Structuralism and Adaptationism: Friends or Foes?

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Abstract:
Historically, the empirical study of phenotypic diversification has fallen into two rough camps; (1) "structuralist approaches" focusing on developmental constraint, bias and innovation (with evo-devo at the core); and (2) "adaptationist approaches" focusing on adaptation and natural selection. Whilst debates, such as that surrounding the proposed "Extended" Evolutionary Synthesis, often juxtapose these two positions, this review focuses on the grey space in between. Specifically, here I look at the motivations behind the "structuralist" and "adaptationist" positions in order to make clear the ways that these two approaches to understanding phenotypic variation are in conflict, along with the ways in which they are commensurable. In doing so, this review makes much clearer (a) the particular value of the evo-devo approach to phenotypic diversity, but also (b) how it properly relates to other predominant approaches to the same issues in evolutionary biology more broadly

Key words:
Phenotypic diversification, selection, development, extended evolutionary synthesis, adaptationism

Introduction

Reading the literature on the "Extended Evolutionary Synthesis" (EES) [1–8] you might reasonably assume that there is a great schism in evolutionary biology, with evolutionary developmental biology (evo-devo) at the core. Advocates for the EES argue for the integration of four important drivers of phenotypic diversity into the existing theory of evolutionary biology (described as "standard evolutionary theory"). These drivers—phenotypic plasticity, niche construction, inclusive inheritance and developmental bias—are, they say, neglected in standard theory, to the detriment of progress in evolutionary biology. What is required is an "extension" to standard evolutionary theory; the so-called "Extended Evolutionary Synthesis" [1–3] . Opponents of the EES respond by rejecting the assertion standard theory "neglects" phenotypic plasticity, niche construction, inclusive inheritance and developmental bias. Rather than being ignored, they say these phenomena are already incorporated into standard theory but lack the degree of "proven explanatory power" necessary for them to hold the type of prominent position that advocates of the EES contend they should have. Standard evolutionary theory, they say, offers "the most powerfully predictive, broadly applicable and empirically validated component of evolutionary theory" and we have no empirical justification for altering it as proposed [1,4,5]. Ultimately EES-sceptics argue that the controversy is nothing but a "a storm in an academic tearoom" whilst EES-advocates claim it is "a struggle for the very soul of the discipline" [1].[1] These diametrically opposed assessments cannot both be right—the EES debate cannot simultaneously be vacuous and of deep import—so, what is going on here, and which assessment is right?

In this critical review I focus on one nexus of disagreement in this debate by digging down into the conceptual origins of evo-devo and evolutionary biology. I make clearer how evo-devo's approach to the question of phenotypic diversity, in particular, relates to that taken in standard evolutionary biology. Three key questions guide the discussion:

1. What is the relationship between the approach to phenotypic diversity typical of research in evo-devo, and that characteristic of so-called "standard" evolutionary biology? (*Section 1: Evo-devo and Evolutionary Biology: A potted history*)
2. What theoretical and empirical differences (if any) motivate these two different research approaches? (*Section 2: Looking Beyond Conflict: Motivating structuralism and adaptationism)*

[1] The following pithy comment from Jerry Coyne, prominent critic of the EES, is indicative of some of the vitriol that the EES has gleaned from some mainstream evolutionary biologists; "Struggle for the soul of our discipline"? That seems a bit dramatic and self-aggrandizing, and is simply untrue. There is no such "struggle" going on, except, perhaps, in the minds of those who feel that their work is not sufficiently appreciated or advertised" [64].

3. How commensurable are these theoretical and empirical motivations? (*Section 3: Friends or Foes? A more nuanced picture of the relationship between evo-devo and standard evolutionary biology*).

Ultimately, I show that, at the heart of at least some of the EES controversy lies two very different attempts to understand phenotypic diversification and the mechanisms that generate it[2]:

(I) "Structuralism": focusing on developmental constraint, bias and innovation and best illustrated by the evo-devo research program.

(II) "Adaptationism"[3]: focusing on adaptation and natural selection, best illustrated by the core research programs of evolutionary biology such as population genetics and behavioural ecology.

There are a number of different motivations (both empirical and theoretical) for adopting one or other of these approaches. Importantly, not all of those adopting any given approach share the same motivations; neither evo-devo, nor standard evolutionary biology are homogenous. Having made this motivational landscape clear, I show there are a number of points of real disagreement behind the call for the EES, but also that there are a number of possible (and actual) points of agreement (or at least commensurability). An appreciation of this is important to making sense of the radically different assessments of the EES offered by its sceptics and its advocates, and also in providing an avenue via which to move on from the controversy.

I begin my analysis (Section 1) by outlining the nature of structuralism and adaptationism, starting with their origins in the early evolutionary biology of the 19th Century.

1. Evo-devo and Evolutionary Biology: A potted history[4]

1.1 Embryology in early evolutionary biology

The structuralism at the core of evo-devo has its origins in the idea of unity of type in biology whose intellectual roots stretch right back to Aristotle [9]. This idea came to the fore in the 19th Century, as researchers tried to make sense of the evolutionary theories of scientists, such as Charles Darwin and Ernst Haeckel, and assess their empirical adequacy. This endeavour required reliable

[2] These two approaches are not exhaustive of the approaches represented in either the EES debate or contributing to contemporary evolutionary biology. "Constructivist" approaches (which focus on the role of the organism in constructing and organising their environments through processes like niche construction [65–67] and "reciprocal causation"[48,49]), for example, are not discussed here. For this reason, I don't claim to offer a comprehensive analysis of the EES debate but focus instead on just one axis of the debate.

[3] While sometimes used as a slur, or criticism (due to Gould and Lewontin's famous *Spandrels* critique [58]), the term "adaptationism" here is not intended to have that value-laden meaning, but more neutrally refer to an approach to evolutionary biology which focuses on adaptation.

[4] This is a very brief sketch of a much richer historical narrative from a philosopher no less. Those wanting more detail should turn to Manfred Laubichler and Jane Maienschein's faboulous edited volume, *From Embryology to Evo-Devo* [11] or Ron Amundson's equally as good monograph, *The Changing Role of the Embryo in Evolutionary Thought* [12].

evidence about the past form of organisms and their relationships, but it was not easy to come by during at this time. The fossil record was only really just being properly explored, and the mechanics of inheritance were poorly understood. Against this empirical background, the unique value the study of embryos and development offered researchers at this time becomes very clear. By looking at the ontogenetic trajectories of different species, researchers were able to reconstruct their phylogenetic relationships and begin to test ideas such as "descent with modification". Now familiar ideas, such a homology, evolutionary novelty and the conservation of traits, were central to this approach [9–12]. As famous evolutionary biologist of the time, William Bateson, put it "Morphology was studied because it was the material believed to be the most favourable for the elucidation of the problems of evolution, and we all thought that in embryology the quintessence of morphological truth was most palpably presented. Therefore every aspiring zoologist was an embryologist, and the one topic of professional conversation was evolution" [10,13].

This continued into the early 20th Century when the role of embryology and development in evolutionary biology shifted dramatically. At this point, Haeckel's theories of ontogeny recapitulating phylogeny were challenged empirically, and real theoretical and empirical traction was made on the question of inheritance. It wouldn't be until the evo-devo "turn" almost a century later that the embryology and development would even begin to gain the same attention within evolutionary biology [9–12].

This big shift was driven by a new approach to understanding phenotypic variation and diversity . By combining Mendelian genetics (which had only just been rediscovered) with the formal tools of statistics, theorists such as Theodosius Dobzhansky, Ronald Fisher, Colin Wright and JBS Haldane were able to make rapid progress on a variety of key questions in evolutionary biology [14,15]. Their approach (which ultimately become the discipline of population genetics) did not rely on the often tedious and slow study of embryos and quickly took over as the main game in evolutionary biology. Later, researchers such as John Maynard-Smith and George R. Price added further complexity to evolutionary biology with their game theoretic approaches to sexual selection and animal communication [16–18]. Other fields branched off this one too. For example, behavioural ecology (whose roots are in the ethological work of Otto von Frisch, Konrad Lorenz and Niko Tinbergen in the mid 20th Century) draws heavily on the theoretical foundation provided by population genetics [19].

1.2 The Modern Synthesis and "adaptationist" status quo

By the mid-20th Century and the period of the Modern Synthesis, the predominant approach to evolutionary biology in the Anglo-American parts of the world is best characterised as "externalist" or "adaptationist". Specifically, there was a focus on accounting for the features of the biological world in terms of an adaptive response to the environment or conspecifics, or drift (i.e. external forces), rather than any other causes internal to organisms (such as

developmental constraint) [5,20–23]. I unpack the details of this further in Section 2, but for current purposes what is most significant is that within this paradigm the study of ontogeny is well and truly side-lined and evolutionary biologists typically treat development like a "black-box"; it is seen as irrelevant to their research interests [14] . Ernst Mayr's famous proximate-ultimate distinction [24,25] reflects this disciplinary division.

According to Mayr there are two domains of enquiry for the biological sciences. The first of these concerns so-called "proximate" causes— those pertaining to the immediate individual-level mechanistic causes of development or physiology—and is the focus of study in fields such as developmental biology, anatomy and physiology. The second concerns so-called "ultimate" causes—the historical, population-level statistical causes of the features of populations—and is the focus of study in evolutionary biology. Although Mayr acknowledged that both of these domains of enquiry are required to achieve a full explanation of a given organismic trait, the distinction is commonly interpreted as delineating two autonomous and distinct domains of enquiry [14]. This has played a key role in shaping the landscape of biology, and evolutionary biology in particular, for the past half century. The long reaching ramifications of this are observable in university infrastructure, for example, where ecology and evolutionary biology are often separate administrative units from genetics, cell biology, and developmental biology [14].

1.3 The return of devo in evo

Despite Mayr's distinction, as our ability to investigate the mechanisms of development, and the genetics underscoring phenotypic diversity, grew in the late 20th Century, various researchers returned to investigating the role of development in the evolution of phenotypic diversity and the original structuralist focus of the 19th Century.[5] Stephen Jay Gould's 1977 book *Ontogeny and Phylogeny* [26] and his work of the same period with Niles Eldridge [27] were seminal to this shift, but so too, were the discovery of fundamental developmental genetic units like the homeobox and master genes like *Pax-6* [10]. In the late 1970s and early 1980s a number of researchers, such as Per Alberch [28–30] , Brian Goodwin [31], Rudy Raff and Thomas Kauffman [32], were working at the intersection developmental biology and developmental genetics and calling for a greater integration of Mayr's domains of proximate and ultimate biology [10]. This momentum only grew over the decades following and the field of evo-devo we see today is directly descends from this renewed interest in the origins of traits, the conservation of traits and the origins of phenotypic disparity as well as diversity. It is the melding of the genetic

[5] Although the mainstream Anglo-American approach at this time was heavily adaptationist, it would be a mistake to claim that *all* work looking at the role of development in evolution ceased over the period from the end of the 19th Century to the 1970s. Conrad Waddington's famous work on developmental canalisation[68], for example, was carried out in the middle years of the 20th Century. So too outside of the Anglo-American scientific community (particularly in Germany and Russia), significant work in comparative embryology was being carried out during this period with a strong influence from Haeckel's evolutionary morphology [34,69].

knowledge of the Modern Synthesis with the much older ideas about development and ontology which characterised early evolutionary biology [10,32–37].

Unlike the externalism of the predominant adaptationist approach, the evo-devo approach is internalist and structuralist in nature. It focuses on accounting for the features of the biological world by reference to internal developmental constraints and biases and other mechanisms such as phenotypic plasticity [22,23]. Given this, it is unsurprising that evo-devo and "standard" evolutionary biology are so often cast as being in conflict. Not only does evo-devo transcend Mayr's popular proximate-ultimate distinction, but it also focuses on studying phenotypic diversity relatively independently of selection and adaptation, something which has been at the heart of evolutionary biology for more than a century. There is obvious potential for empirical disagreement here should researchers from evo-devo and standard evolutionary biology disagree about the relative causal contribution of selection versus constraint in the evolution of a trait, or more broadly the relative causal contribution of selection versus developmental processes in generating the patterns of phenotypic diversity we see across the tree of life. Whilst this potential for disagreement is real, when we delve into the conceptual landscape further, we see that the depth of the disagreement depends on what sort of "selectionist" or "structuralist" you are. Furthermore, the types of very strong views which lend themselves to the most vehement disagreements, are in fact less dominant amongst researchers within evo-devo and evolutionary biology.

2. Looking Beyond Conflict: Motivating structuralism and adaptationism

2.1 Three kinds of adaptationism

Turning to adaptationism first. As already highlighted, the explanations generated by the Modern Synthesis approach to evolutionary biology focus on the role of selection in shaping the tree of life. This includes more than just straightforward natural selection. Other processes, such as sexual selection and frequency-based selection, are a part of this approach. As will become apparent below, it also need not ignore other non-selectionist factors in evolution, such as drift either. Importantly, the focus is largely externalist—concerned with how features external to the mechanistic features of organisms shape evolution [38]. Of course, I am not claiming that *all* work being carried out in typical evolutionary biology departments is like this. Rather, I am simply delineating adaptationism as the central theme or core to research in this domain. Of key significance for us here is the role of background assumptions in motivating this core approach.

Three broad selectionist positions have been identified (Table 1) [20,21,39]. Holding one or more of these motivates engagement in the

externalist selectionist research program. Before I comment in more detail on each of these positions, note, that they are not exhaustive (see [40] for example for a different way of carving up the space). They are also broad views despite the narrow definitions here. More moderate versions of each type of adaptationism are possible and held by various scholars [21]. In this sense, the tripartite division here is best understood as an idealisation, aimed at giving broad landscape of the discipline without necessarily capturing all those engaged in it.

Adaptationist position	Key claims
I. Empirical Adaptationism	1. That selection is a powerful and ubiquitous force, and there are few constraints on the biological variation that fuels it. 2. To a large degree, it is possible to predict and explain the outcome of the evolutionary process by attending only to the role played by selection. 3. No other evolutionary factor has this degree of causal importance.
II. Explanatory Adaptationism	1. That the apparent design of organisms, and the relations of adaptedness between organisms and their environments are the big questions, the amazing facts in biology. 2. Explaining these phenomena is the core intellectual mission of evolutionary theory. 3. Selection is the key to solving these problems—selection is the big answer. 4. Because it answers the biggest questions, selection has unique explanatory importance among the evolutionary factors.
III.Methodological Adaptationism	1. That the best way for scientists to approach biological systems is to look for features of adaptation and good design. 2. Adaptation is a good "organizing concept" for evolutionary research.

Table 1: Three Kinds of Adaptationism
(The definitions here are due to Peter Godfrey-Smith's paper "Three Kinds of Adaptationism" [21]).

Empirical adaptationism in this strong form is not a mainstream contemporary view (nor perhaps has ever been a mainstream view) but weaker forms of the view certainly are expressed in the literature. Empirical adaptationism is a contingent, empirical view about the prevalence of adaptation and the power of natural selection in the biological world [21,41]. This position *if true*, would justify the externalist focus of adaptationism. This is because, if natural selection is indeed, the central causal factor in evolution, evolutionary biologists need not bother with the internal features of organismic systems when developing their evolutionary explanations.[6] Importantly, empirical adaptationists need not (and do not) deny that factors other than the environment are important to evolution but deny them any significant causal role in the shape of the tree of life. For example, they need not deny that mutation is a precursor to evolution by natural selection so long as it not thought to account for the direction of evolutionary change over evolutionary timescales. The real-world testability of empirical adaptationism is undecided. Although theoretically appealing methods have been suggested for evaluating the position [42], their implementation remains problematic [43]. As I say, in its strong form this is not a common contemporary view, but something weaker of this flavour is seen in the writing of at very least Jerry Coyne [44], Richard Dawkins [45] and Daniel Dennett [46]. Dennett, for example, dubs Darwin's theory of evolution by natural selection "universal acid" which "eats through just about every traditional concept, and leaves in its wake a revolutionized world-view, with most of the old landmarks still recognizable, but transformed in fundamental ways" [46] implying both a commitment to the ubiquity of adaptation and the explanatory power of natural selection. Coyne offers a clearer statement of empirical adaptationism, when he says "In essence, the modern theory of evolution is easy to grasp. It can be summarized in a single (albeit slightly long) sentence: Life on Earth evolved gradually beginning with one primitive species—perhaps a self- replicating molecule—that lived more than 3.5 billion years ago; it then branched out over time, throwing off many new and diverse species; and the mechanism for most (but not all) of evolutionary change is natural selection" [44]. Skeptics of the EES also reflect something of this view in claiming that "…it [the Modern Synthesis] laid the theoretical foundations for a quantitative and rigorous understanding of adaptation and speciation, two of the most fundamental evolutionary processes"[1].

[6] As Lewens [40] points out, the causal role attributed to selection by empirical adaptationists need not justify externalism. In particular, empirical adaptationism would not justify externalism if the type of interactionist/constructivist picture of evolutionary causation John Odling-Smee, Kevin Laland, Tobias Uller and associates [48,49] were true. While this is worth noting (especially given the likelihood that the interactionist/constructivist picture is right), no one appears to hold the combination of interactionism/constructivism and empirical adaptationism. There are, however, *explanatory* adaptationists that do hold an interactionist/constructivist view, the implications of this for externalism are discussed when we look to explanatory adaptationism.

In contrast, *explanatory adaptationism* is probably the most prominent contemporary view in evolutionary biology even in a relatively strong form, having been espoused by key figures such as Douglas Futuyma [5], Andy Gardner [47], Richard Dawkins [45] and Daniel Dennett [46].[7] It concerns the "philosophical priority of certain explanations" in the discipline [43]. Explanatory adaptationism motivates abstracting away from factors other than natural selection in our evolutionary explanations by, first, picking out adaptation as the explanatory target for evolutionary biology, and then, purporting that the only explanans for that target is natural selection. If these two assumptions hold then the externalism of adaptationism is justified. Importantly, explanatory adaptationism is not a thesis about the ubiquity of natural selection; it can be true even if natural selection is rare, so long as it accounts for the problem of apparent design [21]. Rather, advocates of explanatory adaptationism are defending a particular theoretical approach to evolutionary biology. We see this view reflected in the comments of leading evolutionary biologists, such as Andy Gardner who argues forcefully for the importance of Darwin's Theory of Natural Selection as "…the only scientific theory of the purpose of adaptation" [47]. The reasons for adopting this approach are complicated and I will not go into them here, suffice to say that there are a variety of aesthetic, political, cultural and social reasons that motivate its adoption.

Methodological adaptationism is a "policy recommendation for biologists". Its proponents have a particular account of what will result in progress in evolutionary biology and advocate a heuristic (i.e., "focus on selection") that reflects this. Methodological adaptationism, unlike the other two forms of adaptationist position, offers purely pragmatic justification for ignoring factors other than natural selection in evolution (although one might justify holding the position by reference to empirical evidence about the ubiquity of selection). We see methodological adaptationism reflected in the views of Mayr [25] who saw the search for adaptations as the default, first step in evolutionary investigation, and non-adaptationist approaches as a last resort, for when the default first step fails [42].

As already mentioned, while the adaptationist positions as presented here are quite strong, more moderate versions of each of them are possible [21,42]. For example, many adaptationists would accept only a weak version of explanatory adaptationism in which *both* adaptedness *and* diversity are the purported important explananda for evolutionary biology. Similarly, many would broadly accept methodological adaptationism, but prefer a slightly weaker formulation of it (i.e., that adaptation, despite clearly being one good "organizing concept" for evolutionary research, is not the only one). As will become apparent later in the paper, the possibility of weaker versions of adaptationism, and a middle ground between adaptationism and other approaches is important for understanding the relationship between

[7] Dennett and Dawkins have argued for all three adaptationist positions at one time or another [21].

adaptationism and structuralism. The tendency in assessments of the adaptationist framework and its rivals thus far to present adaptationism in its stronger form has not been beneficial to theoretical progress in evolutionary biology.

A second feature of the positions to note concerns their independence. The three adaptationist positions are strictly logically independent despite the fact that evidence which supports one can serve to support another [21,42]. To illustrate, although evidence for the truth of empirical adaptation will likely provide support for explanatory adaptation, it need not. Explanatory adaptationists are committed to a claim about the power of selection, not its ubiquity. We see this reflected in the Richard Dawkins who views the project of accounting for adaptation to be of unique importance within evolutionary biology, despite accepting that forces other than natural selection act in evolution [21].

A third, and final, point concerns the role of the three kinds of adaptationism in motivating the adaptationist program. While holding one or more of the three positions can motivate idealizing away from factors other than natural selection in our research, it need not. Laland, a key advocate for niche construction theory, offers a case in point here [48,49]. While committed to some sort of evolutionary explanation and the importance of explaining adaptedness, he is not an externalist in any strict sense, advocating an approach to evolutionary biology that is more constructivist/interactionist. Although accepting adaptation as (at least one of) the central explanatory targets for evolutionary biology, and natural selection as the key explanans for it, according to Laland the adaptation we see in the natural world is a product of a complicated and messy interplay between natural selection, organisms and their environments via processes such as niche construction. Natural selection, on his account, is not a process that can be captured simply by looking at the environment. Thus, although Laland is an explanatory adaptationist of some stripe, he is not an advocate of the strong idealizations seen in the traditional adaptationist research program.

2.2 Three kinds of Structuralism

As outlined in Section 1, in contrast to the selectionist focus of the adaptationist research program, the focus of evo-devo is on the development of internalist explanations for biological systems. In the case of evo-devo, we see this in the explanation of the evolution of organismic traits by reference to internal developmental constraints and biases [22,50]. This approach is motivated by structuralism—a commitment to the importance of studying the internal developmental mechanisms in organismic evolution. There. are roughly three structuralist positions that motivate engagement with evo-devo (Table 2). As with the three adaptationist positions and standard evolutionary biology, these do not represent solid divisions within evo-devo. Rather they track "clumps" in the conceptual space sufficiently enough for them to be useful to us in cashing

out the theoretical heterogeneity of evo-devo. I now outline each in turn beginning with empirical structuralism.

Structuralist position	Key claims
I. Empirical Stucturalism	1. That developmental constraint is a powerful and ubiquitous force in evolution. 2. To a large degree, it is possible to predict and explain the outcome of the evolutionary process by attending only to the role played by developmental constraint. 3. No other evolutionary factor has this degree of causal importance.
II. Explanatory Structuralism	1. Diversity, disparity and complexity are the big questions, the amazing facts in biology. 2. Explaining these phenomena is the core intellectual mission of evolutionary theory. 3. Developmental constraint is the key to solving these problems—it is the big answer. 4. Because it answers the biggest questions, developmental constraint has unique explanatory importance among the evolutionary factors
III. Methodological Structuralism	1. That the best way for scientists to approach biological systems is to look for disparity, diversity and complexity. 2. Investigating developmental constraint and hidden structural unity is the best way to undertake evolutionary research.

Table 2: Three Kinds of Structuralism

Empirical structuralists are committed to a contingent, empirical claim about the biological world. This commitment motivates engagement with evo-devo and its focus solely on providing internalist explanations because, if developmental mechanisms are the sole robust explanations of evolution (as they claim), then we need not be concerned with other factors. There are a number of prominent defenders of this view within evo-devo, notably Stuart Newman, David Wake and Bryan Goodwin. They hold to vary degrees of strength the view that organismal form is highly derived and strongly constrained by a set of

developmental mechanisms. On the picture they advocate natural selection plays only a minor role in determining the organismic form. Rather, development (in particular developmental constraint) is central. For example, according to Wake and Goodwin teleological explanations of traits should be discarded entirely in favour of mechanistic ones [51]. Their view here is in contention with all forms of adaptationism discussed earlier as they deny the utility of the adaptationist project altogether.[8] Importantly, however, their view does not represent the majority opinion. There are (as with the other positions I will discuss here also) stronger and weaker versions of this empirical structuralism. I take it Newman, Wake and Goodwin hold a stronger version of empirical structuralism, while someone like Gerd Müller [52–54] could be said to hold something significantly weaker. Although Müller emphasizes the supreme causal importance of development in evolution (in particular, the central role of development in phenotypic innovation and novelty), he would deny the strength of the second commitment, favouring a view on which development explains the broad structure of the phenotype but selection accounts for variation within that (i.e., development explains how many digits we have but not their exact appearance) [55].

Explanatory structuralism relies on an empirical claim (that developmental mechanisms are the cause of the disparity, diversity and complexity we see in the world), but unlike empirical structuralism (which emphasizes the ubiquity of developmental constraints in causing the outcomes of evolution), however, it can be true even if developmental constraints are rare (i.e., so long as they alone are able to explain diversity, disparity and complexity, then they are the most important evolutionary factor). Explanatory structuralism motivates focusing on development by delineating a particular explanatory domain for evolutionary biology and positing developmental constraint as the central explanatory factor within that domain. On this view, one could feasibly be interested in explaining adaptation (and subsequently the development of selection-based explanations) but would fail to be engaged in the core mission of evolutionary biology. As with the other positions, there are weak and strong versions of explanatory structuralism. One could hold the first commitment but not think that diversity, disparity and complexity are the only amazing facts in biology, for example. Gould's approach in *Ontogeny and Phylogeny* [26] is an illustration of this type of view. While not denying the primacy of natural selection in evolution, Gould emphasizes the importance of explaining disparity and complexity and the failure of natural selection to offer any traction on these explananda. He advocates a less monistic approach to evolutionary biology, in which adaptedness is not the only explanatory target. Gould is not alone in this

[8] It is worth noting, that unlike Amundson [70], I do not think that this is because strong empirical structuralists like Wake and Goodwin are committed to a form of causation that mainstream adaptationists cannot make sense of. Rather, I take it that they are concerned with a project (the production of lineage-based explanations) that can proceed completely independently of the traditional adaptationist program and are committed to a set of structuralist background assumptions that undermine motivation for the development of selection-based explanations altogether.

sentiment. Carroll [56] argues that the range of animal forms is a central explanandum for evolutionary biology and that evo-devo would have been "a cornerstone" of the Modern Synthesis had we had access to contemporary knowledge of development during its construction. Raff [37], offers perhaps the most clear statement of explanatory adaptationism when he says "What constitutes the fundamental problems for a science of evolutionary developmental biology (evo-devo) depends on whether the scientist is a developmental biologist, a palaeontologist or an evolutionary biologist… ". Going on to look at the explanatory interests of each type of researcher and thus the focus of their study with developmental biologists described thus, "For developmental biologists, the principal and inter-related problems are how development has evolved, and how developmental evolution has resulted in changes in particular structures or features of body organization." We see a version of explanatory adaptationism also reflected in Müller's [7] defence of the Extended Evolutionary Synthesis :…it has become habitual in evolutionary biology to take population genetics as the privileged type of explanation of *all* evolutionary phenomena, … the MS theory lacks a theory of organization that can account for the characteristic features of phenotypic evolution, such as novelty, modularity, homology, homoplasy or the origin of lineage-defining body plans…evo-devo, niche construction, systems biology and other areas harbour the capacity to address at least certain aspects of these topics where the classical theory fails."

Unlike the other two positions, *methodological structuralism* does not involve a strong empirical claim of any sort. It is rather a "policy recommendation for biologists". Methodological structuralists hold a particular view about what will progress research in evolutionary biology and advocate a heuristic that reflects this. One way (though not the only way ([57]) of reading at least elements of Gould and Lewontin's *Spandrel's* critique [58], is as advocating this kind of weak view [43,59]. They do not deny the primacy of natural selection in evolution, but rather recognize its explanatory limitations and argue that focusing solely on selection can (in some cases) lead us astray. Thus, we should be interested in other factors aside from natural selection in our investigations.

As with the three adaptationist positions discussed earlier, there are a number of features of the three structuralist positions worth noting. First, while there are relations of support between these three structuralist positions, they are not relations of strict implication. To illustrate, if you are an empirical structuralist you are also likely to be a methodological structuralist, as if development is the central casual player in evolution it suggests that focusing would be a good heuristic for evolutionary research. Importantly, however, you need not hold both theses together. For example, while being an empirical structuralist you might believe the investigation of the role of development in evolution is particularly difficult, or currently beyond our empirical capabilities, in which case you might deny methodological structuralism. Similarly, you can

be an explanatory structuralist while denying empirical structuralism; this being a combination of views I take many in evo-devo to hold. A second feature of the positions to note is that while strong versions of the various structuralist positions have been presented above, weaker versions exist and are held by proponents of evo-devo. Finally, it is important to note that holding any of these structuralist views need not motivate strong internalism. Brian K. Hall [60], for example, takes evo-devo to be "a synthesis of evolution and development with emergent properties not found from analysis of development or evolution alone" and a "synthesis of proximate and ultimate explanations of biology that have been pursued independently for too long". Brakefield [61] appears to hold a similar view.

3. Friends or Foes? A more nuanced picture of the relationship between evo-devo and standard evolutionary biology

Having laid out now three kinds of adaptationism and three kinds of structuralism, in what follows I consider the compatibility of the various positions.

3.1 Empirical Adaptationism and Empirical Structuralism

While strong versions of empirical adaptationism rule out evo-devo and strong versions of empirical structuralism do the same for adaptationism, weaker formulations of the positions permit idealizing away from development in some cases and away from the environment in others. For example, weaker formulations of empirical adaptationism and empirical structuralism (i.e., those which weaken clause (2) and (3) to allow a significant causal role for developmental constraint and natural selection respectively) motivate consideration of both selectionist and developmental factors in evolution; with structuralism and adaptationism merely pragmatic ways of dividing up the problem space. Furthermore, although there exists a small group of strong structuralists (as discussed in Section 2.2), I cannot think of any who would hold to strong adaptationism. As discussed in Section 1 and Section 2, most researchers in both evo-devo and the traditional adaptationist program (if they hold any empirical position at all) are committed to these weaker empirical claims rather than any strong view. Given this, unless progress in either field is hampered by a lack of engagement with the other, conflict is largely empirical and will ultimately be solved that way.

This is, I suggest the source of the response given by many sceptical of the EES. They accept that there is a set of interesting phenomena (such as developmental constraint) which may be of value to evolutionary inquiry but they do not believe there is sufficient evidence of their ubiquity to alter their

adaptationist approach to incorporate structuralism more centrally in evolutionary biology. Advocates of the EES, of course disagree.

One reason why this debate is so challenging is because empirical adaptationism and structuralism are hard to test. Testing claims about the relative causal contribution of any factor to the outcomes of the evolutionary process in general is extremely difficult and even more so when we are looking at large scale patterns in phenotypic diversity, adaptedness etc… A proper assessment of the causal role of constraint, for example, requires detailed analysis of the possibility of alternative evolutionary outcomes to those that actually occurred, which is at best extremely difficult to carry out [62]. Unsurprisingly, therefore, very few but the most hard-headed structuralists are committed empirical structuralism in a strong sense (and, as mentioned, I have struggled to put forward a strong empirical adaptationist). Thus, while a source of conflict on empirical grounds, I don't believe they provide justification for claims of a deep theoretical division between evo-devo and adaptationism. Disagreement here is better understood was being about "relative significance", rather than theory [63].

3.2 Explanatory Adaptationism and Explanatory Structuralism

These two positions differ with respect to the philosophical priority they place on certain types of explanation; explanatory adaptationists place adaptation and natural selection at the centre of evolutionary biology, while explanatory structuralists place constraint, diversity, disparity and complexity there. While strong versions of these positions are in direct conflict as to the question of what should be at the centre of evolutionary biology, the research that they motivate is complementary in nature i.e., on neither view is research into factors that are not considered to have explanatory priority expressly discouraged and research into these other factors is not troublesome (i.e., while externalism is motivated, it is accepted to be not the only approach to evolutionary biology possible). Furthermore, on the weaker versions of explanatory adaptationism and explanatory structuralism held by most protagonists, different idealisations and simplifying assumptions can be seen to be just as motivated as each other. For example, a view in which adaptation, diversity and complexity are considered the big problems in biology and developmental constraint and natural selection the central explanans for them is possible and motivates both the externalist adaptationist research program and the internalist evo-devo program. The compatibility of these views is recognised in discussions of the EES by Douglas Futuyma [5], who, although a "no, all is well" advocate points out that "…the union of population genetic theory with mechanistic understanding of developmental processes enables more complete understanding by joining ultimate and proximate causation; but the latter does not replace or invalidate the former." For Futuyma, his scepticism about the EES appears to lie, not in the merits of evo-devo theoretically, but in other aspects of the EES, such as epigenetic inheritance where he feels that "empirical evidence is needed to

evaluate enthusiastic speculation"[5].[9] This again, highlights the extent to which this is an empirical, rather than theoretical disagreement for sceptics.

3.3 Methodological Adaptationism and Methodological Structuralism

It is with methodological adaptationism and methodological structuralism that the rubber of the EES seems to hit the road for advocates of the EES in a way that is not as obvious in the literature to-date. For most adaptationists, methodological adaptationism is trivially true; the apparent success of evolutionary biology over the past century is evidence, so it seems, of the value of natural selection as an organising principle for evolutionary biology. It seems reasonable then, unless there is significant evidence to the contrary, to continue with selection as the organising principle and therefore reject something like the EES.

Those advocating for the EES argue, however, that this focus on adaptationism overshadows other explanatory interests and skews the empirical data (i.e., by focusing on adaptationist explanations, we do not see any alternatives). In the case of evo-devo, there is a further argument to be made about the availability of ready data and evidence on development now that was not possible before[1]. For all but the most strident empirical adaptationst, whilst methodological adaptationism was a reasonable approach when such data was not available, it seems less viable now and likely to hinder, rather than, benefit progress in the discipline. Thus, in many ways, the push against standard evolutionary theory is methodological in nature rather than focused on empirical issues (even if cast that way by sketpics).

Whilst this is the case, conflict is not inevitable. The division of cognitive labour in evolutionary biology is beneficial to progress [43] and there is a plausible middle ground between strong methodological adaptationism and strong methodological structuralism: the view that both focusing on selection and focusing on developmental constraints are different but useful heuristics for evolutionary research. This is the view I take advocates of the EES to be promoting; that we should be taking alternative the possibility of constraint and other factors (such as epigenetic effects) just as seriously as natural selection because by focusing on selection we are limiting our ability to adequately test our adaptationist assumptions. So long as no-one is a strong adaptationist or strong structuralist, such a view does not hinge heavily on the empirical status of phenomena such as developmental constraint and bias, because it is a claim about how best to make progress in the field.

Conclusion

[9] He also expresses concern over whether "emendation" would be a more appropriate term than "extension" for any changes that ultimately may be made to evolutionary theory which further supports the idea of compatibility.

To conclude, although discussions of the relationship between evo-devo and the traditional adaptationist research program have tended to focus on conflict and disagreement, it may more accurate to understand the two approaches to evolutionary biology as being theoretically commensurable but in conflict both empirically and methodologically. This may help to clarify why it is that calls for an extended synthesis are so often rejected — standard evolutionary theorists typically hold a relatively weak form of explanatory adaptationism that is not in direct conflict with explanatory structuralism but reject anything but a very weak form of empirical structuralism. Although empirical disagreement has been the focus in discussions of the EES and evo-devo, I have shown here how important the methodological divide is to really understanding the push for the EES.

It remains an open question how much, or little, a role either development or natural selection plays in generating the features of the tree of life, and also how far the type of simplifying assumptions and idealisations that those in evo-devo and adaptationism engage in can take us. If recent calls for an EES are correct, then the answer is "not much further" but for others the answer is "much further". Ultimately, it will be an empirical matter which of these things turn out to be true but for many advocates of the EES there is already sufficient evidence of the importance of factors like phenotypic plasticity, niche construction, inclusive inheritance and developmental bias to push us away from the methodological adaptationism that has been the status quo for a century. On their view, even if it ultimately turns out that developmental constraints are relatively rare and plasticity easily incorporated into existing theory, methodological adaptationism is stymying our ability to find out.

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Works Cited:

[1] K. Laland, T. Uller, M. Feldman, K. Sterelny, G.B. Müller, A. Moczek, E. Jablonka, J. Odling-Smee, G.A. Wray, H.E. Hoekstra, D.J. Futuyma, R.E. Lenski, T.F.C. Mackay, D. Schluter, J.E. Strassmann, Does evolutionary theory need a rethink?, Nature. 514 (2014) 161–164. https://doi.org/10.1038/514161a.

[2] K.N. Laland, T. Uller, M.W. Feldman, K. Sterelny, G.B. Müller, A. Moczek, E. Jablonka, J. Odling-Smee, The extended evolutionary synthesis: Its structure, assumptions and predictions, Proc. R. Soc. B Biol. Sci. 282 (2015). https://doi.org/10.1098/rspb.2015.1019.

[3] M. Pigliucci, Do we need an extended evolutionary synthesis?, Evolution (N. Y). 61 (2007) 2743–2749. https://doi.org/10.1111/j.1558-5646.2007.00246.x.

[4] J.J. Welch, What's wrong with evolutionary biology?, Biol. Philos. 32 (2017) 263–279. https://doi.org/10.1007/s10539-016-9557-8.
[5] D.J. Futuyma, Evolutionary biology today and the call for an extended synthesis, Interface Focus. 7 (2017). https://doi.org/10.1098/rsfs.2016.0145.
[6] T.E. Dickins, Q. Rahman, The extended evolutionary synthesis and the role of soft inheritance in evolution, Proc. R. Soc. B Biol. Sci. 279 (2012) 2913–2921. https://doi.org/10.1098/rspb.2012.0273.
[7] G.B. Müller, Why an extended evolutionary synthesis is necessary, Interface Focus. 7 (2017). https://doi.org/10.1098/rsfs.2017.0015.
[8] M. Pigliucci, An extended synthesis for evolutionary biology, Ann. N. Y. Acad. Sci. 1168 (2009) 218–228. https://doi.org/10.1111/j.1749-6632.2009.04578.x.
[9] K.E. Willmore, The Body Plan Concept and Its Centrality in Evo-Devo, Evol. Educ. Outreach. 5 (2012) 219–230. https://doi.org/10.1007/s12052-012-0424-z.
[10] B.K. Hall, Evolutionary Developmental Biology (Evo-Devo): Past, Present, and Future, Evol. Educ. Outreach. 5 (2012) 184–193. https://doi.org/10.1007/s12052-012-0418-x.
[11] M.D. Laubichler, J. Maienschein, eds., From Embryology to Evo-Devo: A History of Developmental Evolution, MIT Press, 2009.
[12] R. Amundson, The changing role of the embryo in evolutionary thought: Roots of Evo-Devo, Cambridge University Press, 2005. https://doi.org/10.1017/CBO9781139164856.
[13] W. Bateson, Evolutionary faith and modern doubts, Science (80-.). 55 (1922) 55–61. https://doi.org/10.1126/science.55.1412.55.
[14] E. Mayr, W.B. Provine, The Evolutionary Synthesis: Perspectives on the Unification of Biology, Harvard University Press, 1980.
[15] S. Sarkar, The Founders of Theoretical Evolutionary Genetics: Editor's Introduction, in: S. Sarkar (Ed.), Founders Evol. Genet., Springer, Dordrecht, 1992: pp. 1–22. https://doi.org/10.1007/978-94-011-2856-8_1.
[16] J.M. Smith, G.R. Price, The logic of animal conflict, Nature. 246 (1973) 15–18. https://doi.org/10.1038/246015a0.
[17] R. Lewontin, Evolution. Retrospective: in memory of John Maynard Smith (1920-2004)., Science (80-.). 304 (2004) 979. https://doi.org/10.1126/science.1099576.
[18] S.A. Frank, George Price's contributions to evolutionary genetics, J. Theor. Biol. 175 (1995) 373–388. https://doi.org/10.1006/jtbi.1995.0148.
[19] L.W. Simmons, 25 years of behavioral ecology, Behav. Ecol. 25 (2014) 1–3. https://doi.org/10.1093/beheco/art108.
[20] P. Godfrey-Smith, J.F. Wilkins, Adaptationism, A Companion to Philos. Biol. (2008) 186–201. https://doi.org/10.1002/9780470696590.ch11.
[21] P. Godfrey-Smith, Three Kinds of Adaptationism, in: S.H. Orzack, E. Sober (Eds.), Adapt. Optim., Cambridge University Press, 2001: pp. 335–357.
[22] R.L. Brown, What evolvability really is, Br. J. Philos. Sci. 65 (2014). https://doi.org/10.1093/bjps/axt014.
[23] P. Alberch, The logic of monsters: Evidence for internal constraint in development and evolution, Geobios. 22 (1989) 21–57. https://doi.org/10.1016/S0016-6995(89)80006-3.
[24] E. Mayr, Cause and Effect in Biology: Kinds of causes, predictability, and teleology are viewed by a practicing biologist, Science (80-.). (1961). https://doi.org/10.1126/science.134.3489.1501.
[25] E. Mayr, Proximate and ultimate causations, Biol. Philos. 8 (1993) 93–94. https://doi.org/10.1007/BF00868508.
[26] S.J. Gould, Ontogeny and Phylogeny, The Belknap Press of Harvard University Press, Cambridge, 1977.
[27] N. Eldredge, S.J. Gould, Punctuated Equilibria: An Alternative to Phyletic Gradualism, in: T.J.M. Schopf (Ed.), Model. Paleobiol., Freeman Cooper, 1972: pp. 82–115.
[28] P. Alberch, Ontogenesis and morphological diversification, Integr. Comp. Biol. 20 (1980) 653–667. https://doi.org/10.1093/icb/20.4.653.

[29] P. Alberch, Developmental Constraints in Evolutionary Processes, Evol. Dev. (1982) 313–332. https://doi.org/10.1007/978-3-642-45532-2_15.
[30] P. Alberch, S.J. Gould, G.F. Oster, D.B. Wake, Size and shape in ontogeny and phylogeny, Paleobiology. 5 (1979) 296–317. https://doi.org/10.1017/s0094837300006588.
[31] B.C. Goodwin, Development and evolution, J. Theor. Biol. 97 (1982) 43–55. https://doi.org/10.1016/0022-5193(82)90275-2.
[32] R.A. Raff, T.C. Kaufman, Embryos, Genes and Evolution: The developmental basis of evolutionary change, Macmillan Publishing, New York, 1983.
[33] W. Arthur, The emerging conceptual framework of evolutionary developmental biology, Nature. 415 (2002) 757–764. https://doi.org/10.1038/415757a.
[34] A.C. Love, R.A. Raff, Knowing your ancestors: themes in the history of evo-devo, Evol. Dev. 5 (2003) 327–330.
[35] S.F. Gilbert, J.M. Opitz, R.A. Raff, Resynthesizing Evolutionary and Developmental Biology, Ontogenez. 28 (1997) 339–343.
[36] J.M. Smith, R. Burian, S. Kauffman, P. Alberch, J. Campbell, B. Goodwin, R. Lande, D. Raup, L. Wolpert, Developmental Constraints and Evolution: A Perspective from the Mountain Lake Conference on Development and Evolution, Q. Rev. Biol. 60 (1985) 265–287. https://doi.org/10.1086/414425.
[37] R.A. Raff, Evo-devo: The evolution of a new discipline, Nat. Rev. Genet. 1 (2000) 74–79. https://doi.org/10.1038/35049594.
[38] P. Godfrey-Smith, Environmental Complexity and the Evolution of Cognition, in: R. Sternberg, J. Kaufman (Eds.), Evol. Intell., Lawrence Earlbaum and Associates, 2001.
[39] P. Forber, Introduction: A primer on adaptationism, Biol. Philos. 24 (2009) 155–159. https://doi.org/10.1007/s10539-008-9150-x.
[40] T. Lewens, Seven types of adaptationism, Biol. Philos. 24 (2009) 161–182. https://doi.org/10.1007/s10539-008-9145-7.
[41] E. Sober, Equilibrium explanation, Philos. Stud. 43 (1983) 201–210. https://doi.org/10.1007/BF00372383.
[42] S.H. Orzack, E. Sober, Optimality Models and the Test of Adaptationism, Am. Nat. 143 (1994) 361–380.
[43] P. Forber, Debating the Power and Scope of Adaptationism, in: K. Kampourakis (Ed.), Philos. Biol. A Companion Educ., Springer Netherlands, 2013: pp. 145–160.
[44] J.A. Coyne, Why Evolution is True, Oxford University Press, Oxford, 2009. https://doi.org/10.5860/choice.46-6781.
[45] R. Dawkins, The Blind Watchmaker: Why the evidence of evolution reveals a universe without design, W.W. Norton & Company, 1987.
[46] D.C. Dennett, Darwin's Dangerous Idea: Evolution and the Meanings of Life, Simon & Schuster, 1996.
[47] A. Gardner, The purpose of adaptation, Interface Focus. 7 (2017). https://doi.org/10.1098/rsfs.2017.0005.
[48] K.N. Laland, K. Sterelny, J. Odling-Smee, W. Hoppitt, T. Uller, Cause and effect in biology revisited: Is Mayr's proximate-ultimate dichotomy still useful?, Science (80-.). 334 (2011) 1512–1516. https://doi.org/10.1126/science.1210879.
[49] K.N. Laland, J. Odling-Smee, W. Hoppitt, T. Uller, More on how and why: Cause and effect in biology revisited, Biol. Philos. 28 (2013) 719–745. https://doi.org/10.1007/s10539-012-9335-1.
[50] B.K. Hall, Evo-Devo: Evolutionary developmental mechanisms, Int. J. Dev. Biol. 47 (2003) 491–495. https://doi.org/10.1387/ijdb.14756324.
[51] T. Lewens, Organisms and Artifacts: design in nature and elsewhere, The MIT Press, Cambridge, Mass., 2004. https://doi.org/10.7551/mitpress/5172.001.0001.
[52] G.B. Müller, Evo-devo as a discipline, Evol. Pathways Key Themes Evol. Dev. Biol. (2008) 5–30. https://doi.org/10.1017/CBO9780511541582.004.

[53] G.B. Müller, S.A. Newman, The innovation triad: An EvoDevo agenda, J. Exp. Zool. Part B Mol. Dev. Evol. 304 (2005) 487–503. https://doi.org/10.1002/jez.b.21081.
[54] J. Kaplan, The end of the adaptive landscape metaphor?, Biol. Philos. 23 (2008) 625–638. https://doi.org/10.1007/s10539-008-9116-z.
[55] G.B. Müller, M. Pigliucci, The So-Called Extended Synthesis and Population Genetics, Biol. Theory. 5 (2010) 275–276. https://doi.org/10.1162/biot_a_00050.
[56] S.B. Carroll, Evo-Devo and an Expanding Evolutionary Synthesis: A Genetic Theory of Morphological Evolution, Cell. 134 (2008) 25–36. https://doi.org/10.1016/j.cell.2008.06.030.
[57] P. Forber, Spandrels and a pervasive problem of evidence, Biol. Philos. 24 (2009) 247–266. https://doi.org/10.1007/s10539-008-9144-8.
[58] S.J. Gould, R.C. Lewontin, The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme, Proc. R. Soc. London. Ser. B. Biol. Sci. 205 (1979) 581–598. https://doi.org/10.1098/rspb.1979.0086.
[59] P. Godfrey-Smith, Adaptationism and the Power of Selection, Biol. Philos. 14 (1999) 181–194. https://doi.org/10.1023/A:1006630232690.
[60] B.K. Hall, Guest editorial: Evo-devo or devo-evo - Does it matter?, Evol. Dev. 2 (2000) 177–178. https://doi.org/10.1046/j.1525-142X.2000.00003e.x.
[61] P.M. Brakefield, Evo-devo and constraints on selection, Trends Ecol. Evol. 21 (2006) 362–368. https://doi.org/10.1016/j.tree.2006.05.001.
[62] R. Sansom, The nature of developmental constraints and the difference-maker argument for externalism, Biol. Philos. 24 (2009) 441–459. https://doi.org/10.1007/s10539-008-9121-2.
[63] J. Beatty, The Evolutionary Contingency Thesis, in: G. Wolters, J.G. Lennox (Eds.), Concepts, Theor. Ration. Biol. Sci., University of Pittsburgh Press, Pittsburgh, 1995: pp. 45–81.
[64] J. Coyne, Does evolution need a revolution? , Why Evol. Is True. (2014). https://whyevolutionistrue.com/tag/evolutionary-theory/ (accessed June 16, 2021).
[65] K. Laland, B. Matthews, M.W. Feldman, An introduction to niche construction theory, Evol. Ecol. 30 (2016) 191–202. https://doi.org/10.1007/s10682-016-9821-z.
[66] J.F. Odling-Smee, K.N. Laland, M.W. Feldman, Niche Construction: The Neglected Process in Evolution, Princeton University Press, Princeton, 2003.
[67] P.J. Odling-Smee, K.N. Laland, M.W. Feldman, Niche construction, Am. Nat. 147 (1996) 641–648. https://doi.org/10.1086/285870.
[68] C.H. Waddington, Canalization of development and the inheritance of acquired characters, Nature. 150 (1942) 563–565. https://doi.org/10.1038/150563a0.
[69] L. Olsson, G.S. Levit, U. Hoßfeld, Evolutionary developmental biology: its concepts and history with a focus on Russian and German contributions, Naturwissenschaften. 97 (2010) 951–969. https://doi.org/10.1007/s00114-010-0720-9.
[70] R. Amundson, Adaptation and Development: On the lack of a common ground, in: S.H. Orzack, E. Sober (Eds.), Adapt. Optim., Cambridge University Press, 2001: pp. 303–334.