E.O. Wilson, groundbreaking figure in evolutionary biology, dead at 92

Philip Guelpa
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Edward O. Wilson, known as E.O. Wilson, who died last month at the age of 92, was a major figure in the field of evolutionary biology. He made significant contributions to the study of animal behavior, biodiversity, and environmental conservation. However, he is perhaps best known for the controversies stemming from his attempt to found a field of study he called sociobiology, which places great emphasis on the genetic determination of animal and human behavior.

During his career, Wilson wrote, cowrote, or edited over 30 books. He was awarded the Pulitzer Prize twice—once for *On Human Nature* (1979) and, as coauthor, for *The Ants* (1991).

Born in Birmingham, Alabama, in 1929, Wilson earned bachelor's and master's degrees at the University of Alabama. He went on to receive his Ph.D. from Harvard University in 1950, and joined the faculty there in 1956, where he remained for a remarkable 46 years.

His early research was focused on insects, ants in particular—how they communicated chemically using pheromones and how they diversified and spread geographically. Through studying the distribution of ant species across islands, he developed mathematical models to predict their spread and differentiation—echoing and expanding on Darwin's study of species diversity in the Galapagos Islands. He has been dubbed by some, "Darwin's natural heir."

Wilson tested his model in the Florida Keys by eradicating all insects from small, uninhabited islands and then documenting how immigrants re-established themselves and achieved stable ecosystems. He also conducted extensive field research in the Caribbean and South Pacific during the 1940s and 1950s. During his career, he is credited with having identified and described over 450 species of ants.

Based on this research, Wilson, in collaboration with biologist Robert MacArthur, wrote *The Theory of Island Biogeography* in 1967, which became a seminal work in the field of ecology. In turn, this approach has been applied to the understanding of biodiversity and the interactions between species, enabling predictions regarding how many species a variety of environments could hold, the impact of habitat destruction on species extinctions and the stability of ecosystems.

Wilson's attention then turned to the study of how natural selection molded animal social behavior, including that of humans. He found that classical evolutionary theory had difficulty explaining the behavior of social animals such as ants. Instead, he drew on the work of William Hamilton, who had proposed the concept of "inclusive fitness."

According to classical evolutionary theory, reproductive success, the passing on of one's genes to offspring, defines the concept of "fitness" of an individual in its environment. The more offspring an individual produces who themselves survive to reproduce, the more that individual's genes increase in its species gene pool (the individual is more "fit"), compared to other individuals who are less successful in a given environment. This was the standard understanding of natural selection.

In effect, organisms are merely mechanisms for the reproduction of genes (i.e., DNA). Genes that promote the survival of those individuals which bear them tend to be perpetuated themselves and increase in frequency within a population or species. Those genes that are less successful in promoting the survival and reproduction of their bearers in a given environment diminish and eventually disappear. Thus, evolution occurs. Under this model, the effective entity subject to natural selection is the individual organism, which is either successful or not in passing on its genetic material.

Hamilton proposed that among social animals, genes may perpetuate themselves and spread by promoting individual behaviors that benefit not only the individual, but the group to which they belong. In this model, genes that promote the survival and reproductive success of close relatives, or the group as a whole, can spread if an individual with those genes promotes the reproduction (fitness) of others who carry the same genes. Thus, among relatives, an individual's fitness may be "inclusive": it may refer not only to their own reproductive success, but to the success of others.

In a 1963 paper, Hamilton described his conception as "inclusive fitness," under which the unit of natural selection is the gene, not the individual. According to this model, if an individual's actions, even to the point of that individual's own demise, and consequent failure to reproduce, promote the propagation of the group's genetic information (e.g., altruistic behavior, such as giving an alarm call that alerts other members of the group to the presence of a predator), that fulfills the evolutionary imperative of reproductive success of that set of genes, even if that particular individual does not reproduce.

Wilson sought to interpret the behavior of ants as gene bearers for such a group, and not merely as autonomous, individually reproducing individuals.

Most ants live in highly structured colonies, with a well-defined division of labor. Each colony is composed of a queen, whose primary function is reproduction. The female offspring, the workers, are normally sterile, performing all the tasks necessary for maintenance of the colony, including the collective raising of offspring. Males have only one function, fertilizing future queens. Species in which members of a group have genetically and/or developmentally determined differential reproductive capacities and other highly defined tasks are termed "eusocial." This is mostly seen in ants, bees, wasps, termites, and a very limited number of mammals (naked mole-rats). From a reproductive perspective, colonies of ants and other eusocial animals may be viewed as the equivalent of a single, multi-cellular organism, rather than a collection of autonomously reproducing individuals.

It should be noted that, in the overwhelming majority of cases, any single gene is not expressed individually but in combination with many other genes to produce the whole organism, greatly reducing the exposure of single genes to direct selective pressure.

The controversy over "Sociobiology"

Nevertheless, Wilson sought to apply a gene-centric model, which gained acceptance among biologists in the context of a burgeoning genetic revolution, to understand the behaviors of all animals. *Sociobiology: The New Synthesis*, published in 1975, presented Wilson's view that "The organism is only DNA's way of making more DNA." Based on this understanding, he argued that social behavior, including that of humans, could be explained as a product of natural selection differentially acting on the variety of genetic material in a species.

The publication of *Sociobiology* initiated a great deal of controversy. So much so that its review in the *New York Times* was placed on the paper's front page. While its proposals regarding social behavior in animals have had an impact on subsequent research, those regarding that of humans have also drawn criticism. Many viewed Wilson's arguments as a form of biological determinism, or "reductionism": the attitude that simple processes may explain complex phenomena that in fact require more sophisticated explanation.

Wilson proposed that humans have a weak form of "eusociality," such that the behavior of individuals and their roles in the social group is partly controlled by genetics. Some critics, including his Harvard colleagues, Stephen Jay Gould and Richard Lewontin, accused Wilson of biological determinism, Social Darwinism, and even alleged that his ideas logically supported eugenics and genocide.

In his preface to the 2000 edition of *Sociobiology*, Wilson pushes back against critics who accuse him of "reductionism." Specifically referring to Gould and Lewontin, whom he describes as the "last of the Marxist intellectuals," Wilson characterizes these critics as advocating a "tabula rasa" view of human behavior—that there is no genetic influence at all, which he says suits their aim for socialism to be "fitted" to the human mind, apparently implying indoctrination.

He goes on to reject the position of other critics, associated with the "New Left," who opposed sociobiology on the grounds that it could lead to the conclusion that behaviors such as "racism, sexism, class oppression, colonialism, and—perhaps worst of all—capitalism!" could be genetically based. In one notorious incident, a protester doused Wilson with water, yelling "Wilson, you are all wet!"

A review of Wilson's discussion of human behavior in *Sociobiology* reveals that while he seems to take a more nuanced view than some critics suggest, fundamentally, despite protestations to the contrary, he fails to appreciate the qualitative difference between human behavior, based on abstract, symbolic thought, and a huge store of culture, and that of other animals.

He states, "Human societies have effloresced to levels of extreme complexity because their members have the intelligence and flexibility to play roles of virtually any degree of specification, and to switch them as the occasion demands." And, furthermore, "Roles in human societies are fundamentally different from the castes of social insects."

In his preface to the second edition of *Sociobiology* (2000), Wilson states, "in the creation of human nature, genetic evolution and cultural evolution have together produced a closely interwoven product." And as well: "The exact process of gene-culture coevolution is the central problem of the social sciences and much of the humanities, and it is one of the great remaining problems of the natural sciences."

Some of his discussion involves behaviors that are so basic as to be likely to have a substantial genetic component. For example, he proposes that there are "epigenetic rules" (i.e., in which non-genetic factors, such as environment or learned behavior, modify genetic expression) which provide general frameworks for such things as classification of color, aesthetic evaluation of shapes, acquisition of fears and phobias, communication via facial expression and body language, "and so on across a wide spread of categories in behavior and thought. Most of these rules are evidently very ancient, dating back millions of years in mammalian ancestry. Others, like the ontogenetic steps of linguistic development in children, are uniquely human and probably only hundreds of thousands of years old."

Culture, class and evolution

However, Wilson's discussion of more complex aspects of human behavior fails to make clear the overwhelming predominance of culture over biology.

An important topic raised by Wilson is that of social class in human societies. "A key question of human biology is whether there exists a genetic predisposition to enter certain classes and to play certain roles."

At first, he states, "A strong initial bias toward such stratification is created when one human population conquers and subjugates another, a common enough event in human history. Genetic differences in mental traits, however slight, tend to be preserved by the raising of class barriers, racial and cultural discrimination, and physical ghettos."

But then, "Yet despite the plausibility of the general argument, there is little evidence of any hereditary solidification of status." And further, "Powerful forces can be identified that work against the genetic fixation of caste differences. First, cultural evolution is too fluid."

Scientific research has demonstrated time and time again that there is absolutely no basis for the proposition that there are any differences in intelligence or any other significant behavioral characteristic within or between various modern human populations. Nevertheless, Wilson, leaves the door open to the possibility that such differences may exist. Is this merely a prudent scientist's caution or does it betray underlying reservations?

With regard to cultural evolution, again Wilson provides contradictory statements. "Ethnographic detail [i.e., different cultures] is genetically underprescribed [i.e., has relatively weak genetic influence], resulting in great amounts of diversity among societies. Underprescription does not mean that culture has been freed from the genes. What has evolved is the capacity for culture, indeed the overwhelming tendency to develop one culture or another."

Few would dispute the first part of this last sentence. However, does this latter statement mean that the humans are somehow genetically driven to cultural diversity? How could that genetic influence be expressed? Again, Wilson is attempting to suggest some degree of genetic influence without providing any evidence to support his contention.

In an even more puzzling statement, Wilson is of the opinion that "Human beings are absurdly easy to indoctrinate—they seek it. If we assume for argument that indoctrinability evolves, at what level does natural selection take place? One extreme possibility is that the group is the unit of selection." This suggests that he believes humans' capacity for independent thought is somehow genetically limited and that some populations may be more susceptible to indoctrination than others.

There are numerous other examples of Wilson's attempt to have it both ways. One of the more troubling is his contention that warfare promoted a number of what he feels are important human traits: "including team play, altruism, patriotism, bravery on the field of battle, and so forth, as the genetic product of warfare." He goes on to suggest that groups with genes for aggressiveness would conquer and replace those that did not, thus creating a positive feedback loop for the spread of aggressive genetics.

But warfare is a recent development in human evolution, a product of class society. To imply that it is somehow a key influencer of human genetics has no scientific basis. Elsewhere, he rejects the contentions of

such popular authors as Konrad Lorenz (*On Aggression*) and Robert Ardrey (*African Genesis*) who claim that aggressive behavior was key to early human evolution.

Wilson rejected accusations that he was promoting a right-wing agenda, labeling them as “academic vigilantism” and criticized Gould and Lewontin in particular for what he labels as their “Marxism,” which he employs as a derogatory epithet without specific content.

There is no indication that he personally held reactionary views. It appears rather that he was led astray by an excessively mechanical view of human development, and as has happened all too frequently, tried to apply the laws of motion of one sphere of the natural world to another and more complicated sphere. Thus, in *Sociobiology*, he argued that ethics should be taken out of the hands of philosophers and, instead, “biologicized.” And, in his later work, *On Human Nature* (1978), he proposed that in the future, with a much deeper understanding of genetics, a “democratically contrived eugenics” could be implemented, indicating, at best, a political naivete with regard to its implications within class society. This clearly goes beyond medical interventions for physical ailments, implying behavioral modification through genetic manipulation.

In a more recent work, *The Social Conquest of Earth* (2012), Wilson appears to step back from rigid determinism. He characterizes humans as the “first truly free species,” and one which can, based on “simple decency” combined with “the unrelenting application of reason,” turn the earth into a “permanent paradise.” This, apparently, is to be accomplished by somehow freeing humans from the otherwise imperious domination of genetics. However, at the same time, he continued to contend that “free will” is an illusion.

Wilson’s conception of human social organization is a gross oversimplification, betraying a lack of knowledge of anthropology and sociology. Firstly, all members of a human social group can, at least potentially, reproduce (barring illness, etc.), contrary to the condition in eusocial species. There are certainly constraints on reproductive success in class-based societies. However, these are the product of social factors, not on any inherent genetically controlled differentiation. The same is true of all productive tasks, which are based on learned behavior.

Fundamentally, Wilson was unable to bridge the contradiction between a genetically constructed brain that evolved under natural selection and its unique capacity for abstract, symbolic thought, whose content is not genetically programmed. In fact, humans have long since evolved beyond behavior that is primarily controlled by their DNA. The problems facing humanity are social and political, not biological.

In retirement, Wilson devoted his energy to environmental conservation, producing many publications on the subject, including his 1992 book, *The Diversity of Life*, which became a best seller. He was an advocate of “Half Earth” which proposed that half of the earth’s surface, both land and water, be devoted to species conservation.

In sum, E.O. Wilson made historic contributions in the fields of ecology, biodiversity, animal behavior, and evolutionary biology. However, his attempt to explain at least a portion of human behavior as significantly controlled by genetics demonstrates a failure to understand that the development of culture as humanity’s primary mode of adaptation has created a qualitatively new level of organization. Just as biology cannot be explained “simply” by physics and chemistry, human behavior cannot be reduced to biology.