

Taxonomic Revisions in the Fabaceae: Implications from Genetic Studies

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Abstract As a highly diverse plant family, the Fabaceae's taxonomic revisions are crucial. Traditional classification methods face numerous challenges in dealing with the diversity and complexity of Fabaceae, while genetic studies provide new perspectives and tools for taxonomy. This study examines the historical background of Fabaceae taxonomy and explores the role and impact of genetic studies, including DNA sequencing and phylogenetic analysis, molecular markers, and genomics. It focuses on the influence of genetic research on Fabaceae taxonomy, such as the reclassification of genera and species, the discovery of cryptic species, and the clarification of evolutionary relationships. Through case studies on the genera *Acacia*, *Lupinus*, and *Phaseolus*, the study demonstrates the practical application of genetics in taxonomic revisions. Additionally, it discusses conservation strategies based on genetic diversity, biodiversity assessments, species richness, and the role of genetics in habitat restoration. Looking forward, the study emphasizes the integration of genetic and morphological data, the role of bioinformatics and big data in taxonomy, and the prospects for automated taxonomy. This study provides important references for the future development of Fabaceae taxonomy.

Keywords Fabaceae; Taxonomic revisions; Genetic research; DNA sequencing; Phylogenetic analysis

1 Introduction

The Fabaceae, also known as the legume family, is the third-largest family of flowering plants, comprising approximately 765 genera and 19 500 species (Zhao et al., 2021). This family holds significant economic and ecological importance, with members including essential crop plants such as soybeans, beans, lentils, and peas (Smýkal et al., 2015). Traditionally, the Fabaceae family has been divided into three subfamilies: Caesalpinioideae, Mimosoideae, and Papilionoideae. However, recent phylogenetic studies have proposed a more refined classification into six subfamilies (Azani et al., 2017). These plants are known for their ability to fix atmospheric nitrogen through symbiotic relationships with rhizobial bacteria, a trait that enhances soil fertility and reduces the need for synthetic fertilizers (Cannon et al., 2015; Zhao et al., 2021).

Taxonomic revisions are crucial for accurately understanding the evolutionary relationships and biodiversity within the Fabaceae family. Traditional classifications based on morphological characteristics have often been found to be incongruent with genetic data, leading to the need for revisions (Liu et al., 2017). Accurate taxonomy is essential for various applications, including conservation, agriculture, and ecological studies. For instance, the discovery of non-monophyletic groups within the Fabaceae has significant implications for the classification and understanding of evolutionary processes within the family (Liu et al., 2017; Azani et al., 2017).

Genetic studies have revolutionized the field of taxonomy by providing robust data for resolving phylogenetic relationships. Techniques such as phylogenomics, which involve the analysis of large-scale genomic data, have been instrumental in clarifying deep-branching relationships within the Fabaceae (Koenen et al., 2019). These studies have revealed complex evolutionary processes such as incomplete lineage sorting, hybridization, and polyploidization, which traditional morphological methods could not adequately address (Koenen et al., 2019; Moghaddam and Kazempour-Osaloo, 2020). For example, the use of nuclear and plastid sequences has provided new insights into the phylogenetic relationships and evolutionary history of various legume genera (Guo et al., 2007; Liu et al., 2017). Additionally, genetic studies have identified multiple polyploidy events and their role in the diversification of the Fabaceae (Cannon et al., 2015).

This study aims to synthesize the current knowledge on taxonomic revisions within the Fabaceae family, particularly focusing on the implications of genetic studies. The study will summarize recent taxonomic changes and their theoretical basis, emphasize the role of genetic data in resolving phylogenetic relationships and uncovering evolutionary processes, and discuss the implications of these taxonomic revisions for conservation, agriculture, and ecological research. By integrating findings from multiple genetic studies, this study hopes to provide a comprehensive overview of the current state of Fabaceae taxonomy and offer insights into future research directions. The ultimate goal is to enhance our understanding of the evolutionary history and biodiversity of this important plant family.

2 Historical Perspective on Fabaceae Taxonomy

2.1 Traditional classification methods

The traditional classification of the Fabaceae family, one of the largest and most economically significant plant families, has historically relied on morphological characteristics. Early taxonomists used features such as flower structure, leaf arrangement, and seed pod morphology to classify and differentiate species within the family. These methods, while foundational, often led to ambiguities and misclassifications due to the high degree of morphological similarity among different species (Ayu et al., 2022; Pinto et al., 2023).

2.2 Major taxonomic changes over the years

Over the years, significant taxonomic revisions have been made within the Fabaceae family, driven by advancements in molecular biology and genetic studies. For instance, the use of nuclear phylotranscriptomics and phylogenomics has provided a highly resolved phylogeny of the family, supporting numerous polyploidization events and offering new insights into the evolutionary history of symbiotic nitrogen fixation in Fabaceae (Zhao et al., 2021). Additionally, DNA barcoding using chloroplast markers such as *matK* and *rbcL* has proven effective in the rapid and accurate identification of Fabaceae species, further refining taxonomic classifications (Ayu et al., 2022).

2.3 Challenges faced in traditional taxonomy

Traditional taxonomy of Fabaceae has faced several challenges, primarily due to the morphological similarities among species, which often led to misidentifications and taxonomic ambiguities. For example, the circumscription of species within the genus *Hymenaea* has been historically challenging, with molecular and morphological studies revealing the need for reclassification to better reflect genetic and morphological distinctions (Pinto et al., 2023). Furthermore, the reliance on phenotypic traits alone has been insufficient in resolving phylogenetic relationships at finer taxonomic levels, necessitating the integration of genetic data to achieve more accurate classifications (Zhao et al., 2021; Ayu et al., 2022).

3 Advancements in Genetic Studies

3.1 Introduction to genetic techniques in taxonomy

Genetic techniques have revolutionized the field of taxonomy, providing tools for more precise and comprehensive classification of species. Traditional taxonomy relied heavily on morphological characteristics, which could be ambiguous and subject to convergent evolution. In contrast, genetic techniques offer a more objective and quantifiable approach to understanding evolutionary relationships. These techniques include DNA sequencing, phylogenetics, and the use of molecular markers, which have been instrumental in resolving complex taxonomic questions and uncovering evolutionary histories.

3.2 DNA sequencing and phylogenetics

DNA sequencing has become a cornerstone in modern taxonomy, allowing researchers to analyze genetic material at an unprecedented level of detail. In the Fabaceae family, extensive DNA sequencing has been employed to construct highly resolved phylogenies. For instance, a study utilizing over 1 500 nuclear genes from newly sequenced transcriptomes and genomes of 391 species provided a robust phylogeny of the Fabaceae, supporting numerous polyploidization events and elucidating the evolutionary history of rhizobial nitrogen-fixing symbiosis

(Zhao et al., 2021). Similarly, the complete chloroplast genome sequencing of *Cercis chuniana* and its comparison with other species in the Caesalpinioideae subfamily has provided valuable insights into phylogenetic relationships and supported the monophyly of Cercidoideae (Liu et al., 2018).

3.3 Molecular markers and genomics

Molecular markers and genomic studies have further enhanced our understanding of genetic diversity and evolutionary processes within the Fabaceae. The use of repetitive DNA analysis in 23 species from the legume tribe Fabeae revealed significant genome size variation driven by the differential accumulation of repetitive elements, particularly Ty3/gypsy LTR-retrotransposons (Macas et al., 2015). This study demonstrated the power of combining low-pass genome sequencing with advanced bioinformatics to analyze genome size evolution within a phylogenetic context. Additionally, the characterization of genetic markers such as simple sequence repeats (SSRs) and the analysis of nucleotide diversity have provided deeper insights into the genetic structure and evolutionary dynamics of legume species (Liu et al., 2018).

These advancements in genetic studies have profound implications for taxonomic revisions in the Fabaceae, enabling more accurate classification and a better understanding of the evolutionary mechanisms driving diversity in this economically and ecologically important plant family.

4 Impact of Genetic Studies on Fabaceae Taxonomy

4.1 Reclassification of genera and species

Genetic studies have significantly impacted the reclassification of genera and species within the Fabaceae family. For instance, the use of nuclear phylotranscriptomics and phylogenomics has provided a highly resolved phylogeny of Fabaceae, supporting the monophyly of subfamilies and revealing numerous polyploidization events (Zhao et al., 2021). This has led to a re-evaluation of traditional morphological taxonomic delimitations, as evidenced by the clustering of species based on seed storage protein profiles, which often do not align with traditional morphological classifications (Omonhinmin and Ogunbodede, 2013). These genetic insights necessitate a revision of the taxonomic framework to better reflect the genetic relationships among species.

4.2 Discovery of cryptic species

The application of genetic diversity studies has also facilitated the discovery of cryptic species within Fabaceae. Proteomic analyses, such as those involving seed storage protein profiling, have uncovered significant genetic polymorphism among species, indicating the presence of hidden genetic subdivisions that were not previously recognized through morphological studies alone (Omonhinmin and Ogunbodede, 2013). This discovery of cryptic species underscores the importance of integrating genetic data into taxonomic studies to uncover the true diversity within the family.

4.3 Clarification of evolutionary relationships

Genetic studies have been instrumental in clarifying the evolutionary relationships within Fabaceae. Phylogenomic analyses have provided robust support for the evolutionary history of the family, including the early radiation of subfamilies and the subsequent divergence of tribe-level clades (Zhao et al., 2021). These studies have also elucidated the evolutionary pathways of key traits, such as rhizobial nitrogen-fixing nodulation, by reconstructing ancestral character states and analyzing related gene families (Zhao et al., 2021). Such genetic insights have refined our understanding of the evolutionary processes that have shaped the diversity and distribution of Fabaceae species.

In summary, genetic studies have profoundly influenced the taxonomy of Fabaceae by enabling the reclassification of genera and species, revealing cryptic species, and clarifying evolutionary relationships. These advancements highlight the necessity of incorporating genetic data into taxonomic frameworks to achieve a more accurate and comprehensive understanding of this diverse and ecologically significant plant family.

5 Case Studies

5.1 Revisions in the genus *Acacia*

The genus *Acacia* is one of the most diverse genera in the Fabaceae family, widely distributed across the world. China is considered a major region rich in *Acacia* species in Asia, with Yunnan Province being the most species-rich and diverse area. Studies have shown that the *Acacia* species in China exhibit a high degree of local endemism, with nearly half of the species being endemic or nearly endemic (Maslin et al., 2019). Traditional classification methods primarily based on morphological characteristics such as leaf shape, inflorescence, and seed structure are often influenced by environmental and developmental factors, leading to classification uncertainties and disputes.

In recent years, genetic research has provided new perspectives for the classification of *Acacia*. Through DNA sequencing and phylogenetic analysis, researchers can more accurately resolve the genetic relationships among different populations. The application of chloroplast DNA (cpDNA) and nuclear DNA (nDNA) markers, in particular, has enabled the tracing of the evolutionary history and phylogenetic relationships of *Acacia* species. A notable case is the study by Maslin et al. (2019) on the broader genus *Acacia* introduced to China, including the genera *Acacia*, *Acaciella*, *Senegalia*, and *Vachellia* (Table 1). The study indicated that the *Acacia* species in China exhibit a high degree of local endemism, with nearly half of the species being endemic or nearly endemic. Through detailed taxonomic treatment and a historical perspective, Maslin et al. (2019) provided a comprehensive overview of the genus in China.

Table 1 Genera comprising *Acacia sens. lat.* (Adopted from Maslin et al., 2019)

Current name	Previous name	No. sp.	Generalised distribution [and occurrence in China]
<i>Acacia (sens. str.)</i>	<i>Acacia</i> subg. <i>Phyllodineae</i>	1 067	Australia, Pacific, SE Asia [12 spp. introduced in China, but <i>A. confusa</i> is both introduced and indigenous in Taiwan]
<i>Vachellia</i>	<i>Acacia</i> subg. <i>Acacia</i>	164	Americas, Africa, Asia, N. Australia [2 spp. introduced in China]
<i>Senegalia</i>	<i>Acacia</i> subg. <i>Aculeiferum</i>	217	Americas, Africa, Asia, NE Australia [21 native & 2 introduced spp. in China]
<i>Acaciella</i>	<i>Acacia</i> subg. <i>Aculeiferum</i> sect. <i>Filicinae</i>	15	Americas [1 species introduced in China]
<i>Mariosousa</i>	<i>Acacia</i> subg. <i>Aculeiferum</i> ('coulteri' group)	13	Americas [Not represented in China]
<i>Parasenegalia</i>	<i>Acacia</i> subg. <i>Aculeiferum</i> ('scleroxylo' group)	7	Americas [Not represented in China]
<i>Pseudosenegalia</i>	<i>Acacia</i> subg. <i>Aculeiferum</i> (<i>pro parte</i>)	2	South America [Not represented in China]

Table 1 lists the classification and number of species included in the broader genus *Acacia*. The comparison of current and previous names illustrates the evolution of classification. The table shows that *Acacia* (sensu stricto) includes 1 067 species, *Vachellia* includes 164 species, *Senegalia* includes 217 species, *Acaciella* includes 15 species, *Mariosousa* includes 13 species, *Parasenegalia* includes 7 species, and *Pseudosenegalia* includes 2 species. The table provides the approximate distribution range for each genus and specifically notes their distribution in China. This information helps understand the geographical distribution and classification evolution of these genera, as well as the significant role of China in the classification of these genera.

5.2 Taxonomic implications for the genus *Lupinus*

The genus *Lupinus*, known for its numerous species and wide distribution, is another important subject of taxonomic study. Traditionally, the classification of *Lupinus* has primarily relied on seed morphology and flower structure. However, these characteristics often exhibit high plasticity under different environmental conditions, posing significant challenges to classification.

Bermúdez-Torres et al. (2021) explored the use of molecular and chemical markers to elucidate the complex diversity of the genus *Lupinus* (Figure 1). By studying secondary metabolites, particularly quinolizidine alkaloids (QA) and piperidine alkaloids as systematic markers, they revealed the complex phylogeny of the genus. The

study found that *Lupinus* can be divided into two major groups based on geographical origin: the Old World/Atlantic America Group and the New World Western Group. This pattern is consistent with molecular data based on nuclear marker ITS. Although QA provides less information at the species level, its differentiation between the two major groups aligns with branches based on DNA molecular characteristics. The combined use of chemical and barcode genetic markers offers a feasible alternative for distinguishing recent evolutionary lineages without the need for expensive and complex molecular equipment such as next-generation sequencing technology.

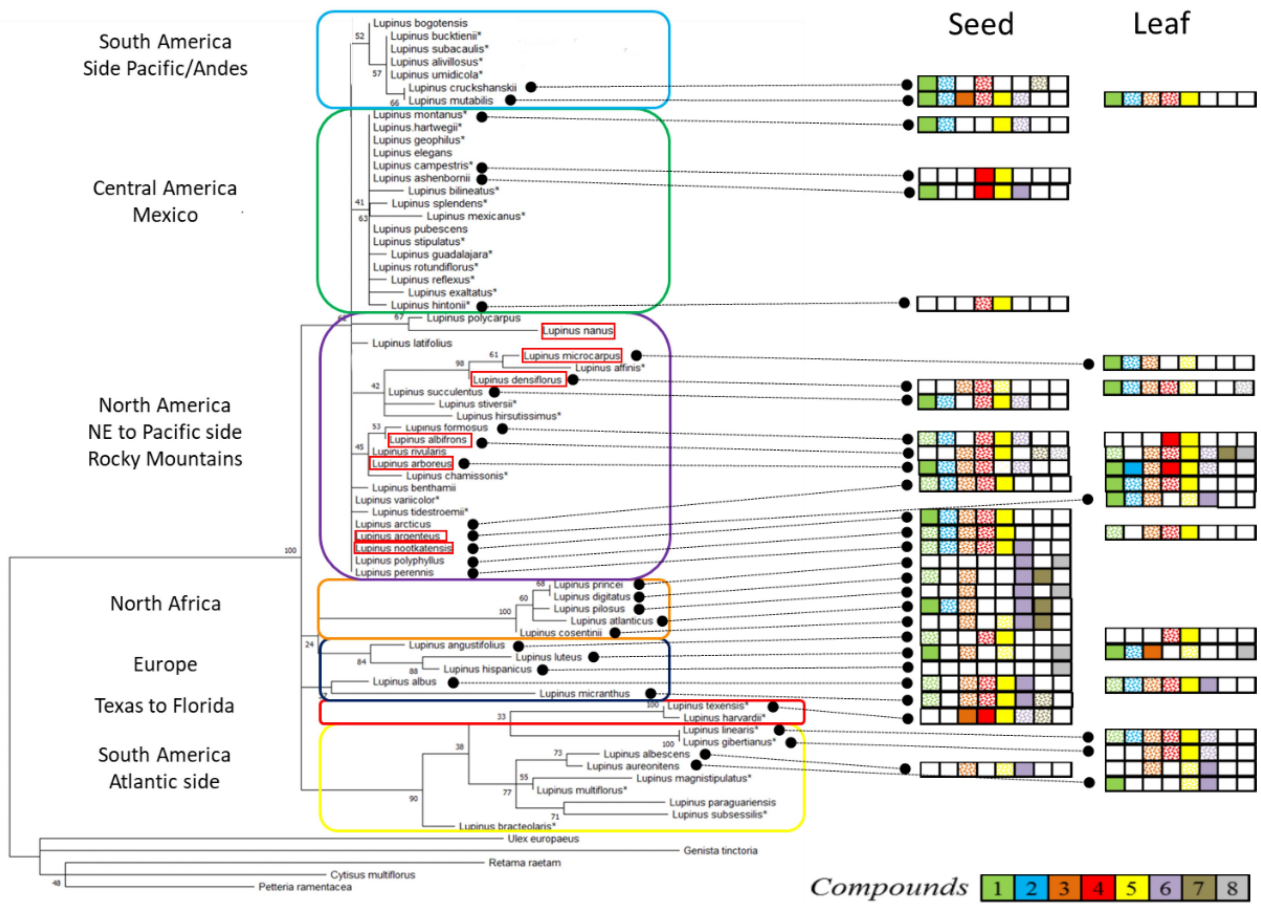


Figure 1 Phylogenetic relationships (maximum likelihood) within *Lupinus* (66 species) (Adopted from Bermúdez-Torres, 2021)

Figure 1 from Bermúdez-Torres et al. (2021) presents a phylogenetic tree of 66 species of the genus *Lupinus* based on ITS sequences. The tree shows that the genus consists of two major clades: the first clade includes Western American species and exhibits two significant subclades from Mexico (Central America and Mexico) and the Andes (South America, Pacific Coast/Andean Mountains). The second clade includes species from the Old World (Europe and North Africa) and Atlantic America. The figure also displays the distribution of seven major quinolizidine alkaloids (QA) and one piperidine alkaloid, illustrating the chemical differences among the geographical groups. The presence of each chemical compound is represented by bar charts, indicating the levels of QA in each species. This figure provides a visual tool for understanding the chemical diversity and geographical distribution of *Lupinus* species.

5.3 Genetic Insights into the genus *Phaseolus*

The genus *Phaseolus*, significant both economically and ecologically within the Fabaceae family, includes many important food crops such as common beans (*Phaseolus vulgaris*) and adzuki beans (*Phaseolus angularis*). Chacón-Sánchez (2021) explored the genetic diversity structure within the two major gene pools of *Phaseolus vulgaris* (the Andean and Mesoamerican gene pools). By analyzing the genetic composition of 349 *Phaseolus*

samples (including wild and domesticated varieties) across 26 microsatellite loci, the study revealed changes in genetic diversity and the importance of gene flow during the domestication process (Figure 2). The results showed that domesticated populations have lower genetic diversity, higher F_{ST} values, and higher linkage disequilibrium (LD), indicating the significant impact of domestication and human selection on gene pool structure. Using STRUCTURE and neighbor-joining analyses, the study identified nine wild or domesticated populations, including four Andean-origin and four Mesoamerican-origin populations, as well as one population considered the wild ancestor of the species (Chacón-Sánchez et al., 2021).



Figure 2 (a) *Phaseolus albiflorus*. (b) *P. chiapasanus*. (c) *P. acutifolius*. (d) *P. talamancensis*. (e) *P. augusti*. (f) *P. xanthotrichus*. (g) *P. dumosus*. (h) *P. lunatus*. (i) *P. vulgaris* (Photo credit: D.G. Debouck)

The study by Chacón-Sánchez et al. (2021) illustrated the floral structures of different species within the genus *Phaseolus*, including *P. dumosus*, *P. coccineus*, and *P. vulgaris*. The figure detailed various parts of the flower, such as the calyx, petals, stamens, and pistils. It also showed pollinating insects (such as bees and butterflies) visiting and extracting nectar from different *Phaseolus* flowers. These images demonstrated the attractiveness and adaptability of different *Phaseolus* flower morphologies to pollinators, further supporting the importance of gene flow within the genus.

Geographical and genetic distances were consistent in wild populations but less so in domesticated populations, possibly reflecting post-domestication seed gene flow. The Andean domesticated variety Nueva Granada showed the highest F_{ST} values and the widest geographical distribution, suggesting a recent origin or selection event. This study revealed the complex domestication and evolutionary history of the genus *Phaseolus* under different geographical and genetic backgrounds, providing an essential foundation for future linkage disequilibrium and association mapping studies.

6 Implications for Conservation and Biodiversity

6.1 Conservation strategies based on genetic diversity

Genetic diversity is a critical factor in the conservation of plant species, including those within the Fabaceae family. The study of the chloroplast genome of *Dipteryx alata* provides valuable genetic information that can be used to design effective conservation strategies. The chloroplast genome sequence of *D. alata* revealed significant genetic variation, including gene losses and rearrangements, which are essential for understanding the evolutionary history and genetic diversity of this species (Antunes et al., 2020). This genetic information can be utilized to develop conservation strategies that maintain genetic diversity, ensuring the long-term survival and

adaptability of *D. alata* and other Fabaceae species.

6.2 Biodiversity assessments and species richness

Biodiversity assessments are crucial for understanding species richness and the ecological roles of different species within the Fabaceae family. The multivariate discrimination study of selected Fabaceae taxa in Nigeria highlights the importance of using mineral element analysis and chemometrics for taxonomic identification and biodiversity assessments (Abdulrahman, 2022). This approach allows for the accurate classification of species based on their mineral content, contributing to a better understanding of species richness and distribution. Additionally, the highly resolved phylogeny of Fabaceae, which includes over 1 500 nuclear genes from 391 species, provides a comprehensive framework for assessing biodiversity and species richness within this diverse family (Zhao et al., 2021).

6.3 Genetic studies in habitat restoration

Genetic studies play a vital role in habitat restoration efforts, particularly for species within the Fabaceae family that are important for ecological restoration. The chloroplast genome sequence of *Dipteryx alata* offers new genetic information that can be used in habitat restoration projects, particularly in the Brazilian Cerrado where this species is native (Antunes et al., 2020). Understanding the genetic makeup of *D. alata* and other Fabaceae species can inform restoration strategies that promote genetic diversity and ecosystem resilience. Furthermore, the phylogenomic analyses of Fabaceae, which support numerous polyploidization events and the evolution of nitrogen-fixing symbiosis, provide insights into the genetic mechanisms that can be leveraged for successful habitat restoration (Zhao et al., 2021).

7 Future Directions in Fabaceae Taxonomy

7.1 Integrating genetic and morphological data

The integration of genetic and morphological data is crucial for resolving taxonomic ambiguities within the Fabaceae family. Recent studies have demonstrated the effectiveness of combining these approaches to achieve more accurate taxonomic classifications. For instance, the study on the *Hymenaea stigonocarpa* complex utilized population genetics and detailed morphological analyses to redefine taxonomic boundaries, leading to the recognition of new taxonomic statuses based on genetic clusters and morphological traits (Pinto et al., 2023). Similarly, the taxonomic revision of the genus *Luetzelburgia* incorporated both morphological and DNA sequence data to clarify species circumscriptions, highlighting the importance of fieldwork and herbarium specimen examination in conjunction with genetic analyses (Cardoso et al., 2014). These examples underscore the potential of integrative approaches to enhance our understanding of Fabaceae taxonomy.

7.2 Role of bioinformatics and big data

Bioinformatics and big data are playing an increasingly significant role in the taxonomy of Fabaceae. The use of next-generation sequencing technologies and advanced bioinformatics tools has enabled the analysis of large genomic datasets, facilitating the resolution of complex phylogenetic relationships. For example, the phylogenomic study of Fabaceae using over 1 500 nuclear genes from 391 species provided a highly resolved phylogeny and insights into polyploidization events and the evolution of nitrogen-fixing symbiosis (Zhao et al., 2021). Additionally, the whole-genome-based taxonomy of the Rhodobacteraceae family, which proposed the reclassification of the "Roseobacter clade" into a new family, demonstrates the power of genomic data in resolving taxonomic inconsistencies (Liang et al., 2021). These advancements highlight the potential of bioinformatics and big data to revolutionize Fabaceae taxonomy by providing comprehensive and robust phylogenetic frameworks.

7.3 Prospects for automated taxonomy

The prospects for automated taxonomy in Fabaceae are promising, driven by advancements in machine learning and artificial intelligence. Automated systems can analyze large datasets of genetic and morphological information, potentially accelerating the taxonomic revision process. For instance, the study on the *Macroptilium gracile* species complex employed multivariate statistical analyses and Bayesian inference to clarify the identity of

taxonomic entities, suggesting that automated approaches could streamline similar analyses in the future (Berlingeri et al., 2020). Furthermore, the integration of chemotaxonomic data with molecular analyses, as demonstrated in the study of *Albizia* species, indicates that automated systems could also incorporate diverse data types to enhance taxonomic resolution (Khodary et al., 2021). As these technologies continue to evolve, they hold the potential to significantly improve the efficiency and accuracy of taxonomic research in Fabaceae.

8 Concluding Remarks

The taxonomic revisions in the Fabaceae family have been significantly informed by recent genetic studies. The use of nuclear phylotranscriptomics and phylogenomics has provided a highly resolved phylogeny of Fabaceae, supporting numerous polyploidization events and elucidating the evolutionary history of rhizobial nitrogen-fixing symbiosis. Additionally, the differential accumulation and elimination of repetitive DNA have been identified as key drivers of genome size variation within the legume tribe Fabaceae, with specific contributions from Ty3/gypsy LTR-retrotransposons. These findings underscore the complexity and dynamic nature of genome evolution in Fabaceae, highlighting the importance of genetic studies in understanding phylogenetic relationships and evolutionary processes.

Continued genetic research is crucial for further refining our understanding of the Fabaceae family's taxonomy and evolutionary history. The insights gained from phylogenomic analyses, such as the identification of whole-genome duplication events and the reconstruction of ancestral character states, provide a robust framework for future studies. Moreover, the application of advanced bioinformatic approaches to analyze repetitive DNA in non-model species demonstrates the potential for uncovering new aspects of genome evolution and diversity. These genetic studies not only enhance our knowledge of Fabaceae but also have broader implications for plant biology, ecology, and agriculture, given the family's economic and ecological significance.

The taxonomic revisions in the Fabaceae family, informed by genetic studies, represent a significant advancement in our understanding of this diverse and ecologically important group of plants. The integration of phylogenomic data has resolved long-standing questions about phylogenetic relationships and divergence times, providing a clearer picture of the evolutionary history of Fabaceae. Additionally, the study of genome size variation and repetitive DNA has revealed the underlying mechanisms driving genome evolution within the family. These findings highlight the importance of genetic research in informing taxonomic revisions and underscore the need for continued exploration of the genetic and genomic diversity within Fabaceae. As we move forward, it is essential to leverage these insights to further refine the taxonomy of Fabaceae and to explore the functional and ecological implications of genetic diversity within the family.

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Conflict of Interest Disclosure

The author affirms that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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