Full Body: The Importance of the Phenotype in Evolution

Abstract  This is a position paper on phenotype-based evolution modeling. It argues that evolutionary complexity is essentially a functional kind of complexity, and for it to evolve, a full body, or, in other words, a dynamically defined, deeply structured, and plasticity-bound phenotype is required. In approaching this subject, we ask and answer some key questions, which we think are interrelated. The questions we discuss and the answers we propose are: (a) How should complexity growth be measured or operationalized in natural and artificial systems? Evolutionary complexity is akin to that of machines, and to operationalize it, we need to study how machinelike organismic functions work and develop. Inspired by studies on causality, we propose the notion of mechanism. A mechanism is a simplified causal system that carries out a function. A growth of functional complexity involves interconversions between a deep (or unused) process and that of a mechanism. (b) Are the principles of natural selection, as they are currently understood, sufficient to explain the evolution of complexity? Our answer is strongly negative. Natural selection helps adapting mechanisms to carry out a given task, but will not generate a task. Hence there is a tradeoff between available tasks and mechanisms fulfilling them. To escape, we argue that competition avoidance is required for new complexity to emerge. (c) What are the environmental constraints on complexity growth in living systems? We think these constraints arise from the structure of the coevolving ecological system, and the basic frames are given by the niche structure. We consider the recently popular idea of niche construction and relate it to the plasticity of the phenotype. We derive a form of phenotype plasticity from the hidden (unused) and explicit (functional) factors discussed in the causality part. (d) What are the main hypotheses about complexity growth that can actually be tested? We hypothesize that a rich natural phenotype that supports causality-function conversions is a necessary ingredient of complexity growth. We review our work on the FATINT system, which incorporates similar ideas in a computer simulation, and shows that full-body phenotypes are sufficient for achieving functional evolution. (e) What language is most appropriate for speaking about the evolution of complexity in living systems? FATINT is developed using advanced agent-based modeling techniques, and we discuss the general relevance of this methodology for understanding and simulating the phenomena discussed.

Keywords  Evolution, complexity, causality, sustained evolution, phenotype plasticity, niche construction, agent-based modeling

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1 Introduction

Full body makes the best of wine and the best of evolution. This article rehearses an argument that is not new, yet little understood, as is clear from the questions in the workshop from which the article has emerged, and the many failed attempts to simulate or mimic evolution in silico or in vitro, or by other methods.

The argument is, in a nutshell, that phenotypes, understood as fully realized material bodies existing in an interactional, relational environment, are of central importance for evolution—in particular, for pushing evolution forward. Without such full bodies (alternatively called fat phenotypes, relational phenotypes, or just phenotypes herein, where the last usage reflects the fact that the biologist's intuition has never been very different), the process of evolution gets stuck at local peaks of adaptation. We outline the structure of this argument and discuss its relevance to a variety of issues related to the modeling and understanding of evolution. The current article is part of the EvoTech project (www.evotech.hu) at Eötvös University and Collegium Budapest.

We attempt to present a comprehensive discussion. This comes with inevitable limitations. For further information on phenotype-based evolutionary modeling, sustained evolution, the relationship to niche construction, and other issues including causality and fat interactions, we refer to previous publications [21, 23–25]. In some ways, the present article (being more theoretical) is complementary to them, and presents a narrative beginning with the first principles of causation up to the philosophy of evolutionary ideas and modeling details. Since this is a position paper, we do not offer a review of or (except where unavoidable) a polemic about other approaches. Discussion of related works is left for subsequent publications.

In approaching the subject, we ask and answer some of the key questions of the call for this special issue, as we think several of them are interrelated. The structure of the argument is shown in the abstract. We begin with the most basic question.

2 Functional Complexity and the Evolution of Mechanisms

How could complexity growth be measured or operationalized in natural and artificial systems?

This question actually has two parts. The first part is, apparently, easy. Evolutionary complexity is, prima facie, a functional kind of complexity. This means that it should serve a “purpose” leading towards the organism. Organisms and ecosystems, and other entities of evolution, are organizations, that is, their different parts constitute an interaction network responsible for the system’s persistence and self-maintenance (as stressed in down-to-earth concepts like autocatalysis and hypercycles, or more avant-garde ones like autopoiesis or chemoton theory). Functional complexity is the kind of complexity that appears in this process. A version of Dobzhansky’s dictum1 applies here: that, biologically speaking, the complexity of organizations—and of their parts—is only meaningful insofar as this complexity arises from the relevant causal interactions in an evolutionary system. This may sound simple, but has important consequences: Anything not “visible” to these causal interactions in an evolutionary system is just a decorative (i.e., epiphenomenal) kind of complexity. (An epiphenomenon is a consequence of a primary phenomenon.) In contrast to functional complexity, epiphenomenal complexity refers to evolutionary properties that just don’t matter. Epiphenomenal complexity is, therefore, empty: As long as a property does not feed back to a causal process, it is really not there—“what does nothing is nothing,” said Bergson [3].

We can draw an important parallel here. Functional complexity is much like the complexity of a machine—a complexity necessary for the machine to work, in order to fulfill a purpose. (“Purpose” here should be understood, as usual in similar discussions, in the mild and well-understood sense of design [9] or proper function [31]). Even the most striking features of an organism, such as the

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1 “Nothing in biology makes sense except in the light of evolution” [10].
giraffe's long neck, would not be part of the definition of the giraffe's functional complexity (and hence its phenotype), therefore, were they not used for something of adaptive value, with a functional role for the giraffe. Current theory [37] says that the giraffe's long neck is mainly used for male sparring (“necking”), and that all other significant byproducts, such as its feeding from upper leaves, or the characteristic clumsy drinking behavior that makes the animal so vulnerable, are consequences. (For the latter maladaptation, a sexual selection advantage, or some other feature, must counterbalance.) Large as it is, the giraffe neck barely has a function, and without this function it disappears from the phenotype. On the other hand (and this should also be obvious), seemingly negligible features such as scent, hardly more than just a few molecules in the air, can serve as sources of a crucial complexity (e.g., in predatory or mating behavior), if other species, or members of the same species, pick it up by their sensors. It all depends on the functional relevance, not on the size, impressiveness, or morphological significance. In the giraffe, the function of the long necks could and—disregarding other factors—would disappear in captivity, where fights are ruled out: It would disappear from the phenotype (from the definition of “what matters”) and later perhaps from the morphology. In short, functional complexity is a complexity of the ever-changing evolutionary functions—and consequently, of the dynamic structures that can support them. The problem of the origin of evolutionary complexity reduces to the study of the relations that make organisms work as machines.

The second part of the question seems to be more difficult. What makes a structure become part of a function? Hence, what makes something complex rather than simple? We propose that understanding causality is the key here. Causal events always have a certain depth, and this makes causal processes complex in a trivial sense. We can safely assume that every natural process is causal; this trivial complexity can be taken for granted. To show nontrivial complexity as exemplified by functional complexity, we propose that a canalization of causal processes will be necessary.

Causal depth is just a fancy name for the fact that any causal event is simultaneous or coextensive with an unbounded number of other causal events, which are hidden inside or come along with the original event in an inexorable way. For instance, the event of the falling of a stone also moves the molecules of the air and each of the stone's individual atoms. The stone also casts a shifting shadow, and glitters in the sunshine. Such events proliferate endlessly and instantaneously, when the original event, in this case the falling of the stone itself, occurs. There is a difference between depth and immediate consequence, but that's not an issue here—in any case, depth formulates an intuition that no causal event stands alone. This is what we meant above by saying that every causal event is complex, albeit in a trivial way.

Could evolution build upon the unbounded complexity of the many physical events hidden in the falling of a stone, for instance? Apparently, not. It's not true, therefore, that just any kind of causal process can be used for hosting a process of functional complexity. Nontrivial complexity needs specific constraints to achieve anything interesting. In machines, the processes that specify functions come along with the possibility of error. An error is the result of an amplification of the trivial complexity hidden in the causal depth of the given function. Turning things around, if we are interested in functions, the origin of functional complexity must closely be related to the problem of how trivial complexity, such as is present in errors of machines, can be constructively used for feedback in order to alter the design of machine functions.

Elaborating this idea, let us briefly discuss the kinds of constraints currently in the foreground of interest in the philosophy of biology, and associated with the notion of mechanism [6, 29]. A mechanism is a specific causal system that is used (and also described and understood) without reference to much of the underlying trivial complexity. The same property, we suggest, may also make it possible to build up functional complexity in the form of the complexity of mechanisms.

To understand mechanisms, we must appreciate how biology is different from physics. Biochemical and ecological mechanisms arise when causal systems reduce to pure functions. Biochemical functions (such as ligase function or end product inhibition), and apparently the majority of biological functions of interest, typically narrow down to a singular causal chain. (“Enterokinase activates trypsinogen,” and forget about the rest.) As a consequence, mechanisms are predictable to the

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point that we need no real physics to operate or understand them. With a little exaggeration, no chemistry is needed for biochemistry. Molecule A does this to molecule B, and B does that to molecule C. This is what a mechanism is about, a chain of highly predictable and causally simple events connected together [7]. (Having understood this, even a falling of a stone, itself not very mechanism-like, can be built into a mechanism using some ingenuity—just by removing the complexities of the process and by narrowing down its outcomes by introducing some constraints, such as letting the irregularly falling stone roll down on a slope towards a switch at the end.)

Mechanisms arise when ordinary causal systems are constrained so that one (or a few) of their causal processes become dominant (e.g., much faster or statistically more reliable) and other elements of the causal halo really just don’t matter any more. In a combustion engine, of all things happening, it’s the mechanical transmission process that forwards most of the energy and does all the useful work. The rest is obsolete or ineffectual, that is, epiphenomenal.

In evolution, we maintain that functional complexity develops when mechanisms grow and diversify while keeping the majority of the constraints that allow them to work. For instance, a prokaryote's mechanism may consist of a few hundred reactions, which form a tiny subset of the chemical processes that may be present in the given system. By the time we have E. coli, the number of components reaches the order of the tens of thousands, and the functional complexity of the different reactions becomes enormous, yet the connectivity of the mechanism (i.e., its dimensionality, in the reaction-network simplification of rate-based chemistry) is of a similarly low degree. In an ecosystem, food webs reiterate the low connectivity: In terms of dynamic stability, the issue was first addressed by the famous May-Wigner theorem, according to which stable dynamic complexity requires low connectivity [11]. In short, a mechanism is a low-dimensional but reliable system that exists in a high-dimensional but unreliable system by simply turning off the rest, and we find various mechanisms at work in evolution.

The conclusion is, if we want to understand the evolution of complexity, we need an understanding of how mechanisms, and indeed many different mechanisms, can arise spontaneously. We discuss this and the conversions between trivial (epiphenomenal) and nontrivial (functional) complexities after some remarks about the controversial role of selection.

3 The Denial of the Fittest

Are the principles of natural selection, as they are currently understood, sufficient to explain the evolution of complexity?

Clearly, the answer to this question should be no. Selection means optimization relative to a task. If a task is given, the basic situation is that optimization either hits a wall or, worse, it does not even hit the wall (more complicated situations will be discussed shortly). In evolution, the functional complexity of the system is strongly limited by the kind of tasks available at a time and by the cost-benefit parameters of the possible local solutions. As a consequence, a given set of selection pressures tends to yield a well-defined set of mechanisms compatible with the pressure, and to a single best (or a best set of) adapted mechanisms as a limiting solution. Else, a limiting solution is not found (as when tasks have several local optima or rugged fitness surfaces), and an itinerancy over the compatible sets occurs. Such an optimization process no doubt produces complexity, but of a limited kind, which is relative to the set of mechanisms compatible with the task. This is not the method of choice for changing the whole set of available mechanisms ad infinitum, in order to give rise to ever new species and higher taxa and hence complexity as it occurs in the open-ended evolution of the real world.

Take a simple example. A cell located in a nutritive environment may adapt to the natural selection pressures that emerge from the kinds and abundance (or scarcity) of the available nutrients. The process may require the cell to introduce new elements in its biochemical mechanism, but in a

2 For a definite subset of E. coli's biochemical mechanism, Ravasz et al. [33] have identified $n = 193, T = 37,056, e = 312, N = 0.0084$ (where $n = \text{number of nodes, } T = \text{total number of reactions over } n \text{ chemicals, } e = \text{number of reactions, } N = \text{connectivity})$. Very low connectivity is typical of all sustained mechanisms.

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limited form. Bacteria that found themselves in a newly oxidizing atmosphere of the Earth (the result of a first environmental pollution that changed the original reducing atmosphere) were forced to invent the oxygen-based energy cycle. The essential meaning of such an adaptation is the shaping and tuning of new functional mechanisms that carry out the task of oxygen-rich metabolism. Once achieved, however, this mechanism stays intact unless some new task is given to the system from the outside, maybe a new pollution [21].

If we want ongoing adaptations, we need new tasks. However, new tasks are not consequences of natural selection. In fact, it opposes them. We propose here the concept of competition avoidance. The name reflects the idea that natural selection yields competition, and competition, in turn, yields winners, which, by the above analysis, excludes a successful innovation of mechanisms (see also [25, 26]). Competition avoidance may, on the other hand, lead to avoiding the very tasks to which competition and selection respond. This opens the door for new tasks.

The notion of competition avoidance generalizes several known concepts, among them, S. Wright's shifting balance theory and the notion of peripheral isolate [43, 44]. Despite much criticism (e.g., [5]), Wright's idea survives as a key concept in evolutionary theory. Wright foresees that populations on fitness landscapes tend to get stuck at adaptive peaks and hypothesizes that subpopulations located in marginal positions on the landscape and reproductively (in a temporary fashion) isolated from the rest may be the key to further evolutionary development. Today's discussion of sympatric and allopatric speciation (i.e., the problem whether a contiguous spatial environment allows for the origin of new species) owes its essence to Wright's original concept. The notion of competition avoidance expresses the same basic idea as Wright's, but without the spatial and fitness-landscape-related connotations—these are factors that may or may not contribute to a given evolutionary situation. Instead of fitness landscapes, which are derived concepts, competition avoidance directly refers to the tasks and causal interactions behind the fitness functions. In other words, competition avoidance is defined as a purely functional “dissent” from the pressure of natural selection.

Functional complexity is limited in its evolution by the nature of selection. Selection must be overcome, yet this may be difficult to achieve.

On the other hand, there is epiphenomenal complexity. Epiphenomenal complexity is free to evolve, and it is only bounded by the physical-chemical constraints that exist in the depth of a causal process (such as the pattern generation dynamics of a reaction-diffusion system). The difference between the evolution of functional and epiphenomenal complexity explains some of the paradoxes of evolutionary modeling. It is hard to find works that successfully address the problem of functional complexity, whereas morphological and other decorative aspects of complexity are easy to grow both naturally and artificially. An example is Dawkins' well-known Biomorph program [8]. Morphological and pattern-based complexity are purely epiphenomenal, yet both produce the illusion of evolutionary complexity. How to use it for real functional complexity is the key issue, and this is the issue we address here.

Many highly acclaimed digital evolutionary systems ultimately fail, in our view, because they don't find a way to achieve competition avoidance, or do this only partially and for a short time. Tierra is a case in point [34, 35]. The assembly language for digital organisms is powerful enough (it can produce any conceivable mechanisms whatsoever, that is, Tierra permits the formation of any finite automaton), and the system's ingenious operation soon produces a wealth of different mechanisms in a simulated evolution process. However, of the evolved Tierra organisms, only those that successfully compete for memory space can survive, and there is no way to permanently overcome this limiting condition in the Tierra system. A temporary solution is the formation of coalitions or symbiosis, exemplified by mutual replication. Yet, the inexorable kinetic competition characteristic of the Tierra system tends to be degenerative; the shortest programs will be the fastest to fill the space with offspring, and, after some time, the system inevitably drowns itself in debris. Avida [1, 4] introduces adaptive radiation as a response to limiting resource competition, which we see as an important recognition that foreshadows the “denial of the fittest” as expressed here; yet the basic setting of the system and the final outcome of the simulations is not fundamentally different from that of Tierra, where the basic functional space of the solutions is given and limited.
Another argument in favor of the notion of competition avoidance comes from the cybernetics of evolution. Formulated in classical control terms, selection incorporates a negative feedback, which has an eliminative effect for most members of the population. For evolutionary novelty and new complexity to develop, a new positive feedback will be necessary that overcomes the existing negative feedback arising from selection. A natural way to achieve this would be by removing the whole population, or part of it, from the realm of the negative feedback, thus freeing the subsidiary positive feedback components present in the system (e.g., density-dependent phenomena [2]). When negative feedback is thus released or decreased, what really happens is that competition is canceled or eased.

There are several known attempts at overcoming the bottleneck of static selection forces. The attempts differ in their treatment of competition. For example, Avida makes use of epistatic landscapes where gene-to-gene interactions modify the fitness values of organisms to explore a combinatorially increased function space, thereby pushing the limits further. Adaptive dynamics models construct scenarios where changes in a population can transform predefined fitness functions, which become multimodal and support the branching off of subpopulations. In our view, these approaches are not very far in spirit (although offering different actual solutions) from the old-negative–new-positive feedback scheme suggested above, which we think has its purest expression in the concept of competition avoidance.

Evolution has found a way to solve the problem, and we suggest that evolution’s solution was radical. In the next section we discuss niche construction and its grounding in trivial-nontrivial complexity conversion as a proposed solution. (Another radical solution would be abandoning the notion of selection and competition altogether, as some current random drift models imply [20].)

4 Niche Construction and Fat Phenotype

What are the environmental constraints of complexity growth in living systems?

The question invites an answer in terms of tradeoffs between environmental and organismic complexity. The backdrop for our analysis will be competition avoidance and task selection as introduced above. The starting point is that organisms that exist under a given set of selection constraints can never be more complex than their environment, from which the selection comes.

Evolution theory has long been struggling with the origin of evolutionary forces. Darwin believed the main factor was geographical and habitat change, such as island formation or migration. Since then, many different candidates have been put forward, from catastrophes [36] to epigenetic factors [14]. What happens if all such opportunities were exploited in a system? Will the process of evolution inevitably come to a halt?

Or, alternatively, is a bootstrapping process possible? Can organisms, to a large extent each other’s environment, define genuine new evolutionary tasks for each other? Some early attempts to tackle the problem, such as the Red Queen hypothesis [42], suggested a first positive answer. The idea is that adaptation in one species means a worsening of the environment for others, and that this leads to a “rat race” (a faster fox makes a better hare, which needs an even faster fox, etc.). Yet such arms race scenarios bring very limited progress, where basic evolutionary tasks and organismic mechanisms do not change fundamentally (it’s still foxes and hares). The recent rediscovery [27] of the organisms’ active role in evolution suggests a new approach (see also [28]; for additional historical references, see [24]).

The task structure of an evolutionary system can be expressed using the concept of ecological niche. In terms of this concept, the evolutionary task space and the selection constraints are consequences, rather than prerequisites, of an evolution process. A niche is understood as a set of complex ecological roles of a species, which include the (biotic and abiotic) resources consumed and produced by the species, together with the many ways in which this may occur. In general, anything that makes coexistence possible without competition with other species pertains to a niche. Fast-growing weeds on a river bank with certain chemical needs constitute a niche; if a new weed growing in a
different part of the season is introduced, this occupies another niche (even if its needs are otherwise
the same).

Niche construction, a recently influential advance, is understood as a process whereby organisms’
self-activity can alter each other's environment, such that the process brings forth new niches. The
activity does not need to be behavior-like: Plants alter the chemistry of the soil, and a large number
of new vegetative niches open (and close) if a plant species invades a territory. Animal behavior too
can initiate niche construction, as in Lewontin’s pivotal example [28] where a bug suddenly decides
to live on the opposite side of a leaf, starting an avalanche of evolutionary micro-events, and poten-
tially grounding a new niche for its own preys and predators. Typical niche construction events
are either behavioral innovations or genetic-morphological mutations, and some authors (e.g., [39])
prefer to consider them in the context of the Baldwin effect. More discussion on niche construction
is found in [32].

Our hypothesis, put forward in earlier writings [21–26], is that niche construction requires a
plasticity of the phenotype and that causal depth can provide this. Phenotype plasticity is the change
of an organism’s evolutionary properties in the lifetime of the individual. Phenotype plasticity can
occur for a variety of much-discussed reasons, many of them genetic and developmental. Causal
depth is complementary to these and offers a new way to overcome mechanisms’ simplicity to de-
velop nontrivial complexity. Our suggestion, emerging from the discussion in this article, is to
achieve competition avoidance by allowing phenotype properties and interactions to change, which
also brings forth a new kind of niche construction.

Like all mammals, the okapi obviously has a neck, but the neck is not part of its functional
phenotype. Or at least, it would be difficult to find an evolutionary task for the okapi’s neck in the
okapi’s own niche—a task where physical properties (such as the length) of the neck would matter.
The situation changes radically when one or several males of the population start to use their necks
for sparring, sidestepping the selection tasks that routine okapi life is all about, yet introducing a new
evolutionary task (try to be a good neck fighter), and with it, a new selection constraint, which comes
from the depth of the organism’s causal interaction potential.

At this point several of the earlier suggestions and formulations of the article converge, and it may
be useful to briefly summarize them. If evolution stops, complexity remains limited; and without
niche construction, evolution will stop. Niche construction, on the other hand, necessitates a con-
tribution from phenotypes. Phenotypes can support a niche construction process by being suitably
flexible; and besides other sources of flexibility, this is possible because phenotypes are full bodies
having an interaction depth that can be utilized for such a change. Finally, this depth is something
never completely exploited, so there is always room for future progress: Depth may be an un-
depletable source of new phenotype complexity and new tasks.

Among the consequences of this train of thought, we single out one: If this picture is to any
degree correct, then complexity in evolution cannot be based on genomic representation and in-
formation alone, and as a result, the genetic and other information-laden structures are no longer
useful in themselves for the study of evolutionary complexity (an idea that may not, by itself, be very
surprising, after the many developments in embodiment and systems biology, yet viewed from a
different angle here).

An interconversion between epiphenomenal and functional (i.e., depth-related and truly evo-
lutionary complexity) may be possible at this point. Traits that exist but are unused, such as the neck
of the okapi or the patterns of the zebra’s skin, may suddenly become parts of an evolutionary task
space, either as sources or as targets of selection (or both), should a phenotype transition occur that
puts them into an interaction mechanism. A good strategy for growing functional complexity can
rely on Darwin’s famous principle of function change: organs that once performed a given function and
became unused afterwards may be resources for new evolutionary change. Darwin foresaw this
mainly on the side of adaptation potential. The above analysis of the role of the phenotypes suggests
that the same principle may be at work in evolutionary task generation as well, and hence in guiding
complexity increase. Tinkering, exaptation, and function change are concepts that have long been
familiar in evolutionary theory, but mainly associated with the organisms’ responses to environmental
change. Now our suggestion is the opposite: Use them for the construction of new evolutionary forces that permit niche construction and evolutionary change leading to new complexity.

Our work on the FATINT system in the framework of the EvoTech project [24, 25] utilizes similar insights to build AI models of sustained evolution using variable phenotype definitions in digital organisms. The model is currently limited in its scope (confined to a proof of principle), as there is (e.g.) no developmental component in the system, and also our artificial ecology is extremely limited. Full bodies are imitated solely by the property of having depth—we use arbitrary methods for changing phenotypes, as if emerging from a preceding full body. Despite these current shortcomings, we believe we have shown the FATINT system to be capable of addressing the issues discussed in this article.

At the core of the FATINT system there is a complete evolutionary engine that uses standard operations that are required in any agent-based evolution model (such as energy uptake, consumption, aging and death, reproduction, mutation, and crossover). The system contains a population of sexually reproducing genderless organisms (e-snails) feeding on a single nonreplicating resource, energy. Organisms run a full autonomous life cycle and perform random mating, based on the assumption that every organism has an identical chance to meet any other. A formal description of the system with simulation results and analysis is found in [24, 25].

Fat interactions and evolutionary change are built at the top of the engine. The realization of selective reproduction is the key to the evolutionary process in the model [24, 25]. In FATINT (v5.0.12), reproduction is based on phenotype similarity defined by a distance function. The organisms’ phenotypes are represented as \( n \)-vectors, and organisms reproduce if two vectors are close enough in the similarity space. The model applies a variety of different similarity measures, from metric (Euclidean) to complementation-based and checksum similarity [25]. The resulting process, still in terms of the basic engine, is that of sexual selection having an emergent center: Organisms with a higher degree of similarity to each other tend to dominate the population after a time, and a single species of interbreeding individuals emerges somewhere in the \( n \)-dimensional space, its exact position and shape being a dynamic result contingent upon many parameters. Phenotype-to-phenotype interaction is confined to mating only. The (sexual) niche occupied by a population is determined by the (sexual) selection forces that arise in an emergent fashion as a consequence of \( n \)-vector similarity—the more similar have more offspring. The process of species convergence is fully analyzed in [25, 26], which will not be repeated here.

We also allow for the dynamic change of phenotypes. The method applied in the model is a direct consequence of the definitions of phenotype and depth used in this article. The role of depth is that it allows for a distinction between used and unused traits to support the induction of phenotype plasticity. We model this feature via its effects, namely, introducing a change of the phenotype definitions at run time. This is carried out by changing the \( n \)-vector that represents the organism (i.e., replacing it with another one, although some restrictions apply). In the best-analyzed version (v5.0.12) of the FATINT system, this happens by adding a new dimension to the \( n \)-vector (which becomes an \( n+1 \)-vector), using random or nonrandom values in the new position. This method underlines one of the fundamental difficulties in the computational modeling of full bodies. A computational model rests, by definition, on an explicit use of information, whereas depth is, also by its definition, implicit. How can (i.e., how far can) depth be incorporated in a computational model? We don't know the answer, and we avoid even the question by random addition of new properties to existing phenotypes.

In other words, phenotype plasticity as currently modeled in FATINT recapitulates the example of the giraffe, where a new sexual trait was turned on (for all organisms simultaneously) when necking began. We studied various realizations of this process by assigning new phenotype values using different methods, such as a type-based method (where every organism with the same genotype obtains and inherits the same changed phenotype), the type-independent method (where the type dependence is relaxed, as in cultural learning, which permits individual differences between identical genotypes), and other methods. We also began to study the effects of phenotype transitions affecting less than the whole population.
Using this system, we were able to test some of the simplest assumptions of our theoretical approach. Is it possible to induce competition avoidance by phenotype change? Can phenotype change lead to a mechanism change (i.e., to the establishment of new selection forces and new subpopulations functionally responding to them)? Can such a system produce several new species and maintain a set of different, dynamically emergent selection forces? The answer to all these questions is positive to the extent that a simple model such as the current one permits. A qualitative description of the results is as follows (for visual results and further analysis see [25, 26]).

Introducing a new phenotype component in the model has the effect of transforming the whole population structure. As a result of a different similarity, where the new traits are also considered, some digital organisms will find themselves removed in similarity space from the vicinity of their usual mating partners and brought closer to new ones, which offers new mating opportunities for them, otherwise excluded. In terms of the entire population, what (under mild conditions) follows next is that the internal variability of the system and of the mating events is temporally increased, and further amplified by the new local positive feedback arising from the new sexual selection events, which are turned on at different new places as determined by the contingent positions of the new phenotypes. Finally, the population (after about 100 generations) usually splits up into some (usually two or three) new stable species, each having its own sexual selection criteria and similarity centers—that is, some organisms continue to reproduce with their old mating partners on the basis of their little-disturbed earlier similarity, whereas new centers emerge where recently established phenotype values allow for new similarity to lead to new reproduction events. In short, in a stable evolutionary system, changing nothing but some relational properties of the phenotypes can lead to speciation and to the appearance of new functional complexity (here in the form of sexual traits)—in principle, continuing indefinitely.

Current work on the model includes testing limitations of finite population size on the number of speciation events, using more realistic phenotype change methods, and studying different genotype-phenotype mappings to assess the generality of the results and their bearing on the problems considered. We nevertheless believe these results make the formulation of a hypothesis already possible.

5 Testability of the Phenotype Hypothesis

What are the main hypotheses about complexity growth that can actually be tested?

Prediction: The changing phenotype hypothesis put forward here predicts that no evolution model and no evolutionary technology or ALife design will be able to produce a sustained evolution process (in the sense of the above) and support the increase of functional complexity without admitting a changing definition space (i.e., a dynamic ontology) for its entities, presumably by also admitting full material bodies that permit the changes of phenotypes as a natural part of an interaction potential, as expressed in the notion of causal depth.

In different words: The basic hypothesis forwarded here boils down to no evolution without phenotypes. Here, to avoid misunderstanding, by “evolution” we mean evolution as we know it, and by “phenotype” we mean phenotypes in the broadest sense of the word, that is, as full material bodies, complete with depth, and linked to germs by a nontrivial development such as that found in real organisms.

6 Use Professional Models, Not Metaphors

Finally, we present a somewhat disconnected plea for a hard-core, professional style of modeling, as opposed to virtual hacks and ad hoc simulations: Which models are (what language is) more appropriate for understanding (speaking about) the evolution of complexity in living systems?

3 "It is interesting to contemplate a tangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent upon each other in so complex a manner, have all been produced by laws acting around us." Origin of Species, 6th ed., beginning of last paragraph.
We believe that the answer is agent-based modeling (ABM), understood properly. ABM’s main tenet is to model the individual, together with all its imperfections (e.g., limited cognitive or computational abilities), idiosyncrasies, and personal interactions [12, 13, 15].

Probably, it is time to put an end to the development of nongeneralizable (i.e., purely ad hoc) models such as cellular automata or Core Wars-like toy systems. A current requirement clearly articulated in ABM is full embeddedness (e.g., [41]). This criterion means that all information necessary for performing a given function (e.g., in reproduction or computation) must be explicitly represented and manipulable, or tokenized. This requirement is akin to that of an explicit ontology [38] as the term has been used in the past 10 years in AI and computational philosophy (e.g., [15]). Agent-based modeling is a tool that comes closest to having formal ontologies for modeling. ABM is strongly grounded in systematic methodology in that it has several roots: ontologies, object-oriented programming, frames of AI, and so on.

Also, ABM defines a system’s behavior strictly from the point of view of the individual. This approach brings about a number of important consequences. In addition to trivial features (e.g., that ABM is a natural bottom-up strategy to define micro rules and seek the emergence of macro behavior), it also implies some subtleties. Most importantly, the agent metaphor encapsulates actors’ state variables, thus allowing for heterogeneity among the individuals. Moreover, since the agents are placed in an environment (be it spatial, network-like, or unstructured, i.e., soup-like), their encapsulation creates an explicit interface (or boundary) between the internal and the external part of the organism (cf. the condition of embeddedness). The actions of the individual are based on the internal state, requiring that everything that crosses the boundary (information needed for the local rules or actions affecting the environment and the other agents) must be modeled explicitly [16]. As a consequence, ABM demands interaction topology to be part (and a dynamic part) of the model description. This is a step forward from traditional computational modeling approaches, where the (interaction) space is typically an ad hoc (and static) choice guided by routine and tradition (at least partly based on implementational and demonstrational feasibility criteria of limited past systems, as in the case of the discrete two-dimensional grid space and display of many computational simulations). In contrast, the relational interaction approach of modern ABM [17–19, 40] allows for the handling of interaction topology as a first-class parameter of the model, which can be subjected to sensitivity analysis along with the other parameters of the system. The relational interaction feature is essential for the modeling of relational phenotypes required for evolutionary growth of complexity, and a key to the generalizability of the results (where “generalizable” is polite jargon for “meaningful”).

The ABM approach makes it possible to rewrite existing models in a standardized style that fulfills the above requirements. For example, a partially embedded system such as Avida may be indispensable as an intuition source. Its remake in the ABM environment would, however, clarify just exactly what hidden assumptions are used with respect to the origin of evolutionary forces or the carrying out of the (digital) organismic functions, or in terms of interaction topology.

Similarly, sensitivity analysis is a technique with which much can be achieved for quality standards and standardization. An intelligent sensitivity analysis toolbox is in development (e.g., supported by EU’s FET and IST, such as the QosCosGrid project, where FATINT is one use-case provider). The proposed sensitivity analysis tools are akin to the Runge-Kutta method for the numerical integration of differential equations, where the idea is to use an adjustable step size: for smooth changes large steps, for sharp changes ever-increasing step refinement, as in the case of chaotic systems. This will allow for the adaptive branching of the parameter space sweep as well, based on previously acquired results, and also for revisiting previously explored areas with increased resolution as needed. This approach is similar to the adaptive nonlinear tests (ANTS) of John H. Miller [30]. Combined, such techniques may open a new era for modeling and simulation, and currently much research, including our own, goes in this direction. FATINT was written in Java-based RePast, using fully encapsulated

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4 ABM development is supported by a number of computational toolboxes, like the Repast system (http://repast.sourceforge.net/). Due to the increasing methodological requirements facing computational modeling in general and ABM in particular, efforts are underway to create standardized, concise, and easy-to-use simulation definition languages, like the Repast-related FABLES/MASS system [18].
agent definitions and allowing for the use of many sophisticated analysis techniques discussed above, some available via the front end.

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