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Floristic composition, structure and diversity of forested swamps in the Damani-Guariviara Wetland, Indigenous Comarca Ngäbe-Buglé, Panama

Composición florística, estructura y diversidad de bosques pantanosos en el Humedal Damani-Guariviara, Comarca indígena Ngäbe-Buglé, Panamá

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Abstract:

Background and Aims: Along the Mesoamerican biological corridor, swamp forests dominated by orey (*Campnosperma panamense*) extend continuously to Caribbean coastal areas. Despite their recognized importance as peat forming ecosystems, little is known about their floristic composition and diversity. In Panama, the Damani-Guariviara Wetland (DGW), on the coast of the Indigenous Comarca Ngäbe-Buglé, holds one of the largest freshwater floodable forests in the country. Our aim is to analyze the floristic composition, structure and diversity of mixed floodable forest, which is the most represented in the wetland.

Methods: We studied ten permanent plots, each covering 0.1 hectares, and inventoried all trees with a diameter at breast height (DBH) of at least 10 cm. We calculated their relative abundance, dominance, frequency and Importance Value Index. Additionally, diametric distribution graphs were obtained. We evaluated sampling effort with a sample coverage estimator and Chao-1 index. We described diversity with species richness (q0) and the Modified Shannon (q1) and Simpson (q2) indexes based on Hill numbers.

Key results: We present a description of the floristics and structure of mixed swamp forests in DGW. *Campnosperma panamense* was the dominant species, followed by *Pterocarpus officinalis* and *Manicaria saccifera*. A sample coverage estimator of 0.9725 was obtained, indicating that the sampling is nearly complete.

Conclusions: The present work contributes to increase knowledge of swamp forests in Panama. The studied mixed floodable forests show heterogeneity in their floristic composition, structure and diversity, what could be related to several factors, mainly to the flooding regime and soil properties.

Key words: *Campnosperma panamense*, floodable forest, orey, peatlands.

Resumen:

Antecedentes y Objetivos: En el corredor biológico Mesoamericano, los bosques pantanosos dominados por orey (*Campnosperma panamense*) se extienden de manera continua hasta las costas del Caribe. A pesar de su reconocida importancia como ecosistemas formadores de turberas, se sabe poco sobre su composición florística y diversidad. En Panamá, el Humedal Damani-Guariviara (HDG), en la costa de la Comarca indígena Ngäbe-Buglé, contiene uno de los bosques inundables de agua dulce más extensos del país. Nuestro objetivo es analizar la composición florística, estructura y diversidad del bosque mixto inundable, el más representado en el humedal.

Métodos: Se estudiaron diez parcelas permanentes de 0.1 hectáreas, donde se inventariaron todos los árboles con un diámetro a la altura de pecho (DAP) de al menos 10 cm. Se calcularon la abundancia, dominancia y frecuencia relativas, y el índice de Valor de Importancia. Adicionalmente se obtuvieron gráficas de distribución diamétrica. Se evaluó el esfuerzo de muestreo con un estimador de cobertura de la muestra y el índice de Chao-1. La diversidad fue descrita con la riqueza de especies (q0) y los índices de diversidad de Shannon (q1) y de Simpson (q2) con base en los números de Hill.

Resultados clave: Se presenta una descripción de la composición florística y estructura de los bosques mixtos inundables del HDG. *Campnosperma panamense* fue la especie dominante, seguida de *Pterocarpus officinalis* y *Manicaria saccifera*. Se obtuvo un estimador de cobertura de la muestra de 0.9725, lo que nos indica que el esfuerzo de muestreo está casi completo.

Conclusiones: Con este trabajo se ha incrementado el conocimiento de los bosques inundables de Panamá. Los bosques mixtos inundables estudiados mostraron heterogeneidad en su composición florística, estructura y diversidad, lo cual pudiera estar relacionado a diferentes factores, principalmente al régimen de inundación y características de los suelos.

Palabras clave: bosque inundable, *Campnosperma panamense*, orey, turberas.

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Introduction

Tropical wetlands are among the most productive ecosystems on the planet (Ellison, 2004). They serve as wildlife refugia, greenhouse gas reservoirs (i.e., CH_4 and CO_2 ; Page et al., 2011; Lezcano and López, 2015; Hoyos-Santillán et al., 2015), and centers of speciation and endemism (Ashton, 1969; Posa et al., 2011). Wetlands can be broadly classified as freshwater or marine, and they can encompass forested, shrubby or herbaceous formations. With the exception of mangroves, forested swamps have been much less studied than lowland and mountain forests in the tropics (Ellison, 2004; López and Kursar, 2007; Junk et al., 2013).

Along the Mesoamerican biological corridor, from Nicaragua to Western Panama on the Caribbean side and from Darién (Panama) to Chocó in Ecuador, on the Pacific side, peat swamp forests with abundant oreo (*Campnosperma panamense* Standl.) are continuous to coastal areas (Ibáñez et al., 2025). These forests represent some of the main peat forming ecosystems in this part of the world (Cohen et al., 1989; Hoyos-Santillán et al., 2016). At the same time, they are presently experiencing enormous socio-economic pressures, which, together with alterations associated to climate change, endanger their sustainability and the ecosystem services they provide (Sjögersten et al., 2011).

Information on the floristic composition and ecology of these forests is limited. In Nicaragua and Costa Rica they have been described as palm swamps (Webb and Peralta, 1998; Urquhart, 1999; Ellison, 2004; Hammel et al., 2004; Myers, 2013; Rueda et al., 2013; Serrano-Sandí et al., 2013), where plant associations dominated by the palms *Raphia taedigera* (Mart.) Mart. and *Manicaria saccifera* Gaertn. develop in poorly drained or waterlogged soils. In general, *Raphia taedigera* dominates flooded areas with extensive hydroperiods and shows a lower floristic diversity, while *Manicaria saccifera* is often found in flooded forests with more complex structure and diversity (Myers, 2013; Rueda et al., 2013).

In Panama, some data on the floristics and vegetation of forested peat swamps is available for the San San Pond Sak (SSPS) Wetland of International Importance, a Ramsar Site, on the northwestern Caribbean coast of the country

(CREHO, 2010). The historical reconstruction of peat accumulation and geomorphology of the SSPS is related to the formation of concentric vegetation rings staggered in successional stages, from open short-grassy fields dominated by the sawgrass *Cladium* sp., passing through dwarf-to-tall vegetation dominated by *Campnosperma panamense*, to *Raphia taedigera* palm forests (see Phillips et al., 1997).

Studies on carbon dynamics, which includes CO_2 , CH_4 , nutrient fluxes and water table hydrological modeling, have been advanced by Hoyos-Santillán et al. (2015; 2016), Baird et al. (2017) and Sjögersten et al. (2020). Microbial community structure was studied by Troxler et al. (2012) and Girkin et al. (2020). These ecosystem-oriented studies highlight the critical importance that SSPS, and all tropical ombrotrophic peat swamps, play in the global equation of greenhouse gases and carbon sequestration (Page et al., 2011).

Also in Panama, a recent work by Ibáñez et al. (2025) describes the floristics, structure and regeneration strategy of monospecific *Campnosperma panamense* mature forests in the Matusagaratí complex of wetlands, in Darién, Pacific watershed. This area has been recently designated as a Ramsar Site (Convention on Wetlands, 2025), where several vegetation types have been described, among which 1267 hectares of swamp forest dominated by *Campnosperma panamense* have been recorded (Ibáñez et al., 2025; Ibáñez et al., in press). The presence of peat in these forests has been verified and its depth preliminary measured by Hoyos-Santillán et al. (in prep.).

The Damani-Guariviara wetland (DGW) is located on the northwestern coast of Panama, within the Ngäbe-Buglé indigenous Comarca (Fig. 1). It has protected status as a Wetland of International Importance and is also a Ramsar Site (CREHO, 2010). The importance of DGW lies in three main aspects: 1) it serves a regulatory function in the storage and sequestration of carbon and other greenhouse gases (e.g., CH_4) due to the extensive deposits of organic matter, >5 meters deep (Hoyos-Santillán, 2014); 2) regulatory function of hydrological processes (e.g. “sponge” effect of the organic matter, Baird et al., 2017), and 3) refuge and center of endemism of flora and fauna. As an example, the Chiriquí Beach, which stretches over 25 km in the



coastal portion of the DGW represents the most important nesting site for leatherback turtles (*Dermochelys coriacea* Vandelli, 1761) in the Caribbean of Central America (Ordóñez et al., 2007). The DGW lagoon complex also harbors meager numbers of the vulnerable Caribbean manatee, *Trichechus manatus* Linnaeus, 1758 (Mou-Sue et al., 1990;

Díaz-Ferguson et al., 2017). The floodable forests in DGW provide shelter for emblematic species such as the jaguar, *Panthera onca* Linnaeus, 1758 (Meyer et al., 2016; 2019).

However, despite the recognized importance of these swamp forests, relatively little is known about their floristic composition and diversity. Limited plant inventories and

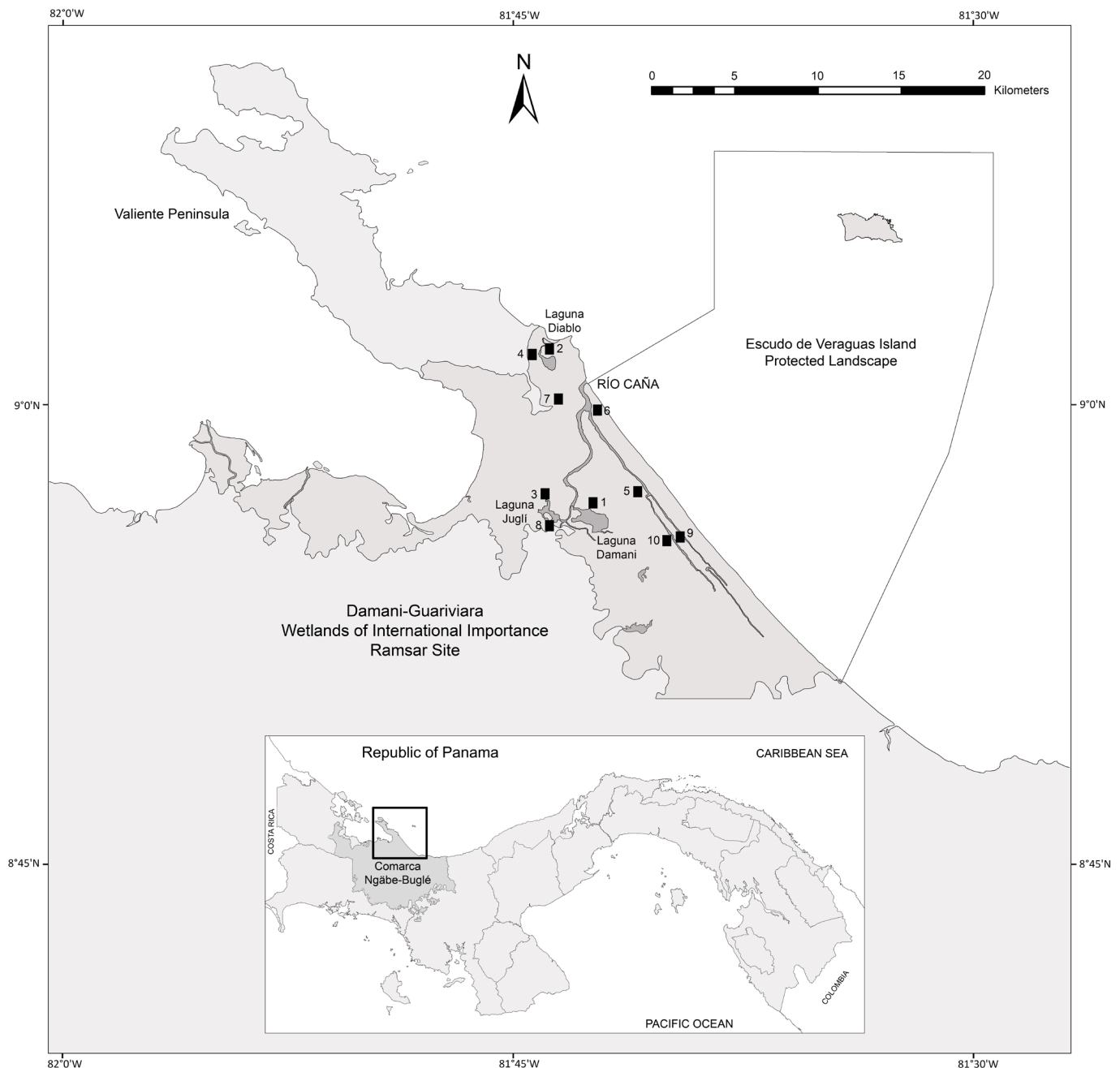


Figure 1: Damani-Guariviara Wetlands in the Indigenous Comarca Ngäbe-Buglé, Panama. The numbers indicate the location of study plots.



descriptions of the vegetation types are available for the area, mostly part of the reports supporting the declaration of the Ramsar Site (Spalding and Gallardo, 2010). Additional surveys of the vegetation of two coastal areas in the DGW were part of a study of carbon dynamics in peatlands (Hoyos-Santillán, 2014). A qualitative floristic survey of the wetland has been carried out by two of the authors and will be published in a separate paper (Ibáñez and Flores, in prep.).

Here we analyze, for the first time, the floristic composition, structure, and diversity of the DGW mixed swamp forests, the most represented vegetation formation of the wetland. We provide a general description of the tree-dominated swamplands that are not monospecific stands (defined as at least 70% of Relative Dominance) (Phillips et al., 1997). We hypothesize that these mixed swamp forests are not a single community, but they represent a heterogeneous habitat due to different underlying environmental factors, such as variable flooding stress, soil properties, proximity to the coast, microtopography, etc. (López and Kursar, 2007; Sjögersten et al., 2011), although none of these factors have been measured in this study. In particular, we aim at addressing basic floristic, forest structure and diversity descriptions, with questions such as: 1) What is the species composition of these forests?, 2) How does the vegetation structure behave in the analyzed forests?, and 3) What are the patterns of richness, abundance and dominance? We hypothesize that 1) The forest is composed of a mixed community where 2-3 canopy species provide over 60% of the relative dominance, 2) The forests exhibit a structure characterized by a reverse J-shaped diameter distribution, and 3) Tree richness, abundance and dominance vary across different zones of the forest.

Materials and Methods

Study site

We carried out this study in the Damani-Guariviara wetland, which covers approximately 24,089 ha (CREHO, 2010) (Figs. 1, 2A). The terrain is flat, poorly drained and characterized by a network of prominent lagoons, such as Damani, Juglí and Diablo, connected by a network of channels, some of which run parallel to the coast. The DGW comprises a

complex of habitats and vegetation types, broadly including beach, mangroves, marshes and lagoons, although most of the area is covered in permanently or temporarily flooded swamp forests, either monospecific *Camposperma panamense* formations or mixed forests (Ibáñez and Flores, in prep.). To the north, south and southwest, the wetland is surrounded by upland forests and agricultural lands and to the northeast by a beach that runs along the coast.

The climate is typical of very humid tropical lowland forests of the Atlantic slope, with a Köppen-Geiger classification of Af (tropical rainforest) (Beck et al., 2018). Mean annual temperature from the Smithsonian Tropical Research Station in Bocas del Toro, around 70 km to the northwest, is 26.3 °C, and average annual rainfall over the last 20 years was 3629 ± 549 mm/yr (Paton, 2023). It rains all year through, although two rainy seasons (April to August, November and December) and two shorter dry seasons with driest months in September and October have been described for the region (Kaufmann and Thompson, 2005).

Plot establishment

We studied ten permanent plots of 0.1 hectares (50 × 20 m), with a total area of 1.0 ha (Fig. 1). In order to maximize the representativeness of the mixed flooded forests, we placed plots across distant areas of the wetland, covering a polygon of approximately 50 km² (Gentry, 1982; Phillips et al., 2003). Trees were permanently marked with a numbered aluminum tag and the diameter of all trees ≥10 cm at breast height (DBH) measured. The height of each tree was estimated. Although we carried out the field survey between May to August 2014, we consider the information to still be valid, as this is a protected area that has not been impacted by people.

All floristic inventory activities were part of a community monitoring project, where members of the Río Caña community were in charge of laying out, measuring, collecting and entering the data in a database, under the supervision and verification of the authors (Fig. 2 B-D), besides outreach of the project (Fig. 2E). It is expected that the ten permanent plots can serve as an initial setting that already trained community members can continue its





Figure 2: Mixed swamp forest in the Damani-Guariviara Wetlands in the indigenous Comarca Ngäbe-Buglé, Panama. A. forest with abundant *Campnosperma panamense* Standl. (taller trees); B.C. local vegetation team carrying out the survey; D. entering plot data; E. outreach by community members about the results of the monitoring project.



long-term monitoring. The information generated will be important for management purposes and forest conservation.

Plant sample collection and identification

We collected voucher specimens for all species represented in the plots. Once dried, the samples were identified using available floras, such as Flora of Panama (Woodson and Schery, 1943-1980), Manual de Plantas de Costa Rica (Hammel et al., 2003-2015), Flora Mesoamericana (Davidse et al., 1994-in progress) and checklists (Correa et al., 2004). Vouchers were compared with specimens from the herbaria of the University of Panama (PMA) and the Missouri Botanical Garden (MO), and difficult ones through consultations with family specialists. All specimens have been deposited in PMA and MO.

Data analyses

To describe the floristic composition and forest structure, we used the most common descriptors reported in the literature. Following Dallmeier et al. (1992), relative abundance (RA, %) was defined as the number of individuals of a species in proportion to the total number of individuals in the entire sample. Similarly, the relative dominance (RD, %) as the basal area of a species in proportion to the total basal area, the relative frequency (RF, %) as the number of quadrants in which a species is present at the rate of total quadrants in the entire sample, and the Importance Value Index (IVI) as the sum of RA + RD + RF (Table 1). Forest structure was also analyzed through diametric distribution graphs.

We evaluated sampling effort through a sample coverage (SC) estimator, with the program iNEXT Online version (Chao et al., 2016). With program SpadeR Online version (Chao et al., 2015), we calculated the expected maximum diversity with the non-parametric estimator Chao-1, which uses the numbers of singletons and doubletons to estimate the number of undetected species, as this information is mostly concentrated on those low frequency counts (Chao, 1984).

We calculated a Modified Shannon Diversity Index (q1), that weights each species in proportion to its

abundance, and a Modified Simpson Diversity Index (q2), that measures the effective number of dominant species. Both Indexes were obtained with the Hill numbers version for the individual plots with the program iNEXT (Jost and González-Oreja, 2012; Hsieh et al., 2016).

Results

Floristic composition

We recorded a total of 655 individuals (661 stems), including trees and palms greater than 10 cm DBH, in 1 hectare of mixed floodable forest. Forty-three species, distributed in 37 genera and 25 families were found (Table 1). Nine species could only be identified to morphospecies level. The tree species, *Camposperma panamense* and *Pterocarpus officinalis* Jacq. and the palm *Manicaria saccifera*, made up 51.30% of the total individuals sampled or 68.91% of relative dominance. *Camposperma panamense* was the dominant species in the mixed forest of the wetland. Nevertheless, its relative abundance varied throughout the plots, from none in plot 2 to 72.05% in plot 4 (Table 2). From a taxonomic point of view, our inventory added one new tree species to science, in the Myrtaceae family, *Eugenia tain* R.R.Flores, B.Holst & A.Ibáñez, whose description has recently been published (Flores et al., 2022).

Forest structure

Forest canopy reaches ca. 20-25 m with emergent trees of up to 40 m (Fig. 2A). Main canopy species are: *Camposperma panamense*, *Pterocarpus officinalis*, *Symphonia globulifera* L.f., *Virola nobilis* A.C.Sm., *Manilkara bidentata* (A.DC.) A.Chev., *Amanoa guianensis* Aubl., *Cespedesia spathulata* (Ruiz & Pav.) Planch., etc. Subcanopy and understory (5-20 m) tree species, beside the abovementioned species, include *Cassipourea elliptica* (Sw.) Poir., *Eugenia tain*, *Iryanthera juruensis* Warb., *Tovomita longifolia* (Rich.) Hochr., *Casearia povedae* (N.Zamora, Aguilar & D.Santam.) T.Samar. & M.H.Alford and the palms *Euterpe precatoria* Mart. and *Manicaria saccifera* (Table 1). At the plot level, *Camposperma panamense* was the most abundant species in the canopy in 8 of the 10 plots. In plot 2 the canopy was dominated by *Pterocarpus officinalis*, while in plot 9 *Virola nobilis* was most abundant (Table 3).



Table 1: Damani-Guariviara Wetland mixed floodable forest in the indigenous Comarca Ngäbe-Buglé, Panama. List of tree species (DBH≥10 cm) and their abundance indexes. N=number of individuals, BA=basal area, RA=relative abundance, RF=relative frequency, RD=relative dominance, IVI=importance value index. In between brackets: Collection Numbers, Initials: AI=Alicia Ibáñez, NF=Noris Flores, RF=Rodolfo Flores; Herbaria: PMA=University of Panama Herbarium, MO=Missouri Botanical Garden Herbarium.

Family	Species	N	BA	RA	RF	RD	IVI
Anacardiaceae	<i>Camptosperma panamense</i> Standl. (AI7287, PMA)	196	17.13	29.92	7.14	46.25	83.31
Fabaceae	<i>Pterocarpus officinalis</i> Jacq. (RF3552, PMA)	55	6.02	8.40	5.56	16.25	30.21
Arecaceae	<i>Manicaria saccifera</i> Gaertn. (NF349, PMA)	85	2.37	12.98	5.56	6.41	24.94
Clusiaceae	<i>Symphonia globulifera</i> L.f. (AI7290, PMA)	26	3.48	3.97	5.56	9.41	18.93
Arecaceae	<i>Euterpe precatoria</i> Mart. (AI8844, PMA)	50	0.89	7.63	6.35	2.39	16.37
Euphorbiaceae	<i>Amanoa guianensis</i> Aubl. (AI8907, PMA)	27	1.36	4.12	6.35	3.67	14.15
Rhizophoraceae	<i>Cassipourea elliptica</i> (Sw.) Poir. (RF1413, PMA, MO)	39	0.67	5.95	5.56	1.81	13.32
Chrysobalanaceae	<i>Licania affinis</i> Fritsch (RF1346, PMA)	33	0.53	5.04	2.38	1.43	8.85
Myrtaceae	<i>Eugenia tain</i> R.R.Flores, B.Holst & A.Ibáñez (AI8915, PMA)	15	0.23	2.29	4.76	0.61	7.66
Myristicaceae	<i>Iryanthera juruensis</i> Warb. (AI8909, PMA)	20	0.46	3.05	3.17	1.24	7.47
Ochnaceae	<i>Cespedesia spathulata</i> (Ruiz & Pav.) Planch. (NF339, PMA)	18	0.35	2.75	3.17	0.93	6.86
Myristicaceae	<i>Virola nobilis</i> A.C.Sm. (RF3549, PMA)	11	0.79	1.68	1.59	2.12	5.39
Sapotaceae	<i>Manilkara bidentata</i> (A.DC.) A.Chev. (RF1406, PMA)	8	0.61	1.22	2.38	1.65	5.25
Lecythidaceae	<i>Grias cauliflora</i> L. (AI7353, PMA)	11	0.29	1.68	2.38	0.77	4.83
Burseraceae	<i>Protium panamense</i> (Rose) I.M.Johnst. (AI8903, PMA)	7	0.13	1.07	3.17	0.36	4.60
Clusiaceae	<i>Tovomita longifolia</i> (Rich.) Hochr. (AI8916, PMA)	6	0.13	0.92	3.17	0.35	4.44
Fabaceae	<i>Zygia latifolia</i> (L.) Fawc. & Rendle (RF3587, PMA)	5	0.07	0.76	3.17	0.19	4.13
Humiriaceae	<i>Sacoglottis trichogyna</i> Cuatrec. (RF3597, PMA)	4	0.23	0.61	2.38	0.63	3.62
Rubiaceae	<i>Chione venosa</i> (Sw.) Urb. (AI8905, PMA)	5	0.09	0.76	2.38	0.23	3.38
Fabaceae	<i>Swartzia oraria</i> R.S.Cowan (RF3594, PMA)	3	0.07	0.46	2.38	0.18	3.01
Elaeocarpaceae	<i>Sloanea</i> sp. 1 (RF3603, PMA)	2	0.17	0.31	1.59	0.45	2.35
Annonaceae	<i>Xylopia macrantha</i> Triana & Planch. (AI8906, PMA)	3	0.05	0.46	1.59	0.14	2.19
Sapotaceae	<i>Pouteria cuspidata</i> (A.DC.) Baehni (AI8902, PMA)	3	0.03	0.46	1.59	0.09	2.13
Rubiaceae	<i>Posoqueria latifolia</i> (Rudge) Roem. & Schult. (RF3553, PMA)	2	0.02	0.31	1.59	0.05	1.94
Bignoniaceae	<i>Tabebuia</i> sp. 1 (RF3557, PMA)	1	0.33	0.15	0.79	0.89	1.83
Burseraceae	<i>Protium tenuifolium</i> (Engl.) Engl. (AI8910, PMA)	3	0.05	0.46	0.79	0.13	1.38
Sapotaceae	<i>Pouteria</i> sp. 1 (RF3604, PMA)	1	0.13	0.15	0.79	0.34	1.29
Meliaceae	<i>Trichilia</i> sp. 1 (No colectada)	1	0.11	0.15	0.79	0.28	1.23
Moraceae	<i>Ficus maxima</i> Mill. (RF3591, PMA, MO)	1	0.05	0.15	0.79	0.13	1.08
Humiriaceae	<i>Humiriastrum diguense</i> (Cuatrec.) Cuatrec. (RF3593, PMA)	1	0.05	0.15	0.79	0.13	1.08
Fabaceae	<i>Jupunba barbouriana</i> (Standl.) M.V.B.Souares, M.P.Morim & Iganci (RF3588, PMA)	1	0.03	0.15	0.79	0.07	1.01
Salicaceae	<i>Casearia povedae</i> (N.Zamora, Aguilar & D.Santam.) T.Samar. & M.H.Alford (RF3559, PMA)	1	0.02	0.15	0.79	0.05	0.99
Aquifoliaceae	<i>Ilex guianensis</i> (Aubl.) Kuntze (RF3589, PMA)	1	0.02	0.15	0.79	0.04	0.99
Myrsinaceae	Myrsinaceae sp. 1 (RF3606, PMA)	1	0.02	0.15	0.79	0.04	0.99
Myrtaceae	Myrtaceae sp. 1 (RF3592, PMA)	1	0.01	0.15	0.79	0.04	0.99
Lepidobotryaceae	<i>Ruptiliocarpon caracolito</i> Hammel & N.Zamora (RF3598, PMA)	1	0.01	0.15	0.79	0.04	0.98
Sapotaceae	<i>Chrysophyllum argenteum</i> Jacq. (RF3585, PMA)	1	0.01	0.15	0.79	0.04	0.98
Rubiaceae	<i>Amaioua glomerulata</i> (Lam. ex Poir.) Delprete & C.H.Perss. (RF3607, PMA)	1	0.01	0.15	0.79	0.03	0.98



Table 1: Continuation.

Family	Species	N	BA	RA	RF	RD	IVI
Melastomataceae	<i>Mouriri gleasoniana</i> Standl. (RF3602, PMA)	1	0.01	0.15	0.79	0.03	0.98
Myristicaceae	<i>Virola fosteri</i> D.Santam. (RF3550, PMA)	1	0.01	0.15	0.79	0.03	0.97
Annonaceae	<i>Guatteria amplifolia</i> Triana & Planch. (AI8827, PMA, MO)	1	0.01	0.15	0.79	0.03	0.97
Rubiaceae	<i>Psychotria</i> sp. 1 (RF3605, PMA)	1	0.01	0.15	0.79	0.02	0.97
Not identified	Indeterminada sp. 1 (RF3592, PMA)	1	0.01	0.15	0.79	0.03	0.98
TOTAL		655	37.04	100	100	100	300

Table 2: Damani-Guariviara Wetland mixed floodable forest in the indigenous Comarca Ngäbe-Buglé, Panama. Number of individual, species and diversity indexes (based on Hill numbers q_0 , q_1 and q_2) of individual plots.

Plot	No. Ind.	Species Richness (Hill numbers- q_0)	Modified Shannon Diversity index (Hill numbers- q_1)	Modified Simpson Diversity index (Hill numbers- q_2)	Orey abundance (RA, %)	No. Singletons
1	74	14	8.35	6.15	29.72	5
2	43	10	4.99	3.36	0	6
3	69	9	4.83	3.79	30.43	4
4	68	5	2.19	1.75	72.05	2
5	47	15	7.83	4.73	8.51	9
6	57	11	6.70	5.31	26.31	5
7	67	15	9.86	8.08	16.41	7
8	87	14	5.71	3.06	55.17	5
9	65	21	14.51	10.91	6.15	10
10	78	12	6.37	4.69	28.20	5

Tree diameter varied across plots and species. Those species with the largest diameters were: *Symphonia globulifera* with 88.5 cm DBH, *Pterocarpus officinalis* with 83.7 cm DBH and *Camposperma panamense* with a largest tree of 68.5 cm DBH. The diameter distribution for the whole forest shows a typical reversed “J” shape skew distribution, with the lowest diameters (10 to 19.9 cm DBH) having the greatest amount of individuals (>61%) (Fig. 3A). *Camposperma panamense*, the most abundant tree species in the DGW, showed a distribution with the greatest amount of individuals in the second lowest diameters (20-29.9 cm DBH), instead of the lowest class (Fig. 3B).

Patterns of richness, abundance and dominance
A sample coverage (SC) estimator of 0.9725 (or 97.25% coverage) indicates that our sampling effort has been very

high. On the other hand, the total number of species in all 10 plots was 43. This is 34% of the expected diversity that according to Chao-1 index is estimated to be around 124 species. We found a total of 18 species in our sampling that were registered only once, and two species of which only two individuals were found, which together, singletons and doubletons, represent about 46.5% in the sample (Table 2).

The diversity analyses showed much variation among plots (Table 2). Species richness ($q=0$) varied from 5 (Plot 4) to 21 (Plot 9). These results were consistent with the value of $q=1$ (Modified Shannon Diversity) that ranged from 2.19 (Plot 4) to 14.51 (Plot 9) and with $q=2$ (Modified Simpson Diversity) that varied from 1.75 (Plot 4) to 10.91 (Plot 9).

When comparing the slope of the Diversity Profile to assess evenness, the steepness of the slope tells us



Table 3: Damani-Guariviara Wetland mixed floodable forest in the indigenous Comarca Ngäbe-Buglé, Panama. Three most abundant tree species in individual plots. In bold, canopy species.

Plot	Tree species	Relative Abundance (%)
P1	<i>Camptosperma panamense</i> Standl.	29.73
	<i>Euterpe precatoria</i> Mart.	16.22
	<i>Manicaria saccifera</i> Gaertn.	16.22
P2	<i>Pterocarpus officinalis</i> Jacq.	48.84
	<i>Symphonia globulifera</i> L.f.	16.28
	<i>Cassipourea elliptica</i> (Sw.) Poir.	16.28
P3	<i>Licania affinis</i> Fritsch	37.68
	<i>Camptosperma panamense</i> Standl.	30.43
	<i>Amanoa guianensis</i> Aubl.	13.04
P4	<i>Camptosperma panamense</i> Standl.	72.06
	<i>Pterocarpus officinalis</i> Jacq.	22.06
	<i>Symphonia globulifera</i> L.f.	2.94
P5	<i>Manicaria saccifera</i> Gaertn.	40.43
	<i>Grias cauliflora</i> L.	17.02
	<i>Camptosperma panamense</i> Standl.	8.51
P6	<i>Camptosperma panamense</i> Standl.	26.32
	<i>Cespedezia spathulata</i> (Ruiz & Pav.) Planch.	26.32
	<i>Symphonia globulifera</i> L.f.	17.54
P7	<i>Euterpe precatoria</i> Mart.	17.91
	<i>Camptosperma panamense</i> Standl.	16.42
	<i>Manicaria saccifera</i> Gaertn.	14.93
P8	<i>Camptosperma panamense</i> Standl.	55.17
	<i>Euterpe precatoria</i> Mart.	6.90
	<i>Manicaria saccifera</i> Gaertn.	6.90
P9	<i>Manicaria saccifera</i> Gaertn.	18.46
	<i>Virola nobilis</i> A.C.Sm.	15.38
	<i>Euterpe precatoria</i> Mart.	7.69
P10	<i>Manicaria saccifera</i> Gaertn.	32.05
	<i>Camptosperma panamense</i> Standl.	28.21
	<i>Cassipourea elliptica</i> (Sw.) Poir.	14.10

how unequal (dominated) the community is (Fig. 4). As an example, comparing Plot 5 and Plot 7, we find they both have the same species richness: 15, but Plot 7 diversity falls from 15 (q0) to 9.86 (q1) and then to 8.08 (q2), meaning that this is a relatively even community. On the other hand, the values for Plot 5 fall drastically from 15 to 7.83 (q1) and to just 4.73 (q2). This means that, although there are 15 species in total, the community is strongly dominated by a few (or even just one) species.

Hence, we can see that Plot 4 presents low diversity and high dominance (Table 2, Fig. 4). It has only 5 species recorded in 68 individuals. Its q1 (2.19) and q2 (1.75) values demonstrate that ecologically it behaves almost like a monoculture, where one species (*Camptosperma panamense*) accounts for the vast majority of the records (Table 3).

On the other hand, plot 9 is by far the most diverse and evenly distributed. It has the highest species richness (q0=21), and its q1 (14.51) and q2 (10.91) values remain



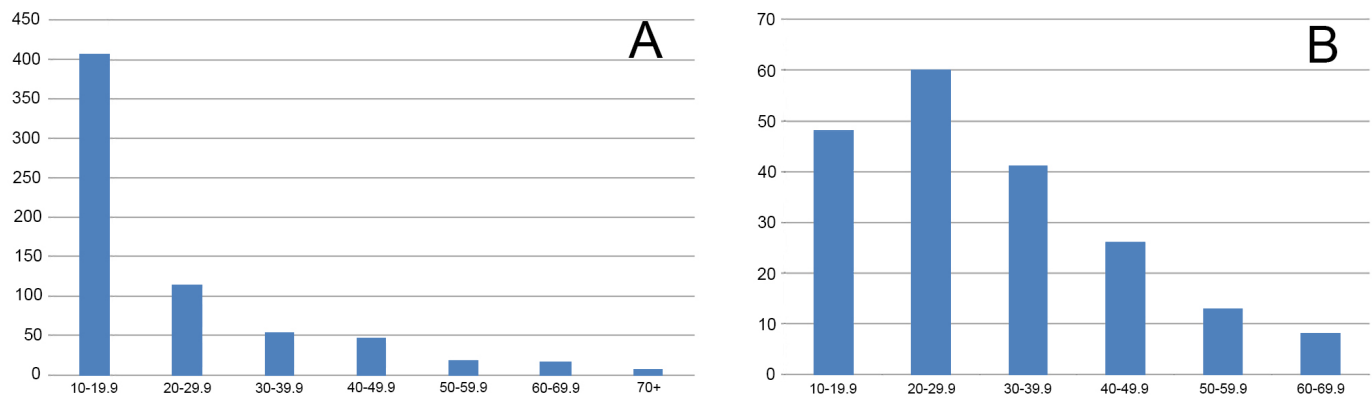


Figure 3: Diametric distributions of mixed inundated forest in the Damani-Guariviara Wetlands in the Indigenous Comarca Ngäbe-Buglé, Panama. A. all tree species included; B. only *Campnosperma panamense* Standl. included.

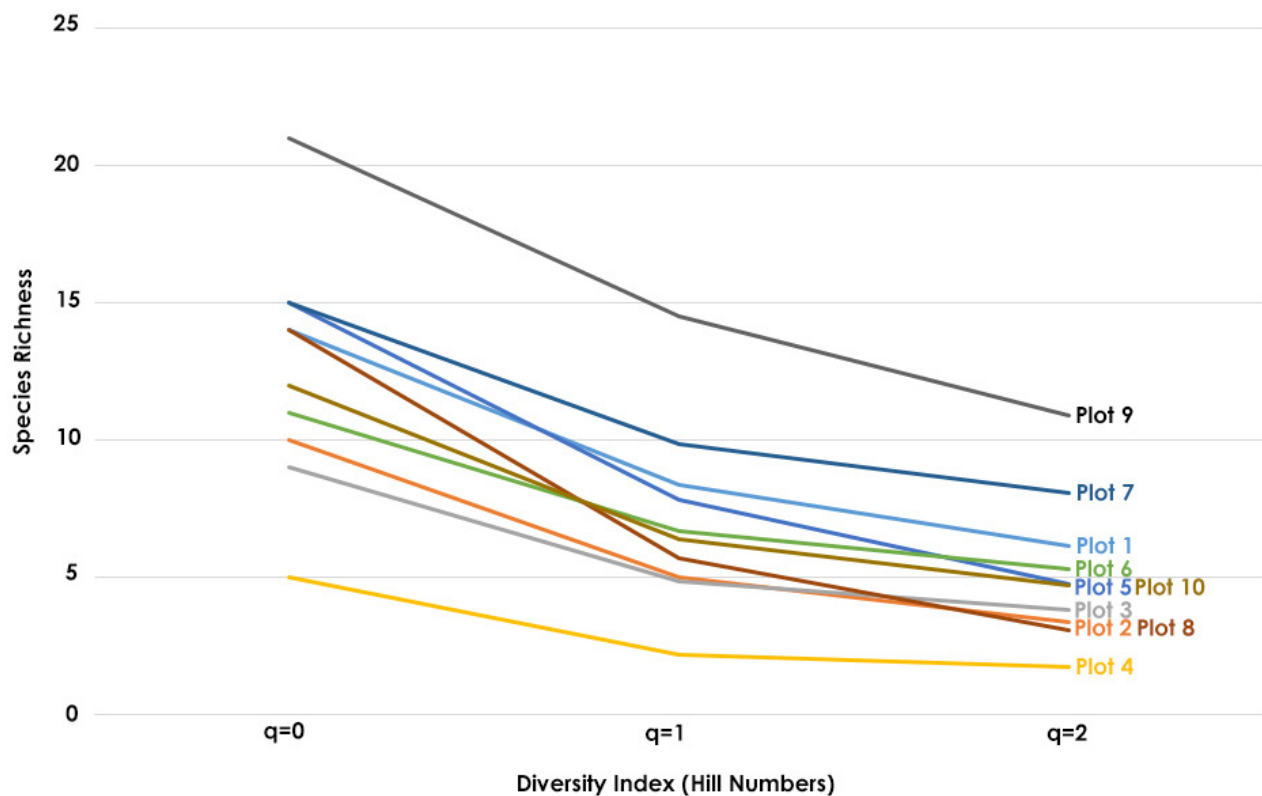


Figure 4: Diversity profile in the wetland forest in the Damani-Guariviara Wetlands in the Indigenous Comarca Ngäbe-Buglé, Panama.

high. There is a much more homogeneous distribution of abundances than in the other sites. The rest of the plots fall within these situations, which means that there is heterogeneity of richness, abundance and dominance within the forested wetland of the DGW.

Discussion

Floristic composition

This is the first quantitative floristic inventory of the mixed swamp forests of the Damani-Guariviara Wetland (DGW), in northwestern Panama. In general, they are dominated by the tree species *Campnosperma panamense* (orey) (46.2% of RD), which together with *Pterocarpus officinalis* and the palm *Manicaria saccifera* make up almost 69% of relative dominance. These results support our first hypothesis of 2-3 tree species dominating the canopy.

The floristic composition and abundance pattern of DGW forest is similar to what has been reported elsewhere in the region. The only previous quantitative inventory of mixed forests of DGW is that of Hoyos-Santillán (2014), where in 0.1 ha, *Campnosperma panamense* showed the highest percentage of the total basal area with ca. 45% (m² ha⁻¹). Their floristic composition and structure are similar to mixed floodable forests of San San Pond Sak, approximately 70 km northeast of DGW, except for the absence of *Raphia taedigera* in DGW.

Phillips et al. (1997) described mixed swamp forest (Phasic community 4) in SSPS as dominated by *Symphonia globulifera*, *Campnosperma panamense*, and other hardwoods (22 species, 5 species in common with DGW). In the same area, Sjögersten et al. (2011) reported a total of 10 species ≥ 10 cm DBH in one 0.1 ha plot of this kind of forest (four species in common with our inventory, *Campnosperma panamense* 43% of the basal area).

The mixed swamp forests of DGW also resemble palm swamps with abundant *Manicaria saccifera* from Caribbean Nicaragua and Costa Rica, where Rueda et al. (2013) reported 44 tree and palm species (773 individuals sampled). We found forty-three species of trees and palms in over 600 individuals of >10 cm DBH and the understory is also dominated by the palm species *Manicaria saccifera*. Nine tree species are shared between their study area and

DGW and although *Campnosperma panamense* was not present in their transects, it has been reported growing in the swamp forest (Rueda et al., 2013).

Mixed swamp forests with abundant *Campnosperma panamense*, such as the ones studied here, have not been reported for other regions of Panama, such as Darién, or Colombia, where monospecific *Campnosperma panamense* forests have been described (Del Valle Arango, 2000; Ibáñez et al., 2025). These kinds of forests are much less diverse than mixed swamp forests. In the Matusagaratí wetland of Darién (*Campnosperma panamense*, 72.66% of RD), 10 species (≥ 10 cm DBH) were found in 0.3 ha or 316 individuals (Ibáñez et al., 2025). Similar numbers were reported from the Pacific coast of Colombia, where in *Campnosperma panamense* forest (70% RD), species diversity reached nine species in 449 individuals per 0.5 ha of sampled area (Del Valle Arango, 2000). Monospecific *Campnosperma panamense* forests also occur in large areas of DGW but have not been studied.

Besides the recently described new tree species, *Eugenia tain*, several other new records for Panama were also found in the region and will be published in a forthcoming paper (Flores et al., in prep.). These findings highlight the importance of this kind of inventory to advance the knowledge of the flora of remote areas of Panama.

Forest structure

As it was hypothesized, the analysis of diameter distributions for the floodable forests with all tree species included, showed a typical J-shaped curve, a common feature of tropical forests that could reflect the aggregation of many species with different mortality rates (Condit et al., 1995) or a high renovation of individuals due to frequent formation of gaps (Lieberman et al., 1985). On the other hand, the analysis with just *C. panamense* (orey) seems to indicate a lack of sufficient young trees for replacement of the older ones in order to maintain the present forest structure. This pattern has also been reported in monodominant oreo forests in Darién (Panama) (Ibáñez et al., 2025), and as in that region, we could infer that these forests may be naturally evolving to a different composition and structure in which oreo is less represented.



Patterns of richness, abundance and dominance

The sample coverage (SC) estimator indicated that our sampling effort has been very high and the sampling is nearly complete. This means that approximately 97.25% of the total individuals in the entire community belong to the species that were already observed. On the other hand, we only recorded 34% of the expected diversity, and this is also reflected in the high number of “singletons” in our sampling. This means that there are still many single species to be detected.

As we had hypothesized, we found that tree richness, abundance and dominance are not uniform throughout the mixed wetland forest of Damani-Guariviara. This is supported by the diversity analyses carried out, where there is ample heterogeneity in those three variables. Patches of very low diversity and high dominance of one species (*Camposperma panamense*) are interspersed with more diverse patches that show low dominance.

Differences in composition and species diversity in wetlands can be related to several factors, but mainly to the flooding regime and soil factors, although these variables have not been studied in the DGW. According to available references on *Camposperma panamense* forests, these tend toward monodominance due to the environmental constraints of saturated soil (Ibáñez et al., 2025). In SSPS, species number and dominance of *Camposperma panamense* seem to be related to a nutrient gradient, with higher diversity and forest height in soils with higher P content (Sjögersten et al., 2011; López, unpublished data).

Additionally, compositional differences between the DGW and other wetlands could influence species diversity. Specifically, the palm *Raphia taedigera* is abundant in SSPS and other wetlands further north but absent in our study area (Urquhart, 1997). The clonal and dense way of growth of this palm makes it the dominant species in large areas (Myers, 2013). In DGW the most common palms are *Manicaria saccifera* and *Euterpe precatoria*, monopodic palms that leave more space for the establishment of other species (observation by the authors). All three palm species are very important to the communities living around the wetlands, as thatching materials (*Raphia taedigera* and

Manicaria saccifera) or edible shoots (*Euterpe precatoria*) (Wake, 2006; Perez and Condit, 2026).

Conclusions

Wetland forests dominated by oreo (*Camposperma panamense*) have a restricted distribution, from Caribbean Nicaragua to western Panama and from Darién in the Pacific to northern Ecuador. In Panama, Damani-Guariviara oreo dominated swamp forests are the most extensive in the country and they need recognition and strict conservation.

The objectives of our research were fully met. In particular, we now have a more precise knowledge of the tree species composition of these wetland forests, the vegetation structure and the patterns of richness, abundance and dominance. Our findings correspond to our expectations, and we can assure that these mixed swamp forests are not a single community, and instead represent a heterogeneous habitat due to varying underlying environmental factors. These factors could be variable flooding stress, soil properties, proximity to the coast, microtopography, etc. and need to be measured in future research. A long-term monitoring program should also be a priority, to record climate change associated phenomena (i.e., salinity increase due to sea level rise, water table changes due to drought, etc.). Finally, there is a need to carry out more rigorous studies about carbon accumulation in the wetland peats, and projections about their capacity to sequester carbon.

Author contributions

Conceptualization: ORL, AI; Methodology: RF; Data curation: AI, RF. Writing – original draft: AI, ORL, RF; Writing – review and editing: AI, ORL, RF.

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Data availability statement

The dataset that supports the results of this study was published in SciELO and can be accessed at <https://doi.org/10.48331/SCIELODATA.JLKOH5>

Declaration of use of Artificial Intelligence

No Artificial Intelligence was used during this study.

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