Trophic structure and dynamical complexity in simple ecological models

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1. Introduction

Dynamical complexity refers to the variety of behaviors that systems can exhibit over time. It can be studied through construction of simple models, and then examination of patterns in temporal evolution in response to changes in model parameters. As such one can attempt to estimate the likelihood of observing predictable (e.g., simple equilibrium, cycles) versus unpredictable (chaotic) dynamics in phase space and determine what causes abrupt changes between these two types of behavior. The more likely the occurrence of unpredictability and abrupt changes in system dynamics, the more dynamically complex a system is understood to be.

Typically, dynamical complexity can be studied by finding the critical parameter values which cause changes in attractor types. Take the classic single population dynamic model studied by May (1975, 1976) and May and Oster (1976). In this model, there is only one parameter to be varied, namely $r$, the intrinsic growth rate. For some range of $r$ values, dynamics reaches a single equilibrium. For another range, the attractor is cyclical. Once it reaches a critical point ($r = 3.5$), chaos is observed. Because there is no interruption in the display of chaotic behavior as $r$ is increased further, we call this type of

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Abstract

We study the dynamical complexity of five non-linear deterministic predator–prey model systems. These simple systems were selected to represent a diversity of trophic structures and ecological interactions in the real world while still preserving reasonable tractability. We find that these systems can dramatically change attractor types, and the switching among different attractors is dependent on system parameters. While dynamical complexity depends on the nature (e.g., inter-specific competition versus predation) and degree (e.g., number of interacting components) of trophic structure present in the system, these systems all evolve principally on intrinsically noisy limit cycles. Our results support the common observation of cycling and rare observation of chaos in natural populations. Our study also allows us to speculate on the functional role of specialist versus generalist predators in food web modeling.

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chaotic dynamics “robust”. This behavior illustrates a very important property: the fact that an extremely simple model (e.g., a single population model) can display dynamical complexity. However, as we shall see, the dynamical complexity of this model is actually relatively low, when compared to more structurally complex ecological models. This is because it has a critical parameter value that clearly divides the phase space into different attractor types (fixed points, stable limit cycles, and chaos).

In this paper, we investigate the dynamical complexity of predator–prey models. The simplest predator–prey model is the Lotka–Volterra model (Lotka, 1920; Volterra, 1931). Because of the existence of two interacting populations, one can argue that this model is structurally more complex than the one studied by May (1976). However, perhaps surprisingly, it does not display greater dynamical complexity. In fact, one can argue that it displays less dynamical complexity than the single population dynamic model because there is no chaotic behavior. Several studies, most of which build upon the work of Lotka, Volterra and May, have however now reported robust deterministic chaos in an appreciable range of a single critical parameter of model predator–prey systems with three or more interacting populations (Gilpin, 1979; Schaffer, 1985; Hastings and Powell, 1991; Rai and Sreenivasan, 1993; Rinaldi and Muratori, 1993; Rinaldi et al., 1993; Vandermeer, 1993; Klebanoff and Hastings, 1991; Rai and Sreenivasan, 1993; Rinaldi and Muratori, 1993; Upadhyay et al., 1998), and (3) by incorporating effect of space in an oscillatory predator–prey system (Pascual, 1993; Medvinsky et al., 2002; Morozov et al., 2004; Petrovski et al., 2004).

In this paper, we examine scenario 1 only. This scenario is appropriate for large interacting populations, which generate well-mixed conditions.

We assume that ecologists generally accept a loose classification of predators into specialists and generalists. Two ecological principles that form the skeleton of the model systems studied in the present paper are: (1) a specialist predator population decays exponentially fast in the absence of its prey and (2) per capita growth of a generalist predator is limited by dependence on its favorite prey and severity of this limitation is inversely proportional to per capita availability of prey at any instant of time.

The Rosenzweig–MacArthur (RM) model (Rosenzweig and MacArthur, 1963) describes the dynamics of a specialist predator and its prey. The model is represented by following coupled ordinary differential equations:

\[
\frac{dX}{dt} = a_1 X \left( 1 - \frac{X}{C_1} \right) \frac{w Y X}{X + D},
\]

\[
\frac{dY}{dt} = -a_2 Y - \frac{w_1 Y X}{X + D_1}.
\]

where \( X \) is prey for specialist predator \( Y \) with Holling type II functional response, \( a_1 \) is the rate of self-reproduction for the prey, \( K \) measures the carrying capacity of the environment for prey \( X \), \( w \) is the maximum rate of per capita removal of prey species \( X \) due to predation by its predator \( Y \), \( D \) is that value of population density of \( X \) at which per capita removal rate is half of \( w \), the parameter \( a_2 \) measures how fast the predator \( Y \) will die when there is no prey to capture, kill and eat; \( w_1 X / X + D_1 \) is the per capita rate of gain in predator \( Y \), \( w_2 \) is its maximum value and \( D_1 \) denotes the population density of the prey at which per capita gain per unit time in \( Y \) is half its maximum value (\( w_2 \)). The assumptions underlying this formulation of predator–prey interaction are as follows: the life histories of each population involve continuous growth and overlapping generations. The predator \( Y \) dies out exponentially in the absence of its most favorite food \( X \). The predator’s feeding rate saturates at high prey densities. The age structure of both the populations is ignored.
A generalist predator differs from a specialist in that it does not die out when its favorite food is absent or is in short supply, but rather its population continues to grow because individuals switch to alternative food options when their most preferred food is in short supply. A model known as Holling-Tanner model (Holling, 1965; TANNER, 1975; Pielou, 1977; May, 2001) describes the dynamics of a generalist predator and its prey:

\[
\frac{dZ}{dt} = AZ\left(1 - \frac{Z}{K}\right) - \frac{w_1 U Z}{Z + D_3}
\]

\[
\frac{dU}{dt} = cU - \frac{w_4 U^2}{Z}.
\]

where \( Z \) is the most favorite food for the generalist predator \( U \), \( A \) the per capita rate of self-reproduction of the predator, and \( K \) is the carrying capacity of its environment. The parameter \( w_1 \) measures the maximum of the per capita rate of removal of the prey population by its predator \( U \). \( D_3 \) is the half-saturation constant for prey \( Z \). \( c \) represents the per capita rate of self-reproduction of the predator \( U \) and \( w_4 \) measures severity of the limitation put to growth of the predator population per capita availability of its prey. It can be seen that the generalist predator \( U \) does not die out exponentially in the absence of its favorite prey \( Z \), instead, grows logistically to \( AZ \), where \( a = c/w_4 \) is the proportionality constant. The underlying assumption of this formulation is that the predator’s carrying capacity is proportional to the population density of its most favorite prey. This assumption is phenomenological (P. Abrams, pers. commun., 2004). The positive aspect of this formulation of predator–prey interaction is that it takes care of our inability to write down growth equations for all the species a generalist predator feeds on. This is simply because it is practically impossible to identify all of them. Although this formulation is too simplistic, yet it has positive features which are not found in other models of predator–prey interaction involving a generalist predator.

Graphical representation of the dynamical structure of the Holling–Tanner model in a 2D parameter space was presented by May (2001). There exists considerably large area in the parameter space where stable limit cycle solutions occur (see May, 2001, p. 192, Fig. A.1). Graphical representation of the dynamics in a 2D parameter space of the Rosenzweig-MacArthur model was presented in the recent work of Rai (2004). It can be noted that the stable limit cycle solutions are confined to a narrow area of the biologically relevant parameter space (\( a_2, K \) (Fig. 1 in Rai, 2004; \( a_1/b_1 = K \)) of RM model. As is well known, a minimum of three degrees of freedom are needed to generate chaos, thus the RM model does not display chaotic dynamics. Rinaldi and colleagues (Rinaldi and Muratori, 1993; Rinaldi et al., 1993) considered sinusoidal variations in model parameters, which drove it into chaos. Recently, Vandermeer et al. (2001) studied phase locking in a seasonally forced RM model. Another ecologically sound way of generating chaos would be to couple two systems dynamically. When parameters are chosen in such a way that both RM and HT systems display regular persistent periodic oscillations, these systems behave as oscillators. When suitably coupled, these systems force each other to generate chaos (Rai, 2004; Rai and Anand, 2004; Rai and Upadhyay, 2004). We have studied some of the models that can be obtained by coupling two subsystems. We found that the nature of ecological interactions affect the observability of chaos, however, the models that we have examined so far have not led to generalizations about these interactions. This is what we study in the present paper.

2.1. Model 1: one generalist, one specialist, two prey

Consider an ecological community with both generalist and specialist predators. This leads to perhaps the most straightforward coupling of RM and HT models. In this, the only effect of the introduction of the generalist predator (and a second prey species) is that the specialist predator population is reduced because of the presence of the generalist predator. This model is given by the following equations:

\[
\frac{dX}{dt} = a_1 X \left(1 - \frac{X}{K}\right) - \frac{wYX}{X + D}
\]

\[
\frac{dY}{dt} = -a_2 Y + \frac{w_1 YX}{X + D_1} - \frac{w_2 Y^2 U}{Y^2 + D_2^2 + Z}
\]

\[
\frac{dZ}{dt} = AZ \left(1 - \frac{Z}{K_1}\right) - \frac{w_3 UZ}{Z + D_3}
\]

\[
\frac{dU}{dt} = cU - \frac{w_4 U^2}{Y + Z},
\]

where parameter \( a_1 \) is the rate of self-reproduction and \( K \) is the carrying capacity of prey \( X \). \( w/(X + D) \) is the per capita rate of removal of prey \( X \) by specialist predator \( Y \). \( D \) is a measure of protection provided by the environment to prey \( X \). \( Y \) is a specialist predator, i.e. \( X \) is the only food for it. Therefore, \( Y \) dies out exponentially in the absence of \( X \). \( w \) is the maximum value that function \( wX/(X + D) \) can attain. \( a_2 \) is the rate at which \( Y \) dies out exponentially in the absence of its prey \( X \). \( w_1 X/(X + D_1) \) denotes the per capita gain in the specialist predator population due to proportionate loss in its prey. \( w_1 \) is the maximum value that this function can take. \( D_1 \) is the half-saturation constant for specialist predator \( Y \). \( a_1/b_1 = K \) and \( K_1 \) are respectively the rate of self-reproduction and carrying capacity for prey \( Z \). The last term in Eq. (3b) represents the functional response of the generalist predator \( U \). It switches its prey whenever its favorite prey \( Z \) is in short supply. The last term in Eq. (3d) describes how loss in abundance of generalist predator \( U \) depends on per capita availability of its prey \( Z \) and \( Y \).

It can be easily seen that this model has been obtained by coupling the RM model with HT model via the term \((-w_2 Y^2 U/(Y^2 + D_2^2 + Z))\). This is the Holling type III functional response term with \( Z \) added to the denominator to signify the fact that the generalist predator switches to \( Y \) whenever it is difficult to find the favorite food \( Z \). Rai (2004) has studied the model with no \( Z \) in the denominator of the coupling term. At this point, it should be noted that the older version of the model is justified if the generalist predator switches its prey only in extreme situations, for example, if there exist
generalist predators whose food requirements are quite low. On the other hand, generalist predators with appreciable food needs are better represented by the present version of the model. We shall compare results of this model and those of Rai (2004). The following schematic diagram represents the model:

A real world ecological community that exemplifies this model involves plantation, vole, weasel and its prey other than the voles. This community is found in northern Fennoscandia and has been studied by many investigators (Turchin, 1996; Turchin and Hanski, 1997; Turchin and Ellner, 2000).

2.2. Model 2: two specialists, two competing prey

In this section, we design a model to represent an ecological situation wherein two different prey are predated upon by two different specialist predators. These two predator–prey systems with strong non-linear interactions are linked via competition between the individuals of prey populations. Vandermeer (2004) terms this as resource–resource (RR) coupling. RR coupling essentially means indirect mutualism between the two consumers (predators). Our aim is to investigate the effect of this on two RM predator–prey systems.
The model is represented by following set of non-linear coupled ordinary differential equations:

\[
\frac{dX_1}{dt} = a_1X_1 \left(1 - \frac{X_1}{K_1} - \frac{X_2}{K_2}\right) - \frac{wY_1X_1}{X_1 + D_1}
\]

\[
\frac{dY_1}{dt} = -a_2Y_1 + \frac{wY_1X_1}{X_1 + D_1}
\]

\[
\frac{dX_2}{dt} = a_3X_2 \left(1 - \frac{X_2}{K_3} - \frac{X_1}{K_1}\right) - \frac{wY_2X_2}{X_2 + D_2}
\]

\[
\frac{dY_2}{dt} = -a_4Y_2 - \frac{wY_2X_2}{X_2 + D_2}
\]

The meaning of the symbols is the same as in Eqs. (1a) and (1b). A population's growth is limited either by the severity of competition among its own individuals or/and by that of competition among individuals of other species, which depend on the same resource. K is the carrying capacity for the prey species X_1 and K_2 for that of X_2. K_1 measures the strength of interference competition between the two prey species. The unit of K_1 is number of individuals per unit volume. The meaning of different symbols will be more clear if one keeps in view the fact that this system is obtained by coupling the two RM oscillators as shown in the following schematic:

![Diagram of RM oscillators](image)

A real world community exemplifying this ecological situation is Epirrita autumnata (a lepidopteran forest insect pest) feeding on the plants in northern Fennoscandia and the voles of the genera Microtus and Clethrionomys feedings on another set of plants. The first herbivore system has 9-year population cycle and the second system has a 5-year cycle (Klemola et al., 2002).

2.3. Model 3: two competing specialists, two prey

Here we again design a model to examine the nature and extent to which dynamics of an ecological system is determined by coupling of two RM oscillators. In this case, the predators can be thought of as specialized on a particular prey, but consume an alternative prey on which another predator specializes (MacArthur, 1970). Vandermeer (2004) refers to this type of coupling as consumer–resource (CR) coupling. CR coupling implies competition between two predators. The model is represented by following set of non-linear coupled differential equations:

\[
\frac{dX_1}{dt} = a_1X_1 \left(1 - \frac{X_1}{K_1}\right) - \frac{wY_1X_1}{X_1 + D_1} + \frac{\beta Y_2}{1 + b(X_1 + \beta X_2)}
\]

\[
\frac{dY_1}{dt} = w(X_1 + \beta X_2)Y_1 - a_2Y_1
\]

\[
\frac{dX_2}{dt} = a_3X_2 \left(1 - \frac{X_2}{K_3}\right) - \frac{wY_2X_2}{X_2 + D_2} + \frac{\beta Y_1}{1 + b(X_1 + \beta X_2)}
\]

\[
\frac{dY_2}{dt} = w(X_2 + \beta X_1)Y_2 - a_4Y_2.
\]

where X_1, X_2 are the two prey and Y_1, Y_2 are corresponding predators. These predators prey on each other’s prey. a_4 and a_3 are per capita reproductive growth rates for the prey X_1 and X_2. K is the carrying capacity for the prey and b is the parameter for the functional response of predators. Parameter \( \beta \) measures the strength of CR coupling. a_2 and a_1 are mortality rates for the two predators. The parameter \( w \) represents the consumption rates of predators. The model is parameterized in such a way that variables take any value between 0 and 1.

2.4. Model 4: one specialist, two competing prey

In this model, two prey species compete for the same resource and each one is predated by the same specialist predator. We thus consider switching behavior in the specialist predator, as no predator is a specialist predator in the mathematical sense encrypted in Eqs. (1a) and (1b). Some specialist predators do switch to alternative prey when their most favorite food is in short supply; e.g. lynx switches to red squirrel when snowshoe hare becomes scarce (O’Donoghue et al., 1998), and the Eurasian badger switches to rabbits when its preferred prey (plants, worms and insects) becomes scarce (Fedriani et al., 1998). The model is described by following equations:

\[
\frac{dX_1}{dt} = r_1X_1 \left(1 - \frac{X_1}{K_1} - \frac{c_2 X_2}{K_2}\right) - f_1F_1(X_1,X_2)Y
\]

\[
\frac{dX_2}{dt} = r_2X_2 \left(1 - \frac{X_2}{K_2} - \frac{c_1 X_1}{K_1}\right) - f_2F_2(X_1,X_2)Y
\]

\[
\frac{dY}{dt} = e_1 f_1 F_1(X_1,X_2)Y + e_2 f_2 F_2(X_1,X_2)Y - dY,
\]

where

\[
f_1 = \frac{\pi X_1}{\pi X_1 + (1 - \pi) X_2}
\]

\[
f_2 = \frac{(1 - \pi) X_2}{\pi X_1 + (1 - \pi) X_2}
\]

where \( \pi \) is the prey preference and takes a value between 0 and 1.

\[
F_i(X_1,X_2) = \frac{A_iX_i}{(1 + B_1 X_1 + B_2 X_2)}
\]
where $A_i$ is the maximum harvest rate of predator $Y$ for prey $X_i$ and $1/B_i$ is proportional to the half-saturation constants. The constants $e_1$ and $e_2$ are conversion rates of prey $X_i$ to predator $Y$.

Setting $f_1$ and $f_2$ equal to 1 in Eqs. (6a)–(6c), one gets the system without switching. This system can be decoupled into two RM oscillators (Rai, 2004). The two oscillators are connected through inter-specific competition.

Gakkhar and Naji (2003) have discovered chaos in the model without switching. However, scans of parameter space were not presented in their publication. The assessment of dynamical complexity is not possible without studying the model in more detail. We performed simulation experiments to investigate dynamical chaos in both versions of the model (with and without switching).

2.5. Model 5: two generalists, two prey

This model is obtained by linking the two HT oscillators. It is assumed that two generalist predators feed on both prey species although they have their own favorite food items ($X$ for $Y$ and $Z$ for $U$). The model is represented by the following set of differential equations:

$$\frac{dX}{dt} = r_1X \left(1 - \frac{X}{K_1}\right) - X \left[\frac{wY}{1 + X + aZ} + \frac{aU}{1 + X + aZ}\right]$$ (7a)

$$\frac{dY}{dt} = c_1Y - \frac{w_2Y^2}{X + aZ}$$ (7b)

$$\frac{dZ}{dt} = r_2Z \left(1 - \frac{Z}{K_2}\right) - Z \left[\frac{bY}{1 + Z + bX} + \frac{w_3U}{1 + Z + bX}\right]$$ (7c)

$$\frac{dU}{dt} = c_2U - \frac{w_3U^2}{Z + bX}.$$ (7d)

where parameters $b$ and $a$ are measures of intensity with which two subsystems are connected to one another. Van dermeer (1993) called them parameters of connection asymmetry (when $b \neq a$). $r_1$, $K_1$, and $r_2$, $K_2$ are per capita growth rates and carrying capacities for the two prey. He found chaos for $a = 0.005$ and $b = 0.008$. Here we present results of detailed simulation experiments, which were performed in the spirit of the methodology in Upadhyay et al. (2001).

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$$\frac{dY}{dt} = c_1Y - \frac{w_2Y^2}{X + aZ}$$ (7b)

$$\frac{dZ}{dt} = r_2Z \left(1 - \frac{Z}{K_2}\right) - Z \left[\frac{bY}{1 + Z + bX} + \frac{w_3U}{1 + Z + bX}\right]$$ (7c)

$$\frac{dU}{dt} = c_2U - \frac{w_3U^2}{Z + bX}.$$ (7d)

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Model 5 contains two types of parameters: (1) connection asymmetry ($a$ and $b$) and (2) driving asymmetry ($r_1$, $r_2$, $K_1$, $K_2$). The

Fig. 2 – Points in 2D parameter space where chaos was observed in Model 2. (a) $0.5 \leq a_1 \leq 1.9; 30 \leq K_1 \leq 65$ with step size (0.1, 5). (b) $0.2 \leq a_2 \leq 0.8; 30 \leq K_1 \leq 60$ with step size (0.05, 5) (c) $0.5 \leq a_3 \leq 1.9; 30 \leq K_1 \leq 60$ with step size (0.05, 5). Fixed values used for relevant cases: $a_2 = 1$, $a_4 = 1$, $a_3 = 1.2$, $K = 35$, $K_2 = 30$, $D = 10$, $D_1 = 10$, $D_2 = 15$, $D_3 = 15$, $w = 1$, $w_1 = 2$, $w_2 = 1$, $w_3 = 2$. 

The figure shows the parameter space for models without switching. The system without switching is decoupled into two RM oscillators (Rai, 2004). The two oscillators are connected through inter-specific competition.
connection asymmetry parameters are measures of predation intensity between the generalist predator and the other prey (the one which is not its most favorite prey). On the other hand, parameters of driving asymmetry are the per capita reproductive rates and carrying capacities for the two prey. We chose both kinds of parameters as control parameters to perform simulation experiments.

3. Methodology

The model systems presented above are multi-parameter systems. A few hundred parameter combinations (choosing two at a time) are possible. It is simply not feasible to scan the system in all the parameter spaces. Application of non-linear dynamics in unison with the knowledge of biology of the system enables one to choose optimal parameter combinations for simulation experiments. Some of the parameters of these systems (e.g., reproductive rates and the carrying capacities) change in response to changes in the environment which changes with the seasons. These can be grouped together to form a parameter combination. Some others undergo slow changes as they are induced by changes in the behavioral traits of the interacting populations. These changes in the behavioral traits are caused by unpredictable fluctuations in the environment of individuals of the constituent

Fig. 3 – Points in 2D parameter space where chaos was observed in Model 3. (a) $0.5 \leq a_1 \leq 3; \ 0.5 \leq w \leq 3$ with step size (0.05, 0.1) for $\beta = 0.015$ (top) and $\beta = 0.0015$ (bottom). (b) $0.5 \leq a_1 \leq 3; \ 1 \leq b \leq 2$ with step size (0.1, 0.05) for $\beta = 0.015$ (top) and $\beta = 0.0015$ (bottom). (c) time-series displaying oscillatory and chaotic dynamics of the specialist predator $Y_1$ for two different initial conditions $Y_{10} = 10, \ 10.01$ for (i) limit cycle $a_1 = 1.0, \ b = 1.3, \ \beta = 0.015$, (ii) chaos $a_1 = 2.5, \ b = 1.5, \ \beta = 0.0015$. The Fixed values for the parameters are $a_1 = 1, \ K = 1, \ w = 2, \ b = 1.3, \ \beta = 0.0015, \ a_2 = 0.1, \ a_3 = 1, \ a_4 = 0.1$. 
populations. To fix the ranges of parameters appearing in parameter combinations for simulation experiments, we use the method suggested by Upadhyay et al. (1998). The system of equations is integrated using standard numerical procedures to generate time-histories for a given set of parameter values.

The distinguishing property of chaos is sensitive dependence on initial conditions. Two initially close trajectories in the state space (or in the phase space) diverge exponentially fast to the extent that after elapse of a certain amount of time, the two appear to originate from two different dynamical systems. We choose this basic feature of chaotic dynamics to detect the presence as well as absence of chaos in these model systems. The system parameters are chosen in such a way that asymptotic dynamics of both the subsystems confine to a stable limit cycle. If the two time-histories (generated by integrating the system of differential equations and recorded after transients are died out) corresponding to two different, but very close, initial conditions overlap each other completely, the absence of dynamical chaos at that particular set of parameter values is inferred. In the case when two histories appear to be quite different, it is understood that chaos exists at the chosen set of parameter values. There is one more important aspect of these simulation experiments: choosing the step size for the variation of a system parameter from a parameter combination within the chosen range. This depends on the nature of the parameter concerned (whether it is a slow varying or fast varying one).

We chose the range of the two critical parameters based on the available information about the parameters (Jorgensen, 1979), which are intrinsic attributes of the system. The critical parameters are varied one at a time in the chosen range. ODE Workbench from AIP (IBM PC Version 1.5; Aguirregabiria, 1994) was used to integrate the system of differential equations numerically. Dormance and Prince 5 (Hairer et al., 1993) was the integration algorithm chosen for the purpose. Comparing two time histories is the most simple and efficient way of detecting the presence as well as absence of chaos in model dynamical systems. This enables one to study two forms of

**Fig. 4 – Points in 2D parameter space where chaos was observed in Model 4 without switching behavior \((f_1, f_2 = 1)\) and with switching behavior.** For (a): (i) \(0.5 \leq r_1 \leq 4.5; \ 50 \leq K_2 \leq 350\) with step size \((0.1, 10)\). (ii) \(1 \leq r_2 \leq 4; \ 50 \leq K_1 \leq 250\) with step size \((0.2, 10)\). The parameter values for limit cycle solutions are: \(r_1 = 2.6, \ r_2 = 2.65, \ K_1 = 150, \ K_2 = 155, \ A_1 = 1.06, \ A_2 = 0.35, \ c_{12} = 0.204, \ c_{21} = 0.208, \ d = 1.21, \ B_1 = 0.54, \ B_2 = 0.55, \ e_1 = 2.5, \ e_2 = 0.52\). For (b) (i) \(1 \leq r_1 \leq 2.8; \ 50 \leq K_2 \leq 350\) with step size \((0.1, 25)\). (ii) \(1.5 \leq r_2 \leq 4; \ 50 \leq K_1 \leq 250\) with step size \((0.25, 25)\). The parameter values for limit cycle solutions are: \(r_1 = 2.6, \ r_2 = 2.1, \ K_1 = 150, \ K_2 = 155, \ A_1 = 1.1, \ A_2 = 0.26, \ c_{12} = 1.1, \ c_{21} = 0.2, \ d = 1.2, \ B_1 = 0.54, \ B_2 = 0.01, \ e_1 = 2.5, \ e_2 = 0.52, \ x = 0.5\).
chaos in dissipative dynamical systems (dynamical chaos as well as intermittent chaos) (Berge et al., 1986; Vandermeer, 1993; Letellier and Aziz-Alaoui, 2002). Of course, the method is not helpful to distinguish between long-lived chaotic transients and chaotic dynamics on a bonafide chaotic attractor. The phenomenon of chaotic transients (Grebowg et al., 1983; Rai and Schaffer, 2001) is more prevalent in spatially extended systems, which we do not study in the present paper. We also mention that we did not use the maximum Lyapunov exponent to detect chaos in the models we studied because the method we chose was time saving. Moreover, a positive maximum Lyapunov exponent does not guarantee dynamical chaos even in a deterministic system (Alligood et al., 1997). Of course, one has to take precautions to detect weak chaos using this methodology. A large number of data points are thrown out as transients so that there is sufficient time for chaos to develop.

We (Rai, 2004; Rai and Upadhyay, 2004) have classified dynamical complexity into two main categories: (1) robust chaos and (2) short-term recurrent chaos (strc). When one finds dynamical chaos to exist in a densely populated region defined by two control parameters of the system, a case for robust chaos is encountered. On the other hand, strc manifests itself as a scatter of points in 2D parameter spaces. Extensive simulation experiments were performed in 2D parameter spaces spanned by per capita reproductive rate ($a_3$) and carrying capacity ($K_3$) of prey $X$; death rate ($a_1$) and the foraging efficiency ($w_1$) of the specialist predator; per capita reproductive rate ($c$) and a measure of dependence of the generalist predator on its most favorite prey ($w_3$) to mention a few.

4. Results

Fig. 1 shows the results of simulation experiments performed on Model 1. Fig. 1a displays robust chaos in a region of relatively high carrying capacity and reproductive rate of the prey. In the rest of the region, strc is found. Fig. 1b displays points where chaos was detected while varying the ratio of per capita reproductive rates of the generalist predator and its most favorite prey. We also varied the parameters ($K_1$, $D_3$) measuring the quality of the environment for these species in the experiments while keeping the ratio of the reproductive rates constant. The distribution of points in the parameter space suggests that robust chaos is a weak possibility and strc may be a dominant mode of the system’s temporal evolution depending on how the relevant system parameters change. We present examples of trajectory convergence (corresponding to a stable limit cycle) and divergence (signifying a strange chaotic attractor in system’s phase space) in Fig. 1c(i and ii) for this model. Chaotic phase is characterized by presence of two time-histories which appear to correspond to different systems because of exponential amplification of the difference in initial conditions.

Results for Model 2 are shown in Fig. 2. The dominant attractor for this system is stable limit cycles. However, chaos rests along straight lines in the space spanned by the chosen set of parameter spaces. For Fig. 2a, these parameters are growth rate ($a_1$) of prey $X_1$ and a measure of the strength of competition between the two prey species ($K_1$). Since $K_1$ is a measure of the competition between the two prey species, we selected parameter pairs in such a way that this is common to all of them. Fig. 2b presents the results of simulation experiments in a 2D space constituted by per capita death rate ($a_1$) of predator $Y_1$ and a parameter that quantifies the intensity of competition between two prey species ($K_1$). Similarly, Fig. 2c reports points where chaos was detected in 2D parameter space defined by per capita reproductive growth rate for $X_2$ ($a_3$) and $K_1$. From these experiments, it appears that chaos is confined to a single parameter value ($K_1 = 30$) and is more sensitive to changes in prey reproductive rates than that of the predator.

We present outcomes of simulation experiments on Model 3 in Fig. 3. Parameters $a_1$, $b$ and $w$ were chosen for two-dimensional parameter scans. The parameter space was scanned for two different values for $\beta$. These values represent weakly and strongly coupled RM oscillators. For lower values of $\beta$ the system supports robust chaos. At higher values of this parameter (strongly coupled RM oscillators), chaos is frequently interrupted by other kinds of attractors (stable focus and stable limit cycles) and, thus, supports strc. We present examples of trajectory convergence (corresponding to a stable limit cycle) and divergence (signifying a strange chaotic attractor in system’s phase space) for Model 3 (cf. Fig. 3c(i and ii)).

Fig. 5 – Points in the 2D parameter space where chaos was observed in Model 5. (a) $0.005 \leq a \leq 0.001$; and $0.005 \leq b \leq 0.05$ with step size (0.001, 0.001). (b) $1.5 \leq r_1 \leq 3.5$; $10 \leq K_2 \leq 90$ with step size (0.1, 5). Fixed values used for relevant cases: $r_1 = 3.5$, $K_1 = 20$, $a = 0.005$, $b = 0.008$, $r_2 = 3.5$, $K_2 = 20$, $c_1 = 0.5$, $c_2 = 0.5$, $w_2 = 0.01$, $w_3 = 0.01$. 

\[
\text{Fig. 5} - \text{Points in the 2D parameter space where chaos was observed in Model 5. (a) } 0.005 \leq a \leq 0.001; \text{ and } 0.005 \leq b \leq 0.05 \text{ with step size (0.001, 0.001). (b) } 1.5 \leq r_1 \leq 3.5; 10 \leq K_2 \leq 90 \text{ with step size (0.1, 5). Fixed values used for relevant cases: } r_1 = 3.5, K_1 = 20, a = 0.005, b = 0.008, r_2 = 3.5, K_2 = 20, c_1 = 0.5, c_2 = 0.5, w_2 = 0.01, w_3 = 0.01.
\]
Fig. 4 shows the results of our simulation experiments on Model 4. We explored parameter spaces spanned by $r_1$, $K_2$ and $r_2$. Results simulation experiments are presented in Figure (a) without and (b) with switching in the diet of the predator. We found few and intermittent occurrences of chaos in general, and in the case of switching, no chaos was observed in the parameter scan in $r_2 - K_2$ space.

Results of simulation experiments to study presence and absence of chaos in Model 5 is presented in Fig. 5. In these experiments, one connection parameter was varied at a time (cf. Fig. 5a). We also study presence and absence of chaos in this model system by varying $r_1$ and $K_2$ (Fig. 5b).

5. Discussion and conclusion

In all the models we studied chaotic dynamics is interrupted by predictable changes in system parameters. The deterministic change in system parameters is to be contrasted with stochastic environmental influences that act on initial conditions. Seasonality is one of the agencies causing these deterministic changes in system parameters (reproductive rates and carrying capacities). Even if one discovers a way to deal with the impact of long-term environmental fluctuations so as to get a suitable time-series which can be analyzed using concepts and techniques from non-linear time series analysis and forecasting (Turchin and Ellner, 2000), the likelihood that an unambiguous case for chaos will be found is small. The on-off character of chaos will render its capture in the wild elusive. In the presence (and absence) of exogenous environmental perturbations, ecological systems will display short-term recurrent chaos (Turchin and Ellner, 2000; Rai, 2004; Rai and Upadhyay, 2004, 2006). The challenge remains the same: to distinguish between deterministic chaos and noisy periodicity (Olsen and Schaffer, 1990; Kendall, 2001; Rai and Schaffer, 2001). We emphasize that the source of this challenge is frequent interruptions in chaotic dynamics caused by non-linear interactions.

We found that in most of the models, the dominant behavior found was stable limit cycles. We hypothesize that the coupling between the dynamics of specialist non-competing predators (herbivorous insects and small mammals, e.g., voles) and their prey (different varieties of plants) explains pronounced population cycles observed in many predator–prey systems, for example the herbivores in northern Fennoscandia (Klemola et al., 2002). No population-extrinsic condition is needed to understand the differences between these observed cycles and ideal cycles. In harsh environments experiencing strong seasonality, the interspecific competition between different prey (functional varieties of plants) may be severe enough to put the parameter ($K_c$) at high values. Thus, occasional chaotic bursts can explain the apparent departures from ideal cycles observed in real population dynamics.

Our study allows us to make some comments about the relationship between trophic structure and dynamical complexity. It appears that the most complex models (Models 1 and 3) displayed dynamical complexity (in the form of strc.). It is interesting to note that Model 1 is the only one that incorporates both generalist and specialist predators. This provides a nice complement to results of Fussman and Heber (2002) who showed that the frequency of chaotic dynamics increases with the number of trophic levels (they did not differentiate between generalist and specialist predators). If we compare the results from an earlier work on a different version of Model 1, which assumes that the switching to alternative prey in the generalist predator’s foraging strategy is infrequent (Rai, 2004), we find that the system’s tendency to exhibit episodes of chaotic dynamics is considerably increased (cf. description of Model 1 in Section 2.1). Model 2 contains two specialist predators whose prey are in competition with each other. In this model, we see a few points where chaotic dynamics exists. This suggests that most likely outcome of models involving the same kind of predators (either the specialist or generalist) in natural systems is cycles not chaos. This could be an explanation for the abundance of population cycles in nature (Kendall et al., 1999). Of course, the observed dynamical patterns will not conform to ideal cycles. These departures are caused by existence of chaotic dynamics in some (albeit small) regions of the parameter space. Thus, non-linear interactions, and not exogenous environmental factors could explain observations of these deviations from ideal cycles. It is interesting to note that coupling two generalists (Model 5) shows more points of observation of chaos than coupling two specialist predators (Model 2) and the model with one specialist predator with switching in its diet (Model 4). This suggests that the generalist behavior may be functionally important for dynamical complexity in these types of systems (Tanabe and Namba, 2005).

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