## Breaking Free from the Common Caricature of Evolution

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Picture a small, secluded lake hidden among the pines of an expansive mountain range. The surface shimmers in the summer sun, obscuring the bustling ecosystem that lives just below. We are, however, only interested in one particular inhabitant: A resilient population of small, yellow fish. These fish have thrived in the lake for millenia, their numbers left unchallenged by the lack of predator species. Below the placid waters, they wander the depths in search of their next meal, moving lazily to conserve energy.

Now imagine, over a long stint of geological time, a river comes to connect several of the neighboring lakes to the home of our yellow fish. The river serves as a highway for a biological exchange that ultimately introduces a large, vicious species of green fish to our beautiful, little lake. The yellow fish population plummets as they are consumed left and right by the green invaders. While the capacity to perform evasive maneuvers hadn't mattered before, amidst the ever-present threat of predation we find that only the most agile of yellow fish survive and reproduce. The offspring of these most elusive individuals tend to take after their parents and are themselves difficult to catch. Eventually, the lethargic species of fish we once knew is entirely replaced by a better adapted, more agile population of yellow fish.

This narrative is an archetypal illustration of evolution by natural selection and represents the fundamental process as Charles Darwin explained it and as most laypeople understand it today. This fact demonstrates that while the last ~160 years of research have illuminated much about the complexity of biological life and expanded on Darwin's model, our understanding of how evolution by natural selection works is often stuck in the past.

I hope to provide a more modern and detailed depiction of evolution by discussing how recent decades have revolutionized our conception of this critical process. To accomplish that task, we can begin by breaking down the prior scenario with our yellow fish.

Although it is intuitive to think about the trait of "agility" being passed down to each generation, we would be sacrificing nuance for simplicity. In reality, we know that there are numerous genes that help determine the traits, or 'phenotypes,' that we perceive as agile. While the fish who host these genes live and die, the genes survive beyond. Through replication the gene becomes the sole survivor of natural selection, and therefore only the genes can be natural selection's primary beneficiary.

This argument was popularized by Richard Dawkins' groundbreaking book The Selfish Gene which reoriented the evolutionary biology community toward a focus on the gene rather than the organism. Dawkins described evolution in terms of replicators and vehicles. In his mind, replicators were the genetic material and the organism was simply a vehicle which facilitated the interaction between a replicator and its environment via gene expression in one direction and selection in the other. The paradigm shift launched by Dawkins' work was challenging, but it seemed to elegantly integrate the observations of evolutionary biology with the current understanding of genetics (Dawkins 1976).

Through this lens, some of the oddest behaviors in the animal kingdom become intelligible. For example, the willingness of individual bees to end their own lives for the wellbeing of the hive seemed a puzzling exception to the competitive selfishness ubiquitous in nature. However, using his conceptual framework, Dawkins explains that "the death of a single sterile worker bee is no more serious to its genes than is the shedding of a leaf in autumn to the genes of a tree" (Dawkins 1984). While we are conditioned to recognize the organism level of the biological hierarchy, using our gained understanding of genetics, we can extend Darwin's theory into places it previously seemed to falter, such as the beehive.

Despite the success of Dawkin's conceptual framework, the theory was not without its critics, especially from the field of philosophy. The philosophy of biology is sometimes perceived as too abstract or not applied enough for many of the more practically-minded biologists, but the leaders of this discipline have an undeniable influence on experimental approach and interpretation within biology. This influence warrants careful consideration of any protest philosophers may pose.

Philosopher and biologist Stephen Gould presents one of the most notable objections to Dawkins' work by advocating for the replacement of the term vehicles with "interactors". Gould argues that it is critical for us to think about how replicators actually interact with their environment and receive selective pressure. In his mind, an organism is not simply a vessel through which genetic material rides, but rather an essential point of communication by which selection confers differential reproduction onto replicators (Gould 2001). Gould pinpoints the distinction between Dawkins and himself by stating that the difference between them lies in casualty. While Dawkins is willing to concede that everything outside of the replicator can ultimately be thought of as merely part of the environment, Gould and other philosophers worry that this framework threatens the fundamental logical application of cause and effect in evolution. This belief is summarized in a rhetorical passage of Gould's The Structure of Evolutionary Theory: "Why don't I just consider higher-level interactors as one aspect of the gene's environment? In that case, why should I talk about higher-level interactors as entities at all? Environment is environment, however constituted, and whether clumped into interactors housing the genes or not? In fact, why even try to identify the environment's forms of dumpiness? Why not, instead, simply average the gene's fitness over all aspects of the environment to achieve a single measure of the gene's evolutionary prowess? This line of argument, as its least attractive feature, relentlessly dissolves causality" (Gould, 2002).

Here we can see that even in Dawkins best case, where his view more accurately reflects the reality of evolution, adopting his terminology requires us to forfeit some of the explanatory power we gain by imagining evolving bodies as replicators and interactors. Gould asserts that if we view organisms and other higher-level entities as humble vehicles they can be lost among the rest of the environment, impeding our ability to make specific causal claims about gene fitness. Using the interactor framework allows us to better isolate and study specific selective pressures and more precisely to predict how changing these variables may alter the course of evolution.

Furthermore, once we accept an evolutionary worldview defined by replicators and interactors, the nature of biological life unfurls into a beautifully complex and connected hierarchy. Since interactor is a flexible term that can apply at any level where selection is occurring, not only can genes and organisms be interactors, but so can groups. As animals whose own evolution is deeply interwoven with socialization and group living, people have been particularly engaged by this idea of group level selection.

One of the prominent authors on group selection is Elliot Sober. In his book The Nature of Selection: Evolutionary Theory in Philosophical Focus, Sober asks us to imagine how different levels of selection interact by using altruism as an example. Grant that there is a group of organisms who are each either altruistic or selfish and that altruistic groups are more productive due to the sharing of resources. Sober posits that being selfish in a group full of altruists provides an individual a huge selective advantage, creating pressure at the organismal level to become more selfish. However, if we compare different colonies originating from this hypothetical population, we will find that the most altruistic of colonies have higher reproductive rates and chances of survival. In this fascinating example, Sober illustrates how selection can not only be imagined at multiple levels, but that the selection at these different levels can be in opposition (Sober 1984).

Leonard Nunney grounds this thought experiment by suggesting that similar mechanisms might have been at play in the evolution of sexual reproduction. In The Maintance of Sex by Group

Selection, Nunney hypothesizes that the early development of sex may have been characterized by a selective battle between the group and organismal level. He argues that, even though organism level selection may favor asexual reproduction where 100% of the genes are passed on to offspring, "the net result of group selection is that sex is maintained because of its lower extinction rate (or higher speciation rate) and because asexual mutants only rarely arise" (Nunney 1989). In groups exhibiting sexual reproduction, we observe a more genetically robust population that can better withstand environmental pressures. We can even extend this hypothesis to think about how groups containing asexual variants of a species might compare to another group of sexual variants. The conferred advantages in genetic diversity may allow one group to out compete the other and change the trajectory of the lineage.

Returning back to our yellow fish, we are now presented with an entirely new range of questions. How do the multitude of genes present in the fish emerge as different degrees of agility? How does our understanding of the evolution of these fish change if we think about their selection on the level of small groups (schools) or even the whole lake population? How does the frequency of "agile genes" change intragroup competition and selection? Engaging with the last 50 years of philosophic debate in biology and the observational findings that have motivated those discussions can help us shed our oversimplified conceptions of evolution and ask new questions.

Even if you are not committed to a career of biological inquiry, there are still takeaways here that are fundamental to how we understand ourselves and the natural processes that gave rise to us. Evolution in the general sense is a closed case, but very real and deep specifics remain a challenge. The debate summarized in this article is testament to the honest and humble struggle humans endure as we attempt to grapple with a process that acts on a time scale and through such complex relationships that its reality is unimaginable to us. We define and debate terminology and concepts that we wield like blunt instruments, scratching only an abstraction of what evolution really is. Science is a method for defining and refining approximations of truth through experimentation, discussion, and observation. We recognize evolution as the incredible process that created us, but a true understanding elicits the even more beautiful, yet frustrating realization that it gave us the curiosity to study it but perhaps not the cognitive ability to fully grasp it.

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