



A mechanistic model for the evolution of multicellularity

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HIGHLIGHTS

- We develop a mechanistic model for the emergence and maintenance of multicellularity.
- The modeling relies on the existence of tradeoffs.
- Division of labor is achieved as optimal configurations.
- Dependence of the different processes on the geometries of the aggregates is studied.

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ABSTRACT

Through a mechanistic approach we investigate the formation of aggregates of variable sizes, accounting mechanisms of aggregation, dissociation, death and reproduction. In our model, cells can produce two metabolites, but the simultaneous production of both metabolites is costly in terms of fitness. Thus, the formation of larger groups can favor the aggregates to evolve to a configuration where division of labor arises. It is assumed that the states of the cells in a group are those that maximize organismal fitness. In the model it is considered that the groups can grow linearly, forming a chain, or compactly keeping a roughly spherical shape. Starting from a population consisting of single-celled organisms, we observe the formation of groups with variable sizes and usually much larger than two-cell aggregates. Natural selection can favor the formation of large groups, which allows the system to achieve new and larger fitness maxima.

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1. Introduction

The formation of new and higher levels of biological organization is a commonplace in evolutionary biology [1,2], being one of the most important transitions the emergence of multicellularity from single-celled organisms. Nowadays, it is well documented that multicellularity has independently occurred in different clades and sometimes even within the same clade [3–5]. The understanding of the mechanisms supporting that process and, in a broader context, the increase of complexity is a matter of longstanding debate in the scientific community [1,6].

The most prominent feature of these events refers to the transition where independent replicators associate and form a higher level unit [1]. As organismal size increases so does the potential to develop division of labor among its lower-level units, which allows the higher-level units to be more efficient under specific conditions, resulting in a fitness advantage. Complexity increases with size as a result of a greater degree of cooperative division of labor within larger entities [4], a feature also observed on economic grounds [7]. But this also holds at the framework of competitive interactions among constituents of the system. Indeed, this has been observed in ecological communities, in which larger areas can harbor more species [8–11].

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As aforementioned, multicellularity have evolved in many distinct occasions and through different mechanisms and modes of development, making use of different aspects of cellular biology [5]. There are some requisites that must be fulfilled for the evolution of multicellular life forms. For instance, there must exist a fitness transfer from a lower-level biological organization (single cell) to a higher-level biological organization (group) [12–14]. This is achieved if, besides cell-to-cell adhesion, some form of communication arises, e.g. biochemical signaling, allowing the cells to communicate and cooperate [5]. A natural following stage of the process is cell specialization (division of labor), which can minimize possible conflicts among competing physiological processes [15]. Though, it is important to highlight that there are benefits at the earlier stages of the emergence of multicellularity even with undifferentiated cells, as increased group size can enhance predation avoidance [3,16], or even create a buffered environment within a group, which can favor the sharing of secreted public goods [17]. Thus, undifferentiated multicellularity introduces an additional advantage for the evolution of specialized cells [18]. Moreover, the insight that the size of an organism affects its ability to evolve new specialized cells is vital for our understanding of how complex multicellular life evolved. The size of a multicellular organism affects its fitness landscape. This augment entails an increase in the dimensionality of phenotype space and the generation of a fitness landscape with new fitness maxima ensues [15,18].

Here we explore the conditions in which the formation of groups of arbitrary sizes is favored. We adopt a mechanistic approach to investigate the evolution of multicellularity. This approach takes into account quite distinct mechanisms driving the dynamics of group size, such as aggregation, dissociation, reproduction and cell death. In the model, there is an important interplay between natural selection and dynamics of group growth as the size of groups strongly impact rates at which cells divide. In the current work, our aim is to observe the emergence of aggregates of arbitrary size thus allowing us to understand the underlying mechanisms that can limit the size of evolving organisms. The problem is simulated within the framework of kinetic theory, where finite populations are assumed and thereby stochastic components of the evolutionary dynamics are naturally incorporated. The problem is formulated within the context of existing tradeoffs. The cells are genetically identical and can complete two tasks, for instance, the production of two metabolites. These two tasks are poorly compatible, which makes room for the appearance of division of labor as bigger organisms arise. The timescale at which signaling processes among cells in a group occur is much shorter than the mechanisms directly affecting group size dynamics, and so one important premise of the modeling is that internal arrangement of cells in a group is the one that maximizes organismal fitness. Note that the establishment of a reproductively integrated phenotype is one of the requirements for multicellularity [19]. This coordination among group members is seen in cellular evolution [20] as well as in social evolution [21]. Once a multicellular organism has been formed, that allows for selection of further size increase, which in its turn will require an increase in complexity, i.e., a further development of division labor through cell specialization. This is dubbed the size-complexity rule [22]. Of course, each newly assembled cell does not add up a new different function. In spite of keeping the number of functions fixed and equal to two, here we show that there exists a selection for “intermediate” organismal size, as a change in organismal size affects the organism phenotypic space, thus allowing the search for new local maxima.

The paper is organized as follows. In Section 2 the model is described. Section 3 presents the theoretical development as well as discusses in detail the formulation which allows us to simulate the problem as a set of chemical reactions, and the type of structures considered in the current work. Section 4 shows the simulation results. And finally, in Section 5 we present our concluding remarks.

2. The model

We propose a model of body formation that assumes the aggregates have well-defined shapes. Besides grouping together to form aggregates, the cells can reproduce and die.

The formation of aggregates of up to two cells has been recently addressed by Ispolatov et al. [15]. In their work, the cells could either give rise to two-cell aggregates or remain in their unicellular form. The generalization of such analysis to aggregates of arbitrary sizes brings about some difficulties. First, one needs to tackle the assumptions underlying fitness optimization within the groups. Instead of maximizing cell's fitness, as originally supposed in Ref. [15], we rather consider that the target of selection is the organismal fitness. The second and troublesome issue is that by designing organisms comprised of an arbitrary number of cells the group structure can no longer be disregarded, as before. Nevertheless, the assessment of groups of arbitrary structures is prohibitively complex. For such reason, we study two situations: in the first case, the cells form linear chains; while in the second, the aggregates are spherically symmetric structures.

The cells are endowed with the capability to perform two tasks. Let us consider, for instance, the production of two metabolites, hereafter denoted by X and Y . The production of these metabolites brings about a benefit $B(x, y)$ and a cost $C(x, y)$. The production of both metabolites cannot grow without a bound, due to the existence of a tradeoff. As such, the production of both metabolites in considerable amounts inflicts a huge cost to the cell. However, both metabolites are considered to be essential for the cells. In order to accommodate these features, we shall assume that the benefit function is given by the standard form

$$B(x, y) = xy, \quad (1)$$

so that if the cell does not produce one of the metabolites the benefit will vanish. On the other hand, we adopt the following cost function

$$C(x, y) = c_x x^3 \exp(y^2) + c_y y^3 \exp(x^2), \quad (2)$$

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