Integrative Bamboo Systematics: Taxonomy, Morphological Diversity, Evolutionary Relationships, and Future Perspectives

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Bamboo (subfamily Bambusoideae, Poaceae) represents one of the most taxonomically complex and evolutionary dynamic lineages within grasses due to irregular flowering cycles, extensive morphological plasticity, frequent hybridization, and widespread polyploidy. These characteristics have historically complicated species delimitation and phylogenetic reconstruction. This review synthesizes recent advances in integrative bamboo systematics, emphasizing the roles of phylogenomics, molecular cytogenetics, DNA barcoding, multi-locus sequencing, and computational morphological analytics in resolving bamboo diversity and evolutionary relationships. Genome-wide sequencing approaches have enabled the detection of hybridization events and reticulate evolutionary histories that were previously difficult to resolve using morphology or single-locus markers. These advances have improved phylogenetic resolution, particularly among closely related bamboo taxa. Nevertheless, major knowledge gaps remain, including incongruence between nuclear and plastid datasets, incomplete lineage sorting, polyploid genome complexity, incomplete taxon sampling, and the limited phylogenomic representation of tropical and Southeast Asian bamboo diversity. Addressing these gaps will require broader geographic and taxonomic sampling, standardized molecular and DNA barcoding protocols, voucher-linked genomic databases, and greater integration of genomic, morphological, anatomical, cytogenetic, and computational evidence. These priorities provide a practical research framework for improving taxonomic stability, biodiversity conservation, and sustainable management within Bambusoideae.

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INTRODUCTION

Classification of bamboo within the Poaceae family has undergone substantial refinement with the advancement of molecular phylogenetics, which uses DNA sequence data to reconstruct evolutionary relationships among organisms, as well as with integrative morphological research. Contemporary systematic frameworks recognize bamboo as

comprising three monophyletic tribes, each representing a group consisting of a common ancestor and all of its descendants, namely Arundinarieae, Bambuseae, and Olyreae. This classification is supported by multilocus phylogenetic analyses and plastome data representing genetic information from the complete chloroplast genome (Saarela *et al.* 2018; Huang *et al.* 2020). Arundinarieae represents temperate woody bamboos and is currently treated without formally recognized subtribes (Zhang *et al.* 2020). Bambuseae encompasses tropical woody bamboos and is subdivided into Bambusinae, Dendrocalaminae, Melocanninae, Hickeliinae, and Racemobambosinae (Saarela *et al.* 2018). In contrast, Olyreae comprises herbaceous bamboos and includes Buergersiochloinae, Olyrinae, and Parianinae (Oliveira *et al.* 2020). While these tribal classifications are broadly supported, intratribal relationships, particularly within Bambuseae, remain partially unresolved, reflecting the complex evolutionary history of the subfamily.

The systematic study of bamboo is uniquely challenged by biological traits that obscure species boundaries and complicate phylogenetic reconstruction. One of the most significant constraints is the prolonged and irregular flowering cycle, which in some taxa may extend up to 120 years (Singh *et al.* 2013). Because traditional plant taxonomy relies heavily on reproductive morphology, the rarity of flowering events restricts access to critical diagnostic characters. Consequently, early classifications were predominantly based on vegetative morphology, including culm characteristics, branching patterns, and leaf anatomy. However, morphological traits in bamboo exhibit considerable phenotypic plasticity, defined as the ability of a genotype to produce different morphological or physiological characteristics in response to environmental conditions. Such phenotypic plasticity may limit their reliability for accurate species delimitation, which is the process of identifying and defining boundaries between species (Khairi *et al.* 2020; Zhuo *et al.* 2023). Although anatomical features, such as leaf epidermal structures, provide valuable taxonomic signals (Yang *et al.* 2008), their diagnostic power is strengthened when interpreted alongside molecular evidence.

Beyond its taxonomic significance, accurate bamboo classification has substantial economic and societal implications. Reliable species identification facilitates the selection of superior germplasm for breeding programs by enabling the identification of desirable traits, including rapid growth, superior culm quality, disease resistance, and environmental adaptability. Accurate taxonomy also strengthens germplasm conservation by distinguishing genetically unique populations and identifying evolutionarily significant units that require protection. From an industrial perspective, different bamboo species exhibit considerable variation in anatomical characteristics, fiber morphology, chemical composition, density, and mechanical performance, all of which influence their suitability for structural engineered bamboo, laminated bamboo, pulp and paper, textiles, furniture, handicrafts, bioenergy, and emerging bio-based materials. Misidentification of commercially important species may result in inconsistent product quality, reduced processing efficiency, inappropriate plantation establishment, and inaccurate certification of sustainable forest products. Consequently, integrative bamboo systematics provides an essential scientific foundation supporting sustainable resource utilization, biodiversity conservation, and the expanding global bamboo bioeconomy (Lobovikov *et al.* 2007; INBAR 2023).

The increasing use of molecular tools has substantially altered our understanding of bamboo evolution. In many cases, classifications based primarily on vegetative morphology have proven insufficient, particularly among closely related taxa exhibiting

high phenotypic plasticity. Techniques such as genome skimming, a low-coverage sequencing approach used to recover high-copy genomic regions, and restriction site-associated DNA sequencing (RAD-seq), which generates genome-wide markers from DNA fragments adjacent to restriction sites, have helped resolve several long-standing taxonomic uncertainties; however, many tropical bamboo groups remain poorly studied compared with economically important East Asian species (Wang *et al.* 2017; Hu *et al.* 2024). Molecular evidence confirms that temperate woody bamboos form a well-supported monophyletic lineage (Wang *et al.* 2017), yet taxonomic distinctions at lower hierarchical levels remain contentious. Polyploidy, the presence of more than two complete sets of chromosomes within an organism, is frequently observed among woody bamboos. This further complicates phylogenetic inference, the reconstruction of evolutionary relationships from biological data, and species delimitation (Saarela *et al.* 2018). The presence of duplicated genomes may generate incongruent phylogenetic signals between nuclear and plastid datasets, thereby obscuring lineage divergence patterns. As a result, integrative approaches that combine molecular, morphological, and anatomical data have become essential for resolving classification ambiguities (Das *et al.* 2007).

With approximately 1,700 recognized species representing 125 genera distributed across tropical, subtropical, and temperate regions, bamboo represents one of the most diverse lineages within the Poaceae family (Bamboo Phylogeny Group 2012; Yeasmin *et al.* 2015; Mustafa *et al.* 2021). This remarkable diversity underscores the evolutionary success of the group but also intensifies the need for robust systematic frameworks capable of accommodating genetic complexity and morphological variability. Malaysia harbors a rich bamboo flora comprising approximately 63 recorded species, yet only a small proportion has been investigated beyond basic taxonomic documentation. Although 13 species are currently recognized for commercial utilization, information regarding their genetic diversity, evolutionary relationships, and conservation status remains fragmented. This knowledge gap may limit both sustainable resource management and future breeding initiatives (Lee *et al.* 2023). The genus *Gigantochloa* dominates the Malaysian bamboo flora, with *Gigantochloa scortechinii* being particularly widespread. Chloroplast DNA (cpDNA) analyses have revealed distinct genetic lineages within this species, highlighting intraspecific variation and its conservation significance (Dhanendiren *et al.* 2015). Beyond resolving taxonomic uncertainties, molecular evidence can identify genetically distinct populations that warrant conservation attention and may influence management decisions.

Beyond taxonomic considerations, bamboo contributes significantly to ecological stability and socioeconomic development. Its rapid growth, extensive rhizome systems, and structural resilience enable effective soil stabilization and carbon sequestration, while also supporting habitat provision in forest ecosystems (Mohamed *et al.* 2007). Sustainable bamboo management has therefore been proposed as a strategy to mitigate deforestation and enhance ecosystem services (Mohamed *et al.* 2007). Furthermore, investigations into bamboo rhizospheres have identified bioactive compounds with pharmaceutical potential, expanding the scientific relevance of accurate species identification (Helaly *et al.* 2009). Misclassification or taxonomic ambiguity may therefore have cascading implications for ecological research, conservation prioritization, and applied utilization.

Bamboo taxonomy has thus evolved from predominantly morphology-based classification toward integrative frameworks that incorporate molecular and genomic evidence (Yu *et al.* 2018). Despite substantial progress, persistent challenges including hybridization, the interbreeding of genetically differentiated species or lineages, polyploidy, morphological plasticity, and incomplete lineage sorting (ILS), the persistence

of ancestral genetic variation across speciation events that can result in gene histories differing from species relationships, continue to hinder full phylogenetic resolution. A comprehensive synthesis of these methodological developments and their implications for understanding bamboo diversity and evolution remains necessary. This review evaluates recent developments in bamboo systematics, with particular emphasis on how molecular, morphological, and phylogenomic approaches, which use genome-scale sequence data to reconstruct evolutionary relationships, have contributed to resolving taxonomic uncertainties. Remaining challenges and research priorities are also discussed. Moreover, the geographic and taxonomic coverage of bamboo phylogenomic research remains uneven. For example, Wang *et al.* (2017) analyzed 39 species representing 19 genera but focused primarily on temperate woody bamboos, while a large-scale chloroplast phylogenetic study analyzed more than 300 species from 40 genera and represented the largest bamboo sampling effort conducted in China (Ma *et al.* 2021). More recently, Liu *et al.* (2024) sampled 175 species from 27 genera of Paleotropical woody bamboos, representing approximately 31.7% of species and 50.9% of genera within this group. Despite these substantial advances, many tropical Southeast Asian lineages remain comparatively underrepresented in genome-scale studies. This imbalance limits comprehensive reconstruction of bamboo evolution and highlights the need for broader geographic and taxonomic sampling across Southeast Asia.

TAXONOMY AND CLASSIFICATION OF BAMBOO

The taxonomy and classification of bamboo have undergone substantial transformation, reflecting the transition from morphology-based systems to integrative phylogenetic frameworks (Table 1). As members of the subfamily Bambusoideae within Poaceae, bamboos constitute a highly diverse lineage of perennial grasses characterized by lignified culms, complex rhizome systems, and rapid growth rates (Akinlabi *et al.* 2017). However, their biological and reproductive characteristics have historically complicated stable classification.

Early taxonomic systems relied predominantly on vegetative and reproductive morphological traits, including culm sheath morphology, branching architecture, and inflorescence structure. Foundational contributions by pioneering taxonomists, such as Gamble in the late nineteenth century, established baseline generic delimitations that shaped subsequent classifications (Yeasmin *et al.* 2015). Nevertheless, the inherent limitations of morphology-based taxonomy became increasingly apparent. Extensive phenotypic plasticity, environmentally induced trait variation, and prolonged flowering intervals resulted in ambiguous species boundaries and inconsistent genus circumscription. As noted by Horn and Häser (2016), the extensive morphological diversity within Bambusoideae does not consistently correspond to phylogenetic relationships, revealing the inadequacy of relying solely on observable traits.

The availability of molecular data revealed that several traditional classifications based solely on morphology were inconsistent with evolutionary relationships. Molecular evidence has generally supported the recognition of three principal tribes within Bambusoideae: Bambuseae, Arundinarieae, and Olyreae. However, some intratribal relationships, particularly within Bambuseae, remain unresolved (Canavan *et al.* 2017). Molecular evidence has reinforced the monophyly of these tribes, particularly supporting Bambuseae as a cohesive evolutionary lineage (Canavan *et al.* 2017). However, intratribal

relationships especially within Bambuseae remain under active revision, reflecting ongoing challenges in resolving lineage diversification.

Chloroplast phylogenomic analyses have significantly enhanced phylogenetic resolution, particularly in groups characterized by rapid evolutionary radiation and limited sequence divergence. Within Arundinarieae, for example, low genetic variation among taxa has historically impeded robust phylogenetic reconstruction, but plastome-scale datasets have improved resolution of intergeneric relationships (Ma *et al.* 2014). Despite these advances, reliance on chloroplast markers alone may obscure signals of hybridization and reticulate evolution, underscoring the need for complementary nuclear genomic data. The increasing application of DNA-based diagnostics has further refined species identification, allowing taxonomists to differentiate morphologically similar taxa through molecular markers (Horn and Häser 2016). These developments demonstrate how molecular approaches have reshaped genus delimitations and clarified previously ambiguous classifications.

Taxonomic revision remains an ongoing process, as new genomic data become available. Recent studies have led to the recognition of additional genera and species, particularly within temperate lineages, necessitating updates to earlier morphological classifications (Ruíz-Sanchez *et al.* 2021). The Bamboo Phylogeny Group has played a central role in synthesizing morphological and molecular evidence into a comprehensive and phylogenetically informed classification framework (Canavan *et al.* 2017). Such collaborative efforts illustrate the movement toward consensus-driven taxonomy grounded in evolutionary relationships rather than solely diagnostic traits. Furthermore, investigations into genetic diversity across bamboo taxa continue to highlight the importance of molecular markers for understanding lineage divergence and speciation processes within Bambusoideae (Li *et al.* 2019). Nevertheless, evolutionary relationships within several woody bamboo groups, particularly the tropical tribe Bambuseae, remain unresolved or controversial. Relationships among closely related genera and species are frequently complicated by hybridization, polyploidization, rapid diversification, and incomplete lineage sorting, which can generate conflicting phylogenetic signals between nuclear and plastid datasets. Consequently, even genome-scale data may produce alternative evolutionary hypotheses when different genomic compartments or analytical approaches are considered. These persistent uncertainties highlight the need for broader taxon sampling and integrative analyses combining nuclear, plastid, cytogenetic, and morphological evidence.

Overall, current bamboo classification should be viewed as an evolving framework rather than a finalized system. Persistent challenges, including low sequence divergence, rapid radiation, hybridization, and conflicting genomic signals, require continued integration of morphological and molecular evidence to improve phylogenetic stability and evolutionary coherence.

Table 1. Scientific Taxonomy of Bamboo

Taxonomic Level	Recognized Groups	Growth Form	Geographic Distribution	Representative Chromosome Number/ Ploidy	Key Evolutionary Features	Major Systematic Challenges
Subfamily	Bambusoideae	Woody and herbaceous grasses	Tropical, subtropical, and temperate regions	Predominantly polyploid; chromo-some numbers vary among tribes	Unique flowering cycles, rhizomatous growth, high morphological diversity	Rare flowering events, morphological plasticity
Tribe	Bambuseae	Tropical woody bamboos	Predominantly tropical regions (Asia, Africa, Americas)	Mostly 2n = 48–72; predominantly polyploid	Frequent polyploidy, rapid diversification, complex genome structure	Hybridization, intratribal phylogenetic resolution, incongruence between plastid and nuclear data
Tribe	Arundinarieae	Temperate woody bamboos	Temperate regions (Asia, North America)	Mostly 2n = 48; predominantly tetraploid	Monophyletic lineage, evolutionary radiation	Low sequence divergence, limited molecular variation
Tribe	Olyreae	Herbaceous bamboos	Tropical forest understory	Commonly 2n = 22–24; predominantly diploid	Distinct reproductive biology, typically non-woody	Limited genomic sampling, underrepresentation in phylogenetic studies
Representative Genera	*Bambusa*, *Dendrocalamus*, *Gigantochloa*, *Phyllostachys*, *Schizostachyum*	Variable	Region-dependent	Chromosome numbers vary among genera	Ecological specialization and adaptive divergence	Species delimitation and cryptic diversity

IMPORTANCE OF BAMBOO IN ECOSYSTEM, ECONOMICS AND CULTURES

Bamboo contributes to ecosystem functioning, economic development, and cultural practices across many regions of the world. Its rapid growth, extensive rhizome networks, and adaptability to diverse climatic conditions enable bamboo to function as a structurally and ecologically dominant component of many forested and semi-forested landscapes. Ecologically, bamboo contributes substantially to carbon sequestration, land restoration, and biodiversity maintenance, while its rapid biomass accumulation makes it attractive for climate mitigation initiatives (Daba 2016). Studies on Moso bamboo (*Phyllostachys edulis*) have demonstrated significant carbon sequestration potential, reinforcing its role in long-term carbon storage dynamics (Xu *et al.* 2011). With reported growth rates reaching up to 17 cm per day, bamboo exhibits exceptional biomass productivity relative to many woody taxa (Shiau and Chiu 2017). Quantitative studies indicate that, depending on species, site conditions, and management practices, bamboo forests can sequester approximately 5 to 12 Mg C ha^{-1} $year^{-1}$, while managed *P. edulis* plantations have been reported to store more than 150 to 300 Mg C ha^{-1} in aboveground biomass and soil carbon pools. Annual biomass productivity may also exceed 30 Mg ha^{-1} $year^{-1}$, further supporting the potential of bamboo for ecological restoration and sustainable bioeconomy development. Nevertheless, substantial variation exists among species and geographic regions, highlighting the importance of accurate species identification and taxonomy when estimating carbon stocks, ecosystem services, and restoration potential (Yen and Lee 2011; Song *et al.* 2011; INBAR 2023).

Beyond carbon dynamics, bamboo forests stabilize soils through extensive belowground rhizome systems that reduce erosion and enhance water retention, particularly in flood-prone and degraded landscapes (Tripathi *et al.* 2024). Dense bamboo stands contribute to hydrological regulation and provide habitat heterogeneity that supports diverse faunal assemblages (Liu *et al.* 2017; Lee 2021). However, the ecological roles of bamboo vary among species and growth forms, highlighting the importance of precise species delimitation in evaluating ecosystem services. Misidentification or unresolved taxonomy may lead to inaccurate ecological assessments and ineffective restoration strategies.

Economically, bamboo constitutes a significant resource base for rural and peri-urban communities, particularly in developing regions. It supports several industries spanning construction, handicrafts, textiles, furniture, bioenergy, and food production (Partey *et al.* 2017; Silva *et al.* 2020). The global bamboo trade generates over USD 2.5 billion annually, with approximately 2.5 billion people relying on bamboo-related activities for their livelihoods (Zhao *et al.* 2018). Its alignment with the United Nations Sustainable Development Goals (SDGs) reflects its capacity to generate green employment opportunities and promote sustainable production systems (Binfield *et al.* 2022). In countries such as Nepal and India, bamboo-based enterprises contribute directly to poverty alleviation and rural income diversification (KC *et al.* 2024). Accurate taxonomic identification is not merely a scientific requirement but also an economic necessity. Misidentification of commercially valuable species may affect material quality assessments, certification processes, plantation planning, and market valuation. This issue is particularly relevant in Southeast Asia, where multiple closely related species are harvested and traded under common vernacular names. Genetic differentiation within commercially important taxa may influence material properties, growth performance, and adaptability, thereby affecting economic valuation.

Culturally, bamboo occupies a prominent position in traditional ecological knowledge systems and artistic expression. In many Asian societies, bamboo is integrated into architecture, tools, daily utensils, and medicinal practices, reflecting its historical and cultural embeddedness (Akinlabi *et al.* 2017; Luo *et al.* 2020). In Indonesia and Nepal, bamboo construction techniques exemplify localized adaptation to environmental conditions, while in China, bamboo-derived instruments, such as the Ti-Tzu flute, illustrate its role in musical traditions (Wang *et al*. 2024b). Festivals, rituals, and artistic symbolism further reinforce bamboo's association with resilience and sustainability (Gong *et al.* 2022; Li 2023). The cultural valuation of bamboo is therefore intertwined with species-specific characteristics, reinforcing the need for systematic clarity to preserve traditional knowledge linked to particular taxa.

From a sustainability perspective, bamboo offers a renewable alternative to conventional timber, often requiring lower energy inputs and generating reduced carbon emissions during production (Nguyen *et al.* 2013). Its adaptability to diverse environmental conditions enhances its potential as a climate-resilient crop capable of supporting food security and economic stability (Hu *et al.* 2020). Nevertheless, effective deployment of bamboo in climate mitigation and sustainable development initiatives depends upon accurate species identification and understanding of evolutionary relationships. Species-level differences in growth form, reproductive biology, and ecological tolerance influence performance in plantation systems and restoration projects.

Collectively, these ecological, economic, and cultural functions demonstrate the broader importance of bamboo diversity and accurate species identification. These roles are influenced by species diversity and evolutionary differentiation within Bambusoideae. Consequently, robust plant systematics provides a foundational framework for linking biodiversity assessment with ecosystem service valuation, sustainable utilization, and cultural preservation. Without taxonomic clarity, conservation planning and sustainable utilization strategies may be undermined by species misidentification and overlooked genetic diversity (Lobovikov *et al.* 2007; Li *et al.* 2025). Figure 1 summarizes the relationships among bamboo phylogenetic diversity, evolutionary processes, integrative systematic approaches, and their ecological, economic, cultural, and conservation implications.

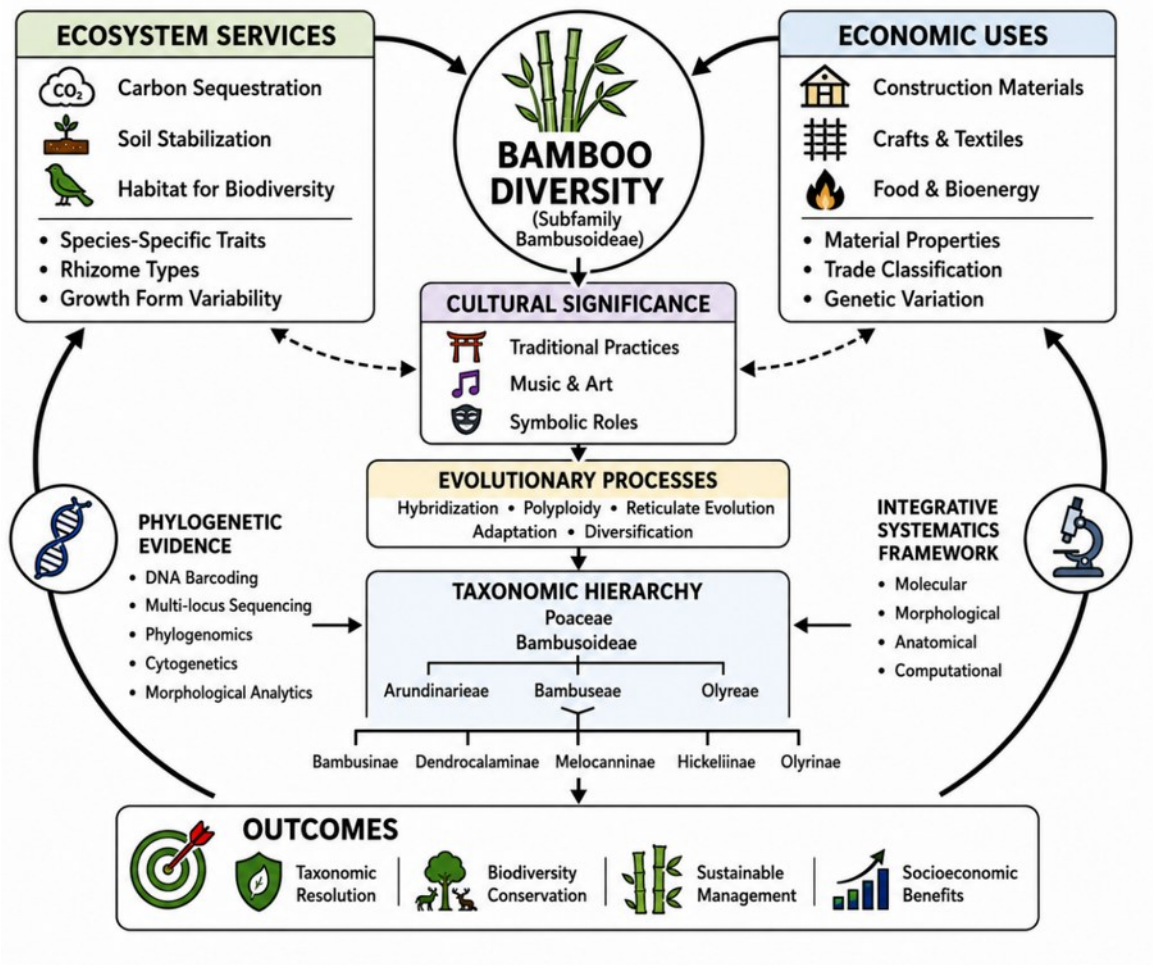

Fig. 1. Linking bamboo systematics to ecosystem services and socioeconomic applications

MORPHOLOGICAL DIVERSITY OF BAMBOO

Morphological characteristics have long served as the foundation of bamboo taxonomy and remain important for field identification. Bamboo species exhibit extensive variation in vegetative and reproductive structures, including culm height and diameter, internode length, branching architecture, leaf morphology, and rhizome type. These traits are shaped by the interplay of genetic inheritance, environmental conditions, and evolutionary history (Liu *et al.* 2024). However, while morphological variation provides essential diagnostic features, its plasticity often complicates taxonomic resolution within Bambusoideae. The principal vegetative characters commonly used for bamboo identification include culm and culm sheath characteristics, branching architecture, rhizome type, and leaf morphology (Fig. 2). These characters provide readily observable diagnostic information, particularly when reproductive structures are unavailable, although their taxonomic interpretation should account for environmentally induced variation.

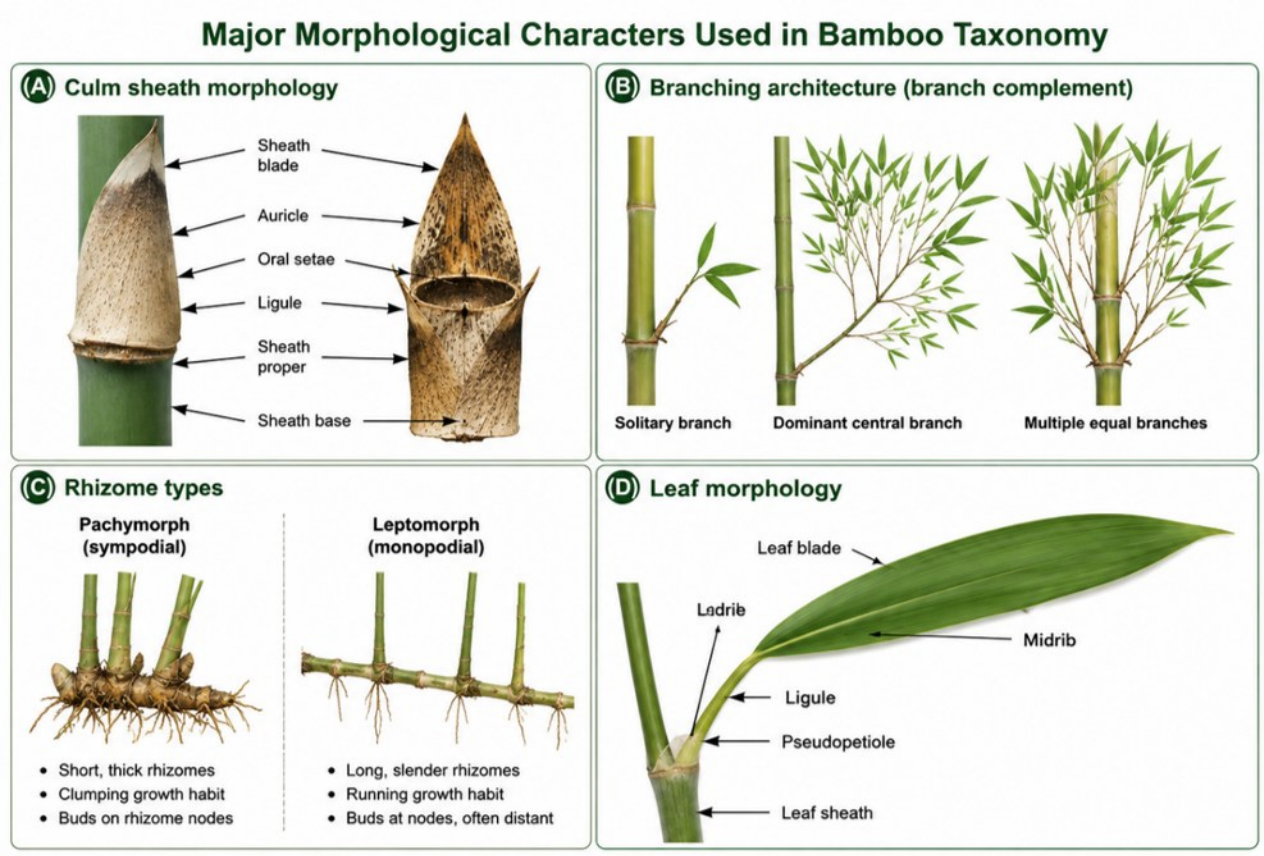

Fig. 2. Representative morphological features used in bamboo taxonomy and field identification: (A) culm sheath morphology, including the sheath blade, auricle, oral setae, ligule, and sheath proper; (B) branching architecture and variation in branch complements; (C) major rhizome types, including pachymorph (sympodial) and leptomorph (monopodial) growth forms; and (D) leaf morphology, including the leaf blade, midrib, pseudopetiole, ligule, and leaf sheath

Culm sheaths differ in the shape and orientation of the sheath blade, development of auricles and oral setae, and ligule characteristics, whereas branch complements provide useful characteristics for distinguishing genera and species. Rhizome architecture also represents an important growth-form character, with pachymorph rhizomes generally associated with clumping or sympodial growth and leptomorph rhizomes associated with running or monopodial growth. Nevertheless, these characteristics should be evaluated collectively because morphological overlap and environmentally induced variation can reduce the diagnostic reliability of individual traits.

Culm morphology is among the most conspicuous and economically relevant characteristics distinguishing bamboo taxa. Variation in culm height, diameter, and wall thickness influences both ecological performance and mechanical utility. For instance, species within the genus *Phyllostachys*, particularly moso bamboo (*Phyllostachys edulis*), are recognized for their rapid growth and substantial culm size, reaching heights of up to 20 m (Zheng *et al.* 2021).

Allometric relationships between culm height and diameter further determine biomechanical stability and competitive capacity in forest ecosystems (Niiyama *et al.* 2024). These structural traits influence light acquisition, canopy dominance, and resource allocation strategies, contributing to interspecific differentiation. Nevertheless,

environmentally induced variation in culm dimensions may reduce their diagnostic reliability when used independently for species identification.

Leaf morphology and micromorphological traits provide additional systematic signals. Stomatal characteristics, rather than gross anatomical features alone, have been shown to regulate photosynthesis and water-use efficiency in moso bamboo (Wen *et al.* 2023).

Such physiological–morphological linkages highlight the adaptive significance of leaf traits in environmental tolerance. Bamboo's capacity to thrive under varying light regimes, including shaded understory conditions, demonstrates morphological and physiological plasticity as an adaptive strategy; however, such environmentally induced responses may produce overlapping patterns among taxa and complicate morphology-based species delimitation (Yu *et al.* 2024).

The evolutionary processes underlying bamboo diversification contribute substantially to its morphological heterogeneity. Independent allopolyploidization events have been identified in both temperate and tropical bamboo lineages, preceding speciation and generating genomic complexity (Triplett *et al.* 2014). Such reticulate evolutionary histories can produce mosaic morphological traits, in which hybrid taxa display intermediate or novel phenotypes that do not conform to traditional taxonomic categories. This pattern, together with homoplasy resulting from convergent adaptation to similar ecological conditions, can obscure phylogenetic affinity despite substantial genomic divergence. Molecular evidence is therefore particularly important for distinguishing shared ancestry from phenotypic convergence in hybrid and polyploid lineages (Triplett *et al.* 2014).

At the anatomical level, cellular architecture further shapes bamboo's distinctive structural properties. Investigations into metaxylem vessel arrangement and vascular bundle organization have elucidated mechanisms supporting rapid growth, efficient water transport, and mechanical resilience (Luo *et al.* 2020). These anatomical features contribute to functional specialization among species and may offer additional characters for systematic evaluation. However, as with macromorphological traits, anatomical variation must be interpreted within a phylogenetic context to avoid conflating adaptive convergence with shared ancestry.

Collectively, morphological and anatomical characters provide valuable taxonomic information but are most informative when evaluated alongside molecular evidence. The appropriate applications, strengths, and limitations of these complementary systematic approaches are compared in Table 2.

Table 2. Comparison of Morphological, Anatomical, and Molecular Approaches in Bamboo Systematics

Approach	Representative Characteristics/Data	Appropriate Applications	Strengths	Limitations
Morphological	Culm height and diameter, culm sheath, branching pattern, leaf morphology, rhizome type, reproductive characters	Field identification, species description, preliminary species delimitation, herbarium taxonomy	Easily observable; relatively low cost; useful for field identification and practical taxonomy	Strongly influenced by environmental conditions and phenotypic plasticity; convergent traits may obscure relationships; reproductive characters are often unavailable because of irregular flowering
Anatomical	Vascular bundle structure, epidermal characters, stomatal traits, fiber and vessel characteristics	Differentiation of morphologically similar taxa, characterization of structural variation, supporting species identification	Provides microscopic diagnostic characters that complement external morphology; useful when macromorphological characters overlap	Requires sample preparation, microscopy, and technical expertise; some characters may vary with culm position, age, or environmental conditions
Molecular	ITS, chloroplast DNA, DNA barcodes, SSRs, SNPs, multi-locus and genome-scale sequence data	Species delimitation, phylogenetic reconstruction, genetic diversity assessment, detection of hybridization and evolutionary relationships	Provides direct genetic evidence; improves resolution of cryptic or morphologically similar taxa; useful for reconstructing evolutionary relationships	Results may be affected by hybridization, polyploidy, incomplete lineage sorting, and nuclear–plastid incongruence; requires laboratory and bioinformatic resources
Integrative	Combined morphological, anatomical, molecular, ecological, and biogeographical evidence	Complex species delimitation, taxonomic revision, phylogenetic interpretation, conservation prioritization	Combines complementary evidence and reduces reliance on a single character or dataset; provides more robust taxonomic conclusions	Requires multiple datasets, greater resources, interdisciplinary expertise, and standardized sampling and analytical procedures

ROLE OF PLANT SYSTEMATICS IN UNDERSTANDING BAMBOO DIVERSITY AND EVOLUTION

Plant systematics provides the conceptual and methodological foundation for resolving bamboo diversity and evolutionary relationships. By integrating morphological and molecular evidence, systematic approaches can address taxonomic uncertainties associated with complex genomic architecture and morphological variability (Wang *et al.* 2020).

The application of molecular markers has resolved several long-standing uncertainties in bamboo phylogeny that could not be addressed using morphology alone. Early applications of Internal Transcribed Spacer (ITS) sequences and chloroplast DNA markers provided critical insights into interspecific relationships and genetic differentiation. ITS-based analyses have proven effective in resolving taxonomic disputes and assessing genetic diversity within bamboo populations (Khanday *et al.* 2022). Similarly, chloroplast-based targeted enrichment approaches have enabled the reconstruction of large-scale phylogenies, as demonstrated by Sawicki *et al.* (2024), who analyzed 412 bamboo species to generate a comprehensive evolutionary framework. Such large phylogenomic datasets have improved resolution at both tribal and generic levels, offering a more robust understanding of lineage divergence across Bambusoideae Recent studies indicate a clear shift from single-marker analyses toward genome-scale datasets, enabling more detailed investigation of hybridization, polyploidy, incomplete lineage sorting, and lineage divergence that were difficult to resolve using conventional molecular approaches.

A defining evolutionary feature of bamboo is its history of allopolyploidization and reticulate evolution. Independent polyploidization events preceding speciation have been documented in both tropical and temperate lineages (Triplett *et al.* 2014). These processes generate complex genomic mosaics that challenge bifurcating tree models traditionally used in phylogenetic inference. The evolutionary significance of reticulate processes therefore underscores the necessity of integrating nuclear and plastid data to disentangle lineage relationships and avoid misleading phylogenetic signals (Triplett *et al.* 2014).

Phylogenetic analyses have prompted reassessment of traditional taxonomic assumptions. Multi-gene region studies have revealed inconsistencies in earlier classifications, including evidence suggesting the non-monophyletic nature of certain woody bamboo groups (Goyal *et al.* 2013). Such findings demonstrate the need for continued systematic refinement and have implications for identifying evolutionarily distinct lineages for conservation. Traditional and genomic taxonomy provide complementary evidence, with the former supporting field-based identification and phenotypic characterization and the latter offering greater resolution of cryptic diversity and complex evolutionary relationships. Their respective strengths, limitations, and applications are compared in Table 3.

Structural traits, such as internode architecture and shoot sheath morphology, remain valuable diagnostic features, particularly when interpreted within a phylogenetic framework (Wang *et al.* 2020). Furthermore, physiological investigations into growth regulation mechanisms, including auxin signaling pathways, contribute to understanding the developmental and evolutionary basis of bamboo's rapid growth and adaptive capacity (Bai *et al.* 2022; Zheng *et al.* 2022). Together, these complementary data provide additional context for interpreting bamboo evolutionary trajectories.

Table 3. Comparison between Traditional Taxonomy and Genomic Taxonomy in Bamboo Systematics

Aspect	Traditional Taxonomy	Genomic Taxonomy
Primary data source	Vegetative and reproductive morphology, including culm, culm sheath, branching, rhizome, leaf, and inflorescence characters	DNA sequences, molecular markers, plastomes, nuclear genes, and genome-wide datasets
Basis of classification	Similarities and differences in observable morphological and anatomical characters	Genetic relatedness, sequence variation, genomic structure, and evolutionary relationships
Major approaches	Field observation, herbarium comparison, morphological measurement, and anatomical examination	DNA barcoding, ITS and chloroplast markers, multi-locus sequencing, targeted enrichment, and phylogenomics
Species identification	Effective when taxa possess stable and distinctive morphological characters	Particularly effective for morphologically similar, cryptic, hybrid, or recently diverged taxa
Major strength	Relatively accessible, cost-effective, and directly applicable to field identification	Provides high phylogenetic resolution and enables direct assessment of genetic and evolutionary relationships
Major limitation	Influenced by morphological plasticity, convergent evolution, and the limited availability of reproductive characters caused by irregular flowering	Requires specialized laboratory and computational resources; results may be affected by incomplete lineage sorting, hybridization, polyploidy, and nuclear–plastid incongruence
Hybridization and polyploidy	Hybrid taxa may be difficult to distinguish because of intermediate or overlapping morphological characters	Nuclear, plastid, and genome-wide datasets can reveal hybrid ancestry, reticulate evolution, and polyploid origins
Phylogenetic resolution	Often limited for closely related or morphologically convergent taxa	Generally higher, particularly when multi-locus or genome-scale datasets are employed
Role in bamboo systematics	Essential for species description, field identification, herbarium taxonomy, and phenotypic characterization	Essential for testing species boundaries, reconstructing evolutionary relationships, and revising classifications
Representative references	Wang *et al.* (2020)	Triplett *et al.* (2014); Khanday *et al.* (2022); Sawicki *et al.* (2024)

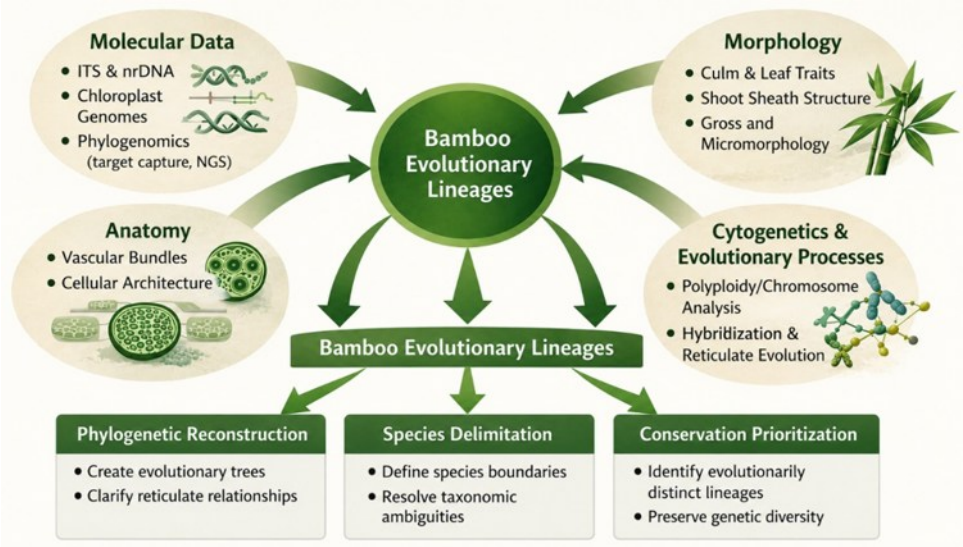

Fig. 3. Integrative plant systematics framework for resolving bamboo diversity and evolution

Collectively, integrative plant systematics provides a framework for reconstructing complex bamboo evolutionary relationships and improving species delimitation and conservation prioritization. Figure 3 summarizes how molecular, genomic, anatomical, morphological, and cytogenetic evidence can be combined to clarify lineage divergence and taxonomic boundaries within Bambusoideae.

ADVANCEMENTS IN MOLECULAR AND MORPHOLOGICAL TECHNIQUES IN BAMBOO TAXONOMY

Early Molecular Markers and Population-level Resolution

The introduction of DNA-based markers marked a turning point in bamboo systematics (Horn and Haser 2016). Microsatellite markers (SSRs) have proven highly effective in detecting genetic variation within and among species, thereby refining taxonomic boundaries and revealing cryptic diversity (Disasa *et al.* 2016). The development of genome-wide microsatellite markers in *Phyllostachys edulis* further strengthened molecular classification frameworks by enabling physical mapping across the genome (Zhao *et al.* 2015). Similarly, inter-simple sequence repeat (ISSR) and amplified fragment length polymorphism (AFLP) markers have been widely employed to assess genetic diversity and population structure (Nilkanta *et al.* 2017; Khairi *et al.* 2020). These marker systems are particularly valuable for distinguishing taxa with similar vegetative characteristics.

DNA Barcoding and Species Identification

DNA barcoding has improved species identification in bamboo, particularly when reproductive structures are unavailable. However, the discriminatory power of commonly used plastid markers remains limited in recently diverged taxa. For this reason, DNA barcoding is often more effective when combined with nuclear markers and complementary morphological evidence (Sawarkar *et al.* 2021). Commonly employed markers include rbcL, matK, trnL-F, and ITS regions, derived from both chloroplast and nuclear genomes (Khairi *et al.* 2020; Meena *et al.* 2020; Gallaher *et al.* 2022; Yong *et al.*

2024). The molecular identification of *Bambusa changningensis*, a natural hybrid, exemplifies the power of genetic markers to resolve taxonomic uncertainties that morphology alone cannot clarify (Zhuo *et al.* 2023). This is especially critical given bamboo's unpredictable flowering patterns and frequent hybridization events (Huang *et al.* 2020). Integration of DNA barcoding with phylogenetic reconstruction can further clarify interspecific relationships (Zhang *et al.* 2020; Ye *et al.* 2022).

Phylogenetic Reconstruction and Multi-gene Approaches

Phylogenetic analysis constitutes a central tool for elucidating bamboo evolutionary history. Sequencing of chloroplast and nuclear loci enables reconstruction of lineage divergence and clarification of taxonomic relationships (Palmer 2019). Chloroplast genes, such as ndhF, psbA-trnH, and rpl16, are frequently employed due to their maternal inheritance and moderate evolutionary rates, making them suitable for examining deeper evolutionary patterns (Palmer 2019; Peng *et al.* 2023; Zhang *et al.* 2024). Nuclear markers, such as GBSSI, provide complementary insights, particularly for detecting hybridization events that are prevalent within Bambusoideae (Zhuo *et al.* 2023). Through multi-locus sequencing, phylogenetic trees can be constructed to reassess generic boundaries, revise classifications, and identify novel taxa (Wang *et al.* 2024a). However, incongruence between nuclear and plastid datasets remains a methodological challenge in hybrid-rich lineages.

While early molecular markers improved species-level discrimination, their limited genomic coverage restricted deeper evolutionary inference. The emergence of next-generation sequencing technologies addressed these limitations by enabling genome-wide phylogenetic reconstruction.

Next-generation Sequencing and Phylogenomics

The introduction of next-generation sequencing has transformed bamboo systematics from marker-based studies to genome-scale analyses. This shift is particularly important for bamboo because many evolutionary processes, including hybridization and polyploidization, cannot be adequately captured using a limited number of loci (Wang *et al.* 2021). Whole-genome sequencing of *Phyllostachys edulis* has provided insights into the genetic basis of rapid growth, wood development, and stress resilience (Fu *et al.* 2024). Techniques, such as Restriction-site Associated DNA Sequencing (RAD-seq), enable the discovery of large numbers of genome-wide markers, facilitating fine-scale analysis of genetic diversity and speciation processes (Guo *et al.* 2019). Additionally, RNA sequencing (RNA-seq) has been applied to investigate gene expression patterns across environmental gradients, linking genomic variation to functional adaptation (Wang *et al.* 2020b). More recently, long-read sequencing platforms, including Pacific Biosciences (PacBio) and Oxford Nanopore Technologies (ONT), have expanded opportunities for resolving complex bamboo genomes. PacBio single-molecule real-time sequencing has been applied to *Phyllostachys edulis*, enabling the identification of full-length transcripts and improving genome annotation and alternative splicing analysis (Zhao *et al.* 2018). In addition, ONT long-read sequencing has been used to generate high-quality genome assemblies across multiple bamboo species, providing improved resolution of repetitive genomic regions, structural variation, and subgenome evolution (Ma *et al.* 2024). These long-read technologies complement conventional short-read sequencing and are particularly valuable for investigating the complex genomic architecture associated with polyploidy and evolutionary diversification in bamboo.

Molecular Cytogenetics and Genome Evolution

Beyond sequence-based methods, molecular cytogenetics has provided crucial insights into genome structure and chromosomal evolution. Bamboo taxonomy is complicated by variable chromosome numbers and diverse levels of polyploidy (Mathu *et al.* 2023). Techniques, such as fluorescence *in situ* hybridization (FISH) and genomic *in situ* hybridization (GISH), allow direct visualization of chromosomal organization and detection of genomic rearrangements (Cheng *et al.* 2023). These approaches are instrumental in identifying hybridization events and elucidating genome evolution patterns (Ma *et al.* 2024). Cytogenetic analyses therefore complement molecular phylogenetics by revealing structural genomic dynamics underlying diversification.

Advances in Morphological Analytics

In parallel with molecular progress, morphological analysis has evolved through technological innovation. Hyperspectral remote sensing combined with machine learning algorithms, including Extreme Gradient Boosting (XGBoost), has enhanced species classification by detecting subtle spectral differences linked to morphological traits (Zhou *et al.* 2022). Such computational approaches enable large-scale species discrimination and provide a data-driven complement to conventional morphological assessment.

Despite substantial methodological advances, no single molecular approach provides sufficient resolution across all taxonomic levels in bamboo. DNA barcoding is efficient for rapid species identification but may provide limited discrimination among recently diverged taxa, whereas multi-locus approaches improve phylogenetic resolution but can generate conflicting signals between nuclear and plastid datasets. RAD-seq provides high-density markers suitable for resolving recent divergence and species complexes, although its application may be constrained by computational requirements and the availability of reference genomic resources. Whole-genome and long-read sequencing provide substantially greater resolution of complex genomic regions, structural variation, and polyploid genomes, but require greater computational resources, high-quality DNA, and advanced bioinformatic analyses. Molecular cytogenetic approaches, including FISH and GISH, are particularly valuable for detecting polyploidy, hybridization, and chromosomal rearrangements, although they provide limited resolution of fine-scale sequence variation. Therefore, the selection of molecular approaches should depend on the taxonomic scale and research objective rather than on the assumption that increased genomic coverage alone can fully resolve bamboo phylogeny. Persistent challenges, particularly hybridization, polyploidy, incomplete lineage sorting, nuclear–plastid incongruence, incomplete taxon sampling, and uneven genomic representation, continue to limit phylogenetic reconstruction and reinforce the need for integrative analyses combining complementary datasets.

Integrative Implications for Taxonomic Precision

The complementary roles of genomic, cytogenetic, and morphological approaches provide a stronger basis for species delimitation and phylogenetic interpretation than any single dataset. The principal techniques applied in bamboo systematics, together with their systematic scales, applications, strengths, and methodological limitations, are summarized in Table 4. Continued methodological development may further improve taxonomic stability and conservation planning by providing more robust assessments of genetic diversity and lineage distinctiveness (Wei *et al.* 2016; Ma *et al.* 2018).

Table 4. Molecular and Morphological Techniques in Bamboo Taxonomy: Applications, Strengths, and Limitations

Technique	Data Source	Systematic Scale	Primary Application in Bamboo	Major Strengths	Key Limitations in Bamboo Context	Representative References
Microsatellites (SSR)	Nuclear DNA	Population to species level	Assess genetic diversity, population structure, clonal variation	High polymorphism, codominant markers, effective for intra-specific variation	Limited resolution for deep phylogeny; allele scoring complexity in polyploids	Zhao *et al.* 2015; Disasa *et al.* 2016
ISSR and AFLP	Nuclear DNA fragments	Population level	Evaluate genetic diversity and genetic differentiation	Cost-effective; useful without prior genome data	Dominant markers; reproducibility issues; limited phylogenetic resolution	Nilkanta *et al.* 2017; Khairi *et al.* 2020
DNA Barcoding (rbcL, matK, trnL-F)	Chloroplast DNA	Species level	Rapid species identification; discrimination among vegetatively similar taxa	Standardized markers; easy amplification	Low variation in recently diverged taxa; maternal inheritance bias	Khairi *et al.* 2020; Meena *et al.* 2020; Gallaher *et al.* 2022; Yong *et al.* 2024
ITS Sequencing	Nuclear ribosomal DNA	Species to genus level	Resolve taxonomic disputes; assess interspecific relationships	Biparental inheritance; higher variability than plastid markers	Concerted evolution; paralog issues; complications in polyploids	Khanday *et al.* 2022
Multi-locus Phylogenetics	Nuclear + plastid genes (*e.g.*, ndhF, psbA-trnH, rpl16, GBSSI)	Genus to tribal level	Phylogenetic reconstruction; detection of incongruence	Improved resolution; detect hybridization signals	Conflicting nuclear *vs* plastid trees; incomplete lineage sorting	Palmer 2019; Peng *et al.* 2023; Zhuo *et al.* 2023; Wang *et al.* 2024a
RAD-seq	Genome-wide SNPs	Population to species complex	Fine-scale genetic differentiation; speciation studies	High marker density; powerful for recent divergence	Computational demand; reference genome dependency	Guo *et al.* 2019
Whole-Genome Sequencing	Entire nuclear genome	Deep evolutionary scale	Investigate genome evolution; identify polyploid origins	Comprehensive genomic insight; gene family evolution	Expensive; complex assembly in large polyploid genomes	Wang *et al.* 2021; Fu *et al.* 2024

Technique	Data Source	Systematic Scale	Primary Application in Bamboo	Major Strengths	Key Limitations in Bamboo Context	Representative References
RNA-seq	Transcriptome	Functional and adaptive evolution	Study gene expression; adaptive traits	Links genotype to phenotype; stress response analysis	Expression varies by tissue and environment; not direct phylogenetic marker	Wang *et al.* 2020
Molecular Cytogenetics (FISH, GISH)	Chromosomal structure	Genome-level	Detect hybridization; analyze chromosomal rearrangements	Visualize polyploidy; confirm genomic composition	Technically demanding; limited resolution for subtle sequence variation	Cheng *et al.* 2023; Ma *et al.* 2024
Hyperspectral Imaging + Machine Learning (*e.g.*, XGBoost)	Spectral morphological signatures	Species classification (landscape scale)	Large-scale species discrimination; remote identification	Non-destructive; scalable; detects subtle trait variation	Requires training datasets; influenced by environmental noise	Zhou *et al.* 2022
Optimized DNA Extraction Protocols	Genomic preparation	Foundational step	Improve DNA quality for molecular integration	Enhances downstream sequencing accuracy	Species-specific optimization required	Silva and Ribeiro 2018
PacBio Long-Read Sequencing	Long-read genomic DNA / full-length transcripts	Genome and transcriptome level	Genome annotation; full-length transcript identification; alternative splicing analysis	Long, high-quality reads; improves transcript and genome annotation; resolves complex regions	Higher cost and requirement for high-quality, high-molecular-weight nucleic acids	Zhao *et al.* 2018
Oxford Nanopore Sequencing (ONT)	Long-read genomic DNA	Genome to comparative genomic level	*De novo* genome assembly; structural variation; repetitive regions; subgenome evolution	Very long reads; improves genome contiguity; useful for complex and polyploid genomes	Requires substantial bioinformatic processing and polishing; sequencing accuracy depends on platform and chemistry	Ma *et al.* 2024

LIMITATIONS IN BAMBOO TAXONOMY

Despite substantial methodological advancements, bamboo taxonomy remains constrained by several intrinsic biological and evolutionary factors that complicate stable classification. These limitations have significant implications for conservation planning, breeding programs, and sustainable resource management.

A primary challenge arises from the sporadic and prolonged flowering cycles characteristic of many bamboo species (Zheng *et al.* 2020). Gregarious flowering may occur after decades of vegetative growth, sometimes at intervals exceeding a century, and may be followed by mass die-off (Chakraborty *et al.* 2021; Yao *et al.* 2023; Dalagnol *et al.* 2018). The resulting scarcity of floral and inflorescence characters, which are important in grass taxonomy, increases reliance on environmentally variable vegetative traits and may contribute to species misidentification and unstable delimitation.

Morphological plasticity further compounds taxonomic uncertainty because climatic conditions, soil type, altitude, and resource availability can modify diagnostic vegetative traits (Rusch *et al.* 2023). Variation in plant height, culm diameter, leaf size, and internode length may complicate discrimination between genetically distinct taxa and environmentally induced forms (Qian *et al.* 2019; Vale *et al.* 2019), increasing the risk of inaccurate species delimitation.

Hybridization and polyploidy create additional uncertainty by generating intermediate morphological characteristics and complex genomic signals that blur species and generic boundaries (Yuan *et al.* 2019; Triplett and Clark 2021; Zhuo *et al.* 2023). Polyploid genomes can further complicate the interpretation of molecular markers, while some hybrid taxa remain genetically similar to their progenitors despite morphological differentiation (Gillespie *et al.* 2020; Ma *et al.* 2024). Plastid capture and incomplete lineage sorting may additionally produce conflicting signals between nuclear and plastid phylogenies, particularly in rapidly radiating woody bamboo clades.

In addition to biological and evolutionary constraints, incomplete taxon sampling remains an important methodological limitation in bamboo phylogenetic studies. Limited representation of species, populations, and geographic regions may reduce phylogenetic resolution and lead to incomplete interpretations of lineage relationships, particularly in species-rich and rapidly diversified groups. Broader taxon sampling can improve phylogenetic resolution by increasing representation of evolutionary diversity across Bambusoideae (Wysocki *et al.* 2015; Wang *et al.* 2017). Inadequate voucher documentation represents a related concern because properly identified and deposited herbarium specimens provide a permanent link between molecular sequence data and taxonomic identity, allowing subsequent verification and reassessment. Incomplete voucher information may therefore reduce the reproducibility and reliability of phylogenetic studies when taxonomic circumscriptions are revised. Future studies should prioritize broader geographic and taxonomic sampling together with well-documented voucher specimens deposited in recognized herbaria.

OPPORTUNITIES IN BAMBOO TAXONOMY

Several recent technological developments may help address taxonomic challenges that have persisted in bamboo research for decades. The future of bamboo systematics lies

in the integration of genomic data, computational analytics, and digitized biodiversity resources to construct more evolutionarily robust classification frameworks.

Continued expansion of genomic resources offers important opportunities for improving species delimitation and evolutionary inference in bamboo (Ramakrishnan *et al.* 2020; Wang *et al.* 2022). Existing approaches, including DNA barcoding, RAD-seq, RNA-seq, and whole-genome sequencing, have demonstrated their value for resolving genetic diversity, speciation, and phylogenetic relationships (Sawarkar *et al.* 2021; Li *et al.* 2022; Ye *et al.* 2024). The *Phyllostachys edulis* genome provides an important reference for comparative genomics and the investigation of complex evolutionary histories (Zhang *et al.* 2018). Expanding comparable genomic resources across underrepresented bamboo lineages could further improve taxonomic resolution, particularly in species complexes characterized by hybridization and reticulate evolution.

Emerging environmental DNA (eDNA) and metabarcoding approaches provide additional opportunities for biodiversity assessment and may complement conventional bamboo surveys and taxonomic studies. Environmental DNA recovered from environmental samples, such as soil and water, can be analyzed using standardized barcode regions to detect plant taxa without direct collection of complete specimens. Recent large-scale studies have demonstrated that soil eDNA metabarcoding can effectively characterize patterns of plant diversity and community composition, although taxonomic resolution remains dependent on the completeness and accuracy of reference sequence databases (Fahner *et al.* 2016; Duley et al. 2023). The integration of eDNA metabarcoding with portable sequencing technologies, particularly Oxford Nanopore Technologies (ONT) MinION, further enables rapid and potentially field-based biodiversity assessment. Recent work in Malaysian tropical ecosystems demonstrated that nanopore-based eDNA metabarcoding can provide cost-effective species detection and complement conventional biodiversity surveys (Munian *et al.* 2024). Although these approaches have yet to be extensively applied to bamboo systematics, their integration with validated bamboo DNA barcode libraries could facilitate rapid detection of bamboo diversity and ecological monitoring, particularly in remote and species-rich tropical regions.

Artificial intelligence (AI) and machine learning offer complementary tools for morphological discrimination and large-scale biodiversity assessment (Correal *et al.* 2022; Tamang *et al.* 2022). Image recognition systems trained on extensive morphological datasets can automate species identification based on culm architecture, leaf morphology, and rhizome characteristics (Watanabe *et al.* 2020). AI-driven algorithms may improve classification consistency and reduce observer bias in morphologically similar taxa (Yabeyen *et al.* 2024), while geometric morphometrics can enhance discrimination among closely related species by quantifying subtle shape variation (Das *et al.* 2023). These computational approaches offer potential for accelerating taxonomic revision and supporting conservation and applied utilization (Sawarkar *et al.* 2024).

The increasing availability of genomic datasets, digitized herbarium specimens, and computational tools is changing how taxonomic studies are conducted and interpreted. By combining high-resolution genetic data with advanced morphological modeling, future bamboo systematics can achieve greater taxonomic stability and more accurate biodiversity assessment.

Despite these technological advancements, several unresolved phylogenomic and systematic challenges continue to constrain the development of a fully stable and evolutionarily coherent bamboo classification framework.

CHALLENGES AND FUTURE DIRECTIONS IN INTEGRATIVE BAMBOO PHYLOGENOMICS

Despite major advances in molecular systematics, several evolutionary and methodological challenges continue to limit the development of a stable and evolutionary meaningful classification system for Bambusoideae.

One of the most persistent problems is incomplete lineage sorting, particularly among woody bamboo lineages that appear to have diversified rapidly (Guo *et al.* 2019; Liu *et al.* 2024). When speciation occurs over a relatively short evolutionary timescale, insufficient genetic divergence may accumulate among descendant lineages, resulting in weakly supported or conflicting phylogenetic relationships. Consequently, even genome-scale datasets may fail to completely resolve certain evolutionary relationships within Bambusoideae.

Another challenge involves the frequent disagreement between plastid-derived and nuclear-derived phylogenies (Triplett *et al.* 2014; Wang *et al.* 2021). Plastid genomes generally reflect maternal inheritance, whereas nuclear genomes capture genetic contributions from both parents. As a result, phylogenetic trees generated from these datasets may support different evolutionary scenarios. Such incongruence is particularly evident in bamboo groups with extensive hybridization histories and highlights the limitations of relying on a single genomic compartment for phylogenetic inference.

Hybridization and polyploidization further complicate bamboo phylogenomics (Triplett *et al.* 2014; Zhuo *et al.* 2023). Evidence from tropical and temperate lineages indicates extensive reticulate evolution, with mixed genomic signatures inherited from multiple ancestral lineages and allopolyploidization generating duplicated genomes (Gillespie *et al.* 2020; Ma *et al.* 2024). Such genomic complexity can produce conflicting evolutionary signals and complicate reconstruction of lineage relationships.

A further limitation of current bamboo phylogenomic research is the uneven distribution of genomic resources. Globally, major regions of bamboo diversity occur across East and Southeast Asia, South Asia and the Himalayan region, Central and South America, and parts of Africa and Madagascar. To date, most large-scale studies have focused on economically important species from China and other parts of East Asia (Khairi *et al.* 2020; Liu *et al.* 2024). In contrast, tropical Southeast Asia, which represents one of the world's major centers of bamboo diversity, remains comparatively understudied. Countries such as Malaysia, Indonesia, Thailand, Myanmar, and the Philippines, harbor numerous species whose evolutionary relationships remain poorly understood. This geographic bias restricts broader interpretation of bamboo evolution and may result in the underestimation of regional biodiversity.

Although AI, machine learning, and computational phylogenomics offer promising opportunities for accelerating species identification and evolutionary analyses (Watanabe *et al.* 2020; Zhou *et al.* 2022), these technologies should not be viewed as standalone solutions. Their effectiveness depends heavily on the quality of underlying reference datasets, accurately identified voucher specimens, and representative taxonomic sampling. Without these foundations, computational approaches may inadvertently reinforce existing taxonomic errors rather than resolve them (Sawarkar *et al.* 2024).

Future progress in bamboo systematics will depend on coordinated international sampling and phylogenomic collaborations, particularly across tropical Southeast Asia, where genomic representation remains limited (Wang *et al.* 2021). Existing resources, such as the Bamboo Genome Database (BambooGDB), demonstrate the value of integrating

genome sequences, transcriptomic data, functional annotations, and analytical tools within a centralized platform (Zhao *et al.* 2014). Future development should expand toward an international bamboo genomic database with broader taxonomic and geographic representation and voucher-linked molecular, morphological, anatomical, ecological, and distributional information. Equally important is the adoption of standardized molecular protocols, including consistent DNA extraction procedures, validated barcode loci, sequencing strategies, voucher documentation, and quality-control criteria, to improve reproducibility and comparability among studies. Standardized DNA barcoding using commonly applied loci, such as *matK* and *rbcL*, could further support species identification and the development of curated reference libraries (Dev *et al.* 2020; Yong *et al.* 2024). Together, internationally coordinated databases, standardized protocols, and expanded collaborative sampling would strengthen comparative phylogenomics and provide a more reliable foundation for bamboo conservation, breeding, and sustainable utilization.

Ultimately, progress in bamboo phylogenomics will depend on broader taxon sampling, coordinated international genomic resources, standardized molecular protocols, and analytical frameworks capable of accommodating reticulate evolution and polyploidy. These priorities will be essential for improving phylogenetic resolution and achieving a more stable classification of Bambusoideae.

CONCLUDING REMARKS

Molecular phylogenetics and phylogenomics have substantially improved our understanding of bamboo diversity and evolutionary relationships while revealing greater evolutionary complexity than suggested by traditional morphology-based classifications. Persistent processes, including hybridization, polyploidization, plastid capture, and incomplete lineage sorting, continue to generate conflicting phylogenetic signals and complicate species delimitation.

Current evidence indicates that no single source of data is sufficient to resolve the systematic complexity of Bambusoideae. Instead, the synthesis supports an integrative framework combining genomic, morphological, anatomical, ecological, and biogeographical evidence to improve species delimitation and phylogenetic interpretation.

A major knowledge gap identified in this review is the unequal geographic representation of bamboo phylogenomic research. While East Asian species have received considerable attention, many tropical Southeast Asian taxa remain underrepresented despite the region's high bamboo diversity. Expanding phylogenomic sampling in this region may improve taxonomic resolution and reveal previously unrecognized evolutionary lineages and cryptic species.

From a practical perspective, accurate taxonomy underpins biodiversity conservation, germplasm management, breeding programs, sustainable harvesting, and industrial utilization. Misidentification can compromise conservation planning, reduce the effectiveness of breeding strategies, and limit the sustainable use of bamboo genetic resources. Therefore, systematic research should be regarded as a fundamental component of bamboo conservation and development rather than solely as an academic exercise.

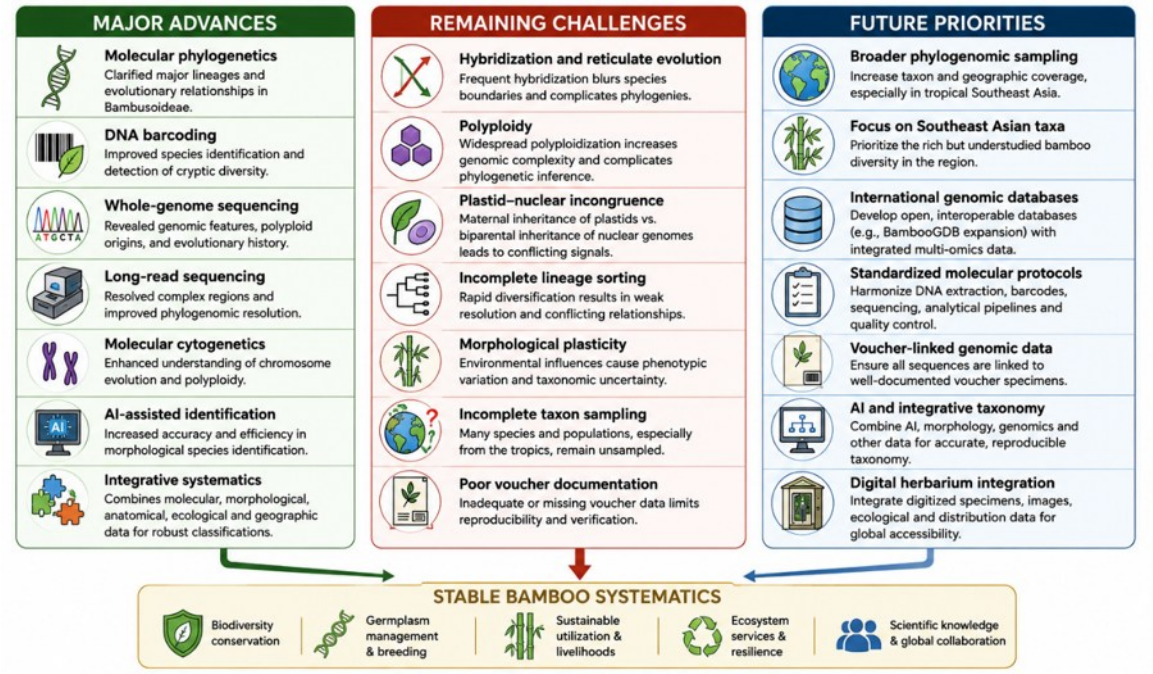

Fig. 4. Major advances, remaining challenges, and future priorities in bamboo systematics. Recent advances in molecular, genomic, cytogenetic, and computational approaches have improved the understanding and resolution of bamboo systematics. However, hybridization, polyploidy, plastid–nuclear incongruence, incomplete lineage sorting, morphological plasticity, incomplete taxon sampling, and incomplete voucher documentation remain important challenges. Future priorities include broader phylogenomic sampling, particularly of Southeast Asian taxa, international genomic databases, standardized molecular protocols, voucher-linked genomic data, AI-assisted integrative taxonomy, and digital herbarium integration.

From the authors' point of view, a key insight emerging from this review is that the major limitation in bamboo systematics is no longer the availability of molecular tools, but their strategic application across underrepresented taxa and geographic regions. Future research should therefore prioritize broader phylogenomic sampling, particularly across tropical Southeast Asia, standardized molecular and analytical protocols, voucher-linked genomic databases, AI-assisted species identification, digital herbarium integration, and stronger international collaboration. These priorities provide a practical roadmap toward resolving persistent taxonomic uncertainties and achieving a more stable and evolutionarily meaningful classification of Bambusoideae. Such efforts will strengthen both scientific knowledge and the sustainable management of one of the world's most important renewable plant resources. The major advances, remaining systematic challenges, and priority directions for future bamboo research are summarized in Fig. 4.

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