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THE PRACTICAL AND THEORETICAL IMPLICATIONS OF THE LIMITS OF EVOLUTIONARY EXPLANATION

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Abstract: The explanatory power of evolution is a topic of debate among scientists and philosophers. Some argue that evolution is a universal acid that can explain all aspects of the natural world, while others believe that there are limits to its explanatory scope. This paper explores the arguments for and against the limitless explanatory power of evolution, and discusses the implications of these arguments for our understanding of the natural world.
Keywords: evolution, explanatory power, universal acid, NOMA, limits of explanation

Introduction:
Are evolution's explanatory powers limitless or limited?

According to philosopher Daniel Dennett (1995, 63), evolution is not only true but universal: the central organizing principle explaining all aspects of the living world. Dennett likens Darwinian theory to an uncontainable _universal acid.' Evolutionary explanations, he declares, corrode every philosophical worldview they touch. People scramble (yet fail, in Dennett's estimation) to keep Darwin's dangerous idea at bay by constantly erecting new barriers while old ones are burnt through, as ―new waves of Darwinian thinking‖ relentlessly erode temporary ―forces of containment.‖ As Dennett states (1995, 63), ―Darwin's idea had been born as an answer to questions in biology, but it threatened to leak out, offering answers—welcome or not—to questions in cosmology and psychology… If mindless evolution could account for the breathtakingly clever artifacts of the biosphere, how could the products of our own _real'minds be exempt from an evolutionary explanation?‖ Yet as Dennett trumpets the extraordinary power of evolutionary explanations, he reminds us of Stephen Jay Gould's _Nonoverlapping magisteria' or NOMA essay (1997, 21), which argues that evolutionary explanations must be strictly contained. *Contra* Dennett, Gould claims that although evolution may be accepted as factual, firm boundaries must be respected.
Modern science offers evolution as the bedrock foundation underlying all features of living systems. Evolutionary explanations (hereafter abbreviated EEs) are presented as logical, mechanistic accounts that help us to understand why the natural world is the way it is. But are EEs limited in explanatory scope and power? Even those who otherwise willingly accept modern science sometimes balk at the sheer audacity of evolutionists to explain every facet of nature, particularly human nature, in evolutionary terms. Social scientists occasionally mock EEs by affirming that, like any explanation that purportedly explains everything, they are effectively useless (Dupré 2001, 74). There is nothing, they tease—no aspect of human behavior, even—that cannot be subsumed within and ultimately explained by evolution. Surely there must be *something* evolution cannot explain. Can Darwinian

theory explain every aspect of nature, or are there distinct, *a priori* limits to its epistemic utility? If so, are the limitations philosophical or scientific in nature? Are they practical or theoretical, real or perceived?

Do limits arise from inadequacies of evolutionary theory itself, or merely from those who misunderstand or misappropriate it? What sorts of naturalistic questions might evolution not be able to answer? Are humans exempt from EEs? These questions carry profound significance for scientists, social scientists, and philosophers alike. Following a historical introduction via two case studies, potential constraints on EEs are considered. A third case study reinforces the conclusion that the stratagem to apply limits to EEs 1) normally occurs in human context and 2) ultimately hinges upon one‘s acceptance or rejection of ontological materialism.

Case Study 1: Thomas Henry Huxley, Darwin’s sometime supporter

The accomplished nineteenth century anatomist and paleontologist Thomas Henry Huxley (1824-1895) is best known today as Charles Darwin‘s colleague. Darwin‘s keen mind and wit made him a fierce debater, but he shunned the spotlight and sought to downplay controversy; he privately fumed at critics but hesitated to take them on in public (Browne 2002, 295). Huxley, in contrast, cherished confrontation as ‗Darwin‘s bulldog,‘ an outspoken champion of evolution. An eager and effective proponent, Huxley defended Darwin from detractors on several occasions, notably in the debate at Oxford on June 30, 1860, against Archbishop Samuel ‗Soapy Sam‘Wilberforce (Desmond and Moore 1992, 492; Hesketh 2009).

Yet Huxley challenged Darwin on key points. Huxley admonished Darwin for arguing that evolution must necessarily be slow and gradual, contending instead that lineages might evolve rapidly: ―You have loaded yourself with an unnecessary difficulty in adopting *Natura non facit saltum* [Nature does not make leaps] so unreservedly‖ (Lyons 1999, 49). Huxley would feel vindicated by today‘s acceptance of variable evolutionary rates in punctuated equilibrium (Eldredge and Gould 1972). Still, Huxley acknowledged that Darwin, more than Wallace, deserved credit for formulating the decidedly non-teleological, non-intuitive, yet remarkably simple idea of natural selection. Upon first grasping this idea, Huxley is said to have remarked, ―How extremely stupid not to have thought of that!‖ (Desmond 1997, 41).

One would suppose that as an ardent convert and supporter of this straightforward scheme, Huxley would fully embrace Darwinian theory, but in at least one notable way Huxley broke with it. In his best known work, *Evolution and Ethics* (1894, 36), Huxley tried to reconcile his dim view of a brutal, nasty nature ‗red in tooth and claw‘ with his idealistic view of humanity. How could something so good arise from something so bad? Well trained, like Darwin, in uniformitarian thinking, Huxley recognized the universal, unalterable permanence of physicochemical laws according to which the world operates; he presumed these axiomatic ‗rules‘ of nature hold in all times and places. But in Huxley‘s mind these rules must somehow have been subverted for ethics to develop in our species. His self-perceived masterstroke was the metaphor of a garden which must ever be tended to stave off disrepair. According to Irvine (1955, 414), Huxley, an avid gardener, was inspired by Voltaire‘s character Candide, who avowed that ―*Il faut cultiver notre jardin*‖ [We must all cultivate our own garden]. Huxley readily embraced this directive. He recognized that only by the gardener‘s never-ending toil and constant energy input could inevitable decay—the entropy called for by thermodynamics—be postponed and ‗progress‘ made.

So far, so good: Darwin would object to nothing here. Gardens evidently require constant care. But Huxley‘s argument culminated by comparing humanity to the symbolic gardener. Only by exercising similar toil, individually and collectively (as society and species), argued Huxley, could humans improve their lot and avoid their bestial nature. Only by removing wicked _weeds‘ can we become moral creatures. Huxley argued (1888) that we overcome a Hobbesian nature solely via cultural practice. In short, Huxley saw ethics as an unnatural innovation (without biological underpinning) triumphing over evolution. As primatologist Frans de Waal notes (2001, 344), this was a case of the bulldog biting his master. Huxley‘s argument deliberately limited evolution‘s explanatory power.

In de Waal‘s words (344), ―Since many people consider morality the essence of our species, Huxley in effect said that what makes us human is too big for the evolutionary framework.‖ Darwin‘s fiercest advocate would not bring himself to subscribe to a universally evolutionary position—Huxley did not imagine a morality explicable in biological terms. As the figurative gardener‘s never-ending struggle attests, Huxley felt EEs could go only so far, despite Darwin‘s unequivocal position (stated in *The Descent of Man*, 1871, 173) of continuity between evolution and human nature, including morality. By contrast, Darwin‘s bulldog plainly recognized curbs to EEs.

Although evolution is the foundation of modern biology—in Dobzhansky‘s famous phrase, ―Nothing makes sense in biology except in light of evolution‖ (1973, 125)—Huxley‘s tenuous position (accepting EEs for all of biology with the exception of human nature) is far from unique. In the century and a half since Darwin‘s idea ascended, many scholars have jumped onto this middle-ground bandwagon. Even Pope John Paul II, in articulating the Vatican‘s official position (1996, 1) by admitting the overwhelming empirical evidence for biological evolution, nonetheless attached strict limits to its relevance in understanding _the truth about man,‘ specifically the _ensoulment‘ of individual human beings.

Case Study 2: John Harlow, Darwin’s unwitting (and unheard) supporter

A similar story lies at the heart of a case the opposite of Huxley‘s. It involves Phineas Gage (1823-1860), the railroad worker whose extraordinary tale is now widely known, in part because it is as gruesome as it is incredible, and because it has gained notoriety in studies of neuroanatomy and cognition (Fleischman 2002; Macmillan 2002; Kean 2014). It is remarkable that Gage was not killed by the iron tamping rod that blew a hole through his brain, and that he soon returned to work. Neurologist Antonio Damasio (1994, 8) extensively described Gage‘s ensuing personality change—from a pleasant, shrewd, ambitious, exemplary employee to a rash, foul-mouthed, unrestrained and unreliable man—and the role of the ventromedial prefrontal cortex in regulating behavior, largely by inhibiting impulsive behavior. Less widely known is the role of Dr. John Martyn Harlow of Cavendish, Vermont, who treated Gage‘s wound the day of the injury (September 13, 1848) and followed his recovery the rest of Gage‘s life (McMillan 2002, 106). Harlow was riveted by Gage‘s ability to survive his grievous injury and by its profound effect on Gage‘s personality, although Kean (2014, 353) casts doubts on the extent of this shift. Harlow grew to appreciate the influence, if not explicit causal link, of brain on behavior. Had he discovered the mythical _moral compass,‘ with the damaged frontal lobe relating directly to sociality (Damasio 1994, 22)?

Harlow‘s work came in the decade following Darwin‘s publication of *Origin*, at a time when mental abilities were first ascribed to specific brain regions. Paul Broca and Carl Wernicke notably described language deficits in speech production and comprehension that could be traced to distinct brain loci (the inferior frontal and superior temporal gyri, respectively). Together, Broca and Wernicke demonstrated an unambiguous link between brain and behavior. Unlike these European academic anatomists, Harlow was a country doctor. Nonetheless, he believed he too had conclusive evidence of a connection between a precise brain region and its corresponding higher order function. Damasio (1994, 85) cites Harlow‘s story as ―the historical beginning of the study of the biological basis of behavior‖ (presuming one does not invoke once-popular but now-debunked ideas about physical traits in 18th century phrenology).

However, the mind-brain link Harlow explored (Macmillan 2002, 114) involved not language but ethics: he speculated on the realm Huxley argued was inexplicable in natural terms. In contrast to Huxley, Harlow suggested that morality—which Darwin himself recognized in *Descent* (1871, 102) as humanity‘s defining feature—was a material phenomenon amenable to scientific investigation. Where Huxley defined clear limits to EE, Harlow saw none. Yet whereas Broca and Wernicke achieved scientific success and popular acclaim, Harlow‘s idea gained no support—at least, none until biologists at the close of the 20th century took up the battle flag and resumed Harlow‘s fight. Where the mighty Huxley had circumscribed limits on evolution‘s explanatory power, Harlow had tried, and failed, to break through.

Defining terms, past and present

What constitutes an evolutionary explanation (EE)? As used here, the term explicitly refers to a scientific hypothesis offering an account of the form or function of any attribute—physical, biochemical, behavioral, etc.—of an organism or taxon (a group of related organisms at any level such as species or kingdom). In a sense an EE is a _just-so story‘purporting to explain how something in the natural world came to be. It provides a historical explanation—a logical inference based on empirical evidence—spelling out how a feature appeared and later predominated in a given environment. As such EEs rely upon the classic algorithmic routine, outlined by Darwin and Wallace, of novel variants (mutations) appearing and being selected for or against, with new iterations occurring in succeeding generations.

Although our understanding of underlying genetic mechanisms has made huge strides, in essence EEs are couched in the same terms Darwin and Wallace used 150 years ago. Commonly known as natural selection, this process involves three step-wise stages: variation, selection, and inheritance. Darwin and Wallace were far from the first to propose organic evolution (non-constancy of species), but they formulated the causal, mechanistic explanation for how such change occurs. Although _natural selection‘ can be taken as roughly synonymous for what is meant here by EE, other elements of selection, including sexual, directional, disruptive, purifying, stabilizing, and artificial selection (human-induced selective breeding) also pertain. Random change due to genetic drift can also occur, as will be discussed.

Nonetheless, when people refer to _Darwin‘s theory of evolution,‘ natural selection is virtually always what they have in mind. Though natural selection remains the centerpiece of modern evolutionary theory it is only one of

Darwin‘s many contributions that remain central today. Indeed, Darwin‘s theory is not a single idea but a suite of interconnected explanatory principles (hence Darwin‘s _theories‘would be a more appropriate name), including common ancestry, gradualness of change, adaptation (link between organism and environment), macroevolution (extension of adaptation to speciation and higher-level evolution), extinction, and convergent (analogous) evolution. Note that Darwin did not initially like the term _evolution,‘ partly because previous theorists, who described a progressive unfolding, offered no causal explanation for how it might occur (Bowler 1975; Desmond and Moore 1992, 293). Instead Darwin described this process as _descent with modification.‘ Only later and reluctantly did Darwin use Herbert Spencer‘s phrase _survival of the fittest‘; he might have preferred _amplification of the aptest‘ (Allchin 2007, 176), given that less fit organisms still survive, even if they have lower fitness and less genetic representation in succeeding generations. It must be emphasized that evolution and development are disparate phenomena (Werth 2014, 9): the former links a chain of organisms by common descent, whereas development refers to programmatic changes during the life history of a single organism. Individual organisms do not evolve. It is also important to distinguish true phyletic adaptation (heritable change in a lineage due to genotypic change) from acute or chronic change in an organism, such as acclimatization to altitude. Such physiological accommodation, although often referred to as adaptation (and likewise fully explicable in causal, mechanistic terms), is not a scenario encompassed by EE.

Among Darwin‘s advances were his emphasis on population-level thinking (Herbert 1977; Ridley 2003) and his characterization of variation not as a flaw to be brushed aside or explained away, but as a key element of EEs in that they furnish the material sculpted by selection. The development of population genetics that led to the _modern synthesis‘of the 1940s paved the way for today‘s gene-centric focus on fitness, which expanded to include behavioral traits in all animals, including humans (i.e., sociobiology and evolutionary psychology, hereafter EP). Although modern studies give greater emphasis to genetic fitness, the essential concept of survival and reproduction of parent and offspring remains unchanged since Darwin and Wallace. There is, however, debate over the level or levels at which selection acts, ranging from gene to individual organism to population (i.e., group selection; Wilson 2012; Pinker 2012). EEs lie at the heart of biology. They are the central organizing principle making biology a *bona fide* science. Evolution is universally accepted as factual by scientists and other scholars. Despite tremendous popular opposition, no viable alternative explanatory framework has been proposed, nor has legitimate contrary empirical evidence been advanced. Nevertheless, the question remains whether this explanatory framework is universal and all-powerful. Can evolution explain *all* features of the living world?

Do evolutionary explanations fit basic tenets of science?

As scientific explanations, evolutionary scenarios are obliged to follow modern science‘s naturalism. EEs depend on empirical data. They must be based on reliable, repeatable, objective evidence rather than mere claims or ideas. EEs must be open to rejection or modification in the face of new evidence. They must be potentially falsifiable, and testability must be intersubjective: independent investigators must be able to challenge and support or disprove claims. EEs are bound by rules of logic. Crucially, EEs must offer more than mere descriptions, for at heart science offers reasoned accounts for *why* things are as they are. Further, such explanations must operate

according to a causal, non-teleological mechanism; they involve proximate (initial mechanistic) rather than ultimate causes (in the sense of purpose).

All explanation must involve wholly and solely natural, material, physical causes, as opposed to supernatural, immaterial, metaphysical phenomena. Though evolution leads to ordered design via selection acting on variation generated by random mutation, there is never appeal to a *telos* or agency beyond nature. Design occurs from the _bottom up‘ rather than _top down‘ (Dennett 1995, 75; Shermer 2006, 65).

Evolution is a _theory‘ in the strict scientific rather than common vernacular sense (i.e., a hunch or guess; Kugler 2002, 341). Further, _Darwin‘s theory‘ is an explanatory framework, not an ideology to be pinned to one man, as in the oft-pejorative phrase _Darwinism.‘ Even if Darwin never developed this idea, which transformed biology from an assemblage of facts into a unified field of study, someone else would have, as Wallace indeed did simultaneously. Science, as a cumulative, collective, objective methodology focused on explanations of the physical world, is, ideally and *in toto*, ultimately independent of individual views (admittedly casting aside vast issues of philosophical realism and sociology of science). Our understanding of evolution increases as a wealth of experimental and observational evidence accumulates.

It might be argued that these basic stipulations (i.e., observability) constitute essential restrictions on EEs. However, EEs that do not fulfill these initial preconditions are scientifically invalid, so this claim is dubious at best. To the extent that EEs represent *bona fide* science, they necessarily abide by such limits *a priori*. EEs published in reputable, refereed publications (as admittedly not all EEs are) are presumed to represent proper science; regrettably, this cannot be accepted as a given. One might argue that error bars, confidence intervals, and statistical findings also place limits on scientific explanations. However, these simply reinforce the provisional nature of EEs, which are not infallible but instead change with evidence.

Do evolutionary explanations fit the real world, or merely a make-believe one?

The best explanations are those with the fewest ontological posits, following the rule of parsimony (_Occam‘s razor‘). But does science actually tell us about nature, or does it only explain how data fit a hypothesis to be tested? Does it just make simplified models that enable us to understand our perceptions of experiential phenomena in the natural world (Godfrey-Smith 2003, 187)? Following Dupré (2001, 10), Holcomb (2002) argues science is limited because it merely models the actual universe, representing certain aspects of our world but not truly or totally characterizing it. Is science merely a metaphor, and terms like _gravity‘ and _gene‘ linguistic placeholders signifying things we scarcely understand?

Natural selection is nevertheless an exceedingly simple mechanistic relationship. Darwin did not need to understand generation of variation to understand how selection operates, just as physicists cannot cleanly link Newtonian mechanics with Einstein‘s relativity to explain gravity. It may be that punctuated equilibrium, involving gaps in the fossil record and non-linear rates of morphological change, is more a *post hoc* descriptive account of why gaps exist than a causal chain explaining, in a predictive sense, why that pattern exists in nature (Hume 1748).

Still, to what extent must scientific explanations give causal accounts, given Darwin himself did not understand inheritance, and at what level of reduction must they attribute cause? Do we explain natural selection in terms of populations, genes, or subatomic particles?

Do evolutionary explanations show causality?

As Godfrey-Smith (2003, 191-2) argues, to explain something in science ―is to show how to derive it in a logical argument… to show that it is to be expected, to show that it is not surprising, given our knowledge of the laws of nature.‖ Under the _covering law‘ model of modern deductive-nomological science (Hempel 1965), to explain is to give an account of something, a reckoning of cause with a relationship of inference. However, an asymmetry problem exists in that whereas we derive conclusions from premises, we cannot always go back to premises from conclusions.

When we predict something we show it is expected, even if it ultimately does not occur, whereas when we explain something ―we know that it has happened already, and we show that it could have been predicted, using an argument containing a law‖ (Godfrey-Smith 2003, 192). Because of this unidirectionality not all explanations can be reversed, and not all good arguments are good explanations.

This *post hoc* rationalization, which Shermer (1997, 216) decries as hindsight bias or _Monday morning quarterbacking,‘ is a frequent critique lodged against EE, where prediction, as in weather forecasting, is theoretically possible if extraordinarily complicated given the number of variables involved. But the inability to predict preceding physical states, given an initial set of conditions and well-understood laws of nature, is not a special problem for EEs; such _overdetermination‘ is a broader issue for science generally.

Another issue is how well EEs link specific events to general patterns, connecting diverse facts under a set of basic explanatory principles. In Godfrey-Smith‘s words (2003, 196), ―[Scientists] try to develop general explanatory schemata that can be applied as widely as possible.‖ In this regard EE is wildly successful: Darwin transformed natural philosophy from scattered anecdotes into modern biology. A basic principle unifies a huge range of natural phenomena—potentially, all such phenomena.

Do evolutionary explanations lack predictive power?

Because of science‘s predictive power, it is concerned with explaining not only what *is* but what *might be*. However, critics contend that EEs are limited by historical contingencies. Evolution might not really explain anything because it cannot specifically predict the sorts of things (structural, behavioral, etc.) that will evolve. Vertebrates evolved with pectoral and pelvic limbs; this is why they have two sets of paired appendages. But why two? Why not three? Unlike Newtonian mechanics or other areas of physical science, where one can calculate a precise end result given a set of initial conditions, EEs seem to offer *ad hoc*, *a posteriori* accounts. Although one can concoct EEs to explain how any aspect of any organism came about, you can‘t predict *a priori* that X or Y will evolve. Could one have expected that eyes or fins or leaves would evolve? Nonetheless, the issue here concerns data, not theory. Those who argue that EEs are necessary but insufficient to explain life‘s diversity fail to acknowledge that given enough information, a biologist could explain specific diversity, just as a meteorologist

could, with sufficient data, predict all weather. The argument is not that EEs should be able to predict perfectly; rather, processes that appear stochastic may when better understood be seen as more deterministic.

The central issue is that EEs are at heart based on statistical probabilities—an inherent element of the algorithmic mechanism proposed by Darwin and Wallace. You need not predict who will win a tennis tournament to be certain someone will emerge as the winner, but knowing something about the competitors, you can offer a statistical argument for who is most likely to win. EEs simply propose that some evolutionary paths are more likely than others, just as it is more likely that a top seed will defeat a #64 seed in a tennis match. The set of organisms that might evolve is infinite, yet one can predict future organisms given today‘s organisms and expected future conditions (e.g., climatic trends). This is the central conceit of books like Dixon‘s *After Man* (1981), which present, as its subtitle explains, *A Zoology of the Future*. Such books are patently speculative, but the conjecture is based on science underlying EEs.

Oddly enough, as Mayr (2001, 277) noted, Darwin was criticized by contemporaries for focusing on specific predictions and deductions rather than grand, abstract ideas. For Darwin, EE fit philosophical as well as methodological naturalism. Darwin‘s view allows for natural, material, physical explanations, as opposed to the supernatural, immaterial, metaphysical explanations so common outside science. EEs do not rule out the possible existence of divine forces, but neither do they require one (Kitcher 2007, 129).

This stripped-down simplicity of EE is, for many critics, a steep hurdle to overcome, especially when compared to the stunning complexity of the living world. How could a simple, blind process result in so much complexity? How can the living world‘s beauty and harmony depend on a probabilistic process? This critique is typically offered not as a limitation on EEs but as a refutation of them in the first place. A common criticism relating to predictive ability is that whereas EE may be seen as *necessary* it is *insufficient* in explanatory power. It can explain that the necks of giraffes and mice have seven cervical vertebrae, but not *why* mammals have 7 instead of 6 or 8. It can explain the prevalence of the pentadactyl hand as a bauplan for tetrapod vertebrates, but not why the common ancestor had five digits rather than some other number.

However, this turns out to be a weak criticism at best; again, the real problem is of limited data, not underlying theory. Given sufficient information, we should be able to explain, via abductive inference, when the next mass extinction will occur and which species will survive it.

That EEs are historical in nature does not preclude scientists from testing them critically (Cooper 2002, 427). EEs are open to the same falsification, via experiment and observation, as all scientific hypotheses. Darwin predicted, given the presumed relationship between humans and apes, that fossils of early human ancestors would be found where chimpanzees and gorillas live, in Africa. This has been borne out by copious evidence. Another example involves the evolutionary link between birds and dinosaurs. Based upon skeletal similarities in the wrist and hip, scientists predicted dinosaur reproduction was like that of modern archosaurs (crocodilians and birds), including laying and brooding eggs in nests. The discovery of fossilized dinosaur eggs in nests confirmed this prediction. Other EE-based predictions such as the stratigraphic and geographic distribution of fossil taxa have likewise been corroborated.

A related issue arises from the reductionism vs. emergence conundrum in that many biological properties (e.g., life, consciousness) cannot easily be distilled—they emerge later, with higher levels of organization, as epiphenomena. Again, the criticism is that something that explains everything explains nothing, and thus EE is a shady, fast-and-loose shell game rather than genuine science. Closer inspection reveals that *given a set of initial conditions*, one could predict the evolution of photoreceptors to sense visual stimuli, or contractile tissues and locomotor structures for movement, or plant organs with photoreactive pigments and high surface area for photosynthesis. There is nothing shifty or underhanded going on, except that the final solution to these scenarios is pragmatically unpredictable: we can‘t easily foretell, with the data we have, which of various possible outcomes will come to pass. As physicist Sean Carroll writes (2016, 293), one can explain giraffes‘ long necks via natural or sexual selection, or by arguing that ―Given the laws of physics, the initial state of the universe, and our location in the cosmos, collections of atoms in the shape of long-necked giraffes came into existence 14 billion years after the Big Bang.‖ This statement is true but not useful, Carroll claims, as it lacks the predictive power of EEs.

Are evolutionary explanations tautological?

Khan (2009) points to the ‗relentless tautologies‘ offered by the evolutionary framework. He refers to the ‗ontological leap‘taken by staunch adherents to EE, particularly social scientists who purport to explain all facets of human art, religion, and history via EP. ‗Survival of the fittest‘ is often unfairly painted as a tautology if one defines fittest as those that survive. However, because EE involves heritability of characters, natural selection does not merely imply that survivors survive. Population genetics demonstrates and predicts when populations will or will not be altered by natural selection (Shermer 1997, 143). Genes conferring adult tolerance to lactose are likely to be selected for in groups of herders with ready access to milk, but not in populations without domesticated cattle, sheep, or goats.

Can evolution create? Does it involve chance?

A potential scientific complaint is that evolution cannot generate new forms because it is eliminative only, removing less fit individuals of a population. Yet elimination can be creative; sculptors create by chiseling away. The ‗adaptationist program‘ criticized in Gould and Lewontin‘s landmark ‗spandrels of San Marco‘ paper (1979) might be seen as a limit to EE. Chance contingencies are not explained by evolution, though they are often subsumed within EE, as Lewontin and Gould noted. Not all organismal features are adaptations demanding a just-so story; some are historical accidents. Adaptationism is a seductive siren, yet just because something makes sense as an adaptation doesn‘t mean it *is* an adaptation. Crucially, as genes are linked, many features just ―come along for the ride‖ without being truly selected for. Much genetic variation is also the result of stochastic drift; ‗neutral‘ DNA is unexpressed and thus not subject to selection. In this sense, as with external aspects of an organism‘s phenotype, features might be attributed to chance events. This poses a potential limitation on the epistemic utility of EE.

Is evolution limited by material constraints?

There appear to be constraints from basic physics (which, for example, limit arthropod size), from genetics/genomics (with a limited toolkit of conserved genes serving similar functions in a wide range of organisms), and from development. This is why, even though birds with aluminum wings or mammals with Gore-Tex coats would be highly favored, they do not exist (Kardong 2012, 3). As Schloss (2009, 41) notes, EEs offer a scenario in which a bat wing or dolphin flipper evolved as variations on the mammalian forelimb, ―but to understand them fully requires concepts outside evolution, like aerodynamics and gravity.‖ Schloss (2009, 41) opines that ―evolution is a search engine that combs possibility space, but to explain what it comes up with, we need to understand both the engine and the space.‖ Why are there no organisms with wheels? Natural selection would greatly favor wheels, or birds with aluminum or Teflon wings or horses with six legs. Such extrinsic (physical) constraints allow a crucial falsifiability to EEs and predictions. As Long (2013, 15) notes, ―Physical models can‘t violate laws of physics,‖ whereas ―every computer model is doomed to succeed.‖ New evolutionary-developmental (‗evo-devo‘) biology seeks explanations incorporating intrinsic (genetic) limitations, helping to broaden EEs‘ explanatory power.

Is evolution limited by irreversibility?

Another prospective scientific limit to EE lies in the irreversibility of evolutionary change. Although it is supposed that random changes in DNA (nucleotide substitutions) can ‗undo‘ earlier changes, ‗Dollo‘s Law‘ states that evolution moves in one direction only: organisms cannot return down a road they have traveled (e.g., losing and later regaining a trait). A study by Bridgham et al. (2009) offers a potential mechanism for one-way evolution, involving mutations (even in ‗neutral‘ or ‗nonfunctional‘ DNA sequences unexpressed in an organism‘s phenotype) that destabilize proteins. A simple genetic reversion would not necessarily ‗undo‘ destabilizing effects of the original change, which would require, without selection pressure, an exceedingly unlikely number of neutral mutations. This ‗one-way‘ path poses a limit, but reflection yields examples of major reversals. Marine mammals arose from quadrupeds; in reverting to an aquatic existence, whales gave up the legs their ancestors evolved when the first terrestrial tetrapods emerged from the sea. The loss of prismatic enamel in cetacean teeth and loss of the complexly folded neocortex in manatee brains (Kelava et al. 2013) are other examples of evolutionary reversal.

Do social norms or sanctions guiding human behavior impose limits?

From the philosophical realm, another stipulation presents a likely limit on EEs: the injunction against using scientific findings as a guide for moral behavior. To borrow a famous phrase attributed to Galileo (1615), scripture ―teaches us how to go to heaven, not how the heavens go.‖ Science is understood not to be used as a model teaching people how to lead their lives.

However, this feeling is not universally shared. Much ink has been spilled concerning ‗social Darwinism‘ and whether it was justifiable to Darwin and other scientists, but that is not what is meant here. Rather, what if EEs shed light on relationships between humans, or between humans and other species, indeed all of nature? If we are morally obligated to yell ―Fire!‖ when we smell smoke in a crowded room, then what if scientists possess superior smoke detectors? Are they bound to share results of findings in ways that could potentially save lives? This is a key question that demands more space and attention than can be given here.

It is essential to distinguish ideal science as an independent societal process from science as a flawed, subjective institution carried out by biased individuals. Sociologists of science have studied, without arriving at a definitive conclusion (Beattie 2007; Dennett 2007), the _chicken-and-egg‘ question of whether people are prone to become scientists because of their philosophical and religious leanings or in contrast, if working as a scientist leads one to develop a secular worldview. Science *per se*, as a literally atheistic process—where explanations involving supernatural causes are not allowed—is separate from scientists, many of whom practice diverse faiths. Science has been ―permeated by groupthink, bias, and financial, political, and personal motivations‖ (Bloom 2015), with false claims and faulty programs—from the Third Reich to Marxism, with eugenics, phrenology, and stifled climate debate—because scientists are human too (Guhin 2016). As Neil DeGrasse Tyson notes, ―In science, when human behavior enters the equation, things go nonlinear. That‘s why physics is easy and sociology is hard.‖ Nonetheless, this demarcation between ontological naturalism (which argues there are only natural phenomena, and that whatever exists or happens is therefore natural) and science‘s purely methodological naturalism poses perhaps the greatest potential curb on EEs, especially for adherents of religious or other teleological worldviews. To the extent that science is limited in theory or practice by social restraints, these must be seen as limitations to evolutionary (and all other scientific) explanations. The general issue of whether science itself has limited explanatory power, especially where it abuts belief, has attracted scrutiny, most notably by Bronowski (1956), Snow (1959), and Medawar (1984). To be clear, science does not *presume* naturalism; rather, science has provisionally *concluded* that naturalism offers the best picture of the world, based on objective empirical evidence (National Academy of Sciences 1998; Plantinga 2011; Carroll 2016). Naturalism is therefore a strength of EEs, not an *a priori* limitation.

Case Study 3: Alfred Russel Wallace and moral (ontological) limitations

Consider Wallace as a counterpoint to Huxley and Harlow. A prominent naturalist who supported Darwin and equaled him as natural selection‘s co-discoverer, Wallace nevertheless eventually, like Huxley, imposed his own limits on EEs‘ utility. Indeed, Wallace is as widely known for his late-life departure from evolutionary theory as for his joint contribution to it. Notably, Wallace ultimately concluded, *contra* Darwin, that evolution is teleological and anthropocentric. Wallace was a remarkably productive scientist but a puzzling person. He saw himself an _utter skeptic‘ (Slotten 2004, 232) and purely scientific thinker, but for half his life was a proponent of spiritualism, though he claimed attempts to contact ghosts in séances involved rational, scientific efforts, given that spirits would be sensed via material means such as sounds, movements, and temperature changes. Wallace publicly claimed he sought to expose fraudulent mystics as sincerely as he sought to communicate with spirits from the beyond (Shermer 2002, 179), but his embrace of mysticism cannot be overlooked. There is no disguising the fact that Wallace, like Huxley, held a different view of evolution‘s generative powers than Darwin.

Whereas Darwin argued that purely physicochemical phenomena could create new, diverse life forms but also, presumably, the first life itself—although evolution is strictly about change in organisms, not the initial appearance of life forms—Wallace saw stark limits to evolution‘s explanatory capacity, espousing the familiar view that material causes are insufficient to explain how life and human cognition arose. He wrote (1889, 478)

that nonmaterial (supernatural) causes in the ―unseen universe of spirit‖ were alone responsible for life‘s origins, for consciousness in ―higher animals,‖ and for man‘s great powers of reason. Indeed, Wallace proudly proclaimed these metaphysical goals as the very purpose of the universe.

Thus Wallace drew the ire of Huxley, who criticized this teleological stance (Raby 2001, 291), and Darwin himself, who wrote in a letter to Wallace, ―I differ grievously from you, & I am very sorry for it… I hope you have not murdered too completely your own and my child‖ (Darwin 1869, Milner 2014, 2). Wallace‘s writings and advocacy of spiritualism, mesmerism, and phrenology have dimmed his luster among modern biologists. Despite a self-professed insistence on pure scientific thinking, Wallace allowed supernatural causes to enter his explanatory framework. Although Wallace‘s myriad contributions to tropical biology and ecology remain seminal—as the father of bioegeography, his name persists in the eponymous Wallace‘s Line and Wallace Effect—in evolutionary theory he lingers mainly as footnote to Darwin. Students learn of Wallace as the humble co-discoverer of natural selection, but the deeper they dig the more they see why Darwin found reasons to shun him (Shermer 2002, xviii).

Two points must be stressed here. First, given that we, as corporeal beings existing in the physical world, can perceive supernatural phenomena only when manifested as empirical events capable of being experienced by our senses, then they are of necessity rendered open to scientific interpretation and analysis. In short, we have no means of perceiving exclusively supernatural (rather than partly or wholly natural) phenomena, or of knowing whether supernatural things even exist—we sense phenomena only via natural means. Supernatural things may well exist, but they have no place in science (thus science‘s methodological naturalism is better characterized as empiricism: knowledge is derived not from thoughts but from experience). Second, teleological explanations are similarly _wrong‘ only in the sense that they are entirely unscientific. In non-scientific contexts (including religious faiths) teleology can be valuable.

Are humans exempt from evolution? Are we bound by determinism?

Astute readers will notice a common thread in the stories of Huxley‘s garden, Harlow‘s brain, and Wallace‘s ghost. All involve a single species: our own. Aside from possible philosophical and scientific objections to EEs noted earlier, all concerns relate to humans alone. We impose limits only upon ourselves. Consider the fundamental importance of this observation. No one who accepts EEs claims that any aspect of a bird, butterfly, or banana is not amenable (in theory) to evolutionary interpretation. Creationists aside, scientists do not argue that a *Paramecium*, pine tree, or porcupine requires a special explanation for its morphology or behavior beyond that outlined by Darwin. Only when a spotlight is turned on our species do we search for additional answers; only then do we explain via ultimate causes. We present ourselves as the first and last exhibit in the list of limits on EE. Aside from arguments that we have _outstripped‘evolution (Gluckman and Hanson 1996, 126), we object for religious or moral reasons.

To reiterate, important questions about the origin of life do not properly fall under the purview of EE. EEs deal with organismal modifications over time; life‘s appearance is a different question. This is not an attempt to hedge or dodge the issue. Any scientific account of life‘s origin must unquestionably adhere to the _rules‘ of science

outlined earlier, including an empirical, natural, non-teleological position (opposite Wallace‘s supernatural explanation). Again, historical explanations are amenable to the scientific methods of observation and experiment, and offer the same predictive power (Cooper 2002, 430).

In short, Darwin presented humans as animals. His view is often construed as—though it was not intended to be—an affront to human dignity and an assault on the doctrine of human exceptionalism and supremacy. If we are just animals, then what keeps us from behaving like animals? How can we exhibit morality? We now study the biological basis of ethics. Morality has evolutionary roots (Allchin 1999), contradicting Huxley‘s claim that ethics must be an exception to evolution. Primatologists like de Waal (2001) argue that moral rudiments exist in other primates, particularly chimpanzees and bonobos. Social apes live in tight groups, with a central social life focused on status in the dominance hierarchy and with violent, sometimes even murderous, impulses. Perhaps not surprisingly, people traditionally viewed apes as aggressive, brutal fighters. But de Waal and colleagues (e.g., Pinker, 2002) highlight clear trends in apes toward peacemaking and reconciliation. They challenge the prevailing Hobbesian (or Huxleyian) view that we are born ruthless and selfish, and that without culture we remain that way. Critics of EE frequently argue humans are no longer bound by the same selective processes that govern evolution of other species, whether because so much change in human populations stems from cultural rather than genetic evolution (Pagel 2012), or simply because, as O‘Hear (1997, 49) writes, ―our reflectiveness and our rationality‖ allow us to ―take on goals and ideals which cannot be justified in terms of survival-promotion or reproductive advantage.‖ We are not bound, as EP generally holds, by our Stone Age past; we make conscious decisions that differ from subconscious desires. We employ such decision-making every time we use birth control, avoid eating desirable calorie-laden foods, submit to painful medical procedures, and aid our enemies (Burnham and Phelan 2012; Cochran and Harpending 2009). Humans alone are seen as transcending biological predispositions, with powers of reason, self-reflection, and cultural transmission that enable us to create new environments, subvert nature‘s tyranny, and exempt ourselves from nature‘s inexorable processes (Midgely 1985; O‘Hear 1997; Ratcliffe 2005).

Gluckman and Hanson (2006, ix) argue that EEs do not apply to us because our bodies and behavior are no longer subject to natural selection. Following a different tack, others argue that humans are exempt from natural selection‘s grasp due to our genetic engineering, particularly the way we can at least potentially alter germline DNA and thus transcend selection. The use of viral vectors to introduce DNA could yield ‗accelerated evolution‘ that surmounts natural processes. Philosophers of science (Dupré 2001, 132; Holcomb 2002; Ruse 2010) use the term metaphysical pluralism in criticizing EP as extending beyond the explanatory reach of evolution and science in general. Critics (Midgley 1985; Freese 2008) disparage EP as faulty (scientifically, philosophically, ideologically) for its emphasis on determinism, mechanism, reductionism, neo-Social Darwinism, and vulgar adaptationism. They accuse EP of embodying bad metaphysics for its scientific imperialism and antienvironmentalism, and for uncritically accepting explanations offered to fit into an evolutionary framework, sometimes with little empirical evidence or with evidence manifestly molded to fit this Procrustean bed.

An admitted problem with EP, and a difference with other sciences, is that it too often projects wildly speculative conjectures with little hard evidence. Whereas peer-reviewed science (taken collectively) hesitates to postulate inferences not backed by hard data, EP seems in many cases eager to offer far-reaching conclusions (such as about human mating or love of music) without nuanced subtlety.

This is leveled as a practical criticism, not a theoretical one. EP explanations need not be limited. Rather, excited writers (often journalists, not sociobiologists) are often guilty of speculating beyond the scope of what limited data imply. This revisits the problem of insufficient information, as well as whether branches of science differ methodologically or in the physical reality they reveal. Are they genuinely, following Wilson‘s model of consilience (1998), points along the spectrum of a larger whole, revealing related aspects of a single truth? Holcomb (2002) criticizes such ‗nothing-butism‘ or ‗one-size fits all‘ explanations as metaphysical monism. O‘Hear (1997, 214) offers a cogent argument that many aspects of our species, particularly moral reasoning and consciousness, are ―unDarwinian‖ or ―not explicable in terms of Darwinian drives.‖ He claims ―We seek truth for its own sake‖ (1997, 204) with no benefit to survival and reproduction, though this is debatable. As with all organisms, just because traits do not exhibit clearly adaptive ‗purpose‘ does not mean they did not or could not have originated evolutionarily.

Darwin was the first to advance a unified, non-teleological theory of evolution that did not seek refuge in Aristotelian final causes. Darwin‘s concept of descent involved no movement toward a goal. Unlike Huxley, Darwin viewed nature as ever-changing but not necessarily improving, or progressing. This was a novel, unpalatable view. In Mayr‘s words (1964, xvi), ―Darwin postulated a brute, mechanical, soulless universe, depending on the whims of accident.‖ Darwin zealously argued that survival is not a matter of mere happenstance: it is a statistically predictable property of an organism‘s makeup.

However, Darwinism seems to rule out choice and free will. As genetic creatures, aren‘t our features, and by extension our lives, predetermined? Evolutionists are quick to distinguish the crucial difference between determinism (―the future is written‖) and potentiality: many paths lie open, some likelier than others. [Some religions involve predestination to a greater extent than geneticists would claim.] In this context one must note that ‗evolution‘ literally refers to unrolling or unfolding, as of a scroll already written but not yet open to view; thus the word evolution itself carries an indelible stamp of teleology on which so much human thinking is predicated. Ever since Darwin biologists have debated the extent to which biological change reflects adaptation to an unpredictable, randomly changing environment, or whether evolution reflects goal-directed progress, as of the unfolding of a grand scheme. Although Huxley is justifiably famous for his formative views on agnosticism, he is also known for espousing a popular view of progress. Then as now, the notion of divinely guided, theistic evolution was a popular middle ground in which people could keep their science and square it with theological worldviews.

Conclusion: Limits lie in the eyes (and worldview) of the beholder

According to lore (Zimmer 2001, ix), an upper-class Victorian lady is said to have remarked, upon the publication of *The Origin of Species*, ―Let us hope this is not true; but if it is, let us hope it will not be generally known.‖

Alas, for this woman and millions of like-minded critics, evolutionary theory is now as universally accepted by scientists as it is widely known by non-scientists, with a deep, enduring, alluring power. As Dennett predicted, evolution has spilled beyond the natural sciences to the social sciences, threatening (some would say) to account for seemingly every aspect, large and small, of humankind, as it has for all other living creatures. The explanatory power of evolutionary accounts might seem limitless.

Science emerges from curiosity and reflects our innate striving to apply an organizing framework to everything we experience. _Science‘derives from the Latin verb _to know,‘ yet although science is our most powerful tool to understand our universe, there is much science cannot answer, including the biggest questions we ask. This baffles opponents of evolution who misunderstand that science seeks explanations about the natural world, but relies on empirical evidence and addresses naturalistic questions. It cannot speak to supernatural claims. It is not suitable for addressing questions about existence, knowledge, or meaning. It cannot tell us how we should behave or what our purpose in the world should be.

At heart, fundamental objections to evolutionary explanations fall into two categories: misunderstanding of the nature of science and ideological or ontological protest to evolutionary implications. If EEs follow basic rules of science (viz. are based on empirical evidence, are falsifiable and predictive, and do not presume a teleological stance), there are no inherent limits *qua* science.

To the extent that one deals with phenomena subject to empirical analysis, there may be no inherent boundaries to evolution‘s explanatory powers. It is potentially applicable to all facets of the natural world, including human culture. In the end, EEs, like any scientific explanations, go only so far as science takes us. For people who feel science can answer everything—that all natural phenomena, including aspects of humanity, can be adequately explained via physical causes—there are no inherent limits to evolutionary explanations. But for the many who feel otherwise, EEs have distinct limits. No one should underestimate the brute force of evolution in providing clear, consistent, consilient explanations of the natural world, but none should overestimate the case for science likewise. Many who accept evolution‘s factual nature hold differing views as to its explanatory power. This was true of key figures in the development and propagation of Darwin‘s theory of evolution, and will likely hold true for the foreseeable future.

The teleological predisposition that lies at the heart of most objections to evolution are so deeply seated in us—both culturally and biologically (through countless generations of neurological hardwiring)—as to be virtually unshakeable. Studies repeatedly show (Kelemen and Rosset 2009) that even when we consciously try to break the teleological paradigm, we subconsciously revert to this heuristic. As intentional creatures, it is our nature to presume agency, to seek reason and purpose in everything. This is not to say no such meaning exists in the world around us—there may well be. But that remains an open question beyond the scope of science. The point is that our default presumption is that there must necessarily be meaning.

For most people, religion is the surest path to the meaning we crave, and herein lies the greatest potential curb to EE, for if there is a grand _meaning to it all‘ (beyond that which we impose ourselves), this scheme has the potential to exist outside the observable bounds of nature, and thus to be outside the reach of evolutionary

explanation. If we wish to believe in a wholly materialistic universe, with nothing exempt from ordinary laws of nature, then we can easily imagine an unalloyed, invincible, omnipotent evolutionary framework—the _universal acid‘ of Dennett‘s metaphor—that truly explains everything in nature. But this is a massive _if,‘ and for most people an impossibly difficult step. The biggest, surest limit to evolutionary explanation is not to be found in the study of nature but rather in the study of ourselves, for it is a limit we willingly or unwillingly yet all too easily apply.

Sheldrake (2012) vigorously critiques modern science‘s unquestioned stance of mechanistic materialism. Haught (2009) likewise argues that some scientists uncritically conflate EEs with a materialist or physicalist worldview such that ―what emerges is not pure science but a belief system.‖ Haught charges that although evolutionary biology is sound, it creeps unwarranted and unprovoked beyond science into ―realms of belief.‖ At issue is Darwin‘s legacy, unintended or not, of extending methodological naturalism to ontological naturalism, a flashpoint of debate for philosophy. If scientists uncritically accept a wholly material worldview as their starting point, their results will be biased, Haught (2009) argues. Recall the essential uniformitarian legacy of Darwin in applying scientific investigations and findings to all times and places, not excluding any portions of the material universe. But is there more to the universe than matter and energy? In Haught‘s view, EEs are about more than science, as they are inherently ―antithetical to religion,‖ excluding the potential for metaphysical explanations. Does Darwin make sense only in a materialist setting? Is EE predicated on a materialist worldview? Obviously not, as many people prefer theistic evolution or progressive creationism. Others, including astronaut John Glenn, see no problem squaring their faith with science (Reid 2016): ―I don‘t see that I‘m any less religious by the fact that I can appreciate the fact that science just records that we change with evolution and time.

The crux of the debate is whether one can be a serious evolutionist without being a materialist. This is a question outside science, which we may never answer to everyone‘s satisfaction. Given that faith does not depend on empirical evidence, this will not soon if ever be resolved in any formal, final way. Like all scientific explanations, evolutionary explanations cannot extend into the realm of belief. This is undoubtedly their strongest, surest _limit.‘ Ultimately it boils down to the worldview one adopts.

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