UNIVERSIDAD
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del Estado de Chile

https://revistammsb.utem.cl | revista.mmsb@utem.cl
ISSN-L: 2735-6817 | ISSN (online): 2735-6817

REVISTA
MMSB
Revista de Modelamiento Matemático de Sistemas Biológicos
Vol.5(2025), pp.1–10, e25R04
https://doi.org/10.58560/rmmsb.v05.e.025.04

Predation and exploitative competition in a two-dimensional system

Depredación y competencia por explotación en un sistema de dos dimensiones

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Recepción: 2025-11-01 | Aceptación: 2025-12-15 | Publicación: 2025-12-30

Recommended Citation: Enith A. Gómez-Hernández *et al.* (2025). *'Predation and exploitative competition in a two-dimensional system'*. Rev. model. mat. sist. biol. Vol.5, e25R04, doi:10.58560/rmmsb.v05.e.025.04

ABSTRACT

Intraguild predation (IGP) arises when two consumer species exploit the same resource and also interact through predation. Classical models of IGP typically include three dynamical variables and describe the resource explicitly. Here we introduce a reduced predator-prey model in which both species depend on a shared resource that is not modeled directly. Instead, resource use is represented through reciprocal reductions of carrying capacities, which captures the main mechanisms of IGP in a two dimensional system that remains analytically tractable. The model exhibits extinction equilibrium, exclusion equilibrium, and up to two coexistence equilibrium. We show that at most one of the coexistence equilibrium is locally stable. These outcomes depend on the balance between prey reproduction and the combined effects of predation and exploitative competition. Prey extinction occurs when its reproductive potential is lower than these antagonistic pressures, while coexistence becomes possible when reproduction is sufficiently high. The analysis also reveals that no local oscillations can arise, which suggests that exploitative competition has a stabilizing effect on the system. This reduced formulation provides a compact mechanistic framework for studying IGP when resource dynamics are assumed constant or secondary. It also serves as a useful basis for extending classical models and examining how asymmetric resource use influences species coexistence or exclusion.

Keywords:

Predator prey dynamics, Intraguild predation, Exploitative competition, Two dimensional models, Local stability, Saddle node bifurcation

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RESUMEN

La depredación intragremial ocurre cuando dos especies consumidoras explotan un mismo recurso y además interactúan mediante depredación. Los modelos clásicos de depredación intragremial suelen incluir tres variables dinámicas y describir explícitamente el recurso. Aquí introducimos un modelo reducido de depredador–presa en el cual ambas especies dependen de un recurso compartido que no se modela directamente; su efecto se incorpora mediante reducciones recíprocas en las capacidades de carga, capturando los mecanismos esenciales de la depredación intragremial en un sistema bidimensional. El modelo presenta equilibrios de extinción, exclusión y por lo menos dos equilibrios de coexistencia, de los cuales a lo sumo uno puede ser localmente estable. Estos resultados dependen de la relación entre la reproducción de la presa y los efectos combinados de la depredación y la competencia por explotación. La presa se extingue cuando su capacidad reproductiva es insuficiente frente a estas presiones, mientras que la coexistencia surge cuando la reproducción es suficientemente alta. El análisis también demuestra que no aparecen oscilaciones locales, lo que indica un efecto estabilizador de la competencia por explotación. Esta formulación ofrece un marco para analizar la depredación intragremial cuando la dinámica del recurso se considera constante o secundaria, y sirve como base para extender modelos clásicos y analizar cómo el uso asimétrico del recurso afecta la coexistencia o exclusión de especies.

Palabras Claves:

Dinámica depredador-presa, Depredación intragremial, Competencia por explotación, Modelos bidimensionales, Estabilidad local, Bifurcación silla–nodo

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2020 AMS Mathematics Subject Classification: Primary: 92B05; Secondary: 92D40

INTRODUCTION

Predation and competition have been extensively studied in ecology, in part because they constitute the basic components of communities Holt and Polis (1997); Bodini (1991). These interactions were mathematically enunciated in the 1920s by Lotka and Volterra. They independently proposed a model to describe the relationship between two species sharing the same resource and then shifted their attention from competition to the effects of predation on population growth Smith *et al.* (1998). Predation has been studied by considering different functional responses, most notably Holling type I, II, and III Holling (1965); Tian and Xu (2011); Chan *et al.* (2017); Sarkar *et al.* (2020). Competition has two main approaches: interference and exploitative competition Nguyen-Ngoc and Nguyen-Phuong (2016). Interference competition occurs when individuals of one species are equivalent to a certain number of individuals of another species. Exploitative competition occurs when the use of the resource by one species reduces the capacity of the environment to support another species by acting on its carrying capacity Jensen (1987).

Intraguild predation is an interaction of competition and predation where two species involved in a predator-prey relationship also compete for a shared resource Arim and Marquet (2004). Generally, three species are involved in mathematical models corresponding to predator, prey, and shared resource. For example, in Kang and Wedekin (2013), they formulate two models of intraguild predation. One has the specialized predator and the other generalist. They found that the model with the generalist predator is more prone to coexistence. In Capone *et al.* (2018), they propose an intraguild model in which the carrying capacity of the prey and the predator is proportional to the biotic resource. They establish different exclusion and coexistence regimes of the populations. In Sen *et al.* (2018), they propose a model in which the predator and the prey compete to remain in the community, and they observe two types of coexistence: steady-state coexistence and oscillatory coexistence.

Intraguild predation is a particular type of omnivory, which is defined as feeding on more than one trophic level in the food chain model Sen *et al.* (2018). According to Hunter (2009), omnivores are generalists that evolve in response to a trade-off between food quality and quantity. A typical example of omnivorous animals are ants that consume animal tissue, seeds, and plants Hunter (2009). In relation to intraguild models of predation mentioned previously an example of an omnivorous predator, a herbivorous prey and a resource for which they compete for exploitation can be found in the periphyton and freshwater amphipods (*Crustacea*) of the genus *Hyalella*. In this case, *Hyalella curvispina* would be an omnivorous predator that feeds on periphyton, but if the algal food supply is low, *H. curvispina* consumes *Hyalella pseudoazteca* , which would be an herbivorous prey, since it only eats algae, so the resource they compete to exploit would correspond to periphyton Casset *et al.* (2001); Carusela *et al.* (2009). Another example, is found in species inhabiting the Antarctic Ocean. Antartic krill *Euphausia superba* is the main food for Antarctic Fur Seals *Arctocephalus gazella* and fishes *Champsocephalus gunnari*, but *A. gazella* also eat fishes *C. gunnari* Doidge and Croxall (1985); Ibáñez (2005).

In this paper, we are interested in developing and analyzing a mathematical model that maintains the simplicity of the Lotka–Volterra framework of two ordinary differential equations, while allowing us to study the population dynamics of a predator and a prey competing for the same resource. Beyond mathematical convenience, dimensional reduction allows for the analytical exploration of ecological systems in which resource dynamics operate on faster time scales or remain approximately constant. This approach preserves the fundamental mechanisms of intraguild predation and exploitative competition, without the need to explicitly incorporate resource dynamics.

For example, this framework can represent an herbivore and an omnivore competing for a primary producer. To achieve this, we include exploitative competition in a two-dimensional model rather than explicitly modeling a three-variable system with separate equations for the predator, the prey, and the shared resource. In our model, the resource for which predator and prey compete is implicit; therefore, the equivalent representation in a three-variable formulation corresponds to equilibrium at which the resource remains positive. With this model, we address the following question: what are the population dynamics of a predator–prey system subject to exploitative competition?

Our analysis shows that the reduced system captures the main dynamical outcomes expected in intraguild interactions. The model admits extinction, exclusion, and coexistence states, with at most one coexistence equilibrium being locally stable. Because the trace of the Jacobian at any interior equilibrium is always negative, stability depends solely on the determinant, and no Hopf bifurcations or oscillatory coexistence can arise. A saddle–node bifurcation separates parameter regions where positive coexistence equilibrium persist from those where coexistence is lost. Ecologically, the analysis reveals two contrasting regimes, when prey reproduction exceeds the predation pressure exerted at the predator carrying capacity, stable coexistence is possible, otherwise, the prey is excluded. Asymmetries in resource exploitation further determine which species dominates at equilibrium.

THE MODEL

We developed a predator–prey model in which both species compete for a shared limiting resource. The formulation relies on the following assumptions:

i. The biological system consists of two state variables: the prey population N_1 and the predator population N_2. Each population experiences gains and losses determined by birth, predation, and competition for resource exploitation.

ii. In the absence of predators, the prey population N_1 follows logistic growth with intrinsic growth rate r_1 and carrying capacity k_1.

iii. The predator exhibits a generalist feeding strategy. Thus, even when the focal prey N_1 is absent, the predator population N_2 follows logistic growth with intrinsic rate r_2 and carrying capacity k_2.

iv. Because both species exploit the same underlying resource, interspecific competition affects their carrying capacities. Specifically, the effective carrying capacity of N_1 decreases by $\eta_1 N_2$, where η_1 represents the per capita resource requirement of the predator relative to the prey's carrying capacity. Symmetrically, the carrying capacity of N_2 decreases by $\eta_2 N_1$.

v. Predation follows a Holling type I functional response. The parameter p denotes the predation efficiency, while ε represents the conversion efficiency by which consumed prey biomass (pN_1) contributes to predator biomass production ($\varepsilon p N_1$).

A conceptual representation of the ecological interactions described by assumptions (i)–(v) is shown in Fig. 1.

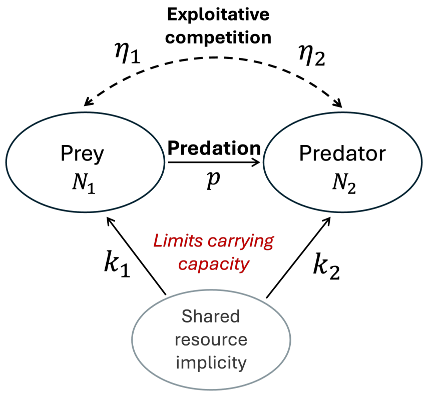

Figure 1: Conceptual diagram of the predator–prey system with exploitative competition mediated by a shared resource. The prey (N_1) and the predator (N_2) interact through direct predation, while both species depend on a common resource that is treated implicitly in the model. Resource availability limits the effective carrying capacities of both populations, generating indirect exploitative competition between prey and predator.

Under these assumptions, the dynamics are described by the system

$$\begin{aligned} \frac{dN_1}{dt} &= r_1 N_1 \left(1 - \frac{N_1}{k_1 - \eta_1 N_2}\right) - pN_1N_2, \\ \frac{dN_2}{dt} &= r_2 N_2 \left(1 - \frac{N_2}{k_2 - \eta_2 N_1}\right) + \varepsilon p N_1 N_2, \end{aligned} \tag{1}$$

with (N_1, N_2) confined to the biologically feasible region

$$\Omega = \left\{ (N_1, N_2) \in \mathbb{R}^2_+ : N_1 < \frac{k_2}{\eta_2},\ N_2 < \frac{k_1}{\eta_1} \right\},$$

and all parameters $r_1, r_2, k_1, k_2, \eta_1, \eta_2, p, \varepsilon$ are strictly positive (see Table 1).

Table 1: Ecological interpretation and units of the model parameters.

Par.	Ecological meaning	Units
r_1	Intrinsic growth rate of the prey	time^{-1}
r_2	Intrinsic growth rate of the predator	time^{-1}
k_1	Effective carrying capacity of the prey	density
k_2	Effective carrying capacity of the predator	density
p	Predation rate on the prey	time^{-1}
m	Predator mortality rate	time^{-1}
η_1	Strength of exploitative competition exerted by the predator on the prey	dimensionless
η_2	Strength of exploitative competition exerted by the prey on the predator	dimensionless

Theorem 1 *All solutions of system* (1) *initiated in* $\mathbb{R}^2_+$ *are uniformly bounded.*

Proof Define the auxiliary function

$$w = \varepsilon N_1 + N_2. \tag{2}$$

Solutions of (1) satisfy

$$N_1 < \frac{k_2}{\eta_2} \quad \text{and} \quad N_2 < \frac{k_1}{\eta_1}. \tag{3}$$

Differentiating (2) along trajectories of (1), we obtain

$$\begin{aligned} \frac{dw}{dt} &= \varepsilon r_1 N_1 \left(1 - \frac{N_1}{k_1 - \eta_1 N_2}\right) + r_2 N_2 \left(1 - \frac{N_2}{k_2 - \eta_2 N_1}\right) \\ &\leq rw - r\left(\frac{\varepsilon N_1^2}{k_1 - \eta_1 N_2} + \frac{N_2^2}{k_2 - \eta_2 N_1}\right), \end{aligned}$$

where $r = \max\{r_1, r_2\}$. Using the bounds in (3),

$$\frac{dw}{dt} \leq rw - r\left(\frac{\varepsilon N_1^2}{k_1} + \frac{N_2^2}{k_2}\right) \leq rw - r\left(\frac{\varepsilon N_1^2}{k} + \frac{N_2^2}{k}\right),$$

where $k = \max\{\varepsilon k_1, k_2\}$. Since

$$\varepsilon N_1 + N_2 = w, \qquad \varepsilon N_1^2 + N_2^2 \geq \frac{w^2}{2},$$

we obtain the simplified inequality

$$\frac{dw}{dt} \leq rw\left(1 - \frac{w}{k}\right).$$

Integrating this logistic-type inequality yields

$$w(t) \leq \left[\left(\frac{1}{w(0)} - \frac{1}{k}e^{-rt}\right) + \frac{1}{k}\right]^{-1}.$$

Thus, $\limsup_{t\to\infty} w(t) \leq k$, which implies that every trajectory eventually enters and remains within the compact region

$$\Omega = \left\{ (N_1, N_2) \in \mathbb{R}^2_+ : N_1 < \frac{k_2}{\eta_2},\ N_2 < \frac{k_1}{\eta_1},\ \varepsilon N_1 + N_2 \leq k \right\}.$$

This proves uniform boundedness of all solutions. ☐

Note 1 *For $N_1(0) > 0$ and $N_2(0) > 0$, the positive quadrant is forward invariant because the right-hand side of system* (1) *vanishes on the coordinate axes. Thus population densities remain non-negative for all $t > 0$.*

RESULTS

From model (1), we obtain four equilibrium points E_i representing different biological situations:

1. The trivial equilibrium $E_0 = (0,0)$, extinction of both species.
2. The axial equilibrium $E_{k_1} = (k_1, 0)$, only the prey at its carrying capacity.
3. The axial equilibrium $E_{k_2} = (0, k_2)$, only the predator at its carrying capacity.
4. The interior (coexistence) equilibrium $E_* = (N_1, N_2)$, where both species coexist.

To explicitly characterize the coexistence equilibrium E_*, we assume $N_1 \neq 0$ and $N_2 \neq 0$ and solve

$$r_1\left(1 - \frac{N_1}{k_1 - \eta_1 N_2}\right) - pN_2 = 0, \tag{4}$$

$$r_2\left(1 - \frac{N_2}{k_2 - \eta_2 N_1}\right) + \varepsilon p N_1 = 0. \tag{5}$$

From (4) we obtain

$$N_1 = \frac{(r_1 - pN_2)(k_1 - \eta_1 N_2)}{r_1}, \tag{6}$$

and substituting this expression into (5) yields a quartic polynomial in N_2 of the form

$$b_4 N_2^4 + b_3 N_2^3 + b_2 N_2^2 + b_1 N_2 + b_0 = 0,$$

where

$$\begin{aligned}
b_4 &= \varepsilon p^3 \eta_1^2 \eta_2, \\
b_3 &= -\left(2\varepsilon p^3 \eta_1 \eta_2 k_1 + 2\varepsilon p^2 \eta_1^2 \eta_2 r_1\right), \\
b_2 &= \varepsilon p^3 \eta_2 k_1^2 + 4\varepsilon p^2 \eta_1 \eta_2 k_1 r_1 + \varepsilon p \eta_1^2 \eta_2 r_1^2 - \varepsilon p^2 \eta_1 k_2 r_1 \\
&\quad + p\eta_1 \eta_2 r_1 r_2, \\
b_1 &= -2\varepsilon p^2 \eta_2 k_1^2 r_1 - 2\varepsilon p \eta_1 \eta_2 k_1 r_1^2 + \varepsilon p^2 k_1 k_2 r_1 \\
&\quad + \varepsilon p \eta_1 k_2 r_1^2 - p\eta_2 k_1 r_1 r_2 - \eta_1 \eta_2 r_1^2 r_2 + r_1^2 r_2, \\
b_0 &= \varepsilon p \eta_2 k_1^2 r_1^2 - \varepsilon p k_1 k_2 r_1^2 + \eta_2 k_1 r_1^2 r_2 - k_2 r_1^2 r_2.
\end{aligned}$$

We note that $b_4 > 0$ and $b_3 < 0$, so the polynomial exhibits at least one sign change. By Descartes' rule of signs, it has at least one positive root. Therefore, there exists at least one interior equilibrium E_* with ecological meaning.

LOCAL STABILITY OF BOUNDARY EQUILIBRIA

To analyze the stability of the equilibria E_{k_i} with $i \in \{1,2\}$, we first compute the Jacobian matrix associated with the linearization of system (1) at a generic equilibrium point $E = (N_1, N_2)$, which is denoted by $J(E)$

$$\begin{pmatrix} r_1\left(1 - \dfrac{2N_1}{k_1 - \eta_1 N_2}\right) - pN_2 & -\dfrac{r_1 \eta_1 N_1^2}{(k_1 - \eta_1 N_2)^2} - pN_1 \\ -\dfrac{r_2 \eta_2 N_2^2}{(k_2 - \eta_2 N_1)^2} + \varepsilon p N_2 & r_2\left(1 - \dfrac{2N_2}{k_2 - \eta_2 N_1}\right) + \varepsilon p N_1 \end{pmatrix}.$$

Evaluating at the trivial equilibrium $E_0 = (0,0)$, we obtain

$$J(E_0) = \begin{pmatrix} r_1 & 0 \\ 0 & r_2 \end{pmatrix},$$

whose eigenvalues are $\lambda_1 = r_1$ and $\lambda_2 = r_2$. Since both are positive, E_0 is unstable.

At the axial equilibrium $E_{k_1} = (k_1, 0)$ we have

$$J(E_{k_1}) = \begin{pmatrix} -r_1 & -pk_1 - \eta_1 r_1 \\ 0 & \varepsilon p k_1 + r_2 \end{pmatrix},$$

with eigenvalues $\lambda_1 = -r_1$ and $\lambda_2 = \varepsilon p k_1 + r_2 > 0$, so E_{k_1} is also unstable.

Proposition 1 (Local stability of the predator-only equilibrium) *The axial equilibrium $E_{k_2} = (0, k_2)$ satisfies the following:*

- *It is locally asymptotically stable if $r_1 < pk_2$,*
- *It is non-hyperbolic if $r_1 = pk_2$,*
- *It is unstable if $r_1 > pk_2$.*

Proof The Jacobian at E_{k_2} is

$$J(E_{k_2}) = \begin{pmatrix} r_1 - pk_2 & 0 \\ \varepsilon p k_2 - \eta_2 r_2 & -r_2 \end{pmatrix},$$

whose eigenvalues are

$$\lambda_1 = r_1 - pk_2, \qquad \lambda_2 = -r_2 < 0.$$

Thus the sign of λ_1 determines the stability of E_{k_2}, giving the three cases above. ☐

Ecologically, the condition $r_1 < pk_2$ indicates that the predation pressure exerted by the predator at its carrying capacity is sufficiently strong to prevent the prey from invading the system. In this case, the predator-only equilibrium persists because prey growth cannot compensate for losses due to predation. Conversely, when $r_1 > pk_2$, the prey has a net positive growth even in the presence of maximal predator density, allowing it to invade and rendering the predator-only state unstable. The case $r_1 = pk_2$ represents an invasion threshold separating these two ecological regimes.

LOCAL STABILITY OF THE COEXISTENCE EQUILIBRIUM

The interior equilibrium E_* of system (1) represents coexistence of both species. Although its coordinates cannot be expressed in closed form, its local stability properties can be analyzed through the Jacobian matrix, complemented by numerical exploration of the parameter space.

Proposition 2 (Sign of the trace) *Let $E_* = (N_1, N_2)$ be any interior equilibrium in the feasible region, i.e. $N_1 > 0$, $N_2 > 0$, $k_1 - \eta_1 N_2 > 0$ and $k_2 - \eta_2 N_1 > 0$. Then the trace of the Jacobian at E_* satisfies*

$$\operatorname{tr} J(E_*) = -\frac{r_1 N_1}{k_1 - \eta_1 N_2} - \frac{r_2 N_2}{k_2 - \eta_2 N_1} < 0.$$

Proof Evaluating the Jacobian at E_* gives

$$\begin{pmatrix} -\dfrac{r_1 N_1}{k_1 - \eta_1 N_2} & N_1 \left(-\dfrac{r_1 \eta_1 N_1}{(k_1 - \eta_1 N_2)^2} - p \right) \\ N_2 \left(\varepsilon p - \dfrac{r_2 \eta_2 N_2}{(k_2 - \eta_2 N_1)^2} \right) & -\dfrac{r_2 N_2}{k_2 - \eta_2 N_1} \end{pmatrix}.$$

All quantities r_i, N_i, and the denominators $(k_i - \eta_i N_j)$ are positive in the feasible region, hence both diagonal entries are negative and the trace is strictly negative. ☐

Note 2 (Absence of Hopf bifurcations) *Because $\operatorname{tr} J(E_*)$ is strictly negative for all feasible interior equilibrium, the real part of the eigenvalues can never vanish while $\det J(E_*) > 0$. Therefore, no Hopf bifurcation can occur at an interior equilibrium of system (1), and limit cycles cannot originate locally from E_*.*

Theorem 2 *Let $E_* = (N_1, N_2)$ be any interior equilibrium of system (1) in the feasible region. If $\det J(E_*) > 0$, then E_* is locally asymptotically stable.*

Proof Since $\operatorname{tr} J(E_*) < 0$ for all feasible interior equilibrium (Proposition 2), the condition $\det J(E_*) > 0$ implies that both eigenvalues of $J(E_*)$ have negative real part. Thus, E_* is locally asymptotically stable. ☐

Note 3 *Let $E_* = (N_1, N_2)$ be an interior equilibrium of system (1) in the feasible region and define*

$$A = k_1 - \eta_1 N_2, \qquad B = k_2 - \eta_2 N_1.$$

Then the determinant of the Jacobian at E_* can be written as

$$\begin{aligned} \det J(E_*) = N_1 N_2 \Bigg[& \frac{r_1 r_2}{AB} + \varepsilon p^2 + \varepsilon p \frac{r_1 \eta_1 N_1}{A^2} \\ & - \frac{p r_2 \eta_2 N_2}{B^2} - \frac{r_1 r_2 \eta_1 \eta_2 N_1 N_2}{A^2 B^2} \Bigg], \end{aligned} \tag{7}$$

where $A > 0$ and $B > 0$ in the feasible region.

The analysis above shows that interior equilibrium may be either locally asymptotically stable or of saddle type, depending solely on the sign of $\det J(E_*)$. Along the curve where $\det J(E_*) = 0$, the equilibrium becomes non-hyperbolic, and numerical continuation in the (η_1, η_2)-plane (Figs. 2–4) reveals that this curve corresponds to the collision and disappearance of two interior equilibria. This behaviour is characteristic of a saddle–node bifurcation. To formalize this observation, and connect the numerical bifurcation diagram with the underlying mathematical structure of system (1), we state the following theorem.

Theorem 3 (Saddle–node bifurcation of interior equilibrium) *Let $\theta = (\eta_1, \eta_2)$ denote the pair of exploitation parameters, and consider system (1) as a one-parameter family with respect to η_1, keeping all remaining parameters fixed.*

Assume that there exist η_1^* and an interior equilibrium $E^* = (N_1^*, N_2^*)$ in the feasible region such that:

(H1) $F(E^*, \eta_1^*) = 0$, where $F = (F_1, F_2)$ is the right-hand side of system (1);

(H2) $\det J(E^*, \eta_1^*) = 0$ and $\operatorname{tr} J(E^*, \eta_1^*) < 0$, so that $J(E^*, \eta_1^*)$ has a simple zero eigenvalue and one strictly negative eigenvalue;

(H3) Let v and w be the right and left eigenvectors associated with the zero eigenvalue. Then the nondegeneracy and transversality conditions

$$w^\top F_{\eta_1}(E^*, \eta_1^*) \neq 0, \qquad w^\top D^2 F(E^*, \eta_1^*)[v, v] \neq 0$$

hold.

Then system (1) undergoes a generic saddle–node bifurcation of interior equilibrium at (E^*, η_1^*). For η_1 on one side of η_1^* there exist exactly two interior equilibria (one stable and one saddle), whereas for η_1 on the other side no interior equilibria exist.

Proof Under (H1) and (H2), the linearization $J(E^*, \eta_1^*)$ has a simple zero eigenvalue and a negative eigenvalue, so the center manifold is one-dimensional. Conditions (H3) ensure nondegeneracy of the unfolding. Standard saddle–node theory (e.g., Sotomayor's theorem; Kuznetsov *et al.* (1998); Guckenheimer and Holmes (2013)) implies that the reduced dynamics on the center manifold is locally equivalent to

$$\dot{z} = \alpha(\eta_1 - \eta_1^*) + \beta z^2 + \mathcal{O}\big(|z|^3 + |\eta_1 - \eta_1^*||z|\big),$$

with $\alpha\beta \neq 0$. This is the normal form of a saddle–node bifurcation, yielding the stated conclusions. ☐

In summary, interior equilibria in system (1) cannot generate oscillatory coexistence through a Hopf mechanism, since their Jacobian trace is always strictly negative. Local stability is determined solely by the sign of the determinant: equilibrium with $\det J(E_*) > 0$ are locally asymptotically stable, whereas those with $\det J(E_*) < 0$ are saddles. The transition between these regimes occurs along the saddle–node curve $\det J(E_*) = 0$, which explains the appearance and disappearance of coexistence states observed in the (η_1, η_2) parameter space.

COEXISTENCE-FAVOURING REGIME: $r_1 > pk_2$

We now investigate how the qualitative dynamics of system (1) vary across the (η_1, η_2) parameter space. These parameters control how strongly each species reduces the other's effective carrying capacity, and therefore the (η_1, η_2)-plane captures how asymmetries in resource exploitation govern coexistence, exclusion, and the emergence of saddle-type interior equilibrium.

First, consider the case in which the exclusion equilibrium $(0, k_2)$ is unstable, i.e. $r_1 > pk_2$, a condition that favours the existence of a stable coexistence equilibrium.

We fix $r_1 = 1.2$, $r_2 = 0.6$, $k_1 = 200$, $k_2 = 100$, $p = 0.01$, $\varepsilon = 0.1$, and treat η_1 and η_2 as bifurcation parameters. In the (η_1, η_2)-plane we distinguish three regions in which the system displays qualitatively different dynamics (Fig. 2(a)).

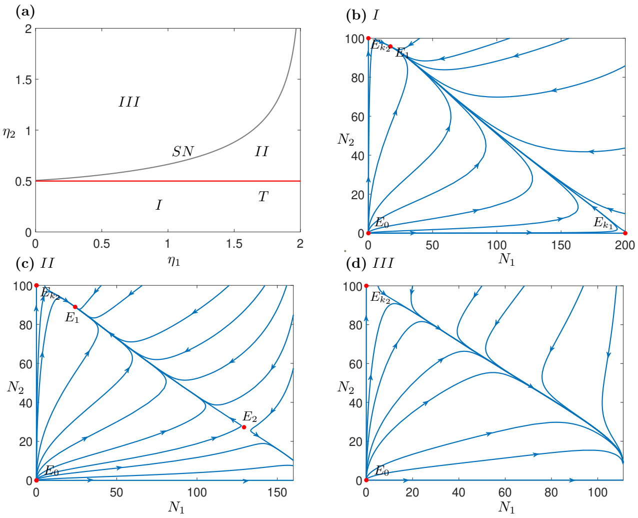

Figure 2: Potential dynamics of model (1). (a) Bifurcation structure in the (η_1, η_2)-plane. The red line T marks the loss of feasibility of E_2, and the grey curve SN denotes the saddle–node locus where two interior equilibria collide and disappear. Regions I–III correspond to qualitatively distinct dynamical regimes. Parameter values: $r_1 = 1.2$, $r_2 = 0.6$, $k_1 = 200$, $k_2 = 100$, $p = 0.01$, $\varepsilon = 0.1$. (b)–(d) Phase portraits illustrating the dynamics in regions I, II and III for $(\eta_1, \eta_2) = (1.2, 0.4)$, $(1.2, 0.6)$ and $(1.2, 0.9)$, respectively. In region I, a single stable coexistence equilibrium E_* attracts all trajectories. In region II, the stable coexistence equilibrium coexists with a saddle E_2. In region III, both interior equilibria are lost and coexistence is no longer possible.

We begin our description in region III, where the system admits no interior equilibria. In this region, the feasible quadrant contains no stable equilibrium, and coexistence of both species is not possible (Fig. 2(d)).

Crossing the gray curve SN from region III into region II generates two interior equilibria through a saddle–node bifurcation: a locally asymptotically stable equilibrium E_1 and a saddle equilibrium E_2 (Fig. 2(c)). Ecologically, E_1 represents a feasible coexistence state in which both species persist, whereas E_2 is unstable and therefore biologically irrelevant.

The red curve T marks the feasibility boundary: the axial equilibrium E_{k_1} becomes unfeasible when $N_1 < k_2/\eta_2$, and the interior saddle E_2 also turns unfeasible as one component becomes negative. Above T, neither E_{k_1} nor E_2 is feasible, whereas below it both lie in the feasible quadrant. Therefore, in region I the system admits four equilibria (E_0, E_{k_1}, E_{k_2}, and E_1). Among them, E_1 is the unique interior equilibrium and is locally asymptotically stable (Fig. 2(b)), corresponding biologically to a regime of robust coexistence in which both species persist despite predation pressure and competition for a shared resource.

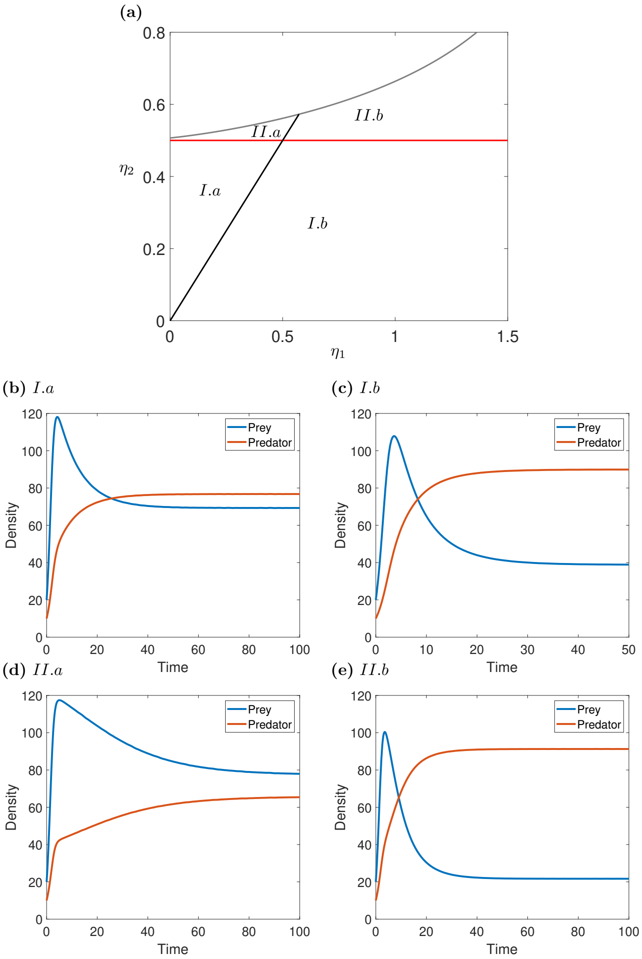

Figure 3: Coexistence regions in the (η_1, η_2) parameter space. (a) Bifurcation diagram showing how the black line $\eta_1 = \eta_2$ intersects four qualitatively distinct subregions (I.a, I.b, II.a and II.b). The red line marks the feasibility boundary for E_{k_1}, and the gray curves correspond to saddle–node collisions of interior equilibrium. Panels (b)–(e) display the temporal dynamics of prey and predator densities at representative points in each subregion: (b) $(\eta_1, \eta_2) = (0.1, 0.3)$ (region I.a), (c) $(0.4, 0.4)$ (region I.b), (d) $(0.52, 0.55)$ (region II.a), and (e) $(1.2, 0.55)$ (region II.b). These simulations illustrate how asymmetries in resource exploitation govern whether prey or predator dominates at equilibrium. All fixed parameter values are the same as in Fig. 2.

Since regions I and II both admit a stable coexistence equilibrium $E_* = E_1$, we next explore how equilibrium densities change across these regions. To this end, we consider points along the line $\eta_1 = \eta_2$, which partitions the coexistence domain into four subregions (Fig. 3(a)).

In subregions I.a and I.b, the predator density always exceeds the prey density at equilibrium. In region I.a, where $\eta_2 > \eta_1$, the predator surplus over the prey is moderate (Fig. 3(b)), whereas in region I.b, where $\eta_1 > \eta_2$, the difference between predator and prey densities is larger (Fig. 3(c)). In contrast, in region II.a the prey density exceeds the predator density (Fig. 3(d)), while in region II.b the predator again dominates (Fig. 3(e)). In summary, when $\eta_1 > \eta_2$ the predator population tends to exceed the prey population. When $\eta_1 < \eta_2$, the prey can dominate numerically, or the species' densities remain relatively similar.

REGIME ALLOWING PREDATOR EXCLUSION OF THE PREY: $r_1 < pk_2$

We now consider the second case, in which the exclusion equilibrium $(0, k_2)$ is locally stable. We fix $r_1 = 1.2$, $r_2 = 0.6$, $k_1 = 200$, $k_2 = 130$, $p = 0.01$, $\varepsilon = 0.1$. In Fig. 4(a), the curves in the (η_1, η_2)-plane divide the parameter space into four open regions, labeled *I–IV*, with qualitatively distinct dynamics.

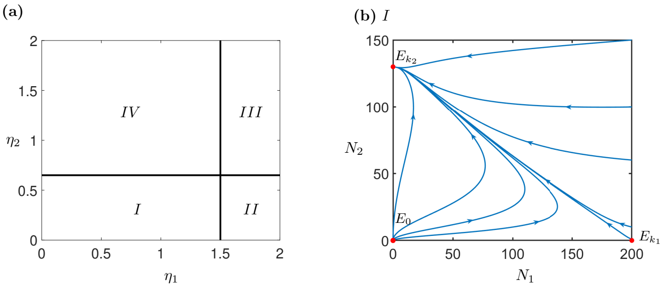

Figure 4: (a) Regions in the (η_1, η_2)-parameter space indicating where exclusion equilibrium and interior equilibrium exist. The horizontal and vertical boundaries separate four qualitatively distinct dynamical regimes. Parameter values: $r_1 = 1.2$, $r_2 = 0.6$, $k_1 = 200$, $k_2 = 130$, $p = 0.01$, $\varepsilon = 0.1$. (b) Phase portrait of model (1) in region I, where the predator-only equilibrium $(0, k_2)$ is globally attracting within the positive quadrant, leading to extinction of the prey.

In region I there is no positive coexistence equilibrium; hence coexistence between both species is not possible. Numerical simulations indicate that $(0, k_2)$ is globally attracting within the positive quadrant (Fig. 4(b)): for any positive initial condition the prey population goes extinct, whereas the predator population converges to its carrying capacity k_2.

In region II the only boundary equilibrium is $(k_1, 0)$, which is always unstable, and no positive coexistence equilibrium with ecological meaning exists. In region III there are no exclusion equilibrium and at least one interior equilibrium in the feasible quadrant, which is of saddle type. Finally, in region IV the only exclusion equilibrium is $(0, k_2)$, and there exists at least one interior equilibrium in the feasible quadrant, which is again of saddle type. In both regions III and IV, trajectories approach either the predator-only state or diverge away from the unstable coexistence equilibrium, depending on initial conditions.

When $r_1 < pk_2$, predators can suppress the prey to extinction, preventing invasion. In contrast, if $r_1 > pk_2$, predators are unable to exclude the prey, allowing a stable coexistence equilibrium to emerge. These two conditions divide the parameter space into qualitatively distinct dynamical regimes.

DISCUSSION

In this paper, we examined the dynamics of a simple predator–prey system in which both species exploit a shared resource. The model preserves the simplicity of the Lotka–Volterra framework while incorporating exploitative competition in an implicit form. This structure is particularly useful for studying intraguild-like interactions when the shared resource remains at a steady density, as assumed in classical ecological theory (Schaffer, 1981). This perspective facilitates ecological interpretation and enables a transparent classification of coexistence and exclusion regimes.

The results show that the exclusion equilibrium E_{k_2} becomes locally stable when the reproductive potential of the prey is lower than the combined effects of predation and shared-resource competition, that is, when $r_1 < pk_2$ and $\eta_1 < k_1/k_2$. Under these conditions, the prey declines to low density or extinction while the predator approaches its carrying capacity. This outcome is ecologically plausible, since predation imposes additional mortality on the prey population (Okuyama and Ruyle, 2003). An illustrative example is the Argentine ant, a globally invasive species that combines exploitative competition with direct predation on native ants, ultimately driving local extinctions (Human and Gordon, 1996; Damas-Moreira *et al.*, 2020). Our model captures this mechanism: an invasive species with both competitive and predatory advantages, often associated with higher reproductive potential (Pöckl, 2009; Jänes *et al.*, 2015), can exclude a native counterpart.

Conversely, coexistence requires the opposite inequality, $r_1 > pk_2$, although this condition alone does not guarantee the existence of a positive equilibrium. For some parameter combinations, no feasible interior equilibrium exists (Fig. 2(d)), consistent with theoretical predictions that prey persistence under omnivory may be rare (Holt and Polis, 1997; Diehl and Feißel, 2000; Mylius *et al.*, 2001; Křivan and Diehl, 2005). Nevertheless, the model also identifies parameter regions where coexistence does occur (regions I and II in Fig. 2(a)), supporting empirical observations that omnivores and their prey often persist together in natural systems (HilleRisLambers *et al.*, 2006; Amarasekare, 2008). When the interior equilibrium E_* exists, it may be locally asymptotically stable, thereby ensuring coexistence for a range of biologically relevant initial conditions (Fig. 2(b)).

The relative strength of resource exploitation by each species further determines their long-term abundances. As

doi: 10.58560/rmmsb.v05.e.025.04

shown in Fig. 3(b) to Fig. 3(e), the ratio between η_1 and η_2 controls which species is numerically dominant at equilibrium. When $\eta_1 > \eta_2$, meaning the prey consumes more resource per capita or exploits it more intensely, the predator eventually outnumbers the prey. When $\eta_1 < \eta_2$, the prey may numerically exceed or match the predator. This pattern resembles coexistence mechanisms observed in marine systems where sessile and mobile species interact through predation while simultaneously competing for oxygen as a limiting resource (Ferguson *et al.*, 2013). Differential exploitation of the shared resource may therefore facilitate coexistence even in the presence of strong antagonistic interactions. From an empirical perspective, the parameters η_1 and η_2—which quantify the intensity of exploitative competition mediated by the shared resource—could be inferred through exclusion experiments or indirectly estimated from consumption rates and measurements of resource availability.

Finally, the model predicts the absence of population cycles for all parameter combinations. Although predator–prey interactions can generate oscillatory dynamics (Erbach *et al.*, 2013), the addition of exploitative competition suppresses such oscillations by imposing mutually negative density effects that stabilize the system (Petren and Case, 1996). Another important factor underlying this result is the assumption of a linear (type I) functional response, which is adopted to focus on the dynamical effects of exploitative competition within a reduced and analytically tractable framework. Extending this work to incorporate nonlinear functional responses, such as type II or type III, would be a natural next step, as these can enable limit cycles and modify the conditions under which coexistence is possible (Fussmann and Blasius, 2005; Abrams and Fung, 2010).

ACKNOWLEDGMENTS

The authors would like to thank Dr. Fernando Momo and Dr. Leonardo Saravia for their insightful comments and suggestions during the initial stage the manuscript.

DECLARATION OF USE OF ARTIFICIAL INTELLIGENCE

The authors declare that no Artificial Intelligence (AI) tools were used for mathematical modeling, figure generation, or any other part of the scientific content of this manuscript. AI assistance was used exclusively to improve the readability of the English writing, without generating original scientific text, ideas, or results. The authors take full responsibility for the content of the manuscript and for ensuring that all scientific claims, derivations, and conclusions are their own.

CONTRIBUTION OF THE AUTHORS (CREDIT)

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Software: Rivera.

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Recommended Citation: Enith A. Gómez-Hernández *et al.* (2025). *‘Predation and exploitative competition in a two-dimensional system’*. Rev. model. mat. sist. biol. Vol.5, e25R04, doi:10.58560/rmmsb.v05.e.025.04