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Composition, structure and regeneration strategy of *Campnosperma panamense* (Anacardiaceae) swamp forests in Darien, Panama

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ABSTRACT

Introduction: Orey (*Campnosperma panamense*) swamp forests are found on the Caribbean coast of Central America, from Nicaragua to Panama, and in the Pacific of Colombia to Northern Ecuador. In Panama, orey grows in monospecific stands or is the dominant species in inundated mixed forests, mainly along the coasts of Bocas del Toro province and Comarca Ngäbe-Buglé. The species was known to occur in Darien province, in the Pacific, although almost no information on its distribution and forest extension in the region existed.

Objective: To describe the structure and floristics of orey forests in Darien, map their extension, and propose a model for their regeneration strategy.

Methods: This work is part of a vegetation mapping project of the Matusagaratí complex of wetlands. It includes the use of drones, ground truthing, vegetation sampling through temporary plots, and general plant collecting. A supervised classification of a Landsat satellite image was performed to delimit the orey forest extension. To study the orey forest regeneration strategy, a digitalization of forest gaps in high resolution WorldView-2 and Planet Scope images was performed. Gap frequency and turnover time for forest stands were calculated.

Results: Several monospecific orey mature forest patches were found in remote areas of the Matusagaratí complex of wetlands, for a total of 1 267 hectares. A description of the floristics and structure of orey forests in Darien is presented. A conceptual model of orey mature forest development and gap regeneration is proposed.

Conclusions: Our knowledge of the floristic composition, structure and distribution of orey forests in the Republic of Panama has increased. For the first time, a model about their regeneration strategy is proposed. These forests seem to be evolving to different formations. Finally, some hypotheses are proposed about how they might respond to changing environmental conditions.

Key words: Matusagaratí; complex of wetlands; swamp forests; orey; Darien; regeneration strategy.

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RESUMEN

Composición, estructura y estrategia de regeneración de los bosques pantanosos de *Campnosperma panamense* (Anacardiaceae) en Darién, Panamá

Introducción: Los bosques pantanosos de orey (*Campnosperma panamense*) se encuentran en la costa Caribe de América Central, desde Nicaragua a Panamá, y desde el Pacífico de Colombia hasta el norte de Ecuador. En Panamá, el orey crece en formaciones monoespecíficas o es la especie dominante en bosques mixtos inundables de la costa de la provincia de Bocas del Toro y la Comarca Ngäbe-Buglé. Se tenía conocimiento que esta especie crece también en la provincia de Darién, en el Pacífico, aunque no había información sobre su distribución y extensión de estas formaciones..
Objetivo: Describir la composición florística y estructura de los bosques de orey de Darién, definir su extensión y proponer un modelo sobre su estrategia de regeneración.
Métodos: Este trabajo es parte de un proyecto de mapeo de la vegetación del complejo de humedales de Matusagaratí, e incluyó el uso de drones, verificación de campo, muestreo de vegetación por medio de parcelas temporales y recolectas de muestras botánicas. Con el fin de delimitar la extensión del bosque de orey, se realizó una clasificación supervisada de una imagen de satélite Landsat. Para estudiar la estrategia de regeneración del bosque de orey se hizo una digitalización de claros del bosque en imágenes de alta resolución WorldView-2 y Planet Scope. Se calculó la frecuencia de claros y el periodo de renovación del bosque.
Resultados: Se encontraron varios parches de bosques maduros monoespecíficos de orey en áreas remotas del complejo de humedales de Matusagaratí, para un total de 1 267 hectáreas. Se presenta una descripción florística y estructural de los bosques de orey en Darién. Se propone un modelo conceptual de desarrollo y regeneración del bosque de orey por medio de claros.
Conclusiones: Nuestro conocimiento sobre la composición florística, estructura y distribución de los bosques de orey en la República de Panamá ha aumentado. Por primera vez se propone un modelo sobre cómo se regeneran este tipo de bosques, los cuales parecen estar evolucionando hacia formaciones diferentes. Finalmente, se presentan hipótesis sobre su posible respuesta ante condiciones ambientales cambiantes.

Palabras clave: Matusagaratí; complejo de humedales; bosques de pantano; orey; Darién; estrategia de regeneración.

INTRODUCTION

Tropical wetlands provide a range of ecosystem services, including ground water recharge, conservation of biodiversity, the removal of excess nutrients from surface waters, and the sequestration and storage of atmospheric carbon (Sjögersten et al., 2011). Tropical forested swamps have been much less studied than lowland and mountain forests, with the exception of mangroves, mainly because of their inaccessibility (Ellison, 2004; López & Kursar, 2007). Knowledge of wetlands tree diversity and ecology at the southernmost end of the Mesoamerican corridor is limited. Particularly in Panama most of these swamp forests are continuous to coastal areas, becoming important conservation assets that have been largely ignored. Information on the floristic composition and ecology of these forests is scarce, which together with the enormous socio-economic pressures that they experience, jeopardize their sustainability, ecosystem services and evolutionary legacy.

The genus *Campnosperma* Thwaites, within the Anacardiaceae, comprises 15 tree and shrub species distributed in SE Asia (5 in Thailand to New Guinea, 1 in Sri Lanka), 5 in Madagascar, 1 in Seychelles, 1 in Micronesia and 2 in the Neotropics (Plants of the World Online [POWO], 2024). Most are restricted to inundated areas, being the dominant species in Southeast Asian peat swamps, mainly by *Campnosperma auriculatum* (Blume) Hook. f. and *Campnosperma coriaceum* (Jack.) Hallier f. In America, 2 species, also from inundated areas, have been described: *Campnosperma gummiferum* (Benth.) Marchand, restricted to the Amazon (from S Venezuela to N Peru) and *Campnosperma panamense* Standl., that grows in the Caribbean of Central America to Pacific Northern South America (POWO, 2024).

Campnosperma panamense was described by Stanley (1920) as "*panamensis*". Since then, the species has been named in both ways in the literature, what has brought a certain degree of confusion about its correct name. The generic name *Campnosperma*, formed by the combination of two Greek words: "kamptein" and "sperma", means the plant has "curved seeds". The ending "ma" in "sperma" is neuter, and so is the generic name derived from it (Stern, 1966). Once the gender of a generic name has been established, the specific epithet to be used must agree with it (Manara, 1991). According to the latest *International Code of Nomenclature* (Turland et al., 2018), it is recommended that the adjective ending in "ensis" should be used for an epithet derived from a geographical name (if the generic name is of masculine gender). Since the genus *Campnosperma* is a neuter generic name, its specific epithet must be neuter (Harper, 2012). Therefore, the word used must end in "ense" which is the neutral way of referring to Panama in Latin.

Campnosperma panamense formations have a limited geographic range in the Caribbean, from Nicaragua to Panama and the Pacific, from the Panamanian region of Darien to Northwest Colombia and Ecuador (Aguirre & Rangel-Ch, 2005; Carrasquilla, 2005), besides Coco Island of Costa Rica (TROPICOS, 2024). In Nicaragua, Ellison (2004) outlined the most relevant vegetational characteristics of swamp forests along the Atlantic coast, emphasizing prominent associations dominated by *Pterocarpus officinalis* Jacq., *Carapa guianensis* Aubl. and *Campnosperma panamense*. Urquhart (1999) examined swamp regeneration in areas mostly dominated by *Raphia taedigera* (Mart.) Mart. and *Campnosperma panamense*. In Costa Rica, flooded forests along the Caribbean coast are found mainly in the Tortuguero floodplain and to a lesser extent in the lower Talamanca region near Limon (Hammel et al., 2004; Webb & Peralta, 1998). In this area, formations dominated by *Campnosperma panamense*, *Manicaria saccifera* Gaertn. and *Raphia taedigera* are common (Hammel et al., 2004), although their composition varies throughout the landscape.

In the coastal region of Chocó in W Colombia and N Ecuador, *Campnosperma panamense* dominates permanently flooded o swamp forests, locally known as "sajales" which have been reported to support few species (Aguirre & Rangel-Ch, 2005; Alvarez-Dávila et al., 2016; Del Valle, 1996).

In Panama, some information on the floristics and vegetation of forested swamps is available for the San San Pond Sak (SSPS) wetland, a Ramsar Site of international importance, located in the Northwest Caribbean coast of the country (Centro Regional Ramsar para la Capacitación e Investigación sobre Humedales para el Hemisferio Occidental, 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. This large peat dome is covered by seven phasic communities, from open short-grassy fields dominated by sawgrass *Cladium* P. Browne in the center, passing through dwarf-to-tall vegetation dominated by *Campnosperma*, to *Raphia* palm forests (Lawson et al., 2014; Phillips et al., 1997; Sjögersten et al., 2011). Troxler et al. (2012) have proposed that vegetational rings, as well as the physiognomy of *Campnosperma* forests in SSPS, are explained by nutrient availability, in particular phosphorus. Studies on carbon dynamics in SSPS, which includes CO_2, CH_4, nutrients fluxes and water table hydrological modeling, have been advanced by Hoyos-Santillan et al. (2015); Hoyos-Santillan et al. (2016) and Sjögersten et al. (2020).

A maybe larger peat dome exists east of SSPS, in the Caribbean side of the Comarca Ngäbe-Buglé, within the Damani-Guariviara Wetlands of International importance, also a Ramsar Site. A few, but limited plant inventories and descriptions of the vegetation are available for this area (López et al., in prep.). Additional surveys in the same region are part of a study of carbon dynamics in peatlands, specifically at the mouth of the Cricamola River and in Guariviara (Hoyos-Santillan et al., 2014).

Until recently, the presence of *Campnosperma panamense* in the Pacific coastal wetlands of the Darien in Pacific Panama was unknown. The species was first reported there in 2000 (Smithsonian Tropical Research Institute (SCZ) Herbarium, Acc. No. 12999; Carrasquilla, 2005), although no information about the extension of its formations existed.

Orey forest regeneration: Turnover within forests is driven by stand development in conjunction with factors influencing tree death and replacement at various temporal and spatial scales. Gap dynamics play an important role in the tropical forest regeneration cycle. Whitmore (1989) recognizes three phases in gap succession in non-inundated mature tropical forests: (a) gap-phase, with an opening of the forest canopy as a result of tree falls; (b) building-phase consisting of young trees, mostly shade-intolerant, growing rapidly to fill the gap and attain the canopy; (c) mature-phase formed by a canopy of large trees.

This process has been also described in mangroves. The most important difference is in the character of small forest gaps. Gaps in terrestrial forests resulting from the fall of large trees are normally elliptic, but those in mangroves are circular and rarely involve falls of large older trees. Instead, mangrove trees usually die standing in small clusters of mixed age cohorts, leaving small circular "scars" or impressions in the forest, that form a mosaic of small regeneration patches reflecting various ages and stages of canopy recovery (Duke, 2001). Duke (2001) described six phases in the mangrove regeneration strategy, starting with a forest showing no gaps, cycles through two creation phases (initiation and opening) and three recovery phases (recruitment, filling and closure), before returning to the original condition. This author also hypothesized that the creation and regeneration of these gaps prevent mangrove forests from reaching senescence stage, hence maintaining the youthful conditions of the forests.

A pattern of circular gaps similar to those in mangroves has been found to be characteristic of not only mangroves but several monospecific peat swamp forests dominated by species such as *Shorea albida* Sym. in Brunei (Becek et al., 2022), and *Campnosperma panamense* in western Colombia (Lamb, 1959) and Caribbean Panama (Lawson et al., 2014; López et al., in prep.). This pattern is also characteristic of the mature orey forests in Darien (this study).

The objective of this paper is to describe the orey swamp forests in the Matusagaratí complex of wetlands, Darien. Their extension has been mapped for the region and information on diversity, floristics and structural composition is presented. To properly understand the role of gap regeneration in orey forest turnover, spatial and temporal gap rates were determined with the use of remote sensed data. A model for their regeneration strategy is also proposed.

MATERIAL AND METHODS

Site description: The study was conducted in the Matusagaratí complex of wetlands, in Darien Province, Pacific Panama. Fieldwork was carried out during 2022 and 2023 (February and March of each year). The Tuira and Balsas rivers are the backbone of these wetlands, one of the largest complex in Central America, covering around 55 750 ha (Ibáñez et al., in prep.). The hydrology and vegetation of this area has been recently studied (Candanedo, 2021; Carol et al., 2020, Carol et al., 2021, Carol et al., 2022; Carol et al., 2024; Ibáñez et al., in prep.). The wetlands include river margins and adjacent floodplains, which contain different vegetation types such as swamp and inundated forests, scrublands and herbaceous formations (Ibáñez et al., in prep.). All these communities are periodically flooded, and their structure and species composition defined by their position in the landscape and the nature and duration of the inundation, which can be from estuarine waters related to daily tides, spring tides, fluvial and/or rainfall flooding (Carol et al., 2022; Carol et al., 2024; Centro de Estudios y Acción Social Panameño [CEASPA], 2015; Grauel, 2004; Ibáñez & Flores, 2020). Rainfall averages around 2 500 mm/year, with a mean annual temperature of 21.6 to 24 °C. There is a pronounced seasonality, with a strong dry season from January to April, and a wet season from May to December (CEASPA, 2015; Grauel, 2004).

Orey forests in the Matusagaratí wetland were mapped. Fig. 1 shows the extent of mature orey monospecific forests in the study area. Besides mature orey monospecific forests which are the objective of this work, there are several other formations in which orey also dominates or grows, such as stunted orey forest and orey scrub, which are preliminary described in Ibáñez et al., (in prep.). Fig. 2 and Fig. 3 illustrate different views of the mature orey forests under study.

Orey forests in Darien remain flooded with freshwater all year round, where tip-up pools are also common (Fig. 2B). Recent hydrological studies show that inundation is mainly due to rainfall, although water from the river influences the lower ground strata. The water table fluctuates in the dry or wet seasons around 1 m relative to the surface (Carol et al., 2024). A peat layer in these forests has been recorded to be of variable depth (30-80 cm) (Hoyos et al., in prep.).

As mentioned in the introduction *Campnosperma panamense* (orey) forests in Darien show a characteristic gap pattern, which has been preliminary studied (Fig. 3).

Drone recording and ground truthing: As part of a general vegetation survey of the wetland region, drone flights were carried out. A Phantom 4 PRO V 2.0 drone was used to film and photograph the different ecosystems and vegetation types in the wetland, as well as the stages of gap formation and regeneration in orey forest (Fig. 3). Ground truthing of the area was later carried out in order to corroborate the identity of the dominant species in the different vegetation types (Ibáñez et al., in prep.).

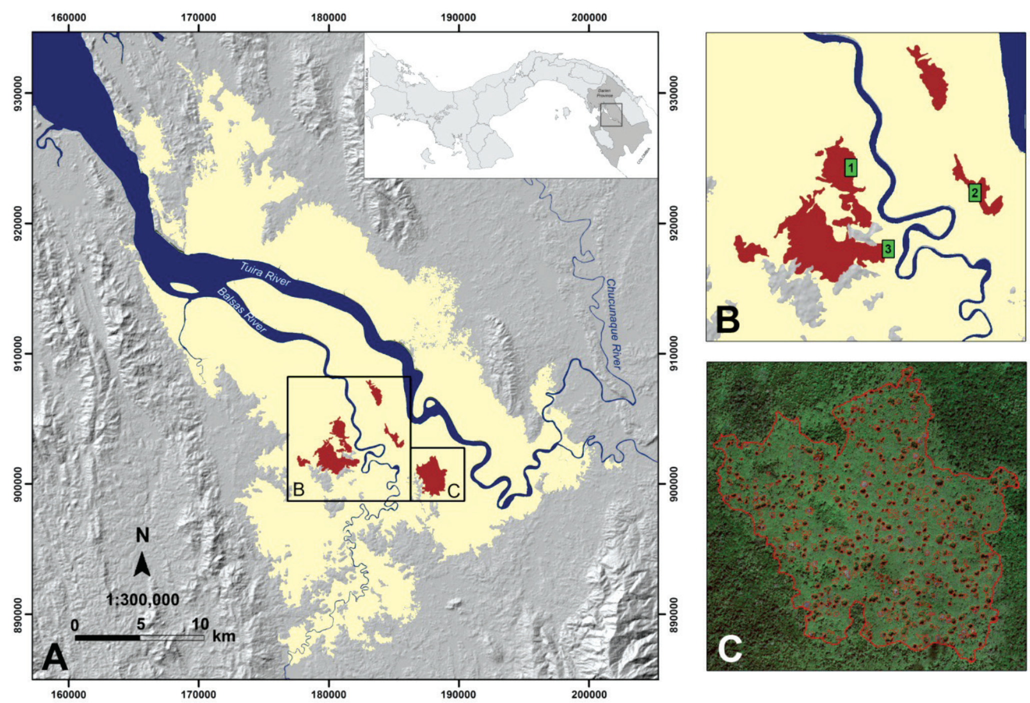

Fig. 1. Orey forest extension in the Matusagaratí complex of wetlands and study areas. **A.** Inundated area of the Matusagaratí complex of wetlands (yellow) and orey forests (dark red). **B.** Field study region in the Balsas river and location of orey research plots (green). **C.** Research area for the regeneration study (WorldView-2 image).

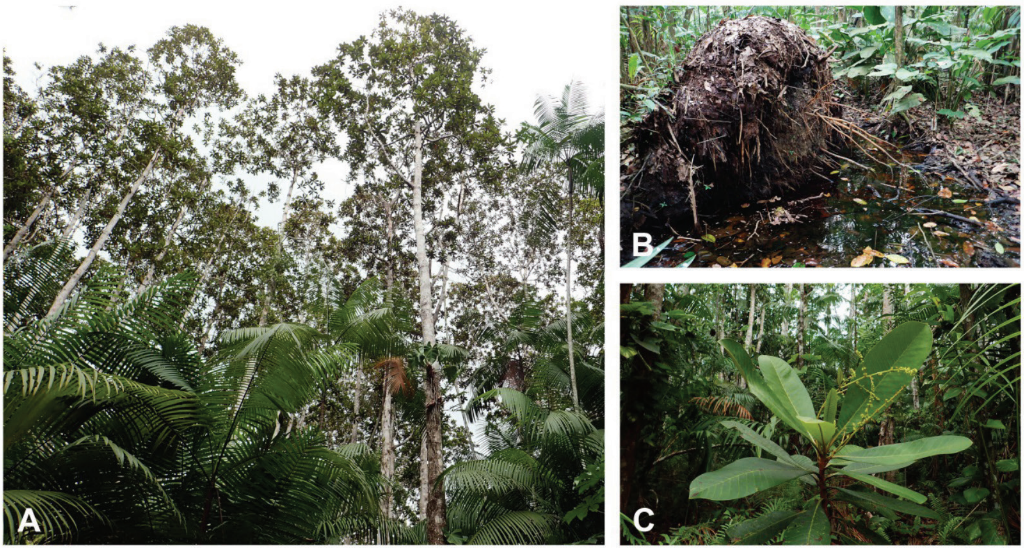

Fig. 2. Orey forest from the field. **A.** Orey (*Campnosperma panamense*) forest. Orey trees in the background, the palm *Euterpe oleracea* in the understory, at front. **B.** Tip-up pool in the forest. **C.** Orey flowering branch. Photos ©Alicia Ibáñez.

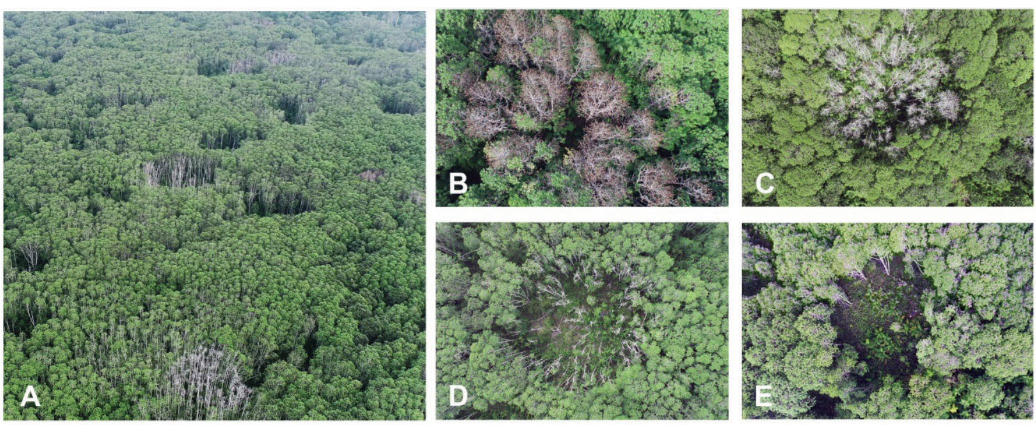

Fig. 3. Aerial view of orey forest and gap formation stages. **A.** Orey forest from the air. **B.** Initiation. **C.** Opening. **D.** Intermediate stage between opening and recruitment. **E.** Recruitment. Photos ©Alexis Baúles.

Satellite image analyses: To map the main vegetation types of the Matusagaratí complex of wetlands, a supervised classification of a Landsat 5 image from 1998 was carried out with the program ERDAS IMAGINE 2018. The results of this mapping process will be published in a separate paper (Ibáñez et al., in prep.). In order to define more precisely orey mature forest patches, a WorldView-2 image from 2017 was used as a base for further delimiting the orey patches found with the Landsat analysis.

Study plots: Three 0.1 ha (20 × 50 m) temporary plots were established in mature orey forest in the Balsas river, near an old logging site known as Cacerete (Fig. 1A, 1B).

Gap mapping techniques: To study the orey mature forest regeneration strategy, one of the forest patches recognized in the field was selected as study site (2.93 km^2) (Fig. 1C). The high resolution WorldView-2 image from January 2017 was used to initially digitize orey gaps

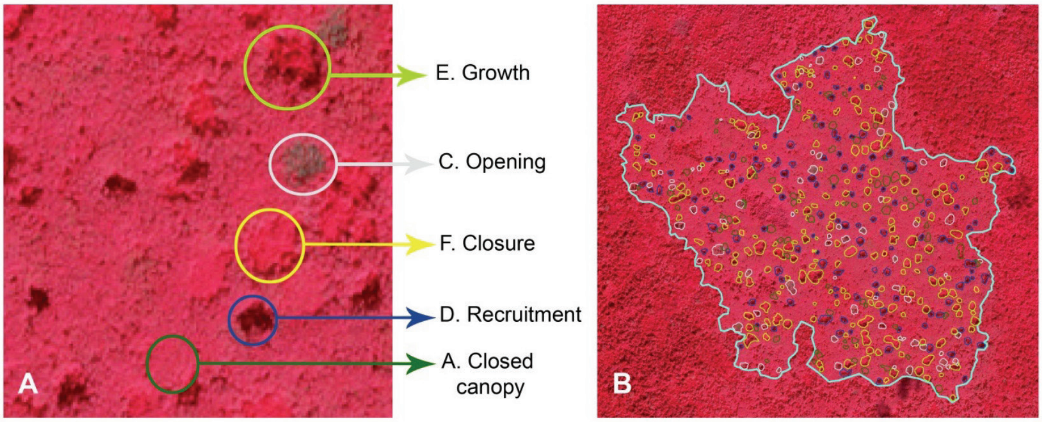

Fig. 4. Orey forest with gaps at various stages of recovery. **A.** Different stages of gap formation and recovery as seen in the WorldView-2 satellite image. **B.** Digitalized gaps at different stages of recovery in the study area. Composite images of bands 4, 3 and 2 (RGB) were used in order to obtain the greatest spectral difference of gaps.

in different states of development, with ArcGIS Pro (Fig. 4). New gaps were mapped and the stages of all gaps evaluated over a 6-year period, from February 2017 to February 2023, using Planet Scope satellite images obtained from Planet Labs (2023) (Fig. 4). The best possible Planet images, those less cloudy, were selected, from the dates: 16 February 2017, 9 December 2017, 13 October 2018, 30 January 2019, 3 November 2020, 20 June 2021, 7 December 2022 and 2 February 2023. They were all georeferenced previous to analyses.

The different gap regeneration stages were defined as follow (adapted from Fig. 2 in Duke, 2001): A: closed canopy, B: the gap is initiating and leaves turn brown (not seen in the images), C: trees died but still standing, D: dead stumps, fallen branches on gap floor, seedlings starting, E: regeneration of forest inside the gap, F: trees in gaps approaching maximal canopy height (Fig. 3, Fig. 4, Fig. 5, Table 1). The number of days each gap was in any of the four stages (C, D, E, F) was counted and the mean calculated for each stage (Table 1).

Vegetation census: To characterize orey mature forest (forest structure and species diversity), vegetation inventories were conducted in the plots; all stems ≥ 5 cm in diameter at breast height (DBH) were mapped, measured and marked. Voucher samples of all species were collected, and their identities verified at the Herbarium of the University of Panama (PMA), following TROPICOS (2024) nomenclature.

To describe the forest structure, the most common descriptors reported in the literature

Table 1
Gap phases, characteristics and estimated age in orey forest in Darien.

Gap Phase	Gap Characteristics	Estimated Age
A. Closed canopy	No gap presence	-
B. Initiation	Leaves brown, still in the trees	unknown
C. Opening	Bare branches and twigs, dead trees standing	1.5 years
D. Recruitment	Dead stumps, fallen branches on gap floor, seedlings starting	2.3 years
E. Growth	Saplings and small trees growing in gap	4.2 years
F. Closure	Trees in gaps approaching site maximal canopy height	3.6 years
TOTAL		11.6 years

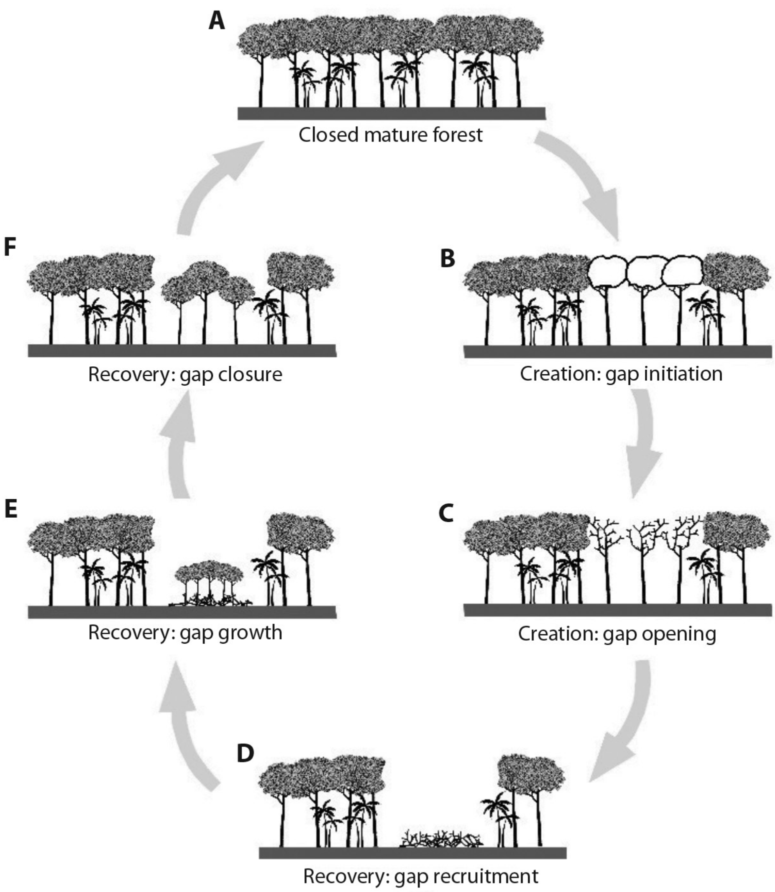

Fig. 5. Six phases in orey forest gap creation and recovery cycle. Adapted from Duke (2001).

were used. The basal area of the tree species found in the plots was calculated from the DBH data. The 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 frequency (RF, %) was calculated as the number of quadrants in which a species is present; the relative dominance (RD, %) as the basal area of a species in proportion to the total basal area, and the Importance Value Index (IVI) as the sum of RA + RF + RD, following Dallmeier et al. (1992) (Table 2). To further assess forest structure, diametric distribution graphs were obtained (Fig. 6).

Sampling effort was evaluated based on the species accumulation curve, using the number of estimated species versus the number of individuals (Fig. 7). The curve was calculated using a random order of the individuals with the program iNEXT (Chao et al., 2016). The expected maximum diversity was calculated with the non-parametric estimator Chao-1, which uses the numbers of singletons and doubletons to estimate the number of undetected species, as undetected species information is mostly concentrated on those low frequency counts (Chao, 1984). The program SpadeR was used (Chao et al., 2015).

Planet Scope imagery limitations: The major benefit of Planet Scope imagery is the availability of at least one image per year through the 6-year period of study, such that

Table 2
List of tree species (DBH ≥ 5 cm) and their abundance indexes.

Family	Species	N	RA	RF	BA	RD	IVI
Anacardiaceae	*Campnosperma panamense*	171	38.26	13.64	9.35	72.66	124.55
Arecaceae	*Euterpe oleracea*	234	52.35	13.64	2.76	21.47	87.46
Arecaceae	*Elaeis oleifera* (Kunth) Cortés	4	0.89	9.09	0.35	2.75	12.73
Aquifoliaceae	*Ilex guianensis* (Aubl.) Kuntze	10	2.24	9.09	0.18	1.38	12.71
Euphorbiaceae	*Alchornea grandis* Benth.	7	1.57	9.09	0.03	0.20	10.86
Moraceae	*Ficus cf. popenoei* Standl.	3	0.67	9.09	0.04	0.35	10.11
Apocynaceae	*Lacmellea panamensis* (Woodson) Markgr.	2	0.45	9.09	0.02	0.14	9.68
Rhizophoraceae	*Cassipourea elliptica* (Sw.) Poir.	10	2.24	4.55	0.06	0.45	7.24
Araliaceae	*Dendropanax arboreus* (L.) Decne. & Planch.	2	0.45	4.55	0.03	0.23	5.23
Malvaceae	*Pseudobombax septenatum* (Jacq.) Dugand	1	0.22	4.55	0.03	0.21	4.98
Euphorbiaceae	*Alchornea* sp. 1	1	0.22	4.55	0.01	0.09	4.86
Chrysobalanaceae	*Parinari chocoensis* Prance	1	0.22	4.55	0.00	0.03	4.80
Melastomataceae	*Henriettea succosa* (Aubl.) DC.	1	0.22	4.55	0.00	0.03	4.80
	TOTAL	447	100	100	12.87	100	300

N: number of individuals, RA: relative abundance, RF: relative frequency, BA: basal area, RD: relative dominance, IVI: importance value index.

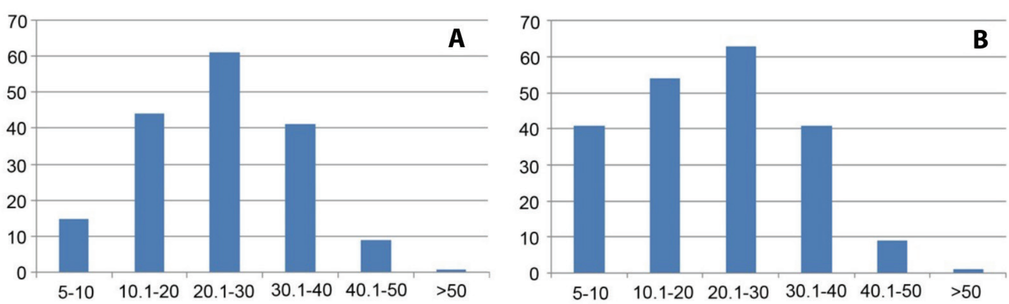

Fig. 6. Diametric distributions of orey forest in Darien. **A.** Only *Campnosperma panamense* included. **B.** All tree species included.

we were able to approximately date gaps and determine gap rate and turnover time. However, there are several disadvantages of using that imagery, including relatively low resolution (compared to WorldView-2) and visibility interference (e.g. edge shadow, cloud shadow).

Gap frequency and turnover time: Gap frequency and turnover time for the study region over a 6 year period were calculated. Gap frequency (Rg, % yr^{-1}) was defined as the percentage of gap area (Ag) per sampled region (As), i.e. Rg = 100 x Ag/As x 1 / 6 yr for all gap area observed during the 6-year study period. Fig. 4B shows the distribution of gaps throughout the study area in the period studied.

The average rate of forest turnover due to gaps (Tg) is the inverse of gap frequency. This metric reflects the time required for gaps to impact all the orey forest, solely based on their rate of occurrence. Table 1 shows an estimated age for the different gap stages according to our data.

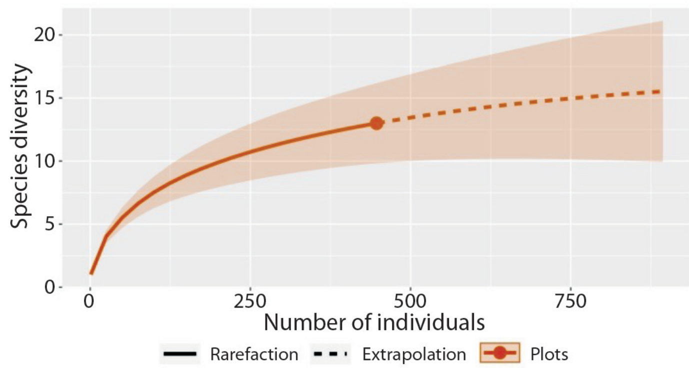

Fig. 7. Species-individuals curve.

RESULTS

Several patches of dense orey forest were identified in the study region, totaling an area of 1 267 hectares. Two of these patches were visited and studied by means of plots (Fig. 1, Fig. 2, Fig. 3).

General findings: A total of 447 individuals (815 stems), including trees and palms greater than 5 cm DBH, were recorded in 0.3 ha. We found 13 species, in 12 genera and 11 families. Two species, *Campnosperma panamense* and the palm *Euterpe oleracea* Mart., made up to 90.60 % of the total individuals sampled and show the highest IVI, 124.55 and 87.46 respectively. They are both the dominant species in this kind of wetland forest (Table 2). While *Campnosperma panamense* forms the canopy, which reaches c. 20 m, the multistemed palm *Euterpe oleracea* is the dominant species in the understory and reaches heights of 2-12 m. Common associates are the shrubs: *Tococa guianensis* Aubl., *Ardisia* sp. 1, *Ardisia* sp. 2, *Psychotria hoffmannseggiana* (Roem. & Schult.) Müll. Arg., *Psychotria poeppigiana* Müll. Arg., *Palicourea triphylla* DC.; herbaceous plants: *Monotagma plurispicatum* (Körn.) K. Schum., *Spathiphyllum phryniifolium* Schott; lianas and epiphytes: *Schradera* sp., *Thoracocarpus bissectus* (Vell.) Harling, *Anthurium clavigerum* Poepp., *Monstera pinnatipartita* Schott, *Philodendron fragrantissimum* (Hook.) G. Don and numerous fern species.

Vernacular names and uses of orey: *Campnosperma panamense* receives different names in its area of occurrence: the name recorded by our team in Darien was "sajo" (only known in the locality of Camogantí), same as in Western Colombia (Del Valle, 1996). The formation is called "sajal" in Darien and Colombia. In other regions of Panama it is called orey, orí (Bocas del Toro) (Phillips et al., 1997), degetda tain (Comarca Ngäbe-Buglé) (Flores et al., 2021) and nusmas (Guna Yala) (TROPICOS, 2024).

No uses were recorded for this species in Darien. Carrasquilla (2005) reports that its wood is used for paper pulp. In the Comarca Ngäbe-Buglé it is used as building material to construct houses (beams, posts and walls) and canoes. Its bark is cooked and used in traditional medicine (Flores et al., 2021). Bioactive flavonoids with antimalarial and anti *Leishmania* activity have been isolated from its leaves (Weniger et al., 2004).

Diametric distribution and stand structure: The analysis of diameter distributions for different tree populations allows us to evaluate the ecological and conservation conditions of the forest. The diameter distribution for *Campnosperma panamense* (Fig. 6A) showed highest proportion (36 %) of individuals in the middle classes (20-30 cm DBH), while 85 % had diameters from 10-40 DBH. Only 15 individuals (9 %) belonged to the lowest class (5-10 cm). A distribution that included all tree species showed similar results, although with higher individuals in the lowest class (Fig. 6B).

Sampling effort: The number of tree species increased as new individuals were sampled (Fig. 7). However, most increment appears up to the 447 trees sampled, after which the extrapolation curve shows few species additions, and seems to almost stabilize. This indicates that our inventory captured much of the orey forest tree diversity.

On the other hand, the total number of species in all 3 plots was 13. This is 76 % of the expected diversity that according to Chao-1 index is estimated to be around 17 species. This would also indicate that the tree inventory is quite complete, and it adequately represents the orey forest tree diversity. Chao-1 is a diversity index sensitive to the number of rare species found in the sample (species that only have one individual "singletons" or two individuals in the entire sample "doubletons") (Colwell, 2009). We found a total of 4 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 % of species in the sample.

Gap frequency and forest turnover: A total of 472 gaps were digitized from the satellite images for the study area in the period under study, with a mean area of 1 046 m^2. Gap recovery in orey forests is characterized in six phases (closed canopy, initiation, opening, recruitment, growth and closure), and it takes about 11.6 years for complete gap recovery (Table 1). Approximately 16.83 % (0.49 km^2) of the orey forest regeneration study area (2.93 km^2) experienced gaps over the 6-year study period. Gap frequency was 2.78 % yr^{-1}, (0.081 km^2 or 8.1 ha/yr^{-1}), which corresponds to a forest turnover time of 35 years.

DISCUSSION

Forest structure and diversity: This is the first study of the orey swamp forests of Darien, Panama, where 1 267 hectares of mature formations were mapped. *Campnosperma panamense* forms large monospecific stands (IVI of 124.55 and 72 % of the basal area) on permanently inundated ground with peat of around 30-80 cm deep. These formations are structurally similar to monospecific forests in SSPS, Bocas del Toro province, Caribbean coast of Panama, where *C. panamense* showed 70 % of the basal area (Phillips et al., 1997; Sjögersten et al., 2011). They are also similar to the "sajo" forests in coastal Western Colombia, with a 74-92 % of *Campnosperma* in their forests (Alvarez-Dávila et al., 2016; Del Valle, 1996). In Darien, middle canopy and understory is dominated by the colonial palm *Euterpe oleracea*, known here as "murrapo", which shows pneumatophores of up to 1 m height, indicating an adaptation to permanently waterlogged conditions. This species does not grow in Caribbean orey forests, where a non-colonial species of the same genus, *Euterpe precatoria* Mart., is common. *Euterpe oleracea* is also abundant in Pacific Colombian sites, where it is called "naidí" (Alvarez-Dávila et al., 2016; Del Valle, 1996).

Tree diversity in orey forests of Darien was low compared to Panamanian lowland forests on mineral soils, which typically contain around 100 sp/ha (e.g. Pyke et al., 2001). Low diversity tree communities are typical of Central and South American wetlands (Ellison, 2004; López & Kursar, 2007; Webb & Peralta, 1998). Species richness (13 sp ≥ 5 cm DBH in 0.3 ha, 10 sp ≥ 10 cm DBH / 0.3 ha, 4-7 sp ≥ 10 cm DBH / 0.1 ha) was similar to SSPS orey forest (7 sp ≥ 10 cm DBH / 0.1 ha) (Sjögersten et al., 2011) and Colombian "sajo" forests (9 sp ≥ 10 cm DBH / 0.5 ha) (Alvarez-Dávila et al., 2016).

In this sense, the low species richness in the tropical swamp forests is generally due to the inability of solid ground species to face the stress conditions that result from the permanent flooding and the acid peat soils typical of *Campnosperma* forests (López & Kursar, 2003;

Sjögerstenet al., 2011). These patterns of low diversity have been described by Richards (1952) and Whitmore (1975) in South East Asian peatland forests dominated by *Campnosperma brevipetiolatum* Volkens (New Guinea), *C. coriaceum* (Malaysia) and *Shorea albida* in Borneo (Whitmore, 1975).

The analysis of diameter distributions, with a higher number of trees within the intermediate size classes, indicates a lack of enough young trees for replacement of the older ones. This lack of regeneration could be explained by human activities (logging) or else a natural ageing trend (Bermadzki et al., 1998). In Darien, orey forests have never been logged or show any other kind of human impact, so we can infer they are naturally evolving to a mixed type or to a more open formation. Inundated mixed forests and more open formations, such as stunted or scrub orey are common in the surroundings of the main mature orey forest patches. The unimodal diametric structure, with mostly contemporary individuals and the lack of enough young trees has also been reported for Colombian orey forests (Lamb, 1959), although there it has been explained by their secondary nature due to logging activities (Del Valle, 2000).

Forest regeneration: A conceptual model of orey forest development and gap regeneration has been proposed. Preliminary evidence shown in this study indicates that orey mature forest regenerates in a similar way to that reported in mangroves by Duke (2001), in which gaps are formed by trees which die standing in small clusters. Gap recovery in orey forests can also be characterized in six phases (closed canopy, initiation, opening, recruitment, growth and closure).

The importance of gap creation on forest turnover can be explored further using the relationship between area of gaps formed in each time and the rate of gap recovery. Our results indicate that orey forests in Darien seem to be very dynamic with a forest turnover time of 35 years. Around 17 % of the area was in gap mode during the 6 years of the studied period, with a gap frequency rate of 8.1 ha/year and only takes 12 years for gaps to recover. As a comparison, for a mangrove forest dominated by *Rhizophora* L. trees in Panama, it took them around fifteen years to achieve early gap closure (Duke, 2001).

Phillips et al. (1997), after evaluating air photos of orey forests in SSPS from 1954, 1981 and 1992, saw striking differences in the distribution of the distinctive *Campnosperma* canopy within the region, and proposed that stands develop rapidly and may be quite short-lived.

It seems that orey forests in Darien are constantly re-newing themselves, with a high frequency of gap formation. Assuming this is correct, turnover in these forests might occur entirely via gap formation rather than via trees getting older. This is why such forests may never reach the senescence phase of stand development.

Factors influencing gap creation: There is no accepted common cause for gap creation in mangroves, although different theories have been proposed, such as windstorms, lightning strikes, frost damage, hail damage, plant pathogens, wood-boring insects, etc. However, the most common gaps in mangroves are small gaps comprising around 10-20 trees and reputedly caused by lightning (Duke, 2001).

In orey forests of Darien, we can hypothesize that they are not caused by lightning. Preliminary evidence showed an initiation stage in which trees in the gap had dried leaves. Although there was no sign of disease, it seems reasonable to think about some kind of plant pathogen. For these forests, still remains the question of what triggers gap creation.

Conservation: Orey forests in Darien are unique ecosystems that need recognition and strict conservation. The orey mature formations described here are included in two protected areas, although they are not managed. Given their remote location and inaccessibility, at present there are no direct threats, except those related with climate change.

Much of the importance of these forests rests in their ecosystemic roles. First of all, the Matusagaratí wetland has a hydrologic function as a buffer for coastal ecosystems, regulating hydrological variations due to rainfall. This function of filtering and buffering is vital for the well-being of marine ecosystems in the region. Second is the value of the wetland as a reservoir of fresh water during the rainy season, as in the dry season, the maintenance of the caudal of the rivers is due to the subterranean flux of water from the wetland. Also, we can highlight the value of these forests as a reservoir of organic carbon, as prospections have shown the presence of peat in these forests (Hoyos et al., in prep.).

Estuarine and continental wetlands, such as the ones in Matusagaratí are very vulnerable to climate change. Hydrological studies indicate that these forests depend on rain water that maintains the water table, so severe drought events seem to be the main threat. Rising sea levels is an important second issue, as orey forests may experience severe disturbances because of salinity. All these changes may suppose the collapse of stands or even of large areas. Such vegetation changes may already be taking place, but they are very difficult to distinguish as few studies are focusing on this issue. A long-term monitoring program should be a priority to record these phenomena and also to study the carbon accumulation process in the peats, in order to estimate the value of the wetland as a carbon reservoir.

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