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Species Complexes Should Be Treated as Staged Research Programs for Discovering, Testing, and Naming Hidden Insect Diversity

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ABSTRACT

Insect species complexes are often treated as delimitation problems whose endpoint is a set of species boundaries. That framing collapses distinct inferential tasks and can obscure whether an observed signal represents overlooked species, population structure, hybridization, marker-specific resolution, a legacy naming problem, or merely an identification problem. This article develops a stage-based taxonomic architecture separating discovery, hypothesis generation, delimitation, independent validation, diagnosis and nomenclature, and post-description reassessment. Discovery is deliberately bidirectional, allowing both hidden diversity and excessive prior splitting. Delimitation is separated from statistical clustering by explicit consideration of gene flow, spatial continuity, model assumptions, preprocessing, and marker choice. Independent validation requires partly nonredundant evidence rather than repetition of the same signal. Naming remains connected to diagnoses, types, and existing nomenclature, while materially new evidence can reopen a completed description. The proposed stage-gate logic treats return to an earlier stage, synonymy, and unresolved status as legitimate outcomes. It is an organizational synthesis, not an empirically validated universal protocol, and requires prospective testing before claims of improved accuracy, efficiency, or stability are warranted.

Keywords: Insect species complexes, Integrative taxonomy, Species delimitation, Cryptic diversity, Phylogenomics, Taxonomic reassessment

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Introduction

An insect species complex is not necessarily a reservoir of undescribed species. It may contain overlooked lineages, structured populations, hybrid entities, weakly differentiated forms, synonyms, or names that no longer map cleanly onto newly recovered variation. Integrative taxonomic work has produced both splitting and synonymization, scalable taxonomic approaches explicitly distinguish preliminary hypotheses from deeper testing, and species recognition can remain provisional as different properties are brought into congruence [1–3]. The problem is therefore bidirectional: a research programme must detect hidden diversity without making "more species" its default success criterion.

The evidential landscape also changes through time. Natural-history collections now provide imaging, distributional, and, where preservation permits, genomic resources that can reopen old complexes [4]. Yet newly

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observed structure does not erase nomenclatural history: new descriptions must still be compared with previously described taxa and supported by usable differential evidence [5]. DNA-barcode clusters can aid sorting and discovery, but they are not automatic substitutes for species descriptions [6]. Discovery, delimitation, diagnosis, and naming thus ask different questions even when they share specimens or characters.

This article proposes treating insect species complexes as staged research programmes rather than single-shot delimitation exercises. The stages are functional, not a universal hierarchy of morphology, genomics, geography, ecology, life history, or reproductive evidence. The key distinction is between a signal that makes a hypothesis worth considering and evidence adequate for a stronger taxonomic claim. A complex may advance, remain unresolved, return for targeted sampling, split, merge, or be redescribed; no direction of change is assumed to be intrinsically preferable.

Materials and Methods

This synthesis organizes taxonomic work by inferential task rather than technique. A stage denotes a change in the claim being evaluated: detecting unexpected structure, specifying candidate lineage or mechanism hypotheses, testing boundaries, validating them with partly independent evidence, linking conclusions to diagnoses and names, and reopening them when materially new evidence appears. No fixed evidence hierarchy is imposed. Phylogenomic inference remains sensitive to sampling, processing, model choice, and systematic error even with large datasets [7], so data volume alone cannot define readiness to advance.

A "gate" is proposed here as a qualitative inferential checkpoint, not a numerical threshold. In the *Temnothorax salvini* group, competing genomic delimitations required arbitration using morphology and geography [8]. In the *Adelges piceae* complex, genetics, reproductive biology, morphology, and hybrid analyses transformed a multi-name problem into a two-species interpretation, showing that hybrid and synonym hypotheses must remain possible [9]. Description of *Neuroterus valhalla* instead linked morphology, phenology, behavior, alternating generations, and a genomic reference, illustrating that naming can require biological connections beyond the output of a delimiter [10].

The proposed process is claim-centered: the same technique can play different roles at different stages. A barcode may discover an anomalous cluster; genome-wide data may test lineage distinctness; morphology may challenge a partition or provide diagnosis; and museum material may later anchor a historical name. A gate remains open when evidence for the stronger claim is largely redundant with the discovery signal, major alternatives remain untested, or the inferred units cannot yet be connected to diagnosis or nomenclature. The architecture therefore makes stopping reasons explicit without prescribing universal thresholds.

Results and Discussion

Discovery should be sensitive to departures from the current taxonomy while remaining agnostic about rank. Molecular screening of Xenidae produced 77–96 putative units across different delimitation procedures, signaling potentially underestimated cryptic diversity but not a corresponding number of confirmed species [11]. Genome-wide analysis of Palearctic *Gymnosoma* produced the opposite warning by failing to distinguish many currently recognized species [12]. A discovery signal is therefore defined here as a reproducible reason to question the existing partition, whether toward splitting or consolidation.

Discordance is itself informative. In the *Nemophora degeerella* complex, ddRAD data strongly separated lineages where genital morphology and several nuclear markers did not, but that case does not establish a universal genomic priority [13]. Historical subspecies within *Metamasius hemipterus* could be retested as phylogenetic hypotheses even though color boundaries were overlapping or weak [14]. Conversely, molecular delimitation in *Gnaptorina* broadly supported existing morphospecies [15]. Discovery can thus expose hidden structure, possible oversplitting, legacy-rank uncertainty, or cross-evidence concordance.

The proposed discovery outputs are therefore candidate split, candidate merge, or documented discordance requiring follow-up. These are organizational labels, not biological categories. Their purpose is to stop early analytical clusters, absences of clustering, or character conflicts from acquiring more taxonomic meaning than the evidence yet supports.

Hypothesis-generation stage

Once a pattern is sufficiently repeatable to merit explanation, the task changes from finding structure to specifying alternatives. In the *Andrena proxima* complex, genomic analyses supported three lineages while phenological separation and *Wolbachia* infection were discussed as possible contributors to boundary maintenance [16]. These observations justify mechanism hypotheses but do not establish causal speciation processes. The proposed architecture therefore keeps lineage hypotheses and mechanism hypotheses on separate evidential tracks.

A competing-hypothesis register is proposed where ecology, demography, and genomic history can generate similar patterns. In *Ectoedemia*, one complex was resolved despite weak morphology or COI, whereas another retained overlap compatible with incomplete lineage sorting or admixture; a host-race explanation was not supported in one focal taxon [17]. Null results and unresolved alternatives must survive into delimitation. The gate to delimitation is reached when candidate partitions and the major processes capable of producing them are explicit enough to test, not when a preferred mechanism has been declared.

Delimitation stage

Delimitation tests candidate partitions, but a statistical partition is not a taxonomic verdict. Multispecies-coalescent analyses can strongly support population splits, gene-flow-aware models address histories that isolation-only analyses may misrepresent, and reproductive-isolation evidence evaluates a different criterion from sequence clustering [18–20]. These methods are valuable because they answer related but nonidentical questions. The proposed delimitation gate therefore asks whether a candidate boundary remains interpretable after relevant model assumptions and alternative criteria are made explicit.

Spatial continuity is a central boundary condition. Parapatric *Melitaea* populations showed genomic differentiation together with admixture, illustrating that boundaries may be continuous rather than sharply separable [21]. Gene flow neither automatically collapses taxa nor confirms their distinctness; it increases the need for geographic sampling and demographic alternatives.

Analytical configuration can also alter inference. In *Monochamus*, allele phasing affected coalescent delimitation, making preprocessing part of the uncertainty structure [22]. In the *Ceratitis* FARQ complex, mitochondrial data failed to resolve species that genome-wide SNPs separated, while genomic analyses also detected gene flow [23]. Marker failure may therefore reflect marker properties, whereas marker success still requires taxonomic interpretation.

Delimitation must also permit consolidation. Integrative phylogenomics of the *Bactrocera frauenfeldi* complex supported five species while synonymizing *B. albistrigata* with *B. frauenfeldi* and finding poor COI diagnostic performance for most examined species [24]. A candidate split may be supported, rejected, merged with an existing name, or remain unresolved. Progress is movement toward a better-supported taxonomic state, not toward a larger species count.

Because these outcomes arise from different failure modes, a prediction-and-test ledger is more informative than a single evidence score. It separates the observed pattern from the alternative interpretation that must remain testable and marks new gate logic as proposed.

Table 1. Delimitation-stage prediction-and-test ledger for separating lineage signal from taxonomic closure

Evidence	Research or test	Interpretive consequence · Limits and uncertainty	Evidential standing · Biological setting
Strong coalescent partition			
Sequence-based partition stabilizes	Test demographic and biological alternatives	Supports lineage structure, not species rank by itself Population structure can mimic species divergence	Proposed gate interpretation Recent divergence or geographic structure
Differentiation with migration			
Structure coexists with admixture	Sample the transition and compare migration-aware histories	Boundary may be continuous Connectivity, introgression, and recent divergence can overlap	Proposed gate interpretation Parapatric or contact-zone systems
Marker discordance			
Marker classes differ in resolution	Match markers to the question	Non-resolution can be evidence-specific Inheritance and information content differ	Evidence-derived pattern

	and seek corroboration		Recent divergence or introgression
		Preprocessing sensitivity	
Phasing or processing changes inference	Require sensitivity analysis before closure	Analytical handling contributes uncertainty Model/data representation is consequential	Proposed checkpoint Multilocus/coalescent analyses
		Cross-evidence concordance	
Partly independent partitions align	Test broader sampling and alternatives	Strengthens a candidate boundary Shared sampling can create dependence	Proposed gate interpretation Multiple biological evidence classes
		Integrative collapse or synonymy	
Multiple evidence classes fail to sustain prior partitions	Retest against geography and name-bearing material	Merge/synonymy can be a valid endpoint Sampling gaps can mimic collapse	Evidence-derived outcome Historically oversplit complexes
		Persistent contradiction	
Discordance exceeds simple measurement variation	Preserve rivals and return to targeted evidence	Closure remains premature ILS, introgression, plasticity, or sampling may explain conflict	Proposed unresolved state Evidence classes support incompatible partitions

The ledger cannot display how specimen evidence, population processes, and analytical models change meaning across scale. **Figure 1** therefore makes the interpretation boundary explicit and shows return paths when method sensitivity or biological continuity prevents taxonomic closure.

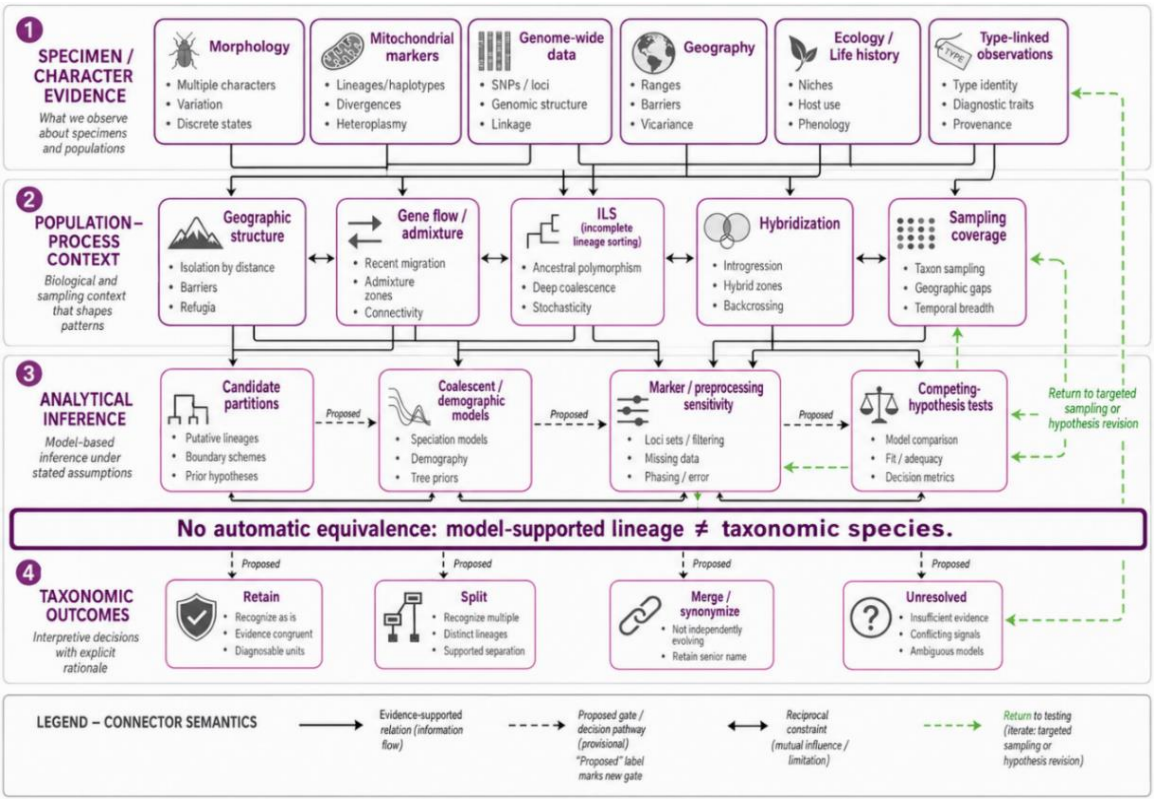


Figure 1. Where delimitation evidence changes meaning across specimen, population, analytical, and taxonomic scales

Independent validation

Delimitation and validation are not synonyms. A delimiter may be internally consistent while responding to the same structure that generated the candidate units. The proposed validation gate therefore seeks evidence partly

independent in measurement, biological basis, sampling frame, or historical anchoring. Complete independence is rarely attainable; the aim is reduced evidential redundancy so that confirmation or contradiction adds information.

Historical types provide one such test because they reconnect newly inferred lineages with nomenclatural anchors. Wing geometric morphometrics have been used to assign type specimens to cryptic bumblebee species, although overlap among some taxa showed that the method is informative rather than infallible [25]. Genome-wide data in the *Melanoplus scudderi* complex instead supported morphology-based species that earlier molecular evidence had complicated, demonstrating that genomic evidence can validate morphology as well as challenge it [26]. Independent validation should therefore be adversarial in design but neutral about whether the outcome is confirmation, revision, or continued uncertainty.

Identification performance is a different validation target. Multimodal convolutional neural-network classification combining molecular and morphological data improved identification across benchmark datasets, but performance depended on reference/training data and was weaker in some subspecies or SNP settings [27]. Such results validate identification against labelled classes; they do not independently establish that those classes are biological species. At this gate, the relevant question is whether a taxonomic hypothesis has survived a meaningful nonredundant challenge and whether remaining contradictions are explicit. Complexes that do not meet that condition should return to targeted sampling or alternative testing rather than being forced into nomenclatural closure.

Diagnosis and nomenclature

Passing delimitation and validation does not by itself produce a taxonomically usable species. The next inferential task is to connect supported lineage hypotheses to the existing nomenclatural system: relevant names, name-bearing types, differential characters, biological states, and practical routes for identification. Earlier evidence already shows why this cannot be reduced to sequence clustering. Existing taxa cannot simply be omitted from comparison [5], barcode groupings are insufficient as automatic descriptions [6], and an integrative description can connect alternate generations and genomic information to the same species hypothesis [10]. Historical types may also require renewed assignment when previously cryptic lineages are recognized [25].

Diagnosis should therefore be treated as evidence translation rather than a second delimitation exercise. A marker that separates research samples may be poorly suited to routine identification, as illustrated by marker-dependent resolution in *Ceratitis* [23] and weak COI discrimination within the *Bactrocera frauenfeldi* complex [24]. Molecular identification protocols for invasive insects can likewise remain inadequate for operational biosecurity even when molecular evidence is taxonomically informative [28]. This does not make easy diagnosis an ontological requirement for species status. It means that a naming decision should state how users can distinguish the proposed taxon, which reference material anchors that distinction, and where diagnostic uncertainty remains.

The proposed nomenclatural gate is therefore passed when a supported taxonomic conclusion has been reconciled with relevant prior names and types and translated into a defensible differential diagnosis. Failure at this gate should return the programme to comparison, specimen acquisition, or diagnostic development rather than encourage a new name detached from the historical taxonomy.

Post-description reassessment

Description is a publication event, not an inference-proof endpoint. New geographic sampling, recovered museum material, higher-resolution data, evidence of hybridization, or improved correspondence between historical names and contemporary populations can change the interpretation of a complex. In *Junonia* from the American southwest and Mexico, integrated geographic, morphological, mitochondrial, nuclear, and life-history information supported five lineages, restoration of *J. grisea* to species rank, and geographically structured hybridization [29]. The presence of hybridization did not itself dictate lumping; instead, it became part of the evidence that had to be interpreted geographically.

Reassessment should nevertheless require materially informative evidence rather than repeated analytical perturbation. Existing cases show multiple directions of legitimate revision: *Adelges* work reduced a multi-name complex to fewer species [9]; *Metamasius* analyses retested historical subspecies and altered rank [14]; and *Bactrocera* phylogenomics combined species recognition with synonymy [24]. The proposed reassessment gate therefore has four admissible outcomes: confirm the current treatment, split or elevate a unit, merge or synonymize units, or retain explicit uncertainty. None is inherently a successful or unsuccessful outcome.

The central decision is whether later evidence changes the mapping among biological lineages, diagnoses, geography, and names. **Table 2** separates these reassessment states without converting them into a confidence score.

Table 2. Post-description reassessment decisions when new evidence changes the mapping between lineages, diagnoses, and names

Reassessment state	Evidence	Interpretation or consequence · Boundary or uncertainty · Interpretive consequence · Limits and uncertainty	Research or test · Status · Evidential standing	Biological setting
Confirmation under extension	Added evidence remains compatible with the published boundary and diagnosis	Existing treatment retained Wider sampling can still expose unrepresented variation	Extend geographic and life-stage coverage where relevant Proposed reassessment outcome	New localities, stages, or specimens
Rank or boundary expansion	New integrative evidence changes the supported partition	Split, elevation, or restoration may be warranted Gene flow or character overlap may persist	Re-test contact zones, types, and differential diagnosis Evidence-derived pattern	Previously named populations or forms gain independent support
Merge or synonymy	New evidence fails to sustain previously named boundaries	Names may be consolidated Sparse sampling can mimic lack of differentiation	Confirm against types, geography, and alternative datasets Evidence-derived pattern	Prior names track morphotypes, hybrids, or weak partitions
Hybrid-zone reinterpretation	Geographic and genetic evidence shows restricted admixture	Species rank may remain compatible with some hybridization Extent, direction, and temporal stability of exchange matter	Sample transects and test alternative demographic histories Evidence-derived pattern	Named taxa meet in contact zones
Diagnostic remapping	New marker, morphology, or type evidence changes assignment rules	Diagnosis revised without necessarily changing species rank Identification performance is reference-dependent	Validate new diagnostics against anchored material Proposed reassessment outcome	Delimitation survives but former identifier fails
Persistent contradiction	No interpretation resolves major discordance	Treatment remains explicitly open ILS, introgression, sampling, or legacy naming may remain confounded	Return to the stage generating the unresolved claim Proposed unresolved state	New evidence conflicts across geography, markers, morphology, or names

A table cannot show how reassessment accumulates through time or how later evidence can feed back to different earlier stages. **Figure 2** therefore treats a described taxonomy as a temporal signal-integration field rather than a terminal node.

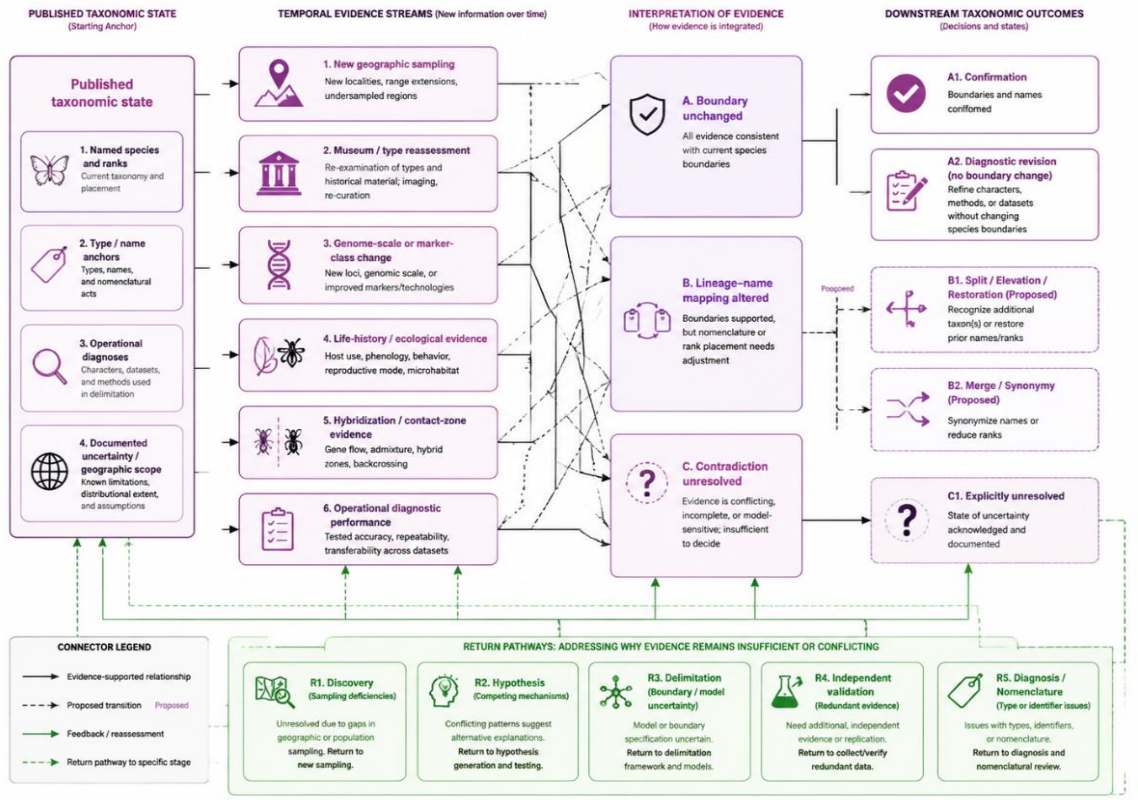


Figure 2. How post-description evidence can preserve, redirect, or reopen a named species boundary through time

Stage-gate architecture for species complexes

The proposed architecture integrates the preceding stages by making claim readiness, rather than data quantity, the criterion for progression. Large-scale integrative taxonomy already demonstrates the usefulness of inexpensive preliminary hypotheses followed by richer testing [2]. Conversely, increasing sequence information can strengthen a population partition without resolving its taxonomic meaning [18], while integrative phylogenomics may ultimately support both recognized species and synonymy [24]. These observations motivate, but do not validate, a stage-gate research programme.

Gate 1 separates discovery from hypothesis generation: an anomalous cluster, discordance, or failure to recover a named unit becomes a candidate problem, not a species. Gate 2 separates hypothesis generation from delimitation: candidate partitions and plausible competing processes must be explicit enough to test. Gate 3 separates delimitation from independent validation: a favored boundary must survive a partly nonredundant challenge. Competing delimitation results in *Temnothorax* show why arbitration can be necessary [8]. Gate 4 separates validation from nomenclatural closure: supported units must be reconciled with existing names, types, and usable diagnoses. Gate 5 is post-description reassessment: materially new evidence can reopen the precise claim that has become uncertain.

A failed gate is not proposed as a negative score. It is a routing instruction. Host-associated *Ectoedemia* patterns show why unresolved alternatives can require renewed hypothesis testing [17], while overlapping morphometric assignments of some historical bumblebee types show why nomenclatural linkage may remain uncertain despite useful independent evidence [25]. The return path should therefore target the source of uncertainty: inadequate sampling returns to discovery; confounded mechanisms to hypothesis generation; model or boundary uncertainty to delimitation; evidential dependence to validation; and unresolved names or identifiers to diagnosis and nomenclature.

This architecture deliberately does not define a universal species concept. Different research programmes may require different evidence to cross a gate because reproductive, ecological, morphological, genomic, geographic, and historical properties are not interchangeable. What remains constant is the requirement that the evidence be appropriate to the claim being advanced and that contradictory evidence remain visible. The proposed architecture

consequently treats unresolved status as a legitimate state and premature closure as progression beyond what the available evidence can support.

The principal contribution of this article is organizational. Insect species complexes are reframed as research programmes in which discovery, explanation, delimitation, validation, naming, and reassessment remain distinguishable even when they use overlapping specimens and technologies. Integrative taxonomy has repeatedly changed conclusions in both directions [1], and species recognition remains provisional in the presence of changing evidence [3]. The stage-gate architecture makes that revisability explicit without claiming that species boundaries are arbitrary or that all evidence classes should carry equal weight in every system.

The strongest reason for staging is inferential non-equivalence. A barcode cluster can be an efficient discovery device but an insufficient description [6]. Genome-wide structure can expose hidden differentiation or undermine older splitting, yet analytical processing and marker choice can change apparent resolution [22]. Gene flow can be a competing demographic explanation without automatically determining species rank [19]. Likewise, classification performance concerns assignment to reference-labelled classes rather than independent validation of those classes [27]. Collapsing these tasks creates the risk that evidence answers a narrower question than the taxonomic conclusion attached to it.

The architecture is also intentionally bidirectional. Hidden insect diversity should not be equated with taxonomic inflation. Genome-scale reassessment of *Gymnosoma* questioned some existing named partitions [12], *Adelges* revision supported substantial consolidation [9], and *Bactrocera* work combined recognized species with synonymy [24]. Conversely, cryptic diversity can remain underestimated, as shown by Xenidae discovery work [11]. A stage-based programme therefore evaluates whether the current taxonomy is too coarse, too fine, or simply organized around the wrong evidence.

Several boundary conditions limit transferability. Evidence availability differs sharply among museum specimens, recently collected material, parasitic life histories, alternating generations, geographically continuous populations, and taxa with sparse reference collections. The biological meaning of gene flow varies with history and spatial configuration, while morphological diagnosability varies among radiations. Genomic scale cannot compensate automatically for biased geographic sampling or unsuitable models [7]. Consequently, the gates are qualitative and claim-specific rather than universal evidential thresholds.

The framework also creates practical costs. Additional stages can increase specimen, analytical, curatorial, and specialist demands, particularly for hyperdiverse dark taxa. Requiring perfect evidential independence would be unrealistic, and waiting for exhaustive knowledge could indefinitely delay useful taxonomy. The architecture therefore calls for proportional rather than maximal evidence: enough nonredundancy and alternative testing to justify the next claim, with residual uncertainty documented. Rapid preliminary hypotheses remain valuable precisely because they can prioritize where deeper work is warranted [2].

A final boundary concerns taxonomic infrastructure. Reassessment is only possible when specimens, metadata, images, sequences, and nomenclatural decisions remain recoverable across time. Entomological collections can provide the material base for such reanalysis, although preservation and accessibility are uneven [4]. Operational diagnostics add another constraint because a formally defensible taxonomy may still be difficult to apply to intercepted or damaged specimens [28]. These limitations reinforce the distinction between species inference and taxonomic usability. The proposed architecture does not require every species to be identifiable by a single character or marker; instead, it requires that limitations of available identifiers be stated and that the evidence linking present hypotheses to historical names remain auditable. This is particularly important where later reassessment depends on comparing newly sampled populations with type-bearing or legacy material rather than merely rerunning the original molecular analysis.

Most importantly, the architecture has not been prospectively validated. Its performance relative to conventional taxonomic workflows is unknown. Future evaluation should compare staged and non-staged programmes across multiple insect orders, geographic configurations, and data-richness conditions. Outcomes could include whether researchers more consistently distinguish discovery from delimitation, whether contradictory evidence is retained rather than suppressed, whether nomenclatural anchoring occurs earlier, and whether later revisions can be traced to the stage where uncertainty was underestimated. These are validation targets, not predicted benefits.

A further research priority is to test gate behavior under deliberately difficult conditions: parapatric gene flow, incomplete lineage sorting, hybrid zones, marker discordance, poor historical types, life-stage polymorphism, and operational diagnostic failure. Such comparisons should avoid treating the number of resulting species as an accuracy metric. A framework intended to organize species-complex research should be judged by whether its

decisions and uncertainties are traceable and scientifically defensible, not by whether it maximizes splitting, lumping, or apparent finality.

Conclusion

Species complexes are most productively treated as sequences of changing inferential questions rather than as single delimitation events. The proposed stage-gate architecture separates discovery, hypothesis generation, delimitation, independent validation, diagnosis and nomenclature, and post-description reassessment while preserving return paths when evidence is contradictory or incomplete. It accommodates splitting, synonymy, confirmation, diagnostic revision, and unresolved status without privileging any outcome. Its central claim is organizational rather than mechanistic or predictive: stronger taxonomic closure requires evidence appropriate to the claim being closed. Whether this architecture improves taxonomic practice remains an empirical question for future comparative validation.

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