The Misunderstood Science of Genetic Bottlenecks

S. Joshua Swamidass (6) in The 2022 Annual Meeting of the American Scientific Affiliation

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The science of genetic bottlenecks is known to many, but often misunderstood. A 2010 article laid out a specific genetic argument against Adam and Eve. This argument was expanded substantially outside peer-review, leading to coverage in *Christianity Today* and coverage by *National Public Radio* (NPR) in 2011. This genetic argument, summarized, was that

- 1. Genetic evidence—primarily linkage disequilibrium (LD) and incomplete lineage disequilibrium (ILS) estimates of effective population size (N_e)—demonstrates that the human lineage was never less than 10,000 individuals going back 18 million years, long before we could remotely be called "human."
- 2. Therefore, we do not all descend from Adam and Eve; "That would be against all the genomic evidence that we've assembled over the last 20 years." 5

This is a theologically potent argument because it appears to disprove the doctrine of monogenesis.

Beyond the scope of this review, the second point does not follow from the first. Universal ancestry does not require a genetic

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Deborah Haarsma, Jim Stump, Loren Haarsma, Ard Louis, and Dennis Venema from BioLogos were also presented a draft of this manuscript, but they did not provide a response.

- Dennis R Venema, 'Genesis and the Genome: Genomics Evidence for Human-Ape Common Ancestry and Ancestral Hominid Population Sizes', Perspectives on Science and Christian Faith, 62.3 (2010).
- 2. Richard N. Ostling, <u>'The Search for the Historical Adam'</u>, *Christianity Today*, 2011.
- Barbara Bradley Hagerty, 'Evangelicals Question The Existence Of Adam And Eve', National Public Radio, 2011 [accessed 10 October 2020].
- 4. Dennis R. Venema, <u>'Vern Poythress, Population Genomics, and Locating the Historical Adam'</u>, <u>BioLogos</u>, 2015 <u>https://doi.org/10.54739/atjo</u>.
- Bradley Hagerty; Scott McKnight and Dennis R. Venema, <u>Adam and the Genome:</u> <u>Reading Scripture after Genetic Science</u>, 2017.

Misunderstood



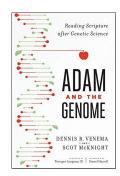
bottleneck and is entirely consistent with large population sizes. ⁶ This review, however, focuses on the first point, which was also incorrect.

The goal of this review is to explain what the evidence in genetics tells us about single-couple bottlenecks, clarifying each line of evidence. The narrow focus is single-couple "genetic bottlenecks," and the findings here do not generalize to most models of Adam and Eve. This is a model in which humanity arises from a single couple with *normal* biology, and there is *absolutely* and *precisely* zero interbreeding between their lineage and others. Findings about genetic bottlenecks do not apply to any model that (1) allows *any* interbreeding *at all* between Adam and Eve's lineage and others, or (2) posits exotic biology in Adam and Eve.

There are three key corrections to the first point.7

- The genetic evidence only rules out a single-couple bottleneck (2, not 10,000) going back about 500,000 years (not 18 million).
- 2. LD, ILS, and N_e are irrelevant lines of evidence, that do not rule out a single-couple bottlenck in any relevant time scale.
- 3. Instead, the primary line of evidence establishing the revised conclusion, the most recent time to 4-alleles (TMR4A), was first reported in 2017.

In 2020, the BioLogos organization acknowledged that they did not accurately represent the scientific evidence. By 2021, the organization deleted or substantially edited all the articles related to and supporting the 2011 coverage by *Christianity Today*. These corrections, however, were not transparent or complete. Consequently, recent academic literature still cites several articles with substantial errors, including articles deleted by the organization.



- 6. Andrew Ter Ern Loke, 'Reconciling Evolution and Biblical Literalism: A Proposed Research Program', Theology and Science, 14.2 (2016), 160–74 https://doi.org/10.1080/14746700.2016.1156328; Kenneth W Kemp, 'Science, Theology, and Monogenesis, American Catholic Philosophical Quarterly, 85.2 (2011), 217–36 https://doi.org/10.5840/acpq201185213; S. Joshua Swamidass, 'The Overlooked Science of Genealogical Ancestry', Perspectives on Science and Christian Faith, 70.1 (2018); S. Joshua Swamidass, The Genealogical Adam and Eve: The Surprising Science of Universal Ancestry (InterVarsity Press, 2019).
- S. Joshua Swamidass, <u>'Heliocentric Certainty Against a Bottleneck of Two?'</u>, 2018 https://doi.org/10.5281/zenodo.1328247.

Rigorous scholarship on any topic engages prior work in detail. The BioLogos organization published more scholarship about genetic bottlenecks than any other group aligned with mainstream science. For this reason, this review engages the organization past and present position, with attention to where corrections have and have not been made. Clarifying the organizations editorial practices, in focused cases, is particularly important where corrections were incomplete, and where mistakes were reasserted.

Going forward, this review is entirely aligned with mainstream science, including evolutionary science. We grant from the outset that the earth looks very old, because it *is* old. The genetic evidence indicates humans also share common ancestors with the great apes: chimpanzees, bonobos, orangutans, and gorillas. This aspect of BioLogos's work was not found in fault.

Genetic bottlenecks, for better or worse, are likely to be discussed for some time to come. If we are to discuss bottlenecks, the scientific claims we make about them should be accurate, and not over-extend to inaccurate claims about models that do not require bottlenecks.

Post-Publication Review of Adam and the Genome

In 2017, Dennis Venema and Scott McKnight published *Adam and the Genome*. Chapter 3 of the book focused on the argument for large ancestral population size as evidence against Adam and Eve. As stated in the book,

All methods employed to date agree that the human lineage has not dipped below several thousand individuals for the last 3 million years or more – long before our lineage was even remotely called "human."

In early 2017, a British evolutionary biologist, Richard Buggs, raised specific concerns about the scientific argument in Chapter 3 of *Adam and the Genome*. This chapter of the book focused on the argument for large ancestral population size as evidence against Adam and Eve. In 2017, BioLogos published two articles by Venema defending this scientific argument from Bugg's criticism. In the forum discussion of the first article, a 514-page exchanged unfolded between several scientists, including Buggs and Venema, but also Stephen Schaffner, Ann Gauger, and S. Joshua Swamidass. Several others were watching closely from the side-lines, including philosopher William Lane Craig, biologist AJ Roberts from Reasons to Believe (RTB), and several secular scientists at Peaceful Science.

In his initial response, Dennis Venema began with a walk-back, stating that he only meant "human" to refer to our species, *Homo sapiens*. ¹² This is a conclusion-altering concession—inconsistent with

- 8. Scott McKnight and Venema.
- Richard Buggs, 'Adam and Eve: A Tested Hypothesis?', Nature Portfolio Ecology & Evolution Community, 2017 [accessed 6 November 2021].
- Richard Buggs, 'Adam and Eve: A Tested Hypothesis?', Nature Portfolio Ecology & Evolution Community, 2017 [accessed 6 November 2021].
- 11. The BioLogos Forum, 'Forum Discussion on "Adam, Eve and Population Genetics: A Reply to Dr. Richard Buggs (Part 1)", 2018 https://doi.org/10.5281/zenodo.1323939.
- 12. Dennis R. Venema, 'Adam, Eve and Population Genetics: A Reply to Dr. Richard Buggs (Part 1)' https://doi.org/10.54739/ju3t.

his prior work and the text of *Adam and the Genome* itself—because this revision allows for a bottleneck at the headwaters of when most scientists teach our lineage is called "human."¹³

Venema also clarified he was only interested in models of a single couple "genetic bottleneck," which he meant to exclude even a single interbreeding event between Adam and Eve's lineage and others.

He thought the evidence ruled out a bottleneck going back 18 million years but was most certain a bottleneck would be ruled out at the origin of *Homo sapiens*, about 200,000 years ago. But if the focus is on our species, this corresponds to a model which excludes all interbreeding between *Homo sapiens* and other hominids. Most old earth creationists and young earth creationists agree Neanderthals and *Homo sapiens* interbreed. He when asked for any evidence that there were never just two *Homo sapiens* amidst a larger population, Venema could not provide any. So, it must be emphasized, Venema's revised conclusion is almost entirely irrelevant to the theological conversation on origins.

Charitably biasing the discussion towards Venema, we focused on determining which lines of evidence (beyond interbreeding) ruled out a bottleneck of two individuals (not several thousand) in at least the last ~200,000 (not 3 million) years, a time that is long after (not long before) archaic "humans" arise about 2 million years ago.

Even under these most favorable of terms, the primary evidence in *Adam and the Genome* did not support the revised conclusion. Several lines of evidence were discussed in detail (Figure 1), but they were all irrelevant, invalid, disputed, or did not cover the relevant time periods. Eventually, another scientist produced a *new* line of evidence that could estimate the minimum possible population size, the time to most recent 4 alleles (TMR4A).

^{13.} Aligned with most biologists, Venema believes Neanderthals are a different type of "human" than *Homo sapiens*.

^{14.} For example, they explain that, if required, they would move to a model in which Adam and Eve are genetic mosaics, with would not limit them to just 4 alleles. John Sanford and others, 'Adam and Eve, Designed Diversity, and Allele Frequencies', Proceedings of the International Conference on Creationism, 8.1 (2018) https://doi.org/10.15385/jpicc.2018.8.1.20.

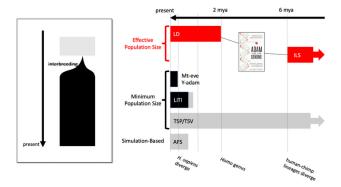


Figure 1: This figure depicts (left) the genetic-bottleneck model on which Venema's revised claim is focused, and (right) the lines of evidence assessed in this review, showing what time ranges they cover (not to scale). Linkage disequilibrium analysis (LD) and incomplete lineage sorting (ILS) are the primary lines of evidence in *Adam and the Genome*, but these are irrelevant lines of evidence that do not rule out a bottleneck (red). Mt-eve and Y-adam rules out the bottleneck any time more recent than ~150,000 years ago, and lineage time inference (LiTI) on autosomal DNA *robustly* rules out a bottleneck as far back as 500,000 years, and possibly up to 600,000 years ago if DNA from archaic humans is included (black). Other lines of evidence, such as trans-species variation (TSV) and simulations of allele frequency spectrums (AFS) are *disputed* (gray).

Irrelevant Lines of Evidence

Since 2010, Venema and the BioLogos organization presented two primary lines of evidence to demonstrate large population sizes in the past. Both these lines of evidence failed to establish their claims.

Linkage Disequilibrium and Effective Population Size

The first line of evidence was linkage disequilibrium, which provides a way of estimating "effective population size" (N_e) in the past. LD features prominently in the 2010 PSCF article, in BioLogos's articles, and in *Adam and the Genome*. The argument goes,

- 1. Linkage disequilibrium (and other methods) estimates our "effective population size" (N_e) in the past. ¹⁵
- 2. N_e estimates are always in the thousands or more.
- 3. N_e is the *minimum* population size consistent with the data. ¹⁶
- Therefore, the human lineage "was never less than" several thousand.

There are also several variations of this basic argument that substitute LD with other methods of estimating N_e in the past. There are, perhaps, dozens of methods that estimate effective population size from genetic data. There are indeed hundreds, if not thousands, of studies that estimate N_e in the past, always computing an N_e of at least several thousand individuals. For many methods, these estimates stretch back 2 million years or so into the past, covering

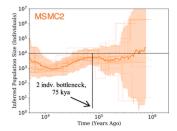
- 15. Brian P. McEvoy and others, 'Human Population Dispersal "Out of Africa" Estimated from Linkage Disequilibrium and Allele Frequencies of SNPs', Genome Research, 21.6 (2011), 821–29 https://doi.org/10.1101/gr.119636.110; Albert Tenesa and others, 'Recent Human Effective Population Size Estimated from Linkage Disequilibrium, Genome Research, 17.4 (2007), 520–26 https://doi.org/ 10.1101/gr.6023607.
- 16. This claim does not appear in the PSCF article, but it was added outside the peer-review process in the discussion of this article. Dennis R. Venema and Darrel R. Falk, 'Does Genetics Point to a Single Primal Couple?', BioLogos, 2010 https://doi.org/10.54739/vqbj.

most of the relevant time-period. Points 1 and 2 are neither controversial nor contested.

Still, in post-publication review, the argument quickly collapsed. First, Venema had claimed that N_e was an estimate of the minimum population size. But this is just not true. N_e is, instead, a harmonic average over a very large time window. Second, Venema thought that a single-couple bottleneck was the most extreme bottleneck possible. But the severity of a bottleneck also depends on its length, and a bottleneck of merely a single generation is exceedingly mild.

Putting these two corrections together, if there truly was a brief population bottleneck to a single couple, it is trivial to show that the $true\ N_e$ is large. So, of course, estimates of N_e are large as well. Put another way, the argument from N_e concludes stock market never crashed in the 2008 financial crisis, because the average rate of return has aways been greater than 10%.

The most straightforward interpretation of this information is that LD, and any other N_e -based method, is an irrelevant line of evidence. Consequently, high estimates of N_e point neither toward nor away from a brief bottleneck. Using a method of computing N_e which more advanced than LD, this fundamental finding, hopefully obvious now, was empirically confirmed in a study published in 2021 (Figure 2).



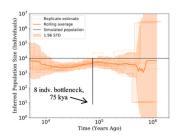


Figure 2: Brief bottlenecks are outside the genetic streetlight. This figure shows the results of applying an advanced, genome-wide method of estimating N_e to simulated data (orange) in which there is a single-couple bottleneck followed by exponential growth (black line). The method does not detect single couple bottlenecks, even when as recent as 75,000 years ago.[^17]

These corrections had cascading consequences, ultimately undermining almost every claim from population genetics made by Venema and BioLogos. In 2019, Reasons to Believe objected when BioLogos, again, overstated the evidence in population genetics against them. ¹⁷ But working independently of BioLogos at the time, Stephen Schaffner agreed with RTB's objection, explaining the corrective,

Estimates of past N_e are point estimates of the most likely value at each point in time, which is quite a different thing from a lower bound on the population size. N_e also represents a kind of average population size over extended times, rather than a precise estimate for every generation; this makes it rather insensitive to very short bottlenecks. ¹⁸

- 17. Anjeanette Roberts, 'How Can Christians Disagree over Adam and Eve?', Reasons to Believe, 2019 [accessed 22 July 2022]. Note that RTB uses the term "sole-progenitor" in a way that explicitly allows for interbreeding between Homo sapiens and other hominids, which is not consistent with BioLogos' usage of the term
- 18. Stephen Schaffner, <u>BioLogos Forum Comment</u>, 2019.

 N_e estimates are not sensitive to brief bottlenecks, even those down to a single couple. Indeed, *any* method based on N_e cannot, even in principle, rule out a brief bottleneck in our ancestral lineage. The BioLogos organization has not yet responded to RTB.

One puzzle remains unsolved. The basic fact—that N_e is an average, not a minimum—is uncontroversial, uncontested, and widely known by biologists. In direct conflict with established consensus science, it is difficult to understand why evolutionary creationists so frequently claimed N_e was a minimum. It is unclear how, for more than a decade, they did so without correction.

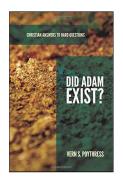
In 2014, Vern Poythress, a theologian, rightly objected that N_e was an average, not a minimum.¹⁹ In his response, Venema conceded that Poythress was correct.²⁰ But then in *Adam and the Genome*, Venema goes on to repeatedly misrepresent N_e as the minimum population size (pp. 44, 52, 53, and 60). When asked for an explanation, BioLogos did not provide one.

LD and N_e are prominent examples where corrections were not transparent. In 2019, Jeff Schloss, a biologist with BioLogos, submitted an article that transparently acknowledged BioLogos misrepresented N_e as a minimum population size, and that any method (such as LD) that relied on N_e could not rule out a single couple bottleneck. ²¹ The organization, instead, published a diffuse statement of error in 2020 that did not mention N_e or LD. In 2020 and 2021, multiple articles that presented LD as evidence against a bottleneck were deleted, including Venema's concession to Poythress. ²²

Incomplete Lineage Sorting

The second line of evidence was incomplete lineage sorting (ILS). In the discussion around the book, Venema's argument from ILS was also quickly dismissed. ILS is another method of computing N_e , but it is notable for making estimates much farther in the past than most other methods.

ILS uses different data than LD, the genomes of multiple species, not the variation within our species. The approach begins by constructing phylogenetic trees of the across all loci of the genome. In most



locations of the genome, humans are closest to chimpanzees, but sometimes there are "discordant" trees, where humans are closer to gorillas. From the details of these discordant trees, we can estimate N_e far deeper into the past than usual, perhaps as far back as 18 million years. But, in the human lineage, ILS estimates of N_e do not extend more recent than 6 million years ago, when the human and chimpanzee lineages diverged.

The argument looks familiar,

- 19. Vern S. Poythress, <u>Did Adam Exist?</u> (P & R Publishing, 2014).
- 20. Dennis R. Venema, 'Vern Poythress, Population Genomics, and Locating the Historical Adam' https://doi.org/10.54739/atjo.
- 21. Personal communication from Jeff Schloss. Used with permission.
- 22. Venema and Falk; Dennis R. Venema, <u>'Adam, Eve and Human Population Genetics'</u>, *BioLogos*, 2014 https://doi.org/10.54739/d670; Dennis R. Venema, <u>'Vern Poythress</u>, Population Genomics, and Locating the Historical Adam'.

- 1. ILS estimates N_e as far back as 9 to 18 million years.²³
- 2. These estimates of N_e are always greater than thousands.
- 3. N_e is the *minimum* population size consistent with the data.
- 4. Therefore, the ILS data demonstrates "large ancestral population sizes throughout the speciation process," back to a time "long before our lineage was even remotely called 'human." ²⁵

In the same way as before, this argument is invalid because N_e is an average, not a minimum. An ILS estimated N_e of thousands is entirely consistent with a brief dip in population down to a single couple. The argument from ILS, moreover, has a conclusion-altering omission; ILS does not tell us anything about population sizes more recent than about 6 million years ago, long before the relevant time period.

The argument from ILS, then, is like, arguing that the US stock market did not crash in 2008, because the average return of the *Chinese* stock market has always been greater than 10%. Averages do not tell us whether or not the market ever crashed, and the Chinese market is not the US stock market.

ILS is a prominent example of an uncorrected mistake. An article published by the BioLogos organization in 2021 (backdated to 2014) states,

...humans, chimpanzees, and gorillas have, within their genomes, the exact pattern of incomplete lineage sorting predicted by...large ancestral population sizes throughout the speciation process.²⁶

In context, this sentence claims that ILS demonstrates the human lineage had "large ancestral population sizes throughout the speciation process." But it is also true that the data matches the exact pattern of ILS predicted by a sharp bottleneck at any point in the speciation of humans. ILS does not estimate N_e "throughout the speciation process." The organization privately acknowledges this is an error, so it is difficult to explain why this claim was reasserted.²⁷

Robust Estimates of Minimum Population Size

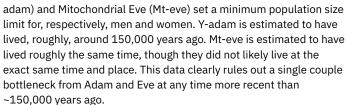
Since 2021, the BioLogos website states that "Population genetics measures the average population, not a minimum population," a claim which is just not true. ²⁸ To the contrary, there is a broad scientific consensus that population genetics *can*, indeed, estimate the *minimum* population size consistent with genetic data, albeit using entirely different methods than effective population size.

- 23. Asger Hobolth and others, <u>'Incomplete Lineage Sorting Patterns among Human, Chimpanzee, and Orangutan Suggest Recent Orangutan Speciation and Widespread Selection'</u>, *Genome Research*, 21.3 (2011), 349–56 https://doi.org/10.1101/gr.114751.110.
- 24. Dennis R. Venema, 'Adam, Eve and Human Population Genetics'.
- 25. Scott McKnight and Venema.
- 26. Dennis R. Venema, 'Adam, Eve and Human Population Genetics'; BioLogos Editorial Team, 'Adam, Eve, and Human Population Genetics', BioLogos, 2021.
- 27. In late 2019, biologist and acting chairman of the BioLogos board, Jeff Hardin, indicated intent to correct several mistakes after personally confirmed with an expert in population genetics that ILS—along with N_e and LD—is not a relevant line of evidence. See the quotation of an organizational communication from Jeff Hardin, in his role as chairman. S. Joshua Swamidass, 'BioLogos Deletes an Article', Peaceful Science, 2021 https://doi.org/10.54739/rv8k.
- 28. See, for example, the note BioLogos attaches to: BioLogos Editorial Team, 'Adam, Eve, and Human Population Genetics'.

At least two lines of evidence robustly estimate the minimum population size, one of which covers the relevant time period: lineage time inference (LiTI) on autosomal DNA, and lineage times of mitochondrial and Y-chromosomal DNA.

Mitochondrial and Y Lineage Times

Though not covering the time period relevant to Venema's book or revised conclusions, Y-Chromosomal Adam (Y-



Nathaniel T. Jeanson

This basic approach to determining minimum population size, lineage time inference, has very broad agreement among scientists, including young earth creationist biologists. For example, Y-adam and Mt-eve feature prominently in Nathaniel Jeanson's two books on Adam and Eve. ²⁹ Jeanson is a biologist with Answers in Genesis, and he reconciles young earth creationism with Y-adam and Mt-eve by using a mutation rate 40x higher than the consensus mutation rate across the genome. ³⁰ This mutation rate is the specific point of contention, on which his argument hinges, but this disagreement is framed by a larger point of agreement: lineage times are a valid and understandable approach to estimating minimum population sizes.

Lineage Times of Autosomal DNA

With the collapse of the LD and ILS arguments, an awkward scramble ensued to identify at least some evidence to support the revised conclusion. After rejecting every line of evidence presented by Venema and Schaffner, Buggs proposed the right way forward:³¹

[compute] the TMR4A for each haplotype block of the human genome... . Until that has been done, I do not think we can say that the bottleneck hypothesis has been rigorously tested.

TMR4A is the "time to most recent 4 alleles," the time needed for mutations and recombinations to generate, from a single couple, the vast majority of observed human genetic variation across the genome. Compared to LD, ILS, and every other line of evidence considered, Venema agreed,

TMR4A is a better way of looking at this overall—it more directly addresses what we're really interested in.³²

- Nathaniel Jeanson, <u>Traced: Human DNA's Big Surprise</u> (Master Books, 2022);
 Nathaniel Jeanson, <u>Replacing Darwin: The New Origin of Species</u> (Master Books, 2017).
- 30. For example, compare the rates reported in these two publications, and references therein. Nathaniel Jeanson, <u>'Evidence for a Human Y Chromosome Molecular Clock"</u>, Answers Research Journal, 2019 [accessed 9 July 2022]; Aylwyn Scally, <u>'The Mutation Rate in Human Evolution and Demographic Inference</u>, Current Opinion in Genetics & Development, 41 (2016), 36–43 https://doi.org/10.1016/j.gde.2016.07.008.
- 31. Swamidass, 'Heliocentric Certainty Against a Bottleneck of Two?'

In defense of Venema's revised conclusions, the TMR4A analysis was implemented and defended almost entirely by another scientist.³³

In the end, TMR4A was the primary evidence supporting Venema and BioLogos's revised conclusions. If the goal is to rule out a single-couple bottleneck, then the most robust and important analysis to present and improve upon are these LiTI estimates of TMR4A.

It had only recently become possible to compute TMR4A across the genome, due to a fascinating advance in population genetics, first was published in 2014. Elegantly accounting for recombination, now several algorithms can infer from genetic variation an "ancestral recombination graph" (ARG), which includes *many* trees arranged in a sequence along the genome. ³⁴ Some ARG inference algorithms are now fast enough to analyze data from thousands of genomes at once.

At each locus of the genome, the ARG's corresponding tree—from the ideal 4-allele starting point— records the most likely count of mutations and recombinations required to exactly reproduce in fine-grain detail the overwhelming majority of observed human genetic variation.³⁵ The TMR4A date itself is estimated by scaling these counts by the mutation (or recombination) rate across the genome. Each locus of the genome yields a distinct TMR4A, and these estimates across the genome are summarized by their median.

What was the median TMR4A date? For humans alive today, the median TMR4A is approximately 500,000 years ago (Figure 3). Any time more recent, the original couple would need to carry more than four alleles, which is not possible with normal human biology. Richard Buggs, AJ Roberts from RTB, Ann Gauger at the Discovery Institute, and secular scientists at Peaceful Science subjected this analysis to intense and searching scrutiny, publicly raising several objections, but finally agreeing this was a robust result. 36

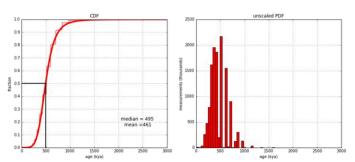


Figure 3: This figure from the 2017 post-publication review of *Adam and the Genome* shows that a single-couple bottleneck is ruled out before 495,000 years ago.[^38] The right figure displays the distribution of TMR4A estimates across the whole autosomal genome. The left figure displays the same data in a different way, as a cumulative probability density function (CDF). The black line identifies the median TMR4A, at 495,000 years ago.

- 32. BioLogos Forum.
- 33. Swamidass, 'Heliocentric Certainty Against a Bottleneck of Two?'
- 34. See a full review in Elliot-Higgins and Swamidass.
- 35. The accuracy of these ARGs and these dates depends on the ratio of the mutation rate to the recombination rate, the higher this ratio the better. As the mutation rate increases, the accuracy increases. This ratio is about 2.0 in humans, high enough for accurate inferences.
- 36. Notably, AFS does not withstand similar scrutiny from Buggs, but Buggs does ultimately refer to AFS positively in the end due to superficially confirmatory results with TMR4A. Richard Buggs, 'Adam and Eve: Lessons Learned' [accessed 8 July 2022]. See the responses to criticism here: Swamidass, 'Heliocentric Certainty Against a Bottleneck of Two?'; BioLogos Forum.

Lineage time inference (LiTI) of TMR4A by this method is both very robust to confounding factors and very resistant to skeptical criticism, ³⁷

- TMR4A estimates do not depend on any simulations of demographic history, which are very difficult to accurately execute and are always subject to valid criticism for neglecting important details.³⁸
- The whole autosomal genome is analyzed, neutralizing any objections that the analysis was biased by cherrypicked regions so as to reduce or increase the TMR4A.
- Several factors push estimates lower or higher than the true TMR4A date at any individual locus of the genome, but none of these factors acts across enough of the genome so as to substantially alter the *median* TMR4A.
- Adding more genomes to the analysis will not decrease the TMR4A date, and empirically new data does not increase the date by much.
- Much as radiometric dating can be crosschecked by comparing independent isotope clocks, TMR4A dates can be computed either using the mutation clock, the recombination clock, or both together.³⁹

A preprint published in 2021 demonstrates that LiTI is very robust indeed, empirically validating TMR4A with several systematic tests. 40

There is one caveat to resolve in future work. This TMR4A is computed only from people alive today. Adding in the DNA from archaic humans, such as Neanderthals and Denisovans is more difficult because ancient DNA has many degradation errors that inflate the inferred date. Due to interbreeding in the past, most of the archaic genomes are already included in the current analysis any ways, so the impact of this data may already be baked in. Perhaps TMR4A might increase to 600,000 or 700,000 years ago or stay the same. We do not yet know.

A Broad and Deep Consensus

The consensus around TMR4A is broad and deep. TMR4A features prominently in William Lane Craigs' response to BioLogos and in his book, 41 which was reviewed favorably by secular scientists. Stephen Schaffner, when writing BioLogos's new position, is silent on the limitations of $N_{\rm e}$, LD, and ILS, but he discreetly cites TMR4A as a "more sophisticated method" than the disputed evidence he presented instead. 42 Reasons to Believe also endorsed the TMR4A

- 37. Elliot-Higgins and Swamidass.
- 38. This is a common point of confusion for many creationists skeptical of the results. No simulations of population history are used, in any way, to infer the ARG and estimate the median TMR4A date.
- 39. At the time, ARG dating algorithms only used a mutation clock, so this crosscheck was not done. However, we know that, on human data, recombination rate-based methods of demography inference produce similar results as mutation-rate based methods, evidence that such a crosscheck, when done, will increase our confidence in the TMR4A.
- 40. Elliot-Higgins and Swamidass.
- 41. William Lane Craig, 'What Became of the Genetic Challenge to Adam and Eve?', Peaceful Science, 2020 https://doi.org/10.54739/e7r9.
- 42. Stephen Schaffner, 'What Genetics Says About Adam and Eve' [accessed 8 July 2022].

analysis too, and used it to guide refinements to their model.⁴³ This analysis has been in public now for almost five years, without uncovering any valid criticism.⁴⁴ Young earth creationists have been largely silent on TMR4A, but the criticism that did arise indicates misunderstanding of the analysis, not any errors.⁴⁵

RTB used TMR4A and "time to most recent 10 alleles" (TMR10A) to update their model. There were eight people on the Ark: Noah, his wife, his three sons, and their three wives, holding 10 lineages at most. ⁴⁶ Looking across the genome, the median TMR10A is approximately 180,000 years ago. Apart from miraculous intervention or interbreeding between Noah's lineage and others, the TMR10A rules out a Noahic bottleneck more recent than this time. So RTB places Noah at about 180,000 years ago, and positing that Eve was created as a genetic mosaic, with different genomes in each her eggs, passing on more lineages than needed to account for the LiTI estimates at the origin of our species. Exotic biology, even in context of one or more miracle, will be judged implausible by many. But this model is not in conflict with the genetic evidence. ⁴⁷

Three Disputed Lines of Evidence

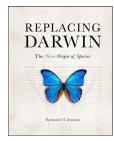
There are, additionally, three disputed lines of evidence that were discussed.

Trans-Species Variation

Leaving no stone unturned, we eventually discussed trans-species variation or polymorphisms (TSV or TSP) in detail, coming to a consensus. This line of evidence was not mentioned in *Adam and the Genome* or any of Venema or BioLogos's work, TSV appears in the formal scientific literature as a test of a single-couple bottleneck. For this reason, it is commonly cited by most biologists when asked questions about Adam and Eve. At Peaceful Science, the discussion continued on with secular scientists for quite some time, eventually arriving to a similar conclusion.

- 43. Anjeanette Roberts, 'Mosaic Eve: Mother of All (Part 1)', Reasons to Believe, 2020 [accessed 5 July 2022]; Anjeanette Roberts, 'Mosaic Eve: Mother of All (Part 2), Reasons to Believe, 2020 [accessed 5 July 2022].
- 44. Swamidass, 'Heliocentric Certainty Against a Bottleneck of Two?'
- 45. Peaceful Science Forum, 'Rob Carter Responds to TMR4A', Peaceful Science, 2018 [accessed 8 July 2022].
- 46. His three sons derive all their DNA from Noah and his wife. Consequently, this bottleneck allows only the DNA that can be held by five individuals. With two copies of the genome in everyone, that means the Noahic bottleneck is down to, at most, 10 lineages.
- 47. Roberts, 'Mosaic Eve (Part 1)'; Roberts, 'Mosaic Eve (Part 2)'.
- 48. Francisco J. Ayala and Ananias A. Escalante, <u>'The Evolution of Human Populations: A Molecular Perspective'</u>, *Molecular Phylogenetics and Evolution*, 5.1 (1996), 188–201 https://doi.org/10.1006/mpev.1996.0013; F J Ayala and others, <u>'Molecular Genetics of Speciation and Human Origins.'</u>, *Proceedings of the National Academy of Sciences of the United States of America*, 91.15 (1994), 6787–94 https://doi.org/10.1073/pnas.91.15.6787.

TSP can, at least in principle, place a minimum population limit from present day back to more than 6 million years in the past, long before we became human. Our genome includes person-to-person variation, different versions, or "alleles," at each locus of the genome. Most of the time, all the variants of a locus within a species are very similar to one another; usually, they are more similar to variants within the species than to variants in other species. In



other words, usually the human variants of a gene are all more similar to other human variants than they are to chimpanzee variants.

This pattern is different in a few locations in our genome, usually at loci important for immunity. At these loci, some human variants are much closer to the variants from other species. In other words, in these immune genes, some human variants are closer to chimpanzee variants than they are to other human variants. This pattern of variation is the hallmark of TSV or TSP.

How does TSV arise? How do different species end up with such similar variants? There are two primary mechanisms: (1) shared history of the genes or (2) convergent evolution due to shared selective pressure. Both mechanisms are valid explanations of TSV, and there is dispute about how much is caused by shared history versus convergent evolution. Only TSP caused by shared history places limits on population size, so convergent evolution confounds estimates of minimum population size based on TSP.

How many TSV lineages are observed, and what limits does this place on population size? This is an area of active research, but in the vast majority of loci there are no TSVs. In the few loci where TSV is observed, almost all have less than 4 trans-species lineages. ⁴⁹ In a few cases, such as the HLA genes, there *may* be up to 10 or 20 shared alleles, though this result has not been replicated. This data, if confirmed and all due to shared history, would place a minimum population limit of 5 to 10 individuals (not thousands) going back 6 million years.

However, HLA genes also show clear evidence of convergent evolution. ⁵⁰ We expect convergent evolution, moreover, in immune genes because different species are often exposed to the same disease-causing organisms. For this reason, TSV-based estimates of minimum population size are lower confidence and disputed.

Simulations of Allele Frequency Spectrum

Allele or Site Frequency Spectrums (AFS or SFS) are a low-information and lossy summary of human genetic variation. This summary is sometimes used in mainstream science to understand population demographics in the somewhat recent past, but the accuracy of AFS inferences degrades rapidly as we look farther back in time. Along with the data underlying LD, the data used by AFS is fully explained and accounted for by the TMR4A estimate.

- Ellen M. Leffler, et al, 'Multiple Instances of Ancient Balancing Selection Shared Between Humans and Chimpanzees' [accessed 8 July 2022] https://www.science.org/doi/10.1126/science.1234070.
- 50. Ali R. Vahdati and Andreas Wagner, 'Parallel or Convergent Evolution in Human Population Genomic Data Revealed by Genotype Networks', BMC Evolutionary Biology, 16.1 (2016), 154 https://doi.org/10.1186/s12862-016-0722-0.

In the context of the post-publication review of *Adam and the Genome*, Stephen Schaffner ran several simulations with stable populations of 10,000 individuals arising from a single couple. From these simulations, he computed the AFS and compared it with the AFS observed in African populations (and nowhere else). The observed and simulated AFS did not match until he moved back the single couple origin to about 500,000 years ago. This approach estimates neither a minimum population size nor an effective population size. Rather, it merely tests the specific hypotheses precisely as they are modeled in simulations, in fine-grained detail. Schaffner presented these results to Buggs, who congratulated the attempt, but quickly dismissed the result due to several factors unaccounted for in the simulations.

Eventually, in 2019, Ann Gauger at the Discovery Institute used simulated AFS to compute a date of 500,000 years ago too. ⁵¹ In 2021 at BioLogos, Schaffner published a different version of the analysis he presented to Buggs, yielding the same date, but using an unnormalized and unscaled AFS. ⁵² At this time, there are at least three reasons this line of evidence is low-confidence and disputed:

- The simulations are dramatically oversimplified in a way that is expected to affect the results, particularly because Schaffner now uses an unnormalized AFS.⁵³
- Creationists published simulations with a much more recent Adam and Eve and different demographic details, generating an AFS matching the observed data. Schaffner does not cite or explain what is invalid about this body of work.⁵⁴
- I was unable to replicate Schaffner's results using simulation software commonly used in the field. His write up was exceedingly terse, without enough information to clarify the source of the discrepancy. Schaffner was non-responsive to questions.

It is possible that future work might develop AFS into a useful line of evidence. The simulations on which the analysis is based need to match both the relevant models of Adam and Eve and the known details of demographic history, also controlling for sampling effects, and systematically determining the starting genotype of the original couple. This sort of modeling is very difficult to do with confidence, and AFS inferences based on simulations will always be vulnerable to criticism for neglecting important details.

Interbreeding and Admixing

There is very good evidence of interbreeding—sometimes referred to as "admixing" or "admixture"—between *Homo sapiens*, Neanderthals

- 51. Unlike Schaffner's write up in 2021, this paper uses a normalized AFS, which is more aligned with the field. Ola Hossjer and Ann Gauger, 'A Single-Couple Human Origin Is Possible', BIO-Complexity, 2019.1 (2019) https://doi.org/10.5048/BIO-C.2019.1.
- 52. Unnormalized AFS is not standard in the field, and is more susceptible to errors introduced by discrepancies in sample size and sampling bias. Schaffner.
- 53. For example, the simulations used a constant population size, but we know that human populations begin to exponentially grow in the last 10,000 years. Simulations that take this into account are expected to render more recent bottleneck times consistent with the AFS data. Other factors have similar confounding effects.
- ${\bf 54.}$ As one example of many, see Sanford and others.

and Denisovans, but the interpretation of this interbreeding is disputed.

Strictly speaking, interbreeding does rule out the genetic-bottleneck model of Venema's revised claims. But *Adam and the Genome*, and the BioLogos organization, made much bigger claims than admixing evidence supports, which is why the book itself just notes interbreeding in passing. For the last decade or more, essentially every creationist organization agreed that *Homo sapiens* and Neandertals interbred. ⁵⁵ If this admixing were all that was claimed, there would have been no controversy.

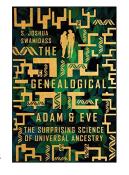
Most critically important, interbreeding between *Homo sapiens* and Neanderthals disconnects the evidence from claims made by BioLogos more recently. Were there ever just two *Homo sapiens*? As was made clear in post-publication review, this question has nothing to do with whether there was a genetic bottleneck down to a single couple in our lineage.

In late 2019, Jeff Schloss, a biologist associated with BioLogos, submitted an article explaining that population sizes estimates do not have "taxonomic specificity." There is no plausible way to sort out how many of our ancestors at the relevant times are *Homo sapiens* or not. Consequently, large "ancestral" population size cannot, even in principle, demonstrate there was never just two *Homo sapiens*.

BioLogos declined to publish this article, in favor of publishing a more diffuse statement of error in early 2020. Ignoring Schloss's correction, this statement went on to present large average ancestral population sizes as evidence that there was never "just two *Homo sapiens*." ⁵⁸

Zombie Science and Defunct Citations

For three reasons, the faith-science conversation may be uniquely susceptible to zombie science from population genetics. First, several false claims based on population genetics are theologically potent, and the change to the consensus is not yet widely known. Second, most scholars in this space do not have the expertise to evaluate claims from population genetics, which are technical and frequently over-extended. Third, quite a bit of scholarship is published in blogs,



books, and other venues with inadequate or non-existent peer review

If we are to discuss genetic bottlenecks, the scientific claims we make about them should be accurate and grounded in good science.

- 55. Young earth creationists and many old earth creationists believe that Neanderthals are fully human and that both species are descendants of Adam and Eve. RTB also agrees that Neandertals and *Homo sapiens* interbred, but they think Neandertals were not fully human and did not descend from Adam and Eve. Either way, this interbreeding is not evidence against the most common creationist accounts of Adam and Eve.
- Deborah Haarsma, <u>'Truth-Seeking in Science'</u>, *BioLogos*, 2020 [accessed 3 July 2022].
- 57. Private communication from Jeff Schloss. Used with permission.
- 58. Deborah Haarsma

And valid claims about bottlenecks should not be over-extended to make negative claims about more sensible models of Adam and Eve, or the theology associated with these models.

Examples of Zombie Science

In 2021, *Perspectives on Science and the Christian Faith* (PSCF) published a series of three articles examining an approach to original sin that does not require descent from Adam and Eve.⁵⁹ Motivating their project, however, the series presumes that the scientific evidence conflicts with universal descent from Adam and Eve, authoritatively citing a defunct article, known since 2018 to be in error.⁶⁰ The series could have still made their theological case, but on a level playing field, without appeals to defunct articles.

A recent book by Loren Haarsma, *When Did Sin Begin?*, repeats several incorrect scientific claims. On the one hand, this book's summary of the evidence presents a very different position than BioLogos held in the past. Recent universal ancestry is presented early on.⁶¹ Viable models of *de novo* creation of Adam and Eve are presented, and the book makes clear that the "humans" of theology need not correspond to specific taxonomic categories, such as *Homo sapiens*.⁶²

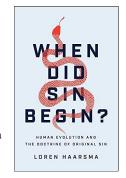
On the other hand, the book makes several defunct scientific claims, referencing several defunct citations in support of these claims, never once engaging corrective scholarship. Most prominently, the book authoritatively references *Adam and the Genome*, without citing or discussing the post-publication review that corrected the book.

The book authoritatively cites a deleted article at BioLogos, 63 claiming LD and ILS, might, after all, rule out a single-couple bottleneck going back millions of years. In a material omission, there is no explanation that estimates of N_e (including LD and ILS) are an average, not a minimum, and are therefore consistent with a brief bottleneck. Extending far beyond the evidence, the book inexplicably concludes that—even if a single-couple bottleneck were shown consistent with the LD and ILS data—the "most probable interpretation of the data would still point towards" a "bottleneck" (i.e., minimum) population size of several thousands.

- 59. Carol A Hill, 'Original Sin with Respect to Science, Origins, Historicity of Genesis, and Traditional Church Views', Perspectives on Science and Christian Faith, 73.3 (2021), 14; George L Murphy, 'The Twofold Character of Original Sin in the Real World', Perspectives on Science and Christian Faith, 73.3 (2021), 6; Roy Clouser, 'Three Theological Arguments in Support of Carol Hill's Reading of the Historicity of Genesis and Original Sin', Perspectives on Science and Christian Faith, 73.3 (2021), 7
- 60. Dennis R. Venema, 'Adam, Eve and Human Population Genetics'.
- 61. Loren Haarsma, 'When Did Sin Begin?' (Baker Academic, 2021). Oddly, the book's scientific explanation does not cite the scholarship that changed BioLogos's position. Swamidass, 'The Genealogical Adam and Eve: The Surprising Science of Universal Ancestry', Swamidass, 'The Overlooked Science of Genealogical Ancestry'.
- 62. The book, however, does not credit, in its references or text, the corrective scholarship that changed BioLogos's position on this matter. Swamidass, <u>The</u> <u>Genealogical Adam and Eve: The Surprising Science of Universal Ancestry</u>.
- 63. See chapter 4, fns. 8 and 12 and associated text in <u>When Did Sin Begin?</u>. The deleted section referenced in the book was republished at <u>Peaceful Science</u>, Dennis R. Venema, <u>'Adam, Eve and Human Population Genetics'</u>.

Without engaging or citing corrective scholarship, the book repeats BioLogos's revised argument, that N_e , LD and ILS are "genetic evidence that the first *Homo sapiens* were a larger group, not just two individuals."

These claims are incorrect and cannot be understood as informed scientific disagreement. This book does not present a new scientific argument, nor does it cite or discuss the scholarship that corrects its references. Without engaging corrective



scholarship or acknowledging the corrections themselves, this book resurrects zombie science that was vanquished long ago by peer-review

Neither Complete nor Transparent

The academic discourse on faith and science is interdisciplinary; we rely on one another to accurately represent the findings of our respective fields.

The BioLogos organization, by 2021, deleted or substantially revised at least 9 articles on their website. ⁶⁴ The article that first brought their scientific argument into the public eye was deleted. ⁶⁵ Every article supporting the *Christianity Today* coverage of BioLogos's scientific position was deleted. ⁶⁶ Venema's articles responding to Buggs were also deleted. ⁶⁷ One deleted article was substantially revised, backdated to 2014, and reposted under new authorship and

- 64. See an incomplete list at S. Joshua Swamidass, 'A U-Turn on Adam and Eve', Peaceful Science, 2021 https://doi.org/10.54739/83rj. Some deleted articles are archived at Peaceful Science to enable ongoing scholarship, http://peacefulscience.org/prints/deleted.
- 65. Venema and Falk.
- 66. For example, Venema and Falk; Dennis R. Venema, 'Adam, Eve and Human Population Genetics'. One article was substantially revised, backdated, and reposted under new authorship with revised conclusions. The note does not disclose that the conclusions were changed.
- 67. Dennis R. Venema, 'Adam, Eve and Population Genetics: A Reply to Dr. Richard Buggs (Part 1)'; Dennis R. Venema, 'Adam, Eve and Population Genetics: A Reply to Dr. Richard Buggs (Part 2)'.

with altered conclusions.⁶⁸ This solitary article is now the lone defense of the coverage by *Christianity Today* in 2011. The revisions removed discussion of LD, but still present ILS as a relevant line of evidence.

BioLogos is a well-respected organization that has done a lot of good, credible in large part due to its founder and former NIH-director, Francis Collins. When asked to make transparent corrections, BioLogos declined, explaining the organization's website is merely a blog. ⁶⁹ The organization does not follow the baseline publication ethics of an academic journal, a research organization, or even a journalistic outlet.

Because they are a credible organization, this response creates a confusion situation, in which defunct citations and scientific errors are propagating.

Conclusions

This review explains what population genetics tells us about single-couple genetic bottlenecks. Special attention was given to explaining each line of evidence, and how our understanding has changed over the last decade.

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Deborah Haarsma, Jim Stump, Loren Haarsma, Ard Louis, and Dennis Venema from BioLogos were also presented a draft of this manuscript, but they did not provide a response.

- 68. Dennis R. Venema, 'Adam, Eve and Human Population Genetics'.
- 69. Swamidass, 'BioLogos Deletes an Article'.

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