HORIZONTAL GENE TRANSFER AS A DRIVER OF ADAPTIVE EVOLUTION IN EXTREMOPHILES: A GENE-CLASS-STRATIFIED REAPPRAISAL OF THE TREE OF LIFE

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Abstract: The image of a single branching tree of life, inherited from Darwin and formalized by molecular phylogenetics, sits uneasily with what genomics now shows about prokaryotes: that genes move sideways across lineages so pervasively that no single gene tree reliably represents an organism's whole history. This article argues that the tree-versus-web dispute has been miscast as a choice between two incompatible topologies and that both camps are partly right, because the answer depends on which genes one asks about. I develop a gene-class-stratified reconciliation framework that models a genome as a vertically inherited informational core — the ribosomal and transcription-translation machinery that remains stubbornly tree-like — embedded in a horizontally acquired operational and stress-response shell that is genuinely network-like. On this account the tree of life is neither a tree nor a web but a tree of cores threaded through a network of shells, and the balance between the two is not fixed but varies across taxa and environments. From the framework I advance the falsifiable Extremity–Reticulation hypothesis: the adaptive contribution of the horizontal shell, quantified by a Reticulation Index that partitions a genome's adaptive genes by functional class and provenance, scales with environmental extremity, so that extremophiles occupy the maximally reticulate end of a continuum. Heuristic scoring across an extremity gradient shows the informational core holding near a Reticulation Index of 0.05–0.08 regardless of environment, while the stress-resistance shell climbs from roughly 0.20 in mesophiles to near 0.60 in polyextremophiles. Extremophiles, in this reading, are not marginal curiosities but the clearest demonstration that adaptive evolution in prokaryotes is driven substantially by acquisition rather than only by mutation, and the tree of life must be reconceived accordingly — as a statement about the informational core alone, explicitly qualified for everything else.

Keywords: *horizontal gene transfer, extremophiles, adaptive evolution, tree of life, phylogenomics, archaea, reticulate evolution.*

INTRODUCTION

The tree of life is one of the most successful images in the history of biology, and it is also, for a large part of the living world, misleading. For animals and plants it works: lineages branch, diverge, and pass their genes vertically from parent to offspring, so that a genealogy really is a tree. For prokaryotes — the bacteria and archaea that constitute most of life's diversity and nearly all of its metabolic range — the picture is different, because genes move not only down the generations but sideways between contemporaries, across species and even across the deepest

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domain boundaries. Horizontal gene transfer, once treated as a curiosity of antibiotic resistance, is now understood as a primary force in prokaryotic evolution, capable of importing whole functional modules in a single step and thereby short-circuiting the slow accumulation of point mutations (Arnold, Huang & Hanage, 2021; Tokuda & Shintani, 2024). The question this raises is not whether the tree is wrong but how wrong, and for which organisms, and about which genes.

Extremophiles bring the question to its sharpest point. Organisms that thrive in boiling acid, saturated brine, ionizing radiation or perpetual cold face selective pressures so severe that the standard tempo of adaptation by mutation is often too slow to keep pace, and for them the ability to borrow a ready-made solution from a neighbor is not a convenience but a survival strategy. Acidophilic archaea acquire metal-resistance and energy-metabolism genes by transfer (Qiu, Tao, Li, Liu, Liu, Nawaz, Wang & Ma, 2025); Antarctic microbial communities are shaped by the horizontal spread of cold-adaptation genes (Manrique-de-la-Cuba, López-Rodríguez, Abades & Trefault, 2025); radiation-resistant lineages assemble their defenses from a patchwork of acquired and evolved components (Bruckbauer & Cox, 2021); and the mechanisms of uptake themselves — natural transformation, conjugation, transduction, gene transfer agents — are demonstrably active in the very environments where transfer would seem hardest (Averhoff, Kirchner, Pfefferle & Yaman, 2021). If horizontal transfer is a general driver of prokaryotic adaptation, extremophiles are where its signal should be strongest, and therefore where the tree of life should break down most visibly.

The central research question of this article is how to reconcile the undeniable reality of pervasive horizontal transfer with the equally undeniable fact that a coherent, tree-like signal survives in the deepest phylogenies — the ribosomal RNA genes on which the three-domain classification rests, and the informational machinery that traces back to a last universal common ancestor (Forterre, 2024; Moody et al., 2024). From this I derive three hypotheses. The first is that the tree-versus-web dichotomy is a false one, because tree-like and network-like signals coexist within every prokaryotic genome, partitioned by gene function rather than mixed uniformly. The second is that the balance between the two is not a constant of prokaryotic life but a variable that responds to ecology, rising toward the network pole as environmental pressure increases. The third follows: that extremophiles occupy the reticulate extreme of this continuum, so that their genomes are the natural test case for measuring how far adaptive evolution is driven by acquisition rather than by mutation.

The original contribution of this article is a gene-class-stratified reconciliation framework together with the falsifiable Extremity–Reticulation hypothesis it generates. The framework partitions a genome into a vertically inherited informational core and a horizontally acquired operational and stress-response shell, and it defines a Reticulation Index that measures, separately for each functional class, the fraction of a lineage's adaptive genetic change attributable to transfer rather than to mutation. The hypothesis is that this index, computed over the adaptive genome, scales with environmental extremity. Unlike prior treatments, which have argued about whether the history of life is fundamentally a tree or fundamentally a web, the framework treats the topology as gene-class-dependent and the reticulation as ecology-dependent, and it turns the old qualitative dispute into a quantitative, testable statement. I should be candid at the outset that the index values I report are heuristic estimates drawn from the recent literature rather than a single uniform re-analysis; their purpose is to give the argument a scorable, disputable form, not to deliver a definitive census of any genome.

A clarification of scope will prevent misreading. I am not claiming that the tree of life is worthless, nor that vertical inheritance is an illusion. The informational core really does descend as a tree, and the framework preserves it as such; that is the sense in which the classical picture survives. What I am claiming is narrower and, I think, more useful: that the tree describes one

stratum of the genome and badly misdescribes another, and that treating the whole organism as if it followed the core's genealogy produces exactly the errors that have fueled the tree-versus-web wars for two decades. The remainder of the article develops the framework, applies it to extremophiles, and draws out what it implies for how the tree of life should be drawn and taught.

The article proceeds through a combined literature review and methodology section that reconstructs the relevant research strands and defines the framework and its index; a results section that presents the Reticulation Index across an extremity gradient without interpretation; three analytical sections treating the mechanistic basis of extremophile transfer, the gene-class partition that reconciles tree and web, and the extremity–reticulation coupling with its consequences for the tree of life; and a conclusion that answers the hypotheses, restates the contribution, and marks the framework's limits.

LITERATURE REVIEW AND METHODOLOGY

Literature Review

The first strand establishes horizontal transfer as a genuine driver of adaptation rather than a background nuisance. The comprehensive synthesis by Arnold, Huang and Hanage (2021) makes the case that transfer supplies bacteria with adaptive novelty faster than mutation can, precisely because it moves pre-tested functional modules rather than single nucleotides. Tokuda and Shintani (2024) trace how mobile genetic elements — plasmids, transposons, integrative elements — mechanize this movement, and Dionisio, Zilhão and Gama (2019) detail the interactions among those elements that determine what actually crosses. The adaptive payoff is measurable: McLeod and Gandon (2025) show formally that transfer, by breaking the linkage that slows selection, can accelerate the speed of adaptation, while Ram and Hadany (2019) analyze how transfer interacts with stress-induced mutagenesis to shape evolvability under pressure. Hall, Whelan, McInerney, Ou and Domingo-Sananes (2020) add the important caveat that transfer is a source of conflict as well as cooperation, so that not every acquired gene is adaptive — a caveat the framework must respect by scoring adaptive contribution specifically rather than raw transfer frequency.

The second strand concerns archaea and extremophiles, where transfer meets its most demanding conditions and where this article's empirical weight lies. Gophna and Altman-Price (2022) review horizontal transfer in archaea from mechanism to genome evolution, establishing that the domain most associated with extreme environments is also thoroughly reticulate. Averhoff and colleagues (2021) document natural transformation operating in Gram-negative bacteria that thrive in extremes, showing that the uptake machinery functions where one might expect it to fail. Case studies accumulate across extremity types: acidophilic archaea gaining adaptive functions by transfer (Qiu et al., 2025), Antarctic communities shaped by horizontal cold-adaptation genes (Manrique-de-la-Cuba et al., 2025), radiation-resistant lineages assembling defenses through experimental and natural evolution (Bruckbauer & Cox, 2021), and genomic islands carrying environmental-adaptation and resistance cassettes as discrete, mobile units (Li & Wang, 2021). This journal has contributed directly to the extremophile-transfer literature with an analysis of horizontal transfer in extremophilic archaea exposed to simulated extraterrestrial regolith chemistry, extending the theme to astrobiological settings (Subotić, 2025). Together these studies make extremophiles the strongest available demonstration that acquisition, not only mutation, drives adaptation.

The third strand is the tree-of-life debate itself, which the framework aims to reconcile rather than adjudicate. At one pole sits the recovery of a deep vertical signal: Forterre (2024) reconstructs the last universal common ancestor of ribosome-encoding organisms, and Moody and

colleagues (2024) date and characterize that ancestor, both efforts resting on the informational genes that resist transfer. At the other pole sits the evidence for reticulation reaching into the deepest branches, including interdomain transfer between bacteria and archaea (Medeiros, Canato, Braz & Paulino, 2024) and the mosaic ancestry of major eukaryotic innovations (Urquhart, Gluck-Thaler & Vogan, 2024). Colnaghi, Lane and Pomiankowski (2020) offer a particularly relevant bridge, modeling how early eukaryotes transitioned from a transfer-dominated to a vertically dominated regime as their genomes expanded — a demonstration that the tree-versus-web balance is itself an evolvable, historically contingent quantity rather than a fixed property. The phylogenomics of Asgard archaea, the closest prokaryotic relatives of eukaryotes, reveals exactly the blend of vertical and horizontal signal the framework predicts (Manzano-Morales & Gabaldón, 2026).

The fourth strand is methodological, because any quantitative claim about reticulation depends on how transfer is detected and measured. The field has moved beyond simple compositional anomaly detection toward phylogenetic and phylogenomic inference: Avni and Snir (2020) develop a phylogenomic approach for quantifying transfer, Yuan, Lu, Li, Nielsen and Kerkhoven (2023) provide automated phylogenetic detection tools, and Mishra and Lercher (2025) refine inference from gene presence–absence patterns. These methods matter for the framework because they make the Reticulation Index computable in principle rather than merely conceptual, and because they expose the uncertainties — false positives from rate variation, false negatives from ancient transfers — that any honest index must acknowledge. Gene transfer agents, virus-like particles that package and disseminate host DNA, add a further mechanism whose evolution is now being reconstructed in detail (Esterman, Wolf, Kogay, Koonin & Zhaxybayeva, 2021; Kogay & Zhaxybayeva, 2024), and the microbiome literature shows the same processes operating in host-associated and gut communities (Moura de Sousa, Lourenço & Gordo, 2023; Peng & Fu, 2025). The uneven distribution of transferred genes across genomes, documented recently by Liu, Wang, Cheewangkoon and Zhao (2025) and within and between species by Smith and Andam (2021), is precisely the non-uniformity the gene-class partition is meant to explain.

What the literature does not yet offer is a single structure that says how the vertical and horizontal signals combine within a genome and how their balance shifts with ecology. The methodology below proposes one.

Research Methodology

The study is conceptual and comparative. It constructs a framework and applies it to an environmental-extremity gradient, drawing all parameters from peer-reviewed work published from 2019 onward. The framework rests on two commitments: a partition of the genome by functional class, and an index of reticulation defined separately within each class.

The partition divides protein-coding genes into three functional strata. The informational core comprises the genes of the transcription–translation apparatus — ribosomal proteins and RNAs, aminoacyl-tRNA synthetases, core RNA polymerase — which are densely interacting, resistant to transfer because a foreign copy rarely integrates into the existing machinery, and therefore tree-like in their inheritance (Forterre, 2024). The operational shell comprises metabolic and biosynthetic genes, which are more modular, more often transferred, and more readily adaptive when acquired (Tokuda & Shintani, 2024). The stress-response shell comprises the genes most directly implicated in surviving extreme conditions — metal and antibiotic resistance, osmotic and thermal protection, radiation repair — which are frequently organized into mobile genomic islands and are the prime currency of adaptive transfer (Li & Wang, 2021; Bruckbauer & Cox,

2021). The partition is functional rather than sharp, and genes can be reassigned as understanding improves, but the three strata capture a real and repeatedly documented gradient in transferability.

The Reticulation Index is defined, within each stratum, as the fraction of a lineage's adaptive genetic change attributable to horizontal acquisition rather than to vertical descent with mutation. An index near 0 means the stratum evolves essentially as a tree; an index near 1 means its recent adaptive history is essentially a network of acquisitions. Crucially, the index scores adaptive contribution, not raw transfer frequency, so that acquired genes that are neutral or deleterious — the conflict side of transfer emphasized by Hall and colleagues (2020) — do not inflate it. From the stratum-level indices I compute a genome-wide adaptive Reticulation Index as their function, weighted by each stratum's contribution to the lineage's adaptation in its environment.

The comparison runs across an environmental-extremity gradient with three reference points: a mesophile baseline, a moderate extremophile, and a hyper- or polyextremophile. For each, I assign stratum-level index values from the case-study literature, using a rubric in which a value near the high end of a stratum's range is assigned when studies directly document extensive adaptive transfer in that stratum at that extremity level, and a value near the low end when transfer is documented but not shown to be adaptively dominant. I assign the scores myself, from the cited literature, and I regard this single-author scoring as the method's chief weakness, to which I return in the limitations. A sensitivity check varies the scores within plausible bands and confirms that the qualitative result — the divergence between a flat informational core and a steeply rising stress shell — is stable. The numbers are ordered estimates meant to structure disagreement, not measurements of any specific genome's reticulation to two decimals.

RESEARCH RESULTS

Applying the gene-class-stratified framework across the extremity gradient produces the Reticulation Index values collected in Table 1. The results organize into three blocks: the behavior of the informational core, the behavior of the two shells, and the genome-wide trend that couples reticulation to extremity.

The informational core is nearly flat across the gradient. It scores a Reticulation Index of about 0.05 in mesophiles, 0.06 in moderate extremophiles, and 0.08 in hyper-extremophiles — low everywhere and only weakly responsive to environment. This is the quantitative signature of tree-like inheritance, and it holds even in the most reticulate organisms, because the transcription–translation machinery resists the integration of foreign parts regardless of external pressure (Forterre, 2024; Moody et al., 2024). The small rise toward the extreme end reflects documented but limited exceptions — occasional transfer of individual informational genes — rather than any breakdown of the core's tree-like character. The core, in short, remains a tree at every extremity level, which is why deep phylogenies built from it recover a coherent branching signal.

The two shells behave oppositely. The operational-metabolic shell rises from a Reticulation Index of about 0.15 in mesophiles to 0.25 in moderate extremophiles and 0.35 in hyper-extremophiles, reflecting the increasing adaptive importance of acquired metabolic modules as environments demand novel energy and biosynthetic strategies (Qiu et al., 2025; Tokuda & Shintani, 2024). The stress-response shell rises far more steeply, from about 0.20 in mesophiles to 0.40 in moderate extremophiles and to nearly 0.60 in hyper- and polyextremophiles, because surviving extreme conditions depends disproportionately on resistance and protection functions that are the prime cargo of adaptive transfer (Bruckbauer & Cox, 2021; Li & Wang, 2021; Manrique-de-la-Cuba et al., 2025). At the extreme end, in other words, the majority of the lineage's recent adaptive change in its most survival-critical stratum is attributable to acquisition rather than to mutation. This is the central empirical pattern the framework isolates.

The genome-wide adaptive Reticulation Index, weighting the strata by their contribution to adaptation, climbs from about 0.14 in mesophiles through 0.28 in moderate extremophiles to 0.45 in hyper-extremophiles. The trend is monotonic and steep, and it is driven overwhelmingly by the stress shell, since the informational core contributes almost nothing to the increase. Two features of the pattern deserve emphasis. First, the divergence between strata widens with extremity: the gap between the tree-like core and the network-like stress shell grows from about 0.15 at the mesophile end to more than 0.50 at the polyextremophile end, so that the two strata become more distinct, not less, as pressure rises. Second, no single genome-wide topology describes any of the three reference organisms, because within each the core is tree-like and the shells are network-like simultaneously; the mislabeling of a whole genome as either a tree or a web is an averaging error that the stratified index exposes.

The sensitivity analysis supports the robustness of the qualitative result. Varying every index value by ±0.08 leaves the informational core flat and the stress shell steeply rising in all combinations tested, and leaves the genome-wide trend monotonic in extremity. To erase the extremity–reticulation coupling one would have to hold the stress-shell index constant across the gradient, which would contradict the case-study literature documenting extensive adaptive transfer of resistance and protection functions specifically in extremophiles (Bruckbauer & Cox, 2021; Qiu et al., 2025). The coupling is thus robust to the scoring, even though the exact index values are not.

Gene functional class	Mesophile (baseline)	Moderate extremophile	Hyper-/polyextremophile
Informational core (transcription–translation)	0.05	0.06	0.08
Operational / metabolic shell	0.15	0.25	0.35
Stress / resistance shell	0.20	0.40	0.60
Genome-wide adaptive R	**0.14**	**0.28**	**0.45**

Table 1. Reticulation Index (R) by gene functional class across an environmental-extremity gradient. R is the fraction of a stratum's adaptive genetic change attributable to horizontal acquisition (0 = fully tree-like; 1 = fully network-like).

Note. Values are heuristic estimates drawn from the cited case-study literature; the scoring procedure is described in the Research Methodology section. The qualitative result — a flat informational core versus a steeply rising stress shell — is stable under ±0.08 perturbation of the scores. R scores adaptive contribution, not raw transfer frequency.

MECHANISM: WHY EXTREME ENVIRONMENTS FAVOUR ACQUISITION OVER MUTATION

The extremity–reticulation coupling would be a mere correlation without a mechanism, and the mechanism is the reason extremophiles sit at the reticulate extreme. Adaptation by mutation is slow because it must wait for a beneficial variant to arise and then sweep, and in a severe environment the waiting time can exceed the time a lineage has before conditions kill it. Adaptation by acquisition is fast because it imports a function that has already been tested by selection in some other lineage, delivering a working solution in a single event rather than building one nucleotide at a time (Arnold et al., 2021; McLeod & Gandon, 2025). Where selective pressure is extreme and time is short, the advantage of the fast route is correspondingly large, and this is the general reason acquisition should dominate adaptation in extremophiles rather than in mesophiles.

The mechanistic literature makes the argument concrete by showing that the machinery of transfer is not merely present but functional in extreme settings. Natural transformation — the uptake of naked environmental DNA — operates in Gram-negative bacteria living in extremes, despite the intuition that such environments should degrade extracellular DNA and disable competence (Averhoff et al., 2021). Gene transfer agents, virus-like particles that shuttle host DNA between cells, provide a further route whose evolutionary reconstruction shows deep integration into host biology (Esterman et al., 2021; Kogay & Zhaxybayeva, 2024). Mobile genetic elements package adaptive functions into transmissible units, and genomic islands assemble resistance and protection cassettes that move as blocks, so that a recipient can acquire an entire survival phenotype in one transfer rather than reconstituting it gene by gene (Li & Wang, 2021; Dionisio et al., 2019). The point is not that any single mechanism is unique to extremophiles but that the full toolkit remains operational under conditions where mutation-based adaptation is least able to keep pace, which tilts the balance toward acquisition exactly where the framework predicts.

The case studies convert this general argument into documented instances. Acidophilic archaea, facing the double challenge of extreme pH and dissolved heavy metals, acquire metal-resistance and energy-metabolism genes by transfer, and the acquisition is adaptive rather than incidental (Qiu et al., 2025). Antarctic microbial communities show cold-adaptation genes spreading horizontally across community members, so that the adaptation is a shared, transmissible resource rather than a lineage-private invention (Manrique-de-la-Cuba et al., 2025). Radiation-resistant lineages assemble their formidable repair and protection systems from a mixture of vertically inherited and horizontally acquired components, and experimental evolution reproduces the assembly under laboratory selection (Bruckbauer & Cox, 2021). In each case the adaptive function that defines the extremophile's niche is, in substantial part, a borrowed one. I find the Antarctic case particularly telling, because it shows adaptation behaving as a community-level property distributed by transfer, which is difficult to square with any strictly tree-like account of how the trait arose.

There is a caveat I want to register rather than bury. Not every gene an extremophile carries that looks acquired is adaptive, and the conflict side of transfer — selfish elements, addiction systems, costly parasitic DNA — is real and can inflate naive counts of "acquired" genes (Hall et al., 2020). This is exactly why the Reticulation Index scores adaptive contribution rather than transfer frequency, and it is a place where the framework's honesty depends on the underlying inference being careful. My scores assume that the case-study literature has, on balance, identified adaptive transfers correctly, but I acknowledge that separating adaptive acquisition from neutral or parasitic acquisition is difficult and that some of my stress-shell values could shift downward if a larger fraction of apparently adaptive transfers proved incidental. The direction of the coupling would survive, but its steepness is more uncertain than the point estimates suggest.

THE GENE-CLASS PARTITION: HOW TREE AND WEB COEXIST IN ONE GENOME

The deepest source of the tree-versus-web dispute is the tacit assumption that a genome must have a single history, so that either the tree wins or the web does. The gene-class partition rejects that assumption. A prokaryotic genome is a composite of strata with different transfer behaviors, and its history is therefore plural: the informational core carries a tree-like genealogy while the operational and stress shells carry network-like ones, all in the same cell at the same time. The dispute dissolves once one stops asking for the history of the genome and starts asking for the history of each stratum, because the two camps turn out to be describing different strata and generalizing each to the whole.

The evidence that the core is tree-like is exactly the evidence the vertical camp has always cited, and the framework grants it in full. The transcription–translation machinery resists transfer because its components interact so densely that a foreign copy seldom functions in a foreign context; a ribosomal protein tuned to one lineage's ribosome does not slot cleanly into another's. This resistance is why deep phylogenies built from ribosomal genes and core informational proteins recover a coherent branching tree and why reconstructions of the last universal common ancestor are possible at all (Forterre, 2024; Moody et al., 2024). The core's Reticulation Index stays near 0.05 even in the most reticulate extremophiles because the mechanism of resistance is intrinsic to the machinery, not dependent on environment. The vertical camp is right about the core, and the framework says so.

The evidence that the shells are network-like is the evidence the horizontal camp has amassed, and the framework grants that too. Operational and stress genes are modular, often self-contained in function, and frequently packaged into mobile units, so that they transfer readily and integrate productively (Tokuda & Shintani, 2024; Li & Wang, 2021). Interdomain transfers move such genes even between bacteria and archaea (Medeiros et al., 2024), and the mosaic ancestry of major functional innovations testifies to how thoroughly the shells reticulate (Urquhart et al., 2024). For these strata a single gene tree is not a faithful account of history, because the genes have moved among lineages that the core tree keeps separate. The horizontal camp is right about the shells, and the framework says that too. What neither camp has done is hold both truths at once, which is what the partition forces.

Colnaghi, Lane and Pomiankowski (2020) supply the framework's most instructive precedent by showing that the balance between the strata is itself historically dynamic. In their model of early eukaryotic evolution, genome expansion drove a transition from a regime dominated by lateral gene transfer to one dominated by vertical inheritance, so that the tree-web balance shifted over evolutionary time. This matters for two reasons. First, it demonstrates that reticulation is a variable, not a constant, which is the premise the extremity coupling builds on. Second, it suggests that the eukaryotic tree became tree-like not because eukaryotes are exempt from transfer but because a particular evolutionary transition suppressed it — a contingent outcome rather than a law. The phylogenomics of Asgard archaea, poised at the prokaryote–eukaryote boundary, shows the intermediate blend one would expect if the balance is indeed a dial rather than a switch (Manzano-Morales & Gabaldón, 2026). My initial intuition was that the tree-web balance would prove roughly constant across prokaryotes; the eukaryogenesis literature convinced me it is better understood as a tunable quantity, and that shift is what made the extremity hypothesis thinkable.

EXTREMITY–RETICULATION COUPLING AND THE TREE OF LIFE RECONCEIVED

If the tree-web balance is a dial, the extremity–reticulation coupling is a claim about what turns it: environmental severity turns it toward the network pole. Bringing the results together, the coupling states that the adaptive contribution of the horizontal shells rises with extremity while the informational core stays fixed, so that extremophiles are not a special exception to prokaryotic evolution but its most pronounced expression. This reconceives the tree of life in a specific way. The tree is not abolished, but its domain of validity is restricted: it is a true statement about the informational core and a progressively worse statement about the rest of the genome as one moves toward extreme environments. Drawn honestly, the tree of life is a tree of cores, and around each branch there is a cloud of shell genes shared reticulately with other branches, a cloud that thickens as the branch's occupants live in harsher places.

The reframing earns its keep by making predictions that could prove it wrong. The sharpest is comparative: across a set of related lineages spanning an extremity gradient, the stress-shell Reticulation Index should rise monotonically with environmental severity while the informational-core index stays flat, and the slope of that rise should be measurable with existing phylogenomic inference tools (Avni & Snir, 2020; Yuan et al., 2023; Mishra & Lercher, 2025). A second prediction concerns the direction of transfer: adaptive stress genes should flow preferentially toward lineages entering more extreme niches and be retained there under selection, a pattern the uneven genome-wide distribution of transferred genes already hints at (Liu et al., 2025; Smith & Andam, 2021). A third, more demanding prediction is that experimentally increasing environmental pressure should increase the adaptive uptake and retention of relevant shell genes, connecting the comparative pattern to a causal mechanism through experimental evolution of the kind already applied to radiation resistance (Bruckbauer & Cox, 2021). None of these is beyond current methods, and each would either sharpen or refute the coupling.

The reframing also has consequences beyond systematics. If adaptive evolution in extremophiles is driven substantially by acquisition, then the search for the genetic basis of an extreme phenotype should look outward to the transferable gene pool of the community as much as inward to the lineage's own mutational history, a shift the microbiome and metagenomic literatures are already making (Moura de Sousa et al., 2023; Peng & Fu, 2025). For astrobiology the implication is pointed: an organism's capacity to colonize an extreme or extraterrestrial environment may depend less on its private genome than on its access to a horizontally shared reservoir of adaptive functions, which is the context in which transfer among extremophilic archaea under simulated extraterrestrial conditions becomes directly relevant (Subotić, 2025). And for evolutionary theory more broadly, the coupling suggests that the relative weight of the two great sources of novelty — mutation and acquisition — is not fixed but ecologically tuned, heaviest on acquisition exactly where life is hardest.

I want to close the analysis by marking what the reframing does not claim, because the temptation to overreach is strong. It does not claim that the tree of life should be discarded; the informational core genuinely descends as a tree, and the framework depends on that. It does not claim that all prokaryotes are equally reticulate; the whole point is that reticulation varies, and mesophiles sit near the tree pole. And it does not claim that extremophiles lack vertical inheritance; their cores are as tree-like as anyone's, and only their shells are heavily networked. The claim is the narrow, quantitative one the index expresses: that the adaptive genome becomes more reticulate as the environment becomes more extreme, and that the tree of life, properly drawn, is a tree only about the stratum that resists this trend. That narrower claim is, I believe, both defensible and testable, which is more than the sweeping either-or positions in the original dispute can say.

CONCLUSION

This article set out to reconcile the pervasive reality of horizontal gene transfer with the survival of a tree-like signal in the deepest phylogenies, using extremophiles as the decisive test case. The three hypotheses that structured the inquiry are supported. The first, that the tree-versus-web dichotomy is false because tree-like and network-like signals coexist within every prokaryotic genome partitioned by function, is borne out by the divergence between a flat informational core and steeply rising operational and stress shells. The second, that the balance between the two responds to ecology, is supported by the monotonic rise of the genome-wide Reticulation Index with environmental extremity. The third, that extremophiles occupy the reticulate extreme, follows directly: their stress shells reach Reticulation Index values near 0.60, meaning that most of

their recent adaptive change in their most survival-critical genes is acquired rather than evolved in place.

The principal original contribution is the gene-class-stratified reconciliation framework and the Extremity–Reticulation hypothesis it generates. By partitioning the genome into a vertically inherited informational core and horizontally acquired operational and stress shells, and by defining a Reticulation Index that measures adaptive contribution separately within each stratum, the framework turns the two-decade tree-versus-web dispute from a clash of incompatible topologies into a quantitative, testable statement about which stratum follows which topology and how the balance shifts with environment. Where prior work argued that the history of life is fundamentally a tree, or fundamentally a web, the framework holds both at once and locates the disagreement precisely — in the gene-class stratum each camp implicitly generalized to the whole. The reconception of the tree of life as a tree of cores threaded through a network of shells is, I think, the framework's most durable product, because it preserves what the classical picture got right while quarantining what it got wrong.

The limitations are substantial and I state them without softening. The Reticulation Index values are heuristic, assigned by a single author from the case-study literature rather than computed uniformly across genomes, so their exact magnitudes carry an unquantified subjectivity; only the qualitative divergence between core and shells, which the sensitivity analysis shows to be stable, should be leaned on heavily. Distinguishing adaptive acquisition from neutral or parasitic acquisition is genuinely hard, and if a larger fraction of apparently adaptive transfers proved incidental, the stress-shell slope would flatten, though not reverse. The three-stratum partition is a simplification of a continuous gradient in transferability, and some genes resist clean assignment. And the extremity gradient itself is coarse, collapsing distinct kinds of extremity — thermal, osmotic, radiative, acidic — that may couple to reticulation differently and deserve separate treatment.

Three directions for future work follow. The first is empirical computation: applying existing phylogenomic inference tools to a curated set of lineages spanning an extremity gradient, to replace the heuristic index with measured values and test the predicted monotonic rise directly. The second is decomposition of extremity: asking whether thermal, osmotic, radiative and acidic pressures each couple to reticulation with the same slope, or whether some kinds of extremity drive acquisition harder than others. The third is the causal test through experimental evolution: imposing graded environmental pressure and measuring whether adaptive uptake and retention of shell genes rise accordingly, closing the loop from correlation to mechanism. Whether the coupling proves as clean as the heuristic suggests is an open question I cannot settle here; but if it holds, then the tree of life is not the whole story of life's history and never was — it is the story of one resistant stratum, around which the rest of the genome has been trading adaptive solutions all along, most vigorously where survival is hardest.

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HORIZONTALNI TRANSFER GENA KAO POKRETAČ ADAPTIVNE EVOLUCIJE KOD EKSTREMOFILA: REEVALUACIJA KONCEPTA „STABLA ŽIVOTA" STRATIFIKOVANA PO KLASAMA GENA

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Sažetak: Slika jedinstvenog razgranatog stabla života, naslijeđena od Darvina i formalizovana molekularnom filogenetikom, teško se miri s onim što genomika danas pokazuje o prokariotima: da se geni kreću bočno između linija toliko rasprostranjeno da nijedno pojedinačno stablo gena pouzdano ne predstavlja cjelokupnu istoriju organizma. Ovaj rad tvrdi da je spor „stablo naspram mreže" pogrešno postavljen kao izbor između dvije nespojive topologije i da su obje strane djelimično u pravu, jer odgovor zavisi od toga o kojim se genima pita. Razvijam okvir stratifikovan po klasama gena koji genom modeluje kao vertikalno naslijeđeno informaciono jezgro — ribosomski i transkripciono-translacioni aparat koji ostaje tvrdoglavo stablolik — ugrađeno u horizontalno stečen operativni i stresni omotač koji je istinski mrežolik. Prema tom pristupu, stablo života nije ni stablo ni mreža nego stablo jezgara protkano mrežom omotača, a ravnoteža između njih nije fiksna nego varira između taksona i sredina. Iz okvira izvodim provjerljivu hipotezu ekstremnost–retikulacija: adaptivni doprinos horizontalnog omotača, kvantifikovan Indeksom retikulacije, raste s ekstremnošću sredine, pa ekstremofili zauzimaju maksimalno retikulatni kraj kontinuuma. Heurističko ocjenjivanje duž gradijenta ekstremnosti pokazuje da informaciono jezgro ostaje blizu vrijednosti 0,05–0,08 bez obzira na sredinu, dok stresni omotač raste od oko 0,20 kod mezofila do blizu 0,60 kod poliekstremofila. Ekstremofili, u ovom čitanju, nisu marginalne rijetkosti nego najjasniji dokaz da je adaptivna evolucija kod prokariota znatno pokretana sticanjem, a ne samo mutacijom, i stablo života mora se u skladu s tim ponovo osmisliti.
Ključne riječi: *horizontalni transfer gena, ekstremofili, adaptivna evolucija, stablo života, filogenomika, arheje, retikulatna evolucija, indeks retikulacije.*