UNIVERSITÉ DU QUÉBEC EN ABITIBI-TÉMISCAMINGUE

RÔLE DE L'HABITAT ET DES RESSOURCES ALIMENTAIRES DANS LA BIODIVERSITÉ DES OISEAUX AQUATIQUES DES LACS SUR ESKERS

MÉMOIRE
PRÉSENTÉ
COMME EXIGENCE PARTIELLE
DE LA MAÎTRISE EN ÉCOLOGIE

PAR

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MARS 2023

UNIVERSITÉ DU QUÉBEC EN ABITIBI-TÉMISCAMINGUE

ROLE OF HABITAT AND FEEDING RESOURCES IN THE WATERBIRD BIODIVERSITY OF ESKER LAKES

THESIS
SUBMITTED
AS A PARTIAL REQUIREMENT
FOR THE MASTER IN ECOLOGY

BY

AKIB HASAN

MARCH 2023

ACKNOWLEDGEMENTS

I am extremely grateful to my supervisor Professor Miguel Montoro Girona for his continuous motivation, guidance, support, and encouragement throughout my master's. I am also extremely grateful to Professor Guillaume Grosbois for his support, motivation, and guidance given to me throughout my research. The support I received from my supervisors for the last two years was incredible. I will never forget the way they helped me to survive in this new country. I want to use this opportunity to thank them deeply. I am also grateful to Professor Louis Imbeau for his wisdom and guidance in my master’s journey. Without the guidance and support from my supervising team, I could not be able to finish my master's successfully.

I would like to acknowledge Professor Jennifer Lento and Professor Anouschka Hof for their great support, valuable suggestions and motivation to improve the quality of this research work. I also thank H. Morin-Brassard, B. Dupuis, C. Scott, P. Blaney, A. Ghose, A. Subedi, S. Kim, H. Bai, F. Bergeron, V. Beaudet, MC. Mayotte, M. Joncas, C. Ferland and E. Drouin for fieldwork assistance and support. I am also grateful to Professor Philippe Marchand, J. Rodriguez, and Professor Fabio Gennaretti for their suggestion in statistical analysis. In addition, I would like to acknowledge H. Lavoie, C. Dany, V. Cloutier, O. Pitre, D. Laporte, M. Lacroix, I. Collin, M.H., Longpré, J.R., Gauthier and all the research, academic and non-academic members of the Forest Research Institute and Groupe de recherche en écologie de la MRC Abitibi

(GREMA) for the great support provided during this journey. I want to thank William Vincent for helping me with the French language correction for my thesis. I want to thank Anoj for helping me with thesis formatting and providing support throughout my master project. I want to acknowledge my office neighbour Sanghyun, Hengyi, Jerry, Aro, Latifa, Abdelaziz, Patrice, Gideon, El Yasse, Miray, Jonathan, Ablo, and Samuel for their time and mental support during countless times in Room 5021 throughout this master's journey.

Finally, I acknowledge my wife and colleague Tasnim Anjum Mou. It is a blessing to have a partner who understands the difficulty of completing a masters. I also want to thank my father (Md. Alamgir), my mother (Most Khursid Jahan) and my uncle (A S M Mostaque) for their support during my master's study.

FOREWORD

The Master thesis is divided into three chapters. The first chapter includes the general introduction which puts into context the research problem, the literature review and the objectives. Chapter II is presented in the form of a scientific article with authors "Akib Hasan, Miguel Montoro Girona, Louis Imbeau, Jennifer Lento, Anouschka Hof, and Guillaume Grosbois" and submitted for publication in the *Ecological Indicator* journal. The project idea and the experimental design were conceptualized by Prof. Guillaume Grosbois, Prof. Louis Imbeau and Prof. Miguel Montoro Girona one year before starting my master project, as well as the study site selection. The interns helped collect the data for bird inventory and fish surveys during the fieldwork in 2021. The fish survey method was approved by the committee of animal care ethics (UQAT) and followed the fishing permit obtained for this study from the Québec Ministère des Forêts, de la Faune et des Parcs (2021-05-27-055-08-SP). I had the main responsibility for analyzing the data and writing the article. My director and research committee members helped and assisted in the interpretation of the results, and critically and constructively revised the content of the article. The whole project and my scholarship were funded by the MRC-Abitibi Research grant obtained by Prof. Miguel Montoro Girona and Prof. Guillaume Grosbois. The third chapter contains the general conclusion, limitations, and implications for forest management and conservation. The appendix includes our research posters, popularised articles, and achievements.

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RÉSUMÉ

Les eskers sont des formations géologiques complexes qui fournissent des ressources cruciales dans les pays nordiques, telles que de l'eau potable, du sable/gravier, du bois et des sites de loisirs en plein air. Cependant, les connaissances sur la biodiversité et le fonctionnement des eskers sont très déficitaires. Les lacs d'esker sont différents des autres lacs boréaux car ils sont principalement alimentés par les eaux souterraines et les précipitations. Ainsi, les lacs d'esker devraient avoir des communautés de poissons réduites ou absentes, ce qui devrait à la fois favoriser l'abondance d'invertébrés aquatiques et une communauté d'oiseaux aquatiques d'eau diversifiée. Ce projet vise à caractériser les communautés d'oiseaux aquatiques associées aux lacs d'esker ainsi que leurs ressources, telles que les poissons et les invertébrés aquatiques, en utilisant une approche de réseau trophique. Cinquante lacs ont été échantillonnés, incluant des lacs situés sur eskers et des lacs sur la ceinture d'argile en Abitibi. Nous avons trouvé un indice de diversité de Shannon significativement plus élevé pour les oiseaux aquatiques dans les lacs d'argile (moyenne ± écart-type = 1,07 ± 0,44) par rapport aux lacs d'eskers (0,72 ± 0,24). L'indice de diversité de Shannon des invertébrés montrait une tendance plus élevée dans les lacs argileux (1,31 ± 0,46), par rapport aux lacs d'esker (1,24 ± 0,36). Pour les poissons, la valeur de l'indice dans les lacs d'argile (0,93 ± 0,29) était significativement plus élevée que dans les lacs sur esker (0,37 ± 0,30). De plus, les concentrations en nutriments, la conductivité et la couverture de macrophytes étaient plus élevées dans les lacs d'argile comparés aux lacs sur esker contrairement à la saturation en oxygène dissous. Les résultats suggèrent que la diversité biologique des lacs d'esker est plus faible à tous les niveaux trophiques du réseau trophique, mais qu'ils fournissent un habitat à quelques communautés rares et importantes. Ce projet représente la première caractérisation de la biodiversité associée aux lacs d'esker et fournira ainsi les informations écologiques de base nécessaires pour établir des stratégies de conservation pour ces écosystèmes vulnérables.

ABSTRACT

Eskers are complex geological formations in northern countries that provide crucial resources such as drinking water, sand/gravel, outdoor recreational sites, and productive forests. The sustainable management of these resources requires baseline ecological knowledge of the ecosystems associated with eskers. 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 lower Shannon diversity index for waterbirds (mean ± standard deviation; 0.7 ± 0.2), fish (0.4 ± 0.3), and 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. 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.

Keywords: Biodiversity, Biological conservation, Ecological indicators, Food webs, Forest management, Macroinvertebrates

CHAPTER 1

GENERAL INTRODUCTION

1.1 Research Context

North and Central America has about one-third of the world's water bodies with an estimated area of 2.5 million km^2 of which 51% is in Canada (Mitsch and Hernandez 2013). These waterbodies produce and store a large amount of carbon in the global environment stabilizing climate, being thus important ecosystems on the planet (Gurney et al. 2017). They recharge underground aquifers, reduce pollution, hold excessive water during the wet season, provide water in the dry season and provide habitat for invertebrates and waterbirds (MEA 2005). Additionally, Canadian freshwater habitats hold a large number of wild animals that depend heavily on aquatic resources for their survival (Slattery et al. 2011). For example, amphibians use wetlands for their reproduction and habitat (Seburn and Seburn 2000), and waterbirds use them for their feeding needs, and brood rearing (Hoppe et al. 1986). However, Canadian freshwater habitats are impacted by anthropogenic activities such as forestry practices and mining (Bradford and Irvine 2000; Chu et al. 2015; Maitland et al. 2016). Anthropogenic impacts in Canadian freshwater are driven by raising demands for fossil fuels, minerals and forest products which result in rapid alteration of the freshwater environment and aquatic biodiversity (Maitland 1995; Laurance and Balmford 2013). As a result, the population of freshwater vertebrates experienced an 84% decline between 1970 and 2014 (Desforges et al. 2022). Therefore, it is very important to understand the ecological functioning and biodiversity pattern of ecosystems associated with eskers, crucial ecosystems for all northern countries. To date, no large-scale systematic characterization of the biodiversity has been done in esker ecosystems in Canada.

Eskers are composed of irregularly stratified sand and gravel which were deposited by subglacial streams running below the ice sheet or in ice tunnels emerging at the ice margin of a retreating glacier (Bates and Jackson 1987). Eskers formed by these subglacial rivers gave rise to extensive fan-shaped deposits (Veillette et al. 2007a). In the Abitibi-Témiscamingue region of Québec (Canada), these eskers and moraines provide more than 73% of the water used for domestic purposes (MDDEP 2000). For example, the Saint-Mathieu/Berry esker located in MRC Abitibi provides fresh water to twenty thousand inhabitants and a commercial water bottle manufacturing company (Nadeau et al. 2015; Statistics Canada 2018). Moreover, eskers are a source of sand and gravel for the construction of roads (Nadeau et al. 2011) and support very productive Jack pine (*Pinus banksiana*) stands. They support forest ecosystems which generate important timber and non-timber products for the local economy. Eskers also provide habitats for biodiversity and wildlife and therefore act as important sites for outdoor activities e.g. hiking, bird-watching, mushroom picking, camping, hunting, and bait fishing (Nadeau et al. 2011). These activities are altering pristine habitats for biodiversity in lakes situated in the esker (Figure 1.1). Although the contribution of these eskers is crucial for economic development, baseline ecological information is lacking to build appropriate sustainable management that can balance the conservation of aquatic biodiversity and natural resource management.

Being ecological indicators, waterbirds play an important ecological role in the aquatic food web and can provide provisioning, regulating, and cultural services (Schummer et al. 2008). Conservation of the diversity of these waterbirds is difficult because their habitats span across different jurisdictions (Batzer et al. 1999; Mitsch and Gossilink 2000; Williams 2007). To implement a successful conservation strategy for these species, we must understand their ecology and feeding behaviour including fish and macroinvertebrates as potential food for waterbirds. Food web approaches are increasing to understand biodiversity patterns, because they can reveal the importance of interactions between taxa (LEVINS 1979; Safina and Burger 1985; Englund et al. 1992; Grosbois et al. 2020, 2022). Interactions between waterbird, fish and invertebrate communities are driven by competition and predation relationships (Kloskowski et al. 2010). Aquatic benthic macroinvertebrates play a very important role in the aquatic food webs providing essential nutrients for higher trophic levels such as waterbirds and fish (Batzer et al. 1999; Mitsch and Gossilink 2000; Williams 2007). Macroinvertebrates thrive in lakes with lower fish predation, which eventually benefits waterbirds that prefer invertebrates and less competition with fish (Eriksson 1979; Eadie and Keast 1982; Hurlbert et al. 1986; van Eerden et al. 1993). In contrast, piscivorous waterbirds benefit from lakes with increased fish populations (Lammens 1999). Therefore, habitat selection for waterbirds is necessary for their survival as it determines their feeding resources and competition with other species. Different species within the community, interact differently with other species. Moreover, the association of species in the community can be useful to understand food web interactions, habitat quality and biodiversity patterns of an ecosystem, this becomes even more important in esker lakes where information about biodiversity remains unknown (Figure 1.1) (Canterbury et al. 2000).

Figure 1.1 A kettle lake on the esker ecosystem. Akib Hasan 2021

1.2 Problem Statement

Esker ecosystems are particularly vulnerable to human pressure such as extraction of sand and gravel, and logging practices. Sand, gravel and log extraction from eskers have consequences to the natural ecosystem including removal of vegetation and soil surface, increase risk of pollution during mechanical activities and alteration of natural slopes (Hatva 1994; Smerdon et al. 2012; Nadeau et al. 2015). On the other hand, logging practices involve road construction for log transportation which has an impact on soil and vegetation, and this could alter the biogeochemical soil processes by changing the forest ecosystem. The alteration includes changes in nutrient uptake rates, microbial activity, water fluxes and soil condition (Kreutzweiser et al. 2008). Although esker ecosystems provide enormous ecological and economical services and are vulnerable to human activities, they are not managed differently from typical boreal forests. A multi-resource management approach should be implemented to reduce conflicts and reach the sustainable management of natural resources in esker ecosystems.

The lakes situated on the eskers (kettle lakes) can be connected to the esker's groundwater aquifers. These lakes are different from other boreal lakes because they are fed by groundwater and precipitations rather than surface inflows and are thus usually not directly connected to other surface aquatic ecosystems (Winter et al. 1998a). Esker lakes often have reduced or absent fish communities (Bourgeois and Nadeau 2013), which may promote the diversity and abundance of aquatic invertebrates at the base of the food web for numerous waterbirds. To our knowledge, no study has evaluated the aquatic biodiversity associated with esker lakes until now and we do not know what its role is in the boreal biodiversity at the landscape scale. However, ecosystems associated with eskers have very important potential from the conservational perspective because of their vulnerability and economical importance. A better understanding of this multi-resource ecosystem will contribute to formulating an effective management and conservation plan.

1.3 State of Knowledge

1.3.1 Eskers

About 20,000 years ago, all of Canada was covered by a thick ice sheet. Then, the glacier began to melt between 11,600 and 9,000 years ago releasing enormous volumes of water resulting in the deposition of sediments, including sand and gravel, in the subglacial tunnels or meltwater channels confined by glacier ice on both sides (Figure 1.3). A fan-like shape is formed with this linear accumulation of sediments. Under this iconic shape, an ancient riverbed is created that we call an esker (Figure 1.2) (Nadeau et al. 2011; Bourgeois and Nadeau 2013; Stroeven et al. 2016). Typically, eskers are very long and winding and can continue for hundreds of km with a height of fewer than ten meters to one hundred meters, however, they can be short and straight as well

(Stroeven et al. 2016). Ridges are usually thin and sinuous, but they can be flat as well and can have several crests or be segmented such as a string of beads (Rogerson 2013).

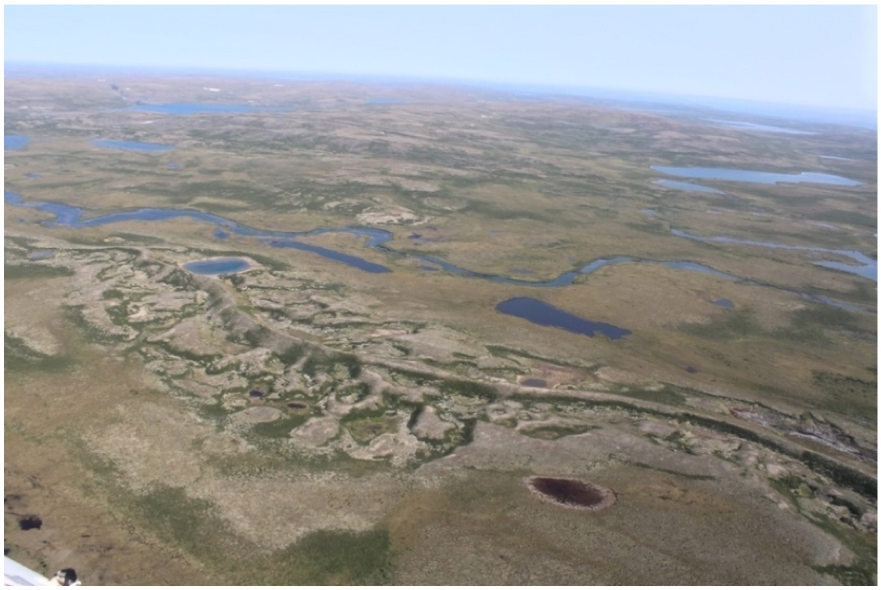

Figure 1.2 Esker ridge in the vicinity of the George River (QC) (Lamarche and Dubé-Loubert 2017)

Eskers are distributed across the areas that were covered by the former Laurentide Ice Sheet (North America), the Eurasian Ice Sheet, and the British-Irish Ice Sheet (Storrar et al. 2013a; Clark et al. 2018). For example, in Sweden, an esker named Uppsalaåsen passes through the city of Uppsala (Björklund 1973). In the United States, the great esker park runs through the back river in Weymouth, Massachusetts, and there are around one thousand eskers situated in the state of Michigan (Onesti and Hinze 1970). In Finland, eskers cover 3% of its land (Särkkä and Mäkelä 1999). In Scotland, esker kemb hills are 5 Km in length (Stone et al. 2010). In Canada, eskers are distributed over all glaciated areas, however, they are well-established and noticeable landmarks on the Canadian Shield (Cummings et al. 2011). The Thelon esker in the Northwest Territories and Nunavut (almost 800 km long) and the Munro esker beside Munro Lake in northern Ontario (250 km long) are the two largest eskers in Canada. In Quebec, several eskers are distributed north to south and formed during the last ice age (Figure 1.3) (Rogerson 2013).

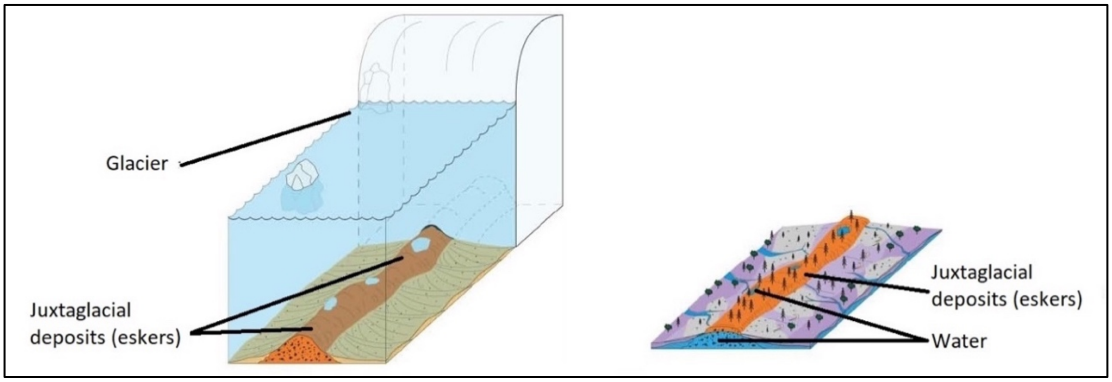

Figure 1.3 Formation of an esker under the glacier during the last ice age (left) and present condition of esker (right). Adapted from Nadeau et al. (2011).

1.3.2 Lakes on Eskers

Lakes play a valuable role in the function of boreal ecosystems and contribute to the global carbon cycle. They recharge underground aquifers, sequester pollutants, hold excessive water during the wet season, provide water in the dry season and provide habitat for invertebrates and waterbirds (MEA 2005). The lakes play an important role to support the breeding of birds with food resources. Throughout the spring, summer, and fall, insects such as midges, mosquitoes, and black flies, emerge in waterbodies in large quantities which is an important element for waterbirds to survive and meet their food demand (Cheskey et al. 2011).

Lakes are sometimes connected to the esker groundwater aquifers, and that groundwater-dependent system provides high ecosystem services such as habitat for aquatic communities (Figure 1.4) (Kløve et al. 2011). The surface runoff on eskers is limited because permeable sandy soil and gravel are deposited over time (Ala-aho et al. 2013). Instead, esker lakes are fed with groundwater subsurface flow which creates a closed basin waterbody. As these lakes are normally connected to the aquifer, their water physico-chemistry is dependent on esker groundwater physico-chemistry (Winter et al. 1998a). This relationship with groundwater also affects the water temperature and nutrients (Hayashi and Rosenberry 2002). Winter et al. (1998) categorized three types of lakes with groundwater flow systems. They are 1. Drainage lake: receive groundwater inflows all over its surface and occur in low elevated groundwater discharge areas. 2. Recharge lake: this kind of lake recharges water from the ground and is located in higher elevated areas. 3. Seepage lakes: These types of lakes are situated in between receiving groundwater in some areas and losing them to others.

Figure 1.4 The beautiful landscape attracts tourists for different lake-based activities. Akib Hasan 2021.

After the last ice age when the glacier melted, large blocks of ice sometimes broke off and then were quickly buried under a thick layer of deposits. As the ice slowly melted very slowly, it leaves a depression called a glacial basin or kettle (Corti et al. 2012; Bourgeois and Nadeau 2013). Some kettles are now dry, but some are filled with water and form kettle lakes. There are mainly two types of kettle lakes, one type is a depression formed from a partially buried ice mass and another type is a depression formed from a completely buried ice mass and by the collapse of overlying sediment. Their water supply comes from precipitation mainly.

1.3.3 Ecosystem Services

Eskers serve both ecological and economical services in Canada (Traynor 2001). Traditionally, they have been used as a source of gravel, sand, and rock which are being used in road construction, preparing concrete blocks, backfill in mines, manufactures of glass, pottery, agricultural activities and water filtration (Bourgeois and Nadeau 2013; Nadeau et al. 2015). Additionally, the esker landform was recognized as a prime location for archaeological sites because of its elevated structure (Epp 1985). This elevated structure serves as a road inside tundra ecosystems and reduces the disturbance with the displacement of insects with the high airflow (Traynor 2001).

Esker aquifers provide freshwater for domestic uses in many areas of the world e.g. Finland (Maries et al. 2017), Sweden (DE GEER 1968), Norway (Kløve et al. 2017), Ontario and Québec (Canada) (Sauriol 2016), Northwest Territories (Canada) (Traynor 2001). The MRC Abitibi region depends completely on esker water for its domestic and commercial uses for 20,360 inhabitants (Nadeau et al. 2011; Statistics Canada 2018). In addition to fulfilling the demand for freshwater for Abitibi, the water from eskers is used in commercial water bottling plant 'Eska' and water wells. This water is recognized as one of the purest fresh water in the world (Veillette et al. 2007b) because water comes through a natural filtration process in eskers. Esker ecosystems provide support to the jack pine stand to produce high-quality timber (Nadeau et al. 2011). Moreover, many people choose the esker environment for leisure activities including biking, birding, canoeing, fishing, hiking, swimming, picking blueberries and mushrooms, skiing, hunting, barbecuing and camping (Figure 1.5). The length of mountain biking trails in the Abitibi region is about 242 km and most of these trails are situated around eskers. Moreover, myco-tourism (mushroom tourism) in eskers is a very popular activity, especially around camping sites. Additionally, wild mushroom collection in the eskers has enormous economic potential. For example, Mutsutake (*Tricholoma matsutake*) observed in the esker ecosystem is considered one of the most expensive (100 mg mushroom = around 140$) mushrooms in the world (Yun and Hall 2004).

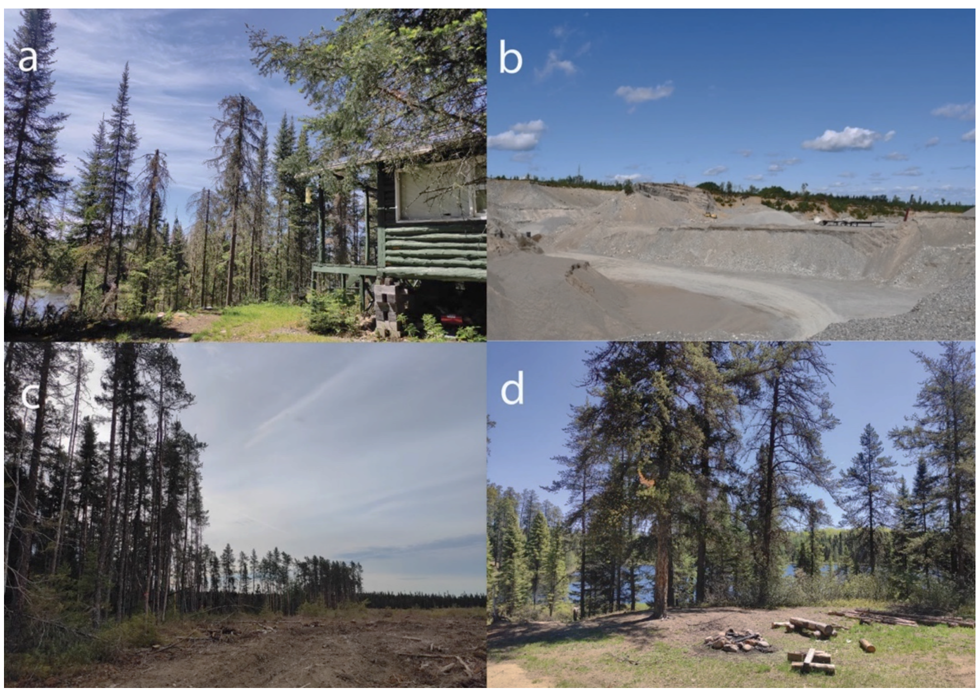

Figure 1.5 Anthropogenic activities around esker lakes, for example, a. summer house b. Sand and gravel extraction from esker in MRC Abitibi, c. forest harvesting around productive jack pine stand, d. Sign of camping around an esker lake. Akib Hasan 2021.

1.3.4 Biodiversity

Eskers of Abitibi fall under the balsam fir-white birch boreal bioclimatic domain and vegetation zone. However, the sandy ridge of eskers is dominated by jack pine (*Pinus banksiana*) and black spruce (*Picea mariana*) because these species are well adapted to arid conditions (Figure 1.6) (Bourgeois and Nadeau 2013). Individuals of most jack pine stands are of the same age because they are regenerated with fire events and are unable to grow in shade (Dubois 2012). The domination of jack pine stand in arid esker environments is successful because of the association with mycorrhizal fungi (Bourgeois and Nadeau 2013). Some of these mushrooms, such as matsutake (*Tricholoma matsutake*), chanterelles (*Cantharellus appalachiensis)*, crab mushroom (*Russula xerampelina*), true morels (*Morchella esculenta*) are edible and have a good commercial value (Miron et al. 2000). Blueberries (*Vaccinium angustifolium*), and sheep laurel (*Kalmia angustifolia*) are the two most common species that can be found in the undergrowth of jack pine stands on eskers. Most of the esker area is dominated by coniferous stands with a few hardwood and mixed stands.

Figure 1.6 Jack pine stands near a lake on esker. Akib Hasan 2021.

The boreal forest covers the eskers of the Abitibi region and provides habitat to 30 mammal species including the emblematic beaver (*Castor canadensis*), moose (*Alces americanus*) and black bear (*Ursus americanus*) (Bourgeois and Nadeau 2013). According to Kitikmeot et al. (2002), wolves (*Canis lupus*) also prefer to establish their den in eskers relative to other habitat types, because it is easier for them to dig in eskers while other types of habitats are dominated by bedrock, boulders, clay or permafrost. Additionally, according to Traynor (2001) migratory birds use eskers as landmarks and travel routes on their migratory journeys.

1.3.5 Factors Affecting Waterbird Habitat

Biotic factors such as food resources, competition with fish and abiotic factors such as pH, depth, water temperature, dissolved oxygen, and light penetration in water may influence directly or indirectly the habitat use of waterbirds in lakes. The availability of food resources such as macroinvertebrates is an important factor that affects habitat use by waterbirds, especially in the breeding season (Sugden 1969; Cheskey et al. 2011; Baschuk et al. 2012). Waterbirds have a very specific need for food when they are young. For example, ducklings eat mainly insects during their first few days and adapt to other kinds of food over time (Collias and Collias 1958; Dessborn et al. 2009). Essential amino acids and fatty acids are very important for waterbirds because they cannot be synthesized in their body *de novo* (Wakil 1989; Wang et al. 2018). Essential fatty acids are synthesized by algal microbial communities using *de novo* lipogenesis and consumed and assimilated by invertebrate communities (Ji et al. 2015). Certain species of waterbirds can therefore meet their diet requirements by consuming aquatic invertebrates, which are very rich in various amino acids and essential fatty acids (Sugden 1969; Bretta et al. 2009; Nyffeler et al. 2018). Highly unsaturated fatty acids for example, docosahexaenoic (DHA) and eicosapentaenoic acids (EPA) are important for the growth, development and immune system of waterbirds and demands for amino acids are higher during the breeding season (Fredrickson and Reid 1988; Hebert et al. 2009). The presence of fish communities in waterbodies is considered an important factor that can affect the abundance of invertebrates in the environment. For example, common goldeneyes (*Bucephala clangula*) prefer lakes that do not have fish or have lower competition with fish for food resources (Figure 1.7c) (Eriksson 1979). Many fish species feed on invertebrates which causes them to compete with birds for food resources (Eadie and Keast 1982; Hunter et al. 1986; Murakami and Nakano 2002). Thus, the presence of fish communities could affect waterbird populations in the waterbodies and affect their breeding success.

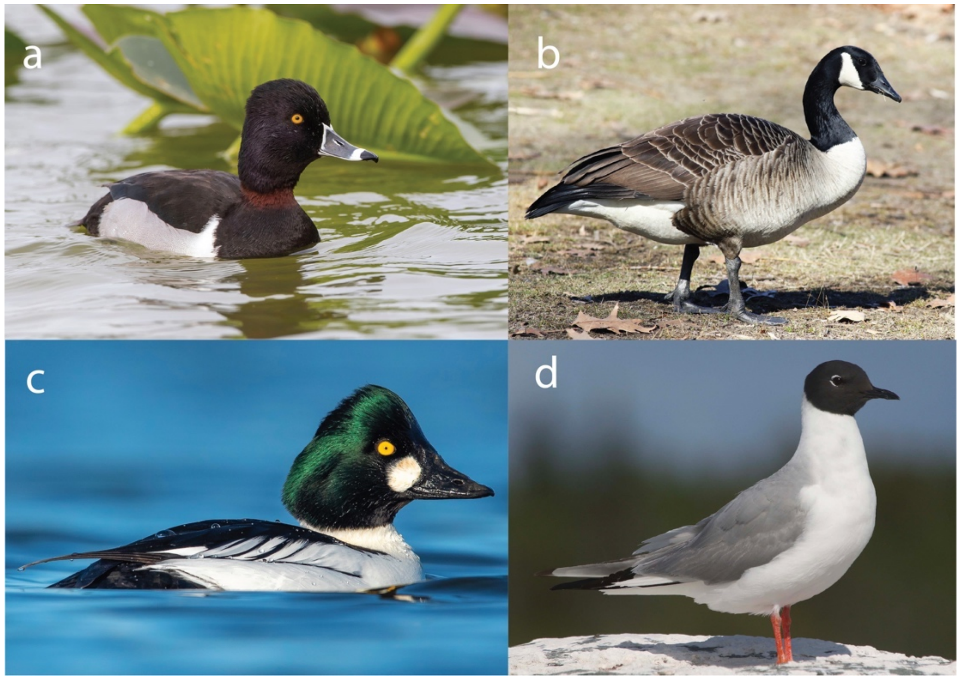

Figure 1.7 a. Ring-necked duck (Aythya collaris), b. Canada goose (Branta canadensis), c. Common goldeneye (Bucephala clangula), d. Bonaparte's Gull (Chroicocephalus Philadelphia) (Photo: eBird, 2022).

1.3.6 Factors affecting aquatic food web

The water pH can have a significant impact on lake biodiversity. The pH affects the invertebrates and fish more than waterbirds. When pH is too high or too low, only a few species can stay in extremely acidic or basic environments (Lacoul et al. 2011). The presence of fish can be reduced with low pH which can positively affect both invertebrate and waterbird populations (Mcnicol et al. 1995). Other physical characteristics of the aquatic ecosystem, namely the depth, temperature, dissolved oxygen, and water clarity, can also affect access to food resources (Pöysä and Virtanen 1994a). Colder groundwater recharge in esker lakes is responsible for higher dissolved oxygen which can provide better habitat for invertebrate and fish communities

(Lancaster and Allan 1995; Rautio and Korkka-Niemi 2011; Justus et al. 2014). Additionally, clear water enables higher light penetration in esker water, thus, increased photosynthesis results in the higher presence of algal food resources for invertebrate communities (Jeppesen et al. 1998). Moreover, the depth of the lake affects the dissolved oxygen concentration as well as invertebrate abundance in lake water (Carroll et al. 2015).

1.3.7 Physical Habitat and Macrophytes Communities

Aquatic plants that grow in or near water, either emergent, submerged or floating, are called macrophytes. The macrophytes can grow in wetlands or in between wetlands and land, and even on shores in periods of low water (Hadad et al. 2006). Aquatic macrophytes can be represented following plant divisions, Cyanobacteria, Chlorophyta, Rhodophyta, Xanthophyta, Bryophyta, Pteridophyta and Spermatophyta (Chambers et al. 2008). In lake ecosystems, macrophytes produce the highest amount of biomass which influences the aquatic communities (Esteves 1988). Moreover, they have a significant impact on the relationship between fish communities and invertebrates (Hupfer and Hilt 2008). They also provide refuge from fish, nutrients and habitat for aquatic invertebrates, recycle carbon dioxide and produce oxygen, and act as a primary food source for some fish and waterbirds (Christie et al. 2009). Macrophytes have impacts on aquatic ecosystems and sunlight penetration in the water (Brix 1997). Because of the underwater environment, macrophytes have limited capacity to access carbon and light and need to practice different adaptation mechanisms to survive (Pedersen et al. 2013). For example, they can uptake CO_2 from bicarbonate substances in the water (Pedersen et al. 2013). Moreover, light is the primary source of energy for all aquatic life in the water. The rates of production of energy in phytoplankton are reliant on the depth and spectral quality of light and optical attributes of water (Tanabe et al. 2019). All green organisms follow one basic chemical equation while producing carbohydrates and dioxygen from CO_2 and water using light energy.

1.3.8 Fish Communities

Fish communities are part of a complex aquatic food web both as a consumer of plants, invertebrates or other vertebrates and as prey to several vertebrates and waterbirds (Traugott et al. 2021). Therefore, understanding the food web interaction is the key to understand the fish community dynamics in an aquatic ecosystem. The ecosystem services provided by fish include regulation of population dynamics of macroinvertebrates, bioturbation, carbon exchange, passive transportation of nutrients, acting as prey to birds, mammals and other vertebrates, purifying water and mitigation of disease spreads (Holmlund and Hammer 1999). Not only fish communities contribute ecologically, but also contribute economically around the world. Further, recreational fishing in lakes is considered a major tourism activity (European Commission 2013). Anthropogenic threats such as habitat alteration, species invasion and pollution are causing fish species extinctions and the decline of native fish communities in both freshwater and marine ecosystem (Reynolds et al. 2008).

1.3.9 Invertebrate Communities

Aquatic invertebrate communities are a very important component in freshwater ecology because they affect the aquatic ecosystem energy transfer and provide food for waterbirds and other dependent aquatic fauna (Teal 1962; De Szalay and Resh 1996; Anderson and Smith 1998). Furthermore, they play the role of synthesizing organic components in the food web (Safran et al. 1997; Anderson and Smith 2000). Due to the complete dependency on invertebrates during the breeding season, waterbirds are affected by the structure and abundance of invertebrate communities (Colwell and

Landrum 1993; Safran et al. 1997; Anderson and Smith 1998). Moreover, the diversity of invertebrates can indicate the lake's hydrological history, wetland functioning capacity and ecological health (Nudds 1983; Anderson and Smith 1998; Twedt and Nelms 1999). For example, Sharma et al. (2006) in India; Masese et al. (2009) in Kenya; Ajuzie (2012) in Nigeria; Garrison Sanders et al. (2011) in USA (Michigan); Bredenhand (2005) in South Africa have studied the use of macroinvertebrates as bioindicators of water quality. Many macroinvertebrates such as the family Diptera begin their life cycle in lakes as being larvae, eggs and nymphs (Figure 1.8b). Then, they leave the water to fly away as pupae or adults. The adult often feeds on a terrestrial environment to reduce competition with the young (Merritt et al. 2009). On the other hand, many macroinvertebrates including crustaceans, amphipods, isopods or insects such as Dytiscidae (Order: Coleoptera) spend their whole life in lakes or the mud on the shore (Yee 2014).

Figure 1.8 a. Macroinvertebrate order Plecoptera, b.order Diptera, c. order Odonata (Photo: Macroinvertebrates.org 2022).

1.3.10 Food web Approach

Esker lakes are different from other boreal lakes because they are fed by groundwater and precipitations rather than surface inflows and are thus usually not directly connected to other surface aquatic ecosystems (Winter et al. 1998a). Esker lakes often have reduced or absent fish communities (Bourgeois and Nadeau 2013), which may promote the diversity and abundance of aquatic invertebrates at the base of the food web for numerous waterbirds. Therefore, understanding the trophic relation among waterbirds, fish and macroinvertebrates is required for the characterization of ecosystems.

Interactions between waterbird, fish and macroinvertebrate populations are related through competition and predation (Kloskowski et al. 2010). Aquatic macroinvertebrates provide essential nutrients for waterbirds and fish (Batzer et al. 1999; Mitsch and Gossilink 2000; Williams 2007). Macroinvertebrates thrive in lakes with lower fish perdition, which eventually benefit waterbirds that prefer invertebrate and less competition with fish (Eriksson 1979; Eadie and Keast 1982; Hurlbert et al. 1986; van Eerden et al. 1993). In contrast, fish-eating waterbirds profit from lakes with an increased fish population (Lammens 1999). Therefore, habitat selection for waterbirds is very important for their survival because they use them for their feeding needs and reproduction (brood rearing) (Hoppe et al. 1986).

1.4 Objective and hypothesis

The main objective of the study is to evaluate the waterbird biodiversity associated to esker lakes and identify its environmental drivers using a food web approach. Our specific objectives are: (i) to assess the aquatic resources for waterbirds in lakes such as the type of habitats, the quantity of macrophytes and macroinvertebrate communities. (ii) to assess the species richness, evenness and diversity of waterbirds and their food resources (fish and macroinvertebrates) and record the occurrence of indicator species for each taxon. Finally, we will compare waterbirds and habitat variables between esker lakes and boreal lakes situated on the clay belt which are the most abundant lakes from the region in order to define the attributes and factors influencing the waterbird biodiversity associated to esker lakes. Based on our goals our hypotheses are:

Hypothesis 1: The abundance and diversity of macroinvertebrates will be higher in esker lakes compared to the lakes on clay because of the higher availability of resources and reduced fish predation. We expect that esker lakes have higher-quality habitats with 1) lower water temperature because of their water recharge from groundwater and as a result, higher dissolved oxygen and 2) higher penetration of light because of water transparency which increases algal and macrophyte production.

Hypothesis 2: The richness, diversity and abundance of waterbirds will be higher in lakes on eskers compared to the lakes on clay because of more availability of their food resources in the kettle lakes i.e., higher abundance and diversity of aquatic invertebrates.

Hypothesis 3: Common goldeneye (*Bucephala clangula*) will be strongly associated with the habitat of kettle lakes on eskers because these lakes can provide the specific habitat required during their breeding period, i.e., less competition with the fish community (Figure 1.9).

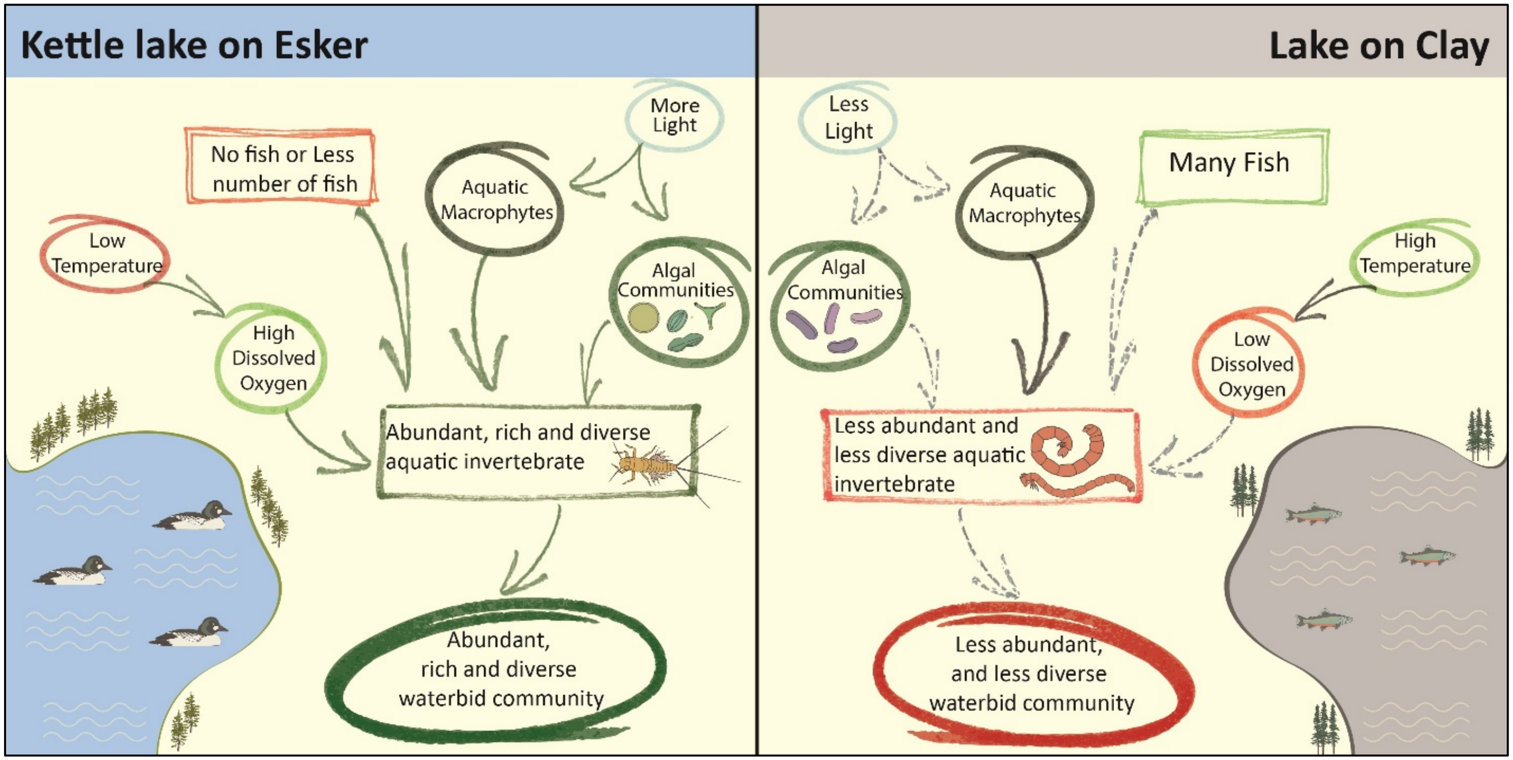

Figure 1.9 Conceptual hypotheses including both types of lakes and associated factors. In the figure, green arrows are representing positive effects while arrows with mezzotint dots are representing negative effects. Here, Left Panel, Tree = Jack Pine, Invertebrate = Mayfly, Algae = Diatoms, Waterbird = Common goldeneye and Right Panel, Tree = Black spruce, Invertebrate = Chironomids, Algae = cyanobacteria, Fish = Brook trout. (Design and illustration by Akib Hasan, idea and framework were made by M. Montoro Girona and G. Grosbois and the organism illustrations by E. Imbeau. Illustration Software: Adobe Creative Cloud 2020)

CHAPTER 2

MANUSCRIPT

Indicator species reveal the physical and biological singularity of esker lake ecosystems

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[1]*The article is submitted to Ecological Indicator in March 2023*

2.1 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 (Monk and Baird 2014; Messager et al. 2016). 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 are driven by rising demands for fossil fuels, minerals, and forest products, resulting in the rapid alteration of the freshwater environment and aquatic biodiversity (Maitland 1995; Laurance and Balmford 2013). 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). As a result, freshwater vertebrate populations experienced an 84% decline between 1970 and 2014 (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 (Nadeau et al. 2011; Bourgeois and Nadeau 2013; 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

(Winter et al. 1998b; Ala-aho et al. 2013). 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 (Winter et al. 1998b; Kløve et al. 2011). 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; Smerdon et al. 2012; Nadeau et al. 2015). 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 1994a). 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 (Steedman and Kushneriuk 2000; Smith et al. 2003; Palviainen et al. 2022).

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 (Eriksson 1979; Eadie and Keast 1982; 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, although piscivorous waterbird are less abundant because of the higher availability of food resources and reduced or absent fish predation. 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.

2.2 Materials and methods

2.2.1 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 more than 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) (Figure 2.1a) (Dyke and Prest 2008; Storrar et al. 2013b). 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).

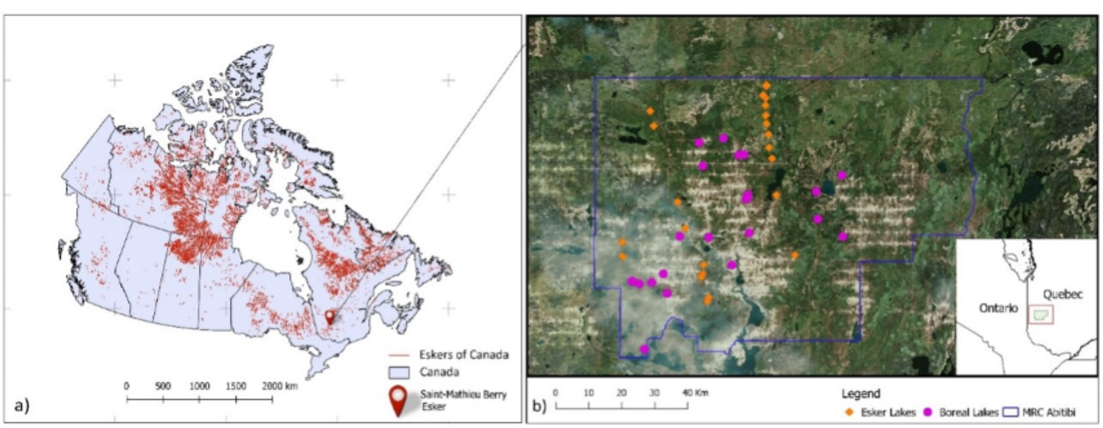


Figure 2.10 (a) Distribution of eskers in Canada and the study area location. Adapted from Storrar et al. (2013b); (b) study sites located in the Abitibi regional county municipality, Quebec, Canada.

2.2.2 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). All selected lakes were at least 1 km apart to limit potential with the same waterbird individuals (Desjardins et al. 2021).

Figure 2.2 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.

2.2.3 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 hours. For DOC analyses, each vial was kept in the oven at 450 °C for 4 hours to remove any potential trace of carbon. The samples were sent to the 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 and key informant interviews whenever applicable.

2.2.4 Biological data compilation

2.2.4.1 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 (Figure 2.3). 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 minutes. 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 (05h00–11h00) when birds search for food on the lake surface (Bennett 1967; Rumble and Flake 1982).

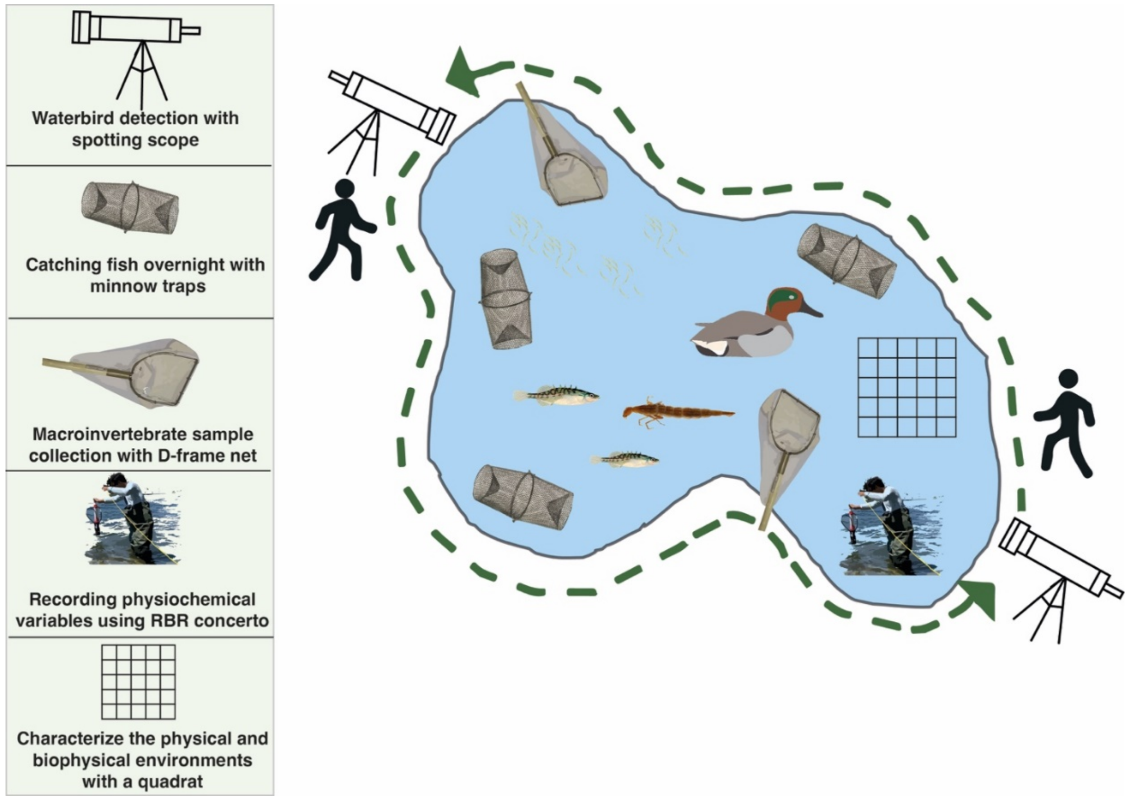


Figure 2.3 Visual representation of 20 minutes of point counts and flush count paths for waterbird surveys, trap locations for fish surveys, D-frame net for macroinvertebrate surveys, and physicochemical measurements for habitat characterization

2.2.4.2 Fish surveys

Three Gee-Feets G-40 minnow traps were set overnight in each lake between June and July 2021 (Figure 2.3) to study fish species richness and abundance. These minnow traps were very effective for the fish communities feeding primarily on macroinvertebrates. As this fishing method was ineffective at catching larger fish such as adult Walleye (*Sander vitreus*) or Brook trout (*Salvelinus fontinalis*), we also walked along the lake margins and counted all sizeable visible fish. 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.

2.2.4.3 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) (Figure 2.3). 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).

2.2.5 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 = $-\sum p_i \log p_i$, where p_i is the proportion of individuals belonging to the ith species) and species evenness were calculated for each lake using the R package vegan (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) with the R package FactoMineR (Lê et al. 2008). Each variable was standardized and tested for collinearity among different variables with the principal components. 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. 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 (Supplemental Material 1) (Boeck et al. 2011). Finally, all data were plotted using the R package ggplot2 (Wilkinson 2011).

2.3 Results

2.3.1 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 (Figure 2.4a,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, Figure 2.4c). The mean pH value was similar in both lake types (t = 1.2, p = 0.2) (Figure 2.4d). 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%) (Figure 2.5e). The mean percentage cover of macrophytes in clay lakes was 80% higher (p = 0.008, t = 2.7) than in esker lakes (24.3%) (Figure 2.4f).

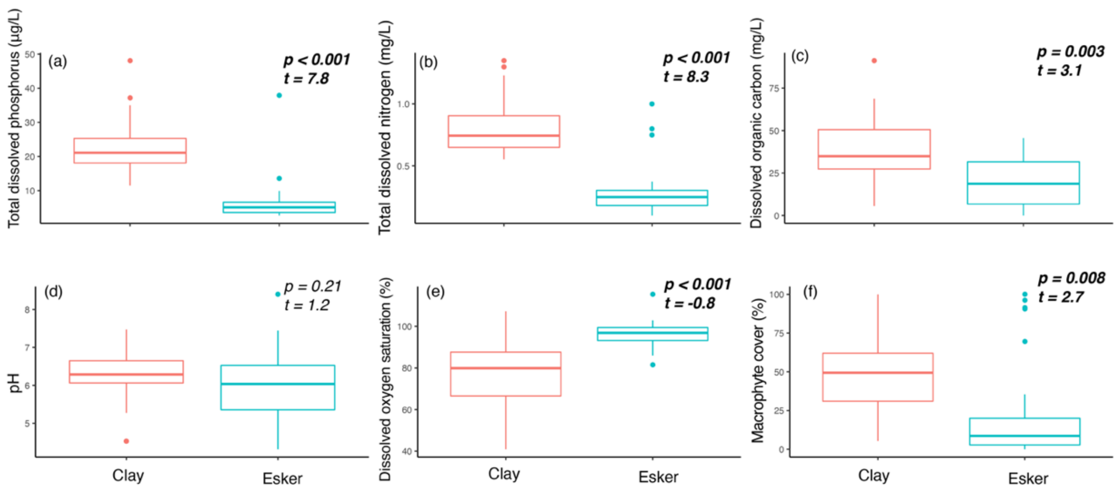


Figure 2.4 Physicochemical and habitat-related variables measured in the esker and clay lakes

2.3.2 Species diversity and abundance

2.3.2.1 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 ($t_{richness}$ = 1.7, $t_{diversity}$ = 2.2, $p < 0.1$ for both; Figure 2.5a,d,g,j).

2.3.2.2 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 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) (Figure 2.5b,e,h,k).

2.3.2.3 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; Figure 2.5c,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).

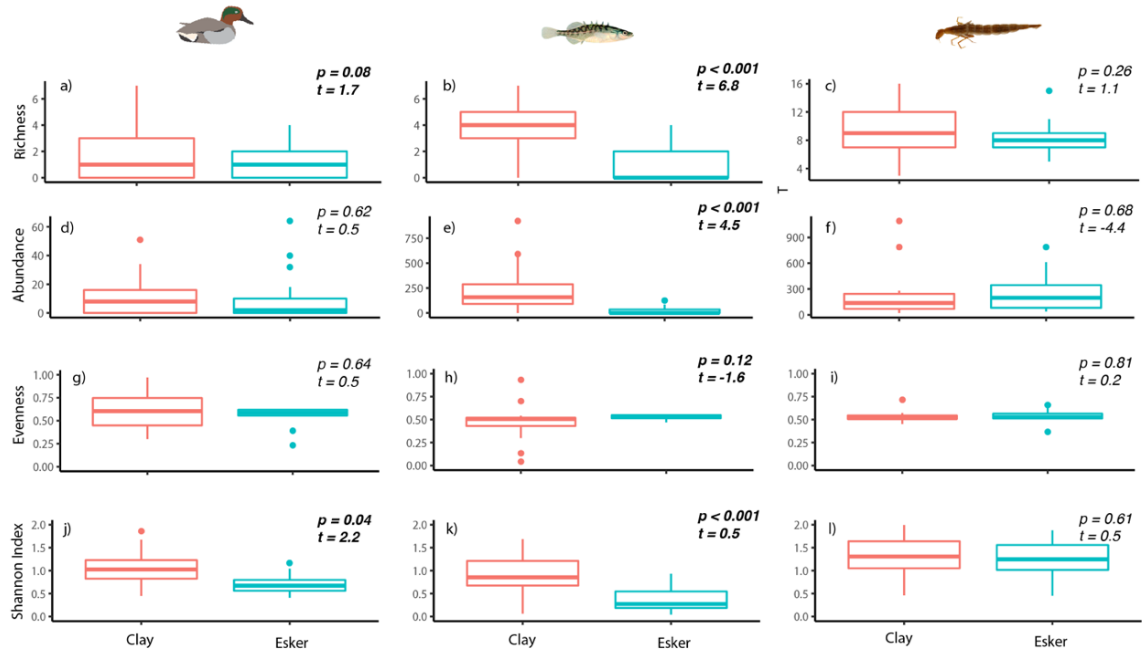
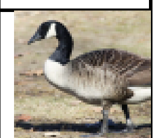
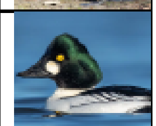
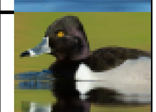


Figure 2.4 Biodiversity indicators of waterbirds, fish, and macroinvertebrates in the esker and clay lakes. Here, richness is the total number of species or families per lake or net catch or sampled surface; abundance is the total number of individuals per lake or net catch or sampled surface; evenness is the distribution of abundance across the species community (scaled 0–1); diversity is the number of different species in the community

2.3.2.4 Indicator species

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 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).

Table 2.1 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	

2.3.3 Factors explaining the food web patterns

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 (Figure 2.6). 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.

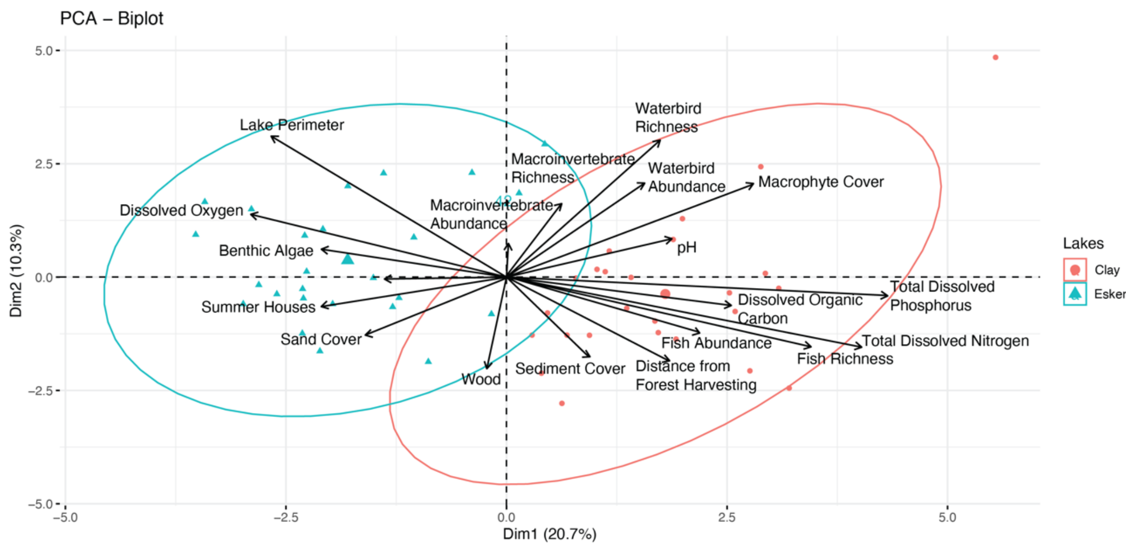


Figure 2.5 Principal component analysis showing all physicochemical, biological, and environmental variables. The red ellipse shows data points from clay lakes; the blue ellipse shows data points from esker lakes, both at a 95% confidence interval

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 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).

Table 2.2 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

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.

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. 2007b). Groundwater is generally cold with specific inorganic ions and nutrients (Winter et al. 1998a; Hayashi and Rosenberry 2002; Ala-aho et al. 2013) that strongly influence the physicochemical properties of esker lakes (Veillette et al. 2007b; Nadeau et al. 2015). 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 (Kloskowski et al. 2010; Sebastián-González and Green 2014; Keppeler et al. 2016; Coccia et al. 2016). 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; McNicol and Wayland 1992; Kloskowski et al. 2010).

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 (Eriksson 1979; McNicol and Wayland 1992; Elmberg et al. 2010; Väänänen et al. 2012). Moreover, the presence of Yellow perch (*Perca flavescens*) reduces the Common goldeneye population (Eriksson 1979; Rask et al. 2001; Nummi et al. 2012) 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 (Post and Cucin 1984; Vitule et al. 2009; Epanchin et al. 2010), 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 (Evans and Day 2002; Corrigan et al. 2011; Cornell Lab of Ornithology 2022).

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 (Keast and Webb 1966; H. and Becker 1984; Cochran and Ellner 1992; 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; Montoro Girona et al. 2018; Girona et al. 2023d). 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 (Steedman and Kushneriuk 2000; Smith et al. 2003; Girona et al. 2023a). 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, 2017). Thus, we recommend 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. 2017, 2023c; Montoro Girona 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. 2007b). 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.

2.5 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 voivinof 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.

Author contributions

GG, MMG, and LI: conceptualization; MMG; GG, and LI: Experimental design and site selection; AH, GG, MMG, and LI: fieldwork and data curation; AH, GG, and MMG: laboratory analysis; GG, MMG, and LI: methodology; MMG and GG: project administration; MMG, GG, and LI: resources; MMG, GG, LI, and AH: result interpretation; supervision; MMG, GG, LI, ARH, JL, and AH: validation; AH, MMG, and GG: visualization and edition; AH: writing-original draft; MMG, GG, LI, JL, and ARH: writing–review; MMG and GG: funding.

Acknowledgements

We thank the Groupe de recherche en écologie de la MRC Abitibi (GREMA) for providing support with equipment and facilities for our project. We also thank H. Morin-Brassard, B, Dupuis, C. Scott, P. Blaney, T. Anjum Mou, A. Ghose, A. Subedi, S. Kim, H. Bai, F. Bergeron, V. Beaudet, MC. Mayotte, M. Joncas, C. Ferland, and E. Drouin for fieldwork assistance and support. We also thank J. Rodriguez, P. Marchand, and F. Gennaretti for statistical advice and validation. We acknowledge Smart Forests Canada for the equipment and support (Pappas et al. 2022) and La Fondation de l'UQAT (The UQAT Foundation) for their financial support. This manuscript is a part of the M.Sc. thesis of AH. The fish survey method was approved by the committee of animal care ethics (UQAT) and followed the fishing permit obtained for this study from the Québec Ministère des Forêts, de la Faune et des Parcs (2021-05-27-055-08-SP).

Funding

This project was funded by the regional development funds from the MRC Abitibi awarded to MMG and GG.

Conflict of interest statement:

The authors declare that the research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

Supplemental material 1

Table 2.3 Generalized linear mixed model results showing estimates and p-values for environmental and biological variables affecting ecological community. Statistically significant variables are noted in bold; *: p ≤ 0.05; **: p ≤ 0.01; ***: p ≤ 0.001.

Biodiversity Indicator	Variables	Estimates	*p*-values
Waterbirds	**Type of lake**	**−2.1**	**<0.05***
	Fish richness	**−0.1**	**<0.1**
	Fish abundance	−0.1	0.2
	Macroinvertebrate richness	0.1	0.3
	Macroinvertebrate abundance	0.1	0.7
	Harvesting distance	−0.5	0.1
	Dissolved oxygen	1.6	0.1
	Lake perimeter	**0.1**	**<0.1***
	Sediment cover	0.1	0.9
	Dissolved nitrogen	−0.7	0.3
	Dissolved phosphorus	0.1	0.4
	Dissolved organic carbon	0.1	0.2
Fishes	**Type of lake**	**−1.8**	**<0.001*****
	Waterbird richness	**−0.1**	**<0.1**
	Waterbird abundance	−0.1	0.9
	Macroinvertebrate richness	−0.1	0.1
	Macroinvertebrate abundance	**−0.1**	**<0.1**
	Dissolved oxygen	0.1	0.3
	Dissolved nitrogen	-0.6	0.3
	Dissolved phosphorus	0.1	0.7
	Dissolved organic carbon	0.1	0.9
	Lake perimeter	0.6	0.4
Macroinvertebrates	Type of lake	-0.1	0.6
	Waterbird richness	0.1	0.8
	Waterbird abundance	-0.1	0.6
	Fish richness	-0.1	0.1
	Fish abundance	**0.1**	**<0.1**
	Dissolved oxygen	0.1	0.7
	Lake perimeter	0.1	0.7
	Sediment cover	0.2	0.6
	Dissolved phosphorus	−0.1	0.7
	Dissolved nitrogen	0.5	0.7
	Dissolved organic carbon	-0.1	0.7
	Macrophyte cover	0.1	0.6

Table 2.4 Waterbird abundance (± sd) in esker and clay lakes.

Common name	**Species name**	**Abundance in clay lakes**	**Abundance in esker lakes**
Common goldeneye	*Bucephala clangula*	22 ± 0.58	55 ± 1.27
Bonapartes gull	*Chroicocephalus philadelphia*	6 ± 0.23	14 ± 0.55
Canada goose	*Branta canadensis*	2 ± 0.11	53 ± 1.49
Wood duck	*Aix sponsa*	9 ± 0.26	4 ± 0.24
Blue-winged teal	*Anas discors*	20 ± 0.46	0
Northern shovler	*Spatula clypeata*	16 ± 0.41	0
American wigeon	*Mareca americana*	12 ± 0.27	12 ± 0.51
Mallard	*Anas platyrhynchos*	35 ± 0.55	37 ± 1.15
American black duck	*Anas rubripes*	15 ± 0.62	12 ± 0.58
Green-winged teal	*Anas carolinensis*	17 ± 0.49	1 ± 0.08
Ring-necked duck	*Aythya collaris*	52 ± 0.64	14 ± 0.45
Bufflehead	*Bucephala albeola*	0	4 ± 0.17
Hooded merganser	*Lophodytes cucullatus*	14 ± 0.27	0
Red-breasted merganser	*Mergus serrator*	4 ± 0.14	0
Sora	*Porzana carolina*	3 ± 0.17	0
Sandhill crane	*Grus canadensis*	12 ± 0.34	1 ± 0.08
Killdeer	*Charadrius vociferus*	12 ± 0.31	0
Wilson’s snipe	*Gallinago delicata*	24 ± 0.61	0
Spotted sandpiper	*Actitis macularius*	16 ± 0.39	13 ± 0.38
Solitary sandpiper	*Tringa solitaria*	1 ± 0.07	19 ± 0.57
Greater yellowlegs	*Tringa melanoleuca*	19 ± 0.35	28 ± 0.45
Common loon	*Gavia immer*	0	12 ± 0.33
Double-crested cormorant	*Phalacrocorax auritus*	12 ± 0.45	0
American bittern	*Botaurus lentiginosus*	19 ± 0.33	0
Great blue heron	*Ardea herodias*	2 ± 0.11	0
Belted kingfisher	*Megaceryle alcyon*	2 ± 0.11	9 ± 0.25

CHAPTER 3

GENERAL CONCLUSION

3.1 Biodiversity in esker lakes

Eskers support natural resources in all northern countries and provide drinking water, sand/gravel, recreational sites and productive forests. However, knowledge gaps exist about the biodiversity and functioning of ecosystems associated with eskers. The primary goal of this thesis was to contribute filling these knowledge gaps by evaluating the biodiversity in esker lakes. To achieve this goal, we implemented a food web approach for the first time in esker lakes. We expected that the macroinvertebrate population will be more abundant and richer supporting a large waterbird population in esker lakes because of the higher-quality habitat and reduced fish population. We found that esker lakes have significantly higher dissolved oxygen concentrations confirming our expectation of higher quality habitat. All physiochemical attributes, except dissolved oxygen, were significantly lower in esker lakes. Therefore, the characteristics of the esker ecosystems are significantly different than clay boreal lakes.

Water physico-chemistry is one of the primary variables that influence waterbird habitat selection (Cintra 2019), and in esker lakes, the physical properties of lakes influenced different waterbird species communities. Moreover, lower macrophyte cover in esker lakes limits waterbird foraging efficiency (Hargeby et al. 1994). Therefore, Waterbird richness and diversity were lower in esker lakes than in clay lakes. However, common goldeneye (*Bucephala clangula*) preferred esker lakes because their population is proven to be affected by competition with the fish community (Eriksson 1979; Pöysä and Virtanen 1994b). Among 5833 fish identified from our study, only 9% of fish was from esker lakes. In fact, half of the esker lakes were fishless. These unique characteristics influence waterbirds such as common goldeneye, to choose esker lakes. Several macroinvertebrate families such as the family Calopterygidae (Odonata order), that thrive in this unique ecosystem because they face less predation from fish. Such macroinvertebrate families can act as a predator in esker lakes. Moreover, esker lakes can provide a better-quality habitat to sustain some important macroinvertebrate families such as Perlidae. This family can survive in esker lakes because they require higher quality habitat (for example higher dissolved oxygen in esker lakes). Although biodiversity in esker lakes was low in every trophic level of the food web, this unique habitat can sustain a very important and demanding species community. Any alteration to this ecosystem might make these communities vulnerable.

Our result suggests that anthropogenic disturbances such as forest harvesting may affect the waterbird occurrence. Physical and chemical impacts from harvesting significantly affect the biological community of the lake ecosystem by decreasing water clarity, increasing temperature, nutrients, organic matter concentration, and sediment loads (Steedman and Kushneriuk 2000; Smith et al. 2003). In esker lakes, waterbird distribution and habitat selection were affected by the distance from harvesting activity. Clear-cutting is being used as the most widely used forest management practice in Canada, including in the esker forest (Bourgeois and Nadeau 2013; Montoro Girona et al. 2018). As a result, this type of management practice could lead to a highly fragmented ecosystem, homogenization of forest stands and decline of biological diversity (Puettmann et al. 2015). Moreover, the waterbird community composition is also affected by the difference in lake types such as esker lakes or clay lakes. Similarly, fish community composition was significantly affected by the difference in lake types. Macroinvertebrate abundance affects fish distribution and fish abundance affects macroinvertebrate community composition. This result connects their trophic relation and establishes their predatory-prey relationship and the significance of our food web approach.

In summary, esker lakes have unique and different physicochemical and biological characteristics. We contributed to eliminating the existing knowledge gap about the esker ecosystem and biodiversity. Esker lakes can provide better habitats to important communities that require this special ecosystem to thrive.

3.2 Contribution of our study

Apart from providing enormous resources for millions of people (Nadeau et al. 2011), esker lakes can provide good quality habitats to a unique species community. We implemented a novel food web approach, that allowed the characterization of this unique biodiversity of esker lakes for the first time and the relationship in the food web.

Our project provides the baseline ecological information on esker lakes, a mandatory element to formulate future conservation plans for esker ecosystems. However, we found that anthropogenic disturbances including forest managerial activities affected the biodiversity of the esker ecosystem. We recommend partial harvest with a wider (> 20m) riparian buffer to minimize the harvesting effects on biodiversity (Figure 3.1). Therefore, our study can be useful to formulate a better management and conservation plan to utilize and protect the esker ecosystem and its unique biodiversity.

3.3 Implication for biological conservation

The biodiversity is declining rapidly through habitat fragmentation, degradation and pollution (Tilman et al. 2017; Hasan et al. 2020; Hernández-Rodríguez et al. 2021). Esker ecosystems provide habitat to a few habitat specialist species. Continuous deterioration of this ecosystem could be very harmful to the species that depend on it, for example, common goldeneye. This waterbird depends primarily on macroinvertebrates and proved to be affected by the presence of fish (Eriksson 1979; McNicol and Wayland 1992; Elmberg et al. 2010; Väänänen et al. 2012). Moreover, several studies showed that the presence of yellow perch (*Perca flavescens*) in lakes reduces the common goldeneye population (Eriksson 1979; Rask et al. 2001; Nummi et al. 2012) because the diet of yellow perch heavily depends on aquatic macroinvertebrates (Brown et al. 2009). We found the presence of yellow perch in 41% of esker lakes with fish and the introduction of yellow perch in esker lakes are linked to anthropogenic activities such as live bait fishing, recreational activities and summer house around esker lakes (Figure 3.16). The anthropogenic threats with the fish introduction in fishless esker lakes could affect the conservation of Common goldeneye because it was observed that the introduction of fish in fishless habitat could alter the whole aquatic food web (Post and Cucin 1984; Vitule et al. 2009; Epanchin et al. 2010). This waterbird species is already vulnerable to hunting with 80,000-1,00,000 individuals hunted between 2019-2020 and a decline of habitat and cavities from traditional forestry practices (clear cut) (Evans and Day 2002; Corrigan et al. 2011; Cornell Lab of Ornithology 2022). Thus, the adaptation of more biodiversity-focused management plans such as partial harvest is mandatory for the conservation of common goldeneye.

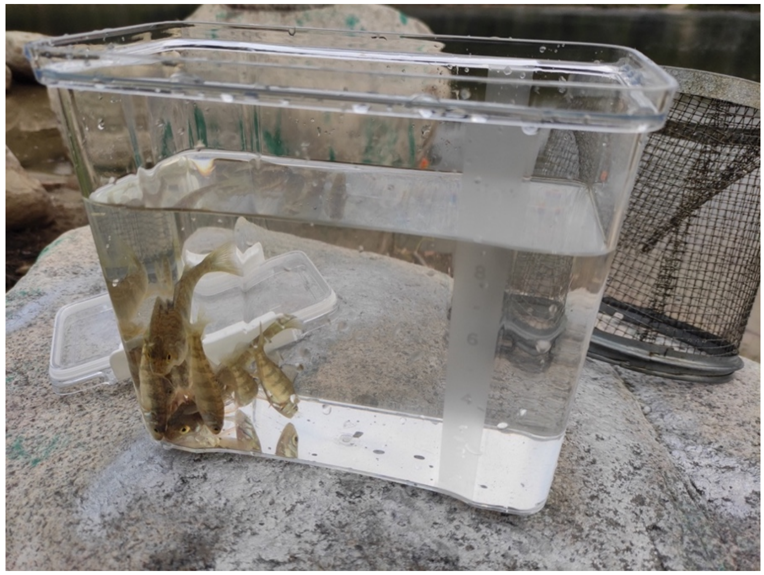


Figure 3.1 Photograph of a group of yellow perch which is an introduced fish species in esker lakes. Akib Hasan 2021.

Macroinvertebrate families such as Perlidae (stonefly) showed a strong association with esker lakes. Macroinvertebrates like stoneflies are frequently used as an indicator of good quality habitat because of their higher requirement of dissolved oxygen in the water (Jerves-Cobo et al. 2017). With the higher dissolved oxygen, fewer nutrients and less fish community, the esker ecosystem is capable of providing a different habitat to some key species communities, thus, protecting this habitat from the gradual changes is mandatory to protect habitat specialist species community depends on this ecosystem. Moreover, for the conservation of biodiversity, it is also mandatory to study how anthropogenic impacts are affecting esker biodiversity and how the severity and vulnerability to these impacts can change over time due to climate change.

3.4 Implication for sustainable forest management

According to the data from 2020, each year around 143 million cubic meters of timber are harvested in Canada, and with a 25 billion $ revenue, forestry represents one of the most important economic contributors to the gross national income of Canada (Canadian Council of Forest Ministers (CCFM) 2020). Eskers are dominated by Jack pine forests that provide a major economic source of timber production (43$/m^3) (Bourgeois and Nadeau 2013). The domination of jack pine stand in arid esker environments is successful because of the association with mycorrhizal fungi. Clear cutting has been practiced as a primary harvesting system in Canada (Montoro Girona et al. 2016). Clear-cutting practice around esker lakes is particularly harmful to the nesting of waterbird species like common goldeneye. They often select a cavity from pileated woodpeckers (*Dryocopus pileatus*) and live very close to the esker lake (Corrigan et al. 2011). For this reason, to reach sustainable forest management of eskers forests, we recommend applying adaptive silviculture using partial cuttings treatments to reduce the impact of forest harvest on biodiversity, provide refugee habitat and promote growth by reducing windthrow (Figure 3.2) (Girona et al. 2017, 2023c, 2019; D'Amato et al. 2023). We recommend applying adaptive silviculture using partial harvest around esker lakes to protect the distinct faunal communities of the esker ecosystem.

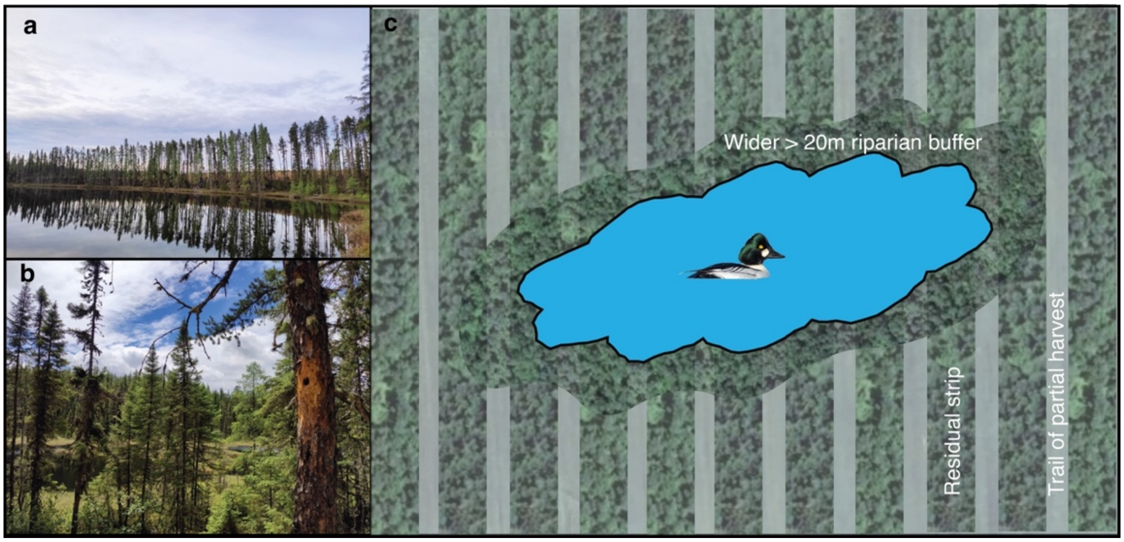


Figure 3.11 Forest management approaches for esker forests ecosystems a. Current management approach in esker forest: clear-cutting with 20m buffer. b. An example of the importance of residual trees for biodiversity is a woodpecker nest in an esker forest. Sometimes, common goldeneye uses the tree cavity of a woodpecker for their summer nesting. c. Our recommended management approach: Partial harvest with keeping wider > 20m riparian buffer. (Idea & framework: Miguel Montoro Girona, Guillaume Grosbois, Louis Imbeau and Akib Hasan. Illustration, design & photograph: Akib Hasan. Illustration Software: Adobe Creative Cloud 2021)

Not only esker ecosystem face threats from harvesting, but also, from mining and recreational activities. Therefore, sustainable resource extraction from the esker ecosystem is essential because of its significance and importance in the context of this changing world. It took more than thousands of years of colder climates the formation of this different ecosystem, thus, any alteration of this ecosystem could be irreversible. As a result, sustainable forest management is compulsory for the conservation of this unique ecosystem. Forest management decisions need to be aligned with the conservation effort of this ecosystem and also a multi-resource management plan will be needed to integrate other economic sides of the esker ecosystem.

3.5 Limitation of the study and Perspectives

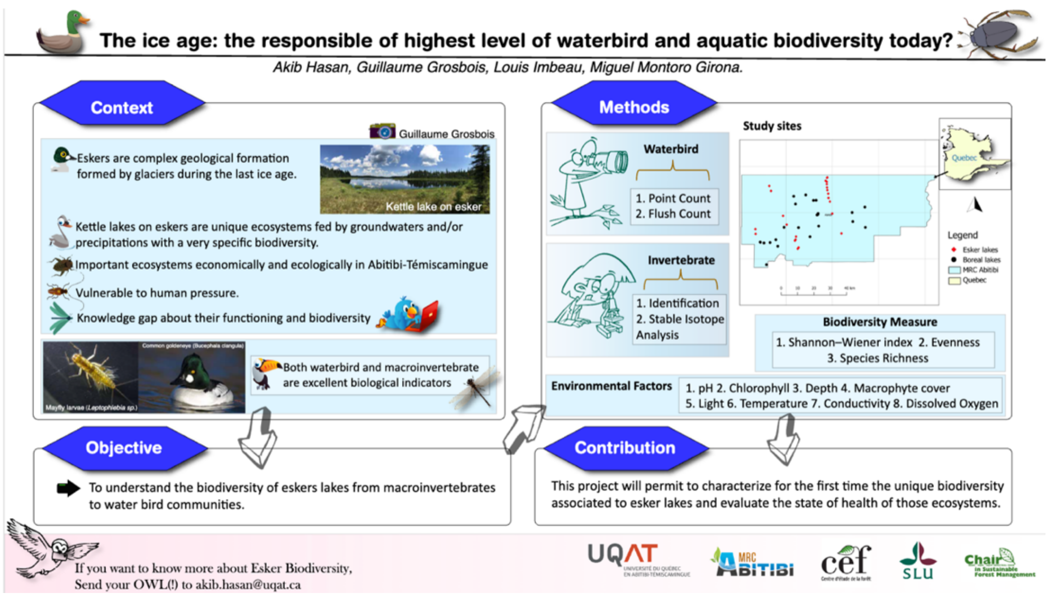
Connecting the trophic relation with stable isotope analysis is a very popular analytical tool in food web ecology (O'Reilly et al. 2002). Initially, we planned to utilize this technique to draw the relationship with the different components of the food web. We surveyed 50 lakes; therefore, it was a big logistic challenge to collect animal specimens (for example waterbirds) from the field within the timeframe of a master. During our field data collection, we collected the feathers and waterbird nest specimens from the field to conduct the stable isotope analysis. However, only a very low number of specimens were found during our fieldwork. As a result, we could not find enough samples to do the stable isotope analysis. However, we managed to connect the trophic structure of the food web efficiently without stable isotopes.

Future studies could characterize pelagic aquatic food web including zooplankton and phytoplankton, and terrestrial species that depend on esker lakes such as herpetofauna and terrestrial insects to have a complete biodiversity characterization of esker lakes because understanding the biodiversity is the primary element to preserve this ecosystem. Moreover, climate change will have a significant impact on boreal biodiversity and the ecosystem in the next few years and contribute to the increasing scarcity of fresh water. This phenomenon is concerning for the esker because the esker ecosystem is strongly dependent on groundwater. Thus, climate change might have severe effects on esker ecosystem functioning and biodiversity. Future studies should assess the vulnerability of the esker ecosystem to this changing climate. As the first characterization of esker biodiversity, this thesis participated in the elimination of the existing knowledge gap about biodiversity and the functioning of eskers and therefore, can act as a baseline ecological study to build sustainable management and conservation for this valuable ecosystem.

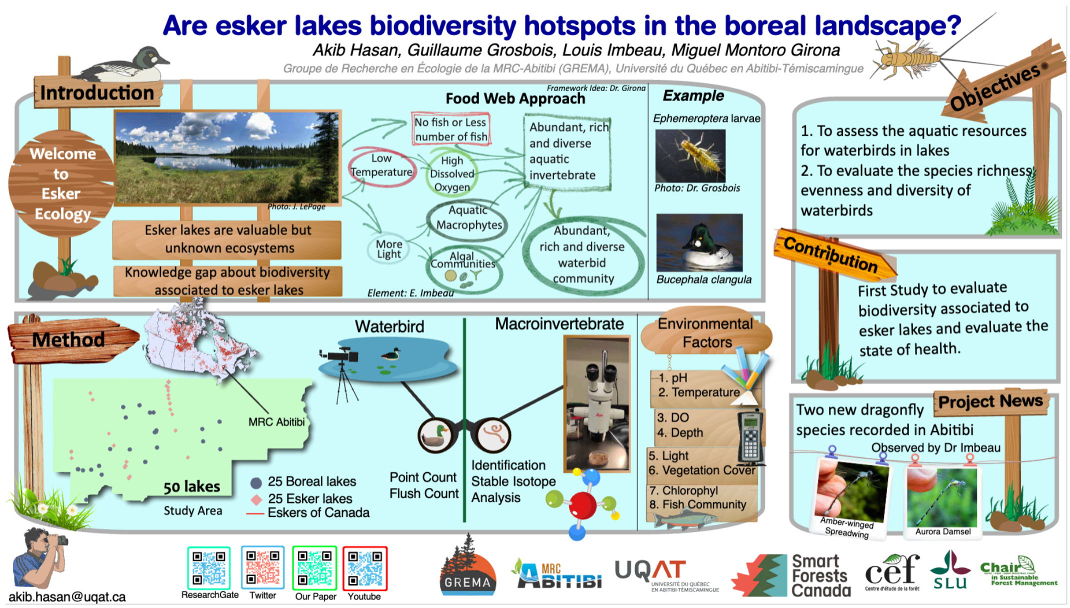
Appendix

The contribution and success of this master project

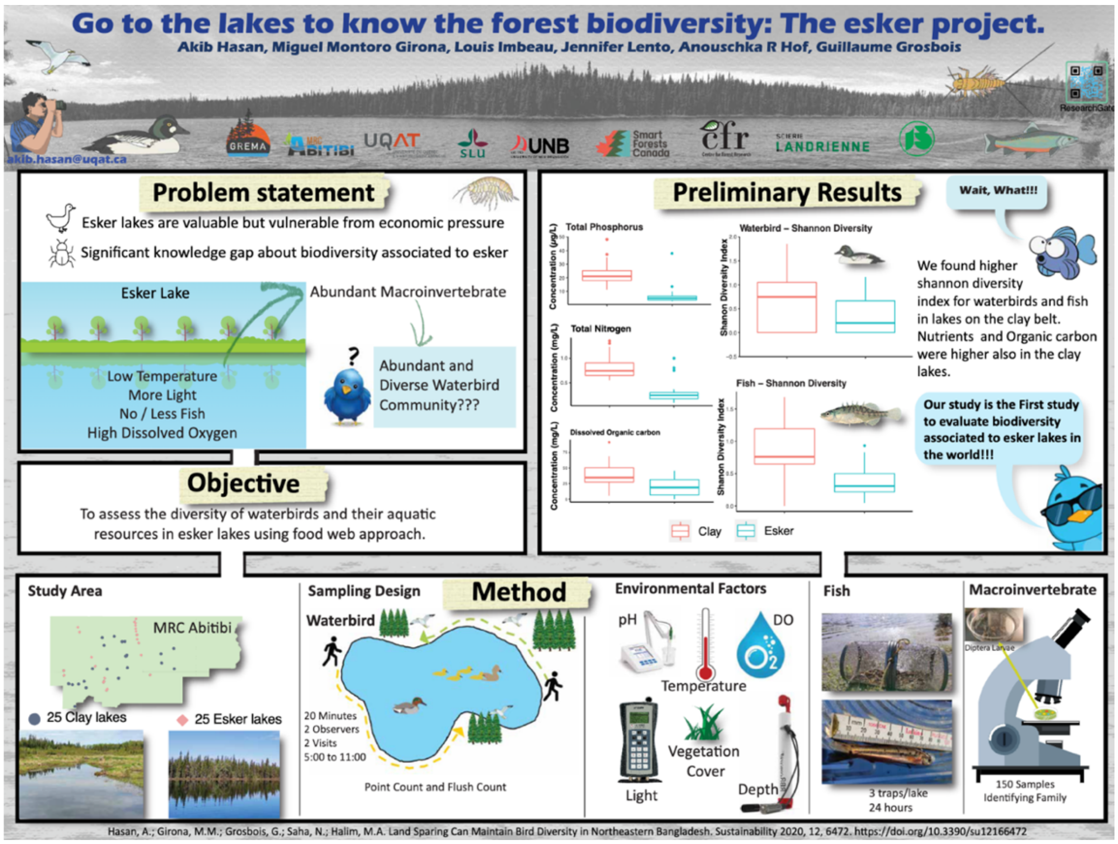
A. Scientific poster: Akib Hasan, Guillaume Grosbois, Louis Imbeau, Miguel Montoro Girona, 2020. <u>The ice age: the responsible of highest level of waterbird and aquatic biodiversity today?</u> Colloque CAFD 2020, Quebec, Canada.



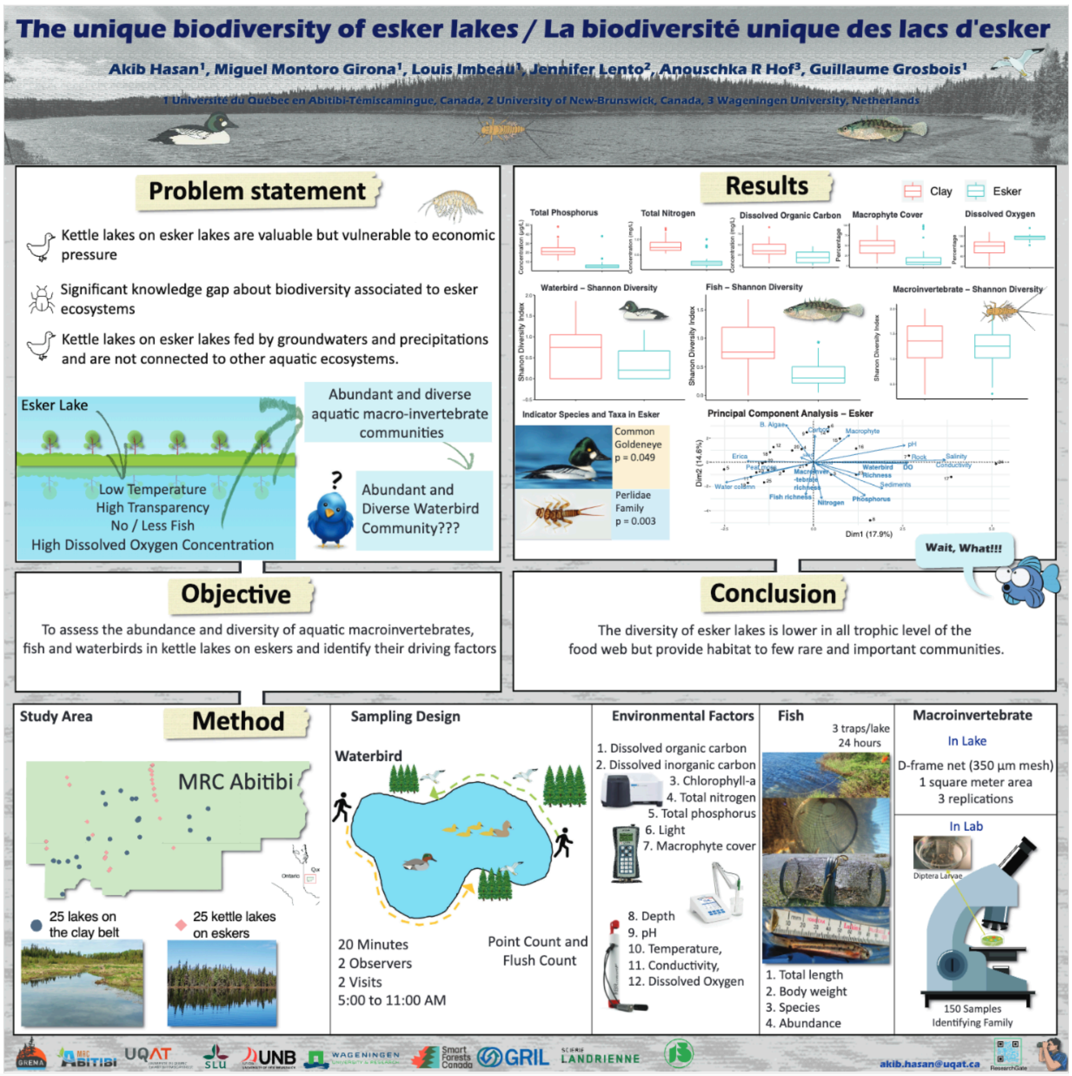
B. Scientific poster: Akib Hasan, Guillaume Grosbois, Louis Imbeau, Miguel Montoro Girona, 2020. Are esker lakes biodiversity hotspots in the boreal landscape? 14e Colloque du CEF, Quebec, Canada.



C. Scientific poster: Akib Hasan, Miguel Montoro Girona, Louis Imbeau, Jennifer Lento, Anouschka R Hof, Guillaume Grosbois, 2021. Go to the lakes to know the forest biodiversity: The esker project. Colloque CAFD 2021, Quebec, Canada.



D. Scientific poster : Akib Hasan, Miguel Montoro Girona, Louis Imbeau, Jennifer Lento, Anouschka R Hof, Guillaume Grosbois, 2021. The unique biodiversity of esker lakes / La biodiversité unique des lacs d'esker. Symposium annuel du GRIL 2022, Quebec, Canada.



E. Popularised article: Akib Hasan, Miguel Montoro Girona, Louis Imbeau, Guillaume Grosbois, 2022, Les Eskers Magiques, https://couvertboreal.com/publications/printemps-2022/

LES ESKERS MAGIQUES

Akib Hasan, Miguel Montoro Girona, Louis Imbeau, Guillaume Grosbois

Les eskers sont des formations géologiques complexes qui ont été créées lors de la dernière glaciation, il y a environ 10 000 ans. Dans la région de l'Abitibi-Témiscamingue, les eskers fournissent des éléments vivants essentiels comme de l'eau potable, du sable, du gravier, ainsi qu'une forêt productive. On soupçonne également les eskers de constituer un habitat pour un ensemble unique de biodiversité. Cependant, il y a peu de connaissances sur cette biodiversité et le fonctionnement des eskers.

Les lacs d'esker sont parmi les lacs d'eau douce naturels les plus spectaculaires au monde. Ce type de lacs diffère des autres lacs boréaux, car ils tirent leur eau des eaux souterraines et/ou des précipitations. Contrairement aux autres lacs boréaux, les lacs d'esker ne sont pas liés à d'autres écosystèmes aquatiques de surface. En raison de cette caractéristique unique, les communautés de poissons y sont souvent réduites ou totalement absentes. Pour la première fois au monde, nous menons une étude sur la biodiversité des eskers en utilisant une approche intégrative du réseau alimentaire. Le but de notre étude est de caractériser les communautés d'oiseaux associées aux lacs d'esker et d'identifier les ressources et les facteurs écologiques qui déterminent leur présence, leur abondance, leur richesse et leur diversité.

Dans la chaîne alimentaire aquatique, les poissons sont l'un des principaux prédateurs des communautés de macro-invertébrés. Par conséquent, les lacs d'esker devraient avoir des communautés de macro-invertébrés abondantes et diversifiées. Les espèces d'oiseaux aquatiques telles que le garrot à œil d'or (*Bucephala clangula*) et la mouette de Bonaparte (*Chroicocephalus philadelphia*) préfèrent souvent les lacs d'esker en raison de ces ressources alimentaires disponibles pendant leur saison de reproduction.

Nous avons exploré 50 lacs au cours des deux dernières années en Abitibi-Témiscamingue. Durant l'été 2021, nous avons identifié 434 oiseaux aquatiques, identifié et mesuré 6 406 poissons ainsi que 200 libellules. Nous avons également découvert deux nouvelles espèces de libellules pour la première fois en Abitibi-Témiscamingue. En laboratoire, nous avons identifié et stocké environ 20 000 macro-invertébrés.

En dehors des travaux de terrain, nous avons trouvé des résultats très intéressants et surprenants. Nous avons trouvé une plus grande diversité d'oiseaux d'eau dans les lacs d'argile que dans les lacs d'esker. Par contre, nous avons remarqué une forte association du garrot à œil d'or avec les lacs d'esker, en démontrant que les communautés des espèces des oiseaux sur les eskers sont plus spécifiques et singulières. Le garrot à œil d'or compétitionne moins avec les poissons pour nourrir les canetons dans les lacs d'esker. Notre hypothèse concernant les poissons était donc correcte. La diversité et l'abondance des poissons dans les lacs boréaux étaient beaucoup plus élevées que dans les lacs argileux. De même, la concentration en nutriments et en carbone organique dissous était plus élevée dans les lacs argileux.

Ce projet sur la biodiversité des eskers est crucial pour la région de l'Abitibi-Témiscamingue, car c'est la première étape pour caractériser la biodiversité aquatique et terrestre associée à ces écosystèmes uniques. Notre étude permettra d'être la base pour établir des mesures de gestion efficace pour aménager de façon durable et conserver la richesse de ces eskers vulnérables, mais magiques.

Photo : GREMA

GREMA

Chaire UQAT - UQAM en aménagement forestier durable

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G. Popularised article: Akib Hasan, Miguel Montoro Girona, Louis Imbeau, Guillaume Grosbois, 2022, Explorer la biodiversité des oiseaux aquatiques des lacs d'esker. "Le Mésangeai". https://www.sloat.org/messangeai, June 2022.

Explorer la biodiversité des oiseaux aquatiques des lacs d'esker

Par Akib Hasan[1], Miguel Montoro Girona[1], Louis Imbeau[1], Guillaume Grosbois[1]
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Retournons 10000 ans en arrière, lorsque 97 % du Canada était recouvert d'une épaisse couche de glace. Cela peut sembler difficile à croire, mais à cette époque l'épaisseur de la glace pouvait atteindre deux kilomètres. Durant cette période, des formations géologiques complexes ont été créées. On les appelle aujourd'hui des eskers. Les eskers sont une accumulation linéaire de sable, de roche et de gravier qui se s'est formée sous cette glace épaisse. La formation des eskers s'est faite sur une longue période, lorsque la température a commencé à augmenter. Aujourd'hui, les écosystèmes situés sur les eskers fournissent des services économiques et écologiques à tous les pays nordiques, y compris le Canada. Dans la région de l'Abitibi-Témiscamingue, les eskers fournissent des services essentiels tels que l'eau potable, le sable, le gravier et la forêt productive de pin gris (*Pinus banksiana*). 73 % de l'eau potable de la MRC d'Abitibi provient des eaux souterraines des eskers et cette eau a déjà remporté le prix de la meilleure qualité d'eau potable en Amérique du Nord.

Les lacs d'esker sont parmi les lacs naturels d'eau douce les plus spectaculaires au monde. Ils sont différents des lacs boréaux normaux, car ils sont reliés au système d'eaux souterraines de l'esker et ne sont pas reliés à d'autres systèmes fluviaux. Cette situation affecte leur température, leur teneur en nutriments et leur biodiversité. L'isolement des lacs d'esker les rend très difficilement accessibles aux poissons qui sont généralement absents de ces habitats. Ces lacs ont également une eau très transparente, qui a été filtrée par les eskers durant des milliers d'années avant de resurgir en surface. Par conséquent, nous soupçonnons que les lacs d'esker abritent une biodiversité unique, notamment d'invertébrés aquatiques et terrestres comme les libellules ainsi que d'oiseaux aquatiques. Ces derniers jouent un rôle de prédateurs en haut de la chaîne alimentaire.

En tant que chercheurs en écologie, nous savons que tout est lié dans les écosystèmes et nous tentons d'élucider les mystères de la nature. Puisque la température des lacs d'esker est régulée par les eaux souterraines, le niveau d'oxygène est plus élevé. L'absence de poissons permet très probablement aux communautés d'invertébrés aquatiques de prospérer dans ces écosystèmes. D'autre part, les oiseaux aquatiques peuvent bénéficier de ces communautés riches en invertébrés pour leur croissance ou leur reproduction. Cela semble être le cas d'une espèce d'oiseau d'eau emblématique : le Garrot à œil d'or (*Bucephala clangula*).

H. Mirror Mirror!!! Where is the best quality water in the world! Jury Award at CAFD Colloque 2020.

I. The sun never stops shining in Abitibi! Best Photo at Landscape category at GREMA Annual meeting 2022.

J. Cône d'or 2022[1] at Chaire AFD UQAT-UQAM 2022.

[1]Best oral presentation award at Chaire UQAT-UQAM en Aménagement Forestier Durable 2022 (Rouyn-Noranda).

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