

## RESEARCH

# Developmental bias in the fossil record

Illiam S. C. Jackson Department of Biology, Lund University,  
Sweden**Correspondence**Illiam S. C. Jackson,  
Lund University, Sweden.  
Email: illiam.jackson@gmail.com**Funding information**Knut och Alice Wallenbergs Stiftelse,  
Grant/Award Number: KAW 2012.0155**Abstract**

The role of developmental bias and plasticity in evolution is a central research interest in evolutionary biology. Studies of these concepts and related processes are usually conducted on extant systems and have seen limited investigation in the fossil record. Here, I identify plasticity-led evolution (PLE) as a form of developmental bias accessible through scrutiny of paleontological material. I summarize the process of PLE and describe it in terms of the environmentally mediated accumulation and release of cryptic genetic variation. Given this structure, I then predict its manifestation in the fossil record, discuss its similarity to quantum evolution and punctuated equilibrium, and argue that these describe macroevolutionary patterns concordant with PLE. Finally, I suggest methods and directions towards providing evidence of PLE in the fossil record and conclude that such endeavors are likely to be highly rewarding.

**KEYWORDS**

cryptic genetic variation, developmental bias, plasticity-led evolution

## 1 | INTRODUCTION

Developmental bias describes the manner in which certain changes to development are more accessible to evolution than others (Arthur, 2004). A key generator of developmental bias, and integral to understanding its role in evolution, is developmental plasticity, which refers to an organism's ability to adjust its phenotype in response to environmental conditions (Laland et al., 2015; Schwab, Casasa, & Moczek, 2019). Developmental bias, framed as a form of constraint, is an important topic studied through the fossil record, but the bias imposed by plasticity has not received similar attention. Investigating plasticity-induced developmental bias ("plasticity-led evolution"; PLE; Levis & Pfennig, 2016) in paleontological data sets necessitates identifying its traces in the fossil record.

In this paper, I outline the process of PLE and core related concepts and discuss how it relates to developmental bias. Thereafter, I predict what kind of patterns

we might expect to result from PLE in the fossil record, anchor these patterns in historical work and suggest methods and future directions for examining PLE using fossil data.

## 2 | CONSTRUCTIVE DEVELOPMENT

Central to understanding the process of PLE is the conceptualization of development as constructive, rather than programmed (Laland et al., 2015). Development has been traditionally viewed as a programmed process, captured in the "genes as blueprint" metaphor (Laland et al., 2015; Moczek, 2012; Noble, 2015; Pigliucci, 2010), perhaps best exemplified by Dawkins (1976) in *The Selfish Gene* where genes are described as "safe inside gigantic lumbering robots, sealed off from the outside world, communicating with it by tortuous indirect routes, and manipulating it by remote control." This view is

starkly at odds with the framing of development as constructive; capable of “[shaping] its own developmental trajectory by constantly responding to, and altering, internal, and external states” (Laland et al., 2015). Informed by the growing field of evo-devo and contemporary understanding of concepts such as developmental plasticity, the relationship between environment and development is increasingly understood as more complex than a unidirectional programmed process, which naturally has ramifications for how we understand evolution (Brakefield, 2011; Moczek, 2015, 2015; Müller, 2007; West-Eberhard, 2003).

For example, the gene regulatory network structure of development (Carroll, 2005; Davidson, 2006; Müller, 2007; Carroll, 2008; Erwin & Davidson, 2009; Uller, Moczek, Watson, Brakefield, & Laland, 2018) facilitates the generation of phenotypic variation by reducing the number of regulatory changes required to achieve evolutionary change (Gerhart & Kirschner, 2007; Wagner, 2011). Given that these regulatory systems can transition between genetic and environmental control (Iwasaki, Tsuda, & Kawata, 2013; Schneider & Meyer, 2017; Schwander & Leimar, 2011; West-Eberhard, 2003), it follows that environmental triggers, through their presence or absence, can act to suppress developmental pathways, shielding them from natural selection and liberating them to accumulate change without malus to the organism (Küttner et al., 2014; Moczek, 2008; Rutherford, 2000; Schlichting & Smith, 2002; Zheng, Payne, & Wagner, 2019). Such unexpressed variation is known as cryptic genetic variation (CGV) and can be understood as a form of evolutionary capacitance that may play an important role in evolution (Gibson & Dworkin, 2004; Levis & Pfennig, 2016; McGuigan & Sgrò, 2009; Moczek, 2008; Paaby & Rockman, 2014; Schlichting, 2008; Schwab et al., 2019).

### 3 | THE ROLE OF CRYPTIC GENETIC VARIATION IN PLASTICITY-LED EVOLUTION

CGV may, but need not necessarily, constitute an adaptive trait. Rather, it can be understood as randomly accumulated variation on a developmental system allowed to persist due to its nonexpression (Küttner et al., 2014; Moczek, 2008; Rutherford, 2000; Schlichting & Smith, 2002; Zheng et al., 2019). Given that this cryptic variation may be sensitive to environmental triggers, it acts as a source of innovation that can be episodically induced and presented to selection (Gibson & Dworkin, 2004; Levis & Pfennig, 2016; McGuigan & Sgrò, 2009; Moczek, 2008; Paaby &

Rockman, 2014; Schlichting, 2008; Schwab et al., 2019; Zheng et al., 2019). It is this form of plasticity, not adaptive plasticity, that plays the central role of driving the process of PLE as described below and discussed throughout this paper. In other words, the plasticity leading evolution in this model of PLE is not an evolved response but rather the periodical accumulation and plastic release of CGV *sensu* Lande’s (2009) “transient evolution of increased plasticity”.

If development indeed operates in this constructive manner then what kind of consequent patterns would we anticipate? A growing body of work is exploring the implications of constructive development and developmental plasticity in extant systems (Levis & Pfennig, 2019; van Bergen et al., 2017) but research from a paleontological perspective has so far been limited. If cryptic genetic variation drives the process of plasticity-led evolution then what kind of traces would we expect to detect in the fossil record?

### 4 | PATTERNS AND PROCESSES IN THE FOSSIL RECORD

The fossil record is the history book of life, preserving patterns of evolutionary change through time. These recorded patterns are regarded as macroevolutionary, that is, broad-scale at the level of species and above (Gould, 2002; Myers & Saupe, 2013). This is the classical understanding of macroevolution as a counterpart to microevolution, which describes processes governing evolutionary change below a species level (Dobzhansky, 1937; Simpson, 1944). Although macroevolutionary patterns are generally assumed to be generated by microevolutionary processes over time (see discussion in Erwin, 2017), the fossil record is more commonly used to map out evolutionary patterns at the level of species and above than to infer microevolutionary processes. But see for example Organ, Copper, and Hieronymus (2015) and Jablonski and Shubin (2015) for an overview of work in such a context. This is due in part to the historical conceptual dichotomy between micro- and macroevolution, but also to the kinds of data and methods available for paleontological studies, to which I will return further on.

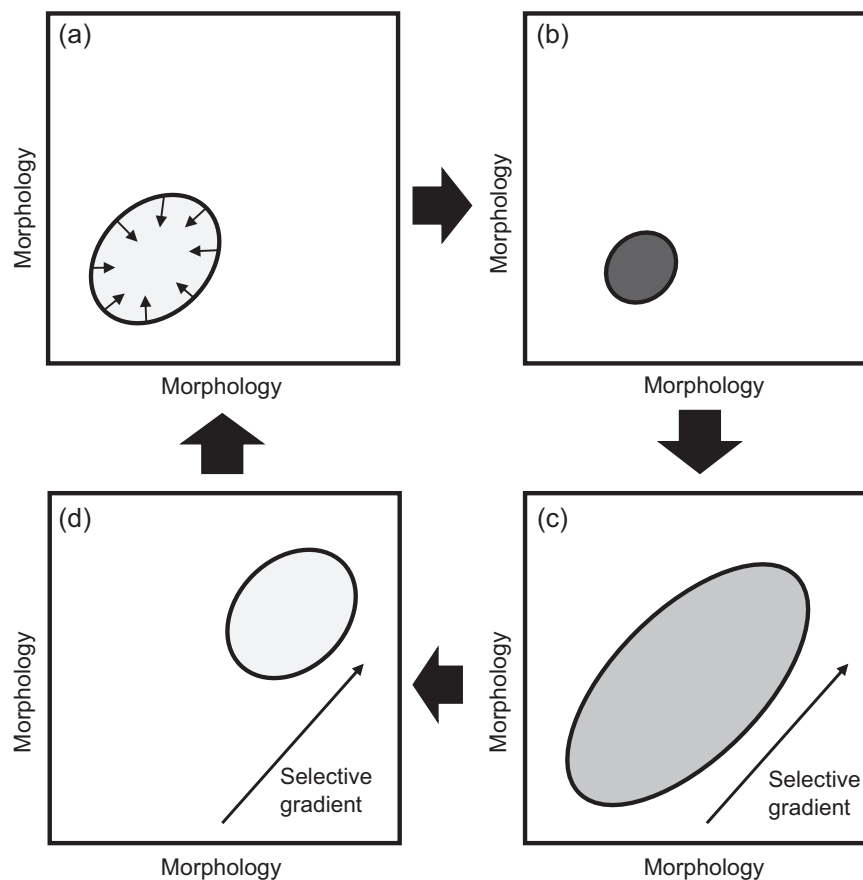
Obviously, in order for microevolutionary processes to be detectable in the fossil record, they must necessarily be theoretically capable of generating a morphological signature that is relevant in a macroevolutionary time-frame. To determine what such a signature of PLE might look like, I first outline the process before going on to draw up strategies for identifying it.

## 5 | PLASTICITY-LED EVOLUTION

PLE, also known as the plasticity-first hypothesis, describes a mode of evolution in which the environment plays a pivotal role in both inducing and, subsequently, selecting for phenotypic variation (Levis & Pfennig, 2016; West-Eberhard, 2003, 2005). It has been investigated in extant organisms such as sticklebacks (Wund, Valena, Wood, & Baker, 2012), house finches (Badyaev, 2009), and spadefoot toads (Levis & Pfennig, 2019), yet how we might approach this process in a paleontological context remains unknown. Here follows a summary of PLE, also illustrated in Figure 1.

A population of organisms well-adapted to its environment is subject to the process of stabilizing

selection, which selects not only for a specific phenotypic optimum but also selects against variation around this optimum (Figure 1a; Schmalhausen, 1949). Apart from the removal of unfit variants this is achieved by reducing developmental sensitivity to any perturbation, including environmental conditions (Gibson & Wagner, 2000; Pertoldi, Bundgaard, Loeschcke, & Barker, 2014; Waddington, 1942; Wagner, Booth, & Bagheri-Chai-chian, 1997). When development is canalized in this manner CGV may accumulate in shielded parts of the genome (Küttner et al., 2014; Moczek, 2008; Rutherford, 2000; Schlichting & Smith, 2002; Zheng et al., 2019) generating evolutionary capacitance (Figure 1b; Gibson & Dworkin, 2004; Levis & Pfennig, 2016; McGuigan & Sgrò, 2009; Paaby & Rockman, 2014; Schlichting, 2008; Schwab et al., 2019).



**FIGURE 1** Illustration of the process of plasticity-led evolution in terms of phenotype, stress, and cryptic genetic variation (CGV). Ellipses represent populations in morphospace. The shading intensity of the ellipses gives their relative level of CGV. (a) Stabilizing selection acting on a population selects both for a phenotypic optimum as well as reduced variation around that optimum. (b) Phenotypic variation is reduced through both the removal of unfit variants as well as decreasing sensitivity to environmental conditions, that is, canalization of development. This shields previously expressed but now hidden developmental pathways from natural selection such that CGV, that is, evolutionary capacitance, can accumulate. (c) An environmental stress is encountered that both induces as well as selects for variation. CGV is revealed by this environmental trigger and phenotypic accommodation occurs generating increasing phenotypic variability. This can be understood as the expenditure of the previously accumulated evolutionary capacitance. (d) Selection acts on the uncovered variation by selecting for the new environmental optimum and genetically accommodating such change that was beneficial, thus restarting this process by undergoing stabilizing selection again and recanalizing development once more

Novel or extreme environmental conditions may reveal this capacitance (Badyaev, 2005; Flatt, 2005) by expressing novel developmental pathways or by downstream effects of mutual adjustment of different parts of the phenotype; a process known as phenotypic accommodation (Figure 1c; Badyaev, 2009; Laland et al., 2015; Schwab et al., 2019; West-Eberhard, 2005). Environmental stress can thus be understood to simultaneously induce and select for novel phenotypes; a process that would facilitate rapid evolutionary change (Gibson & Dworkin, 2004; Levis & Pfennig, 2016; McGuigan & Sgrò, 2009; Paaby & Rockman, 2014; Schlichting, 2008; Schwab et al., 2019).

Due to the internal architecture of developmental systems, which generates integrated modules (Goswami, Binder, Meachen, & O'Keefe, 2015; Schlichting, 1989; Wagner & Zhang, 2011), random genetic mutations may still lead to coordinated phenotypic responses (Jablonski, 2017; Moczek et al., 2011; Uller et al., 2018; West-Eberhard, 2003). For this reason, the effects of the previously cryptic genetic variation may, in fact, cause directed phenotypic change, biased towards functionally integrated phenotypes (Gerhart & Kirschner, 2007; Masel, 2006; Wagner, 2011; Watson & Szathmáry, 2016; Watson, Wagner, Pavlicev, Weinreich, & Mills, 2014). Taken together and in the context of PLE, this implies that accumulated CGV revealed by environmental stress may be biased towards experimental functionality.

Initially, this constitutes a pulse of phenotypic change without genotypic change (Noble, 2015; West-Eberhard, 2003). However, when CGV is thus revealed its phenotypic manifestation nevertheless becomes visible to natural selection, which can select for or against it. More importantly, selection indirectly acts on the developmental system itself, rendering its regulation either more or less sensitive to environmental conditions (Moczek, 2008; Schlichting & Wund, 2014; West-Eberhard, 2005; Wund, 2012). This subsequent process is known as genetic accommodation (Lande, 2009; West-Eberhard, 2003). If nature selects strongly for a novel phenotype, that is, a newly induced variant that is preadapted to its environment, then the process of stabilizing selection starts over and development can begin to canalize once more (Figure 1d). If one such novel phenotype is subjected to very powerful selection it may lose its plasticity entirely and is then said to have been genetically assimilated (Pigliucci, Murren, & Schlichting, 2006; Waddington, 1961; West-Eberhard, 2003).

Given that the modular structure of gene regulatory networks generates patterns in which parts of development interact with the environment whereas others do not (Iwasaki et al., 2013; Schneider & Meyer, 2017), those parts that do interact with, and are intermittently

mediated by, environmental factors become the centers of evolutionary change, and evolution can proceed predominantly by modification of environmentally regulated parts of the developmental system, with consequent phenotypic diversification (Schneider & Meyer, 2017; Uller et al., 2018; Wund, 2012). Thus, this process repeated in isolated populations is likely to direct evolution along particular trajectories.

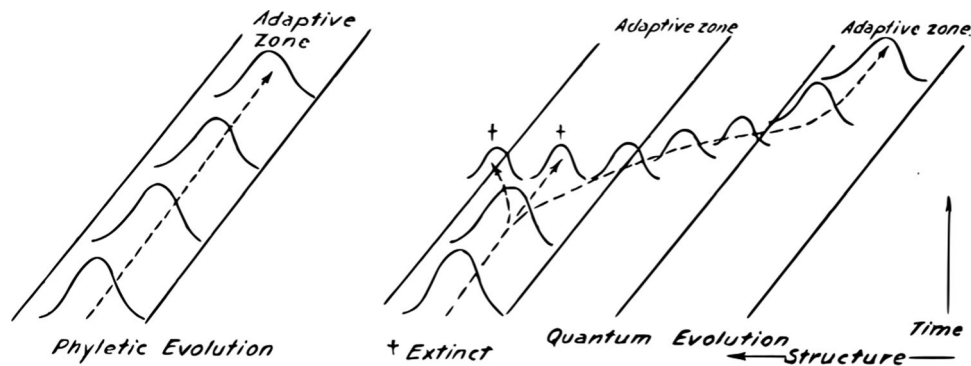
## 6 | PLASTICITY-LED EVOLUTION AS A MODE

The cyclical accumulation and release of CGV, during periods of stabilizing selection and environmental stress respectively, thus describes the operation of PLE. This is similar to Badyaev's (2009) conceptualization of "evolutionary diversifications and maintenance of adaptations probably operating in alternation between the emergence of novel developmental variation and stabilization of locally appropriate organism-environment associations by natural selection" and represents an exciting hypothetical mode of evolution. Indeed, the role of genetic assimilation in evolution, that is, the adoption of genetic management of initially environmentally induced phenotypes, continues to demand attention (Ehrenreich & Pfennig, 2016; Schneider & Meyer, 2017; Schwab et al., 2019).

## 7 | QUANTUM EVOLUTION

As a mode of evolution, this model of PLE constitutes a pattern of periods of stasis, during which capacitance is accrued, followed by rapid bursts of change as this capacitance is expended. In a macroevolutionary context, this is not without historical analogues. Indeed, the distinction between stasis and burst is captured in the contrast between Simpson's (1944) phyletic and quantum evolution (Figure 2), two of his three modes of evolution, the third being speciation. He defines quantum evolution as the "relatively rapid shift of a biotic population in disequilibrium to an equilibrium distinctly unlike an ancestral condition" while phyletic evolution is the "sustained, directional (but not necessarily rectilinear) shift" more commonly observed in the fossil record.

Simpson (1944) considered these two modes of evolution as qualitatively different; to his mind, they fulfill different functions and presumably operate by different mechanisms. Phyletic evolution manages the adaptation of species to their adaptive zone, whereas quantum evolution is a much more radical process capable of generating rapid changes and accommodating



**FIGURE 2** Simpson's (1944) comparison of phyletic and quantum evolution. Phyletic evolution is the selective tracking of a shifting adaptive zone through time with subsequent directional phenotypic gradualism as a result. Quantum evolution, on the other hand, is a rapid evolutionary transition between adaptive zones. Note the preadaptive variation manifest in the ancestral population immediately before quantum evolution

jumps across inadaptable zones to new adaptive zones. In other words, quantum evolution was a suggested solution to the contemporary problem of how a population might cross the valleys of Wright's adaptive landscapes (Wright, 1932), given that evolution proceeds through the gradual accumulation of small changes (cf. Zheng et al., 2019). To this end, Simpson (1944) writes that "preadaptation [is] a necessary element [of quantum evolution, and is] another marked distinction between quantum evolution and phyletic evolution, which is mostly adaptive (and postadaptive)". Furthermore, quantum evolution provided a biological explanation for the long-observed discontinuities in the fossil record; they were not merely artifacts of incompleteness but may, in fact, be indicative of extremely rapid phenotypic transitions.

According to Simpson (1944) quantum evolution progressed through three phases:

*"(1) An inadaptable phase, in which the group in question loses the equilibrium of its ancestors or collaterals.*

*(2) A preadaptive phase, in which there is great selection pressure and the group moves toward a new equilibrium.*

*(3) An adaptive phase, in which the new equilibrium is reached."*

There is a striking concordance between these phases and (a) environmental induction of CGV release, that is, phenotypic accommodation; (b) corresponding environmental selection for novel variants, that is, genetic accommodation and potential assimilation; and (c) stabilizing selection, that is, canalization of development.

Yet at the time, the best candidate for a mechanism by which quantum evolution might proceed was genetic

drift. During the "hardening" of the modern synthesis, as evolutionary explanations became increasingly restricted to selection acting on gradual allelic change (Gould, 1982), the role of genetic drift seemed less significant, leading to Simpson changing his views on quantum evolution and ceasing to see it as a different kind of evolution to phyletic evolution (Gould, 1986). He later wrote that quantum evolution was "not a different sort of evolution from phyletic evolution, or even a distinctly different element of the total phylogenetic pattern. It is a special, more or less extreme and limiting case of phyletic evolution" (Simpson, 1953). In other words, quantum evolution became simply phyletic evolution sped up, and the norm mode of evolution consequently became phyletic gradualism (Eldredge & Gould, 1972; Gould, 1980).

## 8 | PUNCTUATED EQUILIBRIUM

It was against this backdrop that Eldredge and Gould formulated their theory of punctuated equilibrium (Eldredge & Gould, 1972; Gould & Eldredge, 1977, 1993). Similar to Simpson's (1944) quantum evolution, it posits that discontinuities in the fossil record need not necessarily be indicative of incompleteness. Rather, phenotypic evolution may be as intermittently rapid, that is, punctuated, as fossil data suggest. They argue that "the remarkable stasis exhibited by most species during millions of years is ignored (as no data)" (Gould & Eldredge, 1993). In other words, stasis is taken as a lack of evolution and contrasted with directional phenotypic change through time. The assumption that discontinuities are artifacts of incompleteness implies that phyletic gradualism is synonymous with evolution.

Gould and Eldredge (1993) write that we instead ought to "regard stasis and discontinuity as an



expression of how evolution works when translated into geological time” and argue that phenotypic evolution is more closely tied to speciation than previously imagined. Indeed, studies on patterns of change in the fossil record have confirmed that stasis is a far more common observation than phyletic gradualism (Hunt, 2004, 2007; Hunt & Rabosky, 2014), with stasis, in this sense, more accurately regarded as directionless or nonaccumulating morphological fluctuations rather than true stagnance (Gould, 1982; Gould, 2002; Voje, 2016). Furthermore, adaptive phenotypic change may occur so rapidly that it may pass by the record (Hunt, 2010). Yet while the pattern described by punctuated equilibrium is therefore broadly supported by observation, the mechanism by which this pattern arises, particularly the rapid transitions of form, remains unclear (Futuyma, 2015). Around the time of its inception and early reception, the theory of punctuated equilibrium was met with strong critique (e.g., Charlesworth, Lande, & Slatkin, 1982; Gingerich, 1984; Kirkpatrick, 1982) generating a debate that continues to this day (e.g., Lieberman & Eldredge, 2014; Pennell, Harmon, & Uyeda, 2014).

## 9 | FUNDAMENTAL DEBATE

It seems that the same point of contention that led Simpson to dilute his concept of quantum evolution also frames the debate on the theory of punctuated equilibrium as well as the controversy surrounding phenotypic and genetic accommodation; namely, the tension between the understanding of development as programmed or constructive (Laland et al., 2015), itself a manifestation of the differing perspectives of the gene-centered and organism-centered views of evolution (Baedke, 2018; Nicholson, 2014). Clearly, the same currents of thought are manifest in each of these instances, yet the contention remains unresolved.

It is tempting to argue that Badyaev's (2009) alternating “emergence of novel developmental variation” and “stabilization of locally appropriate organism–environment associations by natural selection” are qualitatively different processes, the former approximated by quantum evolution, punctuated equilibria, and plasticity-led evolution, and the latter by phyletic evolution, stasis, and gradualism. Indeed, this would be an approach informed by the distinction between origins and distributional explanations (Erwin, 2017). Yet this does not make sense in terms of our understanding of development.

From a developmental perspective, gradualism and PLE are not qualitatively different processes. Both are

governed by a regulatory network that facilitates variation and buffers genetic and environmental fluctuations towards functionality (Uller et al., 2018). The key difference is simply the phenotypic accommodation of PLE, which may be exaggerated by the release of capacitance in the form of CGV. This facilitates the distinctive rapidity described by quantum evolution (Simpson, 1944) and punctuated equilibrium (Eldredge & Gould, 1972). Thus the difference is quantitative, not qualitative; a matter of thresholds and amounts rather than kinds.

## 10 | MACROEVOLUTIONARY PATTERNS OF PLASTICITY-LED EVOLUTION

PLE as the evolutionary process described above predicts, in my view, in short, two major features in the fossil record: (a) stabilizing selection during periods of environmental stability leading to decreasing phenotypic variation but increasing evolutionary capacitance in the form of cryptic genetic variation, and (b) episodes of environmentally induced phenotypic plasticity facilitating rapid bursts of evolution as this capacitance is expended.

To be clear, in this framework, plasticity-led evolution (PLE), that is, the accumulation and release of cryptic genetic variation (CGV), is a putative generator of those patterns in the fossil record previously described as quantum evolution (Simpson, 1944) and punctuated equilibrium (Eldredge & Gould, 1972). Periods of phyletic evolution or stasis are understood as stabilizing selection acting on an organism. Quantum evolution and the rapid shifts of punctuated equilibria are hypothesized to be facilitated by phenotypic and genetic accommodation. This is not to say that evolution cannot occur through phyletic gradualism, that is, stepwise accumulation of genetic change, nor to say that the fossil record is not incomplete in parts. I only mean to say that PLE provides an alternative explanation for the phenomena mentioned above. While the theory of punctuated equilibrium is associated with speciation and quantum evolution is traditionally discussed in terms of anagenetic evolution, despite Simpson (1944) himself writing that it “may be involved in either speciation or phyletic evolution” and that “certain patterns within those modes intergrade with quantum evolution”, this distinction holds little significance for this model of PLE; the environmentally mediated accumulation and release of CGV can occur in either instance and whether or not speciation occurs is inconsequential.

## 11 | EVIDENCE OF PLASTICITY-LED EVOLUTION IN THE FOSSIL RECORD

When searching for evidence of PLE in the fossil record, it is insufficient to simply point to patterns of stasis or discontinuity. As Gould and Eldredge (1993) point out: “Examples of stasis alone [...] and simple abrupt replacement, although conforming to expectations of punctuated equilibrium, are not direct evidence for our mechanism: for stasis might just be a lull in anagenetic gradualism [...], and replacement might represent rapid transformation without branching, or migration of a distant (phyletic or geographic) relative rather than evolution *in situ*.” Likewise, discontinuities may indeed have geological rather than biological explanations, caused by erosion of fossil-bearing strata or a hiatus in a sedimentary deposition, for example. Furthermore, the processes of phenotypic and genetic accommodation are challenging to study in the fossil record. As Pigliucci and Murren (2003) caution us: “given the hypothesis that [genetic] assimilation can occur within a few generations, it ironically may be too fast for us to catch.” Indeed, the rapidity of phenotypic transitions reported by Hunt (2010) points to a similar problem. These challenges present a problem to the study of PLE in the fossil record.

Beyond these challenges, a further difficulty is that the central macroevolutionary prediction of PLE is superficially identical to that of phyletic gradualism. PLE predicts that novel environments lead to evolutionary change mediated by phenotypic and genetic accommodation. Phyletic gradualism predicts that novel environments lead to evolutionary change mediated by natural selection on gradually accumulating mutations. Thus, the observation of phenotypic change accompanying environmental change is insufficient to support PLE over phyletic gradualism; without access to genetic material, and consequently the underlying processes, we are left unable to determine which explanation is more likely. In general, this is a difficulty faced when investigating the fossil record in search for support for PLE; macroevolutionary patterns have historically proven an inadequate source of discrimination between genetic variation and plasticity (Hopkins, 2014; Schoch, 2014; Webster, 2019).

While the fact that the process of PLE is coherent with the structure of the fossil record should not be ignored as insignificant, it remains the case that to provide definitive support for PLE as a mode of evolution, we need to direct our attention towards identifying evidence that distinguishes it from phyletic gradualism. Approaches towards differentiating these processes rely on the study of processes instead of patterns. In other words, they focus

on providing support for the underlying mechanisms of PLE rather than the broad-scale outcome.

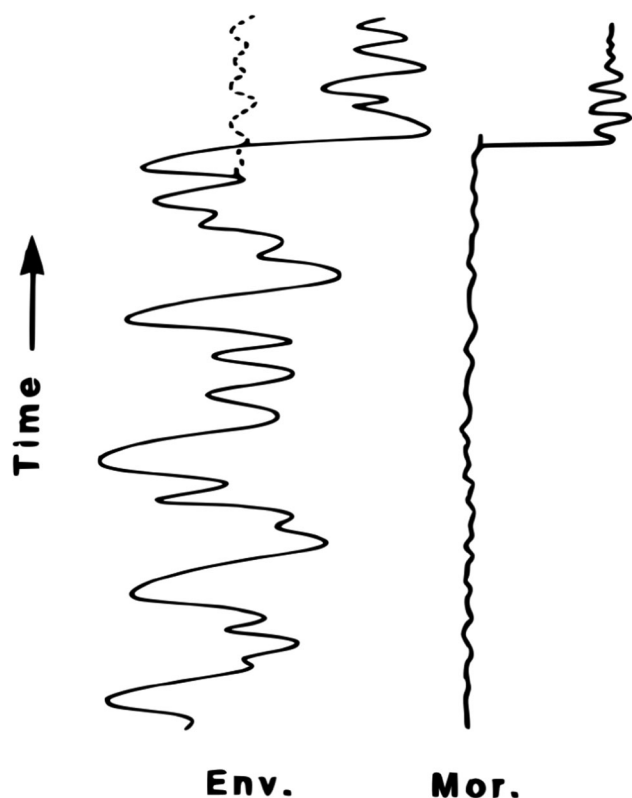
## 12 | ENVIRONMENTAL STRESS AND PHENOTYPIC VARIABILITY

Specifically, the key feature distinguishing PLE from phyletic gradualism is the environmentally mediated developmental plasticity that facilitates rapid phenotypic change. While such change can be measured in the difference between mean morphologies, this does little to help separate hypotheses of PLE and phyletic gradualism, seeing as both predict shifting phenotypic means as a result of environmental change. A stronger indicator of reduced canalization and subsequent increased developmental plasticity is a measure of the morphological variability induced by environmental stress (Hoffmann & Hercus, 2000).

The relationship between environmental stress and morphology is the subject of the *Plus ça Change* model (Sheldon, 1997). In short, it seeks to explain the observation that morphological stasis appears the most common response to fluctuations in environmental conditions in the fossil record. Drawing on a deep-time perspective it argues that long-term generalists are the species most likely to survive such fluctuations and consequently predicts gradualistic phenotypic change under stable or near-stable environmental conditions and phenotypic stasis during periods of strong environmental fluctuations.

In its general sense, this model seemingly suggests the opposite of PLE to manifest in the fossil record. Yet it contains the caveat that upon reaching a critical threshold of stress rapid phyletic evolution may be the result (Figure 3). The parallels between this prediction and the process of PLE outlined above are readily apparent; this model suggests that in a strongly fluctuating environment natural selection favors those organisms that sufficiently canalize their development to best track an underlying phenotypic optimum, yet when an extreme environment is encountered, developmental canalization is overcome and previously cryptic variation is released.

The prediction that environmental stressors can decrease developmental stability by overcoming canalization and releasing CGV implies that phenotypic variability can be regarded as a proxy for developmental instability (Klingenberg, 2019; Webster, 2019; Willmore, Young, & Richtsmeier, 2007). Thus the phenotype–environment association of interest for the study of PLE in the fossil record is that between environmental conditions and phenotypic variability, rather than phenotypic variation.



**FIGURE 3** Sheldon's (1997) Plus ca Change model. Strongly fluctuating environments are predicted to increase selection for stasis, until a threshold is reached and a punctuation, *sensu* Eldredge and Gould (1972), is generated. This model can be interpreted as predicting selection for increased canalization in fluctuating environments until a threshold is reached, at which point cryptic genetic variation is expressed and phenotypic accommodation occurs

This distinction is key for separating the predictions of PLE and phyletic gradualism. Variation, that is, morphological differences between assemblages, associated with environmental change is insufficient to support PLE for the reasons discussed above. However, an association between environmental change and variability, that is, the variance in form within assemblages, informs us about their developmental stability and thus permits investigation into the unique prediction of PLE that environmental stress may overcome canalization and induce the release of CGV with consequent expression of novel variants upon which selection can act. The consequence of this process is an increase in phenotypic variability coupled with a shift in phenotypic mean associated with environmental stress; a pattern not predicted by phyletic gradualism.

Below I provide two examples of approaches towards providing evidence of PLE in the fossil record that use this association. Before discussing them, however, I first present their necessary methodological framework.

### 13 | FRAMEWORK OF ANALYSIS

The focal point for these investigations is the relationship between environmental factors and morphology of fossil assemblages. Morphology is essentially the only biological information available in the fossil record and it is therefore in general of paramount importance to capture and study morphology in as high resolution as possible and with careful consideration of potential taphonomic biases such as disarticulation of hard parts or later structural deformation (Webster, 2019). This is particularly true, however, when studying intraspecific patterns of variation, such as those I will present below. Many modern phylogenetic cladistic analyses rely on discretizing variation into characters, which strongly limits their ability to study intraspecific variation. An alternative approach to analyzing morphological variation is through the use of morphometric methods, which quantify shapes into sets of measurements that can be mathematically analyzed (MacLeod, 2017). Such methods include landmark analyses (Bookstein, 1997), eigenshape analysis (MacLeod, 2002), and elliptical Fourier analysis (Kuhl & Giardina, 1982). These numerical approaches to describing variation in form translate morphology into continuous data and are consequently more suited to the study of the subtle variation exhibited intraspecifically than the use of discrete characters, and indeed are a prerequisite to examining fine-scale patterns of morphological variability.

While straightforward use of statistical variance is often employed in studies on developmental instability (e.g., Imasheva, Loeschke, Zhivotovsky, & Lazebny, 1997), novel methods for quantifying variance specifically stemming from developmental plasticity have seen recent development (Pertoldi & Kristensen, 2015; Pertoldi et al., 2014). Coupling shifts in variability to shifts in phenotypic mean is the key to identifying developmental plasticity in the fossil record, as I will discuss below. The putative confounding effect of time-averaging on morphological variance in fossil specimens has not been supported by empirical studies. Rather, it seems that paleontological and neontological samples have comparable levels of variability (Kidwell & Flessa, 1995; Bush, Powell, Arnold, Bert, & Daley, 2002; Hunt, 2004; Hunt, 2004; Hunt, Bell, & Travis, 2008; Webster, 2019).

To approach the environmental aspect of PLE, it is necessary to identify indications of environmental conditions in fossil assemblages. Patterns of intraspecific variation in fossil species across a geographic and putative environmental range are by no means uncommon (e.g. Hopkins & Webster, 2009; Jackson & Budd, 2017). Such patterns have been studied through the



assessment of associations between morphology and various environmental gradients (e.g. Cisne, Chandlee, Rabe, & Cohen, 1982; Scarponi & Kowalewski, 2004; Webber & Hunda, 2007). Indeed a variety of geochemical proxies are available for the investigation and approximation of depositional environments (Webster, 2019), such as using trace metals as a proxy for paleoredox and paleoproductivity (Tribovillard, Algeo, Lyons, & Riboulleau, 2006), for example. However, care must be taken when interpreting such proxies to minimize environmental variation generated by taphonomic processes such as diagenetic alterations of the rock (Webster, 2019).

The relationship between environmental stress and developmental plasticity by proxy of morphological variability is used in the following two approaches towards providing evidence of PLE as a mode of evolution in the fossil record.

## 14 | EVIDENCE OF PHENOTYPIC AND GENETIC ACCOMMODATION

As mentioned above, both phyletic gradualism and PLE predict a shift in morphology following exposure to novel environments, albeit resulting from different processes, making it difficult to uncover traces definitively of PLE. Gradual adaptive evolution would manifest as an assemblage shifting towards a new phenotypic optimum in response to environmental perturbation. Likewise, PLE would present a similar pattern yet with the environment both inducing as well as selecting for novel variants.

However, PLE predicts a pattern of increasing variability as the expression of CGV is induced by environmental stress, which distinguishes it from phyletic gradualism. In this mode of evolution, phenotypic accommodation increases variability such that the phenotype subsequently genetically accommodated or

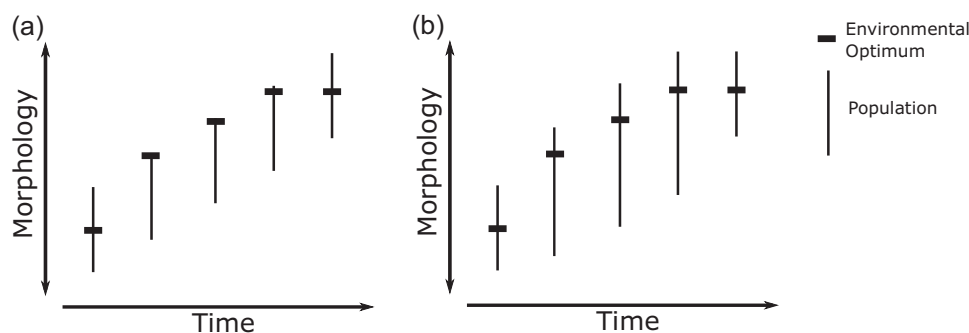
canalized lies outside its ancestral normal range (Figure 4; cf. Figure 1). While developmental instability is known to occur during stress, including on the range margins of populations (Bridle & Vines, 2007; Rieseberg, Archer, & Wayne, 1999), such dynamics do not predict the induction of novel variation outside the ancestral range. Consequently, shifts in mean morphology coupled with strongly increasing variability beyond an ancestrally normal range can be used as an indicator of PLE (Figure 4).

This means that the study of morphological variability across environmental gradients offers an opportunity to test specifically for evidence of the phenotypic and genetic accommodation inherent to PLE as described above.

Naturally, demonstrating this kind of intraspecific pattern requires a fossil organism or lineage with a highly resolved stratigraphy, sufficient abundance, and known presence across temporal and/or environmental gradients (Schoch, 2014). Such research is not uncommon (e.g., Hopkins & Webster, 2009; Schoch, 2014; Webber & Hunda, 2007), yet morphological variability is rarely the focal point, and phenotypic accommodation rarer still.

However, the Cambrian trilobite-like arthropod *Agnostus pisiformis* has been demonstrated to exhibit differentiated patterns of variation and variability across a gradient of dysoxic stress (Jackson & Budd, 2017) implying that environmental conditions may indeed be inducing, as well as selecting for, phenotypic variants.

Further investigation in this framework is needed to properly test the fossil record for evidence of PLE. Patterns of phenotypic variation, and chiefly variability, uncovered by fine-scale studies of fossil morphology (e.g., Dai, Zhang, Peng, & Yao, 2017; Esteve, 2012; Neubauer, Harzhauser, & Kroh, 2013) ought to be considered within the framework of PLE. Likewise, research exploring putative canalization of fossil organisms (e.g., Pimiento, Tang, Zamora, Klug, & Sánchez-Villagra, 2018; Webster,



**FIGURE 4** Illustration of two hypothetical responses of an evolutionary lineage to an environmental perturbation. (a) Natural selection causes an adaptive shift of morphology towards a new environmental optimum in line with the predictions of phyletic gradualism. (b) The environmentally mediated release of cryptic genetic variation increases phenotypic variability, facilitating rapid adaptive evolution towards a new optimum, as per the process of plasticity-led evolution. Stabilizing selection subsequently leads to canalization around this new optimum

2015) could explicitly test for indications of PLE having occurred.

## 15 | EVIDENCE OF DEVELOPMENTALLY BIASED EVOLUTIONARY TRAJECTORIES

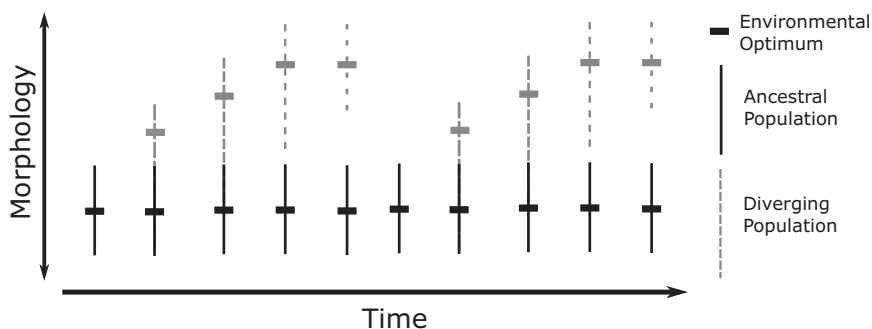
Adaptive radiations represent periods of rapid evolution in which ancestral forms of a lineage diversify in environment, morphology, functionality, and so forth. When such patterns feature repeated evolutionary sequences, such as in the case of the *Anolis* lizards of the Caribbean (Losos, Jackman, Larson, de Queiroz & Rodríguez-Schettino, 1998), they afford us the opportunity to examine the fossil record for evidence of another component of PLE, namely: whether or not repeated patterns of phenotypic evolution are sometimes better explained by developmental bias than convergent selection. At the heart of this issue lies the role of the environment in adaptive radiations. Traditionally, the environment is seen as facilitating such episodes by providing ecological opportunity to diversifying clades (Stroud & Losos, 2016). However, as outlined above, the environment may also act as an inducer of novel variants by interacting with developmental processes. Erwin (2017) describes these perspectives as emphasizing “environmental pull” and “developmental push,” respectively.

West-Eberhard’s (2003) flexible-stem model suggests that plasticity mediated by the regulatory structure of an ancestral population’s development will bias repeated independent diversifications along similar evolutionary trajectories via the processes of phenotypic and genetic accommodation. This represents an alternative or complementary explanation as to why independently derived lineages

of an ancestral population repeatedly evolve similar phenotypes, such as the “ecomorphs” of the *Anolis* lizards mentioned above (Losos et al., 1998; Williams, 1972). While this model has been explored in a neontological context (Gibert, 2017; Parsons et al., 2016; Schneider & Meyer, 2017; Wund, Baker, Clancy, Golub, & Foster, 2008), it has not yet seen attention in a paleontological setting.

Although the identification of adaptive radiations in the fossil record is not a straightforward endeavor (Lieberman, 2012), essentially any sequence of repeated divergence from an ancestral stock population is suitable for investigating the flexible-stem informed model of parallelism. Similarly to the discussion on phenotypic and genetic accommodation above, the focal point of research in such systems should be on the variability of morphology, rather than variation, relative environmental gradients. If it is indeed phenotypic accommodation, that is, the environmentally mediated release of CGV, that directs these repeated evolutionary trajectories, we should predict an increasing degree of phenotypic variability to coincide with these divergences (Figure 5). This coupling of increasing variability and shifting variation is not conventionally anticipated in a pattern of repeated parallel divergences, that is, convergent selection, as explained above.

The positive identification of such patterns in the fossil record would thus provide distinctive support for the underlying processes of PLE both in terms of the suggested environmentally mediated release of CGV, as well as the hypothesized bias exercised by the regulatory nature of development. Research towards uncovering such support should be directed towards reassessing the phenotype–environment associations of studied fossil adaptive radiations (e.g., Abe & Lieberman, 2012; Neige, Dera, & Dommergues, 2013; Neubauer et al., 2013) in the context of PLE.



**FIGURE 5** Repeated divergences from an ancestral or stock population. The bias native to the ancestral developmental network directs morphological change along similar evolutionary trajectories as the successive independently diverging populations encounter the new environment. An increase in morphological variability coupled with such parallelism of phenotypic mean change is predicted by the release of cryptic genetic variation in plasticity-led evolution but not by the conventional process of convergent evolution resulting from similar and repeated selective pressures

## 16 | CONCLUDING REMARKS

Viewing development as constructive is a promising conceptual framework for enriching our understanding of the processes and patterns of evolution. It provides the scaffolding for properly addressing issues of central importance such as the role of developmental biases in directing evolutionary change. However, the majority of efforts towards this end are conducted on extant organisms with minimal reference to paleontological data. This is unfortunate as the fossil record is a fantastically rich source of information that is yet to be fully explored in this intriguing and stimulating context. While microevolutionary concepts such as developmental bias are challenging to approach in the fossil record, I argue that it is manifest in paleontological materials in the form of macroevolutionary patterns concordant with the predictions of plasticity-led evolution. Indeed such predictions recapitulate earlier theories of quantum evolution and punctuated equilibrium.

These predictions are specifically an evolutionary model consisting of two major parts: (a) stabilizing selection during periods of environmental stability leading to a reduction in phenotypic variation but an increase in canalization, CGV and hence evolutionary capacitance; and (b) episodes of environmentally induced plasticity facilitating rapid evolution via the expression of previously cryptic variation.

Research aiming to uncover support for PLE in the fossil record should be directed towards the environment–phenotype association of fossil assemblages. Specifically, towards patterns of correlation between environmental stress and phenotypic variability as a proxy for developmental instability. These may be manifest along single lineages or throughout adaptive radiations. The fossil record offers enormous potential to provide data that, when viewed through the lens of PLE, provides biologically meaningful information about evolution in terms of both patterns and processes.

## ACKNOWLEDGMENTS

I would like to thank Armin Moczek for inviting me to contribute to this special issue on developmental bias in evolution. My thanks to two anonymous reviewers who provided thoughtful, constructive and immensely helpful comments that greatly improved this paper. I am grateful to Graham Budd for our many discussions on this topic over the years. I am thankful to the Uller group at Lund University for formative discussions, particularly Tobias Uller, who also provided valuable comments on an early draft of this paper. My thoughts presented here were greatly informed by the SFI workshop “Developmental

Bias and Evolution,” and I direct my gratitude towards its organizers and participants. This study was funded by the Knut and Alice Wallenberg Foundation grant to Tobias Uller (KAW 2012.0155).

## CONFLICT OF INTEREST

The author declares that there is no conflict of interest.

## ORCID

Illiam S. C. Jackson  <http://orcid.org/0000-0002-7948-2860>

## REFERENCES

- Abe, F. R., & Lieberman, B. S. (2012). Quantifying morphological change during an evolutionary radiation of Devonian trilobites. *Paleobiology*, *38*, 292–307. <https://doi.org/10.1666/10047.1>
- Arthur, W. (2004). The effect of development on the direction of evolution: Toward a twenty-first century consensus. *Evolution & Development*, *6*(4), 282–288. <https://doi.org/10.1111/j.1525-142X.2004.04033.x>
- Badyaev, A. V. (2005). Stress-induced variation in evolution: From behavioural plasticity to genetic assimilation. *Proceedings of the Royal Society B: Biological Sciences*, *272*, 877–886. <https://doi.org/10.1098/rspb.2004.3045>
- Badyaev, A. V. (2009). Evolutionary significance of phenotypic accommodation in novel environments: An empirical test of the Baldwin effect. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, *364*, 1125–1141. <https://doi.org/10.1098/rstb.2008.0285>
- Baedke, J. (2018). Organism, where art thou? Old and new challenges for organism-centered biology. *Journal of the History of Biology*, *52*, 293–324. <https://doi.org/10.1007/s10739-018-9549-4>.
- Bookstein, F. L. (1997). *Morphometric tools for landmark data: Geometry and biology*. Cambridge: Cambridge University Press.
- Brakefield, P. M. (2011). Evo-devo and accounting for Darwin's endless forms. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, *366*(1574), 2069–2075. <https://doi.org/10.1098/rstb.2011.0007>
- Bridle, J. R., & Vines, T. H. (2007). Limits to evolution at range margins: When and why does adaptation fail? *Trends in Ecology & Evolution*, *22*(3), 140–147. <https://doi.org/10.1016/j.tree.2006.11.002>
- Bush, A. M., Powell, M. G., Arnold, W. S., Bert, T. M., & Daley, G. M. (2002). Time-averaging, evolution, and morphologic variation. *Paleobiology*, *28*, 9–25. [https://doi.org/10.1666/0094-8373\(2002\)028%3C0009:TAEAMV%3E2.0.CO;2](https://doi.org/10.1666/0094-8373(2002)028%3C0009:TAEAMV%3E2.0.CO;2)
- Carroll, S. B. (2005). Evolution at two levels: On genes and form. *PLOS Biology*, *3*, e245. <https://doi.org/10.1371/journal.pbio.0030245>
- Carroll, S. B. (2008). Evo-devo and an expanding evolutionary synthesis: A genetic theory of morphological evolution. *Cell*, *134*, 25–36. <https://doi.org/10.1016/j.cell.2008.06.030>
- Charlesworth, B., Lande, R., & Slatkin, M. (1982). A neo-Darwinian commentary on macroevolution. *Evolution*, *36*, 474–498. <https://doi.org/10.2307/2408095>

- Cisne, J. L., Chandler, G. O., Rabe, B. D., & Cohen, J. A. (1982). Clinal variation, episodic evolution, and possible parapatric speciation: The trilobite flexicalymene senaria along an Ordovician depth gradient. *Lethaia*, *15*, 325–341. <https://doi.org/10.1111/j.1502-3931.1982.tb01697.x>
- Dai, T., Zhang, X. L., Peng, S. C., & Yao, X. Y. (2017). Intraspecific variation of trunk segmentation in the oryctocephalid trilobite *duyunaspis duyunensis* from the Cambrian (Stage 4, Series 2) of South China. *Lethaia*, *50*, 527–539. <https://doi.org/10.1111/let.12208>
- Davidson, E. H. (2006). *The regulatory genome*. San Diego: Academic Press.
- Dawkins, R. (1976). *The selfish gene*. Oxford: Oxford University Press.
- Dobzhansky, T. (1937). *Genetics and the origin of species*. New York: Columbia University Press.
- Ehrenreich, I. M., & Pfennig, D. W. (2016). Genetic assimilation: A review of its potential proximate causes and evolutionary consequences. *Annals of Botany*, *117*, 769–779. <https://doi.org/10.1093/aob/mcv130>
- Eldredge, N., & Gould, S. J. (1972). Punctuated equilibria: An alternative to phyletic gradualism. In T. J. M. Schopf (Ed.), *Models in paleobiology* (pp. 82–115). San Francisco, US: Freeman, Cooper & Company.
- Erwin, D. H. (2017). Developmental push or environmental pull? The causes of macroevolutionary dynamics. *History and Philosophy of the Life Sciences*, *39*, 36. <https://doi.org/10.1007/s40656-017-0163-0>
- Erwin, D. H., & Davidson, E. H. (2009). The evolution of hierarchical gene regulatory networks. *Nature Reviews Genetics*, *10*, 141–148. <https://doi.org/10.1038/nrg2499>
- Esteve, J. (2012). Intraspecific variability in paradoxid trilobites from the Purujosa trilobite assemblage (middle Cambrian, northeast Spain). *Acta Palaeontologica Polonica*, *59*, 215–241. <https://doi.org/10.4202/app.2012.0006>
- Flatt, T. (2005). The evolutionary genetics of canalization. *The Quarterly Review of Biology*, *80*, 287–316. <https://doi.org/10.1086/432265>
- Futuyma, D. J. (2015). Can modern evolutionary theory explain macroevolution? In E. E. Serreli, & N. Gontier (Eds.), *Macroevolution. Interdisciplinary evolution research* (2, pp. 29–85). Cham: Springer.
- Gerhart, J., & Kirschner, M. (2007). The theory of facilitated variation. *Proceedings of the National Academy of Sciences*, *104*(suppl 1), 8582–8589. <https://doi.org/10.1073/pnas.0701035104>
- Gibson, G., & Dworkin, I. (2004). Uncovering cryptic genetic variation. *Nature Reviews Genetics*, *5*, 681–690. <https://doi.org/10.1038/nrg1426>
- Gibson, G., & Wagner, G. (2000). Canalization in evolutionary genetics: A stabilizing theory? *BioEssays*, *22*, 372–380. [https://doi.org/10.1002/\(SICI\)1521-1878\(200004\)22:4<372::AID-BIES7>3.0.CO;2-J](https://doi.org/10.1002/(SICI)1521-1878(200004)22:4<372::AID-BIES7>3.0.CO;2-J)
- Gibert, J. M. (2017). The flexible stem hypothesis: Evidence from genetic data. *Development Genes and Evolution*, *227*, 297–307. <https://doi.org/10.1007/s00427-017-0589-0>
- Gingerich, P. D. (1984). Punctuated equilibria—where is the evidence? *Systematic Zoology*, *33*, 335–338. <https://doi.org/10.2307/2413079>
- Goswami, A., Binder, W. J., Meachen, J., & O’Keefe, F. R. (2015). The fossil record of phenotypic integration and modularity: A deep-time perspective on developmental and evolutionary dynamics. *Proceedings of the National Academy of Sciences*, *112*, 4891–4896. <https://doi.org/10.1073/pnas.1403667112>
- Gould, S. J. (1980). Is a new and general theory of evolution emerging? *Paleobiology*, *6*, 119–130. <https://doi.org/10.1017/S0094837300012549>
- Gould, S. (1982). Darwinism and the expansion of evolutionary theory. *Science*, *216*, 380–387. <https://doi.org/10.1126/science.7041256>
- Gould, S. J. (1986). The hardening of the Modern Synthesis. In M. Grene (Ed.), *Dimensions of Darwinism: Themes and Counter-themes in twentieth century evolutionary theory* (pp. 71–93). New York, US: Cambridge University Press.
- Gould, S. J. (2002). *The structure of evolutionary theory*. Cambridge: Harvard University Press.
- Gould, S. J., & Eldredge, N. (1977). Punctuated equilibria: The tempo and mode of evolution reconsidered. *Paleobiology*, *3*, 115–151. <https://doi.org/10.1017/S0094837300005224>
- Gould, S., & Eldredge, N. (1993). Punctuated equilibrium comes of age. *Nature*, *366*, 223–227. <https://doi.org/10.1038/366223a0>
- Hoffmann, A. A., & Hercus, M. J. (2000). Environmental stress as an evolutionary force. *BioScience*, *50*, 217–226. [https://doi.org/10.1641/0006-3568\(2000\)050\[0217:ESAAEF\]2.3.CO;2](https://doi.org/10.1641/0006-3568(2000)050[0217:ESAAEF]2.3.CO;2)
- Hopkins, M. J., & Webster, M. (2009). Ontogeny and geographic variation of a new species of the corynexochine trilobite *Zacanthopsis* (Dyeran, Cambrian). *Journal of Paleontology*, *83*, 524–547. <https://doi.org/10.1666/08-102R.1>
- Hopkins, M. J. (2014). The environmental structure of trilobite morphological disparity. *Paleobiology*, *40*, 352–373. <https://doi.org/10.1666/13049>
- Hunt, G. (2004). Phenotypic variance inflation in fossil samples: An empirical assessment. *Paleobiology*, *30*, 487–506. [https://doi.org/10.1666/0094-8373\(2004\)030%3C0487:PVIIFS%3E2.0.CO;2](https://doi.org/10.1666/0094-8373(2004)030%3C0487:PVIIFS%3E2.0.CO;2)
- Hunt, G. (2004). Phenotypic variation in fossil samples: Modeling the consequences of time-averaging. *Paleobiology*, *30*, 426–443. [https://doi.org/10.1666/0094-8373\(2004\)030%3C0426:PVIFSM%3E2.0.CO;2](https://doi.org/10.1666/0094-8373(2004)030%3C0426:PVIFSM%3E2.0.CO;2)
- Hunt, G. (2007). The relative importance of directional change, random walks, and stasis in the evolution of fossil lineages. *Proceedings of the National Academy of Sciences*, *104*, 18404–18408. <https://doi.org/10.1073/pnas.0704088104>
- Hunt, G. (2010). Evolution in fossil lineages: Paleontology and the origin of species. *The American Naturalist*, *176*(suppl 1), S61–S76. <https://doi.org/10.1086/657057>
- Hunt, G., & Rabosky, D. L. (2014). Phenotypic evolution in fossil species: Pattern and process. *Annual Review of Earth and Planetary Sciences*, *42*, 421–441. <https://doi.org/10.1073/pnas.0704088104>
- Hunt, G., Bell, M. A., & Travis, M. P. (2008). Evolution toward a new adaptive optimum: Phenotypic evolution in a fossil stickleback lineage. *Evolution*, *62*, 700–710. <https://doi.org/10.1111/j.1558-5646.2007.00310.x>
- Imasheva, A. G., Loeschcke, V., Zhivotovsky, L. A., & Lazebny, O. E. (1997). Effects of extreme temperatures on phenotypic variation and developmental stability in *Drosophila melanogaster* and *Drosophila buzzatii*. *Biological Journal of the Linnean Society*, *61*, 117–126. <https://doi.org/10.1111/j.1095-8312.1997.tb01780.x>
- Iwasaki, W. M., Tsuda, M. E., & Kawata, M. (2013). Genetic and environmental factors affecting cryptic variations in gene



- regulatory networks. *BMC Evolutionary Biology*, 13, 91. <https://doi.org/10.1186/1471-2148-13-91>
- Jablonski, D. (2017). Approaches to macroevolution: 1. General concepts and origin of variation. *Evolutionary Biology*, 44, 427–450. <https://doi.org/10.1007/s11692-017-9420-0>
- Jablonski, D., & Shubin, N. H. (2015). The future of the fossil record: Paleontology in the 21st century. *Proceedings of the National Academy of Sciences*, 112, 4852–4858. <https://doi.org/10.1073/pnas.1505146112>
- Jackson, I. S. C., & Budd, G. E. (2017). Intraspecific morphological variation of *Agnostus pisiformis*, a Cambrian Series 3 trilobite-like arthropod. *Lethaia*, 50, 467–485. <https://doi.org/10.1111/let.12201>
- Kidwell, S. M., & Flessa, K. W. (1995). The quality of the fossil record: Populations, species, and communities. *Annual Review of Ecology and Systematics*, 26, 269–299. <https://doi.org/10.1146/annurev.earth.24.1.433>
- Kirkpatrick, M. (1982). Quantum evolution and punctuated equilibria in continuous genetic characters. *The American Naturalist*, 119, 833–848. <https://doi.org/10.1086/283958>
- Klingenberg, C. P. (2019). Phenotypic plasticity, developmental instability and robustness: The concepts and how they are connected. *Frontiers in Ecology and Evolution*, 7, 7. <https://doi.org/10.3389/fevo.2019.00056>
- Kuhl, F. P., & Giardina, C. R. (1982). Elliptic Fourier features of a closed contour. *Computer Graphics and Image Processing*, 18, 236–258. [https://doi.org/10.1016/0146-664X\(82\)90034-X](https://doi.org/10.1016/0146-664X(82)90034-X)
- Küttner, E., Parsons, K. J., Easton, A. A., Skúlason, S., Danzmann, R. G., & Ferguson, M. M. (2014). Hidden genetic variation evolves with ecological specialization: The genetic basis of phenotypic plasticity in Arctic charr ecomorphs. *Evolution & Development*, 16, 247–257. <https://doi.org/10.1111/ede.12087>
- Laland, K. N., Uller, T., Feldman, M. W., Sterelny, K., Müller, G. B., Moczek, A., ... Odling-Smee, J. (2015). The extended evolutionary synthesis: Its structure, assumptions and predictions. *Proceedings of the Royal Society B: Biological Sciences*, 282, 20151019. <https://doi.org/10.1098/rspb.2015.1019>
- Lande, R. (2009). Adaptation to an extraordinary environment by evolution of phenotypic plasticity and genetic assimilation. *Journal of Evolutionary Biology*, 22, 1435–1446. <https://doi.org/10.1111/j.1420-9101.2009.01754.x>
- Levis, N. A., & Pfennig, D. W. (2016). Evaluating 'plasticity-first' evolution in nature: Key criteria and empirical approaches. *Trends in Ecology & Evolution*, 31(7), 563–574. <https://doi.org/10.1016/j.tree.2016.03.012>
- Levis, N. A., & Pfennig, D. W. (2019). Plasticity-led evolution: Evaluating the key prediction of frequency-dependent adaptation. *Proceedings of the Royal Society B: Biological Sciences*, 286, 20182754. <https://doi.org/10.1098/rspb.2018.2754>
- Lieberman, B. S. (2012). Adaptive radiations in the context of macroevolutionary theory: A paleontological perspective. *Evolutionary Biology*, 39, 181–191. <https://doi.org/10.1007/s11692-012-9165-8>
- Lieberman, B. S., & Eldredge, N. (2014). What is punctuated equilibrium? What is macroevolution? A response to Pennell et al. *Trends in Ecology & Evolution*, 29, 185–186. <https://doi.org/10.1016/j.tree.2014.02.005>
- Losos, J. B., Jackman, T. R., Larson, A., de Queiroz, K., & Rodríguez-Schettino, L. (1998). Contingency and determinism in replicated adaptive radiations of island lizards. *Science*, 279, 2115–2118. <https://doi.org/10.1126/science.279.5359.2115>
- MacLeod, N. (2002). Geometric morphometrics and geological shape-classification systems. *Earth-Science Reviews*, 59, 27–47. [https://doi.org/10.1016/S0012-8252\(02\)00068-5](https://doi.org/10.1016/S0012-8252(02)00068-5)
- MacLeod, N. (2017). Morphometrics: History, development methods and prospects. *Zoological Systematics*, 42, 4–33. <https://doi.org/10.11865/zs.201702>
- Masel, J. (2006). Cryptic genetic variation is enriched for potential adaptations. *Genetics*, 172, 1985–1991. <https://doi.org/10.1534/genetics.105.051649>
- McGuigan, K., & Sgrò, C. M. (2009). Evolutionary consequences of cryptic genetic variation. *Trends in Ecology & Evolution*, 24, 305–311. <https://doi.org/10.1016/j.tree.2009.02.001>
- Moczek, A. P. (2008). On the origins of novelty in development and evolution. *BioEssays*, 30, 432–447. <https://doi.org/10.1002/bies.20754>
- Moczek, A. P. (2012). The nature of nurture and the future of evo devo: Toward a theory of developmental evolution. *Integrative and Comparative Biology*, 52(1), 108–119. <https://doi.org/10.1093/icb/ics048>
- Moczek, A. P. (2015). Re-evaluating the environment in developmental evolution. *Frontiers in Ecology and Evolution*, 3, <https://doi.org/10.3389/fevo.2015.00007>
- Moczek, A. P. (2015). Developmental plasticity and evolution—quovadis? *Heredity*, 115, 302–305. <https://doi.org/10.1038/hdy.2015.14>
- Moczek, A. P., Sultan, S., Foster, S., Ledón-Rettig, C., Dworkin, I., Nijhout, H. F., ... Pfennig, D. W. (2011). The role of developmental plasticity in evolutionary innovation. *Proceedings of the Royal Society B: Biological Sciences*, 278, 2705–2713. <https://doi.org/10.1098/rspb.2011.0971>
- Müller, G. B. (2007). Evo-devo: Extending the evolutionary synthesis. *Nature Reviews Genetics*, 8(12), 943–949. <https://doi.org/10.1038/nrg2219>
- Myers, C. E., & Saupé, E. E. (2013). A macroevolutionary expansion of the modern synthesis and the importance of extrinsic abiotic factors. *Palaeontology*, 56, 1179–1198. <https://doi.org/10.1111/pala.12053>
- Neubauer, T. A., Harzhauser, M., & Kroh, A. (2013). Phenotypic evolution in a fossil gastropod species lineage: Evidence for adaptive radiation? *Palaeogeography, Palaeoclimatology, Palaeoecology*, 370, 117–126. <https://doi.org/10.1016/j.palaeo.2012.11.025>
- Neige, P., Dera, G., & Dommergues, J. L. (2013). Adaptive radiation in the fossil record: A case study among Jurassic ammonoids. *Palaeontology*, 56, 1247–1261. <https://doi.org/10.1111/pala.12062>
- Nicholson, D. J. (2014). The return of the organism as a fundamental explanatory concept in biology. *Philosophy Compass*, 9, 347–359. <https://doi.org/10.1111/phc3.12128>
- Noble, D. (2015). Evolution beyond neo-Darwinism: A new conceptual framework. *Journal of Experimental Biology*, 218, 7–13. <https://doi.org/10.1242/jeb.106310>
- Noble, D. (2015). Conrad Waddington and the origin of epigenetics. *Journal of Experimental Biology*, 218, 816–818. <https://doi.org/10.1242/jeb.120071>
- Organ, C. L., Cooper, L. N., & Hieronymus, T. L. (2015). Macroevolutionary developmental biology: Embryos, fossils,



- and phylogenies. *Developmental Dynamics*, 244, 1184–1192. <https://doi.org/10.1002/dvdy.24318>
- Paaby, A. B., & Rockman, M. V. (2014). Cryptic genetic variation: Evolution's hidden substrate. *Nature Reviews Genetics*, 15, 247–258. <https://doi.org/10.1038/nrg3688>.
- Parsons, K. J., Concannon, M., Navon, D., Wang, J., Ea, I., Groveas, K., ... Albertson, R. C. (2016). Foraging environment determines the genetic architecture and evolutionary potential of trophic morphology in cichlid fishes. *Molecular Ecology*, 25, 6012–6023. <https://doi.org/10.1111/mec.13801>.
- Pennell, M. W., Harmon, L. J., & Uyeda, J. C. (2014). Is there room for punctuated equilibrium in macroevolution? *Trends in Ecology & Evolution*, 29, 23–32. <https://doi.org/10.1016/j.tree.2013.07.004>
- Pertoldi, C., Bundgaard, J., Loeschcke, V., & Barker, J. S. F. (2014). The phenotypic variance gradient—a novel concept. *Ecology and Evolution*, 4, n/a–n/a. <https://doi.org/10.1002/ece3.1298>.
- Pertoldi, C., & Kristensen, T. (2015). A new fluctuating asymmetry index, or the solution for the scaling effect? *Symmetry*, 7, 327–335. <https://doi.org/10.3390/sym7020327>
- Pigliucci, M. (2010). Genotype–phenotype mapping and the end of the ‘genes as blueprint’ metaphor. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, 365, 557–566. <https://doi.org/10.1098/rstb.2009.0241>
- Pigliucci, M., & Murren, C. J. (2003). Perspective: Genetic assimilation and a possible evolutionary paradox: Can macroevolution sometimes be so fast as to pass us by? *Evolution*, 57, 1455–1464. <https://doi.org/10.1111/j.0014-3820.2003.tb00354.x>
- Pigliucci, M. (2006). Phenotypic plasticity and evolution by genetic assimilation. *Journal of Experimental Biology*, 209, 2362–2367. <https://doi.org/10.1242/jeb.02070>.
- Pimiento, C., Tang, K. L., Zamora, S., Klug, C., & Sánchez-Villagra, M. R. (2018). Assessing canalisation of intraspecific variation on a macroevolutionary scale: The case of crinoid arms through the Phanerozoic. *PeerJ*, 6, e4899. <https://doi.org/10.7717/peerj.4899>
- Rieseberg, L. H., Archer, M. A., & Wayne, R. K. (1999). Transgressive segregation, adaptation and speciation. *Heredity*, 83, 363–372. <https://doi.org/10.1038/sj.hdy.6886170>.
- Rutherford, S. L. (2000). From genotype to phenotype: Buffering mechanisms and the storage of genetic information. *BioEssays*, 22, 1095–1105. [https://doi.org/10.1002/1521-1878\(200012\)22:12<1095::AID-BIES7>3.0.CO;2-A](https://doi.org/10.1002/1521-1878(200012)22:12<1095::AID-BIES7>3.0.CO;2-A)
- Scarponi, D., & Kowalewski, M. (2004). Stratigraphic paleoecology: Bathymetric signatures and sequence overprint of mollusk associations from upper Quaternary sequences of the Po Plain, Italy. *Geology*, 32, 989–992. <https://doi.org/10.1130/G20808.1>
- Schlichting, C. D. (1989). Phenotypic integration and environmental change. *BioScience*, 39, 460–464. <https://doi.org/10.2307/1311138>.
- Schlichting, C. D. (2008). Hidden reaction norms, cryptic genetic variation, and evolvability. *Annals of the New York Academy of Sciences*, 1133, 187–203. <https://doi.org/10.1196/annals.1438.010>
- Schlichting, C. D., & Smith, H. (2002). Phenotypic plasticity: Linking molecular mechanisms with evolutionary outcomes. *Evolutionary Ecology*, 16, 189–211. <https://doi.org/10.1023/A:1019624425971>
- Schlichting, C. D., & Wund, M. A. (2014). Phenotypic plasticity and epigenetic marking: An assessment of evidence for genetic accommodation. *Evolution*, 68, 656–672. <https://doi.org/10.1111/evo.12348>
- Schmalhausen, I. I. (1949). *Factors of Evolution*. Chicago: The University of Chicago Press.
- Schneider, R. F., & Meyer, A. (2017). How plasticity, genetic assimilation and cryptic genetic variation may contribute to adaptive radiations. *Molecular Ecology*, 26, 330–350. <https://doi.org/10.1111/mec.13880>
- Schoch, R. R. (2014). Life cycles, plasticity and palaeoecology in temnospondyl amphibians. *Palaeontology*, 57(3), 517–529. <https://doi.org/10.1111/pala.12100>
- Schwab, D. B., Casasa, S., & Moczek, A. P. (2019). On the reciprocally causal and constructive nature of developmental plasticity and robustness. *Frontiers in Genetics*, 9, <https://doi.org/10.3389/fgene.2018.00735>.
- Schwander, T., & Leimar, O. (2011). Genes as leaders and followers in evolution. *Trends in Ecology & Evolution*, 26, 143–151. <https://doi.org/10.1016/j.tree.2010.12.010>
- Sheldon, P. R. (1997). The Plus ça change model: Explaining stasis and evolution in response to abiotic stress over geological timescales. In R. Bijlsma, & V. Loeschcke (Eds.), *Environmental Stress, Adaptation and Evolution* (pp. 307–319). Basel: Birkhäuser.
- Simpson, G. G. (1944). *Tempo and mode in evolution*. New York: Columbia University Press.
- Simpson, G. G. (1953). *The major features of evolution*. New York: Columbia University Press.
- Stroud, J. T., & Losos, J. B. (2016). Ecological opportunity and adaptive radiation. *Annual Review of Ecology, Evolution, and Systematics*, 47, 507–532. <https://doi.org/10.1146/annurev-ecolsys-121415-032254>
- Tribouillard, N., Algeo, T. J., Lyons, T., & Riboulleau, A. (2006). Trace metals as paleoredox and paleoproductivity proxies: An update. *Chemical Geology*, 232, 12–32. <https://doi.org/10.1016/j.chemgeo.2006.02.012>
- Uller, T., Moczek, A. P., Watson, R. A., Brakefield, P. M., & Laland, K. N. (2018). Developmental bias and evolution: A regulatory network perspective. *Genetics*, 209, 949–966. <https://doi.org/10.1534/genetics.118.300995>
- van Bergen, E., Osbaldeston, D., Kodandaramaiah, U., Brattström, O., Aduse-Poku, K., & Brakefield, P. M. (2017). Conserved patterns of integrated developmental plasticity in a group of polyphenic tropical butterflies. *BMC Evolutionary Biology*, 17, <https://doi.org/10.1186/s12862-017-0907-1>
- Voje, K. L. (2016). Tempo does not correlate with mode in the fossil record. *Evolution*, 70, 2678–2689. <https://doi.org/10.1111/evo.13090>
- Waddington, C. H. (1942). Canalization of development and the inheritance of acquired characters. *Nature*, 150, 563–565. <https://doi.org/10.1038/150563a0>
- Waddington, C. H. (1961). Advances in genetics. *Advances in Genetics*, 10, 257–293. [https://doi.org/10.1016/S0065-2660\(08\)60119-4](https://doi.org/10.1016/S0065-2660(08)60119-4).
- Wagner, A. (2011). *The origins of evolutionary innovations: a theory of transformative change in living systems*. Oxford: Oxford University Press.
- Wagner, G. P., Booth, G., & Bagheri-Chaichian, H. (1997). A population genetic theory of canalization. *Evolution*, 51, 329–347. <https://doi.org/10.1111/j.1558-5646.1997.tb02420.x>

- Wagner, G. P., & Zhang, J. (2011). The pleiotropic structure of the genotype–phenotype map: The evolvability of complex organisms. *Nature Reviews Genetics*, *12*, 204–213. <https://doi.org/10.1038/nrg2949>.
- Watson, R. A., & Szathmáry, E. (2016). How can evolution learn? *Trends in Ecology & Evolution*, *31*, 147–157. <https://doi.org/10.1016/j.tree.2015.11.009>
- Watson, R. A., Wagner, G. P., Pavlicev, M., Weinreich, D. M., & Mills, R. (2014). The evolution of phenotypic correlations and “developmental memory”. *Evolution*, *68*, 1124–1138. <https://doi.org/10.1111/evo.12337>
- Webber, A. J., & Hunda, B. R. (2007). Quantitatively comparing morphological trends to environment in the fossil record (Cincinnatian Series; Upper Ordovician). *Evolution*, *61*, 1455–1465. <https://doi.org/10.1111/j.1558-5646.2007.00123.x>
- Webster, M. (2015). Ontogeny and intraspecific variation of the early Cambrian trilobite *Olenellus gilberti*, with implications for olenelline phylogeny and macroevolutionary trends in phenotypic canalization. *Journal of Systematic Palaeontology*, *13*, 1–74. <https://doi.org/10.1080/14772019.2013.852903>
- Webster, M. (2019). Morphological homeostasis in the fossil record. *Seminars in Cell & Developmental Biology*, *88*, 91–104. <https://doi.org/10.1016/j.semcd.2018.05.016>
- West-Eberhard, M. J. (2003). *Developmental plasticity and evolution*. Oxford: Oxford University Press.
- West-Eberhard, M. J. (2005). Developmental plasticity and the origin of species differences. *Proceedings of the National Academy of Sciences*, *102*(suppl 1), 6543–6549. <https://doi.org/10.1073/pnas.0501844102>.
- West-Eberhard, M. J. (2005). Phenotypic accommodation: Adaptive innovation due to developmental plasticity. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution*, *304*, 610–618. <https://doi.org/10.1002/jez.b.21071>.
- Williams, E. E. (1972). The origin of faunas. Evolution of lizard congeners in a complex island fauna: A trial analysis. In T. Dobzhansky, M. K. Hecht, & W. C. Steere (Eds.), *Evolutionary Biology*. New York, NY: Springer.
- Willmore, K. E., Young, N. M., & Richtsmeier, J. T. (2007). Phenotypic variability: Its components, measurement and underlying developmental processes. *Evolutionary Biology*, *34*, 99–120. <https://doi.org/10.1007/s11692-007-9008-1>
- Wright, S. (1932). The roles of mutation, inbreeding, crossbreeding, and selection in evolution. *Proceedings of the VI International Congress of Genetics*, *1*, 356–366.
- Wund, M. A. (2012). Assessing the impacts of phenotypic plasticity on evolution. *Integrative and comparative biology*, *52*, 5–15. <https://doi.org/10.1093/icb/ics050>
- Wund, M. A., Baker, J. A., Clancy, B., Golub, J. L., & Foster, S. A. (2008). A test of the “flexible stem” model of evolution: Ancestral plasticity, genetic accommodation, and morphological divergence in the threespine stickleback radiation. *The American Naturalist*, *172*, 449–462. <https://doi.org/10.1086/590966>
- Wund, M. A., Valena, S., Wood, S., & Baker, J. A. (2012). Ancestral plasticity and allometry in threespine stickleback reveal phenotypes associated with derived, freshwater ecotypes. *Biological Journal of the Linnean Society*, *105*, 573–583. <https://doi.org/10.5061/dryad.hb824gd4>
- Zheng, J., Payne, J. L., & Wagner, A. (2019). Cryptic genetic variation accelerates evolution by opening access to diverse adaptive peaks. *Science*, *365*, 347–353. <https://doi.org/10.1126/science.aax1837>

**How to cite this article:** Jackson ISC. Developmental bias in the fossil record. *Evolution & Development*. 2019;e12312. <https://doi.org/10.1111/ede.12312>