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Species Diversity and Endemicity in the Angolan Leguminosae Flora

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Angola has a great diversity of species and ecosystems and a high level of endemism. However, knowledge of the native flora remains very incomplete and outdated. Leguminosae is the largest family in the country, including many species which are of local or more regional economic importance. Based on an extensive review of bibliographic sources, natural history collections, and online databases, the checklist of Angolan Leguminosae plants was updated, including data on their native distribution, conservation status, and principal uses. The endemic taxa were the subject of additional investigation, including the main habitat, the number of collections preserved in herbaria, and the locality of the first collection. We identified 953 Leguminosae taxa occurring in Angola, of which 165 are endemic to the country. Among the 180 genera found, *Crotalaria* (136) and *Indigofera* (96) have the highest number of taxa. Almost half of the studied species have important applications, mainly in traditional medicine (385), forage (267), timber (188), and food (120). Nevertheless, only 27.7% have been assessed according to the IUCN Red List and 10 species are classified as threatened. Thirty-three endemics are known only from the type specimen, revealing the lack of knowledge on these species and the need for further field research. More than 30 type specimens were collected in the Serra da Chela, which highlights the importance of this region for biodiversity conservation.

Keywords: checklist, African flora, endemic taxa, conservation status, herbaria, taxonomy, collection effort

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INTRODUCTION

Angola holds an extraordinary diversity of species and ecosystems (Huntley and Ferrand, 2019). With approximately 1,246,700 km^2, it occupies only 4% of the terrestrial area of Africa but is the second most diverse country in terms of ecoregions, after South Africa (Burgess et al., 2004). Fifteen ecoregions were recognized in this country, from the Atlantic Equatorial coastal forests in Cabinda to the Kaokoveld desert in Namibe (Olson et al., 2001), revealing the great variety of geographic, climatic, edaphic, and biotic conditions.

The country has a rich flora with ca. 6,850 native species and a level of endemism around 14.8% (Goyder and Gonçalves, 2019). Leguminosae (nom. alt.: Fabaceae) is the largest family with more than 900 taxa, occurring in a great diversity of habitats and comprising an extreme diversity of life forms (Lewis, 2005), making it a good case study to understand the main patterns of Angola flora and its main threats.

Recent studies (e.g., Linder, 2001; Darbyshire et al., 2019, 2021; Frazão et al., 2020; Catarino et al., 2021a) revealed important centers of endemism located in Angola, mainly associated with the Angolan Escarpment Zone in Huíla and the Kaokoveld Desert in Namibe, harboring many endemic and range-restricted species. However, 180–200 naturalized species were also identified and some of them are highly invasive, posing a major threat to native biodiversity (Rejmánek et al., 2017; Goyder and Gonçalves, 2019; Figueiredo and Smith, 2022).

Despite the great diversity of species, the knowledge of Angola's flora still presents serious gaps. In previous centuries, collection efforts have been concentrated in the western regions of Angola and some provinces, such as Lunda Norte, Lunda Sul, Uíge, and Moxico, still have few collections (Goyder and Gonçalves, 2019). The first botanical records were made during the seventeenth century by Mason in Luanda and John Kirckwood in Cabinda (Liberato, 1994). Joaquim José da Silva, the first Portuguese collector in Angola, arrived in 1,783 and sent many herbarium specimens to Lisbon, which were taken to the Muséum National d'Histoire Naturelle, Paris during the Napoleonic Peninsula War (Mendonça, 1962). The first major botanical exploration took place in the 1850s. Due to the interest of the Portuguese Government in obtaining scientific information about the products existing on the west coast of Africa, the naturalist Friedrich Welwitsch participated in this expedition and ultimately sent about 11,000 specimens to Portugal, having worked on them until his death, in London (Liberato, 1994). In the following years, the missionaries José Maria Antunes and Eugène Dekindt stood out for the great collections carried out mainly in Huíla, while Hugo Baum explored Cunene and Cuando Cubango (Liberato, 1994; Figueiredo et al., 2009a). The twentieth century was marked by the extensive work of John Gossweiler, who surveyed all provinces of Angola over a period of 50 years (1900–1950), collecting more than 14,000 specimens (Figueiredo and Smith, 2008). Three decades of civil war followed the country's independence in 1975 and hampered existing field research and government efforts to conserve native biodiversity (Huntley, 2017). From the beginning of the twenty-first century, fieldwork resumed and, simultaneously, data about herbaria specimens is being released through GBIF and other data sources (Figueira and Lages, 2019).

Comprehensive and updated lists of the species occurring in this region are an essential tool for managing biological resources and biodiversity conservation planning. During recent decades, some progress has been made with the compilation of several national inventories, but unlike most African countries, Angola was not included in any of the principal regional Flora projects of the twentieth century (Figueiredo and Smith, 2008). Its flora was treated in the *Conspectus Florae Angolensis* edited by Carrisso, Exell, and Mendonça.

The first volume of this Anglo-Portuguese Flora project was published in 1937, so when *Flora Zambesiaca* was initiated in 1960, Angola was explicitly excluded from that wider regional Flora (Dandy and Taylor, 1960). *Conspectus Florae Angolensis* remains incomplete and a large part of the flora is still uncataloged and under-studied, while *Flora Zambeziaca* is already close to completion (Moreira et al., 2006; Soares et al., 2007), with only Commelinaceae, Hyacinthaceae and parts of the Compositae still outstanding.

Figueiredo and Smith (2008) compiled the first checklist of vascular plants, *Plants of Angola*, which has become the baseline for subsequent studies (e.g., Urso et al., 2016; Maquia et al., 2019). According to this work, Leguminosae has 872 native species occurring in Angola, 173 of which are endemic (Figueiredo and Smith, 2008; Figueiredo et al., 2009b). However, with the continuous development of molecular systematics, the taxonomic classification of many taxa of the Leguminosae family has changed in the last few years. Several species were moved from one genus to another, and some species names are now regarded as synonymous with a species previously described due to the existence of multiple names for a single taxon (Miller and Seigler, 2012; Rouhan and Gaudeul, 2014; Hiroyoshi and Kazuaki, 2019). Moreover, a recent study conducted by the Legume Phylogeny Working Group (The Legume Phylogeny Working Group [LPWG], 2017) proposed changing the classification of the traditionally accepted subfamilies (Caesalpinioideae, Mimosoideae, and Papilionoideae) to a new classification, based on six well supported monophyletic subfamilies (Caesalpinioideae, Cercidoideae, Detarioideae, Dialioideae, Duparquetioideae, and Papilionoideae).

Updating checklists, taxonomic data, and the current conservation status of species in the country is an essential step for the conservation of native biodiversity. Conservation actions carried out without accurate taxonomic delimitation can overestimate or underestimate species richness, compromising the sustainable management and effective conservation of the target species (Ely et al., 2017). This is particularly important for legume species, which have a high social and economic value worldwide. This family encompasses important medicinal plants used by local communities, key crops and their crop wild relatives, and important African timber species (Catarino et al., 2019, 2021a). Moreover, they host symbiotic bacteria within nodules in their root systems that fix atmospheric nitrogen, improving soil fertility (The Legume Phylogeny Working Group [LPWG], 2017).

The main goal of this study was to improve the knowledge on the Leguminosae species that occur in Angola, contributing new data to support their sustainable use and future conservation efforts. Specifically, we aimed to: (i) provide a list of Angolan Leguminosae, including their updated taxonomic classification; (ii) gather more data on these taxa, including their native status and life form; (iii) collect updated information on the conservation status and the main uses of each taxon, identifying those that need more conservation efforts; (iv) analyze the endemic taxa and the current knowledge about them through the study of herbarium specimens available electronically; and (v) give a historical perspective on the collection of legume species in Angola, including data on spatial patterns of collection effort.

MATERIALS AND METHODS

Checklist of Leguminosae Taxa

The checklist of Leguminosae taxa that occur in Angola was compiled through an extensive review of different sources. First, we analyzed bibliographic sources focused on Legumes of the flora of Angola and neighboring countries, namely, *Conspectus Florae Angolensis* (Exell and Mendonça, 1956; Exell and Fernandes, 1962, 1966), *Plants of Angola* (Figueiredo et al., 2008), and *Flora Zambeziaca* (Brenan, 1970; Verdcourt, 2000; Mackinder et al., 2001; Pope et al., 2003; Brummitt et al., 2007a,b; Schrire, 2012). Natural history collections are also indispensable sources of data on Angolan species diversity; thus, through the GBIF database (GBIF.org, 2021) and the high-resolution scans of the specimens available online, we analyzed the collections of Leguminosae species held in seven European Herbaria [Herbarium of the Instituto de Investigação Científica Tropical, University of Lisbon (LISC), Herbarium of the Museu Nacional de História Natural e da Ciência, University of Lisbon (LISU), Herbarium of the University of Coimbra (COI), Herbarium of the Royal Botanic Gardens, Kew (K), Herbarium of the Natural History Museum (BM), Herbarium of the Meise Botanic Garden (BR), and Herbarium of the Muséum National d'Histoire Naturelle, Paris (MNHN)]. As herbaria online collections could be biased by the digitizing effort, we also included data from key databases, namely, the African Plant Database (African Plant Database [APD], 2021) and the Plants of the World Online (Plants of the World Online [POWO], 2021).

Scientific names were updated according to the Plants of the World Online (Plants of the World Online [POWO], 2021). This database is sourced from the Royal Botanic Gardens (Kew) and all taxonomic data incorporated reflect the latest peer-reviewed studies on the accepted scientific names and synonyms of plant families. The checklist includes species and subspecies of the Leguminosae family; varieties were not included given the little information available on this taxonomic level and contradictory classifications in the data sources analyzed.

Data on Taxonomy, Distribution, Life Form, Conservation Status, and Main Uses

A database for the identified Leguminosae taxa was constructed, including information on subfamily, native status in Angola, the global area of native distribution, life form, conservation status, and main uses.

The subfamilies were updated following the classification proposed by the Legume Phylogeny Working Group (The Legume Phylogeny Working Group [LPWG], 2017). The native status in Angola was classified as follows: endemic (when the taxa only occur within the political borders of Angola); native (taxa with natural distribution in Angola, but non-endemic); and introduced (taxa originating from other geographic regions; some introduced taxa may become naturalized taxa, i.e., become able to reproduce, grow and disseminate spontaneously in the country; whereas other cannot reproduce or spread without human assistance). The native status and the global native distribution of the taxa were gathered from herbarium specimens, bibliographic sources (Exell and Fernandes, 1962, 1966; Figueiredo et al., 2008), and online databases (African Plant Database [APD], 2021; Plants of the World Online [POWO], 2021). This information was not intended to be exhaustive but rather to show how far the species extends.

Based on the descriptive data of the herbarium specimens and the Plants of the World Online (Plants of the World Online [POWO], 2021), the life form of the taxa was classified into five categories: tree (larger plants in size, with a single woody stem), shrub (plants with several woody main stems growing from the ground), herb (non-lignified plants with unbranched stems), woody climber, and herbaceous climber. Information on the conservation status was retrieved from the IUCN Red List of Threatened Species (International Union for Conservation of Nature [IUCN], 2021) and the evaluations conducted more than 10 years ago that need to be updated were marked with an asterisk. The main uses in Africa were assessed at the species level and categorized as timber, medicinal, forage, and food; these data are available in the Plant Resources of Tropical Africa (Plant Resources of Tropical Africa [PROTA], 2021). For each type of use, a value between 1 and 5 is presented, according to the data available on PROTA. These values were summed to obtain the "total use value," which was applied as a proxy of the anthropogenic pressure imposed on the species and compared with its conservation status.

Collection Data

About 28,270 occurrence records were gathered from GBIF.org (2021), but only 5,331 have geographical coordinates. The geographical data of about 1,200 records were updated with the geographical coordinates assigned in other recent studies (i.e., Catarino et al., 2021a,b). We also identified the type specimen for all endemic taxa and gathered information on the collector's name, number, year, and site of collection. The geographic location of the endemic types was georeferenced, based on the location described on the herbarium specimen label. The georeferencing process was performed using Google Earth Pro 7.3.2.5491 (Serea, 2018) and QGIS v.3.4.4 (QGIS Development Team, 2021), following the Guide to Best Practices for Georeferencing (Chapman and Wieczorek, 2006). The geographical accuracy of the location of each type specimen was estimated based on expert opinion, using a rank scale from 1 to 5, where level 1: $\leq$ 5 km; level 2: $>$ 5–20 km; level 3: $>$ 20–50 km; level 4: $>$ 50–100 km; level 5: $>$ 100 km. Type locations with an accuracy level of 5 were not included in the study.

To ensure the quality and reliability of the data, we deleted the possible duplicated records (i.e., records with the same collector and the same collection number or without collection number). The remaining unequivocal unique herbarium collections were individually checked on the map of Angola; if the description of the collection locality does not correspond to the location

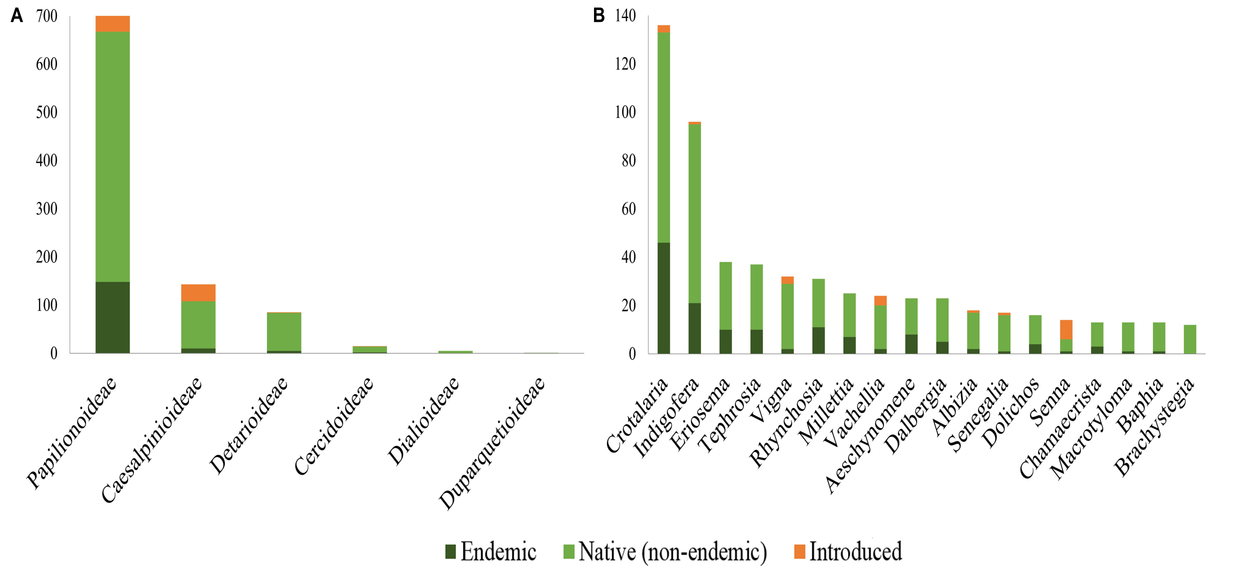

FIGURE 1 | Number of endemic, native non-endemic, and introduced Leguminosae taxa in Angola by **(A)** subfamily and **(B)** genus (only genera with more than ten taxa are represented).

projected on the map, the record was rejected. Despite its limitations, the use of these data is justified by the lack of more georeferenced data.

The final dataset with 3,235 records with geographical coordinates, belonging to 612 species, was used to produce the collection effort maps and the richness maps, using QGIS (QGIS Development Team, 2021) and the FSC QGIS plugin with the function "biological records tool" (FSC Plugin, 2021).

Data on Endemic Taxa

Endemic taxa were the subject of additional investigation. We analyzed the number of collections available on GBIF.org (2021), which includes data of the major international herbaria with large plant collections of Angola (namely, LISC, LISU, COI, K, BM, BR, MNHN). We counted the number of unequivocal unique herbarium collections as a proxy to evaluate the lack of knowledge about each taxon.

To determine the main habitat of an endemic taxon, we analyzed the description of the collection sites from the herbarium specimens and attributed a geographical classification based on the Angolan ecoregions map, established by Olson et al. (2001). We considered the main habitat as the ecoregion that contained the highest number of occurrences. We also recorded the publication of the currently accepted name and the basionym for the taxa that changed their taxonomic classification since the first publication.

RESULTS

Diversity of Leguminosae in Angola

The list of Leguminosae taxa occurring in Angola is presented in **Supplementary Table 1**, including endemic, native, and introduced species and subspecies, which have been described to date and accepted in the Plants of the World Online (Plants of the World Online [POWO], 2021). In total, 953 taxa were identified, including 165 endemics (17.3%), 714 native non-endemics (74.9%), and 74 introduced taxa (7.8%); 933 different species (comprising 70 subspecies) were recognized.

All six Leguminosae subfamilies are present in Angola; Papilionoideae and Caesalpinioideae have the highest number of taxa, with 704 (21.0% endemic) and 143 taxa (7.0% endemic), respectively (**Figure 1A**). Among the 181 genera found, *Crotalaria* has the highest number of taxa, with 136 species accepted, 33.8% of them endemic (**Figure 1B**). *Indigofera* is the second largest genus with 96 taxa (21.9% endemic), followed by *Eriosema* (38 taxa, 26.3% endemic) and *Tephrosia* (37 taxa, 27.0% endemic). Twenty-nine genera only have introduced species, and two genera, *Pseudeminia* (3 taxa) and *Carrissoa* (1 taxon), have only endemic taxa. The list of synonyms, gathered during the review of bibliographic sources and herbarium specimens, is provided in **Supplementary Data 1**.

Concerning the life forms, about 40.2% of taxa are non-climbing herbs, 22.3% are non-climbing shrubs and 27.4% are trees (**Table 1**). In total, about 10.1% of the taxa are climbing plants, specifically 4.4% are herbaceous climbers, and 5.7% are woody climbers.

Main Uses and Conservation of Leguminosae Taxa

According to the Plant Resources of Tropical Africa (Plant Resources of Tropical Africa [PROTA], 2021), 440 of the studied taxa are used in Africa for different purposes (for more details, see **Supplementary Table 1**). Medicinal is the most reported use, with 385 taxa used in traditional medicine, including the Angolan endemics *Droogmansia gossweileri* and *Philenoptera pallescens*.

Forage is the second most reported use (267 taxa), followed by timber (188 taxa) and food (120 taxa) (**Table 2**). Many taxa have been reported for more than one type of use, namely, 43 taxa were reported for four categories of use, 125 taxa for three categories, and 141 taxa for two categories.

Only 264 taxa (27.7%) were assessed in the IUCN Red List of Threatened Species (International Union for Conservation of Nature [IUCN], 2021; **Table 3**) and 65 of them need to be updated. Among the assessed taxa, 240 are classified as Least Concern, four as Near Threatened, and ten in threatened categories. Specifically, *Afzelia bipindensis*, *Afzelia pachyloba*, *Albizia ferruginea*, *Baphia dewevrei* subsp. *marquesii, Brachystegia bakeriana*, *Eriosema laurentii*, and *Copaifera salikounda* were classified as Vulnerable; *Guibourtia pellegriniana,* and *Prioria balsamifera* were classified as Endangered and *Millettia letestui* was classified as Critically Endangered. Also, 10 taxa were classified as Data Deficient and 678 have not yet been evaluated.

Of particular concern are the taxa extensively used in Africa and classified in a threat category (**Figure 2**) or not evaluated. For instance, *Prioria balsamifera* and *Guibourtia pellegriniana* are classified as Endangered, but they continue to be harvested for timber. Classified as Vulnerable, we found *Afzelia pachyloba*, widely used for timber, medicine, forage, and food; *Albizia ferruginea*, used for timber, medicine, and forage; *Afzelia bipindensis* and *Copaifera salikounda*, used for timber and medicine; and *Eriosema laurentii*, used as medicine and food. *Dalbergia melanoxylon* and *Baikiaea plurijuga* are used for three different purposes, timber, medicine, and forage, and are currently classified as Near Threatened; *Daniellia alsteeniana* is classified in the same category and is harvested for timber. Two taxa classified as Data Deficient, namely, *Abrus fruticulosus* and *Dalbergia ealaensis*, and 244 taxa not evaluated are also reported as useful plants for African populations.

TABLE 1 | Life forms (growth habits) of the Leguminosae taxa occurring in Angola.

Habit	Total	Endemic	Native (non-endemic)	Introduced
Tree	261	20	212	29
Shrub (non-climber)	213	45	151	17
Woody climber	54	4	46	4
Herb (non-climber)	383	91	274	18
Herbaceous climber	42	5	31	6

TABLE 2 | The main uses of the Leguminosae taxa occurring in Angola, according to the Plant Resources of Tropical Africa (Plant Resources of Tropical Africa [PROTA], 2021).

Main uses	Total	Endemic	Native (non-endemic)	Introduced
Medicinal	385	2	324	59
Forage	267	0	211	56
Timber	188	0	161	27
Food	120	0	88	32

TABLE 3 | Summary of the conservation status of the Leguminosae taxa occurring in Angola, according to IUCN Red List of Threatened Species (International Union for Conservation of Nature [IUCN], 2021).

Conservation status	Total	Endemic	Native (non-endemic)	Introduced
Critically endangered (CR)	1	0	1	0
Endangered (EN)	2	0	2	0
Vulnerable (VU)	7	1	6	0
Near threatened (NT)	4	0	4	0
Least concern (LC)	240	6	204	30
Data deficient (DD)	10	6	2	2

Collection Effort and Spatial Distribution of Leguminosae Species

The georeferenced data available on the GBIF database (GBIF.org, 2021) includes only a small part of the collections carried out in Angola. However, it is a good proxy for their spatial distribution and allowed us to study the global distribution of the Leguminosae family and the collection activity carried out in the country since the nineteenth century.

After excluding duplicated records and the collections with unprecise coordinates, our dataset includes 3,235 unique records corresponding to 612 species. We only analyzed the data at the species level due to the low infraspecific information in most records. Huíla is the province with the highest number of collections (583) and the highest number of species (211, 34.4% of all the georeferenced species) (**Figures 3A,B**). Namibe, Cunado Cubango, Cuanza Norte, and Malanje have more than 300 collections each. Malanje, with 172 species, has the second-highest richness of Leguminosae species, followed by Namibe (152), Cuanza Norte (135), and Huambo (113). Although Cuando Cubango has a high number of collections, only 73 species were identified in this province. Zaire and Uíge have the lowest values; Zaire has only 19 records of 15 species and Uíge has 36 records of 27 species.

To better understand the spatial distribution of the collection effort, we applied a grid cell of 50 × 50 km resolution. The total number of grid cells in Angola was 575, but only 317 of them include georeferenced records of legume species (**Figure 3C**). The remaining area represents 44.9% of the territory, confirming that botanical collections are still severely biased at the spatial level. Also, ca. 15% of the cells have only one record and 33.6% have five or fewer records (**Figure 3C**). The large areas without collections are mainly located in Zaire, Uíge, Lunda Norte, Lunda Sul, Moxico, Cuando Cubango, and Cunene. The cells with the most intense collection effort are located in Luanda, Cuanza Norte, east of Malanje, central Huambo, and Serra da Chela region between the provinces of Huíla and Namibe. As expected, the cells with the highest species richness are the same (**Figure 3D**).

Furthermore, these data provided information on the distribution patterns of the six recognized subfamilies (**Supplementary Figure 1**). Papilionoideae is distributed across all biomes and provinces; Detarioideae is also found in all provinces, this subfamily contributes an important woody component to Miombo woodlands and has a high frequency in Cabinda, in the Mayombe forests; Cercidoideae is very common in Miombo woodlands and seasonally dry areas; Caesalpiniodeae

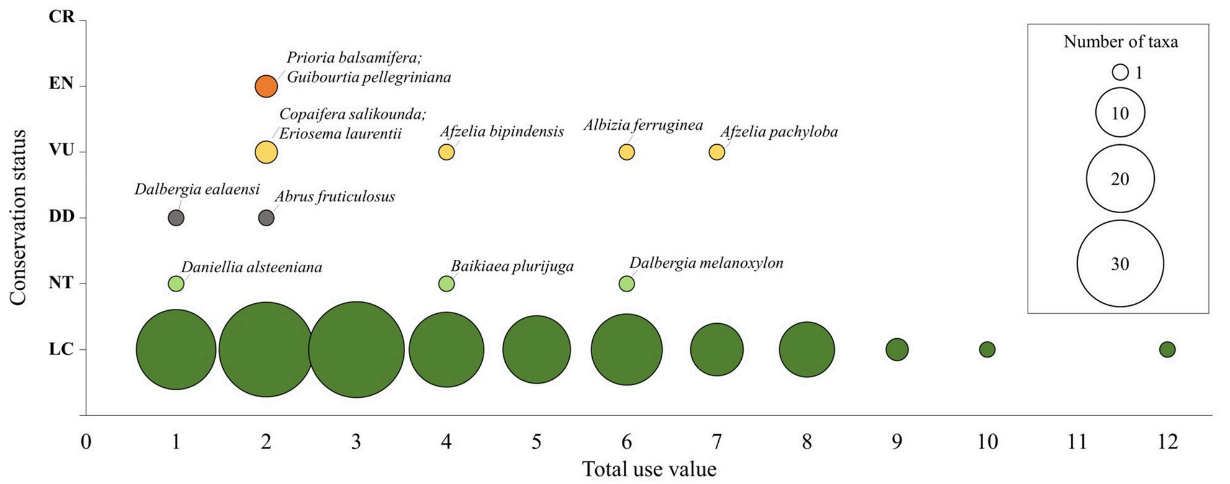

FIGURE 2 | Comparison of the conservation status of the Leguminosae taxa assessed in the IUCN Red List of Threatened Species (International Union for Conservation of Nature [IUCN], 2021) with their total use value, which corresponds to the sum of individual use values (timber, medicinal, forage, and food), classified according to Plant Resources of Tropical Africa (Plant Resources of Tropical Africa [PROTA], 2021). The size of the circles indicates the number of taxa. The figure includes only the 195 taxa with reported uses and included in the IUCN Red List. Conservation status: CR, Critically Endangered; EN, Endangered; VU, Vulnerable; DD, Data Deficient; NT, Near Threatened; LC, Least Concern.

taxa are found mainly in the south and central east Angola, being very common in Namibe and dry regions of Cunene; Dialioideae includes only the genus *Dialium*, with few records in Uíge, Malanje, Lunda Norte, Moxico, Cuando Cubango, and Cunene; Duparquetioideae, with only one species, was recorded in Cabinda but is absent from the map because its record has no geographic coordinates.

Diversity and Conservation of Endemic Taxa

We identified 165 taxa endemic to Angola, including five subspecies (**Supplementary Table 2**). Most of the endemics belong to the subfamily Papilionoideae (90%), but Caesalpinioideae (6%), Detarioideae (3%), and Cercidoideae (1%) also include endemic taxa. This pattern is slightly different from the global pattern observed in Angola, where 79.9% belong to the subfamily Papilionoideae, 15% belong to Caesalpinioideae, 8.9% to Detarioideae, and 1.6% to Cercidoideae.

The main habitat of endemic species was classified using the 15 ecoregions identified in Angola (Olson et al., 2001). Angola Miombo woodlands include more than half of the endemics (84 taxa), followed by Angolan montane forest-grassland mosaic (40 taxa), Angolan scarp savanna and woodlands (11 taxa), Namibian savanna woodlands (10 taxa), Western Congolian forest-savanna mosaic (6 taxa), and Kaokoveld desert (5 taxa) (**Figure 4**). Less than three taxa were found in Southern Congolian forest-savanna mosaic, Zambezian Baikiaea woodlands, Angolan Mopane woodlands, and Atlantic Equatorial coastal forests. The life forms of these taxa are very diverse, including 20 trees, 47 shrubs, and 95 herbs. Endemic taxa have a much lower percentage of IUCN-evaluated taxa than non-endemic natives. Only 13 of the 165 endemics (7.9%) were assessed, six were classified as Least Concern, one as Vulnerable, and six as Data Deficient.

Figure 5 presents the number of unequivocally unique collections available on GBIF.org (2021). For 35 endemic taxa, we only found one collection available in the major herbaria, and 33 of them are globally reported as known only by the type specimen. The other two taxa are *Indigofera astragaloides* and *Indigofera pruinosa,* which have only one collection available on GBIF, but other collections were mentioned in bibliographic sources. Twenty-three taxa have only two collections, 49 taxa have between three and five, 33 taxa have between six and ten, and 25 taxa have more than ten collections. *Chamaecrista huillensis* has the highest number, with 43 collections.

A Historical Perspective of Leguminosae Endemic Taxa

The projected geographic locations of endemic type specimens collected in Angola are presented in **Figure 6**. The early collections were from the coastal provinces. The first type specimen of a Leguminosae endemic taxon was collected by Friedrich Welwitsch in 1855. Between 1855 and 1860, he collected 50 specimens that were later designated as types (**Figure 7**), mainly in Cuanza Norte, Malanje, Namibe, and Huíla.

By 1914 a further 27 new endemic taxa were discovered, mainly in Cuando Cubango and Huíla. John Gossweiler collected the second largest number of new endemic taxa; 30 type specimens were designated from collections he made between 1903 and 1941, in 13 of the 18 provinces of Angola (**Figure 7**). Another important collector was Henry Pearson, collecting seven new endemic taxa in 1908 and 1909. Otto Hundt collected seven new endemics between 1932 and 1933, and Arthur Exell and Francisco Mendonça together collected 15 new endemics in 1937. In Cabinda, Zaire, Lunda Sul, and Huambo, the collection of new endemics was made only between 1915 and 1944.

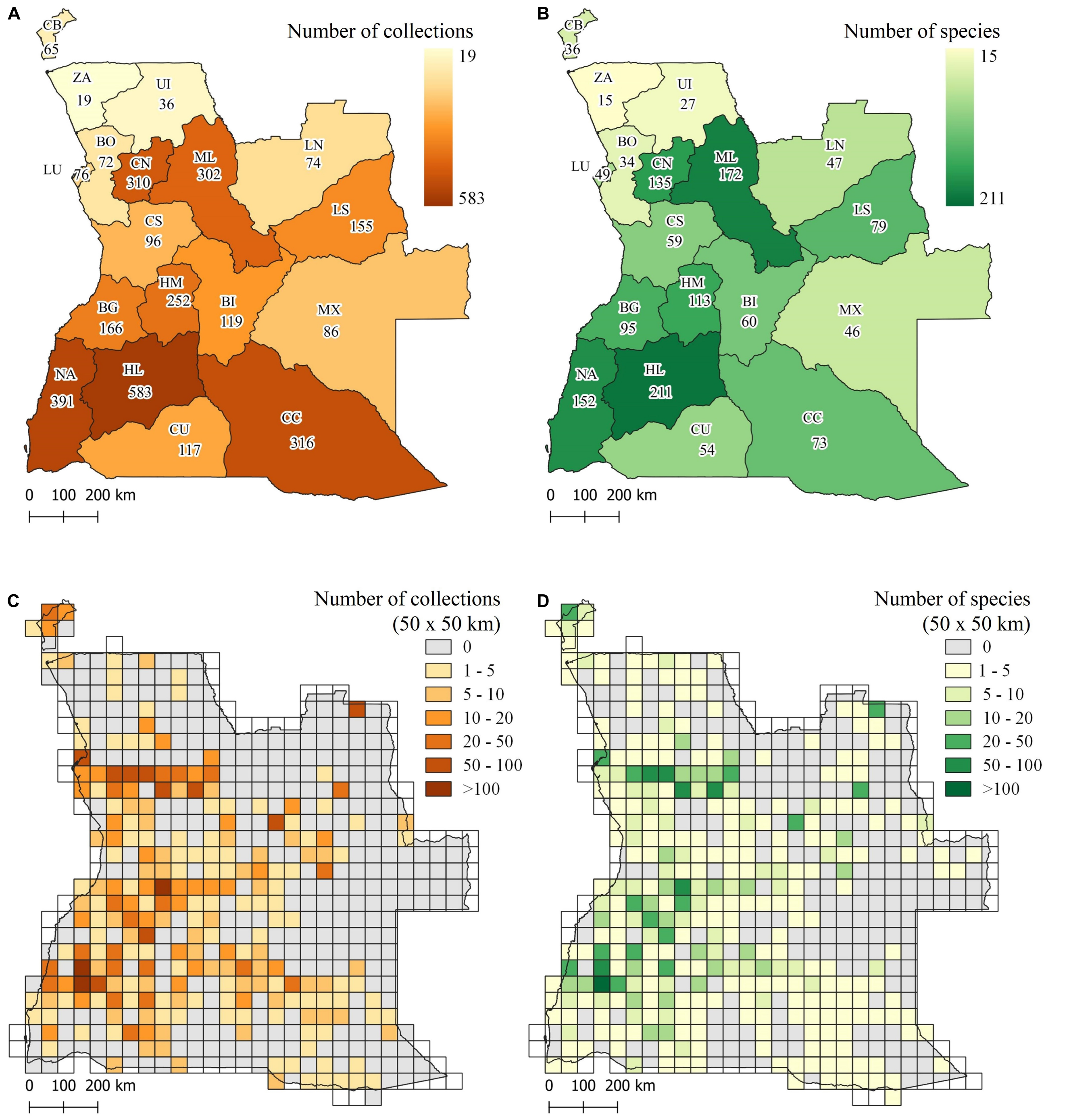

FIGURE 3 | Spatial distribution of collecting activity and species richness in Angola: **(A)** number of collection records in each province; **(B)** number of Leguminosae species richness in each province; **(C)** number of collection records per grid cell of 50 × 50 km resolution; and **(D)** number of Leguminosae species per grid cell of 50 × 50 km resolution. Cells without collections are highlighted in gray. Provinces of Angola: CB, Cabinda; ZA, Zaire; UI, Uíge; LU, Luanda; BO, Bengo; CN, Cuanza Norte; CS, Cuanza Sul; ML, Malanje; LN, Lunda Norte; LS, Lunda Sul; BG, Benguela; HM, Huambo; BI, Bié; MX, Moxico; NA, Namibe; HL, Huíla; CU, Cunene; CC, Cuando Cubango.

Between 1955 and 1966, important collections were made by Eduardo Mendes (8 new endemics), Joaquim Teixeira (7 new endemics) and António Rocha da Torre (6 new endemics). Many of these collections were located near Serra da Chela, in the western border of Huíla province. Currently, Huíla has the largest number of Leguminosae collections, with 44 type specimens (26.5%), Namibe has 22 type collections, Malanje has 15 collections, Cuando Cubango and Cuanza Norte have

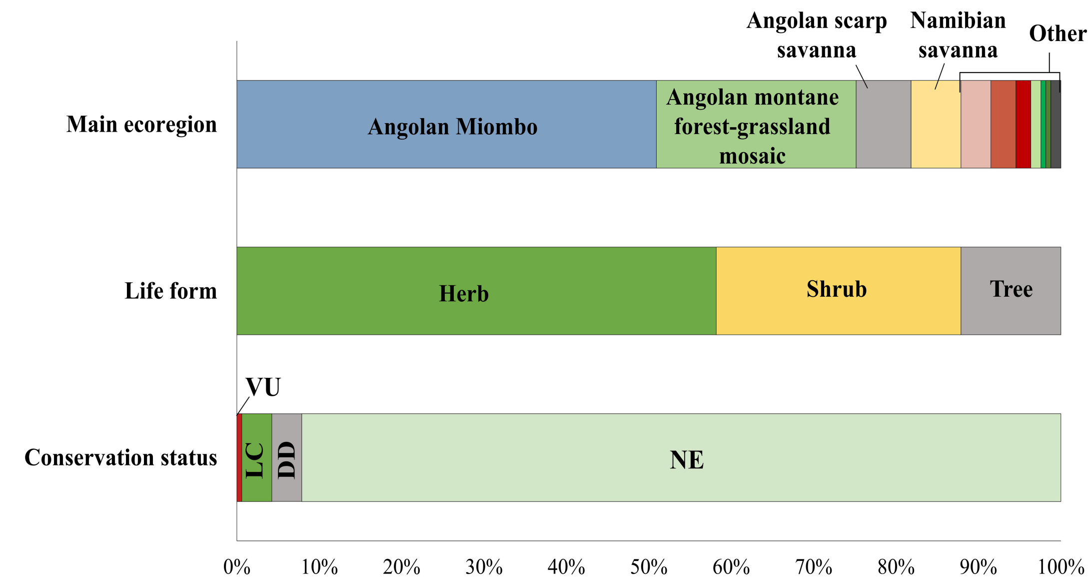

FIGURE 4 | Ecoregion (Olson et al., 2001), life form and conservation status (International Union for Conservation of Nature [IUCN], 2021) of the 165 Leguminosae taxa endemic to Angola.

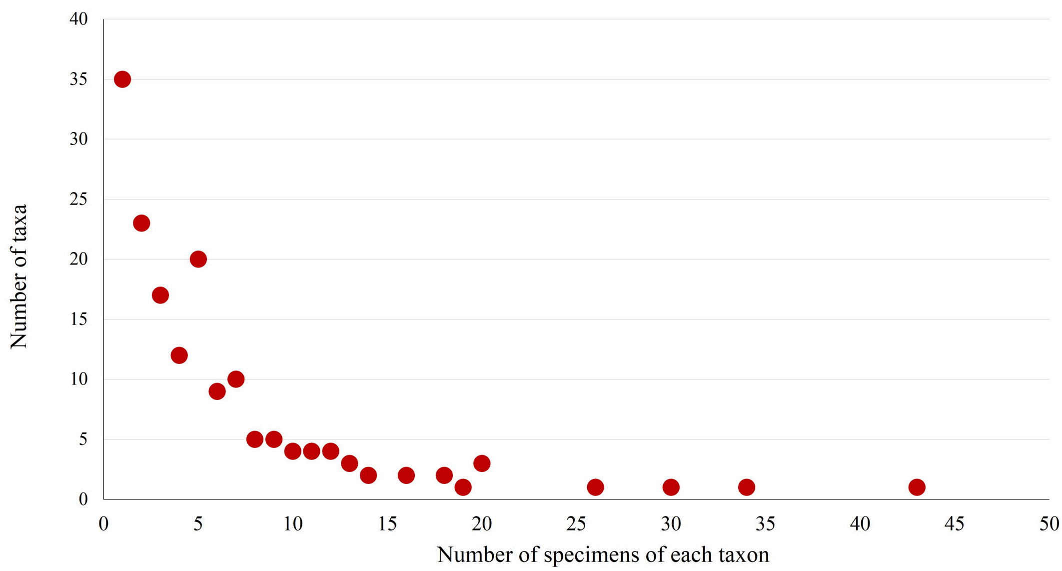

FIGURE 5 | Number of collections available on GBIF.org (2021) for each of the 165 endemic taxa.

12 collections each. Globally, Serra da Chela (Huíla) presents the highest number of new species collections, with 33 types collected in this region.

The chronology of field collection and scientific publication of the currently accepted endemic taxa is presented in **Figure 7**. The first published and currently accepted endemic species was *Indigofera lasiantha* in 1826. However, it is not represented in the chart because the date of collection is unknown. In 1871, the Leguminosae family was published in the Flora of Tropical Africa, which included the first publication of 37 taxa endemic to Angola. In the following years, several species were regularly published in different scientific journals. In 1960, 36 taxa were published in Memórias, Junta de Investigações do Ultramar—Segunda Série. The Boletim da Sociedade Broteriana (Bulletin of the Broterian Society) is also worth noting, as it published 31 Leguminosae taxa since 1933, 18 of them in 1965.

DISCUSSION

The present study focused on the Leguminosae family recognized 953 accepted taxa occurring in Angola. However, this number

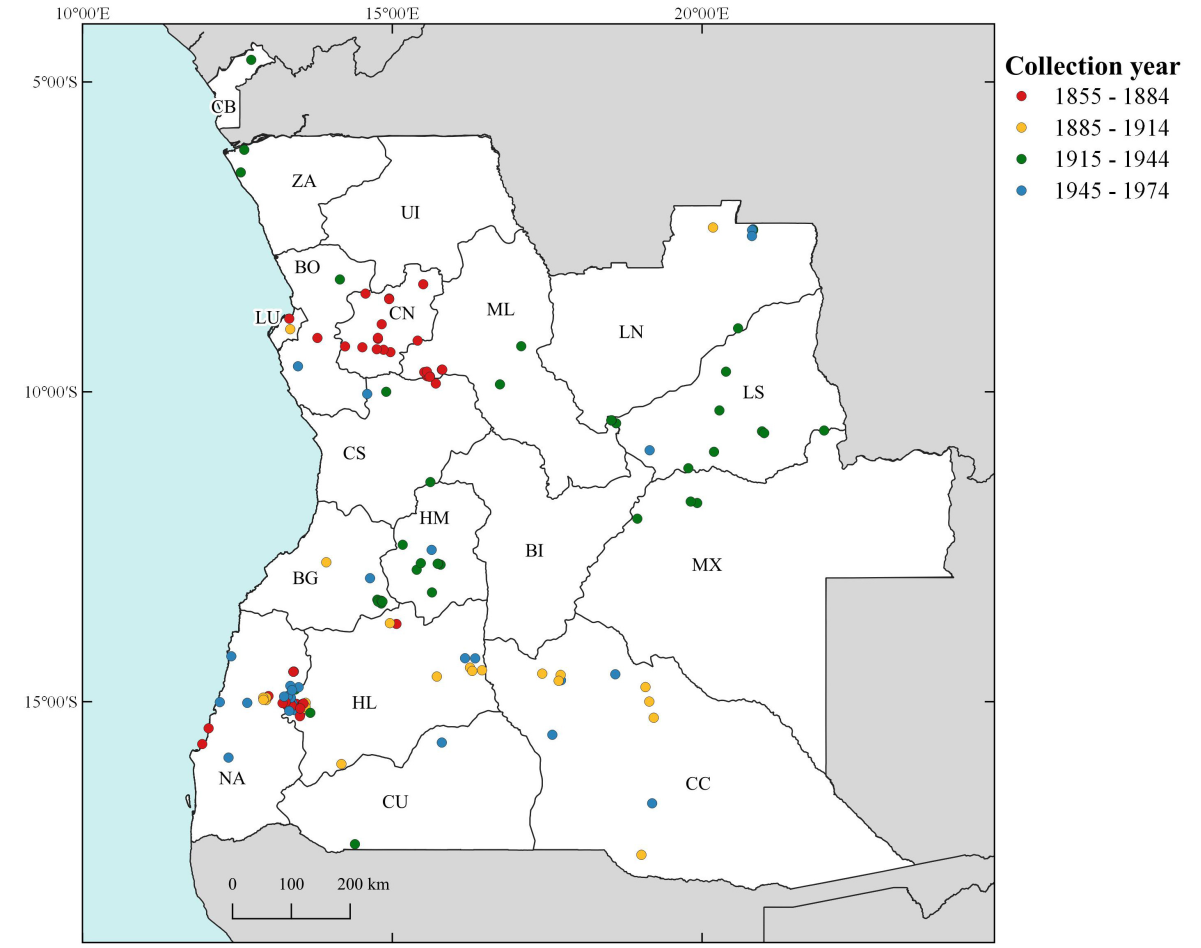

FIGURE 6 | Geographic distribution of the collection sites of the Leguminosae type specimens endemic to Angola. Provinces of Angola: CB, Cabinda; ZA, Zaire; UI, Uíge; LU, Luanda; BO, Bengo; CN, Cuanza Norte; CS, Cuanza Sul; ML, Malanje; LN, Lunda Norte; LS, Lunda Sul; BG, Benguela; HM, Huambo; BI, Bié; MX, Moxico; NA, Namibe; HL, Huíla; CU, Cune-ne; CC, Cuando Cubango.

could be significantly higher since the country's eastern provinces remain very under-surveyed (Goyder and Gonçalves, 2019).

With more than 900 legume species, Angola is one of the richest countries in sub-Saharan Africa. According to Plants of the World Online (Plants of the World Online [POWO], 2021), 752 species of legumes are found in Zambia, 687 in Zimbabwe, and 860 in Mozambique. The Democratic Republic of Congo, the neighboring country to the north, has 1,236 species, while Namibia, in the south, hosts only ca. 350 species (Plants of the World Online [POWO], 2021).

Our results present a lower number of native legume species (863 native species, excluding subspecies) than the previous study of Figueiredo et al. (2009b), which identified 872 species. The taxonomic update of many species can explain this decrease. Some taxa are now classified as synonymous of previously described species; for instance, *Cryptosepalum verdickii* is now a synonym of *Cryptosepalum maraviense* (Govaerts, 1999). Other taxa changed their taxonomic level; for example, *Adenodolichos bussei* is now accepted as the subspecies *Adenodolichos punctatus* subsp. *bussei* (Mackinder et al., 2001), while *Baphia capparidifolia* subsp. *multiflora* and *Bauhinia petersiana* subsp. *macrantha* are now accepted as *Baphia multiflora* and *Bauhinia macrantha*, respectively (Govaerts, 1996; Germishuizen and Meyer, 2003).

Of the 165 legume species and subspecies endemic to Angola, *Albizia angolensis*, *Carrissoa angolensis*, and *Indigofera astragaloides* are reported for the first time, as they were not mentioned by Soares et al. (2007) and Figueiredo et al. (2008), although *Carrissoa angolensis* was reported by Darbyshire et al. (2014) for Lunda Norte.

Profound changes have been made in several genera, and particularly *Acacia* and *Desmodium* had many taxa moved to another genus. About 45 taxa of *Acacia* were previously recognized by Figueiredo and Smith (2008), but these taxa were recently reclassified into different genera. Over the last 10 years, phylogenetic studies have shown that *Acacia* is not a monophyletic genus, and it was divided into five different genera (*Acacia, Vachellia, Senegalia, Acaciella,* and *Mariosousa*) (Kyalangalilwa et al., 2013). The name *Acacia* was conserved for the Australian contingent of the genus as proposed by Orchard and Maslin (2003), and the African taxa were reclassified

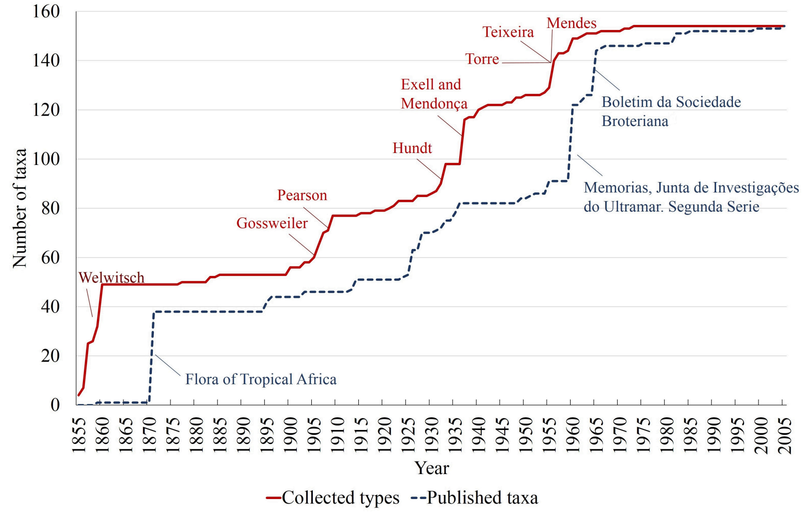

FIGURE 7 | Collection and publication of the Leguminosae taxa endemic to Angola. The cumulative number of taxa is presented by date of collection (red) and description (dark blue). Only the 152 taxa with known years of collection were included. The names of the main collectors and the three most relevant publications are indicated.

as *Senegalia* and *Vachellia* (Lewis, 2005). This proposal and its subsequent adoption have caused controversy, questioning the legitimacy of the procedures (Moore et al., 2010; Thiele et al., 2011). Currently, Angola comprises 24 taxa of the genus *Vachellia*, 17 taxa of *Senegalia,* and three introduced species of *Acacia*.

The genus *Desmodium*, which previously included 18 taxa in Angola, now includes only five species, most of which have been introduced. The remaining taxa were reclassified in the genera *Grona*, *Hylodesmum,* and *Pleurolobus* (Ohashi and Ohashi, 2018, 2019).

All six subfamilies proposed by the Legume Phylogeny Working Group (The Legume Phylogeny Working Group [LPWG], 2017) were found in the country. However, the percentages of taxa belonging to Papilionoideae (73.8%) and Detarioideae (8.9%) subfamilies are higher than the percentages observed globally (71.5 and 3.9%, respectively), while Caesalpinioideae has a lower proportion in Angola (15.0%) than worldwide (22.5%) (The Legume Phylogeny Working Group [LPWG], 2017).

Our results reveal that only 264 (27.7%) of the studied taxa are currently evaluated in the IUCN Red List of Threatened Species (International Union for Conservation of Nature [IUCN], 2021), 65 of which were assessed more than 10 years ago and need to be updated. The assessment of the conservation status, based on IUCN categories and criteria, is recognized as the most comprehensive framework to prioritize the threatened species (Romeiras et al., 2016). Presently, the number of vascular plants evaluated worldwide on the IUCN Red List remains very low. According to Christenhusz and Byng (2016), approximately 308,300 vascular plants are described and accepted, but only 57,987 of them are evaluated in the IUCN Red List (International Union for Conservation of Nature [IUCN], 2021), representing ca. 18.8%. The percentage of native species evaluated in Angola is higher (27.7%), but the percentage decreases to 7.9% among endemics. We observed that most evaluated species are widespread and distributed worldwide, probably accessed by conservation initiatives carried out in other countries, while the restricted taxa remain poorly studied.

Endemic species are especially prone to extinction due to their narrow geographical range, low populations number, and small population sizes (Işik, 2011). Several studies on endemic African flora have shown extremely high levels of threat. For instance, the assessment of the conservation status of the monocotyledon plants endemic to Morocco classifies 95% as threatened species (Rankou et al., 2015); the Red List of endemic plants of Ethiopia and Eritrea reports 81.5% as threatened (Vivero et al., 2006); and The Red List of endemic plants in Cabo Verde identifies 78% as threatened taxa (Romeiras et al., 2016). The number of endangered endemics of Angola can also be very high. Thirty-three of the endemics are known only from the type specimen and there are no recent records, which means that the species may even be extinct. It highlights the need for further studies and extensive fieldwork to understand the distribution and main threats of the most restricted taxa. This is particularly important in Angola because the country has one of the highest rates of deforestation in southern Africa (Romeiras et al., 2014) and is facing numerous threats to biodiversity, including the effects of climatic change, changes in fires regimes, overexploitation of natural resources, and rapid population growth, which cause the degradation of Angolan natural ecosystems (Catarino et al., 2020, 2021b).

Based on collected records of Leguminosae species, this study shows that Angola is still underexplored, and the collection effort is uneven across the country. Since we only include data with available geographical coordinates, our dataset contains only a small part of the field collections carried out in Angola since the first expeditions. This dataset does not allow us to analyze the distribution areas of individual species, but it is a good proxy for studying the spatial patterns of collecting activity across the country, providing new insight into the general distribution patterns of the six subfamilies.

The best collected areas are generally found in central and northern provinces, around larger cities (e.g., Luanda, Lubango, N'Dalatando, Huambo) and near roads and rivers, a pattern commonly found in other tropical countries (Schulman et al., 2007). According to Brundu et al. (2017), in Europe, the geographical distribution of the type collections tends to be positively correlated with the proximity of the coastline and the roads, which could explain the similar pattern found in Angola.

The eastern provinces, such as Lunda Norte, Lunda Sul, Moxico, and Cuando Cubango, have the most extensive areas without collections, which is in line with previous studies (Goyder and Gonçalves, 2019; Frazão et al., 2020; Catarino et al., 2021a).

Many type specimens were collected in Huíla, especially in Serra da Chela (at least 33 types), an elevated region between Lubango and Namibe, corresponding to the Angolan Montane Forest-Grassland Mosaic ecoregion (Olson et al., 2001). These findings suggest a high diversity of endemic legume species in this area. It is in agreement with other studies that identify Serra da Chela as an important hotspot of diversity and endemism of plant species (e.g., Linder, 2001; Frazão et al., 2020; Catarino et al., 2021a), insects (Kipping et al., 2019), amphibians (Conradie et al., 2012) and reptiles (Branch et al., 2019), but the area remains without any legal protection.

Conservation of the natural environment of type specimens, i.e., the geographical locations documented by the publications of a taxon, is of utmost importance. Endemic taxa generally have restricted distributions and are confined to small areas, thus becoming highly vulnerable to extinction (Raedig et al., 2010). Therefore, the endemic species should be considered as a priority for study and conservation. The high number of taxa (33) known only by the type specimen demonstrates the need for further field research. The protection of the type populations is also essential for studies of biosystematics that require the collection of living specimens or germplasm. Only this will ensure that the results obtained will be taxonomically accurate (Brundu et al., 2017). One possible solution could be to implement Protected Areas of small dimensions or Plant Micro-Reserves as defined by Laguna et al. (2013), to promote the *in situ* conservation of endemic taxa.

The temporal distribution of collections was also very biased; field research has been almost completely abandoned for several decades, since 1975, because of the war (Huntley, 2017). However, peace was achieved in 2002, bringing many specialists and recent research projects to Angola, which are also focused on some less studied areas, such as the Okavango basin in Cuando Cubango (National Geographic, 2021). These recent initiatives to document areas of high conservation interest have provided updated information to fill gaps in knowledge of Angolan biodiversity, highlighting the importance of continued investments in inventories and field research.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

SC and MR: conceptualization and methodology. SC: formal analysis, investigation, and writing—original draft preparation. SC, DG, ID, EC, RF, MD, and MR: writing—review and editing. MD and MR: supervision. All authors have read and agreed to the published version of the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.871261/full#supplementary-material

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