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Dealing with variability in ecological modelling: An analysis of a random non-autonomous logistic population model

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This paper presents a methodology to deal with the randomness associated to ecological modelling. Data variability makes it necessary to analyze the impact of random perturbations on the fitted model parameters. We conduct such analysis for the logistic growth model with a certain sigmoid functional form of the carrying capacity, which was proposed in the literature for the study of parasite growth during infection. We show how the probability distributions of the parameters are set via the maximum entropy principle. Then the random variable transformation method allows for computing the density function of the population.

KEYWORDS:
logistic growth model, time-varying carrying capacity, random parameters, probability density function

1 | INTRODUCTION

The logistic equation models the growth of human, plants, animal and bacterial populations [1]. Developed by Pierre-François Verhulst in 1838 [2], it generalizes the exponential growth model proposed by Thomas Robert Malthus in 1798 [3] (which is considered as the first law of population dynamics in the field of population ecology [4]), by taking into account the lack of resources as the population grows. There is thus a limited capacity in the amount of population.

Classically, the carrying capacity has been considered constant. However, some works started to consider it as a function of time, under the principle that a changing environment may result in a significant change in the carrying capacity. From the viewpoint of dynamical systems theory, the logistic equation with time-dependent limiting capacity was studied in [5]. Some applications of this equation, with different functional forms for the carrying capacity, can be found in a variety of works: in [6], for the growth of Earth's human population; in [7], for parasite growth during infection; in [8], for the population histories of England and Japan; and in [9], for the total microbial biomass under occlusion of healthy human skin. In [10], the authors conducted a mathematical analysis of the model from [9] by using an algebraic method.

These types of models, an in general any mathematical model, have three sources of error: model, data and numerical methods errors. The numerical methods error depends on the algorithms and can always be decreased, at least theoretically; moreover, when there is an exact solution, this error does not arise. On the contrary, the model error accounting for the incomplete knowledge on the phenomenon under study, and the data error due to incorrect measurements, lack or scarcity of information, etc. cannot be avoided. Thereby, the process of modelling has associated uncertainty. Accounting for data variability, the parameters of the model should be regarded as random variables with probability distributions, and the solution becomes a random variable that evolves with time, that is, a stochastic process [11].

The maximum entropy principle infers consistent probability laws for the parameters, by maximizing the ignorance on their density functions while not violating physical principles. The ignorance on the density function is usually expressed via the Shannon entropy functional, subject to certain constraints on the statistical moments and the support [12,13,14].

Once the model coefficients follow specific probability distributions, the probability law of the stochastic solution must be found. When a closed-form solution is available, the random variable transformation method gives the exact probability density function under mild conditions. This technique has been employed in different settings: Bertalanffy growth model [15], SIS-type epidemiological model [16], autonomous logistic equation [17,18], and radiative transfer equation [19], for instance. When there is no closed form of the solution, there are hybrid strategies that combine the random variable transformation technique and approximation methods, such as: Monte Carlo simulation, recently applied for the advection linear partial differential equation [20]; finite difference numerical schemes, applied to some linear random differential equations [21] and to the heat partial differential equation [22]; and spectral expansions, such as those of Karhunen-Loève type for the damped pendulum differential equation [23] and the logistic differential equation [24], and those of polynomial chaos type [25]. These approaches capture discontinuity and non-differentiability points of the target density function correctly and are more efficient than non-parametric kernel density estimations. On the other hand, let us mention that Liouville's equation may be used to validate the densities obtained via the random variable transformation method. This equation takes the form of a partial differential equation satisfied by the density function, which, in certain cases, can be explicitly solved by employing the associated Lagrange system [26,27]. Finally, other strategies that only focus on statistics estimations, which rely on simulations and expansions, are available, see [28,29,30] for instance.

In this paper, we deal with the stochastic version of the logistic model proposed in [7], where the carrying capacity varies with time. The structure of the paper is the following. In Section 2, we study the deterministic logistic equation (no randomness) with time-dependent carrying capacity: we solve the model by using the theory on Bernoulli ordinary differential equations and we compare the solution with the cases discussed in [7,9,10]. In Section 3, we randomize the logistic equation, we prove that the randomized solution satisfies the equation in the path-wise and the mean-square senses, and we show how to infer consistent probability distributions for the model parameters via the maximum entropy principle. In Section 4, we derive the probability density function of the solution proposed in [7] by means of a comprehensive application of the random variable transformation method. In Section 5, we carry out numerical test examples. Finally, in Section 6, we discuss the main results and present the conclusions.

2 | NON-AUTONOMOUS LOGISTIC EQUATION

The autonomous logistic equation has the form

$$N'(t) = aN(t)\left(1 - \frac{N(t)}{K}\right), \quad t \geq 0, \quad N(0) = N_0, \tag{1}$$

where $N_0 > 0$ is the initial condition, $a > 0$ is the growth rate parameter and $K > 0$ is the carrying capacity, with $N_0 < K$. The solution to (1) is well-known:

$$N(t) = \frac{KN_0}{K\mathrm{e}^{-at} + N_0(1-\mathrm{e}^{-at})}. \tag{2}$$

Notice that, as expected, $K = \lim_{t\to\infty} N(t)$. As explained in the previous section, we aim at analyzing the non-autonomous logistic equation driven by a time-varying carrying capacity $K(t)$:

$$N'(t) = aN(t)\left(1 - \frac{N(t)}{K(t)}\right), \quad t \geq 0, \quad N(0) = N_0. \tag{3}$$

Different forms of $K(t)$ have been conceived in the existing literature. For instance, [7] employed the sigmoid growth

$$K(t) = \frac{K_0 K_s}{(K_s - K_0)\mathrm{e}^{-ct} + K_0}, \tag{4}$$

while [9] considered the logistic growth

$$K(t) = K_s\left(1 - \left(1 - \frac{K_0}{K_s}\right)\mathrm{e}^{-ct}\right), \tag{5}$$

where $K_0 = K(0)$ is the initial limiting capacity, $K_s = \lim_{t\to\infty} K(t)$ is the saturation (or equilibrium) level, and c is the saturation constant. It is assumed $N_0 < K_0 < K_s$ and $c > 0$. Other functional forms of $K(t)$, which vary sinusoidally, exponentially or linearly, can be consulted in [8,10].

Equation (3) is a Bernoulli ordinary differential equation. It can be solved via the change of variables $M = 1/N$. By differentiating $M(t)$, a linear ordinary differential equation is derived for M:

$$M'(t) = -\frac{N'(t)}{N(t)^2} = -aM(t) + \frac{a}{K(t)}, \quad M(0) = \frac{1}{N_0}.$$

Then

$$M(t) = \frac{\mathrm{e}^{-at}}{N_0} + \mathrm{e}^{-at} a \int_0^t \frac{\mathrm{e}^{as}}{K(s)}\,\mathrm{d}s,$$

so, after undoing the change of variables, the solution to (3) is

$$N(t) = \frac{\mathrm{e}^{at} N_0}{1 + aN_0 \int_0^t \frac{\mathrm{e}^{as}}{K(s)}\,\mathrm{d}s}. \tag{6}$$

When $K(t)$ is given by (5) and is substituted into (6), we have the solution derived in [10]:

$$N(t) = \frac{\mathrm{e}^{at} N_0}{1 + \frac{aN_0}{K_s} \int_0^t \frac{\mathrm{e}^{as}}{1-b\mathrm{e}^{-cs}}\,\mathrm{d}s}, \quad b = 1 - \frac{K_0}{K_s} \in (0,1).$$

To evaluate the integral from the denominator, the authors employed an algebraic trick, by expanding part of the integrand as a series:

$$\frac{1}{1-b\mathrm{e}^{-cs}} = \sum_{n=0}^{\infty} b^n \mathrm{e}^{-ncs}, \quad s > 0,$$

so that

$$\int_0^t \frac{\mathrm{e}^{as}}{1-b\mathrm{e}^{-cs}}\,\mathrm{d}s = \int_0^t \left(\sum_{n=0}^{\infty} b^n \mathrm{e}^{(a-nc)s}\right)\mathrm{d}s = \sum_{n=0}^{\infty} \frac{b^n}{a-nc}\left(\mathrm{e}^{(a-nc)t} - 1\right).$$

In practice, the series is truncated to a finite-term sum. Accurate approximations to the exact solution $N(t)$ are obtained for small orders of truncation. Notice that this method is applicable whenever $K(t)$ can be written as $\tilde{K}(\mathrm{e}^{-ct})$, where $\tilde{K}$ is a decreasing function expressed as a power series $\tilde{K}(u) = \sum_{n=0}^{\infty} \tilde{K}_n u^n$.

On the other hand, when $K(t)$ is defined by (4), we have a closed-form solution (without integrals) after some simple manipulations in (6):

$$N(t) = \frac{\mathrm{e}^{at} N_0 K_s}{K_s + aN_0\left(\frac{K_s - K_0}{(a-c)K_0}\left(\mathrm{e}^{(a-c)t} - 1\right) + \frac{\mathrm{e}^{at}-1}{a}\right)}. \tag{7}$$

In the development from Section 4, we will focus on the closed-form solution (7).

3 | RANDOM NON-AUTONOMOUS LOGISTIC EQUATION

3.1 | Randomization

Model (3) is randomized. Mathematically, there is an underlying complete probability space $(\Omega, \mathcal{F}, \mathbb{P})$, where Ω is the sample space, $\mathcal{F} \subseteq 2^{\Omega}$ is the σ-algebra of events, and $\mathbb{P} : \mathcal{F} \to [0,1]$ is the probability measure. The parameters a and N_0 are random variables and the carrying capacity $K(t)$ is a stochastic process. In this manner, $a(\omega)$, $N_0(\omega)$ and $K(t,\omega)$ depend on the outcome $\omega \in \Omega$ of an experiment. Notice that $K(t)$ is a stochastic process by taking c, K_0 and K_s as random variables, which evaluate at the outcomes of experiments as $c(\omega)$, $K_0(\omega)$ and $K_s(\omega)$. The general solution $N(t)$ to (3), given by (6), is a stochastic process $N(t,\omega)$. It is assumed that, given a population datum at a certain time t, it is just a possible realization of the model solution over all possible realizations $\{N(t,\omega) : \omega \in \Omega\}$. The outcome ω will be implicitly assumed without being systematically written.

3.2 | Stochastic solution

The stochastic process $N(t)$ defined by (6) is the path-wise solution to (3) on $[0,\infty)$ [11, Ch. 3]. Indeed, $N(\cdot,\omega)$ solves (3) almost surely.

Let $\mathrm{L}^p(\Omega)$, $1 \le p < \infty$, be the Lebesgue space of random variables $U : \Omega \to \mathbb{R}$ satisfying $\|U\|_p = (\mathbb{E}[|U|^p])^{1/p} < \infty$, where $\mathbb{E}$ is the expectation operator. When $p = \infty$, $\mathrm{L}^\infty(\Omega)$ is defined as the Lebesgue space of almost surely bounded random variables, and $\|\cdot\|_\infty$ stands for the least upper-bound. The set $\mathrm{L}^p(\Omega)$, $1 \le p \le \infty$, is a Banach space, and for $p = 2$, it is a Hilbert space with the inner product $(U,V) \mapsto \mathbb{E}[UV]$. Convergence in $\mathrm{L}^2(\Omega)$ is referred to as mean-square convergence. Convergence in $\mathrm{L}^p(\Omega)$ preserves the convergence of the statistical moments up to order p; in particular, mean-square convergence implies convergence of the expectation and the variance. Mean-square calculus considers the limits from the definitions of continuity, differentiability, Riemann integrability, etc. in the mean-square sense. Under this alternative calculus, one may solve differential equations with random parameters [11, Ch. 4, 31,32].

It can be proved that the path-wise solution $N(t)$ is also the mean-square solution on $[0,\infty)$, whenever $\|a\|_\infty < \infty$, $K_0(\omega) \leq K(t,\omega) \leq K_s(\omega)$ almost surely for all $t \geq 0$, $\|K_s\|_\infty < \infty$, and $K_0(\omega) > \kappa > 0$ almost surely, for some constant κ. Let $F(t,N,\omega) = a(\omega)N(1-N/K(t,\omega))$ be defined for times $t \geq 0$ and numbers $0 \leq N \leq \|K_s\|_\infty$. The map $F : [0,\infty) \times [0,\|K_s\|_\infty] \times \Omega \to \mathbb{R}$ is Lipschitz: by the triangular inequality,

$$\left|F(t,N_1,\omega) - F(t,N_2,\omega)\right| \leq \|a\|_\infty |N_1 - N_2| + \frac{\|a\|_\infty}{\kappa}|N_1+N_2||N_1-N_2| \leq \|a\|_\infty \left(1 + \frac{2\|K_s\|_\infty}{\kappa}\right)|N_1 - N_2|.$$

By Tietze extension theorem [33, Th. 1], F can be extended to a Lipschitz map $\tilde{F} : [0,\infty) \times \mathbb{R} \times \Omega \to \mathbb{R}$ with Lipschitz constant $\|a\|_\infty(1+2\|K_s\|_\infty/\kappa)$. By [11, Th. 4.3, 32, Th. 5.1.2], the random differential equation problem $N'(t) = \tilde{F}(t,N(t))$ has a unique mean-square solution, for any initial condition $N_0 \in \mathrm{L}^2(\Omega)$. Any mean-square solution is equivalent to the path-wise solution [34, Th. 3(a)]. Suppose that $0 < N_0(\omega) < K_0(\omega)$ almost surely. Then the path-wise solution to $N'(t) = \tilde{F}(t,N(t))$ is the path-wise solution to $N'(t) = F(t,N(t))$ that satisfies $0 \leq N(t,\omega) \leq \|K_s\|_\infty$ for all $t \geq 0$ (more specifically $N_0 \leq N(t) \leq K(t) \leq K_s$). Then the mean-square solution to $N'(t) = F(t,N(t))$ is given by (6), for any initial condition $N_0 \in \mathrm{L}^2(\Omega)$, and we are done. Notice that, in the particular cases of (4) and (5), the parameter $c > 0$ may be unbounded above.

We point out that, as a consequence of [35, pp. 440–441, properties 1–2], the integral from the denominator of (6), $\int_0^t \frac{e^{as}}{K(s)}\,\mathrm{d}s$, can be considered in the mean-square sense (the Riemann sums have mean-square convergence), apart from path-wise.

3.3 | Inverse parameter estimation

In practice, one must set consistent probability distributions for the parameters. Let us see how the Shannon entropy measure is useful here [12,13]. Let θ be any random parameter. Its Shannon entropy is expressed via the functional

$$\mathcal{S}[f_\theta] = -\int_\alpha^\beta f_\theta(\theta)\log f_\theta(\theta)\,\mathrm{d}\theta, \tag{8}$$

where f_θ is the probability density function of θ, $[\alpha,\beta]$ denotes its support (of course, it could be $\alpha = -\infty$ and/or $\beta = \infty$), and log is the natural logarithm (in base e). It is understood here that $0\log 0 = 0$. Prior information on θ is expressed via the following restrictions:

$$\mathbb{E}[\theta^k] = \int_\alpha^\beta \theta^k f_\theta(\theta)\,\mathrm{d}\theta = f^k,\ 0 \leq k \leq m. \tag{9}$$

Here f^k denotes the k-th statistical moment of θ. For instance, $f^0 = 1$ by definition of density function, f^1 is the mean of θ, f^2 is the variance of θ plus its squared mean, etc. The maximum entropy principle maximizes the objective functional (8) subject to (9). This is usually done in the literature via calculus of variations [36]. The Lagrange multipliers method says that

$$\frac{\delta\mathcal{S}}{\delta f_\theta(\theta)} \in \left\langle \left\{ \frac{\delta\mathbb{E}[\theta^k]}{\delta f_\theta(\theta)} : k = 0,\dots,m \right\} \right\rangle,$$

where

$$\frac{\delta\mathcal{S}}{\delta f_\theta(\theta)} = -1 - \log f_\theta(\theta), \quad \frac{\delta\mathbb{E}[\theta^k]}{\delta f_\theta(\theta)} = \theta^k$$

are the functional derivatives with respect to f_θ at θ, determined by means of the Euler-Lagrange equation, and $\langle\cdot\rangle$ denotes the linear span. This gives the solution

$$f_\theta(\theta) = \mathbb{1}_{[\alpha,\beta]}(\theta)\exp\left(-\lambda_0 - \sum_{k=1}^m \lambda_k\theta^k\right), \tag{10}$$

for certain Lagrange constants $\lambda_0,\lambda_1,\dots,\lambda_m \in \mathbb{R}$. These constants are determined by solving the nonlinear system of equations that appears when substituting (10) into (9).

It is worth pointing out that a derivation of (10) using just elementary calculus was proposed in [37]. The idea is simple. Let f_θ be given by (10) and let $\tilde{f}$ be any other non-negative function satisfying the corresponding restrictions (9). From the inequality $\log t \leq t-1$ for $t > 0$, one derives $\tilde{f}(\theta) - \tilde{f}(\theta)\log\tilde{f}(\theta) \leq f_\theta(\theta) - \tilde{f}(\theta)\log f_\theta(\theta)$. By integrating, we have $\mathcal{S}[\tilde{f}] \leq -\int_\alpha^\beta \tilde{f}(\theta)\log f_\theta(\theta)\mathrm{d}\theta = \sum_{k=0}^m \lambda_k \int_\alpha^\beta \tilde{f}(\theta)\theta^k\mathrm{d}\theta = \sum_{k=0}^m \lambda_k f^k = \mathcal{S}[f_\theta]$, and we are done.

Suppose that no information on θ is known, only a bounded support $[\alpha, \beta]$. Then $m = 0$ and (10) becomes the density function of a Uniform distribution on $[\alpha, \beta]$: $f_\theta(\theta) = \mathbb{1}_{[\alpha,\beta]}(\theta)\frac{1}{\beta-\alpha}$. On the other hand, suppose that $\theta > 0$ and its mean $\hat{\theta}$ is known. In this case, $m = 1$, and θ follows the Exponential law, where the rate parameter is $1/\hat{\theta}$: $f_\theta(\theta) = \mathbb{1}_{[0,\infty)}(\theta)(1/\hat{\theta})\mathrm{e}^{-\theta/\hat{\theta}}$. Another well-known case is when θ is defined on the real line, with a certain mean value and standard deviation ($m = 2$), which leads to the Gaussian distribution. Other cases were investigated in [12]. In general, one obtains $\lambda_0, \ldots, \lambda_m$ numerically.

In practice, determining the prior information of a parameter θ is not an easy task. Suppose that we have a single pointwise deterministic estimator of θ, say θ_1. This value could be used as the mean of θ (Exponential distribution for θ), or to define a certain support for θ by adding and subtracting a certain variability around θ_1 (Uniform distribution for θ). But, in any case, the information is vague. A better scenario arises when we have several pointwise deterministic estimators of θ, say $\theta_1, \ldots, \theta_q$, $q \geq 2$. By employing this sample, the mean and the variance of θ can be estimated. Moreover, the support of θ can also be estimated via Markov's inequality (which states that $\mathbb{P}[|\theta - \mathbb{E}[\theta]| > \eta\sigma[\theta]] \leq \eta^{-2}$, $\eta > 0$, where $\sigma[\theta]$ is the standard deviation of θ). In this case, $m = 2$, and the Lagrange constants λ_0, λ_1 and λ_2 satisfying (9) are calculated numerically.

4 | PROBABILISTIC SOLUTION: DENSITY FUNCTION

In this section, we assume that the random parameters of the model (3) with carrying capacity (4) have specific probability distributions, and we aim at computing the probability density function of the solution $N(t)$ given by (7). We employ the random variable transformation method, see [38, Th. 2.1.5].

4.1 | Random variable transformation method

The random variable transformation technique gives the density function of a response X under the relation output-input $X = g(Y)$, where g is a deterministic map called the transformation mapping and Y is a random quantity. It is assumed that the dimensions of X and Y are equal. When g is smooth on an open set containing $\mathcal{D}(Y) = \{Y(\omega) : \omega \in \Omega\}$, one-to-one and with non-vanishing Jacobian $Jg(y) = \det(\frac{\partial g}{\partial y}(y))$, the density function of X is given by

$$f_X(x) = f_Y(h(x))|Jh(x)|, \tag{11}$$

where $h = g^{-1}$ is the inverse of g on its domain. Indeed, for any Borel set B contained in the image of X, we have

$$\mathbb{P}[X \in B] = \mathbb{P}[g(Y) \in B] = \mathbb{P}[Y \in h(B)] = \int_{h(B)} f_Y(y)\,\mathrm{d}y = \int_B f_Y(h(x))|Jh(x)|\,\mathrm{d}x.$$

The requirements may be overcome when the domain of the transformation mapping is divided into sub-domains where the conditions hold [38, Th. 2.1.8].

4.2 | Application

Notice that the solution (7) is a closed-form transformation of the random input parameters N_0, a, c, K_0 and K_s. Then, using (11), the density function of $N(t)$, $f_{N(t)}(N)$, can be expressed in terms of the joint density function of (N_0, a, c, K_0, K_s), $f_{(N_0,a,c,K_0,K_s)}(N_0, a, c, K_0, K_s)$.

The transformation mapping g is

$$g(N_0, a, c, K_0, K_s) = \left(N_0, a, c, \frac{\mathrm{e}^{at} N_0 K_s}{K_s + aN_0 \left(\frac{K_s - K_0}{(a-c)K_0} \left(\mathrm{e}^{(a-c)t} - 1 \right) + \frac{\mathrm{e}^{at}-1}{a} \right)}, K_s \right).$$

This manner of proceeding is usual: one of the components of the transformation mapping is $N(t)$, while the rest of components are fixed; the parameter corresponding to the component $N(t)$ (in this case K_0) must be easily isolated in the equation $N(t) = N$.

The inverse mapping is given by

$$h(N_0,a,c,N,K_s)=\left(N_0,a,c,\frac{K_s}{1-\frac{(a-c)\left(N_0\mathrm{e}^{at}(N-K_s)+N(K_s-N_0)\right)}{aNN_0\left(\mathrm{e}^{t(a-c)}-1\right)}},K_s\right).$$

Its Jacobian is given by

$$Jh(N_0,a,c,N,K_s)=\frac{\partial K_0}{\partial N}=\frac{aK_s^2N_0^2(a-c)\mathrm{e}^{at}\left(\mathrm{e}^{t(a-c)}-1\right)}{\left(cN_0\mathrm{e}^{at}(K_s-N)+aNN_0\left(\mathrm{e}^{at}-\mathrm{e}^{t(a-c)}\right)+aK_s\left(N-N_0\mathrm{e}^{at}\right)+cN(N_0-K_s)\right)^2}>0,$$

where the positivity comes from the fact that $t>0$ and $(a-c)(\mathrm{e}^{t(a-c)}-1)>0$ for all values of a and c (except when $a=c$, but this happens with zero probability when a and c are independent and absolutely continuous random variables). By (11) and marginalizing,

$$f_{N(t)}(N)=\iiiint\limits_{\mathcal{D}(N_0,a,c,K_s)} f_{(N_0,a,c,K_0,K_s)}\left(N_0,a,c,\frac{K_s}{1-\frac{(a-c)\left(N_0\mathrm{e}^{at}(N-K_s)+N(K_s-N_0)\right)}{aNN_0\left(\mathrm{e}^{t(a-c)}-1\right)}},K_s\right)$$
$$\times\frac{aK_s^2N_0^2(a-c)\mathrm{e}^{at}\left(\mathrm{e}^{t(a-c)}-1\right)}{\left(cN_0\mathrm{e}^{at}(K_s-N)+aNN_0\left(\mathrm{e}^{at}-\mathrm{e}^{t(a-c)}\right)+aK_s\left(N-N_0\mathrm{e}^{at}\right)+cN(N_0-K_s)\right)^2}\mathrm{d}N_0\,\mathrm{d}a\,\mathrm{d}c\,\mathrm{d}K_s, \tag{12}$$

where $\mathcal{D}(N_0,a,c,K_s)=\{(N_0(\omega),a(\omega),c(\omega),K_s(\omega)) : \omega\in\Omega\}$ is the image of (N_0,a,c,K_s). To apply the random variable transformation method, we must have the denominator of $Jh(N_0(\omega),a(\omega),c(\omega),N(t,\omega),K_s(\omega))$ distinct from 0 almost surely; this always holds because the solution $N(t)$ is absolutely continuous.

Notice that, given an equation of the form $N(t)=N$, the parameters K_s and N_0 are also easily isolated. Only a and c cannot be explicitly isolated, as they appear within and outside an exponential function. Hence (11) is applicable by isolating K_s and N_0, instead of K_0.

First, for K_s, the transformation mapping is

$$g(N_0,a,c,K_0,K_s)=\left(N_0,a,c,K_0,\frac{\mathrm{e}^{at}N_0K_s}{K_s+aN_0\left(\frac{K_s-K_0}{(a-c)K_0}\left(\mathrm{e}^{(a-c)t}-1\right)+\frac{\mathrm{e}^{at}-1}{a}\right)}\right).$$

Its inverse is

$$h(N_0,a,c,K_0,N)=\left(N_0,a,c,K_0,\frac{\frac{NaN_0}{a-c}\left(\mathrm{e}^{(a-c)t}-1\right)-\left(\mathrm{e}^{at}-1\right)NN_0}{N+\frac{NaN_0}{(a-c)K_0}\left(\mathrm{e}^{(a-c)t}-1\right)-\mathrm{e}^{at}N_0}\right),$$

with Jacobian

$$Jh(N_0,a,c,K_0,N)=\frac{\partial K_s}{\partial N}=\frac{\left(\mathrm{e}^{at}-1-\frac{a}{a-c}\left(\mathrm{e}^{(a-c)t}-1\right)\right)\mathrm{e}^{at}N_0^2}{\left(N+\frac{NaN_0}{(a-c)K_0}\left(\mathrm{e}^{(a-c)t}-1\right)-\mathrm{e}^{at}N_0\right)^2}.$$

Therefore, by (11) and marginalizing,

$$f_{N(t)}(N)=\iiiint\limits_{\mathcal{D}(N_0,a,c,K_0)} f_{(N_0,a,c,K_0,K_s)}\left(N_0,a,c,K_0,\frac{\frac{NaN_0}{a-c}\left(\mathrm{e}^{(a-c)t}-1\right)-\left(\mathrm{e}^{at}-1\right)NN_0}{N+\frac{NaN_0}{(a-c)K_0}\left(\mathrm{e}^{(a-c)t}-1\right)-\mathrm{e}^{at}N_0}\right)$$
$$\times\frac{\left(\mathrm{e}^{at}-1-\frac{a}{a-c}\left(\mathrm{e}^{(a-c)t}-1\right)\right)\mathrm{e}^{at}N_0^2}{\left(N+\frac{NaN_0}{(a-c)K_0}\left(\mathrm{e}^{(a-c)t}-1\right)-\mathrm{e}^{at}N_0\right)^2}\mathrm{d}N_0\,\mathrm{d}a\,\mathrm{d}c\,\mathrm{d}K_0. \tag{13}$$

Now we justify that the term $\mathrm{e}^{at}-1-\frac{a}{a-c}(\mathrm{e}^{(a-c)t}-1)$ coming from the numerator of the Jacobian, does not need to be written with absolute value as indicated in the general formula (11). For this goal, let $t>0$ be fixed, and a and c be positive random variables. Observe that the above-mentioned term can be expressed as

$$\mathrm{e}^{at}-1-\frac{a}{a-c}\left(\mathrm{e}^{(a-c)t}-1\right)=at\left(\frac{\mathrm{e}^{at}-1}{at}-\frac{\mathrm{e}^{(a-c)t}-1}{(a-c)t}\right). \tag{14}$$

Moreover, the function $f(x) = (\mathrm{e}^x - 1)/x$, defined for all $x \in \mathbb{R} - \{0\}$, satisfies that $\lim_{x\to 0} f(x) = 1$, $f(x) > 0$ and $f'(x) > 0$ (i.e. f is increasing). Now we distinguish two cases with respect to the two positive random variables a and c: $a > c > 0$ and $c > a > 0$. Notice that other situations have null probability to occur, by absolute continuity. In both cases, we shall show that expression (14) is positive. Assume that $a > c > 0$. Then $a > a - c$ and $at > (a - c)t$ for $t > 0$. Since f is increasing, $f(at) > f((a - c)t)$, i.e.

$$\frac{\mathrm{e}^{at} - 1}{at} - \frac{\mathrm{e}^{(a-c)t} - 1}{(a - c)t} > 0.$$

Multiplying this last expression by $at > 0$, from (14) one gets the stated result. Now, let us assume that $0 < a < c$. Then, $a > a - c$ and $at > (a - c)t$ for $t > 0$. Now the reasoning follows exactly as before, and we are done.

For N_0, the transformation mapping is defined as

$$g(N_0, a, c, K_0, K_s) = \left(\frac{\mathrm{e}^{at} N_0 K_s}{K_s + aN_0 \left(\frac{K_s - K_0}{(a-c)K_0} \left(\mathrm{e}^{(a-c)t} - 1\right) + \frac{\mathrm{e}^{at}-1}{a} \right)}, a, c, K_0, K_s \right).$$

Its inverse is

$$h(N, a, c, K_0, K_s) = \left(\frac{K_0 K_s N(a - c)}{a\left(N(K_0 - K_s)\mathrm{e}^{t(a-c)} + K_0 \mathrm{e}^{at}(K_s - N) + K_s N\right) - cK_0 \left(\mathrm{e}^{at}(K_s - N) + N\right)}, a, c, K_0, K_s \right),$$

with Jacobian

$$Jh(N, a, c, K_0, K_s) = \frac{\partial N_0}{\partial N} = \frac{K_0^2 K_s^2 (a - c)^2 \mathrm{e}^{at}}{\left(cK_0 \left(\mathrm{e}^{at}(K_s - N) + N\right) - a\left(N(K_0 - K_s)\mathrm{e}^{t(a-c)} + K_0 \mathrm{e}^{at}(K_s - N) + K_s N\right)\right)^2} > 0.$$

By (11) and marginalizing,

$$\begin{aligned} f_{N(t)}(N) = \iiiint_{\mathcal{D}(a,c,K_0,K_s)} & f_{(N_0,a,c,K_0,K_s)}\left(\frac{K_0 K_s N(a - c)}{a\left(N(K_0 - K_s)\mathrm{e}^{t(a-c)} + K_0 \mathrm{e}^{at}(K_s - N) + K_s N\right) - cK_0 \left(\mathrm{e}^{at}(K_s - N) + N\right)}, a, c, K_0, K_s \right) \\ & \times \frac{K_0^2 K_s^2 (a - c)^2 \mathrm{e}^{at}}{\left(cK_0 \left(\mathrm{e}^{at}(K_s - N) + N\right) - a\left(N(K_0 - K_s)\mathrm{e}^{t(a-c)} + K_0 \mathrm{e}^{at}(K_s - N) + K_s N\right)\right)^2} \mathrm{d}a \, \mathrm{d}c \, \mathrm{d}K_0 \, \mathrm{d}K_s. \end{aligned} \tag{15}$$

Two general considerations must be made here. Firstly, when some input random parameter is independent of the rest, then the joint density function can be factored as a product. In fact, when applying the maximum entropy principle, the input random parameters that are distinct are assumed to be independent. Secondly, when some input parameter θ is a constant θ_0, then its probability density function is a Dirac delta function centred at the constant, $f_\theta = \delta_{\theta_0} = \infty \mathbb{1}_{\{\theta_0\}}$. This generalized function is defined via the heuristic property $\int_{-\infty}^{\infty} F(\theta)\delta_{\theta_0}(\theta)\,\mathrm{d}\theta = F(\theta_0)$, for any real function F.

In practice, one chooses between (12), (13) and (15) depending on whether K_0, K_s and N_0 have proper density function, respectively.

Given the density function $f_{N(t)}$, any statistic of $N(t)$ can be determined by using the relation $\mathbb{E}[r(N(t))] = \int_{-\infty}^{\infty} r(x) f_{N(t)}(x)\,\mathrm{d}x$, where r is any deterministic function. Also, given a probability $\alpha \in (0, 1)$, a confidence interval $[i_\alpha, j_\alpha]$ is constructed by using $\alpha \approx \int_{i_\alpha}^{j_\alpha} f_{N(t)}(x)\,\mathrm{d}x$.

An analogous procedure serves to calculate the density function of the carrying capacity $K(t)$ given by (4). Consider the transformation mapping

$$g(c, K_0, K_s) = \left(c, \frac{K_0 K_s}{(K_s - K_0)\mathrm{e}^{-ct} + K_0}, K_s \right).$$

Its inverse mapping, computed by isolating K_0 in the equation $K(t) = K$, is

$$h(c, K, K_s) = \left(c, \frac{K_s K}{K_s \mathrm{e}^{ct} - K\mathrm{e}^{ct} + K}, K_s \right),$$

with Jacobian

$$Jh(c, K, K_s) = \frac{\partial K_0}{\partial K} = \frac{K_s^2 \mathrm{e}^{ct}}{\left(\mathrm{e}^{ct}(K_s - K) + K\right)^2} > 0.$$

By (11) and marginalizing, we obtain

$$f_{K(t)}(K) = \iint\limits_{\mathcal{D}(c,K_s)} f_{(c,K_0,K_s)}\left(c, \frac{K_s K}{K_s \mathrm{e}^{ct} - K\mathrm{e}^{ct} + K}, K_s\right) \frac{K_s^2 \mathrm{e}^{ct}}{\left(\mathrm{e}^{ct}(K_s - K) + K\right)^2} \,\mathrm{d}c\,\mathrm{d}K_s. \tag{16}$$

We can also consider the transformation mapping

$$g(c, K_0, K_s) = \left(c, K_0, \frac{K_0 K_s}{(K_s - K_0)\mathrm{e}^{-ct} + K_0}\right).$$

This selection corresponds to isolating K_s when computing the inverse of g from the equation $K(t) = K$. The inverse mapping is then

$$h(c, K_0, K) = \left(c, K_0, \frac{K K_0 \left(1 - \mathrm{e}^{-ct}\right)}{K_0 - K\mathrm{e}^{-ct}}\right),$$

with Jacobian

$$Jh(c, K_0, K) = \frac{\partial K_s}{\partial K} = \frac{K_0^2 \left(1 - \mathrm{e}^{-ct}\right)}{\left(K_0 - K\mathrm{e}^{-ct}\right)^2} > 0.$$

By (11) and marginalizing, we arrive at

$$f_{K(t)}(K) = \iint\limits_{\mathcal{D}(c,K_0)} f_{(c,K_0,K_s)}\left(c, K_0, \frac{K K_0 \left(1 - \mathrm{e}^{-ct}\right)}{K_0 - K\mathrm{e}^{-ct}}\right) \frac{K_0^2 \left(1 - \mathrm{e}^{-ct}\right)}{\left(K_0 - K\mathrm{e}^{-ct}\right)^2} \,\mathrm{d}c\,\mathrm{d}K_0. \tag{17}$$

Finally, in contrast to the equation $N(t) = N$, we can isolate c in the equation $K(t) = K$; consider

$$g(c, K_0, K_s) = \left(\frac{K_0 K_s}{(K_s - K_0)\mathrm{e}^{-ct} + K_0}, K_0, K_s\right),$$

being

$$h(K, K_0, K_s) = \left(\frac{\log\left(\frac{K(K_s - K_0)}{K_0(K_s - K)}\right)}{t}, K_0, K_s\right)$$

and

$$Jh(K, K_0, K_s) = \frac{\partial c}{\partial K} = \frac{K_s}{Kt(K_s - K)} > 0.$$

Then

$$f_{K(t)}(K) = \iint\limits_{\mathcal{D}(K_0,K_s)} f_{(c,K_0,K_s)}\left(\frac{\log\left(\frac{K(K_s - K_0)}{K_0(K_s - K)}\right)}{t}, K_0, K_s\right) \frac{K_s}{Kt(K_s - K)} \,\mathrm{d}K_0\,\mathrm{d}K_s. \tag{18}$$

Let us summarize the formulae derived in this section. Depending on which parameter θ we can isolate in the equations $N(t) = N$ and $K(t) = K$ and on whether the density function f_θ exists, one chooses the appropriate expression of $f_{N(t)}(N)$ between (12) (when $\theta = K_0$), (13) (when $\theta = K_s$) and (15) (when $\theta = N_0$), and the appropriate expression of $f_{K(t)}(K)$ between (16) (when $\theta = K_0$), (17) (when $\theta = K_s$) and (18) (when $\theta = c$). Notice that N_0 does not play any role in formula (18), since it refers to the carrying capacity. On the other hand, for $f_{N(t)}(N)$, the situations $\theta = a$ and $\theta = c$ are not contemplated because they cannot be isolated in the equation $N(t) = N$ (they appear within and outside an exponential).

All of the integrals that have appeared in this section can be computed via tensorized Gauss quadratures. If the integrand has significant jump discontinuities, a parametric Monte Carlo method may be employed to estimate the integral, instead[39].

5 | NUMERICAL EXAMPLES

In this section we undertake numerical test examples for specific input parameters. In Example 1, we will consider a single pointwise deterministic estimator for each parameter. While in Example 2, we will assume several pointwise deterministic estimators for each parameter.

Example 1. Let us consider the parameters values $a = 0.15$, $c = 0.1$, $K_0 = 0.3$, $K_s = 1$ and $N_0 = 0.2$. The coefficients a and c are measured in time^{-1}, while N_0, K_0 and K_s represent proportions of counts, being K_s the maximum. The parameters values may be fitted experimentally or via least-squares minimization procedures. By using the exact deterministic solution (7), we can forecast the population $N(t)$ for $t \geq 0$. The results are reported in Figure 1, where the fat line refers to $K(t)$ defined by (4), the solid thin line represents $N(t)$ defined by (7), and the dots correspond to the numerical solution employing the classical Runge Kutta scheme for validation. We observe that, as expected, expression (7) and the numerical solution agree. Also, the solution $N(t)$ tends to the carrying capacity $K(t)$ as t increases, at the time when the growth of both functions is decelerated. The slope of the sigmoid trajectory of $K(t)$ depends on the saturation constant c. On the other hand, the slope of the sigmoid trajectory of $N(t)$ depends on both the saturation constant c and the growth rate a.

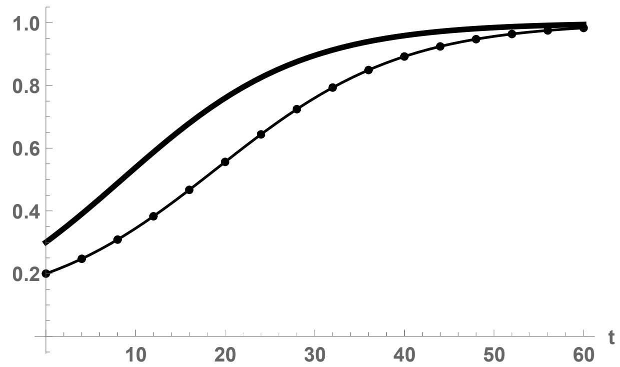

FIGURE 1 Given the parameters values $a = 0.15$, $c = 0.1$, $K_0 = 0.3$, $K_s = 1$ and $N_0 = 0.2$, the fat line refers to $K(t)$ defined by (4), the solid thin line represents $N(t)$ defined by (7), and the dots correspond to the numerical solution employing the classical Runge Kutta scheme. This figure corresponds to Example 1.

Next we study the effect of randomness on the model output. Let us suppose that, by some experimental evidence, N_0 lies within $[0.19, 0.21]$, a is bounded on $[0.13, 0.17]$, $c > 0$ with mean equal to 0.1, and K_0 is bounded on $[0.26, 0.34]$. According to the maximum entropy principle, N_0 has a Uniform distribution on $[0.19, 0.21]$, a follows a Uniform distribution on $[0.13, 0.17]$, c has an Exponential distribution with rate parameter $1/0.1 = 10$, and K_0 is Uniform on $[0.26, 0.34]$. These distributions maximize the ignorance on the random behaviour of N_0, a, c and K_0, while not violating the restrictions on their supports and statistics, if any. The random variables are assumed to be independent. We keep K_s with its constant value 1, as it represents the maximum proportion; its density function may be considered in terms of the Dirac delta function as δ_1. The saturation level being 1 may be seen as a general fact, as it can usually be scaled out of the problem for simplicity. The joint density function $f_{(N_0,a,c,K_0,K_s)}$ is factorized in terms of the marginal density functions:

$$f_{(N_0,a,c,K_0,K_s)} = f_{N_0} \times f_a \times f_c \times f_{K_0} \times \delta_1.$$

As K_s does not have a proper density function, we must consider (12) or (15) for the density $f_{N(t)}(N)$. We take (12). On the other hand, for $f_{K(t)}(K)$, we must consider (16) or (18). We pick (16). Thus, for both density functions, the inverse of the transformation mapping is defined by isolating K_0. The density function (12) is a triple integral in terms of $\mathrm{d}N_0\,\mathrm{d}a\,\mathrm{d}c$, while (16) is a one-dimensional integral with respect to $\mathrm{d}c$. In Figure 2, we plot the density functions (12) and (16) for different times $t = 10$ (solid line), 20 (dashed line), 30 (dotted dashed line) and 40 (dotted line). For (16), the plot has been truncated to $[0, 8]$ in the vertical axis for $t = 20$, $t = 30$ and $t = 40$, otherwise the density functions take too large values near $K = 1$.

The support of $N(t)$ is defined from the value of (7) when $a = 0.13$, $c = 0$, $K_0 = 0.26$, $N_0 = 0.19$ (these values correspond to the left endpoints of the domains of their corresponding distributions) and $K_s = 1$, which is 0.236 for $t = 10$, 0.253 for $t = 20$, 0.258 for $t = 30$, and 0.259 for $t = 40$. Regarding the support of $K(t)$, its left endpoint is 0.26 for any $t \geq 0$. The upper bound for the supports is 1. Notice that small dispersions of the parameters give wide supports for $N(t)$ and $K(t)$: this means that, for small perturbations in the experimental values of the parameters, the response may be sensitive and present large variation. Hence the need of appropriate tools to understand the random behaviour of the response. For standard probability distributions for the

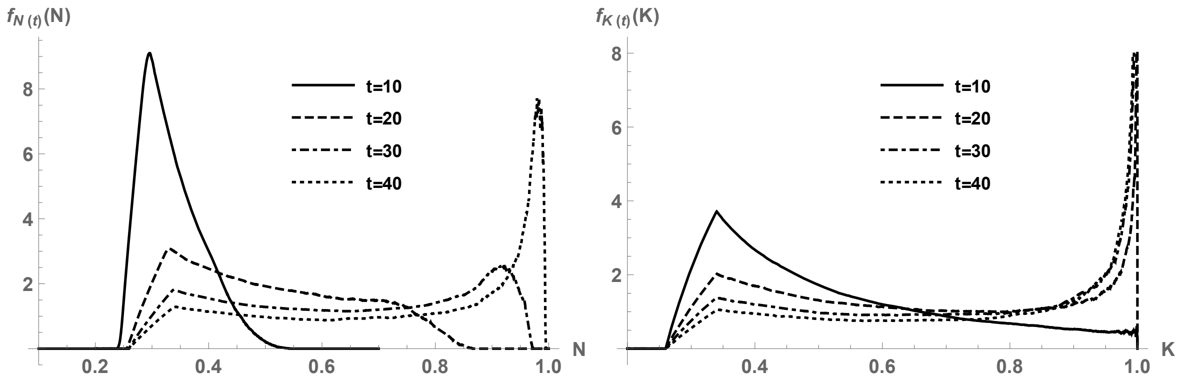

FIGURE 2 Given the probability distributions $a \sim$ Uniform$(0.13, 0.17)$, $c \sim$ Exponential(10), $K_0 \sim$ Uniform$(0.26, 0.34)$, $N_0 \sim$ Uniform$(0.19, 0.21)$ and the total proportion $K_s = 1$, the first panel plots the density $f_{N(t)}(N)$ given by (12) and the second panel shows the density $f_{K(t)}(K)$ given by (16), for different times $t = 10$ (solid line), 20 (dashed line), 30 (dotted dashed line) and 40 (dotted line). This figure corresponds to Example 1.

input parameters, the density functions of $N(t)$ and $K(t)$ may present a wide variety of shapes: asymmetry, multimodality, non-regularity, etc. As t grows, more probability density tends to be concentrated near 1, as the solution and the carrying capacity approach the limiting population.

The evolution of the density function of $N(t)$ can be better understood by means of Figure 3. It shows the contour plot of the densities for locations in $[0, 1]$ and non-negative discretized times. Light colours correspond to large values, being the "outliers" represented in white colour. From f_{N_0} at $t = 0$, the densities spread as t increases and, for large t, they tend to δ_1.

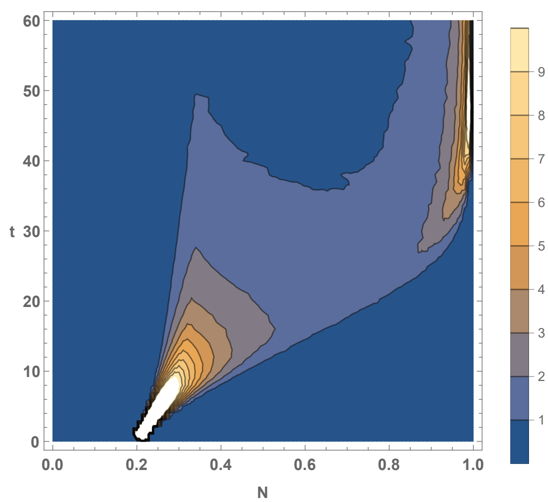

FIGURE 3 Given the probability distributions $a \sim$ Uniform$(0.13, 0.17)$, $c \sim$ Exponential(10), $K_0 \sim$ Uniform$(0.26, 0.34)$, $N_0 \sim$ Uniform$(0.19, 0.21)$ and the total proportion $K_s = 1$, the figure shows the contour plot of the density $f_{N(t)}(N)$ given by (12), for $N \in [0, 1]$ and $t \geq 0$. This figure corresponds to Example 1.

In Table 1, we tabulate the deterministic value of $N(t)$ together with its main statistical information (mean value, standard deviation and 95% confidence range), for times $t = 10$, 20, 30 and 40.

Example 2. Let us suppose several listed values of the parameters N_0 (in proportion of counts), a (in time^{-1}), c (in time^{-1}) and K_0 (in proportion of counts), obtained experimentally or via least-squares minimization procedures from laboratory data that

	deterministic	mean	standard deviation	95% confidence interval
$t = 10$	0.344	0.334	0.054	$(0.26, 0.47)$
$t = 20$	0.556	0.504	0.15	$(0.29, 0.80)$
$t = 30$	0.760	0.642	0.21	$(0.29, 0.94)$
$t = 40$	0.892	0.727	0.23	$(0.33, 0.99)$

TABLE 1 Given $a = 0.15$, $c = 0.1$, $K_0 = 0.3$, $K_s = 1$ and $N_0 = 0.2$, the deterministic value of $N(t)$ is reported for times $t = 10$, 20, 30 and 40. On the other hand, given the randomization $a \sim \text{Uniform}(0.13, 0.17)$, $c \sim \text{Exponential}(10)$, $K_0 \sim \text{Uniform}(0.26, 0.34)$ and $N_0 \sim \text{Uniform}(0.19, 0.21)$, the main statistical information (mean, standard deviation and 95% confidence interval) is tabulated for $t = 10$, 20, 30 and 40. This table corresponds to Example 1.

are replicated at the different time instants of measure:

$$(0.201139, 0.148054, 0.0991566, 0.293589),$$
$$(0.190989, 0.147221, 0.107407, 0.301059),$$
$$(0.205488, 0.142062, 0.114978, 0.280932),$$
$$(0.188831, 0.139132, 0.112557, 0.312992),$$
$$(0.192942, 0.157904, 0.0879763, 0.301962),$$
$$(0.199116, 0.139290, 0.105916, 0.299521),$$
$$(0.199919, 0.164675, 0.0991728, 0.300021),$$
$$(0.210952, 0.156174, 0.0956518, 0.286416),$$
$$(0.206444, 0.156298, 0.113180, 0.293593),$$
$$(0.198279, 0.131121, 0.101008, 0.314752).$$

The parameter K_s is set to 1, as it stands for the maximum proportion in any case. Compared to Example 1, now there is much more information about the parameters, and the conclusions will be robust. The mean and the variance of each parameter are estimated via the corresponding sample of length ten. The support of each parameter is defined by adding and subtracting three times the standard deviation to the mean (this is motivated by the 3σ rule and the Vysochanskii-Petunin inequality, see[40]). When applying the maximum entropy principle, we have $m = 2$, and the Lagrange constants λ_0, λ_1 and λ_2 satisfying the complex nonlinear system (9) are determined numerically by employing Newton's method, with starting value $(-1, 1, 1)$, for each parameter. In Table 2 we report the results, where the values of λ_0, λ_1 and λ_2 have been stopped at the sixth significant digit.

parameter	mean	standard deviation	support	λ_0	λ_1	λ_2
N_0	0.199	0.00706	$[0.178, 0.221]$	384.067	−3892.43	9759.99
a	0.148	0.0105	$[0.116, 0.180]$	93.9733	−1317.20	4444.05
c	0.104	0.00866	$[0.0777, 0.130]$	65.8797	−1344.29	6481.91
K_0	0.298	0.0105	$[0.267, 0.330]$	386.901	−2616.60	4382.95

TABLE 2 For each parameter, we tabulate the mean and the standard deviation estimated from the corresponding sample of length ten. The support of each parameter is defined by adding and subtracting three times the standard deviation to the mean. The Lagrange constants λ_0, λ_1 and λ_2 are determined numerically. This table corresponds to Example 2.

Figure 4 plots the resulting density functions (10) for N_0 (solid line), a (dashed line), c (dotted dashed line) and K_0 (dotted line). As explained in[12,41] based on theory and numerical evidence, whenever the mean, the variance and a compact support are available, the entropy distribution is approximately truncated Gaussian. The density function of K_s is the Dirac delta function centred at 1, δ_1. All of these random variables are assumed to be independent, so their joint density function factorizes.

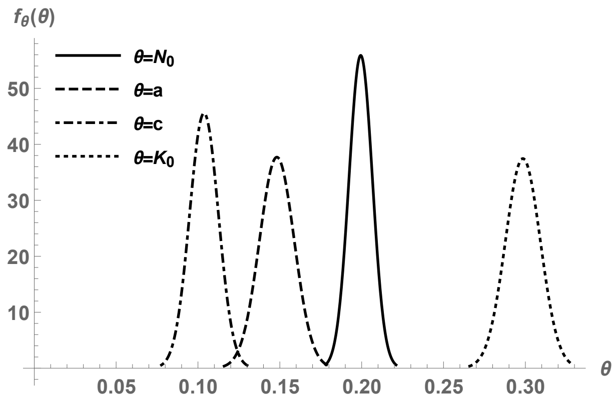

FIGURE 4 Density functions of N_0 (solid line), a (dashed line), c (dotted dashed line) and K_0 (dotted line) determined via the maximum entropy principle. This figure corresponds to Example 2.

As K_s does not have a proper density function, we must consider (12) or (15) for the density $f_{N(t)}(N)$, and (16) or (18) for $f_{K(t)}(K)$. We take (12) and (16), which come from isolating K_0 when defining the inverse of the transformation mapping. In Figure 5, we show the density functions (12) and (16) for different times $t = 10$ (solid line), 20 (dashed line), 30 (dotted dashed line) and 40 (dotted line). On the other hand, in Figure 6 we can see the contour plot of the densities $f_{N(t)}(N)$ for positions $N \in [0, 1]$ and non-negative discretized times t. Light tones are associated to large values, and the "outliers" are painted in white colour.

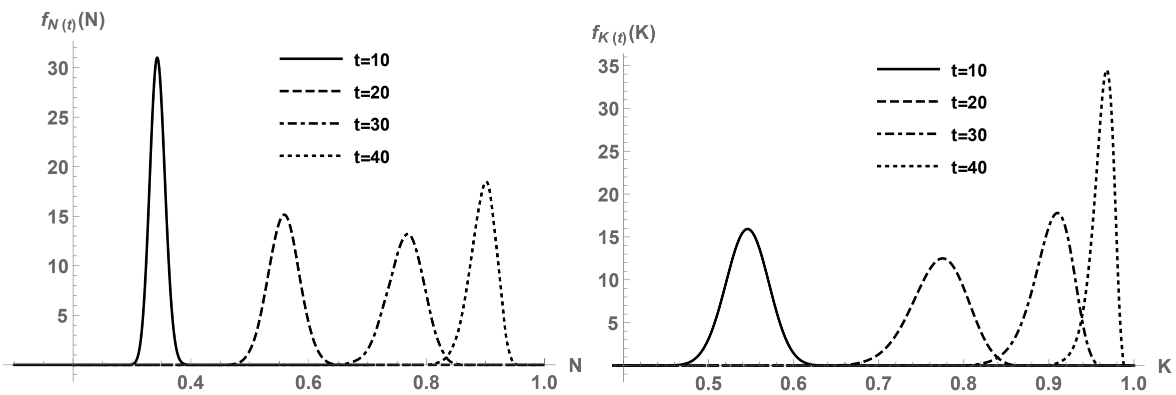

FIGURE 5 Given the distributions of a, c, K_0, N_0, and the total proportion $K_s = 1$, the first panel plots the density $f_{N(t)}(N)$ given by (12) and the second panel shows the density $f_{K(t)}(K)$ given by (16), for different times $t = 10$ (solid line), 20 (dashed line), 30 (dotted dashed line) and 40 (dotted line). This figure corresponds to Example 2.

The left endpoint of the support of $N(t)$ is given by the value of (7) when $a = 0.116$, $c = 0.0777$, $K_0 = 0.267$, $N_0 = 0.178$ and $K_s = 1$, which is 0.273 for $t = 10$, 0.418 for $t = 20$, 0.590 for $t = 30$, and 0.749 for $t = 40$. The left endpoint of the support of $K(t)$ is 0.442 when $t = 10$, 0.633 when $t = 20$, 0.789 when $t = 30$, and 0.891 when $t = 40$. The right endpoint of the support of $N(t)$ is obtained by substituting $a = 0.180$, $c = 0.130$, $K_0 = 0.330$, $N_0 = 0.221$ and $K_s = 1$ into (7), which gives 0.423 for $t = 10$, 0.695 for $t = 20$, 0.884 for $t = 30$, and 0.964 for $t = 40$. The support of $K(t)$ is bounded above by 0.644 when $t = 10$, 0.869 when $t = 20$, 0.961 when $t = 30$, and 0.989 when $t = 40$. When t increases, the density functions converge to δ_1.

In Table 3, we document the deterministic value of $N(t)$ together with its main statistical information (mean value, standard deviation and 95% confidence range), for times $t = 10$, 20, 30 and 40.

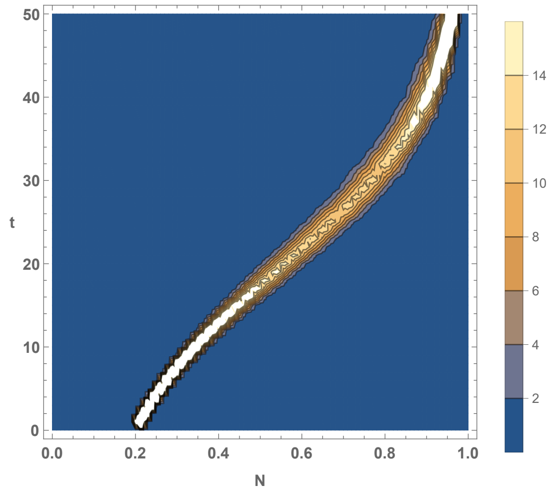

FIGURE 6 Given the distributions of a, c, K_0, N_0, and the total proportion $K_s = 1$, the figure shows the contour plot of the density $f_{N(t)}(N)$ given by (12), for $N \in [0,1]$ and $t \geq 0$. This figure corresponds to Example 2.

	deterministic	mean	standard deviation	95% confidence interval
$t = 10$	0.344	0.343	0.013	(0.32, 0.37)
$t = 20$	0.556	0.558	0.026	(0.50, 0.61)
$t = 30$	0.760	0.764	0.030	(0.70, 0.82)
$t = 40$	0.892	0.894	0.022	(0.84, 0.93)

TABLE 3 Given $a = 0.15$, $c = 0.1$, $K_0 = 0.3$, $K_s = 1$ and $N_0 = 0.2$, the deterministic value of $N(t)$ is reported for times $t = 10$, 20, 30 and 40. On the other hand, given the randomization of a, c, K_0 and N_0, the main statistical information (mean, standard deviation and 95% confidence interval) is tabulated for $t = 10$, 20, 30 and 40. This table corresponds to Example 2.

6 | DISCUSSION AND CONCLUSION

This paper addresses two important issues in ecological modelling: the mathematical analysis of the logistic growth model for time-varying carrying capacity and the incorporation of randomness into the model formulation. The former is motivated by the principle that a changing environment may result in a significant change in the limiting capacity, while the latter is justified accounting for data errors. The study of randomness on the non-autonomous logistic growth model does not seem to have been explored, at least to our knowledge.

With time-dependent carrying capacity, the deterministic logistic equation belongs to the class of Bernoulli ordinary differential equations, which can be solved by a change of variables. The constant parameters (growth rate, saturation rate, saturation level, etc.) can be fitted experimentally or via least-squares minimization procedures. The resulting model can then be used for forecast. In this paper we focus on the model from[7], which described parasite growth during infection.

To analyze the effect of randomness on the model output, first one must set appropriate probability distributions for the input parameters. This can be done via the maximum entropy principle. Given a parameter, its density function is chosen by maximizing the Shannon entropy measure, restricted to certain statistical moments and support usually devised from deterministic fittings and experimental data. For example, if only information on the support of the parameter is available, then the Uniform distribution is selected; if the parameter is positive and only its mean is known, then the Exponential distribution is chosen. In general, the selection of the density function is made numerically. The foundation of these selections is the calculus of variations and Lagrange multipliers. Depending on the amount of data at each time instant of interest, the prior information on the parameters is either more vague or more complete. When there are replicated data at each time instant, the information on the parameters is more significant and the entropy distribution is more reliable; this "multi-data" case is the most desirable scenario in practice. The density function of the exact model solution can be determined via the random variable transformation method. This technique is based on the application of a formula when the transformation mapping between the random quantities is injective (one-to-one) with non-vanishing Jacobian. These requirements may be overcome when the domain of the transformation mapping is divided into sub-domains where these conditions hold.

In this manner, we have a probabilistic solution to the model. Apart from pointwise estimations, other relevant information such as confidence intervals, dispersion and statistical moments can be derived. This supplies a more faithful and complete description of the ecological process.

In the near future, we aim at conducting a similar analysis for the logistic growth model proposed in[10], where the carrying capacity is itself described via a logistic curve. In that paper, the authors modelled the total bacterial biomass during occlusion of healthy human skin. The solution to that model is expressed algebraically by truncating an infinite series. Thus, when the input parameters are random variables, the application of the random variable transformation method shall be analyzed.

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CONFLICT OF INTEREST STATEMENT

The authors declare that there is no conflict of interests regarding the publication of this article.

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