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Invasions in heterogeneous habitats in the presence of advection

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ABSTRACT

We investigate invasions from a biological reservoir to an initially empty, heterogeneous habitat in the presence of advection. The habitat consists of a periodic alternation of favorable and unfavorable patches. In the latter the population dies at fixed rate. In the former it grows either with the logistic or with an Allee effect type dynamics, where the population has to overcome a threshold to grow. We study the conditions for successful invasions and the speed of the invasion process, which is numerically and analytically investigated in several limits. Generically advection enhances the downstream invasion speed but decreases the population size of the invading species, and can even inhibit the invasion process. Remarkably, however, the rate of population increase, which quantifies the invasion efficiency, is maximized by an optimal advection velocity. In models with Allee effect, differently from the logistic case, above a critical unfavorable patch size the population localizes in a favorable patch, being unable to invade the habitat. However, we show that advection, when intense enough, may activate the invasion process.

1. Introduction

Invasions of alien species are widespread phenomena, in principle affecting every ecosystem, usually with dramatic consequences on the native community, constituting a major threat to biodiversity (Vitousek et al., 1997; Mooney and Hobbs, 2000; Pimentel et al., 2000). At the scale of interest for management purposes, i.e. the geographic scale, invasive species move across a heterogeneous landscape characterized by favorable and unfavorable areas. The presence of abiotic heterogeneity, in fact, characterizes most of natural habitats and plays a key role in invasion processes, influencing their rate of spread and outcome (Shigesada and Kawasaki, 1997; Hastings et al., 2005; Melbourne et al., 2007).

Alongside with the empirical interest for the problem, several modeling efforts have been dedicated to the understanding and prediction of the spatial spread of invading organisms in heterogeneous environments. Within the framework of reaction–diffusion models, building on the pioneering theoretical works of Skellam (1951) and Kierstead and Slobodkin (1953) on the "critical patch size" problem, Shigesada et al. (1986) gave a seminal contribution considering the invasion (propagation) of a population through a periodic heterogeneous environment (see also Weinberger, 2002; Kinezaki et al., 2003). The problem was extended including advective transport to study persistence and propagation of passively dispersing populations in oceans (Mann and Lazier, 1991; Abraham, 1998) or rivers (Speirs and Gurney, 2001; Pachepsky et al., 2005; Lutscher et al., 2006). The importance of the interplay between heterogeneity and advection has been recently reviewed by Ryabov and Blasius (2008). Moreover, the role of both advection and landscape spatial structure is clearly relevant also to the dispersal of plants (Hastings et al., 2005), whose seeds are transported by winds.

In this paper, we focus on the interplay between abiotic heterogeneity and advection in invasions. We describe the dynamics in terms of an advection–reaction–diffusion model, which allows for mathematical tractability and quantitative predictions, e.g., on the spreading rates.

We consider an infinite system where a population stably saturates the carrying capacity on one side of the system and possibly invades the remaining part of the environment, which is assumed to be heterogeneous. Our setting is quite general and widely applicable. In particular, it is relevant to situations in which one has a practically infinite biological reservoir of a species invading an empty territory characterized by abiotic heterogeneity. For instance, the above setting may be relevant to situations in which invasions can suddenly become possible for the removal of a climatic barrier due to climate changes (Mooney and Hobbs, 2000). Another relevant case is when a species stably populating a lake invades an effluent characterized by a certain degree of heterogeneity and stream velocity. This is one of the key

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early stage processes related to the spatial control of invasions in lakes' networks (Havel et al., 2002). Other examples concern the spreading of wind-pollinated plants in a heterogeneous environment (Davis et al., 2004) or spores carried by the wind (Kot et al., 1996).

More specifically, the habitat consists of a periodic alternation of unfavorable and favorable patches, as in Shigesada et al. (1986). The population dies at a fixed rate in unfavorable regions, and grows in favorable ones according to either a logistic or an Allee effect dynamics. We are interested in determining the conditions for invasions to be possible and in understanding how invasion speed and efficiency depend on the mechanisms at play.

With the logistic dynamics, in the absence of advection, this problem was pioneered by Shigesada et al. (1986), while Lutscher et al. (2006) considered both advection and heterogeneity in reference to the "drift paradox" problem (Speirs and Gurney, 2001). Going beyond these works, we find asymptotic expressions for both the invasion speed and the rate of increase of the population size. The latter quantity essentially estimates the rate at which the number of invading individuals grows and, thus, provides a suitable measure of the efficiency of the spreading process. Indeed, especially in invasive species control, it is important to quantify the potentiality of growth of an alien population, and not only the speed at which it colonizes the territory. We anticipate that, remarkably, larger invasion speeds do not necessarily imply more efficient invasions.

The logistic case (decreasing *per capita* growth rate) is then contrasted with the case of positive density dependence corresponding to a demographic Allee effect (Allee, 1938; Dennis, 1989), which accounts for a reduced reproductive power at low densities. The importance of Allee effects for the invasion and control of non-native species was emphasized by Taylor and Hastings (2005) and Tobin et al. (2011). It is interesting to mention that even in homogeneous habitats the presence of the Allee effect can decrease the invasion speed or even halt the population spreading if the initially occupied area is too small (Lewis and Kareiva, 1993) (see also Vercken et al., 2011 for recent field observations). We find that the interplay between heterogeneity and advection becomes very subtle in the presence of the Allee effect. In fact it may happen that a persisting population, unable to invade new territory, becomes able to spread in the presence of strong advection. This effect should be taken as a cautionary note from the standpoint of controlling invasive species, telling us that advective transport should be considered. For instance, after strong weather events, or in regions characterized by prevailing winds, neglecting the effects of advection could lead to the erroneous prediction of a population unable to invade, whereas it actually propagates over the territory.

The material is organized as follows. In Section 2 we present the model, and in Section 3 we qualitatively discuss its phenomenology. Sections 4 and 5 present and discuss the main results on invasions with the logistic and the Allee effect model, respectively. Finally, in Section 6 we summarize the results.

2. Model

The evolution of the population, $\theta(x,t)$, is governed by the advection–reaction–diffusion equation:

$$\partial_t\theta+v\partial_x\theta=D\partial_x^2\theta+f(\theta,x). \tag{1}$$

The diffusion coefficient D and the advection velocity v are assumed to be constant. Heterogeneity is introduced in the growth term, $f(\theta,x)$, which depends on the position x. The habitat consists of a periodic alternation of unfavorable and favorable patches of sizes ℓ_u and ℓ_f, respectively. In the elementary cell $[0:\mathcal{L}]$ (where $\mathcal{L}=\ell_u+\ell_f$ denotes the spatial period), we take

$$f(\theta,x)=\begin{cases} g_u(\theta), & 0\le x<\ell_u, \\ g_f(\theta), & \ell_u\le x<\mathcal{L}. \end{cases} \tag{2}$$

In the unfavorable regions the population is assumed to die at a constant rate r_u, so that $g_u(\theta)=-r_u\theta$ $(r_u>0)$. In the favorable regions we consider two dynamics. The first is the classical logistic model (with carrying capacity normalized to one):

$$g_f(\theta)=r_f\theta(1-\theta), \tag{3}$$

r_f being the intrinsic growth rate. Eq. (1) with the logistic term but without advection was first studied by Shigesada et al. (1986). Recently, Lutscher et al. (2006) included advection focusing on the "drift paradox" problem.

Second, accounting for a positive correlation between population density and *per capita* growth rate at small densities—the Allee effect (Allee, 1938; Dennis, 1989)—we consider the threshold model:

$$g_f(\theta)=r_f\ \max\{(\theta-\theta_c)(1-\theta),0\}, \tag{4}$$

prescribing that the population grows only when $\theta>\theta_c$ (otherwise it stays constant). Notice that (4) recovers (3) for $\theta_c=0$. We remark that the model (4) represents an intermediate case between weak and strong Allee effect (Courchamp et al., 2008, see also Section 5 for further discussions). To the best of our knowledge, models with Allee effects have been mostly investigated in homogeneous habitats (Petrovskii and Li, 2003). In heterogeneous habitats we are aware of only a few studies with integrodifference models incorporating different dispersal kernels (see, e.g., the recent work by Dewhirst and Lutscher, 2009; Pachepsky and Levine, 2011).

We now specify the settings in which Eq. (1) is studied. We consider model (1) with boundary condition $\theta(0,t)=1$, mimicking the case in which on the left of the origin $(x<0)$ the population constantly saturates the carrying capacity, while the population is initially absent in the $x>0$ region, i.e. $\theta(x,0)=0$ for $x>0$. With this choice for the boundary conditions the invasion process must be considered from left to right (i.e. from the biological reservoir at $x\le 0$ to the positive real axis). In this case depending on the sign of the advection velocity we can consider (downstream) invasions with the flow (i.e when $v>0$) or (upstream) invasions against the flow (i.e. when $v<0$).

It is useful to formulate the model in non-dimensional variables. To this aim we exploit known results about the logistic growth model without advection, namely the standard FKPP equation (Fisher, 1937; Kolmogorov et al., 1937). The FKPP equation develops traveling fronts characterized by the propagation speed $v_0=2\sqrt{Dr_f}$ and width $\xi_0=\sqrt{D/r_f}$. It is then natural to measure lengths in units of ξ_0, time in units of the inverse growth rate in the favorable patches $1/r_f$, and the advection velocity in units of v_0. We thus define the non-dimensional variables $x'=x/\xi_0$, $t'=tr_f$, $u=v/v_0$. Dropping the primes, Eq. (1) made non-dimensional reads

$$\partial_t\theta+2u\partial_x\theta=\partial_x^2\theta+f(\theta,x). \tag{5}$$

The factor 2 in the advection term results from our choice to fix $u=1$ as the non-dimensional propagation speed in the homogeneous FKPP system. We can now introduce $\epsilon=r_u/r_f$ which is the death over growth rate ratio, and $l_{f,u}=\ell_{f,u}/\xi_0$ which are the non-dimensional sizes of the patches $(L=\mathcal{L}/\xi_0=l_u+l_f)$. In this way, with reference to Eq. (2) we have $g_u(\theta)=-\epsilon\theta$ and

$$g_f(\theta)=\theta(1-\theta) \tag{6}$$