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Biological Processes and Analytical Choices Generate Distinct Forms of Phylogenomic Conflict Across the Insect Tree of Life

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ABSTRACT

Sexuality, which plays an essential and significant role in human life, is provided through healthy sexual organs. Therefore, any disease in the genital area, including vaginitis, can interfere with these tendencies and thus affect the quality of life of the individual. The researchers, therefore, conducted a study aimed at comparing sexual satisfaction in pregnant women with vaginal candidiasis. This is a cross-sectional study to evaluate the effect of *Candida* vaginitis infection on sexual satisfaction that should be considered in healthy individuals and comparative work. Therefore, in this study, 160 pregnant mothers referred to the gynecology clinic, Shahid Beheshti Hospital, Tehran were selected by convenience sampling method and divided into two groups of healthy pregnant women and vaginal candidiasis women (each group 80 people). Data were collected using the Larson Sexual Satisfaction Questionnaire. After data collection, data were analyzed in SPSS software and analyzed by independent t-test. The results showed that sexual satisfaction in healthy pregnant women was slightly higher than pregnant women with vaginal candidiasis, and there was a significant difference between the two groups regarding sexual satisfaction ($p < 0.05$). These results suggest that there is a relationship between sexual satisfaction and *Candida* infection. Regarding the difference of sexual satisfaction in the group of pregnant women with vaginal candidiasis and healthy pregnant women, it can be concluded that the rate of sexual satisfaction with the vaginal candidate will be effected and makes problems and disorders.

Keywords: Gene-tree discordance, Incomplete lineage sorting, Introgression, Orthology inference, Recombination, Species-tree inference.

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Introduction

Genome-scale datasets have transformed insect systematics by increasing access to loci, genomic compartments and historical specimens, while also encouraging integration with morphology, ecology, behaviour and other independent evidence [1]. Yet increasing the quantity of sequence data does not remove a fundamental inferential distinction: gene genealogies are realizations of evolutionary processes, whereas a species tree is a model-based reconstruction of relationships among lineages [2]. Conflict among estimated gene trees therefore cannot be interpreted automatically as conflict in species history.

This distinction becomes consequential when discordance is used as evidence for process. Quartet-frequency patterns can be compared with expectations under the multispecies coalescent, but departure from those

expectations does not uniquely identify the responsible mechanism; substantial gene-tree estimation error or a history more complex than a bifurcating species tree can produce similar departures [3]. Reticulate histories create an additional class of alternatives because introgression or hybridization may generate genomic genealogies that cannot be represented adequately by one tree, while incomplete lineage sorting can itself mimic aspects of network-like conflict [4]. Thus, neither tree disagreement nor a supported network edge is causally self-interpreting.

We argue that this ambiguity is the central phylogenomic-conflict problem. The relevant question is not simply whether loci disagree, but which level disagrees, which processes could produce that pattern, which analytical choices could reproduce it, and which observations discriminate among those alternatives. The article therefore develops a proposed causal conflict taxonomy that keeps biological processes—such as incomplete lineage sorting, introgression, duplication and loss, and recombination—analytically separate from sampling, orthology, alignment, filtering, gene-tree estimation and substitution-model effects. The framework does not assume that these causes are mutually exclusive or that every recalcitrant insect node can be diagnosed uniquely.

Materials and Methods

The framework was constructed as a comparative synthesis of insect phylogenomic case studies and methodological work addressing the origin or interpretation of discordance. Categories were included only when the evidence base supported a specific route by which biological history or analytical treatment can alter gene-tree, genomic-compartment or species-tree inference. Whole-genome analyses of *Neodiprion* sawflies are particularly informative because discordance was associated with several genomic and historical processes rather than a single universal cause [5]. This motivates a taxonomy in which coexistence is permitted by design.

The proposed taxonomy separates four inferential objects. First, an observed conflict state specifies what disagrees: loci, sites, genomic compartments, analytical treatments or higher-level species-tree estimates. Second, a candidate causal class identifies biological or analytical processes capable of generating that state. Third, discriminating evidence asks whether the conflict changes under a perturbation relevant to the proposed cause. Fourth, a residual ambiguity state records explanations that remain viable after that perturbation. These categories are proposed organizational devices rather than validated diagnostic classes.

A critical rule is that model rejection is not causal identification. Departure from coalescent expectations can narrow the range of adequate explanations without determining whether the residual signal reflects reticulation, gene-tree error or another model violation [3]. Likewise, a reticulation model may describe heterogeneous ancestry better than a strictly bifurcating tree without establishing that every inferred network edge represents a uniquely verified hybridization event [4]. We consequently treat analytical perturbations as evidence about causal plausibility, not as experimental proof of historical mechanism.

Results and Discussion

Incomplete lineage sorting is a biological source of conflict because ancestral alleles can persist across successive lineage divergences and coalesce deeper than the species splits being reconstructed. Its phylogenomic signature is therefore expected to be strongest where internodes are short relative to coalescent times, but the magnitude and interpretability of the resulting conflict remain lineage- and method-dependent.

The rapid radiation of alpine *Parnassius* butterflies provides a direct insect example in which extensive gene-tree discordance was interpreted primarily as incomplete lineage sorting [6]. The case supports rapid divergence as a context in which large numbers of loci need not converge on a single dominant genealogy. It does not establish that every rapid insect radiation is ILS-dominated, because demographic history, introgression and estimation error can produce overlapping patterns.

Aphid phylogenomics further illustrates why majority-gene-tree reasoning may fail at particularly short successive branches. Deep relationships within Aphididae were associated with extensive gene-tree discordance, introgression and conditions consistent with the gene-tree anomaly zone [7]. Under such conditions, the most frequent gene-tree topology cannot simply be equated with the species history. Conflict therefore has to be interpreted relative to branch structure and the assumed generative model.

High support values also do not remove this distinction. Phylogenomic analysis of a New Zealand cicada radiation improved resolution of several relationships while retaining substantial gene-tree conflict and strong

mitochondrial–nuclear discordance [8]. Conventional support for an inferred branch and concordance among underlying genomic histories are different quantities; conflating them can make a strongly estimated species-tree edge appear biologically homogeneous when it is not.

Whole-genome data can make this heterogeneity more visible rather than eliminate it. In *Coenonympha* butterflies, pervasive genomic discordance remained compatible largely with ILS, while hybridization contributed to parts of the younger evolutionary history [9]. Similarly, comparative beetle analyses attributed superficially similar mitonuclear disagreement to incomplete lineage sorting in some lineages and mitochondrial introgression in others [10]. The resulting diagnostic principle is proposed but conservative: an ILS explanation becomes more plausible when conflict is distributed in a manner consistent with short internodes and coalescent expectations, yet ILS should remain a candidate rather than a default whenever independent evidence supports reticulation, compartment-specific history or substantial estimation error.

Introgression and hybridization

Introgression differs from ILS because genealogical discordance is produced by ancestry crossing lineage boundaries after divergence rather than solely by persistence of ancestral polymorphism. The distinction is conceptually clear but empirically difficult because both processes can generate discordant local genealogies.

Mitochondrial capture provides one informative asymmetry. In Taiwan–Ryukyu *Ivalia* flea beetles, mitochondrial and nuclear histories were strongly discordant, and the combined evidence supported repeated mitochondrial introgression; consequently, mitochondrial barcode relationships alone would have provided a misleading representation of lineage history [11]. This does not justify treating every mito–nuclear conflict as introgression. Rather, compartmental disagreement becomes diagnostically stronger when nuclear population structure or other genomic evidence supports transfer of mitochondrial ancestry.

Explicit historical models provide a second level of evidence. Full-likelihood genomic analysis of the *Heliconius* erato–sara group supported a complex divergence history incorporating gene flow [12]. Such analyses test richer alternatives than simple comparison of two topologies, but their conclusions remain conditional on the model set, parameterization and genomic information available. A selected gene-flow model is therefore better described as a better-supported historical explanation within the alternatives examined, not as uniquely proven history.

Genomic location supplies another discriminator. Across *Heliconius* genomes, recombination-rate variation was associated with variation in permeability to introgression, with low-recombination regions showing stronger barriers to gene flow [13]. Consequently, reticulation need not leave a spatially uniform genomic signature. A proposed diagnostic use of this result is to ask whether discordant ancestry covaries with recombination and barrier structure; such covariance can strengthen a reticulation interpretation, but recombination alone does not identify the selected loci or prove the causal history of an individual discordant region.

Duplication and loss

Gene duplication and loss create conflict at a different biological level because compared sequences may represent different copies within a gene family rather than divergent histories of the same orthologous locus. Orthology is therefore an inference made before species-tree reconstruction, not a property guaranteed by sequence recovery. Modern orthology methods explicitly reconstruct gene-family relationships to improve delimitation of orthogroups, with benchmark performance varying among algorithms and implementations [14].

This distinction matters because biological paralogy and analytical orthology error should not be collapsed. A duplicated gene can be legitimate phylogenetic evidence if the inference model accommodates multicopy histories. ASTRAL-Pro, for example, extends quartet-based species-tree inference to multicopy gene trees and demonstrates that paralogy can be modeled rather than categorically eliminated [15]. Its existence does not imply that every paralogous dataset becomes reliable; accuracy still depends on the underlying gene trees and assumptions.

Conversely, paralogy is not automatically the dominant source of discordance whenever duplicated genes occur. Simulations and empirical comparisons show that methods developed for ILS can remain comparatively robust to paralogs under tested conditions, while gene-tree estimation error can be similarly or more consequential [16]. The proposed taxonomy therefore separates duplication/loss as biological gene-family history, incorrect orthology assignment as an analytical error, and gene-tree estimation error within correctly identified gene families. These states may interact, but they require different remedies and should not be diagnosed from discordance alone.

Selection and recombination

Recombination changes the scale at which a genealogy is meaningful. A sufficiently recombining genomic region may contain segments with different ancestral trees, so assigning one genealogy to an extended locus can compress genuine local-history variation into an apparent conflict among methods or partitions. Ancestral-recombination-graph approaches formalize this problem by representing transitions among local genealogies along a sequence [17]. A switch between local trees, however, does not by itself distinguish ordinary recombination from introgression, ILS or estimation error.

Tree-mixture models expose the same boundary from another direction. When different subsets of sites are better described by different topologies, a single-tree model can be inadequate even if no biological cause has yet been identified [18]. Detecting heterogeneous tree histories is therefore a different inferential operation from explaining why those histories exist. This distinction prevents a better-fitting multi-tree description from being interpreted automatically as evidence for hybridization, selection or any other specific mechanism.

Selection enters most defensibly when it alters which introgressed or ancestral variants persist across the recombination landscape. In *Heliconius*, genomic permeability to introgression varies with recombination rate, consistent with stronger barriers in low-recombination regions where linked selection can affect larger genomic blocks [13]. The evidence supports a relationship between recombination landscape and introgression, but topology alone does not identify the form, target or adaptive consequence of selection. Selection should therefore be treated here as a potential modifier of the spatial distribution of ancestry rather than as a default explanation for phylogenomic discord.

We propose four analytically distinct states. A recombination-localized genealogy state occurs when neighbouring genomic segments support different histories and the locus boundary itself is biologically inappropriate. A barrier-modulated ancestry state occurs when introgressed ancestry varies with genomic context such as recombination. An unassigned multi-history state occurs when several topologies fit different site subsets but the causal process remains unresolved. Finally, a selection-attribution boundary is reached when genomic heterogeneity is compatible with linked selection but the evidence does not identify a selected target or fitness consequence. These distinctions are diagnostic categories proposed by this article, not empirically validated classes.

Because these states differ in what they permit a phylogenomicist to conclude, a state-and-response ledger is more informative than treating “recombination” as a single source of error.

Table 1. Recombination-structured conflict states and the inferential responses they permit

Biological with observed basis	Defensible interpretation	Interpretive limit	Discriminating check
Recombination-localized genealogy			
<i>Evidence-supported premise; diagnostic use proposed</i>			
Adjacent segments within a nominal locus possess different histories Spatially changing local genealogies or improved fit after recombination-aware representation	One locus may be an inappropriate unit for a single gene tree	Local-tree change does not identify ILS, introgression or selection	Re-estimate histories at recombination-relevant genomic scales
Barrier-modulated ancestry			
<i>Evidence-supported premise; diagnostic use proposed</i>			
Introgressed ancestry varies across genomic regions Discordant ancestry covaries with recombination or barrier structure	Reticulation may be retained unevenly across the genome	Association does not identify a selected locus or prove the origin of every discordant tract	Compare ancestry patterns with recombination landscape and independent evidence of gene flow
Unassigned multi-history signal			
<i>Evidence-supported premise; causal classification proposed</i>			
Different site subsets support different tree histories Multi-tree representation fits heterogeneous sites better than one-tree representation	A single topology may underrepresent the sequence history	The cause of heterogeneity remains unidentified	Test competing biological and analytical explanations rather than labeling the mixture mechanistically

Selection-attribution boundary			
<i>Proposed boundary derived from approved evidence</i>			
Genomic conflict overlaps regions where linked selection could influence ancestry retention	Selection may modify the distribution of ancestry	Tree discordance alone does not reveal target, direction, fitness effect or adaptation	Require population-genomic or functional evidence before assigning selection as a cause
Spatially structured discordance compatible with recombination-mediated barriers			
Cross-scale conflict persistence			
<i>Proposed diagnostic state</i>			
Discord remains after locus boundaries are made more recombination-aware	Remaining conflict requires ILS, introgression, estimation error or other explanations	Recombination correction does not select among residual causes	Carry unresolved alternatives forward into later causal diagnosis
Local genealogies still disagree across independent genomic regions			

The same distinctions become useful for causal triage only if biological history, genomic context and analytical representation remain visibly separate; **Figure 1** therefore places recombination-aware interpretation between the observation of discordance and any attribution to lineage-level process.

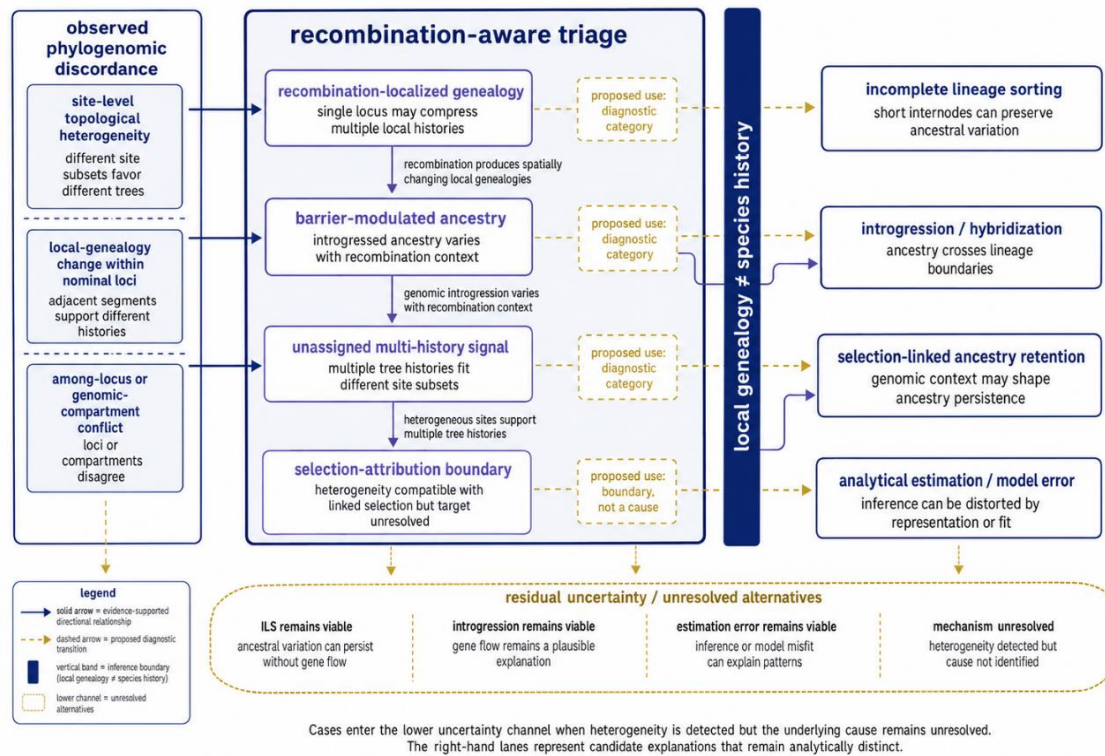


Figure 1. Triage of recombination-structured discordance before attributing insect gene-tree conflict to lineage history

Sampling decisions

Phylogenomic conflict is conditioned before analysis by which lineages, individuals and genomic resources enter the dataset. Published insect phylogenies remain unevenly distributed across diversity, so absence of representation can preserve long branches or omit lineages capable of subdividing apparent conflict [19]. Sampling is therefore not a neutral precursor to causal diagnosis.

In low-coverage whole-genome data from Formica ants, data type, assembly strategy and tree-inference pipeline produced different outcomes, showing that sampling and processing interact rather than operating independently [20]. Historical material can broaden taxonomic representation when living material is difficult to obtain, as target-enrichment museomics demonstrated for Anoplophora and relatives, although preservation quality constrains

comparability [21]. Sample choice can also be formalized under an explicit coalescent objective, but model-aware selection is not equivalent to detecting admixed individuals and may select them under some conditions [22]. We therefore propose treating taxon, individual and genomic-resource selection as diagnostic perturbations: if a relationship changes after biologically justified sampling expansion, sparse representation remains a viable analytical explanation; if conflict persists, other causes remain open.

Alignment and orthology choices

Sequence processing determines which homologous characters are allowed to contribute to a phylogeny. Complex datasets can contain apparently plausible but artifactual orthologues, demonstrating that orthology errors may be introduced during data construction rather than inherited from species history [23]. That empirical demonstration is cross-taxon and does not establish an insect-specific frequency, but it supports the general analytical mechanism.

In Adephaga, excessive trimming and model misspecification generated misleading relationships, showing that removal of difficult sites is not monotonically beneficial [24]. Neuropteridan analyses similarly found that marker class, filtering strategy and substitution treatment interacted in their performance, with no defensible basis for promoting one study-specific combination as universally optimal [25]. Alignment and orthology choices should consequently be interpreted as linked boundaries between biological sequence history and the analytical character matrix.

The distinction is easiest to preserve when the possible failure states are compared explicitly rather than summarized as “data quality”; **Table 2** therefore separates erroneous homology assignment, over-filtering, retained systematic bias and marker-class dependence by the evidence needed to diagnose each state.

Table 2. Analytical boundaries separating sequence-history conflict from alignment and orthology artefacts

Boundary and decisive check	Failure state with evidential standing	Character-level basis	Observable analytical pa and warranted reading
Genuine duplication/loss or estimation error may remain Reassess homology and gene-family history before interpreting species-level discord	Artifactual orthologue state Evidence-supported premise; diagnostic classification proposed	A locus accepted as orthologous does not represent the intended homologous history	Unexpected placement concentrates in particular inferred orthologues or disappears after locus curation Apparent conflict may originate upstream of species-tree inference
Stable conflict may still reflect ILS or introgression Compare orthology strategies with paralogy-aware inference	Paralogy–orthology boundary Proposed boundary	Multicopy gene history is simplified into a single-copy representation	Conflict changes when multicopy-aware or alternative orthology treatments are used Biological duplication should be separated from analytical misassignment
Changes may also reflect model inadequacy Examine stability across biologically defensible filtering levels	Over-trimming state Evidence-supported premise; diagnostic use proposed	Filtering removes sites carrying genuine historical signal together with noise	Topology or support changes disproportionately under stricter trimming More filtering is not inherently more reliable
Biological discord can coexist with model error Couple filtering perturbation to model-adequacy assessment	Retained-bias state Proposed diagnostic state	Alignment retains characters poorly described by the fitted evolutionary model	Conflict persists or shifts with alternative site treatment or model family Analytical bias remains a candidate explanation
True genomic-compartment history and pipeline effects can overlap Compare marker classes without assuming one is intrinsically authoritative	Marker-class dependence Evidence-supported premise; diagnostic use proposed	USCO, UCE, mitochondrial or other partitions encode different signal and error structures	Relationships differ systematically among marker classes Dataset identity is part of the causal interpretation

Because these analytical choices operate in parallel rather than as a single processing sequence, **Figure 2** retains separate lanes for homology, alignment/filtering and marker representation, and places species-history interpretation beyond a shared evidence boundary.

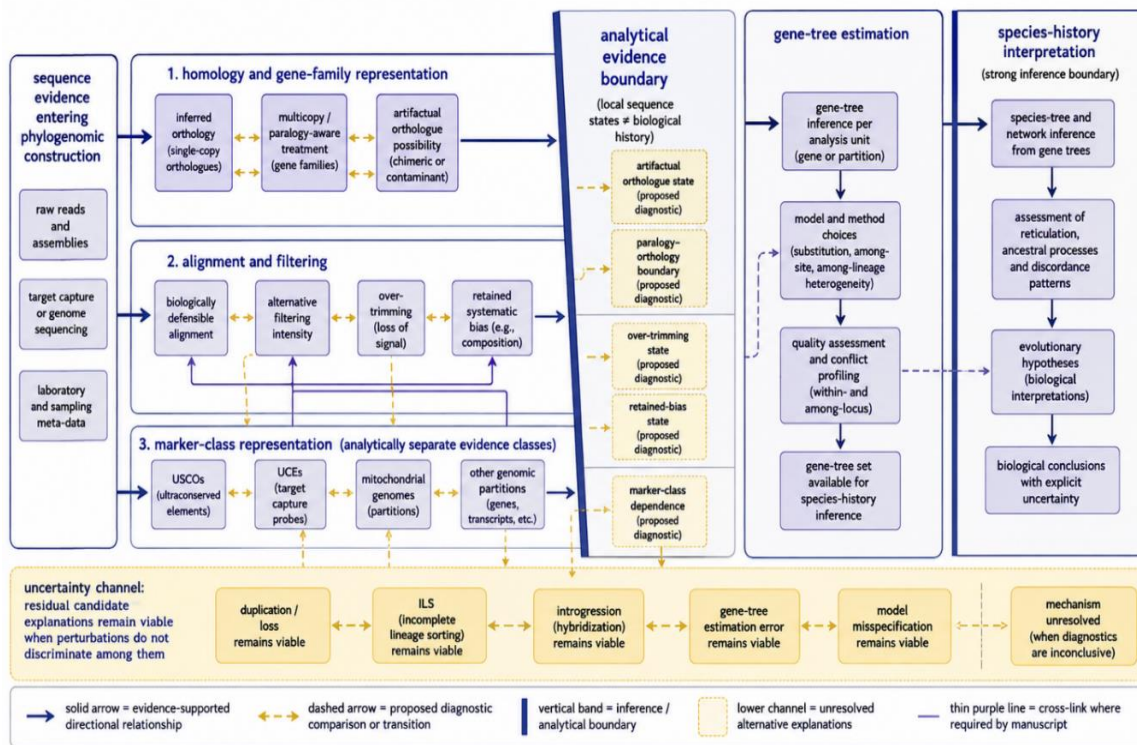


Figure 2. Where sequence construction can create, expose or preserve apparent phylogenomic conflict

Model choice

Model choice can transform persistent discordance without changing the underlying sequences. In deep ant phylogenomics, accounting more adequately for compositional heterogeneity changed a contentious backbone topology, demonstrating that strong support under a misspecified model need not identify a stable historical relationship [26]. Model fit therefore constrains interpretation but does not establish historical truth.

Gene-tree error creates a related problem one level earlier. In fireflies, model-adequacy analyses and simulation attributed much observed gene-tree discordance to estimation error, while divergence-time estimates were comparatively robust across tested locus subsets [27]. This is a clade-specific result, not evidence that biological discord is generally negligible. Whole-genome analyses of diving beetles likewise converged on most relationships while retaining several method-sensitive or weakly resolved nodes [28]. We therefore propose that conflict surviving one model should be challenged with adequacy-aware alternatives before it is assigned to a biological process.

Causal diagnostic matrix

The proposed causal diagnostic matrix is not a classifier assigning one cause to each discordant node. It is a sequence of falsifiable contrasts that asks which candidate explanations remain after targeted perturbation. Expanded planthopper sampling altered and clarified higher relationships [29], whereas dense leafhopper sampling stabilized many nodes while leaving some short deep branches difficult [30]. A response to sampling therefore supports sampling sensitivity; persistence after sampling does not by itself diagnose ILS.

For recalcitrant Bibionomorpha relationships, tree, mitochondrial and network evidence yielded a more complex picture in which a reticulation interpretation remained tentative [31]. Broad UCE sampling in sawflies and woodwasps likewise illustrates how expanded representation can clarify higher relationships without establishing a universal magnitude of sampling benefit [32]. The proposed matrix consequently requires three outputs for every perturbation: the explanation weakened, the explanations still compatible with the evidence, and the scale at which the conclusion applies. A causal label should be withheld when several candidates survive.

A practical application begins with the observed scale of disagreement rather than with a favoured mechanism. Site-level heterogeneity first raises questions about recombination, alignment and substitution process; among-locus conflict adds ILS, duplication/loss and gene-tree estimation; genomic-compartment disagreement raises compartment-specific inheritance or introgression; and instability across taxon sets or pipelines elevates sampling and analytical construction. These are proposed starting positions, not one-to-one mappings. Each candidate then receives a process-matched challenge. Recombination is challenged by local-genealogy analysis, introgression by explicit gene-flow or compartmental evidence, paralogy by gene-family-aware inference, sampling by justified taxon expansion, and model error by adequacy-sensitive alternatives. Failure of a challenge to change the result weakens only the explanation that challenge was capable of testing.

This architecture also clarifies what constitutes a negative diagnostic result. Stability across alternative orthology treatments does not establish ILS; stability under denser taxon sampling does not prove introgression; and improved fit of a multi-tree or network model does not by itself identify hybridization. Instead, each negative result contracts the candidate set while preserving explanations outside the scope of that perturbation. The endpoint can therefore be an unresolved causal set rather than a named mechanism. Treating unresolved status as an acceptable outcome is essential where short internodes, reticulation and estimation error plausibly coexist.

Phylogenomics increases information but also increases opportunities for systematic bias arising from sampling, orthology, alignment and model assumptions [33]. The framework developed here converts that general caution into a proposed causal discipline: first specify the level of observed discordance, then partition biological from analytical candidate causes, challenge those candidates with cause-relevant perturbations, and retain unresolved alternatives explicitly.

The necessity of non-exclusive diagnosis is supported by insect cases in which biological heterogeneity and analytical or estimation effects both contribute to conflict [5, 24, 27]. This prevents a common interpretive shortcut in which persistence of discordance is treated as evidence for a single biological history merely because one analytical explanation has been rejected. Conversely, analytical sensitivity should not be used to erase genuine reticulation, ILS or gene-family evolution.

Sampling deserves equivalent status in this logic because insect phylogenetic coverage is uneven and denser taxonomic representation can alter or stabilize inference [19, 30, 32]. Yet there is no universal perturbation order: recombination-aware subdivision may be crucial for introgressed genomes, paralogy-aware treatment for duplicated gene families, and model-adequacy tests for compositionally heterogeneous deep divergences.

A second limitation concerns transferability. The evidence spans several major insect orders but is uneven across the insect tree, genomic architectures and evolutionary depths. Diagnostic expectations inferred from rapid butterfly radiations should not be transferred quantitatively to deep beetle or hemipteran divergences, and methods validated on non-insect datasets support only methodological principles unless independently demonstrated in insects. The framework therefore predicts no universal threshold of discordance, quartet imbalance, network support or sampling density. Its intended output is a transparent causal argument: what was observed, what alternatives were tested, what evidence changed, and what remains unresolved.

Validation should combine simulations with known generating histories and prospective empirical reanalysis in which diagnostic predictions are declared before alternative pipelines are compared. Until such testing is performed, the taxonomy should be used to organize uncertainty rather than score confidence.

Conclusion

Phylogenomic conflict across insects is not one phenomenon and does not carry its cause in its topology. Biological processes and analytical choices can generate overlapping signatures at different genomic and inferential levels. The proposed causal conflict taxonomy converts discordance into a structured set of competing explanations, discriminating perturbations and residual uncertainties. Its value lies in preventing premature causal attribution while making unresolved conflict scientifically explicit. Prospective validation is required before the framework can be treated as a predictive diagnostic system. It should improve reproducibility by requiring investigators to state why a causal explanation survives alternatives rather than merely reporting support.

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