

How Long Can an Ecological Model Predict?



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Abstract

Prediction of ecological phenomenon needs three components: a theoretical (or numerical) model based on the natural laws (physical, chemical, or biological), a sampling set of the reality, and a tolerance level. Comparison between the predicted and sampled values leads to the estimation of model error. In the error phase space, the prediction error is treated as a point; and the tolerance level (a prediction parameter) determines a tolerance ellipsoid. The prediction continues until the time when the error first exceeding the tolerance level (i.e., the error point first crossing the tolerance-ellipsoid). This time is called the first-passage time. Well-established theoretical framework such as the backward Fokker-Planck equation can be used to estimate the first-passage time-an up-time limit for any model prediction. A population dynamical system is used as an example to illustrate the concept and methodology and the dependence of the first-passage time on the model and prediction parameters.

Keywords: First passage time; Ecological model predictability; Tolerance level; Stochastic forcing; Backward fokker planck equations

Introduction

Most fascinating in ecological systems is their complexity. Not only do ecological communities harbor a multitude of different species, even the interaction of just two individuals can be amazingly complex. For understanding ecological dynamics, this complexity poses a considerable challenge. In conventional mathematical models, the dynamics of a system of interacting species with considering the effect of omnivore on a small food web are described by a specific set of ordinary differential equations [1],

$$\frac{dx^{(1)}}{dt} = S(x^{(1)}) - D(x^{(1)}) - F(x^{(1)}, x^{(2)}) - G(x^{(1)}, x^{(2)}, x^{(3)}) \quad (1)$$

$$\frac{dx^{(2)}}{dt} = \gamma F(x^{(1)}, x^{(2)}) - H(x^{(1)}, x^{(2)}, x^{(3)}) - M(x^{(2)}) \quad (2)$$

$$\frac{dx^{(3)}}{dt} = K(x^{(1)}, x^{(2)}, x^{(3)}) - M(x^{(3)}) \quad (3)$$

Here, $[x^{(1)}, x^{(2)}, x^{(3)}]$ are the densities of prey, predator, and intraguild predator (i.e., top predator). S is the intrinsic gain by reproduction of the prey. F is the interaction between the predator and prey. G and H denote the loss of the resource and consumer from predation by the omnivore. K represents the gain of the omnivore that arises from this predation. $[D, M, M]$ are the mortality, and γ is a constant conversion efficiency. Usually, $S, F, G, H,$ and K are nonlinear functions. Equations (1) - (3) are treated as generalized ecological population model with revealing conditions for the stability of steady states in large classes of systems, identifying the bifurcations in which stability is lost, and providing some insights into the global dynamics of the system [1]. They can be seen as an intermediate approach that has many advantages of conventional equation-based models, while coming close to the efficiency of random matrix models.

It is widely recognized that the uncertainty in the generalized ecological population model (1) - (3) can be traced to three factors:

- A. Observational errors [2],
- B. Model errors such as uncertain model parameters [3-5], and

C. Chaotic dynamics [6-8]. Observational errors cause uncertainty in initial conditions. Discretization causes truncation errors. The chaotic dynamics caused by nonlinearity may trigger a subsequent amplification of small errors through a complex response.

A question arises: How long is the generalized ecological population model (1) - (3) valid since being integrated from its initial state? This has great practical significance. For example, if the model validity time shorter than the biological cycle, the model doesn't have any capability to predict the biological cycle. In this paper, the first-passage time (FPT) is proposed to investigate ecological model predictability.

First passage time

The ecological model (1) - (3) can be generalized by a dynamical system. The state variables are usually defined by $\mathbf{x}(t) = [x^{(1)}(t), x^{(2)}(t), x^{(3)}(t)]$, a point in a three-dimensional phase space. Time evolution of $\mathbf{x}(t)$ from its initial condition \mathbf{x}_0 is governed by the natural law

$$\frac{dx}{dt} = f(X, t) \quad (4)$$

where f is a functional and $X_0 = X(t_0)$. Let $y(t) = [y^{(1)}(t), y^{(2)}(t), y^{(3)}(t)]$ be the prediction point with an initial condition $y(t_0) = y_0, y(t_0)$, and \mathcal{E} be the tolerance level for the prediction. The prediction is valid if the state point $\mathbf{x}(t)$ is situated inside the ellipsoid ($S_{\mathcal{E}}$, called tolerance ellipsoid) with center at $y(t)$ and size \mathcal{E} . When $y(t)$ coincides with $\mathbf{x}(t)$, the model has perfect prediction. The prediction is invalid if the state point $\mathbf{x}(t)$ touches the boundary of the tolerance ellipsoid at the first time from the initial state that is the first-passage time (FPT) for prediction [9,10] (Figure 1). FPT is a random variable when the model has stochastic forcing or initial condition has random error. Its statistics such as the probability density function, mean and variance can represent how long the model can predict. For simplicity and without loss of generality, a one-component population model is used for illustration.

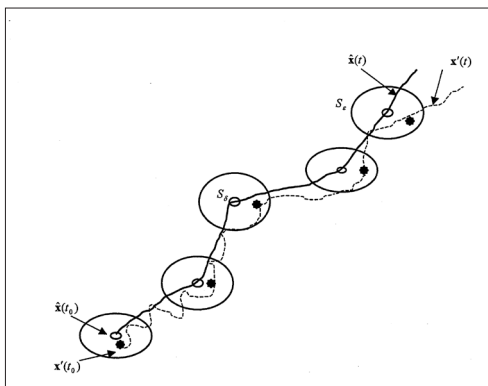


Figure 1: Phase space trajectories of model prediction y (solid curve) and reality x (dashed curve) and error ellipsoid $S_{\mathcal{E}}(t)$ centered at y . The positions of reality and prediction trajectories at time instance are denoted by "*" and "o", respectively). A valid prediction is represented by a time period $(t-t_0)$ at which the error first goes out of the ellipsoid $S_{\mathcal{E}}(t)$.

One component population model

The simplest ecological model contains only one component. The model is based on the assumption that the population density has a maximum capacity K , the migration is proportional to the population density with the migration rate of m . The reproduction is carried out continuously by all its members, without regard to age or sex differences, at an average per capital rate r . The population density (ρ) is normalized by $K, 0 \leq \rho \leq 1$. Usually, the model parameters r and m are difficult to measure. This may lead to the addition of stochastic forcing to the population model [1],

$$\frac{d\rho}{dt} = \sigma\rho - r\rho^2 + v(t)\rho, \quad \sigma = r - m \quad (5)$$

For simplicity, the stochastic forcing is assumed white multiplicative or additive noise,

$$\langle v(t) \rangle = 0, \quad \langle v(t)v(t') \rangle = q^2\delta(t-t'), \quad (6)$$

where the bracket indicates the ensemble average; q represents the strength of the migration; and $\delta(t)$ is a delta function.

FPT Statistics

Let $\hat{\rho}(t)$ be the reference solution which satisfies (5) with the initial condition, $\rho(t_0) = \rho_0$. The forecast error ξ is determined as

$$Z(t) = \hat{\rho}(t) - \rho(t),$$

where $\rho(t)$ is one of individual prediction corresponded to perturbing initial condition and /or stochastic forcing. The conditional probability density function (PDF) of the FPT $(t-t_0)$ with a given initial error Z_0 satisfies the backward Fokker-Planck equation [11],

$$\frac{\partial P}{\partial t} - [\sigma Z_0 - rZ_0^2] \frac{\partial P}{\partial Z_0} - \frac{1}{2} q^2 \frac{\partial^2 P}{\partial Z_0^2} = 0. \quad (7)$$

Integration of PDF over t leads to,

$$\int_{t_0}^{\infty} P[(t-t_0) | Z_0] dt = 1 \quad (8)$$

We multiply equation (7) by $(t-t_0)^n$, integrate with respect to t from t_0 to ∞ , use the condition (8), and obtain the equations of the n^{th} moment of FPT,

$$\frac{q^2 \rho_0^2}{2} \frac{d^2 \tau_n}{dZ_0^2} + [\sigma Z_0 - rZ_0^2] \frac{d\tau_n}{dZ_0} = -n\tau_{n-1}, \quad \tau_0 = 1, \quad (9)$$

which is a linear, time-independent, and second-order differential equation with the initial error Z_0 as the only independent variable. If $|Z_0| = \mathcal{E}$, the model has no predictability initially (i.e., the prediction point hits the error ellipsoid at t_0). FPT of prediction is zero, $t - t_0 = 0$, which leads to the boundary conditions

$$\tau_n = 0, \quad \text{for } |Z_0| = \mathcal{E} \quad (10a)$$

If the initial error reaches the noise level (δ), the boundary condition becomes [12],

$$\frac{\partial \tau_n}{\partial \xi_0} = 0, \quad \text{for } |Z_0| = \delta \quad (10b)$$

Analytical solutions of (9) with the boundary conditions (10a, b) is

$$\tau_n(z_0, \xi, \mathcal{E}, \sigma, q^2) = \frac{2}{q^2} \int_{z_0}^1 y^{\frac{2\sigma}{q^2}} \exp\left(\frac{2\mathcal{E}r}{q^2} y\right), \quad (11)$$

$$\int_{\xi}^y n\tau_{n-1}(x)x^{\frac{2\sigma}{q^2}-2} \exp\left(-\frac{2\epsilon r}{q^2}x\right)dx$$

where $\tau_0 \equiv 1$, and $z_0 \equiv Z_0/\epsilon$, $\xi \equiv \delta/\epsilon$ are non-dimensional initial error and noise level scaled by the tolerance level ϵ . The moments of FPT depend on two types of parameters:

- A. Prediction parameters (z_0, ξ, ϵ),
- B. Model parameters (σ, r, q^2).

Effects of prediction parameters

To investigate the dependence of mean FPT on the prediction parameters (z_0, ξ, ϵ), the three model parameters are taken as $r=1.0$, $\sigma=0.6$, $q^2=0.2$. Figure 2 shows the dependence of $r\tau_1(z_0, \xi, \epsilon)$ [non-dimensional mean FPT scaled by the reproduction rate] on (z_0, ξ) for four different values of $\epsilon(0.01, 0.1, 0.15, 0.2)$. Following features can be obtained:

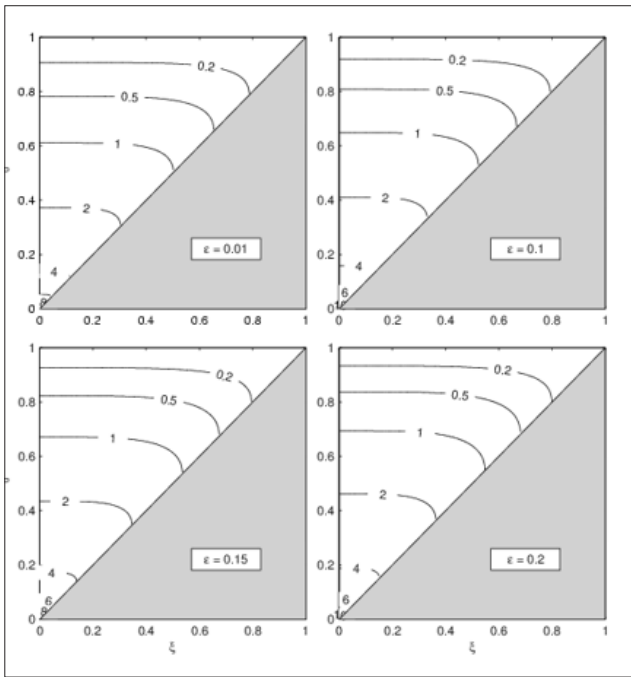


Figure 2: Contour plots of $r\tau_1(z_0, \xi, \epsilon)$ versus (z_0, ξ) for four different values of $\epsilon(0.01, 0.1, 0.15, 0.2)$ using the general production model with model parameters $r = 1, \sigma = 0.6, q^2 = 0.2$. The contour plot covers the half domain due to $z_0 \geq \xi$.

- A. For given values of (z_0, ξ) [i.e., the same location in the contour plots], the mean FPT increases with the tolerance level (ϵ).
- B. For a given value of tolerance level (ϵ), the mean FPT is almost independent on the noise level ξ (contours are almost paralleling to the horizontal axis) when the initial error (z_0) is much larger than the noise level (ξ). The effect of the noise level (ξ) on the mean FPT becomes evident only when the initial error (z_0) is close to the noise level (ξ).

C. For given values of (ϵ, ξ) , the mean FPT decreases with increasing initial error Z_0 .

Effect of model parameter σ

To investigate the sensitivity of mean FPT to the model parameter σ , the other model parameters are taken as $q^2=0.2, r=1.0$. The model parameter σ takes values of 0.3, 0.5, and 0.7. Figure 3 shows the dependence of $r\tau_1(z_0, \xi, \sigma)$ versus Z_0 for two tolerance levels ($\epsilon = 0.1, 0.2$), two noise levels ($\xi = 0.1, 0.6$), and three different values of σ (0.25, 0.5, and 1.0). It is found that the mean FPT decreases with increasing σ for all combinations of noise level ($\xi = 0.1, 0.6$) and tolerance level ($\epsilon = 0.1, 0.2$), which indicates that increase of σ reduces the model valid period.

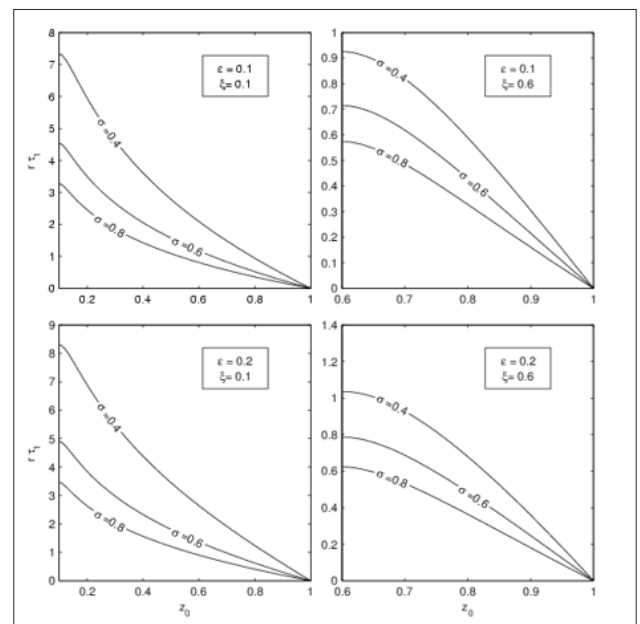


Figure 3: Dependence of $r\tau_1(z_0, \xi, q^2)$ on the initial condition error Z_0 for $q^2 = 0.2, r = 1.0$, and three different values of $\sigma(0.4, 0.6, 0.8)$ using the general production model with two different values of ϵ (0.1, 0.2) and two different values of noise level $\xi(0.1, 0.6)$.

Effect of stochastic forcing

To investigate the sensitivity of mean FPT to the strength of the stochastic forcing, q^2 , the other model parameters are set as $\sigma = 0.6, r = 1.0$. Figure 4 shows the dependence of $r\tau_1(z_0, \xi, q^2)$ on z_0 for two tolerance levels ($\epsilon = 0.1, 0.2$), two noise levels ($\xi = 0.1, 0.6$), and three different values of q^2 (0.1, 0.25, and 0.5) representing weak, normal, and strong stochastic forcing. Two regimes are found:

- A. Mean FPT decreases with increasing q^2 for large noise level ($\xi = 0.6$),
- B. Mean FPT increases with increasing q^2 for small noise level ($\xi = 0.1$).

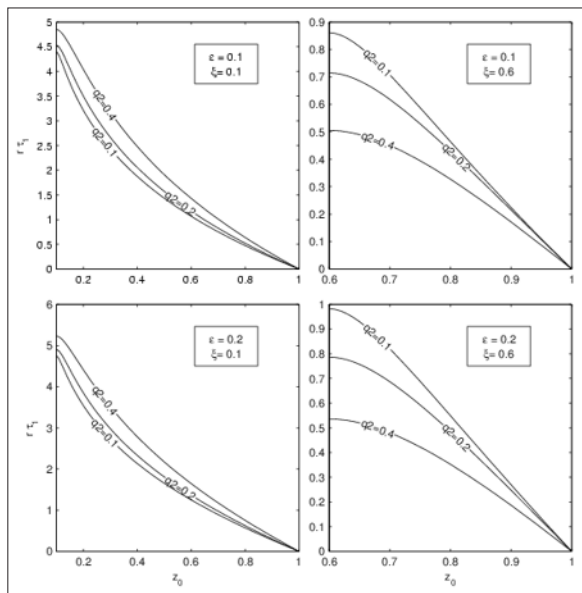


Figure 4: Dependence of $r\tau_1(z_0, \xi, q^2)$ on the initial condition error z_0 for $\sigma = 0.6$, $r = 1.0$, and three different values of q^2 (0.1, 0.2, 0.4) using the general production model with two different values of \mathcal{E} (0.1, 0.2) and two different values of noise level ξ (0.1, 0.6).

This indicates the existence of stabilizing and destabilizing regimes of the dynamical system depending on stochastic forcing. For a small noise level, the stochastic forcing stabilizes the dynamical system and increase the mean FPT. For a large noise level, the stochastic forcing destabilizes the dynamical system and decreases the mean FPT.

Conclusion

The limitation of ecological models' predictability can be represented FPT-the time when the model error first exceeds the tolerance level. FPT is usually a random variable due to model uncertainty such as uncertain initial condition and model parameters. The probability density function of FPT satisfies the backward Fokker-Planck equation. A theoretical framework was developed in this study to determine various FPT moments, which satisfy time-independent second-order linear differential equations with given boundary conditions. This is a well-posed problem and the solutions are easily obtained. For the population model, the mean FPT decreases with increasing initial condition

error, random noise, and model parameter; and increases slowly with increasing tolerance level. Both stabilizing and destabilizing regimes are found in the population model depending on stochastic forcing. For a small noise level, the stochastic forcing stabilizes the population model and increases the mean FPT. For a large noise level, the stochastic forcing destabilizes the population model and decreases the mean FPT.

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