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LIFE HISTORY EVOLUTION AND THE ORIGIN OF MULTICELLULARITY: THE CASE OF DIFFERENT TYPES OF CELLS

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The problem of the unicellular-multicellular transition is one of the main issues that is discussing in evolutionary biology. In [1] the fitness of a colony of cells is considered in terms of its two basic components, viability and fecundity. Intrinsic trade-off function of each cell defines a type of cell. We elaborate models providing in [1]. Assuming that all intrinsic trade-off functions are linear, we construct a model with different cell types and show that the differentiation of these cell types leads to full specialization. In addition, we attempt to consider the fact that environmental factors influence the fitness of the colony. Thus, we introduce an energy restriction to the model and show that the situations can be observed where some cells continue to be specialized while other cells become indifferent between the states in which they can be specialized or unspecialized. It is worth pointing out that the models from [1] are not robust. We try to overcome this disadvantage.

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1. Introduction

The problem of the unicellular-multicellular transition is one of the main issues that is discussing in evolutionary biology. It is necessary to know how colonial organisms transformed into multicellular organisms and what preconditions underlie this transition.

The separation of a body's tissues is the main characteristic of a multicellular organism. This separation means that the majority of the cells in this organism is specialized for one function and loses the potential ability to specialize for other functions.

Some cells in a colonial organism may be specialized for specific functions but may not lose the ability to specialize elsewhere. If conditions that lead the colony to full specialization are performed over a long period of time, it is possible that the unicellular-multicellular transition will occur. Therefore, it is important to determine the conditions that contribute to the full specialization of a colonial organism. For example, it is reasonable to suspect that different cell types may cause full specialization. Another interesting question is the influence of environmental factors on the colony's behavior. We introduce these environmental factors into the model in the form of the total energy constraints consumed by considering colony of cells.

In [1] the model has been illustrated on the example of volvocales green algae. These are flagellated photosynthetic organisms with coherent glycoprotein cell walls and represent the most appropriate system in research of the process of transition under study, because Volvocales linage ranges from the single-cell organisms to undifferentiated, soma-differentiated and germ-soma differentiated organisms arranged according to the size of the colony. Volvocales live in standing waters and so need flagellar beating in order to move toward light and nutrients. Therefore motility is an important factor contributing to viability of Volvocales [2]. Volvocales' type of cell division represents palintomy with multiple fission. Also, useful fact is that the species with increased cell specialization do not have a single origin.

We should note that fundamental models investigated the problem of unicellular – multicellular transition were provided in [1]. These models best illustrate evolution of Volvocalean Green Algae but they may be applied to other lineages as well. That fundamental work [1] provided models which show how cells are specialized. However, the results look non-robust. Because of the identity of all cells in the colony assumed in [1], in optimum it does not matter which cells belong to the sets of soma-specialized cells or germ-specialized cells. So, if we change slightly some characteristics that not reflected explicitly in the model, sets of germ and soma-specialized cells changes – the model only requires that the ratio between their cardinality should remain constant. Thus, small changes in parameters may force soma-specialized cell become germ-specialized immediately. In linear case this non-robustness also lies in a fact that no more than the half cells can be soma-specialized and no more than the half cells can be germ-specialized. These facts have attracted our attention and we provide a new model to overcome above mentioned non-robustness of this beautiful model developed in [1].

Structure of the text

We begin with the model, provided in [1] and describe it in Section 2. Then in Section 3 we propose the model with different cell types, extend this model taking into account energy constraints in Section 4. In section 5 we give a short survey of related works. Section 6 concludes.

2. A survey of the models

In [1], the authors attempt to construct models that explore the fitness trade-offs at both the cell and group levels during the unicellular-multicellular transition. Thus, fitness is considered in terms of its two basic components: viability and fecundity. In [1], the trade-off function (1) is studied, which reflects the intrinsic relationships that link viability and fecundity within the cell due to cell physiology and other constraints.

Let *v* be viability and *b* represents fecundity. Then:

$$v = v_{max} - \alpha * b. \qquad (1)$$

In [1], the authors noted that in unicellular organisms, the cell must contribute to both of the fitness components. In multicellular groups, each cell may be unspecialized, such as in unicellular organisms, or, in contrast, may specialize only in the germ or only in the soma. This fact can lead to the formation of germ – soma (“G-S”) specialization, in which some cells lose their autonomy in favor of the group and, as a result, their fitness and individuality are transferred from the cell level to the group level. In [1], cases in which “G-S” specialization may occur are studied. It is noted as well that the models that are presented in [1] are most applicable to volvocine green algae.

There are two types of models that are considered in [1]: the fitness isocline model and the full optimization model. We discuss only the second model because this model is more general than the fitness isocline model. In the full optimization model, all of the cells are considered simultaneously, and the strategic purpose of the colony is to maximize its fitness. Below, we describe this model in detail to emphasize its advantages and disadvantages and attempt to improve it.

2.1. Full optimization model

Consider a colony consisting of N cells, $i = 1 \dots N$– indices of cells in the colony, b_i –resulting contribution of cell i to the fecundity of the group, v_i – viability-enhancing capability of cell i.

The fitness trade-off function (continuous and determined on a convex hull) is more common than a linear function and should be the same for all of the cells from the colony,

$$v_i = v(b_i). \tag{2}$$

The group’s level of fecundity is an additive function of variable b_i. The group’s level of viability is an additive function of variable v_i,

$$B = \sum_{i=1}^{N} b_i\,; \quad V = \sum_{i=1}^{N} v_i. \tag{3}$$

In [1], it is assumed that the group fitness, which we should maximize, is the product of the group viability and fecundity,

$$W = V * B. \tag{4}$$

In [1], the problem of choosing the correct form of the group fitness function is also discussed. This type of function (4) is based on simple intuition. For instance, imagine that one cell in the group has a high level of fecundity but low viability, and another cell is strictly the opposite, with a high level of viability and low fecundity. Each of these cells by itself would have a low fitness, but together they can achieve a high fitness for the group. Function (4) considers this reasoning in contrast to, for example, the average cell fitness (5):

$$W = \frac{1}{N}\sum_{i=1}^{N} b_i * v_i \tag{5}$$

However, we should note that most of the qualitative points which were made in [1] would still hold even if the fitness submitted a more general function with special properties.

In general, the full optimization model can be written formally as a type of optimization problem (6):

$$\begin{cases} W = \sum_{i=1}^{N} b_i * \sum_{i=1}^{N} v_i \rightarrow max_{b,v} \\ \forall i = 1..N: v_i = v(b_i), \\ b \geqq 0, \\ v \geqq 0. \end{cases} \tag{6}$$

Assume that there is no initial cost of reproduction in the model. In this case, the following results are true:

1. If the function $v(b)$ is strictly concave, then the group of cells should remain unspecialized.

2. If the function $v(b)$ is linear ($v = v_{max} - \alpha * b$), then the group of cells behaves as if there was just one cell; therefore, each cell is indifferent to specialization.

3. If the function $v(b)$ is strictly convex, then the group of cells aims for full specialization. In addition, if there is an even number of cells in the group, then half should specialize in the germ and a half in the soma. If there is an odd

number of cells in the group, $\left[\frac{N}{2}\right]$ of these cells should specialize in the germ, $[\frac{N}{2}]$ should specialize in the soma and one cell should remain unspecialized.

An initial investment is necessary for reproduction. This investment requires an additional spending of energy, which can lead to the appearance of initial costs of reproduction that can be considered within the trade-off function. The initial costs of reproduction lead to full specialization in linear and convex cases of improving the model and provide the opportunity for specialization in the concave case of the full optimization model.

Despite all of the fundamental results of the full optimization model, there are a wide variety of problems that cannot be solved using this model and some disadvantages that are connected strictly with biological processes that this model cannot describe. For instance,

1. The full optimization model does not explain why the cells are jointed into a group and exist in this state instead of continuing to exist separately.
2. The separate form of the fitness function of the group is appropriate in some cases; therefore, it is necessary to obtain results that are robust for any group fitness function to determine the general function.
3. All of the cells in the colony should be identical.
4. There are no energy constraints in the model.
5. The full optimization model is static. A dynamic optimization model exists because we allow cells the opportunity to change their levels of fecundity and viability during the colony’s lifecycle.

In this article, we attempt to construct a model that is based on two important assumptions:

1. Cells within the colony are of different types (different intrinsic trade-off functions).
2. There are some power restrictions in the considered biological system.

In Section 2 the linear model, which satisfies only the first assumption, is studied. In Section 3, we construct the model that satisfies both of the specified assumptions.

3. Full optimization model with different cell types

3.1. Formulation of the problem

In the full optimization model, all of the cells in the colony should be identical, meaning that they have the same intrinsic trade-off fitness functions. However, it may be more reasonable to assume that some subsets of cells within the group are different and that all of the cells belonging to selected subsets have the same trade-off functions.

In order to simplify our analysis we suggest that all of the cells in the colony are unique (this type of model can be easily transformed into the previous one).

Consider a group of N cells, $i = 1 \dots N$ – indices of cells in the colony, b_i – level of fecundity of cell i, v_i – viability of cell i.

The group's level of fecundity is an additive function of variable b_i. The group's level of viability is an additive function of variable v_i,

$$B = \sum_{i=1}^{N} b_i\,; \quad V = \sum_{i=1}^{N} v_i. \tag{7}$$

We agree with [1] and continue to apply type (8) of the group fitness functions because this function reflects the synergetic effects of jointly existing cells in the colony,

$$W = V * B. \tag{8}$$

The main extension of the model from [1] is that each cell has its own parameters of the trade-off function. Additionally, we assume that each individual's trade-off function is linear,

$$\forall i = \overline{1,N}\colon v_i = v_i^{max} - \alpha_i * b_i, \tag{9}$$
$$\forall i = \overline{1,N}\colon \alpha_i \geq 0,$$
$$\forall i = \overline{1,N}\colon v_i^{max} > 0.$$

The main assumption of the full optimization model with different types of cells (strong differentiation of types) is as follows:

$$\alpha_i \neq \alpha_j, \text{ for any } i, j \in \{1, .., N\}, i \neq j. \tag{10}$$

We use formula (10) because it presents the pure form of the differentiation of types in the model and because models with other types of differentiation can be easily transformed in this formula.

Therefore, we can construct the model as a classic optimization model with constraints,

$$\begin{cases} W = \sum_{i=1}^{N} b_i * \sum_{i=1}^{N} v_i \rightarrow max_{b,v} \\ \forall i = \overline{1,N}: v_i = v_i^{max} - \alpha_i * b_i, \\ \qquad \forall i = \overline{1,N}: b_i \geq 0, \\ \qquad \forall i = \overline{1,N}: v_i \geq 0. \end{cases} \tag{11}$$

Additionally, we note that this optimization problem can be transformed into a more convenient form (12):

$$\begin{cases} W = \sum_{i=1}^{N} b_i * \sum_{i=1}^{N} v_i \rightarrow max_{b,v} \\ \forall i = \overline{1,N}: v_i = v_i^{max} - \alpha_i * b_i, \\ \qquad \forall i = \overline{1,N}: b_i \geq 0, \\ \qquad \forall i = \overline{1,N}: v_i \geq 0. \end{cases}$$
$$\leftrightarrow \begin{cases} W = \sum_{i=1}^{N} b_i * \sum_{i=1}^{N} (v_i^{max} - \alpha_i * b_i) \rightarrow max_b \\ \qquad \forall i = \overline{1,N}: 0 \leq b_i \leq b_i^{max}. \end{cases} \leftrightarrow$$
$$\leftrightarrow \begin{cases} W = \sum_{i=1}^{N} b_i * (\sum_{i=1}^{N} v_i^{max} - \sum_{i=1}^{N} \alpha_i * b_i) \rightarrow max_b \\ \qquad \forall i = \overline{1,N}: 0 \leq b_i \leq b_i^{max}. \end{cases} \tag{12}$$

Thus, we should maximize the polynomial of degree two, determined in the hyper parallelepiped in the R^n space. We should analyze the solution to this problem to reveal the optimal behavior of each cell in the group.

3.2. *An analysis of the model*

In this subsection, we provide some propositions that show the nature and important properties of the solution to the optimization problem (12). To correctly describe the characteristics of the solution, we should enter a useful formalism.

Definition 1. Let $\mathcal{P}$ be the class of optimization problems. $p \in \mathcal{P}$ if and only if p is an optimization problem whose form is represented below:

$$\begin{cases} W_p = \left(\sum_{i\in I_1} b_i^{max} + \sum_{i\in I_3} b_i\right) * \left(\sum_{i\in I_2} v_i^{max} + \sum_{i\in I_3} v_i^{max} - \sum_{i\in I_3} \alpha_i * b_i\right) \to max_{b_i, i\in I_3} \\ \forall i \in I_3 \colon 0 \le b_i \le b_i^{max}. \end{cases} \tag{13}$$

$$\text{where } \begin{cases} I_1 \subset \{1,..,N\}; I_2 \subset \{1,..,N\};\ I_3 \subseteq \{1,..,N\}, \\ |I_1| + |I_2| + |I_3| = N, \\ |I_3| \ge 1. \end{cases} \tag{14}$$

Therefore, any task p from class $\mathcal{P}$ has a form (13) and is determined by a triplet sets $\left(I_1^p, I_2^p, I_3^p\right)$ satisfying the conditions (14). For example, problem (12), which is the formal description of the full optimization problem with different types of cells, also belongs to class $\mathcal{P}$ and is matched to the triplet $(\emptyset, \emptyset, \{1,..,N\})$ (denoted as PP).

Additionally, it is necessary to define some sets that will be useful below:

$$F_p = \left\{b \in R^{I_3^p} \colon 0 \le b_i \le b_i^{max}, \forall i \in I_3^p\right\}, p \in \mathcal{P},$$

$$H_p = \{b \in R^N \colon 0 \le b_i \le b_i^{max}, \forall i \in I_3^p;\ b_i = b_i^{max}, \forall i \in I_1^p; b_i = 0, \forall i \in I_2^p\}, p \in \mathcal{P},$$

$$\mathcal{H} = \{H_p, p \in \mathcal{P}\},$$

$$\mathcal{L} = \{H_p, |I_3^p| = 1\}.$$

$F = \{b \in H_{PP}: \exists l \in \mathcal{L},$.

b is a conditional stationary point of the problem $\begin{cases} W_p(b) \rightarrow max \\ b \in l \end{cases}$

Theorem 1. Suppose that assumption (10) is true. Let b^* be the solution to problem (12). Then, the following statement is true:

$$\big(b^* \in Vert(H_{PP})\big) \vee (b^* \in F). \tag{15}$$

In other words, it means, that in the optimum there can be no more than the one unspecialized cell in the colony. The proof of Theorem 1 is provided in Appendix A.

As a result of Theorem 1, in the optimum, there is no more than the one unspecialized cell. Furthermore, there cannot be a situation where all of the cells in a group are soma-specialized or germ-specialized. Thus, we show that cell differentiation in linear cases leads to full specialization, while in linear cases in [1] the cells are indifferent to specialization.

4. Full optimization model with an energy restriction and different types of cells

4.1. Formulation of the problem

All of the previous models have a serious disadvantage: environmental factors do not directly influence the fitness of a colony. Suppose the colony has some way of obtaining energy from available resources. Let C be the level of the energy that is available to the colony by using a fixed way of obtaining energy and fixed environmental characteristics. It is necessary to have k_1 units of energy in order to construct a unit of fecundity and k_2 units of energy in order to support a unit of viability. Considering these judgments, we can construct an energy restriction as follows:

$$k_1 * \sum_{i=1}^{N} b_i + k_2 * \sum_{i=1}^{N} v_i \leq C, \text{where } k_1 > 0, k_2 > 0, C > 0. \tag{16}$$

Using this relationship, we obtain a full optimization model with an energy restriction and different types of cells.

$$\left\{\begin{array}{c} W = \sum_{i=1}^{N} b_i * \sum_{i=1}^{N} v_i \to max_{b,v} \\ \forall i = 1..N: v_i = v_i^{max} - \alpha_i * b_i, \\ k_1 * \sum_{i=1}^{N} b_i + k_2 * \sum_{i=1}^{N} v_i \le C, \\ \forall i = 1..N: v_i \ge 0, \\ \forall i = 1..N: b_i \ge 0. \end{array}\right. \to$$

$$\left\{\begin{array}{c} W(b) = \sum_{i=1}^{N} b_i * \sum_{i=1}^{N} (v_i^{max} - \alpha_i * b_i) \to max_b \\ k_1 * \sum_{i=1}^{N} b_i + k_2 * \sum_{i=1}^{N} (v_i^{max} - \alpha_i * b_i) \le C; \\ \forall i = 1..N : 0 \le b_i \le b_i^{max}. \end{array}\right. \quad (17)$$

The energy restriction can significantly influences the behavior of the colony in the model. However, assume that this restriction allows colony to exist.

4.2. An analysis of the model

In this chapter, we provide some propositions that show the nature and important properties of the solution to optimization problem (17). Problem (17) is a task in which we should maximize a continuously differentiable function in a truncated hyper parallelepiped.

First of all, it is necessary to determine the sets that will be useful below.

$$M = \left\{ b \in R^N : k_1 * \sum_{i=1}^{N} b_i + k_2 * \sum_{i=1}^{N} (v_i^{max} - \alpha_i * b_i) = C \right\},$$

$$M_1 = \left\{ b \in R^N : k_1 * \sum_{i=1}^{N} b_i + k_2 * \sum_{i=1}^{N} (v_i^{max} - \alpha_i * b_i) \leq C \right\},$$

$$Q = F \cap M_1,$$

$$R = \left\{ b \in H_{PP} : b - \text{is a stationary point of the problem } \begin{cases} W(b) \to max_b \\ b \in M \end{cases} \right\}.$$

Theorem 2

Let $b^* \in R^N$ be the solution to problem (17). Then, the following statement is true:

$$(b^* \in Vert(H_{PP}) \cap M_1) \vee (b^* \in Q) \vee \left[\left(b^* \in Vert(H_{PP} \cap M) \right) \wedge (R = \emptyset) \right] \vee [(b^* \in R) \wedge (R \neq \emptyset)] \tag{18}$$

Generally speaking, this theorem determines the location of the optimal point and claims that there can be only three cases, each of them can be realized depending on the values of parameters of the model:

1. All cells in the colony are specialized: some in soma, some in germ.
2. There is the one unspecialized cell in the colony.
3. There exist a set of states, each of them allows colony to achieve the same maximum level of fitness. In some states this cell may be specialized, in some - unspecialized.

We can point out as well that the result of the full optimization model with different types of cells is robust. Indeed, small variation of parameters, which are not reflected explicitly in the model, cannot lead to sharp changes in the solution. The solution either does not change (as in the cases 1 and 2) or change slightly (as in the case 3 due to the fact that optimal set of states is connected). Also, more than half of the cells may specialize in soma or in germ.

The proof of Theorem 2 is provided in Appendix B.

According to the Theorem 1, in some cases we can get an energetic estimation of the optimal value of fitness function:

Let $b^* \in R^N$ be the solution to problem (17). Suppose $R \neq \emptyset$. Then, $W(b^*) \geq \frac{C^2}{4*k_1*k_2}$, meaning that under some circumstances, if the colony has the available level C of the energy, this energy can be transformed into no less than $\frac{C^2}{4*k_1*k_2}$ units of fitness.

Therefore, in the full optimization model with different types of cells, all of the cells in the colony aspire to full specialization, except perhaps one. If we add an energetic restriction to the model, we can model situations where some cells continue to be specialized while other cells become indifferent between states in which they can be specialized or unspecialized. Thus, in some cases, in this model we can obtain a few sets of cell states, each of which can be realized as a solution to the model and each of which yields the same optimal level of colony fitness.

5. A survey of the literature

There are a lot of papers devoted to the problem of unicellular–multicellular transition in terms of fitness and its two basic components – fecundity and viability. Here we provide short descriptions of some articles which characterize precisely main developments in discussed issues.

In [2] the problem of transition from unicellular to multicellular organism is studied using some physical assumptions concerning different processes in the organism in terms of physical laws, for example, hydrodynamic laws.

In [3] very general mathematical model about the division of labor is introduced. The main assumption of the model is that modules can contribute to two different tasks, which connected by a trade-off. It is shown that three factors favor that division of labor – positional effects, accelerating performance functions and interaction between modules.

In [4] the models of social choice have been applied to the problem under study. It has been shown that applying axiomatic approach allows constructing different social welfare functions describing the types of fitness-ranking on the set of alternatives, representing all states of the world that are relevant for considering group. Authors suggest to apply extensive social welfare functions and their axiomatic to describing fitness-functions of colonies and show that this axiomatic doesn’t contradict the fact that transition from unicellular to multicellular organism accompanies to replacing concavity by convexity in trade-offs.

In [5] authors investigate diversity in Volvocalean green algae in terms of process of transition to multicellularity. Authors show that costs of reproduction plays an important role in the evolution of multicellularity in Volvocales. Suggesting model allows explaining the GS – GS/S – G/S form of process of transition to multicellularity.

6. Conclusion

We have explored the fitness trade-offs between the basic components of survival and reproduction at both the cell and group levels during the unicellular-multicellular transition. We have considered a model that describes a colony in which each cell has its own type, reflected in the difference between the intrinsic trade-off functions of the cells (the model, in which some subsets of cells have different types, can be reduced to the model in which each cell has its own type). Note that in the considered version of the full optimization model with different types of cells, all of the intrinsic trade-off functions should be linear. As a result, in the optimum, there is no more than the one unspecialized cell. Furthermore, there cannot be a situation where all of the cells in a group are soma-specialized or germ-specialized. Thus, we have shown that cell differentiation in linear cases leads to full specialization, while in classic linear cases (without the differentiation of types), the cells are indifferent to specialization. Therefore, the difference in the types of cells leads to specialization in the model. Additionally, we noticed that the previous model has a serious disadvantage: environmental factors do not directly influence the fitness of a colony. Therefore, we introduced a power restriction to the model and explored the full optimization model with a power restriction and different types of cells. As a result, we can model situations in which some cells continue to be specialized while other cells become indifferent between states in which they can be specialized or unspecialized. Thus, in some cases using this model, we can obtain a few sets of cell states, each of which can be realized as a solution to the model and each of which yields the same optimal level of colony fitness.

Appendix A

Proof of Theorem 1. First, consider a lemma.

Lemma 1. For each $p \in \mathcal{P}, \left|I_3^p\right| > 1$, let $b_p \in IntF_p$; then, b_p cannot be a solution to optimization problem p.

Proof. Choose any $p \in \mathcal{P}, \left|I_3^p\right| > 1$. Let $b_p \in IntF_p$. Suppose b_p is a solution to optimization problem *p*.

1. $W_p(b_p) \geq W_p(b), \forall b \in F_p,$ because b_p is a solution to optimization problem *p*.

2. $\exists U_\varepsilon(b_p) \subset F_p : W_p(b_p) \geq W_p(b), \forall b \in U_\varepsilon(b_p),$ because b_p is a solution to optimization problems p and $b_p \in IntF_p$. Therefore, b_p is a local extremum point of function W_p.

3. Because W_p is a continuously differentiable function on the entire domain, the necessary condition for a local extremum of the function W_p at b_p has the form $\nabla W_p(b_p) = 0$.

$$\nabla W_p(b_p) = 0 \leftrightarrow$$

$$\leftrightarrow \frac{\partial W}{\partial b_j}(b_p) = \left(\sum_{i\in I_2} v_i^{max} + \sum_{i\in I_3} v_i^{max} - \sum_{i\in I_3} \alpha_i * b_i^p\right) - \alpha_j * \left(\sum_{i\in I_1} b_i^{max} + \sum_{i\in I_3} b_i\right) = 0, \forall j \in I_3;$$

$$\sum_{i\in I_3}(\alpha_i + \alpha_j) * b_i^p = \left(\sum_{i\in I_2} v_i^{max} + \sum_{i\in I_3} v_i^{max} - \alpha_j * \sum_{i\in I_1} b_i^{max}\right), \forall j \in I_3;$$

We obtain the system of the $\left|I_3^p\right|$ linear equations. Because $\left|I_3^p\right| > 1$, we can choose two linear equations: *j*,*k*.

$$\begin{cases} \sum_{i\in I_3}(\alpha_i + \alpha_j) * b_i^p = \left(\sum_{i\in I_2} v_i^{max} + \sum_{i\in I_3} v_i^{max} - \alpha_j * \sum_{i\in I_1} b_i^{max}\right) \\ \sum_{i\in I_3}(\alpha_i + \alpha_k) * b_i^p = \left(\sum_{i\in I_2} v_i^{max} + \sum_{i\in I_3} v_i^{max} - \alpha_k * \sum_{i\in I_1} b_i^{max}\right) \end{cases}$$

Subtract the second equation from the first equation, and note that assumption (10) is true.

$$\sum_{i\in I_3}(\alpha_j-\alpha_k)*b_i^p=-(\alpha_j-\alpha_k)*\sum_{i\in I_1}b_i^{max}$$

$$(\alpha_j-\alpha_k)*\left(\sum_{i\in I_3}b_i^p+\sum_{i\in I_1}b_i^{max}\right)=0$$

$$\sum_{i\in I_3}b_i^p=-\sum_{i\in I_1}b_i^{max}<0\to\exists i\in I_3: b_i^p<0\to b_p\notin F_p$$

We have a contradiction; therefore, b_p cannot be a solution to optimization problem p. Lemma is proved.

Now we prove Theorem 1. Consider the optimization problem (12).

1. If N=1, then, obviously, the statement (15) is true.

2. Suppose N>1. Then, optimization problem (12) belongs to the class $\mathcal{P}$. Consider a point $b\in Int(H_{PP})$, (note, that $H_{PP}=F_{PP}$). According to Lemma 1, b cannot be a solution to optimization problem (12); therefore, the solution to (12) is ∂H_{PP}.

Consider the behavior of function W in ∂H_{PP}. Choose one variable and prescribe it the value 0 or b_i^{max}. Thus, we describe a set $\partial H_{PP}=\bigcup_{p\in\mathcal{P}:|I_3^p|=N-1}H_P$. Therefore, we obtain tasks, each of which would be equivalent to some $p\in\mathcal{P}:\left|I_3^p\right|=N-1$. According to Lemma 1, for each task $p\in\mathcal{P}:\left|I_3^p\right|=N-1$, for all $b\in ReInt(H_P)$, it follows that b is not a solution of a problem (12). Therefore, we should find the solution to (12) in the set $\bigcup_{p\in\mathcal{P}:|I_3^p|=N-2}H_P$ where our conclusions are similar. We should repeat our procedure until we obtain tasks in the edges and vertexes of H_{PP}. The solution to (12) belongs to the vertexes or edges of hyper parallelepiped (12), therefore,

$$\left(b^*\in Vert(H_{PP})\right)\vee(b^*\in F),$$

Q.E.D.

Appendix B

Proof of Theorem 2. First, consider a lemma.

Lemma 2. Consider optimization problem (19):

$$\begin{cases} W(b) = \sum_{i=1}^{N} b_i * \sum_{i=1}^{N} (v_i^{max} - \alpha_i * b_i) \to max_b \\ k_1 * \sum_{i=1}^{N} b_i + k_2 * \sum_{i=1}^{N} (v_i^{max} - \alpha_i * b_i) = C, \\ \forall i = 1..N\colon 0 \le b_i \le b_i^{max}. \end{cases} \tag{19}$$

Let $b^{**} \in R^N$ be the solution to problem (19). Then, the following statement is true:

$$[(b^{**} \in Vert(H_{PP} \cap M)) \wedge (R = \emptyset)] \vee [(b^{**} \in R) \wedge (R \neq \emptyset)] \tag{20}$$

Proof. First, look at the class of optimization problems $\mathcal{U}$. Each $u(I_1^u, I_2^u, I_3^u) \in \mathcal{U}$ has a type (21) (where $I_1^u \subseteq \{1,..,N\}, I_2^u \subset \{1,..,N\}, I_3^u \subset \{1,..,N\}\colon\ |I_1^u| + |I_2^u| + |I_3^u| = N;\ |I_3^u| \ge 2$):

$$\begin{cases} W_u(b) = \left(\sum_{i \in I_1^u} b_i^{max} + \sum_{i \in I_3^u} b_i\right) * \left(\sum_{i \in I_2^u} v_i^{max} + \sum_{i \in I_3^u} v_i^{max} - \sum_{i \in I_3^u} \alpha_i * b_i\right) \to max_{b_i, i \in I_3^u} & (21.1) \\ k_1 * \left(\sum_{i \in I_1^u} b_i^{max} + \sum_{i \in I_3^u} b_i\right) + k_2 * \left(\sum_{i \in I_2^u} v_i^{max} + \sum_{i \in I_3^u} v_i^{max} - \sum_{i \in I_3^u} \alpha_i * b_i\right) = C & (21.2) \end{cases}$$

Each $u(I_1^u, I_2^u, I_3^u) \in \mathcal{U}$ represents a task of maximizing the function of the appropriate form (21.1) on the hyper plane of the appropriate form (21.2) in $R^{|I_3^u|}$ space. We choose and fix every

$u(I_1^u, I_2^u, I_3^u) = u(I_1, I_2, I_3) \in \mathcal{U}$ and simplify the form of optimization problem *u*.

$$\begin{cases} B(b_i | i \in I_3) * V(b_i | i \in I_3) \to max_{b_i, i \in I_3} & (22.1) \\ k_1 * B(b_i | i \in I_3) + k_2 * V(b_i | i \in I_3) = C & (22.2) \end{cases} \tag{22}$$

$$\begin{cases} w\big(B(b_i|i \in I_3)\big) = B(b_i|i \in I_3) * \big(\mathrm{C} - k_1 * B(b_i|i \in I_3)\big) \to max_{b_i, i \in I_3} \\ k_1 * B(b_i|i \in I_3) + k_2 * V(b_i|i \in I_3) = C \end{cases},$$

$$\text{where: } \begin{cases} B(b_i|i \in I_3) = \left(\sum_{i \in I_1} b_i^{max} + \sum_{i \in I_3} b_i\right) \\ V(b_i|i \in I_3) = \left(\sum_{i \in I_2} v_i^{max} + \sum_{i \in I_3} v_i^{max} - \sum_{i \in I_3} \alpha_i * b_i\right) \end{cases}$$

This task is related to the problem below:

$$f(b_i|i \in I_3) = w\big(B(b_i|i \in I_3)\big) = B(b_i|i \in I_3) * \big(\mathrm{C} - k_1 * B(b_i|i \in I_3)\big) \to max_{b_i, i \in I_3} \tag{23}$$

The necessary condition for a local extremum of the function f has the form:

$$\frac{\partial w\left(B\big(b_1; \dots; b_{|I_3|}\big)\right)}{\partial b_i} = \frac{\partial w(B)}{\partial B} * \frac{\partial B(b_i|i \in I_3)}{\partial b_i} = \frac{\partial w(B)}{\partial B} = 0;\ \forall\, i \in I_3$$

This system is equivalent to one equation:

$$\frac{\partial w(B)}{\partial B} = 0 \ \to B = \frac{C}{2 * k_1} \tag{24}$$

Moreover, it is important to note that the function $f(b_i|i \in I_3): R^{|I_3|} \to R$ is concave in $R^{|I_3|}$. This statement follows strictly from the following

1. The function $w(B) = B * (\mathrm{C} - k_1 * B)$ is concave in R.
2. The function $B\big(b_1; \dots; b_{|I_3|}\big) = \big(\sum_{i \in I_1} b_i^{max} + \sum_{i \in I_3} b_i\big)$ is linear in its domain.

Suppose $x \in R^{|I_3|}, y \in R^{|I_3|}$. Then:

$$\begin{aligned} f(\lambda * x + (1 - \lambda) * y) = {} & w(B(\lambda * x + (1 - \lambda) * y)) \\ & = w(\lambda * B(x) + (1 - \lambda) * B(y)) \\ & \geq \lambda * w\big(B(x)\big) + (1 - \lambda) * w\big(B(y)\big) \\ & = \lambda * f(x) + (1 - \lambda) * f(y), \forall \lambda \in [0; 1] \end{aligned}$$

These equalities indicate that each stationary point of the function $f(b_1; \ldots; b_{|I_3|})$ in $R^{|I_3|}$ space represents the point of a local and a global maximum of the function $f(b_1; \ldots; b_{|I_3|})$. Therefore, all of the points of the global maximum of f belong to a ($|I_3|$-1)-dimensional hyper plane, which is described by the equation below:

$$\sum_{i \in I_3} b_i = \frac{C}{2 * k_1} - \sum_{i \in I_1} b_i^{max} \tag{25}$$

Task (22) is equivalent to task (23) with restriction (22.2). This restriction represents a ($|I_3| - 1$)-dimensional hyper plane as well. As a result, all of the points that belong to the intersection of planes (22.2) and (25) are solutions to maximize function (22.1) with restriction (22.2).

Therefore, the solutions to problem (22) satisfy the system of two linear equations:

$$\begin{cases} \sum_{i \in I_3} b_i = \frac{C}{2 * k_1} - \sum_{i \in I_1} b_i^{max} \\ \sum_{i \in I_3} (k_1 - k_2 * \alpha_i) b_i = C - k_1 * \sum_{i \in I_1} b_i^{max} - k_2 * \left(\sum_{i \in I_2} v_i^{max} + \sum_{i \in I_3} v_i^{max} \right) \end{cases} \tag{26}$$

These two planes are parallel when their normal vectors are linear-dependent vectors:

$$\begin{pmatrix} k_1 - k_2 * \alpha_1 \\ \cdots \\ k_1 - k_2 * \alpha_{|I_3|} \end{pmatrix} = a * \begin{pmatrix} 1 \\ 1 \\ 1 \end{pmatrix} \rightarrow k_1 - k_2 * \alpha_1 = k_1 - k_2 * \alpha_{|I_3|} \rightarrow \alpha_1 = \alpha_{|I_3|}$$

According to assumption (10), $\alpha_1 \neq \alpha_{|I_3|}$. As a result, the considered planes have a nonempty intersection; therefore, the solutions to problem (22) belong to a ($|I_3| - 2$)-dimensional plane in $R^{|I_3|}$ spaces that can be described using system (26). Additionally, it is important to mention the statement below:

Let b satisfy (26). Then:

$$W(b) > W(b_1), \forall b_1 \in M, \text{but not satisfying (26).} \tag{27}$$

This proposition follows from the properties of concave functions.

Note that all of the statements considered earlier in this lemma for the fixed optimization problem $u(I_1, I_2, I_3)$ remain valid for each $u(I_1^u, I_2^u, I_3^u) \in \mathcal{U}$.

Now we have a useful approach to investigate problem (19). We emphasize the fact that problem (19) represents the task $\tilde{u}(\emptyset, \emptyset, \{1, .., N\}) \in \mathcal{U}$ with the additional restriction $0 \leq b_i \leq b_i^{max}, \forall i = 1..N$. As found earlier, all of the solutions to task $\tilde{u}$ belong to a (N-2)-dimensional plane, which is why there are two possible cases:

1. There exist points that simultaneously belong to the optimal hyper plane and to the hyper parallelepiped H_{PP}. According to condition (27), these and only these points represent solutions to (19).

2. There is no point that simultaneously belongs to the optimal hyper plane and to the hyper parallelepiped H_{PP}. According to condition (27), we should search for the solution to task (19) in $\partial H_{PP} \cap M$. We also obtain tasks $u(I_1^u, I_2^u, I_3^u) \in \mathcal{U}$, which are determined in appropriate hyper parallelepipeds. Moreover, we know that for each task there is no point that belongs to the optimal hyper plane of the task and also to the appropriate hyper parallelepiped (according to (26)). We can repeat this procedure until we receive the vertices of the set $H_{PP} \cap M$.

Therefore, we show that the following statement is true:

$$\left[\left(b^{**} \in Vert(H_{PP} \cap M)\right) \wedge (R = \emptyset)\right] \vee [(b^{**} \in R) \wedge (R \neq \emptyset)].$$

So, Lemma 2 is proved. According to Theorem 1 and Lemma 2 it is obvious that the following statement is true:

$$(b^* \in Vert(H_{PP}) \cap M_1) \vee (b^* \in Q) \vee \left[\left(b^* \in Vert(H_{PP} \cap M)\right) \wedge (R = \emptyset)\right] \\ \vee [(b^* \in R) \wedge (R \neq \emptyset)].$$

Thus, we have proven Theorem 2.

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Проблема перехода от одноклеточных форм жизни к многоклеточным формам – важнейший вопрос, изучаемый в эволюционной биологии. В [1] жизнеспособность колонии клеток рассматривается в терминах вегетативной и репродуктивной составляющих. Внутренняя функция компромиссов клетки определяет тип этой клетки. Мы развиваем модели, предложенные в [1]. Предполагая линейность всех внутренних функций компромиссов, мы конструируем модель колонии, состоящей из клеток различных типов, и показываем, что дифференциация типов ведет к полной специализации. Кроме того, мы пытаемся учесть, что факторы окружающей среды воздействуют на жизнеспособность колонии. Таким образом, мы добавляем в модель энергетическое ограничение и показываем, что возможны ситуации, когда некоторые клетки продолжают быть специализированными, в то время как другие становятся безразличными между состояниями, в которых они могут быть как специализированы, так и нет. Стоит отметить, что модели, представленные в [1], неробастные. В описываемых здесь моделях мы пытаемся преодолеть этот недостаток.

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