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EVOLUTION WITHOUT VARIATION AND SELECTION

LIANE GABORA AND MIKE STEEL

Abstract. A central tenet of evolutionary theory is that it requires variation upon which selection can act. We describe a means of attaining cumulative, adaptive, open-ended change that requires neither variation nor selective exclusion, and that can occur in the absence of generations (i.e., no explicit birth or death). This second evolutionary process occurs through the assimilation, restructuring, and extrusion of products into the environment by identical, interacting Reflexively Autocatalytic and Food set-generated (RAF) networks. Since there is no self-assembly code, it is more haphazard than natural selection, and there is no discarding of acquired traits (a signature characteristic of natural selection). We refer to this more primitive process evolutionary process as Self–Other Reorganisation because it involves internal self-organising and self-maintaining processes within entities, as well as interaction between entities. In the extreme, it can work with just one entity but it differs from learning because it can operate in groups of entities and produce adaptive change across generations. We suggest that this more primitive process is operative during the initial stage of an evolutionary process, and that it is responsible for both the origin and early evolution of both organic life, and human culture. In cultural evolution, this 'evolution without variation' process can increase homogeneity amongst members of a group and thereby foster group identity and cohesion.

Keywords: autocatalytic network, cultural evolution, evolution, origin of life, social learning

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1. Introduction

A central tenet of evolutionary theory is that evolution requires variation upon which selection can act. This follows from Darwin's theory of natural selection, which holds that evolution is due to differential replication of randomly generated heritable variations in a population over generations, such that some traits become more prevalent than others. Darwin's theory of evolution by natural is the foundation of modern biology and provides a unifying principle for describing species, well after the origin of life. Darwin's theory arose in response to the paradox of how organisms accumulate adaptive change despite traits acquired over a lifetime being eliminated at the end of each generation. His solution was to come up with a population-level explanation: although acquired traits are discarded, inherited traits are retained, so evolution can be explained in terms of preferential selection for those inherited traits that confer fitness benefits on their bearers. However, neither origin of life research nor cultural evolution research is plagued by the problem that acquired changes are extinguished at the end of a generation; therefore, in these domains, the paradox that Darwin's theory was designed to solve does not exist [17]. Accordingly, it would seem appropriate to pay particular attention in these domains to the role of epigenetic and non-Darwinian (e.g. Lamarckian processes) [41, 42, 69]. However, it is widely assumed that any kind of evolutionary process requires variation and selection. Even in research on cultural evolution—which is sometimes (though not universally[1]) regarded as Lamarckian—it is generally assumed that variation and selection are what enables evolution to take place (e.g., [3, 6, 50]).

Indeed, although the term 'evolution' is sometimes assumed to be synonymous with variation and selection, it is increasingly more widely accepted that non-Darwinian processes play a role in evolution. This paper goes a step further: we argue that evolution is possible in the *absence* of variation and selection. Although this has been suggested before [18], here, we formulate

[1]Some maintain that Lamarckism requires genetic transmission to biological offspring, a view held by early biologists (e.g., [58]), though current scholars (e.g., [50]) sometimes take a more equivocal view.

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the argument in a more rigorous fashion, based on the type of structure an entity must have to engage in this kind of evolutionary process. This is important, because although entities of many kinds change due to acquired traits (e.g., a rock tumbling down a stream will acquire rounded edges), this generally cannot be said to be adaptive or to contribute to the entity's survival or replication (indeed, in the case of the rock, the process that rounds its edges culminates in its disintegration.)

The paper begins with a list of definitions of terms and a table of the acronyms used. Next, we introduce the mathematical framework that will be used to develop the argument. We then model evolution in the absence of variation and selection with this framework (with further mathematical details provided in the Appendix). Next, we discuss what sort of structure is able to evolve without variation and selection. We conclude with a discussion of the implications.

2. Preliminaries

We begin by alphabetically listing and defining key terms used in this paper. We believe this is necessary in order to maintain clarity, since some miscommunication has arisen due to inconsistencies in how evolutionary concepts are applied in the sciences and social sciences[2].

- **Acquired trait:** a trait obtained during the lifetime of its bearer (e.g., a scar, a tattoo, or a memory of a song) and transmitted horizontally (i.e., laterally).

[2]Note that vertical and horizontal transmission must be defined with respect to the relevant evolutionary process. A common error is to refer to the transmission of cultural information from parent to offspring as vertical transmission (e.g., [6]). Although the individuals in question are in a parent–child relationship with respect to their status as biologically evolving organisms, with respect to their status as participants in cultural evolution, this need not be the case. Indeed, although childbirth entails one mother and one father, there is no limit to the number of 'parental influences' on the 'birth' of an idea. A related error is to say that in cultural evolution, there is a third form of transmission, namely, oblique transmission, in which traits are transmitted from non-kin members of the parental generation (e.g., [6]), because as far as cultural evolution is concerned it is irrelevant whether the information comes from biological kin or non-kin. In a similar vein, although dual inheritance theorists speak of culture as a second form of inheritance [30, 56, 67, 52], the distinguishing feature of an inherited trait is that it is transmitted vertically (e.g., from parent to offspring) by way of a self-assembly code (e.g., DNA) and is therefore not obliterated at the end of a generation. This is not the case with respect to cultural traits [17], nor is it even the case for all biological traits.

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- **Culture:** extrasomatic adaptations—including behavior and artifacts—that are socially rather than sexually transmitted.
- **Darwinian (or 'selectionist') process:** an evolutionary process —i.e., a process that exhibits cumulative, adaptive, open-ended change—occurring through natural or artificial selection.
- **Darwinian threshold:** transition from non-Darwinian to Darwinian evolutionary process [69, 64].
- **Generation:** a single transition period from the internalized to the externalized form of a trait.[3]
- **Selection:** differential replication of randomly generated heritable variation in a population over generations such that some traits become more prevalent than others. Selection may be natural (due to non-human elements of the environment) or artificial (due to human efforts such as selective breeding), and it can occur at multiple levels, e.g., genes, individuals, or groups [46](Lewontin, 1970).
- **Self-assembly code:** a set of self-replication instructions.
- **Self–Other Reorganisation (SOR):** a theory of how both culture, and early life, evolve through communally exchanging, self-organizing networks that generate new components through their interactions, based on post-modern synthesis theory and findings in biology.

[3]Note that, with respect to biological evolution, a new generation generally (though not in horizontal gene transfer) begins with the birth of one or more organism(s). With respect to cultural evolution, a new generation begins with the expression of an idea (which is considered one transmission event). Thus, over the course of a single discussion, an idea (a cultural trait) may undergo multiple generations. It can be said that cultural evolution proceeds more quickly than human biological evolution, since the lengthy period we associate with biological generations, from birth through to reproductive maturity and parenthood, is in general significantly longer than the stretch of time between when an individual acquires a cultural trait (e.g., an idea) and then expresses (their own version of, or their own take on) that cultural trait.

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It is important to emphasize that we are using the term 'selection' in its technical, scientific sense. The word 'selection' also has an 'everyday' sense in which it is synonymous with 'choosing' or 'picking out'. One could say that selection—in the everyday sense of the term—occurs in a competitive marketplace through the winnowing out of superior products. However, the discussion here concerns selection in the scientific sense of the term.

The acronyms used in this paper are listed alphabetically in Table 1.

Acronym	**Meaning**
CRS	Catalytic Reaction System
RAF	Reflexively Autocatalytic and Food set-generated (F-generated)
OOL	Origin of Life
OOC	Origin of Culture
MR	Mental Representation
CCP	Cognitive Catalytic Process
SOR	Self–Other Reorganisation

Table 1. Abbreviations used throughout this paper.

3. Autocatalytic networks

The type of evolution without variation and selection process that we will describe involves entities that (1) have an organisation that is self-maintaining (i.e., the entities have a structure, and a mechanism for maintaining that structure), and (2) interact with each other by way of their environment. Autocatalytic networks provide a way to model such entities in origin of life (OOL) and origin of culture (OOC) settings.

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The theory of autocatalytic networks grew out of studies of the statistical properties of *random graphs* consisting of nodes randomly connected by edges [10]. As the ratio of edges to nodes increases, the size of the largest cluster increases, and the probability of a phase transition resulting in a single giant connected cluster also increases. The recognition that connected graphs exhibit phase transitions led to their application to efforts to develop a formal model of the OOL, namely, of how abiogenic catalytic molecules crossed the threshold to the kind of collectively self-sustaining, self-replicating, evolving structure we call 'alive' [41, 40]. In the application of graph theory to the OOL, the nodes represent catalytic molecules and the edges represent reactions. It is exceedingly improbable that any catalytic molecule present in the primordial soup of Earth's early atmosphere catalysed its own formation. However, reactions generate new molecules that catalyse new reactions, and as the variety of molecules increases, the variety of reactions increases faster. As the ratio of reactions to molecules increases, the probability increases that the system will undergo a phase transition. When, for each molecule, there is a catalytic pathway to its formation, they are said to be collectively *autocatalytic*, and the process by which this state is achieved has been referred to as *autocatalytic closure* [41]. The molecules thereby become a self-sustaining, self-replicating structure (i.e., a living protocell [36]). Thus, the theory of autocatalytic networks has provided a promising avenue for modelling the OOL and thereby understanding how biological evolution began [70].

Autocatalytic networks have been developed mathematically in the theory of Reflexively Autocatalytic and Food set-generated (RAF) networks [37, 60]. The term *reflexively* is used in its mathematical sense, meaning that every element is related to the whole. The term *food set* refers to the reactants that are initially present, as opposed to those that are the products of catalytic reactions. Autocatalytic networks such as RAFs have proven useful for modelling the origins of both biological evolution [37, 60, 62, 70] and cultural evolution [12, 13, 22, 24, 23][4]. In application of the theory to culture, the products and reactants are not catalytic molecules

[4]For related approaches, see [1, 5, 53]

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but culturally transmittable *mental representations* [5] (MRs) of experiences, ideas, and chunks of knowledge, as well as more complex mental structures such as schemas and scripts. Table 2 summarises how RAF theory terms apply in biological and cultural/cognitive settings. The fact that RAFs have proven useful in both these domains suggests that RAF theory may provide a broad conceptual framework that is applicable to the origins and early stages of diverse evolutionary processes.

RAF Theory	**Origin of Life (OOL)**	**Origin of Culture (OOC)**
node	catalytic molecule	mental representation (MR)
edge	reaction pathway	association
cluster	molecules connected via reactions	MRs connected via associations
connected graph	autocatalytic closure [40, 41]	conceptual closure[6] [12]

TABLE 2. Application of graph theoretic concepts to the origin of life and origin of culture.

We now summarise the key concepts of RAF theory. A *catalytic reaction system* (CRS) is a tuple $\mathcal{Q} = (X, \mathcal{R}, C, F)$ consisting of a set X of molecule types, a set $\mathcal{R}$ of reactions, a catalysis set C indicating which molecule types catalyse which reactions, and a subset F of X called the food set. A *Reflexively Autocatalytic and F-generated* set (i.e., a RAF) is a non-empty subset $\mathcal{R}' \subseteq \mathcal{R}$ of reactions that satisfies the following two properties:

(1) *Reflexively autocatalytic (RA)*: each reaction $r \in \mathcal{R}'$ is catalysed by at least one molecule type that is either produced by $\mathcal{R}'$ or is present in the food set F; and

(2) *F-generated*: all reactants in $\mathcal{R}'$ can be generated from the food set F by using a series of reactions only from $\mathcal{R}'$ itself.

[5]Although we use the term 'mental representation,' our model is consistent with the view (common amongst ecological psychologists and in cognition and quantum cognition communities) that what we call mental representations do not 'represent' but instead act as contextually elicited bridges between mind and world.

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A set of reactions that forms a RAF is simultaneously self-sustaining (by the F-generated condition) and (collectively) autocatalytic (by the RA condition) because each of its reactions is catalysed by a molecule associated with the RAF. A CRS need not have a RAF but when it does, there is a unique maximal one (the maxRAF). Moreover, a CRS may contain many possible RAFs, and it is this feature that allows RAFs to evolve, as demonstrated both in theory and in simulation studies, through selective proliferation and drift acting on the RAFs that are subsets of the maxRAF[37, 62].

In the OOL context, a RAF emerges in systems of polymers (molecules consisting of repeated units called monomers) when the complexity of these polymers (as measured by their maximum length) reaches a certain threshold [41, 51]. The phase transition from no RAF to a RAF incorporating most or all of the molecules depends on (1) the probability of any one polymer catalyzing the reaction by which a given other polymer was formed, and (2) the maximum length (number of monomers) of polymers in the system. This transition has been formalised and analysed mathematically, and by using simulations. Moreover, RAF theory has been applied to real biochemical systems [33, 34, 35, 37, 51], ecology [7] and cognition [22, 24]; the theory has also proven useful for identifying how phase transitions might occur and at what parameter values.

4. A RAF model of evolution without variation and selection

We now demonstrate a more primitive non-Darwinian form of evolution mathematically using RAF networks. We begin by describing a simple process involving a group $\mathcal{G}$ of indistinguishable entities as illustrated in Fig. 1. These entities can be described as identical RAFs. They may be CRSs such as those associated with very early life [2, 8, 16, 27, 38, 59, 64], artificial neural networks in a computational model of cultural evolution (e.g., [11, 25]), human semantic networks or some other structure we have never encountered.

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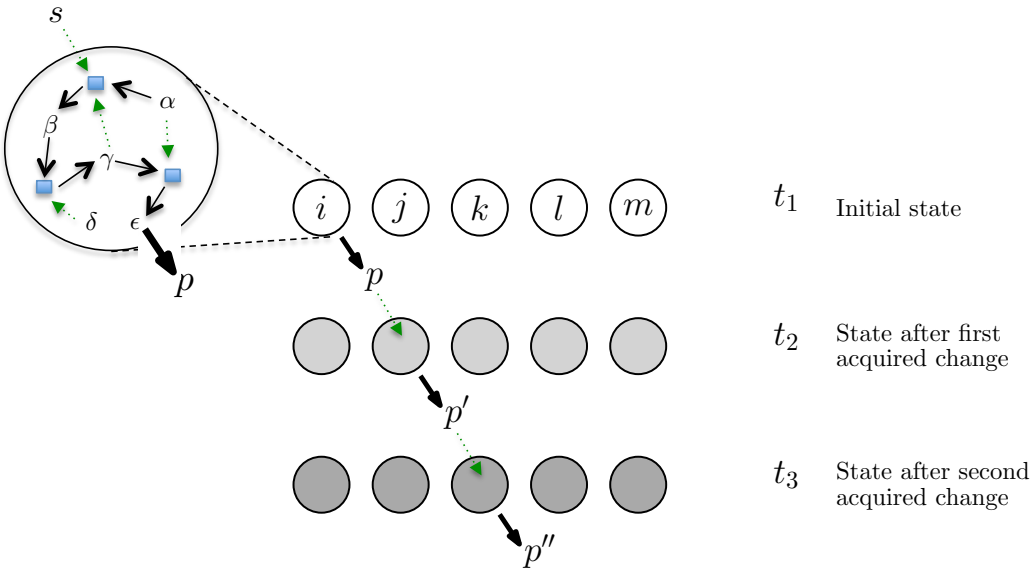

FIGURE 1. Identical entities exhibit cumulative adaptive change over time, as indicated by transition from light to dark, as a result of cumulative environmental changes, indicated by p, $p'\ldots$. The first product p, generated by i due to a stimulus s catalysing a reaction in the RAF structure for entity i. The particular structure illustrated on the left is a schematic example of a simple RAF (with molecule types $\alpha - \epsilon$ and s, reactions indicated by squares, and catalysis shown with dashed arrows; food set here is $F = \{\alpha, \delta, s\}$, and ϵ gives rise to p). The dashed product p in turn catalyses a reaction in the RAF structure of an entity at time t_2 leading to a transformed product p', and so on.

One entity in $\mathcal{G}$, which we call entity i, encounters a stimulus from the environment, which we refer to as s. Stimulus s triggers one or more catalytic reaction(s) in i. In a OOL scenario the reactions would be chemical reactions, while in a OOC scenario, they would be cognitive catalytic processes (CCPs) [22, 24]. This reaction (or chain of reactions) culminates in the generation of a product p into the environment, and product p confers some adaptive benefit on i. The product may have a protective function (for example, it may make the environment less inviting for a predator) or (in a cultural context) it may serve as a source of pleasure that enhances wellbeing (for example, a work of art). We can describe the result of this triggering event as a sequence of one or more reactions within the RAF structure of entity i that generates p and for which the initial reaction in the sequence is catalysed by s. For example, in the cultural

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context, s catalyses the formation of a cognitive catalytic process which is a transient process that is part of the RAF within the mind of individual i, as illustrated in Fig. 2(ii) of [25].

Having generated p, i returns to its initial state. The production of p yields an adaptive benefit for i, making i more resilient to degradation. Since the other entities are identical to i, p has an adaptive benefit for them as well. Moreover, since the other entities have the same structure as i and exist in the same environment as i, the ability to produce p percolates throughout the group $\mathcal{G}$.

The generation of p makes it possible to generate a new product, which confers even greater adaptive benefit than p, making the entities even more resilient. Thus, an entity j assimilates p, which triggers a catalytic reaction in j, resulting in p'. This way, each successive version of p paves the way for a newer version of p. We can view this step as a sequence of one or more reactions within the internal RAF structure of entity j in which p' (sourced from another entity) catalyses the generation of p' from p. Thus entity j benefits from the enhanced adaptive quality of p' over p. The ability to produce p' percolates throughout the group $\mathcal{G}$.

The entities in $\mathcal{G}$ continue to generate increasingly beneficial versions of the original p (e.g., $p', p'', p''', \ldots$), and they collectively come to possess the ability to generate and benefit from this family of products because of the catalysis of the internal RAF structure of entities by the products of other entities. Thus we have cumulative adaptive change over time. Notice that in this model neither the birth nor the death of entities occurs; it is the same set of entities at the beginning as at the end, and there is no competitive exclusion and no selection (as defined above) of entities.

4.1. **Modelling this process.** We consider a simple model, based on two processes (percolation and generation). First, let ρ denotes the rate of percolation of products (or knowledge or 'traces' of these products) through the group $\mathcal{G}$, with contact structure represented by a directed graph $D_{\mathcal{G}}$ (the nodes of this graph are the entities in $\mathcal{G}$, and the arcs indicate directed

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percolation links). For the second (generation) process, we let λ denote the rate (per entity) at which a new product is generated. Provided that the ratio ρ/λ is not too small, the entities evolve via cumulative, adaptive change, with the only variation being between those in $\mathcal{G}$ that have not yet switched to a new product and those that have[7]. Moreover, for large values of ρ/λ, each percolation step will be complete before the next new product is generated and so there will be no variation between the entities of their cultural products.

Conversely, as $\rho/\lambda \to 0$, the entities diverge from each other with respect to the products they generate and their complexity (i.e. the maximal number of improvements of any product at any given time for the entities in $\mathcal{G}$) is expected to be lower than in the previous scenario of shared cumulative adaptive change. We formalise this model more precisely, and provide a justification for these statements above, based on mathematical modelling, in the Appendix.

5. Why evolution without variation and selection is possible

We said earlier that to engage in evolution without variation and selection, the entities in question must possess a certain kind of abstract structure that can be described mathematically by RAFs. The entities must consist of a self-organizing network of components that generate new components through their interactions, and there must be communal interaction amongst these networks. We can refer to the 'evolution without variation and selection' process exhibited by such entities as Self–Other Reorganisation (SOR) [18, 19, 21, 65]. It does not involve competition and the survival of some at the expense of others, but the transformation of all. An entity changes through interactions with its world, which, in turn, alters its potential for future configurations. Like natural selection, SOR has mechanisms for preserving continuity and introducing novelty, but unlike natural selection, it is a low-fidelity Lamarckian process. The distinction between these two is summarised in Table 3 and illustrated in Fig. 2.

[7]This might be likely in an cultural setting when the entity generating a new product is equidistant from all the others or (more particularly in a social media context) where everyone sees something at the same time.

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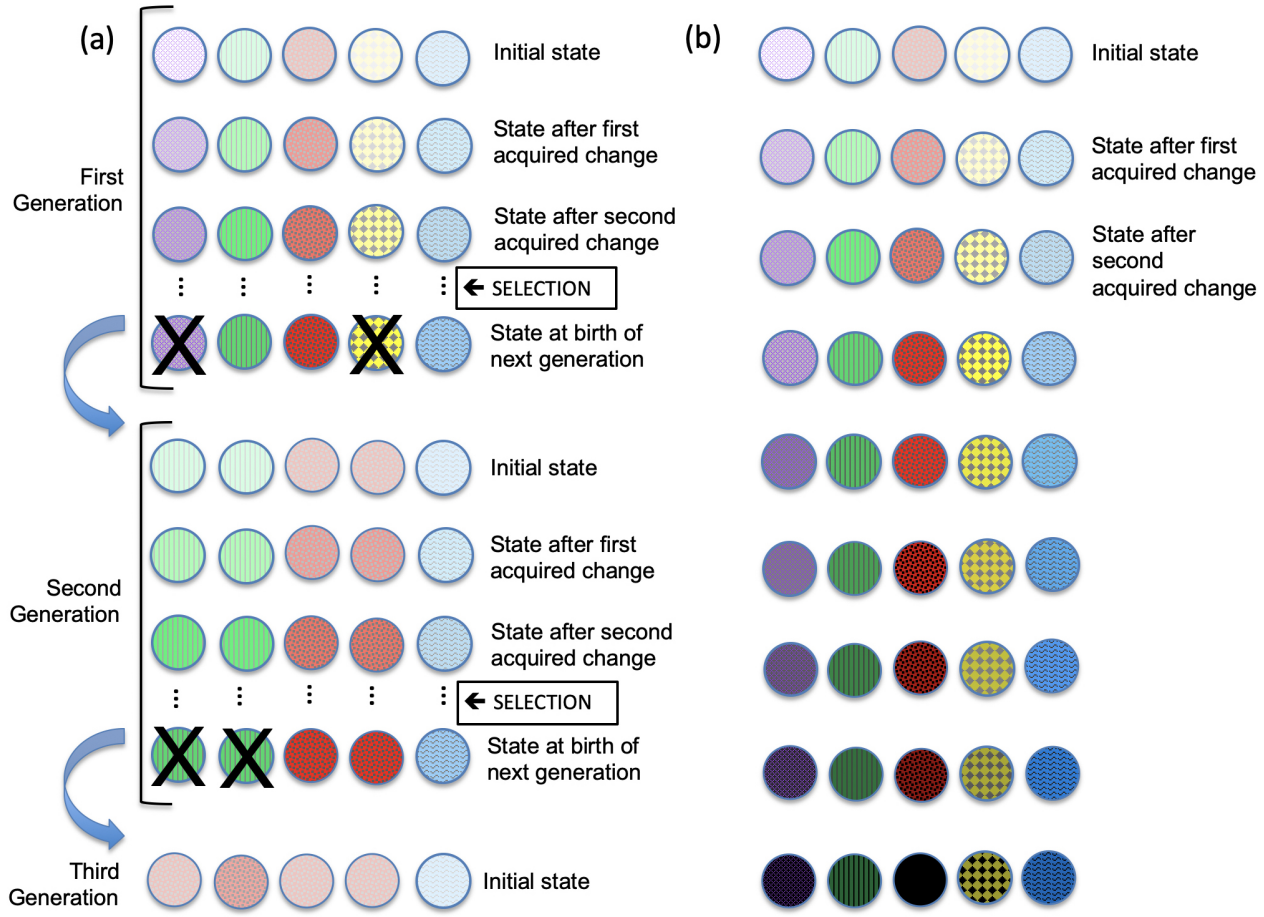

FIGURE 2. Comparison of (a) evolution through natural selection and (b) evolution by Self–Other Reorganisation (SOR). An X indicates that the entity was selected against (i.e., did not contribute to the next generation). (In the example shown in (b), there is variation but there need not be, as illustrated in Fig. 1). Individual entities are represented by circles, with variation among them represented by different patterns. In both (a) and (b), the darker the color the better adapted the individual (regardless of pattern). In (a), the darker color of one of the individuals in the third generation is due to mutation. Both (a) and (b) result in cumulative, adaptive change over time. However, the first is relatively slow because it works due to differential replication of randomly generated heritable variation in a population over generations, such that some traits become more prevalent than others (with acquired changes being discarded). Acquired traits are discarded at the end of each generation. The second is due to acquired change over time.

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Feature	**Variation–Selection**	**Self–Other Reorganisation (SOR)**
Unit of self-replication	Organism	Self-organising autocatalytic network
Preservation of continuity	Reproduction (vertical)	Communal exchange (horizontal)
Generation of novelty	Mutation, recombination	Creativity, catalysis, transmission error
Self-assembly code	DNA or RNA	None
High fidelity	Yes	No
Transmission of acquired traits	No	Yes
Type	Selectionist	Lamarckian (by some standards; see Footnote 1)
Evolution processes explained	Biological	Early life, horizontal gene transfer, culture

TABLE 3. Comparison between evolution through selection and evolution through Self–Other Reorganisation.

SOR is distinctly different from a Darwinian or selectionist process. In selectionist evolution, there are two kinds of traits: (1) inherited traits (e.g., blood type) transmitted vertically from parent to offspring by way of genes, and (2) acquired traits (e.g., a tattoo) obtained during an organism's lifetime, and transmitted horizontally among conspecifics. A selectionist explanation works in biology to the extent that retention of acquired change is negligible compared with retention of selected change; otherwise, the first, which can operate instantaneously, overwhelms the second, which takes generations. Transmission of acquired traits is avoided through use of a self-assembly code (such as the genetic code), which is a set of instructions for how to reproduce. Because a lineage perpetuates itself via a self-assembly code, inherited traits are transmitted but acquired traits are not.

Now let us turn to the earliest structures that could be said to be alive, prior to the evolution of something as complex as a DNA- or RNA-based self-assembly code. Without a self-assembly code, there were no vertically transmitted inherited traits; all change was horizontally transmitted (i.e., acquired). Therefore, the evolution of early life was not due to differential replication of heritable variation in response to selection; it was non-Darwinian [64, 69, 16].

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The situation is analogous for culture. In cultural evolution, there is no self-assembly code, and no vertically transmitted inherited traits; all change is acquired. One might suggest that natural language is a cultural self-assembly code. However, (1) natural language is not a set of encoded instructions for the self-replication of natural languages, and (2) culture does not exhibit the signature characteristics of evolution by way of a self-assembly code: lack of transmission of acquired traits; culture is characterised by horizontal—not vertical—transmission. Therefore, cultural evolution is not due to the mechanism Darwin proposed: differential replication of heritable variation in response to selection [14, 18]. Results from computation modelling suggest that to cross the Darwinian threshold from non-selectionist to selectionist evolution requires the emergence of a self-assembly code [64]. There is no evidence that culture has crossed this threshold, and it does not possess the sine qua non of having crossed it: vertical transmission and lack of transmission of acquired traits. It is, however, possible that culture is moving toward a 'cultural Darwinian threshold'; in other words, it may exist in the state biological life was in before the last universal common ancestor [68].

6. Implications

The feasibility of evolution in the absence of variation and selection (i.e., SOR) and the fact that early life and cultural evolution are both promising candidates for evolution by SOR implies that we must be cautious about applying the concepts and methodologies developed in a Darwinian evolutionary context in these two domains. Since biological acquired traits are usually (though not always) discarded, and since a self-assembly code must stay intact to preserve its self-replication capacity, the joining of bifurcations in biological lineages is infrequent; thus, a phylogenetic tree correctly captures the branching structure. Speciation makes inter-lineage transfers of information relatively rare in biological organisms. By comparison, since cultural acquired traits are not discarded, and there is no cultural self-assembly code, the joining of bifurcations in cultural 'lineages' is commonplace and thus the structure is network-like

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rather than tree-like [15, 47, 61]. Since cultural relatedness frequently arises through not just vertical transmission but horizontal (inter-lineage) transmission, there is extensive blending of knowledge from different sources. Extensive horizontal transmission gives a bushy, reticulated appearance to a phylogenetic tree, which is misleading, because it implies not just chronology but ancestry.

A related concern regarding the applicability of methods developed for selectionist evolutionary processes to culture has to do with convergent evolution, in which similar forms arise independently because they are alternative solutions within similar design constraints. Because biological organisms must solve many problems (reproduction, locomotion, digestion, etc.), the probability that a species will be mis-categorised because of convergent evolution (i.e., on the basis of how it solves any one problem) is low. Cultural artifacts, on the other hand, are generally constructed with a single use in mind (though artifacts developed for use in one context may be used to solve other problems; for example, a screwdriver may be used to open a can of paint. Therefore, for cultural outputs, the probability of mis-categorisation arising through the assumption that similarity reflects homology is significantly higher.

Some have claimed that in practice this does not invalidate the approach [28]. However, such conclusions come from analyses of datasets that involve little horizontal transmission (indeed, the creative blends that are the source of cultural novelty are often treated as 'outliers' and are intentionally discarded from analysis).

Such considerations have led some to develop network-based models of cultural evolution [4, 9, 11, 21, 20, 44, 47, 63]. This body of research suggests that horizontal transmission can significantly alter the pattern of relatedness. For example, a network-based analysis of Baltic psaltery data that incorporated not just superficial physical attributes but also abstract conceptual attributes (such as markings indicative of sacred symbolic imagery), it was possible to resolve ambiguities arising from a phylogenetic analysis and generate a lineage more consistent with other historical data [63]. Horizontal cultural transmission may involve change in

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superficial features despite a preservation of deep structure, as occurs in metaphor [45], analogy [26, 32], and cross-domain transfer, in which a source from one domain (e.g., music) inspires or influences a creative work in another (e.g., painting) [55, 57]. This kind of complexity and hierarchical structure cannot be captured without taking a network approach to cultural evolution, which provides further support for the theory that culture evolves through SOR.

Interestingly, similar issues arise with the simplest life forms. Because of phenomena such as mutualism, lineage reticulation (due to horizontal gene transfer and allopolyploidy—the combining the genomes of different parental species), certain traits evolve with astonishing speed, thereby diminishing the continuity and distinctiveness of species [54, 69]. Indeed, the stability of genetic information is so compromised that sequencing three *Escherichia coli* genomes revealed that fewer than 40% of the genes were common to all three [66]. As a result, the boundaries between many prokaryote species are fuzzy, and exhibit reticulate patterns of evolution, thus calling into question the appropriateness of the notion of the "tree of life" [31, 39, 49]. The limitations of Darwinism as an explanation of the forms and dynamics of living things is increasingly recognised, while the role of epigenetic processes has become increasingly appreciated. Nevertheless, because such phenomena are much less present in biological evolution than cultural evolution, natural selection provides a reasonable approximation.

7. Concluding comments

By using RAF networks, we have shown that evolution is possible in the absence of variation and selection. We refer to this kind of evolution as Self–Other Reorganisation (SOR) because it occurs not through competitive exclusion such that only the fittest reproduce, but through the assimilation, restructuring, and exchange of components. This primitive form of evolution can occur quickly because there is no discarding of acquired traits, and it can take place in the absence of birth or death. Because it does not use precisely coded self-assembly instructions, it is more haphazard that a natural or artificial selectionist process, but is sufficient for cumulative,

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adaptive, open-ended change. In the extreme, SOR could work with just one entity; indeed, learning can be considered a kind of SOR. However, SOR is a broader concept, as it can produce adaptive change in groups of entities biological generations. We suggest that this more primitive process is operative during the initial stage of an evolutionary process, and that it was responsible for both the origin and early evolution of both organic life, and human culture.

As mentioned above, evolution without variation and selection processes as described here requires the entities to have an organisation that is self-maintaining, and able to generate new items by catalysis from items produced by other entities. Since cultural evolution lacks a self-assembly code, and lacks the signature characteristic of Darwinian evolution—discarding of acquired traits at the end of a generation—it seems reasonable to posit that culture evolves through SOR. This is consistent with the proposal that the entities that are evolving through culture are not discrete artifacts or units of behaviour such as songs, jokes or memes, but the minds that generate them [14], which have a structure that is self-organising and self-maintaining [29, 48], and which have been described in terms of RAFs [22, 24, 23]. Since this second evolutionary process does not require variation, it may increase homogeneity among members of a culturally evolving group of individuals. This, in turn, could foster group identity and cohesion [1].

RAFs have proven useful in two quite distinct areas of research – the origin of life and human cultural evolution – where the underlying CRS is based on biochemical reaction networks (in OOL) and semantic networks (in OOC). We further speculate that RAFs may prove useful for modelling the early stage of any evolutionary process and also that human culture may be at a relatively early stage of its evolution. In the case of cultural evolution, SOR may be important in fostering group identity, cohesion and cooperation [65] (see also [1]) because even though it does not require variation, it can increase the amount of shared knowledge and experience among group members.

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8. Appendix: Mathematical modelling and justification for the predictions of cumulative adaptive change vs individual-based change

To help formalise the model described in Section 4, we adopt the following terminology. Given the products $p, p', p'', \ldots$, we say that the entity that first gives rise to one of these products *generates* it. In the case where this product is produced from an earlier item in the series (rather than being the original product p in response to a stimulus), we say the entity *transforms* the existing item to the new one.

We model the increase in the adaptive value of products within $\mathcal{G}$ using two stochastically independent non-deterministic processes.

First, the generation of new products by entity i involves either generating a new product or transforming the most recent version of any product it has available; for simplicity, we assume that these are all equally probable. For example, if entity i has the products (p, p', q, r, r', r'') currently available, then it can either transform p', or q or r'', or generate a new product, with each of these four outcomes having the same probability, namely $1/4$. This process across entities is assumed to be described by independent exponential random variables with a fixed rate per entity of λ (making λ independent of the entity is consistent with the assumption that all entities are initially identical).

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Second, each newly generated product then begins to percolate through the group by moving along the arcs of the directed graph $D_{\mathcal{G}}$ according to a continuous-time random walk on this directed graph at rate ρ. For simplicity, we will treat the two processes (generation and percolation) as stochastically independent.

Let $N = |\mathcal{G}|$ (the number of entities in $\mathcal{G}$). We will assume that the directed graph $D_{\mathcal{G}}$ that describes the community interactions within $\mathcal{G}$ has the property that from each entity in $\mathcal{G}$, it is possible to reach any other entity in $\mathcal{G}$ by following some directed path in $D_{\mathcal{G}}$ (i.e. $D_{\mathcal{G}}$ is 'strongly connected'); however, no further assumptions are made regarding this graph. We now introduce some notation to keep track of the different versions of products that arise in the process described in Section 4. Suppose that product p first arises from entity i_1 and product p is then further modified by entity i_2 and so on, with the last modification (before time t) being made by entity i_k. In that case, we denote the sequence of products thus generated within $\mathcal{G}$ up to time t as: $p(i_1), p(i_1, i_2), p(i_1, i_2, i_3), \ldots$. More generally, we denote such a sequence by writing $(p(i_1), \ldots, p(i_1, i_2, \ldots, i_k) : k \geq 1)$ (thereby allowing the possibility that a product is generated but not transformed, in the case where $k = 1$). We refer to the number k of terms in this sequence as the *complexity* of the final product; thus, when an entity transforms a product, it increases its complexity by 1 (in particular, the first product $p(i_1)$ has complexity 1).

Note that under the assumptions of the model, the entities $i_1, \ldots, i_k$ are not assumed to necessarily be distinct (i.e., an entity may enhance a product more than once, either consecutively or later in the sequence). There may also be several such sequences generated within $\mathcal{G}$; for example, in addition to the previous sequence, one might also have $p(j_1), p(j_1, j_2), \ldots, p(j_1, j_2, \ldots, j_l)$, along with possibly other sequences generated over the time interval $[0, t]$.

Let $T_\rho(i)$ be the expected time for a product generated by entity i to percolate (within $D_{\mathcal{G}}$) to every entity in $\mathcal{G}$, and let $T_\rho = \max\{T_\rho(i) : i \in G\}$. For a wide range of standard percolation processes, the following properties then hold: (i) for $\rho > 0$, we have $\mathbb{E}[T_\rho] < \infty$; (ii) for all $\eta > 0$, $\lim_{\rho \to 0} \mathbb{P}(T_\rho(i) > \eta) = 1$, and (iii) $\lim_{\rho \to \infty} \mathbb{E}[T_\rho] = 0$. This last property implies that

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when ρ is large, items are highly likely to percolate throughout the entire group $\mathcal{G}$ in a short time.

If we start this process at time 0 with no products present, let $\tau_1, \tau_2, \ldots, \tau_k$ be the random variables that describe the time intervals between the generation of products across the collection of entities in $\mathcal{G}$. By the assumptions of the model, the τ_i variables are independent and exponentially distributed, with each variable having an expected value of $1/(N\lambda)$. Thus $\sum_{i=1}^{k} \tau_i$ is the time until k products have been generated (this has a gamma distribution with expected value $k/(N\lambda)$). Let $\mu = N\lambda$. Then, $\mathbb{P}\left(\bigcap_{i=1}^{k}\{\tau_i \geq \eta\}\right) = e^{-\mu k \eta}$ and $\mathbb{P}(T_\rho \leq \eta) \geq 1 - \mathbb{E}[T_\rho]/\eta$ (by Markov's inequality). Let $\mathcal{E}_k$ denote the following event: for each of the first k products generated, each product percolates to each entity in $\mathcal{G}$ before the next new product (in this collection of size k) is generated in $\mathcal{G}$. We then have:

$$\mathbb{P}(\mathcal{E}_k) \geq e^{-\mu k \eta} \cdot (1 - \mathbb{E}[T_\rho]/\eta)^k = (e^{-\mu\eta}(1 - \mathbb{E}[T_\rho]/\eta))^k. \tag{1}$$

Setting $\eta = \sqrt{\mathbb{E}[T_\rho]}$ in (1) and applying Property (iii) above gives:

$$\lim_{\rho \to \infty} \mathbb{P}(\mathcal{E}_k) = 1.$$

Thus, as ρ becomes large, the entities evolve collectively, and any variation is transient and short-lived. We will refer to this limiting case as the *community-based model*. One can model this process by the following novel type of Pólya Urn model:

> Consider an urn that initially has a single white ball. At each step (the timing of which follows a Poisson process at rate r), a ball is selected from the urn uniformly at random. If the selected ball is white, it is returned to the urn along with a ball of a new colour (not present already in the urn). If the selected ball is coloured, it is removed and replaced by a ball of the same colour but a darker shade.

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To connect this urn process to the community-based model described above, note that selecting a white ball corresponds to the generation of a new product, while selecting a ball of a darkest colour corresponds to the transformation of an existing product. Thus $r = N\lambda$.

We now compare the community-based model (corresponding to ρ large) to the opposite extreme, where ρ becomes small. In that case, the probability that there is percolation between any two entities in $\mathcal{G}$ over the interval $[0, t]$ tends to 0, and so products are only generated within entities but not shared between them. We will refer to this limiting case as the *individual-based model*. Note that in this individual-based model, entity i_j may possibly generate a new product $p(i_j)$, or it may generate $p(i_j)$ and then transform it (producing $p(i_j, i_j)$ and so on (or it might not generate any new products at all). Note that, in general, $p(i_j)$ may be different from $p(i_k)$ (for $k \neq j$) (i.e., different entities may produce different products, and similarly for transformed products).

For the individual-based model, we have N independent samples of the above Urn model but with $r = \lambda$. By contrast with the community-based model, we have a single sample of the above Urn model, but with $r = N\lambda$. Note that both models have the same expected number of generation events. However, they have quite different dynamics, as we now describe.

Firstly, in the community-based model there is only short-lived or transient variation among the entities, whereas in the individual-based model, the individuals diverge from each other in terms of the collections of products that are available to them. However, a more subtle difference is that in the community model, the complexity of items is significantly higher than in the individual model, in a sense that we now make precise.

Let $X = X_t$ be the number of balls in the urn at time t and let Y_i be the number of steps of the urn process that an urn that has just arrived at having $i \geq 2$ balls remains with i balls (until it moves to $i + 1$ balls). Then Y_i has a geometric distribution with expected value $\mathbb{E}[Y_i] = i$ for all $i \geq 2$.

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Next, consider the random variable W_t that counts the number of times the first coloured ball is replaced by increasingly darker shades of balls of that same colour up until time t. The expected value of W is given by:

$$\mathbb{E}[W_t] = \mathbb{E}\left[\frac{Y_2}{2} + \frac{Y_3}{3} + \cdots + \frac{Y_{X_t}}{X_t}\right] = \mathbb{E}\left[\frac{2}{2} + \frac{3}{3} + \cdots + \frac{X_t}{X_t}\right] = \mathbb{E}[X_t] - 1.$$

Thus, in the community-based model, one product has expected complexity of at least $\mathbb{E}[X_t]-1$ at time t (and it is easily seen that there are products with expected complexity of $\mathbb{E}[X_t] - 2, \mathbb{E}[X_t] - 3$ and so on). Moreover, we claim that $\mathbb{E}[X_t]$ is bounded below by a term of order $\sqrt{rt}$ (a proof is provided at the end of this Appendix). Thus, since the community-based model has $r = N\lambda$, we arrive at the following conclusion regarding the influence of the size of $\mathcal{G}$ on complexity:

> Over a given period of time, some products in the community-based model have an expected complexity of order at least $\sqrt{N}$.

By contrast, for the individual-based model, we have $r = \lambda$ for each entity, and so we have N independent and identically distributed samples of a process where the maximum complexity of products across each group $\mathcal{G}$ will exhibit a lower (logarithmic) dependence on N (moreover, these complex products are likely to exist only in one or a few entities, rather than being shared across the group). To see this, note that the complexity of any product within an entity (up to time t) is bounded above by the number of generation steps for that entity, which has a Poisson distribution with mean λt, and the maximum of N independent and identically distributed Poisson random variables is known to be dominated asymptotically (with N) by a $\log(N)$ term [43].

Proof that $\mathbb{E}[X_t]$ is bounded below by a term of order $\sqrt{rt}$.

We have: $X_{t+\delta} = X_t + D_t$, where D_t=1 with probability $r\delta/X_t + o(\delta)$ and $D_t = 0$ otherwise (note that the number of balls in the urn increases only if the white ball is selected from the X_t

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balls in the urn at time t). Thus, if we let $\mu(t) = \mathbb{E}[X_t]$, applying the law of total expectation and taking the limit as $\delta \to 0$ gives:

$$\frac{d\mu(t)}{dt} = r\mathbb{E}\left[\frac{1}{X_t}\right]. \tag{2}$$

The initial condition here is $\mu(0) = 1$. Since the function $f(x) = 1/x$ is convex, Jensen's inequality gives:

$$\frac{d\mu(t)}{dt} \geq \frac{r}{\mu(t)}. \tag{3}$$

A straightforward analytic argument now shows that $\mu(t)$ is bounded below by the solution $\tilde{\mu}(t)$ to the differential equation obtained from (3) by replacing the inequality with an equality. This equation has a unique solution satisfying the same initial condition as $\mu(t)$, namely, $\tilde{\mu}(t) = \sqrt{1 + 2rt}$, which exhibits the claimed growth rate.