Exploring autonomy through computational biomodelling*

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Abstract

The question of whether living organisms possess autonomy of action is tied up with the nature of causal efficacy. Yet the nature of organisms is such that they frequently defy conventional causal language. Did the fig wasp select the fig, or vice versa? Is this an epithelial cell because of its genetic structure, or because it develops within the epithelium? The intimate coupling of biological levels of organisation leads developmental systems theory to deconstruct the biological organism into a life-cycle process which constitutes itself from the resources available within a complete developmental system. This radical proposal necessarily raises questions regarding the ontological status of organisms: Does an organism possess existence distinguishable from its molecular composition and social environment? The ambiguity of biological causality makes such questions difficult to answer or even formulate, and computational biology has an important role to play in operationalising the language in which they are framed. In this article we review the role played by computational biomodels in shedding light on the ontological status of organisms. These models are drawn from backgrounds ranging from molecular kinetics to niche construction, and all attempt to trace biological processes to a causal, and therefore existent, source. We conclude that computational biomodelling plays a fertile role in furnishing a proof of concept for conjectures in the philosophy of biology, and suggests the need for a process-based ontology of biological systems.

Keywords: autonomy; computational biomodelling; emergence; enactive evolution; niche construction

COMPUTATIONAL BIOMODELLING IN PHILOSOPHY

‘It is only the beginning of understanding to agree that internal and external factors contribute to phenotype. […] The way in which its genotype and its future environmental sequence influence the fly are themselves effects of the organism as cause’ [1].

The past 10 years have seen a burgeoning of literature on a common theme: ‘Does it make sense to ascribe to a system an existence which is independent of its component parts?’ This question arises in evolutionary biology (‘Does selection act on populations?’ [2]), consciousness research (‘Is mind reducible to its material substrate?’ [3–5]), and religion (‘Can there exist a God transcendent of the material world?’ [6, 7]).

The central issue underlying these debates is ontological emergence. Most authors agree that biological systems are constructed from substantial micro-components, but whereas genocentric theories [8–10] trace the causal efficacy of biological systems to individual genes, dynamical theories [11–14] typically regard certain macro-properties of biological systems as ontologically emergent from their micro-components.

Ontological emergence is the idea that something is ‘there’ in a system which is not ‘there’ in the component parts. Atoms (or quarks or whatever) are supposed to be substantial—they possess intrinsic

*Selected models referred to in this article are available as Matlab and SimBiology simulations from the associated website at: http://www.fh-weihenstephan.de/fh/fakultaet/bb/professoren/palfreyman/autonomy.html.

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micro-properties and exert causal influence, and are therefore 'there'. However we generally assume a macro- (i.e. system-level) property of a system not to be independently 'there', but instead to be supervenient on micro-properties in the sense that it necessarily takes the same value in any two instances of the system possessing identical micro-property values. The usual expression of this intuition is that the macro-property is reducible to micro-properties.

When we cannot reduce some macro-property to micro-properties, we often assume this is due merely to our incomplete knowledge of the system, and ascribe to the macro-property the status of epistemological emergence: a qualitative difference in our knowledge of systems as opposed to components. Yet this ascription clashes with our everyday notion that we humans possess irreducible autonomy. We would like to claim for organisms the ontological emergence of, for example, agency, in the sense that organisms possess a causal efficacy which is irreducible to micro-properties of their component parts.

There are at least two reasons why the question of ontological emergence is important to science. Deacon [15] suggests that it could 'do more than significantly advance our understanding of how life came about [...]. It could possibly also provide new insights into the very nature of physical causality'. Also, existence is intimately bound up with causal efficacy, and the virulence (and hence prevention) of many bacterial infections depends upon the bacteria’s ability to form biofilm communities with distinguishable causal efficacy [15].

Philosophy's tool of choice for tackling questions which resist direct empirical resolution is the thought-experiment based on simple, yet realistic, domains. Simple domains strip issues to their bare essentials, avoiding the overwhelming complexity of even moderately sized biological systems. However, Sterman [16] cautions that we 'cannot simulate mentally even the simplest possible feedback system [...] since we] significantly underestimate exponential growth, tending to extrapolate linearly rather than exponentially'. In the complex realm of biological causality even simple systems resist easy prediction.

Consequently computational biomodelling has a significant role to play in operationalising thought-experiments in philosophy of biology. In the next three sections we review computational models which define emergence respectively in terms of novelty, agency and self-organisation; we conclude that none of these definitions satisfies the strict criteria of ontological emergence. In later sections we investigate models which presuppose an alternative ontology, not of 'things', but of processes, and so offer a convincing basis for ontological emergence.

**EMERGENCE AS NOVELTY**

One starting-point for a discussion of emergence is the development of ontogenetic novelty in organisms: Is the causal efficacy of a complete genome ontologically distinct from that of its individual genes? Nijhout [17] reports a series of simulations demonstrating novel system-level behaviour arising from non-linear genetic interactions. In particular ([17], p. 134) he models the frequency of six co-dominant allele pairs controlling diffusion gradient pattern formation in a population of individuals which are subject to phenotypic selection. While the resulting phenotype in Figure 1A exhibits orderly and gradual change over time, the genetic response (Figure 1B) is more complex, due to the fact that the correlation between any particular gene and the phenotype changes over time (Figure 1C).

Two effects in particular are apparent from Nijhout’s work: the highly non-linear relationship between genetic and phenotypic variation, and the changing relative influence of various genetic determinants on the phenotype. The combination of these effects makes it impossible to talk about the causal influence of any particular genetic or environmental determinant in isolation from its entire genetic and environmental background.

Nijhout’s work demonstrates that non-linear genetic and environmental interactions lead to something which may be called emergence in development. The development of the phenotype in Figure 1 is a historical process which cannot be expressed as an algorithmic function of individual determinants. However ontological emergence requires that the phenotype is not supervenient on these determinants. While the route from genotype to phenotype may not be algorithmic, it is certainly dynamic, and it seems highly probable that identical determinants will in any instantiation lead over time to the same phenotype. Surely any claim of irreducibility stems purely from our predilection for viewing phenotypic traits at the coarse-grained level of organisms, in which case we can at most regard them as epistemologically emergent.
Numerous challenges to evolutionary theory have employed the idea that novel phenotypic forms such as bacterial locomotion [19, 20] are irreducible to the accumulation of individual heritable variation. This led Dawkins [21] to develop the computer simulation *Blind Watchmaker* to demonstrate the surprisingly complex forms which can be generated by accumulation of heritable variation (see [22] for a downloadable version). However Dawkins himself was dissatisfied with *Blind Watchmaker* as a demonstration of the ontological reducibility of organisms, because of its dependence upon artificial selection by a human designer. Krink and Vollrath [23] used the simulation *NetSpinner III* to investigate the evolution of spiders’ webs in interaction with randomly passing prey, and found the simulation reliably generated realistic values for such traits as spiral distance, eccentricity and vertical hub location. Similarly, Ray’s [24] *Tierra* simulation illustrates the evolution of program fragments within an artificial world, including several remarkable examples in which programs spontaneously optimise themselves as if by intelligent design.

These Artificial Life simulations make a powerful case for the reducibility of traits to genetic selection; however this must then make us ask: If traits are determined by genes, and genes are determined by selection, is an organism not simply a machine which is programmed by evolution? Rosen [25] argues that organisms differ from machines in possessing closed paths of efficient causation. Any function of a machine can be traced to an external efficient cause, but functions in an organism can be fully entailed by other functions within the organism.

An example of such internal entailment is symmetry-breaking, modelled for example by the system in Figure 2, constructed by Golubitsky and Stewart ([26]; see article website) to account for sympatric speciation. Four interacting groups of birds with almost identical traits are all assumed to follow a single identical evolutionary rule. Despite virtually identical initial conditions of the four trait groups, this symmetric situation collapses as the groups bifurcate over time into two species with clearly distinguishable trait values (Figure 3).

Symmetry-breaking behaviour arises only in the complete speciation system; it is not present in the individual trait groups. We might therefore regard speciation as an ontologically emergent macro-property. But is this really the case? The divergent behaviour of Figure 3 merely exhibits unpredictability, which we can understand in two alternative ways. If the unpredictability stems from our limited knowledge of the system’s initial state, we have only
demonstrated epistemological emergence; alternatively we might regard this unpredictability of system behaviour as an ontologically emergent consequence of a fundamental probabilistic law of nature. Yet as Bitbol [27] points out, this position is questionable, since there is no particular reason for assuming the law of large numbers to generate deterministic behaviour from underlying probabilistic laws, rather than assuming that probabilistic behaviour derives from underlying deterministic laws. The case for ontological emergence is not yet proven.

Kauffman and Clayton [28] make a deeper point. While speciation behaviour in the above model is merely unpredictable with respect to a finite number of possible histories of the system, if we experiment with individually deleting and inserting the various trait groups, we quickly discover that the number of conceivable system behaviours grows combinatorially with the number of trait groups. If we could pre-specify (i.e. compile a denumerable list of) the traits available in a population, the number of possible interactions between these traits would in general be non-denumerable: the co-evolutionary exaptations which can conceivably evolve from interactions between traits will not be pre-specifiable.

Kauffman and Clayton claim that the non-prespecifiability of exaptations implies that they form a truly existent extension of the system-level trait space. Cohen and Stewart [29] use the illustration of malaria transmission as an exaptation of the blood-mosquito juxtaposition which would be meaningless if only blood or mosquitoes were individually available. But is pre-specifiability really a criterion for existence? It seems unlikely that system-level exaptations ‘exist’ simply by virtue of their non-denumerability. In fact Kauffman and Clayton [30] (p. 503) themselves define existence elsewhere in terms of causal efficacy, to which we now turn.

**AGENCY AND MULTIPLE REALISATION**

Kauffman and Clayton [28] argue that agency necessarily implies emergence, where a system possesses agency if it reproduces itself, performs at least one work cycle, and can make choices. As an example they provide the primitive molecular agent in Figure 4 (see article website), which harnesses an incoming photon to perform the work cycle of replicating a DNA hexamer. This agent can make choices if equipped with motor apparatus to approach or retreat from photon sources.

Dennett [4] would understandably claim that Kauffman and Clayton are adopting an intentional (anthropomorphic) stance when they assign agency to this simple system, however they go on to make a further point. The agent’s approach to food is not determined purely by its physical components, but is also contingent upon processes of natural selection within a particular environment. But natural selection is realisable in multiple ways: we have implemented their agent computationally, but it might equally well be implemented chemically or even optically. For this reason, they claim, the agent’s behaviour is ontologically emergent, since it is contingent upon selection processes which possess intrinsic, realisation-independent existence.

Yet as Bitbol [27] points out, this argument seems flawed. Natural selection operates on populations: a function is adaptive because it is beneficial for an entire population of agents. But this is no guarantee of agency, since true behavioural choice must lie at each instant within the control of the individual agent.

**EMERGENCE AS SELF-ORGANISATION**

The self-organisation approach to emergence draws on the insight that simple interacting components
can organise themselves into well-defined patterns of behaviour which are both unpredictable and history-dependent. There is a wealth of modelling literature exploring this theme [30, 31]. 

Camazine et al. [32] make a strong plea for the use of computational biomodels to investigate self-organisation and emergence (which terms they equate), and present a tutorial of 13 such models. They construct an agent-based model of *Dendroctonus micans*, a parasite of the spruce which evades the tree’s immune reaction through density-dependent cluster formation. This model demonstrates the use of *stigmergy* in the emergence of clustering above a certain threshold of parasite density: agents modify their environment by laying pheromone, and also react to this modification by following the pheromone gradient.

Self-organisation enables *Dendroctonus* to exert system-level influence on its environment; however the question remains whether this influence is supervenient on the individuals’ behaviour. One approach to this question involves cooperation—an important mechanism of self-organisation. Axelrod [33] offers a collection of models illustrating how cooperation between system components can exert causal effects such as the enforcement of norms, creating new political actors and shared culture. But how does cooperative behaviour arise? Is it supervenient on genetic micro-properties [8] or is it a system-level phenomenon?

Sober and Wilson [14] assert that cooperation is in general *not* supervenient on genetic determinants. They present a model demonstrating how altruism can evolve in the parasite *Dicrocoelium dendriticum* through multi-level (i.e.: system-level) selection, as opposed to genocentric kin selection. *Dicrocoelium* eggs (see Figure 5) are eaten by snails, which serve as hosts for two generations of asexual reproduction before excreting the parasites in mucus-covered groups of about 50. This group is then eaten by an ant, whereupon one of the parasites migrates through the stomach wall to the ant’s brain to form a cyst called the brain worm. The brain worm influences the ant’s behaviour, causing it to spend more time on the tips of grass blades and get eaten by livestock, in whose bodies parasites continue their life-cycle. The price the brain worm pays for this is that it foregoes the ability to reproduce itself.

In Sober and Wilson’s model the parasite population initially consists entirely of a selfish strain (S) which cannot cooperate, while the altruistic strain (A) starts as a single mutation which can choose to become a brain worm. We assume that the average snail eats five eggs, including the single A individual. Within the snail the parasites reproduce asexually while maintaining the frequency 0.2 of A individuals, and ants later ingest the parasites in groups of about 50.

At this stage the parasites live in isolated groups in different ants. The majority of groups consist entirely

**Figure 5:** The *Dicrocoelium* model.
of S types, but one group may contain 40 S and 10 A types \((p = 0.2)\). One of the A types in this ant becomes a brain worm, reducing the A frequency, but raising the survival rate of the group from, say, 0.1 to 0.15. The probability of a typical A type not becoming a brain worm and being ingested by livestock is therefore \(0.9 \times 0.15 = 0.135\), whereas the probability of ingestion for a typical S type is only 0.1. Although the frequency of A types in the group diminishes, their frequency in the population will grow to an equilibrium value (Figure 6).

The central message of the Dicrocoelium model is that cooperation can evolve to the extent that A types and S types become concentrated within decoupled groups. If this is true, the system-level causal effects of self-organisation are traceable through cooperation, not only to micro-determinants, but also to downwardly acting selective influences from an encompassing environment.

How do such downward influences function? And how can systems spontaneously form isolated groups subject to multi-level selection?

**DOWNWARD CAUSATION IN DAISYWORLD**

Although not directly concerned with emergence, ecology is nevertheless concerned with mutual interaction between species micro-properties and environmental macro-properties. In particular, downward causation refers to situations in which macro-properties constrain the emergent activity of micro-properties (medium downward causation; see [34]). Gaia theory is an ecological account of homeostasis which makes explicit use of downward causation.

Challenged to defend Gaia theory against charges of anthropomorphism, Watson and Lovelock [35] constructed the Daisyworld computer model, in which just two species (Black and White daisy populations) interact with two environmental forces (solar luminosity and temperature). Daisy growth rate depends on local temperature, but daisies are not merely the objects of environmental forces; by reflecting light, daisies are also the subject of those forces.

Under physically reasonable assumptions Watson and Lovelock were able to show that the Daisyworld system is capable of maintaining temperature homeostasis despite quite drastic changes in solar luminosity (see Figure 7 and article website). It achieves
this by virtue of the macro-property temperature (AvgPlanetTemp) serving as a ‘common currency’ which both combines and then regulates the reflectance of the daisy population.

Daisyworld operationalises the notion of causal macro-properties, in this case temperature, enabling Robertson and Robinson [36] to question its robustness when the daisies’ optimum temperature is subject to adaptation. Lenton and Lovelock [37] later demonstrated (Figure 8) that a Darwinian Daisyworld is indeed also capable of maintaining homeostasis, provided the daisies’ optimum growth temperature is limited in its adaptability.

Is Daisyworld planetary temperature ontologically emergent? It certainly influences the growth rates of Black and White, and so possesses causal efficacy, but is it supervenient on the micro-states Black and White? Temperature is calculated algebraically from solar luminosity (a function of time) and planetary albedo (a function of Black and White). The supervenience of temperature therefore rests on whether we regard luminosity as a micro-property of the system. If so, its time-dependence means that temperature is a function not only of the current micro-properties of the system, but also of past values of luminosity. On the other hand, if the time-dependence indicates the exogenous influence of an external sun, then Daisyworld is a thermodynamically open system, and temperature is a function not only of micro-properties. In both cases temperature is not supervenient on current micro-properties of the system, and is therefore ontologically emergent.

The lesson we draw from Daisyworld is 2-fold. First, it seems that ontological emergence is possible in any thermodynamically open system. The irreducibility of temperature depends crucially on the presence of an open system boundary: without the boundary we have no system, but without external interaction temperature is reducible. Second, Daisyworld indicates the importance of a form of mutual causality in which daisies do not unilaterally define temperature, but in which daisies and temperature are each members of a coupled dynamical system in which each exerts causal influence on the other.

REDEFINING CAUSALITY

Further clues to the nature of ontological emergence come from models seeking to validate the Baldwin effect, a postulated mechanism by which organisms causally influence the genetic inheritance of their descendants. Hinton and Nowlan [38] created a population of neural networks each possessing 20 binary outputs, which are required to learn a target trait pattern consisting of 20 1’s using a genetic algorithm with crossover. Learning occurs in a hostile environment in which only the target has maximal fitness, and all others have zero fitness. To generate the output, each genetic locus in the net contains one of the values {0, 1, ?}, where ‘0’ and ‘1’ represent the genetically fixed traits 0 and 1. When a network is evaluated, 1000 trials are performed in which it produces random combinations of 0’s and 1’s for each locus containing ‘?’. If on the n-th trial the net generates the target pattern, it receives fitness value $20 - 19n / 1000$, rewarding rapid correct ‘guesses’ with high fitness.

The probability of discovering the target pattern without guessing is $2^{-20}$ since even a single 0 in the output pattern returns zero fitness. With guessing the chances are considerably better, for any pattern containing only 1’s and ‘?’s has a chance of finding the target pattern. Once a network guesses the target, it spreads rapidly through the population, and can then improve its fitness by replacing ‘?’s by 1’s in each generation. This model therefore seems to offer a mechanism whereby the organism can exert (non-Lamarckian) causal influence on genetic structure.

Several problems with the Hinton and Nowlan model are addressed by Puenteuera [39]. For example, the coupling of plasticity (?) and trait value (0/1) in a single locus makes the transition from acquired to genetically fixed trait unrealistically easy; Puenteuera rectifies this by decoupling plasticity into a second set of 20 loci. However this model still relies upon genetic assimilation, which predicates a similarity relation between traits: being able to guess some trait correctly increases accessibility of the genetically fixed value 1 for that trait. Consequently, these models demonstrate only gene-to-gene causation.
However, Yamauchi [40] uses a computational model of language evolution to test the validity of an alternative, downward causation based, account of the Baldwin effect due to Godfrey-Smith [41] following Deacon [42], and relying on niche construction. Niche construction, arising from the work of Lewontin [43], Brandon [44] and Odling-Smee [45], emphasizes the influence of organisms in modifying and selecting their own and each other’s niches through their metabolism or behaviour. According to this account of the Baldwin effect, an organism first displays a facultatively acquired skill which then becomes selectively available to other good learners in the population. At this stage the skill is developmentally, but not yet genetically, fixed. However its presence changes selection pressure in the population, since individuals who cannot produce the skill have reduced fitness. The skill will then exhibit positive frequency dependence, becoming more selectively important as it becomes more common. This mechanism enables new genetic mutations even to make partial U-turns in arriving at a genetically polished version of the skill, since they are decoupled from the ability of the organism to learn.

This niche construction account has an interesting causal structure. First, selection appears not as an external shaping force, but rather as co-evolution of organism and social niche. Rather than either gene or organism exerting direct causal influence on genetic structure, the organism participates in the collective social niche, which in turn exerts downward influence on the genetic makeup of its members. In this view, causality is mutual, mediated by an environment which feeds back into the organism shaping it.

Second, we again see the importance of a permeable system boundary for ontological emergence. Precisely because the organism is structurally distinct from its environment, it makes a clear distinction between the upward causation of its internal dynamics and the downward causation of selection. It seems a combination of both is required to avoid supervenience.

**AUTONOMOUS SYSTEMS**

Our review of computational biomodels has led us to an account in which a thermodynamically open system can exert causal influence via its coupling to a common niche which mediates causal influence on other coupled systems. A clear example is the Daisyworld model, in which the black and white daisy populations each possess an individual identity, but their interaction is mediated by planetary temperature. This downward causal influence from the system on the state of its components contrasts with the notion of supervenience, in which the state of components determines the state of the system. Mutual determination of component and system is termed by Thompson [5] *dynamic co-emergence*.

Now a system property is ontologically emergent only if its causal efficacy is non-supervenient; however this seems from our considerations so far to be possible only if the system is coupled to an external niche. Our conjecture is therefore that truly ‘existent’ properties are only possible in dynamically co-emergent systems. But if existence is contingent upon openness to external coupling, we are justified in questioning whether there exist any intrinsic properties. Is information an intrinsic property of a genome, or a relationship between the genome and its environment? Even more fundamentally, is substantiality an intrinsic property of genes, atoms, or whatever, or is it a relationship between the respective entity and its environment?

There have been a variety of answers to this question. Bickhard and Campbell [46] point out that ‘According to our best science, there are no elementary “particles” or basic particulars at all’. Bitbol [27] rejects the whole notion of ontological emergence, concluding that ‘Both [low and high level features] are causally relevant to one another, yet not in any one-directional metaphysical sense.’ Dawkins [8] firmly assigns evolutionary substantiality to the gene, discarding a basis in lower-level nucleotides as simply unhelpful. Oyama [12] insists that information is definitely not intrinsic to the genome.

Some light is shed on this issue by Wilensky’s [47] EACH project, which explores the origins of cooperative behaviour using two populations of computational agents: light-grey altruists and dark-grey selfish agents. At each simulation step, each agent receives a fitness value determined by its four immediate grid neighbours—for each altruistic neighbour the agent increases its fitness by a fixed value. The fitness of the agent is then equal to 1 + its benefit from altruistic neighbours, minus a fixed cost if the agent is an altruist. Agents with altruistic neighbours therefore have higher fitness, but altruists are subject to an additional penalty. The species of agent which appears in the next generation of a cell is determined.
by the fitness of altruistic and selfish agents in the cell’s neighbourhood.

The EACH model is run in two phases: ‘Paradise’ and ‘Adversity’. In the initial Paradise phase the outcome is clear—the fitness of selfish agents is higher than that of altruistic agents. Depending on the relative population densities, after about 200 generations all altruists are extinct (see Figure 9: Light grey indicates altruists and dark grey indicates selfists). This outcome fits well with genocentric expectations.

In the Adversity phase two environmental parameters, harshness and disease, are introduced. Harshness limits population growth by making some empty cells uninhabitable; disease reduces an agent’s chances of reproducing. The introduction of these threats changes the stability of the populations, so that altruists survive better than selfists. When conditions are harsh enough, a lone altruist survives no better than a lone selfist, however groups of altruists can survive harsh conditions through the combined altruistic benefit of their members.

Particularly relevant to our discussion here are the processes which maintain the integrity of altruistic groups in the EACH simulation (Figure 10: black indicates empty space). Observing these processes, three points become apparent:

(i) An altruistic group is embodied as a collection of altruists. This group is not a thing, so much as
a self-constituting process: a collection of life-cycles which recursively reinforce each other in their generation and their realisation as a group.

(ii) An altruistic group is embedded in an environment, from which it constitutes itself as a distinct unity. Since altruists are less likely to reproduce in the company of selfists, light-grey areas retreat in successive generations from contact with dark-grey agents, leaving a black open boundary which protects the group from the ravages of selfists.

(iii) An altruistic group is narratively coupled with its environment through niche construction. This coupling is neither sequential nor algorithmic, but essentially narrative [48]: when approached by selfists, the group does not first perceive and then act to protect its integrity, but rather the selfists and altruists at the meeting point engage in a temporally extended, mutually contingent dynamic which reinstates the group’s integrity.

These three characteristics of an altruistic group qualify it as an autopoietic, or autonomous, system. Thompson [5] defines an autonomous system as one whose internal processes (i) recursively constitutes each other as a network, (ii) constitute the system as a unity distinct from its environment and (iii) determine a set of dynamical interactions with its environment. Condition (ii) is particularly relevant here, since it requires an autonomous system to construct a physical or functional boundary between itself and the environment which enables the altruistic group to form. McMullin and Varela [49] used computational models to investigate the conditions under which such a boundary can spontaneously form and be maintained, and Fontana et al. [50] created a computational model in which generic properties such as narrative coupling reliably arise from a simple set of abstract chemical kinetic laws.

Particularly interesting for our discussion is that despite being distinct from their environment, altruistic groups (and autonomous systems in general) are not so much stable entities as ongoing processes of self-creation whose composition and form are in constant flux. Their influence on other agents is distinctly not unilateral, but arises from mutually causal interaction with their social niche.

AN ONTOLOGY OF PROCESSES
The ontological stance which emerges from work on autonomous systems is known under various headings such as evolutionary developmental biology, enactive evolution [5] and developmental systems theory. All these accounts subscribe to a common world-view dating back in modern times to the process philosophy of Whitehead [51] and the dialectical organism-niche relationships of Lewontin [43]. In this process view, units at all levels are processes, rather than things, which possess ontological status solely by virtue of their autonomous nature. Their identity is embodied in self-organising internal dynamics; their causal efficacy arises from their embedding in a downwardly causal environment; and they achieve ontological autonomy through narrative coupling to this environment.

This approach to biological ontology necessarily blurs the classic biological boundaries, making it difficult to distinguish clearly between the role of genetic and environmental resources in a developmental system, between genetic and group determinants of altruism in Dicrocoelium or between genetic and organismic factors in cancer. Instead, the distinguishable, existent entities of this view of biology are not so much ‘things’, as life-cycle processes implemented in genes, organisms, culture and so on. In this view selection as an exogenous causal mechanism is replaced by the endogenous dynamics of the differential reproduction of life-cycle processes. Biological systems, rather than being mere algorithmic problem-solvers [10], become the prime movers of biology by relinquishing their ‘thingness’ and claiming an inherently dynamic nature.

A crucial feature of this enactive world-view is co-evolution. We have seen that the collective social niche of a species can propagate causal influence, but this niche is also constituted from social agents with their own evolutionary agenda. Kauffman [11] investigates this co-evolutionary perspective in a series of models which allow processes in a lattice to co-evolve with each other subject to two separate constraints: $K$-fold coupling between processes within a single species, and $C$-fold coupling of a species with each of $S$ other co-evolving species. Of Kauffman’s many findings, the following are of most interest to us here:

- As each species evolves, it drastically alters the fitness landscape on which its co-evolving partners evolve, resulting in highly volatile evolutionary dynamics. Some species ‘freeze’ into unchanging stasis for a while, exhibiting robustness in the face of a changing co-evolutionary environment, while
others thrash around in a chaotic attempt to adapt to their changing environment. Between these two extremes Kauffman finds a ‘poised’ area in which species combine robustness with the flexibility to adapt to changes in the environment. Kauffman proposes that the optimum state for a species is precisely this poised combination of robustness and flexibility.

- High values of $K$ (intra-specific, epistatic coupling) increase the flexibility of species, while high values of $C$ (inter-specific coupling) decrease flexibility. Low values of $S$ (number of species in social niche) increase the robustness of species.
- Co-evolving populations tend to tune the numerical parameters $C$, $S$ and $K$ so as to satisfy the poised condition $K \approx S \cdot C$ and the coupling inequality $K > C$. The poised condition reflects the fact that co-evolving populations seek to poise themselves for both robustness and flexibility, while the coupling inequality expresses species’ attempt to maximise their fitness within the constraint of the poised condition.

These findings suggest a number of implications for populations of co-evolving processes. The first is that optimisation may not be a good metaphor for characterising evolution; rather, the suggestion is that species co-evolve to maximise their flexibility and robustness. Stearns [52] refers to this as the satisfying of viable evolutionary trajectories.

A corollary of this perspective is that populations maximise their flexibility and robustness by increasing their value of $K$ with respect to $C$, emphasising intra-group coupling over inter-group coupling. This naturally leads to the formation of a narrative coupling boundary which distinguishes the group from its niche. It seems that co-evolution of processes encourages the formation of multi-level autonomous aggregations with differential rates of reproduction. The structure of these aggregations is defined by richness of narrative coupling between the processes: strong internal coupling defines the group as a unity, while sparse external coupling defines the boundary of the autonomous unity.

**CONCLUSIONS**

From the work reviewed here two things are apparent. First, computational biomodelling is clearly an active player in the philosophy of biology in enabling the exploration of possible biological worlds. Second, it seems we have a choice: If we adhere to a substance ontology, the evidence from computational biomodelling suggests that even our much-treasured intentionality is reducible to mechanical interactions. If on the other hand we assert that organisms (and we) possess causal autonomy, we may need to adopt an ontology founded on processes which enact stable modifications in their embedding niche.

This enactive ontology regards properties, not as intrinsic to entities, but rather as processes, or dynamical relationships between entities. Autonomy then becomes a particular kind of dynamical relationship between entities which we have called narrative coupling. Indeed the idea that entities themselves derive their existential status from their composition out of narratively coupled processes is entirely compatible with current science.

The system properties we are most inclined to call ontologically emergent arise from cooperation between component parts, and multilevel selection models demonstrate that such cooperation predicates a system boundary across which causal influence is sparse. Co-evolutionary models suggest that such boundaries are an expected consequence of viewing evolution as the satisfying of viable trajectories. The behavioural novelty of such an autonomous system derives from its thermodynamic openness to the surrounding niche, and its causal efficacy is enacted through stygmeric interaction with this niche.

We conclude by adapting the following four assumptions of enactive ontology from Thompson [5] (p. 206):

(i) The fundamental ontological unit at any level (atomic, genetic, neural, organism and community) is the organisationally closed, ecologically embedded *autonomous process*.

(ii) Causal interaction between autonomous processes is fundamentally recursive and mediated through narrative coupling to a common niche. Recursively self-reinforcing interactions result in organism-niche constructions of greater or lesser stability.

(iii) Stable constructions support the stygmeric communication necessary for the implementation of higher-level autonomous processes. A *life-cycle* is a high-level process which reconstructs itself stygmerically with greater or lesser fidelity.
(iv) Both interaction and reconstruction preserve life-cycle forms differentially over time, giving rise to co-evolution as the dynamic stabilisation [53] of viable (rather than optimal) life-cycle interactions.

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