Adaptationism and Trait Individuation

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Adaptationism is often taken to be the thesis that most traits are adaptations. In order to assess this thesis, it seems we must be able to establish either an exhaustive set of all traits or a representative sample of this set. Either task requires a more systematic and principled way of individuating traits than is currently available. Moreover, different trait individuation criteria can make adaptationism turn out true or false. For instance, individuation based on natural selection may render adaptationism true, but may do so by presupposing adaptationism. In this paper, we show how adaptationism depends on trait individuation and that the latter is an open and unsolved problem.

1. Introduction. *Adaptationism* is a claim about the significance of adaptations in the process of evolution, or their significance for the study of this process. An *adaptation* is a kind of trait, one that bears a special relationship to natural selection. There is some debate about what this relationship must be in order for a trait to be an adaptation, but most agree that an adaptation is a trait that is in some sense *due to selection*.

Typically, an adaptation has one or more *functions* that it was selected to perform. The existence—and form—of adaptations is due to selection for the performance of these functions in past generations. Although this abstract characterization is straightforward enough, mapping it onto specific traits can be complicated and non-trivial. Take the human chin—is it an adaptation? The shape of the chin has likely undergone some sexual selection (Pampush 2015) and so would be an adaptation under some definitions. However, the chin itself, understood as the bone region of the basal jaw that protrudes beyond the alveolar region, may be a non-adaptive byproduct of other cranial and mandibular modifications, as Gould and Lewontin (1979) famously argued. How one individuates the chin—and whether one identifies the trait with the object (the expanse of bone itself) or the properties born by the object (such as its shape)—is crucial in determining whether it is an adaptation.

Whether a trait is considered an adaptation thus crucially depends on how the trait is individuated as well as how significant a role selection played in its history. We will return to the issue of individuation later—let's shelve it for the moment and ask how adaptations are related to the adaptationism thesis.

Philosophers have distinguished three main forms of adaptationism: methodological, explanatory, and empirical (Godfrey-Smith 2001). Methodological adaptationism is the thesis that the best method for understanding traits is to seek adaptive accounts of their evolution. It is not a claim about the power of natural selection or about the relative frequency of adaptations among all traits. Whereas methodological adaptationism concerns the methods of evolutionary biology, explanatory adaptationism concerns its goals: explanatory adaptationists assert that the study of adaptations is the central goal of evolutionary biology. Again, this is not a claim about the power of selection or the ubiquity of adaptations. It is that adaptations are what evolutionary biology is about.

Empirical adaptationism, in contrast to methodological and explanatory adaptationism, is a thesis about the strength of natural selection in evolution. It is this form of adaptationism that is the focus of this paper, and references to ‘adaptationism’ in what follows should be taken as references to empirical adaptationism. How powerful in shaping traits must selection be in order for the empirical adaptationist hypothesis to be supported? Orzack and Sober (1994, 362) identify three propositions that might be advanced regarding the relationship between natural selection and a trait, *T*:

> (U) Natural selection played some role in the evolution of *T*. (U stands for ubiquitous since we believe this proposition applies to most traits.)
>
> (I) Natural selection was an important cause of the evolution of *T*. (I stands for important.)
>
> (O) Natural selection is a sufficient explanation of the evolution of *T*, and *T* is locally optimal. (O stands for optimal.)

They hold that adaptationists generally assent to (O) and that adaptationism can be defined based on its generalization: “Natural selection is a sufficient explanation for most nonmolecular traits, and these traits are locally optimal” (1994, 364).

There are many things about this definition in need of analysis. For example, what is a *sufficient* explanation and how should *optimality* be assessed? For the purpose of this paper, the important word to point out is ‘most’. References to the ‘majority’ or ‘most’ traits are common in definitions of adaptationism. For instance, Potochnik (2009) says that "adaptationism is taken to be the claim that selection is the only important influence on *most* evolutionary outcomes" (192, emphasis added), and Forber (2009) takes the adaptationist position to hold that "selection is ubiquitous, relatively free from constraints, and provides a sufficient explanation for the evolution of *most* traits" (156, emphasis added).

In order to make a testable claim about most traits, however, there must be a way of producing an exhaustive list of the traits possessed by an individual from which the frequency of adaptations can be deduced. That is, to assess whether *most traits* meet the criteria for being an adaptation, it appears there must be some way of counting *all traits* to support this relative frequency claim. If traits are individuated in an unconstrained way, such that an unlimited number of traits can be defined for any individual, then frequency claims (for example, about the majority of traits) will be ill-founded.

Likewise, if trait individuation is partly or entirely arbitrary, as is often claimed (e.g., West-Eberhard 1992), trait counts will also be ill-founded, making the central claim of adaptationism uselessly indeterminate. It may therefore seem more desirable to formulate adaptationism without a universal quantifier. For example, adaptationism could be the view that *for any given* trait, that trait is likely to be an adaptation. However, if organisms can be carved up into indefinitely many traits, the number of traits an organism possesses will be very large and potentially infinite—certainly larger than the number of traits that could have been shaped by natural selection in a finite evolutionary period. In that case, adaptationism—as a claim about any given trait—will come out as false. Moreover, without some way of excluding arbitrary or non-natural traits—such as being south of the equator on Wednesdays or being part of a species discovered before 1975—the truth or falsity of adaptationism about such traits will lack biological significance.

On top of this problem, the *any given trait* construal is faced with the *representative sample problem*. If we were to test the adaptationism thesis under either this construal or the "most traits" construal, we must produce a representative sample of traits to test. But how can we know that a sample is representative? An answer to this question will be inaccessible for the same reason that we cannot produce an exhaustive list of all traits.

Thus, while the *any given trait* construal may avoid the need to enumerate all traits, it is beset with problems just as significant. What is clear is that under any construal, the problem of trait individuation is central to the assessments of adaptationism and anti-adaptationism. There seems to be no way around advancing a well-founded view of trait individuation if adaptationism (or anti-adaptationism) is to be an empirically meaningful thesis.

Given how sprawling the debate over adaptationism has been in the last decades, the near-total absence of any explicit reflection on how to understand "traits" in this context is especially striking. It may be that authors hold a deflationary presupposition that as long as one is clear about defining the (non-)adaptive traits at issue, there is no need for a broader understanding of how the different *ad hoc* traits fit together in organisms. However, the demand for unambiguous counting implicit in the "most traits" formulation of adaptationism, and the need for excluding arbitrary traits to make such counts biologically meaningful, show that the deflationary presupposition is inadequate. In fact, this point was recognized by Gould and Lewontin (1979) when they criticized adaptationism for proceeding by "atomizing" organisms into traits: "We must omit an extended discussion of the vital issue: 'what is a trait?' Some evolutionists may regard this as a trivial, or merely a semantic problem. It is not" (Gould and Lewontin 1979, 585). However vital the issue, they nonetheless omitted this discussion "for lack of space."

In this paper, we explore the dependency of adaptationism on trait individuation and suggest what this entails for the adaptationist thesis. For adaptationism as a general thesis to be empirically meaningful and testable, we argue, not only must there be a framework for carving organisms into a finite set of traits, this framework must abide by the independence constraint:

> *Independence constraint*: Any trait individuation framework that can support assessments of adaptationism must be independent of the truth or falsity of adaptationism.

This is essential for adaptationism to be empirical and synthetic. If being a trait were conceptually identified with being an adaptation, for example, then adaptationism would be trivially true. Perhaps less obviously, approaches that base trait individuation on selection may also lack the required independence.

The two broad frameworks we will focus on here are *functionalism* and *structuralism*. If we think of evolution as a dual process comprising the generation of variation and the sorting of variants by population-level processes such as selection, structuralism can be characterized as a view that attributes more importance to the generation of variation, whereas functionalism attributes more importance to the sorting of variation by selection. While these perspectives have implications beyond trait individuation, we focus here only on their implied criteria for how traits should be individuated. As we will see, functional approaches have difficulties remaining independent of the truth of adaptationism, but neither succeeds in making the “most traits” formulation of adaptationism tractable. We will begin in the following section with an analysis of functional trait individuation before turning to structuralism.

2. Functional trait individuation. A "functional" conception of trait individuation, as we will call it, is any view that individuates traits with reference to natural selection or fitness differences (for example: Arnold 1983; Brandon 1999; Orr 2000; Violle et al. 2007). The general rationale for this approach is similar to that for evolutionary-functional approaches to biological individuality: it is only insofar as a trait influences fitness that it can be "seen" by selection, and thus only to this extent can it participate in evolutionary processes driven by selection (Orr 2000). These approaches can also be motivated by a type of "screening-off" argument. Traits individuated by contributions to fitness would seem to effectively screen off the influence of structural factors in the sense that, conditional on the fitness effects of functional traits, the underlying structural factors cannot have any additional causal influence on fitness and selection.

If we adopt the view that selection determines what counts as a trait, then it seems that the claim that most traits are adaptations will automatically be true. Functionalist approaches to trait individuation are therefore at risk of failing to constitute an independent test of adaptationism. A subtle example can be found in the tacit reliance on functionalist trait individuation in Reeve and Sherman's (1993) defense of adaptationism. They hold that adaptation is an inherently contrastive concept that represents traits in a space of alternative phenotypes that can be compared as to their contributions to fitness. This space of alternative phenotypes constitutes a "phenotype set" that must be specified in order for claims of adaptation or non-adaptation to be well defined. For example, in saying that vertebrate eyes are adaptations, the contrastive phenotype set could be having eyes versus not having eyes, or it could be different precise arrangements of sensory cells, visual pigments, and lenses (Reeve and Sherman 1993, 10).

They then argue that criticisms of adaptationism on the basis of phylogenetic inertia, genetic correlation, or developmental constraint generally fail to properly specify the relevant phenotype set for comparison. In particular, anti-adaptationist claims citing developmental constraint allegedly neglect to consider the phenotype sets that arise from the deleterious mutations that are constantly being pruned by stabilizing selection. When these are considered, developmental constraints turn out to be nothing other than the operation of stabilizing selection, which is an adaptive process.

Within this perspective, an organism's traits include all phenotypic features that can be contrasted with mutant phenotypes that have been, or would be, distinguishable by selection. The phenotype set then comprises distinct traits corresponding to *any* dimension in phenotype space that is affected by any mutation. For an already adapted organism, the vast majority of fitness-affecting mutations will be deleterious, and so virtually all of the actual organismic phenotypes that can be contrasted with mutational phenotypes will count as adaptations. Thus, if the adaptationist "most traits" is evaluated over Reeve and Sherman's phenotype set, specified in the above manner, then adaptationism will certainly be true.

Traits, in this perspective, are phenotypic contributions to fitness, individuated as the correlates of single-gene variations, most of which are deleterious. It is not obvious, however, that this is the most appropriate background conception of traits for assessing adaptationism. In approaches informed by developmental biology, *networks* of genes organized into modules that—rather than individual genes—are more often the focal units of the causation of phenotypes (Davidson 2010). If phenotypic traits are individuated as correlates of entire developmental-genetic modules or networks, this would lump together into the same trait many of the traits that count as distinct in the single-gene mutational phenotype set. The view of traits as phenotypic contributions to fitness also neglects to distinguish selectively neutral traits. These include traits that do not vary in natural populations—e.g., limb number in tetrapods, viewed as a trait distinct from the various aspects of limbs that contribute to differential fitness. In other words, changing from single-gene phenotype sets and fitness contribution to other criteria of individuation yields different numbers of traits for the same organism, as well as different frequencies of adaptation.

In understanding traits functionally in terms of fitness contribution, the adaptationist all but guarantees that adaptationism will be true. This suggests the possibility that much debate over adaptationism may simply reflect differences between under-theorized stances on the individuation of traits.

How do functionalist approaches articulated more broadly fare on the trait counting problem? Consider first that "functional traits" can be understood either as phenotypic features *actually* undergoing (or having undergone) selection, or phenotypic features *possessing the capacity* to undergo selection. The first option obviously fails the independence constraint: all traits undergoing selection for more than one generation are adaptations, which would make adaptationism trivially true. The second option is less obvious. Any arbitrary phenotypic trait can be selected-for: for example, one can cull a population of laboratory mice based on absolute numerical ratios between heart rate and femur length, thereby making that ratio a functional trait. But for a trait to *respond* to selection by undergoing progressive population-level adaptation, there must be underlying genetic polymorphisms influencing that specific trait. This condition is sometimes referred to as "quasi-independence" (Lewontin 1978) (see below), a property that requires functional traits to be linked to underlying genetic variation (e.g., Brandon 1999) rather than being only phenotypic (e.g., Arnold 1983; Violle et al. 2007).

Functional trait individuation, understood merely in terms of the capacity to undergo selection-for, does meet the independence constraint. It would leave out only traits that cannot undergo selection in a given population because they cannot vary. While there may be many traits that *do not* vary in a given population (e.g., limb number in most tetrapods), it is not clear that there are any that *cannot ever* vary given standard processes of genetic evolution (e.g., mutation, recombination, gene duplication, subfunctionalization, etc.). If functional traits are understood as phenotypic features possessing the capacity for selection plus underlying genetic quasi-independence, this also does not fail the independence constraint because quasi-independence builds a structural condition into an otherwise selection-based formula.

However, even if a functional-capacity view of traits does not presuppose adaptationism, it will not allow for determinate counting of numbers of traits. Arbitrary phenotypic features, including random combinations of biometric values, can undergo selection-for in artificial selection settings. This yields a combinatorial explosion of uncountably many traits. But, perhaps surprisingly, adding in a structural condition of genetic quasi-independence does little to improve the situation. Artificial selection experiments have revealed that novel selection regimes can modify traits that would not otherwise appear to be distinct and cohesive units of the phenotype. For example, in a paper entitled “How small are the smallest domains of selectable form,” Weber (1992) ran artificial selection experiments on fly wings and found that a tiny (<0.2 mm), seemingly arbitrary sub-region of the wing was responsive to selection for altered shape, and that the changes were largely local to that region. He concluded that this implies underlying genetic potential for “dense, fine-grained, autonomous and localized adaptive change” (Weber 1992, 345; see Mezey and Houle 2005). Extrapolating to other body parts, these results suggest that, for any given multicelled organism, the set of traits possessing the capacity to undergo selection as units includes very many nested, partially overlapping and disjoining structures—e.g., the wing as well as many arbitrary sub-regions of it. Different selection regimes can individuate different subsets and supersets of the same biomass, yielding indefinitely many "traits" in the sense of local genotype-phenotype maps responsive to selection.

Traits, understood in terms of the capacity to undergo selection, can only be determinately counted if all selection pressures as well as the variational responses to selection are known. In multicellular organisms this is an impossibly demanding requirement. The genotype-phenotype map has turned out to be exceedingly complex and circuitous and is still not well-understood even in model organisms. Moreover, selection pressures that would individuate many "potential" functional characters have never actually been realized and may never be realized in evolution—whether in nature or in the lab.

While functional trait individuation may be useful for some purposes, it is unsuitable for use in evaluating adaptationism. This is because it either presupposes adaptationism or yields indefinitely many traits that cannot be determinately counted or estimated. If functional trait individuation cannot serve in assessments of adaptationism, let's consider whether the structural alternative fares better.

3. Structural trait individuation. Structural conceptions of trait individuation, as we will call them, include any approach in which phenotypic traits are individuated by the factors that generate and structure variation rather than by selection. Because such approaches do not appeal to selection to identify traits, without positively assuming that selection is *not* involved in shaping the traits individuated structurally, they meet the independence constraint for evaluating adaptationism. Nevertheless, though more promising than functional approaches, they still do not generate the determinate overall trait counts that would be required for evaluating whether "most traits" are adaptations.

One structuralist approach is the developmental-genetic model of character identity developed by Wagner and colleagues (Wagner 2014; DiFrisco et al. 2020, 2022). In its latest version, this model hypothesizes that there are "character identity mechanisms" (ChIMs) with a modular developmental architecture controlling the identity of body parts, distinct from the mechanisms influencing properties or states of the body parts. Morphological characters at different levels of organization have ChIMs with different components but with the same conserved causal profile: thus, cell type identity is based on "Core Regulatory Complexes" of transcription factors, tissue identity is based on networks of autocrine and paracrine signaling between cell types and extracellular matrix, and organ identity is based on networks of cell–cell signaling pathways.

In principle, this model provides structural criteria allowing for the individuation and counting of traits, even though detailed ChIMs have not been empirically worked out most characters. However, the model is designed to apply only to individual body parts—i.e., cell types, tissues, and organs—and not to properties of body parts, quantitative traits, or behaviors. Adaptationism is normally understood as a thesis applying to *all* traits, and it is not clear how including properties, quantities, behaviors, etc. along with body parts would alter the frequency of traits that are adaptations. For the purposes of evaluating adaptationism, this may indicate a need to either further differentiate "most traits" into types (e.g., morphological traits), or to pursue a more abstract structural conception applying to all traits at once.

An example of the latter is the general criterion of "quasi-independence"—which refers to the capacity of something to vary as a unit without causing (much) variation in other units. In his classic article "Adaptation" (1978), Lewontin argued that in order for adaptation to be possible, traits must possess quasi-independence. If traits covary together instead of being quasi-independent, selection cannot cause adaptation in one trait without disrupting other traits. There are two ways of interpreting this claim about quasi-independence, one weaker and one stronger. The weaker claim would be that for adaptation to be possible, the organism must have a modular body plan with *at least some* quasi-independent traits. Complex progressive adaptation would not be possible if everything varies together with everything else. The stronger claim would be that for any given trait to be a trait, or an adaptive trait, *that very trait* must possess quasi-independence. If a described trait/adaptation does not possess quasi-independence, then it should be re-described in terms of a related unit (e.g., at a higher or lower level of composition) that does possess quasi-independence.

The weaker thesis that some organismic modularity is necessary for the evolution of complex adaptations is widely accepted (see, e.g., Wagner et al. 2007), but it does not yield specific constraints on trait individuation. The stronger thesis that traits are just phenotypic units possessing quasi-independence does provide a structuralist criterion of individuation (Brigandt 2007). However, upon closer scrutiny, it is not a criterion that would make traits determinately countable in the sense needed for evaluating whether most traits are adaptations.

Quasi-independence is graded rather than categorical, meaning that different phenotypic features can possess quasi-independence to different degrees. If quasi-independence determines what counts as a trait, then being a trait must also come in degrees. But counting numbers of traits requires that being a trait is categorical or discrete rather than graded. In order to get discreteness from a continuous property, one would have to specify thresholds that demarcate different degrees into categories. Assuming quasi-independence is measurable as a uniform quantity, how much of it is needed for something to be a trait? The threat of arbitrariness and interest-relativity looms large here. It is not obvious that thresholds could be established that would be biologically meaningful rather than merely a matter of formal convenience.

Alternatively, without thresholds, a trait could be viewed as any phenotypic feature with a *non-zero* degree of quasi-independence. However, this leads back to the same problems with the functional capacity view of traits. Recall that in the example of artificial selection on fly wings, the same region of biomass can include multiple nested and partially overlapping sub-regions (Weber 1992). These sub-regions are not only functional traits that can be selected-for, but are also units with some appreciable degree of quasi-independence, as Weber's experiments showed. If *any* degree of quasi-independence is sufficient for being a trait, this would yield indefinitely many traits within the same biomass, most of which would be insufficiently cohesive to make a difference to any process of interest (including adaptation). Such traits are no more countable than the set of traits that possess the capacity to undergo selection.

Essentially, the same line of argument can be repeated for a related genre of structural approaches based on causal rather than variational quasi-independence (sometimes called "near-decomposability"). This is the view that there are body parts wherever there are sets of components that interact more strongly and/or more frequently with each other than with components of the environment (McShea and Venit 2001; Simon 1962). Since interaction strength and frequency come in degrees, "the extent to which a system is a part—its degree of partness—is likewise a continuous variable" (McShea and Venit 2001, 262). This approach leads to the same outcome as the densely articulated fly wing with indefinitely many overlapping sets and subsets of traits. Any given module can have components that strongly interact with distinct sets of components from multiple modules (e.g., transmembrane proteins, morphogens, and hormones) yielding huge numbers of body parts for even a small biomass, and more if we consider the changing dynamics over developmental time. Thresholds or approximations would be needed to tame the inflationary surplus of traits, with the same difficulty of establishing biologically meaningful thresholds. Even if we suppose that certain approximations will simplify the problem (McShea and Venit 2001), a structuralist approach based on interaction strengths between parts still applies only to body parts rather than properties, quantities, and behaviors.

There are likely many biological contexts in which the need to individuate traits is well served by structural approaches. In the present context, however, while they have the advantage of not presupposing the truth or falsity of adaptationism, current frameworks do not provide a straightforward way of counting traits to address the question of whether most traits are adaptations. Further structuralist work may be able to resolve this question, but for now it remains an open problem.

4. Conclusion. Empirical adaptationism, understood as the thesis that most traits are adaptations—or are due in some way to selection—requires a principled way of individuating traits so that the frequency of traits that are adaptations can be counted or estimated. This paper has shown that trait individuation is very much an open and non-trivial problem. Different, independently credible approaches to individuating traits can easily give different results on whether adaptationism comes out true or false. By implication, without further resolution on the trait individuation issue, adaptationism cannot be empirically evaluated as a general thesis—only as a thesis about specific, predefined traits (Orzack and Sober 1994).

The obvious solution for remedying this situation would be to work toward a framework of trait individuation that can make empirical sense of adaptationism as a general hypothesis. We have suggested that structuralist approaches are more promising for this objective. A different solution, however, would be to reinterpret adaptationism in a way that does not require any framework for trait individuation. For example, one could argue that adaptationism is not a claim about "most traits" or "any given trait," but is rather a non-propositional *stance*—i.e., a disposition to seek or assume adaptive explanations for biological phenomena. Recall the discussion above of three kinds of adaptationism, empirical, explanatory, and methodological. One solution is thus to reject empirical adaptationism while retaining explanatory and/or methodological adaptationism.

One reason not to abandon empirical adaptationism because of the challenges of trait individuation is that individuating and counting traits is necessary not only for evaluating empirical adaptationism, but also for other investigative roles such as measuring organismic complexity (McShea and Venit 2001; Orr 2000), weighting rival phylogenetic hypotheses (Winther 2009), and even understanding basic biological concepts like pleiotropy (Wagner and Zhang 2011). The dependence of adaptationism on trait individuation is therefore not a conceptual idiosyncrasy, but points to a deeper, more general unresolved theoretical problem with ramifying influences on biological investigation.

Acknowledgements. The authors wish to thank Alejandro Gordillo García, Andra Meneganzin, and the audience at the PSA 2022 meeting for helpful comments. This work was funded by the Research Foundation – Flanders (FWO) (Grant Nos. 12W1822N and G070122N).

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