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

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A B S T R A C T

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.

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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.