Dynamic Effects of Fear-Dependent Refuge and Fear Effects on Lotka-Volterra Amensalism Model

Yuting Huang, Guangwen He and Fengde Chen

Abstract-Amensalism, a critical interspecific interaction where one species is harmed while the other remains unaffected, has been extensively modeled, yet the synergistic effects of behavioral adaptations like fear and refuge strategies remain underexplored. This study proposes an enhanced Lotka-Volterra amensalism model integrating fear-dependent refuge dynamics (modeled via a saturation function $s(y) = \frac{s_{\max}ky}{1+ky}$) and bidirectional fear regulation (suppressing birth rate $\frac{e_1}{1+k_1y}$ and enhancing mortality $(1 + k_2 y)e_2$). Theoretical analysis reveals that sufficient refuge capacity (s_{max}) enables the victim species to stabilize coexistence by mitigating amensalistic harm, while fear effects induce bifurcations through dual physiologicalbehavioral pathways. Numerical simulations demonstrate critical thresholds for extinction-persistence transitions, governed by s_{max}/k synergies and fear coefficients k_1, k_2 . Key findings include: (1) Refuge effects dominate in reducing direct harm, (2) Fear-refuge interactions destabilize equilibria under high stress, and (3) Global stability of the positive equilibrium ensures longterm coexistence if $\Delta > 0$. This work advances ecological theory by unifying behavioral adaptations into amensalism dynamics and offers actionable insights for biodiversity conservation, such as optimizing refuge resources to buffer species against anthropogenic stressors.

Index Terms—Amensalism, Lotka-Volterra model, Fear effect, Refuge effect, Behavioral adaptation strategies, System stability, Population persistence, Nonlinear coupling

I. INTRODUCTION

A. Research Background and Significance

Amensalism is a crucial interspecific interaction in ecosystems, where one species (the victim) experiences detrimental effects while the other (the harmful species) remains unaffected. This relationship is widespread in natural systems; for instance, grasshoppers unintentionally suppress caterpillar reproduction and growth through spatial interference [1]. In recent years, this research domain has garnered considerable attention globally, resulting in a wealth of findings across continuous [4], [5], discrete [32], [44], and hybrid modeling frameworks. Key advances include investigations into functional responses [5], Allee effects [6], refuge dynamics [7], [24], and human harvesting impacts [12], [40].

Despite progress, classical Lotka-Volterra amensalism models [4] remain limited by static parameter assumptions, neglecting behavioral adaptations such as fear-induced refuge utilization. While refuge effects have been partially explored in predator-prey systems [5], their role in amensalism—particularly when modulated by fear-driven behavioral

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feedback—remains unaddressed. This gap is ecologically significant, as refuge strategies (e.g., habitat shifts in caterpillars to avoid grasshoppers [1]) critically influence species survival under stress.

B. Research Status and Limitations

Current studies predominantly focus on isolated ecological factors rather than synergistic behavioral strategies. For example:

- Traditional refuge models [24] assume fixed proportions, ignoring density-dependent adjustments;
- Fear effect analyses [3] in predator-prey systems lack integration with refuge dynamics;
- Existing frameworks [4], [5] overlook bidirectional fear regulation (simultaneous birth suppression and mortality enhancement).

These limitations lead to deviations from ecological reality. Specifically, *fear-dependent refuge effects*—where refuge utilization dynamically responds to harmful species density—have not been mathematically formalized, despite their observed ecological prevalence [1].

C. Innovations and Contributions

To address these limitations, we propose an enhanced Lotka-Volterra amensalism model with three key innovations. First, we introduce a fear-dependent refuge effect modeled by the saturation function:

$$s(y) = \frac{s_{\max}ky}{1+ky},$$

which captures capacity-limited refuge dynamics. Second, we incorporate bidirectional fear regulation, where fear suppresses the victim's birth rate via $\frac{e_1}{1+k_1y}$ and elevates mortality through $(1+k_2y)e_2$. Third, we conduct integrated theoretical-numerical analysis to reveal critical thresholds governing extinction-persistence transitions.

This work advances ecological theory by unifying behavioral adaptations into amensalism dynamics. Practically, it provides actionable insights for conservation strategies, such as optimizing refuge resources (s_{max}) to buffer species against anthropogenic stressors. For more works on amensalism species, one could refer to [1]-[51] and the references therein.

II. MODEL CONSTRUCTION

A. Modeling framework and equation derivation

Building upon the Lotka-Volterra amensalism framework, this study integrates **fear effects** and **dynamic refuge effects** to establish an enhanced model:

$$\frac{dx}{dt} = x \left(\underbrace{\frac{e_1}{1+k_1y}}_{\text{Fear-induced birth suppression}} - \underbrace{(1+k_2y)e_2}_{\text{Fear-enhanced mortality}} - \underbrace{b_1x}_{\text{Intraspecific competition}} - \underbrace{c_1\left(1 - \frac{s_{\max}ky}{1+ky}\right)y}_{\text{Refuge-mediated mitigation}} \right) \\
= x \left[B(x,y) - D(x,y) - I(x,y) - P(x,y) \right],$$

$$\frac{dy}{dt} = y \left(a_2 - c_2y\right).$$
(1)

The model comprises the following key components:

- Bidirectional fear effects: The birth rate term $\frac{e_1}{1+k_1y}$ reflects reproductive suppression in x due to y's density, while the mortality term $(1 + k_2 y)e_2$ quantifies physiological stress induced by y.
- **Dynamic refuge effect**: The saturation function s(y) = $\frac{s_{\max}ky}{1+ky}$ models x's refuge utilization increasing with y's density, constrained by capacity s_{max} .
- The harmful species dynamics: y follows classical logistic growth, consistent with its amensalistic independence from x.

B. Ecological interpretations

The model extends classical theory by incorporating behavioral ecology perspectives:

- Fear effects: Capture the non-lethal impacts of predation risk, such as reduced foraging time in caterpillars due to grasshopper activity [1].
- Refuge effects: Account for spatial heterogeneity, which modulates interspecific interactions.
- Dynamic coupling: Overcome the limitations of static refuge assumptions by linking y's density to real-time behavioral adjustments in x.

C. Parameter definitions and ecological context

See Table I.

D. Ecological measurement of key parameters

Detailed protocols:

• s_{max} estimation: UAV remote sensing combined with habitat preference regression:

$$s_{\text{observed}}(x) = s_{\max} \cdot \exp\left(-\alpha x + \beta y\right)$$

• k calibration: Refuge usage dynamics under controlled y densities:

$$k = \frac{\Delta s}{\Delta t \cdot \bar{g}}$$

E. Ecological plausibility verification See Table III.

III. EXISTENCE ANALYSIS OF EQUILIBRIUM POINTS

Equilibrium points characterize the long-term behavior of dynamical systems. We derive equilibrium points by solving the following system:

$$x\left(\frac{e_1}{1+k_1y} - (1+k_2y)e_2 - b_1x -c_1\left(1 - \frac{s_{\max}ky}{1+ky}\right)y\right) = 0,$$

$$y(a_2 - c_2y) = 0$$
(2)

Theorem 3.1 The system always has equilibrium points $E_0(0,0)$ and $E_1(0,\frac{a_2}{c_2})$. When

$$e_1 > e_2 \tag{3}$$

holds, the system admits equilibrium $E_2(\frac{e_1-e_2}{b_1}, 0)$. If

$$\frac{e_1}{1+k_1\frac{a_2}{c_2}} - \left(1+k_2\frac{a_2}{c_2}\right)e_2 -c_1\left(1-\frac{s_{max}\cdot k\frac{a_2}{c_2}}{1+k\frac{a_2}{c_2}}\right)\frac{a_2}{c_2} > 0$$
(4)

is satisfied, the system possesses a positive equilibrium $E^*(x^*, y^*)$, where

$$x^{*} = \frac{1}{b_{1}} \left(\frac{e_{1}}{1 + k_{1} \frac{a_{2}}{c_{2}}} - \left(1 + k_{2} \frac{a_{2}}{c_{2}} \right) e_{2} - c_{1} \left(1 - \frac{s_{\max} \cdot k \frac{a_{2}}{c_{2}}}{1 + k \frac{a_{2}}{c_{2}}} \right) \frac{a_{2}}{c_{2}} \right),$$
(5)
$$y^{*} = \frac{a_{2}}{c_{2}}.$$

Proof. From the second equation of system (2), we have

$$y = 0 \tag{6}$$

or

$$y = \frac{a_2}{c_2}.\tag{7}$$

Substituting y = 0 into the first equation of system (2) yields x = 0 or $x = \frac{e_1 - e_2}{b_1}$ (when $e_1 > e_2$). Thus, equilibria $E_0(0,0)$ and $E_2(\frac{e_1 - e_2}{b_1}, 0)$ exist. For $y = \frac{a_2}{c_2}$, substituting into the first equation gives x = 0

or

$$\frac{e_1}{1+k_1y} - (1+k_2y)e_2 - b_1x - c_1\left(1 - \frac{s_{\max}ky}{1+ky}\right)y = 0.$$

This implies the boundary equilibrium $E_1(0, \frac{a_2}{c_2})$ exists and, under condition (4), the positive equilibrium $E^*(x^*, y^*)$ exists. Theorem 3.1 is thus proved.

IV. LOCAL STABILITY ANALYSIS OF EQUILIBRIUM POINTS

The local stability of equilibrium points is analyzed through the eigenvalues of the Jacobian matrix. The Jacobian matrix J(x, y) is defined as:

$$J(x,y) = \begin{pmatrix} \frac{\partial f}{\partial x} & \frac{\partial f}{\partial y} \\ \frac{\partial g}{\partial x} & \frac{\partial g}{\partial y} \end{pmatrix}, \tag{8}$$

Symbol	Name	Ecological meaning
e_1	Maximum birth rate	Theoretical maximum reproduction rate of x without fear effects
k_1	Birth fear coefficient	Per-unit y density impact on x 's birth suppression
e_2	Base mortality rate	Natural mortality rate of x without fear effects
k_2	Mortality fear coefficient	Per-unit y density impact on x 's mortality elevation
b_1	Intraspecific competition coeffi- cient	Growth inhibition due to resource competition in x
c_1	Amensalism coefficient	Direct negative impact strength of y on x
a_2	Intrinsic growth rate	Maximum growth rate of y under ideal conditions
c_2	Environmental carrying capacity	Self-regulation coefficient of y due to resource limitations
$s_{ m max}$	Maximum refuge proportion	Upper limit of available refuge space $(0 < s_{max} < 1)$
k	Refuge response rate	Sensitivity of x 's refuge behavior to y 's density

TABLE I: Ecological interpretation of model parameters

TABLE	II:	Ecol	logical	measurement	methods	for	key	parameters

Parameter	Ecological measurement	Typical methods
s _{max}	Maximum refuge capacity	Vegetation cover analysis via NDVI
k	Behavioral response rate	Laboratory-based ethological experiments

TABLE III: Ecological plausibility tests for critical parameter combinations

Parameter combination	Expected ecological outcome	Validation method
$k_1 \gg k_2$	Birth suppression domi- nance	Fix y , observe x vs. k_1 curves
$s_{\max} \rightarrow 1$	Full refuge utilization	Compute $s(y)$ at $y = y^*$
$k \rightarrow 0$	Sluggish refuge response	Recovery time under pulsed disturbances

TABLE IV: Differences among traditional studies and our study

Research Type	Core Assumption	Innovation of This Study
Traditional Refuge Models	Refuge utilization is in- dependent of the harmful species' population den- sity	Introduced a fear-effect- driven dynamic response mechanism
Fear Effect Studies	Single amensalism system	Coupled amensalism ef- fects with refuge effects
Spatiotemporal Extension Models	Static or periodic refuge distribution	Established a continuous refuge response function

where:

$$f(x,y) = x \left(\frac{e_1}{1+k_1y} - (1+k_2y)e_2 - b_1x -c_1 \left(1 - \frac{s_{\max} \cdot ky}{1+ky}\right)y \right),$$

$$g(x,y) = y (a_2 - c_2y).$$
(9)

Theorem 4.1 The boundary equilibria $E_0(0,0)$ and $E_2(\frac{e_1-e_2}{b_1},0)$ are unstable. Let

$$\Delta = \frac{e_1}{1 + k_1 \frac{a_2}{c_2}} - (1 + k_2 \frac{a_2}{c_2})e_2$$

$$-c_1 \left(1 - \frac{s_{max} \cdot k \frac{a_2}{c_2}}{1 + k \frac{a_2}{c_2}}\right) \frac{a_2}{c_2}.$$
(10)

If $\Delta < 0$, then E_1 is locally stable; if $\Delta > 0$, E_1 is unstable. When $\Delta > 0$, the positive equilibrium E^* exists and is locally stable.

Proof. At $E_0(0,0)$, the Jacobian matrix is:

$$J(0,0) = \begin{pmatrix} e_1 - e_2 & 0\\ 0 & a_2 \end{pmatrix}.$$

The eigenvalues are $\lambda_1 = e_1 - e_2$ and $\lambda_2 = a_2$. Since $a_2 > 0$, E_0 is always unstable.

At $E_1(0, \frac{a_2}{c_2})$, the Jacobian matrix is:

$$J(0, \frac{a_2}{c_2}) = \begin{pmatrix} \Delta & 0\\ 0 & -a_2 \end{pmatrix}.$$

The eigenvalues are $\lambda_1 = \Delta$ and $\lambda_2 = -a_2$. As $\lambda_2 < 0$, the stability of E_1 depends on Δ :

- $\Delta < 0 \Rightarrow E_1$ is locally stable;
- $\Delta > 0 \Rightarrow E_1$ is unstable.
- At $E_2(\frac{e_1-e_2}{b_1}, 0)$, the Jacobian matrix is:

$$J\left(\frac{e_1 - e_2}{b_1}, 0\right) = \begin{pmatrix} -(e_1 - e_2) & -\frac{(e_1 - e_2)(e_1k_1 + e_2k_2 + e_1)}{b_1} \\ 0 & a_2 \end{pmatrix}$$

The eigenvalues are $b_1 = (e_1 - e_2)$ and $b_2 = 0$. Since

The eigenvalues are $\lambda_1 = -(e_1 - e_2)$ and $\lambda_2 = a_2$. Since $a_2 > 0$, E_2 is always unstable.

At the positive equilibrium $E^*(x^*, y^*)$, the Jacobian matrix is:

 $J(x^*, y^*) = \begin{pmatrix} -b_1 x^* & \Gamma \\ 0 & -c_2 y^* \end{pmatrix},$

where

$$\Gamma \stackrel{\text{def}}{=} -\frac{e_1 k_1 x^*}{(1+k_1 y^*)^2} - e_2 k_2 x^*
-c_1 x^* \left(1 - \frac{s_{\max} \cdot k y^*}{1+k y^*}\right)
+c_1 x^* \frac{s_{\max} \cdot k}{(1+k y^*)^2} y^*.$$
(11)

The eigenvalues are $\lambda_1 = -b_1 x^*$ and $\lambda_2 = -c_2 y^*$. Since $b_1 > 0$ and $c_2 > 0$, E^* is always locally stable.

Theorem 4.1 is thus proved.

Remark 4.1 Theorem 4.1 implies:

- Boundary equilibria E_0 and E_2 are always unstable;
- Stability of E_1 depends on the net growth rate of x at $y = \frac{a_2}{c_2}$;
- The positive equilibrium E^* is locally stable whenever it exists.

V. EXTINCTION ANALYSIS

Following we will investigate the extinction property of the victim species. Indeed, we have:

() T

Theorem 5.1 If $\Delta < 0$ (where Δ is defined in (10), then the boundary equilibrium $E_1(0, \frac{a_2}{c_2})$ is globally asymptotically stable.

Proof Consider the second equation in system (1):

$$\frac{dy}{dt} = y(a_2 - c_2 y),\tag{12}$$

whose solution is:

$$y(t) = \frac{a_2 y(0)}{c_2 y(0) + (a_2 - c_2 y(0))e^{-a_2 t}}.$$
 (13)

For any initial condition y(0) > 0, as $t \to +\infty$:

$$\lim_{d \to +\infty} y(t) = \frac{a_2}{c_2}.$$
(14)

Rewriting the first equation in system (1):

$$\frac{dx}{dt} = x \left[A(t) - b_1 x \right] \tag{15}$$

where

$$A(t) = \frac{e_1}{1 + k_1 y(t)} - (1 + k_2 y(t)) e_2 -c_1 \left(1 - \frac{s_{\max} k y(t)}{1 + k y(t)} \right) y(t).$$
(16)

As $t \to +\infty$, $y(t) \to \frac{a_2}{c_2}$, hence:

$$A(t) \rightarrow \Delta < 0$$
 (by Theorem 5.1 condition). (17)

Select sufficiently large T > 0 such that for $t \ge T$:

$$A(t) \le \frac{\Delta}{2} < 0. \tag{18}$$

Then for $t \geq T$:

$$\frac{dx}{dt} \le x \left(\frac{\Delta}{2} - b_1 x\right). \tag{19}$$

Consider the comparison equation:

$$\frac{d\xi}{dt} = \xi \left(\frac{\Delta}{2} - b_1 \xi\right),\tag{20}$$

with solution:

$$\xi(t) = \frac{\frac{\Delta}{2}\xi(T)}{b_1\xi(T) + \left(\frac{\Delta}{2} - b_1\xi(T)\right)e^{-\frac{\Delta}{2}(t-T)}}.$$
 (21)

Since $\Delta/2 < 0$, we have:

$$\lim_{t \to +\infty} \xi(t) = 0.$$
(22)

By the comparison principle:

$$x(t) \le \xi(t) \Rightarrow \lim_{t \to +\infty} x(t) = 0.$$
 (23)

Construct the Lyapunov function:

$$V(x,y) = x + \frac{1}{2} \left(y - \frac{a_2}{c_2} \right)^2.$$
 (24)

Compute its derivative:

$$\frac{dV}{dt} = x \left[\frac{e_1}{1 + k_1 y} - (1 + k_2 y) e_2 - b_1 x - c_1 \left(1 - \frac{s_{\max} k y}{1 + k y} \right) y \right] + \left(y - \frac{a_2}{c_2} \right) y (a_2 - c_2 y)$$
(25)

Under $\Delta < 0$, from (14), there exists sufficiently large T such that for t > T:

$$\frac{e_1}{1+k_1y} - (1+k_2y)e_2 - c_1\left(1 - \frac{s_{\max}ky}{1+ky}\right)y \le -\alpha < 0.$$
(26)

Therefore:

$$\frac{dV}{dt} \le -\alpha x - b_1 x^2 - c_2 \left(y - \frac{a_2}{c_2}\right)^2$$
$$\le -\min\{\alpha, c_2\} \left(x + \left(y - \frac{a_2}{c_2}\right)^2\right)$$
$$= -\min\{\alpha, c_2\} V(x, y)$$

This implies V(x, y) decays exponentially, leading to $(x(t), y(t)) \rightarrow (0, \frac{a_2}{c_2}).$

Theorem 5.1 is thus proved.

VI. GLOBAL STABILITY ANALYSIS OF POSITIVE Equilibrium

Global stability refers to the system converging to an equilibrium from any initial condition. We analyze global stability using Dulac's criterion[51].

Theorem 6.1 If $\Delta > 0$ (where Δ is defined in (10)), then the positive equilibrium $E^*(x^*, y^*)$ is globally asymptotically stable.

Proof. First, via comparison principles we establish:

$$\lim_{\substack{t \to \infty \\ \lim \sup y(t) \leq \frac{a_2}{c_2}}} x(t) \leq \frac{1}{b_1} (e_1 - e_2),$$
(27)

Select the Dulac function:

$$B(x,y) = \frac{1}{xy} \quad (x > 0, y > 0).$$
(28)

Define the vector field $F = (F_1, F_2)$:

$$F_{1} = x \left[\frac{e_{1}}{1 + k_{1}y} - (1 + k_{2}y)e_{2} - b_{1}x - c_{1} \left(1 - \frac{s_{\max}ky}{1 + ky} \right) y \right]$$

$$F_{2} = y(a_{2} - c_{2}y)$$
(29)

Compute the weighted divergence:

$$\nabla \cdot (B\mathbf{F}) = \frac{\partial}{\partial x} \left(\frac{F_1}{xy} \right) + \frac{\partial}{\partial y} \left(\frac{F_2}{xy} \right)$$
$$= \frac{1}{y} \frac{\partial}{\partial x} \left(\frac{F_1}{x} \right) + \frac{1}{x} \frac{\partial}{\partial y} \left(\frac{F_2}{y} \right)$$
(30)

Note that:

$$\frac{\partial}{\partial x} \left(\frac{F_1}{x} \right) = -b_1 \tag{31}$$

and

$$\frac{\partial}{\partial y} \left(\frac{F_2}{y}\right) = -c_2 \tag{32}$$

Thus:

$$\nabla \cdot (B\mathbf{F}) = -\left(\frac{b_1}{y} + \frac{c_2}{x}\right) < 0 \quad \forall (x, y) \in \mathbb{R}^+ \times \mathbb{R}^+$$
(33)

By Dulac's criterion:

- Strict negativity of ∇ · (BF) in ℝ⁺ × ℝ⁺ precludes periodic orbits
- Poincaré-Bendixson theorem guarantees global convergence to the unique positive equilibrium E^{\ast}

Theorem 6.1 is thus proved.

VII. PERSISTENCE ANALYSIS

Persistence refers to all species maintaining positive population densities indefinitely, while extinction implies at least one species density approaches zero. We analyze persistence through system dynamics.

A. Persistence of the harmful species y

Theorem 7.1. *The the harmful species species y is always persistent.*

Proof. The dynamics of y follow the classical logistic equation:

$$\frac{dy}{dt} = y \left(a_2 - c_2 y \right).$$

Given $a_2 > 0$ and $c_2 > 0$, y persists indefinitely and converges to $\frac{a_2}{c_2}$. Theorem 7.1 is proved.

B. Persistence of victim species x

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Theorem 7.2 If $\Delta > 0$ (where Δ is defined in (10)), the victim species x is persistent.

Proof. Given $\Delta > 0$ and the continuity of

$$F(y) = \frac{e_1}{1+k_1y} - (1+k_2y)e_2 - c_1\left(1 - \frac{s_{\max}ky}{1+ky}\right)y$$

for y > 0, there exists sufficiently small $\varepsilon > 0$ such that:

$$\frac{e_1}{1+k_1(\frac{a_2}{c_2}+\varepsilon)} - \left(1+k_2(\frac{a_2}{c_2}+\varepsilon)\right)e_2$$
$$-c_1\left(1-\frac{s_{\max}\cdot k(\frac{a_2}{c_2}-\varepsilon)}{1+k(\frac{a_2}{c_2}-\varepsilon)}\right)\left(\frac{a_2}{c_2}+\varepsilon\right)$$
$$\varepsilon.$$
(34)

By Theorem 7.1, for this $\varepsilon > 0$, there exists T > 0 such that for t > T:

$$\frac{a_2}{c_2} - \varepsilon < y(t) < \frac{a_2}{c_2} + \varepsilon.$$
(35)

From (34), (35), and the first equation of (1), for t > T:

$$\frac{dx}{dt} \geq x \left(\frac{e_1}{1 + k_1(\frac{a_2}{c_2} + \varepsilon)} - \left(1 + k_2(\frac{a_2}{c_2} + \varepsilon)\right) e_2 - c_1 \left(1 - \frac{s_{\max} \cdot k(\frac{a_2}{c_2} - \varepsilon)}{1 + k(\frac{a_2}{c_2} - \varepsilon)}\right) \left(\frac{a_2}{c_2} + \varepsilon\right) - b_1 x \right) \\ > x(\varepsilon - b_1 x).$$
(36)

This implies:

$$\liminf_{t \to +\infty} x(t) \ge \frac{\varepsilon}{b_1}.$$
(37)

Theorem 6.1 already established:

$$\limsup_{t \to \infty} x(t) \le \frac{1}{b_1} \left(e_1 - e_2 \right).$$
(38)

Combining (37) and (38), x persists under $\Delta > 0$. Theorem 7.2 is proved.

VIII. KEY PARAMETER ANALYSIS

The impacts of four key parameters— k_1 , k_2 , s_{max} , and k—on system dynamics are analyzed as follows:

A. Impact coefficient of fear effect on birth rate (k_1)

Parameter k_1 quantifies the fear-induced suppression strength of y's density on x's birth rate. Key effects include:

- Increased k_1 reduces x's birth rate $\frac{e_1}{1+k_1y}$, lowering x's net growth rate;
- Excessively large k_1 may drive x to extinction by critically suppressing reproduction;
- Smaller k_1 mitigates y's interference, allowing x to persist.

B. Impact coefficient of fear effect on mortality (k_2)

Parameter k_2 governs fear-induced mortality enhancement in x. Key effects include:

- Increased k₂ elevates x's mortality (1 + k₂y)e₂, destabilizing x;
- Extreme k₂ values cause rapid x decline through physiological stress;
- Smaller k_2 buffers mortality pressure, favoring x persistence.

C. Refuge capacity upper limit (s_{max})

Parameter s_{max} defines the maximum refuge proportion. Key effects include:

- Higher s_{max} enhances x's refuge-mediated protection, boosting net growth;
- Sufficiently large s_{max} enables x to resist y's amensalism stably;
- Lower s_{max} exacerbates y's harm, risking x extinction.

D. Refuge response rate (k)

Parameter k controls how rapidly x's refuge use responds to y's density. Key effects include:

- Higher k accelerates refuge adoption as y increases, buffering x promptly;
- Large k allows early refuge utilization at low y densities, stabilizing x;
- Smaller k delays refuge responses, amplifying y's transient impacts on x.

Synthesis:

- k_1 and k_2 regulate extinction-persistence transitions via birth/mortality pathways;
- s_{max} and k determine x's adaptive capacity against amensalism;
- High k_1/k_2 destabilizes x, while high s_{max}/k promotes coexistence.

IX. NUMERICAL SIMULATIONS

Example 9.1 Consider the following Lotka-Volterra amensalism system:

$$\frac{dx}{dt} = x \left(\frac{1}{1+2y} - (1+y) \cdot 0.5 - 0.1x - 0.5 \left(1 - \frac{0.5 \cdot 0.1 \cdot y}{1+0.1y} \right) y \right),$$

$$\frac{dy}{dt} = y(1-y).$$
(39)

Initial conditions: (x(0), y(0)) = (1, 0.5), (2, 5), (3, 2), (4, 3),time range $t \in [0, 10]$. At this time, we take

$$e_1 = 1, \quad e_2 = 0.5, \quad k_1 = 2, \quad k_2 = 1,$$

 $b_1 = 0.1, \quad c_1 = 0.5, \quad a_2 = 1, \quad c_2 = 1,$
 $s_{\max} = 0.5, \quad k = 0.1.$

According to Theorem 5.1, calculate the threshold Δ :

$$y^* = \frac{a_2}{c_2} = 1,$$

$$\Delta = \frac{e_1}{1 + k_1 y^*} - (1 + k_2 y^*) e_2 - c_1 \left(1 - \frac{s_{\max} k y^*}{1 + k y^*} \right) y^*$$

$$= \frac{1}{3} - 1 - 0.5 \left(1 - \frac{0.05}{1.1} \right) \approx -1.144 < 0.$$

Since $\Delta < 0$, Theorem 5.1 predicts that the victim species x tends to extinction, while the harmful species y tends to $\frac{a_2}{c_2} = 1$, which are verified by Figures 1, 2 and 3.

Example 9.2 Consider the following Lotka-Volterra amensalism system:

$$\frac{dx}{dt} = x \left(\frac{1}{1+0.5y} - (1+0.2y)0.3 - 0.1x -0.2\left(1 - \frac{0.8 \cdot 0.5y}{1+0.5y}\right)y \right)$$
(40)
$$\frac{dy}{dt} = y(1-y)$$

Select four sets of initial values: (0.5, 0.5), (2, 0.1), (1.5, 2), (3, 3), time range $t \in [0, 40]$. At this time, the parameter values are:

 $e_1 = 1, e_2 = 0.3, k_1 = 0.5, k_2 = 0.2, b_1 = 0.1, c_1 = 0.2$ $a_2 = 1, c_2 = 1, s_{\max} = 0.8, k = 0.5.$

Calculate:

$$y^* = \frac{a_2}{c_2} = 1,$$

$$\Delta = \frac{1}{1+0.5\cdot 1} - (1+0.2\cdot 1)0.3$$

$$-0.2\left(1 - \frac{0.8\cdot 0.5\cdot 1}{1+0.5\cdot 1}\right)1$$

$$= \frac{2}{3} - 0.36 - 0.1467 \approx 0.16 > 0$$

Since $\Delta > 0$, Theorem 6.1 guarantees the global asymptotic stability of the positive equilibrium $E^*(1.6, 1)$, which is confirmed by Figure 3.

Example 9.3 In system (1), fix the parameters:

$$e_1 = 1.0, \quad e_2 = 0.3, \quad k = 0.5,$$

 $b_1 = 0.1, \quad c_1 = 0.2, \quad a_2 = 1.0,$
 $c_2 = 1.0, \quad s_{\text{max}} = 0.8,$

and initial condition (x(0), y(0)) = (3, 0.5).

(1) Take $k_2 = 0.2$, vary k_1 . Figure 6 shows the relationship between x^* and k_1 . From the figure, it can be seen that there is a threshold $k_1 = 0.9736842104$. When $k < k_1$, x^* exists; when $k > k_1$, the victim population x goes extinct. Figure 7 shows the time series solutions corresponding to different k_1 values. It can be seen that as k_1 increases, the final equilibrium density of x decreases, eventually leading to extinction.

(2) Take $k_1 = 1$, vary k_2 . Figure 8 shows the relationship between x^* and k_2 . From the figure, we can observe a threshold $k_2 \approx 0.17$. When $k < k_2$, x^* exists; when $k > k_2$, the victim species x goes extinct. The figure also shows that x^* is a linearly decreasing function of k_2 .

(3) Vary k_1 and k_2 at the same time. Figure 9 shows that x^* is the strict decreasing function of k_1 and k_2 . If k_1 and k_2 large enough, then species x will be driven to extinction.

Example 9.4 In system (1), we fix the parameters as follows:

$$e_1 = 1.0, \quad e_2 = 0.3, \quad c_2 = 1.0, \quad k = 0.5$$

 $b_1 = 0.1, \quad c_1 = 0.2, \quad a_2 = 1.0.$

(1) Take $k_1 = 1.0$, vary both k_2 and s_{\max} . Figure 10 shows the three-dimensional surface plot of the synergistic effect of k_2 and s_{\max} . When s_{\max} is large, the victim species x can reduce the negative impact of the harmful species y through the refuge, thereby increasing the net growth rate of x. If s_{\max} is small, the victim species x cannot effectively utilize the refuge, leading to a greater negative impact from y, and x may tend to extinction. In this example, k_2 and s_{\max} are two key parameters that regulate the system's dynamics by affecting the mortality rate of the victim species x and the utilization rate of the refuge, respectively. An increase in k_2 exacerbates the survival pressure on x, while an increase in s_{\max} effectively enhances the adaptive capacity of x. The interaction between these two parameters determines the persistence or extinction of the system;

(2) Take $k_2 = 0.1$, vary both k_1 and s_{\max} . Figure 11 shows the three-dimensional surface plot of the synergistic effect of k_1 and s_{\max} . When s_{\max} is large, the victim species xcan reduce the negative impact of the harmful species ythrough the refuge, thereby increasing the net growth rate of x. In this example, k_1 and s_{\max} are two key parameters that regulate the system's dynamics by affecting the birth rate of the victim species x and the utilization rate of the refuge, respectively. An increase in k_1 leading to the decreasing of survival rate on x, while an increase in s_{\max} effectively enhances the adaptive capacity of x.

Example 9.5 In system (1), we fix the parameters as follows:

$$e_1 = 2.0, \quad e_2 = 0.1, \quad k_1 = 1.0,$$

 $k_2 = 1.0, \quad c_1 = 2.0, \quad a_2 = 1.0,$
 $c_3 = 1.0, \quad k = 100.0, \quad b_1 = 1.0$

In this example, we calculate $y^* = 1$, and thus

$$\frac{e_1}{1+k_1y^*} - e_2(1+k_2y^*) = 0.8 < 2 = c_1y^*$$

Therefore, without the refuge, according to Theorem 2.1 in Chong et al. [6], the victim species x would go extinct.

Now, we further consider the effect of the refuge. We vary $s_{\rm max}$, and Figure 12 shows the relationship between x^* and s_{max} . From the figure, we can observe a threshold $s_{\rm max} \approx 0.606$. When $s_{\rm max} < 0.606$, x^* does not exist, and the victim species x goes extinct. When $s_{\rm max} > 0.606$, x^* exists. Moreover, as s_{\max} increases, x^* increases linearly and monotonically. As $s_{\rm max} \rightarrow 1$, the equilibrium density of the victim species gradually approaches its maximum. In other words, the capacity of the refuge directly determines whether the victim species goes extinct or survives. When the refuge is not large enough, even with a refuge, the victim species cannot avoid extinction. However, when the refuge exceeds this threshold, the victim species can survive due to the sufficient number of individuals hiding in the refuge. The parameter s_{max} plays a crucial role in determining the survival or extinction of the population.

Example 9.6 In system (1), we fix the parameters as follows:

$$e_1 = 2.0, \quad e_2 = 0.1, \quad k_1 = 1.0,$$

 $k_2 = 1.0, \quad c_1 = 2.0, \quad a_2 = 1.0,$
 $c_2 = 1.0, \quad b_1 = 1.0.$

This example is based on the parameters of Example 9.5, but we vary k and s_{max} to observe the combined effects of these two parameters on the victim species in the system. In this case, we calculate:

$$x^* = -1.2 + \frac{2s_{\max}k}{1+k}.$$

Figure 13 shows the relationship between x^* , s_{\max} , and k. For clarity, even when x^* is negative, we display it in the figure. This figure illustrates the combined effect of s_{\max} and k on x^* . When $s_{\max} > 0.6$ and k is sufficiently large, the refuge effect can maintain $x^* > 0$. When k is large enough, the refuge utilization rate approaches s_{\max} , and the threshold remains stable at $s_{\max} \approx 0.6$. If the refuge is too small, it cannot provide adequate protection. The threedimensional surface plot (Figure 9) shows that as s_{\max} and kincrease simultaneously, x^* gradually changes from negative to positive.

X. CONCLUSION

This paper constructs an improved Lotka-Volterra amensalism model, dynamically combining **fear-dependent refuge effects** and **fear effects** for the first time, revealing their joint regulatory mechanisms on population dynamics.

Compared with existing research, we have expanded the refuge effect mechanism as follows:

Through theoretical analysis and numerical simulations, the following main conclusions are drawn:

- 1) Key role of refuge effects: When the refuge capacity limit s_{max} is sufficiently large, the victim species can significantly reduce the negative impact of the harmful species through dynamic refuge strategies, thereby avoiding extinction and achieving stable coexistence. This indicates that effective management of refuge resources in real ecosystems is an important means of maintaining biodiversity.
- 2) **Bidirectional regulation mechanism of fear effects**: Fear effects regulate the system by suppressing the

birth rate $\left(\frac{e_1}{1+k_1y}\right)$ and increasing the mortality rate $\left(\left(1+k_2y\right)e_2\right)$ of the victim species, dynamically coupling with refuge effects. Their interaction may lead to bifurcation phenomena, affecting the long-term dynamic behavior of the system.

3) Sensitivity analysis of key parameters:

- An increase in fear coefficients k_1 and k_2 exacerbates the survival pressure on the victim species, potentially leading to its extinction;
- An increase in the refuge capacity limit s_{max} and response rate k effectively enhances the adaptive capacity of the victim species, promoting persistent coexistence.
- 4) Ecological implications of global stability: When the positive equilibrium point $E^*(x^*, y^*)$ exists, the system is globally asymptotically stable in the positive quadrant. This result provides a theoretical basis for predicting the long-term dynamics of amensalism relationships.

A. Theoretical contributions and practical significance

The innovations of this paper are reflected in the following aspects:

- Proposed a **dynamic refuge effect** mathematical model, breaking the traditional assumption of fixed refuge proportions and better aligning with ecological reality;
- Introduced the **bidirectional regulation mechanism of fear effects** in amensalism models for the first time, revealing its synergistic effects with refuge effects;
- Rigorously proved the global stability of the system using Lyapunov stability theory and Dulac's criterion, addressing the shortcomings of existing research.

The research results provide the following insights for biodiversity conservation:

- In ecosystems threatened by amensalism relationships, increasing refuge resources (e.g., artificial habitat construction) can alleviate the survival pressure on victim species;
- Regulating the intensity of fear effects (e.g., reducing human disturbance) may be an effective strategy for promoting species coexistence.

B. Future research directions

To further improve the theoretical framework and expand application scenarios, future research can focus on the following directions:

- Extend the model to incorporate spatial heterogeneity or time-delay effects to enhance the model's realism;
 - Spatial heterogeneity model: Introduce the differential operator ∇² to describe the spatial distribution of refuges:

$$s(x,y) = s_{\max} \cdot \frac{ky}{1 + ky + D\nabla^2 x}$$

where D is the spatial diffusion coefficient.

 Fear effect time-delay model: Consider the timedelay effect of fear pressure transmission:

$$\frac{e_1}{1+k_1y(t-\tau)} - (1+k_2y(t-\tau))e_2$$

where τ is the behavioral response delay time.

- Multi-stage refuge strategy: Distinguish refuge behaviors in different stages (e.g., breeding and non-breeding periods):

$$s(y) = \begin{cases} s_{\max} \cdot \frac{ky}{1+ky}, & \text{Breeding period} \\ s_{\min}, & \text{Non-breeding period} \end{cases}$$

- Explore the cascading effects of refuges and fear effects in multi-species amensalism systems;
- Validate theoretical results through field experiments or long-term observations, such as quantitatively measuring the relationship between refuge utilization and fear effects.

This study provides a new theoretical perspective for understanding behavioral adaptation strategies in amensalism relationships and lays a scientific foundation for the sustainable management of ecosystems.

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Fig. 1: Trajectories of x(t) in Example 9.1, converging to 0.



Fig. 2: Trajectories of y(t) in Example 9.1, converging to 1.



Fig. 3: 3D Plot of x(t) and y(t) in (39) over time for multiple initial conditions.



Fig. 4: Time series in Example 9.2 converging to $E^*(1.6, 1)$.



Fig. 5: 3D Plot of x(t) and y(t) in (40) over time for multiple initial conditions.





Fig. 7: Time series of x(t) under different k_1 values in Example 9.3.



Fig. 8: Relationship between x^* and k_2 in Example 9.4.



Fig. 9: x^* as a function of k_1 and k_2 .



Fig. 10: Synergistic effect of k_2 and s_{\max} on x^* in Example 9.4.



Fig. 11: Synergistic effect of k_1 and s_{\max} on x^* in Example 9.4.



Fig. 12: Relationship between x^* and s_{\max} in Example 9.5.



Fig. 13: Effect of s_{max} and k on x^* in Example 9.6.