

A utilitarian approach to evolutionary constraint

Kurt Schwenk

Department of Ecology and Evolutionary Biology, U-43, University of Connecticut, Storrs,
Connecticut 06269-3043, USA

Received: 1. 8. 1994; revised version: 21. 1. 1995; accepted: 30. 5. 1995

Key words: adaptation, natural selection, evolutionary stasis, parallelism, development

Summary

The concept of evolutionary constraint is central to current perceptions of the evolutionary process, but operationally, it is difficult to apply. Much of this difficulty stems from conceptual ambiguity and inconsistent usage. The broadest conception of constraint as “historical contingency” has little pragmatic value because it universalizes constraint to a property of life. Likewise, equation of stabilizing selection with constraint creates unnecessary conceptual redundancy. Conceptions of constraint that emphasize mechanism over phenotypic or phylogenetic patterns tend to eliminate redundancy and restrict constraint to a force that shapes the action of natural selection, and which may oppose it. Constraint is a property of characters, not lineages, and at this level is always negative in the sense of limitation. However, character constraint is neutral to organismal adaptation and, therefore, can have either negative or positive evolutionary effects at the lineage level (i.e., hamper or promote organismal adaptation). Constraint hypotheses can be framed from either a posteriori or a priori perspectives that show that constraint is sensible only when bounded within a relative time-frame. Both stasis and parallelism have been invoked as phylogenetic manifestations of constraint and these alternate conceptions can lead to opposing hypotheses about the time and place of action of constraint. Disallowing pattern as *prima facie* evidence of constraint avoids this conflict. Homology and *Bauplan* might reflect the action of constraint at the level of one and many characters, respectively, but the failure to evolve at any given hierarchical level should not be taken as direct evidence of constraint.

Introduction

Neo-Darwinism has tended to focus on adaptation and the evolutionary lability of phenotypes. This focus emphasizes a positive, or constructive, view of evolutionary change driven by the engine

of natural selection and leading, inevitably, to ever greater refinement of organisms and their parts. The extreme expression of this view has been called the “adaptationist program” and it has been criticized for its failure to consider adequately the possibility that there may be limits imposed on evolutionary change and, therefore, the power of natural selection to shape optimal phenotypes (Gould and Lewontin 1979). As Gould and Lewontin (1979) and others (e.g., Maynard Smith et al. 1985; Stearns 1986; Gans 1989; Hall 1992) pointed out, the concept of evolutionary limitation is not new and is particularly evident in the notion of *Bauplan*, which itself grew out of eighteenth and nineteenth century beliefs in archetypes and idealized forms (Hall 1992). Nonetheless, since Gould and Lewontin’s (1979) seminal paper, there has been an increasing awareness in the literature of the fact that not all evolutionary outcomes are equally likely and that the phenotypic space potentially occupied by an evolving lineage may be bounded – concepts now generally subsumed under the rubric of “evolutionary constraint”.

Heightened awareness of evolutionary constraint has led to a burgeoning literature in which the concept is invoked. The inconsistent manner in which constraint has been used and the confusing terminology surrounding it have led some to question the utility of the concept and to seek controls on its application (e.g., Stearns 1986; Gould 1989; Antonovics and van Tienderen 1991; Perrin and Travis 1992). However, the concept is not only valid, but essential to any complete understanding of evolutionary patterns and processes; therefore, its continued elucidation is worthwhile. My goal here is to make explicit the several ways in which the concept of constraint has been used and to explore some areas of confusion that I perceive in

the literature. I show that different notions of constraint vary in their conceptual utility and degree to which they are redundant with existing theory, and conclude that the most restrictive definitions of evolutionary constraint are of greatest heuristic and practical value.

The series of broadly overlapping topics that follow reflect my subjective interpretation of problem areas and my pragmatic desire to delimit the notion of constraint in such a way as to maximize its utility. I more or less equate the terms phylogenetic constraint and evolutionary constraint, but it should be noted that some approaches to evolutionary constraint (especially the optimality approach of Dullemeijer [1991] and others; see below) do not require an explicit phylogenetic context. Finally, it is not the purpose of this paper to review fully the topic of evolutionary constraint, nor to consider the many comparative methodologies that have been proposed to identify it. For such reviews I refer the reader to Maynard Smith et al. (1985), McKittrick (1993) and Losos and Miles (1994).

Carl Gans has contributed to the concept of phylogenetic constraint (e.g., 1985, 1989), as he has to many topics in evolutionary biology. His writings, in general, have been a source of inspiration in much of my work. Therefore, it is a pleasure to dedicate this essay to Professor Gans.

Evolutionary constraint, in its broadest conception, is a trivial notion

Constraint, especially "phylogenetic constraint", sometimes is defined as any limitation on phenotypic evolution that results from past evolutionary change in a particular lineage (e.g., Schluter 1989; Ligon 1993; Smith 1993). In other words, the direction of future evolutionary change is contingent upon past change. This notion of constraint can be referred to as "historical contingency" (e.g., Gould 1989; Wagner 1989; Wake 1991) and is related to notions of "phylogenetic effect" (Derrickson and Ricklefs 1988), "phylogenetic inertia" (Cheverud

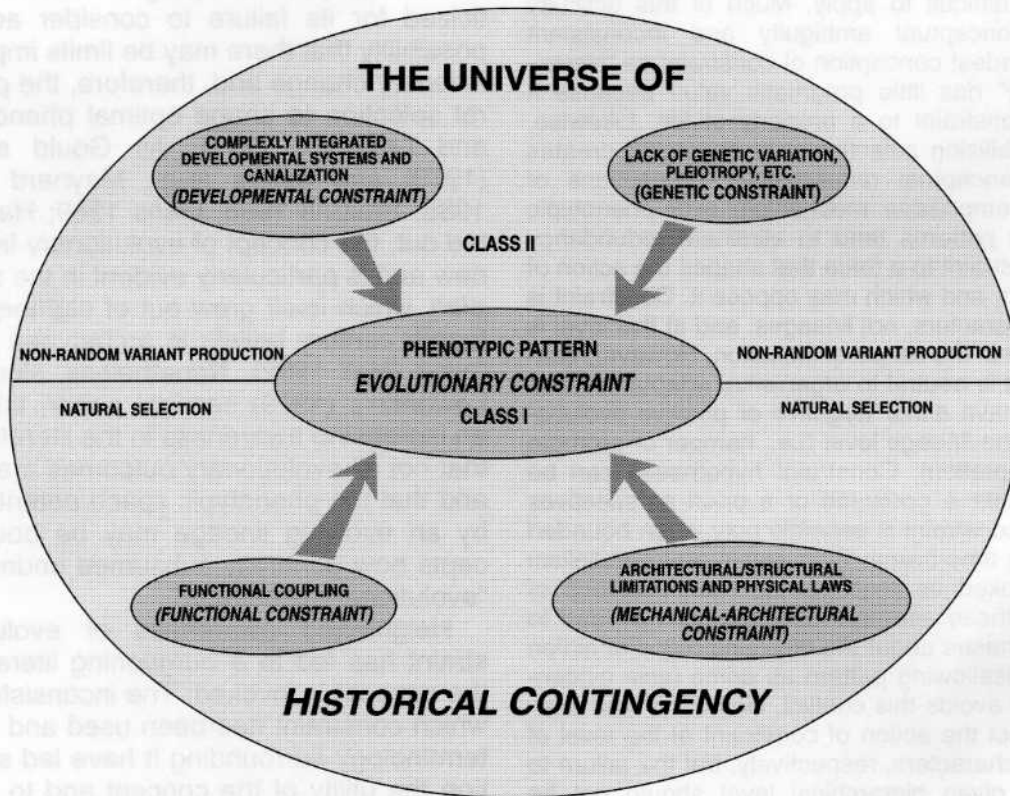


Fig. 1. The notion of historical contingency is equivalent to the total set of constraint concepts. Class-I conceptions of constraint generally are recognized by some phenotypic or phylogenetic pattern. Because they usually are not specific as to the mechanism underlying the putative constraint, they accept natural (stabilizing) selection as one possible cause and posit the pattern as prima facie evidence of constraint. So-called "selective constraints" fall into a variety of types, only a few of which are named here. Class-II constraints, although built by selection, are manifest in the nonrandom production of phenotypic variants upon which further selection can act. These genetic and/or developmental constraints can lead to similar patterns as "selective constraints" and, therefore, must be distinguished by additional investigation into process. As such, Class I and Class II are not mutually exclusive categories, but Class II is more restrictive in that it disallows selection as the process leading to the pattern.

et al. 1985), and "a set of initial conditions" (Thomas and Reif 1993).

While it certainly is true that past history constrains future change, historical contingency is a characteristic of all life at all times. Therefore, it has little value as a definition of evolutionary constraint. Operationally, such a definition leads to the conclusion that all characteristics of all lineages are constrained during the entire course of their existence. Thus, constraint is simultaneously elevated as a universal characteristic of living systems and trivialized as a useful concept, because it becomes tantamount to evolution, as does heterochrony in some recent works (e.g., McKinney and McNamara 1991). I conclude that historical contingency represents the total universe of evolutionary constraint (i.e., the largest possible set; Fig. 1) and, therefore, is an heuristically useful starting point, but of limited operational value. Useful definitions will be much more restricted in their scope.

Likewise, so-called "universal constraints" (Alexander 1985, Maynard Smith et al. 1985; Gould 1989; Wagner 1989; Thomas and Reif 1993), arising from physical laws and invariant properties of matter, do not constitute a useful class of constraints, because of their very universality – i.e., they apply to all life at all times. As Wagner (1989: 1164) noted for the concept of homology, "global and immutable constraints are of little interest, because they cannot account for lineage specificity". Such universal constraints certainly do set boundary conditions for the evolution of phenotypes, but they are ahistorical (in an evolutionary, if not a cosmic, sense) and, therefore, are not part of the universe of historical contingency. Rather, they should be regarded as a fundamental and unchanging part of the environmental milieu, and therefore, a source of selection pressures. Just as an extremely xeric environment will impose strong selective forces on organisms, so too will the force of gravity or the allometry of volume and surface area. These can only be regarded as evolutionary constraints in the broadest formulation of this concept. (See below.)

General classes of evolutionary constraint and the relationship of constraint to natural selection

Two general classes of definition have significant ramifications for the way in which we conceive of evolutionary constraint. In *Class-I* definitions, constraint is broadly envisaged as *evolutionary channeling*. These conceptions of constraint include the notion of "boundary conditions" (e.g., Gould 1980; Lauder 1981; Stearns 1984; Alexander 1985; Dullemeijer 1989, 1991; Thomas and

Reif 1993) and also the observation that some lineages occupy only part of a theoretically possible "morphospace" available to them (e.g., Raup 1966; Gould 1980). Although by no means uniform, these conceptions are similar in that they are based on the idea that the path taken by an evolving lineage through phenotypic space is somehow bounded or limited. They can be regarded as *pattern definitions*, because such a notion of constraint springs from (and is recognized by) some phenotypic pattern. Constraint usually is recognized by the observation of evolutionary stasis (see below), but also comparison of existing phenotypes to theoretically possible phenotypes (the morphospace approach), or comparison to theoretically optimal phenotypes (the optimality approach). Importantly, a variety of underlying mechanisms can lead to such patterns (Fig. 1).

Class-II definitions can be summarized as *the nonrandom production of variants* (e.g., Alberch 1980, 1982; Alberch and Gale 1985; Maynard Smith et al. 1985; Roth and Wake 1989; Wagner 1988a, b; Wagner and Misof 1993; Gould 1989; Oster and Murray 1989; Wake 1991). These usually are called *developmental constraints*, because they reflect a developmental bias in the production of phenotypic variants or a limitation of phenotypic variability stemming from the dynamics of an integrated developmental system (Maynard Smith et al. 1985). Also included here are genetic constraints (e.g., lack of genetic variation; pleiotropy), because these also can limit the availability of certain phenotypes. Class II can be considered *process definitions* of constraint, because they focus on underlying mechanisms that limit the types of new phenotypes produced with little regard to the lineage-level phenotypic or phylogenetic patterns they might generate.

To an extent, these two conceptions of constraint reflect the philosophical dichotomy between neo-Darwinian functionalism (externalism) and biological structuralism (internalism) (Classes I and II, respectively) discussed by Wake and Larson (1987) and Wake (1991). Of critical importance, however, is the distinction between the classes in their relationship to natural selection. Class-I definitions allow that any number of mechanisms can lead to the pattern of phenotypic channeling observed, *including natural selection*. For example, strong stabilizing selection on an integrated functional system can lead to evolutionary stasis. In other words, evolution of a certain character complex is viewed as constrained, because most character changes would tend to disrupt the integration and, therefore, the functionality of the system. In this scenario, there is no reason to suppose that production of variants is anything but random, only that selection weeds them out if they lack function-

nality, or are less functional than the existing, integrated system. The result is phenotypic channeling evident as stasis. If, as in this case, stabilizing selection is acceptable as a mechanism of evolutionary constraint, then the pattern of evolutionary stasis is, itself, *prima facie* evidence of constraint. (See below.) Indeed, most authors accept a class of constraints known as "selective constraints" (e.g. Maynard Smith et al. 1985, Gould 1989, Schluter 1989; Hall 1992; Perrin and Travis 1992; Smith 1993). Upon close examination, many examples of constraint (especially so-called structural, mechanical, and functional constraints) are themselves explicable as manifestations of selection, especially stabilizing selection. In contrast, Class-II definitions disallow the possibility of selection as constraint. In this conception of constraint, the nonrandom production of phenotypes creates a limited variety of phenotypes upon which natural selection can act. As such, *constraint is a concept at once distinct from and in juxtaposition to that of natural selection*. This notion of constraint is consistent with that originally formulated by Gould and Lewontin (1979).

The relationship between constraint and natural selection is much more complex than characterized here and deserves more extensive treatment. For example, although a Class-II constraint is conceived here as a force independent of natural selection, at some level, selection builds and possibly maintains the developmental systems that bias phenotypic variation, thereby causing the constraint (e.g., Maynard Smith et al. 1985; Stearns 1986)! Similarly, if selection moves a phenotype towards an adaptive peak (directional selection), and then acts to maintain it at that peak (stabilizing selection), do we distinguish these types of selection by calling the latter constraint? In other words, once an integrated functional system is evolved, does the fact of its integration qualitatively change the dynamic between phenotype and selection?

A maximally useful conception of evolutionary constraint must exclude natural selection as a causative (mechanistic) agent. A large body of work already deals with stabilizing and directional selection. Why, at this point, should we refer to these well-understood processes as constraint? The conflation of selection and constraint creates a conceptual redundancy that serves little utility. Therefore, we must distinguish between a phenotypic pattern and the causative processes that might lead to that pattern. Because the phenotypic patterns used to invoke constraint might also be explicable as results of natural selection, pattern should not be used as *prima facie* evidence of constraint. Rather, it should be starting point for examining further the potential roles of selection and process (Class II) constraints in creating the observed pat-

tern. If further analysis reveals the action of stabilizing selection as the basis of phenotypic channeling, we should call it just that and not evolutionary constraint. If, on the other hand, we find evidence of constraint on the production of phenotypic variants, then we can study independently the nature of the constraint (the developmental and/or genetic system) and its phylogenetic manifestation (stasis, parallelism, or other pattern; see below). There is no *a priori* reason to suppose that a given pattern reveals a particular type of constraint, or that a type of constraint always produces the same phylogenetic pattern. Thus, the conceptual decoupling of pattern and process helps to clarify the roles of the many different, clade-specific factors potentially involved in creating evolutionary patterns.

Characters, not clades or organisms, are constrained

Even in formal treatments of evolutionary constraint, there is a tendency to slip into an informal vernacular by treating entire clades as the constrained entities (e.g., Maynard Smith et al. 1985; McKittrick 1993). For example, McKittrick (1993) suggested that birds might be phylogenetically constrained relative to mammals as evident in their failure to evolve viviparity. Because birds are highly successful as a vertebrate clade by most any measure of evolutionary success (diversity, distribution, species number, etc.), they hardly can be thought of as "constrained". Of course, implicit in this usage of constraint is that *the suite of characters associated with viviparity* might be constrained in the bird lineage. Nonetheless, this usage leaves the reader with the impression that birds are, somehow, less successful or less adapted than mammals and it is this vague sense of *organismal* limitation (inferiority?) that potentially leads to problems.

Evolutionary constraint is a property of characters, not of organisms or clades. As Dullemeijer (1991: 322) noted, "it is the selection of a *limited part* of the organism or construction that leads to the introduction of the constraint concept" (italics added). The failure to make this distinction may seem trivial, but it has led to further confusion. (See below.) Statements about evolutionary constraint should be restricted explicitly to characters or sets of characters.

Positive versus negative views of constraint and the relationship between constraint and adaptation

Constraint, as envisaged by Gould and Lewontin (1979), acts as a check on the optimizing power

of natural selection and was therefore seen as a limiting or "negative" evolutionary force. Most conceptions follow this lead and emphasize the *limiting* effects of constraint (e.g., limited types of variants produced, limited part of potential morphospace occupied, nonoptimal design features; see above). Some have suggested that constraint is miscast in this negative role and that we should further emphasize its positive, or *directional* role in organismal evolution. For example, Alberch (1982: 313) suggested that discontinuities in the variants produced by development (constraint in the negative sense) can result in "directionality in morphological transformation". Maynard Smith et al. (1985) conceived a positive role for constraint in serving as a "directing force" and Gould (1989: 518) suggested that constraint could act positively by "forcing an action in a particular way." Gould (1989), in particular, wished to emphasize the positive aspect of evolutionary constraint and used the etymology of the word "constraint" as justification for this view. For these authors, the essential point is that constraint can be a positive, or "creative", evolutionary force.

Confusion over whether constraint is a positive or negative evolutionary force arises from a conflation of hierarchical levels. It stems from the failure to distinguish clearly between *what is* constrained (characters) and the potential evolutionary *effect* of the constraint on the *lineage*. If one adopts a Class-II (process) definition and restricts the constrained entities to characters (not whole organisms or clades), then a negative role for constraint (as a force limiting or channeling the effects of natural selection) is inevitable. Pragmatically, this may be the most useful approach. However, while the character(s) may be constrained, the organisms and the clade to which it belongs are not (as pointed out above), and this is where there is apt to be confusion. *The character constraint is neutral to organismal adaptation*. So, while the constraint must always be negative, its effect on the organism may or may not be. Indeed, Wagner (1988a, b) argued that some level of developmental constraint of characters (in the negative sense) may not only increase the rate of adaptive, phenotypic evolution, but may be *necessary* to such evolution. Wagner (1993) further suggested the possibility that developmental constraints might "tune" phenotypic variation to the changing slope of the adaptive landscape so that variants are more likely to fall nearer an adaptive peak, thus promoting "evolvability". Thus, a negative developmental constraint (limitation or bias in the production of phenotypes) can lead to a positive evolutionary result (increasing adaptation) for the lineage evincing the constraint. Conversely, one easily can imagine a scenario in which the constrained production of

phenotypes limits the ability of natural selection to optimize some design parameter, resulting in a negative evolutionary (maladaptive) effect of the character constraint.

Inferring the action of constraint from phylogenetic pattern

In this section, I will consider only phylogenetic notions of constraint. Other approaches to inferring evolutionary constraint, such as comparison to optimization models (e.g., Otten 1985; Barel et al. 1989; Dullemeijer 1989, 1991; Zweers 1991; Galis 1993), are excluded. Such approaches, while valid, provide different kinds of information that are largely independent of particular phylogenetic hypotheses. Because phylogenetic constraint, in the strict sense, is usually taken to be a manifestation of clade-specific historical processes, its recognition will be rooted in referral to an explicit phylogenetic hypothesis (McKittrick 1993; Losos and Miles 1994).

According to the preceding discussion, a conception of phylogenetic constraint should be character-based and it should reflect some notion of restricted or limited character evolution. Given these requirements, the recognition of phylogenetic constraint devolves to a particular pattern of character state distribution across an explicit phylogeny. However, one of the most confusing and problematic aspects of the constraint literature is that there are two, fundamentally different, phylogenetic patterns that have been put forth as evidence of constraint: 1) phenotypic stasis, and 2) repeated, independent evolution of similar forms (parallelism). These patterns can lead to differing hypotheses regarding the time and place of action of constraint. Indeed, hypotheses of constraint so-generated can be in direct conflict with one another. (See below.)

• Stasis as evidence for phylogenetic constraint

Long-term, plesiomorphic character stability (stasis) within a clade in juxtaposition to character change (evolution) in a sister clade. Null model: character change.

Stasis, as defined above, is the most common pattern used to invoke the action of phylogenetic constraint (e.g., Maynard Smith et al. 1985, McKittrick 1993). In this conception of constraint, there is implicit or explicit a null model of evolution as change. (See Antonovics and van Tienderen [1991] for arguments related to the necessity of a null model.) In other words, in the absence of constraint, characters will change through time by whatever process (selection and adaptation, drift,

