THE SIMPLEST MODEL OF SPATIALLY DISTRIBUTED POPULATION WITH REASONABLE MIGRATION OF ORGANISMS

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The simplest model of a smart spatial redistribution of individuals is proposed. A single-species population is considered, to be composed of two discrete subpopulations inhabiting two stations; migration is a transfer between them. The migration is not random and yields the maximization of net reproduction, with respect to the transaction costs. The organisms are supposed to be globally informed. Discrete time model is studied, since it shows all the features of a smart migrations, while the continuous time case brings no new knowledge but the technical problems. Some properties of the model are studied and discussed.

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I. INTRODUCTION

Modelling of the dynamics of biological takes start from the works by V. Volterra [49, 50] (see also [29]). The approach follows, in brief, a chemical kinetics, where reproduction, death and other types of interaction of organisms are described with law of mass action. A spatially distributed population is modelled with the “reaction – diffusion” system, where diffusion is supposed to describe the redistribution of organisms over a space. Good coincidence of the solutions of such “reaction – diffusion” systems to observed dynamics of populations and communities just masks the serious problem.

The point is that the diversity and abundance of possible (structurally stable) regimes of such dynamic systems exceed drastically any really available family of trajectories of real systems. Thus, one always is able to match a differential equation (or a system of differential equation, either ordinary, or partial differential equations) to the dynamic behavior of any really observed system. Doubtlessly, living organisms, even microorganisms, differ drastically in their “microscopic” behavior from the chemical substances and relevant chemical reactions.

Vito Volterra, the founder of the mathematical biology of populations understood pretty well this discrepancy. Later, the comprehension of limitations of this chemical methodology fell off. The situation is going worse when one tends to model a dynamics of spatially distributed populations and communities. Basically, “reaction – diffusion” systems make the basis for modelling of such spatially distributed entities [1, 2, 8, 41, 10, 24, 33, 13, 42, 46, 17]. Famous soviet mathematician Andrew Kolmogorov studied in detail such type of equations [22].

A methodology of modelling of spatially distributed populations based of the reaction – diffusion system has the great discrepancy. It constrains significantly the individual (behavioral) properties of organisms under consideration: one must suppose that the organisms move over a space randomly and aimlessly [26]. Obviously, such assumption does not hold true (see, e.g. [4, 31, 43]), even for microorganisms [17, 23, 37, 14]. The assumption towards the idle transfers of organisms in space is obviously less favorable for the higher organised species.

Modelling methodology based on evolution principles is the way to pass over the discrepancy mentioned above. This approach takes the origin from the evolution studies of J.B.S. Haldane [21]. This is the most general principle prescribing the way biological systems evolve. In brief, it force to evolve a system toward the maximization of net reproduction. This latter is an average number of per capita descendants survived at the course of a series of reproductions over an arbitrary long generation line [12, 13, 14, 39]. Later, they found this principle to be even more general, than just a biological one. Indeed, the principle holds true for any system where the inheritance takes place [3, 15, 30, 34, 51, 52].

A consistent and rational implementation of this principle faces the problem of a lack of knowledge of how the specific biological issues impact the survival of a species. In turn, the question arises, what is an entity to be evolving? An ordinary answer on this question is that the species is an evolving entity. Actually, the situation looks more complicated; not discussing this problem in detail, further we shall follow this idea. The principle formulated above yields the following rule for the model implemented below: evolution optimality in spatial distribution of organisms is equivalent to the maximization of (an average) net reproduction over space, with respect to the evolution trade off for such redistribution. Some further details on this issue could be found in [13, 14, 17, 16].

II. BASIC MODEL OF THE SMART MIGRATION

Consider a population inhabiting two stations; hence, the population consists of two subpopulations. Any movements of individuals within a station must be ne-
glected; thus, only the transfer from station to station is considered as a migration act. No spatial effects in the population dynamics are presumed, for each subpopulation, as soon as no migration occurs. We shall consider a discrete time model; continuous modelling is possible, as well, but it brings no new issues but the serious technical difficulties.

Further, the dynamics of each subpopulation is supposed to follow the Verhulst’s equation \( \frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) \), with the abundances appeared due to migration, at each station, independently.

The first step consists in the determination of the fact of migration, i.e. in the comparison of reproduction coefficients “there” and “here”:
- if \( p \cdot k_l(M) > k_r(N) \), then the migration runs from \( N \)-station to \( M \)-station;
- if \( k_l(M) < p \cdot k_r(N) \), then the migration runs from \( M \)-station to \( N \)-station;
- otherwise no migration takes place.

The second step consists in the determination of the migration flux. Migration yields the change of life conditions measured in the units of reproduction coefficient \( p \cdot k_l(M + p \cdot \Delta) = k_r(N + p \cdot \Delta) \) for the case of migration from \( M \)-station to \( N \)-station, and vice versa:
\[ p \cdot k_l(M + p \cdot \Delta) = k_r(N - \Delta) \]
Here the term \( p \cdot \Delta \) represents the fact of mortality of individuals at the course of migration; this is the way to account the transfer cost, for this model. The migration flux, then, is determined according to
\[ \Delta_{MN} = \frac{pc - a + bN - pdM}{b + p^2d} \]
for the migration from \( N \)-station to \( M \)-station, and
\[ \Delta_{NM} = \frac{pa - c + dM - pbN}{d + p^2b} \]
for the inverse migration.

Finally, the third step consists in the reproduction of organisms in both subpopulations independently, with respect to the abundance (\( \tilde{N}_t \), or \( \tilde{M}_t \), respectively) resulted from the migration:
\[ N_{t+1} = a \cdot \tilde{N}_t - b \cdot \tilde{N}_t^2 \]
and
\[ M_{t+1} = c \cdot \tilde{M}_t - d \cdot \tilde{M}_t^2. \]
It should be stressed, that a reproduction in a station (i.e., at the subpopulations) runs independently, with respect to the abundances occurred due to the migration. If no migration takes place for some time moment \( t \), then \( \bar{N}_t = N_t \) (\( \bar{M}_t = M_t \), respectively).

### III. SOME PROPERTIES OF THE MODEL

The model \( \{4\} \) of the smart migration exhibits various dynamic properties, not observed at the similar population dynamics models with no migration. The dynamics of two (independent) subpopulations runs inside the rectangular \([0, a/b] \times [0, c/d] \), if no migration occurs. As soon as \( p > 0 \), the dynamics runs at the dovetail shown in Fig.4. If a trajectory (i.e. a point representing a couple of abundances \((N_t, M_t)\)) reaches the area 1, then no migration occurs at that time moment \( t \), and no migration will take place, while the trajectory remains at this area. The area is cut off with two solid bold lines. These are determined by the equations

\[
\Delta_{MN} = 0 \quad \text{and} \quad \Delta_{NM} = 0 .
\]

Areas 2 and 3 are the space dynamically available by each subpopulation, independently, when no migration takes place.

On the contrary, the migration expands the dynamically reachable area. Such expansion results from the smart migration: individuals emigrate from the overpopulated station improving the survival of the entire population. Areas 2 and 5 in Fig.4 show this expansion. For any point \((N_t, M_t) \in \Omega \), where \( \Omega \) is a union of these two areas, the migration gives the projection of this point on the bold solid line bordering the area 1, parallel to the solid dashed line shown in this Figure. Thin arrow in this Figure illustrates such projection. Similarly, if a point \((N_t, M_t) \in \Phi \) belongs to the union \( \Phi \) of areas 3 and 4, then the migration maps it to the (lower) solid bold line bordering area 1. Similarly, it is executed in parallel to the thin arrow, shown in the figure.

The tangent of the dashed line bordering the area 5 is equal \(-p^{-1}\); similarly, for the area 4 the tangent is equal to \(-p\). The area 1 expands, as \( p \rightarrow 0 \) occupying the entire rectangular \([0, a/b] \times [0, c/d] \), for \( p = 0 \). The areas 4 and 5 become a (semi-infinite) strip each, of the permanent width. This fact differs the situation of the complete absence of a migration from the infinitely big migration cost \( \mu \). This area collapses into the line (into the intercept, to be exact) defined the the equation

\[
bN - dM + a - c = 0 ,
\]
as \( p \rightarrow 1 \).

Next, the migration expands the allowed parameter values. The parameters \( a \) and \( c \) must meet the constraint

\[
1 \leq a \leq 4 \quad \text{and} \quad 1 \leq c \leq 4 ,
\]
in migration free models \( \{3, 11, 25, 26, 32, 40, 41\} \). The equation \( \{1\} \) (or \( \{11\} \), respectively) exhibits elimination of a population, as \( a \) (\( c \), respectively) exceeds 4: maximum of \( aN_t - bN_t^2 \) may be greater than \( a/b \). The non-zero migration expands the range of the parameter, provided that the overpopulation in one station will be compensated by the emigration into another.

Equation \( \{10\} \) (or \( \{15\} \), respectively) shows various dynamic patterns, for various parameters \( a \) (or parameter \( c \), respectively) value. The diversity of limit regimes of \( \{11\} \) varies from a stable fixed point to a strange attractor as a limit manifold. Similar diversity of regimes could be found at the equation system \( \{10\} \), when the migration occurs. In addition, the system \( \{11\} \) exhibits some other regimes, that are not possible with no migration.

Migration provides a redistribution of individuals over a space. The redistribution is not random; it results in maximization of the average (over two stations) reproduction coefficient \( k_r(N) + k_l(M) \). The reproduction coefficient reaches the maximum in one step; this point results both from the global information accessibility of the data concerning the environmental conditions (coefficients \( a, b, c \) and \( d \)), population density (these are \( N_t \) and \( M_t \) in both stations, at every time moment \( t \)), and the transfer cost \( \mu \) (or the probability of the successful transfer \( p \)). If \( 0 < p < 1 \), the migration results a decrease of a general abundance, since a part of individuals (namely, \( p \cdot \Delta \)) is eliminated, at each time step \( t \). Migration yields no elimination of individuals, as \( p = 1 \).

Various limit regimes occurred due to smart migration effect may be observed. There exists the stable permanent one-side directed flux of individuals. For example, if \( c \) is big enough, and simultaneously \( b \) is sufficiently small (thus increasing the environmental capacity of \( N \)-station), one may observe the permanent one-way migration flux limit regime. Indeed, such regime is determined by the equation

\[
\begin{align*}
N^* &= a \cdot (N^* + p\Delta^*) - b \cdot (N^* + p\Delta^*)^2 \\
M^* &= c \cdot (M^* - \Delta^*) - d \cdot (M^* - \Delta^*)^2 ,
\end{align*}
\]

with \( \Delta^* \) determined by \( \{3\} \):

\[
\Delta^* = \frac{pa - c + dM^* - pbN^*}{d + p^2b} .
\]

To figure out the impact of the smart migration on the population dynamics, let’s consider a particular case of \( b = d = 1 \), and \( p = 1 \). Such choice of the parameters means that the subpopulations differ in their growth rate, only, and no losses of an abundance are resulted from a migration. The equality \( p = 1 \) also means a supreme mobility of an individual. Here \( \Delta \) becomes equal to

\[
\Delta = a - c + M - N ,
\]

and the system \( \{11\} \) changes for

\[
\begin{align*}
N &= a \cdot (M + \lambda) - (M + \lambda)^2 \\
M &= c \cdot (N - \lambda) - (N - \lambda)^2 ,
\end{align*}
\]
with $\lambda = a - c$. Here the asterisks are omitted, since it makes no confusion. This is the system of two polynomials of two variables ($M, N$) of (formally) power 2 each. To solve a system of two polynomials of two variables, one must develop the resultant of the system. This former is the determinant of the following matrix:

$$
\begin{bmatrix}
0 & 1 & -[a(M + \lambda) - (M + \lambda)^2] & 0 \\
0 & 0 & 1 & -[a(M + \lambda) - (M + \lambda)^2] \\
1 & -(2\lambda + c) & \lambda^2 + c\lambda + M & -[a(M + \lambda) - (M + \lambda)^2] \\
0 & 1 & -(2\lambda + c) & \lambda^2 + c\lambda + M
\end{bmatrix}
$$

(7)

for the case (6). Some roots of (7) are the solution of (5). It should be stressed, that the first term at the first line of the matrix (7) becomes non-zero, for the case $b \neq d$.

Suppose, $(N^*, M^*)$ is the solution of (6), and $N^* > 0$, $M^* > 0$. Here the question arises, whether this solution is stable. The answer on this question could be obtained due to linear approximation analysis. Let $N_t = N + \nu_t$ and $M_t = M + \mu_t$, where $\nu_t, \mu_t$ are the small corrections; substituting such $(N_t, M_t)$ into (6) and omitting the terms of the second and higher orders, one gets the following matrix for linear approximation:

$$
\begin{bmatrix}
0 & 1 & -[a(M + \lambda) - (M + \lambda)^2] \\
0 & 0 & 1 \\
1 & -(2\lambda + c) & \lambda^2 + c\lambda + M \\
0 & 1 & -(2\lambda + c)
\end{bmatrix}
$$

(8)

The eigenvalues of matrix (8) are less, than 1, when $|(M + \lambda) \cdot (N - \lambda)| < 1/4$.

Similarly, numerous other limit regimes of different complexity and structure could be found, as well. One hardly can figure them out explicitly; moreover, there is no much sense in detailed determination of these complex regimes. Computer simulation makes them rather obvious.

Here we present the simplest model of a smart migration, strongly opposing the “reaction – diffusion” methodology. The model is rather clear and apparent. The simplicity results from the peculiar feature of the model; this is the case of globally informed individuals. Indeed, an individual makes a decision whether it would migrate, or would stay in the station, referring to the available information concerning the life conditions. So, the key issue is what information towards that matter is available.

Let’s concentrate on some mathematical issues followed from the smart migration. The first one is that the dynamics of a population with smart migration is irreversible in time. Indeed, the migration at the model...
is a projection, from mathematical point of view; thus, a set of different states are transformed into unique one, and there is no regular way to figure out which one was preceding the observed abundance resulted from the migration act.

Another important issue is that it expands both permissible phase space, and the parameters values, in comparison to similar models with no migration. It should be said, that such effects, probably, also could be observed (at least, for some peculiar combinations of the parameters) for the systems with random, or aimless migration. We doubt that the direct comparison of the areas of permissible phase variables, or the parameters, for the case of smart vs. the aimless migration makes much sense. Obviously, the model is rather simple and specific to pretend to describe properly any real biological community. The specificity here manifests in the global information accessibility; in occupation not more than two stations; in the absence of “microscopic” consideration of dynamics within a station.

The main purpose of this paper is to show the methodology of the modelling of spatially distributed populations (and other biological communities) with no chemical analogies, rather than to find out some peculiar dynamic regime pretending to match exactly a dynamics of real biological community.

The model provides that the life conditions at the residence station are converted into a couple of parameters $a$ and $b$ ($c$ and $d$, respectively). Besides, it is supposed that the density of the subpopulation (or its total abundance $N$, or $M$, respectively) is known, as well. Not discussing at the moment the details of the detection of population density, or other conditional parameters per se, suppose that the environmental abundance (density, indeed) and other parameters are detectable for an individual. Besides, the model describes similar parameters, and the abundance are known, at the distant station. Such suggestion makes the individuals to be globally informed. A feasibility of such presumption is doubtful, nevertheless, this assumption is a common place for mathematical population biology.

The methodology presented above is rather powerful, and provides a researcher with the tool for studying spatially distributed populations with no artificial and absolutely unrealistic hypotheses towards the microscopic behavior of individuals, i.e. the randomness and aimlessness of their transfers over a space. One sees the following furthering of the approach described here. First, a two-species (or several species) communities could be described within the framework of the methodology. Again, one should consider a two-station model, where each species (say, predators and preys) migrate from station to station and back. A dynamics within a station might be modelled with the the most common equation (say, with Lotka-Volterra equation), thus explicating the effect of smart migration in the dynamics of a multi-species community.

Both single-species, and multi-species models with smart migration may incorporate various patterns of information accessibility, for individuals. The model presented above is based on the hypothesis of the global accessibility of information to an individual. It means, that an individual knows the conditions of life (expressed in the coefficients, at the case of the model), both at the station of residence, and the station of immigration; it knows the density of each subpopulation. Finally, the an individual knows the transfer cost, in this case.

The hypothesis of total lack of information available to individuals opposes the idea mentioned above. Here an individual operates with the inner, extremely local information, when makes a decision on the change of the location for another one. In brief, such situation could be described like a threshold migration, where the transfer act takes place only when the local conditions become worse than some individually defined level. Still, the situation of the total lack of information is not equivalent to random and aimless migration. The difference becomes clear, if one considers the situation of the transfer act occurrence, while the local density at the occupancy place is still very low. The smart migration under the total lack of information would start up, while chemically-like diffusive migration will not take place, in such case.

All these assumptions seem to be too strong and specific. In general, the individuals operate with a part of information. There are several problems here, both of mathematical origin, and of biological essence. The first one consists in exact and comprehensive definition of what exactly is known to individuals. Next one is the discretion between the behavioral patterns supported by the reasonable choice of the way to behave, and those determined instinctively. Consider the seasonal bird migration. Surely, the fact that some species change a reproduction site for a winter spending site, falls beyond the will of a bird, it does not make a matter of reasonable of self-made choice: that is the instinct forcing them to fly away. On the other hand, the choice of a peculiar site to spend a night (if any) is made by the birds in a flock reasonably, with respect to the detail features and circumstances of the current situation. Finally, the problem arises when one tends to determine how far (in space) the individuals are able to collect and process the information (concerning the living conditions “there”).

The model implies that the transfer cost is symmetrical, and does not depend on the direction of migration. It might be so, while more realistic idea is that the transfer cost should be unsymmetrical. Evidently, the simplest way to figure out the transfer cost is to split it into three parts:

$$\mu = \mu_{\text{out}}(A) + \mu_{\text{in}}(B) + \delta(A, B).$$  \hspace{1cm} (9)

Here $\mu_{\text{out}}(A)$ is the transfer cost of successful emigration from the station $A$; $\mu_{\text{in}}(B)$ is the transfer cost of successful introduction into the station $B$, respectively; finally, $\delta(A, B)$ is the pure transfer cost from station $A$ to station $B$. Obviously, one should expect to face the
asymmetry
\[ \mu_{\text{out}}(A) \neq \mu_{\text{out}}(B) \quad \text{and} \quad \mu_{\text{in}}(A) \neq \mu_{\text{in}}(B), \]
in general. Also, a symmetry of pure transfer cost \( \delta(A, B) = \delta(B, A) \) is doubtful. It should be said, that this point makes no problem in its implementation at the model \([11]\). A dynamical model for synchronisation and for inheritance in microevolution: a survey of papers of A. Gorban, The talk given in the IHES seminar, “Initiation to functional genomics: biological, mathematical and algorithmical aspects”, Institut Henri Poincaré, November 16, 2000.

Another significant constraint of the model \([11]\) is the spatial structure limited with two stations. Indeed, an expansion of the approach presented above for the case of several stations, and, ultimately, for a continuous, or quasi-continuous case of a habitat is strongly desirable. Suppose, a population inhabits three stations; here we presume the global information accessibility, as well. Suppose, further, the conditions (i.e., the abundances and the parameters) make the situation when the individuals from the station A must migrate either to station B, or to station C. No one knows exactly, in advance, what is a proportion of individuals immigrating into the station B vs. those immigrating the station C. This is the main obstacle here. There exists the approach withdrawing this discrepancy; it is based on the interval mathematics \([21,22,23,32]\). The detailed discussion of that issue falls beyond the scope of this paper.

**IV. CONCLUSION**

The model described above implements the methodology of evolution optimality into the problem of the modelling of spatially distributed populations. Migration causes the growth on net reproduction (which is a reproduction rate, in our case), in average, over the space. The model comprises the simplest case of two stations, where the spatial distribution is restricted to a transfer of individuals from station to station and back; the transfer cost is supposed to be symmetrical one. The model shows the expansion of the environment capacity, in comparison to the case of the migration absence.

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