Biology & Philosophy (2024) 39:18
https://doi.org/10.1007/s10539-024-09954-0

Natural selection requires no teleology in addition to heritable variation in fitness

Nathan Cofnas[1]

Received: 1 April 2023 / Accepted: 25 June 2024 / Published online: 7 August 2024

Abstract

According to the standard formulation, natural selection requires variation, differential fitness, and heritability. I argue that this formulation is inadequate because it fails to distinguish natural selection from artificial selection, intelligent design, forward-looking orthogenetic selection, and adaptation via the selection of nonrandom variation. I suggest adding a *no teleology* condition. The no teleology condition says that the evolutionary process is not guided toward an endpoint represented in the mind of an agent, variation is produced randomly with respect to adaptation, and selection pressures are not forward looking.

Keywords Natural selection · Neo-Darwinism · Modern synthesis · Teleology · Artificial selection · Intelligent design

The standard formulation of natural selection

Lewontin (1970: 1) famously identifies three principles that he claims embody "Darwin's scheme" and "the principle of evolution by natural selection." They are: (1) "phenotypic variation," (2) "differential fitness," and (3) "fitness is heritable." He describes these principles as "necessary as well as sufficient conditions for evolution by natural selection" (Lewontin 1985: 76). Godfrey-Smith (2007: 489) approvingly notes that formulations of natural selection tend to "have three or four conditions, where the core requirement is a combination of variation, heredity, and fitness differences." He expounds: "evolution by natural selection in a general sense is the large category of change *due* to variation, heredity, and reproductive differences, in some particular manifestation of those features and in conjunction with other factors" (Godfrey-Smith 2009: 39). Okasha (2011: 212) refers to the "well-known" fact that

---

✉ Nathan Cofnas
nrc48@cam.ac.uk

[1] Faculty of Philosophy, University of Cambridge, Cambridge, UK

the principle of natural selection "says that any entities satisfying [Lewontin's three] conditions will evolve by natural selection." Dennett (1995: 343) says that "[t]he outlines of the theory of evolution by natural selection make clear that evolution occurs whenever" there is "variation," "heredity or replication," and "differential 'fitness.'" Sober (2000: 36) writes that "[n]atural selection occurs when there is heritable variation in fitness." In short, the standard formulation of Darwin's theory of natural selection is that it requires heritable variation in fitness.

This three-part formulation has its dissenters. Regarding the heritability condition, Earnshaw-Whyte (2012) notes that nonheritable variants can proliferate in a population by increasing the lifespan of their possessors. Suppose there are two types in a population, *A* and *B*, both of which have an even chance of giving birth to an *A* or a *B* (i.e., there is no correlation between parent and offspring type). If *A*'s tend to live a long time but *B*'s die quickly, a population composed of half *A* and half *B* will evolve to be predominately *A*, as old *A*'s accumulate faster than old *B*'s. Thus we see apparent natural selection for *A*, but without heritability. Bourrat (2015) counters that it is a mistake to understand heritability as a correlation between parent and offspring type. If the parent survives to the next generation, it should be counted as its own offspring. "From an evolutionary perspective," Bourrat argues, "persisting can be seen as formally equivalent to reproducing" (ibid.: 893). He proposes the concept of "persistence heritability," which is defined as the "linear regression of average parental character in the offspring generation…on parental character in the parental generation" (ibid.: 895). For the purposes of this paper, I leave this and related controversies aside. I accept that natural selection requires heritable variation in fitness, although my main point would stand even if the hereditability condition were rejected.

I argue that the standard formulation is inadequate because it fails to distinguish natural selection from artificial selection by humans, intelligent design by God, forward-looking orthogenetic selection, and adaptation via the selection of nonrandom variation. In the case of artificial selection and intelligent design, natural or supernatural agents intervene in the mutation and/or selection process to drive evolution in a predetermined direction. "Orthogenesis" refers to the idea that evolution follows a predetermined path. ("Ortho" comes from the Greek word for "straight.") In the case of orthogenetic selection, a natural teleological force influences survival and reproduction in order to guide evolution toward a predetermined endpoint. I will also call this "natural teleological selection." Adaptation via the selection of nonrandom variation involves heritable variation arising because it will be favored by selection. All four of these evolutionary processes involve heritable variation in fitness, but, I claim, they should not be classified as natural selection.

In the following section I address the question of why this matters. I argue that there are historical, philosophical, and scientific reasons for distinguishing natural selection from everything else. I then argue that this can be accomplished by adding a *no teleology* condition. Since natural selection is a two-stage process of mutation and selection, teleology can manifest at either stage: mutation can be nonrandom with respect to adaptation, or selection can be forward looking in the sense that it favors traits based on their contribution to future evolutionary outcomes. I then describe two different kinds of teleology that can guide the evolutionary process: agential teleology and natural teleology. Agential teleology refers to deliberate intervention by a goal-directed agent. Natural teleology refers to a natural force or mechanism that is forward looking. The no teleology condition means that evolution is not guided toward an endpoint represented in the mind of an agent, variations are produced randomly with respect to adaptation, and selection pressures are not forward looking.

Why does it matter?

The presence of heritable variation in fitness will (tend to) drive evolutionary change regardless of how the variation was introduced or what determines the fitness of heritable traits. Why is it a problem if we formulate our concept of natural selection so that it includes artificial selection, intelligent design, forward-looking orthogenetic selection, and adaptation via the selection of nonrandom variation? I argue that there are three reasons for distinguishing these processes, which concern history, philosophy, and scientific precedent.

First, the historical. Darwin's revolutionary insight was that something analogous to breeding occurs in nature. His argument for natural selection is based largely on an analogy with artificial selection (Lewens 2007: 50; Okasha 2019: 11; Ruse 1975; Sober 2011: 16, 33, 35–36; White et al. 2021). Chapter 4 of the *Origin* starts with the heading, "Natural Selection—its power compared with man's selection" (Darwin 1859: 80). As White et al. (2021: 1) observe, Darwin chose the term *natural selection* to "mark the relation between selection in the wild and selection on the farm." A formulation of natural selection that does not distinguish natural from artificial selection should not be described as "*Darwin's* scheme" (Lewontin 1970: 1). The same point applies a fortiori to a formulation that does not distinguish natural selection from intelligent design by God.

Darwin (1859: 134–139) did accept the idea that heritable variation sometimes arises nonrandomly—specifically, he endorsed the Lamarckian theory of the inheritance of acquired characteristics, which he called the "effects of use and disuse." However, he saw this means of adaptation as an *alternative* to natural selection (Bowler 1983/2009: 236; Ruse 1975: 343; Sober 2011: 19). Lamarck thought that striving to reach leaves causes successive generations of giraffes to be born with longer and longer necks. This process involves heredity (tall giraffes are more likely to produce tall offspring) but not necessarily variation or differential fitness (Kronfeldner 2007: 497). According to Lamarck's scheme, giraffes *within* each generation may all be the same height. Even if there is intragenerational variation, there need not be selection (i.e., differential fitness). The alleged effects of use and disuse *could* be a source of variation for selection. But the idea that the variation upon which natural selection acts is random with respect to adaptation was a core element of Darwin's theory (Sober 2011: 18). He compares natural selection to an architect who builds a structure with "uncut stones, fallen from a precipice."

> The shape of each fragment may be called accidental; yet the shape of each has been determined by the force of gravity, the nature of the rock, and the slope of the precipice,—events and circumstances, all of which depend on natural laws;

> but there is no relation between these laws and the purpose for which each fragment is used by the builder. (Darwin 1868: 248–249)

This was not just Darwin's personal view. Modern evolutionary theorists also describe natural selection as acting on "random variation" (e.g., Sober 2000: 38; see also Charlesworth et al. 2017: 1) or on variation that arises within populations "in a haphazard and undirected way" (Godfrey-Smith 2009: 1).

As I will discuss presently, the idea that natural selection is not forward looking may not have been fully articulated until *neo-Darwinism*—also known as the *modern synthesis*—took shape in the mid-twentieth century. But this came to be a key tenet of Darwinism as it is currently understood.

Whenever it was made, the separation between natural selection on the one hand and these other (real or hypothetical) means of adaptation on the other was a momentous breakthrough in the history of biology. The standard formulation, which conflates these processes, is therefore misleading from a historical perspective.

Second, the philosophical. Philosophers and scientists often make generalizations about natural selection that are not necessarily true of some or all of the other evolutionary processes mentioned above. Perhaps most notable is the claim that natural selection is *unguided* or *undirected*. According to Weismann: "the philosophical significance of natural selection lies in the fact that it shows us how to explain the origin of useful, well-adapted structures purely by mechanical forces and without having to fall back on a *directive* force" (Weismann 1904: 55; quoted in Haig 2007: 425–426). Ayala (2007: 8567, 8573) writes:

> It was Darwin's greatest accomplishment to show that the complex organization and functionality of living beings can be explained as the result of a natural process—natural selection—without any need to resort to a Creator or other external agent.…In evolution, there is no entity or person who is selecting adaptive combinations.…[N]atural selection does not strive to produce predetermined kinds of organisms.

Dawkins (1986: 9) refers to "[n]atural selection, the blind, unconscious, automatic process which Darwin discovered.…It has no mind and no mind's eye. It does not plan for the future. It has no vision, no foresight, no sight at all." Mayr (2001: 133) says that natural selection "is not teleological (goal-directed)." Kuhn (1962/2012: 171) equates the Darwinian revolution with the "abolition of [a] teleological kind of evolution" and the rejection of a "goal set either by God or nature." Bowler (1983/2009: 236) describes the inheritance of acquired characteristics as an "alternative" to natural selection that "preserve[s] an element of teleology." A related claim is that natural selection does not involve agency. Sterelny and Griffiths (1999: 36) say that it is the "absence of any overseeing agent that makes natural selection natural." Okasha (2019: 11) says that "[i]n natural selection there is no conscious agent." A formulation that (perhaps inadvertently) classifies artificial selection, intelligent design, orthogenetic selection, and the selection of nonrandom variation as natural selection technically makes these claims false, and may therefore be conducive to confusion.[1]

There is a separate historical question of whether *Darwin himself* rejected the idea of direction—or teleology—in evolution. Lennox (1993) brings attention to the fact that he frequently used teleological language. According to Lennox, Darwin did not reject teleology, but "re-invented" it (ibid.: 417). He proposed a radically new form of teleology that allowed him to explain the existence of biological traits by reference to their effects. But this did not imply *direction* in evolution. Darwin's practice of explaining traits "teleologically" as a consequence of their selected effects is, as Lennox notes, consistent with our modern understanding of evolution, and is explicitly endorsed by prominent philosophers of biology including Ayala (1970), Brandon (1981), and Wimsatt (1972). The claim that "flowers have bright petals because they attract pollinators" can be construed as teleological, but it is perfectly acceptable from the perspective of contemporary scientific orthodoxy (Sober 2012; see also Garson 2019: 25–28; Neander 1991b). Ruse (2019: 54) says that neo-Darwinism "is teleological, allowing final-cause explanations," but that "this teleology is all bound up with metaphor….[T]he final causes of biology come into being because of efficient causes." It could be that Darwin metaphorically ascribed teleological final causes to naturally selected traits while, like neo-Darwinians, believing natural selection to be driven by efficient as opposed to teleological causation.

Richards (2013: 24), however, argues that Darwin was a "nineteenth-century thinker" who was unable to shake the habit of thinking in terms of "final causes" in a way that modern science rejects as illegitimate. According to Richards, Darwin saw natural selection as "like a refined and morally concerned agent" whose "teleological goal…was the production of human beings with their moral sentiments" (ibid.: 27, 34). Beatty (1990) notes that the controversy about whether Darwin was a teleologist dates back to the 1860s. At that time, "Darwin was both praised and criticized for abandoning teleology…, but he was also praised and criticized for not doing so" (ibid.: 124). The eminent Swiss physiologist Albert von Kölliker condemned Darwin for being, "in the fullest sense of the word, a Teleologist" (quoted in Huxley 1864: 567; Beatty 1990: 127). In response, "Darwin's bulldog" Thomas Henry Huxley stated that, upon reading the *Origin*, he was "most forcibly" struck by the

> conviction that Teleology, as commonly understood, had received its death blow at Mr. Darwin's hands….If we apprehend the spirit of the 'Origin of Species' rightly then, nothing can be more entirely and absolutely opposed to Teleology, as it is commonly understood, than the Darwinian Theory. So far from being a 'Teleologist in the fullest sense of the word,' we should deny that he is a Teleologist in the ordinary sense at all. (Huxley 1864: 567, 569; partially quoted in Beatty 1990: 131)

---

[1] Sterelny and Griffiths (1999: 37) propose a fourth requirement for natural selection, namely, "the conditions admitting of cumulative selection" should prevail. For example, the mutation rate cannot be too high relative to the strength of selection (ibid.: 36). Although they say that it is the "absence of any overseeing agent that makes natural selection natural" (loc. cit.), their fourth condition does not distinguish natural selection from artificial selection or intelligent design.

On the other hand, the American botanist Asa Gray congratulated Darwin for proposing a theory that, "if we understand it, would leave the doctrines of final causes, utility, and special design just where they were before" (Gray 1860: 412; quoted in Beatty 1990: 125).

Regardless of how Darwin personally conceived natural selection, I think Ghiselin (1994: 489) is right that he "developed a new way of thinking that allows us to dispense altogether with that metaphysical delusion" of teleology (understood in the illegitimate sense). The fact that Darwin might not have succeeded in completely escaping this delusion—that he failed to follow his own line of thinking to its logical conclusion—does not negate the fact that undirectedness came to be recognized as a sine qua non of natural selection by *neo*-Darwinism. To use Ghiselin's apt expression, Darwin allowed *us* to make this leap.

Regarding the third reason for distinguishing natural selection from guided and directed evolutionary processes—scientific precedent—it is true that the models used to describe evolutionary change are generally blind to how variation is introduced or where selection pressures come from. Whether the furin cleavage site in the spike protein of SARS-CoV-2 was the result of genetic engineering or natural mutation makes no difference to how we model the evolution of the virus. Whether the slowest horses in a population are removed from the breeding pool by a human breeder (artificial selection) or by hungry wolves (classic natural selection), the effect on speed in the offspring generation is the same.

However, evolutionary biologists do sometimes distinguish between natural and artificial selection. In a widely used textbook on quantitative genetics, Gillespie (1998: 114–115, 118) treats natural and artificial selection as separate forces that can be opposed to each other. He describes experiments where fruit fly (*Drosophila*) populations are artificially selected to have a larger or smaller number of bristles. It turns out that, when artificial selection ends, the populations revert back to some extent toward the original number. Gillespie writes: "One possible explanation is that there is an optimal number of bristles and that natural selection moves the population back toward the optimum once artificial selection is stopped.…[N]atural selection opposes artificial selection for lower bristle numbers" (ibid.: 115, 118). In another famous textbook, Falconer and Mackay (1996: 343) make similar comments about the same experiment, implying that natural and artificial selection are different: "If artificial selection is carried out and is then suspended before much of the variation has been lost by fixation, natural selection must tend to bring the gene frequencies back toward their equilibrium values, and the mean of the character artificially selected is expected to revert toward its original value." Roff (1997: 154) refers to a scenario where "artificial selection in one direction is opposed by natural selection." If scientists sometimes treat natural and artificial selection as distinct phenomena, it will be helpful to have a criterion to separate them.

The no teleology condition

Natural selection can be distinguished from artificial selection, intelligent design, orthogenetic selection, and adaptation via the selection of nonrandom variation by adding a *no teleology* condition.

No teleology The evolutionary process is not teleological.

On the neo-Darwinian view, natural selection involves the "nonrandom selective retention" of "random variation"—that is, variation produced by random mutation (Sober 2000: 38). In this context, "random mutation" means that "[t]he variation generated by mutation…is not directed to produce a predetermined adaptive end" (Haig 2007: 426), not that all mutations are equally likely (Charlesworth et al. 2017: 1; Futuyma and Kirkpatrick 2017: 95; Haig 2007: 426; Okasha 2019: 16; Sober 2000: 37). Teleology can be introduced at either the mutation stage or the selection stage. First, mutation can be nonrandom with respect to adaptation. Second, selection pressures can be forward looking in the sense that they favor traits based (at least in part) on their contribution to future evolutionary outcomes.

What does it mean to be "teleological" or "forward looking"? To put it in very general (and somewhat circular) terms, a process is "teleological" when it aims at a telos—an end. The paradigm case of teleology is when an agent pursues a goal—the kind of behavior we perform all the time. Aristotle construed the laws of physics as teleological. For example, a rock falls to the ground because it strives toward the center of the earth (its telos). According to the usual story, teleology was jettisoned from physics in the scientific revolution of the sixteenth and seventeenth centuries, but it persisted in biology until Darwin's theory of natural selection provided a mechanistic account of the development of life (cf. Beatty 1990). In Aristotelean terminology, Darwin gave an account based on *efficient causation*.

When God guides evolution in order to achieve his purpose, this is paradigmatically teleological. But it is not clear what it means for there to be a telos in the absence of an agent who intends and strives. There may not be a simple, unifying concept of teleology that covers both goal-directed behavior by agents and (hypothetical) forward-looking natural forces that may or may not be metaphysically reducible to efficient causes. If agential interference in the evolutionary process, orthogenetic selection, and adaptation via the selection of nonrandom variation should not be classified as "natural selection," the *no teleology* condition will have to invoke different concepts of "teleology"—different ways of aiming at a telos. I will classify these under two headings: "agential teleology" and "natural teleology." I address these two types of teleology, in turn, in the following two sections.

Agential teleology

The first concept of teleology can be described as follows:

Agential teleology A process exhibits agential teleology if it is guided toward an end that is represented in the mind of an agent.

The evolutionary process exhibits agential teleology when an agent—such as a breeder, a genetic engineer, or a divine intelligent designer—introduces mutations nonrandomly with respect to, or selects heritable variants with reference to, a mentally represented endpoint. The endpoint could be the species' biological success (however that is defined) or something else valued by the agent, for example, the possession of moral intuitions, a *sensus divinitatis*, a parasite-resistant surface, or greater milk production. Suppose an agent wants to guide the evolution of a corn population toward greater parasite resistance. The agent could directly alter corn genomes to produce this outcome, and/or selectively preserve and plant seeds from the most parasite-resistant plants.

If God created the world and then allowed natural forces to operate unguided, there would be no agential teleology in evolution. Thus natural selection is compatible with deism—the theory that God is an aloof creator. Incidentally, until at least 1860, Darwin took it for granted that natural laws require divine support, and he did not completely abandon this view until the end of that decade (Richards 2013: 31–32).

A process does not display agential teleology merely in virtue of being influenced by an agent—or even in virtue of being influenced by an agent in a predictable way. The agent must direct the process *toward a mentally represented endpoint*. Predation by lions predictably leads to populations of fleeter gazelles. But when lions chase their quarry they do not have a mental representation of this (from their point of view unfortunate) outcome. If anything, their mentally represented endpoint is simply themselves feasting on gazelle meat. It makes no difference if the agent is supernatural. Suppose God never deliberately intervenes in evolution, but occasionally he performs miracles, which, if only via the butterfly effect, cause mutations or result in deaths or births that would not have otherwise occurred. This could result in evolutionary change (i.e., a change in the frequency or combination of genes) on a small or even on a large scale. But if these changes are random with respect to God's plan, as far as evolution is concerned, there is no agential teleology.

Agential teleology does not require conscious awareness in the agents of the effect of their actions. It is possible to guide a process toward a mentally represented telos, but unconsciously.

We can make a distinction between *conscious* and *unconscious* selection, which cuts across the distinction between natural and artificial selection. Conscious selection—what is normally called *breeding* or, when God does it, *intelligent design*—is a paradigm type of artificial selection. It occurs when an agent with some understanding of heritability chooses individuals with certain traits for propagating the next generation in order to bring about a desired evolutionary goal. For example, breeders select the fastest horses to reproduce with each other so their offspring will inherit the ability to win races.

Darwin (1859: 36) coined the term "unconscious selection" to describe what happens when agents preserve organisms with the most desirable characteristics (the sweetest corn, the friendliest wolf) and discard the others without conscious awareness that this will drive evolution toward a specific endpoint. In his words, it is "that which follows from men naturally preserving the most valued and destroying the less valued individuals, without any thought of altering the breed" (Darwin 1868: 193). He explicitly distinguished unconscious selection from natural selection, listing them as separate forces (ibid.: 193–194). He did not think there is a sharp line separating unconscious selection and breeding. He wrote:

> Unconscious selection graduates into methodical, and only extreme cases can be distinctly separated; for he who preserves a useful or perfect animal will generally breed from it with the hope of getting offspring of the same character; but as long as he has not a predetermined purpose to improve the breed, he may be said to be selecting unconsciously….[E]xcept that in the one case man acts intentionally, and in the other unintentionally, there is little difference between methodical and unconscious selection….Unconscious selection so blends into methodical that it is scarcely possible to separate them. (ibid.: 193–194, 210–211)

But Darwin overlooks the distinction between teleological unconscious selection, which is analogous to breeding, and nonteleological unconscious selection, which should be classified as a kind of natural selection. Breeding—what he calls "methodical" selection—is, of course, paradigmatically teleological. On the other hand, unconscious selection can be either teleological or nonteleological depending on whether the agents impose selection pressures based on a *representation* of a telos. *Nonteleological* unconscious selection occurs when the agents *choose what they prefer without reference to a mentally represented paradigm*, and as a side effect drive evolution in a certain direction. For example, by sharing food with the friendliest wolves, people created selection pressures that led to the evolution of dogs, but presumably without having an image of a dog in their minds. In contrast, *teleological* unconscious selection occurs when agents *choose what best conforms to a mentally represented paradigm*, and unintentionally drive evolution toward that outcome. It is teleological for the same reason as breeding, namely, the relevant selection pressures are shaped by agency in response to a mental representation of an endpoint.

Some evolutionary theorists, including Darwin (1859: 88) and Mayr (2001: 137–138), distinguish natural from sexual selection. On my account, *under normal circumstances* sexual selection is nonteleological and therefore a kind of natural selection. It involves selecting a preferred mate among the options available, but generally (and presumably in all nonhuman cases) without having an explicit mental representation of an ideal mate. In humans it is possible to choose a partner based on a mentally represented paradigm, or even as part of a deliberate plan to endow our offspring with certain traits. Sexual selection could theoretically be teleological, and teleological selection may be a (probably minor) component of sexual selection in our species.

According to Boehm's (2012) influential theory, humans evolved a *conscience* via what he calls "social selection." He argues that human societies were originally arranged like those of chimpanzees (*Pan troglodytes*), ruled by an alpha male mainly for his own benefit. When our ancestors made the transition to big-game hunting around 250,000 years ago, coalitions of subordinate males overthrew their alphas and instituted “reverse dominance hierarchies.” They created a “blueprint” (Boehm 1999: 12, 193–194) for what they saw as desirable social arrangements. The blueprint demanded political egalitarianism among adult males as well as group-beneficial behaviors such as meat sharing. People who violated the rules faced fitness-reducing punishments. This created selection pressures for a tendency to internalize group rules—that is, to have a conscience.

The process Boehm describes is a kind of teleological unconscious selection. The scientific merit of his theory is irrelevant for the present purposes. But it is interesting to note that, if the theory is correct, it would mean that our evolved moral faculty is not the product of natural selection—a fact that could have implications for evolutionary debunking arguments in ethics (Cofnas 2023).

Some theorists use the term “social selection” to refer to selection pressures arising from any kind of social interaction (e.g., West-Eberhard 1979; cf. Roughgarden 2007). For example, social selection occurs when individuals compete with each other to be chosen as cooperation partners, which generates selection pressure for qualities that make one an attractive partner (Nesse 2007). Social selection in this sense is a kind of natural selection except in cases where the social selectors favor or disfavor traits under the guidance of a mentally represented paradigm.

Human interventions to control the population numbers of a species do not infuse agential teleology into evolution because they do not aim to produce *evolution*. Evolution is normally defined as a change in the frequency or combination of genes in a population (Sober 2000: 1–4). Although the expansion or contraction of a population can be ecologically significant, it does not per se constitute “evolution” (ibid.: 5). If farmers release green lacewings (*Chrysopidae*) into their fields in order to exterminate as many European corn borers (*Ostrinia nubilalis*) as possible, this may involve agential teleology, but the goal is not to change the course of evolution. Similarly, governments issue hunting licenses with rules designed to keep the ecosystem in what is regarded as a desirable equilibrium. Hunters may be given permission to kill a certain number of deer in order to prevent a population explosion. Such interventions might *cause* heritable variation to be selected, and therefore lead to evolutionary change. For example, they could increase the force of selection for camouflage in corn borers, or skittishness in deer. But this effect is not intended by the human interveners even if they predicted that it might happen. In other words, evolution is not being purposively guided toward this outcome.

Researchers sometimes construct artificial environments to test how populations of, for example, fruit flies will evolve. If they arrange the initial conditions in order to guide the evolution of the population toward a specific outcome, then this is breeding. But in cases where they do not intend to select for a specific outcome, the researchers are analogous to a noninterfering deity who created the world and lets evolution take its course. The unguided evolution of fruit flies in an artificial environment would be driven by natural selection, albeit natural selection operating under unusual circumstances.

Natural teleology

What does it mean for a process to be teleological in the absence of agency? The basic idea can be stated as follows:

Natural teleology A process exhibits natural teleology if it is forward looking with respect to an end that is not represented in the mind of an agent.

But this will not be particularly illuminating until we explain what "forward looking" means.

"Forward looking" in this context cannot mean backward causation—that the final result of the process retroactively causes the earlier stages. Besides the fact that backward causation may be impossible (Black 1956; cf. Horwich 1987: ch. 6), a (natural or agential) teleological process can fail to reach the end stage (Hawthorne and Nolan 2006: 274). A rock that (according to Aristotle) teleologically strives to reach the center of the earth may never make it there. Your soufflé may collapse so that the envisioned product is never realized.

On Lewis's account, a law of nature is a generalization that maximizes *simplicity* and *informativeness* (e.g., Lewis 1999: 41). Hawthorne and Nolan (2006) argue that it could be the case that, according to these criteria, the best formulations of certain laws are teleological. They give the hypothetical example of particles that spontaneously arrange themselves in a pyramidal shape. Given certain assumptions, the simplest and most informative generalization about the behavior of the particles would be framed in terms of their movement toward this end state rather than in terms of "the intrinsic features of the individual particles" (ibid.: 277).

I will not try to come up with a general account of what it means for a natural force to be forward looking. For the present purposes it is sufficient to define narrow concepts of teleology specifically as they apply to evolutionary biology.

Since natural selection involves random variation followed by nonrandom selective retention, natural teleology can be introduced at either stage. There can be *natural teleological mutation* or *natural teleological selection*. Most laypeople misunderstand "natural selection" as a process in which variation arises in response to the organism's needs, and they are oblivious to the fact that selection plays any role at all (Shtulman 2017: ch. 12). Among people who are aware of selection, it is likely that many see this, too, as a forward-looking process, given the natural human tendency to reason teleologically (Kelemen 2012). As I mentioned before, Darwin may have viewed natural selection as being "like a refined and morally concerned agent" aimed at producing human beings with moral sentiments (Richards 2013: 27, 34). Some forms of natural teleology in evolution may be compatible with *science*, but I contend that none are compatible with natural selection as conceived by neo-Darwinism. I address natural teleological mutation and selection in turn.

Natural teleological mutation

Sober (2014) imagines the following scenario. Blue organisms, which are prone to developing mutations that make their offspring red or green, are split into red and green environments. The organism has a selective advantage when its color matches its surroundings, since this provides camouflage. Sober suggests that "guided mutation" occurs when the following conditions are met. First, blues are more likely to produce mutant red offspring in a red than in a green environment. Second, blues in a red environment are more likely to produce mutant red than mutant green offspring. Third, blues are more likely to produce mutant green offspring in a green than in a red environment. Fourth, blues in a green environment are more likely to produce mutant green than mutant red offspring. This pattern of mutation can't be explained as the result of either red or green mutations being inherently more likely than the other, since which one is more likely depends on the environment. And it can't be explained as a result of either red or green environments being more mutagenic, because each environment is associated only with a greater likelihood of the mutation that is adaptive in that environment.

Although Sober does not describe guided mutation as "teleological," his account seems to express the basic idea of what it would mean for a mutation-production process to be forward-looking with respect to adaptation. If a mutation is guided by an agent, it is the product of agential teleology. Now we are interested in cases where a mutation is guided in the absence of agency, so we will have to add the qualification that the mutation is not caused by an agent.

Sober presents his account of guided mutation specifically using the example of blue organisms in red vs. green environments, but his idea can be generalized.

Binary variables M_1, M_2, E_1, and E_2 denote the following:

M_1 = the organism has mutation 1 that is adaptive for environment 1 but not environment 2.

M_2 = the organism has mutation 2 that is adaptive for environment 2 but not environment 1.

E_1 = the organism is in environment 1.

E_2 = the organism is in environment 2.

Natural teleological mutation Natural teleological mutation occurs when the following five conditions hold for some mutations 1 and 2 and some environments 1 and 2: (1) $\Pr(M_1|E_1) > \Pr(M_1|E_2)$. (2) $\Pr(M_1|E_1) > \Pr(M_2|E_1)$. (3) $\Pr(M_2|E_2) > \Pr(M_2|E_1)$ (4) $\Pr(M_2|E_2) > \Pr(M_1|E_2)$. (5) This is not (entirely) the result of agential teleology.

In other words, mutation 1 or 2 is more likely to occur when it is adaptive, this isn't because environment 1 or 2 is more mutagenic or because the organism is inherently more prone to having mutation 1 or 2, and the mutation process is not guided by an agent. (For simplicity, the model assumes that the environment can be in one of two discrete states. A more realistic but complicated model could treat environmental variation as a continuous variable.)

Natural teleological mutation could be the result of mystical Aristotelian forces that are rejected by modern science (e.g., Nagel 2012), but it could also be the result of mechanisms that arose via natural selection itself. As Sober (2011: 138; 2014: 40–41) observes, there is nothing in evolutionary theory that says that a capacity for guided mutation cannot evolve, though considerable evidence suggests that it has not evolved. Haig (2007: 427) notes that the same is true specifically in regard to the inheritance of acquired characteristics, which involves natural teleological mutation.

An evolved biological mechanism that produces natural teleological mutations would have two component parts: one that detects the state of the world (e.g., the environment is red or the giraffe's neck is stretched), and one that responds to this information by causing the appropriate mutation in the germline (e.g., for red coloration or a longer neck). Although the mechanism would not have a mind and therefore could not exhibit agential teleology, there is a naturalistic sense in which it could be said to be forward looking with respect to adaptation. Following Millikan's (1989: 285) naturalistic account of representation, for an evolved mechanism to respond to its environment dynamically, a "producer" device must create a signal that is read by a "consumer," which in turn executes a response. The representational content of the signal corresponds to what must be the case in order for the consumer to perform its function in the normal way. Applying this idea to natural teleological mutation, a Lamarckian giraffe would need to possess a physiological device that detects a stretched neck and produces a signal (by means of some chemical process) with the representational content of *stretched neck*. This signal would be read by another device, which produces a mutation for greater neck length in the germline. This kind of forward-looking control over the mutation process constitutes a means of adaptation that is different from natural selection, although the underlying mechanism (if it existed) would presumably be the product of natural selection.

According to Jablonka and Lamb (2005: 15), "Darwin would no doubt have been amazed to hear that many biologists today think that Lamarckian views about the inheritance of acquired characters contradict the fundamental assumptions of his theory of natural selection. They do not." Darwin would surely have been surprised that many biologists came to reject Lamarckian inheritance as heresy. But, as noted earlier, he saw this process as an alternative to natural selection, and he thought that natural selection depends on "accidental variability" (Darwin 1868: 248). As he said, natural selection is "the main but not the exclusive cause" of evolution (Darwin 1859: 6; quoted in Sober 2011: 19).

Jablonka and Lamb (2005: 7) argue that, as a matter of fact, "not all genetic variation is entirely random or blind; some of it may be regulated and partially directed. In more explicit terms, it may mean that there are Lamarckian mechanisms." They are referring in part to "directed mutation," which comes in two main varieties. First, *induced global mutation* occurs when organisms respond to stressful conditions by ratcheting down the mechanisms responsible for DNA maintenance and repair, leading to an increased rate of mutations in the germline. Second, *local hypermutation* occurs when some regions of the genome—*mutational hot spots*—have higher mutation rates than other regions (ibid.: 94). Both induced global mutation and local hypermutation have been observed in nature (though the former only in bacteria), and are probably evolved adaptations. Stress is a sign that the organism may not be well adapted to the environment and that its progeny would benefit from another roll of the genetic dice—that is, more mutations. Most mutations will be maladaptive, but some offspring could get lucky, and it's better to take a chance with new genes than to stick with old ones that aren't working. Mutational hot spots are formed from certain kinds of sequences that are conducive to errors in copying. They may be found in parts of the genome responsible for producing phenotypes that benefit from continual evolutionary change, such as the protein coat of a pathogen that must evade the host's constantly evolving immune system (ibid.: 323), or the venom of a snake that must defeat evolving venom resistance (ibid.: 96). Jablonka and Lamb say that mutations produced via induced global mutation "are nonrandom because they occur at a *time* when they are likely to be useful." Those produced by local hypermutation are nonrandom because they occur "at a genomic *place* where they are useful" (ibid.: 94). These, they say, are "Lamarckian processes" (ibid.: 102).

But directed mutation does not involve the Lamarckian inheritance of acquired characteristics. Lamarckian inheritance would mean that when an organism acquires phenotypic trait T a mutation arises in the germline that produces T in the offspring. Directed mutations are nonrandom with respect to time or place, but they *are* random with respect to the acquired characteristics of the parent.

Neither induced global mutation nor local hypermutation involves natural teleological mutation as defined above. Induced global mutation in response to stress meets the first condition—namely, a mutation is more likely to occur when it is adaptive—but it fails the second condition, since an adaptive mutation is no more likely than any particular maladaptive one. In the case of local hypermutation, the converse is true: under normal conditions, mutations in the mutational hot spot are more likely to be adaptive than a mutation outside a hot spot, but they are no more likely to occur *when* they are adaptive. That is, local hypermutation does not involve the production of adaptive mutations in response to a signal that represents the state of the world.

Sober (2014: 32) argues that evolutionary theory is *probabilistic* and not causally complete. Therefore, "evolutionary theory is logically compatible" with at least a limited form of divine intervention. "[W]hat biologists mean, or ought to mean, when they say that mutations are unguided says nothing about whether God ever causes a mutation to occur." Whether the mutation was caused by a stray cosmic ray, or by God, or by something else is irrelevant to the truth of the probabilistic statement.

One of Sober's (2014) concerns is to show that evolutionary theory (he avoids the term *natural selection*) can be accepted by religious believers who think that God at least sometimes meddles in evolution. On my account, if God causes a mutation specifically to bring about a desired outcome, this would be an exercise in agential teleology and—at least as far as this mutation and the resulting adaptation are concerned—a case of intelligent design. It may be that evolutionary theory is compatible with a limited amount of intelligent design, but not everything in evolutionary theory is natural selection.

Natural teleological selection

Natural teleological selection is what I originally called "forward-looking orthogenetic selection." This refers to a natural teleological force that influences survival and reproduction in order to guide evolution toward a predetermined endpoint. It can be illustrated with an example.

Suppose giraffes live on an island where foliage grows from zero to 15 feet. According to neo-Darwinism, average height in the population will be determined by the tradeoff between the benefits of being able to reach leaves up to 15 feet high and any other non-food-related benefits, and the costs of being taller. As it happens, the average height of the giraffes is 15 feet.

One day, birds from the mainland introduce seeds from the mythical cactacacia tree, which flourishes and supplants many native species. The cactacacia tree performs photosynthesis with its (to giraffes) inedible stem (like a cactus) until it reaches 20 feet, at which point it sprouts a large, flat crown of nutritious leaves (like an acacia tree). In this scenario, teleological selection would mean that 16-foot giraffes have a survival and reproductive advantage over 15 footers, ditto for 17 footers over 16 footers, and so on up to 20 feet, but they would not have such an advantage—*at least not to the same degree*—in the absence of cactacacia trees.

The idea of forward-looking selection without agency can be expressed as a probabilistic inequality, with the qualification that evolution toward the final trait is not entirely the result of agential teleology or teleological mutation.

Suppose there are three possible variants in a population, A, B, and C. B is an intermediate trait, meaning it is easier for the population to evolve from being predominately A to B to C than it would be to jump directly from A to C. In environment E_2 but not E_1, C would be favored by selection to perform function F, where the *function* of C refers to the effects of C that caused it to be favored by selection (Garson 2019; Millikan 1984: ch. 1; Neander 1991a, b). (E.g., if longnecked giraffes are more likely to survive and reproduce due to greater ability to reach high-up leaves and overpower their rivals, the function of a long neck would be to aid in foraging and fighting.) $A \rightarrow B$ denotes the population evolving from being predominately A to B across generations.

Natural teleological selection Natural teleological selection occurs when the following three conditions hold: (1) Given that B is an intermediate trait between A and C, and that C would be selected to perform function F only in E_2, $\Pr[(A \rightarrow B)|E_2] > \Pr[(A \rightarrow B)|E_1]$. (2) This is not (entirely) the result of B acquiring the ability to perform a function as a result of a shift from E_1 to E_2. (3) This is not (entirely) the result of agential teleology and/or natural teleological mutation.

(The model makes the simplifying assumption that the environment can be in one of two discrete states, and that there are three discrete traits. A more realistic model could treat both environmental and trait variation as continuous variables.)

In combination, conditions (1) and (2) say that the probability that a population evolves from being predominately A to B is sensitive to the probability that a population composed primarily of B's *would* evolve to be primarily C's. This is what is required for evolution to be *forward looking*. Again, the function of a trait is defined as its selected effects. The function of B cannot be to facilitate the evolution of C, because this effect has not happened at the time B was selected for—it is something that may or may not happen in the future. In this scenario, B is undergoing selection although it may have no function at all.

Condition (3) is necessary in order to distinguish natural teleological selection from other forms of forward-looking evolution. Natural teleological selection cannot be the result of agency, or else it would be equivalent to breeding or intelligent design. It cannot be the result of natural teleological mutation, or else it wouldn't be a *selection* process.

Natural teleological selection leading to C does not imply that this outcome is ever achieved. B is favored by selection (at least in part) because it is on the path to C, and C *would be* favored by selection to perform F.

Our giraffes originally averaged 15 feet, so A = being ~15 feet tall. The question is whether they will evolve from A to C = being ~20 feet tall, with intermediate B = being ~17.5 feet tall, in response to the introduction of cactacacia trees. Before the birds brought cactacacia seeds (E_1), the probability that a population of B's would evolve into C's was M. Thanks to the new trees (E_2), the probability is now N, and $N > M$. Neo-Darwinism says that the presence of a potential *future* payoff for C makes no difference to current natural selection for B, so $\Pr(A \to B)$ remains unchanged. In other words, $\Pr[(A \to B)|E_2] = \Pr[(A \to B)|E_1]$.

Neo-Darwinism does not say that it is impossible for the giraffes to ever evolve to reach the cactacacia leaves. Intermediate height may be selected for many reasons—for example, it may confer an advantage in intraspecies competition or signal fitness to potential mates. But *if* natural selection pressures are not sufficient to bring height up to 20 feet, the introduction of cactacacia trees will (ceteris paribus) not change this.

Unlike natural teleological *mutation*, it seems unlikely that natural teleological selection could be achieved via efficient causation. Theoretically, natural selection could fashion a mechanism that produces guided mutations. But, in the absence of agency, it is difficult to see how natural forces could detect the future advantage of certain traits and then manipulate the environment so that organisms with intermediate forms are more likely to survive and reproduce. Natural teleological mutation remains an unsupported but scientifically legitimate hypothesis. Barring radical developments in our understanding of the laws of nature, natural teleological selection will remain implausible.

New formulation

The standard formulation says that variation, differential fitness, and heritability are the core requirements for natural selection. I have argued that this is flawed. For historical, philosophical, and scientific reasons we should distinguish natural selection from certain other (real or hypothetical) means of adaptation that also involve heritable variation in fitness, namely, artificial selection, intelligent design, forward-looking orthogenetic selection, and adaptation via the selection of nonrandom variation. This, I suggested, can be done by adding a *no teleology* condition. The no teleology condition means that the evolutionary process is not guided toward an endpoint represented in the mind of an agent, variations are produced randomly with respect to adaptation, and selection pressures are not forward looking.

New formulation Natural selection requires variation, differential fitness, heritability, and no teleology.

Any population characterized by the four conditions listed in the new formulation will tend to evolve via natural selection. Natural selection does not depend on a specific mechanism of inheritance. Neo-Darwinians have historically focused on biological evolution where information is transmitted between generations by DNA, but DNA per se is not required. (Darwin of course knew nothing about DNA.) Individuals in a population may vary in fitness due to vertically transmitted epigenetic states or cultural practices that arose randomly with respect to adaptation or explicitly represented evolutionary outcomes. In such cases, fitness-promoting epigenetic and cultural variants can proliferate due to natural selection acting on their carriers (cf. Haig 2007: 421; Richerson and Boyd 2005: 76). Natural selection does not even require a biological substrate. If we released von Neumann probes—self-replicating, spacefaring robots—to colonize the galaxy, the probes themselves would be the product of agential teleology. But if random errors in the transmission of magnetically encoded information between generations led to differences in the ability to replicate, there would be natural selection in the probes.

Although it can be and sometimes is driven by natural selection, cultural evolution in our species is shot through with teleology. To varying degrees we are able to critically evaluate alternative beliefs, values, and practices and adopt those that we believe advance our explicitly represented short- and long-term goals. Institutions that are the product of conscious design may create selection pressures that cause people to evolve teleologically to conform to their demands (Boehm 2012; Cofnas 2018). The capacity for culture—while being itself mostly the product of natural selection—allows us to transcend the forces of blind selection and direct even our biological evolution.

Acknowledgements I am grateful to Alexander Bird, Richard Robb, Elliott Sober, Kim Sterelny, and two anonymous reviewers for helpful comments and discussion.

Funding This work was supported by the Leverhulme Trust and the Isaac Newton Trust.

Declaration

Conflict of interest The author declares no conflict of interest.

References

Ayala FJ (1970) Teleological explanations in evolutionary biology. Philos Sci 37(1):1–15

Ayala FJ (2007) Darwin's greatest discovery: design without designer. Proc Natl Acad Sci USA 104(1):8567–8573

Beatty J (1990) Teleology and the relationship between biology and the physical sciences in the nineteenth and twentieth centuries. In: Durham F, Purrington RD (eds) Some truer method: reflections on the heritage of Newton. Columbia University Press, New York, pp 113–144

Black M (1956) Why cannot an effect precede its cause? Anal 16(3):49–58

Boehm C (1999) Hierarchy in the forest: the evolution of egalitarian behavior. Harvard University Press, Cambridge, MA

Boehm C (2012) Moral origins: the evolution of virtue, altruism, and shame. Basic Books, New York

Bourrat P (2015) How to read 'heritability' in the recipe approach to natural selection. Br J Philos Sci 66(4):883–903

Bowler PJ (1983/2009) Evolution: the history of an idea, 25th anniversary edn. University of California Press, Berkeley

Brandon RN (1981) Biological teleology: questions and explanations. Stud Hist Philos Sci 12(2):91–105

Charlesworth D, Barton NH, Charlesworth B (2017) The sources of adaptive variation. Proc R Soc B 284(1855):20162864

Cofnas N (2018) Power in cultural evolution and the spread of prosocial norms. Q Rev Biol 93(4):297–318

Cofnas N (2023) How gene–culture coevolution can—but probably did not—track mind-independent moral truth. Philos Q 73(2):414–434

Darwin C (1859) On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. John Murray, London

Darwin C (1868) The variation of animals and plants under domestication, vol 2. John Murray, London

Dawkins R (1986) The blind watchmaker: why the evidence of evolution reveals a universe without design. Norton, New York

Dennett DC (1995) Darwin's dangerous idea: evolution and the meanings of life. Simon & Schuster, New York

Earnshaw-Whyte E (2012) Increasingly radical claims about heredity and fitness. Philos Sci 79(3):396–412

Falconer DS, Mackay TFC (1996) Introduction to quantitative genetics. Longman, Essex, England

Futuyma DJ, Kirkpatrick M (2017) Evolution, 4th edn. Sinauer Associates, Sunderland, MA

Garson J (2019) What biological functions are and why they matter. Cambridge University Press, Cambridge, UK

Ghiselin MT (1994) Darwin's language may seem teleological, but his thinking is another matter. Biol Philos 9(4):489–492

Gillespie JH (1998) Population genetics: a concise guide. Johns Hopkins University Press, Baltimore

Godfrey-Smith P (2007) Conditions for evolution by natural selection. J Philos 104(10):489–516

Godfrey-Smith P (2009) Darwinian populations and natural selection. Oxford University Press, Oxford

Gray A (1860) Darwin and his reviewers. Atl Mon 6:406–425

Haig D (2007) Weismann rules! OK? Epigenetics and the lamarckian temptation. Biol Philos 22(3):415–428

Hawthorne J, Nolan D (2006) What would teleological causation be? In: Hawthorne J (ed) Metaphysical essays. Oxford University Press, Oxford, pp 265–283

Horwich P (1987) Asymmetries in time: problems in the philosophy of science. MIT Press, Cambridge, MA

Huxley TH (1864) Criticisms on the origin of species. Nat Hist Res 8:566–580

Jablonka E, Lamb MJ (2005) Evolution in four dimensions: genetic, epigenetic, behavioral, and symbolic variation in the history of life. MIT Press, Cambridge, MA

Kelemen D (2012) Teleological minds: how natural intuitions about agency and purpose influence learning about evolution. In: Rosengren KS, Brem SK, Evans EM, Sinatra GM (eds) Evolution challenges: integrating research and practice in teaching and learning about evolution. Oxford University Press, New York, pp 66–92

Kronfeldner ME (2007) Is cultural evolution Lamarckian? Biol Philos 22(4):493–512

Kuhn TS (1962/2012) The structure of scientific revolutions, 50th anniversary edn. University of Chicago Press, Chicago

Lennox JG (1993) Darwin *was* a teleologist. Biol Philos 8(4):409–421

Lewens T (2007) Darwin. Routledge, London

Lewis D (1999) Papers in metaphysics and epistemology. Cambridge University Press, Cambridge, UK

Lewontin RC (1970) The units of selection. Annu Rev Ecol Syst 1:1–18

Lewontin RC (1985) Adaptation. In: Levins R, Lewontin RC (eds) The dialectical biologist. Harvard University Press, Cambridge, MA, pp 65–84

Mayr E (2001) What evolution is. Basic Books, New York

Millikan RG (1984) Language, thought, and other biological categories: new foundations for realism. MIT Press, Cambridge, MA

Millikan RG (1989) Biosemantics. J Philos 86(6):281–297

Nagel T (2012) Mind and cosmos: why the materialist neo-Darwinian conception of nature is almost certainly false. Oxford University Press, New York

Neander K (1991a) Functions as selected effects: the conceptual analyst's defense. Philos Sci 58(2):168–184

Neander K (1991b) The teleological notion of 'function'. Australas J Philos 69(4):454–468

Nesse RM (2007) Runaway social selection for displays of partner value and altruism. Biol Theory 2(2):143–155

Okasha S (2011) Précis of *Evolution and the levels of selection*. Philos Phenomenol Res 82(1):212–220

Okasha S (2019) Philosophy of biology: a very short introduction. Oxford University Press, New York

Richards RJ (2013) Darwin's theory of natural selection and its moral purpose. In: Richards RJ (ed) Was Hitler a Darwinian? Disputed questions in the history of evolutionary theory. University of Chicago Press, Chicago, pp 13–54

Richerson PJ, Boyd R (2005) Not by genes alone: how culture transformed human evolution. University of Chicago Press, Chicago

Roff DA (1997) Evolutionary quantitative genetics. Chapman & Hall, New York

Roughgarden J (2007) Challenging Darwin's theory of sexual selection. Daedalus 136(2):23–36

Ruse M (1975) Charles Darwin and artificial selection. J Hist Ideas 36(2):339–350

Ruse M (2019) The Darwinian revolution. Cambridge University Press, Cambridge, UK

Shtulman A (2017) Scienceblind: why our intuitive theories about the world are so often wrong. Basic Books, New York

Sober E (2000) Philosophy of biology, 2nd edn. Westview, Boulder, CO

Sober E (2011) Did Darwin write the Origin backwards? Philosophical essays on Darwin's theory. Prometheus Books, New York

Sober E (2012) Remarkable facts. Boston Rev. https://bostonreview.net/articles/remarkable-facts/

Sober E (2014) Evolutionary theory, causal completeness, and theism: the case of guided mutation. In: Thompson RP, Walsh D (eds) Evolutionary biology: conceptual, ethical, and religious issues. Cambridge University Press, Cambridge, UK, pp 31–44

Sterelny K, Griffiths PE (1999) Sex and death: an introduction to philosophy of biology. University of Chicago Press, Chicago

Weismann A (1904) The evolution theory. Edward Arnold, London

West-Eberhard MJ (1979) Sexual selection, social competition, and evolution. Proc Am Philos Soc 123(4):222–234

White RM, Hodge MJS, Radick G (2021) Darwin's argument by analogy: from artificial to natural selection. Cambridge University Press, Cambridge, UK

Wimsatt WC (1972) Teleology and the logical structure of function statements. Stud Hist Philos Sci 3(1):1–80