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Original Research Article

Patterns of invasive species spread in a landscape with a complex geometry

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ABSTRACT

Patterns and rates of invasive species spread have been a focus of attention for several decades. Majority of studies focused on the species proliferation in a relatively uniform "open space" thus leaving aside the effects of the landscape geometry as given by size and shape of inaccessible areas. In this paper, we address this issue by considering the spatiotemporal dynamics of an alien species in a domain where two large uniform habitats are connected by a narrow corridor. We consider the case where the species is originally introduced into one of the habitats but not to the other. The alien species is assumed to be affected by a predator, so that mathematically our system consists of two coupled diffusion–reaction equations. We show that the corridor tends to slow down the spread: it takes the alien population an extra time to penetrate through the corridor, and this delay time can be significant in the case of patchy spread. We also show that a sufficiently narrow corridor blocks the spread; simple analytical estimates for the critical width of the corridor are obtained. Finally, we show that the corridor can become a refuge for the alien population. If considered on a longer timescale that includes species adaptation and/or climate change, the corridor may then become a source of a secondary invasion.

1. Introduction

Biological invasion is a phenomenon that has a variety of important implications for ecology (in particular, through species extinctions and biodiversity loss), environment, human wellbeing, agriculture/aquaculture, and sometimes industries beyond agriculture (Keller et al., 2009; Pimentel, 2002; Sandlund et al., 2001). For these reasons, it has been a focus of intense empirical and theoretical research for several decades (Drake et al., 1989; Richardson, 2011; Williamson, 1996). Mathematical modelling is widely accepted as an efficient tool to study biological invasion (Hengeveld, 1989; Lewis et al., 2016; Shigesada and Kawasaki, 1997). Indeed, in the situation when replicated studies are hardly possible,[1] mathematical models along with computer simulations provide a virtual laboratory where the effect of various factors can be refined and analyzed and different hypotheses can be tested safely and at a relatively low cost.

In studies on biological invasion, a central question is how the alien species proliferates into space away from the place of its introduction. In its turn, it evokes the question as to what is the pattern of spread. For several decades, a paradigm of invasive species spread was a travelling population front. A large amount of theoretical work has been done in order to evaluate the speed of the front propagation (Aronson and Weinberger, 1978; Fisher, 1937; Kolmogorov et al., 1937; Skellam, 1951) and to reveal how the propagation can be affected by various factors (Bell et al., 2009; Lewis and Kareiva, 1993; Owen and Lewis, 2001), in particular, by environmental heterogeneity (Andow et al., 1990; Keitt et al., 2001; Petrovskii, 1998; Shigesada et al., 1986). The travelling front paradigm was eventually complemented by an alternative pattern of spread known as patchy invasion (Jankovic and Petrovskii, 2013; Petrovskii et al., 2002, 2005b; Morozov et al., 2006) which is often observed in nature (Davis et al., 1998; Liebhold et al., 1992; Mack, 1981) and predicted by various dispersal-growth models (Lewis, 2000; Mistro et al., 2012; Rodrigues et al., 2015; Shigesada et al., 1995). In the patchy invasion scenario, there is no population front and species spread into space occurs through the dynamics of separate disconnected population patches.

Whether it is a population travelling front or a patchy spread, previous studies on biological invasions have overwhelmingly focused on an idealized case of species spread in an unbounded space. (In case of a simulation study, the domain is bounded but

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[1] Not to mention the transient nature of the weather that makes it virtually impossible to reproduce the initial conditions, a repeated release of an alien species – potentially, a dangerous pest – would be highly controversial and possibly illegal.

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can be chosen 'sufficiently large' in order to imitate an unbounded space.) Even that the effect of environmental heterogeneity was considered in a number of studies, e.g. see the references above, the role of inaccessible areas and hence the effect of landscape geometry on the rate of spread have remained poorly understood. Meanwhile, such a role is likely to be very important. One real world example is the invasion of grey squirrels in the UK. Whilst they successfully colonized most of England and Wales, the rate of their spread being in a good agreement with predictions of relevant mathematical models (Bell et al., 2009; Okubo et al., 1989), they have largely failed to spill over to central and northern Scotland, and the landscape geometry – as given by large areas that are not accessible to squirrels such as swamps or high mountain ranges – is thought to be a reason for that (White, 2013). As another example, it was found in a study on the invasion of nutria in Iran that about one third of the country could potentially be colonized (Farashi and Najafabadi, 2015). In reality, however, having been introduced about one hundred years ago to the sub-Caspian region, this species remains confined to largely the same area. A closer look reveals that different parts of the potential range are poorly connected (e.g. due to the effect of mountain ranges inaccessible to nutria), which is likely to limit species dispersal. In this paper, we consider the effect of the landscape geometry on the invasive species spread by means of mathematical modelling and computer simulations. The "complexity" of the landscape geometry (as is relevant in the context of this study) is represented by a dumbbell-like, "H-shaped" spatial domain consisting of two large habitats connected by a narrow passage or corridor. The initial conditions correspond to the situation where the alien species is present in

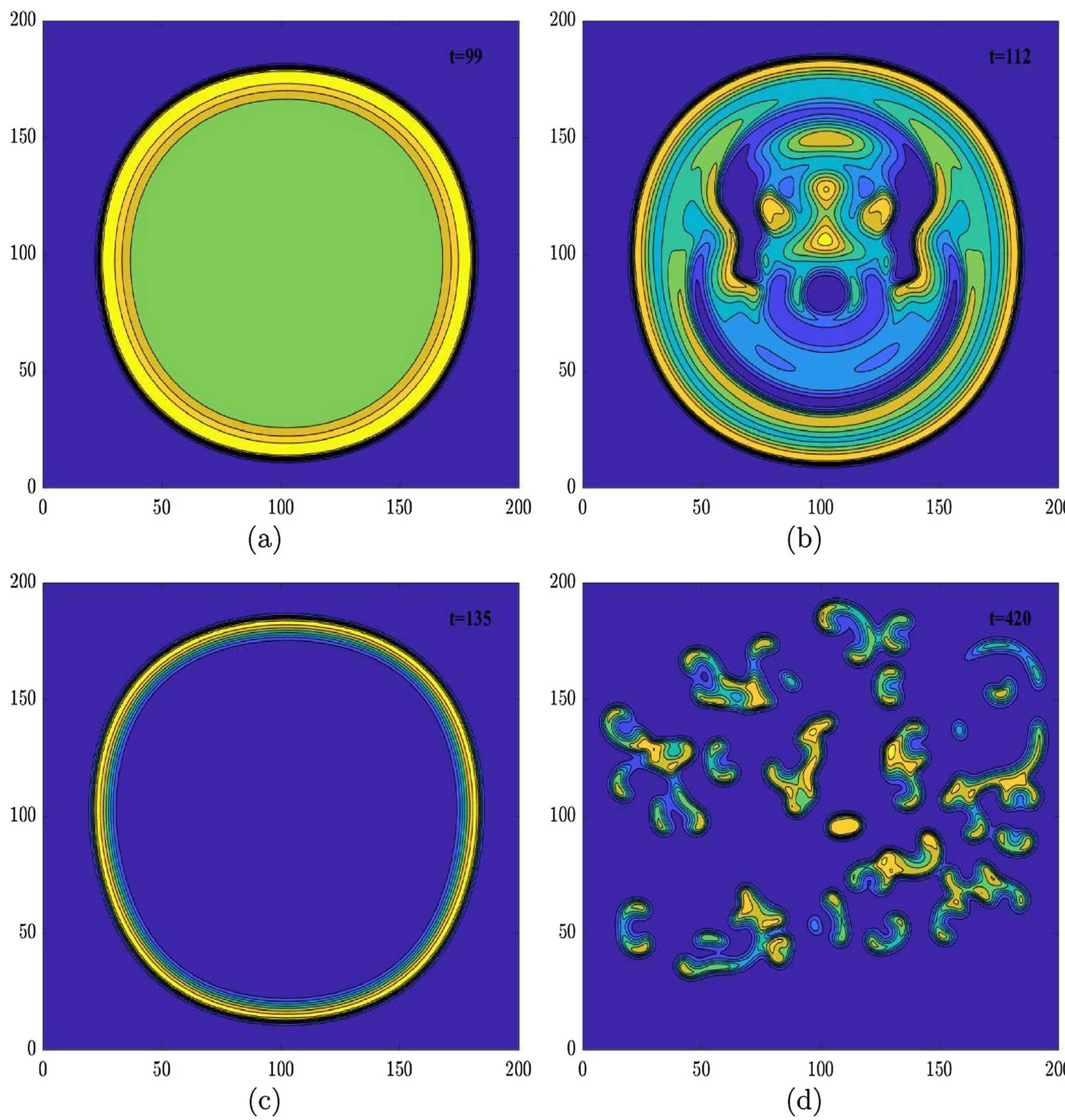

Fig. 1. Snapshots of the spatial distribution of prey (i.e. the alien species) illustrating different scenarios of invasive spread as predicted by Eqs. (5) and (6) obtained in a square domain 200 × 200 for parameters (a) $\delta = 0.63$, (b) $\delta = 0.51$, (c) $\delta = 0.43$ and (d) $\delta = 0.37$. Other parameters are given in the text. Here and below yellow color stands for high population density, green and light blue for intermediate values, dark blue for zero density. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

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