Simple Model for the Formation of a Complex Organism

Barbara Drossel
Theoretical Physics Group, University of Manchester, Manchester M13 9PL, United Kingdom
(Received 18 November 1998; revised manuscript received 2 March 1999)

A simple model for the formation of a complex organism is introduced. Individuals can communicate and specialize, leading to an increase in productivity. If there are limits to the capacity of individuals to communicate with other individuals, the individuals form groups that interact with each other, leading to a complex organism that has interacting units on all scales. [S0031-9007(99)09463-6]

PACS numbers: 02.50.Le, 05.45.Df, 05.70.Ln, 87.10.+e

During the past years, physicists have begun to study complex systems like evolution, ecological systems, human civilization, and economics. The models introduced for this purpose are usually composed of units that interact according to a simple rule and produce a complex large-scale behavior. While these models are still far from a realistic description of the details of the systems under study, they are capable of reproducing some of their essential features. Thus, toy models for evolution can give rise to a power-law size distribution of extinction events [1–4], models for ecological webs generate several trophic layers of species [5,6], models for urban development produce a power-law size distribution of cities [7–9], and models for stock exchange [10] and company growth [11] show the scaling behavior characteristic for those systems.

Most of these models focus on one organizational level, like the formation of cities from interacting individuals, or the formation of food webs from interacting species of variable abundance. However, one important characteristic of complex organisms such as life on earth or human civilization is that they have interactions between units of various sizes. Thus, a biotope consists of several interacting species, a species of interacting individuals, and individuals of cells. Human civilization is structured into countries, which consist of cities, which consist of smaller units like quarters and families, etc.

Phenomena of aggregation and clustering are widespread even in inanimate nature. Thus, atoms may form stable clusters that preserve their identity when aggregating to build a quasicrystal [12]. Aggregation in colloids and aerosols can be successfully described using hierarchical models where clusters are repeatedly joined to form larger clusters [13]. Finally, on a cosmical scale interactions between galaxies within galaxy clusters are important for understanding the features of these clusters [14].

It is the purpose of this paper to introduce a model that produces a complex organism with interacting units on various organizational levels. Rather than trying to model a specific system in some detail (which is done in [15]), we choose a model that contains the essential ingredients in the simplest possible form. The first of these ingredients is the capability of structural units to interact or communicate and to specialize or differentiate, thereby increasing a quantity that is called "fitness" in biology or "utility" in economics, and that will be called "productivity" in this paper. This capability is acknowledged by biologists [16] as well as by authors that adopt an evolutionary view of economics [17,18] and societies [19]. Communication and differentiation alone, however, do not yet lead to several levels of organization. They simply lead to one large group of specialized individuals that has a high productivity. We have to take into account that the size of the groups is restricted due to the limited capacity of individuals to communicate and to travel. This restriction naturally leads to hierarchical structures with several organizational levels, as, for example, in the central place theory of human geography [20]. The reason is that as soon as several groups exist, these groups can communicate with each other *as groups*. In a human society, for instance, messengers are sent back and forth, roads are built, and goods are traded that an independent individual could neither produce nor make use of. This leads to a certain degree of specialization among groups, and to a further increase in productivity. This argument can now be iterated by noticing that groups have also a limited capacity to communicate or to interact. One then obtains supergroups and groups of supergroups, etc.

Taking the above-mentioned basic ingredients into account, we define our model in the following way: Let $P_1(n)$ be the productivity of a group of n individuals, and let $P_1(1)$ be negligible. For small n, the productivity of a given member increases with the number of partners with which it can communicate, the simplest analytical form being a linear law with a parameter g_1 that is the productivity per group member and communication partner. For larger n, the cost of communication must increase faster than this, and we may choose

$$P_1(n) = g_1 n(n-1) - c_1 n^2(n-1)\,, \qquad (1)$$

with $c_1 \ll g_1$. Such a law would, e.g., result if the communication cost was proportional to the number of partners and to the distance to each partner, and if the group extension grew linearly in n. The index 1 indicates that the parameters are associated with the first

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organizational level. The optimum group size, for which the productivity per individual is largest, is $n = (g_1 + c_1)/2c_1$. The maximum possible group size, for which the productivity is not yet negative, is $n = g_1/c_1$. The group size, above which a split into two independent groups of size $n/2$ increases the productivity, is $n = 2(g_1 + c_1)/3c_1$. For unequal splits, the productivity is smaller.

Now let us introduce interaction between groups. When the productivity of a partner group is larger, the gain g_2 per group member due to interaction with this partner will also be larger. Also, a larger group will put more energy into communication. We may therefore write for the total productivity of a "supergroup" consisting of I interacting groups

$$P_2(n) = \sum_{i=1}^{I} P_1(n_i) + g_2 \sum_{i \neq j} n_i P_1(n_j) - c_2 I(I - 1) \sum_{i=1}^{I} n_i \,. \tag{2}$$

The generalization to higher levels of organization is straightforward.

The parameters g_2 and c_2 must lie within certain limits for the model to be meaningful. The productivity of a supergroup that consists of only two interacting groups of ideal size (i.e., $I = 2$), should be of the same order of magnitude as the productivity of two independent ideal groups, leading to $g_2 \simeq c_1/g_1$. The parameter c_2 should not be much larger than $g_1^2/c_1 I$, if P_2 shall be positive for supergroup sizes I.

For the subsequent calculations we assume that the parameters are such that group and supergroup sizes n, I, etc., are large, and $n - 1$ and $I - 1$ can be replaced by n and I, making the analytical expressions simpler. The first term on the right-hand side of Eq. (2) can also be neglected, since it is by a factor $1/I$ smaller than the second term. Furthermore, since the productivity of interacting groups of equal size near the optimum size is larger than the productivity of interacting groups of different sizes (given the same total number of individuals), we assume that all groups, supergroups, etc., have approximately the same size. This is a kind of mean-field approximation. For a fixed total number of individuals, $N = \sum_{i=1}^{I} n_i$, the optimum number of groups is then obtained from the condition $(\partial P_2/\partial I)_N = 0$, leading to

$$-g_1 g_2 N^2 I + 2g_2 c_1 N^3 - 2c_2 I^4 = 0 \,.$$

For $N \ll g_1^4 g_2/c_1^3 c_2$, the last term can be neglected, leading to $I = 2c_1 N/g_1$, implying that the mean group size $\bar{n} = N/I$ is given by the optimum group size. However, when N and I become larger, the last term becomes important, and the mean group size increases.

The optimum values of N and I for supergroups are found from the conditions $(\partial P_2/\partial I)_N = 0$ and $[\partial(P_2/N)/\partial N]_I = 0$, leading to $N = 2g_1 I/3c_1$ and $I = 2g_1^3 g_2/27c_2 c_1^2$. The size of a group within an optimum supergroup is thus $4/3$ times the optimum size of an isolated group. The number of groups within a supergroup is of the same order as the number of individuals n within a group, if c_2 is of the order of $0.1g_1$. (Here, we used the previously derived condition that g_2 is of the order of c_1/g_1, or $1/n$.)

Next, let us estimate how the total productivity increases as a function of N. The productivity of a group of order k has the form

$$P_k = g_k I_k^2 I_{k-1} P_{k-1} - c_k I_{k-1} I_k^3 .$$

Here, I_1 is the number of individuals in a group, I_2 the number of groups in a supergroup, I_3 the number of supergroups in groups of supergroups, etc. The total productivity, divided by the total number of individuals $N = I_1 I_2 \cdots I_k$, is therefore of the order of $g_1 g_2 \cdots g_k N^2/I_k$. All I_k are of the same order, if g_2 to g_k are of the order c_1/g_1, and the c_k are of the order g_1^{2k-3}/c_1^{2k-4}. Then, P_k is of the order $g_1 N^2$, which is comparable to the productivity of a single large group that has no communication cost. The formation of a complex structure with groups and interactions at all levels is a very efficient way of keeping the total communication cost low. This bears some similarity with the formation of networks of rivers or blood vessels, where a hierarchical structure optimizes the drainage of water or the supply with oxygen and nutrients at a minimum cost for transport [21,22].

So far, we have discussed mainly systems where the productivity is globally optimized. However, a realistic system cannot probe all possible configurations in order to find the optimum, and furthermore it is not likely to make rearrangements that require the breaking and reconstruction of a large number of connections. As individuals are added, the growth of a complex organism will follow pathways that increase the productivity without going over larger "barriers," i.e., through large rearrangements. It can be expected that there exists a variety of different growth rules that, although they do not globally optimize productivity, lead to a complex organism of high productivity. The following three examples for explicit growth rules, and the numerical results (see Figs. 1–3) illustrate this: The parameters are for all simulations $g1 = 1, c1 = 0.1, g2 = 0.4, c2 = 0.2, g3 = 0.05$, and $c3 = 0.01$. They are chosen such that the group and supergroup sizes are small in order to facilitate the graphic representation of the growth process. In the first simulation (Fig. 1), individuals are added to a group as long as this increases the productivity of the group. Many isolated groups are formed simultaneously. Then, groups start communicating with each other and aggregate to supergroups. Supergroups grow until the addition of further groups no more increases the productivity of the supergroup. Then, supergroups start to aggregate. We also allow groups that are part of a supergroup to grow further if this increases the productivity of the supergroup. For the parameters used in the simulation, groups

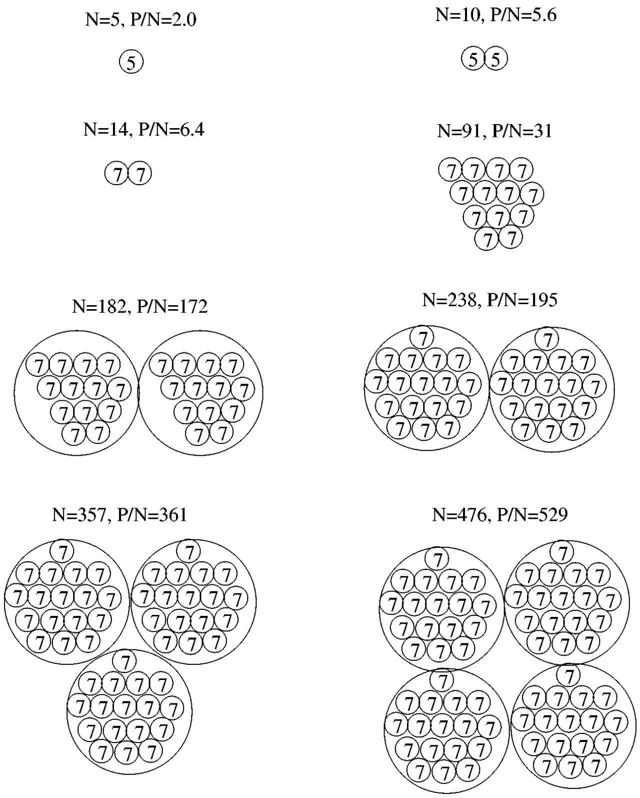

FIG. 1. Growth of the system for the first set of rules. The size n of groups is indicated by the numbers in the small circles. The large circles delimit supergroups. The parameters are $g1 = 1, c1 = 0.1, g2 = 0.4, c2 = 0.2, g3 = 0.05,$ and $c3 = 0.01$.

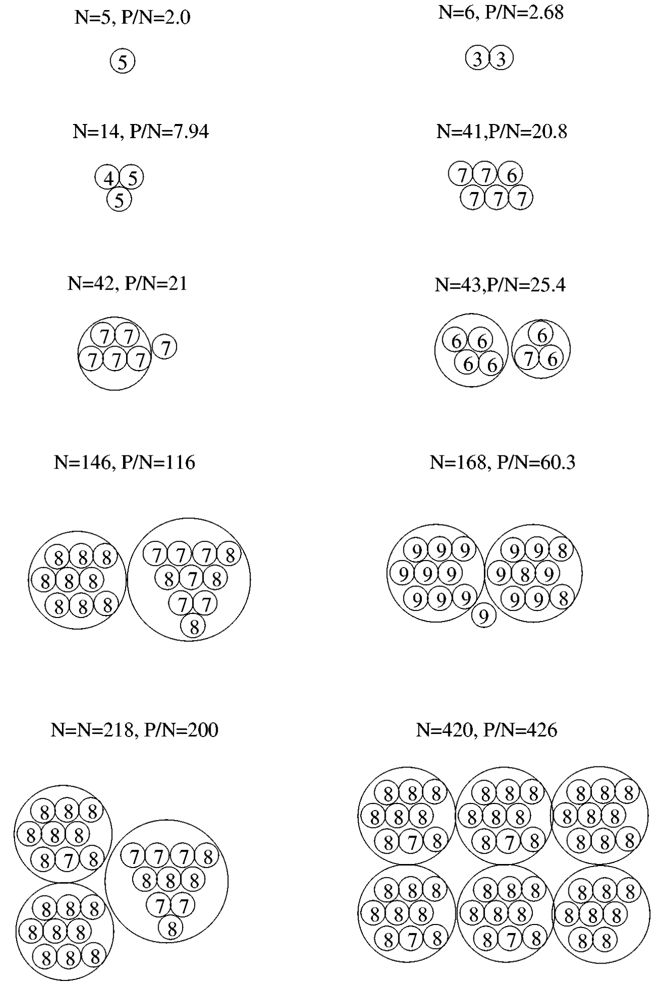

FIG. 2. Growth of the system for the second set of rules.

start to aggregate at size 5 and grow during aggregation further up to size 7. When isolated supergroups reach the size 13, they start communicating with each other to form groups of supergroups. The simulation was stopped at this stage to allow for an easy graphical representation of the result. If it was continued by adding more individuals, several supergroups would form and aggregate to even larger units, etc., thus producing an even higher hierarchy of organizational levels.

In the second simulation (Fig. 2), we grow a complex organism by adding individuals to it. We do not assume that other groups are formed elsewhere that can later get in touch with each other. We allow that individuals move to other groups, if this increases the productivity. Thus, when a new individual is added, it may either join one of the groups, or another individual that is part of a group may join the newly added individual to open a new group, if this increases the productivity. Once a new small group is started, further individuals from larger groups can join it and increase the productivity further. This happens for the parameters used in the simulations when the 6th individual is added. Similarly, we allow a group to split off a supergroup to open a new supergroup (this can be seen in Fig. 2 for $N = 42$ and $N = 168$), and we allow groups to move from one supergroup to another, if this increases the productivity (see, e.g., the step from $N = 42$ to $N = 43$ in Fig. 2). Thus, all moves of single units (individuals, groups, etc.) are allowed that increase the productivity.

In the third simulation (Fig. 3), we also grow a single organism by repeatedly adding individuals to it. As soon as this increases the productivity, the initial group splits into two groups of equal size (this happens in Fig. 3 for $N = 6$). Further individuals are added, until it becomes favorable to perform a reconstruction into three groups of equal size, etc. As the number of groups increases, the cluster of groups splits into two supergroups of equal size, as soon as this increases the productivity (at $N = 38$ in Fig. 3), etc. Among the three rules, the last rules produce the system with the highest productivity, since it allows for the largest rearrangements.

The three sets of rules together illustrate the many possible dynamical pathways that can lead to the formation of a complex organism. This indicates that the formation of a complex organism is a generic phenomenon that can occur under fairly general conditions. The main

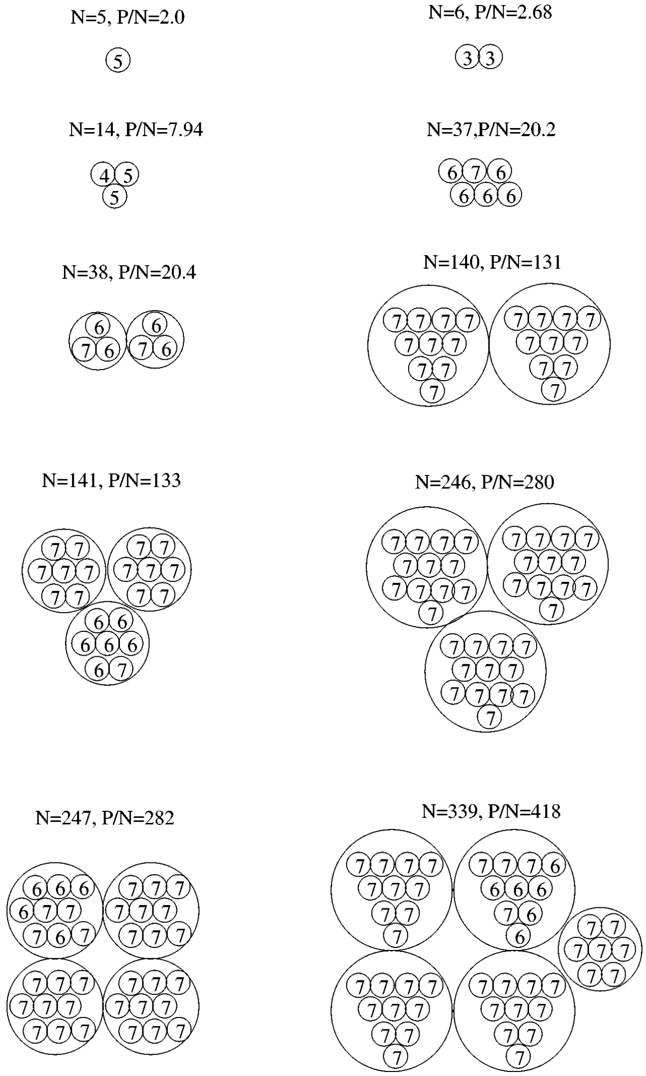

FIG. 3. Growth of the system for the third set of rules.

requirements are that communication increases the productivity, and that the cost of communication exceeds the benefit if too many units are involved. The specific expressions Eqs. (1) and (2) were chosen for their simplicity; however, many other forms of the productivity function are possible.

The model discussed in this paper assumes that all individuals and groups are essentially equal. This is expressed, e.g., by the fact that the parameters c_k and g_k are the same for all groups. One can expect that a release of this restriction will still lead to the formation of a complex organism. Also, the parameters of a complex organism may change with time, which should not destroy the complexity either.

The model presented here does not explicitly take into account that a sufficiently large density of individuals is required for group formation to occur. In the simulations, it was simply assumed that enough individuals are around (or being born) for growth to continue. It would be straightforward to include an explicit dependence on distance in the communication cost, and to allow for the motion of individuals in space. These spatial degrees of freedom were not considered in the present model to make the basic mechanism for the increase in complexity more transparent.

In spite of its simplicity, this model agrees with recent results for complex ecological webs [6]. Explicit models for the interaction between several species show that the web becomes stable if there is a sufficient number of weak links. This condition is naturally satisfied by the model presented in this paper, since each individual interacts strongly only with the individuals in the same group, but weakly with the rest of the system through links between groups.

I thank H. Bokil, M. E. J. Newman, and J. Vaario for comments and hints to the literature. This work was supported by EPSRC Grant No. GR/K79307.

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