



# Turing patterns and long-time behavior in a three-species food-chain model



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## ABSTRACT

We consider a spatially explicit three-species food chain model, describing generalist top predator–specialist middle predator–prey dynamics. We investigate the long-time dynamics of the model and show the existence of a finite dimensional global attractor in the product space,  $L^2(\Omega)$ . We perform linear stability analysis and show that the model exhibits the phenomenon of Turing instability, as well as diffusion induced chaos. Various Turing patterns such as stripe patterns, mesh patterns, spot patterns, labyrinth patterns and weaving patterns are obtained, via numerical simulations in 1d as well as in 2d. The Turing and non-Turing space, in terms of model parameters, is also explored. Finally, we use methods from nonlinear time series analysis to reconstruct a low dimensional chaotic attractor of the model, and estimate its fractal dimension. This provides a lower bound, for the fractal dimension of the attractor, of the spatially explicit model.

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## 1. Introduction

The analysis and modeling of food chains is an active area of research in the biological sciences. These chains comprise the predator–prey relations between species [21]. An interesting subclass of such chains consists of three interacting species. The latter include cases where there is both a specialist predator and a generalist predator. They could also include cases where there are two competing predators. Such systems have many applications in modeling tri-trophic food environments [1]. The interest in three-species food-chain models stems from the seminal work of Hastings and Powell [11] in which they show chaotic dynamics in a food chain of a specialist-top-predator, specialist-middle-predator, and prey. Subsequently, these models have incorporated many kinds of functional responses [41,42]. One of the issues that has motivated much of the research on this problem is the discrepancy between predicted chaotic dynamics in food chain models and actual observations in nature, where such chaos is rarely observed [38,45]. However, there are studies that do report chaos in data from laboratory experiments with food chains [6].

Spatial spread of species in a food chain is ubiquitous in nature. This spread can lead to many interesting spatial patterns, formed

due to the dispersal of species in the search for food, mates, and also due to refuge from predators, such as via camouflage, [21]. Understanding the mechanisms that lead to the formation of these patterns has been an issue of much interest in conservation biology. A priori knowledge of these patterns can assist in conservation efforts for endangered species as well as in predicting biological invasions [30,36]. Among the various patterns that can form, Turing patterns are generated when the species in the food-chain model have different diffusion coefficients. In [37,38] Upadhyay and Rai proposed a model to understand in particular, the reasons why chaos is rarely observed in natural populations, of three interacting species. What sets apart this model from many others in the literature, is that the top predator in this case is a generalist. That is, the predator can change its food source in the absence of its favorite food, as is commonly seen in nature. The model and its variants have been studied by several authors [1,16,23]. Most of these studies have focused on the original model, which is purely temporal. Spatially explicit forms of the Upadhyay–Rai model have not been investigated as thoroughly as their temporal counterparts. In particular there are very few works in the literature on pattern formation in the model, [22].

Our objectives in the current manuscript are to investigate the effect of spatial interactions on the three-species food-chain model, (1)–(3), proposed in [37,38]. To this end we have shown the following.

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(1) We prove global existence of a solution and the existence of a global attractor for the spatial model, and derive upper estimates for its fractal and Hausdorff dimensions, in a certain parameter range. Our results are valid in 1d as well as in 2d spatial domains.

(2) We investigate Turing instability, pattern formation and diffusion induced chaos in this food-chain model, via numerical simulations in 1d as well as in 2d. We show diffusion induced temporal, as well as spatial, chaos in the model. We demonstrate the formation of a wide variety of patterns, such as stripe patterns, mesh patterns, spot patterns, labyrinth patterns and weaving patterns, in certain parameter range.

(3) The estimates of the fractal dimension of the attractor derived via functional analysis (Theorem 3.4 below), are found to be quite large. We are unable to derive lower estimates by standard functional analysis methods. In order to circumvent this difficulty, we use nonlinear time-series analysis, and reconstruct a low dimensional attractor. The upper estimates of the fractal dimension of this attractor, provide us with a lower bound for the attractor dimension of the full PDE system, (4)–(6). We also show that the model possesses diffusion induced temporal chaos as well as spatial chaos.

We briefly present the classical Upadhyay–Rai model. The three species in the model are denoted as  $u, v$ , and  $r$ . Here,  $r$  is the generalist top predator preying on  $v$ , which is its favorite food;  $v$  in turn preys on the prey,  $u$ . This scenario is often seen in nature, such as in a wasp parasitoid-spider-ant food chain, or more generally one could even consider a hyperparasitoid-parasitoid-host food chain [29].

The model takes the following form (as in [37,38]),

$$\frac{du}{dt} = a_1 u - b_1 u^2 - w_0 \left( \frac{uv}{u + D_0} \right), \quad (1)$$

$$\frac{dv}{dt} = -a_2 v + w_1 \left( \frac{uv}{u + D_1} \right) - w_2 \left( \frac{vr}{v + D_2} \right), \quad (2)$$

$$\frac{dr}{dt} = cr^2 - w_3 \frac{r^2}{v + D_3}. \quad (3)$$

There are various parameters in the model:  $a_1, a_2, b_1, w_0, w_1, w_2, w_3, c$  and  $D_0, D_1, D_2, D_3$  are all positive constants. Their definitions are as follows:  $a_1$  is the growth rate of prey  $u$ ;  $a_2$  measures the rate at which  $v$  dies out  $w_i$  is the maximum value that the per-capita rate can attain;  $D_0$  and  $D_1$  measure the level of protection provided by the environment to the prey;  $b_1$  is a measure of the competition among prey,  $u$ ;  $D_2$  is the value of  $v$  at which its per capita removal rate becomes  $w_2/2$ ;  $D_3$  represents the loss in  $r$  due to the lack of its favorite food,  $v$ ;  $c$  describes the growth rate of  $r$  via sexual reproduction.

The above model is very rich dynamically. Simulations of this ODE system [37] show chaotic behavior in various ranges of the parameter space. In addition to chaotic solutions, states of extinction for certain species in certain parameter ranges, stable foci, and limit cycles are also found. However, note that we have recently shown that the original Upadhyay–Rai model as well as the spatially extended model, can exhibit finite time blow-up, in certain parameter range [24,25]. For the spatially extended system, finite-time blow-up of the  $L^p$  norm of  $r$ , for all  $p$ , in the parameter range  $c > \frac{w_3}{D_3}$ , or even if  $c \leq \frac{w_3}{D_3}$  is possible, if  $r_0$  and  $v_0$  are large enough (that is  $\|v_0\|_\infty, \|r_0\|_\infty$  should be larger than some prescribed large constant).

However, it is in the parameter region  $\frac{w_3}{v+D_3} < c < \frac{w_3}{D_3}$ , that one obtains the most interesting dynamics, including chaotic dynamics and rapid fluctuations in the populations as seen via spiking of

the state variables. Our point here is that if one remains in the small data regime (that is  $\|v_0\|_\infty, \|r_0\|_\infty$  should be less than some prescribed small constant), for  $\frac{w_3}{v+D_3} < c < \frac{w_3}{D_3}$ , the above three species model can mimic certain realistic phenomenon, such as rapid spikes/fluctuations in a population, while avoiding blowup. These fluctuations are seen a lot in nature. For example, *C. floridanum*, a species of minute sea snail, is a type of parasitoid where a single parasitoid egg can produce up to 1500 distinct individuals [29]. Thus this model is apt for describing a hyperparasitoid-parasitoid-host food chain [29]. See Fig. 7 for such spiking. Furthermore, such spiking is also seen in insect populations, such as in spruce budworm, where there are seasonal outbreaks in the population, followed by rapid declines [12]. The larch budmoth *Zeiraphera diniana* is also known to go through population cycles where its density can change by 10,000-fold, in roughly eight year cycles [5]. Again, see Fig. 7 for such spiking. These outbreaks can also be of gradient or eruptive type, which are seen in various beetle populations such as bark, spruce and mountain pine beetles [4,31]. Here a rapid change in environmental conditions, for the better, causes the population to quickly jump to a new level. Although mathematically, this particular phenomenon is better described by a shock, or gradient blow up [32], than a spike.

Thus the model is best understood as one where, we segregate the parameter space into “good” or “bad”, depending on the dynamics we would want to see. This is not uncommon in reaction diffusion systems, modeling biological phenomenon. The literature is full of models for realistic phenomenon, such as chemotaxis and neuron firing, that yield blowup in certain parameter regime, and global existence in another [7,15,17]. Here the blowup is understood as concentration phenomenon for bacteria chasing after a food source, or the sharp increase in the amplitude of a pulse along a nerve, leading to firing, or the sharp increase in an insect population from an outbreak. Thus in general, the blow up should be viewed as a means to describe some of these sharp, yet biologically realistic transitions, and not the actual blow up in the limit.

The organization of remainder of the paper is as follows. In Sections 2 and 3, we prove global existence of solution, and the existence of a finite dimensional global attractor for the spatial model, in certain parameter regime. In Section 4, we present the uniform steady-state solutions of the model, perform linear stability analysis, and discuss Turing instability and pattern formation in the model. We also calculate regions of the stable and unstable Turing space with respect to model parameters. In Section 5, a detailed reconstruction of the attractor by nonlinear time series analysis is presented. We also present our results on diffusion induced chaos. We conclude with a discussion of results in Section 6.

## 2. Global existence of solution and the existence of a global attractor

We consider the following diffusive system,

$$u_t = d_1 u_{xx} + a_1 u - b_1 u^2 - w_0 \left( \frac{uv}{u + D_0} \right), \quad (4)$$

$$v_t = d_2 v_{xx} - a_2 v + w_1 \left( \frac{uv}{u + D_1} \right) - w_2 \left( \frac{vr}{v + D_2} \right), \quad (5)$$

$$r_t = d_3 r_{xx} + cr^2 - w_3 \frac{r^2}{v + D_3}, \quad (6)$$

where the subscripts  $t$  and  $x$  denote time and space derivatives of various variables, respectively.

The problem is posed on a domain  $\Omega \times [0, T)$ , here  $\Omega$  is bounded and  $\Omega = [0, L] \subset \mathbb{R}^1$ . We consider the following Neumann boundary conditions:

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