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INTEGRATING MORPHOLOGICAL AND MOLECULAR DATA IN PLANT TAXONOMY

WAJID ZAMAN[1†], ASMA AYAZ[2†] AND SEONJOO PARK[1*]

[1]Department of Life Sciences, Yeungnam University Gyeongsan 38541, Republic of Korea
[2]Faculty of Sports Science, Ningbo University, Ningbo 315211, China
[†] Contributed equally to this study
**Corresponding Author's e-mail: sjpark01@ynu.ac.kr*

Abstract

Integrative taxonomy, which merges traditional morphological data using molecular techniques, is transforming plant taxonomy by creating a more accurate and comprehensive framework for species identification, classification and phylogenetic relationships. While morphology-based taxonomy offers accessible, field-applicable insights, it is limited by phenotypic plasticity, convergent evolution, and cryptic species. Molecular tools, such as DNA barcoding and next-generation sequencing, address these challenges by unravelling genetic relationships and hidden diversity. By combining both approaches, taxonomists can achieve higher taxonomic resolution, enabling more precise species delineation and enhanced understanding of evolutionary relationships and biodiversity. This method supports conservation efforts by facilitating biodiversity assessments, conservation prioritization, and effective invasive species management. Integrative taxonomy also promotes phylogenetic diversity, fostering resilience, and ensuring functional diversity in restored habitats. As emerging technologies, collaborative databases, and interdisciplinary research further advance, integrative taxonomy will be essential for tackling biodiversity loss and supporting sustainable ecological practices.

Key words: Integrative taxonomy, Molecular tools, DNA barcoding, Biodiversity assessment, Conservation prioritization, Phylogenetic diversity.

Introduction

Plant taxonomy is the scientific discipline of naming, describing, and classifying plants. It provides the foundation for organizing and understanding the immense diversity of plant life, which are essential for advancing ecological research, conservation initiatives, and practical applications in agriculture and medicine (Rouhan & Gaudeul, 2020; John *et al.*, 2022). Taxonomy facilitates the systematic cataloging of plant species, enabling scientists to communicate about biodiversity and its uses (Blackmore, 2002). With growing global environmental pressures such as habitat fragmentation or rapidly changing climate, the importance of accurate and comprehensive plant taxonomy has never been greater (Erhan *et al.*, 2021). Understanding the precise identity and relationships among plant species helps comprehend ecosystem dynamics and guide conservation priorities. This understanding also supports key areas, such as pharmacology, where plants contribute directly to the development of medicinal compounds, and agriculture, where taxonomic insights help breed resilient crop varieties (Maestre *et al.*, 2012). The urgency to identify and protect biodiversity hotspots, many of which contain high plant diversity, relies on robust taxonomic frameworks that reflect the evolutionary relationships and functional roles of species within ecosystems (Schweiger *et al.*, 2018; Akira *et al.*, 2023).

Traditional plant taxonomy has primarily relied on morphological characteristics, such as leaf structure, flower shape, and reproductive organs, to identify and classify species (Beerling and Woodward, 1996). This method provides accessible and cost-effective data that can be applied in the field, making it a longstanding approach for studying plants (Munish *et al.*, 2019). However, morphological approaches have limitations, especially when dealing with species exhibiting cryptic diversity—instances where two or more species look identical morphologically but are genetically distinct (Singhal *et al.*, 2018). Additionally, phenotypic plasticity, where a single species can exhibit different physical traits in response to environmental conditions, can complicate identification efforts (Agrawal, 2001). For example, the widespread *Taraxacum officinale* (dandelion) often displays variations in leaf shape and size based on local moisture availability, leading to frequent misclassification in field studies. Hybridization and convergent evolution further present challenges, as unrelated species may independently develop similar traits, leading to potential misclassification (Baocheng *et al.*, 2019). These issues highlight the need for complementary methods that go beyond surface-level observations and incorporate data reflecting underlying genetic differences.

In recent years, molecular approaches like DNA barcoding and next-generation sequencing have become essential tools in plant taxonomy. These methods allow for species identification based on genetic sequences, offering deeper insights into species relationships that traditional morphology alone may not provide (Kress *et al.*, 2005; Ali *et al.*, 2014). DNA barcoding, which uses short, standardized genetic markers (such as *rbcL* or *matK*), has gained widespread adoption due to the stability of these markers across different environmental conditions, including varying temperature, moisture, and light availability, as well as among diverse plant groups (Thomas *et al.*, 2017). For more complex taxonomic challenges, next-generation sequencing (NGS) and whole-genome sequencing offer higher-resolution data, revealing detailed relationships among species and uncovering cryptic diversity (Metzker, 2010). Molecular phylogenetics, which analyzes evolutionary relationships using genetic data, has enabled taxonomists to create more accurate family trees that illustrate how species have diverged over time (Kevin *et al.*, 2009). These molecular tools address taxonomic challenges and open new avenues for studying plant evolution, population genetics, and ecological adaptation (Dorogina and Zhmud, 2020). However, despite their advantages, molecular methods have limitations, including the high cost of sequencing and the need for specialized bioinformatics expertise, highlighting the importance of an integrated approach (Dotolo *et al.*, 2022).

The scope and objectives of integrative taxonomy represent an evolving approach that combines traditional morphological data with molecular tools to establish a comprehensive framework for species identification and classification (Padial *et al.*, 2010). Integrative taxonomy acknowledges that relying solely on either morphology or molecular data has its limitations, as each method offers unique strengths and weaknesses. By merging these datasets, taxonomists can achieve greater accuracy and effectively address complex taxonomic challenges, such as cryptic species, hybrid populations, and evolutionary relationships (Kirilee *et al.*, 2019). For example, an integrative approach can resolve taxonomic ambiguities when morphological data suggests one classification while molecular data indicates another (Padial *et al.*, 2009). Integrative taxonomy is also better suited for ecological and evolutionary research as it considers both the physical traits influenced by an organism's environment and the genetic information that shapes its evolutionary history (Yeates *et al.*, 2011). To solve these challenges, adopting an integrative framework that combines robust sampling strategies, molecular tools like DNA barcoding, and computational phylogenetic models is essential. This comprehensive approach not only deepens our understanding of biodiversity but also underpins applied fields such as conservation biology and environmental management, where precise species identification is crucial for assessing ecosystem health and resilience (Akira *et al.*, 2013). As this review demonstrates, combining morphological and molecular data has significant potential to refine plant taxonomy, enabling more informed and effective efforts strategies for understanding, conserving, and leveraging plant biodiversity.

Morphological data in plant taxonomy: Morphological data, encompassing physical traits such as leaf shape, flower structure, fruit type, and growth form, has long been fundamental to plant taxonomy (Valcárcel & Pablo, 2010). Taxonomists have historically relied on botanical descriptions, illustrations, and herbarium specimens to document biodiversity and classify plants based on observable features(Paterson *et al.*, 2004; Jose *et al.*, 2017). In addition to facilitating species identification, morphological traits provide insights into ecological roles, linking structural adaptations to environmental conditions such as drought tolerance or pollinator attraction (Hoehndorf *et al.*, 2016; Pérez-Harguindeguy *et al.*, 2016). Key diagnostic traits, particularly floral characteristics like petal arrangement and reproductive structures, remain indispensable for accurately distinguishing species (Miho & Fujimoto, 2016; Nina *et al.*, 2020).

Traditional morphological traits used in taxonomy: In plant taxonomy, traditional morphological traits are predominantly characterized by the physical features of a plant's vegetative and reproductive organs (Watson, 2008). Vegetative traits-such as leaf arrangement, stem type, and plant height-serve as preliminary identifiers, aiding taxonomists in distinguishing broad groups of plants (Leishman & Westoby, 1992). For instance, the shape of leaves, whether lobed, toothed, or entire, can indicate specific families or genera. Leaf venation patterns, such as parallel or reticulate, are crucial markers for differentiating major plant groups, like monocots and dicots (Kolivand *et al.*, 2018; Aparecida *et al.*, 2019). Flowers and inflorescences, however, have historically been among the most critical traits for plant classification due to their complexity and diversity, which offer detailed insights into species relationships (Jannice and Harder, 2005). Floral features such as symmetry, petal color, and the structure of stamens and pistils, are often highly conserved within plant families, making them reliable indicators for accurate identification (Raisa *et al.*, 2023).

Beyond flowers, seed and fruit morphology has been instrumental in classifying species, particularly when floral traits may be absent or challenging to observe in the field (Cope *et al.*, 2012). For example, fruit type, such as drupe, berry, or capsule, and seed characteristics, including shape and size, can differentiate closely related species or genera (Primack, 1987). These reproductive traits hold significant value in evolutionary studies, as they often reflect adaptations to specific pollinators or seed dispersers (Jacquemyn *et al.*, 2012). Additionally, certain plants are classified based on specialized structures like thorns, spines, or glandular hairs, which represent adaptive features shaped by environmental pressures such as herbivory (Demis, 2024). By documenting and analyzing these traits, taxonomists can construct a detailed understanding of species' characteristics, relationships, and ecological niches, forming a robust foundation for identifying and organizing plant diversity across various regions and habitats (Duckworth *et al.*, 2000).

Limitations of morphology-based classification: Although morphology is a reliable tool in plant taxonomy, it is not without limitations (Fig. 1). A primary challenge is phenotypic plasticity, where a single species can exhibit diverse physical traits in response to environmental conditions such as sunlight exposure, water availability, or altitude (Parkhurst & Loucks, 1972; Schlichting, 1986). This variability makes it challenging to distinguish true species differences from environmental adaptations, leading to misidentification, particularly in highly variable ecosystems such as mountainous or arid regions (Zamudio *et al.*, 2016). Additionally, hybridization-where two closely related species interbreed to produce offsprings with mixed traits-further complicates morphological classification. Hybrids often display intermediate or entirely novel characteristics, obscuring species boundaries and challenging taxonomists with respect to establishing clear distinctions (Short, 1969; Hörandl, 2022).

Another limitation of morphology-based taxonomy is convergent evolution, where unrelated plant species develop similar traits as adaptive responses to comparable environmental pressures (Huttunen *et al.*, 2018). For example, cacti in Americas and some euphorbias in Africa have evolved thick, fleshy stems and spines to survive in arid environments, even though they are not closely related. Such convergence can create misleading similarities, prompting taxonomists to group unrelated species based on superficial traits (Eggli & Nyffeler, 2009). Furthermore, cryptic species, distinct species that appear nearly identical morphologically, are increasingly being identified, particularly among plants that reproduce vegetatively or lack distinctive floral characteristics (Crawford & Stuessy, 2016). Without molecular data, these cryptic species often remain unrecognized, resulting in the underestimation of biodiversity. These difficulties underscore the importance of integrative approaches that combine the morphological data with molecular tools as molecular data can help resolve ambiguities and reveal hidden diversity that morphology alone may overlook (Leavitt *et al*., 2015). For instance, research on the genus *Dicranopteris* has revealed multiple cryptic species previously unrecognized due to morphological similarities. By applying molecular markers such as *rbcL* and *matK*, phylogenetic analyses uncovered significant genetic differentiation among populations that were indistinguishable morphologically. This study highlights the critical role of molecular tools in uncovering biodiversity and refining taxonomic classifications (Wei *et al*., 2021). Another prime example is genus *Hymenasplenium* and *Asplenium*, combining molecular and morphological data, can reveal cryptic diversity that is not apparent through morphology alone. Molecular markers have been instrumental in uncovering distinct genetic lineages within this genus, highlighting the importance of molecular tools in refining taxonomic classifications and understanding biodiversity (Fujiwara *et al*., 2017; Xu *et al*., 2018).

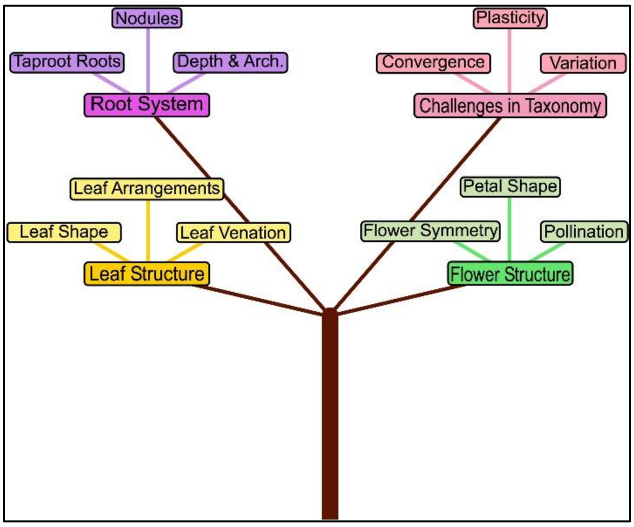

Fig. 1. Mind map of morphological traits and challenges in plant taxonomy.

Molecular tools in plant taxonomy: Molecular tools have revolutionized plant taxonomy by enabling more precise identification and classification through genetic analysis (Rouhan & Gaudeul, 2014). Unlike traditional morphology-based taxonomy, which can be limited by convergent evolution and phenotypic plasticity, molecular approaches rely on DNA sequences that are often conserved within species and provide a more stable basis for identification (Pereira *et al*., 2008). These methods include DNA barcoding, NGS, and phylogenetic analyses, each offering unique insights into plant diversity and evolutionary relationships (Mosa *et al*., 2019). Molecular data allow taxonomists to detect cryptic species, trace lineage divergence, and resolve complex taxonomic challenges, including those arising from hybridization and polyploidy (having multiple sets of chromosomes) (Kartavtsev & Redin, 2019). These tools deepen our understanding of plant biodiversity and support conservation efforts by offering a clear picture of species relationships (Cronn & Wendel, 2004). Integrating molecular data into taxonomy aligns with advancements in bioinformatics, enabling the analysis of extensive genetic datasets and fostering interdisciplinary collaborations (Chavhan *et al*., 2024). This combination of molecular data and traditional taxonomy approaches represents a shift toward the development of a more comprehensive, accurate, and adaptable system for plant classification (Singh *et al*., 2018).

DNA barcoding: DNA barcoding is widely used molecular method in plant taxonomy, providing a standardized approach for species identification through short, specific DNA regions (Table 1) (Hubert & Hanner, 2015). Commonly used barcoding regions in plants include *rbcL* and *matK* (chloroplast genes), which exhibit sufficient variation for species differentiation while remaining relatively conserved within a species (Newmaster *et al*., 2006). However, amplifying *matK* can be challenging due to its high sequence variation, which makes primer design difficult, as well as its low copy number in some plant species. Sequencing these regions allows taxonomists to compare the DNA barcode of an unknown specimen with a reference database, facilitating rapid and accurate identification (Little & Stevenson, 2007). DNA barcoding is especially valuable for distinguishing morphologically similar or cryptic species, where traditional morphological traits may be inadequate (Packer *et al*., 2009). It has also proven essential in biodiversity studies, allowing researchers to catalog species in diverse ecosystems more efficiently (Krishna Krishnamurthy & Francis, 2012). However, DNA barcoding does have limitations, such as its inability to differentiate between very closely related species or detect hybridization events (Rubinoff *et al*., 2006). Despite these challenges, it remains a foundational tool in molecular taxonomy, providing a practical and accessible method for genetic identification (Antil *et al*., 2023).

Next-generation sequencing and genomics: NGS and genomics mark a significant advancement in molecular taxonomy, offering far more detailed genetic data than traditional barcoding methods (Satam *et al*., 2023). Unlike barcoding, which focuses on specific gene regions, NGS enables the sequencing of entire genomes or large genomic segments, providing a comprehensive overview of genetic variation within and between species (Fuentes-Pardo & Ruzzante, 2017). This high-resolution data is invaluable for addressing complex taxonomic questions, such as distinguishing closely related species and analyzing gene flow in hybrid populations (Pareek *et al*., 2011). Genomic data can reveal evolutionary relationships with greater precision, illustrating not only which species are related but also the extent of their connection through shared genetic lineages (Boore, 2006). Furthermore, NGS is crucial for studying polyploidy a common phenomenon in plants where species possess multiple sets of chromosomes, complicating traditional taxonomy (Soltis *et al*., 2016). Although NGS demands substantial resources and bioinformatics expertise, its capacity to generate extensive genetic datasets makes it an increasingly valuable tool for exploring plant evolution, adaptation, and diversity at a genomic level (Kulski, 2016).

Table 1. Common DNA barcode regions and their utility in plant species identification.

Barcode Region	Targeted plant groups	Advantages/Limitations	References
rbcL	Universal; used for wide-ranging plant taxa	Advantage: High amplification success; Limitations: Low resolution at species level	(Group *et al.*, 2009)
matK	Flowering plants, especially dicots	Advantage: High variability; Limitations: Often difficult to amplify	(Lahaye *et al.*, 2008)
ITS (Internal Transcribed Spacer)	Angiosperms, particularly useful for families like Asteraceae	Advantage: High resolution at species level; Limitations: Sequence length variability	(Cowan *et al.*, 2006; Selvaraj *et al.*, 2013)
trnH-psbA spacer	Land plants, especially for herbaceous species	Advantage: Efficient for family-level identification; Limitations: Limited inter-species variation	(Deepak *et al.*, 2018)
psbA-trnH	Land plants, commonly used in ornamental species	Advantage: High success for species identification; Limitations: Limited effectiveness for closely related species	(Wang *et al.*, 2022)
ndhJ	Grass species	Advantage: Highly discriminatory; Limitations: Less commonly used	(Krawczyk *et al.*, 2018)
rpoC1	Gramineae family, monocots	Advantage: High discriminatory power; Limitations: Not universally applicable	(Wong *et al.*, 2002)
YCF5	Used for tropical plants	Advantage: Potential for cryptic species detection; Limitations: Requires complex analysis	(Wang *et al.*, 2022)
trnL-F	Angiosperms, especially in grasses and orchids	Advantage: Short and efficient; Limitations: Lower resolution compared to other regions	(Zhang *et al.*, 2016)
rpoB	Asteraceae and other angiosperms	Advantage: Broad applicability; Limitations: Inconsistency across regions	(Heise *et al.*, 2015)

Phylogenetic and population genetics approaches: Phylogenetic and population genetics approaches utilize genetic data to construct evolutionary trees or phylogenies, which illustrate relationships between species that share a most recent common ancestor (Schraiber *et al.*, 2024). Phylogenetic analysis is a fundamental aspect of molecular taxonomy, providing a framework for understanding the divergence of plant species over time and their evolutionary connections (Patwardhan *et al.*, 2014). By analyzing sequences from multiple genes or entire genomes, taxonomists can create detailed phylogenies that clarify the evolutionary history of plant lineages (Donoghue, 1989). Population genetics, in contrast, focuses on genetic variations within and among populations of a single species (Allendorf *et al.*, 2012). This approach is particularly useful in identifying the population structure, detecting the gene flow, and assessing the genetic diversity, which can help develop conservation strategies by highlighting populations at risk of inbreeding or genetic bottlenecks (Hohenlohe *et al.*, 2021). Combined, phylogenetic and population genetics approaches provide a powerful tool for exploring broad evolutionary relationships among species and fine-scale genetic dynamics within species, making them indispensable for comprehensive plant taxonomy (Stengel *et al.*, 2022).

Integrating morphological and molecular data: Integrating morphological and molecular data has become a cornerstone of modern plant taxonomy, offering a more comprehensive framework for species identification and classification (Karbstein *et al.*, 2024). While traditional morphology-based taxonomy relies on observable traits, it is often limited by factors like convergent evolution, plasticity, and hybridization, which can lead to potential misclassifications (Turgeon *et al.*, 2016). In contrast, molecular data provides genetic insights that can reveal cryptic diversity and clarify evolutionary relationships (Bickford *et al.*, 2007). The combination of these approaches allows taxonomists to capitalize on the strengths of both approaches: morphology provides practical field-based identification and ecological context, while molecular tools provide precision and reveal genetic diversity (Dorogina & Zhmud, 2020). To make integrative taxonomy more practical for researchers, we propose a simplified workflow that combines these methods effectively. The process begins with sample collection and preservation, where both morphological and molecular samples should represent genetic and phenotypic diversity across populations. Morphological samples, such as leaves and flowers, are preserved using herbarium techniques, while molecular analyses require fresh samples stored in silica gel to maintain DNA integrity. Next, data documentation and analysis involve recording diagnostic morphological traits focusing on vegetative and reproductive features and using molecular tools like DNA barcoding (e.g., *rbcL*, *matK*) or NGS for deeper genetic insights. Morphological data can be analyzed using multivariate statistical methods, while bioinformatics tools such as MEGA and RAxML are used to process molecular data. The final step is data integration, where researchers combine morphological and molecular datasets to achieve robust species identification and evolutionary insights. Phylogenetic frameworks and statistical approaches allow taxonomists to cross-validate findings and ensure accurate classifications. This workflow is visually summarized in (Fig. 2), which provides a decision tree outlining the integration process, guiding researchers through key decisions regarding marker selection, sampling strategies, and data analysis tools. This integrative approach leads to a holistic understanding of plant species, encompassing both their physical characteristics and underlying genetic makeup. The synergy between morphological and molecular data also enhances taxonomic resolution, addressing complex classification challenges that may be difficult to solve using a single method (Heikkilä *et al.*, 2015). Overall, this approach aligns with advancements in bioinformatics and phylogenetics, enabling taxonomists to create classifications that more accurately reflect both the ecological and genetic aspects of plant diversity (Steele & Pires, 2011).

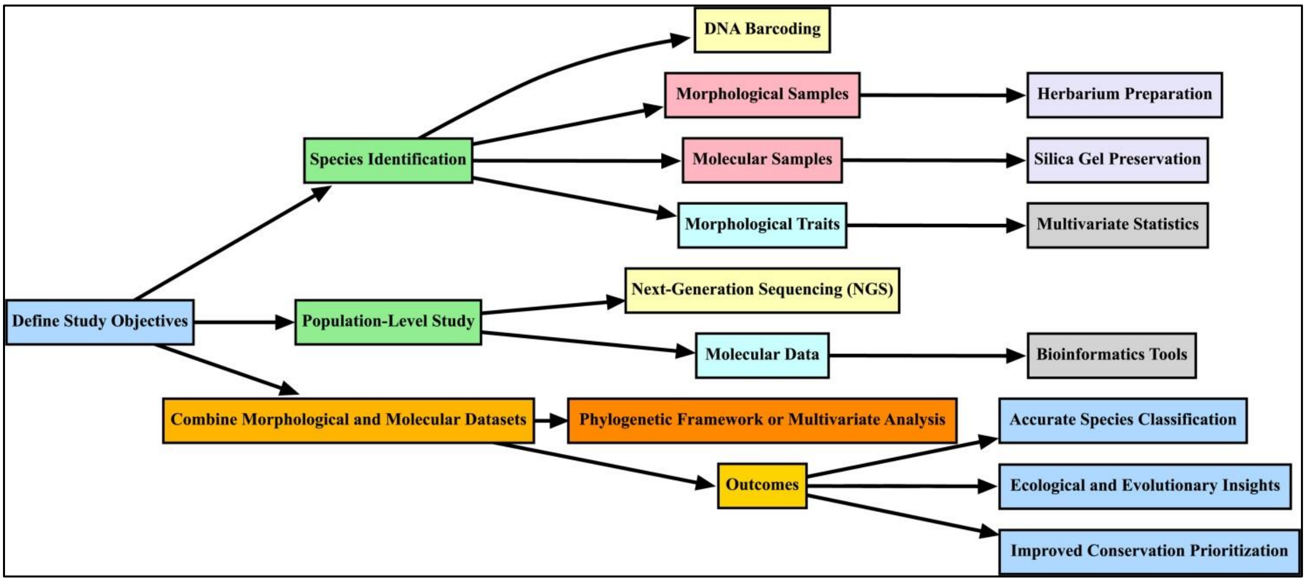

Fig. 2. Decision tree for integrative taxonomy: workflow for combining morphological and molecular data.

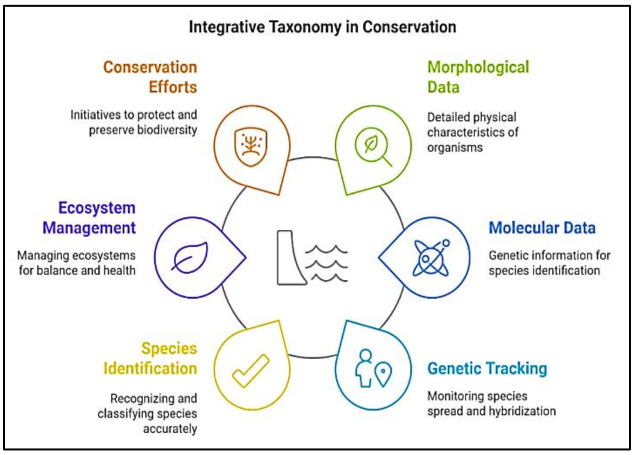

Fig. 3. Conservation and biodiversity impact of integrative taxonomy.

Advantages of an integrative approach: Integrative taxonomy combines the accessibility of morphological data with the precision of molecular tools, enabling a detailed and accurate taxonomic framework (Padial *et al.*, 2010). While morphology remains vital for field identification, its susceptibility to environmental influences highlights the need for molecular data, which provides stable markers unaffected by external factors (Haider, 2011). By cross-validating findings, taxonomists achieve greater confidence in species delineations and a more comprehensive understanding of plant diversity. This combined approach is particularly advantageous for conservation, as it identifies genetically distinct populations, ensuring the protection of unique resources and biodiversity. (Moran, 2002; DeYOUNG and Honeycutt, 2005; Willi *et al.*, 2022; Willi *et al.*, 2022).

Resolving complex taxonomic challenges: Integrating morphological and molecular data is particularly valuable for addressing complex taxonomic challenges that may be difficult to resolve using either approach alone (Yeates *et al.*, 2011). By combining both methods, taxonomists can achieve more reliable classifications, especially in cases involving cryptic species, hybridization, and trait plasticity. This integrated approach is especially transformative for elucidating diversity within closely related groups, where morphological similarities intersect with genetic distinctions (Renner, 2020).

Cryptic species complexes: Cryptic species are distinct entities that are morphologically indistinguishable but genetically different, often present in groups that reproduce clonally or exhibit minimal variation in physical traits (Bickford *et al.*, 2007). Relying solely on morphological data may fail to reveal these hidden diversities, potentially leading to an underestimation of species richness (Tang *et al.*, 2012). Molecular tools, such as DNA barcoding and phylogenetic analysis, are crucial for detecting these genetic differences and identifying cryptic species that have historically been grouped under a single name (Nadler & De León, 2011). The integration of morphological and genetic data allows taxonomists to redefine species boundaries, resulting in more accurate biodiversity assessments. This distinction is particularly important for conservation, as each cryptic species may play unique ecological roles or vulnerability levels, requiring tailored conservation efforts (Steele & Pires, 2011).

Hybridization and polyploidy: Hybridization and polyploidy are significant challenges in plant taxonomy, often resulting in intermediate or variable morphological traits that complicate classification (Hörandl, 2022). Molecular data provide critical insights into the genetic origins of hybrids and polyploids, offering tools to resolve taxonomic ambiguities (Soltis *et al.*, 1993). For instance, sequencing can reveal markers from both parental species in hybrids, confirming their lineage even when morphological traits are unclear (Rieseberg, 1997). By integrating molecular and morphological data, taxonomists refine classifications and gain a deeper understanding of species evolution and diversity (Hörandl, 2022). For instance, in the genus *Quercus* (oaks), hybridization between *Quercus robur* and *Q. petraea* has often led to misclassification due to intermediate morphological traits (Muir *et al.*, 2000). Genomic studies employing SNP markers and whole-genome sequencing successfully identified hybrid individuals and resolved their parental lineages. This integrative approach also elucidated patterns of gene flow and speciation, demonstrating how molecular data complements morphology to address challenges posed by hybridization (Muir *et al.*, 2000; Gugerli *et al.*, 2006).

Trait plasticity and morphology-genotype discordance: Trait plasticity, where a single species exhibits different morphologies based on environmental conditions, challenges morphology-based taxonomy by blurring the line between intraspecific variations and distinct species (Marcisz *et al.*, 2020). For example, *Lupinus arcticus* demonstrates significant morphological variation influenced by soil composition and climate, showcasing the effects of environmental conditions on plant traits (Pieper *et al.*, 2011). In some cases, discordance can occur between morphological traits and genetic identity plants that appear different may belong to the same genetic lineage, or conversely, similar-looking plants may be genetically unrelated (Kool *et al.*, 2012). By integrating genetic data with morphological observations, taxonomists can differentiate between environmental-induced variations and true taxonomic differences (Manoylov, 2014). This combined approach clarifies species boundaries, ensuring that morphological plasticity is accounted for without misidentification of species. Such integration is essential for ecosystems with high environmental variability, where morphological traits alone may not accurately reflect genetic relationships (Stuessy, 2009).

Through this integrative approach, plant taxonomy becomes a more precise and nuanced science, capable of addressing the complexities of nature’s diversity (Kim & Byrne, 2006). Combining morphological and molecular data not only strengthens classification systems but also provides valuable insights into evolutionary processes, population dynamics, and plant ecological roles (Klingenberg, 2008). This holistic perspective supports basic research and applied fields, such as conservation biology and ecological restoration, ensuring that taxonomic frameworks are as comprehensive and adaptable as the plants they describe.

Methodological considerations and challenges: Integrating morphological and molecular data in plant taxonomy presents unique methodological challenges that must be carefully addressed to ensure accuracy and reliability (Yeates *et al.*, 2011). The process involves balancing field-based morphological data collection with laboratory-based molecular analyses, each with specific requirements that can influence data quality (Padial *et al.*, 2010). Key challenges in this integrative approach include ensuring representative sampling, managing potential discrepancies between morphological and genetic data, and handling the large volumes of genetic information generated by molecular techniques (Table 2) (Yeates *et al.*, 2011). In addition, bioinformatics is crucial, as advanced data analysis methods are necessary for interpreting molecular data and integrating it with morphological observations. Addressing these challenges is essential for developing accurate taxonomic frameworks that truly reflect true species diversity and relationships (Kuznetsov *et al.*, 2013). As taxonomy increasingly adopts an integrative approach, establishing clear methodological standards and best practices is vital to account for the unique requirements and potential pitfalls associated with combining different types of data (Schlick-Steiner *et al.*, 2010).

Sampling and data quality: Effective sampling is essential for the success of any taxonomic study, particularly one that integrates both morphological and molecular data (Padial *et al.*, 2010). Sampling should capture the full range of variation within and between species, including different populations and environmental contexts. To mitigate sampling bias, stratified random sampling across geographic and environmental gradients is recommended. Researchers should ensure that their sampling strategy captures both rare and common populations, accounting for phenotypic and genetic variability. Best practices for sampling and preservation are outlined in protocols such as those by Ball-Damerow *et al.*, (2019), which emphasize the importance of comprehensive documentation and maintaining voucher specimens in herbaria. This task can be particularly challenging for species with broad geographic distributions or those exhibiting significant morphological variation (Manoylov, 2014). Field collection should prioritize specimens that reflect habitat diversity, varying environmental conditions, and different growth stages. Moreover, proper sample preservation is crucial for maintaining both morphological integrity and DNA quality; for example, molecular analysis requires fresh or well-preserved specimens to prevent DNA degradation (Pyke & Ehrlich, 2010). DNA integrity can be maintained using silica gel for field preservation or freezing samples at -80°C. Standardized DNA extraction kits, such as Qiagen DNeasy, ensure high-quality results for downstream applications. Researchers should follow protocols like those by Demeke & Jenkins (2010); McDonough *et al.*, (2018) to optimize extraction methods for different plant tissues. While herbarium specimens are invaluable for morphological analysis, they can pose challenges for molecular research due to their age and the condition of preservation (Bieker & Martin, 2018). Ensuring data quality in both morphology and genetics involves systematic field protocols, robust preservation methods, and comprehensive documentation to maintain consistency across datasets (Ball-Damerow *et al.*, 2019).

Interpretation of morphology genotype discordance: Morphology-genotype discordance, where morphological traits do not align with genetic data, is a common challenge in integrative taxonomy (Terraneo *et al.*, 2016). This discordance can arise from various factors, including phenotypic plasticity, where environmental influences cause morphological changes without corresponding genetic differences, or convergent evolution, where unrelated species develop similar traits due to analogous ecological pressures (Nagata *et al.*, 2020). In addition, hybridization and introgression (gene flow between species) can also lead to individuals with mixed morphological and genetic profiles, complicating taxonomic classification. For example, in oaks (*Quercus* spp.), introgression between species has been documented extensively, where genetic exchange blurs species boundaries, creating morphologically intermediate populations with significant taxonomic implications (Muir *et al.*, 2000). Such cases highlight the importance of integrating genetic data to understand the extent and impact of introgression on species definitions. Resolving morphology-genotype discordance requires careful interpretation to avoid erroneous conclusions (Rheindt & Edwards, 2011). Taxonomists must determine whether the observed morphological differences signify true species distinctions or are the result of environmental adaptations, and whether genetic divergence suggests new species or intraspecific variation (Camp & Gilly, 1943). Integrating both morphological and molecular data enables taxonomists to refine species boundaries and address discordances by confirming whether traits are consistent across different populations and environmental contexts, leading to more accurate classifications (Schlick-Steiner *et al.*, 2010).

Table 2. Data quality considerations for morphological and molecular analysis.

Consideration	Description	References
Sample Preservation	The preservation method affects DNA/RNA quality, impacting the success of molecular analyses. Different tissues and storage methods (e.g., ethanol vs. formalin) can influence the integrity of genetic material.	(McDonough *et al.*, 2018)
Contamination Risk	Contamination, whether from environmental sources or cross-sample, can lead to misleading conclusions, particularly in species delineation. Decontamination protocols are crucial.	(Jecha *et al.*, 2024)
Sequencing Depth	Adequate sequencing depth ensures comprehensive data capture, especially for variant detection and accurate species identification. Higher depth increases reliability but also cost.	(Acha *et al.*, 2023)
Extraction Methods	DNA/RNA extraction methods can significantly influence data quality. Protocols such as CTAB-based methods are recommended for high DNA yield from plant tissues, while commercial kits like Qiagen's DNeasy Plant Mini Kit offer consistency and ease of use. Customized protocols may also be necessary for challenging samples (e.g., silica-dried leaves).	(Heera *et al.*, 2015)
Bioinformatics	Bioinformatics tools play a critical role in analyzing large datasets, ensuring accuracy and consistency in molecular identification.	(Clark and Lillard Jr, 2024)
Environmental Factors	Morphological traits can be influenced by environmental factors, making them less reliable for species identification compared to molecular markers.	(Hasan *et al.*, 2021)
Data Standardization	Standardized protocols for molecular analysis help in reducing errors and improving reproducibility in integrative taxonomy studies.	(Matter, 1997)
High-Throughput Screening (HTS)	Ensuring high-quality data in HTS is crucial for accurate biological profiling, avoiding artifacts and low-quality data.	(Stephan, 2002)

Bioinformatics and data analysis: Bioinformatics and data analysis are critical elements of modern molecular taxonomy, enabling researchers to process and interpret the vast amounts of genetic data generated by sequencing technologies (Kushwah *et al.*, 2024). Managing large datasets necessitates sophisticated software tools and computational methods to align sequences, construct phylogenetic trees, and analyze population genetics. Bioinformatics platforms such as MEGA, RAxML, and BEAST support these tasks, providing the computational power needed to model evolutionary relationships and assess genetic diversity (Vello *et al.*, 2024). Additionally, data integration tools are essential for merging morphological and molecular datasets, enabling comprehensive analyses that incorporate different types of data (Boehm *et al.*, 2022). To ensure reproducibility, researchers should use standard data formats, such as FASTA for sequence data, and adhere to metadata standards like Darwin Core to document collection information, ensuring consistency across datasets. However, bioinformatics comes with its challenges, requiring technical expertise in programing, data management, and statistical analysis. Errors in data processing or analysis, such as sequence misalignment or incorrect parameter settings, can lead to inaccurate results (Merelli *et al.*, 2014). To ensure reliable outcomes, taxonomists must be proficient in bioinformatics workflows, understand the limitations of various tools, and carefully validate their findings (Raza and Dey, 2021). As bioinformatics continues to evolve, the integration of morphological and molecular data in taxonomy will become more efficient and accessible, supporting the development of robust, integrative taxonomic frameworks (Sheth & Thaker, 2017).

Applications in conservation and biodiversity studies: Integrating morphological and molecular data in plant taxonomy offers considerable advantages for conservation and biodiversity studies by ensuring accurate species identification, clarifying evolutionary relationships, and revealing hidden diversity (Fig. 3) (Sheth & Thaker, 2017). This integrative approach enhances biodiversity assessments, aids in prioritizing species and habitats for conservation, and supports management strategies for invasive species (Larson *et al.*, 2011). Additionally, by emphasizing phylogenetic diversity, integrative taxonomy plays a crucial role in ecosystem restoration efforts that promote resilience and ecological balance. These applications highlight the practical importance of a robust taxonomic framework for effective conservation (Verdú *et al.*, 2012).

Biodiversity assessment and conservation prioritization: Integrative taxonomy enhances biodiversity assessments by combining physical traits with genetic data, enabling more precise species identification and revealing cryptic diversity. This comprehensive approach helps conservationists in identifying species that may be overlooked when relying solely on morphology, particularly in biodiverse or ecologically complex regions (Schlick-Steiner *et al.*, 2010). For example, the taxonomic resolution of the Darling Downs Earless Dragon (*Tympanocryptis*) through integrative taxonomy revealed it as a distinct species, prompting conservation actions to protect this previously overlooked population in Queensland, Australia (Melville *et al.*, 2014). Similarly, a prioritization study of 24 Australian reptiles identified through integrative taxonomy highlighted the species most in need of conservation, directly influencing policy and resource allocation (Melville *et al.*, 2021). With a clearer understanding of species richness and evolutionary distinctiveness, conservation prioritization correspondingly becomes more targeted and effective, ensuring that resources are directed toward protecting unique and vulnerable species, habitats, and evolutionary lineages (Arponen, 2012). For example, in *Bossiaea vombata*, a rare Fabaceae species, the identification of distinct genetic lineages through next-generation sequencing has guided targeted conservation strategies to protect its unique genetic diversity and prevent inbreeding (Amor *et al.*, 2020). Integrative data also support the preservation of genetic diversity, which is critical for long-term species adaptability and ecosystem health (Hoffmann *et al.*, 2015).

Invasive species detection and management: Invasive species management greatly benefits from integrative taxonomy, as precise species identification is crucial for effectively controlling invasive populations (DiTomaso *et al.*, 2017). Morphological similarities between invasive and native species can lead to misidentification, undermining management efforts. For instance, integrative taxonomy was critical in the case of invasive species in the *Cenchrus* genus in Australia, where genetic data clarified the distinctions between invasive and native species, enabling more targeted and effective control measures (Bonney *et al.*, 2016). Molecular data, meanwhile, can clarify these distinctions, facilitating early detection and intervention before invasive species inflict significant ecological damage (Moffat *et al.*, 2015). By integrating both morphological and genetic data, managers can accurately identify and monitor invasive species, assess their genetic diversity, and develop strategies to curb their spread, ultimately protecting native biodiversity and ensuring ecosystem stability (Cavender-Bares *et al.*, 2022).

Phylogenetic diversity in ecosystem restoration: Phylogenetic diversity, which involves incorporating species with varied evolutionary backgrounds, is vital for ecosystem restoration (Moreno-Mateos *et al.*, 2020). Integrative taxonomy aids in determining phylogenetic relationships, guiding the selection of species that enhance ecosystem resilient and functional diversity (Padial *et al.*, 2010). For example, in grasslands, reintroducing phylogenetically diverse plant species such as nitrogen-fixing legumes and deep-rooted grasses like *Andropogon* gerardii has been shown to improve soil stability and resistance to environmental disturbances, enhancing ecosystem resilience (Hunt *et al.*, 2005). Integrative taxonomy revealed previously unrecognized species critical to ecosystem function and conservation, influencing restoration strategies and resource prioritization (Wang *et al.*, 2021). By including species with different evolutionary histories, restoration projects can promote greater ecosystem stability and adaptability to environmental changes. This approach not only supports species recovery but also re-establishes essential ecological processes, leading to self-sustaining ecosystems capable of withstanding future disturbances. Thus, integrative taxonomy plays a foundational role in ecosystem restoration, aligning biodiversity recovery with evolutionary and ecological principles (Rice & Emery, 2003; Timpane-Padgham *et al.*, 2017).

Future directions: Future directions in integrative taxonomy are driven by technological advancements, collaborative efforts, and increasing demand for interdisciplinary research and training. Emerging technologies, such as high-throughput sequencing, environmental DNA (eDNA) analysis, and AI, are expected to transform the way taxonomists study and classify plant species (Zhang *et al.*, 2023). High-throughput sequencing, for instance, enables rapid and cost-effective genome sequencing across multiple samples, thereby allowing for the detailed genetic analyses of even complex or cryptic species groups. eDNA analysis offers promising applications for detecting rare and elusive plant species by analyzing DNA from environmental samples such as soil, water, and air, enabling biodiversity surveys in challenging or inaccessible habitats (Bohmann *et al.*, 2014; Banerjee *et al.*, 2022).

Meanwhile, eDNA analysis provides a method for detecting plant species from environmental samples, such as soil or water, expanding the potential for biodiversity surveys in hard-to-reach habitats. Meanwhile, AI and machine learning algorithms are increasingly used to analyze large datasets, automate morphological trait analysis, and predict phylogenetic relationships based on genetic markers (He *et al.*, 2024). For example, AI tools such as automated leaf shape recognition algorithms are being developed to identify plant species based on digital herbarium images (Wäldchen *et al.*, 2018; Mäder *et al.*, 2021). Additionally, AI-based platforms can facilitate community-wide DNA barcode classification, allowing rapid species identification from complex datasets, further enhancing biodiversity monitoring efforts. These technologies offer the potential to improve the precision and efficiency of taxonomy, especially when combined with traditional morphological data, ultimately contributing to a more comprehensive understanding of plant diversity.

Developing comprehensive databases and fostering collaborative networks are essential for fully harnessing the potential of integrative taxonomy. As molecular, morphological, and ecological data continue to accumulate, there is an increasing need for centralized, accessible databases that store and standardize this information for use by researchers worldwide (Nelson & Ellis, 2019). Databases, such as GenBank and the Barcode of Life Data Systems, have established a strong foundation. Global networks such as the International Barcode of Life (iBOL) consortium and the Global Biodiversity Information Facility (GBIF) already play critical roles in consolidating data and facilitating large-scale biodiversity studies across regions (Triebel *et al.*, 2012). Expanding these resources to include more diverse species and integrating morphological data will greatly enhance their utility. Collaborative networks that unite experts in taxonomy, bioinformatics, and ecology are crucial for developing these resources and establishing global standards for data collection and analysis (Sarkar & Trizna, 2011). By sharing resources and expertise, these networks can enable large-scale biodiversity studies and conservation planning across regions, bridging gaps in taxonomic knowledge and enhancing global species assessments.

Interdisciplinary research and training are essential for preparing the next generation of taxonomists to excel in an integrative field. Effective integrative taxonomy demands expertise in multiple areas, including molecular biology, ecology, bioinformatics, and traditional morphology (Goulding & Dayrat, 2016). Training programs that combine interdisciplinary coursework with practical experience in fieldwork and laboratory techniques will equip taxonomists to navigate the complexities of modern taxonomy. Additionally, interdisciplinary research promotes collaboration among specialists from different fields, leading to innovative approaches and yielding insights that can address complex taxonomic challenges (Klein, 2010). As taxonomy advances into a more integrative science, it is crucial to provide education and resources that support this transformation, encouraging collaboration and developing expertise in traditional and emerging methodologies (Zwass, 2010). These future directions hold the potential to expand the scope, improve the accuracy, and enhance the applicability of plant taxonomy, reinforcing its importance in biodiversity conservation and ecological research.

Conclusion

Integrative taxonomy merges traditional morphological data with molecular tools to provide a comprehensive and accurate framework for understanding plant diversity. By addressing the limitations of standalone methods-such as the phenotypic plasticity and convergent evolution challenges of morphology-based taxonomy and the resource intensity of molecular methods-this approach delivers more precise species delineation and a deeper understanding of biodiversity. Integrative taxonomy enhances taxonomic resolution, enabling better evaluation of evolutionary relationships, population structures, and ecosystem functions.

In the face of rapid biodiversity loss, climate change, and habitat degradation, integrative taxonomy has become indispensable for modern conservation and ecological studies. It provides a practical framework for swiftly identifying species, assessing conservation statuses, and understanding ecological roles. By prioritizing species and habitats based on genetic distinctiveness and evolutionary history, integrative taxonomy supports targeted conservation strategies. Furthermore, the inclusion of phylogenetic diversity through this approach fosters ecosystem resilience, promoting restoration strategies that incorporate species with diverse evolutionary backgrounds.

As molecular tools become more accessible and integrative methodologies continue to evolve, the adoption of these approaches will be crucial for maintaining a taxonomic system that reflects the genetic complexity and ecological significance of plant species. This shift represents not only an evolution in methodology but also a commitment to protecting biodiversity and supporting sustainable ecological practices in the face of ongoing environmental challenges.

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