

# The Selectionist Rationale for Evolutionary Progress

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Hugh Desmond

## Abstract

The dominant view today on evolutionary progress is that it has been thoroughly debunked. Even value-neutral progress concepts are seen to lack important theoretical underpinnings: (1) natural selection provides no rationale for progress, and (2) natural selection need not even be invoked to explain large-scale evolutionary trends. In this paper I challenge this view by analysing how natural selection acts in heterogeneous environments. This not only undermines key debunking arguments, but also provides a selectionist rationale for a pattern of “evolutionary unfolding”, where life radiates across an increased range of exploitation of environmental heterogeneity.

KEYWORDS: Evolutionary Progress – Natural Selection – Laws – Evolutionary Contingency – Environmental Heterogeneity

## 1. Introduction

In the not-too-distant past, claims that life had made some type of ‘progress’ throughout evolutionary history were considered nearly self-evident, even by prominent biologists:

During the past billion years, animals as a whole evolved upward in body size, feeding and defensive techniques, brain and behavioral complexity, social organisation, and precision of environmental control. (...) Let us not pretend to deny in our philosophy what we know in our hearts to be true (Wilson 1992, p. 187).

Even at the time when Wilson made that statement, evolutionary progress was viewed either with “disdain” (Sober 1994, p. 19), or at least as thoroughly debunked. Today, this stance remains fundamentally the same. While sweeping views of life’s history receive considerable attention via the literatures on evolutionary trends (McShea 1994; McShea and Brandon 2010) and on major transitions (Calcott and Sterelny 2011; Maynard Smith and Szathmary 1995), the concept of evolutionary progress itself no longer receives much attention from philosophers of biology or philosophical biologists. The main academic areas where the concept of

evolutionary progress finds an intellectual home are either among anthropologists interested in understanding why people spontaneously believe in ‘higher’ and ‘lower’ organisms (e.g. Atran 1998), or among science educators interested in weaning students off similar beliefs (e.g. Johnson et al. 2012; Werth 2012).

*Pace* E.O. Wilson, there are some good reasons to distrust intuitions concerning progress. Empirical studies have not yielded support for some of the main concepts of evolutionary progress (McShea 1998, 2001a). Moreover, the concept of evolutionary progress seems to justify practises or policies that are at odds with ethical judgment. Just as the concept of human nature has been used to justify dehumanization (Kronfeldner 2017), concepts of evolutionary progress were used to justify eugenics (see Desmond forthcoming), and the associated distinction between “higher” and “lower” organisms has been used to justify exploiting sentient, non-human species (Singer 2015).

Even while acknowledging how the concept of evolutionary progress can be abused, many evolutionary thinkers have nonetheless defended a value-neutral understanding of progress (e.g. Conway Morris 2003; Dawkins 1997; Dennett 1995; Mayr 1994). As will be spelled out later in the paper, natural selection has played a crucial role in these efforts because it seems to allow the distinction between “better” and “worse” to be spelled out in a way that does not depend on human valuing – but, for instance, in terms of adaptiveness.

The core problem here is that, even if one would grant that concepts of progress can be independent of human valuing, progress still seems to lack any theoretical underpinning in the theory of natural selection. This is why perhaps the most fundamental debunking of progress is a theoretical argument. Natural selection namely does not provide any *rationale* for progress:

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. 467–468, my emphasis).

Here S.J. Gould’s argument echoes earlier statements by G. C. Williams<sup>1</sup>, and is powerful because it brackets other concerns. It brackets the issue whether or not evolutionary progress is inevitably laden with human values. It even brackets the concern whether there is empirical data to support evolutionary progress. The point is that, given the theory of natural selection alone, there is no reason to expect selection to drive anything resembling evolutionary progress.

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<sup>1</sup> “There is nothing in the basic structure of the theory of natural selection that would suggest the idea of any kind of cumulative progress.” (Williams 1966/2018: 35)

Hence this will be termed the *groundedness problem*: there is no selectionist rationale for progress that is *grounded* in the nature of natural selection.

As an example, consider the following rationale: “evolutionary history has ‘progressed’ towards a greater ability to process environmental information because it allows an organism to respond more adaptively to environmental change and hence is selectively favoured across many if not all environments.” What Gould or Williams are saying here is not that such a selectionist rationale is empirically false per se. It may be true that some kind of information processing ability is consistently favoured across selective environments. Their point is that the causal structure of natural selection itself provides no reason to believe that it is true. After all, if suddenly static environments were to become more frequent, either in the future or in some alternative scenario, then information processing would be selected against.

While the groundedness problem is perhaps the most fundamental challenge for value-neutral understanding of progress, it is not the only one. This paper will consider one closely related argument, also promoted by Gould (in Gould 1996), called the *redundancy problem*: selection seems to be simply superfluous for explaining evolutionary trends. For instance, consider the increase in complexity in evolutionary history. Since life started at minimal complexity, it was only a question of time before complexity increased – with or without selection for complexity.

Taken together, the groundedness and redundancy problems seem to provide a knockdown debunking of (value-neutral) evolutionary progress. The groundedness problem undermines selectionist rationales for progress; the redundancy problem discourages any future search for novel selectionist rationales, because even if one could be found that avoided the groundedness problem, it would still be explanatorily useless.

The goal of this paper is to argue that there is at least one selectionist rationale for evolutionary progress that is (1) grounded in the causal structure of natural selection, and (2) not explanatorily redundant. The core proposal is that environmental heterogeneity – change in environments over time and space – does not simply act as a source of contingency, but rather gives rise to selective processes that causally explain a large-scale trend towards species that are better able to exploit environmental heterogeneity. By clarifying the link between natural selection and largest-scale trends, the contribution of this paper lies in showing how progress concepts are not necessarily ungrounded in the theory of natural selection. To this end, two potentially viable concepts are briefly discussed: unfolding progress and competitive progress.

The paper is structured as follows. In the following section I explain what is intended by a ‘selectionist rationale for progress’. In the third and fourth sections I analyse and argue against the neutral view on evolutionary trends. In the fifth section I distinguish between two processes of selection in heterogeneous environments, only one of which can be said to be a source of evolutionary contingency on the largest scales. In the sixth section I make the case for a selectionist rationale for a trend in the exploitation of environmental heterogeneity. This overcomes the groundedness problem, and in closing I suggest what a selectionist rationale for progress could look like.

## **2. The Structure of Selectionist Rationales for Progress**

Claims that evolutionary history has progressed (or progress-claims) are vast generalisations about the history of life and the patterns instantiated throughout that history (Rosslénbroich 2006; Shanahan 2001). Since the danger exists that such claims fall short of all sorts of epistemic standards – and devolve into mere speculation – it is important to analyse the structure of these claims. The following subsections introduce, step-by-step, a formalism by which progress-claims and their selectionist rationales can be evaluated.

**2.1 Laws of Evolutionary History.** Progress-claims aim at generalising over vast time-scales and a vast number of lineages, and so to keep the resulting generalisations manageable, they typically adopt a very narrow scope. To begin with, lineages are characterized by a single feature, such as complexity, body size, genetic information, and so on. Typically this feature is also quantified through some measure  $M$  (e.g., degree of complexity). This quantification allows any given lineage in evolutionary history to be abstractly represented by a number ( $M_0$ ,  $M_1$ , etc.: see Figures 1a, b). In turn this allows a time-slice of evolutionary history to be represented as a frequency distribution that changes over time (Figure 1c).

To further simplify the representation of evolutionary history, progress-claims typically focus on a particular statistical property of this distribution (the maximum, mean, skew, kurtosis, etc.). Its *pattern*  $P$  maps how this property changes over time (Figure 1d). For instance, one could map how the maximum in the degree of complexity changes over time. Finally, progress-claims are typically concerned with one particular type of pattern, namely *trends*: a series of increases in a statistical property. Trends thus can be understood as resulting from stripping away the complexity of evolutionary history, until only a simple quantified representation is left.

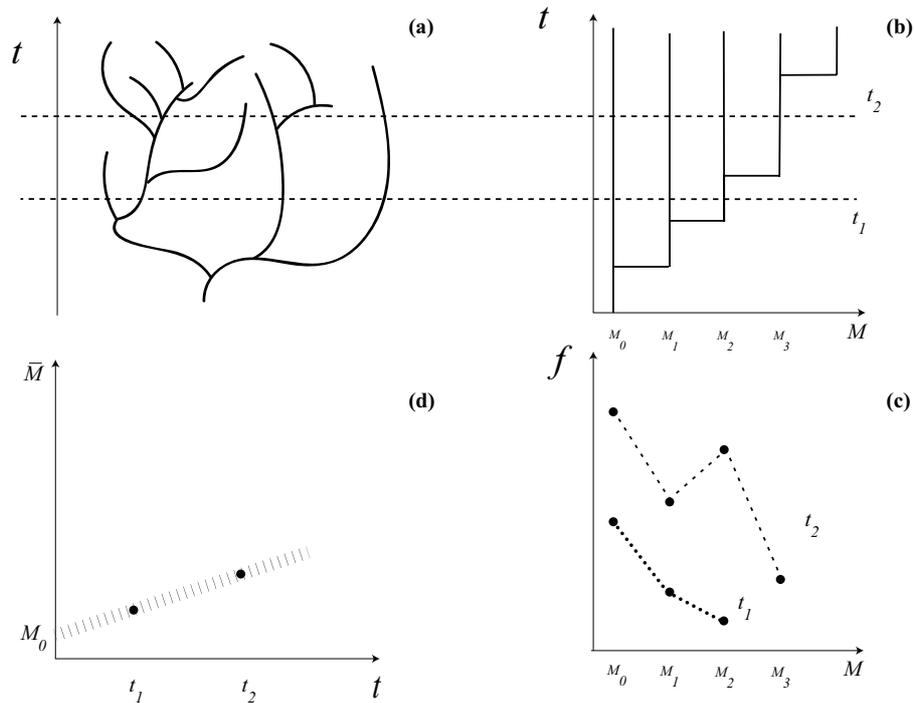


Figure 1: Patterns in Evolutionary History (clockwise from top left): (a) an evolutionary history; (b) the occupation of  $M$ -states over time; (c) absolute frequency distributions of lineages over  $M$ -states at times  $t_1$  and  $t_2$ ; (d) an increase in average  $M$  across all extant lineages over time.

Progress-claims also typically involve a certain degree of counterfactual robustness. After all, not all true generalisations about life’s history are interesting: for instance, nobody contests that organismic body size has in fact increased throughout evolutionary history. The real question is: were such increases in any way *necessary* occurrences? Hence progress-claims concern counterfactually robust evolutionary, or *laws of evolutionary history*:

“All possible evolutionary histories instantiate a trend in  $M$ .”

Here, an ‘evolutionary history’ is the sum total of lineages or ancestor-descendant series, both extant and extinct. These lineages are often grouped together by species boundaries (cf. e.g. Payne et al. 2009).

What does the “all possible” in the definition above mean? Progress-claims involve a modal dimension, but specifying the modal metaphysics of laws of nature is a notoriously vexed issue (Lange 2009). Gould himself offers an intuitive way of side-stepping the issue, namely by representing possible evolutionary histories as “replays of life’s tape” (Gould 1989). In such replays, life restarts its evolution under slightly different physical conditions (even if

these may not seem biologically relevant<sup>2</sup>). In such replays, many features of reality are held constant: the laws of physics, the periodic table, all other regularities in chemistry. The conditions in a replay must also be life-supporting (e.g., not too hot and not too cold). What can vary: asteroids may impact the Earth at different times or not at all; there may be different patterns of global temperature change; different developmental constraints (like body plans) may come to dominate early on in evolution; and so on.

For the purposes of this paper, it would be sufficient to think of “possible evolutionary histories” as replays of life’s tape – both of life as we know it, and of life as it could be elsewhere. The latter refers to how “possible histories” also cover potential life on other planets, where life may face very different conditions. For instance, compositions of the atmosphere and the lithosphere may be so different as to preclude carbon-based life forms. The domains of universal biology and astrobiology can be understood as searching for laws of evolutionary history: can anything (distinctively biological) be predicted about the possible evolutionary histories on other planets (cf. Smith and Mariscal 2020)?

The default stance on such evolutionary laws is that they do not exist – or at least, that they are not distinctively biological. This is encapsulated by the Evolutionary Contingency Thesis, or ECT (Beatty 1995):

All generalisations about the living world: (a) are just mathematical, physical, or chemical generalisations (...) or (b) are distinctively biological, in which case they describe contingent outcomes of evolution (Beatty 1995, pp. 46–47).

Applied to laws of evolutionary history, the ECT means that, if a trend that is counterfactually robust across all possible evolutionary histories, it must be the consequence of facts or features in mathematics, physics, or chemistry.

For instance, candidates for robust generalisations include Dollo’s law (a lineage that has evolved will never return to its initial state; Dollo 1893) and the Zero Force Evolutionary Law (McShea and Brandon 2010). However, these generalisations are grounded in statistics rather than the dynamics of biological processes such as natural selection (see McShea and Brandon 2010, p. 95). At most, generalisations can have the status of ‘rules’. Thus, Cope’s Rule states that populations in the same lineage *tend* to increase in body size over time (i.e., not always).

In general, laws of evolutionary history are not easily tractable from a theoretical perspective. The myriad of contributing causal factors to the course of evolutionary history are

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<sup>2</sup> Beatty would call this “contingency *per se*”: a replay from seemingly identical conditions leading to a different evolutionary outcome (Beatty 2006).

simply too great. However, the progress-claims that are of interest for this paper concern a specific type of law of evolutionary history: those that have a selectionist rationale. These, thankfully, are more tractable.

**2.2 Selectionist Rationales.** “Selectionist rationales” denote a pattern of selection that is grounded in an underlying principle. So, a ‘selectionist rationale for X, entailed by Y’ means that Y grounds a pattern of selection that leads to X. For instance, historical selectionist rationales for progress were grounded in (speculative) principles that certain types of traits (body size, information processing capacity, etc.) are selectively favoured across most environments. The resulting pattern of selection was thought to lead to a trend that could be judged to be “progress”. However, the groundedness problem undermines such rationales across the board. It states that the theory of natural selection (Y) cannot ground a pattern of selection that would lead to evolutionary progress (X). Beatty’s discussion of the ECT implicitly endorses the groundedness problem, since change in environment is listed as one of the sources of evolutionary contingency (Beatty 1995, p. 53). In other words, not only does the ECT deny there to be laws of evolutionary history, but does so for reasons that also imply there cannot be any selectionist rationale for such laws.<sup>3</sup>

A selectionist rationale for increased  $M$  need not imply an observable trend in  $M$ . Selective processes are merely part of the contributing causes of empirical patterns. Hence, the type of robust generalization associated with selectionist rationales concerns only an idealisation of an evolutionary history. To capture this we can introduce a *selectionist law of evolutionary history*:

Given effectively random environments and without long-term constraints on natural selection, all evolutionary histories instantiate a trend in a measure  $M$  that is caused by selection for increased  $M$ .

This adds two provisos to a law of evolutionary history: random environments and no unsurmountable constraints. It is worth unpacking each in more detail.

The first proviso is that evolutionary histories are constrained to those with effectively random environments (over geological time-scales). This means that any resulting trend caused by selection is a consequence of selection’s causal structure, rather than a consequence of particular environments that happened to occur frequently. According to Gould, as well as

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<sup>3</sup> For this reason, there being a (grounded) selectionist rationale would seem to contradict the ECT in spirit, even though the ECT could still be saved in letter since selectionist rationales cannot be used for exceptionless generalisations over actual, empirical evolutionary history.

Beatty, there cannot be any trend that satisfies this condition, since effectively random environments are thought to entail effectively random selective processes.<sup>4</sup>

The second proviso – no long-term constraints on natural selection – is more of an ad-hoc feature, intended to ensure that any genetic or phenotypic constraints in populations would be overcome over time scales of tens to hundreds of millions of years. Thus, even if, for instance, entirely different *Baupläne* survived the Cambrian–Ordovician extinction event (see Gould 1989), a selectionist rationale for *M* would eventually cause a trend in *M* to occur. The condition may even be likely false – there may indeed be constraints that cannot be overcome by selection – but the reason for this condition is to pick out the mechanics of selection alone. This specification of no-constraints is similar to that in the special formulation of the Zero Force Evolutionary Law (ZFEL) (McShea and Brandon 2010, p. 3). (Note that short-term constraints are allowed, because these are necessary for there to be any historicity at all, since otherwise, for instance, eusocial organisms could suddenly appear in a prokaryotic world.)

As a side remark, note that a ‘selection-caused trend’ is not the same as a ‘selection-driven trend’, which is the common term in the literature on largest-scale evolutionary trends (following McShea 1994). In this literature, the qualifiers ‘driven’ and ‘passive’ refer strictly speaking to statistical properties rather than to causes. Thus, driven trends are those where increases in *M* in a lineage are more frequent than decreases. In a passive trend, increases and decreases occur with equal frequency. Not all driven trends are caused by selection: some may be caused by developmental ratchets (e.g., Saunders and Ho 1976), to the accumulation of components (e.g., the ‘neutral ratchets’ in Lukeš et al. 2011). Driven trends do not even need to have specific causes: the (special formulation of the) ZFEL results from the statistical claim that it is more probable that diversity increases than decreases. Conversely, a selection-caused trend can be both driven and passive. (The neutral view, discussed in sections 3 and 4, problematically assumes that all passive trends can be explained without selective causes.)

**2.3 Selectionist Rationales for Progress.** How does progress figure in this picture of selectionist laws? A relatively common view is that the concept ‘evolutionary progress’ is strictly non-scientific, involving the grafting of values onto a scientific concept (i.e., directionality). This stance view is encapsulated by Sober’s pithy formula: “progress =

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<sup>4</sup> See e.g. “The sequence of local environments in any one place should be effectively random through geological time - the seas come in and the seas go out, the weather gets colder, then hotter, etc. If organisms are tracking local environments by natural selection, then their evolutionary history should be effectively random as well.” (Gould 1996, pp. 139–140)

directional change + values” (Sober 1994, p. 20). The view also receives expression in Gould’s colourful verdict that progress is “a noxious, culturally embedded, untestable, nonoperational, intractable idea” (Gould 1988, p. 319).

If this view were true, then all progress-claims could be dismissed without further ado within biological contexts. However, it is not obviously true – and this may also be why Gould himself puts so much effort into undermining the theoretical ground for progress-claims. Upon closer inspection, and as suggested in the introduction of this paper, the link between natural selection and progress is much more intricate than would seem from Sober’s formula alone.

This link is not apparent if natural selection is simply conceptualised in terms of the Lewontin conditions<sup>5</sup> – heritable fitness variation. Rather, the link between selection and progress only can make sense when one adopts a concept of natural selection as involving ‘competition’ of some sort, and/or potential to produce adaptation. Arguing for this would require a separate paper; suffice to say that, in a group of orca and krill, there is heritable phenotypic variation and associated fitness variation, but no natural selection. Darwin himself primarily wrote about the “struggle for life”, which is quite different from heritable fitness variation (for extensive argument, see Lewens 2010) Some recent accounts of natural selection conceive of it as involving reproductive competition (Godfrey-Smith 2009, pp. 49-53).

This is important, because when selection is an adaptation-producing and/or competitive process, the outcomes of a selection-caused trend can be thought of as the ‘victors’ and/or the ‘superiorly adapted’ relative to a given environment. Evolution by natural selection produces ‘better’ outcomes in the following value-neutral sense: they are defined relative to the ‘preferences’ of natural selection, not relative to human moral or societal preferences. The relevant parameters could be better competition, or better adaptation.

This linking of natural selection and progress was present in many historical accounts of evolutionary progress, which relied on an argument that some property – whether complexity, cognition, or something else – allowed general adaptive or competitive superiority across environments (for an overview, see Rosslénbroich 2006). It is present in more recent notions of ‘competitive progress’ (e.g. Vermeij 1987, pp. 419–421) or ‘adaptive progress’ (e.g. Dawkins 1997; Mayr 1994). These specific concepts of progress were perhaps ungrounded – the victors and superiorly adapted are only ‘better’ relative to an environment, and

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<sup>5</sup> As, by the way, Sober explicitly does in (Sober 1984).

environments change<sup>6</sup> – but it does show how the value-neutral usage of ‘progress’ is legitimate and not to be dismissed by default.

This intimate link between selection and progress has been off the table for quite some time, largely because the groundedness and redundancy problems have been seen as insurmountable. If selection cannot ground progress anyway, then Sober’s formula may seem accurate. However, overcoming these problems revives the value-neutral usage of the term ‘progress’, and opens up the possibility that evolutionary trends could also be considered progressive. This is the reason why this paper is not merely about selectionist rationales for evolutionary trends, but also about selectionist rationales for evolutionary progress.

To sum up this section, there are three levels of claim that should be distinguished: generalisations over evolutionary history; selectionist rationales for those generalisations; and the theoretical grounding for selectionist rationales. The groundedness problem states that there is no theoretical grounding for selectionist rationales; the redundancy problem states that, even if there would be theoretical grounding, selectionist rationales are explanatorily superfluous anyway. The following two sections tackle the redundancy problem; sections 5 and 6 address the groundedness problem.

### **3. The Neutral View on Evolutionary Trends**

This section sketches the received view on the redundancy problem: passive trends can be explained parsimoniously as neutral trends. Before a general characterisation, consider the trend in nestedness as an example (McShea 2001a, 2001b). The measure of nestedness, or “hierarchical object complexity” (McShea 1996), has four values – prokaryote, eukaryote, multicellular, colony.<sup>7</sup> Evolutionary history started at the prokaryote level, and maximal nestedness increased monotonically, reaching the upper limit some 800 million years ago (Figure 2). It is not conclusively known whether this trend is driven or passive (see McShea 2001b): for the following, we will assume it is passive.

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<sup>6</sup> So for these particular versions of (selective) competitive and adaptive progress I agree, with Gould and Williams, that natural selection offers no rationale for them. If progress-claim are to be viable, they must involve a different concept of progress.

<sup>7</sup> This taxonomy can be further fine-grained according to the internal differentiation and interaction between parts (see McShea 2001a). This need not further concern us here.

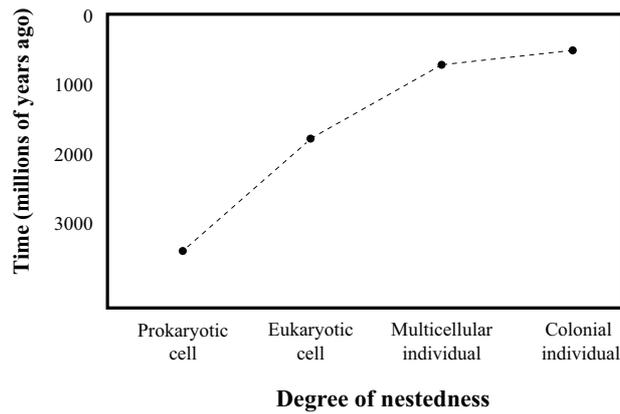


Figure 2. The increase in degree of nestedness across evolutionary history. (Redrawn from McShea 2001b.)

Is selection needed to explain this increase in maximum nestedness? According to the neutral view, most prominently promoted by Gould (Gould 1996), it is not: since life began at the minimum value of nestedness, from that starting point only more nested life could evolve, even if this evolution were a random walk. All one needs is for species to “occasionally wander into previously unoccupied domain” (Gould 1996, pp. 105–106). That, together with starting at the minimum value, is all one needs to generate a passive trend in nestedness.

This parsimonious explanation generalises for any scalar measure  $M$ . A random walk through  $M$ -space, where states are defined as values of  $M$ , can be represented as a game where the player flips a coin and then moves a checker left if the coin lands heads, or right if it lands tails.



Figure 3: Random walk through  $M$ -space (adapted from Sober 1994).

Even with a fair coin it is very probable that a player will have a run of tails, or a sequence where tails far outnumber heads. Hence, if this game is played by a large number of players simultaneously, the expectation is that the checkers will on average move to the right over time.

In an evolutionary context, the coin flip is an idealisation of the sum total of processes affecting the lineage evolution over a certain unit of time. The time step for  $M$ -increase ( $T_{\uparrow}$ ) defines a time-scale where the probability of an  $M$ -increase is  $\frac{1}{2}$  (and similarly for the time step for  $M$ -decrease,  $T_{\downarrow}$ ). A coin flip involves only a single time step ( $T_{\uparrow} = T_{\downarrow}$ ) and is simply the length of time it takes for a person to pick up a coin and flip it. The time-step for changes in nestedness is on the scale of tens to hundreds of millions of years when  $M$ ; for changes in body-size, the relevant time-scale is millions of years.

This explanation of passive trends in  $M$  thus relies on nothing but statistics, i.e., the evolution of the binomial distribution as one conducts an increasing number of Bernoulli experiments. It is a distinctively mathematical explanation (Huneman 2010; Lange 2013) of a biological phenomenon, and hence it is not surprising that it should generalise for any passive trend in any measure  $M$ . This is why Gould can apply it not just to increases in complexity, but also to directional changes in body size or information processing capability: all occur for the same reason as happens if enough people are flipping coins for long enough, the checker will move from the initial state to the right. Moreover, this explanation vindicates Beatty's ECT: largest-scale passive trends are just not interesting evolutionary phenomena, and do not warrant any biological (let alone selectionist) explanation.

Since this is a sweeping explanation of (passive) evolutionary trends, I call this the *neutral view* on trends, in analogy with the neutral theory of molecular evolution (Kimura 1968) and the neutral theories of biodiversity (Hubbell 2001). It is inspired by, but should be distinguished from, the quantitative 'MBL model', constructed by Tom Schopf, S.J. Gould, David Raup, Dan Simberloff, and others in the 1970s. The MBL model represents evolutionary changes in lineages as occurring at fixed intervals with preset probabilities, regardless of how well individuals in that lineage were adapted to their environment (for an in-depth discussion, see Sepkoski 2016 or Turner 2011). In one version of the model, extinction and speciation events were modelled (with the goal of explaining changes in diversity: Raup et al. 1973); in another version, changes in morphology were modelled (Raup and Gould 1974). The neutral view can be understood as taking the basic modelling assumptions of MBL models, and applying them to all passive evolutionary trends.

However, the difference is that the neutral view is not simply a narrowly defined quantitative model with specific conditions of application. It is a sweeping explanation of all passive trends that moreover positions itself as the null view. The status of 'null' explanation of passive trends can be claimed because it is more *parsimonious* than selectionist explanations: why invoke selection when a trend can be explained as resulting from random walks? Moreover, the neutral view has the virtue of avoiding speculation about what selective environments did and did not occur in evolutionary history (and hence it avoids the groundedness problem).

The upshot is that selectionist rationales are deprived of playing any indispensable function in explaining largest-scale evolutionary trends. Perhaps if there were empirical evidence of a largest-scale driven trend (where increases are more likely than decreases for any given lineage), there could be a reason to endorse some relevant selectionist rationale. But as

McShea has documented across a series of empirical studies (e.g. McShea 1998, 2001a), there is not any evidence for such a driven trend.

However, upon a closer look, the neutral view depends on an assumption that is speculative in the same way as assumptions underlying problematic selectionist rationales for progress.

#### **4. Problems with the Neutral View**

Is it so justified that the neutral view can claim the status of ‘null’ explanation? Upon a closer look, the neutral view faces its own type of ‘groundedness’ problem. Of particular interest are two underlying assumptions: (1)  $T_{\uparrow} = T_{\downarrow}$  (so that the evolutionary coin is fair, so to speak), and (2)  $T_{\uparrow}$  is not too large (the evolutionary coin must be flipped often enough). The first condition is a restatement of the explicit assumption that lineages evolve as random walks. The second condition is necessary for the neutral view to work, because if, for instance,  $T_{\uparrow}$  were on the scale of hundreds of billions of years, the neutral view would not predict any observable trend given that life over four billion years old. We will now consider in detail what these two conditions mean when translated in terms of underlying microevolutionary processes (genetic mutation, phenotypic plasticity, selection, drift).

To get a grasp on these processes, we need to operate with some representation of biologically possible states.<sup>8</sup> The reason for this is that the neutral view implicitly operates with some assumptions about these states, namely, that they can be sufficiently explored over the time-scale of one billion years. Hence, to make these assumptions explicit, we need to make some formal – albeit, for purposes here, heuristic – representations of the space of biological possibility. Getting a grasp on “biological possibility” is a notoriously difficult issue (Maclaurin and Sterelny 2008; Mitteroecker and Huttegger 2009). Should we count just possible genotypes, or possible morphologies – or all possible phenotypes (including behaviours)? For purposes here we can opt for number of possible genotypes, partially because this can at least be conceivably quantified, and partially because the exploration of this space can at least plausibly (albeit controversially) be conceived as occurring neutrally without any selection.

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<sup>8</sup> This type of modality should be distinguished from the type involved in “possible evolutionary histories”. The latter are fleshed out in terms of varying conditions faced by life (asteroids, atmosphere composition, etc.). By contrast, biologically possible states are individuated in terms of organismic structure (genotype and/or phenotype). Nonetheless, the two types of modality are related, since a single evolutionary history can be represented as a network of branching paths in the space of biological possibility.

So let  $\Omega_g$  be the space of all possible genotypes in which the evolution of lineages can be represented.<sup>9</sup> Limiting the length of possible genomes to some large number  $N$ , the size of  $\Omega_g$  is unknown but finite, and by all accounts, many times larger than all the protons in the universe (Wright 1932). Other commentators have simply denoted the size of  $\Omega_g$  as “vast” (Dennett 1995) or “hyper-astronomical” (Kauffman 1993).

One way of thinking about what “vast” means is that, if genotypes were sampled randomly, only a vanishingly small subspace of  $\Omega_g$  would ever be explored in evolutionary time. Louis (2016) shows a way how to understand this with some degree of formal precision. He explores the case of protein folding: if a protein were to sample random spatial configurations before finding the right one, it would take in the order of  $10^{120}$  times the age of the universe. (The number of possible protein configurations is about  $10^{150}$ , proteins can sample about 10 trillion ( $10^{13}$ ) configurations per second, and the age of the universe is in the order of  $10^{17}$  seconds.) This, for Louis, is an incontrovertible argument against the idea that protein configurations are sampled randomly.

If we wish to apply a similar reasoning to the case at hand, then the first observation is that the number of possible genotypes is vastly larger than  $10^{150}$ : for haploid genotypes consisting of 1000 genes and 2 possible alleles per gene, there are  $2^{1000} \cong 10^{316}$  possible genotypes. Even this is an underestimation of the size of  $\Omega$ : the number of coding genes is variable, can be much larger than 1000 (humans have around 20.000 of them by latest estimations), many organisms are diploid, many genes polymorphic, and so on. Moreover, the sampling rate is lower than a protein sampling spatial configurations: even if evolution were to consist of a trillion lineages, the sampling rate of genotypes would be much lower than 10 trillion times per second. Thus, random sampling of genotypes would correspond to the exploration of a vanishingly small subregion of  $\Omega$ .

Hence, assuming that  $M$ -states supervene on  $\Omega_g$ -states<sup>10</sup>, and thus partition  $\Omega_g$ , then given the vastness of  $\Omega_g$  and each  $M_i$  region, a lineage randomly sampling genotypes in the  $M_0$  region would most likely never reach the  $M_l$  region. Even the empirically observed time-step

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<sup>9</sup> Phenotypic change can occur without genetic change (due to phenotypic plasticity), so this concept of a space of possible genotypes is just a heuristic. See critical discussion of biological possibility in (Maclaurin and Sterelny 2008).

<sup>10</sup> This is another simplifying assumption. For instance, wolfpacks, or cooperating predatory bacteria (*Myxococcus*), are considered to exemplify multicellularity (Berleman and Kirby 2009; Grosberg and Strathmann 2007). Thus, changes in level of nestedness may be environmentally induced and underdetermined by genotype alone.

of 10-100 million years for increases in nestedness (McShea 2001a) is much shorter than what one would expect if individual lineages were to randomly sample  $\Omega_g$  states.

Thus, for all practical purposes, it is so improbably as to be basically impossible that a random walk through  $M$ -space could be realised by random walks in the lower level space  $\Omega_g$ . So, for the neutral view to be plausible, lineage evolution in the vast lower-level space must be biased. This would remain true if the space of biological possibility was formalized in a different way. The sources of bias are well documented. One important type is mutational biases (as discussed in Louis 2016). Another source of bias, acknowledged by neutral theory of molecular evolution, refers to corridors of functional equivalence dictated by the structure of genotype-phenotype maps (even as sampling within those narrow corridors is random: Kimura 1968). A third is natural selection, which is widely seen (even by proponents of the neutral theory of molecular evolution) as indispensable for explaining the evolution of phenotypes.

Note thus that for the neutral view on evolutionary trends to work, it needs selection operating at the microevolutionary level, and for these selective processes to not translate into a bias in the evolution through  $M$ -space. Thus, the preceding discussion allows us to pinpoint the following crucial assumption underlying the neutral view:

In geological time-scales, where the succession of environments is effectively random,  $M$ -favouring and  $M$ -disfavouring selective environments occur with equal (but not too small) frequencies for any  $M$ .

Note the similarity with Gould's remarks about environments in geological time-scales in footnote 4.

To restate this assumption more informally: the neutral view assumes that all possible measures  $M$  are effectively selectively neutral over geological time-scales. In this way, the neutral view depends on two types of modality: the possible measures  $M$ , and the range of possible selective environments. The inconsistency here, to put it roughly, is that the modal range of possible  $M$  is "much larger" than that of possible selective environments. The neutral view needs to hold for any  $M$  – even biologically implausible or uninteresting  $M$  – because of the distinctively mathematical character of the neutral view. (Recall that this mathematical character is crucial to justify the neutral view's status as null, and hence to present selectionist rationales with the redundancy problem.) However, as will now be argued, there is no reason to expect a measure  $M$  picked randomly to be selectively neutral. In fact, the default expectation could be for a random  $M$  to be selectively *disfavoured*. Thus the mathematical character that

guarantees the neutral view its status as null simultaneously erodes its explanatory power of evolutionary trends.

To unpack this, let us give more precision to what it means to pick out a ‘random’ environments over geological time-scales. One modal sense, call it  $\text{random}_1$ , is that the  $\text{random}_1$  environment is picked randomly from the set of all *metaphysically* possible environments. This is an exceptionally large set, and much larger than would be appropriate in the context of a discussion of evolutionary history, because it includes environments where magic and Lewisian tiny miracles happen (Lewis 2001). A second, more appropriate modal sense,  $\text{random}_2$ , would pick an environment from the set of environments that could be expected to occur during a replay of life’s tape or during a possible evolutionary history (see section 2).

However, concerning possible  $M$ , the distinctively mathematical structure of the neutral view implies that the measure  $M$  can be drawn from a much larger space of possibility than simply the “biologically possible”  $M$ . The neutral view thus would also apply to exaggeratedly artificial  $M$ , such as “the size of horse-sized butterfly-shaped wings”, or “the number of fluorescent feathers that can self-propagate”. Are these traits, on the whole, selectively neutral across the possible<sub>2</sub> environments expected in a replay of life’s tape? There seems to be no good reason why we should not think that such massive and weird wings may be selectively *disfavoured* in most biologically possible environments. One can think of many metaphysically possible environments, replete with magic and miracles, where weird wings may be selectively favoured. However, in most possible<sub>2</sub> environments such wings may be selectively disfavoured. In other words, the neutral view’s assumption that all measures are (effectively) selectively neutral cannot be interpreted as an unproblematic, fall-back assumption. It has the same speculative status as when some proponents of progress assumed that some measures are (effectively) selectively favoured across geological time.

This point holds for more biologically relevant measures, such as body size. What is the exact probability of (biologically possible) environments that favour increased body size in a given lineage? Some have argued that it is larger than  $\frac{1}{2}$  (Bonner 1988), but others have put forth equally good arguments why it would be lower than  $\frac{1}{2}$  (e.g. McShea 1998). In truth, this is a question that no amount of palaeoclimatological, palaeogeological, or palaeoecological investigation will help answer, because they at best only reveal the proportions in *actual* evolutionary history. We should refrain from assigning *any* value to the probability – including the exact value of  $\frac{1}{2}$ . Claiming body size is selectively neutral is as speculative – and in this sense, ungrounded in natural selection itself – as claiming it is consistently selectively favoured.

In conclusion, the neutral view on passive evolutionary trends seems to render selectionist rationales redundant. However, the neutral view is guilty of the same speculation about what environments occur in possible replays of life's tape that some selectionist rationales are guilty of. Or in other words, the neutral view ultimately faces the same groundedness problem as the selectionist rationales it aims to undercut.

## **5. Selection in Heterogeneous Environments**

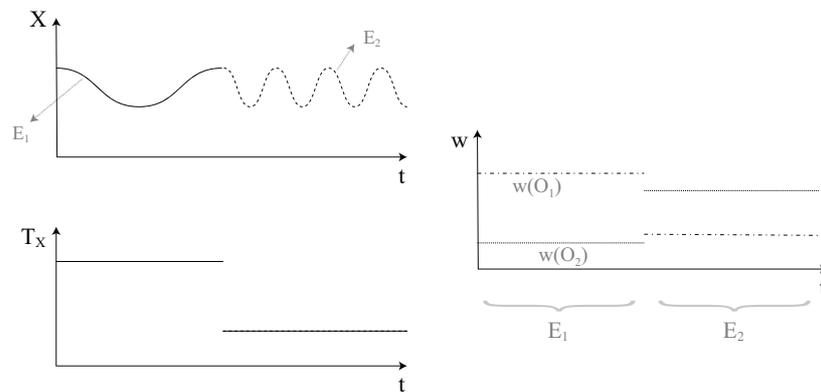
With the redundancy problem neutered, the path is cleared to address the groundedness problem. The groundedness problem is a negative claim (i.e., no selectionist rationale for progress is grounded). Hence it will be countered by a positive proposal. The idea here is to examine the “local changing environments” (Gould 2002, pp. 467–468) the groundedness problem refers to. Because fitnesses in different selective environments are incommensurable (Brandon 1990), this variability seems to preclude any grounded selectionist rationale for progress. This is echoed by Beatty, who assumes environmental heterogeneity is a source of contingency for evolution by natural selection (Beatty 1995). However, this claim was never entirely true: for instance, work on how phenotypic plasticity is selected for in variable environments goes back to Schmalhausen (1949) and Bradshaw (1965). Moreover, in light of current developments in evolutionary ecology, it is increasingly untenable (for an in-depth exploration of the nature of selection in and adaptation to heterogeneous environments, see Desmond 2021).

**5.1 Local and Extended Environments.** What does a “local” environment precisely refer to? Elsewhere Gould goes no further than describing it as the “immediately surrounding environment” (Gould 1996: 139). The example he gives is the woolly mammoth being better adapted to a cold environment than the modern elephant, but that the mammoth no way is a “cosmically better or generally superior elephant” (Gould 1996: 139).

However, it is misleading to think of “local” in a spatiotemporal way, or as designating fixed environmental states. For instance, when the magnitude of environmental fluctuations exceeds the tolerance of individual phenotypes, then environment tracking (e.g., phenotypic plasticity) or mixed strategies (e.g. polymorphism) are selectively favoured (Desmond 2018; Levins 1968). Such adaptations to environmental heterogeneity (EH) are not adaptive to EH as such, but rather to specific patterns of EH. For instance, avian migratory behaviour is adaptive to seasonal variation on a time-scale of months, but not to variation in weather on the scale of hours or days, nor to climatic variation on the scale of tens to thousands of years (Rappole

2013). Induced defences of bryozoans are adaptive only when the density of predators varies on a time-scale that is longer than the reaction time, but shorter than the lifespan (Moran 1992). The motility of bacteria is adaptive only when nutritional resources vary on a spatial scale that is equal to or smaller than the habitat dimensions (Wei et al. 2011).

This means that, for some adaptations, the “local” environment is *necessarily* extended over time (and/or space). not literally the immediately surrounding environment – it is, by virtue of the selective pattern of EH, extended across space and/or time. Figure 5 illustrates this. Heterogeneity here is slower fluctuation in some variable  $X$ , which could represent temperature, concentration of nutrients, presence of predators, and so on. Environment  $E_1$  is characterised by a slow fluctuation in  $X$  (large period  $T_X$ ); environment  $E_2$  is characterised by a fast fluctuation in  $X$  (small period  $T_X$ ).



*Figure 4:* Patterns of EH can individuate selective environments. The two figures to the left are different representations of two environments, one with a long-period variation in  $X$  ( $E_1$ ), and another with a short-period variation in  $X$  ( $E_2$ ). The figure to the right shows how differences in period lead to difference in fitness in two organism types.

**5.2 Adaptations to Novel Environmental Heterogeneity.** When selective environments are defined by patterns of EH they not only become necessarily extended in space and/or time, but the boundaries of the selective environment also become ambiguous. What precisely defines the selective environment: must it be defined in terms of the patterns an organism has already encountered, or can it involve novel patterns the organism has never encountered before? This ambiguity points to a distinction between two types of adaptation to environmental heterogeneity. An example will help introduce a more general characterisation.

Consider migratory behaviour among birds. It is considered to be one of the oldest adaptations of the Aves class, and may be as old as flight itself (Rappole 2013, p. 3). However,

insofar it is adaptive to spatial and temporal variation in food sources, this is not entirely surprising. Such variation characterises a large fraction of avian habitats, both on a regular seasonal basis as well as on irregular shorter time-scales (Rappole 2013, p. 3). Migration thus allows bird species to exploit variation in resources, and according to the pattern of variation there are different types of adaptive migratory behaviour, some of which are difficult to distinguish from mere movement (Rappole 2013, p. 6)

Yet, even though EH is ubiquitous, not all bird species are migratory. Avian adaptations to EH do not simply involve migratory behaviours gaining a selective advantage over resident behaviours in all environments. Because it is often possible for local populations to instantaneously exploit temporary increases in resources (the so-called “irregularity principle” of Willis: see Rappole 2013, p. 162), this leads to what is known as “resource superabundance” (Rappole 2013, p. 160), and allows for migratory species to enter habitats without competing directly with the resident species. So, EH is having two distinct effects on adaptive dynamics: it modifies the selective environment by creating a selection pressure for migratory behaviour, but it creates a new ecological niche in which migrants can avoid selective competition with residents.

In general, this refers to a distinction to be made between two types of adaptive process: adaptation within a common selective environment, and adaptation by avoiding selective competition and exploiting novel ecological opportunities (i.e., adaptive radiation). In the first type, the EH-exploiting type gains a selective advantage over the EH-ignoring type; in the second type, the EH-exploiting type radiates away and does not selectively compete with the EH-ignoring type within a common selective environment. The latter type of adaptive process is incredibly fundamental, even if underappreciated by philosophers of biology: e motility, cooperation, and metabolic adaptations like endothermy are also assigned this adaptive role in the scientific literature (for an overview, see Desmond 2021). A novel, unexploited pattern of EH can refer to novel resources, or to unpopulated habitats (e.g., islands), but also to spatiotemporal patterns of EH that competitors cannot yet detect.

While this process of adapting to novel ecological opportunities is not directly selective (rather, it is one of ecological radiation), it does involve the avoidance of selective competition. Patterns of EH outside the selective environment only become (relative) ecological opportunities when selective competition within the selective environment creates a dearth of opportunity. The latter follows from the basic fact that all resources are limited: this is not just the Malthusian rationale for natural selection within a common environment (Darwin 2008),

but also the precondition for adaptive radiation as a way of escaping selective competition (Grant 2013; Tan et al. 2016).

The reason why this type of adaptive dynamic is relevant for the purposes of this paper is that novel, unexploited patterns of EH are ubiquitous. To take an example from the origins of life: one of the most viable hypotheses about the last universal common ancestor is that it inhabited hydrothermal environments (Weiss et al. 2016). For these early life forms, concentrations of solar radiation represented a type of EH that was still entirely untapped.

From a fundamental thermodynamic point of view, the ubiquity of EH is unsurprising. After, a complete absence of heterogeneity in variables that affect fitness (including concentrations of energy, or concentrations of chemical elements) would imply thermodynamic equilibrium, and thus preclude the gradients (metabolism; formation of cell boundaries) that are essential for life. Moreover, of the 30 chemical elements used in biochemical reactions sustaining living organisms, only 4 are (currently) found in abundance: oxygen, nitrogen, carbon, and hydrogen. All the others occur patchily, and this patchiness is exactly what has driven the evolution of metabolic innovations (e.g., iron metabolism: cf. Frausto da Silva and Williams 2001, p. 512).

It does not seem like the source of novel, unexploited patterns of EH could ever be exhausted, as these are created by the evolution of life itself. For instance, metabolism itself creates exploitable patterns of EH for other organisms: steep gradients in waste products such as H<sub>2</sub>S can be exploited as metabolic inputs by other bacterial organisms (Fenchel 2002). Moreover, the very presence of organisms represent an ecological opportunity for others, favouring the evolution of predation. In fact, predation is one of the oldest adaptations in life's history, and by altering selection pressures, likely influenced evolutionary history to a significant degree. For instance, one leading hypothesis on the origin the eukaryotic cell was one prokaryote predated on another (Pérez et al. 2016). (The other hypothesis is endosymbiosis, but at prokaryotic level, the distinction between endosymbiosis and ingestion seems to be objectively vague: López-García et al. 2017). Predation is also part of the story of how multicellularity originated: predatory wolfpacks are considered to be some of the earliest multicellular organisms (Berleman and Kirby 2009; Grosberg and Strathmann 2007).

Hence, in sum, novel, exploitable patterns of EH are not just a contingent feature of natural environments: they were present at the origin of life, and as life evolves more such patterns are created.

## **6. The Selectionist Rationale for a Trend in EH-exploitation**

We are now in position to propose a concrete selectionist law of evolutionary history. Recall the latter's format:

Given effectively random environments and without long-term constraints on natural selection, all evolutionary histories instantiate a trend in  $M$  that is caused by selection for increased  $M$ .

This section will detail the elements of the selectionist rationale for a trend in EH-exploitation: (1) the measure of EH-exploitation, (2) what the time-steps for EH-exploitation increases are, (3) what the expected trend would look like (under idealised conditions). The upshot is that at least one selectionist rationale for progress is grounded in the causal structure of natural selection.

**6.1 Measure of EH-exploitation.** The degree of EH-exploitation of an organism (or lineage) can be spelled out in terms of the number of patterns to which the organism (or lineage) can react adaptively. Thus, the measure  $M$  (degree of EH-exploitation) supervenes on a space of possible patterns that impact the fitness of organisms. This 'EH-space' (like genotype space, or morphospace) has every indication of being *vast*: it contains all possible spatiotemporal patterns of variation in any primary resource or condition – including biotic variables. In this space, the degree of EH-exploitation of an organism (or lineage) can be thought of as the volume of the region the organism (or lineage) occupies in EH-space.

This measure induces a partial ordering: for some organism-pairs, a direct comparison can be made between degrees of EH-exploitation. For instance, compare the sensory apparatus of cephalopod and bivalve species (see also Desmond 2018). Bivalve ocelli track light intensity change (Gosling 2003, pp. 38–39) or at most can form low-contrast images (in scallop species: Speiser and Johnsen 2008). By contrast, cephalopod eyes can form high-contrast images (Boyle and Rodhouse 2005, p. 3). Concerning tactility, bivalves and cephalopods both have tactile sensors, but those of the latter are sensitive to surface texture (Boyle and Rodhouse 2005, pp. 25–26). By contrast, through proprioception, hearing, or balance, cephalopods can pick up on environmental patterns to which bivalves are completely oblivious (Boyle and Rodhouse 2005, pp. 27–29). It is fair to assign a higher degree of EH-exploitation to cephalopods than to bivalves.

However, the degree of EH-exploitation does not necessarily induce a total ordering. For instance, a deep-sea angler fish is attuned to very different patterns than a European mole living underground. It may not be possible to judge the one being attuned to *more* patterns than

the other. This implies that a trend in EH-exploitation cannot be thought of as a linear increase in some scalar, as passive trends are often represented.

**6.2 The Selectionist Rationale for EH-exploitation.** Recall that for a (passive) trend in measure  $M$  to occur, the probability of increase in  $M$  had an absolute size requirement (it cannot be too low) and a relative size requirement (it cannot be much lower than the probability of decrease in  $M$ ). How do these requirements fare for EH-exploitation?

First, concerning the absolute size requirement: it is a certainty that living organisms inhabit environments with potential for further EH-exploitation. As previously discussed, opportunities for EH exploitation are present at the initial stages of life, and are created as life evolves. This means that the absolute size requirement for a trend is met because novel and exploitable patterns of EH, albeit at varying spatiotemporal scales and in different variables, are present in every natural environment.

Second, the relative size requirement does not matter for a trend in EH-exploitation: there is no need to speculate about how probable the environment of a given lineage will favour EH-exploitation. The rationale for increased EH exploitation employs a different kind of thinking, one where the adaptive process alters the selective environment instead of selective environments exogenously driving the adaptive process. As detailed in section 6.2, increases in EH-exploitation involve exploring novel niches, thereby escaping from selective competition with EH-ignorers. Thus, a trend in EH-exploitation is a ratchet-like increase, involving radiation into new niches, rather than a trend caused by selective environments varying like coin flips.

This means that it no longer makes sense to evaluate the relative frequency of selectively favourable environments. Evolving lineages simply *change* their own selective environments as well as those of other lineages (since lineages constitute each other's environment). Specifically, even if whole clades were to face conditions that favour a decrease in EH-exploitation, this in itself creates novel opportunities for EH-exploitation in other lineages. Environmental heterogeneity is a multi-dimensional, consumable resource that cannot ever be entirely consumed: this is sufficient for a trend in EH-exploitation.

**6.3 The Trend in EH-Exploitation.** Finally, what does the trend in EH-exploitation look like, under the idealised conditions that the trend is caused only by “bare-bones” selection? This question requires separate attention, because selection-caused trends are often thought of as *driven* trends involving scalar increase (see section 2.2). By contrast, because the degree of

EH-exploitation does not induce a total ordering, the implied trend in EH-exploitation has a very different shape. The trend involves a pattern of radiation that could be called *evolutionary unfolding*: over time, different parts of the totality of environmental heterogeneity are “revealed to” (i.e., exploited by) living organisms. At the origin of life only a few environmental variables (sources of energy) may be part of the selective environment, with the other variables being part of the physical environment and with no impact on fitness differences. As the totality of lineages *unfolds* – i.e., as the range of EH-exploitation increases – more environmental variables determine the selective environment of organisms. Biotic environmental variables come to represent novel dimensions of EH, and hence there is no upper limit to the degree of EH-exploitation. As life evolves, new opportunities for EH-exploitation are created.

Due to the ubiquity and necessity of novel exploitable patterns of EH, the trend is robust. Even an episode of a decrease in EH-exploitation across all lineages would subsequently create novel opportunities for other lineages. For instance, the decrease in motility in plants created new ecological opportunities for other lineages to graze on plants. The selectionist rationale for a trend in EH-exploitation remains unaffected by decreases in EH-exploitation.

Teasing out what the concrete empirical implications are of this view would be a separate task, beyond the scope of the discussion here. In any case, what can be said is that tests for driven or passive trends (McShea 1994) would not necessarily be applicable. These tests measure the frequency with which lineages increase and decrease in  $M$ . However, they assume that changes in  $M$  are induced by environmental changes that are independent of evolution itself. By contrast, in the pattern of unfolding, the evolution of a lineage affects both its and other lineages’ selective environment. Thus, an increase in EH-exploitation in a lineage could be followed by a long period of evolutionary stability; a decrease in one lineage could cause an increase in another lineage; and so on.

The main challenge for empirically testing a trend in EH-exploitation would be to develop auxiliary hypotheses, where an observable property is hypothesised to correlate with EH-exploitation in some way. Body size could be one candidate, since it is linked with increased motility and predatory capacity (Bonner 1988). Another candidate could be nestedness, insofar as the transitions to eukaryotes and multicellular organisms are thought to be associated with increases in motility, predatory capacity, and body size in EH-exploitation (Blackstone 2013; Schirmer et al. 2011). Such auxiliary hypotheses would allow changes in EH-exploitation to be observed from the fossil record.

## 7. Discussion: Viable Progress Concepts

Progress concepts have typically been considered dead-on-arrival. Even if the possibility for value-neutral concepts are allowed for, they have been thought to not be grounded in the causal structure of natural selection. However, this judgment rests on a false premise about the role of environmental heterogeneity. When this premise is jettisoned, a very different picture emerges, where selection avoidance drives the exploitation of novel patterns of EH. Even though questions in evolutionary biology often turn on the issue of “how often does it occur?” rather than the issue of “can it occur?”, there seems no *prima facie* reason to believe increased EH-exploitation to be a marginal process. After all, it is involved with various fundamental ecological strategies – cooperation, motility, predation – that have had a major impact on evolutionary history.

The upshot is that the trend in EH-exploitation can be considered lawlike (in a way that seems to challenge Beatty’s ECT, although this will not be further explored here). Moreover, it shows the viability of at least two different value-neutral progress concepts.

The first progress concept is *unfolding progress*, referring to how some species or lineages succeed in exploiting patterns of EH. To revisit the example of cephalopods and molluscs: the former have better succeeded in exploiting EH than the latter. This does not mean they are better adapted in some narrow sense, since they inhabit distinct selective environments. Neither does it mean that the cephalopod has struck on one of a limited number of adaptive solutions to design problems. Unfolding progress is thus to be distinguished from progress concepts inherent in Conway Morris’ highlighting of convergent evolution (Conway Morris 2003, pp. 307ff) or Dennett’s notion of Good Moves in design space (Dennett 1995, p. 306). In unfolding progress, “better” is defined as a life form that can increasingly interact with and exploit a ubiquitous resource (i.e., EH), even though the latter is at all times only partially accessible to extant organisms.

A second potentially viable progress concept is an eco-evolutionary version of *competitive progress*. Here “better” is defined as “more ecologically successful”, attributable to lineages that capture a larger share of energy in ecological networks than their ecological competitors. Ecological success and EH-exploitation are linked in the following way: while the capacity to exploit novel patterns of EH can lead to radiation, it can also allow for competitive (both intraspecific and interspecific) advantages, and for capturing a larger share of energy in foodwebs. For instance, motile organisms can seek ecological opportunity in a way that sessile organisms cannot. This is a concept of success often used (albeit rarely

rigorously defined) by ecologically-minded scientists and philosophers, such as by Wilson (1990), Sterelny (2003), or Henrich (2016).

Since the measure of EH-exploitation does not induce a total ordering, it should not be a surprise that ‘ecological success’, as a proxy for EH-exploitation, does not allow for a total ordering either. There is little sense in comparing the ecological success of whole clades: for instance, the biomass of plants is, by latest estimations, 200 times that of animals (Bar-On et al. 2018). Alternatively, Antarctic krill outweigh all wild mammals – let alone orcas – by at least an order of magnitude (Bar-On et al. 2018). Moreover, while EH-exploitation is linked to ecological success, it is clear that some clades have achieved certain type of ecological success without increased EH exploitation. For instance, sloths pursue a strategy of energy conservation but they account for a quarter of mammalian biomass in jungle habitats (Gilmore et al. 2001). Tardigrades adapt to EH not by flexible avoidance but simply by resilience, for instance by means of cryptobiosis (Møbjerg et al. 2011). Yet, tardigrades are present in every ecosystem (Møbjerg et al. 2011) and seem to have been ecological successful at least in this sense.

What this discussion seeks to illustrate is how a grounded selectionist rationale points to some potentially viable progress concepts. A precise examination of the strengths and weaknesses of such concepts is beyond the scope here. However, given how all value-neutral progress concepts are thought to lack theoretical underpinnings, this shows how there are at least some that have such underpinning.

## **8. Summary and Conclusion**

Any selectionist rationale for progress must (1) be grounded in the nature of natural selection (and, in particular, should not rely on speculation about what types of selective environments are more probable than others), and (2) show how passive trends cannot always be more parsimoniously explained as resulting from random walks. The most common view on this matter is that both hurdles cannot be cleared. By contrast, this paper argued that random walks do not necessarily lead to passive trends, unless one makes speculative assumptions about the probabilities of selective environments. Moreover, environmental heterogeneity need not only be a source of contingency. Heterogeneity itself is ubiquitous, and an exploitable resource. Hence the selection for capacities that exploit novel patterns of environmental change is a sound basis for a selectionist rationale.

The trend implied by this selectionist rationale involves changes in ecology first and foremost, rather than in morphology. Lineages radiate into novel ecological niches, and thus

this trend, where the totality of environmental heterogeneity (EH) unfolds, looks nothing like the classic linear representations of progress. Life as a whole expands into niches where EH is exploited to greater degrees, without necessarily eliminating lifeforms that exploit EH to lesser degrees.

In showing that the hurdles facing selectionist rationales can be cleared, I do not pretend to have presented a full rehabilitation of the concept of evolutionary progress. However, what I do hope to have shown is that the search for a selectionist rationale for progress, grounded in natural selection, is eminently reasonable, and worthy of serious discussion – and not only in the context of science education, or the anthropology of folk biology.

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