

Conservation of Winged Papilionate Flowers: A 30 Million Year Journey

James X. Fang ✉

Hainan Institute of Tropical Agricultural Resources, Sanya, 572025, Hainan, China

✉ Corresponding email: xuanjun.fang@hitar.org

Legume Genomics and Genetics, 2024 Vol.15, No.5 doi: [10.5376/lgg.2024.15.0021](https://doi.org/10.5376/lgg.2024.15.0021)

Received: 02 Sep., 2024

Accepted: 03 Oct., 2024

Published: 14 Oct., 2024

Copyright © 2024 Fang. This is an open access article published under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.

Preferred citation for this article:

Fang J.X., 2024, Conservation of winged papilionate flowers: a 30 million year journey, Legume Genomics and Genetics, 15(5): 210-220 (doi: [10.5376/lgg.2024.15.0021](https://doi.org/10.5376/lgg.2024.15.0021))

Abstract Winged Papilionate flowers, characterized by their unique floral morphology and significant role in legume evolution, represent a fascinating subject of study within evolutionary biology and conservation science. This paper provides a comprehensive review of the evolutionary history, ecological roles, and conservation challenges associated with these flowers. We trace the origins of winged Papilionate flowers from their earliest fossil records to their present-day distribution, emphasizing the evolutionary significance of their unique winged structures and their co-evolution with specific pollinators. The study explores the ecological adaptations that have enabled these flowers to thrive in diverse habitats, highlighting the role of genetic diversity in their ecological success. A focused case study on *Phaseolus* species (common beans) illustrates the agricultural importance of winged Papilionate flowers and the evolutionary adaptations leading to their distinctive morphology. Conservation challenges, including habitat loss, climate change, and genetic erosion, are examined, along with potential strategies such as in-situ and ex-situ conservation approaches, the use of genomic tools, and modern breeding techniques like CRISPR/Cas9. The paper concludes by discussing future research priorities, emphasizing the need for an integrative approach that combines evolutionary and conservation biology, the application of emerging technologies, and the importance of policy and public engagement in conservation efforts. Understanding the evolutionary journey and conservation needs of winged Papilionate flowers is vital for preserving these ecologically and economically significant plant species.

Keywords Papilionate flowers; Winged morphology; Co-evolution; Conservation genetics; *Phaseolus* species

1 Introduction

Papilionate flowers, also known as butterfly-like flowers, are a distinctive floral form within the legume family (Fabaceae). These flowers are characterized by their bilateral symmetry, with petals differentiated into a standard (banner), wings, and a keel that encloses the reproductive organs (Cardoso et al., 2015). This unique floral architecture is not only aesthetically appealing but also functionally significant, facilitating specialized pollination mechanisms. The evolution of papilionate flowers marks a critical phase in legume diversification, contributing to the ecological success and adaptive radiation of this plant family. These flowers play a pivotal role in ecosystem services, including nitrogen fixation, which enhances soil fertility and supports various plant and animal communities (Prenner et al., 2015; Carvalho et al., 2023a).

Winged papilionate flowers exhibit unique morphological traits that distinguish them from other floral forms. Notably, the upper calyx lobes are often enlarged and wing-like, a feature that is particularly prominent in the Dipterygeae clade. This morphological adaptation is believed to enhance the efficiency of pollination by specialized pollinators, ensuring effective reproductive success. The conservatism of these traits over millions of years underscores their evolutionary significance. These flowers maintain stable stamen numbers and a specialized stamen sheath, which are crucial for their interaction with pollinators (Carvalho et al., 2023a; Carvalho et al., 2023b). The role of winged papilionate flowers in plant-pollinator interactions is vital, as they have co-evolved with specific pollinators, leading to mutualistic relationships that benefit both the plants and their pollinators (Prenner et al., 2015).

This study provides a detailed review of the morphological characteristics and evolutionary history of winged papilionaceous flowers, systematically analyzing their ecological roles and interactions with pollinators. The

research thoroughly discusses the implications of the findings for conservation efforts and future research directions, aiming to explore the evolutionary history and ecological significance of winged papilionaceous flowers within the legume family.

2 Evolutionary History of Winged Papilionate Flowers

2.1 Origins in the fossil record

The earliest known fossils of papilionate flowers date back to the Late Cretaceous period. Fossil evidence from this era, such as the winged fruits of *Friisifructus aligeri* from Western North America, provides crucial insights into the diversity and evolutionary history of angiosperms (Tang et al., 2023). Additionally, fossilized flowers from the early Palaeocene of Patagonia, Argentina, with affinities to the Schizomerieae tribe, offer further evidence of early papilionate floral structures (Figure 1) (Jud et al., 2018). The evolutionary significance of winged structures in papilionate flowers is highlighted by their role in effective ecological interactions and dispersal strategies. For instance, the Dipterygeae clade, which has maintained winged papilionate floral traits for approximately 30 million years, demonstrates the evolutionary conservatism of these structures. This conservatism has likely contributed to the clade's successful persistence across various Neotropical biomes (Carvalho et al., 2023a). The presence of winged fruits in the Cladrastis clade also underscores their importance in the biogeographic history and adaptation to different environments (Duan et al., 2019).

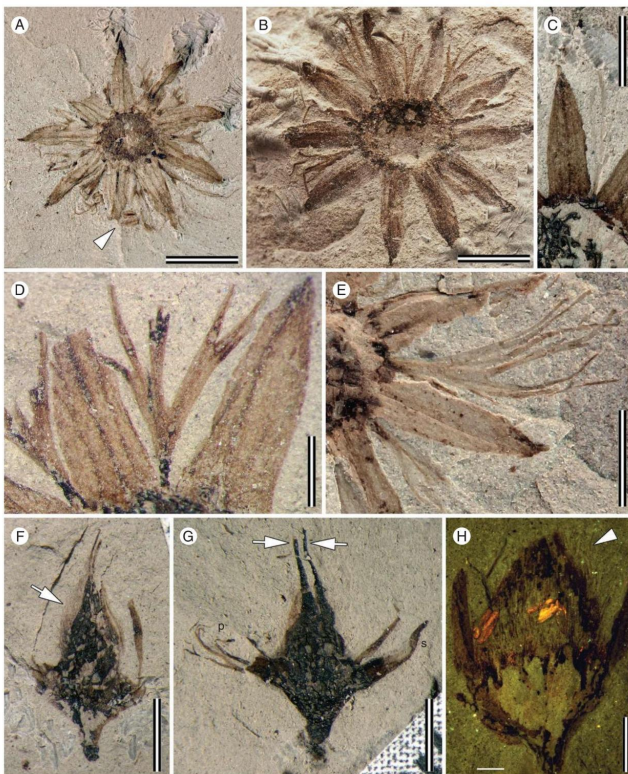


Figure 1 *Lacinipetalum spectabilum* specimens from locality PL-2 (Adopted from Jud et al., 2018)

Image caption: (A) Flower in transverse view, showing 9-merous structure, sepals narrow-lanceolate, laciniate petals alternating with sepals, stamens (at arrowhead) and floral disc 2.5 mm across. MPEF-Pb 8423. (B) Flower in transverse view, showing 10-merous structure, sepals narrow-lanceolate, laciniate petals alternating with sepals, stamens not preserved, and floral disc 3.9 mm across. MPEF-Pb 8517. (C) Detail of sepal venation. Note three main parallel veins supplying the sepals and two faint intramarginal veins. MPEF-Pb 8433a. (D) Close-up of a narrow, flabellate petal incised into at least eight secondary segments. MPEF-Pb 8447a. (E) Close-up of a narrow, flabellate petal incised into nine segments. MPEF-Pb 8414 a. (F) Flower in longitudinal view, showing stout pedicel, shallow floral cup and superior ovary covered in fine trichomes (at arrow) and two free stylodia. MPEF-Pb 8455. (G) Flower in longitudinal view, showing stout pedicel, shallow floral cup, sepals (s), laciniate petals (p) and two stylodia emerging from the apex of the ovary (at arrows). MPEF-Pb 8444a. (H) Flower in longitudinal view illuminated under epifluorescence. Note the two brightly fluorescing anthers and pubescent surface of the ovule (hairs at arrowhead). MPEF-Pb 8452a. Scale bars: (A, B) = 3.0 mm; (C–E) = 2.0 mm; (F, G) = 2.5 mm; (H) = 1.5 mm (Adopted from Jud et al., 2018)

2.2 Phylogenetic relationships

Within the Fabaceae family, several major clades exhibit distinct evolutionary traits. The Dipterygeae clade, for example, is characterized by its unique winged papilionate floral architecture and comprises genera such as *Dipteryx*, *Monopteryx*, *Pterodon*, and *Taralea* (Carvalho et al., 2023a). Another significant clade is the Cladrastis clade, which includes species with compressed, winged fruits and displays an amphi-Pacific distribution. The Bowdichia clade, with fossil evidence from the Paleogene of North America, further illustrates the diversity and evolutionary history within the Fabaceae family (Herendeen et al., 2022). Genetic evidence supports the evolution of winged flowers through comprehensive phylogenetic analyses. Studies on the Dipterygeae clade using nuclear ribosomal ITS/5.8S and plastid matK and trnL intron sequences have strongly supported the monophyly of each genus and the conservatism of winged floral traits. Similarly, the Cladrastis clade's phylogenetic relationships and divergence times have been reconstructed using nuclear and plastid regions, revealing the evolution of winged fruits and their biogeographic history (Duan et al., 2019).

2.3 Co-evolution with pollinators

Winged papilionate flowers have evolved specific adaptations to attract and interact with specialized pollinators. The unique floral architecture of the Dipterygeae clade, including zygomorphy and petal differentiation, has facilitated effective ecological interactions with pollinators, ensuring the protection of young flower buds and developing fruits. The presence of glandular wing petals in *Petaladenium urceoliferum* also highlights the evolutionary adaptations for pollinator attraction and interaction (Prenner et al., 2015). Case studies of co-evolutionary relationships between winged papilionate flowers and their pollinators provide valuable insights into their evolutionary history. For instance, the ancient winged papilionate floral conservatism in the Dipterygeae clade has maintained effective ecological interactions with specialized pollinators, contributing to the clade's evolutionary and ecological persistence (Carvalho et al., 2023a). Additionally, the mid-Mesozoic kalligrammatid lacewings, which exhibited convergent evolution with Cenozoic butterflies, demonstrate the complex co-evolutionary dynamics between flowers and their pollinators (Labandeira et al., 2016; López-Martínez et al., 2023).

3 Ecological Roles and Adaptations

3.1 Habitat preferences

Winged papilionate flowers, particularly those within the Dipterygeae clade, are predominantly found across tropical forests in Central America and the Amazon. They also exhibit ecological dominance in the savannas of the Brazilian Central Plateau (Carvalho et al., 2023a). This wide geographic distribution highlights their adaptability to diverse environmental conditions and their ability to thrive in both forested and savanna ecosystems. The Dipterygeae clade has shown remarkable conservatism in floral architecture over 30 million years, which has likely contributed to their successful adaptation to various environmental conditions. The unique winged papilionate floral structure, characterized by a highly differentiated calyx, has enabled these species to maintain effective ecological interactions with specialized pollinators and protect developing fruits, ensuring their persistence across different biomes. Additionally, the ability of *Vigna caracalla* to adapt its mating system to varying ecological contexts, such as higher elevations with reduced pollinator diversity, further demonstrates the adaptive strategies of papilionate flowers (Etcheverry et al., 2008).

3.2 Pollination mechanisms

Papilionate legume flowers exhibit structural adaptations that facilitate pollination by filtering pollinators based on their ability to exert the necessary strength to access floral rewards. Morphometric traits, particularly those of the keel and wings, are strongly correlated with the operative strength required to open the flowers. This structural complexity forms an intrafloral functional module that ensures only suitable pollinators can access the rewards, thereby enhancing pollination efficiency (Córdoba and Cocucci, 2011). The specialized floral architecture of winged papilionate flowers has fostered symbiotic relationships with specific pollinators. For instance, *Vigna caracalla* relies on pollinators such as *Bombus morio*, *Centris bicolor*, *Eufriesea mariana*, and *Xylocopa eximia* to trigger its pollination mechanism. These relationships are crucial for the reproductive success of these plants, as

evidenced by the higher success rates of hand-crossed fruits compared to hand-selfed ones in *V. caracalla* (Figure 2) (Etcheverry et al., 2008). The long-term conservatism of floral traits in the Dipterygeae clade has also ensured the maintenance of these specialized interactions over millions of years (Carvalho et al., 2023a).



Figure 2 Floral visitors of *V. caracalla* (Adopted from Etcheverry et al., 2008)

Image caption: (A) *Bombus morio* worker, the most frequent pollinator of *V. caracalla* (body length $\frac{1}{4}$ 2 cm). Note the stylar brush contacting the pronotum (arrow). (B) *Xylocopa eximia* (body length $\frac{1}{4}$ 2.6 cm). (C) *Centris bicolor* (body length $\frac{1}{4}$ 1.5 cm); note the cuts on the left wing (arrow), produced by the insect's hind legs during foraging movements. (D) Species of Meliponini acting as a pollen thief (body length approx. 1 cm) (Adopted from Etcheverry et al., 2008)

3.3 Genetic diversity and adaptation

Genetic diversity plays a pivotal role in the ecological success of winged papilionate flowers. The conservatism of floral traits within the Dipterygeae clade, despite the lability in fruit morphology, suggests that maintaining genetic diversity in floral architecture has been key to their evolutionary persistence. This diversity allows for the continuous adaptation to changing environmental conditions and the maintenance of effective pollinator interactions (Carvalho et al., 2023a). Molecular adaptations have enabled winged papilionate flowers to cope with various environmental stressors. The genetic mechanisms underlying the structural complexity of their flowers, such as the differentiation of the calyx and the formation of an intrafloral functional module, have likely evolved to optimize pollination efficiency and reproductive success under different ecological contexts. These adaptations ensure that even in environments with reduced pollinator diversity, such as high elevations, these plants can still achieve reproductive assurance through mechanisms like self-fertilization (Etcheverry et al., 2008; Córdoba and Cocucci, 2011).

4 Case Study: *Phaseolus* Species (Common Beans)

4.1 Importance of *Phaseolus* in agriculture and biodiversity

The genus *Phaseolus* comprises about 70 species, including several that are widely cultivated for food and fodder. This genus is native to the Americas, with a distribution range spanning from the southwestern United States to Argentina. The most economically important species within this genus include *Phaseolus vulgaris* (common bean), *Phaseolus lunatus* (lima bean), *Phaseolus coccineus* (runner bean), and *Phaseolus acutifolius* (teparty bean). These species are notable for their morphological diversity, which includes variations in flower structure, seed shape, and growth habits. The unique winged morphology of the flowers, a characteristic trait of the genus, plays a critical role in pollination biology and has evolved as an adaptive response to attract specific pollinators, such as bees (Chacón-Sánchez et al., 2021; Uebersax et al., 2022).

Phaseolus species are among the most important leguminous crops globally, providing a vital source of protein, fiber, vitamins, and minerals. The common bean (*Phaseolus vulgaris*), in particular, is a staple food in many regions, especially in Latin America and Africa, where it serves as a primary source of plant-based protein. The

economic value of these species extends beyond food production; they are also used in intercropping systems to improve soil fertility through biological nitrogen fixation, thereby reducing the need for synthetic fertilizers. The genetic diversity within *Phaseolus* species, both wild and cultivated, is crucial for breeding programs aimed at improving yield, disease resistance, and climate resilience (Parker and Gepts, 2021).

4.2 Evolution of winged flowers in *Phaseolus*

Phylogenetic studies of the genus *Phaseolus* have revealed a complex evolutionary history shaped by hybridization events, geographical isolation, and natural selection. Molecular phylogenies, based on nuclear and chloroplast DNA markers, have provided insights into the relationships among *Phaseolus* species and their divergence times. The evolutionary trajectory of winged flower morphology in *Phaseolus* suggests multiple independent origins, driven by the selective pressures of pollinator availability and ecological niches. The winged petals, often accompanied by specialized floral structures like the keel and standard, enhance the effectiveness of pollinator visits, thus promoting cross-pollination and genetic diversity within populations (Valderrama et al., 2022; Zheng and Wang, 2024).

The development of winged flowers in *Phaseolus* is an adaptive trait that facilitates efficient pollination. The bilateral symmetry and distinct petal arrangements, including the prominently displayed wings, serve to attract and guide pollinators, particularly bees, to the reproductive organs of the flower. These morphological traits are believed to have co-evolved with specific pollinator behaviors, such as the 'buzz pollination' technique, where bees vibrate flowers to release pollen. Additionally, winged flowers may provide a mechanical advantage by minimizing the energy expenditure required by pollinators, thus increasing the frequency of visits. The interplay between floral morphology and pollinator preferences has likely played a crucial role in the diversification and success of *Phaseolus* species (Figure 3) (Nelson et al., 2020; Wang et al., 2021).

4.3 Conservation challenges and strategies

The conservation of both wild and cultivated *Phaseolus* species is fraught with challenges. Habitat loss due to agricultural expansion, urbanization, and climate change poses significant threats to the genetic diversity of wild relatives, which are invaluable sources of traits for crop improvement. Furthermore, over-reliance on a narrow genetic base in cultivated varieties increases vulnerability to pests, diseases, and environmental stresses. The loss of traditional knowledge and practices related to the cultivation and use of *Phaseolus* species also threatens their conservation (Báez-González et al., 2019; Kovács et al., 2021).

Conservation strategies for *Phaseolus* species must integrate both in situ and ex situ approaches. In situ conservation involves protecting wild populations in their natural habitats, which requires habitat preservation and management, as well as the establishment of genetic reserves. Ex situ conservation efforts include the establishment of germplasm banks and seed repositories that maintain a diverse collection of *Phaseolus* genetic resources. Modern breeding programs, leveraging genomic tools and molecular markers, are crucial for identifying and incorporating desirable traits from wild relatives into cultivated varieties, enhancing resilience to biotic and abiotic stresses. Collaborative efforts among governments, research institutions, and local communities are essential to promote sustainable use and conservation of *Phaseolus* species, ensuring their availability for future generations (Coelho et al., 2020; Werden et al., 2020).

5 Conservation Challenges and Strategies

5.1 Threats to winged papilionate flowers

Habitat loss and fragmentation pose significant threats to the conservation of winged papilionate flowers. The destruction of tropical forests and savannas, where these species predominantly reside, leads to reduced habitat availability and increased isolation of populations. This fragmentation can disrupt ecological interactions, such as pollination and seed dispersal, which are crucial for the survival and reproduction of these plants (Carvalho et al., 2023a). Additionally, habitat fragmentation can alter the distribution of adaptive genetic variation, making it difficult for populations to adapt to changing environmental conditions (Van Daele et al., 2023).

Climate change is another major threat to winged papilionate flowers. Increased temperatures, altered precipitation patterns, and more frequent extreme weather events can affect the growth, reproduction, and survival of these species. For instance, changes in climate can disrupt the phenology of flowering and pollinator activity, leading to mismatches that reduce reproductive success. Furthermore, climate change can exacerbate the effects of habitat fragmentation by imposing additional stress on already vulnerable populations (Van Daele et al., 2023).

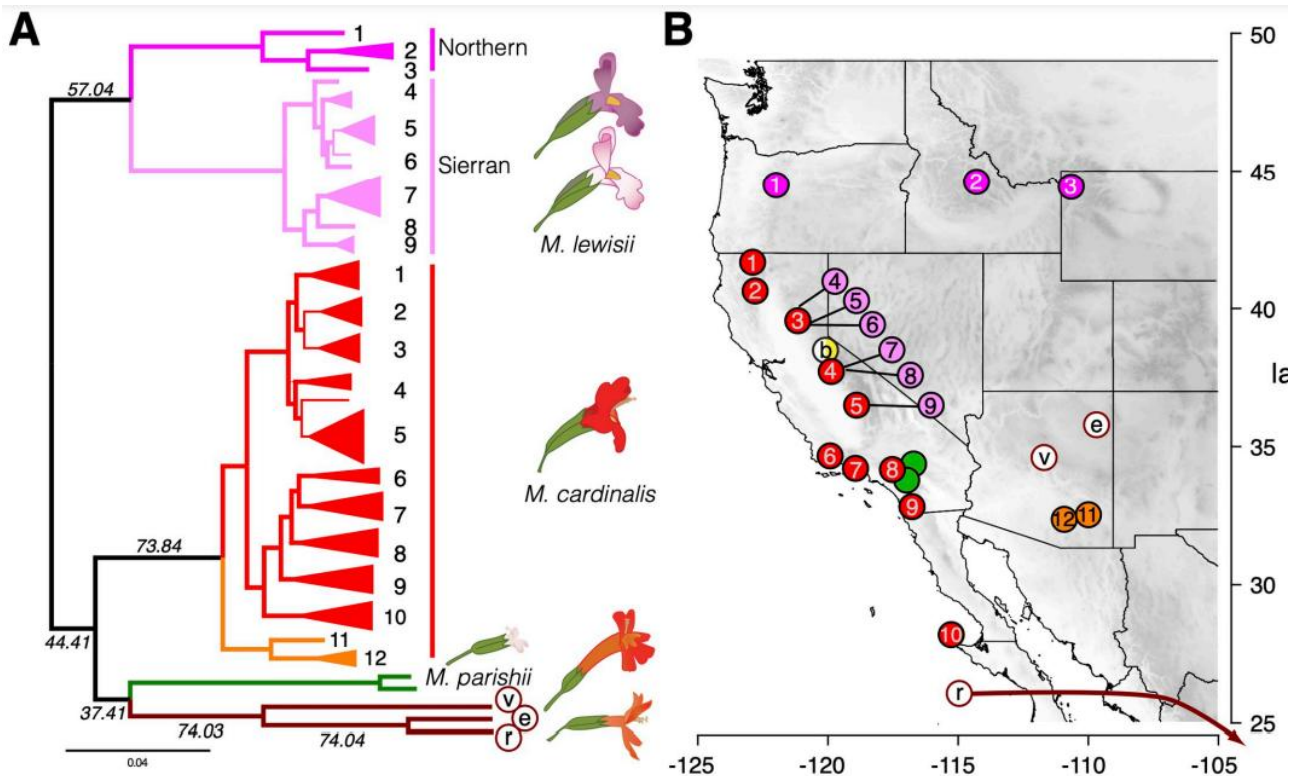


Figure 3 Genome-wide phylogeny of *Mimulus* section *Erythranthe* reveals a single clade containing all hummingbird-pollinated species (Adopted from Nelson et al., 2020)

Image caption: (A) The maximum likelihood phylogeny of section *Erythranthe* rooted to *M. bicolor*. The species level topology is identical to that inferred with ASTRAL 3. Branches with bootstrap support >90% are bold. Quartet scores are also given for branches included in the ASTRAL species tree. Clades representing a single collection location are collapsed (see S18 Fig for the unrooted phylogeny including the branch to *M. bicolor*). Numbers next to *M. lewisii* and *M. cardinalis* tips refer to collection locations in B. (B) Collections of section *Erythranthe* across the American West. Sierran *M. lewisii* collections are offset due to close overlap with *M. cardinalis* collections in the Sierra Nevada Range. Location of the *M. rupestris* accession from Central Mexico not shown (see S1 Table). ‘b’: *M. bicolor*; v: *M. verbenaceus*; ‘e’: *M. eastwoodiae*; ‘r’: *M. rupestris* (Adopted from Nelson et al., 2020)

5.2 Conservation strategies

In-situ conservation involves protecting and managing species within their natural habitats. This approach is essential for maintaining the ecological interactions and evolutionary processes that sustain winged papilionate flowers. Protected areas, habitat restoration, and sustainable land-use practices are key components of in-situ conservation. Ex-situ conservation, on the other hand, involves preserving species outside their natural habitats, such as in botanical gardens and seed banks. This strategy can serve as a backup to in-situ efforts and provide material for research and potential reintroduction programs (Carvalho et al., 2023a).

Botanical gardens and seed banks play a crucial role in the conservation of winged papilionate flowers. These institutions can maintain living collections and seed samples that represent the genetic diversity of threatened species. By doing so, they provide a safeguard against extinction and a resource for future restoration efforts. Additionally, botanical gardens can serve as centers for public education and awareness, promoting the importance of plant conservation and the specific needs of winged papilionate flowers (Cristóbal-Perez et al., 2021).

5.3 Role of molecular techniques in conservation

Genomic tools are increasingly being used to inform conservation strategies for winged papilionate flowers. Techniques such as DNA sequencing and genotyping can help identify genetic diversity and population structure, which are critical for understanding the evolutionary history and adaptive potential of these species. By assessing genetic variation, conservationists can make informed decisions about which populations to prioritize for protection and how to manage genetic resources effectively. Modern breeding techniques, including CRISPR/Cas9, offer new possibilities for the conservation of winged papilionate flowers (Liu et al., 2020; Malabrigo et al., 2023). These technologies can be used to enhance desirable traits, such as disease resistance or climate adaptability, in threatened populations. By precisely editing the genome, scientists can introduce beneficial genetic variations without the need for traditional cross-breeding, which can be time-consuming and less effective. These advanced techniques hold promise for bolstering the resilience of winged papilionate flowers in the face of ongoing environmental challenges (Carvalho et al., 2023a).

6 Future Directions and Research Priorities

6.1 Integrating evolutionary and conservation biology

Understanding the evolutionary history of winged papilionate flowers is crucial for informing conservation strategies. Research must focus on bridging the gap between the evolutionary pathways that led to the development of these unique morphologies and their current conservation needs. This involves utilizing phylogenetic analyses to identify evolutionary significant units (ESUs) and prioritizing these units for conservation. Identifying traits that have been key to survival and adaptation over millennia can inform breeding programs and restoration efforts, particularly in changing climates. Furthermore, knowledge of historical biogeography can aid in predicting potential areas for habitat restoration and identifying refugia that may be crucial under future climate scenarios (Miguel-Peñaloza et al., 2019; Zhao et al., 2019).

The complex challenges facing the conservation of winged papilionate flowers necessitate an interdisciplinary approach. Collaborative efforts between evolutionary biologists, ecologists, geneticists, climate scientists, and social scientists are needed to develop comprehensive conservation strategies. Integrating insights from evolutionary biology with ecological modeling, for instance, can help predict species responses to environmental changes and identify areas of high conservation value. Additionally, socio-economic research is vital to understand the human dimensions of conservation, including the impact of local practices, traditional knowledge, and community engagement. By fostering interdisciplinary collaborations, conservation strategies can be more holistic, incorporating both biological and socio-cultural dimensions (Nelson et al., 2020; Tian, 2024).

6.2 Emerging technologies in conservation

Artificial intelligence (AI) and machine learning (ML) are emerging as powerful tools in conservation biology. These technologies can enhance the monitoring of winged papilionate flower species through automated identification and analysis of large datasets, such as satellite imagery, drone surveys, and camera trap data. AI models can also be used to predict the impacts of climate change, habitat loss, and other anthropogenic factors on these species, allowing for proactive management strategies. Moreover, machine learning algorithms can help identify critical habitats and prioritize conservation areas by analyzing complex ecological data. The integration of AI and ML into conservation planning can increase the efficiency and precision of monitoring efforts, making it possible to respond swiftly to emerging threats (Athanasopoulou et al., 2022; Aggarwal et al., 2023).

Recent advances in genetic and genomic technologies offer new opportunities for the conservation of winged papilionate flowers. Techniques such as CRISPR-based gene editing, genome-wide association studies (GWAS), and genomic selection can be employed to identify and preserve genetic diversity within populations, particularly in the face of environmental stressors. Conservation genomics can also provide insights into the adaptive potential of species, identifying genetic variants associated with resilience to climate change, diseases, and pests. Furthermore, the development of genomic resources, such as reference genomes and gene banks, will be essential for ex situ conservation and the restoration of genetically depauperate populations. These tools can help enhance

the genetic health and viability of both wild and cultivated populations, ensuring their persistence in the long term (Shivaprakash et al., 2022).

6.3 Policy and public engagement

Effective conservation of winged papilionate flowers requires robust policy frameworks that support both in situ and ex situ strategies. Policies should focus on protecting critical habitats, regulating land use changes, and mitigating climate change impacts. International collaborations and agreements, such as the Convention on Biological Diversity (CBD) and the Global Strategy for Plant Conservation (GSPC), are essential to coordinate efforts across borders and ecosystems. National and local policies should also promote sustainable agricultural practices that conserve wild relatives of winged papilionate flowers, particularly those that are important genetic resources for crop improvement. Additionally, policies must be flexible to accommodate new scientific insights and emerging threats, ensuring adaptive management approaches are in place (Ren et al., 2019; Lubis et al., 2022).

Public engagement is a cornerstone of successful conservation efforts. Raising awareness about the ecological and evolutionary significance of winged papilionate flowers can foster a sense of stewardship among local communities and the general public. Educational programs, citizen science initiatives, and community-based conservation projects can empower individuals to participate actively in the protection of these species. Public engagement also involves addressing socio-economic challenges faced by local communities and promoting alternative livelihoods that are compatible with conservation goals. Furthermore, the use of digital platforms and social media can amplify outreach efforts, making it easier to disseminate information and mobilize support for conservation initiatives globally (Ren et al., 2019).

7 Concluding Remarks

The study of winged papilionate flowers within the Dipterygeae clade has revealed significant insights into the evolutionary history and floral conservatism of these species. Over a span of approximately 30 million years, the Dipterygeae clade has maintained a remarkable consistency in its floral architecture, particularly the winged papilionate traits. This conservatism is evident despite the overall lability in floral architecture observed in other early-branching papilionoid legumes. The phylogenetic analyses confirmed the monophyly of the genera within Dipterygeae and highlighted the unique floral synapomorphy of a highly differentiated calyx, which has played a crucial role in the clade's evolutionary success.

The findings from this study have profound implications for conservation biology. The long-term stability of winged papilionate floral traits suggests that these species have developed highly specialized ecological interactions with their pollinators, which are essential for their survival and reproduction. Understanding these interactions can inform conservation strategies aimed at preserving both the plants and their pollinators. Additionally, the structural complexity and functional morphology of these flowers, as demonstrated by their ability to filter pollinators based on strength, underscore the importance of maintaining the integrity of their habitats to support the specific pollinator species they rely on. Conservation efforts should focus on protecting the diverse *Neotropical biomes* where these species thrive, ensuring the continued ecological and evolutionary success of the Dipterygeae clade.

The conservation of winged papilionate flowers is not just about preserving a unique floral architecture but also about maintaining the intricate ecological networks that have evolved over millions of years. The evolutionary conservatism observed in the Dipterygeae clade highlights the resilience and adaptability of these species in the face of environmental changes. However, this resilience is contingent upon the stability of their ecosystems and the availability of their specialized pollinators. As such, conservation strategies must adopt a holistic approach, addressing both the preservation of plant species and the protection of their pollinator communities. By doing so, we can ensure that the remarkable journey of winged papilionate flowers continues for millions of years to come.

Acknowledgments

The author sincerely thanks the two anonymous peer reviewers for their valuable comments and suggestions on the manuscript.

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.

References

- Aggarwal A., 2023, A review on genomics data analysis using machine learning, *Wseas Transactions on Biology and Biomedicine*, (2): 119-131.
<https://doi.org/10.37394/23208.2023.20.12>
- Athanasopoulou K., Daneva G., Adamopoulos P., and Scorilas A., 2022, Artificial intelligence: the milestone in modern biomedical research, *BioMedInformatics*, 2(4): 727-744.
<https://doi.org/10.3390/biomedinformatics2040049>
- Báez-González A., Acosta-Díaz E., Padilla-Ramírez J., Almeyda-León I., and Zavala-García F., 2019, Conservation status of eleven wild bean (*Phaseolus* spp. Fabaceae) species in northeastern Mexico, *Revista Mexicana de Ciencias Agrícolas*, 10(2): 417-429.
<https://doi.org/10.29312/remexca.v10i2.1475>
- Cardoso D., São-Mateus W., Cruz D., Zartman C., Komura D., Kite G., Prenner G., Wieringa J., Clark A., Lewis G., Pennington R., and Queiroz L., 2015, Filling in the gaps of the papilionoid legume phylogeny: the enigmatic Amazonian genus *Petaladenium* is a new branch of the early-diverging Amburaneae clade, *Molecular Phylogenetics and Evolution*, 84: 112-124.
<https://doi.org/10.1016/j.ympev.2014.12.015>
- Carvalho C.S., De Lima H.C., Lemes M.R., Zartman C.E., Van den Berg C., García-Dávila C.R., Coronado E.N.H., Mader M., Paredes-Villanueva K., Tysklind N., and Cardoso D., 2023a, A dated phylogeny of the Neotropical Dipterygeae clade reveals 30 million years of winged papilionate floral conservatism in the otherwise florally labile early-branching papilionoid legumes, *Botanical Journal of the Linnean Society*, 202(4): 449-475.
<https://doi.org/10.1093/botlinnean/boad003>
- Carvalho C., Lima H., Zartman C., and Cardoso D., 2023b, A taxonomic revision of monopteryx (Leguminosae): A florally divergent and ancient papilionoid genus of large amazonian trees, *Systematic Botany*, 48: 447-468.
<https://doi.org/10.1600/036364423X16936046516390>
- Chacón-Sánchez M., Martínez-Castillo J., Duitama J., and Debouck D., 2021, Gene flow in phaseolus beans and its role as a plausible driver of ecological fitness and expansion of cultigens, *Frontiers in Ecology and Evolution*, 9: 618709.
<https://doi.org/10.3389/fevo.2021.618709>
- Coelho N., Gonçalves S., and Romano A., 2020, Endemic plant species conservation: biotechnological approaches, *Plants*, 9(3): 345.
<https://doi.org/10.3390/plants9030345>
- Córdoba S., and Cocucci A., 2011, Flower power: its association with bee power and floral functional morphology in papilionate legumes, *Annals of Botany*, 108(5): 919-931.
<https://doi.org/10.1093/aob/mcr196>
- Cristóbal-Perez E., Fuchs E., Martín-Rodríguez S., and Quesada M., 2021, Habitat fragmentation negatively affects effective gene flow via pollen, and male and female fitness in the dioecious tree, *Spondias purpurea* (Anacardiaceae), *Biological Conservation*, 256: 109007.
<https://doi.org/10.1016/J.BIOCON.2021.109007>
- Duan L., Harris A., Su C., Ye W., Deng S., Fu L., Wen J., and Chen H., 2019, A fossil-calibrated phylogeny reveals the biogeographic history of the Cladrastis clade, an amphi-Pacific early-branching group in papilionoid legumes, *Molecular Phylogenetics and Evolution*, 143: 106673.
<https://doi.org/10.1016/j.ympev.2019.106673>
- Etcheverry Á., Alemán M., and Fleming T., 2008, Flower morphology, pollination biology and mating system of the complex flower of *Vigna caracalla* (Fabaceae: Papilionoideae), *Annals of botany*, 102(3): 305-316.
<https://doi.org/10.1093/aob/mcn106>
- Herendeen P., Cardoso D., Herrera F., and Wing S., 2022, Fossil papilionoids of the Bowdichia clade (Leguminosae) from the Paleogene of North America, *American Journal of Botany*, 109: 130-150.
<https://doi.org/10.1002/ajb2.1808>
- Jud N., Gandolfo M., Iglesias A., and Wilf P., 2018, Fossil flowers from the early palaeocene of patagonia, argentina, with affinity to schizomeriaceae (Cunoniaceae), *Annals of Botany*, 121: 431-442.
<https://doi.org/10.1093/aob/mcx173>
- Kovács Z., Csörgő A., Csontos P., and Höhn M., 2021, Ex situ conservation in botanical gardens-challenges and scientific potential preserving plant biodiversity, 49(2): 12334-12334.
<https://doi.org/10.15835/nbha49212334>
- Labandeira C., Yang Q., Santiago-Blay J., Hotton C., Monteiro A., Wang Y., Goreva Y., Shih C., Siljeström S., Rose T., Dilcher D., and Ren D., 2016, The evolutionary convergence of mid-Mesozoic lacewings and Cenozoic butterflies, *Proceedings of the Royal Society B: Biological Sciences*, 283(1824): 20152893.
<https://doi.org/10.1098/rspb.2015.2893>

- Liu H., Liu Z., Jin X., Gao J., Chen Y., Liu Q., and Zhang D., 2020, Assessing conservation efforts against threats to wild orchids in China, *Biological Conservation*, 243: 108484.
<https://doi.org/10.1016/j.biocon.2020.108484>
- López-Martínez A., Schönenberger J., Balthazar M., González-Martínez C., Ramírez-Barahona S., Sauquet H., and Magallón S., 2023, Integrating fossil flowers into the angiosperm phylogeny using molecular and morphological evidence, *Systematic Biology*, 72(4), 837-855.
<https://doi.org/10.1093/sysbio/syad017>
- Lubis E., and Fauziah M., 2022, Strengthening policy of ex-situ biodiversity management conservation preventing biodiversity loss in cibinong science center botanical garden, *Journal Clean WAS*, 6(2): 40-45.
<https://doi.org/10.26480/jcleanwas.02.2022.40.45>
- Malabrigo P., Tobias A., Witono J., Mursidawati S., Susatya A., Siti-Munirah M., Wicaksono A., Raihandhany R., Edwards S., and Thorogood C., 2023, Most of the world's largest flowers (genus *Rafflesia*) are now on the brink of extinction, *Plants, People, Planet*, 2023: 1-16.
<https://doi.org/10.1002/ppp3.10431>
- Miguel-Peñaloza A., Delgado-Salinas A., and Jiménez-Durán K., 2019, Pollination biology and breeding system of *Desmodium grahamii* (Fabaceae, Papilionoideae): functional aspects of flowers and bees, *Plant Systematics and Evolution*, 305: 743-754.
<https://doi.org/10.1007/s00606-019-01603-4>
- Nelson T., Stathos A., Vanderpool D., Finseth F., Yuan Y., and Fishman L., 2020, Ancient and recent introgression shape the evolutionary history of pollinator adaptation and speciation in a model monkeyflower radiation (*Mimulus section Erythranthe*), *PLoS Genetics*, 17(2): e1009095.
<https://doi.org/10.1371/journal.pgen.1009095>
- Parker T., and Gepts P., 2021, Population genomics of *Phaseolus* spp.: a domestication hotspot, *Population Genomics*, 2021: 1-83.
https://doi.org/10.1007/13836_2021_89
- Prenner G., Cardoso D., Zartman C., and Queiroz L., 2015, Flowers of the early-branching papilionoid legume *Petaladenium urceoliferum* display unique morphological and ontogenetic features, *American Journal of Botany*, 102(11): 1780-1793.
<https://doi.org/10.3732/ajb.1500348>
- Ren H., Qin H., Ouyang Z., Wen X., Jin X., Liu H., Lu H., Liu H., Zhou J., Zeng Y., Smith P., Jackson P., Gratzfeld, J., Sharrock S., Xu H., Zhang Z., Guo Q., Sun W., Ma J., Hu Y., Zhang Q., and Zhao L., 2019, Progress of implementation on the Global Strategy for Plant Conservation in (2011-2020) China, *Biological Conservation*, 230: 169-178.
<https://doi.org/10.1016/J.BIOCON.2018.12.030>
- Shivaprakash K., Swami N., Mysorekar S., Arora R., Gangadharan A., Vohra K., Jadeyegowda M., and Kiesecker J., 2022, Potential for Artificial Intelligence (AI) and Machine Learning (ML) Applications in Biodiversity Conservation, Managing Forests, and Related Services in India, *Sustainability*, 14(12): 7154.
<https://doi.org/10.3390/su14127154>
- Tang K., Smith S., and Atkinson B., 2023, Winged fruits of *Friisifructus aligeri* gen. et sp. nov. from the Late Cretaceous of Western North America, *International Journal of Plant Sciences*, 184: 271-281.
<https://doi.org/10.1086/724745>
- Tian F.F., 2024, Human genetic response to environmental change: biological adaptation to global climate change, *International Journal of Molecular Ecology and Conservation*, 14(1): 18-26.
<https://doi.org/10.5376/ijmecs.2024.14.0003>
- Uebersax M., Cichy K., Gomez F., Porch T., Heitholt J., Osorno J., Kamfwa K., Snapp S., and Bales S., 2022, Dry beans (*Phaseolus vulgaris* L.) as a vital component of sustainable agriculture and food security—a review, *Legume Science*, 5(1): e155.
<https://doi.org/10.1002/leg3.155>
- Valderrama E., Landis J., Skinner D., Maas P., Kramer H., André T., Grunder N., Sass C., Pinilla-Vargas M., Guan C., Phillips H., Almeida A., and Specht C., 2022, The genetic mechanisms underlying the convergent evolution of pollination syndromes in the Neotropical radiation of *Costus* L., *Frontiers in Plant Science*, 13: 874322.
<https://doi.org/10.3389/fpls.2022.874322>
- Van Daele F., Honnay O., Janssens S., and De Kort H., 2023, Habitat fragmentation affects climate adaptation in a forest herb, *Journal of Ecology*, 112(2): 246-264.
<https://doi.org/10.1111/1365-2745.14225>
- Wang G., Zhang X., Herre E., McKey D., Machado C., Yu W., Cannon C., Arnold M., Pereira R., Ming R., Liu Y., Wang Y., Ma D., and Chen J., 2021, Genomic evidence of prevalent hybridization throughout the evolutionary history of the fig-wasp pollination mutualism, *Nature Communications*, 12(1): 718.
<https://doi.org/10.1038/s41467-021-20957-3>
- Werden L., Sugii N., Weisenberger L., Keir M., Koob G., and Zahawi R., 2020, Ex situ conservation of threatened plant species in island biodiversity hotspots: a case study from Hawai'i, *Biological Conservation*, 243: 108435.
<https://doi.org/10.1016/j.biocon.2020.108435>

Zhao Z., Hu J., Chen S., Luo Z., Luo D., Wen J., Tu T., and Zhang D., 2019, Evolution of CYCLOIDEA-like genes in Fabales: Insights into duplication patterns and the control of floral symmetry, *Molecular Phylogenetics and Evolution*, 132: 81-89.

<https://doi.org/10.1016/j.ympev.2018.11.007>

Zheng J.M., and Wang X.C., 2024, Breeding strategies for enhancing medicinal properties of *Lonicera japonica*, *Medicinal Plant Research*, 14(2): 97-106.

<https://doi.org/10.5376/mpr.2024.14.0008>



Disclaimer/Publisher's Note

The statements, opinions, and data contained in all publications are solely those of the individual authors and contributors and do not represent the views of the publishing house and/or its editors. The publisher and/or its editors disclaim all responsibility for any harm or damage to persons or property that may result from the application of ideas, methods, instructions, or products discussed in the content. Publisher remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.
