

Evolution: Limited & Predictable or Unbounded & Lawless?

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Abstract In this brief commentary I compare and contrast two different views of evolution: one of limited (convergent) evolution and mathematical predictability, and one of unbounded diversity and no entailing laws. Clearly these opposing views cannot both be true at the same time. Their disagreement seems to rest on different underlying assumptions, and the challenge is to see if they can be reconciled.

Keywords Convergence · Evolution · No entailing laws · Predictability

1 Introduction

At the Konrad Lorenz Institute (KLI) we recently had the honor of having two distinguished visitors. One was George McGhee (Rutgers University, NJ, USA), and the other Stuart Kauffman (Institute for Systems Biology, WA, USA). Both presented their recent work and ideas, which implied two seemingly opposing views of evolution. McGhee's view is that evolution is limited, with convergent evolution not only ubiquitous but also predictable. On the other hand, Kauffman's view is that evolution enables unbounded diversity, and is not entailed by any laws, hence is fundamentally unpredictable.

In this article I present a brief overview of both these views and their arguments. Since the two views seem to be opposing each other, they cannot both be true at the same time, at least not to their full extent. However, given both McGhee's and Kauffman's previous work and reputations, one would not want to discard either of these views or arguments offhand. Here I try to show that their apparent disagreement rests on different underlying assumptions. An important remaining challenge is to see whether these two views can be reconciled in any way.

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2 Limits and Predictability

McGhee (2011, 2015) argues for limits and predictability in evolution. He demonstrates these limits using theoretical morphospace analysis. A *theoretical morphospace* is a multidimensional hyperspace produced by systematically varying the parameter values of a geometric model of form. An example of such geometric model parameters are the whorl expansion rates for the two parts of a bivalved shell in brachiopods (McGhee, 2015).

A graphical example of a (hypothetical) morphospace is presented in Fig. 1, reproduced from McGhee (2015). The multiple arrows indicate the different dimensions, each one representing a model parameter (such as whorl expansion rate) that can vary within a certain range of values. This, then, gives rise to a multidimensional space of theoretically possible forms.

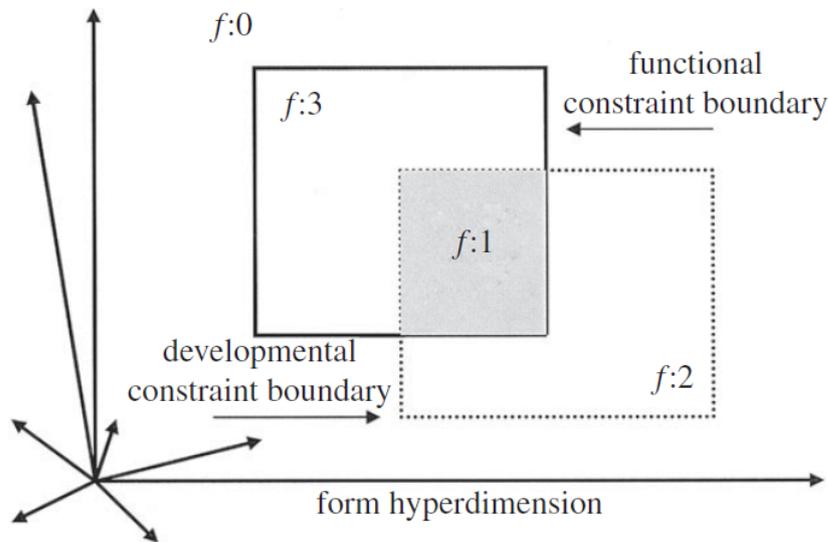


Fig. 1 A hypothetical example of a morphospace with functional and developmental constraint boundaries. Reproduced from McGhee (2015), with permission from the author.

But there are limits on the evolution of form, McGhee (2011, 2015) argues, due to functional and developmental constraints on evolutionary trajectories in morphospace. An example of a functional constraint in biconvex brachiopods, for example, is a lower limit on shell size (or rather, internal volume). Biconvex brachiopods use a pumping organ to filter feed, and because of the organ's structure, the internal shell volume has to be of a minimum size (McGhee, 2015). A shell smaller than this limit will simply not be functional. The (again hypothetical) functional limits in morphospace are indicated by the solid-line rectangle in Fig. 1.

An example of a developmental constraint in brachiopods is that whorl overlap must be avoided in order for both parts of the shell to fit together. If both whorl

expansion rates are too large, an overlap in whorls would be the result, which is developmentally not possible (McGhee, 2015). Developmental limits in morphospace are indicated by the dotted-line rectangle in Figure 1.

The intersection of these two regions (the shaded area) contains forms that are both functional and can (potentially) be developed. Indeed, as McGhee shows with several examples, the actually *evolved* forms of life on earth seem to have converged largely onto specific subregions within morphospace, in many different and unrelated instances. Because of limits in morphospace (functional and developmental), convergent evolution is ubiquitous and (at least to some extent) predictable, McGhee claims.

3 Unbounded Diversity and No Entailing Laws

Kauffman (2016b), on the other hand, presents a rather opposite view of evolution: that of (potentially) unbounded diversity and fundamental unpredictability (Longo et al, 2012; Kauffman, 2016a). He explains his argument by analogy, asking whether one could list all the uses of a screwdriver. It can be used to screw in a screw, open a can of paint, wedge open a door, be tied to a stick to make a spear, and so on, and on, and on. The critical idea here is that the uses of a screwdriver are both *indefinite* and *unordered*. However, this implies that there is no effective procedure (or, more formally, no *algorithm*) to list *all* the uses of a screwdriver.



Fig. 2 The uses of a screwdriver are indefinite and unordered, and can therefore not all be listed by an algorithm (Kauffman, 2016a).

Now transfer this critical idea and its implications to “molecular screwdrivers” such as proteins, or “biological screwdrivers” such as flagella. From this, it follows that there is no effective way to list (or *prestate*) all the relevant variables (or functions) acted on by natural selection. Therefore, it is impossible to write down the “equations of motion” for evolution (Longo et al, 2012). In other words, evolution is not entailed by any laws, and is therefore *fundamentally* unpredictable.

Furthermore, as Kauffman argues, each new use that comes into existence *enables* the evolution of yet more new (but possibly unprestatable) functions. For example, the evolution of a swim bladder enables the evolution of bacteria that live solely in swim bladders. And we can see the equivalent in technological evolution as well. The appearance of the internet allowed companies that sell goods solely online to come into existence. Kauffman (2016b) uses the term *adjacent possible* for this phenomenon: the collection of new “functions” (and organisms, or companies, that “implement” those new functions) that could potentially come into existence given the current state of the biosphere (or economy). However, since this “adjacent possible” changes and expands in ways that we cannot fully prestate, it gives rise to an unbounded (and unpredictable) diversity.

The ultimate conclusion Kauffman derives from this is that the strong reductionist view of a theory that entails the evolution of the biosphere is wrong, and that the end of a physics worldview that has dominated science since Newton has been reached (Longo et al, 2012; Kauffman, 2016b).

4 Comparison and Discussion

In the morphospace analyses as described and used by McGhee, the relevant variables (geometric model parameters), and also the relevant functionality, represented by a fitness landscape, are chosen by the modeler and then remain fixed. However, Kauffman argues that this is not possible, as those qualities are, in general, indefinite and unorderable. In other words, McGhee assumes that relevant variables and functions can be prestate, resulting in limits and predictability, whereas Kauffman assumes this is not possible, resulting in unbounded diversity and unpredictability. Thus, the main difference between the two opposing views seems to lie in their underlying assumptions. In fact, Kauffman and colleagues clearly admit that “*our thesis does not obviate reductive explanations of organisms as synchronic entities, such as an ultimate physical account of the behavior of an existing heart, once evolved*” (Longo et al, 2012), which is basically what McGhee’s morphospace analysis provides. So, perhaps the two views are not that mutually exclusive after all. McGhee focuses on possible *forms*, presuming a particular function, whereas Kauffman focuses on possible *functions*, presuming a particular form. The remaining question (and challenge), then, is whether these two views can be reconciled, and to what extent each one is valid and applicable.

The idea of developmental constraints in evolution is, of course, not new (Riedl, 1977; Oster and Alberch, 1982; Goodwin, 1982), and was probably most influentially argued for by Gould and Lewontin (1979) (see also Amundson (1994) for a clear interpretation and explanation). Unfortunately, though, McGhee (2011) does not directly relate his work to these older ideas, but he does present an impressive compilation of real biological examples, analyzed in a formal way (Powell and Mariscal, 2014).

He also hints at a possible extension of morphospace analysis when commenting on the empty region (beyond the derived limits) in the morphospace of bryozoans: “*This region of space appears to contain only non-functional forms for bryozoans—but are these forms functional for some other evolutionary clade of organisms with a different mode of filter feeding?*” (McGhee, 2015). Indeed, in biological evolution “functionality” (i.e., the fitness landscape) is not fixed. What might be functional

at one point in time may not be functional (or may be less functional) at some other time or in some other place, even if the organism remains the same. Due to changes in the environment, and the (co-)evolution of other species, an organism's fitness landscape changes over time. Combining morphospace analysis with the idea of *coupled fitness landscapes* (Hordijk, 2013) could provide one way of including the possibility of new (or at least changing) functionality. Furthermore, evolutionary adaptations could also give rise to additional variables (geometric parameters), possibly extending an existing morphospace by one or more dimensions. Both of these ideas would bring the "limited evolution" view of McGhee closer to the "unbounded diversity" view of Kauffman.

These notions of unbounded diversity and an ever-changing adjacent possible are not entirely new either, as they are clearly related to the concept of *niche construction* (Odling-Smee et al, 2003). Even the claim of inherent limits to the predictability of evolution is not unique (Day, 2012). However, one can question *how much* of a limitation Kauffman's "no entailing law" really imposes on our practical ability to predict the course of evolution. Claiming the "end of a physics worldview" seems rather extreme. In fact, even within physics itself, fundamental unpredictability (such as in nonlinear dynamical systems) has been known in principle for more than a century, and dealt with in practice for many decades now (Devaney, 1986). But there is another reason why I believe that Kauffman's claim may be too "pessimistic."

It cannot be denied that the possible functions of a (molecular or biological) screwdriver are indefinite and unorderable, and that therefore there is no algorithm to list them all. Hence Kauffman's conclusion that evolution is thus fundamentally unpredictable cannot be countered either. However, it seems that Kauffman implies that since there is no algorithm to list *all* possible functions (known or new) of a screwdriver, that it is not even possible to list at least *some* of them, or to search for at least *some* new ones.

In formal terms, this issue is equivalent to the well-known frame problem in artificial intelligence. The *frame problem* refers to listing all relevant features, variables, and their possible relations necessary to solving a given problem (i.e., a meta-problem). It is indeed true that there is no algorithmic procedure to list *all* of them, precisely because they are indefinite and unorderable. However, this does *not* mean that there are no algorithms that can solve the frame problem at least partially (i.e., approximately). If the frame problem could not even be solved approximately, we would not have any self-driving cars. But because it cannot be solved completely (or optimally), we still occasionally have crashes.

Kauffman seems to rely on the same misinterpretation of the "unsolvability" of the frame problem in a similar argument to claim that the human mind is not algorithmic (Zia et al, 2012). This misunderstanding based on a confusion of two different meanings of the phrase "to solve" (its formal theoretical computer science meaning and its informal colloquial meaning), was already addressed at length elsewhere (Hordijk, 2014). Here, I will elaborate on it in yet another way.

In 1936, Alan Turing published a paper in which he proved that the halting problem is undecidable (Turing, 1936). The *halting problem* refers to the problem of deciding whether a given computer program (formalized as a Turing machine) will eventually halt on a given input, or run forever. Turing himself did not use the phrase "halting problem," but this is how it came to be known. He showed mathematically that there cannot be an algorithm that gives the correct answer

on *all* possible combinations of a program and an input. Whatever algorithm one proposes, there will always be some program/input combinations on which the algorithm will give an incorrect answer.

By Rice's later extension (Rice, 1953), it turns out that this undecidability holds for *any* (non-trivial) property of a computer program, in addition to whether it halts or not. This also includes a program's correctness, i.e., whether it gives the correct (or desired) output on a given input. In other words, program correctness is fundamentally undecidable: it is not possible to construct an algorithm that decides for *all* possible program/input combinations whether the correct answer is returned.

However, writing and selling software to prove program correctness is an entire subindustry within the world of informatics. Indeed, even though the problem of deciding program correctness is *fundamentally* undecidable, it does not mean that it cannot be decided for at least *some* programs. In fact, for *most* programs that are written by humans, and *most* inputs we use, deciding program correctness is far from impossible. In practice there is still much that can be done, to our own benefit, despite the fundamental (theoretical) limit.

Now, to come back to the biological case, the fact that there is no algorithm to list *all* possible functions of a screwdriver (i.e., the equivalent of the frame problem), does not mean that it is impossible to construct an algorithm to list at least some (or perhaps even most) of them, or search for (some) new ones. Based on such an approximate ("as best as we can") solution of the frame problem, we can still write down some (if incomplete) equations of motion for evolution. They may not allow us to predict the *exact* evolutionary trajectory of a given species, as Kauffman argues, just as we cannot predict the exact trajectory of a nonlinear dynamical system. However, even in chaotic dynamical systems there are so-called "strange attractors," i.e., limited subspaces in the phase-space on which the dynamics converge (Devaney, 1986). Similarly, convergent evolution in biology is a very real and perhaps even ubiquitous phenomenon, as McGhee has shown. Not all predictability may be lost.

Indeed, fundamental limits in the predictability of evolution still allow for a less extreme interpretation. In his article, Day (2012) shows formally that the question of whether evolution will (ever) produce a particular genotype, is (in general) undecidable. This question is intimately related to Turing's halting problem, hence its undecidability. Day's result, too, implies that evolution is *fundamentally* unpredictable. However, he interprets this in a more realistic way: "[...] *the theorem presented here does not rule out the possibility that some predictions can be made. For example, it is entirely possible that a theory could still be developed to make [...] predictions about the evolution of drug resistance. The theorem simply says that it will not be possible to make [...] predictions about any arbitrary aspect of evolution [...]*" (Day, 2012). The fundamental unpredictability of evolution that Kauffman (like Day) claims is theoretically correct, no disagreement there. But its impact on our *practical* ability to predict the course of evolution is probably much less dramatic than Kauffman (unlike Day) seems to claim. Indeed, interpreting the unsolvability of the frame problem in a more realistic (and less drastic) way already closes much of the gap between the "no entailing law" view of Kauffman and the "predictable evolution" view of McGhee.

Where exactly in the spectrum between "limited and predictable" and "unbounded and lawless" biological evolution is located remains an open question.

The first extreme seems too narrow, the second one too broad. As with most (seemingly) opposing views in science, the truth probably lies somewhere in the middle. I hope this brief commentary can provide some first steps towards reconciling these two views of evolution.

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