

Essay review

The circle of life

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Cells to Civilizations: The principles of change that shape life.

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The origin of human individuals, and the societies they compose, can be viewed as the product of four processes: evolution, development, learning, and culture. In *Cells to Civilizations*, Coen sets himself the ambitious task of not only examining each of these processes and the relations between them, but also of distilling a unifying set of principles common to all of them: “life’s creative recipe”.

This book does not represent the first attempt to draw common ground between evolution and processes of development, learning, and culture. For example, researchers such as Cavalli-Sforza and Feldman (1981), Richerson and Boyd (2005), and others argue that the social learning of cultural traits is itself a type of Darwinian natural selection, which parallels genetic evolution in important ways. Similarly, research on neural Darwinism posits a process of competition and selection between neural groups inside the brain (Edelman, 1987), allowing learning and behaviour to be themselves viewed as evolutionary processes. But crucially, the approach taken in such work is to show how culture, or learning, can themselves be described as instances of evolution by natural selection. By contrast, while Coen recognises that evolution is fundamental in the sense that it preceded the origin of the other three processes, and so laid the foundation for them, he does not aim to explain development, learning, or culture by framing them in Darwinian terms. Rather, instead of privileging evolutionary explanations, he attempts to identify seven common and fundamental principles that underly all four processes. An important part of Coen’s explanatory strategy is then to focus on feedback cycles between these processes, for example, feedback between competition and cooperation during the major evolutionary transitions (Maynard Smith and Szathmáry, 1995). While I find no particular reason why the seven principles that Coen chooses should be taken as *the* most suitable for explaining life’s transitions, I will argue that Coen is right to emphasise feedbacks. In particular, I suggest that evolutionary and cultural theory could especially benefit from taking them into account more explicitly in future work.

What, then, is life’s creative recipe according to Coen? The first ingredient is *population variation*. The role of this in evolution will be familiar to all – put simply, natural selection relies on some individuals having different traits, for otherwise there is nothing to select between. But the differentiation of cells into specialised types (skin, liver, hair etc.) during the development of a multicellular organism also requires variation. While natural selection works off chance genetic differences (mutations), Coen describes how cellular differentiation relies on variation in protein levels within cells (this variation affects and is affected by cell signalling, which can in turn lead to cellular differentiation). Learning, in turn, requires a population of neurons that vary in their firing rates, while cultural change requires variation in individual talents and ideas.

Now at first blush, there might seem to be only a passing resemblance between these four types of variation. After all, isn’t the differential firing rates of neurons, driven by differences in sensory input, very different from random genetic mutations or creative cultural innovations? What unifies them, Coen argues, is their role in fueling a double feedback loop between *reinforcement* and *competition*, the next two ingredients in our recipe. Reinforcement is a

tendency for things to boost their own levels in a population – to make more of themselves. Individuals reproduce; some molecules can catalyse their own production; neurons that tend to fire together increase the strength of the synaptic connection between them; attractive cultural traits are valued and imitated by other individuals. This leads to a rich get richer process through a positive feedback loop. But reinforcement alone would not lead to interesting outcomes – things would just increase in absolute number. Moreover, an increase in number must inevitably lead to increased competition for limiting resources. Individuals compete for food; chemical reactions consume substrates and/or result in the production of reaction-inhibiting molecules; as an idea spreads, its novelty wears off.

Reinforcement and competition form a double feedback loop: reinforcement initially acts to increase absolute number, but as it does so it creates conditions that put the breaks on itself, leading to negative feedback through increased competition. This double loop of reinforcement (positive feedback) and competition (negative feedback) leads to the fixation of adaptations in a population of individuals, spatial patterns in the development of multicellular organisms, the association of actions with rewards inside brains, and the spread of cultural traits and the human drive to innovate. The feedback loops produce these interesting results because of variation. Variation provides different initial conditions; these initial differences are then magnified by positive feedback.

However, too much variation can be a bad thing. If things continually change, then cumulative adaptations cannot be built, stable patterns of cell differentiation cannot arise, and culture cannot build upon itself over time. In evolution, this problem is known as the trade-off between variation and heredity. Life requires variation, but it also requires *persistence*. Some persistence follows immediately from properties of the physical world, such as chemical stability. But persistence has itself increased through time. For example, the first protocells evolved membranes that prevented their constituent molecules from diffusing away, allowing their molecular patterns to persist through time. Similarly, humans developed the ability to build artifacts, and ultimately written language, allowing cultural innovations to persist in time through the generations. In fact, a defining feature of a major evolutionary transition is the creation of persistence (heredity) at a new level of biological organisation, such as a multicellular organism or a eusocial insect colony (Maynard Smith and Szathmary, 1995). How persistence originates is therefore a fundamental question for understanding all of life’s transitions. However, Coen tends to take it as a given, as something that doesn’t warrant further explanation. For a book that aims to identify the key processes that drove the transitions from cells to civilisations, this is problematic.

Life beyond the first simple replicating molecules would also not be possible without *cooperation*. Persistence of large genomes, and hence the evolution of increasingly complex life, requires accurate copying. But accurate copying requires replicase enzymes. Without these, genomes containing more than approximately one hundred base pairs could not be sustained (Eigen, 1971; Maynard Smith and Szathmary, 1995). However, replicase enzymes must themselves

be coded for by genomes, and a hundred base pairs contains insufficient information to do so. How, then, could the first genome long enough to code for enzymes arise¹? The answer lies in cooperation: several primitive genomes, each less than one hundred base pairs in length, could together code for replicate enzymes. Once achieved, this cooperation then allowed the origin of longer genomes, the persistence of more information, and ultimately, more complex life.

Successful cooperation, however, is not guaranteed. This is an important point, which Coen tends to gloss over at times by writing as if it were inevitable. One problem is that if the cooperating entities consume a common resource, then the type that consumes the resource at the fastest rate will tend to competitively exclude the others² in a “Tragedy of the commons” (Hardin, 1968). This is thought to be the case at the origin of life, where the first replicating molecules would have competed for the common monomers that each needed for their replication. An analogous problem arises when attempting to explain the cooperative production of a shared resource, such as an enzyme that increases the speed or accuracy of replication. Such enzymes would be costly to produce, in terms of the time and energy spent on their production that could otherwise be used directly for replication. Yet because the enzymes are physically separate from the replicators that produce them, they can be used by any molecule nearby. As a result, they are examples of public goods.

The production and consumption of public goods, then, is a universal problem of life, faced by the first molecules through to modern human societies. How is it solved? The answer often involves population structure (Hamilton, 1964; Wilson, 1975). Populations are typically not well-mixed, such that any pair of individuals would be equally likely to interact. Instead populations are often viscous, such that the same individuals, and their offspring, tend to keep on interacting with each other through time. Such spatial structure can favour cooperation in two ways. First, it provides a localisation of the benefits of cooperation. For example, viscosity means that enzymes will tend to stay close to the molecules that produce them, so on average cooperating molecules might receive more enzyme than non-cooperating ones, and hence replicate themselves at a faster rate (Michod, 1983). In the social evolution literature, this is known as direct benefits to cooperation (West et al., 2007). Second, spatial structure means that interacting individuals tend to be genetic relatives. This means that a cooperator is more likely to end up interacting with another cooperator than a non-cooperator would be. Consequently, cooperators are again likely to receive, on average, a greater share of the benefits of cooperation. This is known as kin selection (Hamilton, 1964), or the evolution of cooperation by indirect benefits.

During the early stages of life, both of these routes to cooperation would have been enhanced by the encapsulation of groups of replicators inside cell membranes (Szathmary and Demeter, 1987). Cell membranes would have prevented beneficial enzymes from diffusing away, thus increasing the direct benefits

¹This is known as Eigen’s Paradox (Eigen, 1971).

²This is modelled formally by, for example, the Lotka-Volterra competition equations (see e.g. May 1976).

of cooperation to those molecules that produced them. They would also have ensured that cooperating molecules were more likely to interact with copies of themselves, and so enhanced kin selection. Coen refers to this as the replicators “being in the same boat”, using an analogy borrowed from Dawkin’s (1976) *The Selfish Gene*, and later expanded to encompass other levels of biological organisation by Wilson and Sober (1994). However, such explanations leave unanswered the question of how the individuals get themselves into the same boat in the first place (Powers et al., 2011; Szathmáry, 2011)?

For culture, Coen uses cooperation to refer to systems of reciprocity between individuals (Trivers, 1971), including between master and apprentice (his favourite example is between a young Leonardo da Vinci and his master Andrea Verrocchio), as well as trade and market exchanges. Yet the question of how the social institutions that support such cultural cooperation might arise³ is not raised. Again, how do individuals get themselves into a position where cooperation pays? Coen is silent on this fundamental question, because he tends to assume that the conditions for successful cooperation are entirely the result of exogenous physical factors, such as viscosity. While appealing to an exogenous spatial structure is the classic way of explaining cooperation in evolutionary biology, recent theory has shown that individuals can themselves actively create the conditions that select for increased cooperation (Powers et al., 2011), and that this construction of the social environment is fundamental to explaining the increased cooperation that occurs during major transitions (Szathmáry, 2011). Thus the conditions for successful cooperation, such as the degree of population structure, must be brought inside the system as variables, rather than simply treated as static parameters.

When it comes to development and learning, Coen tends to use the term cooperation to simply refer to the fact that things interact: multiple protein molecules influence the regulation of a gene’s expression, while more than one neuron is required for learning. Unfortunately, this sense of cooperation is quite different from that used in the evolutionary and cultural sections of the book, where cooperation is threatened by selfish interests. By contrast, in development and learning there is no cost to cooperation, and hence no opportunity for selfish behaviour. I would argue that one could view this type of cooperation as a *process*, and hence as one of Coen’s seven principles, while cooperation in the evolutionary and cultural senses is a *product* that is by no means certain to arise.

The next unifying principle of life that Coen identifies is *combinatorial richness*. Combinatorial richness means that there is an exponentially increasing number of ways of combining things, leading to very high dimensional spaces. Consequently the number of possible genomes, or brain states, or societies, is unimaginable. Evolution, development, learning, and culture can all do interesting things because of the vast size of the space of possibilities that they have to work with. However, there are two issues with this. First, Coen takes

³See, for example, North (1990) and Hurwicz (1996) for discussion of the importance and role of social institutions.

combinatorial richness as a given. But for evolution this requires indefinite hereditary replicators⁴, which relies on the origin of template copying. Similarly, combinatorial richness for culture arguably requires human language. As with cooperation, the conditions are presupposed when in fact they themselves require an endogenous explanation. Second, combinatorial richness is not always a blessing; the curse of high dimensionality is well known. Finding meaningful solutions in a high dimensional space often requires modularity (Watson, 2006), be it modularity in a space of possible gene combinations, or modularity in a space of neuron connections. Modularity could therefore just as well be a principle of life as combinatorial richness. This is symptomatic of the fact that Coen does not attempt to justify the particular seven principles that he chooses. While the principles may be pedagogically useful, there is no argument given as to why they are both individually necessary and jointly sufficient to explain life's transitions.

The final ingredient in Coen's recipe is *recurrence*. Processes do not just come to a halt, but instead propel themselves forward. As an adaptation fixes in a population, it raises the bar and creates a new starting point for further mutations, and subsequent rounds of selection, to work from. As one cultural innovation spreads, it spurs others on to build upon these and come up with even better ideas.

So far, I have argued that for *persistence*, *cooperation*, and *combinatorial richness*, Coen does not address why the conditions necessary for their operation themselves obtain. However, he does stress the importance of feedback loops throughout the book, especially between *reinforcement* and *competition*, and *competition* and *cooperation*. Although the role of positive feedback is often overlooked in models of ecological and evolutionary processes (Crespi, 2004), it can explain how persistence, cooperation, and combinatorial richness increase over time.

Consider, for example, the origin of the population structures that support high levels of cooperation. Although some aspects of population structure are provided by the physical environment, population structure is also affected by genetic traits of the individuals that comprise the population. Thus, population structure is itself a product of natural selection, yet this point is often overlooked in models of social evolution. Powers et al. (2011) addressed this by considering a model where individuals carry two heritable traits. The first trait affects their social behaviour (cooperative or selfish), as in standard models. The second trait affects the bearer's population structure (such as a group size preference). Powers et al. then demonstrated that not only does population structure affect selection pressure on a cooperative trait, as in standard theory, but that cooperation in turn exerts indirect selection back on a population-structuring trait, favouring the creation of population structures that support itself. The result is a positive feedback process, where an initial increase in cooperation then selects for population structures that support further cooperation.

⁴These are replicators that can take on a number of states much larger than the number of individuals in the population (Maynard Smith and Szathmáry, 1995).

Such a process provides an explanation for how individuals can start out living in a population structure that supports little cooperation, yet evolve to ultimately live in one that supports large amounts of cooperation. Crucially, this can occur without any exogenous change in population structure, and without any direct selection on the population-structuring trait. In extreme cases, it can lead to the creation of groups with such a cohesive population structure, and such a high level of cooperation between their constituent individuals, that we come to recognise the groups as evolutionary individuals in their own right. Examples include the encapsulation of previously loose groups of replicating molecules inside cell membranes, and the encapsulation of previously unlinked genes into chromosomes. An analogous process may also operate in the cultural domain, leading to the creation of social institutions that foster large-scale cooperation. These can all be viewed as processes of *social niche construction*⁵, where evolution of individual traits (such as individual production of a cell membrane polymer) transforms the social environment into one that selects for much higher levels of cooperation.

Can such a feedback process operate completely from scratch, from an initial condition where no cooperation at all is favoured? The study by Powers et al. (2011) suggests not, since initiation of the positive feedback loop requires that a small, random, change in population structure selects for some small increase in cooperation. When starting from a well-mixed population, this condition is unlikely to hold. However, as Coen stresses, such an initial condition is unrealistic. Physical and chemical properties mean that some degree of viscosity was likely to be present even at the origin of life. This initial spatial structure, which would support some degree of cooperation, could bootstrap the positive feedback process that I have described. Similarly, the creation of human social institutions could bootstrap from the fact that the primate ancestors of humans already lived in cooperative social groups, and were already able to perform social learning.

The creation of cohesive social groupings would also create a new, higher level of persistence. The same feedback process that leads to increased cooperation therefore also leads to increased persistence. For example, by preventing diffusion, the creation of a cell membrane means that copies of the same molecules will keep on interacting with themselves across generations. This is persistence at the group level. Moreover, the process can repeat in a hierarchical fashion: single replicating molecules combined into cells, cells combined into multicellular organisms, and multicellular organisms combined into social groups. This fits with Coen's principle of recurrence. It also fits, I would suggest, with an increase in combinatorial richness – as entities combined to form a new individual, they brought together different, pre-adapted gene combinations⁶ (Watson, 2006; Mills and Watson, 2011). This would allow new parts of genetic space to be accessed.

⁵Following the use of niche construction by Odling-Smee et al. (2003).

⁶This argument applies to the egalitarian major transitions (*sensu* Queller 1997), in which different types or species of individual combined through symbiosis to form a new, higher-level unit. An example would be the origin of the eukaryotic cell.

I think, additionally, that Coen could go further in incorporating feedbacks between learning and evolution. For example, the Baldwin effect (Hinton and Nowlan, 1987) describes a process in which learning can guide genetic evolution, by creating selection pressure favouring those genotypes that are most readily able to learn salient features of the environment. This process ultimately leads to canalisation of the salient environmental feature into the genotype itself. Learning thus allows genetic evolution to find solutions that would otherwise be very difficult to reach.

Likewise, feedback between culture and genetic evolution is also important, yet is overlooked in the book. One obvious example of culture changing selection pressure on genes is the origin of dairy farming, which favoured the spread of mutant genes that continued lactase production into adulthood. Coen is wary to view culture as an evolutionary process, citing the well-known difficulties of treating cultural traits as high fidelity replicators, as is espoused in the memetic approach to cultural evolution (*sensu* Dawkins 1976). However as Boyd and Richerson (2000), Jablonka and Lamb (2005), and others stress, cumulative cultural evolution need not require digital replicators that are the exact analogues of genes, copied intact from brain to brain. What is required to treat culture in a Darwinian fashion is a system of heritable phenotypic variation, but this can arise through the use of (genetically encoded) social learning rules, without exact copies of some underlying mental representation being made. All that matters is that a population of individuals are able to imitate a cultural phenotype to some degree of accuracy (Boyd and Richerson, 2000). The social learning rules and heuristics that allow humans to do this (and the supporting neural circuitry) have presumably co-evolved with culture, in another example of positive feedback.

Consequently, I would argue that Coen is wrong to dismiss Darwinian approaches to understanding cultural change. For not only is a Darwinian approach to culture not hostage to Dawkinsian memetics, it has also proved itself useful in tackling a variety of problems. These range from understanding the rise of hierarchical polities (Turchin and Gavrillets, 2009), to explaining changes in the size and shape of artifacts in the archaeological record, such as handaxes, over time (Kempe et al., 2012). By contrast, the non-Darwinian cultural framework that Coen suggests lacks the analytical foundations to do so. For if we wish to view some cultural traits and institutions as adaptive, as serving a function for their bearers, then there really is no alternative to a Darwinian mode of explanation (Rosenberg, 2012, Chapter 12).

In conclusion, then, while I view Coen's seven principles to be pedagogically useful, I find them less fruitful as analytical research tools when compared to established methods, such as gene-culture co-evolution models. I think, however, that Coen is right to highlight the importance of positive feedback within and between genetic evolution, development, learning, and culture. Here I have expanded further on that point, and have argued that a process of social niche construction – positive feedback between individual traits that affect the social environment and those that affect cooperation – can explain the increased cooperation, persistence, and combinatorial richness that occurred during life's

major transitions.

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