Fitness, Mutational Load, and Eugenics

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Abstract

Eugenic arguments are not a thing of the past. In 2016 prominent geneticist Michael Lynch published an article in *Genetics* arguing that human physical and mental performance is currently and will continue to decline at a rate of 1% per generation, if nothing is done to stop it. This estimate is not based on measurements of physical and mental performance, but on an argument from mutational load: medical interventions are relaxing selection on the human population which will lead to a buildup of deleterious mutations, dragging down human fitness. No policy recommendations were made, but the implication of the argument is clear. In this paper I show that the simple argument from relaxation of selection to fitness declines is invalid. When the argument is made valid it is not clear that there are any significant consequences to human population health.

Introduction

In 2016 geneticist Michael Lynch published a perspective in *Genetics* arguing that human physical and mental performance is declining at a rate of 1% per generation (Lynch 2016a). This estimate was not based on measurements of physical and mental performance, but rather on an argument from mutational load: because medical interventions, such as "surgical procedures, pharmaceuticals, nutritional supplements, and physical and psychiatric therapies" have mitigated the effects of selection on "bad genes," the incidence of deleterious mutations (mutational load) in the human population has, and will continue, to rise.

Lynch is not a fringe figure in the genetics community. He is former president of the Genetics Society of America, the Society for Molecular Biology and Evolution, the Society for the Study for Evolution, and the American Genetic Association, as well as winner of the 2022 Thomas Hunt Morgan Medal for lifetime contributions to genetics. Of his nearly 200 papers, 12 have over 1000 citations and his 2007 textbook, *Genetics and the analysis of quantitative traits*, written with Bruce Walsh, has over 12,000 citations (Google Scholar 2024). With an impact factor of 4.556 at time of publication, the journal *Genetics* is not a minor venue either (BioxBio n.d.).

The mutational load argument is not original to Lynch. It originates in Muller (1950), which urges steps to combat this increase and a subsequent dark future.

Muller consciously chose not to use the word "eugenics" (Paul 1987), but his suggestions are exactly that:

> "[I]t must be pointed out that there is after all one and just one way of avoiding the fiasco of a full fledged resumption of ordinary natural selection. That method, whether we like it or not, is purposive control over reproduction, exercised in such wise as to anticipate and forestall the need for natural selection of the usual, externally imposed type." (Muller 1950)

Unlike Muller, Lynch stops short of advocating for eugenics. In a reply to those who claim his paper advocates for eugenics he says he is "simply highlight[ing] the fact that long-term, population genetic issues merit recognitions and discussions" (Lynch 2016b) Scientists, he says, "have a responsibility to present what we believe to be the facts, and the release of information should not be biased by preconceived notions of what is good vs. bad." I take it, therefore, that Lynch thinks the problem is a distinctively biological one, as opposed to an ethical one. It's hard, however, to escape the conclusion that Lynch thinks this is a serious issue that we ought to do something about. He does nothing to avoid the eugenic conclusion, stating:

> What will it take to promote serious discourse on the slowly emerging, long-term negative consequences of policies jointly promoted by political, social, and religious factors? Should such a discussion even be pursued or should the process of accelerated genetic change simply be allowed to run its course—a slow walk down the path to what Hamilton (2001) called 'the great Planetary Hospital'?"

In spite of this potentially eugenic conclusion, criticism has been muted. Two responses were published in *Genetics*, but neither tackled the core issue. Roth and Wakeley (2016) point out that the argument is nothing new, while Teicher (2018) traced the history of the term "genetic load" to its roots in German eugenic programs. Neither reply, however, seriously challenged the validity of Lynch's argument. On the contrary, Google Scholar lists 129 unique articles citing Lynch's paper—most of them uncritically (Google Scholar n.d.). We are left thinking that, in spite of a lack of novelty and an unfortunate history, the argument itself is good.

The aim of this paper is to show that the argument from genetic load is overblown, if not simply mistaken. The simple version of this argument is invalid. More sophisticated versions might be correct, but do not present us with a problem of great significance.

A note as to the scope of the argument is necessary before I begin. I will not be asking whether individual or population fitness is a morally significant metric or asking the general question of what makes eugenics morally wrong. Both of these, I take it are controversial issues requiring more attention than can be devoted to them here. That said, ethical arguments depending on these biological conclusions have been made in Powell (2015) and Gyngell, Bowman-Smart, and

Savulescu (2019). If the biological conclusions do not hold up to scrutiny, claims based on it may be weakened or undermined as well.

Mutational Load

While most publications, following Crow (1970), give genetic load as the difference in fitness between the maximum fitness genotype in a population and the mean fitness of the population, Muller and Lynch's arguments are better understood as giving load as the expected *number* of deleterious mutations in an individual in a population.[1]

Muller's introduction to this concept is particularly clear. He imagines a delivery company that purchases two new trucks per year (n). The trucks persist (p) in the fleet until they wear out—three years in the example—and are subsequently removed from the fleet. Eventually, an equilibrium is reached and there is a constant number of trucks in the fleet (f). In this case, that number is six. Thus the number of trucks in the fleet at equilibrium may be found by the equation:

$$f = np$$

The same holds for deleterious mutations. Mutations enter the population at a rate proportional to the mutation rate, they persist in the population for a time inversely proportional to the strength of selection, and the expected number of mutations in the population per generation is determined by these values. Muller estimated that the human germline mutational load was eight; that is, a randomly chosen individual could be expected to have eight deleterious mutations. Current estimates put the number at 12-13,000 SNPs—though of course mean effect size is smaller (Henn et al. 2016).

Given the formula above, there are two ways to increase the mutational load of a population. The first is to increase the mutation rate. The second is to relax selection pressure.

Living, as he was, at the beginning of the atomic age, Muller was concerned with an increasing mutation rate due to weapons testing and the proliferation of radioactive devices in medicine, industry, and the home. Crow (1997) speculates that, had he been aware, Muller would also have been concerned by the spread of chemical mutagens. In this he was undoubtedly right. An increase in radioactive and chemical mutagens is a cause for concern. It is likely to result in an increase in both somatic and germline mutations and those mutations that affect fitness are, it is commonly assumed, overwhelmingly likely to be deleterious.

Lynch too is concerned about increases in the mutation rate, though his concern is primarily with increases in germline mutation rate due to paternal age. It is

[1] Genetic load can be separated into load due to mutation, segregation, and heterozygosis, but this is not done in Muller (1950) or Lynch (2016a), which focus on mutational load.

well-known that, because the process of spermatogenesis involves the duplication of cells many times through the male's lifetime, there is an increasing probability of mutations in sperm cells as males age. Thus a trend towards older fathers increases the effective germline mutation rate.

The main target in both papers, however, is the relaxation in selection due to changes in the human environment. Lynch points out that:

> [T]he myriad of clinical procedures for mitigating the consequences of bad genes (e.g., surgical procedures, pharmaceuticals, nutritional supplements, and physical and psychiatric therapies) can only result in the relaxation of natural selection against a broad class of deleterious mutations. (Lynch 2016a)

This is what makes humans "exceptional" per the title of Lynch's paper. We shape our environment and in so doing reduce selective pressures on mutations in the population.[2] This, given the formula above, increases the number of deleterious mutations in the population.

The Simple Argument From Load

The simplest version of the argument, and the easiest to grasp is as follows:

1. Relaxing selection on a population will increase the expected frequency of deleterious mutations.
2. We are relaxing selection on human populations.
3. Therefore, the expected frequency of deleterious mutations in human populations will increase.

This argument is sound, but more is needed to get the required conclusion:

> Human populations will decline in fitness due to an increase in deleterious mutations.

The issue here is that the *number* of deleterious mutations does not necessarily correspond to a reduction in fitness. Fitness depends on selective environment as well as phenotype, but by hypothesis the selective environment has changed, thus we cannot immediately conclude that fitness will decline.

As a concrete example, consider Type 1 diabetes. Type 1 diabetes typically develops in childhood and in the ancestral environment this would likely be a deadly affliction, resulting in a realized fitness of 0. But in our current environment, with early detection, blood sugar monitoring, insulin, and insulin pumps, and so on, individuals with Type 1 diabetes are increasingly likely to survive and reproduce. The expected number of offspring for an individual with

[2]There is a question of whether this truly makes human exceptional. Many organisms shape their environments in ways that reduce selection on various traits (Pascoal et al. 2023). Humans may be exceptional in the extent and rapidity of such shaping, but we hardly seem unique.

Type 1 diabetes now probably approaches that of an individual without. Fitness of the phenotype in the modern environment is not that of the individual in the ancestral environment so it is false that the increased number of deleterious mutations causes a decrease in population fitness.

In fact, holding all else fixed, we can expect an *increase* in absolute fitness due to improved medical technologies. This is especially obvious given how common reproductive assistance technologies have become. Many of us have used or know someone who has used *in vitro* fertilization or other treatments for infertility. Many who would not otherwise have had children now can and do.

Ignoring the fitness effects of change in environment seems like an elementary mistake, but it is one Lynch seems to make in passages like the following:

> For the most extreme case of completely relaxed selection ($s_n = 0$), beneficial alleles will ultimately be lost entirely ($\hat{p}_n = 0$), with the rate of increase of deleterious alleles (with hidden effects) being entirely governed by the mutation rate to defective states.

This raises the obvious question: what is a deleterious allele when there is no selection? Lynch says that the effects are hidden, but the reference environment he uses is the ancestral one, not the current environment. Lynch needs to establish that the ancestral environment is, for some reason, a privileged reference environment and the one that ought to count when we consider the fitness of a population. "Hidden" fitness effects are simply not fitness effects in the current environment. As Pascoal et al. (2023) point out in a study of parental care in the common burying beetle *N. vespilloides*, relaxed selection creates a problem for which it is its own solution.

Roth and Wakeley (2016) points out that our current environment may be very different selectively than our past environment with some things that were advantageous in the ancestral environment being disadvantageous in the current environment and vice versa. This is undoubtedly true for some traits, but Lynch replies that many others, such as psychological conditions and hereditary cancers have "absolute effects in essentially all environments" (Lynch 2016b). This may be correct, cancers seem unlikely to have positive fitness effects (I am less confident about most psychological conditions), but it misses the larger point. That larger point is that in an environment with relaxed selection conditions like psychological disorders and hereditary cancers *by hypothesis* do not have the same fitness effects. This is not a denial that many traits are deleterious in both the ancestral and relaxed environments—the claim is not that selection has been *completely* relaxed. The claim is that the selective effect of these conditions is less than it was in the ancestral environment and so they do not have the same fitness consequences.

Similarly, Lynch argues that even if selection is "soft" deleterious mutations will still have "very real costs." But it is unclear what these costs are. In hard selection, genotypes have the same fitness differences in different environments,

such as a trait that reduces fertility in all environments. But in soft selection, population density makes a difference.

Wallace (1991) used the example of hibernating bears to make this clear. If there are fewer dens to hibernate in than bears, being passive is a disadvantage—an aggressive bear gets a den over a passive bear. But if the number of dens is greater than the number of bears, being passive is no disadvantage at all—every bear gets a den regardless. Whether or not being passive is a disadvantage depends on the selective environment, in this case the population density.

Muller (1950) makes a similar mistake in his argument that an increase in load would be detrimental for the human population, as Wallace (1991) points out. Muller calculates that the decrease in fertility due to human load is approximately 0.2. Because of this the 2.3 children per couple in Western societies (as of 1950) represents the survivors of about 3 zygotes per couple. Doubling the genetic load would then reduce the probability of survival per zygote from about 0.8 to 0.6, leading to only 1.8 children per couple, which is not enough for replacement and will lead to population decline and eventual extinction. What Wallace points out is that this ignores that human reproduction (especially in societies with access to birth control) is based on population density and therefore soft.

If Lynch means that these conditions have constant costs across environments, then he is simply claiming that selection is hard. But that is not obviously true for many of the conditions we might consider. Recall the case of Type 1 diabetes. Arguably selection is soft on this trait because it depends on the availability of medical care. If care is expensive and rare then there will be selection on the trait. But if care is cheap and common there will be no selection on the trait. Obviously the cost and availability of care varies according to condition, so Lynch is right that selection is hard for some traits. But this only shows that the selection against these traits is not as relaxed as it might be. If selection is stronger than we thought then the expected increase in mutational load is also lower. We are left wondering what Lynch means when he says that there are "very real costs." If they are fitness costs, there is less load; if the costs are something else, we do not know what they are.

The Argument from Declining Baseline Human Performance

In order to make the argument that relaxed selection poses a problem for human populations, we need a bridge from the claim that there will be an increase in the number of deleterious mutations to the claim that something bad for the population will happen. In a second version of the argument, rather than a decrease in fitness, an increase in the number of mutations is expected to result in a reduction in "baseline performance." Lynch makes this claim, saying:

> [O]ur current knowledge of the rate and likely effects of mutation in humans suggests a 1% [per generation] decline in baseline performance of physical and mental attributes in populations with the resources and inclination toward minimizing the fitness consequences of mutations with minor effects.

This claim is based on mouse studies by Uchimura et al. (2015) in which a mutator strain of mouse was seen to decrease in offspring number, body weight, and increase in "obvious phenotypic abnormalities." Lynch notes that mice and humans have similar genetic and genomic architectures, thus the inference from mouse to human goes through. This is too quick, however. Even if the inference from mouse to human goes through, Uchimura et al. (2015) is not a study of relaxed selection, but a study of increased mutation rate. Mutator strains of mouse are strains with impaired DNA repair mechanisms and thus a higher mutation rate. As we've seen, relaxing selection is likely to *increase* offspring number, not decrease it, as previously less fit phenotypes now have higher numbers of offspring.

If there is a signal to be seen here it is that we will observe non-fitness differences, such as changes in body weight and "obvious phenotypic abnormalities." But in order to assume that these will affect "baseline human performance" we would have to know 1) what human performance metrics we're looking at and 2) whether these are or have until recently been under selection.

So what are the performance metrics that Lynch is considering? The primary one that Lynch mentions is intelligence. He mentions that several studies have suggested that there has been a decline in intelligence in the US and UK and that, though controversial, these claims give us reason to think that there is a problem (Crabtree 2013; Woodley of Menie 2015). Lynch is right that these studies are controversial, they are extremely problematic for several reasons. One cited study uses socio-economic status as a proxy for intelligence then points to a historical association between socio-economic status and realized fitness to indicate that intelligence has a fitness effect.(Woodley of Menie 2015) Unpacking all that is wrong with this would take some time, but the real problem for Lynch is elsewhere.

The real problem is that these papers assume the conclusion that Lynch wishes to draw—that mutational load is affecting intelligence. Both of the cited papers take it as given that mutational load *is* affecting intelligence and attempt to estimate the amount of decline that has occurred on that basis. But this is exactly Lynch's argument—selective pressure is being reduced, therefore there will be a decline in intelligence. Far from providing independent support for the claim that intelligence has or will decreased, it makes the very same argument that Lynch is making.

There's also the question of what the 1% decrease is with respect to. The way the statement is phrased it might sound like we'll see a 1% decline in sprinting speed, bench press, or measured IQ. This isn't the case. The claim is that the

difference in mean fitness between technological and ancestral environments will decline by 1% per generation due to phenotypic change. That is, it's a claim about the expected decline in fitness in the ancestral environment—just as the previous argument was.

Furthermore, the mapping from fitness measures to phenotypic measures isn't at all obvious. What decline in strength or IQ would equate to a 1% decline in fitness?[3] n the ancestral environment? What aspects of strength or intelligence are under purifying selection in the first place? Much more would need to be said before we can conclude there is a significant worry here.

That said, for traits that were under selection we can expect to see an increase in "obvious phenotypic abnormalities." But again, more needs to be said. Why are these "abnormalities" problematic? Eyeglasses—and more recently laser surgery—could well be reducing selective pressure on visual acuity.[4] If that's right we should expect an increase in the proportion of people needing glasses. But as James Crow pointed out with respect to this question, "Who worries about having to wear spectacles?" (Crow 2000)

Crow's point applies more generally though. Type 1 diabetes was once deadly, but now, with medical care widely available it's neither deadly nor something to be overly concerned about. Today, Crow might have said, "Who worries about having to check their blood sugar?"

In order to make this point stick, Lynch would have to show that some important good is threatened if these conditions were more common. But doing this would move us away from the apparently value-neutral—"presenting the facts as they are"— argument Lynch seems to want and into explicitly ethical territory. By framing the question in terms of "baseline human performance" I take it that Lynch tries to stay in the biological realm while also making a covert value judgment that these performance metrics are or ought to be worrying.

The Argument from the Long-term

This brings us to the third argument that mutational load is a problem in need of a (eugenic) solution. Lynch argues that solutions like eyeglasses and insulin only exacerbate the problem (Lynch 2016b). They further relax selection, leading to greater need for medical intervention. But there's no guarantee that medical technology will keep ahead of the curve.

This argument differs from the previous ones in an important respect. Here the argument isn't that fitness declines with respect to the ancestral environment. The argument is that fitness will decline with respect to the improved baseline

[3]There are good reasons to be skeptical that IQ correlates to anything like "intelligence" but I set aside these worries for now (Gould 1996).

[4]The recent "nearsightedness epidemic" is likely to be due to changes in environment, such as sunlight exposure in childhood, rather than reduced selection on vision, though this does not undermine the possibility that selection has been relaxed as well (Dolgin 2024).

after the introduction of improved sanitation, medicine, and so on. After a sharp jump up, there will be a slow decline back down to equilibrium.

Muller makes the same point in his 1950 paper. He points out that relaxing selection makes no difference in terms of "genetic deaths". In the long run, the effect of a deleterious mutation on the population is the same no matter how weakly or strongly deleterious the mutation is. Even mildly deleterious mutations will be selected against. The only difference is that a mildly deleterious mutation will end up affecting many more individuals than a severely deleterious mutation before it is removed from the population. Eventually a new equilibrium is reached and natural selection is back in full force. Our efforts to cheat natural selection through technology will have been in vain. That's why Muller concluded the only way to avoid a return to full-force natural selection was to take the more humane route of artificial selection—in other words, eugenics.

Lynch builds on Muller's point, arguing that this is not merely about the introduction of *new* mutations into the population. Even if no new mutations were introduced there would be a reduction in fitness due to preexisting deleterious mutations drifting to higher frequencies (Lynch 2016b).

While this is all correct, it is a long-term problem for fitness and does not show that medical intervention was futile. Lynch estimates that if the selection coefficient of a mutation is reduced from 0.01 in the ancestral environment—which he estimates to be the usual size of a deleterious mutation—to 0.001 in the new environment, the halfway point will be reached in ~700 generations—if no further advances in medical technology and availability are made. Until that time there is a reduction in "genetic deaths" from natural selection. Is the fact that we'll eventually reach equilibrium a reason that the reduction in selective force until then was "futile"? It is not obvious that postponing or pausing a problem is a bad thing.

We're all familiar with Keynes' quip that "in the long run we're all dead." His point was in reference to the quantity theory of money. According to the quantity theory of money, increasing the amount of money in an economy makes no difference because eventually prices will simply rise to match. Real prices will not change at all, therefore injecting money into an economy is futile. But as Keynes points out, even if this is true in the long run we may care very much about the short term changes that occur. I don't know what the human population looks like in fourteen thousand years, but I *do* know that there are many more pressing issues for the human population between now and then.

Conclusions

Lynch's main argument that mutational load poses a threat to human populations fails for three reasons:

1. It equivocates on selective environment and therefore on fitness;

2. It conflates the effects of the mutation rate and reduced selection—though both increase the frequency of deleterious mutations, when these affect fitness they do so through different mechanisms;
3. Phenotypic claims about "baseline human performance," cannot be read off of the claimed decline in fitness from an out of equilibrium state.

There are likely further reasons for rejecting Lynch's claims that mutational load is a worry for human populations. These include questions about the relevance of fitness concerns to moral and policy questions, the social impact of healthcare availability on populations, and questions about the value of human diversity. I have focused on fitness effects because that is where I understand Lynch's argument to be targeted—the worry is meant to be a distinctively biological one. If that claim does not hold up to scrutiny then claims based on the supposed biological worry are undermined as well.

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