Studies in History and Philosophy of Biol & Biomed Sci 68–69 (2018) 25–33

Contents lists available at ScienceDirect

Studies in History and Philosophy of Biol & Biomed Sci

journal homepage: www.elsevier.com/locate/shpsc

Natural selection, plasticity, and the rationale for largest-scale trends

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ARTICLE INFO

Keywords:
Trends
Natural selection
Environment
Plasticity
Complexity

ABSTRACT

Many have argued that there is no reason why natural selection should cause directional increases in measures such as body size or complexity across evolutionary history as a whole. In this paper I argue that this conclusion does not hold for selection for adaptations to environmental variability, and that, given the inevitability of environmental variability, trends in adaptations to variability are an expected feature of evolution by natural selection. As a concrete instance of this causal structure, I outline how this may be applied to a trend in phenotypic plasticity.

1. Introduction

Biologists have long been fascinated with the idea that natural selection consistently favors increases in some evolutionary measures (such as organismic complexity), and that this has resulted in natural selection causing large-scale trends: directional increases in the mean or maximum of the measure across species lineages over large time intervals (Bonner, 1988; Rosslenbroich, 2006; Vermeij, 1987). However, the idea that natural selection should consistently privilege some adaptations over others is deeply problematic, certainly when considered at the largest time-scale, encompassing evolutionary history as a whole. As Gould summed up this problem (formulated with regard to progress rather than directional trends): "the bare-bones mechanics of the theory of natural selection provides no rationale for progress because the theory speaks only of adaptation to local changing environments." (Gould, 2002, pp. 467–8).[1]

The two components in the "bare-bones mechanics" to which Gould is referring are the *locality* of natural selection and the *heterogeneity* or *variability* of the environment. Locality refers to the way in which a trait that offers a fitness advantage in temporally and spatially immediate environments may not do so in temporally or spatially distant environment.[2] Variability refers to the multidimensionality of natural environments characterized by many degrees of freedom, and the variation in these degrees of freedom over multiple temporal and spatial scales. Taken together, locality and variability mean that the direction and magnitude of natural selection can be expected to vary greatly on the largest time-scale. In other words, unless environments line up in a very improbable way, there is no reason to expect that natural selection should cause any largest-scale trend.

This does not mean that selection-caused trends cannot occur, even over large time-scales. They do; for instance, there is good evidence that selection induced a trend in increasing body size in mammals during the Cenozoic (Alroy, 1998). The issue rather concerns the counterfactual relation between trends and environment: whether selection-caused trends are always contingent on a particular succession of favorable environments.[3] The fundamental natures of selection and the environment – in particular, the locality of natural selection and variability of the environment – seem to imply that if the tape of life were to be replayed in radically different environments, selection would not cause the same trend to occur. In this light, the absence of a rationale for largest-scale trends can be encapsulated by the following argument (the local selection argument or LSA):

(P1) Products of natural selection are adapted only to the local environment;
(P2) All possible environmental states are equiprobable in

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[1] In a similar vein, Radick (2000) speaks of the "happenstance explanation" of evolutionary progress as the only option available to the "modern selectionist" (Radick, 2000, p. 477). See also Williams (1966, p. 35): "I suspect that no one would ever have deduced progress from the theory [of natural selection] itself. The concept of progress must have arisen from an anthropocentric consideration of the data bearing on the history of life."

[2] Note that every environment of an individual or population is extended in space and time, and that upon closer analysis, it is often not so clear how to demarcate the local from the non-local environment. However, it is widely assumed that the distinction between the local and non-local environment is not arbitrary, and the ongoing challenge is to understand precisely what the criteria of demarcation are (Abrams, 2014; Brandon, 1990; Millstein, 2014). A minimal definition of 'environment', as the instantaneous value of the environmental variables (such as temperature, oxygen levels, vicinity of predators etc.), is sufficient for this paper and thus this issue can be largely sidestepped.

[3] 'Contingency' here is taken in the sense of causal-dependence (Beatty, 2006). Thus, in a replay of life's tape, characterized by different environments, one would likely not see the same selection-caused trend emerging.

https://doi.org/10.1016/j.shpsc.2018.04.002
Received 16 May 2017; Received in revised form 23 January 2018; Accepted 2 April 2018
Available online 09 April 2018

evolutionary history;

∴ (C) Any selection-caused largest-scale trend is contingent on what environments happen to occur in evolutionary history.

Premise (P1) is a statement of the local nature of natural selection. Premise (P2) is added to ensure that no information concerning the likelihood of environments is integrated in the expectation of the trend. In this way, the conclusion is a reflection of the fundamental causal nature (or "bare-bones mechanics") of natural selection.

While the LSA more or less represents the consensus view, it is more problematic than may seem at first and has often been contested in the history of evolutionary theory, going back to Darwin's own discussion of evolutionary progress (see Radick, 2000). The debate about progress no longer grips mainstream evolutionary thought as it once did (mainly because the idea of progress has been criticized as anthropocentric and overly value-laden: see for instance Williams, 1966; Ayala, 1988, pp. 75–96; Gould, 1988; Ruse, 1996), but the one aspect of that debate that still remains controversial is whether, and if so, how, natural selection causes largest-scale evolutionary trends. Often by integrating results from other domains of biology such as ecology and development, it has been argued that selection has caused trends in increasing body size (Bonner, 1988), energy-intensiveness (Vermeij, 1987), autonomy (Rosslenbroich, 2006), information sensitivity (Ayala, 1988, pp. 75–96; Simpson, 1971), functional complexity (Bonner, 1988), and generalized fitness (Van Valen, 1976).[4]

The purpose of this paper is to revisit this long-standing topic from a purely conceptual perspective. I will bracket those issues concerning how well various hypothesized selection-caused trends are empirically supported (although see McShea, 1994, 1996, 1998), or issues concerning whether biologists are implicitly motivated by anthropocentrism (see Gould, 1996; Ruse, 1996; Williams, 1966). Rather, the main question is the following: given the natures of selection and the environment, are selection-caused large-scale trends somehow to be expected or are they merely adventitious? The LSA is an argument for the latter; in this paper I will consider two arguments for the former, one preferable to the other.

The first argument, discussed in the second section, concerns what I term the *generality selection argument* (GSA). In brief, the GSA starts from the observation that some traits ('general adaptations'), such as increased body size or increased functional complexity, are adaptive not just to one specific environment, but across a wide range of environments. For example, increased body size has been claimed to confer a general competitive advantage in many different environments (Bonner, 1988). The general selective advantage causes a trend in the general adaptation, a trend that according to the GSA can be expected in any replay of life's tape. However, I will argue that the GSA fails as a counterargument to the LSA, since a general selective advantage will still be insufficient to guarantee that a selection-caused trend would be robust against unfavorable changes in the environment.

The third section lays out the variability selection argument (VSA), which draws on the claim that environmental variability itself – defined as the temporal or spatial change in the value of a given environmental degree of freedom – may be considered to be an expected property in any replay of life's tape. Based on this, the VSA makes the case that selection-caused trends can be non-contingent features of evolutionary history if they are caused by selection for adaptations to environmental variability (i.e. variability selection).

The VSA as such only elucidates a conceptual relation between environmental variability and selection-driven trends. Lest the VSA be seen as an empty argument, in the fourth section I show how the selection for plasticity – an important type of adaptation to environmental variability – fits the general template of the VSA. The main challenges will be to show how increases in plasticity across species lineages can be meaningfully conceived, and how such increases, despite being adaptive only to some types of environmental variability but not others, are nonetheless robust against unfavorable changes in the environment.

The fifth and final section addresses potential objections and issues, one of which is important to anticipate: how precisely does a conceptual argument such as the VSA relate to empirical reality? The VSA does not concern actual trends and as such is not an empirical generalization. It only concerns to what extent selection-caused trends, regardless of whether they occur or not, are contingent on the environment, and thus only concerns *idealized* replays of life's tape, where no other causal factors besides selection play a role.[5] This, however, does not mean that empirical reality plays no role in making the case for the VSA. For the VSA to be seen as a plausible alternative to the LSA, and as possessing at least *some* potential explanatory force of empirical reality, it is also important to show how empirical research (research concerning plasticity in particular) is consistent with, and can be interpreted along the lines of the general template of the VSA.

2. Trends: patterns and causes

Diagrams representing evolutionary trends are standardly mapped out against two axes, one representing the *measure* of interest (complexity, size, etc.) and the other representing time (e.g. Fig. 1). Each vertical line can be thought of as representing a species, each node a speciation event, and the lineages branching off from the node indicating the daughter species with either increased, decreased or equal measure.

What is of interest is how the *distribution* of the measure over all branches evolves over time. A trend is established when the mean of the measure distribution increases over time. Further, three main types of trend are typically distinguished (following McShea, 1994). When the mean increases but there is no bias for branching events to lead to either increased or decreased measure, the trend is said to be 'passive' (see Fig. 1). What is noteworthy of a passive trend is that the mean increases even though there is no inherent bias, simply because there is a minimum measure — such as a minimum possible size, or degree of complexity. When there is a bias for increase over decrease during branching events, the trend is said to be 'driven'. In this case, a higher percentage of branching events leads to increases. Driven trends are further subdivided into 'weakly driven' trends when minimum measure does not increase over time, and 'strongly driven' trends, when the minimum increases over time.

It is important to note that not just drift, but also natural selection can be the cause of the random walk that characterizes passive trends. As environments vary freely, so does the direction of natural selection, leading to an equal share of increases and decreases in the measure of interests. Within the larger passive trend, there may be zones of driven increase that are a consequence of favorable environments; nonetheless, such zones cancel each other out on average. Thus, a selection-driven trend may have the exact same large-scale pattern as one that is merely a random walk – even though on smaller time scales, the selection-driven trend may consist of strongly driven microtrends.

This allows for a different way of understanding the main question of this paper: given the nature of selection, are selection-caused large-scale trends expected to be indistinguishable random walks at the largest scale?[6] In other words, given the nature of selection, is the average bias at the largest time scale always expected to be zero?

[4] See Rosslenbroich (2006) for a comprehensive overview.

[5] In this way, there are some important parallels between the VSA and the "special formulation" of the Zero Force Evolutionary Law (McShea & Brandon, 2010, p. 3).

[6] Developmental constraints may also cause biases in evolutionary trends. For example, it is often postulated that organismic complexity increases because it is easier to add than to subtract developmental systems (Bonner, 1988; Maynard Smith, 1970; Saunders & Ho, 1976). This increase reflects fundamental properties in developmental systems, and should be distinguished from the selection-caused increases of concern here.

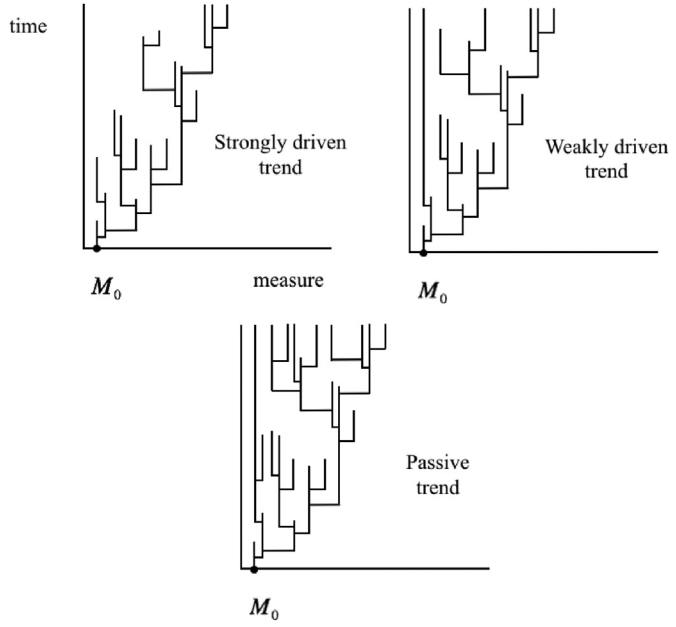

Fig. 1. Different types of trends.

3. The generality selection argument

The generality selection argument makes the case that natural selection consistently favors general adaptations, leading to robust large-scale evolutionary trends that would reoccur in replays of life's tape.[7] In this section, I will reconstruct this argument in more detail, and will argue that it fails to establish a non-contingent generalization.

The starting observation of the GSA (as well as of the LSA) is that environments are complex, characterized by many degrees of freedom, and variable over multiple temporal and spatial scales. However, some features are common to most if not all environments. For instance, in most (though not all) environments, the sources of nutrition are limited and are spread out over space, there are physical stressors (such as heat, cold, or drought), potential mates are in limited supply, and predators threaten survival. There are exceptions, of course, with some species inhabiting environments with few if any physical stressors, or with no natural predators; nonetheless, the selection pressures occasioned by predation or physical stressors are sufficiently common to cause a consistent selection for adaptations to these 'general features' of environments.

It is not necessary that every single environment possess this general feature, only that a 'sufficient' number of environments do, so that *on average* the general adaptation will be selected for. The relative frequency with which the favorable type of environment occurs needs only to reach a certain threshold; this threshold need not be a relative frequency of 1. When the general features are sufficiently widespread, or so the GSA goes, the selection for the corresponding general adaptations will be frequent enough to result in a large-scale trend in that general adaptation.

For instance, besides nutritional resources (Bonner, 1988), body size has been hypothesized to be an advantage in predator-prey interactions (Benton, 2002), competition for mates (Andersson, 1994) and in resisting extreme environments (Peters, 1983). Functional complexity has also been claimed (Bonner, 1988) to be generally adaptive since complexity allows for a division of labor between the parts of an organism. Thus, increased functional complexity allows for increased energy efficiency, which in turn is favored by natural selection in the majority of environments.

As another example, the rough outline of the GSA can also be discerned in Vermeij (1987) complex argument for a global increase in energy-intensiveness. Vermeij understands energy-intensiveness as a banner term, one that can be manifested in different ways, including larger size, longer life-span, higher metabolic rate, a larger number of interactions with the environment, and a larger number of functions. In a competition between an individual with higher energy-intensiveness and one with lower energy-intensiveness, the former will have the edge, and thus selection will favor energy-intensiveness on average, in a process that Vermeij terms 'escalation' (Vermeij, 1987, pp. 49ff). Escalation is not an inevitable process, but rather is dependent on the presence of sufficient environmental resources to support higher energy-intensiveness: for example, climatic warming, the spread of lowland forest, and expanded shallow marine waters are some conditions favorable to escalation (Vermeij, 1987, p. 377). Despite this dependence on favorable conditions, Vermeij characterizes the fitness increase brought on by increased energy-intensiveness as a "nearly universal property" in competitive environments (Vermeij, 1999).

There are two problems with the generality argument. The first is that the GSA is dependent on assumptions about the frequency of favorable environments. In a replay of life's tape, there is no reason why favorable environments should again be sufficiently frequent. For example, with regard to body size, empirical and theoretical research has identified many ways in which increased size can be maladaptive. There are costs, including increased foraging risk (Carlson, Olsen, & Vøllestad, 2008; Dibattista, Feldheim, Gruber, & Hendry, 2007), structure problems, a greater danger of reduced locomotory performance (Lankford, Billerbeck, & Conover, 2001), and a decreased potential for adaptive evolution (Dombroskie & Aarssen, 2010). Whether the benefits of increased size outweigh such costs depend on some key environmental factors, such as nutritional density. When the available nutritional resources diminish (such as during mass extinctions), there is clear selection against size (Alroy, 1998; Arnold, Kelly, & Parker, 1995; LaBarbera, 1986). Another key environmental factor is the stability of environments. In unstable environments, there is selection for an increased number of offspring and shorter generation times (r-selection), which are correlated with decreased body size (Bonner, 1988, p. 48). In sum, without additional assumptions about the types of environment that should occur in evolutionary history (in violation of P2), one cannot automatically hold that general adaptations will be adaptive in a large proportion of possible environments.

Even if the first problem could be overcome, there is no reason to expect that general adaptations are robust against detrimental environmental conditions. An organism bearing a generally adaptive trait could thrive in most environments, yet be not merely maladaptive but non-viable in non-favorable environments. This is the case with a (relatively) large body size, which may offer an advantage in most environments, but which requires a minimum nutrient density to be sustained (Bonner, 1988). This has been proposed as the explanation of the 'island rule', or why large island-dwelling mammals tend to dwarf (Foster, 1964; Van Valen, 1973). It has also been taken to explain why trends in body size are often broken during mass-extinctions (Alroy, 1998; Arnold et al., 1995; Kingsolver & Pfennig, 2004; LaBarbera, 1986). In general, being adaptive in a large proportion of possible environments still does not guarantee that a trend in general adaptations will not be contingent on which environments happen to occur.

In summary, the conceptual argument for natural selection driving a trend towards the increased development of some general adaptation (increased size, increased complexity, etc.) fails because it is dependent on contingent assumptions about which environments happen to occur –assumptions that might fail to hold in reruns of life's tape. Given what we know about the complexity of environmental structure, there is little reason to believe that environments should necessarily line up in just the way demanded by trends in general adaptations. A trait may happen

[7] For instance, Vermeij speaks of "nearly universal properties" (Vermeij, 1999), and Van Valen goes so far as to call his proposed Red Queen dynamic rates an evolutionary "law" (Van Valen, 1973, p. 16).

to be generally adaptive, but there is no reason it should be so in a replay of life's tape, and if it is not universally adaptive, a lethal or severely detrimental environment will occur sooner or later.

4. Plasticity and the variability selection argument

Environmental variability – the temporal or spatial change in the value of a given environmental variable – is necessary in any replay of life's tape since life emerges in a far-from-equilibrium environment characterized by chemical and temperature gradients (e.g. England, 2013). Thus, while all possible life-supporting[8] environmental states are equiprobable (P2), variability itself is inevitable. This suggests the following argument (VSA):

(P1) Products of natural selection are adapted only to the local environment;
(P2) All possible life-supporting environmental states are equiprobable in evolutionary history;
∴ (C) A selection-caused largest-scale trend in a variability adaptation is not contingent on which environments happen to occur.

Not all variability adaptations are good candidates for a largest-scale trend. It is not clear, for instance, what it would mean for phenotypic coin-flipping (where phenotype is expressed randomly, regardless of environment: see Table 1 and Pigliucci, 2001) to undergo cumulative increases. Further, one cannot treat environmental variability in a monolithic way. Not all environments are variable in the same degrees of freedom, and the pace of change is slow for some and quick for others. Thus, an environment is characterized by multiple *patterns of variability*, which themselves can change over time and space. This is important because no single trait is adaptive to all patterns of variability. As we will see, this is true of phenotypic plasticity, which is only adaptive to environmental variability when the characteristic time-scale of the variability is shorter than the organism's generation time, but longer than the organism's behavioral reaction time. In sum, despite the ubiquity of environmental variability, a problem for the plausibility of the VSA is that the selection for variability adaptations is sporadic at best.

The purpose of the following two sections will be to address this issue, namely, to show how sporadic selection for variability adaptations is compatible with a non-contingent ensuing trend. In particular, the discussion will focus on phenotypic plasticity as a type of variability adaptation. I will first introduce the notion of phenotypic plasticity and its conditions of selection.

4.1. Phenotypic plasticity

The plasticity of a trait in a particular environment is standardly modeled by reaction norms (Bradshaw, 1965; Scheiner, 1993; Schlichting & Pigliucci, 1998; Schmalhausen, 1949; Stearns, 1989; Via & Lande, 1985). A reaction norm is a function that maps an environmental variable (e.g. temperature, salinity, etc.) onto a phenotypic variable for a given genotype. If the reaction norm is linear, the degree of plasticity may be identified with the slope of the reaction norm: one genotype is more plastic than another if it exhibits a larger phenotypic change for a fixed amount of environmental change.[9]

Because plasticity may also refer to changes in the biochemistry of an organism (e.g. enzyme or hormone concentrations), a distinction is often made between *active* and *passive plasticity* (Pigliucci, 1996; Whitman & Agrawal, 2009). Passive plasticity refers to the more or less automatic "susceptibility" of an organism that is not the result of any regulated process. Examples of such plasticity include the way in which toxins, poor nutrition, extreme temperatures, acidity, oxygen levels and salinity may affect a range of processes, ranging from the chemical and enzymatic to the cellular and developmental (Whitman & Agrawal, 2009). Active plasticity, by contrast, refers to a highly regulated response to environmental variability, where a host of processes coordinate to produce a particular phenotype in response to the environment.

Table 1
A brief overview of how selection for various types of plasticity depends on patterns of variation in the environment (Adapted from Table 9.1 in Pigliucci, 2001).

Pattern of Temporal variation	Pattern of Spatial variation	Expected Evolutionary Outcome
Scale: Shorter than generation time	/	Plasticity of physiological characters
Scale: Longer than generation time Distribution of variation: random	/	Adaptive coin flipping Genetic polymorphism
Scale: longer than generation Distribution of variation: regular	/	Plasticity by seasonal forms
/	Scale: coarse-grained Distribution of variation: random	Adaptive coin flipping
/	Scale: fine-grained Continuous phenotype	Phenotypic plasticity by continuous modulation
/	Scale: fine-grained Distinct phenotype Time-lag between environmental input and phenotype response	Phenotypic plasticity by development conversion (e.g. sex change)

A further important distinction needs to be made between adaptive and non-adaptive plasticity. Whether plasticity is adaptive depends strongly on the patterns of variability in the environment, and even then, different types of plasticity are favored given different types of variability. Some important parameters that define a pattern of variability are (1) the time scale of temporal fluctuation and (2) the scale of spatial fluctuation. Table 1 shows various permutations of these selective conditions together with the evolutionary outcome that may be expected. Note that some patterns of variation favor non-plastic adaptations to variability, such as genetic polymorphism or phenotypic coin-flipping. Phenotypic plasticity is only favored when the scale of temporal variation is shorter than a generation, and the scale of spatial variation is relatively fine-grained (i.e. lying within the normal range of the organism).

The presence or not of a reliable cue tracking the environment is another condition for the selection of plasticity. If the organism cannot detect a reliable cue, it will not be able to produce an adaptive response to change beyond coin-flipping (Godfrey-Smith, 1996; Moran, 1992; Sober, 1994).

We need not go into any further detail into the conditions under which plasticity is selected (but see Berrigan & Scheiner, 2004; Levins, 1968; Pigliucci, 2001). It is sufficient to note that plasticity is not always adaptive even if there is variability in the environment, and if it is adaptive, that there are different types of plasticity that are adaptive according to the pattern of variability in the environment.

[8] The range of possible environments is here assumed to be limited to those that can support life, since, trivially, if a truly lethal environment were to occur (such as a hypothetical mass extinction, wiping out all life), not only would there not be a trend in any variability adaptation, there would not be any life either.

[9] If the reaction norm is nonlinear, the degree of plasticity will not have a single value, and more sophisticated techniques will be needed to characterize reaction norms (Pigliucci, 2001).

5. The trend in whole-organism plasticity

In this section I will show how the VSA can be applied to selection for plasticity, and thus how a selection-driven trend in plasticity can be expected to reoccur in a replay of life's tape. As preparation, I will first consider how the reaction-norm measure of plasticity can be extended to a measure that is meaningful on the largest time-scales.

5.1. Whole-organism plasticity

As we saw in the previous section, the slope of the reaction norm is a quantitative measure for plasticity: for an organism with a larger degree of plasticity, the same amount of environmental change will result in a 'larger' change in phenotype. However, this plasticity measure is meaningless as a measure by which to compare different organisms or even different species lineages. The slope of a reaction norm is the property of a particular trait of an organism in a specific selective environment (cf. Brandon, 1990). It cannot be attributed to whole organisms, nor to species lineages, which may be characterized by very different traits and inhabit very different environments. Thus, if plasticity were simply to be measured by the slope of the reaction norm of a trait, it would make little sense to speak of a large-scale trend in plasticity.

The reaction norm measure of plasticity is also unsatisfactory as a means of describing phenomena such as homeostasis, where a phenotype is maintained in the face of environmental change across many different parameters[10]. Increased canalization in one trait may require a buffering mechanism and thus an increased plasticity in another trait (Nijhout, 2003). In this way, linkages between different traits, such as occur in homeostasis, make it difficult to analyze the evolution of plasticity in a trait by considering each trait in isolation.

For these reasons, it is worth considering how 'single-trait plasticity' (described by the reaction norm) can be extended to 'whole-organism plasticity', which describes the plasticity organism as a whole (Forsman, 2015; Nicoglou, 2015). How precisely this extension should occur is still controversial. One approach (Schlichting & Pigliucci, 1998) has been to analyze both the correlations between the plasticity of different traits, as well as the plasticity of the correlations between traits (i.e., how the correlation between two traits changes as the environment changes). Given the high degree of integration between traits, composite measures of plasticity then can be introduced to estimate differences in plasticity between organisms (Forsman, 2015).

The other approach is to measure the plasticity of an organism not by the nature of the response, but by the amount of information from the environment that is processed in the production of a response. Thus, in biological systems theory, Kitano and Oda (2006) outline how the capacity of an organism to take countermeasures against environmental variability can be measured by the number of "input networks" (Kitano & Oda, 2006) in an organism. Translated to the context of plasticity, the degree of whole-organism plasticity is understood as the number of environmental variables for which an organism can produce an active plastic response. An increase in whole-organism plasticity thus entails an expansion of the organism's perceived environment, which consists of the environmental variables to which the organism can produce an active plastic response.

A very rough characterization of the two approaches to measure whole-organism plasticity is that the first attempts to express 'how much' response an organism produces as an integrated whole in the face of environmental change, while the second attempts to express 'how much' of the changing environment an organism is able to respond to.

[10] In this respect, whole-organism plasticity is more closely related to what Bradshaw (1965) calls "phenotypic flexibility", which may also include stable responses. For further discussion, see Nicoglou (2015) or Whitman and Ananthakrishnan (2009).

5.2. Illustration: cephalopod and bivalve whole-organism plasticity

In this paper I will adopt the input-based measure of whole-organism plasticity. I will not embark on a detailed discussion of the definition of this measure (for example, how precisely are environments individuated), nor of the precise conditions of selection for increases in whole organism plasticity (for example, which types of variability favor more integrated plastic responses). Instead, a brief discussion of the contrast between bivalve and cephalopod ecology may be useful to illustrate how the input-based measure of whole-organism plasticity is to be understood.

Despite being adapted to very different niches, the degree of whole-organism plasticity of, for instance, *Octopus vulgaris* may be considered greater than that of *Mytilus edulis,* a common species of mussel species. The broad contrast between the species in the two classes of bivalves and cephalopods is an example also of two general points to be discussed later, namely how increases in whole-organism plasticity are robust against unfavorable environments (section 5.3), and how increases in whole-organism plasticity can be realized by changes in functional complexity (section 6.3).

First, consider the selective environment of bivalves. The environmental variables that affect selection on bivalves are divided into physical and biotic factors (variables). Physical factors include aerial exposure, oxygen concentration, currents, water depth, substrate type, food availability, water turbidity, temperature, and salinity, of which temperature and salinity are the most important (Gosling, 2003, p. 55). Biotic factors include the presence of competitors, predators, and disease. Most changes in the selective environment do not elicit a plastic response, but nonetheless, a number of types of plastic responses in bivalve species have been documented. For instance, physiological mechanisms such as respiration, filtration, or heat shock protein production are regulated in response to temperature fluctuation (Gosling, 2003, pp. 57–60). Or, defenses are induced in some bivalve species in response to waterborne cues from crab or gastropod predators (Gosling, 2003, p. 62). Further, bivalves also exhibit some behavioral plasticity: some species of mussel, such the *Perna viridis*, open their valves during emersion (exposure to air), so that the water kept within (in the mantle cavity) is oxygenated and anaerobic end products do not accumulate (Bayne, Thompson, & Widdows, 1976, p. 188; Gosling, 2003, p. 213).

All these plastic responses to changes in the environment are mediated by various sensory organs or receptor cells. For bivalves, the most important types of sensory organ are tactile sensors, chemoreceptors, an olfactory organ, and ocelli (Gosling, 2003, pp. 38–9). In general, bivalve ocelli are only sensitive to rapid changes in light intensity. Scallops are the notable exception here (Speiser & Johnsen, 2008), with ocelli capable of forming low-contrast images, which provide information that is used to identify and swim towards preferred environments.[11]

While cephalopods may inhabit physical environments very similar to those of bivalves, they inhabit very different selective environments, partially due to their ability to recognize different changes in the environment. To generalize broadly, the sensory systems of cephalopod species are sensitive to more changes in the environment than those of bivalve species. Cephalopods possess large eyes capable of detailed and high-contrast image formation (Boyle & Rodhouse, 2005, p. 3), and have more sensitive tactile sensors, sensitive not just to smaller changes but also to different stimuli, such as the quality of surface texture (e.g. in octopus species, see Boyle & Rodhouse, 2005, p. 25). Cephalopods can also pick up on a number of variables to which the bivalves are entirely or almost entirely insensitive: balance and orientation, internal bodily cues (proprioception), mechanoreception and hearing (disturbances in environment due to subtle water movements).

The difference in whole-organism plasticity goes beyond differences

[11] An example of relocation niche construction (see next section).

in sensory systems. Many cephalopod species, such as octopus or cuttlefish species, are capable of learning.[12] This represents an increase in whole-organism plasticity, since learning allows sensitivity to new stimuli in new environments, as these new stimuli are associated (for instance, through conditioning) with opportunity or danger (Boyle & Rodhouse, 2005, pp. 23–25). A final difference in whole-organism plasticity, related more to the output-based measure, is how bivalve species lack a cephalopod's fine nervous control of a muscular body capable of producing a broad array of behaviors (Boyle & Rodhouse, 2005, p. 23). This ability to produce a wide range of possible behavioral responses allows reactions to be more precisely tailored to the state of the local environment.

5.3. Robustness and whole-organism plasticity

For the following I will adopt the input-based measure of whole-organism plasticity, but will abstract away from whatever the precise conditions may be under which selection for increased whole-organism plasticity occurs, and from the way in which these conditions may or may not differ from the conditions of selection for single-trait plasticity. I will merely need to assume that favorable conditions occur with nonzero relative frequency (the significance of this assumption is discussed in the final section).

The purpose will be to show how certain kinds of increases in whole-organism plasticity are robust against unfavorable environmental variability, and hence how they constitute a non-contingent trend. In particular, I will show how prolonged environmental stasis – a condition in which plastic responses are at a disadvantage to non-plastic responses – need not lead to selection for decreased whole-organism plasticity.

Consider first how selection can cause a decrease in the average single-trait plasticity of a species or population. One well-studied mechanism is that of selection-induced genetic assimilation, where a hereditary phenotype is selected for over an environmentally induced phenotype, driving the hereditary phenotype to fixation (Levis & Pfennig, 2016; West-Eberhard, 2003).[13] This occurs in environments where it is advantageous to ignore environmental stimuli – either relatively static environments or environments with unreliable cues (see the discussion in e.g. Godfrey-Smith, 1996). Further, there can be selection against single-trait plasticity in variable environments as well, where, for instance, genetic polymorphism or phenotypic coin-flipping may be favored (see Table 1).

In sum, increases in single-trait plasticity can be reversed, and by extension, there is no reason to expect that increases in whole-organism plasticity cannot be reversed either. However, what makes increases in whole-organism plasticity different from those in single-trait plasticity is that increased whole-organism plasticity can allow an organism to escape from intraspecific and interspecific competition, leading in some cases to speciation (see discussion in West-Eberhard, 1989). If the organism is sensitive to an increased number of environmental variables, the expansion of the perceived environment may cause the organism to inhabit a different *selective* environment, since it is not necessarily in competition for the same resources or space.

To this end, consider how increased whole-organism plasticity can involve niche construction. Niche construction refers to the process by which an organism modifies the selection pressures in its environment (Odling-Smee, Laland, & Feldman, 2003), and is often itself an adaptive response to environmental variability. It has been argued that this reciprocal causation between phenotype and environment can generate a feedback cycle (Laland, Odling-Smee, Hoppitt, & Uller, 2013; Odling-Smee et al., 2003). Not all niche construction behaviors are plastic (for example, the modification of the soil environment by earthworms is not a plastic behavior); however, as Lewontin (1983) notes, many niche construction phenotypes, such as migration, hoarding, habitat selection and thermoregulation, are adaptive plastic responses to temporal variation in environmental resources.

Two important types of niche construction are *perturbation* and *relocation* niche construction (Odling-Smee et al., 2003). In relocation, the selective environment of an organism is changed by an organism migrating to a novel physical environment. By contrast, in perturbation niche construction, the selective environment is actively changed by modifying the environmental state of the organism's current physical environment. In each case the selective environment is changed, but the difference lies in whether the organism actively modifies a physical environment or merely exposes itself to a novel physical environment.

An important type of increase in whole-organism plasticity involves responses to interspecific and intraspecific competition, through the occupation of different “adaptive zones” or niches (West-Eberhard, 1989, pp. 258–9). As a case in point, consider how an organism may respond to changes in the environment and evade competition by relocation. One way is by spatial displacement or motility – probably the oldest form of relocation niche construction. Chemotaxis, flagellar propulsion, and contractile cytoskeleton originated very early on in evolution (Faguy & Jarrell, 1999), and also have re-evolved repeatedly in engineered immotile strains of bacteria (Taylor et al., 2015). One adaptive advantage of motility (in bacteria) is thought to consist in allowing bacteria to distance themselves from competitors and thus have access to more resources (Wei et al., 2011). In general, motility (as a form of habitat choice) is an important strategy for individuals to avoid direct competition with sessile individuals (Edelaar, Siepielski, & Clobert, 2008).

Effective relocation can also occur without spatial displacement: sensitivity to new environmental cues is sufficient to place an organism in a new (effective) environment. In this way, new niches are sought out in the same spatially located environment. For instance, an organism with increased dietary tolerance, or one capable of processing a new nutrient source inhabits an altered selective environment, and will be able to partially avoid competition with its peers (West-Eberhard, 1989).

To summarize: increases in whole-organism plasticity are not just adaptive to patterns of variability in the environment, they also can potentially buffer against variability in those patterns of variability. Even in a period of prolonged stasis in the physical environment, organisms and populations with increased whole-organism plasticity can avoid selective competition with organisms and populations of less whole-organism plasticity because of the capacity to alter the selective environment, through relocation or perturbation. This is thus a special case of the reciprocal causation between phenotype and environment mentioned earlier (Odling-Smee et al., 2003).

The capacity to mold the selective environment entails moving into an empty selective niche (i.e. avoiding competition with those organisms or populations lacking the capacity), but not necessarily vice versa. General adaptations may also help the organism expand into an empty selective niche, thereby avoiding competition with others. This is an important part of Bonner's comprehensive argument for a trend in body size: as body size increases, the organism automatically becomes less sensitive to microchanges in the environment, competes for different resources, and in general avoids competition with other, smaller organisms. As Bonner puts it, “there is always room at the top” (Bonner,

[12] The concept of whole-organism plasticity, like that of single-trait plasticity, is closely related to cognition and proto-cognition. See Calvo Garzón & Keijzer (2011) and Godfrey-Smith (2002).

[13] This mechanism is a significant part of the “plasticity-first” view of evolution where, in rough terms, environmentally-induced phenotypic change is thought to precede genetic change (Levis & Pfennig, 2016; West-Eberhard, 2003). Note that this process basically corresponds to Simpson's interpretation of the Baldwin effect (Simpson, 1953), and that it should be distinguished from Waddington's concept of canalization (see Loison, 2018 for a strong argument). In Loison's reading of Waddington's work (especially Waddington, 1942, 1953), canalization describes a process where environmentally induced phenotypes follow pre-existing developmental pathways, which are inherited by and ‘deepened’ over successive generations in the novel environment (see also Masel, 2004).

1988, p. 59). What distinguishes a variability adaptation such as whole-organism plasticity from a general adaptation such as body size is that a general adaptation is not viable in unfavorable environments, regardless of competition with other individuals. If nutritional density is too low, a large body size will simply not be viable. By contrast, in a static environment a plastic individual will still be able to produce a viable response as long as the environmental state is not too extreme (Langerhans & DeWitt, 2002).

From this discussion we can distill in more detail how the variability selection argument may be applied to the selection for plasticity. Assuming that all environments are equiprobable (P2), the environments favoring an increase in whole-organism plasticity occur with some nonzero relative frequency *p*. This relative frequency may be low, but all that matters is that it is nonzero, since increases in whole-organism plasticity in some lineages are robust against subsequent environmental variability. This means that natural selection causes a ratchet-like increase in whole-organism plasticity, no matter how low *p* is. This increase may be expected to occur in every (purely selection-driven) rerun of life's tape, and hence constitutes a counterexample to the LSA.

6. Objections

6.1. Contingency through the back door?

In the previous section we ascribed a relative frequency *p* to the occurrence of favorable environments, and argued that *p* is nonzero. As long as *p* is nonzero, and increases in plasticity are robust, a trend in plasticity may be expected in idealized (purely selection-driven) reruns of life's tape. However, what about the pathological case where even sporadic selection for increased plasticity does not occur – a rerun of life's tape where favorable patterns of variability never occur? This objection is likely to be purely academic: the universal absence of plasticity-favoring conditions may be incompatible with life-supporting conditions. Furthermore, such a probability may be extremely low, since if one takes *(1-p)* to be the probability of an unfavorable environment at any given time, and if one assumes independence between environments, the probability of favorable environments never occurring over a time period *t* would be proportional to $(1\text{-}p)^t$, which decreases to zero as *t* increases. However, even granted all that, one could still press the point: does the mere possibility of the pathological case not imply that the trend is contingent on a succession of solely unfavorable environments *not* occurring?

The objection provides an opportunity to further clarify the scope of the argument. The trend in plasticity is indeed contingent on favorable patterns of variability occurring at least some of the time. However, there is a difference in kind between assuming that evolutionary history is characterized by *the default structure* of the environment (multidimensionality and multiple patterns of variability in each degree of freedom), and assuming that it is characterized by *a non-default structure* (e.g., one with perpetual high nutrient density). So, not only does the VSA as applied to plasticity make a much weaker assumption about environmental states than the GSA applied to body size does, the assumption it makes is entirely in keeping with what one would expect from a multidimensional, variable environmental structure. While the trend in plasticity is contingent on the environment possessing the default structure (multidimensional and variable), the trend is not contingent on any particular succession of environmental states. By contrast, for the GSA to work, the environment needs to be characterized by a non-default structure. In sum, the VSA as applied to plasticity does not depend on a lucky succession of environments, in contrast to what the LSA claims, but instead is a consequence of natural selection acting in the default environment.

6.2. Constraints and the idealizing assumptions of the VSA

Do constraints on the evolution of single-trait plasticity constitute a problem for the VSA as applied to whole-organism plasticity? The most important types of constraint on the evolution of single-trait plasticity are 'costs' and 'limits' (DeWitt, Sih, & Wilson, 1998). Limits on plasticity prevent plastic traits from expressing extreme phenotypes, such as very elongated plant stems. Costs either arise from the development and maintenance of the structures needed for plasticity ('constitutive' costs), or from the switching of phenotype ('induced' costs): for example, switching the breeding date for birds, or sex changes for fish (DeWitt et al., 1998).

Empirically, there is not much support for the importance of costs and limits. A meta-analysis conducted by Van Buskirk and Steiner (2009) found there were not any widespread costs associated with plasticity. Murren et al. (2015) argue that costs and limits are negligible for the majority of organisms, and instead found the main limiting factor in the evolution of single-trait plasticity to be the presence or absence of optimal selective conditions. These doubts about the importance of costs and limits for the evolution of plasticity are compatible with the view that canalization and plasticity are both forms of gene regulation, and that the costs of plasticity and costs of development are two sides of the same basic phenomenon (Nijhout, 2003; Sultan & Stearns, 2005).

It would be more difficult to disregard developmental constraints on the evolution of whole-organism plasticity. Instances of increase in whole-organism plasticity, such as increased complexity in the sensorimotor system, are more sensitive to constraints than increases in single-trait plasticity. Some lineages of bivalve have never evolved complex sensory organs (allowing sensitivity to additional visual cues), even though they have had sufficient time to do so in their evolutionary history (Morton, 2001). One important reason is thought to lie in constraints. For example, the periostracum (outermost layer of the shell) of bivalves is thought to have been a constraint on the development of complex external sensory organs as seen in other molluscs such as cephalopods (Morton, 2001, p. 193). In general, constraints may prevent a lineage from evolving the sensitivity to environmental change needed for an increase in whole-organism plasticity.

How precisely constraints limit the increase in whole-organism plasticity is not entirely understood (Morton, 2001). If these limits turn out to be important, then one would not expect an increase in whole-organism plasticity in those lineages which are constrained. However, the VSA as such does not make predictive claims about specific lineages. Its general conclusion only holds under two idealizing assumptions: first, that a given lineage should be exposed to all possible environments will equal probability (P2), and second, that there are no other causes involved besides natural selection (such as developmental constraints). Only when these conditions hold can a selection-driven trend in whole-organism plasticity be expected in any rerun of life's tape.[14] In the evolution of many actual lineages these conditions do not hold perfectly. The VSA is an argument for an evolutionary tendency based on an analysis of fundamental concepts, and any empirical test of it would need to take other factors into consideration, including developmental constraints.

6.3. A ratchet in general adaptations?

General adaptations, like increased body size, may also involve forms of niche construction in such a way to as make these adaptations robust against detrimental environments (see e.g. Bonner, 1988; Payne et al., 2009). Could a similar argument not then be made for a robust ratchet-like increase in general adaptations? In response it can be

[14] In that idealized case, one would expect a strongly driven trend, with increasing mean, minimum, and maximum (see section 1).

pointed out that one cannot have niche construction without some sensitivity to cues in the environment; hence, if adaptations such as increased body size are paired with forms of inceptive niche construction, they in fact also represent instances of increased whole-organism plasticity. Furthermore, as mentioned previously, a general adaptation *qua* general adaptation lacks the buffering capacity against detrimental environments, and so general adaptations may not only be not optimally adaptive but also not viable in detrimental environments.

Nonetheless, increases in general adaptations such as body size or complexity can occur in tandem with increases in whole-organism plasticity. For instance, increases in whole-organism plasticity can involve the evolution of new sensory organs or new behavioral responses.[15] In turn, increased body size has been held to be an enabling condition for increased functional complexity (Bonner, 1988) and thus indirectly also increased whole-organism plasticity. In this way, the VSA could be used to argue that driven trends in complexity or body size can be expected to occur *only if* the relevant increases in complexity or body size are also variability adaptations.

7. Conclusion

Given the local nature of natural selection, many have argued that there is no reason to expect that natural selection should drive a large-scale evolutionary trend. As environments have varied considerably in evolutionary history, the traits favored by natural selection have likewise varied considerably.

In this paper I have considered one common but flawed answer to this skepticism, namely that certain traits may be considered 'generally adaptive' – adaptive to causal features common to many environments – and are therefore consistently favored by selection. However, there is no reason why features that are common in actual evolutionary history should also be common in a replay of life's tape. Further, even if they were common they would not be ubiquitous; and since general adaptations are not robust against unfavorable changes in the environment, a trend in general adaptation would be broken should a sufficiently unfavorable environment occur.

By contrast, variability may be considered to be an inevitable property of environments in possible replays of life's tape, since uniformly static environments are not life-supporting. Hence there is bound to be selection for adaptations to variability, even though no known trait is adaptive to every pattern of variability. The variability selection argument relies on this fact, and claims that, given a number of idealizing assumptions such as the absence of constraints, natural selection causes a trend in variability adaptations.

The application of this argument to whole-organism plasticity shows how increases in plasticity may be sporadic, and yet robust against unfavorable environments. By avoiding competition through niche construction, single individuals or a group of individuals may conserve their sensitivity to an increased number of environmental variables. This allows for a ratchet-like increase in whole-organism plasticity. Environments could still line up, however improbably, to preclude a trend in whole-organism plasticity. However, this would require a departure from the default structure of evolutionary environments: multidimensionality and multiple patterns of variability in each degree of freedom. For this reason, the trend in whole-organism plasticity may be considered a property of (idealized) evolution by natural selection – a consequence of the "bare-bone" mechanics of selection acting in default environments.

[15] However, not all increases in complexity – regardless of how complexity should be operationalized (see McShea & Brandon, 2010) – would involve increased whole organism plasticity.

Acknowledgements

The author would like to thank Dan McShea, Andreas De Block, Grant Ramsey, Laurent Loison, as well as three anonymous referees for their helpful comments.

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