Modeling Uncertainty in Population Dynamics

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Abstract

Characterization and analysis of deterministic uncertainties associated with population dynamics models are often of critical importance, especially where pertinent environmental or demographic variables are employed in modeling concepts related to species conservation or invasion. However, uncertainty analysis using conventional methods such as standard Monte Carlo and Hypercube Sampling may not be efficient, or even feasible, for complex, computationally demanding generalized growth models. We use a non-stochastic approach for the analysis of deterministic uncertainty associated with the model parameters for a prototype generalized growth model in population dynamics, which encapsulates a myriad of submodels. Examples are drawn from environmental noise types and estimates of extinction time for observed trends are determined.

1. Introduction

We are constantly faced with the effects of uncertainty in ecological modeling. Incorporating uncertainty or "noise" in such models is usually achieved by either a stochastic approach, where the noise is assumed to have a probabilistic structure, see for example, [1,2,3,4] or a non-stochastic (deterministic) approach, where a deterministic noise, which is not probabilistic in nature is considered [5, 6]. In the stochastic approach, traditional noise, which could be Gaussian or non-Gaussian depending on the modeling scenario being considered, is linearly added. This stochastic approach is usually fraught with problems and there has been several discrepancies in model predictions and observed ecological trends.

In contrast with the stochastic approach to modeling uncertainty, the deterministic approach incorporates an unknown but bounded noise term, which, with the appropriate mathematical formalism, works very well, especially when the data are too few to validate white or colored noise as good representation of the observed fluctuations but are numerous enough to estimate a good bound on them [6]. A realization of the bound hinges on the determination of metric likelihood functional for the anticipated solution, which is usually extracted from a set of desired solutions. Through this process, some qualitative conclusions (see for example, [6] for further details) can be derived for various scenarios for which extinction, for example, is possible.

2. Suite of Growth Models with Uncertainty

Along the lines described above, we present, in this paper, a deterministic uncertainty analysis for a suite of models, which are obtained from a generalized growth model of the form:

$$\begin{cases} \dfrac{dn}{dt} = f\left(n\right) + c(n)g\left(n\right)u(t) \\ n(0) = n_0,\ u(t) \in [-1,1]. \end{cases} \tag{1}$$

where $u(t)$ is the unknown but bounded noise, $n(t)$ is the population density and n_0 is the initial population density. Here, we represent the bound on the noise as $c(n)$. This bound can assume either a constant value or dependence on the population depending on whether one is modeling environmental or demographic noise. It is worth noting that $u(t) \in [-1,1]$ may contain additional information besides its bound $c(n)$, the intrinsic property of which one can use to define the likelihood of the optimal control function for $u(t)$. This presupposes that the noise described by $u(t)$ has no stochasticity. The function $f(n)$ appearing in equation 1 can be written as

$$f(n) = \frac{a}{b} n^{1-b}\left(K^b - n^b\right) \tag{2}$$

where K is the carrying capacity, b is a constant, which describes the rate of growth and density dependence and a is a scaled growth rate. This generalized model is an extension to the one originally described by Schnute [7] for two independent growth model mechanisms. This generalization, in fact, describes a suite of approximately ten (10) submodels for parameter ranges given in Table 1 below.

Parameter Values	Model Type
a < 0, b = 1	Exponential
a > 0, b = -1	Logistic
a > 0, b = 0	Gompertz
a > 0, b < 0	Richards
a > 0, b = 1	Generalized Bertalanfy: Putter No. 1
a > 0, b = 1/3	Generalized Bertalanfy: Putter No. 2
a > 0, b > 0	Generalized Bertalanfy
a = 0, b = 1	Linear
a = 0, b = 1/2	Quadratic
a = 0, b = 0	rth power

Table 1: Parameter Values for a and b.

2.1. Generalized Model with Noise: Fluctuating *a*

To motivate the technique as applied to the generalized model, let a undergo a small perturbation with bound $\varepsilon > 0$. Then, from equations 1 and 2, if $g(n)$ is given by $g(n) = \frac{1}{b} n^{1-b}\left(K^b - n^b\right)$ then the generalized model with fluctuating *a* is given by

$$\begin{cases} \dfrac{dn}{dt} = \dfrac{a+\varepsilon u}{b} n^{1-b}\left(K^b - n^b\right) \\ n(0) = n_0,\ u \in [-1,1] \end{cases} \quad (3).$$

The solution to the perturbed generalized equation 3 is

$$n(t) = \left(K^b - \left(K^b - n_0^b\right)e^{-(a+\varepsilon u)t}\right)^{1/b} \quad (4)$$

which gives a the reachable set *R(t)* for *t>0* of the form

$$R(t) = \begin{Bmatrix} \left(K^b - \left(K^b - n_0^b\right)e^{-(a-\varepsilon)t}\right)^{1/b}, \\ \left(K^b - \left(K^b - n_0^b\right)e^{-(a+\varepsilon)t}\right)^{1/b} \end{Bmatrix} \quad (5)$$

If q is the extinction threshold, then the first time of possible extinction can be obtained from the relation

$$q = \left(K^b - \left(K^b - n_0^b\right)e^{-(a-\varepsilon)T_0}\right)^{1/b} \quad (6)$$

which after rearrangement, becomes

$$T_0\left(n_0, q\right) = \frac{1}{\varepsilon - a}\ln\left(\frac{K^b - n_0^b}{K^b - q^b}\right). \quad (7)$$

By substituting *b=1*, *K=0* for exponential growth and *b=-1* for Logistic growth we get the results of [6].

We can compute the maximum likelihood for the solution of (3). We let

$$L(T,n) = \frac{1}{T}\int_0^T \left(1 - u(t)^2\right)dt \quad (8)$$

and evaluate

$$\min\left(\frac{1}{T}\int_0^T u(t)^2\,dt\right) \quad (9)$$

by alluding to the same membership function $\sigma(u) = 1 - u^2$ (see [6] for details). To do this we assume that $y = \ln\dfrac{1}{\left(\frac{n}{K}\right)^b - 1}$ and substitute this in equation 3 which results in $y' = a + \varepsilon u$. By the convexity of u^2 and Jensen's inequality,

$$\left(\frac{1}{T}\int_0^T u(t)dt\right)^2 \le \frac{1}{T}\int_0^T u(t)^2 dt\ , \quad (10)$$

the minimum functional can be determined as

$$\left(\frac{1}{T}\int_0^T \frac{y' - a}{\varepsilon}\right)^2 = \left(\frac{1}{\varepsilon}\left(\frac{1}{T}\ln\frac{n_0^b - K^b}{\zeta^b - K^b} - a\right)\right)^2 \quad (11)$$

where $n(T) = \zeta$. In other words, ζ is reached by a constant control, u_0 given by

$$u_0 = \frac{1}{\varepsilon}\left(\frac{1}{T}\ln\frac{n_0^b - K^b}{\zeta^b - K^b} - a\right) \in [-1,1]. \quad (12)$$

The likelihood of reaching $\zeta \in R(T)$ can be calculated a

$$L\left(T,\zeta\right) = 1 - \left(\frac{a}{\varepsilon}\right)^2 + \frac{1}{T\varepsilon^2}\left(\left(2a\ln\frac{K^b - n_0^b}{K^b - \zeta^b}\right) - \frac{1}{T}\left(\ln\frac{K^b - n_0^b}{K^b - \zeta^b}\right)^2\right) \quad (13)$$

The likelihood that the population would become extinct in future, $L_e(q)$, is

$$L_e\left(q\right) = \begin{cases} 1 - \dfrac{a^2}{\varepsilon^2} & \text{if } \varepsilon > a \ge 0 \\ 1 & \text{if } a < 0 \end{cases} \quad (14)$$

where

$$L_e\left(q\right) = \sup_{T \ge T_0\left(n_0,q\right)} L_e\left(T,q\right) = \sup_{T \ge T_0\left(n_0,q\right)} \sup_{t \in [T_0\left(n_0,q\right),T]} L\left(t,q\right)$$

Thus every reachable set has the same likelihood. Furthermore, the median metric likelihood extinction time, T_m, is the solution of

$$L(T_m, q) = \begin{cases} \dfrac{1}{2}L_e(q) & \text{if } \varepsilon > a \ge 0 \\ \dfrac{1}{2} & \text{if } a < 0 \end{cases} \quad (15)$$

which gives

$$T_m = \begin{cases} \ln\left(\dfrac{K^b - n_0^b}{K^b - q^b}\right)\dfrac{\left(2a+\sqrt{2\left(\varepsilon^2+a^2\right)}\right)}{\varepsilon^2 - a^2} & ,\text{if } \varepsilon > a \ge 0 \\ \ln\left(\dfrac{K^b - n_0^b}{K^b - q^b}\right)\dfrac{\sqrt{2}}{\varepsilon^2 - \sqrt{2a}} & ,otherwise \end{cases}$$

(16)

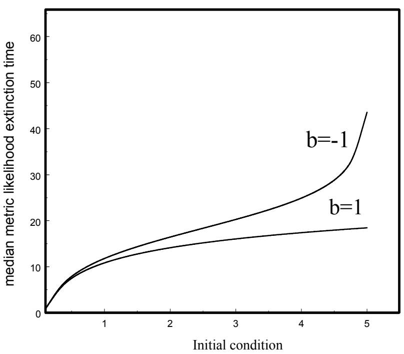

Figure 1. A plot of initial condition n_0 against the median metric likelihood of extinction, T_m, for both exponential and the logistic models with environmental noise. The parameter values are a=0.25, K=5, ε=0.5 and q=0.01. Whereas in the case of exponential the median metric likelihood of extinction is finite, in the case of logistic it grows unboundedly.

2.2. Generalized Model with Noise: Fluctuating *K*

Assuming the impact of environmental noise, the model, with fluctuating K has be form:

$$\begin{cases} \dfrac{dn}{dt} = \dfrac{a}{b} n^{1-b}\left(\left(K+\varepsilon u\right)^b - n^b\right) \\ n(0) = n_0,\ u \in [-1,1] \end{cases} \quad (17)$$

with solution

$$n(t) = \left[\left(K+\varepsilon u\right)^b - \left\{\left(K+\varepsilon u\right)^b - n_0^b\right\}e^{-at}\right]^{1/b}. \quad (18)$$

Equation 17 is not tractable because of the inherent nonlinearities in the $\left(K+\varepsilon u\right)^b$ term. A linearization of equation 17 yields the following approximate differential equation model

$$\begin{cases} \dfrac{dn}{dt} = \dfrac{a}{b} n^{1-b}\left(K^b\left(1+\dfrac{b\varepsilon u}{K}\right) - n^b\right) \\ n(0) = n_0, \quad u \in [0,1] \end{cases} \quad (19)$$

whose solution is

$$n(t) = \left[K^b\left(1+\frac{b\varepsilon u}{K}\right) - \left(K^b\left(1+\frac{b\varepsilon u}{K}\right) - n_0^b\right)e^{-at}\right]^{1/b} \quad (20)$$

A reachable set for $t > 0$ is given by

$$R(t) = \left\{\left[\begin{array}{c} \left(K^b\left(1-\dfrac{b\varepsilon}{K}\right) - \left(K^b\left(1-\dfrac{b\varepsilon}{K}\right) - n_0^b\right)e^{-at}\right)^{1/b}, \\ \left(K^b\left(1+\dfrac{b\varepsilon}{K}\right) - \left(K^b\left(1+\dfrac{b\varepsilon}{K}\right) - n_0^b\right)e^{-at}\right)^{1/b} \end{array}\right]\right., (21)$$

which compares with results of [6] for the logistic and exponential models. If *a<0* then as $t \to \infty$,

$$R(t) \to \left(K\left(1-\frac{b\varepsilon}{K}\right)^{1/b}, K\left(1+\frac{b\varepsilon}{K}\right)^{1/b}\right). \quad (22)$$

Suppose there exist a extinction threshold, q such that

$$q \in \left(K\left(1-\frac{b\varepsilon}{K}\right)^{1/b}, K\left(1+\frac{b\varepsilon}{K}\right)^{1/b}\right) \quad (23)$$

Then the first extinction time is given by

$$T_0 = \frac{1}{a}\ln\frac{K^b\left(K-b\varepsilon\right) - Kn_0^b}{K^b\left(K-b\varepsilon\right) - Kq^b}. \quad (24)$$

If $b \le 0$ then

$$\lim_{n_0\to\infty} T_0 = \frac{1}{a}\ln\frac{K^b(K-b\varepsilon)}{K^b(K-b\varepsilon) - q^b}, \quad (25)$$

if *b>0* then

$$\lim_{n_0\to\infty} T_0 \to \infty.$$

Thus the minimal solution starting from infinity reaches q in a finite time provided $b \le 0$. On the other hand, the minimal solution starting from infinity for *b>0*, will never go extinct.

By making the substitution $y = \dfrac{n^b}{K^b} - 1$, equation 17 becomes $y' = a\dfrac{b\varepsilon u}{K} - ay$. The optimal control can be found in the feedback from as

$$u(t,n) = -\frac{ab\varepsilon}{K}K(t)n(t) \quad (26)$$

where $K(t)$ satisfies the Riccati equation

$$K'(t) = 2aK(t) + \left(\frac{ab\varepsilon}{K}\right)^2 K(t)^2 \quad (27)$$

Solving the differential equation

$$y' = a\frac{b\varepsilon u}{K} - ay \quad (28)$$

where $u = u_0 e^{at}$, $y = \dfrac{n^b}{K^b} - 1$ and $n(0) = n_0$ we obtain

$$n = K\left[\left(1+\frac{b\varepsilon u_0}{2K}e^{at}\right) - \left(1+\frac{b\varepsilon u_0}{2K} - \frac{n_0^b}{K^b}\right)e^{-at}\right]^{1/b}, \quad (29)$$

where u_0 is calculated by setting $n(T)=\zeta$ and isolating u_0, thus

$$u_0 = \frac{2K^{1-b}}{b\varepsilon\left(1-e^{2at}\right)}\left[\left(K^b - n_0^b\right) - e^{at}\left(K^b - \zeta^b\right)\right] \qquad (30)$$

If $u_1(t) = -e^{(t-T)}$ and $u_2(t) = e^{(t-T)}$ are controls corresponding to the optimal solutions n_1, n_2 on *[0, T]* then

$$n_1 = K\begin{bmatrix}\left(1-\frac{b\varepsilon}{2K}e^{a(t-T)}\right) - e^{-at} \\ +\frac{b\varepsilon}{2K}e^{-a(t-T)} - \frac{n_0^b}{K^b}e^{-at}\end{bmatrix}^{1/b} \qquad (31a)$$

and

$$n_2 = K\begin{bmatrix}\left(1+\frac{b\varepsilon}{2K}e^{a(t-T)}\right) - e^{-at} \\ -\frac{b\varepsilon}{2K}e^{-a(t-T)} - \frac{n_0^b}{K^b}e^{-at}\end{bmatrix}^{1/b} \qquad (31b)$$

In the long run

$$n_1 \to K\left[1-\frac{b\varepsilon}{2K}\right]^{1/b} \text{ and } n_2 \to K\left[1+\frac{b\varepsilon}{2K}\right]^{1/b} \qquad (32)$$

Suppose ζ is greater than the maximal solution then let t_2 be such that $0 < t_2 < T$ and define the optimal control to be

$$u(t) = \begin{cases} u_0 e^{at} & 0 \le t \le t_2 \\ 1 & t_2 \le t \le T \end{cases} \qquad (33)$$

then $1 = u_0^+ e^{at_2}$ whence $t_2 = \frac{1}{a}\ln\frac{1}{u_0^+}$. In similar fashion, if ζ is less than the minimal solution then for $0 \le t_1 \le T$ we have $t_1 = \frac{1}{a}\ln\frac{-1}{u_0^-}$. Given these scenarios we can now compute the likelihood of ζ reaching *R(t)* to obtian

$$L(T,\zeta) = \begin{cases} \frac{1}{T}\left(t_2 + \frac{\left(u_0^+\right)^2}{2a}\left(1-e^{2at_2}\right)\right) & \zeta \le n_2(t) \\ \frac{1}{T}\left(t_2 + \frac{u_0^2}{2a}\left(1-e^{2aT}\right)\right) & n_1(t) < \zeta < n_2(t) \\ \frac{1}{T}\left(t_1 + \frac{\left(u_0^-\right)^2}{2a}\left(1-e^{2at_1}\right)\right) & \zeta \le n_1(t) \end{cases} \qquad (34)$$

The evaluation of u_0^- and u_0^+ requires very tedious algebra for the generalized model. However, we can consider individual cases based upon which the control parameter $L(T,\zeta)$ can be obtained. After some algebra, the first extinction time for equation 17 can be written as

$$T_0\left(n_0, q\right) = \frac{1}{a}\ln\frac{\left(K-\varepsilon\right)^b - n_0^b}{\left(K-\varepsilon\right)^b - q^b},$$

which for parameter values associated with exponential and logistic growth (see Table 1), and using data provided in [8], agree very well with the results discussed in [6] and [9].

3. Discussion and Conclusion

As stated in [3], failure to account for demographic and environmental noise associated with stochastic population dynamics has been partially responsible for the decline of many threatened and endangered species and for the overexploitation and collapse of numerous living resources, including commercial fisheries. Several systematic efforts have been made to manage endangered species, and to prevent and control the spread of invasive species, among which are the use of mathematical modeling and evolutionary computational algorithms. A number of different model types have been developed. Some of these models are parameter-sparse and others are not. Models based on differential and integro-difference equations, neural nets, metapopulations, cellular automata, and discrete-event simulation techniques have all been used to predict spatial spread (see, for example, [10, 11, 12]). Two major problems encountered in expanding these models to incorporate more realism are that analytical solutions become very difficult or impossible, and parameter estimations for realistic field data are much more complicated. Also, choosing the correct model is at least as important as fitting model parameters.

Evolutionary algorithmic approach [13,14] is currently being used to select the best model from sets of increasingly complex but potentially more realistic models. Crucial to the problem of model selection is the incorporation of the appropriate “generalized growth dynamic models” based upon which an automated, efficient search technique for the best candidate model for describing invasive species can be found. Here, a combined genetic algorithmic and information theoretic computation approach is used to orchestrate a competition among a community of candidate models that successfully evolves prototype mathematical models for a myriad of ecological and conservation biology problems related to invasive species spread and endangered species modeling.

Given the importance of the definition of the generalized models in evolutionary algorithms, we have discussed the concept of deterministic uncertainty. We have adopted the methodology first proposed by [6] for analyzing deterministic uncertainty and its usefulness in examining parameter variability. This approach permits modeling of uncertainty without the need for probabilistic knowledge of noise. The unknown but bounded noise approach requires no *a priori* knowledge of the noise distribution, and provides a simple analysis of deterministic noise without resorting to gory stochastic details.

Analyses of this generalized model shows that the first possible time to extinction, T_0 and the median metric likelihood of extinction time are both logarithmic, and agree with results obtained in [6]. Moreover, when $b \leq 0$, then any population starting from infinity would go extinct in a finite time (for example Logistic and Gompertz) otherwise it will never go extinct.

Work in in progress to link parameter ranges associated with extinction times to the concept of Allee Effect [8], which occurs when a population goes extinct after falling below a given threshold level. In particular this occurs when the per capita growth rate decreases as density or abundance decreases to low levels.

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