

RESEARCH ARTICLE

Climate-driven spatial and temporal patterns in peatland pool biogeochemistry

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Abstract

Peatland pools are freshwater bodies that are highly dynamic aquatic ecosystems because of their small size and their development in organic-rich sediments. However, our ability to understand and predict their contribution to both local and global biogeochemical cycles under rapidly occurring environmental change is limited because the spatiotemporal drivers of their biogeochemical patterns and processes are poorly understood. We used (1) pool biogeochemical data from 20 peatlands in eastern Canada, the United Kingdom, and southern Patagonia and (2) multi-year data from an undisturbed peatland of eastern Canada, to determine how climate and terrain features drive the production, delivering and processing of carbon (C), nitrogen (N), and phosphorus (P) in peatland pools. Across sites, climate (24%) and terrain (13%) explained distinct portions of the variation in pool biogeochemistry, with climate driving spatial differences in pool dissolved organic C (DOC) concentration and aromaticity. Within the multi-year dataset, DOC, carbon dioxide (CO₂), total N concentrations, and DOC aromaticity were highest in the shallowest pools and at the end of the growing seasons, and increased gradually from 2016 to 2021 in relation to a combination of increases in summer precipitation, mean air temperature for the previous fall, and number of extreme summer heat days. Given the contrasting effects of terrain and climate, broad-scale terrain characteristics may offer a baseline for the prediction of

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small-scale pool biogeochemistry, while broad-scale climate gradients and relatively small year-to-year variations in local climate induce a noticeable response in pool biogeochemistry. These findings emphasize the reactivity of peatland pools to both local and global environmental change and highlight their potential to act as widely distributed climate sentinels within historically relatively stable peatland ecosystems.

KEYWORDS

biogeochemistry, carbon, climate change, climate sentinels, landscape change, nutrient cycling, ponds

1 | INTRODUCTION

Biogeochemical cycles in freshwater bodies are increasingly altered by both large- and small-scale changes in climate and land use that lead to increased loading and processing of carbon (C), nitrogen (N), and phosphorus (P) (Maranger et al., 2018; Pilla et al., 2022). Small lakes or ponds (<0.01 km²) are recognized for having disproportionate influence on local and global C, N and P cycles and GHG emissions (Holgerson & Raymond, 2016) because of their high surface-to-watershed area ratio that increases rates and quantities of biogeochemical processes (Downing, 2010). A large number of small water bodies (often <0.001 km²) consist of pools developing in peatlands, especially in the mid- and high latitudes. Peatlands are globally important ecosystems, covering nearly 5 million km² (UNEP, 2022) and storing >600 Pg C (Yu et al., 2010) and 5–25 Pg N (Yin et al., 2022). However, while they are historically relatively stable ecosystems (Morris et al., 2015), they face challenges related to climate and land-use changes that could modify their current structural and functional state (Juutinen et al., 2018) and that of their components, such as streams and pools. Peatland pools form a relatively homogeneous group of water bodies that develop in similar landscapes of organic matter-rich matrix and that are potentially more biogeochemically dynamic than other aquatic ecosystems (Arsenault et al., 2022). For example, in permafrost-affected peatlands, the relative contribution of small pools to the landscape C budget is proportional to their area, regardless of their size, and peatland water bodies are large contributors to this budget (Polishchuk et al., 2018; Serikova et al., 2019). Despite this potential, the response of peatland pool biogeochemical patterns and processes to major drivers such as climate change and land-use modification, and their role in global biogeochemical cycles remain poorly understood.

Temperature and precipitation are broad-scale (>10 km) climate drivers of spatial and temporal variability in the biogeochemistry of freshwater bodies (Collins et al., 2019), but such factors often vary in response to small scale (<1 km) land use and terrain differences (Cao et al., 2020). In permafrost-free temperate and boreal peatland pools, C and nutrient processing have been shown to be partly driven by local temperature and summer precipitation variations due to their effect on microbial activity dynamics, and on mass concentration, dilution, and transfer from the surrounding soil (Arsenault et al., 2018; Prijac et al., 2022). At larger scales, for a given set of

terrain characteristics, spatial and possibly temporal patterns in biogeochemistry that follow climatic gradients may emerge in lakes (Soranno et al., 2019), but to our knowledge, this has not yet been studied in more structurally homogeneous systems like peatland pools. Hence, it is difficult to predict how climate change affects peatland pool structure and functioning as the influence of climate on spatial and temporal patterns in peatland pool biogeochemistry, compared with that of other potentially important drivers, remains unclear.

Water balance and biogeochemical patterns and processes in most aquatic ecosystems are largely influenced by their connectivity to the watershed and other water bodies, and by surrounding land use and terrain structure (e.g., morphometry, elevation, geology) (Covino, 2017). Peatland pools are, however, biogeochemically distinct from typical lentic freshwater bodies because of the very small area of their watershed that limits external nutrient inputs and because of the nature of the soil in which they develop that may influence the lateral flow of water and mass (C, N, and P) (Arsenault et al., 2022) especially when peat hydraulic conductivity is elevated (Holden et al., 2018). In ombrotrophic settings, pools from both raised (i.e., dome-shaped) or blanket (i.e., peatlands that follow the landscape morphology) peatlands have little to no hydrological and biogeochemical connectivity with the surrounding landscape and groundwater (Fraser, Roulet, & Lafleur, 2001; Holden & Burt, 2003). Locally, pool biogeochemistry, therefore, relies almost entirely on intrinsic controls, related to their morphology, the composition of the surrounding vegetation, and soil chemistry (Arsenault et al., 2018, 2019; Prijac et al., 2022). These factors are constrained at a larger scale by altitudinal, topographical, and hydrological influences (Belyea, 2007; Rydin & Jeglum, 2013). Regional dissimilarities in pool biogeochemistry emerging in Scotland and Northern Ireland have been related to peatland continentality, peat structure and composition, and pool morphology (Turner et al., 2016), highlighting the influence of broad-scale terrain factors on pool biogeochemistry. Landscape position, hydrological connectivity, and morphometry also mediate the response of freshwater bodies to climate variability by regulating ecosystem metabolism, but these factors often co-occur with climate gradients (Lapierre et al., 2015; Oleksy et al., 2022). It is, therefore, challenging to disentangle broad-scale controls of terrain on freshwater body biogeochemistry from climate influences.

Spatiotemporal variations in aquatic ecosystem biogeochemistry result from a combination of small- and broad-scale terrain and climatic drivers, that, respectively, control the origin of mass and the rates at which it is received, produced, and processed by the systems (Dodds et al., 2019; Oleksy et al., 2022). The development of peatland pools is driven by both terrain- and climate-related mechanisms (Belyea, 2007), but it is unclear to what extent these geographic factors dictate peatland pool biogeochemistry hence limiting our ability to understand and predict their function in both local and global biogeochemical cycles under rapidly occurring environmental change. In this context, the goal of this research was to assess how climate and terrain (peatland elevation and pool depth and area) drive the broad-scale spatial and local-scale interannual patterns in peatland pool C, N, and P biogeochemistry. More specifically, we first determined the main drivers of spatial variations in pool biogeochemistry, by comparing peatland pools from different geographic settings (in eastern Canada, the United Kingdom, and southern Patagonia). We then assessed the interannual variation in pool C, N, and P biogeochemistry from an undisturbed peatland of eastern Canada, based on five ice-free season surveys over the 2016–2021 period.

2 | MATERIALS AND METHODS

2.1 | Sites description

A total of 240 pools were sampled between 2011 and 2021 in 20 undisturbed peatlands of eastern Canada, the United Kingdom, and southern Patagonia (Table 1). The peatlands were in different geographic settings, from maritime to more continental locations, and from sea level to >550m in altitude to ensure a broad array of climatic variability was captured. Mean annual precipitation ranged from ~400 to >2000mm per year and mean annual air temperature ranged from -0.7 to 9.2°C over the 1991–2020 period (Harris et al., 2020). All peatlands were classified as raised or blanket bogs and had numerous pools at their surface.

2.2 | Pool sampling and chemical analyses

Pools from eastern Canada and southern Patagonia were sampled between 2016 and 2021 during the growing season (May to October in Canada, January to February in Chile; Table 1). They were selected to cover not only a wide range of depth, area, and surrounding vegetation composition but also accessibility and water availability. The pools we sampled were not in contact with the mineral substrate of the peatlands and their bottom was composed of peat and limnic material. There was, therefore, little to no connectivity to groundwater and lithology. Sampling and water analyses are further described in Arsenault et al. (2018). Pools from the United Kingdom were sampled between 2011 and 2014, and pool measurements,

and water sample collection and analyses were performed as reported by Brown et al. (2016) and Turner et al. (2016).

To assess interannual variation in pool biogeochemistry, nine pools from one peatland in eastern Canada (Grande plée Bleue—GPB, a raised bog) were sampled repeatedly during the 2016, 2017, 2019, 2020, and 2021 growing seasons (from May to October). These pools were selected to represent three pool archetypes found at the study sites: three large (>1200m²) and moderately deep (~1m) pools, three small (<400m²) and shallow (<0.8m) pools, and three small (<400m²) and deep (>1.8m) pools (Arsenault et al., 2018). All pools were sampled on the same day, between 4 and 10 times per growing season. Water samples were analyzed for pH, DOC, total nitrogen (TN), total phosphorus (TP), water color at 254nm (A254), specific UV absorbance at 254nm (SUVA), and dissolved CO₂ and CH₄ concentrations.

2.3 | Data handling

For the spatial component of the study, most pools were sampled only once and during the growing season (Table 1). When pools were sampled repeatedly, means were calculated for all variables to average sampling effects of covariates. Given the influence of pool morphology (Arsenault et al., 2018) and regional variations in pool biogeochemistry (Turner et al., 2016), analyses considered the effects of variables describing climate (mean annual air temperature [MAAT], mean annual precipitation [MAP], potential evapotranspiration [PET], annual number of days with precipitation [wet days], annual number of frost days [frost days], and precipitation to potential evapotranspiration ratio [P:PET]) and terrain (elevation, and pool area and depth). We used global gridded climate data (Harris et al., 2020) to ensure consistency in our analyses because most peatlands did not have nearby meteorological stations and those that did, did not report all the variables of interest.

For the temporal component, to deal with uneven sample sizes and irregular sampling dates between years at our study site, we averaged data for each pool for 50-day windows between day of year (DOY) 150 and 300 to encompass all sampling dates while reducing data repetition to a minimum (Legendre & Legendre, 2012). Averages of all biogeochemical parameters (pH, A254, SUVA, and DOC, TN, TP, and dissolved CH₄ and CO₂ concentrations) were calculated for each window (days of the year 150–200, 175–225, 200–250, 225–275 and 250–300). For example, DOY 175 and 200 were used to compare pool biogeochemistry for windows 150–200 and 175–225, respectively. We used the windows to assess changes in pool biogeochemistry patterns among and within years, and between groups of pools. To assess the effect of climate on temporal changes in pool biogeochemistry, we collated meteorological data from the nearest station with complete data (Saint-Michel station, 13 km east from the study site; Environment Canada, 2022) for each year: mean summer temperature, number of summer days where maximum temperature exceeded 30°C, mean previous spring, winter and fall temperature,

TABLE 1 Description of the sites where pools were sampled.

Region	Site	Latitude	Longitude	Peatland type	N pools sampled	N sampling events (year range)	Elevation (m)	MAAT (°C)	MAP (mm)	PET (mm)	
Eastern Canada	Grande plée Bleue	46.781	-71.052	Raised bog	53	1 (2016)	87	3.9	1329	641	
	Grande plée Bleue	46.781	-71.052	Raised bog	9	28 (2016–2021)	87	3.9	1329	641	
	Rivière-au-Tonnerre	50.315	-64.927	Raised bog	10	1 (2019)	80	1.5	962	506	
	Kegaska	50.194	-61.556	Raised bog	10	1 (2019)	35	1.4	1022	446	
	Havre-Saint-Pierre	50.256	-63.445	Raised bog	10	1 (2019)	32	1.7	901	487	
	La Romaine	50.523	-63.206	Raised bog	10	1 (2019)	109	-0.7	962	445	
	Saint-Alexandre-de-Kamouraska	47.740	-69.610	Raised bog	11	8 (2020–2021)	126	3.2	1055	530	
	Miscou	47.940	-64.526	Raised bog	9	1 (2021)	7	4.7	1198	655	
	United Kingdom	Cross Lochs	58.373	-3.959	Blanket bog	6	5 (2013–2014)	211	7.6	1109	472
		Loch Lier	58.388	-3.783	Blanket bog	6	5 (2013–2014)	185	7.6	1109	472
Munsary		58.396	-3.343	Blanket bog	6	5 (2013–2014)	105	8.3	1247	436	
Silver Flowe		55.128	-4.400	Blanket bog	22	1 (2013)	280	7.6	2046	449	
Slieveanorra		55.085	-6.193	Raised bog	15	1 (2013)	307	9.2	1164	488	
Garron Plateau		55.004	-6.073	Blanket bog	11	1 (2013)	337	9.2	1164	504	
Upper Midhope		53.475	-1.722	Blanket bog	10	3 (2011–2012)	515	8.9	1177	530	
Moor House		54.690	-2.388	Blanket bog	5	3 (2011–2012)	571	7.4	1199	460	
Cold Fell		54.892	-2.604	Blanket bog	5	3 (2011–2012)	546	8.5	1216	513	
Southern Patagonia		Navarino	-54.937	-67.888	Blanket bog	11	1 (2019)	300	4.4	501	620
	Punta Arenas	-53.396	-71.25	Blanket bog	9	1 (2019)	256	5.9	419	691	
	Karukinka	-54.532	-68.795	Raised bog	6	1 (2019)	36	3.9	537	665	
	Cape Horn	-55.963	-67.229	Blanket bog	6	1 (2019)	45	4.9	763	467	

Note: Peatland elevation estimates were taken from Google Earth. Climate variables for the 1991–2020 period were taken from the Climate Research Unit gridded Time Series (Harris et al., 2020). Abbreviations: MAAT, mean annual air temperature; MAP, mean annual precipitation; PET, potential evapotranspiration.

total summer and previous spring, winter and fall precipitation, and number of summer precipitation days.

2.4 | Statistical analyses

2.4.1 | Spatial variation

In the multivariate analyses of spatial variation in pool biogeochemistry, we only included pools for which pH, SUVA, DOC, TN, TP, and dissolved CO₂ and CH₄ concentrations data were available ($n=150$). We first performed a multiple analysis of variance (MANOVA) after transforming the non-normally distributed data to determine if biogeochemistry was different among the three studied regions. We then ran individual Tukey HSD post-hoc tests on individual biogeochemical variables when differences were found. We also performed a one-way analysis of variance to determine if terrain variables (elevation, pool area, and depth) were related to peatland type (blanket or raised bog). We used Kruskal–Wallis followed by pairwise Wilcoxon rank-sum tests on non-transformed data to determine if climate and terrain influenced pool biogeochemistry, and isolate dissimilar sites. To assess how each climate and terrain variable influenced the individual biogeochemical variables while dealing with the several tied ranks in the distributions, we ran Kendall rank correlations.

To determine the effect of climate and terrain predictors on pool biogeochemistry, we used partial least-square regressions (PLSR) because they are robust even if there is collinearity among variables (Lindgren et al., 1993), as was the case for climate predictors. Both dependent and independent matrices were standardized to a mean of 0 and a standard variation of 1. We then calculated the variable importance in projection (VIP) to determine which of the climate and terrain predictors mostly influenced the spatial variation in pool biogeochemistry, using a threshold of $VIP > 1$ (Farrés et al., 2015). We used variance partition to differentiate the effect of “climate” (i.e., combined effect of MAAT, MAP, PET, P:PET ratio, annual number of wet days, and annual number of frost days) from that of the terrain (i.e., combined effect of pool area and depth, and peatland elevation) on pool biogeochemistry. We finally used generalized linear mixed effects models to determine the response of the variables with the most variation explained by the PLSR (DOC and TN concentrations) to changes in climate and terrain. We used *gamma* distribution family for both DOC and TN. We rejected from the models the predictors that showed collinearities (P:PET ratio, annual number of wet days, and annual number of frost days) and kept MAAT, MAP, PET, peatland elevation, and pool area and depth as fixed effects. These variables were scaled to a mean of 0 and a standard deviation of 1 to standardize units. Peatland type and regions were added as random intercepts to the models.

2.4.2 | Temporal variation

We first ran a principal component analysis (PCA) based on biogeochemical variables from each group of pools at every DOY to assess

the temporal changes and the effect of morphology on pool biogeochemistry. In the PCA, we also added climate data (MAAT and total annual precipitation) recorded at the nearest meteorological station to allow cross-comparison with the spatial component of the research. We performed two-way MANOVAs with interactions and Tukey HSD post-hoc tests to determine how pool biogeochemistry varied among years, across growing seasons, and among groups of pools, and how pool morphology influenced pool biogeochemical response over time. We then used linear mixed-effects models to assess the random effect of pool morphology on temporal changes in pool biogeochemistry and tested fixed effects using analyses of variance for likelihood ratio. We also ran Kendall rank correlations to assess the relationships between pool biogeochemistry, time, and meteorological variables regardless of pool morphology. To identify the main drivers of temporal variations of pool biogeochemistry at the GPB site, we conducted PLSR of biogeochemical vs meteorological variables based on three principal components and calculated VIPs. While the experimental design at the study site was originally built to compare the effect of pool size, we here focused on meteorological drivers because within-pool controls on biogeochemistry had previously been established (Arsenault et al., 2018, 2019). For each biogeochemical variable and at every DOY, we then averaged the data of all pools regardless of their size.

For both spatial and temporal variation analyses, except for Kruskal–Wallis and Wilcoxon tests and Kendall correlations, variables that were not normally distributed were \log_{10} -transformed to fulfill the normality condition prior to all analyses. All statistical analyses were undertaken using R, version 4.2.0 (R Core Team, 2022), and packages ‘pls’ and ‘plsdepot’ for PLSR, ‘vegan’ for variance partition, and ‘lme4’ for generalized linear mixed-effects models.

3 | RESULTS

3.1 | Spatial variation in pool biogeochemistry

There were large variations in peatland pool morphological and biogeochemical properties among the three studied regions. Peatland type (raised or blanket bog) was related to peatland elevation, pool area, and depth, with blanket bogs in our dataset developing at higher altitude and having shallower and smaller pools than raised bogs (ANOVA, $p < .001$). Overall, pools from Canada were deeper, more acidic and had higher concentrations in dissolved CH₄, pools from the United Kingdom were smaller and had lower concentrations in DOC, and pools from southern Patagonia had higher concentrations in TN and TP than other regions (Table 2). There was no difference in dissolved CO₂ between regions, and pool SUVA was similar between Canada and the United Kingdom, but higher in Patagonia. On average, pools from all regions were supersaturated in CH₄, especially in eastern Canada where the lowest concentration was around three times that of the atmosphere but went up to 250-fold, while CO₂ concentrations were on average slightly below atmospheric values (Table 2). There were also large within-site

TABLE 2 Morphological and biogeochemical parameter means \pm standard error (minimum–maximum) for peatland pools of Canada, the United Kingdom, and southern Patagonia.

	Eastern Canada	United Kingdom	Southern Patagonia
Area (m ²)*	_a 1067 \pm 249 (23–24,542); n = 122	_b 130 \pm 39 (4–1757); n = 59	_a 1419 \pm 675 (2–21,328); n = 32
Depth (cm)*	_a 73 \pm 4 (13–219); n = 122	_b 29 \pm 2 (3–60); n = 86	_b 34 \pm 7 (4–142); n = 32
pH	_a 4.07 \pm 0.02 (3.72–4.80); n = 122	_b 4.34 \pm 0.02 (3.90–4.90); n = 86	_b 4.47 \pm 0.06 (4.04–5.48); n = 32
DOC (mg L ⁻¹)*	_a 25.7 \pm 0.8 (6.7–51.7); n = 122	_b 17.9 \pm 1.7 (3.1–85.2); n = 86	_a 28.6 \pm 3.0 (8.0–73.1); n = 32
TN (mg L ⁻¹)*	_a 0.6 \pm 0.0 (0.3–1.9); n = 122	_a 0.7 \pm 0.0 (0.3–1.8); n = 66	_b 1.1 \pm 0.1 (0.4–3.6); n = 32
TP (μ g L ⁻¹)*	_a 17 \pm 1 (6–102); n = 122	_a 19 \pm 1 (6–76); n = 66	_b 55 \pm 15 (7–409); n = 32
SUVA (Lmg C ⁻¹ m ⁻¹)	_a 2.83 \pm 0.10 (0.87–6.04); n = 120	_a 2.99 \pm 0.16 (0.76–7.21); n = 66	_b 3.57 \pm 0.10 (2.12–4.77); n = 32
Dissolved CH ₄ (μ g L ⁻¹)*	_a 76.9 \pm 11.8 (3.8–336.5); n = 67	_b 16.2 \pm 2.2 (0.2–93.0); n = 66	_b 21.0 \pm 6.9 (0.5–159.3); n = 26
Dissolved CO ₂ (mg L ⁻¹)*	_a 0.7 \pm 0.06 (0.09–2.1); n = 67	_a 0.7 \pm 0.05 (0.2–2.0); n = 66	_a 0.8 \pm 0.2 (0.2–5.4); n = 26

Note: Letters in indices show differences and similarities between regions as determined by Tukey HSD tests (\log_{10} -transformed variables for the analyses are indicated by an asterisk).

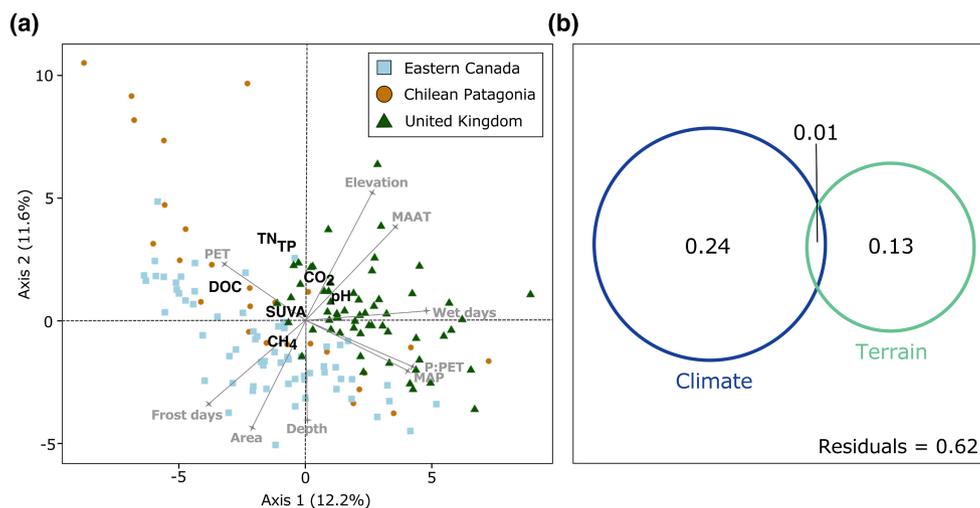


FIGURE 1 Peatland pool biogeochemistry varies across space. (a) Partial least square regressions of biogeochemical (black) vs. climate and terrain (gray) variables for pools of eastern Canada, the United Kingdom and southern Patagonia. Only depth (0.90) was a predictor with a VIP score < 1. (b) Partition of the variance in peatland pool biogeochemistry explained by climate (MAAT, MAP, PET, P:PET ratio, annual number of wet days, and annual number of frost days) and terrain (area, depth, and elevation) predictors.

variations in biogeochemistry, especially in terms of DOC, TP, and dissolved CH₄ concentrations (Table S1).

Multivariate analyses showed how peatland pool biogeochemistry tended to be much more similar within than among regions, and how spatial variations in climate and terrain both drive clear geographic patterns in peatland pool biogeochemistry among the three regions (Figure 1). Overall, the six-component PLSR explained 34.9% of the variance in pool biogeochemistry, with the first axis being driven by climate predictors (MAP, PET, and P:PET ratio) and mostly explaining variations in DOC concentration and aromaticity (SUVA). The second axis of the PLSR was driven by peatland elevation and pool area and mostly explained variations in TN, TP, and dissolved CH₄ concentrations. However, differences in pool biogeochemistry among regions and sites were not systematically attributed to variations in the same sets of climate and terrain predictors (Figure 1a; Figures S3–S11). For example, the different regions were mainly discriminated along the bottom-left (higher number of frost days

and pool area) to top-right (higher MAAT and peatland elevation) axis, but pool biogeochemistry appeared mainly driven by wetness conditions (Figure 1a). In particular, DOC, TN and TP concentrations seemed higher under the high PET typically found in Patagonia (except for Cape Horn) and continental eastern Canada (Grande plée Bleue site) (Table 1). At the terrain level, however, TN and TP were both correlated to peatland elevation, and pool area and depth ($p < .001$), but DOC was not correlated to any of these predictors ($p > .1$) (Figures S3–S5).

The independent effect of climate and terrain was supported by the partition of the variance in pool biogeochemistry explained by both sets of predictors (Figure 1b). Among the three regions, climate (24% of the variance) and terrain (13% of the variance) drove almost entirely distinct parts of the spatial variation in pool biogeochemistry, with only 1% of the variation explained by their joint effect. This means that while there was co-variation between terrain and climate properties, with pool morphology being correlated to climate

and peatland elevation (Figures S1 and S2), there was virtually no overlap in the effect these predictors have on pool biogeochemistry as they did not influence the same biogeochemical properties (Figures S3–S11).

In particular, generalized linear mixed effects models showed a strong influence of climate and terrain predictors on DOC and TN concentrations which were the two variables with the most variation explained by the PLSR (Figure 1a, upper-left quadrant). The random effects of peatland type and region showed clear patterns of increasing DOC with MAAT and elevation (Figure 2a,c) but decreasing with MAP and pool area and depth (Figure 2b,d,e). The relationships of TN to climate and terrain were not as clear as for DOC, with the strongest relationships being with elevation (positive, Figure 2h) and depth (negative, Figure 2j). For either DOC or TN, PET was not a driver of variation. In both models, the estimated among-type variance was much lower than among-region variance, meaning that peatland type only had a small influence on DOC and TN concentrations compared with peatland location. Overall, region and peatland type had little influence on TN variation compared with climate and terrain predictors (Table S3).

3.2 | Temporal variation in pool biogeochemistry

Meteorological conditions at the Grande plée Bleue site (eastern Canada) considerably varied between 2016 and 2021. For example, total summer rain ranged from 317 mm in 2017 to 472 mm in 2021 (~50% difference), and there were more than twice the number of days of high heat (>30°C) in 2020 (14) and 2021 (13) than in 2017 (6) (Table S7). Pools at the GPB site also exhibited highly variable

biogeochemistry during this period (MANOVA, $p < .001$, Table S4), both seasonally ($p = .01$) and among pools of different morphology ($p < .001$). For example, SUVA, DOC, TN and CO₂ concentrations increased gradually from 2016 to 2021, with the highest numbers systematically recorded in the shallowest pools (blue signs, Figure 3), and generally at the end of the growing seasons (Figures 3 and 4; Table S8). There was usually no interaction between the effects of time and morphology ($p \geq .05$; Figure 3). When adding a random effect of pool morphology on biogeochemistry, only DOC and CO₂ concentrations changed over the growing seasons ($p < .05$), but all parameters varied over the 2016–2021 period ($p < .1$), highlighting the influence of climate variations on pool biogeochemistry (Table S5). For each pool, morphology and surrounding vegetation composition did not change over the study period.

The multi-dimensional representation of the different variables highlighted the effect of both pool morphology and time on pool biogeochemistry (Figure 4a). Shallower pools (circle signs in the upper right quadrant) tended to have higher concentrations in DOC, TP and dissolved CO₂ and CH₄ concentrations, and lower pH than deeper pools, and for all variables there was a general increasing trend from 2016 (orange) to 2021 (gray) in relation to higher MAAT and lower total annual precipitation. The PLSR further emphasized the seasonal and interannual variability in the biogeochemistry of pools regardless of their size (Figure 4b). The three components of the analysis together explained 62.8% of the variance in pool biogeochemistry, with the first axis (22.4% of the variance) highlighting the interannual pattern of increasing DOC, TN and CO₂ concentrations and higher A254, SUVA and pH from 2016 to 2021. This pattern was driven by a combination of increasing summer precipitation, increasing mean air temperature the previous fall and the higher number

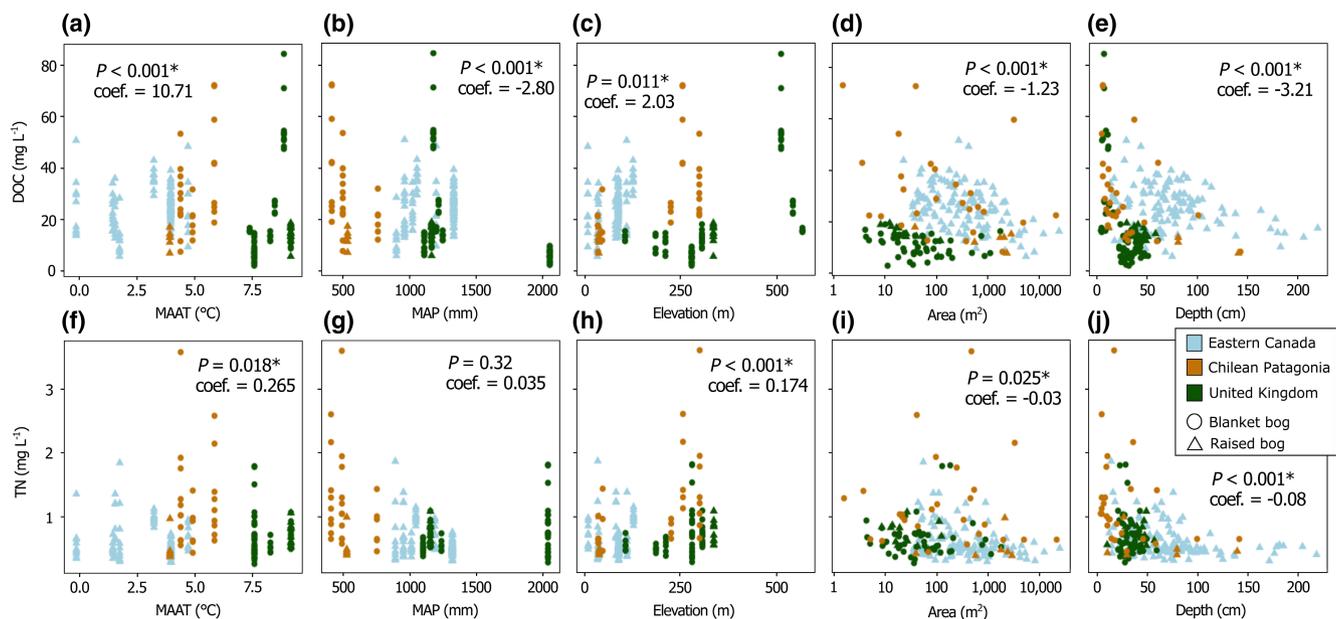


FIGURE 2 Spatial patterns among regions emerged when comparing dissolved organic carbon (DOC, boxes a–e) and total nitrogen (TN, boxes f–j) concentrations to climate and terrain predictors. Coefficient estimates (coef.) and p -values (p) of the generalized linear mixed-effects models of DOC and TN concentrations to predictors, with peatland type and regions as random effects, are shown for each plot. Asterisks (*) indicate models with p -values (p) < .05.

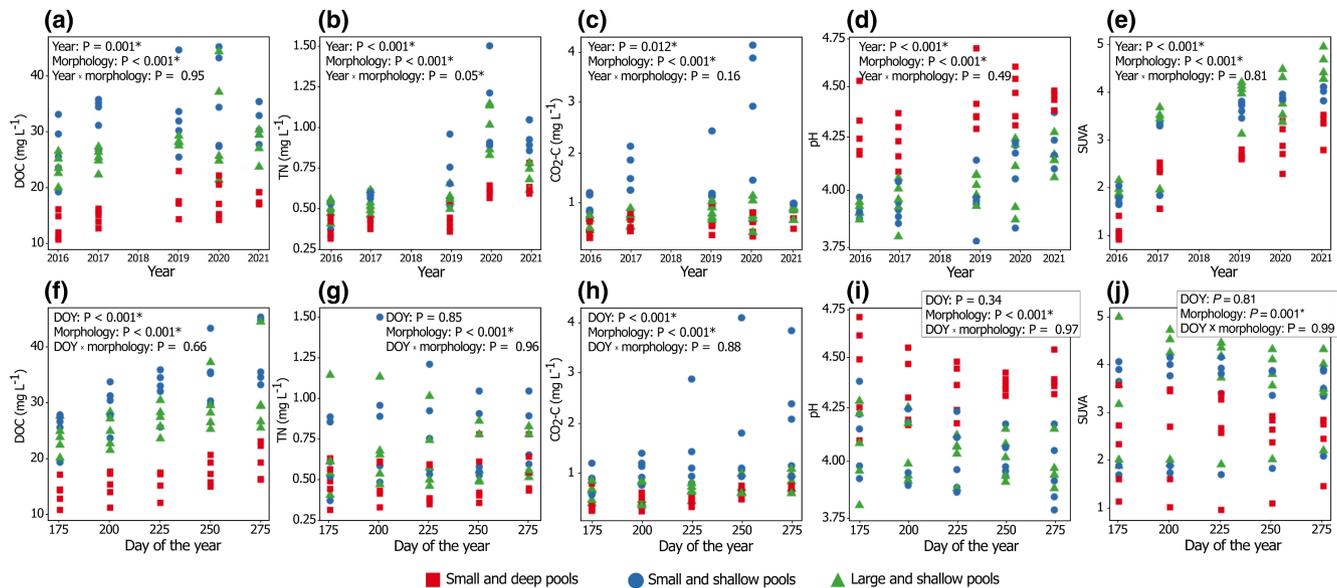


FIGURE 3 Interannual (upper boxes) and seasonal (lower boxes) variations in pool dissolved organic carbon (DOC), total nitrogen (TN), and dissolved carbon dioxide (CO_2) concentrations, pH, and specific UV absorbance (SUVA) in pools of different sizes at the Grande plée Bleue site (eastern Canada). Each dot represents the mean for a specific day of the year (DOY), between 2016 and 2021. Results (p -values, p) of analyses of variance with interactions among time (year or DOY) and groups of pools (morphology) are shown, with asterisks (*) indicating p -values $< .05$.

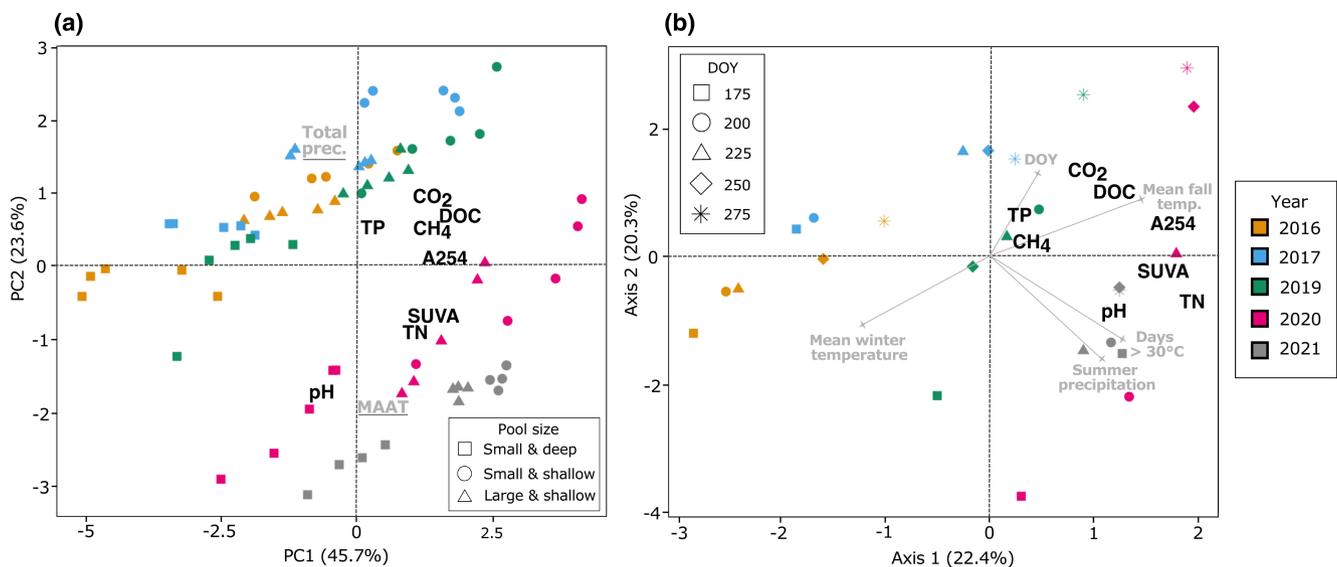


FIGURE 4 At the Grande plée Bleue site (eastern Canada), peatland pool biogeochemistry varies over time in response to local variations in climate. (a) Principal component analysis of pool biogeochemistry (black) and climate (mean annual air temperature [MAAT] and total annual precipitation; gray) evolution from the GPB site over the 2016–2021 period. Dot shapes represent pools of different sizes, color represent year of sampling. (b) Partial least square regressions (PLSR) showing annual (color) and seasonal (shape) variation in pool biogeochemistry (black) versus meteorological (gray) variables. Each dot is the average of all nine pools sampled at different days of the year (DOY). Only predictors with a VIP score > 1 are shown on the PLSR graph.

of extreme heat days in 2020 and 2021 (Table S6). The second axis (20.3% of the variance) showed the seasonal pattern of increasing DOC and CO_2 concentrations from early summer (square signs in the lower quadrants) to early fall (star signs in the upper quadrants) (Table S7).

4 | DISCUSSION

Our results show that both spatial and temporal variations in the biogeochemistry of peatland pools are controlled by sets of distinctive processes related to climate and terrain. At a broad scale, climate

has the largest influence, explaining 24% of the variation in pool biogeochemistry, and mostly drives pool organic C concentrations and aromaticity (Figure 1). Similarly, local temporal patterns of C, N, and P biogeochemistry are driven by small-scale differences in pool morphology in addition to seasonal and interannual fluctuations in temperature and precipitation (Figure 4). The fact that climate and terrain predictors did not influence the same biogeochemical predictors suggests that there may be factors driving pool biogeochemistry that were not considered in our analysis, such as peatland hydrology or peat thickness under the pools (Fraser, Roulet, & Moore, 2001; Holden et al., 2018; Pokrovsky et al., 2014). Nevertheless, due to the strong independent effects of terrain and climate (Figure 1b), this means that any given change in climate conditions may impact pool biogeochemistry regardless of terrain properties, and likewise, that any alteration in peatland terrain characteristics (e.g., water table drawdown) may similarly impact pool biogeochemistry in any given climate. It is, thus, crucial to distinguish the effects of terrain and climate because both may independently dictate future directions of pool biogeochemistry but at different time scales. In undisturbed conditions, variations in climate, indeed, occur faster than peatland terrain changes (Morris et al., 2015). Climate variations are, however, accelerating (IPCC, 2022) and atmospheric deposition chemistry is changing (Monteith et al., 2007), which will drive structural and functional changes in peatland ecosystems (Bridgman et al., 2008), further limiting our understanding of current and future peatland pool function in both local and global biogeochemical cycles.

4.1 | Terrain characteristics as a baseline for the prediction of pool biogeochemistry

Morphology is a fundamental driver of peatland pool biogeochemistry (Figure 3; Arsenault et al., 2018; McEnroe et al., 2009; Pelletier et al., 2014) and is constrained by altitudinal and topographical factors (Belyea, 2007). Our results show that differences in pool morphology, and indirectly in pool biogeochemistry, among regions may first be attributed to peatland types, with pools from blanket bogs being smaller and shallower than pools from raised bogs, where thicker peat deposits allow pool deepening (Foster & Wright Jr, 1990). In blanket bogs, pools develop perpendicularly to the surface gradient, which limits their maximum areal extent in comparison with less sloping raised bogs (Belyea, 2007; Foster & Glaser, 1986). The raised and blanket bogs contrast then partially drives the biogeochemical differences among eastern Canada (raised bogs) and the United Kingdom and southern Patagonia (mostly blanket bogs) (Table 1, Figure 1), with shallower and smaller pools having higher concentrations in DOC and TN in every region (Figure 2).

Pools from southern Patagonia had higher TN and TP concentrations than elsewhere. Given its remoteness, this region receives little atmospheric pollution (Kleinebecker et al., 2008); pool TN and TP concentrations in southern Patagonia are, therefore, associated to local controls, possibly related to maritime influence

that increases nutrient inputs from oceanic sources to the pools (Vizza et al., 2017) or the distinctive vegetation of Patagonian peatlands (Kleinebecker et al., 2008; Mathijssen et al., 2019). It is also possible that higher TN and TP concentrations were related to dry and wet deposition of dust in more continental parts of southern Patagonia (Kleinebecker et al., 2008) or to the positive effect volcanic ash has on OM decomposition and nutrient cycling and loading (Broder et al., 2012; Modenutti et al., 2013). Similarly, spatial trends in pH and SUVA may reflect differences in plant diversity among regions, as pool acidity and the aromaticity of DOC have been related to the composition of vegetation surrounding the pools (Arsenault et al., 2019; Prijac et al., 2022). Pools in our dataset represented a wide range of depth, area, and vegetation, and the 20 peatlands that were compared cover large gradients of altitudinal and topographic parameters. Under a rapidly changing climate, given the strong relationships that emerge between terrain and pool biogeochemistry and the distinct effect climate and terrain have (Figure 1b), broad-scale and more stable terrain characteristics may, therefore, offer a baseline for the estimation of small-scale pool biogeochemistry from temperate and boreal settings. Predictive relationships between pool terrain and their biogeochemistry could thus be incorporated into upscaling efforts and for better integration of peatland pools in global biogeochemical models.

4.2 | The broad- and small-scale influence of climate

Broad-scale climate patterns drove spatial variations in pool biogeochemistry, with increasing DOC, TN, and TP concentrations in regions with higher PET and lower MAP, and increasing pH and dissolved CO₂ in warmer climates (Figure 1a). These patterns in pool biogeochemistry followed gradients in peatland structure that also correlate with increases or decreases in climate properties. For example, warmer MAT favors greater DOC export from peatlands (Rosset et al., 2022) because of changes in vegetation composition and increased decomposition rates (Dieleman et al., 2015, 2016). A lowered water table under warmer and drier climates also stimulates the production of DOC (Strack et al., 2008) and CO₂ (Huang et al., 2021) in the upper layer of the peat profile by exposing labile C to newly created aerobic conditions. The produced DOC and CO₂ can then be transported to and processed in the pools. Dry summers have also previously been associated with high DOC and dissolved CO₂ and CH₄ concentrations in peatland pools (Chapman et al., 2022). Our findings support the importance of these climate-driven mechanisms in controlling peatland pool biogeochemistry, and further suggest that climate may be the overarching driver of broad patterns at the cross-regional scale, where other sources of variation may not be as strongly expressed.

The broad-scale climate effect is coherent with the relatively higher concentrations (up to 250-fold supersaturation), variation, and climate response of CH₄ than CO₂ across the studied sites. Part

of this effect could be directly linked to climate, considering that CH_4 production is more sensitive than CO_2 to temperature (Yvon-Durocher et al., 2014). This pattern could further be explained by indirect climate effects linked with carbon turnover. The lower DOC and dissolved CO_2 and CH_4 concentrations in larger and deeper pools further suggest that slower water turnover time in large pools enables the processing of C over a longer period of time leaving more recalcitrant, high-SUVA C in the pools (Holden et al., 2018). C emissions from pools have previously been positively correlated to DOC concentrations and SUVA (Pelletier et al., 2014). If pool DOC concentrations and SUVA were to increase in drier conditions, as proposed by our results, then the C balance of pools, and incidentally of peatlands, from regions expected to experience smaller P:PET ratio in the future may, therefore, be affected, potentially increasing C emissions from pools, especially CH_4 , and decreasing overall C sequestration in peatlands.

At a small scale, the magnitude of temporal variations in pool biogeochemistry at the GPB site in eastern Canada was in the range of what was reported in the spatial component of the study (Table 1, Table S5), even if there was high within-site variability from 1 year to another (Table S4). This means that the climate effect on pool biogeochemistry at GPB may be transposable and used to foresee changes in peatland pool biogeochemistry in other temperate and boreal regions. In particular, increased TN concentrations and pH may be broadly expected in eastern Canada in response to projected higher summer precipitation and number of extreme heat days (Figure 3b, Prairie Climate Centre, 2019). Increases in TN concentrations could be related to higher N cycling and fixation in and around the pools under warmer summer temperatures and increased soil wetness (Weedon et al., 2012; Živković et al., 2022). Mechanisms leading to higher pH are, however, less clear but could be explained by lower phenolics coming from the surrounding peat because of more intense water table fluctuations during wet summers (Kim et al., 2021). Similarly, the sustained increases in SUVA, A254 and DOC, TN, TP, and dissolved CO_2 and concentrations measured at GPB between 2016 and 2021 were driven by warmer temperature in the falls preceding the growing seasons we sampled (Figure 4b). These trends may be related to differences in decomposition and production rates in the pools during the warmer falls. Warmer temperatures may sustain elevated decomposition processes late after the end of the growing season and release nutrients that can not be taken up efficiently because of slower production rates under low photointensity and photoperiod, and a decrease in temperature right after. It is also possible that changes in DOC concentration and composition in peatland pools reflect the worldwide trend of inland water browning under warmer climate and higher soil pH (Evans et al., 2006; Freeman et al., 2001). While our results do not provide a definitive explanation for the underlying mechanisms behind these climate-driven trends, they suggest that the biogeochemical dynamism of pools could increase under a warming climate, altering small-scale biogeochemical cycles and possibly overall peatland functions.

Capturing a climate signal in freshwater ecosystems within only 6 years is difficult as climate parameters rarely follow monotonic

relationships (Soranno et al., 2019). Our results nonetheless show that relatively small year-to-year variations in climate induce a noticeable response in pool biogeochemistry, possibly due to the fast reaction of these small waterbodies to changes. Fast reaction times can be caused by their small water content and high surface-to-volume ratio, and by the relative stability of their terrain characteristics compared with other freshwater ecosystems (Oleksy et al., 2022). Here, we demonstrate that even short-term variations in climate can induce ecologically meaningful increases in pool reactivity, which may inform future predictions of peatland pool function under an increasingly warmer climate.

5 | CONCLUSION

Our results show that freshwater bodies in peatlands are highly susceptible to terrain and climate variations that influence biogeochemical patterns at both local (e.g., Arsenault et al., 2018) and regional (e.g., Turner et al., 2016) scales. Given the relatively large influence that intrinsic controls exert on their biogeochemistry and their distinctiveness among aquatic ecosystems, peatland pools would, therefore, be at the forefront of freshwater body response to local and global environmental change. It is indeed likely that peatland pools act as climate sentinels (i.e., Williamson et al., 2009), where small variations in temperature or precipitation induce large structural and functional changes. In fact, peatland pools appear to be even more responsive than previously defined freshwater climate sentinels (i.e., lakes and reservoirs; Williamson et al., 2009) as we showed that relatively small and short-term climate variations within a 6-year period had a considerable impact on C and nutrient cycles. Considering the relatively stable influence terrain exerts on pool biogeochemistry, the role climate plays in controlling variability at both small and broad scales may then increase if it keeps changing rapidly, bringing a considerable level of uncertainties to future predictions of peatland pool biogeochemistry and its effects on the local and global environment. Further survey and monitoring efforts conducted in understudied terrain and climate settings should thus be pursued to reduce this uncertainty.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Zenodo at <https://doi.org/10.5281/zenodo.7826229>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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