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CHARACTERISTICS AND
DETERMINANTS OF ENDEMIC
PLANT TAXA IN THE GABONESE
AREA OF ENDEMISM¹

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ABSTRACT

Endemism is one of the most important concepts in biogeography and is often used to guide biodiversity conservation, yet our understanding of the determinants of endemism in many biodiverse tropical regions is limited. This is true for western Central

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Africa, a region with one of the highest levels of plant diversity in tropical Africa, where endemism is poorly documented. This study examines the Gabonese Area of Endemism (GAE) and explores the main characteristics and determinants of its vascular plant endemism with regard to taxonomy, growth form, habitat, distribution, and range size. We compiled a comprehensive, verified specimen database of vascular plant taxa restricted to the GAE, comprising 19,876 occurrences of 1145 species and infraspecific taxa, and we characterized the habitat and habit for each taxon. We then calculated the proportion of taxa in the regional flora that are endemic to the GAE. A Wilcoxon rank-sum test was used to investigate range size among endemic taxa exhibiting different growth forms, and Fisher exact tests were used to explore the association between their habit and habitat, and to test the distribution of these attributes among higher-level taxa and growth forms compared to patterns in the regional flora as a whole. We found that endemic taxa represent ca. 13% of the GAE flora, and that the rate of endemism varies considerably among taxonomic groups and growth forms. Endemism is highest among shrubs (22%) and lowest in herbs (8%), especially monocotyledons (e.g., 5% among Poales). Most endemic taxa grow preferentially in forest habitats, the dominant vegetation type of the region. Endemic trees, which structure forest ecosystems, have significantly larger ranges than endemic herbs, climbers, and shrubs. About 17% of the flora of Gabon is endemic or subendemic to the country. Our results show that the dispersal capacity of taxa and the biogeographical history of the region appear to be critical factors in explaining differences in the rate of endemism among growth forms and taxonomic groups. Our findings also highlight the benefits of carefully building a comprehensive and verified database for studying rare and range-restricted plants, and they underscore the necessity to strengthen botanical exploration throughout western Central Africa in order to develop improved and better-informed conservation strategies.

Key words: Biodiversity, dispersal, Gabon, growth form, Lower Guinea, rate of endemism, taxonomy, tropical forest, vascular plants, western Central Africa.

Documenting and understanding patterns of biodiversity is one of the most important and challenging tasks for today's ecologists and biogeographers (Gaston, 2000). Elucidating the determinants of plant endemism in tropical areas has always been challenging due to significant gaps in our knowledge of the floras in these regions, largely because reliable data on species distributions are often scarce and/or difficult to access (Küper et al., 2006; Collen et al., 2008; Feeley & Silman, 2011; Stropp et al., 2016). The range of a species is an important indicator of historical, ecological, and evolutionary processes that have shaped the current distribution of biodiversity (Harold & Mooi, 1994; Sosef, 1994; Jansson, 2003). Endemism is a central concept in biogeography (Anderson, 1994; Brown et al., 1996) and is also highly relevant for biodiversity conservation, especially in areas where many endemic species occur (Myers et al., 2000; Brown et al., 2013; Bland et al., 2015).

Mega-databases of georeferenced records of vascular plant species have recently become available at both a global (BIEN, 2021; GBIF, 2021) and continental scale (Dauby et al., 2016), facilitating broad-scale biogeographical and conservation research initiatives (Droissart et al., 2018; Stévant et al., 2019). Studying patterns and characteristics of endemism at a regional scale generally requires accurate and verified distributional data, as narrowly distributed species are often known from only one or a few records (Texier et al., 2021), making it particularly important to assure that identification and georeferencing are highly accurate. Unfortunately, the information available from mega-databases is sometimes erroneous (Maldonado et al., 2015; Zizka et al., 2019), resulting from recurrent issues such as the difficulty of georeferencing old specimens and the presence of duplicate records of a given collection that

bear different geo-coordinates or have been identified to different species (Sosef et al., 2017). Moreover, despite the recent digitization of collections in many large herbaria (Soltis, 2017), the data associated with these collections often remain to be captured, such as those in the herbarium of the Muséum National d'Histoire Naturelle in Paris, the Royal Botanic Gardens, Kew, and the Conservatoire et Jardin botaniques de la Ville de Genève (Sosef et al., 2017). These shortcomings constitute significant obstacles when attempting to utilize these mega-databases to determine the distribution of rare species or to study the patterns and characteristics of endemism at a local or regional scale (Beck et al., 2013).

Botanical knowledge of the flora of western Central Africa (WCA) is very heterogeneous. This territory, which broadly corresponds to the Lower Guinea sub-center of plant endemism of the Guineo-Congolian forests (White, 1979; Droissart et al., 2018), includes some areas that are very poorly known, such as the Republic of the Congo and Nigeria, whereas Gabon, situated in the center of WCA and possessing a forest cover that exceeds 85% (Mayaux et al., 2004), hosts one of the best-known and well-digitized floras in tropical Africa (Sosef, 2016a; Sosef et al., 2006, 2017). The rare and endemic species of the region are of significant importance for conservation (Texier et al., 2021). These species have also figured significantly in research that has sought to explain the current distribution of biodiversity in WCA in a historical biogeographic context in which the area occupied by African rainforest is hypothesized to have been fragmented and reduced in area and extent during the Pleistocene ice ages (Sosef, 1994; Maley, 1996; Rietkerk et al., 1996; Robbrecht, 1996). Because national boundaries in WCA do not correspond to natural or biological limits, endemic spe-

cies tend to be concentrated toward the center of a given country, and as a consequence, considerations of endemism with regard to political or administrative areas are therefore of limited value (Texier et al., 2021). An alternative approach involves focusing studies on meaningful floristic bioregions, i.e., areas of endemism (Morrone, 1994; Texier et al., 2021).

The Gabonese Area of Endemism (GAE), defined to encompass the biogeographical territories connected to the ecosystems found in Gabon (see below under Materials and Methods), has a vascular plant flora comprising more than 8000 specific and infraspecific taxa, representing one of the highest levels of plant diversity in tropical Africa and making it one of the continent's richest centers for plant endemism (Linder, 2001; Kier et al., 2005; Sosef et al., 2017; Droissart et al., 2018). Although patterns of endemism within this area have been described for some taxonomic groups (Sosef, 1994; Droissart, 2009; Lachenaud, 2019), they have not been explored broadly, largely due to the lack of an up-to-date and well-verified database that documents endemism for the entire flora of the area.

The goal of this paper is therefore to document the main characteristics of vascular plants whose distributions are restricted to the GAE, in particular with regard to their taxonomy, growth form, habitat, distribution, and range size, and to explore the factors explaining the rate of endemism in this area. Using the largest verified database of restricted-range vascular plant species ever compiled at a regional scale in tropical Africa, we specifically aim to (1) characterize the biology and ecology of the taxa endemic to the study area and (2) explore potential determinants of the rate of endemism by analyzing the proportion of endemics within the regional flora with regard to various taxonomic ranks and growth forms.

MATERIALS AND METHODS

STUDY AREA

The study area was defined to encompass all the territories that have a strong biogeographical connection to the ecosystems found in Gabon. We delineated this territory based on a preliminary analysis of areas of endemism at the scale of the Lower Guinea subcenter of endemism (as defined by White, 1979) using the occurrences of vascular plants available in the RAINBIO database (Dauby et al., 2016) and employing three different methods: (1) a hierarchical clustering method applied to a presence-absence dissimilarity matrix, and using the beta-sim index (β_{sim}) and the Ward hierarchical clustering method (Koleff et al., 2003; Kreft & Jetz, 2010); (2) modeling of the distribution of species (Phillips et al., 2006) associated with the hierarchical

clustering method in (1); and (3) a bipartite network approach (Vilhena & Antonelli, 2015), using the web application “Infomap Bioregion” (Edler et al., 2017). The study area, which we refer to as the GAE, was delineated by considering all the areas of endemism that overlapped partially or fully with Gabon based on a consensus of the results from these three methods and the literature dealing with areas of endemism and phylogeography in the region (Sosef, 1994; Robbrecht, 1996; Droissart, 2009; Duminil et al., 2013; Hardy et al., 2013; Dauby et al., 2014a; Lachenaud, 2019) (methodology explained in Supplementary Material 1).

The study area (Fig. 1) extends from 4.5°N, i.e., predominantly along the Sanaga River in Cameroon, to 6°S, i.e., along the mouth of the Congo River, and from the Atlantic Ocean in the west to 19°E, covering an area of ca. 1,155,000 km². It encompasses all of Gabon, the Republic of the Congo, and Rio Muni (Equatorial Guinea), along with forested areas in several adjacent countries: (1) southern Cameroon; (2) the rainforest of southwestern Central African Republic (CAR); (3) the floodplain of the Sangha River and the Congo River in both the Republic of the Congo and the Democratic Republic of the Congo (DRC), respectively, regarded by White (1979) as marking the separation between the Lower Guinea and the Congolian subcenters of endemism; (4) the forest/savanna mosaic extending from the Plateaux Batéké in Gabon to the region of Kinshasa in the DRC; and (5) the Mayombe chain extending from Gabon to the DRC. The Cameroon Volcanic Line lies to the north of the study area, and while part of the Lower Guinea domain, it represents a distinct area of endemism that is not connected to Gabon (White, 1979; Sosef, 1994; Robbrecht, 1996; Droissart, 2009; Lachenaud, 2019).

Based on the land cover map of Africa from Mayaux et al. (2004), 74.5% of the GAE is covered by forest, 13.8% by woody or shrubby savannas, 6.2% by cropland, 4.3% by grasslands, 1.2% by water bodies, and 0.1% by urbanized areas (Fig. 1).

DATA ACQUISITION

To develop a list of species that are found only in the GAE, we first compiled a list of range-restricted species that occur in the study area, based on a compilation of three extensive, publicly available databases:

- The RAINBIO database, developed by Dauby et al. (2016), which contains 205,505 records for the study area (out of a total of 613,873 records for tropical Africa). It notably integrates information from the databases of the main herbaria with collections from Central Africa (BR, BRLU, MO, WAG; acronyms according to Thiers, 2021), as well as from the database

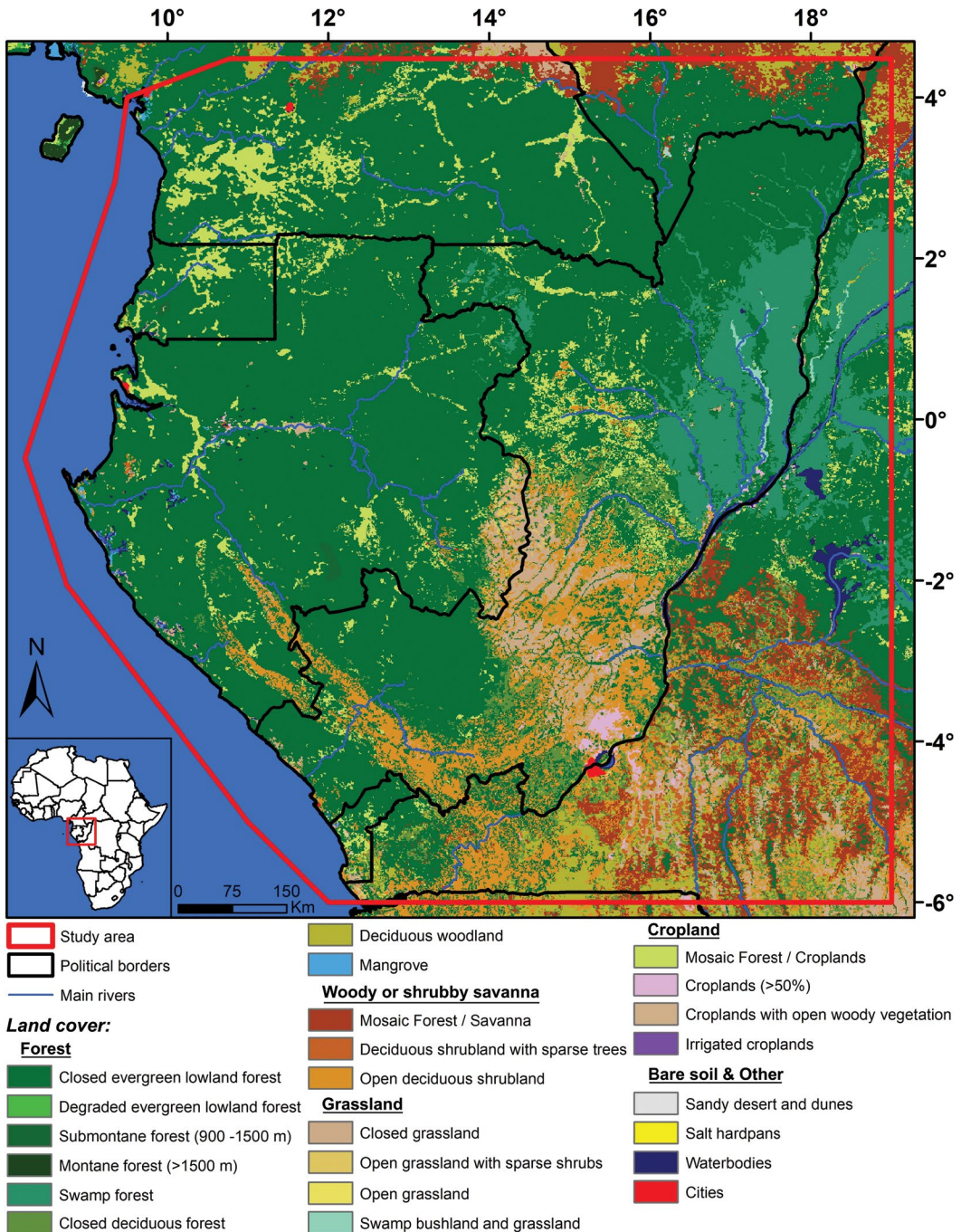


Figure 1. Land cover of the Gabonese Area of Endemism (GAE). The study area, delimited by a red line, encompasses the southern parts of Cameroon and the Central African Republic, Rio Muni (Equatorial Guinea), Gabon, the Republic of the Congo, the western part of the Democratic Republic of the Congo, and the Cabinda region of Angola. Land cover data are adapted from Mayaux et al. (2004).

of Gabonese plant material managed by Naturalis, and other relevant sources, such as the database of Rubiaceae and Orchidaceae endemic to Atlantic Central Africa (Droissart et al., 2011) and the Central African tree plot occurrence database (Dauby et al., 2014b).

- Tropicos® (<<https://tropicos.org/>>), the database of the Missouri Botanical Garden, which comprises 61,901 records from the study area (as of 17 April 2020), including 8562 recent collections made after the completion of RAINBIO.
- The GBIF database (<www.gbif.org>), which contains 249,293 records from the study area (as of 17 April 2020).

Using this compilation, a preliminary list of 2031 restricted-range species occurring in the GAE was established based on georeferenced specimen records. Specialists of the Central Africa flora (see Acknowledgments) then helped to verify and correct this preliminary list. Because the compilation contained many duplicate records, it was subjected to an iterative process of standardization, verification, additions, and correction, according to the following workflow.

1. Nomenclatural standardization and removal of taxonomic ambiguities

Family names for angiosperms were standardized according to the APG IV system (The Angiosperm Phylogeny Group, 2016). Names of specific and infraspecific taxa were generally aligned to the African Plant Database (African Plant Database, 2020) except for a few cases in which another name is published or has been more recently accepted (e.g., *Renzorchis pseudoplatycoryne* Szlach. & Olszewski). To avoid errors due to taxonomic uncertainty, taxa belonging to 10 genera currently under revision (such as *Croton* L. and *Tessmannia* Harms) or in need of a taxonomic revision according to experts (e.g., *Allophylus* L. and *Beilschmiedia* Nees) were not included in the database (see Supplementary Material 2A). A total of 66 additional taxa for which there is current disagreement regarding species delimitation (such as *Noronhia mannii* (Soler.) Hong-Wa & Besnard) or in need of a taxonomic revision or currently under revision (e.g., *Acridocarpus camerunensis* Nied.) were also excluded.

2. Establishment of a comprehensive, accurate list of specimens

The compilation of data from RAINBIO, Tropicos®, and GBIF initially resulted in ca. 14,500 unique records of vascular plant species with restricted ranges in the GAE. While these databases are the largest available, collectively they nevertheless do not include all

records for each restricted-range taxon, so several further steps were undertaken to compile additional information from other sources. First, published references with cited specimens (floras, revisions, monographs, publications of new species, and checklists of various parts of Central Africa) were reviewed for records of restricted-range taxa occurring in the study area, and new records were incorporated into the database. Then ca. 600 new and updated records from the database of the herbarium of the Université Libre de Bruxelles (BRLU) not present in RAINBIO, Tropicos®, and GBIF were added. This was followed by an examination of scans of specimens of the restricted-range taxa available via the online platforms of several herbaria (B, BM, BR, COI, E, HBG, K, L, LISC, MA, P, U, and WAG). Finally, more than 3600 specimens deposited in key European herbaria with significant holdings from the study area (BR, BRLU, P, and WAG) were examined between 2017 and 2019 in order to supplement previously captured information and to verify the identification of doubtful specimens. These steps generated a total of 5333 additional records obtained primarily from (1) historical data that were not captured at key institutions (such as P), (2) recent collections made after the compilation of RAINBIO, not yet incorporated in GBIF, and not present in Tropicos®, and (3) collections listed in the literature but not available in the main European institutions. The 5333 additional records represent 26.8% of the total of 19,876 occurrences of our database.

3. Identification of duplicate records

Because our database initially was compiled from different sources and therefore contained two or more entries for many collections, each individual record was carefully reviewed and duplicates were merged. When duplicate records had different species identifications and/or georeferences, the most accurate or reliable information was retained. When dates were indicated for identifications, the most recent one performed by a taxonomic expert familiar with the group was kept, or if dates were not given, the correct identification was obtained from a taxonomic expert of the group. When discrepancies in geographical coordinates were found, those with the highest level of precision were retained and checked, or when two records had the same level of precision but different coordinates, the locality data were verified using ArcGis® software and/or Google Earth®.

4. Post-facto georeferencing and verification

Georeferencing was done post facto for collections that lack geographical coordinates, provided that the

locality information was sufficiently precise. Coordinates were assigned based on those from other collections made at the same locality, as well as on information from online gazetteers (e.g., <<http://www.geonames.org>>) and Google Earth®. An accuracy code, similar to the one used by RAINBIO (Dauby et al., 2016), was assigned to each newly georeferenced record. Finally, the distribution of each species was mapped and checked using ArcGis® software and Google Earth®.

5. Verification of identifications

Each specimen that had not been identified by a taxonomic specialist (e.g., not cited in a recent flora, monograph, or revision) was tagged in the database as being potentially doubtful. The distribution of these doubtful specimens was then compared with that of reliably identified specimens and any that represented outliers were verified, when possible with input from a taxonomic expert.

6. Defining endemic and subendemic taxa

A taxon was considered endemic to the study area if its known distribution is strictly limited to it (Anderson, 1994). Later in this paper, the term “taxon” or “taxa” refers to species and/or infraspecies (subspecies and variety). A total of 1145 taxa were considered endemic to the GAE, represented by 19,876 occurrence records.

The term subendemic was used by Sosef et al. (2006) in their checklist of Gabonese vascular plants to refer to taxa whose distribution is centered in Gabon but whose range partly exceeds the limits of the country. A taxon is often determined to be subendemic to a particular area based on a threshold for the number of records that must fall within that area, but there does not appear to be a consensus regarding where this threshold should be placed. For example, Sosef et al. (2017) set the limit at 80% of the records, whereas Noroozi et al. (2019) placed it at 90%. In a biologically defined region such as the GAE, where botanical knowledge is insufficient and exploration is very heterogeneous, applying this kind of threshold to define subendemism would lead to inconsistencies because the determination of whether a taxon would qualify is heavily influenced by sampling effort. We therefore prefer to use the term subendemic to refer to a taxon that is present in a particular country (in our case, Gabon) and is restricted to a biogeographical zone specifically designed to study the flora of the country in question (here, the GAE), but whose range extends into one or more other political entities (i.e., countries). A taxon is thus considered subendemic to Gabon if it occurs in Gabon and one or more adjacent countries but

is restricted to the GAE. This definition has the advantage of being independent of both past and future sampling efforts in the region, and it furthermore allows for analyzing and discussing endemism in an explicitly biogeographic framework, i.e., according to the distribution of ecosystems found in a particular area of study.

BIOLOGY AND ECOLOGY OF ENDEMIC PLANTS

Growth form and habitat

The habit and habitat of each taxon endemic to the study area were determined based on the available literature (articles containing species descriptions, flora accounts, etc.), information on specimen labels, and for six species, from the information provided by RAINBIO. Four habit types were recognized: trees (woody, erect plants more than 5 m tall), shrubs (woody, erect plants less than 5 m tall), climbers (both herbaceous and woody), and herbs. These were selected because they were deemed to be the easiest to recognize, including for species whose biology is not well known, which enabled us to assign a habit type of all but one taxon (*Hibiscus elongatifolius* Hochr.). For taxa that express multiple growth forms, the most frequently indicated habit was used. Taxa were also classified according to habitat type: forests (applied to taxa that occur primarily in forested habitats), open areas (mainly present in areas such as lowland savannas and herbaceous inselbergs), and ecotones (mainly present in the forest/savanna transition or with equal frequency in both forests and open habitats). Only 29 taxa lacked any data on habitat type and were therefore not considered in the analyses.

We investigated whether the growth form of endemic taxa is habitat dependent by assessing the association between the habit and the habitat type of taxa by means of a Fisher exact test on 2-way contingency tables under the null hypothesis of no association (Fisher, 1950). Each habit was tested for each habitat against the sum of all other habits and habitats.

Range size distribution

The range size of each taxon was estimated by calculating the area within the convex hull formed by all collection localities. The convex hull is the smallest polygon that contains all occurrences and in which no internal angle exceeds 180°. Because the extent of occurrence (EOO) used for assessing the risk of extinction based on the Categories and Criteria of the IUCN Red List (IUCN, 2012) is also based on a convex hull, we used the function ‘EOO.computing’ and the parameter ‘method.less.than3’=“arbitrary” from the ConR R package (Dauby et al., 2017). An arbitrary minimum

range size of 1 km² was assigned for the 176 taxa (15% of the total) that are known from a single georeferenced specimen or for which the estimated EOO was less than 1 km².

We then investigated whether there were any differences in range size among taxa exhibiting different growth forms by testing pairwise differences of range size between each of the four habits using a Wilcoxon rank-sum test under the null hypothesis of no difference. To control for type I errors, the false discovery rate (FDR) was maintained below 5% by applying the “fdr” *P* value-adjusted method within the Wilcoxon test.

DETERMINANTS OF THE RATE OF ENDEMISM AT THE REGIONAL SCALE

To assess the relative prevalence of endemic taxa in the regional flora among higher-level taxonomic groups (orders, families, and genera) and growth forms, a plant database of the GAE was compiled that encompassed unverified records from the RAINBIO database, recent collection records from Tropicos®, and data for other collections of taxa endemic to the study area. This database comprises 219,731 georeferenced specimens and documents the botanical sampling effort in the GAE (Supplementary Material 3).

Taxonomy

We investigated whether the proportions of endemic taxa varied among orders, families, and genera. We tested the null hypothesis that the proportion of endemics in a particular group does not differ from the proportion in all other groups by using Fisher exact tests on 2-way contingency tables (Fisher, 1950). Each order, family, and genus containing at least 20 taxa present in the study area was tested against the sum of all other groups at the same rank. Genera and families primarily comprising taxa in genera currently under study or in need of a taxonomic revision were not considered (Supplementary Material 2B).

Growth form

We also investigated whether the prevalence of endemic taxa varies among growth forms. For this, we tested the null hypothesis that the proportion of endemic taxa within a growth form category does not differ from the proportion of endemic taxa exhibiting all other growth forms by using Fisher exact tests on 2-way contingency tables (Fisher, 1950). Taxa considered as a “vine” and “climber” in the RAINBIO database were treated as climbers, “myco-heterotrophs” and “aquatics” were considered as herbs, and “epiphyte” and

“parasitic” were classified either as trees, shrubs, herbs, or climbers depending on the characteristics of the taxon. Within the GAE, the “epiphytic” habit is found mainly in members of the family Orchidaceae (26 endemic taxa) and some members of the families Acanthaceae, Balsaminaceae, Begoniaceae, and Hymenophyllaceae, representing 34 endemic taxa in total (3% of the flora endemic to the GAE), and was therefore not regarded as relevant for analysis. Taxa for which the habit was not specified in RAINBIO were not included in the analysis.

RESULTS

BIOLOGY AND ECOLOGY OF ENDEMIC PLANTS

A total of 1145 taxa (1093 species, 37 subspecies, and 15 varieties) are considered endemic to the GAE (Fig. 1), represented by 19,876 occurrence records, 13,887 (70%) of which are from Gabon. A total of 915 (80%) of these endemic taxa are recorded from Gabon (875 species, 27 subspecies, and 13 varieties), whereas the remainder occur in one or more adjacent countries. On average, each endemic taxon is known from 17 occurrences (median = 8, max = 700), but 124 (10.8%) are represented by a single occurrence, 633 (55.3%) by fewer than 10 occurrences, and only 161 (14.1%) by more than 30 occurrences (Fig. 2A).

These taxa belong to 93 families and 388 genera. Nearly a third of the endemic taxa belong to just two families, Rubiaceae (20.3%) and Fabaceae (11.9%), and the genus *Psychotria* L. (Rubiaceae) alone represents 6.5% of the endemic taxa. Of the 388 genera, 21 have more than 10 endemic taxa, which together comprise 34.5% of all endemics, whereas 210 genera have just a single endemic taxon. The most endemic-rich families and genera are presented in Figures 3 and 4. There are 26 genera endemic to the GAE, which collectively comprise 38 species (3.3%), and 19 of these genera are monotypic (Table 1).

Shrubs are the most frequently represented habit, comprising 34.6% of the endemic taxa, followed by trees (26.1%), herbs (20.5%), and climbers (18.7%) (Fig. 2B, Table 2). Endemic shrubs mainly belong to Rubiaceae (41.6% of all shrubby taxa) and Violaceae (7.1%), and in particular to their largest respective genera, *Psychotria* (18.4%) and *Rinorea* Aubl. (6.8%). Endemic tree taxa mainly belong to Fabaceae s.l. (31.8%), in particular to the genus *Gilbertiodendron* J. Léonard (5.7%), whereas most endemic herbs belong to Orchidaceae (15.3%), Begoniaceae (14.9%), Podostemaceae (9.3%), and Cyperaceae (8.9%). Some families that contain numerous endemic herbs are represented by a single highly diverse and endemic-rich genus, such as *Begonia* L. (Begoniaceae) and *Impatiens*

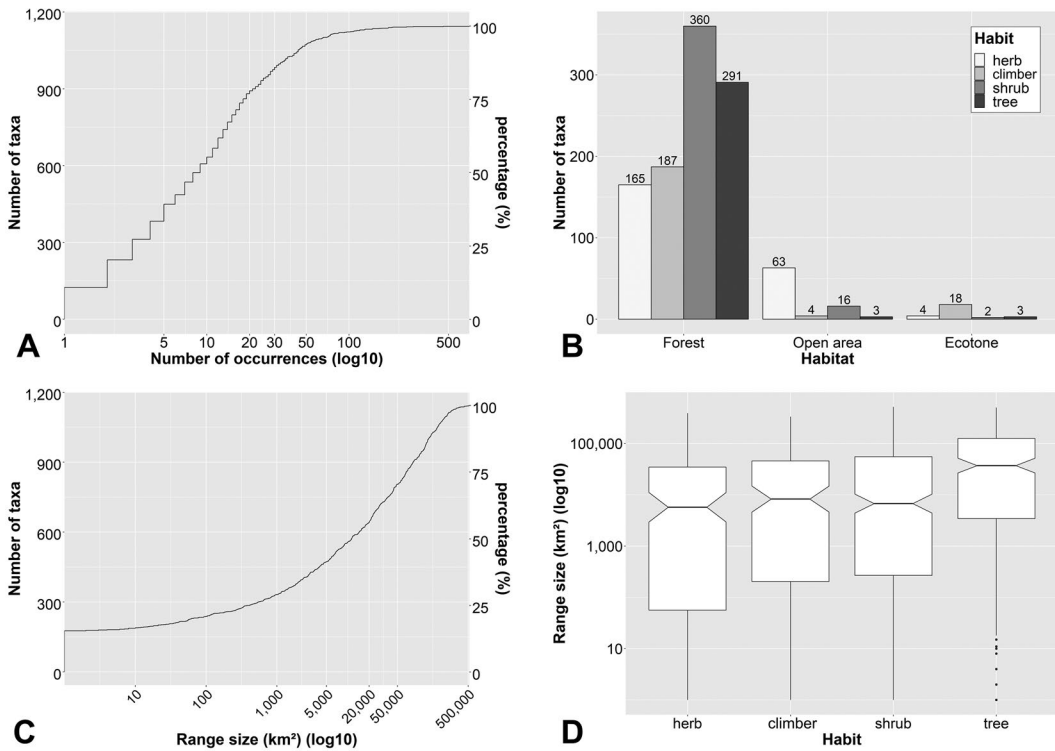


Figure 2. General characteristics of taxa endemic to the study area. —A. Number of occurrences known per endemic taxon (cumulative values). —B. Number of endemic taxa per habitat type and per growth form types within each habitat. —C. Range size per endemic taxon (cumulative values). The thresholds for considering a species as potentially threatened with extinction according to IUCN Red List subcritereon B1 (IUCN, 2012) [EEO < 100 km² (Critically Endangered), < 5000 km² (Endangered), and < 20,000 km² (Vulnerable)], and for considering a species as range restricted and therefore as a Critical Habitat trigger under Performance Standard 6 of the International Finance Corporation (2019) [EEO < 50,000 km²], are indicated to visualize the potential conservation importance of the taxa. —D. Range size distribution of endemic taxa per habit type. The black line inside each boxplot represents the median of the range sizes. A confidence interval around the median is shown in the form of notches. If the confidence intervals of two boxes do not overlap, this suggests that the medians are significantly different (Wickham, 2016).

L. (Balsaminaceae). Other families contain several genera, only one or two of which are notably diverse and endemic-rich, e.g., *Mapania* Aubl. (Cyperaceae), *Palisota* Rechb. ex Endl. (Commelinaceae), and two genera of Podostemaceae, *Inversodicraea* Engl. and *Ledermanniella* Engl., whereas endemic Orchidaceae belong to numerous genera. Endemic climbers are more evenly distributed among the families in which this habit is represented, although many belong to Rubiaceae (17.3%), Fabaceae (12.6%), and Dichapetalaceae (11.2%), along with the genera *Sabicea* Aubl. (11.7%), *Dichapetalum* Thouars (11.2%), and *Combretum* Loeffl. (7.9%) (Fig. 4).

The vast majority of endemic taxa are found in forests (87.6%), far greater than in open areas (7.5%) and along ecotones (2.4%) (Fig. 2B). Podostemaceae, represented only by herbaceous riverine species growing

in waterfalls and rapids, have the largest number of nonforest endemics, with 24 of the 113 taxa (21.2%). The genus *Sabicea* is well represented along ecotones, with 11 taxa that mostly occur in this habitat, representing 40.7% of the total (27 taxa). Regarding the proportion of the four habit types represented in these three habitats, trees and shrubs are, by definition, overrepresented within forests, whereas herbs are overrepresented within open areas and underrepresented in forests, and climbers are overrepresented along ecotones (all P values < 0.001, Fisher exact test). Moreover, climbers are underrepresented in open areas, and shrubs are underrepresented in both open areas and ecotones (P values < 0.01; Supplementary Material 4).

A comparison of range size distributions shows that 56% of the endemic taxa occur in an area of less than

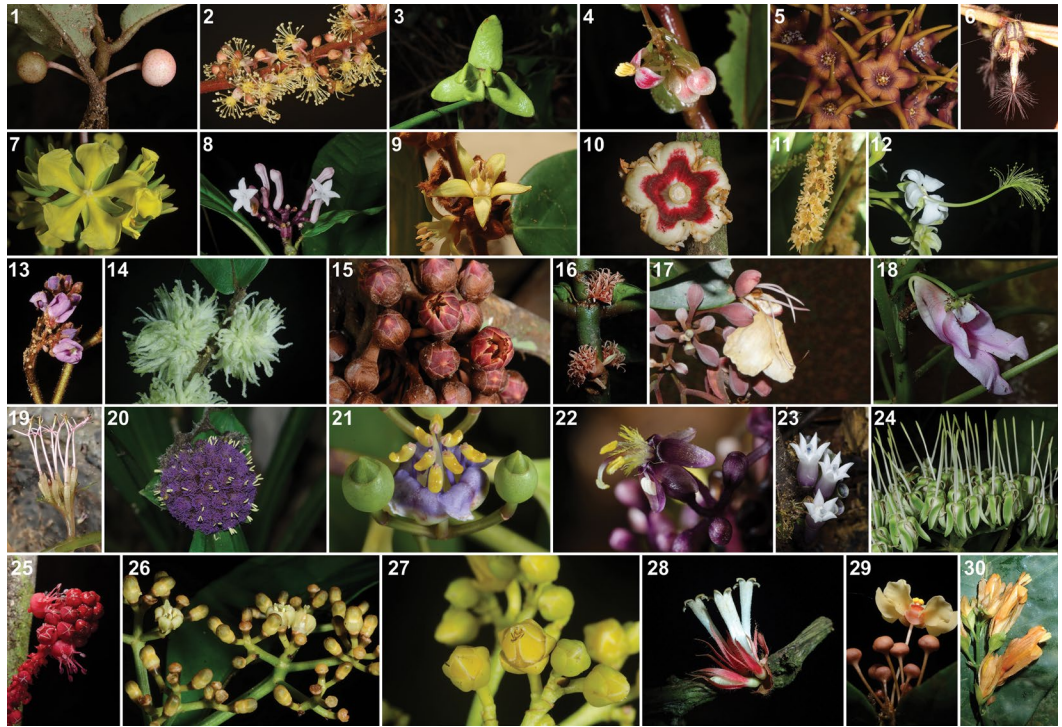


Figure 3. Representatives of the 20 most endemic-rich families and genera in the study area. 1. *Ardisia sadebeckiana* Gilg (Primulaceae); 2. *Argomuellera sessilifolia* Prain (Euphorbiaceae); 3. *Artabotrys crassipetalus* Pellegr. (Annonaceae); 4. *Begonia auriculata* Hook. f. (Begoniaceae); 5. *Brachystelma letestui* Pellegr. (Apocynaceae); 6. *Bullbophyllum pauwelsianum* Stévant & Droissart (Orchidaceae); 7. *Campylosperrum glaucifolium* Biss. (Ochnaceae); 8. *Chassalia ichibangensis* Pellegr. (Rubiaceae); 9. *Cleistanthus bambidianus* Breteler (Phyllanthaceae); 10. *Cola tsandensis* Pellegr. (Malvaceae); 11. *Combretum rupestre* Jongkind & Texier (Combretaceae); 12. *Dactyladenia pallescens* (Baill.) Prance & F. White (Chrysobalanaceae); 13. *Dalbergia fouilloiana* Pellegr. (Fabaceae); 14. *Dichapetalum leucocarpum* Breteler (Dichapetalaceae); 15. *Englerophytum gigantifolium* O. Lachenaud & L. Gaut. (Sapotaceae); 16. *Eumachia letouzeyi* (Robbr.) Razafim. & C. M. Taylor (Rubiaceae); 17. *Gilbertiodendron uninjugum* (Pellegr.) J. Léonard (Fabaceae); 18. *Impatiens mackeyana* Hook. f. subsp. *clari* (N. Hallé) Grey-Wilson (Balsaminaceae); 19. *Ledermanniella nicolasii* C. Cusset (Podostemaceae); 20. *Mapania purpuriceps* (C. B. Clarke) J. Raynal (Cyperaceae); 21. *Memecylon diluviorum* Exell (Melastomataceae); 22. *Palisota alboanthera* Burg & E. Bidault (Commelinaceae); 23. *Pauridiantha cauliflora* (R. D. Good) Smedmark & B. Bremer (Rubiaceae); 24. *Pavetta puberula* Hiern (Rubiaceae); 25. *Placodiscus resendeanus* Exell & Mendonça (Sapindaceae); 26. *Psychotria breteleri* O. Lachenaud (Rubiaceae); 27. *Rinorea verrucosa* Chipp (Violaceae); 28. *Sabicea desseini* Zemagho, O. Lachenaud & Sonké (Rubiaceae); 29. *Salacia diplasia* N. Hallé (Celastraceae); 30. *Whitfieldia rutilans* Heine (Acanthaceae). Photograph credits: Ehoam Bidault (1, 4, 5, 7, 8, 10, 12–15, 20–27, 29), Gilles Dauby (17), Tariq Stévant (2, 6), and Nicolas Texier (3, 9, 11, 16, 18, 19, 28, 30).

20,000 km² and that 21% are very narrowly distributed, with a total recorded range of less than 100 km². Only 30% of the endemic taxa have an EOO exceeding 50,000 km² (Fig. 2C). However, some species with a large EOO have in fact discontinuous distributions and only occur in a small portion of their overall range (e.g., *Combretum robustum* Jongkind, *Massularia stewartiana* Sonké, E. Bidault & Droissart, *Xylopia paniculata* Exell, *Palisota fadenii* Burg & E. Bidault, and *Ledermanniella pusilla* (Warm.) C. Cusset). Trees have on average significantly larger ranges than taxa in the three other habit types, with a median range size of 38,135 km² versus less than 8500 km² for shrubs,

climbers, and herbs (*P* values < 0.001, Wilcoxon rank-sum test; Fig. 2D).

DETERMINANTS OF THE RATE OF ENDEMISM AT THE REGIONAL SCALE

The strict rate of endemism within the GAE is 13.4% (1145 endemic taxa among 8513 species and infraspecific taxa) and 7.3% within Gabon (369 endemic species among the 5039 published species currently known to occur in the country; but see discussion below). We estimate that 875 species are endemic and subendemic to Gabon, representing 17.4% of the country's flora.

Taxon	Total number of species in the study area	Number (% of species endemic to study area)	Result of Fisher exact test for proportion of endemics in regional flora	Number of endemics present in Gabon	Mean range size of endemics (km ²)	Proportion of growth form among endemics	Proportion of habitat among endemics
Acanthaceae	225	22 (9.8)	n.s.	18	42968		
Annonaceae*	146	40 (27.4)	excess	36	67632		
Apocynaceae*	259	32 (12.4)	n.s.	29	74340		
Balsaminaceae†	32	10 (31.2)	excess	9	23356		
<i>Impatiens</i>	32	10 (31.2)	n.s.	9	23356		
Begoniaceae	102	34 (33.3)	excess	28	35820		
<i>Begonia</i>	102	34 (33.3)	excess	28	35820		
Burseraceae†	20	10 (50)	excess	10	225064		
Celastraceae	172	20 (11.6)	n.s.	17	37415		
<i>Salacia</i>	107	14 (13.1)	n.s.	12	46239		
Chrysobalanaceae†	53	12 (22.6)	n.s.	11	45500		
<i>Dactyladenia</i>	23	10 (43.5)	excess	9	48223		
Combretaceae	84	17 (20.2)	n.s.	17	38828		
<i>Combretum</i>	70	17 (24.3)	n.s.	17	38828		
Commelinaceae	89	14 (15.7)	n.s.	10	59411		
<i>Palisota</i>	22	10 (45.5)	excess	9	56838		
Cyperaceae	282	20 (7.1)	deficit	18	54663		
<i>Mapania</i>	35	13 (37.1)	excess	13	84324		
Dichapetalaceae	90	31 (34.4)	excess	29	42737		
<i>Dichapetalum</i>	82	25 (30.5)	excess	24	45518		
Euphorbiaceae*	183	18 (9.8)	n.s.	14	61832		
Fabaceae*	885	133 (15)	n.s.	121	62652		
<i>Dalbergia</i>	44	12 (27.3)	n.s.	12	40538		
<i>Gilbertiodendron</i>	27	18 (66.7)	excess	16	66059		
Malvaceae*	225	35 (15.6)	n.s.	23	23245		
<i>Cola</i>	65	12 (18.5)	n.s.	10	38025		
Melastomataceae	146	41 (28.1)	excess	29	43448		
<i>Memecylon</i>	33	14 (42.4)	excess	9	61746		
Ochnaceae	66	12 (18.2)	n.s.	11	73305		
<i>Campylospermum</i>	43	12 (27.9)	n.s.	9	59109		
Orchidaceae	489	36 (7.4)	deficit	30	27247		
Phyllanthaceae	139	13 (9.4)	n.s.	9	55342		
Podostemaceae	42	22 (52.4)	excess	15	24063		
<i>Ledermanniella</i> †	21	8 (38.1)	excess	7	60311		
Primulaceae†	35	12 (34.3)	excess	8	27207		
<i>Ardisia</i>	28	12 (42.9)	excess	8	27207		
Rhizophoraceae†	21	9 (42.9)	excess	7	11026		
Rubiaceae	1217	229 (18.8)	excess	178	53411		
<i>Chassalia</i>	37	10 (27)	n.s.	7	80710		
<i>Eumachia</i>	40	10 (25)	n.s.	9	87240		
<i>Pauridiantha</i>	34	14 (41.2)	excess	13	59256		
<i>Pavetta</i>	65	11 (16.9)	n.s.	8	88538		
<i>Psychotria</i>	208	74 (35.6)	excess	51	39298		
<i>Sabicea</i>	79	29 (36.7)	excess	27	44147		
Sapindaceae*	94	14 (14.9)	n.s.	12	61815		
Sapotaceae*	101	24 (23.8)	excess	23	45393		
Violaceae	100	34 (34)	excess	19	29766		
<i>Rinorea</i>	91	31 (34.1)	excess	17	27944		

Figure 4. Characteristics of endemism within the most endemic-rich families and genera in the study area and those with a significantly greater proportion of endemic taxa compared to all other families or genera, respectively (Fisher exact test). An asterisk (*) indicates families in which some genera were excluded from the analyses (see Material and Methods section and Supplementary Material 2). A dagger (†) indicates a family or genus that has a significantly greater proportion of endemic taxa compared to the regional flora but is not among the 20 most endemic-rich families or genera of the study area. Growth form and habitat are depicted by colors: herb (light green), shrub (yellow), climber (purple), tree (brown), forest (dark green), open area (orange), ecotone (blue). n.s.: not significant.

Table 1. Genera endemic to the study area and their number of species.

Endemic genera	Number of species
Annonaceae	
<i>Letestudoxa</i> Pellegr.	3
<i>Pseudartabotrys</i> Pellegr.	1
<i>Sirdavidia</i> Couvreur & Sauquet	1
Apocynaceae	
<i>Crioceras</i> Pierre	1
Burseraceae	
<i>Aucoumea</i> Pierre	1
Erythroxylaceae	
<i>Pinacopodium</i> Exell & Mendonça	1
Euphorbiaceae	
<i>Afrotrewia</i> Pax & K. Hoffm.	1
<i>Aubletiana</i> J. Murillo	2
Fabaceae	
<i>Augouardia</i> Pellegr.	1
<i>Gabonius</i> Mackinder & Wieringa	1
<i>Librevillea</i> Hoyle	1
<i>Neochevalierodendron</i> J. Léonard	1
<i>Oddoniodendron</i> De Wild.	6
<i>Sindoropsis</i> J. Léonard	1
Menispermaceae	
<i>Dialythea</i> Exell & Mendonça	1
<i>Sarcophilium</i> Troupin	1
Ochnaceae	
<i>Testulea</i> Pellegr.	1
Orchidaceae	
<i>Halleorchis</i> Szlach. & Olszewski	1
<i>Veyretella</i> Szlach. & Olszewski	2
Passifloraceae	
<i>Paropsiopsis</i> Engl.	2
Rubiaceae	
<i>Temnopteryx</i> Hook. f.	1
Salicaceae	
<i>Mocquersia</i> Hua	2
<i>Trichostephanus</i> Gilg	2
Sapindaceae	
<i>Pseudopancovia</i> Pellegr.	1
Sapotaceae	
<i>Letestua</i> Lecomte	1
Simaroubaceae	
<i>Iridosma</i> Aubrév. & Pellegr.	1

Fisher exact tests revealed that endemic taxa are not randomly distributed among higher-level taxa (Fig. 5). Among orders, Cucurbitales, Ericales, Gentianales, Malpighiales, and Myrtales are overrepresented by endemic taxa (17% to 22%) compared to an average value of 11%, whereas Asparagales, Asterales, Caryophyllales, Lamiales, Poales, Polypodiales, and Rosales exhibit a highly significant deficit in endemic taxa compared to the other orders represented within the study area, with 0% to 8% of their taxa being endemic (P values < 0.001; Fig. 5A, Supplementary Material 5).

Table 2. Association between the rate of endemism and growth forms within the regional flora. The last two columns indicate the percentage of taxa of each growth form that are endemic to the study area and the associated P value from a Fisher exact test on 2-way contingency tables; statistically significant results are in bold (P value < 0.05). Only taxa for which a growth form has been identified are considered.

Habit	Total number of taxa	Total number of endemic taxa	% of taxa endemic	P value
Shrub	1794	396	22.1	9.5E-27
Tree	1957	299	15.3	0.06
Liana	1451	214	14.8	0.34
Herb	2992	235	7.8	5.0E-36
Total	8194	1144	14	

Endemism at the family level varies from 0% to 52%, with a mean value of 13.8%. Twelve families present a significantly greater proportion of endemic taxa compared to all other families, in particular Podostemaceae (52%), Burseraceae (50%), and Rhizophoraceae (43%), along with several families containing one or two large genera that are particularly diverse within the region, such as Dichapetalaceae (*Dichapetalum*), Primulaceae (*Ardisia* Sw.), Rubiaceae (*Psychotria* and *Sabicea*), Sapotaceae (*Englerophytum* K. Krause and *Synsepalum* (A. DC.) Daniell), and Violaceae (*Rinorea*) (Figs. 4, 5B, Supplementary Material 5). The families with the highest proportion of endemic taxa are generally moderately rich in species and are often characterized by taxa that occur only in narrowly restricted habitats, such as Podostemaceae, whose members grow exclusively on rocks in rapids and waterfalls, as well as Balsaminaceae (*Impatiens*) and Begoniaceae, whose species preferentially occur in hyper-humid habitats, particularly in submontane vegetation. Conversely, 12 families have a significantly lower proportion of endemic taxa (Fig. 5B, Supplementary Material 5), including several that are very rich in species in the study area (e.g., Cyperaceae, Orchidaceae, and Poaceae; Fig. 5B, Supplementary Material 5).

At the level of genus, rates of endemism vary from 0% to 67%, with a mean value of 17%. Thirteen genera have significantly more endemics than the mean, including *Ardisia*, *Dactyladenia* Welw., *Gilbertiodendron*, *Memecylon* L., and *Palisota*, more than 40% of whose members are endemic to the GAE, while 19 genera have a significantly smaller proportion of endemics, such as *Bulbophyllum* Thouars (4.9%) and *Cyperus* L. (1.6%) (Figs. 4, 5C, Supplementary Material 5). It is noteworthy that only 11 of the 77 genera represented by 20 or more taxa contain no endemics. Most are monocotyledons (*Bulbostylis* Kunth, *Chlorophytum* Ker

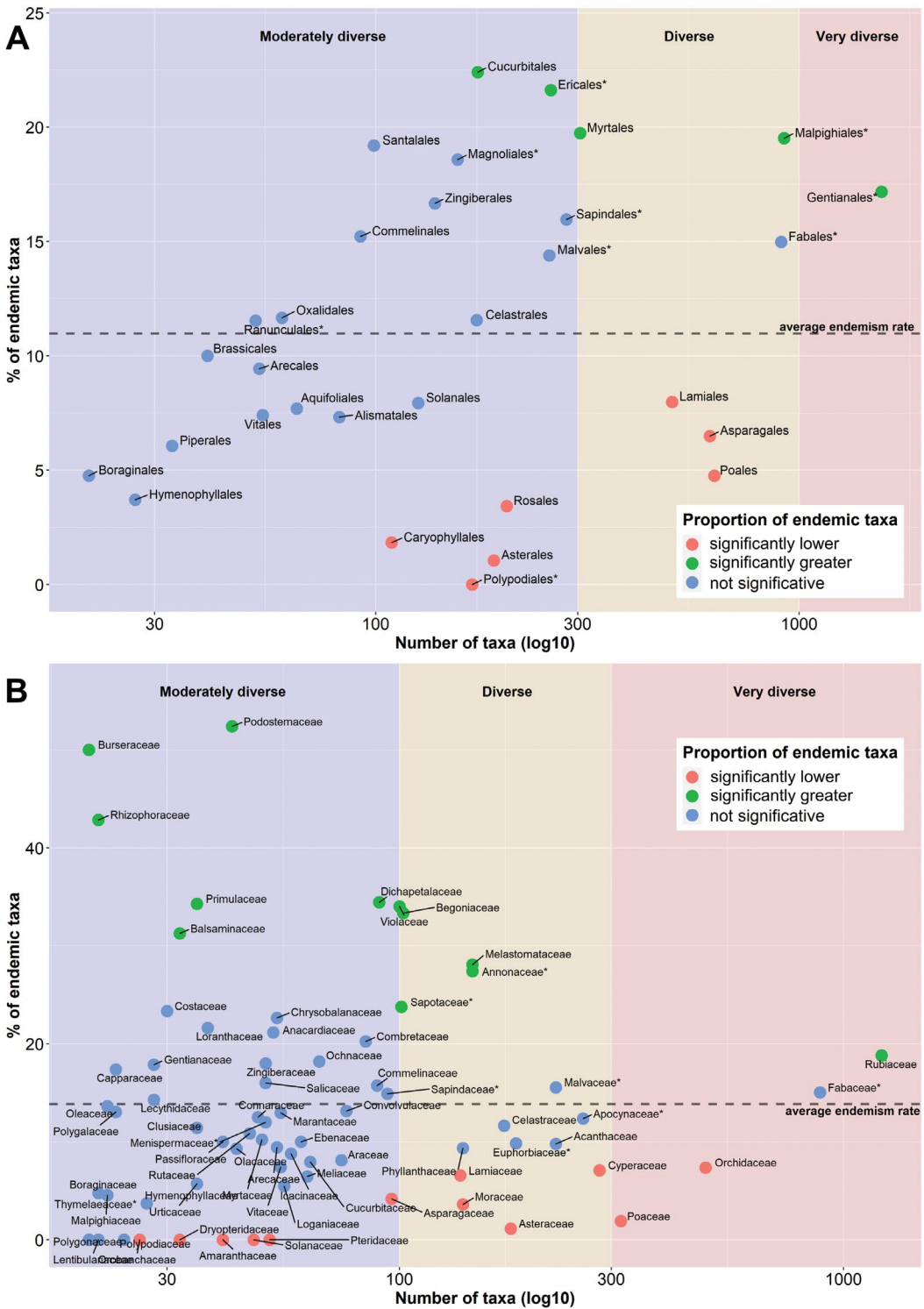


Figure 5A, B. Species richness and proportion of endemic taxa among orders (A) and families (B) represented by at least 20 species in the study area. Each taxon is plotted according to its species richness (x-axis) and proportion of species endemic to the study area (y-axis). An asterisk (*) indicates that some of their constituent taxa were excluded from the analyses (see Material and Methods section and Supplementary Material 2B). The color of each point reflects the result of a Fisher exact test

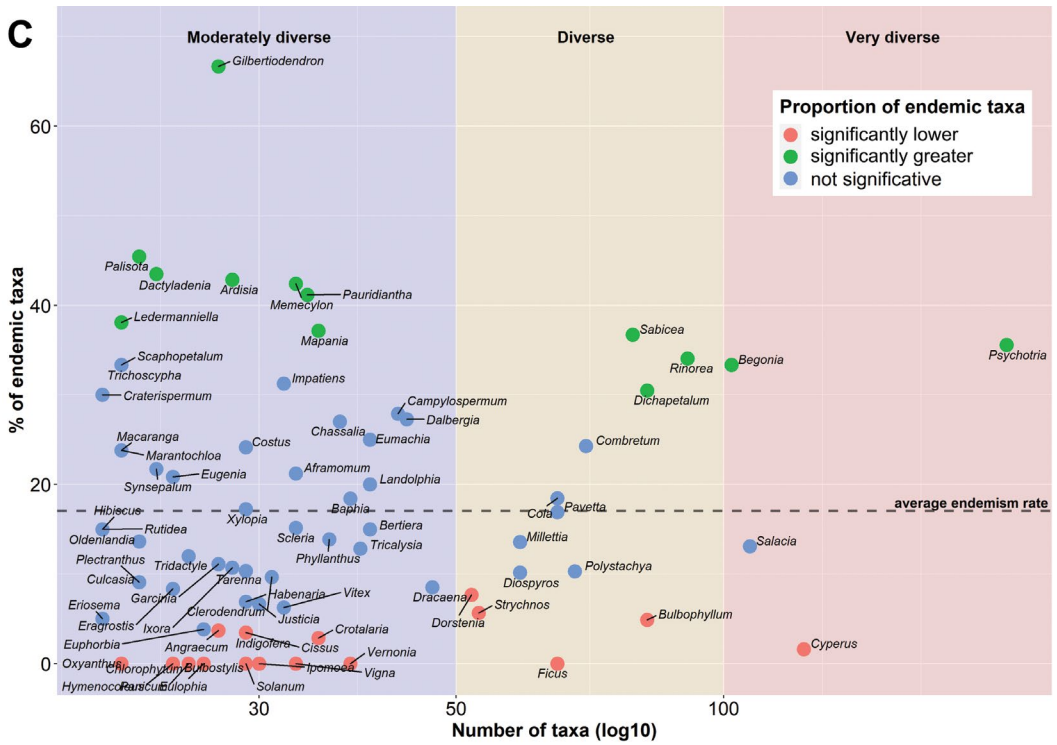


Figure 5C. Species richness and proportion of endemic taxa among genera (C) represented by at least 20 species in the study area. Each taxon is plotted according to its species richness (x-axis) and proportion of species endemic to the study area (y-axis). The color of each point reflects the result of a Fisher exact test to assess whether the proportion of endemics in a given taxon (order, family, or genus) is statistically different from that for endemics in all other taxa. Taxa with a significantly lower proportion of endemics are depicted in red, those with a significantly higher proportion in green, and those for which the Fisher exact test indicates a difference that is not statistically significant are depicted in blue. The horizontal dashed line represents the average rate of endemism for all taxa. The background of the plot has been divided into three different colors to distinguish between taxa (orders, families, and genera) that are moderately rich (blue), rich (orange), and very rich (red) in species.

Gawl., *Eulophia* R. Br., and *Panicum* L.) and/or occur in open areas or along forest edges (*Ipomoea* L., *Solanum* L., *Vernonia* Schreb., and *Vigna* Savi).

Regarding habit, endemic taxa are overrepresented among shrubs and underrepresented among herbs (*P* values < 0.001, Fisher exact tests; Fig. 4).

DISCUSSION

NEW ESTIMATES OF RATES OF ENDEMISM

A total of 13.4% of the taxa occurring in the portion of WCA studied here are endemic to this area, a rate

that is much lower than the recently published estimate of 24.2% endemism for Lower Guinea as a whole (Droissart et al., 2018). However, the spatial extent of our study area differs in two important ways from that considered by Droissart et al. (2018). First, we included areas regarded as transition zones between the Lower Guinea and Congolia bioregions (i.e., the southern part of the Central African Republic, the Republic of the Congo, and the western part of the Democratic Republic of the Congo), whose rate of endemism is lower and which contain species not present in Lower Guinea (Droissart et al., 2018). Second, the Lower Guinea bioregion partly includes the Cameroon Volcanic Line

←
to assess whether the proportion of endemics in a given taxon (order, family, or genus) is statistically different from that for endemics in all other taxa. Taxa with a significantly lower proportion of endemics are depicted in red, those with a significantly higher proportion in green, and those for which the Fisher exact test indicates a difference that is not statistically significant are depicted in blue. The horizontal dashed line represents the average rate of endemism for all taxa. The background of the plot has been divided into three different colors to distinguish between taxa (orders, families, and genera) that are moderately rich (blue), rich (orange), and very rich (red) in species.

(CVL), in particular the Mount Cameroon area, whose rate of endemism is known to be very high (Gehrke & Linder, 2014; Lachenaud, 2019) and which shares numerous taxa endemic to Lower Guinea with our study area. Moreover, the species-level diversity indicated by Droissart et al. (2018) for Lower Guinea is probably underestimated because a significant number of occurrences were either recently recorded or have not yet been added to key databases and are thus not in RAINBIO (ca. 27% of our database was not included in RAINBIO). Finally, several families and genera had to be excluded from our analyses because they require taxonomic revision and contain many species that are difficult to distinguish, a high proportion of which may have restricted distributions (e.g., Bidault & van der Burg, 2019). Their inclusion would likely result in a slight increase in both the number of endemic taxa and the rate of endemism. It is worth noting that the rate of endemism we report for the GAE (13.4%) is actually much lower than it would have been if our calculation had been based solely on the data in RAINBIO without verification (19.7%), confirming the value of carefully compiling a comprehensive and verified database. Comparison of the rate of endemism of vascular plants in the region with other groups of organisms is difficult, either due to insufficient knowledge (e.g., bryophytes; Patiño & Vanderpoorten, 2018) or a total lack thereof (e.g., insects). Groups of larger animals have lower rates of endemism, e.g., only seven species of birds are endemic to the region, representing ca. 1% of the total avifauna (BirdLife International, 2021a, 2021b; <<http://datazone.birdlife.org>>), and about 7% of large mammals are endemic to the Lower Guinea and Congo-Gabon centers of endemism taken together (Turpie & Crowe, 1994). Lower endemism among these animal groups is likely due to their greater capacity for migration within the Guineo-Congolian forests compared to plants.

Our database provides the most up-to-date and comprehensive source of information for assessing the endemism rate among plants in Gabon. Brennan (1978) was the first to attempt a calculation, estimating that 18% of the flora was restricted to the country based on data in the first 23 volumes of *Flore du Gabon*. Subsequently, Sosef et al. (2006) listed 508 taxa they considered endemic to the country, 10.8% of the 4710 taxa reported in their checklist of Gabonese vascular plants. More recently, Lachenaud et al. (2018) took into consideration unpublished species and used several unverified lists of specimens to estimate that ca. 650 (12.6%) of the 5175 species in Gabon are endemic. Using our current count of 5039 published species in Gabon and our updated list of the country's endemics (Texier et al., 2021), and factoring in taxa excluded from our analyses as well as several recently published new species (Lachenaud et al., 2020a, 2020b), we ob-

tain a total of 396 species that are strictly endemic to Gabon, for a rate of endemism of 7.9% (excluding infraspecific taxa). This notable reduction in the estimated rate of endemism in Gabon can largely be attributed to increased information on the occurrence of taxa in adjacent countries, in particular in the Republic of the Congo and Equatorial Guinea, many parts of which have habitats similar to those in Gabon, including some that are poorly sampled (Lachenaud, 2009; Sosef et al., 2017; Supplementary Material 3), and also to revisions of taxonomic concepts (Texier et al., 2021) that have led to extensions of the known distribution of several species. On the other hand, we have shown that 875 species are endemic to the GAE, i.e., a rate of endemism of 17.4% for Gabon if we consider taxa that are subendemic to the country. This rate of endemism for the GAE should remain fairly stable in the future as it is only weakly dependent on the sampling effort in the countries adjacent to Gabon. Moreover, it is more meaningful than calculations of strict country-level endemism since it concerns a biologically coherent area rather than an arbitrarily delimited political entity.

OVERREPRESENTATION OF ENDEMICS AMONG SHRUBS AND UNDERREPRESENTATION AMONG HERBS

In the GAE, the most species-rich taxonomic groups are also the most endemic rich, a pattern commonly documented for plants (Beard et al., 2000). More than 87% of endemic taxa grow in forest habitats, which are by far dominant in the study region, covering more than 85% of the area (Fig. 1; Mayaux et al., 2004). It logically follows that the overall distribution of endemics among the four habit types (Fig. 2B) largely reflects their distribution among forest taxa (Supplementary Material 4), with a dominance of shrubs (34.6%) followed by trees (26.1%), a result that is consistent with the findings of Droissart et al. (2018) for Lower Guinea. However, only shrubs exhibit a significant overrepresentation of endemic taxa (P value < 0.001, Fisher exact test; Fig. 4). This could be explained in part by the fact that shrubby species are adapted to all habitat types occurring in the region (Sosef et al., 2017), which could account for the fact that open habitats have five times more endemic shrub species than trees (Fig. 2B). Moreover, trees typically have significantly larger geographic ranges than shrubs, herbs, and climbers (Fig. 2D). The larger average extent of occurrence of tree species may be related to their fruits being borne higher above the ground, favoring dispersal over greater distances (van der Burgt, 1997) or to the fact that they may have fleshy fruits (White, 1994) that are eaten and dispersed by large mammals such as elephants or great apes (Haurez et al., 2015, 2018) over large distances (Corlett, 2009). Species that reach the canopy, such as

tall trees and the largest climbers (e.g., *Acridocarpus* Guill. & Perr., some lianescent species of *Dalbergia* L. f.) are also regularly dispersed by canopy birds or wind over great distances (Clark et al., 2001; Corlett, 2009). It is worth noting that the tree genus with the highest rate of endemism, *Gilbertiodendron*, is characterized by heavy seeds that disperse by gravity over short distances (barochory). Because wind dispersal is likely infrequent in the understory of closed-canopy equatorial rainforests, other agents are favored that result in dispersal over shorter distances than wind or large mammals (Corlett, 2009). Also, although many shrub species are dispersed by fruit-eating birds, the average distance over which they transport diaspores is shorter than for bird species that disseminate the fruits and seeds of canopy trees (Corlett, 2009; Wotton & Kelly, 2012). It should also be noted that it is more difficult for botanists to access the flowers and fruits of trees that reach the upper stratum and these taxa are therefore less often collected, which explains why the species-level taxonomy of some groups remains uncertain (e.g., Ewédjè et al., 2020). The advent of phylogenetic methods has led to the breakup of some tree species that were previously regarded as having wide distributions but are now recognized as several distinct species, including some that are endemic to our study area (Lissambou et al., 2018; Ikabanga et al., 2019), although this taxonomic bias is not exclusive to tree species (Supplementary Material 2).

By contrast, herbaceous taxa endemic to the GAE are significantly underrepresented in forests (16.5%; Supplementary Material 4), reflecting the low proportion of herbs in these ecosystems in tropical Africa (Sosef et al., 2017) and the fact that endemic taxa are not a taxonomically random assemblage (Supplementary Material 5). Indeed, the most species-rich orders and families of monocotyledons (i.e., Poales, Asparagales and their respective families Cyperaceae, Poaceae, and Orchidaceae) and dicotyledonous families that mainly comprise herbs (e.g., Asteraceae) have proportions of endemic taxa that are significantly below the average for the regional flora (Fig. 5B). These terrestrial and epiphytic herbaceous groups are, in fact, particularly rich in endemic taxa that occur in open areas and/or high mountains (Droissart, 2009; Gehrke & Linder, 2014; Droissart et al., 2018), two habitats that are poorly represented in our study area. Orchidaceae, although very speciose and comprising numerous endemics in Lower Guinean forests (Droissart, 2009), include many species that also occur north of the Sanaga River and/or in the islands of the Gulf of Guinea, both of which lie outside the area of study. Most herbaceous species present in open areas are probably commonly dispersed by wind over great distances (Corlett, 2009), resulting in a low rate of endemism.

As a consequence, 71% of the herbaceous species endemic to the GAE are primarily found in forest habitats. The processes of diversification and endemism in this region are often considered to be related in large part to the contraction and expansion of forest cover associated with glacial and interglacial periods, and to the persistence of forest refugia during the drier and cooler periods, which are thought to have acted as cradles and museums of forest species diversity (Maley, 1996; Plana, 2004; Dagallier et al., 2020), in particular for shrub and tree species (but see Sosef, 1994; Janssens et al., 2010). The rarity of endemic herbs in forests could also partly be explained by the very low levels of sunlight received at ground level in closed-canopy, lowland terra firme forest, which usually requires that herbs wait in a vegetative state until a gap opens in the canopy (Chazdon, 1988), which in turn leads to a low rate of speciation, although there may be exceptions, for example, in the genera *Begonia* (Sosef, 1994), *Impatiens* (Janssens et al., 2015), *Mapania* (Lye, 2014), and *Palisota* (Bidault & van der Burg, 2019). Most endemic herbaceous forest taxa occur in habitats that occupy restricted areas, such as submontane formations (e.g., Begoniaceae and Balsaminaceae) or along rivers (*Mapania*), where there are high levels of microscale heterogeneity and which are thought to constitute areas where forest refugia occurred during Pleistocene ice ages (Maley, 1996; Leal, 2001). According to the theory of diversification in mountainous forest refugia (Sosef, 1994; Maley, 1996), taxonomic groups with low dispersal capacity should have species with ranges that are restricted to a single mountain range. Our results show that genera with low dispersal capacity that are well represented in these habitats (such as *Begonia* and *Impatiens*) have some of the smallest average range sizes (Fig. 4), which is consistent with this theory.

Finally, we note that another herbaceous family, Podostemaceae, whose members are all aquatic, growing exclusively on rocks in rapids and waterfalls, have the highest rate of endemism in WCA, with 52% of the currently recognized species endemic to the study area (Fig. 4). The precise level of endemism may prove to be somewhat different as Podostemaceae are still largely underdocumented in Central Africa and recent collections from Gabon belonging to the genus *Ledermanniella* have shown that it is still in need of revision, which could lead to substantial changes in the number, delimitation, and distribution of its species.

THE NEED FOR FURTHER BOTANICAL EXPLORATION IN WESTERN CENTRAL AFRICA

Although WCA is one of the best-explored areas in tropical Africa, many of its endemic taxa nevertheless

remain poorly known. Indeed, more than half of the area's species are documented by fewer than 10 occurrences, whereas only 13.7% of the taxa are represented by more than 30 occurrences, a common pattern in the tropics (Borchsenius, 1997). The flora of a large part of our study area is still very poorly documented, especially in the Republic of the Congo, the Central African Republic, and the Democratic Republic of the Congo, where most areas have less than one record per km² (Supplementary Material 3; Sosef et al., 2017). This situation is compounded by the fact that data capture from herbarium collections is also incomplete (Sosef, 2016b; Sosef et al., 2017), leaving gaps in the available records of many taxa that are endemic or have restricted ranges. Major changes in the estimated rate of endemism in Gabon reported over the last 15 years reflect this situation, as noted previously by Küper et al. (2006). While no country in tropical Africa can be regarded as botanically well explored (Sosef et al., 2017), rapid changes in patterns and practices of land use, such as expanding agriculture and forestry, oil palm plantations, and urbanization, increasingly threaten native habitats and their flora. It is therefore increasingly urgent to strengthen botanical exploration, to expand and complete the scanning and data capture of herbarium collections and make them available via publicly accessible databases in order to facilitate our understanding of the distribution of rare species (Beard et al., 2000; Küper et al., 2006), and to describe new species before they become extinct. Improved documentation of the flora of WCA would also enable a more accurate assessment of endemism and would reduce the number of instances in which a species is considered to be endemic when in fact it is not, a situation referred to as “endémisme par ignorance” by Gaussen and Leredde (1948).

Expanded botanical exploration and an improved understanding of endemic and range-restricted species are also urgently needed in order to develop better conservation strategies and to identify conservation priorities in a world where biodiversity is rapidly moving toward collapse (Barnosky et al., 2011; Ceballos et al., 2015). The distribution of species is a key parameter for assessing their conservation status (IUCN, 2012; IUCN Standards and Petitions Committee, 2019). Taxa with restricted ranges are widely regarded as top conservation priorities because most or all of their population may be threatened with rapid extinction (International Finance Corporation, 2019). Our data suggest that 56% of the taxa endemic to WCA could be regarded as narrowly distributed, with an extent of occurrence (EOO) of less than 20,000 km² (Fig. 2C), and could therefore potentially be classified as threatened according to the IUCN Red List criteria (IUCN, 2012). Moreover, 70% of the endemics identified in our study

are considered to be range restricted according to the definition provided by Performance Standard 6 of the International Finance Corporation (2019) (i.e., with an EOO < 50,000 km²) and therefore constitute Critical Habitat triggers. The governments of Central African countries have a unique responsibility for the conservation of these regionally endemic species, including those that are known to be threatened as well as those not yet published on the IUCN Red List (see Stévant et al., 2021). While only a few tree species exploited for timber are formally protected in Central Africa (such as *Baillonella toxisperma* Pierre and *Guibourtia tessmannii* (Harms) J. Léonard), most range-restricted species, whose entire population can very rapidly be subjected to significant threats and which are generally shrubs, herbs, and climbers (Fig. 2C), are neglected and their conservation importance remains underappreciated.

BUILDING A DYNAMIC AND EXPERT-MANAGED DATABASE FOR CENTRAL AFRICA

When RAINBIO was published (Dauby et al., 2016), it was described as the most comprehensive and accurate distributional database for tropical African plants, and in particular for western Central Africa, and it was thought that data from this area had been compiled for most herbarium collections (Sosef et al., 2017; Droissart et al., 2018). The step-by-step compilation of data undertaken for the present study shows, however, that a large number of records are missing from RAINBIO, including those for recent collections and for herbarium specimens whose data have not yet been captured. For example, an average of more than 3000 collections are currently made per year in Gabon, resulting in a 30% increase over the last 15 years (Lachenaud et al., 2018), and specimens at the Meise Botanical Garden were only recently scanned and the accompanying data captured (Vissers et al., 2017). To date, 613 collections of endemic taxa, representing 3% of the total, have been made since the completion of RAINBIO, and the identifications of an additional 929 collections (5%) made prior to 2015 have been updated in the last six years (see also Goodwin et al., 2015). Likewise, while the data served by GBIF probably contain most of these new or updated records, this widely used database nevertheless presents several significant deficiencies, in particular the presence of many duplicate entries for a given collection bearing different identifications (only one of which can be correct) as well as erroneous georeferencing. These problems lead to an overestimate of species richness in certain regions and an overestimate of the distributional range of many taxa (Beck et al., 2013; Maldonado et al., 2015), which are important issues when studying range-restricted entities. When

conducting studies at a regional scale, such as in Central Africa, a dynamic (i.e., regularly updated), online, and publicly available database managed by taxonomic experts would be of great value and would significantly improve the quality and accuracy of studies focusing on biogeography, conservation, ecology, and many other fields. A collaborative, multi-institutional effort involving taxonomists, ecologists, and online database managers would ensure that quality and accuracy are maintained. Until such an endeavor is undertaken, the most reliable source of information on the flora of the region is Tropicos®, the online, publicly accessible database of the Missouri Botanical Garden, which systematically integrates data from the numerous field expeditions conducted by its staff and collaborators, regularly incorporates new identifications of material deposited in several herbaria, and systematically integrates taxonomic changes. In order to provide the most up-to-date information possible on the Central African flora, we have fully integrated the data compiled for the present study into Tropicos® in the hope that this will further advance research on and the conservation of plants in this exceptionally rich region.

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