Mathematical Biosciences 275 (2016) 51–56

Contents lists available at ScienceDirect

Mathematical Biosciences

journal homepage: www.elsevier.com/locate/mbs

Formulating spread of species with habitat dependent growth and dispersal in heterogeneous landscapes

Andriamihaja Ramanantoanina[a,b,*], Cang Hui[a,b]

[a] Centre for Invasion Biology, Department of Mathematical Sciences, Stellenbosch University, Matieland 7602, South Africa
[b] Mathematical and Physical Biosciences, African Institute for Mathematical Sciences, Cape Town 7945, South Africa

ARTICLE INFO

Article history:
Received 26 August 2015
Revised 31 December 2015
Accepted 28 February 2016
Available online 8 March 2016

Keywords:
Biological invasion
Range expansion
Boom-and-bust
Lag phase
Habitat heterogeneity
Dispersal strategy

ABSTRACT

Habitat heterogeneity can have profound effects on the spreading dynamics of invasive species. Using integro-difference equations, we investigate the spreading dynamics in a one-dimensional heterogeneous landscape comprising alternating favourable and unfavourable habitat patches or randomly generated habitat patches with given spatial autocorrelation. We assume that population growth and dispersal (including emigration probability and dispersal distance) are dependent on habitat quality. We derived an approximation of the rate of spread in such heterogeneous landscapes, suggesting the sensitivity of spread to the periodic length of the alternating favourable and unfavourable patches, as well as their spatial autocorrelation. A dispersal-limited population tends to spread faster in landscapes with shorter periodic length. The spreading dynamics in a heterogeneous landscape was found to be not only dependent on the availability of favourable habitats, but also the dispersal strategy. Estimates of time lag before detection and the condition for boom-and-bust spreading dynamics were explained. Furthermore, rates of spread in heterogeneous landscapes and corresponding homogeneous landscapes were compared, using weighted sums of vital rates.

1. Introduction

Landscape heterogeneity can affect the behaviour of biological invasions at different stages, especially when established species start to become invasive and spread into heterogeneous landscapes [1–3]. Empirical investigations have suggested that the spatial heterogeneity of landscapes can influence the rate of spread of invasive species [4] as demography and dispersal are both context based (i.e. sensitive to spatial heterogeneity) [1,5]. While many robust estimates of the asymptotic rate of spread on homogeneous landscapes have been formulated [6], the effects of spatial heterogeneity on the spreading dynamics of species with habitat sensitive demography and dispersal demand more attention [7,8].

Invasion dynamics in heterogeneous landscapes has long been theoretically explored using continuous time frameworks such as partial differential equations. In particular, Shigesada et al. [9] simulate spatial heterogeneity by alternating homogeneously favourable and unfavourable habitat patches on an infinite one-dimensional environment, with the growth rate and diffusion coefficient assumed as periodic step functions of locations. It emphasises the effect of the lengths of periodically alternating favourable and unfavourable patches on the rate of spread. In contrast, Kinezaki et al. [10] consider the effect of spatial heterogeneity by allowing vital rates to vary sinusoidally in space, representing a continuous change in habitat quality. It emphasises the role of both the amplitude and periodic length of habitat heterogeneity on the rate of spread. In both models, when the periodic length of alternating habitat quality is short, the initial population will propagate from the introduction point into periodic travelling waves, with the rate of spread being $c = 2\sqrt{\langle r\rangle_A \langle D\rangle_H}$, where $\langle r\rangle_A$ and $\langle D\rangle_H$ denote the spatial arithmetic mean of the growth rate and the spatial harmonic mean of the diffusion coefficient, respectively.

When the focal species does not follow a diffusion-type movement, integrodifference equations (IDEs) are commonly used for modelling the spatiotemporal dynamics of biological invasions [11]. For instance, Kawasaki and Shigesada [7] have examined the spreading dynamics with an exponentially damping (Laplace) dispersal kernel in a patchy landscape with alternating favourable and unfavourable patches, while assuming that dispersal is insensitive to habitat heterogeneity. They found that the presence of unfavourable patches can dramatically reduce the rate of spread, although the population can always spread with wide enough favourable habitats. Dewhirst and Lutscher [8] expanded this

---

[*] Corresponding author at: Mathematical and Physical Biosciences, African Institute for Mathematical Sciences, Cape Town 7945, South Africa. Tel.: +27 725569814.
E-mail address: mihataims@gmail.com, ar@aims.ac.za (A. Ramanantoanina).

http://dx.doi.org/10.1016/j.mbs.2016.02.013
0025-5564/

model by considering habitat dependent dispersal behaviours, with individuals from unfavourable habitats dispersing farther in an attempt to find favourable habitats. These works put the emphasis on the existence of a minimum proportion of favourable habitats for successful invasions and spread. Gilbert et al. [12] further consider the effects of the landscape periods on the spread of a structured population.

We here formulate the spread of a species with non-overlapping generations in a heterogeneous patchy landscape as defined by Shigesada et al. [9]. Besides assuming a habitat-dependent population growth, dispersal behaviours are further affected by habitat quality in the following two ways. First, the dispersal distance of migrating individuals is dependent on the habitat quality, with individuals from unfavourable locations dispersing farther for locating favourable habitats [13,14]. Second, only a fraction of the local population emigrates (defined as emigration probability) while others remain sedentary - the number being dependent on habitat quality. We also perform numerical simulations to investigate the instantaneous rate of spread, and derive an estimate for the asymptotic rate of spread in randomly generated patchy landscapes with different levels of spatial autocorrelation.

2. Model

We consider a population with non-overlapping generations undergoing growth and dispersal at separate times, using integrodifference equations (IDEs). With the vital rates affected by spatial heterogeneity, we have the following IDE model,

$$u(x,t+1) = \int [d(y)k(x-y,y) + (1-d(y))\delta(x-y)] \times g(u(y,t),y)dy, \tag{1}$$

where $u(x,t)$ denotes the population size at location x and time t. The function g gives the population growth (more specifically, fecundity in species with non-overlapping generations). It is a non-negative function satisfying density dependent recruitment, $g(u, x) \leq R(x)$ with $R(x) = \partial g/\partial u|_{u=0}$ being the intrinsic growth rate at location x. In the Ricker (1954) model, we have $g(u(x,t),x) = ue^{r(x)-u(x,t)}$ and $R(x) = e^{r(x)}$.

We considered two factors in formulating the habitat dependent dispersal strategy [14,15]. First, the dispersal kernel k in Eq. (1) gives the probability distribution that an individual from location y disperses to location x. The dispersal distance effectuated by an individual during a dispersal event can be influenced by the habitat quality [13,14]. That is, $k(x-y,y)$ not only depends on the distance between location x and y but also the habitat quality of the originating location y. For instance, a Gaussian dispersal kernel is thus

$$k(x-y,y) = (1/\sqrt{2\pi\sigma^2(y)})\exp(-(x-y)^2/(2\sigma^2(y))),$$

and a Laplace dispersal kernel

$$k(x-y,y) = (1/\sqrt{2\sigma^2(y)})\exp(-\sqrt{2}|x-y|/\sqrt{2\sigma^2(y)}).$$

Second, spatial heterogeneity can also influence the probability, $d(y)$, of an individual emigrating from its original location y to other patches, often following a ‘good-stay, bad-disperse’ rule [5]. Therefore, $1 - d(y)$ gives the proportion of individuals remaining sedentary, with $\delta(x-y)$ in Eq. (1) being 1 if $x = y$ and 0 otherwise.

Here we focused on periodically alternating habitats of favourable and unfavourable patches, with lengths L_1 and L_2, respectively [7,9]. The habitat was laid out with a periodic length of L $(=L_1+L_2)$ and a proportion of p $(=L_1/L_2)$ favourable habitats in the landscape. The intrinsic growth rate $R(x)$ is given by R_1 $(>1$ to ensure population growing) in favourable habitats and R_2 (>0) in unfavourable habitats. Similarly, we also defined the emigration probability, $d(x)$, being d_1 and d_2, and the variation of dispersal kernel, $\sigma^2(x)$, being σ_1^2 and σ_2^2 in favourable and unfavourable habitats, respectively.

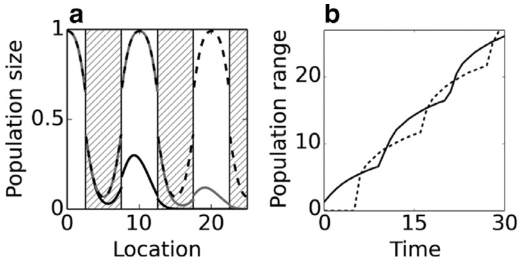

Fig. 1. (A) Travelling periodic waves in a heterogeneous landscape. Dashed black line represents the periodic steady state of the model. Solid black and grey lines indicate the population size at time $t = 15$ and $t = 25$ respectively. Hatched region indicate unfavourable patches. (B) Population range front for the initial population introduced in favourable (solid line) and unfavourable (dashed line) locations. While the former started to spread immediately, the population introduced into an unfavourable habitat experienced a lag between the introduction and detected spread. Parameter values are $p = 0.5$, $R_1 = e$, $R_2 = e^{-0.5}$, $d_1 = 0.75$, $d_2 = 1$, $\sigma_1{}^2 = 1$, $\sigma_2{}^2 = 1$.

To study the dynamics of the above IDE model, we first investigate its non-trivial steady states by replacing $u(x,t+1)$ and $u(y,t)$ in Eq. (1) with $v(x)$ and $v(y)$, and numerically solving the equation using the routine *optimize.fsolve* in the Python library SciPy [16]. To investigate the spreading dynamics, we ran the model for 100 generations and calculated the population range at time t as $x^*(t) = \max\{x; u(x,t) \geq u*\}$ for a threshold of detection $u*$. The corresponding instantaneous and average rate of spread can be given as $c_I(t) = x^*(t+1) - x^*(t)$ and $c_A(t) = x^*(t)/t$. The time lag before range expansion is defined as the first time when the population was detected after its introduction, $T(u^*) = \min\{t; x^*(t) > 0\}$. The spreading dynamics was also compared with the dynamics in homogenous landscape with normalised vital rates (e.g. $d = p \cdot d_1 + (1-p)d_2$).

3. Results

3.1. General behaviour

The model exhibited a periodic steady state, with obvious gaps between the population sizes in favourable and unfavourable habitats (Fig. 1A). The gap size is more sensitive to changes in emigration probability (d) than to changes in dispersal distance (σ^2), with even higher sensitivity observed when increasing dispersal probability from favourable habitats than when increasing the same factor in unfavourable ones. When the proportion of favourable habitats (p) increased, population sizes remained largely unchanged in favourable habitats whilst population sizes in unfavourable habitats increased notably. Similarly, increasing only the periodic length of spatial heterogeneity (L) notably reduced the populations in unfavourable habitats.

Unless the population eventually became extinct, it was found to expand its range in both directions from the introduction location, in the form of a periodic travelling wave (i.e.$u(x+L; t+t') = u(x;t)$ for some $t' > 0$) (Fig. 1A). (We note that Fig. 1 and the remaining figures in this section were obtained using Gaussian dispersal kernel) A time lag was often observed before the detection of the population after its initial introduction in an unfavourable patch (Fig. 1B). The time lag can be shortened by increasing the initial population size or the vital rates (growth and dispersal rates). Time lags on the other hand can be prolonged for larger thresholds of detection or wider unfavourable patches. Nonetheless, the spreading dynamics remained the same for populations in landscapes with different periodic lengths but a common proportion of favourable habitats (p), regardless of whether it was initially introduced into a favourable or unfavourable patch.