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Biogeochemical Distinctiveness of Peatland Ponds, Thermokarst Waterbodies, and Lakes

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Abstract Small lentic freshwater ecosystems play a disproportionate role in global biogeochemical cycles by processing large amounts of carbon (C), nitrogen (N), and phosphorus (P), but it is unlikely that they behave as one homogenous group for the purpose of extrapolation. Here, we synthesize biogeochemical data from >12,000 geographically distinct freshwater systems: lakes, peatland ponds, and thermokarst waterbodies. We show that peatland ponds are biogeochemically distinct from the more widely studied lake systems, while thermokarst waterbodies share characteristics with peatland ponds, lakes, or both. For any given size or depth, peatland ponds tend to have dissolved organic carbon concentrations several-fold higher and are 100-fold more acidic than lakes because of the organic matter-rich settings in which they develop. The biogeochemical distinctiveness of freshwater ecosystems highlights the need to account for the fundamental differences in sources and processing of organic matter to understand and predict their role in global biogeochemical cycles.

Plain Language Summary Small freshwater bodies are major (but under-studied) contributors to the global cycling of carbon and nutrients. A large number of these ecosystems develop in climate-sensitive organic soils. Using a dataset of >12,000 geographically distinct freshwater bodies, we show that many of these ecosystems, namely peatland ponds and some waterbodies developing in permafrost, are structurally and functionally different than their more widely studied lake counterparts. Peatland ponds have distinct combinations of pH, nutrients, and organic carbon concentrations compared to lakes, and they are commonly much more acidic and richer in organic carbon for any given size or depth. Biogeochemically, permafrost waterbodies behave either as peatland ponds, as lakes, or as a combination of both. Our results emphasize the need to consider the distinction between peatland ponds, permafrost waterbodies, and lakes to better understand and forecast the role of small freshwater ecosystems in global biogeochemical cycles.

1. Introduction

Small waterbodies are major components of global biogeochemical cycles, despite their limited areal extent, as they display high biogeochemical processing rates compared to larger lakes, terrestrial, or marine ecosystems (Downing, 2010; Kortelainen et al., 2006). Very small waterbodies (<0.001 km²) have been estimated to account for 15% of the carbon dioxide (CO_2) and ~37% of the diffusive methane (CH_4) emissions from lentic systems, despite only representing 8.6% of the global area of static surface freshwater bodies (Holgerson & Raymond, 2016; Rosentreter et al., 2021). An unquantified portion of small waterbodies consists of ponds commonly found in peatlands (Belyea & Lancaster, 2002), and thermokarst waterbodies (lakes and ponds) that form following water accumulation in soil depressions after the subsidence of thawing permafrost (Vonk et al., 2015). Thermokarst waterbodies account for approximately 25% of the total area covered by open freshwaters in the Arctic (Wauthy et al., 2018) and are estimated to cover a total of ~1,300,000 km² of the northern circumpolar permafrost region (Olefeldt et al., 2016). Estimates of the extent of peatland ponds are currently limited to the boreal-arctic domain where peatland waterbodies cover ~260,000 km² (Olefeldt et al., 2021). Thermokarst waterbodies and peatland ponds are highly reactive, with CO_2 and CH_4 fluxes estimated to be up to 10- and 2-fold higher, respectively,

than lakes and impoundments, but these estimates are based on scarce data when compared to lakes (DelSontro et al., 2018; Hamilton et al., 1994; Kuhn, Varner, et al., 2021; Laurion et al., 2010; Pelletier et al., 2014; Serikova et al., 2019).

Lakes and ponds have no clear-cut definition, and their distinction is usually based on size, mostly surface area. Beyond size, the interaction of peatland ponds and thermokarst waterbodies with the surrounding landscape is different to non-thermokarst and non-peatland lakes and impoundments developing in geological depressions (hereafter simply referred to as lakes) because of the absence of extended watersheds (Arsenault et al., 2019; Holden et al., 2018; Kokelj & Jorgenson, 2013). Peatland ponds, especially, differ from lakes because they develop in organic-rich peat deposits. Thermokarst waterbodies are included in a vast group of systems formed by periglacial processes and comprise lakes and ponds that develop either in mineral or organic-rich permafrost and yedoma (carbon-rich, fine-textured, frozen aeolian sediments) (Elder et al., 2018; Kokelj & Jorgenson, 2013; Laurion et al., 2010). This results in a wide variety of transparencies and trophic conditions (Vonk et al., 2015; Wauthy et al., 2018) that often occupy extreme ends of lake gradients, but few studies have differentiated the effect of the surrounding matrix (organic or mineral) of thermokarst waterbodies on their biogeochemistry (Heslop et al., 2015). Hence, we postulate that while waterbodies form a continuum along environmental gradients, systems generally identified as peatland ponds and thermokarst waterbodies differ from lakes because of the large influence that climate and surficial material have on their development (Foster, King, et al., 1988; Kokelj & Jorgenson, 2013) and biogeochemistry (Kuhn, Thompson, et al., 2021; Wik et al., 2016).

Despite the growing interest in studying peatland ponds and thermokarst waterbodies given their responses to global change (Karofeld & Tõnisson, 2014; Serikova et al., 2019; Walter Anthony et al., 2018), knowledge of these systems is lagging behind other freshwater ecosystems. Because of the unique settings in which they develop, peatland ponds and thermokarst waterbodies are likely to show atypical combinations of morphometric and chemical properties among lentic systems. Recent studies have described the distribution and characteristics of peatland ponds and thermokarst waterbodies in specific regions of the world (e.g., Kuhn, Varner, et al., 2021; Stolpmann et al., 2021; Wik et al., 2016) or characterized the biogeochemistry of globally distributed freshwater systems without differentiating the matrix in which they develop (e.g., Abell et al., 2012; Sobek et al., 2010). However, currently, most freshwater models do not consider the heterogeneity in the biogeochemical processes among different types of lentic systems (Jones et al., 2018), limiting the robustness of regional estimates of C fluxes (Zwart et al., 2018) and their integration in earth system models. In this context, our aim was to identify the common and distinguishing features of lakes, peatland ponds and thermokarst waterbodies, in order to determine if these different ecosystems should warrant system-specific scaling relationships and aid our understanding of such waterbodies. We focus on biogeochemical indicators that are central to ecosystem functioning and that are widely reported: pH, dissolved organic carbon (DOC), total nitrogen (TN), and total phosphorus (TP) concentrations.

2. Methods

2.1. Data Compilation

We initially classified lentic freshwater ecosystems in three broad categories, based on the nomenclature used in the articles from which data were extracted: (a) lakes, which develop in geological depressions not created by periglacial processes and in non-peatland settings; (b) thermokarst waterbodies, created by periglacial processes regardless of the matrix (organic or mineral) in which they develop; and (c) peatland ponds, defined as water filled depressions in organic soils not influenced by permafrost. All waterbodies found in peatlands of the continuous and discontinuous permafrost regions were considered as the result of thawing processes and thus categorized as thermokarst waterbodies.

We gathered morphometrical (area, depth) and chemical (pH, DOC, TN, TP) data for 11,357 lakes worldwide, 827 thermokarst waterbodies from the Arctic circumpolar and the Himalaya regions, and 291 peatland ponds from North America, Europe, and Patagonia, from published and unpublished sources (Figure 1, Text S1, S2, and S3 in Supporting Information S1). We excluded systems that were clearly another type of aquatic ecosystem than lake, thermokarst waterbody, or peatland pond (e.g., hydroelectric reservoirs, retention basins, vernal
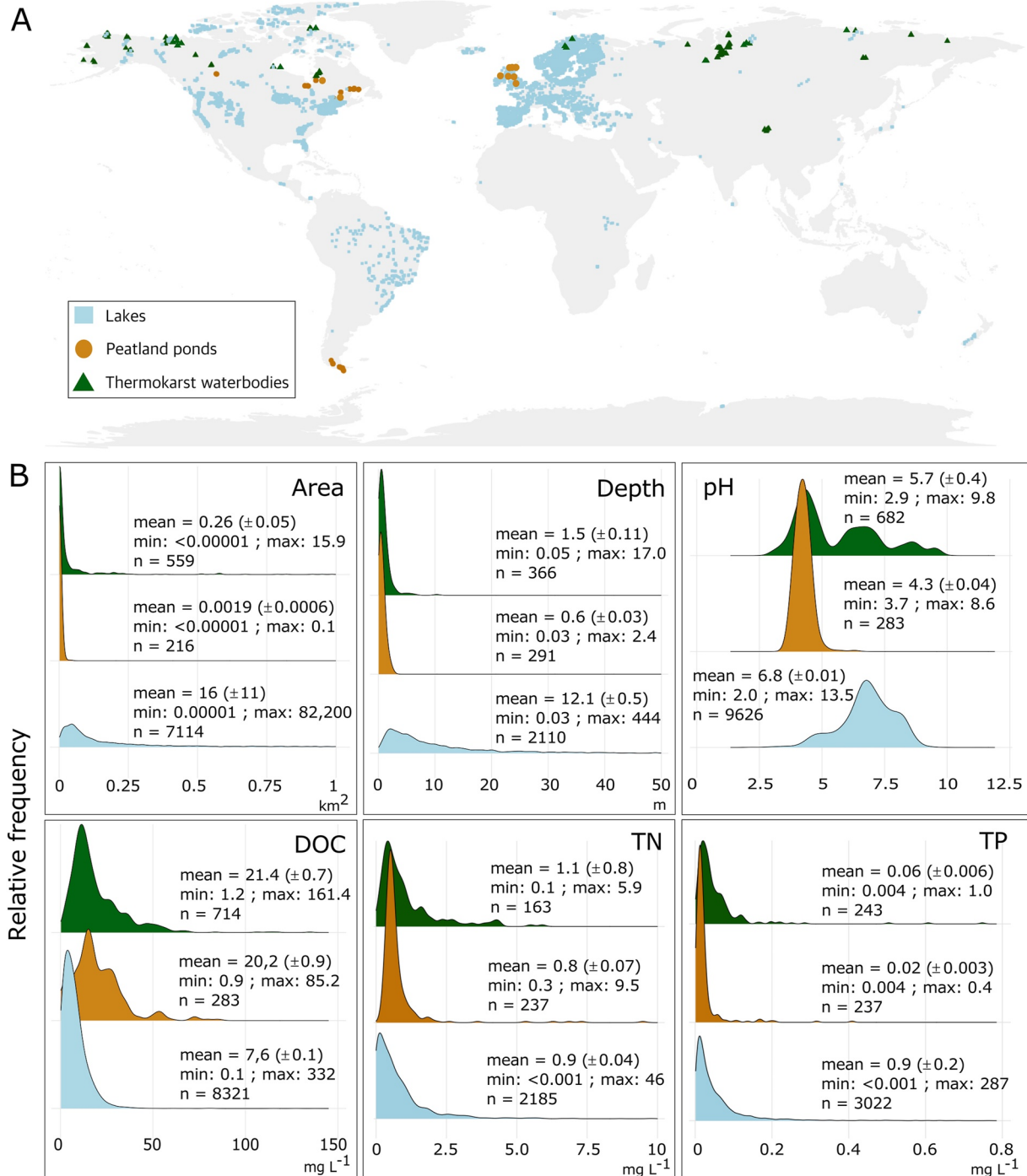
Figure 1. Biogeochemical properties of globally distributed peatland ponds, thermokarst waterbodies, and lakes. (a) Global distribution of freshwater ecosystems for which we gathered morphometrical and chemical data. (b) Relative frequency distributions, and mean (± standard error), minimum, and maximum values for area, depth, pH, dissolved organic carbon (DOC), total nitrogen (TN), and total phosphorus (TP) concentrations.

ponds). To avoid pseudoreplication and double-counting issues, we excluded duplicates from our dataset based on matching coordinates. Where repeated datasets were available for a variable in a single waterbody, means were calculated and used to average sampling effects of covariates such as seasonality and/or sample collector effects.

2.2. Statistical Analysis

The categories (lakes, thermokarst waterbodies, and peatland ponds) we compared were broad representations and include systems found in relatively distinct environmental conditions. To compare the properties of freshwater ecosystems according to these groupings, we first ran general linear models (GLM) with biogeochemical variables as response variables and categories as predictors. However, to uncover in greater detail the environmental gradients associated with waterbody biogeochemistry and test the a priori classification, we used data-driven k-means analyses followed by principal component analyses, and a discriminant analysis. We also created a classification tree to determine the variables linked to each ecosystem's distinctiveness (see Text S3 in Supporting Information S1 for the detailed methodology).

3. Results and Discussion

3.1. The Biogeochemistry of Globally Distributed Peatland Ponds, Thermokarst Waterbodies, and Lakes

The dataset we assembled encompasses a total of 12,475 observations, ranging from small and shallow freshwater ecosystems located in agricultural settings, permafrost regions, and peatlands, to very large and deep lakes with watersheds spanning thousands of square kilometers (Figure 1). This mosaic of landscapes includes a highly diverse range of aquatic ecosystems, with large variations in dissolved C and nutrient concentrations. The small amount of available data from peatland ponds and thermokarst waterbodies compared to lakes results in imbalanced sample sizes but our results nonetheless highlight major differences among the systems in both morphometrical (area and depth) and chemical variables (DOC, pH, TN, and TP), especially when comparing lakes to peatland ponds (Figure 2).

The a priori classification of our dataset shows that area and depth, which are often used to define lakes and ponds, are typically lower in peatland ponds and thermokarst waterbodies than in lakes (GLM: $n = 7,678$; $P < 0.001$, and $n = 2,563$; $P < 0.001$, respectively, Figure 1b, Table S1 in Supporting Information S1). There may be a bias for data availability toward large versus small lakes (Stanley et al., 2019), as we report that 50% of lakes are >0.32 km^2 (Figure 1b). This differs from remote-sensing studies that estimated that 96% of the world's lakes are <0.1 km^2 (Cael et al., 2017; Verpoorter et al., 2014), but it is unclear whether or not small peatland ponds and thermokarst waterbodies are included as lakes in these analyses. Regardless, peatland ponds in our dataset never exceeded 0.1 km^2 and 66% of thermokarst waterbodies were <0.01 km^2, suggesting that there is a true difference in the mean and upper limit for area and depth for peatland ponds compared to lakes, and that thermokarst waterbodies cover a range that encompasses both lakes and peatland ponds, while being skewed toward smaller values. Lake depth and area are limited by the geomorphology of the landscape and the mass water balance of the system. Peatland ponds and thermokarst waterbodies are dynamic systems that expand and contract over time, sometimes on a daily basis (Karofeld & Tõnisson, 2014), in relation to climatic, biological, and physicochemical factors. In contrast, most lake depths and areas are rather stable in time when the landscape is undisturbed by human activities (Downing, 2010; Wetzel, 2001). Peatland ponds and thermokarst waterbodies can shrink and disappear following drainage (Bouchard et al., 2020; Foster, Wright Jr., et al., 1988), terrestrialization through vegetation growth, peat accumulation (Payette et al., 2004), or increased evapotranspiration (Riordan et al., 2006). These systems can, albeit rarely, reach thousands of square meters in extent for peatland ponds and several square kilometers for thermokarst systems as adjacent waterbodies may coalesce after bank erosion or soil organic matter (OM) decomposition (Bouchard et al., 2020; Foster & Fritz, 1987; Kokelj & Jorgenson, 2013), releasing millennial-old C in the process (Walter Anthony & Anthony, 2013). With permafrost regions and temperate wetlands being highly sensitive to global change, future trends in peatland pond and thermokarst waterbody coverage and their influence on global biogeochemistry are particularly uncertain.

There are very few data on the biogeochemistry of peatland ponds, and those that exist originate primarily from temperate peatlands characterized by an organic and acidic matrix. This results in higher DOC concentrations (GLM; $P < 0.001$) and lower water pH ($P < 0.001$) when compared to lakes (Figures 1b and 2, Table S1 in Supporting Information S1). In colder climates, many thermokarst waterbodies similarly develop in OM-rich soils, coherent with the higher DOC concentrations ($P < 0.001$) and lower pH ($P < 0.001$) than lakes (Figures 1b and 2). In these peatland ponds and thermokarst waterbodies, the extensive interface between the oxygenated and DOC-concentrated water, and the anoxic character of the surrounding organic soil, creates ideal conditions for high biogeochemical activity. This sustains both elevated C emissions (peatland ponds, range = 20–103 g
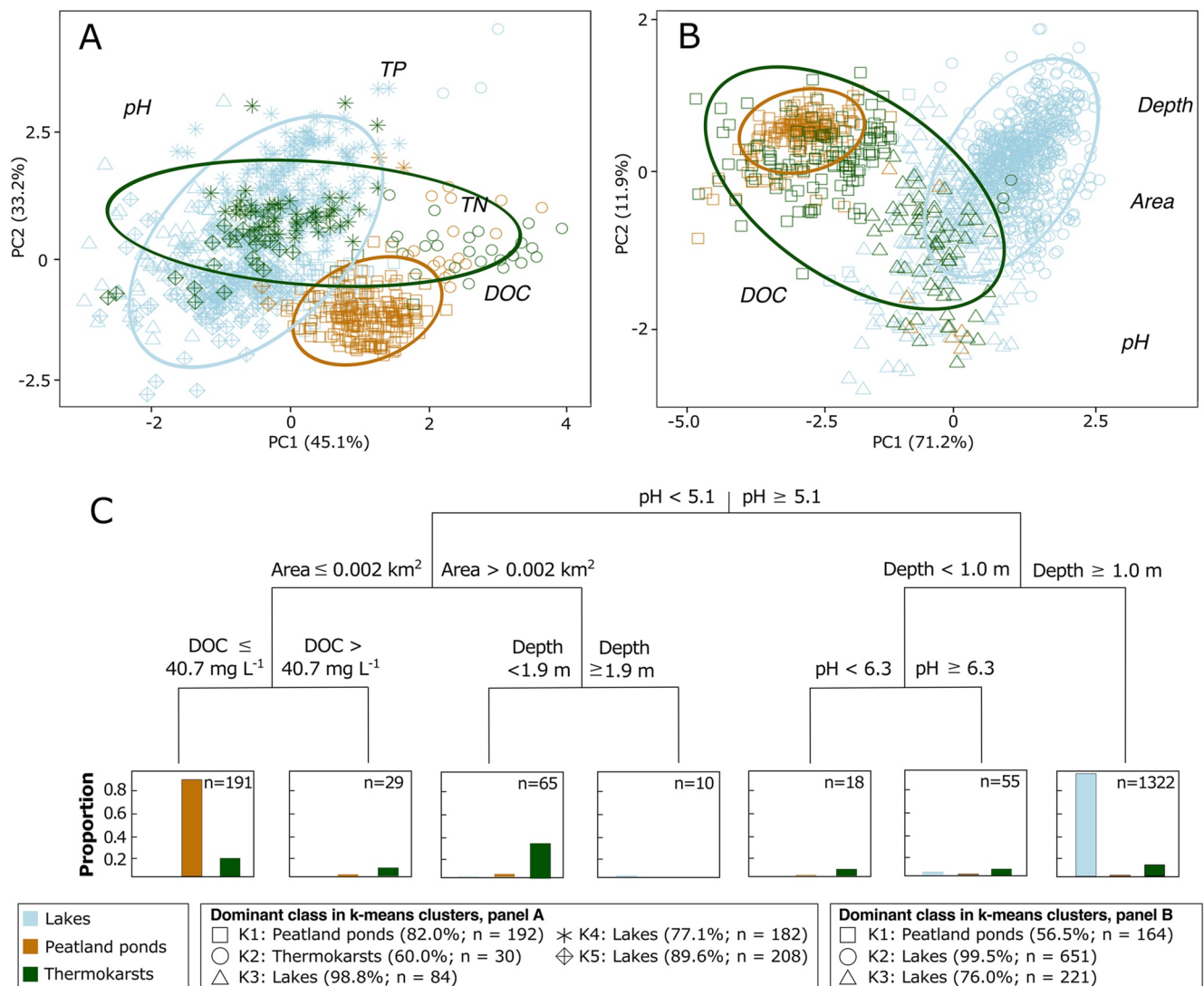
Figure 2. The distinctiveness of peatland ponds, thermokarst waterbodies, and lakes is highlighted when comparing their different morphometric and biogeochemical properties. Principal component analysis of (a) water chemistry focusing on sites for which pH, dissolved organic carbon (DOC), total phosphorus (TP), and total nitrogen (TN) concentrations were available ($n = 837$), and (b) small waterbodies of less than 0.1 km² for which data for morphometric properties and DOC and pH were available ($n = 1,235$). Color code represents a priori classification mentioned in previous studies, whereas shape of the signs corresponds to k-means clusters (see Tables S2 and S3 in Supporting Information S1 for details). (c) Classification tree showing the distinction between lake and peatland pond biogeochemistry, and the ambivalent behavior of thermokarst waterbodies ($n = 1,690$, including 1,347 lakes, 166 peatland ponds, and 177 thermokarst waterbodies). Leaves of terminal nodes show the number of categorized waterbodies ($n=$) and the proportion of the systems predicted.

C m⁻² yr⁻¹; thermokarst waterbodies, range = 219–1934 g C m⁻² yr⁻¹), and nutrient release from decomposition processes as previously documented (McEnroe et al., 2009; Pelletier et al., 2014; Sepulveda-Jauregui et al., 2015; Serikova et al., 2019).

A large quantity of nutrients is processed within lakes where light penetration and water temperature influence their biogeochemical cycling (Cory & Kling, 2018; Maranger et al., 2018). However, generally lakes receive most of their nutrients from their watershed and nutrient concentrations are therefore not only linked to within-lake biogeochemical cycling but also to patterns and processes occurring upstream and in the surrounding land-scape. Large variations in lake-landscape contexts in our dataset could thus explain the high range of observed nutrient data in lakes (Figure 1b) (Soranno et al., 2009). Indeed, lakes drain much larger catchments, sometimes perturbed by human activity, from which they receive OM and nutrients (Walter et al., 2020). On the other hand, nutrient concentrations vary less in peatland ponds and in thermokarst waterbodies presumably because of their

development in smaller, and likely more homogeneous landscapes, and with much lower freshwater volumes (Arsenault et al., 2019; Holden et al., 2018; Kokelj & Jorgenson, 2013) compared to lakes.

3.2. Distinguishing Freshwater Ecosystem Types

Peatland ponds and thermokarst waterbodies for which data were available had relatively narrower geographical contexts (Figure 1a) compared to lakes. It is unclear how the available data represent the true distribution of peatland ponds as we were unable to find datasets from tropical areas and large portions of temperate regions. By definition thermokarst waterbodies will naturally be found in cold climates with little human land use. Nonetheless, despite these major differences in geographic coverage, there were no clear differences between the biogeochemical properties of thermokarst waterbodies and lakes and peatland ponds, but appreciable distinction emerged between lakes and peatland ponds (Figure 2).

By aggregating the systems solely according to their biogeochemistry, the k-means clustering highlights the contrasting characteristics of peatland ponds, thermokarst waterbodies, and lakes (Table S2 in Supporting Information S1). It emphasizes how ecosystems a priori identified as lakes are scattered among four of the five clusters, with a wide range of biogeochemical properties, whereas ecosystems a priori identified as peatland ponds are mostly clustered in a fifth cluster (squares in Figure 2a). Ecosystems a priori classified as thermokarst waterbodies were mostly found among lake-like clusters, with 69% of the systems ($n = 74$) found in two clusters dominated largely by lakes ($n = 390$, 76% of lakes) rather than by peatland ponds ($n = 4$, 2% of peatland ponds). This shows the similarity of thermokarst waterbodies to lake biogeochemistry, meaning that they tend to have similar concentrations, but also combinations of DOC, TN, TP, and pH. The ordination of the k-means in a reduced space further supports the differences and similarities between the freshwater ecosystems (Figure 2a). The observed pattern also holds when comparing freshwater ecosystems of all area and depth: peatland ponds and lakes form distinct types of ecosystems, clearly differentiated by their pH, while thermokarst waterbodies have multiple combinations of physical and chemical characteristics (Figure 2c).

Overall, lakes and peatland ponds thus behave as two divergent freshwater ecosystems with very little overlap in terms of the combination of their morphometric and chemical properties (Figure 2). This apparent pattern is supported by a discriminant analysis model that correctly predicts 94.2% ($n = 340$) of lakes and 95.3% ($n = 142$) of peatland ponds but fails to correctly identify 66.6% ($n = 50$) of the thermokarst waterbodies (Table S4 in Supporting Information S1). In fact, most of the thermokarst waterbodies (65.3%; $n = 49$) were predicted as lakes. This suggests that systems that have been identified as thermokarst waterbodies may not represent a homogenous group with a distinct combination of biogeochemical properties, but rather behave either as a peatland pond, a lake, or as a combination of both (Figure 2). Although many lakes and ponds of the permafrost regions are considered thermokarst waterbodies because of the mechanisms leading to their formation, it is well known that these systems develop in a wide variety of matrices that influence their biogeochemistry (e.g., Elder et al., 2018; Sepulveda-Jauregui et al., 2015). This is supported by their bimodal distribution for pH, as well as the multiple shoulders in nutrients and DOC concentrations that align well with either lake or peatland pond distributions (Figure 1).

We suggest that the OM-rich setting in which peatland ponds develop represents the fundamental difference that positions typical lakes and peatland ponds at opposite ends of the biogeochemical gradients, and that the underlying matrix for thermokarst waterbodies determine whether they behave as a lake or a peatland pond. For example, many thermokarst waterbodies primarily form in OM-rich permafrost, showing increasing pH with developmental stages (Peura et al., 2020), but decreasing pH with latitude because of the reduced peat thickness in higher latitudes from which to receive acidic OM (Pokrovsky et al., 2014). Thermokarst waterbodies may also form in mineral-rich soils and yedoma and have neutral to alkaline pH (Calmels et al., 2008; Rautio et al., 2011; Sepulveda-Jauregui et al., 2015) (Figure 1b), leading to large spatial variations in chemical and biological characteristics of these freshwater ecosystems (Rautio et al., 2011; Vonk et al., 2015). Like thermokarst waterbodies, previous studies have reported waterbodies in peatlands with different levels of transparency and pH close to neutral (Quenta et al., 2016). These were however typically found over very shallow peat deposits (<40 cm) of mountainous regions and had inorganic bed material, contrary to most other peatland ponds, supporting the idea that within the broad categories defined here, there is an array of possible conditions controlling pond biogeochemistry that are ultimately linked to the surrounding matrix and developmental mechanisms.

3.3. The Distinct Biogeochemistry of Peatland Ponds: More Than Small Lakes

Both a priori and data-driven classifications showed that peatland ponds and thermokarst waterbodies were typically smaller and shallower than lakes (Figures 1b and 2). It is well known that larger lakes tend to have lower concentrations of elements because of higher retention times and smaller interfaces with C- and nutrient-rich sediments and soils (Downing, 2010; Holgerson & Raymond, 2016). If peatland ponds and thermokarst waterbodies behaved as small lakes, it could be possible to make global predictions for these systems based on widely available lake data. If, on the other hand, they display a distinct biogeochemistry, then knowledge and scaling relationships derived from lakes cannot be transposed to predict the role of peatland ponds and thermokarst waterbodies in global biogeochemical cycles.

Even when comparing only freshwater ecosystems of small extent (<0.1 km²), our results suggest that peatland ponds do not function simply as small lakes (Figure 2b, Table S3 in Supporting Information S1). The intermediate and more variable patterns for the population of thermokarst waterbodies (Figures 1 and 2) also hold even when considering size- or depth-specific patterns (Figure 3), likely because this category of aquatic ecosystems includes systems developing in both mineral- and OM-rich matrices. In particular, our results demonstrate that peatland ponds and thermokarst waterbodies are ecosystems that are more connected to their surroundings than
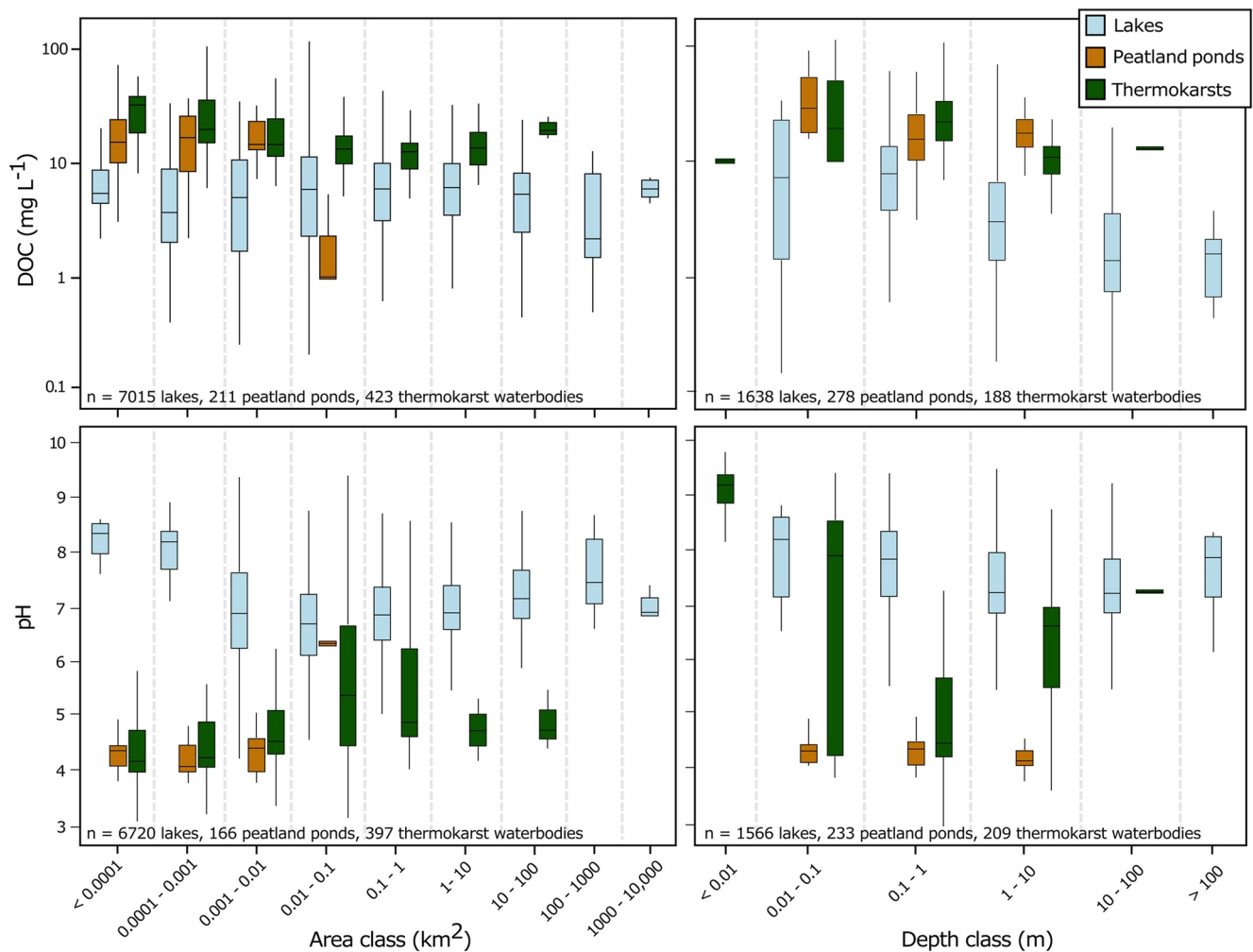
Figure 3. Distribution of dissolved organic carbon (DOC) concentration and pH in relation to area and depth for peatland ponds, thermokarst waterbodies, and lakes. Generalized linear models show that variations in DOC concentrations are only related to freshwater system type, and not to area or depth (GLM, $P > 0.1$; Table S4 in Supporting Information S1). Interactions between the type of system and area may, however, explain variations in pH between lakes, peatland ponds, and thermokarst waterbodies (GLM, $P < 0.05$; Table S4 in Supporting Information S1). Boxes show the median and the 25th and 75th percentiles of the distributions, and whiskers show the 10th and 90th percentiles.

lakes, with the DOC available for biological and photochemical reactions being on average more than twice higher than for lakes, as well as a pH that can be as much as four orders of magnitude more acid, especially for the smaller peatland ponds and thermokarst waterbodies (Figure 3). Moreover, TN and TP concentrations in peatland ponds (GLM; TN: $P = 0.381$, and TP: $P = 0.135$; Table S1 in Supporting Information S1) and thermokarst waterbodies (GLM; TN: $P = 0.206$, and TP: $P = 0.145$; Table S1 in Supporting Information S1) are comparable to those observed in lakes, although lakes drain much larger watersheds from which to receive nutrients (Arsenault et al., 2019; Kokelj & Jorgenson, 2013; Walter et al., 2020). Then, if TN and TP concentrations in freshwater ecosystems were to be compared in terms of units of drained area, nutrient concentrations would be much higher in peatland ponds and thermokarst waterbodies than in lakes, highlighting the distinctiveness of such systems.

Globally, lentic ecosystems emit 1.25–2.3 Pg C yr^{-1}, most of which likely originates from small freshwater systems (DelSontro et al., 2018). Most estimates of greenhouse gas emissions from limnological systems are based on the size of the systems and their C content (Bastviken et al., 2011; DelSontro et al., 2018; Raymond et al., 2013), and little attention has been given to the distinctive nature of a large portion of the world's small freshwater systems apart from those located in the boreal-arctic region (e.g., Kuhn, Varner, et al., 2021; Matthews et al., 2020; Wik et al., 2016). Here, we have shown that peatland ponds and, to a lesser extent, thermokarst waterbodies, that account for a substantial proportion of small waterbodies worldwide, have distinct combinations of morphometric and chemical properties that are not observed in lakes. While lakes receive most of their OM and nutrients from their watersheds, peatland pond biogeochemistry is mostly influenced by internal cycling and exchanges with the surrounding peat (Figure 4) (Arsenault et al., 2018, 2019). For thermokarst waterbodies developing in OM- or mineral-rich permafrost, the surrounding matrix influences their biogeochemistry but lateral exchanges are not as important as in peatland ponds because of the frozen soil that reduces permeability (Figure 4) (Vonk et al., 2019). However, with permafrost regions experiencing warming temperatures, the relative contribution of the surrounding thawing soils to thermokarst waterbody OM and nutrient loading is expected to increase in the future (Pokrovsky et al., 2013), perhaps making peatland ponds better models than lakes for predicting future evolution of these waterbodies.

Deepening our knowledge of the biogeochemistry of peatland ponds, especially in lower latitudes where data are particularly scarce, and of thermokarst waterbodies will improve prediction of the fate of climate-sensitive wetland and permafrost regions dominated by unique freshwater systems. Because of their distinct functional relationships with their surroundings, it is likely that peatland ponds and lakes will respond differently to climate forcing. Our results suggest that predictive relationships developed for lakes would not translate well to peatland
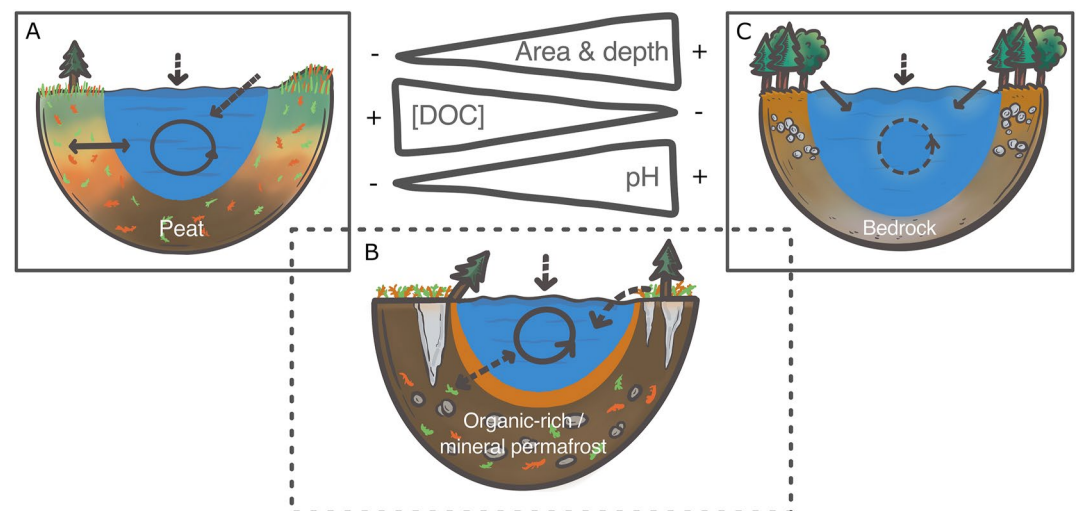
Figure 4. Relative contribution of landscape, internal cycling, and atmospheric inputs to organic matter (OM) and nutrient sources to (a) peatland pond, (b) thermokarst waterbody, and (c) lake biogeochemistry. Area, depth, and pH are lower and dissolved organic carbon (DOC) is higher in peatland ponds than in lakes, but thermokarst waterbodies show mixed biogeochemical patterns combining morphological and chemical characters of both lakes and peatland ponds, depending on the surrounding soil characteristics. We explain the distinct biogeochemistry of these freshwater systems by the different settings in which they develop, influencing the relative contribution of OM and nutrient sources.

ponds and most thermokarst waterbodies. This warrants the development of distinct scaling relationships for the integration of freshwater ecosystems in the next generation of land-surface components of earth system models. It also highlights the critical need for more data on peatland ponds and thermokarst waterbodies to feed such models.

Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

Data Availability Statement

The data used in this study and the list of articles from which we built the dataset are available on Zenodo at http://www.doi.org/10.5281/zenodo.5619484. The list of references is also available in Supplementary information Text S1 and S2.

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