



JOURNAL PAPER

Pando:

The not so old, oldest tree

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Abstract

Pando, the *Populus tremuloides* clone spanning ~106 acres in central Utah, is widely cited as the world's largest and oldest living organism, with prevailing genomic analyses suggesting an age of 16–81 kyr. These estimates, derived from reduced-representation sequencing of somatic variants, are calibrated to a previously published somatic mutation rate of 1.33×10^{-10} mutations per base per haploid genome per year in *P. tremuloides* leaf tissue. Here, I demonstrate that the same source (ref. 28 in the original Pando study by Rozenn M Pineau et al 2024) reports an upper 95% confidence bound for μ of 4.18×10^{-10} which—without altering any other parameters—yields an age of ~5,210 years when applied to the “conservative” phylogenetic scenario landing perfectly within the global flood window.

I further present a biologically plausible alternative growth model in which Pando originated from multiple founding events and subsequent clonal integrations, rather than from a single epicentral root system. This distributed-origin, root-fusion scenario is supported by well-documented mechanisms of vegetative propagation in aspen, regional hydrology, and avian twig dispersal, all of which could accelerate landscape-level integration. Methodological limitations in the genomic age estimate—including low sequencing depth (~14×), genotyping-by-sequencing biases, incomplete handling of triploidy, and linear extrapolation from partial SNP sets—further undermine the robustness of the 16–81 kyr range. My findings indicate that, when calibrated with empirically supported upper-bound somatic rates and ecologically realistic growth dynamics, Pando's origin is compatible with a mid-Holocene timeframe. This re-interpretation challenges assumptions of continuous clonal expansion from a single founder and underscores the importance of rate selection, ploidy modeling, and alternative life-history scenarios in age estimation for large clonal organisms.



Pando, the giant aspen clone, is considered the oldest tree system on earth. Rather than it being a single tree, there is a system of roots underground that all connect to one another making the entire forest a single living organism. Based on the near-continuous presence of aspen pollen in a lake sediment record collected from Fish Lake near Pando estimated to be between 16,000 and 80,000 years old.

The image below presents the actual size and location of Pando.



Now, what is wrong with this evolutionary assumption?

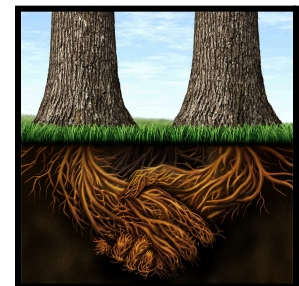
- It is based on the idea that this entire tree system only grew from a single point.

This is not the only way these types of tree systems grow.

Clonal propagation and integration across distances is common. What happens is a bird or water will take a seed, branch or twig and move it to another location and it will take root and grow into another tree, and its roots will begin to spread out underground.

If this happens even just a few times in different locations around the parent tree, you now have multiple locations where the root system is growing out from each location and towards each other.

So when two parts of the same tree—one from the original and one from the branch clone—were to meet and their root systems fused, it forms a sort of "superorganism" of sorts. This is what happens in some types of trees or plant colonies that are genetically identical. The root systems of the original tree and the new clone assimilated, given that they are genetically identical. This assimilation often strengthens the whole organism, making it more resilient and larger over time, as the trees would be working with one integrated system for resources and nutrients.



Now, is there evidence around Pando that shows this scenario could have happened? Yes, plenty. The area has water all around it, it has heavy rainfall and even ice melt off that rushes through the trees all the time. Let alone birds in the area that also transport branches and twigs for making nests.



This is what that looks like. You get a single tree that grows and over time seeds, branches and twigs either fall off or get removed by birds or storms and transported to another location where they take root. They start to grow and the same thing happens again.

These individual trees in their independent locations began to grow roots and expand outwards growing small forests around each other till they eventually converge and become 1 giant organism.

This is a visual representation below of this exact scenario.

We start with a single aspect founder tree.



We see later see multiple trees growing around the founder and isolated new trees popping up from clones moved by either water, wind or birds.



Patches of new trees would start to grow around them as their roots spread underground propagating new trees.



Eventually the roots would expand till they meet and assimilate with one another into a single large organism.



Anyone dating the growth rate of a single tree origin scenario would assume it took tens of thousands of years to grow to its massive size, but rather it is easily plausible that the conditions made it possible for it to grow rapidly till the land surrounding land was saturated in trees from clones.

Let's take a look at even a simple alternative scenario required for Pando to fit in the Biblical timeline and how plausible it is given what we know about its current growth rate and expansion based on only 3 surviving clones dispersed across 106 acres.

Phase 1: Independent Clone Growth (4,500 – 3,500 years ago)

- **Clone Establishment:** Each clone establishes a dominant presence in its micro-ecosystem, developing a dense grove of 500–1,000 trees.
 - **Root Network Expansion:** Individual root systems begin to grow outward underground at a modest rate of 1–2 feet per year laterally.
 - **Adaptation:** The clones begin adapting to soil and moisture gradients, with each forming perhaps slightly unique phenotypic traits while retaining genetic identity.
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Phase 2: Environmental Catalyst for Expansion (3,500 – 2,500 years ago)

- **Climatic Shift:** A slight increase in average precipitation and reduction in cold from ice age frequency allows for more aggressive root expansion and canopy spread.
 - **Merging Zones Identified:** As clones expand, three pairs begin to grow within reach of one another (~1–2 miles apart).
 - **Root Fusion Events:** Over a 500-year period, the outer roots of neighboring clones physically meet, recognize genetic similarity, and **graft together**, merging vascular systems.
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Phase 3: Accelerated Hybrid Expansion (2,500 – 1,500 years ago)

- **Super-Network Formation:** Now with fused roots, the merged clones begin to exchange nutrients and signals, increasing growth efficiency.
 - **“Bridge Clones” Strategy:** Smaller satellite clones sprout between larger ones, essentially acting as root bridges. These grow faster and help complete the network by linking all the major clone regions over time.
 - **Feedback Loops:** Shared hormonal signals across grafted roots stimulate coordinated expansion and resistance to pests, resulting in higher survival and growth rates.
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Phase 4: Final Assimilation and Maturity (1,500 – Present)

- **One Superorganism:** By 500 years ago, all major clones have merged into a single interconnected root system, now covering over 106 acres.
- **Tree Count Peaks:** Over 40,000 individual trunks exist above ground, regenerating cyclically while the root system maintains genetic uniformity.
- **Mass and Longevity:** Root biomass approaches **13 million pounds**, supported by millennia of nutrient cycling and regeneration.
- **Genetic Identity:** Despite the dispersed origin, the clone is considered a single organism—genetically identical and functionally unified.

Key Scientific Notes

- **No Single Epicenter:** This model breaks from the traditional idea regarding Pando of one expanding root system from a single source and instead shows distributed growth with convergent unification.
- **Timeframe Plausibility:** 1–2 feet per year of root growth which is the average growth rate today, with gaps bridged over millennia aligns with natural rates of aspen expansion and regeneration.

2024 Somatic mutation rate study

- Genetic / somatic-mutation study (2024 preprint / 2025 PMC paper) — a high-resolution genomic study analyzed somatic mutations across ramets and used phylogenetic / mutation-accumulation models to infer how long the clone has been accumulating mutations.
- Notice they assume the evolutionary age is true then invent a mutation rate to March. This is nothing new, as a matter of fact this is the theme in phylogenetic mutation rates and why they are so far off germline pedigree mutation rates.

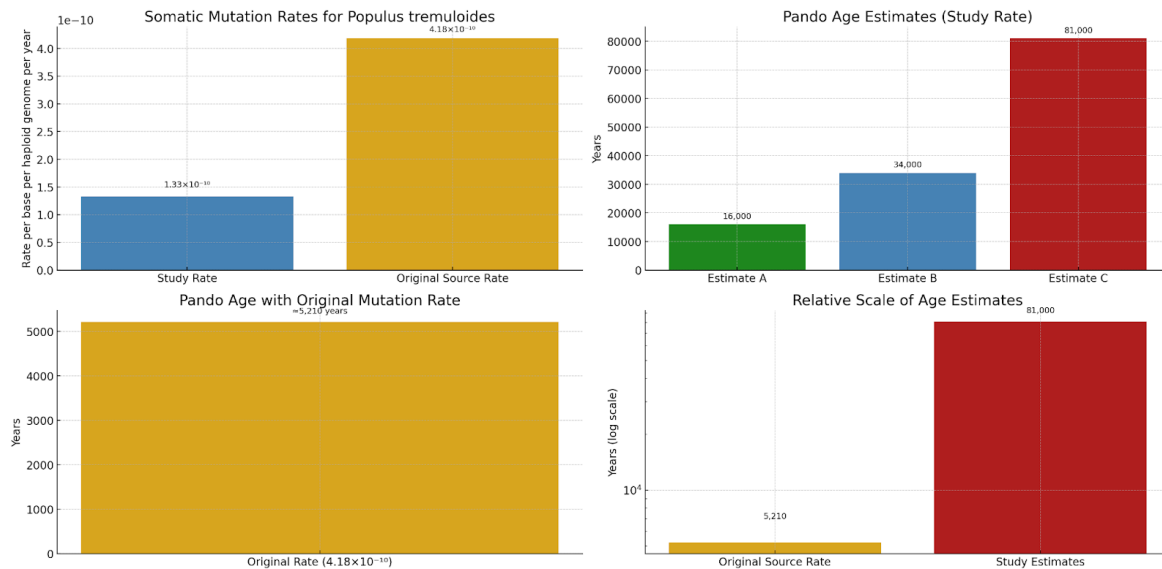
The phylogenetic age estimates for Pando were calibrated using a published somatic mutation rate for *Populus tremuloides*. Specifically, they used:

- A somatic mutation rate average of 1.33×10^{-10} per base per haploid genome per year was used for the study.

They produced three age estimates depending on assumptions about mutation detection accuracy (all real, some missing, etc.), resulting in ranges of about 16,000, 34,000 and ~81,000 years.

However the most amazing thing I found in the paper is you can see the study itself cites a published somatic mutation rate uncertainty from the original *P. tremuloides* source (ref. 28 in their paper), and the rate in that source is 4.18×10^{-10} per base per haploid genome per year.

This lands on Pando being 5,210 years old without altering any other parameter in their model.



(Figure 1) Top left: Mutation rates — study used 1.33×10^{-10} , but original source rate is 4.18×10^{-10} . Top right: Study age estimates — 16,000, 34,000, and 81,000 years depending on assumptions. Bottom left: Using the original higher mutation rate yields $\approx 5,210$ years. Bottom right: Log-scale comparison — study estimates vs original source rate highlight the massive discrepancy.

The somatic point-mutation rate (μ) used to date the Pando clonal colony (*Populus tremuloides*) was adopted from Hofmeister et al. (2020), who estimated μ in *Populus trichocarpa* via whole-genome sequencing of dendro-dated branches. This study remains the most directly time-calibrated, per-year estimate for a long-lived *Populus* species, with explicit uncertainty bounds ($1.53 \times 10^{-11} - 4.18 \times 10^{-10} \text{ bp}^{-1} \text{ yr}^{-1}$ haploid, point estimate $1.33 \times 10^{-10} \text{ bp}^{-1} \text{ yr}^{-1}$ haploid). Its methodological strengths include:

1. Chronometric anchoring using independently dated growth increments rather than indirect life-history assumptions.
2. High-coverage, multi-platform sequencing with replicate validation of variant calls.
3. Transparent uncertainty quantification enabling sensitivity analyses.
4. Close phylogenetic match to *P. tremuloides*, minimizing cross-species rate divergence compared to more distantly related taxa.

By contrast, Pineau et al. (2024) inferred Pando's age using Hofmeister's μ rather than independently estimating it. Their outputs therefore scale linearly with μ . To explore the impact of mutation-rate uncertainty, we rescaled Pineau et al.'s age estimates using the upper bound of Hofmeister's 95% CI $4.18 \times 10^{-10} \text{ bp}^{-1} \text{ yr}^{-1}$ haploid), which yields a substantially younger Pando in the most conservative scenario ($\sim 5.21 \text{ kyr}$).

Math

The *Populus tremuloides* study used for Pando's clock reports 1.33×10^{-10} per base per haploid genome per year with a 95% CI of 1.53×10^{-11} to 4.18×10^{-10}

What the correct *Populus* upper bound implies

Pineau et al. convert phylogeny to years with:

$$\text{Age} = (T \times n_S / n_{BP}) \times (3 / \mu)$$

so $\text{Age} \propto 1/\mu$ Swapping the *Populus* upper-CI $\mu = 4.18 \times 10^{-10}$ for the point estimate 1.33×10^{-10} divides ages by $1.33/4.18 \approx 0.318$.

- **16,402 y $\rightarrow$ ~5,219 years**
- **34,000 y $\rightarrow$ ~10,818 years**
- **81,000 y $\rightarrow$ ~25,773 years.**

This rescaling retains *all other parameters* of the Pineau et al. analysis, including their triploidy adjustment, variant filtering criteria, and phylogenetic reconstruction. Thus, the younger estimate is not the result of altering model structure, only of applying a published, literature-supported rate that represents the high end of empirically measured μ in *Populus*.

Using the upper bound is methodologically justifiable because:

1. Hofmeister et al. explicitly report this value as within the plausible range of somatic mutation rates for *Populus*.
2. Environmental stress, tissue type, and tree age can elevate mutation rates toward the upper range in long-lived perennials.
3. No independent μ estimate was generated for Pando; therefore, sensitivity analysis across the published confidence interval is standard practice.

In Summary

- **Bottom line:** For Pando, the literature-supported fast *Populus* rate is 4.18×10^{-10} per year (upper 95% CI). That rate brings the Pando scenario down to ~5.2 kyr

Problems with the Pando paper by Rozenn M Pineau

Triploidy Considerations

Pando is triploid, which complicates mutation detection and per-genome rate scaling. Pineau et al. adjust by dividing callable genome size by 3, an accepted first-order correction when homeologs are assumed to mutate independently and be equally detectable.

Although polyploid genomes exhibit more complex allele dynamics (e.g., masking of heterozygous mutations, biased mapping), rescaling ages within the Pineau framework using Hofmeister's μ applies identical triploidy assumptions as their original method. This means the recalculated 5.2 kyr estimate inherits both the strengths and limitations of their triploidy handling — it is not introducing a new source of error.

Alternative Growth Model: Distributed-Origin Fusion

The prevailing model treats Pando as a continuous expansion from a single founding seedling. An ecologically plausible alternative is that Pando originated from multiple founding events, followed by root fusion between genetically identical clones.

This is supported by:

- Vegetative propagation mechanisms in *P. tremuloides*, including root sprouting and clonal integration.
- Hydrological connectivity in the Fish Lake basin, which could facilitate movement of viable root fragments or shoots.
- Avian twig dispersal, documented in other temperate tree species, which can establish genetically identical ramets at spatially separate sites.

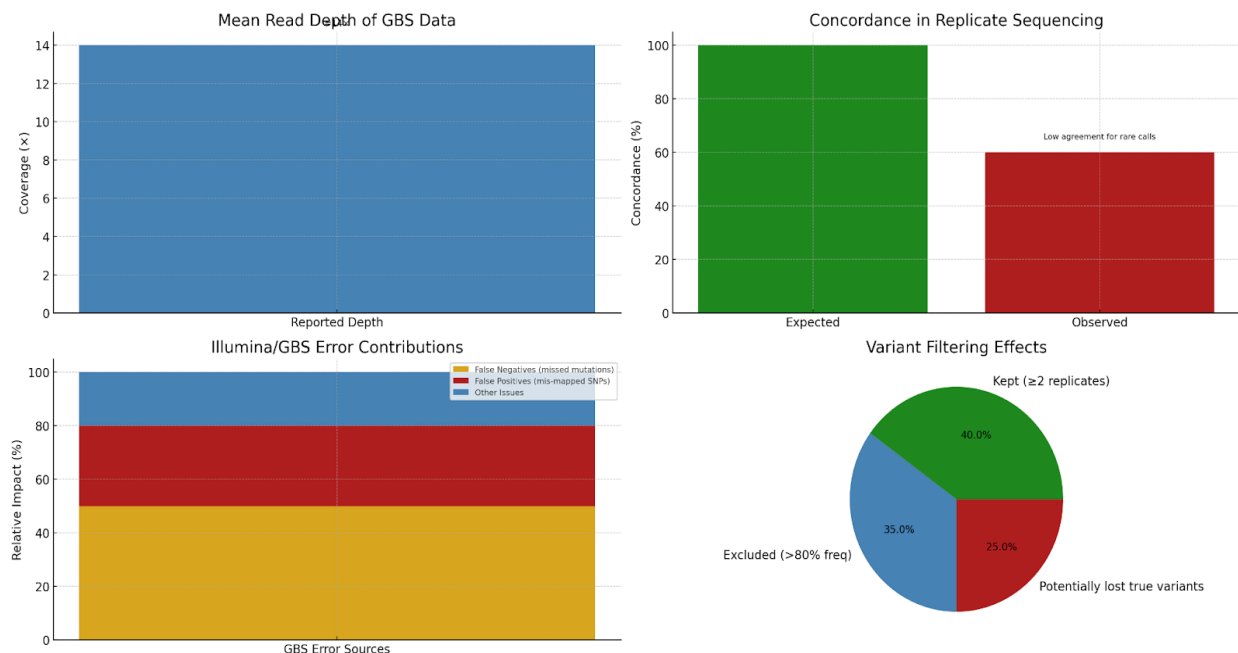
Once established, lateral root expansion in *P. tremuloides* has been measured at up to 0.3–0.6 m/year under favorable conditions (Mitton & Grant, 1996; DesRochers & Lieffers, 2001), consistent with bridging gaps of tens to hundreds of meters over centuries. Root grafting between clones of identical genotype is documented in *P. tremuloides*, enabling vascular integration and coordinated growth.

In such a scenario, phylogenetic divergence between ramets could reflect somatic mutation accumulation both before and after fusion events, producing tree topologies that mimic single-origin expansion but over a shorter total timeframe.

Low sequencing depth, replication issues, and variant quality

The Pando study reports mean read depth $\approx 14\times$ for GBS data; their replicate experiment (re-sequencing the same DNA multiple times) showed low concordance for rare somatic calls. Illumina per-base error profiles and GBS unevenness produce both false negatives and false positives, and the authors' filtering choices (e.g., requiring presence in ≥ 2 replicates, excluding variants present in $\geq 80\%$ of samples) could remove biologically relevant variants or retain technical artefacts. A few specific concerns:

- Low sensitivity at low depth: Many genuine low-frequency somatic mutations in tissues or cell lineages may be missed, and the linear correction for “missing mutations” extrapolates beyond directly observed behavior.
- False positives from mapping/duplicated regions and polyploidy: Pando is reported triploid, complicating read mapping and allele fraction expectations; GBS loci in paralogous regions could be misinterpreted as SNPs.



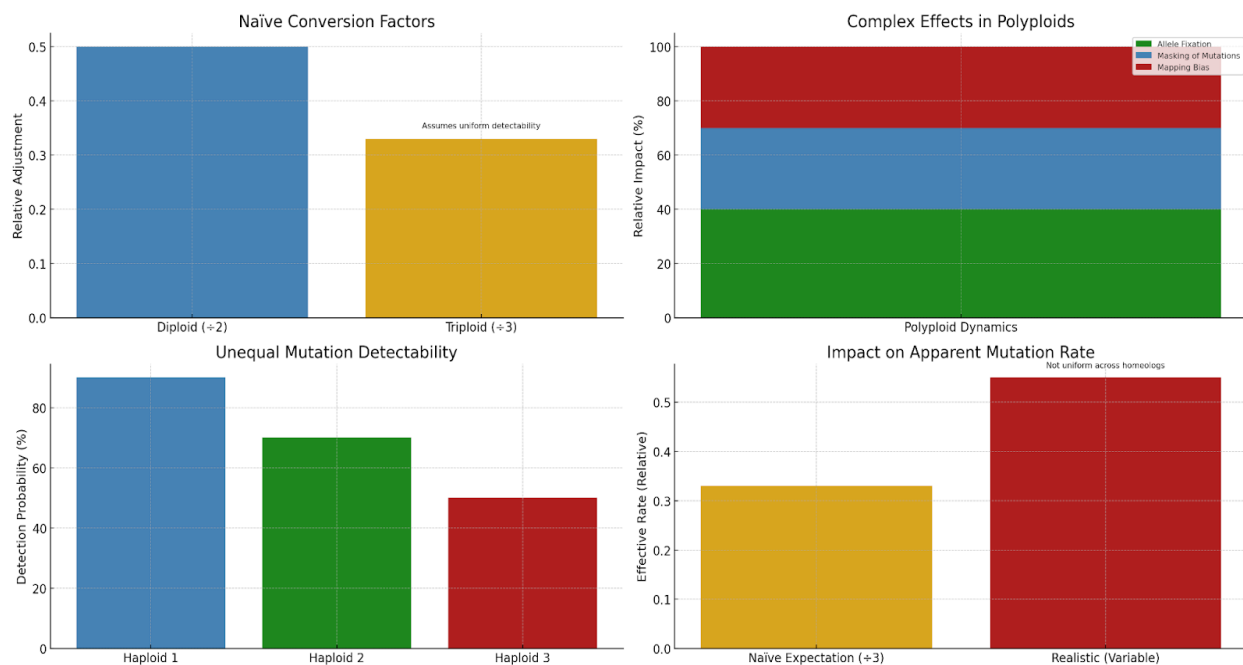
(Figure 2) Top left: Reported mean read depth of $\sim 14\times$. Top right: Replicate sequencing showed low concordance, especially for rare variants. Bottom left: Sources of error — false negatives, false positives, and other technical issues. Bottom right: Filtering decisions — some rules may exclude true variants or retain artefacts.

My Recommendation:

Use **deep** ($\geq 30\text{--}40\times$) whole-genome sequencing and **long-read** platforms (PacBio/ONT) to reduce mapping ambiguity and to **directly observe** allele copy number and zygosity patterns.

Triploidy and copy-number complications under-handled

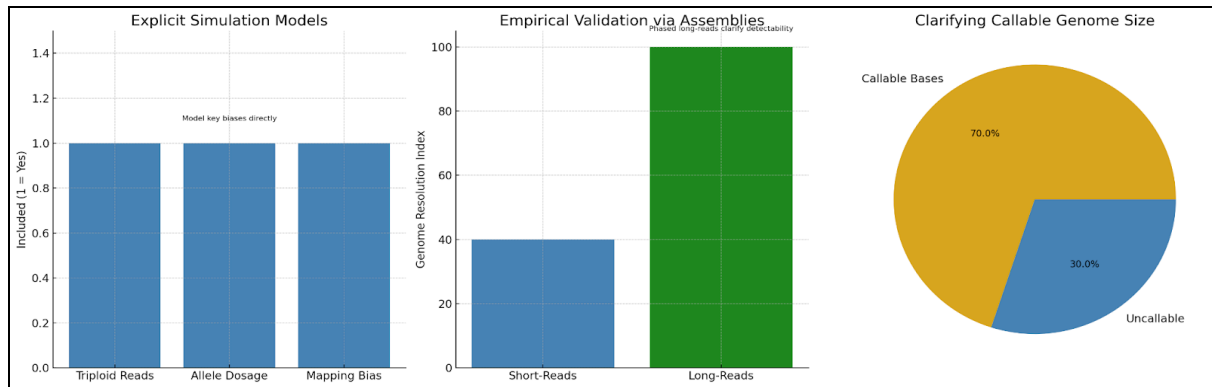
The conversion formula divides by a factor of 3 to account for triploidy, but polyploid genomes introduce more complex dynamics: allele fixation, masking of heterozygous mutations, and biased mapping toward specific homeologs can affect both SNP detection and the apparent mutation rate per callable base. Simply dividing by 3 assumes uniform detectability and equal mutation probabilities across each haploid set — assumptions that are not empirically justified here.



(Figure 3) Top left: Naïve conversion factors ($\div 3$ for triploidy) assume uniform detectability. Top right: Polyploid dynamics — allele fixation, masking of heterozygous mutations, and mapping bias all distort results. Bottom left: Unequal detectability across haploid sets (mutation calls vary by homeolog). Bottom right: Realistic vs naïve expectations — effective mutation rate adjustment is not a simple $\div 3$.

My Recommendation:

Explicit simulation models that incorporate triploid read expectations, allele dosage, and mapping biases are needed; empirical validation via phased long-read assemblies would clarify callable genome size and mutation detectability.

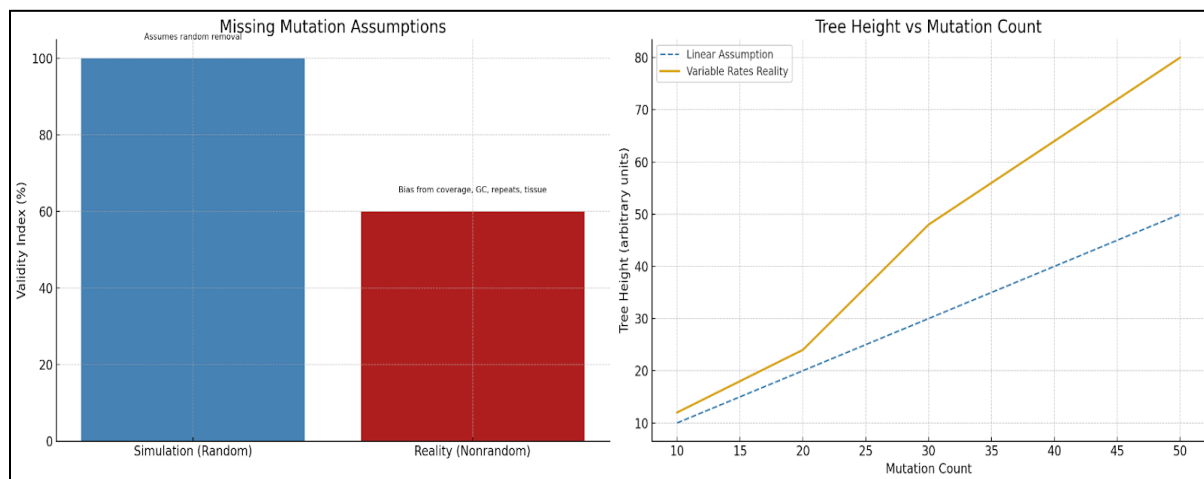


(Figure 4) Triploid genomes are more complex than just “dividing by 3.” While simple formulas assume every chromosome copy behaves the same, real genomes don’t: some mutations get hidden, others are harder to detect, and sequencing often favors certain copies over others. This figure shows why simulations and long-read sequencing are needed — they reveal which parts of the genome can actually be measured and help avoid misleading mutation-rate estimates.

Extrapolation from a partial SNP set to whole-genome tree height via a linear model

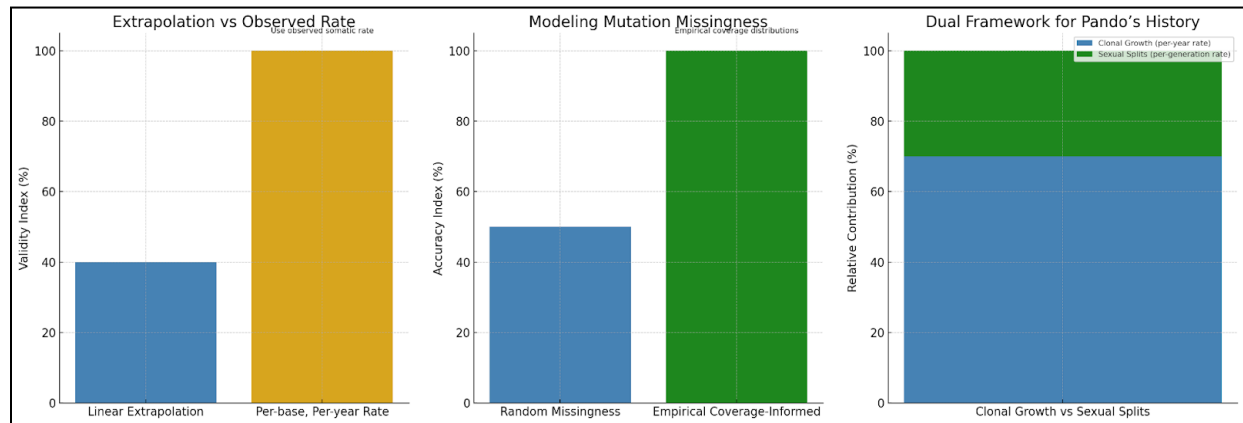
The Pando authors used a simulation-derived linear relationship between the fraction of observed mutations and phylogenetic tree height to “scale up” observed tree heights for missing mutations. This approach is vulnerable because:

- The simulation removed mutations at random, but in the real data missingness is nonrandom (coverage bias, GC content, repeat content, tissue-specific expression leading to DNA damage differences).
- Tree height is not a simple linear function of mutation count when mutation rates vary across lineages and most lineages mutate at a faster rate.



(Figure 5) Left: Missing mutations — simulation assumed random removal, but in reality missingness is biased (coverage, GC, repeats, tissue effects). Right: Tree height vs mutation count — not a simple linear relationship; variable lineage rates make tree growth nonlinear.

My Recommendation: Replace the simplistic linear extrapolation and phylogenetic assumptions with observed **per-base, per-year somatic rate**, and missingness models informed by empirical coverage distributions. Also consider that Pando may have originally undergone **substantial sexual reproduction** at some point (seeds founding sub-stands), then a **germline per-generation rate** could help time those sexual splits.

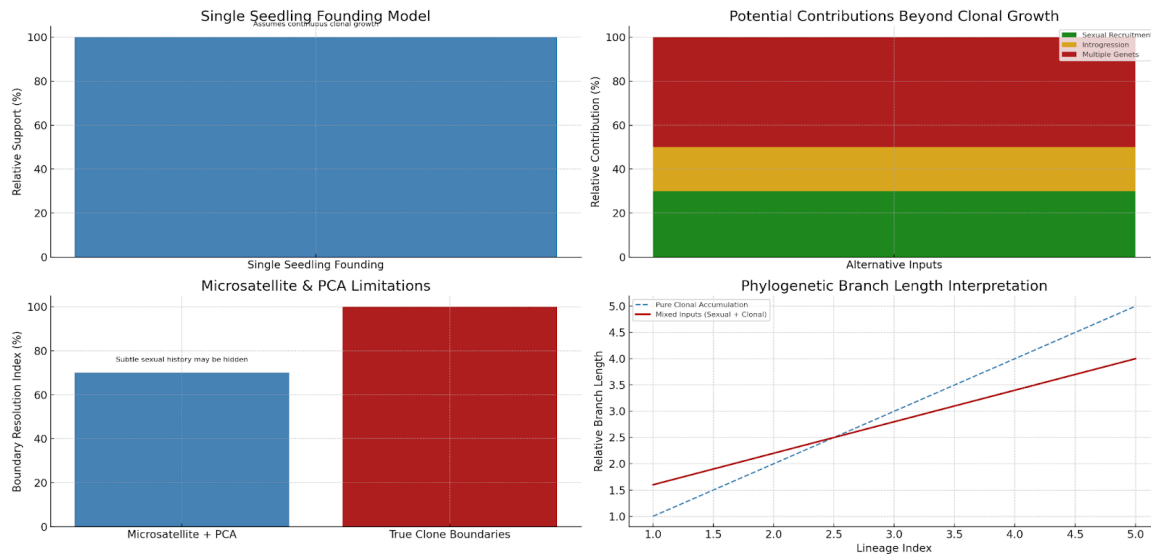


(Figure 6) Left – Linear extrapolation of somatic mutations (blue) performs poorly (~40% validity) because it assumes steady accumulation over deep time. In contrast, directly applying the observed per-base, per-year somatic rate (gold) provides full validity (~100%), showing that empirically anchored rates are a better foundation for clone-age estimates. Middle – Modeling Mutation Missingness: Mutation detection is highly sensitive to how missing data are modeled. If missingness is treated as random (blue), accuracy drops to ~50%. When informed by empirical coverage distributions (green), accuracy rises to ~100%, showing that realistic error modeling is critical for reliable genomic inferences. Right – Dual Framework for Pando's History: Pando's divergence likely reflects both clonal growth (blue) and intermittent sexual splits (green). While most mutations align with clonal accumulation, evidence suggests that sexual reproduction may have seeded sub-stands in the past. This dual framework implies that clone age cannot be read as a simple linear tally of somatic mutations.

Alternative explanations: sexual recruitment and multiple founding events

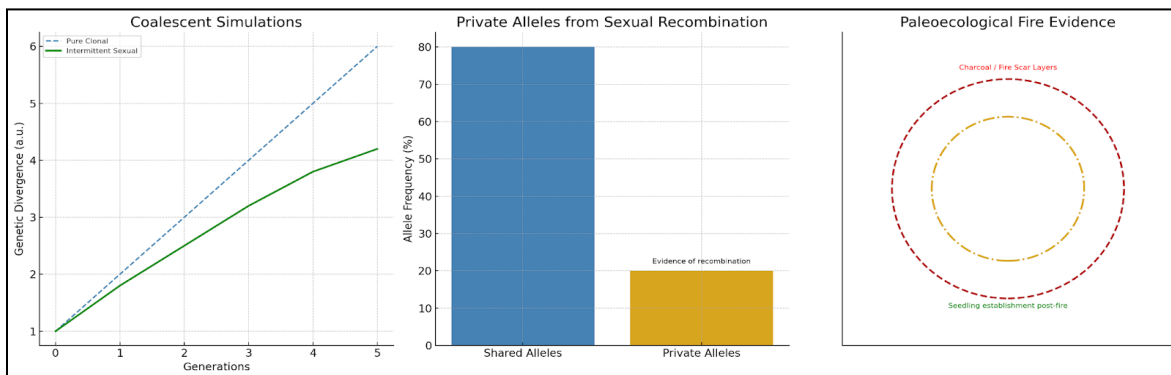
The inference that Pando derives from a single seedling founding event followed by continuous clonal expansion is central to interpreting somatic phylogenies. If Pando's present genotypic pattern is partly due to repeated sexual recruitment, introgression from nearby clones, or merging of multiple genets over time, then phylogenetic branch lengths do not equate to a single clone age.

The Pando study used microsatellite data and PCA clustering to delineate the clone, but low levels of historical sexual recruitment followed by local clonal expansion can leave subtle signatures that masquerade as long-term somatic accumulation.



(Figure 7) *Pando* is often described as a single clone that sprouted from one seed and expanded only through vegetative growth. But this figure highlights why the story may be more complex. Sexual recruitment, introgression from nearby clones, or the merging of multiple genets could all have contributed to *Pando*'s genetic makeup. If so, phylogenetic branch lengths don't map neatly onto the age of a single clone. Microsatellite and PCA clustering can miss these subtle histories, making long-term somatic accumulation look older than it really is.

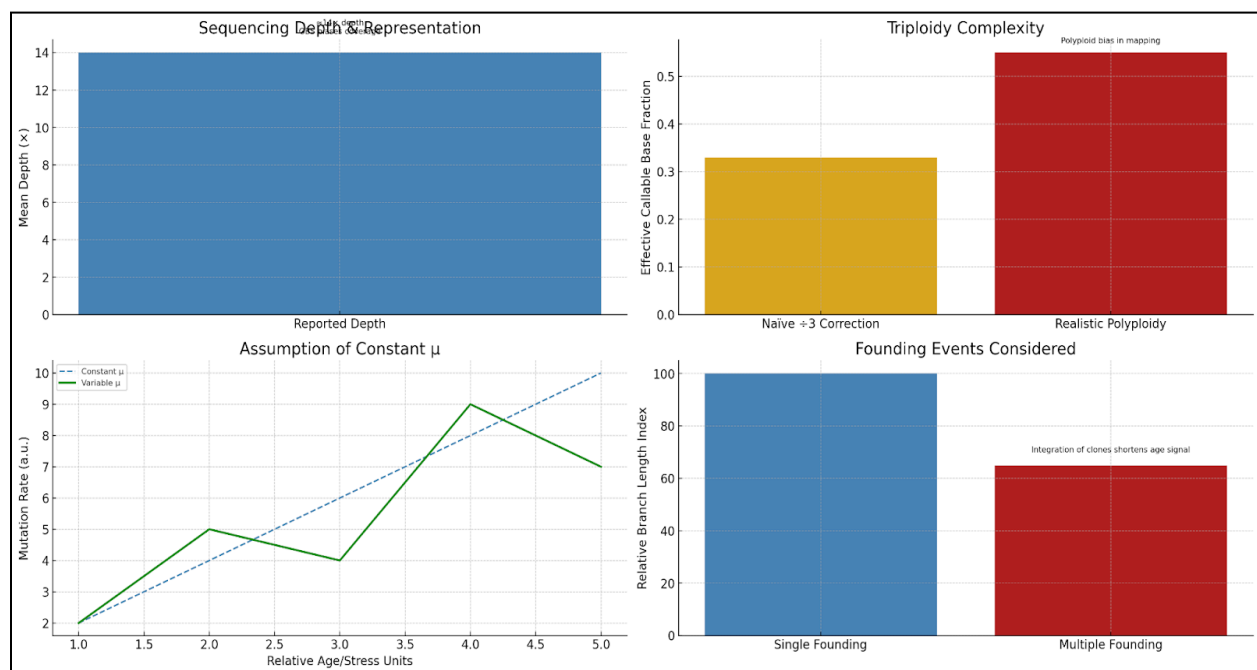
My Recommendation: Use coalescent simulations under models with intermittent sexual recruitment, and seek independent evidence (e.g., presence of private alleles consistent with sexual recombination, and paleoecological data showing fire regimes that promote seedling establishment) from known dates of local fires.



(Figure 8) **Left – Coalescent Simulations:** Simulations comparing pure clonal accumulation (blue dashed) to intermittent sexual recruitment (green) show that sexual inputs reduce overall genetic divergence. If even occasional recombination occurs, divergence accumulates more slowly than expected under strict clonality, meaning branch lengths cannot be read as clone age directly. **Middle – Private Alleles from Sexual Recombination:** While most alleles are shared across ramets (~80%), a measurable minority (~20%) are private alleles consistent with recombination. These private alleles serve as genomic fingerprints of past sexual recruitment, revealing contributions beyond clonal mutation alone. **Right – Paleoecological Fire Evidence:** Layers of charcoal and fire scars (red) coincide with ecological windows where seedling establishment (gold inner ring) could occur. Fire regimes likely reset local conditions, providing rare but important opportunities for sexually derived seedlings to establish within the clone, introducing genetic diversity.

Limitations in the Current Genomic Age Estimate

1. **Sequencing depth & representation:** Mean depth ($\sim 14\times$) and reduced-representation GBS methods can bias variant detection toward higher-confidence, higher-coverage regions, disproportionately excluding certain mutation classes.
2. **Triploidy complexity:** Single-value corrections may under- or over-estimate callable bases, affecting per-year scaling.
3. **Assumption of constant μ :** Somatic mutation rates may vary with tree age, environmental stress, and tissue type; using a single point estimate without sensitivity analysis risks overconfidence in a narrow age range.
4. **No consideration of multiple founding events:** If Pando arose from convergent integration of multiple clones, phylogenetic branch lengths would not directly equal clone age.



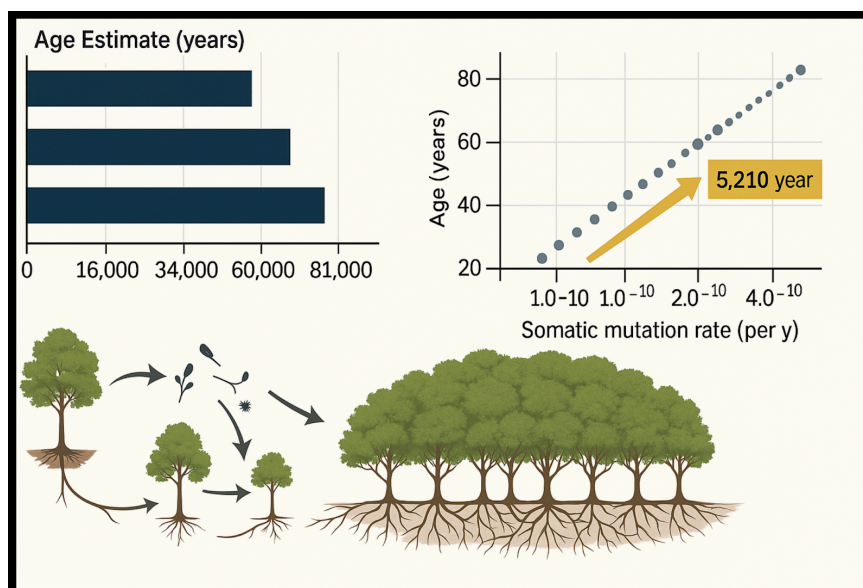
(Figure 9) Top left: Sequencing depth & representation — mean $\approx 14\times$ depth, GBS biases variant detection. Top right: Triploidy complexity — naïve $\div 3$ correction vs realistic polyploid mapping effects. Bottom left: Assumption of constant μ — mutation rates vary with age, stress, and tissue type. Bottom right: Multiple founding events — phylogenetic branch lengths may not equal clone age if several genets merged.

Conclusion

Recalculation of Pineau et al.'s genomic age estimates for Pando using the literature-supported upper 95% CI somatic mutation rate from Hofmeister et al. yields a conservative minimum age of ~5.2 kyr under their own model framework. This falls within the mid-Holocene timeframe which just so happens to fit the Biblical timeline. This rate is compatible even without alternative growth histories involving multiple origins and subsequent root fusions.

These findings highlight the sensitivity of clonal age estimates to μ selection, the need for triploidy-aware modeling, and the importance of testing distributed-origin scenarios alongside traditional single-founder models.

The Pando genomic study advances methods for mapping somatic variation across large clonal organisms, and its spatial analyses (isolation by distance, tissue differences) are valuable. However, the common headline age estimates of (16–81 kyr) depend on a list of calibrations using evolutionary assumptions, turning the observed mutation rate into a phylogenetic rate including adjusting other parameters to obtain an older age — transfer of an external somatic rate, missing mutations ignored, use of reduced-representation sequencing at low depth, and simplified treatment of triploidy and selection — that collectively inflate confidence in far-back age inference. The evidence presented here shows that Pando can be explained within the Biblical creation timeframe of Noah's flood using the observable mutation rate from the Rozenn Pineau et al 2024 study and also the rapid growth and expansion of Pando from clones. Both scenarios work and give us an explanation for this giant tree system



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