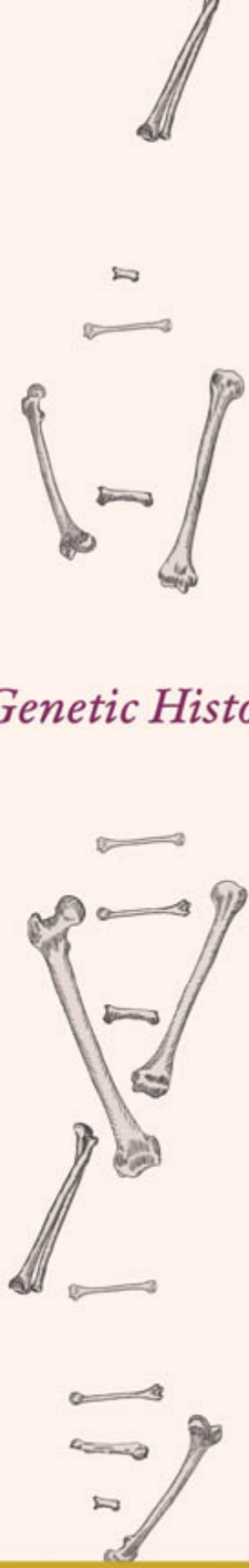
INEQUALITY

A Genetic History



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Preface

History is a nightmare from which I am trying to awake
—James Joyce, *Ulysses*

When I was a child, there were many history books at home that my father had bought—but that sadly, he never had the time to read. Even the street where we lived, in the Gothic Quarter of Barcelona, was made of history, with most of its buildings dating back to the Middle Ages. Ancient history was a matter of conquerors, dramatic quotes, bloody battles, and deaths. But the anonymous folks, the common people—the bulk of the population—were never even mentioned. Although my career gravitated toward evolutionary biology, history always remained my main intellectual interest. (One might argue, of course, that the two disciplines, along with astronomy, share one element: the time dimension.)

After years of working on Neanderthal genetics, I grasped that the novel DNA sequencing technologies could help us explore the recent human past using a new, multidisciplinary approach that integrated genetics, archaeology, anthropology, and even linguistics. In 2014, I led the retrieval of the first European forager genome from an eight-thousand-year-old skeleton and the next year the first early farmer genome from the Mediterranean.[1] In subsequent years, I continued this research with more projects, examining different archaeological horizons, mainly in collaboration with Harvard researcher and pioneer in the field David Reich. And as we moved closer to the present, we also started incorporating information from historical sources into the general picture—and sometimes challenging it. A common finding from these studies is that migration, and not just the propagation of ideas, was a prevalent phenomenon of the past and that modern human

populations were in fact shaped by successive layers of different genomic ancestries associated with these past population movements.[2]

One day, in a casual conversation about my work, my wife said that I tended to look into the past through a man's eyes and that the history of humanity—in fact a long road of suffering and discrimination, still going on for many—included women, no less than half the world's population. And she was right; though women are largely ignored in the old history books, they crucially bear each new generation of humankind. Just think how differently a legendary tale like the kidnapping—and by modern standards, subsequent rape—of Sabine women by Romulus and his companions in the early history of Rome, abundantly represented in art in a rather heroic manner, might be told from the female rather than the usual male perspective.

I realized that directly or indirectly, the new genetic studies were in fact revealing numerous layers of inequality in past societies, from the potential

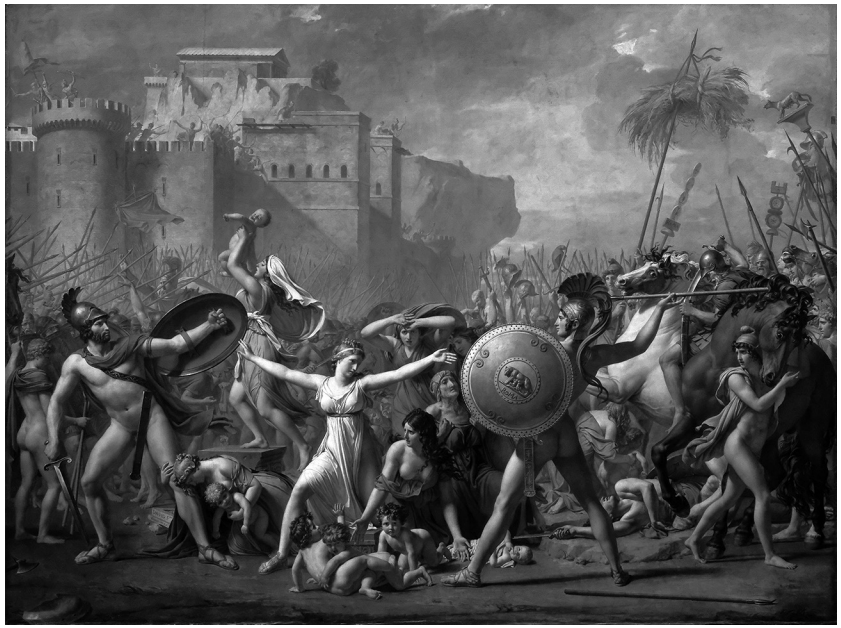

Figure 0.1
The Intervention of the Sabine Women, painted by Jacques-Louis David (1748–1825) in 1799 (on display at the Louvre Museum, Paris). This episode, recounted by Livy and Plutarch, was frequently depicted since the Renaissance as an inspiring example of ancient Roman heroism.

gender biases that we were unearthing in those migrations to the social structures implemented to maintain such inequalities as well as correlating wealth and social status with sex, kinship, and ancestry in cemeteries.[3] Powerful men of the past could have more offspring, from different women, than contemporaneous men that were left with no children—or with children who had less chance to survive.

Some recent studies set out to analyze the genetic composition of African slaves, and in conjunction with genomic analysis from recently admixed modern populations—notably those of the Americas—it was possible to reconstruct unequal reproductive patterns. Again, if we shift our point of view, certain anecdotes of the past, such as that George Washington's dentures were possibly made from teeth pulled out of the mouths of Black slaves, are all the more shocking and quite understandably have generated a broad range of reactions.[4]

Crucially, such patterns of inequality all left genetic marks that can be recognized in the genomes of ancient and modern human populations. Whenever I looked at a new genetic study, I saw new evidence of inequality and discrimination in different times and periods, and I decided to write this book to speak for those past figures who suffered the consequences. A number of baffling ideas came out of these observations. To mention but a few: those who sustained inequality in the past and had more offspring are more likely to be among our genetic ancestors, and if wealthy men could mate with multiple women and this was a prevalent pattern, then clearly women have contributed more than men to modern human genetic diversity.

Philosopher Walter Benjamin was right when he said, "It is a more arduous task to honor the memory of anonymous beings than that of famous persons."[5] But with genetic data, this task is now possible to achieve. The main observation is that history—the history of heroic acts, wars, and conquests—has indeed been a tale of inequality that modeled the genomes of humankind.

That said, inequality is not just a curiosity of the past. When I started this book, I predicted that inequality would differentially influence mortality in the current COVID-19 pandemic, and a few weeks later, my hunch was confirmed. Inequality is entangled in our genomes, but it also casts a long shadow over the future of society. We'll need to decide sooner than later how we want to face it.

1 The Age of Inequality

> Inequality was the unalterable law of human life.
> —George Orwell, *1984*

We live in an age of growing inequality, and to such an extent that the concept has become a social concern. In Google searches, the word "inequality" has been on the rise, especially since the year 2004. In a database of millions of books published since 1800 on Google Ngrams, the frequency of the word "inequality" remains almost undetected from 1800 to 1960; thereupon it surges continuously. In 2013, President Barack Obama said that income inequality is "the defining challenge of our time," and one year later, Pope Francis stated, "Inequality is the root of social evil." According to Oxfam's 2020 report, the 2,153 richest people on the planet have amassed more wealth than 60 percent of humankind, and according to Swiss bank UBS, the global billionaire wealth climbed to a new record of $10.2 trillion during the peak of the COVID-19 pandemic, between April and July 2020.[1]

Parallel to a general public interest in present-day disparity in incomes there has been an academic interest in understanding the causes and consequences of its increase. In this context, the success of the 2014 book by the French economist Thomas Piketty, *Capital in the Twenty-First Century*, might not be that surprising. According to the author, at the global level, 1 percent of the population has more than twice as much wealth as 6.9 billion people, while 70 percent of the population altogether accounts for just 3 percent of the world's wealth. In the United States, the richest 10 percent possess more than 72 percent of the national wealth. In countries such as France, Germany, Great Britain, and Italy, the richest 10 percent possess

around 60 percent of the national wealth, while the poorest half the population have a low income, collectively owning just 10 percent. In countries as diverse as China, Germany, Egypt, and Thailand, income inequality in the year 2000 looked strikingly similar to what it was in 1820. And places like Mexico and Brazil are more unequal now than when military and political leader Simón Bolivar was alive.[2] For those hoping to make the world a better place to live, it is a startling revelation.

If we consider the world as a single population and work with the Gini coefficient—named after the statistician and sociologist Cirrada Gini, who proposed it in 1912—which ranges from 0 (all people are equal and have the same income) to 100 (a single person owns everything), we discover, according to Piketty, that the figure has increased from 43 in 1820 to 66 in the year 2000. But the increase has not been steady across this period; in fact, it has been growing sharply since 1980, especially in places like the United States, where in 2012 it was at a staggering 85.2 out of 100 on the scale.[3] Despite criticisms of the use of this index and controversies surrounding Piketty's interpretations, one thing that we can all agree on is that no one can predict the limit to this increase in the world's inequality.

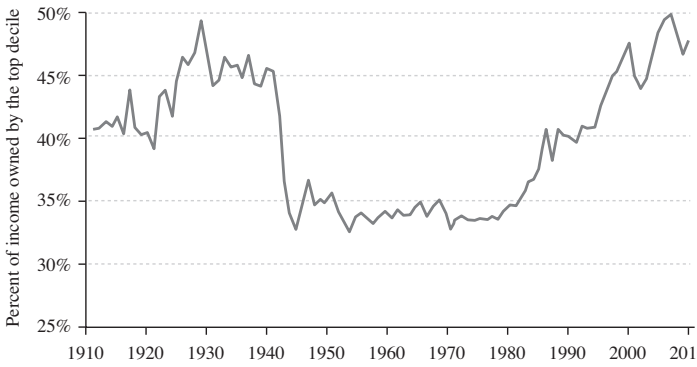

Figure 1.1
Income inequality in the United States over the last one hundred years, shown by the percent of the country's income that is owned by the richest 10 percent of the population. Despite a significant reduction, mainly associated with World War II, there has been a continuous increase over the last forty years. *Source*: T. Piketty, *Capital in the Twenty-First Century* (Cambridge, MA: Belknap Press of Harvard University Press, 2014).

Perhaps in no other nation has the growth in inequality been so evident or studied in such detail as in the United States. Throughout the twentieth century, and despite continuous economic growth, the wealthiest have accumulated much more than ever before, while the bottom 50 percent of national income shares have remained stagnated or even gotten poorer in some places.[4] Between 1979 and 2007, the real income for the wealthiest 1 percent of the nation tripled, while that of the middle class increased by only 25 percent (and even so, due to an increase in working hours and labor mass). In Piketty's words, income inequality derived from work in the United States "is probably higher than in any other society at any time in the past, and anywhere in the world including societies in which skill disparities were extremely large."[5]

Such social factors as the aging of the population, the globalization phenomenon, and migratory movements from poor to rich countries as well as the growing threat of climate change and the current COVID-19 pandemic indicate that inequality will likely continue to grow, mainly because state resources must be shifted from diverse redistributive policies to basic public services. Also, new technologies and industrial automation suggest that the income gap between the qualified and unqualified workforce will continue to increase in the near future. In his 2018 book *Enlightenment Now: The Case for Reason, Science, Humanism, and Progress*, the Canadian evolutionary psychologist Steven Pinker emphasizes the fact that at the planetary level, inequality *between* countries is lower now than at any time in the past and that there has been a rise in the number of poor people becoming middle class in developing countries—cause for optimism in his view.[6] According to Oxford University economist Ian Goldin, however, globalization has also led to a dramatic increase in systemic risks, including global warming and the degradation of the world's ecosystems.[7] Moreover, Pinker downplays the fact that inequality is effectively growing within each country (this is one of the reasons that he, along with others such as Hans Rosling, are sometimes dubbed the "New Optimists").[8] And the maxim that differences in technological societies will be primarily meritocratic is likely false; the economy will be dominated by inherited wealth.[9] The ongoing robotization of production, for instance, means that inequality will continue to rise, at least in the near future, and that large segments of society—those with fewer qualifications—will remain jobless.

The essential point of Piketty's work is that nowadays, the return on financial capital is much higher than what is yielded by economic growth (equivalent to human capital)—a process that in turn enables wealth to accumulate faster. The market economy, unrestrained by any form of regulation, contains divergent forces that favor a much quicker increase in wealth than salaries and production can provide, and in the absence of a solution—here Piketty proposes a global tax on capital—this trend will continue to increase inexorably. Although a number of economists have jumped into the arena criticizing aspects of the French researcher's thesis from his methodology to his conclusions and proposals, there seems to exist a general consensus within academic circles that inequality—understood as differential access to wealth—is effectively larger now than before the 2008 crisis. Also, some researchers have argued that this long trend of rising inequality can be considered an unavoidable epiphenomenon of the progress that civilization has experienced since the Middle Ages; that is, inequality is the toll to pay for progress.

Whatever the magnitude, the existence of such rampant inequality is no trivial matter, and beyond moral considerations, has an important impact on health, prosperity, and even life expectancy throughout society. Several studies have shown that citizens from the most disadvantaged strata in a highly unequal society have a higher chance of becoming obese, sick, or psychologically afflicted, and are more likely to populate its prisons. We have now learned that they are more likely to die during a pandemic too. These results, beyond the negative consequences at the personal level, mean that inequality undermines the productivity of any economy due to the large costs of maintaining public health systems as well as security enforcement. And in the long term, the situation will probably favor the emergence of authoritarianism to ensure the persistence of current inequality—or rather paradoxically, to claim to fight against it—as well as the parallel advent of political extremisms that could eventually destabilize the system. Some observers have warned of signs associated with both phenomena—the former in the United States and within some Asian powers, and the latter in some European countries.

If inequality has grown to become a distinctive sign of our society, what can be done to fight it? To Stanford University professor Walter Scheidel, there are four mechanisms for correcting inequality that have worked historically and are much more effective than those suggested by economists:

war, revolution, state collapse, and deadly natural disasters—including pandemics.[10]

In the first case (war), conflicts must be paid for through an increase in taxes on the wealthiest (in some cases, as in both world wars, such taxes reached 90 percent) as well as social mechanisms for the underprivileged classes to compensate for the cost in human lives. In the second case (revolution), social movements such as the Russian and Chinese Revolutions erased the ruling social class in a quick and effective way. Something similar occurred in the United States during the Great Depression. But revolutions aren't always effective in modifying inequality; according to Piketty, the French Revolution only represented a small drop in the country's inequality levels, with the wealthiest 1 percent in Paris owning 55 percent of all private property in 1780 versus 49 percent in 1810 under Napoléon. Meanwhile, the third case (state collapse) is associated with a number of phenomena. For example, the fall of the Western Roman Empire was followed by a large-scale decrease in inequality, yet this was achieved through the undesirable process of the impoverishment of the entire population. Finally, in the fourth case, dramatic natural disasters or large-scale pandemics, if they indiscriminately affect the whole society, can also decrease levels of inequality. The best known of these past pandemic events, the Black Death, which killed off between 30 and 50 percent of Europeans during the fourteenth century, rather than destroying the social order, freed the few surviving workers to look for better employers; this process triggered the end of the Middle Ages as well as the emergence of a middle class and urban population centers.[11] In fact, studies of tax records in Italy by researchers Guido Alfani and Matteo Di Tullio show that the Black Death was the only time in the past few hundred years when inequality decreased in that country.[12]

There are in addition local phenomena. In the United States, for instance, inequality experienced a decrease after the Civil War, mainly due to the emancipation of slaves in the southern states. Moreover, according to Scheidel, none of these mechanisms that have operated in the past will have the same effect on modern inequality, which is much more complex and interconnected on a global scale.[13] In conclusion, there seems to be no easy solution to this problem, and the past is not likely to help us find suitable mechanisms—unless, of course, we accept a world catastrophe as a leading force for change.

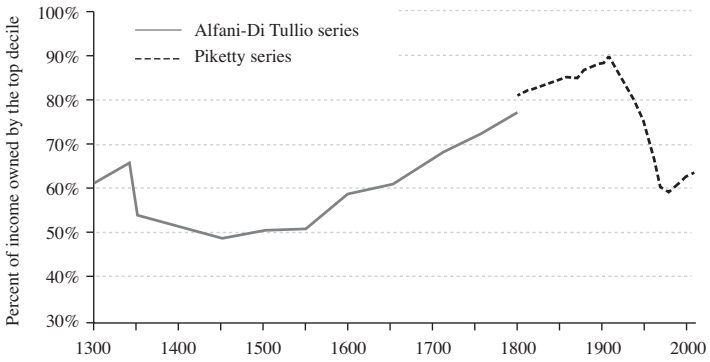

Figure 1.2
Evolution of the share of wealth of the richest 10 percent in European societies from 1300 to 2010. During this entire period the only two episodes of significant decline in inequality are related to catastrophic events: the Black Death in 1347 and subsequent years and the two world wars. The share of the richest 10 percent today is about the same as that in Europe (or Italy, at least) immediately before the Black Death. The Alfani-Di Tullio series (2019) is an average of the Sabaudian state, the Florentine state, and the kingdom of Naples (before 1600, only information from the first two is available). The Piketty series (2014) is an average from France, the United Kingdom, and Sweden. *Source*: G. Alfani and M. Di Tullio, *The Lion's Share: Inequality and the Rise of the Fiscal State in Preindustrial Europe* (Cambridge: Cambridge University Press, 2019) and T. Piketty, *Capital in the Twenty-First Century* (Cambridge, MA: Belknap Press of Harvard University Press, 2014).

If we would like to fight inequality, however, a pertinent question to ask from the field of social psychology is to which extent people view it as a problem that needs to be addressed; for example, a recent poll about income inequality in the United States showed that less than half of North Americans consider it a serious concern.[14] Researchers on social psychology and moral economics have explored the innate bases of social differences, finding that in many cases people seem to prefer societies with inequalities (or a certain amount of inequality) over equal ones.[15] Some researchers think that this conclusion can be explained because what really seems to worry people is not inequality per se but instead economic unfairness—different concepts that sometimes get mixed up. This trend seems to be universal (though some studies indicate that people don't realize the magnitude of inequality in our current society). Various transcultural tests conducted on children suggest that humans do favor fair over merely equal

distribution, and that in situations of conflict between justice and equality, people tend to prefer fair inequality over unfair equality.

In social games performed under controlled conditions, the perception of justice is prevalent in all human interchanges, even beyond rational considerations. Unfair players are often punished, even where their opponent forfeits all potential benefits. An innate altruism, influenced by considerations of social prestige, seems to be a common conclusion in such experiments.

The most common of these social experiments, the "ultimatum game" (designed in 1982 by researchers from the University of Cologne in Germany) concludes that a perception of fairness is a fundamental element in human exchanges, even more than rationality.[16] In the game, two players share a certain amount of money (say, ten dollars); one makes a single, final offer to the other, who may accept or reject it. If rejected, both players are left with nothing. The experiment has been repeated many times with different players and communities, and the obtained results are always similar: obviously unfair proposals (such as a distribution of nine to one) are rejected, even those that yield a net gain for the second player. (We might think, from a purely rational point of view, that one dollar in profit is better than nothing at all.) Most transactions accepted are close to what is perceived as fair—five to five—while offers below two are generally rejected by the second player. If the proposal is not fair, it is preferable to punish the greedy player, leaving them with nothing. Brain scanners performed on the second player during the decision process showed an activation of the dorsal striatum, where reward perceptions reside in the brain. The satisfaction experienced in teaching greedy opponents a lesson seems to dominate the player's visceral response. Of course, there are quite a lot of intercultural variations in these fairness judgments, and yet what seems to underlie them is the existence of a general psychological mechanism adapting to different conditions in which the second player never behaves like a rational economic maximizer.[17]

That's not all; unbalanced offers are usually not proposed because the first player knows that a markedly unfair offer will be rejected and prefers not to run the risk of being punished. Obviously if this is the case and the first player is making a strategic decision, then we should believe that offers are rationally constructed, which is what conventional economic theory says. That said, other researchers have suggested an alternative, altruistic

explanation to this bias: those who make an offer prefer to set a more equitable partition from the outset.

In a variant of the game, the first player is a machine and the second one is aware of this circumstance. In this case, when the offer is unfair, the other player—the human being—accepts it because there would be no point in teaching a moral lesson to a machine.

In the "dictator game," there is a variant: the player who receives the offer is a passive subject and cannot reject it.[18] Despite the potential impunity of the first player, it could be seen that the second player ends up with amounts smaller than those from the ultimatum game, but nevertheless higher than zero. It is difficult to know whether or not the altruistic component is in this case overtaken by matters of social prestige. In some variants of the game, it is explained to player one that their opponent will never know who they are—and therefore no one will ever know that they are greedy—and then it turns out that this person makes more unfair transactions, protected by this feeling of social impunity. Some people have argued that in real life, and with much larger amounts of money at risk, the other players would behave more rationally, insisting that such economic games are not representative of human realities, which are much more complex and unpredictable, and subject to more intangible personal variables and special circumstances.

While such criticisms may be fair, a common conclusion that can be drawn from all these experiments is that economic transactions, rather than cold, rational activities, are largely based on emotional reactions in human societies (something that marketing experts are well aware of). This is important because our civilization has been built on the basis of commercial exchanges, especially since the development of farming—and the possibility of having food surpluses to trade. Integration in a social context is thus a determinant in the generosity of economic transactions.

Surprisingly, the emotional component is not exclusive to humans. Experiments undertaken with capuchin monkeys showed that they could tell when something was fair or not by having some of them watch others being rewarded with a grape instead of a less tasty cucumber. In the experiment, monkeys were taught to exchange a token for a grape; if they were in isolation, they felt satisfied with either a grape or cucumber, but in the presence of more monkeys, they become quite irate if they found themselves

at the short end of an inequitable distribution of rewards.[19] I suppose many non-monkey readers will identify with this feeling.

Based on all these observations, some researchers suggest that an idea of equity—defined as a benefit according to relative contribution—exists because it has been naturally selected in humans as the best psychological strategy to be integrated into a cooperative environment in which humans evolved.[20] (By the way, inequity and inequality are different concepts; the former is an unfair or unjust state of being, and the latter is an imbalance that may or may not depend on inequity.)

And yet we all would agree that common experience indicates that inequity is ubiquitous in our societies. If both fairness and equity—as well as inequality and inequity—are so prevalent, they might have a biological basis; consequently we might ask ourselves if they can be considered to some extent unavoidable.

And following this, one might hypothesize as well that inequity is somehow related to innate aggressiveness and dominant behavior, which in the natural world could result in differences in strength and body size.[21] (Interestingly, humans show a level of sexual dimorphism—understood as systematic physical differences between both sexes—that could also be associated with ancestral differences in aggression levels between males and females.)

Can we study aggression from an evolutionary perspective? When one of our closest relatives among the great apes, the common chimpanzees, are studied, researchers describe solidarity among fellow primates, but also aggression and competition associated with the highly hierarchical structures of chimpanzee groups; wars are even waged between rival groups, and dominant males tyrannize female members. (In contrast, the bonobos or pygmy chimpanzees use sex to maintain a peaceful social structure.) According to British primatologist Richard W. Wrangham, two different types of aggression may be distinguished here: proactive (similar to offensive, planned, controlled, or cold aggression) and reactive (defensive, emotional, or hot aggression). Cold, tactical proactive aggression is more pronounced in humans as compared to other primates, while hot, reactive aggression is more frequent among chimpanzees. The low propensity for reactive aggression in humans could be constrained, according to Wrangham, by a tendency toward extensive within-group tolerance and even cooperation.[22]

Cold, proactive aggression might have been favored among early hominins if altruism genes in the group increased the chances of winning conflicts against neighboring groups by enhancing intragroup cooperation bonds. For this mechanism to operate effectively, genetic differentiation between hunter-gatherer groups had to be sufficiently high in the past—something that seems to be at odds with present genetic evidences for widespread admixture among African forager groups prior to the advent of farming.[23] Proactive aggression, however, also existed within groups, with the possibility of enforcing norms through such measures as capital punishment that might have selective consequences. Some researchers disagree with Wrangham's two categories of aggression, arguing that more than two basic types can be distinguished.[24] Notwithstanding this controversy, the notion that aggression might have been a driving force in our evolution remains powerful.

One potential source of evidence for the study of the evolutionary trajectory of aggression is the fossil record, where we can study what are in all likelihood our closest extinct relatives, the Neanderthals. We can speculate that if there were behaviors that helped our species to survive, then differences in the outcome of both modern humans and Neanderthals might have resulted from such behaviors. We find evidence of compassion among Neanderthals, with disabled individuals surviving for years under the group's care. But we see signs of violence too, with an abundance of trauma and cannibalism. These somewhat contradictory findings are in fact quite humanlike, and we can recognize ourselves in them, both for good and evil. Nevertheless, the evidence of aggression and cooperation doesn't tell us how prevalent the two types of behaviors were, much less what kind of aggression was occurring.

From a demographic point of view, we now know that Neanderthals experienced a long process of population decline—well before their encounter with modern humans—while our species underwent a continuous expansion after the out-of-Africa migration—or migrations—that took place around sixty-five thousand years ago. It can be demonstrated from genetic data that there were various episodes of interbreeding not only between Neanderthals and Homo sapiens but also between both and yet another archaic hominin group from Asia, the Denisovans.[25] Still, no sign of gene flow from our ancestors into the latter Neanderthals (those dated to the potential contact period, between forty to fifty thousand years

ago) has been detected so far. It seems that modern humans were able to tolerate hybrids but not vice versa. It could be that hybrids were rejected from Neanderthal groups—or maybe even killed—yet their absence could just be the consequence of a greater demographic fragmentation or even existing genetic differences. In fact, the Y chromosome sequence of some Neanderthal individuals showed specific mutations in three genes that could account for an incompatibility of hybrids with a Neanderthal father only.[26] Whether these patterns represent fundamental differences in aspects such as social structure or aggression, or are just a reflection of biological incompatibilities, is something that remains to be explored. But so far there is no evidence of Neanderthal–modern human hybrids living in the small, endogamous, and kin-structured Neanderthal groups.[27] One might be tempted to think that accepting admixed people as equals could hold clues to our success as a species, at least in these distant periods.

Yet if proactive aggression was a driving force in the successful expansion of Homo sapiens across all continents, is this a trait, we might ask ourselves, that has been increasing in tandem with our current demographic explosion? Did we become more abundant by becoming coldly aggressive? In his 2011 book *The Better Angels of Our Nature: Why Violence Has Declined*, Pinker argues that despite what people may perceive and the dramatic statistics from the two world wars, the number of deaths in violent conflicts (corrected for the rise in population) is continuously decreasing.[28] Moreover, some researchers reported that forager groups suffer from higher homicide and war occurrence rates than previously assumed.[29] This conclusion has been criticized by some historians and ethnographers alike, partly because of the inherent difficulties in estimating the number of deaths from past conflicts and partly because recent ethnographic studies suggest that the basic pattern of interaction among forager groups is to get along with neighbors rather than attacking them.[30] Meanwhile, economist and essayist Nassim Taleb has also questioned Pinker's idea that humanity is entering a period of "lasting peace," as he calls it. Taleb argues that world-scale armed conflicts do not follow a predictable pattern because of the long interarrival time existing between conflicts and therefore Pinker's results can be considered a "statistical illusion."[31]

The conclusion of this controversy is that we do not know if past forager groups were peaceful or inclined toward violence. But beyond the academic debate over the past and future of war, one thing seems evident: rather

than arising out of the sedentary lifestyle of the first farming communities, violence and conflicts are part of the emergence of human nature, as are their counterparts, altruism and solidarity. Despite some opposite claims, the former is not just a recent phenomenon; there are some examples of deliberate interpersonal violence and resulting lethal trauma in fossils from the Middle Pleistocene, such as in a skull from the famous Sima de los Huesos site in Atapuerca (Spain) that received multiple, deadly blows.[32] The issue of war mortality before the Pleistocene is still hotly debated, though.

Summing up, there are different approaches to the study of innate human behavior, and most seem to conclude that cooperation as well as competition—including aggression—are prevalent within and between social groups.[33] It can be hypothesized, perhaps controversially, that inequity is rooted in this innate behavior and thus might never be eradicable. By the same token, inequalities deriving from unfair conditions, a kind of cold proactive structural violence, might also be impossible to eliminate. Therefore a crucial question for evolutionary biologists is whether inequality does in fact have a biological basis, rooted in proactive violence. It is likely that if we are to understand inequality, we must understand violence and its evolution.

Beyond this debate and irrespective of its nature, we're still interested in analyzing not the basis but rather the consequences of this inequality over the genetic structure of human populations, both past and present. How we can measure it?

The study of the accumulation of resources—that is, wealth—is key to understanding inequality in premodern societies. Such study requires one to quantify the different classes of wealth—material, embodied, and relational—and the mechanisms of their transmission across generations (though some argue that these different classes are not independent of each other). Material wealth refers to those goods—land, livestock, household, or objects—that can be possessed and accumulated; embodied wealth refers to health, immunity, physical strength or body weight, knowledge, and practical skills stored in human bodies; and relational wealth consists of the individual social links that derive from social status or family ties.[34] Transmission of material goods between generations, usually referred to as "inheritance," is a defining human trait rarely found in nature.[35] Some studies on modern African agricultural societies suggest that material and relational wealth are likely more important in the emergence and persistence

of inequality than embodied wealth, and that ownership rights in land and stock are more significant factors in determining the levels of inequality than the use of domesticated animals itself.

The study of inequality in all its aspects can to some extent be based on the analysis of quantitative data from the foraging, agriculturalist, and pastoralist groups of recent times. For most of our evolutionary history, humans have been foragers (or hunters and gatherers). Due to fluctuating and uncertain resources, foraging groups are constantly on the move, and hence cannot accumulate goods or even food. Therefore these foragers are typically described by ethnographers and cultural anthropologists as having formed more egalitarian societies—including sex equality—than agriculturalist and pastoralist groups.[36]

But how can we understand—if we can—the extent and level of potential inequality in the distant past? Sustained economic inequalities usually leave archaeological signatures, although they can be difficult to interpret with our eyes, which are those of a rich society. Their generalized absence (in the form of rich funerary assemblies, for instance) prior to the Neolithic period has been interpreted as evidence of scant economic differentiation between and within foraging groups, with the possible exception of those occupying abundant fishing sites.[37] As we have seen, observations based on modern foraging groups have lent support to this interpretation, but it is difficult to know how well present-day anthropological data can be extrapolated to the past. Are modern forager groups comparable to those of the past?

Actually, some rather elaborate graves have indeed been found dating as far back as the foraging groups of the Upper Paleolithic—long before either permanent settlements or agriculture—that bear marks of symbolic behavior such as ochre soil scattered over an interred body, or stone tools or animal bones that seem to have been deposited alongside. The most ornate example of such burials is in Sunghir near Vladimir (Russia), where an adult male and two juveniles dated to about thirty-four thousand year ago were excavated between 1957 and 1977. There were about three thousand mammoth ivory beads on the adult skeleton (originally sewn onto their clothing), plus twelve pierced fox canines and twenty-five mammoth ivory armbands; all these items of personal decoration required hundreds of hours of manufacturing. But the juveniles, approximately ten and twelve years old, and buried head to head, were even more spectacularly decorated,

with about five thousand mammoth ivory beads each.[38] What do these mean in terms of hierarchy, group membership, and social structure? Are they signs of a certain status among these foraging groups, or simply well-preserved burials in particular contexts?[39] Also, numerous examples of the Paleolithic Venus figurines—representing women with exaggerated anatomical traits related to fertility—have been found across Europe, but do they mean that women were held in higher regard, perhaps due to their involvement in fertility rituals, than in subsequent periods, or do they just reflect hopes for survival in harsh times?[40] Again the problem is, What can be deduced and generalized from archaeological findings in terms of social stratification and gender roles?[41]

The difficulties in understanding potential signs of inequality in the fossil and archaeological records can be easily grasped by looking at the most basic data that one can hope to get from the past: the gender of the people involved. Let's look, for instance, at the famous Upper Paleolithic triple burial dating from around thirty-one thousand years ago from Dolní Vêstonice in the Czech Republic. The three individuals in this burial (labeled DV13, DV15, and DV14 by archaeologists) are intriguing for a number of reasons. DV13—which corresponds to a male teenager—had a thick wooden pole driven through his hip and was found with his hands on the pubic region of the central individual, DV15. Flanking DV15, a second male teenager, DV14, was buried facedown.[42] The central individual, who obviously had a preeminent status, had usually been characterized as female, although the real sex was controversial due to a pathological condition affecting the curvature of the spine, pelvis, and teeth.[43] Until recently, the biological sex of skeletal remains had to be assessed via morphological indications as, on average, males have larger and more robust bones than females, and in this case it was unclear. One popular interpretation was that the middle individual was a high-status female who died during childbirth—because they had ochre over their pelvic bones—and the man on the right was possibly a kind of shaman who was executed for failing to save her life. Our view of this triple burial might alternatively be considered the result of a tragic love triangle with the central character being female or all three bodies being male (which would not of course rule out the possibility of a love triangle). Genomic data generated from the three individuals and published in 2016 eventually revealed that all three were in fact male, thus ruling out some of the previous interpretations and changing the way

that we perceived this remarkable burial—and also the potential social relationships within the group.[44]

Not only the genetic sex can now be unveiled, but the kinship. The genetic analysis of the Sunghir skeletons revealed, for instance, that the two immature individuals buried together were not—despite previous suggestions—family related.[45] These are but two examples of how genetic data can shed new light on the study of the past, resolving even for seemingly unresolvable mysteries.

In the last five thousand years, signs of inequality in funerary contexts have increased, yet the paucity and gaps in the archaeological record impose restrictions on the conclusions that can be drawn from different times and periods. Apart from the discovery of spectacular burials of wealthy people, it is difficult to really grasp what the archaeological record has to tell us about how unequal those societies actually were.

Even in recent history and Western societies, we have some evidence to suggest a surprising connection between genetics and social inequality. Some recent studies have exposed the persistence of social status—or to put it another way, a low level of social mobility—existing even in a society like Sweden, considered a model of social democracy. An economist from the University of California at Davis, Gregory Clark, surveyed for surnames and income among present-day Swedes. The underlying idea was that no new aristocratic houses were created after the seventeenth century, and all existing by then have been recorded in the House of Nobility (or Riddarhuset); noble surnames among the general population had to have been derived patrilineally—that is, transmitted only through male relatives—from past aristocrats. (To name just a few, Björnstjerna, Cedercreutz, Falkenberg af Sandemar, Lövenskjöl, Meijerfeldt, Oxenstierna af Croneborg, Silfverschiöl, Wallenstedt, and Wrangel.) By contrast, common Swedes tend to have the patronymic particle "son" added to the end of their surnames. Clark found that despite tens of generations, false paternity events, and of course the ups and downs of fortune, the surname was still a good predictor of social status in twenty-first-century Sweden—along with such variables as wealth, occupation, education, and even longevity.[46] This correlation between surname and status has been replicated in other Western countries, including Denmark, Ireland, and Great Britain, and even in places like China and Korea, and the conclusion is that social mobility is lower than traditionally measured and at the same levels as in preindustrial times. In general, it takes

at least four hundred years for elite surnames to converge with average-income families in society. Even in today's Britain, Norman surnames (Baskerville, Darcy, Mandeville, Montgomery, Percy, Neville, Punchard, and Talbot) are overrepresented among the country's elites.[47] Why this long persistence happens is unclear; obviously there seems to be a strong transmission within families of the attributes needed for social success. Whether these are genetic or environmental, or a combination of the two, is more difficult to unravel. While Clark controversially argues for the inheritance of some of the traits that lead to social success, such as intelligence, attractiveness, self-determination, and so on, others interpret these observations as a result of well-established social networks. Clark's work has also received some methodological criticism, as surname-level income averages capture a diverse set of individual- and group-level factors, and these cannot be disentangled in a comprehensive way without additional information.[48]

Despite potential statistical flaws, it seems evident that intergenerational social mobility is lower than we might think in our societies, and this is notably due to the existence of marked assortative mating—that is, people with similar phenotypes tend to mate more often than would be expected if mating were random. Even though we share environments in daily life, small details such as spoken accents or dress can indicate one's social status, wealth, or educational level to a high degree of precision. Whether conscious or unconscious, assortative mating likely helps perpetuate past social differences.

And even if we were to conclude that such structures are not as rigid and endogamous as those seen in societies like India, it is also obvious that people tend to marry others of the same socioeconomic status. This tendency has increased, paradoxically, with the access of women to higher education and the job market. (It might be partially correlated as well with the fact that married couples were much younger one generation ago, before they had attained their final educational and job level.) To put it simply, some decades ago doctors married nurses, and now doctors marry other doctors (in United States, approximately one in four women physicians are married to doctors, according to a report from the American Medical Association). In a study carried out in 2011 within member states of the Organization for Economic Cooperation and Development, it was observed that about 40 percent of couples had similar salaries, against a 33 percent figure just twenty years before.[49] If the previous tendency of couples with dissimilar

incomes had held, present-day inequality would instead be around 25 to 30 percent lower. And it is likely that this is happening everywhere; in Spain, for example, over 40 percent of the children whose mothers have a PhD are fathered by men who have a doctorate too.[50] This cultural trend contributes to an increase in inequality, along with the aforementioned weight of one's past family status.

One way or another then, unequal societies can clearly be linked to biological factors: wealthy people can raise and feed more children as well as live longer than ordinary people. (Interestingly, this trend seems to be reversed today, with wealth and education inversely correlated to fertility, although it is unlikely that this was the case in the past.) Where such wealth can be effectively inherited, children will also have more children over several generations because they are more resilient in the face of economic turmoil. This will have consequences for the future of that population because each generation hinges on the fertility dynamics of the previous one. We need not refer back to the extreme reproductive asymmetry of Ottoman sultans who had literally hundreds of children; Clark demonstrated in 2005 that in England's pre–Industrial Revolution period, the poorest had, at the moment of their death, 2.2 surviving offspring on average, while the wealthiest had 4.1.[51] If anything, the Industrial Revolution tended to increase the differences in fertility—or at least the chances of survival—between social classes. The possibility of leaving more offspring of course has genetic consequences for upcoming generations. As we belong to those subsequent generations, we can take a look back and try to understand our own genesis.

The number of our ancestors doubles with each generation (we have two parents, four grandparents, eight great-grandparents, etc.). In a few more generations, the numbers of our genealogical ancestors will rise to such vast numbers—more than the number of people who've ever inhabited this planet—that only the enormous number of interconnecting links between them all could explain this paradox. In short, many of our ancestors are shared, in the same way, for instance, that first cousins share two grandparents (two unrelated people have eight unconnected grandparents instead of the four unconnected ones that first cousins do). That is, we do not have as many different ancestors as theoretically estimated because many of them are repeated; this is quite evident in small, endogamous populations such as those found in remote islands.

Nevertheless, it is apparent that some among our genetic ancestors must be overrepresented—not necessarily among our genealogical ancestors. Those who had a disproportionately high number of descendants in one particular generation—and maybe also their descendants through subsequent generations—are expected to have contributed more than average to the genetic ancestry of modern populations. These people would then necessarily be overrepresented among our genetic ancestors, partly reversing the previous trend of genetic dilution described by population geneticists as we go back one generation after another.

While this overcontribution of some genetic ancestors is expected to happen in the natural world as well, especially in non-monogamous species—think, for instance, of polygynous species in which a single male mates with multiple females—a human-specific trait that I want to elucidate in this book is whether differences in wealth give some individuals advantages over others in reproduction, thus entangling social and genetic factors in a complex way, and effectively modifying the genomic composition of subsequent generations. Consequently, if this is in fact the case, we can safely assume that we carry a higher genomic fraction from those who benefited from inequality in the past, if only by probability. I think this in itself is an interesting thought; let's keep it rolling in our minds for a while.

To understand the past of human inequality in new ways, beyond recent historical information such as that used by Piketty, we now have new technical tools that enable the retrieval of hundreds of ancient genomes generated from hundreds of skeletons distributed in space and time. The second-generation sequencing platforms, developed after 2008, now enable the retrieval of literally billions of DNA fragments from minute dental or bone samples from up to tens of thousands of years ago. These DNA fragments are computationally mapped onto the human reference genome and can then be analyzed with genetic statistical algorithms, along with other contemporaneous ancient genomes as well as modern ones from the same geographic areas. These extremely powerful analytic tools can discern different genetic compositions derived from each individual's ancestors as well as provide solid information about kinship and sex. Without doubt, this is a genetic revolution with a continuous impact on all levels of the reconstruction of the past, and it is unlikely to conform to previous notions.

Of course, there are limitations in genetics too; DNA degrades under certain environmental conditions and over time, being less likely to survive in

hot climates such as those found in most of Africa and Southeast Asia, and the samples that can be analyzed are most likely a biased representation of all those who ever lived (in fact, we will never have data on everyone who ever lived and left descendants). And sometimes we do not have the remains of past individuals for analysis either because they haven't been found or haven't been preserved in the ground.

Current genetic tools, however, are so powerful that in many cases we don't even need to have the dead. For instance, we can study a substantial genomic fraction of someone from the past without having their remains, as a recent study on the descendants of a certain Hans Jonathan demonstrates.[52] Jonathan was born into slavery on the Caribbean island of Saint Croix in 1784, and was the son of an African slave and someone of European origin, most likely the secretary of the plantation's owner, who was Heinrich Ludvig Ernst von Schimmelmann. Later on, the Schimmelmanns moved to Copenhagen and took Jonathan with them; once there, Jonathan joined the Danish Navy and fought bravely in the Napoleonic Wars. Afterward, however, Schimmelmann died and his widow had Jonathan arrested, claiming that he was her property and she wanted to sell him in the West Indies. The Danish court—despite the fact that slavery was abolished by then in the country—sentenced Jonathan to be returned to the Caribbean. Before that could happen, he escaped to Iceland in 1802, settling in a small fishing village, Djúpivogur, where he had a couple of surviving children with a local woman, Katrín Antoníusdóttir, before his death in 1827.[53] It is somehow remarkable that he was accepted in Iceland, by then one of the world's most isolated communities, which nevertheless had less racial prejudice than Jonathan faced in continental Europe. Today, there are almost 900 living descendants of Jonathan, and from the analysis of 182 of them, it has been possible to reconstruct about 38 percent of his "African" genome (that is, 19 percent of his complete genome), which shows affinities with the present-day populations of Benin, Nigeria, and Cameroon. His descendants carry a small fraction of non-European DNA, while most of their genome is overwhelmingly similar to the rest of modern Icelanders. In fact, Iceland is probably one of the most genetically homogeneous populations in the world today, and Jonathan's African genes are but a single drop in the Icelandic gene pool. That said, his African genome, even if fragmented, is still discernible because it was so different from the rest. This is undoubtedly the true genetic meaning of leaving a

legacy, and this book will provide many examples of such links between past and present.

It is worth emphasizing that geneticists could have conducted the Icelandic study without any historical record about the existence of Jonathan. Nevertheless, genetics does not stand alone in the task of reconstructing human history; the fields of archaeology and anthropology also play a role in this new view of the past. For instance, wealthy people have a higher than average social status in any time and period—a fact that can sometimes be recognized at archaeological sites. Burial ritual reflects the transition of this status to the other world, and thus there is a strong relationship between graves and the existing social organization. Genetic analysis of the dead therefore holds clues to understanding the societies where they lived, and both archaeology and anthropology add significant information. We are not advocating for an independent view of past controversies based solely on the genetic evidence; we are in fact pursuing a real interdisciplinary interpretation that was previously impossible to achieve. But archaeology won't be the only tool employed; underestimating genetics, archaeological academia runs the risk of being ignored by mainstream science, which may view it as entrenched in untested, ideological hypotheses.

The various links that exist between social structure and biology remain crucial to us because they may address a number of hypotheses, usually posed by archaeology, but previously untestable, about how prevalent inequality was in the past. Thanks to the potential of ancient DNA, we can now explore how dramatically ancestral shifts associated with past migrations have unequally shaped the genomes of humankind. We can also unravel how sex biases and new social structures associated with these past population movements have implemented the genomic change, effectively influencing future generations. We can elucidate the magnitude of some of the most obvious examples of inequality in human history: those related to underprivileged classes, minority groups, and enslaved people, but those suffered by women too (by and large, the most oppressed human beings in all historical periods; it is worth remembering as well that the greatest genetic difference within our species is between males and females). And this can be done on the collective and individual level; sometimes powerful men contribute disproportionally to subsequent generations by monopolizing women, and this shapes paternal chromosomes.

Until now, skeletons in themselves could not tell us anything about the link between social status and the ancestry of their possessors, but this is changing definitively. Through their DNA, ancient skeletons have much to tell us, and we're listening to their anonymous stories of inequality and suffering, and at the same time developing a new, objective, and multidisciplinary reconstruction of human history. Amazingly, this technical revolution was unforeseen even by people like me who have been working for two decades in the field of ancient DNA. What was impossible ten years ago is now becoming mainstream. This is what is happening.

We can thus ask for the first time (we, the outcome of these entangled social and biological processes), To what extent has inequality shaped the genomes of humans?

Notes

Preface

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