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POPULATION DYNAMICS IN HETEROGENEOUS ENVIRONMENTS: A DISCRETE MODEL

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We study the dynamics of a multidimensional coordinate-dependent mapping governing the time evolution of a population spread over a one-dimensional lattice. The nonlinearity is of mean-field type and the dependence on coordinates, given by the so-called fitness, allows to take into account the spatial heterogeneities of the habitat. A global picture of the dynamics is given in the case without diffusion and in the case with diffusion when the fitness is homogeneous and leads to a periodic orbit. Moreover it is shown that, periodic fitnesses close to homogeneous ones impose their periodicity on the asymptotic dynamics when the latter is time-periodic.

1. Introduction and Definitions

The time evolution of spatially extended systems may be represented by multidimensional nonlinear dynamical systems, such as PDEs, systems of coupled ODEs, Coupled Map Lattices, etc. [Cross & Hohenberg, 1993; Kaneko, 1993]. Often these models are chosen homogeneous to comply with the assumption that the dynamics should not depend on the spatial location but only on the field variable.

However for some systems, it may be more realistic to consider dynamics which also depend on the spatial location. For instance, in a model representing the time evolution of a population spread over some habitat, the spatial dependence means that changes in the local quality of the habitat are allowed. In such systems, a specific question arises: How do these heterogeneities affect the asymptotic dynamics?

There are essential results related to the effects of heterogeneities in reaction–diffusion equations representing the dynamics of populations (see e.g. [Cantrell & Cosner, 1991] and references therein). In these models, the dynamics is based on a logistic law depending on a local variable, and the interaction is of diffusive type. Precisely, at each spatial point, the nonlinear term compensating the linear growth depends only on the local population density. Adding the coupling, the evolution at each spatial point depends essentially on states in a (small) spatial neighborhood of this point.

However, assuming the information propagates sufficiently fast, the local nonlinear evolution may be influenced by all the states of the habitat rather than only by the neighboring states. The model we propose takes this effect into account. The model is also based on a logistic law and on a diffusive interaction, but the nonlinear compensation depends

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on the total population through a mean-field term, i.e. is given by the sum of local populations. The goal of the paper is to investigate the asymptotic behavior in this model.

The model represents the time evolution of a population spread over a lattice of finite length, say $L \in \mathbb{N}$. At each site $1 \leq s \leq L$ of the lattice, we have a local population density denoted by u_s with $u_s \in [0, 1]$. The total population should be bounded. Up to normalization, this bound can be set to 1. Hence the phase space is a simplex contained in the Euclidean unit cube of dimension L

$$\mathcal{M} = \left\{ u \in [0, 1]^L : \sum_{s=1}^{L} u_s \leq 1 \right\},$$

endowed with the ℓ^1-norm. A vector $u = \{u_s\}_{s=1}^L$ is called a configuration.

The evolution of the population is given by the iterations of the map T defined on $\mathcal{M}$ by

$$(Tu)_s = f_s u_s \left(1 - \sum_{r=1}^{L} u_r\right) + D(u_{s-1} - 2u_s + u_{s+1}), \quad 1 \leq s \leq L$$

with periodic boundary conditions (i.e. $x_0 = x_L$ and $x_{L+1} = x_1$) or Neumann boundary conditions (i.e. $x_0 = x_1$ and $x_{L+1} = x_L$). Each initial condition u in $\mathcal{M}$[1] generates an orbit $\{u^t\}_{t\in\mathbb{N}}$ for which the state u^t represents the population density configuration at time t.

The configuration $f = \{f_s\}_{s=1}^L \in \mathbb{R}^L$ is called the fitness. Its coordinates f_s are assumed to be non-negative. We will use in the sequel its minimum and maximum values

$$m = \min_s f_s \quad \text{and} \quad M = \max_s f_s .$$

$D \geq 0$ is the diffusion coefficient.

It would be more sensible to replace the term $1 - \sum_r u_r$ in the definition of T by $(1 - \sum_r u_r)/L$ to indicate that each local population grows linearly with a rate proportional to a local term which is the same ratio of the global population. But this correction would be the same as dividing the fitness f_s by L. The present definition has the advantage of dealing with a fitness independent of L, and thus normalized in this sense.

As argued in [Tereshko & Lee, 1999], the map T can be used to represent the foraging behavior of a honeybee colony. From this point of view, the variable u_s^t represents the local employed foragers density and then $1 - \sum_r u_r$ is the total density of unemployed foragers. Our model indicates that the recruitment rate of employed foragers at each site is assumed to depend on the total population of unemployed foragers.

For $L = 1$, the map T reduces to the logistic map $x \to f_1 x(1 - x)$ (see e.g. [Collet & Eckmann, 1981; Katok & Hasselblatt, 1995] for the corresponding dynamical properties). Hence, for $L > 1$, the map T can be viewed as a multidimensional extension of the logistic map.

In the sequel, we investigate the dynamics of T. Firstly, we give conditions for this dynamics to be meaningful and we analyze a simple fixed point (Sec. 2). Then we study the regime without diffusion (Sec. 3) and the cases of homogeneous and periodic fitnesses with diffusion when the dynamics is time-periodic (Secs. 4 and 5). In the latter cases, we show the existence of periodic orbits, with a shape imposed by the shape of the fitness, and we study their stability. Stability is always understood as asymptotic stability.

2. Basic Properties

2.1. *Conditions for the existence of meaningful dynamics*

Firstly we notice that if $u_s = \delta_{s,1}$ for all s, where $\delta_{s,n}$ is the Kroenecker's symbol, we have $u \in \mathcal{M}$ and, since $(Tu)_1 = -2D$, $Tu \notin \mathcal{M}$ if $D > 0$, which is meaningless.

To be sure that the states of any orbit are always non-negative, the phase space is restricted to a (positively) invariant set contained in $\mathcal{M}$. Thanks to the boundary conditions we have for any $u \in \mathcal{M}$

$$\sum_{s=1}^{L} (Tu)_s \leq M \sum_{s=1}^{L} u_s \left(1 - \sum_{r=1}^{L} u_r\right) \leq \frac{M}{4} .$$

Therefore we consider the dynamics in the following simplex

$$\mathcal{M}_M = \left\{ u \in \mathcal{M} : \sum_{s=1}^{L} u_s \leq \frac{M}{4} \right\} .$$

[1]In the entire paper, we discard the superscript 1 of initial conditions, i.e. $u^1 = \{u_s^1\}_{s=1}^L$ is denoted by $u = \{u_s\}_{s=1}^L$.

Sufficient conditions for this set to be invariant are given in the following statement.

Proposition 2.1. *For periodic or Neumann boundary conditions, we have*

(i) *If* $0 \le M \le 4$ *and* $0 \le D \le m(4-M)/8$, *then* $T(\mathcal{M}_M) \subset \mathcal{M}_M$.

(ii) *If* $M \le 4$ *and* $D > m(4-M)/8$, *or if* $M > 4$ *and* $D \ge 0$, *then there exists* $u \in \mathcal{M}_M$ *such that* $Tu \notin \mathcal{M}_M$.

If $M > 4$, then the condition $D \le m(4-M)/8$ implies $D < 0$, which makes no sense. Statement (ii) shows that for $M > 4$, though $D \ge 0$, some orbits have negative states, and the dynamics may be meaningless.

Henceforth, we assume the inequalities in (i) to be satisfied.

Proof.

(i) According to the inequalities at the begining of this section, one has only to check the conditions on D for $(Tu)_s$ to be positive. Since $D \ge 0$ for any $u \in \mathcal{M}_M$ we have
$$(Tu)_s \ge u_s\left(f_s\left(1-\sum_{r=1}^{L} u_r\right) - 2D\right) \ge u_s\left(m\frac{4-M}{4} - 2D\right),$$
and consequently if $D \le m(4-M)/8$, then $(Tu)_s \ge 0$ for all s.

(ii) If $M \le 4$ and $D > m(4-M)/8$, let r be such that $f_r = m$ and let $u_s = (M/4)\delta_{s,r}$ for all s. Then $(Tu)_r = (M/4)(m(4-M)/4 - 2D) < 0$. If $M > 4$ and $D \ge 0$, let $u_s = M/4L$ for all s. Then $(Tu)s = f_s(M/4L)(1-(M/4)) < 0$. ■

2.2. *The trivial fixed point*

For any value of the parameters, the configuration $u = 0$ (i.e. $u_s = 0$ for all s) is a fixed point. It means that if there is no population at some time, then no population is created at the following times. Moreover, if the environment is not sufficiently appropriate, then for any initial population, the subsequent states asymptotically vanish. Indeed, if $M < 1$, 0 is globally attracting. On the opposite, if the environment is sufficiently appropriate, then only special (initial) populations may asymptotically die. Indeed if $M > 1$, 0 is unstable. We now prove these claims.

For any configuration $u \in \mathcal{M}_M$ we have for any $t \ge 0$, $\sum_{s=1}^{L}(T^t u)_s \le M^t \sum_{s=1}^{L} u_s$ and if $M < 1$, then $\lim_{t\to\infty}\sum_{s=1}^{L}(T^t u)_s = 0$ and therefore $\lim_{t\to\infty}(T^t u)_s = 0$ for all s.

Now if $M > 1$, let r be such that $f_r = M$ and let $u_s = \varepsilon\delta_{s,r}$ for all s where $0 < \varepsilon < \min\{M/4, (M-1)/M\}$. We have $u \in \mathcal{M}_M$ and $\|Tu\|_1 = M\varepsilon(1-\varepsilon) > \varepsilon = \|u\|_1$. This shows that 0 is unstable if $M > 1$.

Although $M > 1$, (the Jacobian at) 0 may have some contracting directions. However, the stronger condition $m - 4D > 1$ ensures that all the directions are expanding.

In fact, if $L > 2$, the Jacobian J at 0, for T with periodic boundary conditions, has the following expression
$$J_{s,r} \ne 0 \quad \text{iff} \quad r = (s-1) \mod L,\ s \quad \text{or} \quad (s+1) \mod L,\ 1 \le s \le L\,,$$
and $J_{s,s} = f_s - 2D$, $J_{s,(s-1) \bmod L} = J_{s,(s+1) \bmod L} = D$. (The notation $r \mod L$ stands for $L - R$ where R is the remainder of the Euclidean division r/L, i.e. $r = kL + R$, $k \in \mathbb{Z}^+$, $0 \le R < L$.) By the Levy–Hadamard's theorem (see e.g. [Bodewig, 1959]), the eigenvalues of J are contained in the union of Gershgorin's disks $\bigcup_{s=1}^{L} D(f_s - 2D, 2D)$ where $D(x, y)$ is the disk in $\mathbb{C}$ of radius y centered at x.

Still for $L > 2$, the Jacobian at 0, for T with Neumann boundary conditions, is given by
$$J_{s,r} \ne 0 \quad \text{iff} \quad \begin{cases} 1 < s < L & \text{and} \quad r = s-1,\ s \text{ or } s+1 \\ s = 1 & \text{and} \quad r = 1 \text{ or } 2 \\ s = L & \text{and} \quad r = L-1 \text{ or } L \end{cases},$$
and $J_{s,s} = f_s - 2D$, $J_{s,s-1} = J_{s,s+1} = D$, $1 < s < L$, $J_{1,1} = f_1 - D$, $J_{L,L} = f_L - D$ and $J_{1,2} = J_{L-1,L} = D$. In this case, the union of Gershgorin's disks is $D(f_1 - D, D) \bigcup \bigcup_{s=2}^{L-1} D(f_s - 2D, 2D) \bigcup D(f_L - D, D)$.

If $L = 2$, we have for both boundary conditions
$$J = \begin{pmatrix} f_1 - D & D \\ D & f_2 - D \end{pmatrix}$$
and then the union of Gershgorin's disks is $D(f_1 - D, D) \bigcup D(f_2 - D, D)$.

Therefore, if $m - 4D > 1$, in all the cases, the union of Gershgorin's disks, and thus the eigenvalues of J, are outside $D(0, 1)$, showing that 0 is expanding.

3. The Diffusion-Free Regime

We investigate the case $D = 0$ as a starting point. In this case, one can entirely characterize the asymptotic behavior when taking into account the property $u_s = 0$ implies $u_s^t = 0$ for all $t > 0$. The conclusion is at all the sites where the fitness is not maximal (if any), there is extinction. In other words, only populations living in the most favorable sites can survive. On the remaining sites, the dynamics is governed by the logistic map.

Proposition 3.1. *For $D = 0$ and any $u \in \mathcal{M}_M$, we have*

$$f_s < M \implies \lim_{t\to\infty} u_s^t = 0\,.$$

Proof. According to the comment preceeding the statement, we can assume that for all s, $f_s > 0$ and $u_s^t > 0$ for all $t \in \mathbb{N}$. We obtain for any $t > 0$

$$u_{s'}^t = \left(\frac{f_{s'}}{f_s}\right)^t \frac{u_{s'}}{u_s} u_s^t\,.$$

Since $u_s^t \le 1$, if $f_{s'} < f_s$ then $\lim_{t\to\infty} u_{s'}^t = 0$ and the proposition follows. ■

The ratio of local populations on the remaining site(s) of maximum fitness is constant and the asymptotic dynamics is governed by the logistic map. Indeed the following statement is a consequence of Lemma 4.1 below.

Corollary 3.2. *Assume $f_s = \mu$ for all s and define the sum $U_0^t = \sum_{s=1}^L u_s^t$. We have*

$$U_0^{t+1} = \mu U_0^t (1 - U_0^t)\,, \quad t \ge 0\,.$$

If, in addition $D = 0$ and $U_0^t \neq 0$ for all t, then for any s, the ratio u_s^t / U_0^t does not depend on t.

In particular, if the logistic map $U_0 \mapsto \mu U_0(1 - U_0)$ has a (hyperbolic) periodic orbit $\{U_0^t\}_{t\in\mathbb{N}}$ different from 0, then the system without diffusion has a multiparameter family of marginally stable periodic orbits, the states u^t being given by

$$u^t = \left\{\alpha_1 U_0^t,\, \alpha_2 U_0^t, \dots,\, \alpha_{L-1} U_0^t,\, \left(1 - \sum_{s=1}^{L-1} \alpha_s\right) U_0^t\right\}\,,$$

$$t \in \mathbb{N}\,,$$

where $\alpha_s \ge 0$ and $\sum_{s=1}^{L-1} \alpha_s \le 1$. The neutral directions of perturbations correspond to changes in the α_s. The hyperbolic direction corresponds to changes in U_0^1. This direction is stable (respectively unstable) if the periodic orbit $\{U_0^t\}_{t\in\mathbb{N}}$ is stable (respectively unstable) for the logistic map.

4. The Homogeneous Case

We now consider the homogeneous case with diffusion. In this case and with periodic boundary conditions,[2] under the Fourier transform, the system becomes a skew-product with linear factors, the base being the logistic map. As a consequence, if the fitness $f_s = \mu$ is such that $x \to \mu x(1 - x)$ has a stable periodic orbit and if $0 < D < \mu(4 - \mu)/8$, then for (Lebesgue-almost) any initial condition, the asymptotic population is homogeneous and periodic.

To see this recall that the Fourier transform in $\mathbb{R}^L$ is the mapping $\mathcal{F}$ such that $\mathcal{F}u = U$ for any $u \in \mathbb{R}^L$ and $(\mathcal{F}u)_k = \sum_{s=1}^L u_s e^{(2i\pi ks/L)}$, $0 \le k < L$. Applying this mapping to T, we obtain the following statement.

Lemma 4.1. *The following conjugacy holds $\mathcal{F} \circ T = G \circ \mathcal{F}$, where $G : \mathcal{F}(\mathbb{R}^L) \to \mathcal{F}(\mathbb{R}^L)$ is defined by*

$$(GU)_k = \frac{1 - U_0}{L} \sum_{j=0}^{L-1} F_j U_{k-j \mod L} + \lambda_k D U_k\,,$$

$$0 \le k < L\,,$$

with $\lambda_k = -4\sin^2(\pi k/L)$ and $F = \mathcal{F}f$.

Using this conjugacy for a mapping T with homogeneous fitness $F_j = F_0 \delta_{j,0}$, one obtains a global picture in the time-periodic case. We assume the following conditions to hold.

(H) The fitness is homogeneous, $f_s = \mu$ for all s, and is such that the map $x \to \mu x(1 - x)$ has

[2]From now on, we impose periodic boundary conditions.

an orbit $\{x^t\}_{t\in\mathbb{N}}$ with $x^{t+\tau} = x^t$ for some $\tau \in \mathbb{N}$ and any $t \in \mathbb{N}$. The diffusion coefficient satisfies the inequalities $0 < D < \mu(4-\mu)/8$.

These conditions allow to give a global picture through the following technical result.

Proposition 4.2. *If the conditions* (H) *hold, then for any* $u \in \mathcal{M}_\mu$ *such that* $U_0 = x^{t_0}$ *for some* $t_0 \in \mathbb{N}$, *we have* $U_0^t = x^{t+t_0}$ *for all* $t \in \mathbb{N}$ *and*

$$\lim_{t\to\infty} \max_{0<k<L} |U_k^t| = 0\,.$$

Proof. If the fitness is homogeneous, then $(GU)_0 = \mu U_0(1-U_0)$. In this case, let $\{U^t\}$ be an orbit of G such that $U_0^t = x^{t+t_0}$. By reindexing the sequence $\{x^t\}$, we can always assume $t_0 = 1$. If $U_0^t = 0$ for some t, then $U_k^t = 0$ for all $1 \le k < L$ since $u \in \mathcal{M}$ and then $U_k^{t+1} = 0$ for all k and the result holds. If U_0^t never vanishes we have for any $1 \le t \le \tau$ and any $0 \le k < L$

$$|U_k^{t+\tau}| = \prod_{j=0}^{\tau-1} \left|\frac{x^{t+j+1}}{x^{t+j}} + \lambda_k D\right| |U_k^t|\,.$$

If $k > 0$ then $-4 \le \lambda_k < 0$. Thus if $D(\tau) = 1/2 \min_{1\le t\le\tau} x^{t+1}/x^t > 0$ and $0 < D < D(\tau)$, then for any k and any $1 \le t \le \tau$ we have

$$\left|1 + \lambda_k D \frac{x^t}{x^{t+1}}\right| < 1\,,$$

and the periodicity of $\{x^t\}$ implies that

$$|U_k^{t+\tau}| = \prod_{j=0}^{\tau-1} \left|1 + \lambda_k D \frac{x^t}{x^{t+1}}\right| |U_k^t|\,.$$

Iterating we conclude that $\lim_{t\to\infty} |U_k^t| = 0$. Using the inequality $U_0^t \le \mu/4$ valid for $t \in \mathbb{N}$ we obtain $D(\tau) \ge \mu(4-\mu)/8$ and the proposition follows. ■

If μ is such that $\max_{1\le t\le\tau} x^t < \mu/4$ then one may allow $D = \mu(4-\mu)/8$ in the statement, and thus cover entirely the allowed region for D.

Recall that if the logistic map has a periodic orbit, then it has a periodic orbit of smaller period in the Sharkovsky ordering [Katok & Hasselblatt, 1995]. Moreover, for a given μ, at most one periodic orbit is stable and its basin of attraction is of full Lebesgue measure [Collet & Eckmann, 1981]. It is then easy to conclude about the asymptotic dynamics of T with homogeneous fitness if $x \to \mu x(1-x)$ has a periodic orbit.

Corollary 4.3. *If the conditions* (H) *are satisfied, then the following assertions hold.*

(i) *An orbit of* T *is periodic iff it is homogeneous and its states are equal to the states of a periodic orbit of the logistic map.* (*In particular, both periods are equal.*)

(ii) *If the latter is stable, then the corresponding homogeneous periodic orbit of* T *is globally stable in the following sense. There exists a subset* $\mathcal{S}$ *of* $[0, 1]$ *with full Lebesgue measure such that any orbit with initial condition in* $\mathcal{M}_\mu$ *and the sum of coordinates in* $\mathcal{S}$, *asymptotically converges to the homogeneous periodic orbit.*

(iii) *If the periodic orbit of the logistic map is unstable and is not 0, then the corresponding homogeneous periodic orbit of* T *is hyperbolic with a codimension 1 stable manifold. Let* $\{E_k\}$, $(E_k)_j = \delta_{k,j}$, $0 \le j < L$ *be the canonical basis in* $\mathcal{F}(\mathbb{R}^L)$. *The tangent subspace spanned by* E_0 (*resp. by* $\{E_k\}_{k>0}$) *is an unstable* (*resp. stable*) *subspace for* G.[3]

It is simple to deduce from the definition of T that the system has a homogeneous periodic orbit when the logistic map has a periodic orbit. The present result shows that, if the fitness is homogeneous $f_s = \mu$ and $0 < D < \mu(4-\mu)/8$, then no nonhomogeneous orbit can be periodic and all the (homogeneous) periodic orbits are periodic orbits of the logistic map.

As an example, a schematic phase portrait in the case of periodic orbits of period 2 is represented in Fig. 1. This picture shows the stable and unstable homogeneous periodic orbits and the corresponding invariant directions. As given by Proposition 4.2, the unstable manifolds corresponding to perturbations of the Fourier modes U_k, $k > 0$, are hyperplanes orthogonal to the direction U_0. In the picture, they are represented by straight lines.

Notice that the damping of the modes $\{U_k\}_{k=1}^{L-1}$ holds, not only for initial conditions in $\mathcal{F}(\mathcal{M}_\mu)$ but also for any initial condition with $\{U_k\}_{k=1}^{L-1} \in \mathbb{C}^{L-1}$.

[3]If $D = 0$, the subspace spanned by $\{E_k\}_{k>0}$ is precisely the marginal one (see Sec. 3).

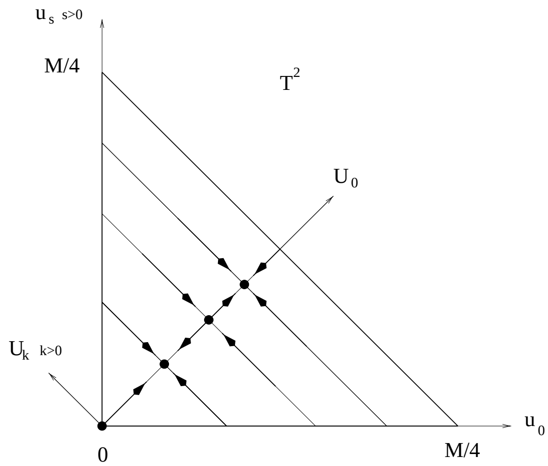

Fig. 1. The phase portrait of T^2 in the homogeneous case with periodic boundary conditions and diffusion. The corresponding logistic map as a periodic orbit of period 2.

5. Periodic Fitnesses

An extension of the previous section is to consider (space) periodic fitnesses. In this case, one also obtains a skew-product system with linear factors, acting on higher dimensional variables, and the results are similar to those obtained with homogeneous fitnesses. The problem is that we do not know in advance if the system has space-time periodic orbits (in $\mathcal{M}_M$) as we knew the existence of homogeneous periodic ones.

To begin, we suppose the existence of $p \in \mathbb{N}$, $1 < p < L$ such that $p|L$ and we consider a p-periodic fitness, i.e. $f_{s+p} = f_s$ for all s. (We assume p is the minimal period.) Equivalently we assume that if $k \neq j(L/p)$ for all $0 \leq j < p$ then $F_k = 0$.

Now for $0 \leq n < L/p$ we define $W_{\underline{n}} = (U_{n+jL/p})_{j=0}^{p-1}$ and we endow the corresponding space of vectors $W = \{W_j\}_{j=0}^{p-1} \in \mathbb{C}^p$ with the ℓ^1-norm. The map G induces the following dynamics $W_{\underline{0}}^{t+1} = \mathcal{A}_F(W_{\underline{0}}^t)$ and for $n > 0$ $W_{\underline{n}}^{t+1} = A_{F,n,U_0^t}(W_{\underline{n}}^t)$ where the maps write

$$(\mathcal{A}_F(W))_j = \frac{1 - W_0}{L} \sum_{k=0}^{p-1} F_{k\frac{L}{p}} W_{j-k \mod p} + \lambda_{j\frac{L}{p}} D W_j, \quad 0 \leq j < p,$$

and

$$(A_{F,n,U_0}(W))_j = \frac{1 - U_0}{L} \sum_{k=0}^{p-1} F_{k\frac{L}{p}} W_{j-k \mod p} + \lambda_{n+j\frac{L}{p}} D W_j, \quad 0 \leq j < p,$$

The space-time periodic orbits are obtained using a continuation argument, and are shown to have spatial period not larger than p, and to have the same stability properties as the original homogeneous periodic orbits.

Proposition 5.1. *If the conditions (H) are satisfied, then the following statements hold.*

(i) *There exists $\varepsilon_0 > 0$ such that for any $0 \leq \varepsilon < \varepsilon_0$ and any f such that $f_{s+p} = f_s$ for all s and $\sum_{s=1}^{L} |f_s - \mu| < \varepsilon$, the corresponding map $\mathcal{A}_F$ has a τ-periodic orbit, denoted by $\{W_{\underline{0}}^t(\varepsilon)\}_{t\in\mathbb{N}}$.*
(ii) *There exists $\varepsilon_1 \leq \varepsilon_0$ such that for any $0 \leq \varepsilon < \varepsilon_1$ this periodic orbit is locally stable (resp. hyperbolic) if the corresponding logistic orbit is stable (resp. unstable).*
(iii) *There exists $0 < \varepsilon_2 \leq \varepsilon_0$ such that for any $0 \leq \varepsilon < \varepsilon_2$ and any $u \in \mathcal{M}_M$ such that $W_{\underline{0}} = W_{\underline{0}}^{t_0}(\varepsilon)$ for some $t_0 \in \mathbb{N}$*

$$\lim_{t\to\infty} \max_{0<n<\frac{L}{p}} \|W_{\underline{n}}^t\| = 0\,.$$

Proof.

(i) Let $\tilde{\mathcal{A}}_F = \mathcal{A}_F^\tau - \mathrm{Id}$ where Id is the identity map in $\mathbb{C}^p$. The map $\tilde{\mathcal{A}}_F$ is a C^1 map and $\tilde{\mathcal{A}}_{\hat{F}}(\hat{W}_{\underline{0}}^0) = 0$ where $\hat{F}_k = L\mu\delta_{k,0}$ and $(\hat{W}_{\underline{0}}^0)_k = x^0\delta_{k,0}$. By Corollary 4.3 for $0 < D < \mu(4-\mu)/8$ the homogeneous orbit $\hat{U}_k^t = x^t\delta_{k,0}$ is either globally stable, and in particular linearly stable, or hyperbolic for G^τ with $F = \hat{F}$. In both cases $\mathrm{spec}(D\tilde{\mathcal{A}}_{\hat{F}}(\hat{W}_{\underline{0}}^0)) \not\ni 0$ and then $D\tilde{\mathcal{A}}_{\hat{F}}(\hat{W}_{\underline{0}}^0)$ is invertible. By the implicit function theorem there exists $\varepsilon_0 > 0$ such that for $0 < \varepsilon < \varepsilon_0$ and $\|F - \hat{F}\| < \varepsilon$, the equation $\tilde{\mathcal{A}}_F(W_{\underline{0}}) = 0$ has a solution $W_{\underline{0}}^0(\varepsilon)$, the unique continuation of $\hat{W}_{\underline{0}}^0$.
(ii) The spectrum of the differential $D\mathcal{A}_F^\tau(W_{\underline{0}}^t(\varepsilon))$ is a continuous function of ε. Therefore the hyperbolic properties of $W_{\underline{0}}^t(\varepsilon)$ are preserved under if ε is sufficiently small.

In the case where the orbit of the logistic map is stable, the periodic orbit of $\mathcal{A}_F$ is linearly stable for $\varepsilon = 0$. It is then linearly stable, and thus locally stable, provided ε is small enough, say $\varepsilon < \varepsilon_1$.

In the case where the orbit of the logistic map is unstable, the periodic of $\mathcal{A}_F$ is unstable for $\varepsilon = 0$. It is then unstable provided ε is small enough, say also $\varepsilon < \varepsilon_1$.

(iii) From the proof of Proposition 4.2 we have for any $1 \le t \le \tau$

$$\left\| \prod_{j=0}^{\tau-1} A_{\hat{F}, n, \hat{U}_0^{t+j}} \right\| \le \delta \,,$$

where $\delta = \max_{1\le t\le\tau} \max_{0<n<L/p} \max_{0\le j<p} |1 + \lambda_k D x^t / x^{t+1}| < 1$. On the other hand, from (i) we have for any t and n

$$\lim_{\varepsilon\to 0} \left\| \prod_{j=0}^{\tau-1} A_{F, n, U_0^{t+j}(\varepsilon)} \right\| = \left\| \prod_{j=0}^{\tau-1} A_{\hat{F}, n, \hat{U}_0^{t+j}} \right\| .$$

Hence there exists $\varepsilon_2 > 0$ such that if $0 \le \varepsilon < \varepsilon_2$ then

$$\max_{1\le t\le\tau} \max_{0<n<\frac{L}{p}} \left\| \prod_{j=0}^{\tau-1} A_{F, n, U_0^{t+j}(\varepsilon)} \right\| < 1 \,.$$

By induction, the limit in (iii) then holds for $0 \le \varepsilon < \varepsilon_2$. ■

As in Corollary 4.3, the combination of (ii) and (iii) shows that if $\{W_{\underline{0}}^t(\varepsilon)\}$ is stable, any initial condition with $W_{\underline{0}}$ in the basin of attraction of $W_{\underline{0}}^{t_0}(\varepsilon)$ for some t_0, asymptotically converges to the orbit with $W_{\underline{0}}^t = W_{\underline{0}}^{t+t_0}(\varepsilon)$ and $W_{\underline{n}}^t = 0$ for $0 < n < L/p$.

If one assumes $m < \mu < M$ for the pertubed periodic fitness, then $m(4-M)/8 < \mu(4-\mu)/8$ so that the condition $D < \mu(4-\mu)/8$ is satisfied once $D < m(4-M)/8$. Moreover, if μ is such that $\max_{1\le t\le\tau} x^t < \mu/4$, then the continued orbit belongs to $\mathcal{M}_M$ provided ε is sufficiently small.

The map $\mathcal{A}_F$ can be viewed as a linear map with a time-dependent parameter if one writes $(1-U_0)/L$ instead of $(1-W_0)/L$, i.e. $\mathcal{A}_F(W) = W A_{F,U_0}$ where A_{F,U_0} is a $p \times p$ matrix. Under this point of view, a periodic orbit of $\mathcal{A}_F$ is an eigenvector of $\prod_{j=0}^{\tau-1} A_{F,U_0^j}$. If $F \ne \hat{F}$ and $U_0 \ne U_0'$, then the maps A_{F,U_0} and $A_{F,U_0'}$ and hence the maps A_{F,n,U_0} and $A_{F,n,U_0'}$ do not commute. Consequently the periodic orbit cannot be composed of a common eigenvector of the A_{F,U_0^j} as it was the case for $F = \hat{F}$. This shows that the orbit's shape changes in time, since the Fourier modes change in a nonproportional way from a time step to the following one. Also it is not sufficient to have contraction at each step, i.e. $\|A_{F,n,U_0^j}\| < \|A_{F,U_0^j}\|$ to ensure the damping of the modes $W_{\underline{n}}$ for $n > 0$ because $\prod_{j=0}^{\tau-1} \|A_{F,U_0^j}\| > 1$. This explains the argument developed in the proof of (iii). In other words one has to control the expansion rate over the period, and not only at each step, to ensure damping.

6. Concluding Remarks

A space-time discrete model for the dynamics of populations on heterogenous lansdcape has been introduced. Optimal conditions on the parameters for the dynamics to be meaningful have been given. The dynamics has then been investigated on the corresponding invariant set.

The first result has shown that if the habitat is not sufficiently appropriate, then the populations asymptotically vanish.

When the fitness is sufficiently large, in the diffusion-free regime, the model selects the most favorable sites. This is a characteristic effect of the mean-field coupling. Indeed, in models such as in [Cantrell & Cosner, 1991] or in coupled map lattices [Kaneko, 1993], where the term $1 - \sum_r u_r$ in the definition of the dynamics is replaced by a local term $1 - u_r$, the limit $D = 0$ is an uncoupled system (i.e. the dynamics at each site is independent of the other sites), and the previous selection of best sites does not occur.

When diffusion is added and the fitness is chosen homogeneous and such that the system has a periodic orbit, the dynamics asymptotically becomes homogeneous, the choice of the (phase of the) orbit depending only on the sum $\sum_s u_s$ of the components of the initial conditions.

If the fitness is chosen homogeneous and such that the logistic map has a dense orbit $\{x^t\}_{t\in\mathbb{N}}$ in some set,[4] then there exists a sequence $\{t_j\}_{j\in\mathbb{N}}$ with $t_j \in \mathbb{N}$, such that $x^{t_{j+1}} < x^{t_j}$. Using arguments similar to those in the proof of Proposition 4.2, we conclude that if the initial condition is chosen such that $U_0^1 = x^1$, then the sequence $\{\sum_{k=1}^{L-1} |U_k^{t_j}|\}$ converges to 0. In other words, the t_j-states of such orbits are more and more homogeneous when j increases. However, the orbit may not converge to a homogeneous one because the sequence $\{t_{j+1} - t_j\}$ may not be bounded. In this case, the system then may be

[4] for instance, on the Feigenbaum's accumulation point of bifurcation values of periodic orbits.

intermittent, as described in [Platt *et al.*, 1993]. If that be the case, homogeneity of the fitness would not be sufficient to force asymptotic homogeneity in aperiodic situations.

Back to periodic cases, for space periodic fitnesses close to homogeneous ones, the results are similar to those obtained with periodic fitnesses: the asymptotic orbit always has the spatial periodicity of the fitness. Moreover, though the fitness is close to homogeneous, its heterogeneity provokes important changes on the orbits' shape within a period, in the sense that various Fourier modes can be excited independently at different times.

Finally, we notice that the results extend to multidimensional lattices without any supplementary difficulty other than notations. However, they do not extend easily to infinite lattices. Indeed, if the phase space is chosen to be

$$\mathcal{M}_M = \left\{ u \in \ell^1(\mathbb{Z}) : u_s \geq 0 \quad \text{and} \quad \sum_{s\in\mathbb{Z}} u_s \leq \frac{M}{4} \right\},$$

and the fitness is a bounded configuration, i.e. $f \in \ell^\infty(\mathbb{Z})$, then the condition for the existence of a dynamics, the analysis of the trivial fixed point (apart the condition ensuring expansivity which requires additional work) and the results in the diffusion-free regime, adapted to the infinite-dimensional case, extend. The problem comes from the Fourier transform of T which does not decompose in the convolution of Fourier transforms as in the finite-dimensional case. This is because $u \in \ell^1$ and $f \in \ell^\infty$ do not belong to the same spaces. Therefore, our analysis for homogeneous and periodic fitnesses does not apply and one has to carry out a direct analysis to conclude in this case.

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