

MODELLING ENVIRONMENTAL STOCHASTICITY IN A STAGE-STRUCTURED POPULATION APPLYING STOCHASTIC DIFFERENTIAL EQUATIONS

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ABSTRACT. This work presents a new approach to incorporating environmental stochasticity into stage-structured models by combining population dynamics with stochastic differential equations theory. Random fluctuations were treated as Brownian motion, where the stochastic diffusion process here was the population size. The resulting SDEs model was discussed in terms of existence, uniqueness and stability of the solution. Numerical analyses were investigated in this work to analyze and visualize our model. Our approach allowed us to project the population behavior and to calculate the stochastic growth rate. The quasi-extinction risk was also studied by setting a threshold population size under different conditions. The proposed method was applied to a real dataset of a plant species populations, and the obtained results were in excellent agreement with previous studies. Therefore, our method can be an alternative way to incorporate stochasticity in such structured population models.

1. INTRODUCTION

The development of population models with stochastic differential equations (SDE_s) have been on the rise in last years as a result of new interest (see for example [20], [15], [16], [17], [30] and [32]). The SDE_s models were considered as an appropriate modelling to describe population data, since SDE_s have showed more accurate and closer approximation to the actual data than other stochastic models [33]. However, its application remains so limited in population dynamics, especially for the multidimensional models as the case for structured populations, except for a few studies (see for example [2], [11]). In such stochastic approach in population dynamics, the number of individuals in each class can be treated as diffusion processes to describe the stochastic fluctuations in population size. Most previous studies have shown that knowledge of stochasticity is essential for understanding the temporal changes in populations, finding approximations to the stochastic growth rate and predicting extinction risk, focusing on both theoretical and numerical analyses ([6], [18] and [22]). Thus, more complex phenomena may be revealed in such noisy systems than in deterministic systems.

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Most biological populations are subject to various sources of demographic and environmental stochasticity, where the environmental noise should be an essential component of any population model (see [6] and [32]). Demographic stochasticity is due to the independent probability of transition and reproduction among individuals, which can be studied as Markov chains [2]. Environmental stochasticity results from perturbations that affect the birth and death rates of all individuals in a population ([13], [25] and [29]). In the majority of natural populations, the observed temporal variations in population dynamics are of an environmental source, which are considered to exert a stronger influence on population persistence than those of a demographic source. Moreover, unlike to demographic stochasticity, environmental stochasticity is important in both large and small populations [11]. Such *noise*, can be accurately modelled as a diffusion process (see [25] and [32]). In fact, diffusion models are employed in a multitude of biological phenomena, in our particular case, the stochastic process $N(t)$ represents the population size, solution of a SDE describing an exponential growth model ([11], [15]).

In our work we developed a *Matrix Population Model* which describes the dynamics of a stage-structured population by incorporating the environmental type of stochasticity. Such structured models treat the processes of moving among stage classes as alternating. A deterministic model is then given as a matrix equation based on a square matrix containing transition parameters [6]. In the presence of stochastic fluctuations, stochasticity can generally be incorporated into population models by randomly selecting one entire matrix transition at each time step (sampling with replacement) from all existing matrices (see for example [9], [10] and [22]). An alternative to random selection of matrices is random selection of matrix elements, by drawing values from the *joint* probability distribution of vital rates ([6]). Such approaches require longer-term surveys, which explains why most population dynamics studies have treated only the deterministic model based on a few years of data [9]. In contrast, in the approach proposed here, we considered the number of individuals at each stage as a diffusion process, solution of a stochastic differential equation, which requires only the average transition parameters from fewer numbers of projection matrices.

SDEs in applications arose by incorporating random fluctuations (noise) into deterministic models, where the notion of Brownian motion processes had been introduced with the associated white noise models ([3],[11], [14], [15], [26], [30]). Such noise is called additive (if it acts externally) when the diffusion coefficient does not depend on the studied stochastic process, and in this case these integrals have a unique value. In the case of a parametric (multiplicative) white noise, where the diffusion coefficient depends on the stochastic process, the integral has infinite values depending on the position of the point in the discretisation interval [16]. In such analyses, two methods of stochastic calculus are distinguished, namely Itô and Stratonovich, which differ in the stochastic integral employed. However, in the case of additive noise, the two representations are equivalent (see [16] and [18]).

In most studies that developed SDEs for modeling and analysing realistic phenomena, theoretical analyses became less important especially when it may not

be possible to find an explicit solution. Thus, numerical methods are becoming an indispensable tool in a variety of disciplines, relating the developed theory of SDEs and their application to specific examples ([23] and [31]). In this case, if the solution exists, it can be approximated using a discrete-time approximation ([23], [5]). The current progress in the development of numerical tools has enabled many theoretical problems involving SDEs to be solved [18]. There are already a number of open source packages that are able to carry out stochastic analysis in the R software environment. In fact, the R language is a powerful programming language that is well adapted to express advanced mathematical processes. There are several packages that address continuous time (SDE) models in R, most of them focusing on single topic issues. These include **sde** [21], **yuima** [4], **cts** [39], and **ctsem** for more complex continuous time models [12]. Here we used the package **Sim.DiffProc** [18], which allows us to simulate, estimate and analyse the dynamics of stochastic systems using both symbolic and numerical computation. All numerical approaches used in this package are of high order of convergence [18].

The structure of this paper is as follows: we have described in Section 2 the way to introduce stochasticity into deterministic population growth models, and some properties of the resulting diffusion processes. The proposed approach is presented in Section 3. Numerical analyses were carried out in detail in Section 4. The obtained results were applied to a real dataset of a plant species in Section 5. Finally, a brief conclusion is given in the last section.

2. DIFFERENTIATING A DETERMINISTIC POPULATION MODELZ

We consider a single-species biological population with no migration. The corresponding population growth model is given by an ordinary differential equation

$$\frac{dN(t)}{dt} = a(t)N(t); \quad (2.1)$$

given that $N(t)$ represents the population size at time t and $a(t)$ is the relative population growth rate.

However, biological populations can be exposed to environmental stochasticity. Thus, the relative growth rate $a(t)$ will be subject to random fluctuations caused by various random effects such as the meteorology, habitat and the general environmental conditions. Such noise is usually studied as a stochastic (Wiener) process and, in especially, as a Brownian motion process [32].

Note that a Wiener process, $W(t)$, $t \geq 0$, represents a stochastic process that has the following characteristics ([15], section 3.1):

- (i) $W(0) = 0$.
- (ii) $W(t) - W(s)$, $s < t$, is independent of the past.
- (iii) $W(t) - W(s)$ has a normal distribution with parameters $\mu = 0$ and variance $\sigma^2 = t - s$. For $s = 0$ the process $W(t)$ has the distribution $N(0, t)$.
- (iv) $W(t)$, $t \geq 0$ represents a continuous function of t .

Under these conditions, the equation (2.1) can be rewritten as the following SDE form

$$\frac{dN(t)}{dt} = (r(t) + \alpha(t) \cdot \xi_t)N(t) \quad (2.2)$$

where $r(t)$ and $\alpha(t)$ are given functions of t and the noise term ξ_t is the stochastic process called *White noise* and is given by $\xi_t = \dot{W}(t) = dW(t)/dt$. It represents the time derivative of the Wiener process (Brownian motion) $(W(t))_{t \geq 0}$ with $W(0) = W_0 = 0$ (see [32], sections 4.1 and 6.3).

Then the equation (2.2) becomes

$$dN(t) = r(t)N(t)dt + \alpha N(t)dW(t), N(0) = N_0, t \geq 0. \quad (2.3)$$

In the general case, the stochasticized model is given as the SDE of the form

$$dN(t) = f(N(t), t)dt + g(N(t), t)dW(t), t \geq t_0, \quad (2.4)$$

with the initial state $N(t_0) = N_0$, assuming that N_0 is a random variable independent of $W(t) - W(t_0)$, and $E(|N_0|^2) < +\infty$ (see [32], section 5.1).

In such models, f is called the drift coefficient function, which can be considered as a measurement of short-term growth, and g the diffusion coefficient function, which represents short-term variability. Thus, a sufficient regularity is assumed for these functions (Lipschitz, bounded growth conditions), which ensure the existence and uniqueness of the solution (see Theorem 2.1).

Theorem 2.1. (*Theorem of existence and uniqueness*)

If the drift and diffusion functions (f and g) of the SDE (2.4) verify the conditions:

(a) *Uniform Lipschitz Condition*

$$|f(x, t) - f(y, t)| + |g(x, t) - g(y, t)| \leq k|x - y| \quad (2.5)$$

for a given constant k and all $t \in [t_0, T]$, $T > 0$.

(b) *Linear Growth Condition*

$$|f(x, t)|^2 + |g(x, t)|^2 \leq k^2 (1 + |x|^2) \quad (2.6)$$

for a given constant k^2 and all $t \in [t_0, T]$, $T > 0$.

Then the equation (2.4) has for all t in the interval $[t_0, T]$ a unique continuous solution $N(t)$ with probability 1, that satisfies the initial condition $N(t_0) = N_0$. This means; under the same initial value N_0 , if $N(t)$ and $\tilde{N}(t)$ are two continuous solutions of (eq. 2.4), then we have

$$P \left[\sup_{t_0 \leq t \leq T} |N_t - \tilde{N}_t| > 0 \right] = 0,$$

so that the solution $N(t)$ is unique.

(See Section 5.2 in [32] and Section 6.2 in [3] for the proof).

Stochastic stability for such models is well investigated in ([2]; Section 4.2, and [32]; Section 5.4 and [28]; Section 4). The stability of the solution of SDEs must be formulated in probabilistic sense. Assume that the following hypotheses are fulfilled :

- (a) The conditions in Theorem 2.1 are satisfied;
- (b) the initial state $N(t_0) = N_0 \in \mathbb{R}$ is supposed to be a constant with probability 1, and
- (c) the equation (eq. 2.4) has a unique global solution, for a given N_0 independent of $W(t), t \geq t_0$, with continuous sample paths and finite moments; and
- (d) $N(t) \equiv 0$ is the unique solution corresponding to the initial state $N(t_0) = N_0 = 0$, since for all $t \geq t_0$ we have $f(0, t) = 0$ and $g(0, t) = 0$.

Then the trivial or equilibrium solution is called stochastically stable or stable in sense of probability if for every $\varepsilon > 0$

$$\lim_{N_0 \rightarrow 0} P \left(\sup_{t_0 \leq t \leq +\infty} |N_t(t_0, N_0)| \geq \varepsilon \right) = 0, \quad N(t_0) = 0. \quad (2.7)$$

When this is not the case, it is considered as stochastically unstable solution [28]. We have an asymptotic stochastic stability of the equilibrium solution, if it satisfies in addition to stochastic stability; the property

$$\lim_{N_0 \rightarrow 0} P \left(\lim_{t \rightarrow +\infty} N_t(t_0, N_0) = 0 \right) = 1. \quad (2.8)$$

This result can also be considered for multidimensional stochastic systems (see [2]; Section 4.2 and [28]).

In natural systems, the notion of stability consists to the fact that the changes in the initial state (conditions) do not lead to large changes in the population behavior. However, in most research of biological populations systems, analyzing the stability behaviors is extremely difficult, therefore numerical simulations and visualizations are often used to treat such questions.

3. CONSTRUCTION OF THREE-DIMENSIONAL STOCHASTIC SYSTEM

3.1. Matrix Projection Models. In this paper, we have focused on stage-structured populations and, in particular, populations with three stage classes. The dynamics of such populations are studied based on the matrix projection model given by

$$N(t+1) = AN(t), \quad (3.1)$$

where $N(t)$ is a three dimensional vector representing the number of individuals in each stage class at time t ($t = 0, 1, 2, \dots$), and the square matrix A contains the non-negative elements representing transition parameters between different stage classes [6]. In this case, the projection matrix A has dimension (3×3) and is constructed from the vital rates a_{ij} representing transitions from stage j to stage i . The projection matrix has the form

$$A = \begin{pmatrix} a_{11} & a_{12} & a_{13} \\ a_{21} & a_{22} & a_{23} \\ a_{31} & a_{32} & a_{33} \end{pmatrix}. \quad (3.2)$$

If the projection matrix is primitive, the population growth rate can describe the long-term dynamics of the studied population. This growth rate (denoted λ_1) is calculated as the dominant eigenvalue of the projection matrix A . In such cases,

when the final population behavior does not depend on the initial conditions, the population is called *ergodic* [6].

A key hypothesis in our modeling approach is that projection matrices change over time in such a way that each of the elements, or vital rates, from a (multivariate) stationary time series. For example, the projection matrix entries are drawn at each time step with a multivariate distribution, independent of previous time (see [24],[38] and [11]). The vital rates could be correlated within each time step, however no serial correlation exists between rates at different times. In this case the model is called an independent and identically distributed (iid) [38].

3.2. The 3d Stochastic Differential Equations. In this section we rewrite the matrix equation (3.1) as a system of three equations representing the number of individuals in each stage class, as follows

$$\begin{cases} X(t+1) = a_{11} X(t) + a_{12} Y(t) + a_{13} Z(t) \\ Y(t+1) = a_{21} X(t) + a_{22} Y(t) + a_{23} Z(t) \\ Z(t+1) = a_{31} X(t) + a_{32} Y(t) + a_{33} Z(t) \end{cases}$$

where $X(t), Y(t)$ and $Z(t)$ are the three components of the vector $N(t)$ and a_{ij} are the entries of the projection matrix A .

The proposed method is to transform the previous system into a 3d stochastic system (following Section 2), since the numbers of individuals $X(t), Y(t)$ and $Z(t)$ were assumed to be diffusion processes, which could be represented mathematically as stochastic differential equations [11]. Thus, we introduced the noise term (Brownian motion) as explained above, considering the case of a scalar SDE driven by three Wiener processes. We obtained the three-dimensional SDEs of the form :

$$\begin{cases} dX(t) = (a_{11} X(t) + a_{12} Y(t) + a_{13} Z(t)) dt + g_1(X(t), t) dW_1(t) \\ dY(t) = (a_{21} X(t) + a_{22} Y(t) + a_{23} Z(t)) dt + g_2(Y(t), t) dW_2(t) \\ dZ(t) = (a_{31} X(t) + a_{32} Y(t) + a_{33} Z(t)) dt + g_3(Z(t), t) dW_3(t) \end{cases} \quad (3.3)$$

where g_1, g_2 and g_3 represent diffusion functions and $dW_1(t), dW_2(t), dW_3(t)$ are three Wiener processes.

Note that the noise can be introduced as an additive, linear or nonlinear multiplicative term, with correlated or independent Wiener processes [18].

For this type of SDE, the unique continuous global solution to (eq. 3.3) always exists. In fact, the coefficients of the obtained stochastic system (a_{ij}) are all real constants, which represents a system of autonomous, homogeneous SDEs. The drift and diffusion functions (f and g) are both independent of time t , therefore the assumptions underlying in Theorem 2.1 are verified (see [32] Section 5.2).

3.3. Population Dynamics Analyses. From the obtained stochastic system (3.3), we numerically approximate the solution at each stage class ($X(t), Y(t), Z(t)$). Projections were simulated based on 1000 stochastic iterations, each representing stochastic fluctuations in the number of individuals in each stage class over a fixed period of time. The initial population size N_0 used to start our simulations

was calculated from the *stable stage distribution* (see [6] and [19]). In this method we used the scaled right eigenvector w which satisfies

$$A w = \lambda_1 w$$

where λ is the dominant eigenvalue and A is the projection matrix of the studied population.

More importantly, our projection allowed us to calculate the stochastic population growth rate λ_s from trajectories representing the total population size (by summing the number of individuals from the three stage classes). For a given trajectory, we calculated the corresponding growth rate λ_j using the following formula

$$\lambda_j = \exp \left[\frac{\ln(n_j(T)) - \ln(n_j(0))}{T} \right], \quad (3.4)$$

where $n_j(T)$ and $n_j(0)$ represent the population size of the j^{th} trajectory at the final time T and the initial time $t = 0$, respectively. Thus, the stochastic growth rate λ_s was calculated as the median of λ_j over 1000 trajectories [6].

In our resulting model we can also study the *quasi-extinction*, since such stochastic models do not permit extinction ([6], [11] and [24]). Under the random variations of the Wiener drift model, $N(t)$ could potentially reach any lower threshold population size [11]. For this, we have specified a lower *threshold size* $N(t) = N_Q$, so that the quasi-extinction threshold θ is given by

$$\theta = \frac{N_Q}{N_0}$$

which is a fixed percentage of the initial population size [6]. Thus, the eventual quasi-extinction probability at a given time t was calculated as the number of trajectories for which $N(t) = N_Q$ over the total number of trajectories. The *quasi-extinction time* T_Q corresponds to the first time for which N_t reaches N_Q , and was calculated as the median of 1000 values. Indeed, for such parameters, the median is generally a more representative, since the mean value can be influenced by the extrem values of $N(t)$ ([6]; Section 14.8 and [11]).

4. NUMERICAL ANALYSIS AND SIMULATIONS

In the current study we used the open source R-package Sim.DiffProc to simulate the solutions of the studied population models. In fact, this package contains a variety of R functions that can be used to perform simulations and stochastic analyses. Different tools are available to estimate, analyse and visualize the dynamics of scalar and multivariate systems, of Itô and Stratonovich SDEs driven by Wiener processes (see [18]).

First, we numerically approximated the solution of the stochastic system, using the R-function *snssde3d()*, after specifying the R-expressions of the *drift* and *diffusion* coefficients and the initial conditions.

Secondly, we have carried out a symbolic calculation and numerical approximation of the means, variances and covariances of the SDEs, by solving a system

of ordinary differential equations, which provides a first understanding of the dynamics of stochastic systems. This can be done in *R* by applying the R-function *MEM.sde()* (Moment Equations Method) to the stochastic system [18].

Then, based on the obtained stochastic trajectories, we calculated the stochastic growth rate λ_s , the quasi-extinction probability and the time to quasi-extinction, as explained in the previous section. All stochastic analyses were implemented using the open source R-studio (version 4.2.2).

5. APPLICATION ON A PLANT SPECIES

We have studied in this section an endemic plant species (*Centaurea corymbosa*) which has a life-cycle composed of three stage-classes: seedlings (individuals < 1 year), rosettes (vegetative plants older than 1 year) and flowering plants. The corresponding projection matrix is given by

$$A = \begin{pmatrix} 0 & 0 & fs_0 \\ s_1(1 - \alpha_1) & s_2(1 - \alpha_2) & s_3(1 - \alpha_3) \\ s_1\alpha_1 & s_2\alpha_2 & s_3\alpha_3 \end{pmatrix} = \begin{pmatrix} 0 & 0 & 5.104 \\ 0.351 & 0.586 & 0.024 \\ 0.0111 & 0.120 & 0.038 \end{pmatrix},$$

where fs_0 represents the fecundity term, s_i survival probabilities and α_i the flowering probabilities. The transition parameters have been estimated in previous studies (see for example [19] for more details).

Thus, from the matrix model $N(t+1) = AN(t)$, and when differentiating the system, we obtained the following form

$$\begin{cases} dX(t) = 5.104 Z(t)dt \\ dY(t) = 0.351 X(t)dt + 0.586 Y(t)dt + 0.024 Z(t)dt \\ dZ(t) = 0.011 X(t)dt + 0.120 Y(t)dt + 0.038 Z(t)dt \end{cases}$$

Using the proposed method we stochasticized the previous system, by introducing a linear multiplicative noise term where the strength of stochasticity depends on the current state of the system. We obtained the following three-dimensional SDEs

$$\begin{cases} dX(t) = 5.104 Z(t) dt + \sigma_1 X(t) dW_1(t) \\ dY(t) = (0.351 X(t) + 0.586 Y(t) + 0.024 Z(t)) dt + \sigma_2 Y(t) dW_2(t) \\ dZ(t) = (0.011 X(t) + 0.12 Y(t) + 0.038 Z(t)) dt + \sigma_3 Z(t) dW_3(t) \end{cases} \quad (5.1)$$

where σ_1, σ_2 and σ_3 represent the diffusion coefficients corresponding to three independent Standard Brownian motion (using the R-command *corr=NULL*).

To approximate the solution of (5.1), we used $N_0 = (2152, 2487, 377)$ the initial population size based on the obtained stable stage distribution

$$w = (42.90\%, 49.59\%, 7.51\%),$$

(see Section (3.3)), with a total population size obtained from the exhaustive survey (see Appendix A in [19]). We did not observe any effect on the results when changing the type of approximation, we then used *Euler-Maruyama* approximation [18].

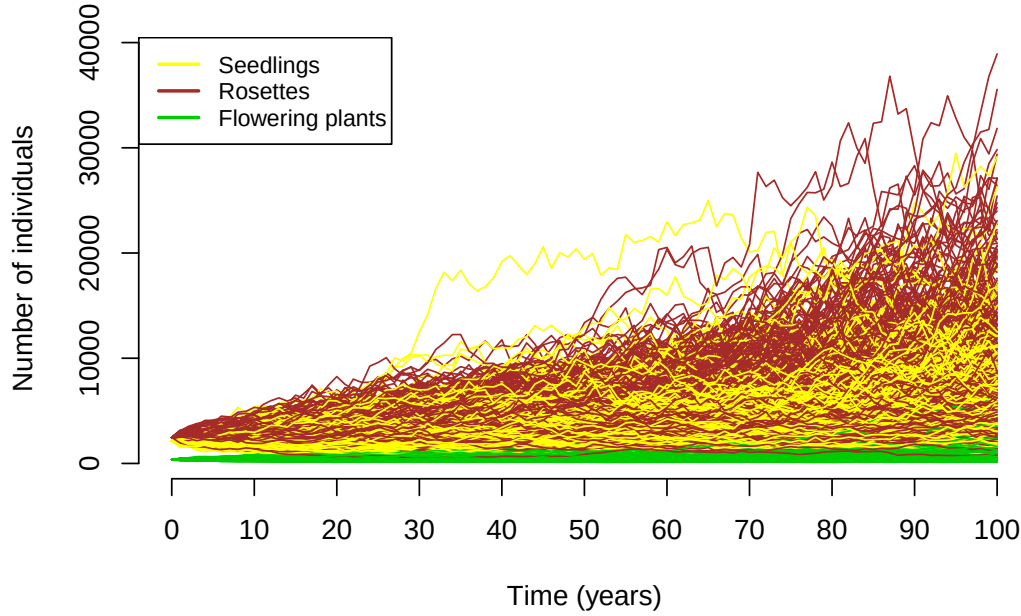


FIGURE 1. Numerical approximation of the solution of the 3d system (5.1). The trajectories represent the number of individuals per stage class of *C. corymbosa* populations. Simulations were performed with parameter values $t_0 = 0, T = 1, N = 100, \Delta = 0.01, M = 1000, x_0 = N_0$ and $\sigma_1 = \sigma_2 = \sigma_3 = 0.8$. The time $T = 1$ represents the ending time of 100 years and other parameters were left as default.

5.1. Trajectories analyses per each stage class. We approximated the numerical solution of the resulting 3d stochastic system (5.1) based on 1000 simulations (see Fig. (1)), where trajectories corresponded to the number of individuals in each stage class (Seedlings, Rosettes and Flowering plants). Here, we used 3d drift and diffusion coefficient functions as follows

$$f(x, y, z) = ((5.104 * z), (0.351 * x + 0.586 * y + 0.024 * z), (0.011 * x + 0.120 * y + 0.038 * z))$$

and

$$g(x, y, z) = (\sigma_1 * x, \sigma_2 * y, \sigma_3 * z),$$

with the start time $t_0 = 0$ and the ending time $T = 1$ representing 100 years in our study. Δ is the integration step size (mesh size). Our results were simulated under the assumption of high frequency (see [18]) :

$$T = n\Delta \text{ is fixed, } \Delta \rightarrow 0 \text{ as } n \rightarrow \infty .$$

This result showed a weak increase in the number of individuals, especially for flowering plants. We observed that the variability of the stochastic fluctuations increased with time (Fig. 1).

We thus calculated the moments equations given as a system of ordinary differential equations, that represents the dynamics of the means, variances, and covariances of the system (5.1) (see [34], [35]). This system can replace the SDEs system and leads directly to solutions for the moments of the state variables [18]. We obtained the symbolic moments equations for our model (means (m_i), variances (S_i) and covariances (C_{ij})) using the R function *MEM.sde*, as the following system of ODEs:

$$\left\{ \begin{array}{l} \frac{d}{dt}m_1(t) = a_{13} m_3(t) \\ \frac{d}{dt}m_2(t) = a_{21} m_1(t) + a_{22} m_2(t) + a_{23} m_3(t) \\ \frac{d}{dt}m_3(t) = a_{31} m_1(t) + a_{32} m_2(t) + a_{33} m_3(t) \\ \frac{d}{dt}S_1(t) = 2 (a_{13} C_{13}(t)) + \sigma_1^2 (S_1(t) + m_1(t)^2) \\ \frac{d}{dt}S_2(t) = 2 (a_{21} C_{12}(t)) + 2 (a_{23} C_{23}(t)) + S_2(t) (2 a_{22} + \sigma_2^2) + \sigma_2^2 m_2(t)^2 \\ \frac{d}{dt}S_3(t) = 2 (a_{31} C_{13}(t)) + 2 (a_{32} C_{23}(t)) + S_3(t) (2 a_{33} + \sigma_3^2) + \sigma_3^2 m_3(t)^2 \\ \frac{d}{dt}C_{12}(t) = a_{13} C_{23}(t) + a_{21} S_1(t) + a_{23} C_{13}(t) + C_{12}(t) (a_{22} + \sigma_1 \sigma_2) + \sigma_1 \sigma_2 m_1(t) m_2(t) \\ \frac{d}{dt}C_{13}(t) = a_{13} S_3(t) + a_{31} S_1(t) + a_{32} C_{12}(t) + C_{13}(t) (a_{33} + \sigma_1 \sigma_3) + \sigma_1 \sigma_3 m_1(t) m_3(t) \\ \frac{d}{dt}C_{23}(t) = a_{21} C_{13}(t) + a_{23} S_3(t) + a_{31} C_{12}(t) + a_{32} S_2(t) + C_{23}(t) (a_{22} + a_{33} + \sigma_2 \sigma_3) \\ \quad + \sigma_2 \sigma_3 m_2(t) m_3(t) \end{array} \right. \quad (5.2)$$

The exact solutions of the obtained system (5.2) can be given explicitly. Here we were interested in the numerical approximation of the obtained moment equations at a fixed time t . The dynamic plots of the results (mean $m(t)$, variance $S(t)$ and covariances $C(t)$) are shown in Fig. (2). This result is in a good agreement with the result in Fig. (1), since the means curves increased slowly over the 100 years representing the weak positive tendency in population size, especially for flowering plants (green curve). The variances increased rapidly, particularly during the last years, which can be explained by the increased temporal fluctuations in the number of individuals. The highest covariance curve was observed between seedlings and rosettes (C_{12}), which can be interpreted as a positive relationship between the number of seedlings and the number of rosettes. This was not the case for the flowering plants, as the covariance curves with other stage classes did not show any important trend (see C_{13} and C_{23} in Fig. (2)).

5.2. Total population dynamics. The population dynamics analyses required the total number of individuals, which was obtained as the sum of the number of individuals per stage class. The resulting stochastic trajectories thus represent the random fluctuations of the total population size over 100 years (see Fig. (3)), which allowed us the calculation of the stochastic growth rate λ_s (see Section

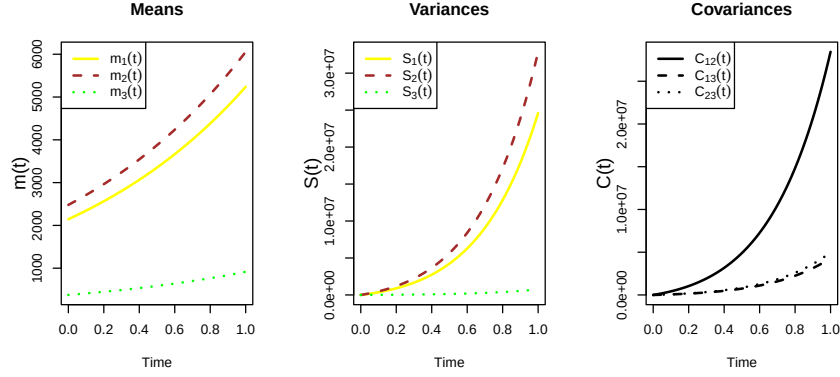


FIGURE 2. Numerical approximations of the moments equations of the system (5.2) with initial values $m_1 = 2145$, $m_2 = 2479$, $m_3 = 375$, $S_1 = 0$, $S_2 = 0$, $S_3 = 0$, $C_{12} = 0$, $C_{13} = 0$, $C_{23} = 0$. The time value $t = 1$ represents the ending time (100 years in our study).

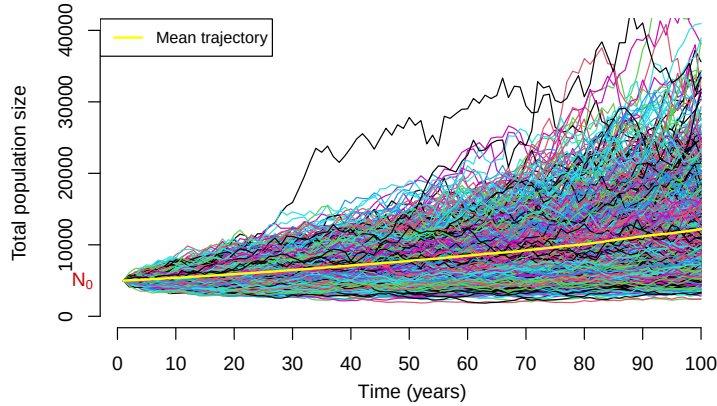


FIGURE 3. Stochastic fluctuations in total population size over 100 years, obtained by summing the number of individuals in each stage class in Fig. (1).

(3.3)). The simulations were realized using the same parameters as in the previous section.

For the studied populations, we obtained $\lambda_s = 1.007$ ranging from $\min = 0.989$ to $\max = 1.024$, (confidence interval's upper and lower bounds were too close to λ_s). This result explains the fact that the obtained trajectories of population size show a weak growth over years (see the mean trajectory in Fig. 3).

An essential issue in the dynamics analysis of such stochastic models is: How to measure the introduced diffusion coefficient? There are no easy solutions of this problem and the collaboration of population biologists is necessary. Indeed, in this work, we tested the influence of diffusion coefficients on the stochastic

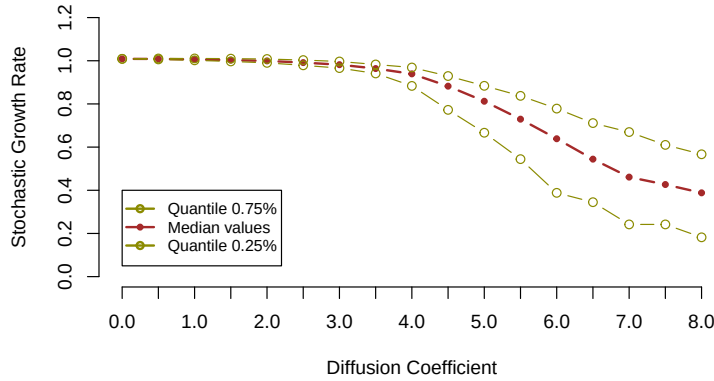


FIGURE 4. The obtained stochastic growth rates λ_s when increasing diffusion coefficients σ_i with their first quantile (0.25%) and third quantile (0.75%).

growth rate (see Fig. (4)). Not surprisingly, the stochastic growth rate was mainly influenced by the magnitude of the stochastic fluctuations, as it decreased as the diffusion coefficients σ_i increased. The decrease was more important for $\sigma_i \geq 4$ (see Fig. (4)). This result is in a good agreement with the previous works studying the dynamics of *C. corymbosa* populations, since the increase in environmental and demographic stochasticity increased extinction probabilities; which was due to low stochastic growth rates (see [19]).

To analyse the quasi-extinction of the populations, we set a threshold size N_Q of 500 individuals, corresponding to 10% of the initial population size (5000 individuals, sum of $N_0 = (2152, 2487, 377)$) which gives to $\theta = 0.10$. Using diffusion coefficients $\sigma_i = 0.8$, there were no trajectories that reached the threshold size. We assumed that stochasticity increases due to environmental changes, which can be explained by an increase in the diffusion coefficients σ_i in the model. In this case, by taking $\sigma_1 = \sigma_2 = \sigma_3 = 3$ and $\theta = 0.10$, the stochastic growth rate decreased to $\lambda_s = 0.980 < 1$, leading to decreasing trajectories. We obtained in Fig. 5 (left side) the distribution of quasi-extinction time, where the corresponding quantiles are given by $Q_1 = 14, Q_2 = 56, Q_3 = 76, Q_4 = 91$, and $Q_5 = 100$. This result shows that after 14 years, the trajectories begin to reach the threshold population size N_Q . However, 50% of the trajectories reached N_Q after 77 years, which represents the median value of the quasi-extinction time ($T_Q = 77$ years). This result implies that there is an even chance that the population will be reduced to 10% of the initial population size within 77 years.

The right side of the Fig. (5) shows an increase in the quasi-extinction probability over years, that does not reach $P_{Ext} = 0.45$. This result changes when the diffusion coefficients in the model are changed. Therefore, we have shown in Fig. (6) the quasi-extinction probability as a function of both time (years) and diffusion coefficient (σ_i varying from 0 to 8). Correspondingly with both Fig. (4) and Fig. (5), for lower values of the diffusion coefficients (which means

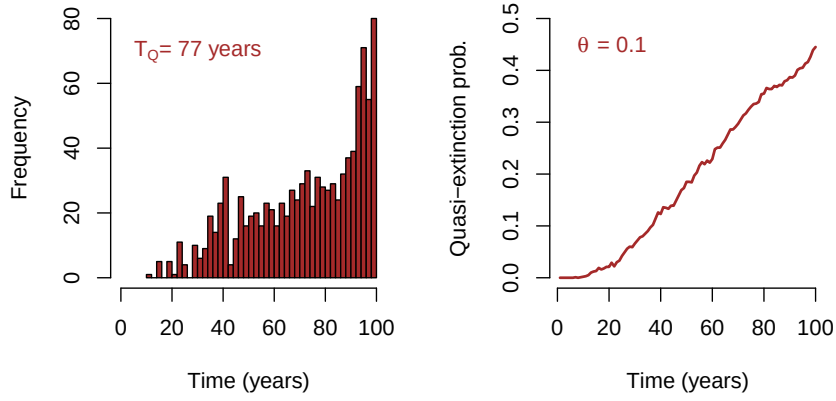


FIGURE 5. (Left) The distribution of the quasi-extinction time for *C. corymbosa* populations resulting from 1000 stochastic trajectories, with diffusion coefficients $\sigma_1 = \sigma_2 = \sigma_3 = 3$. T_Q represents the median value. (Right) the quasi-extinction probability over 100 years. The threshold used was $\theta = 0.10$ corresponding to a threshold size of 500 individuals.

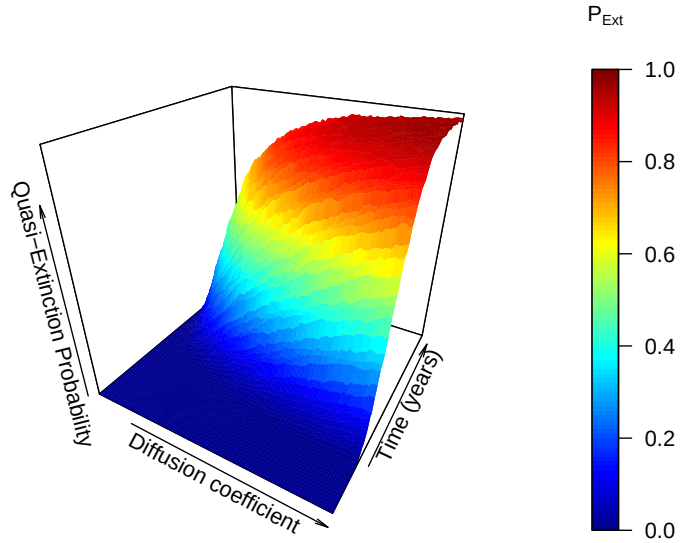


FIGURE 6. The quasi-extinction probability as a function of both time and the diffusion coefficients (σ_i from 0 to 8) with threshold $\theta = 0.10$.

a weak stochastic effect), the quasi-extinction risk does not increase over years. Also, during the first period of time (30 years), the quasi-extinction probability was close to zero (blue area, with $P_{Ext} < 0.2$), even for the highest values of the diffusion coefficients. This can be explained by the fact that the environmental stochasticity does not affect the population dynamics for the studied species in the short term. Thus, such biological systems could persist a certain period under a high level of stochasticity. However, this probability increased rapidly after a certain number of years, reaching its maximum values ($P_{Ext} \simeq 1$) at the ending time (100 years) and a diffusion coefficient $\sigma_i = 8$.

5.3. Biological implications. In this work, we aimed to simplify the use of theoretical principles such as SDEs in practical problems such as biological and ecological phenomena, particularly with real datasets. The proposed method has been accompanied with explicit details to be applied to a given population species using the open source software R-Studio, which contains different packages that allow us to realize an analysis, visualizations and simulations of the studied model. An interesting application of the present approach is to investigate a comparative stochastic study of several species. For that, the database COMPADRE can be useful since it contains the populations matrices of hundreds species ([8]). In our model, the initial parameters are not difficult to introduce, except for the diffusion coefficient, which requires a rigorous discussion. The initial population size was not important for the simulations rather than the stable stage distribution (noted w), this can be related with the notion of stability of the stochastic system. To reduce the error rate, the user should project a significant number of trajectories, for example for the studied species, taking 1000 trajectories were sufficient to obtain a reduced confidence interval for λ_s .

Furthermore, the present work can contribute to biological conservation management, since we have treated here the main indices of population performance (as mentioned in [6], (section 18.1)); in the case of environmental stochasticity the major indices concern the stochastic growth rate, the stochastic projections, the variance-covariance and the quasi-extinction probability. The long-term population dynamics depend on the obtained stochastic growth rate, since in the case of $\lambda_s < 1$ (resp. $\lambda_s > 1$), the population declines (resp. explodes), whereas in the case of $\lambda_s \simeq 1$ the population remains stable around the initial size. The projection of the number of individuals in each stage class reveals an important finding for biological populations analysis, which was not possible using the previous methods. This result makes it possible to visualize separately the long-term behavior of individuals in each stage class, and to analyze which one is the most influenced by environmental stochasticity.

The notion of the means, variances and covariances of the approximated solution at each life stage could also contribute significantly to conservation management. Indeed, the means curves illustrate the trend in the number of individuals at each life stage over years. More importantly, the variances and covariances curves allow us to understand how individuals from different stage classes are related under stochasticity. For example, in Fig. (2) the covariance between

seedlings and rosettes is extremely higher than the other covariances. This means that an increase in the number of seedlings leads to an increase in the number of rosettes, contrary to what we assume that an increase in flowering plants leads to an increase in seedling individuals (C_{13}). Therefore, for management strategies we should target the seedling stage rather than the flowering stage in order to maintain the population persistence.

The results presented in both Fig. (4) and Fig. (6) can be used to predict the magnitude of the changes in the population dynamics under the accelerated environmental change (eg. the climate change). For example, in Fig. (6), the populations can persist for at most 30 years, after which the quasi-extinction risk increases rapidly, requiring the introduction of a rigorous conservation policy.

6. CONCLUSION

In the present work, we introduced a new approach to treat the environmental stochasticity in stage-structured population models. Our proposed method was based on the combination of the SDEs theory with stochastic population dynamics. We discussed the existence and uniqueness of the solution of the obtained three-dimensional model. We were interested on numerical analyses, where the R-package Sim.DiffProc was used for dynamic analyses and simulations of the numerically approximated solution. All implemented numerical approaches in this package have a high degree of convergence. The population dynamics was projected over years under environmental stochasticity. Our simulations allowed us to calculate the stochastic growth rate and to study explicitly the quasi-extinction risk. The proposed method was applied to a real dataset of a plant species, and the results obtained were biologically relevant. Our approach can be an alternative way to the existing methods, in particular, it becomes more interesting for populations structured with small projection step, for example bacterial species.

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REFERENCES

1. Allen, E. (2007). Modeling with Itô Stochastic Differential Equations. volume 22 of Mathematical Modelling: Theory and Applications. 1st edition. Springer-Verlag.
2. Arató, M. (2003). A Famous Nonlinear Stochastic Equation (Lotka-Volterra Model with Diffusion). Mathematical and Computer Modelling, 38, 709-726. [https://doi.org/10.1016/S0895-7177\(03\)90056-2](https://doi.org/10.1016/S0895-7177(03)90056-2).
3. Arnold, L. (1974). Stochastic Differential Equations : Theory and Applications. John Wiley and Sons, Montreal, Canada.
4. Brouste, A., Fukasawa, M., Hino, H., Iacus, S. M., Kamatani, K., Koike, Y., Masuda, H., Nomura, R., Ogihara, T., Shimuzu, Y. & al. (2014). The **yuima** Project: A Computational Framework for Simulation and Inference of Stochastic Differential Equations. Journal of Statistical Software, 57(4), 1-51. <https://doi.org/10.18637/jss.v057.i04>
5. Burrage, K., Burrage, P., Higham, D. J., Kloeden, P. E. & Platen, E. (2006). Comment on "Numerical Methods for Stochastic Differential Equations". Physical Review E., 74, 068701. <https://doi.org/10.1103/physreve.74.068701>

6. Caswell, I. H. (2001). *Matrix Population Models: Construction, Analysis, and Interpretation*. 2nd edition. Sinauer Associates Inc., U.S., Sunderland, Mass.
7. Caswell, H. (2019) *Sensitivity Analysis: Matrix Methods in Demography and Ecology*. Springer International Publishing. Amsterdam, The Netherlands. <https://doi.org/10.1007/978-3-030-10534-1>
8. COMPADRE plant matrix database. <https://compadre-db.org/Species/46616>, Accessed: 10/12/2024.
9. Crone, E.E., Menges, E.S., Ellis, M.M., Bell, T., Bierzychudek, P., Ehrlén, J., Kaye, T.N., Knight, T.M., Lesica, P., Morris, W.F., & al., (2011). How do plant ecologists use matrix population models? *Ecol. Lett.* 14, 1–8. <https://doi.org/10.1111/j.1461-0248.2010.01540.x>
10. Crone, E. E., Ellis, M. M., Morris, W. F., Stanley, A., Bell, T., Bierzychudek, P., Ehrlén, J., Kaye, T.N., Knight, T.M., Lesica, P., & al., (2013). Ability of matrix models to explain the past and predict the future of plant populations. *Conserv. Biol.* 27, 968–978. <https://doi.org/10.1111/cobi.12049>
11. Dennis, B., Munholland, P. L. & Scott, J. M. (1991). Estimation of Growth and Extinction Parameters for Endangered Species. *Ecological Monographs*, 61(2), 115–143. <https://doi.org/10.2307/1943004>
12. Driver, C. C., Oud, J. H. L. & Voelkle, M. C. (2017). Continuous Time Structural Equation Modeling with R Package **ctsem**. *Journal of Statistical Software*, 77(5). <https://doi.org/10.18637/jss.v077.i05>
13. Engen, S., Bakke, Ø. & Islam, A., (1998). Demographic and environmental stochasticity concepts and definitions. *Biometrics*, 54, 840–846. <https://doi.org/10.2307/2533838>
14. Faye, I., Diouf, M. & BocarBa, D. (2024). Stochastic fractional integro-differential equations with jumps: Application on a averaging principle. *Gulf Journal of Mathematics*, 17(2), 51–72. <https://doi.org/10.56947/gjom.v17i2.2067>
15. Fima, C. K. (2012). *Introduction to Stochastic Calculus with Applications*. Third edition. London: Imperial College Press. <https://doi.org/10.1142/p821>
16. Floris, C. (2019) On the Effects of Different Interpretations of Stochastic Differential Equations. *Applied Mathematics*, 10, 876–891. <https://doi.org/10.4236/am.2019.1011063>
17. Fuchs, C. (2013). *Inference for Diffusion Processes: With Applications in Life Sciences*. Springer-Verlag.
18. Guidoum, A. C. & Boukhetala, K., (2020) . Performing Parallel Monte Carlo and Moment Equations Methods for Itô and Stratonovich Stochastic Differential Systems: R Package Sim.DiffProc. *Journal of statistical software*, 96, 2. <https://doi.org/10.18637/jss.v096.i02>
19. Hadjou Belaid, A., Maurice, S., Fréville, H., Carbonell, D. & Imbert, E. (2018). Predicting population viability of the narrow endemic Mediterranean plant *Centaurea corymbosa* under climate change. *Biological Conservation*, 19–33. <https://doi.org/10.1016/j.biocon.2018.04.019>
20. Han, X. & Kloeden, P. E. (2017). Random ordinary differential equations and their numerical solution. Volume 85 of *Probability Theory and Stochastic Modelling*. Springer-Verlag. <https://doi.org/10.1007/978-981-10-6265-0>
21. Iacus, S. M. (2008). *Simulation and Inference for Stochastic Differential Equations, With R Examples*. 2nd edition. Springer-Verlag New York. <https://doi.org/10.1007/978-0-387-75839-8>
22. Kaye, T. N. & Pyke, D. A. (2003). The effect of stochastic technique on estimates of population viability from transition matrix models. *Ecology* 84, 1464–1476. <https://doi.org/10.1890/0012-9658>
23. Kloeden, P. E., Platen, E. & Schurz, H. (2003). *Numerical Solution of SDE Through Computer Experiments*. Universitext, 3rd edition. Springer-Verlag.

24. Lande, R. & Orzack, S. H. (1988). Extinction dynamics of age-structured populations in a fluctuating environment. *Proc. Natl. Acad. Sci. USA*, 85, 7418-7421. <https://doi.org/10.1073/pnas.85.19.7418>
25. Lande, R. (1993). Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *Am. Nat.* 142(6), 911–927. <https://doi.org/10.1086/285580>
26. Lundquist, K. (2011). A comparative study of stochastic and deterministic population models. *Biology, Mathematics course*. <https://api.semanticscholar.org/CorpusID:41230682>
27. Lurding, A. (1974). *Stochastic Differential Equations : Theory and Application*. 2nd edition. New York: John Wiley and Sons,.
28. Mao, X. (2007). *stochastic differential equations and applications*. 2nd edition. Woodhead Publishing Limited, UK.
29. Melbourne, B. A. & Hastings, A. (2008). Extinction risk depends strongly on factors contributing to stochasticity. *Nature* 454(7200), 100–103. <https://doi.org/10.1038/nature06922>
30. Moujahid, A. & Vadillo, F. (2021) A Comparison of Deterministic and Stochastic Susceptible-Infected-Susceptible (SIS) and Susceptible-Infected-Recovered (SIR) Models . *Open Journal of Modelling and Simulation*, 9, 246-258. <https://doi.org/10.4236/ojmsi.2021.93016>
31. Naciri, T. & Aminataet, A. (2014). On the numerical solution of fractional-order fredholm-volterra integro-differential and multi-fractional order integro-differential equations. *Gulf Journal of Mathematics*, 2(4), 14-31. <https://doi.org/10.56947/gjom.v2i4.204>
32. Panik, M. J. (2017). *Stochastic Differential Equations. An Introduction with Applications in Population Dynamics Modeling*. 1st edition. John Wiley and Sons, Inc., West Hartford, CT, USA.
33. Radzi, N. A. M., Haliza, A. R., Syed, J. S. S. & Arifah B. (2022). Exponential Growth Model and Stochastic Population Models: A Comparison via Population Data. *Malaysian Journal of Fundamental and Applied Sciences*, 18 (1) , 60-69. <https://doi.org/10.11113/mjfas.v18n1.2402>
34. Rodriguez, R. & Tuckwell, H. C. (1996). Statistical Properties of Stochastic Nonlinear Dynamical Models of Single Spiking Neurons and Neural Networks. *Physical Review E*, 54, 5585–5590. <https://doi.org/10.1103/physreve.54.5585>
35. Rodriguez, R. & Tuckwell, H. C. (2000). A Dynamical System for the Approximate Moments of Nonlinear Stochastic Models of Spiking Neurons and Networks. *Mathematical and Computer Modelling*, 31(4–5), 175–180. [https://doi.org/10.1016/s0895-7177\(00\)00036-4](https://doi.org/10.1016/s0895-7177(00)00036-4)
36. Shryock, D. F. , Esque, T. C. & Lee Hughes, (2014). Population viability of *Pediocactus bradyi* (Cactaceae) in a changing climate. *American Journal of Botany*. 101(11), 1944–1953. <https://doi.org/10.3732/ajb.1400035>
37. Tomé, T. & de Oliveira, M. J. (2023). Stochastic Approach to Population Dynamics. *Braz J Phys* 53, 43. <https://doi.org/10.1007/s13538-022-01254-w>
38. Tuljapurkar, S. D. (1989). An uncertain life: demography in random environments. *Theoretical Population Biology* 35(3) 227-294. [https://doi.org/10.1016/0040-5809\(89\)90001-4](https://doi.org/10.1016/0040-5809(89)90001-4)
39. Wang, Z., (2013). *cts*: An R Package for Continuous Time Autoregressive Models via Kalman Filter.” *Journal of Statistical Software*, 53(5), 1-19. <https://doi.org/10.18637/jss.v053.i05>

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