Race and Human Genomic Variation Rasmus Grønfeldt Winther Professor of Humanities University of California, Santa Cruz www.rgwinther.com ; info@rgwinther.com October 21, 2021

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Abstract

How much do different groups of humans differ genetically? Starting from a thought experiment, this chapter shows that we differ less than we might think—and that, in a sense, *we are all Africans*. I draw on several key findings: that compared to many other species, *Homo sapiens* has relatively little genomic variation; that of all continental regions, African genomic variation is the richest and most distinctive; that population-level genetic variation decreases with distance from Africa; and that most genomic variation is found within local human populations (with only about 6% or so found across continental groups). This is not to deny that there are—small but somewhat systematic—group-level differences, but it is also important to recognize that these should not matter ethically or politically.

A Thought Experiment¹

A few months after your intergalactic expedition left Earth, you arrive in a far-off world.² Departing your ship, you come upon some of the planet's inhabitants. They all seem to look the same. They are all more-or-less one meter tall and have the same muscular body and rounded facial features. You know that people sometimes say that other groups of people "all look the

¹ Parts of this book chapter were adapted from chapters 6 and 9 of Winther 2021a, and from Winther 2021b.

² I first presented this thought experiment in Winther 2018. This work was completed in 2015.

same," but in this case it seems nearly true: finding a distinguishing mark on any one of them is a challenge.

"Greetings, traveler," you hear through a universal translation device held up to the mouth of a single inhabitant who has emerged to meet you on the rock where you stand. "Please be at ease." You are told that every person on the planet looks the same; your greeter is no exception. You learn that centuries ago there was a Great Tragedy brought on by ethnic conflict including a calamitous civil war. Committed to preventing further destruction, the survivors agreed that for the rest of time they would engage in random breeding to avoid ethnic strife.

Call this Planet Unity.

Now, let's imagine a different scenario, perhaps a little more familiar: Imagine the Galápagos Islands, the natural experimental laboratory where Darwin studied evolution, with their wide variety and number of finch and tortoise species. Let's in our minds populate these islands—or any analogous archipelago—with identical small populations of early humans. Let's then add a few more dozen islands that are larger, mutually unreachable, and have distinct environments: Some are relatively cool and rainy, while others are hot and arid. What happens after tens of millions of years of evolution? Will the populations become more alike, similar to Planet Unity? Just the opposite, of course: Unlike on Planet Unity, the populations on these islands have come to be quite different from each other—not just in body and behavior, but in culture, as well.

Call this Galápagos-Writ-Large.

Now the real question: are modern humans more like the inhabitants of Unity or Galápagos-Writ-Large? (Figure 1) Where do we fall between these extremes?



Fig. 1. From Galápagos-Writ-Large to Planet Unity

The extreme ends of the thought experiment on human population structure: (left) Galápagos-Writ-Large and (right) Planet Unity. The Galápagos map includes equidistant contour lines at 250m on land and 500m in the ocean. (Concept by Rasmus Grønfeldt Winther, illustrated by Larisa DePalma (aliens) and Mats Wedin (Galápagos map) © 2021 Rasmus Grønfeldt Winther.)

When we look around us on the street or in a Zoom meeting, we can easily see differences in people's eyes, skin tone, height, and the rest. Identical twins might be a partial exception! This isn't just a point about individuals: some *groups* of people seem to share physical traits in common. And this would seem to be an argument for humans fitting the Galápagos-Writ-Large scenario.

I'm going to use this chapter to suggest the opposite: the Planet Unity scenario is a much better description of our situation. To help convince you, we'll review our best genomic evidence for the (relative) unity of the human species.

It was only in the middle of the 20th century—long after Darwin's death—that scientists started unlocking the mysteries of genetic inheritance at the molecular level. The environment is an essential part of making you what you are, but the other side of the matter is that molecule called DNA, which encodes our genes.

A reasonable starting point for examining human diversity, then, is to ask how genes differ, if at all, between individuals and groups. How similar or dissimilar genetically is anybody from anybody else, really? Let's have a look.

The genomics of recent decades has had some surprising findings. We have learned that, compared to many other species, *Homo sapiens* has relatively little genomic variation; that of all continental regions, African genomic variation is the richest and most distinctive; that population-level genetic variation decreases with distance from Africa; and that most genomic variation is found within local human populations (with only about 6% or so found across continental groups).

What does this mean? As I will show, it means *we are all Africans*. But groups also differ, and these small but somewhat systematic group-level differences explode with highly charged and controversial political and ethical debates and implications.

Relatively Little Homo sapiens Intraspecies Genomic Variation

Among species for which we have good data, *Homo sapiens* has rather low average nucleotide variation. At roughly 999 base pairs out of 1000 (on average), all members of *Homo sapiens* are basically identical.³ Given our total, haploid genome size of 3 billion nucleotides, two individuals will typically and on average differ at approximately 3 million nucleotides—only a difference of about 0.1%. Our closest cousins are on either side of us in this measure, but not too far: bonobos differ by 0.077%, chimpanzees by 0.134%, and gorillas by 0.158%.⁴ By contrast, the most classic model organism for genetic studies, *Drosophila* fruit flies, differ from each other by 1% on average, or about 10 times our nucleotide diversity. And maize has even more nucleotide diversity than *Drosophila*.⁵

In short, there is, according to our best genomic data, a *single overarching* human race, at least as compared to less unified species.

Out of Africa Migrations

³ Li and Sadler 1991, Yu et al. 2002, Auton et al. 2015, Biddanda et al. 2020, Winther 2021a.

⁴ Yu et al. 2004.

⁵ Brown et al. 2004.

Even so, we do differ in small ways, both at the individual level and the group level. This is what makes human evolutionary genomics so fraught and so interesting. Are there alleles associated with cancer, running speed, or intelligence, and might they be distributed unevenly across human populations? If so, what are the consequences for medicine, social policy, and our self-understanding?

It is crucial to recognize that our basic evolutionary pattern is *Out of Africa migration*. You may know the story: our species originated in Africa with a few small and highly related populations. Several times, groups left Africa, grew in size and range, and underwent evolution by natural selection, random genetic drift, and mutation. (Some migration *back* to Africa also occurred.) In this way, different human populations spanned the world, occasionally interbreeding, especially in the last tens of thousands of years.⁶

Of All Continental Regions, African Genomic Variation is the Richest and Most Distinctive

African human populations are the most genetically variable in the world. African populations have roughly double the nucleotide diversity of other populations. In other words, two people whose recent ancestors are of African origin differ on average by about 1:900 nucleotides (.11%), whereas two people whose recent ancestors are of European origin differ on average by only approximately 1:1600 (.063%).⁷ Another study found that Mandinka peoples from Mali, Guinea, and the Ivory Coast and the San peoples of South Africa harbored nucleotide diversities of .12% and .126%, respectively, while Han Chinese and Basque peoples had, respectively, .081% and .087%.⁸ According to Rosenberg 2011, Africa has approximately half of the world's "private alleles"—that is, alleles at a locus unique to a geographic region.⁹ Many more pieces of evidence indicate that genomic variation is generally much higher in Africa, in part due to the long periods of time of human population differentiation across the African continent. Given our Out of Africa picture, none of this is surprising.

⁶ For a nuanced, yet somewhat non-standard view of Out of Africa migrations, see: Templeton 1997, 1999, 2002.

⁷ Yu et al 2002.

⁸ Wall et al. 2008, Table 1, p. 1355; cf. Campbell and Tishkoff 2008.

⁹ Rosenberg 2011, p. 667.

Genomic heterozygosity of populations decreases with increasing distance from Africa, along human migration routes

Early humans had to pass through northeastern Africa to leave it, and following this path leads to interesting insights. Genetic variation in human populations reduces in proportion to its distance from Africa, as measured along historical human migration routes. This means that the further apart two populations are along these lines, the more they differ. Here we can talk about human migration as well as *genetic* migration, or the process of gene exchange when populations mix. Genetic migration also tends to diminish along human migration routes as they move farther from Africa.¹⁰



Fig. 2. Heterozygosity to Distance from Eastern Africa Global Pattern. The amount of heterozygosity of each of approximately 40 worldwide populations diminishes as a function of their respective distance, along (approximate) migration routes, from Addis Ababa. (Source: Figure 4A, p. 15946, Support from the relationship of genetic and geographic distance in human populations for a serial founder effect originating in Africa by Sohini Ramachandran, Omkar Deshpande, Charles C. Roseman, Noah A. Rosenberg, Marcus W. Feldman, L. Luca Cavalli-Sforza. Proceedings of the National Academy of Sciences. Nov 2005, 102 (44) 15942-15947; DOI: 10.1073/pnas.0507611102 © (2005) National Academy of Sciences, U.S.A. Reprinted with permission from PNAS.)

The Out of Africa migration model also aligns with the data on the decline in genomic variation as you move away from our evolutionary cradle, providing very strong evidence for a general Out-of-Africa scenario of human evolution (Figure 2). This occurs because when a species migrates, relatively few individuals typically move and survive. Even fewer make it when

¹⁰ See Figure 1B of Ramachandran et al. 2005, 15943; similar results are found and presented by Serre and Pääbo 2004; Lawson Handley et al. 2007.

difficult barriers such as mountains are crossed. This means two things. First, due to random genetic drift (random changes in allele frequencies across generations), small populations tend to lose genetic variation over generations (more so the smaller they are). Second, migrating natural populations experience genetic bottlenecks or a "founder effect" whenever a small group inhabits new areas.¹¹ Each time this happens, the founder population represents only some of the genetic variation of its parent population. These factors combine to lower the amount of genomic variation, especially outside of Africa, the home of our originary genetic variation. Interdisciplinarity and acceptance of multiple models and methods will also help paint the full picture here. For instance, archaeological and paleontological evidence can deepen and broaden our analysis.

Africa is indisputably the capital of Planet Unity—as well as the most diverse part of that planet. This is not to deny, of course, that we can see features of Galápagos-Writ-Large as a consequence of human migration and local adaptation to distinct environments.

Two Groundbreaking Episodes

In 1972, biologist Richard Lewontin studied the distribution of alleles across individuals from numerous groups around the globe.¹² He used genes coding for blood proteins to compare genetically different individuals within a population to individuals from other populations, both within and across continental regions. Here is his list of seven continental regions, into which he pooled populations that had been sampled and whose allele distributions (or allele frequencies) had been identified: Africans, Europeans, Asians, Southeast Asians, Indigenous Americans, Oceanians, Australian Aborigenes.

Lewontin found something astonishing: genetically, speaking, you are almost as different from someone chosen at random from your group as you are from a random person from anywhere on the globe. Our familiar racial categories are not backed up by the genetics. The human species has very little genetic variation, and it is mostly between individuals within groups—not between groups.

¹¹ Hartl and Clark 1989; Ramachandran et al. 2005; Lawson Handley et al. 2007.

¹² Lewontin1972. For a more recent study confirming these results, see Barbujani et al. 1997. I explore Lewontin's aims and methods in Winther 2014, 2018.

Nevertheless, 40 years later, a group of researchers led by Noah Rosenberg showed that even these small between-group differences provide enough information to correctly assign someone to a racial group based on knowing about 20-30 of her genes.¹³

What are we to make of this mix of results? Lewontin's work seems to suggest that races and other large human populations aren't, genetically speaking, "really real." But then how could it be possible to assign you a race with a small sample of your genes? This is not an idle question. Biologists and doctors—not to mention big pharma and insurance companies—have large stakes in understanding this puzzle.

The full answer as to why this mix of findings can co-exist would take more detail than available here. What I have elsewhere called Lewontin's "variance partitioning" and Rosenberg's "clustering analysis" are two sides of the same coin, mathematically (Winther 2020). The twofold truth is this: human populations are similar in allele frequencies at many genes—but whenever we *aggregate* information about small differences across two populations, we can use this information to cluster and classify individuals into populations. Knowing an individual's multilocus genotype provides just this information. Although some refer to "Lewontin's Fallacy" (Edwards 2003), I see no fallacy here: Lewontin and Rosenberg were interested in two different sets of questions and methods.

Recall our thought experiment: Planet Unity and Galápagos-Writ-Large are extremes on a spectrum. Yet, in general and on average, our species fits the Planet Unity model surprisingly well. This makes sense in light of Lewontin's results. And, in at least some places on Earth especially big multicultural cities—our children are becoming even more Unity-like, both genetically and culturally. We see Galápagos-Writ-Large properties when we zoom in to a finer grain to explore specific genes or small populations. Admittedly, for some genes there are very large frequency differences in different parts of the world. This shows the validity of Rosenberg and colleagues' results.

Is Race Biologically Real?

¹³ Rosenberg et al. 2002. See also Rosenberg 2018.

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Some claim that our best science indicates that human races are biologically *real* entities (e.g., Robin Andreasen, Charles Murray, Neven Sesardić, Quayshawn Spencer¹⁴). According to this view of *racial realism*, racial groups are clearly genetically differentiated. I believe that our best genomics obviously undercuts such a view. A subset of racial realists—call them "hereditarians"—argue further that the existence of biological populations explains and justifies certain social inequalities (e.g., Jensen 1969, Herrnstein and Murray 1995, Rushton 1995, Lynn and Vanhanen 2002, Murray 2020). For them, multiple social and political inequalities, both within and between nations, are due largely to hereditary differences in the (average) innate abilities of races (as this concept is usually conceived)—intelligence, for instance. This view gives us a Galápagos-Writ-Large picture of biological race. Many hereditarians stand on the political right (e.g., conservatives, libertarians).

Compare the *racial antirealism* view developed in the wake of Lewontin's 1972 paper "The Apportionment of Human Genetic Diversity" (e.g., Joshua Glasgow, Adam Hochman, Naomi Zack¹⁵). For the racial anti-realist, races are social fictions without a biological basis. Such a view is widespread throughout the social sciences,¹⁶ and is widely held by those who identify with the academic left. It can be thought of as the *liberal consensus* on race. In my view, this position goes too far and is somewhat disingenuous—it simply ignores some data.

This controversy is riddled with *burden of proof arguments*: both sides like to argue that the burden lies with the other side. The left wants the right to show strong genetic evidence for specific traits, while the right wants the left to prove that no genetic explanation for between-group differences can be given.

I would suggest that our global genome leaves it open to interpretation whether we can say that racial groups exist or not. The story is complex. Interpretation differs depending on the trait—blood proteins, skin color, behaviors, etc. At any rate, our best genomic studies in the last decade have shown that racial groups aren't very strongly identifiable and don't explain very much.¹⁷ Moreover, the Out of Africa paradigm is basically correct. Ample genomic evidence show, beyond a doubt, that Africa is the capital of our Planet Unity (albeit the most internally

¹⁴ Andreasen 2000, 2007, Herrnstein and Murray 1995, Murray 2020, Sesardić 2010, 2013, Spencer 2013, 2014, 2015, 2019.

¹⁵ Glasgow 2009, Hochman 2013, 2016, Zack 2002.

¹⁶ For instance: Reardon 2005; Fujimura et al. 2014.

¹⁷ For scientific and philosophical reviews of a vast literature, see, e.g., Kaplan and Winther 2014, Winther 2019.

diverse part). Even so, while we are all quite similar, there may be real heritable differences that could, potentially, be politically controversial, especially if they inspire public policy or medical interventions.

We should also bear in mind that the story of race, however we conceive this fraught concept and category, is not, for the most part, a genetic story. Cultural narratives, questions of identity and belonging, are central in our attempts to understand all human groups and populations, racial or otherwise. As we will see below, whether or how race is biologically real is a separate issue from whether or how it might be socially real.

Philosophy and Post-Racial Futures

I believe philosophical analysis of genomics of race shows that race must be characterized in both realist (social race) and antirealist (biological race) terms. (And in *conventionalist* terms for genomic race.) It all depends on which "race" you're talking about. Mills (1988) provides a useful taxonomy of views, ranging from the denial of races' existence (Glasgow 2009) to the belief in deep biological racial "essences." To me, Mills' "objective constructivism" seems the most plausible: races are socially real and are shaped by ongoing social practices. Ásta (2018) provides a similar "conferralist" framework for analyzing the social construction of race and other categories such as sex and gender. For Ásta, race is defined by a social property, namely, "social status consisting in constraints on and enablements to the individual's behavior in a context" (2018, 2). Finally, psychiatrist and philosopher Frantz Fanon illustrates the reality and consequences of social race (e.g., structural racism), in the European colonial context.¹⁸

Crucially, the social construction process of race is historical and contingent.¹⁹ This means that racial categories could always be otherwise. In *When Maps Become the World*, I defended a practice of *imagining "What if...?"*:

In posing this most capacious question, philosophy opens up a space for memories, feelings, hopes, and imagination. When we ask "What if . . . ?," we swap one set of assumptions for another and follow the world-making consequences of each, whether in the future or in potential existence more generally. Perhaps this is a kind

¹⁸ Fanon, Franz. 1952/2008, and 1961/2004.

¹⁹ Hacking 1999 provides a refreshing discussion of realism and constructivism. See also the last chapter "Map Thinking Science and Philosophy" of Winther 2020.

of future-oriented pluralistic ontologizing. ... What if social relations were structured with institutions, values, and behaviors dramatically different from those in place here, today? (Winther 2020a, p. 253)

Let us here briefly address one "what if...?" possibility, that of post-racial societal futures.

A post-racial future is one in which perceived membership in a racial category is no longer associated with differential access to social goods, including dignity, trust, and opportunity. For such a future to exist, we must rip up what Charles Mills calls *the racial contract*. According to Mills, the seemingly neutral social contract theory tradition—including such philosophical luminaries as Thomas Hobbes, John Locke, Jean-Jacques Rousseau, Immanuel Kant, and John Rawls—has effectively posited a social contract between just the *people who count*, which is to say white people. Plausibly, he suggests that "White supremacy is the unnamed political system that has made the modern world what it is today." A post-racial future, then, requires struggles for recognition, power, land, and a decent standard of living—for an expanded social contract that includes all.²⁰

I do believe that post-racial societies are possible, and desirable. They are possible if, per some of the above discussions, each of us is willing to do the hard, critical work of simultaneously feeling a sense of belonging to our respective groups and to *all of us*, and *to all of life*. In so doing, I believe, we must also work hard not to reify and naturalize social expectations and prejudice. The result of the work need not be societies in which people no longer "see" race as a social organizing principle. For instance, social race, as I have defined it, may continue to have some relevance, but not for oppressive or negatively discriminatory purposes—perhaps only to celebrate differences, as some like to say, in culture, music, or food. Whether such a society, in the absence of stereotypical racial judgments, would be more inclined to reward people based on any number of *individual* qualities, such as work ethic or charm, is a matter for further "what if...?" discussion.²¹

²⁰ Mills 1997, pp. 3, 1. For critical analysis of whiteness, racism, and colonialism, in addition to Fanon, see, e.g., Alcoff 2015, Coulthard 2014, Galeano 1973, and Kendi 2019. TallBear 2013 and Happe 2013 show how genomics could undermine such struggles.

²¹ A starting point for such a discussion might be Sandel 2020.

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Allow me to put my point starkly: *genomics simply shouldn't matter to politics*.²² Regardless of genomic results and what they could or could not tell us, we must continue to work towards equality and dignity—also for non-human life—premised on ethics and law instead of on scientific information. Normative equality simply does not depend upon factual equality. Abstracting away from genomics, I encourage us to strengthen moral and legal frameworks to guarantee equality and protection to all.

Coda: Who Are We?

Who am I? It no longer makes sense for us to ask this question. Here, on this pale simulacrum of Planet Unity, we learn more about ourselves as individuals when we ask about the collective: Who are *we*? Who *were* we? Where did *we* come from—from what places and what ancestors? Whence humanity?

These questions include another as their flipside: Who are we not? *Homo sapiens*—that collection of us oddball apes—is not *Homo erectus* or *Homo heidelbergensis*, let alone *Australopithecus anamensis*. Nor are we Neanderthals or Denisovans, although here there is much more overlap. There are morphological and (postulated) behavioral differences between all hominin species and sub-species, including differences in average brain size, presence or absence of air sacks, and the production of particular forms of tools and weapons.

Neanderthals and Denisovans both likely emerged out of Africa. Neanderthals also evolved in Europe and western Asia, and Denisovans called eastern and southern Asia—and later Oceania—their home. There are reasonably good African *Homo* fossils before 400,000 years and after 260,000 years ago. In between lies a gap. Europe, meanwhile, has a solid fossil record for Neanderthal throughout this period (Hublin 2013).

These two subspecies or sister species of *Homo sapiens* elicit much interest. After all, most humans outside of Africa today have a few percentage of Neanderthal DNA, some of

²² I develop this point in detail in Rasmus Grønfeldt Winther. 2021. *Our Genes: A Philosophical Introduction to Human Evolutionary Genomics*. Cambridge University Press. See also Rasmus Grønfeldt Winther and Jonathan M. Kaplan. 2013 "Ontologies and Politics of Bio-Genomic 'Race.'" *Theoria. A Journal of Social and Political Theory (South Africa).* 60 (3): 54-80.

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which is adaptive, for example, in fighting viruses.²³ And Oceanian peoples such as Papuans and Australian aborigines often have more than 5% Denisovan DNA.²⁴ Recent research finds Neanderthal DNA even in contemporary African individuals, suggesting that there were "Back to Africa" migrations, perhaps even by European *Homo sapiens*, themselves carrying Neanderthal DNA, over the last 20,000 years or so.²⁵

Still, we have no evidence of Neanderthal or Denisovan mitochondrial DNA or Ychromosomal haplotypes in any modern human population. Perhaps male fetuses with Neanderthal fathers and human mothers were inviable.²⁶ I leave it to the interested reader to draw out various mating combinations, in order to see that both Neanderthal mitochondrial DNA and Y-chromosomes can be lost in two generations, while autosomal DNA easily introgresses into the human genealogy.²⁷

While we have a few answers, many more remain: The history of *Homo* cannot but raise questions about how to untangle our DNA, "whose" DNA it is, and why Neanderthals went extinct approximately 40,000 years ago.²⁸ Taking a wider view, we can ask which species—and places—gave rise to our nearest contemporary cousins: bonobos, chimpanzees, and gorillas. Such questions bring us closer to our ancestors, inviting a sense of connection and belonging

²⁵ Chen et al. 2020.

²³ E.g., Enard and Petrov 2018. The divergence between Neanderthals and modern humans, *Homo sapiens* can be estimated. Mendez et al. (2016) use Y-chromosome DNA from a Neanderthal to estimate divergence time to be around 588,000 years ago; Langergraber et al. (2012) find the temporal range for the split to be 400-800,000 years ago; Gómez-Robles (2019) uses fossil teeth, not genetics, to place the split at no less than 800,000 years ago.

²⁴ Many central, south, and east Asian populations, as well as indigenous Americans, have small amounts of Denisovan DNA (Jacobs et al. 2019). Typically, because of chromosomal recombination over many generations, the regions of the Neanderthal genome interspersed in our genome are less than a hundred kilobases long (Sankararaman et al. 2014). For further reviews and citations, see also Nielsen et al 2017, Bergström et al. 2020, and Winther 2021a, especially chapter two.

²⁶ See, e.g., Mendez et al. 2016, p. 732. Or maybe any such haplotype lineages in *Homo sapiens* died out due to selection or chance (See Prüfer et al. 2014, Nielsen et al. 2017, <u>https://humanorigins.si.edu/evidence/genetics/ancient-dna-and-neanderthals/interbreeding</u>).

²⁷ Of course, it is possible that we have yet to discover a new Neanderthal Y-chromosome or mitochondrial DNA haplotype from archaic remains, perhaps present somewhere in a human population, either already sampled or not. (On the converse point of human introgression into the Neanderthal lineage, see, e.g., Raff 2017.)

²⁸ Chen et al. 2020; Vaesen et al. 2019.

across the branches of the tree of life. Our best genomics blurs all kinds of putative boundaries, showing the deep and broad connection of all life.



Fig. 3. Our Cousins: Bonobos

Bonobos (*Pan paniscus*) are known for their empathy, matriarchal society, relative peacefulness, and rampant sexual activity across a range of relations (e.g., de Waal 2013, 2019). Bonobo mothers frequently permit other group members to handle their infants; 96% of these interactions were positive in one study (Boose et al. 2018). (Illustrated by Daphné Damoiseau-Malraux. © 2020 Rasmus Grønfeldt Winther.)

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