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RESEARCH ARTICLE

Morphological redescription and ecological niche modelling of *Gustavia santanderiensis* (Lecythidaceae), with a key for the genus in the Magdalena Valley, Colombia

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Abstract

Background and aims – *Gustavia santanderiensis* is a tree species from the Magdalena Valley described around a century ago. Despite the species' morphological plasticity, restricted range, and ecology, the species has been greatly understudied. This study aims to establish a clear taxonomic framework for the species based on its morphology and to determine its distribution and predicted range, ecological niche, and conservation status.
Material and methods – A careful revision of herbarium specimens was performed along with field work in the type locality. We used the occurrence records to build an Ecological Niche Model (ENM) using the maximum entropy algorithm through the kuenm package. The accessibility area was constructed by overlapping the records with the ecoregions that encompass the Magdalena Valley. The model was generated using a unique set of bioclimatic variables, with their contributions and permutation importance estimated.
Key results – The flower colour in *Gustavia santanderiensis*, previously described by Knuth and Mori as white petals, varies considerably. Surprisingly, none of the specimens cited by Mori and Prance (1979) in their monograph corresponds to *G. santanderiensis*. Its geographic range is more restricted than previously known, excluding its occurrence in Brazil, and it is now endemic to Colombia. According to the ENM, the species occurs between 100 and 680 m in areas where the annual mean temperature and annual precipitation range do not vary significantly. The annual mean temperature, isothermality, and temperature seasonality were the variables with the highest contributions and permutation importance in the model.
Conclusion – *Gustavia santanderiensis* is an endangered, endemic species of the Magdalena Valley, characterised by remarkable flower colour variation that warrants further investigation. In addition to redescribing this species, we provide the first taxonomic key for *Gustavia* in the Magdalena Valley, which will serve as a diagnostic tool for the species in one of Colombia's most diverse yet fragmented regions.

Keywords

endemism, flower colour variation, inter-Andean valleys, Lecythidoideae, tropical America

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INTRODUCTION

Lecythidaceae is a pantropical family with around 280 tree species in the order Ericales (Mori et al. 2017). It is classified into either five (The Angiosperm Phylogeny Group 2016) or three subfamilies (Huang et al. 2015; Mori et al. 2017): Foetidioideae with species in Madagascar, the Mascarene Islands, and western Africa; Barringtonioideae with species in Asia and Africa, and Lecythidoideae which is restricted to tropical America and includes 16 genera (Kubitzki and Ziburski 1994; Prance 2008; Vargas et al. 2024), where the latter classification is the more commonly used (Huang et al. 2015; Mori et al. 2017; Vargas et al. 2019; Vargas and Dick 2020). Lecythidoideae is the most species-rich subfamily, containing ca 240 species (Vargas et al. 2024) with several new species described each year (i.e. Cornejo et al. 2023; Aymard-Corredor et al. 2024), ranking as one of the most important tree groups of primary forests in Central and South America (Gentry 1982a; Gentry 1982b; Tsou and Mori 2007; ter Steege et al. 2013; Guevara Andino et al. 2019). The subfamily locates Lecythidaceae within the 20 most-species-rich families of trees in the lowland Amazon forests (Cardoso et al. 2017), and third in terms of stem numbers and biomass (ter Steege et al. 2013), providing critical ecological services such as carbon sequestration (Milton et al. 2022) and food resources for pollinators and seed dispersers (Mori et al. 2010).

The classification of the subfamily Lecythidoideae has been relatively stable due to the monographs published by Prance and Mori (1979) and Mori et al. (1990). Molecular phylogenies using chloroplast markers (Thomson et al. 2018), the internal transcribed spacer (ITS) (Mori et al. 2017), and 343 targeted nuclear sequences for Lecythidaceae (Vargas et al. 2019; Vargas et al. 2024) have also recovered two main sister clades in Lecythidoideae: the *Gustavia* + *Grias* clade, where the flowers are always actinomorphic—radial symmetry that characterises the floral morphology in *Gustavia santanderiensis* R.Knuth—, and the clade with mostly zygomorphic flowers—bilateral symmetry—which includes six genera besides the Bertholletia clade.

Since the centre of species richness of Lecythidoideae is in the Amazon Basin (Mori et al. 2017; Vargas and Dick 2020), most studies in the subfamily have focused on species that occur in this biogeographical region. However, Lecythidoideae ranges from Mexico to Paraguay, including Central America, northwestern South America, the Atlantic Forest, and the inter-Andean valleys (Mori et al. 2007; Medellín-Zabala et al. in review), where *Gustavia* L. is the second most diverse genus in the subfamily after *Eschweilera* Mart. ex DC. s.s. (Vargas et al. 2024). Previous works have shown that the Magdalena Valley of Colombia contains a considerable number of species (Prance and Mori 1979), many of which are restricted and some of which are threatened (Calderón et al. 2002; MADS 2024). However, the distribution of the species is not uniform throughout the valley, with higher richness in the tropical wet forests of the Middle Magdalena Valley (Idárraga et al. 2016) compared to the tropical dry forests of the valley (Mendoza-C. 1999; Pizano and García 2014). One approach to understanding species distribution patterns is to evaluate the contribution of climatic variables through ecological niche models (ENMs). ENMs are valuable tools that enable researchers to associate species occurrence data with the broad environmental characteristics of their habitats, thereby facilitating a better understanding of species' distribution patterns and helping to predict their geographic distribution (Cobos et al. 2019; Simões et al. 2020; Menezes et al. 2021).

Gustavia santanderiensis was initially described by Reinhard Knuth in his monograph of Lecythidaceae (Knuth 1939). The description was based on a unique flowering specimen collected by Oscar Haught in the Middle Magdalena Valley, presumably near Cimitarra, Santander. Later, Scott Mori monographed the genus (Prance and Mori 1979), including the type specimen along with six additional specimens of *G. santanderiensis*: two collections from the Colombian Amazonia (*Fernández 2253*, COL; *Fernández 2292*, US), two from the Brazilian Amazonia (*Oliveira 2199*, IAN; *Pires & Silva 8071*, IAN), one from the Upper Magdalena Valley (*Murillo 297*, COL), and one from the Colombian Caribbean region (*Cruz 470*, COL)—none of these specimens were collected in the Middle Magdalena Valley, which is the type locality of the species. Given the morphological characters of *G. santanderiensis* observed in the field, which we find to be new to previous descriptions, such as the wide variation in petal colour, we performed a careful revision of herbarium specimens from the type locality and the Middle Magdalena Valley to corroborate their plasticity. Here, we present a new description of *G. santanderiensis* that examines its phenotypic variation, conservation status, and an ENM for the species, documenting and predicting its distribution given its restricted range. In addition, we present the first taxonomic key for the species of *Gustavia* that occur in the Magdalena Valley.

MATERIAL AND METHODS

Identification and description

All specimens of *Gustavia* were physically studied from COL, FAUC, HUA, JAUM, JBB, UDBC, and UIS herbaria (Thiers 2025), along with images from virtual herbaria B, F, IAN, and US, giving special attention to those specimens cited by Scott Mori as *G. santanderiensis* (Prance and Mori 1979). Vegetative and reproductive structures were measured with a digital vernier calliper (resolution 0.1 mm, accuracy ± 0.2 mm), following Mori et al. (2010). We coined the term "appearing terminal" inflorescence instead of "suprafoliar" inflorescence, following more recent descriptions for some *Gustavia* species (i.e. Cornejo and Mori 2019; Cornejo et al. 2023).

Field work and phenology

Natural populations were visited to describe and document the habitat, ecology, and phenotypic variation of the species. Fieldwork was carried out in the Middle Magdalena Valley, in the department of Caldas, in the municipalities of La Dorada, Norcasia, Samaná, and Victoria, in January of 2021, June of 2022, and April, July, August, and September of 2024. In addition, exsiccate were prepared and deposited in the JBB, FAUC, and UIS herbaria. The phenological data were obtained from all fertile examined specimens and categorised as flowering, fruiting, or both, and visualised using the R package ggplot2 v.3.5.2 (Wickham 2016; R Core Team 2024).

Ecological niche modelling (ENM)

Occurrence data and accessibility area (M)

We used occurrence records from the revised herbarium specimens, our fieldwork collections, and records available in the Global Biodiversity Information Facility (GBIF 2024) to build the ENM. The 29 compiled records were cleaned and curated. Duplicates were removed, and the occurrence data were cleaned to include just one record per 1 km^2. The records were overlapped with the terrestrial ecoregions proposed by Dinerstein et al. (2017) to delimit the accessibility area (M). Thus, we included the ecoregions of the Magdalena Valley dry forests, Magdalena montane forests, and Magdalena-Urabá moist forests to build the accessibility area. Thereafter, we created a projection M that included the ecoregions Northwest Andean montane forests and Chocó-Darién moist forests due to connectivity between the Magdalena Valley and the Chocó region (Myers et al. 2000; Gutiérrez 2007; Dinerstein et al. 2017; Bocanegra-González et al. 2024).

Bioclimatic variables

We downloaded 19 bioclimatic variables from WorldClim 2.0 (Fick and Hijmans 2017) at a spatial resolution of 30s (~1 km^2) to select the appropriate variable set for the ENM. The variables BIO8: Mean temperature of wettest quarter, BIO9: Mean temperature of driest quarter, BIO18: Precipitation of warmest quarter, and BIO19: Precipitation of coldest quarter were deleted since they showed errors by integrating precipitation and temperature data into a single layer, producing spatial irregularities and unusual discontinuities between adjacent pixels (Escobar et al. 2014). In addition, we used the Pearson correlation coefficient to exclude variables with high correlations ($r > |0.8|$). This was performed to avoid overfitting the model and to improve the accuracy of simulations affected by variable correlation (Changjun et al. 2021). Subsequently, we created a single data set with the following bioclimatic variables: BIO1 (Annual mean temperature), BIO3 (Isothermality (BIO2/BIO7) (×100)), BIO4 (Temperature seasonality (standard deviation ×100)), BIO7 (Temperature annual range (BIO5-BIO6)), BIO12 (Annual precipitation), BIO14 (Precipitation of driest month), and BIO15 (Precipitation seasonality (Coefficient of variation)).

Calibration and evaluation of the model

To estimate the predicted geographic distribution of *Gustavia santanderiensis*, we built an ENM using the maximum entropy algorithm (MaxEnt) through the kuenm v.1.1.10 R package (Cobos et al. 2019; R Core Team 2024). The model was generated with a unique set of bioclimatic variables and calibrated with 14 regularisation multipliers (0.1–1.0 with intervals of 0.1, 2–5 with intervals of 1) and seven combinations of the feature classes (l = linear, q = quadratic, and p = product features). The more accurate, simpler parametrisation, and better-performing model was diagnosed based on three criteria thresholds: partial ROC as a measure of statistical significance, omission rates, and delta AICc ≤ 2 (Cobos et al. 2019).

Preliminary IUCN Red List assessment

The preliminary IUCN Red List assessment of the extent of occurrence (EOO) and area of occupancy (AOO) was estimated from specimen-based geographical data using the ConR v.2.1 R package (Dauby and de Lima 2023; R Core Team 2024). We used the Convex Hull method to compute EOO, setting 2 × 2 km grid cells. This grid was randomly overlaid 100 times to calculate AOO. The IUCN Red List category for the species was assessed following the guidelines of the International Union for Conservation of Nature v.16 (IUCN 2024). The data and materials related to the ENM, phenology, and IUCN Red List assessment can be found in the GitHub Repository: https://github.com/davidbiol/Gustavia-santanderiensis-data.

TAXONOMIC TREATMENT

Gustavia santanderiensis R.Knuth. (Knuth 1939: 24)

Figs 1–4; Table 1

Type. COLOMBIA – **Santander** • Vicinity of Puerto Berrío [Cimitarra], between Carare and Magdalena Rivers; 100–700 m; 10 Jul. 1935; fl.; *O. Haught 1834*; holotype: B n.v., probably destroyed; isotypes: F [V0061935F] image, US [00117405] image.

Description. Trees 2–7 m tall, 9–15 cm diam. at breast height; many branched. Bark slightly roughened, lenticellate, inner bark pinkish-orange. Twig 3.1–5.5 mm diam., glabrous. Leaves spirally-alternate, anisophyllous, clustered in groups of 5–9, clusters spaced by 2.7 cm or more. Small leaves with petioles (0.2–)0.7–1.5 cm long, 0.7–1.2 mm wide medially, subterete, slightly flattened adaxially, winged on the distal half, glabrous or occasionally with 0.01 mm erect sparse hyaline trichomes; blades (3.5–)7.1–15.1 × (1.3–)2.5–5.3 cm, elliptic to oblong, chartaceous when dry, glabrous on both sides, base round to cuneate, margin entire to distally weakly denticulate, apex acuminate; venation brochidodromous, conspicuous towards the apex, secondary veins 9–12 pairs, moderately ascending, emerging at 60–65°, tertiary venation scalariform to reticulate, 1.0–1.5 cm apart along the midrib medially. Large leaves with petioles 4.1–12.0 cm long, 1.0–2.2 mm wide medially, subterete, slightly flattened adaxially, distal half alate, glabrous or occasionally with 0.01 mm erect sparse hyaline trichomes; blades 22–35 × (6.5–)8.0–13.5 cm, oblong to elliptic, rarely lanceolate, chartaceous when dry, glabrous on both sides, occasionally abaxially sparsely puberulous along the midvein, trichomes ca 0.01 mm, hyaline, base attenuate to cuneate, margin entire to sparsely denticulate distally, apex acuminate; venation brochidodromous, conspicuous towards the apex, secondary veins 11–14(–16) pairs, moderately ascending, emerging at 60–65°, tertiary venation scalariform to reticulate, 1.8–2.7 cm apart along the midrib medially. Inflorescences appearing terminal, racemose, 4–5 flowered, 1–3 open simultaneously; rachis 0.3–2.2 × 0.4–0.7 cm, green to brown; floral bract 1.8–2.4 × 1.5–1.9 mm, base truncate, apex acute, dark brown, glabrous to puberulous, usually deciduous; pedicels ascending, 1.6–2.7 cm × 0.1–0.3 cm, green, pubescent, trichomes hyaline 0.1–0.2 mm, between distal quarter and proximal quarter bearing 2 bracteoles, 2.7–3.3 × 1.6–2.1 mm, ovate, reddish orange, dorsally keeled, puberulous, trichomes ca 0.01 mm, one bracteole deciduous to both bracteoles persisting. Flowers 9–10 cm diam.; floral buds green to green tinted pink, puberulous; hypanthium without costae, light green, glabrous; calyx 1.3–1.5 mm long, entire, greenish-white, occasionally pale purple, glabrous to puberulous; petals 8(–9), 5.0–5.9 × 2.7–3.2 cm, oblanceolate, white to tinged magenta at apex to almost completely magenta, glabrous, apex rounded; staminal ring 0.7–1.2 cm high, white to pale yellow, glabrous, many filaments, outermost filaments 1.7–2.0 cm long, 0.7–1.1 mm wide, yellow to tinged magenta at apex to completely magenta, glabrous, connective 0.01–0.05 mm long, white, glabrous, anthers 2.9–3.2 × 0.6–1 mm, poricidal, dehiscent by 2 apical pores, yellow, glabrous, base truncate to sagittate, apical pores 0.6–1.3 mm long, oblong; ovary 4-locular, ovules arranged in axillar, summit of the ovary ca 1.4 cm diam., yellow, hirsute to villous, trichomes 0.1–0.6 mm long, hyaline, style ca 2 mm long, slightly obconical, yellowish-brown, pubescent, trichomes equal to the ones on the summit of the ovary, stigma with four not fully developed lobes, yellowish-brown, glabrous. Fruits 2.4–4.8(–5.1) × 3.5–5.8 cm, subglobose, smooth to slightly longitudinally striate, glabrous to lenticellate with orange-brown trichomes, truncate at apex; calycine rim deciduous, infracalycine zone round to truncate at base, green to brown to cream-coloured at maturity, glabrous; supracalycine zone truncate, occasionally prominent, green, villous, trichomes 0.1–0.2 mm long, simple, hyaline; exocarp 4–5 mm thick, leathery; pulp white. Seeds 9–10, 2.2–2.6 × 1.4–1.7 cm, ovoid to subglobose, yellow to dark vinaceous; funicular aril 4–12 mm long, generally well-developed, white to cream when immature, yellowish-brown when mature, slightly adpressed to the seed.

Distribution. Endemic to Colombia, distributed mainly in the Middle Magdalena Valley, in the departments of Santander, Boyacá, Antioquia, and Caldas, from 100–680 m a.s.l. There is an additional and isolated population in the Upper Magdalena Valley, in the department of Cundinamarca. Although Prance and Mori (1979) initially proposed its distribution as a disjunction between the Magdalena Valley and northwestern Amazonia, many years later, Mori et al. (2010) refined the description of some *Gustavia* species. They proposed the distribution of *G. santanderiensis* as only known from a single locality, near the border between the departments of Santander and Antioquia, between Puerto Berrio and Puerto Nare (Mori et al. 2010). The latter description made more sense with the distribution we found for the species than the

Figure 1. Flower colour variation of *Gustavia santanderiensis*. **A**. White petals and yellow stamens. **B**. White petals and stamens ranging from yellow to magenta. **C**. White petals and magenta stamens. **D**. Magenta petals and magenta stamens. Photos: A by Álvaro Idárraga (specimen cultivated in Jardín Botánico de Medellín); B by Juan Mauricio Posada (*Posada 1325*, FAUC); C by María Camila Ángel (*Ángel 003*, FAUC); D by Luis Fernando Coca (*Coca & Jaramillo 15472*, JBB).

former one. Probably Mori had realised that the species has a more restricted distribution (Nathan Smith pers. comm.) but never explained the reasons for discarding the other specimens he initially proposed as belonging to the species.

Habitat and ecology. *Gustavia santanderiensis* mainly inhabits wet tropical forests from the Magdalena Middle Basin. Usually recorded under the canopy of conserved forests, with an isolated population in the Upper Magdalena Valley.

Phenology. *Gustavia santanderiensis* has two flowering-fruiting peaks per year. The first flowering peak goes from November to January, and the fruiting peak from December to January. The second flowering peak occurs

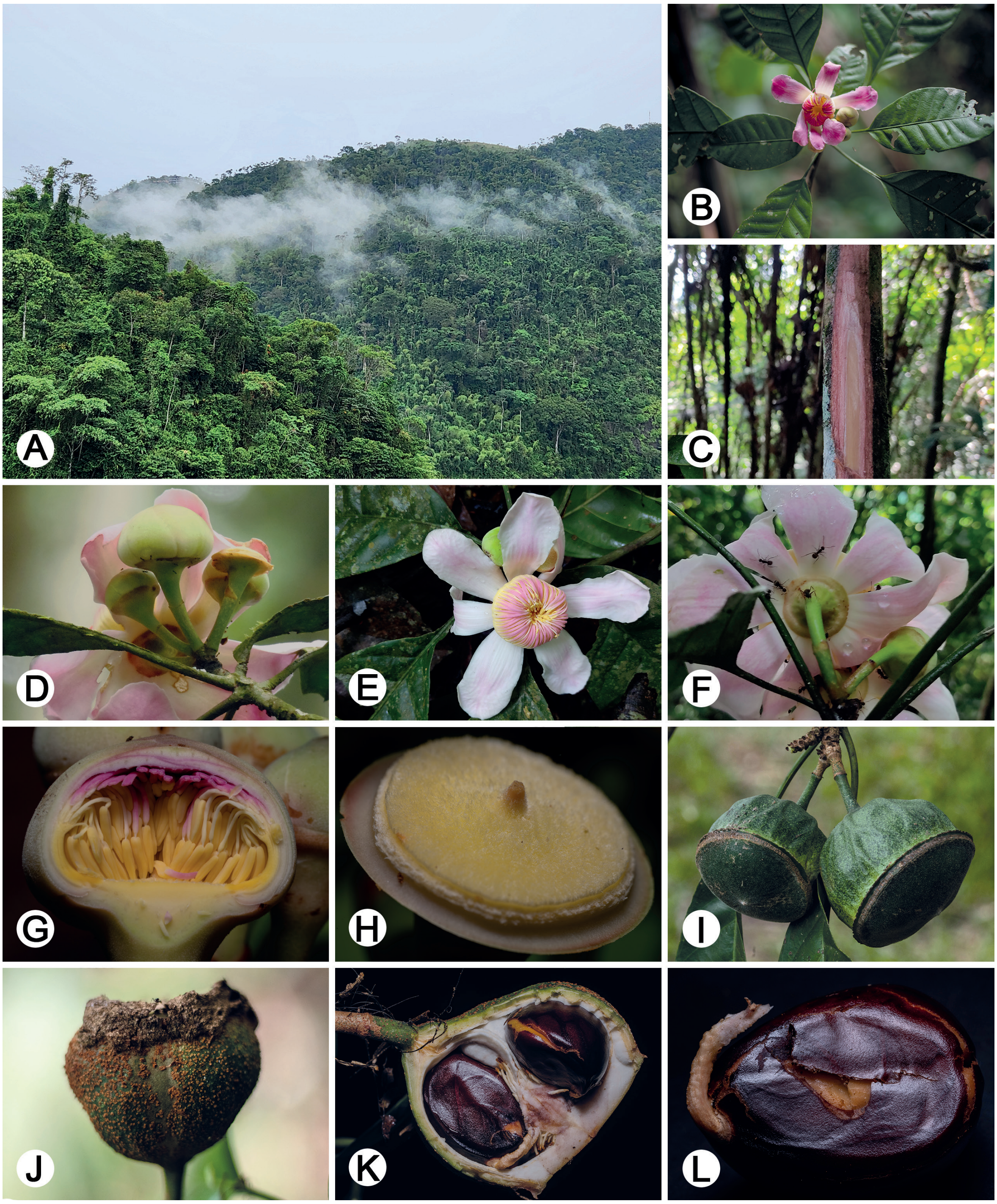

Figure 2. Key morphological characters of *Gustavia santanderiensis*. **A**. Habitat in Norcasia, Caldas. **B**. Habit and leaves. **C**. Bark. **D**. Inflorescence. **E**. Flower. **F**. Entire calyx. **G**. Longitudinal section of flower bud. **H**. Detail of the summit of the ovary. **I**. Immature fruit. **J**. Mature fruit. **K**. Longitudinal section of the fruit. **L**. Seed with funicle. Photos: A by Diana Medellín; B, G, H, J–L by Luis Fernando Coca (*Coca & Jaramillo 15472*, JBB); C, E, F by María Camila Ángel (*Ángel 003*, FAUC); D by David Gutiérrez (*Gutiérrez et al. 360*, FAUC); I by Juan Mauricio Posada (*Posada 1325*, FAUC).

from June to September, with fructification from July to September (Fig. 3).

Etymology. In the protologue, Knuth (1939) did not mention the origin of the specific epithet *santanderiensis*. Nonetheless, the type locality (*O. Haught 1834*) probably lies in the municipality of Cimitarra, in the department of Santander. The name might refer to it.

Notes. Flower colour in *Gustavia santanderiensis* ranges from white petals with yellow stamens (Fig. 1A) to petals apically tinged with magenta, and magenta stamens (Fig. 1D). The staminal ring is more constant in colour, ranging from white to yellowish, but never magenta. Knowledge of flower colour variation within the genus is limited (Mori and Cornejo 2013); however, similar variation has been observed in other species, e.g. *G. augusta* L. (Mori et al. 2010), *G. poeppigiana* O.Berg (Wilmar Guzmán pers. comm.), and *G. romeroi* S.A.Mori & García-Barr. (MCAV pers. obs.).

Ecological niche model. In total, we found 24 occurrences of *Gustavia santanderiensis*, distributed between 100–680 m a.s.l., in zones where the annual average temperature and the annual precipitation range between 24.6–27.8°C and 1940–2960 mm, respectively. *Gustavia santanderiensis* occurs in the departments of Antioquia, Caldas, Cundinamarca, Boyacá, and Santander (Fig. 4A).

Using a single set of variables, along with 14 multiple regularisers, and the seven combinations of the feature classes mentioned above, 98 candidate models were developed. The best-performing and most parsimonious ENM was the one using a regularisation multiplier of 1 and the *lqp* feature classes. This model exhibited an AUC of 0.964, a significant partial ROC, an omission rate of 5%, a delta AICc of 0, and an AICc value of 439.346. The environmental variables with the highest contributions in the model were BIO1, BIO3, and BIO4, which accounted for 90.9% of the total contribution (Table 1).

According to the predicted distribution shown by the ENM (Fig. 4B), the largest number of areas that meet the habitat suitability requirements for the species are in the Middle Magdalena Valley between the Central and Eastern Cordilleras of the Andes in the departments of Antioquia, Boyacá, Caldas, Cundinamarca, Santander, and Tolima. However, high suitability values are also observed in the Urabá region of Antioquia, in the Chocó region, and on the western slope of the Western Cordillera, in the departments of Cauca and Nariño. These results expand the predicted distribution range of the species within the country, primarily driven by the BIO1, BIO3, and BIO4 climatic variables.

Preliminary IUCN conservation assessment. *Gustavia santanderiensis* has been recently proposed as Least Concern by the IUCN Red List of Threatened Species (Morales and Lopez-Gallego 2023). This may be explained by earlier considerations of the species distribution spanning from the Magdalena Valley to northwestern Amazonia. However, given the material revised and the current species description, we found that its geographic range is more restricted than previously known, excluding its occurrence in northwestern Amazonia. The extent of occurrence (EOO) was estimated to be 8731 km^2, with an area of occupancy (AOO) of 80 km^2. Therefore, the species is preliminarily proposed as Endangered (EN) under IUCN Red List assessment criteria: EN B2ab(iii) (IUCN 2024). The main threat to the species is habitat degradation. Concerningly, the Middle Magdalena Valley has been heavily impacted by timber extraction, cattle, and agriculture (Balcázar-Vargas et al. 2000; IGAC 2005; Idárraga et al. 2016). As a result, 13 out of the 26 *Gustavia*

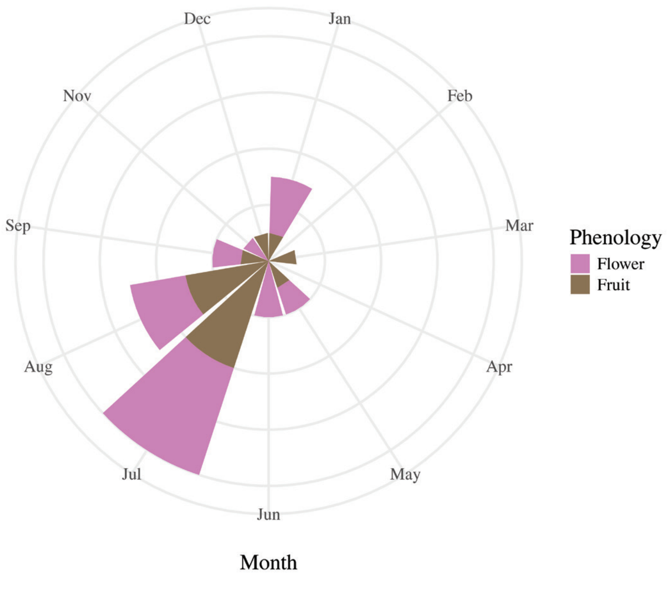

Figure 3. Phenology of *Gustavia santanderiensis*. Magenta and brown slices indicate flowering and fruiting specimens, respectively. The size of each slice represents the number of specimens that were in flower and/or fruit per month. (n = 21).

Table 1. Environmental variables included in the ecological niche modelling, percentage of contribution, and permutation importance in predicting the distribution of *Gustavia santanderiensis*.

Bioclimatic variables	Description	Percentage of contribution (%)	Permutation importance (%)
BIO1	Annual mean temperature (°C)	53.6	47.1
BIO3	Isothermality (BIO2/BIO7) (×100)	19.4	0.4
BIO4	Temperature seasonality (standard deviation ×100)	17.9	46.6
BIO7	Temperature annual range (BIO5-BIO6)	6.7	2.5
BIO12	Annual precipitation (mm)	1.3	3.2
BIO14	Precipitation of the driest month	1.1	0.1
BIO15	Precipitation seasonality (Coefficient of variation)	0.1	0.2

species in Colombia (50%) are listed as Endangered or Vulnerable (Cornejo et al. 2023; MADS 2024).

Additional material examined. COLOMBIA – **Antioquia** • Puerto Nare: vereda Serranías; 257 m; 14 Jul. 2013; fr.; *J. Jiménez et al. 141*; HUA. – **Boyacá** • Puerto Boyacá: Corregimiento de Puerto Pinzón, predio de don Gerardo; 5°58’4.7”N, 74°13’23.2”W; 400 m; 6 Aug. 2022; fr.; *J.D. Mora et al. 2*; JAUM, UDBC • Hacienda Colorados; 6°02’56.0”N, 74°17’40.0”W; 289 m; 12 Sep. 2019; fl.; *R.D. Jurado et al. 1786*; JBB. – **Caldas** • La Dorada: vereda La Habana; 5°38’19.3”N, 74°46’39.1”W; 250 m; 27 Jan. 2000; fr.; *Bustos 169*; COL • Vereda Pontoná, finca La Alcaparrosa; 5°34’28.91”N, 74°40’7.34”W; 174 m; 22 Jul. 2022; fl., fr.; *J.M. Posada et al. 1325*; FAUC • Vereda La Atarraya, Margen del río La Miel, Finca Los Achiles, relictos de bosque al margen del río; 5°41’03.9”N, 74°44’16.4”W; 285 m; 30 Jan. 2021; fl.; *D. Sanín et al. 7699*; JBB; UIS • Vereda La Atarraya, Los Achiles, Jardín Botánico del Magdalena, bosque de los macondos; 5°40’01.8”N, 74°44’15.3”W; 186 m; 10 Aug. 2024; fl., fr.; *L.F. Coca & D. Jaramillo 15472*; JBB • Norcasia: vereda San Roque, Reserva de la sociedad civil Río Manso; 5°40’08.2”N, 75°45’09.8”W; 213 m; 26 Nov. 2005; fl.; *D. Sanín & N. Castaño 1579*; FAUC • Vereda Quiebra de Roque, Reserva Natural Riomanso; 5°40’34.7”N, 74°46’00.3”W; 222 m; 23 Mar. 2012; fr.; *J. Ramírez et al. 266*; FAUC • Reserva Natural Riomanso, localidad Alejandría; 5°40’34.5”N, 74°45’58.8”W; 204 m; 20 Jul. 2012; fr.; *J. Ramírez et al. 295*; FAUC • Reserva Natural Riomanso, localidad Alejandría; 5°40’34.5”N, 74°45’58.8”W; 204 m; 20 Jul. 2012; fr.; *J. Ramírez et al.*

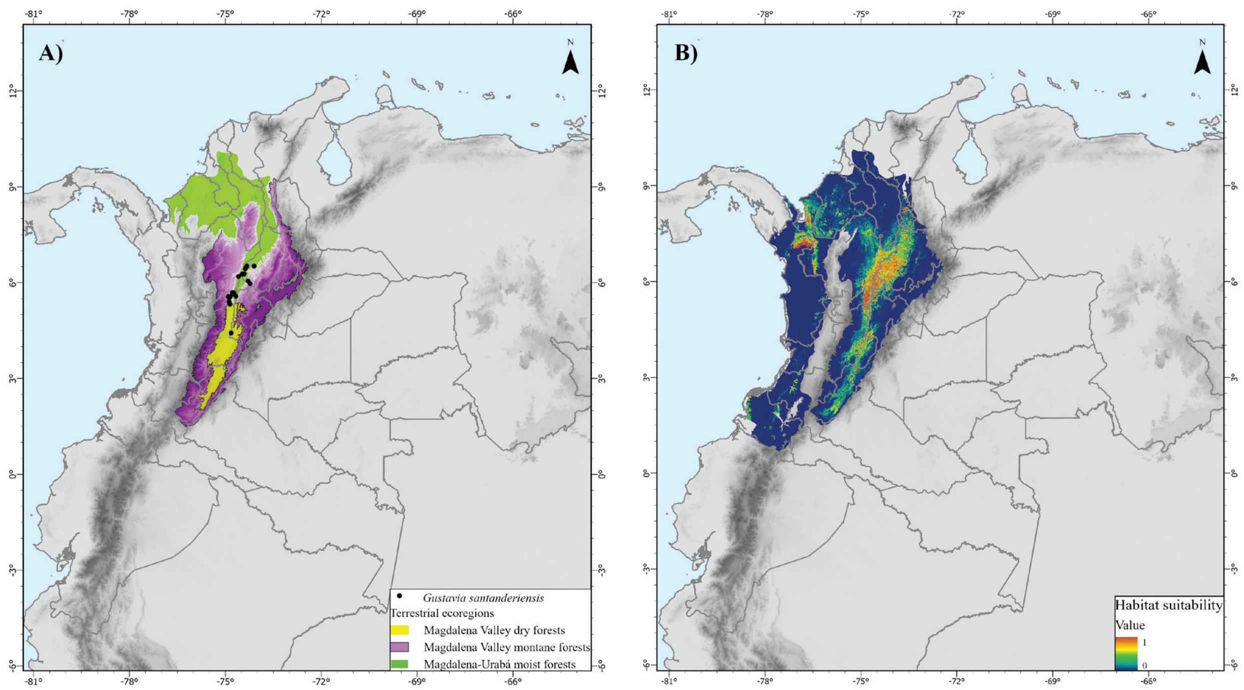

Figure 4. Geographical range of *Gustavia santanderiensis*. **A**. Distribution of *G. santanderiensis* in Colombia (occurrence records, n = 24). This species is found in the Magdalena Valley dry forests (yellow), Magdalena Valley montane forests (purple), and Magdalena-Urabá moist forests (green). **B**. Habitat suitability for the predicted distribution of *G. santanderiensis* in Colombia. Areas in red represent the most likely sites for establishment, while blue areas are unsuitable for the species.

301; FAUC • Embalse Amani, vereda Planes; 5°33'33.7"N, 74°54'35.0"W; 505 m; 16 Apr. 2024; st.; *D. Medellín et al. 969*; FAUC • same data as for preceding; *D. Medellín et al. 970*; FAUC • same data as for preceding; *D. Medellín et al. 971*; FAUC • Embalse Amani, vereda Planes; 5°33'33.85"N, 74°54'34.38"W; 546 m; 2 Jul. 2024; fl.; *M.C. Ángel 002*; FAUC • Embalse Amani, vereda Planes; 5°33'33.60"N, 74°54'34.32"W; 554 m; 2 Jul. 2024; fl.; *M.C. Ángel 003*; FAUC • Samaná: Embalse Amani, vereda La Mula; 5°34'07.2"N, 74°54'02.3"W; 592 m; 15 Apr. 2024; st.; *D. Medellín et al. 960*; FAUC • same data as for preceding; *D. Medellín et al. 961*; FAUC • same data as for preceding; *D. Medellín et al. 962*; FAUC • Embalse Amani, vereda La Mula; 5°34'07.2"N, 74°54'02.3"W; 592 m; 1 Jul. 2024; fr.; *M.C. Ángel 001*; FAUC • Embalse Amani, vereda La Mula; 5°34'07.2"N, 74°54'02.3"W; 592 m; 10 Sep. 2024; fl.; *M.C. Ángel 004*; FAUC • Victoria: franja protección, río La Miel; 475 m; 18 Aug. 2003; fr.; *E. Correa et al. 59*; FAUC • Sitio El Cuatro, Gravillera el Llano; 5°19'22"N, 74°51'16"W; 300–350 m; 18 Jan. 2006; fl.; *J.A. Pérez et al. 2322*; FAUC • Vereda Carrizal, borde de río; 5°32'42.7"N, 74°51'33.9"W; 347 m; 3 Jun. 2022; fl.; *D. Gutiérrez et al. 360*; FAUC • Vereda La Habana, hacienda Pozo Redondo; 5°38'36.9"N, 74°46'14.9"W; 194 m; 2 Aug. 2023; fl.; *A. Jara et al. 4398*; COL. – **Cundinamarca** • Nariño: vereda Mendoza, finca El Caucho, cerca de la antena de comunicaciones; 4°25'27.3"N, 74°49'00.9"W; 640 m; 8 Jun. 2017; fl.; *J. Navarro 3350*; UDBC. – **Santander** • Cimitarra: V. Albania, Finca la Hermosa, entrando por el caserío La Pequeña (Tierradentro); 6°16'26"N, 74°24'23"W; 145 m; 2 Oct. 1998; st.; *W. Rodríguez et al. 1538*; JAUM • Hacienda Monterrey; 6°15'45.7"N, 74°28'24.4"W; 152 m; 12 Dec. 2020; fr.; *D. Cabrera & P. Piñeros 5784*; JBB • Corregimiento de Puerto Olaya, Hacienda El Bosque; 6°28.285'N, 74°21.116'W; 160–190 m; 27 Jul. 1999; fl.; *A. Idárraga et al. 1319*; COL • Corregimiento Puerto Olaya, Hacienda Piamonte; 6°26'17"N, 74°22'7"W; 123 m; 29 May 2015; fr.; *A. Idárraga et al. 6039*; HUA • Corregimiento Puerto Olaya, Hacienda Piamonte; 6°26'25"N, 74°22'22"W; 132 m; 23 Jul. 2015; fl., fr.; *A. Idárraga et al. 6134*; HUA • Corregimiento de Puerto Araujo; 100 m; 19 Sep. 1979; fr.; *Rentería et al. 1783*; COL.

Taxonomic key to the species of *Gustavia* in the Magdalena Valley

1. Inflorescence appearing terminal or axillary **2**
– Inflorescence cauline **7**
2. Hypanthium costate, calyx 6-lobed, persistent in fruit; fruit costate **3**
– Hypanthium ecostate, calyx entire or 4-lobed, deciduous in fruit; fruit ecostate **4**
3. Petioles semicircular in cross-section, blades coriaceous; calyx lobes triangular-sagittate, margin revolute; fruits brown at maturity; seeds with expanded funicles .... ***Gustavia longifuniculata***
– Petioles subterete in cross-section, blades chartaceous; calyx lobes triangular, margin flat; fruits yellowish-brown at maturity; seeds with inconspicuous funicles .... ***G. dubia***
4. Inflorescence axillary .... ***G. gentryi***
– Inflorescence appearing terminal **5**
5. Inflorescence rachis 20–60 mm long; pedicel 40–90 mm long; petals white, filaments yellow, ovary (4–)6-locular; often cultivated, fruits edible .... ***G. speciosa***
– Inflorescence rachis 3–30 mm long; pedicel 13–30 mm long; petals white to magenta, filaments yellow to magenta, ovary 4-locular; not cultivated **6**
6. Leaves clearly anisophyllous; leaf blades ovate, ovate-elliptic, elliptic to rarely lanceolate-elliptic; leaves less than three times as long as wide; staminal ring white to yellow, not magenta; seeds with well-developed funicles .... ***G. santanderiensis***
– Leaves not anisophyllous or not conspicuously so; leaf blades narrowly elliptic to oblanceolate; leaves equal or more than three times as long as wide; staminal ring white to magenta, rarely yellow; seeds without well-developed funicles .... ***G. verticillata***
7. Leaves sessile or subsessile (petioles generally less than 2 cm long) **8**
– Leaves clearly petiolate (petioles generally more than 2 cm long) **10**
8. Trees unbranched or rarely one-time branched; leaf margin entire to minutely serrulate: leaves with 40 or more pairs of secondary veins .... ***G. excelsa***
– Trees sparsely branched; leaf margins serrate to distinctly serrulate; leaves with 30 or fewer pairs of secondary veins **9**
9. Leaves broad, more than 5 cm wide; ovary (5)6-locular .... ***G. superba***
– Leaves narrow, less than 5 cm wide; ovary 4-locular .... ***G. gracillima***
10. Leaves oblanceolate to broadly oblanceolate; calyx often entire, slightly lobed to clearly 4-lobed **11**
– Leaves elliptic, narrowly elliptic to narrowly oblanceolate; calyx clearly 4-lobed **12**
11. Leaf margins serrate; petioles semicircular in cross-section; pedicels bearing bracteoles at or below the middle .... ***G. superba***
– Leaf margins entire; petioles terete to subterete in cross-section; pedicels bearing bracteoles at the distal third .... ***G. latifolia***
12. Leaves elliptic; leaf blades 17–21 × 6–7 cm; leaf margins entire; leaves with 12–14 pairs of secondary veins; flowers with 11–12(–18) petals .... ***G. romeroi***
– Leaves narrowly elliptic to narrowly oblanceolate; leaf blades 25–46 × 2.0–3.5 cm; leaf margins serrulate; leaves with 22–29 pairs of secondary veins; flowers with 8 petals .... ***G. gracillima***

DISCUSSION

Taxonomic notes

Gustavia santanderiensis is vegetatively similar to *G. nana* subsp. *rhodantha* (Standl.) S.A.Mori. However, the study species differs due to its margin entire to distally sparsely denticulate, inflorescence appearing terminal, and mainly found in the Middle Magdalena Valley (vs margin serrulate, inflorescence cauline, and mainly found in the Chocó region). These morphological and geographic differences are supported by the most recent phylogenetic and biogeographic reconstructions of *Gustavia*, in which *G. santanderiensis* is nested in a clade mostly diversified across the Magdalena Valley, whereas *G. nana* is nested in a clade with species from the Chocó and Western Amazonia (Medellín-Zabala et al. in review). *Gustavia santanderiensis* could also be easily confused with *Gustavia verticillata* Miers. The flowers and fruits are almost identical, and it may seem that they are the same species. However, both species appear segregated as sister taxa in the phylogeny (Medellín-Zabala et al. in review). The primary differences among these species are evident in their leaves, staminal rings, and distribution patterns. *Gustavia santanderiensis* differs from *G. verticillata* by the leaf-blades that are oblong to elliptic to rarely lanceolate, and less than three times as long as wide (vs narrowly elliptic to oblanceolate, and equal or more than three times as long as wide in *G. verticillata*), the staminal ring is white to yellow (vs white to magenta, rarely yellow), and has a distribution primarily in the wet forests of the Middle Magdalena Valley (vs mainly in tropical dry forests of the Upper and Lower Magdalena Valley).

Specimens cited in Flora Neotropica

In the *Gustavia* monograph, Prance and Mori (1979) described *G. santanderiensis* including the type specimen along with six additional specimens. The identity of each of these specimens is discussed hereafter. The specimens from Colombian Amazonia *Fernández 2253* (COL) and *Fernández 2292* (COL) have 6-lobed calyx (different from the entire calyx of *G. santanderiensis*). The Brazilian specimens *Oliveira 2199* (IAN) and *Pires & Silva 8071* (IAN) are in fruit, so the calyx lobes are indistinguishable. However, the latter two specimens are more similar to those of the Amazonian region of Colombia than to those from the Magdalena Valley. Probably all four of these specimens correspond to the same unknown species, which is required to be collected with more complete characters (e.g. trunk branching, flower) in order to assign them to a taxonomic identity.

Regarding the other two specimens cited in Prance and Mori (1979), the first one was collected in the Colombian Caribbean region (*Cruz 470*, COL). This one differs from *G. santanderiensis* by presenting a lustrous adaxial surface. The identity of this specimen is uncertain due to the fragmentary nature of the collection. The second one was collected from the Upper Magdalena Valley (*Murillo 297*, COL), it does not correspond to *G. santanderiensis*, which can be distinguished from the species by broader leaves (8.0–13.6 cm wide in *G. santanderiensis* vs 5–8 cm wide), longer petioles (4–12 cm in *G. santanderiensis* vs 3–5 cm long), and seeds with well-developed funicles (vs seeds without well-developed funicles). This specimen probably corresponds to *G. verticillata*. As a result, we conclude that none of the specimens cited by Mori corresponds to *G. santanderiensis*, thereby excluding its occurrence in Brazil, and excluding its occurrence in the Colombian Caribbean region.

Gustavia in the Magdalena Valley

Based on this study, we recognise 11 species for the genus along the Magdalena Valley, with most of them occurring in the middle basin, and seven of them classified as threatened (MADS 2024). Some species typically considered to belong to the Magdalena Valley are excluded from the taxonomic key presented above. We doubt the presence of *Gustavia grandibracteata* Croat & S.A.Mori and *G. petiolata* S.A.Mori in the Magdalena Valley. Regarding *G. grandibracteata*, we have not observed any fertile specimens for this species in the study area, only from the Chocó region. Mori cited *Daniel 2083* (US) from the Middle Magdalena Valley (in Prance and Mori 1979). However, it corresponds to a sterile specimen, and its identification could not be confirmed. The *G. petiolata* type collection is from southern Colombia in the Chocó region. It has a 4-costate hypanthium, which differs from the smooth hypanthium found in some specimens typically identified as *G. petiolata* in the Middle Magdalena Valley. These specimens correspond to *G. speciosa* (Kunth) DC.

Ecological niche modelling

It is widely recognised that abiotic environmental factors determine plant distribution ranges, as they define the basic conditions necessary for survival (Huang et al. 2024). In this context, our results support the notion that variables such as annual mean temperature, isothermality, and temperature seasonality shape the distribution of angiosperms (Huang et al. 2021). Specifically, these variables are known to influence plant growth, seed germination, plant recruitment, and phenological development (Bahuguna and Jagadish 2015; Rosbakh and Poschlod 2015; Piri Sahragard and Karami 2024). Thus, temperature may be influencing the distribution of *Gustavia santanderiensis* by setting the frequency of its flowering periods, which are observed during the dry season (Fig. 3). This pattern of flowering periods during the dry season has also been observed in *G. montana* Cornejo, Gut.-Duque & Arango-Gonz. (Cornejo et al. 2023), *G. superba* (Kunth) O.Berg (Mori and Kallunki 1976) and several species of the family (Prance and Mori 1979). Also explained by the rapid rainy syndrome in some species of *Gustavia*, where, before the dry season begins, there is a pattern of fruiting and germination during the rainy season (Sork 1985).

In addition to climatic variables, the evolutionary history of *Gustavia* might also influence the observed and predicted distributions of *G. santanderiensis*. Although we know little about the diversification of the genus, Vargas and Dick (2020) suggested that *Gustavia* originated in the Transandean region around 20.4 Ma. A more recent biogeographical reconstruction indicates that *Gustavia* is older, having originated in the Late Eocene, approximately 36 Ma, and encompasses two main lineages: (1) an Amazonian clade, and (2) a more diverse trans-Andean clade, within which the *Gustavia* species from the Magdalena Valley are nested (Medellín-Zabala et al. in review). Additionally, the latest study reveals that the *Gustavia* species found in the Chocó region, which have diversified more recently within the group (~Late Miocene), have different origins, including the Magdalena Valley. This finding confirms the association between the Chocó-Magdalena Valley, suggested in previous studies (Lynch and Suárez 2004; Fagua and Ramsey 2019; Bocanegra-González et al. 2024), which might shape the distribution patterns in Lecythidaceae and other biological groups.

Although several species of *Gustavia* occur in the Magdalena Valley, most do not occur in the Chocó region (e.g. *G. santanderiensis*, *G. excelsa* R.Knuth, and *G. romeroi*). Vice versa, there are species occurring in the Chocó region but not in the Magdalena Valley (e.g. *G. sessilis* S.A.Mori, *G. monocaulis* S.A.Mori, and *G. grandibracteata*). Nonetheless, a few known species are shared between the two regions; one well-known example is *G. dubia* (Kunth) O.Berg (Batista-Guerra and Ortíz 2020). This pattern suggests that, although some climatic variables between the Magdalena River humid system and the Chocó region are similar (Bocanegra-González et al. 2024) and may be shaping the predicted distribution of *G. santanderiensis* (Fig. 4B), species of *Gustavia* occurring in both ecoregions are rare. Therefore, the evolutionary history and additional local conditions may shape the diversity patterns in *Gustavia*. Also, this result highlights the need for a more extensive survey in the Chocó region, as the absence of the species in this area has not yet been verified. However, it is important to note that ENMs are based on presence-only data. Therefore, the apparent absence of the species in this region may represent pseudo-absences rather than true absences.

CONCLUSION

Gustavia santanderiensis is an endangered endemic species to the Magdalena Valley, primarily found in the moist forests of the Magdalena-Urabá and the Magdalena Valley montane forests. According to the ENM built for the species, climatic conditions such as the annual mean temperature, isothermality, and temperature seasonality are highly correlated. They could help predict these forests as suitable habitats for the species. However, the species could also occur in the northern and southern areas of the Chocó region, given the connectivity between the Magdalena-Chocó regions, the climatic variables, and the predicted distribution suggested by the ENM. Thus, this finding suggests a broad exploration of the Chocó region, as the absence of the species in this area has not been confirmed. Although *G. santanderiensis* was described by Knuth (1939) based on a single flowering specimen from Cimitarra, Santander—*O. Haught 1834*, Middle Magdalena Valley—, we found that the specimens cited for the species in the genus monograph by Prance and Mori (1979) do not represent the original description for *G. santanderiensis*. Our description includes a curated and detailed revision of herbarium and field specimens, along with taxonomic notes and observations about the remarkable colour variation in the species' flowers, which merits further research at the population level, the presence of anisophylly, and the circular shape of the calyx; characters that have not been previously described, and that have helped to segregate the species in the study area. Finally, we present the first taxonomic key for *Gustavia* in the Magdalena Valley, which will serve as a diagnostic tool for the species in one of the most diverse yet underexplored and fragmented regions of Colombia.

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