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The impact of diffusive migration on ecosystem stability

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ABSTRACT

In the present paper, we investigate the stability of two non-identical ecological systems, which are spatially separated, but connected through migration. We assume that the population distributions in two different patches are governed by Hastings–Powell and Upadhyay–Rai models, respectively. We also assume that all the populations are free to migrate from one patch to another. The migration and its direction are regulated by the population densities. Here, we consider that the direction of the diffusive migration is bi-directional. We propose and analyze the coupled system. Our results suggest that increase in the rate of migration can stabilize the ecosystems, which are chaotic in isolation. Extensive numerical experiments are performed to illustrate the rich dynamics of the coupled system.

1. Introduction

One of the most important discoveries in nonlinear dynamics is chaos, which gives a new hope to providing simple mathematical models for exploring, and ultimately controlling chaos in several fields of research, such as physics, chemistry, engineering, economics, ecology and so on [1–4]. Occurrence of chaos in a simple ecological system makes chaos as a subject of considerable interest among theoretical ecologists [4–7]. Earlier studies on ecological modeling mainly focused on the local stability and persistence, whereas the recent studies have a tendency in investigating extensive dynamical behaviors such as bifurcation and chaos. Hastings and Powell [4] showed chaotic dynamics in a continuous three species food chain model, and they suggested that chaos is common in natural systems. Although the literature of chaos is vast, the evidence of chaos in the real-world population dynamics is rare, except the experimental results of Beck et al. [8]. Becks et al. [8] experimentally showed chaos in the predator-prey interaction between bacterivorous ciliate and two bacterial prey species. Despite the complexity and unpredictability of chaotic behavior [4,9], it has been known that it can be controlled [10]. In ecology, until now, many researchers have investigated three species food chain/web models with an aim of exploring and/or controlling the chaos by incorporating several biological phenomena [1,11–16,18–20].

In the last few decades, there has been a growing interest on the role of space in determining population dynamics [21]. Well-mixed ecological systems could have very different dynamics if the movements of the individuals are limited. In well-mixed systems, the dynamics could be synchronized in the sense that the dynamics will be same at different patches [22]. In the population dynamics of interacting species, oscillations in population densities are common [4,16,18]. The spatial interaction is one of the most important factors that can regulate the population distribution, which have a tendency to oscillate in isolation. A simple formalism to describe spatially interacting population is provided by metapopulation models [23–26]. Levins [23] proposed metapopulation theory and applied to a pest control situation over a large region, within which local population would fluctuate in asynchrony. Metapopulation ideas play an increasingly important role in landscape ecology and conservation biology. A metapopulation consists of a set

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of local populations, living in patches in which individuals are allowed to migrate to nearby patches. Lecmote et al. [27] designed an experiment on metapopulation dynamics, which consist of 16 patches of lizard populations (Lacerta vivipara), half of which were connected by dispersal. They experimentally showed that connection stabilized population fluctuations by homogenizing population size, which decreases the metapopulation extinction probability. They suggested that dispersal could prevent metapopulation extinction by buffering the stochastic processes.

Migration of species is a common biological phenomenon, which plays a major role on the stability of ecosystems. The effects of species migration between patches have received a great attention in ecology. Migration has been described and studied in a variety of taxa from insects to higher vertebrates [23,28–30]. Migration can have a stabilizing effect in the stability of an ecosystem [15,31–34]. Holt [34] showed that passive dispersal between source and sink habitats can stabilize an otherwise unstable predator–prey interaction. Stone and Hart [33] have investigated the effect of constant immigration in a single-species discrete-time model. They observed that migration can stabilize an otherwise chaotic system. Chowdhury et al. [31] showed that migration in the middle predator can stabilize a tri-trophic food chain system. Recently, Samanta et al. [15] also observed that cascading migration in three species food chain system can increase the stability and persistence of the system. Furthermore, population migration can simplify the ensemble dynamics in the sense that individually chaotic systems can be stabilized to simple periodic dynamics [35,36]. Silva et al. [37,38] also observed that migration was able to synchronize chaotic orbits. In metapopulation dynamics, many studies focused on the simplest coupled systems consisting of two single-species sub-populations linked by migration, in order to examine the effects of migration rate on the dynamics and the stability of coupled populations [32,35,36,39–41]. These studies elucidated the important effects of migration, especially the stabilizing effects of coupling two sub-populations with chaotic dynamics. Most of the above studies, investigated the effect of migration in single species discrete models and/or single species metapopulation models. Although, food-web models framed in a spatial context are emerging, the analysis of complex trophic interactions in a spatial framework is difficult and there exists a little theory for spatial food webs.

In this paper, we have considered a simple metapopulation dynamics of tri-trophic food chain systems, which are spatially separated, but connected through migrations. We have also considered that in each food chain system, species interact differently depending on the availability of resources and the local climate. The main aim of the present study is to investigate the effect of migration on the stability behavior of two different chaotic systems while they are coupled through diffusive migration. To achieve our goal, we consider Hastings–Powell and Upadhyay–Rai models, and investigated the stability dynamics of the coupled system.

2. Model formulation

2.1. Hastings–Powell model

In 1991, Hastings and Powell [4] proposed and analyzed a three species food chain model with Holling type-II functional responses. The model is being famous for exhibiting chaos for the first time in a continuous-time food chain model. Here, both the middle predator and top predator are the specialist predators, i.e., the middle predator depends on the prey population, and the top predator depends on the middle predator. The dimensionless Hastings and Powell model is given below.

$$\begin{aligned}\frac{dx}{dt} &= x(1-x) - \frac{a_1xy}{1+b_1x},\\ \frac{dy}{dt} &= \frac{a_1xy}{1+b_1x} - \frac{a_2yz}{1+b_2y} - d_1y,\\ \frac{dz}{dt} &= \frac{a_2yz}{1+b_2y} - d_2z.\end{aligned} \tag{2.1}$$

Where x, y and z be the concentration of prey, middle predator and top predator populations, respectively. The other parameter values are interpreted as follows: a_1 and a_2 are the maximum predation rates of middle predator on prey and top predator on middle predator respectively. b_1 and b_2 represent the half-saturating constant of the middle predator and top predator, respectively. The natural mortality rate of the middle predator and the top predator populations are d_1 and d_2, respectively.

Hastings and Powell [4] studied the above three species food chain model numerically and showed the chaotic dynamics for biologically feasible parameter values. They also suggested that chaos was common in natural systems (interacting tri-trophic food chains). Later, the dynamical behavior of the model has been extensively studied by many authors with an aim to control or synchronize chaos [1,11–15,18].

2.2. Upadhyay–Rai model

Upadhyay and Rai [17,18] have proposed and analyzed a tri-trophic food chain model, where the middle predator is a specialist predator, and the top predator is a generalist predator. It is to be noted that the generalist predator is sexually reproducing species. They assumed that males and females are equal in the number, and every individual has got equal opportunity to meet an individual of opposite sex. Upadhyay and Rai [17,18] extensively studied the system and numerically explored that if the intrinsic growth rate of the prey population is increased, then the system shows chaotic behavior.

The prey-specialist predator-generalist predator system is governed by the following equations [17,18].

$$\begin{aligned}\frac{dx}{dt} &= m_1x - n_1x^2 - \frac{wxy}{x+D},\\ \frac{dy}{dt} &= -n_2y + \frac{w_1xy}{x+D_1} - \frac{w_2yz}{y+D_2},\\ \frac{dz}{dt} &= cz^2 - \frac{w_3z^2}{y+D_3}.\end{aligned} \tag{2.2}$$

Where x, y and z be the concentration of prey, middle predator, and top predator populations, respectively. The other parameter values are interpreted as follows: m_1 is the growth rate of prey population; n_1 denote the coefficient of intraspecific competition for the resources. w, w_2, w_3 are the maximum values, at which, per capita consumption rate can