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Complex Discrete Dynamics from Simple Continuous Population Models

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The concept of chaos in ecological populations is widely known for non-overlapping generations since the early theoretical works of May [1974, 1976], and successively applied to laboratory and field studies [Hassell et al., 1976]. A classical approach using very simple models consist of using discrete, first-order non-linear difference equations for populations with N_i individuals at time i of the form $N_{t+1} = f(N_t)$, where $f(N_t) = aN_tg(N_t, \dots, N_{t-j})$ and $g(N_t, \dots, N_{t-j})$ is some nonlinear function describing some degree of density-dependence with time delay j . In fact, a well-known equation describing a full range of dynamic behaviors was developed by Ricker (1954): $N_{t+1} = \mu N_t e^{-bN_t}$, where μ stands for the discrete initial growth rate, and the initial population N_t is exponentially reduced as a function of some mortality rate $b > 0$.

The use of discrete models, although very popular due to their simplicity, contains serious drawbacks if some biological within-generation properties are to be taken into account. A given population may indeed reproduce at certain fixed time steps; however, its mortality might not be constant, but conditioned by the starvation rate, which in turn depends on the quantity of resources available for the population and its consumption along time between successive generations. How this resource-consumer interaction affects the behavior of the population and how it is related to classical discrete models is crucial if a well-defined dynamic scenario is required.

Continuous models displaying chaos require a minimum of three variables unless: (i) time is explicitly introduced (as when external forcing is considered) or (ii) time delays are at work. In this sense, it is not obvious how to recover the complex dynamics of discrete maps from a continuous formulation of single-species, within-generation dynamics. A fruitful approach was followed by Gyllenberg et al. [1997]. By assigning discrete time steps for reproduction and continuous dynamics for the mortality and population-environment interactions, they concluded that non-monotone maps (such as the Ricker map) would appear in a unstructured population only if an adjustable reproductive strategy was at play (i.e, $\mu = f(x)$, being x an environmental state variable). In this letter we show that this condition is not necessary. In fact, if we describe a mortality rate as dependent on the evolution of the environment itself through a general, population-environment interaction in the continuous phase, we will be able to track a full one-dimensional map in a unstructured population with fixed reproductive strategy.

The Model

We modelled within-generation dynamics with the following simple ODE system of resource-consumer interactions developing on time units t' :

$$\frac{dR}{dt'} = -C \frac{R}{\Gamma} \quad (1)$$

$$\frac{dC}{dt'} = -m \left(1 - \frac{R}{\Gamma}\right) C \quad (2)$$

where m stands for the intrinsic mortality rate in the absence of resources, which is reduced when resources are highly available and Γ is the size of the system (here $R \leq \Gamma$). Let us note that resources (the environmental interaction variable) are only depleted by consumption whereas consumers may constantly die in the absence of resources, or avoid mortality when the system is plenty of available food. Although there is an oversimplification due to the particularity that the consumption efficiency rate has the same value than the mortality rate, the system is able to reproduce the whole set of dynamic behaviors observed in the Ricker map. When the continuous dynamics (after several integration steps) reach the threshold value of within-generation time τ , the discrete phase takes place. Fig. 1a shows a realization in τ within-generation steps .

The updating rules taking place at each discrete step are:

1. After τ steps, surviving individuals reproduce at a growth rate μ .
2. Next, the within-generation process takes place. We have now $R_0(t + \tau) = R^*$, $C_0(t + \tau) = \mu C(t + \tau)$.

Observe that resource levels replace themselves to R^* each discrete $(t + \tau)$ iteration step

Taking τ as the basic iteration step, the resulting dynamics (fig. 1b,c) for resources and consumers may follow, under certain combinations of parameter values, chaotic trajectories describing Ricker-like behavior. Surprisingly, both the continuous-discrete and the discrete Ricker approaches produce similar richness in their dynamic behavior. This agreement suggests that the continuous equation plus the discrete updating at the end of each generation lead to a dynamical system which behaves as a discrete map. This link is easy to prove:

Let us assume, for simplicity, the case when $m = 1$. A separation of variables in eq. 1 gives

$$\frac{dR}{R} = -\frac{C}{\Gamma} dt'$$

which, after integration, becomes

$$R(t + \tau) = \Gamma \exp\left(-\frac{1}{\Gamma} \int_0^\tau C(t') dt'\right)$$

and substituting into eq. 2,

$$C(t + \tau) = C_0(t) \exp\left\{-\left[1 - \exp\left(-\frac{1}{\Gamma} \int_0^\tau C(t') dt'\right)\right] \Delta t\right\} \quad (3)$$

where Δt defines a discrete, unit time step. Now, from numerical resolution (see fig. 1a), we can assume that, for long within-generation times (i.e., $\tau \gg 0$), $C(t + \tau) \sim C_0(t) \exp(-\alpha\tau)$. Thus, we can solve the integral from eq. 3:

$$\int_0^\tau C(t') dt' = \frac{C_0(t)}{\alpha} [\exp(-\alpha\tau) - 1] \quad (4)$$

which, due to the assumption $\tau \gg 0$, becomes $\int_0^\tau C(t') dt' = C_0(t)/\alpha$. Thus, eq. 3 now reads

$$C(t + \tau) = C_0(t) \exp\left(-\frac{C_0(t)}{\Gamma\alpha} \Delta t\right)$$

Recalling our first assumption of exponential decay of consumers within the generation time, $\alpha = \sqrt{C_0(t)/\Gamma}$, and taking a discrete step of one iteration, finally the continuous-discrete scheme can be simplified after applying the reproductive rate:

$$C_0(t + \tau) = \mu C_0(t) \exp\left(-\sqrt{\frac{C_0(t)}{\Gamma}}\right) \quad (5)$$

If we relax the first assumption and assume $\tau \rightarrow 0$, then a Taylor series expansion of eq. 4 gives $\int_0^\tau C(t') dt' = -C_0(t)\tau$, giving eq. 3 the form

$$C(t + \tau) = C_0(t) \exp\left(-\frac{C_0(t)\tau}{\Gamma} \Delta t\right)$$

Thus, assuming exponential decay of consumers, and taking a discrete iteration step, the discrete approximation of the hybrid model now reads

$$C_0(t + \tau) = \mu C_0(t) \exp\left(-\frac{C_0(t)\tau}{\Gamma}\right) \quad (6)$$

Not surprisingly, the system reduces in both eqs. 5 and 6 to a first-order difference Ricker-like map (Fig. 1b) under the two limit approaches (i.e., $\tau \rightarrow 0$ and $\tau \rightarrow \infty$). In these two limit cases, the stability conditions, for the non-trivial fixed points $C_{\tau \rightarrow \infty}^* = \Gamma (\log \mu)^2$ and $C_{\tau \rightarrow 0}^* = \Gamma (\log \mu) / \tau$ are $\mu_{\tau \rightarrow \infty}^* = e^4$ and $\mu_{\tau \rightarrow 0}^* = e^2$, respectively. The corresponding bifurcation diagram for the original continuous-discrete system (Fig. 1d for $\tau = 10$) shows, under the range of τ considered in our model, that the second approximation is closer to our original model (where $\mu^* \sim \tau \parallel 4 \leq \mu^* \leq 11$).

Individual-based approach: handling space availability

Our hybrid model incorporates a within-generation dynamics that introduces new degrees of complexity into the Ricker-like dynamics. One might argue that perturbations of this continuous motion should strongly modify the discrete dynamics. The most likely source of change is the stochastic nature of individual behavior, and here we show that our results are robust. In pursuit of realism, it is necessary to account for an explicit representation of random demographic fluctuations in the search of food by individuals (as a form of indirect competition). In order to model the stochastic, continuous-discrete dynamics we proceeded to build a model based on individual rules featuring a Ricker-like system. Thus, interactions taking place in the individual-based model come as random series of instantaneous events [Wilson, 1998]. The model, simplified from Solé et al. [1999], is a well-mixed system of Γ cells, where one unit of resource r_i , $R = \sum r_i$ and/or consumer c_i , $C = \sum c_i$ may (or not) be present. For the simplest case, let us assume $m = 1$. In this case individual rules for within-generation dynamics are:

$$\text{If } c_i = 1 \text{ and } r_i = \begin{cases} 1 & \rightarrow r_i = 0 & \text{Resource consumption} \\ 0 & \rightarrow c_i = 0 & \text{Consumer death} \end{cases}$$

Next, consumers move to a randomly chosen cell (i.e., the system shows global mixing) and individual rules start again until the within-generation time τ is accomplished. At this point, every surviving individual lays μ newborns and dies and another generation starts with $R = \Gamma$. Typically, $C_0(t + \tau) \leq \Gamma$, so redistribution of newborns is another process of competition for available space. Dispersal must be as well a source of stochasticity. In a well-mixed model the probabilistic events taking place for dispersal may come by assigning a handling time in the search for available space in newborns. In a metapopulation-like context, this handling time resembles the searching parameter for juveniles in Lande’s model for the northern spotted owl [Lande, 1987]. For example, if a newborn falls in a cell that is already occupied by another newborn, it has the opportunity to look for free space during certain “time-steps”. Let us indicate the potential number of newborns as $N_t = \mu C(t + \tau)$. There is a handling time of search for free cells h . Then, the probability for a newborn i of finding a free space follows the distribution (see Fig. 2c)

$$P(i, h) = 1 - \left(\frac{i-1}{\Gamma}\right)^h \tag{7}$$

and thus

$$C_0(t, h) = \sum_{i=1}^{N_t} P(i, h) \tag{8}$$

Fig. 2a,b presents two simulations where the individual model behaves as a unimodal Ricker map. For high h , the results match those of the continuous-discrete deterministic counterpart, but with some noise added to the system. Low values of h decrease the number of newborns appearing at discrete steps, thus, the initially chaotic behaviour becomes an almost two-point cycle dynamics with random noise. This probabilistic approach to the dispersal and redistribution of offspring may represent a new constraint to the saturation of environmental resources by some populations and consequently, to the capacity of the population to amplify its range of dynamic behavior by means of a simple density-dependence restriction.

This approach, though simplistic, match very well the results obtained from the deterministic model.

We have tested the same model, but with non-constant m , and the results do not vary the qualitatively strong behavior offered by the Ricker map. A straight mean-field model approach including the handling time restriction would require solving eq. 8:

$$C_0(t, h) = N_t - \frac{1}{\Gamma^h} \sum_{i=1}^{N_t} (i-1)^h \quad (9)$$

Taking the sum and integrating over N_t we get:

$$\int_1^{N_t} (x-1)^h dx = \frac{(N_t-1)^{h+1}}{h+1} \quad (10)$$

Thus, the corrected initial population at the beginning of the discrete step is defined as

$$C_0(t, h) = N_t - \frac{(N_t-1)^{h+1}}{(h+1)\Gamma^h} \quad (11)$$

Finally, under the assumption of exponential decay in the within-generation dynamics, the application of a handling time in eqs. 5 and 6 would involve two new maps:

$$C_0(t + \tau) = \left[\mu C_0(t) - \frac{(\mu C_0(t) - 1)^{h+1}}{(h+1)\Gamma^h} \right] \exp \left(-\sqrt{\frac{C_0(t)}{\Gamma}} \right) \quad (12)$$

$$C_0(t + \tau) = \left[\mu C_0(t) - \frac{(\mu C_0(t) - 1)^{h+1}}{(h+1)\Gamma^h} \right] \exp \left(-\frac{C_0(t)\tau}{\Gamma} \right) \quad (13)$$

respectively. Numerical simulations have showed a strong fit between these equations and the results obtained from the individual-based models in fig. 2a,b.

Conclusions

The characterization of chaotic dynamics by means of a well-suited model with basic rules of individual behavior has been presented. In order to achieve a better comprehension of ecological processes, biological plausibility must pervade in future models of population dynamics. Thus, the modelling of non-overlapping generations must account, in some cases, for the continuous dynamics present when some events such as resource consumption, predation, interaction and mortality are at play. As some authors advocate, a proper

mathematical representation must define functional responses on a continuous basis and reproduction on a discrete basis in order to solve controversies such as the old one on prey- and ratio-dependent theory [Abrams and Ginzburg, 2000]. As we show, the basic constraints that must be present in non-overlapping populations in order to fit a unimodal map are: (i) some density-independent mortality and strong consumption efficiency in a continuous phase and (ii) high reproductive rates at the end of the generation. Furthermore, we add a new restriction (by means of the handling time as a surrogate for density-dependent space occupation) that is able to modify the spectrum of behaviours.

Our approach (the deterministic, the analytical approximation, the individual based stochastic and the handling-time restriction models) matches the dynamics resulting from the application of a simple unimodal Ricker equation, and gives support in ecology to the increasing use of continuous-discrete hybrid models in control systems, as well as some related time-series techniques (such as intervention analysis).

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Abstract

Non-overlapping generations have been classically modelled as difference equations in order to account for the discrete nature of reproduction events. However, other events such as resource consumption or mortality are continuous and take place in the within-generation time. We have realistically assumed an hybrid ODE bidimensional model of resources and consumers with discrete events for reproduction. Numerical and analytical approaches showed that the resulting dynamics resembles a Ricker map, including the doubling route to chaos. Stochastic simulations with a handling-time parameter for indirect competition of juveniles may affect the qualitative behavior of the model.

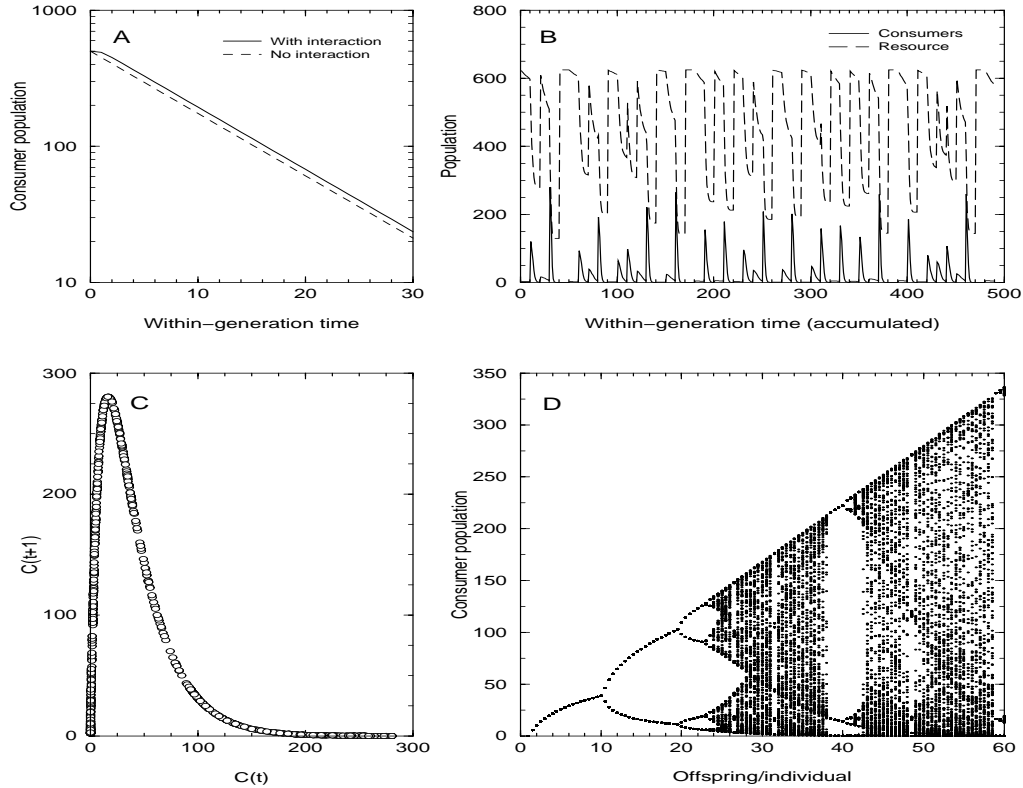


Figure 1: Deterministic hybrid Ricker model. A, exponential decay of consumers within the generation time with and without resource-consumer interaction. We can see a very well defined exponential decay. B, time response of consumers and resource. C, Ricker map resulting from a realization of the hybrid model. D, bifurcation diagram, showing 200 discrete steps after a transient of 200 has been discarded. Here, $\Gamma = 625$, $m = 1$, $\mu = 50$; $\tau = 10$ for B-D. Deterministic hybrid Ricker model. A, exponential decay of consumers within the generation time with and without resource-consumer interaction. We can see a very well defined exponential decay. B, time response of consumers and resource. C, Ricker map resulting from a realization of the hybrid model. D, bifurcation diagram, showing 200 discrete steps after a transient of 200 has been discarded. Here, $\Gamma = 625$, $m = 1$, $\mu = 50$; $\tau = 10$ for B-D.

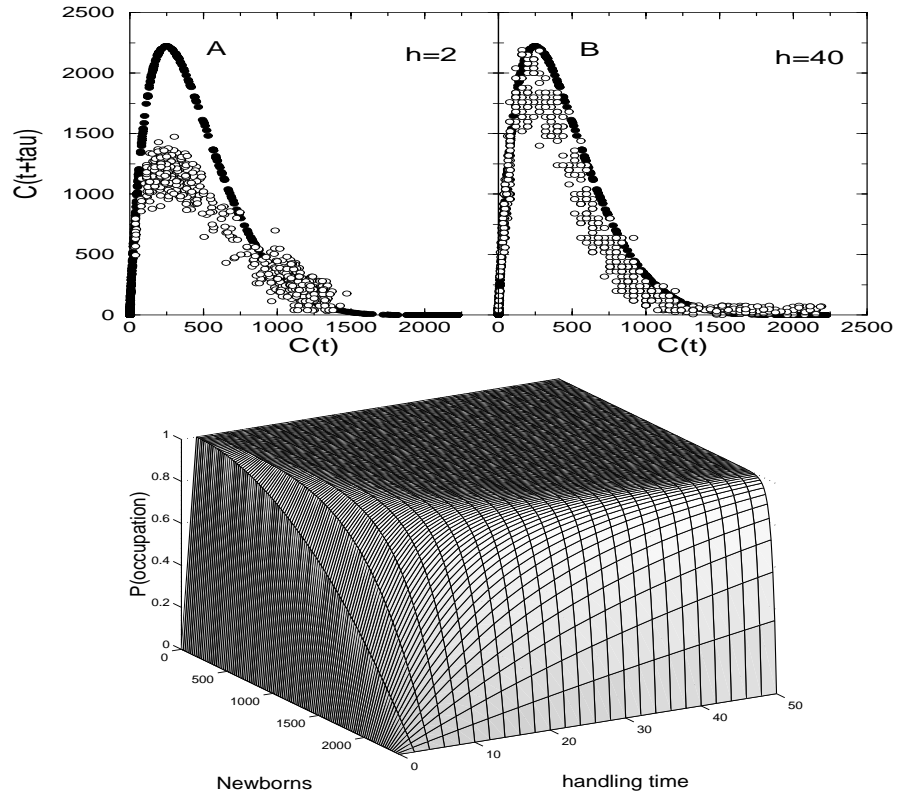


Figure 2: State-space maps for the individual model (open circles), showing the matches with the deterministic model (filled circles) for: A, $h = 2$; B, $h = 40$. C: probability of a newborn to get a free space with handling time h (eq. 7). $\Gamma = 2380$, $m = 1$, $\mu = 40$, $\tau = 5$.