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Integer-based modeling of population dynamics: Competition between attractors limits predictability

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Real populations consist of a finite number of discrete individuals, and discreteness of the populations cannot always be neglected (Jackson, 1989; Coulson et al., 2004). Here we show that the discrete-state population dynamics are impacted by competition between non-chaotic attractors. These attractors emerge as a result of splitting of a continuous-state chaotic attractor when passing from continuous-state description of the population dynamics to discrete-state models. Taking into account that ecological systems are inherently noisy, we show that predictability of the regular discrete-state population dynamics is limited by noise driven transitions between the competing non-chaotic attractors. In the event that the noise can be neglected, predictability of the discrete-state dynamics is shown to be dependent on the time scale. At the comparatively short time scales, the discrete-state population size oscillations can be chaotic while at larger time scales, the discrete-state time series, which consist of many periodically repeating chaotic sections, are regular and highly predictable.

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1. Introduction

Population dynamics is often complex and difficult to predict. As an example, the input of nutrients in a lake (e.g., with runoff from adjacent fields treated with mineral fertilizers) does not necessary lead to an increase in the productivity of aquatic communities in this lake, as could be expected, but, conversely, can be lethal to hydrobiots (Scheffer, 1998). Poor predictability of the population dynamics appears to arise from both a plethora of external impacts and intrinsic instability of the dynamics of the populations. The role of different factors in population functioning has been a hotly debated subject (Bolliger et al., 2005). Revealing these factors is a challenging task since the time series obtained in the course of field observations are often too short to reveal true mechanisms underlying hardly predictable variations in the population size (Bobryev et al., 2012). Therefore, an essential role in research on population dynamics belongs to mathematical modeling.

Usually, the variables in the models of population dynamics are assumed to take real values, which is to say that the population densities vary in a continuous way. Indeed, the population densities being averaged in space are real numbers. However, each of the unit areas of a habitat contains a whole number of organisms. Also, a total population size is naturally expressed as a whole number. Hence modeling with the use of discrete instead of continuous variables would provide more realistic description of population dynamics (Coulson et al., 2004). At first glance, the difference between, for example, 1000 animals inhabiting a unit area and the value of 1000.5 as a spatially averaged population density is too small to lead to significant effects. However, it has been shown that a discrete-state analog of a continuous-state model exhibits purely cyclic behavior (Henson et al., 2001), whereas the continuous-state models demonstrate a larger variety of dynamical regimes, including chaotic ones (Henson et al., 2001; Solé and Bascompte, 2006; Medvinsky, 2009).

Predictability of the intrinsically cyclic dynamics (in contrast to chaotic dynamics) can be broken down by influence of external stochastic factors. Here we show that limits of predictability of the discrete-state dynamics can arise naturally due to a noise treatment of competing discrete-state regular attractors, which are resulted from splitting of a continuous-state chaotic attractor.

2. The models

We illustrate integer-based effects with discrete-state analogs of continuous-state discrete-time models, which have gained wide acceptance in mathematical ecology. They are the logistic difference equation, the Ricker map, and the Gompertz difference equation.
The logistic difference equation can be presented in the form

\[ N_{t+1} = rN_t \left( 1 - \frac{N_t}{K} \right) + N_t, \]  

(1)

where \( N \) is the population size, \( t \) is time, \( K \) is the carrying capacity, and \( r \) is a model constant. This equation describes the dependence of the population size \( N \) at time \( t+1 \) on the population size at time \( t \). The logistic equation has been extensively studied beginning with the seminal works of May (May, 1974, 1976). In Eq. (1), the factor \( R = r(1 - (N_t/K)) \) represents the population growth rate, which obviously is a function of the population size \( N \). Namely, increase of \( N \) finally leads to a decrease in the population growth rate. The logistic difference model (1) has been shown to give a rise to both regular and chaotic dynamics (Ott, 2002).

The discrete-state analog of Eq. (1) is

\[ N_{t+1} = \text{int}[rN_t \left( 1 - \frac{N_t}{K} \right) + N_t], \]  

(2)

where \( \text{int}[x] \) denotes the integer part of \( x \).

The Ricker map (Ricker, 1954)

\[ N_{t+1} = rN_t \exp \left( -\frac{c}{K}N_t \right), \]  

(3)

where \( N \) is the population size, \( t \) is time, \( K \) is the carrying capacity, \( r \) and \( c \) are model constants, was put forward to describe fish recruitment depending on \( N \). As is seen from Eq. (3), growth of the population abundance \( N \) initially leads to increasing recruitment, but as the abundance exceeds the critical value \( (K/c) \ln r (r > 1) \) the recruitment begins to decrease. The Ricker map (3) can exhibit complex dynamics, including chaos (Solé and Bascompte, 2006). The discrete-state analog of the Ricker map is

\[ N_{t+1} = \text{int}[rN_t \exp \left( -\frac{c}{K}N_t \right)]. \]  

(4)

One more model, which can exhibit complicated dynamical behaviors, is the Gompertz difference equation. Originally, it was

![Bifurcation diagrams](image)

**Fig. 1.** Bifurcation diagrams of continuous-state dynamics (left column) and their discrete-state counterparts (right column). \( K = 1000 \), 4000 iterates are shown for each of the parameter \( r \) values. (a) The continuous-state logistic model (1). Examples of regular time series (at \( r = 2.2 \)) and irregular time series (at \( r = 2.8 \)) are displayed in the upper and lower insets, correspondingly. For the irregular time series the dominant Lyapunov exponent \( \lambda = +0.44 \). Positive Lyapunov exponent is a hallmark of chaos (Boccara, 2004). To calculate the Lyapunov exponents, we followed the method given in [Kantz and Schreiber, 1997]. (b) The discrete-state logistic model (2). Time series at \( r = 2.2 \) and at \( r = 2.8 \) are displayed in the upper and lower insets, correspondingly. (c) The continuous-state Ricker model (3), \( r = 17, K = 1000, c = 1 \). (d) The discrete-state Ricker model (4), \( r = 17, K = 1000, c = 1 \). (e) The continuous-state Gompertz model (5), \( r = 2.7, K = 1000 \). (f) The discrete-state Gompertz model (6), \( r = 2.7, K = 1000 \).
worked out by Benjamin Gompertz (Gompertz, 1825) in order to describe human mortality in the assumption that a person’s resistance to death decreases exponentially as his years increase. The Gompertz equation also appears in fisheries ecology (Fox, 1970). Here, we use the Gompertz map in the form:

\[ N_{t+1} = -rN_t \ln \frac{N_t}{K} + N_t. \]  

(5)

In Eq. (5) \( N \) is the population size, \( t \) is time; the population growth rate \( \dot{R} = r \ln(N_t/K) \), where \( K \) is the carrying capacity, and \( r \) is a model constant. The discrete-state version of the Gompertz difference equation (5) is

\[ N_{t+1} = \text{int}\left[ -rN_t \ln \frac{N_t}{K} + N_t \right]. \]  

(6)

In order to assess the role of noise treatment, we consider two types of the treatment. Specifically, the noisy analogs of Eq. (2) are

\[ N_{t+1} = \text{int}\left[ r(1 + \sigma \nu)N_t \left( 1 - \frac{N_t}{K} \right) + N_t \right] \]  

(7)

and

\[ N_{t+1} = \text{int}\left[ rN_t \left( 1 - \frac{N_t}{K(1 + \sigma \nu)} \right) + N_t \right]. \]  

(8)

Here and throughout the paper \( \sigma \) measures the intensity of the noise, while \( \nu \) is a standard normal random variable.

The noisy analogs of Eq. (4) are

\[ N_{t+1} = \text{int}\left[ r \exp(\sigma \nu)N_t \exp\left( -\frac{C}{K}N_t \right) \right] \]  

(9)

and

\[ N_{t+1} = \text{int}\left[ rN_t \exp\left( -\frac{C}{K(1 + \sigma \nu)}N_t \right) \right]. \]  

(10)

Notice that Eq. (9) coincides with Eq. (3) in Henson et al. (2001). Finally, the noisy analogs of Eq. (6) are

\[ N_{t+1} = \text{int}\left[ -r \ln(e + \sigma \nu)N_t \ln \frac{N_t}{K} + N_t \right] \]  

(11)

and

\[ N_{t+1} = \text{int}\left[ -rN_t \ln \frac{N_t}{K(1 + \sigma \nu)} + N_t \right]. \]  

(12)

It is obvious that at \( \sigma = 0 \) Eqs. (7)–(12) become noise free and describe purely deterministic changes in the population size.

3. Integer-based deterministic dynamics

Fig. 1 allows to compare the bifurcation diagrams of the continuous-state models (1) (Fig. 1a), (3) (Fig. 1c) and (5) (Fig. 1e) with the bifurcation diagrams, which are obtained with the discrete-state versions of the models above, i.e. with the use of Eqs. (2), (4) and (6) (Fig. 1b, d and f, correspondingly). The continuous-state bifurcation diagrams show transition from steady states to regular oscillations (as an example see the upper inset in Fig. 1a), and then through the period-doubling routes to chaotic dynamics (an example of the chaotic oscillations is shown in the lower inset in Fig. 1a). At first glance, the discrete-state bifurcation diagrams in the right column (Fig. 1) look similar to those of the continuous-state models (the left column in Fig. 1). The only visible difference is the greater rarefaction of the discrete-state diagrams in the “chaotic” regions in comparison with their continuous-state counterparts.

However, the seemingly irregular oscillations (as an example, see the lower inset of Fig. 1b), which arise as a result of the period-doubling bifurcations in the discrete-state models (2), (4) and (6), in fact turn out to be non-chaotic. Fig. 2 demonstrates the power spectra of the time series, sections of which are shown in the lower insets in Fig. 1a and b. One can see that the power spectrum of the continuous-state dynamics (Fig. 2a) has the broad continuous component that is a hallmark of chaotic dynamics (Ott, 2002). In contrast to the spectrum shown in Fig. 2a, the power spectrum of the discrete-state dynamics (Fig. 2b) consists of discrete components, which are typical of a regular, non-chaotic behavior.

The difference in the nature of the continuous-state and discrete-state dynamics is also evident from comparison of the appropriate recurrence plots (Fig. 3). The recurrence plots depict how phase trajectories return or repeat itself. Fig. 3a depicts the recurrence plot for the chaotic time series generated by the continuous-state model (1). This recurrence plot has a complicated structure typical of chaotic dynamics (Eckmann et al., 1987). However, the discrete-state analog (2) of the model (1) under the same parameter values generates the regular recurrence plot, which reflects periodic changes of the population size (Fig. 3b), even though the section of the time series (the lower inset in Fig. 1a) looks as irregular.

![Fig. 2. Power spectra. (a) The chaotic dynamics, which arise in the continuous-state logistic model (1); (b) The dynamics arising in the discrete-state model (2) at the same value of the parameter \( r \) as in (a). In both cases \( r = 2.8, K = 1000 \).](image)
Noteworthy that periodicity in the discrete-state dynamics can collocate with the sensitive dependence on initial conditions that is often considered as a hallmark of chaotic behavior. In the simplest case, a change in initial conditions just leads to a phase shift in the population size oscillations. Fig. 4 gives an example of such sensitive dependence. One can see how a section of the time series displaces in time as the initial population size is slightly changed. Notice that the non-chaotic discrete-state time series, which are parametrically correspond to chaotic continuous-state time series, often consist of periodically repetitive sections of the irregular population size oscillations.

Fig. 5 represents an example of even more dramatic changes in the character of population size oscillations resulting from the sensitive dependence of the discrete-state population dynamics on initial conditions. Namely, one can see three types of regular oscillations (Fig. 5), which are a result of changes in the initial population size \( N_0 \). We performed massive calculations with the use of all three discrete-state models: (2), (4) and (6), in order to reveal the different attractors, which correspond to different \( N_0 \) values. Fig. 6 presents five attractors of the discrete-state Ricker model (4), which arise at different values \( N_0 \). The model parameter values remain unchanged and the same for each of these competitive attractors. Fig. 7 demonstrates four competitive regular oscillatory regimes (attractors) in the Gompertz model (6). All the discrete-state competitive attractors (Figs. 5–7) arise under the model parameter values, which correspond to chaotic continuous-state dynamics (see Fig. 1).

Fig. 8 presents an example of an extended description of the dependence of the population dynamics on initial conditions. The three attractors, which are seen in Fig. 8 (see also Fig. 5), differ in the length \( L \) of the periodically repetitive sections of which the time series are composed. Within each of the sections the population abundance can oscillate in an irregular way. One can see (Fig. 8) that in this case the time series with \( L = 14 \) are more probable since they occur with a greater frequency than the others, i.e. with \( L = 9 \) and \( L = 4 \).

The integerized models (2), (4) and (6) are noise free. However, environmental noise can have an essential impact on population
Namely, added noise is expected to make integer-based model systems behave similarly to their continuous-state counterparts (Scheuring and Domokos, 2007). It has been shown, however, that added noise does not necessarily lead to either purely stochastic or chaotic dynamics (King et al., 2002). With the use of models (7)–(12), we evaluate effects of noise treatments on predictability of the model integer-based population dynamics.
4. Noise treatments

In order to assess quantitatively the predictability of irregular oscillations, which arise in models (7)–(12), we use the algorithm proposed in Kaplan and Glass (1995). This algorithm makes possible the comparison of “real” oscillations and predicted changes of the population size $N_t$. Namely, for a time series $N_t$ where $t \in [0, T]$, this algorithm implies:

(1) construction of the vector 
$$N_{T/2} = (N_{T/2}, N_{(T/2)-1}, N_{(T/2)-2}, \ldots, N_{(T/2)-d}).$$

where $d$ is the so-called embedding dimension (Ott, 2002);

(2) searching at the interval $[0, T/2]$ the $d$-dimensional vectors 
$$\tilde{P}_i = (P_{i}, P_{i-1}, P_{i-2}, \ldots, P_{i-(d-1)}), \quad i = 1, 2, \ldots, m,$

such that 
$$|N_{T/2} - \tilde{P}_i| < \varepsilon \ll 1;$$

(3) prediction of the value 
$$N_{T/2+1} = \frac{1}{m} \sum_{i=1}^{m} \tilde{P}_{i+1};$$

(4) construction of the vector $N_{T/2+1}$ according to item (1) above and taking into account that the value $N_{T/2+1}$ is known now;

(5) the next iteration at the interval $[0, T/2+1]$, and following iterations until the point $T$ is reached.

(6) calculation of the prediction error. The prediction error is given as (Medvinsky and Rusakov, 2011)
$$E = \frac{1}{N_{1-T/2+1}} \sum_{i=1}^{N_{1-T/2+1}} |N_{i} - N_{i-1}| \quad (13)$$

To assess quantitatively the horizon of predictability ($t_H$) we specify a limiting value $E_L \ll 1$ (in our case, $E_L = 0.1$). The horizon of predictability is a point, where predictability moves into uncertainty (Kraivtsov and Kadtk, 1996). You can see clearly up to this horizon but not beyond it. The horizon of predictability of chaotic time series has been shown to be dependent on the value of the dominant Lyapunov exponent (Boleta et al., 2002) and also on the characteristic size of the chaotic attractor (Medvinsky and Rusakov, 2011).

Fig. 7. Attractors of the discrete-state Gompertz model (6) under different initial conditions: (a) $N_0 = 389$; (b) $N_0 = 404$; (c) $N_0 = 405$; (d) $N_0 = 429$. In all the cases $r = 2.7$, $K = 1174$.

Fig. 8. The dependence of the length ($L$) of the periodically repetitive sections of which the time series are composed on initial conditions for the discrete-state logistic model (2). Here, $N_0 \in [200, 450]$. The model parameters: $r = 2.8$, $K = 1268$. 
reach the limiting value $E_r$, is equal to 28 time steps. The value $E$ varies from one computer experiment to another; in the average the horizon of predictability $t_H$ for the map (9) under $\sigma = 0.0001$ is roughly equal to 20 time steps. Notice that the imposition of the same noise on continuous-state chaotic Ricker dynamics yields $t_H$ to be, on average, equal to 15 time steps. The difference between the values of $t_H$ obtained for the continuous-state chaotic Ricker dynamics and their discrete-state noisy counterparts dies out as the noise intensity $\sigma$ increases. Under $\sigma = 0.01$ the averaged values of the horizon of predictability of the discrete-state and continuous-state dynamics become practically identical and equal to 10 time steps. It is self-evident that for the noise free regular dynamics, which is given by the deterministic skeleton (4), $t_H = \infty$. In contrast to the map (9), the noisy analogs (7) and (11) of logistic and Gompertz skeletons demonstrate transformation of oscillatory regimes into stationary states. In this case the population size does not change in time, and $t_H = \infty$.

Stationary states do not appear if external noise is superimposed on the carrying capacity $K$; see Eqs. (8), (10) and (12). For all these models $t_H$ is approximately 15 time steps at $\sigma = 0.0001$ and almost halved at $\sigma = 0.005$. Nearly the same $t_H$ values are found under the noise treatment of continuous-state chaotic dynamics.

5. Concluding remarks

Paradoxically, many features of complex population dynamics are shown to be described with the use of simple deterministic mathematical models (May, 1976; Hanski, 1999; Kot, 2001; Malchow et al., 2001; Medvinsky et al., 2002; Malchow et al., 2004; Petrovskii and Li, 2006; Schoen, 2006; Solé and Bascompte, 2006). Such models, dealing with only a few basic properties common to different ecosystems, are referred to as conceptual mathematical models (Medvinsky et al., 2002). The logistic difference equation (1), the Ricker map (3) and the Gompertz equation (5) belong to the category of the continuous-state discrete-time conceptual models. The usefulness of conceptual continuous-state models has been demonstrated in a number of studies. For example, predator–prey limit-cycle oscillations and generation and drift of planktonic patches were found in a conceptual phytoplankton–zooplankton interaction model (Malchow, 1993, 1994). Patchy environment has been shown to play an essential role in raising chaotic regimes in plankton dynamics (Medvinsky et al., 2001). However, although continuous-state modeling is accepted widely, it is impossible to ignore that real populations consist of a finite number of discrete individuals. Hence, discrete-state models appear to be biologically more realistic (Coulson et al., 2004).

Interestingly, in contrast to the continuous-state Ricker model (Ricker, 1954), where chaotic regimes can occur, a discrete-state counterpart of the Ricker map has been demonstrated to display only cyclic behavior (Henson et al., 2001). Seemingly, the regular cyclic dynamics should be fully predictable. What we show in this paper (Figs. 4–7) is that regular dynamics can manifest the sensitivity to initial conditions, which is usually considered as a hallmark of chaos (Kaplan and Glass, 1995). Earlier, it has been shown (Medvinsky et al., 2001) that even in the absence of any external impacts coexistence of chaotic and regular attractors resulting from the diffusive interaction between different habitats in a patchy marine environment can lead to virtually unpredictable population size oscillations. In our case, however, the dependence of the regular discrete-state dynamics on initial conditions is a consequence of competition between separate non-chaotic attractors.

We show that emergence of the competing regular attractors in noise free models (2), (4) and (6) is due to splitting of the chaotic attractor when passing from continuous-state description of the population dynamics to the discrete-state models. The corresponding non-chaotic time series are characterized by various values of
the length \( L \) of the periodically repetitive time series sections (Fig. 8). It is remarkable that within these regularly repetitive sections the population abundance is often found to oscillate in an irregular way (see Fig. 4 as an example). In Fig. 8, the length \( L \) takes moderate values: 4, 9 and 14. However, as the carrying capacity \( K \) increases, the range of \( L \)'s enlarges. For example, at \( K = 5 \times 10^5, L \) in the discrete-state logistic model (2) can be of order \( 10^3 \). In order to evaluate numerically chaoticity of the irregular oscillations within the time series sections we use the algorithm, which has been proposed by Kantz and Schreiber (1997). This algorithm let us calculate a value of the dominant Lyapunov exponent (\( \lambda \)). For reasonably large values of \( L \) the values of \( \lambda \) are shown to be positive (as an example, \( \lambda = +0.41 \) under \( r = 2.8, K = 5 \times 10^5 \) for the discrete-state logistic model (2)). Hence, the corresponding irregular oscillations can be considered as chaotic (some examples of the chaotic oscillations are shown in Fig. 10). Notice, that since the sections of the chaotic (but noise free) changes in the population size are repeated periodically, the whole noise free time series appear to be regular, non-chaotic and highly predictable, i.e. the prediction error \( E \) (Eq. (13)) remains to be much less than 1. Such a combination of regular and chaotic features is presented pictorially in Fig. 11, where the regular stripes, which reflect periodicity of the whole time series, are seen to be superimposed on the “chaotic” background (see Fig. 3 for a comparison). Although the time series, which consist of many periodically repeating chaotic sections, are yet highly predictable, there is a factor, which essentially limits predictability of population dynamics on all time scales. This is the noise-induced competition between separate coexisting regular attractors.

As a result of the competition between attractors, even minor changes in the population size stemming from an external noise lead to sudden transitions from one regular attractor to another; therefore predictability of the integer-based population dynamics can be adversely affected. Notice, however, that in models (7) and (11) the external noise induces transition to fully predictable stationary attractor states \( N = K \), which do not depend on the noise intensity \( \sigma \) (in contrast to the “stationary” attractor \( N = (K/c) \ln(re^{\alpha}) \) of the noisy Ricker map, Eq. (9)). The model noise accounts for fluctuations of environmental factors, such as interspecific competition, climatic effects or anthropogenic changes that are not included into the deterministic skeletons (2), (4), and (6). As a result, the noise treatment can lead to fluctuations of the value of \( r \) (as in Eqs. (7), (9) and (11)) that are especially significant at \( N \ll K \), and/or to irregular changes in the carrying capacity \( K \) (see Eqs. (8), (10) and (12)). Investigations of dynamical regimes arising in the noise free deterministic models can be nevertheless useful because they can help us specify the effects associated with an external noise.

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