História, Ciências, Saúde-Manguinhos
ISSN: 0104-5970
ISSN: 1678-4758
Casa de Oswaldo Cruz, Fundação Oswaldo Cruz

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História, Ciências, Saúde-Manguinhos, vol. 26, no. 1, 2019, January-March, pp. 281-297
Casa de Oswaldo Cruz, Fundação Oswaldo Cruz

DOI: https://doi.org/10.1590/S0104-59702019000100016

“A most bountiful source of inspiration:” Dobzhansky’s evolution of tropical populations, and the science and politics of genetic variation

“A mais abundante fonte de inspiração”: Dobzhansky e sua evolução sobre as populações dos trópicos, a ciência e a política da variabilidade genética

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Received on 23 Jan. 2018.
Approved on 28 May 2018.

http://dx.doi.org/10.1590/S0104-59702019000100016

CARVALHO, Tito. “A most bountiful source of inspiration:” Dobzhansky’s evolution of tropical populations, and the science and politics of genetic variation. *História, Ciências, Saúde – Manguinhos*, Rio de Janeiro, v.26, n.1, jan.-mar. 2019, p.281-297.

Abstract

Theodosius Dobzhansky has been studied for how he integrated field naturalism and laboratory experimentation in ways that helped produce the Modern Synthesis, as well as how he leveraged biological expertise to support liberal and cosmopolitan values amidst Second World War and the Cold War. Moreover, Dobzhansky has been central in analyses of the institutionalization of genetics in Brazil, where he spent several years. This article situates Dobzhansky’s Brazilian research within the science of variation and the politics of diversity. I conclude by raising questions about how the ways in which science figured in politics depended on ideas about the role of scientists in society whichwere advanced in parallel, suggesting research on the “co-production” of natural and social orders.

Keywords: evolutionary genetics; transnational science; eugenics; race; tropics; Theodosius Dobzhansky (1900-1975).

Resumo

Theodosius Dobzhansky tem sido estudado pelo modo como ele integrou o naturalismo de campo e a experimentação científica, que deram origem à síntese moderna, assim como a alavanca que ele deu ao conhecimento biológico para apoiar valores liberais e cosmopolitas em meio à Segunda Guerra Mundial e à Guerra Fria. Além disso, Dobzhansky tem sido fundamental para a análise da institucionalização da genética no Brasil, onde ele morou e trabalhou por muito tempo. O trabalho contextualiza a pesquisa brasileira de Dobzhansky dentro da ciência da variabilidade e nas políticas de diversidade. A conclusão levanta questionamentos sobre como a ciência figurava na política dependendo das ideias sobre o papel dos cientistas na sociedade, que foram avançando em paralelo, sugerindo uma pesquisa na coprodução das ordens social e natural.

Palavras-chave: genética evolutiva; ciência transnacional; eugenia; raça; trópicos; Theodosius Dobzhansky (1900-1975).

The Russian-American evolutionary biologist Theodosius Dobzhansky has been the subject of considerable philosophical and historical scholarship, including how he integrated the methods of field naturalism and laboratory experimentation in ways that helped produce the Modern Evolutionary Synthesis and how he leveraged his biological expertise to defend liberal, cosmopolitan, and democratic values in the midst of the Second World War, the Cold War, and the problematization of race (Lewontin, 1974; Gould, Lewontin, 1979; Mayr, Provine, 1980; Beatty, 1987a, 1987b; Paul, 1987; Adams, 1994; Gould, 2002; Gannett, 2013; Subramanian, 2014; Yudell, 2014; Jackson, Depew, 2017). Moreover, Dobzhansky has been at the center of analyses on the institutionalization of genetics as a science in Brazil, where he spent most of his time outside of Russia and the US with the support of the Rockefeller Foundation (Glick, 1994, 2008; Cunha, 1998; Marinho, 2001; Pavan, Cunha, 2003; Araújo, 2004; Sião 2007; Formiga, 2008; Souza et al., 2013; Magalhães, Vilela, 2014; Souza, Santos, 2014; Santos, Silva, Gibbon, 2015). This article bridges both sets of literature by situating Dobzhansky's work in Brazil within the mid-twentieth-century science of genetic variation and the politics of diversity. To a considerable extent, Dobzhansky's framing of natural selection as a creative mechanism in evolving adaptations was based on his research on the genetics of spatially dispersed tropical *Drosophila* populations in relation to their diverse environments; this also served as an empirical and scientific basis for his defense of the social values of liberal cosmopolitanism. I conclude the piece by raising questions about how the ways in which the science of genetic variation figured in the politics of diversity – as a source of knowledge and as a locus of rational and ostensibly extra-political authority – depended on ideas about democracy and the proper role of scientists in society that were advanced in parallel. I suggest further research on the "co-production" of natural and social orders and the exportation of these models to different national contexts and their reception (Jasanoff, 2004).

"The evolution of Theodosius Dobzhansky:" the full breadth of his life and thought?

Born in Nemirov, Ukraine, on January 29, 1900, Theodosius Dobzhansky was one of the major architects of the Modern Evolutionary Synthesis, integrating his Russian training in natural history, entomology, and field biology with the genetics problems under investigation in laboratories like those of Thomas Hunt Morgan in the United States. By 1937, his masterpiece *Genetics and the origin of species* was the first of a number of books and other publications to assimilate myriad biological disciplines within an overarching evolutionary paradigm. Subsequent works included Ernst Mayr's 1942 *Systematics and the origin of species*, George Gaylord Simpson's 1944 *Tempo and mode in evolution*, and G. Ladyard Stebbins's 1950 *Variation and evolution in plants*. In 1938, Dobzhansky, along with M.L. Queal (1938), published an article entitled "Chromosome variation in populations of *Drosophila pseudoobscura* inhabiting isolated mountain ranges;" this was the first piece in what would become his influential anthology *Genetics of natural populations, I-XLIII,* and indeed the essential resource in the field of population genetics for the next four decades.

Yet despite his crucial role in articulating modern evolutionary biology, Dobzhansky was not the subject of much philosophical and historical scholarship until the "reopening of Russia" in the late 1980s and early 1990s, especially in comparison with other major twentieth-century evolutionary biologists such as R.A. Fisher, J.B.S. Haldane, and Sewall Wright. Cold War politics meant that Dobzhansky (who emigrated to the US in 1927) was shunned in the Stalinist-Lysenkoist Soviet Union. In fact, as late as the mid-1970s and just a few years before his death in December 1975, he was denied a visa to return to his country of origin for a final visit. Fortunately, the International Symposium on Theodosius Dobzhansky was held in Leningrad in September of 1990, and questions about how his Russian background related to his successive contributions to modern evolutionary biology began to be answered. Following this symposium, Mark Adams edited the excellent 1994 volume *The evolution of Theodosius Dobzhansky: essays on his life and thought in Russia and America*, in which a number of Russian authors reflected on the origins of Dobzhansky's pioneering methods and insights and American scholars wrote about Dobzhansky's later years at the Morgan lab, his influence on other biological disciplines, and his social, political, and religious ideas.

Thanks to their knowledge of published sources in the Russian language and the archival materials which had recently been made available, the Russian scholars who contributed to Adams's volume offered novel insights about Dobzhansky's upbringing as a young naturalist in Kiev and Leningrad, and the genesis and development of his quintessential contributions. Entitled "Russian roots," the first section of the book explored Dobzhansky's shaping as an entomologist, with Nikolai Krementsov (1994) arguing that the practices of early twentieth-century Russian entomology deeply influenced Dobzhansky's subsequent population genetics research and formed the foundation of his understanding of speciation, as well as the biological species concept with which he has been credited. Daniel Alexandrov (1994) also underscored the entomological element of Dobzhansky's early work in his chapter on a comparative analysis of Dobzhansky and his mentor, Yuri Filipchenko, considering the young Dobzhansky's publications in Russian for the first time. Lastly, Mikhail Konashev (1994) offered his findings after several years of archival research on Dobzhansky's family history and work in Kiev and in Filipchenko's Leningrad laboratory, clarifying how the collaboration and friendship between the two scientists influenced the development of genetics in that country. Entitled "The Morgan lab," the second section of Adams's *The evolution of Theodosius Dobzhansky* examined his activities after joining Thomas Hunt Morgan's group in the US in 1927. Drawing on interviews with Dobzhansky in the late 1960s, Garland Allen (1994) considered Dobzhansky's role within Morgan's lab in connecting field naturalism and laboratory experimentation. In the following chapter, William Provine (1994) focused specifically on the years leading to the publication of *Genetics and the origin of species*, examining the impact that this book had not only as a source of novel evolutionary genetics insights, but also as a re-articulation of theoretical and mathematical population genetics in empirical terms. Robert Kohler (1994) continued the analysis by expanding on his previous work on the centrality of the *Drosophila* model system in twentieth-century biology, contending with Dobzhansky's population genetics approach to evolutionary questions as a "novel system of scientific production" centered on wild populations of *Drosophila pseudoobscura* as opposed to standardized laboratory specimens of *Drosophila melanogaster*. Lastly, Richard Burian (1994) pressed forward on questions related to how Dobzhansky departed from his own scientific tradition, for example by overcoming Filipchenko's objections to neo-Darwinian extrapolations from micro- to macro-evolution, as he argued for the continuity of evolutionary mechanisms at all taxonomic levels.

In the next section, "The scientific legacy," three evolutionary biologists considered the lasting impacts of Dobzhansky's work two decades after his death. Scott Gilbert (1994) addressed Dobzhansky's predilection for the views of Schmalhausen over those of Waddington in integrating embryology with the Modern Synthesis. One of Dobzhansky's most prominent students, Bruce Wallace (1994), drew on their decades-long relationship to explore the development of his mentor's thinking on the question of coadaptation. And yet another prominent student of Dobzhansky, Charles Taylor (1994), brought the section to a close by recollecting the discussions that they had on evolution's "larger issues" regarding social, political, and philosophical questions, and how Taylor's own research with computer modeling and artificial life has addressed these questions.

The fourth and final part of the volume, "Dobzhansky's worldview," focused on his social, political, philosophical, and religious ideas. In the opening chapter, Dobzhansky's student Costas Krimbas (1994) reviewed Dobzhansky's comprehensive evolutionary perspective, tracing the connections between his biological research and his wider interests in heredity, evolution, meaning, destiny, and religion. John Beatty contended with Dobzhansky as a "biologist of democracy," examining his vision of the ethical and social consequences of genetic variation and measuring the impact that his years at Columbia University in the late 1930s and 1940s, which was a hotbed of liberal politics, hadon his own political philosophy (more on the "biology of democracy" below). Diane Paul (1994) examined how an evolving nature-nurture debate placed Dobzhansky on different sides of the controversy atvarious points in time. And Michael Ruse (1994) scrutinized Dobzhansky's understanding of progress in the broadest sense, exploring the apparent paradox between his materialist evolutionary ontology vis-à-vis his interest in Teilhard de Chardin, and ultimately finding systematicity and synthesis – epistemic, moral, political, and spiritual – to be latent, for Dobzhansky, in living systems.

The evolution of Theodosius Dobzhansky thus captured a broad swath of his life and work, including his scientific practices, critical contributions to the development of the Modern Synthesis, and social and political philosophy. But surprisingly, not a single word was written on the decades of work Dobzhansky did in Brazil, nor on the tropical species of *Drosophila*, save for one mention in the introduction to the volume by Dobzhansky's daughter, Sophie Dobzhansky Coe. She stated that the opportunity to travel to Brazil gave her father "a chance to indulge in his love for the tropics. He often referred to passages in Charles Darwin's *Voyage of the Beagle* as his intellectual precedent for his delight in the abundance of tropical life" (Coe, 1994, p.24). But Dobzhansky did not simply travel to explore exotic, romantic lands; he labored in many ways to develop the science of population genetics in several countries in collaboration with many international colleagues, which in turn had a considerable impact on the direction of his own science and politics. It consequently cannot be said, as Adams (1994, p.9) remarked in the opening pages of the book, that it "reflects the full breadth of Dobzhansky's life and thought." As I argue below, Dobzhansky's work with tropical populations, especially of the species *Drosophila willistoni*, was fundamental for his articulation of the modern theory of evolution by adaptive natural selection. In particular, these experiences shaped his position in the controversy against Hermann Joseph Muller (known as the “classical-balance debate”) over the direction of selection and the extent of genetic variation in natural populations. As such, Dobzhansky’s research on evolution in the tropics was also an important source of his support for liberal, cosmopolitan, and democratic principles in the contexts of the Second World War, the Cold War, and the question of race, indicating the extent to which he believed that scientific expertise and accurate representation of the world were the appropriate responses to pressing social and political issues, and raising questions about his role in spreading scientific rationality as a global political project.

Dobzhansky and the institutionalization of genetics in Brazil

In the same year that Adams’s volume was published, 1994, so was Marcos Cueto’s *Missionaries of science: the Rockefeller Foundation in Latin America*; this book contained a chapter by Thomas Glick on how, between the 1940s and 1950s, Dobzhansky introduced a circle of Brazilian scientists to the methods of *Drosophila* genetics, trained them in population biology and neo-Darwinian evolutionary theory, and conducted research on evolutionary mechanisms in tropical *Drosophila* species (see also Glick, 2008). Although Dobzhansky’s work with his Brazilian group effectively ended in 1956 after a failed experiment in the islands of Angra dos Reis, off the coast of Rio de Janeiro, his Brazilian colleagues carried on with the science of population genetics in the South American country, expanding it to other experimental systems and eventually including human populations.[1]

As with *D. melanogaster* and *D. pseudoobscura,* work on the tropical species *D. willistoni* marked methodological and conceptual developments in twentieth-century evolutionary biology, with significant implications for social and political ideologies.

As Glick (1994) pointed out, genetics in Brazil can be traced back to 1917, when the subject was studied as an applied agricultural science at the Escola Superior de Agricultura Luiz de Queiroz (see also Araújo, 2004; Souza et al., 2013). By the mid-1930s, the Brazilian physician André Dreyfus (who was self-taught in genetics) chaired the faculty of biology at the newly founded University of São Paulo. Dreyfus thought it important to introduce the emerging synthesis of evolutionary theory and genetics to his students. Along with the Rockefeller Foundation representative to Latin America, Harry Miller, Dreyfus therefore arranged for Dobzhansky to visit Brazil, as Dobzhansky himself had conveyed interest to Miller in studying the genetics of tropical *Drosophila* populations, a matter which up to that point had been overlooked in the emerging field of population genetics.[2] Accordingly, Dobzhansky’s work in Brazil was the outcome of a confluence of Brazilians’ own concern with furthering the science of genetics in their country, the Rockefeller Foundation’s presence in Latin America as it endeavored to spread its model of scientific rationality and governance, and Dobzhansky’s interest in the study of evolution in the tropics.

With regard to this latter point, Dobzhansky’s research had previously shown that the frequencies of chromosomal polymorphisms in populations of *D. pseudoobscura* inhabiting different localities in southern California changed seasonally, suggesting that these polymorphisms affected the adaptive value of their carriers under differing winter, spring, summer, and fall conditions (Dobzhansky, 1943). But little was known about tropical populations that were assumed to experience few seasonal variations throughout the year, even though Dobzhansky had collected *Drosophila azteca* and other species from tropical regions of Mexico and Guatemala in the mid-1930s.[3] It was therefore important for Dobzhansky to know "whether or not the mutation rates were low and the migration rates reduced to a minimum," as well as whether "the diversification of the population in local races was high and proceeding to a considerable extent along non-adaptive lines" (Dobzhansky to Miller, cited in Glick, 1994, p.151). As he later recalled for a Columbia University oral history project,

> in collaborating with [Sewall] Wright I had, of course, been very excited about this problem of genetic drift. ... Now, one of the important variables there, or so it seemed to me at that time, is that in temperate climates, where you have summer and winter seasons, the populations of many animals, including *Drosophila*, pass every year through a series of contractions and expansions. The flies hibernate almost certainly as adults, and during the winter season most of them die out, so that by spring only a few survive, presumably chiefly impregnated females, also some males are left, and they start the ball rolling from the beginning. As the season progresses, and more fruits and other food is available, the population grows very large. It is this periodic reduction of the population to small size which seemed important as a possible agency bringing about this genetic drift. That led to a very simple idea: if the genetic drift is due to seasonal alternations, chiefly winter resulting in destruction of the flies, then what would happen in a tropical climate where winter never comes? There, season after season the population should be large enough to eliminate genetic drift (Dobzhansky's reminiscences, 1962, cited in Araújo, 2004, p.470).

Upon arriving in Brazil in August of 1943, Dobzhansky taught evolutionary genetics for four months at the University of São Paulo, as part of his arrangement with Dreyfus and Miller, and participated in local genetics conferences that had been organized around his presence in the country. He then left the city with a few selected students to begin collecting *Drosophila* at a number of sites in Brazil. During the next few years, Dobzhansky hosted many of these students in his own laboratory at Columbia University, where they worked on chromosomal analysis of the tropical *Drosophila* specimens that had been captured. This work resulted in the identification of several new species, as well as descriptions of many others that were already known but seldom collected. Most notably, they found that *D. willistoni* in particular contained the greatest number of inversion polymorphisms of any species studied in this manner, with as many as fifty different chromosomal inversions eventually recorded (Cunha et al., 1959).

As Dobzhansky later recalled for the aforementioned Columbia oral history project, his motivation to compare temperate and tropical *Drosophila* populations with regard to seasonal variables "proved to be wrong" because "in the tropics, seasonal changes are by no means absent" (Dobzhansky's reminiscences, 1962, cited in Araújo, 2004, p.470). Instead, he returned to Brazil during his sabbatical year (1948-1949) to conduct a new study, measuring the frequencies of genetic polymorphisms in populations of *D. willistoni* with regard to spatial rather than temporal variation in different parts of the species distribution. Specifically, Dobzhansky and his co-authors rated different parts of the territory in terms of the variety of ecological niches available, correlating it with the mean number of inversion polymorphisms in local *D. willistoni* populations from each area. Their findings ultimately supported the working hypothesis that polymorphisms constituted a method by which populations mastered multiform environments (Glick, 1994, 2008). Although the initial research was conducted during the 1948-1949 sabbatical (Cunha, Burla, Dobzhansky, 1950; Burla, Cunha, 1950), additional studies were done for several more years (Cunha, Dobzhansky, 1954; Dobzhansky, Cunha, 1955; Cunha et al., 1959), strengthening Dobzhansky's belief that natural selection preserved a wealth of genetic variations in natural populations. Ultimately, as he and his associates mounted an empirical and scientific basis for the politics of diversity, the genetics of tropical populations afforded the strongest evidence that the principles of democratic equality should be advanced because, not in spite of, known evolutionary dynamics. In the following section, I develop this claim with regard to a related series of scientific and political controversies.

Evolution in the tropics and the creativity of natural selection

Becoming acquainted with tropical nature is, before all else, a great esthetic experience. Plants and animals of temperate lands seem to us somehow easy to live with, and this is not only because many of them are long familiar. Their style is for the most part subdued, delicate, often almost inhibited. Many of them are subtly beautiful; others are plain; few are flamboyant. In contrast, tropical life seems to have flung all restraints to the winds. It is exuberant, luxurious, flashy, often even gaudy, full of daring and abandon, but first and foremost enormously tense and powerful. Watching the curved, arched, contorted, spirally wound, and triumphantly vertical stems and trunks of trees and lianas in forests of Rio Negro and the Amazon, it often occurred to me that modern art has missed a most bountiful source of inspiration. The variety of lines and forms in tropical forests surely exceeds what all surrealists together have been able to dream of, and many of these lines and forms are endowed with dynamism and with biological meaningfulness that are lacking, so far as I am able to perceive, in the creations exhibited in museums of modern art (Dobzhansky, 1950, p.209).

The relative importance of Dobzhansky's genetics of tropical populations can be evaluated against three interrelated scientific and political questions: the "hardening of the Synthesis," the "classical-balance debate," and the "paradox of viability." As Stephen Jay Gould and a number of other scholars have observed, the Synthesis's original works by Dobzhansky and others in the late 1930s and early 1940s were rather pluralistic in their approach to assessing admissible mechanisms of evolutionary change. In other words, although natural selection was considerable, it was by no means considered the dominant force of evolution. As the Synthesis unfolded in the mid-1940s, 1950s, and 1960s, however, a predominantly selectionist paradigm took hold (Gould, 1982, p.XXXV-XXXIX; see also Gould, Lewontin, 1979; Mayr, Provine, 1980; Beatty, 1987a, 1987b; Gould, 2002, p.524-528). The growth of this program (which was known as the "hardening of the Synthesis" due to its Darwinian character) was first expressed in the changes that Dobzhansky made between 1941 and 1951 for the third and final edition of *Genetics and the origin of species*. For this version Dobzhansky deleted much of the material on non-adaptive or non-selected genetic changes and instead added a new chapter, "Adaptive polymorphisms," with a discussion of the tropical *D. willistoni*.

Before getting to *D. willistoni*, however, it is necessary to note that Dobzhansky's famous 1943 paper, "Temporal changes in the composition of populations of *Drosophila pseudoobscura,*" already provided clear evidence of adaptive natural selection. In this paper he inferred that the standard, Chiricahua, and "sex-ratio" gene arrangements in populations of *D. pseudoobscura* inhabiting Mt. San Jacinto, California affected the adaptive value of their carriers because of cyclic (seasonal) and year-to-year changes in their frequencies. Nevertheless, historians of the Synthesis such as Gould and John Beatty have expressed incredulity that these results alone, "a small sample of evolutionary events" (Beatty, 1987b, p.274), could have prompted the "hardening." Gould states he did "not fully understand why this hardening occurred," and regarded it "as an important topic of historical research" (Gould, 1982, p.XXVIII). Beatty, in turn, argued that in addition to Dobzhansky's empirical findings, the importance of natural selection became increasingly compelling from his point of view due to "value considerations" – that is, "it had evolutionary consequences that were very 'desirable' for Dobzhansky in a value-laden sense" (Beatty, 1987b, p.275). To understand why, Beatty argued, one must take into account the "classical-balance debate" between Dobzhansky and Hermann Joseph Muller which took place parallel to the "hardening of the Synthesis." This debate, as Beatty and others have pointed out, was as political as it was scientific, since it simultaneously considered the amount of genetic variation that should be expected in natural populations, the role of natural selection in this variation (in other words, was natural selection mainly a mechanism to preserve or eliminate variations), and accordingly, the kinds of social policies for governing populations (for example, different forms of eugenics programs).

Dobzhansky's most famous student, Richard Lewontin, has shed light on the technical aspects of this debate, which we shall see before returning to Beatty's point about Dobzhansky's "value considerations" (see also Dobzhansky, 1955). As Lewontin explained in his own magnum opus, *The genetic basis of evolutionary change* (1974), Hermann Joseph Muller believed that at nearly every locus every individual was homozygous for a "wild-type" gene (i.e. the statistical norm in the population), and additionally, each individual was thought to be heterozygous for rare deleterious alleles at a handful of loci, on the order of one hundred out of tens of thousands of genes, though a very small proportion of the population would be so unfortunate as to be homozygous for a rare deleterious gene and thus be severely handicapped (Lewontin, 1974, p.23-31). This hypothesis, Lewontin pointed out, was fully described by Muller in his 1950 article titled "Our load of mutations," in which Muller estimated that a typical person would be heterozygous for a deleterious gene at eight to eighty loci, depending upon various assumptions about the number of loci in the genome, mutation rates, and degrees of dominance. This image also agreed with the assumption in biochemical genetics at the time that there was one functional or best form of an enzyme, and that other forms specified by alternative alleles as the structural gene locus would have defective enzyme activity (Lewontin, 1974, p.23-31). Muller thus presumed that the chief action of natural selection was to remove mutations from the population – or to purify the gene pool – and that the fittest genotypes were the homozygotes for the "wild-type" alleles at all loci. In other words, for Muller, genetic changes were nearly always for the worse, and the function of natural selection was to prevent species degeneration by maintaining the type. Approvingly quoting Muller two decades later, geneticists Motoo Kimura and Tomoko Ohta wrote, "the gene, through the long course of evolution, has finally found itself in man" (Kimura, Ohta, 1971, p.166, cited in Lewontin, 1974, p.30).

As Diane Paul (1987) has emphasized, however, Muller's chief concern was not with severely deleterious and rare genetic mutations, but rather the cumulative effects of only slightly deleterious mutations, which were generally submerged in heterozygosis. Most human ailments, Muller contended, resulted from these kinds of genotypes, which persisted much longer in populations and thus acted as a heavy burden (or "load") on the species. Moreover, Muller's anxiety about this genetic load was exacerbated during an age of medical and other bonafide social advances that he saw as checks on natural selection, as well as the increased use of atomic radiation, which he believed would increase the number of genetic mutations in populations. Consequently, beyond merely articulating a theory of evolution according to a classical view of natural selection, Muller also advocated for certain social policies, notoriously proposing mass artificial insemination of women from sperm banks derived from an ostensible genetic elite of "great men" such as Lenin, Newton, Leonardo, Pasteur, Beethoven, Omar Khayyam, Pushkin, Sun Yet Sen, and Karl Marx (Muller, 1935; see also Paul, 1984). And although Muller himself did not promote eugenics along racial lines, Lewontin has observed that the classical view did assign considerable biological importance to race as a taxonomic category, since from this viewpoint most genetic diversity within polymorphic species (including *Homo sapiens*) would be inter-populational, which was to say interracial. In addition, another basis for racism also streamed from the concept of the wild type, since if there were an optimum genotype of the species, populations that fail to correspond to it must be inferior (Lewontin, 1974, p.25-26).

In contrast with Muller's "classical" view of natural selection, Dobzhansky believed that individuals from sexually reproducing, cross-breeding populations were heterozygous at nearly all of their loci, and that a locus would only rarely be homozygous, except in offspring from closely-related mates (Lewontin, 1974; Dobzhansky, 1955). This view had two concomitants: first, there was no allele that could be properly designated the "wild type" since normal individuals in the population were thought to be heterozygous, a point that Dobzhansky most forcefully expressed with his Brazilian co-author Antônio Rodrigues Cordeiro in their 1954 article entitled "Combining ability of certain chromosomes in *Drosophila willistoni* and invalidation of the 'wild-type' concept," and second, the number of alleles segregating in the population would be so large at each locus (since otherwise, ordinary Mendelian laws would cause homozygosity from random segregation and mating) that not only were most loci heterozygous, but the loci that happened not to be would be homozygous for different alleles. This view was most clearly stated by Dobzhansky's student Bruce Wallace in the paper "The role of heterozygosity in *Drosophila* populations," delivered during the X International Congress of Genetics in Montreal, Canada in 1958, which extensively cited the work by Dobzhansky and his Brazilian colleagues on *D. willistoni*, such as Cunha, 1946; Cunha, Burla, and Dobzhansky, 1950; and Dobzhansky and Cunha, 1955 (Wallace, 1958).

In accordance with his scientific opposition to Muller, Dobzhansky also opposed eugenicists' tinkering with populations, arguing that the so-called genetic load was actually an important source of variation that populations used to adapt to environmental changes. Dobzhansky believed that free choice in marriage would actually result in a more eugenically optimal society than short-sighted (if not altogether blind) manipulation by eugenicists (Paul, 1984). Ultimately, as Joseph Felsenstein (1975, p.589) described in his review of Lewontin's *The genetic basis of evolutionary change,* Muller's "classical school" (at least as described by Lewontin) was "the conservative ideology of eugenic engineers, rationalizing the status quo," while Dobzhansky's "balance school" was "an optimistic, pluralistic view that sees nature as process rather than product."

Returning to Beatty's point about Dobzhansky's "value considerations," the empirical findings from *D. willistoni* precisely addressed the value problems that Dobzhansky encountered even as he articulated the alternative "balance hypothesis" of natural selection. This is where the "paradox of viability," or the notion that the long-term viability of a population depended on possessing genetic variations that decreased the viability of individual carriers at any given point in time, came into play. Environments were so dynamic and changeable, Dobzhansky thought, that populations needed mechanisms to balance genetic variations which would permit adaptedness at the present time with others that could allow future adaptation. "Heterosis," also known as "heterozygote advantage," was one such mechanism; whenever heterozygosis afforded higher fitness than any other possible homozygous combination, for example by engendering developmental plasticity, a balance between the frequencies of each genetic variation would hold (Lewontin, 1981; Beatty, 1987b). Yet the nature of Mendelian inheritance was such that heterosis caused less fit individuals to always be present in the population, since the superior heterozygotes give rise to some less fit homozygotes in every generation. In other words, it "hardly did away with the individual costs of maintaining variation within a population" (Beatty, 1994, p.212). On the other hand, Dobzhansky's 1948 research on *D. willistoni* in Brazil mentioned above surveyed genetic polymorphisms in spatially dispersed populations, not temporally successive ones, ultimately supporting the idea that polymorphisms were a method with which populations mastered complex, multiform environments such as the tropics. Importantly in this case, however, was the implication that the "paradox of viability" did not apply, since more complex environments accommodated a greater variety of genotypes. In other words, to dissolve the paradox, Dobzhansky looked beyond genetic diversity within the population, simultaneously accounting for the diversity of ecological opportunities available in the population's territory.

In addition to addressing the "paradox of viability," Dobzhansky's research on *D. willistoni* also offered a stronger guarantee of genetic variation against the classical position than his previous research on temporal changes in *D. pseudoobscura*. By 1943, Dobzhansky had surveyed the fluctuating frequencies of only five gene arrangements of *D. pseudoobscura* populations, three of which were considerably more common in all five localities of the distribution he examined in southern California, and two of which were more common in two of the localities. In other words, while this research suggested a model of balancing selection, it nevertheless fell short of depicting ubiquitous genetic variation in natural populations to juxtapose with Muller's view. In contrast, and as mentioned in the opening of this essay, the greatest number of inversion polymorphisms of any species of *Drosophila* (or for that matter, of any organism studied in this respect) was found in *D. willistoni*, with as many as fifty different inversions recorded. Populations in central Brazil were the most notably diverse, possessing thirty-four such inversions (Cunha et al., 1959). Ultimately, whether Dobzhansky adopted a selectionist program due to either his empirical research or value considerations is a trivial question. He understood human society within a biological register, and brought political and ethical considerations to bear on his scientific research. As his work on genetic variation in *D. willistoni* specifically exemplifies, he sought to resolve normative problems, such as the conflict between the welfare of populations and the welfare of individuals, by using empirical evidence. In the following section I address how Dobzhansky applied the lessons of tropical *D. willistoni* to human society, suggesting that he was just as concerned with the characteristics of environments as he was with the characteristics of populations.

"Applicable to *Drosophila* as well as to man:" multiform environments and equality of opportunity

As many scholars have underscored, and as this essay has suggested up to this point, Dobzhansky was a committed social activist devoted to using scientific knowledge to address social, political, and philosophical questions. "Although a biologist may do his research on mice, *Drosophila* flies, or bacteria," he argued, "the ultimate aim should be to contribute toward the understanding of man and his place in the universe" (Dobzhansky, 1973, cited in Paul, 1987, p.334). His work on tropical *D. willistoni* was no exception, as he drew direct connections between evolution in the tropics and human society.

In the late autumn of 1970, in the twilight of his career, Dobzhansky received a letter in which his dear friend and famed systematist Ernst Mayr asked if he could "single out" what he considered to be his "major scientific contributions." In response, he listed three: first, being one of a small group of geneticists responsible for transitioning from laboratory study of *D. melanogaster* to studying natural populations of *D. pseudoobscura* in 1931; second, his observation of cyclic changes in the frequencies of certain inversion polymorphisms in these populations between 1940 and 1942; and third, his idea, "starting around 1948 [his sabbatical year in Brazil]," that "a population can cope with diversity of environments either by having genetic variety or by having genotypes with adaptively flexible manifestations." The latter idea was "clearly applicable to *Drosophila* as well as to man," Dobzhansky continued. "In *D. willistoni* the extent of polymorphisms is, on the whole, proportional to the variety of habitats the populations occupy in different parts of the distribution. Man, on the other hand, controls many environments not so much by a diversity of genotypes as by one basic genetically controlled trait – the ability to acquire a learned culture" (Dobzhansky, 15 Dec. 1970). This communication between Mayr and Dobzhansky raises two questions: First, how did Dobzhansky connect *Drosophila* genetics with human culture and society? And second, in making this connection (at least as he did with Mayr), why did he mention *D. willistoni* in particular, and not *D. pseudoobscura*?

Dobzhansky articulated his understanding of evolution, culture, and society over several decades in a number of publications addressed to both scientific and lay audiences. Essentially, he believed that the process of organismic evolution that is common to all species led sapient humans in particular to a new phase of cultural evolution, because whenever possible, natural selection promoted flexible traits, and learning was a most flexible method for coping with environmental changes. Dobzhansky further supposed that the flexibility or plasticity afforded by the capacity for learning was particularly significant for human beings, since in addition to otherwise expected environmental changes, our species vigorously engages in transforming our own environments; indeed, Dobzhansky believed that selection for this ability was so vital for humans that it became a common trait across all populations and races (Dobzhansky, Montagu, 1947; see also Dunn, Dobzhansky, 1946; Dobzhansky, 1956, 1962b, 1967, 1973; for secondary literature, see Beatty, 1994; Jackson, Depew, 2017). It should be noted, however, that although this is not how he expressed his views to Mayr in 1970, Dobzhansky continued to argue on many occasions that underlying genetic variation was important for human populations, even as our species entered this new phase of cultural evolution made possible by the generation of such developmentally plastic characteristics as educability. After all, developmental plasticity was augmented in heterozygosis. In the case of human learning in particular, Dobzhansky believed that all kinds of human differences, including the ability to learn and perform different tasks and jobs well, must have had at least some genetic component or influence, and consequently benefited from genetic variation in human populations (Beatty, 1994; Paul, 1994).

While this is not the place to review the work of Dobzhansky's pupils, it is worth noting that Francisco Ayala continues today to develop a similar line of argumentation, reasoning that moral evaluation of actions emerges from the human capability for rationality, and consequently is a necessary implication of the biological makeup of our species. This is not to be confused with crude biological determinism, however; Ayala (1987, 2010) posits a modest biological ability for morality (as opposed to a genetically determined content of moral codes), maintaining that the norms human beings use to judge good and evil are largely learned from culture, although he adds that they may be conditioned by some biological predispositions such as parental care.

As for the second question raised above, whether Dobzhansky specifically referred to *D. willistoni* as opposed to *D. pseudoobscura* in connection to human evolution and culture in responding to Mayr, I believe that the answer goes back to Dobzhansky's (1973, p.44, cited in Paul, 1994, p.227) belief that "any human society, from the most primitive to the most complex, needs a diversity of men adapted and trained for a diversity of functions." In other words, as Paul has noted (and as previous sections of this essay have implied), Dobzhansky (1973, p.44, cited in Paul, 1994, p.227) prized human differences, believing that "all kinds of people were needed to do the world's work." Moreover, he also prized democratic equality as the sociopolitical environment in which individuals were free to pursue their preferences and talents. Thus, for Dobzhansky, the ideal polity and society must have been much like tropical populations and environments: teeming with various types, though not as a “price to be paid” for the long-term welfare of the population, but rather as a method with which to master the various niches available.

Final considerations: the problem of race and the ethos of science

Dobzhansky not only leveraged his work on the diversity of tropical life against Muller’s classical view of evolution by natural selection and the morally and politically troubling policies that it supported, he also did away with the paradox between the welfare of populations and the welfare of individuals which his own previous research had generated. Accordingly, our attention to Dobzhansky’s work in Brazil provides a fuller picture of how the science of genetic variation and the politics of diversity unfolded in the mid-twentieth century. But were we to stop here, we would assume a relationship between science and society that itself must be interrogated as a historical, political project. From a more distanced level of analysis, the question is not be so much about the substantive content of (and connections between) Dobzhansky’s science and politics, but rather about how, in formulating a political ideology based on science, Dobzhansky simultaneously advanced a particular notion of the proper way to frame social and political problems and to define the relevant stakeholders.

Enjoying a form of extra-political authority, Dobzhansky positioned himself as arbiter of what is the case – how evolution has taken place and what populations are like – and what must be done about it. His strategy of calling the politics of eugenics and racism into question by retaining eugenical and racial science conceived that the way to resolve concerns of shared norms, the common good, and public life was through disinterested and expert knowledge, “speaking truth to power.” This was made plain in how Dobzhansky responded not to Mullerbut to the anthropologist Frank Livingstone, on the question of the biological existence of human races. “To say that mankind has no races,” Dobzhansky (1962a, p.280) argued, “plays into the hands of race bigots, and this is least of all desirable when the ‘scientific’ racism attempts to rear its ugly head.”

Analytically, I believe that this notion can be developed by comparison Dobzhansky’s argumentative strategies with those of his pupil Richard Lewontin. While the focus of this essay is not Lewontin’s scholarship, suffice it to say that he is well-known partly because of his rejection of the biological category of race, a stance he took for fundamentally political reasons, not scientific ones; recall that he recommended abandoning race as a taxonomic category, stating that its negative impact on social relations outweighed its admittedly limited genetic significance (Lewontin, 1972, p.397). Therefore, in contrast with his mentor who sought to expand the reach of population genetics science to claim authority over public concerns about race, Lewontin contended with the problem of race by demarcating narrower boundaries around population genetics science.

On a final note, I find that here one can also see the exportation of a new, humble scientific approach to the problem of race, as the disposition toward this problem among subsequent generations of Brazilian population geneticists more closely resembled Lewontin's approach than Dobzhansky's. For example, in his forward to the English edition of *Problems in human biology: a study of Brazilian populations*, the 1970 classic by the Brazilian population geneticists Francisco Salzano and Newton Freire-Maia, Charles Wagley, the Franz Boas Professor of Anthropology at Columbia University, wrote: "Sociologists and social anthropologist study what people 'believe to be true' and what actions people take as a consequence of their attitudes and beliefs … The authors of this book are human biologists of the new breed and they are fully aware of, and make use of, the historical and sociological setting in which the biological process occurs" (Wagley, 1970, p.XIX-XX).

NOTES

[1] On human population genetics in Brazil, see Santos, Lindee, Souza (2014); Santos, Silva, Gibbon (2015); Dent (2016) and Dent, Santos (2017).

[2] On the activities of Rockefeller Foundation at the University of São Paulo specifically, see Marinho (2001).

[3] On how Dobzhansky contributed to the emergence and institutionalization of genetics in Mexico, see Barahona, Ayala (2005).

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