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Evolution, Complexity, and Life History Theory

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Abstract

In this paper, we revisit the long-standing debate of whether there is a pattern in the evolution of organisms towards greater complexity, and how this hypothesis could be tested using an interdisciplinary lens. We argue that this debate remains alive today due to the lack of a quantitative measure of complexity that is related to the teleonomic (*i.e.* goal-directed) nature of living systems. Further, we argue that such a biological measure of complexity can indeed be found in the vast literature produced within life history theory. We propose that an ideal method to quantify this complexity lays within life history strategies (*i.e.,* schedules of survival and reproduction across an organism's life cycle), as it is precisely these strategies that are under selection to optimise the organism's fitness. In this context, we set an agenda for future steps: (1) how this complexity can be measured mathematically, and (2) how we can engage in a comparative analysis of this complexity across species to investigate the evolutionary forces driving increases or for that matter decreases in teleonomic complexity.

Keywords: biological complexity; evolutionary trends; fitness; goal directedness; life history theory; life history complexity; optimality; teleonomy.

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1 Introduction

In a 1991 paper in this journal, Daniel McShea criticised the longstanding conviction among evolutionists, ever since Darwin (1859), that the complexity of species increases over evolutionary time, in addition to the closely related idea of progressive evolution (see Levit and Olsson 2006). Aiming to question these ideas, McShea argued that there is almost no empirical evidence supporting this belief in a kind of directionality of evolution and that biologists may simply be misled by their own biased presuppositions. Further, he suggested that research should shift from more theoretical model-building work to empirical inquiries into actual increases in complexity offering several avenues for future research. Unfortunately, such a shift has not yet taken place. Rather, it seems that the interest among evolutionary biologists in the notions of complexity and progress has been waning for at least three decades, with the exception of their own work (McShea 1996a,b, 2021; McShea and Brandon 2010). Despite the scepticism advocated by McShea, however, it appears that biologists (as opposed to philosophers of biology) have nevertheless remained convinced in the consensus idea of an increase in complexity through evolutionary time.

The goal of this programmatic paper is to argue that McShea may have been incorrect in attributing this belief to mere cultural or perceptual biases among biologists. While we agree with his call for more empirical research, we do not share his dismissal of theoretical model-building work to understand complexity. Our core argument in this paper is that the natural phenomenon driving most of these ideas and intuitions regarding the directedness of evolution towards complexity is not any kind of complexity, but a special kind of complexity, distinct to the study of living systems, that has been increasing ever since the origin of life. We argue that this debate remains unresolved because of the lack of a distinctive biological measure of complexity that is related to the *teleonomic* nature of living systems.

Importantly, we use Pittendrigh's (1958) definition of the term 'teleonomic', as an evolutionary replacement of pre-Darwinian teleological explanations, *i.e.* that life is to be explained in terms of its purpose (often associated with a designer) rather than the mechanisms that gave rise to it. The concepts of goals, purposes, functions, and the like were revolutionized in the light of Darwin's theory of evolution by natural selection that explained them in causal terms. For instance, the goal of an organism is the maximization of fitness - not because that is true for any living system, but because natural selection has selected for such individuals in the past, which gives us predictive power to theorize about individuals in the present. Thus, as we use 'teleonomic' in this article, we define 'teleonomic' as the goal-directedness of living systems towards fitness-maximization. While the term teleonomic is also relevant for discussions of the 'functions' of traits, that is not the focus of this article, which is also why measures of functional complexity do not successfully capture the goal-directness of organisms (see McShea 2000 for an overview of this literature). By using this teleonomic lens, we conceptualize teleonomic complexity in terms of how complex the strategies are that organisms have evolved in order to achieve this goal. Some of these strategies are recognizably more complex and our goal here is to emphasize the need to measure and study this complexity.

Furthermore, we argue that such a biological measure of complexity is already available within the rich arsenal of metrics provided by life history theory and comparative demography. It is only in assessing the complexity of life history strategies that we are provided with a teleonomic measure of complexity that assesses the degree of complexity within evolved life history strategies in the pursuit of the goal of fitness-maximization. In addition, we conclude by outlining two directions for future research, one concerning how this complexity can be measured mathematically, and the other for how we can engage in a comparative analysis of this complexity across species to gain key insights toward understanding the evolution of organismal complexity.

Article Outline

This programmatic paper is structured as follows. In Section 2, we outline the debate on the evolution of complexity and argue that we should not be interested in any kind of complexity when it comes to the evaluation of progressive views of evolution without considering teleonomic complexity. In Section 3, we discuss how to measure teleonomic complexity, one must turn to life history theory. Finally, Section 4 outlines avenues for further research into the evolution of complexity.

2 Complexity and Evolution

We agree with McShea (1991) in that discussions of biological complexity have been present among a long row of evolutionists dating back to Darwin[1], Lamarck (1984), Cope (1871), Spencer (1890), Huxley (1953), Rensch (1960), Simpson (1961), and that these discussions have been of particular importance in the investigation of macro-evolutionary trends in paleobiology (Æble 2005; Jablonski 2005; Lowery & Fraass 2019). Despite some critiques of the idea, the last century saw great confidence in the idea that evolution increases complexity:

> [I]ncreasing complexity is still the conventional wisdom. Clear statements that complexity increases can be found in the work of Stebbins (1969), Denbigh (1975), Papentin (1980), Saunders and Ho (1976; 1981), Wake et al. (1986), Bonner (1988), and others. And lately the new thermodynamic school of thought has added its voice to the chorus: Wicken (1979; 1987), Brooks and Wiley (1988), and Maze and Scagel (1983) have all argued that complexity ought to and does increase in evolution. In my own experience, the consensus extends well beyond evolutionary biology and professional scientists. People seem to know that complexity increases as surely as they know that evolution has occurred.
>
> – Daniel McShea (1991, p. 303)

Much of the writing on biological complexity has unsurprisingly focused on the evolution and explosion of multicellular life and body-plans in the Cambrian. And yet, despite this conventional impression and the search for evidence for this thesis, very little evidence either in favour or against the hypothesis has been obtained. As McShea (1991) notes, few have actually empirically investigated whether complexity increases with evolutionary time. Yet, there have been many attempts at developing adaptive rationales for why an increase in complexity is beneficial and ought to be expected.

Biologists have long confidently maintained that 'organismal' or 'biological complexity' will increase throughout evolutionary history. Indeed, this is an idea that, as McShea (1991) points out, "extends well beyond evolutionary biology and professional scientists. People seem to know that complexity increases as surely as they know that evolution has occurred" (p. 304). This strange attraction to the idea that complexity inevitably increases with evolutionary time may be especially perplexing since it sits uncomfortably close to older vitalist and teleological views of

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[1] Though as McShea (1991) notes, Darwin only discussed his views on marcoevolutionary trajectories toward complexity in his Notebook E, not in his *Origin* (see Darwin 1987, p. 422).

progressive evolution or as it is sometimes called 'orthogenesis' (Ruse 2019). It is thus unsurprising that McShea (1996b) has been critical of attempts to revive Herbert Spencer's ideas of progressive evolution and the adaptive rationales of complexity and mind (Godfrey-Smith 1996), though also noting that the idea of progressive evolution remains "essentially the conventional wisdom even today" (p. 469). While we do not agree that the idea of progressive evolution is conventional wisdom today (or for that matter, even in 1991), the seeming increase in complexity in organisms such as during the Cambrian explosion (Valentine et al. 1994) has certainly come to inspire a lot of speculation (e.g., Carroll 2001; Zhang et al. 2014). If there is no evidence for an increase in complexity over evolutionary time-scales, however, there would appear to be little point in offering an adaptive explanation for a phenomena that may merely be a myth - perhaps as other critics of the idea alongside McShea (1991), such as Williams (1966), Lewontin (1968), Hinegardner and Engelberg (1983) hint at, a remainder of earlier hierarchical views of the biological world with humans placed on top that biologists have largely abandoned, though remain popular among the public.

McShea (1991) highlights how both empirical and theoretical studies have lacked rigor. For instance, most studies and perspectives miss concise discussions of what complexity actually means. Admittedly, while the concept has long puzzled philosophers and scientists alike, it seems reasonably clear that complexity is a *phenomenon* in nature. Complexity is as our folk understanding of the term rightly suggests opposed to the idea of simplicity, but this understanding does not give us much purchase on making the notion precise. Parts of nature can be readily placed on a continuum from simplicity to complexity. A frog catching a fly is more complex than a stone washed up at a beach. So one might be hopeful that we could develop a straightforward and unified measure of complexity to capture this phenomena in nature - a way of ranking systems on a single scale of complexity. Yet, attempts to operationalize complexity have resisted consensus.

We believe that part of the challenge here has been especially due to attempts to provide biologically neutral measures of complexity that could in principle be applied to any non-biological system. These neutral measures miss out on what we think has driven most advocates of the view that natural selection would select for greater complexity. For example, McShea (1991) repeatedly emphasizes that it is *morphological complexity*, rather than genetic complexity or ecosystem complexity, that he is interested in. And as he makes clear, the way this complexity should be measured has largely been inspired by researchers in information theory whose operationalizations of complexity could be applied to living and non-living systems alike.However, we argue the complexity that matters for biological systems should be informed by the drivers of evolutionary change; a teleonomic measure of complexity that assesses how the complexity of different strategies organisms have evolved to achieve their goal of fitness maximization.

One rough-and-ready measure of biological complexity in terms of heterogeneity is found, as Godfrey-Smith notes, in Bonner's 1988 book *The Evolution of Complexity*, where he measures complexity as a function of distinctive cell types in a multicellular organism, a move typical in discussions on cell-differentiation, division of labour, and the evolution of multicellularity (see Márquez-Zacarías et al. 2021). While this measure certainly is closer to the kind of teleonomic complexity we are interested in, it is only a proximate measure at best since it makes no reference to the complex trade-offs organisms undergo in the pursuit of fitness maximization. Furthermore, this definition in terms of heterogeneity lacks scale. For example, a patch of one cell is less complex than a patch of three cells. But, what if they can be differentiated? How does a patch of five cells of the same type compare to a patch of two cells of different types? The definition falls under the weight of its own constraints - in turn lacks scale. This shortcoming emphasizes the necessity of scalability in a measure of biological complexity. The metric must be exhaustive in the parameter space it can describe. In turn, the biological complexity of an *Escherichia coli*, a gopher and a giant squid from the depths must exist at some point in the same parameter space quantifying biological complexity.

In explaining ideas about biological complexity, many have drawn on Shannon's (1948) information theory published in "A Mathematical Theory of Communication", sometimes referred to as 'Shannon information' or 'Shannon entropy'. Following Godfrey-Smith (1996), Shannon information can be calculated as follows: for any system that has an exhaustive number of possible states, there is a probability of being in that state *i* denoted as P_i, "then the complexity or disorder of the system is measured as: $E = -\sum P_i \log_2 (P_i)$" (p. 28). If there are few possible states or most of the probability space is exhausted by a few options, entropy or thermodynamic probability is low, *i.e.* there is little uncertainty. If there are many alternative states with similar likelihoods, however, then uncertainty is high and the system is more complex. The higher the entropy, the higher the (potential) informational content of the states. Here, both organisms and environments can be understood as complex or simple the number and probability of their possible states. However, what these measures are lacking is a link to the 'goal' of biological systems, *i.e.* fitness. While these measures of entropy are certainly useful to capture uncertainty, variability, changeability, heterogeneity, and disorder of systems (Godfrey-Smith 1996), we are skeptical that it captures the kind of complexity that is important to living systems (Smith 1975). This skepticism is so because, as mentioned above, they do not recognize the complex strategic trade-offs organisms undergo to maximize their fitness. Indeed, in the measure of entropy there is no connection to the biological notion of reproduction and survival, the building blocks of organismal fitness.

Finally, to understand teleonomic complexity, we have to understand the population rather than the individual, which is neglected in many such measures of biological complexity. As van Groenendael et al. (1994) note, "Variation in life history traits among individuals within populations is ubiquitous in both plants and animals" (p. 2410). Nevertheless, the fact that life history strategies can be very complex also makes them very difficult to study. As such, we are happy to take up the task McShea (1991) has left to the discipline: "I leave it to others to discover the extent to which my remarks apply in other complexity domains" (p. 305). Why does the teleonomic complexity of species increase over evolutionary time? As we shall argue in the next section, the means for this task are to be found in life history theory as *the theory* of organismal strategies we find in nature.

3 Life History Theory and Teleonomic Complexity

Life history theory originated out of the study of the trade-offs between survival and reproduction. Some of these were very simple mathematical models (e.g. Leslie and Lefkovitch matrix population models: Leslie 1945; Lefkovitch 1965), while others were quite complex to understand the schedules of survival and reproduction can impact fitness (see especially Stearns 1992; Roff 1992). As Veit (2023) puts it: "To understand a species' teleonomic strategy is to understand their species-specific trade-offs between costly investments of resources into development, fecundity, and survival, with fitness providing an ultimate 'common currency' for this economic decision problem, or 'game' against nature" (p. 13). Trade-offs are universal and so the so-called Darwinian demon cannot evolve. Because of the myriad factors that have to be traded off against each other, it is no surprise that Morbeck et al. (1997) has nicely described life history theory as providing us with "a means of addressing the integration of many layers of complexity of organisms and their worlds" (p. xi). It is here that we find ourselves provided with the theoretical means to understand teleonomic complexity.

While Lewontin criticized adaptationism for not being able to deal with trade-offs and treating organisms as mere robotic bundles of traits (Lewontin 1985; see also Gould and Lewontin 1979), life-history theory offers an adaptationist framework to make sense of just such trade-offs. These trade-offs can be seen as the result of natural selection shaping traits such that a life history agent is able to pursue their goal of maximizing fitness:

> In life-history theory, [...] numerous aspects of an organism's life-cycle, such as the timing of reproduction or the length of its immature phase, can be understood by treating the organism as if it were an agent trying to maximize its expected number of offspring-or some other appropriate fitness measure-and had devised a strategy for achieving that goal.
>
> – Samir Okasha (2018, p. 10)

As evolution gives rise to more complex life history strategies, it is easy to see why many early evolutionists were convinced of the idea of progressive evolution. With fitness-maximization being both the teleonomic ‘goal’ and cause of organisms, life histories allow us to study the varying degrees of complexity organisms use to achieve this goal (e.g., from the relatively simple and fatally semelparous salmon to the relatively complex immortal jellyfish, *Turritopsis dohrnii*, that can reproduce sexually and asexually aswell as switch back and forth between sexual mature and sexually immature stages). We, therefore, think that our notion of teleonomic complexity offers an elegant way of explaining the connection between complexity and ‘progress’ that has often been made in this debate without necessarily having to explain it away as a mere cognitive bias.

Interestingly, such a teleonomic perspective does not have to imply that increases in complexity are inevitable. Indeed, because increases in complexity are typically associated with costs there is also an evolutionary drive towards simplicity, i.e. organisms developing less complex strategies. Two excellent examples that make this obvious are annualism and dwarfism.

While most animals typically reproduce over multiple reproductive cycles, many plants such as annual weeds are *annualists*, i.e. their life cycle involves only a single breeding season before the individual dies (Hautekèete, Piquot & Van Dijk 2001; Friedman 2020). On the other side, we find *perenniality*, i.e. life cycles lasting more than one year. Should we expect natural selection to inevitably move species towards perenniality? When chance of survival is low it makes sense for species to evolve very short life cycles and invest everything in one of few reproductive cycles. Natural selection thus often makes life history strategies less complex by moving from complex trade-offs towards investing everything in one breeding season (Bena et al. 1998; Fox 1990). Furthermore, species often switch quite rapidly (in evolutionary terms) from one strategy to the other or for that matter back again, suggesting that there is a lot of evolutionary pressure on the costs of more complex life history strategies (Friedman 2020). Similarly, we can find dwarfism in many species, i.e. individuals or species becoming significantly smaller in response to selection. Examples include the pygmy marmoset, *Callithrix pygmaea* (Montgomery & Mundy 2013), which stands in opposition to the common observation that animal size increases over time (Alroy 1998). The selective pressures that lead to dwarfism are manifold, though the most often discussed factor is related to the isolation of breeding populations to islands (Foster 1964). As we hope to have thus made clear, we should not expect some general explanation that can explain changes in life course complexity across all of life. Our explanations will have to be more fine-grained than that. Steiner and Tuljapurkar (2022), for instance, have recently shown using life history data that much of the non-environmental and non-genetic variability of phenontypes in a population cannot simply be categorized as neutral in respect to evolution, or for that matter selected for or against. The variability of life courses within even a single population remains a major puzzle within the field (see also Flatt 2020) and we hope that the development of our framework will help us move closer towards an understanding of how and why life history strategies change over evolutionary time. Thus, let us now turn to how this complexity can be understood in the context of life history theory.

Life History Strategies and Complexity

A life history strategy is the eco-evolutionary equivalent of a bar of soap in the bathtub; the firmer you try to grip its definition, the more the blighter lurches further from grasp. From parental care (Klug & Bonsall 2010) to dispersal (Bonte & Dahirel 2016), a plethora of phenotypes are required to fully characterise life histories across the tree of life. Simply put, a life history strategy is not a physical characteristic of a population one can extract and manipulate. In turn, when we discuss a life history strategy we must require our discourse to be general across form, temporal and spatial scales. Life histories are combinations of life history traits, and the latter refer to key moments along the life cycle of a species (e.g., age at maturity, frequency of reproduction, rate of development and generation time; Stearns 1992).

With this in mind, we propose we define a life history strategy as the time points and actions across an individual's lifespan that allow the population to persist in the face of ecological perturbations. Using this definition, let us build the archetype of a life history strategy – in its simplest form:

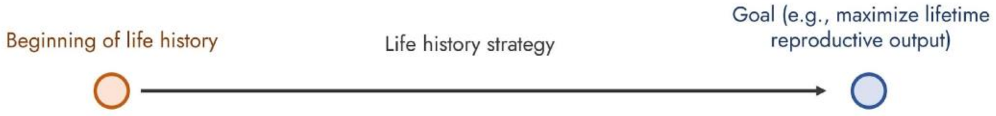

Figure 1: The goal of life history strategies

All life history strategies are defined by a schedule starting from the start of a life history (*e.g.*, birth, fission, cloning). This beginning is followed by a life history strategy that directs the individual towards a goal (*e.g.*, maximizing lifetime reproductive output or inclusive fitness).

Now that we have built our archetypal life history strategy, let us explore life history complexity. We can define life history complexity as being informed by two components of the aforementioned life history strategy. Firstly, life history complexity is informed by the number of paths individuals of the same population can take from the beginning of their life history to their goal - a term known as individual heterogeneity in life history theory (Tuljapurkar et al. 2008, Vindenes & Langangen 2015). Secondly, life history complexity is informed by the relative contribution of each of the paths toward the goal. For example, here are two life history strategies with different levels of life history complexity due to the number of possible paths.

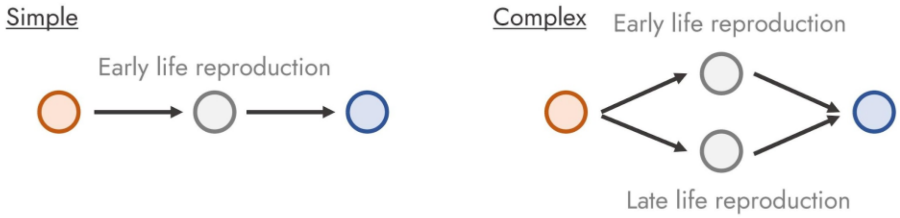

Figure 2: Complex and simple life history strategies

Furthermore, here are two life history strategies that differ in their complexity based on the evenness in importance of paths for individuals to reach their goal.

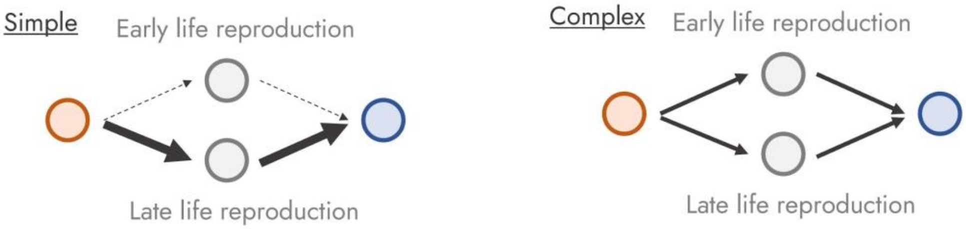

Figure 3: Complex and simple life history strategies

In short, by analysing the number and importance of paths in a life history, we are able to (even if only relatively) create a framework for life history complexity that is both based on the necessary properties of a life history strategy - shown in the archetypal example – and scalable across modes of life history research (e.g., from demography to behavioural ecology to developmental biology).

While we will not go into the mathematical measurement of this complexity in this paper here, we will nevertheless note that it will be straightforward to calculate this complexity by drawing on available matrix population models - a discrete time stage/age structured mathematical model where survival, growth and reproduction values are coerced into matrix form - of different species' demographic data to assess their life history strategies. As Van Groenendael et al. (1994) have argued, matrix models have shown themselves to be extraordinarily useful for the mathematical analysis of complex life history strategies (see also van Groenendael et al. 1988), which is why we believe it will provide the ideal resource to measure life history complexity.

4 Conclusion and Further Directions

Our goal in this paper was to introduce a set of conceptual ideas on how to assess a distinctive kind of biological complexity unique to living systems that we have called *teleonomic complexity*. In his seminal paper, McShea (1991) assumed that we should think of ideas about the evolution of complexity as being about morphological complexity. Yet, we have argued that the seemingly progressive evolution views of these authors can be naturalized in a less problematic sense in terms of an increase in teleonomic complexity without thereby invoking the idea of orthogenesis. As we hope to have made clear here, the apparent belief of many evolutionists in progress towards greater complexity can in principle be naturalized in a Darwinian way by restating this thesis as one about an increase in teleonomic complexity. That is, over evolutionary time, more complex life history strategies will emerge and it is this teleonomic complexity that we should be interested in.

That this complexity should be measured through the lens of life history theory was the second argument of our paper. All species have evolved life history strategies to achieve their teleonomic goals of maximizing their genetic representation in the next generation. These fitness differences can be mapped out in different ways to assess the diversity of life and one important dimension along which we can assess this diversity is of course complexity. Some life history strategies are more complex than others and natural selection is leading to an ever-growing exploration of more complex life history strategies (Giménez et al. 2004; Sebert-Cuvillier et al. 2007; Higgins et al. 2015). We are, of course, not endorsing the simplistic orthogenesis view that evolution leads to perfection and greater complexity as an end in itself. However, complex design solutions to the problems animals, plants, and other organisms face do not come out of nowhere. Their history is one from successively more complex strategies upon which more complex strategies can come to be explored. Natural selection provides an entirely unproblematic kind of progress if it is defined in a teleonomic manner, since we can expect it to come up with new and more 'ingenious' strategies that make sense of the apparent directness of evolution. We have thus argued against the suggestion by McShea that biologists may have fallen victim to their own cultural and perceptual biases forces *scala naturae* thinking into our view of life.

Nevertheless, while we have offered an explication of the idea of teleonomic complexity here, it remains a difficult problem to show how we can measure this complexity in practice. Acknowledging the difficulty of this task, we are currently working on a follow-up paper, where we will draw on graph theory to demonstrate how life history complexity can be mathematically measured such that others could engage in the same kinds of analyses to us of the same or other data sets. This task, however, will be left for another paper.

While we have argued that McShea depicts theoretical work unfairly, he was certainly right that there is a need for more empirical work to fill out what has largely remained a data and inference vacuum. We are carefully optimistic that teleonomic complexity can be expected to increase over evolutionary time, yet we acknowledge the need to provide further evidence for this view both in virtue of theoretical models and empirical studies. In another paper, we will apply our new life history complexity measure to the COMADRE (Salguero-Gómez et al. 2016) and COMPADRE (Salguero-Gómez et al. 2015) databases offering matrix population models of hundreds of animal and plants species to offer a comparative analysis of the complexity of life history strategies across a broad range of taxa.

Finally, we hope that our programmatic paper will raise interest in the teleonomic complexity of different species, which should not be confused with other notions such as morphological or functional complexity. It is our hope that both biologists and philosophers will contribute to its investigations and in order to understand under which conditions life history strategies become more complex or for that matter become more simple.

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