A Literature Review of the Kolmogorov Population Model: Foundations, Disambiguation, and Modern Extensions

Biomathematics and Dynamical Systems Expert Group

November 12, 2025

Abstract

This report provides an exhaustive literature review of the mathematical frameworks associated with Andrei Kolmogorov in population dynamics. The central "Kolmogorov population model" is a non-monolithic term, and this review disambiguates and analyzes its three principal pillars. The first, and most common referent, is the 1936 general predator-prey system, a class of autonomous ordinary differential equations (ODEs) that established a new, qualitative approach to dynamical systems in ecology. We detail its mathematical formulation, the core biological assumptions embedded in its partial derivatives, and the celebrated Kolmogorov theorem on the existence of stable equilibria or limit cycles. The second framework is the 1937 Kolmogorov-Petrovsky-Piskunov (KPP) reaction-diffusion equation, a partial differential equation (PDE) that models the spatial propagation of populations (or genes) and is foundational to the theory of traveling waves. The third is the 1931 Kolmogorov Forward Equation (Fokker-Planck equation), a PDE for probability densities that provides the mathematical basis for stochastic population models, including the diffusion approximation of the Wright-Fisher model in population genetics. The review explores generalizations of the 1936 model to n-species competition, food chains, and stochastic differential equation (SDE) formulations, unifying the 1936 and 1931 frameworks. Finally, we assess the limitations of these models and explore future directions, culminating in the emerging use of Kolmogorov-Arnold Networks (KANs)—a novel machine learning architecture based on Kolmogorov's 1957 representation theorem—to discover the general, non-parametric interaction functions of Kolmogorov-type systems directly from ecological data.

Contents

1 Introduction: Kolmogorov's Legacy in Population Dynamics

1.1 The Kolmogorov Population Model: A Critical Ambiguity

The term "Kolmogorov population model" appears with significant frequency in the literature of biomathematics, theoretical ecology, and applied probability. A critical analysis of the literature, however, reveals that this term is not monolithic. It is used to refer

to at least three distinct, though thematically related, mathematical frameworks pioneered by Andrei Kolmogorov during his profoundly creative period in the 1930s. These frameworks, developed in collaboration with colleagues and spanning ordinary differential equations (ODEs), partial differential equations (PDEs), and the foundations of stochastic processes, have each become cornerstones of modern theoretical biology.[1, 2, 3, 4]

An expert-level review must therefore begin not with a single definition, but with a careful disambiguation of these contributions. Failure to distinguish them obscures the specific nature of Kolmogorov's insights and the distinct applications of each framework.

1.2   The Three Pillars of Kolmogorov's Population Modeling

The literature implicitly organizes Kolmogorov's contributions to population dynamics into three pillars, distinguished by their mathematical structure and domain of application:

1. **The 1936 General Predator-Prey System:** This is the most common referent for the "Kolmogorov population model" in theoretical ecology.[1, 5] Published in his 1936 paper, "Sulla teoria di Volterra della lotta per l'esistenza" [6, 7], it is a system of two autonomous ODEs that provides a sweeping generalization of the Lotka-Volterra predator-prey model.[6, 8] Its primary contribution was a qualitative analysis of the entire *class* of predator-prey interactions.

2. **The 1937 Reaction-Diffusion (KPP) Equation:** Developed with I.G. Petrovsky and N.S. Piskunov, this framework was presented in their 1937 paper on reaction-diffusion equations.[9, 10] Often called the Fisher-KPP equation, due to R.A. Fisher's independent work in the same year [3, 11], this PDE models the spatial propagation of a population or an advantageous gene.[4, 12, 13]

3. **The 1931 Stochastic Process Equations:** Arising from Kolmogorov's 1931 foundational work on the analytical methods of probability theory [2, 14], these are the Kolmogorov Forward (KFE) and Backward (KBE) equations. The KFE, identical to the Fokker-Planck equation [15, 16], is a PDE that governs the probability density function of continuous-time Markov processes. In biology, it is the fundamental tool for diffusion approximations of stochastic population processes, most notably the Wright-Fisher model of genetic drift.[17, 18]

1.3   The Unifying Theme: A Shift from Mechanics to Qualitative Dynamics

These three pillars, while mathematically distinct, are unified by a revolutionary conceptual approach. Kolmogorov's predecessors and contemporaries typically proposed specific, mechanistic models. Volterra, for instance, "had an arbitrary postulate of linear rates of increase," which was justifiable only as a first approximation.[6] Similarly, Fisher's 1937 paper proposed the specific logistic reaction term $F(u) = ru(1 - u)$.[11]

In each case, Kolmogorov's contribution was to abstract the problem. He shifted the focus from analyzing a *single* equation to defining the *class* of all equations that share fundamental properties.

For the 1936 predator-prey model, he did not specify the interaction functions S and W. Instead, he postulated "minimal conditions" on their partial derivatives—such as

$\frac{\partial S}{\partial y} < 0$ (predation) and $\frac{\partial W}{\partial y} < 0$ (predator self-regulation)—that were rooted in basic biological principles.[6] He then proved general theorems about the dynamics of *any* system satisfying these conditions. For the 1937 KPP model, he and his co-authors defined a general *class* of reaction functions $F(u)$ satisfying certain convexity and root properties.[4, 19] For his 1931 work, he sought to derive the theory of *all* continuous-time Markov processes, classifying them into jump and diffusion types.[2]

This "qualitative analysis" [1] was a profound shift. It moved mathematical biology from a collection of specific, fragile models (whose results might be artifacts of their simplifying assumptions) to a robust, general theory based on qualitative, observable properties.

1.4 Report Structure

This report is structured to reflect the primacy of the 1936 ODE system while providing essential context from the other frameworks.

- **Section 2** provides a detailed analysis of the 1936 general predator-prey system, its mathematical formulation, its core assumptions, and the dynamical consequences (isoclines, stability, and limit cycles).

- **Section 3** explores generalizations of this ODE framework, including multi-species competition models and n-dimensional food chains, and identifies the limitations of the Kolmogorov form.

- **Section 4** reviews the modern synthesis of the 1936 model with the 1931 framework, leading to stochastic Kolmogorov systems (SDEs) and the analysis of persistence versus extinction.

- **Section 5** provides a comparative review of the other two pillars: the 1937 KPP spatial model and the 1931 KFE application in population genetics, clarifying their distinctions from the 1936 model.

- **Section 6** offers a critical assessment of the models' limitations and explores the future directions of the field, highlighting an emerging unification of Kolmogorov's work in ecology and machine learning.

2 The 1936 General Predator-Prey System: A Qualitative Revolution

2.1 Context: Beyond the Lotka-Volterra Model

The development of mathematical population dynamics in the 1920s was dominated by the work of Alfred J. Lotka [20] and Vito Volterra.[7, 20] Their canonical predator-prey model, a system of non-linear ODEs, was a foundational achievement.[21] However, its predictions were biologically problematic. The model exhibits neutral stability, where the populations oscillate in cycles whose amplitude and period are determined entirely by the initial conditions.[22] This "ephemeral" and "delicately balanced" result [22] is structurally unstable; any small perturbation to the model's form (e.g., adding logistic self-limitation) completely changes its dynamics.[22]

Kolmogorov, in his 1936 paper "Sulla teoria di Volterra della lotta per l'esistenza" [6, 7], recognized that the "arbitrary postulate of linear rates of increase" was the source of this fragility.[6] He sought to build a more general framework that incorporated "more realistic biological assumptions" and was capable of a "qualitative analysis" of population dynamics.[1, 6]

2.2 Mathematical Formulation

The Kolmogorov general predator-prey model is defined as a system of two autonomous differential equations [1, 23]:

$$\frac{dx}{dt} = \dot{x} = x \cdot S(x, y)$$

$$\frac{dy}{dt} = \dot{y} = y \cdot W(x, y)$$

Here, $x(t)$ represents the population density of the prey and $y(t)$ represents the population density of the predator. The functions $S(x, y)$ and $W(x, y)$ are the per-capita growth rates of the prey and predator, respectively. The crucial step taken by Kolmogorov was to *not* specify these functions, but to assume only that they are continuously differentiable (C^1) in the positive quadrant ($x \geq 0, y \geq 0$).[6, 23, 24]

2.3 The Core Kolmogorov Conditions

Kolmogorov's innovation was to replace specific functional forms (like $S(x, y) = \alpha - \beta y$) with a set of "minimal conditions" on the partial derivatives of S and W.[6] These conditions are not arbitrary mathematical conveniences; they are direct translations of fundamental ecological principles. These are summarized in Table 1.

Table 1: The Kolmogorov (1936) General Predator-Prey Conditions

Condition	Variable(s)	Interpretation	Implication
$\frac{\partial S}{\partial y} < 0$	S (Prey rate), y (Predator)	More predators eat more prey.	Defines the act of predation. [6]
$\frac{\partial W}{\partial x} > 0$	W (Predator rate), x (Prey)	More prey leads to more predator births.	Defines the predator's functional response. [25]
$\frac{\partial W}{\partial y} < 0$	W (Predator rate), y (Predator)	More predators compete for resources.	Predator self-regulation (intraspecific competition). [6]
$\frac{\partial S}{\partial x} \leq 0$	S (Prey rate), x (Prey)	More prey compete for resources.	Prey self-regulation (logistic growth). [24, 26]
$W(0, y) < 0$	W (Predator rate)	Predators starve with zero prey.	Predators are specialists and cannot survive without prey x.

This table summarizes the core qualitative assumptions of the 1936 Kolmogorov predator-prey model. The conditions on the partial derivatives translate basic ecological observations into a general mathematical framework.

The most critical of these assumptions, in terms of its dynamical consequences, is $\frac{\partial W}{\partial y} < 0$. This condition introduces intraspecific competition for the predator. It was

notably absent from the original Lotka-Volterra model [6] and is the primary mechanism that prevents the unrealistic neutral stability of that system. The condition $\frac{\partial S}{\partial x} \leq 0$ similarly introduces self-limitation for the prey, ensuring it has a finite carrying capacity in the absence of predators.[26]

2.4 Isocline Analysis

The qualitative conditions on the partial derivatives have immediate and powerful geometric consequences for the system's nullclines (curves where $\dot{x} = 0$ or $\dot{y} = 0$).

1. **The Prey Isocline ($\dot{x} = 0$):** This is defined by $x = 0$ (the y-axis) or $S(x, y) = 0$. The conditions $\frac{\partial S}{\partial x} \leq 0$ and $\frac{\partial S}{\partial y} < 0$ imply that if the isocline $S(x, y) = 0$ exists in the positive quadrant, y can be expressed as a non-increasing function of x. In typical predator-prey models (like Rosenzweig-MacArthur), this isocline is a "humped" curve, but in the simplest Gause-Kolmogorov type, it is often a downward-sloping line, representing the prey's carrying capacity K at $y = 0$ and its decline as predator pressure y increases.

2. **The Predator Isocline ($\dot{y} = 0$):** This is defined by $y = 0$ (the x-axis) or $W(x, y) = 0$. The conditions $\frac{\partial W}{\partial x} > 0$ and $\frac{\partial W}{\partial y} < 0$ necessarily imply that this isocline must be an upward-sloping function of x.[6] This curve represents the minimum prey density x required to sustain a given predator population y.

This geometric arrangement—a downward-sloping (or humped) prey isocline and an upward-sloping predator isocline—guarantees that if they intersect in the positive quadrant, they do so at a unique point (x^*, y^*).[6] This unique intersection is the non-trivial coexistence equilibrium for the system.

2.5 Kolmogorov's Theorem on Coexistence and Cycles

By combining this geometric isocline analysis with the Poincaré-Bendixson theorem (which applies to 2D autonomous systems), Kolmogorov's 1936 work established a powerful dichotomy for the long-term behavior of *any* predator-prey system meeting his general conditions.[24]

Theorem 2.1 (Kolmogorov, 1936). *A general Kolmogorov-type predator-prey system satisfying the conditions in Section 2.3 can have only two possible long-term outcomes (attractors) in the positive quadrant:*

1. ***A stable equilibrium (fixed point):*** *If the coexistence equilibrium (x^*, y^*) is locally asymptotically stable, it is globally stable in the positive quadrant. All populations starting with $x > 0, y > 0$ will converge to this steady state.*

2. ***A stable limit cycle:*** *If the coexistence equilibrium (x^*, y^*) is unstable (e.g., a repelling spiral), then the system possesses at least one stable limit cycle, and all populations will converge to a state of persistent, self-sustaining oscillations.*

This theorem is a profound result in theoretical ecology. It demonstrates that the pathological neutral stability of the Lotka-Volterra model is a non-robust artifact of its extreme linearity.[22] By incorporating the minimal and biologically realistic non-linearity of self-regulation (especially $\frac{\partial W}{\partial y} < 0$), the system is forced into one of two structurally stable, biologically meaningful behaviors: a stable steady state or a stable, robust oscillation.[24, 26]

2.6 Modern Stability Analysis: The Role of Lyapunov Functions

While Kolmogorov's original proof relied on the geometric and topological methods of the Poincaré-Bendixson theorem, modern analysis of the global stability of the coexistence equilibrium (x^*, y^*) often relies on the construction of a suitable Lyapunov function.[27, 28]

A Lyapunov function $V(x, y)$ is a scalar-valued function that is positive definite with respect to the equilibrium and whose time derivative $\dot{V} = \frac{\partial V}{\partial x}\dot{x} + \frac{\partial V}{\partial y}\dot{y}$ is negative semi-definite along the system's trajectories. Constructing such a function proves that all trajectories converge to the equilibrium. A significant body of literature in mathematical biology is dedicated to finding appropriate Lyapunov functions for various classes of Kolmogorov systems, which serves to rigorously establish the conditions for global stability.[29]

3 Applications of the Kolmogorov ODE Framework

The mathematical structure $\dot{x}_i = x_i H_i(\vec{x})$, where x_i is the population of species i and H_i is its per-capita growth rate, is not limited to two-species predator-prey interactions. This general form, now widely known as a Kolmogorov system, provides a unifying framework for modeling a vast array of ecological interactions, including competition, mutualism, and complex food webs.[21]

3.1 Kolmogorov-Type Competition Models

The classic Lotka-Volterra competition equations are a prime example of a planar Kolmogorov system.[21, 30] For two competing species, N_1 and N_2, the model takes the form [30]:

$$\frac{dN_1}{dt} = \rho_1 N_1 \left(1 - \frac{N_1}{K_1} - a_{12}\frac{N_2}{K_1} \right)$$

$$\frac{dN_2}{dt} = \rho_2 N_2 \left(1 - \frac{N_2}{K_2} - a_{21}\frac{N_1}{K_2} \right)$$

This system fits the Kolmogorov form $\dot{N}_i = N_i H_i(N_1, N_2)$. The qualitative analysis pioneered by Kolmogorov, based on the geometry of the nullclines, leads to the four canonical outcomes of interspecific competition, based on the relative strengths of intraspecific vs. interspecific competition (a_{12}, a_{21}) [30]:

1. **Stable Coexistence:** If interspecific competition is weaker than intraspecific competition for both species, the system converges to a stable equilibrium where $N_1^* > 0$ and $N_2^* > 0$.

2. **Exclusion (Species 1 wins):** If species 1 is a strong competitor and species 2 is weak, the system converges to the boundary equilibrium $(K_1, 0)$.

3. **Exclusion (Species 2 wins):** The reverse of the above; the system converges to $(0, K_2)$.

4. **Bistability (Founder Control):** If interspecific competition is stronger than intraspecific competition for both species, the coexistence equilibrium is unstable.

The system converges to either $(K_1, 0)$ or $(0, K_2)$, depending on the initial population densities.

This framework can be extended to general "competitive systems" (where $\frac{\partial H_i}{\partial x_j} \leq 0$ for $i \neq j$) and "cooperative systems" (where $\frac{\partial H_i}{\partial x_j} \geq 0$ for $i \neq j$), for which a rich mathematical theory of monotone dynamical systems now exists.[31]

3.2 Multi-Species (n-Dimensional) Kolmogorov Systems

The framework naturally extends to n interacting species, represented by the system [32, 33]:

$$\dot{x}_i = x_i H_i(x_1, \ldots, x_n), \quad i = 1, \ldots, n$$

This general form can model complex food webs, including three-species food chains (prey-predator-superpredator).[6] However, a critical finding is that the "simple" dynamics of the 2D Kolmogorov system are completely lost in higher dimensions. The Poincaré-Bendixson theorem, which forbids chaos in 2D autonomous systems, does not apply for $n \geq 3$.

As early as 1976, it was shown that three-species Lotka-Volterra competition models could be chaotic. Later work on three-species food chains confirmed that Kolmogorov systems can exhibit complex, chaotic dynamics.[6, 34] This implies that, in contrast to 2D models, the long-term behavior of complex ecosystems can be aperiodic and fundamentally unpredictable.[6]

3.3 Predator-Two Prey Models and Non-Kolmogorov Systems

A "predator-two prey" model is a 3-species system that can be formulated in the Kolmogorov form.[34, 35, 36] Analysis of these systems reveals complex behaviors not seen in the 2D case, including:

- **Multistability:** The coexistence of different stable attractors (e.g., a stable steady state and a stable limit cycle) for the same set of parameters.[35, 36]

- **Multiple Limit Cycles:** The presence of more than one stable oscillatory solution.[35]

This results in a strong sensitivity to initial conditions, where the final state of the ecosystem (steady or oscillating) depends entirely on the starting populations.[35, 36]

This research also highlights a crucial limitation of the Kolmogorov framework. Studies often contrast Kolmogorov models with non-Kolmogorov models, such as a predator-prey-subsidy system.[34, 35, 36] A subsidy model, which includes an allochthonous resource... provided to the system exogenously [35], is no longer Kolmogorov in form.[34, 35, 36]

The reason for this distinction is fundamental. A system $\dot{x}_i = x_i H_i(\vec{x})$ has the mathematical property that the axes are invariant: if $x_i(0) = 0$, then $\dot{x}_i(t) = 0$ for all t. This means the model cannot, by definition, include processes like immigration or external subsidies, which would be represented by an additive term (e.g., $\dot{x}_i = x_i H_i(\vec{x}) + C_i$). Such an "exogenous forcing term" [35] breaks the Kolmogorov structure. Thus, the framework is intrinsically limited to modeling closed, self-contained biotic interactions.

4 Stochastic Kolmogorov Systems: Environmental Fluctuations

4.1 From Determinism to Stochasticity

The 1936 Kolmogorov model is deterministic. It assumes that the per-capita growth rates S and W are fixed functions of the current population sizes. However, real-world biological and environmental parameters (e.g., birth rates, predation success) fluctuate randomly.[37] A major line of modern research extends the Kolmogorov framework to include this "environmental noise," recasting the deterministic ODEs as stochastic differential equations (SDEs).[32, 37]

4.2 Formulation as Stochastic Differential Equations (SDEs)

An n-dimensional stochastic Kolmogorov system is a diffusion process $X(t)$ in $\mathbb{R}^n_+$ that solves a system of SDEs, typically of the Itô form [37]:

$$dX_i(t) = X_i(t)f_i(X(t))dt + X_i(t)g_i(X(t))dW_i(t), \quad i = 1, \ldots, n$$

Here, f_i represents the deterministic part of the per-capita growth rate (as in the 1936 model), $W_i(t)$ is a standard Brownian motion (or Wiener process) representing "white noise" fluctuations, and g_i scales the magnitude of this noise.[37, 38] The multiplicative noise term $X_i g_i dW_i$ is often considered more biologically realistic, as it implies that the magnitude of random fluctuations scales with the population size.

4.3 Conceptual Unification: The SDE and the Kolmogorov Forward Equation

This SDE formulation creates a powerful synthesis of two of Kolmogorov's major contributions. The 1936 model provides the deterministic "drift" term $X_i f_i dt$, while the 1931 framework provides the machinery to analyze the resulting stochastic process.

Specifically, the probability density function $p(\vec{x}, t)$ of the state vector $X(t)$ of the SDE system is governed by the **Kolmogorov Forward Equation (KFE)**, also known as the Fokker-Planck equation.[38, 39] For a single population SDE $dX = f(X)dt + g(X)dW$, the KFE is the PDE:

$$\frac{\partial p(x,t)}{\partial t} = -\frac{\partial}{\partial x}[f(x)p(x,t)] + \frac{1}{2}\frac{\partial^2}{\partial x^2}[g^2(x)p(x,t)]$$

Thus, Kolmogorov's 1931 work on Markov processes provides the exact mathematical tools needed to analyze the probabilistic outcomes (like extinction probabilities or stationary distributions) of his 1936 population model once it is generalized to a stochastic setting.

4.4 The Central Question: Coexistence vs. Extinction

In the deterministic 1936 model, the central question is the stability of the coexistence equilibrium (a fixed point or a limit cycle). In the stochastic framework, this question is reframed as **coexistence vs. extinction**.[37, 40, 41, 42, 43]

- **Strong Stochastic Persistence (Coexistence):** The system is considered persistent or coexistent if it has a unique stationary (invariant) probability measure π^* whose support is in the *interior* of the positive quadrant (i.e., $\pi^*(\{\vec{x} : x_i > 0 \text{ for all } i\}) = 1$). This represents a long-term probabilistic steady state where all species survive.[37]

- **Extinction:** The system (or a subset of its species) goes extinct if the process converges to an invariant measure that is supported on the *boundary* of the domain (i.e., where at least one $x_i = 0$).[37, 40]

A key finding is that environmental fluctuations can either facilitate or, more commonly, negate coexistence.[37, 41] For a simple stochastic logistic model $dX = X(r - aX)dt + \sigma X dW$, the condition for persistence is not $r > 0$, but $r - \sigma^2/2 > 0$.[41] The term $-\sigma^2/2$, an artifact of Itô calculus, acts as a noise-induced reduction in the effective growth rate, demonstrating that environmental variability itself can drive a population to extinction even when its deterministic counterpart would survive.

4.5 Analytical Methods: Invariant Measures and Lyapunov Exponents

The stability of stochastic Kolmogorov systems is analyzed by "a careful study of the properties of the invariant measures of the process that are supported on the boundary of the domain".[37, 40] The method involves calculating the "stochastic growth rate," or more formally, the principal Lyapunov exponent $\lambda_i(\mu)$ for each species i with respect to each boundary invariant measure μ.[37]

- If for every invariant measure μ on the boundary, there is some species j (currently extinct in μ) that has a positive growth rate ($\lambda_j(\mu) > 0$), then the boundary is "repelling" as a whole, and the system is stochastically persistent.[37]

- If there exists a boundary measure μ that is a "sink" (i.e., all $\lambda_i(\mu) \leq 0$), then extinction is possible or guaranteed.[37]

This modern approach provides "sharp conditions" for coexistence and extinction in n-dimensional, non-compact domains, extending Kolmogorov's qualitative analysis into the stochastic realm.[32, 37, 40, 42]

5 Related Frameworks: Kolmogorov's Contributions to Spatial and Genetic Dynamics

To complete the literature review, it is essential to detail the other two major frameworks associated with Kolmogorov, as they are often confused with the 1936 model and with each other.

5.1 The Kolmogorov Petrovsky Piskunov (KPP) Equation

This is a partial differential equation (PDE) for reaction-diffusion, and it is fundamentally a *spatial* model.

5.1.1 Definition and Origin

Published in 1937 by Kolmogorov, Petrovsky, and Piskunov [9, 10, 19], and independently by R.A. Fisher [3], the KPP equation (or Fisher-KPP equation) describes the spatial and temporal evolution of a population density $u(x, t)$.[3, 12] In its one-dimensional form, it is [4, 44]:

$$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2} + F(u)$$

Here, D is the diffusion coefficient (modeling spatial dispersal) and $F(u)$ is the nonlinear reaction term (modeling population growth).[3, 44]

5.1.2 Original Application and the Reaction Term

The 1937 KPP paper explicitly applied this model to a "biological problem," namely the spread of an advantageous gene in a population.[4, 13, 19] The variable u represented the frequency of the new gene, from $u = 0$ (absent) to $u = 1$ (fixed).

True to the Kolmogorov approach, the authors did not fix $F(u)$ (as Fisher did with the logistic $F(u) = ru(1 - u)$), but defined a general *class* of "KPP-type" functions satisfying [4, 19, 45]:

1. $F(0) = 0$ and $F(1) = 0$ (unstable and stable equilibria, respectively).

2. $F(u) > 0$ for all $u \in (0, 1)$.

3. $F(u)$ is sufficiently smooth, with $F'(0) = \alpha > 0$ and $F'(u) < \alpha$ for $u \in (0, 1]$ (growth is fastest at the lowest density).

5.1.3 Key Result: Traveling Waves

The seminal contribution of the KPP paper was the proof of the existence of *traveling wave* solutions, $u(x, t) = U(z)$ where $z = x - ct$. These waves represent a stable front of the invading population (or gene) propagating through space. The key result is that for any KPP-type function $F(u)$, there is a continuous family of wave speeds $c \geq c^*$, but that a "pushed" wave (from localized initial data) will asymptotically select the minimum speed [4, 12, 46]:

$$c^* = 2\sqrt{DF'(0)}$$

This formula provides a powerful, predictive link between microscopic parameters (diffusion D, initial growth α) and a macroscopic phenomenon (invasion speed c^*). This model is now a cornerstone of spatial ecology, used to model biological invasions, tumor growth, and epidemic spread.[12, 44, 47]

5.2 The Kolmogorov Equations for Markov Processes (1931)

This framework is the most mathematically abstract but provides the foundation for all modern stochastic population modeling.

5.2.1 Definition and Origin

In his 1931 paper, Kolmogorov laid the axiomatic foundations of probability theory and derived the "analytical methods" for describing continuous-time Markov processes.[2, 8, 14] He found that such processes fall into two categories: "jump processes" and "diffusion processes".[2] For each, he derived a pair of equations:

1. **The Kolmogorov Forward Equation (KFE):** This PDE describes the time evolution of the *probability density function* $p(x, t)$ of the process being in state x at time t. It is now universally known in physics and biology as the **Fokker-Planck equation**.[2, 15, 16]

2. **The Kolmogorov Backward Equation (KBE):** This is the adjoint PDE, which describes how the probability of reaching a future state depends on the *starting* position and time.

5.2.2 Application in Population Genetics (Wright-Fisher Model)

The KFE finds its most classical biological application in the diffusion approximation of the Wright-Fisher model of genetic drift.[17, 18] The discrete Wright-Fisher model describes the change in allele frequency X in a finite population of size N due to random sampling. In the limit of large N (the diffusion limit), the allele frequency $x = X/N$ evolves as a continuous Markov process.[18]

The probability density function $u(x, t)$ of this allele frequency x at time t (measured in generations) is a solution to the KFE [18]:

$$\frac{\partial u(x, t)}{\partial t} = \frac{1}{2} \frac{\partial^2}{\partial x^2} \left[V(x)u(x, t) \right] - \frac{\partial}{\partial x} \left[M(x)u(x, t) \right]$$

In the simplest case of pure drift (no mutation or selection), the drift coefficient $M(x) = 0$ and the diffusion coefficient $V(x) = x(1 - x)/N$ (reflecting the binomial sampling variance). This equation allows for the calculation of fundamental quantities in population genetics, such as the probability of allele fixation or loss.[18]

5.3 Comparative Summary

The distinctions between these three foundational frameworks are critical and are summarized in Table 2. The 1936 model is a non-spatial, deterministic ODE system for species *interaction*. The 1937 KPP model is a spatial, deterministic PDE for *propagation* of a single population. The 1931 KFE is a spatial (in state-space), stochastic PDE for the *probability* of a population process.

6 Critical Assessment and Future Directions

6.1 Limitations and Critiques of the 1936 Model

While the 1936 Kolmogorov model was a revolutionary step towards biological realism, its general assumptions are still simplifications and have been the subject of extensive refinement.

Table 2: Comparison of Kolmogorov's Population-Related Frameworks

Feature	1931 Stochastic Model	1936 Predator-Prey Model	1937 KPP Model
Full Title	"Über die analytischen Methoden..."	"Sulla teoria di Volterra..."	"Étude de l'équation de la diffusion..."
Mathematics	PDE (for probability density)	System of 2 ODEs	PDE (for population density)
Domain	Probability Theory (Markov Processes)	Theoretical Ecology (Dynamical Systems)	Population Genetics / Spatial Ecology
Key Eq(s)	Kolmogorov Forward/Backward Eqns.	$\dot{x} = xS(x,y),\ \dot{y} = yW(x,y)$	$u_t = Du_{xx} + F(u)$
Variables	$p(x,t)$: probability density	$x(t), y(t)$: population densities	$u(x,t)$: population density at (space, time)
Core Concept	Diffusion/Jump Processes	Qualitative stability, Limit cycles	Traveling waves, Invasion speed
Spatial	No (models state-space)	No (models well-mixed)	**Yes** (models spatial spread)
Stochastic	**Yes** (foundational)	No (deterministic base)	No (deterministic base)
Primary App.	Wright-Fisher diffusion approx. [18]	Generalizing Lotka-Volterra [6]	Spread of an advantageous gene [13]

This table provides a high-level comparison of the three primary mathematical frameworks developed or co-developed by A.N. Kolmogorov and applied to population dynamics.

- **Violated Assumptions:** The "minimal conditions" are not universally true. For example, the predator self-regulation condition $\frac{\partial W}{\partial y} < 0$ (predator competition) can be violated in species that engage in cooperative hunting, where an increase in predator density (for small y) might *increase* hunting success.[6]

- **Omitted Biological Phenomena:** The general C^1 framework of the 1936 model, in its basic form, omits many biological mechanisms that are now known to be critical in shaping population dynamics.[20, 48] Modern predator-prey modeling routinely incorporates:

  - **Allee Effects:** The reduction of per-capita growth at low densities, which violates the $S(0,y) > 0$ assumption.[20, 49]

  - **Fear Effects:** Anti-predator behavior in prey (e.g., reduced foraging) that can affect prey reproduction even without direct consumption.[20, 49]

  - **Cannibalism:** Intraspecific predation, which can have strong stabilizing (or destabilizing) effects.[20, 49]

  - **Time Delays:** Delays from gestation, maturation, or resource regeneration, which are known to be a powerful source of instability and oscillations.[50, 51]

- **Structural Limitations:** As identified in Section 3.3, the $\dot{x}_i = x_i H_i$ structure is a fundamental limitation. It cannot, by definition, model systems with exogenous inputs, such as resource subsidies or population immigration.[34, 35, 36]

6.2 Open Problems in Kolmogorov Dynamics

The study of Kolmogorov-type systems remains a vibrant and challenging area of mathematical research.

1. **The $n \geq 3$ Problem:** As noted, 3D and higher-dimensional Kolmogorov systems can be chaotic.[6] A general classification of their dynamics, analogous to the 2D Kolmogorov theorem, is impossible. A key open problem, highlighted in the literature, is that for n-dimensional systems, there exist "open sets of Kolmogorov equations" for which it is impossible to predict from a local analysis (e.g., stability of equilibria) whether all species will survive. Only a "dynamic global study" can account for the complexity, and this remains a formidable analytical challenge.[6]

2. **Stochastic Persistence:** While the theory of stochastic persistence is well developed, finding the sharp conditions for coexistence in n-dimensional, non-compact domains (i.e., for $X(t) \in \mathbb{R}_+^n$) remains a highly active research frontier. [37, 43]

3. **Spatial Dynamics:** The classic KPP model has its own limitations. For example, it cannot simulate population extinction, which gives rise to a "spreading-extinction dichotomy" that the KPP model fails to capture.[12, 44] This has led to new classes of spatial models, such as the Fisher-Stefan model, which involve free boundaries and pose significant new analytical challenges.[12, 44, 47]

6.3 Emerging Frontiers: Unifying Kolmogorov's Legacies with KANs

The central challenge of the 1936 Kolmogorov model has always been the nature of the functions $S(x, y)$ and $W(x, y)$. For nearly a century, theoretical ecology has consisted of *proposing* simple, parametric forms for S and W (e.g., Holling Type II, Beddington-DeAngelis, Ivlev) and testing their consequences. A long-standing goal has been to *discover* these functions directly from data.

This data-driven discovery of dynamical systems is notoriously difficult.[52, 53, 54]

- **Sparse optimization** methods (like SINDy) work well for simple physical laws but fail for "a large variety of ecosystems," which are not "sparse" (i.e., their governing equations are not sums of a few simple mathematical terms).[52, 53, 54]

- **Traditional deep learning** e.g., Multi-Layer Perceptrons or MLPs can be trained to predict system behavior but function as "black boxes," offering little insight into the underlying functional forms of S and W.[53, 55]

A remarkable new development, however, points to a unification of Kolmogorov's many legacies. A novel neural network architecture called the **Kolmogorov-Arnold Network (KAN)** has emerged as a powerful tool in scientific machine learning.[56, 57, 58]

The profound connection is this: KANs are not based on the universal approximation theorem (like MLPs), but on the **Kolmogorov-Arnold Representation Theorem** (Kolmogorov, 1957), another of Kolmogorov's foundational mathematical achievements.[59] KANs are "interpretable" by design and are being used to "discover" the symbolic governing equations of complex dynamical systems that are not sparse.[53, 56, 57, 60]

Researchers are already applying KANs integrated with ODE solvers (termed KAN-ODEs) to ecological models, including the Lotka-Volterra system, and demonstrating superior accuracy and interpretability compared to traditional neural ODEs.[60, 61] This new technology is uniquely suited to tackle the core challenge of the 1936 Kolmogorov model: discovering the complex, non-sparse, and non-parametric functional forms of $S(x, y)$ and $W(x, y)$ directly from ecological time-series data.[53, 54]

The future of the "Kolmogorov population model" may therefore be a grand synthesis: using a machine learning framework derived from Kolmogorov's 1957 theorem to discover the true functional forms of the general ecological framework he proposed in 1936, and using the stochastic calculus he pioneered in 1931 to analyze their probabilistic behavior.

7 Conclusion: A Unified View of Kolmogorov's Influence on Theoretical Biology

This review has navigated the complex and multifaceted legacy of Andrei Kolmogorov in population dynamics. The "Kolmogorov population model" is not a single entity but a tripartite foundation of modern theoretical biology.

1. **The 1936 General Predator-Prey System (ODE):** This framework fundamentally shifted ecological modeling from the analysis of specific, mechanistic equations (like Lotka-Volterra) to the *qualitative analysis* of entire *classes* of models defined by their fundamental biological properties. Its theorem on the dichotomy between stable equilibria and stable limit cycles resolved the problematic neutral stability of earlier models and remains the cornerstone of 2D population dynamics.

2. **The 1937 KPP Equation (PDE):** This provided the mathematical theory for spatial propagation in biology, defining the concepts of reaction-diffusion traveling waves and minimum invasion speeds that are now indispensable in spatial ecology, genetics, and epidemiology.

3. **The 1931 Kolmogorov Forward Equation (KFE):** This work provided the mathematical "engine" for all modern stochastic modeling, allowing discrete, random processes (like genetic drift or demographic stochasticity) to be analyzed as continuous diffusion processes.

Kolmogorov's unifying contribution across all three fields was the introduction of a new level of mathematical abstraction, focusing on the general, qualitative properties of classes of functions rather than the behavior of specific, arbitrary postulates. This approach built a far more robust and general foundation for theoretical biology.

Today, this legacy is evolving. The limitations of the 1936 model are well-understood, and the frontiers of research have pushed into n-dimensional, stochastic, and spatial-temporal systems that exhibit complex chaos and require sophisticated analytical methods. The most exciting frontier, however, is one that brings Kolmogorov's work full circle. The emergence of Kolmogorov-Arnold Networks (KANs) promises, for the first time, a method to *discover* the general, non-parametric interaction functions $S(x, y)$ and $W(x, y)$ that Kolmogorov posited in 1936. This suggests that the next era of theoretical ecology will be defined by the unification of Kolmogorov's 1936 ecological framework, his 1931 stochastic calculus, and his 1957 representation theorem.