

Emergence of diverse life cycles and life histories at the origin of multicellularity

Merlijn Staps¹, Jordi van Gestel^{1,2,3,4,5*} and Corina E. Tarnita^{1*}

The evolution of multicellularity has given rise to a remarkable diversity of multicellular life cycles and life histories. Whereas some multicellular organisms are long-lived, grow through cell division, and repeatedly release single-celled propagules (for example, animals), others are short-lived, form by aggregation, and propagate only once, by generating large numbers of solitary cells (for example, cellular slime moulds). There are no systematic studies that explore how diverse multicellular life cycles can come about. Here, we focus on the origin of multicellularity and develop a mechanistic model to examine the primitive life cycles that emerge from a unicellular ancestor when an ancestral gene is co-opted for cell adhesion. Diverse life cycles readily emerge, depending on ecological conditions, group-forming mechanism, and ancestral constraints. Among these life cycles, we recapitulate both extremes of long-lived groups that propagate continuously and short-lived groups that propagate only once, with the latter type of life cycle being particularly favoured when groups can form by aggregation. Our results show how diverse life cycles and life histories can easily emerge at the origin of multicellularity, shaped by ancestral constraints and ecological conditions. Beyond multicellularity, this finding has similar implications for other major transitions, such as the evolution of sociality.

The evolutionary history of life on Earth features multiple major transitions during which biological entities assembled into higher-order structures^{1–5}. A key example of such a transition is the evolution of multicellular life from unicellular ancestors^{6–9}. Multicellularity has evolved repeatedly and is widespread across the tree of life, ranging from the canonical examples of multicellular organisms (animals, plants, fungi) to filamentous bacteria or aggregating social amoebae. Independent evolutionary origins of multicellularity have given rise to a wide variety of multicellular life cycles^{9–18} that differ in their mode of group formation (how groups are built from single cells), the mode of group propagation or reproduction (how groups give rise to new groups), and in the resulting life history traits (for example, group size, longevity, or timing of group reproduction). For example, group formation can occur via cells staying together after division (ST, or clonal development), cells coming together (CT, or aggregation) or via a mix of CT and ST^{6,9,19,20}, whereas group reproduction modes can range from binary fission (groups splitting into two) to the release of single-celled propagules or even the complete dissolution of groups into single cells^{21–23}. How diverse multicellular life cycles and life histories can come about remains an open question.

Our understanding of the life cycles that arise at the very origin of multicellularity has been greatly illuminated by recent empirical advances^{24–28,29}. Experimental evolution studies have demonstrated that multicellular life cycles can readily emerge given the right pre-adaptations and ecological conditions^{30–34}. Comparative genomics studies have shown that transitions to multicellularity are facilitated by the reorganization of molecular pathways that are already present in the unicellular ancestor, thus revealing the important role of the unicellular ancestor in shaping primitive multicellular life^{35–38}. Despite these empirical developments, the emergence of multicellular life cycles from unicellular ancestors has received surprisingly

limited theoretical attention. Instead, theoretical studies tend to take the emergence of a multicellular life cycle for granted (but see refs. ^{39–41}) and examine how different life cycles may be favoured under different ecological conditions^{19,21,42,43,44} or how group properties (such as group integrity or the division of labour between group members) may evolve in the context of a given life cycle^{45–50}. There have been no theoretical studies that, starting from the unicellular ancestor, have systematically explored the multicellular life cycles and life histories that can originate.

Here, we approach this question by developing a mechanistic model for the evolution of multicellularity that explicitly accounts for the unicellular ancestor and its ecology (see Methods for full details and Table 1 for parameters). In this model, group formation results from cell stickiness, which we assume to arise as a promiscuous function of an ancestral gene. Evolution acts on the regulation of this gene, leading to the emergence of multicellular life cycles. Because the life cycle is an emergent feature of the model, this bottom-up approach allows us to explore, without *a priori* expectations, what life cycles may arise starting from a unicellular ancestor and how those life cycles are shaped by ecological conditions and ancestral constraints.

Specifically, we consider a finite population of haploid, asexually reproducing cells that undergo density-dependent population growth and experience two sources of mortality—one intrinsic and one due to predation. Since many unicellular organisms face fluctuating environmental conditions, such as the feast and famine cycles in soil-dwelling amoebae or the diurnal cycle in photosynthetic algae, we assume that our cells live in a fluctuating environment. For simplicity, we consider only two alternating environments of equal length. In each environment, selection favours (via a reproductive benefit) the expression of a different gene—gene A in environment 1 and gene B in environment 2. To allow selection to act on gene

¹Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ, USA. ²Department of Evolutionary Biology and Environmental Studies, University of Zürich, Zürich, Switzerland. ³Swiss Institute of Bioinformatics, Lausanne, Switzerland. ⁴Department of Environmental Systems Science, ETH Zürich, Zürich, Switzerland. ⁵Department of Environmental Microbiology, Swiss Federal Institute of Aquatic Science and Technology (EAWAG), Dübendorf, Switzerland. *e-mail: jordivangestel@gmail.com; ctarnita@princeton.edu