

# The nature of developmental constraints and the difference-maker argument for externalism

Roger Sansom

Received: 29 March 2007 / Accepted: 19 June 2008  
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**Abstract** One current version of the internalism/externalism debate in evolutionary theory focuses on the relative importance of developmental constraints in evolutionary explanation. The received view of developmental constraints sees them as an internalist concept that tend to be shared across related species as opposed to selective pressures that are not. Thus, to the extent that constraints can explain anything, they can better explain similarity across species, while natural selection is better able to explain their differences. I challenge both of these aspects of the received view and propose a hierarchical view of constraints.

**Keywords** Constraints · Natural selection · Explanation · Adaptationism · Identity conditions · Heirarchical view of constraints

## Introduction

Perhaps no intellectual division in evolutionary biology has run as long and deep as that between internalist and externalist explanations of organism form. In Darwin's (1859) terms, these are explanations in terms of "unity of type" and "conditions of existence." Ever since Darwin, externalist explanation has focused on adaptivity and natural selection. The most widely used internalist concept of today is the notion of "developmental constraint" (e.g. Kauffman 1983; Maynard Smith et al. 1985; Gould 1989; Schlosser 2007). Maynard Smith et al. (1985) defined a developmental constraint as "a bias on the production of variant phenotypes or a limitation on phenotypic variability caused by the structure, character, composition,

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R. Sansom (✉)  
Department of Philosophy, Texas A&M University, College Station, TX, USA  
e-mail: r-sansom@philosophy.tamu.edu

or dynamics of the developmental system” (p. 266).<sup>1</sup> This definition means that constraints determine the probabilities of descendents with various combinations of trait values appearing in subsequent generations. Developmental constraints determine variants available to natural selection (Maynard Smith et al. 1985; Gould 1989) and natural selection favors those variants that are most adaptive. Even pluralists like Gould and Lewontin (1979), who argue for the importance of constraints, accept the primary importance of natural selection in evolution. Some all but assume that natural selection is primary, but others offer arguments for the explanatory primacy of natural selection (e.g. Dawkins 1996; Dennett 1995; Sober 1996; Sterelny and Griffiths 1999), which would grant the primacy of externalism (Godfrey-Smith 1996).

Enough participants in the debate are sufficiently agreed on some matters to describe a limited received view. First, developmental constraints are an internalist concept (Gould 1989; Godfrey-Smith 1996). Second, constraints tend to be shared across related species while selective pressures are not (Gould 1989; Amundson 1998; Sterelny and Griffiths 1999). Thus, to the extent that constraints can explain anything, they can better explain similarity across species, while natural selection is better able to explain their differences. To this received view, Sterelny adds the claim that the adaptive diversity of organisms poses the \$64,000 question in evolutionary biology, and natural selection is the answer (Sterelny and Griffiths 1999). This makes Sterelny an explanatory adaptationist (Godfrey-Smith 2001). I call Sterelny’s argument for explanatory adaptationism the “difference-maker” argument and challenge that argument in this paper.

I shall challenge both premises of the received view. First, I will argue that the environment plays a significant role in developmental constraints. I will propose a way to distinguish the influence of constraints from that of natural selection, but this view denies that developmental constraints are a purely internal concept. Second, I will argue that it is hard to identify constraints such that the claim that constraints tend to be shared across species is the empirical one that Sterelny takes it to be. My arguments hold a mixed lesson for the fate of internalism. Constraints cease to become a purely internal concept, but that mixed concept gains explanatory power. In presenting these arguments, I will develop a hierarchical view of constraints.

## Clarifying constraints

Much effort has gone into the theoretical analysis of natural selection in evolutionary explanation, but far less has gone into the analysis of constraints (although, see Whyte 1965; Gould and Lewontin 1979; Alberch 1980, 1982, 1989; Dullemeijer 1980; Wake 1982; Gould 1989; Schwenk 1994, 2001; Webster and Goodwin 1996; Wagner and Schwenk 2000; Sansom 2003; Schlosser 2007).

There is a general ambiguity in the term “constraint.” It can refer to a limitation of the capacity of a process, which I call a “capacity constraint.” For example, if I

<sup>1</sup> While Maynard Smith et al. (1985) also discuss selective constraints, this paper will only deal in developmental constraints.

am handcuffed, my capacity to move my hands is limited. It can also refer to the mechanism, system, or process that is limiting my capacity (e.g. the handcuffs themselves). We may refer to the handcuffs as constraints even when they are not around anyone's wrists and, therefore, are not actually constraining anyone. I call this second meaning of constraints a "constraint mechanism." A capacity constraint is explained by the relevant constraint mechanism.

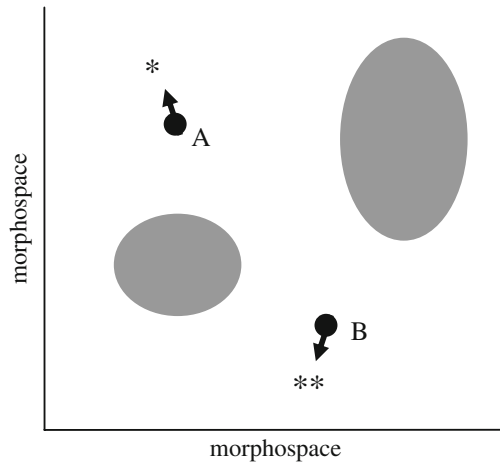
Capacity constraints and constraint mechanisms are determined relative to a process. When evolutionary theorists refer to constraints in evolutionary theory, they typically refer to a capacity constraint on evolution that is discovered by observation of variation. For example, Nijhout discovered that there is an inverse relationship in *Onthophagus acuminatus* (a horned beetle) between size of horn and size of eyes (each relative to body size) (Nijhout and Emlen 1998; Nijhout 2003). This is a capacity constraint on the development of *Onthophagus acuminatus* (i.e. they cannot develop variants with large horns and large eyes). Nijhout and Emlen hypothesize that this is due to the fact that the development of these two features draws from the same limited pool of nutritional resources. Their hypothesis proposes a constraint mechanism for the development capacity constraint. One can induce from Nijhout and Emlen's work that large horned and eyed *Onthophagus acuminatus* cannot evolve, which is a capacity constraint on their evolution, which is partially explained by another capacity constraint—the limitation in developmental variation, which is explained by a constraint mechanism—Nijhout and Emlen's hypothesis that they develop from shared resources.

### The environmental relativity of stability constraints

The capacity constraint on the evolution of a population along with the fitness of each variant determines the probabilities of change from each generation of a population to the next. The conceptually simplest constraints to analyze are the constraints that determine that certain trait value combinations are logically impossible. Gould has offered us the following example concerning the whorled shells of *cerion*; "If the adult size of a shell lies within a limited range, then an increase in the size of the whorls requires that the adult shell contain a smaller number of whorls" (Gould 1989, p. 520). This jigsaw constraint is explained by the fact that if the size of anything is limited, then an increase in the size of pieces requires a reduction in their size. These constraints prohibit certain combinations of trait values for all phyla, although the relevance of most constraints is limited. Gould's constraint is highly relevant to *cerion*, because they have whorled shells, but irrelevant to *homo sapiens*. This constraint that tells us why there are no *cerion* with small shells made up of a large number of large whorls is purely internal. Nothing about anything external to the organisms is required. In particular, there is no mention of function or natural selection.

We can represent the influence of developmental constraints like Gould's jigsaw constraint in a diagram of morphospace (see Fig. 1), in which developmental constraints (shown as shaded areas) impose "no go" zones and selection pressures are forces moving populations through morphospace. On this view, populations

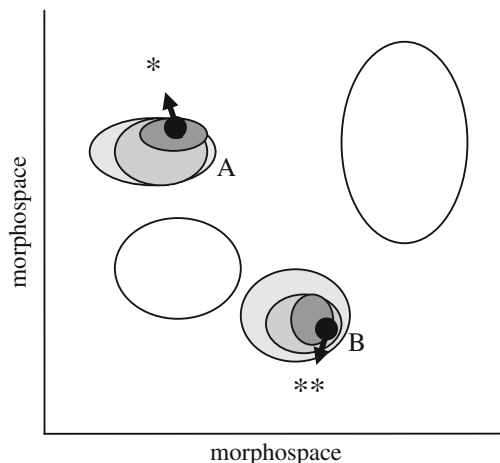
**Fig. 1** Evolution through morphospace with universal constraints



(A and B) must avoid the same morphospace ruled out by common constraints (shown in gray), but, populations in different environments are moved in different directions through morphospace, perhaps as they are attracted by natural selection to different local optima (\* and \*\*).

I want to suggest that a better way to think about constraints is represented in Fig. 2. In this figure, the same constraints of impossible organisms are represented (as white no-go zones), but so are limits of where a population can get to (within some number of generations) given its current position in morphospace. The most accessible morphologies are dark gray, less accessible morphologies in light gray, and white areas are completely inaccessible. Considering position constraints allows us to take into account phenomena, such as the fact that elephants are perfectly possible organisms, but it is impossible for a guinea pig to have anything similar to an elephant as a descendent (in the short term at least).

**Fig. 2** Evolution through morphospace with universal and position constraints



The more generations into the future we look, the broader the possibilities will be for any population. Just how many generations down the line should we think about when talking about constraints? There are a number of options here, but I shall raise one concern that if we look more than one generation down the line, natural selection will itself become a factor in determining developmental constraints. If mutation X makes mutation Y more likely, then the probability of Y occurring some number of generations in the future will be greater the more X is favored by natural selection. This mixing of natural selection and developmental constraint is certainly problematic for any who would wish to privilege one factor over the other. The problem may not even be solved by limiting oneself to thinking of only constraints on the very next generation, because sexual selection, etc. can also play a role in determining that. This is one reason why I think that it is difficult to understand developmental constraints as a purely internal concept.

A further reason for the environmental relativity of certain developmental constraints concerns the environmental relativity of what Schlosser names “stability constraints” (Schlosser 2007). Stability constraints determine that logically possible systems will not develop because they are physically unstable for some reason. Many structures are logically possible, but physically unstable, because they cannot support their own weight, etc. Physical stability is not a purely internal notion. Technically, it is contingent on things like the size of the planet (and, therefore, the force of gravity on the structure). Although this external feature is shared by all life that we know, other environmental factors vary. Some vary in obvious ways. For example, a structure that could not support its own weight above ground may be able to under water and structures under water can be crushed by water pressure that is not faced by structures above ground.

Other stability constraints vary in ways that are more interesting. The inactive *L-gulonolactone oxidase* enzyme of the haplorrhini primates (including humans), guinea pigs, and bats, results in an incapacity to synthesize ascorbic acid, which is essential for the life of all organisms. Organisms with this condition are unstable in environments without foodstuffs rich in ascorbic acid, because they cannot produce a component essential for successful development, but organisms can get sufficient ascorbic acid in environments with the right food.

The received view supposes that constraints are about internal features of the organism, but this analysis of stability constraints shows that they are conceptually entwined with the external environment. This presents a challenge for many potential purely internal explanations in biology. I shall offer a response to the challenge that is something of a tactical retreat for the internalist. Externalist explanations focus on natural selection. I propose that explanations that appeal to natural selection can be kept distinct from explanations that appeal to developmental constraints if we distinguish the *selective environment* from the *nonselective environment*. The selective environment includes all factors that determine which viable phenotypes are more adaptive than others. It is conceptually distinct from the nonselective environment, which includes all factors that determine viability and therefore stability constraints. For example, the widespread presence of food rich in ascorbic acid in the historic environments of haplorrhini primates determined that those with an inactive *L-gulonolactone oxidase* enzyme were viable. Those variants

were not removed by developmental constraints. In these terms, developmental constraints are determined by the non-selective environment, which, in this case, had an adequate concentration of food rich in ascorbic acid. Furthermore, the fixation of the inactive enzyme in haplorrhini primates populations suggests that variants with an active enzyme were no more adaptive than those without. In these terms limited vitamin C rich food was not a factor in the selective environment.

This type of analysis allows us to say that the maintenance of the active enzyme is explained by developmental constraints in populations that have inhabited environments with so little ascorbic acid rich food that those with an inactive enzyme were not viable. In contrast, the active enzyme is maintained by natural selection in environments that have enough ascorbic acid to make variants without it viable but less adaptive. Admittedly, there may be borderline cases of environments where there is just enough ascorbic acid for a variant with an inactive enzyme to have a very small chance of reproducing, but that is true of many useful distinctions.

The dependence of stability constraints on the environment shows that not all explanations that appeal to developmental constraints are entirely internal. However, distinguishing between the nonselective environment that plays a role in determining constraints, from the selective environment that does not, allows the distinction between explanations that appeal to constraints from those that appeal to natural selection, which has been the contemporary version of the internalist/externalist debate. Empirical work has been undertaken to distinguish between phenomena that are the result of developmental constraints from phenomena that are the result of natural selection. For example, Anderson and Roopnarine (2005) work hard to explain the conservation of some trait values in *Caryocorbula* in terms of constraints and others in terms of stable selection. Their results are complex and not entirely conclusive, but developmental constraints and selection must be conceptually distinct for the project to even get off the ground. Acknowledging the environmental relativity of stability constraints turns the developmental constraints/natural selection debate from a pure internalism versus pure externalism debate to an internalism *and* externalism versus pure externalism debate.

### The range of constraints

Maynard Smith et al. (1985) do not acknowledge the environmental relativity of constraints, but they do acknowledge that developmental constraints vary in their scope. “Universal constraints” cover all physical systems, because they “do not depend on any distinctive features of the organism” (p. 267). Their example is the law of the lever: “any uncompensated change in the shape of a skeleton that increases the speed with which some member can be moved will reduce the force which that member can exert” (Maynard Smith et al., p. 267, also discussed in Maynard Smith and Savage 1956). In contrast, “local constraints”, are limited to particular taxa because they do depend on a feature of the organism. Maynard Smith et al. (1985) take an example from the majority of monocotyledons (palms), whose variation in growth is constrained because their trunks are quite uniform in diameter, because they have not evolved secondary thickening, unlike

dicotyledons.<sup>2</sup> They take themselves to be describing the ends of a continuum of constraint scope.<sup>3</sup>

The received view accepts that a population might be under local and universal constraints. The notion of local constraints raises the question of just how local constraints can get. If there is at least a class of constraints that are not typically shared across populations, this will spell difficulty for the second thesis of the received view. In what follows, I will argue for just such a notion of constraints.

*Drosophila sechellia* is endemic to the Seychelles archipelago in the Indian Ocean, where it specializes on the fruit of *Morinda citrifolia* (Tsacas and Bachli 1981). This species is morphologically almost identical to *D. simulans* and *D. mauritiana*. However, only *D. sechellia* is resistant to the fruit's primary toxin—octanoic acid (Legal et al. 1992, 1994; Farine et al. 1996). At least five genes are cumulatively involved in *D. sechellia*'s resistance (Jones 1998). R'Kha et al. (1997) have suggested that the resistance evolved gradually as more resistant variants were able to exploit initially less rotten and then less ripe fruit, with its increasing octanoic acid concentration. This increased resistance led to increased specialization of *D. sechellia* on the fruit, probably leading to its reproductive isolation (Jones 1998).

This clear case of gradual evolution by natural selection for increased resistance to a toxin resulted in a change in the mean trait value of variants produced by the populations that came later in the transition. New variants after selection were biased toward greater resistance than new variants were before selection. If we accept that any “bias on the production of variant phenotypes or a limitation on phenotypic variability caused by the structure, character, composition, or dynamics of the developmental system” is a constraint, then the higher octanoic acid resistance in only *D. sechellia* became a new developmental constraint. This change may well be isolated to a particular population.

Any heritable change in mean trait value will change what I call an “exact constraint” on that population. The position constraints discussed in the previous section are the full set of exact constraints that a population is under. Because populations vary from each other and exact constraints are so narrow, they may often not be shared by other populations of the same species, let alone distinct species. Accepting exact constraints would deny that constraints tend to be shared across species—a crucial premise in Sterelny's difference-maker argument for externalism.

### Are exact constraints acceptable?

There may be good conceptual reasons to be suspicious of exact constraints because they are so narrow. How constraining can a constraint so easily broken really be?

<sup>2</sup> The constraints that take into account a population's position in morphospace discussed in the previous section of this paper are local, but not all local constraints take account of position in such a specific way.

<sup>3</sup> They also take universality to be a measure of the “bindingness” of a constraint. I shall ignore that issue for now and concentrate only on scope.

The idea behind them is that even when you shed one constraint you only acquire another (similar) one, but I admit that constraints that are so easily shed may not seem very constraining in the first place.

To deny that exact constraints are genuine developmental constraints is to deny that just any bias in the production of phenotypes is a constraint. In the case of increased octanoic acid resistance in *Drosophila sechellia* in the Seychelles archipelago, it seems reasonable to say that the constraints have not changed, but selection has maneuvered the population within its developmental constraints.

There are a number of other ways to try to avoid adopting exact constraints. One might drop the “bias on the production of variant phenotypes” from Maynard Smith’s definition and leave just the “limitation of phenotypic variability”. The idea behind such a move would presumably be that while an increase in octanoic acid resistance might bias variants, it will not change which variants are possible. This option denies that changes in quantitative traits change the possibilities for the population. Taken to its logical conclusion, this move really denies local constraints altogether. I recommend against this option because only local constraints explain why, for example, a guinea pig cannot give birth to an elephant, because elephants per se are eminently possible.

Even if we take the absolute limits of variants of *Drosophila sechellia* to remain constant over an increase in octanoic acid resistance, I think that dropping the “bias” from the definition would still be a mistake, because I take it that many constraints are not absolute prohibitions of variants, but rather determine their probabilities (although, in many cases they determine their probabilities to be very low). If a change reduces the probability of a variant by several orders of magnitude (which seems quite reasonable if the variant requires certain additional mutations after the change), then I contend that it is appropriate claim that the change has altered the constraints on the population.

Another way to avoid this result may be to stipulate that constraints are not about the variations in the very next generation, but rather changes in variants that might occur within a significant number of generations. These constraints may be more stable, particularly if you think that natural selection can typically undo what it has done if the environment changes, such as to later reduce the need for reduce octanoic acid resistance, for example. This objection does bring up the general point of whether constraints are determined by possible variants in the next generation or more distant descendants. We may be able to talk about different constraints on different time scales, although the longer the time scale, the greater the potential external influence of natural selection (see section “The environmental relativity of stability constraints”).

The issue of whether exact constraints are legitimate is a grain issue of how finely to distinguish one constraint from another similar one. Constraints are metaphysically murky notions, clouded in the realm of possibilities. While I have alluded to an intuition that a constraint easily changed is no constraint at all (apparently shared by Sterelny and Griffiths 1999 and Gould 1989). I think that intuitions quickly run out of steam when it comes to determining the identity conditions of constraints. For example, we are confident that constraints prevent Zebras from evolving machine guns (Krebs and Nicholas 1981), but consider the following questions: How many



constraints determine that Zebras cannot evolve machine guns? Is this the same constraint that prevents Zebra fish from evolving dart guns? These distinctly odd questions concern the identity conditions of constraints. The difference-maker argument for explanatory adaptationism appears contingent on the answers to the same type of questions.

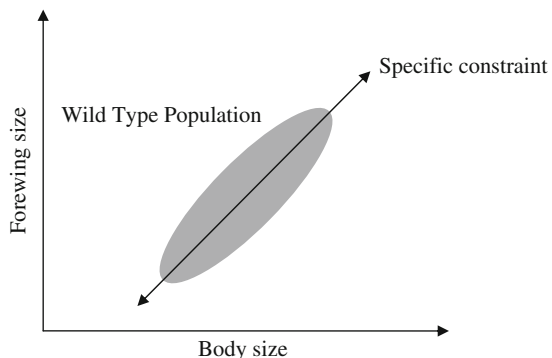
### Identifying constraints

Philosophers of natural science who claim to have discovered a potentially irresolvable metaphysical problem should always be concerned that scientists have in practice solved it. Empirical studies on constraints provide a good place to look for ideas about how we should fill out the requirements for a bias in production of variants to be a legitimate constraint. Brakefield and colleagues (Frankino et al. 2005) accept Maynard Smith's definition of constraints in their investigation on the developmental constraints concerning the allometric relationship between forewing area and body size in the butterfly *Bicyclus anynana*. Their empirical results are excellent investigations of how the structure, character, composition, or dynamics of the developmental system bias the production of phenotypic variability. They provide a useful case study for thinking about the identity conditions of developmental constraints.

Brakefield measured the wild type variation of combinations of two traits of all individuals in a population born into a particular generation and found that not all combinations were represented. Organisms with high body mass are biased toward having high forewing area. Figure 3 represents his result in a simplified form. Combinations of body size and forewing area of each member of *Bicyclus anynana* fall within the shaded area and the line of best fit is calculated from this distribution.

Having noted this positive allometric relationship between body size and forewing area in the population, we would expect selection for higher body size to result in a population of higher forewing area, too. Therefore, I interpret Fig. 3 as representing a constraint about how selection for changes in body size will change forewing area. After all, such a correlation between traits is an example of a limitation on phenotypic variability caused by the structure, character, composition,

**Fig. 3** Positive correlation between body size and forewing area in wild type *Bicyclus anynana*



or dynamics of the developmental system. Allometric relationships appear to be one of the simplest examples of a developmental constraint. Let us call it a “specific constraint.” This way of thinking about constraints is much like the way Nijhout thinks of the constraint between size of horn and size of eyes in *Onthophagus acuminatus*, which is just such a correlation and was even shown with a very similar graph (2003, p. 16).

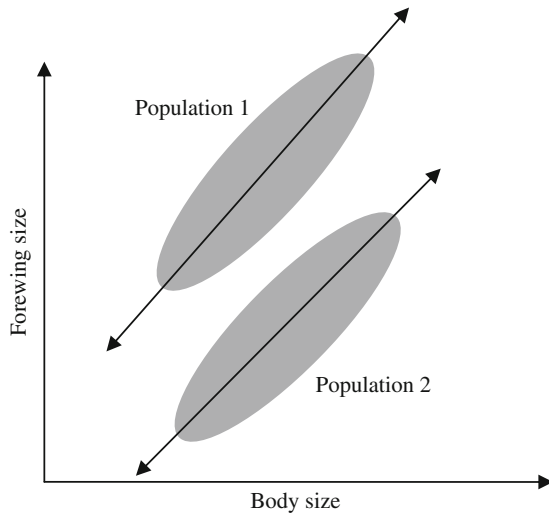
Specific constraints appear to be a good candidate for the constraints of practicing biologists and also are in contention for being the constraints needed for the difference-maker argument. Figure 3 shows the wild type’s specific constraint on the allometric relationship between forewing area and body size. If a subpopulation were selected for increased body size, we would expect it to increase its forewing area at the level determined by the specific constraint. The population would move along the same constraint to a point that has higher body size and forewing area. Interestingly, this way of identifying constraints assumes that such a change would be reversible, because if the same subpopulation were subsequently selected to again have the body size of the wild type, then the *same* constraint would determine that it should return to having the same forewing area as the wild type as well.

In the previous section I discussed how the legitimacy of exact constraints poses a challenge to the difference-maker argument for externalism, because exact constraints will so rarely be shared across populations. Specific constraints may appear to be a step in the right direction for the defender of the argument, because they can be shared by populations with different trait values. However, as we shall see, even specific constraints are themselves variable, which leads to the similar conceptual problems at a higher level of generality.

The ratio of body size to wing area is called wing loading. It is directly related to flying ability (Vogel 2003). Flying ability is directly related to fitness, because flying is important in male competition and courtship of females (Joron and Brakefield 2003). We can think of wing loading as a trait in itself. Different points along the specific constraint shown in Fig. 3 have similar wing loading (bigger individuals have on average around 20% greater wing loading than smaller individuals). Brakefield and his colleagues investigated whether wing loading could be changed with selection. They artificially select for low wing loading in Population 1 and high wing loading in Population 2. Given that there is some variety in the ratio in the wild type population, it is not surprising that they are able to produce divergence between wing loading mean values in the two populations in just a few generations, shown in Fig. 4.

If we accept the specific constraint shown in Fig. 3 to be a developmental constraint, then Brakefield has shown that it can be easily changed. This result is not surprising because wing loading varies across butterfly species (Vogel 2003). The great diversity of insects suggests that their allometric relationships are highly variable. This poses a challenge to the defender of the difference-maker argument for externalism. If specific constraints are legitimate and vary, then they too explain biological diversity according to difference-maker logic. Brakefield does not consider this specific constraint to be legitimate, because he showed it to be too variable to count as constraints in the first place. He concludes that; “it is not

**Fig. 4** Positive correlation between body size and forewing area in *Bicyclus anynana* artificially selected for high and low wing loading (simplified from Frankino et al. 2005, p. 719)



internal developmental constraints, but rather external natural selection that is the primary force shaping the short-term evolution of morphological allometries in insects” (p. 720). Finding morphological allometries highly malleable by selection, he apparently concluded that they are no constraints at all. Brakefield takes his work to support externalism for reasons entirely in accord with the difference-maker argument. Specific constraints face the problem faced by exact constraints of not being constraining enough.

Interestingly, the variation of wing loading is itself constrained. While the selection was on the wing loading ratio, the variation in wing loading was due primarily to changes in forewing area (resulting in populations ending up above and below each other in Fig. 4) rather than body size (which would result in populations lying to the left and right of each other). For Brakefield, “[T]he pattern of response exhibited by forewing area and body size indicates a strong bias [or developmental constraint (Maynard Smith et al. 1985)] in how these traits respond indirectly to direct selection on their scaling relationship” (p. 719).

There is a way to reconcile the view that allometric relationships are constraints that vary between butterfly species with Brakefield’s conclusion that allometric relationships are the result of selection and are themselves constrained. Brakefield’s work shows that body size is relatively more fixed than forewing area. This is another constraint, because it is another bias in the production of phenotypes. It could have been different—selection for increased wing loading could have reduced forewing area more than it increased body size.

Brakefield has shown that the allometries of *Bicyclus anynana* are highly flexible. While many combinations of forewing area and body size are possible, this work shows that there are tendencies in the directions that populations can travel through morphospace. The populations of *Bicyclus anynana* are under specific constraints that increase body size and forewing area in such a way that they can relatively easily increase or decrease both and remain with quite similar wing loading. These

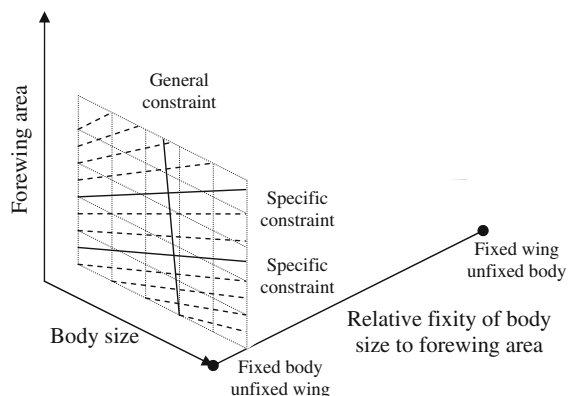
specific constraints can also be quite easily broken and when they are it is primarily through changes in forewing area rather than body size. I suggest that we provisionally call this constraint on specific constraints a “general constraint”, which is represented in Fig. 5.

The specific constraints shown in Fig. 4 are represented in Fig. 5 as *solid lines*, which show how selection for change in body size affects forewing area. Note that they get slightly steeper with an increase in wing loading as also represented for the two populations in Fig. 4. Theoretically, there is a value of the direction of the specific constraint for every point on the plain, but only a sample of additional estimated specific constraints are shown (as *dotted lines*). These represent the values of another dimension. Representing more than three dimensions is difficult, but by showing the values of these samples, we get an idea of the values of every point on the plane.

In this case, we do not know if all points along the specific constraints share the same relative fixity of body size, so for simplicity I have assumed that they do. If they did not, their values on the relative fixity of body size to forewing area axis of the specific constraints would change and the plain that they are on would curve. The line that represents the general constraint of Fig. 4 is actually redundant in Fig. 5, because it represents the same information as the plain’s location on that axis. If the line had been vertical, then the plain would be moved to the extreme left of the axis.

Just as Fig. 3 shows how a population of *Bicyclus anynana* can be moved through morphospace after selection on body size, while remaining under the same specific constraint, the plain on Fig. 5 shows the positions in morphospace that a population of *Bicyclus anynana* can be moved to by selection on body size, forewing area, and wing loading, while remaining under the same general constraint. Do other species fall under Brakefield’s general constraint? The great variety of wing loading and allometric relations among butterflies is well documented. For example, *Itaballia demophile* and *Itaballia pandosia*, both of the subfamily *Pieridae Pierinae* have similar wing length (26.8 and 25.2 mm), but quite different wing loading (0.74 and 0.53 N/m<sup>-2</sup>) (Dudley and Srygley 1994). Knowing these trait values is not enough to show that they do not share the same general constraint as *Bicyclus anynana* or

**Fig. 5** General constraint on *Bicyclus anynana*

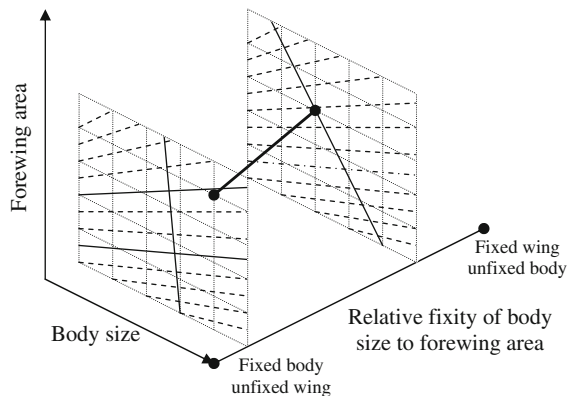


each other. In order to do so, we would have to know how they have changed or would change under selection for changes in wing loading. Repeating Brakefield's experiment on these species could show, perhaps, that selection for increased wing loading resulted in smaller wings in one or both of these species, more than larger bodies. Such a result would show that they are under a different general constraint than *Bicyclus anynana*.

Could a population of *Bicyclus anynana* be removed from this general constraint by selection? That is an empirical question, but it can be tested with another artificial selection experiment. The experiment would be complicated by the fact that it would not be selecting for different trait values but for a different way of evolving under selection. For example, subpopulations of the wild type could be selected for increased wing load. The population that most decreased wing area, rather than increased body size would be selected for further generations of selection. If the general constraint could be changed by artificial selection, we would expect that the way that it changed would also be constrained. That constraint on a general constraint I call a "very general constraint". Representing such a high order constraint gets tricky, but an attempt is made in Fig. 6.

The general constraint from Fig. 5 is shown in Fig. 6 along with another constraint of lesser relative fixity of body size to forewing area wing area fixity. Both general constraints share equivalent specific constraints although this is not necessary and may not be expected. The lesser relative fixity of body size to forewing area is indicated by the angle of the solid line on the second plain, which is redundant because it contains the same information as the plain's position on the relative fixity of body size to forewing area axis. The line between them represents a possible constraint on how a population selected for greater relative wing area fixity would move from a point on the first general constraint to the second, showing that the population would reduce body size more than it reduced forewing area. It shows a bias in how a population can change its general constraint and is thereby an aspect of what I call a very general constraint. This line is only an aspect of the very general constraint, just as the solid and dotted lines on the general constraint represent a sample of information about the directions of change that would tend to occur within the general constraint. If we were to learn the direction of additional

**Fig. 6** Possible very general constraint on *Bicyclus anynana*



transitions from the first general constraint to the second, we could plot them on the graph and show more about the nature of the very general constraint.

In the section “The range of constraints”, I introduced the notion of an exact constraint, which limits the variation of trait values to those similar to the current trait values of the population. In this section, I introduced the idea of a specific constraint, which is a constraint on the way trait values can change; a general constraint, which is a constraint on the way a population can change the way that it changes; and a very general constraint, which is a constraint on the way it can change the way it changes the way it changes. While constraints at high orders of complexity get complicated to represent and would require a great deal of empirical work to investigate, they remain mathematically tractable in  $n$ -dimensional hyperspace. Accepting the legitimacy of all or these constraints suggests the view I call the ‘hierarchical view of constraints’.

### **The hierarchical view of constraints’ challenge to the difference-maker argument for externalism**

Accepting exact, specific, general, and very general constraints as developmental constraints suggests the following view. Constraints are correlations between trait values in any generation before there is selection on that generation. A constraint may also be considered a trait value. Such a constraining trait value may itself be constrained by a higher order constraint. We can think of exact constraints as first order constraints, specific constraints as second order constraints, and so on. Adopting this approach does not suggest any conceptual limit to the number of orders of constraints on an organism (see also Sansom forthcoming).<sup>4</sup>

The difference-maker argument for externalism requires that it is an empirical truth that species tend to share constraints. The hierarchical view of constraints proposes a challenge to this argument, because species that do not share one order of constraint can be shown to share a higher order of constraint. In the case with the two populations of *Bicyclus anynana* that did not share a specific constraint between wing area and body size (shown in Fig. 4), we were able to show that they do share a higher order constraint, by introducing another variation variable of relative fixity of body size to forewing area (shown in Fig. 5). Figure 6 shows conceptually how populations that did not share the same general constraint could share the same very general constraint.

A population under constraint of some order can either change its trait values according to that constraint or free itself from that constraint and thereby acquire a new constraint of the same order. We would expect the acquisition of a new constraint to be constrained (by a higher order constraint). The only way that it might not be constrained is if there is no bias at all in the way that the population changed constraints. Even if this is a conceptual possibility, it seems an empirical

<sup>4</sup> Nijhout (2007) describes how  $n$ -dimensional genotypes between  $n$  quantitative phenotypic values can be described in an  $n$ -dimensional hyperspace. This is a representation of all of possible morphospace, which was assumed in Figs. 1 and 2. Although Nijhout had a different project to mine, his work inspired my view of higher order constraints described here.

improbability. Therefore, given that there is no theoretical limit to the order of constraints, it appears possible to show that any two species that share a common ancestor may be shown to share a constraint with regard to some trait value, because they will share some way of changing the way they change. The only question remaining is how high the order of the common constraint. On the hierarchical view of constraints, the sharing of constraints becomes metaphysically trivial, rather than the empirical tendency Sterelny takes himself to be relying on. Below, I consider two possible ways of avoiding this challenge to the difference-maker argument for externalism.

The first approach offers the following strategy for explaining trait values. First, find a trait value that differs between species. Second, show that both species share a pre-specified order of constraint (perhaps a specific constraint) that governs that trait value. Third, show that the trait value of each species is more adaptive than the alternatives (i.e. the selection regimes regarding that trait value in isolation for both species differ appropriately). Thus, the trait value difference is explained by selection rather than developmental constraints.

Such an explanatory strategy holds the laudable feature of possibly failing for empirical reasons when applied to a particular trait value difference between species. For example, the selection regime may be the same for that trait value  $T_1$  considered in isolation, but the difference in  $T_1$  would be due to different selection on value of trait  $T_2$  that is constrained by  $T_1$  (e.g. in each species  $T_2$  may be constrained by  $T_1$  and the adaptive value of  $T_2$  differs between species). In such a case, the externalist will be tempted to point to  $T_2$ 's different value and look to explain it in terms of a different selection regime on that trait value considered in isolation. Again, the selection regimes for  $T_2$ , considered in isolation, may be the same for both species, but the constraints may differ. The externalist can continue working her way through constrained trait values until she discovers a different selection regime. At that point, she will have an externalist explanation of the last trait value in the sequence, but will only have an explanation involving natural selection and constraints for the rest.

One cause of concern for this strategy is that the relatively high level of integration in an organism means that, even if the order of constraints is specified, each trait is likely to be under many constraints of that order. For example,  $T_1$  may covary with  $T_2$  and also  $T_3$ . Does the difference-maker argument require only that we find one specific constraint on  $T_1$  that is shared across species, or do they all have to be? If only one constraint must be shared, then we should be concerned about the objectivity of any difference-maker argument in cases when most constraints are not shared. If they all have to be shared, then, given the difference in other trait values between species, it is a good bet that many of the specific constraints are different too (i.e. only high level general constraints will be shared). The different constraints should then play an important part of the explanation of the difference between the species.<sup>5</sup> If the selection regimes are the same, then difference-maker logic favors internalism over externalism. More likely (in my

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<sup>5</sup> For example, the selection pressures faced by population A, with A's constraints, would have had different effects on population B, with B's constraints.

opinion) the selection regime will differ too, leaving difference-maker logic unable to support either internalism or externalism over the other.<sup>6,7</sup>

My other concern with this approach is that it assumes that we can legitimately pre-specify the appropriate order of constraint. I am concerned about the legitimacy of any such starting point, because the trait values used in the examples cited here, like body size, are already gross generalizations about the organism. Body size can itself be thought of as an abstract fact about the process of ontogeny. So when dealing with such high level abstractions, I worry that we can appropriately calibrate the order of constraints to be studied.

Consensus in the approach of biologists concerning the order of constraint studied could possibly reduce this concern to a metaphysician's tit-bit—another “grue” problem that we would do better to get over (Goodman 1954). While I cannot rule this out, I take Brakefield's work to be an example of science running into the metaphysical issue and not offering an answer clear or rigorous enough to justify what the difference-maker argument for externalism needs.

The second approach deals with the distinction between capacity constraints from constraint mechanisms that I made at the beginning of this paper. Maynard Smith's definition of developmental constraints is the definition of a capacity constraint and the practice of biologists has focused on limitations on the capacities of development of members of a population. On this view, different mechanisms may be responsible for the same limit on a developmental capacity shared by species and species may share the same mechanism, but it may be responsible for different constraints in each.

It is worthwhile to also consider the alternative of identifying developmental constraints not with capacity constraints, but instead with constraint mechanisms and seeing whether or not this might solve the constraint identity problem for the difference-maker argument for externalism. Constraint mechanisms could be inherited from a common ancestor, whether they are defined narrowly (in terms of what links the trait value with just one other trait value) or broadly (in terms of what links the trait value with multiple other trait values). However, such mechanisms would be expected to mutate and with those mutations would come changes in the effects of the mechanism. According to this approach, the same developmental constraint that is responsible for one capacity limit between the values of traits  $T_1$  and  $T_2$  in one species could be responsible for the capacity limit between the values of traits  $T_3$  and  $T_4$  in another. Looking at the details of the shared mechanism would encourage us to see that there is something shared, which could allow constraints to be shared across species when selection differs, which is just what the difference-maker argument for externalism requires.

I reject this approach to saving the difference-maker argument for externalism, because I do not think mechanisms are developmental constraint. This is to say that

<sup>6</sup> Convergent evolution poses some threat to this, but it is relatively rare and selection regime detail might still differ.

<sup>7</sup> Speciation events probably involve the splitting of a population. Both subpopulations may have just the same constraints but might not. However, the fact that speciation happens is not the \$64000 question. It is not the existence of variety, but the existence of adaptive variety that natural selection is supposed to explain in terms of difference according to the difference-maker argument.



I agree with Maynard Smith et al. (1985) when they defined developmental constraints in terms of capacities, rather than mechanisms. That is the approach that is currently taken by Brakefield, Nijhout, etc. This approach could be usurped by one that named mechanisms as constraints. However, this would be a pickwickian way for this argument for externalism to be saved, because it would change what it was defending, because it would be the lesser importance of developmental mechanisms, rather than the lesser importance of developmental capacities. That said, I think that the practice of science should be the primary arbiter of how such terms are defined, so the pickwickian defense remains a possibility for the future.

## Conclusion

Arguments for explanatory adaptationism have focused on the relative explanatory power of natural selection and developmental constraints. Accordingly, the arguments for externalism have had to make assumptions about developmental constraints. These assumptions are dangerous because evolutionary theorists have paid relatively little attention to analysis of developmental constraints, and developmental constraints deal in the theoretically difficult realm of possibilities. I have criticized two widely held views about constraints. First is the view that developmental constraints are a purely internal concept. I have argued that it is generally difficult to separate developmental constraints from natural selection, and that constraints must be understood as relative to the nonselective environment. Second is the view that constraints tend to be shared across species, while natural selection is not, leaving only natural selection as explanatory of biodiversity. I have suggested that exact constraints, which are not shared, may be legitimate and proposed the hierarchical view of constraints that suggests that it is a metaphysical tautology that some order of constraint will be shared by any species with a common ancestor.

I have offered the hierarchical view of constraints and some lessons about their nature. In general, I propose that without careful analysis of developmental constraints, arguments about their relative explanatory importance should be approached with caution.

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