

Evo-devo beyond development: The evolution of life cycles

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Abstract

In principle, development is only a part of a life cycle, as a life cycle can include more than one ontogeny and reproductive phase. Here I argue that evolution should be viewed as the “change of life cycles with time”, rather than ontogenies, as the basic evo-devo rationale is generally summarized. Each different segment of a life cycle can provide scope for evolutionary change, and the articulation of life cycles into multiple segments can itself vary and evolve, as the diversity of life cycles in the tree of life shows. This more inclusive perspective may have valuable consequences for the evo-devo research agenda.

Introduction

As a very general statement, the evolutionary developmental biology (*evo-devo*) approach to the study of evolutionary patterns and processes is motivated by the idea that, in order to explain evolution, it is crucial to take development into consideration (Hall, 1992; Amundson, 2005; Minelli and Fusco, 2008). Considering the processes of sorting of extant variation operated by natural selection and random drift, in association with the generative processes of variation that derive from the developmental systems, provides more complete explanations of observed evolutionary patterns (Müller, 2007). This idea is often synthesized by a formula that states that *evolution is the change of ontogenies with time*, rather than simply the modification of genotypes and phenotypes (Gilbert *et al.*, 1996).

Here I will argue that this formulation should be replaced by a more inclusive one, that substitutes *life cycles* for *ontogenies*, thus acknowledging that development – which comprises all the transformations of an individual, from its onset until disappearance – is often only a segment of an organisms’ life

cycle. In many taxa, the life cycle involves a sequence of more than one individual, each with its own developmental processes and reproductive phases. Every different segment of a life cycle can provide scope for evolutionary change, and the articulation of life cycles into multiple segments can itself vary and evolve, as the diversity of life cycles in the tree of life shows.

Life cycles¹

Everybody has an intuitive idea of what a life cycle is. It is the series of transformations and events which, from a given life stage of a given organism, leads to the same stage in a next generation of the same organism: from a zygote to a zygote, but also from an adult to an adult, or from an embryo to an embryo. In a cyclic process, the choice of the 'initial stage' cannot be other than an arbitrary or conventional choice, as the egg-chicken dilemma beautifully illustrates.

That said, the description of a cycle has necessarily to start somewhere, and as an example let us concisely describe the life cycle of the fruit fly *Drosophila melanogaster*, starting from the zygote stage. Within the egg case, the zygote proliferates by mitosis during embryonic development and builds up, through complex and highly coordinated morphogenetic processes, the body of a worm-like individual that at some point will be ready to interact with the external world. Hatching occurs after about 12 h of embryonic development at 25 °C. During the subsequent free-living larval period (about 4 days at 25 °C), the insect grows by feeding on rotten fruit while moulting twice (after about 24 and 48 h from hatching), so that the larval period is partitioned by moult into three stages (or instars). The third larval stage develops into the pupa stage, which, while sheltered by the exoskeleton of the final larval stage (the puparium), undergoes a four-day-long metamorphosis. This is a process of profound transformation of the individual, where large parts of its body lose the larval organization and a completely new body organization is built. Once the metamorphosis is complete, an adult fly emerges from the puparium. Fruit flies reproduce sexually: males and females mate, and from the fusion of their gametes the zygotes of the next generation are produced. The development of a fly, from zygote to adult, is considered to be complex, because metamorphosis separates two very different segments of the insect's post-embryonic life, the larva and the adult. For this reason it qualifies as a kind of *indirect development*.

However, despite the complex developmental path from zygote to adult, in the panorama of the diversity of life cycles, that of the fruit fly actually appears to be relatively simple, because the whole cycle is traversed by a single devel-

¹ This section draws extensively from Fusco and Minelli (in press)

oping and reproducing individual. This is not the case for a multitude of plants, animals, fungi and microorganisms.

As an example of a more complex life cycle, let us concisely describe that of a fern, like *Polypodium*, starting from the better known phase of a macroscopic plant, with roots, stem and fronds. A mature leafy fern plant (a diploid phase called *sporophyte*), reproduces sexually (by means of recombination) and uniparentally (i.e., without the need of a partner) by producing haploid spores by meiosis. Spores disperse and germinate on the ground, each developing into a tiny multicellular haploid plant called *prothallus* (*gametophyte* phase). Prothallia, which bear both male and female reproductive organs, reproduce sexually (through fertilization) and biparentally (i.e., through cross-breeding) by producing gametes that will fuse to form diploid zygotes, the founding cells of the sporophytes of the next cycle. During early development, the sporophyte is retained on the parent gametophyte that nourishes it, until it produces the first leaves and roots and becomes independent. In the cycle of a fern there are at least two generations (a sporophyte and a gametophyte), which constitute two distinct *organizational forms*, i.e. two kinds of individual of the same species, each with its own ontogeny. In the case of the fern, one form starting from a zygote develops into a macroscopic diploid leafy plant, the other form starting from a spore develops into a haploid tiny thallus. The two generations are separated by two reproductive phases: the production of spores by the sporophyte and the production and the fusion of gametes of the gametophyte.

The cycle of the fruit fly is an example of a *monogenerational life cycle*, that is, a cycle in which the same developmental phase (e.g., the first larval stage) of the single organizational form of the organism is repeated after one generation. In contrast, the cycle of the fern is an example of a *multigenerational life cycle*, because the cycle passes through a given developmental stage (e.g., the fully-formed thallus) of a given organizational form (in this case, the gametophyte) after more than one generation, in this case two (Minelli and Fusco, 2010). In multigenerational life cycles there are reproductive phases where offspring are generated that are not of the same kind (of the same organizational form) as the parent(s), so that more than one generation is required to return to a starting form.

Multigenerational life cycles, also called *cycles with alternations of generations*, are widespread in the tree of life. In addition to the aforementioned cycles with an alternation of haploid and diploid generations, which are found in many groups of algae and in all land plants, there are cycles with alternation of sexual and asexual generations (*metagenetic cycles*; e.g., many cnidarians, cestodes, polychaetes, tunicates), alternation of amphigonic and parthenogenetic

generations (*heterogonic cycles*; e.g., monogonont rotifers, cladocerans, aphids), alternation of unicellular and multicellular generations (e.g., mycetozoans) and many others (review in Fusco and Minelli, in press). Really complex, multigenerational life cycles include multiple organizational forms which can exhibit a different genetic make-up (e.g., haploid vs. diploid in mosses), a different morphology (e.g., winged vs. wingless in aphids), a different living environment (e.g., a different host in parasitic flatworms), a different mode of reproduction (e.g., sexual vs. asexual in pelagic tunicates), and/or a different kind of development (e.g., direct vs. indirect in cnidarians). In many organisms, the route through which the life cycle closes on itself can be very tortuous.

Evolutionary change

The central claim of evo-devo, that to better explain evolutionary change, development has to be taken into account (Robert, 2004), has been synthesised in various ways. For instance by stating that *evolution is the change of ontogenies with time* (McKinney and Gittleman, 1995), or that *evolution proceeds by developmental repatterning* (Arthur, 2011).

Recognizing development as a part of the life cycle, and acknowledging the “life cycle as a unit of evolution” (Minelli, 2009, p. 155), both of the above claims can be rewritten by substituting “life cycle” for “development”, thus reading either *evolution is the change of life cycles with time*, or *evolution proceeds by life cycle repatterning*.

The rationale behind these two new claims has not changed with respect to those centred on development. The main idea remains that the production of variation can significantly affect the direction of evolution, no less than selection and drift (Stern, 2000). This is possible because such variation is structured, rather than isotropic, and thus instructive – i.e., potentially able to influence the direction of evolution – rather than merely permissive – i.e., only necessary for evolution under natural selection (Fusco, 2015; Jaeger, 2019 this volume). From the “more elevated” view point of the life cycle, however, it is possible to contemplate the possible source of variation more inclusively. There are many kinds of evolutionary change that cannot be qualified as changes in developmental pathways or their control, and that are instead modifications of specific features of the structure of the life cycle, such as its articulation into one or more organizational forms, or the specific mode of reproduction of one of these to the next.

Life cycle evolution

In the view of a variational approach to the study of evolutionary change (Wagner and Altenberg, 1996; Salazar-Ciudad, 2006), one of the directions of development of the so called *extended evolutionary synthesis* (Müller, 2017), the evolution-of-life-cycle perspective exposes a multidimensional space of variation that goes beyond the already vast space of developmental variation with its genetic and environmental modulations (Moczek, 2019 this volume; Gilbert, 2019 this volume), and that obviously includes it as a subspace.

Selectable variation can emerge at any developmental stage of any organizational form of the organism. Sorting at the level of variation within an organizational form is standard (although developmentally informed) phenotypic evolution. However, other changes at the level of the whole cycle can occur. Here are a few examples.

- *A new organizational form can be added to the cycle.* The life cycle of many red algae (e.g., *Polysiphonia*) includes three generations: gametophyte, carposporophyte and tetrasporophyte. The diploid carposporophyte, which develops from a fertilized egg cell and asexually generates tetrasporophytes by means of diploid (unreduced) carpospores, intercalates between a gamete-producing gametophyte generation and a (meio)spore-producing sporophyte generation. This three-generation life cycle is thought to have evolved from a primitive cycle with biphasic alternation between gametophyte and sporophyte generations (Yang *et al.*, 2016). While the tetrasporophyte seems to correspond to the primitive sporophyte, actually the carposporophyte qualifies as an evolutionary novelty (Minelli and Fusco, 2005). However, homologies in life cycle traits, especially if a strictly historical concept of homology is applied (see Minelli and Fusco, 2013), are not easy to establish (see DiFrisco, 2019 this volume)
- *A primitive organizational form can be suppressed in the cycle.* In some brown algae (e.g., *Fucus*), the primitive haplodiaplontic cycle with alternation of generations has evolved into a monogenerational diplontic cycle. The gametophytic organizational form has been suppressed and the diploid sporophyte, by meiosis, produces haploid gametes, rather than spores, in a cycle that structurally does not significantly differ from that of mammals. In the cnidarian class Cubozoa (box jellyfish), the primitive multigenerational metagenetic cycle, with an alternation of a sexually reproducing medusa and an asexually reproducing polyp, has evolved into a monogenerational cycle. Cubozoan polyps go through a metamorphosis and become medusae, rather than asexually generating them. In these cnidarians the polyp generation has been assimilated into the medusa generation as an early develop-

mental phase of the latter. The polyp organizational form as such has been suppressed.

- *The relative predominance (however defined) of different organizational forms can be altered.* In modern angiosperms, the sporophyte generation (the generally macroscopic, autotrophic plant) is dominant with respect to the generation of the gametophyte, that at maturation consists only of the few cells of the embryo sac (female gametophyte) and pollen grain (male gametophyte). Both male and female gametophytes conduct a non-autonomous existence, protected and nourished by the parental sporophyte. However, according to the so called *antithetic theory* of land plant evolution (see Haig, 2008), this condition has evolved from the opposite condition, where the dominant generation was that of the gametophyte, with the sporophyte actually parasitic on it (a condition similar to that found in extant mosses) (Kenrick, 2017).
- *The reproductive mode of one or more organizational forms can be modified.* Parthenogenesis has evolved independently multiple times from amphigonic reproduction in monogenerational (e.g., fish, amphibians and squamate reptiles) and multigenerational (e.g., cladocerans among crustaceans and aphid among the insects) life cycles of animals (Simon *et al.* 2003), as well as in plants, where processes related to parthenogenesis are commonly referred to as apomixis (e.g., *Hieracium* and *Taraxacum*; Van Dijk, 2009).

There are important taxonomic groups in which interspecific diversity is largely a matter of variation in life cycle. Among these are the green algae (Gastineau *et al.*, 2014), red algae (Lee, 2008), cnidarians (Fautin, 1992) and trematodes (Galaktionov and Dobrovolskij, 2003). In all these cases, speaking about a “typical life cycle” is more a mystification than a simplification.

Difficulties around the corner

The characterization of a life cycle, a necessary step for any comparative analysis in an evolutionary context, strongly depends on the possibility of distinguishing the reproductive events, with the value of a transition to a new generation, from the developmental processes, which are instead transformations of the individual. This is not always as easy as it might seem (see DiFrisco, 2019, this volume; Fusco and Minelli, in press), and cases that are difficult to classify are not rare. Evolutionary processes of change are evidently not compelled to respect the limits imposed by our categories. For instance, there are situations where metamorphosis (a developmental process) can fade into asexual reproduction, when, as in many marine invertebrates, most of the larval body is discarded and the young derives from a small number of *set-aside cells*, or

even, as in the bivalve *Mutela bourguignati*, from a larval bud (Fryer, 1961). Are there one or two generations in the cycle of this bivalve? Yet another example is when reproduction blends into development, a very common situation found in many colonial marine invertebrates, like bryozoans or corals. Here, the asexual reproduction of the zooids actually takes on the meaning of growth at the level of the whole colony. A final example will further highlight how much our pre-established classifications can condition the interpretation of an organism's life cycle. All mammals are considered to have a monogenerational diplontic life cycle. However, the armadillos of the genus *Dasypus* exhibit obligate polyembryony, i.e. more than one embryo constitutively develops from a single zygote. If one considers polyembryony as a form of asexual reproduction at a very early (embryonic) stage of development, these mammals actually exhibit an alternation of sexual and asexual generations, a metagenetic cycle not different from that of most cnidarians.

Conclusions

Beyond introducing a new slogan for evo-devo, "life cycles evolve", this more inclusive view on the "unit of evolution" has some more profound implications. It exposes the fact that both development and reproduction are incomplete causal factors in the continuity of life through generations. At the same time, it shows that the way development and reproduction are associated in the life cycle, and the capacity of the life cycle to change in time (life cycle evolvability) are actually the means through which living systems can persist across vast spans of time. The life cycle and its evolution is the core of the persistence of life.

A sparse but lively literature demonstrates that life cycle evolution is a challenging subject of study (Valero *et al.*, 1992), where different kinds of evidence and theories meet, from palaeobiology (e.g., Taylor *et al.*, 2009), life-history trait evolution (e.g., Louhi *et al.*, 2013), gene expression (e.g., Bowman *et al.* 2016; Kenrick, 2017), natural selection (e.g., Mable and Otto, 1998; Szövényi *et al.*, 2013; Rescan *et al.*, 2016; Scott and Rescan, 2017), to evolvability (e.g., Minelli and Fusco, 2010). A merger between these diverse lines of investigation, together with a new awareness of the place of development within the broader context of the life cycle in ongoing research in developmental evolution, may have valuable consequences for the evo-devo research agenda.

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