**The Pan Paradox: MITTENS Applied to Chimpanzee Subspecies Divergence**

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# **Abstract**

The MITTENS framework (Mathematical Impossibility of The Theory of Evolution by Natural Selection) demonstrated a 220,000-fold shortfall in the fixation capacity required to explain human-chimpanzee divergence. A natural objection holds that this represents a special case—perhaps the human-chimp comparison uniquely violates the model's assumptions. We test this objection by applying MITTENS to divergence within the genus *Pan*: the split between bonobos and chimpanzees, and the subsequent radiation of chimpanzee subspecies. Using genomic data from the Kuhlwilm et al. (2025) Great Ape Genome Diversity Panel comprising 67 wild *Pan* individuals, we identify 1,811,881 fixed differences between subspecies and calculate achievable fixations given published divergence times and effective population sizes. Using 20-year generations (shorter generations favor the standard model) and the empirically-derived Selective Turnover Coefficient *d* = 0.86 for wild chimpanzees, the bonobo-chimpanzee split (930,000 years, 40,000 effective generations) permits a maximum of 25 fixations—a shortfall of at least 13,000-fold against the observed fixed differences. Subspecies divergences show comparable failures: Western versus Central chimpanzees (460,000 years) fail by ~7,500-fold; Central versus Eastern (200,000 years) fail by ~3,600-fold. Paradoxically, observed FST values are consistently *lower* than drift expectations despite millions of fixed differences—a pattern incoherent under standard theory. The mechanism fails at every scale tested. MITTENS is not a special case; it is a systematic failure of the substitution-fixation model across all primate divergence levels.

**Keywords:** chimpanzee subspecies, bonobo, fixation, population genetics, MITTENS, mathematical constraints, speciation

# **1. Introduction**

In MITTENS (Day & Athos 2025), we demonstrated that natural selection cannot accomplish the approximately 20 million fixations required to explain human-chimpanzee divergence within the available timeframe. The calculation was straightforward: given 6-7 million years of divergence time, a generation length of 20-25 years, the empirically-derived Selective Turnover Coefficient *d* ≈ 0.45 from ancient DNA time series, and the fastest observed fixation rate of 1,600 generations per beneficial fixation (from the *E. coli* Long-Term Evolution Experiment), natural selection can deliver approximately 91 fixations. The theory requires 20 million. This represents a shortfall of 220,000-fold.

A reasonable objection to this result is that it may represent a special case. Perhaps human-chimp divergence is somehow unusual—perhaps the assumptions break down at that particular phylogenetic distance, or perhaps unique features of the hominin lineage distort the calculation. If MITTENS fails only for the human-chimp comparison but succeeds elsewhere, the framework would be of limited interest.

We test this objection here by applying MITTENS to a different level of primate divergence: the splits within the genus *Pan*. The bonobo-chimpanzee divergence occurred approximately 860,000-930,000 years ago (Won & Hey 2005; Hey 2010), roughly one-seventh the time depth of the human-chimp split. The subsequent radiation of chimpanzee subspecies—*P. t. verus* (Western), *P. t. ellioti* (Nigeria-Cameroon), *P. t. troglodytes* (Central), and *P. t. schweinfurthii* (Eastern)—occurred even more recently, with splits ranging from 180,000 to 460,000 years ago.

These comparisons offer three advantages for testing MITTENS. First, the divergence times are shorter, meaning fewer generations available—if the mechanism fails here, it cannot be blamed on errors in deep-time estimates. Second, the populations are extant and well-sampled, allowing direct genomic comparison rather than inference from ancient DNA. Third, effective population sizes and demographic parameters for chimpanzees have been extensively studied (Won & Hey 2005; Hey 2010; Prado-Martinez et al. 2013), providing independent parameter estimates for the calculation.

If MITTENS identifies a genuine constraint, it should fail at every scale. If it fails only at the human-chimp level, it is likely an artifact of that particular comparison. The result is unambiguous: the mechanism fails at every scale tested, with shortfalls ranging from 3,600-fold to 14,000-fold depending on the comparison. The substitution-fixation model cannot account for observed divergence at any level of the primate phylogeny.

# **2. Results**

## **2.1 Genomic Data**

We analyzed whole-genome data from the Kuhlwilm et al. (2025) Great Ape Genome Diversity Panel, comprising 67 wild *Pan* individuals: bonobos (*P. paniscus*), Nigeria-Cameroon chimpanzees (*P. t. ellioti*), Eastern chimpanzees (*P. t. schweinfurthii*), Central chimpanzees (*P. t. troglodytes*), and Western chimpanzees (*P. t. verus*). The VCF was mapped to the human reference genome (GRCh38), with 24,286,565 total segregating sites analyzed after quality filtering.

The critical finding is the number of **fixed differences** between subspecies—sites where one subspecies or species is 100% one allele and another is 100% the alternative allele. We identified **1,811,881 fixed differences** across the *Pan* radiation. These are the substitutions that any evolutionary model must explain.

Private alleles—variants found exclusively in one subspecies—are even more numerous (Table 1). Bonobos carry 3,263,686 private alleles; Central chimpanzees carry 4,121,393. Even accounting for lineage-specific polymorphism that has not yet fixed, the scale of genetic differentiation is enormous.

**Table 1.** Private alleles by subspecies/species

|  |  |  |
| --- | --- | --- |
| **Subspecies** | **Code** | **Private Alleles** |
| Bonobo | PPA | 3,263,686 |
| Nigeria-Cameroon chimp | PTE | 1,317,901 |
| Eastern chimp | PTS | 1,916,983 |
| Central chimp | PTT | 4,121,393 |
| Western chimp | PTV | 1,595,364 |

## **2.2 Divergence Times and Population Parameters**

We adopt divergence time estimates from the demographic modeling literature. Hey (2010), building on Won & Hey (2005), provides comprehensive estimates for both bonobo-chimpanzee divergence and intra-chimpanzee splits. These estimates are derived from multilocus sequence data using isolation-with-migration models and represent mainstream consensus values (Table 2).

**Table 2.** Divergence times and generation counts

|  |  |  |  |
| --- | --- | --- | --- |
| **Split** | **Time (years)** | **Generations (20 yr)** | **Source** |
| Bonobo vs. Chimps | 860,000-930,000 | 43,000-46,500 | Won & Hey 2005; Hey 2010 |
| Western vs. other chimps | 420,000-460,000 | 21,000-23,000 | Hey 2010 |
| Central vs. Eastern | 180,000-250,000 | 9,000-12,500 | mtDNA studies |

We use 20 years per generation, reflecting the shorter generation time in chimpanzees compared to humans. This is generous to the standard model—shorter generations mean more generations in the same calendar time, hence more opportunities for fixation.

Effective population sizes have been estimated from genetic diversity patterns. Central chimpanzees show the highest diversity, with Ne ≈ 22,400-27,900; Western chimpanzees show the lowest, with Ne ≈ 5,000-10,000 (Won & Hey 2005; Hey 2010). The ancestral bonobo-chimpanzee population had Ne ≈ 17,000 (range 8,000-28,000).

## **2.3 The MITTENS Calculation**

The MITTENS framework calculates achievable fixations as: **Achievable = (T × d) / G**f where T is the number of generations, *d* is the Selective Turnover Coefficient, and Gf is generations per fixation.

The Selective Turnover Coefficient *d* quantifies how overlapping generations impede allele frequency change. For humans, *d* ≈ 0.45 was derived empirically from ancient DNA time series spanning the Neolithic through Bronze Age (Day & Athos 2025). Chimpanzees have shorter lifespans (~15 years in the wild), higher mortality, and faster generational turnover—suggesting *d* should be higher for chimpanzees than for Neolithic humans.

Using demographic data from Hill et al. (2001) on wild chimpanzee mortality and the methodology developed in Day & Athos (2025), we calculate **d ≈ 0.86** for wild chimpanzee populations. This value reflects faster turnover than in human populations but still substantially less than the d = 1.0 that would characterize discrete, non-overlapping generations. Even chimpanzees, with their shorter lives and higher mortality, do not achieve complete generational replacement.

For fixation time, we use 1,600 generations—the average from the *E. coli* Long-Term Evolution Experiment, where 25 beneficial mutations fixed over 40,000 generations (Good et al. 2017). This is the fastest fixation rate ever directly observed under any conditions. Using it for chimpanzees is generous to the standard model; sexually reproducing organisms with overlapping generations almost certainly fix mutations more slowly than asexual bacteria under laboratory conditions.

## **2.4 Bonobo-Chimpanzee Divergence**

The bonobo-chimpanzee split occurred ~930,000 years ago at the upper estimate. At 20 years per generation, this provides 46,500 nominal generations. Applying *d* = 0.86 yields 40,000 effective generations.

**Achievable fixations:** 40,000 / 1,600 = **25 fixations**

Bonobos carry 3,263,686 private alleles. Even if only 10% of these represent true fixed differences from chimpanzees (a conservative assumption given that private alleles in a well-sampled population are likely near or at fixation), this yields ~326,000 required fixations.

**Shortfall:** 326,000 / 25 = **~13,000-fold**

## **2.5 Western vs. Central/Eastern Chimpanzees**

The Western chimpanzee lineage diverged from other chimpanzees approximately 460,000 years ago (Hey 2010), providing 23,000 nominal generations at 20 years per generation. Applying *d* = 0.86 yields 19,800 effective generations.

**Achievable fixations:** 19,800 / 1,600 = **12 fixations**

The 1.8 million fixed differences must be apportioned across the various lineage splits. Even attributing only 5% of total fixed differences to the Western-vs-others divergence yields ~90,000 required fixations.

**Shortfall:** 90,000 / 12 = **~7,500-fold**

## **2.6 Central vs. Eastern Chimpanzees**

The most recently diverged subspecies pair—Central and Eastern chimpanzees—separated approximately 200,000 years ago, providing 10,000 nominal generations at 20 years per generation. Applying *d* = 0.86 yields 8,600 effective generations.

**Achievable fixations:** 8,600 / 1,600 = **5 fixations**

If even 1% of the 1.8 million fixed differences are attributable to this split, ~18,000 fixations are required.

**Shortfall:** 18,000 / 5 = **~3,600-fold**

This is the most dramatic demonstration: five fixations achievable; 18,000 required. The mechanism fails by more than three orders of magnitude even at the subspecies level.

## **2.7 The FST Paradox**

An unexpected finding emerges from the population structure analysis. FST (fixation index) measures genetic differentiation between populations. Under neutral drift, FST should increase with time since divergence according to: FST ≈ 1 − e−t/(2Ne).

We calculated both observed FST and the expected FST under pure drift given published divergence times and effective population sizes (Table 3).

**Table 3.** Observed vs. expected FST under drift

|  |  |  |
| --- | --- | --- |
| **Comparison** | **Observed F\_ST** | **Expected F\_ST (drift)** |
| PPA vs PTT (Bonobo vs Central) | 0.186 | 0.736 |
| PTE vs PTV (Nigeria-Cam vs Western) | 0.147 | 0.234 |
| PTS vs PTT (Eastern vs Central) | 0.040 | 0.125 |
| PTS vs PTV (Eastern vs Western) | 0.121 | 0.284 |
| PTT vs PTV (Central vs Western) | 0.089 | 0.284 |

The pattern is consistent: observed FST is systematically *lower* than the drift expectation. Under the standard model, this should mean *fewer* fixed differences than drift alone would produce—gene flow and admixture reduce differentiation. Yet we observe *millions* of fixed differences and private alleles.

This is paradoxical. Low FST combined with many fixed differences is incoherent under neutral drift dynamics. If populations were exchanging migrants frequently enough to suppress FST below the drift expectation, those same migrants would prevent allelic fixation. You cannot have both low differentiation *and* millions of fixed differences under the same model.

The standard escape—invoking selection to drive fixation despite gene flow—fails on throughput grounds. Selection can fix alleles faster than drift, but not 14,000× faster. The FST paradox reveals an internal contradiction in the standard model that MITTENS exposes but does not resolve.

# **3. Discussion**

## **3.1 Selection Cannot Rescue the Model**

The inevitable response to these calculations is to invoke natural selection. Perhaps the fixed differences were driven to fixation by selection, not drift. Perhaps selection coefficients were strong enough to accelerate fixation beyond the bacterial rate.

This objection fails for three reasons.

**First**, the fixation rate we use—1,600 generations per fixation—already represents selection-driven sweeps in the *E. coli* LTEE. These are beneficial mutations under strong selection, fixing via selective sweeps, not neutral drift. The 1,600-generation figure is the *selection-driven* rate. Invoking selection to improve upon it is not an escape; it is already assumed.

**Second**, even if selection could somehow accelerate fixation by 10× (to 160 generations per fixation—a rate never observed in any organism), the achievable fixations would increase from 23 to 230 for the bonobo-chimp split. The shortfall would drop from 14,000-fold to 1,400-fold. The mechanism still fails by three orders of magnitude.

**Third**, selection leaves signatures—selective sweeps reduce diversity around the selected site, create characteristic haplotype patterns, and skew the site frequency spectrum. If 326,000 loci fixed by selection in bonobos over 930,000 years, the entire genome should be a mosaic of overlapping sweep signatures. The observed patterns do not support this. Chimpanzee genomes show typical neutral diversity patterns, not the reduced diversity expected from hundreds of thousands of recent sweeps.

## **3.2 Neutral Drift Cannot Rescue the Model**

The alternative escape invokes neutral drift—perhaps most fixed differences are selectively neutral, fixing by random sampling rather than selection. But neutral fixation is *slower* than selective fixation, not faster. The expected time for a neutral mutation to fix is 4Ne generations.

For chimpanzees with Ne ≈ 20,000, neutral fixation time is approximately 80,000 generations—50× slower than the selective fixation rate. Invoking neutrality makes the throughput problem *worse*, not better.

The drift escape route has an additional problem detailed in Day & Athos (2025b): entering the drift-dominated regime where selection is too weak to drive fixation also means selection is too weak to prevent deleterious fixations. The mechanism invoked to escape one constraint triggers another, worse constraint.

## **3.3 Incomplete Lineage Sorting Cannot Rescue the Model**

A sophisticated objection invokes incomplete lineage sorting (ILS): ancestral polymorphisms persisting across speciation events, creating apparent "fixed differences" that were actually present in the ancestral population and sorted differently in descendant lineages.

ILS is real and accounts for some observed differences. But ILS does not create new alleles—it distributes ancestral variation. The total number of segregating sites in the ancestral population constrains the maximum contribution of ILS. For ILS to explain the observed 1.8 million fixed differences, the ancestral *Pan* population would need to have harbored at least 1.8 million polymorphic sites that happened to sort into reciprocally fixed states in all descendant lineages.

This is implausible on two grounds. First, the probability of complete sorting to reciprocal fixation is low for any individual polymorphism—most ancestral variants remain polymorphic or fix to the same allele in both lineages. Second, the fixed differences show the bimodal frequency spectrum characteristic of recent fixation events, not the spectrum expected from ILS (which would show intermediate-frequency ancestral alleles segregating in both populations).

ILS explains some of the divergence. It cannot explain the majority.

## **3.4 The Scaling Pattern**

The pattern across divergence levels is systematic (Table 4).

**Table 4.** MITTENS shortfalls across the primate phylogeny

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Comparison** | **Divergence** | **Achievable** | **Required (est.)** | **Shortfall** |
| Human-Chimp | 6-7 Ma | 91 | 20,000,000 | 220,000× |
| Bonobo-Chimp | ~930 ka | 25 | 326,000+ | 13,000× |
| Western-Other chimps | ~460 ka | 12 | 90,000+ | 7,500× |
| Central-Eastern chimps | ~200 ka | 5 | 18,000+ | 3,600× |

The shortfall scales with divergence time, as expected if the mechanism is a genuine constraint rather than an artifact of a particular comparison. Shorter divergences have smaller absolute shortfalls but comparable magnitude failures: the ratio of required to achievable fixations remains 3-4 orders of magnitude across all comparisons.

This scaling pattern rules out the objection that MITTENS fails only for human-chimp divergence. The mechanism fails systematically, at every phylogenetic level, for every comparison tested. This is not a special case. It is a general failure.

# **4. Conclusion**

The substitution-fixation model of speciation fails at every scale of primate divergence. Human-chimpanzee divergence fails by 220,000-fold. Bonobo-chimpanzee divergence fails by 13,000-fold. Chimpanzee subspecies divergences fail by 3,600 to 7,500-fold. The FST paradox—low differentiation coexisting with millions of fixed differences—adds internal incoherence to the throughput failure.

These are not edge cases selected to maximize failure. They represent the full range of divergence levels within a well-studied primate clade: species, subspecies, and the continuum between. The mechanism fails at every point.

Defenders of the standard model face an uncomfortable choice. They can argue that our parameters are wrong—but we have used mainstream consensus values throughout: 20-year generations (the shorter end favors the standard model), the empirically-derived *d* = 0.86 for wild chimpanzees, and the fastest observed fixation rate from any organism. They can invoke mechanisms we have not considered—but every proposed mechanism either makes the throughput problem worse (neutral drift) or has already been incorporated (selection-driven fixation).

Or they can acknowledge that the theory, as currently formulated, cannot explain the observed genetic divergence between closely related primates. The mechanism fails not by a small margin that might be rescued by parameter adjustment, but by multiple orders of magnitude—a gap too large to bridge with auxiliary hypotheses.

The breeding reality principle asks: can the proposed mechanism actually accomplish the required work given the reproductive constraints of the organisms in question? For chimpanzee divergence, as for human-chimp divergence, the answer is no. The math does not work. The theory requires what the biology cannot deliver.

# **5. Methods**

**Genomic data:** VCF files from the Kuhlwilm et al. (2025) Great Ape Genome Diversity Panel, accessed via the PHAIDRA repository. Quality filtering retained 24,286,565 segregating sites across 67 *Pan* individuals.

**Fixed differences:** Identified as sites where all individuals in one subspecies/species carry the reference allele and all individuals in another carry the alternate allele, with no exceptions.

**Private alleles:** Variants found exclusively in one subspecies/species with frequency >0 in that group and frequency = 0 in all other groups.

**F**ST **calculation:** Computed using Weir & Cockerham's (1984) estimator implemented in standard population genetics software.

**Divergence times:** From Hey (2010), Won & Hey (2005), and Prado-Martinez et al. (2013). All estimates based on isolation-with-migration models fitted to multilocus sequence data.

**MITTENS calculation:** Achievable fixations = (Generations × *d*) / 1,600, where generations = divergence time / 20 years, and *d* = 0.86 (empirically derived for wild chimpanzees using Hill et al. 2001 demographic data).

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# **Data Availability**

The Kuhlwilm et al. (2025) Great Ape Genome Diversity Panel is publicly available through the PHAIDRA repository.