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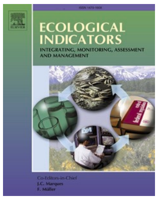

Indicator species reveal the physical and biological singularity of esker ecosystems

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ABSTRACT

Eskers are complex geological formations shaped with a linear accumulation of sand and gravel under the glaciers during the last ice age and that provide crucial resources such as drinking water, sand/gravel, outdoor recreational sites, and productive forests. Surrounding sand and gravel and connection with the groundwater influences the physicochemical properties of lakes on esker which can benefit different biotic communities in the food web. The sustainable management of resources provided by eskers requires baseline ecological knowledge of these ecosystems. However, very little information exists about the ecology of freshwater ecosystems on eskers. This study uses a food web approach to identify the environmental variables, biological diversity, and indicator species associated with esker lakes to better understand their ecological functioning and biodiversity patterns to benefit their sustainable management and conservation. Fifty lakes were sampled in the Abitibi-Témiscamingue region (Canada), half on eskers and half on the surrounding boreal clay belt to include the most abundant lake ecosystems of the region. Physicochemical, environmental, and anthropogenic variables measured in the two lake types showed that esker lakes differed markedly from clay lakes. Nutrient concentrations, conductivity, and macrophyte cover were significantly lower in esker lakes than in clay lakes, whereas dissolved oxygen saturation and concentration showed the opposite trend. Three interconnected trophic levels of the esker lake food webs—waterbird, fish, and macroinvertebrate communities—were characterized for biological diversity and the associated species. We found a significantly lower Shannon diversity index for waterbirds (mean ± standard deviation; 0.7 ± 0.2), fish (0.4 ± 0.3), and a tendency for a lower value for macroinvertebrates (0.9 ± 0.3) in esker lakes than the clay lakes (1.1 ± 0.4, 0.9 ± 0.3, and 1.3 ± 0.5, respectively). Common goldeneye (*Bucephala clangula*) and Canada goose (*Bucephala clangula*) were associated significantly with esker lakes and identified as indicator species for esker lakes. In contrast, ring-necked duck (*Aythya collaris*) and hooded merganser (*Lophodytes cucullatus*) were associated significantly with clay lakes. Perlidae was similarly associated with esker lakes as an indicator for macroinvertebrates. Anthropogenic activities such as forest harvesting have altered the waterbird community, and recreational activities around the lakes have modified the fish and macroinvertebrate communities. We conclude that esker lakes differ from other regional lakes and are associated with specific environmental and biological variables and indicator species. The biological diversity in esker lakes is lower than that of clay lakes for all studied trophic levels of the food web, but these waterbodies provide preferential habitats for some species. This research provides the first baseline ecological information necessary to establish sustainable management and conservation strategies for this vulnerable ecosystem.

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1. Introduction

With 60% of Earth's total freshwater lakes and approximately 2 million lakes, Canada contains the most abundant and diverse pool of freshwater ecosystems in the world (Messager et al., 2016; Monk and Baird, 2014). Lakes provide many ecosystem services, including carbon storage, resources for use by humans, and habitats to support aquatic and terrestrial communities (Gurney et al., 2017). Canadian freshwater systems hold complex food webs that depend heavily on the excellent quality of these habitats (Slattery et al., 2011). However, Canadian freshwater habitats are impacted by anthropogenic activities such as forestry and mining (Bradford and Irvine, 2000; Chu et al., 2015; Maitland et al., 2016). Anthropogenic effects on Canadian freshwater systems include rising demands for fossil fuels, minerals, and forest products, resulting in the rapid alteration of the freshwater environment and aquatic biodiversity (Laurance and Balmford, 2013; Maitland, 1995). For example, forest harvesting around lakes can strongly affect the trophic interactions of the aquatic food web (Berger et al., 2013; Girona et al., 2023b). Consequently, freshwater vertebrate populations experienced an 84% decline between 1970 and 2014 and forest harvesting is one the leading cause behind this decline (Desforges et al., 2022).

Eskers are geological formations found in previously glaciated regions of northern countries and are composed of irregularly stratified sand and gravel deposited by subglacial streams at the margin of retreating glaciers (Bates and Jackson, 1987). Under the fan-like shape of eskers, an ancient groundwater riverbed is created (Bourgeois and Nadeau, 2013; Nadeau et al., 2011; Stroeven et al., 2016). Esker lakes are kettle lakes created by ice blocks left behind by retreating glaciers. Esker lakes can be connected to the groundwater aquifers, or they can be perched and therefore dependent only on precipitation (Kløve et al., 2011). Connection with groundwater influences the physicochemical properties of these lakes and lowers the lake's water temperature (Ala-aho et al., 2013; Winter et al., 1998). Sand and gravel from eskers reduce surface runoff to esker lakes; therefore, these lakes obtain limited amounts of nutrients from the surrounding forest ecosystem (Ala-aho et al., 2013). Moreover, these lakes have transparent waters and higher dissolved oxygen concentrations to provide high-quality habitats for aquatic biodiversity (Kløve et al., 2011; Winter et al., 1998). Esker lakes and surrounding habitats provide crucial resources such as drinking water, wildlife habitat, sand and gravel for construction, and productive forest timber, and they support extensive recreational activities (Nadeau et al., 2011). The overexploitation of resources such as sand, gravel, and timber impacts natural ecosystems, including the removal of vegetation and soil, increased risks of pollution associated with resource extraction, e.g., oil from heavy equipment, and alteration of natural slopes (Hatva, 1994; Nadeau et al., 2015; Smerdon et al., 2012). A multi-resource management approach is needed to reduce land-use conflicts and achieve the sustainable management of natural resources to preserve biological diversity. Understanding the biological diversity of esker lakes and the impact of anthropic activities on these systems is crucial, where balancing ecological and economic resources remains a major challenge (Nadeau et al., 2015).

An improved understanding of the ecological functioning and biodiversity patterns of esker-associated ecosystems is urgent because, to date, there has been no assessment of the biodiversity of esker ecosystems in Canada. This information is needed to establish conservation strategies and manage the ecosystem sustainably. Understanding biodiversity patterns and the faunal relationships with habitat is complex because abiotic and biotic factors affect the food web differently. Abiotic factors, including climate change and the physicochemical properties of aquatic ecosystems, can alter habitats and the distribution of communities (Meier et al., 2010). Physicochemical parameters of the aquatic ecosystem, such as water clarity, water temperature, and dissolved oxygen concentrations, can affect aquatic food webs (Pöysä and Virtanen, 1994). A more transparent water column enables deeper light penetration (i.e., as observed in esker waters) and promotes a greater abundance of algal food resources for invertebrate communities (Jeppesen et al., 1998). In groundwater-dependent ecosystems such as esker lakes, relatively colder groundwater recharge is responsible for higher dissolved oxygen concentrations in the lakes, which improves the habitat for some invertebrate species (Croijmans et al., 2021). Macroinvertebrates having gills or underwater respiratory mechanisms depend directly on the dissolved oxygen concentration in the water (Justus et al., 2014; Rautio and Korkka-Niemi, 2011; Verberk et al., 2016). Other physicochemical parameters, such as nutrients and dissolved organic carbon (DOC), can also determine macroinvertebrate and fish communities because nutrients, e.g., dissolved phosphorus and nitrogen, directly influence primary production. Additionally, DOC also plays a key role in controlling water transparency and light penetration in a lake's water column, which affects the abundance and distribution of primary producers (Jia et al., 2021; Pilière et al., 2014; Wang et al., 2008). Besides abiotic factors, anthropogenic activities such as forest harvesting affect the aquatic environment by decreasing water clarity and increasing water temperature, organic matter, and nutrient concentrations (Palviainen et al., 2022; Smith et al., 2003; Steedman and Kushneriuk, 2000).

Biotic factors also directly impact esker lake food webs (Gilliam and Fraser, 2001). Macrophytes compete with other primary producers, such as phytoplankton and benthic algae, although these plants serve as habitats for macroinvertebrate communities (Burks et al., 2002; Duggan et al., 2001; Schad et al., 2020). However, because of lower nutrient concentrations, macrophyte communities are less abundant in esker lakes than in surrounding lakes. Introducing fish into lakes significantly impacts aquatic ecosystems, especially those of esker lakes (Epanchin et al., 2010). These lakes typically do not have fish because of the lakes' higher elevations and a lack of connection to current river systems (Bourgeois and Nadeau, 2013). Introduced and invasive fish species markedly alter the aquatic food web and biotic interactions between waterbirds and macroinvertebrate communities (Pinel-Alloul et al., 2022). Therefore, biotic, abiotic, and anthropogenic factors combine to determine the structure and functioning of an aquatic ecosystem, and understanding their respective roles is critical for explaining biodiversity patterns.

Food web approaches contribute to understanding biodiversity patterns because they identify the importance of interactions between taxa (Englund et al., 1992; Grosbois et al., 2020, 2022; Levins, 1979; Safina and Burger, 1985). Competition and predation relationships drive interactions between waterfowl, fish, and invertebrates (Kloskowski et al., 2010). Aquatic benthic macroinvertebrates play a vital role in the aquatic food web of small lakes because they provide essential nutrients (e.g., proteins, lipids, and energy) for higher trophic levels such as waterbird and fish (Batzer et al., 1999; Mitsch and Gosselink, 2000; Williams, 2007). Macroinvertebrates thrive in lakes with lower fish predation; the abundance of macroinvertebrates eventually benefits waterbird that prefer invertebrates and a reduced competition with fish (Eadie and Keast, 1982; Eriksson, 1979; Hurlbert et al., 1986; van Eerden et al., 1993). In contrast, piscivorous waterbirds benefit from lakes having larger fish populations (Lammens, 1999). Habitat selection for waterbird is crucial for their survival as it determines their feeding resources and competition with other species. However, little is known about such interactions in esker lakes, for which the dominant biotic factors and diversity patterns remain unknown (Canterbury et al., 2000).

Here we use a food web approach to evaluate the environmental variables, biological diversity, and indicator species associated with esker lakes. To our knowledge, no studies have evaluated the aquatic biodiversity and ecosystem functioning of lakes associated with eskers despite their importance from an economic and conservation perspective (Nadeau et al., 2015). Furthermore, along with baseline ecological information, identifying biological indicators for the ecosystem is also an essential element for biodiversity conservation. We hypothesize that esker lakes provide high-quality habitats for benthic macroinvertebrates because of the lakes' high dissolved oxygen concentrations, sandy and gravel substrates, and high benthic primary production. We also hypothesize that rich macroinvertebrate communities in these lakes support waterbird communities because of the higher availability of food resources. Finally, we predict that indicator species requiring a high-quality environment will be more abundant in esker lakes than in the other regional lakes. This study aims to provide baseline information about the biodiversity of esker lakes in Canada.

2. Materials and methods

2.1. Study area

The study was conducted in the Abitibi regional county municipality, Québec, Canada. This region, situated in the fir–white birch forest bioclimatic domain (Blouin and Berger, 2002), covers 64,878 km^2 and contains>20,000 boreal and esker lakes (Beaulne et al., 2012). The cold and humid continental climate is characterized by a mean annual temperature of 2.5 °C and an average annual precipitation varying from 800 to 900 mm (Blouin and Berger, 2002; Rey et al., 2018). The regional surficial geology is heterogeneous because of eskers and glaciolacustrine deposits from proglacial lake Ojibway–Barlow and the clay deposits covering most of the region territory related to Lake Ojibway–Barlow (Veillette, 1988). Jack pine (*Pinus banksiana*) forests are generally found on well-drained sandy soil sites of the regional eskers and moraines. In contrast, black spruce (*Picea mariana*), aspen (*Populus tremuloides*), and white birch (*Betula papyrifera*) stands are the predominant forests across the clay plains. Forest harvesting practices have removed 20% of the regional forest over the last 20 years from this region's esker ecosystems and clay plains (Molina et al., 2022). Moreover, part of the land is cultivated mainly to feed cattle, and farmland for fodder production accounts for a high proportion of the cultivated area. Large-scale sand and gravel extraction from esker sites are another major anthropogenic disturbance in this region (Nadeau et al., 2011).

During the last glacial period, the Wisconsinan in North America, the Laurentide ice sheet covered most of Canada east of the Rocky Mountains. Ice advances/retreats and subglacial streams produced respectively 20,186 large eskers and moraines (>2 km in length) (Fig. 1a) (Dyke and Prest, 1987; Storrar et al., 2013). Six eskers and moraines are found in the Abitibi regional county municipality. In terms of hydrological characteristics, the regional moraines are similar to the eskers; therefore, we referred to both as *eskers* in this study (Nadeau et al., 2011). We selected three large eskers and moraines: the Saint-Mathieu-Berry esker, the Launay esker, and the Harricana moraine (Bourgeois and Nadeau, 2013). The Saint-Mathieu-Berry esker covers 100 km^2 and runs over approximately 76 km. It provides groundwater for 20,000 inhabitants and supplies a commercial water bottling company (Nadeau et al., 2015; Statistics Canada, 2018).

2.2. Experimental design

Preliminary site selection was carried out in the summer of 2020, and we relied on three criteria: lake size (0.3–20 ha), substrate (clay/sand-gravel), and accessibility. We selected lakes smaller than 4 ha after ground-truthing to conduct an effective waterbird survey and to cover the entire lake surface. We used satellite imagery from the Quebec government's "Forêt ouverte" and regional geological maps from the groundwater research group (GRES) of the University of Québec in Abitibi-Témiscamingue to carry out a preliminary selection of 80 lakes. After ground-truthing, we selected 50 lakes (25 lakes in the clay belt and 25 kettle lakes on eskers or moraines (Fig. 2). All selected lakes were at least 1 km apart to limit potential with the same waterbird individuals (Desjardins et al., 2021).

2.3. Characterization of the aquatic food web and habitat

We used a quadrat (1 m^2) to characterize the physical and biophysical environments for macroinvertebrates. Five quadrats were sampled along the shore systematically every 2 m along a 10 m transect to measure the cover percentage of sand, sediments, macrophytes, benthic algae, and wood debris. We used a multi-parameter probe (RBR Concerto, Ottawa, Canada) to measure the dissolved oxygen saturation (%) and pH. To estimate dissolved elements, including dissolved organic carbon (DOC), total dissolved phosphorus (TDP), and total dissolved nitrogen (TDN), we filtered a 1 L water sample using a 0.7 μm glass fiber filter. Samples were collected at a shallow depth about 2 m from the shore (Cytiva, Marlborough, USA). Before preserving the filtrated water for TDN and TDP, each vial was treated in a 10% HCl bath for 24 h. The nutrient vials were then dried in an oven at 200 °C for 4 h. For DOC analyses, each vial was kept in the oven at 450 °C for 4 h to remove any potential trace of carbon. The samples were sent to the Groupe de

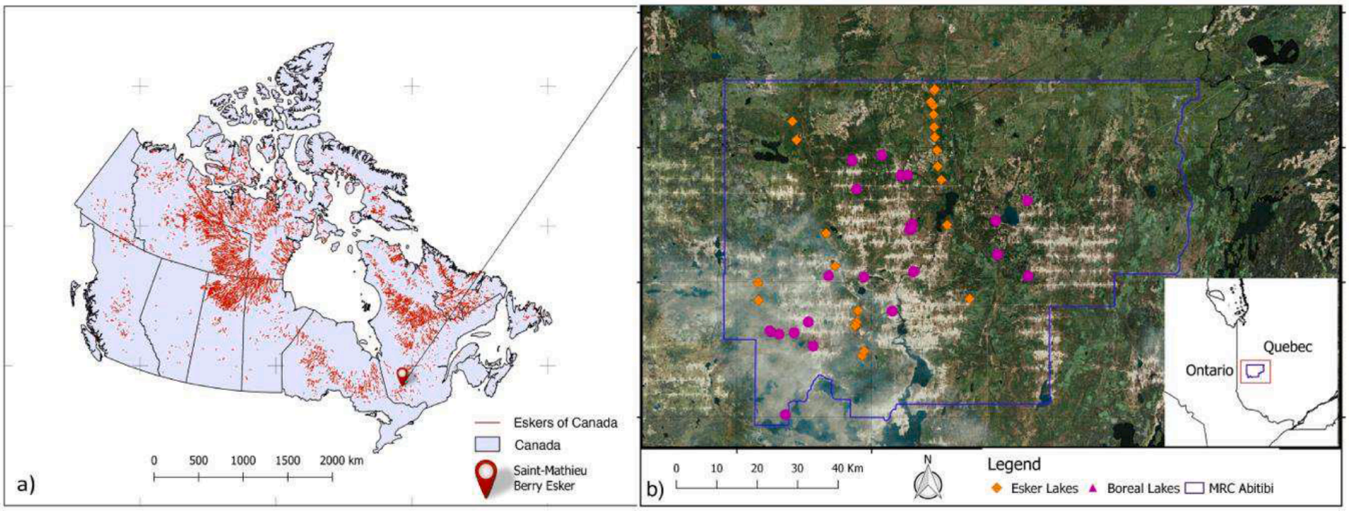


Fig. 1. (a) Distribution of eskers in Canada and the study area location. Adapted from Storrar et al. (2013); (b) study sites located in the Abitibi regional county municipality, Quebec, Canada.

Fig. 2. Two types of study lakes: a) esker lake with a jack pine stand and b) a lake on the boreal surrounding clay belt with emergent macrophytes in a marsh habitat with black spruce, aspen, and white birch in the surrounding forest.

Recherche Interuniversitaire en Limnologie (GRIL) laboratory of the University of Québec in Montreal to measure nutrient and carbon concentrations (Wetzel and Likens, 2000).

We estimated the linear distance to all large-scale clear-cut harvesting activity within 1000 m of the study lakes using the measuring tool of Google Earth Pro version 7.3.4 (imagery: CNES/Airbus, July 2021). We identified anthropogenic disturbances around the lake using visual observations. We also noted the presence and number of houses, including summer houses, semi-permanent recreational vehicles (in place for at least two weeks), and fishing cottages via visual observations

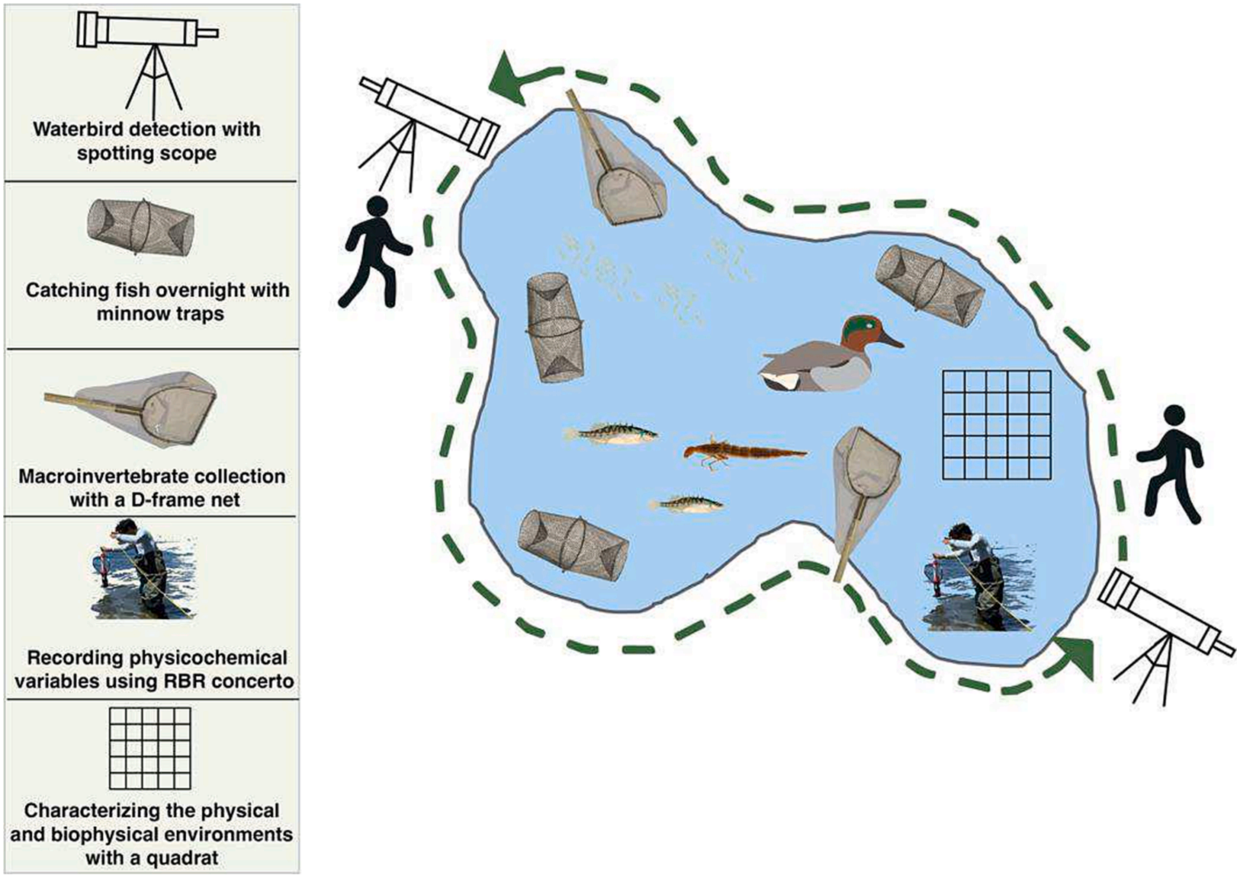


Fig. 3. Representation of 20 min of point counts and flush count paths for waterbird surveys, trap locations for fish surveys, D-frame net for macroinvertebrate surveys, and physicochemical measurements for habitat characterization.

and key informant interviews whenever applicable.

2.4. Biological data compilation

2.4.1. Waterbird surveys

We defined waterbird as birds primarily associated with lakes and species belonging to Anatidae, Phalacrocoracidae, Ardeidae, Podicipedae, Rallidae, and Recurvirostridae (Garrett-Walker et al., 2020). We counted waterbirds both male and female at each lake through fixed-point counts and perimeter searches (Desjardins et al., 2021). All the detected waterbirds from these two methods were recorded as the number of species and individuals present per lake. Two independent observers visited each lake twice over one month, from 24 May to 24 June 2021 (Fig. 3). The observers approached the lake as quietly as possible and positioned themselves on each side of the lake. The observers were camouflaged to limit the impact of their presence on the surrounding fauna. They counted and identified the individuals on the lakes for 20 min. The observers used binoculars (Nikon, Japan. 10 × 42 mm) and a spotting scope (Vortex, Middleton, USA. 20–60 × 80 mm) to identify each observed waterbird individuals. The inventories were carried out immediately after sunrise (05 *h*00–11 *h*00) when birds search for food on the lake surface (Bennett, 1967; Rumble and Flake, 1982).

2.4.2. Fish surveys

Three Gee-Feets G-40 minnow traps were set overnight in each lake between June and July 2021 (Fig. 3) to study fish species richness and abundance. These minnow traps were very effective for the fish communities feeding primarily on macroinvertebrates (McNicol and Wayland, 1992). We identified each fish from the minnow traps before releasing the fish, and we measured fork length, total length, and body weight for the first ten individuals from each taxon of each trap.

2.4.3. Macroinvertebrate surveys

At each lake, macroinvertebrate samples were collected between June and July 2020 to characterize the food resources of fish and waterbirds. They were collected at two randomly selected sites using a D-frame net (350 µm mesh, 305 × 254 mm) and following the kick and sweep method for 30 s at each site in the littoral zone (Gurney et al., 2017) (Fig. 3). We sampled two 0.1525 m^2 zones at each site. Each sample was preserved using a 90% ethanol solution. Macroinvertebrates were then sorted, counted, and identified in the laboratory. Each sample was mixed with water to prepare a 2 L solution. Each sample was replicated into two portions using the Huntsman Marine Laboratory (HML) beaker technique (van Guelpen et al., 1982). One portion of the sample was identified with a stereomicroscope (Discovery V.12, Zeiss, Oberkochen, Germany). The final counts of macroinvertebrates were adjusted depending on the portions that were sorted for each sample. Taxa were identified at the genus level for mollusk gastropods and insects and at the family level for other taxa. We used taxonomic manuals and keys, e.g., Thorp and Covich's key for freshwater invertebrates (Flannagan, 1979; Thorp and Rogers, 2015). We also calculated water quality index following Biological Monitoring Working Party (BMWP) average score per taxon (ASPT) scoring system (Armitage et al., 1983).

2.5. Statistical analysis

We categorized waterbirds, fish, and macroinvertebrate richness and abundance, defined as the number of species and individuals found per lake, after averaging observations from four visits for waterbirds, three traps for fish, and two replications for macroinvertebrates. All statistical analyses and calculations were performed using the statistical software R version 4.2.2 (R Development Core Team, 2016). The Shannon diversity index ($H = -\sum pi \log pi$, where pi is the proportion of individuals belonging to the *i*th species) and species evenness were calculated for each lake using the R package vegan with the function diversity and evenness (Oksanen et al., 2023). The data set for each variable was tested for normality and homoscedasticity when required by test assumptions. We used Welch's *t*-tests to compare the mean difference in richness, abundance, evenness, and diversity of biological communities and the differences between the physicochemical variables at the esker and clay lakes. To assess the differences in species associations between the esker and clay lakes, we used the *multipatt* function of R package indicspecies (de Cáceres and Legendre, 2009). Three separate species matrices were used to formulate multi-level pattern with 999 permutations to determine the indicator species for each lake type. To visualize the relationship between the diversity of waterbirds, fish, and macroinvertebrates with lake water quality and the biological characteristics of lakes, we performed a principal component analysis (PCA) combing variables from both type of lakes and two multiple factor analysis (MFA) for each lake types with the R package FactoMineR (Lê et al., 2008). Each variable was standardized and tested for collinearity among different variables with the principal components. Variables were divided into 5 groups for multiple factor analysis namely Fish, Macroinvertebrate, Waterbird, Abiotic factors, and Biotic Factors. To understand the influence of environmental and ecological variables on waterbirds, fish, and macroinvertebrate abundance and diversity, we used three community similarity matrices, one for each type of community. Permutational multivariate analysis of variance (PERMANOVA) was run using the adonis function from the R package vegan to test the effects of environmental and ecological variables on a community similarity matrix (Oksanen et al., 2023). The model included both the physicochemical characteristics of lakes (total dissolved nitrogen, total dissolved phosphorus, dissolved organic carbon, dissolved oxygen, lake perimeter, distance from harvesting, and sediment cover) and biological parameters (macrophyte cover, abundance and richness of waterbirds, fish, and macroinvertebrates) as fixed effects with 9999 permutations. As the explanatory variables used are continuous variables, PERMANOVA acts like linear regressions. Biological community compositions (matrix of species/taxon in column and abundance in each lake in rows) were used as response variable in the PERMANOVA analysis. All used variables were continuous except type of lakes that was categorical. We confirmed the effects of environmental and ecological variables on a community matrix with redundancy analysis (see supplementary material Table S3). We used three generalized linear mixed models using the R package lme4 with a Poisson distribution to validate the model estimates for the continuous variables. We tested the effects of environmental and ecological variables on biological communities using species (Supplementary Material 1) (Boeck et al., 2011). Finally, all data were plotted using the R package ggplot2 (Wilkinson, 2011).

3. Results

3.1. Physicochemical characteristics

All physicochemical parameters, except pH and dissolved oxygen, were significantly lower in esker lakes than in clay lakes. Total dissolved phosphorus ($t = 7.8$) and total dissolved nitrogen ($t = 8.3$) concentrations were significantly lower ($p < 0.001$) in the esker lakes. The mean concentrations of total dissolved phosphorus and nitrogen in esker lakes were respectively four and three times lower than in clay lakes (Fig. 4a, b). The mean dissolved organic carbon concentration in esker lakes (mean = 20.6 mg/L) was 44% lower than in clay lakes (mean = 36.5 mg/L, $p = 0.003$, Fig. 4c). The mean pH value was similar in both lake types ($t = 1.2$, $p = 0.2$) (Fig. 4d). The dissolved oxygen water saturation in the water was 16% higher ($t = -0.8$, $p < 0.001$) in esker lakes (96.1%) than in clay lakes (79.6%) (Fig. 5e). The mean percentage cover of macrophytes in clay lakes was 80% higher ($p = 0.008$, $t = 2.7$) than in esker lakes (24.3%) (Fig. 4f).

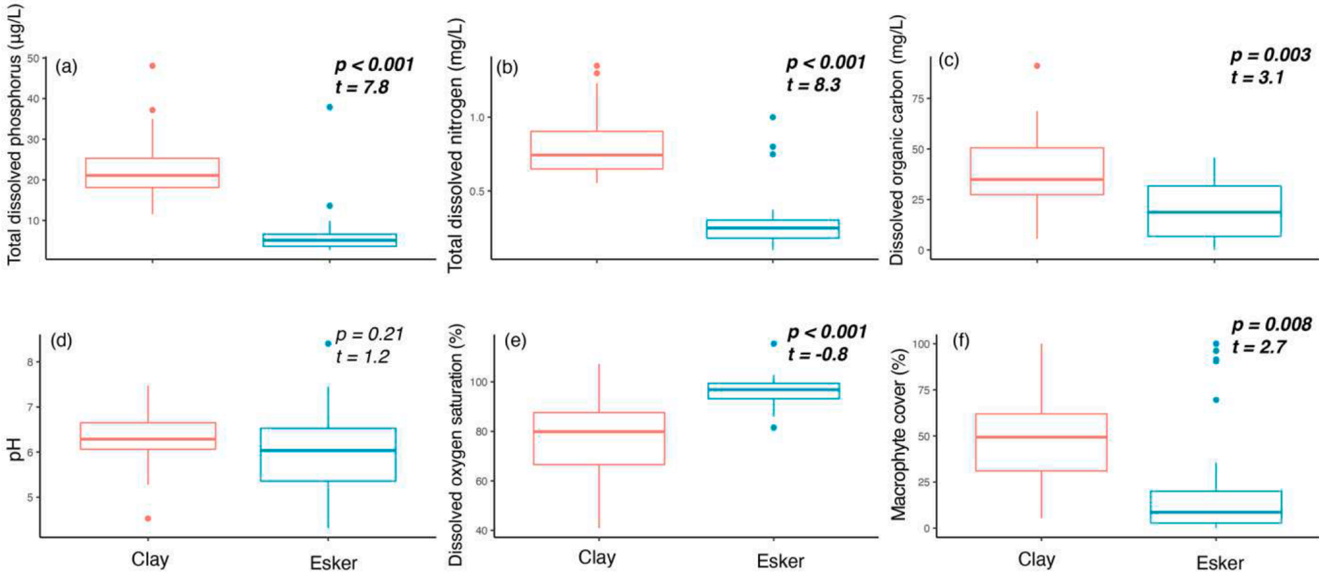


Fig. 4. Physicochemical and habitat-related variables measured in the esker and clay lakes.

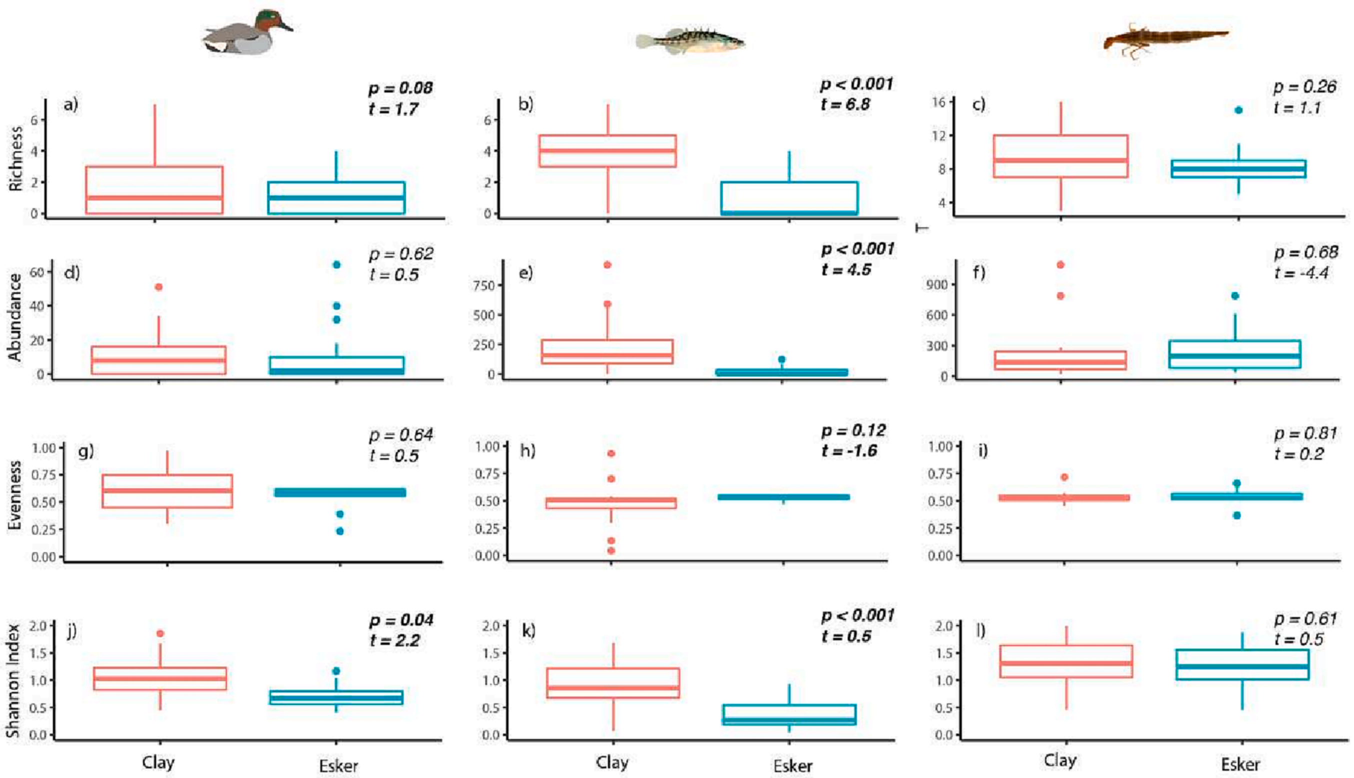


Fig. 5. Biodiversity indicators of waterbirds, fish, and macroinvertebrates in the esker and clay lakes. Here, richness is the total number of species or families per lake or net catch or sampled surface; abundance is the total number of individuals per lake or net catch or sampled surface; evenness is the distribution of abundance across the species community (scaled 0–1); diversity is the number of different species in the community.

3.2. *Species diversity and abundance*

3.2.1. *Waterbirds*

We recorded 634 individuals from 26 waterbird species for both lake types. Esker lakes had a total abundance of 288 with an average of 11.5 individuals per lake, and clay lakes had a total abundance of 346 with an average of 13.8 individuals per lake. Common goldeneye (*Bucephala clangula*) was the most abundant (average 2.2 individuals/lake) in esker lakes, and ring-necked duck (*Aythya collaris*) was most abundant (average 2.1 individuals/lake) in clay lakes. Additionally, we found a higher species richness in clay lakes (24) than in esker lakes (16) and a higher diversity index for waterbirds in clay lakes (mean ± standard deviation = 1.1 ± 0.4) relative to esker lakes (0.7 ± 0.2), although neither was statistically significant ($t_{\text{richness}} = 1.7$, $t_{\text{diversity}} = 2.2$, $p < 0.1$

for both; Fig. 5a, d, g, j).

3.2.2. Fish

Ten fish species and 5833 individuals were recorded from both lake types. Half (48%) of the esker lakes were fishless, and 4% of the clay lakes were fishless. The thirteen esker lakes with fish had a total abundance of 573 fish (mean of 44.1 individuals per lake), and the 24 clay lakes had a total abundance of 5260 (mean of 219.2 individuals per lake). Brook stickleback (*Culaea inconstans*) was the most abundant species (12 individuals/lake) in the esker lakes ($t = 2.1$, $p < 0.05$), and northern redbelly dace (*Chrosomus eos*) was the most abundant (100 individuals/lake) in the clay lakes. Additionally, the mean Shannon diversity index for fish in the clay lakes (0.9 ± 0.3) was significantly higher ($t = 0.5$, $p < 0.001$) than in the esker lakes (0.4 ± 0.3) (Fig. 5b, e, h, k).

3.2.3. Macroinvertebrates

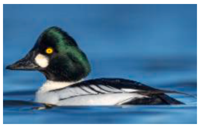
The mean abundance of macroinvertebrates was similar between the esker and clay lakes (156.4 and 164.2 individuals on average, respectively). Chironomidae (non-biting midges) was the most abundant family in both lakes. Amphipods were highly abundant in esker lakes, whereas Corixidae (water boatmen) were highly abundant in clay lakes. However, diversity was similar among lake types (mean Shannon Diversity index for esker lakes = 1.2 and for clay lakes = 1.3), and macroinvertebrate richness, abundance, evenness, and diversity did not differ significantly between the clay and esker lakes ($p > 0.1$; Fig. 5c, f, I, l). The water quality index calculated using individual scoring of each taxon tended to be higher ($p < 0.1$) in the esker lakes (mean = 8.3) than in the clay lakes (7.47).

3.2.4. Indicator taxa

Indicator species analyses were performed for the food web taxa at the species level for birds and fish and at the family level for invertebrates. For birds, we determined that Canada goose (*Branta canadensis*) and common goldeneye were significantly associated ($p < 0.05$) with esker lakes. In contrast, the ring-necked duck (*Aythya collaris*) and hooded merganser (*Lophodytes cucullatus*) were waterbird indicators for clay lakes. In the case of fish, yellow perch (*Perca flavescens*) was associated with the esker lakes, and northern redbelly dace (*Chrosomus eos*) and fathead minnow (*Pimephales promelas*) represented indicators for

Table 1

Indicator species strongly associated with esker and clay lakes in the Abitibi region, Quebec, Canada.

Category	Associated lake type	Common name	Species or family name	Abundance in clay lakes (Mean ± SD)	Abundance in esker lakes (Mean ± SD)	p-value	Pictures
Waterbirds	Esker	Canada goose	*Branta canadensis*	2 ± 0.11	53 ± 1.49	**0.031**	
		Common goldeneye	*Bucephala clangula*	22 ± 0.58	55 ± 1.27	**0.049**	
	Clay	Ring-necked duck	*Aythya collaris*	52 ± 0.64	14 ± 0.45	**0.020**	
		Hooded merganser	*Lophodytes cucullatus*	14 ± 0.27	0 ± 0	**0.021**	
Fish	Esker	Yellow perch	*Perca flavescens*	0 ± 0	38 ± 1.8	0.105	
	Clay	Northern redbelly dace	*Chrosomus eos*	2520 ± 59.6	79 ± 5.5	**0.001**	
		Fathead minnow	*Pimephales promelas*	1703 ± 37.1	4 ± 0	**0.001**	
Macroinvertebrates	Esker	Common stonefly	Perlidae	5 ± 0.1	60 ± 2.3	**0.003**	
		Spread-winged damselfly	Lestidae	2 ± 0.1	23 ± 0.8	**0.035**	
	Clay	Predaceous diving beetle	Dytiscidae	37 ± 1.4	4 ± 0.1	**0.009**	
		Giant water bug	Belostomatidae	14 ± 0.3	0 ± 0	**0.036**	

clay lake fish. For invertebrates, with an abundance of 60 individuals (mean ± SD = 6.7 ± 3.8) from nine esker lakes, the common stonefly (Perlidae) was strongly associated with esker lakes. Moreover, spread-winged damselfly (Lestidae) was also significantly associated with esker lakes. The predaceous diving beetle (Dytiscidae) and giant water bug (Belostomatidae) were macroinvertebrate indicators for the clay lakes (Table 1).

3.3. Factors influencing the biological communities

The first two axes of the PCA captured 31% of the variation in the biological and environmental variables, with 21% explained by axis 1 and 10% by axis 2 (Fig. 6A). The PCA illustrated that eskers and clay lakes differed in terms of their biological and physicochemical properties. Total phosphorus and total nitrogen contributed 19% and 17%, respectively, in explaining variability along the first axis Macrophyte cover and waterbird richness contributed 14% and 13%, respectively, to the variability along axis 2. Among the biological variables, fish richness, waterbird richness, and fish abundance contributed 14%, 11%, and 9%, respectively. The PCA also highlighted the positive correlation of macrophyte cover, pH, and macroinvertebrate richness with waterbird richness and abundance. Additionally, there was a strong positive correlation of pH and nutrients (total phosphorus, total nitrogen, and dissolved organic carbon) with fish richness and abundance. Both lake types were separated along the first axis of the PCA. Clay lakes are positively correlated with fish richness, nutrients, and macrophyte cover. In contrast, esker lakes are positively correlated with lake size, dissolved oxygen, sand cover, the presence of summer houses, and benthic algae. The first two axis of MFA with the variables from esker lakes explained 35% of variation (Fig. 6B) and MFA with the variables from clay lakes explained 42% of variation (Fig. 6C). Variables from esker lakes showed negative correlation between waterbird (richness and abundance) and fish. Moreover, negative correlation also observed between fish and macroinvertebrate. Similarly, with the MFA from the clay lake variables waterbird showed negative correlation with fish. However, Macroinvertebrate showed correlation with waterbird in clay lakes.

We then aimed to understand the factors driving the similarity and differences among lakes for each fauna category. When sites were assessed using the waterbird community, the PERMANOVA model

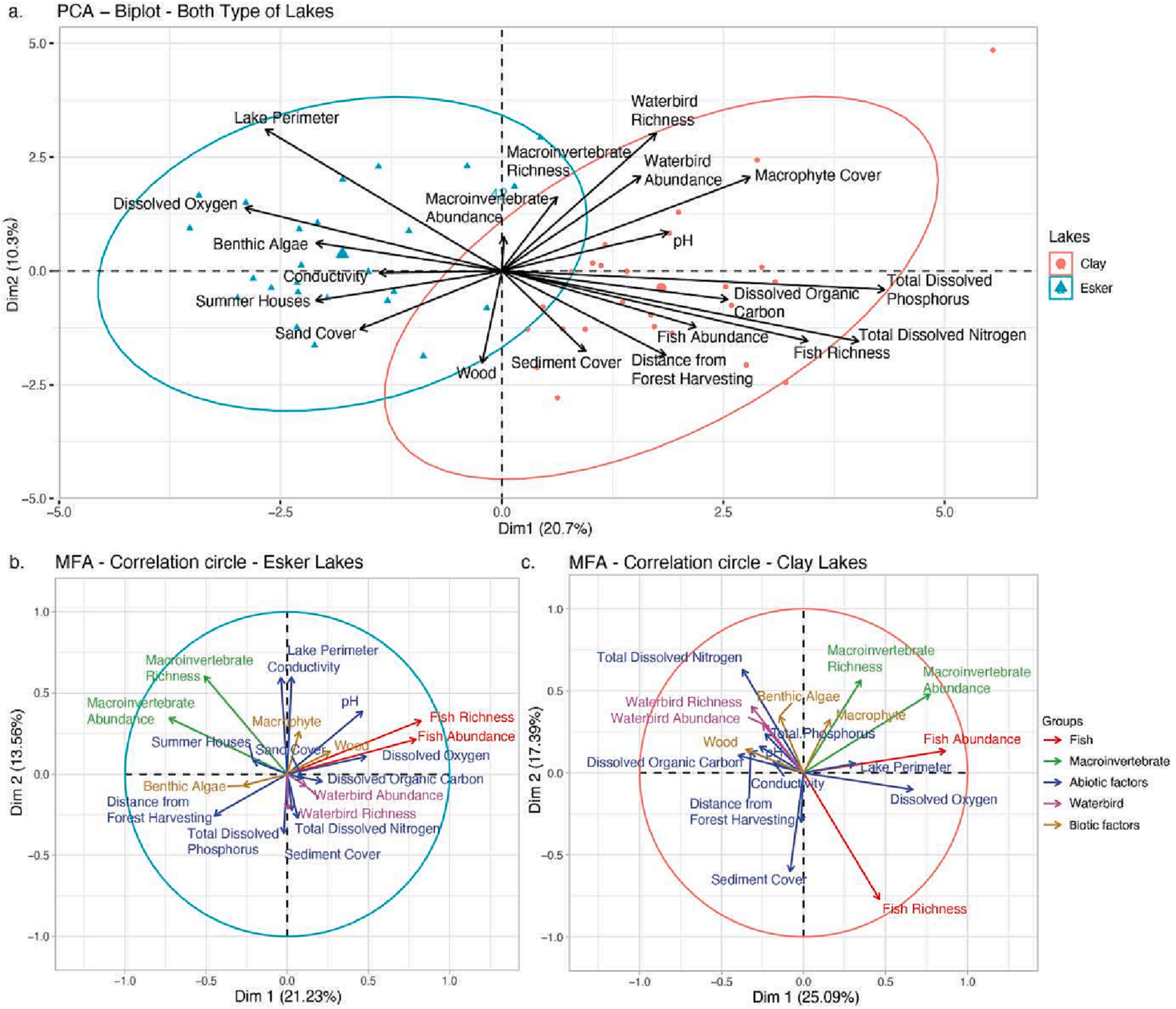


Fig. 6. A. Principal component analysis showing all physicochemical, biological, and environmental variables. The red ellipse shows data points from clay lakes; the blue ellipse shows data points from esker lakes, both at a 95% confidence interval. B. Multiple factor analysis showing variables differentiated in 5 groups from esker lakes. C. Multiple factor analysis showing variables differentiated in 5 groups from clay lakes. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

explained 29% of the variation in the similarity matrix. Lake type (clay or esker) and harvesting distance were the explanatory variables most strongly associated with differences between sites ($F = 1.7$ and 1.9, respectively; $p < 0.1$; Table 2), although pseudo-F values were also high for dissolved oxygen, dissolved organic carbon, and sediment.

The PERMANOVA based on fish community composition explained 26% of the variation in the similarity matrix. Fish communities differed significantly between lake types ($F = 9.9$, $p < 0.001$; Table 2). Moreover, lake size and macroinvertebrate abundance were significantly ($p < 0.05$) associated with differences among sites based on fish community composition.

For macroinvertebrate community composition, the PERMANOVA model explained 41% of the variation in the similarity matrix. There was no evidence of significant differences among sites based on lake type (Table 2). Instead, fish abundance had the strongest effect in the model ($F = 19.9$, $p < 0.05$; Table 2).

4. Discussion

Eskers provide multiple resources for millions of people (McLoughlin et al., 2004; Nadeau et al., 2011) and quality habitats for unique species communities. We found that biodiversity patterns in esker lakes differed from boreal lakes on the surrounding clay belt and reflected biotic interactions and habitat use of associated species communities because of strong associations among organism groups. Although the overall diversity found in the esker lakes was lower than that observed in clay lakes, the species present in esker lakes indicate these elevated water bodies offer higher quality habitats and communities specific to this ecosystem. We also found that anthropogenic activities have altered the esker communities; half of the studied esker lakes had introduced fish species, and forest harvesting has potentially affected waterbird diversity. Therefore, developing adequate protection measures are mandatory for conserving esker ecosystems.

Table 2

PERMANOVA results showing pseudo-F values and p-values for environmental and biological variables affecting the waterbird, fish, and macroinvertebrate community composition. Statistically significant variables are noted in bold *: p ≤ 0.05; **: p ≤ 0.01; ***: p ≤ 0.001.

Category	Variables	Pseudo-F values	R^2	p-values
Waterbird community composition	**Type of lake**	**1.7**	**0.03**	**0.07**
	Fish abundance	0.4	0.01	0.6
	Macroinvertebrate abundance	0.8	0.02	0.4
	Harvesting distance	**1.9**	**0.03**	**0.09**
	Dissolved oxygen	1.5	0.03	0.1
	Lake perimeter	0.4	0.01	0.9
	Sediment cover	1.6	0.05	0.1
	Dissolved phosphorus	0.5	0.01	0.6
	Dissolved organic carbon	1.4	0.02	0.2
Fish community composition	**Type of lake**	**9.9**	**0.21**	**<0.001******
	Waterbird richness	0.1	0.01	0.9
	Waterbird abundance	0.1	0.01	0.9
	Macroinvertebrate richness	1.9	0.02	0.1
	Macroinvertebrate abundance	**3.9**	**0.18**	**0.02***
	Dissolved oxygen	1.1	0.01	0.3
	Dissolved nitrogen	1.1	0.02	0.3
	Dissolved phosphorus	0.3	0.03	0.7
	Dissolved organic carbon	0.1	0.01	0.9
	Lake perimeter	**2.7**	**0.01**	**0.09**
Macroinvertebrates community composition	Type of lake	0.6	0.01	0.6
	Waterbird richness	0.2	0.01	0.7
	Waterbird abundance	0.2	0.01	0.6
	Fish richness	0.4	0.01	0.6
	Fish abundance	**19.9**	0.32	**0.01***
	Dissolved oxygen	0.1	0.01	0.2
	Lake perimeter	0.7	0.01	0.3
	Sediment cover	0.2	0.01	0.6
	Dissolved phosphorus	0.12	0.01	0.8
	Dissolved nitrogen	0.5	0.01	0.4
	Dissolved organic carbon	1.3	0.02	0.7
	Macrophyte cover	0.1	0.02	0.3

We found that esker lakes differed from boreal lakes in terms of their physicochemical makeup and biological communities. The physical and chemical properties of lakes depend highly on watershed properties and inflows (MacLeod et al., 2016). Esker lakes are fed by groundwater and precipitation and are isolated from the regional surface hydrological network (Veillette et al., 2007). Groundwater is generally cold with specific inorganic ions and nutrients (Ala-aho et al., 2013; Hayashi and Rosenberry, 2002; Winter et al., 1998) that strongly influence the physicochemical properties of esker lakes (Nadeau et al., 2015; Veillette et al., 2007). Groundwater dominance, sediment filtration, and the eskers' higher (perched) elevation lead to lower carbon and nutrient concentrations and higher dissolved oxygen levels (Winter, 1976). Soils on eskers are highly permeable sand and gravel; therefore, surface water runoff is minimal (Ala-aho et al., 2013). Minimal runoff causes esker lakes to receive relatively low inputs of nutrients from the forest, which can also explain their significantly lower nutrient and dissolved organic carbon concentrations. Moreover, groundwater naturally has low phosphorus concentrations (Re et al., 2020), explaining the significantly lower (300% lower) total phosphorus concentrations observed in the groundwater-dependent esker lakes. Furthermore, groundwater-fed esker lakes contain greater dissolved oxygen levels because of the colder water influx (Håkanson, 2006). These particular physical characteristics of esker lakes influence the associated biological communities.

Lake productivity significantly affects waterbird populations via the types of aquatic communities and habitats (Paszkowski and Tonn, 2000). Waterbird community composition differed between lake types (esker vs. clay) largely because of differences in the physicochemical makeup of the water and available feeding resources. Water physicochemistry is one of the primary factors influencing waterbird habitat selection (Cintra, 2019), and the particular nature of the physical properties of esker lakes influenced the local waterbird communities. Similarly, fish community composition differed between lake types (esker or clay), confirming our expectations about the fish communities in esker lakes. Among the sampled esker lakes, 48% were fishless. Naturally, esker lakes often lack or have a reduced fish community, as previously observed by Bourgeois and Nadeau (2013) for the lakes of the Saint-Mathieu-Berry esker. Species invasions in pristine ecosystems such as eskers can have severe negative ecological consequences (Vitule et al., 2009). The introduction of non-native fishes in esker lakes, such as yellow perch (*Perca flavescens*), brown bullhead (*Ameiurus nebulosus*), and golden shiner (*Notemigonus crysoleucas*), is closely linked to human activities, such as live bait fishing, the presence of summer houses, camping, and hunting (Brown et al., 2009).

Characterizing the biodiversity patterns using waterbird, fish, and macroinvertebrate communities allows us to explain the habitat selection of biological communities from their trophic interactions (Coccia et al., 2016; Keppeler et al., 2016; Kloskowski et al., 2010; Sebastián-González and Green, 2014). Macroinvertebrate abundance significantly influences fish community composition and abundance as a food resource for fish (Sanders et al., 2011). For example, the absence of fish species in esker lakes influences predatory macroinvertebrate orders (such as Order Odonata) in these lakes. Although lake type influenced waterbird and fish communities, lake type affected macroinvertebrate communities less. However, the absence of (or minimal occurrence of) fish communities in esker lakes influenced predatory macroinvertebrate orders, e.g., Odonata, in esker lakes. We found a significant association of Lestidae (Odonata) with esker lakes having minimal or no fish communities, establishing the importance of trophic interactions for species habitat use. This fish–macroinvertebrate coupling determines both the trophic positions and abundance of macroinvertebrate families (González-Bergonzoni et al., 2014) and the habitat selection of waterbird from different feeding guilds (Eadie and Keast, 1982; Kloskowski et al., 2010; McNicol and Wayland, 1992).

Relative to the surrounding clay lakes, esker lakes are nutrient poor, lack macrophyte cover, have fewer fish, and are characterized by lower organic carbon concentrations. In turn, these lakes also have a lower waterbird diversity. However, species such as common goldeneye were strongly associated with esker lakes and were observed at a higher abundance in these water bodies. Common goldeneye feeds mainly on macroinvertebrates, and its abundance at a site is influenced by the presence of fish—preferring fishless sites—explaining its higher abundance around esker lakes (Elmberg et al., 2010; Eriksson, 1979; McNicol and Wayland, 1992; Väänänen et al., 2012). Moreover, the presence of yellow perch (*Perca flavescens*) reduces the common goldeneye population (Eriksson, 1979; Nummi et al., 2012; Rask et al., 2001) because the diet of yellow perch depends heavily on aquatic macroinvertebrates (Brown et al., 2009). We observed yellow perch in 41% of the esker lakes containing fish. Furthermore, brook stickleback, the most abundant fish in our esker lakes, is omnivorous and shares a similar diet as waterbirds such as the common goldeneye (Wieker et al., 2016). Therefore, fishless esker lakes are a potential high-quality habitat for waterbirds that require these particular habitats to feed and raise their ducklings throughout the summer. However, the anthropogenic threat of fish introduction into fishless esker lakes could therefore affect the conservation of common goldeneye (Epanchin et al., 2010; Post and Cucin, 1984; Vitule et al., 2009), which is already vulnerable because of hunting (80,000–100,000 hunted in 2019 through to 2020) and the loss of habitat and nesting cavities because of traditional clear-cutting forestry practices (Cornell Lab of Ornithology, 2022; Corrigan et al., 2011; Evans and Day, 2002).

In contrast, lakes on the clay belt had higher levels of nutrients, dissolved organic carbon, and macrophyte cover to support a higher species diversity of waterbirds and fish. In clay lakes, the primary dietary preference of the most abundant waterbird, the ring-necked duck, is aquatic macroinvertebrates and macrophytes (Hohman, 1985). The most abundant fish in the clay lakes, the northern redbelly dace, prefers habitats having extensive macrophytes and woody debris; this species is omnivorous, feeding on small macrophytes and macroinvertebrates from the entire water column (Cochran and Ellner, 1992; H and Becher, 1984; Keast and Webb, 1966; Stasiak, 2006). Macrophytes strongly affect the relationship between the fish and macroinvertebrate communities, soil chemistry, nutrient cycling, and sunlight penetration in the water (Brix, 1997; Hupfer and Hilt, 2008). A reduced macrophyte cover negatively affects macroinvertebrate communities and waterbird foraging efficacy (Hargeby et al., 1994). Macrophyte cover can thrive in nutrient-rich waterbodies (Preiner et al., 2020), explaining their predominance in clay lakes relative to the esker lakes.

Macroinvertebrate families such as Perlidae (stonefly) are strongly associated with esker lakes. We found 60 stoneflies in 36% of the esker lakes (in 4% of the clay lakes); this difference likely relates to the substrate and higher dissolved oxygen in the esker lakes (Hynes, 1976). Dissolved oxygen saturation favors macroinvertebrate presence, especially that of macroinvertebrates having delicate gills or respiratory systems (e.g., Perlidae; Verberk et al., 2016; Croijmans et al., 2021). Moreover, clay can clog the respiratory systems or gills (Hynes, 1976). The orders Hemiptera and Coleoptera were significantly associated with clay lakes, and these aquatic insects avoid problems of being in lower-quality water by absorbing oxygen directly from the atmosphere (Thorp and Rogers, 2015). Although clay lakes have lower-quality habitats compared with esker lakes, higher nutrient content and greater macrophyte cover provide abundant resources for producing as abundant species communities at all trophic levels. In contrast, the higher-quality habitat of esker lakes supports specific and distinct species communities.

In 2020, 143 million m^3 of forest was harvested in Canada, and forestry represents one of the country's most important economic activities, providing $25 billion CDN (2020) to the gross national income (Canadian Council of Forest Ministers (CCFM), 2020). In Canada, clear-cutting is the most widely used forest practice, including in esker forests (Bourgeois and Nadeau, 2013; Girona et al., 2023c; Montoro Girona et al., 2018). This management practice creates highly fragmented ecosystems, homogenizes forest stands, and reduces biological diversity (Puettmann et al., 2015). Therefore, ecological impacts from forest harvesting affect the biological community of lake ecosystems by increasing organic matter inputs, decreasing water transparency, and increasing water temperatures, nutrients, and sediment loading (Girona et al., 2023a; Smith et al., 2003; Steedman and Kushneriuk, 2000). In esker lakes, the degree to which waterbird community composition and habitat selection are affected by harvesting depends on the distance from the harvesting. Eskers are dominated by jack pine forests, representing a major regional economic resource for timber production ($43.8 CDN/$m^3$) (Bourgeois and Nadeau, 2013). Clear-cutting practices around esker lakes are particularly harmful to nesting waterbird species such as common goldeneye because these waterfowl often use a cavity produced by pileated woodpeckers (*Dryocopus pileatus*) and live very close to the lake (Corrigan et al., 2011). Additionally, increased sediment load from clear-cutting negatively affects macroinvertebrates dependent on higher dissolved oxygen levels, transparent waters, and rocky substrates (Grosbois et al., 2023). Partial harvesting, however, a promising option to promote growth, guarantee adequate levels of regeneration, minimize tree mortality, and preserve biodiversity in forest and lake ecosystems (Montoro Girona et al., 2016; Montoro Girona et al., 2018, 2019; Moussaoui et al., 2020; Hernández-Rodríguez et al., 2021; Kim et al., 2021; Kwon et al., 2021; Bose et al., 2023). Partial harvesting can reduce the sedimentation in lakes and therefore be beneficial to macroinvertebrates, e.g., Perlidae (Grosbois et al., 2023; Grosbois et al., 2017). Thus, we recommend to develop an adaptive silviculture in eskers forests (D'Amato et al., 2023), and replacing clear-cutting with partial-cutting treatments around esker lakes to reduce the ecological impact of forest harvesting on these lakes, protect habitats, and maintain forest biodiversity (Girona et al., 2023c; Montoro Girona et al., 2017).

Our study focused on the eskers of the Abitibi region because this region has three large eskers that provide drinking water to 20,360 inhabitants and the Eska commercial water bottling plant (Nadeau et al., 2011; Statistics Canada, 2018). Groundwater from this region is recognized as one of the purest fresh waters in the world (Veillette et al., 2007). Numerous lakes on the eskers of this region act as the heart of the entire ecosystem providing support to each trophic level of esker food webs. Ecosystem services related to eskers, such as sand and gravel deposits, freshwater extraction, and forest harvesting, contribute to a significant portion of the regional economy. However, this economic exploitation can negatively affect the esker ecosystem (Nadeau et al., 2015). Eskers contribute to the economy and provide critical ecological support to mammals, birds, insects, herpetofauna, forest vegetation, and fungi (Nadeau et al., 2011). Conserving this unique ecosystem is essential, and this goal requires an integrated resource-based and conservation-focused management plan to preserve esker biodiversity, ecosystem functioning, and resources.

5. Conclusions

Our study demonstrated that esker lake ecosystems differ from the surrounding boreal clay lakes, supporting different aquatic and waterfowl communities. We found that esker lakes have a relatively low fish diversity and provide a healthy ecosystem characterized by different physicochemical properties from typical boreal lakes. Similarly, the diversity in esker lakes is lower than in clay lakes at other trophic levels. Nonetheless, esker lakes sustain particular species communities within each category of fauna. For example, common goldeneye and the macroinvertebrate Perlidae require this particular habitat for their survival. Anthropogenic activities, such as forest harvesting practices, species introductions, economic resource exploitation, and recreational activities, alter the biodiversity and habitats of these unique esker ecosystems. We recommend applying partial harvesting silviculture around esker lakes to protect the distinct faunal communities of the esker ecosystem. Our study helps reduce the existing knowledge gap about esker lakes and serves as a baseline ecological study for sustainably managing the esker ecosystem and its valuable resources.

CRediT authorship contribution statement

Akib Hasan: Data curation, Visualization, Formal analysis, Investigation, Writing – original draft, Writing – review & editing. **Miguel Montoro Girona:** Conceptualization, Data curation, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Funding acquisition, Investigation, Writing – review & editing. **Louis Imbeau:** Conceptualization, Data curation, Methodology, Resources, Supervision, Validation, Investigation, Writing – review & editing. **Jennifer Lento:** Validation, Writing – review & editing. **Anouschka R. Hof:** Validation, Writing – review & editing. **Guillaume Grosbois:** Conceptualization, Data curation, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Funding acquisition, Investigation, Writing – review & editing.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Miguel Montoro Girona reports financial support was provided by MRC Abitibi.

Data availability

Data will be made available on request.

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Research ethics

The research methodology was approved by the Research Ethics Committee of Université du Québec en Abitibi-Témiscamingue. No animal was killed/hurt during field measurements of fish and waterbirds.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2023.110612.

References

Ala-aho, P., Rossi, P.M., Kløve, B., 2013. Interaction of esker groundwater with headwater lakes and streams. J. Hydrol. (Amst.) 500, 144–156. https://doi.org/10.1016/j.jhydrol.2013.07.014.

Armitage, P.D., Moss, D., Wright, J.F., Furse, M.T., 1983. The performance of a new biological water quality score system based on macroinvertebrates over a wide range of unpolluted running-water sites. Water Res. 17 (3), 333–347. https://doi.org/10.1016/0043-1354(83)90188-4.

Bates, R.L., Jackson, J.A., 1987. Glossary of geology, 3rd ed. American Geological Institute.

Batzer, D.P., Shurtleff, A.S., Robinette, J.R., 1999. Managing fish and invertebrate resources in a wood stork feeding pond. J. Freshwater Ecol. 14, 159–165. https://doi.org/10.1080/02705060.1999.9663667.

Beaulne, J.S., Lucotte, M., Paquet, S., Canuel, R., 2012. Modeling mercury concentrations in northern pikes and walleyes from frequently fished lakes of Abitibi-Témiscamingue (Quebec, Canada): A GIS approach. Boreal Environ. Res. 17, 277–290.

Bennett, C.L., 1967. A new method for estimating numbers of duck broods. J. Wildl. Manag. 31, 555–562. https://doi.org/10.2307/3798139.

Berger, A.L., Palik, B., D'Amato, A.W., Fraver, S., Bradford, J.B., Nislow, K., King, D., Brooks, R.T., 2013. Ecological impacts of energy-wood harvests: Lessons from whole-tree harvesting and natural disturbance. J. For. 111, 139–153. https://doi.org/10.5849/jof.12-020.

Blouin, J., Berger, J.-P., 2002. Guide de reconnaissance des types écologiques : Région écologique 5a : plaine de l'Abitibi. Direction des inventaires forestiers, Forêt Québec, Ministère des ressources naturelles, Québec, QC.

Bose, A.K., Alcalá-Pajares, M., Kern, C.C., Montoro-Girona, M., Thiffault, N., 2023. Complex regeneration responses of eight tree species to partial harvest in mixedwood forests of northeastern North America, 120672 For. Ecol. Manage. 529. https://doi.org/10.1016/j.foreco.2022.120672.

Bourgeois, G., Nadeau, S., 2013. Portrait de l'esker aquifère Saint-Mathieu-Berry. Société de l'eau souterraine Abitibi-Témiscamingue (SESAT), Université du Québec en Abitibi-Témiscamingue.

Bradford, M.J., Irvine, J.R., 2000. Land use, fishing, climate change, and the decline of Thompson River, British Columbia, coho salmon. Can. J. Fish. Aquat. Sci. 57, 13–16. https://doi.org/10.1139/f99-283.

Brix, H., 1997. Do macrophytes play a role in constructed treatment wetlands? Water Sci. Technol. 35, 11–17. https://doi.org/10.2166/wst.1997.0154.

Brown, T.G., Runciman, B., Bradford, M.J., Pollard, S., 2009. A biological synopsis of yellow perch (*Perca flavescens*). Can. Manuscr. Rep. Fish. Aquat. Sci. 2883, 28.

Burks, R.L., Lodge, F.M., Jeppesen, R., Lauridsen, T.L., 2002. Diel horizontal migration of zooplankton: costs and benefits of inhabiting the littoral. Freshw. Biol. 47 (3), 343–365. https://doi.org/10.1046/j.1365-2427.2002.00824.x.

Canterbury, G.E., Martin, T.E., Petit, D.R., Petit, L.J., Bradford, D.F., 2000. Bird communities and habitat as ecological indicators of forest condition in regional monitoring. Conserv. Biol. 14, 544–558. https://doi.org/10.1046/j.1523-1739.2000.98235.x.

Canadian Council of Forest Ministers (CCFM), 2020. Harvest - National forestry database. http://nfdp.ccfm.org/en/data/harvest.php.

Chu, C., Minns, C.K., Lester, N.P., Mandrak, N.E., Rosenfeld, J., 2015. An updated assessment of human activities, the environment, and freshwater fish biodiversity in Canada. Can. J. Fish. Aquat. Sci. 72 (1), 135–148.

Cintra, R., 2019. Waterbird community composition in relation to lake physical traits and wetland limnological conditions in the Amazon basin. Hydrobiologia 826, 43–65. https://doi.org/10.1007/s10750-018-3676-y.

Coccia, C., Vanschoenwinkel, B., Brendonck, L., Boyero, L., Green, A.J., 2016. Newly created ponds complement natural waterbodies for restoration of macroinvertebrate assemblages. Freshw. Biol. 61, 1640–1654. https://doi.org/10.1111/fwb.12804.

Cochran, M.E., Ellner, S., 1992. Simple methods for calculating age-based life history parameters for stage-structured populations. Ecol. Monogr. 62, 345–364. https://doi.org/10.2307/2937115.

Cornell Lab of Ornithology, 2022. Common goldeneye life history. Retrieved December 2, 2022 from. https://www.allaboutbirds.org/guide/Common_Goldeneye/lifehistory.

Corrigan, R.M., Scrimgeour, G.J., Paszkowski, C., 2011. Nest boxes facilitate local-scale conservation of common Goldeneye (*Bucephala clangula*) and Bufflehead (*Bucephala albeola*) in Alberta, Canada. Avian Conserv. Ecol. 6, art1. https://doi.org/10.5751/ACE-00435-060101.

Croijmans, L., De Jong, J.F., Prins, H.H.T., 2021. Oxygen is a better predictor of macroinvertebrate richness than temperature—a systematic review. Environ. Res. Lett. 16 (2), 023002.

D'Amato, A.W., Palik, B.J., Raymond, P., Puettmann, K.J., Girona, M.M., 2023. Building a Framework for Adaptive Silviculture Under Global Change. In: Boreal Forests in the Face of Climate Change: Sustainable Management. Springer International Publishing, Cham, pp. 359–381.

De Cáceres, M., Legendre, P., 2009. Associations between species and groups of sites: Indices and statistical inference. Ecology 90, 3566–3574. https://doi.org/10.1890/08-1823.1.

Desforges, J.E., Clarke, J., Harmsen, E.J., Jardine, A.M., Robichaud, J.A., Serré, S., Chakrabarty, P., Bennett, J.R., Hanna, D.E.L., Smol, J.P., Rytwinski, T., Taylor, J.J., Martel, A.L., Winegardner, A.K., Marty, J., Taylor, M.K., O'Connor, C.M., Robinson, S.A., Reid, A.J., Creed, I.F., Gregory-Eaves, I., Lapointe, N.W.R., Cooke, S. J., 2022. The alarming state of freshwater biodiversity in Canada. Can. J. Fish. Aquat. Sci. 79 (2), 352–365.

Desjardins, E., Imbeau, L., Darveau, M., Mazerolle, M.J., Fenton, N.J., 2021. Waterfowl use of mine tailing ponds in comparison with beaver ponds in boreal eastern Canada. Avian Conserv. Ecol. 16, art24. https://doi.org/10.5751/ACE-02003-160224.

Duggan, I.C., Green, J.D., Thompson, K., Shiel, R.J., 2001. The influence of macrophytes on the spatial distribution of littoral rotifers. Freshw. Biol. 46, 777–786. https://doi.org/10.1046/j.1365-2427.2001.00718.x.

Dyke, A.S., Prest, V.K., 2008. Late Wisconsinan and Holocene history of the Laurentide ice sheet. Géographie Physique et Quaternaire 41, 237–263. https://doi.org/10.7202/032681ar.

Eadie, J.M., Keast, A., 1982. Do goldeneye and perch compete for food? Oecologia 55, 225–230. https://doi.org/10.1007/BF00384491.

Elmberg, J., Dessborn, L., Englund, G., 2010. Presence of fish affects lake use and breeding success in ducks. Hydrobiologia 641, 215–223. https://doi.org/10.1007/s10750-009-0085-2.

Englund, G., Johansson, F., Olsson, T.I., 1992. Asymmetric competition between distant taxa: Poecilid fishes and water striders. Oecologia 92, 498–502. https://doi.org/10.1007/BF00317841.

Epanchin, P.N., Knapp, R.A., Lawler, S.P., 2010. Nonnative trout impact an alpine-nesting bird by altering aquatic-insect subsidies. Ecology 91, 2406–2415. https://doi.org/10.1890/09-1974.1.

Eriksson, M.O.G., 1979. Competition between freshwater fish and goldeneyes *Bucephala clangula* (L.) for common prey. Oecologia 41, 99–107. https://doi.org/10.1007/BF00344840.

Evans, D.M., Day, K.R., 2002. Hunting disturbance on a large shallow lake: The effectiveness of waterfowl refuges. The Ibis 144, 2–8. https://doi.org/10.1046/j.0019-1019.2001.00001.x.

Flannagan, J.F., 1979. An introduction to the aquatic insects of North America. J. Fish. Res. Board Can. 36 (2), 231.

Garrett-Walker, J., Collier, K.J., Daniel, A., Hicks, B.J., Klee, D., 2020. Design features of constructed floodplain ponds influence waterbird and fish communities in northern New Zealand. Freshw. Biol. 65, 2066–2080. https://doi.org/10.1111/fwb.13602.

Gilliam, J.F., Fraser, D.F., 2001. Movement in corridors: Enhancement by predation threat, disturbance, and habitat structure. Ecology 82, 258–273. https://doi.org/10.1890/0012-9658(2001)082[0258:MICEBP]2.0.CO;2.

Girona, M.M., Aakala, T., Aquilué, N., Bélisle, A.C., Chaste, E., Danneyrolles, V., Díaz-Yáñez, O., D'Orangeville, L., Grosbois, G., Hester, A., Kim, S., Kulha, N., Martin, M., Moussaoui, L., Pappas, C., Portier, J., Teitelbaum, S., Tremblay, J.P., Svensson, J., Gauthier, S., 2023a. Challenges for the sustainable management of the boreal forest under climate change. In: Girona, M.M., Morin, H., Gauthier, S., Bergeron, Y. (Eds.), Boreal Forests in the Face of Climate Change: Sustainable Management. Springer International Publishing, pp. 773–837. https://doi.org/10.1007/978-3-031-15988-6_31.

Girona, M.M., Morin, H., Gauthier, S., Bergeron, Y. (Eds.), 2023b. Boreal Forests in the Face of Climate Change: Sustainable Management. Springer International Publishing. https://doi.org/10.1007/978-3-031-15988-6.

Girona, M.M., Moussaoui, L., Morin, H., Thiffault, N., Leduc, A., Raymond, P., Bosé, A., Bergeron, Y., Lussier, J.M., 2023c. Innovative silviculture to achieve sustainable forest management in boreal forests: Lessons from two large-scale experiments. In: Girona, M.M., Morin, H., Gauthier, S., Bergeron, Y. (Eds.), Boreal Forests in the Face of Climate Change: Sustainable Management. Springer International Publishing, pp. 417–440. https://doi.org/10.1007/978-3-031-15988-6_16.

González-Bergonzoni, I., Landkildehus, F., Meerhoff, M., Lauridsen, T.L., Özkan, K., Davidson, T.A., Mazzeo, N., Jeppesen, E., 2014. Fish determine macroinvertebrate food webs and assemblage structure in Greenland subarctic streams. Freshw. Biol. 59, 1830–1842. https://doi.org/10.1111/fwb.12386.

Grosbois, G., del Giorgio, P.A., Rautio, M., 2017. Zooplankton allochthony is spatially heterogeneous in a boreal lake. Freshw. Biol. 62, 474–490. https://doi.org/10.1111/fwb.12879.

Grosbois, G., Vachon, D., Del Giorgio, P.A., Rautio, M., 2020. Efficiency of crustacean zooplankton in transferring allochthonous carbon in a boreal lake. Ecology 101, e03013.

Grosbois, G., Power, M., Evans, M., Koehler, G., Rautio, M., 2022. Content, composition, and transfer of polyunsaturated fatty acids in an Arctic lake food web. Ecosphere 13. https://doi.org/10.1002/ecs2.3881.

Grosbois, G., Lau, D.C.P., Berggren, M., Girona, M.M., Goedkoop, W., Messier, C., Hjältén, J., del Giorgio, P., 2023. Land and freshwater complex interactions in boreal forests: A neglected topic in forest management. In: Girona, M.M., Morin, H., Gauthier, S., Bergeron, Y. (Eds.), Boreal Forests in the Face of Climate Change: Sustainable Management. Springer International Publishing, pp. 719–745. https://doi.org/10.1007/978-3-031-15988-6_29.

Gurney, K.E.B., Clark, R.G., Slattery, S.M., Ross, L.C.M., 2017. Connecting the trophic dots: Responses of an aquatic bird species to variable abundance of macroinvertebrates in northern boreal wetlands. Hydrobiologia 785, 1–17. https://doi.org/10.1007/s10750-016-2817-4.

H, C., Becher, G.C., 1984. Review of Fishes of Wisconsin, by G. C. Becker. Copeia 1984 (1), 274–276. https://doi.org/10.2307/1445079.

Håkanson, L., 2006. The relationship between salinity, suspended particulate matter and water clarity in aquatic systems. Ecol. Res. 21, 75–90. https://doi.org/10.1007/s11284-005-0098-x.

Hargeby, A., Andersson, G., Blindow, I., Johansson, S., 1994. Trophic web structure in a shallow eutrophic lake during a dominance shift from phytoplankton to submerged macrophytes. Hydrobiologia 279–280, 83–90. https://doi.org/10.1007/BF00027843.

Hatva, T., 1994. Effect of gravel extraction on groundwater. IAHS Publication No, In Future groundwater resources at risk, p. 222.

Hayashi, M., Rosenberry, D.O., 2002. Effects of ground water exchange on the hydrology and ecology of surface water. Ground Water 40, 309–316. https://doi.org/10.1111/j.1745-6584.2002.tb02659.x.

Hernández-Rodríguez, E., Escalera-Vázquez, L.H., García-Ávila, D., Montoro Girona, M., Mendoza, E., 2021. Reduced-impact logging maintain high moss diversity in temperate forests. Forests 12, 383. https://doi.org/10.3390/f12040383.

Hohman, W.L., 1985. Feeding ecology of ring-necked ducks in northwestern Minnesota. J. Wildl. Manag. 49, 546–557. https://doi.org/10.2307/3801670.

Hupfer, M., Hilt, S., 2008. Lake restoration. In: Jørgensen, S.E., Fath, B.D. (Eds.), Encyclopedia of Ecology. Academic Press, pp. 2080–2093. https://doi.org/10.1016/B978-008045405-4.00061-6.

Hurlbert, S.H., Loayza, W., Moreno, T., 1986. Fish-flamingo-plankton interactions in the Peruvian Andes. Limnol. Oceanogr. 31, 457–468. https://doi.org/10.4319/lo.1986.31.3.0457.

Hynes, H.B.N., 1976. Biology of Plecoptera. Annu. Rev. Entomol. 21, 135–153. https://doi.org/10.1146/annurev.en.21.010176.001031.

Jeppesen, E., Lauridsen, T.L., Kairesalo, T., Perrow, M.R., 1998. Impact of submerged macrophytes on fish-zooplankton interactions in lakes. In: Jeppesen, E., Søndergaard, M., Søndergaard, M., Christoffersen, K. (Eds.), The Structuring Role of Submerged Macrophytes in Lakes. Springer, New York, pp. 91–114. https://doi.org/10.1007/978-1-4612-0695-8_5.

Jia, Y., Jiang, Y., Liu, Y., Sui, X., Feng, X., Zhu, R., Chen, Y., 2021. Understanding trophic structure variation in fish assemblages of subtropical shallow lakes: Combined effects of ecosystem size, productivity, and disturbance, 107924 Ecol. Ind. 129. https://doi.org/10.1016/j.ecolind.2021.107924.

Justus, B.G., Mize, S., Wallace, J., Kroes, D., 2014. Invertebrate and fish assemblage relations to dissolved oxygen minima in lowland streams of southwestern Louisiana. River Res. Appl. 30, 11–28. https://doi.org/10.1002/rra.2623.

Keast, A., Webb, D., 1966. Mouth and body form relative to feeding ecology in the fish fauna of a small lake, Lake Opinicon, Ontario. J. Fish. Res. Board Can. 23, 1845–1874. https://doi.org/10.1139/f66-175.

Keppeler, F.W., Cruz, D.A., Dalponti, G., Mormul, R.P., 2016. The role of deterministic factors and stochasticity on the trophic interactions between birds and fish in temporary floodplain ponds. Hydrobiologia 773, 225–240. https://doi.org/10.1007/s10750-016-2705-y.

Kim, S., Axelsson, E.P., Girona, M.M., Senior, J.K., 2021. Continuous-cover forestry maintains soil fungal communities in Norway spruce dominated boreal forests, 118659 For. Ecol. Manage. 480. https://doi.org/10.1016/j.foreco.2020.118659.

Kloskowski, J., Nieoczym, M., Polak, M., Pitucha, P., 2010. Habitat selection by breeding waterbirds at ponds with size-structured fish populations. Naturwissenschaften 97, 673–682. https://doi.org/10.1007/s00114-010-0684-9.

Kløve, B., Ala-aho, P., Bertrand, G., Boukalova, Z., Ertürk, A., Goldscheider, N., Ilmonen, J., Karakaya, N., Kupfersberger, H., Kværner, J., Lundberg, A., Mileusnić, M., Moszczynska, A., Muotka, T., Preda, E., Rossi, P., Siergieiev, D., Šimek, J., Wachniew, P., Angheluta, V., Widerlund, A., 2011. Groundwater dependent ecosystems. Part I: Hydroecological status and trends. Environ. Sci. Policy 14 (7), 770–781.

Kwon, S., Kim, S., Kim, J., Kang, W., Park, K.H., Kim, C.B., Girona, M.M., 2021. Predicting post-fire tree mortality in a temperate pine Forest, Korea. Sustainability (Basel) 13, 569. https://doi.org/10.3390/su13020569.

Lammens, E.H.R.R., 1999. The central role of fish in lake restoration and management.In: Harper, D.M., Brierley, B., Ferguson, A.J.D., Phillips, G. (Eds.), The ecological bases for lake and reservoir management. Dordrecht, pp. 191–198.

Laurance, W.F., Balmford, A., 2013. Land use: A global map for road building. Nature 495, 308–309. https://doi.org/10.1038/495308a.

Lê, S., Josse, J., Husson, F., 2008. FactoMineR : An R package for multivariate analysis. J. Stat. Softw. 25 (1), 1–18. https://doi.org/10.18637/jss.v025.i01.

Levins, R., 1979. Asymmetric competition among distant taxa. Am. Zool. 19 (4), 1097–1104. https://doi.org/10.1093/icb/19.4.1097.

MacLeod, J., Keller, W., Paterson, A.M., Dyer, R.D., Gunn, J.M., 2016. Scale and watershed features determine lake chemistry patterns across physiographic regions in the far north of Ontario, Canada. J. Limnol. 76 (1) https://doi.org/10.4081/jlimnol.2016.1553.

Maitland, P.S., 1995. The conservation of freshwater fish: Past and present experience. Biol. Conserv. 72, 259–270. https://doi.org/10.1016/0006-3207(94)00088-8.

Maitland, B.M., Poesch, M., Anderson, A.E., Pandit, S.N., 2016. Industrial road crossings drive changes in community structure and instream habitat for freshwater fishes in the boreal forest. Freshw. Biol. 61, 1–18. https://doi.org/10.1111/fwb.12671.

McLoughlin, P.D., Walton, L.R., Cluff, H.D., Paquet, P.C., Ramsay, M.A., 2004. Hierarchical habitat selection by tundra wolves. J. Mammal. 85, 576–580. https://doi.org/10.1644/BJK-119.

McNicol, D.K., Wayland, M., 1992. Distribution of waterfowl broods in Sudbury area lakes in relation to fish, macroinvertebrates, and water chemistry. Can. J. Fish. Aquat. Sci. 49, 122–133. https://doi.org/10.1139/f92-307.

Meier, E.S., Kienast, F., Pearman, P.B., Svenning, J.C., Thuiller, W., Araújo, M.B., Guisan, A., Zimmermann, N.E., 2010. Biotic and abiotic variables show little redundancy in explaining tree species distributions. Ecography 33, 1038–1048. https://doi.org/10.1111/j.1600-0587.2010.06229.x.

Messager, M.L., Lehner, B., Grill, G., Nedeva, I., Schmitt, O., 2016. Estimating the volume and age of water stored in global lakes using a geo-statistical approach. Nat. Commun. 7, 13603. https://doi.org/10.1038/ncomms13603.

Mitsch, W.J., Gosselink, J.G., 2000. The value of wetlands: Importance of scale and landscape setting. Ecol. Econ. 35, 25–33. https://doi.org/10.1016/S0921-8009(00)00165-8.

Molina, E., Valeria, O., Martin, M., Montoro Girona, M., Ramirez, J.A., 2022. Long-term impacts of forest management practices under climate change on structure, composition, and fragmentation of the Canadian boreal landscape. Forests 13, 1292. https://doi.org/10.3390/f13081292.

Monk, W.A., Baird, D.J., 2014. Biodiversity in Canadian lakes and rivers. Canadian Biodiversity: Ecosystem status and trends 2010.

Montoro Girona, M., Morin, H., Lussier, J.M., Walsh, D., 2016. Radial growth response of black spruce stands ten years after experimental shelterwoods and seed-tree cuttings in boreal forest. Forests 7, 240. https://doi.org/10.3390/f7100240.

Montoro Girona, M., Rossi, S., Lussier, J.-M., Walsh, D., Morin, H., Zang, RunGuo, 2017. Understanding tree growth responses after partial cuttings: A new approach. PLoS One 12 (2), e0172653.

Montoro Girona, M., Lussier, J.M., Morin, H., Thiffault, N., 2018. Conifer regeneration after experimental shelterwood and seed-tree treatments in boreal forests: Finding silvicultural alternatives. Front. Plant Sci. 9, 1145. https://doi.org/10.3389/fpls.2018.01145.

Montoro Girona, M., Morin, H., Lussier, J.M., Ruel, J.C., 2019. Post-cutting mortality following experimental silvicultural treatments in unmanaged boreal forest stands. Front. For. Glob. Change 2, 4. https://doi.org/10.3389/ffgc.2019.00004.

Moussaoui, L., Leduc, A., Girona, M.M., Bélisle, A.C., Lafleur, B., Fenton, N.J., Bergeron, Y., 2020. Success factors for experimental partial harvesting in unmanaged boreal forest: 10-year stand yield results. Forests 11, 1199. https://doi.org/10.3390/f11111199.

Nadeau, S., Cloutier, V., Daigneault, R., Veillette, J., 2011, August. Volume estimate of granular deposits and groundwater reserves of the Abitibi-Témiscamingue eskers. Geohydro2011, Joint IAH-CNC, CANQUA and AHQ conference, Quebec City, QC.

Nadeau, S., Rosa, E., Cloutier, V., Daigneault, R.A., Veillette, J., 2015. A GIS-based approach for supporting groundwater protection in eskers: Application to sand and gravel extraction activities in Abitibi-Témiscamingue, Quebec, Canada. J. Hydrol. Reg. Stud. 4, 535–549. https://doi.org/10.1016/j.ejrh.2015.05.015.

Nummi, P., Väänänen, V.M., Rask, M., Nyberg, K., Taskinen, K., 2012. Competitive effects of fish in structurally simple habitats: Perch, invertebrates, and goldeneye in small boreal lakes. Aquat. Sci. 74, 343–350. https://doi.org/10.1007/s00027-011-0225-4.

Oksanen, J., Simpson, G.B.F., Kindt, R., Legendre, P., Minchin, P., O'Hara, R., Solymos, P., Stevens, M., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., De Caceres, M., Durand, S., Evangelista, H., et al., 2023. vegan: Community ecology package. R package version 2.6-5. https://doi.org/10.4135/9781412971874.n145.

Palviainen, M., Peltomaa, E., Laurén, A., Kinnunen, N., Ojala, A., Berninger, F., Zhu, X., Pumpanen, J., 2022. Water quality and the biodegradability of dissolved organic carbon in drained boreal peatland under different forest harvesting intensities, 150919 Sci. Total Environ. 806. https://doi.org/10.1016/j.scitotenv.2021.150919.

Pappas, C., Bélanger, N., Bergeron, Y., Blarquez, O., Chen, H. Y. H., Comeau, P. G., De Grandpré, L., Delagrange, S., DesRochers, A., Diochon, A., D'Orangeville, L., Drapeau, P., Duchesne, L., Filotas, E., Gennaretti, F., Houle, D., Lafleur, B., Langor, D., Lebel Desrosiers, S., et al., 2022. Smartforests Canada: A network of monitoring plots for forest management under environmental change. In: R. Tognetti, M. Smith, P. Panzacchi (Eds.), Climate-Smart forestry in mountain regions (pp. 521-543). Springer International Publishing. https://doi.org/10.1007/978-3-030-80767-2_16.

Paszkowski, C.A., Tonn, W.M., 2000. Community concordance between the fish and aquatic birds of lakes in northern Alberta, Canada: The relative importance of environmental and biotic factors. Freshw. Biol. 43, 421–437. https://doi.org/10.1046/j.1365-2427.2000.00512.x.

Pilière, A., Schipper, A.M., Breure, A.M., Posthuma, L., de Zwart, D., Dyer, S.D., Huijbregts, M.A.J., 2014. Comparing responses of freshwater fish and invertebrate community integrity along multiple environmental gradients. Ecol. Ind. 43, 215–226. https://doi.org/10.1016/j.ecolind.2014.02.019.

Pinel-Alloul, B., Giani, A., Taranu, Z.E., Lévesque, D., Marinescu, I., Kufner, D., Mimouni, E.A., Robert, M., 2022. Foodweb biodiversity and community structure in urban waterbodies vary with habitat complexity, macrophyte cover, and trophic status. Hydrobiologia 849, 3761–3787. https://doi.org/10.1007/s10750-021-04678-8.

Post, J.R., Cucin, D., 1984. Changes in the benthic community of a small Precambrian lake following the introduction of Yellow perch, *Perca flavescens*. Can. J. Fish. Aquat. Sci. 41, 1496–1501. https://doi.org/10.1139/f84-184.

Pöysä, H., Virtanen, J., 1994. Habitat selection and survival of Common Goldeneye (*Bucephala clangula*) broods - preliminary results. Hydrobiologia 279–280, 289–296. https://doi.org/10.1007/BF00027862.

Preiner, S., Dai, Y., Pucher, M., Reitsema, R.E., Schoelynck, J., Meire, P., Hein, T., 2020. Effects of macrophytes on ecosystem metabolism and net nutrient uptake in a groundwater fed lowland river. Sci. Total Environ. 721, 137620 https://doi.org/10.1016/j.scitotenv.2020.137620.

Puettmann, K.J., Wilson, S.M., Baker, S.C., Donoso, P.J., Drössler, L., Amente, G., Harvey, B.D., Knoke, T., Lu, Y., Nocentini, S., Putz, F.E., Yoshida, T., Bauhus, J., 2015. Silvicultural alternatives to conventional even-aged forest management - what limits global adoption? For. Ecosyst. 2, 8. https://doi.org/10.1186/s40663-015-0031-x.

R Development Core Team, 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing.

Rask, M., Pöysä, H., Nummi, P., Karppinen, C., 2001. Recovery of the perch (*Perca fluviatilis*) in an acidified lake and subsequent responses in macroinvertebrates and the goldeneye (*Bucephala clangula*). Water Air Soil Pollut. 130, 1367–1372. https://doi.org/10.1023/A:1013967604076.

Rautio, A., Korkka-Niemi, K., 2011. Characterization of groundwater-lake water interactions at Pyhäjärvi, a lake in SW Finland. Boreal Environ. Res. 16 (5), 363–380.

Re, V., de Filippis, G., Viaroli, S., di Curzio, D., 2020. Groundwater (Freeze and Cherry, 1979). ora disponibile anche in italiano. 9 (1), 89–90. https://doi.org/10.7343/as-2020-453.

Rey, N., Rosa, E., Cloutier, V., Lefebvre, R., 2018. Using water stable isotopes for tracing surface and groundwater flow systems in the Barlow-Ojibway Clay Belt, Quebec, Canada. Can. Water Resour. J. / Revue canadienne des ressources hydriques 43 (2), 173–194. https://doi.org/10.1080/07011784.2017.1403960.

Rumble, M.A., Flake, L.D., 1982. A comparison of two waterfowl brood survey techniques. J. Wildl. Manag. 46, 1048. https://doi.org/10.2307/3808238.

Safina, C., Burger, J., 1985. Common tern foraging: Seasonal trends in prey fish densities and competition with bluefish. Ecology 66, 1457–1463. https://doi.org/10.2307/1938008.

Sanders, T.G., Biddanda, B.A., Stricker, C.A., Nold, S.C., 2011. Benthic macroinvertebrate and fish communities in Lake Huron are linked to submerged groundwater vents. Aquat. Biol. 12 (1), 1–11.

Schad, A.N., Kennedy, J.H., Dick, G.O., Dodd, L., 2020. Aquatic macroinvertebrate richness and diversity associated with native submerged aquatic vegetation plantings increases in longer-managed and wetland-channeled effluent constructed urban wetlands. Wetl. Ecol. Manag. 28, 461–477. https://doi.org/10.1007/s11273-020-09724-1.

Sebastián-González, E., Green, A.J., 2014. Habitat use by waterbirds in relation to pond size, water depth, and isolation: Lessons from a restoration in Southern Spain. Restor. Ecol. 22, 311–318. https://doi.org/10.1111/rec.12078.

Slattery, S.M., Morissette, J.L., Mack, G.G., Butterworth, E.W., 2011. Waterfowl conservation planning: science needs and approaches. In: Wells, J.V. (Ed.), Boreal Birds of North america: a Hemispheric View of Their Conservation Links and Significance. Studies in Avian Biology 41. University of California Press, pp. 23–40.

Smerdon, B., Mendoza, C., Devito, K., 2012. The impact of gravel extraction on groundwater dependent wetlands and lakes in the Boreal Plains, Canada. Environ. Earth Sci. 67 (5), 1249–1259. https://doi.org/10.1007/s12665-012-1568-4.

Smith, D.W., Prepas, E.E., Putz, G., Burke, J.M., Meyer, W.L., Whitson, I., 2003. The Forest Watershed and Riparian Disturbance study: A multi-discipline initiative to evaluate and manage watershed disturbance on the Boreal Plain of Canada. J. Environ. Eng. Sci. 2, S1–S13. https://doi.org/10.1139/s03-030.

Stasiak, R., 2006. Northern Redbelly dace (Phoxinus eos): A technical conservation assessment. USDA Forest Service, Rocky Mountain Region, Omaha, NE, 1846–3363). Retrieved from.

Statistics Canada, 2018. Canada's population estimates: Total population, July 1, 2018. Ottawa, ON: The Daily: Component of Statistics Canada catalogue no. 11-001-X.

Steedman, R.J., Kushneriuk, R.S., 2000. Effects of experimental clearcut logging on thermal stratification, dissolved oxygen, and lake trout (*Salvelinus namaycush*) habitat volume in three small boreal forest lakes. Can. J. Fish. Aquat. Sci. 57, 82–91. https://doi.org/10.1139/f00-112.

Storrar, R.D., Stokes, C.R., Evans, D.J.A., 2013. A map of large Canadian eskers from Landsat satellite imagery. J. Maps 9, 456–473. https://doi.org/10.1080/17445647.2013.815591.

Stroeven, A.P., Hättestrand, C., Kleman, J., Heyman, J., Fabel, D., Fredin, O., Goodfellow, B.W., Harbor, J.M., Jansen, J.D., Olsen, L., Caffee, M.W., Fink, D., Lundqvist, J., Rosqvist, G.C., Strömberg, B., Jansson, K.N., 2016. Deglaciation of Fennoscandia. Quat. Sci. Rev. 147, 91–121. https://doi.org/10.1016/j.quascirev.2015.09.016.

Thorp and Covich's Freshwater Invertebrates, 2015. Elsevier, p. ii.

Väänänen, V.M., Nummi, P., Pöysä, H., Rask, M., Nyberg, K., 2012. Fish–duck interactions in boreal lakes in Finland as reflected by abundance correlations. Hydrobiologia 697, 85–93. https://doi.org/10.1007/s10750-012-1172-3.

van Eerden, M.R., Piersma, T., Lindeboom, R., 1993. Competitive food exploitation of smelt *Osmerus eperlanus* by great crested grebes Podiceps cristatus and perch *Perca fluviatilis* at Lake IJsselmeer, The Netherlands. Oecologia 93, 463–474. https://doi.org/10.1007/BF00328953.

van Guelpen, L., Markle, D.F., Duggan, D.J., 1982. An evaluation of accuracy, precision, and speed of several zooplankton subsampling techniques. ICES J. Mar. Sci. 40, 226–236. https://doi.org/10.1093/icesjms/40.3.226.

Veillette, J.J., 1988. Former southwesterly ice flows in the Abitibi-Timiskaming region: Implications for the configuration of the Late Wisconsinan ice sheet, Reply. Can. J. Earth Sci. 25, 353. https://doi.org/10.1139/e88-038.

Veillette, J.J., Cloutier, V., de Corta, H., Gagnon, F., Roy, M., Douma, M., Bois, D., 2007. A complex recharge network, the Barraute esker. OttawaGeo2007, Ottawa, ON.

Verberk, W.C.E.P., Durance, I., Vaughan, I.P., Ormerod, S.J., 2016. Field and laboratory studies reveal interacting effects of stream oxygenation and warming on aquatic ectotherms. Glob. Chang. Biol. 22, 1769–1778. https://doi.org/10.1111/gcb.13240.

Vitule, J.R.S., Freire, C.A., Simberloff, D., 2009. Introduction of non-native freshwater fish can certainly be bad. Fish Fish. 10, 98–108. https://doi.org/10.1111/j.1467-2979.2008.00312.x.

Wang, H.-J., Liang, X.-M., Jiang, P.-H., Wang, J., Wu, S.-K., Wang, H.-Z., 2008. TN:TP ratio and planktivorous fish do not affect nutrient-chlorophyll relationships in shallow lakes. Freshw. Biol. 53 (5), 935–944. https://doi.org/10.1111/j.1365-2427.2007.01950.x.

Wetzel, R.G., Likens, G.E., 2000. Limnological analyses (Third ed.). Springer. https://doi.org/10.1007/978-1-4757-3250-4.

Wieker, J.E., Schoonover, C.M., Gaines, R.K., Jones, A., Mattes, C., Moses, K., Perry, J., Prior, K., Smith, S., Swilling, B., Rule, M., Joyner-Matos, J., 2016. Effects of Introduced Brook stickleback (*Culaea inconstans*) on benthic macroinvertebrate communities in the nearshore area of lentic systems in Turnbull National Wildlife Refuge, Washington. Northwest Sci. 90, 278–289. https://doi.org/10.3955/046.090.0306.

Wilkinson, L., 2011. ggplot2: elegant graphics for data analysis by WICKHAM, H. Biometrics 67, 678–679. https://doi.org/10.1111/j.1541-0420.2011.01616.x.

Williams, D.D., 2007. The biology of temporary waters (online edition). Oxford University Press. https://doi.org/10.1093/acprof:oso/9780198528128.001.0001.

Winter, T.C., 1976. Numerical simulation analysis of the interaction of lakes and ground water. USGS Numbered Series, Professional Paper 1001. U.S. Government Printing Office, Washington, D.C.

Winter, T.C., Harvey, J.W., Franke, O.L., Alley, W.M., 1998. Ground water and surface water: A single resource. USGS Numbered Series, Circular 1139. Denver, CO: U.S. Geological Survey, North Dakota Water Science Center, Toxic Substances Hydrology Program, Dakota Water Science Center.