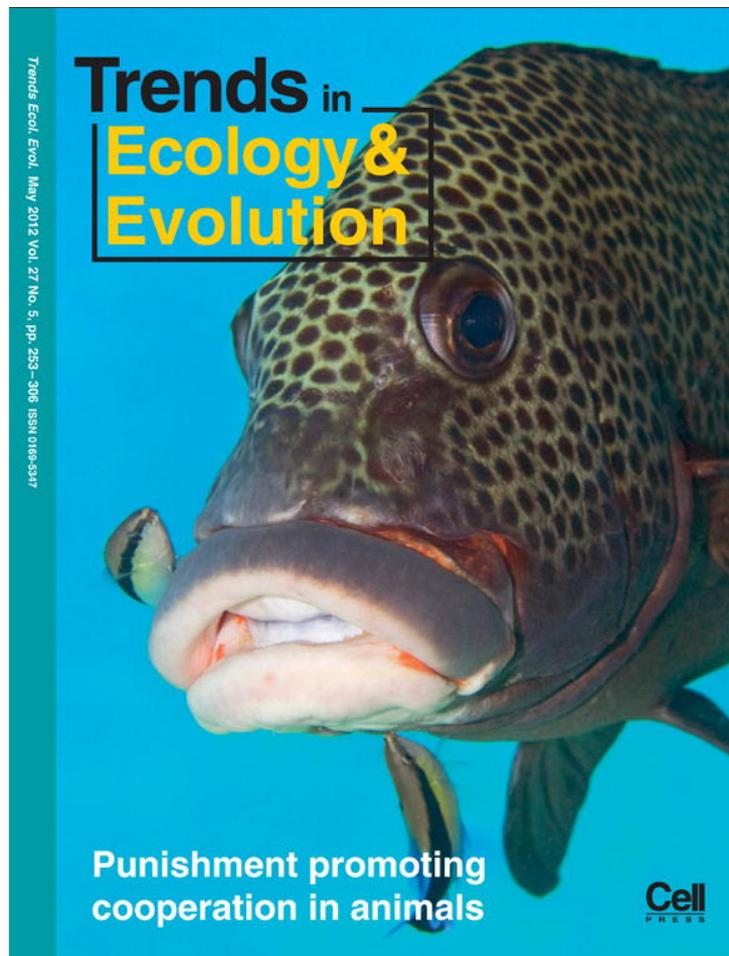


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The developmental renaissance in adaptationism

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From an adaptation perspective, unoccupied patches of morphological space are inferred to be empty because they are of low fitness and selected against. These inferences hinge on venturesome assumptions, because emptiness is explained by low fitness and low fitness is inferred from emptiness. Moreover, non-adaptive factors, such as developmental constraint, could also plausibly account for empty morphospace. In response, biologists increasingly study ontogeny to test the assumption that unobserved phenotypes could be produced if selection were to favor them; finding that empty space morphologies can be readily produced in development helps reject constraint and lends support to adaptive hypotheses. This developmental approach to adaptation calls on manifold techniques, including embryology, artificial selection and comparative methods. Belying their diversity, all of these methods examine the causes of empty morphospace and mark a return of development, long excluded from traditional evolutionary biology, to adaptationist practice.

Adaptation, constraint and development

Adaptation (see [Glossary](#)), manifest in the fit between organismal form, function and the environment, often seems so obvious and widespread that it scarcely inspires scientific testing. A walk in the woods near my house reveals endless apparent examples: plants with hollow stems that distribute their scant tissue in a way that is near-optimal mechanically; crab spiders that perfectly mimic the flowers they lurk on; or highland rabbits, whose tiny, frost-resistant ears seem ideal for hunkering down on cold mountains. However, for all its apparent pervasiveness, adaptation is hard to study because multiple, even non-adaptive, explanations can often account for the same set of observations.

With their famous essay on the ‘spandrels’ⁱ of San Marco, Gould and Lewontin [1] changed the way that adaptation is studied, precisely because they forcefully argued that biologists need to take seriously non-adaptive explanations of organismal form [2,3]. Foremost among their alternatives to adaptation was the notion of constraint, the idea that some morphologies are unobserved

not because they are eliminated by natural selection but because of inherent tendencies of development ([Box 1](#)). The Spandrels paper ensured that no student of adaptation would ever again fail to think about constraints, but what Gould and Lewontin did not provide was a conceptual and empirical framework up to the task of integrating constraints into studies of adaptation. The result has been a confusing literature with contradictory adaptive and non-adaptive explanations for the same data. For example, there seems to be a positive linear relationship between basal metabolic rate and body size across animal groups, as in [Figure 1a](#). One camp says that patterns of this sort, which span many taxa and are often called ‘scaling laws’, ‘are presumed to be consequences of natural selection’ [4]; that is, they reflect adaptation. Referring to the same observations, other authors take a completely different

Glossary

Adaptation: the process by which form comes to reflect function as the result of the action of natural selection; also an organismal ‘part’ that reflects this process [75].

Adaptationism: thinking of adaptation as the cause of the form–function fit; this term has no necessary negative connotation. The ‘adaptationist program’, by contrast, is an often pejorative term for the combination of the tendency to explain all organismal features as adaptations, protecting adaptive hypotheses from rejection with ad-hoc explanations, reluctance to entertain non-adaptive hypotheses and the willingness to accept any plausible sounding adaptive story [2].

Allometric engineering: surgical alteration of organ proportionalities to examine the performance of trait values not observed in nature.

Allometry: a proportionality relationship between organismal variables, as in [Figure 1](#) (main text) [30].

Constraint: see [Box 1](#).

Development: the processes involved in the production of new structures or new individuals; applicable to all organisms, not just complex multicellular ones.

Developmental potential: the sum of all morphologies produced throughout the ontogeny of all individuals of a species, juvenile to adult and ordinary to teratological.

Externalism: the view that developmental potential is so vast that the outstanding directors of evolution are factors external to the organism; for example, the ‘abiotic environment’ [2,10]. Often a synonym for adaptationism.

Internalism: the view that the dynamics of the developmental system so channel developmental potential that they are the primary directors of the evolutionary process [10,61].

Morphospace: a depiction of developmental potential created by plotting two or more organismal variables against one another. [Figure 1](#) (main text) shows a bivariate morphospace in which the black dots represent the observed and the empty spaces the imaginable but unobserved.

Ontogeny: see development.

Serial homology: repeated structures, such as centipede segments, vertebrae, or flower parts, which are thought to derive from greater or lesser degrees of evolutionary modification of identical repeated parts present in an ancestor.

Teratology: the study of abnormal morphologies; this field shows that developmental potential is not haphazard but reveals underlying order impossible to explain via adaptation, and that nothing separates the normal from the abnormal, merely the common from the uncommon. Atavisms are teratological ‘throwbacks’ to ancestral conditions, as in [Figure 2g](#) (main text) [14].

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ⁱ The full title of their essay was ‘The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme’. It is often just called Spandrels for short, a convention followed here.

Box 1. A constraints lexicon

'Constraint' is a wastebasket term, with different authors throwing different things into it [68,76–78], often making different uses of the term incommensurable. This list offers a (partial) guide to common meanings, but more important than terminology is framing questions clearly. Avoiding the term in favor of more precise wording (e.g. tradeoffs, low trait variance, etc.) might provide the clearest communication.

- Developmental constraints: as used in practice by adherents of the developmental approach to adaptation (and, therefore, in this review), regions of morphospace that are developmentally inaccessible.
- Quantitative genetic constraints: the breeder's equation $r = h^2s$, in which r is the response to selection (intergenerational change in population mean), s is the intensity of selection, and h^2 is the heritable genetic variance in a trait, highlights low trait variance as a 'constraint' to change because r disappears as h^2 drops. This sense offers conceptual challenges for all of evolutionary biology, for example whether population-level statistical summaries such as variances can be considered as real directors of evolution or whether they are simply convenient tools to guide thinking [33,67,79,80].
- Phylogenetic constraints: the tendency for closely related species to resemble one another; a pattern, rather than a process. Often shorthand for 'such a long way in morphospace from A to B as to seem impossible' [77,81].
- Selection in constraint's clothing: many uses of the term 'constraint' upon inspection turn out to refer to the action of natural selection. Terms such as 'selective constraint', 'adaptive constraint' and even 'architectural constraint' (Box 4) often diagnose this sense [82].
- Attractors: if development is thought of from a systems perspective, some parts of developmental space, known as attractors, will be almost inevitably occupied, whereas fringes of morphological space distant from attractors will never or only transiently be produced, leading to unoccupied, 'constrained' space [65,83–85].
- Tradeoffs: when two or more features compete for the same developmental resources, the developmental possibilities will be limited; for example, the same pool of resources can produce many small or one large egg, but not many large eggs [18,30].
- Ontogenetic cascades: parts that differentiate late in development share more in their fate than parts that diverge early, limiting the evolutionary flexibility of late diverging parts [68].

position, that '[t]he conclusion here is inescapable, that the driving force for these invariant scaling laws cannot have been natural selection', instead invoking constraint [5]. Both camps make untested and often unarticulated

assumptions that are legacies of the missing framework for studying constraints and adaptation. In this review, I chart the emerging framework that evolutionary biologists have been quietly building in many independent strands toward a post-Spandrels consensus with the exploration of development as its centerpiece.

This framework, the developmental approach to adaptation, is motivated by thinking about empty morphospace (Box 2). Most patterns demanding the attention of students of adaptation include generally unobserved but plausibly imaginable phenotypes, such as six limbs in vertebrates, eight cervical vertebrae in humans, or the morphologies corresponding to the blatant empty triangles above and below the scaling line in Figure 1a. If the pattern in Figure 1a is considered to reflect adaptation, then it would be expected that the empty space morphologies are readily produced in development but of low fitness and eliminated by selection (Figure 1b). By contrast, constraint hypotheses imply that the pattern is observed because the morphologies above and below the scaling line are developmentally very rare or impossible (Figure 1c). Either way, to address these issues empirically, biologists must explore development [6,7].

To explore development in testing hypotheses of adaptation and constraint, biologists deploy the battery of empirical approaches I turn to next. After surveying the three main strategies embodied by these approaches, I conclude that what is being witnessed is much more than the simple fulfillment of the Spandrels mandate to entertain non-adaptive hypotheses. Although this has surely happened, what is also occurring is the construction of common ground to unite the scientists who see adaptation as the foremost cause of organismal form with those who see development as the primary director of form. In the process, the developmental approach represents a move away from the daunting but common question of 'what are all the imaginable ways that evolution could be constrained?' [1] to the much more tractable 'why do I see this particular empty space in my data?' Most importantly, I show how the developmental approach strengthens inferences of adaptation and identifies essential research priorities.

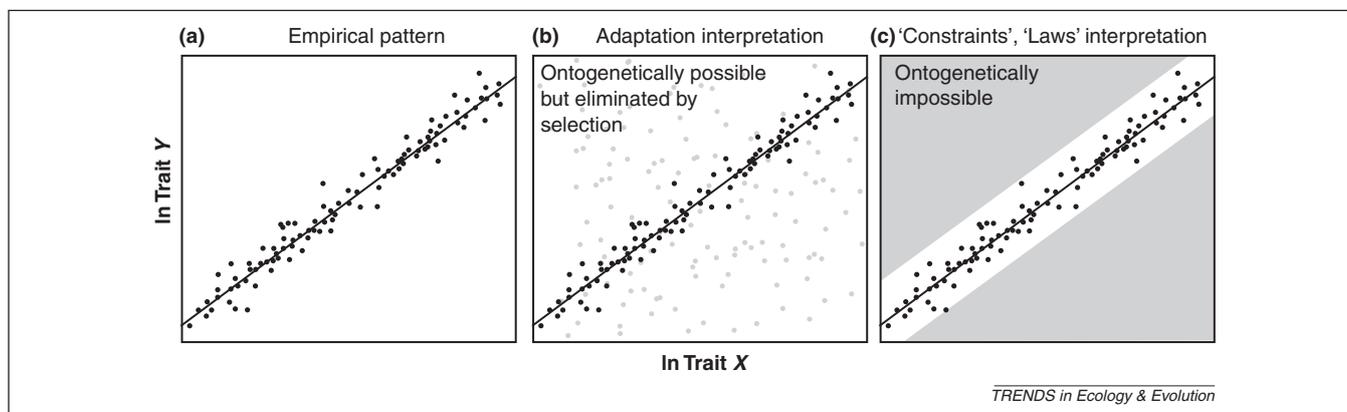


Figure 1. 'Adaptation' and 'constraints' explanations for the same data, and the common ground of ontogeny. (a) Empirical data present a pattern to be explained, a striking scaling relationship and conspicuous empty spaces. The black points represent observed data, which could be individuals within a species or even species mean values, the line a regression fit. (b) From the point of view of adaptation, an allometric scaling relationship between two traits is assumed to correspond to the highest fitness trait combinations. The empty areas are assumed to be ontogenetically accessible, but if produced (gray points) would be of lower fitness than the observed ones. (c) By contrast, from a constraints perspective, exactly the same data would be interpreted as indicating areas of difficult or impossible developmental access (gray fields). Without studies of developmental potential, it is impossible to distinguish between these positions.

Box 2. Doing the adaptationist two-step: adaptive patterns and developmental potential

Studies of adaptation from a developmental perspective have two broad steps, one that documents a potentially adaptive pattern of trait variation, followed by exploration of developmental potential using one or more of the three main strategies: embryological, manipulation or comparative. Using a comparative strategy, Swartz and Middleton [86] constructed an empirical morphospace depicting limb bone proportions of terrestrial mammals from tiny shrews to huge gorillas (Figure 1a). Such relationships are often described as being inescapable owing to 'laws' or 'constraints' [1,5,87], which would mean that the morphologies corresponding to the empty spaces above and below the allometric scaling line are ontogenetically impossible. To test this idea from a comparative perspective, data from other groups can be added; Swartz and Middleton added data from bats. With their very long, slender bones, the bats fell far above the terrestrial mammals (Figure 1b), vividly showing that the space above the terrestrial allometric line is indeed ontogenetically

accessible. Adding whales shows that the occupied space is even wider (Figure 1c). Bringing to bear embryological–teratological methods, bone disorders show that multiple relationships, such as skeletal proportions or bone size–density relationships, are readily altered ontogenetically [88,89], surely making the space of possibilities wider still (Figure 1d). All told, that these 'empty' areas of morphospace are developmentally accessible means that the scaling pattern observed across the terrestrial mammals in Figure 1a is almost certainly the signature of selection, reflecting the bone proportions favored in terrestrial situations. Based only on Figure 1a, it might be inferred that variants not falling on the scaling line would have bones 'too thin' or 'too thick' for terrestrial life, but this supposition is built on the rickety reasoning that 'if these variants were the fittest we would observe them; we do not observe them, so they must not be the fittest'. The developmental approach to adaptation helps fortify such inferences (Box 3).

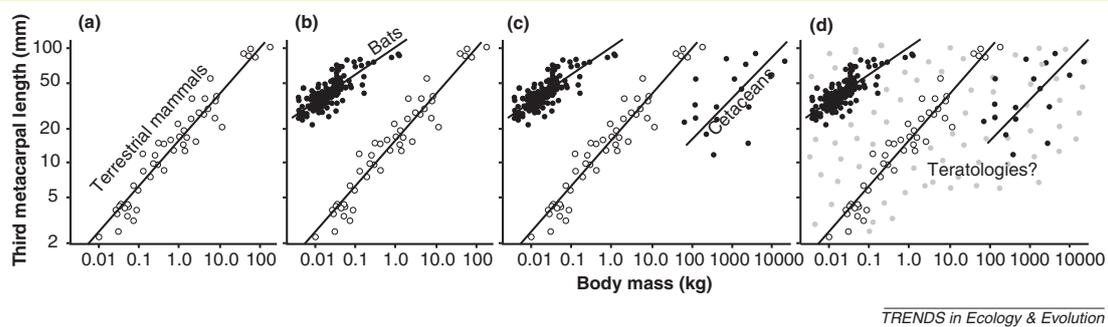


Figure 1. Application of the comparative and teratological approaches to bone–body size scaling patterns. Because the empty spaces are largely filled (b–d), the pattern in (a) is probably the result of selection, not constraint. Bat and terrestrial mammal data kindly provided by Sharon Swartz; cetacean data from the Australian Museum, Sydney, and the Institute of Biology, UNAM.

Exploring developmental potential: possible dogs, impossible centipedes and lizard surgery

The developmental approach to adaptation distinguishes between the ontogenetically impossible and the possible but unfit with an array of techniques that can be grouped into three main strategies: embryology, manipulation and comparative studies.

Embryology

The embryological strategy focuses on the array of morphologies produced in development within species, from the normal to the abnormal [8]. The variation produced across the arc of a typical ontogeny is broad, although often hidden in embryonic or juvenile stages [9]. Uncommon variants describe a still more prodigious array, and teratology, the study of deformities, gives particularly striking information regarding what can and cannot be produced developmentally (Figure 2) [10–14]. Every morphology along a developmental trajectory, and every freak or sport, is precious data for the evolutionist, because it shows what might be if selection were to favor it. Works such as Isidore Geoffroy Saint-Hilaire's studies of teratology, Gould and Pyle's 1896 *Anomalies and Curiosities of Medicine*, Wilder's early 20th-century systematization of human facial deformations and, more recently, Pere Alberch's all too short career [10,11] spotlighted developmental potential, showing that morphospace apparently empty when looking at common morphologies is actually a vast and often ordered constellation of possibilities (Figure 2, Box 2) [12].

Although of hoary heritage [15], teratological approaches are enjoying a resurgence. In a clever if ghoulish study, Galis *et al.* [16] examined cervical vertebra number in humans, seeking variation from the standard seven. Prowling for expired children in an Amsterdam hospital, they found that higher numbers of cervical vertebrae are common, but often associated with deleterious conditions. In the terms of Figure 1b, eight vertebrae is a condition surely accessible ontogenetically, but of low fitness. In a less cadaverous but equally ingenious botanical example, Flores-Rentería *et al.* [17] used teratologies to examine the evolution of bisexuality in pines. Pines usually bear separate male and female cones, but Flores-Rentería *et al.* scoured trees for rare teratological bisexual cones. Careful histological work and controlled crosses showed that bisexual cones are perfectly functional, bearing live pollen and setting viable seed. The authors concluded that pines seem capable of producing bisexual cones if selection were to favor them, and that unisexuality is probably the result of selection favoring outcrossing. Variation occurring naturally within species, from the normal to the teratological, is therefore a major source of information regarding which morphologies can or cannot be presented to selection. Sometimes, however, this variation is just not enough, driving biologists to take matters into their own hands.

Manipulation

Sometimes, biologists wish to study morphologies that are only very rarely observed in nature. In these cases, they

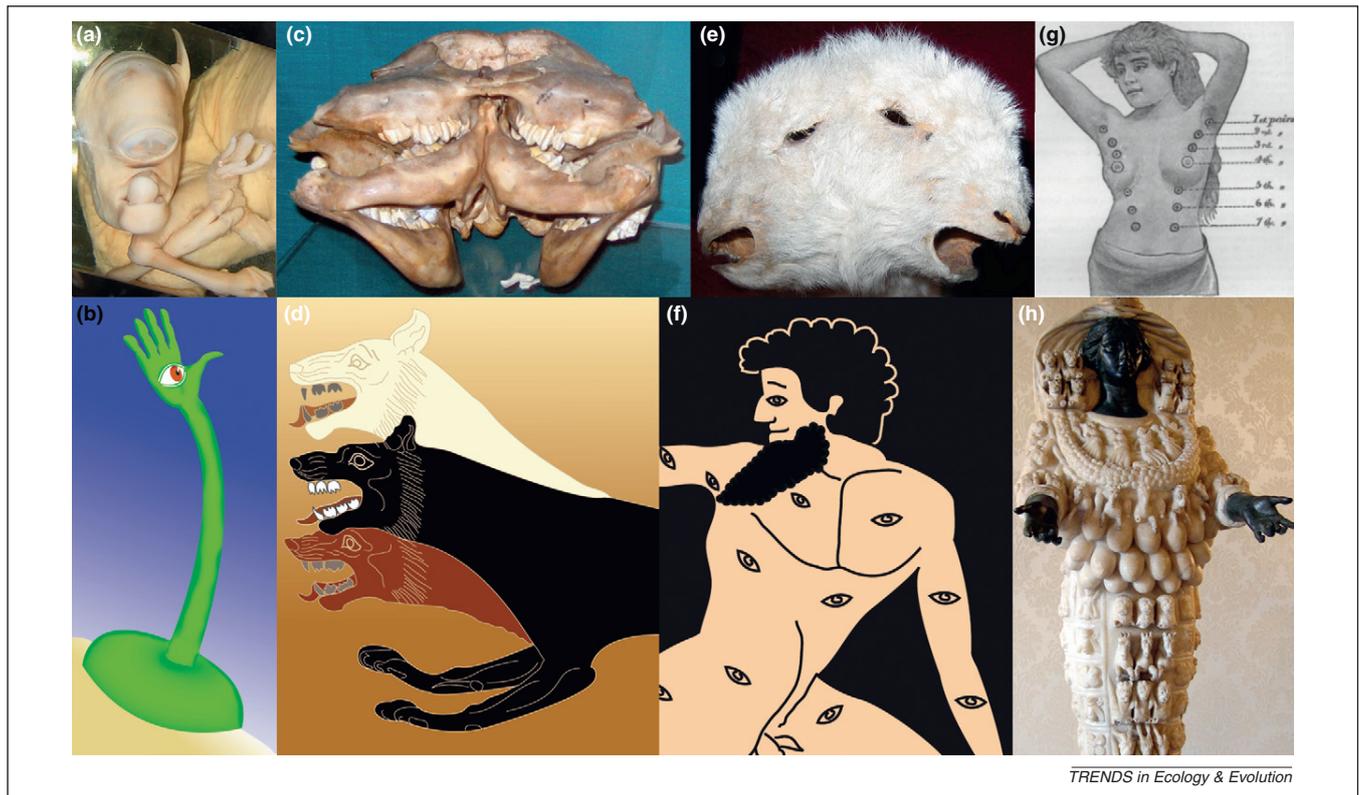


Figure 2. Teratologies ('abnormal' but possible morphologies, top row), imaginable but unobserved forms (bottom row) and order in development. (a) Individuals with single eyes generally have them along the midline, as in this calf fetus, and not in other imaginable places, as on the hands of Trafamadorians (b), extraterrestrials from Kurt Vonnegut's fiction. (c) Some triplications are possible, whereas others seem developmentally forbidden. This calf had three eyes as the result of diprosopia, a condition in which the forebrain is very wide with respect to the midline and the face widens or duplicates accordingly [12]. So, whereas partial duplication of the face can produce three eyes, having three heads seems to be found only in legend [10], such as this Cerberus from an Etruscan vase (d) or Fluffy of Harry Potter fame. (e) When multiple eyes are present, their position is predictable, as in this diprosopic lamb with four eyes, in contrast to the imaginable but unobserved morphology of Argos Panoptes of Greek myths (f). Williams's late 19th-century rumination on nipples [74] noted that 'There is no evidence whatever that such structures can arise just anywhere... on the contrary, I have shown that they only arise in positions which correspond with those occupied normally by the glands of polymastic animals' (g), making a multiple-breasted morphology, such as this Artemis from Roman Turkey (h), unlikely. Few adaptive explanations have been proposed for many of the predictable patterns in teratologies. That developmental possibilities are only a small subset of the imaginable and, moreover, are to an extent orderly, is one of the most compelling arguments for the importance of mapping developmental potential for studies of adaptation. (a), (c), and (e) from the Dugès Museum, Guanajuato, Mexico; (d) after a Cerveteri vase in the Louvre; (f) after an Attic vase in the Museum für Kunst und Gewerbe, Hamburg; (g) from [74]; (h) from the Capitoline Museums, Rome.

can use artificial selection or surgical intervention to drag individuals to areas of morphospace that they do not typically occupy, and even assess the performance or fitness of these variants. Recall that the adaptationist's interpretation of Figure 1 is that the empty-space morphologies can be produced developmentally, but that the observed morphologies must be the fittest ones, otherwise they would be selected against and so not observed (Figure 1b, Box 2). In a surgical approach dubbed 'allometric engineering', Sinervo and Licht [18] asked why side-blotched lizards, which lay an average of 4.6 eggs per clutch, rarely lay clutches of just one or two eggs. Laying one or two eggs is presumably associated with low fitness, but this assumption is hard to test because the variation observed in natural populations is so low. Sinervo and Licht lowered egg number surgically, and found that when few eggs developed, they became very large and often bound in the oviduct or ruptured upon laying. Laying many eggs, by contrast, would lead to tiny hatchlings with low survivorship. Clutches of around five, then, seem the fittest of the possible variants. Surgical manipulation is applied to great effect not only in animals, but also in plants and microorganisms [19–25].

A less invasive if slower approach is artificial selection, which can be applied in the lab or studied in domesticated organisms. With humans exerting often thousands of years of selection, domesticated organisms provide spectacular study systems. Selection in many opposing directions has made domestic dog skull shape diversity far exceed that of wild canids [26]. This shows that, were selection in the wild to favor a Chihuahua-type morphology, it would surely be possible, although mercifully Mother Nature has spared us from this. Whereas domesticated organisms provide systems that have been under selection for generations, organisms with short life cycles give scientists the chance to exert their own selection [27–30]. A series of remarkable studies on wild radish [27] shows that wild-type stamen length and petal length scale with a tight positive relationship, longer petals being associated with longer stamens, similar to Figure 1a. Because petals and stamens are serially homologous structures, it would seem plausible that they should share crucial developmental machinery limiting their mutual developmental independence and, indeed, quantitative genetic studies suggest that correlation between their lengths involves shared genes. From this point of view, the empty spaces in radish flower

allometric space could be the result of developmental inaccessibility. Under laboratory selection, however, the spaces turn out to be readily reached. Rather than reflecting developmental impossibilities, the empty spaces above and below the wild-type allometric scaling line seem certainly selected against, as in Figure 1b rather than Figure 1c. Excellent recent overviews of manipulation studies [30,31] make it unnecessary to go into more detail here beyond noting that this strategy shares with the previous one a focus on phenotypes beyond those commonly observed, to determine whether they are ontogenetically possible and even assess their performance once generated. Both the embryological and manipulation strategies provide fine developmental and functional detail, but to gauge the relevance of their observations to diversification, biologists turn to cross-species comparisons.

Comparative studies

This strategy documents the ways that multiple species fill morphospace to see which parts are filled and which seem to be empty; in Figure 1 the points would represent species rather than individuals. This is perhaps the perspective that has produced the most compelling evidence for developmental constraint. The vast and, for the most part, inexplicable morphological discontinuities between animal phyla, or the insistence on having no more than four limbs in tetrapods or five petals in most angiosperms, seem conspicuously hard to address with appeals to selection [2,10,32]. Scientists examine these gaps using the two main categories of this strategy: empirical and theoretical morphospaces [33].

The first category begins with empirical observations and focuses special attention on apparently unoccupied morphospace [34–38]. A celebrated example is segment number in the geophilomorph centipedes, in which none of the over 1000 species is known to have an even number of segments, not even in species that vary in segment number [39]. All plausible hypotheses for this conspicuous restriction involve an ontogenetic segmentation mechanism utterly precluding even numbers. Study of the mechanism is apace, rhythmic patterns of gene expression seeming to be major players [40], and helping to explain why, even if selection were somehow to favor an even segment number, its evolution is unlikely.

In contrast to the geophilomorphs, which are bound by an apparent constraint, the membracid treehoppers could provide evidence against one. These widespread insects are extremely hard to spot. Largely responsible for their crypsis is a unique helmet that surges from the thorax in often extravagant proportions in the shape of bark, fungi, lichens, thorns or even other insects. Prud'homme *et al.* recently suggested that gene expression patterns show the helmet to be derived from the fusion of paired structures serially homologous to wings [41] (although see [42]). If so, then the two additional wing homologs of the Membracidae would provide evidence that insects have four wings rather than six, not because six is a developmental impossibility but probably because it is not favored by selection. The essence of the comparative strategy, distilled by geophilomorphs and membracids, is that the patterns of morphospace occupation (no even segments, six wings) emerge not

from the study of a few individuals but become conspicuous because they emerge from comparison of multiple, even thousands, of species. Conspicuous holes in empirical morphospaces are one way of looking for constraint, and another is to ask whether morphologies that can be imagined exist, the starting point of the other main category of the comparative strategy.

The second main category within the comparative strategy starts with a theoretical morphospace, an approach credited to David Raup's 1960s studies of imaginable and observed ammonite shell shapes [35,43,44]. These studies fill a priori spaces defined by two or more variables with a full range of possibilities [33,45,46]. Niklas [47] used variables describing branching, length and taper of cylindrical stem segments to define a multivariate morphospace describing almost the entire arc of plant form, from whisk fern-like to Christmas tree-shaped or flat-topped acacia habits. The most striking observation of his studies for the purposes here was that every morphology Niklas generated corresponded to real plants either living or extinct. No 'holes' suggested an entirely prohibited morphology, showing that what is pathological in one context, say a tree unable to support its own weight, can be adaptive in another, as in the stems of a rainforest liana. Again, these observations summarize variation seen across thousands of species. Thanks to friendly and thorough recent reviews [43,48], it is safe not to go into more detail on this extremely fruitful approach so that I can turn to other crucial points, the empirical connections and conceptual threads linking all of the methods discussed.

Empirical and conceptual connections between strategies

Sometimes, biologists draw on more than one strategy of the developmental approach to adaptation in the same study. The most common interaction is for comparative studies to highlight major morphospace lacunae for detailed developmental study [32,49–54]. The comparative observation that so many mammals have just seven cervical vertebrae [16] has motivated painstaking studies of ossification patterns, which concluded that the 'extra' cervical vertebrae of sloths (they seem to have up to ten) are in fact ribless thoracic vertebrae [55]. Scientists also can combine comparative and manipulation strategies [27,38,56,57]. For example, molecular biologists start with a naturally occurring protein and synthesize its putative ancestors, creating a constructed comparative protein space analogous to a morphospace. From a manipulation point of view, they then test directly the idea that the 'ancestors' should confer sequentially higher performance, as measured by attributes such as antibiotic resistance or binding affinity, toward a peak corresponding to the currently observed protein [58]. Jordan and Harder's [59] study of differences in bumblebee flower visitation behavior before an array of artificial inflorescences represents a similar comparative–manipulation approach to morphology. Despite scattered empirical connections such as these, the three strategies for exploring developmental possibility are not explicitly united in a conceptual current. For example, the reviews of Brakefield [60] and Frankino *et al.* [30] chiefly examined artificial selection, whereas

Box 3. The adaptationist abduction

Understanding how inferences regarding adaptation are constructed shows ways to make them stronger. Many inferences in evolutionary biology, and most of those regarding adaptation, include reasoning that at first blush might seem circular. Darwin famously noted that 'The existence of closely allied or representative species in any two areas, implies, on the theory of descent with modification, that the same parents formerly inhabited both areas' [90]. He invoked common descent to explain the geographical distribution of taxa, but also cited global patterns of geographical distribution as critical evidence in favor of common descent. In inferences of adaptation, it is argued that unobserved morphologies must be of low fitness and eliminated; it is inferred that these morphologies are of low fitness precisely because they are not observed (Figure 1a). Biologists spurn circular arguments, but loopy reasoning may be an essential part of biological inference.

Important work by philosopher Paul Griffiths has called attention to the 'adaptationist abduction', referring not to aliens but to an

inferential strategy also known as inference to the best explanation (Figure 1b) [91]. In abductive reasoning, the conclusions shore up confidence in the assumptions [92]. Geographical distribution is still one of the main observations cited in support of common descent, and common descent can still be cited to explain the distribution of taxa [93]. In the 150 years since Darwin, biologists have tested many of the assumptions that he had to invoke with little evidence, including mechanisms of inheritance, plate tectonics, climate change and molecular similarities among taxa. Data from all of these sources now form a web strengthening confidence in common descent. By recognizing the abductive structure of the inferential strategies that researchers use, it is possible to search explicitly for the weakest loops. In studies of adaptation, assumptions about developmental potential (Figure 1) are crucial; the means to test them is the developmental approach to adaptation.

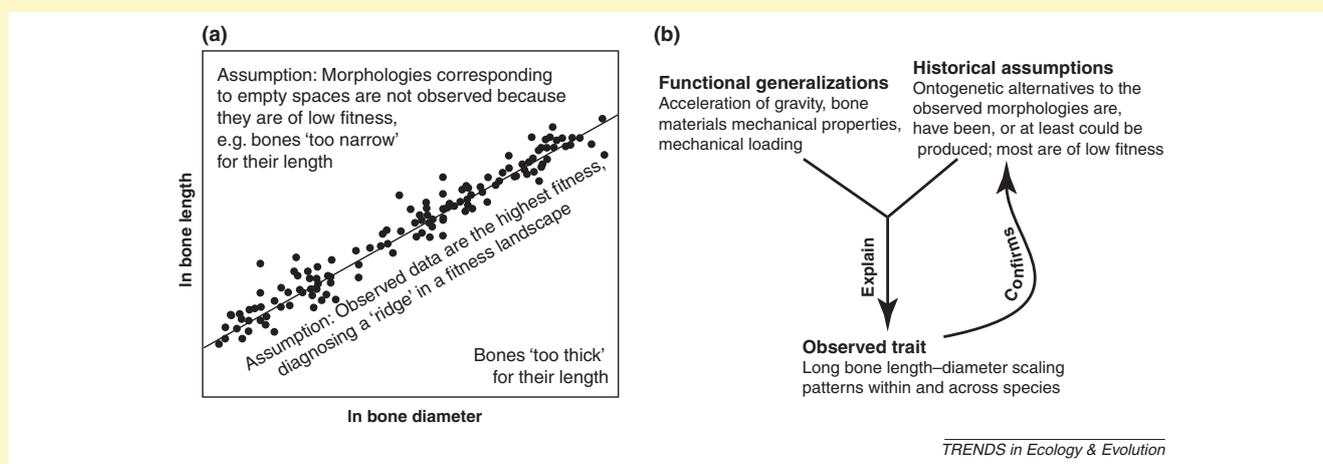


Figure 1. The structure of adaptationist inferences. (a) Most inferences of adaptation make assumptions regarding developmental potential and fitness, assumptions that can only be tested using the developmental approach to adaptation. (b) The 'adaptationist abduction', the inferential strategy behind studies of adaptation, here modified from [91] to reflect the example in (a). With kind permission of Paul Griffiths and Oxford University Press.

McGhee [43] discussed theoretical morphospaces, and no work spans the three strategies. Yet, regardless of the exact methods used, all three share the same underlying reasoning with respect to the causes of empty morphological space (Box 2). When seen as a united current, the developmental approach fills an important void in traditional evolutionary biology.

Developmental potential as the missing link of the Synthesis

One of the most notorious aspects of the Modern Synthesis has been its elision of development, treating it as a trivial, more or less deterministic black box between the genome and the phenotype [12,46,61–66]. At the same time, the main cause of morphological differences between species in the thinking of the Synthesis was adaptation. Because examining developmental potential is essential for testing adaptation hypotheses (Box 3), excluding development left the Synthesis without a crucial tool. The developmental approach outlined here is a clear extension of the Synthesis view. Traditionally, mutations cause phenotypic changes in any direction and the morphology of a population can go anywhere the whims of selection might take it [63,64,67]. In the developmental view, the possibilities of selection are limited by the array of morphologies that can be produced in development, an array that is often restricted and

discontinuous [10,12,39,65,68–70]. With the developmental approach, it is no longer possible to accuse students of adaptation of being blind to these points, thereby answering exhortations such as those of Spandrels to take non-adaptive hypotheses seriously.

Important as heeding the call of Spandrels might be, the developmental approach addresses the even more profound issue of how to structure inferences regarding adaptation. Adaptations are shaped by natural selection, and natural selection acts on variation within populations. Variation is produced in development. Therefore, any statement that this or that structure is an adaptation implies that developmental variation is, or at least once was, present for selection to act upon. Inferences of adaptation consequently include the following tacit reasoning: 'unoccupied patches of morphospace are empty because they are of low fitness and eliminated by selection; I infer that they are of low fitness and eliminated because they are empty' (Box 3). By examining empty spaces directly, the developmental approach tests the central but perennially unexamined assumption that phenotypes currently unobserved could become common if selection were to favor them (Box 2).

As an additional bonus, the ontogenetic approach helps resolve the supposed conflict between externalism versus internalism by highlighting the common ground of

ontogeny. Externalists are biologists who interpret organismal form as reflecting adaptations culled from a vast and continuous space of alternatives, the traditional position of the Synthesis. Internalism is the view that the properties of development so snugly circumscribe the forms available for production in nature that selection can only occasionally choose among a narrow pool of variants [2]. These views are often seen as mutually inimical, neither side agreeing on the cause of organismal form. However, both views make predictions about ontogeny and neither denies the action of selection, just the amplitude of the field available for its action [6]. The coincidence between these two views reveals itself on the empirical front. Whether internalist or externalist, empirically the issue at hand is whether empty spaces, such as those in Figure 1, are ontogenetically accessible, and both sides turn to the methods described above, mapping out their common ground as they do so.

Conclusion: fusing the three strategies into a united developmental approach

The developmental approach to adaptation has been a long time in establishing, its antecedents traceable across many decades. Embryology long pre-dates evolutionary thought,

whereas variation, including asking how performance might compare between uncommon and common morphologies, has always been central to Darwinism. Even theoretical morphospaces have been a part of evolutionary biology for 50 years. However, it was not until insistence on the importance of developmental constraint by workers such as Gould and Alberch [1,10] that these traditions began to weave together with studies of adaptation. More recently, with the broad resurgence of developmental thinking [7–12,60,71,72], students of adaptation have begun to ask how their interests fit into evolutionary developmental biology [7,60]. So, although the antecedents of the developmental approach to adaptation span many decades, it is not until the past five years or so that it has burgeoned. More and more researchers, from comparative morphologists to quantitative geneticists, are testing the developmental accessibility of unobserved morphologies and even exploring their performance relative to the commonly observed and presumably fitter ones. These researchers turn to the developmental approach as a response to traditional discussions of ‘constraint,’ which often use the term to refer to so many things (Box 1) that it becomes hopelessly vague. Instead, the studies cited above have the virtue of being built on clear empirical

Box 4. A developmental perspective on a confusing analogy

The Spandrels of San Marco [1] were supposed to illustrate two things: architectural constraint and exaptation. Spandrels admirably illustrate exaptation, which refers to existing structures co-opted evolutionarily to new functions, because the Spandrels of San Marco (gray triangles in Figure 1c) were built to support a dome but co-opted for decorations. By contrast, the notion of ‘architectural constraint’ has caused decades of confusion, precisely because of the lack of a developmental perspective. By architectural constraint, Gould and Lewontin meant that Spandrels were an inevitable consequence of putting a round dome atop a square building. They argued that the presence of Spandrels might be explained with vivid and convincing stories about their utility. Based on these stories, it might be concluded that Spandrels represent adaptations, honed by trial and error from among a vast field of contenders. Gould and Lewontin went on to suggest that, although Spandrels might indeed have uses, because there is simply no other way to build a dome on a square building, the assumption that Spandrels represent the best among many options is incorrect. Gould and Lewontin’s biological lesson was that just because an organismal structure has a function does not mean that it is optimal or the best of

many possibilities, but that sometimes there are simply no alternatives. If there are no alternatives, then the inference that a given structure is an adaptation, understood as the fittest among a field of developmental contenders, is incorrect.

However, there is an endless number of ways to put a round dome on a square building, most of which cannot support the weight of a large dome (Figure 1a,b), obstruct the view inside the church (Figure 1d,e), or fall down at once (e.g. supporting the dome with cotton candy). That is, of the possibilities, ‘Spandrels’ (actually called ‘pendentives’) are the variant that works best (Figure 1c) [94]. In other words, the space of ‘ontogenetic’ possibilities is as vast as the capacity for imagination, but pendentives represent the variant with the highest ‘fitness.’ To be sure, there are many constraints, such as building styles, that affect the way religious buildings are built. Squinches (Figure 1a), for example, are more common in medieval mosques, whereas most Renaissance churches have pendentives. However, with regard to ‘architectural constraint,’ the developmental approach to adaptation quickly shows that there is no constraint here, just run-of-the-mill natural selection.

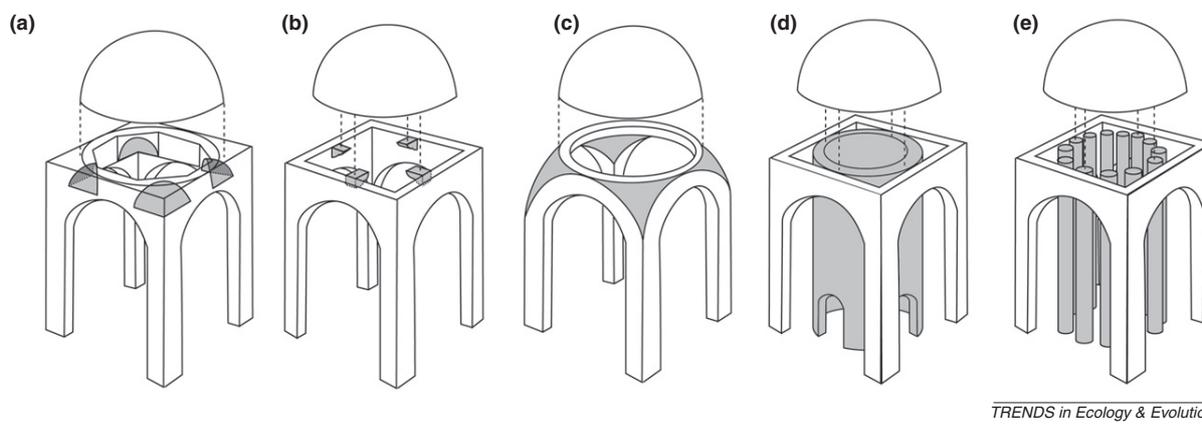


Figure 1. Some of the ‘ontogenetic’ alternatives to supporting a dome on a square building (a–e). The variant that is structurally and architecturally most sound are pendentives (‘Spandrels’), shown in (c).

Box 5. Outstanding questions

- How do organisms fill morphospace? If developmental potential determines what can and cannot be acted on by natural selection, and if the way that organisms fill morphological space is neither random nor comprehensive, then a mandate of evolutionary biology is to map morphospace, be it comparative, ontogenetic, teratological, living or extinct [35,37,38,44]. Because morphospaces are entirely defined by the variables measured, which variables to choose and how to compare them across morphologically disparate groups are paramount issues [33].
- What is meant by 'constraint'? In Box 1, I show a small slice of notions regarding 'constraint', some of which are incompatible with one another. Much clarification remains to be required to separate these contradictory concepts, to forge terminology with maximum conceptual content and minimal redundancy, and to determine the limits to the meaningfulness of the constraint-adaptation dichotomy [67,95].
- For that matter, what is meant by adaptation? It is common to refer to adaptations as 'parts', for example, 'the bird wing is an adaptation for flight', but it is not clear how to partition organisms into parts non-arbitrarily. Adaptation can also be seen as a process [65], a perspective emphasizing tradeoffs and covariation between

traits, such that no clear delimitation of 'parts' emerges [38]; the 'parts' and 'process' conceptions of adaptation are not always compatible.

- Where are the limits to developmental potential? Development must have ultimate limits in maximum and minimum values, for example beyond the space of Figure 1 (main text); where these limits lie and what causes them are, in almost all cases, outstanding issues.
- What causes major 'constraints'? Awaiting understanding are many inscrutable examples of stasis where alternatives would seem possible and often advantageous [7,32]. Tetrapod limb design [50,53] and limb number, gaps between animal phyla, or five petals in the bulk of the flowering plants are conspicuous examples.
- Where do organisms and novelties come from? The more that is understood about the detailed dynamics of development, the more it becomes clear that ontogeny is not a simple reading of a pre-written genetic program but a process of coral reef complexity. Forsaking simple genes to phenotype notions for a view of ontogeny as contingent self-construction might be the greatest challenge facing all of evolutionary biology [64–67,95–97]. Several recent books offer excellent and accessible introductions to developmental thinking [12,39,68,98,99].

questions; for example, 'are the morphologies corresponding to the empty spaces defined by my data readily accessible developmentally?'

To address its questions, three separate strategies of the developmental approach to adaptation (embryology, manipulation and comparative studies) have sprung up, and making explicit the connections between them gives clear avenues for future work. Each strategy offers distinct advantages. The comparative approach offers generality, with inferences spanning many species, and is based on the products of natural, not laboratory, evolution. Studies of ontogeny of single species provide mechanistic detail, and manipulation methods can examine performance or fitness of variants directly. All are means to explore developmental potential in an adaptive context, to determine what is common, what is possible and what is prohibited. Deliberately combining strategies would fortify inferences by drawing on the strengths of all three [60]. Developmental thinking also helps identify when 'constraint' is no constraint at all but simply veils reference to natural selection (Box 4). Additionally, recognizing that developmental potential defines the domain of natural selection mandates the redoubling of efforts to map all of organismal morphospace, juvenile, adult, teratological, living and extinct, as the foundation on which all inferences of adaptation must be overlain (Box 5) [73]. Because it maps this crucial foundation, the emerging conceptual and methodological consensus that marks this renaissance of ontogeny in adaptationism is easily one of the most important developments in recent evolutionary biology.

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