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Evolutionary Transitions in Individuality and Life Cycle Closure

Guilhem Doulcier[1,2], Peter Takacs[3], and Pierrick Bourrat[1,3]

[1]Macquarie University, Department of Philosophy, North Ryde, Australia

[2]Max Planck Institute for Evolutionary Biology, Plön, Germany

[3]Charles Perkins Center, University of Sydney, Australia

Abstract

We propose a novel account of evolutionary transitions in individuality as *life cycle closure*: that is, the emergence of a new embedding life cycle. To characterize this process, we show how the life trajectory of lower-level entities (e.g., cells) can be *coarse-grained* into classes of a higher-level entity. We argue that only higher-level entities displaying two necessary conditions for the existence of a life cycle (e.g., multicellular organisms) have achieved life cycle closure. Throughout, we illustrate our point with stage-structured demographic models that yield a rigorous characterization of the conditions for life cycle closure.

Introduction

Evolutionary transitions in individuality (ETIs) are events during the history of life where entities at one level of organization (e.g., genes, cells, individuals), hereafter *particles*, become embedded in a higher-level entity or *collective* (e.g., chromosomes, multicellular organisms, eusocial organizations). The completion of an ETI leads to the emergence of a new level of organization. For instance, following the ETI from unicellularity to multicellularity, multicellular organisms constitute a new level of organization and can participate in evolutionary processes at that level (Okasha, 2006, chap. 8; Maynard Smith and Szathmáry, 1995).

According to this *entity-centered view*, an ETI represents a transition from one type of entity to another. In the most familiar form of this view, ETIs are understood in spatial terms (i.e., particles embedded in collectives) without fully considering the temporal dimension (Godfrey-Smith, 2016, p. 85). We argue that this does not align well with the fact that individuals are *both* spatial *and* temporally extended entities. To address this shortcoming, we propose a complementary approach according to which individuals are viewed through the lens of entire life cycle from birth to reproduction and death. We term this a switch from an entity-centered to a *life cycle–centered* view of ETIs.

Thinking in terms of life cycles in the context of evolutionary biology has some precedence in the literature. For instance, following the developmental system tradition, Griffiths and Gray (1994) argue for a link between developmental processes and evolutionary explanation on the grounds that biological traits are not copied ready-made from generation to generation but necessarily reconstructed by the complex interactions of diverse resources. The literature on ETIs has also been concerned with the origin of life cycles, from the emergence of prebiotic hypercycles of autocatalytic molecules (Eigen et al., 1981) to nascent life cycles that naturally emerge in early multicellular organisms (Ratcliff et al., 2017; Staps et al., 2022). In both cases, switching to a life cycle perspective highlights the dynamical nature of biological individuals and how they develop over time.

In this paper, we lay the groundwork for a life cycle–centered view in the context of ETIs. We discuss the diversity of life cycles (Section 1), then describe how our life cycle view is rooted in a statistical method involving coarse-graining individual states into classes of *life stages* that reoccur over time (Section 2). This method permits defining and recognizing a life cycle at any level of organization. We then deploy this view to account for the emergence of a new life cycle at the collective level from the population dynamics of the particles constituting it during an ETI. We refer to this emergence as *life cycle closure* (Section 3).

1 Life Cycles and Their Diversity

The living world displays a broad diversity of life cycles, characterized by an organism's various changes from birth to reproduction and, ultimately, death. The most familiar life cycle is that of metazoans (Figure 1a). After sexual reproduction, a zygote grows and continuously develops into a new fertile adult. More abstractly, if we adopt the convention to start the cycle at syngamy (i.e., when gametes fuse into a zygote), this cycle can be described in three steps: aggregation (here, syngamy), transformation (when the zygote develops and grows), and multiplication (when a single individual produces several gametes through meiosis, starting the life cycle of a new individual). These three processual categories are not specific to the life cycle of metazoans; they are encountered in all life cycles. Additionally, each process can occur numerous times, at various points of a cycle, and be variably complex. While a complete characterization of these processes is beyond the scope of this manuscript, several defining characteristics are worth highlighting for our purpose.

Sexually reproducing organisms exhibit the familiar process of aggregation through syngamy. However, some life cycles do not involve an aggregation step, such as those of unicellular and multicellular organisms that reproduce asexually. Conversely, other life cycles (e.g., the social cycle of the amoeba *Dictyostelium discoedum*) display several aggregative phases involving the "coming together" of many cells to form a larger entity (Bonner, 2015).

Transformation might include continuous growth, as found in some plants. However, some life cycles feature drastic qualitative changes in the organism's morphology and behavior. The metamorphosis of holometabolous insects represents a vivid example of this phenomenon (Moran, 1994).

The life cycle of metazoans exhibits a single step of multiplication: gametes produced through meiosis. Each haploid gamete produced can lead to the production of a new organism. However, plants exhibit alternation between haploid and diploid phases (termed *alternation of generations*), each of which involves a multiplicative step. A diploid gametophyte produces several haploid gametes (through meiosis) that can grow into a multicellular sporophyte, which produces multiple spores, each of which can aggregate (through syngamy) into a different gametophyte (Qiu et al., 2012). The relative importance of these two phases varies from species to species.

In addition to being characterized by the three processes, some life cycles have optional branches. A single cell of *Dictyostelium discoedum* (Figure 1a) can bypass the social and sexual phases of the cycle and instead follow a unicellular vegetative cycle, depending on environmental conditions (Bonner, 2015). Thus, a life cycle might not be characterized by a unique *life trajectory* (i.e., a fixed sequence of aggregations, transformations, and multiplications) repeated at each generation.

Representing organisms' life trajectories with a life cycle comprising these three processes, as illustrated in the graph in Figure 1a, is a convenient way to summarize all relevant information about the dynamics of these trajectories. However, such a representation rests on several assumptions and a process of coarse-graining, as detailed in the next section.

2 Coarse-Graining the Tree of Life

Identifying and describing a life cycle involves three steps. It requires 1) identifying *life stages* (Figure 1b-I), 2) establishing transition probabilities between these stages (Figure 1b-II), and finally 3) encoding this information in a life cycle graph (Figure 1b-III). We detail these steps in this section.

Life cycles present a challenging case of identity through time. Consider an individual organism, such as an adult chicken. If one followed its states back in time, one would see a succession of states—chicken, chick, egg, zygote, and gametes—that would eventually reach the previous generation. However, at no point would the states of the previous generations be *exactly* the same (atom-to-atom) as the current one. To claim that the lineage exhibits a succession of generations (i.e., a successful realization of a given life cycle), one must first have a criterion of identity for each stage of the life cycle. From there, each occurrence that satisfies this criterion is considered an instance of this *life stage*. To find the relevant set of criteria for the purpose of identifying a life cycle from the observations of a lineage, a statistical method is required that identifies what kind of heterogeneities in the lineage can be discarded without compromising accurate prediction. This operation can be described as a *coarse-graining* procedure, whereby the phenotypic space is divided into life stages (e.g., juveniles, adults, gametophytes, imago, pupa) linked by biological processes (e.g., growth, meiosis, syngamy). In the previous

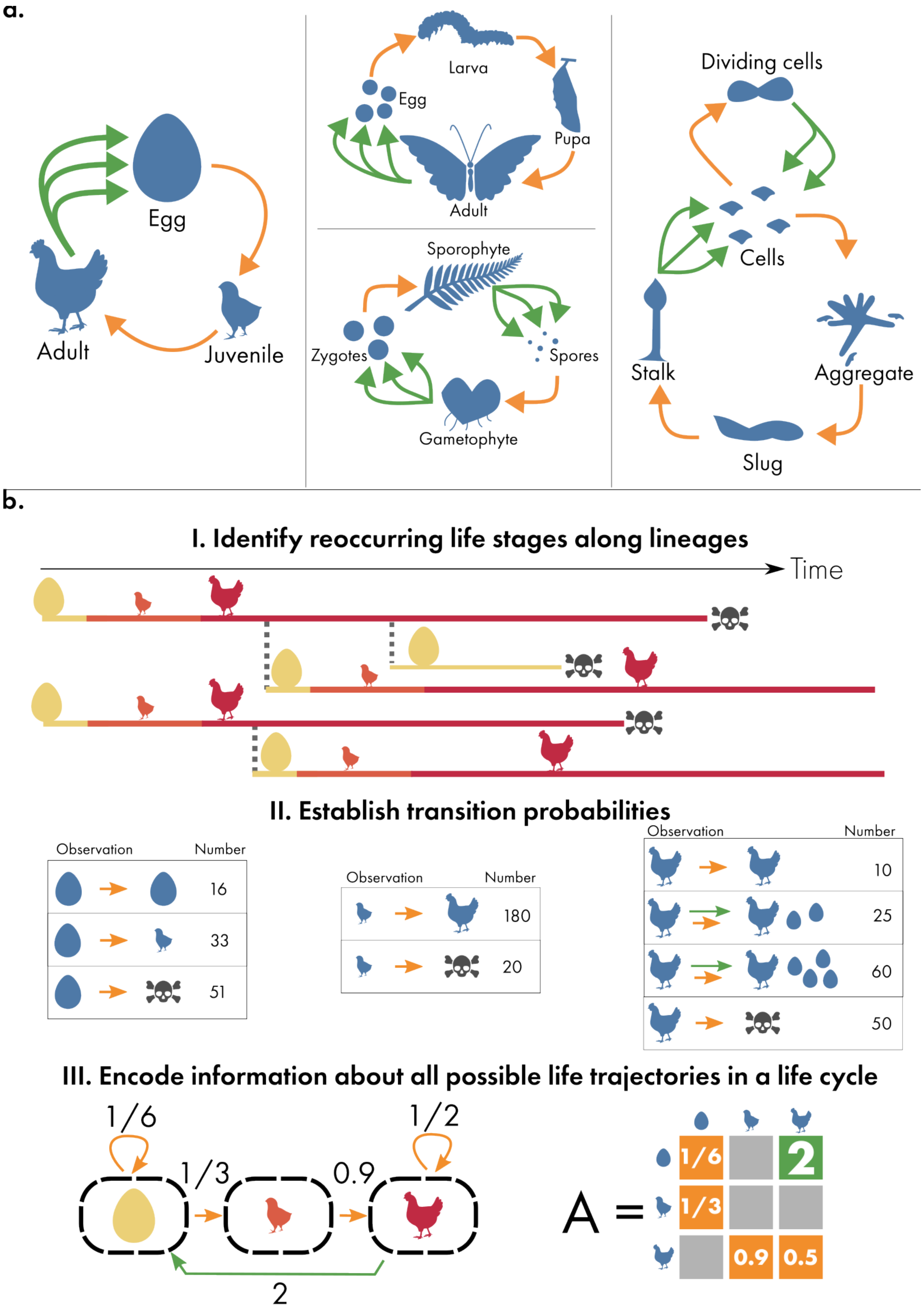

Figure 1: Describing and identifying a life cycle. **(a)** Biological examples. **(b)** The three coarse-graining steps involved in identifying a life cycle.

section, we argued that all life cycles can be described as exhibiting three processes: transformation, aggregation, and multiplication. In doing so, we implicitly discarded some of the differences between different processes and kept only several key commonalities—we, thereby, "coarse-grained" these biological processes.

An illustration of the coarse-graining operation is presented in Figure 1b-I, where the lineage is coarse-grained into three stages (egg, chick, chicken), two transformation processes (from egg to chick, and chick to chicken), and one multiplication process (gamete production). Note that those stages and processes could be further partitioned. The grain chosen will depend on explanatory goals and material limitations (models with more stages require more observations), not on a priori reasoning.

In practice, the coarse-graining of a lineage into different stages and processes forming a life cycle is done through a "stage-structured model" (or "age-structured model," if the stages are defined solely by individuals' ages). In the following, we present their simplest formalization: matrix population models.

Matrix population models (see Caswell, 1989, for a classic treatment of the subject) involve a discrete (i.e., non-continuous) representation of time and stages. They offer us a class of linear models, which do not feature density-dependant effects. While these models are fully deterministic, they can represent the expected behavior of more complex stochastic models.[1]

In such a model, the state of a population at time t is described by counting the number of individuals belonging to each coarse-grained stage. These numbers are collected in a vector $\mathbf{n}_t$. In a graph representation of the model, a stage or element of the state vector n_t corresponds to a

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[1] More sophisticated models are generalizations of this core idea by including chance and infinitesimal differences between classes (see e.g., Haccou et al., 2007; Perthame, 2006).

node. The transitions between different stages—representing aggregation, transformation, and multiplication—are encoded in the associated projection matrix $\mathbf{A}$, where an element represents the expected flux between two stages. In a graph representation, this corresponds to an edge between two nodes. Traditionally, in demography, two kinds of fluxes are distinguished: survival and fertility, corresponding to the transformation and multiplication processes of a life cycle,[2] respectively.

This demographic model is used to establish projections of a population's future state. In demography, a projection is a special kind of prediction where some conditions (here, the fluxes) are assumed to remain constant (Keyfitz and Caswell, 2005). In the context of matrix population models, this projection is achieved by a simple matrix product $n_{t+1} = \mathbf{A}n_t$. Through this product, each stage is associated with inbound and outbound fluxes toward and from other stages. These fluxes are then tallied over a unit of time.

An important feature of class-structured models, required for projection, is that all individuals in a given stage are independent and have the same propensities to transform and multiply into other life stages. By propensities, we follow here a physical interpretation along the line of Rosenthal (2010), where, roughly, an object's "propensity" is a set of dispositional properties in its reference environment (i.e., a set of boundary conditions). Considered as such, only object–environment systems that are invariant in their probability distribution over outcomes have well-defined physical probabilities.

In practice, transition probabilities are established empirically from actuarial tables and sam-

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[2] We here ignore aggregative processes, as is often done in demography, by either considering specific organisms (e.g., non-aggregating asexual organisms) or focusing on one sex only in sexual organisms ("mother models").

ple observations of life trajectories (Keyfitz and Caswell, 2005). For example, in Figure 1b-II, a hundred eggs are observed for one unit of time: 16 persist without change, 33 become chicks and 51 die. Based on these observations, the probability for an egg to persist in the egg stage is estimated to $\frac{16}{100} \approx \frac{1}{6}$, and the probability to transform into a chick is $\frac{33}{100} \approx \frac{1}{3}$. Because these probability distributions are invariant for a given stage and independent between individuals, the law of large numbers applies: the average fluxes between stages (encoded in the elements of $\mathbf{A}$) are the expected values of these distributions. Thus, $\frac{1}{3}$ of the eggs become chicks, and there are 2 new eggs for each chicken in a unit of time.

Thus, stage-structured models provide a way to summarize information about any potential life trajectory of an individual as a life cycle. These models contain all the information about the probability of an individual transforming (and multiplying) into different coarse-grained stages. They are an example of population thinking (Mayr, 1994), a statistical abstraction that represents the diversity of unique life trajectories. The ability to make projections renders them an invaluable tool for demography and evolutionary biology more broadly (Caswell, 1978). In particular, they provide a way to describe the evolutionary implications of biological changes to a life cycle (i.e., changes in the transition probabilities between stages) in terms of changes to long-term growth rate,[3] the latter of which can be regarded as fitness following the propensity interpretation of fitness (Pence and Ramsey, 2013). Thus, remarkably, matrix population models can straightforwardly connect changes in life history to fitness, the primary commodity of evolutionary explanations.

From a technical perspective, this link between probabilities of changes and fitness hinges on

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[3] This method is called sensitivity analysis. A full description is beyond the scope of this article; classic textbooks (e.g., Caswell, 1989) explore the topic in detail.

some very general results of matrix theory. Provided that the matrix **A** is *irreducible*—meaning that any class is eventually reachable from any other class (a concept that will become crucial in the next section)—the Perron-Froebenius theorem ensures the existence and uniqueness of a dominant eigenvalue r that corresponds to the long-term growth rate (i.e., fitness) of the population.[4] The associated eigenvectors ($\mathbf{v}$ and $\mathbf{w}$) correspond to the asymptotic stage distribution (the stable stage distribution toward which the population converges in time) and the reproductive value (the contribution of each stage to the future population state), respectively. Provided that the matrix describing the coarse-graining verifies the conditions outlined above, these quantities (dominant eigenvalue and eigenvectors) are 1) characteristic of the whole life cycle and of the lineage, not of a specific stage that would be reified as *the* individual, and 2) well-defined. These two properties are particularly desirable for a definition of fitness (Akçay and Van Cleve, 2016).

So far, we have argued that a life cycle description is a powerful approach to evolution because it encompasses the whole life of organisms through time (from birth to death, with an explicit account of development) that would be lost in a purely entity-centered view. The relevant information to predict the dynamics of a population is kept by coarse-graining possible phenotypes into stages and transition processes that are subsequently connected. Matrix population models represent a simple operationalization of this life cycle–centered view.

Having presented what life cycles are and how they can be efficiently represented and integrated into a powerful evolutionary model, we now turn to their emergence during evolution, particularly ETIs.

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[4] The theorem also assumes an aperiodicity condition that we do not detail here because it is not biologically relevant in our context of application.

3 Evolutionary Transitions in Individuality

As mentioned in the introduction, life has a nested structure; developing and multiplying populations are embedded into one another (Okasha, 2006). This nestedness has been described by Griesemer (2016) as a “double recursion of development and reproduction” across levels, which bottoms out with the simple duplication of molecules: a minimal development that is the simplest life cycle observed. Importantly, the link between development or reproduction across successive levels is not necessarily one-to-one. For example, the development of a collective is a combination of potentially many instances of particle development and reproduction combined in complex ways. Recognizing the nested organization of life immediately raises the question of its origin(s). In this section, we show that our life cycle–centered view can help answer this question and provides a novel account of ETIs.

Classically, accounting for an ETI from a purely entity-centered view consists in defining what types of collections of particles become a collective-level individual. Our life cycle–centered view defines a collective-level individual as a collection of particles that exhibits a life cycle on its own. To move from a state where a population of particles does not exhibit a life cycle to a state where it does, this population must achieve what we call *life cycle closure*. We contend that achieving life cycle closure is enough to characterize an ETI. Further, this approach brings substantial clarity to the dynamical nature of ETIs.

To abstract away from the details of these mechanisms and see how life cycle closure is pivotal for all ETIs, consider any collection of particles in a metapopulation (e.g., cells). This collection has a state (the characteristics and position of the cells within it) and dynamics (governed by cell births, deaths, and migrations) that change its state. We call such a collection a *candidate collective individual*.

In principle, there is nothing preventing us from applying the statistical method outlined in the previous section to describe the state of this candidate collective individual as belonging to one coarse-grained stage (of potentially many). A stage can be defined, for example, by the number and relative position of the particles. Similarly, the probability for a candidate collective individual of a given stage to transition (by aggregation, multiplication, and transformation) to another stage in the next unit of time can be calculated. The candidate collective transition probabilities can be either constructed experimentally from the study of large collections of recorded life trajectories or even deduced from the composition of particle-level probabilities in the case of simple models.

There are numerous ways one could coarse-grain a population of particles in candidate collective individuals (including the number of stages for their candidate life cycle, and the spatial extent of each stage). However, the stage-structured models outlined in the previous section offer an objective way to distinguish descriptions that correspond to genuine collective life cycles and thus to individuals. Assuming classes (stages and processes) with well-defined probability distributions, the method assesses whether the candidate meets two conditions: 1) the existence of at least one multiplicative stage and 2) the closure of the life cycle. These two conditions capture the notion of a life cycle as the re-establishment of traits at each generation through development and the re-occurrence of life stages over time when following a lineage. We now illustrate why if either of these conditions goes unfulfilled, the candidate is not a collective individual.

If a coarse-grained collective cycle exhibits no multiplicative stage, as in Figure 2a, a lineage follows a trajectory with coarse-grained stages. A stage can potentially reoccur over time, but no branching lineages are initiated because no new collective-level entities are produced. Since no generations marked by multiplication events can be defined at that level, any given candidate collective individual follows a succession of stages akin to perpetual development. An instance

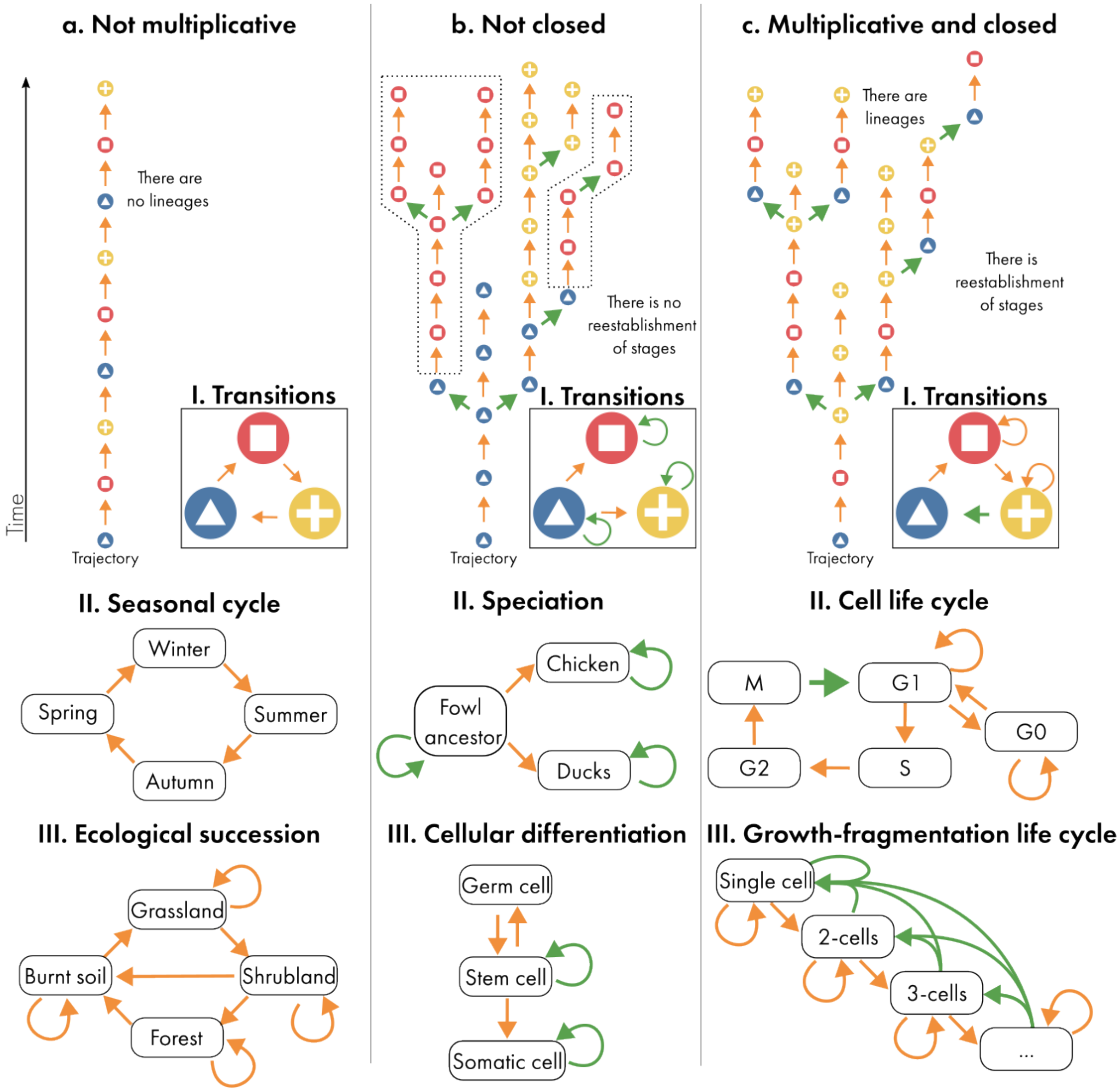

Figure 2: Two necessary conditions for establishing a life cycle: multiplication and closure. Stages are colored disks. Multiplicative transitions are in green; transformative transitions are in orange.

of this situation occurs if we take life as a whole as a candidate individual, as in some versions of the Gaia hypothesis. With adequate coarse-graining, seasonal cycles may appear as displaying a recurrence of biosphere-wide stages every year (Figure 2a-II). However, because there is no multiplication, this description does not delimit a life cycle. At smaller scales, the same pattern can be observed if we consider ecological successions in a single ecosystem such as the effect of wildfires on forests (Figure 2a-III).

As was mentioned in the previous section, a coarse-graining satisfies the condition of multiplication if it includes some transitions that result in the production of a new candidate individual belonging to one of the existing coarse-grained stages. In matrix population models, this condition translates to the existence of at least one fertility flux between two classes.

Let us now turn to the condition of life cycle closure. Assume a population of particles coarse-grained in a finite number of stages such that at least one is a multiplicative stage. For the condition of life cycle closure to be satisfied, there must exist a path (i.e., a sequence of stages linked by processes) that goes from any stage to any other stage (during one or over several generations). If this is not the case (Figure 2b), lineages may get stuck in different subsets of stages indefinitely and, thus, cannot be considered to have the same life cycle. This type of situation occurs, for instance, if we consider diverging populations of particles as a candidate collective individual (Figure 2b-II). To see this, suppose a coarse-graining that would encompass chickens, other birds such as ducks, and their common fowl ancestor. From such a description—where a candidate collective individual is a population of one of the different bird species—there is no developmental path from a duck egg to an adult chicken. The cycle is not closed; thus, a population of one bird species, in this context, is not an individual because speciation is not a mechanism for reproduction in a putative life cycle of species. In other words, since there is no cycle at the coarse-grained level of a meta-population of bird species, the species level does not represent an adequate level of individuality.[5] At smaller scales, the same pattern can be observed if we consider cell differentiation (Figure 2b-III). There is no developmental path from somatic to germs cells. The cycle of the “gerrymandered” candidate individual with separated germ and soma is not closed.

In the matrix population model formalism, the life cycle closure condition corresponds to the irreducibility of the projection matrix **A**—the property that there is a succession of (potentially many) stages that link any starting stage to any other stage. Recall that when this property is verified, there is a unique long-term growth rate (dominant eigenvalue) associated with the matrix and a unique stable stage distribution (the associated eigenvector), which together describe the long-term projected demographic trajectory of the population and characterize the life cycle. If this property is not verified, there is no unique long-term behavior, but one for each irreducible set of stages (i.e., one for ducks and one for chickens in the example (Figure 2b-II)).

When both conditions are fulfilled (Figure 2c), a life cycle exists at the level described by the coarse-graining featuring lineages and reestablishment of stages (as shown in Figure 1 for metazoans; Figure 2c-II for the life cycle of cells).

Several mechanisms promoting the inception of collective life cycle closure have been suggested in the literature. Here, we briefly review two cases: the ecological scaffolding of collective properties and the emergence of growth-fragmentation cycles in early multicellularity. When ETIs occur under the ecological scaffolding scenario (Bourrat, 2022), a collective multiplies by migration of several of its constitutive particles to new niches. This can lead to the

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[5] Our notion of individuality, as an entity with a developmental and a multiplication phase, is more restricted than that of Hull (1978, 336), who defines individuals as “spatiotemporally localized cohesive and continuous entities (historical entities).”

closure of a simple life cycle if the collective composition is reestablished in offspring niches "by chance." This unreliable mechanism has been called a "stochastic corrector" (Maynard Smith and Szathmáry, 1995, p. 55). The reliability of the closure can be increased dramatically by the subsequent selection of specific kinds of particle interactions within collectives (Doulcier et al., 2020). In the case of clonal multicellularity, incomplete separation of cells after reproduction can naturally be described in terms of stages (e.g., clusters of 2, 3, 4, . . . cells; Figure 2c-III) where cluster fragmentation defines multiplication events. The emergence of growth-fragmentation life cycles can stem from a single point mutation (ACE2 in snowflake yeast systems; Ratcliff et al., 2015) or plastic changes (in cyanobacteria filaments; Tang et al., 2023).

Conclusion

Starting from the observation that collective-level life cycles embed particle-level life cycles both spatially and temporally, we have sketched a view of ETIs that fully integrates this temporal dimension. According to this view, an ETI is complete only when *closure* of a new collective life cycle is achieved—that is, collective stages are reliably reestablished. Although we have only briefly mentioned some of the mechanisms by which life cycle closure can be achieved, a more systematic review of the mechanisms underlying ETIs would demonstrate the generality of this account.

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