



Floristic and phytogeographic analysis of the Sabanas Miravalles in Costa Rica

Análisis florístico y fitogeográfico de las Sabanas Miravalles, Costa Rica

José Esteban Jiménez^{1,2,3,4,8} , Gerardo Avalos^{5,6} , Mario A. Blanco^{3,5,7} 

Abstract:

Background and Aims: The savanna ecosystem in Costa Rica, which covers small areas along the Pacific slope (100-1500 m a.s.l.), and particularly the Sabanas Miravalles, on the western flank of Volcán Miravalles (Cordillera de Guanacaste), remain floristically understudied. The aims of this study are to inventory the vascular flora of Sabanas Miravalles, assess its ecological importance, evaluate spatial heterogeneity's impact on composition, and compare their phytogeographic affinities with other Neotropical savannas.

Methods: We identified the vascular flora within 25 plots of 50 × 10 m, classified by life form following Raunkjær, and divided into woody and herbaceous (graminoid and non-graminoid herbs) species. We analyzed the composition and floristic affinity with species accumulation curves, Chao1 index, Relative Importance Value (RIV), Bray-Curtis and Sørensen indices.

Key results: A total of 54 families, 161 genera, and 228 species were documented. Fabaceae was the most diverse family, and *Polygala* and *Rhynchospora* were the most diverse genera. Non-graminoid herbs and hemicryptophytes were dominant. *Miconia sericea*, *Polygala glochidata*, and *Trachypogon plumosus* were the most abundant in their growth form. Floristic composition exhibited clear elevation-driven shifts, with three main groups identified. Most species exhibited wide Neotropical distributions. The flora of the Sabanas Miravalles showed the greatest similarity to the Venezuelan Llanos, with 70% of species in common.

Conclusions: The flora of the Sabanas Miravalles represents 2.1% of Costa Rica's ~10,712 vascular plant species. Although its origin is uncertain, Pleistocene floristic exchanges, volcanic eruptions, and fire have likely shaped its composition. Understanding its origin, phytogeographic affinities, and physical drivers is essential for effective management and conservation.

Key words: floristics, *Miconia sericea*, phytogeography, *Polygala glochidata*, savanna ecosystem, *Trachypogon plumosus*.

Resumen:

Antecedentes y Objetivos: El ecosistema de sabana en Costa Rica, el cual cubre áreas pequeñas en la vertiente del Pacífico (100-1500 m s.n.m.), y particularmente las Sabanas de Miravalles, ubicadas en el flanco occidental del Volcán Miravalles (Cordillera de Guanacaste), permanecen florísticamente no estudiadas. Los objetivos de este estudio fueron inventariar la flora vascular de las Sabanas de Miravalles, describir su importancia ecológica, evaluar el impacto de la heterogeneidad espacial en la composición de especies y comparar sus afinidades fitogeográficas con otras sabanas neotropicales.

Métodos: Se identificó la flora vascular en 25 parcelas de 50 × 10 m, clasificando las especies por forma de vida según Raunkjær y dividiéndolas en especies leñosas y herbáceas (graminoides y no graminoides). Analizamos la composición y afinidad florística con curvas de acumulación de especies, índice Chao1, Valor de Importancia Relativa (VIR), e índices Bray-Curtis y Sørensen.

Resultados clave: Se documentaron 54 familias, 161 géneros y 228 especies. Fabaceae fue la familia más diversa, y *Polygala* y *Rhynchospora* los géneros más diversos. Las hierbas no graminoides y las hemicriptófitas fueron dominantes. *Miconia sericea*, *Polygala glochidata* y *Trachypogon plumosus* fueron las especies más abundantes en su respectiva forma de crecimiento. La composición florística mostró claros cambios asociados a la altitud, identificándose tres grupos principales. La mayoría de las especies presentaron amplia distribución neotropical. La flora de las Sabanas de Miravalles mostró mayor similitud con los Llanos Venezolanos, compartiendo 70% de las especies.

Conclusiones: La flora de la Sabana de Miravalles representa 2.1% de las ~10712 especies de plantas vasculares de Costa Rica. Aunque su origen es incierto, intercambios florísticos durante el Pleistoceno, las erupciones volcánicas y los incendios influyeron en su composición. Comprender su origen, afinidades fitogeográficas y los factores físicos es esencial para mejorar su manejo y conservación.

Palabras clave: ecosistemas de sabana, fitogeografía, florística, *Miconia sericea*, *Polygala glochidata*, *Trachypogon plumosus*.

⁸Author for correspondence: gaiadendron.jej@gmail.com

Affiliations are shown on the next page.

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Introduction

Savannas are ecosystems dominated by a continuous herbaceous matrix, primarily composed of grasses and sedges, interspersed with a discontinuous layer of small trees, shrubs, and palms at varying densities (Beard, 1953; Gómez and Herrera, 1986). They cover approximately 10% of the Earth's continental surface, making them one of the most extensive ecosystems worldwide (Furley, 2004). In the Neotropics, savannas are second only to rainforests in extent, spanning about 3 million km² (Huber, 1987). Savannas are located in seasonal regions with nutrient-poor, poorly drained, acidic, and rocky soils (Beard, 1953; Harris, 1980; Sarmiento, 1984; Gómez and Herrera, 1986; Huber, 1987).

In Costa Rica, savannas are confined to small areas on the Pacific slope, which is characterized by a pronounced dry season (Beard, 1953). They have a range of distribution from Guanacaste to Puntarenas (Gómez and Herrea, 1986; Zamora et al., 2004; Artavia-Rodríguez and Avalos, 2020). The historical origins of these savannas have been debated, with arguments for both anthropogenic (Budowski, 1956; Montoya, 1966; Gómez and Herrera, 1986) and natural origins linked to edaphic, geological, and climatic factors (Vargas, 1985; Gómez and Herrera, 1986; Zamora et al., 2004). Despite this, their origin remains unresolved (Artavia-Rodríguez and Avalos, 2020). This debate mirrors broader discussions in tropical ecology regarding the difficulty of distinguishing natural savannas from anthropogenic pastures due to their physiognomic similarity and landscape modification (López-Olmedo et al., 2007).

Although some ecological and phytogeographic studies of Costa Rican savannas exist (Vargas, 1985; 1987; 1988a; 1988b; 2001; Elizondo and Jiménez, 1988; Vargas and Cortés, 2000), comprehensive floristic analyses are rare. The Sabanas Miravalles, located on the Cordillera de Guanacaste's volcanic western flank, have been overlooked despite their designation as natural savannas since the 19th century (Wagner and Scherzer, 1856). This lack of research

underscores the need for detailed investigations into their biodiversity and ecological dynamics.

This study aimed to 1) inventory the vascular flora of the Sabanas Miravalles, 2) determine the species' ecological importance value, 3) evaluate the influence of the spatial heterogeneity on floristic composition, and 4) analyze the species' geographic distribution and their floristic similarity to other Neotropical savannas. These objectives fill critical knowledge gaps, providing a foundation for effective conservation and management strategies for these ecosystems.

Materials and Methods

Study area

The Sabanas Miravalles are located on the western slope of Volcán Miravalles in the Cordillera Volcánica de Guanacaste (10°43'-10°46'N and 85°10'-85°12'W) and cover approximately 309 hectares. They are part of the Miravalles National Park (72.3% of the area), span an elevation range of 640-1545 m, and form a cohesive group of savanna fragments embedded within lowland and pre-montane forests (Fig. 1), according to the Holdridge life zone system (Holdridge, 1967). Locally, these savannas are known as "Sitio Las Mesas" and "Sitio Miravalles;" however, for the purposes of this study, we refer to them collectively as "Sabanas Miravalles". The region's topography is irregular, with slopes averaging 16±9°, and the soils are of volcanic origin with exposed rocky surfaces (Vargas, 2008). Annual precipitation averages 2500 mm, and the mean annual temperature is 24 °C (Vargas, 2008). The area experiences strong NE winds during the dry season (November to March) coming through the depression between the Miravalles and Rincón de la Vieja volcanoes (Vargas, 2008). There is a brief dry spell in August (Fig. 2). The Miravalles volcanic system is estimated to have originated approximately one million years ago, and the last lava flow occurred 8000 years ago on its western flank, precisely where the Sabanas Miravalles are currently located (Alvarado, 2011).

¹University of Florida Herbarium, Florida Museum of Natural History, 379 Dickinson Hall, 1659 Museum Rd., Gainesville, Florida 32611, USA.

²University of Florida, Department of Biology, Gainesville, Florida 32611, USA.

³Universidad de Costa Rica, Centro de Investigación en Biodiversidad y Ecología Tropical, Herbario Luis A. Fournier Origgí (USJ), P.O. Box 11501-2060, San José, Costa Rica.

⁴Research Associate, Universidad de Costa Rica, Jardín Botánico Lankester, P.O. Box 3027050, Cartago, Costa Rica.

⁵Universidad de Costa Rica, Escuela de Biología, Apdo. 11501-2060, San Pedro, San José, Costa Rica.

⁶The School for Field Studies, Center for Ecological Resilience Studies, Apdo. 150-4013 Atenas, Costa Rica.

⁷Universidad de Costa Rica, Jardín Botánico Lankester, Apdo. 302-7050, Cartago, Costa Rica.



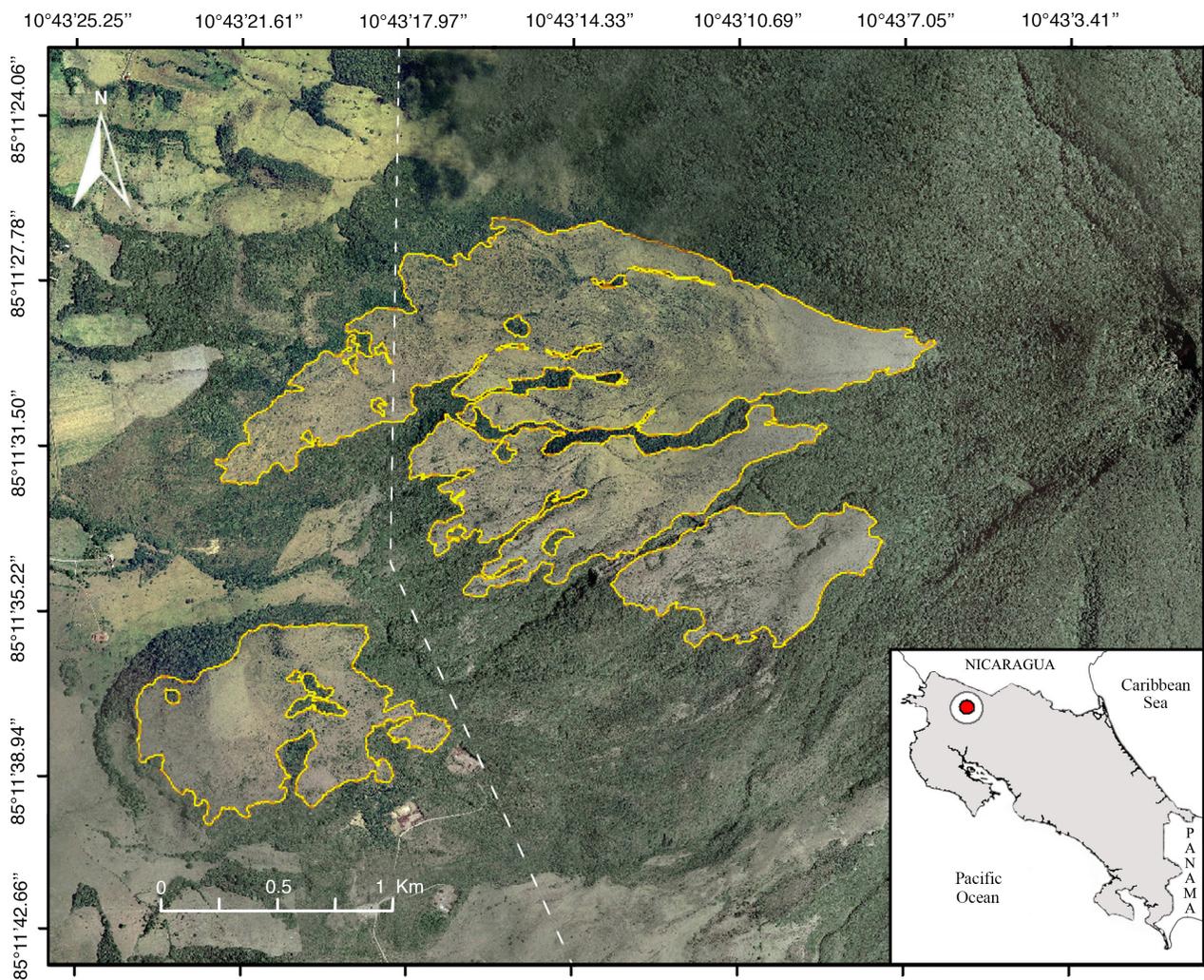


Figure 1: Location of the Miravalles Savannas, Guanacaste Mountain Range, Costa Rica. The area to the right of the dotted line is Volcán Miravalles National Park. Landsat satellite image (U.S. Geological Survey, 2011).

Collection of botanical specimens

Vascular plant specimens were collected over 20 days during 10 field trips (2012–2015) in both dry and rainy seasons. Specimens were deposited in the herbarium USJ, and databases from CR (Museo Nacional de Costa Rica, 2025), MO (TROPICOS, 2025), and USJ (no public database available) herbaria were consulted for historical records. Herbarium acronyms follow Thiers (2025). Taxonomic identification was based on literature, herbarium specimens, and expert consultations.

Establishment of plots

A systematic plot sampling design with nested subplots was employed following the methodology of Farruggia et al. (2008). According to this approach, 25 plots measuring 50

× 10 m were established, with the longer side aligned parallel to the dominant slope and spatially distributed homogeneously throughout the study area. Each plot was divided into five segments of 10 × 10 m. In the center of each segment, a 1 × 1 m subplot was established to sample herbaceous vegetation.

Although the initial locations of the plots were spatially randomized within the study area, the plots were established accessibility in the field based on access, starting from the lower elevations near the main entrance of the site and progressing upslope. As a result, plot numbers (P1 to P25) reflect the order of implementation and partially align with their relative spatial position along the elevation gradient.

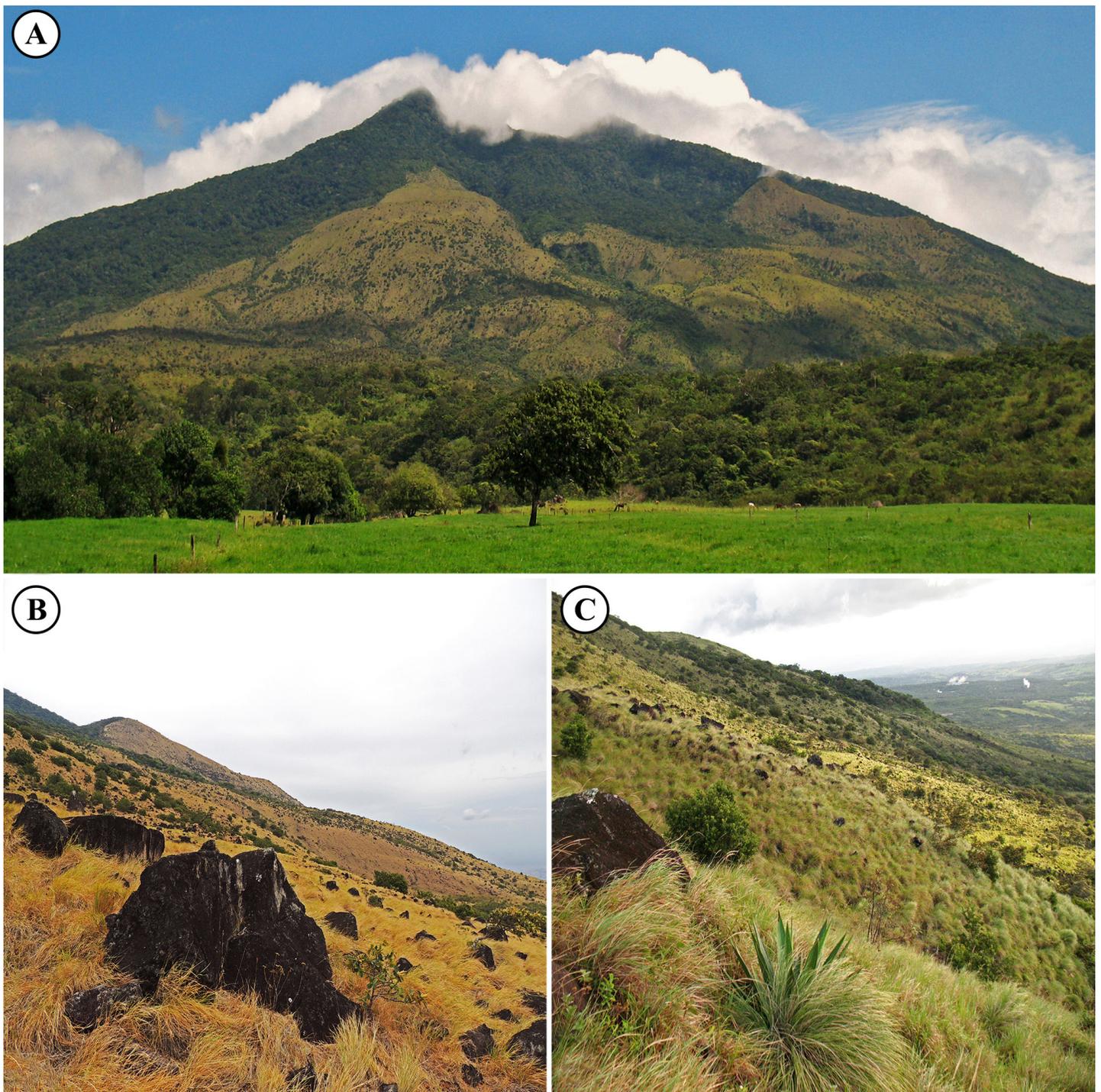


Figure 2: Sabanas Miravalles, Costa Rica. A. view of the Volcán Miravalles from Guayabo de Bagaces to the west of the volcano (the yellowish areas are the savannas); B. savanna landscape during the dry season; C. savanna landscape during the rainy season. Photographs by José Esteban Jiménez.

The presence and abundance of woody plants, graminoid, and non-graminoid herbs were recorded, and their physiognomic structure was documented. For woody vegetation and non-graminoid herbs, abundance was determined as the number of individuals per plot. A total

of 125 subplots were initially established, but 36 were excluded because more than 30% of their area was occupied by a tree or a superficial rock, leaving 89 subplots for sampling. For graminoid herbs, abundance was quantified as the percentage of ground cover within the subplots using

the point-intercept method (Mueller-Dombois and Ellenberg, 2002). Epiphytes were excluded from this part of the study due to their relatively low abundance.

Species inventory

An inventory of vascular plants was carried out based on the species registered in the 25 plots plus aleatoric collections of plants encountered throughout the savanna matrix not recorded in the plots. The checklist was compiled and organized by family and genus for Lycophytes, Monilophytes, and Spermatophytes. The taxonomy and nomenclature of seed plants followed the classification of the Angiosperm Phylogeny Group (APG, 2016), while Lycophytes and ferns were identified according to the criteria of Christenhusz et al. (2011). Species were categorized by life form using the Raunkiaer system (Raunkiaer, 1934), and by growth habit following Font-Quer (1982). Although epiphytes were excluded from the quantitative sampling conducted in the plots, they were recorded during the floristic survey and included in the checklist.

Sampling effort

To assess sampling representativeness, the Chao1 index (Chao, 2005) was used to estimate the maximum expected richness of woody plants and non-graminoid herbs. Also, a species-accumulation curve was performed using R software v. 4.3.1. (R Core Team, 2023), assembling a presence-absence matrix (plots × species) using composite plots (woody, graminoid, and non-graminoid records), then computed a randomized species-accumulation curve with 1000 permutations using `specaccum()` function from the Vegan package (Oksanen et al., 2020).

Characterization of species composition

The Relative Importance Value (RIV) was calculated for each species, representing the sum of relative abundance and relative frequency (Mueller-Dombois and Ellenberg, 2002). Changes in species composition were evaluated using presence/absence and abundance data, applying the Bray-Curtis similarity index (Krebs, 1999). A cluster analysis using the single linkage method was conducted based on the Bray-Curtis similarity matrix to compare

species composition across the 25 plots. The similarity calculations were performed using R software v. 4.3.1 (R Core Team, 2023). The `vegdist()` function from the vegan package (Oksanen et al., 2020) was employed to calculate Bray-Curtis similarity, while the `ggplot()` function from the `ggplot2` package (Wickham, 2016) was used to generate and customize the visualizations.

Species composition of Sabanas Miravalles in a Neotropical context

Native species were categorized by their distribution into seven mutually exclusive geographical groups: (A) Endemic to Costa Rica, (B) Present in Mesoamerica, (C) Present in the Neotropical region of the Northern Hemisphere, (D) Present throughout the Neotropics, (E) Present in both the Neotropics and Nearctic region, (F) Panropical, and (G) Cosmopolitan. Exotic species were excluded from this classification. Geographical distribution data were obtained from the TROPICOS database (TROPICOS, 2025). Category C was defined based on Lenthall et al. (1999), who identified the Neotropics of the Northern Hemisphere as extending from Ecuador (including the Venezuelan/Colombian Llanos, the Guianas, and the Orinoco) to the Tropic of Cancer. Category E included species with distributions extending beyond the Neotropics. It is important to note that this categorization was intended solely to reflect present-day geographic distribution patterns, not to infer the evolutionary or historical origin of the taxa.

This categorization was compared with the proportion of endemic species in Costa Rica (Zamora et al., 2004) and floristic data from other Neotropical savannas, including those of Belize (Goodwin et al., 2013), the Venezuelan Llanos (Duno de Stefano et al., 2007), and the Brazilian Cerrado (Castro et al., 1999; Batalha, 2001; Ratter et al., 2003), using the Sørensen similarity index. A cluster analysis was performed based on the resulting similarity matrix. All statistical analyses were conducted using R software v. 4.3.1. (R Core Team, 2023). The `vegdist()` function from the vegan package (Oksanen et al., 2020) was used to calculate Bray-Curtis similarity, while the `ggplot()` function from the `ggplot2` package (Wickham, 2016) was utilized to create and customize the visualizations.



Results

Floristic inventory of the Sabanas Miravalles

We identified 54 families, 161 genera, and 228 species of vascular plants, supported by 362 botanical specimens (Appendix). No records of previously collected specimens from the study site were found. The grasses *Hyparrhenia rufa* (Nees) Stapf and *Eleusine indica* (L.) Gaertn., along with the herb *Alysicarpus vaginalis* (L.) DC., were the only exotic and invasive species recorded at the site.

Spermatophytes constituted the majority of vascular plants, with 223 species, representing 92.5% of families, 97.5% of genera, and 97.8% of species. Lycophytes and ferns exhibited low diversity, with one and four species, respectively. The five families with the highest genus and species richness were Fabaceae (18 gen./28 spp.), Asteraceae (20 gen./25 spp.), Poaceae (17 gen./24 spp.), Orchidaceae (15 gen./19 spp.), and Cyperaceae (7 gen./18 spp.). Together, they accounted for nearly half of the documented vascular flora (114 species and 48% of the genera). The remaining 49 families were represented by eight or fewer species, with 23 of these families consisting of only a single species. The genera *Polygala* L. and *Rhynchospora* Vahl were the most diverse, with eight species each, followed by *Chamaecrista* (L.) Moench with five species, and *Paspalum* L. with four (Appendix).

This survey also yielded significant distributional records that expand the known flora of the region. Four species are reported here for the first time in the Cordillera de Guanacaste: *Fimbristylis complanata* (Retz.) Link, *Rhynchospora rugosa* (Vahl) Gale, *Malaxis macrostachya* (Lex.) Kuntze, and *Cologania procumbens* Kunth. Also, four additional angiosperm records for Costa Rican flora were identified and subsequently published: *Eriocaulon fuliginosum* C. Wright ex Griseb., *Polygala pseudocelosoides* Chodat, *Trimezia martinicensis* (Jacq.) Herb., and *Utricularia subulata* L. (Jiménez, 2017). Furthermore, this study provides the first record of *Polygala incarnata* L. (Polygalaceae) for Costa Rica (Appendix, Fig. 3), a species previously known from the United States of America to Nicaragua (TROPICOS, 2025).

Non-graminoid species constitute the most diverse growth habit (37% of total species), followed by shrub-herbs (21%) and graminoid herbs (18%). Among woody plants, shrubs were the most diverse growth habit, account-



Figure 3: *Polygala incarnata* L. (Polygalaceae) as a new record for the Costa Rican flora, documented in the Sabanas Miravalles, based on voucher J. E. Jiménez 2301 (USJ).

ing for 15% of species. Trees and vines exhibited low diversity, representing only 5% and 4% of species, respectively. Hemicryptophytes were the most diverse life form, comprising nearly half of the flora (111 spp.), followed by phanerophytes, which represented 20% of species. Chamaephytes, cryptophytes, epiphytes, and therophytes had a similar number of species, each contributing 7-9% of the savanna flora (Fig. 4).

A total of 120 species of woody and non-graminoid herbaceous species were recorded, representing 37 woody species and 83 non-graminoid herbaceous ones. We obtained a Chao1 index of 138 ± 3 species, while the observed number of species in these groups was 120. This suggests that the sampling effort was close to capturing the estimated species richness, with the observed number approaching the expected value predicted by the Chao1 index. Also, the randomized species-accumulation curve showed a clear asymptotic trend with narrowing confidence bounds towards the final sampling units, indicating that our survey captured most of the expected species richness and that sampling effort was adequate (Fig. 5).

Ecological importance value of species

Miconia sericea (D. Don) Michelang. was the woody species with the highest RIV (35.2%), followed by *Stachytarpheta frantzii* Pol. and *Byrsonima crassifolia* (L.) Kunth, with RIVs of



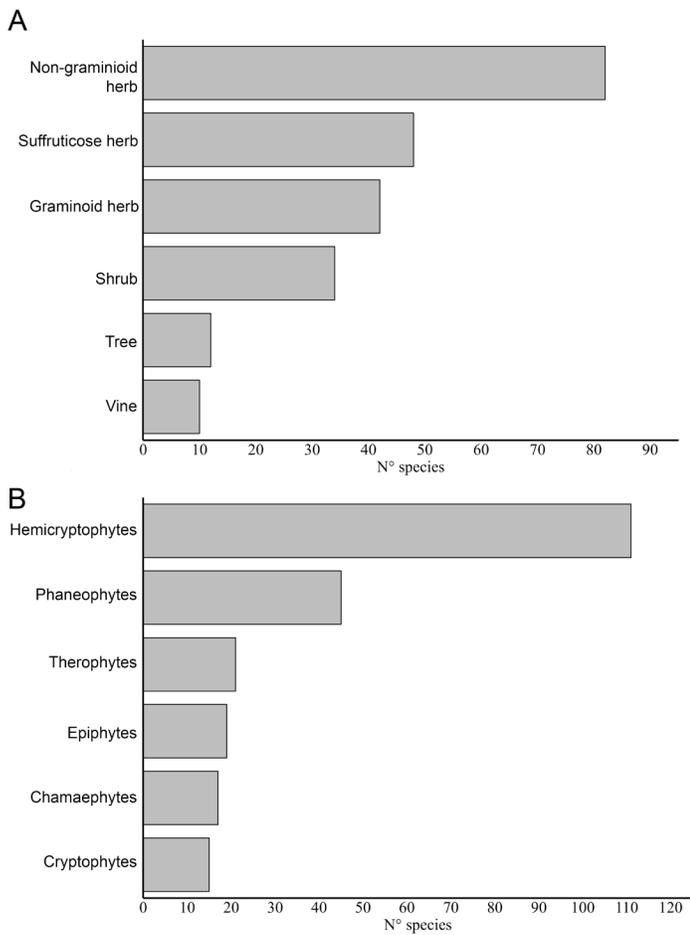


Figure 4: Number of vascular plant species of the Sabanas Miravalles, Costa Rica, by: A. habit; B. life form.

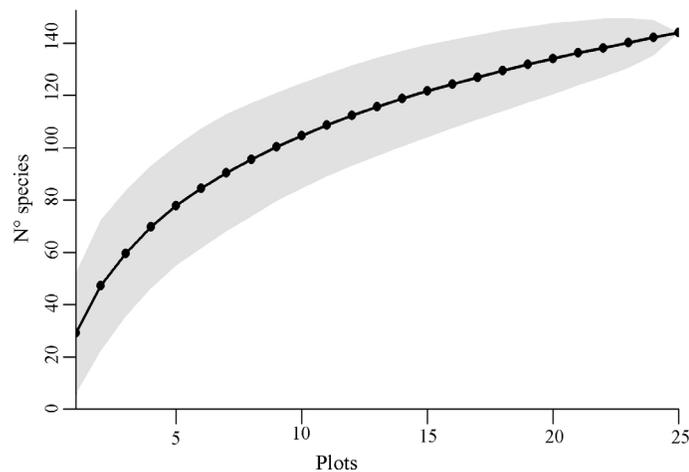


Figure 5: Species-accumulation curve across 25 plots (mean ± 95% CI from random 1000 permutations) carried out between 2012-2015 in the Sabanas Miravalles, Costa Rica.

17.1 and 16.1%, respectively. These three species accounted for 68.4% of the total RIV, while the remaining 34 woody species contributed the rest (Table 1). Among non-graminoid herbaceous species, *Polygala glochidata* Kunth had the highest RIV (37.8%), with a maximum density of 22 individuals/m². *Polygala longicaulis* Kunth and *Sauvagesia tenella* Lam. were the second and third most important non-graminoid herbaceous species, with RIVs of 11.9 and 11.3%, respectively. The grass *Trachypogon plumosus* (Humb. & Bonpl. ex Willd.) Nees was the most abundant and dominant graminoid herbaceous species, with 59.6% abundance and 70.3% RIV. *Paspalum centrale* Chase and *Rhynchospora barbata* (Vahl) Kunth followed, with RIVs of 23.1% and 17.3%, respectively. Together, these three graminoid species accounted for 86.1% of total graminoid species abundance (29 species, Table 1, Fig. 6).

Table 1: Abundance, frequency, and relative importance value (RIV) of the three main species by growth habit of the vascular flora of the Miravalles Savannas, Costa Rica. Abun.=Relative Abundance, Freq.=Relative Frequency, RIV=Relative Importance Value.

Woody plants			
Species	Abun.	Freq.	RIV
<i>Miconia sericea</i> (D. Don) Michelang.	24.1	11.1	35.2
<i>Stachytarpheta frantzii</i> Pol.	11.2	5.8	17.1
<i>Byrsonima crassifolia</i> (L.) Kunth	7.3	8.8	16.1
Other 34 spp.	57.4	74.3	131.7
Total	100	100	200
Non-graminoid herbs			
Species	Abun.	Freq.	RIV
<i>Polygala glochidata</i> Kunth.	30.4	7.4	37.8
<i>Polygala longicaulis</i> Kunth.	5.9	5.9	11.9
<i>Sauvagesia tenella</i> Lam.	8.4	3.0	11.3
Other 75 spp.	55.3	83.7	139.0
Total	100	100	200
Graminoid herbs			
Species	Abun.	Freq.	RIV
<i>Trachypogon plumosus</i> (Humb. & Bonpl. ex Willd.) Nees	59.6	10.8	70.3
<i>Paspalum centrale</i> Chase	19.5	3.6	23.1
<i>Rhynchospora barbata</i> (Vahl) Kunth	7.0	10.3	17.3
Other 26 spp.	14.0	75.4	89.4
Total	100	100	200



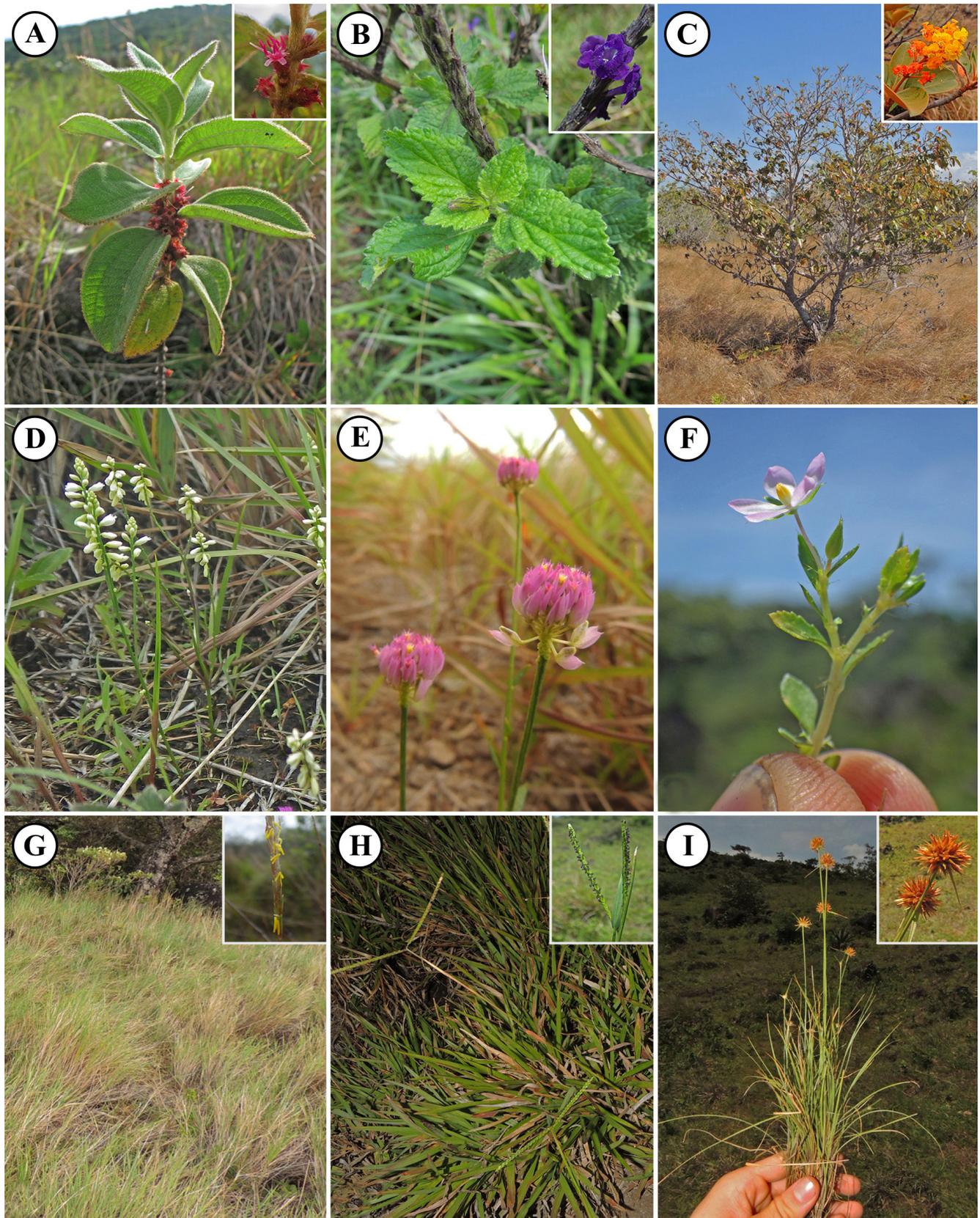


Figure 6: Most abundant woody plants, non-graminoid herbs, and graminoid herbs in the Miravalles Savannas, Costa Rica. Woody plants: A. *Miconia sericea* (D. Don) Michelang. (Melastomataceae); B. *Stachytarpheta frantzii* Pol. (Verbenaceae); C. *Byrsonima crassifolia* (L.) Kunth (Malpighiaceae). Non-graminoid herbs: D. *Polygala glochidata* Kunth (Polygalaceae); E. *Polygala longicaulis* Kunth (Polygalaceae); F. *Sauvagesia tenella* Lam. (Ochnaceae). Graminoid herbs: G. *Trachypogon plumosus* (Humb. & Bonpl. ex Willd.) Nees (Poaceae); H. *Paspalum centrale* Chase (Poaceae); I. *Rhynchospora barbata* (Vahl) Kunth (Cyperaceae). Photographs by José Esteban Jiménez.

Spatial heterogeneity of vegetation

Cluster analysis revealed spatial heterogeneity among the 25 plots in the Miravalles Savannas, with a clear elevation-driven effect on floristic composition. However, because plots were numbered sequentially in the field starting from the lower entrance of the study area to higher elevations, the clustering of plot numbers also partially reflects their spatial proximity along the elevational gradient. The dendrogram identified three main groups at a dissimilarity threshold of 0.45-0.55. Notably, Plot P16 emerged as a distinct outlier, indicating unique species composition, confirming its differentiation from the other plots. The remaining plots formed two primary clusters: one encompassing plots P12 to P8 and the other including plots P1, P3, P5, P2, and P4 (Fig. 7).

The first group, located at an elevation of 922 m and consisting solely of Plot P16, harbors several species found exclusively in this single sampling unit. These include graminoids such as *Homolepis aturensis* (Kunth) Chase, *Steinchisma laxum* (Sw.) Zuloaga, *Paspalum clavuliferum* C. Wright, *Setaria parviflora* (Poir.) Kerguelen, *Eleocharis geniculata* (L.) Roem. & Schult., *Fimbristylis complanata* (Retz.) Link, *Cyperus salzmannianus* (Steud.) Batters, and *Rhynchospora filiformis* Vahl, alongside non-graminoid herb species such as *Acisanthera quadrata* Pers., *Burmannia capitata* (Walter ex J.F. Gmel.) Mart., *Eriocaulon fuliginosum* C. Wright ex Griseb., *Melananthus guatemalensis* (Benth.) Soler., and *Polygala tenella* Willd. The second cluster, located exclu-

sively within an elevation range of 640-1240 m, encompasses 76% of the plots (P6 to P25, excluding P16). This region accounts for the majority of the savanna's floristic diversity. It is characterized by the dominance of *Paspalum centrale* as the most abundant grass, along with the presence of the abundant non-graminoid herb *Polygala longicaulis* and woody species such as *Miconia sericea*, *Stachytarpheta frantzii*, and *Byrsonima crassifolia*. The third group, situated at elevations of 1300-1580 m and comprising Plots P1 to P5, exhibits a distinct pattern. This cluster is dominated by the grass *Trachypogon plumosus* and shares the presence of the non-graminoid herb *Polygala glochidata* and the woody plant *Pernettya prostrata* (Cav.) DC.

Geographic distribution and phytogeographic relationships

Most species in the Sabana Miravalles had broad latitudinal distributions. A total of 33.8% exhibited extensive Neotropical distributions (category D), with some species extending into subtropical and temperate regions (category E). Species restricted to the Neotropics of the Northern Hemisphere comprised 17.3%. No endemic species were recorded for Costa Rica, and the representation of Mesoamerican endemics (category B) was low (7.6%). Pantropical (category F) and cosmopolitan (category G) species were also minimally represented (6.7% and 2.7%, respectively, Fig. 8).

The flora of Sabana Miravalles showed the greatest similarity to that of the Venezuelan Llanos (Duno de Stefano et al., 2007), sharing 70% of species (159 spp.). Both were more similar to the Brazilian Cerrado (Castro et al., 1999; Batalha, 2001; Ratter et al., 2003) than to the savannas of Belize (Goodwin et al., 2013). The Miravalles savanna shared 45% (102 spp.) of its species with the Brazilian Cerrado and 36% (82 spp.) with the Belizean savannas (Fig. 9).

Discussion

Floristic inventory and comparison with other Neotropical savannas

Although there is ongoing debate about the historical origin of savannas (Archibald et al., 2019), their contemporary presence in the American tropics depends on the balance between moisture availability, fire incidence, and water stress (Beckage et al., 2019). As humidity increases, woody

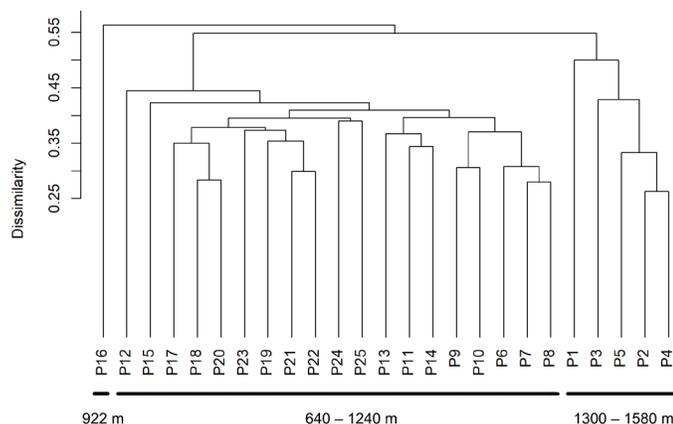


Figure 7: Dendrogram based on the Bray-Curtis index of the 25 plots in the Sabanas Miravalles, Costa Rica.

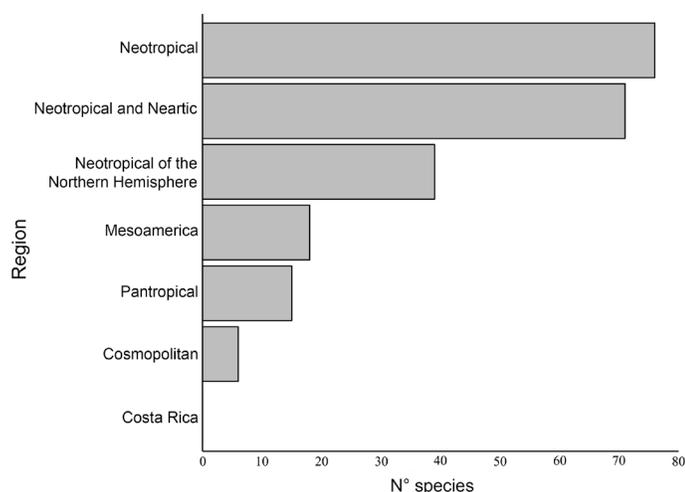


Figure 8: Abundance of phytogeographic distribution categories of the vascular flora of the Miravalles Savannas, Costa Rica.

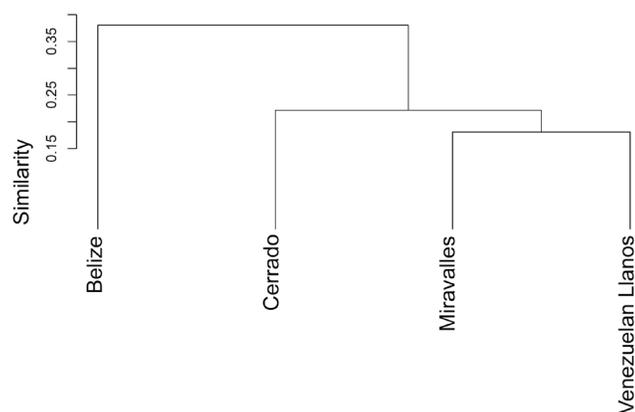


Figure 9: Floristic affinity between the Miravalles Savannas, Costa Rica, and three Neotropical savannas with well-documented floras compared with the Bray-Curtis distance and the single linkage method.

vegetation expands until a closed-canopy forest is established. However, recurrent fires and water stress during the dry season can limit woody vegetation and promote the expansion of herbaceous vegetation, establishing savannas as a stable alternative state (Beckage et al., 2019).

There are no contemporary historical records of anthropogenic fires in the Miravalles Savannas. Nevertheless, the presence of herbaceous species that depend on fire for dispersal, the abundance of the tree *Byrsonima crassifolia*,

and the prevalence of fire-resistant traits in the flora suggest that fire has significantly influenced the species composition of this savanna. In southern Costa Rica, anthropogenic fires are essential for the persistence of wet savannas (Artavia Rodríguez and Avalos, 2020), as they reduce the dominance of the arboreal component. This may also apply to the Sabanas Miravalles. Research on Costa Rican savanna flora remains in its early stages, leading to scarce comparative data, both in terms of geographic distribution (Elizondo and Jiménez, 1988) and the role of recurrent fires, which are vital for the existence and persistence of these ecosystems (Gómez and Herrera, 1986; Artavia-Rodríguez and Ávalos, 2020).

Structural and floristic distinctions between natural savannas and anthropogenic pastures have been demonstrated in other Neotropical savannas, highlighting the importance of historical land use, fire regimes, and edaphic constraints in shaping savanna vegetation (López-Olmedo et al., 2007). These findings support the idea that fire-driven ecological filters contribute to the differentiation and long-term persistence of natural savannas.

The flora of the Sabanas Miravalles represents 2.1% of the approximately 10,712 species of vascular plants in Costa Rica, despite occupying only 0.006% of the country's continental territory (Ávalos, 2019). Although this ecosystem is vulnerable to colonization by invasive plants, the percentage of introduced species was very low, suggesting that this community has not been significantly altered by human activity (Pivello et al., 1999), at least in the recent past. The presence of only a few exotic grasses is surprising, considering that the surrounding areas are subjected to extensive livestock farming, which relies on introduced African grasses such as *Hyparrhenia rufa*.

The species richness pattern by family and genus in the Miravalles Savannas was similar to other savannas in the Neotropics, and was characterized by many monospecific families and genera, and relatively few families and genera with multiple species (Castro et al., 1999; Ratter et al., 2003; Batalha and Martins, 2007; Goodwin et al., 2013). Fabaceae was the most diverse family, accounting for 12.3% of the total number of species and 4.7% of the vascular flora recorded in Costa Rica. Fabaceae was also the most diverse family in the savannas of Belize (Goodwin



et al., 2013) and the Cerrado of Brazil (Castro et al., 1999; Batalha, 2001). The high diversity of Fabaceae is likely due to their production of orthodox seeds, an adaptation for survival in regions with high dehydration and temperature (Weber et al., 2005). Their association with nitrogen-fixing bacteria offers a significant advantage in nutrient-poor soils subjected to seasonal water stress, as these bacteria enhance nutrient and water uptake, improving plant tolerance to such conditions (Sánchez-Navarro et al., 2020).

The families Asteraceae, Cyperaceae, Poaceae, and Rubiaceae were also among the most diverse in both the Sabanas Miravalles and other Neotropical savannas (Batalha, 2001; Duno de Stefano et al., 2007; Goodwin et al., 2013). Additionally, the genus *Rhynchospora* was one of the two most diverse genera in the Miravalles Savannas, as well as in the savannas of Belize (Goodwin et al., 2013) and the Venezuelan Llanos (Duno de Stefano et al., 2007; Ramírez et al., 2007).

The Sabanas Miravalles exhibited a higher richness of non-graminoid herbs compared to other Neotropical savannas, which are typically dominated by graminoid herbs (Batalha, 2001; Duno de Stefano et al., 2007; Goodwin et al., 2013). The hemicryptophyte life form recorded the highest number of species, a pattern observed in other Neotropical savannas as well (Batalha, 2001; Pérez-García and Meave, 2006; Duno de Stefano et al., 2007; Goodwin et al., 2013). The dominance of hemicryptophyte species is likely due to their axillary buds at ground level and basal leaves, which enhance drought and fire resistance, and facilitate vegetative dispersal after fires (Pérez-García and Meave, 2006). In contrast, the low representation of chamaephytes, cryptophytes, and therophytes in these savannas (Ellenberg and Mueller-Dombois, 1967) may be due to the higher water availability requirements of these groups (Riina et al., 2007).

Low tree species richness in the Sabanas Miravalles is typical of Central American savannas (Bridgewater et al., 2002), but contrasts with the greater tree diversity in South American savannas, such as the Cerrado (Ratter et al., 1997; Duno de Stefano et al., 2007). Greater tree diversity is often associated with increased topographic and edaphic variation (Lenthall et al., 1999). This variability is evident in the presence of depressions or holes in the Sabanas Mira-

valles, which may act as refuges that facilitate tree seed and seedling regeneration during fire events, like what has been observed in the humid savannas of the southern Pacific region of Costa Rica (Artavia-Rodríguez et al., 2024). We observed that trees and their seedlings tend to concentrate in these depressions, likely because runoff deposits organic matter and nutrients that accumulate in these areas, facilitating tree regeneration. Furthermore, these depressions or holes may protect seedlings from the desiccating effects of intense dry-season winds. The pronounced seasonality and low humidity of this ecosystem likely contribute to the limited species richness of lycophytes and ferns (Riina et al., 2007).

Regarding herbaceous plants, the floristic composition of the Sabanas Miravalles was similar to other Neotropical savannas, characterized by a low abundance of woody species and graminoid herbs and a more balanced abundance of non-graminoid herbs (Parsons, 1955; Furlley, 1997; Ramírez et al., 2007). The fire-resistant species *Byrsonima crassifolia* was the most abundant tree in the Miravalles Savannas. This is one of the four most abundant tree species in the savannas of Central and northern South America (Lenthall et al., 1999; Souza et al., 2002; Duno de Stefano et al., 2007; Farruggia et al., 2008).

The dominance of the grass *Trachypogon plumosus* in the Sabanas Miravalles partially agrees with the classification developed by Gómez and Herrera (1986), who proposed the name “open savannas of *Trachypogon plumosus*” for those on the Pacific slope of the Cordillera de Guanacaste. However, our study found that this grass is dominant only above 900 m, while *Paspalum centrale* dominates at lower elevations. Furthermore, the documentation of a woody stratum across the Sabanas Miravalles does not align with Gómez’s description of “open savannas”. This discrepancy suggests the need for a revised classification of Costa Rican savannas based on quantitative and qualitative data from individual communities.

Species with the highest ecological importance

Unlike other Neotropical savannas, in the Miravalles Savannas, *Miconia sericea* and *Polygala glochidata* were the most abundant woody and non-graminoid herbaceous species, respectively. Both species are widely distributed

throughout the Neotropics. Notably, as observed in other natural savannas of Mesoamerica, *Polygala* is often exclusive to savanna habitats and absent from adjacent pastures, suggesting long-term ecological differentiation and the persistence of floristically distinct assemblages (López-Olmedo et al., 2007).

Effects of spatial heterogeneity on floristic composition

We observed differences in species composition, both herbaceous and woody, based on elevation, especially above 1300 m a.s.l. In addition to elevation, factors such as the density of exposed rocks, terrain slope, topographic variations (e.g., depressions or holes), and wind speed and exposure are likely to influence species distribution. It is also necessary to evaluate the effects of nutrient distribution, soil texture, and variations in temperature and humidity.

Sarmiento (1984) demonstrated that the floristic composition of savannas changes along an altitudinal gradient, a pattern also observed in forest ecosystems, with greater diversity at lower elevations. Our results contrast with those of Renvoize (1998), who proposed that savanna species typically have wide altitudinal distributions. In the Sabanas Miravalles, we observed clear differences in species composition, particularly above 1300 m. This higher-elevation cluster (1300-1580 m) is characterized by increased exposure to strong winds, steeper slopes, and a higher abundance of rocky outcrops, which likely contribute to differences in microhabitat conditions. These factors can potentially limit soil moisture retention, influence nutrient availability, and create environmental stress that favors species adapted to drier and more exposed conditions, such as *Trachypogon plumosus*, *Polygala glochidata*, and *Pernettya prostrata*. The unique floristic composition found in Plot P16 may be explained by the microtopographic conditions compared to other plots, as it is located in an unusual flat area compared to the other plots. The reduced slope likely promotes temporary surface water accumulation during the rainy season, creating a moist condition that persists longer. Such conditions may favor the establishment of species with greater affinity for humid or seasonally wet environments.

The identified clusters suggest that floristic composition is shaped by environmental heterogeneity, likely influ-

enced by factors such as soil types and elevation gradients. The Sabanas Miravalles are distinct in being distributed along a wide altitudinal gradient, which is uncommon in other floristic studies that typically focus on lowland savannas with narrower altitudinal ranges. These groupings highlight the strong influence of environmental heterogeneity on the vegetation patterns of the savanna, emphasizing the need for a more detailed evaluation of how physical factors, particularly wind exposure, soil characteristics, and terrain structure, shape species composition at different elevations.

Consequently, the apparent correlation between plot number and cluster membership is largely a byproduct of logistical field access along the elevational gradient. While this does not undermine the observed floristic turnover associated with elevation, future analyses should incorporate explicit spatial modeling to further disentangle the effect of elevation and geographic distance.

Phytogeographic relationships and geographic distribution of species

The phytogeographic relationships of the flora of the Sabanas Miravalles are complex, as many herbaceous species exhibit extra-tropical distributions. Most species have wide distributions throughout the Neotropics, a pattern shared with the savannas of the Venezuelan Llanos, the Brazilian Cerrado, and Bolivia (Lenthall et al., 1999; Duno de Stefano et al., 2007). The dominance of species with broad Neotropical distributions suggests that many species in the Sabanas Miravalles originated in South America and extended into Central America, likely during the Miocene and Pleistocene, which were characterized by cycles of greater regional aridity (Graham, 2011). This hypothesis is supported by increased grass pollen in fossil records from Panama during these periods (Burnham and Graham, 1999). In addition, local historical factors such as floristic exchange during the last glacial period of the Pleistocene, volcanic activity, and recurrent fire events may have shaped the current floristic composition of the Sabanas Miravalles, reinforcing the role of both geological and climatic dynamics in the origin of this ecosystem.

A similar biogeographic pattern has been reported for the seasonally dry tropics of Mexico, where floristic elements show affinities with Central and South Amer-



ican savannas, likely shaped by tectonic processes and Pleistocene climate dynamics (Pérez-García et al., 2012). These trans-isthmian links suggest that the presence of drought-adapted taxa in Central America, including in the Sabanas Miravalles, may reflect an ancient dispersal corridor connecting Mesoamerican and South American dry ecosystems.

The Sabanas Miravalles displayed greater floristic affinity with South American savannas than with those in northern Central America. A similar pattern was identified by Lenthall et al. (1999). The savannas of Belize, however, have a distinctive floristic composition, with many herbaceous species (44%) appearing endemic to the region (Goodwin et al., 2013). The similarities in species composition of the Sabanas Miravalles with other natural savannas in the Neotropics suggest that the latter have a natural origin. There are no endemic elements in the Sabanas Miravalles, which contrasts with the high proportion of species with wide distributions. This may be related to the relatively short existence of Costa Rican savannas (Graham, 2011), and the brief history of the Sabanas Miravalles, which may have formed after the last lava flow of the Miravalles Volcano approximately 8000 years ago (Alvarado, 2011). The prevalence of species with broad geographic distributions is characteristic of ecosystems dominated by herbaceous plants with great ecological and latitudinal amplitude, attributed to their high dispersal capacity and wind pollination (Sarmiento, 1984). The absence of endemism in our study also contrasts with the estimated number of endemic plant species in Costa Rica (900-1000 species; Zamora et al., 2004) and the higher endemism recorded in other Neotropical savannas, where nearly half or more of the flora is endemic. Understanding the origin, phytogeographic affinities, and the influence of physical factors on the development of savanna flora is essential for improving conservation strategies and the management of this ecosystem. While savannas have often been considered anthropic environments and given secondary importance in scientific analysis and conservation efforts, their ecological significance must be recognized (López-Olmedo et al., 2007). They harbor a considerable diversity of species adapted to extreme climatic conditions, which may provide resilience in the face of advancing climate change.

Authors contributions

Project administration: JEJ; Conceptualization: JEJ, MAB; Investigation: JEJ; Data Curation: JEJ; Methodology: JEJ, GA, MAB; Formal analysis: JEJ; Funding acquisition: JEJ; Visualization: JEJ; Validation: JEJ, GA, MAB; Resources: JEJ, GA, MAB; Software: JEJ; Supervision: GA, MAB; Writing – original draft: JEJ; Writing – review & editing: JEJ, GA, MAB.

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Data Availability Statement

The dataset supporting the findings of this study was published in SciELO Data and can be accessed at: <https://doi.org/10.48331/SCIELODATA.1BJD40>

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Appendix: Vascular flora of the Miravalles Savannas, Costa Rica. Classification of Life Forms (LF): Ca=Chamaephytes, Cr=Cryptophytes, E=Epiphytes, H=Hemicryptophytes, F=Phanerophytes, T=Therophytes. Habit (Ha): A=Tree, Ar=Shrub, B=Vine, Hg=Graminoid herbs, H=Non-graminoid herbs, Hs=Suffruticose herbs. All vouchers were collected by the first author and were deposited in the herbarium USJ. The new record for Costa Rica, for the Cordillera de Guanacaste, the endemic species, and the exotic species are indicated with letter N (^N), asterisks (*), the letter E (^E), and letter I (^I) at the end of the scientific name, respectively.

Taxa	LF	Ha	Voucher(s)
LYCOPHYTA			
Selaginellaceae			
<i>Selaginella minima</i> Spring	H	H	2467
PTERIDOPHYTA			
Anemiaceae			
<i>Anemia oblongifolia</i> (Cav.) Sw.	H	H	3049
<i>Anemia pastinacaria</i> Moritz ex Prantl	H	H	2098
Dennstaedtiaceae			
<i>Pteridium caudatum</i> (L.) Maxon	Cr	H	2294
Pteridaceae			
<i>Mildella intramarginalis</i> (Kaulf. ex Link) Trevis.	H	H	2101
SPERMATOPHYTA			
MONOCOTS			
Asparagaceae			
<i>Furcraea cabuya</i> Trel.	H	H	1385
Bromeliaceae			
<i>Catopsis micrantha</i> L.B. Sm.	E	H	1263, 3077
<i>Pitcairnia heterophylla</i> (Lindl.) Beer	E	H	2103
<i>Tillandsia pruinosa</i> Sw.	E	H	2465
Burmanniaceae			
<i>Apteria aphylla</i> (Nutt.) Barnhart ex Small	T	H	1838
<i>Burmannia capitata</i> (Walter ex J.F. Gmel.) Mart.	T	H	968, 2474
Cyperaceae			
<i>Bulbostylis junciformis</i> (Kunth) C.B. Clarke	H	Hg	1854
<i>Bulbostylis tenuifolia</i> (Rudge) J.F. Macbr.	H	Hg	2463, 3012
<i>Cyperus flavescens</i> L.	H	Hg	3020
<i>Cyperus haspan</i> L.	H	Hg	3015
<i>Cyperus salzmannianus</i> (Steud.) Bauters	H	Hg	3019
<i>Eleocharis geniculata</i> (L.) Roem. & Schult.	H	Hg	3023
<i>Fimbristylis complanata</i> (Retz.) Link*	H	Hg	3027, 3053
<i>Fimbristylis spadicea</i> (L.) Vahl	H	Hg	3054
<i>Rhynchospora barbata</i> (Vahl) Kunth	H	Hg	1030, 3026
<i>Rhynchospora eximia</i> (Nees) Boeckeler	H	Hg	3013
<i>Rhynchospora filiformis</i> Vahl	H	Hg	3024
<i>Rhynchospora globosa</i> (Kunth) Roem. & Schult.	H	Hg	3358
<i>Rhynchospora hirsuta</i> (Vahl) Vahl	H	Hg	2466
<i>Rhynchospora holoschoenoides</i> (Rich.) Herter	H	Hg	3006, 2749
<i>Rhynchospora nervosa</i> (Vahl) Boeckeler	H	Hg	2725
<i>Rhynchospora rugosa</i> (Vahl) Gale*	H	Hg	1032, 2304, 3055
<i>Scleria distans</i> Poir.	H	Hg	2926

Appendix: Continuation.

Taxa	LF	Ha	Voucher(s)
<i>Scleria tenella</i> Kunth	H	Hg	2090, 3011, 3069
Eriocaulaceae			
<i>Eriocaulon fuliginosum</i> C. Wright ex Griseb.	T	H	2472, 3022
Hypoxidaceae			
<i>Curculigo scorzonrifolia</i> (Lam.) Baker	Cr	H	2283
<i>Hypoxis humilis</i> Kunth	Cr	H	2759
Iridaceae			
<i>Cipura campanulata</i> Ravenna	Cr	H	1830, 3064
<i>Trimezia martinicensis</i> (Jacq.) Herb.	Cr	H	946, 1831, 1850
Orchidaceae			
<i>Bletia purpurea</i> (Lam.) DC.	Cr	H	2292
<i>Christensonella uncata</i> (Lindl.) Szlach., Mytnik, Górniak & Śmiszek	E	H	940, 1277, 2088
<i>Cyclopogon guayanensis</i> (Lindl.) B.M.Carvalho & Meneguzzo	Cr	H	2724, 2747
<i>Dichaea panamensis</i> Lindl.	E	H	2309
<i>Encyclia ceratistes</i> (Lindl.) Schltr.	E	H	2727
<i>Epidendrum centropetalum</i> Rchb. f.	E	H	1270
<i>Epidendrum congestoides</i> Ames & C. Schweinf.	E	H	1275
<i>Epidendrum stangeanum</i> Rchb. f.	E	H	974
<i>Habenaria lankesteri</i> Ames ^E	Cr	H	1843, 3051
<i>Habenaria trifida</i> Kunth	Cr	H	1845, 3060
<i>Malaxis macrostachya</i> (Lex.) Kuntze*	Cr	H	3050
<i>Platystele stenostachya</i> (Rchb. f.) Garay	E	H	943
<i>Prosthechea fragrans</i> (Sw.) W.E. Higgins	E	H	1274
<i>Rhetinantha friedrichsthalii</i> (Rchb. f.) M.A. Blanco	E	H	942
<i>Sacoila lanceolata</i> (Aubl.) Garay	Cr	H	2281
<i>Scaphyglottis imbricata</i> (Lindl.) Dressler	E	H	1276
<i>Scaphyglottis prolifera</i> (Sw.) Cogn.	E	H	2082
<i>Sobralia bradeorum</i> Schltr.	E	H	1259, 2300
<i>Specklinia grobyi</i> (Bateman ex Lindl.) F. Barros	E	H	941
Poaceae			
<i>Andropogon bicornis</i> L.	H	Hg	2714
<i>Andropogon gerardi</i> Vitman	H	Hg	2306
<i>Aristida capillacea</i> Lam.	H	Hg	2110
<i>Axonopus aureus</i> P. Beauv.	H	Hg	1010, 2305
<i>Dichantherium acuminatum</i> (Sw.) Gould & C.A. Clark	H	Hg	3014
<i>Dichantherium strigosum</i> (Muhl. ex Elliott) Freckmann	H	Hg	959, 2743
<i>Dichantherium viscidellum</i> (Scribn.) Gould	H	Hg	2756, 2091, 2094, 3072, 3073
<i>Digitaria bicornis</i> (Lam.) Roem. & Schult.	H	Hg	2693
<i>Eleusine indica</i> (L.) Gaertn. ¹	H	Hg	2709
<i>Eragrostis pectinacea</i> (Michx.) Nees	H	Hg	2699
<i>Homolepis aturensis</i> (Kunth) Chase	H	Hg	3017
<i>Hyparrhenia rufa</i> (Nees) Stapf ¹	H	Hg	3057
<i>Ischaemum latifolium</i> (Spreng.) Kunth	H	Hg	1029



Appendix: Continuation.

Taxa	LF	Ha	Voucher(s)
<i>Muhlenbergia lehmanniana</i> Henrard	H	Hg	2108, 2307
<i>Panicum laxum</i> Sw.	H	Hg	3028
<i>Paspalum centrale</i> Chase	H	Hg	2733, 3032
<i>Paspalum clavuliferum</i> C. Wright	H	Hg	3034
<i>Paspalum pectinatum</i> Nees ex Trin.	H	Hg	3076, 3171
<i>Paspalum pilosum</i> Lam.	H	Hg	3030
<i>Paspalum plicatulum</i> Michx.	H	Hg	3031
<i>Schizachyrium brevifolium</i> (Sw.) Nees ex Buse	H	Hg	3065
<i>Schizachyrium sanguineum</i> (Retz.) Alston	H	Hg	1013, 3029, 3074
<i>Setaria parviflora</i> (Poir.) Kerguélen	H	Hg	3016
<i>Trachypogon plumosus</i> (Humb. & Bonpl. ex Willd.) Nees	H	Hg	952
EUDICOTS			
Acanthaceae			
<i>Ruellia geminiflora</i> Kunth	H	Hs	1244, 2703, 2723
Apiaceae			
<i>Eryngium ebracteatum</i> Lam.	Cr	H	3018
Apocynaceae			
<i>Asclepias curassavica</i> L.	Ca	H	3035
Asteraceae			
<i>Ageratum petiolatum</i> (Hook. & Arn.) Hemsl.	H	Hs	956, 1019, 2722, 2757
<i>Ayapana amygdalina</i> (Lam.) R.M. King & H. Rob.	Ca	Hs	1382, 2282
<i>Baccharis trinervis</i> Pers.	F	Ar	2704, 3086
<i>Brickellia kellermanii</i> Greenm.	F	Ar	2107
<i>Calea prunifolia</i> Kunth	F	Ar	1282
<i>Campuloclinium macrocephalum</i> (Less.) DC.	H	H	1835
<i>Chaptalia nutans</i> (L.) Pol.	H	H	2720
<i>Chaptalia runcinata</i> Kunth	H	H	1851
<i>Chromolaena collina</i> (DC.) R.M. King & H. Rob.	F	Ar	1234
<i>Chromolaena glaberrima</i> (DC.) R.M. King & H. Rob.	F	Ar	1294
<i>Chrysanthellum integrifolium</i> DC.	H	H	1852, 2721
<i>Clibadium leiocarpum</i> Steetz	F	Ar	1021
<i>Comaclinium montanum</i> (Benth.) Strother	H	H	1254
<i>Conyza bonariensis</i> (L.) Cronquist	H	H	2701
<i>Conyza laevigata</i> (Rich.) Pruski	H	H	2700
<i>Delilia biflora</i> (L.) Kuntze	T	H	3009
<i>Elephantopus mollis</i> Kunth	H	Hs	1255, 2097
<i>Gnaphalium attenuatum</i> DC.	Ca	Hs	1256, 2092
<i>Lepidaploa canescens</i> (Kunth) H. Rob.	F	Ar	2084, 2298
<i>Melanthera nivea</i> (L.) Small	F	Ar	2695, 2751
<i>Pseudelephantopus spicatus</i> (Juss. ex Aubl.) C.F. Baker	Ca	Hs	2708
<i>Tridax procumbens</i> L.	H	Hs	1242
<i>Verbesina guatemalensis</i> B.L. Rob. & Greenm.	Ca	Hs	923



Appendix: Continuation.

Taxa	LF	Ha	Voucher(s)
<i>Verbesina turbacensis</i> Kunth	F	Ar	1024
Boraginaceae			
<i>Varronia guanacastensis</i> (Standl.) J.S. Mill.	F	Ar	1283
Campanulaceae			
<i>Lobelia laxiflora</i> Kunth	Ca	Hs	2299
<i>Lobelia xalapensis</i> Kunth	T	H	2100
Clethraceae			
<i>Clethra lanata</i> M. Martens & Galeotti	F	A	3046
Convolvulaceae			
<i>Evolvulus filipes</i> Mart.	T	H	1235, 2471
<i>Evolvulus sericeus</i> Sw.	H	Hs	2734
<i>Ipomoea batatas</i> (L.) Lam.	F	B	1289
<i>Ipomoea capillacea</i> (Kunth) G. Don	Cr	H	1828
Ericaceae			
<i>Macleania insignis</i> M. Martens & Galeotti	E	Ar	1272, 2280
<i>Pernettya prostrata</i> (Cav.) DC.	Ca	Ar	2296, 3071
<i>Satyria meiantha</i> Donn. Sm.	E	Ar	2286
Erythroxylaceae			
<i>Erythroxylum macrophyllum</i> Cav.	F	Ar	1262, 2308
Euphorbiaceae			
<i>Croton trinitatis</i> Millsp.	H	Hs	2293
<i>Dalechampia cissifolia</i> Poepp.	F	B	1290, 1826, 2085
<i>Euphorbia hirta</i> L.	H	H	2692
<i>Euphorbia thymifolia</i> L.	H	H	2710
Fabaceae			
<i>Alysicarpus vaginalis</i> (L.) DC. ¹	H	H	1827
<i>Centrosema angustifolium</i> (Kunth) Benth.	F	B	1840
<i>Centrosema molle</i> Mart. ex Benth.	F	B	970, 1249
<i>Chamaecrista diphylla</i> (L.) Greene	H	Hs	1269, 2106
<i>Chamaecrista hispidula</i> (Vahl) H.S. Irwin & Barneby	H	Hs	1239, 1378, 2755
<i>Chamaecrista kunthiana</i> (Schltdl. & Cham.) H.S. Irwin & Barneby	H	Hs	1268, 2728
<i>Chamaecrista nictitans</i> (L.) Moench	H	Hs	1025, 2087
<i>Chamaecrista rotundifolia</i> (Pers.) Greene	H	Hs	2105, 3180
<i>Clitoria guianensis</i> (Aubl.) Benth.	Cr	Hs	3063
<i>Cologania procumbens</i> Kunth*	Cr	Hs	2291, 2706, 2745
<i>Dalbergia calycina</i> Benth.	F	A	1034, 1847
<i>Desmodium barbatum</i> (L.) Benth.	H	Hs	3059
<i>Desmodium incanum</i> (Sw.) DC.	Ca	Hs	1247, 2713, 2726, 2744
<i>Eriosema crinitum</i> (Kunth) G. Don	H	Hs	2279, 2711, 2730
<i>Eriosema diffusum</i> (Kunth) G. Don	H	Hs	1012
<i>Galactia argentea</i> Brandegees	F	B	2738, 3052
<i>Helicotropis linearis</i> (Kunth) A.Delgado	F	B	1248, 2705, 2750
<i>Indigofera lespedezioides</i> Kunth	Ca	Hs	2707, 2740



Appendix: Continuation.

Taxa	LF	Ha	Voucher(s)
<i>Lonchocarpus schiedeanus</i> (Schltdl.) Harms	F	A	1377
<i>Macroptilium gracile</i> (Poepp. ex Benth.) Urb.	F	B	1264, 2093, 2473, 2731
<i>Mimosa pudica</i> L.	H	Hs	3070
<i>Mimosa skinneri</i> Benth.	H	Hs	973, 3056
<i>Rhynchosia reticulata</i> (Sw.) DC.	F	B	1287, 2095
<i>Senna hayesiana</i> (Britton & Rose) H.S. Irwin & Barneby	F	Ar	1288
<i>Stylosanthes guianensis</i> (Aubl.) Sw.	H	Hs	1016, 2089
<i>Stylosanthes scabra</i> Vogel	H	Hs	3061
<i>Stylosanthes viscosa</i> (L.) Sw.	H	Hs	1381, 2712
<i>Zornia gemella</i> Vogel	H	Hs	2737
<i>Zornia reticulata</i> Sm.	H	Hs	969, 1014
Gentianaceae			
<i>Curtia tenella</i> (Mart.) Cham.	T	H	2287
<i>Schultesia guianensis</i> (Aubl.) Malme	T	H	1832
Gesneriaceae			
<i>Achimenes longiflora</i> DC.	H, E	H	931, 1823
<i>Gloxinia erinoides</i> (DC.) Roalson & Boggan	H, E	H	928, 3075
Hypericaceae			
<i>Hypericum thesiifolium</i> Kunth	T	H	953
Lamiaceae			
<i>Cantinoa mutabilis</i> (Rich.) Harley & J.F.B.Pastore	H	Hs	1252
<i>Hyptis lantanifolia</i> Poit.	H	Hs	955, 1022
<i>Hyptis savannarum</i> Briq.	H	Hs	1020
<i>Marsypianthes chamaedrys</i> (Vahl) Kuntze	T	H	2702
<i>Mesosphaerum suaveolens</i> (L.) Kuntze	H	H	1293
<i>Salvia lasiocephala</i> Hook. & Arn.	T	H	1265
<i>Salvia pteroura</i> Briq.	F	Ar	1028, 2297, 2102
Lentibulariaceae			
<i>Utricularia amethystina</i> Salzm. ex A. St.-Hil. & Girard*	T	H	965, 1836
<i>Utricularia pusilla</i> Vahl	T	H	966, 1853
<i>Utricularia subulata</i> L.	T	H	967, 1837
Lythraceae			
<i>Cuphea appendiculata</i> Benth.	F	Ar	1292, 2753
<i>Cuphea carthagenensis</i> (Jacq.) J.F. Macbr.	H	Hs	3025
Malpighiaceae			
<i>Byrsonima crassifolia</i> (L.) Kunth	F	A	1240
Malvaceae			
<i>Helicteres guazumifolia</i> Kunth	F	Ar	1284, 1824
<i>Melochia villosa</i> (Mill.) Fawc. & Rendle	F	Ar	951, 1009, 1236, 2752
<i>Pavonia cancellata</i> (L.) Cav.	C	H	1238
<i>Peltaea trinervis</i> (C. Presl) Krapov. & Cristóbal	F	Ar	1237
<i>Sida ciliaris</i> L.	H	Hs	3021
<i>Sida hirsutissima</i> Mill.	H	Hs	3058



Appendix: Continuation.

Taxa	LF	Ha	Voucher(s)
<i>Sida linifolia</i> Juss. ex Cav.	H	Hs	1257
<i>Waltheria indica</i> L.	F	Ar	926
Marcgraviaceae			
<i>Souroubea loczyi</i> (V.A. Richt.) de Roon	F	B	932
Melastomataceae			
<i>Acisanthera quadrata</i> Pers.	T	H	961
<i>Blakea maurofernandeziana</i> (Cogn.) Penneys & Almeda	E	Ar	1279
<i>Miconia sericea</i> (D. Don) Michelang.	F	Ar	929, 1260
<i>Miconia xalapensis</i> (Bonpl.) M.Gómez	F	A	3067
<i>Tibouchina longifolia</i> (Vahl) Baill.	Ca	Hs	1271
Myricaceae			
<i>Morella cerifera</i> (L.) Small	F	A	924
Myrtaceae			
<i>Psidium guajava</i> L.	F	A	3038
<i>Psidium guineense</i> Sw.	Ca	Ar	938, 1241, 2742, 2754
<i>Psidium salutare</i> (Kunth) O. Berg	Ca	Ar	1825, 1848, 2099
Ochnaceae			
<i>Sauvagesia erecta</i> L.	T	H	934
<i>Sauvagesia pulchella</i> Planch. ex Seem.	T	H	3037
<i>Sauvagesia tenella</i> Lam.	T	H	1829, 3036
Onagraceae			
<i>Ludwigia octovalvis</i> (Jacq.) P.H. Raven	H	Hs	3007
Orobanchaceae			
<i>Buchnera pusilla</i> Kunth	H	H	1251, 2278, 2729
<i>Buchnera weberbaueri</i> Diels	H	H	1849, 2096, 2746
<i>Castilleja arvensis</i> Schltldl. & Cham.	H	H	933, 1015
<i>Lamourouxia viscosa</i> Kunth	H	Ar	1844, 2086, 2741
Oxalidaceae			
<i>Oxalis frutescens</i> L.	H	Hs	1243, 2735
Phyllanthaceae			
<i>Phyllanthus caroliniensis</i> Walter	T	H	3085
Plantaginaceae			
<i>Mecardonia procumbens</i> (Mill.) Small	H	Hs	2691
<i>Russelia sarmentosa</i> Jacq.	F	Ar	944
<i>Scoparia dulcis</i> L.	Ca	Hs	1384
Polygalaceae			
<i>Polygala glochidata</i> Kunth	H	H	963, 2303
<i>Polygala hygrophila</i> Kunth	H	H	964, 1842, 2080, 2302
<i>Polygala incarnata</i> L. ^N	H	H	922, 1841, 2301
<i>Polygala longicaulis</i> Kunth	H	H	962, 1834
<i>Polygala paniculata</i> L.	H	H	1031, 2464, 3066
<i>Polygala pseudocoelosioides</i> Chodat	H	H	2081, 2469
<i>Polygala tenella</i> Willd.	H	H	958, 2739, 3033



Appendix: Continuation.

Taxa	LF	Ha	Voucher(s)
<i>Polygala violacea</i> Aubl.	H	H	2732
Primulaceae			
<i>Anagallis pumila</i> Sw.	T	H	960, 3008
<i>Myrsine coriacea</i> (Sw.) R. Br. ex Roem. & Schult.	F	A	1026
Proteaceae			
<i>Roupala montana</i> Aubl.	F	A	3044
Rhamnaceae			
<i>Gouania velutina</i> Reissek	F	B	1286
Rosaceae			
<i>Rubus urticifolius</i> Poir.	F	Ar	2288
Rubiaceae			
<i>Arachnothryx buddleioides</i> (Benth.) Planch.	F	A	930, 1261, 3045
<i>Coccocypselum hispidulum</i> (Standl.) Standl.	H	H	950, 971
<i>Declieuxia fruticosa</i> (Willd. ex Roem. & Schult.) Kuntze	H	Hs	1011
<i>Diodia apiculata</i> (Willd.) K. Schum.	H	Hs	947, 1266, 2736
<i>Diodia teres</i> Walter	H	Hs	2697
<i>Richardia scabra</i> L.	H	Hs	2696, 3010, 3068
<i>Spermacoce ocymifolia</i> Willd. ex Roem. & Schult.	H	Ar	1250
<i>Spermacoce verticillata</i> L.	H	Hs	949, 1017, 1267, 2694
Salicaceae			
<i>Casearia sylvestris</i> Sw.	F	A	1281
Sapindaceae			
<i>Dodonaea viscosa</i> Jacq.	F	Ar	1846, 2104, 2284
Solanaceae			
<i>Melananthus guatemalensis</i> (Benth.) Soler.	T	H	3062
<i>Schwenckia americana</i> D. Royen ex L.	H	Hs	3047
<i>Schwenckia lateriflora</i> (Vahl) Carvalho	Ca	Ar	1291
<i>Solanum lanceolatum</i> Cav.	F	Ar	1258, 2295, 2748
Styracaceae			
<i>Styrax argenteus</i> C. Presl	F	A	1027
Verbenaceae			
<i>Lantana camara</i> L.	Ca	Ar	1253, 2698
<i>Stachytarpheta frantzii</i> Pol.	Ca	Ar	925

