Response to Comments made in a Letter by Guedes et al. on "The Out of Africa Hypothesis, Human Genetic Diversity and Comparative Development"

Quamrul Ashraf and Oded Galor

This is a response to the criticisms of our research in a letter by Guedes et al. As discussed in detail below, these criticisms are scientifically baseless and ultimately reflective of a misunderstanding of our empirical methodology, potential unfamiliarity with the statistical techniques that we employ, and a misinterpretation of our findings. Indeed, some of the arguments raised in the letter are so trivially and gravely erroneous that we have wondered whether the contents of the letter truly reflect the informed viewpoint of the scholars who have signed it.

First, on the statistical front, our critics have falsely suggested that we treat socioeconomic and genetic data as if populations are independent of one another. On the contrary, our empirical analysis accounts for the possibility of spatial dependence across observations, including analytical methods that correct for spatial autocorrelation in "error terms" and bootstrapping. This criticism of our work thus reflects either a misunderstanding of the techniques that we employ or a superficial reading of our work.

Second, on the conceptual front, our critics have raised several concerns. They challenge our findings that diversity can be beneficial for innovative activity, stating in their letter that our hypothesis must be fundamentally flawed because it "implies that the Maya and Aztecs should not have been able to achieve high population densities because of their low genetic diversity." Such an inference is based on a misunderstanding of basic empirical methodology. In simple terms, it is equivalent to suggesting that if we were to observe a 100-year-old person who smokes then research that concludes that smoking is harmful must be flawed.

In following this line of argumentation, our critics have fallen prey to the trap of conducting thought experiments without holding everything else constant. Indeed, Amerindian populations in general have the lowest degree of diversity worldwide but, as we establish empirically, additional factors have contributed to the prosperity of some of these populations and the stagnation of others. Our research does not suggest that diversity is the only determinant of development. In fact, we consider variations in numerous other observed factors across societies that contribute to their economic development. Thus, in order to use the example of the Maya (or the Aztecs) to falsify our hypothesis, the right thought experiment is to ask: if we were to take another society that is *identical* to the Maya (or the Aztecs) with respect to *all* factors other than in the extent of intra-population diversity, how would the level of development in that society differ from that of the Maya (or the Aztecs)? Framed differently, given that actual societies differ from one another in many respects (geographical, institutional, cultural, etc.) and not just in their levels of diversity, once all these other differences have been used to explain not only their comparative development but also the differences in their levels of diversity, is the unexplained variation in development related to the unexplained variation in diversity? Indeed, this is precisely the question that is answered by a regression analysis of the type that we conduct, one that not only controls for differences across populations in observed factors other than diversity

but also addresses the issue of correlation vs. causality that arises when differences in unobserved factors (as captured by variation in the "error terms" in a regression model) are statistically correlated with differences in diversity.

This brings us to the issue of correlation vs. causality. Our critics claim that we have erroneously ascribed a causal interpretation to the statistical relationship that we uncover between economic development and diversity. The prime argument that they offer is that innovation and cooperation are highly complex social outcomes that must have more than a genetic basis to them. Here again, our critics have misinterpreted our work. If anything our work not only conforms to this argument but it actually subsumes it. The key is that the measure of intrapopulation genetic diversity that we employ should be interpreted as a *proxy* (i.e., a correlated summary measure) for diversity amongst individuals in a myriad of observable and unobservable personal traits that may be physiological, behavioral, socially-constructed, or otherwise.

In many respects, our research builds upon mature and well-established literatures in economics, political science, and sociology that attempt to link measures of *ethnic* diversity with outcomes at the societal level. However, a major issue with empirical studies that attempt to link diversity with various economic and sociopolitical outcomes is that diversity is codetermined with these outcomes, thereby making it challenging to disentangle causal effects from correlations. Another issue with conventional measures of ethnic and cultural diversity is that they cannot account for differences across individuals within a group and they are necessarily based on ad hoc assumptions about what constitutes an ethnic group or what cultural traits should matter for socioeconomic outcomes, an issue that anthropologists are intimately familiar with and that many of our critics from the field of cultural anthropology have eloquently raised in their own work. Our research surmounts all these predicaments by using a measure of intra-population genetic diversity, variation in which (across populations) was determined tens of thousands of years ago during the "out of Africa" migration process of humans to the rest of the globe.

A careful reading of our research should make it apparent that our use of the measure of genetic diversity from the field of population genetics does not imply that our hypothesis is one of biological determinism, nor does it imply that DNA material is directly important for economic outcomes or that some genes are more important than others for economic success. The fact that the measure of genetic diversity we use is based on variation across individuals in non-protein-coding regions of the genome (and, thus, in genomic characteristics that are not necessarily phenotypically expressed so as to be subject to the forces of natural selection) is clear reason why our findings should be interpreted through the lens of our measure serving as a proxy for diversity more broadly defined.

The more relevant question to ask therefore is to what extent the measure we use can reasonably be considered a proxy for diversity in unobserved phenotypic or socially-constructed characteristics. There is indeed an emerging body of scientific evidence that establishes remarkable correlations in this regard. For instance, in articles published in *Science* and *Nature* in the past few years, researchers have shown that variation in migratory distance from East Africa, which explains global spatial variation in genetic diversity across populations (due to what population geneticists call a *serial founder effect* of the prehistoric "out of Africa" migration process), also happens to explain global spatial variation in *phonemic* diversity across

languages (Atkinson, *Science*, 2011) as well as variation in observable *phenotypic* characteristics across populations (Manica et al., *Nature*, 2007). In other words, the scientific evidence suggests that the "out of Africa" migration process generated not only variation in the measure of genetic diversity that we employ but also correlated shifts in other dimensions of diversity. It is remarkable that the "out of Africa" migration has left its mark on all these dimensions of diversity, one that persists to the present day despite tens of thousands of years of population mixings in both biological and cultural dimensions. Indeed, it is this very mark that we exploit in our research in order to overcome statistical issues of reverse causality.

In particular, even though the specific measure of diversity we employ should be viewed as a proxy for diversity more broadly defined, we needed to ensure that the statistical relationships we uncover based on this measure are not tainted by reverse causality or that they do not reflect latent effects otherwise attributable to variation in other factors like geography or the quality of sociopolitical institutions. To this end, our work employs migratory distance from East Africa (i.e., distance along land-connected routes) as an "exogenous" source of variation in intrapopulation diversity across regions. Put differently, rather than directly employing the observed diversity measure, which may be tainted by genetic admixtures resulting from movements of populations across space in response to spatial differences in economic prosperity, we employ the variation in the diversity measure that is *predicted* by distance along prehistoric migration routes from East Africa.

Nevertheless, this still leaves open the possibility that prehistoric migratory distance from East Africa may itself confer an effect on economic outcomes either directly or via channels other than the diversity channel (i.e., as proxied by our employed measure). To surmount this issue, the empirical analysis in our research follows two strategies. First, we show that in an empirical "horse race" between migratory distance and observed genetic diversity only the latter appears as a statistically significant predictor of economic outcomes, suggesting that migratory distance itself does not affect economic outcomes other than through the diversity channel. Second, we account for variation across societies in an exhaustive list of measurable geographical, institutional, and cultural factors to ensure that diversity (as predicted by migratory distance) does not capture the latent effects of these other potential determinants of economic outcomes. As such, we are confident that our findings do indeed reflect a causal effect of the diversity channel broadly defined.

Finally, our critics argued that hunter-gatherer societies, in which humans have lived for 95% of the time since *Homo sapiens* evolved, were highly cooperative societies regardless of genetic background and that variation in the extent of cooperation only arose after the Neolithic Revolution. While we certainly agree with the claim that hunter-gatherer societies were highly cooperative, what our critics are essentially saying is that there was no heterogeneity whatsoever in terms of the *extent* of cooperation (and, potentially, in other aspects of human social interaction) across hunter-gatherer societies. However, this argument from our critics violates the principles of "cultural relativism" and "historical particularism" that the field of cultural anthropology largely draws upon. In the absence of data on variation (or lack thereof) in the extent of cooperation across pre-Neolithic societies, this argument cannot be made on scientific grounds in an attempt to falsify our hypothesis regarding the effects of diversity broadly defined.

It is unfortunate that our critics have not communicated with us directly before publicizing their viewpoint in order to clarify potential misconceptions that often arise with research that traverses different fields of intellectual inquiry. One germane example of how misconceptions can arise due to the methodological gaps between disciplines is the following. It is standard practice in economics for authors to interpret their empirical findings in the context of thought experiments. It is also common knowledge amongst economists that, depending on the context of the study, such thought experiments are not to be interpreted as policy directives. We feel that awareness of such methodological subtleties on the part of our critics may have prevented the non-scientific rhetoric in their letter.

In conclusion, it is apparent that all of the criticisms raised are scientifically baseless, reflecting a misunderstanding of our empirical methodology, potential unfamiliarity with the statistical techniques that we employ, and a misinterpretation of our findings. Moreover, our work should not be misconstrued as being suggestive of biological determinism and, thus, of any distressing inferences that one may derive from such potential misinterpretation. Given that our work crosses disciplinary boundaries, misconceptions by researchers from other fields are not entirely unexpected, but we hope that our response clarifies the issues raised by our critics and will move the discussion regarding our research towards more productive academic avenues. In particular, there are important questions that ought to be addressed. For instance, what are the different potentially-measurable dimensions of diversity that are important for social and economic outcomes? Can more evidence be brought to bear regarding the precise mechanisms through which diversity confers costs and benefits on productivity? Are there institutional mechanisms that augment the beneficial effects of diversity and mitigate its detrimental effects? These are some of the fascinating questions that we hope will be explored in future research, enhanced by scientifically-productive interdisciplinary dialogue.