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Integrative Taxonomy in Plant Systematics: Advances in Species Delimitation, Evidence Integration and Emerging Challenges

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Abstract

Plant taxonomy and systematics provide the framework through which plant diversity is identified, named, classified and interpreted in an evolutionary context. The expansion of molecular phylogenetics, DNA barcoding, genome-scale methods, ecological analysis and digitised botanical collections has broadened the evidence available for species delimitation. At the same time, these developments have made taxonomic decisions more complex. Morphological variation may not correspond neatly to evolutionary lineages; gene trees may disagree because of incomplete lineage sorting, hybridisation or introgression; and different analytical methods can produce boundaries that depend on sampling and model assumptions. Integrative taxonomy addresses these challenges by evaluating complementary lines of evidence rather than treating a single character system as universally decisive. This review critically discusses the conceptual foundations of integrative taxonomy, the contributions and limitations of morphological, anatomical, cytological, reproductive, ecological, geographical and molecular evidence, and the role of phylogenomics and emerging computational approaches. It also considers the distinction between species discovery, species delimitation, taxonomic classification and nomenclatural decisions under the International Code of Nomenclature for algae, fungi, and plants. Particular attention is given to evidence discordance, hybrid and polyploid plant groups, cryptic diversity, reproducibility and the risk of interpreting clusters as species without sufficient biological justification. The review argues that robust taxonomic conclusions require explicit species concepts, transparent sampling, critical evaluation of evidence independence, careful treatment of uncertainty and accessible documentation of specimens and analytical decisions. Rather than proposing a universal algorithm, it identifies practical priorities for a pluralistic but disciplined integrative workflow. These include preregistered or clearly stated analytical choices where appropriate, open access to vouchers and sequence records, explicit reporting of conflicting evidence, and closer coordination between taxonomic expertise and computational methods.

Keywords: plant systematics; integrative taxonomy; species delimitation; DNA barcoding; phylogenomics; hybridisation; polyploidy; taxonomic uncertainty; botanical nomenclature

1. Introduction

Taxonomy is more than the assignment of names to organisms. It is a scientific activity that establishes hypotheses about biological identity, recognises diagnosable groups, describes variation and provides a stable means of communicating biodiversity. Systematics places these tasks within an evolutionary framework by investigating relationships among organisms and the processes responsible for their diversification. Reliable taxonomy is consequently important to ecology, conservation, agriculture, pharmacognosy, plant pathology and environmental monitoring. When species boundaries are uncertain, estimates of distribution, endemism, extinction risk and ecosystem function may also become uncertain.

Traditional plant taxonomy has relied heavily on comparative morphology, including vegetative, floral, fruit and seed characters. These observations remain indispensable because they can be examined directly, are often available from herbarium specimens and support identification in the field. Yet morphology alone may be insufficient in groups with convergent traits, phenotypic plasticity, reduced or seasonally unavailable structures, or recent evolutionary divergence. Conversely, molecular differences do not automatically demonstrate that populations represent separate species. The challenge is not to replace one evidence type with another, but to understand what each source can and cannot establish.

Integrative taxonomy emerged as a response to this challenge. Dayrat (2005) argued for species delimitation informed by multiple perspectives, while Schlick-Steiner et al. (2010) described a multisource approach to biodiversity research. Integrative approaches seek explanations that account for the total evidence rather than treating morphology, genetics, ecology or reproductive biology as isolated authorities. In plant systematics, the approach is particularly relevant because reticulate evolution, hybridisation and polyploidy can complicate simple branching models of diversification (Rieseberg, 1997; Hörandl, 2022).

The growth of DNA barcoding, phylogenomics and computational species delimitation has expanded analytical capacity but has not removed conceptual uncertainty. The recommended plant barcode combination of *rbcl* and *matK* offers a standardised basis for specimen identification, yet the discriminatory power of barcode loci varies among plant groups and closely related species may share or exchange genetic variants (CBOL Plant Working Group, 2009). Genome-scale data can resolve relationships that were previously inaccessible, but large datasets can also reveal gene-tree conflict and increase dependence on analytical assumptions. Karbstein et al. (2024) describe these issues as part of a broader transition toward more standardised, integrative and computationally assisted species delimitation.

The Indian context illustrates both the importance and the practical challenges of integrative plant systematics. India's varied biogeographic regions, high floristic diversity and endemic plant lineages make reliable identification and documentation important for biodiversity assessment and conservation. The Botanical Survey of India's floristic and revisionary work provides a foundational taxonomic resource, while Indian studies show how molecular evidence can complement, but not simply replace, morphological assessment. Sheth and Thaker (2017) reviewed the value of combining DNA barcoding with traditional taxonomy for biodiversity conservation, and Joshi and Agarwal (2021) discussed the progress and prospects of integrative taxonomy in the Indian subcontinent. Empirical studies of Indian plant groups also demonstrate that barcode performance is taxon-dependent: universal loci may fail to resolve some closely related species in *Berberis* (Roy et al., 2010), whereas supplementary nuclear or plastid regions can improve discrimination in selected groups, including tropical trees (Tripathi et al., 2013). These examples support a context-sensitive approach in which specimen-based identification, regional floras, expert taxonomic knowledge and molecular data are evaluated together.

This review synthesises the principal evidence types used in plant taxonomy, evaluates their respective strengths and limitations, and considers how they can be combined without overstating what any single method demonstrates. The central argument is that integrative taxonomy is most useful when integration is treated as a reasoned process of hypothesis evaluation rather than the simple accumulation of data. A strong taxonomic conclusion should identify the species concept being applied, explain the relevance of each evidence source, investigate discordance, and separate biological interpretation from nomenclatural procedure.

2. Review scope and approach

This article is a critical narrative review rather than a systematic review or meta-analysis. It draws on influential conceptual papers, methodological studies and selected recent contributions relevant to plant species delimitation, molecular identification, phylogenetics, hybridisation, polyploidy and botanical nomenclature. No new field observations, laboratory experiments or original dataset analyses were conducted for this manuscript. The purpose is interpretive synthesis: to compare the roles of different evidence types, identify recurring methodological difficulties and formulate practical priorities for taxonomic research.

The literature discussed here is illustrative rather than exhaustive. A submission intended for a specific journal should include a reproducible search strategy, explicit databases and search dates, inclusion and exclusion criteria, and a screening record if the manuscript is to be presented as a systematic or scoping review. The current narrative format should not be represented as a systematic review, and no claim of comprehensive coverage is made.

3. Conceptual foundations of integrative taxonomy

3.1 Species concepts and the delimitation problem

Species are often treated as the fundamental units of biodiversity, but their boundaries are not always straightforward to infer. The biological species concept emphasises reproductive isolation, whereas phylogenetic approaches commonly emphasise ancestry and diagnosability. Ecological concepts focus on niche differentiation, while lineage-based approaches consider whether populations form separately evolving entities. De Queiroz (2007) argued that many species concepts emphasise different properties associated with the process of lineage separation. Under this interpretation, reproductive isolation, diagnosability and ecological differentiation may provide evidence of divergence without serving as universally necessary criteria in every case.

The practical implication is that taxonomists should state the question and concept guiding a delimitation study. A method designed to detect genetic clusters does not necessarily test reproductive isolation; a morphological key is not a direct test of evolutionary independence; and a niche model cannot alone establish that two ecological groups are separate species. Different methods may be appropriate for different questions, but their outputs must be interpreted in relation to the biological hypothesis under consideration.

3.2 Integrative versus iterative taxonomy

Integrative taxonomy combines complementary evidence to evaluate species hypotheses, while iterative taxonomy emphasises repeated refinement of hypotheses as new information becomes available. Yeates et al. (2011) discussed the relationship between integrative and iterative approaches and highlighted the importance of treating taxonomy as an ongoing process of hypothesis testing. In practice, the two approaches

can be complementary: a taxonomist may integrate several evidence types in one analysis and then revise the interpretation when additional populations, specimens or genomic information become available.

The aim is not necessarily to achieve agreement among all datasets. Discordance may reveal biological processes such as introgression, incomplete lineage sorting, hybrid origin or ecological adaptation. It can also expose technical limitations, such as inadequate sampling, misidentification, contamination or inappropriate analytical assumptions. A defensible integrative analysis investigates these possibilities rather than averaging conflicting results or selecting whichever result supports a preferred classification.

4. Morphological and anatomical evidence

Morphology remains the operational foundation of much plant identification. Characters such as leaf arrangement, venation, indumentum, floral structure, fruit morphology and seed traits are often observable on herbarium material and can be translated into diagnoses and identification keys. Morphological evidence is also essential for linking molecular results to named taxa because sequence clusters must ultimately be connected to specimens and taxonomic descriptions.

Its limitations arise when character states overlap, vary with age or environment, or evolve convergently in unrelated lineages. Vegetative traits may be strongly influenced by water availability, light, nutrient conditions or developmental stage. Reproductive characters can be highly informative but may be absent from sterile specimens or available only during a limited season. Preservation may also distort colour, texture or dimensions. A rigorous study therefore defines characters precisely, documents measurement procedures, samples variation adequately and distinguishes stable diagnostic features from traits that are environmentally or developmentally labile.

Anatomical and micromorphological characters can reveal differences not visible to the unaided eye, including epidermal structure, trichome types, stomatal features, pollen morphology and seed-coat patterns. Such characters can be especially useful in morphologically similar groups. Nevertheless, they should not be treated as intrinsically more reliable than macromorphology. Their value depends on repeatability, sampling, preparation methods and their demonstrated relevance to the taxonomic problem.

5. Cytology, reproductive biology and genome evolution

Chromosome number, ploidy level, genome size and reproductive behaviour can provide important evidence about plant diversification. Polyploidy is widespread in plant evolution and may contribute to the formation of lineages with distinctive genetic, ecological or reproductive properties. Hybridisation can create combinations of parental genomes and phenotypes, while introgression may transfer genetic material across species boundaries. These processes complicate the assumption that species relationships can always be represented by a simple bifurcating tree (Rieseberg, 1997; Hörandl, 2022).

Cytological evidence can help distinguish diploid and polyploid cytotypes, clarify reproductive compatibility and identify possible routes of lineage formation. However, chromosome-number differences do not automatically determine taxonomic rank, and shared chromosome numbers do not prove conspecificity. Reproductive evidence also requires careful interpretation: observed crossing compatibility under controlled conditions may not reflect mating patterns in nature, while lack of observed hybrids may reflect limited sampling rather than complete reproductive isolation.

In suspected hybrid groups, an integrative study should consider whether morphology, cytology, nuclear markers, organellar genomes and reproductive behaviour tell a coherent evolutionary story. Discordant patterns may be expected under reticulate evolution. The task is to explain how the evidence arose, not to require every evidence source to recover an identical branching pattern.

6. Molecular systematics and DNA barcoding

DNA sequence data have transformed plant systematics by providing characters that can be compared across life stages and, in many cases, across preserved material. Molecular phylogenetics can test hypotheses of relationship, reveal cryptic lineages and help identify specimens that lack diagnostic reproductive structures. DNA barcoding applies selected standardised regions to specimen identification. The CBOL Plant Working Group (2009) recommended the combination of *rbcl* and *matK* as a core barcode for land plants, balancing recoverability, sequence quality and discriminatory performance.

DNA barcoding is best understood as an identification aid rather than a universal species-delimitation test. Closely related species may share barcode sequences because divergence is recent, ancestral polymorphism persists or hybridisation has transferred genetic variants. In other cases, within-species variation may be substantial. A barcode match is therefore only as reliable as the reference library, taxonomic identification and geographic representation underlying the comparison. Voucher specimens and traceable sequence accessions are essential for checking unexpected matches and revising identifications.

Evidence from Indian plant research reinforces this caution. Roy et al. (2010) found that standard plant barcode loci did not consistently resolve closely related Indian *Berberis* species, while Tripathi et al. (2013) evaluated several candidate loci in tropical Indian tree species and highlighted the value of considering supplementary regions alongside the standard markers. In applied identification, Mishra et al. (2016) further showed the relevance of DNA barcoding to the authentication of medicinal plant materials. Collectively, these studies indicate that marker choice should be validated for the target taxonomic group and that sequence-based assignments should remain linked to authenticated voucher specimens and conventional taxonomic evidence.

Molecular phylogenetics also requires attention to the distinction between gene trees and species trees. Individual loci record genealogical histories that may differ from the history of species because of incomplete lineage sorting, introgression, gene duplication or loss. Concatenating loci can improve resolution under some conditions, but it may conceal heterogeneity among gene histories if the model is inappropriate. Coalescent-based methods and explicit tests of reticulation can help address these complexities, although their assumptions and sampling requirements must be evaluated rather than treated as automatic solutions.

7. Phylogenomics and emerging computational methods

Phylogenomics uses large numbers of loci or genome-scale information to investigate evolutionary relationships. Its potential advantage is the availability of many informative characters, which may improve resolution for recent or rapid radiations. Yet more sequence data do not eliminate the need for sound taxon sampling, orthology assessment, model choice and interpretation of gene-tree conflict. Large datasets may produce highly supported trees that remain sensitive to systematic error or to the biological processes generating discordance.

Computational species-delimitation methods range from distance-based and tree-based approaches to multispecies coalescent models, clustering algorithms and machine-learning procedures. Their outputs depend on assumptions about population structure, gene flow, sampling and the meaning of a species boundary. A statistically distinct cluster is not automatically a taxonomic species: population structure within a species can generate clusters, while recently diverged species may remain genetically intermixed at some loci.

Karbstein et al. (2024) discuss the prospects and challenges of integrating multi-approach data with artificial intelligence in species delimitation. Computational systems may assist with image classification, specimen sorting, character extraction, sequence analysis and the identification of candidate groups. However, they are dependent on training data, taxonomic coverage and the quality of reference identifications. Their predictions should remain auditable and linked to specimens and expert assessment. Artificial intelligence is best viewed as a tool for managing complexity, not as a substitute for taxonomic reasoning.

8. Ecological, geographical and biogeographical evidence

Ecological differentiation can contribute to species delimitation when lineages occupy distinct habitats, exhibit consistent niche preferences or maintain differentiation despite opportunities for contact. Geographical distribution can reveal allopatric lineages, disjunctions and patterns consistent with historical isolation. These sources may be particularly informative when morphological differentiation is subtle or when the evolutionary processes shaping a group are not fully resolved by molecular data alone.

However, ecological and geographical evidence can be confounded by incomplete sampling, environmental plasticity and spatial population structure. Populations separated by distance may show genetic differentiation without constituting separate species. Conversely, distinct lineages can occur sympatrically and remain difficult to distinguish by habitat alone. Ecological niche models depend on occurrence records, background selection, spatial resolution and assumptions about environmental suitability. They should therefore be interpreted as evidence about potential distributions or ecological differentiation, not as direct proof of species status.

Geographical data also raise practical issues of provenance and uncertainty. Records may be misidentified, imprecisely georeferenced or based on cultivated material. Integrative studies should document the origin and reliability of occurrence records and distinguish observed distributions from modelled predictions. When records are used to infer evolutionary history, the limitations of sampling and the possibility of unsampled populations should be stated clearly.

9. Evidence integration: from multiple data types to defensible conclusions

The central challenge of integrative taxonomy is deciding how different evidence sources should influence a species hypothesis. Simply collecting more data types does not guarantee a stronger conclusion. Evidence may be redundant, of unequal quality or directed at different biological questions. A morphological character can diagnose a taxon without establishing its evolutionary independence; a molecular cluster can reveal population structure without proving species status; and an ecological difference may be environmentally induced rather than genetically fixed.

A defensible workflow begins with a clearly stated taxonomic question and species concept. The study then defines the relevant evidence, sampling units and analytical methods. Each evidence source is evaluated for

reliability, discriminatory capacity and possible dependence on other sources. Agreement among complementary evidence may strengthen a hypothesis, while disagreement should prompt investigation of biological and methodological explanations. The conclusion should reflect the total evidence and its limitations rather than the output of a single method.

A useful distinction is between evidence that is independent in its data-generation process and evidence that is independent in its biological meaning. Two datasets may be generated by different methods but reflect the same underlying process. Conversely, two character sets collected through similar methods may represent different biological mechanisms. Independence must therefore be considered in relation to the question and the causal structure of the evidence, not merely the disciplinary label.

Evidence source	Principal contribution	Common limitation	Recommended practice
Morphology and anatomy	Diagnosis, identification and observable character variation	Plasticity, convergence, developmental variation and preservation effects	Define characters, sample variation and distinguish diagnostic utility from lineage evidence
Cytology and reproductive biology	Ploidy, chromosome evolution and reproductive relationships	Intraspecific variation; laboratory compatibility may not equal natural isolation	Interpret with phylogenetic, morphological and population evidence
DNA barcoding	Standardised specimen identification and reference-library matching	Low resolution in recent radiations; incomplete or misidentified reference libraries	Link sequences to vouchers and avoid treating a barcode match as definitive species proof
Phylogenetics and phylogenomics	Evolutionary relationships and lineage-history hypotheses	Gene-tree conflict, model sensitivity, introgression and sampling bias	Report assumptions and investigate discordance among loci or methods
Ecology and geography	Niche differentiation, distribution patterns and biogeographic context	Spatial structure, environmental plasticity and biased occurrence records	Document provenance and avoid equating geographical separation with species status
Computational and AI methods	Pattern detection, candidate discovery and scalable analysis	Training bias, limited taxonomic coverage and opaque decisions	Make workflows reproducible and retain expert review and specimen traceability

The table is a conceptual synthesis rather than a quantitative ranking. No evidence type is universally superior; its value depends on the biological question, the organisms involved and the quality of the information available.

10. Species complexes, cryptic diversity and taxonomic uncertainty

Species complexes are groups in which species boundaries or relationships remain difficult to resolve. Cryptic species may be morphologically similar while representing distinct evolutionary lineages, whereas highly variable species may contain substantial morphological and genetic variation without warranting taxonomic splitting. Integrative methods can help distinguish these situations by testing whether multiple evidence sources support the same boundary and by investigating alternative explanations for observed patterns.

Taxonomic uncertainty should be reported rather than concealed. Uncertainty may arise from inadequate sampling, conflicting gene trees, incomplete type information, overlapping morphology or unresolved nomenclature. A provisional conclusion can still be useful if it states which parts of the problem are resolved and which require further evidence. This is preferable to presenting a cluster or character difference as conclusive proof when competing explanations remain plausible.

The recognition of cryptic diversity has implications for conservation, particularly when overlooked lineages have restricted distributions or distinct ecological requirements. However, taxonomic splitting can also affect conservation priorities, legal protection and estimates of endemism. Species delimitation should therefore be rigorous, transparent and linked to accessible vouchers and diagnostic information so that subsequent researchers can evaluate and revise the decision.

11. Botanical nomenclature and taxonomic stability

Biological species hypotheses and the names applied to them are related but separate matters. The International Code of Nomenclature for algae, fungi, and plants provides rules for the formation and application of scientific names. The Madrid Code was published in 2025 following amendments adopted at the Twentieth International Botanical Congress in 2024 (Turland, 2025). Authors preparing taxonomic revisions should consult the current Code and relevant nomenclatural literature rather than relying exclusively on older guidance.

A taxonomic revision may involve synonymising names, reinstating a previously recognised taxon, changing rank or describing a new species. Each action requires appropriate evidence and compliance with nomenclatural rules. Type specimens anchor the application of names, while priority and valid publication influence which name is correct under the Code. A biological interpretation cannot by itself settle every nomenclatural question, and a nomenclatural act does not independently validate a species hypothesis.

Taxonomic stability should not be confused with resistance to change. Stability is supported by clear diagnoses, accessible evidence, transparent nomenclatural reasoning and careful treatment of uncertainty. When new evidence justifies a change, a well-documented revision helps other researchers understand why the classification has changed and how previous names relate to the revised treatment.

12. Reproducibility, open science and taxonomic infrastructure

Reproducibility in plant systematics depends on the ability to trace conclusions to specimens, character observations, sequence records, analytical workflows and nomenclatural sources. Voucher deposition, persistent identifiers, public sequence accessions, version-controlled scripts and explicit reporting of analytical parameters can make taxonomic decisions easier to verify. Digitised herbarium collections and shared biodiversity infrastructures increase access to specimens and occurrence information, although digitisation does not remove the need to verify identifications or assess data quality.

Open science should include meaningful documentation, not merely the release of files. A sequence without a reliable voucher, an occurrence record without clear provenance or a script without its parameter settings may be difficult to interpret. Researchers should describe how specimens were selected, how missing data were handled, which methods were compared and why a particular delimitation was accepted. Where access to sensitive locality information is restricted for conservation reasons, the restriction should be explained while preserving as much reproducibility as is appropriate.

Taxonomic expertise remains essential in open and computational workflows. Automated tools can accelerate processing, but taxonomic names and reference identifications may contain historical errors. Curated reference libraries, expert verification and the ability to correct records are therefore necessary for reliable infrastructure. The long-term value of integrative taxonomy depends on maintaining links between analytical outputs and the physical or digital evidence on which those outputs rest.

13. Emerging challenges and future priorities

One continuing challenge is the absence of a single species-delimitation method that is appropriate for all plant groups. Different evolutionary histories require different evidence and assumptions. A method designed for recently diverged sexual lineages may perform poorly in clonal, hybrid or polyploid groups. Future research should therefore prioritise explicit biological assumptions, comparative evaluation of methods and transparent explanations of why a particular workflow was selected.

A second challenge concerns evidence integration at scale. Genome-scale datasets, high-resolution imaging, environmental information and machine-learning outputs can be difficult to combine because they differ in structure, quality and inferential meaning. Methods for data fusion should preserve the distinction between observation, model output and taxonomic interpretation. Standardised reporting may help, but standardisation should not impose an inflexible algorithm that ignores the biology of particular groups.

A third priority is the integration of taxonomic research with conservation needs. Many plant groups remain poorly sampled or taxonomically unresolved, and some lineages may disappear before their diversity is adequately documented. Rapid tools can assist candidate discovery, but formal taxonomic conclusions still require appropriate evidence, nomenclatural care and accessible documentation. Capacity-building, herbarium support and collaboration among regional specialists are therefore as important as technological innovation.

Finally, the field needs clearer ways to communicate uncertainty. Rather than reporting only a final tree or cluster assignment, studies should explain the stability of the result across reasonable analytical choices, identify conflicting evidence and state what additional observations could change the interpretation. This practice would make taxonomic conclusions more informative to conservationists, ecologists and other users who need to understand both the accepted classification and its limitations.

14. Conclusion

Integrative taxonomy is an important approach to plant systematics because no single type of evidence can resolve every species-delimitation problem. Morphology and anatomy remain central to diagnosis; cytology and reproductive biology illuminate genome evolution and reproductive relationships; molecular methods reveal genetic differentiation and evolutionary history; and ecological and geographical information place lineages in their environmental and biogeographic contexts. Computational approaches can extend the scale of analysis, but their outputs remain dependent on biological assumptions, sampling design and the quality of reference information.

The central lesson is that integration requires critical interpretation rather than the simple accumulation of data. Strong taxonomic decisions define the question being addressed, assess the limitations and possible dependence of each evidence source, investigate discordant results, and distinguish biological conclusions from nomenclatural acts. They also document specimens and analytical procedures so that other researchers can evaluate the basis of the proposed classification.

Future progress will depend on combining methodological innovation with taxonomic expertise, traceable research infrastructure, explicit reporting of uncertainty and sensitivity to the diverse evolutionary histories of plants. Integrative taxonomy is most effective when it uses multiple evidence types critically, makes its reasoning transparent and remains open to revision as new biological information becomes available.

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