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# Darwin endures, despite disparagement

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## ABSTRACT

*Evolution lies at the heart of the life sciences, and Charles Darwin is a towering historical figure within evolutionary science. One testimony to his lasting influence is that declaring Darwin to have been wrong all along remains a provocative way to command attention. The present paper discusses various strands of “Darwin was wrong” partisans and their divergent views and motives: some are looking to Darwin to justify or condemn the political ideologies that they support or reject; others are concerned with the corrupting influence that the bleak cosmic outlook of evolution is deemed to exert on the moral or religious rectitude of impressionable minds, or regard Darwinism as a direct assault on religion; philosophers question the very coherence of the entire enterprise; and certain biologists aspire to go down in history as even greater than Darwin. It is sobering to reflect that this diverse group is united only by their poor grasp of Darwin’s theory of natural selection.*

Keywords: *Charles Darwin, Social Darwinism, evolution, creationism, Alvin Plantinga, Jerry Fodor*



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## 1 Introduction

Charles Darwin is one of the few scholars who have become emblematic of an epoch-making scientific innovation. It is true that such icons tend to attract more than their fair share of the credit, but they also become a lightning rod for the misgivings evoked by the paradigm shift they represent. Since Darwin’s theory of natural selection seems to have something to say on several aspects of life, at least in the eyes of the disgruntled, the sport of “Darwin bashing” continues to this day. Interesting historical, philosophical, religious, and scientific questions tend to get caught up in the melee, and here I propose to separate some of the wheat from the chaff, with a view mainly directed towards elucidating misconceptions and highlighting outstanding conceptual difficulties associated with evolutionary theory, rather than gratuitously exposing the errors of the anti-Darwinists.

## 2 Social Darwinism and myth-making

“If you take seriously that evolution has to do with the transition of life forms, and that life and death are just natural processes, *then* one gets to be liberal about abortion and euthanasia. All of those kinds of ideas seem to me to *follow* very naturally from a Darwinian perspective—a deprivileging of human beings, basically.”<sup>1</sup> The added italics emphasise where the speaker, sociologist S. Fuller, commits the naturalistic fallacy of viewing natural phenomena (facts, processes, mechanisms) as somehow justifying or motivating normative positions, e.g. on abortion or euthanasia, or that human beings are less special because their biological make-up points to kinship with other forms of life. However, one simply cannot conclude that anything *ought to be so* in the affairs of humans because *it is so* in those of Nature, even if we are in the final analysis part of Nature.

If the naturalistic fallacy were admissible, then perhaps science might claim credit for many a lofty ideal? Alas, it is often made a scapegoat: “Compassion and empathy leads you to a very glorious place, and science leads you to killing people” according to political activist B. Stein<sup>2</sup>. For instance, the mechanism of evolution can be characterised, somewhat uncouthly, as “selective breeding” and those who would apply this to civilised society might hide behind Darwin, even if selective breeding of animals and plants predates Darwin and, indeed, was a major source of inspiration for his theory. Are we to believe that eugenics would never have occurred to the noble minds of political thinkers had it not been for the corrupting influence of the theory of evolution?

The catch phrase “survival of the fittest” was merely intended as a catchier rendition of “differential survival of individuals, and hence via the effects this has on their life-time reproductive outputs, and thus on the propensity of their types to persist, expand, or perish over trans-generational time.” This complex technical meaning is wholly discarded when “survival of the fittest” becomes, instead, the slogan of Social Darwinism, “a political ideology whose leading advocates take wealth to be a sign of individual and social virtue, whose advocates believe its concentration in fewer and fewer hands is not something for a democratic country to worry about, toy with the idea of getting rid of child-labour laws, regard unemployment and other social insurance as forms of coddling the unworthy poor, and hold health care to be a personal option for which the individual is responsible.”<sup>3</sup> *This* would seem to be a kind of Darwinism that suits the economic right, as opposed to the kind that vexes their friends of the religious right who condemn evolutionary theory for its perceived support for abortion or euthanasia.

Capitalism could equally well be justified by declaring the ability to accumulate wealth through professional success to be a divine sign that one belongs to the Chosen Few. Thus the doctrine of predeterminism becomes the culprit. Far less from shifting the blame to religion, this argument shows that metaphysical ideas, no matter their original intent and provenance, are all too easily gang-pressed into lending respectability to base purposes.



**Figure 1: Bones of contention.** Some creationists continue to reject the fossil evidence outright. Shown here is a specimen of *Rhamphorhynchus*, a long-tailed pterosaur that lived during the late Jurassic.

Still, could it not be said that evolution exudes a particularly nihilistic, barren bleakness that infects and corrupts the moral fibre of the general population, no matter how diligently we lecture on the naturalistic fallacy and similar flaws of reasoning? Would American politician R. Santorum not have a point when he says that, whether or not this is scientifically legitimate, “it is used to promote to a worldview that is anti-theist, that is atheist”<sup>4</sup>?

There are two distinctions to be made. The first is that between a natural phenomenon and a theory that purports to describe it, or bring order to our insights and understanding surrounding that phenomenon. One can take a stance on any number of theoretical approaches towards gravitation, but no sensible person would deny the existence of gravity *qua phenomenon* (or perhaps gravity-deniers are little heard of as they tend to have very bad falls). So it is with evolution: regardless of one’s feelings about any particular theory of evolution, the natural phenomenon as such is well-attested and should be beyond reproach (Fig. 1). This first distinction matters since any inherent bleakness (or grandeur, depending on one’s sensibilities) is already inherent in the facts of the matter.

The second important distinction is that between pragmatic and dogmatic belief. The former is always provisional, held with a less-than-complete degree of confidence, and subject to revision when new empirical evidence becomes available, or else when new insights turn the received wisdom into a quaint and obsolete way of looking at things. There are of course gradations: we can be as sure as anything that gravity and evolution happen, for instance, and we have every reason to expect that future observations will further



**Figure 2: The fifth day of creation.** Woodcut with watercolours by Michael Wolgemut (1493). Does evolution amount to a doctrine that is set to replace religious or humanistic teachings? And is the hand of the creator to be replaced by that of Darwin?

consolidate our confidence in the existence of, say, the Higgs boson or gravitational waves. Dark matter is less well-understood and accordingly no astrophysicist is claiming a definitive understanding. Dogmatic belief, on the other hand, rules out any future revision in advance and demands conviction. The point here is not that dogmatic belief need be inherently inferior: it is possible for a person to practice either of them as circumstances may demand.

Both these distinctions are blurred or even denied in creationist debates, and thus when we hear “belief in evolution” being disparaged, we must wonder whether the speaker intends to speak of pragmatic or dogmatic belief and whether evolution *qua phenomenon* or evolution *qua theory* is meant. Accusations of dogmatism, incidentally, so liberally hurled at evolutionary thinkers, seem to be rhetorical flourishes rather than thoughtful reflections on the distinction evoked here; dogmatism does not mean the mere unwillingness to accede to an untenable position. These two crucial distinctions need not even mean anything at all to the speaker, as seems evident when, for instance, creationist B. Feijen claims that evolution is the *religion* of the atheist<sup>5</sup>.

Historian A. N. Wilson combines the ills of Social Darwinism and the theme of evolution-as-religion by casting Darwin himself as the author of both<sup>6</sup>, offering “the emergent Victorian middle classes a consolation myth [an ersatz religion to the effect that] there was something inexorable, natural about their superiority to the working class.” In particular, “their land-grabs in Africa, their hunger for stock-market wealth in the face of widespread urban poverty, their rigid class system and their ever-lasting wars were not things to be ashamed of, but actually part of the processes of nature.” It is perhaps not surprising that Wilson does not even come close to correctly describing Darwin’s actual theory and fails to achieve basic accuracy with regard to biographical details<sup>7</sup>; but it certainly audacious to lampoon Darwin as the “Victorian mythmaker”: an ambitious (albeit flatulent) social climber who cared little for scientific accuracy and more for currying favour with his contemporaries.

### 3 Progress, complexity, entropy, and statistics

There is an almost irresistible temptation to organise life into a chain of being, proceeding relentlessly and ineluctably from “lower” to “higher” forms. It could well be a primal motif born from marvelling at our own place in the natural world. We readily discern unique abilities in ourselves, and yet we also discern our kinship with other forms of life, according to a decreasing scale of affinity. At the top of this scale we naturally see fit to place ourselves.

This stratified, linear view of life, as a great chain or ladder, recurs throughout the world’s mythologies. A temporal or evolutionary connection in the modern sense, that of descent, is not implied: the idea is rather that of a hierarchy of structural perfection. Nevertheless, the chain motif has become a staple of popular accounts of evolution, exacerbated perhaps by a careless reading of the fossil record. There can be no real objection to theists who would regard evolution as a divinely guided process. However, if we retain the rhetoric, except for replacing every mention of the divine by a reference to natural selection, we are creating an unintended impression that we seek to usurp the supreme being and put Darwin on the throne (Fig. 2). If this conception of evolution were correct, the creationist objections would make rather more sense: we should then have cause to ask what endows the process with such a consistent impetus toward higher forms over the course of millions of years. And, blindly groping for advancement, how is it possible that evolution attains this goal, when natural processes tend not to create order spontaneously? Does this not violate fundamental thermodynamic principles? Actually, spontaneous creation of order is perfectly common-place even in the realm of dead matter: for instance, magnesium sulphate ions dissolving in water create more ordering in hydration shells than they abandon in the solid-form lattice. What matters is not just whether order is created or not, but the sign of the change in thermodynamic potential.

#### 3.1 The Second Law, entropy, and order

If evolution is the attainment of higher order and complexity, it would seem to be reducing entropy, contrary to the law that it must always increase. But only the entropy of the universe as a whole must increase; locally, entropies can and do increase all the time.

It is true that entropic arguments play a substantial role in biological complexity at the molecular level. Consider, for instance, the entropy decrease associated with the formation of a peptide bond: let us suppose that it is about  $25 \text{ J mol}^{-1}\text{K}^{-1}$ . However, amino acids in solution would give rise to a mixture of peptides, whereas the cell requires the amino acid residues in a protein to be in a particular order. This requirement adds a configurational entropy of circa  $-k_B \ln 20 \approx -25 \text{ J mol}^{-1} \text{ K}^{-1}$  per peptide bond, where  $k_B$  is Boltzmann’s constant. In view of the enthalpy change of peptide bond formation ( $\Delta H \approx -14 \text{ kJ mol}^{-1}$ ) this additional decrease in entropy is enough to tip the balance in favour of being thermodynamically unfavourable, as the reader may care to verify, taking e.g.  $T = 300 \text{ K}$

and using the formula  $\Delta G = \Delta H - T \Delta S$  where  $\Delta G$  is the change in Gibbs energy and  $\Delta S$  is the change in entropy. In bioenergetics we learn that the thermodynamically unfavourable formation of ordered biopolymers is balanced by coupling to reactions that are thermodynamically highly favourable; and the latter are replenished by the exchange of distinct species of chemical compounds with the environment; in the case of proteins this coupling is indirectly mediated by the process of peptide chain elongation effected by the ribosomes<sup>8</sup>. The question of *rates* is a related, but distinct one—few reactions in metabolism have a sufficiently large spontaneous rate that they do not require catalysis by enzymes.

In principle, this elementary rejoinder –biota are thermodynamically open systems– should suffice to put paid to the objection from entropy. Undeterred, mathematician G. Sewell has proposed that the Second Law be reformulated to render the objection unassailable: “Natural (unintelligent) forces do not do macroscopically describable things that are extremely improbable from a microscopic point of view.”<sup>9</sup> Ironically, “macroscopically describable” is nearly co-extensive with “entropically negligible” as any kind of supramolecular order that we perceive as “organised” or “structured” does not translate into measurable  $\Delta S$ .

The configurational entropy associated with the complex organisation of ostensibly higher-grade organisms hardly affects the thermodynamic balance sheet of such organisms. Suppose that the synaptic wiring complexity of a human brain has a Kolmogorov complexity of  $2^K$  with  $K = 10^{13}$ . This is (roughly) saying that  $K$  bits are needed to describe the brain’s wiring in some suitable description language. The configurational entropy equals  $k_B K \ln 2 \approx 10^{-10} \text{ J K}^{-1}$ , which is negligible compared to the configurational entropy in the peptide sequences of the brain’s  $\sim 0.1 \text{ kg}$  of protein, which is equivalent to  $25 \text{ J K}^{-1}$ . Even if our somewhat careless estimate for the Kolmogorov complexity of the brain’s wiring underestimates its true complexity by many orders of magnitude, this would make no difference whatsoever to the qualitative conclusion.

A similar exercise may be carried out at the level of subcellular organisation. The reader may care to estimate the Kolmogorov complexity of subcellular organisation (i.e., compartmentalisation into organelles), by observing first that, if there are  $M$  macromolecules to be assigned to  $D$  spatial domains, then  $2^K = D^M$  ( $M \sim 10^{10}$ ,  $D \sim 10^3$ ) and subsequently comparing the configurational entropy of subcellular organisation to that of the primary sequences of the nucleic acids and the proteins.

The overall conclusion must be that the exquisite histological and anatomical structuring, so characteristic of multicellular organisms, hardly amounts to anything much from the thermodynamical point of view, which perceives *Amoeba proteus* and *Homo sapiens* as equally “ordered” (in the thermodynamical sense) to a disconcertingly good degree of approximation. It is certainly true that the regulation and coordination of histological/anatomical organisation requires a host of signalling molecules. In fact, these

signalling factors and pathways associated with regulation and development account for a large portion of the genome and the proteome; this is the true correlate of our intuitive perception of certain organisms belonging to a higher grade than others. On the other hand, it is at the level of primary structure of these molecules that a substantial additional configurational-entropic cost is incurred. Questions of order and disorder are dominated by what happens at the atomic level and the level of macromolecular aggregations.

It should not be thought that faulty application of thermodynamical ideas is the sole purview of the anti-Darwinists. Mainstream evolutionary biologists are just as liable to produce complete nonsense when entropy meets evolution<sup>10</sup>.

### 3.2 Probabilistic arguments

The randomness inherent in the generation of genomic variants sits uneasily with those who are rightly impressed with the complexity of the traits that have appeared in evolution but unimpressed with what may be wrought by mere randomness. No one in their right mind would detonate a scrapheap in the expectation that the debris, falling back down to earth, arranges itself in the form of a jetliner. A. N. Wilson believes that the evolutionist's answer to this poser simply relies on billions of years' worth of time. Consistent with this misunderstanding, he thinks that Darwinism relies on extreme gradualism over geological time<sup>6</sup>.

In reality, Darwin's account of evolution involves an interplay between random mutations and directed selection. It is perhaps this juxtaposition of randomness and non-randomness that leads to confusion. The generation of mutants is not entirely random, as some mutants arise more readily than others. Moreover, a chance element remains in selection, since the fecundity of individual organisms remains subject to stochastic variation—selection only works through an average. The sheer improbability of a complex innovation indicates that natural selection would not normally be effective if all it did was waiting for a radically advanced mutation. A fairly elementary calculation shows why we should rather expect complexity to evolve by means of a series of small increments. Let us estimate  $T$ , the number of generations required to evolve a trait with Kolmogorov complexity  $2^K$  in a population of size  $N$  (which, for the sake of simplicity, is assumed to be the same in all generations). The "hopeful monster" model would estimate the probability of a mutant with this trait arising as  $2^{-K}$ . With  $N$  individuals in every generation, the probability that a generation fails to bring forth the hopeful monster equals  $\exp\{-N2^{-K}\} \approx 1 - N2^{-K}$  (the term on the left is a Poisson probability, and the approximation on the right is admissible when  $2^K \gg 1$ , which is certainly true since we are thinking of  $K$  as a large number). The required number of generations before the monster arrives then follows a geometric distribution with expectation  $2^K/N$ .

Some monsters are improbable, but not unfeasibly so. For instance, whereas humans do not typically survive for much more than half an hour in near-freezing water, the rare

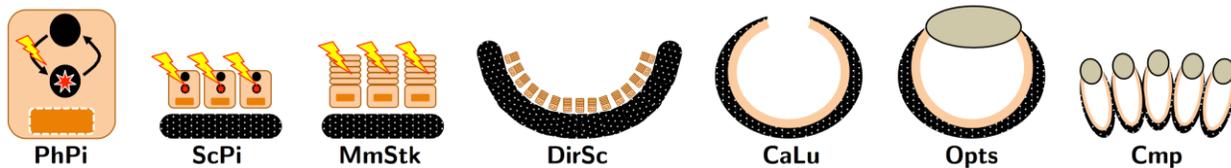
individual who is at the far end of the various bell curves for several relevant physiological traits can survive for several hours. Since we know of at least one such person<sup>11</sup>, the probability is better than  $10^{-10}$ . Indeed, marine mammals, which are secondarily aquatic, have evolved several times independently (pinnipeds, cetaceans, and sirenians), with the harsh marine environment imposing a stringent, but by no means desperate, selection differential.

On the other hand, if the trait arises through a series of intermediates and if  $p$  is the probability that the mutant with the next increment arises in a given organism, then the probability that a generation fails to bring forth the increment is  $\exp\{-pN\} \approx 1 - pN$ . The probability  $p$  and the increment  $\Delta K$  are related by  $p = 2^{-\Delta K}$  (we treat  $p$  and  $\Delta K$  as constants, for the sake of simplicity). The expected number of generations to the next increment is  $(pN)^{-1}$ . The total number of generations  $T$  is therefore given by  $(pN)^{-1}(K/\Delta K)$ .

Comparing the results, we find:  $\ln T$  scales as  $K - \ln N$  for the hopeful monster model and as  $\ln K - \ln N + \ln p^{-1}$  for the incremental model, which indicates that the incremental model requires far fewer generations to generate complex traits. The “hopeful monster” mode of evolution is exponentially less efficient than the incremental mode and we should therefore not be surprised to find that it is the dominant mode of evolution.

One last refuge of the probabilistic argument against evolution is that incremental evolution is inherently implausible, since a complex trait typically relies on many components functioning together. An analogy often invoked to convey the idea is that of a watch: all the cogs and springs work together and the mechanism is entirely non-functional without everything being just so: if the watch evolved out of an ancestor watch with one cog slightly too small or too big (say), then that ancestor could not have been functional at all. Interdependence of intricate parts is an all-or-none sort of phenomenon, precluding a prehistory of gradual improvement.

The fact of the matter is that incremental innovation is not only possible, but routinely observed. For instance, in the animal kingdom we find light-sensors ranging from neurones that can be irritated by photons, to sensors that are directionalised by pigment cups to one side, to pits that form a pinhole camera, which can then be equipped with focussing crystalline substances—lenses (Fig. 3).



**Figure 3: Innovations in the evolution of the eye.** At each stage, the incremental change confers adaptive value. **PhPi**: a photopigment that is activated by light and readily regenerable (cells at this stage are involved in perceiving the light/dark cycle rather than image formation); **ScPi**: a screening pigment that confers a degree of directionality (no image is formed, but the animal can distinguish the approach of danger and escape in the safest direction); **MmStk**: a stack of membrane invaginations supporting an array of photopigment (enhancing the photon capture rate and thus allowing vision in dark and murky environments); **DirSc**: directed screening achieved by locating the photosensitive cells in a more or less shallow pit (which makes the eye more sensitive to stimuli coming from specific directions); **CaLu**: the pigment cup can form a *camera lucida* (rudimentary image formation); **Opts**: the introduction of optics permits image formation at higher resolutions; **Cmp**: compound eyes form an alternative to the single-camera eye.

Whereas every innovation must confer adaptive advantage, innovations also act as *exaptations*: certain innovations are only adaptive provided others have been established<sup>12</sup>. For instance, incremental increases in neurone density and precision of connections and local circuitry in the image plane cannot contribute to fitness (and hence be favoured) before the focussing optics has evolved. It is possible and quite common, however, that a structure or process mediating function  $\phi$  (and initially being selectively favoured because of this) becomes co-opted into fulfilling a different secondary function  $\phi'$  (which may ultimately play a much larger role in the organism's biology); the exaptation is then called a pre-adaptation<sup>12</sup>. The end result is an eye with a retina and a lens, neither of which makes functional sense without the other.

## 4 Philosophical feints

As we have seen, proving Darwin wrong on scientific grounds is fraught with difficulty, as those more conversant with physics, chemistry, mathematics, and biology stand ready to come to his aid. An attack on philosophical grounds, by contrast, holds the promise of being both more elegant and definitive: if a fundamental inconsistency or other irreparable conceptual flaw can be brought to light, a stake can be put through the heart of Darwinism once and for all. Three interesting attempts will be discussed here.

### 4.1 Belief in evolution as irrational and self-refuting

Theist philosopher A. Plantinga introduced what might loosely be called an application of

Gödel's theorem to evolutionary science: if one wishes to be regarded as rational, one is logically compelled to reject evolution precisely when one commits to its truth: "you have to give up your belief that evolution is true [...] The belief that both materialism and evolution are true is self-refuting. [...] Therefore it cannot rationally be held."<sup>13</sup>

To arrive at this position, Plantinga first observes that, on a *materialist* view of the world, beliefs have to be understood as quasi-irrelevant byproducts of neurophysiological states or properties that correlate with adaptive behaviour. Here, "quasi-irrelevant" means that the truth or falsehood of the beliefs is wholly subservient to whether or not the beliefs (conceived of purely as neurophysiological states, i.e. certain configurations of certain collections of atoms in the universe) are adaptive. The adaptive value does not necessarily reside in any or all of the beliefs being actually true. This does not bode well for belief systems that involve many propositions, for if such a system rests on  $N$  beliefs with  $p_i$  being the probability that the  $i$ th of these beliefs is warranted (subscribes to a truth rather than a falsehood), then the probability of the entire system amounting to a truth collectively is  $\prod_{i=1}^N p_i$ . Put differently, if  $L$  is the average value of  $\ln\{1/p_i\}$  among these beliefs, the collective likelihood of truth is  $\exp\{-NL\}$ : reliability of belief systems decreases exponentially in their elaborateness<sup>14</sup>.

One might object that it is not all that clear just how to count the beliefs that compose such a system, but in the spirit of our foregoing thermodynamical arguments we might allow that the qualitative conclusion remains the same as long as  $N$  is large enough. Another objection is that beliefs that have proven to be adaptive should not be expected to be arbitrarily true or false: surely the hardwired manner in which our brains fashion a picture of the world around us out of sense impressions should be expected to be a *sensible* one? This is the trap Plantinga has set: the naive biologist taking this tack is bound to get lost in the thickets of analytical philosophy.

However, the fatal objection is that empirical evidence causes the scientist to *adjust* the values of the  $p_i$  (this is precisely what Bayesian statistics is all about), and, even more importantly, in coherent belief systems the  $p_i$  tend to be *correlated* in the way they react to empirical evidence, whereas Plantinga's formula requires that the beliefs be statistically independent (he says: "remember that the probability that all of a group of beliefs are true is the multiplication of all their individual probabilities"<sup>13</sup> which sounds rather as if he genuinely does not know that this is true only of statistically independent events—otherwise he is being deliberately disingenuous which, for a devout Calvinist, is much worse than mere incompetence). Plantinga's argument amounts to little more than dubious statistics.

If we momentarily overlook the problem of statistical dependence, how then does Plantinga's own belief system escape? One might suppose that his system comes off better since  $N = 1$  in his case, but Plantinga's argument is slightly more subtle (and anyway he appears to state that  $N \approx 12$  for his own belief system<sup>13</sup>). The formula  $\exp\{-N L\}$  *only*

applies to belief systems that reside in brains having evolved under a *materialistic* reading of Darwinism, and that is what makes evolution and materialism incompatible.

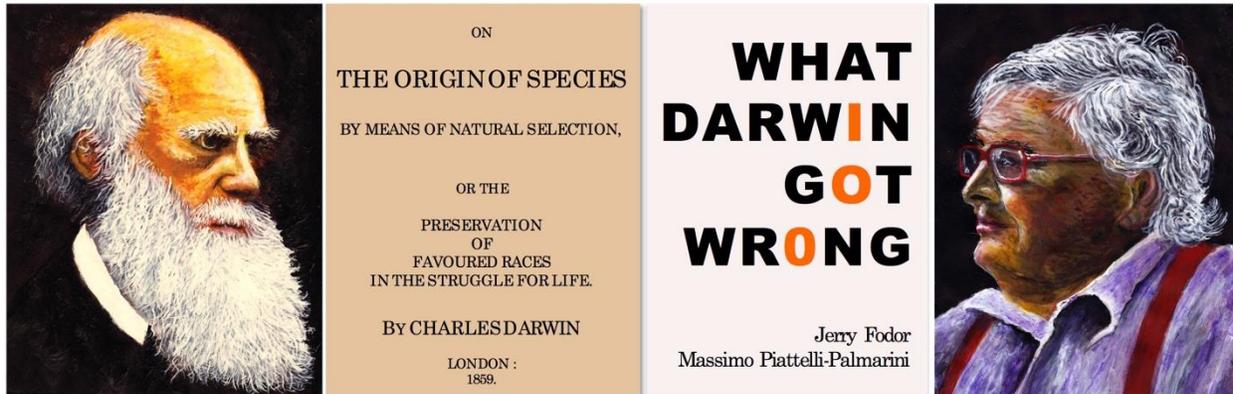
On the other hand, on a *theistic* reading of Darwin, belief systems fare a good deal better (or at least some of them). Here the supreme being purposely guided the process of evolution (Fig. 2), resulting in humans that are equipped with the *sensus divinitatus*<sup>15</sup>, an inborn inclination to form correct beliefs about God directly, experientially (this *sensus* is apparently not functioning properly in agnostics and atheists, presumably due to some form of intellectual immaturity). Plantinga insists that Christians should believe in evolution, on his theistic reading<sup>15</sup>. In this respect he is more demanding than materialist evolutionists, who only ask that the evidence be contemplated.

## 4.2 Fitness as a tautological concept

If fitness is understood to be whatever allows a given type to become more prevalent over trans-generational time, and certain types are said to become more prevalent over trans-generational time *because* they possess higher fitness, are we then not presented with a prime example of circular reasoning? Newcomers to ordinary differential equations often express similar misgivings, as both sides of the equation seem to suppose that one has already worked out what is on the other side. These two objections, however different at first glance, have a point of commonality: their respective resolutions are similar.

One fact of the matter is that some types do become more prominent over trans-generational time, and another fact of the matter is that such trends do correlate with the genes that are transmitted through subsequent generations. “Fitness” is merely an index that quantifies this phenomenon; defining it in all generality is a matter of applied dynamics, complicated to no small degree by the fact that subtle aspects of stochasticity and contingency have to be properly taken into account<sup>16</sup>.

The critics may well cry foul over this rejoinder, inasmuch as fitness was touted as a universal causal explanation and has now been reduced to mere parameter. One could shrug and glibly state that this is bound to happen whenever a science matures into mathematisation and recall how heat, energy, space-time and the like have gone the same way. Nevertheless, the presumed correlation between fitness values and genomic states still needs to be attested and documented in detail. This is not impossible in principle, but often tremendously challenging since the connection between genes and traits (which incur fitness values) involves all of functional biology. Since the latter is quite variegated and we do not have (or even aspire to having) a unified mathematical theory that encompasses all of functional biology<sup>17</sup>, evolutionary theory becomes essentially pluralistic at this point<sup>18,19</sup>. It might be better to acknowledge that evolutionary theory should be regarded rather as a kind of Kantian schema. These themes will be explored more fully in the following sections.



**Figure 4: Clash of the titans.** Charles Darwin (left), Jerry Fodor (right), together with frontispieces of their contributions to scholarship in evolutionary science.

### 4.3 Traits as impervious to natural selection

Philosopher of mind J. Fodor offered a philosophical argument against Darwinism which is particularly interesting since it seems to leave almost all of evolutionary theory intact: differential reproductive success, correlated with genetic variation, giving rise to certain types persisting through evolutionary time for much longer than others. Since this is evolutionary theory in a nutshell, one may well wonder how Darwinism is going to receive its *coup de grâce*. It is thus: evolution cannot possibly explain why certain traits are thus-and-so, since natural selection simply cannot tell one trait from the next. If we look to natural selection to provide a central and universal mode of explanation in evolutionary theory, we must find that it utterly fails in this regard, in essence because of the pervasive co-extensiveness of traits in the life histories of actual organisms.

Somewhat like Wilson, Fodor presented his ideas in a book<sup>20</sup> burdened with a vulgar title (Fig. 4) and myriad factual errors, duly savaged by numerous knowledgeable critics<sup>21–24</sup>. In several respects, Fodor's subsequent polemic with the critics makes for more interesting and worthwhile reading, as there Fodor abandoned every pretense of caring one whit about biological details<sup>25</sup>.

In its simplest form, “Fodor’s paradox” states that natural selection can never favour one trait and disfavour the other, since it does not deal with traits directly, but rather with entire life histories, which are inextricable *bundles* of traits<sup>20</sup>. If a rabbit has 2, or 3, or 5, 8, 13... offspring in its lifetime, who is to say that this is a particular reward for one trait or another (say the mass of its thigh muscles)? And come to think of it, is the lifetime reproductive output of any particular rabbit not mostly a matter of good or bad luck? All true, but natural selection operates over averages of many rabbits, and their correlations between genes, traits, and reproductive output are picked up and exert their effect. This response would seem to be all that needs to be said<sup>23</sup>, but Fodor insisted that he assented to this generally accepted account of natural selection which, however, is *not* what he understood to be the “Darwin bit”<sup>25</sup> — a truly startling proposition tantamount to stating that virtually all



**Figure 5: A single trait, or many?** From left to right: wild-type homozygous, mutant heterozygous, and mutant homozygous individuals of the zebra fish *Danio rerio* with a mutation at a locus that encodes an inward-rectifying potassium channel<sup>26</sup>. Among the countless trait descriptors associable with this mutation are: *defective Kir7.1*, *loss of stripes*, *deficient  $\alpha_2$ -adrenoceptor signal*, *reduced melanophore mobility*, *elevated intracellular  $[Ca^{2+}]$* . On which of these, if any, would natural selection focus, and how does it matter?

evolutionists have hitherto failed to grasp the essence of Darwinism. Let us attempt to gain an understanding of what, in Fodor's eyes, the "Darwin bit" came to.

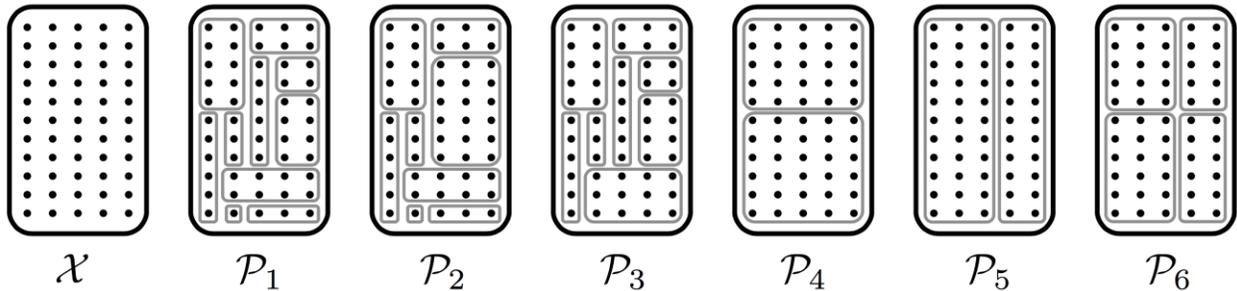
#### 4.3.1 Traits: seemingly in the eye of the beholder

Imagine a species of moth in which certain individuals are capable of hearing a bat approach and respond with a sudden evasive manoeuvre. The ones that exhibit this trait are capable of having more offspring, on average, and these offspring tend to display the same trait, insofar as the possession of this trait is genetically determined, and in subsequent generations, the portion of individuals with this trait tends to increase. Imagine also that, whenever a moth has this ability, it is also the case that a particular nucleus in its brain is pigmented and would show up purple if we were to open its head and cut up its a brain. Just what is being favoured by natural selection: the trait *detection and evasion* or the trait *purple nucleus*?

We might discover that the purple nucleus is involved in flight manoeuvring, and its increased degree of pigmentation related in some way to the evasive capabilities (this is not nearly as far-fetched as it might first appear; see Fig. 5 for a real-life example which if anything is more outlandish than our hypothetical example). This would certainly be in keeping with the observed perfect correlation between the two traits. In fact, once the requisite molecular and neurophysiological research has been done to establish the link, a workaday physiologist would not hesitate to regard *detection and evasion* and *purple nucleus* as descriptors of the *same* trait, two descriptors that are only different in outward appearance, which is ultimately immaterial.

What if, for whatever reason, our field work had never yielded observations of *detection and evasion* but we were able to collect observations on the colour of that brain area? Should we then conclude that *purple nucleus* was being "selected for" and would that be

an egregious error? It does not matter from the point of view of those physiologists who *know* that the co-extensiveness of the trait descriptors can be attributed to the correlation in functional biology, because for them these descriptors are different names for the same trait anyway. However, those not privy to that additional knowledge would observe that natural selection



**Figure 6: Equivalent probe maps.** A probe is conceived as a mapping from a set of life histories  $X$  to a set  $Y$  of trait values (trait descriptors). Partitioning the elements in  $X$  such that all the elements in each given subset of the partition are mapped to the same element of  $Y$ , and no elements not in that subset are sent to that particular element of  $Y$ , one arrives at the partition induced by the probe; each subset can be thought of as uniquely labelled by a trait value. The partitions  $P_1$ – $P_6$  are discussed in the text.

favours the *nucleus purpureus* and have debates regarding the presumptive adaptive value of having purple neurones in hidden places. Is the notion of an operative trait that is “selected for” tenable, given that natural selection does not “see” individual traits, but only the bundles that constitute the life histories of the organisms concerned, and given that we name them through the prism of imperfect knowledge and understanding?

#### 4.3.2 Regimented traits

If traits such as are the object of natural selection truly are in the eye of the beholder, this would *prima facie* entail a conflict with our more general supposition that science ought to be an objective endeavour, dealing in intersubjective concepts. At the very least, it would appear that we must be more careful when speaking of traits.

A trait is a property that an organism might have, typically having a genetic correlate or at least some degree of genetic determination, alongside environmental factors. Properties of the genome itself correlate perfectly (albeit trivially) with genetics, even if such properties are not considered as traits in common biological parlance; this can be understood from the way the genotype/phenotype distinction arose historically.

*Property* is a notoriously problematic notion<sup>27</sup>; the phrases we use as trait descriptors may suffer from referential opacity<sup>28</sup>. Different competent language users may differ where they cease to agree that a pea can still be said to be *yellow*. More worryingly, trait descriptors

might be suggestive of adaptive quality, purpose, or mechanism, and these suggestions may point us towards proper biological understanding, but could just as well lead us astray.

To reign in the confusion engendered by trait descriptors, we recast the discussion in terms of *regimented traits*. First, let a *set of trait values* be a set of trait descriptors, such as  $\{\textit{green}, \textit{yellow}\}$ . The set as a whole is the *trait* (although each element may also be spoken of as a trait, biological terminology being perennially sloppy): thus *pea colour* for the set  $\{\textit{green}, \textit{yellow}\}$ , or *body length* standing for the interval of physiologically allowed values. Let us also assume that we can associate the life histories of the organisms concerned to a given set of trait descriptors. There may well be theoretical and pragmatic questions surrounding observability, precision of measurement, access to the organism, and so on; let us assume that such issues can be resolved to everyone's satisfaction. Finally, let us regard the act of associating to each life history (full developmental path) an element in a given set of trait values as a mapping, which we shall call a *probe*, to emphasise its role of an idealised observer.

If we partition the set of life histories  $X$  into groups such that all members of each group map to the same value in the co-domain  $Y$  of a given probe, and no elements of  $X$  outside that group map to that trait value, we obtain the partition *induced by* that probe. In other words, this is a division of  $X$  into subsets each of which is labelled by the trait value that all of its members are sent to. Fig. 6 shows Venn diagrams of a set  $X$  together with various partitions.

Two probes are said to be equivalent if they induce the same partition. A class of equivalent probes is called a *regimented trait* and each of its members can be taken as a representative, bearing in mind that the semantics of the probes' co-domain elements (the trait values), and the biological explanations they suggest, may well be different. One could think of the regimented trait as the partition of  $X$  rather than the probes that induce the partition.

Probes can be similar; for instance, one may locally be a refinement of the other. That is to say,  $X$  can be split into two complementary sets respecting both their partitions and such that in the first of these sets the first partition is a refinement of the second, and in the second set the second partition is a refinement of the first. The partitions  $P_2$  and  $P_3$  in Fig. 6 are compatible in this sense: neither one is a refinement of the other, since both have a subset of life histories where they are coarser than the other. However, any two such compatible probes can be crossed to produce a maximal refinement, by taking all non-empty intersections between the elements of their induced partitions. The result for  $P_2$  and  $P_3$  is the partition  $P_1$  which is a refinement of both  $P_2$  and  $P_3$ .

The partitions  $P_4$  and  $P_5$  in Fig. 6 are not compatible; their crossing is the refined partition  $P_6$ , which can be regarded as a regimented trait in its own right; Boolean conjunction can be used to form the labels of a probe for this partition out of two representative probes for

$P_4$  and  $P_5$ , respectively. Conversely,  $P_4$  and  $P_5$  can be regarded as projections of the regimented trait corresponding to  $P_6$ .

#### 4.3.3 Weak and strong forms of Fodor's paradox

Regimented traits allow us to interpret Fodor's paradox in various ways. In its weakest form, it is merely a word of caution: always be aware that the probe you are working with is no more than a representative of an equivalence class (the regimented trait): its semantics and its connotations may be misleading. In the words of Block and Kitcher: ". . . among these options [the probes], you can talk as you like. *Any* of them will distinguish the selection process."<sup>21</sup>

A stronger form of Fodor's paradox is that what he called the "Darwin bit" becomes vacuous as soon as we restrict our attention to regimented traits. In particular, what drops out is the notion that the observed trait values are *explained* by natural selection or have arisen *because* of its adaptive value<sup>25</sup>. If indeed "you may talk as you like" then any particular choice of talk would seem to become meaningless. What is interesting about Fodor's objections is that he did not deny the partitioning of  $X$  induced by any of the equivalent probes. The "fact of the matter about which of the correlated traits causes increased reproductive success" is not at stake<sup>25</sup>, that is, he countenanced the partition, and acknowledged that this partition represents differential reproductive success. But to Fodor, this was the crux of the matter: natural selection responds to this partition and *only* to the partition: it is blind to *any* of the probes that induce the partition. In his words, natural selection is "unable to distinguish the causes of fitness from their local confounds [i.e. other probes in the same regimented traits]"<sup>21</sup>. Consequently, it "makes no sense at all to speak of the aspects of a causal history that selection focuses on [...] Selection does not focus: it just happens"<sup>25</sup>. Fodor granted that we can take the partition as our cue to uncover what is happening at the level of functional biology, but he dismissed any such case-by-case investigation as an epistemological side-issue, because the explanatory power then accrues to the incidentals of the case at hand, and not to the theory of natural selection. For Fodor, the principle of natural selection fails as a (causal) law because it fails to clarify what all adaptations have in common "as such"<sup>22,25</sup>.

There is an unambiguous procedure that allows us to associate differential fitness values to the elements of any given partition of  $X$ , the set of life histories<sup>16</sup>. Thus, it is mathematically possible to determine such fitness values for all possible partitions, and thereby discover which ones are associated with the largest fitness differentials. If there exists a unique maximising partitioning in this sense, it can be taken to define the direction of the selection gradient and hence the "natural" coordinate system for trait space. This identifies an *evolutionarily most salient regimented trait*. The evolutionist's thesis is that among the probes pertaining to this most salient trait, there will nearly always be ones that correctly identify the relevant functional biology via "semantic" denotation.

#### 4.3.4 Contingency and the resolution of traits

Taking stock, we see that much of Fodor's misgivings overlap with those noted in Section 4.2: causal connections are local and must be treated on a case-by-case basis, which renders evolutionary science pluralistic, to such a degree that its status as providing general explanations must be called into question. One stance that could be adopted in the face of such charges is that concerns of this nature tend to recede into the background whenever a discipline becomes mathematised: naive notions of causality are replaced by precise mathematical constraints, and opinions regarding what does and what does not constitute an explanation are just that: opinions.

On the other hand, once a science becomes mathematised, some other issues come more sharply into focus. One such issue, closely related to Fodor's paradox, is that natural selection does not operate on life histories in a general, abstract space, but on a finite (and comparatively speaking minute) set of such life histories within a limited time frame. In other words, evolution is *contingent* and it is not clear that the theory has properly come to terms with this difficulty<sup>12</sup>.

Life histories travelled by real organisms do not necessarily collectively sample what we intuitively envisage as the "full space" of possibilities, not merely because the realised histories are contingent on external inputs such as environmental catastrophes (such "external" contingencies can be suppressed, at least in a formal sense, by conditioning on the time paths of the relevant inputs) but more importantly because of the irreducible randomness of the mutational process, the results of which are ultimately frozen in the genotype and thereby influence the phenotypic effect of any future mutations. For instance, the non-compatible probes, of which partitions are shown as  $P_4$  and  $P_5$  in Fig. 6, can be made compatible in various ways by deleting selected life histories. More generally, regimented traits will coalesce when elements are removed from  $X$ . In fact, all traits become one and the same when  $X$  is a singleton set; such extreme coalescence represents Fodorism in its purest form. The upshot is that along with any regimented trait, the set  $X$  should be specified.

The simplest instantiation of  $X$  is perhaps  $X_t$ , the set of life histories of the organisms extant (alive) at time  $t$  in the population (or species) of interest. If an evolutionary selection process takes place between times  $t_0$  and  $t_1$ , then the union  $X_{t_0:t_1} = \cup_{t_0 \leq t \leq t_1} X_t$  is the relevant set to define regimented traits that were "selected for" i.e., the subject to selection over that time interval. Godfrey-Smith<sup>29</sup> carefully discusses the issue of delineating the interval  $[t_0, t_1]$ , i.e., the relevant portion of history in his account of the precise meaning of biological functions (which he defines as dispositions or effects associated with a trait).

A more sophisticated version of Fodor's paradox can now be formulated: there is no way

to be sure, in general, that  $X_{t_0:t_1}$  resolves the operative regimented trait with sufficient refinement to identify the relevant functional-biological causal factors.

Another way of looking at this objection is that we can imagine cloning the world an infinite number of times at time  $t_0$  and taking the union of the versions of  $X_{t_0:t_1}$  from each of these clone worlds. The result  $X_\Omega$  may allow for a refined identification of causal factors in a way that the historical set  $X_{t_0:t_1}$  does not. We should perhaps hasten to add that  $X_\Omega$  is invoked here only as the result of a thought experiment; the universe over which we allow our cloned worlds to vary is not *a priori* well-defined (for the present purposes, a rough idea will do). Moreover, provided that we are willing to countenance optimality principles in evolutionary processes, we may find life histories in  $X_\Omega$  that are *superior* in some suitable technical sense.

Evolutionists have long been familiar with *spandrels*, which are traits (physiological processes, anatomical structures) that would seem mystifying until it is discovered that they are natural concomitants of operative traits; by the latter is meant that the spandrel arises because of the way the organism's ontogeny, physiology, or ecology is set up<sup>12</sup>. For instance, the moth in the introductory example may have wing notches that, on first sight, "serve no purpose" which raises the question why they have been "selected for." In the language of regimented traits, spandrels are not particularly problematic, as they are simply probes belonging to relevant regimented traits that happen to have a semantics (labelling in the set of trait values) that can engender confusion.

However, Fodor was not concerned with spandrels, but with *true free riders*: coalesced traits that, in the history  $X_{t_0:t_1}$  such as it happened, just were always co-occurring with the operative factors, with Hume-like haplessness. The set  $X_\Omega$  might have eliminated any spurious co-extensiveness, but, Fodor says, natural selection never saw enough of  $X_\Omega$ . The fact that  $X_{t_0:t_1}$  and  $X_\Omega$  can lead to different conclusions reflects the central importance of contingency in evolution.

The evolutionist's working hypothesis is that evolutionary histories can generally be expected to resolve salient regimented traits<sup>23</sup>. The final state of affairs, when the selection process is concluded, may lead us to underestimate the resolving power of  $X_{t_0:t_1}$ ; that is, for  $t > t_1$ , the set  $X_t$  will tend to coalesce traits which  $X_{t_0:t_1}$  resolves (nearly) as well as  $X_\Omega$ . Once traits become fixed, there is less variability and an increased level of correlation, perhaps even with tight supergene-type linkage (genes whose alleles are highly compatible in specific combinations tend to aggregate in tight clusters known as supergenes, which are a pervasive feature of genetic architectures<sup>30,31</sup>). By contrast, there tends to be much more variability during the process of selection; variability that can be regarded as the fuel that drives evolutionary processes. Periods of rapid evolution tend to occur at times of geophysical upheaval, when populations migrate, are subjected to a wider range of evolutionary pressures and new opportunities, and hybridise with closely related

(sub)species<sup>32,33</sup>; all these processes promote the generation of variability and thus act to disturb Fodor's perfect correlations.

If  $X_{\Omega}$  seems to be too fanciful a construction, we may consider a more modest expansion of the historical set  $X_{t_0:t_1}$  by performing suitable experiments (which might involve painting polar bears orange, or setting them free on pacific islands, to determine whether their fur is adaptive in being white, being thermo-conservative, or being arctic camouflage). One fears that the resulting set of life histories  $X_{\text{exp}}$  would also have been repudiated by Fodor since they contain counterfactuals which natural selection could never have entertained. Nevertheless,  $X_{\text{exp}}$  may often turn out to be a suitable proxy for  $X_{t_0:t_1}$ .

## 5 Outlook : enduring greatness

If evolutionary science accords Darwin a special place in the pantheon, it is in recognition of the thoughtful and cogent way he put forward the central ideas of natural selection, supported by data he gathered during his famous voyage on the Beagle. Of course a great many aspects of the relevant biology were unknown in his day, and we can hardly blame him for his ignorance in such matters.

The developments in genetics and developmental biology greatly expanded the scope of Darwinism: there was hardly any sort of consensus that Darwin had been made obsolete by these advances, but rather that his theory had been enriched with a firm grounding. This integration is commonly known as the *Modern synthesis*<sup>34</sup> and it owes its stability to the coherent mathematical framework in which Darwin's 19th-century ideas, Mendelian genetics (and its consequences at the population level), and 20th-century insights into the molecular and cellular nature of genes, traits, and development were reconciled. This framework matured into the theory of evolutionary population genetics<sup>35-37</sup>, which has have been extended with formal systems at various levels of abstraction, such as adaptive dynamics<sup>38</sup>, Rice's geometric treatment of Price fitness<sup>39</sup>, or the ensemble-based principle of fitness<sup>16</sup>.

More recent advances have been assimilated in the same vein: much more is now known about the interplay between genomic reorganization events and the reconfiguring of developmental processes, the role of phenotypic plasticity, the alphabet of inheritable information is considerably extended by the phenomenon of epigenetics, we know more about how larger aggregations of organisms co-evolve, we consider natural selection at a meta-level by treating "evolvability" as a trait in its own right, and so on<sup>16</sup>. Perhaps unavoidably, these developments prompt dreams about a new paradigm shift rivalling Darwin's original one (with fanciful names such as "post-modern synthesis" or "extended synthesis") and there has been no shortage of upstarts who would play Einstein to Darwin's Newton (although invariably lacking the mathematical sophistication that such a feat would most likely require), giving rise to an unpleasant kind of careerist disparagement of Darwin

that, coming as it does from within, strikes one as so much more deeply deplorable than the jejune misunderstandings offered by politicians, historians, or philosophers.

## References

- [1] S. Fuller, quote taken from the documentary film Expelled: No Intelligence Allowed written by and starring B. Stein.
- [2] B. Stein, quote taken from televised discussion moderated by Paul Crouch on the *Trinity Broadcasting Network*, April 24 2008.
- [3] Packer, G. Iceberg to the right: From the Titanic to Paul Ryan. *The New Yorker*. April 9 2012, accessed online.
- [4] R. Santorum, quote taken from an address to the *Oxford Centre for Religion & Public Life*, August 1 2008.
- [5] <http://www.basfeijen.nl/evolution/>.
- [6] Wilson, A. N. (2017). *Charles Darwin: Victorian Mythmaker*. London: John Murray. (Yes, *that* John Murray, of Darwin's *Origin*.)
- [7] van Wyhe, J. Reduced fact content. *New Scientist*. September 2 2017, p.46.
- [8] Harold, F. M. (1986). *The Vital Force: A Study of Bioenergetics*. New York: Freeman.
- [9] Sewell, G. (2013). Entropy and evolution. *BIO-Complexity*, 1–5.
- [10] Morowitz, H. (1986). Entropy and nonsense. *Biol. Philos.* 1, 473–476.
- [11] Keatinge, W. R., S. R. Coleshaw, C. E. Millard, and J. Axelsson (1986). Exceptional case of survival in cold water. *Br. Med. J. (Clin. Res. Ed.)* 292, 171–172.
- [12] Gould, S. J. (2002). *The Structure of Evolutionary Theory*. Harvard: Harvard University Press.
- [13] A. Plantinga, quote taken from an interview with G. Gutting, *The New York Times* February 9 2014, accessed online.
- [14] Plantinga, A. (2011). *Where the Conflict Really Lies: Science, Religion, and Naturalism*. Oxford: Oxford University Press.
- [15] A. Plantinga, quote taken from an interview with J. Schuessler, *The New York Times* December 13 2011, accessed online.
- [16] van den Berg, H. A. (2015). *Evolutionary Dynamics: The Mathematics of Genes and Traits*. Bristol: Institute of Physics.
- [17] van den Berg, H. A. (2017). Inceptions of biomathematics from Lotka to Thom. *Science Progress* 100, 1–18.
- [18] van der Steen, W. J. (1991). Natural selection as natural history. *Biology and Philosophy* 6, 41–44.

- [19] van der Steen, W. J. (2000). *Evolution as Natural History: A Philosophical Analysis*. London: Praeger.
- [20] Fodor, J. and M. Piattelli-Palmarini (2010). *What Darwin Got Wrong*. New York, USA: Farrar, Straus, and Giroux.
- [21] Block, N. and P. Kitcher (2010, March). Misunderstanding Darwin: Natural selection's secular critics get it wrong. *Boston Review*.
- [22] Sober, E. (2010). Natural selection, causality, and laws: What Fodor and Piattelli-Palmarini got wrong. *Philosoph. Sci.* 77, 594–607.
- [23] Futuyma, D. J. (2010). Two critics without a clue. *Science* 238, 692–693.
- [24] Ruse, M. Origin of the specious. *The Boston Globe* February 2010, accessed online.
- [25] Fodor, J., S. Blackburn, T. Lewens, I. Cross, J. Coyne, P. Kitcher, D. Dennett, and S. Why pigs don't have wings. *London Rev. Books* 29. October 2007, accessed online.
- [26] Iwashita, M., M. Watanabe, M. Ishii, T. Chen, S. L. Johnson, Y. Kurachi, N. Okada, and S. Kondo (2006). Pigment pattern in *jaguar/obelix* zebrafish is caused by a Kir7.1 mutation: Implications for the regulation of melanosome movement. *PLoS Genetics* 2, 1861–1870.
- [27] Swoyer, C. and F. Orilia (2014). Properties. In E. N. Zalta (Ed.), *The Stanford Encyclopedia of Philosophy* (Fall 2014 ed.). Stanford University.
- [28] Bell, J. M. (1973). What is referential opacity? *J. Philosoph. Logic* 2, 155–180.
- [29] Godfrey-Smith, P. (1994). A modern history theory of functions. *Noûs* 28, 344–362.
- [30] Joron, M., L. Frezal, R. T. Jones, N. L. Chamberlain, S. F. Lee, C. R. Haag, A. Whibley, M. Be-cuwe, S. W. Baxter, L. Ferguson, P. A. Wilkinson, C. Salazar, C. Davidson, R. Clark, M. A. Quail, H. Beasley, R. Glithero, C. Lloyd, S. Sims, M. C. Jones, J. Rogers, C. D. Jiggins, and R. H. ffrench Constant (2011). Chromosomal rearrangements maintain a polymorphic supergene controlling butterfly mimicry. *Nature* 477, 203–206.
- [31] Schwander, T., R. Libbrecht, and L. Keller (2014). Supergenes and complex phenotypes. *Curr. Biol.* 24, R288–R294.
- [32] Hassanin, A. (2015). The role of Pleistocene glaciations in shaping the evolution of polar and brown bears. Evidence from a critical review of mitochondrial and nuclear genome analysis. *C. R. Biologies* 338, 494–501.
- [33] Stearns, S. C. and R. F. Hoekstra (2005). *Evolution: An Introduction*. Oxford: Oxford University Press.
- [34] Huxley, J. S. (1942). *Evolution: The Modern Synthesis*. London: GeorgeAllen & Unwin.
- [35] Maynard Smith, J. (1989). *Evolutionary Genetics*. Oxford: Oxford University Press.
- [36] Bell, G. (2008). *Selection: The Mechanism of Evolution*. Oxford: Oxford University Press.
- [37] Hamilton, W. D. (1998). *Narrow Roads of Gene Land: The Collected Papers of W. D. Hamilton*. Oxford: Oxford University Press.

[38] Metz, J. A. J., S. A. H. Geritz, G. Meszéna, F. J. A. Jacobs, and J. S. van Heerwaarden (1996). Adaptive Dynamics, a geometrical study of the consequences of nearly faithful reproduction. In S. J. van Strien and S. M. V. Lunel (Eds.), *Stochastic and Spatial Structures of Dynamical Systems*, Volume 45 of *KNAW Verhandelingen, Afd. Natuurkunde*, pp. 183–231. North Holland.

[39] Rice, S. H. (2004). *Evolutionary Theory: Mathematical and Conceptual Foundations*. Sunderland: Sinauer.