Stochastic Modified Lotka-Volterra Competition Model with N Interacting Species

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Abstract—**In this paper, based upon the Gompertz model of population growth, we have reformulated the stochastic Lotka-Volterra Competition model with N interacting species. By means of Ito's lemma and some simple changes of variables, we have succeeded in deriving the N-dimensional joint probability density function of the stochastic modified multi-species Lotka-Volterra model in closed form. With this joint probability density function, an analytical likelihood function can be constructed readily, and thus model-fitting procedures become feasible and efficient.**

Keywords: Lotka-Volterra Competition, Gompertz growth model, Fokker-Planck equation, joint probablity density function

1 Introduction

Competition is by all means ubiquitous in the natural world. Whenever there is a limited supply of common resources, organisms of the same or different species inevitably need to compete for the limited resources. For instance, plants often compete for access to a limited supply of nutrients, water, sunlight and space, whilst animals compete for food, water and space to live. Intraspecific competition occurs when individuals of the same species vie for access to essential resources, and becomes intense whenever populations of a species are crowded. On the other hand, interspecific competition plays a prominent role if individuals of different species are crowded and have similar requirements of resources. Mathematical models have been proposed to study ecological competition which affects the community structure in an ecosystem and places evolutionary pressure on the development of adaptations in a population. One particular model, which has been studied extensively because of its theoretical and practical significance, is the classical Lotka-Volterra Competition (LVC) model with N interacting species $[1, 2]$:

$$\frac{dx_i}{dt} = x_i \left\{ b_i - \sum_{j=1}^{N} a_{ij} x_j \right\} \tag{1}$$

for $i = 1, 2, 3, ..., N$, where x_i and b_i denote the population size and intrinsic growth rate of the i-th species at time t, respectively. Here a_{ii} is the intraspecific competition rate of the i-th species, and a_{ij} is the interspecific competition rate between the i-th and j-th species. It should be noted that all model parameters are positive definite.

Since population systems are naturally subject to environmental noises, a better model is needed to reflect the external randomness that affects the dynamical behaviour of the system. The simplest stochastic version can be derived via assuming that the variability of environmental conditions induces fluctuations in the intrinsic growth rate b_i of the i-th species. By assuming that the intrinsic growth rate varies in time according to [3]

$$\theta_i (t) = b_i + \sigma_i \varepsilon (t) \tag{2}$$

for $i = 1, 2, 3, ..., N$, where b_i is the constant mean value of $\theta_i (t)$, σ_i is the diffusion coefficient, and $\varepsilon (t)$ is a Gaussian white noise process, the stochastic LVC model is defined by the system of stochastic differential equations (s.d.e.'s):

$$dx_i = x_i \left\{ b_i - \sum_{j=1}^{N} a_{ij} x_j \right\} dt + \sigma_i x_i dW_i \tag{3}$$

for $i = 1, 2, 3, ..., N$, where dW_i denotes the standard Wiener process. Unfortunately, the stochastic LVC model does not have an analytical N-dimensional joint probability density function (p.d.f.), so details of the dynamical behaviour of the system needs to be uncovered in an indirect manner $[3 - 8]$. In the absence of an analytical likelihood function, the only methods available to fit the model to data are thus simulation based, *i.e.* the LVC model has to generate simulated data for each proposed set of parameters in order to calculate any measure of fit. As a result, model-fitting procedures are extremely slow, and a thorough investigation of model-fitting procedures, recoverability and identifiability of the LVC model has not been performed for multi-species cases. Accordingly, it is the aim of this communication to propose a new reformulation of the LVC model such that the N-dimensional joint p.d.f. can be derived in closed form readily.

*Manuscript received January 18, 2023; revised April 22, 2023.

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2 Modified LVC model

First of all, by taking a closer look at the classical LVC model, one can easily realize that it is a simple extension of the logistic growth model for N interacting species [1, 2]. When the N species are growing independently and only intraspecific competition is present, their population growth is governed by the first-order differential equaton defining the logistic growth model:

$$\frac{dx_i}{dt} = x_i \{b_i - a_{ii} x_i\} \tag{4}$$

for $i = 1, 2, 3, ..., N$. It is well known that the Gompertz model is an alternative popular approach of modelling population growth and can be derived from Eq.(4) via simply substituting the term $a_{ii}x_i$ by $a_{ii} \ln x_i$ [9, 12]. By including the interspecific competition in a similar manner, the classical LVC model can be reformulated as follows:

$$\frac{dx_i}{dt} = x_i \left\{ b_i - \sum_{j=1}^{N} a_{ij} \ln x_j \right\} \tag{5}$$

for $i = 1, 2, 3, ..., N$.

Next, in order to account for the impact of environmental noises on the dynamical behaviour of the system, we may derive a stochastic version of the modified LVC model by assuming that the environmental noises induce fluctuations in the intrinsic growth rate b_i of the i-th species in accordance with Eq.(2). The stochastic modified LVC model is then defined by

$$dx_i = x_i \left\{ b_i - \sum_{j=1}^{N} a_{ij} \ln x_j \right\} dt + \sigma_i x_i dW_i \tag{6}$$

for $i = 1, 2, 3, ..., N$, where dW_i denotes the standard Wiener process. For simplicity, it is reasonable to assume that $\sigma_i = \xi$, $a_{ii} = \kappa$ and $a_{ij} = \beta$ for $i \neq j$, where κ and β represent the common intraspecific and interspecific competition rates, respectively. Accordingly, Eq.(6) can be rewritten as

$$\frac{dx_i}{x_i} = \left\{ b_i - \kappa \ln x_i - \beta \sum_{j \neq i}^{N} \ln x_j \right\} dt + \xi dW_i \ . \tag{7}$$

Beyond question, the number of model parameters is dramatically reduced while most of the basic features of the system are being retained.

In the following section we demonstrate how to derive the closed-form N-dimensional joint p.d.f. of the stochastic modified LVC model, which in turn enables us to construct an analytical likelihood function for model-fitting.

3 Probability density function

Prior to deriving the joint p.d.f. $P(\{x_i\}, t)$ associated with the stochastic variables $\{x_1, x_2, x_3, \ldots, x_N\}$, we first apply multi-dimensional Ito's lemma (see Appendix A; [13]) to express Eq.(7) in terms of the new stochastic variables $\{y_i = \ln x_i\}$ as

$$dy_i = \left\{ I_i - (\kappa - \beta) y_i - \beta \sum_{j=1}^{N} y_j \right\} dt + \xi dW_i \ , \tag{8}$$

where $I_i = b_i - \frac{1}{2}\xi^2$. It should be noted that the logarithm of population size of each species can assume any real values and follow the Ornstein-Uhlenbeck (OU) process in the absence of interspecific competition, *i.e.* $\beta = 0$. Then, by means of the change of variables:

$$z_i = y_i e^{(\kappa-\beta)t} + \eta_i(t) \ , \tag{9}$$

where

$$\eta_i(t) = \frac{\beta \left(\sum_{j=1}^{N} I_j \right)}{\kappa + \beta (N-1)} \left\{ \frac{e^{(\kappa-\beta)t} - 1}{\kappa - \beta} - \frac{1 - e^{-\beta N t}}{\beta N} \right\} - I_i \left\{ \frac{e^{(\kappa-\beta)t} - 1}{\kappa - \beta} \right\} , \tag{10}$$

Eq.(8) is reduced to

$$dz_i = -\beta N \bar{z} dt + \xi e^{(\kappa-\beta)t} dW_i \ , \tag{11}$$

where $\bar{z}$ is simply the mean of the stochastic variables $\{z_1, z_2, z_3, \ldots, z_N\}$:

$$\bar{z} = \frac{1}{N} \sum_{i=1}^{N} z_i \ , \tag{12}$$

in accordance with multi-dimensional Ito's lemma (see Appendix A; [13]). Obviously, every member of the set of s.d.e.'s in Eq.(11) has the same drift, *i.e.* $-\beta N \bar{z}$, and diffusion coefficient, *i.e.* $\xi e^{(\kappa-\beta)t}$, implying that the stochastic variables $\{z_1, z_2, z_3, \ldots, z_N\}$ are statistically-independent and are all distributed in the same way.

The joint p.d.f. $P(\{z_i\}, t)$ associated with the stochastic variables $\{z_1, z_2, z_3, \ldots, z_N\}$ can be derived by solving the associated multi-dimensional Fokker-Planck equation:

$$\sum_{i=1}^{N} \frac{\partial}{\partial z_i} \left\{ \left(\frac{1}{2} \xi^2 e^{2(\kappa-\beta)t} \frac{\partial}{\partial z_i} + \beta \sum_{j=i}^{N} z_j \right) P(\{z_i\}, t) \right\} = \frac{\partial P(\{z_i\}, t)}{\partial t} \ . \tag{13}$$

By a simple change of variables:

$$\mathcal{Z}_N = \frac{1}{N} \sum_{j=i}^{N} z_j \quad \text{and} \quad \mathcal{Z}_i = z_i - \frac{1}{N} \sum_{j=i}^{N} z_j \tag{14}$$

for $i = 1, 2, 3, ..., N-1$, Eq.(13) can be re-written as

$$\frac{\partial}{\partial \mathcal{Z}_N} \left\{ \left(\frac{1}{2N} \xi^2 e^{2(\kappa-\beta)t} \frac{\partial}{\partial \mathcal{Z}_N} + \beta N \mathcal{Z}_N \right) P(\{\mathcal{Z}_i\}, t) \right\} + \sum_{i=1}^{N-1} \sum_{i=1}^{N-1} \frac{1}{2} \xi^2 e^{2(\kappa-\beta)t} \left(\delta_{ij} - \frac{1}{N} \right) \frac{\partial^2 P(\{\mathcal{Z}_i\}, t)}{\partial \mathcal{Z}_i \partial \mathcal{Z}_j} = \frac{\partial P(\{\mathcal{Z}_i\}, t)}{\partial t} \ . \tag{15}$$

It is not difficult to show that the stochastic variables $\{\mathcal{Z}_1, \mathcal{Z}_2, \mathcal{Z}_3, \ldots, \mathcal{Z}_N\}$ satisfy the set of s.d.e.'s:

$$d\mathcal{Z}_N = -\beta N \mathcal{Z}_N dt + \frac{\xi}{\sqrt{N}} e^{(\kappa-\beta)t} d\mathcal{W}_N \tag{16}$$

$$d\mathcal{Z}_i = \sqrt{1-\frac{1}{N}}\xi e^{(\kappa-\beta)t} d\mathcal{W}_i \tag{17}$$

for $i = 1, 2, 3, ..., N-1$, where the two distinct Wiener processes $d\mathcal{W}_i$ and $d\mathcal{W}_j$ are correlated as

$$d\mathcal{W}_i d\mathcal{W}_j = \rho_{ij} dt = -\frac{1}{N-1} dt \tag{18}$$

for $i \neq j$. Obviously, the stochastic variable $\mathcal{Z}_N$ follows an OU process with a time-dependent varaince and a long-term mean equal to zero, whilst the remaining $N-1$ stochastic variables are described by a $(N-1)$-dimensional normal process with a time-varying covariance matrix. The corresponding closed-form joint p.d.f. is then given by

$$\begin{aligned} & P\left(\{\mathcal{Z}_i\}, t\right) \\ = & \frac{1}{\sqrt{(4\pi)^{N-1}\det\left(\mathbf{\Omega}\right)}} \times \\ & \exp\left\{-\frac{1}{4}\sum_{i,j=1}^{N-1}\left(\mathcal{Z}_i - \mathcal{Z}_{i0}\right)\left(\mathbf{\Omega}^{-1}\right)_{ij}\left(\mathcal{Z}_j - \mathcal{Z}_{j0}\right)\right\} \times \\ & \frac{e^{\beta N t}}{\sqrt{2\pi\Delta(t)}} \exp\left\{-\frac{\left(e^{\beta N t}\mathcal{Z}_N - \mathcal{Z}_{N0}\right)}{2\Delta(t)}\right\} \end{aligned} \tag{19}$$

where

$$\Delta(t) = \frac{\xi^2}{N}\left\{\frac{e^{2[\kappa+(N-1)\beta]t}-1}{2\left[\kappa+(N-1)\beta\right]}\right\} . \tag{20}$$

Here the $(N-1)\times(N-1)$ matrix $\mathbf{\Omega}(t)$ is defined by its elements as follows:

$$\Omega_{ij}(t) = \frac{\xi^2}{2}\left[\frac{e^{2(\kappa-\beta)t}-1}{2(\kappa-\beta)}\right]\left(\delta_{ij} - \frac{1}{N}\right) , \tag{21}$$

and $\mathbf{\Omega}^{-1}(t)$ is its inverse.

4 Discussion and conclusion

The Monte Carlo method based upon the strong order 1.5 Taylor scheme [14] is employed to generate the time series of the stochastic modified LVC model. With the closed-form joint p.d.f., maximum-likelihood analyses are then applied to calibrate the model parameters and check whether the actual values can be recovered. In Table 1 the input model parameters and the calibrated values (based upon 100 simulated time series) are presented for the case of two species. The corresponding standard errors and z-scores of the calibrated values are tabulated, too. It is evident that the calibrated values are in excellent agreement with the exact values. Table 2 presents the same set of informations for the case of three species, and the same conclusion is reached. Hence, the calibration of parameters is both efficient and accurate. Furthermore, the calibration is carried out using a 4.7GHz Intel Core i7-10700K PC, and the average elapsed time for the maximum-likelihood estimation per time series for the two illustrative cases is less than a second. In fact, the calibration can be completed within a minute even for a large number of species.

Table 1: Calibrated results for the case of two species

	κ	β	I_1	I_2	ξ
exact value	4	1	0.9	1.1	0.25
calibrated value	4.02	1.00	0.904	1.11	0.254
standard error	0.10	0.11	0.03	0.03	0.00045
z-score	39.9	10.0	26.45	32.3	560

Table 2: Calibrated results for the case of three species

	κ	β	I_1	I_2	I_3	ξ
exact value	4	1	0.9	1.1	0.98	0.25
calibrated value	4.02	1.00	0.904	1.11	0.987	0.254
standard error	0.12	0.09	0.025	0.025	0.025	0.0003
z-score	68.8	11.5	35.7	43.7	39.0	679

In conclusion we have reformulated the stochastic LVC model by simply replacing the competition term $-\sum_{j=1}^{N} a_{ij}x_j$ in Eq.(3) by $-\sum_{j=1}^{N} a_{ij}\ln x_j$ as shown in Eq.(6). In other words, whilst the classical LVC model is a simple extension of the logistic growth model for N interacting species, the modified LVC model is derived from the Gompertz model of population growth. By means of Ito's lemma and some simple changes of variables, we have succeeded in deriving the N-dimensional joint p.d.f. of the stochastic modified LVC model in closed form. With the joint p.d.f., an analytical likelihood function can be constructed readily, and thus model-fitting procedures become feasible and efficient. In addition, we have demonstrated that the calibration of model parameters based upon the Monte Carlo simulated time series is indeed both efficient and accurate.

Acknowledgement

The author would like to thank Mr. Ian Ho-Yan Ip for his help in performing the calibration analyses.

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