Ecological Complexity 20 (2014) 264–270

Contents lists available at ScienceDirect

Ecological Complexity

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

Original Research Article

Can climate change lead to gap formation?

Henri Berestycki [a,*], Laurent Desvillettes [b], Odo Diekmann [c]

[a] Centre d'analyse et de mathématique sociales – UMR 8557, Ecoles des hautes études en sciences sociales – CNRS, 190-198, avenue de France, 75244 Paris Cedex 13, France
[b] CMLA, ENS Cachan, CNRS, 61 Av. du Pdt., Wilson F-94230 Cachan Cedex, France
[c] Department of Mathematics, Utrecht University, P.O. Box 80010, 3508 TA Utrecht, The Netherlands

ARTICLE INFO

Article history:
Received 5 February 2014
Received in revised form 14 October 2014
Accepted 15 October 2014
Available online 11 November 2014

Keywords:
Reaction–diffusion system
Competing species
Climate change
Gap formation

ABSTRACT

Consider a situation where spatial heterogeneity leads to a cline, a gradual transition in dominance of two competing species. We first prove, in the context of a simplified competition–diffusion model, that there exists a stationary solution showing that the two species coexist in a transition zone. What happens then if, owing to climate change, the environmental profile moves with constant speed in space? We show here that, when the speed with which the environmental condition shifts exceeds the Fisher invasion speed of the advancing species, an expanding gap will form. We raise the question of whether such a phenomenon has been or can be observed.

1. Introduction

In this note we consider two competing species in a one-dimensional domain characterized by an environmental gradient such that species 1 is favoured far to the left (corresponding, say, to the South) and species 2 is favoured far to the right (corresponding to the North). One expects that a cline will form as a result, with species 1 being replaced gradually by species 2 when one moves from South to North. We indeed establish this property in the context of a simple reaction-diffusion model for such a situation. We prove the existence of a stationary solution of the system showing that the two species coexist in a transition region.

But what do we expect to see when the environmental conditions themselves are "on the move"? In particular, what if due to climate change the species-specific indicators of local suitability are not fixed for a given spatial position x but are in fact a function of $x - ct$ where t denotes time and c is the speed at which isolines of environmental quality move up North?

In this short note we show that, in this context of the simple reaction–diffusion system modelling such a situation, gap formation can occur. By this we mean the following. The speed at which species 2 is forced to retreat towards the North is exactly c. An upper bound for the speed with which species 1 can occupy the region from which species 2 has withdrawn is the Fisher invasion speed c_0. We show here that whenever $c_0 < c$ an ever increasing gap will form in which species 2 is already brought down to a very low density while species 1 is yet to attain a substantial density. Thus, in particular, we will see in this case a phase separation such that, in the limit, the two species do not interact.

The underlying reason is an asymmetry in the effect of a moving climate depending on whether suitable habitat expands or retracts. In the first case, the invasion speed sets an upper bound for the ability to follow, while in the second case the speed of retreat is forced by the climate and hence is independent of dispersal. Our aim is to substantiate the claim that the speed of rising cannot exceed the intrinsic invasion speed by providing simple estimates for solutions of a system of two reaction–diffusion equations.

By formulating explicitly the theoretical possibility of gap formation we hope to trigger ecological awareness such that, perhaps, the phenomenon can be related to actual observations of shift in competitive balance. Clearly, ecological reality is far more complex than our simplified description does capture. Here we focus on the single aspect of a moving competition framework. But many other phenomena can come into play and deserve to be studied. For instance, one can imagine that, in addition to climatic conditions, competition involves food and that the food population will grow to higher than usual levels in the gap. Thus the phenomenon may take the form of a moving succession of patterns involving two speeds, c and c_0 and possibly other parameters.

In this paper we report a precise theoretical result and ask whether it can be related to field observations. The aim here is not

* Corresponding author.
E-mail addresses: hb@ehess.fr (H. Berestycki), desville@cmla.ens-cachan.fr (L. Desvillettes), o.diekmann@uu.nl (O. Diekmann).

http://dx.doi.org/10.1016/j.ecocom.2014.10.006
1476-945X/

to survey the manifold aspects of modelling the impact of climate change on population dynamics. The recent references (Leroux et al., 2013; Sorte, 2013) provide an entrance to the rapidly growing literature. The modelling approach of the present paper overlaps with the approach in the references (Berestycki et al., 2009; Lutscher et al., 2007, 2010; Potapov and Lewis, 2004; Vasilyeva and Lutscher, 2012; Zhou and Kot, 2011).

In a subsequent work we plan to study the case when $c < c_0$ for which we prove that coexistence occurs in the form of a joint travelling wave solution. Here, we already study the existence of stationary solutions for the case $c = 0$. More precisely, for $0 \le c < c_0$, we intend to establish in Berestycki et al. (in preparation) the existence, uniqueness and global stability of a traveling wave solution $u(x - ct), v(x - ct)$ of speed c for the system (1) and (2) below. This behavior is illustrated by numerical simulation in Section 5 below (compare Fig. 5). Here, we prove the case $c = 0$. Thus, this case gives rise to a different behavior from the one we derive here.

2. Cline formation

We consider the system of two equations:

$$\partial_t u(t,x) - d_1\, \partial_{xx} u(t,x) = u(t,x)\,(r_1(x - ct) - u(t,x) - v(t,x)), \qquad (1)$$

$$\partial_t v(t,x) - d_2\, \partial_{xx} v(t,x) = v(t,x)\,(r_2(x - c\,t) - u(t,x) - v(t,x)). \qquad (2)$$

Here, $t \in \mathbb{R}_+, x \in \mathbb{R}, u := u(t,x)$ and $v := v(t,x)$ are the number densities of two different species, $d_1, d_2 > 0$ are their respective diffusion rates. The per capita growth rates (when $u = v = 0$) $r_1, r_2 : \mathbb{R} \to \mathbb{R}$ satisfy the following conditions: r_1, r_2 are continuous, monotone, with values in $[-L, K]$, and have the following limits

$$r_1(-\infty) = K > 0, r_1(+\infty) = -L < 0, \qquad r_2(-\infty) = -L, r_2(+\infty) = K. \qquad (3)$$

Here K, $-L$ represent the asymptotic (when $x \to \pm\infty$) low density growth rates of the species.

We begin with a result concerning the situation when $c = 0$. We show that in that case, there exists a nontrivial steady state for system (1) and (2), in which the first species (u) is dominant when $x \to -\infty$, and the second species (v) is dominant when $x \to +\infty$. More precisely, we show the following result.

Theorem 1. *We consider the system (1) and (2), when $c = 0$, that is*

$$\partial_t u(t,x) - d_1\, \partial_{xx} u(t,x) = u(t,x)\,(r_1(x) - u(t,x) - v(t,x)), \qquad (4)$$

$$\partial_t v(t,x) - d_2\, \partial_{xx} v(t,x) = v(t,x)\,(r_2(x) - u(t,x) - v(t,x)). \qquad (5)$$

Then, there exists a stationary solution to system (4)–(5), denoted by $(U(x), V(x))$, such that $0 \le U(x), V(x) \le K$. Moreover, U is decreasing on $\mathbb{R}$, V is increasing on $\mathbb{R}$, and $\lim_{x\to-\infty} U(x) = K, \lim_{x\to-\infty} V(x) = 0, \lim_{x\to+\infty} U(x) = 0, \lim_{x\to+\infty} V(x) = K$.

This theorem is proven in Section 4.

In the forthcoming paper (cf. Berestycki et al. (in preparation)), we shall study the issues related to uniqueness and global stability for system (4)–(5), and make more precise the asymptotic behavior of U and V.

3. Gap formation

We now consider $c > 0$ a given constant. For the initial value problem we complement the system (1)– (2) with some suitable initial data

$$u(0,x) = u_0(x), \quad v(0,x) = v_0(x), \qquad \text{for all} \quad x \in \mathbb{R}. \qquad (6)$$

In the absence of species 2, and if r_1 were the constant given by $r_1(x) \equiv K$, then the classical Fisher – KPP invasion speed of u would be given by

$$c_0 := 2\sqrt{d_1 K}.$$

In the present note we focus on the case $c > c_0$, that is, when there is a fast change of climate. The aim is to provide estimates that characterize the large time behaviour. Our main result states that in a region of asymptotic size $(c - c_0)\,t$ the density of individuals of *both* species decreases exponentially. Accordingly we call this region a gap. Thus, there is a phase separation with widening gap. We now state precisely the result.

Theorem 2. *Assume $c > c_0$. Let $u_0, v_0 \in L^\infty(\mathbb{R})$ (that is, u_0 and v_0 are bounded) be initial data such that for all $x \in \mathbb{R}, u_0(x) \ge 0, v_0(x) \ge 0, u_0(x), v_0(x) \le K$ and the support of u_0 is bounded from above, that is, there exists $R \in \mathbb{R}$ such that $u_0(x) = 0$ for all $x \ge R$.*

Then the unique bounded solution of Eqs. (1)–(2) with the initial condition (6) satisfies for all $t \ge 0, x \in \mathbb{R}$: $u(t,x) \ge 0, v(t,x) \ge 0, u(t,x), v(t,x) \le K$. Furthermore, for all c_1, c_2 satisfying $c_0 < c_1 < c_2 < c$, and for all constants $b_1, b_2 \in \mathbb{R}$

$$\forall t \ge 0, \qquad \sup_{x \ge c_1 t + b_1} u(t,x) \le A_1\, e^{-\alpha_1 t}, \qquad (7)$$

$$\forall t \ge 0, \qquad \sup_{x \le c_2 t + b_2} v(t,x) \le A_2\, e^{-\alpha_2 t}, \qquad (8)$$

where the positive constants A_2, $\alpha_2 > 0$ only depend upon $K, L, r_2^{-1}(-L/2), d_2, c, c_2, b_2$ and A_1, $\alpha_1 > 0$ only depend upon K, d_1, c_1, b_1, R.

This theorem is proved in Section 4.

Remarks.– (i) Actually, the assumption $u_0(x), v_0(x) \le K$ is used only for presentation convenience, the proof below can be adapted to the more general case of merely bounded nonnegative initial data.

(ii) The condition that the support of u_0 be bounded from above by some R could also be replaced by the hypothesis of a sufficiently fast exponential decay for the right tail of u_0.

(iii) Lastly, the assumption that $-L \le r_1, r_2 \le K$ is not needed, and the same is true for the assumption that r_1, r_2 are monotone. We assume it here to somewhat simplify the argument. However, the result holds only under the requirement of the limiting conditions (3). This will be further detailed in Berestycki et al. (in preparation).

(iv) In that paper, we also intend to show that in the present case $c_0 < c$, then, c_0 and c are sharp in the following sense. First for all u_0, v_0 with $u_0 \not\equiv 0$, let γ_1 be any real such that $\gamma_1 < c_0 < c$, then,

$$\lim_{\{t\to\infty; -\gamma_1 t \le x \le \gamma_1 t\}} u(t,x) = K,$$

Likewise, for all u_0, v_0 with $\lim_{\{x\to\infty\}} v_0 > 0$, let γ_2 be any real such that $c_0 < c < \gamma_2$, then,

$$\lim_{\{t\to\infty; x \ge \gamma_2 t\}} v(t,x) = K.$$

Thus, c is the exact asymptotic speed of retreat of v and c_0 is the exact asymptotic speed of advance of u.

4. Proof of the theorems

Proof of Theorem 1: We start with a lemma in which we summarize the results of existence, uniqueness and qualitative behavior for one reaction–diffusion equation with inhomogeneous coefficients of the type:

$$-d\, \partial_{xx} w(x) = w(x)\,(R(x) - w(x)). \qquad (9)$$