A mathematical model of competitive self-organization

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Abstract

A simple mathematical model describing the co-evolution of species and their ecological niches in hyperspace of the quantitively parametrised biological properties ("characters") is considered. It is shown that competition and selection described in the frame of the model may promote self-organization in a multi-species system in their characters' space.

General principles of structure formation delineated in this paper can be applied to different examples, from mechanical multi-body dynamical systems to complex economical systems consisting of large amounts of subsystems.

1. Introduction

The creation of structural order in complex systems is natural and well known. The phenomenon is represented in physics by cooperative light emission in lasers and Benar's cells that appear in liquid due to thermal convection, the famous Belousov-Zhabotinsky reaction can serve as an example in chemistry; for living organisms one could mention the oscillating ATP synthesis in *Dictyostelium discoideum* (see e.g. Nicolis and Prigogine (1989)).

The self-organising nature of ecological systems is commonly recognized by scientists, although modelling of general ecological systems involves extremely high levels of complexity, and the hierarchy of interactions involved can also be debated (Jorgersen *et al.*, (1992)). Nevertheless remarkable progress in ecological modelling and significant understanding of the problems related to spontaneous ordering and self-organization of

different structures in nature has been achieved by employing modern concepts and methods of theoretical physics (see for example Ricotta (2000), Flyvbjerg *et al*. (1995) and references therein).

In this context we can also mention some early works of one of the authors (A. F.). In early studies (Filippov, (1984), (1993)) a relatively simple model was introduced that accounts, self-consistently, for a reaction of the environment on the presence of a species. A transformation of ecological niche due to reaction of the environment follows the species in a parametric space of its characters and causes a specific state of "pursuit" in this space. In some particular cases such a pursuit really appears as a result of the adaptation of the predator to the prey, it is an interaction among species or species and components of the environment. In this approach it is convenient to consider species as a group of specimens closely distributed near the same peak of fitness in the space of characters. The position of this peak moves in the space of characters to produce a sufficiently functional type towards the state (generally dynamical), that may have a survival advantage and allow reproductive success for a species. The dynamics of such a development may be plausibly modeled by a system of first-order differential equations. These differential equations can be derived as a continuous limit of discrete equations for mutation and adaptation of species (Filippov, 1993).

The main purpose of the present publication is to show that for a large number of the species their collective motion in the parametric space can cause some specific ordering. This ordering could be treated as a self-organized structure that arises spontaneously via interactions among species.

2.   Methods

Consider a two-dimensional space of characters $r = (x, y)$. This also could be a two-dimensional resource spectrum, sustaining a number of species. Let r_j be the position of the fitness peak of the *j*-th species in this spectrum. From here we equate the point r_j to the j-th species in the characters space. Depending on their interaction we separate all *N* species into two groups { r_{1j} } and { r_{2j} }, which could be conven-tionally considered as "predators" and "preys".

The dynamics of "predators" and "preys" in the space of their characters can then be described by the set of equations:

$$\gamma_{1j}\, \partial r_{1j}/\partial t = \sum_k F_{11}(r_{1j} - r_{1k}) + \sum_m F_{12}(r_{1j} - r_{2m}),\, j = 1, \dots, M_1;$$

$$\gamma_{2j}\, \partial r_{2j}/\partial t = \sum_k F_{21}(r_{2j} - r_{1k}) + \sum_m F_{22}(r_{2j} - r_{2m})\, j = 1, \dots, M_2; \qquad (1)$$

$$M_1 + M_2 = N.$$

Here parameters γ_{nj} determine time scales, e.g. there could be slowly evolving species and species that are able to change their characters relatively fast. $F_{nm}(r_{nj} - r_{mk})$ characterise the interactions in the system; n=1,2.

For simplicity we use the same space dependence for all these interactions

$$F_{nm}(r_{1j} - r_{1k}) = A_{nm} \cdot (r_{1j} - r_{1k}) \cdot \exp\left[-(r_{1j} - r_{1k})^2/ a_{nm}\right]. \qquad (2)$$

This "force" corresponds to an effective potential $U_{nm}(\mathbf{r}_{1j} - \mathbf{r}_{1k}) \sim \exp[-(\mathbf{r}_{1j} - \mathbf{r}_{1k})^2 / a_{nm}]$ with a (limited) maximum energy of evolutionary pressure from close neighbours $\mathbf{r}_{1j} \rightarrow \mathbf{r}_{1k}$. It is supposed that each "predator" is attracted to all "preys". In its turn, each "prey" repulses from all "predators". Besides, a slight repulsive interaction is assumed for all "prey" and "predator" respectively. It means that:

$$A_{11} > 0; A_{12} > 0; A_{21} < 0; A_{22} > 0 \text{ and } A_{nn} \ll A_{nm}. \tag{3}$$

The same inequality is assumed for the characteristic scale of the interactions:

$$a_{nn} \ll a_{nm}. \tag{4}$$

Generally speaking, the space of the characters (or resources) is not uniform and without interaction every species $\mathbf{r}_{1j}$ has a preferable position $\mathbf{r}_{1j}^0$ in this space. From the mathematical point of view it could be reflected by including some forces $f_n(\mathbf{r}_{1j})$ in the dynamical system (1) ($f_n(\mathbf{r}_{1j}) > 0$, if $\mathbf{r}_{1j} < 0$; $f_n(\mathbf{r}_{1j}) < 0$, if $\mathbf{r}_{1j} < 0$ and $f_n(\mathbf{r}_{1j}) = 0$, if $\mathbf{r}_{1j} = 0$), which puts natural bounds to the phase space of the dynamical system under consideration. The reason why these terms are omitted in the system (1) is to make clear that coupling itself produces an ordered state. Being a simplification from the conceptual point of view, the assumption that the interacting points $\mathbf{r}_{nj}$ are embedded into the uniform space creates some numerical difficulties. In that case one has to deal with unbounded motion of the points $\mathbf{r}_{nj}$. To avoid this problem it is reasonable to apply a technique that is commonly used in numerical studies of (pseudo-) infinite systems in physics.

Suppose that initially all points are located inside a finite box $0 < x < L_x; 0 < y < L_y$ (L_x and L_y could coincide with the natural limitations of changes for x and y). The following mapping

$$x \rightarrow x - L_x \text{ if } x > L_x \; ; \; x \rightarrow x + L_x \text{ if } x < 0$$
$$y \rightarrow y - L_y \text{ if } y > L_y \; ; \; y \rightarrow y + L_y \text{ if } y < 0. \tag{5}$$

transforms the space into a torus. The transformation should be completed by a relevant extension of interaction terms (see e.g. Braun *et al.* (1998)*,* Vakarin *et al.* (1998)).

The numerical simulations of the system (1) were performed for the following set of parameters:
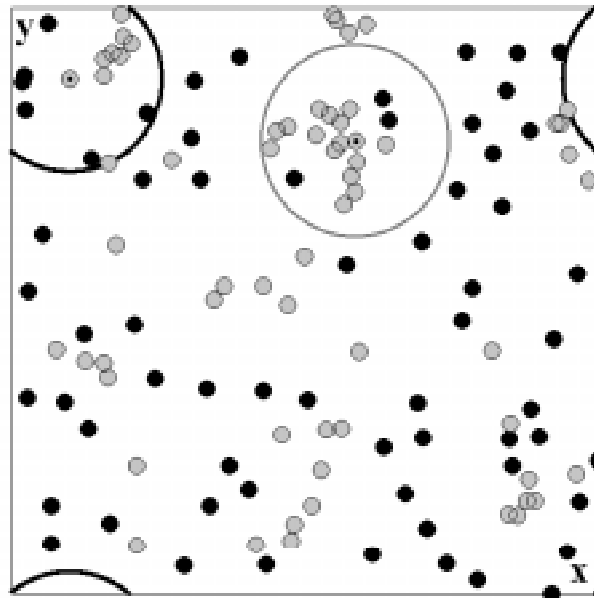
$N_1 = N_2 = 64; L_x = L_y = 125$;

$A_{11} = 1.0; A_{12} = 1.0; A_{21} = -0.3; A_{22} = 1.0;$

$a_{21} = a_{12} = 100; a_{22} = a_{11} = 10,$

and $\gamma_{1j} = \gamma_{2j} = 1$.

This choice of parameters corresponds to the case that all changes of $\mathbf{r}_{1j}$ take place in the same time scale. Later on we will consider some extension of the case and note the effect, which is entirely due to different scales of interactions. It is supposed that initially at $t = 0$ values $\mathbf{r}_{1j}$, $\mathbf{r}_{2j}$ are randomly distributed in the resource spectrum. In real nature they are not, but in the present study we are concentrating on the space structure which is due to the interaction only.

3.   Results and Discussion

The repulsive interaction among "prey" is less than the repulsion of a "prey" from any "predator". It is relatively obvious that in the neighborhood of any given "prey" it is more likely to find another "prey" than a "predator". At the same time all "predators" are attracted strongly to the places densely occupied by a large number of "prey" and they push "prey" out to another place in the space of characters. The repulsive interactions among each group of species do not allow either "prey" or "predator" to be packed very closely in the space. This results in the interactions leading to regular fluctuations of the density of species in any region of the space of characters. The numerical simulations of the system (1) are aimed at showing that these fluctuations are correlated in both space and time.

The results of the simulation are summarized in figures 1-4. A typical instant configuration of the system is shown in figure 1. The black and gray circles show the coordinates of the "predators" and "prey" respectively.

Figure 1. Instant configuration of the system. The coordinates of the "predators" and "prey" are shown by the black and gray circles respectively. The circular lines specify the neighborhoods of arbitrary "prey" (marked by dotted circles), that were chosen to calculate the population densities around them.

As is clear from the above, the important question is how closely the species are packed in their characters' space. This proximity in the space of characters is closely related to the problem of limiting similarity of the species in the resource spectrum, which has been under study by traditional ecologists for a number of years (see May, 1973).

To study the proximity effect we define a local neighborhood of any "prey" as a circle with a radius R=20. This value is chosen to be equal to the spatial dispersion of the main interactions in the system $R = (0.5\ a_{12})^{1/2} = (0.5\ a_{21})^{1/2}$. The corresponding region around a particular, but arbitrarily chosen, "prey" is shown in figure. 1 by a circular gray line.

If a chosen "prey" happens to be closer than R to L_x or L_y , then because of conditions (5) the circle around it will look as it is shown by a black line in figure 1.

If the population r_{1j} is not structured, but randomly distributed in the space one can expect the mean population for both "prey" and "predators" inside the circle of the radius R to be equal to $<N_{1,2}> = \pi(R/L_x)^2 N/2 = 5.14$. However, our simulations show that the proximity of any 'prey" is much more populated by the other "prey" and under-populated by the "predators". The averaging was performed over $T=256$ time units (the number $256=2^8$ is chosen to simplify further numerical calculations of correlation functions). The calculated mean values are equal to $<N_1> \cong 9$ and $<N_2> \cong 1.9$ for the "preys" and "predators" respectively.
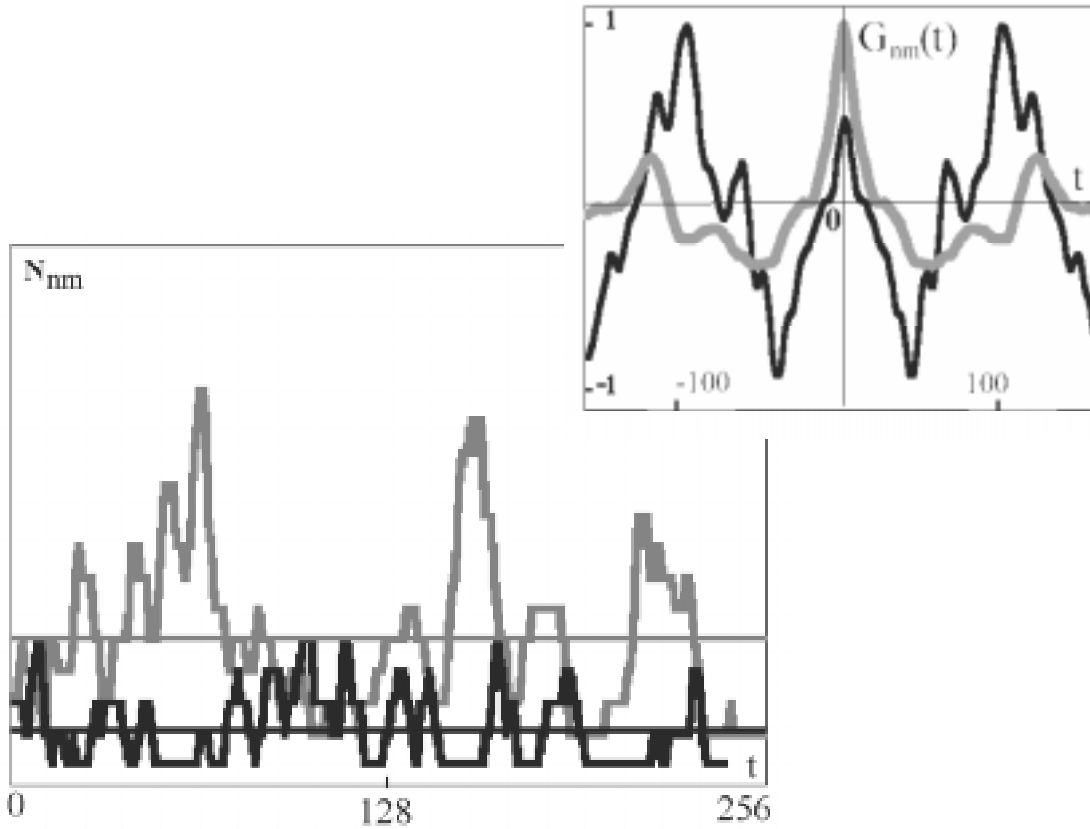

Figure 2. A fragment of the two correlated time dependencies of local "predator" and "prey" populations (black and gray lines respectively) in the vicinity of a chosen "prey". Straight lines of the same colors denote the mean values of the populations accumulated over the observation time. The "prey-prey" $G_{11}(t)$ (gray line) and "prey-predator" $G_{12}(t)$ (black line) correlation functions are presented in the insert.

These mean values are shown by the straight lines in the main plot of figure 2. This plot presents the typical behaviour of the "prey" and "predator" populations (gray and black lines in the figure) inside the proximity circle described above. Some correlation between the functions $N_1(t)$ and $N_2(t)$ displayed in figure 2 is seen directly. To make this clear we calculated the correlation functions $G_{nm}(t)$. By the formal definition one has:

$$G_{nm}(t) = \frac{1}{T} \int_{T_0}^{T_0+T} N_n(t') N_m(t-t') dt' \tag{6}$$

Here T_0 is some time after which the system has forgotten the random initial conditions that happen naturally in all self-organised systems. After time T the average values $<...>$ do not depend on the time of averaging. Actual numerical calculation of these functions is done by means of consecutively applied direct and inverse standard Fast Fourier Transformation of the variables $N_{1,2}(t)$. Resulting time-correlation functions are presented in the insert to figure 2. The "prey-prey" $G_{11}(t)$ function is plotted by gray lines and "prey-predator" $G_{12}(t)$ by black lines. Quasi-periodic oscillations of the density of the species are obvious.

Let us consider the instant space structure of the population. In fact, such a structure can be visually recognized from the snap-shot in figure 1 already. To make the consideration more rigorous we calculated a 2D space-correlation function. The space order in the system under consideration can be described by three correlation functions: "prey-prey", "predator-predator" and "prey-predator". The mathematical structure of all these correlation functions is the same. Let the function $G_{11}(r_{1j}- r_{1k})$ for the "prey-prey' correlation serve as an example:

$$G11(r1j- r1k) = \int_\Omega \rho 1(r- r') \rho 1(r') \, d \, r' /\Omega \,. \qquad (7)$$

The integration $\int_\Omega d \, r' /\Omega$ is performed here over the whole system volume $\Omega = L_x{\times}L_y$ and the local density $\rho_l(r)$ is given by the relation:

$$\rho 1(r) = \Sigma j \, \delta(r - rj) \qquad (8)$$

where $\delta(r - r_j)$ are the Dirac delta-functions.

In figure 3 we plot the gray-scale map of a Fourier-transform $G_{11}(q)$ of the function $G_{11}(r_{1j}- r_{1k})$

$$G11(q) = G11(qx,qy) = \int_\Omega G11(r1j- r1k) \exp [i \, q \, (r1j- r1k) \,] \, d \, rs /\Omega. \qquad (9)$$

For consistency, it is calculated for the same instant spatial configuration that is shown in figure 1. It is seen directly that the function $G_{11}(q_x,q_y)$ has a set of secondary maximums and it manifests clearly a presence of ordered structure in the system.

The configuration of r_{nk} evolves with time and all space correlation functions $G_{nm}(q)$ change as well. However, some long-term correlation structure also exists and can be obtained by averaging the dynamical correlation function over time. Note that with time this structure tends to become an isotropic one because of the chosen interactions in the system (1). But for the space structure the memory of the initial distribution of r_{1k} can last for a relatively long time. To smooth away remaining peculiarities, one can integrate 2D functions $G_{nm}(q_x,q_y)$ over the angle. The result of averaging over time and angle is shown in the insert to figure 3. The averaging has been performed over the same time period as for the mean values shown in figure 2. To complete an impression about structure of correlation functions in the system this time we present the "prey-predator" correlation function $G_{12}(q)$ averaged over time
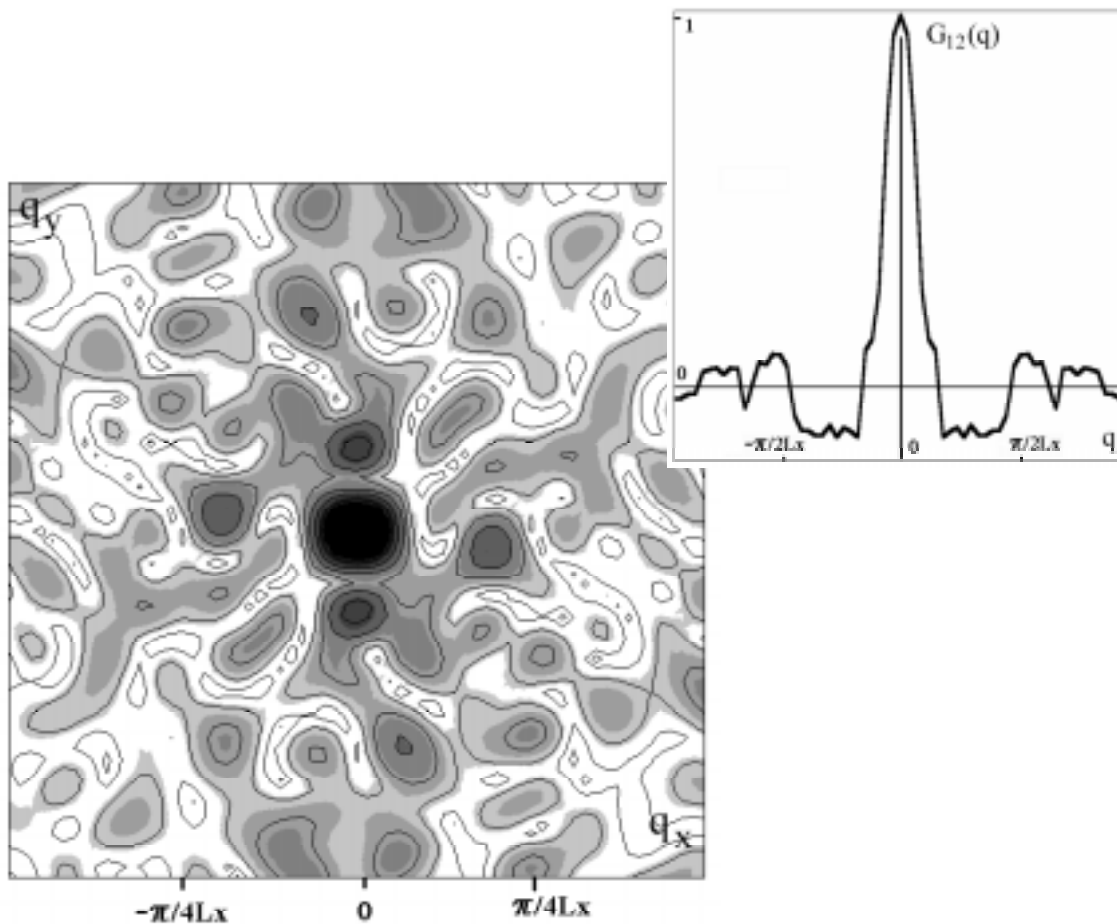
Figure 3. Gray-scale map of the Fourier-transform $G_{11}(\boldsymbol{q}_x,\boldsymbol{q}_y)$ calculated for the instant spatial "prey-prey" correlation function $G_{11}(\boldsymbol{r}_{1j}-\boldsymbol{r}_{1k})$. The insert presents "predator-prey" function $G_{12}(q_x,q_y)$ during an observation averaged over time and the angle.

and angle. One can clearly see here a region of an "anti-correlation", where the function $G_{12}(q)$ is negative. So, mutual interaction and collective dynamics create preferable positions for some species with respect to the other.

It is important that qualitative behavior of the system does not depend on a particular choice of parameters in the set of equations (1). Generally speaking, here one deals with a common feature of so-called strange attractor behavior. When a nonlinear system attracts to a specific configuration in a multidimensional phase space, its density of states creates a non-uniform distribution in any projection onto some sub-space (real physical space, in particular), and this is observable as a "self-organized spatial structure".

Although a more specific choice of parameters can produce some interesting behavior it cannot be observed in the system with the time scale as before. In a natural situation the timing parameters γ_{nj} can be different for the different groups of species, e.g. some of them can be correlated with seasonal changes. Below we show that the presence of groups of species with different characteristic times γ_{nj}^{-1} of their evolution is quite important for the self-organisation process.

For definiteness let us assume that there are two groups of "prey" and "predators" with two different time scales $\gamma^{(1)}_{nj}$ and $\gamma^{(2)}_{nj}$ ($\gamma^{(2)}_{nj} = 10\gamma^{(1)}_{nj}$) We suppose also that there is the same strong interaction inside each group, but the interaction amongst different groups is represented by a short range (weak) repulsion only

$$A^{(12)}_{11} = A^{(12)}_{12} = A^{(12)}_{21} = A^{(12)}_{22} = 0.5;$$

$$a^{(12)}_{11} = a^{(12)}_{12} = a^{(12)}_{21} = a^{(12)}_{22} = 10.0;$$

For clearness and brevity we continue to use the terms "prey" and "predator", although in that particular case we have to say about four groups of species. Starting from the random initial conditions, both slow and fast subsystems form their own structures more or less independently. Later, the dynamics of the fast subsystem can be considered as a motion in a "frozen" effective potential (landscape in the space of the characters), created by the slow subsystem.

As an example, in figure 4 (a-c) we show a sequence of three consequent snap-shots of the complex dynamical system. Small black and gray circles represent fast subsystems, slow species are denoted by big squares. The square frame in figure 4 allows the easy following of a group of fast species moving in an effective potential valley. In fact, the "frozen" potential plays the role of a niche structure for the quick subsystem. In turn, slow species move in the background of a time-averaged structure of the quick one.

(a)   (b)   (c)
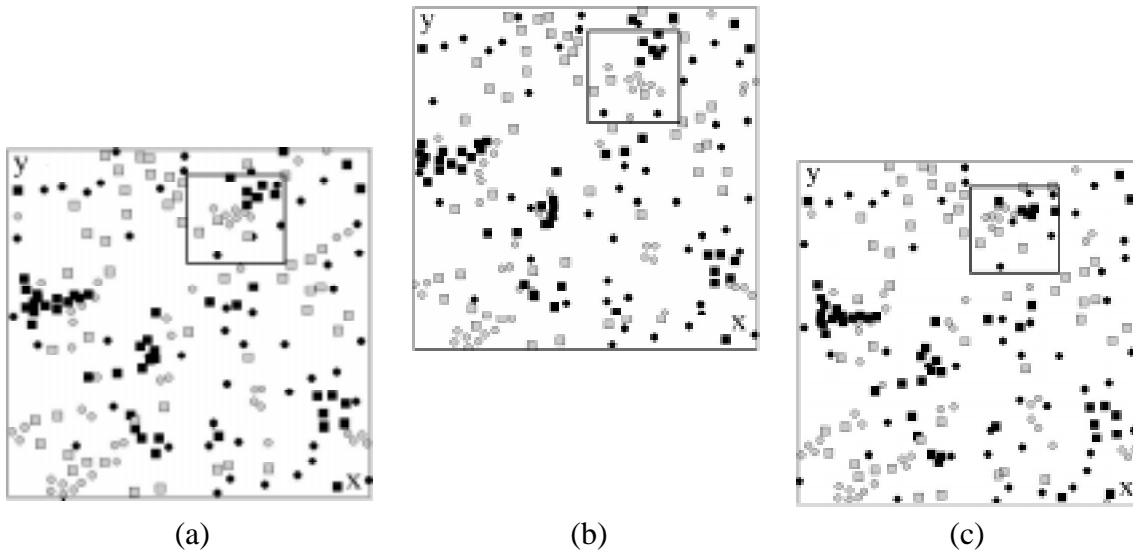
Figure 4. A sequence of three snap-shots depicting a short time evolution of the system that consists of two subsystems with different characteristic time constants. Small black and gray circles and big squares denote fast and slow subsystems respectively.

However, this averaged essentially non-uniform structure is strongly correlated with the current valleys of the potential caused by the slow subsystem. It means that both subsystems self-consistently create niche structures for each other.

4.   Conclusions

The above description could be applied to an extremely large class of objects ranging from different multi-particle physical systems to complex super-systems in sociology or micro-economy. The latter ones could consist of a number of smaller, relatively stable sub-systems of different types with different scales of interaction. On the other hand many continuous physical systems can be considered as a continual limit of the system (1) as N tending to infinity. The authors dealt with very similar behavior in the physical system, describing superconducting current in Josephson junctions (Filippov *et al.*, 1993). The actual reason for this is the tendency of complex dynamical systems of different natures to demonstrate strange attractor behavior.

The interaction of the sub-systems with different time scales plays an important role in a lot of evolutionary stages and forms. In particular, it is well known as an "adiabatic" interaction in physics and chemistry. Recently the similar Brownian dynamics technique was applied to study the hydrogen bonding in giant DNA molecules (Samoletov and Filippov, 1998). It is believed also that the tertiary structure of proteins could be explained as a self-organization in a complex system with a few time scales.

Acknowledgements

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