

**Phylogenomics, Biogeography, and Taxonomy of *Senna***  
**(Leguminosae, Caesalpinioideae)**

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Ph.D. Thesis



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National School of Tropical Botany

2026

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**Abstract**

The legume genus *Senna* comprises more than 300 species that have colonized a wide range of habitats, from deserts and seasonally dry tropical forests to wet tropical forests and savannas, from sea level to nearly 4,000 m in the Andes. The genus is notable for its long history of human use, with medicinal applications documented since at least the ninth century AD, as well as numerous ornamental species cultivated worldwide and invasive species that affect natural ecosystems and agriculture. The flowers of *Senna* display a set of morphological and functional traits associated with buzz pollination, which have been the subject of extensive study in the last two decades. Despite this attention, significant gaps remain about the taxonomic and evolutionary knowledge of *Senna*, including problematic species complexes, undescribed species, the absence of a comprehensive phylogenetic analysis, and the lack of studies on its biogeographic history across continents. In this context, my thesis addresses these gaps through an integrated approach. **Chapter I** presents the most comprehensive phylogenomic analysis of *Senna* to date, covering approximately 86% of the species in the genus, together with a new infrageneric classification and a synthesis of current knowledge on the genus, including updated information on diversity, ecology, evolution, and human uses. **Chapter II** provides the first comprehensive biogeographic analysis of *Senna*, examining the role of transoceanic long-distance dispersal in shaping its pantropical distribution. **Chapters III–VI** comprise taxonomic studies focused on Neotropical species of *Senna*, including integrative studies of species complexes based on genomic and morphometric data, comprehensive taxonomic revisions, and the description of seven new species. Finally, an **Appendix** includes a co-authored paper addressing the phylogeny and taxonomy of the tribe Cassieae, to which *Senna* belongs. Together, these studies provide a fundamental contribution to the taxonomy and evolutionary understanding of *Senna* and establish a framework for future research, conservation, and sustainable use of the species of *Senna*.

### Svensk sammanfattning

Legumsläktet *Senna* omfattar mer än 300 arter som har koloniserat en stor variation av habitat, från öknar och säsongsmässigt torra tropiska skogar till fuktiga tropiska skogar och savanner, från havsnivå till nästan 4 000 m i Anderna. Släktet är anmärkningsvärt för sin långa historia av mänsklig användning, med medicinska tillämpningar dokumenterade sedan åtminstone 800-talet e.Kr., liksom ett stort antal prydnadsarter som odlas världen över samt invasiva arter som påverkar naturliga ekosystem och jordbruket. Blommorna hos *Senna* uppvisar en uppsättning morfologiska och funktionella egenskaper som är kopplade till vibrationspollinering (buzz pollination), vilka har varit föremål för omfattande studier under de senaste två decennierna. Trots denna uppmärksamhet kvarstår betydande kunskapsluckor om *Senna* taxonomi och evolution, inklusive problematiska artkomplex, obeskrivna arter, avsaknaden av en omfattande fylogenetisk analys samt bristen på studier av släktets biogeografiska historia över kontinenterna. Mot denna bakgrund behandlar min avhandling dessa kunskapsluckor genom ett integrerat angreppssätt. **Kapitel I** presenterar den mest omfattande fylogenomiska analysen av *Senna* hittills, som omfattar cirka 86 % av arterna i släktet, tillsammans med en ny infragenerisk klassificering och en syntes av nuvarande kunskap om släktet, inklusive uppdaterad information om mångfald, ekologi, evolution och mänskliga användningar. **Kapitel II** presenterar den första omfattande biogeografiska analysen av *Senna*, där rollen av transoceanisk långdistansspridning undersöks för att förklara dess pantropiska utbredning. **Kapitel III–VI** omfattar taxonomiska studier med fokus på neotropiska arter av *Senna*, inklusive integrativa studier av artkomplex baserade på genomiska och morfometriska data, omfattande taxonomiska revisioner samt beskrivningen av sju nya arter. Slutligen innehåller ett **Appendix** en medförfattad artikel som behandlar fylogeni och taxonomi hos tribus Cassieae, till vilken *Senna* hör. Tillsammans utgör dessa studier ett grundläggande bidrag till taxonomin och förståelsen av *Senna* evolution och etablerar en ram för framtida forskning, bevarande och hållbart nyttjande av arter inom *Senna*.

**Resumo**

O gênero *Senna* (Leguminosae) compreende mais de 300 espécies que colonizaram uma ampla variedade de habitats, desde desertos e florestas tropicais sazonalmente secas até florestas tropicais úmidas e savanas, ocorrendo desde o nível do mar até quase 4.000 m de altitude nos Andes. O gênero é notável por sua longa história de uso humano, com aplicações medicinais documentadas desde pelo menos o século IX d.C., além de numerosas espécies ornamentais cultivadas mundialmente e espécies invasoras que afetam ecossistemas naturais e a agricultura. As flores de *Senna* apresentam um conjunto de características morfológicas e funcionais associadas à polinização por vibração (buzz pollination), que têm sido objeto de extensos estudos nas últimas duas décadas. Apesar dessa atenção, ainda permanecem lacunas significativas no conhecimento taxonômico e evolutivo do gênero, incluindo complexos de espécies problemáticos, espécies ainda não descritas, a ausência de uma análise filogenética abrangente e a falta de estudos sobre sua história biogeográfica em escala continental. Nesse sentido, a minha tese aborda essas lacunas: o **Capítulo I** apresenta a análise filogenômica mais abrangente de *Senna* realizada até o momento, cobrindo aproximadamente 86% das espécies do gênero, juntamente com uma nova classificação infragenérica e uma síntese do conhecimento atual sobre o gênero, incluindo informações atualizadas sobre diversidade, ecologia, evolução e usos humanos. O **Capítulo II** apresenta a primeira análise biogeográfica abrangente de *Senna*, examinando o papel da dispersão transoceânica de longa distância na distribuição Pantropical de *Senna*. Os Capítulos **III–VI** compreendem estudos taxonômicos focados em espécies neotropicais de *Senna*, incluindo estudos integrativos de complexos de espécies baseados em dados genômicos e morfométricos, revisões taxonômicas abrangentes e a descrição de sete novas espécies. Por fim, um **Apêndice** inclui um artigo em co-autoria que aborda a filogenia e a taxonomia da tribo Cassieae, à qual *Senna* pertence. O conjunto de trabalhos da minha tese estudos fornece uma contribuição fundamental para o conhecimento taxonômico e evolutivo de *Senna*, estabelecendo também uma base para futuras pesquisas, conservação e uso sustentável das espécies do gênero.

### **Acknowledgements**

I am deeply grateful to God for guiding me throughout this PhD journey and for giving me strength and clarity during the challenging moments.

I am deeply grateful to my family, my mother Rose, my father Elcio, my brother Luiz, and my grandparents Iracema, Francisco, and Fernando, for their love, and encouragement.

I am deeply grateful to my supervisors Christine Bacon, Marcelo Trovó, and Vidal Mansano, for their trust, inspiration, and honest conversations. Thank you for supporting me, and for challenging me to think critically – you are true academic inspirations to me!

I am deeply grateful to Bengt Oxelman and Leandro Pederneras, examiners of my PhD, for their valuable contributions to my academic career, and for their insights on plant systematics more broadly.

I thank Vinicius Castro Souza, my undergraduate and master's supervisor, who first introduced me to the wonderful genus *Senna* and has always believed in me and my work – your enormous contributions to the taxonomy and conservation of the Brazilian flora are inspiring!

I thank Juliana de Paula Souza, Juliana Rando, and Roseli Bortoluzzi who are great references in plant taxonomy for me and with whom I have had the pleasure of collaborating on legume projects. I look forward to a long and productive partnership.

I thank Adrian Hill, Alena Wichmann, Brigitte Marazzi, Britt Wassmur, Carolin Rutgersson, Claes Gustafsson, Claes Persson, Claudio Nicoletti, Colin Hughes, Diego Gonzaga, Diego Nunes, Diego Silva, Elenice Fortes, Ellen Larsson, Elizabeth Stunz, Flávia Pezzini, Guilherme Silva, Gwilym Lewis, Haissa Caitano, Haroldo Lima, Heléne Aronsson, Henrique Zamengo, Jenny Egardt, Joel Kokk, Leonardo Borges, Luciano Paganucci, Luiz Sena, Lukas Gabriel, Manuela Santos, Marcus Falcao, Maria Tereza, Ntwae Moiloa, Olga Kourtchenko, Paola Ferreira, Rafaela Forzza, Ryan Folk, Sebastián Giraldo, Søren Faurby, Tony Verboom, Ulf Swenson, Victoria Keller, Wallace Silva, Wellerson Picanço, and William Tejler who generously shared insights and feedback, supported me during fieldwork, lab work, or donated samples to my research.

I thank the curators of all herbaria that I consulted during my PhD, especially ESA, GB, K, P, and RB, where I spent a significant part of my research.

I thank all the staff of the graduate programmes and departments, especially Angela Wulff, Åsa Arrhenius, Cassia Sakuragui, Charlotte Nordangård, Claudia Elisa, Giovana de Oliveira, Henrik Aronsson, Hevelise Peregrino, Ingela Dahllöf, Lovisa Stenbäcken, and Sven Toresson – your support was fundamental throughout my PhD journey!

I'm deeply grateful to the Botanical Garden of Rio de Janeiro (JBRJ), which for more than two centuries has greatly contributed to Brazilian science in support of the research and conservation of Brazilian and South American plants. I also thank the Escola Nacional de Botânica Tropical, which is dedicated to training new generations of botanists — I am proud to be part of this!

I am equally grateful to the University of Gothenburg (GU), the Department of Biological and Environmental Sciences (BioEnv), and the Gothenburg Global Biodiversity Centre (GGBC) for providing me with a wonderful opportunity for learning and research within a highly collaborative and productive community — the commitment to a better world I have found here is truly inspiring!

I am grateful to the following institutions for the financial support that was essential for the completion of this project: Idea Wild, International Association for Plant Taxonomy, Royal Swedish Academy of Sciences, the Society of Systematic Biologists, Stiftelsen Lars Hiertas Minne Foundation. To the Transmitting Science Foundation for providing scholarships for courses.

Finally, I am grateful to the dear friends I made at ESALQ, GU, and JBRJ, who welcomed me warmly and made my days lighter and joyful.



“A conversation with Rupert C. Barneby sparkles like a sunny day in April. Just ask him how he became one of the world's experts on beans. "They choose you," he said. "I don't think I chose them"

After England and Hollywood, Beans Win Out. The New York Times, New York, 18 Apr. 1992. Section 1, p. 23.

In honor of Rupert Charles Barneby (1911–2000), recognized as one of the greatest legume experts worldwide. Born in Monmouthshire, Wales (UK), he studied History and Modern Languages at the University of Cambridge. It was his passion for plants, however, and his remarkable capacity for self-directed learning that shaped his life, leading him to the United States and eventually to a long career at The New York Botanical Garden lasting approximately 50 years. There he produced his major publications, including *Atlas of North American Astragalus* (1964) and *The American Cassiinae: A Synoptical Revision of Leguminosae Tribe Cassieae Subtribe Cassiinae in the New World* (1982). Beyond the more than 7,000 pages he published and the more than 1,000 new taxa he described, he left a lasting example of enthusiasm and scientific rigor that continues to inspire generations, including myself.

<b>Abstract</b>	3
<b>Acknowledgements</b>	6
<b>Introduction</b>	10

#### **Unpublished Chapters**

Chapter 1: Unveiling the Economically Important Legume Genus <i>Senna</i> : Phylogenomics, Taxonomy, and a State-of-the-Art Synthesis	21
Chapter 2: Ocean Currents, Not Ancient Land Bridges: Long-Distance Dispersal Explains the Global Distribution of <i>Senna</i> (Leguminosae)	98
Chapter 3: Beyond Morphological Convergence: Genomic, Morphometric, and Ecological Data Unravel the Systematics of the Widely Cultivated <i>Senna macranthera</i> Complex (Leguminosae)	117

#### **Published Chapters**

<b>Lima, A. G.</b> , V. F. Mansano, M. Trovó & C. D. Bacon. 2025. Morphometric and taxonomic studies of <i>Senna</i> ser. <i>Coriaceae</i> (Leguminosae, Caesalpinioideae, Cassieae), including a new species from Chapada Diamantina, Bahia, Brazil. Brazilian Journal of Botany 48: 18. <a href="https://doi.org/10.1007/s40415-024-01054-3">https://doi.org/10.1007/s40415-024-01054-3</a>	181
<b>Lima, A. G.</b> , M. Trovó, R. L. C. Bortoluzzi, J. G. Rando, C. D. Bacon & V. F. Mansion. 2024. Taxonomic revision of <i>Senna</i> ser. <i>Spinescentes</i> (Leguminosae, Cassieae) including two new South American species. Annals of the Missouri Botanical Garden 109: 413–427. <a href="https://doi.org/10.3417/2024877">https://doi.org/10.3417/2024877</a>	219
<b>Lima, A.G.</b> , Trovó, M., Bacon, C.D., Queiroz, L.P., Souza, V.C. & Mansano, V.F. (2023). Taxonomic novelties in <i>Senna</i> ser. <i>Bacillares</i> (Leguminosae, Cassieae). Nordic Journal of Botany. <a href="https://doi.org/10.1111/njb.03947">https://doi.org/10.1111/njb.03947</a>	252

#### **Appendix**

Rando J.G., Cota M.M.T., <b>Lima A.G.</b> , Bortolozzi R.L.C., Marazzi B. & A.S. Conceição (2024) 5. Tribe Cassieae In: Bruneau A, Queiroz LP, Ringelberg JJ (Eds) Advances in Legume Systematics 14. Classification of Caesalpinioideae. Part 2: Higher-level classification. PhytoKeys 240: 83–102. <a href="https://doi.org/10.3897/phytokeys.240.101716">https://doi.org/10.3897/phytokeys.240.101716</a> .	283
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## INTRODUCTION

### 1. Plant Taxonomy in the Genomic Era: Herbaria and Fieldwork are fundamental

#### 1.1. A Brief History of Plant Taxonomy

Taxonomy is the scientific discipline concerned with the description, delimitation, naming, and classification of organisms. The word taxonomy was coined in the early nineteenth century by the Swiss botanist Augustin-Pyramus de Candolle in his *Théorie élémentaire de la Botanique* (1813), where he introduced taxonomy as the “*théorie des classifications ou taxonomie végétale*” (theory of classification or plant taxonomy). In his work, Candolle defined taxonomy as a method for navigating the diversity of plants by dividing them into groups, which offers a reliable path to recognizing a particular plant and accessing the knowledge previously established about it.

Taxonomy is an ancient science that predates the term coined by de Candolle. Theophrastus (372–287 BC) studied plants beyond their utilitarian functions and contributed to the foundations of taxonomy as a scientific discipline by naming plants and providing early insights into plant classification based on life form and floral characteristics (Pavord, 2005; Rouhan and Gaudeul 2021). Millennia later, the first translations of Theophrastus’ works by Theodore Gaza (ca. 1398–1475) to Latin took place during the Renaissance in 1483 and helped disseminate his ideas, a process further accelerated by Gutenberg’s invention of the printing press in the 15th century (Hort 1916).

The Age of Exploration (from the early fifteenth to the early seventeenth century) was marked by the discovery of new territories, with explorers collecting vast amount of biological, geological, archaeological, and ethnographic specimens that were transported back to Europe (Arnold, 1983; Attenborough et al. 2007). These specimens were often acquired by members of the nobility and wealthy families and organized into collections known as cabinets of curiosities, or *Kunst- und Wunderkammern* (from the German, meaning “art and wonder chambers”) (Raffaini, 1993). These collections became particularly popular in Europe during the sixteenth and seventeenth centuries, as they housed rare and curious artifacts that revealed a world still unknown. Some of the most notable examples of cabinets of curiosities belonged to the Danish physician and antiquarian Ole Worm (1588–1654) and to the Neapolitan apothecary Ferrante Imperato (c. 1525–1615). Over the following centuries, many of these collections were traded or donated, and incorporated into universities, museums and

herbaria, thereby highlighting the scientific role of such collections (Pomian, 1986; Raffaini, 1993; Loureiro, 2007).

Botanical gardens have also played a central role in plant taxonomy. Although historical records of gardens date back millennia, such as the Lyceum in Athens (Greece), the foundations of modern botanical gardens are generally considered to have been established during the Renaissance (Hill, 1915; Kaiser, 2022). These gardens were associated with medical faculties, such as the Botanical Garden of the University of Padua (Italy), where the teaching of botany was generally integrated as a discipline of medicine (Azzi-Visentini, 1984; Tomasi, 2005). Yet the Renaissance contributed to plant taxonomy not only through living collections. The Italian physician and botanist Luca Ghini (1490–1556) developed a method for preserving plant specimens by drying, pressing, and fixing plant parts between the pages of books, an innovation regarded as the origin of contemporary herbaria collections (Funk et al. 2005; Rouhan and Gaudeul 2021).

The works published by Carl Linnaeus (1707–1778; Sweden) were fundamental to the history of taxonomy, establishing the binomial nomenclature, simplifying species names into a genus and a specific epithet, and also proposing a classification system based on plant reproductive structures (Linnaeus 1753, 1758; Blunt, 2004; Paterlini, 2007). The binomial replaced the long phrase names then in use and provided a standardized framework for formally naming species. Pre-Linnaean names are not considered valid under current nomenclatural codes (Knapp 2020; Rouhan and Gaudeul 2021). He also introduced an artificial classification system based on the number and arrangements of stamens and pistil (the sexual system), by first selecting a number of characters and then grouping species accordingly (Bremer, 2007).

After Linnaeus, new insights into plant classification emerged from French botanists, particularly through the ideas of Bernard de Jussieu and his nephew Antoine Laurent de Jussieu, the latter formalizing these concepts in *Genera Plantarum* (1789). The natural system presented in this work relied on multiple characters and implied that not all characters are equally informative at the same level of classification, and introduced the idea of a hierarchy known as the subordination of characters (Rouhan and Gaudeul 2021)

The rise of evolutionary thought, mainly based on Charles Darwin and Alfred Russel Wallace's works, transformed taxonomy by establishing common ancestry and that species change over time. A major turning point in systematics occurred with the publication of Willi

Hennig's works (1950, 1966), which formalized phylogenetic methodology and emphasized classification based on synapomorphies and strictly monophyletic groups (1950, 1966). Advances in molecular data and computational tools in the late twentieth century formalized phylogenetic systematics as an evolutionary framework for taxonomy.

Plant taxonomy has undergone a profound transformation. Despite these advances, the effects of climate change, habitat loss, and the inattention to plants (known as “plant blindness”) represent major challenges (Stagg and Dillon, 2022; Maarten et al., 2025). Accelerating the documentation of biodiversity is therefore essential for effective conservation and sustainable use strategies. Paradoxically, fieldwork and herbaria, historically central to taxonomy, are often undervalued in the genomic era. Here, I argue that both fieldwork and herbaria are now more essential than ever for expanding our understanding and conservation of plant diversity and were fundamental components throughout all chapters of my doctoral thesis. In this context, I discuss their importance, existing gaps, and proposals for rethinking modern taxonomy.

## **1.2. Herbarium Collections**

Herbaria are fundamental repositories of plant diversity, providing verifiable documentation of taxa (Funk, 2003). Each herbarium specimen represents a temporal and spatial representation of a plant species and its morphological, ecological, and genetic diversity, thus serving as a reference for the study of taxonomy and evolution. The value of herbaria is based not only in the specimens themselves but also in the associated metadata (e.g., collection date, locality, habitat), which are invaluable to biogeographic and ecological studies (Soltis, 2017; Heberling and Isaac, 2017; Gasper et al., 2020; Fortier et al. 2024).

Herbarium specimens are indispensable for taxonomic research, serving as nomenclatural types for species descriptions and as voucher material for taxonomic revisions and floristic studies (Funk, 2003). Herbaria serve as reference archives for ecological restoration, biodiversity monitoring, and studies of species distributions and climate change. By comparing historical and contemporary records, researchers can track geographical distribution shifts, local extinctions, and changes in phenology in response to climate change (Wheeler et al., 2012; Davis et al., 2015; Meineke et al., 2018). Advances in DNA extraction have made herbarium collections central to phylogenetic and genomic research

(herbariomics) enabling the recovery of genetic data from specimens collected decades or even centuries ago. Such developments allow the integration of population and phylogenomic approaches to investigate plant evolution across both macro- and micro-evolutionary scales (Kristler et al. 2020; Card et al. 2021; Davis, 2023; Marín-Rodulfo et al. 2024).

In addition to the research function, herbaria play an important educational role. They provide infrastructure for training new generations of taxonomists and plant biologists, developing skills in observation, identification, and curation (Funk, 2003). Herbaria can also promote outreach and communication, connecting science and society through exhibitions, citizen-science projects, and digital platforms that democratize access to plant diversity information (Funk, 2003; Marín-Rodulfo et al. 2024). Through global initiatives such as Global Biodiversity Information Facility (GBIF) (<https://www.gbif.org/>), and regional initiatives such as REFLORA Virtual Herbarium (<https://reflora.jbrj.gov.br>), herbarium data have become part of a digital network, expanding their relevance far beyond physical collections and allowing large-scale analyses of biodiversity patterns and conservation priorities (Soltis, 2017; Drew et al. 2017; Rønsted et al., 2020).

### **1.2.1. Challenges and Gaps**

Natural history collections, including herbaria, face challenges related to infrastructure, funding, and recognition. Many collections suffer from chronic underfunding, thus a scenario of inadequate facilities for specimen preservation, digitization, and data management. The maintenance of climate-controlled storage, specialized equipment, and curatorial staff requires permanent investment. A further concern is the loss of technical expertise, since trained curators, taxonomists, and collection managers become scarce as institutional support and professional positions decline (Dalton, 2003; Canhos et al., 2015)

Particularly in the Global South, which encompasses most of the world's megadiverse countries, underfunding and inadequate infrastructure are more pronounced. Consequently, many plant groups remain underrepresented in herbarium collections, limiting our understanding of plants. Long-term funding is therefore needed not only for physical infrastructure but also for digital infrastructure, such as virtual herbarium networks. Addressing these gaps requires recognition of herbaria as essential scientific infrastructure, repositories not only of specimens, but also of historical records and potential for advancing

our understanding and conservation of plant diversity (Canhos et al., 2015; Zhigila et al., 2025; Boldgiv et al., 2025).

### **1.3. Fieldwork**

Naturalists such as Alexander von Humboldt (1769–1859) and Aimé Bonpland (1773–1858) were prominent explorers in the 18–19th centuries. During their expeditions in the Americas, they carried out detailed field observations and collected numerous specimens. By integrating biological and geographical perspectives, they provided fundamental contributions to the development of biogeography and ecology (Egerton, 2009; Hoorn et al., 2022). Charles Darwin's voyages aboard the HMS Beagle were essential to the development of his theory. Other naturalists such as von Martius, Spix, and Wied-Neuwied, in addition to collecting vast amounts of biological and mineral specimens in the New World, through their written records and illustrations, allowed Europeans to see the natural world far beyond their own borders (Kury, 2001). The combination of fieldwork, observation, and theoretical reflection, not only shaped disciplines such as taxonomy and evolution but also influenced modern field teaching and research.

Among the benefits of fieldwork is capturing details on morphology and ecology that may not always be clear in herbarium specimens. In addition, field observations serve as a critical source of insight for formulating hypotheses concerning the evolution and ecology of organisms and adopting the best conservation strategies (Grant and Grant, 2002; Rafiq et al., 2024). Beyond enabling direct observation of organisms, fieldwork is also important for the collection of specimens, which continuously enriches herbarium collections, contributing to the understanding of plant diversity across space and time (Holmes, et al. 2016; Ramírez-Castañeda et al., 2022)

#### **1.3.1. Challenges and Gaps**

Despite its importance, fieldwork faces growing challenges. Opportunities for field training have declined, with less time devoted to direct observation of organisms in their habitat and increasing emphasis on the analysis of secondary data. This shift not

only weakens the training of new taxonomists but also limits the capacity to document and monitor plant diversity worldwide (Rafiq et al., 2024; Ríos-Saldaña et al. 2018).

Fieldwork and its associated infrastructure remain geographically uneven between the Global North and South, with the latter facing more pronounced limitations in access to long-term funding and research opportunities. At the same time, most of global plant diversity is concentrated in Latin America, Africa, and Asia, regions that largely comprise the Global South. Expanding fieldwork initiatives and strengthening institutional support in these countries is therefore fundamental to improve sampling efforts and advance a more equitable understanding of global plant diversity (Holmes et al. 2016; Simões et al. 2025)

#### **1.4. Golden Rules for Taxonomy**

Here I propose a set of recommendations as pathways for strengthening plant taxonomy through fieldwork and herbarium collections.

**1. Integrate approaches:** fieldwork and herbarium research are complementary. *In situ* observation and the examination of herbarium specimens should be combined with molecular techniques, next-generation sequencing, georeferencing, high-resolution imaging, and digital curation, in order to enhance plant taxonomy and evolutionary studies.

**2. Prioritize underrepresented regions:** global plant diversity knowledge is uneven, with the flora of Global South countries still underrepresented. Fieldwork should focus on these gaps to collect new specimens, while herbaria should ensure their preservation, digitization, and integration into national and global digital databases.

**3. Collaborative practices:** conducting fieldwork and managing collections should involve collaboration with local research partners and respect to national and international regulations. Collaborations should ensure that both fieldwork and herbarium activities benefit local institutions and researchers and the global scientific community.

**4. Training:** taxonomist training should emphasize skills such as field observation, morphological analysis, plant nomenclature, and herbarium curation, integrated with genomic and bioinformatic techniques and digital data management. Integrative training preserves traditional taxonomic expertise while allowing researchers to apply modern tools. Fieldwork

and the curation of biological collections should receive more emphasis in undergraduate and graduate curricula in biodiversity related programs, with adequate course offerings and contact hours.

**5. Funding and infrastructure:** Long-term and continuous investment is required to support fieldwork, herbarium maintenance, digitization, taxonomist training, and molecular studies. Funding mechanisms should facilitate access to modern tools and strengthen institutional capacity, particularly in Global South countries. Resources must be allocated to both large and smaller herbaria to ensure inclusive research infrastructure.

**6. Outreach:** fieldwork and herbarium collections can engage society, support citizen science, and provide education opportunities. By integrating outreach communication with plant taxonomy research, institutions strengthen societal awareness of plant diversity, promote popularization of plants and conservation.

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