

# Chaotic oscillations and cycles in multi-trophic ecological systems

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## Abstract

A set of multi-trophic population models are described, all of which yield an interesting form of chaotic dynamics—namely, the populations cycle in a periodic fashion, yet the peak abundance within each cycle is erratic and irregular over time. Since there are many ecological and biological systems that are characterized with this same form of “uniform phase-growth and chaotic amplitude (UPCA),” these models should be useful in a range of applications. We discuss their relevance to the well-known Canadian hare-lynx system, and other small mammal foodwebs which together comprise wildlife’s unusual “four and ten year cycle.” The dynamics of the model equations are analysed and an explanation is given as to the source of the UPCA dynamics in the new class of foodweb systems presented, and in others found in the literature.

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## 1. Introduction

The cycling of predator–prey populations has long been of great fascination to animal naturalists and must surely be viewed as one of the major research themes in Ecology over the last century (Seton, 1912; Elton and Nicholson, 1942; Hanski et al., 1993; Bascompte et al., 1997; Stenseth et al., 1997). From a theoretical perspective, the mechanisms that lead to these (often periodic) cycles were successfully explained by Lotka and Volterra in their now famous two-species predator–prey model which admit neutrally stable limit cycle solutions (Lotka, 1925; Volterra, 1926). In a more recent study, Hastings and Powell (1991) examined the complex nonlinear behaviour of three-species continuous-time ecological models and found them to be characterised by a far richer spectrum of dynamics than their well studied two species counterparts. In particular, they highlighted that three-species foodweb models are able to generate chaotic oscillations and thus have relevance for the study of more complex population dynamics. Two-species autonomous models, on the other hand, can never yield chaotic dynamics (as a direct consequence of the

Poincaré–Bendixon Theorem). The Hastings and Powell (1991) study initiated a concerted effort amongst theoretical ecologists who sought to analyse the subtle dynamics of these nonlinear multi-trophic models (Klebanoff and Hastings, 1994; Rinaldi et al., 1996; McCann and Hastings, 1997; De Feo and Rinaldi, 1998; Kuznetsov et al., 2001; Vandermeer, 1996).

Here we extend previous work on continuous time ecological models by providing a new class of foodweb equations that are specifically designed to match realistic features observed in many population cycles, but often overlooked in theoretical analyses. The class of models we have in mind should be able to reproduce the two following characteristics (c.f. Krebs and Myers, 1974; Schaffer, 1984):

1. The frequency of the population “cycle” must be relatively constant.
2. In contrast, the amplitude of the population fluctuations is highly variable.

As Schaffer, 1984 emphasized, the classic Canadian hare-lynx cycle has a relatively stable period of approximately 10 years yet the amplitude of each cycle has remarkable

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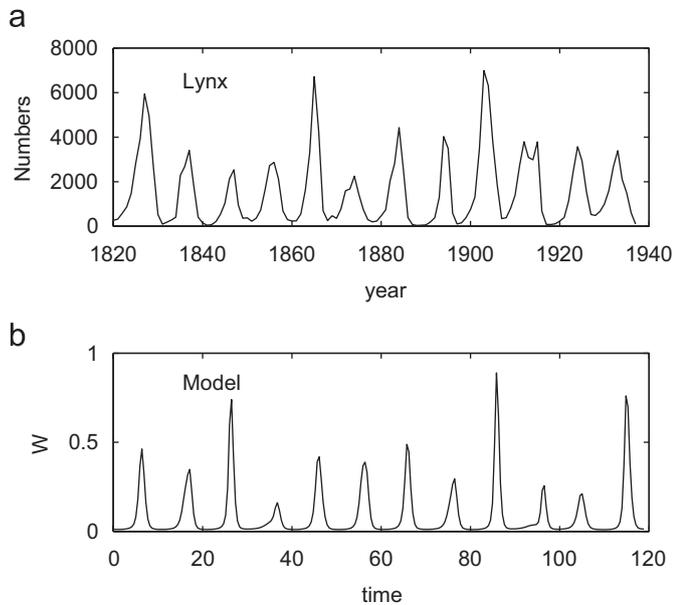


Fig. 1. (a) Ten-year cycle in the Canadian lynx in the Mackenzie river area (1821–1937) after (Elton and Nicholson, 1942) and (b) chaotic time-series of top predator,  $w$ , in the foodweb model (1).

irregularity (see Fig. 1). According to the historical record, this cycle has persisted for at least a quarter of a millenia (Elton and Nicholson, 1942). The same sort of pattern has been observed for many other small mammal cycles. Krebs and Myers (1974) wrote that: “Vole and lemming populations undergo fluctuations which comprise one of the classic unsolved problems of animal ecology. Two facets of these fluctuations have interested ecologists: their cyclic periodicity and their [erratic] amplitude.” Many seasonally forced systems also exhibit this phenomenon. Annual phytoplankton blooms, for example, regularly recur at the same time of year but with unpredictable amplitude.

Although other models are capable of producing oscillations with chaotic abundances, they fail to reproduce the regular frequency (or ‘rhythm’) that is associated with the hare-lynx, and many other animal cycles. The two features of Uniform Phase evolution (i.e., constant rhythm) and Chaotic Amplitudes—henceforth UPCA—are common in many biological settings, yet few realistic models are capable of producing this dynamic (see Blasius et al., 1999; Blasius and Stone, 2000).

Fig. 1 gives a comparison of Canada lynx cycle and chaotic time series of foodweb model we describe soon below.

The Hastings and Powell (1991) model was an important contribution to ecological theory, because it made clear that simple tritrophic “vertical” foodweb systems are nevertheless capable of yielding complex chaotic oscillations—a possibility that had not been exploited until their study. For the three-species system with populations ( $X, Y, Z$ ), chaos was achieved by choosing “parameter values that would lead to cycling in the pair of species  $X$  and  $Y$ , with  $Z$  absent, and also, with  $X$  constant, the pair  $Y$

and  $Z$ .” The two oscillations at different time-scales successfully induced chaotic dynamics. Other techniques have been exploited to drive three-species systems into chaos. Inoue and Kamifukumoto (1984), and Vandermeer (1996) have shown that the Lotka–Volterra predator–prey system yields complex oscillations if driven by periodic forcing. See also the works of Kot et al. (1992); Gragnani and Rinaldi (1995) and Stone et al. (2007) for descriptions of other forced chaotic ecological and epidemiological models. May and Leonard (1975) and Gilpin (1973) demonstrated that systems of cyclic competition could also develop chaotic oscillations. A variety of other ecological and epidemiological models appear in the literature. But, again, none of these model foodweb structures produced the UPCA dynamics we seek to describe.

## 2. “UPCA” foodweb models

We study a vertical foodweb structure with vegetation ( $x$ ) grazed on by herbivores ( $y$ ) which in turn are fed on by predators ( $z$ ) with the following model:

$$\begin{aligned}\dot{x} &= a(x - x_0) - \alpha_1 f_1(x, y), \\ \dot{y} &= -b(y - y_0) + \alpha_1 f_1(x, y) - \alpha_2 f_2(y, z), \\ \dot{z} &= -c(z - z_0) + \alpha_2 f_2(y, z),\end{aligned}\quad (1)$$

where  $a$ ,  $b$  and  $c$  represent the respective growth/mortality rates of each trophic species in the absence of interspecific interactions. Without loss of generality the equations may always be rescaled so that  $a = 1$ . In Blasius et al. (1999) and Blasius and Stone (2000) prey–resource interactions ( $f_1$ ) were incorporated into the equations via a Holling type II term, while predator–prey ( $f_2$ ) interactions were represented by a standard Lotka–Volterra term. We also included the possibility of modelling a scenario in which the predator has alternative food sources ( $z_0$ ) available when its usual prey  $y$  is scarce (Gotelli, 1995). This allows the predator ( $z$ ) to maintain a low equilibrium level  $z = z_0$  even though its usual prey ( $y$ ) is rare. The effect may be made more general by further supposing that other alternative consumers and predators can affect both  $x$  and  $y$  as well, through the terms  $x_0$  and  $y_0$ .

The above model should, for example, sketch the major ecological transfers involved in the Canadian lynx-hare-vegetation foodweb, whose dynamics are dependent on three vertical trophic levels (Keith, 1963; Stenseth et al., 1997). There is a known strong vertical structure in this foodweb. That the hare population is an absolutely vital component of the lynx diet is best understood from Seton’s (1912) early study of the lynx: “It lives on Rabbits, follows the Rabbits, thinks Rabbits, tastes like Rabbits, increases with them, and on their failure dies of starvation in the unrabbitted woods.” More recently, however, it has been found that alternative prey (eg., the red squirrel) may also sometimes be of importance to the lynx population (O’Donoghue et al., 1998), but the overwhelming foodweb structure is “vertical.” Furthermore, current wisdom

suggests that the classical two-level system (i.e., hare and lynx only) is too simplistic, and vegetation is a third key variable that must be included in any model if it is to reflect the dynamical features of this system accurately (Stenseth et al., 1997).

Here we examine one of the simplest possible foodweb models which is able to generate UPCA dynamics. All species interaction terms are taken to be purely of the bilinear Lotka–Volterra form:

$$\begin{aligned} \dot{x} &= (x - x_0) - \alpha_1 xy, \\ \dot{y} &= -by + \alpha_1 xy - \alpha_2 yz, \\ \dot{z} &= -c(z - z_0) + \alpha_2 yz \end{aligned} \tag{2}$$

The model is simpler than that studied in Blasius et al. (1999) which used nonlinear Holling Type II interactions. The simplification also makes the model more amenable to mathematical analysis, as will be seen.

Fig. 2 gives time-series of the system which reveals the UPCA dynamics of model equations (2). The graphs make clear how all variables cycle very regularly in phase yet the amplitude dynamics are quite unpredictable. The chaotic nature of the system is also captured in Fig. 2 which shows a projection of the attractor in the  $(x, y)$  plane. The trajectory spirals chaotically around an unstable focus almost, but not quite, following a closed circle.

### 3. The heart of the UPCA mechanism

The above UPCA foodweb models have similarity, both in structure and dynamics, to the Rössler equations which are widely used in nonlinear physics, and which also possess UPCA dynamics. Consider then the Rössler

equations:

$$\begin{aligned} \dot{x} &= -y - z, \\ \dot{y} &= x + ay, \\ \dot{z} &= z(x - c) + b \end{aligned} \tag{3}$$

with  $a = 0.2, b = 0.2$  and  $c = 5.7$ .

In Fig. 3 we plot the time series and the attractor of the Rössler equations. By comparing this with Fig. 2, one immediately sees the similarity between the Rössler and foodweb models, both in terms of the UPCA dynamics and the structure of the attractor. However, as written in the form above, the Rössler equations have little ecological relevance since:

- (a) the  $x$  and  $y$  variables of the Rössler model take on negative values. The variables of the foodweb model on the other hand, once in the positive orthant, remain there for all time i.e. the positive orthant is invariant. It is wrong to believe that a trivial change of coordinates to the Rössler will result in this property. Such a change of coordinates might be helpful in ensuring that the final attractor remains in the positive orthant, but due to the lack of invariance, the Rössler trajectory still has the potential to leave the positive orthant after a perturbation.
- (b) The structure of the Rössler equations does not appear to translate directly into ecological terms, and appears to lack the vertical tritrophic form of the foodweb model.

Note that the second criticism (b), is somewhat misleading. The vertical structure of the Rössler equations

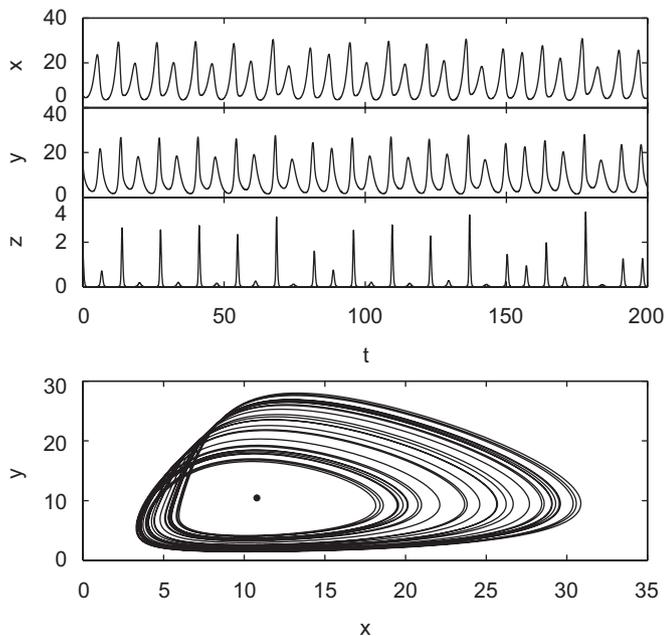


Fig. 2. Simulation results of model equations (2). Time series of  $x, y, z$  and projection of attractor into the  $(x, y)$  plane. Parameters:  $(b = 1, c = 10, \alpha_1 = 0.1, \alpha_2 = 0.6, x_0 = 1.5, z_0 = 0.01)$ .

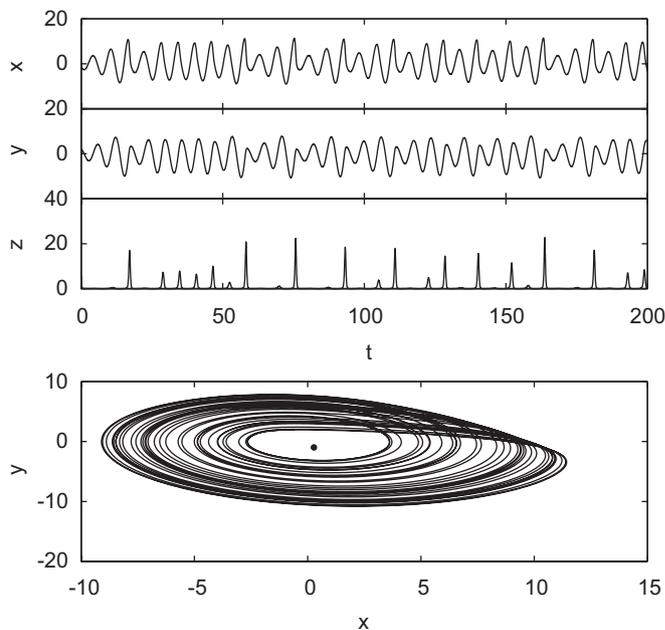


Fig. 3. Simulation results of the Rössler model equations (3). Time series of  $x, y, z$  and projection of attractor into the  $(x, y)$  plane. Parameters:  $a = 0.2, b = 0.2, c = 5.7$ .

becomes more transparent after the simple change of variables  $u = -y, v = x, w = z$  which gives

$$\begin{aligned} \dot{u} &= au - v, \\ \dot{v} &= u - w, \\ \dot{w} &= w(v - c) + b. \end{aligned} \tag{4}$$

In this form, the Rössler equations might describe a system in which  $w$  eats  $v$  which consumes  $u$  and for which all interactions but one are linear.

We now explain in simple terms, the mechanism which leads to UPCA in the Rössler equations (3) since it helps understand the similar dynamics of the foodweb model. Consider first the two variable system ( $z = 0$ ):

$$\dot{x} = -y, \quad \dot{y} = x + ay, \tag{5}$$

which are the classical equations for damped simple harmonic motion, with fixed point at the origin  $(x^*, y^*) = (0, 0)$ . Equivalently these equations can be written in the form of the second order ODE:

$$\ddot{x} - a\dot{x} + x = 0. \tag{6}$$

When  $a = 0$  the equation yields the usual simple harmonic motion (SHM) with  $x(t) = A \cos(t) + B \sin(t)$ . When there is damping ( $a \neq 0$  and  $|a| < 2$ ), the solution then reads  $x(t) = \exp(at/2)[A \cos(\sqrt{1 - (a/2)^2} t) + B \sin(\sqrt{1 - (a/2)^2} t)]$ . Hence when  $0 < a < 2$ , the fixed point is unstable and the solution is an exponentially growing cycle spiralling in the  $(x, y)$  plane.

For the full 3-variable system,  $z$  acts as a trigger variable. Whenever  $x$  is less than the threshold value  $c$ , then  $z$  may be approximated as  $z = b/(c - x)$  and being small, has little effect on the unstable cycle as it ‘stretches’ (or amplifies) in the  $(x, y)$  plane (Fig. 2c). However, when  $x$  grows larger than the threshold level ( $x > c$ ), the growth rate of  $z$  changes from negative to positive. At this point,  $z$  triggers and increases in growth exponentially, but only later to decrease as  $x$  (undergoing spiral motion) drops below the threshold. This drop in  $z$  ‘folds’ the system back towards the origin, and acts as a reset by preventing the  $x$  and  $y$  variables from increasing with unbounded growth. The stretching and folding act together to generate chaos.

Consider now the foodweb model equations (2). Some preliminary insights can be gained from a study of the model’s fixed points. As shown in Appendix A, the foodweb model has three unstable equilibrium points. For the relevant regime where  $z_0 \ll 1$ , two of these unstable equilibria are non-negative and for the given parameter values may be estimated as (see Appendix):  $E_1: (x^*, y^*, z^*) = (x_0, 0, z_0) = (1.5, 0, 0.01)$   $E_2: (x^*, y^*, z^*) \approx (b/\alpha_1, 1/\alpha_1 - x_0/b, cz_0/(c - \alpha_2 y^*)) = (10, 8.5, 0.02)$ .

It is evident from Fig. 2 that the chaotic cycle seen in the  $(x, y)$  plane is centred about the unstable fixed point or focus,  $E_2$ , around which it spirals. The frequency of the rotation is almost constant and may be estimated from a study of the fixed point’s eigenvalues as we show shortly.

Similar to the Rössler equation, the oscillatory nature of the foodweb model derives from the subsystem comprised of the two lower trophic levels. To see this better, consider the foodweb model equations (2) after removing the top-predator ( $z$ ):

$$\begin{aligned} \dot{x} &= (x - x_0) - \alpha_1 xy, \\ \dot{y} &= -by + \alpha_1 xy. \end{aligned} \tag{7}$$

The system has two equilibria.

- (a)  $E_1: (x^*, y^*) = (x_0, 0)$  with eigenvalues  $\lambda_1 = 1, \lambda_2 = -b + \alpha_1 x_0 < 0$ , for the parameters given here. The eigenvalues tell us that this is a saddle point.
- (b)  $E_2: (x^*, y^*) = (b/\alpha_1, 1/\alpha_1 - x_0/b)$  with eigenvalues  $\lambda_{1,2} = p \pm iq$  where  $p = \alpha_1 x_0/2b$  and  $q = \sqrt{b - x_0 \alpha_1 - (\alpha_1 x_0/2b)^2}$ .

Since  $p > 0$ , the latter equilibrium is an unstable focus whereby the trajectory spirals about the unstable fixed point  $E_2$  with frequency  $q$ .

Note that should  $x_0 = 0$ , the system reduces to a standard Lotka–Volterra model with a neutrally stable limit cycle of frequency  $\Omega = \sqrt{b}$ . But since  $x_0 > 0$ , this small constant loss of resources that might arise because of alternative consumers, leads to instability in the cycle ( $p > 0$ ). The unstable oscillation between the lower trophic levels of the food chain is analogous to the unstable SHM in the  $x$  and  $y$  variables of the Rössler equations.

Refer now to the full three variable foodweb model (2). Again similar to the Rössler equations, the  $z$  variable acts to fold the system back to the  $(x, y)$  plane and reset the unstable growth by dampening the otherwise exponential growth in  $y$ . Hence the foodweb model inherits uniform phase growth due to the underlying unstable Lotka–Volterra oscillator (Eq. (7)), but the instability is kept in check through the folding mechanism which leaves a bounded chaotic attractor.

From this analysis, one sees that the top predator acts to control the unstable vegetation-herbivore cycle. This has the interesting implication that the foodweb model is governed by a form of “top-down” control. In the next section, a “bottom-up” controlled UPCA model will also be discussed.

#### 4. UPCA in the Hastings–Powell model

We now turn to the Hastings and Powell (1991) tritrophic model:

$$\begin{aligned} \dot{x} &= rx(1 - Kx) - f_1(x)y, \\ \dot{y} &= -d_1 y + f_1(x)y - f_2(y)z, \\ \dot{z} &= -d_2 z + f_2(y)z, \end{aligned} \tag{8}$$

where  $f_1 = a_1 x/(1 + b_1 x); f_2 = a_2 y/(1 + b_2 y)$  with the same parameters as used by these authors (see Legend). This differs from the foodweb equations (2) in that all

interactions are Holling Type II rather than bilinear, and the vegetation  $x$  has logistic growth in the absence of herbivores.

The time-series for vegetation, herbivore and predator and its associated “tea cup” attractor are plotted in Fig. 4. Unlike the UPCA foodweb model (2) discussed above, there are two visible fundamental frequencies; the relatively high frequency of the spikey vegetation-herbivore system, and the smoother low frequency cycle of the predator-herbivore system. Note that the top-predator’s low frequency cycle superimposes itself upon the vegetation and herbivore time-series. According to Hastings and Powell (1991), it is the nonlinear interaction of these two frequencies that yields chaos. (See Kuznetsov and Rinaldi (1996) and Kuznetsov et al. (2001) for an alternative explanation).

For the purpose of modelling population cycles we found these characteristics problematical from several points of view. Note that the top-predator population has an amplitude that fluctuates between 7.5 and 11 and the peak amplitude has very little variability at all. As such this provides a poor characterization of the Canadian lynx cycle and other North American mammals where the cycle amplitude variability (the ratio of maximum to minimum) can vary from 15 to 200 fold (Korpimäki and Krebs, 1996). Furthermore, to our knowledge, the two frequencies of the vegetation-herbivore and top predator systems are not so glaringly observed in the empirical data, if they exist at all. In addition, the high frequency spikey cycle makes it difficult to investigate synchronization of coupled models, as can be done with the UPCA foodweb model equations (1).

However, as Hastings and Powell (1991) hint at, there is something regular about this model’s oscillations: “[It’s]

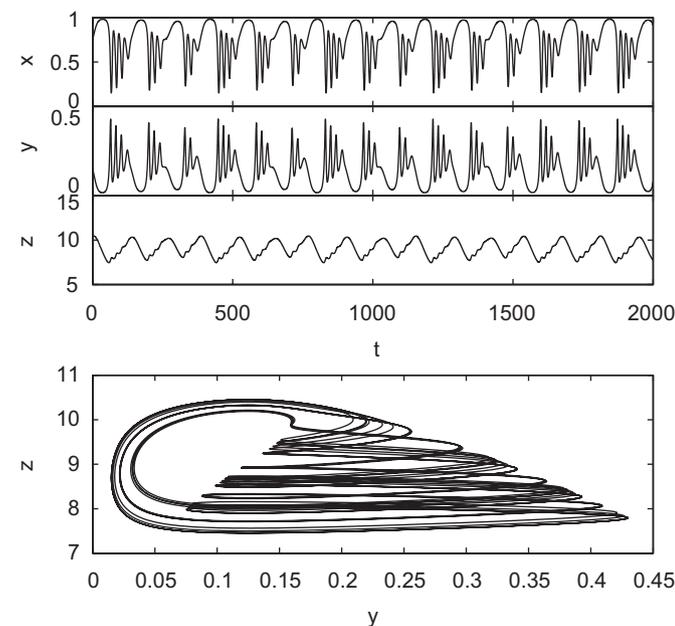


Fig. 4. Simulation results of Hastings–Powell model equations (8). Time series of  $x$ ,  $y$ ,  $z$  and projection of attractor into the  $(y, z)$  plane. Parameters:  $K = r = 1$ ;  $a_1 = 5$ ;  $a_2 = 0.1$ ;  $b_1 = 3$ ;  $b_2 = 2$ ;  $d_1 = 0.4$ ;  $d_2 = 0.01$ .

Chaotic behaviour ...need not lead to an erratic and unpatterned trajectory in time that one might infer from the usual (not mathematical) connotation of the word ‘chaos.’ Rather, the term ‘regular oscillations’ better describes the curves of  $x$ ,  $y$ , and  $z$  vs.  $t$  as seen in Fig. 2.” Further inspection reveals that the low-frequency oscillation of the top-predator population ( $z$ ), although lacking strong amplitude variability, appears to keep a uniform phase evolution which is partially inherited by the other variables ( $x$  and  $y$ ). In a sense, the Hastings and Powell (1991) model has many of the elements of a UPCA model, but not in its purest form as generated from, say, Eq. (2).

Given the similarities between the Hastings and Powell (1991) model and the foodweb equations (1), one suspects that there might be a parameter regime in which the former model exhibits UPCA oscillations. In fact, after a painstaking search, it was found that this indeed proves to be the case. Fig. 5 plots the time-series of the model time-series in the UPCA regime and the projection of the attractor in the  $(y, z)$  plane. Comparing this with the equivalent graphs of the foodweb model (Fig. 2), and the Rössler equations (Fig. 3), one sees the similarity of all three systems. We have also found another parameter regime even closer to that of the original Hastings–Powell model. These parameters yield oscillations as given in Fig. 6. Although technically speaking, the model generates UPCA oscillations, the variability in the predator variable is considerably reduced. Note that, unlike the UPCA model equations (2), the latter parameters have the predator mortality rate  $d_2 < d_1$  to match the assumption that average life span of predators is usually larger than herbivores. However, if the predator undergoes large UPCA oscillations as seen in, say Fig. 2, large predator

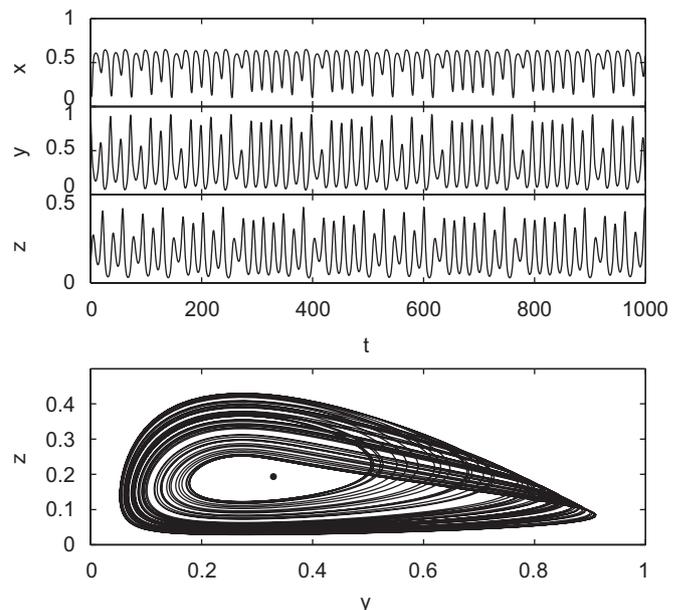


Fig. 5. Simulation results of Hastings–Powell model equations (8). Time series of  $x$ ,  $y$ ,  $z$  and projection of attractor into the  $(y, z)$  plane. Parameters ( $K = 1.5$ ,  $r = 2.5$ ,  $a_1 = 4.0$ ,  $a_2 = 4.0$ ,  $b_1 = 3.0$ ,  $b_2 = 3.0$ ,  $d_1 = 0.4$ ,  $d_2 = 0.6$ ).

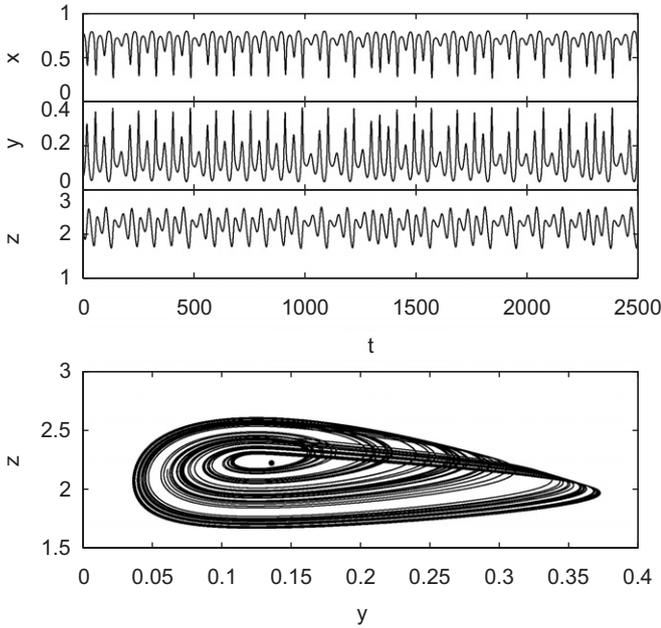


Fig. 6. Simulation results of the modified Hastings–Powell model equations (8). UPCA time series of  $x$ ,  $y$ ,  $z$  and projection of attractor into the  $(y, z)$  plane. Modified parameters:  $K = r = 1.2, a_1 = 5.0, a_2 = 0.4, b_1 = 3.0, b_2 = 2.0, d_1 = 0.4, d_2 = 0.04$ .

mortality rates are required to rapidly reduce the population levels. In the case of the hare-lynx cycle the large predator mortality  $d_2$  is realistic and due to the combined effects of intense hunting and harsh environmental conditions (see e.g. Gamarra and Solé, 2000).

The UPCA produced by the Hastings–Powell model, as seen in Fig. 5, seems to derive from a different mechanism than the models discussed so far. When the top-predator is removed (by setting  $z = 0$ ) the vegetation-herbivore subsystem is found to oscillate at twice the frequency of the full three species foodweb as shown in Fig. 7. In contrast, when the vegetation is removed from the foodweb or held constant ( $x = c$ ), the system becomes unstable. Unlike the UPCA foodweb models of Section 2, the predator–prey subsystem is reset and remains bounded in a manner that appears to be governed by the lower trophic levels—a kind of “bottom-up” control. We suspect this is because of the strong logistic stabilization of the vegetation in the Hastings and Powell (1991) model (absent in Eqs. (1)), which acts to control the oscillation of the higher levels. Nevertheless, the final frequency of the 3-species foodweb is half that of the herbivore-vegetation system indicating that the foodweb oscillation is slowed considerably due to the presence of the predator. Appendix B explains why this is so.

### 5. Model comparison and basins of attraction

Here we compare the characteristics of three types of UPCA models already discussed.

- (a) The UPCA foodweb model equations (2) in which all interactions are bilinear.

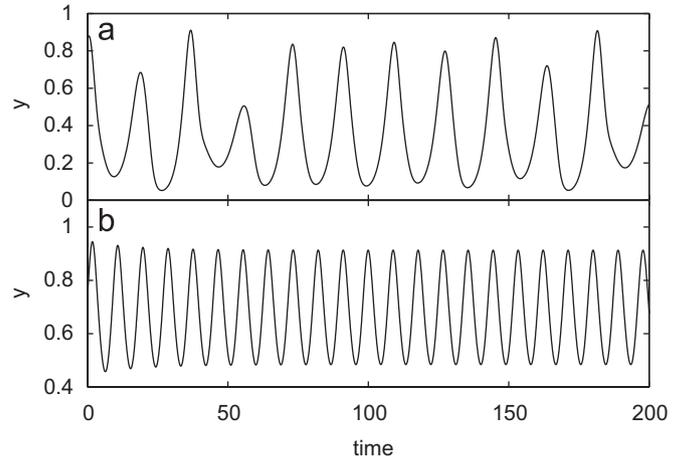


Fig. 7. Simulation results of modified Hastings–Powell model equations (8). Time series of  $y$  (a) comparing with  $y$  of the subsystem  $(x, y)$  with fixed  $z = 0$  (b); Parameters:  $K = 1.5, r = 2.5, a_1 = 4.0, a_2 = 4.0, b_1 = 3.0, b_2 = 3.0, d_1 = 0.4, d_2 = 0.6$ .

- (b) A related UPCA model in which the herbivore-vegetation is Holling Type II interaction while the predator-herbivore interactions are bilinear (see Legend Fig. 8).
- (c) The Hastings–Powell model equations (8) in which all interactions are Holling Type II, and vegetation grows logistically (rather than exponentially as in other models) in the absence of herbivores.

In Fig 8, we provide bifurcation diagrams of the three models where the maxima of the predator population  $z$  are plotted as a function of the control parameter representing herbivore mortality. The latter is  $b$  in the case of the first two models, and  $d_1$  for the Hastings–Powell model.

The first UPCA model is unstable for  $b \leq 0.865$  and the trajectory follows unstable exponential growth. As seen in the bifurcation diagram of Fig. 8a, a boundary crisis occurs at  $b \approx 0.865$ . A boundary crisis is a well-known mechanism for destroying (or creating) a chaotic attractor by variation of one parameter: at the moment of the boundary crisis bifurcation the chaotic attractor touches the boundary of its own basin of attraction.

When  $b > 0.865$  the model exhibits UPCA dynamics and there are intervals for  $b$  in which there are periodic solutions or equilibrium. Fig. 8(b) shows that the introduction of a single Holling Type II interaction seemingly removes the unstable behaviour of the model with bilinear interactions. The Holling interaction introduces a bifurcation reversal (Stone, 1993) which acts to stabilize the model for relatively smaller levels of  $b$ . The Hastings–Powell model also inherits this bifurcation reversal in the bifurcation diagram (Fig. 8(c)).

Alongside the bifurcation diagrams are projections of the models’ associated basins of attraction (when the parameter  $b = 1$  and  $d_1 = 0.4$ ). In these diagrams,  $(x_0, y_0, z_0)$  denotes the models’ initial conditions, and we plot the projection for which  $z_0 = 0.1$  is fixed. When  $x_0$  and

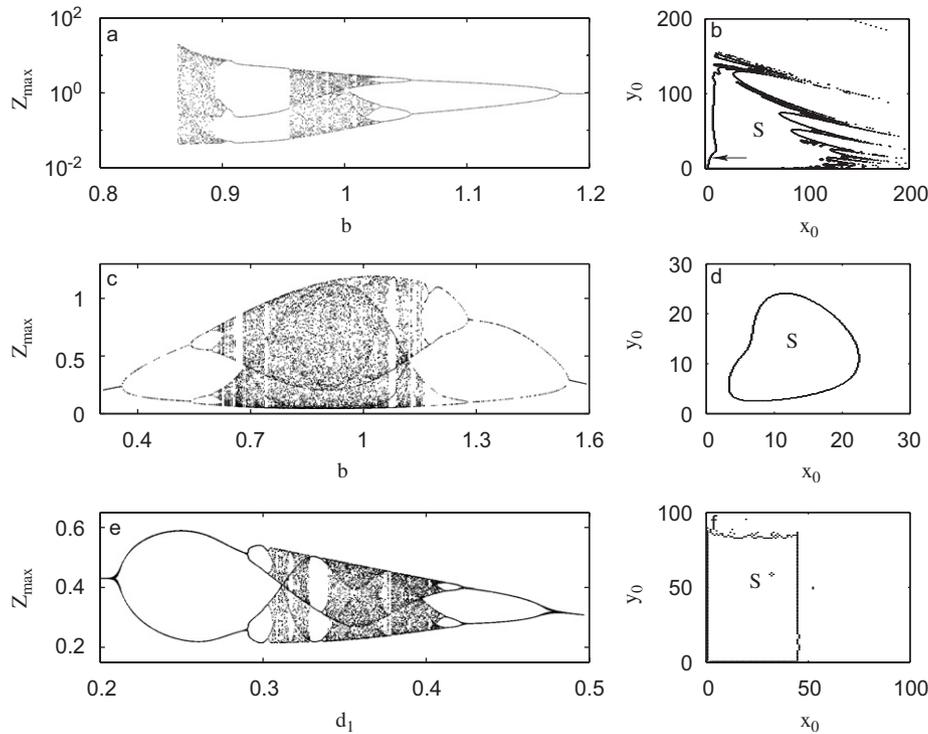


Fig. 8. Bifurcation diagrams (left panels) and basins of attraction (right panels). (a and b) Model equations 2. Maxima of  $z$  plotted as a function of control parameter  $b$ . Other parameters as in legend to Fig. 2. (b)  $b = 1$ ,  $z = 0.1$ . (c and d) Model equations (1) as in Blasius et al., 1999,  $f_1 = xy/(1 + k_1x)$ ,  $f_2 = yz$ ,  $a = b = \alpha_2 = 1$ ,  $c = 10$ ,  $\alpha_1 = 0.2$ ,  $k_1 = 0.05$ ,  $z_0 = 0.006$ ; Maxima of  $z$  plotted as a function of control parameter  $b$ . (e and f) Hastings–Powell model (parameters as in legend to Fig. 5);  $d_1$  is control parameter.

$y_0$  lies in the region demarked by ‘S,’ there is a stable chaotic attractor. When  $x_0$  and  $y_0$  lies outside  $S$  the model is unstable and the trajectory follows exponential growth.

Surprisingly, of the first two models the one with the stabilizing Holling interaction term appears to have the smaller basin of attraction. The Hastings–Powell model, however has a basin of attraction that is equally as large. Unlike the other models, the Hastings–Powell model fails to reach an unstable state should  $x$  and/or  $y$  reach small population levels. This is presumably an outcome of the stabilizing logistic growth of the vegetation.

## 6. Discussion

Over the last decade there have been a number of extremely detailed mathematical studies of the Hastings–Powell and related ecological models. In Boer et al. (1998), De Feo and Rinaldi (1998), Gragnani and Rinaldi (1995), Kooi and Boer (2003), Kuznetsov and Rinaldi (1996), Kuznetsov et al. (2001) bifurcation theory is used to study the dynamics of the model and to explain the origin of chaos. These studies show that a family of homoclinic bifurcations are the organizing centres of the overall bifurcation scenario and structure the chaotic region. The latter is fractalized in subregions of chaotic and/or periodic behaviour, and the coexisting attractors (cycles and strange attractors) are characterized by different geometries, namely by a different number of prey–predator oscillations.

These studies are important contributions giving a deep mathematical understanding of the potential complexities of ecological cycles. Our study here takes a different approach with the specific and perhaps more modest goal of focusing only on the UPCA dynamics of foodweb models, which, to our knowledge, has been otherwise overlooked. This extends the study of continuous time chaotic foodweb models in several significant ways.

- (i) The models we have introduced might be considered to be simpler in structure than that of Hastings and Powell (1991). In the latter model it was found necessary to use Holling Type II interaction terms with their nonlinear saturation effects to generate chaos. However, the foodweb models we have described achieve similar results even when bilinear Lotka–Volterra interaction terms are used.
- (ii) The UPCA properties of the foodweb models extends the range of behaviours available in existing ecological models. For some purposes, the UPCA characteristics have great realism for there are many ecological and biological processes that maintain a regular rhythm but show signs of being irregular or chaotic in amplitude. Furthermore, the UPCA dynamics can be taken advantage of to explore new theoretical possibilities. For example, we are using these models to analyse synchronization of chaotic systems and spatially synchronized travelling waves (Blasius et al.,

- 1999). Considerable progress in these areas can only be achieved with a continuous time model that has regular oscillations (in phase) so that synchronization may be achieved.
- (iii) The underlying mechanism that leads to chaos in the foodweb model is different to that suggested for Hastings and Powell’s (1991) model. Rather than requiring two subsystems which oscillate at different frequencies, the UPCA foodweb model becomes chaotic with only one oscillating subsystem that is itself unstable.
  - (iv) Numerical analysis indicates that the mechanism that resets unstable population growth and causing the attractor to fold, thus generating chaotic oscillations rather than unbounded growth, may be controlled by both “top-down” mechanisms (as in model equations (2)) or “bottom-up” mechanisms (as in model 8).

There are numerous ecological implications in finding that simple, biologically realistic, continuous-time, food chain models yield chaotic dynamics. For example, Hassell et al. (1976) previously argued, that if discrete-time models are a representative guide to population dynamics then it would be unlikely to find chaotic population fluctuations unless real world interactions are far more nonlinear than empirical data suggests. Continuous time chaotic foodweb models add a new dimension to the modelling approach, if only by pointing to the need to revise these earlier conclusions drawn from the logistic map (see also Hastings and Powell, 1991). UPCA foodweb models extend the scope even further since they allow one to gain some control in the actual design of the foodweb dynamics since the underlying type of oscillation may be specified in advance. In addition, these models open up many new avenues for the theoretical study of complex ecological systems, including the assembly, build up, persistence and extinction characteristics of interacting communities far from equilibrium.

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**Appendix A**

The equilibrium values of the populations  $N^* = (x^*, y^*, z^*)$  for model equations (2) must satisfy

$$\begin{aligned} (x^* - x_0) - \alpha_1 x^* y^* &= 0, \\ -by^* + \alpha_1 x^* y^* - \alpha_2 y^* z^* &= 0, \\ -c(z^* - z_0) + \alpha_2 y^* z^* &= 0. \end{aligned} \tag{9}$$

By inspection, one equilibrium is

$$E_1 : (x^*, y^*, z^*) = (x_0, 0, z_0). \tag{10}$$

To find the other equilibria note that the above equations yield:

$$\begin{aligned} x^* &= (\alpha_2 z^* + b)/\alpha_1 = x_0/(1 - \alpha_1 y^*), \\ z^* &= cz_0/(c - \alpha_2 y^*). \end{aligned} \tag{11}$$

Solving for  $y^*$  one obtains the two solutions  $y_{1,2}^*$  of

$$qy^{*2} + ry^* + s = 0, \tag{12}$$

where  $q = \alpha_1 \alpha_2 b$ ;  $r = \alpha_1 \alpha_2 x_0 - \alpha_1 bc - \alpha_1 \alpha_2 cz_0 - \alpha_2 b$ ; and  $s = bc + \alpha_2 cz_0 - \alpha_1 cx_0$ .

With  $y_{1,2}^*$  known, it is an easy matter to calculate  $x_{1,2}^*$  and  $z_{1,2}^*$  from Eqs. (11).

When  $z_0 \ll 1$  (and hence  $z^*$  relatively small), it is possible to approximate one of the solutions by considering the two-species model:

$$\begin{aligned} \dot{x} &= (x - x_0) - \alpha_1 xy, \\ \dot{y} &= -by + \alpha_1 xy. \end{aligned} \tag{13}$$

Setting  $\dot{x} = \dot{y} = 0$ , the equilibria are found to be  $(x^*, y_1^*) = (b/\alpha_1, 1/\alpha_1 - x_0/b)$  or  $(x^*, y_1^*) = (x_0, 0)$ .

Note that the above equilibrium solutions must closely approximate that of the full system 2 when  $\alpha_2 z^* \ll b$ . This can always be achieved by choosing, for example, a small enough  $z_0$ . The other equilibrium solution of the full system equations (2) associated with the root  $y_2^*$  is not relevant since population abundances are negative.

The non-negative equilibria of the full system (2) are thus:

$$\begin{aligned} E_1 : (x^*, y^*, z^*) &= (x_0, 0, z_0), \\ E_2 : (x^*, y^*, z^*) &= (b/\alpha_1, 1/\alpha_1 - x_0/b, cz_0/(c - \alpha_2 y^*)). \end{aligned} \tag{14}$$

The Jacobian Matrix at the equilibrium  $(x^*, y^*, z^*)$  is

$$\begin{bmatrix} 1 - \alpha_1 y^* & -\alpha_1 x^* & 0 \\ \alpha_1 y^* & 0 & -\alpha_2 y^* \\ 0 & \alpha_2 z^* & \alpha_2 y^* - c \end{bmatrix}. \tag{15}$$

For the given parameter values, the eigenvalues for equilibrium  $E_1$  are  $\lambda_1 = 1$ ,  $\lambda_2 = -10$ ,  $\lambda_3 = -0.856$  (saddle-node point). The eigenvalues for equilibrium  $E_2$  are  $\lambda_{1,2} = 0.0689 \pm 0.9195i$ ,  $\lambda_3 = -4.8879$  (saddle-focus point).

A reviewer has pointed out that in Kuznetsov and Rinaldi (1996) and De Feo and Rinaldi (1998) singular perturbation theory is used to relate the dynamics of the subsystem with the appearance of chaotic behavior of the full system.

**Appendix B**

The frequency of oscillations in the Hastings–Powell model equations (8) can be estimated as follows. Consider the model when  $z$  is artificially set to zero so that only the first two equations of (8) need be studied. (Incidentally, this situation is relevant when  $d_2 > 0.89$ , since then  $z$  converges to  $z^* = 0$ , and  $x$  and  $y$  oscillate about an unstable focus in

$x$ - $y$  plane. The equilibrium is then  $(x^*, y^*)$  where  $x^* = d_1/(a_1 - b_1 d_1)$ ,  $y^* = rx(1 - Kx^*)/f_1(x^*)$  with Jacobian matrix

$$J = \begin{bmatrix} J_{11} & J_{12} \\ J_{21} & J_{22} \end{bmatrix} = \begin{bmatrix} r - 2rKx^* - y^* \frac{df_1}{dx} \Big|_{x=x^*} & -d_1 \\ y^* \frac{df_1}{dx} \Big|_{x=x^*} & 0 \end{bmatrix}. \quad (16)$$

For the given parameter values there is a pair of complex eigenvalues  $\lambda_{1,2}$  with imaginary part setting the frequency of the cycle around the focus with period  $T \approx 8.48$ .

When  $d_2 < 0.825$ , e.g.,  $d_2 = 0.6$ , there is a positive fixed point  $(x^*, y^*, z^*)$ , having Jacobian matrix

$$J = \begin{bmatrix} J_{11} & J_{12} & J_{13} \\ J_{21} & J_{22} & J_{23} \\ J_{31} & J_{32} & J_{33} \end{bmatrix} = \begin{bmatrix} r - 2rKx^* - y^* \frac{df_1}{dx} \Big|_{x=x^*} & -f_1(x^*) & 0 \\ y^* \frac{df_1}{dx} \Big|_{x=x^*} & -d_1 + f_1(x^*) - z^* \frac{df_2}{dy} \Big|_{y=y^*} & -d_2 \\ 0 & z^* \frac{df_2}{dy} \Big|_{y=y^*} & 0 \end{bmatrix}. \quad (17)$$

It is not hard to show that near the Hopf bifurcation point the system has a negative real eigenvalue  $\lambda_1 = J_{11} + J_{22}$  and a pair of purely imaginary eigenvalues setting the frequency of the cycle as  $\Omega = \text{Im}(\lambda_{2,3}) = \text{Im}(\sqrt{J_{32}J_{23} + J_{12}J_{21} - J_{11}J_{22}})$ . For the given parameter settings the period is  $T \approx 16.8$  i.e. double the former one. Furthermore, we have found numerically that the dominant term in the expression for  $\Omega$ , allows us to roughly approximate the frequency as  $\Omega \approx \sqrt{J_{32}J_{23}}$ , implying that the predator-prey relationship has the most affect on the system's ultimate frequency.

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