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GLOBAL STABILITY IN MODELS OF POPULATION DYNAMICS WITH DIFFUSION. II. CONTINUOUSLY VARYING ENVIRONMENTS

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Dedicated to Paul Waltman on the occasion of his 60th birthday

ABSTRACT. A class of models of single-species dynamics is considered where the diffusion coefficient and reaction term continuously depend on spatial position. It is shown that, under our prescribed conditions, there is a unique, positive, globally asymptotically stable steady state.

1. Introduction. Over the past several decades there have been thousands of papers written which deal with mathematical models and/or analyses of ecological dynamics. The majority of these papers consider dynamics in a closed environment with no diffusion and constant carrying capacities [**4**]. In nature, however, spatial effects quite often need to be considered. If one thinks of growth in a forest, the various species diffuse among the forest area. Further, changing soil conditions, elevations, foliage cover, etc., create a continuously changing carrying capacity.

A technique often employed by ecological field workers in aid of their analysis is to draw a transect through the environment and analyze the ecological dynamics along the transect, thus reducing the spatial considerations to one dimension. It is the main purpose of this paper to carry out the analysis of a diffusing single species along such a transect.

Such models have been considered in [**2, 3**] where the growth law of the species is logistic without a stability analysis and in [**5, 6, 7**] where the environment is divided into a finite number of patches, each with constant diffusion and constant carrying capacities. Here we continuously vary the diffusion and the carrying capacity spatially.

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We do assume, however, that the population can be maintained at its carrying capacities at the ends of the transect.

We model the above ecological dynamics by a semilinear parabolic initial boundary value problem

(1.1)
$$u(x,t) = (D(x)u_x(x,t))_x + u(x,t)g(x,u(x,t)), \qquad 0 \le x \le 1,\ 0 < t < \infty$$
$$u(0,t) = K(0), \qquad u(1,t) = K(1), \qquad 0 \le t < \infty$$
$$u(x,0) = \eta(x), \qquad 0 \le x \le 1$$

where we normalize the spatial transect as going from 0 to 1. Here D and K are positive C^1 functions on $[0,1]$, g is also C^1 from $[0,1] \times \mathbf{R}_+$ to $\mathbf{R}$, $g(x,K(x)) = 0$ for all $x \in [0,1]$, $g(x,\cdot)$ is nonincreasing and $\eta \in C([0,1],\mathbf{R}_+)$ satisfying $\eta(0) = K(0)$, $\eta(1) = K(1)$.

A result of Sattinger [**17, 18**] (cf. also Fujita [**8**]) on monotone methods in elliptic and parabolic boundary value problems can be applied to problem (1.1). From their results it follows that if the boundary value problem

$$\begin{aligned} &(D(x)U'(x))' + U(x)g(x,U(x)) = 0, \qquad 0 \le x \le 1 \\ &U(0) = K(0), \qquad U(1) = K(1) \end{aligned} \tag{1.2}$$

has a unique nonnegative solution $U(x)$, then this solution is a globally asymptotically stable steady state solution of (1.1), that is, for any initial value $\eta(x)$, the unique solution of (1.1) converges toward $U(x)$ as $t \to \infty$.

The only nontrivial task in the application of the above mentioned result is to prove uniqueness for problem (1.2) and this is the primary purpose of the present paper. The existence of at least one solution of (1.2) easily comes from [**17**] (see also [**1**]) and the fact that there are upper and lower solutions. In the uniqueness proof the monotonicity assumption on the second variable of g is crucial. Without this monotonicity, uniqueness for (1.2) and global asymptotic stability in (1.1) are not necessarily true.

The paper is organized as follows. In Section 2 we give the definitions and some preliminary results. The uniqueness and stability of the steady state solution are proved in Section 3. Finally, Section 4 contains a brief discussion of our results and some relevant biological implications.

2. Preliminaries. In the following we always assume that the functions D, K, g and η satisfy

(2.1) $\quad D, K \in C^1([0,1];(0,\infty)), \qquad g \in C^1([0,1] \times \mathbf{R}_+; \mathbf{R})$

(2.2)

$$g(x, K(x)) = 0 \quad \text{and} \quad g(x, \cdot) \text{ is nonincreasing for all } 0 \le x \le 1$$

(2.3) $\quad \eta \in C([0,1]; \mathbf{R}_+), \qquad \eta(0) = K(0), \qquad \eta(1) = K(1).$

By a *solution of* (1.1) we mean a nonnegative classical solution, that is, $u \in C([0,1] \times \mathbf{R}_+; \mathbf{R}_+)$ such that u_t and u_{xx} exist and are continuous, and that (1.1) holds. A *solution of* (1.2) is a function $U \in C^2([0,1]; \mathbf{R}_+)$ satisfying (1.2).

A function $U_0 \in C^2([0,1]; \mathbf{R}_+)$ is said to be an *upper solution* of (1.2) if

$$(D(x)U_0')' + U_0 g(x, U_0) \le 0, \qquad U_0(0) \ge K(0),\ U_0(1) \ge K(1).$$

A *lower solution* of (1.2) is defined by reversing the above inequalities.

A solution U of the boundary value problem (1.2) is *stable* if given any $\varepsilon > 0$ there exists a $\delta > 0$ such that if $\max_{0 \le x \le 1} |\eta(x) - U(x)| < \delta$, then $\max_{0 \le x \le 1} |u(x,t) - U(x)| < \varepsilon$ for all $t \ge 0$, where u satisfies the initial value problem (1.1). U is *asymptotically stable* if, in addition, $\max_{0 \le x \le 1} |u(x,t) - U(x)| \to 0$ as $t \to \infty$. U is *globally asymptotically stable* if, in addition, $\max_{0 \le x \le 1} |u(x,t) - U(x)| \to 0$ as $t \to \infty$ for all initial values η satisfying (2.3).

The results stated in the following theorem can be obtained from [**17**].

Theorem 2.1 (Sattinger [**17**]). *Let U_0 and V_0 be upper and lower solutions of* (1.2) *with $0 \le V_0(x) \le U_0(x)$, $0 \le x \le 1$. Then the following statements are true*:

(i) *The boundary value problem* (1.2) *has at least one solution U such that $V_0(x) \le U(x) \le U_0(x)$, $0 \le x \le 1$.*

(ii) *If $V_0(x) \le \eta(x) \le U_0(x)$, $0 \le x \le 1$, then the initial value problem* (1.1) *has a unique globally defined solution u which satisfies $V_0(x) \le u(x,t) \le U_0(x)$, $0 \le x \le 1$, $0 \le t < \infty$.*

(iii) *If the boundary value problem* (1.2) *has exactly one solution U with $V_0(x) < U(x) < U_0(x)$, $0 \le x \le 1$, then U is asymptotically stable.*

From conditions (2.2) on g, it easily follows that the constant functions U_0 and V_0, satisfying $U_0 \geq \max_{0\leq x\leq 1} K(x)$ and $0 \leq V_0 \leq \min_{0\leq x\leq 1} K(x)$, are upper and lower solutions of (1.2), respectively. Therefore, Theorem 2.1 implies the following corollaries.

Corollary 2.2. *Problem* (1.2) *has at least one solution.*

Corollary 2.3. *If problem* (1.2) *has exactly one solution* $U(x) > 0$*, then* U *is globally asymptotically stable.*

By using condition (2.2) on g and the maximum principle for elliptic boundary value problems, we obtain the following lemma.

Lemma 2.4. *Any solution* U *of problem* (1.2) *satisfies*

$$\min_{0\leq x\leq 1} K(x) \leq U(x) \leq \max_{0\leq x\leq 1} K(x), \qquad 0 \leq x \leq 1.$$

3. Uniqueness and stability of the steady state solution. In this section we state and prove the main results of this paper.

Theorem 3.1. *Problem* (2.1) *has a unique solution.*

Theorem 3.2. *The unique solution of* (2.1) *is a globally asymptotically stable steady state solution of problem* (1.1).

By Corollary 2.3, only Theorem 3.1 requires a proof. Before proving Theorem 3.1, we need the following lemma.

Lemma 3.3. *Let* $(V_i(t), W_i(t))$*,* $i = 1, 2$*, be two solutions of the first order system*

$$\begin{aligned} V'(t) &= W(t)/D(t) \\ W'(t) &= -V(t)g(t, V(t)) \end{aligned} \tag{3.1}$$

on the interval $[t_0, t_1]$ *such that*

$$V_2(t) > V_1(t) > 0, \qquad t_0 \leq t \leq t_1, \tag{3.2}$$

and

$$\frac{W_1(t_0)}{V_1(t_0)} = \frac{W_2(t_0)}{V_2(t_0)}, \tag{3.3}$$

where $0 \le t_0 < t_1 \le 1$ *and* D *and* g *satisfy* (2.1) *and* (2.2). *Then*

$$\frac{W_2(t)}{V_2(t)} \ge \frac{W_1(t)}{V_1(t)}, \qquad t_0 \le t \le t_1. \tag{3.4}$$

Proof. Let $\varepsilon > 0$ and consider

$$\begin{aligned} V'(t) &= W(t)/D(t) \\ W'(t) &= -V(t)[g(t, V(t)) - \varepsilon V(t)]. \end{aligned} \tag{3.5}$$

Let $(V_{\varepsilon,i}(t), W_{\varepsilon,i}(t))$, $i = 1, 2$, be two solutions of system (3.5) with initial conditions

$$V_{\varepsilon,i}(t_0) = V_i(t_0), \qquad W_{\varepsilon,i}(t_0) = W_i(t_0), \qquad i = 1, 2.$$

Let us define

$$\beta(t) = \frac{W_2(t)}{V_2(t)} - \frac{W_1(t)}{V_1(t)}, \qquad \beta_\varepsilon(t) = \frac{W_{\varepsilon,2}(t)}{V_{\varepsilon,2}(t)} - \frac{W_{\varepsilon,1}(t)}{V_{\varepsilon,1}(t)}.$$

From the continuous dependence on parameters of solutions of (3.5), it follows that $(V_{\varepsilon,i}(t), W_{\varepsilon,i}(t))$, $i = 1, 2$, exist on $[t_0, t_1]$ for sufficiently small $\varepsilon > 0$ and $(V_{\varepsilon,i}(t), W_{\varepsilon,i}(t)) \to (V_i(t), W_i(t))$ uniformly in $t \in [t_0, t_1]$ as $\varepsilon \to 0$. Therefore, (3.2) implies that

$$V_{\varepsilon,2}(t) > V_{\varepsilon,1}(t) > 0, \qquad t_0 \le t \le t_1, \tag{3.6}$$

for small enough $\varepsilon > 0$, say $\varepsilon < \varepsilon_0$, and

$$\beta_\varepsilon(t) \to \beta(t) \quad \text{uniformly in } t \in [t_0, t_1] \text{ as } \varepsilon \to 0. \tag{3.7}$$

If $\varepsilon \in (0, \varepsilon_0)$, $t \in [t_0, t_1]$ and $\beta_\varepsilon(t) = 0$, then, by using (3.5), we have

$$\begin{aligned} \beta'_\varepsilon(t) &= [g(t, V_{\varepsilon,1}(t)) - g(t, V_{\varepsilon,2}(t))] \\ &\quad + \varepsilon[V_{\varepsilon,2}(t) - V_{\varepsilon,1}(t)] + \frac{1}{D(t)}\left[\frac{W^2_{\varepsilon,1}(t)}{V^2_{\varepsilon,1}(t)} - \frac{W^2_{\varepsilon,2}(t)}{V^2_{\varepsilon,2}(t)}\right] > 0 \end{aligned} \tag{3.8}$$

because of $\beta_\varepsilon(t)=0$, (3.6) and the nonincreasing property of $g(t,\cdot)$.

From (3.3), we have $\beta_\varepsilon(t_0)=0$, and thus $\beta_\varepsilon'(t_0)>0$. Consequently, $\beta_\varepsilon(t)>0$, $t\in(t_0,t_0+\delta)$, for some sufficiently small $\delta>0$. Then $\beta_\varepsilon(t)>0$, $t_0<t\le t_1$, follows. Indeed, if β_ε has a zero on $(t_0,t_1]$, then it has a smallest zero t_2 in $(t_0,t_1]$, where $\beta_\varepsilon'(t_2)>0$ by (3.8). This is a contradiction, since $\beta_\varepsilon(t)>0$, $t_0<t<t_2$.

Now, from (3.7), we also conclude that $\beta(t)\ge 0$, $t_0\le t\le t_1$, and the proof is complete. □

Proof of Theorem 3.1. Let U_1 and U_2 be two different solutions of (1.2). Then $U_1'(0)\ne U_2'(0)$. Assume $U_2'(0)>U_1'(0)$. Since, by Lemma 2.4, $U_i(x)\ge\min_{0\le x\le 1}K(x)$, $i=1,2$, the function $\alpha:[0,1]\to R$, defined by

$$\alpha(x)=\frac{D(x)U_2'(x)}{U_2(x)}-\frac{D(x)U_1'(x)}{U_1(x)},\qquad 0\le x\le 1,$$

is continuous. From $U_2(0)=U_1(0)$ and $U_2'(0)>U_1'(0)$ it follows that $U_2(x)>U_1(x)$, $0<x<\delta$, for some $\delta>0$. By $U_2(1)=U_1(1)$, we may define

$$\hat{x}=\min\{x\in(0,1]:U_2(x)=U_1(x)\}$$

and $0<\hat{x}\le 1$. Since $U_2(\hat{x})=U_1(\hat{x})$ and $U_1\ne U_2$, we cannot have $U_2'(\hat{x})=U_1'(\hat{x})$. If $U_2'(\hat{x})>U_1'(\hat{x})$, then U_2-U_1 is strictly increasing in a neighborhood of $\hat{x}$ contradicting the definition of $\hat{x}$. Therefore, $U_2'(\hat{x})<U_1'(\hat{x})$ and

$$\alpha(0)=D(0)\frac{U_2'(0)-U_1'(0)}{K(0)}>0,\qquad \alpha(\hat{x})=D(\hat{x})\frac{U_2'(\hat{x})-U_1'(\hat{x})}{K(\hat{x})}<0.$$

Hence

$$\tilde{x}=\max\{x\in[0,\hat{x}]:\alpha(x)=0\}$$

is well defined, $\tilde{x}\in(0,\hat{x})$ and

$$\alpha(\tilde{x})=0,\qquad \alpha(x)<0,\ \tilde{x}<x\le\hat{x}. \tag{3.10}$$

Now Lemma 3.3 can be applied with

$$(V_i(t),W_i(t))=(U_i(t),D(t)U_i'(t)),\qquad i=1,2,\ t_0=\tilde{x},\ t_1=(\hat{x}-\tilde{x})/2.$$

From (3.4) it follows that $\alpha(x) \geq 0$ for $x \in [\tilde{x}, (\hat{x} - \tilde{x})/2]$, which contradicts (3.10). Therefore, we cannot have two different solutions, and the proof is complete. $\square$

Remark 3.3. If the monotonicity condition of $g(x, \cdot)$ is dropped, then the statements of Theorems 3.1 and 3.2 may not be true. The example given in [**5**] for a discontinuous situation can be easily modified to show this.

4. Discussion. In this paper we have considered a model of a single species with continuous diffusion along a transect in an environment with continuous carrying capacity. We have shown that there exists a unique globally stable positive steady state solution in the case of environments maintained at the carrying capacity levels at the endpoints of the transect.

Such boundary conditions are valid in some circumstances, for instance, if the carrying capacity is relatively constant near the environmental boundaries but changes in the interior. (Think of a forest with a stream running through it. The carrying capacity may be relatively constant away from the stream but vary drastically near and across the stream.)

A problem of interest would be where no-flux boundary conditions hold. This would represent a situation where environmental conditions where diffusion in or out is impossible (drastic change in soil conditions or elevation for a forest). Other problems of interest would be to consider two spatial dimensions (in which case the shape of the boundary plays an essential role) and/or to consider several interacting populations such as predator-prey or competitors. We leave such considerations to the future.

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