

The Generalized Selective Environment

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Abstract

As the principle of natural selection is generalized to explain (adaptive) patterns of human behavior, it becomes less clear what the selective environment empirically refers to. While the environment and individual are relatively separable in the non-human biological context, they are highly entangled in the context of moral, social, and institutional evolution. This chapter brings attention to the problem of generalizing the selective environment, and argues that it is ontologically disunified and definable only through its explanatory function. What unifies the selective environment is that it explains adaptation in a non-agential way, by screening off various forms of agency, whether divine, organismic, or human. This explanatory function of the selective environment helps avoid some sources of confusion when the theory of natural selection is applied to humanities and social sciences.

Keywords: Natural selection – Human Agency – Cultural Evolution – Memetics – Evolutionary Psychology

1. Introduction

At a basic, almost folkbiological level of analysis, the concept of natural selection implies that there is an environment “doing” the selecting. More precisely, the selection is done by the “selective environment” of a population, consisting of those attributes or processes in the external environment that influence fitness differences between individuals in the population (Brandon 1990). For instance, if a population of moths consists of both dark and light types, and if the color of tree bark influences

fitness differences between moth types, then the color of the bark of trees in the external environment can be counted as part of the selective environment.

In the context of biological evolution, the concept of selective environment is clear enough. A field biologist might still have difficulty identifying the selective environment for a given population, given how real environments are highly heterogeneous. However, such challenges do not give conclusive grounds for doubting that there is some “selective environment” to which the trait or organism type in question is adapting.

By contrast, once the principle of natural selection is applied outside of biology, the concept of selective environment becomes much less clear. In fields such as cultural evolutionary theory or evolutionary psychology, natural selection acts on products of human cognition: patterns of behavior, social and/or moral norms, social institutions, or even scientific theories. For instance, in evolutionary approaches to scientific change, some scientific theories are “selected for” over others. What does the selective environment then consist of? Does it consist of the humans doing the selecting? Does it consist of the community of scientists, or some type of “invisible hand” determining which theories come out as winners? Or the mind-independent reality that determines the predictive success of a theory?

My proposal in this chapter is, first, that we run into confusion if we try to find a naïvely realist account of what selective environment is. Instead, I argue that what unifies various generalizations of the selective environment is an explanatory function. In particular, the explanatory function of the generalized selective environment concept is to *screen off* the explanatory role of agency in explanations of adaptation. This function can be realized in different ways, depending on what agency refers to. Agency can refer to non-human organismic agency, human agency, and divine agency. The focus in this paper will be mainly on how natural selection screens off human agency. This can be done in many ways and to varying degrees, and disambiguating between these ways and degrees helps clarify the distinctions between types of generalization of natural selection.

The paper is structured as follows. In the next section I will review the reasons why it is not fruitful to think of the selective environment as part of the furniture of the world, but that we should think of it as an epistemic or explanatory category instead. I then (section 3) will focus on four types of explanation of changes of honor norms – evolutionary psychology, memetics, dual inheritance theory, and cultural

niche construction – and will identify the selective environment concept present in each, and contrast it with agential explanations (section 4). Based on this analysis of the selective environment of a moral norm, I will argue how it can be extrapolated and will present an account of the generalized selective environment (section 5).

2. Defining the Boundaries of the Selective Environment

As an illustration of the problem for this chapter, consider evolutionary approaches to scientific change. The change in time of scientific theories, as many products of human cognition, lends itself easily to the evolutionary metaphor. Science is like a population of jostling, competing theories, each struggling for dominance. In one of the first evolutionary accounts of science, Hull (Hull [1988] 2010) proposed a memetic analysis of the phenomenon, where scientific ideas (hypotheses, methodologies, epistemic values, etc.) play the role of replicators and books, journals, and scientists that of interactors.¹ Ideas shape the brains of scientists and cause these scientists to produce particular locution that persuade other scientists, thus allowing for the replication of the idea. In this way, science is the history of different ideas competing by colonizing human minds.

Now, what is the “environment” in which the selection of scientific theories takes place? After all, to speak of natural selection presupposes fitness differences (or, depending on one's concept of natural selection, a struggle or competition), and fitness is always defined relative to an environment. So, what is the “environment” of a scientific idea (hypothesis, methodology, value)? The obvious proposal is that the environment consists of the *minds* of individual scientists: these are the “space” that ideas can “colonize”. This answer is closest to core rationale of Dawkins’s memetics, where, memes were originally presented as “parasitizing” human minds (see Dawkins [1976] 2006).

A problem with this line of analysis is that Dawkins seems to primarily have had fashions, hypes, or ideologies in mind (see Dawkins [1976] 2006, 192 ff.). By contrast, it is implausible to think the success of, for instance, Newtonian dynamics is entirely

¹ In his words: “elements of the substantive content of science-beliefs about the goals of science, proper ways to go about realizing these goals, problems and their possible solutions, modes of representation, accumulated data, and so on.” (Hull 1988, 434). Dawkins himself suggests that the true replicator is a “unit of information residing in the brain” (Dawkins 1982, 109), with words, music, images etc. the interactor.

similar to the changing fashions regarding, for instance, beard length. While science is not immune to such dynamics -- the psychological appeal of a scientific theory (e.g., simplicity, elegance) plays its part in theory selection -- an idea must also generate *empirical success* in order to replicate successfully in a scientific community. In other words, mind-independent reality also determines the (long-term) fitness of scientific ideas. Moreover, the wide variety of epistemic attitudes scientists can hold towards ideas – varying degrees of credence, or instrumentalizing views – is not captured by a category so crude as “colonization”. While it may be attractive to explain fashion trends as memes “colonizing” human minds, it is a much less attractive approach to understanding scientific trends.

So should one analyze the selective environment more broadly, as including features of mind-independent reality? Thus, the fitness of Newtonian dynamics compared to, say, Aristotelian dynamics is not determined by the preferences of scientists, but by the real properties of mass, force, and movement. One specific way of construing this option, would be to view the scientist as the extended phenotype through which scientific ideas interact with each other and with the mind-independent reality. However, this option seems implausible in different ways. The minds of scientists cannot be analyzed as extended phenotypes of ideas in their interaction with empirical, mind-independent reality. For instance, scientists can keep on supporting ideas even if they seem “maladaptive to” (i.e., falsified by) the empirical environment (the Duhem-Quine thesis). Sometimes this support is irrational (as if the idea has colonized the scientist’s mind), but sometimes this support can be grounded in the conviction that the relevant empirical evidence is just not available yet.

Is the human mind part of the selective environment, or should the selective environment be placed outside of the human mind? When phrased at this higher level of abstraction, it becomes clear that we run into similar problems if we would enquire about the selective environment of corporations and social entities, moral norms, technological know-how, or languages. It is also a problem that arises specifically as the theory of natural selection is applied to human phenomena. To explain why cetaceans evolved in the direction of limbless streamlined bodies, it seems very plausible to refer to a mind-independent reality, namely the aqueous environment. By contrast, products of human cognition often cannot be entirely explained through a process of adaptation to the physical environment, and they are both shaped and shape human minds and human communities.

Figure 1 schematizes some of the difficulties in defining the selective environment: where should the boundary be drawn? What precisely is the environment that an entity such as a scientific theory “adapts” to? Does it consist only of mind-independent reality, or also of the human minds (and communities)? Each option runs into difficulties.

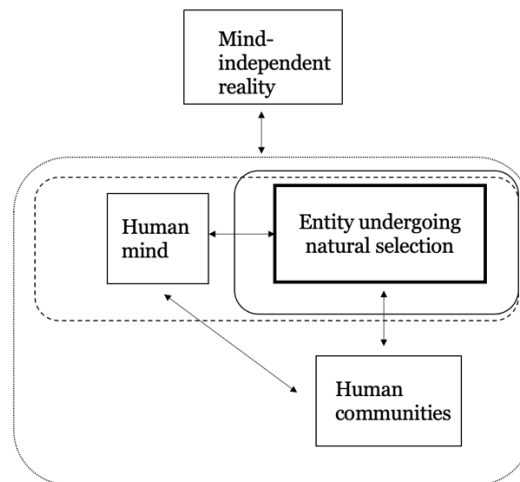


Figure 1: Where should the boundary between the selective environment and the (extended) evolving entity be drawn?

3. Heterogeneity and Reciprocity Blur Boundaries

Why exactly is it so difficult to pinpoint what the selective environment is for entities such as scientific theories? Why do these same problems not seem to be as pressing in the context of biological evolution? What are the deeper reasons for this? In this section I will suggest two reasons: the heterogeneity of the external environments and the reciprocal interactions between an individual and its environment. It is also helpful to take a slight detour into the grounds of the concept of the selective environment.

The history of the concept of environment indicates some of the difficulties. Naturalists, including Darwin in *On the Origin of Species*, originally only spoke of a concrete plurality of “circumstances” impinging on the organism. The term “environment” traces back to the translation of Comte’s term of *le milieu* or perhaps Goethe’s term of *Umgebung* (see Pearce 2010, 248). Spencer is usually credited with popularizing the notion in the English-speaking scientific community through his *Principles of Psychology* (Spencer 1855). Darwin only started using the term from

1875 on, but without any explicit reasoning being given for the adoption (Darwin 1875; Pearce 2010, 249). At a certain point, for unclear reasons, there was a scientific need to reify the concrete plurality of circumstances in the abstraction of “the environment”.

This abstraction inevitably raises the question what it precisely refers to, and even in the biological context one tends to find ontological disunity. After all, the environment concept is the dual of the individuality concept: the environment contains everything that is “not” the individual. According to one’s concept of individuality, one obtains different concepts of the environment. For instance, if one defines individuals by their outer physical membranes or surfaces, the “environment” then becomes all processes or features that are spatially outside these surfaces. If one defines individuals by means of what their immune systems accepts (Pradeu 2012), then the “environment” contains all processes or features that are rejected by the immune system, including features that may be physically inside the individual (e.g. invading pathogens). If one defines individuals as Gibsonian agents, then the environment becomes a landscape of affordances that is unique to each individual (Walsh 2015). And crucially for our purposes, if one defines individuals as units of selection, the associated environment concept is the “selective environment” (Brandon 1990). The selective environment is thus merely one possible environment concept among many.

What then is the selective environment? In textbook representations of natural selection, this is often represented as unproblematic. The process of natural selection is highly idealized and represented as taking place in an environment that can be represented by a single, binary variable, such as the “presence” or “absence” of sooted trees (for examples of this kind, see textbooks such as Ridley 2004; Futuyma and Kirkpatrick 2017). This is a significant idealization for the field biologist trying to determine the selective environment of a population. For them it may be genuinely unclear what processes or features contribute to selection, due to various forms of environmental heterogeneity. What are the types of process that should be included in their determination of the selective environment? What are the truthmakers of the selective environment?

The first challenge lies in environmental heterogeneity as the default state of natural environments. In general, environments are continually changing due to exogeneous factors, including geological processes or climatological processes. Environments change as individuals radiate into new habitats, for instance due to

intragroup competition. They may also change as rival species evolve, with new patterns of predation or symbiosis occurring. This does not mean that a biologist cannot assign a “habitat” or some relatively fixed environment to an organism or population, where the habitat consists of with a number of “expected” processes or features that can go into defining the selective environment. For instance, stable patterns, or approaches to equilibrium, could be taken as evidence of a well-defined selective environment (for more detail on this, see Desmond 2018). However, not all variation allows for a well-defined pattern to be inferred (this is argued in more detail in Desmond 2022, 84–87). There is always a fallible epistemic leap from observations of recurrent phenomena to the probability with which they occur². This suggests a hypothesis why the selective environment is a lot more difficult to pin down the generalized evolutionary setting: in such settings, where the “environment” is influenced by the action of individual human beings, it is much more difficult to identify stably recurring patterns, and hence to define selective environments.

A second conceptual roadblock in the way of attempts to pin down the generalized selective environment, is that boundaries between individual and environment can become objectively blurred once there is “mutual interaction”, sometimes also called “entanglement” or “reciprocity”: the individual exerts a causal influence on the environment, which in turn changes the causal influence the environment exerts on the individual (for an overview, see Baedke, Fábregas-Tejeda, and Prieto 2021). An organism may behave – through niche construction – in ways that alter the selection pressures on itself and its kin. In such cases, to fully explain how lineages evolve by natural selection, one cannot simply refer to processes in the selective environment as if these are wholly external to the organism. The explanans must also include the behavior, development, or even metabolism of organisms within (and beyond) the lineage, and how these properties impact the selective environment. The selective environment thus becomes an intermediary in the causal link between organismic behavior and evolution.³

² On this point, I am in agreement with (Abrams 2009; Bourrat 2020). A once-off occurrence (lightning strike) may significantly impact the expected number of offspring, but if the occurrence is truly once-off, there will be no way of verifying what exactly the probabilities are underlying the expectation number. This is why, when a freak environmental occurrence significantly alters reproductive numbers in an otherwise relatively stable environment, we tend to speak of “drift” instead of “selection”.

³ This is the underlying rationale for viewing niche construction as an *agential process*: not all alterations of the selective environment can be categorized niche construction, but only alterations that are been effected in an agential way by the organism. This view is developed to some extent in (Aaby and Desmond 2021).

At what point does the environment-organism distinction break down? Quite a number of philosophers and biologists have endorsed the conclusion that organism and environment form a single system (see the discussion of "ontological co-constitution" in Baedke, Fábregas-Tejeda, and Prieto 2021). This is not the place to embark on an extended analysis of this issue, but for purposes here I wish merely to draw attention to how the environment-organism distinction is much easier in some cases of reciprocal interaction than in others.

For instance, the dam that the beaver builds can be seen as the beaver modifying its environment, but also as the genotype of the beaver expresses itself through a particular phenotype (Dawkins 1982). It may be difficult to choose whether dam should be viewed as an extension of the organism, or as part of the environment that affects the beaver. In fact, this is the rationale for Dawkins's notion of the extended phenotype: part of the external environment constitutes the organism. Nonetheless, there is still a clear criterion for distinguishing between dam and, for instance, the beaver's tail: persistence over time. Once the first generation of beavers has constructed the dam, the dam may continue to exist regardless of the behavior or even existence of subsequent generations of beaver. Hence for subsequent generations of beaver, for whom the dam predates them, the parts of the dam that persist can more appropriately be judged as being part of the selective environment rather than as extensions of the organism.

Nonetheless, as environment and individual become increasingly entangled, it becomes increasingly hopeless to try to pinpoint where precisely the unit of selection stops and where the selective environment begins. This entanglement may not be extreme in the case of the beaver and the dam, because neither the beaver nor the dam depends directly on each other for their continued existence. That is different with scientific theories, moral norms, or corporations. Their continued existence *does* depend on the continued existence of their selective environment (composed of humans who cognize the theories, norms, or institutions). In this sense, the entanglement between such units of selection and the selective environment is much more extreme in the case of cultural evolution. The next section will illustrate in more concrete detail just how difficult it is to pin down what the selective environment is in the context of cultural evolution, and how entanglement is a significant reason for this difficulty.

4. The Environment in Evolution of Honor Cultures

As a further case study, let us take a specific instance of cultural evolution: the evolution of honor norms, which are a type of moral norms. In particular, I will build on the work of Stefan Linquist (Linquist 2016) who teases apart the diverging predictive implications of different models of cultural evolution. Identifying how these models generate divergent predictions forces clarity on two core questions: what are the units of selection, and what types of ontological factors determine the selective environment.

What are honor cultures? They describe communities characterized by norms that endorse violence as a morally justified response to insults, slights, or other reputation-lowering actions. They appear to be more common among pastoral communities than among horticultural communities. Hence the question arises whether honor cultures are adaptive to the types of environmental circumstance faced by pastoral community.

The general adaptationist rationale for honor cultures, is that in some “socioecological environments” (Linquist 2016, 215) it is adaptive to have a low threshold for violent retaliation and escalation against reputation-lowering behavior. Reputation-lowering action (e.g., insults) can be damaging to the affected individual, as it can snowball into theft, conflict, and exclusion of the insulted person. So, reacting violently to reputational threats can shut down this snowball process and send others the message that it will be costly to enter into conflict. However, reacting violently can lead to a proliferation of conflicts as well as to costly misunderstandings. What degree of sensitivity to reputational threats is optimal as societal norm depends on the circumstances. In any case, in honor cultures, a relatively high degree of sensitivity is the *norm*, and individuals furthermore adopt certain behaviors (e.g., threats of retaliation) that signal to others that they adhere to such honor norms.

Under what circumstances precisely are honor cultures adaptive? The main hypothesis here is that their adaptiveness depends on two variables in the socioecological environment (see Linquist 2016, 216): (1) whether or not individuals depend on easily stealable resources, and (2) whether individuals can rely on a legal or social corrective mechanism to address perceived injustices. In pastoral

communities, resources are easily stolen, namely, livestock, as opposed to, for instance, housing or agricultural land. Moreover, pastoral communities tend to be spread out geographically (to allow for grazing), which means most will live too far from any type of communal norm enforcement to be able to rely on the latter. Together, this means that violence and dominance from others can have a very significant impact on an individual's livelihood, and that an individual will not be recompensed for any suffered violence or dominance. In such circumstances it is adaptive for individuals respond actively (and, often, violently) to potential challenges to their social status.

3.1 Four types of selective cultural environment

What are the units of selection and the selective environment in this adaptationist rationale for honor cultures? Linquist introduces the notion of the “socioecological environment” and distinguishes between two types of *evolutionary* unit: psychological phenotypes (patterns of behavior that characterize an individual) and cultural phenotypes (the norms of a community). Whether these units are also units of selection depends on the model of cultural evolution employed. The following starts from his analysis of four models of cultural evolution – evolutionary psychology, memetics, dual inheritance theory, and cultural niche construction – and zooms in on the question how precisely each model conceptualizes the selective environment.

Memetics. First, in the model of memetics, cultural variants are virus-like units hosted by human minds. The paradigmatic type of memetic evolution is the spread of a catchy tune, or the rise and fall of fashions. Here the unit of selection is the cultural phenotype, and the selective environment is the human mind. More sophisticated construals of memetics are possible, but they stretch the original conceptual fabric and are ultimately less satisfactory.⁴ The units of selection spread by appealing to psychological dispositions of individual human beings.

⁴ For instance, instead of interpreting the human mind as the environment for the meme, one could potentially view it as the extended phenotype of the meme. In this view, the selective environment would consist of the social and ecological conditions acting on individual humans. However, in this alternative construal, memetics no longer presents a distinctive model to e.g. dual inheritance theory, where human organisms are the main unit of selection and where cultural variants are understood as a fitness-enhancing trait. Second, this compromises memetics' explanatory simplicity for the core cases of fashion trends or catchy tunes – and hence brings memetics further away from why it got uptake in the

For this model to successfully explain the evolution of honor norms, one pattern the data would need to show is that the spread of honor norms to be relatively independent of varying the fitness benefit or cost to individuals. As circumstances change, but the makeup of the human mind presumably does not⁵, the memetic model predicts that honor norms would be able to continue to hijack human psychology with success. (Linguist find that this is not borne out by the data.)

Evolutionary Psychology. The second model is that of evolutionary psychology, or more precisely, canonical evolutionary psychology (see Nettle, this volume). Here the human mind is hypothesized to have evolved through selection for cognitive modules in the “environment of evolutionary adaptedness” (EEA), which comprises, roughly, the types of general conditions that are hypothesized to characterize ancestral hunter-gatherer societies. On this view, cognitive evolution tracks genetic evolution, and moreover, cognitive modules develop in a canalized fashion and thus are relatively insensitive to changing physical or social conditions. Note that this does not imply that habits of behavior or of preference will develop uniformly among individuals: cognitive modules will express themselves differently in different circumstances. Even though there may be little plasticity in the development of cognitive modules, evolutionary psychology still allows in principle for plasticity in the expression of behavior (though see footnote 6). In any case, in canonical evolutionary psychology, the units of selection are genotypes, and the selective environment consists of the social and ecological factors that characterized the EEA (small communities; subsistence through hunting of game and the gathering of other forms of nutrition).

This model of cultural evolution predicts honor norms to be a quasi-universal cultural pattern: patterns of behavior that are robustly manifested despite cultural or

first place. When Dawkins introduced the concept, he cites approvingly the gloss his colleague N. K. Humphrey gave of it: “When you plant a fertile meme in my mind you literally parasitize my brain, turning it into a vehicle for the meme's propagation in just the way that a virus may parasitize the genetic mechanism of a host cell.” (Dawkins 1976, p. 192) It's also the construal of memetics that was later promoted enthusiastically to a broader audience (e.g. Blackmore 1999). So with these caveats in mind, it is fair to restrict memetics to the view where the human mind is exploited or harvested by memes in much the same way organisms may exploit the physical environment.

⁵ Again, one could attempt a more sophisticated interpretation of memetics here, where the makeup of the human mind can change in response to change in the environment. Human minds are, after all, highly plastic and can develop differently (in some respects) in different cultures. This interpretation of memetics would account for how some variants find more “fertile soil” in some cultures rather than others. However, this interpretation runs into the same problems as the interpretation above.

ecological variation.⁶ These are the predictions that are born out, with some plausibility (though not without controversy) with regards to mating preferences and strategies that differ (on a population level) between male and female genders and with regards to perception and reactions to social status and reputation (Buss 2019). Hence one would expect similar patterns with regard to the distribution of honor norms and behaviors. (Linguist finds little support for this prediction in the data he considers.)

Dual-Inheritance Theory. The third model is gene-culture dual inheritance theory (DIT). The paradigmatic phenomenon for DIT is the spread lactose tolerance in human populations, since this involved the spread of the alleles responsible for the lifelong ability to digest lactose, as well as the spread of know-how regarding animal husbandry. Lactose tolerance thus must be explained through genetic evolution as well as cultural evolution working in tandem. In DIT there are two units of selection that propagate through two forms of inheritance: genotypes through genetic inheritance (i.e., biological reproduction) and cultural variants through cultural inheritance (i.e., social learning). In contrast to memetics, the cultural variant is not conceptualized as the unit of selection; rather, the variant is a property that affects the fitness of the *biological* unit of selection. Depending on one's view of natural selection this may be the individual or the genotype. The predictions of DIT are close to those of CNCT and are discussed next.

Cultural niche construction theory. The fourth model is cultural niche construction theory (CNCT), where the idea is that cultural variants allow humans to create both social and ecological niches. For instance, a skill such as knowing how to construct artificial shelter allows humans to carve out new ecological niche in colder climates. However, niches can also concern social roles or functions: a skill such as shamanism allows individuals to carve out social niches in communities with a division of labor. As in the case of DIT, in CNCT the units of selection consist of both cultural variants and genotypes.

⁶ Again, also evolutionary psychology could be interpreted in a more sophisticated fashion, where some plasticity would be allowed for. Thus the expression of cognitive modules might modulate in response to varying environmental input. However, the more plasticity is allowed, the weaker the distinctive explanatory power of evolutionary psychology is, and the more one needs to refer to concepts such as social and individual learning which feature more centrally in gene-culture inheritance theory and cultural niche construction theory.

How do DIT and CNCT differ? Here it can be proposed (and this is where I depart from Linquist's presentation) that they differ in their conceptualization of the selective environment. In CNCT, the selective environment has an explicitly cultural character: behavior adapts to the norms in the social environment, and one norm can evolve to adapt to other, more established norms. By contrast, in DIT, the selective environment does not have this cultural component. The environment that determines the coevolution of genes for lactose tolerance and animal husbandry behaviors is an ecological environment: for instance, consisting of those agricultural variables that determine whether the environment can support cattle. In their original presentation of DIT, Boyd and Richerson characterize the selective environment in physical terms. In particular, they refer to high frequency temporal and spatial heterogeneity as the property of the environment that cultural evolution (but not genetic evolution) can accurately track (Boyd and Richerson 1985, chapter 4).

For Linquist, the difference between DIT and CNCT lies in the degree of functional integration of the cultural variants. In dual inheritance theory, cultural variants evolve as autonomous units, and have a more one-to-one relation to behavioral patterns. By contrast, in cultural niche construction, cultural variants form interlocking complexes or "traditions" to which individual human beings then adapt. Because humans adapt to the complex whole, a change in one of the elements of the tradition may not produce any material change in behavior. Honor cultures thus are characterized by reputation-maintenance norms (views on what types of response to behavior or threat may be considered "normal"), gender norms (views on what "normal" female and male behaviors are), and educational norms (what views can be passed on to the next generation). All of these tend to coincide, but on the cultural niche construction theory, a variation in, say, gender norms might not produce material change in behavior.

I believe this to be an accurate analysis, but incomplete in that it does not account for why functional integration matters. On my account, functional integration is what ensures that cultural complexes become decoupled from individual behavior, in such a way that cultural complexes become constitutive of the selective environment for individual humans. In other words, in CNCT but not in DIT, there is a "cultural selective environment" that is distinguishable (though not entirely separate) from the "physical-ecological selective environment". In DIT, cultural variants are units of selection, but in CNCT cultural variants do not evolve as autonomous units in response

to ecological change, but instead interlock and decouple both from individual behavior and ecological change. This is why ensembles of cultural variants can be conceptualized as a selective environment acting on individuals.

There are other accounts of the difference between DIT and CNCT. Sterelny accounts for the difference in terms of “cultural scaffolding” (Sterelny 2003), where the transmission of complex cultural require guided learning where the cultural variant is broken down into components which then can separately be imitated. For instance, manufacturing stone hand axes is a process composed of multiple steps, each of which are taught separately. Thus, for the cultural variant of stone hand axes to be transmitted, and the associated niche it allows for, there must be a teacher that acts as a scaffolding for this transmission process. (And once the transmission is complete, the scaffolding can be removed: hence the term “scaffold”.) This account reduces to Linquist’s notion of functional integration, since each one of the pedagogical components of stone hand axe construction may be transmissible but is useless, and they only assume functional value when they are integrated into a whole. It also reduces to my proposal in the following sense: the learning process set up by the teacher (i.e., the scaffolding) forms a “cultural selective environment”, to which the learner must adapt (and which the learner does not construct or affect through their own activities) and which follows a rate of change that is decoupled from change in the ecological environment.

Table 1 summarizes this discussion of the four models of cultural selection. The explanandum target by all four models is the observed pattern of human behavior across cultures, but different explanantia are posited. In particular, different types of environment are posited to play the role of “selective environment”.

Model	Explanans		
	Unit of selection	Mode of Inheritance	Selective environment
Memetic	Cultural variants	Social learning	Human minds (preferences of various kinds: biased cognitive mechanisms, prejudices, needs, desires)
Evolutionary psychology	Genotypes (esp. those predisposing the canalized development of certain cognitive programs)	Genetic	Ancestral socio-ecological environment (esp. that of hunter-gatherer societies: the EEA)
Dual inheritance theory	Cultural variants and Genotypes/Individuals*	Social learning and genetic	Ecological environment

Cultural niche construction	Cultural variants and Genotypes/ Individuals*	Social learning and genetic	Cultural environment (proximal)	Ecological environment (distal)
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Table 1: Explanans categories across cultural evolution models. The explanandum for all four models is the same: patterns of human behavior, both across as well as within cultures.

* For purposes here, genotypes and individuals can be considered as equivalent units of selection.

3.2 Ontological disunity

What is the selective environment in cultural evolution? The lesson from the preceding discussion is that there is no single answer to the question. It does seem possible to pin down the *kind of thing* a selective environment is. There are different models of cultural evolution, which make different empirical predictions which may or may not be borne out by the empirical observations.

In biological settings, it can be difficult to pin down what processes or features of the environment can be considered as part of the selective environment when there is a lot environmental heterogeneity (Desmond 2022); however, it is not in doubt that the selective environment possesses a spatial character. It refers to processes “outside of” different organisms that impact fitness differentials. By contrast, in the context of cultural evolution, it seems undecided whether the selective environment has a spatial nature. In some models of cultural evolution, such as dual inheritance theory (or at least, according to the construal above), the selective environment has a relatively straightforward spatial character. By contrast, in memetics, the selective environment consists of an ensemble of cognitive mechanisms. The meme itself is not a tangible entity occupying a certain volume of space: Dawkins characterized it as a “unit of information residing in the brain” (Dawkins 1982, 109).

Whether a selective environment is made up of cognitive mechanisms, or of ecological processes, or of some ensemble of social norms, seems to mainly depend on explanatory purposes. In the specific case of evolution of honor norms, Linquist concludes that cultural niche construction theory best predicts the data given by the Human Relations Area File (Linquist 2016, 230–34). Evolutionary psychology is discounted by evidence that differences in norms of aggression do not always correlate with the distinction between pastoral and horticulturalist conditions (Linquist 2016, 233–34). This suggests that there is no automatic cognitive module responsible for

honor norms that is triggered by specific conditions. Dual inheritance theory, in turn, is discounted by the fact that specific norms towards aggression covaried with the behavior that parents expected or tolerated among children. This suggests that there is something as a “cultural environment”, and not just distinct cultural variants, that is responsible for the spread and maintenance of honor norms.

Even if cultural niche construction theory may offer the best explanation of the evolution of honor norms, that does not mean that CNCT is the best theory of cultural evolution. For instance, if one were to explain the dynamics of some fashion trend that seems to run counter to some aspect of normal biological functioning – think of as the practice of foot binding – memetics would seem to be an elegant and parsimonious explanatory model for that phenomenon. Alternatively, if one were to explain why individuals attach great importance to social status – regardless of culture, gender, age, or personality (see Anderson, Hildreth, and Howland 2015) – the model offered by (canonical) evolutionary psychology might offer a more appropriate explanation. It would seem appropriate to explain our desire for status by referring to our ancestral hunter-gatherer environment in which cooperation was crucial for reproduction and survival and where one needed to maintain status in the eyes of others in order to be included in collaborative networks.

In sum, it does not seem fruitful to try to pin down what “things” the generalized selective environment empirically refers to. The selective environment can be generalized in many different ways, and no single ontological property seems to be held in common by these various generalizations of the selective. One cannot even claim that the selective environment *surrounds* or *envelops* the organism in any basic spatial sense (this was the original rationale for speaking of “the” environment). For instance, in memetics, the unit of selection (meme) supervenes on its environment (human brain). And it makes no sense to either affirm or deny that the human brain envelops a meme in any spatial sense. Thus, attempts to pin down any “real” distinction between unit of selection and selective environment -- in the way that the temperature, moisture, acidity of the soil and atmosphere constitute the “environment” of a plant – only runs into frustration in the generalized setting.

5. The Contrast class: Agential explanations of Honor Culture

The preceding discussion could give credence to a pluralist and instrumentalist reading of the generalized selective environment: the selective environment simply refers to a multitude of environment concepts that can be used if they are explanatorily expedient. On this view, the selective environment is a modelling tool, but not much more can be said of it. However, even if we accept this view, it raises a further question that cannot be easily answered in a pluralist-instrumentalist fashion: what *epistemic* or *explanatory* features are held in common by the different generalizations of the selective environment? The question to ask is, under what conditions can the concept of selective environment – regardless of how precisely it is generalized – be dispensed with in scientific explanations?

In the remainder of the paper, I would like to develop the idea that the correct contrast class of selectionist explanations is agential explanations. For instance, the contrast class for explaining honor norms as an outcome of evolution by natural selection is explaining honor norms as the product of a reasonable deliberation (or lack thereof) by an agent. An agential explanation thus appeal to the *intentions* and/or *reasons* humans have for adhering to or rejecting honor norms. What agential explanations mean in non-human biological context is a different and ongoing question (see also Desmond and Huneman 2020), but for purposes of this paper can simply be construed as explaining organismic behavior *as if* the organism were acting like an intentional agent.

Even in human context, agential explanations may assume different forms. As an illustration, consider two types of explanation of honor cultures, “pragmatic explanations” and “moral explanations”. In *pragmatic explanations*, the behavior is explained by (1) an agent acting to maximize benefit (however defined), and (2) the belief of the agent that the explanandum behavior maximizes benefit. In order to apply this to the case of honor norms, we can introduce some more detail from Nisbett and Cohen’s classic account of honor culture in the Southern United States. According to their account, violent responses (or threats thereof) to reputational threats can be understood as a (rational) strategy of deterrence of future threats. Thus, a pragmatic explanation refers to a process of adaptation to the social environment, but the process of adaptation is not explainable by natural selection alone. Rather, honor cultural is produced by rational agents that perceive and understand certain challenges in their social environment and choose their response accordingly. The agent may make mistakes, and wrongly calculate which strategy is the benefit-maximizing one.

However, also here the core explanans is the agential reasoning process. No reference needs to be made to a selective environment (such as a socioecological environment): the “ought” of agential reasoning screens off the “is” of the selective environment.

Such pragmatic explanations are most familiar to evolutionary thinkers, as they are interpreted as the “maximizing agent analogy”, a shorthand for a selectionist explanation (Sober 1998; Martens 2016; Okasha 2018). However, pragmatic explanations – as I intend them – do not involve the maximizing agent analogy. This analogy may hold for a human whose behavior is determined by automatic modules shaped in the ancestral environment, but such a human is in that case not manifesting itself as an agent because their behavior can be entirely explained by the inputs from their immediate environment interacting with a trait shaped by natural selection.

The contrast between selectionist and agential explanations is even clearer when it comes to moral explanations of behavior. *Moral explanations* refer to a different type of reasoning principle compared to that inherent in pragmatic explanations: the agent acts not in order to maximize benefit, but in order to maximize a moral value.⁷ What could a moral explanation of honor culture look like? One version of a moral explanation could assume that honor is an intrinsic good that can and should be pursued for its own sake, independently of any type of personal benefit, whether wealth, avoidance of suffering, or even happiness. And as Dan Demetriou documents, this is exactly how individuals inhabiting honor cultures experience honor norms (Demetriou 2014). They construct an honor *morality*, consisting of various norms, including the norm of fair play in honor competitions, or the norm that one should respond to challenges to one’s honor (Demetriou 2014, 902). The moral explanation of the evolution of honor morality is that honor cultures are *morally right*, and that agents have simply chosen to live in accordance with this moral truth.

However, this is not the only possible moral explanation of honor cultures. If one adopts liberalism as the background moral framework, the value of human autonomy is prioritized over honor. The core norms in a liberal society are norms such as: the right to property or the right to pursue one’s life as one sees fit (without harming others). From the perspective of a liberalism, honor cultures would simply appear to be *morally wrong*. However, this is also a type of moral explanation of the evolution

⁷ On this analysis, utilitarianism could be seen as an intersection between pragmatic and moral explanations (“benefit” is narrowly defined as pleasure and pain, which is an intrinsic good in for instance hedonistic utilitarianism). By contrast, for a deontologist such as Kant, there is a clear distinction between benefit (pleasure, success, power) and the good (the good will).

honor cultures: honor cultures are explained as due to a lack of moral agency. The individuals in honor cultures are “biased”, “prejudiced”, or “ignorant”: and this state of affairs may in turn be explained by a lack of education by material deprivation. In other words, if one adopts the assumptions of a liberal morality, the main explanans in such a (liberal) moral explanation is the widespread presence of a curtailed or truncated agency, such that individuals are incapable of (morally) reasoning correctly.

Although it will not be further pursued here, this line of argumentation suggests where the tension between evolutionary (selectionist) and traditional rationalist perspectives on morality should be sought: not in issues about the existence or nonexistence of objective moral truth (e.g. Street 2006; Sterelny and Fraser 2017), but in the competition between two types of explanation -- selectionist and agential -- for the status of the best explanation of behaviors which appear to be driven by moral reasoning. An agent may *believe* that their behavior is driven by moral reasoning, but the question at hand is whether their behavior is *in fact* driven by moral reasoning. Selectionist explanations explain away moral reasoning as a secondary phenomenon, and locate the true causes in cultures and norms evolving to adapt to certain ecological conditions. Taking such a selectionist stance on the evolution of honor cultures seems to be relatively uncontroversial; by contrast, the selectionist stance on the evolution of liberal morality is of course much more controversial, where the dominant view is that the rise of liberal morality must be explained agentially.

In sum, in agential explanations, the main explanans is the agent and its process of reasoning or deliberation. This suggests a more general, yet more accurate way of characterizing the generalized selective environment, namely as an explanatory principle that screens off any need to appeal to agency. This account is developed in more detail in the next section.

6. Generalized Selective Environment

Based on these considerations, we can now propose an account of the generalized selective environment:

The **generalized explanatory function** of the selective environment is to be used as an explanans of adaptive evolution in such a way that agential causes of adaptation are screened off.

This explanatory function can be realized in different ways: some selective environment concepts screen off the role of agency *entirely*, whereas others only do so partially. Let us first apply this account to the models of cultural evolution previously discussed. Then, I will suggest how the generalized selective environment can be understood even more generally, in contrast to three forms of agency: divine agency, organismic agency, and human agency.

6.1 The selective environment in various models of cultural evolution

What does the selective environment “do” in the various models of cultural evolution? Let us start with memetics. Here the selective environment is represented by the human mind as a resource to be harvested, exploited, parasitized, invaded. In other words, not only is there no role for human agency, but the human mind is represented as an entirely passive quantity, like a natural resource that can be mined. Any explanatory role that some reasoning process *could* play is screened off by the exploitable cognitive modules involved in that reasoning process. The *gestalt*-switch involved here is that an active reasoning process is presented as a process that is controlled by memes. This control by memes becomes the explanans that screens off the explanans of human agency. (The only problem is that this mode of explanation has only limited success, and somewhat surprisingly Dawkins affirms the reality of moral agency and thus implies that memetics has limited explanatory scope (Dawkins [1976] 2006, 2).)

In evolutionary psychology, agency is not necessarily an epiphenomenon as it is in memetics—reason itself, after all, may be the outcome of a process of selection (Mercier and Sperber 2017) – but again agency does not play any crucial explanatory role. There are of course rather extreme and implausible construals of evolutionary psychology where all human behavior is determined by cognitive modules. However, even the more plausible explanations in evolutionary psychology concern the explananda where it is potentially plausible to screen off the role of human agency. For instance, in being attracted to certain properties in potential mates, men and women may believe they *themselves* are the source of this desire or preference. For instance, they may believe they are attracted to the opposite sex because of “beauty”. However, evolutionary psychology explains away such reasoning processes as secondary

phenomena that produced by cognitive modules for mate preference that were shaped by natural selection in the ancestral environment.

Both dual inheritance theory and cognitive niche construction theory also screen off agency as explanans, but do so in subtly differing ways. Both posit the importance of social learning, and thereby imply that a lot of human behavior can be explained through the presence of external cultural norms (and variants). However, DIT and CNCT have different construals of the process of social learning, and thus screen off agency in different ways. In DIT, the tendency is to model the spread of cultural variants (such as animal husbandry know-how) as a diffusive process: individuals imitate successful cultural variants. Here there is no explanatory need to invoke real intentionality or choice.⁸ In CNCT, by contrast, there seems to be a limited role for agency. If an individual learns to construct stone hand axes in a certain way, then this is partially due to the existence of a selective cultural environment, to which individuals have no choice but to adapt. In this respect, cultural niche construction screens off the explanatory role of human agency. However, during the social learning process, the individual cannot necessarily be adequately represented as a passive receptacle for the knowledge imparted by the teacher. For instance, the skill of hand axe construction needs to be divided into component parts, and while each of these component skills could perhaps be learned by a process of imitation, the learner is still responsible themselves for the integration of the component skills. Thus, the learner is conceptualized as an agent in this limited respect. Nonetheless, cultural evolutionary theory, by explaining the adaptiveness of human behavior through natural selection (and selection by the environment), serves to undermine the idea that humans are autonomous, self-determining agents (this relation between cultural evolutionary theory and autonomy is explored further in Desmond 2021b).

How does this contrast between agential and selectionist explanations play out more generally? How does this help to revisit the selective environment in biological context from a new perspective? The following three sections distinguish between three broad categories of agency: divine, organismic, and human agency.

⁸ Of course, this statement is conditional on the underlying cognitive neuroscience of imitation (see Frith et al. 2003). Can imitation be fully explained in a basic mechanistic way, such as in terms of firing up mirror neurons? Or does one need to also refer to the capacity to create mental representations of the skill in order to successfully imitate it? In the latter case, some agential capacity creeps in.

5.2 Screening off Divine Agency

It may seem strange to include divine agency in the list, but screening off divine agency was, historically, the most important feat of Darwin's theory of natural selection. Darwin's contemporaries (e.g. Paley) were concerned whether adaptive complexity in nature required divine agency as an explanans. They were aware that human agency could lead to significant evolution within domesticated species (e.g., the varieties of dog bred through artificial selection on the European wolf). However, it was unclear how the adaptive complexity found across wild species could be explained through anything other than divine agency.

The concept of natural selection provided a plausible alternative explanation, which did not involve a Paleyan divine agency who designed organisms like a master watchmaker might design a watch. Against this background, a lot of the initial explanatory force of *On the Origin of Species* can be understood as charting an explanatory course that makes such divine agency superfluous. Explanations by natural selection did not involve any action from an agent, but rather what some philosophers have called population-thinking (Ariew 2008): a sufficiently long succession of a large number of insensible variations, some with a slight edge over others, that over time leads to large changes.

5.3 Screening off Organismic Agency

Invoking the selective environment can also function as a way to screen off organismic agency. Historically, this explanatory role positioned natural selection as rival to Lamarckian adaptation (where actions of the organism would determine evolution). However, the screening off of organismic agency by natural selection has never been as conclusive as that of divine agency. Moreover, Darwin himself seemed to hesitate. While it is relatively clear that Darwin did not believe in the necessity to invoke divine agency as an explanans, he is much more ambivalent about organismic agency. For instance, there are suggestive passages in the *Descent of Man* where he ascribes an evolutionary role to aesthetic preferences independently on their impacts on fitness (roughly: peacock tails are explained because peahens find them beautiful, and not because peahens have been shaped by natural selection to select for costly signals of fitness).

Today, many of the developments in the extended synthesis, ranging from niche construction (Laland, Matthews, and Feldman 2016) to plasticity-first evolution (Levis and Pfennig 2016; West-Eberhard 2003), suggest that organisms may have an “active” role to play in explanations of adaptive evolution, in such a way that their role cannot simply be reduced to processes of natural selection. From the perspective of this paper, such developments in biological thinking show that that doubts remain whether organismic agency can be entirely screened off as explanans in evolutionary explanations.

For instance, take phenotypic plasticity, one of the core phenomena deemed to illustrate the “active” role that organisms can play. Phenotypic plasticity need not be agential, and in some instances can be perfectly well explained as the product of natural selection. Think of the adaptive elongation of a plant stem in response to an environmental input. Is agency really indispensable to account for this process of development adaptation? Referring to a developmental mechanism shaped by natural selection may suffice. However, the selective pressure for plasticity is only well-defined when the environmental patterns of heterogeneity are themselves well-defined (in the sense described in Desmond 2022, in turn drawing on Levins 1968). Forms of phenotypic plasticity that produce adaptive behavior in ill-defined heterogeneous environments would be good candidates for agential forms of plasticity. So, whether the principle of natural selection truly succeeds in screening off organismic agency remains an open question.

5.4 Screening off Human Agency

As the selective environment is generalized to new domains, the screening off of human agency more obviously becomes the most important explanatory dimension of the selective environment. After all, in many of the domains “invaded” by evolutionary, human agency plays a core explanatory role. The list of novel evolutionary domains in introduction to this volume amply demonstrates this: economics, anthropology, sociology, psychology, epistemology, ethics, aesthetics, literary studies, archaeology, history, history of science, history of technology. These domains are traditionally analyzed to significant extents by various processes of human agency (e.g., the intentions of an author, the intentions of historical figures, the personality and past

experiences of an individual). In evolutionary approaches, such agential processes are typically bracketed. This is illustrated in Table 2.

Domain	Explanandum	Classic Explanans (agent)	Darwinian explanans (selective environment)
Economics	Formation of corporations Division of labor	Utility-maximizing agents	Markets
Sociology	Structure of institutions	Group agency	Socio-ecological environment
Literary studies	Structure of a text	The intentions of the author; the norms and values of the author's contemporaries	Socio-ecological environment
History	Salient events in human past	Human agents	Ecological or socio-ecological environment
Epistemology	Claims to "know" certain propositions	Rational agent deliberating about evidence and prior beliefs	Socio-ecological environment where such claims give some advantage (biological fitness, social status, power)
Ethics	Endorsements of certain actions as "good".	Rational agent deliberating about standards of good	Socio-ecological environment where such endorsements give some advantage (biological fitness, social status, power)
Aesthetics	Endorsements of certain objects as "beautiful"?	Rational agent deliberating about standards of beauty	Socio-ecological environment that associates those objects with an advantage (biological fitness, social status, power)
History of science/technology	Patterns of adoption and rejection of ideas and technologies	Rational agents deliberating about the merits and demerits of ideas and technologies	The ensemble of mechanisms, biases, preferences characterizing human minds

			OR The socio-ecological environment where ideas and technologies may give benefits
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Table 2: A contrast between evolutionary and “traditional” approaches in terms of different explanantia, for a selection of domains in the humanities and social sciences.

In a second category of domains, briefly illustrated in Table 3, the “evolutionary” approach consists of replacing the human designer by a selective environment. These evolutionary approaches do not *entirely* banish human agency, as the human agent is still expected to engineer the selective environment.

Domain	Goal	Classic approach (agent)	Darwinian approach (environment)
Evolutionary medicine	Health-promoting interventions on the human body	Medical scientist who understands physiological mechanisms, and can manipulate outcomes accordingly.	Set of ecological factors that favor certain physiological mechanisms over others
Evolutionary computation	Efficient algorithms	Computer scientist who designs an algorithm that produces a solution.	Set of incentives (or values) that favor some possible solutions over others.

Table 3: A contrast between evolutionary and “traditional” approaches in terms of different explanantia, for a selection of domains in the medical and engineering sciences.

This characterization of evolutionary approaches beyond evolutionary biology helps account for why evolutionary approaches in sciences such as physics or chemistry have seen so little uptake. This is not self-evident if one analyzes generalizations of Darwinism in terms of the abstract criteria of variation, differential reproduction, and inheritance (e.g. Hodgson and Knudsen 2006). There is nothing in these criteria that would predict why the principle of natural selection is taken up so

enthusiastically in comparative psychology but so much less so in solid-state physics. It is not that natural selection cannot be applied: for instance, Quantum Darwinism uses natural selection to offer a resolution, or at least a frame of analysis, of the measurement problem (Blume-Kohout and Zurek 2006). So why has the application of Darwinian explanatory schemes to psychology spawned a whole subfield in the way that Quantum Determinism has not? The explanatory function of the selective environment suggests why: agency has never played any explanatory role in modern physics or chemistry, and hence there was no explanatory need for natural selection.

A full detailed analysis of how natural selection is applied in these various domains may not be possible here; however, it is plausible to expect that the screening off of human agency will never be entirely successful when it comes to individual and social human phenomena. Evolutionary approaches are never likely to completely displace “traditional” approaches.

7. Conclusion

One of the roadblocks preventing a fruitful analysis of selective environment in a generalized setting is that it is an ontologically disunified concept. The various models of cultural evolution demonstrate how the selective environment may be identified with the minds that cultural variants infect (memetics), or with the socioecological environment of hunter-gatherers (evolutionary psychology), or with a collection of the social norms and ecological features impacting the biological fitness of individual humans (dual inheritance theory). It does not seem fruitful to look for spatiotemporal processes held in common by these various selective environments. Instead, this paper sought to unify various generalizations of the selective environment through *explanatory* they fulfill. I argued that this function is essentially contrastive: the selective environment supplants agency as the dominant explanans. This account of the generalized selective environment captures very well what Darwin originally intended with his concept of natural selection (supplanting divine agency), and captures how the concept of natural selection was further developed in the Modern Synthesis (with the effect of supplanting organismic agency). Today, it is especially as a rival to human agential explanations that the theory of natural selection is attracting most attention.

However, the screening-off of human agency does not happen uniformly, and can be done in different ways for different phenomena. Acknowledging these differences, and with it, the different ways the selective environment can be invoked as explanatory principle, can help avoid confusion associated with attempts to find what characterizes “the Darwinian” approach. While one could arguably identify a “pure” Darwinian approach with screening off agency entirely (i.e., doing to human agency what Darwin did to divine agency), in practice, fruitful Darwinian approaches in domains such as psychology or anthropology will only screen off agency partially, and will sometimes model humans as resources to be exploited, and sometimes as expressions of underlying cultural variants.

References

- Aaby, Bendik Hellem, and Hugh Desmond. 2021. “Niche Construction and Teleology: Organisms as Agents and Contributors in Ecology, Development, and Evolution.” *Biology & Philosophy* 36 (5): 47. <https://doi.org/10.1007/s10539-021-09821-2>.
- Abrams, Marshall. 2009. “What Determines Biological Fitness? The Problem of the Reference Environment.” *Synthese* 166 (1): 21–40. <https://doi.org/10.1007/s11229-007-9255-9>.
- Anderson, Cameron, John Angus D. Hildreth, and Laura Howland. 2015. “Is the Desire for Status a Fundamental Human Motive? A Review of the Empirical Literature.” *Psychological Bulletin* 141 (3): 574–601. <https://doi.org/10.1037/a0038781>.
- Ariew, André. 2008. “Population Thinking.” In *The Oxford Handbook of Philosophy of Biology*, edited by Michael Ruse. <https://doi.org/10.1093/oxfordhb/9780195182057.003.0004>.
- Baedke, Jan, Alejandro Fábregas-Tejeda, and Guido I. Prieto. 2021. “Unknotting Reciprocal Causation between Organism and Environment.” *Biology & Philosophy* 36 (5): 48. <https://doi.org/10.1007/s10539-021-09815-0>.
- Blackmore, Susan. 1999. *The Meme Machine*. Oxford: Oxford University Press.
- Blume-Kohout, Robin, and W. H. Zurek. 2006. “Quantum Darwinism: Entanglement, Branches, and the Emergent Classicality of Redundantly Stored Quantum Information.” *Physical Review A* 73 (6): 062310. <https://doi.org/10.1103/PhysRevA.73.062310>.
- Bourrat, Pierrick. 2020. “Natural Selection and the Reference Grain Problem.” *Studies in History and Philosophy of Science Part A* 80 (April): 1–8. <https://doi.org/10.1016/j.shpsa.2019.03.003>.
- Boyd, Robert, and Peter Richerson. 1985. *Culture and the Evolutionary Process*. Chicago: The University of Chicago Press.
- Brandon, Robert N. 1990. *Adaptation and Environment*. Princeton University Press.
- Buss, David M. 2019. *Evolutionary Psychology: The New Science of the Mind*. 6th Edition. New York: Routledge.

- Darwin, Charles. 1875. *The Variation of Animals and Plants Under Domestication*. 2nd ed. London: John Murray.
- Dawkins, Richard. 1982. *The Extended Phenotype: The Long Reach of the Gene*. Oxford University Press.
- . (1976) 2006. *The Selfish Gene*. Oxford University Press.
- Demetriou, Dan. 2014. “What Should Realists Say About Honor Cultures?” *Ethical Theory and Moral Practice* 17 (5): 893–911. <https://doi.org/10.1007/s10677-014-9490-3>.
- Desmond, Hugh. 2018. “Selection in a Complex World: Deriving Causality from Stable Equilibrium.” *Erkenntnis* 83 (2): 265–86. <https://doi.org/10.1007/s10670-017-9889-z>.
- . 2021. “In Service to Others: A New Evolutionary Perspective on Human Enhancement.” *Hastings Center Report* 51 (6): 33–43. <https://doi.org/10.1002/hast.1305>.
- . 2022. “Adapting to Environmental Heterogeneity: Selection and Radiation.” *Biological Theory* 17: 80–93. <https://doi.org/10.1007/s13752-021-00373-y>.
- Desmond, Hugh, and Philippe Huneman. 2020. “The Ontology of Organismic Agency: A Kantian Approach.” In *Natural Born Monads: On the Metaphysics of Organisms and Human Individuals.*, edited by Andrea Altobrando and Pierfrancesco Biasetti, 33–64. Berlin: De Gruyter.
- Frith, C.d., D.m. Wolpert, Andrew N. Meltzoff, and Jean Decety. 2003. “What Imitation Tells Us about Social Cognition: A Rapprochement between Developmental Psychology and Cognitive Neuroscience.” *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 358 (1431): 491–500. <https://doi.org/10.1098/rstb.2002.1261>.
- Futuyma, Douglas J., and Mark Kirkpatrick. 2017. *Evolution*. Sunderland: Sinauer.
- Hodgson, Geoffrey M., and Thorbjørn Knudsen. 2006. “Why We Need a Generalized Darwinism, and Why Generalized Darwinism Is Not Enough.” *Journal of Economic Behavior & Organization* 61 (1): 1–19. <https://doi.org/10.1016/j.jebo.2005.01.004>.
- Hull, David L. 1988. *Science as a Process: An Evolutionary Account of the Social and Conceptual Development of Science*. University of Chicago Press.
- Laland, Kevin, Blake Matthews, and Marcus W. Feldman. 2016. “An Introduction to Niche Construction Theory.” *Evolutionary Ecology* 30: 191–202. <https://doi.org/10.1007/s10682-016-9821-z>.
- Levins, Richard. 1968. *Evolution in Changing Environments: Some Theoretical Explorations*. Princeton, NJ: Princeton University Press.
- Levis, Nicholas A., and David W. Pfennig. 2016. “Evaluating ‘Plasticity-First’ Evolution in Nature: Key Criteria and Empirical Approaches.” *Trends in Ecology & Evolution* 31 (7): 563–74. <https://doi.org/10.1016/j.tree.2016.03.012>.
- Linquist, Stefan. 2016. “Which Evolutionary Model Best Explains the Culture of Honour?” *Biology & Philosophy* 31 (2): 213–35. <https://doi.org/10.1007/s10539-015-9515-x>.
- Martens, Johannes. 2016. “Inclusive Fitness and the Maximizing-Agent Analogy.” *The British Journal for the Philosophy of Science*, June, axw003. <https://doi.org/10.1093/bjps/axw003>.
- Mercier, Hugo, and Dan Sperber. 2017. *The Enigma of Reason*. Cambridge, Massachusetts: Harvard University Press.
- Okasha, Samir. 2018. *Agents and Goals in Evolution*. Oxford: Oxford University Press.

- Pearce, Trevor. 2010. "From 'circumstances' to 'Environment': Herbert Spencer and the Origins of the Idea of Organism-Environment Interaction." *Studies in History and Philosophy of Biological and Biomedical Sciences* 41 (3): 241–52. <https://doi.org/10.1016/j.shpsc.2010.07.003>.
- Pradeu, Thomas. 2012. *The Limits of the Self: Immunology and Biological Identity*. Oxford ; New York: Oxford University Press.
- Ridley, Mark. 2004. *Evolution*. 3rd ed. Malden, MA: Blackwell Publishers.
- Sober, Elliott. 1998. "Three Differences between Deliberation and Evolution." In *Modeling Rationality, Morality, and Evolution*, edited by Peter Danielson, 15. New York: Oxford University Press.
- Spencer, Herbert. 1855. *The Principles of Psychology*. Williams and Norgate.
- Sterelny, Kim. 2003. *Thought in a Hostile World: The Evolution of Human Cognition*. Wiley.
- Sterelny, Kim, and Ben Fraser. 2017. "Evolution and Moral Realism." *The British Journal for the Philosophy of Science* 68 (4): 981–1006. <https://doi.org/10.1093/bjps/axv060>.
- Street, Sharon. 2006. "A Darwinian Dilemma for Realist Theories of Value." *Philosophical Studies* 127 (1): 109–66. <https://doi.org/10.1007/s11098-005-1726-6>.
- Walsh, Denis. 2015. *Organisms, Agency, and Evolution*. Cambridge: Cambridge University Press. <https://doi.org/10.1017/CBO9781316402719>.
- West-Eberhard, Mary Jane. 2003. *Developmental Plasticity and Evolution*. New York, NY: Oxford University Press.