Journal of Mathematical Biology (2025) 91:61
https://doi.org/10.1007/s00285-025-02288-9

Mathematical Biology

Studying the role of phenotypic change in biological invasion success through mathematical modeling

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Received: 29 December 2024 / Revised: 25 August 2025 / Accepted: 13 September 2025

Abstract

When an exotic species is introduced outside its natural range, new interspecific interactions with native species may arise. These interactions can induce phenotypic changes, which may originate from phenotypic plasticity or adaptive processes. Phenotypic change may play an important role in biological invasions, either by promoting or by preventing its success. In this work, a mathematical modeling approach is used to study a native predator-prey system exposed to an exotic species that predates on the native species and that also competes by interference with the native predator. This proposed approach allows to describe the eco-evolutionary dynamics involving the inducible defense of the prey and the inducible offense of both predators. The model is represented by a system of ordinary differential equations (ODEs), analyzed using advanced analytical and numerical methods. Specifically, we applied the qualitative theory of ODEs and developed numerical algorithms for parameter sweeps. Parameter values for the numerical experiments were based on the American mink, one of the most harmful invasive species in Europe and South America. The results show that the role of phenotypic change in invasion success depends on three components: the efficiency of the new trait values, the associated costs, and the speed of trait change. The specific conditions that lead to an unsuccessful invasion are: the prey's defense efficiency against the exotic predator is higher than its defense efficiency against the native predator. The cost imposed by the exotic predator is greater than the cost imposed by the native predator. Lastly, the speed of phenotypic change is faster in the native predator than in the exotic predator.

Keywords Eco-coevolutionary dynamics · Phenotypic change · Inducible defense · Inducible offense · Ordinary differential equations

Mathematics Subject Classification Primary: 92D25 · 92B05 Secondary: 92D40 · 37N25 · 65L07

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1 Introduction

Invasive exotic species are one of the main direct drivers of biodiversity loss worldwide (IPBES et al. 2019). Unfortunately, approximately 200 new exotic species are recorded annually (Roy et al. 2023). Many of these species are classified as threats only after their negative impacts have been identified (Hulme 2009; Simberloff et al. 2013; Early et al. 2016). When an exotic species is introduced outside its natural range, new interspecific interactions with native species may arise. For instance, the exotic species may compete with native species for resources (Catford et al. 2018; Byers 2000), act as a potential predator (Blackburn et al. 2004; Schuettler et al. 2008), or even become harmful prey for native predators (Sanches et al. 2012; Castorani and Hovel 2015). When an exotic species simultaneously assumes the roles of competitor and predator, increased damage to native species is likely to occur, and the negative impacts of these types of invasive species on ecosystems and biodiversity are of major concern (Salo et al. 2007; Doherty et al. 2016; Anton et al. 2020; Taillie et al. 2021).

New interspecific interactions can induce phenotypic changes, which may results from phenotypic plasticity or adaptive processes (Agrawal 2007; Hendry 2017; Gutiérrez et al. 2022). In fact, evolutionary changes have been documented in the context of biological invasions on very short timescales, sometimes less than a decade (Whitney and Gabler 2008; Ruland and Jeschke 2020). These changes play an important role in regulating population dynamics over ecological timescales (Yoshida et al. 2003; Hairston Jr et al. 2005; DeLong et al. 2016; Bell 2017; Yamamichi and Letten 2021). Therefore, studying population trends and the dynamics of relevant phenotypic traits could help determine when or under what conditions an exotic species becomes invasive, *i.e.*, when the invasion is successful. Information from this eco-evolutionary framework may help to improve predictions of potential damage resulting from invasions.

It is not entirely clear to what extent phenotypic changes can favor the success of an invasion (Habit et al. 2015; Rudman et al. 2017). For instance, in a native predator-prey system exposed to an exotic predator, the prey may undergo a phenotypic change related to the defense against both predators, *i.e.*, inducible defense (Becks et al. 2010; Agrawal et al. 2012). Similarly, the native predator and the exotic predator may undergo a phenotypic change related to the offense against the prey, *i.e.*, inducible offense (Mougi and Iwasa 2011; Tien and Ellner 2012). The result of this eco-coevolutionary dynamic may depend on the efficiency of the phenotypic change. For instance, the efficiency of the native prey against the native predator could be greater than its efficiency against the exotic predator, contributing to the success of the invasion (Strauss et al. 2006; Ehlman et al. 2019). Therefore, the efficiency of the phenotypic change in the prey against its predators influences the outcome of the biological invasion.

In addition, there may be interference competition between the two predators, particularly in their strategies for attacking the prey (van Riel et al. 2007). For example, the exotic (or native) predator may undergo a phenotypic change that enhances its offensive capabilities against the native prey. This change could not only improve its hunting efficiency but also alter its competitive interactions with the native (or exotic) predator. As a result, interference competition could intensify, with one predator's strategies potentially disrupting or inhibiting the other predator's access to the shared prey resource (Song et al. 2021). However, this competition could lead to differential benefits from these phenotypic changes, that is, the efficiency of the phenotypic change may be greater in one predator than in the other (Amarasekare 2002).

Although these phenotypic changes may enhance the organism's offensive or defensive capabilities, a change in the relevant trait may come at an increased cost. The expression of new phenotypic traits, whether due to adaptive responses or other mechanisms such as phenotypic plasticity, can require significant energy, potentially impacting other vital functions of the organism (DeWitt et al. 1998; Roff et al. 2002; Benard and Fordyce 2003). For instance, an improvement in defense against predators or in offense against prey may lead to decreased reproduction or increased mortality (Van Buskirk 2000; Relyea 2001). These associated costs may limit the benefits of phenotypic change, thereby limiting the success of biological invasions (Blossey and Notzold 1995; Sakai et al. 2001; Lee 2002).

Finally, the speed of phenotypic change may differ significantly between native and exotic species. If the native prey can improve its defenses faster than the predator can improve its offense, the native prey may be better able to avoid predation, resulting in a reduction in predation pressure. Conversely, if the exotic predator can improve its offensive traits more quickly than the improvement of the prey defensive traits, the exotic predator may be more successful when preying. Therefore, the success of an invasion may be significantly influenced by the speed at which phenotypic changes occur (Agrawal 2007; Ruland and Jeschke 2020).

Mathematical models are a powerful tool for studying the complex feedback mechanisms of eco-evolutionary dynamics (Mougi 2012a; Cortez 2015; Van Velzen and Gaedke 2017). These models incorporate the mean value of a phenotypic trait distribution into key parameters such as birth rate, attack rate, and mortality rate, allowing for feedbacks between traits and demographic parameters that change over time. A common approach is to assume that the rate of change of the mean trait is proportional to the change in the per capita growth rate with respect to the mean trait (the fitness gradient) (Abrams et al. 1993; DeLong et al. 2016). Consequently, phenotypic change has the potential to modify the parameter space, leading to changes in dynamic patterns.

In this study, we use a mathematical model to explore how differences between native and exotic species in efficiency, associated costs, and speed of trait change may influence the success of an exotic predator invasion in a native predator-prey system. The exotic predator preys on native species while also competing through interference with a native predator. The study uses parameter values from the literature, and focuses specifically on the American mink (*Neovison vison*), an invasive predator known to cause significant damage to native communities (Anderson et al. 2006; Schuettler et al. 2008). Understanding the impact of phenotypic change on population dynamics is crucial for predicting the factors that contribute to the success of a biological invasion and, consequently, in species conservation and management.

2 The model

Based on a previous work Rivera-Estay et al. (2024), we formulated a mathematical model to describe the dynamics of a native predator-prey system exposed to an exotic predator, where the exotic predator consumes native prey and simultaneously competes by interference with the native predator. As a result of these interactions, the prey and predator can change their defense and offense, respectively (Miner et al. 2005; Kishida et al. 2009, 2010; McGhee et al. 2013). Specifically, inducible offenses are changes in predator traits that occur in response to the presence of prey, allowing for more effective hunting. Similarly, inducible defenses are changes in the prey's traits triggered by the risk of predation that help it avoid being consumed (Mougi et al. 2011). This modeling approach considers a trait for each species, representing inducible defense in the prey species and inducible offense in predator species, which we will simply refer to as defense and offense, respectively. As the prey invests more in defense, both predators need to invest more in offense to maximize their consumption. Conversely, as the predators invest more in offense, the prey must invest more in defense to minimize consumption (Mougi and Iwasa 2011; Tien and Ellner 2012; Cortez 2015). Furthermore, since both predators interact through interference competition, the predator that invests more in offense becomes a better competitor. Based on this, it is possible to define some model parameters as functions of the species' traits.

The following system with positives variables and parameters is considered:

$$\begin{cases} \dfrac{dX}{dt} = X\left[r(u)\left(1-\dfrac{X}{K}\right) - d_1(u,v)Y - d_2(u,w)Z\right], \\ \dfrac{dY}{dt} = Y\left[p\cdot d_1(u,v)X - b_1(v,w)Z - q(v)\right], \\ \dfrac{dZ}{dt} = Z\left[s(w)\left(1-\dfrac{Z}{n\cdot d_2(u,w)X+c}\right) - b_2(w,v)Y\right], \end{cases} \tag{1}$$

where densities of the native prey, the native predator and the exotic predator are denoted by $X = X(t)$, $Y = Y(t)$ and $Z = Z(t)$, respectively. The phenotypic trait of prey, native predator and exotic predator are denoted by u, v and w, respectively. Also, $r(u)$, $q(v)$, $s(w)$, $d_1(u, v)$, $d_2(u, w)$, $b_1(v, w)$, $b_2(w, v)$ are functions that explicitly depend on the traits (see Figure 1), and are defined in sections 2.1, 2.2 and 2.3 and are defined in subsections and 6. The parameters K, n, c, p are positive (see Table 1).

The prey population follows a logistic growth with intrinsic growth rate $r(u)$ and carrying capacity K. The prey population decreases with encounters with both predators, where $d_1(u, v)$ and $d_2(u, w)$ are the attack rates of native and exotic predator, respectively.

The native predator population follows an exponential growth that is dependent on the consumption of prey and a conversion coefficient p. Its growth decreases due to intrinsic mortality at a rate q and encounters with the exotic predator through interference competition, where $b_1(v, w)$ is the competition coefficient. This coefficient represents the negative effect of the exotic predator on the native predator (and $b_2(w, v)$ represents the reciprocal effect).

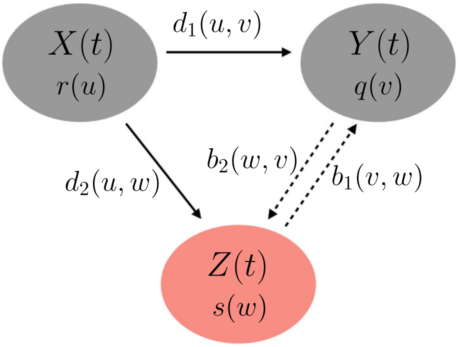

Fig. 1 Interactions diagram between native and exotic populations. Solid arrows denote the decrease in prey population due to predation, where $d_1(u, v)$ and $d_2(u, w)$ are the attack rates of the native and exotic predators, respectively. Dashed arrows indicate the population decrease due to competition between both native and exotic predator populations, where $b_1(v, w)$ and $b_2(w, v)$ are competition coefficient. Intrinsic parameters $r(u)$, $q(v)$ and $s(w)$ depend on the main trait value

The exotic predator population follows a modified logistic growth, in which its carrying capacity depends on the consumption of prey, where n is an enlarger parameter and c is the minimum carrying capacity of exotic predator population guaranteed by the alternative food. This approach represents a generalist exotic predator whose carrying capacity depends not only on the native prey but also on alternative food resources. This modeling choice ensures the predator's persistence even in scenarios where the native prey, explicitly included in the equation system, goes extinct (Rivera-Estay et al. 2024). In other words, the exotic predator can survive in the absence of this prey by consuming other native prey species that are not explicitly included in the model. This assumption is ecologically supported, as empirical studies have documented that trophic generalism is a common characteristic among successful invasive predators, facilitating their establishment and persistence across different ecosystems (Salo et al. 2007; Mooney and Cleland 2001).

2.1 Attack rates

According to Mougi et al. (2011); Mougi (2012a); Van Velzen and Gaedke (2017), the attack rate functions should reach the maximum when the offense is sufficiently higher than the defense and approach zero when the defense is sufficiently higher than the offense. Therefore, a sigmoidal function of the difference between two traits is an appropriate choice.

The attack rate function of the native predator d_1, which depends on defense u and offense v, is defined as follows:

$$d_1(u, v) = \frac{\delta_1}{1 + \exp(\theta_1(u - v))}, \tag{2}$$

and the attack rate function of the exotic predator d_2, which depends on defense u and offense w, is defined as follows:

Table 1 Parameters values to the simulation of the model (1)

Par.	Ecological meaning	Values	Unit	Ref.
r_0	Maximum intrinsic growth rate of the native prey	1.2	$year^{-1}$	(Tanner 1975)
K	Carrying capacity of native prey	100	$indiv.$	
p	Conversion coefficient: food intake to new native predator	$[0.025, 0.05]$	unitless	(Schuettler et al. 2008)
q_0	Maximum mortality rate of the native predator	$[0.01, 0.25]$	$year^{-1}$	(Caudera et al. 2021)
s_0	Maximum intrinsic growth rate of the exotic predator	0.2	$year^{-1}$	Tanner (1975)
c	Carrying capacity minimum of exotic predator guaranteed by the alternative food	5	$indiv.$	(Anderson et al. 2006)
n	Enlarger of carrying capacity	10	$year \cdot indiv.$	(Anderson et al. 2006)
δ_1	Maximum attack rate of the native predator	$]0, 1]$	$indiv.^{-1} year^{-1}$	(Schuettler et al. 2008)
δ_2	Maximum attack rate of the exotic predator	$]0, 1]$	$indiv.^{-1} year^{-1}$	(Schuettler et al. 2008)
θ_1	Efficiency of phenotypic change in prey to enhance its defense against a native predator	$(0, 6]$	unitless	
θ_2	Efficiency of phenotypic change in prey to enhance its defense against an exotic predator	$(0, 6]$	unitless	
β	Maximum coefficient competition	$[0.001, 0.02]$	$indiv.^{-1} year^{-1}$	(Bonesi et al. 2004; Schuettler et al. 2008)
σ_1	Efficiency of phenotypic change in the native predator to become a better competitor	$(0, 6]$	unitless	
σ_2	Efficiency of phenotypic change in the exotic predator to become a better competitor	$(0, 6]$	unitless	
c_S	Costs associated with phenotypic change $S \in \{X, Y, Z\}$	$(0, 2]$	unitless	
G_S	Speeds of phenotypic change, $S \in \{X, Y, Z\}$	$(0, 1]$	unitless	(Mougi 2012a; Van Velzen and Gaedke 2017)

$$d_2(u, w) = \frac{\delta_2}{1 + \exp(\theta_2(u - w))}, \tag{3}$$

where δ_1 and δ_2 are the maximum attack rates of the native and exotic predators, respectively, which are reached when $v \gg u$ and $w \gg u$, respectively. Conversely, when defense exceeds offense, *i.e.*, $u \gg v$ or $u \gg w$, the capture rate approaches zero. The parameters θ_1 and θ_2 represent the efficiency of prey defense against the native and exotic predators, respectively, and serve as the shape parameters of the functions $d_1(u, v)$ and $d_2(u, w)$, controlling the steepness of the transition between high and low capture rates.

Remark 1 When defense is greater than offense ($u > v$ and $u > w$) and $\delta_1 = \delta_2$, if $\theta_1 > \theta_2$, the efficiency of prey defense against the native predator is greater than against the exotic predator. Conversely, when $\theta_1 < \theta_2$, the efficiency of prey defense against the native predator is lower than against the exotic predator.

Remark 2 The choice of a sigmoidal function is motivated by both biological and mathematical considerations. Biologically, predation success is expected to transition smoothly from low to high as the offensive trait surpasses the defensive trait, rather than changing abruptly. Mathematically, the sigmoidal function ($d(\mu, \nu) = \delta/\left[1 + \exp\left(\theta(\mu - \nu)\right)\right]$, where μ denotes defense and ν denotes offense) is a common choice in ecological modeling because it provides a continuous and differentiable approximation of threshold-like processes, capturing asymptotic behaviors at both extremes ($\nu \gg \mu$ and $\mu \gg \nu$). Additionally, the parameter θ allows flexibility in adjusting the steepness of the transition, which is key for modeling varying levels of defensive efficiency across species.

2.2 Interference competition

The competition coefficient captures the same idea as in the previous paragraph, if the trait value of the native predator v is much greater than the trait value of the exotic predator w ($v \gg w$), then the native predator is a better competitor than the exotic predator. Conversely, when $v \ll w$, then the exotic predator is better competitor than the native predator. It is defined sigmoidal functions:

$$b_1(v, w) = \frac{\beta}{1 + \exp(\sigma_1(v - w))}, \tag{4}$$

$$b_2(w, v) = \frac{\beta}{1 + \exp(\sigma_2(w - v))}, \tag{5}$$

where the parameter β represents the maximum competition coefficient reached when $v \gg w$ in (4) and $w \gg v$ in (5). Letter σ_i ($i = 1, 2$) is the shape parameter of the function, which determines the steepness of the transition between high and low competition coefficients.

2.3 Trade-off

In general, phenotypic changes are subject to trade-offs (Abrams 2000; Nuismer et al. 2007; Mougi 2012a; Van Velzen and Gaedke 2017). Following this, the model considers that there are costs associated with investing in offense and defense for predators and prey, respectively. Specifically, as native prey invests in defense, its intrinsic growth rate decreases. Similarly, as both predators invest in offense, the mortality rate of the native predator and the intrinsic growth rate of the exotic predator decrease. To capture the effect of this trade-off and ensure the presence of a threshold beyond which the effect is amplified. Specifically, where intrinsic growth decreases more rapidly and mortality increases at an accelerated rate. The following functions are considered:

$$r(u) = r_0 \exp(-c_X u^2/2), \qquad q(v) = q_0 \exp(c_Y v^2/2), \qquad s(w) = s_0 \exp(-c_Z w^2/2),$$

where $r(u)$ and $s(w)$ are decreasing and concave-convex, with inflection points at $\sqrt{1/c_X}$ and $\sqrt{1/c_Z}$, and $q(v)$ is increasing and convex. The parameters r_0, q_0 and s_0 represent the maximum intrinsic growth rate of the prey, the minimum mortality rate of the native predator, and the maximum intrinsic growth rate of the exotic predator, respectively. These values are all achieved when $u = 0$, $v = 0$, and $w = 0$, respectively. However, these maximum values are never reached because u, v and w only approach zero. The parameter c_X denotes the associated cost of inducible defense, while c_Y and c_Z represent the associated cost of inducible offense. These parameters determine the rate at which $r(u)$, $q(v)$, and $s(w)$ decrease or increase with increasing u, v, and w.

Remark 3 Note that, $r'(u)/r(u) = -c_X u$ implies that the relative rate of change of the function $r(u)$ is proportional to the mean trait u with the parameter c_X representing the cost associated with changes in u. This means that we are measuring how $r(u)$ changes with respect to u, not in absolute terms, but relative to the current value of $r(u)$. Similarly, for the functions $q(v)$ and $s(w)$, their relative rates of change are proportional to the mean traits v and w, respectively.

2.4 Evolutionary dynamics

The evolutionary dynamics are incorporated as phenotypic change, meaning that the mean of a certain distribution of traits can change over time. There is a feedback between ecological and evolutionary dynamics, such that they influence each other. In fact, evolutionary changes have been observed on ecological timescales, making it reasonable to consider both ecological and evolutionary dynamics on the same timescale (Prentis et al. 2008). The rate of trait change is proportional to the fitness gradient (Abrams 2001). The fitness gradient represents the instantaneous response of fitness to changes in the trait, *i.e.*, the partial derivative of the fitness function with respect to the trait, evaluated at the current trait value and ecological state (Abrams et al. 1993). This quantity is also commonly referred to as the selection gradient in evolutionary biology (Lande and Arnold 1983; Dieckmann and Law 1996). The fitness functions of prey and predators are defined as the net per capita growth rates $W_S =$

$1/S{\cdot}dS/dt$ (the logarithmic derivative for $S \in \{X, Y, Z\}$). When computing the partial derivative $\partial W_X/\partial u$ (and analogously for v and w), the ecological variables (X, Y, Z) are treated as constants only within the differentiation operator, thereby capturing the direct effect of the trait on fitness. Immediately after, the resulting expression is evaluated at the instantaneous ecological state $(X(t), Y(t), Z(t))$, which evolves according to the ecological dynamics. Therefore, the selection gradients remain time-dependent and reflect the fully coupled nature of ecological and evolutionary dynamics.

The rate of adaptive change for each trait is:

$$\begin{cases} \dfrac{du}{dt} = G_X \dfrac{\partial W_X}{\partial u} \exp(-\epsilon/u), \\ \dfrac{dv}{dt} = G_Y \dfrac{\partial W_Y}{\partial v} \exp(-\epsilon/v), \\ \dfrac{dw}{dt} = G_Z \dfrac{\partial W_Z}{\partial w} \exp(-\epsilon/w), \end{cases} \tag{6}$$

where the selection gradients $\partial W_X/\partial u$, $\partial W_Y/\partial v$, and $\partial W_Z/\partial w$ are evaluated at $u(t)$, $v(t)$, $w(t)$, $X(t)$, $Y(t)$, and $Z(t)$, ensuring that they incorporate the instantaneous ecological conditions and thus the eco-evolutionary coupling.

The parameters G_X, G_Y and G_Z are positive and represent the speed of phenotipyc change of each species trait (Lee 2002; Prentis et al. 2008; Kishida et al. 2010). In line with previous modeling studies (Mougi and Iwasa 2011; Cortez and Weitz 2014; Mougi 2012b; Van Velzen and Gaedke 2017), G_X, G_Y and G_Z are kept constant within each simulation run. The exponential functions in (6) are boundary functions restricting the dynamics of u, v and w to positive values by decreasing the speed of phenotipyc change when u, v or w very closely approach zero ($\epsilon = 0.001$).

When the fitness gradient is positive, the rate of change of the trait is positive. Conversely, if the fitness gradient is negative, the rate of change of the trait is negative (Abrams et al. 1993; Abrams 2001). In addition, when there is no phenotypic change, $G_S = 0$ for $S \in \{X, Y, Z\}$, meaning that the traits remain fixed over time according to the initial conditions considered. Thus, the model proposed and analyzed in Rivera-Estay et al. (2024) is recovered.

2.5 Model Analysis

The model is represented by the coupled system of ordinary differential equations defined by equations (1) and (6). First, the main properties of the model, such as positivity and boundedness of solutions, are studied using analytical mathematical tools. Then, the model representing the native system without the exotic predator ($Z = 0$) is analyzed using both analytical and numerical tools. Finally, the native system with the exotic predator is studied using numerical methods, specifically through a computational implementation that allows studying the model's dynamics under different parameter spaces via numerical integration routines.

Regarding the computational implementation, a maximum time interval of $\left[0, 10^4\right]$ is considered, which is sufficient for most simulations to reach convergence. It is important to clarify that convergence here refers strictly to the numerical trajectories of the full eco-evolutionary system reaching a steady state within the simulation window, and does not imply a quasi-equilibrium assumption. In some cases, particularly when the evolutionary speed parameter G_S (with $S \in \{X, Y, Z\}$) is small, traits evolve slowly and may not reach their asymptotic values within the fixed time horizon, even though the ecological variables (*i.e.*, population densities) may have already stabilized.

To ensure that eco-evolutionary dynamics remain fully coupled, the selection gradients are updated at each integration step using the current values of all ecological and trait variables, so that no variables are held fixed during the simulation.

The parameter values of the model were derived from bibliographic sources and are shown in Table 1. These values correspond to the example of the American mink (*Neovison vison*), which is responsible for declines in native prey worldwide, including birds (Craik 1997) and mammals (Barreto et al. 1998). This invasive species also imposes serious negative impacts on native competitors such as *Lutra lutra* in Europe and *Lontra provocax* in South America (Bonesi et al. 2004; Schuettler et al. 2008).

Regarding the model parametrization, some parameter values are fixed (see Table 1). For instance, the maximum intrinsic growth rate of the American mink (s_0) is set as an approximate average based on values reported by Tanner (1975). For the carrying capacity, the parameters n and c were chosen such that the resulting values fall within the empirical range of mink densities observed on Navarino Island ($0.79 - 1.32\ individuals/km^2$; Anderson et al. (2006)), under plausible prey densities. For the maximum intrinsic growth rate of the prey r_0, we assumed a value representative of a short-lived, high-fecundity species. This choice is consistent with the demographic traits commonly observed in prey species subject to strong predation pressure and rapid population turnover. Additionally, the prey's carrying capacity was fixed at 100, a plausible value that allows for population persistence and realistic predator-prey dynamics, without introducing unnecessary complexity into the system. The native predator's mortality rate (q_0) was supported by Schuettler et al. (2008), where empirical calibration in similar species indicates a low mortality rate. The conversion coefficient p was derived from the typical energy efficiency observed in aquatic mammals, aligning with the species' biological and energetic requirements (Caudera et al. 2021).

To assess the extent of predation and competition pressures exerted by the exotic predator, the parameters δ_i, β (with $i = 1, 2$) were used for parameter scanning. Also, to evaluate the efficiency of phenotypic change, the parameters θ_i, σ_i (with $i = 1, 2$) were considered. Finally, to evaluate the associated cost and the speed of phenotypic change, the parameters c_S and G_S were considered, respectively (with $S \in \{X, Y, Z\}$). The numerical study was conducted through a two-parameter sweep, where in some cases it was necessary to optimize the codes to improve memory usage and simulation time (see the Appendix A for the algorithms).

In all simulations, initial conditions were kept constant to isolate the effects of parameter variation. While this approach facilitates comparison across scenarios, we acknowledge that system dynamics may depend on initial conditions, which is an aspect that could be explored in future studies.

3 Results

3.1 Model properties

The model is represented by a system of nonlinear ordinary differential equations, defined by equations (1) and (6). The following theorem ensures the well-posedness of the model by establishing the existence, uniqueness, non-negativity, and boundedness of the solutions in the set:

$$\Omega = \Big\{(X, Y, Z, u, v, w) \in \mathbb{R}^6 / X, Y, Z \geq 0 \text{ and } u, v, w > 0\Big\}.$$

Theorem 1 *The system represented by equations (1) and (6) with any initial condition in the set* Ω *admits a unique and non-negative solution.*

Proof Note that the eco-evolutionary dynamics are modeled by a set of continuously differentiable functions in Ω. Therefore, the classical theory of ordinary differential equations assures that the system represented by equations (1) and (6) admits a unique solution for any associated initial condition in Ω.

Now, consider the system (1) with initial conditions $X(0) \geq 0$, $Y(0) \geq 0$, $Z(0) \geq 0$, $u(0) > 0$, $v(0) > 0$ and $w(0) > 0$. The goal is to show that $X(t) \geq 0$, $Y(t) \geq 0$, $Z(t) \geq 0$, $u(t) > 0$, $v(t) > 0$ and $w(t) > 0$ for all $t \geq 0$.

From the first equation of (1), we have

$$\frac{dX}{dt} = \left[r(u)\left(1 - \frac{X}{K}\right) - d_1(u, v)Y - d_2(v, w)Z\right] \cdot X = W_X(X, Y, Z, u, v, w) \cdot X.$$

We consider the differential equation

$$\frac{dX}{dt} - W_X(t) \cdot X(t) = 0,$$

and solve it by multiplying both sides by the integrating factor $\exp\left(-\int_0^t W_X(\omega)d\omega\right)$, obtaining

$$\left[\frac{dX}{dt} - W_X(t) \cdot X(t)\right] \cdot \exp\left(-\int_0^t W_X(\omega)d\omega\right) = 0.$$

Observe that the left-hand side is the derivative of a product

$$\frac{d}{dt}\left[X(t) \cdot \exp\left(-\int_0^t W_X(\omega)d\omega\right)\right].$$

Indeed, applying the product rule yields:

$$\begin{aligned}\frac{d}{dt}\left[X(t)\cdot\exp\left(-\int_0^t W_X(\omega)d\omega\right)\right] &= \frac{dX}{dt}\cdot\exp\left(-\int_0^t W_X(\omega)d\omega\right)\\ &\quad - X(t)\cdot W_X(t)\cdot\exp\left(-\int_0^t W_X(\omega)d\omega\right),\\ &= \left[\frac{dX}{dt} - W_X(t)\cdot X(t)\right]\cdot\exp\left(-\int_0^t W_X(\omega)d\omega\right).\end{aligned}$$

Therefore,

$$\frac{d}{dt}\left[X(t)\cdot\exp\left(-\int_0^t W_X(\omega)d\omega\right)\right] = 0,$$

which implies that the quantity inside the derivative is constant over time,

$$X(t)\cdot\exp\left(-\int_0^t W_X(\omega)d\omega\right) = X(0).$$

Solving for $X(t)$, we obtain:

$$X(t) = X(0)\cdot\exp\left(\int_0^t W_X(\omega)d\omega\right).$$

Since $X(0)\geq 0$ and the exponential function is strictly non-negative, it follows that $X(t)\geq 0$ for all $t\geq 0$.

The same integrating factor technique can be applied to the second and third equations of (1), which yield:

$$Y(t) = Y(0)\exp\left(\int_0^t W_Y(\omega)d\omega\right),\quad \text{and}\quad Z(t) = Z(0)\exp\left(\int_0^t W_Z(\omega)d\omega\right),$$

where $dY/dt = W_Y\cdot Y$ and $dZ/dt = W_Z\cdot Z$. Thus, $Y(t)\geq 0$ and $Z(t)\geq 0$ for all t whenever $Y(0)\geq 0$ and $Z(0)\geq 0$, respectively.

Now, from the equations (6), we have

$$\begin{aligned}\frac{du}{dt} &= G_X\left\{-c_X r_0\exp\left(-c_X u^2/2\right)\left(1-\frac{X}{K}\right)u + \frac{\delta_1\theta_1\exp\left(\theta_1(u-v)\right)Y}{\left[1+\exp\left(\theta_1(u-v)\right)\right]^2}\right.\\ &\qquad\left.+\frac{\delta_2\theta_2\exp\left(\theta_2(u-w)\right)Z}{\left[1+\exp\left(\theta_2(u-w)\right)\right]^2}\right\}\exp(-\epsilon/u),\\ &\geq -G_X c_X r_0\exp\left(-c_X u^2/2\right)\left(1-\frac{X}{K}\right)u\exp(-\epsilon/u),\\ &\geq -G_X c_X r_0\exp\left(-c_X u^2/2\right)\alpha_X u\exp(-\epsilon/u),\end{aligned}$$

where

$$\alpha_X = \max_{0 \le X < K} \left\{ \left(1 - \frac{X}{K} \right) \right\}.$$

By adding and subtracting the same quantity, we obtain

$$\begin{aligned}\frac{du}{dt} &\ge -G_X c_X r_0 \exp\left(-c_X u^2/2\right) \alpha_X u + G_X c_X r_0 \exp\left(-c_X u^2/2\right) \alpha_X u \\ &\quad -G_X c_X r_0 \exp\left(-c_X u^2/2\right) \alpha_X u \exp(-\epsilon/u), \\ &= -G_X c_X r_0 \exp\left(-c_X u^2/2\right) \alpha_X u + G_X c_X r_0 \exp\left(-c_X u^2/2\right) \alpha_X u(1 - \exp(-\epsilon/u)).\end{aligned}$$

Note that the function $f(u) = u(1 - \exp(-\epsilon/u))$ is strictly positive and continuous for all $u \neq 0$. Therefore,

$$\frac{du}{dt} > -G_X c_X r_0 \exp\left(-c_X u^2/2\right) \alpha_X u.$$

Similarly, from the equations for $v(t)$ and $w(t)$, we obtain

$$\begin{aligned}\frac{dv}{dt} &= G_Y \left\{ -c_Y q_0 \exp\left(c_Y v^2/2\right) v + \frac{p\delta_1\theta_1 \exp\left(\theta_1(u-v)\right) X}{\left[1 + \exp\left(\theta_1(u-v)\right)\right]^2} \right. \\ &\quad \left. + \frac{\beta\sigma_1 \exp\left(\sigma_1(v-w)\right) Z}{\left[1 + \exp\left(\sigma_1(v-w)\right)\right]^2} \right\} \exp(-\epsilon/v), \\ &\ge -G_Y c_Y q_0 \exp\left(c_Y v^2/2\right) v \exp(-\varepsilon/v), \\ &= -G_Y c_Y q_0 \exp\left(c_Y v^2/2\right) v + G_Y c_Y q_0 \exp\left(c_Y v^2/2\right) v \\ &\quad -G_Y c_Y q_0 \exp\left(c_Y v^2/2\right) v \exp(-\varepsilon/v), \\ &= -G_Y c_Y q_0 \exp\left(c_Y v^2/2\right) v + G_Y c_Y q_0 \exp\left(c_Y v^2/2\right) v(1 - \exp(-\epsilon/v)), \\ &> -G_Y c_Y q_0 \exp\left(c_Y v^2/2\right) v.\end{aligned}$$

and

$$\begin{aligned}\frac{dw}{dt} &= G_Z \left\{ -c_Z s_0 \exp\left(-c_Z w^2/2\right) \left(1 - \frac{Z}{\frac{n\delta_2 X}{1+\exp(\theta_2(u-w))} + c} \right) w + \frac{\beta\sigma_2 \exp\left(\sigma_2(w-v)\right) Y}{\left[1 + \exp\left(\sigma_2(w-v)\right)\right]^2} \right. \\ &\quad \left. + \frac{s_0 n\delta_2\theta_2 \exp\left(-c_Z w^2/2\right) \exp\left(\theta_2(u-w)\right) XZ}{\left[1 + \exp\left(\theta_2(u-w)\right)\right]^2 \left(\frac{n\delta_2 X}{1+\exp(\theta_2(u-w))} + c \right)^2} \right\} \exp(-\epsilon/w), \\ &\ge G_Z \left\{ -c_Z s_0 \exp\left(-c_Z w^2/2\right) \left(1 - \frac{Z}{n\delta_2 X + c} \right) w \right\} \exp(-\epsilon/w),\end{aligned}$$

$$\begin{aligned}
&\geq -G_Z c_Z s_0 \exp\left(-c_Z w^2/2\right) \alpha_Z w \exp(-\epsilon/w), \\
&= -G_Z c_Z s_0 \exp\left(-c_Z w^2/2\right) \alpha_Z w + G_Z c_Z s_0 \exp\left(-c_Z w^2/2\right) \alpha_Z w \\
&\quad -G_Z c_Z s_0 \exp\left(-c_Z w^2/2\right) \alpha_Z w \exp(-\epsilon/w), \\
&= -G_Z c_Z s_0 \exp\left(-c_Z w^2/2\right) \alpha_Z w + G_Z c_Z s_0 \exp\left(-c_Z w^2/2\right) \alpha_Z w (1 - \exp(-\epsilon/w)), \\
&> -G_Z c_Z s_0 \exp\left(-c_Z w^2/2\right) \alpha_Z w,
\end{aligned}$$

where

$$\alpha_Z = \max_{0 \leq Z < n\delta_2 K + c} \left\{ \left(1 - \frac{Z}{n\delta_2 X + c} \right) \right\}.$$

Therefore, for each trait variable $\varrho(t) \in \{u(t), v(t), w(t)\}$ we have shown that it satisfies an inequality of the form

$$\frac{d\varrho}{dt} > -H_\varrho(\varrho) \cdot \varrho,$$

where the function $H_\varrho(\varrho)$ is strictly positive and continuous for all $\varrho \in \{u, v, w\}$. The form of H_ϱ may vary including terms such as $\exp\left(c_S \varrho^2/2\right)$ or $\exp\left(-c_S \varrho^2/2\right)$ with $S = \{X, Y, Z\}$, but these differences do not affect the argument that follows.

Now, consider the auxiliary function $\phi(t)$ defined by the differential equation

$$\frac{d\phi}{dt} = -H_\varrho(\phi)\phi, \quad \phi(0) = \varrho(0) > 0.$$

Applying the method of separation of variables, we obtain

$$\int_{\phi(t)}^{\phi(0)} \frac{1}{H_\varrho(\omega)\omega} d\omega = t.$$

The integrand is strictly positive and continuous on the interval $]0, \phi(0)]$. Therefore, the associated improper integral

$$\int_0^{\phi(0)} \frac{1}{H_\varrho(\omega)\,\omega}\, d\omega$$

diverges to $+\infty$ as the lower limit approaches 0. In the separation-of-variables formula, the value of this integral from $\phi(t)$ to $\phi(0)$ equals the elapsed time t. If $\phi(t)$ were to reach 0 at some finite time $\hat{t} > 0$, this integral would have to be finite (equal to $\hat{t}$), contradicting its divergence. Therefore, $\phi(t)$ cannot reach zero in finite time and must remain strictly positive for all $t \geq 0$.

Since $\varrho(t)$ satisfies a differential inequality of the same form and with the same initial condition, the comparison principle implies that

$$\varrho(t) > \phi(t) > 0 \quad \text{for all} \quad t \geq 0.$$

In particular, $\varrho(t)$ remains strictly positive for all $t > 0$, provided that $\varrho(0) > 0$. □

By definition, the solutions of a system of differential equations are said to be uniformly bounded if, for every solution $\gamma(t)$, regardless of the initial conditions, there exists a constant $B > 0$ such that

$$\|\gamma(t)\| \leq B \quad \text{for all} \quad t \geq t_0.$$

In contrast, a system is said to be uniformly ultimately bounded if there exist constants $R > 0$ such that, for every $r > 0$, there exists a time $T = T(r, R) > 0$, independent of the initial time t_0, such that

$$\|\gamma(t_0)\| \leq r \Rightarrow \quad \|\gamma(t)\| \leq R \quad \text{for all} \quad t \geq t_0 + T.$$

This means, all trajectories that start within a ball of radius r eventually enter and remain within a ball of radius R, after a finite time T that depends only on the initial size r, not on the initial time t_0 (Khalil and Grizzle 2002).

We deliberately use B and R to distinguish between the constants associated with uniform boundedness and uniform ultimate boundedness, respectively.

In the following theorem, it is proven that the ecological variables (X, Y, and Z) of the system given byequations (1) and (6) are uniformly ultimately bounded.

Theorem 2 *For any solutions of the system defined by equations (1) and (6) with initial condition in Ω:*

(i) The population densities $X(t)$, $Y(t)$, $Z(t)$ are uniformly ultimately bounded.
(ii) The trait $v(t)$ is bounded.
(iii) The traits $u(t)$ and $w(t)$ remain positive and cannot blow up in finite time. In particular, they grow at most linearly in time.

Proof The boundedness of $X(t)$ can be established using the Comparison Theorem for differential inequalities (Birkhoff and Rota 1989). Since $r(u) = r_0 \exp(-c_X u^2/2) < r_0$ for all $u > 0$, we have

$$\begin{aligned}\frac{dX}{dt} &= rX\left(1 - \frac{X}{K}\right) - d_1XY - d_2XZ < r_0X\left(1 - \frac{X}{K}\right) - d_1XY - d_2XZ, \\ &\leq r_0X\left(1 - \frac{X}{K}\right),\end{aligned}$$

so $X(t)$ remains bounded, as the right-hand side corresponds to a logistic growth function with carrying capacity K.

For $X \geq 0$ and $Y \geq 0$, the dynamics of Z satisfy

$$\frac{dZ}{dt} = Z\left[s(w)\left(1 - \frac{Z}{nd_2(u,w)X + c}\right) - b_2(w,v)Y\right].$$

Since the term $-b_2(w,v)Y$ is non-positive, we obtain the upper bound

$$\frac{dZ}{dt} \leq s(w)Z\left(1 - \frac{Z}{nd_2(u,w)X + c}\right),$$

which corresponds to a logistic-type differential inequality. The solution of this inequality is bounded above by the solution of the associated logistic equation. Hence, we deduce that

$$Z(t) \leq nd_2(u,w)X(t) + c \leq n\delta_2 K + c.$$

Therefore

$$\limsup_{t\to\infty}\{Z(t)\} \leq n\delta_2 K + c.$$

Note that,

$$\frac{r_0}{K}(K - X)^2 \geq 0 \Leftrightarrow r_0K - r_0X - \left(r_0X - \frac{r_0}{K}X^2\right) \geq 0 \Leftrightarrow r_0K - r_0X \geq r_0X - \frac{r_0}{K}X^2,$$

similarly,

$$\begin{aligned}\frac{s_0}{n\delta_2K + c}(n\delta_2K + c - Z)^2 \geq 0 &\Leftrightarrow s_0(n\delta_2K + c) - s_0Z - \left(s_0Z - \frac{s_0}{n\delta_2K + c}Z^2\right) \geq 0\\ &\Leftrightarrow s_0(n\delta_2K + c) - s_0Z \geq s_0Z - \frac{s_0}{n\delta_2K + c}Z^2.\end{aligned}$$

Let

$$M(t) = X(t) + \frac{1}{p}Y(t) + Z(t),$$

then

$$\begin{aligned}\frac{dM}{dt} &\leq \left[r(u)X\left(1 - \frac{X}{K}\right) - \delta_1XY\right] + \frac{1}{p}\left(p\delta_1XY - q(v)Y\right) + s(w)Z\left(1 - \frac{Z}{nd_2X + c}\right)\\ &\leq r_0X - \frac{r_0}{K}X + s_0Z - \frac{s_0}{n\delta_2X + c} - \frac{q_0}{p}Y\\ &\leq r_0K - r_0X + s_0(n\delta_2K + c) - s_0Z - \frac{q_0}{p}Y\end{aligned}$$

$$\begin{aligned}&\le r_0K + s_0(n\delta_2K + c) - \left(r_0X - \frac{q_0}{p}Y - s_0Z\right)\\&\le \mathcal{Q} - \eta M,\end{aligned}$$

where

$$\mathcal{Q} = r_0K + s_0\,(n\delta_2K + c)$$

and

$$\eta = \min\left\{r_0, \frac{q_0}{p}, s_0\right\}.$$

Hence,

$$\frac{dM(t)}{dt} + \eta M(t) \le \mathcal{Q}.$$

Applying the Comparison Theorem for differential inequality (Birkhoff and Rota 1989), we have

$$0 \le M(t) \le \frac{\mathcal{Q}[1 - \exp(-\eta(t - t_0))]}{\eta} + M\,(t_0)\exp(-\eta(t - t_0)), \quad \text{for all } t \ge t_0.$$

Let $r > 0$, such that $M(t_0) \le r$, then

$$M(t) \le r\exp(-\eta(t - t_0)) + \frac{\mathcal{Q}}{\eta}.$$

Since $\exp(-\eta(t - t_0))$ decreases to zero as $t \to \infty$, we can choose $R > \mathcal{Q}/\eta$, such that

$$r\exp(-\eta(t - t_0)) + \frac{\mathcal{Q}}{\eta} \le R,$$

which is equivalent to

$$r\exp(-\eta(t - t_0)) \le R - \frac{\mathcal{Q}}{\eta}.$$

Solving for t, we obtain

$$t - t_0 \ge \frac{1}{\eta}\ln\left(\frac{r}{R - \mathcal{Q}/\eta}\right),$$

so it suffices to take

$$T(r, R) = \frac{1}{\eta} \ln \left(\frac{r}{R - Q/\eta} \right).$$

Therefore, for all $t \geq t_0 + T(r, R)$, we have $M(t) \leq R$. This shows that the system is uniformly ultimately bounded, for every $r > 0$, there exists $T = T(r, R) > 0$, independent of t_0, such that if $M(t_0) \leq r$, then $M(t) \leq R$ for all $t \geq t_0 + T$.

Since $X, Y, Z \geq 0$ and $M = X + \frac{1}{p}Y + Z$, it follows that $X(t) \leq M(t)$, $Z(t) \leq M(t)$ and $Y(t) \leq p\,M(t)$ for all $t \geq t_0$. Hence, for all $t \geq t_0 + T(r, R)$,

$$X(t) \leq R, \qquad Y(t) \leq pR, \qquad Z(t) \leq R,$$

which proves that X, Y, Z are uniformly ultimately bounded (with ultimate bounds $R_X = R$, $R_Y = pR$, $R_Z = R$ and entrance time $T(r, R)$).

Next, we derive an upper bound for dv/dt as follows:

$$\begin{aligned}
\frac{dv}{dt} &= G_Y \left\{ -c_Y q_0 \exp\left(c_Y v^2/2\right) v + p d_1(u, v)\theta_1 X \cdot \frac{\exp\left(\theta_1(u - v)\right)}{1 + \exp\left(\theta_1(u - v)\right)} \right. \\
&\quad \left. + b_1(v, w)\sigma_1 Z \cdot \frac{\exp\left(\sigma_1(v - w)\right)}{1 + \exp\left(\sigma_1(v - w)\right)} \right\} \exp(-\epsilon/v), \\
&\leq G_Y \{-c_Y q_0 \exp\left(c_Y v^2/2\right) v + p d_1(u, v)\theta_1 X + b_1(v, w)\sigma_1 Z\} \exp(-\epsilon/v), \\
&\leq G_Y \{-c_Y q_0 \exp\left(c_Y v^2/2\right) v + p\delta_1\theta_1 K + \beta\sigma_1(n\delta_2 K + c)\} \exp(-\epsilon/v), \\
&\leq G_Y \{-c_Y q_0 \exp\left(c_Y v^2/2\right) v + B\} \exp(-\epsilon/v),
\end{aligned}$$

where $B := p\delta_1\theta_1 K + \beta\sigma_1(n\delta_2 K + c)$.

Given that $\exp(-\epsilon/v)$ and $c_Y q_0 \exp\left(c_Y v^2/2\right) v$ are increasing on $v > 0$ and $c_Y q_0 \exp\left(c_Y v^2/2\right) v$ tends to infinity as v increases, there exists $V > 0$ such that for all $v \geq V$, $dv/dt \leq -G_Y \exp(-\epsilon/v) < 0$. Hence every trajectory enters $[0, V]$ in finite time and remains there thereafter, proving that v is bounded.

Now, it has been established that $u(t)$ and $w(t)$ can grow at most linearly as $t \to \infty$.

$$\begin{aligned}
\frac{du}{dt} &= G_X \left\{ -c_X r(u) \left(1 - \frac{X}{K}\right) u + d_1(u, v)\theta_1 Y \cdot \frac{\exp\left(\theta_1(u - v)\right)}{1 + \exp\left(\theta_1(u - v)\right)} \right. \\
&\quad \left. + d_2(u, w)\theta_2 Z \cdot \frac{\exp\left(\theta_2(u - w)\right)}{1 + \exp\left(\theta_2(u - w)\right)} \right\} \exp(-\epsilon/u), \\
&\leq G_X \left\{ -c_X r_0 \exp(-c_X u^2/2) u \left(1 - \frac{X}{K}\right) \right. \\
&\quad + \delta_1\theta_1 Y + \delta_2\theta_2 Z \} \exp(-\epsilon/u), \\
&\leq G_X \{\delta_1\theta_1 Y + \delta_2\theta_2 Z\} \exp(-\epsilon/u), \\
&\leq A_u(R),
\end{aligned}$$

where $A_u(R) = (\delta_1\theta_1 p + \delta_2\theta_2)R$.

Integrating from t_0 to t gives, $u(t) \leq u(t_0) + A_u(R)(t - t_0)$. Thus u grows at most linearly and cannot blow up in finite time.

Similarly w,

$$\begin{aligned}
\frac{dw}{dt} &= G_Z\left\{-c_Z s(w)\left(1 - \frac{Z}{nd_2(u,w)X + c}\right)w + \frac{b_2(w,v)\sigma_2\exp\left(\sigma_2(w-v)\right)Y}{1+\exp\left(\sigma_2(w-v)\right)}\right.\\
&\quad\left.+\frac{s(w)nd_2(u,w)\theta_2\exp\left(\theta_2(u-w)\right)XZ}{\left[1+\exp\left(\theta_2(u-w)\right)\right](nd_2(u,w)X+c)^2}\right\}\exp(-\epsilon/w),\\
&\leq G_Z\left\{-c_Z s_0\exp\left(-c_Z w^2/2\right)\left(1-\frac{Z}{nd_2(u,w)X+c}\right)w\right.\\
&\quad\left.+\beta\sigma_2 Y + \frac{s_0 n\delta_2\theta_2 XZ}{c^2}\right\}\exp(-\epsilon/w),\\
&\leq G_Z\left\{\beta\sigma_2 Y + \frac{s_0 n\delta_2\theta_2 XZ}{c^2}\right\}\exp(-\epsilon/w),\\
&\leq A_w(R),
\end{aligned}$$

where $A_w(R) = \beta\sigma_2 pR + \left(s_0 n\delta_2\theta_2 R^2\right)/c^2$.

Integrating from t_0 to t gives, $w(t) \leq w(t_0) + A_w(R)(t - t_0)$. Thus w grows at most linearly and cannot blow up in finite time. □

Remark 4 The ecological variables $X(t)$, $Y(t)$, and $Z(t)$ are uniformly ultimately bounded, while the evolutionary traits satisfy the following: $v(t)$ remains uniformly bounded, and $u(t)$, $w(t)$ exhibit at most linear growth. Hence no finite–time blow-up occurs in the full system, although uniform boundedness of u and w is not guaranteed.

3.2 Native system

To understand what happens with the native system before the arrival of the exotic predator, we will study the dynamics of the native species, which are represented by the system

$$\begin{cases}
\dfrac{dX}{dt} = X\left[r(u)\left(1-\dfrac{X}{K}\right) - d_1(u,v)Y\right],\\
\dfrac{dY}{dt} = Y\left[pd_1(u,v)X - q(v)\right],\\
\dfrac{du}{dt} = G_X\dfrac{\partial W_X}{\partial u}\exp\left(-\epsilon/u\right),\\
\dfrac{dv}{dt} = G_Y\dfrac{\partial W_Y}{\partial v}\exp\left(-\epsilon/v\right),
\end{cases} \tag{7}$$

where $W_S = 1/S \cdot dS/dt$ with $S \in \{X, Y\}$. In Rivera-Estay et al. (2024), this system does not account for phenotypic change in species, meaning the variable u and v are not included. That study shows that the system has three equilibrium points: $(0, 0)$,

$(0, K)$, and (X^*, Y^*), where X^* and Y^* are positive. Moreover, when the positive equilibrium exists, it is always stable. Thus, the conditions for its existence ensure the coexistence of the native system. Here, phenotypic change has been included as shown in equations (7), resulting in a positive equilibrium point of the form (X^*, Y^*, u^*, v^*). The existence conditions are given in the following theorem.

Theorem 3 *Assume there exists a value* $v^* \in]0, \theta_1/c_Y[$ *satisfying the following two conditions:*

1. $pd_1(v^*)K - q(v^*) > 0$, *and*
2. $\exp(\theta_1 v^*(c_Y - c_X)/c_X) \cdot (\theta_1 - c_Y v^*) = c_Y v^*$.

Then, the system admits a positive equilibrium point of the form

$$\left(X^*, Y^*, u^*, v^*\right) = \left(\frac{q(v^*)}{pd_1(v^*)}, \frac{r(u^*)\left[pd_1(v^*)K - q(v^*)\right]}{pd_1^2(v^*)K}, \frac{c_Y v^*}{c_X}, v^*\right),$$

with $u^* = c_Y v^*/c_X$.

Proof Considering the equations of the system (7)

$$X\left[r(u)\left(1 - \frac{X}{K}\right) - d_1(u, v)Y\right] = 0, \tag{8}$$

$$Y\left[pd_1(u, v)X - q(v)\right] = 0, \tag{9}$$

$$G_X \frac{\partial W_X}{\partial u} \exp\left(-\epsilon/u\right) = 0, \tag{10}$$

$$G_Y \frac{\partial W_Y}{\partial v} \exp\left(-\epsilon/v\right) = 0. \tag{11}$$

Solving for X in (9), we obtain $X(u, v) = q(v)/pd_1(u, v)$. Then, by replacing X and solving for Y in (8), we obtain $Y(u, v) = \{r(u)\left[pd_1(u, v)K - q(v)\right]\}/d_1(u, v)^2$ pK. Therefore, for a positive equilibrium point to exist, the following condition must be satisfied

$$pd_1(u^*, v^*)K - q(v^*) > 0, \tag{12}$$

where u^* and v^* represent the coordinates of the positive equilibrium point.

Replacing X in equation (10), it is obtained that

$$0 = G_X\left\{-c_X r_0 \exp\left(-c_X u^2/2\right)\left(1 - \frac{X}{K}\right)u + \frac{\delta_1\theta_1 \exp\left(\theta_1(u - v)\right)Y}{\left[1 + \exp\left(\theta_1(u - v)\right)\right]^2}\right\}\exp(-\epsilon/u),$$

$$
\begin{aligned}
&= G_X \left\{ -c_X r_0 \exp(-c_X u^2/2) \left(1 - \frac{q(v)/pd_1(u,v)}{K} \right) u \right. \\
&\quad \left. + \frac{\delta_1 \theta_1 \exp\left(\theta_1 (u-v)\right) r(u) \left[pd_1(u,v)K - q(v) \right] / d_1^2(u,v) pK}{\left[1 + \exp\left(\theta_1(u-v)\right)\right]^2} \right\} \exp(-\epsilon/u), \\
&= G_X \left\{ -c_X r_0 \exp(-c_X u^2/2) \left(\frac{pd_1(u,v)K - q(v)}{pd_1(u,v)K} \right) u \right. \\
&\quad \left. + \frac{\delta_1 \theta_1 \exp\left(\theta_1 (u-v)\right) r_0 \exp(-c_X u^2/2) \left[pd_1(u,v)K - q(v) \right]}{d_1^2(u,v) pK \left[1 + \exp\left(\theta_1(u-v)\right)\right]^2} \right\} \exp(-\epsilon/u), \\
&= G_X \left\{ -r_0 \exp(-c_X u^2/2) \left(pd_1(u,v)K - q(v) \right) \left[\frac{c_X u}{pd_1(u,v)K} \right. \right. \\
&\quad \left. \left. + \frac{\delta_1 \theta_1 \exp\left(\theta_1(u-v)\right)}{d_1^2(u,v) pK \left[1 + \exp\left(\theta_1(u-v)\right)\right]^2} \right] \right\} \exp(-\epsilon/u), \\
&= G_X \left\{ -r_0 \exp(-c_X u^2/2) \left(pd_1(u,v)K - q(v) \right) \left[\frac{c_X u}{pK\delta_1/[1+\exp(\theta_1(u-v))]} \right. \right. \\
&\quad \left. \left. + \frac{\delta_1 \theta_1 \exp\left(\theta_1(u-v)\right)}{pK \left[1 + \exp\left(\theta_1(u-v)\right)\right]^2 \delta_1^2 / \left[1 + \exp\left(\theta_1(u-v)\right)\right]^2} \right] \right\} \exp(-\epsilon/u), \\
&= G_X \left\{ -r_0 \exp(-c_X u^2/2) \left(pd_1(u,v)K - q(v) \right) \left[\frac{c_X u [1+\exp(\theta_1(u-v))]}{pK\delta_1} \right. \right. \\
&\quad \left. \left. - \frac{\theta_1 \exp\left(\theta_1(u-v)\right)}{pK\delta_1} \right] \right\} \exp(-\epsilon/u), \\
&= G_X \left\{ \frac{-r_0 \exp(-c_X u^2/2) \left(pd_1(u,v)K - q(v) \right)}{pK\delta_1} \left[c_X u + c_X u \exp(\theta_1(u-v)) \right. \right. \\
&\quad \left. \left. - \theta_1 \exp\left(\theta_1(u-v)\right) \right] \right\} \exp(-\epsilon/u),
\end{aligned}
$$

then

$$
c_X u + c_X u \exp\left(\theta_1(u-v)\right) - \theta_1 \exp\left(\theta_1(u-v)\right) = 0,
$$

equivalently to

$$
c_X u - \exp\left(\theta_1(u-v)\right) \left(\theta_1 - c_X u\right) = 0. \tag{13}
$$

Now, by replacing Y in equation (11), it is obtained that

$$
\begin{aligned}
0 &= G_Y \left\{ -c_Y q_0 \exp(c_Y v^2/2) v + \frac{p\delta_1 \theta_1 \exp\left(\theta_1(u-v)\right) X}{\left[1 + \exp\left(\theta_1(u-v)\right)\right]^2} \right\} \exp(-\epsilon/v), \\
&= G_Y \left\{ -c_Y q_0 \exp(c_Y v^2/2) v + \frac{p\delta_1 \theta_1 \exp\left(\theta_1(u-v)\right) q(v)/pd_1(u,v)}{\left[1 + \exp\left(\theta_1(u-v)\right)\right]^2} \right\} \exp(-\epsilon/v),
\end{aligned}
$$

$$= G_Y \left\{ -c_Y q_0 \exp(c_Y v^2/2) v + \frac{\delta_1 \theta_1 \exp\left(\theta_1 (u-v)\right) q(v)}{\left[1+\exp\left(\theta_1(u-v)\right)\right]^2 d_1(u,v)} \right\} \exp(-\epsilon/v),$$

$$= G_Y \left\{ -c_Y q_0 \exp(c_Y v^2/2) v + \frac{\delta_1 \theta_1 \exp\left(\theta_1 (u-v)\right) q(v)}{\left[1+\exp\left(\theta_1(u-v)\right)\right]^2 \delta_1 / \left[1+\exp\left(\theta_1(u-v)\right)\right]} \right\}$$

$$\exp(-\epsilon/v),$$

$$= G_Y \left\{ -c_Y q_0 \exp(c_Y v^2/2) v + \frac{\theta_1 \exp\left(\theta_1 (u-v)\right) q(v)}{1+\exp\left(\theta_1(u-v)\right)} \right\} \exp(-\epsilon/v),$$

$$= G_Y \left\{ -c_Y q_0 \exp(c_Y v^2/2) v + \frac{\theta_1 \exp\left(\theta_1 (u-v)\right) q_0 \exp(c_Y v^2/2)}{1+\exp\left(\theta_1(u-v)\right)} \right\} \exp(-\epsilon/v),$$

$$= G_Y \left\{ q_0 \exp(c_Y v^2/2) \left[-c_Y v + \frac{\theta_1 \exp\left(\theta_1 (u-v)\right)}{1+\exp\left(\theta_1(u-v)\right)} \right] \right\} \exp(-\epsilon/v),$$

$$= G_Y \left\{ \exp\left(c_Y v^2/2\right) q_0 \left[\frac{-c_Y v \left[1+\exp\left(\theta_1(u-v)\right)\right] + \theta_1 \exp\left(\theta_1(u-v)\right)}{1+\exp\left(\theta_1(u-v)\right)} \right] \right\}$$

$$\exp\left(-\epsilon/v\right),$$

then

$$-c_Y v - c_Y v \exp\left(\theta_1(u-v)\right) + \theta_1 \exp\left(\theta_1(u-v)\right) = 0,$$

if and only if

$$\exp\left(\theta_1(u-v)\right)\left(\theta_1 - c_Y v\right) = c_Y v,$$

equivalently to

$$\exp\left(\theta_1(u-v)\right) = \frac{c_Y v}{\theta_1 - c_Y v}. \tag{14}$$

Replacing (14) in (13) we have

$$c_X u - \frac{c_Y v}{\theta_1 - c_Y v}\left(\theta_1 - c_X u\right) = 0,$$

if and only if

$$\frac{c_X u \left(\theta_1 - c_Y v\right) - c_Y v \left(\theta_1 - c_X u\right)}{\theta_1 - c_Y v} = 0,$$

then

$$c_X u - c_Y v = 0,$$

equivalently to

$$u = c_Y v / c_X. \tag{15}$$

Replacing (15) in (13) and (12), it follows that v^* must satisfy

$$\exp(\theta_1 v^* (c_Y - c_X)/c_X) \cdot \big(\theta_1 - c_Y v^*\big) - c_Y v^* = 0, \tag{16}$$

and

$$p d_1(v^*) K - q(v^*) > 0. \tag{17}$$

Therefore, if there exists a value $v^* \in]0, \theta_1/c_Y[$ satisfying both condition (16) and condition (17), then setting $u^* = c_Y v^*/c_X$, we obtain a positive equilibrium point of the form:

$$\big(X^*, Y^*, u^*, v^*\big) = \left(\frac{q(v^*)}{p d_1(v^*)}, \frac{r(u^*)[p d_1(v^*) K - q(v^*)]}{d_1(v^*)^2 p K}, \frac{c_Y v^*}{c_X}, v^* \right).$$

Note that inequality $v^* < \theta_1/c_Y$ is automatically satisfied as a consequence of condition (16). This completes the proof. □

Theorem 3 is stated under the assumption that a value $v^* \in]0, \theta_1/c_Y[$ satisfying the required conditions exists. The existence of such a value follows from a standard application of the Intermediate Value Theorem (Rudin 1976), since the function involved is continuous on the interval, positive near zero, and negative near the upper bound.

We now highlight a biological interpretation related to the equilibrium values of the traits.

Remark 5 Note that there is a linear relationship between u and v in the equilibrium state, such that $u^* = m v^*$, where $m = c_Y/c_X$. When the offense and the defense are equal in the equilibrium state ($u^* = v^*$), then the cost associated with phenotypic change is the same for both species ($c_X = c_Y$). However, due to the trade-off, if the offense is lower than the defense in the equilibrium state ($u^* > v^*$), then the cost associated with phenotypic change for the predator is greater than the cost for the prey ($c_X < c_Y$). Conversely, if the offense is greater than the defense in the equilibrium state ($u^* < v^*$), then the cost associated with phenotypic change for the prey is greater than the cost associated with phenotypic change for the predator ($c_X > c_Y$).

From the existence conditions of the positive equilibrium point, $p d_1(u^*, v^*) K - q(v^*) > 0$, we can deduce that if $c_X > c_Y$, the likelihood of coexistence increases, because $d_1(u^*, v^*)$ could take a sufficiently large value compared to $q(v^*)$ when $u^* < v^*$. Conversely, if $c_X < c_Y$ the likelihood of coexistence decreases, because $d_1(u^*, v^*)$ could not take a sufficiently large value compared to $q(v^*)$ when $u^* > v^*$. However, in this case, the persistence condition strongly depends on other parameters: δ_1, θ_1, p and q_0. Figure 2 shows two scenarios of the native model in the parameter space (δ_1, θ_1) for different values of λ such that $q_0 = \lambda p$. Note that there is a threshold

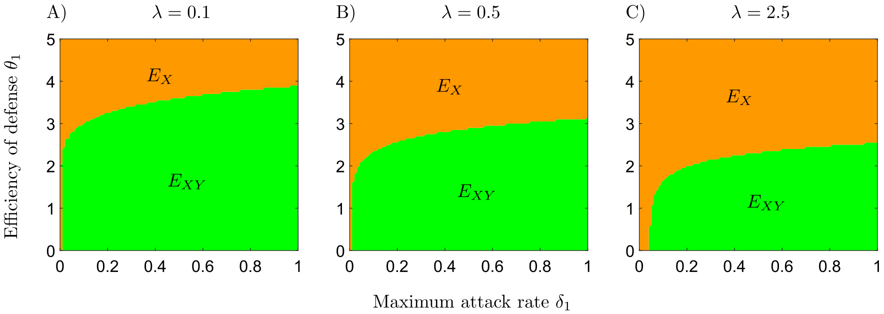

Fig. 2 Two scenarios of the native model in parameter space (δ_1, θ_1) for different values of λ such that $q_0 = \lambda p$. All other parameters are fixed: $r_0 = 1.2$, $K = 100$, $p = 0.1$, $e = 0.001$, $\theta_1 = 3$, $c_X = 0.5$, $c_Y = 1$, $G_x = 0.01$, $G_y = 0.01$. Initial conditions are: $X(0) = 15$, $Y(0) = 9$, $u(0) = 0.01$, $v(0) = 0.01$

for θ_1 such that, if the defense efficiency exceeds this value, coexistence becomes impossible, even when δ_1 approaches one (orange region). This threshold decreases as λ increases, implying that as the predator's minimum mortality increases, the efficiency of defense must also decrease to ensure coexistence (green region). Thus, the attack rate increases, as it depends inversely on θ_1, so that $pd_1(u^*, v^*)K - q(v^*)$ could be positive.

3.3 The native system with an exotic predator

When considering the arrival of an exotic predator to the native system, two additional equations are added to the previous system, as shown in section 2. This increases the complexity of the algebraic manipulation of the model. Therefore, we analyzed the model numerically (see section 2.5 for more details).

According to Rivera-Estay et al. (2024), the model has four different ecological scenarios. When the exotic species enters the native predator-prey system, it may fail to establish (E_{XY}). In another scenario, the new predator can establish alongside the native species, ensuring the persistence of both native species over time (E_S). In the last two scenarios, either the native predator become extinct (E_{XZ}), or the native prey goes extinct, which subsequently leads to the extinction of the native predator (E_Z). These latter scenarios represent successful invasions because the exotic predator establishes and leads to the extinction of one or both native species. The occurrence of each of these scenarios depends on the interplay between predation and competition, which in turn are influenced by the phenotypic changes that the species may undergo. The effects of the efficiency, associated costs, and speed of phenotypic change on invasion success were studied.

Figure 3 illustrates these scenarios in the parameter space (δ_1, δ_2), which correspond to the maximum attack rates of the native predator and the exotic predator, respectively. In this figure, the efficiency, associated costs, and speed of phenotypic change are the same for all species (it means $c_X = c_Y = c_Z$ and $G_X = G_Y = G_Z$), and the scenarios E_{XY}, E_S, E_{XZ} and E_Z are represented as green, blue, yellow and red region, respectively.

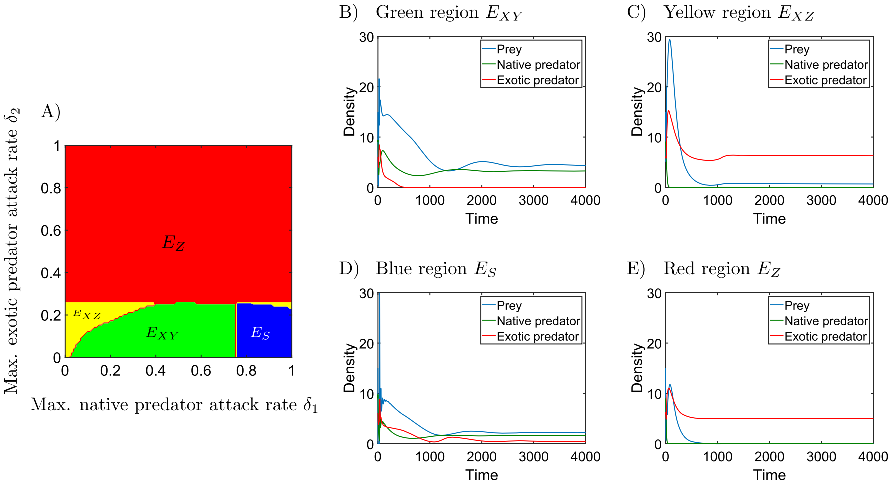

Fig. 3 Different scenarios of the model. In panel A), a partition of the parameter space (δ_1, δ_2) is shown. In panels B) to E), species densities over time for each region shown in panel A) are depicted. All other parameters are fixed: $r_0 = 1.2$, $s_0 = 0.2$, $K = 100$, $n = 10$, $c = 5$, $p = 0.1$, $q_0 = 0.05$, $e = 0.001$, $\beta = 0.0125$, $\theta_1 = 3$, $\theta_2 = 3$, $\sigma_1 = 3$, $\sigma_2 = 3$, $c_X = 2$, $c_Y = 2$, $c_Z = 2$, $G_x = 0.01$, $G_y = 0.01$, $G_z = 0.01$. Initial conditions are: $X(0) = 15$, $Y(0) = 9$, $Z(0) = 6$, $u(0) = 0.01$, $v(0) = 0.01$, $w(0) = 0.01$

From Figure 3, panel A), there exists a threshold δ_2^* for the maximum attack rate of the exotic predator, such that if δ_2 exceeds δ_2^*, the native system will go extinct (red region). When δ_2 is below δ_2^*, the exotic predator may not establish (green region). If $\delta_1 > \delta_2$, the native predator will always become extinct, even when $\delta_2 < \delta_2^*$ (yellow region). Additionally, there is a threshold δ_1^* for the maximum attack rate of the native predator, such that if δ_1 exceeds δ_1^*, the exotic predator can establish within the native system, provided that $\delta_2 < \delta_2^*$ (blue region). However, as δ_2 approaches δ_2^*, the native predator may go extinct (yellow region).

Figure 4 shows the effect of the maximum competition coefficient β on the scenarios, when the efficiency, associated costs, and speed of phenotypic change are the same for all species. Both thresholds mentioned earlier are affected as β increases. Specifically, the threshold for the maximum attack rate of the native predator, δ_1^*, disappears, while the threshold for the maximum attack rate of the exotic predator, δ_2^*, increases until it also disappears as β increases. In fact, the green region, which represents unsuccessful invasion, increases when β increases. Therefore, an intensification of competition may help to prevent the establishment of the exotic predator. Appendix B.1 presents a brief sensitivity analysis that illustrates the existence of this threshold and its influence across scenarios.

3.3.1 The efficiency of phenotypic change

The potential for phenotypic change to enable successful invasion depends on the efficiency of defense of the native prey against both native and exotic predators, θ_1

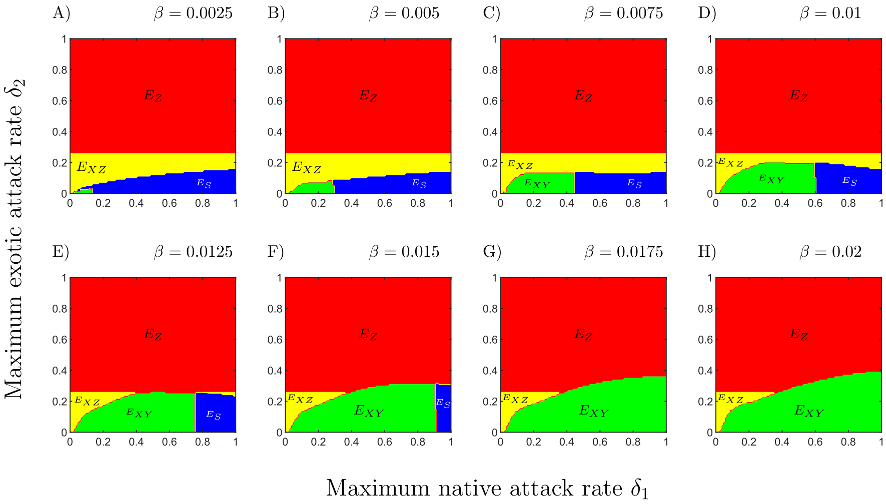

Fig. 4 Scenarios of the model in the parameter space (δ_1, δ_2) for different values of β. All other parameters are fixed: $r_0 = 1.2$, $s_0 = 0.2$, $K = 100$, $n = 10$, $c = 5$, $p = 0.1$, $q_0 = 0.05$, $e = 0.001$, $\theta_1 = 3$, $\theta_2 = 3$, $\sigma_1 = 3$, $\sigma_2 = 3$, $c_X = 2$, $c_Y = 2$, $c_Z = 2$, $G_x = 0.01$, $G_y = 0.01$, $G_z = 0.01$. Initial conditions are: $X(0) = 15$, $Y(0) = 9$, $Z(0) = 6$, $u(0) = 0.01$, $v(0) = 0.01$, $w(0) = 0.01$

and θ_2, respectively, and the efficiency of interference competition between the exotic and native predators, σ_1 and σ_2, respectively.

Considering that $\sigma_1 = \sigma_2$, when $\theta_1 < \theta_2$, the establishment of the exotic predator is less likely than when $\theta_1 \geq \theta_2$. In fact, the entire native system does not go extinct when the efficiency of the prey's defense against the exotic predator is greater than its efficiency against the native predator (see Figure 5 panels A.1 and A.2).

Considering that $\theta_1 = \theta_2$, if $\sigma_1 < \sigma_2$, the establishment of the exotic predator and the persistence of the native system are not possible, while they are possible when $\sigma_1 \geq \sigma_2$. Additionally, when the predation pressure by the exotic predator is low and the predation pressure by the native predator is high, if $\sigma_1 < \sigma_2$, the invasion could be unsuccessful, even if the competition pressure is very low (see Appendix B.2). However, if $\sigma_1 \geq \sigma_2$, the competition pressure must increase to prevent the establishment of exotic predator (see Figure 5 panels B.1 and B.2).

Based on the above, the native system will not go extinct as long as the prey's defense efficiency against the exotic predator is greater than its defense efficiency against the native predator ($\theta_1 < \theta_2$). This is a strong condition to prevent a successful invasion, which does not depend on the efficiency of phenotypic change that allows one predator to become a better competitor (see Appendix B.2). In other words, an invasion is unsuccessful, when $\theta_1 < \theta_2$ does not depend on the relation between parameters σ_1 and σ_2 (see Figure 5 panels C.1 and C.2).

3.3.2 Associated cost of phenotypic change

The phenotypic change that improves the prey's defense and the predators' offense has a relative cost due to a trade-off. For the prey, its intrinsic growth decreases

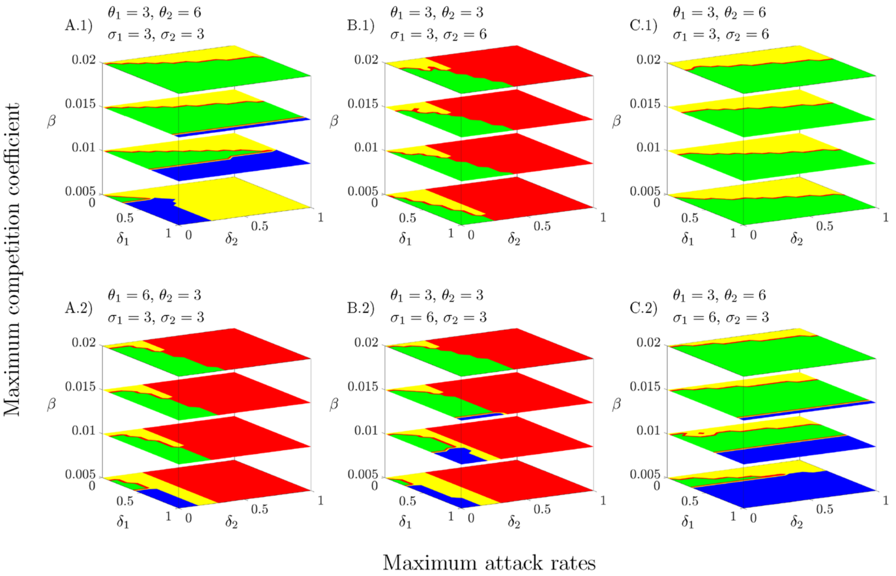

Fig. 5 Scenarios of the model in the parameter space (δ_1, δ_2) for different values of β, θ_1, θ_2, σ_1 and σ_2. Red, yellow, blue, and green regions represent the scenarios E_Z, E_{XZ}, E_S, and E_{XY}, respectively. All other parameters are fixed: $r_0 = 1.2$, $s_0 = 0.2$, $K = 100$, $n = 10$, $c = 5$, $p = 0.1$, $q_0 = 0.01$, $e = 0.001$, $c_X = 2$, $c_Y = 2$, $c_Z = 2$, $G_x = 0.01$, $G_y = 0.01$, $G_z = 0.01$. Initial conditions are: $X(0) = 15$, $Y(0) = 9$, $Z(0) = 6$, $u(0) = 0.01$, $v(0) = 0.01$, $w(0) = 0.01$

as its defense increases. For the native predator, its mortality increases as its offense increases. For the exotic predator, its intrinsic growth decreases as its offense increases. The relative cost of improving the prey's defense against both predators is represented by the parameter c_X. The relative cost of improving the predator's offense to capture the prey is represented by the parameters c_Y and c_Z for the native and exotic predators, respectively.

Figure 6 shows different scenarios of the model in the parameter space (c_Y, c_Z) for three different values of c_X. In the top panels, values for the maximum attack rate of the native predator δ_1 and the maximum attack rate of the exotic predator δ_2 are chosen such that all three species can persist (E_S, blue region). In bottom panels, In the bottom panels, values for δ_1 and δ_2 are chosen such that the exotic predator cannot establish (E_{XY}, green region). The black line in each panel represents the point where the relative phenotypic change cost of both predators are equal, $c_Y = c_Z$. Values below the line indicate that $c_Y > c_X$, while values above the line indicate that $c_Y < c_X$.

Starting from E_S, when $c_Y > c_Z$, the invasion will be successful because the exotic predator can persist (blue and yellow regions). However, if $c_Y < c_Z$, the invasion may not be successful as long as c_Y and c_Z are within the green region. Conversely, if c_Y and c_Z are within the blue region, then the exotic predator can establish and persist. When $c_Y < c_Z$, there is a threshold for the relative phenotypic change cost of the native predator c_Y^* such that if $c_Y < c_Y^*$, the exotic predator can not establish. Therefore, the invasion will not be successful if $c_Y < c_Z$ and c_Y is below this threshold. In addition,

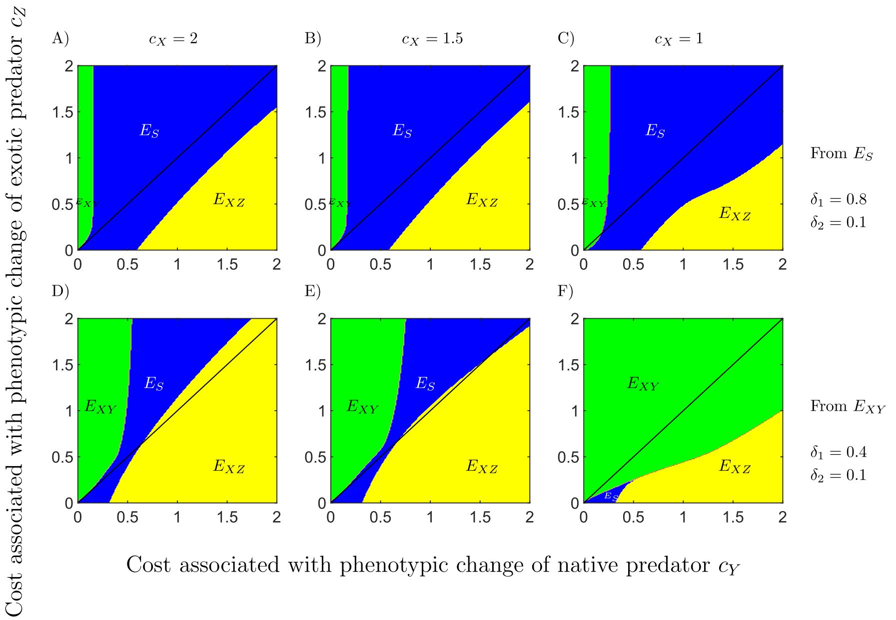

Fig. 6 Scenarios of the model in the parameter space (c_Y, c_Z) for different values of c_X, starting from E_S (top panel) and E_{XY} (bottom panels). All other parameters are fixed: $r_0 = 1.2$, $s_0 = 0.2$, $K = 100$, $n = 10$, $c = 5$, $p = 0.1$, $q_0 = 0.05$, $e = 0.001$, $\beta = 0.01$, $G_x = 0.01$, $G_y = 0.01$, $G_z = 0.01$, $\theta_1 = 3$, $\theta_2 = 3$, $\sigma_1 = 3$, $\sigma_2 = 3$. In top panels $\delta_1 = 0.8$ and $\delta_2 = 0.1$. In bottom panels $\delta_1 = 0.4$ and $\delta_2 = 0.1$

this threshold increases as c_X decreases, implying that the decrease in the relative phenotypic change cost of the prey contributes to an unsuccessful invasion.

Starting from E_{XY}, the likelihood of an unsuccessful invasion may be higher because the green region in the bottom panels is larger than the green region in the top panels. In fact, when $c_Y < c_Z$, the threshold c_Y^* increases until it disappears as c_X decreases, but now the green region shifts below the black line. Therefore, the decrease in the prey's cost still contributes to an unsuccessful invasion, even when $c_Y > c_Z$.

In summary, when the relative phenotypic change cost of the native predator is lower than the relative phenotypic change cost of the exotic predator, the biological invasion may be not successful. There is a threshold for c_Y such that when c_Y is below this threshold, the invasion cannot be succeed. The value of this threshold depends on the relative phenotypic change cost of the prey, c_X. As c_X decreases, the likelihood of a successful invasion decreases. Conversely, if the relative phenotypic change cost of the native predator is higher than the relative phenotypic change cost of the exotic predator, the likelihood of a successful invasion is higher. However, if c_X decreases this likelihood also decreases (see Appendix B.3).

3.3.3 Speed of phenotypic change

The speed of phenotypic change may influence the success of biological invasions. Let G_X, G_Y, and G_Z represent the speed of phenotypic change of the prey, native

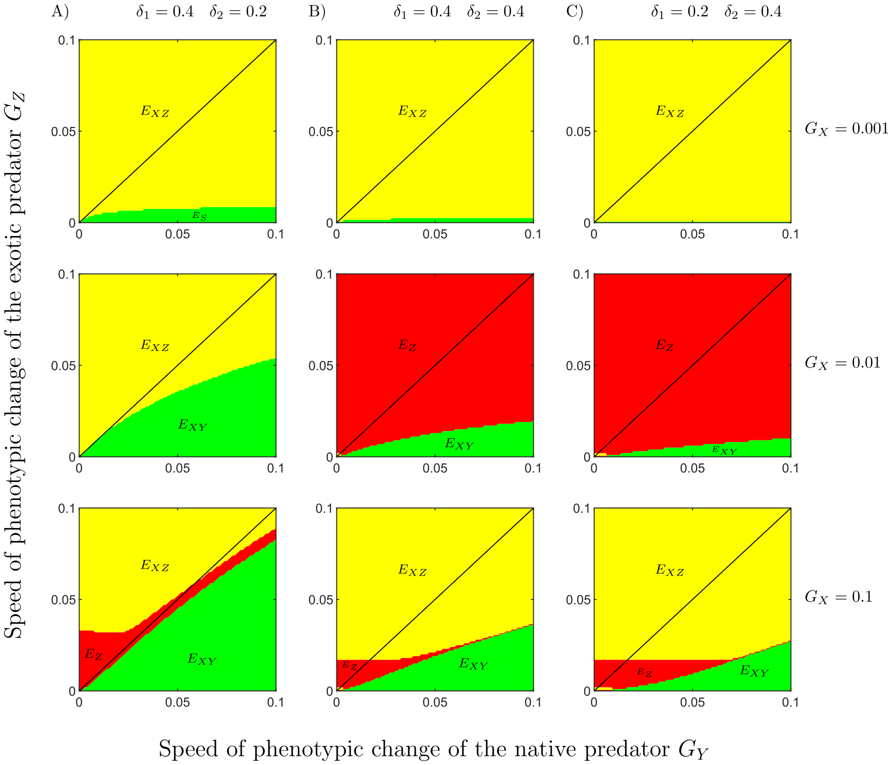

Fig. 7 Scenarios of the model in the parameter space (G_Y, G_Z) for three different values of G_X and three different combination of δ_1 and δ_2. In panel A) $\delta_1 = 0.4$ and $\delta_2 = 0.2$. In panel B) $\delta_1 = 0.4$ and $\delta_2 = 0.4$. In panel C) $\delta_1 = 0.2$ and $\delta_2 = 0.4$. All other parameters are fixed: $r_0 = 1.2$, $s_0 = 0.2$, $K = 100$, $n = 10$, $c = 5$, $p = 0.1$, $q_0 = 0.01$, $e = 0.001$, $\beta = 0.01$, $\theta_1 = 3$, $\theta_2 = 3$, $\sigma_1 = 3$, $\sigma_2 = 3$, $c_X = 1$, $c_Y = 1$ and $c_Z = 1$

predator, and exotic predator, respectively. Figure 7 shows the model scenarios in the parameter space (G_Y, G_Z) for three different values of G_X, as well as for various combinations of δ_1 and δ_2. The black line represents the scenario where the speed of phenotypic change of both predators is the same $(G_Y = G_Z)$. Above this line, the region corresponds to $G_Z > G_Y$, and below it, to $G_Z < G_Y$.

When $G_Z > G_Y$, the exotic predator always establishes, with or without prey. When $G_Z < G_Y$, there is a possibility that the exotic predator does not establish. This possibility depends on the speed of phenotypic change of the prey and the relationship between both maximum attack rates. In fact, the likelihood of invasion success decreases as the speed of phenotypic change of the prey increases (see Appendix B.4). However, if the maximum attack rate of the exotic predator is greater than that of the native predator, the likelihood of invasion success increases, even if $G_Z < G_Y$ (see panels B and C of Figure 7). Below a certain threshold, the system does not show sensitivity to either G_Y or G_Z. The exotic predator can establish if $G_Z < G_Y$, however, if $G_Z > G_Y$, its establishment is prevented.

4 Discussion

Although it is well known that biological invasions are a major threat to biodiversity, a large number of exotic species are introduced each year, as a result of increased industrial activity, international trade and human population growth (Meyerson and Mooney 2007; Hulme 2009, 2021). Unfortunately, the number of exotic species that are considered a threat is underestimated. In fact, by the time an exotic species is declared invasive, the damage has already been done. Therefore, predicting the potential negative impacts of an exotic species could help support more informed control and eradication actions aimed at preventing successful invasions (Simberloff et al. 2013). In order to predict the negative impacts of exotic species, it is necessary to consider the key factors in the biology of invasions. One of these factors is the phenotypic change experienced by both native and exotic species (Simberloff 2009, 2013).

Phenotypic change could occur through plasticity or adaptation processes that involve changes in the distribution of specific traits, where these traits correspond to specific morphological, physiological, or behavioral characteristics (Hendry 2017). This study explores the role of phenotypic change in the invasion success of an exotic predator in a native predator-prey system. The traits involved are related to the defense of the prey and the offense of both the native and exotic predators. Our results suggest that, in the context of our model, the potential role of phenotypic change to prevent a successful invasion depends strongly on the efficiency, relative cost, and speed of phenotypic change.

The efficiency of prey defenses against predators plays a critical role. If the efficiency of defense against the exotic predator is lower than or equal to that against the native predator, the exotic predator could become establish, potentially leading to the extinction of the native species, as long as its maximum attack rate exceeds a certain threshold. This may be interpreted as an instance of ineffective prey escape responses to novel predators (Anton et al. 2020). For example, native water voles (*Arvicola amphibius*) respond to the presence of American mink (*Neovison vison*) by seeking refuge in burrows. However, this defense is ineffective against female mink, which are small enough to enter the burrows, resulting in high predation on the water voles by this exotic predator (Macdonald and Harrington 2003). However, if the efficiency of defense against exotic predator is greater than the efficiency against native predators, the likelihood of exotic predator establishment decreases. In this scenario, the exotic predator may establish with the one or both of the native species considered. In New England, mussels (*Mytilus edulis*) have thickened their shells as a defense against the invasive Asian shore crab (*Hemigrapsus sanguineus*). Therefore, the efficiency of this phenotypic change appears to have facilitated the coexistence between native prey and invasive predators (Freeman and Byers 2006).

Our model suggests that an increase in competition may help prevent the establishment of exotic predators, under specific conditions. Particularly, as the maximum competition coefficient increases, the probability of an unsuccessful invasion increases. However, this scenario depends on two conditions: 1) the maximum attack rate of the exotic predator must be below a given threshold (Rivera-Estay et al. 2024), and 2) the efficiency of phenotypic change in the native predator must be greater than that of the exotic predator to become a better competitor. If either condition 1) or

2) is not met, the exotic predator will be able to establish itself and even displace the native species. These simulation results are consistent with the findings of Amarasekare (2002), who proposed that exotic species that displace native species in a system are superior resource exploiters with strong interference effects. From this, the likelihood of a successful invasion is high because exotic predators may exhibit higher attack rates than native predators (Salo et al. 2007; Sih et al. 2010; Ehlman et al. 2019; Anton et al. 2020). Therefore, condition 1) fails.

Although our conclusions are based on model simulations, they can inform conservation strategies and mitigation measures to manage biological invasions. First, promoting strategies that enhance the ability of native prey to adapt more effectively to exotic predators. For instance, establishing refuge zones to reduce predation pressure from exotic predators. These zones could provide protection for native prey while also imposing an adaptation cost on exotic predators, potentially limiting their establishment and spread (Boon et al. 2023). Second, regulating the establishment of exotic predators could be achieved by reducing their competitive advantage over native predators. This could be accomplished through the restoration of native vertebrate predator populations or by restoring the ecosystem structure to favor native predators, including implementing measures to reduce prey availability for exotic predators, thereby benefiting native ones (Gurevitch and Padilla 2004; Twining et al. 2022). Additionally, in environments where exotic predators are already established, it may be crucial to focus on reducing their phenotypic plasticity or slowing their rate of adaptation to mitigate their impact on native systems (Allendorf and Lundquist 2003).

The proposed eco-evolutionary model was formulated under the assumption of directional trait selection, meaning that the mean of trait distribution can either increase or decrease. Although there are other types of selection, this type is particularly appropriate for studying eco-evolutionary processes in a predator-prey system because the defenses of the prey and the offensive traits of the predator may follow a coevolutionary trend in which the trait values of both species are reciprocally regulated (Abrams et al. 1993). Typically, these models consider only two species and two traits, or three species and one trait, which explore the form of the cycles that emerge in the predator-prey dynamic.

The works by Mougi et al. (2011) and Van Velzen and Gaedke (2017) both studied how the evolutionary adaptation of both species in a predator–prey system affects population dynamics. Our work extends this by introducing a new exotic predator with its corresponding trait, leading to a model that considers three species and three traits. We built on previous studies by defining rates as trait functions and further extended this approach to include interference competition between predators. These studies examined the conditions under which adaptation by predator and prey leads to population oscillations or a stable equilibrium, as well as the amplitudes of the oscillations and the phase differences between the two species. For example, they found that if the predator adapts faster than the prey, the dynamics tends to be more stable, promoting the persistence of the system. In contrast, if the prey adapts faster, the system becomes more prone to large fluctuations, increasing the risk of extinction. In our work, this result also depends on the speed of phenotypic change of the newly introduced species, the exotic predator. Our study focuses on persistence or extinction scenarios, which effectively represent invasion success dynamics. This allowed us to describe complex dynamics in the context of biological invasions, where phenotypic change feedback between exotic and native species plays a key role. We believe that studying the nature of the cycles emerging in the predator-prey dynamics of our model, particularly their amplitude and antiphase patterns, could be particularly insightful. However, chaotic dynamics may arise.

Additionally, the complexity of our model makes a full analytical treatment intractable. Nonetheless, we were able to perform an analytical analysis on a simplified native subsystem with evolving traits (see Section 3.2), where we derived conditions for coexistence and trait relationships at equilibrium. Our current model is an extension of a previous version that excluded phenotypic change, for which a full analytical study was conducted to characterize the stability of equilibria and the conditions for coexistence, extinction, or successful invasion (Rivera-Estay et al., 2024). In the present study, the inclusion of phenotypic traits introduces dynamic parameters. However, all trait-dependent functions, such as the attack rates $d_1(u, v)$ and $d_2(u, w)$, the growth and mortality rates $r(u)$, $s(w)$, and $q(v)$, and the competition coefficients $b_1(v, w)$ and $b_2(w, v)$, remain continuous and bounded. This implies that the system retains the same qualitative behaviors as the constant-parameter model. Therefore, the ecological scenarios observed in the trait-free model, such as species coexistence or extinction, are still expected to arise in the trait-dependent framework. The analytical results presented for the native subsystem with evolving traits (Section 3.2) reinforce this interpretation and provide theoretical support for the general patterns observed in the numerical simulations of the full model.

Significant advances have been made in mathematical models that allow a better understanding of the biology of invasions (Meng et al. 2015; Lewis et al. 2016; Kang et al. 2017; Rivera-Estay et al. 2024). Using numerical and analytical tools, a mathematical modeling approach enables the assessment of multiple scenarios simultaneously with different sets of assumptions (Kot 2001; Turchin 2013). Additionally, since the modeling costs are lower compared to empirical methods, the use of mathematical models could help to optimize the resources allocated to prevention and control measures. Given the consistency of our results with biological invasion theory, we suggest that mathematical models, especially eco-evolutionary models, can be valuable tools in studying biological invasions. Some projections for future research include incorporating propagule pressure, temperature dependence, habitat fragmentation, or control measures into the modeling, as well as extending this model into an allometric framework.

Lastly, in Rivera-Estay et al. (2024), it was shown that invasion success depends on the initial exotic predator density (Z_0), above a certain threshold the invasion succeeds, while below it fails. Although our study fixed initial conditions to isolate parameter effects, these conditions are inherently linked to propagule size, a key factor in invasion dynamics. Propagule pressure can influence invasion results by increasing predation and competition pressures, or by introducing individuals with low genetic variability, thus limiting effective phenotypic adaptation (Lockwood et al. 2005; Catford et al. 2018; Lee 2002). Propagule size, event frequency, and timing are important variables to consider when evaluating invasion success. Future model extensions might benefit from incorporating propagule pressure, for instance, transitioning to a metapopulation framework with dispersal and trait diffusion terms.

5 Conclusion

This study explores the role of phenotypic change in the success of biological invasions using an eco-evolutionary model. Our results indicate that its role may depend on the efficiency, relative cost associated with, and the speed of phenotypic change. First, a native system was studied analytically and numerically. An interesting result from the analytical part was that when the populations are in equilibrium, there is a trade-off between offense/defense and the cost associated. In addition, when the efficiency of phenotypic change in the prey exceeds a critical threshold, the native predator goes extinct, even if its maximum attack rate is high. This suggests that, in our model, beyond this threshold, phenotypic change allows the prey to escape predation pressure, ultimately leading to the extinction of the predator.

Second, an exotic predator was introduced into the native system. At this point, the model equations become more complex to analyze analytically. Therefore, all results were obtained through numerical routines, that allowed us to perform parameter sweeps to explore different scenarios of the model. The model represents four different scenarios, with only one of them representing an unsuccessful invasion. The occurrence of these scenarios depends on predation and competitive pressure, as described in [48]. However, in this case, the occurrence also depends on the efficiency, the associated costs, and speed of phenotypic change, which are represented by parameters in the model.

Starting with efficiency, it is found that if the phenotypic change in the prey is more efficient in response to the exotic predator than to the native predator, the entire native system has a chance of avoiding extinction. This means that the worst-case scenario may be avoided. However, under these conditions, the exotic predator could establish itself within the native system or only with the prey (see Figure 5 panels A.1, C.1 and C.2). Conversely, if the phenotypic change in the prey is more efficient in response to the native predator than to the exotic predator, the entire native system could become extinct. This scenario strongly depends on the maximum attack rate of the exotic predator. In fact, simulations reveal a threshold for the predator's maximum attack rate, which increases until it disappears as the intensity of competition rises (see Figure 5, panels A.2, B.1, and B.2).

The efficiency of phenotypic change of the predator influences in the fact that exotic predator could establish with both prey and native predator (blue region). In fact, when the efficiency of phenotypic change in the native predator is greater than that of the exotic predator in becoming a better competitor, the exotic predator cannot establish itself within the entire native system, and the likelihood of its establishment decreases. This suggests that, under certain conditions, the native predator could contribute to an unsuccessful invasion as long as its efficiency of phenotypic change helps it to be a better competitor, and the maximum attack rate of the exotic predator is below the threshold and smaller than the maximum attack rate of the native predator (see green region in Figure 5 panels B.1 and C.1).

Regarding the associated cost and the speed of phenotypic change. The results suggest that preventing the establishment of the exotic predator could be possible as long as the associated cost for the exotic predator is higher than that for the native predator. However, this prevention also depends on the associated cost for the native predator being below a certain threshold. Additionally, decreasing the associated cost for the prey can also help prevent the establishment of the exotic predator (see Figure 6). Similarly, the speed of phenotypic change for the native species needs to be considerably lower in our simulations, compared to the speed of phenotypic change of the exotic predator, in order to prevent its establishment (see Figure 7). In both cases, the likelihood of a successful biological invasion depends on the maximum attack rates of both predators. Specifically, the maximum attack rate of the exotic predator must be below the threshold and also lower than that of the native predator to reduce the likelihood of a successful invasion.

Appendix A Algorithms Implemented for Numerical Analysis

Algorithm 1 Two-Parameter sweep to classify system scenarios

```
Input: Model with predetermined parameters, initial conditions and umbral
Output: Matrix $R$
Procedure:
  1. Define parameters and configurations
       • Initialize $\delta_1 = [0 : 0.01 : \delta_{1,end}]$ and $\delta_2 = [0 : 0.01 : \delta_{2,end}]$
       • Create a zero matrix $R$ with dimensions $length(\delta_1) \times length(\delta_2)$
  2. Iterate over $\delta_1$ and $\delta_2$
for $i = 1 : length(\delta_1)$ do
  for $j = 1 : length(\delta_2)$ do
    Solve the system of differential equations represented by equations (1) and (6) using ode45 over the interval [0, 10.000] with $\delta_1(i)$ and $\delta_2(j)$
    if $X_{end} >$ umbral and $Y_{end} >$ umbral and $Z_{end} >$ umbral then
      $R(i, j) = 1$
    else if $X_{end} >$ umbral and $Y_{end} <$ umbral and $Z_{end} >$ umbral then
      $R(i, j) = 2$
    else if $X_{end} <$ umbral and $Y_{end} <$ umbral and $Z_{end} >$ umbral then
      $R(i, j) = 3$
    else if $X_{end} >$ umbral and $Y_{end} >$ umbral and $Z_{end} <$ umbral then
      $R(i, j) = 4$
    end if
  end for
end for
```

Appendix B Sensitivity Analysis

From the results obtained in Section 3.3, a brief sensitivity analysis is presented, in order to enhance the previous simulations' robustness. Based on Richard et al. (2015), the sensitivity of key parameters.

Algorithm 2 Solve the system with `ode45` until convergence

```
Input: Model parameters $P$, initial conditions $x_0$, total time, time step, threshold, and tolerance.
Output: Solution matrix sol.
Procedure:
Define model parameters $r_0, s_0, K, n, c, d_1, d_2, b, \theta_1, \theta_2, \sigma_1, \sigma_2, p, q_0, e, c_x, c_y, c_z, G_1, G_2, G_3$.
Set initial conditions: $x_0 = [x_1, x_2, x_3, x_4, x_5, x_6]$.
Define the total simulation time: $total\_time = 10000$ and the time step: $time\_step = 200$.
Set threshold for small or negative values: $umbral = 1e - 6$.
Set tolerance for consecutive solutions: $tol = 0.000001$.
Initialize a cell array to store solutions: sol = cell(1, total_time / time_step).
Initialize $x_0$ as the initial conditions.
for $i = 0 : time\_step : total\_time$ do
    Define the current time span: $tspan = [i, i + time\_step]$.
    Solve the ODE system represented by equations (1) and (6) using ode45 on the interval $tspan$.
    Adjust small or negative values:
    if $y(end, 1) < umbral$ then
        $y(end, 1) = 0$
    end if
    if $y(end, 2) < umbral$ then
        $y(end, 2) = 0$
    end if
    if $y(end, 3) < umbral$ then
        $y(end, 3) = 0$
    end if
    Store the solution in sol.
    Check for convergence by comparing consecutive solutions:
    if $index > 1$ then
        Calculate the errors for each component:
        $error1 = \mathrm{mean}(|sol(index)(:, 1) - sol(index - 1)(:, 1)|)$
        $error2 = \mathrm{mean}(|sol(index)(:, 2) - sol(index - 1)(:, 2)|)$
        $error3 = \mathrm{mean}(|sol(index)(:, 3) - sol(index - 1)(:, 3)|)$
        $error = \mathrm{mean}([error1, error2, error3])$
        if $error < tol$ then
            break                                   ▷ Stop simulation if convergence is reached
        end if
    end if
    Update the initial conditions: $x_0 = y(end, :)$.
end for
```

B.1 Sensitivity to maximum attack rates and maximum competition coefficient: δ_1, δ_2, and β

We conducted a sensitivity analysis on the maximum attack rates (δ_1 and δ_2) and the maximum competition coefficient (β). These parameters govern the intensity of interspecific interactions and thus play a crucial role in shaping population dynamics. Figures 8 and 9 show the time series of population densities and the corresponding sensitivities of these state variables with respect to δ_1 and δ_2, respectively. Three values were considered for both δ_1 and δ_2. Consistent with previous results, different dynamical outcomes emerge depending on the value of each parameter.

Regarding sensitivity, when $\delta_1 = 0.2$ (in the E_{XZ} scenario), $S_{X_{\delta_1}}$, $S_{Y_{\delta_1}}$, and $S_{Z_{\delta_1}}$ are almost zero, indicating low sensitivity of the system to changes in δ_1 at this value. This suggests a stable dynamic where the populations are relatively unaffected by

Algorithm 3 General sensitivity analysis with respect to a parameter $P(i)$

```
Input: Vector of fixed parameters $P$, index $i$ of the parameter to be varied, vector of test values $V$, initial conditions $x_0$, time interval $tspan$, and threshold $\varepsilon$.
Output: Final population densities and sensitivity metrics for each value of $P(i)$.
Procedure:
Initialize result matrix $R$ of size $m \times (1 + d)$, where $m = \texttt{length}(V)$ and $d$ is the number of state variables.
for $j = 1$ to $m$ do
    Set $P(i) \leftarrow V(j)$
    Solve the system of differential equations with parameters $P$ and initial conditions $x_0$ over the interval $tspan$.
    Extract the final state: $Y_{\text{final}} = Y(t = t_{\text{end}})$
    Apply threshold: set $Y_{\text{final}}(k) = 0$ if $Y_{\text{final}}(k) < \varepsilon$
    Store the result: $R(j, :) = [V(j),\ Y_{\text{final}}]$
end for
Compute the range of variation for each state variable:
    $\Delta_k = \max_j R(j, k + 1) - \min_j R(j, k + 1)$
Compute the relative variation:
    $\text{RV}_k = \frac{\Delta_k}{\min_j R(j, k + 1)} \times 100$
Estimate numerical sensitivity using finite differences:
    $S_{j,k} = \frac{R(j + 1, k + 1) - R(j, k + 1)}{V(j + 1) - V(j)}$   for $j = 1, \dots, m - 1$
Optionally, plot final densities and sensitivities versus $V$.
```

small changes in δ_1. When $\delta_1 = 0.4$ (in the E_{XY} scenario), $S_{X_{\delta_1}}$ and $S_{Y_{\delta_1}}$ are negative, while $S_{Z_{\delta_1}}$ is zero. This negative sensitivity suggests that the populations of X and Y decrease as δ_1 increases, implying a destabilizing effect at this value of the parameter. When $\delta_1 = 0.8$ (in the E_S scenario), $S_{X_{\delta_1}}$ is zero, while $S_{Y_{\delta_1}}$ and $S_{Z_{\delta_1}}$ are negative and positive, respectively, showing a shift in the system's response, where the populations of Y decrease and Z increase with increasing δ_1.

In contrast, when $\delta_2 = 0.1$ (in the E_{XY} scenario), $S_{X_{\delta_2}}$, $S_{Y_{\delta_2}}$, and $S_{Z_{\delta_2}}$ are almost zero, indicating minimal sensitivity to changes in δ_2 at this level. When $\delta_2 = 0.2$ (in the E_{XZ} scenario), $S_{Y_{\delta_2}}$ is zero, and both $S_{X_{\delta_2}}$ and $S_{Z_{\delta_2}}$ are negative, suggesting that an increase in δ_2 leads to a decrease in the populations of X and Z. Finally, when $\delta_2 = 0.4$ (in the E_Z scenario), $S_{Y_{\delta_2}}$, $S_{X_{\delta_2}}$, and $S_{Z_{\delta_2}}$ are all zero, indicating that at this value of δ_2, the system reaches a state of insensitivity, where the populations no longer respond to changes in this parameter.

To further investigate the effect of key parameters on system dynamics, the sensitivity analysis was extended over a range of values for δ_1, δ_2, and β. Figure 10 shows the final population density (top panels) and the corresponding sensitivity values (bottom panels) for each parameter. Notably, clear thresholds emerge for each parameter, marking abrupt transitions in system behavior. These thresholds represent points where the system shifts from one scenario to another, such as the exclusion or

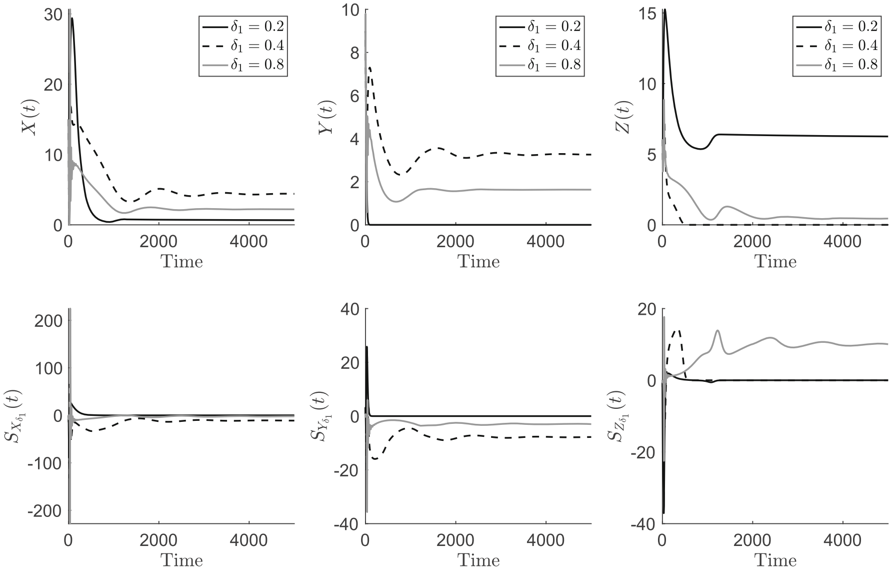

Fig. 8 Time series of population densities (top panels) and their sensitivities to δ_1 (bottom panels). Solid black line $\delta_1 = 0.2$, dashed black line $\delta_1 = 0.4$ and gray line $\delta_1 = 0.8$. All other parameters are fixed: $r_0 = 1.2$, $s_0 = 0.2$, $K = 100$, $n = 10$, $c = 5$, $p = 0.1$, $q_0 = 0.05$, $e = 0.001$, $\delta_2 = 0.2$, $\beta = 0.0125$, $\theta_1 = 3$, $\theta_2 = 3$, $\sigma_1 = 3$, $\sigma_2 = 3$, $c_X = 2$, $c_Y = 2$, $c_Z = 2$, $G_x = 0.01$, $G_y = 0.01$, $G_z = 0.01$. Initial conditions are: $X(0) = 15$, $Y(0) = 9$, $Z(0) = 6$, $u(0) = 0.01$, $v(0) = 0.01$, $w(0) = 0.01$

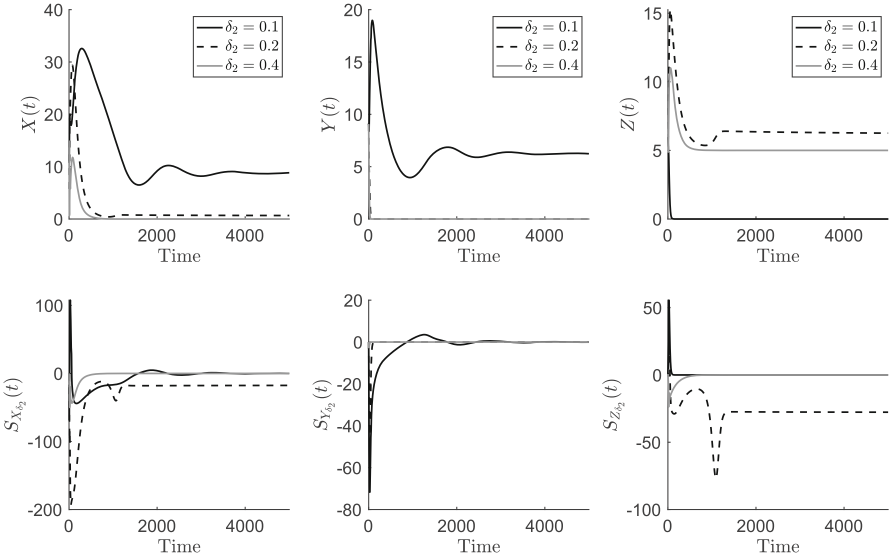

Fig. 9 Time series of population densities (top panels) and their sensitivities to δ_2 (bottom panels). Solid black line $\delta_2 = 0.1$, dashed black line $\delta_2 = 0.2$ and gray line $\delta_2 = 0.4$. All other parameters are fixed: $r_0 = 1.2$, $s_0 = 0.2$, $K = 100$, $n = 10$, $c = 5$, $p = 0.1$, $q_0 = 0.05$, $e = 0.001$, $\delta_1 = 0.2$, $\beta = 0.0125$, $\theta_1 = 3$, $\theta_2 = 3$, $\sigma_1 = 3$, $\sigma_2 = 3$, $c_X = 2$, $c_Y = 2$, $c_Z = 2$, $G_x = 0.01$, $G_y = 0.01$, $G_z = 0.01$. Initial conditions are: $X(0) = 15$, $Y(0) = 9$, $Z(0) = 6$, $u(0) = 0.01$, $v(0) = 0.01$, $w(0) = 0.01$

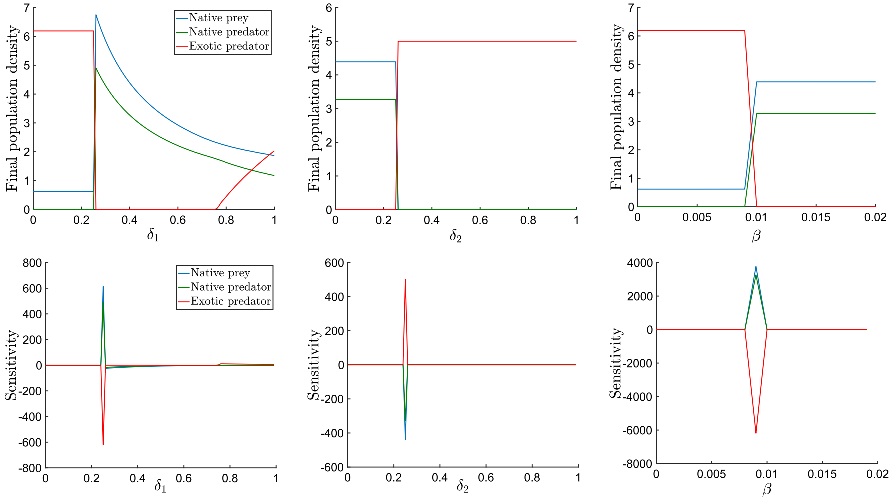

Fig. 10 In top panels final population densities in a range of δ_1, δ_2 and β (left, center and right panel, respectively) and their sensitivities (bottom panels). All other parameters are fixed: $r_0 = 1.2$, $s_0 = 0.2$, $K = 100$, $n = 10$, $c = 5$, $p = 0.1$, $q_0 = 0.05$, $e = 0.001$, $\delta_1 = 0.4$, $\delta_2 = 0.2$, $\beta = 0.0125$, $\theta_1 = 3$, $\theta_2 = 3$, $\sigma_1 = 3$, $\sigma_2 = 3$, $c_X = 2$, $c_Y = 2$, $c_Z = 2$, $G_x = 0.01$, $G_y = 0.01$, $G_z = 0.01$. Initial conditions are: $X(0) = 15$, $Y(0) = 9$, $Z(0) = 6$, $u(0) = 0.01$, $v(0) = 0.01$, $w(0) = 0.01$

establishment of the exotic predator. At these transition points, the sensitivity tends to increase sharply, highlighting regions where small changes in parameter values have large impacts on population outcomes.

B.2 Sensitivity to efficiency of phenotypic change: θ_1, θ_2, σ_1, and σ_2

We conducted a sensitivity analysis on the parameters δ_1, δ_2, σ_1, and σ_2, which are associated with the efficiency of phenotypic change. On the one hand, δ_1 and δ_2 represent the efficiency of induced defense against the native and exotic predator, respectively. Figure 11 shows the final population densities (top panels) and the corresponding sensitivity values (bottom panels) for these parameters in a specific range. Note that there is a threshold value of θ_1 at which the dynamics shift, specifically, the system transitions from a scenario of biological success to one of biological failure as θ_1 crosses this threshold. The sensitivity of population densities with respect to θ_1 is close to zero before reaching the threshold. For values slightly above the threshold, the sensitivity of the exotic predator population becomes negative, while the sensitivity of the native species (prey and predator) becomes positive. This means that a small increase in θ_1 just beyond the threshold tends to reduce the exotic predator population, while promoting the persistence or growth of the native species. For values of θ_1 further away from the threshold, the sensitivity exhibits irregular behavior, taking both positive and negative values. This could be a consequence of oscillatory trajectories; in this case, the persistence of native species might occur through a limit cycle. In contrast, the sensitivity to parameter θ_2 iremains close to zero, and the system does not undergo a change in scenario. Therefore, θ_1 has a stronger influence on the system dynamics.

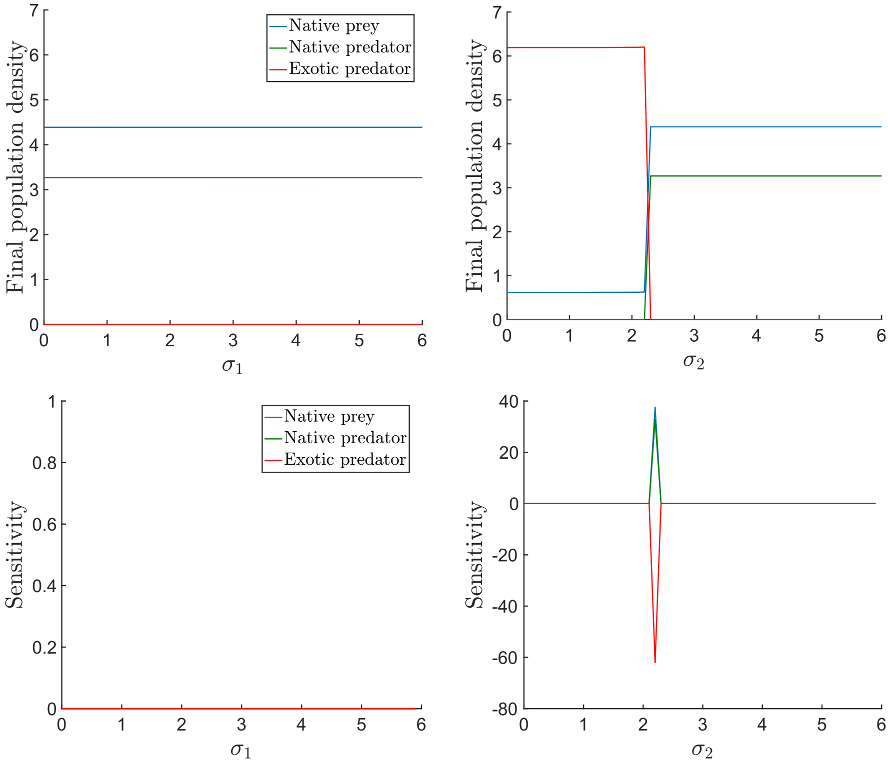

Fig. 11 In top panels final population densities in a range of θ_1 and θ_2 (left and right panels, respectively) and their sensitivities (bottom panels). All other parameters are fixed: $r_0 = 1.2$, $s_0 = 0.2$, $K = 100$, $n = 10$, $c = 5$, $p = 0.1$, $q_0 = 0.05$, $e = 0.001$, $\delta_1 = 0.4$, $\delta_2 = 0.2$, $\beta = 0.0125$, $\theta_1 = 3$, $\theta_2 = 3$, $\sigma_1 = 3$, $\sigma_2 = 3$, $c_X = 2$, $c_Y = 2$, $c_Z = 2$, $G_x = 0.01$, $G_y = 0.01$, $G_z = 0.01$. Initial conditions are: $X(0) = 15$, $Y(0) = 9$, $Z(0) = 6$, $u(0) = 0.01$, $v(0) = 0.01$, $w(0) = 0.01$

On the other hand, Figure 12 shows the final population densities (top panels) and the corresponding sensitivity values (bottom panels) for these parameters over a specific range. There is a threshold value of σ_2 beyond which the system's dynamics change and the invasion becomes unsuccessful. The parameter σ_2 represents the efficiency of phenotypic change in the exotic predator to become a better competitor. Therefore, when $\sigma_1 < \sigma_2$, the invasion may fail. In contrast, the sensitivity to σ_1 remains zero, and the system dynamics do not change.

B.3 Sensitivity to relative cost of phenotypic change: c_X, c_Y and c_Z

Figure 13 shows the final population densities (top panels) and the corresponding sensitivity values (bottom panels) for c_X, c_Y and c_Z. There are threshold values for all three parameters at which the system dynamics can change. However c_X presents an additional threshold that also leads to a change in the system's dynamics. This suggests that the system is more sensitive to variations in c_X which may reflect a stronger regulatory role of the corresponding trait in determining population outcomes

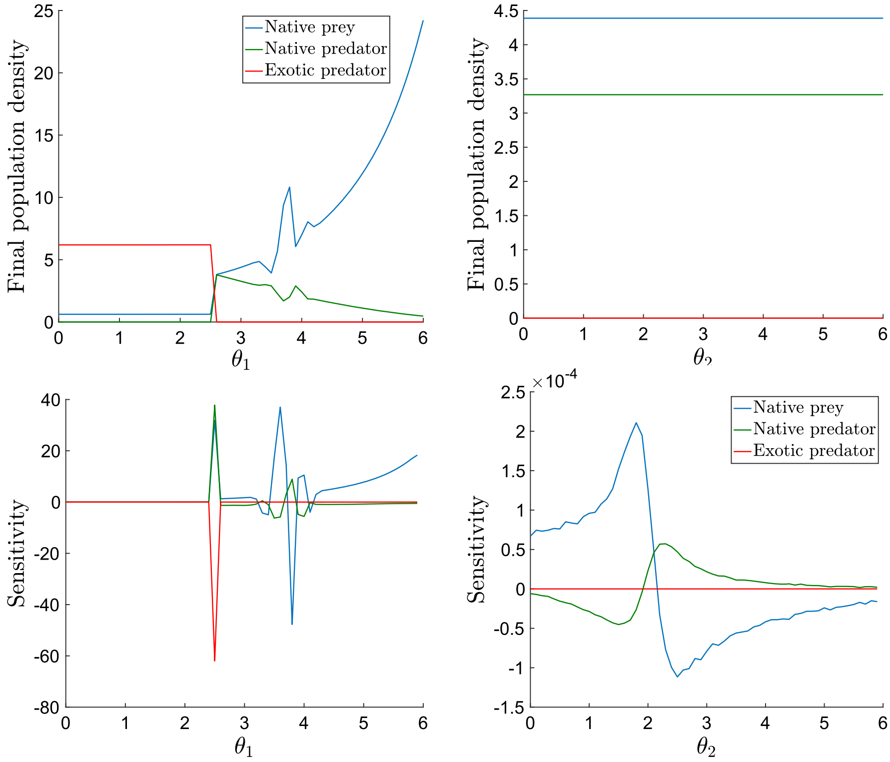

Fig. 12 In top panels final population densities in a range of θ_1 and θ_2 (left, center and right panel, respectively) and their sensitivities (bottom panels). All other parameters are fixed: $r_0 = 1.2$, $s_0 = 0.2$, $K = 100$, $n = 10$, $c = 5$, $p = 0.1$, $q_0 = 0.05$, $e = 0.001$, $\delta_1 = 0.4$, $\delta_2 = 0.2$, $\beta = 0.0125$, $\theta_1 = 3$, $\theta_2 = 3$, $\sigma_1 = 3$, $\sigma_2 = 3$, $c_X = 2$, $c_Y = 2$, $c_Z = 2$, $G_x = 0.01$, $G_y = 0.01$, $G_z = 0.01$. Initial conditions are: $X(0) = 15$, $Y(0) = 9$, $Z(0) = 6$, $u(0) = 0.01$, $v(0) = 0.01$, $w(0) = 0.01$

or species interactions. Additionally, the cost thresholds associated with both the native and exotic predators play a key role in determining the success of the invasion. For the native predator, the relative cost must remain below a critical threshold to prevent the establishment of the exotic predator. In contrast, the exotic predator can only establish if its own relative cost lies below a corresponding threshold. Thus, invasion success depends on both thresholds: high costs for the native predator facilitate invasion, while high costs for the exotic predator prevent it.

B.4 Sensitivity to speed of phenotypic change: G_X, G_Y and G_Z

Figure 14 shows the final population densities (top panels) and the corresponding sensitivity values (bottom panels) with respect to G_X, G_Y, and G_Z. Notably, there is a threshold value for G_X below which the system exhibits a wide range of sensitivity values, including both positive and negative responses. In this region, the system displays a complex sensitivity pattern, suggesting high instability or strong nonlinear

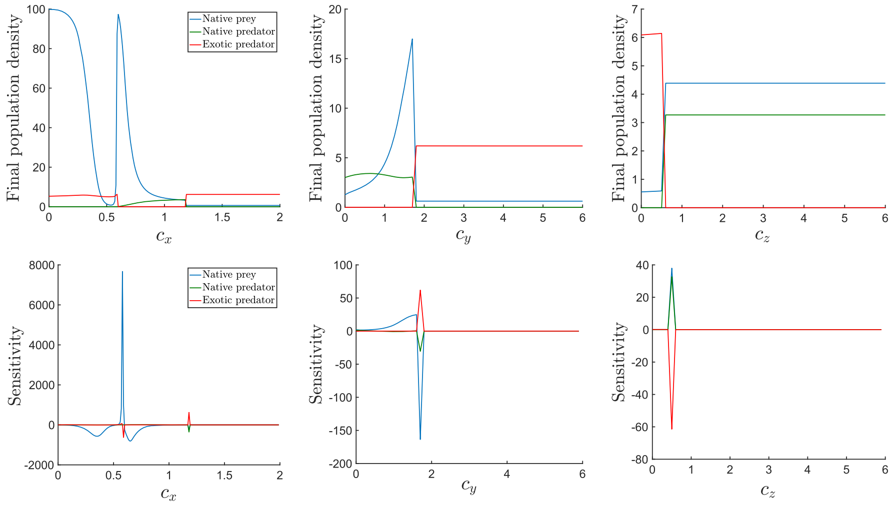

Fig. 13 In top panels final population densities in a range of c_X, c_Y and c_Z (left, center and right panel, respectively) and their sensitivities (bottom panels). All other parameters are fixed: $r_0 = 1.2$, $s_0 = 0.2$, $K = 100$, $n = 10$, $c = 5$, $p = 0.1$, $q_0 = 0.05$, $e = 0.001$, $\delta_1 = 0.4$, $\delta_2 = 0.2$, $\beta = 0.0125$, $\theta_1 = 3$, $\theta_2 = 3$, $\sigma_1 = 3$, $\sigma_2 = 3$, $c_X = 2$, $c_Y = 2$, $c_Z = 2$, $G_x = 0.01$, $G_y = 0.01$, $G_z = 0.01$. Initial conditions are: $X(0) = 15$, $Y(0) = 9$, $Z(0) = 6$, $u(0) = 0.01$, $v(0) = 0.01$, $w(0) = 0.01$

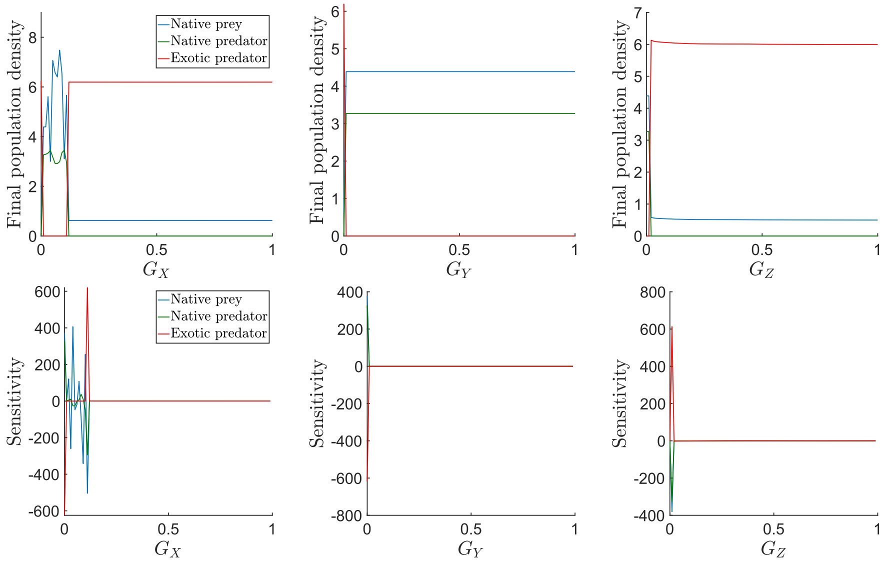

Fig. 14 In top panels final population densities in a range of G_X, G_Y and G_Z (left, center and right panel, respectively) and their sensitivities (bottom panels). All other parameters are fixed: $r_0 = 1.2$, $s_0 = 0.2$, $K = 100$, $n = 10$, $c = 5$, $p = 0.1$, $q_0 = 0.05$, $e = 0.001$, $\delta_1 = 0.4$, $\delta_2 = 0.2$, $\beta = 0.0125$, $\theta_1 = 3$, $\theta_2 = 3$, $\sigma_1 = 3$, $\sigma_2 = 3$, $c_X = 2$, $c_Y = 2$, $c_Z = 2$, $G_x = 0.01$, $G_y = 0.01$, $G_z = 0.01$. Initial conditions are: $X(0) = 15$, $Y(0) = 9$, $Z(0) = 6$, $u(0) = 0.01$, $v(0) = 0.01$, $w(0) = 0.01$

effects in response to small changes in G_X. After the threshold, sensitivity drops to zero, and the exotic predator fails to establish. Therefore, if the prey's rate of phenotypic change remains above this threshold, and both predators exhibit equal rates of phenotypic change (*i.e.*, $G_Y = G_Z = 0.01$) it may prevent the establishment of the exotic predator. In contrast to G_X, parameters G_Y and G_Z show limited impact on population densities across most of their respective ranges. For G_Y, both the final densities and their sensitivities remain nearly constant, indicating that the system is insensitive to changes in this parameter. For G_Z , only very low values lead to notable changes, particularly in the exotic predator's density, but the system quickly stabilizes, with sensitivity dropping to zero as G_Z increases.

Acknowledgements V.R.E. gratefully acknowledges the Agencia Nacional de Investigación y Desarrollo of Chile (ANID, Doctorado Nacional Scholarship No. 21211263) and the Vicerrectoría de Investigación y Postgrado, Universidad Católica del Maule, for financial support through a grant for conference participation and short research stays. This paper forms part of V.R.E.'s Ph.D. thesis in the Doctorado en Modelamiento Matemático Aplicado program at Universidad Católica del Maule, Talca, Chile. H.B thanks the project ANID ANILLO ATE230025 and Millennium Science Initiative Program – ICN2021_002. The paper's authors would like to express our sincere gratitude to the Laboratory of Technological Research in Pattern Recognition (LITRP), Faculty of Engineering Sciences, Universidad Católica del Maule, 3480112, Talca, Chile, for providing us with access to their computational cluster, which facilitated our research.

Author Contributions V.R.E, F.N.M.G, F.C.L, R.G and H.B. conceived the study. V.R.E carried out the mathematical modeling and manuscript writing under the advice and supervision of F.N.M.G, F.C.L, R.G and H.B. All authors reviewed and edited the final version of the manuscript.

Declarations

Conflicts of Interest The authors declare that they have no conflict of interest.

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