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Constraints and Spandrels in Gould's *Structure of Evolutionary Theory*

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Abstract. Gould's *Structure of Evolutionary Theory* argues that Darwinism has undergone significant revision. Although Gould succeeds in showing that hierarchical approaches have expanded Darwinism, his critique of adaptationism is less successful. Gould claims that the ubiquity of developmental constraints and spandrels has forced biologists to soften their commitment to adaptationism. I argue that Gould overstates his conclusion; his principal claims are compatible with at least some versions of adaptationism. Despite this weakness, Gould's discussion of adaptationism – particularly his discussions of the exaptive pool and cross-level spandrels – should provoke new work in evolutionary theory and the philosophy of biology.

Key words: adaptationism, constraint, evolvability, Gould

1. Introduction

For 30 years, Steven Jay Gould's eloquent prose has challenged evolutionary biologists, stimulated philosophers of biology, and enlightened the general public. Out of his early work on punctuated equilibrium grew a series of essays exploring the importance of hierarchy and the possibility of species selection (e.g., Vrba and Gould 1986). In the late 70s, Gould criticized adaptationism (Gould and Lewontin 1979) and challenged us to pay greater attention to developmental biology (1977). Throughout the 80s and 90s, Gould developed these themes and added new ones: He explored the relationship between science and religion (1999), argued that the history of life is strongly shaped by contingencies (1989), drew attention to the problem of disparity, and argued that disparity may have actually decreased since the Cambrian (1989, 1991). All the while, he enlightened lay readers with a steady stream of meditations on the history and contemporary state of biology. *The Structure of Evolutionary Theory* weaves together many of the themes of his previous work to leave us with a final and magisterial statement of Gould's perspective – an eloquent tribute to the "grandeur" of his view of life.

Gould's work has been with me from my very first course in evolutionary biology to the present. I will write in the present tense to recognize that his ideas are very much with us. Rather than emphasizing the hierarchical aspects of his theory (with which I agree), I will critically examine his claim that the ubiquity of constraints and spandrels undermines adaptationism. Though his critique of adaptationism does not fully succeed, Gould's emphasis on the problem of morphospace occupation, the exaptive pool, and cross-level spandrels should spur new work in evolutionary biology and the philosophy of biology.

2. A short summary of a long book

The Structure of Evolutionary Theory offers a new analysis of the structure of "Darwinism" and, based on this analysis, argues that Darwinism has undergone significant revision and expansion. Gould uses an architectural metaphor drawn from Darwin's correspondence to make this point more vivid. Darwin speculated that the "framework" of his theory would stand. Falconer replied by suggesting that Darwin had "laid the foundations" for a correct theory. The difference is subtle but important. Consider the fact that the foundations of many European cathedrals were laid centuries before the cathedrals were completed. The finished cathedrals often differed from the designs envisioned by those who laid the foundations. Thus, "laying the foundations" does not fix the "framework" of the building: many different structures can be built on the same foundation. So, too, with theories. Gould suggests that building upon the foundation laid by Darwin, evolutionary biologists have constructed a theory which differs in important ways from Darwin's account.

To make this thesis more precise, Gould argues that "Darwinism" involves four essential theses. The "core" of the theory is the claim that natural selection is a "true cause" of evolutionary change. Darwin supplemented the core with three further claims. Taken together, these auxiliaries guarantee the centrality of natural selection within evolutionary theory. The first claim ("agency") is that natural selection works primarily at the organismic level. The second claim ("efficacy") holds that natural selection explains the origin of all major evolutionary novelties. Finally, Darwin held that microevolutionary causes have sufficient "scope" to explain all macroevolutionary phenomena. Gould claims that this analysis accurately depicts the structure of Darwin's theory. Furthermore, questions about agency, efficacy, and scope have been primary foci of evolutionary debate for 150 years. This structure is implicit in Mayr's encapsulation of the synthetic theory: "all evolution is due to the accumulation of small genetic changes, guided by natural selection, and that transpecific evolution is nothing but an extrapolation and magnification of the events that take place within populations and species" (1963: 586). Gould describes these auxiliaries as "Darwin's tripod" because they support the "core" and keep natural selection at the center of the theory. (Alternatively we can view the core as the root of a tree with the three auxiliary claims being the principal branches.) Gould claims that these four theses constitute the "essence" of Darwinism. Even though no essential element has been completely rejected, the three supporting claims have been extensively revised: "I argue, as the major thesis of this book, that modern debates have developed important and coherent auxiliary critiques on all three branches of essential Darwinian logic, and that these debates may lead to a fundamentally revised evolutionary theory with a retained Darwinian core" (p. 61).

How have the three legs of the tripod been challenged? From 1859 to roughly 1920, critics attempted to completely reject one or more legs of the tripod. The historical portion of the book documents these challenges and argues that none succeeded (Chapters 2–7). Critics writing in the second half of the 20th century opt for a different approach: working from *within* Darwinism, they have reformulated the three legs of the tripod. The three "branches of Darwinian logic" persist, but in such an altered form that we must conclude that the theory has changed in fundamental ways. The thesis of "agency" was challenged by the hierarchical theory of selection (Chapter 8). The thesis of efficacy was revised to recognize the importance of developmental, historical, and structural constraints (Chapters 10–11). Finally, Gould argues that extrapolationism fails because mass extinctions prevent us from smoothly extrapolating the dynamics of evolution from short to long time scales (Chapter 12). Gould bolsters this familiar critique with a new argument: "evolvability" is a crucial aspect of evolution that cannot be understood in microevolutionary terms. The second argument merits a closer look because it illustrates how Gould's themes dovetail to form cohesive and revised Darwinism.

Gould argues that an adequate theory of evolution must recognize the causal role played by evolvability (i.e., a lineage's "flexibility" or ability to respond to changing conditions). Explaining differences in evolvability, however, requires attending to factors other than selection at the level of organisms and hence requires us to abandon both efficacy and agency. Because selection is not forward-looking and cannot favor attributes that will help future organisms, selection is an unlikely candidate to explain evolvability. Gould suggests we focus, instead, on the "exaptive pool" – the set of resources which can be coopted for future (adaptive) evolution.

While adaptations certainly form *part* of this pool, non-adaptations (such as spandrels) and developmental constraints provide important resources that enhance evolvability. Since spandrels and constraints play crucial roles in the origin of novel traits, we must reject stronger versions of efficacy (e.g., that selection alone is sufficient to explain the origin of all major novelties). Furthermore, since evolvability is a property of *lineages* (rather than organisms), a theory of evolvability must be hierarchical: we must consider the possibility that selection is acting at multiple levels. (One particularly interesting and novel suggestion emerges when Gould puts spandrels in a hierarchical context: he suggests that we can have "cross-level" spandrels. More on this below.) In sum, Gould argues although Darwin's "foundation" is intact, the legs of the tripod have been substantially revised. We can see the extent of the changes in our thinking about evolvability:

1. Differences in evolvability are crucial to explaining patterns of macroevolution.
2. To explain differences in evolvability, we must (a) adopt a hierarchical perspective, and (b) recognize developmental constraints and spandrels as parts of the exaptive pool.
3. Therefore, we cannot explain macroevolution by extrapolating microevolutionary explanations (in which selection acts at the level of organisms).

Gould's critiques of "agency" (2a) and efficacy (2b) come together to challenge the claim of scope. Thus, Gould's reflections on evolvability bear out his claim that Darwinism has undergone a significant revision.

3. Hierarchy and extrapolationism: General observations

Gould claims to have isolated the "essence" of Darwinism. Like David Hull (1988), I am skeptical about such claims and prefer to think of theories and research programs as forming lineages that are capable of indefinite modification. Setting this worry aside, Gould's survey of the history of evolutionary biology shows that the legs of the "tripod" have been central axes of debate. Thus, the tripod is a useful tool for organizing the history of evolutionary theory. More to the point, have the theses of agency, efficacy, and scope have been substantially revised? I will argue that the central thesis of *Structure of Evolutionary Theory* is well-supported by the weight of the arguments contained in this book (pardon the pun). This section dogmatically sets out the reasons for this positive assessment. In short, the hierarchical expansion of evolutionary theory is an important conceptual development. Furthermore, hierarchical approaches undermine traditional statements of extrapolationism. Thus, two legs of the tripod (agency and scope) have been modified in significant ways. Sections 4 and 5 qualify this positive assessment, arguing that Gould's challenge to efficacy is less successful.

Chapter 8 explains how evolutionary theory has been expanded to address selection at a number of levels, ranging from genes to organisms, demes, and species. Gould endorses the "interactor approach" of Hull and Brandon: selection occurs at a level when the differential interaction of entities at that level (with one another and with their environment) influences their reproductive success. Gould articulates this familiar position well, emphasizing the importance of species selection. Since the late 80s, he has abandoned Vrba's more restrictive conception of species selection in favor of Lloyd's "emergent fitness" approach (e.g., Lloyd and Gould 1993). Gould also includes a detailed account of the concept of "individuality," arguing that because different kinds of individuals occur at different hierarchical levels, selection behaves differently at different levels. Given that Gould's view on hierarchy and species selection nearly coincides with my own (Grantham 1995, 2001, 2002), I wholeheartedly endorse Gould's position, including the claim that the development of a hierarchical perspective was a significant expansion of Darwinism.

In Chapter 12, Gould argues that mass extinctions undermine extrapolationism. Like Sterelny and Griffiths (1999), I do not think the occurrence of mass extinctions provides compelling evidence against extrapolationism. Even though the observed patterns of evolution may change during mass extinctions, these patterns can (in general) be explained by ordinary evolutionary processes acting in a highly unusual environment. Hence mass extinctions do not require any fundamental change in evolutionary *theory*. Even though the argument from mass extinctions fails, Gould's evolvability argument (discussed above) undercuts extrapolationism. Insofar as one accepts the reality of irreducible higher-level processes (such as species selection), macroevolution cannot be reduced to microevolution (i.e., evolutionary processes occurring among organisms within a population).[1] Thus, the failure of extrapolationism is, at base, a consequence of the hierarchical expansion of evolutionary theory. Gould recognizes this point when he notes that "the *biological* [as opposed to geological] aspects of the critique for the third theme of extrapolationism lie mainly within expansions and revisions of Darwinism on the first two legs" (p. 1313).

While Gould's revisions of "agency" and "scope" appear to be sound, his extensive discussion of constraints and spandrels is harder to assess. It is to these topics that I now turn.

4. Constraints, efficacy, and adaptationism

Chapters 10 and 11 argue that the thesis of "efficacy" has been significantly revised, but not completely abandoned. The arguments of these chapters are hard to pin down – in part because the target of criticism (i.e., "efficacy") is slippery. For example, although one of the targets is "adaptationism," Gould never explains which versions of "adaptationism" he would reject and which are acceptable. In what follows, I attempt to reconstruct and assess Gould's arguments against "efficacy." Gould is correct to claim that adaptationism has softened since the high point of the "hardening" of the synthesis (Rose and Lauder 1996; Pigliucci and Kaplan 2000) but in other respects Gould's arguments are less than satisfying. In particular, Gould's critique of efficacy appears to be compatible with some influential adaptationist theses. This section asks how developmental constraints bear on the theses of efficacy and adaptationism. Section 5 examines Gould's claim that the ubiquity of spandrels undermines adaptationism.

Several different conceptions of "efficacy" lurk in these chapters. Efficacy is initially defined as the claim that natural selection is not merely a negative force, but is capable of generating novel traits (p. 14). Later, "efficacy" is defined as the view that selection is "virtually the sole creative force in evolutionary change" (p. 1313). In Chapter 10, where the target is supposed to be efficacy, Gould argues that we cannot explain the distribution of species in morphospace in purely selectionist terms. Trying to explain the distribution of forms in morphospace "poses a different kind of challenge to our usual views about the power and range of natural selction in the explanation of functional design" (p. 1056). In Chapter 11, Gould claims that a high frequency of spandrels "would introduce a significant non-adaptationist element into evolutionary theory" – without ever clarifying the precise form of the adaptationism he rejects (p. 1286). At least four distinct statements of "efficacy" can be found in these passages:

E1: natural selection is capable of generating some evolutionary novelties.
E2: natural selection is a necessary part of the correct explanation of all major evolutionary novelties.
E3: natural selection is sufficient to explain all major evolutionary novelties.
E4: natural selection is sufficient to explain the distribution of species in morphospace.

Roughly, Gould accepts E1 and E2 but rejects E3 and E4. All of these statements emphasize the explanation of "novelties"[2] because, for Gould, the issue of efficacy hangs on whether natural selection is "the only potent source of creative evolutionary change" (p. 60).

Gould challenges the thesis of efficacy in two ways. Chapter 10 maintains that developmental constraints influence the direction of evolution and the occupation of morphospace. Chapter 11 claims that the because that non-adaptations (such as spandrels) are a crucial component of the "exaptive pool" – the set of resources which allow species to evolve in new directions – a full account of the emergence of novelties must recognize the role played by structures that are, in first appearance, not adaptations. These chapters maintain that evolutionary biologists have tempered their claims about the power of natural selection and should reject E3 and E4. Gould's intent is to integrate the externalist/functionalist perspective of Darwinism with internalism/structuralism to yield a richer and more successful Darwinism.

Gould suggests that evolutionary biologists have failed to recognize the *positive* aspect of constraints. Whereas constraints are often viewed as limits to the power of natural selection (negative constraints), they can also be seen as "channels" which facilitate evolution in particular directions (positive constraints). Gould invokes an analogy between developmental canalization and the evolution of species. Just as the genome can "channel" development toward certain end-points (making certain adult phenotypes more likely), a genome can make certain evolutionary outcomes more likely. A simple illustration of this idea comes from studies of allometry. Because beak length and depth are correlated, selection for longer beaks tends to increase beak depth. Thus, there is an "evolutionary channel" which facilitates the evolution of certain morphologies (deeper and longer beaks, less deep and shorter beaks), while making deeper and shorter beaks harder to achieve (Grant 1986; see Pigliucci and Kaplan 2000 for additional examples). As this illustration suggests, "positive" constraints are not categorically different from negative constraints. Rather, channels are implicitly defined by combinations of traits that are harder to attain (negative constraints).

According to Gould, recent work in evolutionary developmental genetics demonstrates that positive constraints are a powerful factor controlling the paths of evolution and the occupation of morphospace. Even when natural selection impels a lineage along a trajectory, the trajectory is accessible because of properties of the underlying genetic and developmental architecture:

> The pool cue of natural selection may always do the actual pushing, but if internal channels – set by history, and grafted into the genetic and developmental architecture of current organisms – designate a limited set of possible pathways as conduits for selection's pushing, then these internal constraints can surely claim equal weight with natural selection in any full account of the causes of any particular evolutionary change (pp. 1173–1174).

If positive constraints are a crucial part of the causal story – if a full explanation of the origin of major novelties often requires appeal to aspects of the developmental architecture – then E3 is false.

The phenomenon of parallelism illustrates the importance of positive constraints. According to Gould, parallelism involves cases in which two lineages independently follow very similar trajectories of morphological evolution *because they share a homologous "generating structure."* The evolution of maxillipeds provides a nice illustration. Typical crustaceans have two distinct kinds of appendages: Gnathal segments have specialized feeding appendages (maxillae) while thoracic segments have appendages specialized for locomotion. However, a number of species also possess appendages of intermediate appearance (maxillipeds) that are used for food handling. The interesting point is this: although maxillipeds have evolved independently in a number of distinct lineages, the genetic mechanism is the same in every case examined so far. The Ubx and abdA genes – genes that are typically expressed in thoracic segments – are suppressed whenever thoracic segments produce maxillipeds. Thus, Gould claims that the prevalent pattern of gene expression is a homologous developmental/genetic resource that, by its structure, facilitates the evolution of maxillipeds. Similarly, Gould argues that the independent evolution of eyes different taxonomic groups – a phenomenon traditionally conceptualized as convergence – is in fact a case of parallel evolution because of the presence of homologous *Pax* genes that appear to have the same function in cephalopods, vertebrates, and insects. Even though the latter case is splashy, Gould suggests that the mundane but more numerous cases (such as maxillipeds) will provide the most persuasive evidence for the role of positive constraints.

If, as Gould claims, positive constraints and parallelism are common, this fact would undermine the thesis of efficacy. Because constraints facilitate similar trajectories in independent lineages, then internal factors (developmental constraints) must be added to get a complete account of the parallel evolution of novelties, thereby undermining E3 and E4. How do these claims relate to recent discussions of adaptationism? Let me briefly outline what I take to be the implications of Gould's argument.

Peter Godfrey Smith (2001) distinguishes three different conceptions of adaptationism, two of which are particularly relevant for our purposes. *Empirical* adaptationism asserts that natural selection is (empirically) the most important cause of evolution. This broad conception can be articulated in various ways (e.g., "most traits are shaped by natural selection" or "most traits are optimal.") In contrast, *explanatory* adaptationism holds that natural selection is the most important force because explaining adaptation is the central problem of evolutionary biology and natural selection is the only explanation for adaptation. On the face of it, Gould seems to be challenging empirical adaptationism but this appearance may be deceptive in two ways. First, Gould's critique of efficacy is compatible with some important forms of empirical adaptationism. Second, Gould implicitly challenges explanatory adaptationism.

Gould's critique of efficacy is compatible with some definitions of empirical adaptationism. For example, Reeve and Sherman (1993) argue that the theory of natural selection makes the following empirically testable prediction, a generalization we can roughly equate with adaptationism: "among a specific set of alternatives, the most adapted phenotype will be the one that predominates" (p. 14). Similarly, Sober defines adaptationism as the thesis that "Natural selection has been the only important cause of most of the phenotypic traits found in most species" (1996: 72). I regard these approaches as similar because both (implicitly) rely on optimality models: adaptationism is upheld if optimality models make accurate predictions about most traits. This "optimality" approach is compatible with Gould's claim that developmental architectures limit the range of available phenotypes and channel evolution toward specific outcomes. Adaptationism asserts that, given a set of actual variants, the best adapted will come to predominate (at least most of the time). Even if developmental constraints were extremely common or extremely powerful, the best adapted *actual* variant might generally predominate. Thus, even though developmental constraints limit the range of actual variation, they don't undermine the adaptationist claim that selection will bring the best adapted *actual* variant to predominance (Sober 1996). The fact that Gould's argument is compatible with substantive forms of adaptationism suggests that his argument is not entirely successful.

On the other hand, one might argue that the compatibility between optimality approach and developmental constraints reveals a weakness in this way of defining adaptationism. Imagine a continuum of possible worlds. At one extreme, development only weakly constraints selection (e.g., trait covariances generated by the mechanisms of development are easily modified by selection). At the other extreme, developmental constraints permanently block access to large regions of morphospace. Moving toward the "strong constraint" end of the spectrum should, at some point, undermine adaptationism (the view that natural selection is the most important force shaping phenotypic evolution). Furthermore, since the question of where our world fits along this continuum is an empirical question, discovering that development strongly constrains evolution should undermine *empirical* adaptationism. An adequate conception of "empirical adaptationism" ought to recognize that empirical data on the strength of developmental constraints is relevant to the assessment of adaptationism. Curiously, advocates of the "optimality" approach hold that empirical evidence about the strength of developmental constraint is *not* relevant to assessing adaptationism. The fact that developmental constraints are compatible with the optimality approach reveals a weakness – either in Gould's argument or in this conception of adaptationism.

Proponents of the optimality approach might try sidestep this worry by suggesting that Gould's real target is explanatory adaptationism, not empirical adaptationism. Gould claims that explaining the inhomogeneous occupation of morphospace is a central problem for evolutionary biology. Assuming that factors other than adaptation are crucial for explaining this distribution, then this problem would be both distinct from the problem of adaptation and central to evolutionary biology. Thus, Gould does reject explanatory adaptationism. However, interpreting Gould as rejecting *only* explanatory adaptationism would mis-represent his position. Gould argues (whether correctly or incorrectly) that there is good empirical evidence for the potency of developmental constraints. He claims that this body of empirical evidence provides a compelling reason to reject E3 and E4. Thus, it would be a mistake to read Gould as criticizing *only* explanatory adaptationism.

I suspect that the optimality approach does not adequately capture some dimensions of empirical adaptationism. The following claim seems reasonable: an empirical demonstration that developmental constraints powerfully shape the distribution of species in morphospace should lead us to weaken our commitment to adaptationism. Yet this intuition is lost in the optimality approach. Despite this weakness, the optimality approach offers an important insight: Selection operates on a set of actual variants, whereas constraints act to limit which phenotypes appear in the pool of actual variants. Because these two "forces" operate in different "spheres," direct comparisons of the strength of selection and developmental constraint are at least very difficult, perhaps conceptually confused. I hope that Gould's book will push philosophers and biologists to develop an account of adaptationism which recognizes that developmental constraints are relevant to the assessment of empirical adaptationism without sacrificing the conceptual clarity gained by the optimality approach.

5. Cross-level spandrels

In Chapter 11, Gould turns his attention from developmental constraints to spandrels. According to Gould, spandrels are the "automatic and non-adaptive sequalae or side consequences of changes in other features, or at other levels" (p. 1280). In the classic architectural example, supporting a dome with four arches necessarily creates triangular spaces ("spandrels") in the corners, where two arches meet at right angles. In biology, similar "structural" side effects can occur. For instance, if a snail shell grows by coiling a tube around an axis, then the shell must contain a cylinder (the "umbilicus") along this axis. The umbilicus is a spandrel – a necessary consequence or "side effect" of the primary structure (the coiled shell). Although spandrels originate as non-adaptations, they can be "exapted" to perform functions. For example, the umbilicus was originally a non-adaptative side effect but was subsequently shaped by selection to function as a brood chamber in some snails.

In traditional spandrels, the evolution of one organismic trait (the coiled shell) necessarily creates an architectural side effect *at the same level* (the umbilicus). If one adopts a hierarchical framework, however, it becomes possible to consider *cross-level* effects. Such cross-level effects are, for Gould, a special kind of spandrel: "The key property of spandrels lies in their automatically consequential character as things necessarily enjoined by other changes. Cross-level effects fit this definition in all ways" (p. 1288). Any trait "arising at one level and injected into another must enter its new domain adventitiously and without reference to the norms and needs of its adopted 'home' " (p. 1288). Whenever a change at one level produces immediate structural changes at adjoining levels, then these effects are regarded as cross-level spandrels. Consider, for example, a gene that is duplicated within the genome. Regardless of how this gene duplication occurs, it is not (at first appearance) an adaptation at the level of the organism. It originates as an effect of lower-level processes and becomes part of the organism-level exaptive pool. Viewed at the level of organisms, this gene is a spandrel.

Although spandrels can be co-opted to perform functions ("exapted"), Gould argues that spandrels present a deeper challenge to Darwinism than exaptations *per se*. In ordinary cases of exaptation, a trait which has been shaped by natural selection to serve one purpose is co-opted to perform a new service. Exaptation does not challenge Darwinian functionalism because "quirky functional shifts" are still guided by selection. Consider a standard case of exaptation – the evolution of feathers. According to one common hypothesis, feathers originate for thermoregulation and are subsequently co-opted for a different purpose (flight). Gould maintains that cases such as these do not threaten adaptationism because the trait remains "adaptive throughout" (p. 1247). By contrast, spandrels

> emplace a genuinely nonadaptationist component into the heart of evolutionary explanation – for if many features originate as nonadaptations, and if nonadaptations . . . [occupy] a substantial percentage of the exaptive pool, then evolutionary explanations for both the origin of novelties, and for the differential capacity of lineages to enjoy future phyletic expansion

> and success, will require a revised and expanded version of Darwinism (p. 1286).

Gould argues that spandrels represent a particularly potent challenge because they are ubiquitous. His judgement about the frequency of spandrels is driven largely by his decision to expand the category to include "cross-level" spandrels. Including cross-level effects makes spandrels more common and should, according to Gould, lead us to reject some forms of empirical adaptationism. Cross-level spandrels are "the key addition that elevates spandrels to a position of central importance in evolutionary theory" (p. 1280).

The concept of cross-level spandrels should stimulate new work in evolutionary biology but I remain uncertain about the extent to which it challenges adaptationism. I suspect that many cross-level effects do not challenge the core commitments of adaptationism. Here is my worry. Gould argues that "quirky functional shifts" require us to become more sophisticated adaptationists – but that we can still remain adaptationists. If so, then sophisticated adaptationists should (by parity of reasoning) be able to handle cross-level spandrels. To cite a well-known example, suppose that natural selection drives a shift from planktotrophic to direct development in a mollusc species. Because direct development decreases larval dispersal, organismic evolution has immediate impact on gene flow among populations (a species-level trait). Suppose further that by decreasing gene flow, direct development elevates speciation rate and therefore becomes more common through species selection. In this scenario, the changes in gene flow count as a spandrel – this change is "injected" at the species level from below and was not introduced by selection *at that level*. It is unclear, however, why this scenario should be thought to challenge adaptationism. The organismic trait (direct development) is an adaptation. This adaptive process has an effect (on gene flow) which initiates another selection process at the species level. The process appears to be driven by selection (albeit at different hierarchical levels).

My hypothetical scenario shows that cross level spandrels are compatible with at least some of the core commitments of adaptationism. As we've just seen, selection can be the primary engine of change – first driving evolution at the lower level and then co-opting the higher-level effects of this change. The only "moment" of non-adaptationist reasoning is the original appearance of the new population structure. Adaptationists will be inclined to downplay the importance of this moment of non-adaptation. First, adaptationists are principally concerned with *organism-level* traits; Gould's claim that some higher-level traits are not adaptations does not threaten the claim that most organismic traits are adaptations. Notice, however, that this argument is not, by itself, an adequate reply. For just as organism-level changes can produce species-level effects, genic changes produce organismic effects. Thus, Gould would argue that many organism-level traits are not, in first appearance, adaptations. They appear as "passive effects" of lower-level processes and are only later co-opted to become organism-level aptations. (Recent work on the duplication of *Hox* genes makes this an intriguing hypothesis.) At this point, adaptationists are likely to avail themselves of a second reply: Why be so concerned with first appearance? An adaptationist who holds that most phenotypic traits are currently well-adapted won't be concerned by the fact that some traits were, for (brief?) periods, not adaptations.

6. Conclusion

Has the Darwinism "framework" been substantially revised? The hierarchical expansion of Darwinism was a significant change. Furthermore, its acceptance forced us to modify traditional views of extrapolationism (i.e., by undermining the claim that macroevolution is reducible to microevolution). It is harder to judge Gould's success regarding "efficacy." On the one hand, Gould's claim that evolutionary biology is less adaptationist than it was at the peak of the synthesis is correct. Contemporary theorists have a greater awareness of and concern for alternative (non-adaptationist) explanations. In addition, Gould's emphasis on the "occupation of morphospace" challenges explanatory adaptationism. Finally, two of Gould's conceptual innovations (the exaptive pool and cross-level spandrels) provide important resources for addressing central evolutionary problems (such as evolvability). On the other hand, section 4 argued that developmental constraints are compatible with some versions of empirical adaptationism. The message of section 5 is similar. Gould argues that the high frequency of spandrels undermines adaptationism. He establishes this high frequency by including cross-level effects within the category of spandrels. However, it is likely that at least some cross-level spandrels are compatible with the core commitments of adaptationism. My own judgement is that Gould's defense of the hierarchical approach to evolutionary theory is more successful than his attack on adaptationism. Although the argument against efficacy is not fully successful, Gould's discussion of constraints and spandrels provides several new concepts and arguments which should engage philosophers of biology.

In Chapter 10, Gould offers a "symphony" of four movements – a meditation on the role of historical constraints in evolution. Although Gould's symphony has classical *form*, the book as a whole is more like Mahler than Mozart. Many will ignore the book for this reason. But those who do so will miss something quite special: a fully articulated vision of the history and current status of evolutionary thought, written by one of the most influential biologists of the 20th century. The only book I know of with comparable scope is Mayr's *Growth of Biological Thought*. Those with "classical" taste (i.e., those who find the sheer length of Gould's book daunting) can easily read specific chapters without reading the whole. Those with more "romantic" taste will find that investing some time in this book is worthwhile.

Notes

[1] Even though micro-reduction fails (because we cannot reduce higher-level selection to lower-level selection), a hierarchically expanded evolutionary theory can probably explain the domain of macroevolutionary phenomena. In other words, while micro-reduction fails, the prospects for a "subsumptive reduction" (where the theory of microevolution is subsumed within the hierarchically expanded theory) are quite good.

[2] This is true even of E4, which does not explicitly mention novelties, because Gould is interested in the occupation of (or failure to occupy) new regions of morphospace, which correspond (at least roughly) to major evolutionary novelties.

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