

# Self-reproducing systems: structure, niche relations and evolution

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A formal definition of a self-reproducing system is proposed using Petri nets. A potential self-reproducing system is a set of places in the Petri net such that the number of tokens in each place increases due to some sequence of internal transitions (a transition is called internal to the marked subset of places if at least one of its starting places and one of its terminating places belongs to that subset). An actual self-reproducing system is a system that compensates the outflow of its components by reproduction. In a suitable environment every potential self-reproducing system becomes an actual one. Each Petri net can be considered as an ecosystem with the web of ecological niches bound together with trophic and other relations. The stationary dynamics of the ecosystem is characterized by the set of filled niches. The process of evolution is described in terms of niche composition change. Perspectives of the theory of self-reproducing systems in biology are discussed.

*Keywords:* Self-reproduction; Petri net; Niche structure; Natural selection.

## 1. Introduction

A wide range of systems can reproduce themselves. These include autocatalytic systems in chemistry and among biological populations (Rudenko, 1976; Eigen and Schuster, 1979). There is a hypothesis that thinking is based on self-reproduction and selection of some elementary structures in the brain (Dawkins, 1976; Edelman and Mountcastle, 1978). New self-reproducing systems (SRS) appeared with the origin of man. They include tools, cultural traditions, languages and so on (Wilson, 1980; Boulding, 1981; Csányi, 1982). According to these authors, evolution of social organization in human populations has the same base as the biological evolution of animal species. Social equivalents to the genotype, phenotype, mutation, niche and natural selection are considered. Human ideas, inventions, traditions are replicated with some changes (mutations) when transferring between people and this is a sort of self-reproduction (Csányi, 1982).

SRSs have some common features. They can increase in number infinitely. Complicated SRSs can evolve and increase their organization. It was pointed out that quite different SRSs have common features in their structure and in the pattern of their evolution (Boulding, 1981; Sarychev, 1981; Csányi, 1982; Brennenstuhl, 1982). Thus it is important to develop the general theory of SRSs for deduction of some common features of such systems from their ability to reproduce themselves.

Many different mathematical and mechanical models of self-reproduction have been developed (Neumann, 1966; Arbib, 1969; Moore, 1962). Many of these mimic, to some extent, molecular and genetic processes in living beings (Eigen and Schuster, 1981; Ratner, 1986). But each of these models deals with only one sort or one specific class of SRSs. Thus they are not useful for a general theory of self-reproduction.

Kull and Leht (1984) were the first who gave a general definition of self-reproduction. They used the traditional kinetic approach, consider-

ing system dynamics to be formed by a set of elementary processes, resembling chemical reactions. A complex process is defined as a connex (web) consisting of a set of components (object species) with all elementary processes connecting these components. A definite connex is a connex with those and only those processes which connect its components. A definite connex is called multiplicative, if concentrations of all its components infinitely increase. A multiplicative definite connex represents a SRS.

This approach to the theory of SRSs demands some improvement. First potential and actual SRSs have to be distinguished (Sharov and Kull, 1990). Infinite growth in numbers occurs only in potential SRSs. Actual SRS as any population of animals cannot realize infinite growth because of resource limitation. Another requirement is to increase the rigor of mathematical apparatus used in the theory.

In the present work, a new variant of the theory of SRSs is proposed and applied to the description of processing and evolution in ecological systems. Potential SRSs are defined using the Petri net theory that has been already used for description of chemical systems (Gánty 1979). In the definition of actual SRSs the ability for infinite increase is replaced by the demand of compensating the outflow of components by reproduction. The niche structure and evolution are defined within a Petri net.

## 2. Potential self-reproducing systems

Our definition of potential SRS is based on the mathematical theory of Petri nets (Peterson, 1981). A Petri net consists of (1) a finite set of places  $P$  (empty circles in Fig. 1), (2) a finite set of transitions  $T$  (line segments in Fig. 1), (3) two functions  $B_t$  and  $E_t$  from  $T$  to  $N^p$ , where  $N$  is a set of natural numbers. These functions are shown by arrows in Fig. 1. If we choose some  $t \in T$ , then we shall write  $B(t)$  as  $B_t$  and  $E(t)$  as  $E_t$ . They are functions from the set  $P$  to  $N$ .  $B_t(p)$  is the number of arrows going from the place  $p$  to the transition  $t$ , and  $E_t(p)$  is the number of arrows going from the transition  $t$  to the place  $p$ .

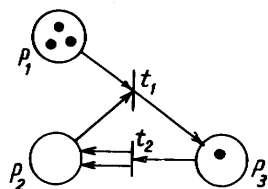


Fig. 1. An example of a Petri net (for explanations see the text).

Places may contain tokens (points inside empty circles in Fig. 1). A distribution of tokens among places is called a marking. Formally, a marking is a function  $M : P \rightarrow N$ . A transition  $t$  becomes executed if one token disappears from the starting places, followed by the appearance of one token in the terminal place of each arrow directed from the transition. Thus every transition changes the marking of the Petri net. The transition can be executed only if there are enough tokens in starting places.

In real systems tokens are interpreted as objects, places as object species and transitions as processes. For example, in chemical systems tokens become molecules, places become species of molecules, and transitions become reactions. In Fig. 1 transition  $t_1$  corresponds to the reaction of synthesis and  $t_2$  corresponds to the reaction of decay. Organisms and non-living components are objects in ecological systems. Object species are not equivalent to biological species. For example, conspecific organisms distinguished by sex or by stage of development belong to different object species. Transitions are interpreted as ecological processes: reproduction, death, foraging, migration etc. The transition  $t_1$  in Fig. 1 represents the feeding of organisms  $p_2$  on food items  $p_1$ , and  $t_2$ , the division of an organism into two. Space-distributed systems can be modeled by Petri nets as well. In this case the place will correspond to the position of an object in space.

Two special sets of places are associated with each transition  $t$ : the starting set  $b_t = \{p \in P \mid B_t(p) > 0\}$  and the terminate set  $e_t = \{p \in P \mid E_t(p) > 0\}$ . The transition  $t$  is called internal for some subset of places  $Q \subseteq P$ , if  $b_t \cap Q \neq \emptyset$  and  $e_t \cap Q \neq \emptyset$ . The other transi-

TABLE 1  
Change of the marking of the Petri net in Fig. 1.

Place	The marking of the net					
	Initial	After executing of transitions				
		$t_2$	$t_1$	$t_1$	$t_2$	$t_1$
$p_1$	3	3	2	1	1	0
$p_2$	0	2	1	0	2	1
$p_3$	1	0	1	2	1	2

tions we call external. The sets of all internal and all external transitions are designated as  $In(Q)$  and  $Ex(Q)$ , respectively.

The place  $p$  is called a resource for some set of places  $Q \subseteq P$  if  $p \notin Q$  and  $p \in b_i$  for some  $t \in In(Q)$ .

A non-empty subset of places  $Q \subseteq P$  is called a potential SRS, if there exists the sequence of internal transitions  $t_1, \dots, t_n$ , that increases the number of tokens in all places of the subset  $Q$ . Obviously, the number of tokens in each place can grow infinitely if the mentioned sequence of internal transitions is repeated again and again, and if there are enough resources.

The set  $Q = \{p_2, p_3\}$  in Fig. 1 is an example of potential SRS. Execution of transitions  $t_2, t_1, t_1, t_2, t_1$  leads to the final marking of the net which is strongly greater in the subset  $Q$  than the initial marking (Table 1).

In Fig. 2 there is another more complicated example of potential SRS – a population of hypothetical bisexual animals. The upper cycle corresponds to females and the lower to males. Fertilized females ( $p_1$ ) produce female ( $p_2$ ) and

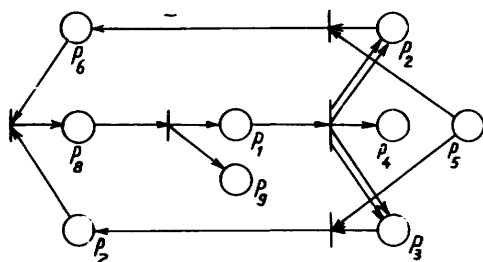


Fig. 2. Bisexual population represented by a Petri net.

male ( $p_3$ ) progeny and die after that ( $p_4$ ). Progeny assimilate some resources ( $p_5$ ) and copulate after completing their development ( $p_8$ ). Males die after copulation ( $p_9$ ) while fertilized females ( $p_1$ ) start their reproduction.

The set  $Q = \{p_1, p_2, p_3, p_6, p_7, p_8\}$  is a potential SRS. This example is interesting for  $Q_1$  has two smaller SRS:  $Q_2 = \{p_1, p_2, p_6, p_8\}$  and  $Q_2 = \{p_1, p_3, p_7, p_8\}$  inside.  $Q_1$  corresponds to female and  $Q_2$  to male subpopulations. Males serve as resources for female self-reproduction and in the same manner females are resources for male self-reproduction.

Now some features of SRSs revealed by Kull and Leht (1984) are formulated using Petri net formalism:

(1) Each potential SRS has at least one internal transition, the execution of which increases the number of tokens in the system. This feature is obvious.

(2) If the law of conservation of mass is true for each internal transition  $t$  of some potential SRS  $Q$ , i.e. there is a positive real function  $\mu$  on the set of places  $P$  ( $\mu(p)$  is interpreted as the mass of the object in the state  $p$ ) and

$$\sum_{p \in P} \mu(p)B_t(p) = \sum_{p \in P} \mu(p)E_t(p) \tag{1}$$

then  $Q$  has at least one resource. The proof can be obtained by summing up equation (1) for the sequence of internal transitions mentioned in the definition of potential SRS.

The set of places  $Q$  will be called a cycle if any place  $p_1 \in Q$  can be attained from any other place  $p_2 \in Q$  going by internal transitions. The potential SRS  $Q$  will be called minimal, if the formula  $Q_1 \subseteq Q \Rightarrow Q_1 = Q$  is true for any potential SRS  $Q_1$ .

(3) Each minimal potential SRS is a cycle.

For the proof we need an additional notion. The basic cycle of the set of places  $Q$  we define as a non-empty subset  $Q_1 \subseteq Q$  such that (i) any place  $p_1 \in Q_1$  can be attained from any other place  $p_2 \in Q_1$  going by transitions  $t_i \in In(Q)$ , (ii) if there exists a transition  $t \in In(Q)$  leading from the place  $p_3 \in Q$  to the place  $p_1 \in Q_1$ , then  $p_3 \in Q_1$ . It is easy to show that a basic cycle is a cy-

cle and that any set of places  $Q$  has at least one basic cycle.

**Lemma 1.** If  $Q$  is a potential SRS then any of its basic cycles  $Q_1$  is also a potential SRS.

**Proof.** According to the definition of potential SRS there is some sequence of transitions taken from the set  $\text{In}(Q)$  which increases the number of tokens in each place  $p \in Q$ . The subsequence of transitions which belong to the set  $\text{In}(Q_1)$  will increase the number of tokens in all places  $p \in Q_1$ , because  $e_t \cap Q_1 \neq \emptyset$  only for those transitions  $t$  which belong to the set  $\text{In}(Q_1)$ . Thus  $Q_1$  is a potential SRS.

Now we can prove the third feature of potential SRSs. According to Lemma 1, the basic cycle  $Q_1$  of the potential SRS  $Q$  is a potential SRS itself. But  $Q$  is a minimal SRS and therefore,  $Q_1 = Q$  and  $Q$  is a cycle.

It follows from feature (3) that any minimal potential SRS consists of one or several cycles. Each potential SRS contains some minimal potential SRS and therefore has at least one cycle.

### 3. Actual self-reproducing systems

Before giving the definition of an actual SRS we have to introduce certain laws of execution of transitions in the Petri net. Let there be a sufficient number of tokens in each place. Then the dynamics of the system can be considered as a continuous process and be described by differential equations. In this case we shall use concentration of objects  $c_p$  in the place  $p$  instead of their numbers. The rate  $v_t$  of the process  $t$  (the rate of executing of the transition  $t$ ) satisfies the law of mass action:

$$v_t = k_t \prod_{p \in P} c_p^{B_t(p)} \quad (2)$$

where  $k_t$  is the coefficient of the process rate. We shall call the Petri net, where the process rates are defined by (2) a kinetic system. Its state is characterized by concentrations of ob-

jects in all places and its dynamics corresponds to differential equations:

$$\frac{dc_p}{d\tau} = \sum_{t \in T} v_t(E_t(p) - B_t(p)) \quad (3)$$

where  $\tau$  is time.

Let  $\varphi_p(T_1)$  be the rate of the object concentration change in the place  $p$  by the action of all processes from some subset of transitions  $T_1 \subseteq T$ , i.e.

$$\varphi_p(T_1) = \sum_{t \in T_1} v_t(E_t(p) - B_t(p)) \quad (4)$$

Average rates of processes can be estimated in kinetic systems with stationary dynamics. Systems with stable equilibrium, limit cycle, or strange attractor will exhibit this kind of dynamics. In this case one is able to find the mean value of  $\varphi_p(T_1)$  that will be signed as  $\Phi_p(T_1)$ .

An actual SRS is a set of places  $Q$  in the kinetic system, if there is a stationary dynamics and  $\Phi_p(\text{In}(Q)) > 0$  for all places  $p \in Q$ .

This definition means that internal processes support the increase of object concentrations in all places of an actual SRS. In other words, production is generated by internal processes. The dynamics of the kinetic system is considered to be stationary and therefore internal and external processes must compensate each other on average. Thus, external processes ensure the outflow of production:  $\Phi_p(\text{Ex}(Q)) < 0$  for all places  $p \in Q$ . The significant feature of actual SRSs is their ability to exist in conditions of permanent outflow of its components.

Definitions of actual and potential SRSs are interrelated. Each actual SRS is a potential SRS. The proof can be obtained if the number of executions of internal transitions in the sequence, mentioned in the definition of potential SRSs is taken proportional to the rates of corresponding processes in actual SRSs. On the other hand, any potential SRS will become an actual one in a suitable kinetic system (the proof is given in the Appendix).

#### 4. Niche structure

It was mentioned previously that a Petri net can be interpreted as an ecological system. Thus, the question arises whether a niche structure, comparable with that in the ecosystems, can be revealed in any given Petri net. It will be shown that it is possible.

The first step is to define the elementary unit of the niche structure, i.e. a niche. One must bear in mind that it is not a real ecological niche but a pure abstraction, comparable with the ideal gas in theoretical physics. Not every potential SRS can be considered as a niche. If two such systems cannot exist separately, each producing some indispensable resource for the other, they both occupy the same niche. For example in the bisexual population (Fig. 2) there are two potential SRSs: male and female, but they cannot exist separately because males are resources for female reproduction and vice versa females are resources for male reproduction. Thus they share the same niche.

Let us introduce some auxiliary terms. The transition  $t$  will be called active for the set of places  $Q \subseteq P$ , if  $b_t \subseteq Q$ . The set of all active transitions for the set of places  $Q$  we shall sign as  $Ac(Q)$ .

The set of places  $Q$  will be called autonomous if the following conditions hold:

(A1) for each transition  $t$  the implication  $b_t \subseteq Q \Rightarrow e_t \subseteq Q$  is true,

(A2) there exists a sequence of active transitions  $t_1, \dots, t_n$  ( $t_i \in Ac(Q)$ ), such that after their execution the terminate marking of the set  $Q$  will be strictly greater than the initial one.

If  $Q$  is an autonomous set of places and  $b_t = \emptyset$  for some transition  $t$ , then  $e_t \subseteq Q$ . It can be derived from the condition A1. Thus all the places with input transitions (with  $b_t = \emptyset$ ) are common for all autonomous sets.

Let us assume that all places of the set  $Q$  are filled with tokens while the other places are empty. An enlargement of the set  $Q$  (signed as  $E(Q)$ ) is the set of all places which can be filled after the execution of some transition  $t \in Ac(Q)$ . Formally  $E(Q) = \{p \in P \mid p \in Q \vee (p \in e_t \& t \in Ac(Q))\}$ . The set  $Q$  is called closed\* if

$E(Q) = Q$ . It is obvious that the set  $Q$  is closed if and only if it satisfies the condition A1.

The set of places  $\bar{Q}$  is called a closure\* of the set  $Q$  if there is a sequence of sets  $U_1, U_2, \dots$  such that  $U_{i+1} = E(U_i)$  for all  $i$ ,  $U_1 = Q$ , and  $U_n = U_{n+1} = \bar{Q}$ . The closure of any set of places is a closed set.

**Lemma 2.** If some set of places  $Q$  satisfies the condition A2 then its closure is an autonomous set (see the proof in the Appendix).

**Lemma 3.** If  $Q$  is a closed set of places, and  $Q_1 \subseteq Q$ , then  $\bar{Q}_1 \subseteq Q$ .

**Proof.** Let us assume that the statement is wrong. Then there is some minimal integer  $k$  for which the set  $U_k$ , mentioned in the definition, will contain a place  $p$  outside of the set  $Q$ . Then there is some transition  $t$  and  $p \in e_t$  and  $b_t \in Q$ . Thus  $Q$  is not closed. The contradiction obtained finishes the proof.

**Lemma 4.** The intersection of two closed sets  $Q_1$  and  $Q_2$  is closed.

**Proof.**  $b_t \in Q_1 \cap Q_2 \Rightarrow b_t \in Q_1 \& b_t \in Q_2 \Rightarrow e_t \in Q_1 \& e_t \in Q_2 \Rightarrow e_t \in Q_1 \cap Q_2$ .

In each Petri net there exists at least one autonomous set of places: it is the closure of the empty set. It is autonomous according to Lemma 2 and obviously is included in any other autonomous set. It will be called the least autonomous set. It is empty if and only if  $b_t \neq \emptyset$  for all transitions  $t$ .

In Fig. 3 all autonomous sets of places for a definite Petri net are shown. These sets we consider as the modes of existence of the ecosystem, represented by the net. The least autonomous set consist of only two places  $p_1$  and  $p_2$  that will be interpreted as non-living components of the ecosystem. If only these places are filled by tokens, all other places will remain empty in the course of the system dynamics. Now, let us suppose that an object (an organism) has appeared in the place  $p_3$ . Then it will start reproducing itself using objects in the place  $p_1$

\*Notions closed set and closure are not topological, because the union of two closed sets of places is not always closed.

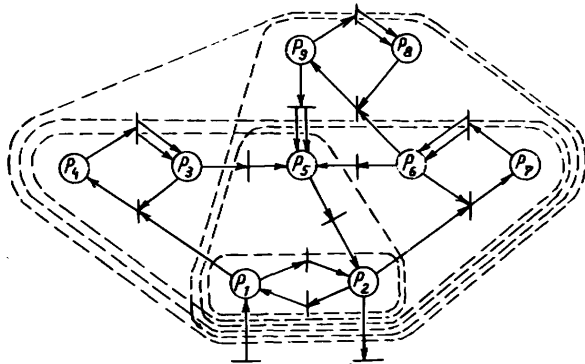


Fig. 3. A Petri net with autonomous sets of places encircled with a dashed line.

as the resource. In result the system will grow to the extent of another autonomous set of places  $\{p_1, p_2, p_3, p_4, p_5\}$ . All these places will be filled with tokens, while other places will remain empty. Then, if the object  $p_6$  is added to the system, then the system will again enlarge to the extent of the autonomous set  $\{p_1, p_2, p_3, p_4, p_5, p_6, p_7\}$  and so on.

The basic cycle for the difference  $Q = Q_1 \setminus Q_2$  of two non-equal autonomous sets of places ( $Q_2 \subset Q_1$ ) will be called a niche. The basic cycle has to be taken because the niche must not contain places for non-living objects, produced by the organisms, such as faeces and dead bodies. For example, the set of places  $\{p_3, p_4, p_5\}$  in Fig. 3 is the difference of two autonomous sets, and its basic cycle is  $\{p_3, p_4\}$ . The basic cycle does not contain the place  $p_5$ , which is considered to be the state of dead organisms.

**Theorem 1.** A niche is always a potential SRS.

**Proof.** First we shall prove that the difference  $Q = Q_1 \setminus Q_2$  of two including one another autonomous sets of places is a potential SRS. Let us assume that  $e_t \cap Q \neq \emptyset$  for some transition  $t \in T_1$ , where  $T_1 = Ac(Q_1) \setminus In(Q)$ . If  $b_t \cap Q \neq \emptyset$  then  $t \in In(Q)$ , and if  $b_t \cap Q = \emptyset$  then  $b_t \subseteq Q_2$  and therefore the set  $Q_2$  will be not autonomous. In both cases there is a contradiction. Thus,  $e_t \cap Q = \emptyset$  for any transition  $t \in T_1$ . According to the definition of an autonomous set, there is a sequence of transitions  $t_1, \dots, t_n$  ( $t_i \in Ac(Q_1)$ ), which increases the number of tokens

in all places  $p \in Q_1$ . The subsequence of transitions, belonging to the set  $In(Q)$  has to be chosen from it. This subsequence will increase the number of tokens in all places  $p \in Q$ , because all other transitions ( $t_i \in T_1$ ) cannot increase the number of tokens in these places ( $e_i \cap Q = \emptyset$ ). The initial number of tokens in all places must be great enough for all transitions to be executed. Thus  $Q$  is a potential SRS. Then, according to Lemma 1, its basic cycle, i.e. the niche, is also a potential SRS.

Niches can intersect each other, and can be included one into another, as shown in Fig. 4. They may be occupied not by the whole population, but by part, specializing on some particular resource. An interesting example is a hypercycle (Eigen and Schuster, 1979). It is a number of elementary niches united by one great niche.

**Theorem 2.** For two unequal autonomous sets  $Q_1$  and  $Q_2$  there is some niche  $N$  which is filled only in one of them. In other words, any autonomous set has its specific composition of niches.

**Proof.** If  $Q_1 \subseteq Q_2$  then our statement is evident. Thus we shall consider only the difficult case, when neither of two autonomous sets includes the other one. Let  $Q_3$  be the greatest autonomous set which is included in the intersection  $Q_1 \cap Q_2$ . Let  $N$  be the basic cycle of the set  $Q_1 \setminus Q_3$ . According to the definition  $N$  is a niche. We shall assume that  $N \subseteq Q_2$ . If  $e_t \cap N \neq \emptyset$  for some transition  $t \in Ac(Q_1)$ , then  $t \in Ac(Q_3 \cup N)$  because otherwise  $N$  will be not a

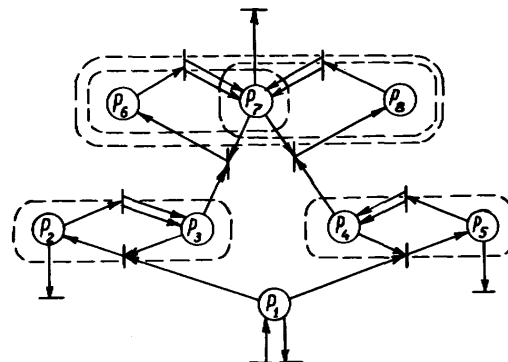


Fig. 4. A Petri net with intersecting niches (niches are encircled).

basic cycle. Furthermore,  $t \in \text{In}(N)$  because otherwise transition  $t$  will not correspond to the condition A1 for the autonomous set  $Q_3$ . According to A2, there is a sequence  $S_1$  of transitions taken from the set  $\text{Ac}(Q_1)$ , which increases the number of tokens in all places of the set  $Q_1$ , and in particular in all places of the niche  $N$ . The subsequence  $S_2$  obtained by the exclusion of all transitions  $t \notin \text{Ac}(Q_3 \cup N) \cup \text{In}(N)$  will also increase the number of tokens in all places of the niche  $N$ , because all excluded transitions are not terminated in  $N$ . All resources for  $N$  accumulated in the course of execution of this sequence of transitions are located in the set  $Q_3$ . The number of resource tokens taken from the place  $p \in Q_3$  will be signed as  $v_p$ . According to A2, there is a sequence  $S_3$  of transitions taken from the set  $\text{Ac}(Q_3)$ , which increases the number of tokens in each place  $p \in Q_3$  by some positive value  $w_p$ . Let  $p'$  be the place with the highest value of  $v_p/w_p$ . Then combining  $\text{Int}(v_{p'}/w_{p'}) + 2$  copies of the sequence  $S_3$  (where  $\text{Int}(x)$  means the integer part of real number  $x$ ) with the sequence  $S_2$  we shall obtain the sequence of transitions taken from the set  $\text{Ac}(Q_3 \cup N)$  which increases the number of tokens in all places of the set  $Q_3 \cup N$ . According to Lemma 2,  $Q_3 \cup N$  is an autonomous set. The set  $Q_1 \cap Q_2$  is closed because of Lemma 4, and thus  $Q_3 \cup N \subseteq Q_1 \cap Q_2$  according to Lemma 3. Therefore  $Q_3$  is not the greatest autonomous subset in  $Q_1 \cap Q_2$ . We have come to the contradiction, and thus  $Q_2$  does not include the niche  $N$ . The theorem is proved.

There are various relations between niches.

TABLE 2

Types of relations (R,E,F,I) between the niche  $N$  and some place  $p \in N$ .

The type of transition $t$ connecting $p$ and $N$	Localization of the place $p$	
	In the set $b_t$	In the set $e_t$
Internal	R	F
Input external	I	-
Output external	E	F

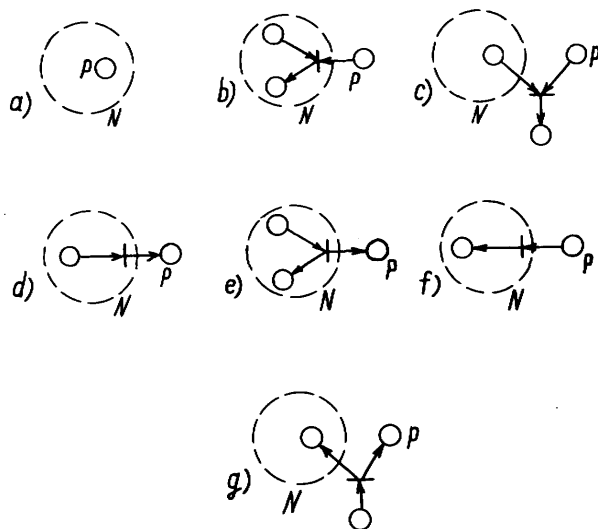


Fig. 5. Types of relations between the place  $p$  and the niche  $N$ : (a) S-relation; (b) R-relation; (c) E-relation; (d),(e) F-relation; (f) I-relation; (g) the absence of relation.

To analyze them we need to classify relations between a niche  $N$  and some place  $p$ . There are five main types of such relations signed by the letters S, R, E, F and I (Fig. 5). S-Relation means that  $p \in N$  (Fig. 5a). Other relations when  $p \notin N$  are represented by Table 2. Input (or output) external transition means that  $b_t \cap N = \emptyset$  &  $e_t \cap N \neq \emptyset$  (or  $b_t \cap N \neq \emptyset$  &  $e_t \cap N = \emptyset$ ). Examples are given in Fig. 5b-f. R-, E-, F- and I-relations can be interpreted as links between the niche and its resource, inimical agent, excrements or dead bodies, and immigrants, respectively. The dash in Table 2 corresponds to the situation, shown in Fig. 5g. In this case neither the niche affects the number of objects in the place  $p$ , nor the objects in the place can affect the niche. Thus we do not consider it as a form of relation.

Now we can characterize the relation between niches  $N_1$  and  $N_2$  by the relation of some place  $p$  to each of these niches. For example, if the place  $p$  is F-related with  $N_1$  and R-related with  $N_2$  then the relation between these niches will be signed by the formulae FR (or RF). All possible combinations are shown in Fig. 6 and in the Table 3. In the table there are two bases for the classification of inter-niche relations. The first is

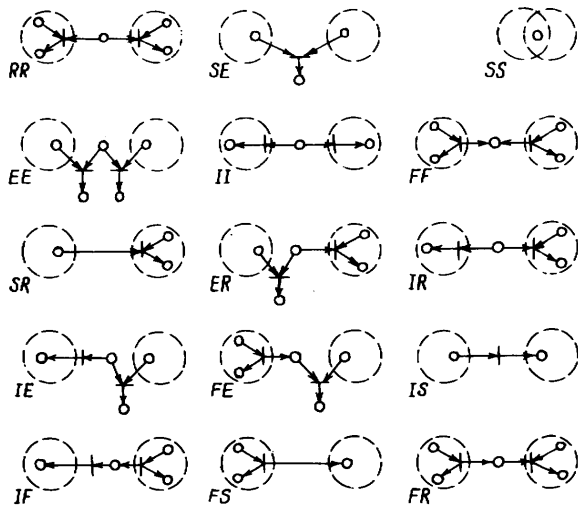


Fig. 6. Types of inter-niche relations: SS, intersection; RR, competition; EE, relation by common inimical agent; FF, II, neutral relations; SR, consumption; SE, annihilation; FS, IS, IF, transitions; ER, refinement; FR, utilization; IR, IE, relations with no biological interpretation; FE, contamination.

the distinction between direct relation, where the formulae have the letter S, and indirect relation, which goes through the outside connection place and has no letter S in its formulae. The second is the sign of relation. According to Odum (1971), inter-species relations are characterized by a pair of signs: ++, --, 00, +-, 0-, 0+, where + denotes a positive effect of one population upon another, - a negative effect, and 0 is the neutral effect. We adopt this

TABLE 3

Types of inter-niche relations.

The type of relation, after Odum (1971)	Relations	
	Direct	Indirect
--	SE	RR
++	SS	EE
00	-	II, FF
+ -	SR	ER
0 -	-	IR, FE
0 +	IS, FS	IF, IE, FR

classification for niches. It is important that the sign of the inter-niche relation corresponds to Table 3 only if there are no additional relations and no feedback loops ending in the external connection place. Otherwise the sign of the effect of one niche onto another may change to the opposite one.

The types of inter-niche relations are the following. RR is competition for a common resource. SE is annihilation: two objects from different niches perish when they run into each other. An example is the parasitism on the non-adequate host species, which leads to the death of both the parasite and its host. SS is niche intersection. The object located in the place of intersection can go either to one niche or to another depending on the resource available. EE is a relation by common inimical agent. For example, organisms of two populations are destroyed by some agent. When an organism dies it accumulates these agents, and that diminishes mortality in the other population. That is why this relation belongs to the ++ type. II and FF are neutral relations. SR is consumption; examples are preying and parasitism. ER is refinement. For example, filtrator organisms exclude small particles from the aquatic environment which are harmful for some other species. IR, IE - these relations have no analogies in biology. FE is contamination. This relation binds together populations one of which producing harmful agents (e.g. toxins) for another. IS, IF, FS are transitions of objects from one niche to another. Animal migration and distribution of seeds are examples of this kind of relations. FR is utilization. It has a place if excrements or dead bodies are resources for organisms of another population, e.g. for dung-beetles.

In more complicated cases there are two or more relations between niches. For example, if a parasite does not prevent the host reproduction then there are two relations between niches: the consumption of the host by the parasite (at the invasion) and the transition of invaded host offspring to the host niche.

Inter-niche relations with the resource component R in the formulae are the most important in biological world, and are called trophic rela-



tions. According to the set of resources niches can be classified into several trophic groups.

A niche will be called autotrophous if all its resources belong to the least autonomous set of places. All other niches are heterotrophous. Autotrophous niches can exist independently from the other niches, while heterotrophous niches are dependent. In Fig. 3 niches  $\{p_3, p_4\}$  and  $\{p_6, p_7\}$  are autotrophous and niche  $\{p_8, p_9\}$  is heterotrophous.

A heterotrophous niches which has at least one resource located in another niche, is called phagotrophous. The other heterotrophous niches are called saprotrophous. The niche  $\{p_8, p_9\}$  is phagotrophous. If its resource were the place  $p_5$  instead of  $p_6$  it would be saprotrophous.

Thus, a set of niches with different interrelations can be revealed in any Petri net. Niches can be classified according to their trophic relations.

### 5. Evolution in self-reproducing systems

Natural selection and evolution can be considered in the frame of the described model. Evolution is a natural potentially infinite process of occupation of new niches (Boulding, 1981). For any stationary dynamics of the kinetic system, where the rates of transition execution are defined by the mass action law, the set of places with positive object concentrations is autonomous. All niches included in this set are filled. The niche will be called opened, if after addition of some objects to it a new stationary dynamics will be established with this niche being filled. All filled niches are considered to be opened. A niche is called free if it is opened but not filled. Theorem 2 allows us to trace any evolutionary trajectories as the change of the composition of filled niches.

A new niche may become occupied by accidental invasion from outside or by mutation. Both processes are not represented in the Petri net. If they were in the net there would be no niches. These processes are considered to have much lower rate coefficients than the processes represented by transitions in the net. The niche

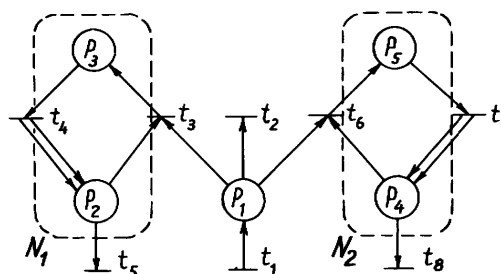


Fig. 7. A Petri net with two competing niches (encircled).

structure allows us to predict evolution only if there are few free niches. In this case mutational processes affect only the rate, but not the direction of evolution. If there is a great variety of free niches, then the role of mutations in directing evolution will increase.

The process of evolution can be illustrated by an example of competition exclusion (Fig. 7). There are two niches  $N_1 = \{p_2, p_3\}$  and  $N_2 = \{p_4, p_5\}$  competing for the common resource  $p_1$ . Transitions  $t_1$  and  $t_2$  ensure the stream of resources through the system. If there is only one niche filled, the stable resource concentration will be  $c' = k_5/k_3$  for  $N_1$ , and  $c'' = k_8/k_6$  for  $N_2$  where  $k_i$  is the coefficient of the rate of the  $i$ th process (transition). Let us assume that primarily only the niche  $N_1$  is filled and  $c' > c''$ . Then the niche  $N_2$  will be free because the resource concentration ( $c'$ ) will be greater than the least value ( $c''$ ) that can support reproduction in this niche. If an object will appear in  $N_2$  due to some mutation, then it will reproduce itself. This will lead to the decrease of resource concentration. The number of objects in the niche  $N_1$  will decrease because they need higher resource concentration for their reproduction than objects in the niche  $N_2$ . At the end the niche  $N_1$  will become empty and closed because it cannot be occupied again. Competitive exclusion of one niche by another may be interpreted as a natural selection. So, natural selection can operate in arbitrary SRS, described by a Petri net.

Maynard Smith (1982) suggested to analyze evolutionary attractors for qualitative description of the direction of natural selection. When

applied to evolution of animal behavior an attractor was called an evolutionary stable strategy – “a strategy such that, if all the members of a population adopt it, then no mutant strategy could invade the population under the influence of natural selection” (Maynard Smith, 1982, p.10). This approach can be adopted for Petri nets: a stationary dynamics of kinetic system is evolutionary stable if it is not sensitive to the introduction of a small number of any kind of objects. In the previous example, a stationary dynamics with single filled niche  $N_2$  is evolutionary stable. It is obvious that there are no free niches for evolutionary stable dynamics. But the absence of free niches is not a sign of evolutionary stability. For example, the niche of a pathogen is not free if its invasion leads to the destruction of the host population and to the subsequent death of the pathogen; but the stationary dynamics of the host population without pathogen is not evolutionary stable. The analysis of evolutionary stable dynamics is very important for understanding trends of evolution.

Thus, evolution by natural selection is a general feature of SRSs with mutations. Simple systems without macromolecules being involved, cannot provide long evolution because the types of mutations are very limited (it may be only few isomers). Only complicated systems can perform a potentially infinite spectrum of mutations, and thus only they can evolve without certain limits.

In the real world no ecological system exists in a stationary environment. That is why our definitions of niches and evolution are abstractions. Nevertheless they are useful because for each time scale it is possible to ignore trends, performed in a larger scale. It is possible to analyze changes of the niche structure during long-scale evolution and to reveal the rate of adaptability of niches by their persistence in the environment with non-stationary trends. Therefore this approach can be applied to the theory of adaptability developed by Conrad (1983).

## 6. Quasi-evolution

A very important problem concerns the evolu-

tion of systems without self-reproduction. Physicists are talking about the evolution of elementary particles and sky bodies, geographers, about the landscape evolution; biologists are discussing the pre-biological evolution of catalytic complexes. The question arises if it is a true evolution, and if it is, what are its differences from biological evolution.

A Petri net without potential SRS has no niches. Thus the evolution (if it may be called so) of non-living objects is qualitatively different from biological evolution. I am not against the wide interpretation of the term evolution, but it is necessary to distinguish between evolution of SRSs and of physical systems without self-reproduction. For the former I will use the term eu-evolution and for the latter, quasi-evolution.

Now we shall clarify some features of quasi-evolution. The minimal difference between two closed sets including one another will be called a quasi-niche. Each closed set of places is characterized by a certain composition of quasi-niches. But there is no stationary dynamics which keeps quasi-niches filled. The number of tokens in them may be increased only by mutations from other quasi-niches. Thus there are no opened or closed quasi-niches and no evolutionary stable dynamics. That is the main difference of quasi-evolution from eu-evolution. The absence of stationarity enforce us to consider the quasi-niche to be occupied only if it has at least some critical number of tokens.

In pre-biological evolution the number of objects in quasi-niches must be very low and comparable with the mutation rate. Only few of the most stable quasi-niches can accumulate a considerable number of objects, and even then the process of accumulation will take a large stretch of time. All these circumstances prevent the appearance of long chains of mutations leading across a number of quasi-niches. Thus quasi-evolution has limited scope if it will not turn into eu-evolution.

It is interesting that quasi-evolution became highly developed in biological systems due to its interaction with eu-evolution. For example, consider evolution of immune system in higher animals. The immune system is formed by selec-

tive propagation of plasmatic cells with special antigen receptors. But there is no real self-reproduction because plasmatic cells cannot proliferate infinitely. Their quality changes in this process and after several divisions they stop their reproduction. It is quite important for an organism, because real SRSs can escape from its control and will turn into a cancer. Development of immune reaction is a sort of quasi-evolution when some new quasi-niche becomes filled. There is a cascade of pseudo-reproduction which provides an amplifying effect, causing a global response of an organism to few antigens.

Learning is also a sort of quasi-evolution. It can be described as the filling of some mental quasi-niches which correspond to different algorithms of behavior (Edelman and Mountcastle, 1978). We do not know exactly what structures are propagated in the brain, but it seems that the process is very alike the immune reaction.

The question arises why quasi-evolution is so highly developed in living beings. The answer is that it has developed in the course of eu-evolution taking place on another structural level – the level of organisms. Internal quasi-evolution improves the adaptability of an organism and therefore it is supported by natural selection. Such combination of eu- and quasi-evolution operating on different structural levels may be called a hyper-evolution.

Social evolution is a kind of hyper-evolution. It comprises evolutionary processes on population, organism and sub-organism levels. There is a great variety of niches in human evolution: these are professions in the broad sense with all their social and matter surroundings. Producing of tools and machines is necessary for sustaining of certain human niches. For example, the car industry sustains the profession of a driver.

An essential feature of social evolution is that all new human niches have to be invented first, so they originate from mental quasi-niches. Here we see the highest interaction between two levels of evolution. Social evolution may spread to the super-organism level. Culture is the property of a big social group. These groups in the past were considerably isolated and thus

group selection was possible. Presently, I think human evolution goes mainly at organism and sub-organism levels.

## 7. Conclusion

The present mathematical formalism is very convenient for theoretical biology, especially for ecology and evolutionary biology. The majority of the most important ecological problems can be formulated using Petri nets. These are problems concerning the ecosystem structure, trophic nets, niche and ecosystem dynamics, evolutionary ecology.

The theory has significant applications in the field of global evolution. It can be used in biology, physics, linguistics, sociology and other branches of science for all systems which can be described by Petri nets. It allowed us to analyze three main modes of evolution: quasi-, eu- and hyper-evolution. Boulding (1981) and Csányi (1982) tried to develop such a synthesis using verbal models. Our approach may be considered as an attempt at mathematical explication of their ideas.

Unfortunately, at present the model cannot be used for simulation of systems with hierarchical structure. Therefore it is not suitable for description of group selection and hyper-evolution. It is quite important to develop a generalized variant of Petri nets for modeling hierarchically organized systems.

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## Appendix

**Theorem 3.** Any potential SRS can become a real SRS in a suitable kinetic system.

**Proof.** Let  $Q$  be a potential SRS in the Petri net. For each place  $p$  there must be an input transition  $t$  (with  $b_t = \emptyset$  and  $e_t = \{p\}$ ), and an output transition  $t'$  (with  $b_{t'} = \{p\}$  and  $e_{t'} = \emptyset$ ). If these transitions are absent, they must be added to the Petri net. According to the definition of potential SRSs there is a sequence of internal transitions for  $Q$  which leads to the increase of token numbers in all places of the set  $Q$ . Let the coefficient of the rate of each internal transition  $t$  be equal to the number of its entries ( $n_t$ ) in that sequence. The coefficient of the rate of input transition to each place  $p$  will be equal to  $\alpha$  and the coefficient of the rate of output transition from the place  $p$  will be equal to

$$\alpha + \sum_{t \in \text{In}(Q)} n_t (E_t(p) - B_t(p)) \quad (\text{A.1})$$

where  $\alpha$  is a positive constant, which is big enough for all output transitions to have positive coefficients according to (A.1). Coefficients of the rate of all the other transitions in the net will be assumed to be zero. Then the state of the

kinetic system with concentrations of all object species equal to 1 will be an equilibrium state. If it is not stable, the constant  $\alpha$  has to be increased until this state will become stable. It is possible, because the limit of the matrix of the linearized model, when  $\alpha$  is increased infinitely, is equal to  $-\alpha I$ , where  $I$  is a unity matrix, and therefore the characteristic values will have negative real parts.

**Lemma 2.** If for the set of places  $Q$  there is a sequence  $S_1$  of active transitions which increases the number of tokens in all places of this set, then  $Q$  is an autonomous set.

**Proof.** A closure of any set is closed, and thus the set  $Q$  satisfies the condition A1. According to the definition of a closure there is a sequence of sets  $U_1, U_2, \dots$ , such that  $U_1 = Q$ ,  $U_{i+1} = E(U_i)$  for all  $i$  and  $U_n = U_{n+1} = Q$ . Let  $U_0 = \emptyset$ . We shall define the rank  $\rho(p)$  of each place  $p \in Q$  as the greatest number  $i$  for which  $p \in U_i$ . The rank of the transition  $t \in \text{Ac}(Q)$  we define as the greatest rank of places in the set  $e_t$ . Let  $S_i$  be the sequence of all transitions of the rank  $i-1$ , which has at least one terminate place with the rank  $i$ . Execution of the sequence of transitions  $S_i$  where  $i = 1, \dots, n$  increases the number of tokens in all places of the rank  $i$  by

positive value  $w_p$  and never diminishes the number of tokens in the places with the rank greater than  $i$ . The sequence of transitions  $S$  which increases the number of tokens in all places of the set  $\bar{Q}$  has to contain in chain  $m_1$  copies of the sequence  $S_1, \dots, m_i$  copies of the sequence  $S_i, \dots$  and  $m_n$  copies of the sequence  $S_n$ . Let  $v_p$  be the number of tokens in the place  $p$  which are utilized when all transitions of the

rank greater or equal to  $\rho(p)$  taken from the sequence  $S$  have been executed. Numbers  $m_i$  are estimated one by one from  $m_n$  to  $m_1$  using the formulae:  $m_i = \text{Int}(x) + 2$ , where  $\text{Int}(x)$  is the integer part of  $x$  - the greatest value of  $v_p/w_p$  among the places  $p$  of the rank  $i$ . Thus, the condition A2 is satisfied and so  $\bar{Q}$  is an autonomous set.