Stability and Bifurcation Patterns in Multi-Species Predator–Prey Systems

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Abstract

Mathematical models of three-species predator-prey systems are essential for understanding complex ecological dynamics, as these 3D continuous models represent the minimum dimension capable of exhibiting deterministic chaos. This paper reviews the analytical methodologies and dynamical implications associated with stability and bifurcation in tri-trophic food chains and intra-guild predation (IGP) systems. Local asymptotic stability of coexisting equilibrium points (E^*) is rigorously assessed using the Routh–Hurwitz criterion on the characteristic polynomial of the Jacobian matrix, an algebraic test critical for analyzing highly nonlinear systems without explicit root calculation. Bifurcation analysis reveals how parameter variations drive qualitative shifts in dynamics: Transcritical bifurcations govern species invasion/extinction, while Hopf bifurcations generate self-sustained population oscillations (limit cycles). In discrete systems, the analogous Neimark–Sacker bifurcation leads to quasi-periodic behaviour. A key challenge involves the destabilizing influence of ecological modifications, such as gestation time delays, which induce stability switches by repeatedly moving the characteristic equation roots across the imaginary axis. Conversely, realistic non-consumptive effects like prey refuge and adaptive foraging behaviour are shown to be powerful stabilizing forces, capable of collapsing chaotic dynamics to stable states, provided critical trophic efficiency conditions are met. Advanced geometrical methods, such as singular perturbation analysis, demonstrate that deterministic Shilnikov chaos is structurally guaranteed under explicit conditions of extreme time-scale separation ($\zeta \ll 1$) and high trophic efficiency ($\epsilon > \epsilon_0$ of the top predator). This synthesis underscores the delicate balance between structural realism and analytical tractability in mapping complex ecological interactions to stable or unstable outcomes.

Keywords: Predator-Prey, Bifurcation, Routh-Hurwitz, Tri-Trophic, Chaos, Stability.

Introduction

The pioneering work of Lotka and Volterra laid the mathematical foundation for analyzing population dynamics, establishing the paradigm of oscillatory behaviour in two-species predator-prey systems. However, natural ecosystems invariably involve multiple trophic levels and complex interaction topologies. The transition from two-dimensional to three-dimensional (3D) models marks a critical juncture in dynamical systems theory, as three coupled ordinary differential equations represent the minimum system capable of exhibiting deterministic chaotic behaviour. Consequently, the mathematical analysis of three-species systems—such as the hierarchical tri-trophic food chain or the intricate intra-guild predation (IGP) topology—is essential for uncovering the mechanisms driving stable coexistence, periodic oscillations, and the emergence of chaotic cycling in complex food webs.

The core objectives of mathematical ecology in this domain are to derive conditions for the existence and stability of coexisting populations and to identify the critical parameter thresholds (bifurcations) that trigger qualitative shifts in system behaviour. The challenge lies in navigating the trade-off between mathematical tractability and ecological realism; while simple models are analytically soluble, they often fail to capture complexities like time delays or sophisticated functional responses that are ubiquitous in nature. This paper synthesizes the specialized analytical techniques and key ecological findings from high-impact literature. It begins by establishing the canonical model structures and the crucial role of nonlinear functional responses. It then details the rigorous analytical methods employed for stability assessment, particularly the application of the Routh–Hurwitz criteria. Finally, the review explores the codimension-one and higher-order bifurcation phenomena, including delay-induced Hopf bifurcations and the geometric mechanisms leading to chaos, providing a comprehensive overview of dynamic complexity in tri-dimensional ecological systems.

I. Foundational Framework and Model Typology

Three-species dynamical models are a key focus in mathematical ecology because they are the simplest continuous systems capable of showing deterministic chaos. Their complexity reflects real ecosystems. Studying stability and bifurcations in these models involves advanced methods to link multidimensional parameters with outcomes like coexistence, extinction, or population cycles.

I.A. Canonical Structures of Three-Species Systems

Three major ecological structures are central to three-species predator–prey research, each with distinct dynamical behaviour. The most examined is the **Tri-Trophic Food Chain (P–M–T)**, where a basal prey X is consumed by a middle predator Y, which is in turn eaten by a top predator Z. Classical Lotka–Volterra and Hastings–Powell models use this framework, often with time delays to generate oscillations. Another important structure is the **Intra-Guild Predation (IGP) System**, where Z feeds on both Y and X, combining predation and competition, and strongly shaping ecosystem outcomes.**I.B.**

The Critical Role of Functional Responses

The mathematical representation of predation success—the functional response—is paramount to determining the system's stability profile. Changes in functional form can drastically alter predicted outcomes. **Holling Types and Nonlinearity** are pervasive in 3D modelling. The choice among Holling Type I, II, or III functions dictates how the predator's consumption rate changes with prey density. Simple linear responses (Type I) often destabilize the system, contributing to the "paradox of enrichment". However, the introduction of nonlinearity, such as the sigmoidal **Holling Type III** response, is known to stabilize the system by removing periodic orbits. This stabilization occurs because the Type III function, characterized by slow consumption at low prey densities, dampens the rapid population fluctuations that drive oscillatory behaviour, thereby restricting the domain where instability can emerge. Moreover, the inclusion of defense mechanisms, such as group defense in the prey population, further complicates the required functional form and strongly influences the resulting dynamical outcomes. More complex ecological interactions necessitate **Alternative Functional Responses**, such as the Beddington–DeAngelis functional response, which accounts for predator mutual interference, or the Crowley-Martin functional response, useful for modelling interference alongside saturation effects. These responses are essential for achieving models that balance analytical tractability with ecological realism in higher-dimensional systems, particularly where interference or complex behavioural traits are involved.

I.C. Existence and Classification of Equilibrium Points

Stability analysis begins with identifying the system's stationary states. In a general 3D system, these include the **Trivial Equilibrium** (0,0,0) and various **Boundary Equilibria** (where one or two species are extinct). The transitions between these boundary states and the interior coexistence state are often governed by **Transcritical Bifurcations**, which mathematically describe the ecological threshold for species invasion or long-term survival.

The ultimate focus of dynamical analysis is the **Coexistence Equilibrium (E^*)**, where all three species maintain positive densities. Researchers rigorously derive the conditions for the existence of a unique positive $E*$ using algebraic techniques, such as solving the system of nonlinear nullcline equations. A significant complexity arises when the system permits **Multiple Co-existing Stationary Points**. The simultaneous intersection of system nullclines at several points in the positive orthant leads to multi-stability. This implies that the system's long-term fate (which stable state it settles into) is highly dependent on the initial population densities. From a biological standpoint, multi-stability complicates ecological prediction and suggests potential hysteresis in the population response to environmental changes.

II. Analytical Methods for Stability and Persistence

The assessment of population dynamics in 3D predator-prey systems requires two complementary approaches: local stability analysis to understand short-term behaviour near equilibrium points, and global analysis to guarantee long-term outcomes across the entire phase space.

II.A. Local Stability Analysis via Jacobian Eigenvalues

Local stability is determined by linearizing the system around an equilibrium point $E^*=(x^*,y^*,z^*)$ using the Jacobian matrix $J(E^*)$. For a continuous 3D system defined by $X=f(X)$, where $X=(x,y,z)^T$, the stability is dictated by the eigenvalues (λ_i) of $J(E^*)$, which are the roots of the characteristic equation:

$$P(\lambda)=\det(J-\lambda I)=\lambda^3+a_2\lambda^2+a_1\lambda+a_0=0$$

where a_0 ,a_1, a_2 are functions of the system parameters.

The Routh–Hurwitz Stability Criterion (RHC)

The Routh–Hurwitz criterion provides a necessary and sufficient algebraic test to confirm if all roots (λ_i) of the characteristic polynomial have negative real parts, thereby establishing local asymptotic stability. This algebraic procedure is particularly useful for highly nonlinear ecological systems where explicitly calculating the roots of a third-order polynomial derived from complex biological parameters is computationally difficult. The RHC links the stability property directly to the sign and magnitude of the coefficients of the characteristic polynomial.

For a 3D continuous system, local asymptotic stability is achieved at E^* if and only if the following conditions are satisfied :

1. $a_i > 0 \; for \; all \; i = 0,1,2.$
2. The Routh array condition: $a_2 a_1 - a_0 > 0$.

If any coefficient a_i is negative, the system is unstable, as this implies that either the sum of the roots or the product of the roots must be positive, which is impossible if all roots have negative real parts. The Routh–Hurwitz criteria translate the dynamic condition $\mathrm{Re}(\lambda_i)<0$ into clear algebraic inequalities involving these ecological parameters, effectively mapping the parameter space to the region of stable coexistence.

Table I: Routh-Hurwitz Criteria for 3D ODE Stability

Equilibrium Stability Type	**Mathematical Condition on Eigenvalues (λ_i)**	**Routh-Hurwitz Criteria (for P(λ)=** $\lambda^3+a_2\lambda^2+a_1\lambda+a_0$	**Ecological Interpretation**
Asymptotically Stable	$\mathrm{Re}(\lambda_i)<0$ for all i	$a_0>0$, $a_1>0$, $a_2>0$, and $a_1a_2-a_0>0$	long-term coexistence (or stable boundary state) without persistent oscillation.
Critical Hopf Bifurcation	One pair $\lambda_{1,2}=\pm i\omega$, one real $\lambda_3<0$	$a_1a_2-a_0=0$	System is poised for self-sustained oscillations (limit cycle formation).
Unstable (Saddle or Repelling Focus/Node)	At least one $\mathrm{Re}(\lambda_i)>0$	$a_0\leq 0$ or $a_1a_2-a_0<0$	Population fluctuations grow unboundedly or converge to a different attractor (e.g., chaos or extinction).

II.B. Global Stability and Persistence

While local stability guarantees convergence near an equilibrium, **Global Stability** ensures convergence to a single state regardless of the initial population sizes. Proving global stability for highly nonlinear 3D systems remains an arduous challenge in theoretical ecology. Global analysis is often performed using Lyapunov Functions in conjunction with LaSalle's Invariance Principle to prove global asymptotic stability of the coexistence steady state. The construction of an appropriate Lyapunov function is non-trivial for complex non-linear systems. For models incorporating Stochasticity, such as environmental white noise or Lévy jumps, the analysis shifts from deterministic stability to proving persistence (long-term survival) or extinction. Stochastic differential equations (SDEs) are used to model abrupt environmental changes (Lévy jumps) or continuous noise (Wiener processes). For these systems, specific Lyapunov functional constructions are utilized to establish sufficient conditions for the upper bound of population densities and confirm persistence, even in the presence of random environmental fluctuations. Studies have shown that environmental Brownian motion can sometimes suppress population explosions in comparison to deterministic models.

III. Codimension-One Bifurcation Spectrum

Codimension-one bifurcations are critical events in the dynamical landscape where a single parameter variation causes a change in the qualitative dynamics of the system, typically involving one or two eigenvalues crossing the imaginary axis.

III.A. Real Eigenvalue Bifurcations (λ=0)

These bifurcations occur when a real eigenvalue crosses zero. The most relevant examples in ecological modelling are the transcritical and saddle-node bifurcations. A Transcritical Bifurcation involves two equilibrium points colliding and exchanging stability as a control parameter passes through a critical value p^*. For example, this mechanism governs the exchange of stability between a predator-free boundary equilibrium and the interior coexistence equilibrium. Mathematically, this occurs precisely when the constant term of the characteristic polynomial, $a_0=0$. Ecologically, transcritical bifurcations define invasion or extinction thresholds, such as the minimum birth rate required for a species to establish itself in the ecosystem. A Saddle-Node Bifurcation also occurs when $\lambda=0$, but it involves the simultaneous creation or annihilation of a pair of equilibrium points (one stable, one unstable), signifying sudden population collapse or emergence.

III.B. The Hopf Bifurcation ($\lambda=\pm i\omega$)

The Hopf Bifurcation is the critical mechanism that generates self-sustained population oscillations (limit cycles) from a previously stable equilibrium. In a continuous 3D system, this occurs when a complex conjugate pair of eigenvalues crosses the imaginary axis (One pair $\lambda_{1,2} = \pm i\omega$, one real $\lambda_3<0$). The necessary algebraic condition is the collapse of the Routh–Hurwitz criterion, such that $a_1a_2-a_0=0$.

Delay-Induced Hopf Bifurcation

In ecological systems, time is rarely instantaneous. **Time Delays** (e.g., gestation, maturation, or digestion time lags) are often incorporated, transforming the system into Differential Delay Equations (DDEs). This results in an infinite-dimensional phase space and introduces complex dynamics. In DDEs, the delay parameter (τ) often acts as the bifurcation parameter. Finding the critical delay thresholds (τ_k) that induce a Hopf bifurcation requires analyzing the roots of a transcendental characteristic equation, where roots cross the imaginary axis at $\lambda=i\omega$. This non-linear relationship between the delay parameter and the stability boundary leads to complex spectral analysis. A profound finding in delayed 3D systems is the existence of

Stability Switches. Increasing the delay parameter can cause the system to transition from stable to unstable, then back to stable, and finally back to instability.

To determine the ecological realism of the resulting oscillation, the **Direction and Stability** of the bifurcating limit cycle is assessed. The standard procedure involves applying the Center Manifold Theorem and Normal Form method to calculate the first Lyapunov coefficient. A negative coefficient indicates a supercritical (stable) limit cycle, while a positive coefficient indicates a subcritical (unstable) cycle.

IV. Complex Dynamics and Routes to Chaos

Since continuous 3D systems can exhibit deterministic chaos, researchers focus on identifying the mathematical mechanisms that drive the transition from stable orbits to strange attractors.

IV.A. Discrete Systems and Neimark–Sacker Bifurcations

Discrete-time models, often representing populations with non-overlapping generations, are mathematically significant because they tend to reveal complex dynamical behaviours (such as chaos) more readily than continuous models. It is essential that these discrete models be formulated using dynamically consistent schemes to ensure the conservation of equilibrium points, thus validating the biological relevance of the observed complex dynamics.

In discrete systems, the analogue of the Hopf bifurcation is the **Neimark–Sacker Bifurcation** (sometimes called discrete Hopf). This occurs when a pair of complex conjugate eigenvalues of the discrete Jacobian matrix crosses the unit circle (i.e., $|\lambda|=1$). This bifurcation signals the birth of a quasi-periodic invariant curve, or torus, which often precedes chaotic dynamics. Discrete systems also commonly exhibit flip (period-doubling) bifurcations leading directly to chaos.

IV.B. High-Codimension Bifurcations and Resonance

Codimension-two and higher bifurcations represent multiple critical stability conditions occurring simultaneously, resulting in even richer dynamics. Discrete predator-prey models have been shown to exhibit **Strong Resonances** at the interior fixed point, specifically 1:2, 1:3, and 1:4 resonances. These strong resonances are critical indicators that ecological complexity is not simply random noise; rather, it is governed by underlying mathematical structure. These points are associated with the destruction of a torus, which is a key route to the generation of strange attractors and complex quasi-periodic orbits.

IV.C. Geometric Singular Perturbation and Shilnikov Chaos

A fundamental and rigorous mechanism for chaos generation in continuous tri-trophic models relies on the geometry of the system when component species operate on vastly different time scales. This involves **Time Scale Separation**, where one species (e.g., prey) is fast, and the predators are slow or superslow (represented by a small perturbation parameter $\zeta \ll 1$). The **Shilnikov Homoclinic Orbit Mechanism** is a specific geometric structure proven to generate chaos in these singularly perturbed food chain models. Chaos arises when the system possesses a saddle-focus equilibrium point and a trajectory connecting that point back to itself (a homoclinic loop). The existence of a singular Shilnikov saddle-focus homoclinic orbit (G_0) is established under explicit conditions on the top predator’s efficiency ratio (ϵ) and the predator/prey reproduction rate ratio (ζ):

1. The singular limit condition $\zeta=0$ (or $0<\zeta\ll 1$) must hold, representing the large disparity in time scales.
2. The ratio ϵ of the top-predator's maximum growth rate over the intermediate predator's maximum growth rate must exceed a modest threshold value ϵ_0 ($\epsilon>\epsilon_0$).

3. The saddle-focus equilibrium must align with the Pontryagin landing curve, requiring a specific condition on a death rate parameter, $d_2 = y_{spk}/(y_{spk} + b_2)$.

This analysis demonstrates that high trophic specialization (high top predator efficiency) coupled with highly disparate growth rates are the *sufficient structural conditions* to guarantee the emergence of deterministic chaos in food chain models. The resulting complex dynamics are often characterized by **Mixed-Mode Oscillations (MMOs)** and relaxation oscillations, which qualitatively resemble observed natural cycles in small mammals and insects.

V. Drivers of Dynamic Complexity in Realistic Models

To enhance ecological realism, 3D systems often incorporate additional biological phenomena that introduce new layers of complexity or provide stabilizing effects.

V.A. The Dual Influence of Time Delays

As noted previously, time delays are critical components, especially in tri-trophic systems where gestation or consumption processing times are significant. The analysis of stability switches in these systems reveals that delays lead to complex non-monotonic behaviour. Studies suggest that in managing population fluctuations, attempting to reduce delays (e.g., through faster resource utilization) may inadvertently destabilize a system that was previously stabilized by an intermediate time lag. Furthermore, analyzing the direction and stability of bifurcating periodic solutions is crucial for understanding the ecological relevance of delay-induced cycles.

V.B. Spatial Dynamics: Turing Instabilities

When species movement is considered, the 3D ODE system is extended to a **Reaction-Diffusion System** (Partial Differential Equations, PDEs). This framework allows for the analysis of spatio-temporal dynamics and pattern formation. **Turing Instability** describes a condition where a homogeneous steady state, which is stable in the absence of diffusion, becomes unstable when diffusion is introduced, leading to the spontaneous formation of spatial patterns (e.g., spots or stripes). This requires the interacting species (activators and inhibitors) to diffuse at critically different rates. Specific inequality conditions for Turing instability have been derived for 3D systems, confirming that population-level patterning is a feasible dynamic outcome in tri-trophic webs. Furthermore, studies have shown that the interplay between external forces, such as harvesting, and species diffusion can trigger Turing instability. This implies that localized human interventions may inadvertently generate large-scale, persistent spatial heterogeneity in population densities, a crucial consideration for management strategies that rely on uniform population distributions.

V.C. Modelling Indirect Ecological Effects (Fear and Refuge)

Beyond direct consumption, the behavioural responses of species to risk—Non-Consumptive Effects (NCEs)—significantly modify system stability.

Fear of Predation models account for the psychological effect where prey species reduce their reproduction rates due to the perceived risk of predation. Studies show that fear and its carry-over effect (COE) can be highly effective in controlling chaotic behaviour, acting as a stabilizing factor by regulating prey recruitment and thereby preventing extreme population oscillations. Similarly, the inclusion of **Prey Refuge**—mechanisms representing habitat complexity that reduce encounter rates—has a stabilizing influence. Even introducing a small amount of refugia to a previously chaotic system can collapse the complex dynamics to stable limit cycles or fixed points, confirming that structural complexity is a powerful buffer against instability. The vigilance effect, where prey actively search for and utilize refuges, further influences the dynamics of fractional-order models.

VI. Mechanisms for Stabilization and Ecological Control

The research highlights both inherent ecological traits and external management actions that serve to stabilize complex 3D systems.

VI.A. Adaptive Behaviour as an Intrinsic Stabilizer

Adaptive foraging behaviour, particularly in the intra-guild prey component of an IGP system, is a potent, biologically inherent mechanism that promotes stability. When the intra-guild prey dynamically adjusts its foraging effort to maximize its *per capita* growth rate (fitness-seeking behaviour), the resulting system exhibits a significantly expanded region of parameter space leading to stability compared to non-adaptive models. Rigorous analysis suggests that the stable region of the non-adaptive system is always contained within the stable region of the adaptive system. This systemic stabilization occurs because adaptive strategies introduce an effective negative feedback loop that limits large-amplitude oscillations, functionally widening the parameter domain that satisfies the Routh-Hurwitz criteria. The adaptive behaviour will always promote stability, meaning it will never push a stable system toward instability.

This stabilizing effect is strictly conditional upon two requirements:

1. A **finite optimal foraging effort must exist**, implying that the optimization function is dome-shaped and achievable.
2. The **trophic transfer efficiency** from the resource to the top predator *via* the intra-guild prey must be greater than the efficiency of the direct path from the resource to the top predator. This is known as the **Trophic Upgrading Criterion** and is recognized as a general requirement for the feasibility of intra-guild predation itself.

Adaptive dynamics thus exert a powerful regulatory control. Where simple deterministic models predict instability and chaos, incorporating realistic adaptive behaviour often reveals an underlying structural stability, suggesting that highly complex dynamics may be less prevalent in natural systems with sophisticated behavioural traits.

The table below summarizes the key dynamic influences of various ecological modifiers discussed in this report.

Table II: Dynamic Influence of Ecological Modifiers in 3-Species Systems

Ecological Modifier	**Mechanism of Influence**	**Typical Dynamic Outcome**	**Stabilizing/Destabilizing Role**
Adaptive Foraging	Optimal fitness-seeking behaviour of IGP prey.	Expansion of the stable parameter region; damping of large-amplitude oscillations	Strongly Stabilizing
Time Delay (τ)	Non-instantaneous gestation/digestion (infinite-dimensional phase space).	Delay-induced Hopf bifurcation; stability switches; chaotic oscillation	Typically Destabilizing (though switches occur)
Prey Refuge	Reduced encounter rates/escape from predation.	Collapse of chaotic dynamics to stable limit cycles or equilibria.	Stabilizing

Singular Perturbation ($\zeta \ll 1$)	Disparate growth rates (time scale separation).	Shilnikov homoclinic orbits; Mixed-Mode Oscillations (MMOs); Chaos.	Destabilizing (Geometric Chaos Generator)
Fear Effect	Reduced prey reproduction due to non-consumptive predation risk.	Can control/eradicate chaotic behaviour; can induce multi-stability.	Context-Dependent (Can Stabilize or Induce Complexity)
Stochastic Noise/Jumps	Environmental fluctuations modeled by Wiener process or Lévy jumps.	Modified conditions for persistence/extinction; suppression of explosive dynamics.	Stabilizing/Modifying Persistence

VI.B. Control Strategies and Management Parameters

External pressures such as **Harvesting and Alternative Food Sources** are often tunable parameters that can be used to manage system dynamics. Research indicates that both harvesting (of prey and intermediate predators) and the availability of alternative food sources can stabilize chaotic dynamics, leading the system back toward stable states through mechanisms such as the reversal of period-doubling cascades. The finding that alternative food sources have a stabilizing effect is crucial for ecological protection and management. This emphasizes that these factors may be considered key biological parameters for controlling chaos. Furthermore, non-smooth harvesting strategies (e.g., switched linear/constant rates) introduce unique bifurcation structures, including the appearance of stable and unstable limit cycles via Hopf and saddle-node bifurcations.

For systems already exhibiting chaos, specific mathematical intervention strategies exist. Methods like the **OGY (Ott, Grebogi, Yorke) feedback control** are implemented in discrete systems to stabilize the system by controlling orbits near unstable fixed points, particularly useful in systems experiencing flip or Neimark–Sacker bifurcations.

VII. Synthesis and Unsolved Problems

VII.A. The Trilemma of Ecological Modelling

The rigorous analysis of 3D predator-prey systems is constrained by an inherent trade-off between mathematical tractability and ecological realism. Simple Lotka-Volterra formulations allow for straightforward local stability analysis using the Routh–Hurwitz criterion, but they often fail to capture real-world phenomena like time delays, stochastic environmental noise, or adaptive behaviour. Conversely, highly realistic models incorporating multiple nonlinearities, non-smooth functions (e.g., switched harvesting), or stochastic elements, rapidly lose analytical tractability, necessitating extensive reliance on numerical simulations.

This tension underscores the **Structural Stability Challenge**. Dynamical studies have repeatedly shown that the qualitative outcome (e.g., stable limit cycle versus chaos) is profoundly sensitive to the exact choice of functional form or the level of interference modeled. Since empirical ecological data are often inadequate to distinguish between slightly differing functional relationships, the structural stability of the system must be explicitly analyzed. If minor functional changes lead to significant bifurcations, the model's predictive reliability in a fluctuating environment is inherently low.

VII.B. Global Dynamics and Future Directions

Despite significant advances in local stability and bifurcation analysis, obtaining general conditions for **Global Asymptotic Stability** remains a major unsolved problem in 3D nonlinear ecological systems. Researchers must often rely on numerical continuation techniques (e.g., using specialized software like MATCONT) to map the global parameter space and investigate coexistence steady states.

Furthermore, the theoretical understanding of **Stable Coexistence** in multi-predator scenarios, particularly those involving intraguild predation and high competition, remains challenging. The presence of multi-stability (multiple stable attractors) implies that the classical idea of a single, deterministic, long-term state may not apply, thereby complicating the theoretical framework of community assembly.

The robust identification of the **Shilnikov chaos mechanism** demonstrates that specific structural characteristics—namely extreme time-scale separation and high trophic efficiency—are the necessary preconditions for deterministic chaos. Future research must focus on quantifying the ubiquity of these structural features in natural populations to determine the true prevalence of chaotic cycling versus stable or periodic dynamics. The exploration of fractional-order derivatives in these models also presents a new avenue for analysis, as these models can sometimes exhibit greater stability compared to their integer-order counterparts.

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