Master thesis

Discrete time population dynamics model for exploitative competition between native and alien predators

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1 Introduction

Today numerous species are experiencing habitat shifts potentially driven by climate change. Invasion of an alien predator species into a native prey-predator system could lead to substantial ecological consequences. The limiting dynamics of the predator and prey populations are shown to depend substantially on what ages of prey are eaten by predators [1]. Cases have been observed where more than one predator species predate on the same prey species but at different life stages. In such cases, new features of biological importance could emerge that are not present in simpler models. They include limits to the length of juvenile periods (both upper and lower) for stability, and the possibility that increases or decreases in any of the model parameters can be stabilizing or destabilizing [2]. McNair [3] presented in his findings that the conclusion of previous studies of simple models is due to biologically extreme restrictions on certain parameter values. When they are relaxed, age-dependent predation becomes equally capable of a stabilizing or destabilizing effect, just as in more complex models [3]. In large animals only adults participate in direct predation, while sucking feeds on milk from adult predators and juveniles depend on the prey population killed by the adult predators; states Mishra et al. [4], emphasizing the importance of stage structure in predators. Conversely, when considered in terms of the prey species, such a stage structure provides more insights in the prey-predator dynamics.

In this work we consider a discrete time prey-predator dynamics with an exploitative competition between two predator species sharing the common prey. We examine a scenario where a native prey-predator system is invaded by an alien predator and we will try to discuss how the difference of predation stage could be related to the consequence of the competition for the common prey, especially with respect to the invasion success/failure of the alien predator, while also considering the possibility of coexistence.

2 Assumptions

The setup examines the population dynamics in a native ecosystem where a resident predator coexists with its prey. The focus is on the impact of an alien predator entering this environment, competing with the native predator through exploitative, indirect competition for the common prey. We assume the following for our modeling:

- Predator is a specialist, dependent solely on a specific prey species for survival and reproduction. Without the presence of the prey, the predator goes extinct.
- The native prey-predator system experiences the invasion of an alien predator species. The alien new predator competes with the native predator, targeting the same prey and introducing novel predation pressures and competitive dynamics.
- Predation is stage-structured, that is the native and alien predators target different stages of the prey's life cycle. One predator primarily consumes the juvenile prey, while the other consumes the adult prey.
- Both prey and predator populations are assumed to have non-overlapping generations, where adults die after the breeding season, and only their offspring continue the population cycle.In other words, the lifespan is annual.
- The prey population features an intra-specific competition based on population density, for example, where the individuals compete over certain resources that help in reproduction.

3 Modeling

3.1 NICHOLSAN-BAILEY MODEL

Nicholson-Bailey model is well known as a classic model to describe the interactions between a prey (or host) population and a predator (or parasitoid) population. Predator predation limits prey growth, leading to a decline in predators due to reduced host availability. Let us consider a prey population first without the enemy with the difference equation model

$$H_{n+1} = F(H_n), \tag{3.1}$$

where H_n is the adult prey population density of the n^{th} season. Function F gives the offsprings that survive to become the adults in the next generation and in turn produce their own offsprings and die out because we have assumed that adults only survive for one reproductive season, which means that after reproducing once, the adults die out and only the offspring can survive to become adults in the next generation. Now let us consider the prey-population dynamics with an enemy species that predates on the prey. If the enemy targets the juvenile prey, then the prey population dynamics is given by the difference equation

$$H_{n+1} = e^{-aP_n} F\left(H_n\right), \tag{3.2}$$

where e^{-aP_n} gives the probability for the juvenile prey to escape predation and survive to become adults and

- P_n is the predator population density at the n^{th}generation.
- Positive parameter a represents the attack rate or the efficiency with which the predator locates and consumes prey.

In contrast, if the enemy targets the adult prey, it follows the difference equation

$$H_{n+1} = F\left(e^{-aP_n} H_n\right). \tag{3.3}$$

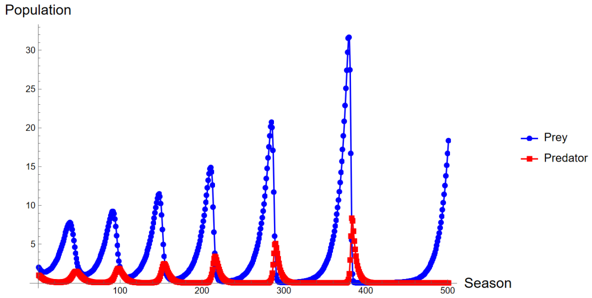

Figure 3.1: Numerical example of the temporal variation for the Nicholsan-Bailey model. $r_0 = 1.1$, $c = 0.3$, $a = 0.2$.

Here the adult prey population is the target of predation and F includes the offsprings of the surviving adults, that is, the adults that escaped predation.

Next, let us consider the predator population dynamics, which is now given as the difference equation

$$P_{n+1} = c\left(1 - e^{-aP_n}\right) F\left(H_n\right), \tag{3.4}$$

where the predator targets the juvenile prey. Positive parameter c is the coefficient of the predator reproduction of the predator. The offsprings produced by the adult prey that are unable to escape predation, provide energy for the reproduction of the predator. Along with (3.1) we get

$$\begin{cases} H_{n+1} & = e^{-aP_n} F\left(H_n\right), \\ P_{n+1} & = c\left(1 - e^{-aP_n}\right) F\left(H_n\right). \end{cases} \tag{3.5}$$

For the predator targeting the adult prey, from (3.3) and (3.4) we get

$$\begin{cases} H_{n+1} & = F\left(e^{-aP_n} H_n\right), \\ P_{n+1} & = c\left(1 - e^{-aP_n}\right) H_n. \end{cases} \tag{3.6}$$

Notice that change in the target of predation ends up providing a different system for the prey-predator population dynamics.

When we consider a Malthusian growth-based model, we get the definition

$$F(H_n) = r_0 H_n, \tag{3.7}$$

where r_0 is the expected number of offspring an adult produces. The prey population shows an exponential growth without the presence of a predator. Applying (3.12) to (3.5), we get

$$\begin{cases} H_{n+1} &= e^{-aP_n} r_0 H_n, \\ P_{n+1} &= c\left(1 - e^{-aP_n}\right) r_0 H_n. \end{cases} \tag{3.8}$$

While applying (3.7) to (3.6), we get

$$\begin{cases} H_{n+1} &= r_0 e^{-aP_n} H_n, \\ P_{n+1} &= c\left(1 - e^{-aP_n}\right) H_n. \end{cases} \tag{3.9}$$

The well known Nicholsan-Bailey model is typically referred with the system of difference equations given by (3.8) or (3.9), mostly in the context of host-parsite population dynamics. Figure 3.1 gives a numerical example of the temporal variation with the model (3.8) with $r_0 > 1$. The prey and predator populations show an excited oscillation to diverge as $n \to \infty$. For $r_0 \leq 1$, both prey and predator populations go extinct, that is, converge to zero as $n \to \infty$. The prey-predator dynamics by (3.9) has the same mathematical nature. Remark that the prey population dynamics with (3.7) does not match the assumption that the prey population undergoes the intra-specific competition. It includes no such intra-specific density effect. In the next section, we will introduce the other function F with such a density effect for our modeling in this work.

3.2 BEVERTON-HOLT MODEL

In the absence of predators, the prey population is assumed to follow a density-dependent growth pattern governed by the Beverton-Holt model. To introduces the effect of intra-specific competition on the prey population dynamics, we consider the following function for F in our modeling:

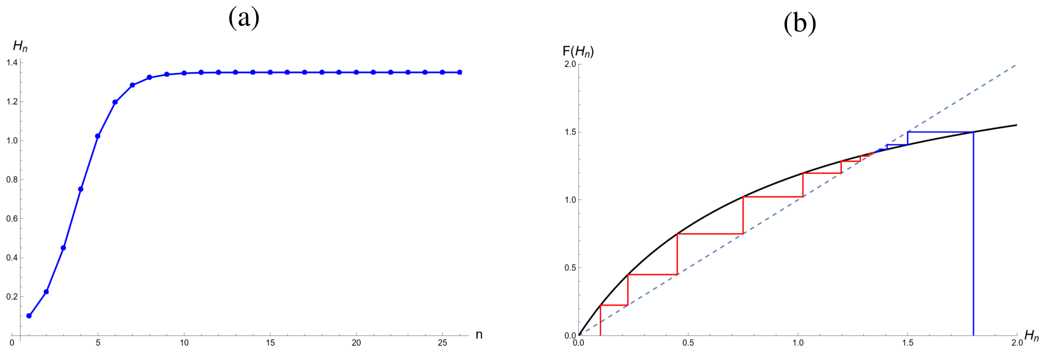

Figure 3.2: Numerical example of the cob-webbing and temporal variation for the Beverton-Holt density model given by (3.1) with (3.10). For both (a) and (b), $r_0 = 2.5$, $\beta = 0.9$. We have checked for two different initial values, $H_0 = 0.1$ and $H_0 = 1.8$.

$$F(H_n) = \frac{r_0}{1 + H_n/\beta} H_n, \tag{3.10}$$

where β is the coefficient of density effect, representing the intensity of intra-specific competition. Larger values of β correspond to a weaker density-dependent effect, allowing the population to sustain higher densities.

The population dynamics model (3.1) with (3.10) is frequently called Beverton-Holt model. It implies that the prey population growth is limited as the population density approaches a threshold, or a carrying capacity, defined as

$$H^* = \beta(r_0 - 1), \tag{3.11}$$

provided $r_0 > 1$. The equilibrium value H^* represents the carrying capacity for the prey population to which the population size converges in the absence of predator. If $r_0 \leq 1$, the prey population size declines to zero, as the growth rate is insufficient to sustain the population. If $r_0 > 1$, the prey population size exhibits a monotonic convergence to the carrying capacity H^* given by (3.11), as seen when in Figure 3.2. This behavior forms the baseline dynamics of the prey population, providing a foundation for examining interactions with predator populations in subsequent sections.

3.3 NATIVE PREY-PREDATOR POPULATION DYNAMICS

In this work we consider two distinct models — Model J and Model A — each representing a case where the life stage of prey that the native targets is different. The foundation of these models is the Nicholson-Bailey model. Later we will assume an alien predator that invades these native systems targeting the same prey but at a different stage.

Model J

We consider a prey-predator interaction where the native predator targets the juvenile stage of the prey population. The prey population is reduced by predation at the juvenile stage, influencing both its survival and the subsequent adult population density in the next generation. The prey population dynamics fundamentally follows Beverton-Holt model, with the density-dependent reproduction described by (3.10) with the intrinsic growth rate r_0 and the density effect parameter β. The equations to govern the population dynamics are given as

$$\begin{cases} H_{n+1} &= e^{-a_1 P_n} \dfrac{r_0}{1 + H_n/\beta} H_n, \\ P_{n+1} &= \rho_1 \left(1 - e^{-a_1 P_n}\right) \dfrac{r_0}{1 + H_n/\beta} H_n, \end{cases} \tag{3.12}$$

where

- P_n is the predator population size, specifically targeting the juvenile stage of the prey;
- a_1 is the attack efficiency of the predator P;
- ρ_1 is the coefficient of the predator reproduction.

The parameter ρ_1 means the conversion of energy gained by consuming the preys to the reproduction of predator offsprings.

Model A

The native predator targets the adult stage of the prey population, altering the population dynamics at a different life stage. The equations for the native prey-predator population dynamics in Model A are given as

$$\begin{cases} H_{n+1} &= \dfrac{r_0}{1+e^{-a_2Q_n}H_n/\beta}e^{-a_2Q_n}H_n, \\ Q_{n+1} &= \rho_2\left(1-e^{-a_2Q_n}\right)H_n, \end{cases} \tag{3.13}$$

where

- Q_n is the predator population size, specifically targeting the adult stage of the prey;
- a_2 is the attack efficiency of the predator Q;
- ρ_2 is the coefficient of the predator reproduction.

Remark that, differently from Model J, the intra specific density effect for the prey population is influenced by the predation. This is because the density effect is now introduced in the reproductivity, and thus the reduction in the adult population size by the predation changes the per capita reproductivity since the decrease of the adult density weakens the density effect on it.This predator-driven mortality impacts the number of reproducing individuals, influencing the prey population size in the subsequent generations.

3.4 POPULATION DYNAMICS WITH INVADING ALIEN PREDATOR

In this section, we extend the dynamics of the native prey-predator population dynamics model to incorporate an invading alien predator, which results in a three-species system: prey H, predators P and Q. The system expresses the interactions between these populations, capturing the effects of exploitative competition between two predators that target different life stages of the prey population. Its dynamics are governed by the following set of difference equations:

$$\begin{cases} H_{n+1} = e^{-a_1P_n}\dfrac{r_0}{1+e^{-a_2Q_n}H_n/\beta}e^{-a_2Q_n}H_n, \\ P_{n+1} = \rho_1\left(1-e^{-a_1P_n}\right)\dfrac{r_0}{1+e^{-a_2Q_n}H_n/\beta}e^{-a_2Q_n}H_n, \\ Q_{n+1} = \rho_2\left(1-e^{-a_2Q_n}\right)H_n, \end{cases} \tag{3.14}$$

This system applies both for model J and A. In this system, both the native and alien predators indirectly compete through their shared prey H. Predator P primarily targets the juvenile prey, while predator Q targets the adult prey. Remark that the difference in the target stage of predation indicates no interference reaction between predators P and Q because the predation seasons must be different for two predators depending on the seasons of juvenile and adult stages for the prey.

To simplify analysis, we non-dimensionalize the system by introducing scaled variables for prey and predator population sizes as well as parameters. Let

$$h_n = \frac{H_n}{\beta}, \quad p_n = a_1 P_n, \quad q_n = a_2 Q_n, \quad \alpha_1 = a_1 \rho_1 \beta, \quad \alpha_2 = a_2 \rho_2 \beta.$$

Using these variable and parameter transformations, we can derive the following system of difference equations mathematically equivalent to (3.14):

$$\begin{cases} h_{n+1} = e^{-p_n} \dfrac{r_0}{1 + e^{-q_n} h_n} e^{-q_n} h_n, \\ p_{n+1} = \alpha_1 \left(1 - e^{-p_n}\right) \dfrac{r_0}{1 + e^{-q_n} h_n} e^{-q_n} h_n, \\ q_{n+1} = \alpha_2 \left(1 - e^{-q_n}\right) h_n. \end{cases} \tag{3.15}$$

The introduction of an alien predator alters the dynamical nature of the system by intensifying competition for prey resources and modifying predation rates. Depending on α_1, α_2, and r_0, the system may exhibit various stationary states. This model provides a foundation for analyzing the conditions under which an alien predator can successfully invade and persist with the native prey, as well as the ecological impacts on the native predator population.

3.5 BASIC PREDATOR REPLACEMENT RATE

In this section, we define the basic predator replacement rate $\mathscr{R}_0$ means the supremum of the reproductive success of a predator in terms of its ability to replace itself. It is defined here as the supremum for the number of offsprings produced by a single predator at the reproduction season.

Model J

For Model J, the adult population of native predator P produces offspring at the n-th reproduction season as

$$\rho_1 \left(1 - e^{-a_1 P_n}\right) \frac{r_0}{1 + H_n/\beta} H_n.$$

Hence the averaged number of offsprings produced by a single predator in the nth season can be formulated as

$$\rho_1 \left(1 - e^{-a_1 P_n}\right) \frac{r_0}{1 + H_n/\beta} H_n \cdot \frac{1}{P_n}.$$

This expression represents the number of offspring produced per predator as a function of prey availability and predator density. From the conceptual definition given above, the basic predator replacement rate can be defined by the supremum of this formula for possible values H_n and P_n, that is, the basic replacement rate $\mathscr{R}_0^{\mathrm{P}}$ for predator P is now defined as

$$\mathscr{R}_0^{\mathrm{P}} := \sup_{H,P} \left[\rho_1 \left(1 - e^{-a_1 P}\right) \frac{r_0}{1 + H/\beta} H \cdot \frac{1}{P}\right].$$

The prey population size H cannot exceed its carrying capacity, $\beta(r_0 - 1)$. We can easily prove that the term

$$\frac{1 - e^{-a_1 P}}{P}$$

achieves its supremum at a_1 for $P \to +0$. Therefore,the above supremum can be given for $H \to \beta(r_0 - 1)$ and $P \to +0$. As a result, we can get the following expression of the basic predator replacement rate $\mathscr{R}_0^{\mathrm{P}}$ for predator P:

$$\mathscr{R}_0^{\mathrm{P}} = \rho_1 a_1 \beta(r_0 - 1).$$

If $\mathscr{R}_0^{\mathrm{P}} \leq 1$, then the predator P must go extinct because it means that a single predator cannot produce more than one predator in the next season. In contrast, the predator population size P_n increases only if $\mathscr{R}_0^{\mathrm{P}} > 1$. Remark that, even if $\mathscr{R}_0^{\mathrm{P}} > 1$, the predator P may go extinct with the effect of competition with the successful invasion of alien predator Q, which will be investigated later.

Model A

For Model A, the number of offspring produced by the alien predator population in the nth season is given by

$$\rho_2 \left(1 - e^{-a_2 Q_n}\right) H_n.$$

Hence the average number of offspring produced by a single predator can be formulated as

$$\rho_2 \left(1 - e^{-a_2 Q}\right) H_n \cdot \frac{1}{Q_n}$$

Taking the supremum over H and Q as we did in the above for Model J, gives the basic reproduction number for predator Q is now given by

$$\mathscr{R}_0^{\mathrm{Q}} = \rho_2 a_2 \beta (r_0 - 1).$$

If $\mathscr{R}_0^{\mathrm{Q}} > 1$, the predator Q's population can grow in the native prey-predator system, potentially establishing itself in the system. Conversely, if $\mathscr{R}_0^{\mathrm{Q}} \leq 1$, the predator Q is unlikely to persist, as it cannot replace itself across generations. This analysis provides insights into the dynamics of predator invasion and coexistence within the ecosystem.

4 Analysis on Native Prey-Predator System

4.1 PREDATOR EXTINCTION EQUILIBRIUM

The persistence of a predator population in a native prey-predator system is determined by its ability to maintain a positive population over time. This section discusses the condition under which the predator population persists by analyzing the native prey-predator systems of Model J and Model A, focusing on the predator extinction equilibrium E_{+0}.

Native systems and predator extinction equilibrium

The native prey-predator systems are governed by the systems (3.12) and (3.13), that is, the following non-dimensionalized systems:

$$\text{Model J}\begin{cases} h_{n+1} = e^{-p_n}\dfrac{r_0}{1+h_n}h_n, \\ p_{n+1} = \alpha_1\left(1-e^{-p_n}\right)\dfrac{r_0}{1+h_n}h_n, \end{cases} \tag{4.1}$$

$$\text{Model A}\begin{cases} h_{n+1} = \dfrac{r_0}{1+e^{-q_n}h_n}e^{-q_n}h_n, \\ q_{n+1} = \alpha_2\left(1-e^{-q_n}\right)h_n, \end{cases} \tag{4.2}$$

For both models, the predator extinction equilibrium E_{+0} is given by$E_{+0} = (h^*, 0) = (r_0-1, 0)$ where h^* is the prey population density at equilibrium in the absence of predators.

Stability of predator extinction equilibrium

The local stability of E_{+0} determines the possibility of predator extinction. The Jacobian matrices for E_{+0} about those models are

$$\mathscr{J}(E_{+0}) = \begin{pmatrix} \dfrac{1}{r_0} & -h^* \\ 0 & \mathscr{R}_0^P \end{pmatrix}$$

for Model J and

$$\mathscr{J}(E_{+0}) = \begin{pmatrix} \dfrac{1}{r_0} & -h^* \\ 0 & \mathscr{R}_0^Q \end{pmatrix}$$

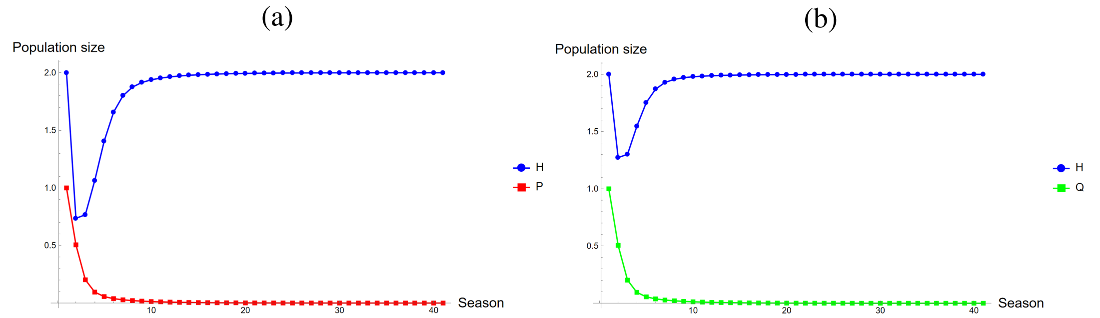

Figure 4.1: Numerical examples of the predator extinction for native prey-predator systems of Model J and A. (a) Model J: $r_0 = 3$, $\alpha_1 = 0.4$; (b) Model A: $r_0 = 3$, $\alpha_2 = 0.4$.

for Model A, where $\mathscr{R}_0^P$ and $\mathscr{R}_0^Q$ are the predator's basic replacement rate for Model J and A respectively defined as

$$\mathscr{R}_0^P = \alpha_1(r_0 - 1) \quad \text{for Model J}, \quad \mathscr{R}_0^Q = \alpha_2(r_0 - 1) \quad \text{for Model A}.$$

The eigenvalues of these Jacobian are $\lambda_1 = 1/r_0$, and $\lambda_2 = \mathscr{R}_0^P$ or $\mathscr{R}_0^Q$ for Model J and A respectively. Therefore, we can obtain the following result on the local stability of E_{+0} for Model J and A:

Lemma 1. *The predator extinction equilibrium E_{+0} for the native prey-predator system is:*

- *Locally asymptotically stable if $\mathscr{R}_0^P < 1$ and $\mathscr{R}_0^Q < 1$ for Model J and A.*
- *Unstable if $\mathscr{R}_0^P > 1$ and $\mathscr{R}_0^Q > 1$ for Model J and A, indicating that the predator population can persist in the native prey-predator system.*

4.2 PERSISTENCE OF PREDATOR

In this section we examine the existence and local stability of the coexistent equilibrium E_+ for the native prey-predator system. If it exists and it is locally asymptotically stable, the system may converge to it. In such a case, the native prey and predator coexist, whereas there could be another stationary state to which the system may converge, for example, an oscillatory state or the predator extinction equilibrium. The convergence depends on the detail of dynamics, which cannot be determined only by the local stability.

Model J

For Model J, the system dynamics are governed by the discrete-time equations of (4.1).

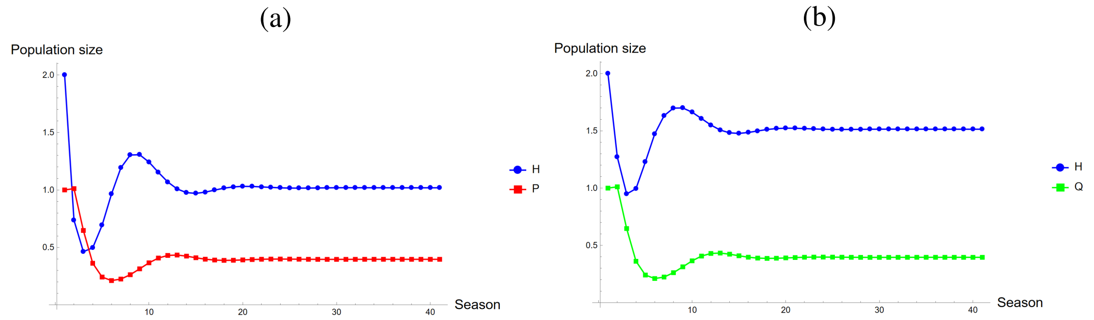

Figure 4.2: Numerical examples of the predator persistence for native prey-predator systems of Model J and A .(a)Model J: $r_0 = 3$, $\alpha_1 = 0.8$ (b)Model A: $r_0 = 3$, $\alpha_2 = 0.8$.

The coexistent equilibrium $E_+^{\mathrm{J}} = (h^*, p^*)$ satisfies the following steady-state conditions:

$$\begin{cases} e^{-p^*} \dfrac{r_0}{1 + h^*} = 1, \\ p^* = \alpha_1 r_0 \dfrac{(1 - e^{-p^*})h^*}{1 + h^*}. \end{cases} \tag{4.3}$$

Then, we find that the equilibrium densities of prey (h^*) and predator (p^*) satisfy the following equations mathematically equivalent to (4.3):

$$h^* = r_0 x^* - 1, \quad p^* = \alpha_1 r_0 \left(\frac{1 - x^*}{x^*} \right) \left(x^* - \frac{1}{r_0} \right), \tag{4.4}$$

where $x^* = e^{-p^*}$.

Figure 4.2 shows a numerical example such that the system converges to a coexistent equilibrium E_+^{J} at which both the prey and the predator exist togther. The existence of E_+^{J} requires $x^* \in (1/r_0, 1)$, which ensures that $h^* > 0$ and $p^* > 0$. The equilibrium size of the predator population satisfies:

$$x^* = e^{-p^*} \in \left(\frac{1}{r_0}, x_c \right) \subset \left(\frac{1}{r_0}, 1 \right)$$

with:

$$x_c = \frac{1}{2 r_0 \alpha_1} \left(1 + \sqrt{1 + 4 r_0 \alpha_1^2} \right).$$

This range defines the predator's equilibrium density based on its reproductive rate α_1 and the prey's carrying capacity r_0. As α_1 increases, x_c shifts, reflecting the predator's capacity to maintain a stable population.

We can prove the following theorem on the existence and stability of E_+ for Model J (Appendix A):

Theorem 1. *The coexistent equilibrium E_+^{J} for the native prey-predator system of Model J exists and is locally asymptotically stable if one of the following three conditions is satisfied:*

- $F_1(x_-) > 0$ *or* $F_1(x_+) < 0$ *with* $r_0 \in \left(1, \frac{4}{3}\right]$ *and* $\alpha_1 > \frac{1}{r_0 - 1}$*,*
- $r_0 > \frac{4}{3}$ *and* $\alpha_1 \in \left(\frac{1}{r_0-1}, \frac{4}{r_0}\right)$*,*
- $F_1(x_-) > 0$ *or* $F_1(x_+) < 0$ *with* $r_0 > \frac{4}{3}$ *and* $\alpha_1 \geq \frac{4}{r_0}$ *where,*

$$F_1(x) := \alpha_1 r_0 \left(x - \frac{1}{r_0}\right) - g(x), \quad g(x) = -\frac{x \ln x}{1 - x},$$

and $x_\pm$ *are given by*

$$x_\pm := \frac{\alpha_1}{2}\left(1 \pm \sqrt{1 - \frac{4}{\alpha_1 r_0}}\right).$$

Model A

For Model A, the dynamics are governed by the discrete-time equations of (4.2).

The coexistent equilibrium $E_+^A = (h^*, q^*)$ satisfies the following steady-state conditions:

$$\begin{cases} \dfrac{r_0}{1 + e^{-q^*} h^*} e^{-q^*} = 1, \\ q^* = \alpha_2 (1 - e^{-q^*}) h^*. \end{cases} \tag{4.5}$$

Then, we find that the equilibrium densities of prey (h^*) and predator (q^*) satisfy the following equations mathematically equivalent to (4.5):

$$h^* = r_0 - \frac{1}{y^*}, \quad q^* = \alpha_2 r_0 \left(\frac{1 - y^*}{y^*}\right)\left(y^* - \frac{1}{r_0}\right), \tag{4.6}$$

where $y^* = e^{-q^*}$.

The equilibrium exists if $y^* \in (1/r_0, 1)$, ensuring $h^* > 0$ and $q^* > 0$. The equilibrium size of the predator population satisfies:

$$y^* = e^{-q^*} \in \left(\frac{1}{r_0}, y_c\right) \subset \left(\frac{1}{r_0}, 1\right)$$

with:

$$y_c = \frac{1}{2 r_0 \alpha_2}\left(1 + \sqrt{1 + 4 r_0 \alpha_2^2}\right).$$

We can prove the following theorem on the existence and stability of E_+ for Model J (Appendix B):

Theorem 2. *The coexistent equilibrium* E_+^A *for the native prey-predator system of Model A exists and is locally asymptotically stable if one of the following three conditions is satisfied:*

- $F_2(y_-) > 0$ *or* $F_2(y_+) < 0$ *with* $r_0 \in \left(1, \frac{4}{3}\right]$ *and* $\alpha_2 > \frac{1}{r_0 - 1}$,
- $r_0 > \frac{4}{3}$ *and* $\alpha_2 \in \left(\frac{1}{r_0-1}, \frac{4}{r_0}\right)$,
- $F_2(y_-) > 0$ *or* $F_2(y_+) < 0$ *with* $r_0 > \frac{4}{3}$ *and* $\alpha_2 \geq \frac{4}{r_0}$ *where,*

$$F_2(y) := \alpha_2 r_0 \left(y - \frac{1}{r_0}\right) - g(y), \quad g(y) = -\frac{y \ln y}{1 - y},$$

and the $y_\pm$ *are given by*

$$y_\pm := \frac{\alpha_2}{2}\left(1 \pm \sqrt{1 - \frac{4}{\alpha_2 r_0}}\right).$$

Lemma 2. *The coexistent equilibrium* E_+ *uniquely exists if and only if* $\mathscr{R}_0^{\mathrm{P}} > 1$ *with* $r_0 > 1$ *and* $\mathscr{R}_0^{\mathrm{Q}} > 1$ *with* $r_0 > 1$ *for Model J and Model A respectively.*

Lemma 3. *When the coexistent equilibrium* E_+ *exists, the equilibrium size of the native predator population satisfies* $x^* \in (1/r_0, x_c)$ *for Model J and* $y^* \in (1/r_0, y_c)$ *for Model A, where* x_c *and* y_c *are as defined above.*

4.3 BIFURCATION FOR NATIVE PREY-PREDATOR SYSTEM

In this section, we investigate the bifurcation of solutions for the native prey-predator system under the critical conditions where the stability of equilibria is lost. Using the results on the local stability of equilibria for $r_0 > 1$, we analyze the bifurcation behavior for both predator extinction and coexistent equilibria.

Predator extinction equilibrium

From Theorem 1, the stability of the predator extinction equilibrium is lost at the critical condition $\mathscr{R}_0 = 1$. When $\mathscr{R}_0 > 1$, the eigenvalues for the predator extinction equilibrium consist of:

- One eigenvalue less than 1, specifically $1/r_0$, which satisfies $1/r_0 < 1$,

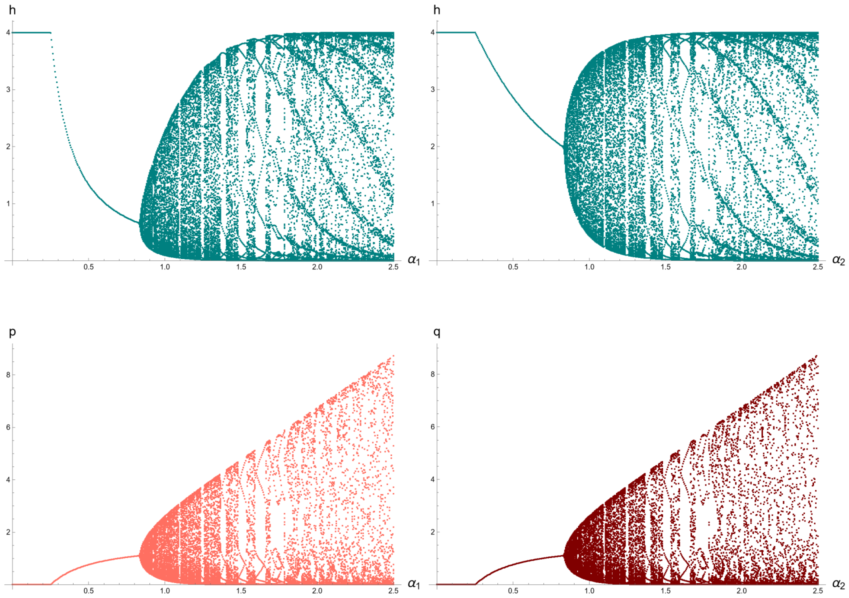
(a) (b)

Figure 4.3: Numerical examples of (4.1) and (4.2) showing bifurcation for native prey-predator systems of Model J and A, respectively, with $r_0 = 5$. (a) corresponds to Model J while (b) corresponds to Model A.

- Another eigenvalue greater than 1, specifically $\mathscr{R}_0 > 1$.

This indicates that the bifurcation occurring at $\mathscr{R}_0 = 1$ is of the saddle-node bifurcation type. Such a bifurcation reflects the emergence of a stable equilibrium alongside an unstable one, with $r_0 > 1$ ensuring a sufficient growth rate for the prey to sustain this transition.

Coexistent equilibrium

The stability of the coexistent equilibrium, E_+^J for Model J and E_+^A for Model A, is determined by the eigenvalues of the Jacobian matrix $\mathscr{J}_+^\bullet$ at the equilibrium. These eigenvalues are the roots of the characteristic equation:

$$\Phi^\bullet(\lambda) := \lambda^2 - (\mathrm{tr}\,\mathscr{J}_+^\bullet)\lambda + \det \mathscr{J}_+^\bullet = 0. \tag{*1}$$

From the local stability analysis, it has been shown that the condition,

$\mathrm{tr}\,\mathscr{J}_+^\bullet < 1 + \det \mathscr{J}_+^\bullet$

is necessarily satisfied when the coexistent equilibrium exists.

Since $\operatorname{tr} \mathscr{J}_+^\bullet > 0$ holds when the coexistent equilibrium exists, the characteristic equation never has roots at $\lambda = 1$ or $\lambda = -1$ under these conditions. Consequently, at the bifurcation point where the stability of the coexistent equilibrium is lost, the eigenvalues must include imaginary values with absolute value 1.

This analysis reveals that the instability of the coexistent equilibrium $E_+^\bullet$ corresponds to a Naimark-Sacker bifurcation which can also be seen in Figure 4.3. Near the bifurcation point, the system exhibits quasi-periodic behavior with chaotic variations.

5 Invadability of Alien Predator

5.1 FAILURE OF ALIEN PREDATOR INVASION

This section analyzes the invasion failure of the alien predator in the native prey-predator systems. The discussion focuses on the stability of E_{++0} for Model J and E_{+0+} for Model A, considering scenarios where the alien predator fails to establish itself.

Invadability of alien predator in model J

For Model J, $E_{++0} = (h^*, p^*, 0)$ represents the equilibrium where the prey h and native predator P coexist in the absence of the alien predator Q. The equilibrium values are given by:

$$h^* = r_0 x^* - 1, \quad p^* = \alpha_1 r_0 \left(\frac{1 - x^*}{x^*} \right) \left(x^* - \frac{1}{r_0} \right), \quad x^* = e^{-p^*}.$$

The critical eigenvalue for the alien predator Q is

$$\lambda_3 = \mathscr{R}_Q = \alpha_2 h^* = \alpha_2 (r_0 x^* - 1).$$

Theorem 3. *Provided that the equilibrium E_+^J for the native prey-predator system of Model J is asymptotically stable, the equilibrium E_{++0} is locally asymptotically stable if one of the following two conditions is satisfied*

- $\alpha_2 \le \alpha_1$,
- $\alpha_2 > \alpha_1$ *and* $F_1\left(\frac{1}{r_0}\left(1 + \frac{1}{\alpha_2}\right)\right) > 0$,

Conversely, E_{++0} is unstable if

- $\alpha_2 > \alpha_1$,
- $F_1\left(\frac{1}{r_0}\left(1 + \frac{1}{\alpha_2}\right)\right) < 0$

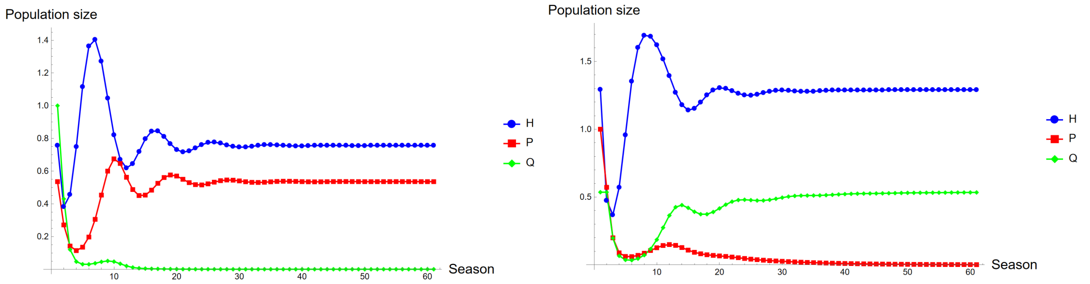
(a) (b)

Figure 5.1: Numerical examples for the invasion failure of the alien predator in the case of both Model J and A.(a) Model J: $r_0 = 3$, $\alpha_1 = 1$, $\alpha_2 = 0.9$ (b) Model A: $r_0 = 3$, $\alpha_1 = 0.7$, $\alpha_2 = 1$.

Invadability of alien predator in model A

For Model A, $E_{+0+} = (h^*, 0, q^*)$ represents the equilibrium where the prey h and alien predator Q coexist in the absence of the native predator P. The equilibrium values are given by

$$h^* = r_0 - \frac{1}{y^*}, \quad q^* = \alpha_2 r_0 \left(\frac{1 - y^*}{y^*}\right) \left(y^* - \frac{1}{r_0}\right), \quad y^* = e^{-q^*}.$$

The critical eigenvalue for the native predator P is

$$\lambda_2 = \mathscr{R}_P = \alpha_1 h^* = \alpha_1 \left(r_0 - \frac{1}{y^*}\right).$$

Theorem 4. *Provided that the equilibrium E_+^A for the native prey-predator system of Model A is asymptotically stable, the equilibrium E_{+0+} is locally asymptotically stable if one of the following two conditions is satisfied*

- $\alpha_1 \leq \dfrac{1 + \alpha_2}{r_0}$,
- $\alpha_1 \in \left(\frac{1+\alpha_2}{r_0}, \alpha_2\right)$ *and* $F_2\left(\frac{1}{(r_0 - 1/\alpha_1)}\right) > 0$,

Conversely, E_{+0+} is unstable if one of the following 2 conditions is satisfied:

- $\alpha_1 \geq \alpha_2$,
- $\alpha_1 \in \left(\frac{1+\alpha_2}{r_0}, \alpha_2\right)$ *and* $F_2\left(\frac{1}{(r_0 - 1/\alpha_1)}\right) < 0$

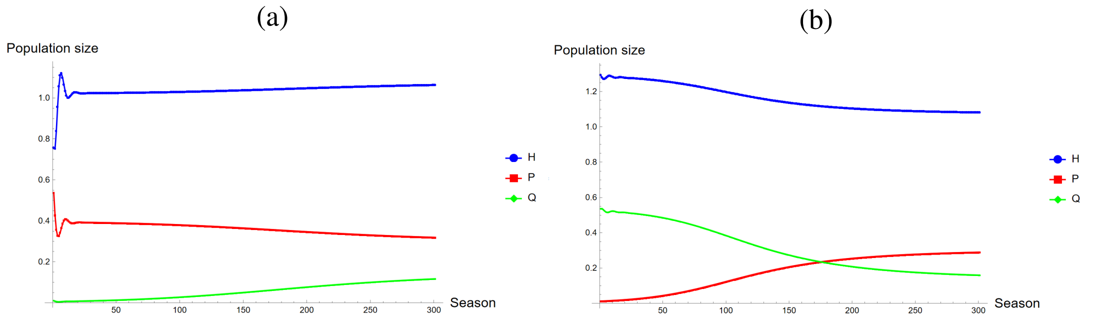

Figure 5.2: Numerical example of the possible coexistence between the 3 species in both model J and A.(a) Model J: $r_0 = 3$, $\alpha_1 = 0.8$ and $\alpha_2 = 1$. Here, Q is the invading species and initial values of H and P are taken from equilibrium state.(b) Model A: $r_0 = 3$, $\alpha_1 = 0.8$ and $\alpha_2 = 1$. Here, P is the invading species and initial values of H and Q are taken from equilibrium state.

5.2 COEXISTENT EQUILIBRIUM OF NATIVE AND ALIEN PREDATORS

This section explores the conditions under which prey, native predator P, and alien predator Q coexist in a shared ecosystem. The equilibrium, referred to as E_{+++}, represents a state where all three populations persist over time with positive densities. Understanding the coexistence dynamics is critical for analyzing the interactions between native and invasive species and their collective impact on the prey population. The coexistent equilibrium E_{+++} arises in ecosystems where the prey population is capable of supporting the growth and survival of two predator species. Both predators exert predation pressure on the prey, but their ability to coexist depends on a balance between resource availability and competition. The presence of the alien predator Q introduces an additional layer of complexity, as it competes with the native predator P for the same prey resource.

Existence of Coexistence

For E_{+++} to exist, several ecological conditions must be met:

- The prey population must have a sufficiently high growth rate (r_0) to compensate for the combined predation pressures from P and Q.
- The native predator (P) and alien predator (Q) must have reproductive rates (α_1 and α_2) that allow them to maintain positive densities without driving each other or the prey population to extinction.

- There must be a balance between predation efficiency and saturation effects, ensuring that neither predator becomes overly dominant.

The coexistence of all three populations as seen from Figure 5.2, is a dynamic outcome of these interacting ecological forces. Factors such as resource partitioning, predator interference, and density-dependent prey growth further shape the conditions for E_{+++}.

Stability of Coexistence

The stability of E_{+++} refers to the system's ability to return to equilibrium after small perturbations in population densities. Stability is influenced by:

- The intrinsic growth rate of the prey population (r_0), which determines the system's overall resource availability.
- The competitive interactions between P and Q, which must not destabilize the system by driving one predator to extinction or causing runaway dynamics.
- The strength of predation saturation effects, which limit the predators' impact at high densities and prevent overexploitation of the prey.

A stable E_{+++} indicates that the ecosystem can maintain a balance between prey replenishment and predation pressures, ensuring the long-term coexistence of all three populations. By combining theoretical analysis with visual representations, this section provides a comprehensive understanding of the factors driving coexistence in prey-predator systems with native and alien species.

5.3 CONSEQUENCE OF THE SUCCESSFUL INVASION OF ALIEN PREDATOR

The invasion of the alien predator in the native system of Model J and Model A where Q and P are the invading predators respectively, has different possible outcomes depending on the parameter values. See Figure 5.3 where the bifurcation diagram shows the different regions. In Model J, where predator Q is the invader,in a certain range of α_2 H and P exist together in a stable state and the invasion is unsuccessful. If α_2 increases beyond that range, all 3 species coexist where predator Q starts establishing itself in the native environment and predator P starts declining. If α_2 increases further, the model enters in a state of competitive exclusion where the native predator P goes extinct and the invading predator Q exists with the prey H in a

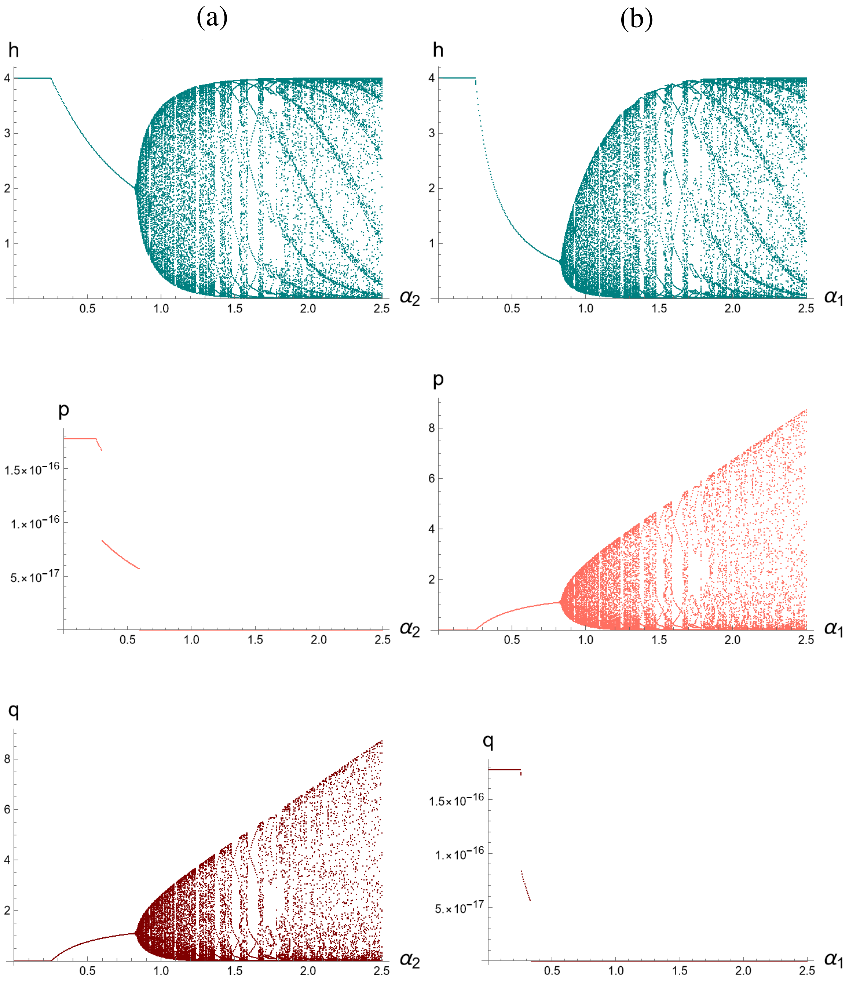

Figure 5.3: Numerical examples of (3.15) showing bifurcation for native prey-predator systems of Model J and A with alien predator invasion, respectively, with $r_0 = 5$. (a) corresponds to Model J with $\alpha_1 = 0.2$ while (b) corresponds to Model A with $\alpha_2 = 0.2$.

stable state and then in an oscillatory state. Similar regions can be observed in Model A where P is the invader.

The instability of E_{++0} for Model J and E_{+0+} for model A means the invadability of the native prey-predator system by the alien predator, provided that the native prey-predator system stays at the asymptotically stable equilibrium with persistent native prey and predator before the invasion of the alien predator. Figure 5.4 gives the numerical result about the (α_1, α_2)-dependence of the invasion success of the alien predator at the coexistent equilibrium of the native prey-predator system in Model J and A respectively, making use of the conditions given in Theorems 3 and 4. The invasion of the alien predator is successful only with a sufficiently large α_1 or α_2, depending on the model J or A. Coexistence seems to be difficult and very likely

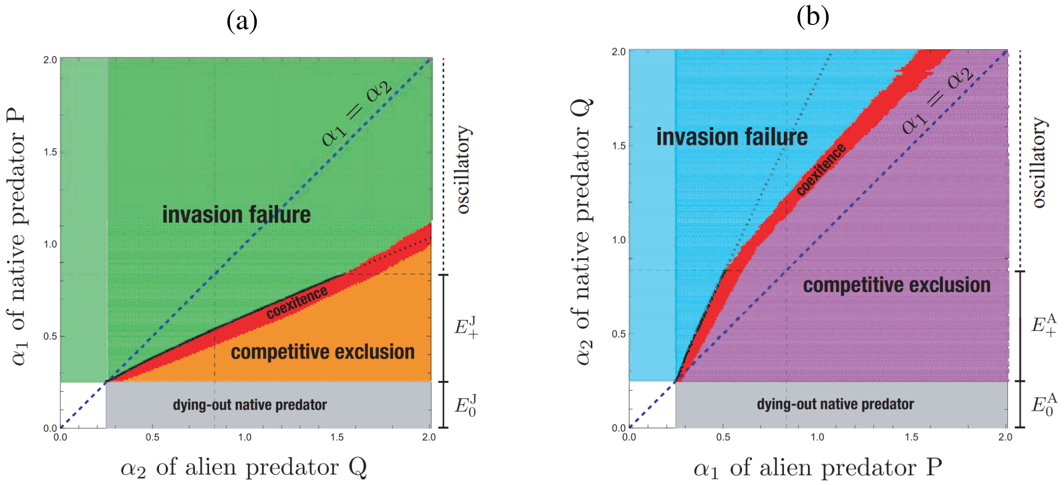

Figure 5.4: (α_1, α_2)-dependence of the final state after the invasion of alien predator in (a) Model J; (b) Model A. Numerically estimated with the temporal variation of population sizes generated by the three dimensional system (3.14) for $r_0 = 5.0$.

to cause competitive exclusion, that is, the extinction of the nativ predator species.

Corollary 1. *Provided that the native prey-predator system stays at the asymptotically stable coexistent equilibrium before the invasion of the alien predator, the alien predator* P *with* $\alpha_1 \geq \alpha_2$ *successfully invades the native prey-predator system of Model A, while the alien predator* Q *with* $\alpha_2 > \alpha_1$ *may fail to invade the native prey-predator system of Model J.*

This result indicates that the invasion of predator Q in the native prey-predator system with predator P is harder to be successful than that of predator P in the native prey-predator system with predator Q. Especially when $\alpha_1 = \alpha_2$ for predators P and Q, we can see that the invasion of predator P in the native prey-predator system of Model A is successful, while that of predator Q in the native prey-predator system of Model J is unsuccessful. Hence, 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 invasion of the alien predator, the native prey-predator system of Model J is more resistant to the invasion of the alien predator than that of Model A. In other words, the invasion of the alien predator preying on the juvenile stage is more successful than that preying on the adult stage.

6 Concluding Remarks

As seen from Figure 5.4, the coexistence between native and alien predators is possible only for a relatively narrow region of (α_1, α_2), about the coexistent equilibrium for the native prey-predator system. Further, similarly to the result of Corollary 1, the invasion of alien predator Q in Model J is more hardly successful than that of alien predator P in Model A even at the oscillatory state of native prey-predator system. Therefore, the numerical result implies that, independently of what stationary state the native prey-predator system stays at, the native prey-predator system of Model J is more resistant to the invasion of alien predator than that of Model A, and the invasion of alien predator preying on the juvenile stage is more successful than that preying on the adult stage.

The native prey-predator system represented by Model J demonstrates greater resistance to the invasion of an alien predator compared to Model A. This enhanced resistance is attributed to the interaction dynamics between the native predator and prey, where the native predator preys on juvenile prey stages. The saturation effect in predation and the ability of the prey population to sustain higher reproductive rates contribute to the stability and persistence of the native predator population, even in the presence of an invader.

In contrast, the invasion of an alien predator targeting the juvenile stage, as modeled in Model A, proves to be more successful than an alien predator preying on adult prey. This success stems from the heightened vulnerability of juvenile prey to predation, which limits their transition to reproductive stages and subsequently reduces the prey population's growth potential. As a result, the alien predator in Model A can establish itself more effectively, often leading to destabilization or competitive exclusion of the native predator.

These findings underscore the critical role of life stage-specific interactions in determining the outcomes of species invasions. The dynamics observed in Models J and A reveal the importance of prey population structure and predator-prey interaction efficiencies in shaping ecosystem resilience to invasions. In conclusion, this work highlights the nuanced interplay between native and alien predators in prey-predator systems, providing a foundation for further exploration of invasion dynamics and ecosystem stability. Future research may extend these models to account for additional ecological factors such as environmental variability, multi-predator interactions, and adaptive behaviors in prey and predators.

A Proof for Theorem 1

From (4.3) and (4.4) we get

$$\ln x = \alpha_1 r_0 \left(1 - \frac{1}{x}\right)\left(x - \frac{1}{r_0}\right),$$

that is,

$$\alpha_1 r_0 \left(x - \frac{1}{r_0}\right) = g(x) := -\frac{x \ln x}{1 - x}.$$

and alternatively

$$F_1(x) := \alpha_1 r_0 \left(x - \frac{1}{r_0}\right) - g(x), \quad g(x) = -\frac{x \ln x}{1 - x}. \tag{A.1}$$

From the same result we can also get

$$f_1(x) := \left(1 - \frac{1}{x}\right)\left(x - \frac{1}{r_0}\right) - \frac{1}{\alpha_1 r_0} \ln x = 0,$$

and for the derivative

$$f_1'(x) = \frac{1}{x^2}\left(x^2 - \frac{1}{\alpha_1 r_0} x - \frac{1}{r_0}\right).$$

From the Jacobi matrix for the native prey-predator system of Model J, we have:

$$\mathscr{J}_+^J := \begin{pmatrix} r_0 \frac{x^*}{(1+h^*)^2} & -r_0 \frac{x^* h^*}{1+h^*} \\ \alpha_1 r_0 \frac{1-x^*}{(1+h^*)^2} & \alpha_1 r_0 \frac{x^* h^*}{1+h^*} \end{pmatrix} = \begin{pmatrix} \frac{1}{r_0 x^*} & -(r_0 x^* - 1) \\ \alpha_1 \left(\frac{1}{x^*} - 1\right) & \alpha_1 (r_0 x^* - 1) \end{pmatrix}, \tag{A.2}$$

where we used the equations (10) to determine the equilibrium values at E_+^J with $x^* := e^{-p^*}$.

Then, the determinant and trace of $\mathscr{J}_+^J$ are:

$$\det \mathscr{J}_+^J = \frac{\alpha_1}{x^*}\left(1 - \frac{1}{r_0 x^*}\right) > 0, \quad \mathrm{tr} \mathscr{J}_+^J = \frac{1}{r_0 x^*} + \alpha_1 (r_0 x^* - 1) > 0,$$

since $r_0 x^* > 1$ for E_+^J.

Here, we apply the Jury stability criterion, which provides the sufficient condition for the characteristic equation $\lambda^2 + c_1 \lambda + c_2 = 0$ to have roots with absolute values less than 1. The conditions are:

$$c_2^2 < 1, \quad c_1^2 < (1 + c_2)^2,$$

where $c_1 = -\mathrm{tr}\mathscr{J}_+^J$ and $c_2 = \det \mathscr{J}_+^J$. Substituting these, the eigenvalues of $\mathscr{J}_+^J$ have absolute values less than 1 if:

$$\begin{cases} \det \mathscr{J}_+^J < 1, \\ \mathrm{tr}\mathscr{J}_+^J < 1 + \det \mathscr{J}_+^J, \end{cases}$$

since $\det \mathscr{J}_+^J > 0$ and $\mathrm{tr}\mathscr{J}_+^J > 0$ as shown above.

This results in the conditions:

$$\begin{cases} \psi_1(x^*) := (x^*)^2 - \alpha_1 x^* + \frac{\alpha_1}{r_0} > 0, \\ \psi_2(x^*) := (x^*)^2 - \frac{1}{\alpha_1 r_0} x^* - \frac{1}{r_0} = (x^*)^2 f_1'(x^*) < 0, \end{cases}$$

where $f_1(x)$ and its derivative $f_1'(x)$. If the above conditions are satisfied, the coexistence equilibrium E_+^J is locally asymptotically stable. Conversely, if any of these conditions is reversed, E_+^J becomes unstable.

For $\psi_1(x^*) > 0$, the discriminant of $\psi_1(x)$ is negative if and only if $\alpha_1 < \frac{4}{r_0}$. This means that $\psi_1(x^*) > 0$ is always satisfied when $\alpha_1 < \frac{4}{r_0}$. Taking into account the existence condition for E_+^J, ($\mathscr{R}_0^P > 1$, i.e., $\alpha_1 > \frac{1}{r_0 - 1}$), the condition $\alpha_1 < \frac{4}{r_0}$ is satisfied only if $r_0 > \frac{4}{3}$ when E_+^J exists.

The discriminant of $\psi_1(x)$ becomes non-negative if $\alpha_1 \geq \frac{4}{r_0}$. For such cases:

$$x^* < x_- \quad \text{or} \quad x^* > x_+,$$

where $x_\pm$ are the roots of $\psi_1(x) = 0$, given by:

$$x_\pm = \frac{\alpha_1}{2}\left(1 \pm \sqrt{1 - \frac{4}{\alpha_1 r_0}}\right).$$

Finally, from previous arguments, the condition $x^* < x_-$ is equivalent to $F_1(x_-) > 0$, and $x^* > x_+$ corresponds to $F_1(x_+) < 0$. From this, we get the proof for Theorem 1.

B Proof for Theorem 2

From (4.5) and (4.6) we get

$$\alpha_2 r_0 \left(y^* - \frac{1}{r_0} \right) = g(y^*),$$

that is,

$$F_2(y^*) := \alpha_2 r_0 \left(y^* - \frac{1}{r_0} \right) - g(y^*) = 0.$$

where

$$g(y) = -\frac{y \ln y}{1-y}. \tag{B.1}$$

For the Jacobi matrix of the native prey-predator system of Model A, we have:

$$\mathscr{J}_+^A := \begin{pmatrix} r_0 \frac{y^*}{(1+y^*h^*)^2} & -r_0 \frac{y^*h^*}{(1+y^*h^*)^2} \\ \alpha_2(1-y^*) & \alpha_2 y^* h^* \end{pmatrix} = \begin{pmatrix} \frac{1}{r_0 y^*} & -\frac{1}{y^*}\left(1 - \frac{1}{r_0 y^*}\right) \\ \alpha_2(1-y^*) & \alpha_2(r_0 y^* - 1) \end{pmatrix}, \tag{B.2}$$

where $y^* := e^{-q^*}$.

The determinant and trace of $\mathscr{J}_+^A$ are:

$$\det \mathscr{J}_+^A = \frac{\alpha_2}{y^*}\left(1 - \frac{1}{r_0 y^*}\right) > 0, \quad \mathrm{tr} \mathscr{J}_+^A = \frac{1}{r_0 y^*} + \alpha_2(r_0 y^* - 1) > 0,$$

since $r_0 y^* > 1$ for E_+^A from Lemma 4.

Similarly to the arguments for the native prey-predator system of Model J, we apply the Jury stability criterion. The eigenvalues of $\mathscr{J}_+^A$ have absolute values less than 1 if:

$$\det \mathscr{J}_+^A < 1, \quad \mathrm{tr} \mathscr{J}_+^A < 1 + \det \mathscr{J}_+^A,$$

since $\det \mathscr{J}_+^A > 0$ and $\mathrm{tr} \mathscr{J}_+^A > 0$ for E_+^A.

These conditions are mathematically equivalent to those in Appendix A, substituting y^* and α_2 for x^* and α_1, respectively. Using the function F_2 and defining:

$$y_\pm := \frac{\alpha_2}{2}\left(1 \pm \sqrt{1 - \frac{4}{\alpha_2 r_0}}\right), \tag{22}$$

corresponding to similar equation for Model J, we obtain the result regarding the local stability of E_+^A for the native prey-predator system of Model A. From this we get the proof for Theorem 2.

C Proof for Theorem 3

The Jacobi matrix for E_{++0} is given as

$$\mathscr{J}_3(E_{++0}) = \begin{pmatrix} r_0\frac{x^*}{(1+h^*)^2} & -r_0\frac{x^*h^*}{1+h^*} & -r_0\frac{x^*h^*}{(1+h^*)^2} \\ \alpha_1 r_0\frac{1-x^*}{(1+h^*)^2} & \alpha_1 r_0\frac{x^*h^*}{1+h^*} & -r_0\frac{(1-x^*)h^*}{(1+h^*)^2} \\ 0 & 0 & \alpha_2 h^* \end{pmatrix}$$

Therefore, its eigenvalues contain those of the Jacobi matrix $\mathscr{J}_+^{\mathscr{J}}$ given in (A.2) for the native prey-predator system of Model J and another eigenvalue $\lambda_J^* := \alpha_2 h^* = \alpha_2(r_0x^* - 1) > 0$. Hence, provided that the coexistent equilibrium E_J^+ for the native prey-predator system of Model J is asymptotically stable, the equilibrium E_{++0} is asymptotically stable if $\lambda_J^* < 1$, while it is unstable if $\lambda_J^* > 1$.

The condition for the local stability $\lambda_J^* < 1$ holds if and only if

$$\frac{1}{r_0}\left(1 + \frac{1}{\alpha_2}\right) > x^*. \tag{C.1}$$

Remark that $\frac{1}{r_0}\left(1 + \frac{1}{\alpha_2}\right)$ is not necessarily less than 1 when the coexistent equilibrium E_J^+ is asymptotically stable. If $\frac{1}{r_0}\left(1 + \frac{1}{\alpha_2}\right) < x^*$, then $\lambda_J^* > 1$, and the equilibrium E_{++0} is unstable.

Since $x^* < 1$, the condition (C.1) necessarily holds if $\frac{1}{r_0}\left(1 + \frac{1}{\alpha_2}\right) \geq 1$, which is equivalent to $\mathscr{R}_Q^0 \leq 1$. Thus, we have found a sufficient condition for the local stability of E_{++0}.

When $\mathscr{R}_Q^0 > 1$ with $r_0 > 1$, we have $\frac{1}{r_0}\left(1 + \frac{1}{\alpha_2}\right) < 1$. Again, from the arguments on the existence of E_J^+ with the function g defined by (A.1), the condition (C.1) is equivalent to

$$F_1\left(\frac{1}{r_0}\left(1 + \frac{1}{\alpha_2}\right)\right) > 0,$$

with F_1 defined as

$$F_1\left(\frac{1}{r_0}\left(1 + \frac{1}{\alpha_2}\right)\right) = \alpha_1 r_0\left\{\frac{1}{r_0}\left(1 + \frac{1}{\alpha_2}\right) - \frac{1}{r_0}\right\} - g\left(\frac{1}{r_0}\left(1 + \frac{1}{\alpha_2}\right)\right) = \frac{\alpha_1}{\alpha_2} - g\left(\frac{1}{r_0}\left(1 + \frac{1}{\alpha_2}\right)\right) > 0. \tag{C.2}$$

When $\mathscr{R}_Q^0 > 1$ with $r_0 > 1$, the condition (C.1) holds if and only if the condition (C.2) is satisfied. Since $g\left(\frac{1}{r_0}\left(1 + \frac{1}{\alpha_2}\right)\right) < 1$ for $\frac{1}{r_0}\left(1 + \frac{1}{\alpha_2}\right) < 1$ from the nature of the function g defined by (A.1), we find that the condition (C.2) necessarily holds if $\frac{\alpha_1}{\alpha_2} \geq 1$.

In contrast, the condition $\frac{1}{r_0}\left(1+\frac{1}{\alpha_2}\right) < x^*$ is equivalent to $F_1\left(\frac{1}{r_0}\left(1+\frac{1}{\alpha_2}\right)\right) < 0$ with $\frac{1}{r_0}\left(1+\frac{1}{\alpha_2}\right) < 1$, that is, with $\mathscr{R}_Q^0 > 1$.

With these conditions obtained, we have the proof for Theorem 3.

D Proof for Theorem 4

According to the eigenvalues, the following matrix is mathematically equivalent to $J_3(E_{+0+})$:

$$\mathscr{J}_3(E_{+0+}) = \begin{pmatrix} \frac{1}{r_0 y^*} & -\frac{1}{y^*}\left(1-\frac{1}{r_0 y^*}\right) & -r_0 h^* \\ \alpha_2(1-y^*) & \alpha_2(r_0 y^*-1) & 0 \\ 0 & 0 & \alpha_1 h^* \end{pmatrix}$$

derived from $J_3(E_{+0+})$ by the permutations of the second and third columns, and subsequently the second and third rows. Therefore, the eigenvalues of $J_3(E_{+0+})$ contain those of the Jacobi matrix J_+^A for the native prey-predator system of Model A, and another eigenvalue, $\lambda_A^* := \alpha_1 h^* = \alpha_1\left(r_0 - \frac{1}{y^*}\right) > 0$. Hence, provided that the equilibrium E_+^A is asymptotically stable, the equilibrium E_{+0+} is locally asymptotically stable if $\lambda_A^* < 1$, while it is unstable if $\lambda_A^* > 1$.

The condition for the local stability $\lambda_A^* < 1$ holds if and only if:

$$\frac{1}{y^*} > r_0 - \frac{1}{\alpha_1}. \tag{D.1}$$

$\mathscr{R}_Q^0 > 1$ for the existence of E_+^A, which is equivalent to $\frac{1}{r_0}\left(1+\frac{1}{\alpha_2}\right) < 1$, so that $\alpha_2 > \frac{1}{r_0-1} > \frac{1}{r_0}$, whereas $\alpha_1 > \frac{1}{r_0}$ does not necessarily hold for Model A.

If the right side of (D.1) is non-positive, that is, if $\alpha_1 \leq \frac{1}{r_0}$, the condition (D.1) is satisfied for E_{+0+} with a positive y^* of E_+^A. If $\alpha_1 > \frac{1}{r_0}$, the condition (D.1) becomes equivalent to:

$$\frac{1}{r_0 - 1/\alpha_1} > y^*.$$

Then, for $y^* \in (0,1)$, if $\frac{1}{r_0-1/\alpha_1} \geq 1$, that is, if $\mathscr{R}_0^P \leq 1$, the condition (D.1) is necessarily satisfied.

When $\mathscr{R}_0^P > 1$ with $r_0 > 1$, we have $\frac{1}{r_0-1/\alpha_1} \in (0,1)$. In this case, from the arguments for the existence of E_+^A, we have $\frac{1}{r_0-1/\alpha_1} > y^*$ if and only if:

$$F_2\left(\frac{1}{r_0-1/\alpha_1}\right) > 0,$$

with F_2, that is,

$$F_2\left(\frac{1}{r_0-1/\alpha_1}\right) = \alpha_2 r_0\left(\frac{1}{r_0-1/\alpha_1} - \frac{1}{r_0}\right) - g\left(\frac{1}{r_0-1/\alpha_1}\right) = \frac{\alpha_2}{\alpha_1}\left(r_0 - \frac{1}{\alpha_1}\right) - g\left(\frac{1}{r_0-1/\alpha_1}\right) > 0, \tag{D.2}$$

where we used the equality $g\left(\frac{1}{x}\right) = \frac{1}{x}g(x)$ for $x > 0$.

When $\mathscr{R}_0^P > 1$ with $r_0 > 1$, the condition (D.1) holds if and only if the condition (D.2) is satisfied. Since $g\left(\frac{1}{r_0 - 1/\alpha_1}\right) < 1$ for $\frac{1}{r_0-1/\alpha_1} \in (0, 1)$ from the nature of the function g defined by (B.1), we find that the condition (D.2) necessarily holds if:

$$\frac{\alpha_2}{\alpha_1}\left(r_0 - \frac{1}{\alpha_1}\right) \geq 1,$$

that is, $\alpha_1 \leq \frac{1+\alpha_2}{r_0}$.

For $\mathscr{R}_Q^0 > 1$ with $r_0 > 1$, we have $\frac{1+\alpha_2}{r_0} < \alpha_2$. Thus:

$$\left(\frac{1}{r_0 - 1}, \frac{1+\alpha_2}{r_0}\right] \subset \left(\frac{1}{r_0 - 1}, \alpha_2\right].$$

On the other hand, when $\frac{\alpha_2}{\alpha_1} \leq 1$, we have $F_2\left(\frac{1}{r_0-1/\alpha_1}\right) < 0$ from (D.2), because $g\left(r_0 - \frac{1}{\alpha_1}\right) > 1$ for $\mathscr{R}_Q^0 > 1$ with $r_0 > 1$, that is, for $\frac{1}{r_0-1/\alpha_1} \in (0, 1)$, and $g(x) > 1$ for $x > 1$. This indicates that $\frac{1}{r_0-1/\alpha_1} < y^*$ when $\alpha_1 \geq \alpha_2$. Subsequently, we obtain the following result on the instability of E_+^A:

When $\alpha_1 > \frac{1+\alpha_2}{r_0}$, the condition $\frac{1}{r_0-1/\alpha_1} > y^*$ is equivalent to $F_2\left(\frac{1}{r_0-1/\alpha_1}\right) > 0$.

With these conditions obtained, we have the proof for Theorem 4.

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