A statistical interpretation of the logistic equation

A. Samoletov*, B. Vasiev**

The University of Liverpool, Liverpool, UK

Abstract

The logistic equation is one of the established paradigms in modelling population growth. Here we propose a statistical interpretation of the logistic equation. This interpretation is based on modelling the population–environment relationship, the mathematical theory of which we discuss in detail. By applying this theory, we obtain stochastic evolutionary equations, for which the logistic equation is a limiting case. The prospect of modifying logistic population growth is discussed.

Keywords: logistic equation, ecological temperature, dynamic principle, population–environment coevolution, stochastic dynamics

1. Introduction

Dynamics of a single species population is a prototype for mathematical modelling in ecology and is commonly described by the following differential equation,

$$\dot{x} = xf(x), \tag{1}$$

where x is the population density and $f(x)$ describes the *per capita* growth. The observed upper limit for population growth determines the level of saturation known as carrying capacity. The simplest form of the associated dynamics, the Verhulst-Pearl [1, 2] logistic equation,

$$\dot{x} = rx\left(1 - \frac{x}{K}\right), \tag{2}$$

where r is a time scale so that rt is dimensionless time and K is the carrying capacity, is often and successfully used to model population growth [3]. The modelling of population dynamics using equation (1) is based on a special choice of mathematical expressions for the laws governing population growth, that is, the function $f(x)$, so that the environment is treated as a static reservoir. The logistic equation (2) inherits the requested generic properties of the equation (1). To substantiate a choice $f(x) = r\left(1 - K^{-1}x\right)$, the data of experimental observations and heuristic reasoning are usually used [1–3].

⋆This document is a collaborative effort.
*Corresponding author
**Corresponding author
Email addresses: `A.Samoletov@liverpool.ac.uk` (A. Samoletov),
`B.Vasiev@liverpool.ac.uk` (B. Vasiev)

Another approach to justifying the equation (2) was initiated by Volterra [4] and was based on finding a certain minimum principle leading to the logistic law of population growth, that is, to the equivalent Euler-Lagrange equation. The problem is to find the Lagrangian that has the required form. This approach was discussed in the literature and several forms of the Lagrangian were proposed [4–8]. Also some speculations were made regarding the universality of the functional approach in the context of ecological problems [7–9].

Philosophically, one can trivially assert that all subsystems of the ecosphere are in interaction and interdependence. However, this statement is meaningless, since only a relatively small number of characteristic variables need to be taken into account in specific models. Since reliable information about the actual state of the entire ecosphere is unknown, its impact on small ecosystems can only be accounted for phenomenologically, based on plausible reasoning.

A statistical approach to population dynamics, which can be either deterministic or stochastic, is as follows. Consider an ensemble of identical populations, differing only in initial size, together with the corresponding phase space. Assuming that the ensemble is initially characterised by a probability density on the phase space, we interpret the population dynamics as an evolution of this ensemble, and we are interested in the asymptotic density at large times. Traditional deterministic population dynamics can be represented by a stable asymptotic behaviour [10], so that the resulting densities are singular. If the dynamics can be perturbed in some way, we must consider smooth density functions. In the context of dynamical systems theory we are interested in invariant densities. Ergodicity means equivalence of ensemble averaging and time averaging. This property is the basis of statistical approach to dynamics, and therefore the ergodic hypothesis is necessary for our analysis.

By moving towards a mathematical formulation of a statistical approach to population dynamics, we recognise that natural populations do not exist and grow in isolation, but are in dynamic contact with the environment. It is clear that population evolution is influenced by changes in static (or quasi–static) environmental conditions, but to better understand population growth, dynamic models must also account for population–environment interactions, environmental responses to a growing population, and internal population and environmental processes that may be only partially known, introducing a degree of uncertainty into population dynamics. Indeed, any population placed in the environment must perturb it to some extent and will itself be subject to the backward influence of this perturbation. Depending on the time scale of the population growth the environment can be divided into two parts: the part involved in the joint dynamics with the population and the unperturbed part, which determines the general statistical properties of the population–environment co-evolution and the long-term homeostasis of the population, if it exists.

To ensure an equilibrium state, population growth must be controlled by resource balance, population abundance and a variety of other mechanisms. The dynamic processes of fluctuation and relaxation must be defined accordingly. However, we do not specify explicit mechanisms. Instead, we define general statistical hypotheses that cover many different biological processes. Specific biological processes need to be considered separately.

In the context of population dynamics and ecosystem evolution, the statistical approach, as we formulate it, contains the possibility of implementing different scenarios of transition from the initial state to the asymptotic state of

statistical equilibrium, which implies qualitatively different dynamic scenarios. In our case, the goal is the statistical interpretation of a very special process - the logistic law of population growth.

To present a statistical interpretation of the logistic equation, that is, a rather simple but important mathematical model of population growth, we begin with a brief statement of the relevant mathematical assumptions that combine the dynamic principle for ensemble control tools, the definition of the environmental temperature and the corresponding invariant density, the ergodic hypothesis and methods of stochastic analysis [11–14]. Then, based on plausible probabilistic reasoning, we formulate and explore the statistical interpretation of the logistic equation.

2. Mathematical formalism

In this section, we briefly summarise the mathematical concepts necessary to understand the statistical interpretation of the logistic equation.

Let a population $\mathscr{P}$ be placed in an environment $\mathscr{E}$, a system of large (infinite) number of phase variables, that determines the general statistical properties of the entire ecosystem. The population has to disturb the environment to some extent, and will be affected by this disturbance. Let the environment $\mathscr{E}$ be divided into the part participating in the joint dynamics with the population, $\mathscr{E}^*$, and the rest of the ecological system, $\mathscr{E} \setminus \mathscr{E}^*$, which determines statistical properties of population and environment coevolution, and long-term population homeostasis. Subsystems $\mathscr{P}$ and $\mathscr{E}^*$ interacting with the global environmental reservoir $\mathscr{E} \setminus \mathscr{E}^*$ can be fluctuating, while $\mathscr{E} \setminus \mathscr{E}^*$ remains unchanged, determining the general statistical properties of the whole system, $\mathscr{P} + \mathscr{E}^*$. Let us make an important assumption that the population $\mathscr{P}$ and its environment $\mathscr{E}^*$ participating in the joint dynamics are statistically independent in equilibrium. Of course, the actual description of $\mathscr{E}^*$ cannot be done in advance and depends on the population, the environment and the experiments used to extract information on population growth, as they determine the temporal and spatial scales of measurements and the corresponding interpretation of data. Thus, the system $\mathscr{E}^*$ is not predetermined, but depends on a number of factors that do not affect the asymptotic statistical behaviour of the population. Among these factors, the possibility of various evolutionary transients should be emphasised. The study of transients in population dynamics and ecology is an intensively studied problem [15, 16]. Practically, to describe $\mathscr{E}^*$, one can try one or another set of variables to construct consistent coevolution equations and investigate their properties.

To consider the interaction and joint evolution of systems $\mathscr{P}$ and $\mathscr{E}^*$ as described above, we first need to define the dynamical system, $\mathscr{S} = (\mathcal{M}^+, G(z))$, which is a direct product of noninteracting (autonomous) systems $\mathscr{P} = (\mathcal{M}, g(x))$ and $\mathscr{E}^* = (\mathcal{M}^*, g^*(y))$, that is, $\mathscr{S} = \mathscr{P} \times \mathscr{E}^* = (\mathcal{M} \oplus \mathcal{M}^*, g(x) \times g^*(y))$, where $\mathcal{M}$ and $\mathcal{M}^*$ are phase spaces of systems $\mathscr{P}$ and $\mathscr{E}^*$ correspondingly. In other words, we consider a simple combination of two independent systems into one so that $z = (x, y) \in \mathcal{M}^+ = \mathcal{M} \oplus \mathcal{M}^*$ and $\dot{z} = G(z)$, where $G(z) = g(x) \times g^*(y)$. When $\mathscr{P}$ and $\mathscr{E}^*$ are considered as systems involved in joint evolution, such a separation into noninteracting systems becomes impossible and we have to

consider dynamics in the general form,

$$\dot{z} = G^+(z). \tag{3}$$

However, it is important that, as in the case of noninteracting systems, the invariant density σ^+ for the combined system $\mathscr{S}$ is the direct product of the invariant densities σ and σ^* for the systems $\mathscr{P}$ and $\mathscr{E}^*$,

$$\sigma^+(z) = \sigma(x) \times \sigma^*(y), \tag{4}$$

that is, the systems $\mathscr{P}$ and $\mathscr{E}^*$ are statistically independent in the equilibrium state, provided that the equilibrium state of the entire ecosystem exists, where $\mathscr{P}$ and $\mathscr{E}^*$ are small subsystems.

As preparation for what follows, we briefly summarise two important concepts: (1) ecological temperature and (2) the dynamic principle for statistical ensemble control tools.

Ecological temperature

The concept of temperature expression [11, 12].

Let the probability density $\sigma(x)$, $x \in \mathcal{M}$ be given. Define the function $h(x) : \mathcal{M} \to \mathbb{R}$, $h(x) \propto -\vartheta \ln \sigma(x)$, where $\vartheta > 0$ is a parameter, so that $h(x)$ is a sufficiently smooth function, bounded from below and growing at infinity, $h(x) \geq a|x|^b$ for some $a > 0$, $b > 0$, that is, a coercive function. Let us represent the probability density function as,

$$\sigma_\vartheta(x) \propto \exp\left\{-\vartheta^{-1}h(x)\right\}, \quad x \in \mathcal{M}. \tag{5}$$

The density $\sigma_\vartheta^*(y) \propto \exp\left\{-\vartheta^{-1}h^*(y)\right\}$, $y \in \mathcal{M}^*$ is understood in the same way.

The function $\Theta(x,\vartheta)$, $\Theta : \mathcal{M} \times \mathbb{R}_+ \to \mathbb{R}$ is called an ecological temperature expression (abbreviated as ϑ-expression) if it explicitly depends on the parameter ϑ and satisfies the conditions,

$$\mathbb{E}_\vartheta\{\Theta(x,\vartheta)\} = 0 \quad \text{for all} \quad \vartheta > 0, \tag{6}$$

where $\mathbb{E}_\vartheta\{\ldots\} = \int_\mathcal{M}(\ldots)d\mu_\vartheta(x)$ is the mathematical expectation, and $d\mu_\vartheta(x) = \sigma_\vartheta(x)dx$ is the probability distribution. The ϑ-expression (6) is defined up to a constant factor, possibly depending on ϑ, and an additive function $\psi(x)$ such that $\int_\mathcal{M}\psi(x)d\mu_\vartheta(x) = 0$. We consider $\Theta(x,\vartheta)$ as an analytic function of the real parameter ϑ, $\Theta(x,\vartheta) = \Theta_0(x) + \Theta_1(x)\vartheta + \ldots$, whose first term $\Theta_0(x)$ has a nonzero expectation $\mathbb{E}_\vartheta\{\Theta_0(x)\} \neq 0$. Usually $\Theta(x,\vartheta)$ is a polynomial in ϑ [12]. This is the context in which definition (6) should be understood. In practice, although $\psi(x)$ functions are not true ϑ-expressions, they can nevertheless be used to generate deterministic equations of motion consistent with the dynamic principle, as defined below. However, in this case the required property of ergodicity seems to be more than doubtful (e.g. [17]).

We consider $\mathscr{P}$ and $\mathscr{E}^*$ as parts of a large, infinitely large, ecosystem that determines the equilibrium statistical properties of both the population $\mathscr{P}$ and environment $\mathscr{E}^*$, provided that such an equilibrium state exists. Thus, it should be assumed that the ecological temperatures of the population $\mathscr{P}$ and the environment $\mathscr{E}^*$ coincide (see [18] to argue for this). This equality of the parameter ϑ has direct implications for the mathematical formulation of the theory.

The set of all ϑ-expressions for an arbitrary but fixed value of the parameter ϑ is a linear system in which the operations of addition and multiplication by numbers are defined in the usual way. In order to study and use the properties of ϑ-expressions, it will be necessary to interpret them as elements of either the space L_1 (summable expressions) or L_2 (square summable expressions). Such an interpretation is appropriate here, since the ϑ-expressions we are considering are bounded from below and grow at infinity no faster than a polynomial.

For the combined system $\mathscr{S}$ a temperature expression satisfies the condition,

$$\int_{\mathcal{M}^+} \Theta^+(z,\vartheta)d\mu_\vartheta^+(z) = \int_{\mathcal{M}^+} \Theta^+((x,y,\vartheta),\vartheta)d\mu_\vartheta(x)d\mu_\vartheta^*(y) = 0 \quad \text{for all} \quad \vartheta > 0,$$

and, provided that $\int_{\mathcal{M}} |\Theta^+(z,\vartheta)| \, d\mu_\vartheta(z) < \infty$, it follows from Fubini's theorem that

$$\int_{\mathcal{M}} \Theta^+(z,\vartheta)d\mu_\vartheta(x) = \Theta^*(y,\vartheta) \quad \text{and} \quad \int_{\mathcal{M}^*} \Theta^+(z,\vartheta)d\mu_\vartheta^*(y) = \Theta(x,\vartheta)$$

are ϑ-expressions as defined above. For more information about the properties and selection of ϑ–expressions, see [12].

Dynamic principle

The dynamic principle [11, 12] for development of statistical ensemble control tools is based on the assumption of ergodicity, that is, the averaging can equally be interpreted either as an ensemble average or as a time average for a single trajectory. To unify the notation, we denote the result of the averaging by " $\sim$ " and write, for example, in relation to the ϑ-expression, $\Theta(x,\vartheta) \sim 0$, assuming that $\lim_{t\to\infty} \frac{1}{t} \int_0^t \Theta(x(t'),\vartheta)dt' = 0$.

In the statistical description of a dynamical system $\dot{x} = g(x)$, the concept of the first integral plays a central role [18]. The function $h(x)$ is the first integral if and only if $\nabla h(x) \cdot g(x) = 0$ for all $x \in \mathcal{M}$. When populations are involved in coevolution with the environment, then $h(x)$ is no longer the first integral. This is also true when the effects of the ecosystem on the population are treated as random perturbations. To describe such coevolution with a given invariant measure, the dynamic principle for ensemble control tools is used, which leads to consistent dynamic equations. The invariant measure can be *a priori* or can be derived from experimental data. Let us assume that the equations of motion are of the form (3) and denote $\Gamma(z) \equiv \nabla_z h^+(z) \cdot G^+(z)$. Then the dynamic principle postulates the following functional relationship:

$$\Gamma(z) \propto \Theta^+(z,\vartheta) \sim 0, \tag{7}$$

or $\mathbb{E}_\omega \{\Gamma_\omega(z)\} \propto \Theta^+(z,\vartheta) \sim 0$ in the case of stochastic dynamics. Solutions to the functional equation, $\Gamma(z) = \Theta^+(z,\vartheta)$, represent possible transient population evolution scenarios compatible with a given invariant density. To find a particular solution to the equation $\Gamma(z) = \Theta^+(z,\vartheta)$, it is necessary to specify an invariant density and select an admissible ϑ–expression corresponding to this density. The criterion of such a selection is determined by the nature of the problem to be solved, for example, it can be the simplest admissible ϑ–expression. However, the range of possible selections is wide [11–14].

To understand the practical value of this rather abstract mathematical scheme, let us start simple and consider a conceptual example. To this end, we will consider a statistical interpretation of the logistic equation.

3. Statistical interpretation of the logistic equation

3.1. Preliminaries

Consider $\mathscr{P}$ as a single species homogeneous population with density $x \in \mathbb{R}_+$, placed in an environment such that a state of equilibrium exists. This is not a static equilibrium. Population growth depends on available resources and other environmental conditions, as well as the size of the population itself, to ensure a dynamic statistical equilibrium. These processes, which involve the environment in coevolution, must have balanced dynamics where the fluctuation and relaxation processes must be appropriately specified. To formulate a statistical approach to population dynamics, we will assume that the state of equilibrium and the corresponding ecological temperature ϑ are determined by the ecosystem as a whole, of which the population is a small part.

According to the theoretical scheme presented in Section 2, we must first establish the invariant density for the system $\mathscr{S} = \mathscr{P} + \mathscr{E}^*$, i.e. $\sigma_\vartheta^+ (z) = \sigma_\vartheta (x) \times \sigma_\vartheta^* (y)$.

3.1.1. The environment

Assume that the environment $\mathscr{E}^*$ is characterised by a variable $y \in \mathbb{R}$ with a probability density $\sigma_\vartheta^*(y)$. By necessity, y is a collective variable that incorporates a number of environmental factors and processes. Thus, it is reasonable to guess the Gaussian statistics, that is,

$$\sigma_\vartheta^*(y) \propto \exp\left\{-\vartheta^{-1}\frac{1}{2}y^2\right\}, \tag{8}$$

where y is a dimensionless variable. The ecological temperature ϑ defines the intensity of the environmental fluctuations. The Gaussian statistics is completely characterised by the first two cumulants: $\mathbb{E}_\vartheta (y) = 0$, $\mathbb{E}_\vartheta \left([y - \mathbb{E}(y)]^2\right) = \mathbb{E}_\vartheta \left(y^2\right) = \vartheta$. Thus, a linear combination of y and $\left(y^2 - \vartheta\right)$ is a ϑ–expression. It should be noted that even in the case of Gaussian statistics, it is only the simplest ϑ–expression associated with the environment. There are also other ϑ-expressions of higher order in ϑ [12].

3.1.2. The population

Let us accept the invariant probability density $\sigma_\vartheta (x)$ in the form (5), where the coercive function $h(x)$ is a subject to define. The ϑ parameter is the same as in $\sigma_\vartheta^*(y)$. The simplest ϑ-expression associated with the population has the form,

$$\Theta(x,\vartheta) = xh'(x) - \vartheta, \tag{9}$$

where prime denotes derivative (Lagrange notation). The proof is by direct calculation. For more advanced ϑ–expressions, see [12].

3.2. Logistic equation

To proceed to the statistical interpretation of the logistic equation, it is necessary to solve the functional equation (7) that includes at least the ϑ–expression associated with the environment, that is, the equation

$$\mathbb{E}_\omega \left\{h'(x) g(x,y) + yg^*(x,y)\right\} \propto \Theta^*(y,\vartheta) \sim 0, \tag{10}$$

where $\dot{x} = g(x,y)$, $\dot{y} = g^*(x,y)$. If we take a ϑ–expression of the form $\Theta^*(y,\vartheta) = ay + b\left(y^2 - \vartheta\right)$, in accordance with Section 3.1.1 $\mathbb{E}_\vartheta\left(\Theta^*(y,\vartheta)\right) = 0$, where a, b are constant coefficients and $b \neq 0$, then among the solutions of equation (10) there are only stochastic equations [11]. The algorithmic scheme for finding a solution to the functional equation (10) is based on a specific technique of stochastic analysis [11]. In order to stay within reasonable mathematical limits, we will skip the relevant details. Let us examine the following solution,

$$\dot{x} = \lambda xy,$$
$$\dot{y} = -\lambda\Theta(x,\vartheta) - \gamma y + \sqrt{2\gamma\vartheta}\xi(t), \tag{11}$$

where $\xi(t)$ is the standard Gaussian white noise, $\mathbb{E}_\omega\left\{\xi(t)\right\} = 0$, $\mathbb{E}_\omega E\left\{\xi(t)\xi(t')\right\} = \delta(t - t')$, $\lambda > 0$ and $\gamma > 0$ are parameters that actually define two time scales.

First of all, we check the ϑ-expression for the environment, $\Theta^*(y,\vartheta)$, by direct calculation,

$$\mathbb{E}_\omega\left\{h'(x)\lambda xy + y\left[-\lambda\left(xh'(x) - \vartheta\right) - \gamma y + \sqrt{2\gamma\vartheta}\xi(t)\right]\right\}$$
$$= \mathbb{E}_\omega\left\{\lambda\vartheta y - \gamma y^2 + \sqrt{2\gamma\vartheta}y\xi(t)\right\} = \lambda\vartheta y - \gamma\left(y^2 - \vartheta\right) = \Theta^*(y,\vartheta),$$

as required. Then, we prove that the density,

$$\sigma_\vartheta^+(x,y) \propto \exp\left\{-\vartheta^{-1}h(x)\right\} \times \exp\left\{-\vartheta^{-1}\frac{1}{2}y^2\right\}, \tag{12}$$

is invariant for dynamics (11). Indeed, the Fokker-Planck equation corresponding to stochastic differential equation (11) has the form $\partial_t\sigma = \boldsymbol{\mathcal{F}}^*\sigma$, where

$$\boldsymbol{\mathcal{F}}^*\sigma = -\frac{\partial}{\partial x}\left[\lambda xy\sigma\right] - \frac{\partial}{\partial y}\left\{\left[-\lambda\left[xh'(x) - \vartheta\right] - \gamma y - \gamma\vartheta\frac{\partial}{\partial y}\right]\sigma\right\},$$

is the Fokker-Planck operator. We prove the identity, $\boldsymbol{\mathcal{F}}^*\sigma_\vartheta^+(x,y) = 0$, by direct calculation, implying that $\sigma_\vartheta^+(x,y)$ (12) is the invariant density for dynamics (11). One would expect that for the stochastic evolution equation (11) the dynamics would be ergodic.

We have arrived at fairly simple population–environment coevolution equations (11). We can now ask how these dynamic equations relate to the conventional population growth equations (1), in particular the logistic equation (2). To answer this question, consider the limiting case, $\gamma \gg 1$ (relaxation processes are extremely fast) and $\vartheta \to +0$ (the environment is in static equilibrium). In this procedure we follow an analogy with the Kramers problem [19, 20]. As a result, we arrive at deterministic dynamics involving only the population variable. Note that the corresponding mathematically consistent passage to the limit is not trivial, but intuitively the result seems quite clear.

Thus, passing to the limit $\gamma \gg 1$, $\dot{y} = 0$, and $\vartheta \to +0$, we get $y = -\gamma^{-1}\lambda\, xh'(x)$, and hence the correspondence

$$xf(x) = -\lambda^2\gamma^{-1}x^2h'(x).$$

For the logistic population growth rate, that is, $f(x) = r\left(1 - K^{-1}x\right)$, setting $\lambda^2\gamma^{-1} = r$, we get the following expression for the function $h(x)$,

$$h(x) = K^{-1}x - \ln x. \tag{13}$$

We shall say that $h(x)$ (13) is the logistic h–function. Let us now substitute this h–function into the equations (11) and thus obtain a stochastic analogue of the logistic equation (2), which to some extent describes the coevolution of the population and the environment,

$$\dot{x} = \lambda xy,$$
$$\dot{y} = -\lambda \left[K^{-1} \left(x - K \right) - \vartheta \right] - \gamma y + \sqrt{2\gamma\vartheta}\xi(t), \tag{14}$$

where $\lambda^2 \gamma^{-1} = r$.

To illustrate the difference between the population evolution described by the (2) and (14) equations, we performed a test numerical simulation of these dynamic equations. This simulation also allowed us to test the validity of our basic assumptions. We simulated these equations using the Euler scheme with a time step $dt = 0.001$. In all simulations, we keep $K = 1$, $\lambda = 1$, and $\gamma = 50$ (the latter to stay close to the logistic equation (2)), but vary the values of ϑ.
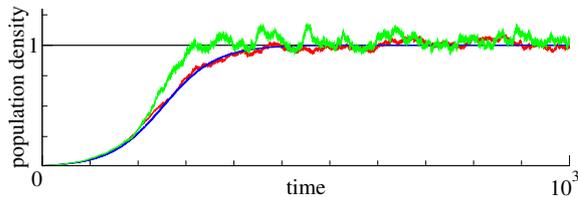
Figure 1: (colour online) Population density versus time. The various curves correspond to the Verhulst-Pearl logistic equation (2) (blue curve) and a stochastic analogue of the logistic equation (14) at two values of the ϑ parameters: $\vartheta = 0.001$ (red curve) and $\vartheta = 0.005$ (green curve). Initial values are $x = 0.01$, $y = 0$.
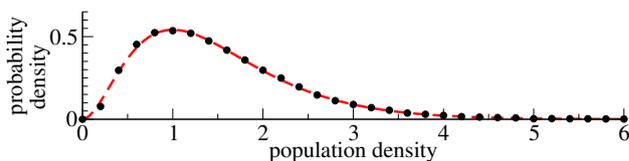
Figure 2: (colour online) Population probability density versus population density. The (red) dash lines show the theoretical result given by the logistic h–function. The (black) circles show the normalised histogram generated at $\vartheta = 0.5$ by running numerical simulation for quite a long time, up to $t_{max} = 10^5$. Observe, the circles follow the theoretical curve exactly.

The results of the simulations confirm our assumptions and expectations. Figure 1 shows that the concept of a statistical approach to interpreting the logistic equation is reasonable. In the case of $\gamma = 50 \gg 1$, the agreement with the logistic curve becomes particularly good as the ambient temperature decreases. Note that this good agreement corresponds to short relaxation times of the environmental variable, $\gamma^{-1} = 0.02 \ll 1$, which is in line with our theoretical assumptions. The variation of the time scales γ^{-1} and λ^{-1} requires further research. Figure 2 confirms the validity of the ergodic hypothesis. It can be seen that the numerically obtained population density distribution fits the theoretical curve.

4. Discussion

On a fairly simple but conceptually important example, we have presented the way of probabilistic reasoning and the mathematical structure underlying the statistical approach in modelling evolutionary processes in ecology and population dynamics. This example is rather a particular implementation of the idea of the proposed statistical approach. In this context, a natural question arises: What perspectives, in a wide sense, does the statistical approach potentially provide in modelling ecological processes, if any? Indeed, if mathematical ideas are formulated in general terms, then it is necessary to clarify the further prospect of their possible application.

Population growth models differ in how to model the transition to the most probable state of the population. This distinction is central to understanding ecological evolution in general. The availability of a variety of mathematical descriptions of transient processes offers the prospect of implementing qualitatively different models of evolution. In this context, let us consider the following concrete example in order to answer, at least in part, the question posed.

Without over-complicating the evolutionary dynamics (14), we modify these equations on the assumption of non-Gaussian statistics of the environment variable, while keeping the logistic h–function (13) unchanged. More precisely, we consider the equilibrium (invariant) density of the form,

$$\sigma_\vartheta^+(x, y) \propto \exp\left\{-\vartheta^{-1} h(x)\right\} \times \exp\left\{-\vartheta^{-1} h^*(y)\right\}, \tag{15}$$

where $h^*(y)$ is the environment h–function. Let the ϑ-expression be chosen in the form

$$\Theta^*(y, \vartheta) = \lambda \vartheta h^{*\prime}(y) - \gamma\left[\left(h^{*\prime}(y)\right)^2 - \vartheta h^{*\prime\prime}(y)\right].$$

The proof that $\Theta^*(y, \vartheta)$ is indeed a ϑ-expression is done by direct calculation [12]. Under these assumptions, we arrive at the (stochastic) equations of motion,

$$\begin{aligned}
\dot{x} &= \lambda x h^{*\prime}(y), \\
\dot{y} &= -\lambda\left[x h'(x) - \vartheta\right] - \gamma h^{*\prime}(y) + \sqrt{2\gamma\vartheta}\,\xi(t).
\end{aligned} \tag{16}$$

The density $\sigma_\vartheta^+(x, y)$ (15) is invariant for dynamics (16). The proof is by direct calculation. In the case $h^*(y) = y^2/2$, ϑ-expression and dynamic equations coincide with those considered earlier. Note that if we put $\gamma \equiv 0$, we obtain a system of ordinary differential equations with the required invariant density (easily checked by direct calculation). However, in this case the ergodicity condition is problematic [17].

The choice of admissible function $h^*(y)$ introduces noticeable freedom in the modelling of transients. As an example, let us consider two variants of the bimodal probability density function $\sigma_\vartheta^*(y)$, symmetric and asymmetric. First, let the symmetric density be defined by the expression

$$h^{*\prime}(y) = y\left(y + \sqrt{m}\right)\left(y - \sqrt{m}\right), \tag{17}$$

where $m > 0$ is a parameter. For the shortened ordinary differential equation, $\dot{y} = -\gamma h^{*\prime}(y)$, the equilibria $y = \pm\sqrt{m}$ are stable, while $y = 0$ is an unstable equilibrium.

To deepen the discussion, consider a hypothetical situation where changes in the environment are associated not only with population size, but also with changes in the phenotype of the population itself, when an additional environmental resource becomes available to the population and affects its growth and terminal size. The asymptotic result would be a change in the value of the most probable population density. We now focus on describing such a process.
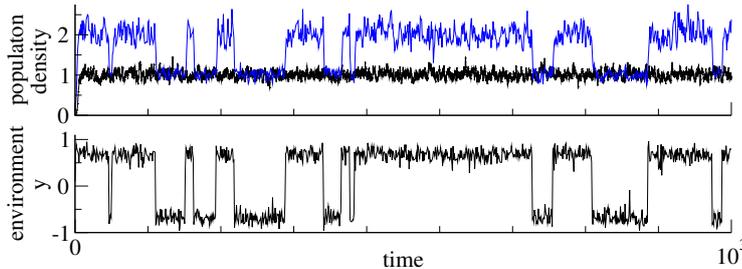
Figure 3: (colour online) Population density x (top) and environment variable y (bottom) versus time for the symmetric bimodal equilibrium probability density of variable y (equation(17)) in two modes: in the absence (black) and in the presence of functional population–environment relationship (blue). The parameters used in the simulation are as follows: $m = 0.5, \vartheta = 0.01, r = 1, \gamma = 50, \lambda = \sqrt{50}$.

To solve this problem, we assume that the functional relationship between the population and the environment has the form $K[y] = 1 + H(y)$, where $H(y)$ is a Heaviside function. Although this piecewise linear relationship is speculative and oversimplified, it reflects an important qualitative feature of the phenotype–environment relationship responsible for the transition between two equilibrium population densities. It would be more correct to relate K to its own dynamics, but for our illustrative purposes such a complication is unnecessary.

Qualitatively, this dependence can be explained as follows: the transition of the environment from one steady state to another is associated with a change in the phenotype of the population such that an additional environmental resource becomes available to the population.

To test the intended perspective, we perform numerical simulations. The parameters used in the simulation were chosen to remain close to the logistic dynamics. Figure 3 shows the population density x (top) simultaneously with the corresponding environmental variable y (bottom) versus time, in two different modes: in the absence (black curve) and in the presence (blue curve) of a functional relationship between population and environment $K[y]$. The random fluctuations of the population density synchronised with the environment can be clearly identified.

This behaviour provides the basis for the following important modification of the bimodal density $\sigma_\vartheta^*(y)$. Namely, a conceptually important example is the asymmetric bimodal probability density $\sigma_\vartheta^*(y)$, defined by the expression

$$h^{*\prime}(y) = Dy(y - a)(y - 1). \tag{18}$$

The detuning parameter a in this expression satisfies $0 < a < 1$, and the parameter $D > 0$. Thus, for the shortened ordinary differential equation, $\dot{y} = -\gamma h^{*\prime}(y)$, the equilibria $y = 0, 1$ are stable, while $y = a$ is an unstable

equilibrium. Let there be a functional relationship between the population and the environment of the form $K[y] = 1 + H(y - a)$. This piecewise linear dependence should, under certain conditions, determine the long-term transition from the initial equilibrium population density to the new one. To check this, we carry out numerical simulations. The parameters used in the simulation are chosen to remain close to the logistic equation. Figure 4 shows population density x as a function of time in two different modes: in the absence (black curve) and in the presence (blue curve) of functional relationship $K[y]$ between population and environment. For the selected asymmetric bimodal density parameters, it is observed a clear transition to a new equilibrium state in the population size. Mathematically, a backward transition to the initial population size is possible, but the average waiting time is expected to be long and may exceed the lifetime of the population [21]. We omit the discussion of the relevant mathematical details.
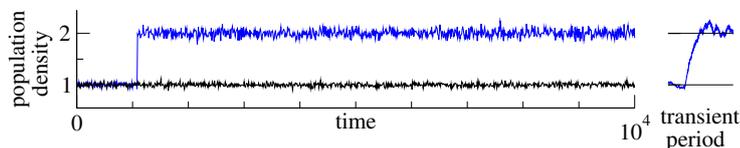
Figure 4: (colour online) Population density versus time for the equilibrium asymmetric bimodal probability density of variable y (equation (18)), in two different modes: in the absence (black) and in the presence (blue) of functional population–environment relationship. Note that the transition to a new population density persists for a long time ("forever"). The parameters used in the simulation are as follows: $D = 4, a = 0.25, \vartheta = 0.001, r = 1, \gamma = 50, \lambda = \sqrt{50}$.

When we use the term ecological temperature, we refer to the parameter ϑ, which in turn is related to the key definition of the ϑ–expression in Section 2. For the presented statistical interpretation of the logistic equation, the specific value of ϑ is immaterial. To give ϑ an appropriate value, one should choose a special device, an ecological thermometer. The analogy with thermodynamics can be useful. However, a discussion of this issue is beyond the scope of this article. In an extended context, other parameters in addition to ϑ may be necessary, for example, when considering the processes of emigration and immigration of the population.

Finally, we should make a note about the random term in the system (16). If we put $\gamma \equiv 0$, we obtain a system of ordinary differential equations for which the density (15) is invariant (this is easy to check). However, these equations of motion are not ergodic for the given density (note that there exists the integral of motion, $I = h(x) - \vartheta \ln x + h^*(y) = const$), so the dynamical scenarios discussed earlier have no place.

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