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Introgression and Reticulate Evolution Must Be Incorporated Explicitly Into Insect Species Histories and Classification

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ABSTRACT

Genome-scale data have made reticulation increasingly visible in insect systematics, yet the inferential consequences are often compressed into a single bifurcating species tree or treated as secondary discordance. This perspective argues that introgression should be carried explicitly from detection through historical interpretation to classification whenever the evidence warrants it. The central difficulty is not simply detecting gene flow, because incomplete lineage sorting, recombination, substitution-rate heterogeneity, unsampled donor lineages and analytical model choice can generate competing explanations. Nor does evidence of hybridization automatically imply erosion of species boundaries. Drawing on recent insect phylogenomics, this article develops a proposed reticulation-aware classification logic that separates evidence class, historical interpretation, genomic distribution, temporal placement and taxonomic consequence. The framework treats networks as complements to, rather than substitutes for, species trees; distinguishes genome-wide admixture from local genealogical mosaicism; and requires mitochondrial, nuclear, morphological and diagnostic evidence to remain analytically separable. Reticulation therefore becomes an explicit component of species history where supported, but not a default explanation for discordance. The proposed approach is intended to improve transparency in insect classification while preserving uncertainty, alternative histories and cases in which contact or discordance occurs without substantial introgression.

Keywords: Introgression, Phylogenetic networks, Genomic mosaicism, Incomplete lineage sorting, Species delimitation, Insect systematics

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Introduction

Insect systematics is increasingly confronted with genomes that record more than bifurcating descent. Comparative genomic work across multiple insect groups shows that hybridization and introgression can materially affect the interpretation of lineage histories and species boundaries [1]. This does not make reticulation a universal property of insect diversification, but it does make its omission consequential when supported by the data. A classification that reports only a preferred branching topology may therefore suppress part of the historical signal that generated the present-day genome.

Reticulation is also not synonymous with gene-tree disagreement. Phylogenomic analyses distinguish reticulate evolution from incomplete lineage sorting (ILS), recombination, sampling artefacts and other sources of discordance, and they increasingly provide network and model-based approaches for evaluating those alternatives [2]. The relevant systematic question is consequently two-stage: first, whether a non-tree history is supported; second, whether that history changes how lineage relationships or taxonomic boundaries should be represented.

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Direct insect studies demonstrate historical introgression in sampled *Drosophila* radiations, deep ancestral introgression in Odonata and strong asymmetric gene flow in *Melitaea* butterflies [3–5]. These examples establish possibility and diversity of outcome, not a frequency estimate for insects as a whole.

The central problem addressed here is the tendency for reticulation evidence to disappear between phylogenomic analysis and the final species-history statement. A paper may detect introgression, yet the taxonomic narrative is subsequently reduced to a tree whose branches imply cleaner separation than the genome itself supports. The opposite error is equally serious: treating every discordant marker, network edge or hybrid zone as evidence that species boundaries have collapsed. This perspective therefore proposes a reticulation-aware classification logic that separates detection, historical interpretation and taxonomic consequence. The logic is conceptual rather than empirically validated, and it is intended to preserve competing explanations rather than select reticulation by default.

Materials and Methods

The proposed logic begins with evidence class. Introgression can be investigated through site-pattern statistics, gene-tree distributions, local genealogies, phylogenetic networks, demographic models and multispecies-coalescent approaches, but these methods do not share identical assumptions or infer the same historical quantity [6]. A reticulation-aware classification should therefore record which signal supports gene flow and whether independent evidence converges on the same interpretation. A single statistic is insufficient as a universal decision rule because the alternative processes producing similar patterns differ among datasets.

The second step is confound triage. Among-species substitution-rate variation can alter site-pattern expectations and generate misleading introgression inference under some conditions [7]. Unsampled or extinct donor lineages create a different identifiability problem: alternative ghost-introgression histories may require gene-tree topology together with branch-length information for discrimination [8]. These are not reasons to reject introgression tests generally. They are reasons to state which alternative histories remain plausible after analysis.

The third step is method sensitivity. Reanalysis of *Drosophila* genomic data with a full-likelihood multispecies-coalescent-with-introgression approach recovered a materially different set of gene-flow events from some earlier interpretations [9]. The appropriate conclusion is not that one framework is universally correct, but that event number, direction and placement can depend on model structure. Classification should therefore distinguish a robust broad conclusion—such as evidence that gene flow occurred—from a less certain reconstruction of exactly where or when every event occurred.

Finally, reticulation can distort temporal inference. Models that ignore cross-species gene flow may bias estimated divergence times under some conditions, although the magnitude and even practical importance of that bias depend on the timing and extent of gene flow and on sampling [10]. The proposed classification logic therefore treats topology, temporal history and taxonomic consequence as separate outputs. A lineage can have a useful species-tree placement while still requiring an explicit qualification that some branch lengths, divergence times or local genomic histories are conditional on reticulation.

Results and Discussion

The strongest reason for separating introgression from shared ancestry is empirical heterogeneity among insect radiations. Whole-genome studies of *Neodiprion* sawflies, alpine *Parnassius* butterflies and Aphididae all recover substantial gene-tree discordance, yet the processes underlying that discordance differ [11–13]. This contrast rejects a one-mechanism interpretation of conflict. It also provides the basis for a proposed discordance-triage principle: discordance should be classified first by plausible generating process before it is translated into species history.

In *Neodiprion*, whole-genome analyses indicate that ILS, introgression and data-related effects can contribute to discordance within the same radiation [11]. This is important because a single species tree may still recover well-supported relationships even when local genealogies have heterogeneous origins. By contrast, rapid diversification in *Parnassius* produces extensive conflict that is primarily consistent with ILS rather than prominent introgression [12]. The latter is an essential negative comparator: high discordance alone is not evidence that a lineage history is reticulate.

The distinction is also visible within a single model-rich genus. Broad genomic analysis supports repeated historical introgression across *Drosophila* [3], while later full-likelihood reanalysis shows that the inferred placement and number of specific events can change with analytical framework [9]. Thus, "introgression occurred" and "this precise reticulation event occurred on this branch" are not equivalent statements of certainty. A classification should be capable of carrying the first statement while qualifying the second.

Hybridization networks

A bifurcating topology is a compact representation of ancestry, but it is not always a complete representation. In *Heliconius*, radiation-scale genomic analyses recover extensive admixture connecting lineages that would otherwise be depicted only as successive splits [14]. A network can therefore expose historical relationships hidden by a single tree. However, an inferred edge is an analytical claim about ancestry, not automatically a taxonomic instruction.

The same distinction applies to diversification. Genomic evidence indicates that hybridization contributed to diversification within *Spialia* butterflies [15], whereas Holarctic *Vanessa* history is better explained through a combination of long-distance dispersal and introgression rather than gene flow alone [16]. Reticulation can therefore interact with biogeography rather than replace it as an explanatory axis. A network that omits geographic history may be as incomplete as a tree that omits gene flow.

Heliconius elevatus provides a stronger and more specific case. Population-genomic and trait-mapping evidence supports a hybrid-speciation history involving multilocus introgression of ecological traits [17]. This is a high-evidence example of reticulation altering lineage origin, but it should not be generalized into a rule that hybrid ancestry establishes species status. The contrast among *Heliconius*, *Spialia*, *Vanessa* and *Melitaea* instead supports a proposed network-to-classification separation rule: network structure describes inferred ancestry; classification requires a second evaluation of diagnosability, lineage differentiation and the persistence or erosion of boundaries.

The analytical question is therefore not merely which lineages are connected, but what kind of historical connection is represented and what, if anything, follows for classification. **Table 1** compresses these distinct network states without assigning an unsupported score or taxonomic threshold.

Table 1. Hybridization-network states that require different historical and classificatory interpretations

Radiation and diversification histories			
Hybridization history comparison dimension	**Radiation-wide admixture**	**Diversification with hybrid contribution**	
Biological context and evidence	Closely related species within a rapid radiation Recurrent genomic support for cross-lineage ancestry	Lineages whose ancestry includes hybridization during diversification Concordant genomic ancestry signals	
Historical interpretation	A bifurcating tree is an incomplete historical summary	Hybridization is part of lineage history without automatically defining species rank	
Classification boundary	Individual edges may remain model-sensitive	Diversification can also involve nonhybrid processes	
Research test and proposed state	Compare network support with local genealogies and alternative histories Evidence-supported pattern	Test whether ancestry signal coincides with persistent lineage differentiation Evidence-supported pattern	
Dispersal, hybrid-speciation, and retained-differentiation histories			
Hybridization history comparison dimension	**Dispersal plus introgression**	**Multilocus hybrid-speciation case**	**Introgression with retained species differentiation**
Biological context and evidence	Geographically disjunct or mobile lineages Population-genomic and biogeographic evidence	Lineage with hybrid ancestry tied to ecological-trait loci Genomic ancestry plus trait-associated loci	Species exchanging substantial ancestry yet remaining differentiated Genome-wide ancestry plus species-level differentiation
Historical interpretation	Range history and gene flow must be interpreted jointly	Reticulation contributes directly to inferred lineage origin	Gene flow does not automatically erase boundaries

Classification boundary	Introgression alone may not explain distribution	Strong evidence in one system is not a universal criterion	No universal ancestry threshold follows
Research test and proposed state	Integrate demographic and geographic models Evidence-supported pattern	Require independent evidence for origin, trait association and lineage persistence Evidence-supported case	Evaluate where differentiation persists and whether diagnosis is stable Evidence-supported pattern
Unresolved network edge			
Hybridization history comparison dimension	**Network edge awaiting taxonomic interpretation**		
Biological context and evidence	Any inferred reticulation lacking independent boundary evidence Network or gene-flow signal alone		
Historical interpretation	Historical connection is reported, but taxonomic consequence remains unresolved		
Classification boundary	Edge direction, timing or donor identity may be uncertain		
Research test and proposed state	Seek independent genomic, morphological, ecological or reproductive evidence **Proposed interpretive rule**		

Genomic mosaicism

Reticulate histories are often heterogeneous within genomes. In the *Heliconius* radiation, genome-scale analyses show that different genomic regions can support different evolutionary histories, making a single whole-genome topology an incomplete description of ancestry [18]. This is genomic mosaicism in a phylogenetic sense: local genealogies need not share one reticulation history even when they belong to the same named species.

The distribution of introgressed ancestry is also conditioned by genomic context. Comparative work in *Heliconius* shows that recombination-rate variation is associated with heterogeneous barriers to introgression across genomes [19]. Related contact-zone work in *Iphiclides* indicates that some genomic regions can retain stronger long-term barriers to gene flow than genome-wide averages imply [20]. Neither observation licenses a universal genomic rule. It does show why classification should not translate one mean admixture estimate into a species-boundary conclusion.

More generally, recombination-aware phylogenomics emphasizes that recombining genomes are mosaics of local genealogies and that species-tree summaries should be interpreted at the scale relevant to the question being asked [21]. Species trees remain useful for summarizing dominant branching relationships, but local histories can be indispensable when reticulation, barrier loci or marker-specific ancestry affect systematic interpretation.

These findings motivate a proposed mosaicism-to-boundary firewall: evidence that a genome is reticulate should first be localized by genomic scale and only then evaluated for taxonomic consequence. **Figure 1** makes that firewall explicit by separating observed discordance, competing historical causes, genomic distribution and classification inference.

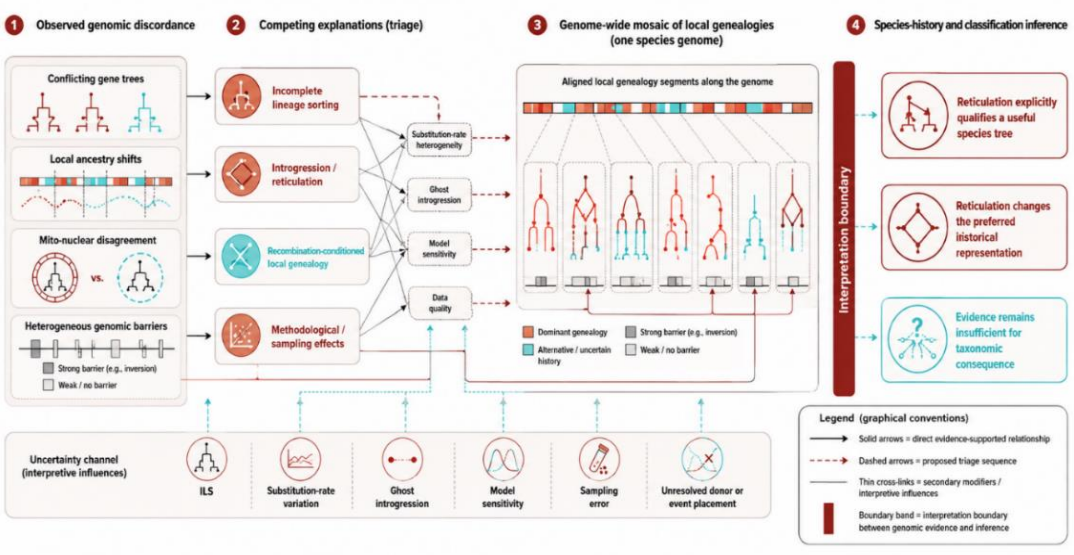


Figure 1. Genomic discordance triage across local genealogy, reticulation inference and species-history interpretation

Species-tree distortion

Reticulation can distort species-history inference without destroying the possibility of classification. In dacine fruit flies, the *Anastrepha fraterculus* complex and *Cletus* bugs, restricted marker or gene histories can conflict with broader nuclear or genomic evidence relevant to species interpretation [22–24]. These cases justify a distinction between a discordant data layer and a failed species concept: conflict may signal that a particular marker, genomic region or tree is an incomplete historical proxy rather than that no lineage structure exists.

The dacine case is especially instructive because genome-wide data reveal entities that mitochondrial COI diagnostics alone can fail to separate reliably in the affected complex [22]. That result should not be generalized into a rejection of DNA barcoding. It instead establishes a boundary condition: a marker with introgressed or lineage-specific inheritance may be inadequate when its history is decoupled from the broader genomic history relevant to diagnosis.

The *Anastrepha fraterculus* complex demonstrates a complementary outcome. Extensive gene-tree discordance and introgression need not eliminate useful species-level genomic structure or the possibility of identifying diagnostic loci [23]. In *Cletus*, mitochondrial introgression produced strong mito-nuclear disagreement, while nuclear SNPs and morphology retained differentiation among closely related taxa [24]. Together these studies show why classification should retain evidence classes separately rather than resolve conflict by privileging whichever marker is most familiar.

Independent nuclear evidence can also test historical hypotheses first suggested by mitochondrial patterns. In hybridizing swallowtail butterflies, nuclear phylogenomics was used to evaluate mitochondrial clues of archaic ancestry rather than treating the mitochondrial genealogy itself as the species history [25]. This supports a broader proposed distortion taxonomy in which reticulation may alter topology, branch length or divergence-time interpretation, marker diagnosis, or the apparent coherence of local genomic histories. These are different failure modes and should not be merged under a single label of "discordance."

Table 2 reconciles these failure modes by asking what each type of conflict can and cannot justify at the level of species history.

Table 2. Reconciling species-tree distortion without converting discordance into automatic reticulation

Conflict state	Context and evidence	Inference allowed versus unresolved	Reconciliation test and proposed state
Coalescent and mixed-cause discordance			
ILS-dominant gene-tree conflict	Rapid radiation Many gene trees disagree while coalescent evidence favours shared ancestral polymorphism	Species-tree conflict can arise without prominent introgression Exact local histories may remain uncertain	Compare coalescent expectations with explicit gene-flow models Evidence-supported distinction
Mixed-cause discordance	Radiation with multiple historical and data processes ILS, introgression and error each explain parts of the conflict	More than one mechanism may operate simultaneously Relative contribution can be model-sensitive	Partition signal across data quality, gene trees and reticulation tests Evidence-supported distinction
Model, rate, and time distortion			
Rate- or model-sensitive reticulation signal	Any phylogenomic dataset using site-pattern or model-based tests Inference changes under rate heterogeneity or alternative models	Reticulation remains a candidate history Event number, donor, direction or timing may be unstable	Reanalyse with methods that address the identified confound Evidence-supported methodological boundary
Divergence-time distortion	Lineages with cross-species gene flow Estimated times differ when gene flow is ignored versus modelled	Gene flow can affect temporal inference Magnitude and relevance are scenario-dependent	Compare models with and without gene flow Evidence-supported methodological boundary
Marker and local-genome conflict			
Mito-nuclear or barcode conflict	Closely related taxa with mitochondrial introgression	Marker history may be decoupled from species history	Test mitochondrial inference against genome-wide and nonmolecular evidence

	Mitochondrial clustering conflicts with nuclear genomic or morphological structure	Taxonomic consequence requires independent evidence	Evidence-supported distinction
Local-genome versus species-tree conflict	Recombining genomes with mosaic ancestry Different genomic regions support different genealogies	One species tree may summarize only the dominant history Which local histories matter for classification may remain uncertain	Localize ancestry signal and evaluate barrier or diagnostic relevance **Proposed reconciliation rule**
Recoverable diagnosis			
Discordance with recoverable diagnosis	Species complex showing reticulation and gene-tree conflict Genomic structure and diagnostic loci remain identifiable	Introgression does not necessarily preclude diagnosis Long-term lineage independence may still require further evidence	Separate identification performance from historical reconstruction Evidence-supported pattern

Classification under reticulate histories

Classification under reticulate histories requires more than choosing between a tree and a network. Genomic species delimitation itself remains sensitive to model assumptions, population structure, geographic sampling and the distinction between historical gene exchange and continuing lineage cohesion [26]. Consequently, reticulation-aware classification should not replace one automated decision rule with another. The proposed approach instead treats delimitation output as one evidence layer whose biological meaning must be reconciled with ancestry, diagnosability and the persistence of lineage-specific structure.

Hybrid origin provides an especially important test of that separation. Whole-genome evidence supports a hybrid origin for the insular butterfly lineage *Aricia horkei*, yet demonstrating hybrid ancestry is not identical to demonstrating that hybridization alone establishes a completed species boundary or a particular taxonomic rank [27]. Historical origin and present classification are therefore analytically distinct questions. The former asks where ancestry came from; the latter asks whether the resulting lineage is sufficiently differentiated and diagnosable under the evidential standards appropriate to the taxonomic problem.

The opposite boundary is demonstrated by secondary contact. Replicated contact zones between highly differentiated *Erebia* sibling species show that rare hybridization can occur while substantial contemporary or historical introgression remains weak or undetected [28]. Contact therefore cannot be translated directly into a major reticulation edge, just as a reticulation edge cannot be translated directly into taxonomic fusion. This negative case is critical because a framework designed only around positive examples would systematically overcall reticulation.

The proposed reticulation-aware classification logic therefore distinguishes four questions. First, is gene flow supported rather than merely compatible with the data? Second, how broadly is that signal distributed across the genome and through time? Third, does the signal alter the preferred reconstruction of lineage history? Fourth, does it affect diagnosability, lineage differentiation or another taxonomically relevant property? Only the final question concerns classification directly. Earlier stages establish evolutionary history but do not predetermine rank.

When reticulation changes taxonomic boundaries

Reticulation becomes taxonomically consequential when it changes the interpretation of evidence used to delimit or diagnose lineages. Mitochondrial introgression can obscure boundaries that remain apparent in nuclear genomic and morphological evidence [24], whereas strong genomic introgression can coexist with recognizable lineage differentiation, as shown in *Melitaea* [5]. These contrasting outcomes preclude a universal ancestry proportion at which species boundaries should be considered erased.

The strongest cases require evidence escalation rather than a numerical threshold. In *Heliconius elevatus*, genomic ancestry, multilocus ecological-trait introgression and lineage history together support a hybrid-speciation interpretation [17]. In *Aricia horkei*, hybrid origin is strongly supported but the taxonomic endpoint remains a separate inference [27]. The difference is not that one lineage crossed an arbitrary admixture boundary. It is that the evidential connection between ancestry, lineage formation and present differentiation is stronger and more specific in one case than in the other.

Reticulation may also alter only part of the evidential architecture. Persistent genomic barriers in *Iphiclides* show that gene flow can be spatially heterogeneous within the genome [20], while genomic delimitation methods

themselves can respond differently to population structure and gene flow [26]. A taxonomic decision based on genome-wide average ancestry could therefore obscure regions that retain long-term differentiation, whereas a decision based on a few resistant loci could exaggerate their importance. Neither direction supplies a universal rule.

The proposed boundary criterion is consequently qualitative: reticulation should change classification only when the total evidence indicates that it changes how lineage independence, ancestry, diagnosability or another taxonomically relevant property should be interpreted. Detection of gene flow alone is insufficient. Equally, failure to detect substantial introgression in one contact zone does not prove permanent reproductive isolation. The appropriate outcome may be taxonomic change, explicit historical qualification without taxonomic change, or continued uncertainty.

This staged distinction is compressed in **Table 3**, while **Figure 2** separates the evidence lanes that must remain independent before a taxonomic decision is reached.

Table 3. Inference stages at which reticulation can alter, qualify or leave taxonomic boundaries unchanged

Detection, historical reconstruction, and differentiation			
Reticulation to classification comparison dimension	**Detection**	**Historical reconstruction**	**Genomic differentiation**
Reticulation state and taxonomic context	Gene flow supported Any lineage pair or radiation	Reticulation changes ancestry history Hybrid-origin or introgressed lineage	Introgression is heterogeneous Genomes containing permeable and resistant regions
Evidence required	Convergent genomic evidence beyond unexplained discordance	Direction, genomic distribution and temporal placement of ancestry	Local ancestry and barrier evidence
Classification consequence	No automatic taxonomic change	Species history requires explicit qualification	Genome-wide averages should not alone determine boundaries
Boundary and decision implication	ILS, model error and unsampled donors may remain alternatives Proceed to historical interpretation	Donor identity or event timing may remain uncertain Report tree plus reticulation where appropriate	Resistant loci need not define species independently Compare local and genome-wide structure
Diagnosis and lineage formation			
Reticulation to classification comparison dimension	**Diagnosis**	**Lineage formation**	
Reticulation state and taxonomic context	Marker history conflicts with broader evidence Mito-nuclear or barcode discordance	Hybrid ancestry contributes to origin Putative hybrid lineage	
Evidence required	Independent nuclear, morphological or diagnostic evidence	Ancestry plus evidence linking hybridization to lineage formation	
Classification consequence	Marker-based classification may require revision	Taxonomic consequence may become substantive	
Boundary and decision implication	Conflict may be marker-specific Weight evidence by biological scale	Hybrid origin alone does not establish rank Escalate evidence before rank change	
Secondary contact and final classification			
Reticulation to classification comparison dimension	**Secondary contact**	**Final classification**	
Reticulation state and taxonomic context	Hybridization with little substantial introgression Differentiated taxa in contact	Evidence remains mixed Any reticulate or potentially reticulate history	
Evidence required	Contact-zone genomic evidence	Integrated historical, genomic and diagnostic evidence	

Classification consequence	Existing boundaries may remain supported	Retain, revise or qualify classification
Boundary and decision implication	Low detected gene flow is not absolute isolation Do not infer major reticulation from contact alone	No universal admixture threshold **Apply proposed reticulation-aware classification logic**

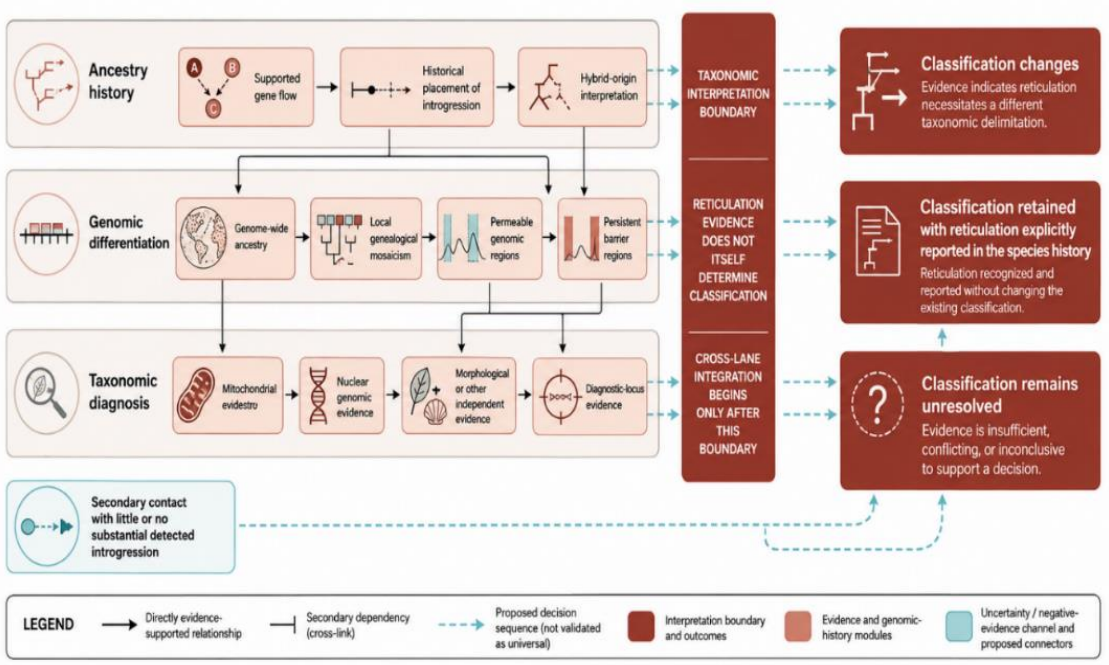


Figure 2. Taxonomic boundary decisions after reticulation evidence is separated into ancestry, genomic differentiation and diagnosis

Reporting reticulation explicitly

Explicit reporting should begin with the evidence class. Site-pattern support, network placement, local genealogy, demographic inference and full-likelihood coalescent models do not make identical claims [6]. A manuscript should therefore state what was detected, by which class of evidence and under which competing models, rather than summarize all outcomes as "introgression present."

Relevant confounds should then be reported selectively. Rate heterogeneity can alter some introgression tests [7]. Unsampled donors can complicate the identity of the inferred source lineage [8]. Alternative full-likelihood analyses can also revise event placement [9]. These limitations need not be listed mechanically in every study; they should be tested or discussed when the data and method make them plausible.

Scale is equally important. Recombination can create local genealogical histories that differ across a genome [21], mitochondrial histories can diverge from nuclear genomic structure [24], and mitochondrial hypotheses can be tested using independent nuclear evidence [25]. Reporting should therefore identify whether a conclusion concerns a marker, genomic region, population, species tree or broader lineage history.

The final reporting step is to separate reticulation from its taxonomic consequence. Strong introgression may coexist with differentiated species [5], whereas some contact zones exhibit little substantial introgression [28]. The proposed reporting architecture therefore requires two explicit statements: the preferred evolutionary history and the resulting classification interpretation. Where those conclusions differ in certainty, the difference should remain visible.

The central argument of this perspective is deliberately narrower than a claim that insect evolution is fundamentally network-like. Some insect radiations show extensive introgression, but others show discordance dominated by ILS [12], and secondary contact can occur without substantial genomic exchange [28]. Reticulation-aware classification must therefore begin with discrimination among alternatives rather than with an expectation that reticulation will be found.

Trees and networks should likewise not be treated as mutually exclusive representations. Networks can recover cross-lineage ancestry that a single bifurcating topology omits [14], while species trees remain efficient summaries of dominant branching structure when their assumptions fit the question [2]. The appropriate representation may therefore be a species tree explicitly qualified by one or more reticulation events, a more strongly network-based history, or a tree accompanied by unresolved discordance.

The taxonomic consequences are even less uniform. *Melitaea* demonstrates that extensive introgression can coexist with recognizable lineage differentiation [5]. *Heliconius elevatus* provides a substantially stronger case in which multilocus introgression is implicated in hybrid lineage formation [17]. Dacine fruit flies show how mitochondrial diagnostics can become unreliable within a reticulate complex [22], while comparative work on genomic species delimitation shows that analytical methods themselves can over- or under-split structured lineages [26]. These outcomes cannot be reduced to one ancestry threshold.

The proposed framework therefore treats taxonomic consequence as an evidence-integration problem. Its main advantage is transparency: the reader can see whether uncertainty lies in detection, historical placement, genomic distribution, diagnosis or classification. Its principal limitation is equally important. The framework has not been prospectively validated and is derived from a literature heavily represented by Lepidoptera and Diptera, with fewer examples from several other insect orders. Broader testing should examine whether the same inferential separation remains useful across deeper divergences, poorly sampled radiations and taxa for which high-quality genomes or replicated contact-zone data are unavailable.

Validation should also focus on whether the proposed logic improves reproducibility of historical interpretation, not whether it mechanically produces more taxonomic changes. A useful reticulation-aware system should sometimes preserve existing classifications, sometimes qualify them and sometimes motivate revision. If it systematically increases splitting, lumping or network complexity regardless of evidence, it would have failed its central purpose.

Conclusion

Introgression belongs explicitly in insect species histories when the evidence supports it, but it should not be presumed from discordance, hybridization or contact alone. Gene trees, local genomic histories, mitochondrial markers, network edges and species boundaries represent different inferential levels and should remain distinguishable. The proposed reticulation-aware classification logic links these levels without imposing a universal ancestry threshold or requiring networks to replace species trees. Its central principle is simple: reticulation should remain visible through the transition from genomic evidence to species history and, only where justified, to classification. Making that transition explicit offers a more faithful representation of complex evolutionary histories while preserving uncertainty, negative evidence and taxonomic restraint.

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References

1. San Jose M, Doorenweerd C, Rubinoff D. Genomics reveals widespread hybridization across insects with ramifications for species boundaries and invasive species. Curr Opin Insect Sci. 2023;58:101052. doi:10.1016/j.cois.2023.101052
2. Bjornson S, Verbruggen H, Upham NS, Steenwyk JL. Reticulate evolution: Detection and utility in the phylogenomics era. Mol Phylogenet Evol. 2024;201:108197. doi:10.1016/j.ympev.2024.108197
3. Suvorov A, Kim BY, Wang J, Armstrong EE, Peede D, D'Agostino ERR, et al. Widespread introgression across a phylogeny of 155 Drosophila genomes. Curr Biol. 2022;32(1):111-23.e5. doi:10.1016/j.cub.2021.10.052

4. Suvorov A, Scornavacca C, Fujimoto MS, Bodily P, Clement M, Crandall KA, et al. Deep ancestral introgression shapes evolutionary history of dragonflies and damselflies. Syst Biol. 2022;71(3):526-46. doi:10.1093/sysbio/syab063
5. Hinojosa JC, Marques V, Sánchez Mesa L, Dapporto L, Dincă V, Vila R. Can species endure massive introgression? Genomic evidence of asymmetric gene flow in Melitaea butterflies. Syst Entomol. 2024;49(4):583-95. doi:10.1111/syen.12631
6. Hibbins MS, Hahn MW. Phylogenomic approaches to detecting and characterizing introgression. Genetics. 2022;220(2). doi:10.1093/genetics/iyab173
7. Koppetsch T, Malinsky M, Matschiner M. Towards reliable detection of introgression in the presence of among-species rate variation. Syst Biol. 2024;73(5):769-88. doi:10.1093/sysbio/syae028
8. Pang XX, Zhang DY. Detection of ghost introgression requires exploiting topological and branch length information. Syst Biol. 2024;73(1):207-22. doi:10.1093/sysbio/syad077
9. Ji J, Roberts T, Flouri T, Yang Z. Inference of cross-species gene flow using genomic data depends on the methods: Case study of gene flow in Drosophila. Syst Biol. 2025;74(4):566-82. doi:10.1093/sysbio/syaf019
10. Tiley GP, Flouri T, Jiao X, Poelstra JW, Xu B, Zhu T, et al. Estimation of species divergence times in presence of cross-species gene flow. Syst Biol. 2023;72(4):820-36. doi:10.1093/sysbio/syad015
11. Herrig DK, Ridenbaugh RD, Vertacnik KL, Everson KM, Sim SB, Geib SM, et al. Whole genomes reveal evolutionary relationships and mechanisms underlying gene-tree discordance in Neodiprion sawflies. Syst Biol. 2024;73(5):839-60. doi:10.1093/sysbio/syae036
12. He B, Zhao Y, Su C, Lin G, Wang Y, Li L, et al. Phylogenomics reveal extensive phylogenetic discordance due to incomplete lineage sorting following the rapid radiation of alpine butterflies (Papilionidae: Parnassius). Syst Entomol. 2023;48(4):585-99. doi:10.1111/syen.12592
13. Owen CL, Miller GL. Phylogenomics of the Aphididae: Deep relationships between subfamilies clouded by gene tree discordance, introgression and the gene tree anomaly zone. Syst Entomol. 2022;47(3):470-86. doi:10.1111/syen.12542
14. Kozak KM, Joron M, McMillan WO, Jiggins CD. Rampant genome-wide admixture across the Heliconius radiation. Genome Biol Evol. 2021;13(7). doi:10.1093/gbe/evab099
15. Hinojosa JC, Dapporto L, Pitteloud C, Koubínová D, Hernández-Roldán J, Vicente JC, et al. Hybridization fuelled diversification in Spialia butterflies. Mol Ecol. 2022;31(10):2951-67. doi:10.1111/mec.16426
16. Palahí A, García-Berro A, Dincă V, Vodă R, Dapporto L, Backström N, et al. Trans-Atlantic dispersal and introgression explain Holarctic disjunct distributions in Vanessa butterflies. Mol Ecol. 2025;34(11). doi:10.1111/mec.17781
17. Rosser N, Seixas F, Queste LM, Cama B, Mori-Pezo R, Kryvokhyzha D, et al. Hybrid speciation driven by multilocus introgression of ecological traits. Nature. 2024;628(8009):811-7. doi:10.1038/s41586-024-07263-w
18. Edelman NB, Frandsen PB, Miyagi M, Clavijo B, Davey JW, Dikow RB, et al. Genomic architecture and introgression shape a butterfly radiation. Science. 2019;366(6465):594-9. doi:10.1126/science.aaw2090
19. Martin SH, Davey JW, Salazar C, Jiggins CD. Recombination rate variation shapes barriers to introgression across butterfly genomes. PLoS Biol. 2019;17(2). doi:10.1371/journal.pbio.2006288
20. Ebdon S, Laetsch DR, Vila R, Baird SJE, Lohse K. Genomic regions of current low hybridisation mark long-term barriers to gene flow in scarce swallowtail butterflies. PLoS Genet. 2025;21(4). doi:10.1371/journal.pgen.1011655
21. Burbrink FT, DeBaun D, Foley NM, Murphy WJ. Recombination-aware phylogenomics. Trends Ecol Evol. 2025;40(9):900-12. doi:10.1016/j.tree.2025.06.011
22. Doorenweerd C, San Jose M, Geib S, Barr N, Rubinoff D. Genomic data reveal new species and the limits of mtDNA barcode diagnostics to contain a global pest species complex (Diptera: Tephritidae: Dacinae). Syst Entomol. 2024;49(2):279-93. doi:10.1111/syen.12616
23. Congrains C, Dupuis JR, Rodriguez EJ, Norrbom AL, Steck G, Sutton B, et al. Phylogenomic analysis provides diagnostic tools for the identification of Anastrepha fraterculus (Diptera: Tephritidae) species complex. Evol Appl. 2023;16(9):1598-618. doi:10.1111/eva.13589
24. Dong X, Zhang H, Zhu X, Wang K, Xue H, Ye Z, et al. Mitochondrial introgression and mito-nuclear discordance obscured the closely related species boundaries in Cletus Stål from China (Heteroptera: Coreidae). Mol Phylogenet Evol. 2023;184:107802. doi:10.1016/j.ympev.2023.107802

25. Dupuis JR, Sperling FAH. Phylogenomic test of mitochondrial clues to archaic ancestors in a group of hybridizing swallowtail butterflies. Mol Phylogenet Evol. 2020;152:106921. doi:10.1016/j.ympev.2020.106921
26. Hausdorf B. Species delimitation using genomic data: Options and limitations. Mol Ecol. 2025;34(8). doi:10.1111/mec.17717
27. Boman J, Nolen ZJ, Backström N. On the origin of an insular hybrid butterfly lineage. Evolution. 2025;79(4):510-24. doi:10.1093/evolut/qpaf017
28. Augustijnen H, Lucek K. Beyond gene flow: (Non)-parallelism of secondary contact in a pair of highly differentiated sibling species. Mol Ecol. 2024;33(17). doi:10.1111/mec.17488