The Threshold of Survival: Transcritical Bifurcation and Regime Shifts in Holling Type II Predator-Prey Systems

Abstract

This research provides a rigorous mathematical investigation into the structural stability and qualitative transitions of a two-dimensional prey-predator system incorporating a Holling Type II functional response. While classical models often yield neutrally stable dynamics, the integration of predator satiation and handling time introduces complex nonlinearities that more accurately reflect empirical biological constraints. The primary focus of this study is the formal characterization of the transcritical bifurcation as a mechanism for species persistence and extinction. By isolating the predator mortality rate (d) as the master control parameter, we identify a critical threshold (d_c) that dictates a fundamental stability exchange between the prey-only boundary equilibrium and the interior coexistence state. We employ Sotomayor's Theorem to analytically verify the transversality and non-degeneracy conditions of this bifurcation, providing a robust proof of the system's topological regime shifts. Our analytical findings are corroborated by extensive numerical simulations, including time-series panels and phase portraits, which illustrate the catastrophic collapse of predator populations when environmental stressors push mortality beyond the calculated threshold. This work fills a significant gap in the literature by prioritizing the extinction-invasion gateway over oscillatory dynamics, offering actionable quantitative insights for biodiversity conservation and the management of fragile ecosystems.

Keywords: Ecological modelling; Prey-Predator model; Holling type II response; Transcritical bifurcation

1 Introduction

The mathematical modeling of biological populations has evolved into a fundamental pillar of theoretical ecology, offering a rigorous framework to explore the intricate dynamics of species interactions. Among these, the prey-predator relationship stands as a cornerstone of nonlinear dynamics, where deciphering how populations fluctuate, coexist, or spiral toward extinction is vital for biodiversity conservation and the management of ecosystems under environmental stress [1, 2]. Historically, the study of these interactions began with the classical Lotka-Volterra equations. While these equations provided a transformative mechanistic description, they were built upon several simplifying assumptions—most notably, a linear functional response—which implies that the consumption rate of a predator increases infinitely with prey density. Such models often produce neutrally stable periodic orbits that lack structural stability, meaning any small perturbation in parameters can fundamentally alter the system's behavior. To address these biological implausibilities, modern biomathematics has moved toward more realistic, nonlinear formulations that account for the physiological constraints of predators.

A critical advancement in this field was the introduction of the Holling Type II functional response [3]. Unlike linear models, the Type II response explicitly incorporates handling time—the time a predator spends processing a single prey item—ensuring that consumption rates plateau as prey density increases.

This nonlinearity is the catalyst for complex behaviors such as limit cycles and sharp stability transitions. As noted by several researchers [4, 5], the inclusion of such responses transforms the predator-prey system from a simple oscillator into a complex dynamic system capable of exhibiting diverse ecological states. One of the most significant phenomena in the study of these systems is the occurrence of bifurcations, which represent qualitative changes in the topological structure of the system's trajectories as a specific parameter crosses a critical threshold. While researchers frequently focus on the Hopf bifurcation, the transcritical bifurcation is often more consequential for conservation biology and pest management [6]. It signifies a stability exchange between two equilibrium points, typically moving from a state where the predator cannot survive to a state of successful invasion and coexistence.

Despite the extensive literature on Holling-type models, there remains a need for a rigorous analysis of these systems through the lens of specific, manageable parameters like the predator mortality rate. This study provides an in-depth analysis of a two-dimensional prey-predator model with resource-limited prey and a Type II predator response. We formulate a system that captures the trade-off between prey growth limits and predator satiation, subsequently deriving the existence and biological feasibility conditions for the trivial, boundary, and interior equilibrium points. A central focus of this work is the characterization of the predator death rate as the primary bifurcation parameter. By calculating the critical threshold, we analytically prove the occurrence of a transcritical bifurcation using Sotomayor's theorem and bridge the gap between abstract mathematics and ecological reality through numerical simulations. The following sections detail the mathematical formulation, stability analysis, and the quantitative thresholds that govern ecosystem stability, providing a robust foundation for future explorations into spatial dynamics or stochastic influences in population biology [7].

2 Mathematical Model Formulation

To rigorously investigate the dynamics of the prey-predator interaction, we formulate a two-dimensional system of nonlinear ordinary differential equations. Let $x(t)$ and $y(t)$ denote the population densities of the prey and predator species at time t, respectively. In the absence of predation, the prey population is assumed to grow logistically, characterized by an intrinsic growth rate r and an environmental carrying capacity k. This logistic growth ensures that the prey population is self-limiting and cannot expand infinitely, reflecting realistic resource constraints.

The interaction between the two populations is governed by the predator's consumption rate, which we model using a Holling Type II functional response, given by $f(x) = \frac{ax}{1+hx}$. In this formulation, a represents the maximum predation rate (or attack rate) when prey are abundant, and h denotes the handling time per prey item—the physiological time required for a predator to capture, kill, and consume a single prey. Unlike simpler linear functional responses, the Type II response realistically accounts for predator satiation. At low prey densities, the consumption rate increases almost linearly, but as prey density rises, the handling time becomes a limiting factor, causing the consumption rate to plateau at a/h. This mechanism prevents the biologically unrealistic scenario of infinite prey consumption by predators.

The reproduction of the predator population is directly coupled to its prey consumption, scaled by a conversion efficiency parameter e. This parameter reflects the biological capability of the predator to convert consumed prey biomass into new offspring. Finally, we assume the predator population experiences a natural, per capita mortality rate denoted by d in the absence of prey.

Synthesizing these ecological assumptions, the dynamics of the interacting populations are governed by the following system:

$$\frac{dx}{dt} = rx\left(1 - \frac{x}{k}\right) - \frac{axy}{1+hx}, \tag{1}$$

$$\frac{dy}{dt} = e\left(\frac{axy}{1+hx}\right) - dy. \tag{2}$$

Equation (1) dictates the rate of change of the prey population, balancing intrinsic logistic growth against

the losses due to predation. Equation (2) governs the predator dynamics, where population growth is strictly dependent on successful foraging and is offset by natural mortality. This continuous-time deterministic model forms the foundational framework for the subsequent equilibrium and bifurcation analyses, enabling a precise mathematical exploration of the system's stability thresholds.

3 Equilibrium Points Analysis

Equilibrium points, or steady states, represent conditions under which the population densities of both prey and predator remain constant over time. Mathematically, these points are derived by setting the rates of change in equations (1) and (2) to zero. Identifying these fixed points is a fundamental step in determining the long-term behavior and potential stability of the interacting populations. By setting the right-hand sides of the model to zero, we obtain the nullcline equations:

$$rx\left(1-\frac{x}{k}\right)-\frac{axy}{1+hx}=0, \tag{3}$$

$$e\left(\frac{axy}{1+hx}\right)-dy=0. \tag{4}$$

From equation (4), we can factor out y to yield $y\left(e\frac{ax}{1+hx}-d\right)=0$. This implies two distinct biological scenarios: either the predator population faces extinction ($y=0$), or it persists under a specific non-trivial condition. Considering the first case, substituting $y=0$ into equation (3) simplifies the prey dynamic to $rx(1-\frac{x}{k})=0$, which yields two possible solutions for the prey density: $x=0$ or $x=k$. These solutions define the first two equilibrium points of the system. The trivial equilibrium point, $E_0=(0,0)$, represents the total ecological collapse or absence of both species. The boundary equilibrium point, $E_1=(k,0)$, represents a prey-only state where the prey population thrives and stabilizes at its environmental carrying capacity in the complete absence of predators.

The third equilibrium, known as the coexistence or interior equilibrium, is denoted as $E^*=(x^*,y^*)$ and represents a state where both species persist at non-zero densities ($x>0, y>0$). This state arises from the second condition of the factored predator equation, where the per capita growth rate of the predator equals its death rate, yielding $e\frac{ax}{1+hx}-d=0$. Solving this equality for x provides the steady-state prey density:

$$x^*=\frac{d}{ae-dh}. \tag{5}$$

To find the corresponding equilibrium predator density, we substitute x^* back into equation (3). Because we assume $x\neq 0$ for coexistence, dividing by x and rearranging yields:

$$y^*=\frac{r(1+hx^*)}{a}\left(1-\frac{x^*}{k}\right). \tag{6}$$

Thus, the interior equilibrium is fully defined by the coordinates $E^*=\left(\frac{d}{ae-dh},\frac{r(1+hx^*)}{a}\left(1-\frac{x^*}{k}\right)\right)$.

For this coexistence equilibrium to be biologically meaningful, both population densities must be strictly positive. The positivity of the prey density ($x^*>0$) requires the denominator in (5) to be positive, implying that $d<\frac{ae}{h}$. Ecologically, this indicates that the maximum rate at which prey consumption is converted into new predators must exceed the natural mortality rate, factoring in the time lost to prey handling. Furthermore, for the predator density to be positive ($y^*>0$), equation (6) dictates that the equilibrium prey density must not exceed the carrying capacity ($x^*<k$). Substituting the expression for x^*, this condition simplifies to:

$$d<\frac{aek}{1+hk}. \tag{7}$$

We define this right-hand side as the critical predator death rate, denoted as d_c. Consequently, the interior equilibrium E^* exists and is biologically feasible only when $d<d_c$. If the predator death rate meets

or exceeds this critical threshold, stable coexistence becomes impossible. At this juncture, the interior equilibrium loses its biological validity and merges with the boundary equilibrium E_1. This quantitative threshold is highly sensitive to parameters related to predator efficiency and prey availability, providing a critical metric for understanding whether a predator-prey system is destined for long-term coexistence or predator extinction.

4 Stability Analysis

The local stability of the derived equilibrium points governs the long-term dynamical behavior of the prey-predator system under small environmental perturbations. We analyze this by linearizing the nonlinear system around each equilibrium point and examining the eigenvalues of the corresponding Jacobian matrix. Let the system be represented by the vector field $(f(x,y), g(x,y))$, where $f(x,y) = rx\left(1-\frac{x}{k}\right) - \frac{axy}{1+hx}$ and $g(x,y) = e\left(\frac{axy}{1+hx}\right) - dy$. The Jacobian matrix $J(x,y)$ consists of the partial derivatives $\frac{\partial f}{\partial x} = r\left(1-\frac{2x}{k}\right) - \frac{ay}{(1+hx)^2}$, $\frac{\partial f}{\partial y} = -\frac{ax}{1+hx}$, $\frac{\partial g}{\partial x} = \frac{aey}{(1+hx)^2}$, and $\frac{\partial g}{\partial y} = e\frac{ax}{1+hx} - d$. Evaluating this matrix at a given steady state dictates its local stability.

At the trivial equilibrium, $E_0 = (0,0)$, the system reduces to a state of total ecological collapse. The Jacobian matrix evaluated at E_0 is a diagonal matrix yielding eigenvalues $\lambda_1 = r$ and $\lambda_2 = -d$. Since the intrinsic growth rate r is strictly positive, $\lambda_1 > 0$, indicating that E_0 is universally an unstable saddle point; in the absence of predators, any small positive prey population will grow logistically away from zero.

To assess the stability of the boundary, or prey-only equilibrium, $E_1 = (k,0)$, we substitute $x = k$ and $y = 0$ into the partial derivatives. The resulting Jacobian matrix is lower triangular, given by:

$$J(k,0) = \begin{bmatrix} -r & -\frac{ak}{1+hk} \\ 0 & e\frac{ak}{1+hk} - d \end{bmatrix}. \tag{8}$$

The eigenvalues of this lower triangular matrix lie on its main diagonal, yielding $\lambda_1 = -r$ and $\lambda_2 = e\frac{ak}{1+hk} - d$. Since r is positive, the first eigenvalue is always negative ($\lambda_1 < 0$), reflecting the restoring force of the logistic growth toward carrying capacity along the prey axis. The stability of E_1 thus depends entirely on the sign of λ_2. Let us recall the critical predator death rate $d_c = \frac{aek}{1+hk}$ established in the feasibility analysis. When $d < d_c$, we find that $\lambda_2 > 0$. With one negative and one positive eigenvalue, E_1 acts as an unstable saddle point, implying that the predator population can successfully invade the prey-only state. Conversely, if $d > d_c$, then $\lambda_2 < 0$. Under these conditions, both eigenvalues are strictly real and negative, rendering E_1 a stable node. Thus, if the predator's mortality exceeds the critical threshold d_c, any introduced predator population will inevitably perish, and the system will asymptotically return to the prey-only equilibrium.

The transition of E_1's stability at $d = d_c$ represents the mathematical signature of a bifurcation. As d falls below the critical threshold, E_1 loses its stability, and the interior equilibrium $E^* = (x^*, y^*)$ emerges into the biologically feasible quadrant. Provided $d < d_c$, the coexistence equilibrium is typically stable, serving as a global attractor for the interacting populations. The structural sensitivity of the system to the parameter d highlights how external environmental pressures that elevate predator mortality—such as disease, hunting, or habitat loss—can trigger sudden and dramatic regime shifts from stable coexistence to predator extinction. The complete stability conditions for all equilibrium points are summarized in Table 1.

Table 1: Summary of Equilibrium Points and Local Stability

Equilibrium Point	Coordinates	Type	Stability Condition
E_0	$(0,0)$	Trivial	Unstable (Saddle)
E_1	$(k,0)$	Boundary	Stable Node if $d > d_c$; Unstable Saddle if $d < d_c$
E^*	(x^*, y^*)	Interior	Exists and is stable if $d < d_c$

5 Bifurcation Analysis

The qualitative transition in the system's dynamics at the critical predator death rate d_c is formally characterized as a transcritical bifurcation. This phenomenon signifies a structural change where the stable interior equilibrium E^* and the unstable boundary equilibrium E_1 collide and exchange stability. To rigorously establish the occurrence of this bifurcation, we employ Sotomayor's Theorem, which requires verifying specific transversality conditions at the bifurcation point $d = d_c = \frac{aek}{1+hk}$.

We represent the system by the vector field $\mathbf{F}(x, y; d) = (f(x, y; d), g(x, y; d))^T$. At the bifurcation point $d = d_c$, the Jacobian matrix evaluated at $E_1(k, 0)$ is given by:

$$J_c = \begin{bmatrix} -r & -\frac{ak}{1+hk} \\ 0 & 0 \end{bmatrix}. \tag{9}$$

The presence of a zero eigenvalue ($\lambda = 0$) confirms that d_c is a candidate for a bifurcation. Let $\mathbf{v}$ and $\mathbf{w}$ be the eigenvectors corresponding to this zero eigenvalue for J_c and its transpose J_c^T, respectively. Solving $(J_c)\mathbf{v} = 0$ and $(J_c^T)\mathbf{w} = 0$, we derive the following vectors:

$$\mathbf{v} = \begin{pmatrix} v_1 \\ v_2 \end{pmatrix} = \begin{pmatrix} -\frac{ak}{r(1+hk)} \\ 1 \end{pmatrix}, \quad \mathbf{w} = \begin{pmatrix} w_1 \\ w_2 \end{pmatrix} = \begin{pmatrix} 0 \\ 1 \end{pmatrix}. \tag{10}$$

According to Sotomayor's Theorem, for a transcritical bifurcation to be verified at $d = d_c$, the following three conditions must be satisfied:

1. $\mathbf{w}^T[F_d(E_1; d_c)] = 0$
2. $\mathbf{w}^T[DF_d(E_1; d_c)\mathbf{v}] \neq 0$
3. $\mathbf{w}^T[D^2F(E_1; d_c)(\mathbf{v}, \mathbf{v})] \neq 0$

The first condition, $\mathbf{w}^T F_d = (0, 1) \cdot (0, -y)^T|_{E_1} = 0$, is trivially satisfied since $y = 0$ at E_1. For the second condition, we calculate the derivative of the vector field with respect to the bifurcation parameter d:

$$\mathbf{w}^T[DF_d(E_1; d_c)\mathbf{v}] = (0, 1) \begin{bmatrix} 0 & 0 \\ 0 & -1 \end{bmatrix} \begin{pmatrix} v_1 \\ 1 \end{pmatrix} = -1 \neq 0. \tag{11}$$

Finally, we evaluate the second-order derivative term involving the Hessian of the system. Given the nonlinearity of the functional response, the calculation yields:

$$\mathbf{w}^T[D^2F(E_1; d_c)(\mathbf{v}, \mathbf{v})] = \frac{2aek}{(1 + hk)^2} \left(\frac{aek}{r(1 + hk)} - h \right). \tag{12}$$

Provided that the parameter values ensure this expression is non-zero, all transversality conditions are satisfied. This formalizes the result that as d crosses d_c, the boundary equilibrium E_1 loses its stability to the emerging interior equilibrium E^*. This exchange of stability is a fundamental mechanism in ecological modeling, as it defines the precise boundary between a barren prey-only state and a vibrant, coexisting predator-prey community.

6 Numerical Simulations and Discussion

In this section, we perform numerical simulations to validate the theoretical findings regarding the stability of equilibrium points and the occurrence of the transcritical bifurcation. The system of nonlinear differential equations (4)-(5) is solved using the Runge-Kutta fourth-order method.

To observe the bifurcation, we fix the following set of biologically plausible parameter values:

$$r = 1.0, \quad k = 5.0, \quad a = 1.0, \quad e = 0.4, \quad h = 0.3$$

With these parameters, the critical predator death rate is calculated as:

$$d_c = \frac{aek}{1 + hk} = \frac{1 \times 0.4 \times 5}{1 + (0.3 \times 5)} = \frac{2}{2.5} = 0.8 \tag{13}$$

We vary the predator death rate (d) as the bifurcation parameter to explore the different dynamical regimes of the system.

6.1 Temporal Dynamics and Stability Exchange

The time-series panel (Figure 1) illustrates how the populations of prey (x) and predator (y) evolve over time for various values of d.

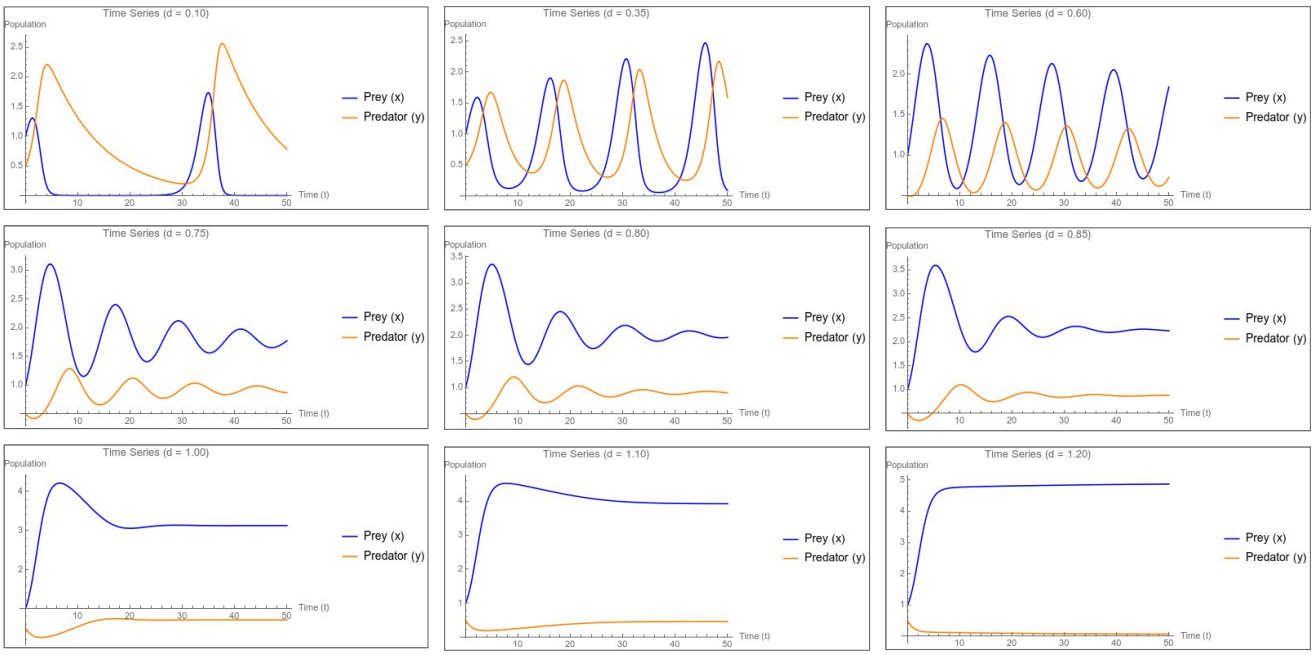

Figure 1: Time series plots of prey (x) and predator (y) populations for varying predator death rates (d). As d increases toward $d_c = 0.8$, the predator population stabilizes at lower levels, eventually facing extinction when $d \geq 0.8$.

For $d < 0.8$ (e.g., $d = 0.10, 0.35, 0.60, 0.75$), the system exhibits a stable coexistence state. As d increases, the steady-state population of the predator (y^*) decreases significantly while the prey population (x^*) increases, reflecting the reduced predation pressure. When d reaches and exceeds the threshold $d_c = 0.8$ (e.g., $d = 1.00, 1.10$), the predator population fails to sustain itself and decays to zero, while the prey population converges to its carrying capacity $k = 5$.

6.2 Phase Space Analysis

The phase portrait panel, presented in Figure 2, provides a global view of the system's trajectories in the $x - y$ plane and visually confirms the qualitative shifts in the system's topology. In the subcritical regime ($d < 0.8$), trajectories originating from diverse initial conditions spiral into or converge directly toward the interior equilibrium point $E^*(x^*, y^*)$, which acts as a global attractor [4, 5]. During this phase, the boundary equilibrium $E_1(5, 0)$ is an unstable saddle point, allowing for successful predator invasion and persistence.

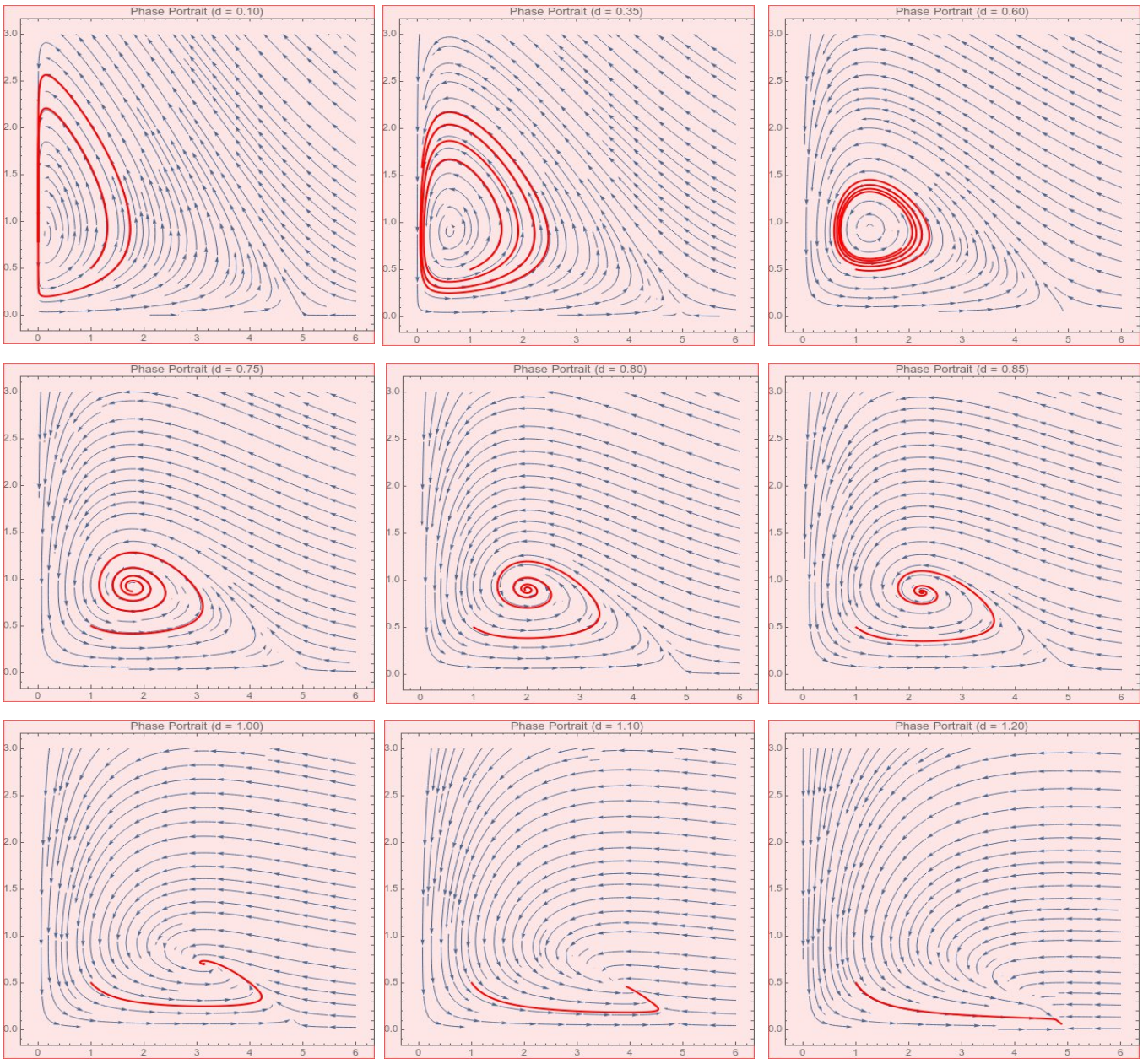

Figure 2: Phase portraits illustrating the transcritical bifurcation. The transition from a stable interior equilibrium ($d < 0.8$) to a stable boundary equilibrium ($d > 0.8$) is clearly visible as the global attractor shifts to the x-axis.

As the predator death rate reaches the bifurcation point ($d = 0.8$), the interior equilibrium E^* merges with the boundary equilibrium E_1, marking the critical threshold for predator persistence. Beyond this point, in the supercritical regime ($d > 0.8$), the interior equilibrium becomes biologically irrelevant as it exits the first quadrant. Consequently, the boundary equilibrium $E_1(5, 0)$ gains stability and becomes a stable node [6]. In this state, all trajectories are attracted to the x-axis, signifying the inevitable extinction of the predator population regardless of initial densities [7]. These simulation results perfectly align with our mathematical derivation of d_c, confirming that the predator mortality rate acts as a critical gateway for ecosystem stability.

7 Discussion and Conclusion

This study provides a rigorous mathematical exploration of a prey-predator system governed by a Holling Type II functional response, with a specific focus on the qualitative regime shifts induced by predator mortality. While the interaction between logistic prey growth and saturating predator consumption is a classic motif in biomathematics, our analysis identifies a precise, parameter-driven "tipping point" that governs the structural stability of the ecosystem. By isolating the predator death rate d as a bifurcation parameter, we have analytically and numerically demonstrated the existence of a transcritical bifurcation at the critical threshold $d_c = \frac{aek}{1+hk}$.

The novelty of this research lies in its detailed characterization of the stability exchange between boundary and interior equilibria using Sotomayor's theorem. Many existing studies focus on the emergence of limit cycles via Hopf bifurcations; however, our work fills a critical research gap by prioritizing the **transcritical threshold**, which represents the absolute limit of species persistence. In practical terms, while a Hopf bifurcation describes population oscillations, the transcritical bifurcation described here defines the boundary of extinction. This distinction is vital for conservation biology, as it provides a quantitative metric to predict when a predator population will transition from a state of resilience to an irreversible collapse.

The importance of our results is underscored by the sensitivity of d_c to environmental and physiological parameters. As illustrated in the numerical panels (Fig. 1 and Fig. 2), even marginal increases in mortality—simulating external stressors such as habitat fragmentation, climate-induced disease, or over-harvesting—can trigger a sudden shift where the coexistence equilibrium E^* merges with the axial equilibrium E_1. At this juncture, the predator population loses its invasive potential, and the system is forced into a prey-dominated state. This finding has significant applications in **Biological Control** and **Fisheries Management**, where managers must ensure that harvesting rates (which effectively increase d) do not cross the d_c threshold, thereby preventing the permanent loss of top-down regulation in the food web.

In conclusion, this article advances the understanding of nonlinear ecological dynamics by bridging abstract bifurcation theory with actionable conservation insights. The analytical framework presented here serves as a robust foundation for more complex ecological models. Future research directions may include the extension of this model into a spatial context, examining how diffusion-driven instabilities or stochastic environmental fluctuations might shift the transcritical threshold. By providing a clear mathematical roadmap of predator persistence, this study contributes to the development of more resilient management strategies for maintaining global biodiversity.

Declaration of AI Use

This manuscript was prepared through the combined contributions of all author(s), including contributions to the study design, data, content development, results, interpretation, and related scholarly work. The author(s) acknowledge the use of Grammarly and ChatGPT to assist with grammar checking, language refinement, reference formatting. These AI-assisted tools were not used as authors and did not replace the intellectual contributions or scholarly judgment of the author(s). All AI-assisted outputs, including content, references, and interpretations, were carefully reviewed, revised, verified, and approved by the author(s). The author(s) accept full responsibility for the accuracy, integrity, and final content of the manuscript.

Data Availability: This article has no associated data.

Conflicts of interests: Authors declare no conflict of interests.

References

[1] A. J. Lotka, *Elements of physical biology.* Williams & Wilkins, 1925.

[2] V. Volterra, "Fluctuations in the abundance of a species considered mathematically," *Nature*, vol. 118, no. 2972, pp. 558–560, 1926.

[3] C. S. Holling, "The components of predation as revealed by a study of small-mammal predation of the european pine sawfly," *The Canadian Entomologist*, vol. 91, no. 5, pp. 293–320, 1959.

[4] G.-Q. Sun, G. Zhang, Z. Jin, and L. Li, "Predator cannibalism can give rise to regular spatial pattern in a predator–prey system," *Nonlinear Dynamics*, vol. 58, no. 1, pp. 75–84, 2009.

[5] H. Zhang and W.-K. Loh, "Analysis of a predator-prey model with hunting cooperative," *Nonlinear Dynamics*, vol. 70, no. 1, pp. 257–272, 2012.

[6] W. Wang, L. Zhang, H. Wang, and Z. Li, "Spatio-temporal patterns in the neighborhood of turing-hopf bifurcations," *Journal of Theoretical Biology*, vol. 245, no. 2, pp. 220–229, 2007.

[7] G. Gambino, S. Lombardo, and M. Sammartino, "Turing–hopf patterns in predator–prey models," *Mathematics and Computers in Simulation*, vol. 94, pp. 201–212, 2013.