Do Humans Have Continental Populations?

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In this article I show that population geneticists are acknowledging a kind of biological population that has hitherto been unappreciated by philosophers. The new population talk occurs when population geneticists call continent-level human genetic clusters 'populations' in population structure research. My theory is that the kind of population being referred to is the K population, which is, roughly, a biological population whose members are united by common genomic ancestry and in which population membership is graded. After presenting and defending the theory, I show that the K population is indeed a kind of biological population. Finally, I address likely objections.

1. Introduction. There is a recent trend among population geneticists to call the continent-level human genetic clusters inferred from *structure-like* algorithms 'populations'.[1] For example, Bamshad et al. (2003, 584–85) call Africans, East Asians, Europeans, and Indians "continental populations" when conducting population assignment with *Alu* insertions and microsatellites. McEvoy et al. (2010, 297) call Africans, East Asians, Eurasians, Native Americans, and Oceanians "geographic populations" when using *frappe* and *structure* to detect human population structure. Feldman and Lewontin (2008, 90) call these same continental groups "geographical populations" when summarizing two landmark studies on human population structure.

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1. The term "*structure-like*" is Weiss and Long's (2009, 704). I will define the term in sec. 4.

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Furthermore, Zhivotovsky, Rosenberg, and Feldman (2003, 1183) call both East Asians and Eurasians "a metapopulation" when doing human genetic clustering research. However, this linguistic pattern raises two philosophically interesting questions.

First, what kind of population are population geneticists referring to when they call continent-level human genetic clusters 'populations'?[2] Second, is the kind of population being referred to a biological population? The second question requires some clarification. Philosophers who study populations in biology agree that there are many ways that biologists legitimately divide living things into populations.[3] However, there is a consensus among these experts that the kind of population that is minimally appropriate for evolutionary biology is the *biological population*—where biological populations are groups that evolve (descend with modification).[4] Perhaps Millstein (2009, 268) puts it best when she says, "Populations are the entities that evolve, prior to any evolution of species." Sometimes the members of biological populations interact in evolutionarily significant ways, but sometimes they don't. For instance, Gannett (2003, 997) has shown that population geneticists sometimes identify populations as "breeding units" and sometimes as "genealogical units." Hence, the second question can be restated as, "Is the kind of population being referred to one that requires populations to be groups that evolve?"

The two questions above are philosophically interesting for multiple reasons. Not only is it interesting to figure out whether continental groups like Native Americans cohere in the right way to form biological populations, but also the work done here will inform two ongoing debates in philosophy of biology. One is about whether there is a single, best conception of a biological population for evolutionary biology.[5] The other is about whether any of the human continental groups that population geneticists call 'populations' can be legitimately understood as races in any biological or ordinary sense.[6]

2. Notice that I do not question whether the continental groups called 'populations' by population geneticists are really populations. Like Stegenga (2016, 2), I agree that a population is whatever a linguistic group calls a 'population'.

3. For evidence, see Gannett (2003), Millstein (2009, 269), Barker and Velasco (2013), and Stegenga (2016).

4. For instance, Gannett (2003, 990), Millstein (2009, 268), Stegenga (2016, 2), Barker and Velasco (2013, 973), Gildenhuys (2014, 437), and Reydon and Scholz (2014, 7) are all interested in populations understood as groups that evolve.

5. For contributions to this debate, see Gannett (2003), Millstein (2009, 2015), Barker and Velasco (2013), and Stegenga (2016), among others.

6. For contributions to this debate, see Glasgow (2003), Kaplan and Winther (2014), Spencer (2014), and Millstein (2015), among others.

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My answer to the first question is that the kind of population being referred to in this context is the *K population*. This answer constitutes *K population theory*. While a K population cannot be understood without jargon from fuzzy set theory and perdurantist metaphysics, it's roughly a biological population whose members are united by common genomic ancestry and whose members can have graded membership. My answer to the second question is that the K population is indeed a biological population. Note that, in this article, I do not answer whether continent-level human genetic clusters are biological populations. That would be an enormous project that would require defending the sampling scheme, study design, and other methodological assumptions that go into identifying continent-level human genetic clusters. Rather, what I do is provide the metaphysical framework for legitimately calling continent-level human genetic clusters 'populations'.

I begin by presenting jargon from fuzzy set theory and perdurantist metaphysics that serves as background assumptions for K population theory. Second, I define the K population. Third, I defend the K population as the kind of population being referred to when population geneticists call continent-level human genetic clusters 'populations'. Fourth, I defend the K population as a kind of biological population. Fifth, I address potential objections to K population theory. I end with concluding remarks.

2. Background Jargon. The mathematical and metaphysical jargon that I will use to define the K population is the following. Suppose that *crisp sets* are the objects called 'sets' in Zermelo–Fraenkel set theory. Let an *object space* X be a crisp set of objects. Suppose that a *membership function* μ is a function such that $X \xrightarrow{\mu} [0, 1]$. Then, a *fuzzy set* $\tilde{A}$ is a pair $(X_{\tilde{A}}, \mu_{\tilde{A}})$. Unlike crisp sets, '$\in$' has no meaning for fuzzy sets. The analogous relation is *belonging*. Suppose that $\mu_{\tilde{A}}(x)$ is x's *grade of membership* (or *strength*) in $\tilde{A}$. Then, x *belongs* to $\tilde{A}$ just in case $x \in X_{\tilde{A}}$ and $\mu_{\tilde{A}}(x) > 0$.

An important point to note is that all of the objects that belong to a fuzzy set need not have a partial membership in that set. In fact, it could be the case that all of the objects that belong to a fuzzy set have a strength of 1. In such a case, we say that the fuzzy set's membership function is a *characteristic function*, which is a μ such that $X \xrightarrow{\mu} \{0, 1\}$. But here are some more useful terms. Suppose that the *support* of $\tilde{A}$ is the crisp set of all objects that belong to $\tilde{A}$.[7] Furthermore, $\tilde{A}$ is *empty* iff nothing belongs to it.[8] Finally, the *cardinality* of $\tilde{A}$ is equal to $\sum_{x \in X_{\tilde{A}}} \mu_{\tilde{A}}(x)$.[9]

7. This definition is needed to articulate condition v in the definition of a fuzzy K partition.

8. This definition is needed to articulate condition ii in the definition of a fuzzy K partition.

9. This is really the sigma-count cardinality. But I'll use 'cardinality' for convenience. Also, while this definition is not needed to define a fuzzy K partition, it is needed to articulate the definition of a K population.

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Now suppose that we have a crisp set of fuzzy sets A. Then, a fuzzy set $\widetilde{B}$ is the *union* of all members of A just in case (a) $|A| \geq 2$, (b) the object space of $\widetilde{B}$ is identical to the object space of each member of A, and (c) each $\mu_{\widetilde{B}}(x)$ is identical to the maximum value among all strengths of x in each member of A.[10] Next, suppose that we have a finite, crisp set A. Then, a crisp set B is a *fuzzy K partition* of A just in case (i) each member of B is a fuzzy set, (ii) each member of B is nonempty, (iii) $|B| = K$, (iv) $2 \leq |B| < |A|$, (v) the support of the union of all members of B equals A, and (vi) for any object x that belongs to any member of B, the sum of each grade of membership that x has in each member of B is 1. Furthermore, let a member of a fuzzy K partition be a *part*.[11] Thus, an important point to remember is that a fuzzy K partition is itself a crisp set, but it's called 'fuzzy' because its parts are all fuzzy sets.

Now suppose that an object *persists* iff it exists at different times, an object *perdures* iff it persists and it is only partially present at any time it exists, an object that perdures is a *perduring object*, and a *temporal part* is any part of a perduring object that constitutes its partial presence when it exists.[12] Now I am ready to define the K population.

3. The K Population. Let L be a sexually reproducing species that forms a lineage or a lineage of such species, but not both.[13] For instance, L could be the species *Pan troglodytes* (the common chimp) or the *Pan* genus (the common chimp and the bonobo).[14] Let L_t be a crisp set of organisms that constitutes all of the members of L at a time t. Now suppose that any member of L_t has a genome that consists of a sequence of distinct loci, with one or more alleles at each locus.[15] For instance, if L_t consists of diploid organisms, then each member of L_t will usually have two alleles at each locus. Now I will articulate how L can be subdivided into K populations. Let's start with the notion of a genomic ancestry partition.

10. This definition is needed to articulate condition v in the definition of a fuzzy K partition.

11. All fuzzy-set theoretic definitions are from Zadeh (1965) or Zimmermann (2012).

12. These definitions are from Lewis (1986, 202).

13. The point of defining L in this way is twofold. First, it ensures that members of the same K population are conspecific. Second, it allows an entire species to be a K population.

14. For the phylogenetic evidence that both the common chimp and *Pan* form lineages, see Gonder et al. (2011).

15. By an *allele* I mean any unique nucleic acid sequence at a locus. Furthermore, this is exactly how population geneticists talk about alleles in the context of structure-like population structure analysis. For evidence, see Pritchard, Stephens, and Donnelly (2000) and Tang et al. (2005).

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Suppose that a *crisp genomic ancestry partition* of L_t is a fuzzy K partition of L_t such that the object space for each part in the partition is L_t, each part in the partition is the temporal part of an isolated breeding group, each L_t member's degree of membership in each part is equal to the proportion of its genome inherited from an organism in the breeding group that the part represents, and each part's membership function is a characteristic function. Also, it will be useful to call each organism that belongs to a part in a crisp genomic ancestry partition an *unmixed* organism.

Now, suppose that L_u and L_v are distinct crisp sets that constitute all of the members of L at distinct times u and v, respectively, and that u occurs before v. Also, suppose that u is the last time before v when L has a crisp genomic ancestry partition into K parts due to hybridization after u. Thus, hybridization could have begun at v or at some time between u and v. Let C be a crisp genomic ancestry partition of L_u into K parts. Then, a *fuzzy genomic ancestry partition* of L_v into K parts, call it F, is a fuzzy K partition of L_v such that the object space for each part in F is L_v, there is a one-to-one correspondence between C and F, each L_v member's degree of membership in each part is equal to the proportion of its genome inherited from an organism that belongs to the part in C that corresponds to the part in F under consideration or else an unmixed organism descended from such an organism, and not every part's membership function is a characteristic function. Also, it will be useful to call any organism that belongs to a part in a fuzzy genomic ancestry partition and has a grade of membership in that part in (0,1) a *mixed* organism.

For clarity, the hybridization model I am presupposing is the following:

> 1. Isolated breeding groups undergo hybridization in such a way that none of the groups involved become extinct.

Model 1 is one of three biological possibilities for hybridization between breeding groups. The second and third are below:

> 2. Isolated breeding groups undergo hybridization in such a way that all of the groups involved become extinct.

> 3. Isolated breeding groups undergo hybridization in such a way that some, but not all, of the groups involved become extinct.

The fact that I am presupposing model 1 as the hybridization model for K population theory will be relevant to how K population theory avoids certain objections. In any case, let a *genomic ancestry partition* be a crisp ge-

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nomic ancestry partition or a fuzzy genomic ancestry partition. Now, I will define K population parts, which are the temporal parts of K populations.

Suppose that we call a part in a genomic ancestry partition a *K population part* (or *KP part* for short). Thus, while KP parts must be indexed to at least one time, they need not exist at exactly one time. Rather, KP parts can exist through time. Now I'm going to make some distinctions among KP parts in order to define K populations as, roughly, sequences of KP parts through time.

Suppose that $\tilde{A}$ and $\widetilde{B}$ are KP parts. Then, $\widetilde{B}$ is an *offspring* of $\tilde{A}$ and $\tilde{A}$ is a *parent* of $\widetilde{B}$ iff $\widetilde{B}$ originated from a change in $\tilde{A}$'s object space or membership function. For instance, suppose that at time t_1 we have a fuzzy set of Hadza people that counts as a KP part of humans, call it '$\widetilde{H}_1$'. Then, at a later time t_2 a human dies but not a Hadza person. Also suppose that the latter event produces a new KP part of humans, call it '$\widetilde{H}_2$', that has the same support and membership function as $\widetilde{H}_1$. Then, it is safe to say that $\widetilde{H}_2$ originated from changing the object space of $\widetilde{H}_1$, and thus $\widetilde{H}_2$ is an offspring of $\widetilde{H}_1$ and $\widetilde{H}_1$ is a parent of $\widetilde{H}_2$.

Now, suppose that two or more KP parts *merge* iff their offspring is their union, two or more KP parts *fuse* iff they merge and they're approximately equal in cardinality, and two or more KP parts *join* iff they merge but do not fuse. Furthermore, let a parent with much lower cardinality in a joining be a *minor parent.* Then, a *KP beginning* is any KP part that originated from its parent(s) through hybridization, budding, splitting, or fusion. In contrast, a *KP end* is any KP part that has no offspring after multiple generation times for its species, has offspring that arose from splitting, has offspring that arose from fusion, or is a minor parent and has offspring that arose from joining. We are finally in a position to define a K population.

> **Definition 1.** A *K population* is, essentially, a perduring object such that all of its temporal parts are unique KP parts, its successive temporal parts are related as parent and offspring, its first temporal part is a KP beginning, and it perdures until one of its temporal parts is a KP end.

Thus, K populations are, roughly, perduring objects whose temporal parts are fuzzy sets of conspecific organisms that cohere via common genomic ancestry. Here are some final terms that will be useful for talking about K populations. First, an organism is a *member* of a K population at a time *t* iff it belongs to that K population's temporal part at *t.* Second, an organism's *grade of membership* in a K population at a time *t* is equal to its grade of membership in that K population's temporal part at *t.* Now that I have introduced what a K population is, we can turn to answering whether population geneticists are actually referring to K populations when they call continent-level human genetic clusters 'populations'.

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4. The Evidence for K Population Theory. There is plenty of evidence that population geneticists are referring to the K population when they call continent-level human genetic clusters 'populations'. But first, here's some clarification. The linguistic context in which continental population talk is used in population genetics is population structure analysis that utilizes structure-like clustering algorithms. Structure-like clustering algorithms (*structure*, *frappe*, *admixture*, etc.) attempt to infer population structure in a group of organisms using an algorithm that searches for the fuzzy K partition that maximizes allele frequency differences among parts using genotype data from the organisms. Sometimes what's investigated is the optimal partition into *K* parts, and other times the task is to find the optimal partition at each *K* level. Suppose that we call any population structure analysis that uses a structure-like clustering algorithm 'structure-like PSA'. Then, two examples of structure-like PSA are Gonder et al.'s (2011) use of *structure* to identify the population structure of chimpanzees and Li et al.'s (2008) use of *frappe* to identify the population structure of humans.

If the continent-level human genetic clusters inferred in structure-like PSA are K populations, then we can explain how population geneticists model, sample, talk, and otherwise behave in structure-like PSA. With respect to modeling, the representations in the models used in structure-like algorithms are what we would expect if the populations being inferred are K populations.

For example, one important model assumption of structure-like algorithms is that populations leave behind a genetic trail. This is because structure-like algorithms represent populations as sequences of allele frequencies (Pritchard et al. 2000, 947; Tang et al. 2005, 290). However, K population theory predicts this model assumption nicely because the fact that K populations leave behind a genetic trail in the form of a sequence of allele frequencies can be derived from what a KP part is.

Second, K population theory explains why population geneticists sample in the way that they do. For example, the widespread practice in fuzzy PSA of sampling "ancestry informative markers" for cluster analysis suggests that what is being sought are genealogical groups, which K populations are by definition (Tishkoff and Kidd 2004, S23, S25). In fact, one population geneticist, Marcus Feldman (2010, 157), coined the term 'ancestry group' to talk about continent-level human genetic clusters.

Third, K population theory predicts how population geneticists talk in fuzzy PSA. For example, population geneticists have no problem saying that continent-level human genetic clusters originated thousands of years ago, which would make little sense unless the clusters were perduring objects, like K populations.[16] Finally, K population theory explains many other

16. For an example, see Wang et al. (2007, 2060).

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behaviors of population geneticists in structure-like PSA that would otherwise be peculiar. For one, K population theory explains why population geneticists check the accuracy of structure-like algorithms in the way that they do. For example, Shringarpure and Xing (2014, 904) tested the accuracy of *admixture*'s population membership grade assignments by judging how well it predicted "the proportion of YRI ancestry" in individuals of a fabricated admixed population.[17]

Nevertheless, one objection is that K population theory is pointless because the actual population concept being used here is inconsistent. For example, some population geneticists, such as Feldman and Lewontin (2008, 81, 90), have no problem calling the continental clusters both 'geographical populations' and 'ancestry groups', while others, such as Weiss and Long (2009, 709), are fine calling the clusters 'geographic populations' but find the 'ancestry group' label misleading.

While it is true that there is no consensus among population geneticists about how to define 'population' when using it to talk about continent-level human genetic clusters in structure-like PSA, K population theory is not a project in conceptual analysis; it's a theory about what 'population' refers to in a particular context. This project is compatible with there being inconsistent beliefs about what 'population' means as long as we adopt a referential semantics for 'population'. Yet another concern is that even if K population theory is right, it still remains to be shown that the K population is a biological population. So to that I now turn.

5. Why K Populations Are Biological Populations. Remember that biological populations must be, at the very least, groups that evolve. Thus, if K populations are not, at least, groups that evolve, then the population geneticists who are acknowledging continental populations in humans are using the word 'population' in a way that is not helpful for evolutionary research. However, K populations are groups that evolve, and this fact can be derived from the definition of a K population.

Suppose that we have an arbitrary K population p and we want to know how it originated. By definition, the first temporal part of p is a KP beginning. Furthermore, KP beginnings, by definition, are offspring from one or more KP parts that are distinct from it. But for a KP part to be an offspring it must be a modified version of its parent, either in its object space or in its membership function. Thus, p will be a modified descendant the moment its first temporal part originates. Nevertheless, it's an empirical question whether p originated from another K population since the KP part that p originated from could be a temporal part of a different kind of biological

17. 'YRI' is shorthand for 'Yoruba Nigerians from Ibadan'.

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population.[18] In any case, it's easy to see how K populations form evolutionary networks.

6. Objections and Replies. There are a few objections that one could have with K population theory. First, in a recent article, Millstein (2015, 9–10) has offered some healthy skepticism about interpreting continent-level human genetic clusters as biological populations. Millstein rightly points out that another possible interpretation is that continent-level human genetic clusters are not populations, but are just ancestry groups (in Feldman's sense) of organisms descended from members of past populations.

While Millstein's suggestion is a plausible interpretation of some inferred clusters in structure-like PSA, it's not a plausible interpretation of continent-level human genetic clusters. This is because the hybridization model that Millstein is using, which is model 2, is not the model that best fits how population geneticists talk about continental clusters. In order for Millstein's model to be correct, population geneticists would have to think that continent-level human genetic clusters represent only past nonrandom mating structure. However, population geneticists regularly talk about continent-level human genetic clusters as reflecting current nonrandom mating structure. Here is an example: "Each of the large population groups (the Sub-Saharan African farmers, Eurasia, and East Asia) can be considered as a metapopulation consisting of populations with some genetic exchange between them and with a common ancestry" (Zhivotovsky et al. 2003, 1183).[19] These authors do not sound like they're just talking about past nonrandom mating structure. Of course, this way of talking is easily explained if we accept that population geneticists intend continental clusters to represent extant breeding groups. Furthermore, if that is true, then the appropriate hybridization model is model 1, not model 2, which is the model used in K population theory. For clarity, I am not saying that population geneticists are correct in using model 1 to model hybridization among continental groups of humans. All I am saying is that the hybridization model that they are in fact using when they call continent-level human genetic clusters 'populations' is model 1.

Second, both Millstein (2009, 269) and Gildenhuys (2014, 434–37) have claimed that a respectable notion of biological population must be able to explain how populations are modeled in evolutionary dynamics. For instance, Millstein (2009, 269) claims that migration modeling in population genetics (the source-sink model, the island model, etc.) requires that migration amounts to organisms wholly leaving one population and wholly join-

18. This quirk is intentional since it allows K populations to have evolved from a more primitive kind of biological population.

19. See Zhivotovsky et al. (2003, 1174) for what they mean by "farmers."

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ing another population. However, since organisms are born into K populations in virtue of their genomic ancestry, it's hard to imagine how the members of K populations can migrate in the sense given above.

This is a good concern. The members of K populations are indeed born into them. And barring the extinction of one's K population or one's species, it's impossible for a member of a K population to leave her population. However, the latter is a concern only if one presupposes "monism" about classifying individuals into biological populations, as Millstein (2015, 6) does.[20] However, if one does not presuppose monism, but rather accepts the possibility of "population pluralism"—which Stegenga (2016, 1) defines as the view that "there are many ways that a particular grouping of individuals can be related such that the grouping satisfies the conditions necessary for those individuals to evolve together"—then the fact that the members of K populations don't migrate is not a flaw.[21] Rather, it's just an example of how classifying organisms into K populations is not going to be useful in all research projects in population genetics.

In fact, Mishler and Brandon (1987, 401) would call K populations "historical entities" because they're essentially genealogical groups (e.g., monophyletic groups). Furthermore, because they're historical entities, they're useful in history-oriented population-genetic research, such as research on "the history of human migrations" and "human evolutionary history" (Rosenberg et al. 2002, 2381, 2384).[22]

7. Conclusion. In this article, I have attempted to show that there is a legitimate metaphysical basis for calling continent-level human genetic clusters 'populations'. Namely, these groups could be biological populations in virtue of being K populations. I defended my position by first articulating a K population as, roughly, a biological population whose members are united by genomic ancestry and in which population membership is graded. However, the precise definition was given in definition 1. Next, I provided evidence that population geneticists are referring to the K population in population structure analyses that use structure-like clustering algorithms.

20. It's worth noting that Millstein (2015, 6) considers her monism a "defeasible monism," since she's more interested in knowing whether there is a definition of 'population' that can legitimately be used in all of ecology and evolutionary biology than in defending the view that all ecologists and evolutionary biologists should use a single definition of 'population'.

21. Other supporters of population pluralism are Gannett (2003) and Barker and Velasco (2013).

22. Note that 'migration' is being used here in a very different sense from how it's used in evolutionary dynamics research. Here it means 'geographic relocation' as opposed to 'leaving one population and joining another'.

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After this, I defended K populations as authentic biological populations. Finally, I defended K population theory against two objections.

REFERENCES

Bamshad, M., S. Wooding, W. Watkins, C. Ostler, M. Batzer, and L. Jorde. 2003. "Human Population Genetic Structure and Inference of Group Membership." *American Journal of Human Genetics* 72:578–89.

Barker, M., and J. Velasco. 2013. "Deep Conventionalism about Evolutionary Groups." *Philosophy of Science* 80 (5): 971–82.

Feldman, M. 2010. "The Biology of Ancestry: DNA, Genomic Variation, and Race." In *Doing Race: 21 Essays for the 21st Century*, ed. H. Markus and P. Moya, 136–59. New York: Norton.

Feldman, M., and R. Lewontin. 2008. "Race, Ancestry, and Medicine." In *Revisiting Race in a Genomic Age*, ed. B. Koenig, S. Lee, and S. Richardson, 89–101. New Brunswick, NJ: Rutgers University Press.

Gannett, L. 2003. "Making Populations: Bounding Genes in Space and Time." *Philosophy of Science* 70 (5): 989–1001.

Gildenhuys, P. 2014. "Arbitrariness and Causation in Classical Population Genetics." *British Journal for the Philosophy of Science* 65:429–444.

Glasgow, J. 2003. "On the New Biology of Race." *Journal of Philosophy* 100 (9): 456–74.

Gonder, M., S. Locatelli, L. Ghobrial, M. Mitchell, J. Kujawski, F. Lankester, C.-B. Stewart, and S. Tishkoff. 2011. "Evidence from Cameroon Reveals Differences in the Genetic Structure and Histories of Chimpanzee Populations." *Proceedings of the National Academy of Sciences* 108 (12): 4766–71.

Kaplan, J., and R. Winther. 2014. "Realism, Antirealism, and Conventionalism about Race." *Philosophy of Science* 81 (5): 1039–52.

Lewis, D. 1986. *On the Plurality of Worlds.* Oxford: Blackwell.

Li, J., et al. 2008. "Worldwide Human Relationships Inferred from Genome-Wide Patterns of Variation." *Science* 319:1100–1104.

McEvoy, B., J. Lind, E. Wang, R. Moyzis, P. Visscher, S. van Holst Pellekaan, and A. Wilton. 2010. "Whole-Genome Genetic Diversity in a Sample of Australians with Deep Aboriginal Ancestry." *American Journal of Human Genetics* 87:297–305.

Millstein, R. 2009. "Populations as Individuals." *Biological Theory* 4 (3): 267–73.

———. 2015. "Thinking about Populations and Races in Time." *Studies in History and Philosophy of Biological and Biomedical Sciences* 52:5–11.

Mishler, B., and R. Brandon. 1987. "Individuality, Pluralism, and the Phylogenetic Species Concept." *Biology and Philosophy* 2:397–414.

Pritchard, J., M. Stephens, and P. Donnelly. 2000. "Inference of Population Structure Using Multilocus Genotype Data." *Genetics* 155:945–59.

Reydon, T., and M. Scholz. 2014. "Searching for Darwinism in Generalized Darwinism." *British Journal for the Philosophy of Science* 66:561–89.

Rosenberg, N., J. Pritchard, J. Weber, H. Cann, K. Kidd, L. Zhivotovsky, and M. Feldman. 2002. "Genetic Structure of Human Populations." *Science* 298 (5602): 2381–85.

Shringarpure, S., and E. Xing. 2014. "Effects of Sample Selection Bias on the Accuracy of Population Structure and Ancestry Inference." *G3: Genes, Genomes, Genetics* 4 (5): 901–11.

Spencer, Q. 2014. "A Radical Solution to the Race Problem." *Philosophy of Science* 81 (5): 1025–38.

Stegenga, J. 2016. "Population Pluralism and Natural Selection." *British Journal for the Philosophy of Science* 67 (1): 1–29.

Tang, H., J. Peng, P. Wang, and N. Risch. 2005. "Estimation of Individual Admixture: Analytical and Study Design Considerations." *Genetic Epidemiology* 28:289–301.

Tishkoff, S., and K. Kidd. 2004. "Implications of Biogeography of Human Populations for 'Race' and Medicine." *Nature Genetics* 36 (11): S21–S27.

Wang, S., et al. 2007. "Genetic Variation and Population Structure in Native Americans." *PLoS Genetics* 3 (11): e185.

https://doi.org/10.1086/687864 Published online by Cambridge University Press

Weiss, K., and J. Long. 2009. "Non-Darwinian Estimation: My Ancestors, My Genes' Ancestors." *Genome Research* 19:703–10.
Zadeh, L. 1965. "Fuzzy Sets." *Information and Control* 8:338–53.
Zhivotovsky, L., N. Rosenberg, and M. Feldman. 2003. "Features of Evolution and Expansion of Modern Humans, Inferred from Genomewide Microsatellite Markers." *American Journal of Human Genetics* 72:1171–86.
Zimmermann, H. 2012. *Fuzzy Set Theory and Its Applications*. 4th ed. New Delhi: Springer.

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