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Fish-mediated impacts highlight the conservation value of esker kettle lakes

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Kettle lakes on eskers, formed during glacial retreat and isolated from surface hydrological networks, represent unique ecosystems that provide high-quality habitats for aquatic biodiversity and offer essential services such as drinking water. However, their ecological integrity is increasingly threatened by fish introductions and forest harvesting. We assessed the effects of fish presence on waterbird and macroinvertebrate communities in esker kettle lakes of Eastern Canada, using these taxa as indicators of ecosystem health. Comparisons were made with clay-belt lakes, the region's most common and typically fish-bearing waterbodies. Physicochemical conditions differed markedly between esker and clay-belt lakes but not between fishless and fish-bearing esker lakes. Waterbird richness and abundance varied among lake types, with several species negatively affected by fish presence. Macroinvertebrate communities were also shaped by fish, while fish assemblages differed between esker and clay-belt lakes. In esker lakes, fish richness was positively correlated with a forest disturbance index reflecting human access, forestry, agriculture, housing, and recreational activities. Our results highlight the distinctive species assemblages of fishless esker lakes and their high vulnerability to anthropogenic pressures. Protecting these ecosystems is essential for biodiversity conservation, and our findings provide a scientific basis for sustainable management integrating lake and forest ecosystems.

Keywords Biodiversity, Disturbances, Fishless lakes, Food webs, Macroinvertebrate, Waterbird

Human activities exert increasing pressure on natural systems, leading to widespread ecosystem degradation[1,2]. This degradation is primarily driven by habitat destruction, overexploitation, pollution, and the spread of invasive species[3]. Freshwater taxa are among the most threatened, with freshwater vertebrate populations in Canada declining by 84% between 1970 and 2014[4]. The human-mediated introduction of fish contributes substantially to freshwater ecosystem degradation[5]. This impact is especially severe in hydrologically isolated lakes, which often function as biodiversity hotspots distinct from the more homogenized communities of connected systems[6].

Kettle lakes located on eskers are formed by detached ice blocks during glacial retreat and are typically isolated from surface hydrological networks because of their higher altitude[7]. As a result, fish communities are often absent, with little possibility of natural colonization. However, when introduced, fish drastically alter the entire aquatic food web[8]. Because of their hydrological isolation, esker kettle lakes are primarily connected to groundwater and receive minimal external inputs from the surrounding watershed. This results in clear-water habitats with high dissolved oxygen concentrations, driven by oxygen-rich groundwater inflows and low rates of organic matter degradation. Such conditions create favorable habitats for species with high oxygen requirements[9].

Hasan, et al.[10] demonstrated that esker lakes differ markedly from the more abundant clay-belt lakes in the region. Esker lakes exhibited lower nutrient concentrations and conductivity but higher oxygen saturation (96% vs. 80%). In contrast, clay-belt lakes supported greater fish species richness, abundance, and diversity, as well as higher waterbird species diversity.

In addition to providing high-quality habitat for biodiversity, esker lakes deliver essential ecosystem services such as drinking water, recreation, boating, and swimming[11]. However, rising demands for critical trace elements for high technology and for forest products are placing increasing pressure on esker forests, with cascading

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impacts on lake biodiversity and ecosystem services[12]. Mineral extraction, such as sand and gravel removal, can alter natural slopes and increase organic matter inputs to the esker lakes[13].

In the terrestrial esker environment, Jack pine (*Pinus banksiana*), a valuable timber species (\$43.8 CDN/m^3), thrives and contributes significantly to the local economy[14]. Clearcutting simplifies stand structure and reduces biodiversity and sustainability, while also increasing temperature, organic carbon, nutrients and sediment inputs, and decreasing dissolved oxygen and water clarity in adjacent lakes[15].

Among human pressures, fish introductions can directly alter the structure and functioning of aquatic food webs. Kettle lakes on eskers are subject to both legal and illegal fish stocking, as sport fishing represents one of the main recreational activities of the region. Because these lakes are often easily accessible and appreciated for their sandy shores and transparent water, fish stocking by local residents is believed to be frequent. However, such introductions can be highly detrimental, as fishless kettle lakes on eskers host species often naïve to fish predation. Their ecological consequences on aquatic communities remain poorly understood. Understanding the biodiversity of fishless esker lakes and its relationship to anthropogenic pressures is crucial for developing conservation strategies and adaptive management of these unique ecosystems[13].

In this study, we reanalyzed data from Hasan, et al.[10], which included 48 lakes in the Abitibi-Temiscamingue region, to compare the physicochemistry and biological communities of esker lakes with and without fish, using clay-belt lakes as a reference. No additional field sampling was conducted for this study. While lakes in the clay belt are geomorphologically and biologically distinct from kettle lakes on eskers, they represent the vast majority of waterbodies in the region[16], allowing a meaningful comparison between the unique biological communities of esker lakes and the more widely distributed clay-belt lakes. We focused on waterbird and macroinvertebrate communities as indicator of ecosystem health. We also evaluated the relative importance of fish introductions compared to forest disturbances. Our hypotheses were that in esker lakes, fish presence modifies (i) lake physicochemistry through the excretion of nutrients and organic matter, (ii) waterbird communities through competition, and (iii) macroinvertebrate communities through predation. We further hypothesized that (iv) forest disturbances, defined as the presence or absence of (1) access to the lake, (2) agricultural activity, (3) forest harvesting, (4) houses, and (5) recreational activities, increase the likelihood of the presence of fish, and therefore reduce the abundance of waterbirds and macroinvertebrates in esker lakes. Results.

Lake physicochemistry

All values of physico-chemical variables were higher or similar in clay lakes compared to esker lakes with fish, which in turn had higher or similar values compared to esker lakes without fish (Table 1, see Figure S1 in supplementary material). pH values in clay lakes with fish (6.3 ± 0.6) were not significantly different from those in esker lakes with fish (6.4 ± 0.9) or without fish (5.8 ± 1.0), although values in esker lakes without fish tended to be lower than in esker lakes with fish ($p = 0.09$).

Lake biological communities

In total, 523 waterbird individuals from 23 species were identified to species. Waterbird species richness was higher in esker lake with fish (1.5 ± 0.3) than in clay lake with fish (1.0 ± 0.7; $p = 0.003$; Fig. 1). In average, 2.3 ± 1.5 individuals were observed in esker lakes without fish, 2.0 ± 0.7 in esker lakes with fish, and 1.4 ± 1.0 in clay lakes ($p = 0.008$; Fig. 2).

	Clay lake with fish **$N = 23$**	**Esker lake with fish** **$N = 12$**	**Esker lake without fish** **$N = 13$**	***p*-value**	**Post hoc test**
Water temp. (°C)	16.2 ± 4.9	17.3 ± 3.8	18.5 ± 1.8	0.334	a a a
O_2 (%)	79.6 ± 15.7	98.9 ± 5.6	93.4 ± 6.4	**< 0.001**	a b b
Spec. Cond. (mS/cm)	0.045 ± 0.035	0.03 ± 0.04	0.01 ± 0.02	**< 0.001**	a b b
pH	6.3 ± 0.6	6.4 ± 0.9	5.7 ± 1.0	0.09	a a a
TDP (μg/L)	23.5 ± 8.1	6.6 ± 3.1	6.9 ± 9.4	**< 0.001**	a b b
TDN (mg/L)	0.8 ± 0.2	0.3 ± 0.2	0.3 ± 0.3	**< 0.001**	a b b
DOC (mg/L)	36.5 ± 20.8	25.6 ± 15.8	16.0 ± 13.3	**0.006**	a ab b
Sand (%)	0.0 ± 0.0	7.9 ± 23.5	3.0 ± 6.4	**< 0.001**	a b ab
Sediments (%)	17.3 ± 23.9	7.3 ± 24.9	12.9 ± 29.1	**0.03**	a b ab
Wood (%)	11.0 ± 20.4	20.7 ± 33.2	5.2 ± 12.1	0.1	a a a
Rock (%)	0.1 ± 0.4	7.6 ± 24.2	0.5 ± 1.2	0.605	a a a
Benthic algae (%)	7.8 ± 18.6	18.4 ± 30.2	35.8 ± 32.6	**0.03**	a ab b
Macrophyte (%)	49.1 ± 28.8	33.5 ± 42.0	15.8 ± 24.7	**0.004**	a ab b
Peat moss (%)	0.0 ± 0.0	0.0 ± 0.0	0.6 ± 1.5	**0.05**	a ab b
Ericaceae (%)	0.4 ± 1.4	5.1 ± 9.4	7.0 ± 9.8	**0.002**	a b b

Table 1. Physico-chemical and habitat variables (mean ± SD) for each type of lakes. Water temp. = Water temperature, O_2 = Dissolved oxygen saturation, Spec. Cond. = Specific conductivity, TDP = Total dissolved phosphorus, TDN = Total dissolved nitrogen, DOC = Dissolved organic carbon, Sand, Sediment, Wood, Rock, Benthic algae, Macrophyte, Peat moss, Ericacea are % cover of littoral zone.

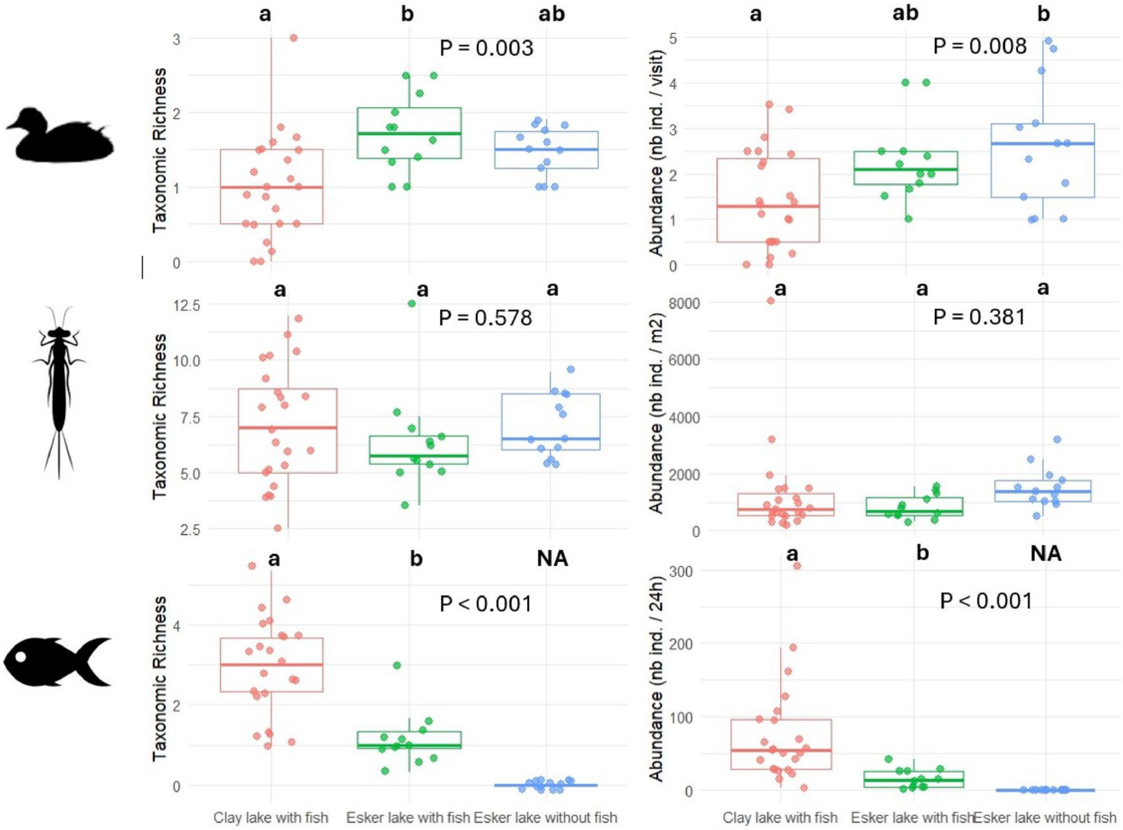

Fig. 1. Taxonomic richness and abundances of waterbirds, macroinvertebrates and fish assessed in clay lakes with fish (*N* = 23), esker lakes with fish (*N* = 12) and esker lakes without fish (*N* = 13). P values are from one-way ANOVA tests and significant differences are determined by Tukey tests and indicated by letters. Fish data have been tested with t-tests, excluding the category 'Esker lake without fish', which contains only zero abundances, providing null variance and violating ANOVA's model assumptions.

Five species were observed on esker lakes only: Bufflehead (*Bucephala albeola*), Common loon (*Gavia immer*), Marsh wren (*Cistothorus palustris*), Osprey (*Pandion haliaetus*) and Rusty blackbird (*Euphagus carolinus*). Three species were observed in lakes with fish only: Belted kingfisher (*Megaceryle alcyon*), Sandhill crane (*Antigone canadensis*) and Wood duck (*Aix sponsa*) and two species were observed in esker lakes without fish only (Marsh wren and Bufflehead).

In esker lakes with fish, the most abundant species were the Bonapart gull (*Chroicocephalus Philadelphia*), followed by the Ring-necked duck (*Aythya collaris*) and the Greater yellowlegs (*Tringa melanoleuca*) (Fig. 2). In esker lakes without fish, The Common goldeneye (*Bucephala clangula*) and Canada goose (*Branta canadensis*) were the most abundant species followed by the Mallard (*Anas platyrhynchos*). Fish presence did not affect waterbird community composition ($F_{(1,24)} = 1.19$, $p = 0.21$; Figure S2). However, it affected Common loon ($p = 0.004$, $p_{adj} = 0.04$), Belted kingfisher ($p = 0.0008$, $p_{adj} = 0.02$) and Rusty blackbird abundances ($p = 0.007$, $p_{adj} = 0.05$) (Fig. 3). Also, it tended to affect Common goldeneye ($p = 0.03$; padj = 0.16) and Canada goose abundances ($p = 0.03$, $padj = 0.15$).

A total of 5,727 fish individuals from 10 different species were caught. Fathead minnows (*Pimephales promelas*) and Finescale dace (*Phoxinus neogaeus*) were caught only in clay lakes, whereas Golden shiner (*Notemigonus crysoleucas*), Yellow perch (*Perca flavescens*), and Slimy sculpin (*Cottus cognatus*) were caught only in esker lakes. Fish species abundances were also higher in clay lakes (75.0 ± 69.0) than in esker lakes (15.4 ± 12.8; Fig. 1). In clay lake, the most abundant species was the Northern redbelly dace (*Chrosomus eos*), followed by the Fathead minnow. In esker lakes, the most abundant species was the Brook stickleback (*Culaea inconstans*), followed by Northern redbelly dace. Fish species composition was significantly different in clay lakes compared to esker lakes ($F_{(1,34)} = 4.08$, $p = 0.001$). Northern redbelly dace ($p < 0.001$), Fathead minnow ($p < 0.001$), Pearl dace ($p < 0.001$) and Finescale dace ($p < 0.001$) were significantly more abundant in clay lakes. Yellow perch ($p < 0.001$) and Golden shiner ($p = 0.03$) were significantly more abundant in esker lakes.

A total of 7,313 individuals from 35 macroinvertebrate taxa were identified. Macroinvertebrate taxa richness did not differ significantly among the three lake types ($F_{(2,46)} = 0.56$, $p = 0.58$; Fig. 1). Macroinvertebrate abundance was also not significantly different ($F_{(2,\ 46)} = 0.99$, $p = 0.38$), although higher abundances tended to occur in esker lakes without fish (Fig. 1). However, macroinvertebrate community compositions differ between the three types of lakes ($F(2,47) = 2.27$, $p = 0.007$) and between esker lake with and without fish ($F_{(1,24)} = 2.22$, $p = 0.03$). Chironomidae ($p = 0.004$, $p_{adj} = 0.11$) and Libellulidae ($p = 0.02$, $p_{adj} = 0.24$) were the taxa that differ the most

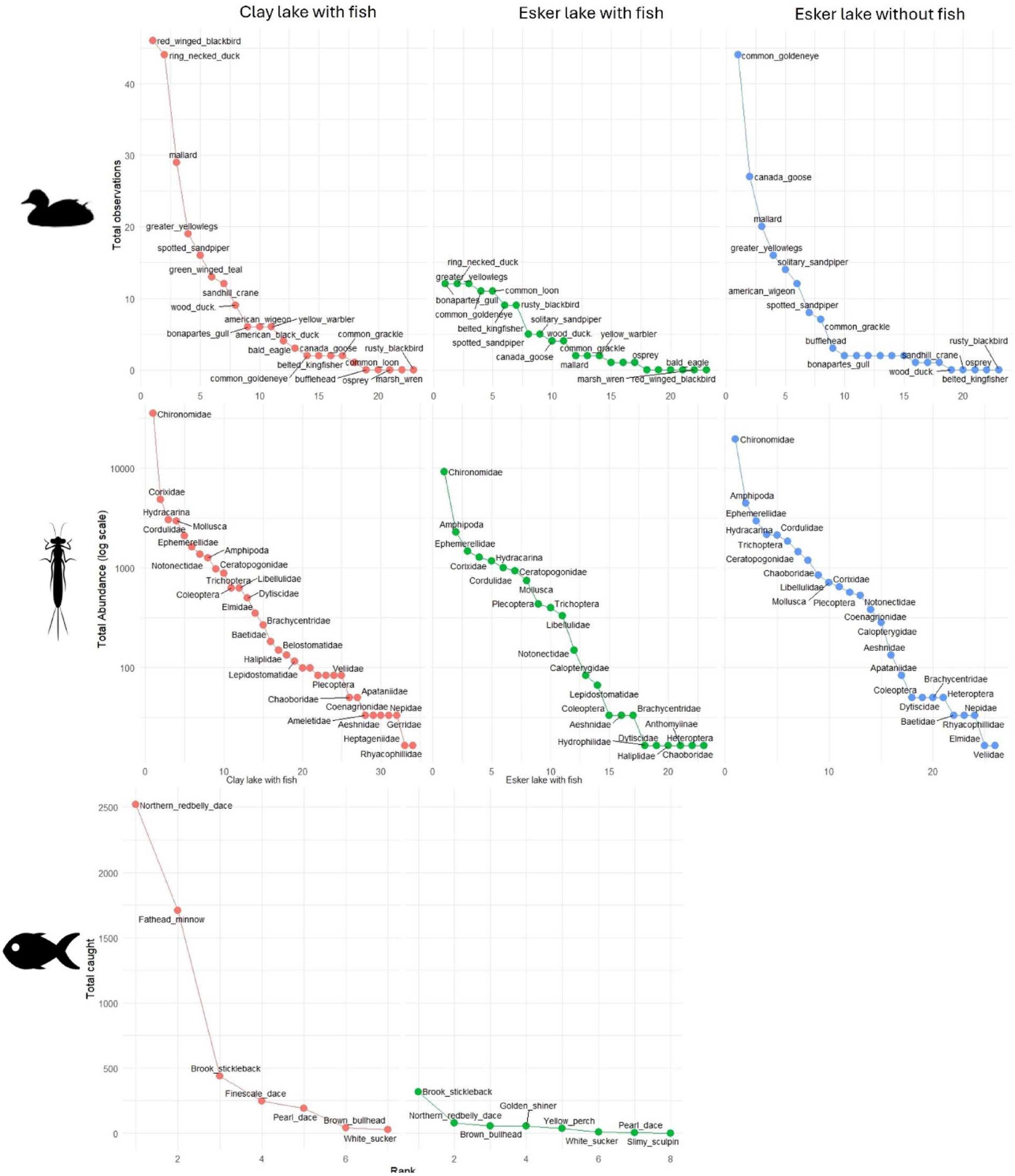

Fig. 2. Rank-abundance graph of the waterbird, fish and macroinvertebrate communities in the three types of lake. Waterbirds are total observations, and fish are total number of individuals caught per type of lake. Macroinvertebrates are log(total abundance) per type of lake as chironomids abundances overwhelmed each type of lake.

between the two lake types (Fig. 3). No taxa were only found on esker lakes. *Ameletidae*, *Gerridae*, *Belostomatidae* and *Heptageniidae* were only found in clay lakes. Moreover, in esker lakes with fish, no *Apataniidae*, no *Baetidae*, no *Coenagrionidae*, no *Elmidae*, no *Nepidae*, no *Rhyacophillidae* and no *Veliidae* were found. In esker lakes without fish, no *Anthomyiinae*, no *Haliplidae*, no *Hydrophilidae* and no *Lepidostomatidae* were found. In average, 1,221 ± 1,629 individuals were identified in clay lakes, 823 ± 423 in esker lakes with fish and 1,503 ± 714 in esker lakes without fish. In all lakes, the most abundant taxon was *Chironomidae* (Fig. 2). In clay lakes, the following most abundant taxa were *Corixidae*, *Hydracarina*, *Mollusca*, *Cordulidae* and *Ephemerellidae*. In esker lakes with fish, the following most abundant taxa were *Amphipoda*, *Ephemerillidae*, *Corixidae*, *Hydracarina* and

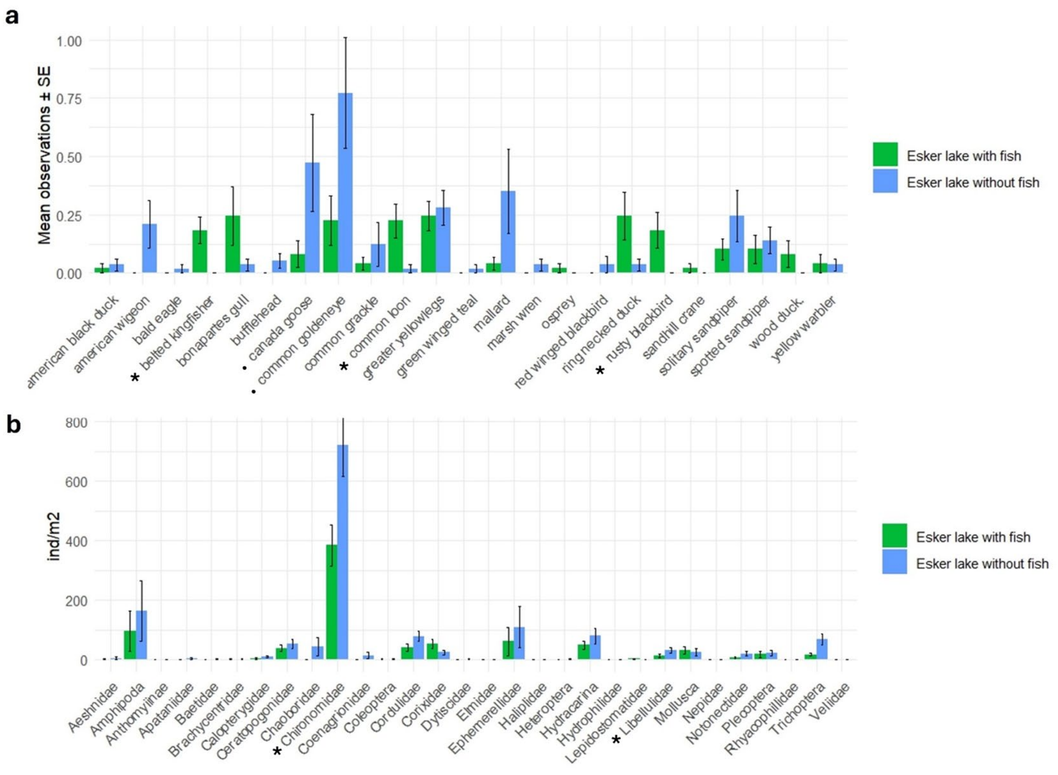

Fig. 3. Waterbird and macroinvertebrate abundances in esker lakes with and without fish. Stars indicate differences in abundances with statistical significance (p < 0.05) and dots indicate tendencies to significance (p < 0.05 but p_{adj} > 0.05).

Cordulidae and in esker lakes without fish, they were *Amphipoda*, *Ephemerellidae*, *Hydracarina* and *Cordulidae* and *Trichoptera* (Fig. 2).

Fish introduction and forest disturbances

The disturbance index was significantly higher in esker lakes with fish (estimate = 0.22, p = 0.048) compared to esker lakes without fish (Fig. 4). Taking separately, the only significative difference between the two types of lakes was regarding recreational activities. Esker lakes with fish were significantly more impacted by recreational activities (75% impacted, estimate = 0.31, p = 0.03) than esker lakes without fish with 31% impacted (Fig. 4). All esker lakes with and without fish were impacted by access (gravel or mud road). Agricultural activities had minor impact on both lakes, impacted 17% of esker lakes with fish and no lakes without fish. Harvesting and summer houses both impacted esker lakes with fish at 67%. Harvesting was the second most important disturbance affecting the esker lakes without fish (62%) and summer houses was the third (46%). The forest disturbance index had a significant impact on fish richness, but not on waterbird or macroinvertebrate richness (Table 2). Fish abundance was also significantly affected, but negatively, by the elevation of the lakes.

Discussion

Here, we show that fish presence in esker kettle lakes influences both waterbird and macroinvertebrate assemblages, even though lake physicochemistry did not differ between esker lakes with and without fish. We also found that forest disturbances correlate with fish richness, indicating that the presence of several fish species is largely due to human introductions.

Most of physico-chemistry variables of kettle lakes on esker differed from lakes on the clay belt but were not affected by the presence or absence of fish (Table 1). pH, water temperature, cover of wood detritus and cover of rocks did not differ between clay and esker lakes and lakes with and without fish (Table 1). Only pH tended to be lower in esker lakes without fish (p = 0.09), supporting the hypothesis that pH values may limit fish colonization in these lakes[17], although this needs to be investigated further.

Concentration in DOC, cover in benthic algae and in macrophytes were different between clay lakes with fish and esker lakes without fish. DOC concentration was highest in clay lakes, intermediate in esker lakes with fish and lowest in esker lakes without fish. The limited input of organic matter in esker lakes contributes to the lower DOC concentrations, along with limited nutrient inputs, which also restrict the growth of primary producers such as macrophytes and phytoplankton that release DOC[18]. Fish also contribute to the DOC pool and, therefore, to the higher DOC concentrations observed in lakes with fish[19]. As DOC of both terrestrial and aquatic origin feeds the microbial loop, it supports the entire lake food web[20] which likely affect macroinvertebrate, fish and waterbird communities. A shift in the dominance of primary producers was observed: from macrophyte-

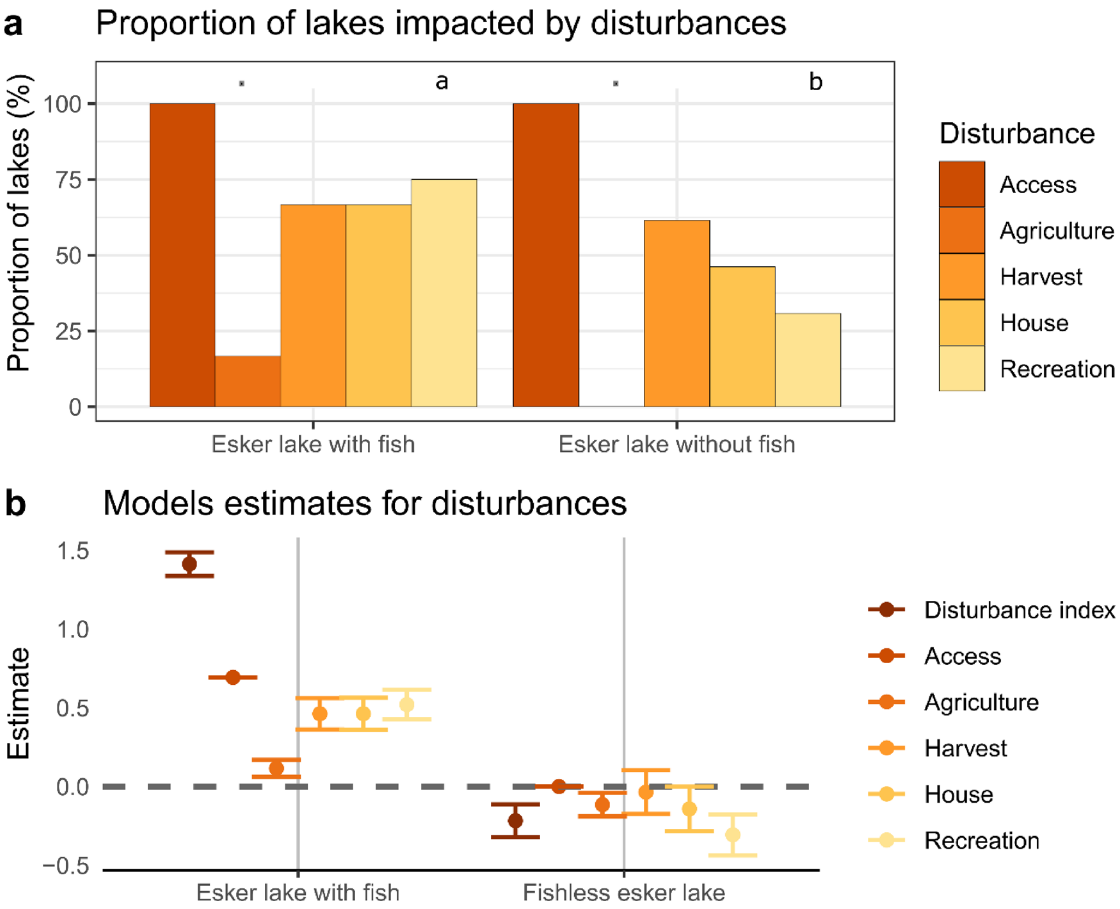

Fig. 4. Influence of forest disturbances in the two types of esker lakes, showing: (**a**) Proportion of lakes impacted by the five types of disturbances: Access, Agriculture, Harvest, House, and Recreation. Different letters indicate significant differences ($p \leq 0.05$) while dots indicate tendency to significant differences (. = $p \leq 0.1$); (**b**). Influence of each forest disturbance on the presence of fish, with parameters estimates and 95% confidence intervals from generalized linear models showing the predicted number of lakes impacted by each disturbance in esker lake with and without fish.

dominated clay lakes to benthic algae-dominated esker lakes without fish. Esker lake water is favorable to the growth of benthic algae as it is clearer than the turbid clay lake water[10]. Low nutrient concentration in the water column limits the growth of pelagic phytoplankton which diminished the competition with benthic algae that can access the nutrients from lake sediments similarly to the oligotrophic Arctic lakes[21,22]. In clay lakes, benthic algae and phytoplankton receive less light than macrophytes, which extend to or above the water surface[23]. Dominance of benthic, pelagic or littoral primary producers determine the entire lake food webs[24].

Sand cover was highest in esker lakes with fish, intermediate in esker lakes without fish and absent from clay lakes.Sandy or gravel substrates provide essential spawning grounds for many fish species[25]. For example, Pearl dace, Yellow perch, and Slimy sculpin require such habitats and were all found in esker lakes. Hasan et al.[10] captured Yellow perch (*Perca flavescens*) in 41% of sampled esker lakes and in none of the clay-belt lakes, suggesting local introductions of forage fish for predatory species such as walleye[26]. The presence of golden shiner (*Notemigonus crysoleucas*), a popular live-bait species in Eastern Canada[27], also points to the release of baitfish despite a provincial ban since 2017 (Government of Québec. (n.d.)). Together, these findings indicate that fish communities in kettle lakes on eskers are strongly influenced by human-mediated introductions. Waterbird species richness was higher in kettle lakes on esker than in lakes on the clay belt contrarily to fish species richness that was higher in lakes on clay and taxonomic richness of macroinvertebrates that was similar in all types of lakes. Five waterbird species were only found in esker lakes and no species were only found in clay lakes. Among the species only found in esker lakes, the Rusty Blackbird has a *Vulnerable* status on the International Union for Conservation of Nature's Red List of Threatened Species[28] and is designated as a species of *Special Concern* in Canada[29]. Other species were Bufflehead, Common loon, Osprey and Marsh wren that all serve as indicators of aquatic ecosystem health because they are sensitive to pollutants and habitat degradation. For example, Osprey have historically been affected by DDT and other contaminants, which caused eggshell thinning, but populations are now recovering[30]. The vulnerable IUCN status of the Rusty blackbird is mainly due to habitat degradation, such as wetland drainage, forest harvesting, and conversion of habitats for agriculture[31]. Rusty blackbird and Marsh wren, for instance, feed on a variety of aquatic and terrestrial prey[32,33] and therefore

Response Variable	Predictor	Estimate ± SE	*p*-value
Waterbird abundance	Macroinvertebrate Abundance	0.002 ± 0.001	0.018 *
	Fish Abundance	-0.005 ± 0.016	0.780
	Waterbird richness	-0.135 ± 0.200	0.506
	Macroinvertebrate richness	0.137 ± 0.116	0.249
	Fish richness	-0.329 ± 0.340	0.343
	Disturbance Index	-0.276 ± 0.374	0.461
	Elevation	0.003 ± 0.01	0.787
Macroinvertebrate Abundance	Fish Abundance	-0.017 ± 0.006	0.002 **
	Waterbird richness	-0.142 ± 0.074	0.055 .
	Macroinvertebrate richness	0.113 ± 0.055	0.039 *
	Fish richness	-0.114 ± 0.128	0.377
	Disturbance Index	-0.269 ± 0.145	0.062 .
	Elevation	0.003 ± 0.005	0.521
Fish Abundance	Waterbird richness	0.306 ± 0.245	0.212
	Macroinvertebrate richness	-0.211 ± 0.188	0.262
	Fish richness	2.412 ± 0.367	0.000 ***
	Disturbance Index	0.154 ± 0.367	0.680
	Elevation	-0.026 ± 0.012	0.036 *
Waterbird richness	Macroinvertebrate richness	0.036 ± 0.080	0.648
	Fish richness	0.066 ± 0.176	0.709
	Disturbance Index	0.216 ± 0.206	0.293
	Elevation	-0.002 ± 0.007	0.815
Macroinvertebrate richness	Fish richness	-0.018 ± 0.057	0.755
	Disturbance Index	0.022 ± 0.066	0.739
	Elevation	0.001 ± 0.002	0.637
Fish richness	Disturbance Index	0.454 ± 0.231	0.049 *
	Elevation	-0.013 ± 0.007	0.081 .

Table 2. Results of generalized linear models showing relationships among forest disturbance index, lake elevation, and the abundance and richness of biological communities (waterbirds, fish, and macroinvertebrates). Asterisks indicate statistically significant effects (*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$), and Dots indicate marginal significance (.$p < 0.10$). SE = Standard Error.

require healthy boreal biome with numerous terrestrial - aquatic interactions[34]. Aquatic prey, such as insect larvae, are rich in essential molecules such as polyunsaturated omega-3 fatty acids[35,36], while terrestrial berries, like blueberries, are rich in antioxidants[37]. Both molecules families are essential for the growth, immune system and reproduction of birds.

Fish species richness and abundance were significantly higher in the clay lakes compared to the esker lakes. Yellow perch and Golden shiner were significantly more abundant in the esker lakes, while Slimy sculpin were found only in these lakes. Sandy environments are important for yellow perch reproduction, invertebrates provide food for golden shiner, and clear, oxygenated waters favor Slimy sculpin, which explains their distribution[38].

Fish presence in esker lakes did not affect waterbird and macroinvertebrate taxonomic richness or abundance but did influence macroinvertebrate community composition and affected Belted kingfisher, Common loon and Rusty blackbird. It also tended to reduce the abundance of two waterbird species: Common goldeneye and Canada goose. These species feed on aquatic plants and invertebrates and may benefit from the absence of competition with fish. Eriksson[39] demonstrated through field experiments that Goldeneye compete with several fish species and prefer lakes without fish. Some duck species may also avoid lakes with predatory fish to reduce the risk of duckling predation. Dessborn, et al.[40] found that Goldeneye ducklings were significantly less abundant in lakes with Pike (*Esox lucius*), and adults spent less time on such lakes. Macroinvertebrate community composition differed between esker lakes with and without fish, primarily driven by Chironomidae and Libellulidae, which were more abundant in lakes without fish. Because Libellulidae and many Chironomids species are predators, they benefit from the absence of fish through reduced predation and competition[41].

Macroinvertebrate data were collected in 2020, whereas fish and waterbird data were collected in 2021. Although this temporal offset may introduce some variability, both years exhibited comparable climatic conditions and hydrological regimes[42]. As our analysis focuses on structural community differences among lake types, rather than on temporal dynamics, this difference is unlikely to have influenced the overall patterns observed. Additionally, our survey methods for waterbirds, fish, and macroinvertebrates likely captured the most common and abundant species, but rare or transient species may have been underrepresented. As a result, observed species richness may be slightly underestimated. Our study revealed that access roads (gravel or mud roads) are the primary disturbances impacting esker lakes, regardless of fish presence. Access roads are typically constructed to facilitate resource extraction, particularly timber[43]. The variable “harvest” was the second most important disturbance for esker lake without fish. Forest harvesting alters water physicochemistry by increasing inputs of organic matter and nutrients, leading to short-term declines in water quality[44], and long-term impacts when tree windthrow reduces the protective function of riparian buffers[45]. The majority of the boreal forest in Canada is managed using clear-cutting[46], which maximizes nutrient inputs from logged areas into aquatic environment and can lead to harmful algal blooms, toxin release, and eutrophication[47]. Sustainable land management such as partial cutting, on the contrary, reduce the nutrient loading from forest to aquatic environments[48] and reduce the impact of natural disturbances (e.g. insect outbreak) on boreal ecosystems[49,50]. Furthermore, land-sparing management practices such as partial harvesting and the maintenance of riparian buffers provide important habitats for bird communities[51]. Future sustainable land management should therefore not only expand the use of partial harvesting in forest management but also integrate both terrestrial and aquatic environments to more effectively conserve landscape integrity and boreal biodiversity[52], particularly in esker ecosystems that host unique species assemblages[10].

Following the variable "access", the second most important disturbance was "recreation" for esker lake with fish. Access roads often created with forest harvesting open previously isolated ecosystems to human activity, introducing a range of environmental impacts such as fishing, camping, and boating. These recreational activities are associated with an increased risk of accidental species invasions[53]. Because invasive species are often more flexible than native species in habitat use and diet[54], they can outcompete natives and, in worst-case scenarios, drive local extinctions. This effect is even more pronounced in isolated ecosystems, such as islands[55], and may therefore be particularly significant in isolated esker lake ecosystems. Humans have long introduced fish into lakes for recreational fishing and, through the release of live bait, have inadvertently facilitated the spread of invasive species[56]. This is also supported by the disturbance index, which indicates higher fish richness and suggests that the presence of several fish species in our study lake is partly due to human introductions. In contrast, lake elevation was negatively associated with fish abundances. This likely reflects natural colonization patterns, as lakes at higher elevations are less connected to the surface hydrological network and were more difficult to colonize following glacial retreat[57]. In esker lakes, we found that macroinvertebrate abundance was positively associated with waterbird abundance but negatively associated with fish abundance. This relationship likely reflects the complex interactions among the three components of esker food webs.

Conclusion

Our study demonstrates that fish presence in esker lakes influences macroinvertebrate and waterbird communities. It underscores the biological uniqueness of fishless kettle lakes on eskers and their vulnerability to fish introductions, as well as to forest disturbances. The marked contrasts in community composition between esker and clay lakes, including the occurrence of the Rusty blackbird (*Euphagus carolinus*), a species listed as *Vulnerable* by the IUCN, emphasize the need for tailored management and targeted conservation efforts. Kettle lakes on esker are particularly isolated ecosystems that can support distinctive and poorly documented species assemblages. Moreover, differences in waterbird communities indicate that these ecosystems sustain not only aquatic specialist but also broader aquatic-terrestrial food webs. Future research on the ecological consequences of fish introductions for food web functioning and community structure will provide essential knowledge to guide conservation policies in the face of growing anthropogenic pressures on these fragile ecosystems.

Methods

Study area

The studied area is located in the MRC Abitibi territory of the Abitibi-Témiscamingue region, Quebec, eastern Canada, within the fir–white birch forest bioclimatic domain[58]. The climate is continental, cold, and humid, with a mean annual temperature of 2.5 °C and an average annual precipitation of 800–900 mm[59]. This region is characterized by clay deposits related to proglacial Lake Ojibway–Barlow and the presence of esker[60]. Stands on sandy eskers are dominated by Jack pine forests, whereas clay plains are dominated by Black spruce (*Picea mariana*), trembling aspen (*Populus tremuloides*), and white birch (*Betula papyrifera*)[14,61,62].

In this study, both eskers and moraines are referred to as eskers, since despite their different geological origins, they share similar geomorphological characteristics[63]. Forest harvesting is the dominant anthropogenic activity in this territory, with 2,0 million m^3 of timber harvested in 2023, representing about 200–400 km^2 of harvested area[64–66]. A significant portion of the studied region is cultivated, primarily to feed cattle, with fodder accounting for a large proportion of the cultivated area[63]. In addition, tourism activities, including camping and hunting around esker ecosystem, are highly popular in the region[14].

All environmental and biological data used in this study originate from Hasan et al.[10]; no new field sampling was conducted.

Experimental design

Study lakes were selected based on two criteria: lake size (0.3–20 ha) and substrate type (clay/esker). We focused on lakes smaller than 4 ha to compare similar ecosystems and conduct a robust waterbird survey. A total of 48 lakes were selected from Hasan, et al.[10], including 23 clay lakes and 25 esker lakes (Fig. 5). Lakes were chosen based on the presence or absence of fish: 13 esker lakes with fish and 12 esker lakes without fish. The results presented here constitute a reanalysis of data from Hasan et al.[10] using this modified selection framework. All lakes were at least 1 km apart to minimize the likelihood of observing the same individual waterbirds across multiple lakes.

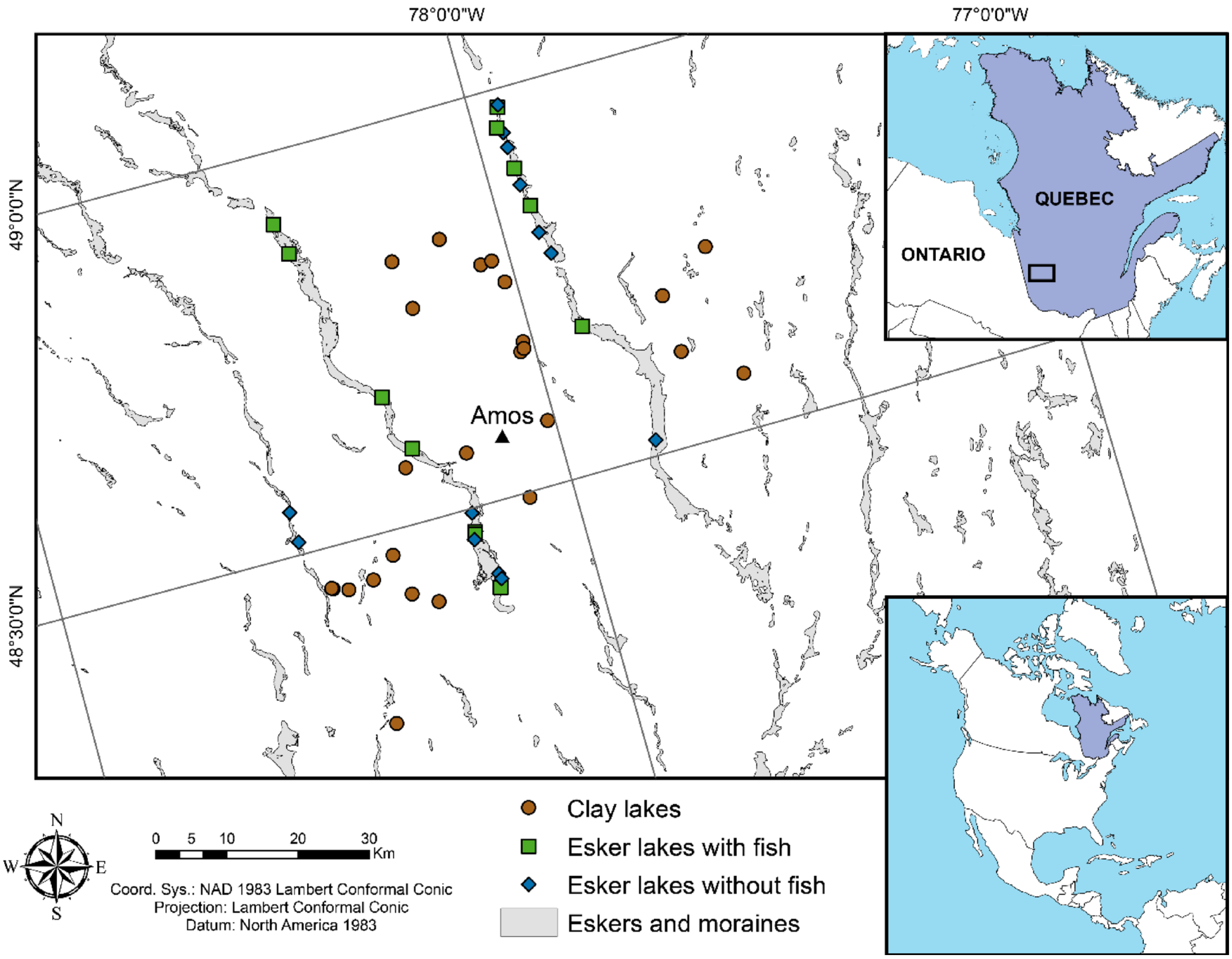

Fig. 5. Studied esker and clay lakes, with and without fish, in the Abitibi-Témiscamingue region, Québec, Canada. The map was created using ArcGIS Desktop v.10.8 (Environmental Systems Research Institute [ESRI], 2021; available at https://www.esri.com, by integrating georeferenced field plots with spatial data on lake types for the studied region obtained from Veillette, et al.[67].

Sampling design

Lake physicochemistry

Field sampling methods followed Hasan et al.[10], from which all data used in this study were obtained. In the original study, a 10-m transect was established along the shoreline in the littoral zone of each lake. At 2-m intervals, a 1 m² quadrat was placed to estimate covers of sand, sediments, rocks, woody debris, benthic algae, macrophytes, and mosses. Using a multi-parameter probe (RBR Concerto, Ottawa, Canada), Hasan et al.[10] measured specific conductivity (mS/cm), oxygen saturation (%), water temperature (°C), and pH at depth of 50 cm below the surface from the shore. To determine dissolved organic carbon (DOC), total dissolved phosphorus (TDP), and total dissolved nitrogen (TDN), Hasan et al.[10] collected 1-L water samples at the same point. Samples were filtered through 0.7-µm glass fiber filter (Cytiva, Marlborough, USA) immediately upon arrival at the laboratory on the same day. Filtered samples were then transferred into acid-washed 50-ml glass vials and sent to the GRIL laboratory at the University du Québec à Montreal, following Guimond, et al.[45].

Biological communities

Waterbird surveys Waterbirds were defined as species associated with aquatic environments during at least one stage of their life cycle. They belonged to the families Accipitridae, Alcedinidae, Anatidae, Gaviidae, Gruidae, Icteridae, Laridae, Pandionidae, Parulidae, Scolopacidae and Troglodytidae[68]. Fixed-point counts and perimeter searches were used to record individuals. Two independent observers identified and counted birds twice within a month, between May 24 and June 24, 2021. After a 5-minutes acclimatation period, both observers conducted a 20-minute waterbird survey. Binoculars (Nikon, Japan. 10 × 42 mm) and a spotting scope (Vortex, Middleton, USA. 20–60 × 80 mm) were used to detect and identify species. Surveys were carried out immediately after sunrise (05:00–11:00 am) when bird activity is highest[69].

Fish surveys Three Gee-Feets G40 minnow traps were deployed overnight in each lake during June and July 2021 to capture fish that primarily feed on macroinvertebrates. Captured fish were identified to species and released safely back into the water.

Macroinvertebrate surveys At two randomly selected sites in each lake during June and July 2020, macroinvertebrate samples were collected using a D-frame net (350 µm mesh; sampled surface area = 0.0604 m^2) by sweeping horizontally in the littoral zone for 30 s[70]. Samples were preserved in 90% ethanol. In the laboratory, the Huntsman Marine Laboratory (HML) beaker technique was used to replicate the samples[71]. Sorting and identification were performed using a stereomicroscope (Discovery V.12, Zeiss, Oberkochem, Germany). Taxa were identified using the key of Thorp and Covich (2014) for freshwater invertebrates[72], as well as the open-source data portal (macroinvertebrate.org).

Disturbance index measurement

To assess disturbances from the surrounding forested environment that may affect the lakes, we developed a forest disturbance index. Five variables were evaluated around each lake: (1) access to the lake (e.g., gravel or mud road); (2) agricultural activities within 100 m of the lake; (3) forest harvesting activities within 100 m of the lake, both measured using Google Earth Pro (version 7.3.4; imagery: CNES/Airbus, July 2021); (4) presence of summer houses or recreational vehicles occupied for at least one month during the sampling period; and (5) visible signs of recreational activities (e.g. campfires), recorded visually. The forest disturbance index was calculated for each lake by scoring the presence (1) or absence (0) of five disturbance types, resulting in values from 0 (undisturbed) to 5 (highly disturbed). Because the relative effects of these disturbances may differ among ecological components (e.g., fish introductions, fish abundance, waterbird abundance, and macroinvertebrate abundance), all disturbance types were weighted equally to ensure consistent treatment across lakes. In the absence of empirical evidence to assign differential weights, this approach provides a balanced and transparent representation of cumulative disturbance. Moreover, lake elevations were extracted from Google Earth Pro.

Statistical analyses

We compared physicochemical and biological variables between (1) esker lakes with fish, (2) esker lakes without fish, and (3) clay lakes with fish, used as a reference. Taxonomic richness and abundance of each biological group (waterbirds, fish, and macroinvertebrates) were calculated from the mean of four observations per lake (two visits × two observers) for waterbirds, three minnow traps for fish, and two net replicates for macroinvertebrates. One-way ANOVA and Tukey post hoc tests were performed to compare differences between taxonomic richness, abundance and physicochemical variables between the three types of lakes. Student's t-tests were performed to compare fish species richness and abundances between 'Esker lakes with fish' and 'Clay lakes with fish', excluding 'Esker lakes without fish', which contain only zero abundances. Null abundances do not provide the necessary variance to apply statistical tests such as ANOVA or generalized linear models. Rank-abundance curves were performed to highlight common and rare species in the three types of lakes[73].

To display the differences between the waterbird and macroinvertebrate community composition across esker lake with and without fish, Non-metric Multidimensional Scaling Analyses (NMDS) were executed. Differences in community composition between the two types of esker lakes were tested using Permutational Multivariate Analysis of Variance (PERMANOVA) with 999 permutations and Jaccard distances, which account for skewed distributions caused by zeros[74]. Wilcoxon rank-sum tests were used to assess differences in abundance for each waterbird and macroinvertebrate taxa. To account for multiple comparisons, p-values were adjusted using the Benjamini–Hochberg procedure (FDR correction).

To determine the influence of each disturbance and the disturbance index in the two types of esker lakes we practiced generalized linear model with normal distribution. Log transformations were applied when normality and homogeneity of variances of the residuals were not respected. Tukey post-hoc tests have been performed to examine the differences. To determine the response of the three biological groups to the disturbance index, elevation, and between themselves, we used generalized linear model with Poisson or negative binomial distribution.

All the analyses were performed using the R software[75] (version 4.0.3, R core Team 2015). Generalized linear models were fitted using the glm() function from the "stats" package.

Data availability

The datasets used during the current study are available from the corresponding author on reasonable request.

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Author contributions

Conceptualization: GG, MMG; Experimental design and site selection: MMG, GG; Fieldwork and data curation: AH, GG, MMG; Laboratory analysis: AH, GG, and MMG; Statistical analysis: MN, AH; Methodology: GG, MMG; Result interpretation: MN, MMG, GG, and AH; Validation; AH, MMG, and GG; Visualization and edition: MN, AH; Writing-original draft: MMG, GG; Writing–review: MN, MMG, GG; Supervision: MMG, GG; Project administration: MMG and GG; Funding: MMG and GG.

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Declarations

Competing interests

The authors declare no competing interests.

Additional information

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