The Selectionist Rationale for Evolutionary Progress

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Abstract

A widespread view on evolutionary progress is (1) that natural selection offers no rationale for it, and (2) that a neutral model, where lineages evolve randomly starting at some minimal state, is sufficient to explain large-scale evolutionary trends. In this paper, I first undermine the view that the neutral model should be the default view, and then offer what I argue can be the only selectionist rationale for evolutionary progress, based on an analysis of how natural selection acts in heterogeneous environments. The concept of evolutionary unfolding is proposed, where evolutionary history is characterized by an increased range of exploitation of environmental heterogeneity.

1. Introduction. In the not too distant past, claims that life has made progress throughout evolutionary history – or 'progress-claims' for short – 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 organization, 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).

This has very much become a minority view, to the extent that the default view on the thesis of evolutionary progress is that the thesis is thoroughly debunked. Instead, beliefs in evolutionary progress are largely assigned to folkbiology, where they are of interest to educators (Johnson et al. 2012; Werth 2012).

However, while other folkbiological belief such as teleology or species essentialism have received philosophical rehabilitations, the concept of evolutionary progress remains thoroughly debunked.[1] Besides changes in the wider culture, there are many different reasons for this. One class reason concerns the role of chance in evolution, ranging from mass extinctions to the importance of random genetic mutation, to how some chance, irreversible

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[1] Few if any believe that the functions or species are an entirely anthropomorphic construct, yet such a position is rather common with regard to evolutionary progress.

evolutionary changes can yet constrain all future variation on which selection acts (the 'frozen accident' argument: Crick 1968). However, one of the most powerful reasons against evolutionary progress lies in an analysis of very concept of natural selection. Echoing earlier statements by G.C. Williams[2], here is S. J. Gould's formulation:

> 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)

In other words, to say that natural selection has consistently favored adaptive increases in some measure (whether 'complexity' or 'intelligence') reflects a misunderstanding of the concept of natural selection. Adaptive evolution is caused by spatially and temporally immediate ("local") environment of an organism, since this is what determines the organism's fitness; moreover. environments have changed continuously and dramatically over the past 4 billion years.

Even though this argument has been, on the whole, seen as decisive, it is based on an abstraction that is often left unquestioned. 'Local environment' is intended to contrast with future, or spatially distant environments, and is referred to across the scientific literature (Thompson 1999). However, if the concept is analyzed at a finer grain, it becomes problematically vague. In reality, a process of selection occurs in temporally and spatially extended environments: just as starters, an organism's fitness may be determined by many different environments the organism is exposed to in its lifetime. This may not matter when environments are static or uniform, but all natural environments are characterized by varying degrees of environmental heterogeneity (EH), which is defined as: a large number of independent variables, such as temperature, humidity, or the presence of predators, all varying at different rates, across time and/or space. And environmental heterogeneity engenders its specific selection pressures (Levins 1968): selection in extended, heterogeneous environments cannot be modeled as selection in a local, homogeneous environment.

In this paper I seek to inquire into the precise link between selection, environment, and evolutionary progress in light of the reality of environmental heterogeneity. While the importance of EH for selection has been long recognized (Bradshaw 1965; Levins 1968), its implications for eco-evolutionary dynamics (Hairston et al. 2005; Thompson 1999), and for major events in evolutionary history (Berleman and Kirby 2009; Pfeiffer and Bonhoeffer 2003;

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[2] "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)

Wei et al. 2011) are only beginning to be charted. In any case, the philosophical implications for evolutionary progress have not been drawn (or so I will argue).

In any case, the upshot will be a defense of a (partial) rehabilitation of the concept of progress. To do so, I will draw on Hutchinson's distinction between a 'condition' and 'resource' variable[3], and will both outline a rationale as well as illustrate of how EH can be both be modeled as both kind of variable. Interpreting EH as a resource variable has macroevolutionary implications: since EH as a resource is ubiquitous, selection for exploitation of EH can give rise to a largest-scale counterfactually robust pattern, a small number of evolutionary lineages increasingly exploit EH as resource.

The paper is structured as follows. I will first clarify the different forms a 'law' of evolutionary history may take, especially in relation to the evolution contingency thesis (Beatty 1995). I will then argue that contingency alone cannot explain large-scale patterns in evolutionary history, and by looking more closely at the relation between ecology and laws of evolutionary history, I will argue that the only way progress can be rehabilitated is as an increase in exploitation of EH.

2. Laws of Evolutionary History

Drawing on Ayala (Ayala 1974), Elliott Sober has pithily summarized the concept of evolutionary progress as "direction + value" (Sober 1994). The first element, direction, can be ascribed to a lineage (e.g., an increase in complexity or intelligence) or across many lineages (e.g., an increase in the average complexity or intelligence). The second element refers to how progress-claims involve an evaluative judgement, where evolution has progressed towards 'higher' or 'better' (so, e.g., higher complexity is in according to some values 'better' than lower complexity). In some versions of progress, this involves a mixing of moral values with scientific theory is perhaps the underlying reason why, without too much exaggeration, Sober's diagnosis that evolutionary progress is "a phrase that many evolutionary biologists now view with disdain" is true today as much as it was in 1994. However, 'value' can also be defined on the basis of non-moral evaluative judgments – hence 'more complex', 'more genetic information' (Kimura 1961), 'better at survival' (Thoday 1953). However, as Ayala (1988) points out, it is impossible to speak of progress without some conception of 'higher/lower' or 'better/worse', and such evaluative judgments cannot be grounded in biological theory alone.

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[3] Hutchinson himself uses the terms 'scenopoetic' and 'bionomic' (G. Evelyn Hutchinson 1957). (CITE)

In this section, I will introduce a different analysis of progress-claims, eschewing talk of directionality in favor of analyzing progress-claims as 'laws'. This will make the conceptual tools in the wider philosophy of science more readily usable, in particular, by allowing counterfactual and causal structures to be analysed more powerfully. In general, progress-claims need not involve laws. One can also claim that that life has factually progressed (categories I and II in Table 1), whether in complexity, moral virtue, or intelligence. These claims are uncontroversially true; however, where the debate lies is whether this progress is a lawful feature of evolution as it has occurred on this planet. Progress claims that are lawful are much more controversial – *a fortiori*, they remain basically debunked at the moment. Leaving aside progress in moral values (category III), this paper focuses on progress-claims in category IV.

		Value	
		Moral	**Non-moral**
Generalization	**Contingent**	I	II
	Lawful	III	IV

Table 1: Varieties of Evolutionary Progress

Basic definitions. I will now situate progress claims (type IV) within a larger context of 'laws of evolutionary history', and will define precisely what type of progress claims are under investigation in this paper. A generalization 'all Fs are G' is a *law of evolutionary history* when the generalization has the following format:

"All possible evolutionary histories instantiate a pattern P"

An *evolutionary history* is the sum total of lineages, both extant and extinct. A lineage is an ancestor-descendant series (Simpson 1951). So the quantification over all possible evolutionary histories includes not just the set of all lineages, both extant and extinct, but also all counterfactual sets of lineages. It includes all of life as it actually evolved on our planet, but also life as it (possibly) evolved on other planets, and life as it could have evolved on our planet, were the initial conditions and boundary conditions different.

An evolutionary history is constituted by a very large number of sequences of individuals; however, fine-grained data at the individual level is typically unavailable in the fossil record. Hence most if not all large-scale studies in paleontology concern generalizations at the level of species (e.g. Payne et al. 2009). A history of species is a model of evolutionary history, where individual organisms standing in ancestor-descendant relations to each other

have been grouped together according to species (species delimitation remains a controversial area, cf. De Queiroz 2007).

In progress-claims, only a certain aspect of evolutionary history is of interest, whether complexity, body size, genetic information, and so on. Hence a measure *M* (corresponding to non-moral values above) is introduced that assigns a real number to any given lineage; in this way a time-slice of evolutionary history induces a frequency distribution, which changes over time. A *pattern P* is a further abstraction of this frequency distribution, obtained by isolating one particular statistical property of this distribution. For instance, a pattern can concern the maximum of the frequency distribution over time. An evolutionary law that concerns the maximum of a measure is Cope's Law[4]:

> In all possible evolutionary histories, the maximum body size of any lineage increases with time.

Patterns can also concern the or the minimum, or the average – or any statistical property for that matter (skew, kurtosis, etc.). When the pattern concerns a monotone increase in the statistical property, it can be called a *trend*[5]. Thus cyclical or chaotic patterns are not trends; however, the focus in this paper, as well as most of the scientific literature on macroevolutionary patterns, will be on trends.
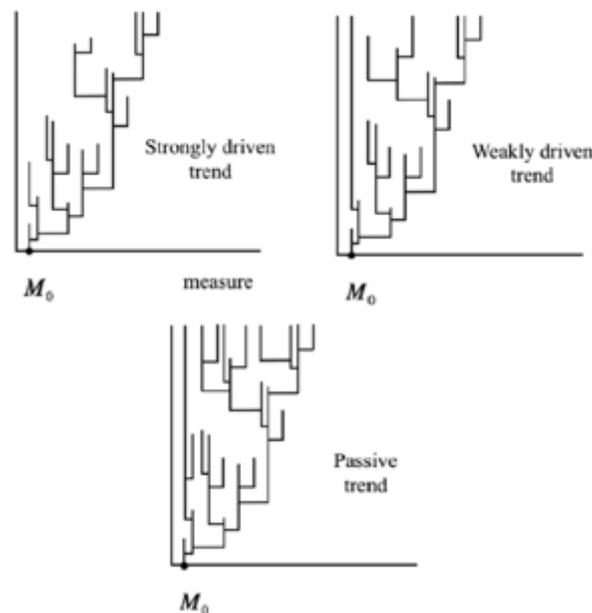

Figure 1: Patterns in Evolutionary History

Contingency and Causes. There is good reason to believe that laws of evolutionary history – that is, exceptionless generalizations over all possible evolutionary histories – do not exist. Any evolutionary history can be massively influenced by contingent events – i.e., events that may happen in one possible world, but not another – such as asteroid impacts at a certain time *t* after the origin of life, or a chance mutation constraining all subsequent lineages. The view that there are no laws of evolutionary history is implied by the Evolutionary Contingency Thesis, or ECT (Beatty 1995):

> All generalizations about the living world: (a) are just mathematical, physical, or chemical generalizations (…) 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 implies that any pattern P that is instantiated across all possible evolutionary histories (i.e., non-contingent patterns) must be the consequence of theories in mathematics, physics, or chemistry. There is no pattern that is the consequence of distinctively biological processes, such as genetic mutation, drift, or natural selection.

However, the focus in this paper does not concern empirical generalizations, but rather the rationale inherent in natural selection for progress. This 'rationale' can be formulated by means *selectionist laws of evolutionary history*, a particular type of ceteris-paribus generalization (Hempel 1988):

> *Given no constraints on natural selection*, all possible evolutionary histories instantiate a pattern P *that is causally explainable by natural selection*.

The 'no constraints' proviso refers to an idealized evolutionary history where natural selection is given free reign and is not counteracted by constraints or other evolutionary processes. Thus neither developmental constraints nor genetic constraints prevent adaptive phenotypes from being introduced into a population. Neither do strong drift processes (e.g., during a founder effect) lead to a suboptimally adaptive phenotype being fixated in the population.

The second element of selectionist laws of evolutionary history is that the pattern be 'causally explainable' by natural selection. Even if there are no constrains on natural selection, some patterns in evolutionary history can follow from mathematical principles. For instance, zero-force evolutionary law (McShea and Brandon 2010) refers to such a pattern, where an increase in number of part-types follows with mathematical necessity from the foundations of probability theory (McShea and Brandon 2010, 108–9).

Note that in the scientific literature an orthogonal distinction is typically made between 'driven' and 'passive' trends: in a driven trend, increases in the measure *M* are more frequent

than decreases in an individual, whereas in a passive trend, increases and decreases occur with equal frequency. Some driven trends may be causally explained by natural selection (e.g. increases in *M* are more adaptive), but others may have occurred in absence of natural selection (e.g., if there is constraint on decreases, which is known as a neutral ratchet, cf. e.g. Lukeš et al. 2011).

3. The Neutral Theory of Evolutionary Trends

Just as there is a neutral theory of molecular evolution (Kimura 1968) and a neutral theory of the ecology of biodiversity (Hubbell 2001), so too there is a neutral theory – albeit it one that is intended as a critique of progress, and less well developed than other the neutral theories – of evolutionary progress, where no biological causes are invoked to explain trends. Instead, trends follow from the random walk of lineages over macroevolutionary timescales. Even though he draws on (Stanley 1973), in the following I take Gould's formulation (Gould 2011) to be the *locus classicus* of the neutral theory.

Consider an important type of trend in complexity: the trend in nestedness (McShea 2001a, 2001b). One entity is 'nested' within the other when the latter physically contains or includes the former. The measure of nestedness, or "hierarchical object complexity" (McShea 1996) has four values – prokaryote, eukaryote, multicellular, colony – and evolutionary started at the prokaryote level, and maximal nestedness increased monotonically, reaching the upper limit some 800 million years ago (Figure 2). The trend in nestedness thus covers some of the major transitions (Maynard Smith and Szathmary 1995), and is a relatively precise operationalization of the concept of complexity.

Consider following generalization:

(C-1)   'The maximum degree of nestedness increases in any possible evolutionary history'.

This lawlike generalization seems to be true in actual evolutionary history. Depending on how one defines multicullarity it may have evolved as early as 1.8 bya and as late as 700 mya. However, even within this extremely large margin of error, one can still safely conclude that eukaryotes evolved before multicellular organisms. Similarly, multicellular organisms evolved before colonies. So the generalization is verified pretty convincingly on our planet. However, what about (C-1) across *possible* evolutionary histories? While much remains still to be understood, the transitions in nestedness do not seem to be contingent once-off events that are unlikely to occur in other possible evolutionary histories. Both multicellularity and eusociality have evolved numerous times (Grosberg and Strathmann 2007; Hughes et al. 2008; Wilson and

Hölldobler 2005), even though eukaryotes seem, somewhat puzzlingly, to have only evolved once (Blackstone 2013).
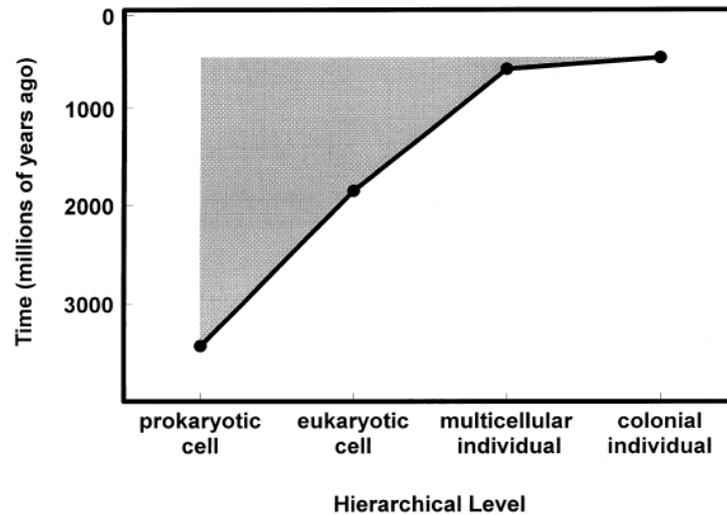

Figure 2. The increase in degree of nestedness across evolutionary history. (From McShea 2001)

However, is selection needed to explain the lawlike trend in nestedness? Consider the selectionist version of C-1:

(C-2)   Given no constraints on natural selection, the increase in maximum nestedness in any possible evolutionary history is causally explainable by natural selection.

The neutral theory undermines C-2 as explanatorily dispensable: C-1 can be adequately explained by the statistics of random walks, and there is no need to invoke natural selection.

First, consider how life necessarily began at the minimum mode of complexity (assuming eukaryote, multicellular, or colonial life could only appear if prokaryote life already existed), then from that starting point, only more complex life could evolve. Then, even if there is no causal principle at work favoring a phylogeny to increase or decrease complexity, and that the degree of complexity of lineages increases or decreases according to some random walk, we can still expect the complexity maximum to increase over time. In his own words:

> "Since space remains available away from the left wall and toward the direction of greater complexity, new species occasionally wander into this previously unoccupied domain, giving the bell curve of complexity for all species a right skew, with capacity for increased skewing through time (…) Such an extension of the right tail will occur in a regime of entirely random motion for each item, so long as the system begins at a wall." (Gould 2011, pp. 105–106)
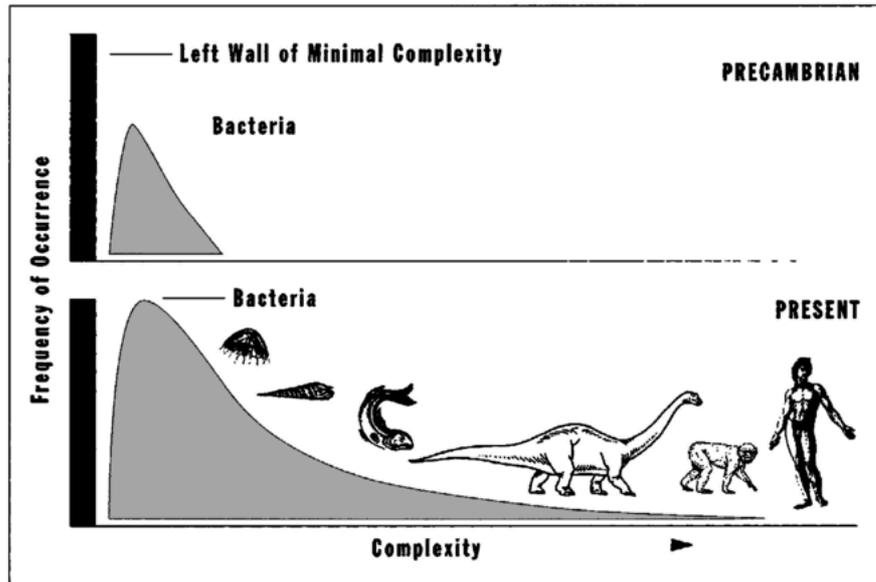
FIGURE 29
The frequency distribution for life's complexity becomes increasingly right skewed through time, but the bacterial mode never alters.

In this way, just as Hubbell's neutral theory of ecology is an instance of a distinctively mathematical (topological) explanation (Huneman 2010; Lange 2013), this explanation of the trend in complexity draws on nothing but statistics, i.e., the evolution of the binomial distribution as one conducts an increasing number of Bernouilli experiments. In other words, complexity increases in evolution for the same reason that, if enough people flip a coin for long enough, someone is bound to have a long run of heads. Moreover, categorizing the neutral theory as a distinctively mathematical explanation is a vindication of Beatty's ECT: the increase in complexity in evolution may be lawlike, in the sense that the pattern will reoccur in any evolutionary history, but the law is not distinctively biological in that it is not explained by any distinctively biological processes or causes.

Why prefer the neutral theory over a selectionist explanation? There are three reasons. First, it is more parsimonious, since it does not invoke any controversial hypotheses (such as, increased complexity being selectively advantageous in most environments). Second, it is consistent with the assumption that selective environments have varied effectively randomly in evolutionary history. There is no conceptual rationale that natural selection should favour certain traits more often than not. Third, even if natural selection would, on average, favour increased complexity, one would expect what is called a 'weakly driven trend': a trend where in any given lineage unaffected by constraints increases in complexity are more frequent than decreases. When tested for this (the 'ancestor-descendant test': McShea 1994) there is no

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empirical evidence with regards to a weakly driven trend in complexity (regardless of how precisely complexity is measured).

While I have called it the 'neutral theory' in order to expose the underlying argumentative structure, Gould's argument against progress is not intended so much as an explanation of progress, but rather as a critique or an attempt to deflate the concept of progress. As he states, "the vaunted progress of life is really random motion away from simple beginnings, not directed impetus toward inherently advantageous complexity." (Gould 2011, p. 173) Why precisely should this deflate the "vaunted" progress of life? The answer lies in the distinctively mathematical character of the neutral theory. While Gould's argument is directed towards the increase of complexity, it really generalizes for any passive trend in measure M. Not just increases in complexity, but also increases in body size, information processing capability, and even increases in baseball hitting averages: they are all occur for the same reason that, if enough people are flipping coins for long enough, somebody is bound to throw many more heads than they throw tails. Trends in complexity, or any measure for that matter, are therefore just not interesting evolutionary phenomena.

The neutral theory has been very influential – not just Gould's formulation of it, but also as an 'attractor', if you will, for scientific and philosophical thought (e.g., (Raup 1988), (Sober 1994), or (Turner 2011) outline the same basic analysis of a directional pattern). Yet, it is not as neutral as it seems, and in the following section I will argue that an effectively random evolution of individual lineages makes significant assumptions about how natural selection operates on macroevolutionary scale.

4. Problems with the Neutral Theory

The neutral theory assumes that lineage evolution can be modeled as a random walk. A random walk describes a dynamics where an entity can transition into 'nearby' states with equal probability. Let us define this with more precision. Let M be the measure of interest, and 'M-space' the set of all possible values of M. A random walk then describes how a lineage moves through M-space, either by increases in M with probability ½ or decreases with probability ½ each time step. The 'time step' defines a time-scale where the expected probability for the expectancy for a M-increase (or M-decrease) is ½. The time-step for a coin flip is the length of time it takes for a person to pick up the coin and flip it again. The time-step for changes in nestedness is on the scale of 10s-100s of millions of years when M; for changes in body-size, the relevant time-scale is millions of years.

A random walk is an idealized model of causal processes responsible for lineage evolution, and does not correspond to any single causal process. So, to get a better grasp on what is precisely entailed by "random motion away from simple beginnings", we should translate the random walk in M-space in terms of fundamental variation-producing processes (genetic mutation, phenotypic plasticity) and variation-spreading processes (natural selection, drift) acting in genotype space.

Let Ω be the space of all possible genotypes. Then evolution of any one parent-offspring lineage is a trajectory within this space Ω. The evolution of a species includes many such individual trajectories, and can be represented as a single species lineage, averaging over individual lineages in the monophyletic group. Evolutionary history as a whole refers to the sum total of all individual lineages, which in turn may be represented as the sum total of species lineages.[6] Limiting the length of possible genomes to some large number N, the size of Ω 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 Ω as "vast" (Dennett 1995) or "hyper-astronomical" (Kauffman 1993). Let us further assume that each genotype in Ω corresponds to a unique degree of M, but a single degree of M may correspond to a large number of genotypes: M-states supervene on Ω-states.[7]
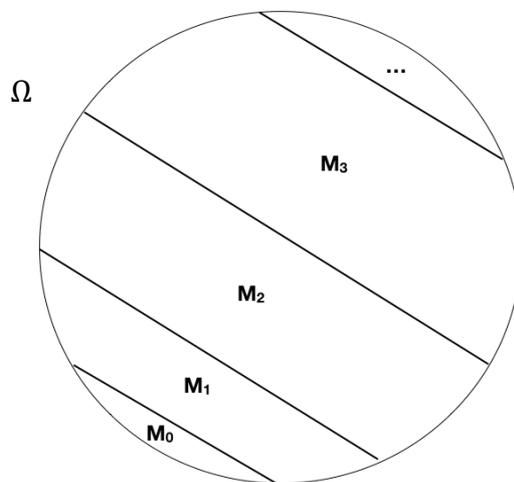

Figure 3: Levels of Complexity in Genotype Space

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[6] Whether such an explanation is particularly *explanatory* is another question (and a controversial one); that it is possible to describe evolutionary history in this way is not controversial.

[7] This assumption need not be true. For instance, wolfpacks, or cooperating predatory bacteria (*Myxococcus*), are considered to exemplify multicellularity (Berleman and Kirby 2009; Grosberg and Strathmann 2007). Such cooperative behaviors are environmentally induced, and thus genotype alone underdetermines level of nestedness. However, if environmental states were to be included among micro-level states (upon which M-states) supervene, this would support the account presented later on in the paper, since

Within this framework, the question now becomes, what is required for a lineage to wander 'occasionally' into areas with a higher degree of M? The size of the time-step matters here. In microcanonical thermodynamics, heat will also 'occasionally' flow from cold to hot, but the scale of the time-step involved here is in the order of tens of billions of years. This is why the second law of thermodynamics is a "statistical" instead of "deterministic" law (Schrödinger 1992): it offers mere quasi-universality. In the evolutionary case, given the size of Ω, an evolutionary history could easily spend tens of billions of years in the M_0 state, if lineages sampled Ω randomly through genetic mutations[8]. Specifically, for nestedness, the empirically documented time-step involved in increases in nestedness is on the scale of 10-100 million years (McShea 2001a): this cannot be explained simply by random mutation through Ω. Moreover, multicellularity and eusociality have evolved numerous times (Grosberg and Strathmann 2007; Hughes et al. 2008; Wilson and Hölldobler 2005), so transitions in nestedness cannot be modeled as entirely random. Some bias needs to be involved in the navigation of Ω.

If unaccompanied by some selective advantage, the appearance of a phenotype with increased nestedness (e.g., cooperative bacterial predation) would likely disappear within a few generations due to swamping by drift (even the neutral theory of molecular evolution allows for natural selection at phenotypic level). A random walk through M-space therefore involves that M-favoring selective environments occur just as often as M-disfavoring selective environments (and that neither is too infrequent in comparison to M-neutral environments).

Yet it is very significant to assume that M-favoring selective environments occur just as often as M-disfavoring selective environments. There is no *a priori* reason to support this assumption. For instance, say that M is 'level of beauty', 'level of moral goodness', then most selective environments actually disfavor M. Just as most genetic mutations are deleterious, most measures imaginable should be disfavored by selection. The same applies for measures of complexity: if one would model the succession of environments in evolutionary history as effectively random (as Gould does[9]), one should expect nestedness decreases to happen over a

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[8] See (Louis 2016) for a calculation, on the basis of an estimation of the size of space of possible protein configurations, of how long it would take for a single protein of length 150 to find the correct spatial configuration: in the order of 10^{133} times the age of the universe. In reality, proteins fold in microseconds: strong evidence that spatial configurations are not sampled randomly.

[9] "If a sequence of local environments could elicit progressive advance through time, then some expectation of progress might be drawn from natural selection. 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

shorter time-scale than increases. The default expectation for a random measure in a random environment is that the measure will disfavored.

This argument undercuts the (widespread) neutralist assumption that trends in the maximum of a measure (i.e., passive trends, where the minimum measure remains occupied) are best explained by a random walk in the lineages, and do not reflect anything of interest about evolution. If a measure is not privileged by evolutionary processes, and selective environments vary with true randomness, then not even a trend in the maximum can be expected.

In the next section I will suggest we should question the concept of a local environment. Upon closer analysis, there is no such thing as a local environment, in the sense of spatio-temporally immediate environment, and if one replaces that with the alternative – evolution in heterogeneous, spatio-temporally extended environments – one obtains a very different picture of the 'bare-bone mechanics' of natural selection, with very different implications then for the question of progress.

5. Selection in Heterogeneous Environments

Among the sources of contingency that preclude the existence evolutionary laws, John Beatty includes "natural selection in changing environments" (Beatty 1995, p. 53). By contrast, in this section, I aim to show how natural selection in changing environments is an important source of counterfactual robustness (and hence predictability) for evolutionary trends. I will start by undermining the common idea that natural selection occurs in local environments.

5.1 Local and Extended Environments

What does "local" precisely refer to when saying that natural selection concerns only adaptation to "local changing environments"? Gould goes no further than describing it as "immediately surrounding environment" (Gould 1996: 139), and illustrating it by noting how the woolly mammoth evolved a coat as an adaptation to a cold environment, but in no way is a "cosmically better or generally superior elephant".

However, while it is true that fitness can only be defined relative to an environment – thus the fitness of a woolly mammoth would be different in cold versus hot environments –

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are tracking local environments by natural selection, then their evolutionary history should be effectively random as well." (Gould 2011, pp. 139–140)

one must distinguish between the physical and the selective environment (Brandon 1990). The physical environment is defined by the sum total of abiotic and biotic processes: temperature, terrain features, precipitation, presence of predators, presence of potential mates, etc. The physical environment can change substantially without the selective environment changing, since the latter tracks fitness differentials throughout time and space. The temperature in the immediately surrounding environment of any one woolly mammoth will undergo considerable variation during its lifetime; what matters for selection pressures would not be fine-scale variation (e.g., on a day-to-day basis) but rather coarser features, such as the average annual temperature, the maximum temperature, the minimum temperature. Lowering the minimum temperature may increase selection pressure for a thicker coat, but increasing the rate of change of temperature during a season may not.

Only certain changes in the physical environment matter, but it is a far from easy task from determining which changes matter. In fact, some have argued that there is no privileged way of doing this: fitness is a mere bookkeeping device to track births and deaths in a population, and no privileged measure of fitness can be introduced for the same fundamental reasons why, in general, no privileged reference class can be assigned to estimate the probability of an event type (cf. analysis in Desmond 2018). Hence, we only reconstruct what environmental factors mattered for this after evolution has already taken place (Walsh 2007).

However, even if it can be done, one obtains different answers what the fitness values – and hence what the selection pressures – are according to the time-scale that one adopts. If the average annual temperature is low for two generations, the selection pressures for a population of elephants will favor those with thicker coats; if after those two generations, the temperature rises significantly, the selection pressure will favor those with thinner coats. So on a time-scale of two generations, selection has a direction; on a slightly longer time-scale, average selection may have another direction (or none at all); and so on. This is what is known as 'compound selection' (Brandon 1990): the selective environment changes over time.

Significant changes in physical environment do not always occasion compound selection; as is well known, they can create specific selection pressures for increased degrees of phenotypic plasticity (Bradshaw 1965; Levins 1968). Phenotypic plasticity is an instance of a wider class of adaptations to heterogeneity, which can include degree of developmental homeostasis, and at the population level, polymorphism and spatial differentiation. Depending on the *pattern* of heterogeneity in the physical environment (the scale of spatial and temporal heterogeneity), different types of adaptations can be favored (for an overview, see Pigliucci 2001, chapter 9).

Why this is significant is that, the selective environments which favor adaptations to heterogeneity are *necessarily* extended over time and/or space. A heterogeneity adaptation cannot, per definition, be adaptive to an "immediately surrounding" environment, but is adaptive to an environment that is spatiotemporally extended. The selective environment cannot be considered local in a vague spatiotemporal sense. Rather, locality is now defined by the pattern of heterogeneity across time and/or space, and there is a multitude of different adaptations, each suited to different patterns.

In sum, Gould's remark about "immediately surrounding" environments is inaccurate: selection for variability adaptations necessarily occurs in environments that are spatially and/or temporally extended. However, as we will now see, by itself this does suffice to undermine Gould's basic point about the causal structure of natural selection.

5.2 Selection in Heterogeneous Environments

Adaptations to environmental heterogeneity are always adaptations to particular *spatiotemporal scales* of heterogeneity. Avian migratory behavior is adaptive to seasonal variation, but not to variation in weather (time-scale of hours or days), nor to climatic variation (time-scale of tens to thousands of years). Induced defenses of bryozoans are adaptive only when the density of predators vary on a time-scale that is longer than the reaction time, but shorter than the lifespan. Motility of bacteria is adaptive only when nutritional resources vary on a spatial scale that is equal or smaller to the habitat dimensions.

In general, different scales of heterogeneity in the same variable may be superposed, to create a *pattern of EH* (not to be confused with a pattern of evolutionary history)[10]. An organism may take a single scale of change to be a signal, or may take a combination of scales to constitute a signal or cue which will produce a reaction. For the sake of simplicity, the following discussion will be limited to regular heterogeneity at well-defined time-scales.

Figure 4 illustrates how selective environments can be individuated according to a spatiotemporal scale of heterogeneity: in this case, the period or characteristic time-scale of the fluctuation of some variable X, which could represent temperature, food, presence of predators, and so on. Environment E_1 is characterized by a slow fluctuation in X (large period T_X); environment E_2 is characterized by a fast fluctuation in X (small period T_X).

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[10] And conversely, any pattern of change in an environmental variable can be decomposed into periodic sinusoidal oscillations at different frequencies (the Fourier series, cf. e.g. Boyce and DiPrima 2008).
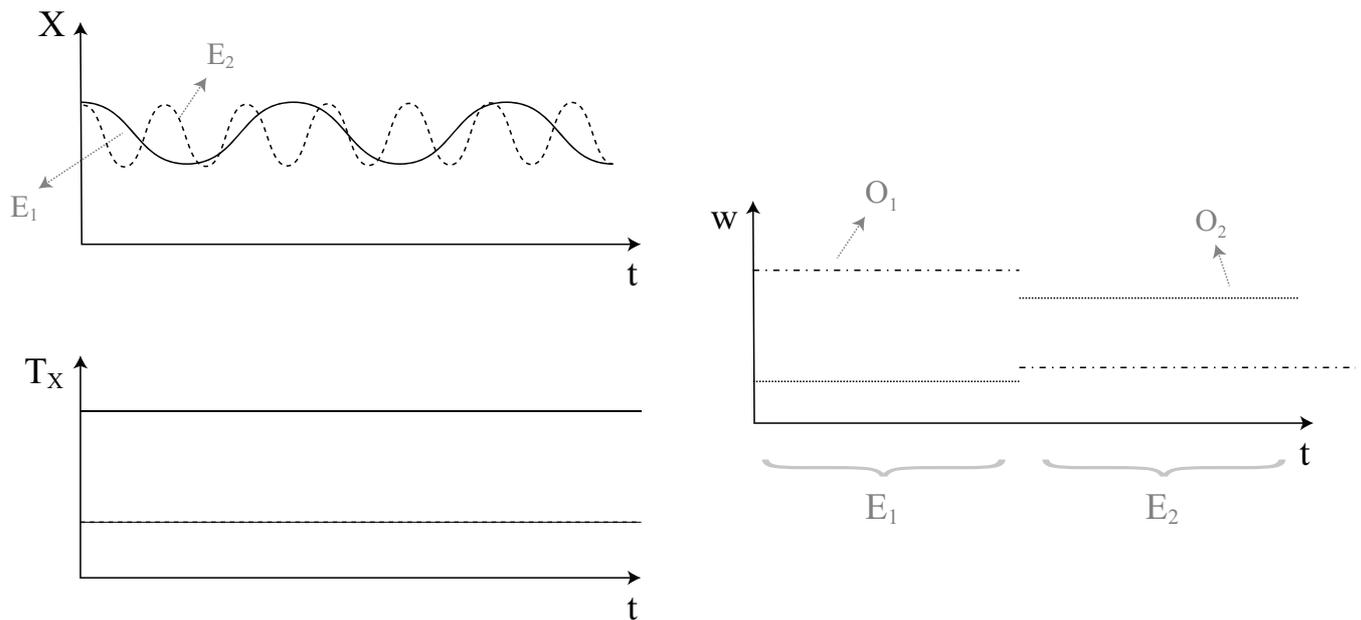
Figure 4: Patterns of EH individuate selective environments. The two figures to the left are different representations of two environments, one with a long-period variation in X (*E₁*), and another with a short-period variation in X (*E₂*). The figure to the right shows how differences in period lead to difference in fitness in two organism types.

The physical environment is continuously changing to varying degrees and in different variables X, but not all of these changes necessarily matter for evolution by natural selection. Only when these changes occasion fitness differences do they become part of the selective environment. This is illustrated by the fitness graph in Figure 4: in environment E_1 there is selection for O_1 over O_2, whereas in environment E_2 there is selection for O_2 over O_1. There may be a large number of other environments characterized by yet other values of T_X which do not occasion fitness differences.

Because spatiotemporal scales of EH themselves vary, the adaptation to EH cannot provide a rationale for evolutionary progress. Even though environmental heterogeneity is *ubiquitous*, and can be considered a necessary property of natural environments in any evolutionary history, this does not translate into a ubiquitous selection pressure. On the largest time-scale, the expected average direction of selection is still zero.

This does not mean that selection for adaptations to particular spatiotemporal scales of EH cannot cause significant evolutionary trends. Because a very significant source of EH is biotic (e.g., the variable presence of competitors, predators, prey, etc.), *effects* of selection for adaptations to a scale of EH in turn cause changes in the very scale of EH. For instance, organisms of prey-population A may selectively compete to avoid predator-population B. The

selective environment of prey-population A therefore includes a variable X, defined as 'vicinity of predators B'. Conversely, the selective environment of predator-population B includes a variable Y, defined as 'vicinity of prey A'. Both X and Y fluctuate over time[11]; A-individuals compete to adapt to fluctuations in X, whereas B-individuals compete to adapt to fluctuations in Y. The results of selective competition between A-organisms results in better capacities to escape B-organisms. This leads to changes in the spatiotemporal variation of Y, and hence modifies the selection pressure on B-organisms, resulting in further adaptations among B-organisms, and so on.

This is, of course, a Red-Queen dynamic (Van Valen 1973), which can lead to evolutionary arms races. The Red-Queen dynamic has been hypothesized to be at the basis of a number of evolutionary trends, including a trend in increased body size (Bonner 1988), or energy intensiveness (Vermeij 1987). However, the Red-Queen dynamic, by itself, does not offer any rationale for a selection-driven evolutionary law. It describes a causal feedback between two populations and two selective environments, but the feedback will collapse if conditions in the wider physical environment, shared by both predators and prey, are no longer supportive, such as offering sufficient nutrients to prey (Vermeij 1987, p. 377). Since such variability in the wider physical environment is to be expected in an evolutionary history, trends based on the Red-Queen dynamic exemplify how natural selection in changing environments is a source of contingency.

5.3 Two Eco-Evolutionary Roles of Environmental Heterogeneity

If this were the only thing that could be said about natural selection in heterogeneous environments, the preceding discussion would constitute at most be a further nuance on the neutralist critique. However, heterogeneity plays two distinct ecological roles, and taken together present a case why the bare-bone mechanics of natural selection does provide a rationale for progress. I will first give an example.

Migratory behavior among birds is, as one would expect, an adaptation to EH. Temporal variation in temperature or precipitation is present for a large fraction of habitats, both on a regular seasonal basis as well as on irregular shorter time-scales, and a consequence of this is considerable variation in the resources available for the ecosystems in those habitats. Migration allows bird species to take advantage of this variation, and is in fact considered to

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[11] Necessarily so, since if B-individuals were always close to A-individuals, A would not exist, and if B were never close to A, B would be deprived of its food source and would die off.

be a trait that is likely as old as flight itself (Rappole 2013: 3) – in other words, migration likely goes back to the origin of the Aves class. There are many different types of migratory behavior (Rappole distinguishes between ten different types: Rappole 2013: 6), but not all of them should be considered as specifically avian adaptations: the boundary between migration and movement is vague. Nonetheless, the near-ubiquity of EH means that migratory behavior, in its various forms, is one of the oldest adaptations of the Aves class.

Yet, even though EH is ubiquitous, not all bird species are migratory. Because it is often possible for local populations to instantaneously exploit temporary increases in resources ("irregularity principle" of Willis 1966:221), this leads to what is known as "resource superabundance" (Rappole 2013, p. 160), and allows for migratory species to enter the habitats without competing directly with resident species. So EH can be viewed in two ways: as modifying the selective environment by creating a selection pressure for migratory behavior (because migrants will be able to exploit the heterogeneity in resources), and as creating an a new selective environment, by placing migrants in their own ecological niche so they avoid selective competition with residents. This is why, even though EH is ubiquitous and even though migratory behavior has evolved numerous times, not all bird species are migratory.

The example illustrates how scales of EH can act as two types of ecological variable (Begon et al. 2006; George Evelyn Hutchinson 1978): resource and condition variables. Condition variables refer to slow-changing, usually abiotic features of the environment which are not consumed and hence not affected by levels of competition. Examples include terrain features, precipitation, temperature. Resource variables are consumed and hence affected by levels of competition between organisms, and can often (though not necessarily) fluctuate on much shorter time-scales than condition variables. Hutchinson's original terms for these two types of variable were, respectively, "bionomic" and "scenopoetic": the latter set the scene, whereas the former govern interactions among biota.

This distinction can be applied to environmental heterogeneity as follows. For instance, the temporal scale S of heterogeneity in variable X can itself be represented as a value of variable T_X (as in in Figure 4). Therefore $T_X = S$ sets the scene for selective competition in a population (i.e., right graph in Figure 4). In this way, the variable T_X can represent a condition variable that is nearly constant in a selective environment, in the same way that average annual temperature, or terrain features such as forests or wetlands can.

Condition variables have been linked with Grinnellian niches (Soberón 2007). This niche concept is defined by basic abiotic variables in the environment, and is used to explain coarse-grained properties of species. Thus, for instance, water is part of the physical

environments of fish, whales, seals, and penguins, and has driven similar adaptations in an aquatic environment (Brandon 1990: 69). Similarly, seasonality can be represented as a variable in a Grinnelian niche, in which all populations and species adjust to this seasonality. This eco-evolutionary role of EH is the one of interest in the investigation of the evolution of phenotypic plasticity, where models are constructed when plastic phenotypes are selected for over fixed phenotypes (Godfrey-Smith 1996; Moran 1992).

The second eco-evolutionary role of EH refers to how a scale of can act as a resource variable to be exploited by individuals. Resource variables, ranging from food and nesting sites, to shelter and mating opportunities, define Hutchinsonian niches, where each resource variable defines an axis a n-dimensional hyperspace (Hutchinson 1957). Generalizing from the avian migration example, a particular S of EH can also act as a resource variable in this hyperspace. Once an organism or a group of organisms evolves that is capable of exploiting $S,$ it may at first be at a selective advantage over those who are incapable of exploiting $S.$ At this stage, S-exploiters and S-ignorers share a single selective environment. However, after some time, there will increased competition between S-exploiters, i.e., between behavioral and/or developmental strategies to exploit S as efficiently as possible. Thus new selection pressures are created, and the selective environments of S-exploiters and S-ignorers diverge. In this way, inhabiting separate Hutchinsonian niches has prevented fitness differences between S-exploiters and S-ignorers to constitute selective competition (see Desmond and Ramsey ms. for further analysis on the selective environment).

Despite some ambiguity attached to niche models of biodiversity[12], such models are still largely seen as explanatorily indispensable to explain stability properties of species coexistence in the same physical habitat ('niche partitioning', cf. Chase and Leibold 2003). In sum, modeling scales of heterogeneity as axes in Hutchinsonian niche therefore has several implications.

First, a heterogeneity scale only matters for evolution by natural selection when it engenders a fitness difference between two organisms. For instance, as long as there is no motile organism that can exploit spatial variation in food sources, this spatial variation does not play any role in the selective environment.

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[12] Some having constructed models that predict patterns of biodiversity based on ecological drift (Hubbell 2001). However Hubbell himself was not an eliminativist on niches (Hubbell 2001, p. 11).

Second, scales and patterns of EH can only function as resource variables because there are primary resource variables in the habitat: without heterogeneity in primary resource variables, heterogeneity would never be a resource.

Third, EH as a resource is not limited by physical constraints such as limits on quantity of free energy in a physical environment: patterns can be superimposed upon patterns, at varying temporal and spatial scales, without limit. As a secondary resource variable, EH is effectively infinite. Thus, if there are n-independent resource variables, then each variable vary at m distinct spatial or temporal scales. The classic Hutchinsonian niche is n-dimensional; the space of possible EH-patterns is n^m-dimensional.

5.4 Summary

In sum, selection in heterogeneous environments occurs in two distinct ways. In the first, a specific pattern π of EH can occasion a specific selection pressure, which means: there is selective competition between a group of individuals that possess a trait that is adaptive to π (e.g., plasticity, or polymorphism, or spatial differentiation, or endothermy, cf. Levins 1968) and those individuals which lack that trait. As long as π is present in the environment, one group will be selectively favored over the other group. However, the environment changes, π may be replaced by a different pattern π' of EH, and selection pressures may be reversed.

The second way EH can impact evolution by natural selection is by creating a new ecological niche, defined by a specific pattern π of EH. In this case, π does not cause selective competition; rather, it causes the *avoidance* of selective competition. One group of organisms may evolve an adaptation to π and thereby avoid competition with another group that is not adapted to π. Seasonal variation creates a niche for seasonal migration in birds, but those groups of birds that exploit the seasonal variation are not in selective competition (or, not strong selective competition: selective environments can be shared to varying degrees, see analysis in Desmond and Ramsey ms.) with non-migratory birds.

These two eco-evolutionary roles of EH may be present in varying degrees at the same time. Bacteria use motility both to gain a selective advantage over sessile bacteria, as well as to avoid competition. One role may also precede the other role: in initial stages, a pattern of EH may engender selective competition, but at a certain point, the intragroup selective competition among EH-exploiters may become greater than the intergroup selective competition, leading to diverging evolutionary trajectories, and ultimately separate ecological niches. However, this ratchet is not a consequence of changes in unit of selection (Maynard Smith and Szathmary 1995) nor due to evolutionary-developmental reasons of it being easier

to add rather than eliminate developmental programs (Saunders and Ho 1976), nor due to basic probabilistic considerations (McShea and Brandon 2010). The rationale for the ratchet is based on the causal structure of natural selection in heterogeneous environments.

6. Reconstructing the Trend in Nestedness

The preceding analysis of EH can be made more concrete by applying it to the case of nestedness. What follows now is *how-plausibly* narrative of how exploitation of EH drives the evolution of nestedness – alternative hypotheses are not thus not discounted. Instead, the narrative is intended as an illustration of how selection for adaptations to EH-as-resource can causally explain to a lawlike trend.

Life started at the unicellular stage, with organisms drawing on a number of different resources: solar sources of energy, chemical sources, and so on. Initially, the vast space of possible EH-patterns remained untapped: patterns in spatial and/or temporal variation of these energy sources, but also biotic sources of energy. A number of ecological strategies emerged to exploit the various categories of EH. Motility exploited the first category: motile organisms have a selective advantage over sessile organisms when nutrients are heterogeneous over time and/or space (Wei et al. 2011). However, motility can also be used to avoid competition with sessile organisms (Hibbing et al. 2010), and in such cases, selective competition between motile organisms is stronger than that between motile and sessile organisms. The second category of EH is exploited by predation, which often are motile as well (Pérez et al. 2016, p. 771), and which likely has evolved many times (Jurkevitch and Davidov 2007). Different predatory strategies include enveloping the prey (epibiotic predation), invading the cell membrane of the prey (endobiotic predation), and cooperation between predator cells to degrade the prey cell.

Predation, cooperation, and motility have been linked to the transitions in nestedness. The two leading hypotheses on the origin of eukaryotes is that it occurred either through phagy or through symbiosis of plasmids or mitochondria (Blackstone 2016; O'Malley 2010)[13]. The origin of multicellularity is similarly explained as either resulting from combinations of cooperation and predation: cooperative hunting, cooperation for excretion of enzymes, or cooperation to produce anti-predator toxins (Pfeiffer and Bonhoeffer 2003). Finally, the role

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[13] An alternative hypothesis, compatible with the framework presented here, is that prokaryotes and eukaryotes have a common ancestor that was neither a prokaryote nor an eukaryote (Forterre 2013). Forterre proposes that "the ancestors of archaea (and bacteria) escaped protoeukaryotic predators by invading high temperature biotopes, triggering their reductive evolution toward the "prokaryotic" phenotype" (Forterre 2013, p. 1).

of EH for the origin of eusociality is more ambiguous. Some have proposed that eusocial strategies outcompete egalitarian and solitary strategies when resources are scare and unevenly distributed (Fronhofer et al. 2018); others that eusocial colonies draw on the resources that are present in large quantities, and leave solitary organisms to "fill in the cracks" (Wilson 1990, p. 52). Nonetheless, Wilson lists eusociality as offering clear advantage in responding to spatial heterogeneity in nesting sites, as well as temporal heterogeneity in the physical environment through creating a homeostasis in the nesting environment (Wilson 1990, p. 98).

While there may not be a rationale why natural selection should cause an increase in complexity (or cognition for that matter), there is a rationale why natural selection should cause an increase in EH-exploitation capacity. For many of the transitions in nestedness, it is in fact quite well accepted that they represent ways to increase EH-exploitation. However, there is nothing privileged about increases in nestedness per se: if decreases in nestedness were a better way to increase EH-exploitation, than the bare-bone mechanics of natural selection would offer a rationale for a trend in decreased nestedness.

In all of this, selection never ubiquitously favors those organisms that are able to exploit EH. Prokaryotes, unicellular organisms, and solitary organisms still populate the biosphere. While an increased capacity to exploit EH may be an initial selective advantage, as the population of EH-exploiters grows, selective competition between EH-exploiters becomes more intense, until EH-exploiters and EH-ignorers occupy separate niches. This means that the evolutionary success of the former need not imply the extinction of the latter; furthermore, it also means that once environments change significantly, the groups of EH-exploiters are relatively shielded from competition from non-exploiters.

Thus, there may be developmental reasons why the origin of eukaryotes or multicellular organisms was an irreversible event in evolutionary history, but there is also a selective one. Eukaryotes, due to their larger size, have superior motility, are less encumbered by viscosity (lower Reynolds numbers), and robustness against predators (Blackstone 2013).

In sum, increases in nestedness seem to line up, more or less, with increases in EH-exploitation, and insofar they do, a law-like increase in nestedness explainable by natural selection can be expected in any evolutionary history (assuming no constraints on selection). However, unlike the increase in EH-exploitation, this conclusion about the increase in nestedness is not purely conceptual, and depends on empirical research. Thus, EH may be shown to not matter for the selection of eusocial (over solitary) strategies, and in such a case, the proposed framework of selectionist laws of evolutionary history does not apply.
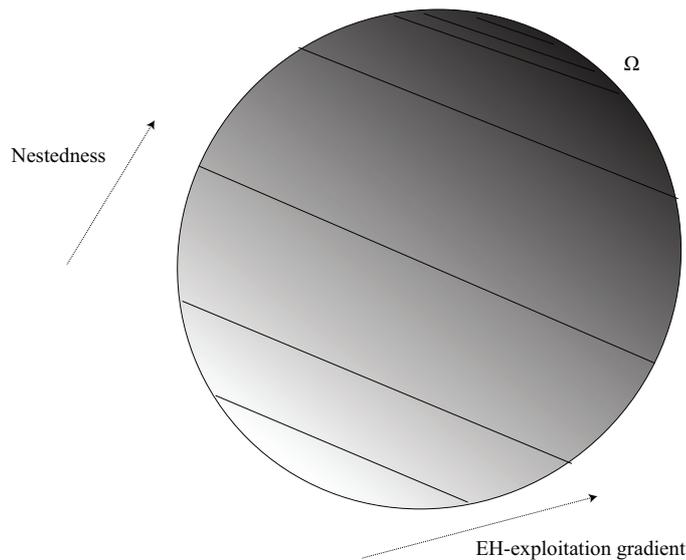
Figure 5: Increases in nestedness need not correlate with increases in EH-exploitation, but the state-of-the-art implies that, on the whole, it does.

7. Discussion and Conclusion: The Pattern of Evolutionary Unfolding

A process is said to 'unfold' when its future states are either known ahead of time, or are present as latent potentialities. Thus, a contingent process, where any replay of the process might lead to a different outcome, does not 'unfold' in this sense. To give a more everyday example, a blanket or newspaper can be unfolded. In folded state, the different parts of the larger sheet of linen or paper are not visible, but as the blanket or newspaper is unfolded, then these parts become visible. The time sequence of events serves merely to reveal the different parts of a whole.[14]

In the account constructed in this paper, a process of evolutionary unfolding reveals different parts of the totality of environmental heterogeneity to living organisms.[15] Most dimensions of environmental heterogeneity remain unexploited at the initial stages of life, and as evolution unfolds these are increasingly exploited. This unfolding is neutral on the issue of convergence (e.g. Morris 2003), as it is on traditional measures of progress, such as complexity, body size, or cognition. There is not an end-state to this unfolding either, since evolutionary outcomes can create new sources of environmental heterogeneity, for instance, through

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[14] Systematically exploring the metaphysical implications of unfolding are beyond the scope of this paper.

[15] Ironically, the word 'evolution' comes from the Latin word for unrolling or unfolding (*e-volvere*). Darwin himself initially preferred the terms 'transmutation' or 'descent with modification', since 'evolution' had the preformationist connotations of the unrolling of a predetermined plan, usually from a simple beginning to a more complex final state (Bowler 1975). Thus the term evolution was associated with the concept of progress from the start (what precisely Darwin's own views on progress were remains controversial: cf. Ruse 1996, 136–77; Richards 1988). Needless to say, the account presented in this paper is not a rehabilitation of preformationism.

ecological interactions of predation, competition, or cooperation, as well as when organisms themselves become the source of signals in the environment of others (Searcy and Nowicki 2010).

Unfolding is entailed by the selectionist rationale for progress, and entails a number of properties the ensuing pattern in (idealized) evolutionary history has. As such it is potentially compatible with the many different measures of evolutionary progress proposed in the past. Reviewing the literature going back to the early 20th century, Bernd Rosslenbroich counts thirty distinct measures. The main purpose of the account proposed were was not to add another one to this list, but rather to clarify how natural selection in changing environments is not merely a source of contingency (cf. Beatty 1995). Instead, the basic causal structure of natural selection in changing environments does offer a selectionist rationale for evolutionary progress.

Nonetheless, an abstract measure does suggest itself: the degree to which environmental heterogeneity is exploited by an organism. No attempt was made to operationalize this measure (i.e., how precisely should environmental heterogeneity be measured), but the definition given here was sufficient to offer a rationale why the maximum of the measure should increase monotonically in evolution. Going back to Rosslenbroich's overview, this measure has (perhaps unsurprisingly) been anticipated in historical literature. It is closely related to following measures:

"Perception of signals from the environment and ability to react to environmental stimuli"; "Occupancy of ecospace", "plasticity of structures and functions", "flexibility of behavior", "autonomy", "ecological possibilities", "control over the environment" (Rosslenbroich 2006, pp. 55–57)

There is not sufficient space here to discuss how precisely environmental heterogeneity is related to these measures, but based on the preceding discussion, it should at least be intuitively clear.

The main philosophical work done by selectionist rationale for progress is that it places a *necessary condition* on any candidate selectionist law of evolutionary history. If a proposal is made that some pattern *P*, causally explainable by natural selection, is instantiated in any possible evolutionary history (given no constraints on natural selection), then it must be causally explainable by natural selection increasing the degree to which environmental heterogeneity is exploited by an organism. Given the ubiquity of EH, this is the only underlying selective process that can deliver on the counterfactual robustness needed for the generalization to count as a law.

[9041 words]

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