

Poland TM, Patel-Weynand T, Finch DM, Miniat CF, Hayes DC, Lopez VM (2021) Invasive Species in Forests and Rangelands of the United States: A Comprehensive Science Synthesis for the United States Forest Sector. Springer Cham Switzerland. https://doi.org/10.1007/978-3-030-45367-1

Preisser EL, Elkinton JS (2008) Exploitative competition between invasive herbivores benefits a native host plant. Ecology 89(10):2671–2677. https://doi.org/10.1890/08-0299.1

Ricker WE (1954) Stock and recruitment. Journal of the Fisheries Board of Canada 11(5):559–623. https://doi.org/10.1139/f54-039

Robinson R (2012) An Introduction to Dynamical Systems: Continuous and Discrete, Second Edition, Pure and Applied Undergraduate Texts, vol 19. American Mathematical Society, Providence, Rhode Island

Royama T (1992) Analytical Population Dynamics. Springer Dordrecht. https://doi.org/10.1007/978-94-011-2916-9

Sala OE, Stuart Chapin FI, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A, Leemans R (2000) Global biodiversity scenarios for the year 2100. Science 287(5459):1770–1774. https://doi.org/10.1126/science.287.5459.1770

Saleem M (1984) Egg-eating age-structured predators in interaction with age-structured prey. Math Biosci 70(1):91–104. https://doi.org/10.1016/0025-5564(84)90048-8

Saleem M, Siddiqui SU, Gupta V (1987) A mathematical model with young predation. J Math Biol 25:89–101. https://doi.org/10.1007/BF00275890

Seebens H, Blackburn TM, Dyer EE, Genovesi P, Hulme PE, Jeschke JM, Pagad S, Pyšek P, Van Kleunen M, Winter M, Ansong M, Arianoutsou M, Bacher S, Blasius B, Brockerhoff EG, Brundu G, Capinha C, Causton CE, Celesti-Grapow L, Dawson W, Dullinger S, Economo EP, Fuentes N, Guénard B, Jäger H, Kartesz J, Kenis M, Kühn I, Lenzner B, Liebhold AM, Mosena A, Moser D, Nentwig W, Nishino M, Pearman D, Pergl J, Rabitsch W, Rojas-Sandoval J, Roques A, Rorke S, Rossinelli S, Roy HE, Scalera R, Schindler S, Štajerová K, Tokarska-Guzik B, Walker K, Ward DF, Yamanaka T, Essl F (2018) Global rise in emerging alien species results from increased accessibility of new source pools. Proc Natl Acad Sci 115(10):E2264-2273. https://doi.org/10.1073/pnas.1719429115

Seno H (2022) A Primer on Population Dynamics Modeling: Basic Ideas for Mathematical Formulation. Springer Singapore Singapore. https://doi.org/10.1007/978-981-19-6016-1

Seno H (2025) Persistent prey species in the Lotka-Volterra apparent competition system with a single shared predator. J Math Biol 90:19. https://doi.org/10.1007/s00285-025-02184-2

Seydel R (2010) Practical Bifurcation and Stability Analysis, Third Edition, Interdisciplinary Applied Mathematics, vol. 5. Springer-Verlag, New York https://doi.org/10.1007/978-1-4419-1740-9

Siddiqui JA, Bamisile BS, Khan MM, Islam W, Hafeez M, Bodlah I, Xu Y (2021) Impact of invasive ant species on native fauna across similar habitats under global environmental changes. Environ Sci Pollut Res 28:54362–54382. https://doi.org/10.1007/s11356-021-15961-5

Singh A, Emerick B (2022) Coexistence conditions in generalized discrete-time models of insect population dynamics. Ecol Model 474:110148. https://doi.org/10.1016/j.ecolmodel.2022.110148

Smith RH, Mead R (1974) Age structure and stability in models of prey-predator systems. Theor Popul Biol 6(3):308–322. https://doi.org/10.1016/0040-5809(74)90014-8

Solomon ME (1949) The natural control of animal populations. J Anim Ecol 1:1–35. https://doi.org/10.2307/1578

Tang S, Cheke RA (2008) Models for integrated pest control and their biological implications. Math Biosci 215(1):115–125. https://doi.org/10.1016/j.mbs.2008.06.008

Tang S, Chen L (2002) Chaos in functional response host-parasitoid ecosystem models. Chaos Solitons & Fractals 13(4):875–884. https://doi.org/10.1016/S0960-0779(01)00063-7

Thompson WR (1929) On the effect of random oviposition on the action of entomophagous parasites as agents of natural control. Parasitology 21(1–2):180–188. https://doi.org/10.1017/S0031182000022885

Turbelin AJ, Malamud BD, Francis RA (2017) Mapping the global state of invasive alien species: patterns of invasion and policy responses. Glob Ecol Biogeogr 26(1):78–92. https://doi.org/10.1111/geb.12517

Wainright CA, Muhlfeld CC, Elser JJ, Bourret SL, Devlin SP (2021) Species invasion progressively disrupts the trophic structure of native food webs. Proc Natl Acad Sci 118(45):e2102179118. https://doi.org/10.1073/pnas.2102179118

Wauters LA, Lurz PW, Santicchia F, Romeo C, Ferrari N, Martinoli A, Gurnell J (2023) Interactions between native and invasive species: A systematic review of the red squirrel-gray squirrel paradigm. Front Ecol Evol 11:1083008. https://doi.org/10.3389/fevo.2023.1083008

Weide V, Varriale MC, Hilker FM (2019) Hydra effect and paradox of enrichment in discrete-time predator-prey models. Math Biosci 310:120–127. https://doi.org/10.1016/j.mbs.2018.12.010

Wignall VR, Campbell Harry I, Davies NL, Kenny SD, McMinn JK, Ratnieks FL (2020) Seasonal variation in exploitative competition between honeybees and bumblebees. Oecologia 192:351–361. https://doi.org/10.1007/s00442-019-04576-w

Wilson JK, Casajus N, Hutchinson RA, McFarland KP, Kerr JT, Berteaux D, Larrivée M, Prudic KL (2012) Climate change and local host availability drive the northern range boundary in the rapid expansion of a specialist insect herbivore. Papilio cresphontes Front Ecol Evol 9:579230. https://doi.org/10.3389/fevo.2021.579230

Wu Y, Tang G, Xiang C (2023) Dynamics of a class of nonlinear pest-natural enemy discrete model. Mathematical Methods in the Applied Sciences 46(5):5245–5261. https://doi.org/10.1002/mma.8829

Ziska L (2022) Invasive Species and Global Climate Change. CABI Wallingford UK doi 10(1079/9781800621459):0000