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ORIGINAL RESEARCH

Stability and Bifurcation in a Delayed Predator–Prey Model with Environmental Stress and Dynamic Carrying Capacity

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Abstract

We develop a delayed predator–prey model that integrates nonlinear environmental stress and a dynamic carrying capacity into the prey's growth function. The model introduces a discrete time delay in the predator's response, capturing ecological lags such as gestation or behavioral adaptation. Unlike previous studies, our framework couples environmental degradation and biological delay, two destabilizing forces often treated in isolation, to examine their combined impact on ecosystem dynamics. We derive analytical conditions for the local and global stability of equilibrium states and identify critical Hopf bifurcation thresholds as functions of the delay and environmental stress level. The model reveals how interactions between these parameters govern transitions between extinction, stable coexistence, and sustained oscillations. Notably, we extend the classical Wangersky–Cunningham framework by incorporating feedback-regulated carrying capacity. Numerical simulations validate the theoretical predictions and map resilience boundaries that highlight tipping points in ecological regimes. The results have practical implications for biodiversity conservation and adaptive ecosystem management, especially under anthropogenic stress and delayed biological feedbacks.

Keywords Delayed response · Predator–prey model · Environmental stress · Variable carrying capacity · Hopf bifurcation · Ecological resilience

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Introduction

Predator-prey interactions are fundamental to theoretical ecology and remain central to understanding population dynamics, species persistence, and trophic stability. Classical models pioneered by Lotka [1] and Volterra [2] provided elegant, deterministic frameworks to describe such interactions. However, these early models rely on simplifying assumptions, such as fixed carrying capacities, instantaneous predator responses, and unchanging environments [3, 4], which limit their applicability to real-world ecological systems. Contemporary ecosystems are increasingly exposed to dynamic environmental pressures, ranging from climate change and pollution to habitat fragmentation and anthropogenic exploitation. These perturbations significantly alter species interactions and demographic rates, often in nonlinear and unpredictable ways, requiring comprehensive modeling approaches that integrate deterministic, stochastic, and thermodynamic perspectives [5]. Recent studies have significantly advanced our understanding of fractional-order and delayed ecological models. Pramodh Bharati et al. [6] investigated the effect of fear in a fractional-order prey–predator model with time-delayed carrying capacity, revealing how psychological factors interact with temporal delays. Subrata Paul et al. [7] analyzed the dynamical behavior of fractional-order SEIR epidemic models with multiple time delays, providing insights into disease dynamics applicable to eco-epidemiological systems. Similarly, Mahata et al. [8] examined stability and Hopf bifurcation in fractional-order SEIRV models, demonstrating the critical role of time delays in infected populations. Paul et al. [9] extended this work by analyzing imprecise fractional-order eco-epidemiological models with various prey refuges and predator harvesting strategies. Furthermore, Mahata et al. [10] studied two-species prey-predator models in imprecise environments with maximum sustainable yield (MSY) policies under different harvesting scenarios, highlighting the importance of considering uncertainty in ecological modeling. In this context, the primary scientific motivation of our work is threefold. First, existing predator–prey models predominantly assume static environmental conditions or treat time delays and environmental stress as independent phenomena, failing to capture their synergistic effects on ecosystem stability. Second, real-world ecosystems exhibit feedback mechanisms where environmental degradation dynamically alters carrying capacity, a critical feature overlooked in classical formulations. Third, there is a pressing need to identify quantifiable thresholds, bifurcation boundaries in parameter space, that distinguish stable coexistence from oscillatory or extinction regimes under combined stress and delay. By integrating these elements into a unified mathematical framework, our model addresses a fundamental gap: understanding how ecological memory (time delays) and environmental forcing (stress-induced carrying capacity reduction) jointly govern resilience and regime shifts in trophic systems. This approach is essential for predicting tipping points in ecosystems subjected to anthropogenic pressures, where delayed responses to environmental change can trigger irreversible collapses. Empirical evidence has documented how environmental stress impacts survival, fecundity, and recruitment across diverse taxa, including red deer [11], marine fisheries [12, 13], seabirds [14], and Soay sheep [15]. Climatic indices such as the North Atlantic Oscillation (NAO) synchronize biological responses across trophic levels and spatial scales [16–18]. As ecosystems are pushed beyond their resilience thresholds, environmental stressors tend to amplify existing instabilities, giving rise to chaotic or cyclical population dynamics [19]. These stress-induced shifts have led to collapses in critical populations, such as cod [12] and herring [13], indicating the need for predictive models that can anticipate regime transitions. These collapses often exhibit hysteresis and irreversibility, highlighting the necessity of identifying early warning signals before the system crosses critical thresholds. In this context, modeling approaches that incorporate ecological memory, time delays, and feedback loops become indispensable for capturing the full scope of dynamic behaviors observed in empirical ecosystems.

Time delays are inherent in ecological systems due to gestation, prey digestion, nutrient cycling, recruitment lag, and behavioral adaptation. These delays introduce memory effects that can drive feedback lags between current population levels and their actual influence on the growth or decay of interrelated species. Delay differential equations (DDEs) provide a powerful and widely used framework to investigate such phenomena [20–26]. When delays are ignored, important dynamical features, such as sustained oscillations, stability switches, or even chaotic transients, may be overlooked. Indeed, numerous studies have shown that including delay terms can lead to bifurcations, whereby a system transitions from stable equilibrium to persistent cycles or more complex dynamics, with environmental stress further modulating these transitions in both ecological and epidemic contexts [27]. As such, time delay is not merely a technical artifact, but a biologically essential feature of predator-prey systems. Simultaneously, recent advances in ecological theory emphasize the destabilizing role of environmental degradation. Environmental stress can operate through multiple pathways: reducing the effective carrying capacity of habitats, suppressing reproductive rates, increasing mortality, or altering trophic structures. Many of these effects are nonlinear, creating feedback loops that accelerate ecosystem decline [28, 29]. In mathematical models, this is often captured by making the carrying capacity a function of population density and environmental burden. The inclusion of stress-responsive carrying capacity yields a more flexible and realistic depiction of ecological resilience under anthropogenic pressure [30–33]. Environmental stress can reduce the buffer zones that allow ecosystems to withstand natural fluctuations, thereby pushing them closer to bifurcation points. Recent advances in predator-prey modeling have significantly enriched our understanding of complex ecological dynamics through the incorporation of diverse biological mechanisms. Modified Leslie-Gower models with nonlocal competition and Beddington-DeAngelis functional responses have revealed intricate bifurcation structures, including Hopf-Hopf bifurcations and spatially nonhomogeneous patterns [34, 35]. Spatially inhomogeneous bifurcating periodic solutions induced by nonlocal competition demonstrate how spatial interactions coupled with additional food sources can fundamentally alter predator-prey dynamics [36]. The integration of fear effects, where prey populations exhibit behavioral changes in response to predation risk, has been shown to fundamentally alter system stability and generate novel spatiotemporal patterns [37, 38]. Turing pattern formation in predator-prey systems with double Allee effects demonstrates how demographic Allee effects at both low and high densities can drive spatial heterogeneity and influence species coexistence [39]. Furthermore, studies on spatially inhomogeneous bifurcating periodic solutions induced by nonlocal competition highlight the importance of spatial interactions in determining long-term population dynamics [40, 41]. Recent work on delayed predator-prey models with square root functional responses [42] and eco-epidemic systems incorporating disease in predators [43] underscores the critical role of time delays in destabilizing equilibria and inducing oscillatory dynamics. The interplay between gestation delays, hunting cooperation, and anti-predator behaviors has been examined through weighted state-dependent impulsive control frameworks [44, 45], revealing how management interventions can prevent population extinction while maintaining biodiversity. These studies collectively emphasize that contemporary predator-prey modeling must integrate multiple ecological mechanisms, including delays, spatial diffusion, behavioral responses, and environmental stress, to accurately capture the complexity of natural ecosystems and inform conservation strategies. Despite the separate acknowledgment of delay and environmental feedback in the literature, their combined effects remain relatively unexplored, particularly in the context of stability boundaries and bifurcation thresholds. While delay may independently cause instability, its interplay with environmental stress may exacerbate or suppress bifurcation phenomena in unexpected ways. For example, an otherwise stable system may become unstable under a critical delay threshold only in the presence of moderate environmental degradation. Conversely, extreme stress may eliminate oscillatory behavior entirely by destabilizing all coexistence equilibria, driving predator extinction. Motivated by this gap, we propose a novel delayed predator-prey model that integrates: a nonlinear environmental stress term affecting prey carrying capacity, and a discrete time delay in the predator's functional response to prey density.

Our model extends the classical Wangersky-Cunningham framework [33], and is informed by recent advances in resilience theory [28, 29], delay dynamics [20, 21], and climate, ecology coupling [16]. It offers a unifying structure for examining how internal biological lags and external environmental degradation interact to shape predator-prey dynamics across multiple regimes. We derive analytical conditions for the existence and stability of steady states, explore delay-induced bifurcations via Hopf theory, and determine resilience thresholds that delineate regime transitions. Importantly, our framework allows for direct interpretation of how environmental degradation and time lags jointly influence the long-term dynamics and resilience of ecological systems. Our analysis also supports policy-relevant insights, such as identifying parameter domains where ecological restoration or management interventions are most likely to succeed. Numerical simulations are used to validate the theoretical findings, reveal the impact of varying the delay and stress parameters, and provide insight into resilience boundaries relevant to conservation and ecosystem management. In this way, our model provides both theoretical advancement and practical applicability. This study contributes to the theoretical foundation for understanding ecological resilience under coupled stress and delay mechanisms and offers quantitative insight into managing systems vulnerable to tipping points. Our results highlight the importance of addressing both biological feedback lags and environmental degradation in designing effective ecological interventions. Although the present framework is grounded in mathematical theory, it is motivated by and directly applicable to several real ecological systems where both time delays and environmental stress play critical roles. In marine fisheries, for instance, the delayed predator response can represent gestation periods in fish populations such as North Sea cod, while the environmental stress parameter (β) captures the effects of pollution, overfishing, or temperature changes that reduce the effective carrying capacity of prey populations. Similarly, Arctic ecosystems provide compelling examples of predator-prey dynamics, such as lynx-hare or arctic fox-lemming interactions, where climate-induced habitat degradation ($\beta < 0$) directly affects prey carrying capacity, and predator reproduction involves seasonal delays due to extended gestation or behavioral adaptation periods. Another practical application arises in agricultural pest control through integrated pest management strategies, where natural predators such as ladybugs are used to control crop pests. In these systems, pesticide use degrades the environmental quality and reduces pest carrying capacity, while predator population responses are delayed due to reproductive cycles and dispersal dynamics. These examples illustrate that our model framework is not merely an abstract mathematical construction but provides a realistic and flexible tool for understanding and predicting ecosystem dynamics under simultaneous environmental and biological constraints.

The remainder of the paper is organized as follows: In Section 2, we present the model formulation and nondimensionalization. Section 3 provides a comprehensive mathematical analysis of the system's equilibrium, stability, and bifurcation structure. Section 4 offers numerical simulations to validate and visualize the analytical results. Finally, Section 5 summarizes the findings and outlines future research directions.

Model Formulation

In this section, we develop a delayed predator-prey model that incorporates two critical ecological mechanisms: environmental stress impacting prey growth, and a time delay in the predator's response to prey availability. Unlike classical models, which typically assume a constant carrying capacity and instantaneous interactions, our formulation accounts for the nonlinear feedback effects of environmental degradation and biologically realistic response lags. This approach extends the foundational model of Wangersky and Cunningham [33]. The dimensional form of the model is given by:

$$\begin{cases} \dfrac{dx(t)}{dt} = rx(t)\left[1 - \dfrac{x(t)}{C_0 + \beta x(t)}\right] - ax(t)y(t), \\ \dfrac{dy(t)}{dt} = eax(t-\tau)y(t-\tau) - \mu y(t), \end{cases} \tag{1}$$

In this system, $x(t)$ and $y(t)$ represent the prey and predator densities at time t, respectively. The prey population follows logistic growth with intrinsic rate $r > 0$, limited by a dynamic carrying capacity that depends on prey density and a crowding coefficient $\beta < 0$, representing environmental degradation (e.g., pollution, habitat fragmentation). In the absence of degradation, the carrying capacity is $C_0 > 0$. The term $ax(t)y(t)$ captures predation, where $a > 0$ is the predation rate. The predator gains biomass from past prey abundance with a fixed time delay $\tau > 0$, modeling biological lags such as gestation or tracking delays. The coefficient $e > 0$ denotes the efficiency of converting consumed prey into predator biomass, while $\mu > 0$ is the predator's natural mortality rate. This model introduces nonlinear prey regulation via a density-dependent carrying capacity, along with a delayed functional response that reflects ecological memory effects. To reduce the number of parameters and facilitate analysis, we nondimensionalize the system using the following substitutions:

$$\bar{x} = \frac{x}{C_0}, \quad \bar{y} = \frac{y}{eC_0}, \quad \bar{\tau} = r\tau, \quad \bar{t} = rt. \tag{2}$$

Substituting (2) into system (1), and dropping the bars for simplicity, yields the dimensionless model:

$$\begin{cases} \dfrac{dx(t)}{dt} = x(t)\left[1 - \dfrac{x(t)}{1+\beta x(t)}\right] - \phi x(t)y(t), \\ \dfrac{dy(t)}{dt} = \phi x(t-\tau)y(t-\tau) - \psi y(t), \end{cases} \tag{3}$$

where the dimensionless parameters are defined by:

$$\phi = \frac{eaC_0}{r}, \quad \psi = \frac{\mu}{r}.$$

Here, ϕ measures the strength of predation and conversion efficiency, while ψ reflects the predator's mortality relative to prey growth. The effect of environmental stress appears in the nonlinear feedback term $x/(1+\beta x)$, consistent with empirical findings reported by Renwick et al. [46] and Clark et al. [12]. For clarity and ease of reference, all model parameters and their biological interpretations are summarized in Table 1.

To complete the initial value problem, we impose delay-dependent initial conditions:

$$x(\theta) = \eta_1(\theta) > 0, \quad y(\theta) = \eta_2(\theta) > 0, \quad \forall\theta \in [-\tau, 0],$$

where η_1 and η_2 are continuous and bounded history functions. Under these assumptions, the theory of functional differential equations ensures the existence, uniqueness, and positivity of solutions. This nondimensional system forms the foundation for the analytical investigation, where we derive equilibrium points, assess their stability, and study the condi-

Table 1 Model parameters and their biological interpretation

Parameter	Range	Biological Interpretation
$x(t)$	$x > 0$	Prey population density at time t (dimensionless)
$y(t)$	$y > 0$	Predator population density at time t (dimensionless)
r	$r > 0$	Intrinsic growth rate of prey population
C_0	$C_0 > 0$	Baseline carrying capacity in absence of environmental stress
β	$\beta < 0$	Environmental stress coefficient; represents crowding effects and habitat degradation (negative values indicate reduced carrying capacity)
a	$a > 0$	Predation rate (consumption rate of prey by predators)
e	$e > 0$	Conversion efficiency of consumed prey into predator biomass
μ	$\mu > 0$	Natural mortality rate of predators
τ	$\tau > 0$	Time delay in predator response, representing gestation period, digestion lag, or behavioral adaptation time
ϕ	$\phi > 0$	Dimensionless predation-conversion parameter: $\phi = eaC_0/r$ (ratio of predation impact to prey growth)
ψ	$\psi > 0$	Dimensionless predator mortality parameter: $\psi = \mu/r$ (ratio of predator death rate to prey growth rate)

tions under which time delay and environmental stress induce bifurcations. These dynamics reveal critical ecological transitions, as demonstrated by Bena et al. [25] and Aiello et al. [22].

Model Dynamics

In this section, we undertake a rigorous examination of the dynamical behavior of the delayed predator-prey model formulated in Section 1. The model incorporates two critical ecological mechanisms: environmental degradation, which reduces the effective carrying capacity of the prey population through a negative crowding parameter $\beta < 0$; and a discrete delay $\tau > 0$, representing the time lag in the predator's response to prey availability. These features reflect realistic feedbacks such as pollution-induced suppression of prey growth or delayed predator reproduction due to gestation. Our objective is to characterize the qualitative behavior of the system under biologically meaningful conditions. Specifically, we investigate conditions under which the species coexist stably, when sustained oscillations or extinction may emerge, and how the interplay between time delay and environmental stress induces bifurcation phenomena. To this end, we analyze equilibrium points, their stability (both local and global), and identify threshold conditions for Hopf bifurcation. These findings offer not only mathematical insights but also valuable ecological interpretations. Understanding thresholds that determine stability, persistence, or collapse is vital for designing effective conservation policies and ecological interventions. We begin with the foundational result on the well-posedness of the model.

Existence and Uniqueness of Solutions

We verify that the system (3) is well-posed, admitting a unique and strictly positive solution for all $t > 0$, given positive initial functions.

Theorem 1 *Let* $\eta_1(\theta), \eta_2(\theta) \in C([-\tau, 0], \mathbb{R}_+)$*, with* $\eta_1(\theta) > 0$*,* $\eta_2(\theta) > 0$ *for all* $\theta \in [-\tau, 0]$*. Then the initial value problem defined by system (3) admits a unique global solution* $(x(t), y(t)) \in \mathbb{R}_+^2$ *for all* $t > 0$*, and this solution remains strictly positive.*

Proof Let $\mathcal{C} := C([-\tau, 0], \mathbb{R}^2)$ denote the Banach phase space equipped with the supremum norm $\|\eta\| = \sup_{\theta \in [-\tau,0]} \|\eta(\theta)\|$. We rewrite system (3) as a functional differential equation:

$$\frac{dX(t)}{dt} = F(X_t), \quad \text{with } X(t) = \begin{pmatrix} x(t) \\ y(t) \end{pmatrix}, \quad X_t(\theta) = X(t+\theta),$$

where the functional $F : \mathcal{C} \to \mathbb{R}^2$ is defined componentwise by

$$F_1(x_t, y_t) = x(0)\left[1 - \frac{x(0)}{1+\beta x(0)}\right] - \phi x(0)y(0),$$
$$F_2(x_t, y_t) = \phi x(-\tau)y(-\tau) - \psi y(0).$$

The functional F is locally Lipschitz on $\mathbb{R}^2_+$, since all terms are continuously differentiable and $1 + \beta x > 0$ for $x > 0$ (given $\beta < 0$). Hence, by the standard theory of functional differential equations, a unique local solution exists. To show positivity, consider the prey equation:

$$\frac{dx}{dt} = x\left(1 - \frac{x}{1 + \beta x}\right) - \phi xy \geq -\phi xy,$$

from which it follows that

$$\frac{d(\ln x)}{dt} \geq -\phi y(t) \quad \Rightarrow \quad x(t) \geq x(0) \exp\left(-\phi \int_0^t y(s)\, ds\right) > 0.$$

For the predator:

$$\frac{dy}{dt} = \phi x(t-\tau)y(t-\tau) - \psi y(t) \geq -\psi y(t),$$

yielding

$$\frac{d(\ln y)}{dt} \geq -\psi \quad \Rightarrow \quad y(t) \geq y(0)e^{-\psi t} > 0.$$

Since solutions remain bounded and positive on any compact time interval, standard continuation theorems ensure that the local solution extends globally for all $t > 0$. □

This result confirms that the model is both mathematically well-posed and biologically meaningful. Population densities remain strictly positive and finite, avoiding pathological behaviors. From a practical perspective, this guarantees that simulations based on this model can be used with confidence for long-term ecological forecasting, adaptive management planning, and impact assessments under environmental stress scenarios.

Equilibrium Points and Their Feasibility

With the assurance of existence and uniqueness of positive solutions established in Theorem 1, we now identify and characterize the equilibrium points of system (3). These correspond to biologically meaningful steady states where population densities remain constant over time.

Theorem 2 *System (3) admits the following equilibrium points:*

1) *Trivial equilibrium:* $E_0 = (0, 0)$*, always exists.*
2) *Predator-free equilibrium:* $E_1 = \left(\frac{1}{1-\beta}, 0\right)$*, exists if and only if* $\beta < 1$.
3) *Coexistence equilibrium:*

$$E_* = \left(\frac{\psi}{\phi}, \frac{\phi + (\beta - 1)\psi}{\phi(\phi + \beta\psi)} \right),$$

which is feasible $(i.e., \ x_* > 0, \ y_* > 0)$ *if and only if*

$$\beta < -\frac{\phi}{\psi} \quad \text{or} \quad \beta > 1 - \frac{\phi}{\psi}.$$

Proof To find the equilibrium points, we set the right-hand sides of system (3) to zero and analyze each case.

1) Trivial equilibrium. Setting $x = 0$, $y = 0$ satisfies both equations, hence $E_0 = (0, 0)$ always exists.
2) Predator-free equilibrium. Set $y = 0$. Then the first equation becomes:

$$x \left(1 - \frac{x}{1 + \beta x} \right) = 0,$$

yielding $x = 0$ or solving $x/(1 + \beta x) = 1$ gives $x = 1/(1 - \beta)$, which is valid only when $\beta < 1$. Thus, the predator-free equilibrium is $E_1 = (1/(1 - \beta), 0)$.
3) Coexistence equilibrium. Assume $x > 0$, $y > 0$. From the second equation:

$$\phi xy - \psi y = 0 \quad \Rightarrow \quad x = \frac{\psi}{\phi}.$$

Substituting into the first equation:

$$1 - \frac{x}{1 + \beta x} - \phi y = 0 \quad \Rightarrow \quad \phi y = 1 - \frac{\psi/\phi}{1 + \beta(\psi/\phi)}.$$

Simplifying the right-hand side:

$$\phi y = \frac{(\beta - 1)\psi + \phi}{\phi + \beta\psi} \quad \Rightarrow \quad y = \frac{(\beta - 1)\psi + \phi}{\phi(\phi + \beta\psi)}.$$

Hence, the coexistence equilibrium is

$$E_* = \left(\frac{\psi}{\phi}, \frac{(\beta - 1)\psi + \phi}{\phi(\phi + \beta\psi)} \right).$$

This equilibrium is feasible (i.e., all components positive) if the numerator $(\beta - 1)\psi + \phi > 0$, which occurs when $\beta < -\phi/\psi$ or $\beta > 1 - \phi/\psi$.

□The feasibility of each equilibrium has clear ecological meaning. The trivial equilibrium E_0 denotes total extinction, while the predator-free state E_1 reflects prey-only survival under mild environmental stress ($\beta < 1$), often due to predator collapse in degraded ecosystems. The interior equilibrium E_* is feasible when stress is either low or sufficiently strong to induce stabilizing feedback. Its viability depends sensitively on predator efficiency (ϕ), mortality (ψ), and environmental degradation (β).

Remark 1 Stable coexistence is achievable through reduced environmental stress or improved predator fitness. Actions such as lowering β (e.g., pollution control), increasing e, or reducing μ can enlarge the feasible domain of E_*, enhancing ecological resilience and biodiversity.

Remark 2 The existence conditions for equilibria reveal critical ecological benchmarks. The condition $\beta < 1$ for the predator-free equilibrium E_1 represents a fundamental viability threshold: when environmental degradation becomes severe ($\beta \geq 1$), prey populations cannot sustain themselves even without predation pressure, leading to total ecosystem collapse. For the coexistence equilibrium E_*, the threshold conditions $\beta < -\phi/\psi$ or $\beta > 1 - \phi/\psi$ delineate two distinct ecological regimes. In severely degraded habitats (β strongly negative), coexistence paradoxically becomes possible because reduced carrying capacity prevents prey from overwhelming the system, maintaining balance through resource limitation. Conversely, in moderately stressed environments (β near zero), coexistence requires sufficiently efficient predation (ϕ large relative to ψ) to regulate prey populations. Ecosystems operating near $\beta = 1$ are highly vulnerable to catastrophic transitions, while those near coexistence boundaries may exhibit bistability and hysteresis, once lost, stable coexistence may be difficult to restore even if conditions improve.

Local Stability Analysis

We now analyze the local stability of the equilibria of system (3) under the assumption that the delay parameter vanishes, i.e., $\tau = 0$. This analysis is based on the linearization of the system at each equilibrium point and the examination of the corresponding Jacobian matrix. We begin with the trivial equilibrium, which always exists but lacks biological viability.

Lemma 1 *The equilibrium point $E_0 = (0, 0)$ is a saddle point.*

Proof Evaluating the Jacobian at E_0 gives:

$$J(E_0) = \begin{bmatrix} 1 & 0 \\ 0 & -\psi \end{bmatrix}.$$

The eigenvalues are $\lambda_1 = 1 > 0$ and $\lambda_2 = -\psi < 0$, which confirms that E_0 is a saddle. □

Next, we consider the predator-free equilibrium, where the prey persists in the absence of predators. Its feasibility and stability depend on the environmental stress parameter β.

Lemma 2 *The predator-free equilibrium E_1 is locally asymptotically stable if $\beta < 1 - \phi/\psi$, and a saddle point if $1 - \phi/\psi < \beta < 1$.*

Proof At E_1, we have $x_* = 1/(1 - \beta)$. The Jacobian becomes:

$$J(E_1) = \begin{bmatrix} 1 - \dfrac{2x_* + \beta(x_*)^2}{(1+\beta x_*)^2} & -\phi x_* \\ 0 & \phi x_* - \psi \end{bmatrix}.$$

This upper triangular matrix yields eigenvalues:

$$\lambda_1 = 1 - \frac{2x_* + \beta(x_*)^2}{(1+\beta x_*)^2}, \quad \lambda_2 = \phi x_* - \psi = \frac{\phi}{1-\beta} - \psi.$$

Clearly, $\lambda_1 < 0$ for all $\beta < 1$. The sign of λ_2 determines the stability of E_1. Solving $\lambda_2 < 0$ yields:

$$\frac{\phi}{1-\beta} < \psi \quad \Leftrightarrow \quad \beta < 1 - \frac{\phi}{\psi}.$$

Hence, E_1 is asymptotically stable when $\beta < 1 - \phi/\psi$, and a saddle otherwise. □

We now turn to the biologically meaningful interior equilibrium where both species coexist. Its existence and stability are governed by the balance between predation efficiency, predator mortality, and environmental stress.

Theorem 3 *The coexistence equilibrium E_* is locally asymptotically stable whenever it exists; i.e., when $\beta < -\phi/\psi$ or $\beta > 1 - \phi/\psi$.*

Proof Let $E_* = (x_*, y_*)$. The Jacobian at E_* is:

$$J(E_*) = \begin{bmatrix} A - \phi y_* & -\phi x_* \\ \phi y_* & \phi x_* - \psi \end{bmatrix},$$

where

$$A = \frac{1 - 2x_* + \beta(x_*)^2}{(1+\beta x_*)^2}.$$

The characteristic polynomial is:

$$\lambda^2 + b\lambda + c = 0,$$

with

$$b = \phi y_* + \psi - A, \quad c = (\phi x_* - \psi)(A - \phi y_*) + \phi^2 x_* y_*.$$

Substituting the expressions for $x_* = \psi/\phi$ and $y_* = [\phi + (\beta - 1)\psi]/[\phi(\phi + \beta\psi)]$, we obtain:

$$b = \frac{\phi\psi}{(\phi + \beta\psi)^2} > 0, \quad c = \frac{\phi\psi + (\beta - 1)\psi^2}{\phi + \beta\psi}.$$

Since feasibility requires $y_* > 0$, which implies $\phi + (\beta - 1)\psi > 0$, the denominator is positive and the numerator is also positive. Thus, $c > 0$. Therefore, the characteristic roots have negative real parts, and E_* is locally asymptotically stable whenever it exists. □

Local stability implies that if the populations start sufficiently close to equilibrium, they will return to this steady state over time. The condition $\mathrm{Tr}(J) < 0$ ensures that small perturbations are damped, while $\det(J) > 0$ guarantees the absence of eigenvalues with positive real parts. Biologically, this means the predator-prey system can resist small environmental or demographic fluctuations and tend toward stable coexistence, provided delay is negligible and stress parameters remain within viable ecological thresholds.

Remark 3 Local stability analysis reveals how ecosystems respond to small perturbations such as seasonal variations, disease outbreaks, or temporary habitat disruptions. When E_* is locally stable, populations exhibit resilience: after a disturbance (e.g., harsh winter reducing prey abundance, or disease outbreak in predators), the system naturally returns to equilibrium without management intervention. The trace condition $\mathrm{Tr}(J) < 0$ ensures damping of oscillations, meaning population fluctuations diminish over time rather than amplify. This property is crucial for ecosystems harvested by humans, stable systems allow for consistent, predictable yields. The determinant condition $\det(J) > 0$ prevents runaway growth or collapse by ensuring feedback mechanisms (predation pressure on prey, prey availability for predators) maintain balance. Species with rapid reproductive rates (high *r*) or efficient predators (high ϕ) typically exhibit stronger stabilizing feedbacks. Conservation implications include: protecting predator populations to maintain top-down regulation; reducing environmental stress to keep β within stable domains; and recognizing that locally stable systems can still collapse under large perturbations or if stress pushes parameters beyond critical thresholds.

Global Stability Analysis

We now investigate the global stability properties of system (3) under the assumption of no delay ($\tau = 0$). Unlike local stability, which characterizes dynamics near equilibria, global stability concerns the asymptotic behavior of all trajectories originating in the positive quadrant. We establish sufficient conditions under which the system converges globally to either the predator-free equilibrium or the interior coexistence equilibrium, depending on the ecological regime.

Global Stability of the Predator-Free Equilibrium

We begin by analyzing the global behavior of the predator-free equilibrium E_1, which exists whenever $\beta < 1$. This equilibrium corresponds to the extinction of predators and persistence of prey at a density determined by stress-adjusted carrying capacity.

Theorem 4 *Suppose $\beta < 1$ and $\beta < 1 - \phi/\psi$. Then the predator-free equilibrium E_1 is globally asymptotically stable in $\mathbb{R}^2_+ \setminus \{0\}$; that is, any solution with initial data $(x_0, y_0) \in \mathbb{R}^2_+$, $y_0 > 0$, satisfies*

$$\lim_{t\to\infty} (x(t), y(t)) = E_1.$$

Proof Consider the predator equation from system (3) with $\tau = 0$:

$$\frac{dy}{dt} = y(\phi x - \psi).$$

The predator declines whenever $x < \psi/\phi$. Since E_1 is given by $x_* = 1/(1-\beta)$, the assumption $\beta < 1 - \phi/\psi$ implies:

$$x_* = \frac{1}{1-\beta} < \frac{\psi}{\phi} \quad \Rightarrow \quad \phi x_* - \psi < 0.$$

Define the Lyapunov function $V(y) = y$, which is positive definite in $y > 0$. Then:

$$\frac{dV}{dt} = y(\phi x - \psi).$$

As $x(t) \to x_* < \psi/\phi$, there exists $\varepsilon > 0$ and $T > 0$ such that for $t > T$, $\phi x(t) - \psi < -\varepsilon$. Hence:

$$\frac{dV}{dt} \leq -\varepsilon y,$$

which implies $y(t) \to 0$ as $t \to \infty$. For the prey dynamics, as $y(t) \to 0$, the equation reduces to:

$$\frac{dx}{dt} \approx x\left(1 - \frac{x}{1+\beta x}\right),$$

which admits a globally stable steady state at $x_* = 1/1 - \beta$. Therefore, $x(t) \to x_*$, completing the proof. □

This result indicates that under moderate environmental stress ($\beta < 1$) and weak predator efficiency ($\phi < \psi(1-\beta)$), predators cannot persist. The prey population stabilizes at a nonzero level, governed by the degraded carrying capacity. This reflects the vulnerability of predator populations in stressed environments lacking strong trophic interactions.

Global Stability of the Coexistence Equilibrium

We now consider conditions under which the interior coexistence equilibrium E_* attracts all positive solutions, assuming again that $\tau = 0$.

Theorem 5 *Assume that the coexistence equilibrium E_* is feasible; i.e., $\beta < -\phi/\psi$ or $\beta > 1 - \phi/\psi$. Then, in the absence of delay, the equilibrium E_* is globally asymptotically stable in $\mathbb{R}^2_+$.*

Proof Define the Lyapunov function:

$$V(x,y) = x - x_* - x_* \ln\left(\frac{x}{x_*}\right) + y - y_* - y_* \ln\left(\frac{y}{y_*}\right),$$

where $x_* = \psi/\phi$, $y_* = [\phi + (\beta - 1)\psi]/[\phi(\phi + \beta\psi)]$. The function $V(x, y)$ is positive definite and radially unbounded over $\mathbb{R}^2_+$. Taking the time derivative along trajectories:

$$\frac{dV}{dt} = \left(1 - \frac{x_*}{x}\right)\frac{dx}{dt} + \left(1 - \frac{y_*}{y}\right)\frac{dy}{dt}.$$

Substituting system (3):

$$\begin{aligned}\frac{dV}{dt} &= \left(1 - \frac{x_*}{x}\right)\left[x\left(1 - \frac{x}{1+\beta x}\right) - \phi xy\right] + \left(1 - \frac{y_*}{y}\right)[\phi xy - \psi y] \\ &= (x - x_*)\left(1 - \frac{x}{1+\beta x}\right) - \phi(x - x_*)y + (y - y_*)(\phi x - \psi).\end{aligned}$$

At equilibrium:

$$\phi x_* = \psi, \quad 1 - \frac{x_*}{1+\beta x_*} = \phi y_*.$$

Using these, the derivative simplifies to:

$$\begin{aligned}\frac{dV}{dt} &= (x - x_*)\left[\phi y_* - \frac{x}{1+\beta x} + \frac{x_*}{1+\beta x_*}\right] - \phi(x - x_*)(y - y_*) + \phi(x - x_*)(y - y_*) \\ &= (x - x_*)\left[\frac{x_*}{1+\beta x_*} - \frac{x}{1+\beta x}\right].\end{aligned}$$

Define the function $h(x) = x/(1 + \beta x)$, which is strictly increasing in $x > 0$. Thus:

$$(x - x_*)\left[h(x_*) - h(x)\right] \le 0,$$

with equality if and only if $x = x_*$. Hence, $dV/dt \le 0$, and V is a strict Lyapunov function. By LaSalle's Invariance Principle, all trajectories converge to the largest invariant subset where $dV/dt = 0$, which occurs only at $(x, y) = (x_*, y_*)$. Therefore, E_* is globally asymptotically stable. □

This result confirms that, in the absence of delay, the coexistence equilibrium E_* globally attracts all strictly positive trajectories, provided it is feasible. This global convergence reflects strong ecological resilience: both species persist and stabilize despite initial fluctuations, as long as environmental degradation and predator dynamics remain within viable bounds. Effective conservation strategies should therefore aim to maintain or restore system parameters to regions supporting coexistence.

Hopf Bifurcation: Instability Induced by Delay

We now explore the destabilizing effects of the delay parameter $\tau > 0$ in the predator's response to prey abundance. Although previous sections established global stability under certain parameter regimes for $\tau = 0$, the introduction of delay can destabilize the coexistence equilibrium E_* and generate persistent oscillations. This phenomenon is commonly characterized by a Hopf bifurcation, wherein a pair of complex conjugate eigenvalues cross the imaginary axis as τ varies. Linearizing system (3) at the coexistence equilibrium E_*, the characteristic equation takes the form:

$$f(\lambda, \tau) = \lambda^2 + \bar{a}_1\lambda + \bar{a}_3 + (\bar{a}_2\lambda + \bar{a}_4)e^{-\lambda\tau} = 0, \tag{4}$$

where the constants $\bar{a}_i$ are given by:

$$\bar{a}_1 = \frac{\phi\psi}{(\phi + \beta\psi)^2} + \psi, \quad \bar{a}_2 = -\psi,$$
$$\bar{a}_3 = \frac{\phi\psi^2}{(\phi + \beta\psi)^2}, \quad \bar{a}_4 = \frac{\psi\phi + (\beta - 1)\psi^2}{\phi + \beta\psi} - \frac{\phi\psi^2}{(\phi + \beta\psi)^2}.$$

Seeking purely imaginary roots $\lambda = i\delta$, with $\delta > 0$, and separating equation (4) into real and imaginary parts, we obtain:

$$-\delta^2 + \bar{a}_2\delta\sin(\delta\tau) + \bar{a}_4\cos(\delta\tau) + \bar{a}_3 = 0, \tag{5}$$

$$\bar{a}_1\delta + \bar{a}_2\delta\cos(\delta\tau) - \bar{a}_4\sin(\delta\tau) = 0. \tag{6}$$

Squaring and adding both equations (5),(6) yields the following biquadratic equation:

$$g(\delta) = \delta^4 + (\bar{a}_1^2 - \bar{a}_2^2 - 2\bar{a}_3)\delta^2 + \bar{a}_3^2 - \bar{a}_4^2 = 0. \tag{7}$$

The discriminant of this equation is:

$$\Delta = \left(\bar{a}_1^2 - \bar{a}_2^2 - 2\bar{a}_3\right)^2 - 4(\bar{a}_3^2 - \bar{a}_4^2).$$

Depending on the sign and size of Δ, several bifurcation scenarios can emerge. As a first case, we identify conditions under which the equilibrium remains stable for any delay. This offers a robust stability criterion that is independent of τ.

Lemma 3 *(Uniform Delay-Independent Stability) If $\bar{a}_1^2 - \bar{a}_2^2 - 2\bar{a}_3 > 0$ and $\bar{a}_3^2 - \bar{a}_4^2 > 0$, then equation (7) has no positive real root. Hence, E_* remains locally asymptotically stable for all $\tau \geq 0$.*

Proof Under the given assumptions, the polynomial $g(\delta)$ is positive for all $\delta > 0$ because all coefficients are positive. Therefore, it has no positive real roots. Thus, no purely imaginary roots $i\delta$ exist for any τ, and the equilibrium E_* remains stable for all $\tau \geq 0$. □

This result guarantees unconditional stability: the equilibrium remains unaffected by any amount of delay. We now consider a contrasting situation in which delay induces instability through a Hopf bifurcation. This leads to the emergence of limit cycles and persistent oscillations.

Lemma 4 *(Existence of Hopf Bifurcation) If $\bar{a}_1^2 - \bar{a}_2^2 - 2\bar{a}_3 > 0$ and $\bar{a}_3^2 - \bar{a}_4^2 < 0$, then equation (7) admits a unique positive root $\delta_+ > 0$. Consequently, there exists an infinite sequence of critical delays $\{\tau_n^+\}_{n=0}^{\infty}$ such that the system undergoes Hopf bifurcation at each τ_n^+.*

Proof Since $g(\delta) \to \infty$ as $\delta \to \infty$, and $g(0) = \bar{a}_3^2 - \bar{a}_4^2 < 0$, the Intermediate Value Theorem guarantees that $g(\delta) = 0$ has exactly one positive root $\delta_+ > 0$. Substituting $\delta = \delta_+$ into equations (5) and (6), we can solve for τ such that the characteristic equation (4) has purely imaginary roots $\lambda = i\delta_+$. Because the exponential function is periodic in its imaginary argument, there will be an infinite sequence of such τ values:

$$\tau_n^+ = \frac{1}{\delta_+}\left\{tan^{-1}\left[\frac{\delta_+^2 - \bar{a}_3 - i(\bar{a}_1\delta_+)}{\bar{a}_2\delta_+ + i\bar{a}_4}\right] + 2\pi n\right\}, \quad n \in \mathbb{N}.$$

Thus, Hopf bifurcation occurs at each τ_n^+. □

This scenario corresponds to a classic delay-induced Hopf bifurcation, where increasing τ leads to the onset of sustained oscillations. We now examine a richer bifurcation structure: the presence of two critical frequencies introduces alternating bands of stability and instability as the delay varies.

Lemma 5 *(Double Root and Multiple Stability Switches) Suppose $\Delta > 0$, $\bar{a}_1^2 - \bar{a}_2^2 - 2\bar{a}_3 < 0$, and $\bar{a}_3^2 - \bar{a}_4^2 > 0$. Then equation (7) has two distinct positive roots $\delta_- < \delta_+$, yielding alternating intervals of stability and instability in τ.*

Proof Equation (7) is now a biquadratic polynomial with a negative coefficient for the quadratic term and a positive constant term. Given that the discriminant is positive, the equation admits two distinct positive real roots, denoted by $\delta_- < \delta_+$. These roots correspond to purely imaginary eigenvalues, indicating that the system may undergo Hopf bifurcations at two separate critical frequencies. As the delay parameter τ increases, the system crosses the stability boundary at discrete values $\tau_n^{\pm} = \tau(\delta_{\pm})$. This results in alternating intervals of stability and instability, leading to the phenomenon of multiple stability switches driven by delay. □

Here, the system can switch repeatedly between stable and unstable regimes as the delay increases, indicative of complex bifurcation structure. Finally, we consider a degenerate case in which the mathematical conditions for a bifurcation exist, but the dynamic transition does not occur due to lack of transversality.

Lemma 6 *(Degenerate Bifurcation) If $\Delta = 0$ and $\delta_0 > 0$ is a repeated root, the transversality condition fails. Thus, no Hopf bifurcation occurs despite the presence of purely imaginary eigenvalues.*

Proof If $\Delta = 0$, then equation (7) has a repeated root $\delta_0 > 0$. However, the Hopf bifurcation theorem requires not only that a pair of purely imaginary eigenvalues exist, but also that they cross the imaginary axis with non-zero speed (transversality condition). At a repeated root, the derivative $d\mathrm{Re}(\lambda)/d\tau|_{\tau=\tau_0} = 0$, and the imaginary root does not cross the imaginary axis transversely. Therefore, the bifurcation is degenerate and does not produce periodic solutions. □

In this setting, despite the apparent presence of a bifurcation, the system remains dynamically unchanged and exhibits no oscillatory behavior.

Remark 4 These results show how the feedback delay τ and ecological stress parameter β jointly determine whether the system exhibits stable coexistence or destabilizing oscillations. Bifurcation patterns include single critical thresholds, periodic transitions, or full delay-robust stability, depending on the algebraic structure of the characteristic equation.

To determine whether a Hopf bifurcation truly occurs, we must verify that the pair of purely imaginary eigenvalues crosses the imaginary axis with non-zero speed as τ passes through the critical value. This is known as the transversality condition. Assume $\lambda = i\delta$ is a root for some $\delta > 0$. Differentiating both sides of (4) implicitly with respect to τ, we obtain:

$$\frac{d\lambda}{d\tau} = -\frac{\partial f_\tau}{\partial f_\lambda}.$$

Explicitly computing these partial derivatives and simplifying the expression leads to the following identity:

$$\left(\frac{d\lambda}{d\tau}\right)^{-1} = \frac{2\lambda + \bar{a}_1 + \bar{a}_2 e^{-\lambda\tau}}{\lambda e^{-\lambda\tau}(\bar{a}_2\lambda + \bar{a}_4)} - \frac{\tau}{\lambda}.$$

Evaluating at $\lambda = i\delta$, we extract the real part to determine the sign of the crossing speed:

$$\mathrm{Re}\left(\frac{d\lambda}{d\tau}\right) = \left[\frac{d\mathrm{Re}(\lambda)}{d\tau}\right]_{\tau=\tau_n^\pm}.$$

Using trigonometric identities and separating real and imaginary parts in the characteristic equation, the transversality condition can be reformulated as:

$$\mathrm{sign}\left(\frac{d\mathrm{Re}(\lambda)}{d\tau}\right) = \mathrm{sign}\left[\bar{a}_1^2 - \bar{a}_2^2 - 2\bar{a}_3 + 2\delta^2\right],$$

or, alternatively, in terms of the discriminant Δ,

$$\mathrm{sign}\left(\frac{d\mathrm{Re}(\lambda)}{d\tau}\right) = \mathrm{sign}\left(\pm\sqrt{\Delta}\right).$$

To fully characterize the impact of the transversality condition on the system's dynamics, we distinguish the following three cases based on the sign of $\mathrm{Re}(\lambda)/d\tau$:

i) $\mathrm{Re}(\lambda)/d\tau > 0$. In this case, the pair of complex-conjugate eigenvalues crosses the imaginary axis from left to right as the delay τ increases. This implies that the real parts of the eigenvalues change from negative to positive, leading to a loss of stability of the equilibrium E_*. As a result, the system undergoes a supercritical Hopf bifurcation, and stable limit cycles (i.e., persistent oscillations) are born. This scenario describes a transition from steady coexistence to sustained predator–prey cycles, driven by increasing delay in the predator's response.
ii) $\mathrm{Re}(\lambda)/d\tau < 0$. Here, the eigenvalues move from the right half-plane to the left as τ increases, indicating that stability is regained. In this regime, the system transitions from an oscillatory or unstable state back to a stable steady state. This reverse crossing of the imaginary axis signifies the extinction of periodic behavior, potentially restoring equilibrium conditions in the predator–prey interaction.
iii) $\mathrm{Re}(\lambda)/d\tau = 0$. This degenerate case corresponds to a situation where the eigenvalues lie on the imaginary axis but do not cross it as τ varies. Consequently, the transversality condition fails, and a Hopf bifurcation does not occur, even though purely imaginary roots exist. The system remains structurally unchanged, and no qualitative transition in stability or dynamics is induced by delay. This scenario typically reflects a boundary case where the bifurcation is suppressed due to higher-order effects or parameter degeneracy.

Building upon the previous analytical findings regarding the characteristic equation, the transversality condition, and the delay-dependent stability behavior of the system, we now formalize the main dynamical consequences in the following theorems.

Theorem 6 *(Existence of Hopf Bifurcation) Let E_* be the coexistence equilibrium of system (3). Assume that the characteristic equation at E_* admits a pair of purely imaginary roots $\lambda = \pm i\delta$ for some critical delay value $\tau = \tau^*$. If the transversality condition*

$$\left.\frac{dRe(\lambda)}{d\tau}\right|_{\tau=\tau^*} \neq 0,$$

is satisfied, then a Hopf bifurcation occurs at $\tau = \tau^*$. That is, the equilibrium E_* loses stability, and a family of periodic solutions bifurcates from it.

This result guarantees the local birth of periodic solutions from the steady state when the delay crosses a critical value. However, to understand the system's behavior more completely, we must also determine the direction in which the bifurcation occurs.

Theorem 7 *(Direction of Stability Switch) Suppose that all parameters of the system ensure the existence of a unique positive root δ^* of the characteristic equation at the bifurcation threshold τ^*. Then:*

1) *If $d\mathrm{Re}(\lambda)/d\tau|_{\tau=\tau^*} > 0$, the eigenvalues cross the imaginary axis from left to right as τ increases. The equilibrium E_* becomes unstable, and stable periodic oscillations emerge (supercritical Hopf bifurcation).*

2) *If* $d\mathrm{Re}(\lambda)/d\tau|_{\tau=\tau^*} < 0$, *the eigenvalues cross from right to left, and the equilibrium* E_* *regains stability while oscillations vanish.*
3) *If* $d\mathrm{Re}(\lambda)/d\tau|_{\tau=\tau^*} = 0$, *the transversality condition fails, and no Hopf bifurcation occurs.*

The previous two theorems concern the onset of instability near a single threshold. In some parameter regimes, however, the system may experience multiple transitions between stability and instability as the delay increases. This more complex behavior is captured in the following result.

Theorem 8 *(Multiple Stability Switches and Delay-Induced Instability) If the characteristic equation admits two distinct positive imaginary roots* $\delta^+ > \delta^- > 0$, *with corresponding critical delays* τ_n^+ *and* τ_n^-, *then there exists an integer* $m \geq 1$ *such that:*

$$E_* is\ stable\ for \tau \in [0, \tau_0^+),\ (\tau_1^-, \tau_1^+), \ldots, (\tau_{m-1}^-, \tau_m^+),$$

and unstable in the complementary intervals:

$$\tau \in (\tau_0^+, \tau_1^-),\ (\tau_1^+, \tau_2^-), \ldots, (\tau_m^+, \infty).$$

This implies that delay can induce alternating regimes of stability and instability, and oscillatory behavior may reappear at larger delay values.

Remark 5 The preceding theorems clearly show that the transversality condition determines whether a Hopf bifurcation occurs and whether the system shifts toward or away from stability as the delay increases. We have seen that a positive derivative signals the onset of destabilizing oscillations, while a negative value indicates a return to equilibrium. Ecologically, even short delays in predator response (e.g., due to gestation or foraging lags) can trigger prey outbreaks and predator collapse. Economically, this may lead to fluctuations in harvest yields and the loss of ecosystem services. Mitigating delays through early warning, faster feedback, or adaptive management is therefore critical to maintaining both ecological balance and economic resilience.

Remark 6 Hopf bifurcation marks a fundamental transition in ecosystem dynamics–from stable equilibrium to sustained oscillations. The critical delay τ_0 represents the maximum biological lag an ecosystem can tolerate before losing stability. For species with long gestation periods (e.g., large carnivores: wolves 63 days, bears 60–270 days), or slow-maturing fish populations (e.g., cod reaching maturity at 2–4 years), inherent delays push systems closer to bifurcation thresholds. Environmental degradation (more negative β) further reduces τ_0, meaning stressed ecosystems become unstable at shorter delays. Post-bifurcation oscillations manifest as cyclic boom-bust dynamics observed in lynx-hare systems (10-year cycles), lemming populations (3–4 year cycles), and insect pest outbreaks. Supercritical bifurcations produce stable limit cycles with predictable amplitude and period, allowing for anticipatory management, harvest quotas can be adjusted cyclically. Subcritical bifurcations are more dangerous: small perturbations cause abrupt jumps to large-amplitude oscillations or alternative stable states, with limited warning. Conservation strategies must shorten response times through real-time monitoring and rapid intervention; buffer environmental quality to increase τ_0; recognize that ecosystems near bifurcation exhibit critical slowing down, recovery from perturbations becomes increasingly sluggish, serving as an early warning signal for impending regime shifts.

Numerical Analysis and Results

In this section, we numerically examine how the time delay parameter τ and the environmental stress parameter β interact to determine the long-term dynamics of the predator–prey model. While the analytical results in Section 3 provide rigorous bifurcation conditions and stability thresholds, the following simulations offer concrete insights into the system's behavior under biologically relevant scenarios. Following the parameter setup in [47], we fix the dimensionless predation rate at $\phi = 2$ and the predator mortality rate at $\psi = 0.2$, which reflect moderate predator conversion efficiency and low mortality. These values lie within ecologically meaningful ranges and provide a suitable baseline for exploring the impact of delayed feedback and environmental degradation. Under the baseline configuration, the coexistence equilibrium takes the form $E_* = (1/10, (9+\beta)/[2(10+\beta)])$,, which is biologically feasible whenever $\beta > -9$ or $\beta < -10$. This constraint reflects the role of environmental degradation in regulating carrying capacity and ensuring viable predator–prey interactions. We systematically vary the delay τ and stress parameter β to illustrate the main dynamical regimes identified in our theoretical analysis. These regimes include globally stable coexistence, delay-induced oscillations via Hopf bifurcation, tipping points due to environmental collapse, and combined delay–stress interactions. The simulation results, summarized in Figures 1 through 4, reveal how different ecological scenarios unfold in time and phase space.

Case 1: Global Stability for All Delays (No Positive Roots)

We first explore a parameter regime in which the auxiliary characteristic equation admits no positive real roots $\delta > 0$. In this case, the coexistence equilibrium E_* is globally asymptotically stable for all values of the delay parameter $\tau \geq 0$, regardless of its magnitude. This scenario is illustrated using $\beta = -6$, a level of environmental degradation that still permits stable predator–prey coexistence. Under this choice, the equilibrium becomes $E_* = (1/10, 3/8)$, and the characteristic roots are $\lambda = -0.3125 \pm 0.2288i$. This parameter configuration represents a highly resilient ecosystem that maintains stable population levels in the face of both biological delays and moderate environmental stress. Simulations confirm that trajectories converge to the coexistence equilibrium regardless of initial conditions or delay length. The time series and phase portraits exhibit damped transients followed by asymptotic stability. From a practical perspective, this regime reflects ecological systems where recovery and equilibrium are robust to disturbances, including gestation lags, tracking delays, or seasonal feedback cycles.

Remark 7 From an ecological perspective, this result indicates a highly resilient ecosystem capable of absorbing both environmental stress and time-delayed feedback without destabi-

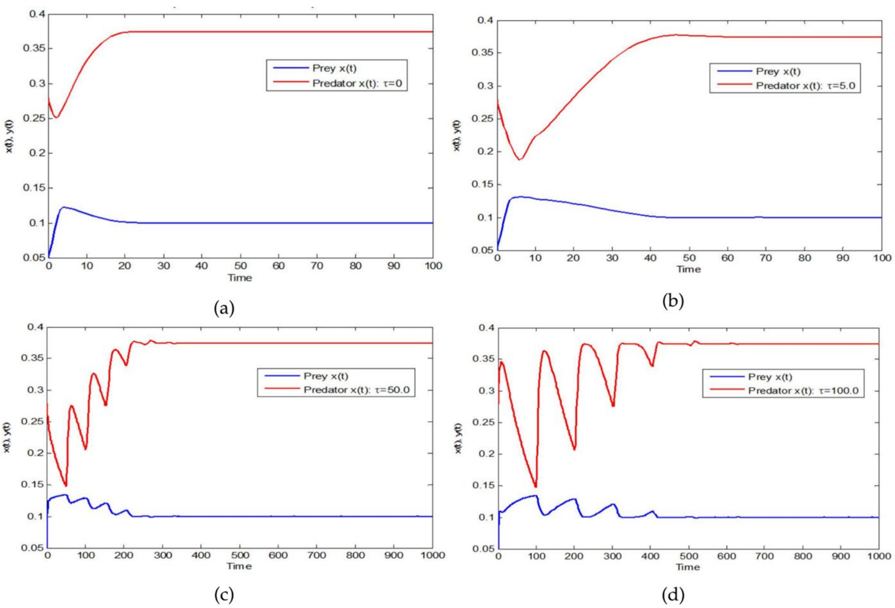

Fig. 1 Time series of prey $x(t)$ and predator $y(t)$ for $\beta = -6$ under increasing delay values. (**a**): $\tau = 0$ (negligible delay); (**b**): $\tau = 5$; (**c**): $\tau = 50$; (**d**): $\tau = 100$. All trajectories converge to the coexistence equilibrium E_*, demonstrating the system's global stability for all τ. Increasing the delay slows the convergence and amplifies transient oscillations

lizing. The predator and prey populations recover from perturbations and settle into a steady coexistence state. Such robust dynamics are particularly valuable in ecosystems where biological lags (e.g., gestation, foraging delay) are unavoidable. Economically, the absence of sustained oscillations implies predictability in population dynamics, which translates to stable resource yields. Fisheries or wildlife harvesting strategies operating in this regime can maintain consistent output levels without requiring frequent recalibration. The system's stability under long delays suggests that even delayed policy responses (e.g., seasonal quotas or adaptive measures) may not lead to collapse, making it an ideal scenario for long-term resource planning.

Case 2: Hopf Bifurcation at Critical Delay

We now consider a regime in which the characteristic equation admits a unique positive real root $\delta > 0$, giving rise to a Hopf bifurcation at a critical delay threshold τ_0^+. For this case, we fix $\beta = -4$, which corresponds to moderate environmental stress. The coexistence equilibrium becomes $E_* = (1/10, 5/12)$, and a Hopf bifurcation occurs at approximately $\tau_0^+ \approx 1.395$.

The simulation results in Fig. 2 show that for $\tau < \tau_0^+$, the system converges to the coexistence equilibrium with minor transient oscillations. At the critical delay, the system exhibits near-harmonic oscillatory behavior. As τ exceeds the threshold, the equilibrium loses stability, and persistent limit cycles emerge. This behavior is consistent with a supercritical Hopf bifurcation as predicted by Theorems 7 and 8.

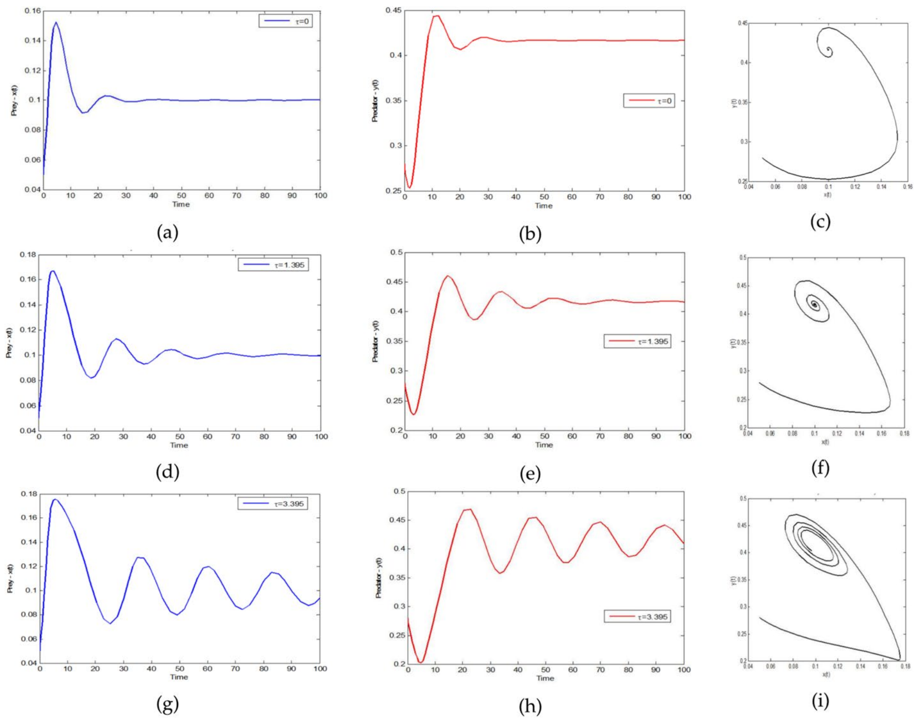

Fig. 2 Transition from stability to oscillation near the Hopf bifurcation point for $\beta = -4$. (**a**)–(**c**): $\tau = 1.2 < \tau_0^+$ stable convergence to E_*. (**d**)–(**f**): $\tau = 1.395 = \tau_0^+$ critical oscillatory onset. (**g**)–(**i**): $\tau = 1.6 > \tau_0^+$ emergence of sustained periodic oscillations

Remark 8 Ecologically, this regime shows that even modest delays in predator response can destabilize an otherwise resilient system, shifting dynamics from equilibrium to persistent oscillations. Such behavior reflects common patterns of prey booms and predator declines under anthropogenic stress or behavioral inertia. Economically, delay-induced cycles hinder reliable biomass estimation and increase the risk of overharvesting or missed yields. These findings underscore the need for responsive management that minimizes feedback lags through timely monitoring, adaptive quotas, and proactive policy intervention.

Case 3: Nonexistence of Double Roots and Multiple Stability Switches

Although the theory permits multiple stability switches due to two positive roots of the auxiliary equation, no biologically feasible value of β satisfies the required conditions. For $\phi = 2$ and $\psi = 0.2$, the characteristic polynomial never admits two distinct positive roots, ruling out alternating stability–instability cycles driven by delay alone. To examine this further, we fix $\tau = 0.0001$ (near-instantaneous response) and vary β near the bifurcation threshold. As shown in Fig. 3, the system becomes highly sensitive to environmental stress even under negligible delay.

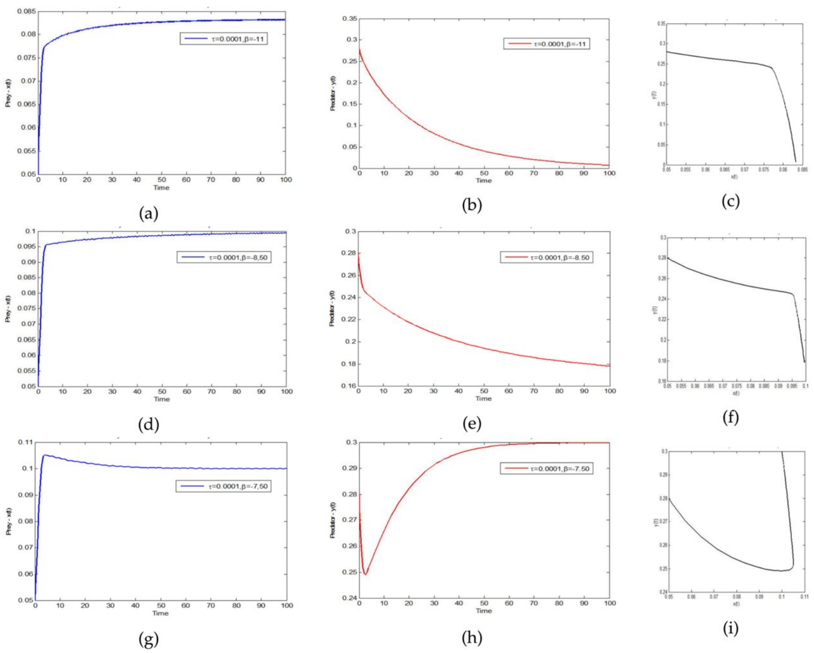

Fig. 3 Predator-prey dynamics under near-zero delay ($\tau = 0.0001$) for increasing levels of environmental stress. (**a**)–(**c**): $\beta = -11 E_*$ becomes infeasible and the system diverges. (**d**)–(**f**): $\beta = -9.5$ marginal stability regained. (**g**)–(**i**): $\beta = -7.5$ stable convergence to E_* resumes

Remark 9 Ecologically, this analysis illustrates a regime shift driven by environmental degradation. For $\beta = -11$, the equilibrium E_* is no longer feasible, and population trajectories diverge, potentially leading to extinction or uncontrolled growth. As β increases to -9.5, the system becomes marginally stable, and further improvements to $\beta = -7.5$ restore robust convergence to equilibrium. This behavior suggests a tipping-point-like phenomenon in which small changes in environmental conditions can induce large qualitative shifts in system behavior. From a resource management standpoint, this finding underscores the importance of maintaining environmental stress below critical levels. Sudden deterioration in habitat quality, pollution, or climate stressors may render formerly stable population levels unsustainable. Conversely, modest restoration efforts that improve environmental quality can help re-establish ecological balance and safeguard ecosystem services.

Case 4: Interaction of Delay and Environmental Stress

To investigate the combined effect of predator response delay and environmental stress, we fix the delay at a moderate level $\tau = 5.0$ and examine dynamics for two values of β: -5.5 and -3.5. Both configurations support a feasible coexistence equilibrium, but differ in how strongly environmental degradation affects system resilience. The results are presented in Fig. 4.

For $\beta = -5.5$, the system exhibits moderate, low-amplitude oscillations. These remain bounded and do not threaten species persistence, though they deviate from the steady equilibrium. When the stress level increases to $\beta = -3.5$, the amplitude of oscillations grows

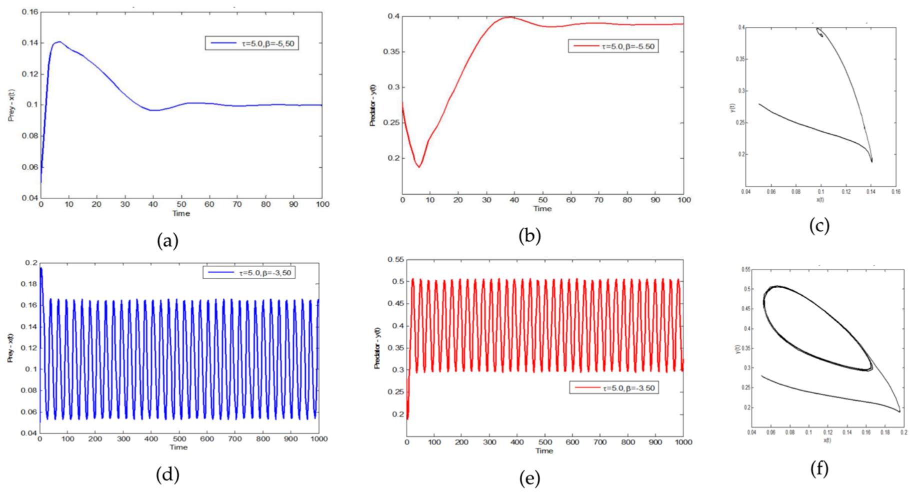

Fig. 4 Time series of prey $x(t)$ and predator $y(t)$ for fixed delay $\tau = 5.0$ under varying environmental stress levels. (**a**)–(**c**): $\beta = -5.5$; (**d**)–(**f**): $\beta = -4.5$. As environmental conditions improve, the system transitions from damped oscillations to sustained cycles, indicating the loss of asymptotic stability

significantly, indicating a more profound bifurcation effect. The feedback delay and environmental stress act synergistically, pushing the system into a regime of sustained, large-scale cycles.

Remark 10 Ecologically, these dynamics illustrate how combined biological lags and environmental stressors can destabilize predator–prey interactions, leading to prey outbreaks or predator collapse. Effective management must address both feedback delays (e.g., through habitat restoration) and environmental quality. Economically, such coupled stress amplifies risk: systems stable under either factor alone may become volatile when both are present, complicating planning and necessitating adaptive, real-time strategies.

Delay-Driven Dynamics and Management Implications

In this section, we explore the dynamic regimes of the delayed predator–prey model through simulations, focusing on the interaction between time delay τ, environmental degradation β, predation strength ϕ, and predator mortality ψ. Beyond confirming theoretical predictions, these results highlight the ecological impact of delayed feedback and its implications for resource governance. Figure 5 shows that small delays support stable coexistence, while longer delays trigger Hopf bifurcations and sustained cycles. Higher ϕ and lower ψ accelerate this transition, underscoring the role of trophic feedback sensitivity.

Remark 11 Biologically, this behavior reflects the loss of equilibrium due to slow predator response, common in systems with gestation lags or behaviorally delayed foraging. Economically, oscillations introduce uncertainty in prey abundance, complicating stock assessments and increasing the risk of overharvesting during peaks or underutilization during troughs.

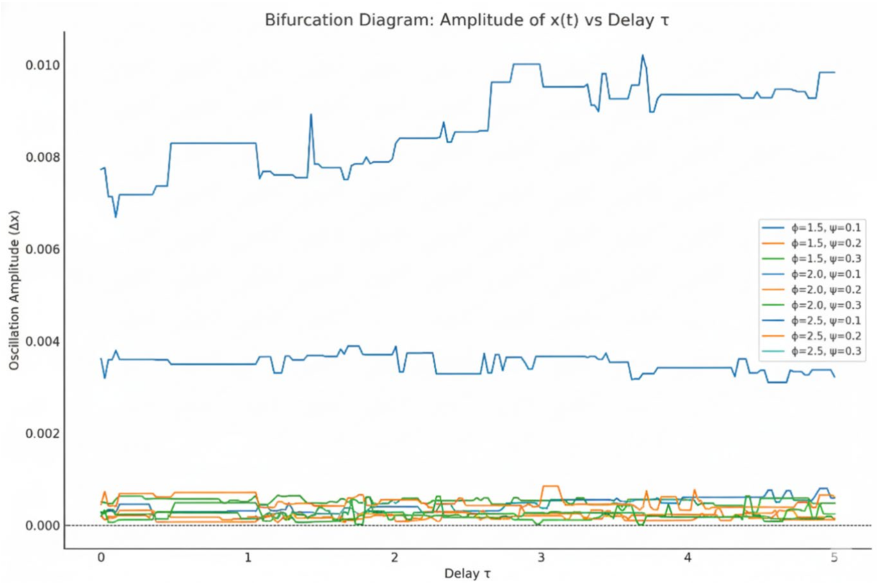

Fig. 5 Bifurcation diagram showing oscillation amplitude Δx as a function of delay τ for various combinations of predation strength ϕ and predator mortality ψ

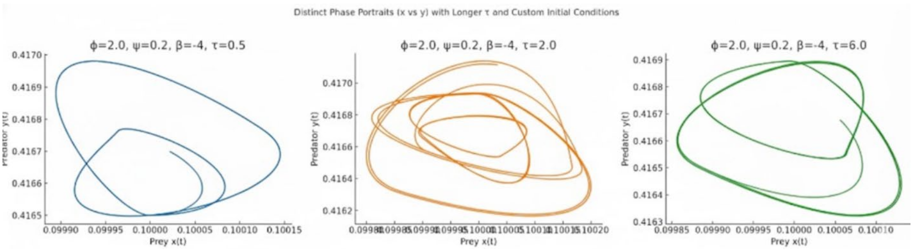

Fig. 6 Phase portraits ($x(t)$, $y(t)$) for different values of the delay τ with fixed $\phi = 2.0$, $\psi = 0.2$, and $\beta = -4$

To further explore these transitions, we simulate three representative regimes with increasing values of τ, shown in the phase portraits of Fig. 6. When $\tau = 0.5$, the system rapidly converges to a stable interior equilibrium, suggesting well-regulated population dynamics. At $\tau = 2.0$, small-amplitude oscillations emerge, indicating proximity to a bifurcation point. When τ increases to 6.0, the system exhibits a large-amplitude limit cycle, confirming that delay alone can drive sustained predator–prey cycles. These simulations highlight how even moderate delays in predator response can shift the system from equilibrium to persistent fluctuations.

Remark 12 Ecologically, this corresponds to scenarios where prey populations overshoot due to slow predator regulation, potentially leading to population crashes and trophic imbalance. Economically, such cyclic behavior complicates harvest planning and increases the risk of resource mismanagement, particularly in systems that rely on delayed population assessments or inflexible quota adjustments.

Summary of Numerical Insights

The numerical simulations presented across Subsections 4.1–4.5 complement the analytical findings of Section 3 and reveal critical delay-driven ecological transitions under environmental stress. They elucidate the nonlinear and sometimes abrupt shifts in predator–prey dynamics induced by the interplay between feedback delay (τ) and environmental degradation (β), offering valuable insights for both ecological understanding and policy design.

- Case 1) Delay-Resistant Coexistence: For strong environmental degradation (e.g., $\beta = -6$), the system remains globally stable across all delays, including large τ values. The resilience of the ecosystem is high, and predator–prey coexistence is delay-independent.
- Case 2) Delay-Induced Hopf Bifurcation: At moderate stress levels (e.g., $\beta = -4$), increasing delay τ beyond a critical threshold ($\tau_0^+ \approx 1.395$) induces a supercritical Hopf bifurcation, leading to sustained population oscillations. This confirms the destabilizing effect of biological lags predicted analytically.
- Case 3) Sensitivity to Stress Near Bifurcation Boundaries: Despite theoretical feasibility, no biologically relevant parameters produced double Hopf bifurcations or multiple stability switches. However, even negligible delays ($\tau \approx 0$) exhibited sharp sensitivity to β, underlining the existence of ecological tipping points.
- Case 4) Synergistic Effects of Delay and Stress: Combined increases in τ and β yield nonlinear amplification of oscillatory behavior. For instance, with $\tau = 5$ and β increasing from -5.5 to -3.5, the system transitions from mild damped oscillations to large-amplitude limit cycles, despite feasibility of coexistence.
- Case 5) Delay-Driven Regime Classification and Management: Section 4.5 highlighted how increasing τ alone, even under fixed β, can drive the system through distinct dynamical regimes: convergence to equilibrium, onset of small oscillations, and full-scale limit cycles. Simulations in Figure 6 further illustrate this progression, reinforcing the policy-critical need to monitor ecological delays in real time.

The resilience of predator–prey systems is governed not solely by trophic interaction strengths (such as ϕ and ψ), but by the interplay between internal biological delays and external environmental pressures. Our findings emphasize that delay, though inherent to ecological systems, constitutes a manageable risk when addressed through timely monitoring, early detection, and adaptive feedback mechanisms. Management strategies that neglect time-lagged responses or address environmental stressors in isolation may fail to detect early-warning signals of instability, thereby underestimating the likelihood of critical transitions or regime shifts. Effective conservation and harvesting policies must account for both environmental conditions and the temporal structure of biological feedbacks. Failure to do so can result in prey overabundance, predator collapse, or oscillatory dynamics that complicate sustainable resource use. Ensuring ecological balance requires the integration of real-time assessment tools, flexible intervention frameworks, and a dual focus on reducing anthropogenic stress while managing delay-driven risk.

Conclusion and Future Research

This study developed a delayed predator–prey model that incorporates two fundamental ecological mechanisms: environmental stress, modeled through a feedback-regulated carrying capacity, and time-delayed predator responses that capture biological lags such as gestation and behavioral adaptation. By unifying these destabilizing forces within a single mathematical framework, the model offers new insights into how ecological systems transition between extinction, stable coexistence, and sustained oscillations. Analytical results established clear conditions for the existence and stability of equilibria, as well as Hopf bifurcation thresholds that mark the onset of oscillatory dynamics. Numerical simulations further illustrated how the interplay between delay and environmental degradation can induce critical transitions, shaping long-term population trajectories and revealing tipping points in ecosystem resilience. These findings contribute to both theoretical ecology and applied resource management, emphasizing the importance of accounting for feedback delays and environmental degradation when assessing system stability.

Our mathematical analysis yields several key biological insights with direct implications for ecosystem management and biodiversity conservation. First, we identify precise threshold conditions for ecosystem viability: the boundary $\beta = 1$ represents a point of no return beyond which prey populations cannot sustain themselves, providing a quantitative target for habitat restoration efforts. Second, our results demonstrate that environmental stress and biological delays interact synergistically rather than additively, an ecosystem stable under moderate delay may become unstable when environmental quality declines, even if the delay itself remains unchanged. This suggests that climate change and habitat degradation can destabilize populations not by directly affecting vital rates, but by reducing the ecosystem's capacity to absorb inherent biological lags. Third, the approach to Hopf bifurcation exhibits critical slowing down, whereby populations take progressively longer to recover from perturbations. This phenomenon provides an early warning signal for impending regime shifts and can be monitored through recovery rate metrics following natural or experimental disturbances. Fourth, our framework supports evidence-based management strategies: priority should be given to reducing environmental stress (improving β) in systems with inherently long delays, such as marine mammal populations or old-growth forest ecosystems. For systems near bifurcation thresholds, interventions should focus on shortening response times through assisted migration, supplemental feeding programs, or predator-prey rebalancing initiatives. Finally, harvesting and culling programs must explicitly account for both current stress levels and biological lags to avoid inadvertently pushing systems past tipping points, policies that ignore time-lagged responses may underestimate collapse risk and overestimate sustainable yield.

Looking ahead, several directions offer rich potential for extending this work. Introducing stochastic processes into the model could allow for the exploration of noise-induced transitions and extinction risks, aligning the analysis more closely with the inherent unpredictability of natural systems. Expanding the model into spatially structured environments would capture the influence of dispersal, habitat fragmentation, and local disturbances on global system behavior. Incorporating state-dependent or distributed delays would provide a more refined representation of biological feedbacks and potentially uncover more complex dynamical regimes. Empirical calibration of the model using real-world data could improve its predictive accuracy and enhance its practical relevance for conservation planning. Furthermore, embedding the model within an adaptive management framework could support proactive ecological interventions by identifying policy levers that stabilize predator–prey dynamics under changing environmental conditions.

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Declarations

Conflict of Interest The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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