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The presence of peat and variation in tree species composition are under different hydrological controls in Amazonian wetland forests

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Abstract

The peat-forming wetland forests of Amazonia are characterized by high below-carbon stocks and supply fruit, fibres and timber to local communities. Predicting the future of these ecosystem services requires understanding how hydrological conditions are related to tree species composition and the presence, or absence, of peat. Here, we use continuous measurements of water table depth over 2.5 years and manual measurements of pore-water pH and electrical conductivity to understand the ecohydrological controls of these variables across the large peatland complex in northern Peruvian Amazonia. Measurements were taken in permanent forest plots in four palm swamps, four seasonally flooded forests and four peatland pole forests. All trees ≥10 cm diameter were also measured and identified in the plots to assess floristic composition. Peat occurs in eight of these twelve sites; three seasonally flooded forests and one palm swamp are not associated with peat. Variation in tree species composition among forest types was linked to high flood levels (maximum flooding height) and pH: seasonally flooded forests experience high flood levels (up to 3.66 m from the ground surface) and have high pH values (6–7), palm swamps have intermediate flood levels (up to 1.34 m) and peatland pole forests experience shallow flooding (up to 0.28 m) and have low pH (4). In contrast, the presence of peat was linked to variation in maximum water table depth (i.e. the depth to which the water table drops below the ground surface). Surface peat is found in all forest types where maximum water table depth does not fall >0.55 m below the ground surface at any time. Peat formation and variation in tree species composition therefore have different ecohydrological controls. Predicted increases in the frequency and strength of flooding events may alter patterns of tree species composition, whereas increases in drought severity and declines in minimum river levels may pose a greater risk to the belowground carbon stores of these peatland ecosystems.

1 | INTRODUCTION

The Pastaza-Marañón Foreland Basin (PMFB) in northern Peruvian Amazonia contains the largest peatland complex in South America (Draper et al., 2014; Page et al., 2011). Here, a range of ecosystem types, including palm swamps, peatland pole forests, open herbaceous swamps and seasonally flooded forests are associated with the presence of peat (Draper et al., 2014; Lähteenoja et al., 2012; Lähteenoja et al., 2009a; Ruokolainen et al., 2001). These ecosystems store large amounts of carbon below ground (Draper et al., 2014; Honorio Coronado et al., 2021; Hastie et al., 2022) and provide natural resources to local communities, supporting livelihoods and the regional economy (Padoch, 1988; Kvist & Nebel, 2001; Schulz et al., 2019). However, climatic changes related to the increased variability of the hydrological cycle leading to more locally severe drought and flooding events, as well as drainage associated with increasing demand for agricultural land, may lead to dramatic changes in the hydrological regime of these ecosystems (Baker et al., 2019; Gloor et al., 2013; Roucoux et al., 2017; Zulkafli et al., 2016). As a result, there is a need to understand the hydrological controls on variation in species composition and the presence, or absence, of peat in these wetland forests.

Observations of the distribution of the different ecosystem types (palm swamps, peatland pole forests, open herbaceous swamps, and seasonally flooded forests; see Materials and Methods) and peat deposits in the PMFB suggest that the controls on peat formation do not correspond with hydrological controls on tree species composition. Peat formation can be associated with very different species composition above-ground: for example, herbaceous swamps that look like open savannas with scattered stems of the palm *Mauritia flexuosa*, and peatland pole forests that have a closed canopy and are dominated by thin-stemmed woody species, contain different species but both consistently have thick peat deposits (Honorio Coronado et al., 2021). Sites within the same forest type with similar species composition also vary in whether they are associated with the presence of peat. For example, palm swamps – closed canopy forests dominated by *M. flexuosa* – typically, but not always, have surface peat, and seasonally flooded forests are only occasionally associated with peat formation (Draper et al., 2014; Draper et al., 2018; Honorio Coronado et al., 2021). These observations highlight that there is little knowledge of the hydrological thresholds that are associated with the presence of peat in these wetlands and how those controls differ from the determinants of variation in species composition.

Understanding the controls on both peat formation and tree species composition is important for mapping these ecosystems. Maps of the distribution of tropical peatland forests based on remote sensing data often assume that there is a perfect match between variation in aboveground forest structure and composition, and the presence or absence of peat belowground (Draper et al., 2014; Dargie

et al., 2017). However, if specific ecosystem types are not always associated with peat formation, this approach will inevitably lead to inaccuracies in peatland mapping. An alternative approach is to predict the presence of peat by estimating soil wetness using temporal MODIS optical or PALSAR images (e.g. Gumbricht et al., 2017; Bourgeau-Chavez et al., 2021, Hastie et al., 2022). However, we do not know the range and variation in water table depths that are associated with the presence of peat to calibrate and validate this approach effectively. A better understanding of the underlying hydrological controls on both species composition and the presence of peat would allow more accurate mapping of both the biodiversity and total carbon stocks of these ecosystems.

Understanding how water levels influence the properties of wetland forests would also help to improve predictions of how larger fluctuations in river levels linked to climate change will impact these ecosystems. In Amazonia, more severe flooding events have been reported over recent years (Espinoza et al., 2016; Gloor et al., 2013) and this trend is predicted to increase in the future (Barichivich et al., 2018). Such climatic changes will likely impact local populations by affecting the supply of fruits, fibres, timber, and meat (Bodmer et al., 2018; Langerwisch et al., 2013; López Gonzales et al., 2020), particularly from palm swamps, which are of high economic importance due to the harvesting and consumption of fruits of *M. flexuosa* (Baker et al., 2019; Hidalgo Pizango et al., 2022; Padoch, 1988; Virapongse et al., 2017). Alterations to hydrological regimes could also lead to changes in carbon cycling in these ecosystems (Flores et al., 2017; Langerwisch et al., 2013) but we lack information about the sensitivity of peat accumulation to flooding. Understanding the specific ecohydrological conditions associated with the different forest types in this region is therefore important for understanding the stability of these ecosystems in the future and their long-term role in supplying resources to local populations.

Here, we use long-term measurements of water table depth and manual measurements of pore-water pH and electrical conductivity to (1) compare the variation in water table depth among the principal wetland forest types and to (2) understand the ecohydrological controls on variation in tree species composition and the presence of peat in northern Peruvian Amazonia.

2 | MATERIALS AND METHODS

2.1 | Study area

The study was carried out in 12 permanent forest plots established or recensused in 2017 as part of this study (Table 1). The plots are in the PMFB along the four main river basins of the Amazon, Marañón, Tigre and Ucayali rivers in the region of Loreto in northern Peruvian

TABLE 1 Diversity, stem density and ecohydrological variables in the 12 forest plots in the northern Peruvian Amazonia that were used in this study.

Forest type	River basin	Plot	Site	Year of establish-ment	Area (ha)	No. of species	Species diversity	No. of stems (ha^{-1})	Peat thickness (m)	pH	EC (µS/cm)	Min. WTD (m)	Max. WTD (m)	Range of WTD (m)
Pole forest	Amazon	SJO-01	San Jorge	2010	0.5	13	2.51	892	5.56	3.83	80	−0.23	0.45	0.67
	Marañón	OLL-01	Ollanta	2013	0.5	25	5.60	960	3.27	4.32	24	−0.15	0.19	0.34
	Tigre	AUC-01	Aucayacu	2017	0.5	34	8.66	862	8.22	3.88	44	−0.17	0.34	0.50
	Tigre	NYO-03	Nueva York	2014	0.5	30	7.33	864	5.19	4.08	27	−0.28	0.27	0.55
Palm swamp	Amazon	QUI-01	Quistococha	2010	0.5	21	4.72	800	3.39	5.33	28	−0.52	0	0.53
	Marañón	PRN-01	Parinari	2014	0.5	38	11.37	620	1.10	5.68	79	−0.72	0.52	1.24
	Tigre	PIU-02	Piura	2017	0.5	60	19.58	800	0.00	5.43	14	−1.24	0.67	1.91
	Ucayali	JEN-14	Jenaro Herrera	2009	0.5	38	12.86	468	1.61	5.98	101	−1.34	0.55	1.89
Seasonally flooded	Amazon	BVA-01	Buenavista	2010	1	46	13.03	432	4.00	6.17	72	−3.66	0.19	3.85
	Marañón	OLL-05	Ollanta	2017	1	78	23.17	648	0.00	5.92	86	−1.76	1.10	2.86
	Tigre	PIU-01	Piura	2017	1	101	38.21	499	0.00	5.32	28	−2.40	3.60	6.01
	Ucayali	JEN-19	Jenaro Herrera	2017	1	150	81.49	432	0.00	6.10	240	−3.50	2.16	5.67

Notes: EC, electrical conductivity; WTD, water table depth, which has a positive value when water table is below the ground surface and a negative value when flooded. Minimum, maximum and range of water table depths are provided for each plot.
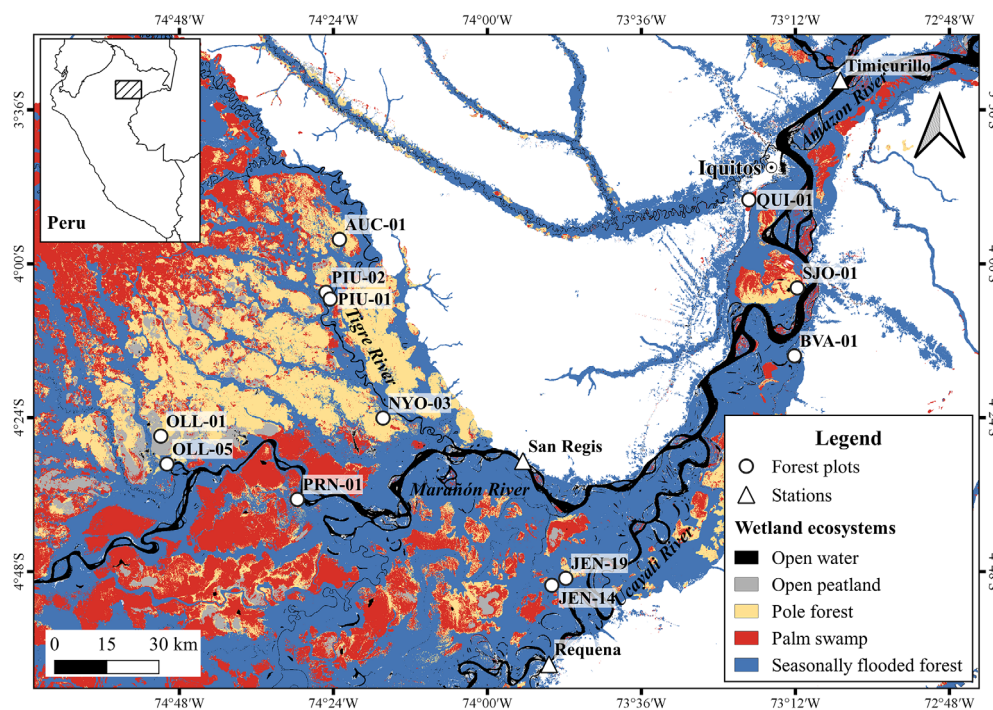
FIGURE 1 Location of the forest plots and hydrological and meteorological stations studied in the Amazon, Ucayali, Tigre and Marañón river basins in the northern Peruvian Amazonia. Water table depth was measured in palm swamps (JEN-14, PIU-02, PRN-01, QUI-01), peatland pole forests (AUC-01, NYO-03, OLL-01 and SJO-01) and seasonally flooded forests (BVA-01, JEN-19, OLL-05 and PIU-01). The spatial distribution of wetland ecosystems follows Honorio-Coronado et al. (2021).

Amazonia (Figure 1). In each plot, we measured variation in water table depth, pore-water pH and electric conductivity, tree species composition and peat depth. The plot network incorporates the main natural forested wetland types in this region (palm swamp, peatland pole forest and seasonally flooded forest), with four plots in each ecosystem type. Palm swamp forests, locally known as 'aguajales', are dominated by the arborescent palm *M. flexuosa*. These forests occur on poorly drained soils that are often flooded (Encarnación, 1985) and typically, but not always, have surface peat (Lähteenoja et al., 2009a; Lähteenoja et al., 2012; Honorio Coronado et al., 2021). This wetland type is most common in the Ucayali and Marañón river basins (Draper et al., 2014). Peatland pole forest, locally known as 'varillal hidromórfico', is dominated by a few species of thin-stemmed trees (Draper et al., 2018; Honorio Coronado et al., 2021). These forests occur typically on deep peat deposits and are rarely flooded (del Aguila-Pasquel, 2017; Draper et al., 2014). This wetland type is most commonly found between the Tigre and Marañón rivers (Draper et al., 2014; Honorio Coronado et al., 2021). Seasonally flooded forests are more diverse than palm swamps and pole forests (Draper et al., 2018), and occur on areas that flood for two to nine months during the year (Kvist & Nebel, 2001) and only occasionally have peat (Draper et al., 2014; Honorio Coronado et al., 2021; Hastie et al., 2022). Seasonally flooded forests occur alongside the major rivers of all basins but are particularly extensive alongside the Ucayali river (Draper et al., 2014).

2.2 | Plot inventory data

The forest plots are 0.5 ha in the peatland pole forest and palm swamp ecosystems types, and one hectare in the seasonally flooded forests. Plots of 0.5 ha are sufficient to capture local variation in species richness and forest dynamics in peatland pole and palm swamps because these ecosystem types have a lower diversity and lower canopy than seasonally flooded forests. In each plot, all stems with a diameter at breast height (dbh at 1.3 m height) equal to or greater than 10 cm were measured in 2017 as part of this study. Plot establishment and tree measurement followed the standard methods described in the RAINFOR protocol (http://www.rainfor.org/en/manuals/in-the-field). Botanical samples of trees were collected for each species and deposited at the Herbarium Herrerense (HH) in Iquitos. Palms were identified in the field and a photograph was taken for species confirmation. All identifications and morphospecies were applied consistently across all plots. The dataset included 5180 individuals of which 0.7% did not have a determination and were excluded from analyses of floristic composition. Fisher's alpha was used as an index of species diversity (Fisher et al., 1943). The plot data are managed at ForestPlots.net (ForestPlots.net, 2021; Lähteenoja & Page, 2011; Lopez-Gonzalez et al., 2009; Lopez-Gonzalez et al., 2011; Lähteenoja & Page, 2011; ForestPlots.net, 2021).

In the centre of each plot, peat thickness was measured from the surface to the point of the transition between peat and underlying inorganic sediment (pale grey sandy to silty clay) using an extendable metal rod. The rod was introduced into the soil until it reached the bottom of the peat. Peat was identified as partially decomposed, wet, dark brown organic matter.

2.3 | Ecohydrological variables

Water table depth was measured using two pressure sensors in each plot. One measured the barometric pressure (LT Barologger Edge,

Solinst) and the other the total pressure below the water table (LT Levelogger Edge M5). The Leveloggers were installed in dipwells at a depth of ca. 3.5 m and the Barologgers more than 10 m above the ground in trees close to the Leveloggers to be well above any extreme flood events and for security. The pressure data was collected every 30 min for 2.5 years, from 1 December 2017 to 31 July 2020. The water table depth was obtained by subtracting the values of the Barologger from the values of the Levelogger and calibrating with manual water table depth measurements taken using a tape measure during the installation of the instruments and during the subsequent visits to the plots to download the datasets in mid-2018, mid-2019 and mid-2020. Water table depth has positive values when the water table is below the ground surface and negative values when the site is flooded.

pH and electrical conductivity (EC) of the pore-water were measured three times at each plot in 2017 using a LAQUAtwin B-71X portable pH meter (Horiba Scientific) and a LAQUAtwin B-771 portable conductivity meter (Horiba Scientific). The measurements were made by making a hole in the ground and sampling the water that accumulated, after waiting for the soil material to settle.

River level and daily precipitation data were downloaded from the National Service of Meteorology and Hydrology of Peru (SENAMHI, 2020) for the hydrological and meteorological stations at Timicurillo on the Amazon river, San Regis on the Marañón river and Requena on the Ucayali river (Figure 1). Data from San Regis was used to compare with the water table records from sites on the Tigre river, as this is the nearest monitoring station to this basin.

2.4 | Data analysis

The variation over time in water table depth among plots was explored in three ways. First, we compared the minimum, maximum and range of water table depths recorded in each plot during the study period. Second, we compared the cumulative proportion of time that each forest plot experienced different water table depths during the 2.5 years of the study (Ingram, 1983). Thirdly, we used a categorical approach to address the same issue: we compared the proportion of time that the water table resides at six different depth ranges (periods with water table more than 0.5 m above the ground (subsequently referred to as category A), between 0.25 and 0.50 m above the ground (B), between 0 and 0.25 m above the ground (C), between 0 and 0.25 m below the ground (D), between 0.25 and 0.50 m below the ground (E) and more than 0.50 m below the ground (F)).

We used a Kruskal–Wallis test and Dunn's tests of multiple comparisons to assess whether the ecohydrological variables (i.e. pH, EC, minimum and maximum WTD and variables A-F) were significantly different among the three different wetland types. We used Wilcoxon rank sum tests to compare these variables between sites with, and without, peat. Non-parametric tests were used because the residuals of some datasets following parametric analysis were non-normally distributed (Shapiro test: *p* < 0.001).

We explored whether variation in the level of the nearest river, or precipitation, exerts the greatest control on variation in water table within each plot by using cross-correlation analysis.

Finally, we used non-metric multidimensional scaling multivariate analysis (NMDS) to explore the floristic similarity among forest plots. For this analysis, we constructed a floristic distance matrix using the Bray-Curtis distance for relative abundance data and optimized the axes of the ordinations using the 'vegan' package (Oksanen et al., 2007) in R. We used a non-parametric permutational multivariate analysis of variance (PERMANOVA) of the Bray-Curtis distance matrix as the response variable to test whether species composition varied significantly among the three wetland types and/or between sites with, and without, peat. To assess which ecohydrological variables are associated with the composition of different wetland types, we fitted the ecohydrological variables onto the ordination based on the strength of the correlation of each variable with the main axes. All statistical tests were run in R 3.5.3 (R Development Core Team, 2019).

3 | RESULTS

3.1 | Diversity, stem density and peat thickness

Overall, the 12 forest plots contained 5144 individuals corresponding to 339 species and morphospecies, 180 genera and 51 families in the 2017 census. Species diversity varied significantly among the three wetland types (Kruskall–Wallis: p < 0.05), with the highest alpha diversity in the seasonally flooded forest (Mean ± 95% CI: 38.98 ± 48.01), followed by the palm swamp (12.13 ± 9.70) and peatland pole forest (6.03 ± 4.23; Table 1). The density of individuals per hectare also varied among wetland types (Kruskall-Wallis: p < 0.05) with the highest stem density in the peatland pole forest (890 ± 82 stems ha⁻¹) and the lowest stem density in the seasonally flooded forest (503 ± 162 stems ha⁻¹). Average peat depth was also significantly different among forest types (Kruskall-Wallis, p < 0.05) and was highest in the peatland pole forest (5.56 ± 3.24 m). Palm swamp forests had lower peat depths (1.53 ± 2.25 m) and only one of the seasonally flooded forests had peat (BVA-01: 4.00 m; Table 1).

3.2 | Variation in water table depth

The hydrological regimes varied substantially among the different wetland forest types (Figure 2a). Seasonally flooded forests have the largest range of water table depths, with values from 3.86 to 6.01 m (Table 1) and 3–4 months of annual flooding (Figure 2a). These forests spend, on average, 60% of their time either with water more than 0.5 m above or more than 0.5 m below the ground surface (Figure 3). The palm swamps have a smaller range of water table depths, from 0.53 to 1.91 m (Table 1) with 1–11 months when the water table is above the surface (Figure 2a). In these forests the water table spends, on average, 83% of the time between 0.50 m above the ground and 0.25 m below the ground (Figure 3). Peatland pole forest sites do not
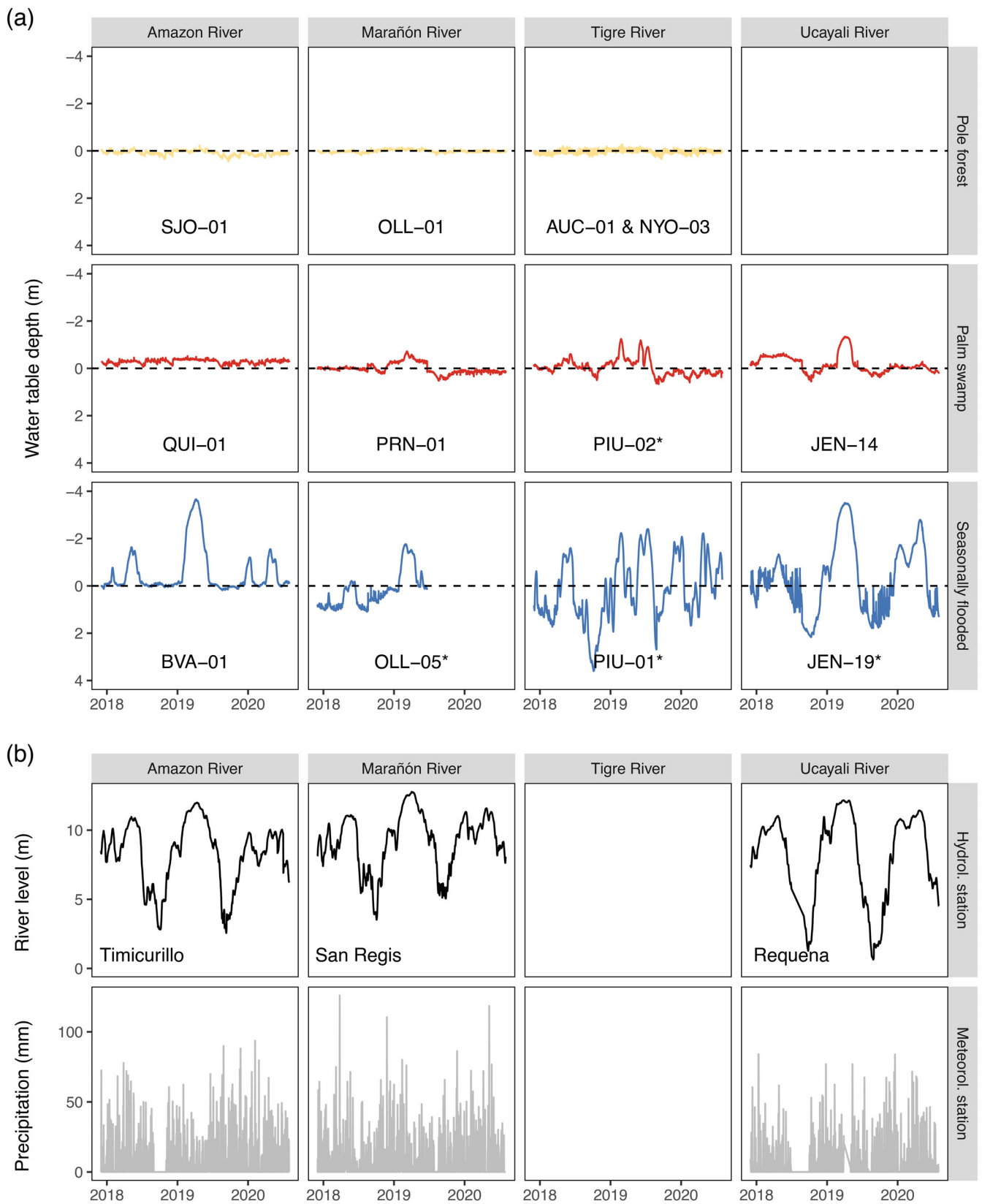
FIGURE 2 (a) Water table depths inside 12 forest plots classified by wetland type and river basins and (b) river level and precipitation of hydrological and meteorological stations in northern Peruvian Amazonia. Empty graphs indicate combinations where no data are available. The dashed horizontal line indicates ground level inside the plots. Water table depth is positive when the water level is below the ground and negative when flooded. Plots without peat are indicated with an asterisk.
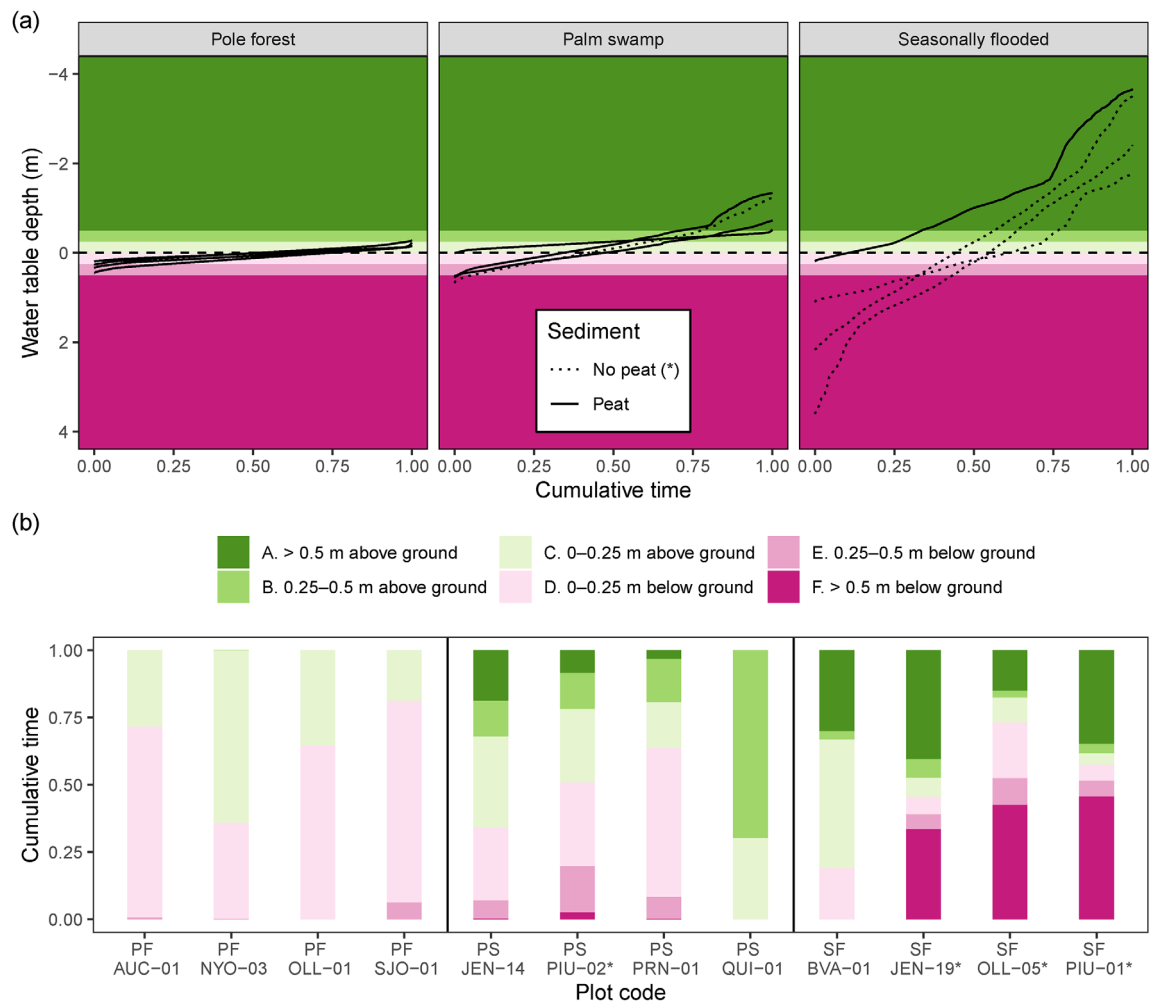
FIGURE 3 (a) Cumulative proportion of time and water table depth and (b) proportion of time that the water table resides at six different depth ranges relative to the ground, in twelve plots in peatland pole forest (PF), palm swamp (PS) and seasonally flooded (SF) forests. Plots without peat are indicated with an asterisk

have pronounced variations in water table depth (Figure 2a), with ranges from 0.34 to 0.67 m (Table 1). These forests spend 99% of their time with the water table within 0.25 m above or below the ground surface (Figure 3).

The key difference among the hydrological regimes of the different forest types is the significant variation in the depth of flooding (shown as negative water table depths in Table 2). The plots in seasonally flooded forest plots all experience deeper flooding (ie more negative water table depths) than the plots in palm swamps, which in turn all experience greater flooding than the plots in peatland pole forest (Figure 2a; Table 2). In contrast, the presence or absence of peat is more strongly related to variation in maximum water table depths (ie the depth to which the water table falls below the ground surface; shown as positive water table depths in Table 2). Maximum water table depth was significantly greater in sites without peat (Table 2). In all the plots with no peat, that is, three seasonally flooded forests (JEN-19, OLL-05, PIU-01) and one palm swamp (PIU-02), the maximum water table depth was more than 0.55 m; that is, during part of the study period, the water table dropped more than 0.55 m below the ground surface (Table 1, Figure 3b). Conversely, the water table

was permanently within 0.55 m of the ground surface in all the plots with peat – all four peatland pole forest plots, three palm swamp plots and one seasonally flooded forest plot (Figure 3b).

The river level was generally highest in April or May in the Amazon and Marañón rivers but reached its peak one month earlier in the Ucayali river (March or April; Figure 2b). The lowest river levels were during September or October in the Amazon and Marañón rivers and during August or September in the Ucayali river (Figure 2b). Maximum river level was 1–2 m higher in 2019 in all rivers than in 2018 and 2020, and greater flooding indicated by a more negative minimum water table depth was observed in 2019 in all ecosystem types: pole forests (PF: from −0.2 to −0.3 m), palm swamps (PS: from −0.5 to −1.3 m) and seasonally flooded forests (SF: from −1.8 to −3.7 m) compared to the other two years (PF: from 0 to −0.2 m; PS: from 0 to −0.6 m; SF: from −1.2 to −2.8 m; Figure 2a).

Fluctuations in water table depth in the plots were related to variation in river levels in all ecosystem types, with higher correlation values in seasonally flooded forest sites ($r = 0.67$–0.88) compared to the other wetland forest types (0.34–0.69; Table 3). However, when river levels were high, water tables in the plots were also higher even

TABLE 2 Mean (± 95% CI) values of the ecohydrological variables grouping plots by wetland type and the presence/absence of peat

Variable	Wetland type			p	Presence of peat		p
	Pole forest	Palm swamp	Seasonally flooded		Peat	No peat	
No. of plots	4	4	4		8	4	
pH	4.03 ± 0.35ᵃ	5.61 ± 0.46ᵇ	5.88 ± 0.61ᵇ	**0.02**	4.91 ± 0.82	5.69 ± 0.60	0.31
EC (µS/cm)	44 ± 41	56 ± 65	107 ± 145	0.44	57 ± 25	92 ± 156	0.87
Min. WTD (m)	−0.21 ± 0.09ᵃ	−0.96 ± 0.63ᵃᵇ	−2.83 ± 1.44ᵇ	**0.01**	−0.88 ± 0.99	−2.23 ± 1.55	0.07
A (%)	0ᵃ	8 ± 13ᵃᵇ	30 ± 17ᵇ	**0.01**	**7 ± 10**	**25 ± 24**	**0.05**
B (%)	0ᵃ	28 ± 44ᵇ	4 ± 3ᵃᵇ	**0.01**	13 ± 20	7 ± 8	0.55
C (%)	37 ± 31	27 ± 11	17 ± 33	0.25	**34 ± 13**	**12 ± 17**	**0.02**
D (%)	62 ± 28ᵃ	28 ± 34ᵃᵇ	13 ± 12ᵇ	**0.03**	43 ± 23	16 ± 19	0.15
E (%)	2 ± 5	8 ± 11	5 ± 7	0.38	3 ± 3	10 ± 9	0.10
F (%)	0	1 ± 2	30 ± 33	0.06	**0**	**31 ± 31**	**0.01**
Max. WTD (m)	0.31 ± 0.18	0.44 ± 0.47	1.76 ± 2.33	0.21	**0.31 ± 0.16**	**1.88 ± 2.08**	**0.01**

Notes: Comparisons among wetland types were made using Kruskal–Wallis tests, followed by Dunn's test of multiple comparisons between groups. Comparisons between sites with and without peat were made using Wilcoxon-rank sum tests. Comparisons with overall significant differences shown in bold. Min. WTD, the minimum water table depth (ie greatest depth of flooding) measured during the study; Max. WTD, the maximum water table depth measured during the study. The letters A–F indicate the proportion of time that water table resides within different depth ranges: A, >0.5 m above the ground; B, 0.25–0.50 m above the ground; C, 0–0.25 m above the ground; D, 0–0.25 m below the ground; E, 0.25–0.50 m below the ground; F, >0.5 m below the ground. ᵃᵇIndicate groups that are significantly different.

TABLE 3 Pearson's Product Moment Correlation coefficients between river level or precipitation and water table depth in 12 forest plots, with lag = 0.

Forest type	River basin	Plot	Station	Person's *r* correlation	
				River level	Precipitation
Pole forest	Amazon	SJO-01	Timicurillo	**0.64**	−0.05
	Marañón	OLL-01	San Regis	**0.42**	0.05
	Tigre	AUC-01	San Regis	**0.34**	−0.04
	Tigre	NYO-03	San Regis	**0.62**	0.02
Palm swamp	Amazon	QUI-01	Timicurillo	**0.39**	−0.05
	Marañón	PRN-01	San Regis	**0.57**	0.02
	Tigre	PIU-02	San Regis	**0.51**	−0.01
	Ucayali	JEN-14	Requena	**0.69**	0.01
Seasonally flooded	Amazon	BVA-01	Timicurillo	**0.67**	−0.08
	Marañón	OLL-05	San Regis	**0.73**	0.03
	Tigre	PIU-01	San Regis	**0.67**	0.01
	Ucayali	JEN-19	Requena	**0.88**	0.06

Notes: We used data from hydrological and meteorological stations located 30–70 km from the plots. Only correlations with river level are statistically significant (*p* < 0.001; shown in bold).

in the peatland pole forest sites, which are typically the most distant forest type from the main river channel (Table 3; Figure 4). Daily precipitation did not correlate with water table depth in any plot using unlagged data (Table 3) or for any positive or negative lag time using cross-correlation analysis.
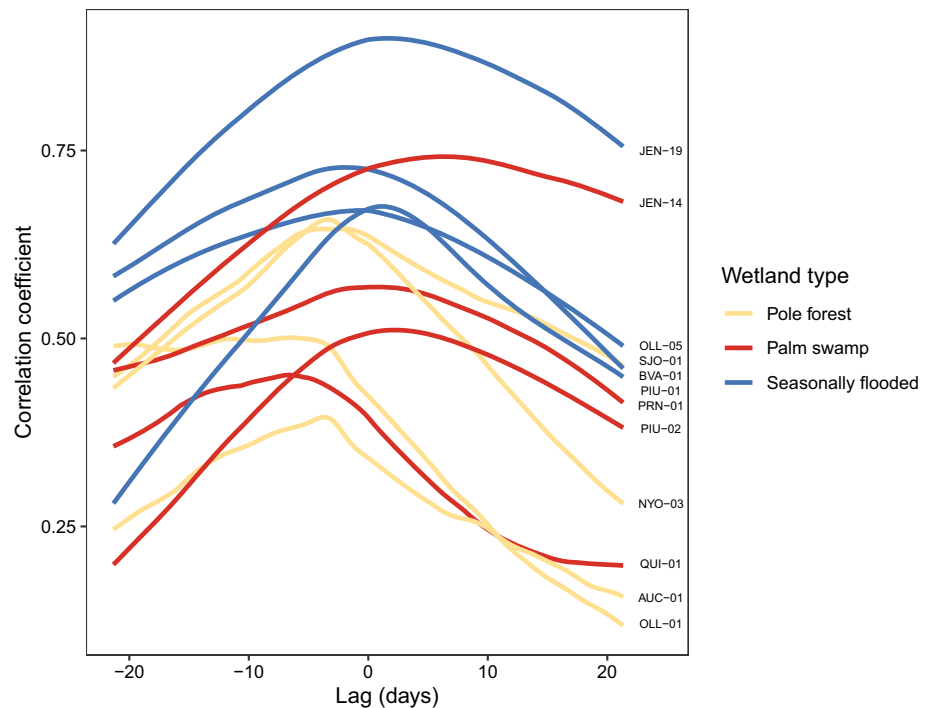
3.3 | Variation in floristic composition

Non-metric multidimensional scaling analysis (NMDS) shows the expected strong differences in floristic composition among the different wetland forest types (Figure 5a). The key species that determined

these patterns were the high abundances of *Platycarpum loretense*, *Calophyllum brasiliense*, *Pachira nitida*, *Hevea guianensis*, *Xylopia GLF1848*, and *Macrolobium GFL1805* in peatland pole forests; *M. flexuosa*, *Mauritiella armata*, *Tabebuia insignis* and *Virola pavonis* in palm swamps; and *Pseudolmedia laevigata*, *Inga stenoptera* and *Vatairea guianensis* in seasonally flooded forests (Figure 5a). Variation in floristic composition is also associated with the presence of peat (PERMANOVA, *p* < 0.05) but less strongly than with forest types (PERMANOVA, *p* < 0.01). This pattern was found because although all pole forest sites had peat, only three palm swamps (QUI-01, PRN-01, JEN-14) and just one seasonally flooded forest site (BVA-01) was found with peat (Table 1).

FIGURE 4 Variation in cross-correlation coefficients for the relationship between water table depth within each plot and nearby river level for 12 plots in three different wetland types of the northern Peruvian Amazon. A positive lag means river levels were correlated with water table depths a number of days later while a negative lag means river water levels were correlated with water table depths from the preceding few days.

3.4 | Links between species composition, the presence of peat and ecohydrology

The NMDS also showed the ecohydrological factors that are associated with the variation in floristic composition among the different ecosystem types. A high proportion of time with a water table more than 0.5 m above the ground (Figure 5b; Category A) is associated with the floristic composition of seasonally flooded forest sites; palm swamps are characterised by intermediate levels of flooding (Figure 5b; Category B) and the composition of peatland pole forests is associated with a water table that is always close to the ground surface (Figure 5b; Categories C and D). Variation in pH is also related to the variation in floristic composition among forest types: mean pH in peatland pole forest sites was significantly lower (4.03 ± 0.35; Kruskal-Wallis, $p < 0.05$) than pH in the palm swamps (5.61 ± 0.46) and seasonally flooded forests (5.88 ± 0.61; Table 2 and Figure 5b).
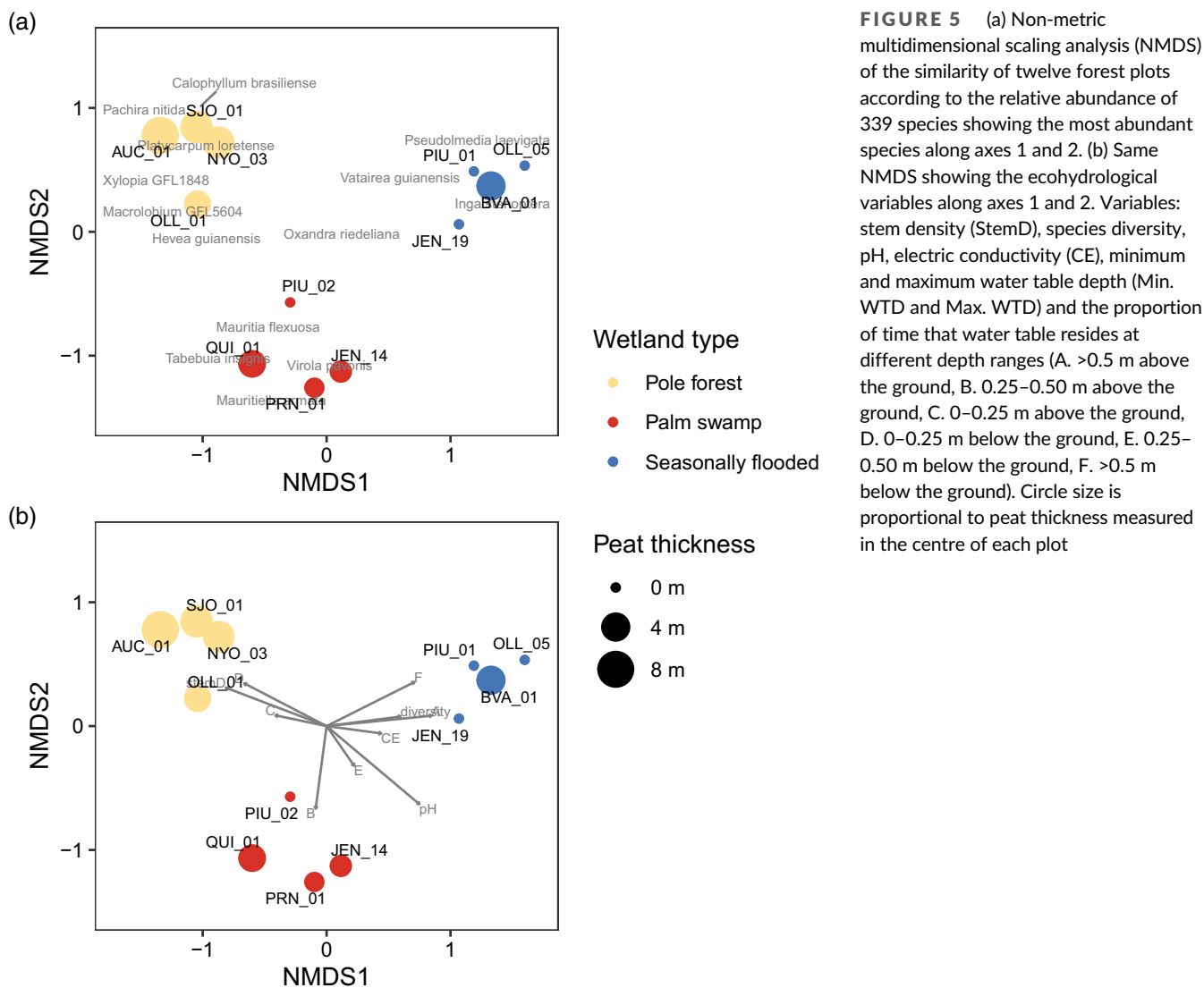
4 | DISCUSSION

This comparative study of the water table depth, pore-water pH and electrical conductivity of peat-forming Amazonian wetlands in the PMFB shows that species composition and peat formation have different ecohydrological controls. Whilst variation among sites in the highest flood levels (minimum water table depth) and pH are closely associated with variation in tree species composition, the presence of peat is associated with sites where the water table depth does not drop far from the ground surface. Our study therefore demonstrates that spatial variation in tree species composition and forest types cannot be used as a simple predictor of the presence or absence of peat. We discuss below the implications of these results for: (1) understanding how to map peatland

extent using remote sensing products, (2) understanding how shifts in the structure and composition of these wetland types may occur over time, and (3) predicting the impact of climate change on carbon accumulation rates and forest-dependent livelihoods in this region.

4.1 | Determinants of the presence of peat and mapping peatland extent

Our results show that maintaining a water table close to the ground surface throughout the year is closely associated with the presence of peat within all the major ecosystem types in the PMFB (Tables 1 and 2; Figure 3). This finding has important implications for mapping the distribution of tropical peatlands as maps based on remote sensing data have typically assumed a direct link between ecosystem types based on their structure and floristic composition and the presence of peat (Dargie et al., 2017; Draper et al., 2014). Our work supports approaches that use remote sensing products, such as ALOS PALSAR and particularly PALSAR's L-band synthetic aperture radar that penetrates the forest and can detect the presence of surface water (Tsuji et al., 2021; Hess et al., 2003, Hastie et al., 2022). Approaches that use multi-temporal PALSAR images are particularly promising for indicating permanent waterlogged conditions suitable for peat accumulation (e.g. Bourgeau-Chavez et al., 2021). However, PALSAR images will need to be carefully calibrated with water table depth data within each ecosystem type, because forest structure influences the reflectance signal (Draper et al., 2014) and forest structure strongly varies among wetland forests (Table 1; Draper et al., 2018; Honorio Coronado et al., 2021).

Our results are consistent with the need for permanent waterlogging, related to high precipitation and poor drainage, for the

(a)

(b)

FIGURE 5 (a) Non-metric multidimensional scaling analysis (NMDS) of the similarity of twelve forest plots according to the relative abundance of 339 species showing the most abundant species along axes 1 and 2. (b) Same NMDS showing the ecohydrological variables along axes 1 and 2. Variables: stem density (StemD), species diversity, pH, electric conductivity (CE), minimum and maximum water table depth (Min. WTD and Max. WTD) and the proportion of time that water table resides at different depth ranges (A. >0.5 m above the ground, B. 0.25–0.50 m above the ground, C. 0–0.25 m above the ground, D. 0–0.25 m below the ground, E. 0.25–0.50 m below the ground, F. >0.5 m below the ground). Circle size is proportional to peat thickness measured in the centre of each plot

development of peat in Amazonia (Ruokolainen et al., 2001). The PMFB meets this condition due to high precipitation (>2500 mm annual rainfall), the lack of a dry season (no monthly rainfall <100 mm), and, importantly, because it is a foreland basin that collects water from upper Amazon tributaries that flow from the Andes (Baker et al., 2019). Spatial variation in the degree of waterlogging within the PMFB is also modified by physiographic features such as abandoned river channels (oxbow lakes) and levees (Kalliola et al., 1991; Salo et al., 1986) that form due to lateral movement of rivers and sediments. For example, the one seasonally flooded forest site (BVA-01) which has peat, had a maximum water table depth of only 0.19 m during the study period, which is unusual compared to other seasonally flooded forests (Figure 2a). The lack of deeper water tables at this site, which otherwise shows a strong flood peak similar to other seasonally flooded forests, is related to a levee which separates it from the nearby Tahuayo river, which prevents drainage when the river level is low. Similar permanently waterlogged conditions as a result of the physiography of the terrain within normally seasonally flooded forests also occur in other parts of Amazonia. For example, a study in the

Solimões river basin in the Brazilian Amazon found similar deposits of peat related to permanently waterlogged conditions in a *chavascal*, another unusual type of seasonally flooded forest (Lähteenoja et al., 2013; Wittmann et al., 2004, 2010). At this site, a surface layer of clayey peat and leaf litter had an average thickness of 1.45 m (Lähteenoja et al., 2013). The importance of fine scale variation in the physiography of the landscape for determining spatial variation in the presence of peat also needs to be incorporated in approaches that use remote sensing products to map peatland extent. In particular, approaches that use high resolution products representing the elevation of the terrain, such as SRTM and height above the nearest drainage, are needed to detect these physiographic features in Amazonia, and should be used in combination with PALSAR images, to map and understand the full distribution of peat-forming wetland ecosystems (e.g. Hastie et al., 2022).

The association between the presence of peat and a water table that does not fall far from the ground surface suggests that a low decomposition rate is the underlying mechanism that determines peat accumulation in these sites. However, our study is not able to

disentangle the role that other mechanisms may also play in determining the distribution of peat today, such as variation in the productivity of organic matter, or the length of time since conditions arose that permit peat accumulation. For example, the palm swamp site, PIU-02, has no peat but spent just 2.5% of the study period with a water table between 56 and 67 cm below the ground (Figure 3). This site may be close to the threshold of hydrological conditions that are required for peat formation and it is possible that even this short period with a deep water table is sufficient to elevate decomposition rates and prevent the accumulation of peat (Jauhiainen et al., 2005). Alternatively, the production of organic matter may be reduced in this site compared to other palm swamps, although this seems unlikely as the stem density is greater than several comparable palm swamps that are associated with peat (Table 1). Third, an intriguing possibility is that permanently waterlogged conditions have only arisen recently at this site, as nearby rivers have migrated across the landscape. Studies of the productivity and decomposition rates of organic matter in palm swamps where peat is absent, as well as where it is present, are required to understand the mechanisms that determine the absence of peat in sites that appear hydrologically suitable.

4.2 | Understanding the long-term vegetation dynamics of tropical peatlands

Our results also have important implications for interpreting patterns of change in the vegetation of these wetland ecosystems in the past. In particular, our findings provide further evidence that past changes in floristic composition may have been driven by changes in the degree of flooding. Palaeoecological studies in Amazonian peatlands have demonstrated that the vegetation type that is found in any given location changes repeatedly over time, and that these transitions can occur over just decades (Kelly et al., 2017; Roucoux et al., 2013). For example, the pollen record at the peatland pole forest in San Jorge (taken from plot SJO-01) was used to infer that this ecosystem type developed over a period of 50 years, 150–200 years ago, after ~1700 years as a *Mauritia* palm swamp (Kelly et al., 2017). Similarly, expansion of trees into an initially open habitat during the earliest stages of vegetation development of the peatland at Quistococha (taken from plot QUI-01) occurred in <100 years, and the current palm swamp developed approximately ~1880 years ago (Roucoux et al., 2013). Our data suggests that transitioning from a seasonally flooded forest into a palm swamp and later into a pole forest requires a reduction in minimum water table depth, or flooding depth, from approximately −2.83 m, the average minimum water table depth across our seasonally flooded forest sites (Table 2), to at least −1.34 m as observed in the palm swamp in plot JEN-14 (Table 1), to approximately −0.21 m, the average for the peatland pole forests (Table 2). Such a reduction in minimum water table depth could result at least in part from the build-up of peat itself, but lateral movement of a river channel away from a floodplain site will also reduce its influence on the water table (Kalliola et al., 1991). This mechanism is consistent with the lower correlations of river level data with variation in

water table depth in the peatland pole forest compared to the seasonally flooded forest sites (Figure 4).

In terms of the spatial patterns of peatland vegetation in wetland ecosystems, our results add to the evidence that pole forest is an ecologically distinctive ecosystem type (Draper et al., 2014), rather than a formation that occurs as a result of degradation by human activity (Bhomia et al., 2019; Hergoualc'h et al., 2017). Peatland pole forests have only recently been scientifically described in Amazonia and have a distinctive tree, bird and soil microbial composition, as well as the deepest peat deposits of all forest types in this region (Draper et al., 2014, 2018; Díaz-Alván et al., 2017; Finn et al., 2020; Honorio Coronado et al., 2021). Our results indicate that peatland pole forest also has a distinctive ecohydrological regime, with a low pH, a water table permanently close to the surface and a range in water table depth of less than 0.70 m. This ecohydrological regime would not be found if this forest type was derived from a palm swamp through selective harvesting of female *M. flexuosa* palms for their fruit, as palm swamps are associated with a greater range of water table depths and higher levels of flooding than peatland pole forests (Figure 2). A similar sex ratio of adult male:female individuals of *M. flexuosa* in palm swamps and peatland pole forests in the Tigre river basin also supports the argument that these two forest types are different natural formations (Honorio Coronado et al., 2021). Peatland pole forests therefore appear to be analogous to the small stature forests growing on domed ombrotropic peatlands in Southeast Asia (Draper et al., 2018; Lähteenoja et al., 2009b), rather than a degraded version of other forest types.

4.3 | Impact of climate change on peat accumulation and forest-dependent livelihoods

The significant links between ecohydrological conditions, tree species composition and the presence of peat mean that changes in river fluctuations due to climate change could affect the biodiversity and function of these ecosystems as a carbon store, and in turn, impact local livelihoods. Long-term records of river level from the Amazon River have shown that extreme flooding and low river level events are now occurring more frequently, with one extreme flooding event every 4 years on average since 2000, and extremely low river levels recorded in 2005 and 2010 (Barichivich et al., 2018; Gloor et al., 2013). Our results indicate that this intensification of flooding and drought events will likely affect different aspects of these peatland ecosystems. Firstly, severe flooding events could cause large-scale reorganization of the ecosystem types across this landscape, by triggering mortality of *M. flexuosa* if the maximum flooding levels for palm swamps recorded here, corresponding to a minimum water table depth of −1.34 m, are exceeded. Examples of such large-scale mortality events of *M. flexuosa* have been observed, with large numbers of standing dead trees in areas that have been rapidly inundated linked to high siltation rates of their aerial roots (Kalliola et al., 1991). Extreme flood events also reduce populations of animals that rely on the terrestrial habitats in these wetlans (Bodmer et al., 2018) and high

mortality of animals and *M. flexuosa* palms would have a negative impact on livelihoods because local communities depend on hunting and fruit harvesting within these forests for consumption and income (Bodmer et al., 2018; Hidalgo Pizango et al., 2022; Virapongse et al., 2017). In contrast, the association between the presence of peat and a maximum water table depth of 0.55 m, suggests that even modest increases in drought frequency could reduce peat accumulation rates as the increase in oxic conditions in the near surface promotes the decomposition of litter and peat and release of CO_2 to the atmosphere (Jauhiainen et al., 2005).

5 | CONCLUSIONS

In this study, we show that species composition and peat formation have different ecohydrological controls in the PMFB. Variation in minimum water table depth (ie flooding level) and pH are associated with variation in tree species composition, whilst the maintainance of the water table close to the ground surface throughout the year is associated with the presence of peat. Overall, the different hydrological controls on tree species composition and the presence of peat in this landscape, suggest that predicted increases in the frequency and strength of flooding events may alter patterns of tree species composition, whereas increases in drought severity and declines in minimum river levels pose a greater risk to peat accumulation and the ability of these ecosystems to act as a store and sink of carbon.

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DATA AVAILABILITY STATEMENT

The dataset of water table depth can be requested from the corresponding author and the forest plot dataset can be requested through http://www.forestplots.net.

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