

Personification as ‘Epistemic Practice’ in Evolutionary Biology

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Abstract

I scrutinise the epistemic practices used in the initial formulation and subsequent development of the theory of Darwinian evolution and its subsequent gene-centric turn. Drawing on Charles Darwin’s *On the Origin of Species* (1859), I argue that *heuristic personification* was instrumental to the discovery and formulation of Darwin’s theory. Furthermore, three seminal papers by the sociobiologist W.D. Hamilton (1964, 1971, 1972) reveal that this same practice was used to render intelligible the ‘kin selection’ explanations of altruism rooted in game-theoretic mathematical models. I propose that this heuristic is sufficiently distinct from recognised epistemic practices in the existing literature that it deserves its own, special category.

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1) Introduction

In *Ways of Knowing* (2004), John V. Pickstone proposes three categories of epistemic practices in the natural sciences: *natural history* (describing and classifying), *experimentation* (controlling phenomena and systematically creating novelties), and *analysis* (explaining complex phenomena by reducing them to simpler constituents). By showing how technological developments made their way into scientific practice, the book attempts to narrow the gap between the history of ways of knowing (science) and histories of ways making and doing (technology) (2004, pp. 19-20).

I will first show how Pickstone's epistemic practices map onto the development of Darwinian theory of evolution by natural selection and its subsequent refinement by the biologist W.D Hamilton. Having done that, I will show that a close reading of Charles Darwin's *Origin of Species* (1859) (hereafter "the *Origin*") and W.D Hamilton's seminal papers in sociobiology (1964, 1971, 1972) reveal Pickstone's categories to be insufficient to accurately categorise a key epistemic practice for both Darwin and W.D Hamilton, which I will call *heuristic personification*.

By *heuristic personification* I mean the metaphorical attribution of rational agency to a biological entity as a means to explain a biological phenomenon, with the simultaneous denial of the reality of such agency. This is consistent with how the term "personification" has been used in discussions by Darwin (1859), Dawkins (1976), and Gillian Beer (1996). I will argue that *heuristic personification* was an indispensable tool for generating knowledge for Charles Darwin (1809–1882) and W.D Hamilton (1936–2000). More concretely, I will show that the initial discovery and formulation of the theory of evolution by natural selection would have been implausible without the personification of *Nature* as a 'selecting agent', a tool which allowed Darwin to explore the parallels between human breeders and natural selection. Moreover, the introduction of game-theoretic mathematical models to explain altruism by W.D Hamilton in the late 1960s and early 1970s is only coherent in light of the *personified gene*. After all, game theory implies the existence of a game, which implies the existence of players with rational motives.

Having established that the initial formulation and subsequent mathematisation of Darwinian theory has depended heavily on the epistemic practice of *heuristic personification*, I will attempt to field two potential criticisms: First, that *heuristic personification* ought to be regarded as a special case of *analysis*, in the Pickstonian sense. And second, that it ought to be seen as a special case of vitalism.

2) Darwinian Evolution in Three Epistemic Practices

We begin by showing how Pickstone’s categories allow us to understand the epistemic practices used in the initial formulation and subsequent gene-centric mathematical re-formulation of Darwinian evolution.

2.1) Natural History

For Pickstone, *natural history* relies on “describing and collecting, identifying and classifying, utilising and displaying” (2004). It thus relies both on the accumulation and dissemination of facts and objects as well as the journeys and expeditions necessary for their collection

Darwin’s *Origin of Species* (1859) is littered with natural history. Whether it is wheat (1859, p. 9), ducks (p. 12) or dogs (p. 17), *Lobelia fulgens* (Cardinal Flower) (p. 76), Cirripedes (p. 78), *Ornithorhynchus* (Platypus), or a *Lepidoriren* (lungfish) (p. 100), Darwin is constantly citing his own observations as well as those made by his fellow naturalists such as Asa Gray (p. 88) or Étienne Geoffroy Saint-Hilaire (p. 113). In fact, the “Register of writers referred to in the text of the *Origin*” in the 2008 *Oxford Classics* re-print contains 75 entries (1859/2008, p. 361). Still, Darwin reminds the reader that due to space constraints he can only reveal a small sliver of the “long array of facts I have collected” (p. 114).

For each organism he cites, he argues that many of its peculiar characteristics appear more likely on the theory of evolution than on the “ordinary view of each species having been independently created” (1859, p. 121). Darwin illustrates this by observing that “a part developed in any species in an extraordinary degree or manner, in comparison with the same part in allied species, tends to be highly variable” (1859, p. 114). The orang-utan provides a clear case: its distinctive long arms—the very feature that separates it from other apes—also happen to be the anatomical part exhibiting the greatest variation between individuals. While Darwin sees “no explanation” for this phenomenon under the “view of each species [being] independently created” (p. 116), it becomes a logical necessity under the framework of natural selection. He argues that if a species has undergone recent, significant transmutation, we should expect the most radically altered part to remain the most variable in the present generation (p. 116). After all, Darwin sees individual variation as “generative” (p. 117) of natural selection, since variations afford “the materials for natural selection to accumulate” (p. 38).

Another application of natural history is Darwin’s insistence that species are not ‘natural kinds’. That is to say, they are invented, rather than discovered. Darwin’s *species nominalism* is most apparent from the following quote:

[...] it will be seen that I look at the term *species*, as one arbitrarily given for the sake of convenience to a set of individuals closely resembling each other, and that it does not essentially differ from the term *variety*, which is given to less distinct and more fluctuating forms. The term *variety*, again, in comparison with mere individual differences, is also applied arbitrarily, and for mere convenience' sake

— (Darwin, 1859), p. 43

To support this view, Darwin points out the difficulties that naturalists have faced in drawing the line between a “strongly-marked variety” and a “doubtful species”, or between “sub-species” and “species” (p. 39-42). Darwin is brought to his view using existing plant and animal catalogues: “How many of those birds and insects in North America and Europe, which differ very slightly from each other, have been ranked by one eminent naturalist as undoubted species, and by another as varieties” (p. 47). In addition, he draws on his own experience on the expedition of the *Voyage of the Beagle* (Darwin, 1839) to argue the same point: “Many years ago, when comparing and seeing others compare, the birds from [...] the Galapagos Archipelago [...], I was much struck how entirely vague and arbitrary is the distinction between species and varieties” (p. 40). Since natural history relies on classification, Darwin thus uses the *difficulties* encountered by the practice of natural history to argue that “varieties do not essentially differ from species” (p. 132), thus priming the reader to be more receptive to the mutability of species, for “[t]he differences [between species] blend into each other in an insensible series; and a series impresses the mind with the idea of an actual passage” (p. 42).

2.2) Experiment

We can illustrate the *experimental* way of knowing with another example from the *Origin*. He starts by explaining the ‘standard view’ that he is arguing against:

The view generally entertained by naturalists is that species, when intercrossed, have been specially endowed with the quality of sterility, in order to prevent the confusion of all organic forms.

— (Darwin, 1859, p. 47)

The belief in the “universal sterility of distinct species of animals when crossed” (p. 188) is a matter of fact about the world which can be settled by experiment. Drawing on Currie and Levy’s *Why Experiments Matter*, we can say that experiments provide privileged access to certain “focal properties”, that is to say, essential properties, of a specimen: in this case the supposed “universal” sterility of its cross with another species (Currie & Levy, 2019). Darwin is sceptical that this sterility is actually universal, and brings to bear decades of experimental evidence on plant hybridism by Kölreuter and Gärtner, concluding that the “two most careful experimentalists who have ever lived, have come to diametrically opposite conclusions [...]”

about the sterility of the crosses of various species, suggesting that intercross-sterility is not a *specially endowed quality*, but an *accidental one* based on the physical incompatibility of reproductive organs. Darwin concludes that “some degree of sterility, both in first crosses and in hybrids, is an extremely general result; but that it cannot, under our present state of knowledge, be considered as absolutely universal” (p. 189). For Darwin, this makes it less likely to have been specially endowed by a Divine hand.

The shift in evolutionary biology that led to the cementing of the ‘gene’ as an epistemic object was also heavily influenced by experimental practice, first as breeding experiments in the 1890s confirmed Mendel’s laws of inheritance (Rheinberger, 2008, p. 5), and later when Herman J. Muller reported on the induction of Mendelian mutations in *Drosophila* using X-rays in 1927 (Rheinberger, 2008, p. 6). And, perhaps most famously, the elucidation of the structure of DNA as a macromolecular double helix by Crick, Watson, and Rosalind Franklin allowed biologists to identify it as *the* autocatalytic hereditary entity, or ‘basic unit’ of heredity (Rheinberger, 2008, p. 8).

2.3) Analysis

Pickstonian *analysis* is the practice of “reducing complex phenomena to simple principles” (2004, p. 56). We can illustrate this with the following example from one of W.D Hamilton’s seminar papers (1971): how do we explain that animals tend to form clusters or herds? In 1971 W.D Hamilton published his “Selfish Herd” model, a mathematical model that predicts the clustering behaviour by simulating prey organisms minimising their own probability of being attacked. When prey use their neighbours as living shields, groups and herds form, with very few assumptions about the organisms in question (1971). Hamilton is said to use *analysis*, in the Pickstonian sense, because he has explained a complex behaviour as a natural consequence from a simple rule (an organism’s desire for self-preservation).

3) Heuristic Personification: The Fourth Practice

While Pickstone's three categories are remarkably well-suited to cover a large portion of epistemic practices underlying the genesis and development of Darwinian evolutionary theory, we will next show that a careful reading of the *Origin* and three papers by the biologist W.D Hamilton (1964, 1971, 1972) as well as their popularisation in Richard Dawkins' *Selfish Gene* 1976 reveals that *heuristic personification* (defined in §1) has been a distinct, fourth epistemic practice in evolutionary biology.

3.1) In Darwin's *Origin of Species*

Darwin personifies *Nature* and *natural selection*. Thus, we read that that “man by selection can [...] produce great results, [...] through the accumulation of [...] useful variations, **given to him by the hand of Nature**,” (1859, p. 50), or that “natural selection should have **preserved or rejected** each little deviation of form **less carefully** [for unspecialized than specialized anatomical parts]” (1859, p 114), or that variations “**will be taken advantage of** by natural selection” (p. 258), or of variations “being **preserved and accumulated** by natural selection” (p. 91). We read that “Natural Selection, it should never be forgotten, **can act** on each part of each being, solely **through and for its advantage**” (p. 114), or that “natural selection would **have free scope for the work of improvement**” (p. 64). In each of these cases, natural selection appears personified - as if it had intelligence, discernment, agency and the desire to shape an organism a certain way.

Darwin didn't literally believe in a Personified Nature, as he explicitly clarifies¹ in the third edition:

So again it is difficult to avoid personifying the word Nature; but I mean by Nature, only the aggregate action and product of many natural laws, and by laws the sequence of events as ascertained by us.

— Darwin (1861/1959) [p. 165]

Darwin claims that his Personified Nature is merely a short-hand for the natural laws gleaned from empirical observations of nature. So, why do I insist it should be viewed as an epistemic practice? Should we not view the personification of Nature in the same light as Darwin's other similes and metaphors, such as when he compares species to languages: “a breed, like a dialect of a language, can hardly be said to have had a definite origin” (p. 33). Why don't I argue that the language-simile was an epistemic practice?

¹Darwin's exasperation is evident in a private letter to his publisher, saying he has made many “corrections, or rather additions, which I have made in hopes of making my many rather stupid reviewers at least understand what is meant” 1959 [p. 20]

My argument hinges on showing that *heuristic personification* was indispensable for Darwin to have his key insight, by enabling him scrutinise what others ignored: individual differences. It is commonly understood that Darwin revolutionised biology by making the first compelling case for the transmutation of species and giving a plausible dominant mechanism (*natural selection*). What is less understood is the method that led him to this conclusion: namely the careful scrutiny of *individual differences* between organisms, a topic that, as he pointed out, was much-ignored by his fellow naturalists:

[...] I look at individual differences, though of small interest to the systematist, as of high importance for us, as being the first step towards such slight varieties as are barely thought worth recording in works on natural history.

— (Darwin, 1859), p. 42

Gillian Beer has argued that this was Darwin’s key contribution, and what separated him from other evolutionists like his grandfather Erasmus or his French predecessor Jean-Baptiste Lamarck (1996, p. xviii). Indeed, Darwin sees these individual differences as “*generative variability*” (e.g. p. 117), meaning that they generate evolutionary change. Whether they are used by Man or by Nature, in both cases they lie at the root of species change.

Whereas “the systematists” quoted by Darwin ignored individual differences, Victorian breeders were absolutely dependent on them. In keeping with Beer’s interpretation, Pickstone has pointed out that the analogy with an active human selector or breeder was the key insight that led Darwin to formulate his theory 2004. Citing Desmond and Moore’s biography of Darwin (1991), Pickstone highlights the influence that commercially-driven human selection had on Darwin:

In Britain from 1750, cattle and sheep were changed radically as breeders sought marketable characteristics and faster growth. [...] the theory of evolution by natural selection [...] can be shown to have built on this shift in breeding technology.

— (Pickstone, 2004, p. 30)

Indeed, Darwin dedicates his first chapter ‘Variation under Domestication’ to discussing man-made selection, using examples from horses, sheep, dogs, and pigeons (Darwin, 1859, pp. 9-37). In fact, Darwin tells us that his study of individual differences between domesticated forms led him to take up the breeding of domestic pigeons, and even gaining entry into “two of the London Pigeon Clubs” (p. 18-19). Darwin undoubtedly sharpened his eye for individual differences through his pigeon-breeding, and brought this sharpened breeders’ eye to bear on biological systematics. Breeding and man-made selection is ever present throughout *Origin*, even in discussions of Natural Selection. For example, in the fourth Chapter (‘Natural Selection’) he seamlessly switches between discussing a human and a ‘natural’ selector: “Though nature

grants vast periods of time for the work of natural selection [...] In man’s methodical selection, a breeder selects for some definite object” (p. 79).

Darwin’s personification of nature is absolutely essential for drawing the parallel between an artificial and a natural selector, as is clear from the following quote:

as man can certainly produce great results by adding up in any given direction mere individual differences, so could Nature, but far more easily, from having incomparably longer time at her disposal

— (Darwin, 1859, p. 64)

It follows that *heuristic personification* of nature enabled Darwin to apply a certain logic of artificial breeding (“Multiply, vary, let the strongest live and the weakest die” (1859, p. 181)) to the action of Nature. We have thus shown that it is an epistemic practice - a way of producing knowledge.

3.2) In W.D. Hamilton’s Game-Theoretic Explanations of Altruism

Charles Darwin struggled to explain how altruistic traits could be ‘naturally’ selected if they disadvantaged the altruist (Okasha, 2020). His explanation was to argue that these traits would benefit the group, thus introducing the idea of ‘group selection’. Group selection fell into disrepute in the 1960s however, after the work of G.C. Williams (1966) and J. Maynard Smith (1964) showed that group selection was an inherently weak evolutionary force, hence unlikely to promote interesting altruistic behaviours (Okasha, 2020). In 1964, W.D. Hamilton’s “The Genetical Evolution of Social Behaviour,” 1964 contained a game-theoretic mathematical proof showing that altruism can evolve as a trait as long as the benefits of altruistic acts fell on individuals that were genetically related to the donor 2026. Hamilton’s rule gave the conditions by which one individual would likely behave altruistically toward another: An altruistic trait will be favoured by natural selection if the relatedness of the recipient (r) multiplied by the benefit to the recipient (B) exceeds the reproductive cost to the donor (C) (Hamilton, 1964):

$$rB > C$$

Hamilton’s core insight was that a gene’s success isn’t tied solely to the survival of one specific body. Because relatives share a significant portion of their DNA, a “replica” of a gene can exist in a sibling, cousin, or nephew just as easily as in a direct descendant (1972 p. 192).

By helping a relative survive and reproduce, an organism is indirectly ensuring the survival of its own genetic material. To account for this, Hamilton expanded the definition of fitness into ‘Inclusive Fitness’, which combines an individual’s own reproductive success with the success of their relatives. Under this logic, the gene—not the individual—is the fundamental unit of

selection; the individual is merely the “vehicle” that carries the gene into the next generation (Dawkins, 1976; Segerstrale, 2026).

Hamilton’s highly mathematical paper concludes by employing heuristic personification to interpret the result of his mathematical proof:

*in the world of our model organisms, whose behaviour is determined strictly by genotype, we expect to find that no one is prepared to sacrifice his life for any single person but that everyone will sacrifice it when he can thereby save more than two brothers, or four half-brothers, or eight first cousins [...] Clearly **from a gene’s point of view** it is worthwhile to deprive a large number of distant relatives in order to extract a small reproductive advantage*

— (Hamilton, 1964)

Thus, the prediction is made by pure mathematics, but the interpretation is made by taking “the gene’s point of view”. In a later paper using kin selection to explain the sterility of worker ants, Hamilton defends his method of attributing “to the genes, temporarily, intelligence and a certain freedom of choice” (Hamilton, 1972, p. 195).

Richard Dawkins enthusiastically promotes Hamilton’s work in his highly popular *Selfish Gene* 1976. In particular, he defends and extends Hamilton’s personification of the gene. Thus, Dawkins states that “natural selection for selfish genes tends to favour **cooperation among genes**” (p. xi), ascribing to the gene the quality of *cooperation*. For Dawkins, personification of this kind is not “just a quaint didactic device” (p. xii). He explains how it is a *tool* for biologists who have to make sense of the dense algebra of game theory:

“[in] Darwinian calculations of altruism and selfishness [...] it is very easy to get the wrong answer. Personifying genes, [...] often turns out to be the shortest route to rescuing a Darwinian theorist drowning in muddle”.

— (Dawkins, 1976, *Introd. p. xii*)

Thus, *heuristic personification* of the ‘gene’ became a way to navigate the complex, mathematics-heavy turn of the modern synthesis. It is thus a tool for generating knowledge - an epistemic practice.

4) Objections to Heuristic Personification as Epistemic Practice

It may be contended that *heuristic personification* is simply vitalism in disguise. But, as we have seen in §3.1, Darwin rejected a literal view of personified Nature. In his defense of W.D Hamilton, Dawkins is even more forceful in denying the reality of the personified *gene*:

Personification of genes really ought not to be a problem, because no sane person thinks DNA molecules have conscious personalities, and no sensible reader would impute such a delusion to an author.

— (Dawkins, 1976, Prologue)

The rejection of the reality of the very agency that is so useful as an epistemic tool is why it ought to be considered a *useful fiction*. This makes *heuristic personification* different from vitalism, which holds that biological entities *really do* have irreducible agency (for example Hans Driesch’s “entelechy” - “an organising, directive force that consumed no energy, was immaterial, but was the factor that distinguished living from non-living matter” (Allen, 2005, p. 271)).

It may be contended that *heuristic personification* is merely a type of *analysis* in the Pickstonian sense. This contention is easy to refute. For Pickstone, *analysis* concerns the “decomposition of ‘compounds’ into their various elements, and the reduction of systems to the ‘flow’ of single elements” (p. 85). Importantly, the simple elements which are used to explain complex behaviour are always implicitly taken to be real. It would stretch the concept to the point of meaninglessness if we expanded “analysis” to include *useful fictions* like *heuristic personification*.

5) Conclusion

We have seen that, for Darwin and W.D Hamilton, *heuristic personification* was far more than rhetoric: it did real conceptual work. Personifying Nature was essential to Darwin’s core argument in the *Origin of Species*. When we realise that natural selection implies a selector, we are led to the key insight that led Darwin to see what others missed: that human breeding was a minified version of the work of nature - an that is only possible with *heuristic personification*. Similarly, for W.D Hamilton, the personification of the *gene* allowed him to justify the application of game-theoretic models to explain altruism as ‘kin selection’. Indeed, without personified (rational) actors there can be no “game” in “game theory”. And as Dawkins pointed out, it also served as an epistemic shortcut for practising biologists: a way to navigate complex mathematical probabilities and quickly arrive at an answer without having to explicitly go through the mathematical proofs offered by Hamilton.

These considerations lead us to the conclusion that Pickstone’s account of epistemic practices are not sufficient to understand the the conceptual development of Darwinian evolution. Thus, we must elevate *heuristic personification* to its rightful place as a distinct epistemic practice in evolutionary biology.

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