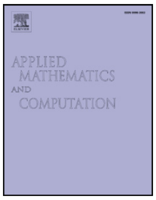
Applied Mathematics and Computation 320 (2018) 371–379

Contents lists available at ScienceDirect

Applied Mathematics and Computation

journal homepage: www.elsevier.com/locate/amc



Predicting population extinction from early observations of the Lotka–Volterra system

Alex Skvortsov[a,*], Branko Ristic[b], Alex Kamenev[c]

[a] Maritime Division, Defence Science and Technology, Melbourne, Australia
[b] School of Engineering, RMIT University, Melbourne, Australia
[c] William I. Fine Theoretical Physics Institute and School of Physics and Astronomy, University of Minnesota, Minneapolis, USA

ARTICLE INFO

Keywords:
Population biology
Lotka–Volterra system
Bayesian estimation

ABSTRACT

Population extinction is one of the central themes in population biology. We propose a statistical algorithm for long-term prediction of an extinction event in the paradigmatic predator–prey model. The algorithm is based on noisy and sporadic observations of the Lotka–Volterra (LV) system at the early stages of its evolution, when the system is still very far from extinction. There are two stages in the algorithm: first, the unknown parameters (reaction rates) of the LV system are estimated using the Approximate Bayesian Computation method; then an analytical expression for the time-scale of extinction (which involves the estimated parameters) is applied to compute the probability density function of extinction time. The proposed algorithm is validated by numerical simulations for the case of a stochastic LV system specified by the birth–death rate equations. The algorithm can be seen as an initial step in the quest for long-term prediction of rare “catastrophic” events in complex stochastic dynamic systems (epidemics, host-parasite dynamics, enzyme kinetics, dynamic trading, etc.).

1. Introduction

The process of population extinction is governed by many unpredictable factors that include environmental and demographic variability (food availability, diseases, genetic diversity, etc.) [1–6]. Understanding this process and estimation of the expected time to extinction is important not only for preserving biodiversity and for planning responsible consumption of natural resources [7,8], but also for predicting abrupt changes (catastrophic events) in biological and social systems driven by random fluctuations (virus mutations, transcriptional bursting in gene regulations, host-parasite convolution, stock-exchange trading, etc.), see [9–11] and references therein. The phenomenology of population extinction is one of the central themes in population biology and there is a vast body of literature on this subject (see [1,6,12–15], and references therein). It has been well-recognized that population extinction is an inherently stochastic event, therefore the analytical models of this phenomenon heavily engage the theory of stochastic processes [6,13,15]. In fact, these models describe the population growth as a random process, for which randomness is caused by either environmental factors (i.e. climate change, water quality) or by demographic stochasticity (finite number of individuals in population, variability of individual parameters across the population) [5,16–19]. From this perspective the event of extinction occurs when the fluctuating population crosses a given

---

[*] Corresponding author.
E-mail address: alex.skvortsov@dsto.defence.gov.au (A. Skvortsov).

https://doi.org/10.1016/j.amc.2017.09.029

threshold. Mathematically, the time of extinction may be viewed as the first passage time for the random process to cross the threshold.

In the present study, we consider only the demographic stochasticity (noise induced by finite population size). In other words, we assume that there are no ‘deterministic’ trends that drive population toward extinction, so the very existence of an extinction event is entirely caused by demographic noise. Obviously this extinction does not occur (and therefore cannot be accurately predicted) in pure deterministic limit (i.e. in the limit of infinity large population).

For the case of a single species population, the stochastic properties of the extinction time have been studied in a number of publications [5,12,15–19]. They observed that in a large class of models the population size undergoes diffusion motion, leading to the *Inverse Gaussian distribution* of extinction times [5,18]. In line with the above comments, the Inverse Gaussian (IG) distribution is well known in the context of the first-passage statistics of stochastic processes [20].

For the case of structured populations, consisting of multiple interactive groups, the statistical estimation of extinction time becomes much more challenging. This is due to the strong temporal correlations between population in the groups which may drive a complex and versatile set of extinction scenarios [1,13]. Prediction of the statistic properties of extinction time is such settings is a difficult analytical task and to the best of our knowledge the IG model has never been proposed and validated in this context (and it is intuitively unclear why the IG model is relevant to these settings).

Close to extinction the system exhibits strong fluctuations and becomes analytically intractable. The conventional approach to overcome this difficulty is to invoke simplifying assumptions (e.g., moments closure scheme [16,17]). These assumptions can lead to a tractable problem, but often have a limited validity (for comments on the inconsistency of the moment closure approach see [21]) or impose a significant constraint on model parameters (e.g., diffusion approximation is valid only for large population sizes [21]). For any model of interacting species with demographic stochasticity the extinction time (and its statistical moments) depends on the initial population size and satisfies the backward Kolmogorov differential equation [22], which is a linear partial differential equation with variable coefficients. Unfortunately, finding a parametric analytical solution of this equation poses severe technical challenge, and without such a solution a path for the development of any predictive algorithm for population extinction is unclear. A novel approach to predict the extinction event was reported in recent studies (see [13] for a review), which demonstrated that the long-time phenomenology of population extinction can be described by methods borrowed from theoretical physics [23–26] and their applications to predator–prey dynamics [15,27–30]. In particular, according to Refs. [29,30] the statistics of extinction time in the stochastic version of the Lotka–Volterra (LV) predator–prey model still follows a well defined statistical distribution with the parameters that can be related to the parameters of the underlying population model. It was also found [6,15] that in such Lotka–Volterra systems the mean extinction time is proportional to the system size (although the probability distribution for the extinction times has not been given).

The present study builds on this analytic progress to develop and validate a practical algorithm to forecast extinction events in a simplified model of stochastic population dynamics driven by strong demographic noise. Given noisy and sporadic observations of the predator–prey dynamics, collected at the early stages of its evolution (when it is far from extinction), we predict the long-time probability distribution of extinction events. The idea is to use the early-time observations to estimate the unknown LV system parameters via a Bayesian Monte Carlo method. These parameters along with the analytical results are then used to find the probability density function of population extinction time.

2. Model of population extinction

Our conceptual model of structured and interacting populations is based on the conventional LV predator–prey model. This model forms the backbone to simulate complex processes of population dynamics [31,32]. In the context of the present study our rationale resides on its ability to describe oscillating dynamics of species population (even in a deterministic limit) which being affected by the stochastic demographic fluctuations can potentially obscure any long-term trends leading to extinction. This environment creates a challenging setting for the evaluation of any prediction algorithm [33].

The dynamics of the LV system can be summarized by the three reactions (birth–death processes) [21,31]:

$$Q_1 \overset{\sigma}{\to} 0, \quad Q_2 \overset{\mu}{\to} 2Q_2, \quad Q_1 + Q_2 \overset{\lambda}{\to} 2Q_1, \tag{1}$$

where Q_1 represents the predator and Q_2 is the prey population. The prey species reproduces at the rate μ and the predators die at the rate σ. The third reaction states that the predator consumes a prey at the rate λ in order to reproduce.

In the mean-field approximation, the two populations are taken to be continuous and the system's evolution is governed by deterministic differential equations. If q_1 signifies the predator population and q_2 signifies the prey population, the equations are [21]

$$\dot{q_1} = -\sigma q_1 + \lambda q_1 q_2, \tag{2}$$

$$\dot{q_2} = \mu q_2 - \lambda q_1 q_2. \tag{3}$$

Following the conventional approach [26,29,30,33] we study the LV system for which the λ coefficient, in the nonlinear (interacting) term, is the same in both (2) and (3) equations. This allows to employ the analytical framework developed in Refs. [29,30].