



RESEARCH ARTICLE OPEN ACCESS

Ecohydrological Response of a Tropical Peatland to Rainfall Changes Driven by Intertropical Convergence Zone Variability

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Received: 18 April 2024 | **Revised:** 21 October 2024 | **Accepted:** 5 November 2024

Funding: This work was supported by the Quaternary Research Association (UK) and the Secretaría Nacional de Ciencia, Tecnología e Innovación (Panama).

Keywords: climate change | ecohydrology | palaeoenvironments | precipitation change | tropical ecology | wetlands

ABSTRACT

Aim: Tropical peatlands are globally significant carbon stores, increasingly threatened by human activities and climate change. However, their ecohydrological responses to shifting water availability remain poorly understood. In this study, we investigate the connections between climate change, hydrology and vegetation dynamics in a coastal tropical peatland in Panama, aiming to understand the effects of future drying on peatland dynamics.

Location: Bocas del Toro, Panama (9°22'54"N, 82°21'59"W).

Taxon: Angiosperms.

Methods: High-resolution multiproxy palaeoecological data, including pollen and plant macrofossils (vegetation), testate amoebae (water-table depth) and physical peat properties, are used to explore the relationships between climate change, hydrology and vegetation in a coastal tropical peatland over the past 700 years. Downscaled climate simulations are integrated with this process-based understanding to project the likely future responses of this coastal peatland to climate change.

Results: We identify a clear connection between precipitation variability, driven by shifts in the Intertropical Convergence Zone and water-table dynamics, which subsequently influence changes in the peatland vegetation mosaic. Historical drier periods are marked by the expansion of shrub communities into the open peatland plain.

Main Conclusions: Palaeoecological studies incorporating climate and hydrological proxies are essential for understanding both recent and future ecohydrological dynamics of tropical peatlands. Our findings suggest that in response to future climate change, water tables will lower and shrub communities will expand due to rising temperatures and reduced precipitation. Additionally, future sea-level rise, combined with declining rainfall, may result in seawater intrusion and significant vegetation shifts in coastal tropical peatlands.

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1 | Introduction

Tropical peatlands are globally important ecosystems in terms of their biodiversity, their influence on groundwater and hydrology and the large amount of carbon they store above and below ground (Girkin et al. 2022; Green and Page 2017). Tropical peatlands contain an estimated 104.7 petagrams (1Pg = 10^{15} kg) of carbon globally (Page, Rieley, and Banks 2011), and although long recognised in Indonesia and Malaysia (Page, Rieley, and Wüst 2006), recent investigations have uncovered their extent and depth in the Congo (Dargie et al. 2017) and Amazonian basins (Draper et al. 2014; Kelly et al. 2017). Tropical ecosystems differ from their temperate counterparts in that they are typically forested (Hoyos-Santillan et al. 2015), with a spatially complex vegetation structure incorporating elements of flooded forest and palms (Phillips, Rouse, and Bustin 1997). Tropical peatlands have become highly vulnerable to exploitation and clearance for palm oil and banana plantation (Cole et al. 2022). Climate change poses a further threat, as the redistribution of precipitation patterns and increased evapotranspiration, bring an uncertain future to tropical peatland ecosystems. There are few studies on the interaction between climate and hydrology in tropical peatlands, but existing studies have shown clear hydrological shifts occurring in tropical peatlands in response to climate change and long-term peatland development (Swindles, Baird, Kilbride, Low, and Lopez, 2018; Swindles, Morris, Whitney, et al. 2018).

Our limited understanding is further complicated by the diversity of tropical peatland types and their climatological envelope globally; for example, the American tropical and subtropical coastal peatlands combine elements of both forested and open domed vegetation structures (e.g., Läähteenoja and Page 2011). Here, we investigate vegetation and hydrological change from a Central American coastal peatland over the last 700 years. Using palaeoecological methods, identified shifts in hydrology are compared with other indicators of environmental change, including vegetation and peat composition. We use instrumental and proxy climate data to understand the relationship between peatland dynamics and climate in these understudied systems and place these findings in the context of future climate scenarios.

2 | Study Site

Oropel swamp is located within the Changuinola coastal peatland complex of Bocas del Toro, northern Panama ($9^{\circ}22'54''\text{N}$, $82^{\circ}21'59''\text{W}$) (Figure 1). The region lacks a distinctly pronounced dry season with a mean annual precipitation of 3200 mm and mean annual temperature of 26°C . The swamp is bounded by the Atlantic Ocean on the northeastern side and a NE–SW oriented coastline situated leeward of the Bocas del Toro archipelago. The study site is situated less than 500-m from this protected coastline. Further descriptions of the Oropel swamp are provided in Baird et al. (2017) and Swindles, Baird, Kilbride, Low, and Lopez (2018), which describe the peatland as ombrotrophic despite its proximity to the sea and its low elevation (<1 m asl) owing to low pH and electrical conductivity. Sea ingress may be prevented by a series of ridges that form a barrier between the site and the coastline, although the mangrove peats

at the margin are influenced by tidal waters (Baird et al. 2017). Surface microtopography is variable across the peatland and is characterised by the aforementioned ridges, tree-root hummocks, hollows and pools. Areas of forest cleared for agriculture (including banana plantations) are located as close as 5 km from the peatland (Figure 1).

Previous studies of the Changuinola peatland complex delineated a maximum of seven modern phasic vegetation zones (Phillips, Rouse, and Bustin 1997) along a gradient originating in the coastal mangrove vegetation to the central bog plain in the central dome of the ombrotrophic peatland. Despite the absence of a dome, Oropel swamp contains a subset of five distinctive vegetation zones which exhibit similar composition to those identified by (Phillips, Rouse, and Bustin 1997); (i) central *Cladium*-dominated plain; (ii) stunted *Camposperma panamensis* forest with *Cladium*; (iii) *Camposperma panamensis*—*Symphonia globulifera* hardwood forest; (iv) mixed *Camposperma panamensis*—*Euterpe precatoria*—*Raphia taedigera* forest; and (v) *Cassipourea elliptica* and *Chrysobalanus icaco* scrub in the brackish mangrove edge (Swindles, Baird, Kilbride, Low, and Lopez, 2018).

3 | Materials and Methods

3.1 | Field Surveys and Peat Extraction

A NE–SW transect was established across the major vegetation types and a sampling station was established within each distinct vegetation zone (Figure 1, Figure S1 in ‘Supporting Information’). At each point, peat thickness was tested using a 3-cm diameter Dutch-head auger. A Russian D-section corer with a 5-cm diameter and 50-cm long chamber (De Vleeschouwer, Chambers, and Swindles 2010; Jowsey 1966) was used to extract a 200-cm core from the interior of the peatland (*Cladium* (sawgrass) plain) at the deepest sampled point for a detailed multiproxy palaeoecological analysis. A series of dipwells were installed along the transect to examine the hydrological dynamics of Oropel swamp. Four litter samples measuring ca. 5-cm^3 each were extracted adjacent to each dipwell for analysis of modern testate amoeba communities. Environmental variables (water-table depth, surface elevation, vegetation, electrical conductivity of water in the dipwells, moisture content) were sampled at each point to determine the ecological preferences of testate amoeba species and develop a transfer function to reconstruct past water-table depths using subfossil assemblages (see ‘3.4 Testate amoebae’ below). Forty modern samples were included in the modern training set; the transfer function was applied to 49 fossil samples in this study. Full details of modern sampling and the testate amoeba community data are found in (Swindles, Baird, Kilbride, Low, and Lopez, 2018).

3.2 | Radiocarbon Dating and Age-Modelling

Peat samples were sieved at $63\ \mu\text{m}$ (retaining the $<63\ \mu\text{m}$ fraction) and all rootlets were picked out before acid–alkali–acid treatment. AMS ^{14}C Dating was carried out at the André E. Lalonde AMS Laboratory, Ottawa, Canada. Calibration was carried out using Calib 7.1 and the IntCal20 calibration dataset (Reimer et al. 2020).

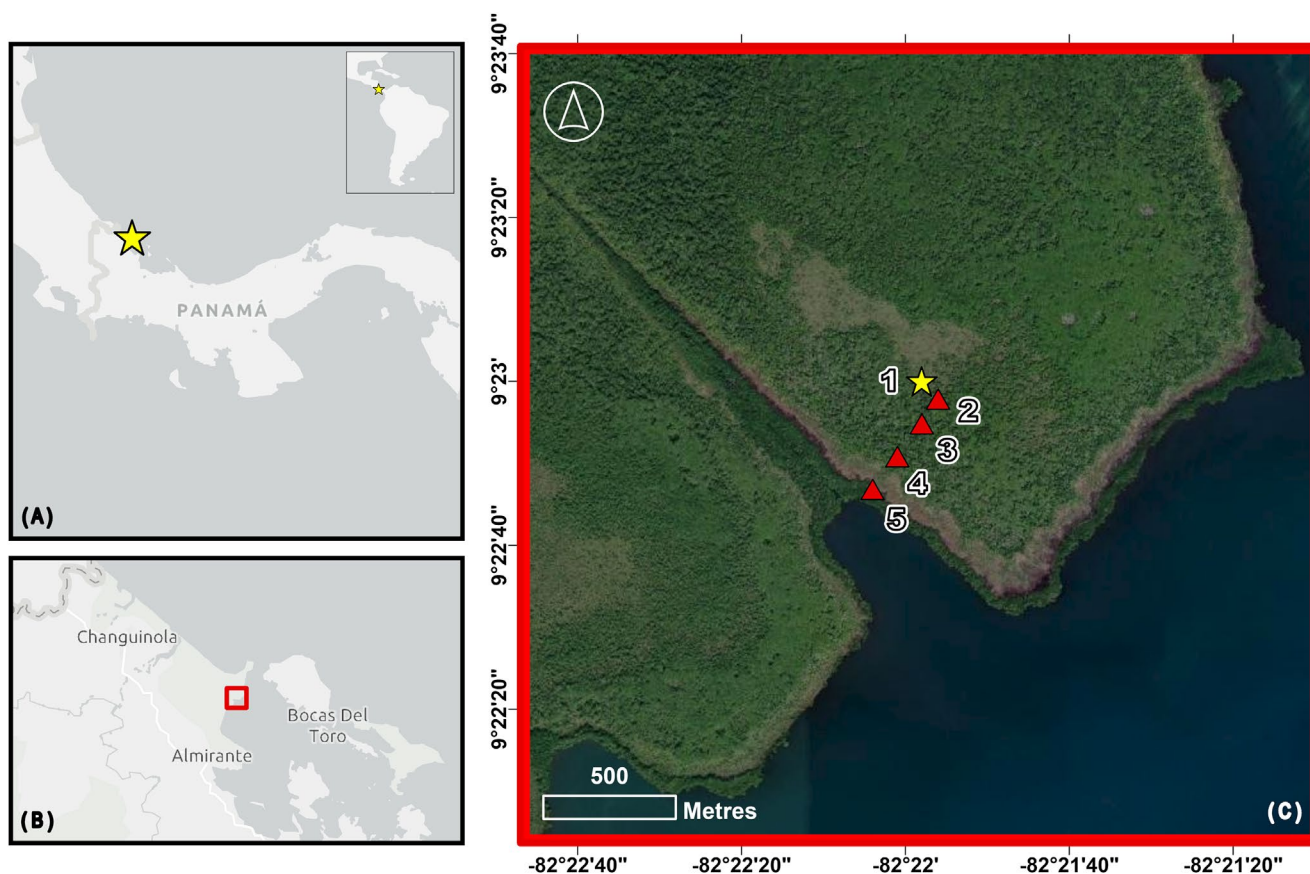


FIGURE 1 | [A] Map showing the location of Oropel swamp, Panama, inset with global location. [B] Map of core study location within Panama showing geographical area and extent of satellite map. [C] Satellite imagery illustrating the five main sampling locations and complexity of the vegetation mosaic from mangrove fringe, forest to open bog plain. The location of the analysis core is shown ("1"). Satellite image: MAXAR 2023. Oropel Swamp: 9°22'53.9"N 82°21'58.6"W.

The basal date at our sampling location is 2200–1900 BCE (Before Common Era); however, only the top 150-cm was subjected to a detailed palaeoecological analysis owing to the poor preservation of testate amoeba communities in the lower portion of the peat profile. An age model based on six ^{14}C dates from the top 150-cm and an assumed modern core top were constructed using Bacon, a Bayesian piecewise linear accumulation model, where the accumulation rate of sections depends to a degree on that of the preceding sections (Blaauw and Christen 2011) (Figure S1). Details of all radiocarbon dating results are available in Table S1. The a priori accumulation rate was assumed to be 5 year cm^{-1} and 5-cm thick sections were used. Markov chain Monte Carlo (MCMC) iterations estimate the accumulation rate for each of these sections. Mean ages calculated for each depth horizon were used for description and plotting of results.

3.3 | Peat Properties

The analysis core was subsampled in contiguous 1-cm sections. Moisture content, dry bulk density and loss-on-ignition (LOI; ash content) were determined at every 2-cm interval using standard methods on 1 cm^3 samples of peat (Chambers, Beilman, and Yu 2011). C, N and H percentages were measured every 10-cm on a Thermo Scientific Flash 2000 Series CHNS/O Analyser. Full results are presented in Figure S1.

3.4 | Testate Amoebae

Testate amoebae were extracted from the peat samples through sieving at $300\ \mu\text{m}$ and back-sieving at $15\ \mu\text{m}$ following (Booth, Lamentowicz, and Charman 2010). Testate amoebae were counted under transmitted light at $200\text{--}400\times$ magnification and were identified using morphology, composition, size and colour to distinguish taxa. At least 200 specimens were counted in each sample to ensure statistical reliability (e.g. Patterson and Fishbein 1989). Testate amoebae were identified using several sources (Charman, Hendon, and Woodland 2000; Mazei and Tsyganov 2006; Meisterfeld 2002; Meisterfeld and Badewitz 2006; Ogden and Hedley 1980; Siemensma 2019). The taxonomy used a morphospecies approach in certain circumstances, where a designation that includes other species or several morphotypes is referred to as a 'type'.

Water-table depths and moisture content were reconstructed using the transfer function from the same site (Swindles, Baird, Kilbride, Low, and Lopez, 2018). Transfer functions for water-table depth (cm) and moisture content (%) were developed from contemporary testate amoeba community data using weighted averaging partial least-squares regression and were found to perform well under 'leave-one-out' cross-validation ($R^2=0.80$, $\text{RMSEP}=4.64\text{ cm}$; $R^2=0.89$; $\text{RMSEP}=1.57\text{ cm}$). Sample-specific errors of prediction were generated for the subfossil data through

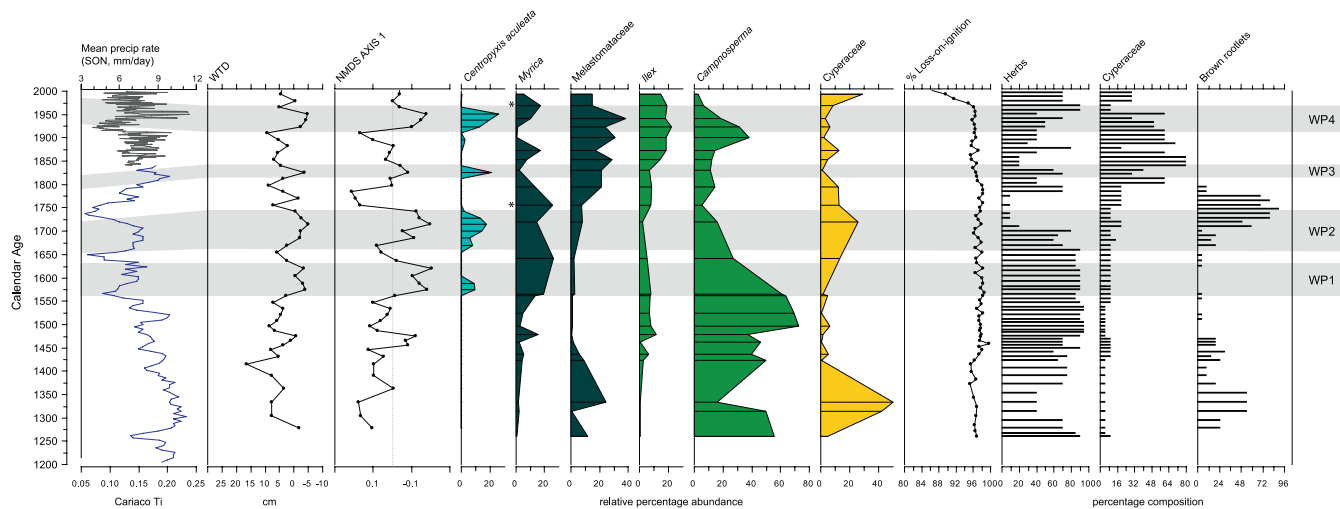


FIGURE 2 | Summary diagram presenting multiproxy palaeoecological data from Oropel Swamp, alongside the proxy rainfall record from the Cariaco Basin (Ti) in blue (Haug et al. 2001) and mean daily precipitation rates for the three wettest months in black. Grey bars highlight wet periods identified through testate amoeba-inferred water-table depths (WTD) and NMDS Axis 1 scores, which align with periods of increased precipitation observed in the independent climate records. Wet periods are inferred when the reconstruction shows near-surface water tables at or above 0 cm. The presence of the unambiguous wet-indicator testate amoeba *Centropyxis aculeata* is marked by turquoise shading. The pollen data visualization uses a color-coded scheme to distinguish between different vegetation types: dark grey shading represents shrubs, green represents trees, and orange shading represents herb taxa. Percentage loss-on-ignition (LOI) data are also displayed, with bars indicating major peat components as determined by plant macrofossil analysis. An asterisk denotes samples with a pollen count of less than 50. Please refer to Supporting Information to view the complete dataset.

999 bootstrap cycles. Non-metric multidimensional scaling (NMDS) was applied to the subfossil data using the Bray–Curtis dissimilarity calculation using the Vegan ecological package in R (Oksanen et al. 2022). The water-table depth reconstruction was compared with NMDS axis 1 scores to determine whether the transfer function was reconstructing the main patterns in the subfossil data. Key testate amoeba indicators are plotted in Figure 2 and full results are presented in Figure S1.

3.5 | Plant Macrofossils

Plant macrofossils were analysed at 5-cm intervals. Samples were washed and sieved under a warm-water spray using a 0.20-mm mesh sieve. The volume percentages of different vegetative remains (rootlets, leaves, wood fragments) were estimated to the nearest 5% with a stereoscopic microscope. Macroscopic charcoal pieces (> 1 mm) were counted during plant macrofossils analysis. The number of carpological and insect remains was counted separately and expressed as absolute numbers (Figure S1).

3.6 | Pollen

Peat samples measuring 1-cm³ were analysed for pollen at approximately every 5–10 cm with 22 samples prepared. Standard sieving and chemical digestion methods (e.g., Fægri and Iversen 1989) were used to concentrate the pollen, specifically, 10% NaOH, sieving at 250 μm to remove large plant fragments, acetolysis and hydrofluoric acid treatments. Residues were dehydrated with isopropanol before mounting in silicone oil for microscopic analysis. Counts of 300 pollen excluding spores were obtained for 19 samples, but the pollen was poorly preserved at 10 cm and 56 cm and

counts of < 50 grains were obtained. A count of only 115 grains was achieved at 94 cm, but a full count was achieved at 95 cm. Identifications were performed with the aid of (Phillips, Rouse, and Bustin 1997; Roubik and Moreno Patino 1991) (Figure 2). Key pollen indicators are plotted in Figure 2 and full results (including 95% confidence intervals) are presented in Figures S1 and S1.

3.7 | Climate

Daily mean temperature and precipitation data were taken from the NOAA-CIRES-DOE Twentieth Century Reanalysis V3 dataset covering the period 1836–2015 (Compo et al. 2011; Slivinski et al. 2019). The dataset is the first ensemble of sub-daily global atmospheric conditions spanning more than a century, making it suitable for climate analyses extending back into the 19th century. The data were downloaded from KNMI Climate Explorer (<https://climexp.knmi.nl/>) for the 1° longitude × 1° latitude grid box within which the study site is located. Data were aggregated for three averaging periods—the wettest 3 months of the wetter season (September, October and November), the drier season (December–August) and the entire annual average. Trends were calculated based on the difference between the starting year (1836) and end year (2015) when a line of best fit is drawn. Modelled climate data for the years 1995–2100 for the same location were downloaded from KNMI Climate Explorer for four future scenarios for both mean temperature and precipitation—the Coupled Model Intercomparison Project 6 (CMIP6) mean driven by shared socioeconomic pathways (SSP) 126, 245, 370 and 545 (Riahi et al. 2017). The climate model data were bias corrected and downscaled to the same spatial resolution as the reanalysis data using the change factor method (e.g. (Hawkins et al. 2014)), by subtracting model output for the period 1995–2014 from the

reanalysis data for the same time period and then adding the difference to the model output for the period 2015–2100 (on a monthly basis) (Figure 4).

The Titanium (Ti) record from the anoxic Cariaco Basin, off the Venezuelan coast, is used to infer variations in the hydrological cycle over our study region in the Late Holocene (Haug et al. 2001). This palaeoclimate record documents changes in precipitation driven by shifts in the mean latitude of the Atlantic Intertropical Convergence Zone (ITCZ).

4 | Results

The age-model indicates the peat core covers the last 700 years with no obvious hiatuses or age reversals (Figure S1). Quantitative reconstructions of water-table depth (WTD) are presented alongside key vegetation and peat composition indicators and the Cariaco basin Ti record (Haug et al. 2001) in summary Figure 2. The physical properties of the peat (e.g., LOI) are unvarying through most of the record except for a reduction in LOI (by 10%) in the most recent decades. The influx of minerogenic dust particles in the top of the core most probably originates from land use change owing to banana plantations and farmland surrounding the study site. The anthropogenic influences on Oropel swamp are apparent in our palaeoecological data from the mid-20th century until present. We interpret environmental changes prior to this date to have been largely driven by natural factors, although we cannot rule out some impacts of earlier human activity.

The pollen-based vegetation reconstruction of the Oropel swamp shows a transition from closed-canopy forest (*Camnosperma* monodominant stands) towards an open or broken canopy shrub bog plain (characterised by *Myrica* and *Ilex*) after 1560 CE (Common Era) (Figure 3). We infer this change to an open and shrubby bog plain to have been driven by vegetation

succession. We find no clear evidence for earthquake-induced hydrological shifts as previously suggested by Phillips, Bustin, and Lowe (1994), as the timings of major hydrological shifts do not correspond to known earthquake events in this region. We do not discount the possibility of precipitation-driven hydrological change, but the Cariaco record shows a generalised drying trend from 1200 to 1560 CE, the opposite pattern to what would be expected if the establishment of an open bog environment was driven by climate change. This upper half of the record represents a mix of stunted forest and open bog plain, both of which are characterised by a high water table with pools of standing water at the base of the shrubs and sedges (Phillips, Rouse, and Bustin 1997) and contain the highest relative abundance of *C. aculeata* in the modern training set. Wetter conditions at the very bottom of the core (137–150 cm, 1260–1360 CE), though not consistently present, may be suggested by a high relative abundance of Cyperaceae pollen and the presence of *Cladium* fruits as sedges are indicative of wet conditions in tropical peatlands.

The peatland environment of the open bog plain is highly variable, as shown by quantitative water-table depth values and changes in relative abundance of *Myrica* which vary in anti-phase with periods of wetness (as suggested by the presence of *C. aculeata*). Prior to ca. 1560 CE (85 cm), the testate amoeba-inferred wet periods were less pronounced during the forested phasic community, despite the Cariaco record showing the highest precipitation in the Oropel record. The dense closed-canopy forest before 1560 CE was described as short-lived and successional (Phillips, Rouse, and Bustin 1997). Although the modern testate amoeba training set was not sampled from within monodominant *Camnosperma* stands, its closest vegetation community analogue in the modern study (mixed and hardwood forest ridges) has lower water tables and an absence of *C. aculeata*, a species ecologically restricted to open standing pools of water (Swindles, Baird, Kilbride, Low, and Lopez, 2018). Therefore, although precipitation was high, the monospecific forest stand

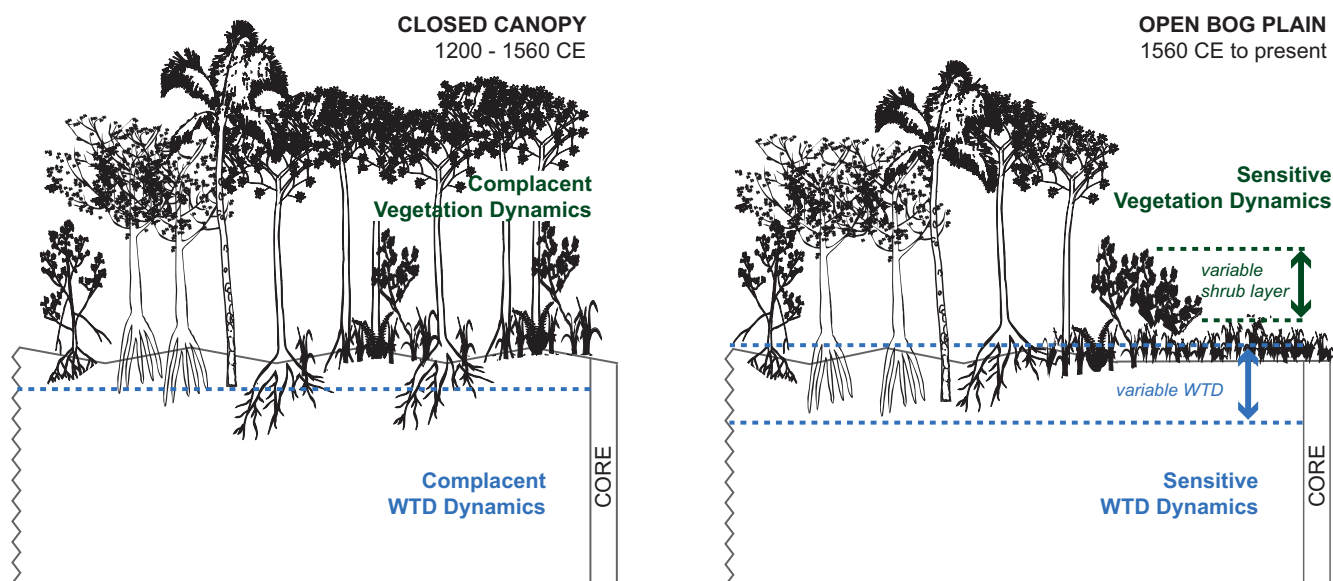


FIGURE 3 | Conceptual diagram illustrating the impact of precipitation variability on hydrology and vegetation dynamics in the closed forest peatland (left) and open bog plain (right).

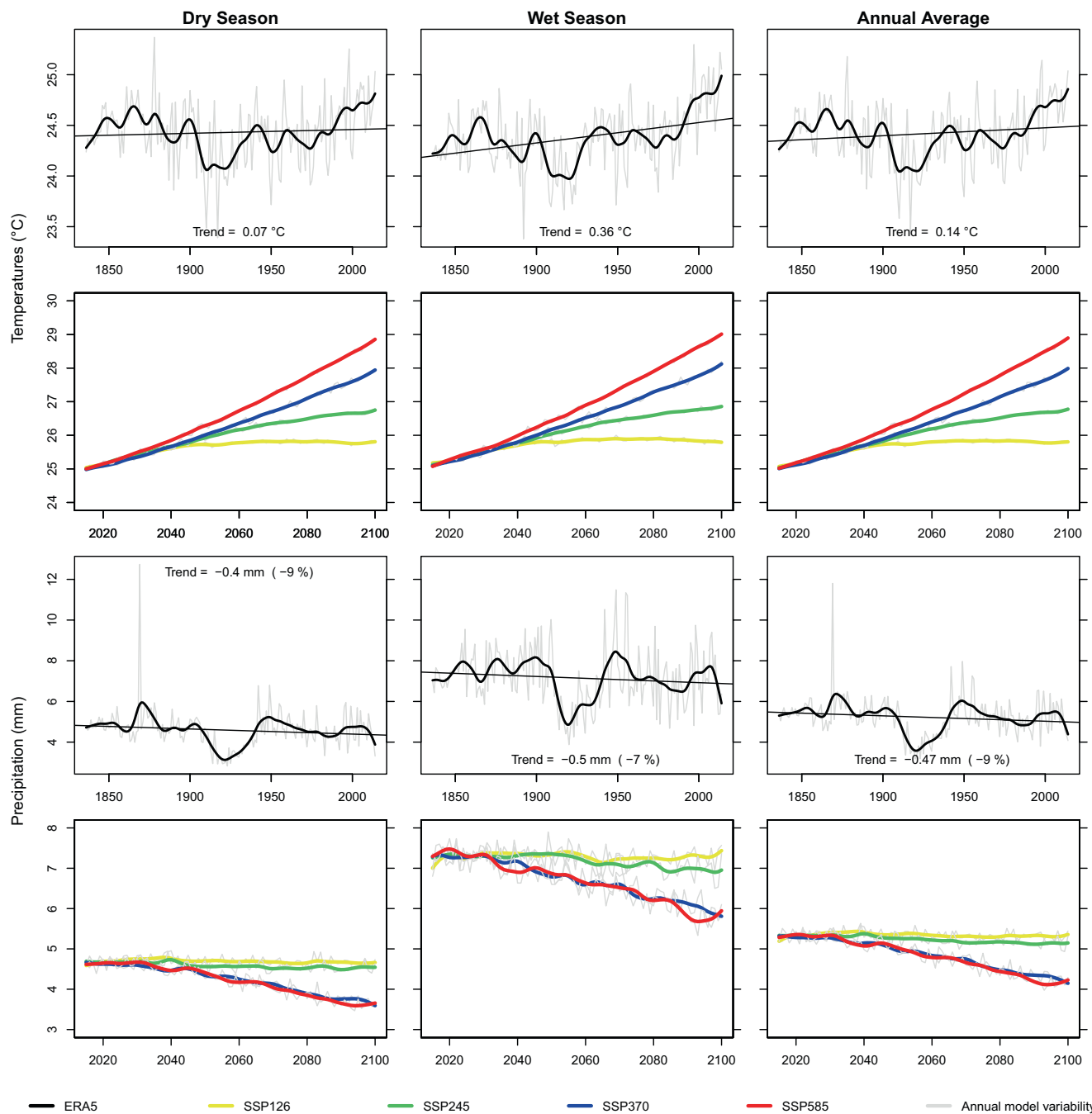


FIGURE 4 | Historical reanalysis (1836–2015) temperature and precipitation (upper and third rows) and projected (2015–2100) temperature and precipitation (under four contrasting SSPs for the CMIP6 mean) for the study site (second and fourth rows), averaged for the drier season (December–August—left column), the wetter season (September–November—middle column) and the annual average (right column).

covering the core location had a moderating effect on local peat hydrology to any precipitation change.

After the canopy opens, there are four distinctive wet periods identified in the water-table reconstruction (WP1=1560–1630 CE; WP2=1655–1740 CE; WP3=1810–1830 CE; WP4 = 1910–1965 CE) (Figure S1). These wet periods co-occur with episodes of higher precipitation as indicated by the Cariaco basin Ti record (Haug et al. 2001) and wet season daily precipitation averages for the period 1836–2015 CE (Compo et al. 2011),

which are inferred to be driven by variability in the position of the ITCZ. Furthermore, once shifted to a structurally open vegetation type, composite community species vary in response to precipitation-driven hydrological change, in particular, the relative abundance of *Myrica* varies in anti-phase to the inferred wet periods as this shrub would not tolerate standing pools of water. We hypothesise that the opening of the canopy increased the sensitivity of peatland hydrology and vegetation to precipitation change (wetting), which may be related to changing interception and evapotranspiration losses.

5 | Discussion

Climate-driven changes in carbon accumulation, linked to vegetation community shifts, have been proposed for closed-canopy Amazonian forested peatlands (Swindles, Kelly, Roucoux, and Lawson, 2018; Swindles, Morris, Whitney, et al. 2018), but the relationship between vegetation structure (open vs. closed), hydrological dynamics and climate change is poorly understood. The vegetation-determined sensitivity to precipitation change we describe is corroborated by recent observations of the modern open bog plain where standing-water pools have been observed (Phillips, Rouse, and Bustin 1997), and the highest moisture contents of the modern peatland surface were recorded (Swindles, Baird, Kilbride, Low, and Lopez, 2018). The high surface wetness coinciding with an open canopy is perhaps surprising given that evapotranspiration is a strong determining factor in the hydrology of ombrotrophic peatlands, a mechanism that is expected to be exacerbated in a hot climate. However, transpiration and interception losses would be greater for trees than lower-stature open plain vegetation. In addition, the central plain may be relatively less windy compared to the upper tree canopy.

The Oropel swamp, once transitioned to an open canopy structure, showed clear hydrological shifts associated with excursions in the ITCZ, but the peat core represents hydrology and vegetation at only one site located in the southwest of the complex. Given the vegetation of the Changuinola peatland is a complex mosaic of vegetation communities, the observed patterns would have exhibited spatial, as well as temporal variability, and climate sensitivity to any shifts in precipitation patterns would be dependent on the dominant phasic vegetation zone at any given location. The radiocarbon-dated ages on previous palaeoecological investigations (Phillips, Rouse, and Bustin 1997), although limited, suggest the timing of the vegetation transitions is spatially and temporally variable. Therefore, it is likely that ITCZ-driven precipitation changes influenced peatland hydrology in areas of the complex that had transitioned to an open canopy prior to 1560 CE and which remain unobserved from our single core.

Oropel swamp has among the highest hydraulic conductivity values recorded for peatlands, similar to those of unconsolidated gravel (Baird et al. 2017). We have previously reported that the highest values of hydraulic conductivity occur within the hardwood forested vegetation zones (Baird et al. 2017). This together with our core results implies that the intrinsic peat properties may be linked to differences in open and closed canopy vegetation. The distinctive plant communities each interact differently with peat hydrological dynamics and climate change; therefore, plant community and structural diversity could enable the peatland to alter and reorganise under new climate scenarios and provide adaptability to future change. However, the complex linkages between climate, peatland hydrological conditions and vegetation structure (Figure 3), and their interactions and feedbacks require further investigation to understand how tropical peatlands will respond to future climate change.

A southward shift in ITCZ is predicted for the eastern Pacific and Western Atlantic in the next century (Mamalakis et al. 2021), which will potentially lead to drier conditions on Oropel

swamp (Figure 4). A marked decrease in precipitation across the remainder of the 21st century is suggested by SSP 370 and 585, whereas precipitation shows more modest reductions in SSP126 and 245. SSP370 and 585 should be interpreted with caution as these scenarios are deemed to be ‘unlikely’ and ‘highly unlikely’, respectively, involving a reversal of some current climate policies that would lead to a global temperature rise of +4°C and +5°C. SSP245 is deemed more likely given current policies, leading to a global temperature rise of 2.5°C (Hausfather and Peters 2020). Alongside a projected decrease in precipitation is an increase in temperature across all SSPs—including up to 2°C under the most likely scenario of SSP245—which will lead to greater evapotranspiration (Figure 4). Our recent palaeoenvironmental record suggests there will be a shift to greater shrub cover (most likely *Myrica*) in Oropel swamp as water tables deepen in response to increased temperature and lower precipitation. However, relative sea levels will rise at the same time as rainfall declines in this region. In this scenario, the constant flushing of the peatland by freshwater may be compromised as saline water periodically penetrates the peatland which would lead to significant vegetation change, including migration or expansion of the mangrove fringe.

Author Contributions

G.T.S., B.S.W. and A.J.B. led the research project, carried out analysis and wrote the paper. All other authors carried out analysis and assisted with writing the paper. R.L. and R.O.L. also assisted with fieldwork.

Acknowledgements

Permission to work at the study site in the Changuinola peat swamp was granted by Autoridad Nacional del Ambiente (Natural Environmental Authority), Republic of Panama. No numbered permits were required. The work was partly supported by a grant from the Quaternary Research Fund (Quaternary Research Association, UK) to GTS. ROL was funded by the National Research System (SNI) of SENACYT, Panama. Deyvis Gonzalez assisted with the field work and kept us safe from the field site's many venomous snakes. GTS currently holds research grants from the Dutch Foundation for the Conservation of Irish Bogs, the Quaternary Research Association, the Natural Environment Research Council (UKRI-NERC) and the Leverhulme Trust (RPG-2021-354).

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data for this study is available at <https://doi.org/10.5061/dryad.3r2280gsd>.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.