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Analysis of a Schnute postulate-based unified growth mode for model selection in evolutionary computations

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Abstract

In order to evaluate the feasibility of a combined evolutionary algorithm-information theoretic approach to select the best model from a set of candidate invasive species models in ecology, and/ or to evolve the most parsimonious model from a suite of competing models by comparing their relative performance, it is prudent to use a unified model that covers a myriad of situations. Using Schnute's postulates as a starting point, we present a single, unified model for growth that can be successfully utilized for model selection in evolutionary computations. Depending on the parameter settings, the unified equation can describe several growth mechanisms. Such a generalized model mechanism, which encompasses a suite of competing models, can be successfully implemented in evolutionary computational algorithms to evolve the most parsimonious model that best fits ground truth data. We have done exactly this by testing the effectiveness of our reaction-diffusion-advection (RDA) model in an evolutionary computation model selection algorithm. The algorithm was validated (with success) against field data sets of the Zebra mussel invasion of Lake Champlain in the United States.

Keywords

Schnute's postulates; Unified growth model; Allee effect; Invasive species; Model selection; Evolutionary computations; Zebra mussels

1. Introduction

Evolutionary algorithm-information theoretic formalism is a powerful approach for selecting the best model from a suite of models. This approach is applicable to several fields of study, one of which is invasive species modeling. These algorithms can be used to evolve the most parsimonious model mechanism that describes an observed ecological trend through a procedure similar to biological evolution. Thus, through a combination of the evolutionary algorithm and information theoretic methods, a competition among a suite of candidate models can be initiated, and the best model for describing an observed biological trend can be realized. The process can be facilitated if one has the appropriate generalized differential equation model for the automated search algorithm through which the most parsimonious model can be realized.

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To evolve the most parsimonious model from a set of competing models by comparing their relative performances, it is prudent to use a unified model that covers a myriad of situations. In the ecological literature, for example, several growth models abound. Typical examples are the Malthus (1798), Gompertz (1832), Verhulst (1838), Richards (1959), Blumberg (1968), and Schnute (1981). In an attempt to unify some of these growth models, Turner et al. (1976a) proposed a hyperlogistic model with four parameters but the biological significance of all the parameters was not clearly evident. Oftentimes the model parameters are fraught with uncertainties (Bentil et al., 2003). Quite recently, Tsoularis (2001) proposed a five-parameter model, which encompasses most growth curves but some of the model parameters cannot also be interpreted biologically. In another paper, Tsoularis and Wallace (2002) presented a comparative study of a generalized logistic equation. In particular, they discussed a generalized logistic growth function with several parameters, which may potentially have a wider applicability than Schnute's equations. The Tsoularis and Wallace (2002) model had several parameters and it had limited use for our purposes.

We have successfully combined Schnute's ordinary differential equation system into a single (unified) model with the added advantage that this single, unified equation could be incorporated into an evolutionary algorithm for studying the dynamics and spread of invasive species, such as Zebra mussels in Lake Champlain situated in the Northeastern part of the USA. A further extension to the unified model incorporates the Allee effect. The Allee effect describes the scenario when a population cannot persist below a critical population density known as Allee threshold (Allee, 1931,1938). When considered in its entirety, the generalized equation (with Allee effect) could be an extremely useful model to adopt for invasive species modeling via evolutionary computation techniques (see, for example, Hoffmann et al., 2004). For completeness in this exposition, the paper is organized as follows: we give a brief description of the derivation of the unified model from Schnute's postulates. This is done in Sections 2 and 3. We then allude to the generalized model in Section 4, and embody this model in an evolutionary computation algorithm in Section 5. Discussions and concluding remarks are given in Section 6.

2. Schnute's postulates and the unified equation

In his classic paper, Schnute (1981) considered accelerated growth of fish populations from the viewpoint of "relative growth rate of the relative growth rate." In Schnute's model derivation, it was assumed that

- i. the relative growth rate, k, of a population with density, N, was given by (1/N)(dN/dt) = k;
- ii. the relative growth rate, of the relative growth rate, k, was a linear quantity of the form (1/k)(dk/dt) = -(a + bk).

Here, the parameter *a* defined a fixed growth rate, and *a/b* was the scaled growth rate. The parameter *b* was assumed *dimensionless*. It was defined as a *shape* parameter, which determined the point (on a population-time graph) at which an initial "accelerated" or "faster" growth changed to a "slower" growth. Through this reasoning, Schnute (1981) considered the accelerated growth rate of species, and solved the model system:

$$\frac{dN}{dt} = Nk, \qquad \frac{dk}{dt} = -k(a+bk), N(t_1) = N_1, \qquad N(t_2) = N_2$$
(1a)

where t_1 and t_2 are initial and final times and N_1 and N_2 are the initial and final population densities, respectively. Model equation (1a) assumes a solution of the form:

$$N(t) = \left(N_1^b + \left(N_2^b - N_1^b\right) \frac{1 - e^{-a(t-t_1)}}{1 - e^{-a(t_2 - t_1)}}\right)^{1/b}$$
(1b)

For a given set of parameter values, the model system and associated solution (Eqs. (1a) and (1b)) describe 10 growth equations (see Table 1).

Based upon Schnute's postulates, the ensuing equations and their respective solutions, we can derive a unified model for use in evolutionary computations. We motivate the derivation of the unified model from the reasoning given below. Suppose for some fixed positive growth rate *a* of Eq. (1b), the time difference, $t_2 - t_1$, is large enough. Then,

 $N_1^b + ((N_2^b - N_1^b)(1 - e^{-a(t_2 - t_1)})) \rightarrow N_2^b$. Given that, in theory, the final population density, N_2 , cannot exceed the carrying capacity, in the limit where $N_2^b \rightarrow K^b$, we obtain:

$$N_1^b + \frac{N_2^b - N_1^b}{1 - e^{-a(t_2 - t_1)}} \sim K^b$$
⁽²⁾

where K^b is the *b*-dependent carrying capacity. Following Schnute's assumptions, the parameter *b* modulates the shape and form of the growth curve and its corresponding carrying capacity. Indeed, if the population grows long enough, the final population can approach the *b*-dependent carrying capacity K^b . Using assumption (ii) and differentiating Eq. (1b), after a little bit of algebra and rearrangement, one obtains a single differential equation of the form:

$$\frac{\mathrm{d}N}{\mathrm{d}t} = \frac{a}{b} N^{1-b} \left(K^b - N^b \right) = \frac{a}{b} N \left[\left(\frac{K}{N} \right)^b - 1 \right], \text{for} \quad b \le 1$$
(3)

This (single) differential equation, which we term the unified model, describes all of the growth models given in Table 1.

The beauty of Eq. (3) is that it has fewer parameters, that is (a, b, K), and it allows for a more realistic interpretation of the parameters biologically. For example, differentiating Eq. (3) and equating to zero, one can examine the behavior of the parameter b at the point of inflexion. Fig. 1 illustrates this relationship.

Here, a gradual increase of *b* from $-\infty$ to 1 corresponds to a nonlinear decrease in the point of inflexion from the value of *K* to 0, which implies a gradual decrease in the intensity of density dependence. Thus, as the population grows and the number of individuals increase, the relative growth rate decreases, which clearly illustrates the effect of population size on itself. Biologically, we can restate the problem as follows:

rate of change of population=biotic potential - intra-specific competition

Without intra-specific competition, that is, the negative feedback of density dependence, there is only exponential growth, i.e. b = 1. Intra-specific competition increases with decreasing b. Therefore, the parameter b determines the strength of density dependence indeed. In addition, b also scales the relative growth rate, r, in which case we can assume that b is a complex parameter that modifies density dependence as well as the relative growth rate. Perhaps, it should be emphasized, here, that growth rate is a demographic and/or ecological term; it measures the rate at which the number of individuals in a population increases whereas the relative growth rate is the growth rate per individual in the population. Fig. 2 illustrates the behavior of typical growth curves.

3. Solution to the unified model equation

The exact solution to the unified model equation (Eq. (3)) can be obtained, in closed form, as

$$N(t) = \left(N_1^b + \frac{N_2^b - N_1^b}{1 - e^{-a(t_2 - t_1)}} - \frac{(N_2^b - N_1^b)e^{-a(t-t_1)}}{1 - e^{-a(t_2 - t_1)}}\right)^{1/b}$$

= $\left(K^b - (K^b - N_1^b)e^{-a(t-t_1)}\right)^{1/b}$ (4a)

This is analogous to the solution (Eq. (1b)) to Schnute's two model equation system (Eq. (1a)). At any given initial time, $t_1 = 0$, and corresponding initial population density $N_1 = N(0) = N_0$, one obtains, after substituting these initial conditions in Eq. (4a), the solution:

$$N(t) = \left(K^{b} - \left(K^{b} - N_{0}^{b}\right)e^{-at}\right)^{1/b}$$
(4b)

A rearrangement of Eq. (4a) yields:

$$N(t) = \left(K^{b}\left(1 - e^{-at}\right) + N_{0}^{b}e^{-at}\right)^{1/b}$$

= $K^{b}\left(1 - \left(1 - \left(\frac{N_{0}}{K}\right)^{b}\right)e^{-at}\right)^{1/b}$ (4c)

For the special case when b = 0 we have the limiting solution:

$$N(t) = N_0 e^{\left(\frac{1}{\ln - \kappa} - \ln - N_0\right)\left(1 - e^{-rt}\right)}$$
(4d)

We note, here, that these model solutions (Eqs. (4b-d)) have only three parameters, that is a, b and K, while Schnute's original model had six parameters. The parameters in our unified model are indeed amenable to experimental interpretations.

Because the unified model has fewer parameters it has an inherent advantage over Schnute's model; it distinctly reduces the parameter search domain in evolutionary computation algorithms. In the case of the exponential growth model where there is no carrying capacity, the *b*-dependent parameter, K^b , is set to 0. Biologically, this means there is no limit to growth since there is no carrying capacity. On the other hand, the Gompertz model is obtained by taking the limiting value of the model (Eq.(4c)) as $b \rightarrow 0$. Fig. 3 shows some typical behaviors of the time variation in population density for various values of the shape parameter *b*. Table 2 below shows the parameter ranges for various models mimicked by the model.

4. Extension of unified equation to include Allee effect

In this section we extend the unified model (Eq. (3)) to include the Allee effect. We call this the generalized model. The generalized model encompasses a myriad of models and submodels, which are particularly useful in evolutionary computations. The Allee effect (Allee, 1938) occurs if the intrinsic growth rate decreases as density or abundance decreases to low levels (see, for example, Robertson, 1921;Courchamp et al., 1999;McCarthy, 1997). This implies that there exists a population threshold of size q, say, which for $N_0 < q$, population declines, perhaps due to harsh environmental conditions, and eventually becomes extinct, whereas for $N_0 > q$ the population can grow to a certain level (and below the *b*-dependent carrying capacity). This is illustrated in Fig. 4a and b.

Indeed, the functional form of the right-hand side (RHS) of the unified model (Eq. (3)) is a quadratic equation with domain $N \in [0, K]$, where from a linear analysis of the RHS, the steady state N = 0 is unstable and N = K is stable. Here, the axiom of parenthood (Hutchinson, 1978) is naturally satisfied. Based upon biologically realistic assumptions for the occurrence of the Allee effect (Allee, 1938) given above, a pragmatic extension of model Eq. (3) yields a *b*-dependent cubic function for the RHS defined in the same population density domain, $N \in [0,K]$, but with three steady states occurring at N = 0, q, K such that N = 0, K are stable and N = q is unstable (see Fig. 4a). With a little bit of algebra and rearrangements, one obtains a generalized model that encapsulates all of the growth models described earlier, and, in addition, encapsulates the Allee effect. Such an equation is given by

$$\frac{\mathrm{d}N}{\mathrm{d}t} = \frac{a}{b} N^{1-2b} \left(K^b - N^b \right) \left(N^b - q^b \right) \tag{5}$$

We also note, here, that if b = -1, a > 0 and $q \neq 0$ one obtains a logistic growth model with Allee effect. Also, for q = 0, one obtains the unified model (Eq. (3)).

We note that Eqs. (3) and (5) describe just the local phenomenon (i.e. time-dependence only). Given the generalized model equations described above, we can then incorporate spatial effects that encompass both dispersal (in the form of diffusion) and advection (in the form of convective flow). This gives us a reaction-diffusion-advection (RDA) model. A prototype RDA model, which incorporates some of the characteristics described above, can be written as

$$\frac{\partial N}{\partial t} = D\left(\frac{\partial^2 N}{\partial x^2} + \frac{\partial^2 N}{\partial y^2}\right) - v_x \frac{\partial N}{\partial x} - v_y \frac{\partial N}{\partial y} + \frac{a}{b} N^{1-2b} \left(K^b - N^b\right) \left(N^b - q^b\right)$$
(6)

where *D* and v_x , v_y are the diffusion rates and advection velocities in the *x* and *y* directions, respectively, and the other model parameters are as described in the text. Here, for simplicity, we have assumed that the diffusion coefficient is constant but the model equation could easily be extended to incorporate density-dependent diffusivity. We describe below an evolutionary computational test of our unified RDA model and discuss its advantages.

5. Evolutionary computation test of the unified equation

As a test of the effectiveness of Eq. (6), we used this model in an evolutionary computation model selection algorithm that was applied to field data set of the Zebra mussel invasion of Lake Champlain (United States). Lake Champlain occupies a north-south geological fault zone and is long (193 km) and narrow (19 km at its widest point). It is located at 44.50 latitude and -73.25 longitude, and is the sixth largest lake in the United States. The predominant flow is north into the Richelieu River in Quebec, Canada, and the mean hydrologic residence time is 3.3 years. Additional information can be found at

http://www.worldlakes.org/lakedetails.asp?lakeid=8518.

The Zebra mussel data consists of a 10-year time series of the densities of veliger larvae, juveniles, and adult forms of this invasive species at 23 locations in the lake. Data are available at (http://www.anr.state.vt.us/dec/waterq/lakes/htm/lp_lczebramon.htm). These data are considered the best whole-lake Zebra mussel data set in existence due to the consistency of the methods used in collecting them and the fact that the initial sampling occurred at the very beginning of the invasion in 1993. Zebra mussels were first discovered in the extreme southern portion of the lake and over the next 10 years spread northward throughout the entire lake. A succinct summary of the life history of this invasive species is available at http://nis.gsmfc.org/nis_factsheet.php?toc_id=131.

We note, here, that the hydrodynamic features of the lake are extremely crucial for modeling the etiology of the spread of invasive species, hence the use of the unified model, the characteristics and assumptions, some of which we describe below will be important here. Indeed, the "true" model is unknown when using field data, so for these tests it is necessary to use the known facts of the life history stages of Zebra mussels (specifically, the passively dispersed veliger larval stage), and the known hydrodynamic features of Lake Champlain as criteria for judging whether these tests can evolve the "correct" unified model. The larvae are released by the adults in large numbers (~10⁶ per adult) from late spring to early fall (a period of approximately 4 months when the water temperature of Lake Champlain is sufficiently warm to allow spawning). This stage of their life history is planktonic for approximately 1 month and occurs more or less continuously during this 4-month period. Thus, it is reasonable to expect that the large-scale hydrodynamic features of the lake (predominant northward flow) will dominate the passive *dispersal* of the veliger spread dynamics on an annual time scale. Therefore, a "correct" model of their dynamics should show strong anisotropic *advection* in the northern direction, and the magnitude of the advection should approximate the known

average annual northward flow rate of the lake. There is also an extremely high fecundity of the mussels and large-scale mixing of the planktonic larvae, so it suffices to use the generalized *growth term* with or without the Allee effect, and negative density dependence (as the ground truth data suggest) in the dynamics of the model.

To see if the evolutionary algorithm would evolve a model structure consistent with these three expectations, namely reaction terms in the form of growth, diffusion and advection, we used our RDA model on a gridded spatial domain of the lake with a cell size of approximately 1.4 km². Despite the recognized high quality of the Lake Champlain data set, the observed veliger larvae densities show considerable variability typical of field data, and furthermore constitute a sparse data matrix in time and space. It was, therefore, necessary to process the data before conducting these tests. First, the data were averaged over the 4-month spawning period for each station in each year of the time series-this some-what smoothed and effectively transformed the data to the appropriate time scale for comparison to the known large-scale annual hydrodynamic features of the lake. Second, the original data were supplemented with linearly interpolated values to fill in the empty grid cells, and then locally averaged to smooth further the training data. Only the first 7 years of the 10-year time series were used for these feasibility tests because this time period best depicts the onset and subsequent spread of the invasion, whereas the more recent years show stagnation and possible decline in densities. Local investigators are currently researching the cause of the stagnation and possible decline; however, no consensus of causal factors has emerged yet.

The evolutionary (or specifically genetic) algorithm used a genome encoding for the complete seven-parameter generalized model. The genome also included switch genes, which determined the components of the generalized model that would be active for that individual. To avoid over-fitting, the more complex models were given a higher fitness penalty as guided by the Akaike (1973) information criterion. Specifically, the algorithm orchestrates a competition among different models that ultimately results in the evolution of the most parsimonious model that best describes the data. The evolutionary algorithm software package used for these tests is a public domain, parallel genetic algorithm function library written in ANSI C, known as PGAPack (Levine, 1996), and is available from the United States DOE Argonne National Laboratory (ftp://ftp.mcs.anl.gov/pub/pgapack). The fitness function and models were coded in C, optimized, and parallelized for SMP (symmetrical multiple processors) in circumstances where global memory space was not an issue. We used NAG (The Numerical Algorithms Group, Inc., Downers Grove, IL) numerical partial differential equation solver, and optimized in FORTRAN for SMP. Computation times on dual-processor Xeon workstations took approximately 6 h of CPU time. See Hoffmann et al. (2004) for more specific details of this algorithm and method.

Our results have confirmed the potential for the use of this generalized model in evolutionary computational algorithms. Fig. 5 shows the population density predictions of one typical "correct", evolved model of the spread dynamics of the veliger larvae compared to the field data for Zebra mussel veliger densities in Lake Champlain. It is interesting to note that 29 of 36 experiments using the Lake Champlain veliger density data evolved the "correct" model structure with appropriate parameter values (a "correct" model is defined as including the three expectations of anisotropic northward advection, some negative density dependence, and no Allee effect). The "correct" models had an average parameter value for the northward advection of the larvae of 62.9 km/year (S.D. \pm 2.5), which compared favorably with the independently estimated average of 60 km/year calculated from the known hydrologic residence time and length of Lake Champlain. The average value of the density-dependent parameter *b* in the "correct" model was -1.67 (S.D. \pm 0.16), and suggests a negative non-linear density dependence. All of the "correct" models had evolved a model structure in which the switch for the Allee effect gene was turned off, thus indicating no significant positive density dependence.

Although this model over estimated the spread rate in years two and three of the invasion, the general pattern of the predicted dynamics over the 7-year time period was consistent with the observed field data.

6. Discussion and conclusion

The key to using mathematical models in ecology effectively lies in applying theoretical work to experimental observations, and deriving a theory from experiment-driven hypothesis. To make predictions from models, one should be able to estimate the important parameters that govern the phenomenon under consideration.

By reducing Schnute's model to a single differential equation, we have obtained a unified model (Eq. (3)), and then a generalized model (Eq. (5)) with biologically meaningful parameters. Our models describe as many as eleven known growth model equations, and other growth models that are yet to be related to field data. In particular, we have included the Allee effect and incorporated spatial effects into the unified model. It is clear that the unified model includes both linear and non-linear density dependence, and spatial effects, and it is a novel one. Also, it has fewer parameters that are verifiable experimentally.

Given the generalized model, we have incorporated it in an evolutionary computation model selection algorithm to evolve the most parsimonious model that best fits ground truth data. There is, however, the danger in blindly accepting the best model selected from any model selection procedure, and often there is no single best model and the model parameters are fraught with uncertainties (see, for example, Bentil et al., 2003; Hoffmann et al., 2004; Osei et al., 2005). Since evolutionary algorithms are, in general, stochastic search procedures, many replicate searches were conducted to produce several best evolved models out of which the most parsimonious model was chosen. The major limitation of this approach to model selection and fitting is the computational intensity and time needed to adequately search both model and parameter spaces simultaneously. The use of ecologically realistic models with fewer parameters indeed allowed for considerably less CPU time.

In conclusion, we note, here, that global warming is predicted to alter the range of species and increase the number of disruptive invasions. Managing invasions in complex ecosystems depends on good predictive models of invasive species dynamics. The use of this generalized RDA model will directly benefit ecosystem scientists and environmental managers who need better predictive tools and understanding of invasive species dynamics for directing their control efforts.

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Fig. 1.

Normalized population density (at the point of inflexion) plotted as a function of the parameter b. Points on curve indicate corresponding points of inflexion on the population time graph for different models. Note that the graph asymptotes at K since that is the maximum point that the inflexion point can attain. The value of b therefore determines the strength of density dependence.



Fig. 2.

A plot of population density (*N*) against time (*t*) for relative growth rate r = 0.69, and carrying capacity K = 10. For b = 1 the growth is exponential and therefore there is no point of inflexion. For b = -1 (logistic) the point of inflexion is at N = 5. Note that apart from b = 1, which is a unique case, the point of inflexion moves up towards K as b decreases. Also note that changes in b affect the relative growth rate. In this graph adjustments have been suitably made to make sure that the relative growth rate is always the same (0.69).



Fig. 3.

As *b* decreases the inflexion point moves up along the population-time graph, thus *b* determines the change from *accelerating* growth to slow growth due to density dependence. For example at b = 1 the point of inflexion is at 0 density. This means that for the population time graph with an initial population $N_0 > 0$, the growth has no inflexion point, whereas at b = -1 (logistic) the inflexion point is halfway along the population time graph.

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Fig. 4.

(a) Functional form of the RHS of the generalized model with Allee effect for b = -1 (logistic model) and a = 0.69. For the given choice of parameter values, the steady states for the normalized population density were 0, 0.3 and 1. The threshold population, 0.3 is unstable and allows for the occurrence of the Allee effect. (b) A qualitative solution of the generalized model with the Allee effect. The threshold population, q, is 0.3 and carrying capacity is 1. The five initial conditions are $N_0 = 0.1, 0.2, 0.4, 0.6, and 0.9$. For initial populations less than 0.3, the populations go extinct with time whereas for populations above 0.3 the populations can rise up to some maximal population below the carrying capacity.



Fig. 5.

Time series of the Zebra mussel veliger densities in Lake Champlain. The spatial domain of the lake is graphically shown here as the set of 1.4 km^2 grid cells used to model the veliger larvae spread dynamics. The upper panel depicts the unified model predictions and the bottom panel depicts the processed field data. The noticeable light area in the northern portion of the lake in 1994 is due to the veliger larvae not reaching that region of the lake in that year. The small square region in the northern portion of the lake represents islands.

Table 1

A list of parameter ranges suggested by Schnute and their model types

Values of <i>a</i> and <i>b</i>	Model type
a < 0, b = 1 a > 0, b = -1 a > 0, b = 0 a > 0, b < 0 a > 0, b = 1 a > 0, b = 1/3 a > 0, b = 1 a = 0, b = 1 a = 0, b = 1/2 a = 0, b = 0	Exponential Logistic Gompertz Richards Generalized von Bertalanfy: Putter No. 1 Generalized von Bertalanfy: Putter No. 2 Generalized von Bertalanfy Linear Quadratic <i>r</i> th power

 Table 2

 Parameter values for the unified equation and their model types

Values of <i>a</i> and <i>b</i>	Model type	
a < 0, b = 1, K = 0 a < 0, b = 1, K > 0 a > 0, b = -1, K > 0 a > 0, b = 0, K > 0 a > 0, b = 0, K > 0 a > 0, b < 0, K > 0 a > 0, b = 1, K > 0 a > 0, b > 0, K > 0 a > 0, b = 1, K > 0 a = 0, b = 1, K > 0 a = 0, b = 1, K > 0 a = 0, b = 1/2, K > 0	Exponential Monomolecular Logistic Gompertz Richards Generalized von Bertalanfy: Putter No. 1 Generalized von Bertalanfy: Putter No. 2 Generalized von Bertalanfy Linear Quadratic	
a = 0, b = 0, K > 0	<i>r</i> th power	