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O. DIEKMANN

CLINES IN A DISCRETE TIME MODEL IN POPULATION GENETICS

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Clines in a discrete time model in population genetics*)

by

O. Diekmann

ABSTRACT

Motivated by a model from population genetics, we study the nonlinear integro-difference equation

$$u_{n+1}(x) = \int_{-\infty}^{\infty} g(y,u_n(y))k(x-y)dy, \qquad -\infty < x < \infty.$$

We show that certain conditions on g and k guarantee the existence, the uniqueness and the global asymptotic stability of a monotone increasing equilibrium solution (a so-called cline).

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*) This report will be submitted for publication elsewhere.

1. INTRODUCTION

The perhaps simplest deterministic model in population genetics takes the form of the difference equation

$$(1.1) \qquad u_{n+1} = g(u_n),$$

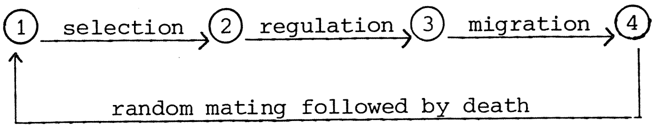
where

$$(1.2) \qquad g(u) = \frac{\alpha u^2+\beta u(1-u)}{\alpha u^2+2\beta u(1-u)+\gamma(1-u)^2},$$

for some $\alpha,\beta,\gamma \in (0,1)$. This model originated from the works of Mendel, Fisher, Wright and Haldane and it describes the influence of selection on the genetic composition of a diploid population which consists of synchronized, nonoverlapping generations and whose members are distinguished according to the genotype with respect to one diallelic locus. In fact u_n represents the fraction of alleles of one type, say a, amongst the total number of alleles in the n-th generation. The parameters α, β and γ, the so-called survival fitnesses, are by definition the fractions of the neonates of the three genotypes aa, aA and AA which reach the reproductive stage. Finally, the model assumes that mating occurs at random.

One may verify, by some elementary but amusing calculations, that $g'(u) > 0$ for $u \in [0,1]$. Consequently the dynamics of (1.1) on the invariant set $[0,1]$ can be described in all detail and one easily arrives at a classification in terms of the parameters α, β and γ (see HADELER [8] and WEINBERGER [16]).

Since the dynamics of (1.1) are so simple, we are in an ideal situation for investigating the consequences of spatial dependence, if we bring this somehow into the model. So let us now, following WEINBERGER [16] and others, assume that the population is continuously distributed in a habitat Ω, which we think of as a closed subset of $\mathbb{R}^m$, and that the life cycle is given by the following scheme:



The chance that an arbitrary individual will survive the transition from stage 1 to stage 2 depends on both genotype and position. In the next two steps the genotype is irrelevant. First the total population size is cut down to the local carrying capacity C(x) and subsequently individuals may migrate from their original position to a new one near by. In fact we suppose that we know a function $K_1 = K_1(\xi,\eta)$, the forward migration kernel, with the property that the number of those who migrate from a neighbourhood $\omega(y)$ of y to a neighbourhood $\omega(x)$ of x is given by

$$\int_{\omega(x)} \int_{\omega(y)} K_1(\xi,\eta)C(\eta)\,d\eta\,d\xi.$$

Since then the total population density at x after migration is given by

$$\int_{\Omega} K_1(x,\eta)C(\eta)\,d\eta$$

we conclude that the fraction of those in $\omega(x)$ who came from $\omega(y)$ is given by

$$\int_{\omega(x)} \int_{\omega(y)} K_2(\xi,\eta)\,d\eta\,d\xi,$$

where K_2, the so-called backward migration kernel, is given by

$$K_2(\xi,\eta) = \frac{K_1(\xi,\eta)C(\eta)}{\int_{\Omega} K_1(\xi,\zeta)C(\zeta)\,d\zeta}\ .$$

We observe that K_2 describes how frequencies, like u, transform as a consequence of migration, and that we can express K_2 explicitly in K_1 as a result of the regulation mechanism which brings about that the total population density before and after migration is independent of the generation. Finally, the life cycle is completed by the production of offspring after random mating, followed by the death of the old generation.

The analogue of equation (1.1) is given by

$$(1.3) \qquad u_{n+1}(x) = \int_{\Omega} g(y,u_n(y))K_2(x,y)\,dy,$$

where g(y,u) is the function defined in (1.2), but now with α, β and γ being functions of y. We shall restrict our attention to the special case $\Omega = \mathbb{R}$ and $K_2(x,y) = k(x-y)$. If α, β and γ are constant, then, roughly speaking, the asymptotic behaviour is locally the same as it was in the space independent situation (however, there are some interesting new phenomena like travelling waves and an asymptotic speed of propagation; see WEINBERGER [16]). Here we concentrate on the case where α, β and γ do depend on position (for instance, as a result of variations in temperature, humidity or soil composition) and we are interested in nonconstant stable equilibrium solutions of (1.3). Thus, in other words, we investigate whether both alleles can be preserved in the population as a consequence of an inhomogeneous environment.

The effect of an inhomogeneous environment has been analysed in the context of other, related, mathematical models. For diffusion equations the problem has been studied by HALDANE [9], STATKIN [15], NAGYLAKI [12], FLEMING [7], FIFE & PELETIER [6], PELETIER [14] and others. Problems in discrete time and discrete space have been analysed by, for instance, KARLIN & RICHTER-DYN [10] and NAGYLAKI [13]. A reference pertaining to the present model is DOWNHAM & SHAH [4].

2. EXISTENCE, UNIQUENESS AND GLOBAL ASYMPTOTIC STABILITY OF A CLINE

In this section we shall study the difference equation

$$(2.1)\qquad u_{n+1} = Tu_n, \qquad u_0 \text{ is given,}$$

where $u_n \in C = C(\mathbb{R}; [0,1])$ and where the operator $T: C \to C$ is given by

$$(2.2)\qquad (T\phi)(x) = \int_{-\infty}^{\infty} g(y,\phi(y))k(x-y)dy.$$

Throughout we assume that k and g satisfy:

$$H_k: k \in L_1(\mathbb{R}); \quad k \geq 0; \quad \int_{-\infty}^{\infty} k(x)dx = 1;$$

$$k(-x) = k(x); \text{ k has a compact support.}$$

$$H_g^1: g: \mathbb{R} \times [0,1] \to [0,1] \text{ is a } C^1\text{-mapping;}$$

$$g(x,0) = 0 \text{ and } g(x,1) = 1, \forall x \in \mathbb{R};$$

$$\frac{\partial g}{\partial u} > 0 \text{ on } \mathbb{R} \times [0,1].$$

Further assumptions on g will be introduced later.

From these assumptions we infer that the operator T has fixed points ϕ_0 and ϕ_1 defined by $\phi_0(x) = 0$, $\phi_1(x) = 1$, $\forall x \in \mathbb{R}$. These we call trivial fixed points. They correspond to a situation where one of the alleles is absent from the population. In principle, we want to obtain answers to the following questions. Does there exist a nontrivial fixed point of T? If so, is it stable as an equilibrium solution of the difference equation (2.1)? If so, what is its domain of attraction (i.e., how are the functions u_0 characterized for which the sequence u_n defined by (2.1) converges towards the fixed point as $n \to \infty$)? We remark that in this context monotone nontrivial fixed points are called clines.

An important consequence of the assumptions, notably of the nonnegativity of k and the monotonicity of g with respect to u, is that the operator T is monotone (or, order-preserving): if $\phi \geq \psi$ then $T\phi \geq T\psi$ (here and in the following $\phi \geq \psi$ means $\phi(x) \geq \psi(x)$, $\forall x \in \mathbb{R}$). This observation suggests that we might try to construct suitable upper and lower solutions and subsequently use monotone iteration. In order to obtain candidates for comparison functions we first pay attention to linear convolution inequalities.

LEMMA 1. *Let* $\nu > 1$. *There exists a continuous, nonnegative function* q *with compact, nonempty support, such that*

$$\nu(q * k) \geq q.$$

For a constructive proof of this lemma see WEINBERGER [16] or [2; Lemma 3]. We point out that the support of q becomes larger as ν decreases to 1. This can be concluded from the following result, which is due to ESSÉN [5; Theorem 3.1].

LEMMA 2. *Let* ψ *be a bounded continuous function which satisfies* $\psi * k \geq \psi$. *Then* ψ *is constant.*

Our second assumption on g:

H_g^2: there exist for $i = 1,2$, $x_i \in \mathbb{R}$, $v_i \in (0,1)$, $\nu_i > 1$, such that
(i) $g(x,u) \geq \nu_1 u$ for $x \geq x_1$ and $0 \leq u \leq v_1$,
(ii) $g(x,u) \leq 1 - \nu_2(1-u)$ for $x \leq x_2$ and $1 - v_2 \leq u \leq 1$.

expresses that the allele a is protected far to the right whereas the allele A is protected far to the left. Since translation, multiplication and convolution commute, it is clear that the functions $\underline{\psi}$ and $\overline{\psi}$ defined by

$$\underline{\psi}(x;\delta,\xi) = \delta q(x-\xi),$$

$$\overline{\psi}(x;\delta,\xi) = 1 - \delta q(x+\xi),$$

satisfy $T\underline{\psi} \geq \underline{\psi}$ and $T\overline{\psi} \leq \overline{\psi}$ if we choose for q a solution of the inequality $\min\{\nu_1,\nu_2\}(q * k) \geq q$ (cf. Lemma 1) and if we choose $\delta \leq (\max q)^{-1}\min\{v_1,v_2\}$ and $\xi \geq \max\{x_1 - \min(\text{support } q), \max(\text{support } q) - x_2\} + \max(\text{support } k)$. Moreover, for δ small and/or ξ large, $\underline{\psi} \leq \overline{\psi}$. Hence,

$$\phi_0 \leq \underline{\psi} \leq T\underline{\psi} \leq \ldots \leq T^n\underline{\psi} \leq \ldots \leq T^n\overline{\psi} \leq \ldots \leq T\overline{\psi} \leq \overline{\psi} \leq \phi_1. \tag{2.3}$$

Consequently both $T^n\underline{\psi}$ and $T^n\overline{\psi}$ converge, as $n \to \infty$, to a limit (in fact, as one can deduce from the Arzela-Ascoli theorem, uniformly on compact subsets). Invoking Lebesgue's monotone convergence theorem we conclude that the limit is a fixed point of T. Subsequently (2.3) shows that this fixed point is nontrivial. With the definition

$$X = \text{set of nontrivial fixed points of } T,$$

we can formulate this result as follows.

THEOREM 3. (Existence). X *is nonempty.*

Now suppose for a while that we know that $X = \{w\}$, a singleton, then both $T^n\underline{\psi}$ and $T^n\overline{\psi}$ converge to w as $n \to \infty$. But likewise the monotonicity of T implies that for any u_0 with $\underline{\psi} \le u_0 \le \overline{\psi}$ the sequence u_n defined by (2.1) converges to w as $n \to \infty$. In the next lemma we extend the applicability of this idea by showing that, except for ϕ_0 and ϕ_1, any $u_0 \in C$ yields after a finite number of iterations with T a function which can be sandwiched between $\underline{\psi}$ and $\overline{\psi}$ if δ is chosen sufficiently small.

LEMMA 4. *Let* $u_0 \in C$ *and* $u_0 \neq \phi_0, \phi_1$, *then there exist* $m = m(u_0)$ *and* $\varepsilon = \varepsilon(u_0)$ *such that* $\underline{\psi} \le u_m \le \overline{\psi}$ *provided* $\delta \le \varepsilon$.

PROOF. We shall give a proof only for the case that, for some $\eta > 0$, $[-\eta,\eta] \subset \operatorname{support} k$. Define $J_n = \{x \mid u_n(x) > 0\}$ and let $[\xi_1,\xi_2]$ be a nonempty interval contained in J_0. Then $[-n\eta + \xi_1, \xi_2 + n\eta] \subset J_n$ and consequently, for fixed ξ, support $\underline{\psi}(\cdot;\xi,\delta) \subset J_n$ for n sufficiently large, say $n \ge m$. Hence $u_m \ge \underline{\psi}$ if we take $\delta \le \varepsilon = (\max q)^{-1}\min\{u_m(x) \mid x \in \operatorname{support} \psi\}$. Essentially the same argument applied to $1 - u_n(x)$ shows the correctness of the right inequality. In the general case the proof is based on the same idea, but one has to consider properties of the support of iterated convolutions of k with itself, cf. [3; Lemma 2.1]. □

COROLLARY 5. (Uniqueness implies global asymptotic stability). *Suppose* $X = \{w\}$. *Let* $u_0 \in C$, $u_0 \neq \phi_0,\phi_1$. *Then* $\lim_{n\to\infty} u_n = w$.

Motivated by this result we shall now concentrate on finding conditions on g which guarantee that X is a singleton indeed. Our next assumption

$$H_g^3\colon \frac{\partial g}{\partial x} > 0 \text{ on } \mathbb{R} \times (0,1),$$

expresses that the environment changes in a monotone way. Under this assumption the operator T has the additional property that it leaves the set of nondecreasing functions invariant: if ϕ is nondecreasing then so is $T\phi$. Starting from the same function q as before we define nondecreasing functions $\underset{\sim}{\psi}$ and $\tilde{\psi}$ by

$$\underset{\sim}{\psi}(x;\delta,\xi) = \delta \sup\{q(x-\eta) \mid \eta \ge \xi\},$$

$$\tilde{\psi}(x;\delta,\xi) = 1 - \delta \sup\{q(x+\eta) \mid \eta \ge \xi\}.$$

Again assumption H_g^2 implies that $T\underset{\sim}{\psi} \ge \underset{\sim}{\psi}$ and $T\tilde{\psi} \le \tilde{\psi}$ if δ is small and ξ is large.

LEMMA 6. *Either* X *consists of one increasing function or* X *contains at least two such functions* w_1 *and* w_2 *with* $w_1 \ge w_2$.

PROOF. Let $w \in X$ be arbitrary. By some rather technical arguments one can show that $\lim_{x\to+\infty} \inf w(x) \geq v_1$ and $\lim_{x\to-\infty} \sup w(x) \leq 1 - v_2$, where v_1 and v_2 are defined in H_g^2 (this part of the proof is essentially the same as the proof of Theorem 5.3 in [1], so we omit it). Hence $\underset{\sim}{\psi} \leq w \leq \tilde{\psi}$ if we choose δ and ξ properly. Consequently the sequences $T^n\tilde{\psi}$ and $T^n\underset{\sim}{\psi}$ converge monotonically to monotone elements w_1 and w_2 of X and $w_1 \geq w \geq w_2$. So if $w_1 = w_2$ then $w = w_1 = w_2$ for any $w \in X$, whereas $w_1 \neq w_2$ yields precisely the other alternative of the lemma (note that H_g^3 implies that any nondecreasing element of X is in fact increasing). □

On account of Lemma 6 it is sufficient to show uniqueness among increasing fixed points of T to conclude uniqueness in general. So let w_1 and w_2 be two increasing fixed points of T such that $w_1 \geq w_2$. We define a nonnegative function h by the relation

$$w_1(x) = w_2(x + h(x)).$$

Since w_1 and w_2 are increasing, h is uniquely defined and continuous. Next, let the number $\bar{h}$ be defined by

$$\bar{h} = \sup\{h(x) \mid -\infty < x < \infty\}.$$

It is our intention to show that $\bar{h} = 0$ and the following result is a first step in that direction.

LEMMA 7. *If* $\bar{h} > 0$ *then* $h(x) < \bar{h}$ *for all* $x \in \mathbb{R}$.

PROOF. Since the result is trivially true in case $\bar{h} = \infty$, we assume $0 < \bar{h} < \infty$. Then we can write

$$\begin{aligned}
w_2(x + h(x)) &= w_1(x) \\
&= \int_{-\infty}^{\infty} g(y, w_1(y))k(x-y)\,dy \\
&= \int_{-\infty}^{\infty} g(y - \bar{h}, w_1(y-\bar{h}))k(x+\bar{h}-y)\,dy \\
&= \int_{-\infty}^{\infty} g(y - \bar{h}, w_2(y-\bar{h}+h(y-\bar{h})))k(x+\bar{h}-y)\,dy \\
&< \int_{-\infty}^{\infty} g(y, w_2(y))k(x+\bar{h}-y)\,dy \\
&= w_2(x+\bar{h}).
\end{aligned}$$

□

Our final assumption:

H_g^4: there exist $x_3 \in \mathbb{R}$ and $\mu, \rho \in (0,1)$ such that

(i) $g(x,u) > u$ for $u \in (0,1)$ and $x \geq x_3$,

$\frac{\partial g}{\partial u}(x,u) \leq \rho$ for $u \in [1-\mu,1]$ and $x \geq x_3$,

(ii) $g(x,u) < u$ for $u \in (0,1)$ and $x \leq -x_3$,

$\frac{\partial g}{\partial u}(x,u) \leq \rho$ for $u \in [0,\mu]$ and $x \leq -x_3$,

is intended to get hold on the behaviour of $h(x)$ for $x \to \pm\infty$. The assumption implies that, in the absence of migration, the alleles A and a are doomed to disappear from the population far away to the right and to the left, respectively. Also it implies that for any $w \in X$, $w(-\infty) = 0$ and $w(+\infty) = 1$ (cf. the proof of Lemma 6).

THEOREM 8. (Uniqueness). $X = \{w\}$, *a singleton.*

PROOF. Let w_1, w_2, h and $\bar{h}$ be as above and suppose $\bar{h} > 0$. Then, on account of Lemma 7, either $\bar{h} = \lim_{x\to+\infty} \sup h(x)$ or $\bar{h} = \lim_{x\to-\infty} \sup h(x)$. Let us assume that the first alternative holds. We define numbers $\tilde{x}$, $\bar{x}$, b and $\tilde{h}$ as follows:

$$\tilde{x} = \inf\{x \mid w_i(\xi) > 1 - \mu \text{ for } \xi \geq x \text{ and } i = 1,2\},$$

$$\bar{x} = \max\{x_3, \tilde{x}\},$$

$$b = \max(\text{support } k),$$

$$\tilde{h} = \max\{h(x) \mid \bar{x} - b \leq x \leq \bar{x}\},$$

and we choose a number $d \in (\tilde{h}, \bar{h})$. Hence $h(x) < d$ for $\bar{x} - b \leq x \leq \bar{x}$ and there exists $x_0 > \bar{x}$ such that $h(x_0) > d$. So if we define a function v by $v(x) = w_1(x) - w_2(x+d)$ then $v(x) \leq 0$ for $\bar{x} - b \leq x \leq \bar{x}$ and $v(x_0) > 0$. Since both w_1 and w_2 are fixed points of T we can write:

$$v(x) = \int_{-b}^{b} \{g(x-\xi, w_1(x-\xi)) - g(x+d-\xi, w_2(x+d-\xi))\}k(\xi)d\xi$$

$$\leq \int_{-b}^{b} \{g(x-\xi, w_1(x-\xi)) - g(x-\xi, w_2(x+d-\xi))\}k(\xi)d\xi.$$

Furthermore, defining sets $\Sigma(x)$ by

$$\Sigma(x) = \{\xi \mid w_1(x-\xi) \geq w_2(x+d-\xi)\}$$

and taking $x \geq \bar{x}$, we deduce

$$\begin{aligned} v(x) &\le \rho \int_{\Sigma(x)} v(x-\xi)k(\xi)d\xi \\ &\le \rho \sup\{v(\xi) \mid \xi \ge \bar{x} - b\} \\ &= \rho \sup\{v(\xi) \mid \xi \ge \bar{x}\}. \end{aligned}$$

Since $\rho < 1$ this implies $\sup\{v(\xi) \mid \xi \ge \bar{x}\} = 0$ which is, however, in contradiction with $v(x_0) > 0$. Similarly one can exclude the second alternative, $\bar{h} = \lim_{x\to-\infty} \sup h(x)$. Hence our assumption $\bar{h} > 0$ must be false and we conclude that $w_1 = w_2$. This in turn implies, by Lemma 6, the conclusion of the theorem. □

An example of a function g satisfying $H_g^1 - H_g^4$ is obtained by taking $\alpha(x) = 1 + c(x)$, $\beta(x) = 1$ and $\gamma(x) = 1 - c(x)$ in (1.2), where $c'(x) > 0$ and $-1 < c(-\infty) < 0 < c(+\infty) < 1$.

Our results show that spatial variation in survival fitness can lead to a cline with strong stability properties. The same conclusion appears from the work on diffusion equations and from that on discrete habitat models. So this work adds to the robustness of that conclusion.

Also we hope that this paper shows some of the flavour of working with convolution equations. Recently these have shown up in various mathematical models from population dynamics (see, for example, [1,11,16]) and it looks as though this will happen increasingly in the near future.

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