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Understanding the interplay between density dependent birth function and maturation time delay using a reaction-diffusion population model

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ABSTRACT

The present work employs a nonlocal delay reaction-diffusion model to study the impacts of the density dependent birth function, maturation time delay and population dispersal on single species dynamics (i.e., extinction, survival, extinction-survival). It is shown that the maturation time and the birth function are two major factors determining the fate of single species. Whereas the dispersal acts as a subsidiary factor that only affects the spatial patterns of population densities. When the birth function has a compensating density dependence, maturation time delay cannot destabilize the population survival at the positive equilibrium. Nevertheless, when the birth function has an over-compensating density dependence, the population densities of single species fluctuate in the spatial domain due to the increased maturation time delay. With the Allee effect and over-compensating density dependence, the increases in the maturation time may cause extinction of the single species in the entire spatial domain. The numerical simulations suggest that the solutions of the general model may temporarily remain nearby a stationary wave pulse or a stationary wavefront of the reduced model. The former indicates the survival of single species in a narrow region of the spatial domain. Whereas the latter represents the survival in the entire left-half or right-half of the spatial domain.

1. Introduction

Mathematical models in population biology and epidemiology are becoming more sophisticated and therefore more challenging. In the last two decades, there has been a significant progress in mathematical modeling of spatially structured populations. Two contemporary modeling approaches that have been the center of attention are known as Britton's and Smith-Thieme approaches. Namely, the Britton's approach Britton (1989, 1990) takes into account the aggregation mechanism of the population through a spatio-temporal convolution, whereas the Smith-Thieme approach Smith and Thieme (1991) incorporates age structures into the population models. Employing either of these approaches, various nonlocal delay diffusive models have been proposed Gourley et al. (2004), Liang et al. (2005), Weng et al. (2008). Analyses of these models are mainly focused on the existence and behavior of traveling wave solutions Gourley et al. (2004), Liang and Wu (2003), So et al. (2001). Nonetheless, there is a need to compare the possible outcomes of the new models with those of the traditional models. Specifically, the spatio-temporal patterns resulting from the new models may reveal population dynamics and crucial factors that have been overlooked by the traditional models.

In the present work we study the possible outcomes of the general age-structured population model proposed by So et al. (2001). The model has been developed using the Smith-Thieme approach for one-dimensional unbounded domain. In particular, let $u(x, a, t)$ denote the population density of the single species at time $t \geq 0$, age $a \geq 0$, and location $x \in (-\infty, \infty)$. Then the authors start with the following age-structured model proposed in Metz and Diekmann (1986).

$$\frac{\partial u}{\partial t} + \frac{\partial u}{\partial a} = D(a)\frac{\partial^2 u}{\partial x^2} - d(a)u, \tag{1}$$

where $D(a)$ and $d(a)$ are the diffusion and death rates, respectively. Let τ be the total time spent from birth until becoming a sexually

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mature adult. Then the total mature population at time t and position x is given by

$$w(x,t) = \int_{\tau}^{\infty} u(x,a,t)da. \quad (2)$$

By taking the integral from both sides of (1) and assuming that $u(t, \infty, x) = 0$, $D(a) = D_m$ and $d(a) = d_m$, we get

$$\frac{\partial w(x,t)}{\partial t} = u(x,\tau,t) + D_m \frac{\partial^2 w(x,t)}{\partial x^2} - d_m w(x,t), \quad (3)$$

where parameters D_m and d_m are diffusion and death rates of mature population, respectively. Using the method of separation of variables and Eq. (1), $u(x, \tau, t)$ can be replaced with an integral term. Then the nonlocal delay reaction-diffusion (RD) model of mature population is given by

$$\frac{\partial w(x,t)}{\partial t} = D_m \frac{\partial^2 w(x,t)}{\partial x^2} - d_m w(x,t) + \epsilon \int_{-\infty}^{\infty} b(w(y,t-\tau)) f_\alpha(x - y)dy, \quad (4)$$

where $x \in \mathbb{R}$ and $0 < \epsilon \le 1$. The first term on the right hand side of (4) reflects the spread of adults in the spatial domain and the second term corresponds to the mortality of adults. The function $b(w)$ is known as the birth function and $f_\alpha(x) = (1/\sqrt{4\pi\alpha})e^{-x^2/4\alpha}$ is the standard heat kernel which relates to random movement of individuals. Here $\alpha = \tau D_I > 0$, where D_I is the diffusion rate of immature population.

The integral term is a weighted spatial average that takes into account the local increase in the mature population due to migration of all individuals born elsewhere Gourley et al. (2004). In particular, the current mature population $w(x, t)$ at location x is increased by the weighted birth rates $b(w(y, t - \tau))$ at the previous time $t - \tau$ and all locations $y \in \mathbb{R}$. The term ϵ represents the survivorship of immature individuals from the time of birth until they are mature. This is given by

$$\epsilon = \exp\{-\int_0^{\tau} d_I(\theta)d\theta\}, \quad (5)$$

where $d_I(\theta)$ is the death rate of the immature population at age θ. Specifically, taking ϵ inside the integral term in (4) and considering $\epsilon b(w)$ as a single term, we may realize that the portion $(1 - \epsilon)b(w)$ of individuals did not survive and therefore removed from the equation. This is similar to models that consider the mating probability $p(w)$ as a limiting factor of reproduction and include $p(w)b(w)$ rather than $b(w)$ Dennis (1989), McCarthy (1997), Wells et al. (1998).

Considering specific birth functions, the traveling wave solutions of model (4) have been previously studied Bani-Yaghoub and Amundsen (2014), Liang and Wu (2003), Liang et al. (2005). Moreover, model (4) has been further extended to RD models with two-dimensional spatial domains Liang et al. (2005), Weng et al. (2008), where the existence of traveling wave solutions Liang et al. (2005) has been investigated. Nevertheless the possible outcomes of model (4) in regards to extinction, survival or extinction-survival of a population remain poorly elaborated. The present work studies these outcomes by considering the general birth function $b(w)$, the maturation time τ and the diffusion rate D_m and D_I.

Similar to discrete models Anazawa (2009), the behavior of $b(w)$ can be classified into four categories: Indefinite Population Growth (IPG), Compensating Density Dependence (CD), Overcompensating Density Dependence (OCD) and Allee effect (AE), which are shown in Fig. 1. The OCD and the CD are two self-limiting mechanisms that arise from scramble competition and contest competition, respectively Nicholson (1954). The former represents a single species whose birth rate declines after it reaches a maximum value. Whereas the latter corresponds to a population with monotonic increase in the birth rate until it reaches some asymptotic value. The IPG occurs when $b(w)$ is increasing for all $w \ge 0$. Moreover, $b(w)$ may exhibit an AE Allee (1927, 1933) which often occurs at low population densities. The main concept of AE is

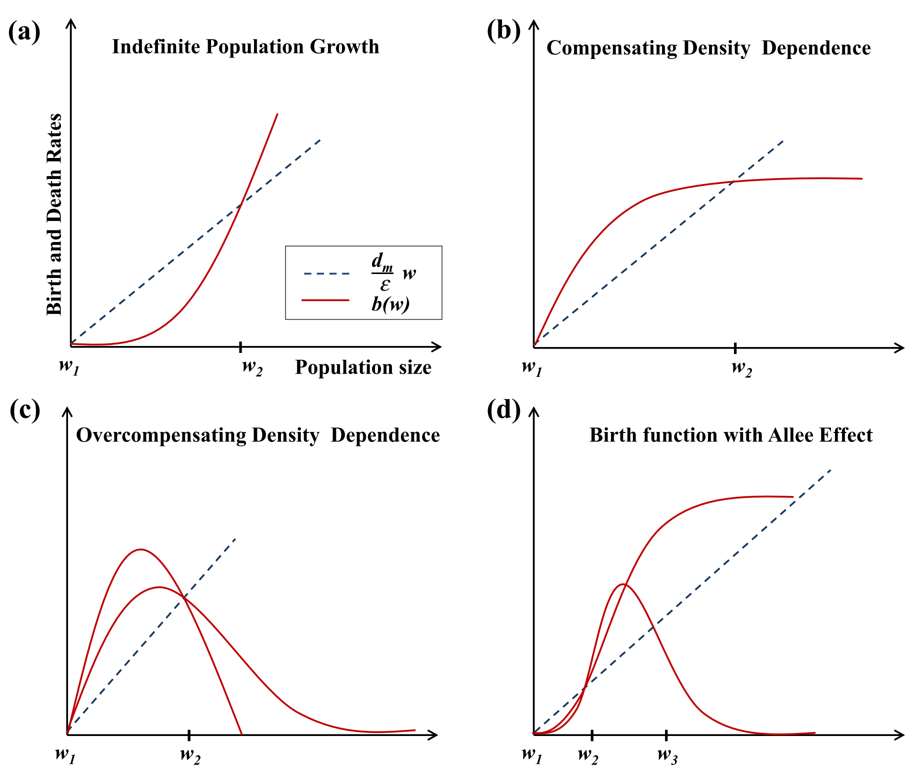

Fig. 1. A schematic representation of the density dependent birth function $b(w)$. Possible behaviors of $b(w)$ are indicated in each panel. The slope (d_m/ϵ) of the dashed lines indicates the ratio of the mature population death rate over immature population survival rate. The constant equilibria of model (4) are shown with w_1, w_2 and w_3.