ELSEVIER

Contents lists available at ScienceDirect

# **BioSystems**

journal homepage: www.elsevier.com/locate/biosystems





# The information continuum model of evolution

Rasmus Skern-Mauritzen a,\*, Thomas Nygaard Mikkelsen b

- <sup>a</sup> Institute of Marine Research, 5005, Bergen, Norway
- <sup>b</sup> Geco Global, 4174, Jystrup, Denmark

ARTICLE INFO

Keywords:
Heredity
Evolution
Hereditome
Modern synthesis
Natural selection
Extended evolutionary synthesis

#### ABSTRACT

Most biologists agree that evolution is contingent on inherited information shaped by natural selection. This apparent consensus could be taken to indicate agreement on the forces shaping evolution, but vivid discussions reveal divergences on how evolution is perceived. The predominant Modern Synthesis (MS) paradigm holds the position that evolution occurs through random changes acting on genomic inheritance. However, studies from recent decades have revealed that evolutionary inheritance also includes DNA-methylation, RNA, symbionts, and culture, among other factors. This has fueled a demand of a broader evolutionary perspective, for example from the proponents of the Extended Evolutionary Synthesis (EES). Despite fundamental disagreements the different views agree that natural selection happens through dissimilar perpetuation of inheritable information. Yet, neither the MS, nor the ESS dwell extensively on the nature of hereditary information. We do - and conclude that information in and of itself is immaterial. We then argue that the quality upon which natural selection acts henceforth is also immaterial. Based on these notions, we arrive at the information-centric Information Continuum Model (ICM) of evolution. The ICM asserts that hereditary information is embedded in diverse physical forms (DNA, RNA, symbionts etc.) representing a continuum of evolutionary qualities, and that information may migrate between these physical forms. The ICM leaves theoretical exploration of evolution unrestricted by the limitations imposed by the individual physical forms wherein the hereditary information is embedded (e.g. genomes). ICM bestows us with a simple heuristic model that adds explanatory dimensions to be considered in the evolution of biological systems.

### 1. Introduction

Evolution of life is contingent on changing hereditary information relayed through time. For a generation of biologists trained under the neo-Darwinian Modern Synthesis (MS) paradigm, the basic heuristic model of evolution maintains that the hereditary information is found in the genome (Dawkins 1974; Wray et al., 2014; Laland et al., 2015). The genome, in turn, is shaped by natural selection among a collection of genomes created by random mutations, recombinations, integrations, and reorganizations. Furthermore, according to the MS, while the genome dictates which phenotypes an organism can display, adaptive information is not transferred to the germline other than through differential survival. This means that adaptations are not transferred to the offspring and that the changing information, on which evolution is contingent, arises by random changes in the germline. Hence, the prevailing conception is that evolutionary adaptation takes place during the transition of generations, and since the genome is the hereditary information, interchanging the two terms would not matter much. The above may righteously be argued to be an oversimplification of MS (Wray et al., 2014) - but this oversimplification describes our applied heuristic MS model of evolution too well to be ignored (Laland et al., 2014; Laland et al., 2015; Jablonka 2017; Noble and Noble 2017; Noble 2018). The fallacies of a simplified gene-centric model of evolution have become evident in light of the cumulative evidence that inheritance is more than just genomes, and includes epigenetic methylation, RNA, proteins, and culture, among other factors (Laland et al., 2014; Laland et al., 2015; Noble 2016; Noble 2018; Corning 2020). These emergent weaknesses of a monolithic gene-centric model of evolution has brought in its wake a demand for a widening of the gaze, and it has been contended that the dominating gene-centric MS has been an obstacle to progress, by ousting proponents of MS-deviant views and curbing the financing of MS-conflicting research (Laland et al., 2014; Noble 2016; Jablonka 2017; Noble and Noble 2017; Noble 2018; Corning 2020). In a sense, the MS's singular focus on genes and genomes has since its rise served as the "one ring to rule them all", to cite J.R.R. Tolkien. Among the contenders of emerging approaches, the advocates of the Extended Evolutionary

E-mail address: rasmus@hi.no (R. Skern-Mauritzen).

<sup>\*</sup> Corresponding author.

Synthesis (EES) argue that to understand evolution one should put less emphasis on natural selection and genetic inheritance, and attain a broader focus that includes developmental bias - the propensity of particular forms to emerge among the forms possible, developmental plasticity - the range of forms an organism can acquire, niche construction - the modifications of environmental states, and inclusive inheritance heredity defined to comprise all factors leading to resemblance between offspring and their peers, including genomes (Laland et al., 2015). Despite disagreements, the different views of evolution agree that natural selection happens through dissimilar perpetuation of inherited information (Dawkins 1974; Laland et al., 2014; Wray et al., 2014). However, neither the Modern Synthesis, nor the Extended Evolutionary Synthesis, dwell extensively on the nature of the substrate of natural selection: inherited information. We investigate the qualities of inherited information that render it amenable to natural selection, and formulate the findings and their consequences into a coherent heuristic model: the information continuum model of evolution (ICM). After introducing the model, we investigate its inherent conceptual, practical, and philosophical implications.

#### 2. The information continuum model of evolution

#### 2.1. The immaterial nature of information

All scholars and laymen familiar with evolution would agree that natural selection acting on inheritable information in genomes is a key process in evolution. However, it is important to recognize that the genome is not hereditary information. If a string of bacterial DNA comprising a gene is placed in a eukaryotic cell, it will not be translated into protein because bacteria use different combinations of A, T, C, and G to code for amino acids and protein termination than eukaryotic cells. But if the exact same string of DNA is placed in the mitochondria of a eukaryotic cell, it can be translated into protein, because the mitochondria uses the prokaryotic code to interpret the sequence. The material string of DNA is unchanged, yet in one situation it enshrines information and in another it does not. This demonstrates that while the genome is material, information is immaterial. The immateriality is further illustrated by information's ability to change its physical representation. This article, for instance, has changed from biochemical representations in the minds of the authors, to electronic representation in a computer, to physical form on a printed page, and all the way back – many times. Likewise, the information underlying a digestive proteolytic enzyme migrates from DNA via transcription into mRNA and then through translation into a protein. The information hence is physically transformed twice, before the resulting protein is finally secreted and activated to perform its function. The above encompass the first assertation of the ICM: Information is immaterial by nature.

Information, by virtue of its immaterial nature, may be conceptually illusive. In an evolutionary context, it makes sense to define inheritable information as the inherited quality required to materialize as a phenotypic trait. This quality may be embedded in single or multiple genes or, as we shall see later, in other physical carriers of information. The immaterial nature of information does not imply that ICM resorts to supernatural explanations of evolution; information depends on a physical representation for its existence, and natural selection acts through differential propagation of immaterial information mediated by differential survival of the physical form(s) wherein the information resides (e.g. genomes). This recognition of the immaterial nature of information is not entirely new. For instance, David Haig distinguish between the material genes, the informational gene and memes (Haig 2012, 2020). Likewise, George C. Williams distinguished between the material domain and the (immaterial) codical domain (Williams 1992). While both these authors recognize the immaterial nature of information, the information affected by natural selection and evolution is generally considered to be entirely dominated by information in genomes (Dawkins 1974; Williams 1992; Wray et al., 2014; Haig 2020).

While this may be correct, it may also not be correct. And the possibility for the latter warrants an earnest scrutiny considering the widespread implications for evolutionary theory, ethics and philosophy. To reiterate: The genome is not information, just as a book is not a story but a representation of language that may be interpreted as a story. The genome contains a representation of hereditary information, and the information inferred depends on the living system in which the representations are interpreted by the cellular machinery (Noble 2018). This may seem an unimportant distinction to some. But consider the weight of its significance: a vital mitochondrial gene is non-sensical to the cytosolic ribosomal machinery only micrometers away; the same genome produces cells as different as those found in brains and muscles; or the fact that when transferring the nucleus of one fish species to the enucleated egg of another, the resulting fish is not representative of the species from which the nucleus originated (Sun et al., 2005). The living world is rife with examples illustrating that genomes contain representations of information that may be read in very different ways, just as religious texts are interpreted in very different ways by scholars.

## 2.2. Inherited information is found in many forms

Genomes are important repositories of inheritable information – but they are not the sole repositories (Noble 2016; Jablonka 2017): Information embedded in epigenetic methylation is inheritable and affects genome organization and gene expression (Jimenez-Useche et al., 2013; Gaydos et al., 2014; Jeremias et al., 2018; Perez and Lehner 2019). In Daphnia magna, for instance, exposure to increased salinity induces a stress gene-related epigenetic DNA methylation response that persists in generations of asexual formation after exposure (Jeremias et al., 2018). Mitochondria also harbor information that is passed, primarily maternally, through generations. The mitochondrial information interacts with the information in the nuclear genome, and combining a mitochondria with a 'host' cell containing an unsuitable nuclear genome can have deleterious effects. This is nicely illustrated in studies of the intertidal rock-pool copepod Tigriopus californicus, where hybridization between rock-pools can lead to paternal nuclear alleles occurring in combinations with less compatible maternally-derived mitochondria, resulting in reduced viability, development, and fecundity in later generations (Ellison and Burton 2008). Inheritable information may also be conveyed by RNA molecules with no corresponding representation in the nuclear genome. Such RNA molecules may be acquired from pathogens, as seen with nodavirus-derived viRNAs that can confer non-mendelian inheritance of viral resistance in Caenorhabditis elegans (Rechavi et al., 2011). The viRNAs can be amplified by RNA dependent RNA-polymerases and persist for generations, and they can be transferred between generations via both sperm and oocytes (Rechavi et al., 2011). Information may also be relayed by proteins. For instance, inheritable conformation change in one prion-like element in unicellular bakers' yeast can induce transgenerational obligate multicellularity (Holmes et al., 2013), while conformation change in another prion-like element governs transition from being a metabolic specialist to a generalist strategy (Jarosz et al., 2014a). The latter trait can persist for hundreds of generations and interestingly, is induced by bacteria with mutual benefits for both bacteria and yeast (Jarosz et al., 2014a,b). Furthermore, inherited information does not need to rely on a single physical representation for its transmission between generations. Epigenetic methylation patterns are mirrored in the pattern of DNA binding proteins. While methylation is lost during post-zygotic demethylation, it is apparently reinstated based on protein binding patterns, hence upholding the general methylation pattern - an intriguing example of information being relayed via alternating routes of methylation and protein binding (Kremsky and Corces 2020). While the examples above all concern information embedded in molecules transmitted via germ cells, symbionts may also serve as living carriers of inherited information. An example of this is seen in the microbial flora of termites, which demonstrate colony-to-offspring inheritance (among

other modes of inheritance) and is vital for the symbionts' joint digestion of plant biomass (Bourguignon et al., 2018; Ahmad et al., 2020). Another example is the fetal colonization of maternal bacteria found in humans, that have lifelong effects on children's health (Duranti et al., 2017; Walker 2017). Information may also be inherited through routes of hitherto less clearly defined physical bodies. Culture, for instance, is a source of evolutionary important information affecting the fitness, and the evolution of those sharing it (Foote et al., 2016; Whiten 2017). An elegant non-human example of this stems from archeological excavations revealing culturally-transmitted use of nut cracking stone tools over millennia in west African chimpanzees (Mercader et al., 2007; Whiten 2017). One point should be very clear from above examples; hereditary information of evolutionary importance has numerous representations and sometimes travel along alternating routes. The combined inherited representations embody the total information available for evolutionary tinkering. Strangely, we lack a word for the full gamut of physical carriers and their embedded hereditary information; we propose here the term 'hereditome', which we adopt and use from here. The above is the basis for the second assertation of the ICM: Hereditary information is embedded in diverse physical representations that collectively constitutes the hereditome.

# 2.3. The evolutionary properties of inherited information is dependent on its' physical forms

The hereditome compartments have distinct properties and this affects the evolutionary dynamics for the embedded information. Some hereditome compartments are stable while other are more dynamic; some are readily modified by external cues while other are more static; some may cross species boundaries with relative ease whereas others do not (Jarosz et al., 2014a; Dalia and Dalia 2019; Perez and Lehner 2019). The genomic hereditome, for instance, is usually inherited from both parents and remarkably constant, while crucial variability is ensured by mutations, reconfigurations, and recombinations. In contrast, the mitochondrial hereditome is generally maternally inherited and does not exhibit recombination, which renders it with different evolutionary properties (Allio et al., 2017). While both the nuclear and mitochondrial genetic hereditomes are quite stable across generations, the epigenetic methylation hereditome is more dynamic with potential for rapid modifications within both generations and cell types (Phillips and Roth 2019). Where the epigenetic methylation hereditome relay hereditable differences associated with the genome, the RNA hereditome and protein hereditome may be equally dynamic, but are able to confer information not represented in the genome (Rechavi et al., 2011; Jarosz et al., 2014a). In addition, the RNA and protein hereditomes are inherited in a non-mendelian manner, as is the maternally inherited bacterial flora (Rechavi et al., 2011; Jarosz et al., 2014a; Bourguignon et al., 2018). While their physical representations are less defined, cultural and knowledge-based inheritance also have adaptive significances and therefore are compartments of the hereditome - compartments with capacity for very rapid evolution affecting all sharing members. The above examples are not exhaustive and additional hereditome compartments, with yet different evolutionary characteristics, exist. Further hereditome compartments likely remain to be identified. It should be noted that dynamic parts of the hereditome and the embedded information may change very rapidly, and evolution should therefore be considered a continuous process, not a dotted line of events occurring at the transition of generations (Rechavi et al., 2011; Jarosz et al., 2014a; Chen et al., 2016; Jeremias et al., 2018). The above frames the third assertation of the ICM: Hereditome compartments are diverse and encompass a continuum of evolutionary properties.

Sometimes hereditary information switches between hereditome compartments on the journey through time, as previously exemplified by information alternating between representation through epigenetic methylation and representation through the pattern of DNA binding proteins (Kremsky and Corces 2020). At other times, information more

permanently moves from one hereditome compartment to another, a point well illustrated by the migration of mitochondrial genes to the nuclear genome (Fox 1983). Another good example of this is the migration of viral envelope genes into the genomes of placental mammals happening through permanent retroviral inhabitation of becoming placental mammal genomes. The Envelope protein is required for the formation of the placental interface between the mother and the developing fetus, and migration of the underlying information therefore represented a vital stepping stone in the evolution of mammals (Dunlap et al., 2006; Roossinck 2011). Information may also be assisted in its migration between hereditome compartments as illustrated by information underlying human insulin production travelling from its original position in the human genome via human intervention into yeast – only to be purified and injected into the bodies of humans in need. These examples illustrate the fourth assertation of the ICM: Information can migrate between hereditome compartments.

The information in the hereditome compartments do not act in isolation. For instance, the almost absent consequences of bubonic plague in the 21st century, contrasted to its devastating effects earlier in history, cannot be explained based on the human genetic hereditome alone – it is only understandable when taking also into consideration the human knowledge-based and cultural hereditomes. This illustrates that traits are manifestations of information conveyed by multiple hereditome compartments, and it makes sense to conceptually think of immaterial information as a quality, rather than as parcels behaving as we expect singular physical entities to. In reality, this is not much different from how eukaryote evolution is conceived under the Modern Synthesis; after all, the expression of any gene is dependent on the products of multitudes of genes scattered on separate chromosomes with divergent evolutionary characteristics (Noble and Noble 2017) (e.g. autosomes, sex chromosomes, and chromosomes with different recombination rates). While we generally consider organisms as separate entities, information underpinning vital traits may be embedded in the combined hereditomes of more than one organism. This may be exemplified by obligate symbionts, where the participants are mutual repositories of hereditary information bestowing traits depending on their intertwined hereditomes (McCutcheon and von Dohlen 2011; Roossinck 2011). This fits nicely into the concept of biological relativity captured by the statement that 'biology has no privileged level of causality' (Laland et al., 2015; Noble 2016), in that obligate symbionts may be considered to have a collective hereditome. For instance, the success of termites is best, if not only, understood by considering both information embodied in the microbial and genetic hereditome compartments (Bourguignon et al., 2018). The above is the basis of the fifth assertation of the ICM: Information in the hereditome compartments interact.

## 2.4. The substrate of natural selection is information

There is widespread agreement that cellular life originated about four billion years ago, that it originated only once, and that it was likely preceded by primitive noncellular 'life' in the form of replicating RNA molecules (Vazquez-Salazar and Lazcano 2018; Weiss et al., 2018). It is also generally agreed that evolution is the process that, through continuous proliferation and modification, has propagated life from its earliest forms to the living systems we are part of today. It thus appears undisputed that there is an unbroken continuity from the dawn of life to present day - but a continuity of what? While a body of information may constantly be found in the same hereditome compartment as it descends through time (e.g. in the genome), information oftentimes moves from one representation to another. This can be exemplified by the HIV virus that, during its proliferation, alternates between having its hereditome embedded in a retroviral HIV RNA genome and in the human host's nuclear DNA genome (Schroder et al., 2002). Such discontinuity in physical inheritance show that it is not the physical representations of inherited information the constitutes the continuous what (although the predominance of DNA in our present understanding of inheritance can

make it seem so). Indeed, if the cellular world of today was preceded by an RNA-world, the very earliest steps in the evolution of life likely represent a giant discontinuity of material inheritance. This argument is echoed in the observation that the physical hereditome compartments are composed of atoms and elementary particles that are unable to replicate themselves - and that the physical compartments therefore are discontinuous by nature. When a chromosome is copied it is not the physical chromosome that proliferates - it is the embedded information that does so by the reorganization of matter into a copy of the molecule. Hence it appears that although the information is contingent on a physical form for its existence, it is only the immaterial information that transcends through time, leaving behind a trail of physical representations to wither and perish. Thus, natural selection determines if information persists or not by regulating information proliferation, based on the differential survival of the physical hereditome compartment wherein the information resides. The above frames the sixth and final assertation of the ICM: The substrate of natural selection is immaterial information. This does not mean that ICM promotes the view that natural selection alone explains evolution; propagating information constrains the possible forms and actions of living systems, but this does not entail that inheritance governs the forms and actions within the set constraints (Laland et al., 2015; Noble 2016; Noble and Noble 2017).

#### 2.5. A summary the information continuum model

In summary ICM contends that: hereditary information is immaterial. The hereditary information is embedded in physical hereditome compartments as illustrated in Fig. 1. The hereditome compartments have divergent evolutionary properties and thereby strongly influence the possible evolutionary trajectories of the embedded information. The adaptive capacity of the hereditome ranges from relatively low, for genes residing on regularly recombing autosomes for example, to very



Fig. 1. A conceptual representation of the Information Continuum Model. Hereditary immaterial information is represented in the hereditome compartments. The represented information is expressed through interpretation and integration by the system the hereditome compartment is part of. Natural selection acts on the manifested integrated expression and governs the continuous propagation of information in the hereditome compartments. The hereditome compartments illustrated here are, from left (most stable) to right (most adaptable): DNA, mitochondrion, RNA, epigenetic methylation, proteins, microbiome, knowledge, and culture. The compartments list is not exhaustive, and the localizations along the stability-adaptability axis are tentative.

high, such as by cultural adaptation or acquisition of symbiotic bacteria through fecal microbiota transplants (Vrieze et al., 2012). Information can migrate between hereditome compartments, for instance from genomic Y chromosome region that never recombines to an autosome that regularly do, and thereby alter its hereditome dependent evolutionary properties. The information in the various hereditome compartments interacts with information in other compartments as it is interpreted and integrated. It is the immaterial information that replicates and diversifies and thereby is the substrate for natural selection.

# 2.6. Implications of ICM

The implications of ICM are conceptual, practical, and to those so inclined, philosophical. ICM regards living systems as the physical manifestation of immaterial information propagating, in essence, by reorganizing matter. Furthermore, ICM states that evolution through natural selection acts by differential propagation of immaterial information that descends with modification. The immaterial information 'substrate' of ICM alleviates the conceptual need for scales and units. Hereditary information can emerge, persist, and disappear at any timescale - it may emerge by acquiring an information-carrying molecule (e.g. viRNA) at one point in time and disappear by the discontinued proliferation of molecules harboring the information seconds or eons later. Hereditary information can also exist at any physical scale – it can be a represented by a single molecule proliferating at the same rate as it degrades, or it can be imbedded in the culture of millions of organisms. The traits underpinned by the inheritable information may manifest itself at any organizational level, from resistance against antiviral pharmaceuticals in a single virion (Irwin et al., 2016) to the collaborative knowledge-based problem solving in multicellular primates (Dolgin 2021). A conceptual implication of ICM is therefore that evolution is continuous and that it takes place at the level (cell, tissue, individual, population, species etc.) which forms the base of the proliferating information.

There is a tendency for heuristic conceptual models to gravitate towards single-factor explanations: to understand global warming - look to CO<sub>2</sub>; to understand author importance – look to their H-index; to assess a legal entity's successfulness - look to their monetary income; to assess the importance of a paper - look to the citation number; to deem a person's intelligence - look to their grades; to understand evolution look to the genomes. While the predominant singular focus on genomes in the Modern Synthesis (MS) is one of its most criticized qualities (Laland et al., 2014; Laland et al., 2015; Jablonka 2017; Noble and Noble 2017; Noble 2018), it is probably also among the qualities that has made it successful: it is both elegant and conceptually tractable. ICM offers the same conceptual heuristic simplicity as the MS because it allows interpreters to concern themselves only with "information". Nonetheless, ICM's multiple hereditome compartments, and the continuity of evolutionary properties they bestow on the hereditary information, will hopefully allow a nuanced consideration of inheritance in biology and serve to avoid monotheistic tendencies.

In practical terms the ICM brings forth a concept that encompasses all inherited information existing at any scale, which affects how we should design studies and interpret scientific data. For example, experimental organisms collected in the field are prone to have dissimilar histories and divergent hereditomes that may affect the results. Potential influence from all hereditome compartments should therefore be considered in biological studies. This is not necessarily straightforward and ICM may initially appear unappealing, as deciphering the potential contribution from a multitude of hereditome compartments interacting at all temporal scales can seem intractable. However, while the interactions in multifaceted hereditomes can yield an indefinite number of phenotypes, the *range* of the phenotypes is not indefinite. In fact, since the various hereditome compartments contribute cumulative delimitations to the possible phenotypes, unravelling the individual hereditome compartments' contributions will likely simplify matters, and

allow for explanation of a proportion of the hitherto inexplicable phenotypic variation and developmental bias. As such, ICM may partly bridge the apparent gap between MS and EES. Furthermore, in an age of rapid environmental change, understanding the temporal aspect of adaptive potential is of crucial importance (Bonduriansky et al., 2012; Corning 2020) and likely requires systematic identification and study of the more adaptable hereditome compartments (residing on the right side in Fig. 1). ICM offers a conceptual framework that promotes identification of the more dynamic quarters of information residence.

Beyond the direct instrumental value, ICM also bestows us with a framework for generating hypotheses about the role of hereditary information based on the hereditome compartment wherein it resides – and a tool for identifying probable hereditome compartments carrying the information underpinning a certain trait. For instance, information related to traits under recurrent adaptational pressure, such as recurrent environmental stress, are expected to reside in more adaptable parts of the hereditome, such as in the DNA-methylation hereditome (Jablonka 2017; Heckwolf et al., 2020). Since natural selection is the result of the dissimilar ability of information to propagate itself, introduction of variation in the hereditome during propagation is indispensable for adaptation. So, in contrast to the common notion that natural selection should promote fidelity (Dawkins 1974), ICM predicts that evolution must promote mechanisms that strikes the degree of information replication *infidelity* just right.

This section shows how ICM may affect the academic approaches to biological systems. We contest that ICM also have countless philosophical implications and find that the most fundamental question the model rises is: what defines life? According to ICM, living systems are manifestations of immaterial information propagating through time, in essence, by reorganizing matter. Also, according to ICM, evolution of life happens through differential propagation of diversifying immaterial information. We argue that the implication of this is that information that propagates is life and that reserving the quality of life for a subset of information embedded in physical forms with certain arbitrary, anthropogenically-defined attributes is inconsistent. However, discussions regarding the definitions of the interconnected conceptions of life, free will, and the nature of the self, have always thrived within the branches of Philosophy. Accordingly, we recognize that one may disagree with our definition of life, but defend the view that the concept of life has connotations related to values and rights and that it should therefore at least be defined consistently. In this respect ICM offers a platform for further transdisciplinary discussions between what C.P. Snow identified as "The Two Cultures" represented by human and natural sciences (Snow 1993). That would seem befitting as this paper sprouted from conversations between a biologist (RSM) and a science philosopher (TNM). However, additional discussions of these aspects are beyond the intentions of the present paper and we will therefore here refrain from further exploration of the relationship between matter, information and the self.

# 3. Summary

- 1. Information is immaterial by nature but must have a physical form to
- 2. Inherited information may be found in many forms.
- The forms have divergent properties and information may over time change its physical form.
- 4. We suggest the term 'hereditome' to refer to the sum of inherited information and its forms.
- 5. The substrate of natural selection is immaterial information.
- The Information Continuum Model is a simple heuristic model that allows evolution and natural selection to be investigated without conceptual restrictions imposed by the properties of individual hereditome components.

 The conceptual nature of Information Continuum Model enables it to serve as an interdisciplinary platform for collaboration between natural and social sciences.

### Declaration of competing interest

The authors declare that they have both contributed to the conception, design and writing of the manuscript.

The authors declare that the manuscript is not under consideration at another journal or publishing venue.

The authors declare that they have no affiliation with any organization with a direct or indirect financial interest in the subject matter discussed in the manuscript.

The Authors declare they have read and approved the manuscript.

#### Acknowledgements:

We are thankful to Søren Grove, Mette Skern-Mauritzen, Samantha Bui, Kevin Alan Glover, Grace Wyngaard and Sussie Dalvin for their remarks and questions - without their efforts it is likely that no one would have understood what we were trying to say.

#### References

- Ahmad, F., Yang, G.Y., Liang, S.Y., Zhou, Q.H., Gaal, H.A., Mo, J.C., 2020. Multipartite symbioses in fungus-growing termites (Blattodea: termitidae, Macrotermitinae) for the degradation of lignocellulose. Insect Sci.
- Allio, R., Donega, S., Galtier, N., Nabholz, B., 2017. Large variation in the ratio of mitochondrial to nuclear mutation rate across animals: implications for genetic diversity and the use of mitochondrial DNA as a molecular marker. Mol. Biol. Evol. 34. 2762–2772.
- Bonduriansky, R., Crean, A.J., Day, T., 2012. The implications of nongenetic inheritance for evolution in changing environments. Evol Appl 5, 192–201.
- Bourguignon, T., Lo, N., Dietrich, C., Sobotnik, J., Sidek, S., Roisin, Y., Brune, A., Evans, T.A., 2018. Rampant host switching shaped the termite gut microbiome. Curr. Biol. 28, 649
- Chen, Q., Yan, W., Duan, E., 2016. Epigenetic inheritance of acquired traits through sperm RNAs and sperm RNA modifications. Nat. Rev. Genet. 17, 733–743.
- Corning, P.A., 2020. Beyond the modern synthesis: a framework for a more inclusive biological synthesis. Prog. Biophys. Mol. Biol. 153, 5–12.
- Dalia, A.B., Dalia, T.N., 2019. Spatiotemporal analysis of DNA integration during natural transformation reveals a mode of nongenetic inheritance in bacteria. Cell 179, 1499–1511 e1410.
- Dawkins, R., 1974. The Selfish Gene. Oxford University Press, New York.
- Dolgin, E., 2021. How COVID unlocked the power of RNA vaccines. Nature 589, 189–191.
- Dunlap, K.A., Palmarini, M., Varela, M., Burghardt, R.C., Hayashi, K., Farmer, J.L., Spencer, T.E., 2006. Endogenous retroviruses regulate periimplantation placental growth and differentiation. In: Proceedings of the National Academy of Sciences of the United States of America, 103, pp. 14390–14395.
- Duranti, S., Lugli, G.A., Mancabelli, L., Armanini, F., Turroni, F., James, K., Ferretti, P., Gorfer, V., Ferrario, C., Milani, C., et al., 2017. Maternal inheritance of bifidobacterial communities and bifidophages in infants through vertical transmission. Microbiome 5.
- Ellison, C.K., Burton, R.S., 2008. Interpopulation hybrid breakdown maps to the mitochondrial genome. Evolution 62, 631–638.
- Foote, A.D., Vijay, N., Avila-Arcos, M.C., Baird, R.W., Durban, J.W., Fumagalli, M., Gibbs, R.A., Hanson, M.B., Korneliussen, T.S., Martin, M.D., et al., 2016. Genomeculture coevolution promotes rapid divergence of killer whale ecotypes. Nat. Commun. 7.
- Fox, T.D., 1983. Mitochondrial genes in the nucleus. Nature 301, 371-372.
- Gaydos, L.J., Wang, W., Strome, S., 2014. Gene repression. H3K27me and PRC2 transmit a memory of repression across generations and during development. Science 345, 1515–1518.
- Haig, D., 2020. From Darwin to Derrida: Selfish Genes, Social Selves, and the Meaning of Life. The MIT press, Cambride, Massechusetts.
- Haig, D., 2012. The strategic gene. Biol. Philos. 27, 461–479.
- Heckwolf, M.J., Meyer, B.S., Hasler, R., Hoppner, M.P., Eizaguirre, C., Reusch, T.B.H., 2020. Two different epigenetic information channels in wild three-spined sticklebacks are involved in salinity adaptation. Science Advances 6.
- Holmes, D.L., Lancaster, A.K., Lindquist, S., Halfmann, R., 2013. Heritable remodeling of yeast multicellularity by an environmentally responsive prion. Cell 153, 153–165.
- Irwin, K.K., Renzette, N., Kowalik, T.F., Jensen, J.D., 2016. Antiviral drug resistance as an adaptive process. Virus Evolution 2.
- Jablonka, E., 2017. The evolutionary implications of epigenetic inheritance. Interface Focus 7.
- Jarosz, D.F., Lancaster, A.K., Brown, J.C.S., Lindquist, S., 2014a. An evolutionarily conserved prion-like element converts wild fungi from metabolic specialists to generalists. Cell 158, 1072–1082.

Jarosz, D.F., Brown, J.C.S., Walker, G.A., Datta, M.S., Ung, W.L., Lancaster, A.K., Rotem, A., Chang, A., Newby, G.A., Weitz, D.A., et al., 2014b. Cross-kingdom chemical communication drives a heritable, mutually beneficial prion-based transformation of metabolism. Cell 158, 1083–1093.

- Jeremias, G., Barbosa, J., Marques, S.M., De Schamphelaere, K.A.C., Van Nieuwerburgh, F., Deforce, D., Goncalves, F.J.M., Pereira, J.L., Asselman, J., 2018. Transgenerational inheritance of DNA hypomethylation in Daphnia magna in response to salinity stress. Environ. Sci. Technol. 52, 10114–10123.
- Jimenez-Useche, I., Ke, J.Y., Tian, Y.Q., Shim, D., Howell, S.C., Qiu, X.Y., Yuan, C.L., 2013. DNA methylation regulated nucleosome dynamics. Sci. Rep. 3.
- Kremsky, I., Corces, V.G., 2020. Protection from DNA re-methylation by transcription factors in primordial germ cells and pre-implantation embryos can explain transgenerational epigenetic inheritance. Genome Biol. 21, 118.
- Laland, K., Uller, T., Feldman, M., Sterelny, K., Muller, G.B., Moczek, A., Jablonka, E., Odling-Smee, J., 2014. Does evolutionary theory need a rethink? - POINT Yes, urgently. Nature 514, 161–164.
- Laland, K.N., Uller, T., Fellman, M.W., Sterelny, K., Muller, G.B., Moczek, A., Jablonka, E., Odling-Smee, J., 2015. The extended evolutionary synthesis: its structure, assumptions and predictions. In: Proceedings of the Royal Society B-Biological Sciences, 282.
- McCutcheon, J.P., von Dohlen, C.D., 2011. An interdependent metabolic patchwork in the nested symbiosis of mealybugs. Curr. Biol. 21, 1366–1372.
- Mercader, J., Barton, H., Gillespie, J., Harris, J., Kuhn, S., Tyler, R., Boesch, C., 2007. 4,300-year-old chimpanzee sites and the origins of percussive stone technology. Proc. Natl. Acad. Sci. U. S. A. 104, 3043–3048.
- Noble, D., 2018. Central dogma or central debate? Physiology 33, 246–249. Noble, D., 2016. Dance to the Tune of Life Biological Relativity. Cambridge University
- Noble, D., 2016. Dance to the Tune of Life Biological Relativity. Cambridge University Press, Cambridge.
- Noble, R., Noble, D., 2017. Was the watchmaker blind? Or was she one-eyed? Biol. Bull. 6.
- Perez, M.F., Lehner, B., 2019. Intergenerational and transgenerational epigenetic inheritance in animals. Nat. Cell Biol. 21, 143–151.

- Phillips, N.L.H., Roth, T.L., 2019. Animal models and their contribution to our understanding of the relationship between environments. Epigenetic Modifications, and Behavior. Genes 10.
- Rechavi, O., Minevich, G., Hobert, O., 2011. Transgenerational inheritance of an acquired small RNA-based antiviral response in C. elegans. Cell 147, 1248–1256.
- Roossinck, M.J., 2011. The good viruses: viral mutualistic symbioses. Nat. Rev. Microbiol. 9, 99–108.
- Schroder, A.R.W., Shinn, P., Chen, H.M., Berry, C., Ecker, J.R., Bushman, F., 2002. HIV-1 integration in the human genome favors active genes and local hotspots. Cell 110, 521–529.
- Snow, C.P., 1993. The Two Cultures. Cambridge University Press, Cambridge, UK.
- Sun, Y.H., Chen, S.P., Wang, Y.P., Hu, W., Zhu, Z.Y., 2005. Cytoplasmic impact on cross-genus cloned fish derived from transgenic common carp (Cyprinus carpio) nuclei and goldfish (Carassius auratus) enucleated eggs. Biol. Reprod. 72, 510–515.
- Vazquez-Salazar, A., Lazcano, A., 2018. Early life: embracing the RNA world. Curr. Biol. 28, 1166–1167.
- Vrieze, A., Van Nood, E., Holleman, F., Salojarvi, J., Kootte, R.S., Bartelsman, J.F.W.M., Dallinga-Thie, G.M., Ackermans, M.T., Serlie, M.J., Oozeer, R., et al., 2012. Transfer of intestinal microbiota from lean donors increases insulin sensitivity in individuals with metabolic syndrome. Gastroenterology 143, 913.
- Walker, W.A., 2017. The importance of appropriate initial bacterial colonization of the intestine in newborn, child, and adult health. Pediatr. Res. 82, 387–395.
- Weiss, M.C., Preiner, M., Xavier, J.C., Zimorski, V., Martin, W.F., 2018. The last universal common ancestor between ancient Earth chemistry and the onset of genetics. PLoS Genet. 14.
- Whiten, A., 2017. Culture extends the scope of evolutionary biology in the great apes. Proc. Natl. Acad. Sci. U. S. A. 114, 7790–7797.
- Williams, G.C., 1992. Natural Selection: Domains, Levels, and Challenges. Oxford University Press, New York.
- Wray, G.A., Hoekstra, H.E., Futuyma, D.J., Lenski, R.E., Mackay, T.F.C., Schluter, D., Strassmann, J.E., 2014. Does evolutionary theory need a rethink? COUNTERPOINT No, all is well. Nature 514, 161(. -+).