From Developmental Constraint to Evolvability

How Concepts Figure in Explanation and Disciplinary Identity

Ingo Brigandt

Department of Philosophy, University of Alberta
2-40 Assiniboia Hall, Edmonton, AB T6G2E7, Canada
brigandt@ualberta.ca

Abstract The concept of developmental constraint was at the heart of developmental approaches to evolution of the 1980s. While this idea was widely used to criticize neo-Darwinian evolutionary theory, critique does not yield an alternative framework that offers evolutionary explanations. In current Evo-devo the concept of constraint is of minor importance, whereas notions as evolvability are at the center of attention. The latter clearly defines an explanatory agenda for evolutionary research, so that one could view the historical shift from 'developmental constraint' towards 'evolvability' as the move from a concept that is a mere tool of criticism to a concept that establishes a positive explanatory project. However, by taking a look at how the concept of constraint was employed in the 1980s, I argue that developmental constraint was not just seen as restricting possibilities ('constraining'), but also as facilitating morphological change in several ways. Accounting for macroevolutionary transformation and the origin of novel form was an aim of these developmental approaches to evolution. Thus, the concept of developmental constraint was part of a positive explanatory agenda long before the advent of Evo-devo as a genuine scientific discipline. In the 1980s, despite the lack of a clear disciplinary identity, this concept coordinated research among paleontologists, morphologists, and developmentally inclined evolutionary biologists. I discuss the different functions that scientific concepts can have, highlighting that instead of classifying or explaining natural phenomena, concepts such as 'developmental constraint' and 'evolvability' are more important in setting explanatory agendas so as to provide intellectual coherence to scientific approaches. The essay concludes with a puzzle about how to conceptually distinguish evolvability and selection.

This essay investigates historical and philosophical questions about the concepts of developmental constraint and evolvability. The concept of constraint was cen-

tral for developmental approaches to evolution in the 1980s but faded into the background throughout the 1990s, seemingly replaced by more important notions, such as evolvability (Section 1). The historical part of my discussion presents two diverging accounts as to why the concept of developmental constraint moved into the background while the concept of evolvability became more salient. On the first account, the concept of constraint was used to criticize adaptationism but did not underwrite evolutionary explanations, and thus was replaced by the concept of evolvability, which in contrast provides a positive explanatory project (Section 2). On the second historical account, the concept of constraint has always been part of a positive explanatory project in evolutionary research and thus is continuous with the notion of evolvability (Section 3). There is some truth to both of these perspectives, yet the second one turns out to be historically more adequate and intellectually more revealing than the first. The two accounts offer different portrayals of how the concept of constraint was understood and employed, so that my historical discussion sheds light on the roles and meaning of the concept of developmental constraint.

Section 4 turns to philosophical questions about the concepts of constraint and evolvability. Here the epistemological project is to understand the different intellectual purposes for which scientific concepts are used. Of course the concept of evolvability nowadays figures in scientific explanations, but I argue that other biological concepts (e.g., modularity) are more crucial for explaining evolvability. Rather than providing explanations, the concept of evolvability more effectively fulfills a second, distinct intellectual purpose—setting an explanatory agenda so as to provide intellectual identity to a scientific discipline. One of the central aims of evolutionary developmental biology (Evo-devo) is to account for evolvability, and thus the concept of evolvability contributes to its disciplinary identity. In a similar fashion, the concept of developmental constraint provided intellectual coherence to developmental approaches to evolution in the 1980s. In contrast to prevailing assumptions, the agenda-setting function of a certain concept can be as or more salient than the explanatory capacity of this concept, which suggests that more philosophical attention should be devoted to the diverse functions of scientific concepts. I conclude my discussion with remarks about the relationship between evolvability and natural selection (Section 5).

1 Historical Background

During the 19th century, evolution and development were generally conceived of as closely related phenomena (Bowler 1988). Haeckel's biogenetic law viewed ontogeny and phylogeny as parallel patterns, and postulated a mechanistic link between the two processes. Even those who were less convinced of recapitulationism studied development to understand evolutionary change (Hall 2000). However, this was to change substantially. With the advent of Mendelian genetics, genetics

and embryology became separate fields, severing the previously related notions of heredity and development. While genetics and evolutionary theory formed the basis of the Modern Synthesis, embryology and developmental biology were largely irrelevant to evolutionary biology throughout most of the 20th century (Amundson 2005). Apart from a few isolated instances, such as the notion of heterochrony (de Beer 1930; Gould 1977; Brigandt 2006), only in the last three decades has the possibility of a new (or renewed) link between evolution and development come into view (Bonner 1982). Evo-devo is typically construed as an (emerging) synthesis that actualizes this possibility.

In the 1980s, one focal point for demonstrating how developmental biology mattered to evolutionary biology was the concept of developmental constraint (Seilacher 1974; Gould and Lewontin 1979; Gould 1980a, 1980b, 1989; Alberch 1980, 1982, 1983; Oster and Alberch 1982; Alberch and Gale 1985; Maynard Smith et al. 1985). This was clearly on display in the discussions at the 1981 Dahlem Conference 'Evolution and Development' (Bonner 1982). The question as to how cellular, developmental, and morphological properties restrict possible evolutionary trajectories was addressed directly by three different discussion groups: 'The cellular basis of morphogenetic change' (Gerhart et al. 1982), 'Adaptive aspects of development' (Horn et al. 1982), and 'The role of development in macroevolutionary change' (Maderson et al. 1982). Additionally, it served as the central theme in the individual essay 'Developmental constraints in evolutionary processes' (Alberch 1982).

Despite its historical centrality, the concept of constraint increasingly moved to the background of Evo-devo's discourse throughout the 1990s. Although it remains relevant for contemporary biologists (Wagner et al. 2000; Schwenk and Wagner 2003), constraint appears secondary to other concepts now prominent at the intersection of evolution and development, such as evolutionary novelty (Müller and Wagner 1991, 2003; Müller and Newman 2005) and evolvability (Kirschner and Gerhart 1998; Gerhart and Kirschner 2003; Hendrikse et al. 2007). How did this transition occur, and why?

2 'Constraint' as a Critique of a Selection-Centered Approach

One reason for the centrality of the concept of constraint to developmental approaches to evolution in the 1980s is as part of a critique of a neo-Darwinian explanatory framework based on natural selection; constraint is thereby construed in opposition to selection. Even though this concept was introduced, endorsed, and actively used by paleontologists, morphologists, and developmentally oriented biologists investigating evolution, the term 'developmental constraint' became widely known within evolutionary biology largely due to Stephen J. Gould and Richard Lewontin's (1979) vehement critique of what they called the 'adaptationist program.' While offering several different criticisms of

adaptationism, the existence of developmental constraints was their central argument.[1] 'Spandrels' are non-adaptive outcomes of morphological evolution arising not from selection but from architectural-developmental constraints (Gould 1980a, 1980b, 1989). In addition to the occurrence of non-adaptive traits, other authors in this period addressed the fact that constraints make the production of certain phenotypes impossible (Raup 1967; Alberch 1980, 1983; Alberch and Gale 1985). Natural selection is irrelevant if a variant cannot be generated due to developmental constraints, even if it would have been strongly favored by selection had it arisen. If there are large ranges of developmentally impossible phenotypes in morphological space, then the distribution of form observed across taxa is not so much to be explained by selection but the action of constraints (Alberch 1982).

In addition to grounding a critique of a selection-centered approach, the concept of developmental constraint yielded an indirect critique of the neo-Darwinian framework by way of its commitment to a phyletic gradualism. It primarily was Gould who advertised punctuated equilibrium as an 'alternative paradigm' (Eldredge and Gould 1972), while the punctuated equilibrium model was originally introduced by Niles Eldredge (1971) in a form largely compatible with neo-Darwinism (using allopatric speciation as the explanation for rapid change). Still, the punctuated equilibrium model was generally construed as contrary to neo-Darwinian phyletic gradualism, and this model was discussed approvingly by proponents of developmental approaches to evolution, including the Dahlem 1981 conference participants (Maderson et al. 1982). Punctuated equilibrium was one of several macroevolutionary phenomena taken to be significant and related to the concept of constraint because the main explanation for the absence of net morphological change during periods of stasis was attributed to developmental constraints (Maderson et al. 1982). Thus, in addition to the concept of constraint being opposed to adaptationism, it supported the theory of punctuated equilibrium by accounting for phyletic stasis, resulting in a further (but indirect) critique of neo-Darwinism (Gould 1980b).

Developmental constraints frequently have been conceived in opposition to selection (Burd 2006; Pagel 2002; Schwenk 2002). In particular neo-Darwinists saw the idea of constraint as a direct challenge to their evolutionary framework, and reacted to the perceived opposition (Charlesworth et al. 1982, Reeve and Sherman 1993, Amundson 1994). A variety of counterarguments were given, some of which were quite dubious or even disingenuous. Charlesworth, Lande, and Slatkin (1982) claimed that "the concept of organism, including constraints of history, development and architecture, which Gould (1980) seeks to restore to evolutionary biology, has always been an integral part of the neo-Darwinian theory" (480), but this is in tension with their critique of macroevolutionary approaches based on de-

[1] "Ever since Gould and Lewontin (1979) raised the specter of nonadaptive architectural constraints in evolution, the invocation of developmental constraints for explaining why certain phenotypes occur has been popular among those skeptical of purely adaptationist approaches" (Reeve and Sherman 1993, 20; see also Schwenk and Wagner 2003).

velopmental constraints and their stated defense of neo-Darwinism—a theory in which "selection is regarded as the main guiding force of phenotypic evolution" (474). Despite maintaining that constraints were integral to neo-Darwinism, none of the population-genetic models used by Charlesworth et al. (1982) took the influence of developmental constraints into account effectively. Overall, the main reaction to the threat posed by the idea of developmental constraints was to acknowledge the existence of constraints but claim that their influence on the course of evolution was comparatively small and usually did not override the effects of selection. Developmental constraint and natural selection were viewed as two forces acting in opposite directions, with neo-Darwinists considering the latter as the stronger and more effective force.[2]

Although the concept of developmental constraint can be used to argue against adaptationism (and against any explanatory framework centered on natural selection), this is a limited epistemic role for the concept to play. Merely criticizing an approach and its putative explanations falls short of providing an alternative that explains evolutionary phenomena—and putting forward explanations is the main criterion of adequacy for any scientific approach. This can be illustrated vividly by intelligent design creationism. All that intelligent design proponents have to offer are arguments against evolutionary theory. These arguments may be vacuous and recycled versions of repeatedly debunked traditional creationist arguments, but the most blatant defect of intelligent design is that it does not offer any alternative theory that would explain biological phenomena (such as the structural commonalities and differences across species or their geographical distribution). An analogous point can be made about the concept of developmental constraint. No matter how good it is at exposing the problems of neo-Darwinian theory, only arguing against an explanatory framework does not yield a positive account that actually explains evolutionary phenomena.

On my first historical account, this limitation is one possible reason why the concept of constraint has largely faded in contrast to other concepts such as evolvability, which embody a positive explanatory project germane to evolutionary change. Evolvability is the ability of organisms to generate heritable and viable phenotypic variation, which forms the mechanistic basis of morphological change. Thus, an explanation of evolvability addresses an evolutionary phenomenon. While considerations about development are essential to an account of evolvability, unlike developmental constraint (as portrayed above), evolvability is not set in opposition to selection, but, in fact, operates on a *different dimension* than selection. In every generation, heritable phenotypic variation is first generated—the manifestation of evolvability—and then natural selection acts on the available variation. Selection presupposes the availability of phenotypic variation, and therefore evolvability, which means that an account of evolvability need not

[2] "[This empirical case] casts considerable doubt on the idea that developmental constraints restrict the power of selection to accumulate small changes in the phenotype" (Charlesworth et al. 1982, 477).

be in conflict with an evolutionary theory centered on natural selection; instead, a theory of evolvability *completes* evolutionary theory. Marc Kirschner and John Gerhart (2005) frame the issue in this fashion: "The Three Pillars of Darwin's Theory of Evolution [are] a theory of natural selection, a theory of heredity, and a theory about the generation of variation in the organism" (10). Darwin had an adequate account of how natural selection works. His theory of heredity (pangenesis, endorsing the inheritance of acquired characters) turned out to be false, but classical genetics filled this gap by offering an adequate account of heredity. Kirschner and Gerhart emphasize that the third 'pillar' is still missing—we are in need of a theory of how phenotypic variation is generated, i.e., an account of evolvability that completes evolutionary theory based on natural selection.

This first historical portrayal stressed how the concept of developmental constraint was construed as being in opposition to selection. The concept was primarily used to criticize adaptationism but it could not deliver evolutionary explanations. A primarily negative depiction of constraint goes some way toward illuminating why biologists came to shift away from 'developmental constraint' and focus on 'evolvability, setting aside a concept whose only function was critical for one that could be part of a positive explanatory agenda in evolutionary biology (and is not in conflict with the idea of selection). But there is more to the history of the concept of developmental constraint.

3 'Constraint' as an Explanatory Project in Evolution

In his justly famous analysis entitled "Two concepts of constraint," Ron Amundson (1994) demonstrated that constraints are not just limits on adaptation, which opens up the possibility that 'constraint' need not be in conflict with an evolutionary theory centered on selection. Amundson agreed that there is one construal of constraint, used especially by neo-Darwinists, which conceives of them as constraints on adaptation (constraint$_A$). If one's agenda is to explain *adaptation*, then a natural strategy to use is an optimality model. If a predicted optimal character state does not match the observed state, then the modeling assumptions may be wrong or the selectively optimal state cannot be reached due to constraints. Thus, constraint is conceived as restricting adaptation and resulting in suboptimal traits. This is the portrayal of constraint laid out in the previous section, which portrays constraint and selection as antagonistic forces.

Amundson pointed to a curious implication of this notion of constraint. The only way to infer constraints$_A$ is from the presence of suboptimal traits, which presupposes an optimality model. If the only reason for postulating constraints is a prior adaptation hypothesis, then there is no room for a concept of constraint outside of a selectionist framework. However, Amundson emphasized that developmental approaches to evolution introduced a concept of developmental constraint that was independent of a selectionist framework. This distinct conception was

constraint on form ($constraint_F$), which focused on the how the generation of morphological form is shaped by developmental processes. Thus far my historical discussion has dealt primarily with critiques of adaptationism and thus with $constraint_A$, but $constraint_F$ is the construal of constraint frequently used by those who introduced the concept of developmental constraint. This complicates the story about why biologists adopting a developmental approach to evolution shifted their focus away from 'constraint' toward other notions such as 'evolvability.' Most importantly, Amundson (1994) argued that whereas from the $constraint_A$ perspective developmental constraints were not operative for optimally adapted traits (so that no developmental considerations are of explanatory relevance), "Developmentalists would claim that their contributions are a proper part of the full explanation of even the most wonderfully adapted trait" (585). This points to a possible *positive explanatory role* for the concept of developmental constraint in the 1980s. If $constraint_F$ plays a role in the explanation of any trait ("even the most wonderfully adapted trait"), then developmental constraint might be the flipside of evolvability.

In my view, defended in more detail elsewhere (Brigandt 2007), evolvability and developmental constraint are identical phenomena, or at least two aspects of one phenomenon. Evolvability is the ability to generate viable and heritable phenotypic variation. This variation has a certain structure, where some variants are more likely to occur than others and changes in some characters tend to be correlated. An account of evolvability is meant to explain why in a given taxon (or for given characters) a certain probability distribution and covariation structure obtains with respect to phenotypic variation (Hendrikse et al. 2007). But developmental constraint—as already construed in the 1980s—is not only the impossibility of certain variants being produced, but any "bias on the production of variant phenotypes … caused by the structure, character, composition, or dynamics of the developmental system" (Maynard Smith et al. 1985, 266). Therefore, evolvability and constraints both pertain to the way in which heritable phenotypic variation is structured. The concept of evolvability may focus on positive biases (generation of viable phenotypes), whereas the concept of constraint often focuses on negative biases (restrictions on the regular production of some phenotypes), but they refer to different aspects of the same phenomenon.

In Section 2 I emphasized that evolvability is fully compatible with selection, as it operates on a different dimension: first phenotypic variation is generated due to evolvability, and then, second, selection acts on some of the available variation. The historical portrayal of 'constraint' in this previous section assumed that constraint was viewed as a force on the same dimension as but operating in opposition to selection. Although this is the case for the notion of $constraint_A$, it does not hold for a construal that conceptualizes constraint as the flipside of evolvability, such as $constraint_F$. $Constraint_F$ was in fact the understanding used by George Oster and Pere Alberch (1982, Fig.11): first random genetic change leads to non-random change among available phenotypes due to developmental properties including constraints, and subsequently natural selection acts and results in the eventually

realized phenotypes. From this perspective, constraint is not in opposition to selection but rather an orthogonal mechanism.

Apart from making the concept of developmental constraint compatible with evolutionary explanations involving selection, a construal that views constraint and evolvability as two aspects of one phenomenon has the major advantage that it assigns a positive explanatory agenda to the concept of developmental constraint. Accounting for constraint is at the same time accounting for evolvability, so that any study of constraint sheds light on the possibilities for generating phenotypic variation and novelty. To be sure, this is a way one *can* understand the notion of developmental constraint, but for the purposes of my historical discussion the crucial question is whether this *was* the case in the 1980s, i.e., whether in this period constraint was seen as tied to what nowadays goes by the name of evolvability.

Did research on constraint of the 1980s have the generation of morphological variation and novelty in view? We have already seen one reason in support: Amundson's (1994) characterization of constraint$_F$ shows that development was understood to be part of the explanation of the evolution of any trait. A closer look at the primary literature of this period bolsters this interpretation. Even though the term 'evolvability' was not common in the 1980s, the published reports of the 1981 Dahlem conference contain the following notions that were seen as tied to developmental constraint: evolutionary "adaptability" (Bonner 1982, 308), "facilitating" evolutionary change (302, 308), evolutionary "opportunity" (90, 101, 103, 217, 221, 329), and (macro-)evolutionary "potential" (108, 109). These terms are closely related to what nowadays is dubbed 'evolvability' (and the possibility of novelty). The developmental properties of organisms were seen as generating this capacity for morphological change: "the opportunities a particular developmental mechanism might hold for future evolutionary change" (107), "developmental mechanisms facilitating macroevolutionary change" (302). Even though there is an impression that developmental approaches to evolution in the 1980s were all about how development restricts evolutionary change and makes the generation of some phenotypes impossible, morphological transformation and macroevolutionary change were of major concern at the Dahlem 1981 workshop—including the issue of evolutionary "novelty" (33, 35, 41, 79, 80, 219, 220, 232, 282, 283, 294, 301, 308, 309, 318). Most importantly for our purposes, evolvability (to use the current term) was seen as the flipside of constraint:

> Developmental factors not only provide constraints but may also be a prerequisite for explaining adaptations of higher organisms. … Development specifically deals with the origin and limits of morphological novelty and phenotypic transformation (Bonner 1982, 307, 329).[3]

[3] Further language of this kind is found throughout the volume: "each mechanism [to build organisms] implies a specific set of opportunities and a specific set of constraints" (Bonner 1982, 242); "innumerable constraints and opportunities based upon inheritance and architecture" (343); "evolutionary potentials and constraints" (229); "Constraints and Opportunities in Tetrapod Limb Evolution" (300). See also Sander (1983): ontogenetic networks yield "(a) network-

Occasionally constraint was equated directly with evolvability: "constraints as such and as evolutionary opportunities" (218, 220); "constraint (what novelties are possible and also – the positive side – what novelties are facilitated)" (308).

Let us take a closer look at how developmental constraint was construed in this period. Five basic effects of constraints were acknowledged:

a) Constraints make the generation of certain phenotypes impossible (Alberch 1982).
b) Constraints can result in spandrels, i.e., the adaptive evolution of one trait entailing another trait as a developmental by-product (Gould and Lewontin 1979). Although this pertains to the generation of traits (a more constructive role for constraint), it was used by Gould to emphasize non-adaptive aspects of evolution (Gould 1980a, 1980b, 1989).
c) Constraints can lead to discontinuous morphological evolution due to thresholds in morphogenetic mechanisms (Alberch 1982). As a result, constraints explain how morphological change can be non-gradual.
d) Constraints lead to specific sets of available developmental trajectories, such as the bifurcation of developmental pathways (Oster and Alberch 1982). They determine what routes of morphological evolution are possible (and not merely what evolutionary outcomes are impossible). This sense of constraint plays a clear-cut role in explaining morphological evolution: "[development's] contribution will be to provide an understanding of the possible morphological transformations" (Alberch 1982, 327).
e) Constraints can lead to such coordination among traits that they vary in an integrated and functional manner (Wagner 1986), shaping the potential for the future evolutionary change and the evolution of complex characters.

In addition to these five basic effects attributed to constraints, developmental approaches to evolution in the 1980s had three distinct but compatible ways of using the concept of constraint as part of a positive explanatory agenda, which often were jointly employed by researchers. *First*, morphological evolution was explained as being due to the influence of both constraints and natural selection (Maderson et al. 1982). For example, David Wake (1991) argued that homoplasy can be due not only to convergent evolution based on selection but also arise from developmental constraints. Instead of replacing selection-based explanations with accounts in terms of constraint, Wake's endeavor was to analyze in what ways selective forces and developmental constraint had influenced the evolution of a certain phylogenetic lineage. A combination of external (selective) and internal (developmental) factors explains morphological trends.

Second, the reduction or loss of a developmental constraint opens up the possibility for subsequent morphological change and innovation: "These departures from the ancestral growth patterns involve a release from developmental constraints, permitting the introduction of new growth programs" (Maderson et al.

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dependent opportunities for evolutionary innovation and (b) network-dependent restraints effecting evolutionary conservation" (139).

1982, 303). In the context of the punctuated equilibrium model, constraints are not only the cause of morphological stasis (Section 2), but the disappearance of constraint was seen as leading to periods of rapid, punctuated morphological change. The origin of novelties can stem from the breaking up of developmental constraints that prevailed in ancestral lineages and therefore the concept of constraint was germane to explaining morphological evolution: "certain basic constraints may be set on development and evolution by the properties of cells themselves, and … evolutionary 'escapes' from these constraints may mark macroevolutionary change" (Gerhart et al. 1982, 107).

Third, developmental constraints provide the possibility of morphological variation and novelty. This is the most interesting explanatory use of the concept, as developmental constraints are not just viewed as preventing novelty (to be broken for novelty to arise), but as evolutionary opportunities (Wake et al. 1991). To use a modern term, some developmental constraints undergird evolvability. One context in which this explanatory role of the concept of constraint was visible was complex and coordinated phenotypic change. Viable and functional evolutionary modification of a complex character requires that changes in many individual traits are coordinated. Günter Wagner argued that developmental constraints can play the role of ensuring coordinated structural variation and integrated morphological evolution:

> [the] evolution of functionally coupled characters is highly dependent on an appropriate allocation of variance and thus depends on an appropriate pattern of developmental constraints. (Wagner 1986, 150; see also Wagner 1988; Müller 1989)

This explanatory task was already in view at the Dahlem conference discussions: "the crucial role that such ontogenetic buffers play in the evolution of novel structure and function; a novelty is of no use unless it can be functionally integrated with what is already there" (Horn et al. 1982, 220).

Another example from the Dahlem conference of constraints conceptualized as opportunities is the dependence of metazoan cell division and migration on a cell's contact and interaction with other cells. This feature of cells permits the evolution of complex metazoan cellular organization in the first place:

> This dependence would seem to constrain cell behavior, but at the same time it provides the wherewithal, the 'opportunity,' for multicellularity, for the integrated activity of cells in tissues (Gerhart et al. 1982, 90–91).

These ideas are manifested currently in the viewpoint that structures and processes may be conserved because they are governed by certain constraints, which at the same time allow for modularity and thus evolvability at higher levels of organization (Kirschner and Gerhart 2005; Gerhart and Kirschner 2007). At the 1981 Dahlem conference, structures above the cellular and histological level were seen as entailing constraints as well as creating the ability for morphological change and innovation in the case of adaptive radiations.

> The evolutionary 'choice' of a particular developmental pattern early in the evolution of the body plan of a group of organisms limits the range of future adaptations in a lineage. Yet it may provide unique opportunities for adaptations that are not open to other groups

> with other body plans. A particularly instructive example, where much is known about both evolution and development, is the five-part radial symmetry of starfish and their relatives, which imposes severe limitations on development and on body form, yet allows extensive adaptive radiation (Horn et al. 1982, 221).

Developmental constraint and evolutionary opportunity were intimately related in this period:

> Every time that someone mentioned a 'constraint,' someone else reinterpreted it as an 'evolutionary opportunity' for a switch to a new mode of life, and a third person would bring up the subject of the complementary 'flexibility' (Horn et al. 1982, 217).

This close connection to (what is now called) evolvability also obtained for theories using notions closely tied to the concept of developmental constraint, such as Rupert Riedl's concept of burden (Riedl 1978; Wagner and Laubichler 2004) and William Wimsatt's concept of generative entrenchment (Wimsatt and Schank 1988).

In the first historical portrayal (Section 2), the concept of developmental constraint was *exclusively* (or at least primarily) used to object to a selection-centered explanatory agenda in evolution. On this interpretation, it could only criticize explanations—not yield an alternative explanatory framework—and steadily came to be replaced by concepts supporting a positive explanatory agenda, such as evolvability. But this is not the whole story. Although neo-Darwinians construed constraint as a force antagonistic to selection (in line with the first historical account), the forerunners of Evo-devo often saw constraint and selection as orthogonal issues: developmental mechanisms account for how heritable phenotypic variation is biased or limited, and a subsequent, independent question is how natural selection operates on the available variation. Constraint was tied to what is now called evolvability in that development was conceived as the basis for the biasing as well as the generating of phenotypic variation. Most importantly, the concept of developmental constraint was part of an explanatory project in evolutionary research of the 1980s; developmental approaches to evolution aimed to account for the possibility of morphological transformation in terms of constraints and other developmental features of organisms. Thus, rather than a concept that did not support an explanatory agenda being replaced with a concept that does, the second and more adequate historical story reveals much more continuity in the shift from 'constraint' toward 'evolvability.' It is largely a rhetorical move, from the limiting aspects towards the enabling aspects that development has for morphological evolution.[4]

To be sure, such a rhetorical shift may matter substantially for the general perception of Evo-devo, and deemphasizing 'constraint' while emphasizing

[4] In agreement with several other contemporary Evo-devo biologists, Wallace Arthur views constraint and evolvability as related but deplores the traditional focus on the label 'constraint': "It is important, in relation to this question, to acknowledge that such a role for developmental bias is potentially both positive and negative. This is particularly so because in much previous literature the overuse of 'constraint' has painted too negative a picture of the evolutionary role of developmental processes" (Arthur 2006, 1; see also Arthur 2000).

'evolvability' may well help this approach be accepted by evolutionary biologists beyond the Evo-devo community. Why does developmental constraint primarily retain negative associations? In the late 19th and early 20th centuries, natural selection was often seen as only negative—exclusively eliminating variants. Many were skeptical about selection being able to produce novel and functional phenotypes. Nowadays it is generally acknowledged that the negative and positive impacts of selection go together; selection reduces the prevalence of maladapted characters and increases the presence of well-adapted characters. Why is it so hard for many evolutionary biologists to view the positive flipside of constraint (i.e., evolvability), instead of identifying it only with restricting the possibility of phenotypic variants? We need not answer this question to recognize the continuity between the concepts of constraint and evolvability, which I emphasize here to highlight neglected facts about the historical understanding and use of the concept of developmental constraint in the 1980s. But it may be that the acceptance of Evo-devo's explanatory contribution will remain decidedly mixed until these negative connotations are transcended. And, despite this perspective of 'constraint'-based research from the 1980s being in continuity with current 'evolvability'-centered Evo-devo, the latter is not generally accepted as being compatible with traditional neo-Darwinian evolutionary theory even though evolvability and selection operate on different dimensions. Not every evolutionary biologist is happy to embrace the relevance of evolvability (and constraint) for the study of adaptive morphological evolution.[5]

4 How Concepts Figure in Explanation and Disciplinary Identity

A philosophical issue contained in this discussion of the concepts of developmental constraint and evolvability is the different scientific purposes for which concepts are used. This raises epistemological questions about the use of mental representations in scientific practice. Concepts are mental representations, which represent features of the external world. Psychologists construe concepts as cognitive structures, as they contain knowledge (or at least assumptions) about the phenomena they represent. Words or terms are used to verbally express a concept. Concepts—both scientific and ordinary—figure in cognition and reasoning, and can serve multiple, different intellectual functions. Many concepts are used for the purposes of classification. Often concepts are used in combination to draw various kinds of inferences; for instance, assessing how likely the occurrence of an event is (prediction), determining whether some objects have a property given that other

[5] Likewise, even current Evo-devo biologists focusing on the 'evolvability' label (and pursuing Evo-devo questions rather than being preoccupied with criticizing adaptationism) point to false assumptions embedded within the traditional neo-Darwinian model, such as the tenets that phenotypic variation is largely unbiased and only gradual morphological change is possible.

objects are known to have it (category induction, analogical reasoning), or assessing how likely a claim is given background knowledge (hypothesis confirmation). Apart from classifying objects and predicting events, some scientific concepts are used for the purpose of explaining events and other phenomena. Concepts as mental representations support explanations if these representations include causally relevant features, e.g., causal processes, mechanisms, or causal laws.

Given that explanation is one of the prime functions of scientific concepts, how does the concept of evolvability fare on this count?[6] To answer this I have to start with some remarks on dispositions, since evolvability is a disposition (Love 2003). For every disposition (propensity), there is also the disposition's characteristic manifestation, and the physical basis of the disposition. Consider the disposition of solubility in water. Salt has this disposition, which manifests itself by the salt dissolving when put in water. A sample of salt has this disposition even if it never dissolves (e.g., because it never comes into contact with water). Thus, dispositions are present even if never manifested. The reason why a disposition obtains is the disposition's physical basis. Salt is water-soluble because of its ionic crystal structure. While the disposition obtains whenever its physical basis is present, one can know the disposition without knowing the physical basis: one can ascertain that salt is water-soluble without knowing why. Now consider evolvability, an organism's disposition to generate viable and heritable variation. The manifestation of this disposition is the actual occurrence of some phenotypic variation in future generations. (In the long run, evolvability also manifests itself in phylogenetic patterns of character change, though this pattern is due both to a taxon's particular evolvability and the effects of natural selection.) The physical basis of this disposition is the developmental basis of evolvability—whatever internal and developmental features of organisms make them and their characters evolvable. An account of evolvability is meant to shed light on the developmental basis of evolvability, where this developmental basis may differ across taxa.

Does the concept of evolvability support explanations? The disposition of evolvability is the cause of its manifestation (actual variation generated), so that the concept 'evolvability' refers to a cause of phenotypic variation. However, this concept offers a rather shallow or superficial explanation—just like the dormative virtue in Molière's *Le Malade imaginaire*. In this play the doctor 'explains' why opium makes people fall asleep with reference to the substance's dormative virtue (its ability to make people sleepy). But an appeal to a 'dormative virtue' seems to be nothing more than a redescription of the phenomenon to be explained. To be sure, the doctor identifies a genuine cause (opium) rather than pointing to a causally irrelevant factor. But a complete explanation only comes from laying out the physical basis of opium's ability to make people fall asleep, i.e., how physical aspects of the substance trigger certain physiological reactions. In the same fashion,

[6] Equivalent considerations apply to the concept of developmental constraint, given that constraint and evolvability are two aspects of the same phenomenon, as discussed in Section 3.

the concept of evolvability refers to a causal disposition, and technically speaking explains the disposition's manifestation—albeit in a shallow fashion. A deep explanation of a taxon's evolvability (including the relative likelihood of different variants) only comes from an account of the *developmental basis* of evolvability. Such an account of evolvability is not given by invoking the mere term or concept 'evolvability'; instead, other biological concepts that describe this developmental basis do the explaining. For those who are convinced that evolvability is largely explained by gene regulatory architecture (Erwin and Davidson 2009), the concepts of gene regulatory network (GRN), GRN kernel, GRN plug-in, GRN I/O-switch, and gene differentiation battery will be major explanatory ingredients. In Gerhart and Kirschner's theory of facilitated variation, the concepts of weak regulatory linkage, state selection, and exploratory behavior (which are not exclusively manifested at the genetic level, but apply to features on different levels of organization) are central notions used to account for evolvability (Kirschner and Gerhart 2005; Gerhart and Kirschner 2007). Another relevant concept is modularity (Bolker 2000; Schlosser and Wagner 2004). Sorting out the significance of these different concepts for successfully explaining evolvability is an empirical question, to be settled by ongoing research. Some set of these concepts (jointly employed) will play the primary role in explanations concerning evolvability and the generation of phenotypic variation because they causally account for the developmental basis of the disposition of evolvability.

Given that the concept of evolvability can support only shallow explanations on its own, it suggests that we ought to search for another epistemic function of this concept. Consider the question of what kind of discipline Evo-devo is and how it is related to other biological fields. One possible reply is that Evo-devo is an autonomous discipline, with its own methods, concepts, and explanatory models; it determines its major problems and acceptable answers on its own. While the idea of Evo-devo as an autonomous discipline suggests a significant distance from other disciplines, an alternative is to emphasize the integrative nature of Evo-devo and its close connection to other disciplines. Indeed, a much more common position is to characterize Evo-devo as an emerging synthesis of at least evolutionary biology and developmental biology, if not also paleontology, phylogeny, and morphology (Gilbert et al. 1996; Pigliucci 2009; Wagner and Laubichler 2004; Wake 1996). Although these connections to various biological disciplines are real, a vision of several biological fields merging into a unified whole—even forming one discipline—may well be too optimistic and at odds with the partial disciplinary specialization of contemporary science (Brigandt 2010; Bechtel 1986). A more cautious third view is that Evo-devo is an intersection of different approaches, or a coordination with and among different disciplines.

The characterization of Evo-devo, both in terms of composition and boundaries, is a controversial question (Brigandt and Love 2010). Evo-devo's identity is still in flux, and it does not yet have all the institutional characteristics of a genuine discipline (Gerson, this volume). But we do not have to settle on any specific answer about the disciplinary identity and institutional nature of Evo-devo in order

to observe that the problem of evolvability provides a significant amount of intellectual coherence. Hendrikse, Parsons, and Hallgrímsson (2007) argue that evolvability is (or ought to be) the central problem of Evo-devo, noting that not all research currently carried out under the label 'Evo-devo' speaks to this core concern. If we acknowledge that there might be several main problems on the Evo-devo agenda, then the explanation of the origin of evolutionary novelty is another obvious candidate. Indeed, Alan Love (2005, 2006, 2008) has already emphasized that novelty is what he calls a problem agenda (i.e., a set of interrelated questions). His insight is that problem agendas come with criteria of explanatory adequacy that set standards for what would count as a satisfactory explanation. In the case of evolutionary novelty, the criteria of adequacy entail that the intellectual resources of and ideas from several biological disciplines have to be used (developmental biology, paleontology, phylogeny, etc). The problem agenda's interrelated component questions and criteria of explanatory adequacy give some idea of how the different intellectual components have to be integrated; a problem agenda coordinates interdisciplinary research (see also Brigandt 2010). In a similar vein, I view the *concept* of evolvability as setting a problem agenda, and thereby providing intellectual identity to Evo-devo (even though there are other problems that bear on Evo-devo's identity). The problem of evolvability implies which approaches and disciplines contribute to an explanation of evolvability, guiding interactions among researchers and the efforts devoted to solving this problem. My point is that the concept of evolvability provides a significant amount of intellectual identity to Evo-devo *without* having to answer what kind of discipline Evo-devo is or what its institutional boundaries are. The systematic pursuit of the problem agenda of evolvability will result in an explanatory framework, but we do not have to decide whether this explanatory framework will correspond to exactly one discipline (e.g., by a theory of evolvability being the theoretical core of the discipline of Evo-devo).

I interpret the concept of developmental constraint as having played an analogous scientific-epistemic role in the 1980s. Developmental approaches to evolution at this time clearly did not constitute a discipline, but the concept of constraint did set a problem agenda that provided intellectual coherence to these approaches (even if this fell short of a disciplinary identity). Moreover, the concept of developmental constraint led to research coordination. Although not as systematic and influential as current Evo-devo efforts, this coordination did guide interaction among researchers from different disciplines—some were paleontologists, some were primarily developmental biologists, and others were morphologists.

One of the primary epistemic functions (intellectual purposes) of scientific concepts is to explain natural phenomena. Some concepts have a higher explanatory impact than others. The concepts of evolvability and developmental constraint support explanations in a weak fashion only (because evolvability and constraint are explained primarily by other biological concepts), but this does not belittle the scientific importance of these concepts. On the contrary, my discussion points to another important role that scientific concepts can have—to set a problem agenda.

And in the case of the concept of evolvability, the problem agenda provides some of the disciplinary identity for Evo-devo. As a result, the concept of evolvability fulfills a major epistemic function—it is more important in setting an explanatory agenda than in explaining phenomena. This is analogous to how the concept of evolutionary novelty may be more valuable in setting an explanatory agenda than in categorizing biological traits (Brigandt and Love 2010). The definition of 'novelty' is contested, the issue being how to distinguish novel from non-novel structures, with some arguing that a clear line between a quantitative variant and a qualitative morphological difference cannot be drawn. Some scientific concepts must draw clear boundaries in order to serve the epistemic function of classification. If this was the primary function of the concept of novelty, then its prospects would be dim given the debates about what counts as novel. However, another—and in my view more important—function of the concept of novelty is to set an explanatory agenda. Even if a trait is counted by some definitions as novel but by others as non-novel, a mechanistic explanation of its evolutionary origin is an intellectual achievement. By setting a problem agenda the concept of novelty can play an important scientific role even if its definition remains contested.[7]

5 Conclusion: How to Distinguish Evolvability and Selection?

My discussion has focused on the historical shift away from the concept of developmental constraint toward the concept of evolvability. One possible historical account is that the concept of constraint—as used prominently in the 1980s—was *exclusively* employed in a critique of selection-centered neo-Darwinian explanations. This would be a major limitation of this concept, since merely criticizing an explanatory framework does not yield an alternative explanation. The modern concept of evolvability undoubtedly figures in an explanatory project about the mechanisms underlying evolutionary change. On this historical interpretation the transition from 'constraint' to 'evolvability' is the replacement of a concept that cannot support an explanatory project by a concept that can. However, a closer look at the history shows that even though the concept of developmental constraint was used to criticize adaptationism, it was also used by its proponents as part of an explanatory project that attempted to understand how the developmental properties of organisms make integrated morphological change and the generation of novel forms possible—very much akin to how an account of evolvability is understood nowadays. Thus, there is a large amount of historical continuity because the transition from 'constraint' to 'evolvability' was not a substantial intellectual shift

[7] Setting an explanatory agenda is an epistemic function that is of a very different kind than most other functions of concepts (Brigandt 2012). Scientific concepts typically have the function of representing the natural world by classifying natural phenomena, predicting natural phenomena, or explaining natural phenomena. A problem agenda is not a representation of the natural world, but a goal for scientific practice.

but more of a rhetorical change. I have also addressed different epistemic purposes for which concepts can be used. An obvious intellectual function of a scientific concept is to give explanations. The concept of evolvability does support explanations, but to a small degree only in that the phenomenon of evolvability is actually explained by other biological concepts (e.g., modularity), which lay out what the ability to generate morphological variation consists in. Still, the concept of evolvability fulfills a vital epistemic function by setting out a problem agenda. Accounting for evolvability is one (though not the only) item on the Evo-devo agenda, so that the concept of evolvability contributes to defining the intellectual and disciplinary identity of evolutionary developmental biology. I have argued that the same applied for the concept of developmental constraint in the 1980s, where it generated intellectual coherence and coordinated research even though developmental approaches to evolution did not form a genuine discipline.

I conclude with a puzzle about the relation of evolvability and selection. The manifestation of evolvability is heritable phenotypic variation, and phenotypic change across generations is due to both evolvability and natural selection. It may be hard to distinguish the influence of each empirically in concrete cases, but the question I want to raise instead is what distinguishes them *in principle*. One possibility is that evolvability and selection are two ontologically distinct processes. In each generation, first phenotypic variation is created due to evolvability, and then on a second, separate level selection operates on the existing variation. An advantage of this two-level scheme is that it offers some clarification to different terminologies surrounding constraint. Biologists may speak of developmental constraints, morphological constraints, ecological constraints, and selective constraints (among others), which some have taken as an indication that the notion of constraint is hopelessly muddled (Antonovics and van Tienderen 1991). On a two-level scheme, developmental and morphological constraints belong to the first level (i.e., the generation, biasing, and restriction of phenotypic variation). So-called ecological and selective 'constraints' are not constraints on the generation of variation at all, but they reflect the influence of natural selection and thus belong to the second level.

While it is attractive to construe evolvability and selection as operating on ontologically distinct levels, this neat separation may not be possible given biological reality. The two levels cannot be understood as temporal stages. It is not the case that in each generation there is first a period of time where phenotypic variation is created followed by a period where the variation is selected. On the contrary, evolvability can lead to phenotypic variation at any point of an organism's life cycle, and likewise selection can favor traits at any point of a life cycle. Selection having any actual impact logically presupposes that relevant variants are present, but the variation in a specific character at a particular life-stage need not *temporally* precede the presence of natural selection (favoring or disfavoring some states of this character at this life-stage).

A more promising strategy is to suggest that evolvability is determined by factors internal to organisms, whereas natural selection (selection pressure) is deter-

mined by factors external to organisms. However, there are extended phenotypes in the case of behavioral characters, niche construction, and symbioses, so that such heritable phenotypic characters (manifestations of evolvability) are not solely determined by the internal constitution of an organism. Due to phenotypic plasticity, even characters that are within organisms are influenced by external factors. Evolvability is context-dependent—putting organisms in a different environment may change their evolvability (Love 2003). Thus, evolvability cannot be exclusively determined by internal factors. Likewise, what characters are favored by natural selection is not solely determined by factors external to organisms. Organisms from different species can occupy the same environment, but they face quite different adaptive problems and selective pressures—due to the internal differences among organisms from different species.

My diagnosis of this issue is that evolvability, being about generating viable heritable variation, necessarily has to include considerations about the viability of organismal features and the reproductive ability of organisms. Such considerations about viability and reproductive ability are also the core of natural selection, which means evolvability and selection are entwined. Evolvability and selection pertain to the functioning of organismal systems (developmental processes and an organism's interaction with other organisms and its abiotic environment), but I have argued that partitioning the various causally interrelated factors bearing on functioning into internal versus external does not yield an acceptable distinction between evolvability and selection.[8] Changing the internal constitution of a taxon's organisms (e.g., their genome) changes the taxon's evolvability, but may also impact the selection regime. Since some material factors impact *both* evolvability and selection, it is not possible to separate material features into those constituting evolvability and those constituting selection pressure.

This question is broadly analogous to recent philosophical debates about how to interpret selection and drift, and how to construe their relation (Beatty 1984; Brandon 2006; Matthen and Ariew 2002; Millstein 2002; Stephens 2010; Walsh et al. 2002). While some maintain that selection and drift are distinct forces, others argue that selection and drift are not causes but features of a statistical theory. Some even suggest that selection and drift cannot be separated in principle. As opposed to the above strategy of attempting to argue that evolvability and selection are *ontologically* distinct processes, another possibility is that it is only a *conceptual* distinction made by us. Our mathematical models (e.g., as found in quantitative genetics) simply assume that heritable variation and natural selection are distinct entities without an account of how material factors (features of organisms and their environment) ontologically determine the generation of variation and ac-

[8] Although the two-level model could assign developmental constraints, morphological constraints, ecological constraints, and selective constraints to one or the other level (suggesting that the levels can be distinguished), it is less clear what to make of so-called 'functional constraints.' Given that functional constraints concern an organism's developmental dynamics/internal mechanics, as well as the effects on survival and reproductive ability, they seem to touch on both evolvability and selection.

tion of selection as separate processes. From this vantage point, evolvability and selection may be seen as two different *epistemological* perspectives. One explanatory project is to account for evolvability. Here selection is taken as a background condition (whatever features precisely determine selection pressure), and the task is to lay out the factors that result in the generation of heritable morphological variants in a taxon or that bias the generation of some morphological traits over others. Another explanatory project is to account for adaptation. Here the generation of heritable morphological variation is taken for granted (whatever its cause evolvability involves), and the task is to explain why certain traits have been favored in ancestral environments, resulting in adaptive evolutionary change. To some it may seem unsatisfactory to say that evolvability and selection are not distinct in nature but only a conceptual separation that we make in our minds. I acknowledge this reaction but leave the issue for future reflection and scholarly debate.

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