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One Kind of Adaptationism

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Abstract

There is only one kind of adaptationism: explanatory adaptationism. Explanatory adaptationism claims that adaptation is the "big question" in evolutionary biology and that natural selection is the "big answer" to that question. In recent decades, philosophers of biology have largely come to agree, first, that explanatory adaptationism is only one kind of adaptationism among many (at the high end, seven) and, second, that these kinds are logically independent and so can, in principle, be accepted or rejected in any combination. On the surface, this is true. Beneath the surface, it is not. When the arguments supporting various forms of allegedly non-explanatory adaptationism are interrogated closely, each turns out to essentially rely on explanatory adaptationism. That is, all kinds of adaptationism are *justificatorily dependent* on explanatory adaptationism. The different kinds of adaptationism should be recognized as different ways of articulating the import of explanatory adaptationism. In the last analysis, every adaptationist is an explanatory adaptationist.

1. Many kinds of adaptationism

The preponderance of organisms swarming the earth, their diversity of form and form of life, and their ability to maintain their existence even in hostile environments—these are striking phenomena, and biologists have been duly struck. The consensus explanation is evolutionary: extant life descended (with modification) from a single origin. Beyond this consensus is murk. What causes drive this process? How do they interact with each other? Are any of them either logically or empirically primary? How

best can we study them? And, lastly, which processes and products of evolution are most *important* to study?

From this murk emerge the longstanding debates over adaptationism. Adaptationism privileges the role of natural selection in evolutionary explanations. But there are many ways to do so (Godfrey-Smith 2001)—perhaps as many as seven (Lewens 2008). Natural selection might be, in some specifiable and testable sense, the most *powerful* evolutionary factor ("empirical adaptationism"). Or natural selection might be the most *useful* evolutionary factor: we best learn about the evolutionary history of traits by first testing selective hypotheses ("methodological adaptationism"). Or natural selection might be the most *interesting* evolutionary factor, because it answers the "big question": the origin of adaptations ("explanatory adaptationism").

These views are logically independent: one might accept any subset of them, including the empty set and the improper subset. Distinguishing them is essential to avoiding pseudo-disputes. Reeve and Sherman (1993, 2) long ago correctly complained about "quasi-empirical claims that are really disguised assumptions about what aspects of evolution are most important"—imprecise and irresolvable mingling of empirical and explanatory adaptationism.

This may satisfy the logician, but not the philosopher, who wants to know not just what the views *say* but also how they are *justified*. Which, if any, kinds of adaptationism should biologists and philosophers accept? This question is controversial, and the mere logical independence of the different kinds of adaptationism by no means entails that they can justifiably be accepted separately. I shall argue that, when the threads of justification are laid bare for inspection, the independence that so impresses the logician proves to be of modest importance. Different adaptationist positions appear together in regular, structured ways.

In particular—here is my central contention—***explanatory adaptationism plays a central, ineliminable role in justifying adaptationist positions.*** Methodological and empirical

adaptationism, historically, do not appear in isolation from explanatory adaptationism. Arguments supporting them prove, upon examination, to essentially rely on explanatory adaptationism. When this support is removed, there are methodological and empirical claims that survive, but these claims are much more modest than those at stake in debates over adaptationism.

More simply: there is one kind of adaptationism. Every adaptationist is an explanatory adaptationist.

2. Explanatory adaptationism

2.1. Explanatory adaptationism

Godfrey-Smith (2001, 336) describes explanatory adaptationism as the bipartite view that (1) adaptation is the "big question" in evolutionary biology and (2) natural selection is the "big answer". Adaptation is here understood as organism-environment fit (however it arises), which stands in need of explanation (Brandon 1990, sec. 1.7). Natural selection is then the primary cause that explains adaptation (Brandon 1990, sec. 5.2).

Neither claim is empirical; both are claims about significance. The first concerns the centrality of explaining adaptation within the problem space of evolutionary theory. It regards that problem as possessing outsized importance relative to other problems. This might be defended on grounds internal to biology: perhaps adaptation uniquely serves as a useful organizing concept that helps us to understand the significance of other evolutionary processes (Mayr 1983). It might also be defended on grounds external to biology: perhaps adaptation is especially important because adaptation is theism's last line of defense, and thus naturalistically explaining adaptation is important for establishing a thoroughgoing secularism (Dennett 1996). My focus below will be on forms of explanatory adaptationism concerned with the importance of adaptations for evolutionary theory.

The second claim concerns the centrality of natural selection in explaining adaptation. It regards selection as the most significant cause of the evolution of adaptations. This may be defended on various

grounds: because selection is the most powerful cause involved in producing adaptations, or because selection is especially methodologically useful for learning about evolutionary processes, but it is not identical to either claim. I regard this claim as of secondary importance for characterizing explanatory adaptationism, for two reasons. First, it is the acceptance of adaptation as the "big question" that allows us to recognize the adaptationist program as part of a larger history of functionalist approaches to biology (Boucher 2015, 396–97). Second, my arguments to follow will focus on the ways in which biologists' choice of questions shape the problem space in which they work; the specific answers at which they arrive play less of a role. Thus, in what follows, I focus on the first claim.

Most fundamentally, I understand the claim that adaptation is the "big question" in evolution as a claim about *the structure of the problem space* of evolutionary research. Evolutionary biologists ask a great many questions about evolutionary history and evolutionary processes. These questions do not exist as an unstructured mass; there are relations between them, and these relations are themselves subject to debate. Consider the following from Gareth Nelson (1994, 135):

> If homology pervades biological data then all of biology relates to homology. All manner of biological investigations may be viewed as contributing to yet unsolved problems of systematics. One might be tempted to say even that "nothing in biology makes sense except in the light of systematics," but Dobzhansky already said it (inexplicably, he used the word "evolution" instead of "systematics").

This is a (non-adaptationist) claim about the structure of the evolutionary (and not just evolutionary) problem space, one that places the problems of systematics in a central position. Nelson's argument is ***methodological***. The data used to address any biological problems is pervaded by hypotheses of homology. But it is systematics that supports such hypotheses. So all biological problems are inseparable from the problems of systematics. So the questions of systematics are the "big questions". (We might give this view the ugly moniker "explanatory systematicism".)

For explanatory adaptationism specifically, Charles Darwin (1859, 206) furnishes a classic example:

> It is generally acknowledged that all organic beings have been formed on two great laws—Unity of Type, and the Conditions of Existence. ... On my theory, unity of type is explained by unity of descent. The expression of conditions of existence... is fully embraced by the principle of natural selection. ... Hence, in fact, the law of the Conditions of Existence is the higher law; as it includes, through the inheritance of former adaptations, that of Unity of Type.

Darwin notes two fundamental problems in the study of organic beings: explaining adaptation (conditions of existence) and explaining "fundamental agreement in structure" (unity of type). Of these, the former is the "higher law". Darwin's argument is ***explanatory***: unity of type is explained by unity of descent, but unity of descent is just "the inheritance of former adaptations". Unity of type is thus a byproduct of natural selection exerting its effects over time. Explanations of adaptations have a privileged place in the overall chain of explanations, so explaining adaptations is of central importance.

Such "subordination arguments" (Novick 2023, sec. 4) seek to show that the problem space of a scientific discipline has (or ought to have) a particular structure. They are ubiquitous in the history of biology, frequently contributing to the non-empirical aspects of biological controversies. In what follows, we will track the role of such arguments in defenses of empirical and methodological adaptationism. While explanatory adaptationists sometimes simply assert that adaptation is the "big question" in evolutionary biology, the justification of this commitment takes the form of subordination arguments. In this regard, the invocation of adaptationist subordination arguments is a reliable mark of explanatory adaptationism. My arguments below will (a) show that we find this mark throughout defenses of allegedly empirical and allegedly methodological adaptationism and (b) explain why this ubiquity is no accident.

2.2. Preliminaries

I can now clarify my central thesis. Commitments to particular ways of structuring the problem space of evolutionary biology routinely appear in defenses of empirical and methodological adaptationism. These commitments play a special role in these arguments: they are what make them arguments *for adaptationism*. There are empirical and methodological claims that can be defended without attaching a commitment to explanatory adaptationism. However, these claims are modest: they do not rule out the kinds of views traditionally opposed to adaptationism (e.g., structuralism). If we take it as desirable that our analysis capture the ways in which adaptationists (and functionalists more generally) are committed to a big picture view of evolution—one that excludes adaptationism's traditional rivals—the commitment to explanatory adaptationism cannot be done without.

My argument takes the form of a No True Scotsman. Empirical and methodological "adaptationism", when purged of explanatory adaptationism, are not *true* kinds of adaptationism. Running such an argument requires a clear account of what adaptationism is. To start getting a grip on this, consider the epistemological form of "adaptationism" that Lewens (2008, 178) introduces:

> *Epistemological optimism* is the view that our capacities for gathering evidence and comparing hypotheses about the functions and origins of organic traits are good enough to be able to provide strong support for these hypotheses.

Lewens acknowledges that this sort of optimism is not really specific to adaptationism: a neutralist or structuralist should be equally epistemologically optimistic about their ability to provide support for their preferred hypotheses. Nonetheless, Lewens argues that, historically, critics of adaptationism have generally run epistemologically pessimistic arguments, and thus that epistemological optimism is a characteristic element of the adaptationist program as it actually existed.

I agree with Lewens about this last point: epistemological optimism is indeed a strand of the adaptationist program. I deny, however, that such optimism is itself a *kind* of adaptationism. I deny it

for the reason Lewens gives: acceptance of such optimism does not yet distinguish adaptationists from non-adaptationists. Adaptationism, whatever its specific content, is bold and general, and stands opposed to its comparably bold and general rivals. It was such competition between rival, *incompatible* visions of evolutionary science that characterized historical debates over the adaptationist program (and which continue to shape our understanding of contemporary debates, even where those have mellowed). "Adaptationism" as a philosophical tool should help us to make sense of these debates and their aftermath. In insisting that adaptationism be understood as bold and general, I am asking for some trust at the outset; further justification will come below as I show in detail the role of explanatory adaptationism in justifying nominally "empirical" and "methodological" positions (§§3-4), as well as in a general discussion of how my approach makes good sense of the historical material (§5.1).

In the meantime, here is a general principle undergirding my subsequent arguments: if a claim can be accepted by a structuralist (or by defenders of any other major rival of adaptationism), that claim is not by itself a kind of adaptationism. In other words, *anything that we call "adaptationism" should be strong enough to exclude non-adaptationist rivals*. That does not mean that weaker claims cannot be an important part of a broader package of adaptationist views, just that they are not kinds of adaptationism on their own.

The claim I defend below can be understood as a claim about the source of adaptationism's boldness and generality: it arises, in all cases, because of a commitment regarding the structure of the evolutionary problem space. There are empirical and methodological claims that were part of the adaptationist program, but they do not acquire general significance without resting on explanatory adaptationism. Eliminate that commitment to explanatory adaptationism and we are left, not with adaptationism, but with a pluralistic view of evolutionary theory in which adaptationist answers given to some empirical questions and adaptationist methodologies are adopted for some research agendas—but no longer the "most important" questions, no longer the "most central" agendas. I will discuss the implications of this

later (§5).

3. Empirical adaptationism

Empirical adaptationism, broadly conceived, is the view that most traits are adaptations (Forber 2009; Potochnik 2009). Lewens identifies three specific ways of understanding this claim: pan-selectionism (§3.1), good designism (§3.2), and gradualism (§3.3).

3.1. Pan-selectionism

Pan-selectionism has been given its clearest statements in the work of Orzack and Sober (1994; 1996; 2001). They treat adaptationism as a thesis concerning the frequency with which the fittest traits go to fixation. Expressed generally, the thesis is: "Natural selection is a sufficient explanation for most nonmolecular traits, and these traits are locally optimal" (Orzack and Sober 1994, 364). This generalizes over claims with the following form: "(O) Natural selection is a sufficient explanation of the evolution of [some trait T], and T is locally optimal" (Orzack and Sober 1994, 362).

So long as claims of the form **(O)** can be made sufficiently precise to take definite truth-values, pan-selectionism can be understood as a matter of degree: the more traits for which selection is a sufficient explanation, the truer pan-selectionism is. Moreover, it can vary by domain, as Orzack and Sober acknowledge when they restrict their attention to a claim about "nonmolecular traits": pan-selectionism is likely truer of morphological and physiological traits than of molecular traits (where neutralism is best-supported). But all of this turns on making particular claims of the form **(O)** precise.

Making **(O)** precise requires specifying (a) when a phenotype is optimal and (b) when natural selection is a sufficient explanation of a trait. Orzack and Sober (1994, 361) specify (a) as follows: "A phenotype of an individual is optimal (relative to a variety of alternatives) because it outperforms the other phenotypes and thereby results in a higher fitness." In other words, given a set of variant

phenotypes of a particular trait, the optimal trait in a particular environment is that with the highest fitness. They specify (b) in terms of the predictive abilities of "censored" models, i.e. models that consider only natural selection and no other evolutionary forces: "Natural selection... provides a sufficient explanation [when] taking other factors into account could not significantly enhance the predictive accuracy of the optimality model", where the other factors in question are "mutation, migration, genetic drift, and genetic and phylogenetic constraints" (Orzack and Sober 1994, 363).

This formula can indeed be used to generate empirical claims, but I will argue that they fall short of anything we might regard as a properly empirical *adaptationism*—unless, of course, we add a commitment to explanatory adaptationism. I draw on the recent critique of Mingjun Zhang (2022), who argues that empirical adaptationism is not actually a testable thesis. Zhang's (2022, 3–8) critique concerns how we understand the interactions between different evolutionary factors. Zhang puts forth three cases (pleiotropic linkage, shifting balance theory, and drift eliminating fit new mutants) that share the same basic structure: (1) it is true that natural selection is responsible for driving the final phenotype to fixation, and (2) natural selection can do so only thanks to the inseparable contribution of some other factor (linkage in case one, drift in cases two and three). In what sense, Zhang asks, can selection be highlighted as the "most important" factor?

Orzack and Sober purport to offer a meaningful way of making this distinction: if including other factors does not improve the optimality model, then selection is the most important factor. This does indeed make empirical sense of claims of type **(O)** (as Zhang concedes). But, I contend, Orzack and Sober manage this only by *writing off certain questions as irrelevant to explaining the evolution of a trait*. In particular, Orzack and Sober's strategy treats questions about *outcome* as more important than questions about *process*.

Consider Zhang's shifting balance case. This involves a population divided into partially isolated subpopulations. It has three stages: (1) genetic drift allows one subpopulation to cross an adaptive valley,

moving it into the region of a higher adaptive peak, (2) each subpopulation evolves (via selection) to reach its local peak, and (3) migration introduces the fittest variant to all subpopulations, allowing it to go to fixation in the entire population. In this case, the fittest variant does indeed go to fixation, as the optimality model predicts, and thus selection provides a "sufficient answer". However, it provides exactly the same answer in the quite different case where there is a single panmictic population with the same variants present. If all we care about is outcome, these two cases are the same. If, however, we care about *how* these two populations achieved the same outcome, they require different explanations.

It is one thing to be more concerned with outcomes than processes. It is quite another to slide from "natural selection is a sufficient explanation of *outcome questions* about T" to "natural selection is a sufficient explanation *of T*". As Van Fraassen (1980, chap. 5) taught us long ago, questions of the form "why X?" are generally elliptical for questions with a contrastive form: "why X, *rather than Y*?". In this sense, what appears like a single question ("why X?") actually contains within it indefinitely many questions. Questions about trait evolution ("why T?") fit this form. We might be asking, "why did T evolve, rather than other available variants?" Orzack and Sober provide reasonable grounds for identifying when selection provides a sufficient answer to *this* question. But we might also be asking, "why was T evolutionary accessible at all, rather than precursors to T (in the adaptive valley) being eliminated?" This question is unanswerable without explaining how drift allowed the crossing of said valley—natural selection is *not* a sufficient answer.

Moreover, satisfying Orzack and Sober's criteria does not even show that natural selection is sufficient for answering outcome questions concerning the trait evolution. Consider the following two outcome questions:

Q1 Why did T evolve, rather than X, Y, Z *available* variants?

Q2 Why did T evolve, rather than A, B, C *unavailable* variants?

Orzack and Sober's approach provides, at least in principle, a sufficient answer to **Q1** (but see Brandon

and Rausher 1996 for critique). However, it not only fails to answer **Q2**, it *necessarily* fails to do so, because unavailable variants are excluded from the optimality model at the outset (Sansom 2003, 502–5). But, of course, not all unavailable variants are alike: some merely fail to appear, others are impossible to generate (e.g., for developmental reasons). Variants of the latter type are, of course, central to structuralist explanations.

There is a caveat here: Orzack and Sober (1994, 372) do allow that developmental constraint might be factored into an optimality model. This can happen in two ways. First, unavailable variants might be explicitly considered among the possibly optimal phenotypes (cf. Reeve and Sherman 1993, in particular the discussion of the phenotype set). We will consider this possibility below (§3.2). The second approach—which Orzack and Sober favor—involves distinguishing global from local optimality. What concerns evolutionary biologists is not the optimal solution to an environmental problem *in a vacuum*, but rather the optimal solution accessible to a particular population. On this approach, constraints structure the space of possible solutions. If natural selection selects the best of these possible solutions, then it provides a "sufficient explanation" of T's evolution.

Both the shifting balance critique and the constraint critique push the panselectionist into the same dilemma. **(Horn 1)** Accept (a) that natural selection provides (in principle) a sufficient answer to a restricted set of contrastive why-questions concerning trait evolution (those like **Q1**) and (b) that it provides (in principle) no answer to other such questions (those like **Q2**). Accept, further, that this means that natural selection is not necessarily a sufficient explanation of trait evolution as such. This concession, however, renders panselectionism too weak to rule out alternatives to adaptationism. It is an empirical thesis (provided it can answer the criticisms of Zhang 2022; DiFrisco and Ramsey 2023), and that empirical thesis may be part of a broader adaptationist program, but it is not itself a kind of adaptationism.

Alternatively, the panselectionist can **(Horn 2)** argue that, if selection provides an adequate answer

to questions of type **Q1**, then selection provides a sufficient explanation of trait evolution as such. Answers to other questions are regarded either as irrelevant (cf. Reeve and Sherman 1993, 20–22; see below, §3.2) or as subordinate, as important for identifying the relevant problem space but not truly part of the explanation of trait evolution (as when constraints help determine what counts as locally optimal; see below, §4). For example, those contrastive why-questions that admit of structuralist answers may be relegated to the status of mere "proximate"— and thus not genuinely *evolutionary*—explanations (Mayr 1961). To take this horn is to argue that, of the indefinitely many contrastive questions contained within the non-contrastive question, "Why did T evolve?", a certain subset of questions are central and other questions are peripheral. It thus goes beyond a mere segregation of questions into those explicable by different evolutionary factors: questions answerable by selection are prioritized over others. That is a commitment to a particular way of structuring the problem space of evolutionary theory—in other words, explanatory adaptationism.

3.2. Good designism

Good designism is the view that "evolutionary processes tend to result in organisms with suites of well-designed traits," conjoined with the claim that "most lineages are highly evolvable" (Lewens 2008, 162). Lewens (2008, 164) distinguishes good designism from panselectionism because "there are worlds where pan-selectionism is true, yet because constraints on the availability of variants are so strong, organisms show nothing like 'good design' in any traditional senses of the term." We saw above that Orzack and Sober, in distinguishing local from global optimality, incorporate constraints into their understanding of the evolutionary problem to be solved. Good designism, by contrast, concerns global optimality: the claim is that organisms are overall "well-designed".

A first problem for good designism, as a form of empirical adaptationism, is that it is not obvious that it is an empirical thesis. While panselectionism as a general thesis suffers from important ambiguities

(Zhang 2022), it is at least easy to see how individual claims of type **(O)** are empirically testable. Good designism does not share this virtue. To put it glibly, "good" is a value term, and "well-designed" sure *sounds* like a value judgment. This worry goes beyond the glib. There are a few ways one might try to make precise the claim that an individual trait (or interconnected suite of traits) is "well-designed". One way would be to say that a trait is "well-designed" if it is globally optimal. This faces two difficulties. The first difficulty is that this is not actually what adaptationists believe. If any trait counts as well-designed, the tetrapod eye is well-designed, but it is notoriously (Darwin 1859, chap. 6) not globally optimal.

The second difficulty is that global optimality is a phantom (Maynard Smith 1978; Gilchrist and Kingsolver 2001). Any notion of optimality requires some conception of the evolutionary problem to be solved. This requires imposing *some* constraints on the potential solutions to that problem. (Teleportation is not an optimal solution to problems of locomotion.) One may include more or fewer such constraints, but not none. For instance, Orzack and Sober include developmental constraints in their conception of evolutionary problems, and this makes their understanding of optimality more local than one that includes all the same information *except* developmental constraints. But there can be no model that includes *no* information in its problem conception, and so there are really only more and less "local" conceptions of optimality. Nor is there a single obvious minimum of information that must be included to define an evolutionary problem (which might be treated as the relevant problem for determining global optimality). Thus, there is not any well-defined notion of "global" optimality to use as a comparison point.

That approach is a non-starter. A better way might be to understand good design in terms of crossing some threshold: so long as traits do *well enough* at solving evolutionary problems, one can dispense with any comparisons to "optimal" solutions, however conceived. But this has its own difficulties. Unless there is a way to measure precisely how well some (suite of) trait(s) solves an evolutionary problem, this is an aesthetic and not an empirical judgment. Undoubtedly, such a measure can be developed for particular

traits and particular conceptions of evolutionary problems. More dubious is that any such measures will be *comparable* across traits in a way that makes a generalization like "evolutionary processes tend to result in organisms with suites of well-designed traits" an empirically meaningful claim. An attempt to make this generalization precise has been offered by Grafen (2014; discussed further below); it has been critiqued by Birch (2014) precisely on the grounds that, while it formalizes *something*, what it formalizes is not "apparent design". As such, I agree with Lewens' (2008, 167) judgment that good designism "resists precise characterization".

So I think the glib worry—that "good designism" is, as its name suggests, an aesthetic judgment masquerading as an empirical hypothesis—is in fact rather severe. Let us, however, lay it aside, and presume that some notion of "good design" that is not essentially dependent on aesthetic judgments can be found. Let us presume, for instance, that Grafen (2014), *pace* Birch, has successfully formalized our intuitive notion of good design. There remains a further issue, which throws the adaptationist onto a new version of the old dilemma.

Consider the following passage from Lewens (2008, 166):

> Consider a creature that runs on its hind legs. Let us suppose that long hind-limbs are better than short, for these make the creature run faster. The creature makes no use of its forelimbs. Short forelimbs are consequently better for this creature than long ones, for long forelimbs get in the way. Now suppose that development is set up in such a way that increases in the length of hind-limbs are accompanied by increase in the length of forelimbs. Our creature can have four long limbs, or four short limbs. But it cannot have long hind-limbs and short forelimbs, even though this would be the fittest combination. Suppose, finally, that selection ends up eliminating short forelimbs from the population. The question is whether this is merely a failure of the fittest *properties* to reach fixation, or whether it is also a failure of the fittest *traits* to reach fixation.

The choice here is the same choice that faced Orzack and Sober: the conception of the evolutionary problem to be solved cannot even be characterized without some conception of what the relevant evolving traits are.

Neither choice about how to conceive the situation renders good designism an empirical form of adaptationism. If "good design" merely requires that sufficiently well-designed *traits* evolve, then good designism is subject to the same arguments I raised in the case of panselectionism: constraints are entirely subordinated to questions of the operation of selection, since constraints are part of what determines *what a trait is* (Gould and Lewontin 1979; DiFrisco and Ramsey 2023). Grafen illustrates this nicely. His formalization of the notion of "good design" turns on the notion of an "optimization program". Grafen (2014, sec. 3) writes:

> An optimization program contains three elements. One variable, the *instrument*, is regarded as under the control of the implicit optimizer, who selects a value of the variable from some set of possible values, the *constraint set* or *feasible set*. A real-valued function defeined on that set, the *maximand*, indicates the degree of success of each possible choice. A choice of instrument is said to *solve* the program if it achieves the highest possible value of the maximand within the feasible set.

From here, Grafen goes on to argue that, if one can predict actual phenotype sufficiently well using this approach, then one can ignore genetic architecture as explanatorily irrelevant. But, of course, this is accomplished by a combination of strategies we have already seen. One is the prioritization of *outcome questions* over process questions. Another is the building of structural considerations into the definition of the evolutionary problem to be solved, thereby subordinating them to functional considerations. Lewens (2019) is thus entirely correct to regard Grafen as "neo-Paleyan", where what is "Paleyan" is precisely "having identified the central problem for the natural historian"—that is, a commitment to the structure of the problem space.

If, by contrast, good designism is a claim that evolution produces organisms with sufficiently well-designed *properties*, constraints are allowed a role: they can serve as *constraints on adaptation*, by preventing the fittest suites of properties from being generated. But, as Amundson (1994; cf. 2005) showed three decades ago, constraints on adaptation are not the concern of structuralist biologists. Structuralists are concerned with *constraints on form*: with patterns of possible and impossible variation that shape evolutionary trajectories over long periods of evolutionary history. For the structuralist, such patterns are of interest in their own right, not for their effects on preventing (or not) suites of well-designed properties from evolving.

The good designist, however, treats constraints on form as *invisible* unless they manifest as constraints on adaptation (Amundson 1994). Reeve and Sherman (1993, 20–22) furnish a clear example. In their discussion of constraints as an alternative explanation to selection, they critique structuralists for failing to conduct "the *crucial* thought experiment," namely, "What would be the evolutionary result if a mutant alternative trait arose and competed with the observed trait?" If the mutant, had it arisen, would have been fitter than the observed trait, then there is a constraint on adaptation; if, by contrast, the mutant would have been less fit, there is no constraint on adaptation and so developmental constraint is irrelevant. The structuralist's concern for constraints on form is altogether written off by the nature of the question asked.

The good designist is thus thrown back on the old dilemma. **(Horn 1)** If they restrict their concern only to questions of how well organisms solve evolutionary problems, they (*maybe*) have an empirical claim. However, this claim is simply orthogonal to the concerns of structuralists, because it considers constraints on form as subordinate to constraints on adaptation, rather than as independent phenomena of interest. Constraints might be quite strong and evolutionarily important without preventing organisms from being well-designed; if so, they simply go unnoticed by the good designist. **(Horn 2)** If, however, they treat questions of good design as central and other problems as peripheral, then they have

a view that genuinely subordinates structuralist approaches. But this, of course, rests on a commitment to explanatory adaptationism.

3.3. Gradualism

Gradualism may be addressed more swiftly. Gradualism, as Lewens (2008, 162) defines it, is the view that "adaptation is always the result of selection acting on gradual variation." "Gradual variation" refers to effect size (mode), not evolutionary rate (tempo): gradualism thus involves the accumulation of mutations of small effect size (Simpson [1944] 1984). Gradualism is a two part-thesis: first, adaptation results from the accumulation of mutations of small effect size and, second, this accumulation is the "result" of selection.

Both can be satisfied without yielding an adaptationist view. Indeed, gradualist commitments have been leveraged to support some of the most powerful "structuralist" explanations arising from evo-devo: those that rely on the deep conservation of gene regulatory networks (Novick 2019). At the core of these explanations is an understanding of the hierarchical structure of gene regulatory networks (Davidson and Erwin 2006; Peter and Davidson 2011; 2015). These networks are easier to modify at their terminal nodes than at their core, and the reasons why are structuralist: it is *easy* to generate gradual variation at the periphery and *hard* to generate gradual variation at the core. This basic pattern can then be leveraged to explain broad patterns in the evolution of characters (Wagner 2014). The full explanatory chain in these explanations involves both structuralist and functionalist explanatory patterns (Novick 2023, sec. 3.3).

These explanations clearly satisfy the first part of the gradualist thesis: character evolution involves the accumulation of mutations of small effect size. What about the second part? Are any adaptations involved the "result" of selection? The question is ambiguous, and the ambiguity raises the now-familiar dilemma for "empirical" adaptationism. The ambiguity turns on whether we examine each adaptation

individually or whether we examine patterns that are visible only from considering many different adaptations.

Suppose we consider each adaptation individually. On this approach, we attempt to understand each variant of the tetrapod limb in relation to its particular history. Even if we accept the foregoing view of character evolution, we might very well find that each of these variants arose via selection acting on mutations of small effect size. In this sense, gradualism is true: the evolutionary mode was gradualist, and selection explains adaptations. This latter claim, that selection explains adaptations, is identical (or at least highly similar) to the weaker, genuinely empirical interpretation of pan-selectionism considered above (§3.1). Like pan-selectionism (in its empirical form), this interpretation simply ignores background structural factors and so falls short of genuine adaptationism.

These background structural factors become most relevant when we seek to explain, not individual adaptations, but broader patterns. Why is the distribution of adaptations clumpy, with many different variant limbs and many different variant fins, and only a single historical transition from fin to limb (Wagner 2014, chap. 10)? The explanation for this (if Wagner, Davidson, and collaborators are correct) lies in the structure of the gene regulatory networks driving fin and limb development, which shapes *where adaptation is possible*. This basically structuralist interpretation of the view (favored explicitly by Wagner) is ruled out only if we adopt the stronger, not-fully-empirical interpretation of pan-selectionism, on which problems of the generation of variation are subordinated to problems of adaptation.

On the first approach, gradualism is too weak to rule out structuralist views. On the second approach, gradualism is genuinely adaptationist, but only because it commits to a particular way of structuring the problem space—i.e., because it rests on explanatory adaptationism. This familiar pattern arises because gradualism amounts to the conjunction of a claim about evolutionary mode and a claim about the operation of selection. The former claim is best understood as similar to epistemological optimism in this respect: it is possibly part of a larger package of adaptationist views, but it is not adaptationist in

itself. The latter claim is just pan-selectionism, in one of its forms, and suffers the same dilemma.

4. Methodological adaptationism

So much for empirical adaptationism; let us turn our attention now to methodological concerns. Methodological adaptationism is the view that regarding traits as adaptations is a good *starting point* for evolutionary research, even if such traits ultimately prove not to be adaptations. Lewens (2008, 162) distinguishes two forms, one weaker and one stronger. The weaker form says, "those traits that are adaptations are likely to be correctly recognised as such only if we begin by assuming that all traits are adaptations"—i.e., that this is a *good* method for identifying *adaptations*. The stronger form says, "only by beginning to think of traits as adaptations can we uncover their true status, whether they are adaptations or not"—i.e., that this is a *necessary* method for identifying *both adaptations and non-adaptations*. (Basic combinatorial thinking allows us to recognize two further positions of intermediate strength.) I will discuss both the stronger and weaker forms together, since my argument for their reliance on explanatory adaptationism is the same in each case (and also covers the intermediate cases).

Alternative starting points are possible. One potential alternative is methodological structuralism (Brown 2022; Novick 2023, sec. 4), in which one begins by identifying the range of possible variation affecting a trait before even asking whether or not it might be an adaptation (e.g., Alberch and Gale 1985). Another alternative is Lloyd's (2015) "evolutionary factors" framework, which asks, neutrally, "what evolutionary factors account for the form and distribution of this trait?" (We shall see below that these alternatives involve distinctive conceptions of the evolutionary problem space.)

My argument for the reliance of methodological adaptationism on explanatory adaptationism is, frankly, banal. Here it is. Methods are means to ends. They are valuable insofar as (a) they achieve those ends and (b) those ends are worth achieving. Any method is thus evaluable along two axes: 1. Does the method achieve its end? 2. Is the end worth achieving? The ends of methodological adaptationism can

be read off Lewens' characterization: either *to identify adaptations* (weak) or *to identify both adaptations and non-adaptations* (strong).

At this point, the familiar dilemma arises. Methodological adaptationism, in either form, posits itself as a good way to answer the question, "what was the role of natural selection in the evolution of T?", where T is some trait of interest. **(Horn 1)** If this question is taken to be merely one question that might be asked about the evolution of a trait, then the relevant evaluative question to ask is just the first: is methodological adaptationism a good way to identify adaptations (and perhaps non-adaptations)? Even this is controversial, but that's beside the point here. The resulting position is modest: methodological adaptationism is not a view about the best starting point for *evolutionary research*; rather, it is a view about the best starting point for answering one particular question about evolution (Green 2014). Such a modest view falls short of being genuine adaptationism. Alternatively, **(Horn 2)** the question may be taken to be a particularly central one: questions about the role of selection are *the* questions to ask in evolutionary biology, with all other questions subordinated. This is, of course, a view about the structure of the problem space of evolutionary theory, i.e., explanatory adaptationism.

Though this argument rests on a trivial point about the subservience of methods to goals, it illuminates the actual nature of debates over methodological adaptationism. I'll give two examples. First, consider again Lloyd's (2015) evolutionary factors approach. Lloyd raises two critiques of methodological adaptationism. One critique concerns its efficacy as a method for its stated purposes: it is not especially good at identifying (and correctly characterizing) adaptations (as argued at length in Lloyd 2006). The other critique, however, concerns those purposes as such. Lloyd's approach asks, "what evolutionary factors account for the form and distribution of this trait?" This question is neutral as to which factors matter most. The first question to ask about a trait is not, "is T an adaptation?", but rather, "how did T evolve?". In this way, Lloyd presumes a different structure of the evolutionary problem space from the explanatory adaptationist, one on which adaptation is *a question* but not *the big question*. To

reduce Lloyd's critique to a mere critique of efficacy is to miss much of her point. A similar point holds for methodological structuralism: it presumes an interest in the effects of constraints independent of their influence on selection (Alberch 1989).

An even more striking example can be seen in Mayr's (1983) defense of methodological adaptationism from Gould and Lewontin's (1979) critique. At the core of Gould and Lewontin's critique are questions of trait individuation: adaptationists, in their eagerness to identify adaptations, treated linked features of organisms as capable of independently evolving. In light of this, they suggested five alternative processes affecting trait evolution. The first alternative was evolution without either selection or adaptation (e.g., by pure genetic drift). The other four all involved selection operating, but operating in ways that did not allow for an adaptationist answer to some particular question of interest. For example, their second alternative involved traits linked pleiotropically or allometrically, in which there might be *selection of* one trait without it being *selected for* (Sober 1984).

How does Mayr address this charge? Like so (Mayr 1983, 330):

> Indeed, when we look at Gould and Lewontin's "alternatives to immediate adaptation," we find that all of them are ultimately based on natural selection, properly conceived. It is thus evident that the target of their criticism should have been neither natural selection nor the adaptationist program as such, but rather a faulty interpretation of natural selection and an improperly conducted adaptationist program. Gould and Lewontin's proposals are not "alternatives to the adaptationist program," but simply legitimate forms of it.

This is both an entirely sensible response and a quite outrageous one—depending on how one understands the relevant problem. It is outrageous in that Mayr wholly misses Gould and Lewontin's point. In advocating a plurality of explanatory strategies, they are identifying evolutionary phenomena of independent interest. Yes, selection is involved *somewhere* in many of their explanations, but selection

is not the main feature of interest: it is merely part of a fuller explanation. For Mayr to say that, since selection plays a role, the explanation is really adaptationist after all is just to say that all other factors involved in the explanation are subordinate to selection.

On the other hand, this is exactly what we should expect Mayr say: it is the *obvious* response. It is the obvious response because, for Mayr, adaptation is the big question. Because adaptation is the big question, the phenomena Gould and Lewontin highlight appear to Mayr only insofar as they bear on our understanding of adaptation. We may need a more sophisticated view of trait adaptation than his atomizing peers favored, but, for Mayr, the only *evolutionary* relevance of the phenomena Gould and Lewontin highlighted was to help us better understand how selection operates. So things appear to the explanatory adaptationist.

For the explanatory adaptationist, once selection enters the picture, the questions stop. That is one particular sense in which adaptation is treated as the "big question" in evolutionary theory. What I have tried to show here is that, even in disputes that seem like disputes over methodology, questions about the structure of the problem space of evolutionary theory are ineluctable.

5. One kind of adaptationism

If my arguments above succeed, I have established my central contention: that there is really only one kind of adaptationism, to wit, explanatory adaptationism. Even as we recognize the logical independence of empirical and methodological adaptationism from explanatory adaptationism (and from each other), we should understand that they are justificatorily intertwined: the strong forms of empirical and methodological adaptationism that drive historical debates over adaptationism essentially depend on explanatory adaptationism. Two tasks remain: first, to explain what this means for how we understand adaptationism (§5.1); second, to consider what this can tell us about evolutionary theory more generally (§5.2).

5.1. Articulating explanatory adaptationism

My overarching argument has taken the form of a No True Scotsman. This might reasonably occasion the worry that the foregoing has ultimately all been a verbal dispute, a question of what deserves the appellation, "adaptationism". My response to this worry is that "adaptationism" is an analytical tool available that we (biologists and philosophers of biology) can use to make sense of historical and present debates in evolutionary biology. We should understand it in the way that makes it the best tool. That means characterizing adaptationism in a way that makes sense of the actual debates surrounding adaptationism. What I have tried to show in the foregoing is that these debates have, again and again, come to turn on assumptions about *how different evolutionary questions relate*: which are fundamental, and which are subordinate? When I exclude most of the various positions identified by Godfrey-Smith and Lewens as genuine forms of adaptationism, my contention is that, while those positions might have been defended and critiqued in historical debates over adaptationism, what was fundamentally *at stake* in those debates was explanatory adaptationism: is adaptation the "big question"?

In light of this, I want to propose a new interpretation of what Godfrey-Smith and Lewens are really identifying. Lewens' (2008) seven kinds of adaptationism are not actually distinct *kinds of adaptationism*; instead, they are distinct *strands of the adaptationist program*. This was a diverse program comprising numerous biologists (and philosophers), not all of whom had identical commitments. That is why the logical independence of the different strands matters: it allows us to make sense of the differing commitments of different biologists. It is useful to have clear characterizations of the different kinds of commitments that these biologists made. However, where Godfrey-Smith and Lewens conceive adaptationists on a family resemblance model (where they have overlapping sets of commitments, drawn from among those strands), I have argued that explanatory adaptationism is *not* a strand like the others. It is the core commitment that held the program together.

In itself, however, explanatory adaptationism is not self-sufficient. There is a large gap between adopting the view that adaptation is the "big question" and actually practicing evolutionary biology. Boucher's (2015; 2025) analysis of adaptationism as a stance captures this nicely. A stance is not a belief about the world; it is an orientation toward it (Van Fraassen 2002; Boucher 2014). It is essential to this conception that a single stance be compatible with a wide range of particular beliefs and scientific practices. To say that adaptation is the "big question" in evolutionary theory is, likewise, an orientation and not a belief. It does not, by itself, determine how one should study the traits of organisms nor what one should ultimately believe about the role of selection in their evolution. This is not to say that explanatory adaptationism has no content of its own—it involves commitment to particular ways of structuring the evolutionary problem space—but this content stands in need of further articulation.

My contention is that the strands of the adaptationist program that Godfrey-Smith and Lewens distinguish are *ways of articulating explanatory adaptationism*. Explanatory adaptationism, on its own, does not actually interact with the world, but stands forever motionless in its stance. Any biologist who takes this stance will have to take on further commitments, whether empirical, methodological, or both. Thus, to account for the views of adaptationist biologists, explanatory adaptationism is necessary but not sufficient. The minimum viable adaptationist package comprises explanatory adaptationism plus at least one of the other strands. Note that, on this understanding, we might still speak of distinct "kinds of adaptationism", tracking differences in the particular packages of views that adaptationists accepted. This, however, would be a classification orthogonal to those of Godfrey-Smith and Lewens.

One advantage of understanding adaptationism in this way is that it can help us make sense of the structure of particular disputes over adaptationism. These disputes commonly occur at two levels. On the first level, there are local empirical and methodological disputes. The local empirical disputes concern the answers to particular contrastive why-questions about the evolution of some trait; the local methodological disputes concern particular ways of answering these questions. On the second level,

there is a fight for the *recognition* of particular problems as genuinely evolutionary. The rise of evolutionary developmental biology, for instance, did not only involve empirical discoveries about how developmental constraints shape evolution. It also required fighting for the recognition of constraints on form as (a) distinct from constraints on adaptation (Amundson 1994) and (b) worth asking about in their own right, rather than merely as "proximate" mechanisms (Amundson 2005).

Understanding adaptationism in this way allows us to disentangle these two levels of dispute. Once we do so, it is easy to see why "adaptationists agree with much of what anti-adaptationists claim they should not, and anti-adaptationists feel cheated by this" (Sansom 2003, 496): the "cheat" lies in subordinating questions about the phenomena anti-adaptationists highlight to questions about the operation of selection—in other words, it lies at the second level. At the first level, by contrast, there are simply certain kinds of evolutionary questions for which selection is a powerful answer, and there are other kinds for which it is less powerful (Wilkins and Godfrey-Smith 2009).

These disagreements at the second level generate "incommensurability" (Chang 2012, chap. 1; Feyerabend 1981, chap. 4; Kuhn [1962] 2012) between rival approaches to evolution: a failure to understand and recognize each other's central concepts and problems. Happily, however, such incommensurability is resolvable by carefully disentangling why questions, recognizing that non-contrastive questions ("why did T evolve?") contain many smaller contrastive questions within them ("why did T evolve, rather than...?") (Novick 2023, sec. 2). Doing so involves separating out the explanatory adaptationism from apparently empirical or methodological claims, thereby returning those claims to their more modest forms. Insofar as it is true that "debates over adaptationism are subsiding, with most researchers now taking a more nuanced view" (Wilkins and Godfrey-Smith 2009, 200), I suggest that this is a result precisely of the subsiding of explanatory adaptationism, allowing a clearer focus on first-level questions about methods and results.

5.2. Adaptation explanations and the structure of evolutionary theory

At this point, I want to turn my attention from adaptationism in particular to evolutionary theory more generally. I have argued that explanatory adaptationism involves commitments about the structure of the evolutionary problem space. I now want to discuss an important nuance of this claim. There are two different things we might mean when we talk about the structure of a problem space. The first concerns the structure that appears *within* particular explanations (i.e., relations between their parts). Explanations themselves have a structure: minimally, they contain an explanandum and an explanans, with an asymmetric relation between them (the latter explains the former). The explanans may then have further parts which play distinct roles. The second concerns the structure that appears *between* explanations (i.e., relations between distinct explanations). In this sense, structure concerns how different kinds of explanation fit together.

Let us revisit Mayr's (1983) response to Gould and Lewontin (1979). We saw that Mayr subordinated problems of trait individuation to problems of identifying and explaining adaptations. This may be understood as either kind of subordination: within or between explanations. Understood as a claim about subordination between explanations, it says that problems of trait individuation gain their explanatory power only insofar as they contribute to explanations of adaptations. Mayr appears to have intended a claim of this sort: all of the explanatory patterns Gould and Lewontin identified contribute to explaining adaptation, which is the central question of evolutionary theory, and thus they are best understood as parts of a sophisticated adaptationist program. Explanations of trait individuation are (generally) subordinate to explanations of adaptation.

Mayr might, however, have limited himself to a weaker claim: that the phenomena Gould and Lewontin identify have a subordinate role to play *within adaptation explanations*. I take the term "adaptation explanations" from Brandon (1990, sec. 5.2). Brandon's notion is useful because he identifies five types of information required for an ideally complete explanation of an adaptation. Each

of these types of information has a role to play within the overall structure of an adaptation explanation. For instance, phylogenetic information is required. While phylogeny might be studied (mostly) independently of any questions of adaptation, *within adaptation explanations*, phylogenetic information is subordinate: it matters for its relevance to explaining adaptation. While Brandon's list does not explicitly include information relevant to trait individuation (Brandon simply takes trait identities for granted), a more modest Mayr might be interpreted as making a similar point about trait individuation: *within adaptation explanations*, information about trait individuation is subordinate.

What Brandon (1990, chap. 4) recognizes more clearly than Mayr is that an adaptation explanation is not the only *evolutionary* explanation to give. Foregrounding other aspects and subordinating adaptation and selection generates other explanatory patterns. Phylogeny is again illustrative. It is not quite true to say that phylogeny can be studied independently of any questions of adaptation. Rather, the selection regimes to which portions of the genome tend to be exposed affects the strength of their phylogenetic signal. For instance, deeply conserved genes are often especially useful phylogenetically, whereas fast-evolving genes may generate noisier signals (e.g., Fox et al. 1977). In this sense, *within phylogenetic explanations*, adaptive information is subordinated.

Distinguishing these two kinds of subordination allows the following general remark: claims about subordination within explanations are generally clearer and more defensible than claims about subordination between explanations. I confess that I do not find it so clear what it means to think that adaptation is the "big question" in evolutionary biology (a claim about subordination between explanations). Even if this claim can get articulated through particular empirical and methodological theses (§5.1), those theses do not exhaust its content—this is the flip side of the logical independence of Godfrey-Smith's (2001) three kinds of adaptationism. By contrast, claims about subordination within explanations can be given a precise articulation in terms of the specific roles that information about adaptation (the generation of variation, phylogeny, etc.) plays within particular explanatory structures

(Novick 2023).

This, I suggest, tells us something about debates within evolutionary theory as a whole. Evolutionary theory concerns a motley array of problems that may not possess any single general structure (Love 2013; Booth, Mariscal, and Doolittle 2016; Novick and Doolittle 2019). Some explanations center adaptation, but others do not, and a singular focus on adaptation can obscure the existence of these independent explanatory questions, as we have seen. In addition to non-adaptive explanations, there are also cases where adaptive and structural explanations are interwoven, with neither having priority (Novick 2019; 2023, sec. 3), as well as cases that mix adaptive and neutral explanations (Stoltzfus 1999; 2012; Brunet and Doolittle 2018; Muñoz-Gómez et al. 2021).

My suggestion is that a great many pseudo-disputes in evolutionary theory arise from attempting to find global patterns of subordination, that is, to identify some problem as central to evolutionary theory as such. In fact, however, we are really dealing primarily with local subordination: subordination within the structure of *particular* problems and *particular* explanations. While I cannot defend this at length here, I think attending to this would go a long way to clarifying what is at stake in current debates over the "extended evolutionary synthesis" (Laland et al. 2015; Lala et al. 2024; for clarificatory efforts along the lines I suggest, cf. Buskell 2019; 2020; Hazelwood 2023).

6. No kinds of adaptationism

I have sought to show that all forms of adaptationism rest, ultimately, on explanatory adaptationism. This is, on the surface, a relatively modest aim. I have said nothing about whether or not explanatory adaptationism is viable. The work has simply been clarificatory: though it is true that the various kinds of adaptationism are logically independent, in other ways they are interdependent.

I would be remiss, however, not to admit my ulterior motive. If all forms of adaptationism depend, for their justification, on explanatory adaptationism, the natural consequence is that adaptationism as

such has a single critical point of failure. If explanatory adaptationism is indefensible, every kind of adaptationism is indefensible.

Explanatory adaptationism is indefensible (Novick 2023, sec. 5); therefore, every kind of adaptationism is indefensible. I do not say this because I am a partisan of some other explanatory *-ism*—structuralism, say (Amundson 2005, chap. 11). Explanatory adaptationism (and therefore all adaptationism) should be abolished, and replaced with *nothing* (for a critique, see Boucher 2025).

I have not defended this here, and will not, beyond a simple note. I share with Reeve and Sherman (1993, 2) a distaste for disputes over "quasi-empirical claims that are really disguised assumptions about what aspects of evolution are most important". They hoped that a suitable definition of "adaptation" would save their own view from this fate; it did not. I have tried to show that their failure is due, not to insufficient ingenuity, but rather the task itself: there is *no* definition of "adaptation" that will save the adaptationist from having to rest, at the last, on a judgment about which evolutionary questions most matter.

But this is only a partial defense. For one who believes that such judgments (and disputes over them) are essential drivers of scientific progress (Kuhn [1962] 2012; Boucher 2014; 2019; 2025), I have at best clarified, but not resolved, the debate over adaptationism. I think such judgments are predominantly impediments to progress (cf. Chang 2012), but the question is too large to attempt here. Still, it seems only fair to acknowledge where I am going, and where I hope you will follow.

Bibliography

Alberch, Pere. 1989. "The Logic of Monsters: Evidence for Internal Constraint in Development and Evolution." *Geobios*, Ontogenèse Et Évolution, vol. 22 (January): 21–57. https://doi.org/10.1016/S0016-6995(89)80006-3.

Alberch, Pere, and Emily A. Gale. 1985. "A Developmental Analysis of an Evolutionary Trend: Digital Reduction in Amphibians." *Evolution* 39 (1): 8–23. https://doi.org/10.1111/j.1558-5646.1985.tb04076.x.

Amundson, Ron. 1994. "Two Concepts of Constraint: Adaptationism and the Challenge from Developmental Biology." *Philosophy of Science* 61 (4): 556–78. https://doi.org/10.1086/289822.

Amundson, Ron. 2005. *The Changing Role of the Embryo in Evolutionary Thought: Roots of Evo-Devo*. Cambridge Studies in Philosophy and Biology. Cambridge University Press. https://doi.org/10.1017/CBO9781139164856.

Birch, Jonathan. 2014. "Has Grafen Formalized Darwin?" *Biology & Philosophy* 29 (2): 175–80. https://doi.org/10.1007/s10539-013-9421-z.

Booth, Austin, Carlos Mariscal, and W. Ford Doolittle. 2016. "The Modern Synthesis in the Light of Microbial Genomics." *Annual Review of Microbiology* 70 (July): 279–97. https://doi.org/10.1146/annurev-micro-102215-095456.

Boucher, Sandy C. 2014. "What Is a Philosophical Stance? Paradigms, Policies and Perspectives." *Synthese* 191 (10): 2315–32. https://doi.org/10.1007/s11229-014-0400-y.

Boucher, Sandy C. 2015. "Functionalism and Structuralism as Philosophical Stances: Van Fraassen Meets the Philosophy of Biology." *Biology & Philosophy* 30 (3): 383–403. https://doi.org/10.1007/s10539-014-9453-z.

Boucher, Sandy C. 2019. "An Empiricist Conception of the Relation Between Metaphysics and Science."

Philosophia 47 (5): 1355–78. https://doi.org/10.1007/s11406-018-0040-4.

Boucher, Sandy C. 2025. "Functionalism and Structuralism in Biology: Stances or Explanatory Strategies?" *Synthese* 206 (1): 1–23. https://doi.org/10.1007/s11229-025-05128-x.

Brandon, Robert N. 1990. *Adaptation and Environment*. Princeton University Press.

Brandon, Robert N., and Mark D. Rausher. 1996. "Testing Adaptationism: A Comment on Orzack and Sober." *The American Naturalist* 148 (1): 189–201. https://doi.org/10.1086/285918.

Brown, Rachael L. 2022. "Structuralism and Adaptationism: Friends? Or Foes?" *Seminars in Cell & Developmental Biology*, ahead of print, March 8. https://doi.org/10.1016/j.semcdb.2022.02.022.

Brunet, T. D. P., and W. Ford Doolittle. 2018. "The Generality of Constructive Neutral Evolution." *Biology & Philosophy* 33 (1): 2. https://doi.org/10.1007/s10539-018-9614-6.

Buskell, Andrew. 2019. "Reciprocal Causation and the Extended Evolutionary Synthesis." *Biological Theory*, ahead of print, September 5. https://doi.org/10.1007/s13752-019-00325-7.

Buskell, Andrew. 2020. "Synthesising Arguments and the Extended Evolutionary Synthesis." *Studies in History and Philosophy of Science Part C: Studies in History and Philosophy of Biological and Biomedical Sciences*, January 6, 101244. https://doi.org/10.1016/j.shpsc.2019.101244.

Chang, Hasok. 2012. *Is Water H2O?: Evidence, Realism and Pluralism*. Boston Studies in the Philosophy of Science 293. Springer.

Darwin, Charles. 1859. *On the Origin of Species by Means of Natural Selection, Or the Preservation of Favoured Races in the Struggle for Life*. John Murray, Albemarle Street.

Davidson, Eric H., and Douglas H. Erwin. 2006. "Gene Regulatory Networks and the Evolution of Animal Body Plans." Review. *Science* 311 (5762): 796–800. https://doi.org/10.1126/science.1113832.

Dennett, Daniel C. 1996. *Darwin's Dangerous Idea: Evolution and the Meanings of Life*. Simon and Schuster.

DiFrisco, James, and Grant Ramsey. 2023. "Adaptationism and Trait Individuation." *Philosophy of Science*, February 17, 1–15. https://doi.org/10.1017/psa.2023.28.

Feyerabend, Paul K. 1981. *Realism, Rationalism and Scientific Method: Volume 1: Philosophical Papers*. Cambridge University Press.

Forber, Patrick. 2009. "Introduction: A Primer on Adaptationism." *Biology & Philosophy* 24 (2): 155–59. https://doi.org/10.1007/s10539-008-9150-x.

Fox, George E., Kenneth J. Pechman, and Carl R. Woese. 1977. "Comparative Cataloging of 16S Ribosomal Ribonucleic Acid: Molecular Approach to Procaryotic Systematics." *International Journal of Systematic and Evolutionary Microbiology,* 27 (1): 44–57. https://doi.org/10.1099/00207713-27-1-44.

Gilchrist, George W., and Joel G. Kingsolver. 2001. "Is Optimality Over the Hill: The Fitness Landscapes of Idealized Organisms." In *Adaptationism and Optimality*. Cambridge University Press.

Godfrey-Smith, Peter. 2001. "Three Kinds of Adaptationism." In *Adaptationism and Optimality*, edited by Steven Hecht Orzack and Elliott Sober. Cambridge University Press.

Gould, Stephen J., and Richard C. Lewontin. 1979. "The Spandrels of San Marco and the Panglossian Paradigm: A Critique of the Adaptationist Programme." *Proceedings of the Royal Society B* 205 (1161): 581–98. https://doi.org/10.1098/rspb.1979.0086.

Grafen, Alan. 2014. "The Formal Darwinism Project in Outline." *Biology & Philosophy* 29 (2): 155–74. https://doi.org/10.1007/s10539-013-9414-y.

Green, Sara. 2014. "A Philosophical Evaluation of Adaptationism as a Heuristic Strategy." *Acta Biotheoretica* 62 (4): 479–98. https://doi.org/10.1007/s10441-014-9232-x.

Hazelwood, Caleb. 2023. "Reciprocal Causation and Biological Practice." *Biology & Philosophy* 38 (1): 5. https://doi.org/10.1007/s10539-023-09895-0.

Kuhn, Thomas. (1962) 2012. *The Structure of Scientific Revolutions*. 50th Anniversary. University of

Chicago Press. https://press.uchicago.edu/ucp/books/book/chicago/S/bo13179781.html.

Lala, Kevin N., Tobias Uller, Nathalie Feiner, Marcus Feldman, and Scott F. Gilbert. 2024. *Evolution Evolving: The Developmental Origins of Adaptation and Biodiversity*. Princeton University Press.

Laland, Kevin N., Tobias Uller, Marcus W. Feldman, et al. 2015. "The Extended Evolutionary Synthesis: Its Structure, Assumptions and Predictions." *Proceedings of the Royal Society B: Biological Sciences* 282 (1813): 20151019. https://doi.org/10.1098/rspb.2015.1019.

Lewens, Tim. 2008. "Seven Types of Adaptationism." *Biology & Philosophy* 24 (2): 161. https://doi.org/10.1007/s10539-008-9145-7.

Lewens, Tim. 2019. "Neo-Paleyan Biology." *Studies in History and Philosophy of Science Part C: Studies in History and Philosophy of Biological and Biomedical Sciences* 76 (August): 101185. https://doi.org/10.1016/j.shpsc.2019.101185.

Lloyd, Elisabeth A. 2006. *The Case of the Female Orgasm: Bias in the Science of Evolution*. Harvard University Press.

Lloyd, Elisabeth A. 2015. "Adaptationism and the Logic of Research Questions: How to Think Clearly About Evolutionary Causes." *Biological Theory* 10 (4): 343–62. https://doi.org/10.1007/s13752-015-0214-2.

Love, Alan C. 2013. "Theory Is as Theory Does: Scientific Practice and Theory Structure in Biology." *Biological Theory* 7 (4): 325–37. https://doi.org/10.1007/s13752-012-0046-2.

Maynard Smith, John. 1978. "Optimization Theory in Evolution." *Annual Review of Ecology and Systematics* 9: 31–56.

Mayr, Ernst. 1961. "Cause and Effect in Biology." *Science* 134 (3489): 1501–6. https://doi.org/10.1126/science.134.3489.1501.

Mayr, Ernst. 1983. "How to Carry Out the Adaptationist Program?" *The American Naturalist* 121 (3): 324–34. https://doi.org/10.1086/284064.

Muñoz-Gómez, Sergio A., Gaurav Bilolikar, Jeremy G. Wideman, and Kerry Geiler-Samerotte. 2021. "Constructive Neutral Evolution 20 Years Later." *Journal of Molecular Evolution* 89 (3): 172–82. https://doi.org/10.1007/s00239-021-09996-y.

Nelson, Gareth. 1994. "Homology and Systematics." In *Homology: The Hierarchical Basis of Comparative Biology*, edited by Brian K. Hall. Academic Press.

Novick, Aaron. 2019. "Cuvierian Functionalism." *Philosophy, Theory, and Practice in Biology* 11 (20190821). https://doi.org/10.3998/ptpbio.16039257.0011.005.

Novick, Aaron, and W. Ford Doolittle. 2019. "How Microbes 'Jeopardize' the Modern Synthesis." *PLOS Genetics* 15 (5): e1008166. https://doi.org/10.1371/journal.pgen.1008166.

Novick, Rose. 2023. *Structure and Function*. Cambridge University Press.

Orzack, Steven Hecht, and Elliott Sober. 1994. "Optimality Models and the Test of Adaptationism." *The American Naturalist* 143 (3): 361–80. https://doi.org/10.1086/285608.

Orzack, Steven Hecht, and Elliott Sober. 1996. "How to Formulate and Test Adaptationism." *The American Naturalist* 148 (1): 202–10. https://doi.org/10.1086/285919.

Orzack, Steven Hecht, and Elliott Sober. 2001. "Adaptation, Phylogenetic Inertia, and the Method of Controlled Comparisons." In *Adaptationism and Optimality*, edited by Steven Hecht Orzack and Elliott Sober. Cambridge University Press.

Peter, Isabelle S., and Eric H. Davidson. 2011. "Evolution of Gene Regulatory Networks Controlling Body Plan Development." *Cell* 144 (6): 970–85. https://doi.org/10.1016/j.cell.2011.02.017.

Peter, Isabelle S., and Eric H. Davidson. 2015. *Genomic Control Process: Development and Evolution*. Academic Press. https://resolver.caltech.edu/CaltechAUTHORS:20151001-085324137.

Potochnik, Angela. 2009. "Optimality Modeling in a Suboptimal World." *Biology & Philosophy* 24 (2): 183–97. https://doi.org/10.1007/s10539-008-9143-9.

Reeve, Hudson Kern, and Paul W. Sherman. 1993. "Adaptation and the Goals of Evolutionary Research."

The Quarterly Review of Biology 68 (1): 1–32. https://doi.org/10.1086/417909.

Sansom, Roger. 2003. "Constraining the Adaptationism Debate." *Biology and Philosophy* 18 (4): 493–512. https://doi.org/10.1023/A:1025581622161.

Simpson, George Gaylord. (1944) 1984. *Tempo and Mode in Evolution*. Columbia Classics edition. Columbia University Press.

Sober, Elliott. 1984. *The Nature of Selection*. University of Chicago Press. https://www.press.uchicago.edu/ucp/books/book/chicago/N/bo3621916.html.

Stoltzfus, Arlin. 1999. "On the Possibility of Constructive Neutral Evolution." *Journal of Molecular Evolution* 49 (2): 169–81. https://doi.org/10.1007/PL00006540.

Stoltzfus, Arlin. 2012. "Constructive Neutral Evolution: Exploring Evolutionary Theory's Curious Disconnect." *Biology Direct* 7 (1): 35. https://doi.org/10.1186/1745-6150-7-35.

Van Fraassen, Bas C. 1980. *The Scientific Image*. Clarendon Press.

Van Fraassen, Bas C. 2002. *The Empirical Stance*. Yale University Press.

Wagner, Günter P. 2014. *Homology, Genes, and Evolutionary Innovation*. Princeton University Press. https://press.princeton.edu/books/hardcover/9780691156460/homology-genes-and-evolutionary-innovation.

Wilkins, Jon F., and Peter Godfrey-Smith. 2009. "Adaptationism and the Adaptive Landscape." *Biology & Philosophy* 24 (2): 199–214. https://doi.org/10.1007/s10539-008-9147-5.

Zhang, Mingjun. 2022. "Empirical Adaptationism Revisited: Is It Testable and Is It Worth Testing?" *Biology & Philosophy* 37 (6): 51. https://doi.org/10.1007/s10539-022-09879-6.