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LIST OF ABBREVIATIONS

ACM	Airport Creek Marsh
ANC	Anderson Creek
BDD	Baie Du Doré
CRW	Coffin Rock Wetland
CWS	Collingwood Shores Wetlands
DRR	Detroit River Marshes
ECCC	Environment et Changement Climatique Canada
EM	Emergent marsh
FOX	Fox Creek Marsh
FPM	Francis Point Marsh
GL	Great Lakes
GLPI	Great Lakes Protection Initiative
GRM	Grand River Mouth Wetlands
HBH	Hay Bay
HIW	Hill Island East
HGB	Hog Bay
HKC	Hurkett Cove
IJC	International Joint Commission
JSM	Jordan Station Marsh
KRW	Key River Wetland
THO	Long Point
LCM	Lynde Creek Marsh
MIM	Mission Marsh
NPE	Non-Persistent Emergent
RON	Rondeau Bay
SAM	Saint Anne's Marsh
SAV	Submerged Aquatic Vegetation
SCS	Lake St. Clair Marsh
SCP	Systematic conservation planning
SPP	Selkirk Provincial Park Marsh
SOB	South Bay Marsh
SS	Swamp
TRB	Treasure Bay
WEM	Wesleyville Marsh
WM	Wet meadow
WHW	Whiskey harbour Wetland

RÉSUMÉ

Résumé

Les milieux humides jouent des rôles écologiques, économiques et sociaux indispensables qui découlent de leur riche biodiversité fournissant un habitat essentiel pour une grande variété d'espèces. De plus, ils atténuent les changements climatiques, offrent une protection côtière et participent à la purification de l'eau. Récemment, les milieux humides des Grands Lacs (**GL**) se dégradent à un rythme alarmant en raison de l'augmentation des facteurs de stress anthropiques, du changement climatique et des espèces envahissantes. Les espèces exotiques et envahissantes continuent de se répandre à grande vitesse et sont responsables d'une multitude de changements dans l'écosystème des GL. Avec l'évolution rapide de la succession des milieux humides, une analyse à jour de la répartition actuelle des espèces de plantes des milieux humides est nécessaire. Travaillant de pair avec l'Initiative de protection des Grands Lacs (IPGL), ce mémoire vise à comprendre la répartition et la biodiversité actuelles des espèces végétales le long de l'hydrosère des milieux humides des GL en analysant une base de données acquise par Environnement et Changement Climatique Canada (**ECCC**). Cette base de données couvre 26 sites distribués du côté canadien des GL et compte plus de 8500 quadrats échantillonnés durant les étés 2018 et 2019. Une approche multi-échelle a été adoptée pour examiner la diversité alpha-bêta-gamma des espèces végétales présentes dans les milieux humides des GL. L'analyse quantifie et compare la richesse spécifique, la diversité Shannon-Weaver, l'équitabilité des espèces (Pielou), la couverture des espèces exotiques et l'unicité des espèces via une analyse de diversité bêta (Contribution locale à la diversité bêta; **CLDB**). Les résultats démontrent un gradient latitudinal important le long des GL; les milieux humides du sud étant beaucoup plus dégradés que les milieux humides du nord et donc moins diversifiés. De plus, la classe de milieux humides la plus touchée par cette dégradation le long de l'hydrosère est la communauté végétale des marais émergents. À la lumière des résultats, ce mémoire offre un cadre conceptuel pour aider les gestionnaires des milieux humides dans leurs efforts de priorisation afin de conserver et restaurer les milieux humides basé sur des données d'utilisation des terres et de biodiversité.

Mots-clés

Zone humide. Plantes. Espèces exotiques. Espèces envahissantes. Grands Lacs. Biodiversité. Beta-diversité. Richesse spécifique.

ABSTRACT

Abstract

Coastal wetlands play essential ecological, economic, and social roles which stems from their rich biodiversity that provide crucial habitat for a large variety of species, mitigate climate change, offer coastal protection and water purification. Recently, the Great Lake (**GL**) wetlands are being degraded at an alarming rate due to increasing anthropogenic stressors, climate change and invasive species. Exotic and invasive plant species have recently expanded tremendously and have been found responsible for a multitude of ecosystem changes in the GL. With the fast-changing successional nature of wetlands, an updated analysis of the current distribution of wetland plant species of the GL is now needed. Working along with the Great Lake Protection Initiative (**GLPI**), this study aims to understand the current distribution and diversity of plant species along the hydrosere of the Canadian GL wetlands by analysing a dataset acquired by Environment and Climate Change Canada (**ECCC**) sampled in the summer of 2018-2019. This dataset includes 26 sites along the GL, in Canada, and over 8500 quadrats. A multiscale approach was adopted to perform alpha- beta- and gamma-diversity analysis. Analysis including species richness, species diversity (Shannon-Weaver) species evenness (Pielou index), exotic species cover and species composition uniqueness (Local contribution to Beta-diversity; **LCBD**) show an important latitudinal gradient along the GL, and where wetlands from the south are being much more degraded than wetlands in the north. Furthermore, the wetland class that is the most affected along the hydrosere is the emergent marsh vegetation community. Furthermore, this study offers a conceptual framework to assist wetland managers in their conservation and restoration efforts.

Keywords

Wetland. Plants. Exotic species. Invasive species. Great Lakes. Biodiversity. Beta-diversity. Species richness.

CHAPTER I: GENERAL INTRODUCTION

1.1. Wetland formation and functions

Wetlands occur in all regions of the world and the term “wetland” has no single, scientific, universal meaning. Wetland is a generic term used to define environments subject to being inundated or saturated at or near the surface for periods long enough to create anaerobic conditions, promoting the development of hydric soils or substrate, and favoring the establishment of hydrophytic vegetation (Tiner, 2016). Hydrology is the driving factor of wetland creation and maintenance. All wetlands have seasonally or annually fluctuating water levels. Some have standing surface water for extended periods of time while others have saturated soils with little or no surface water. The main factors influencing the availability of water for wetland formation is climate, topography, local weather, surficial geology, soils, vegetation, and human activities (Tiner, 2016) .

Wetlands act as a sponge and provide many ecological services including soaking up floodwaters after rains and spring snowmelt and filtering of contaminants before they enter lakes and rivers (Derosier *et al.*, 2005). This filtration process removes excess nutrients, sediments and pollutants from the water making it healthier for drinking, swimming and for supporting a rich community of plants and wildlife (Derosier *et al.*, 2005). Wetlands also reduce the frequency and intensity of floods by acting as natural buffers, and effectively perform waste assimilation and detoxification (Zedler & Kercher, 2005). As water flows through a wetland, the vegetation slows down the flow, allowing sediments to settle, therefore reducing the risk of flooding and erosion as well as helping with soil formation and maintenance. Most importantly, wetlands provide essential habitat for a vast array of wildlife (Derosier *et al.*, 2005). The presence of water, high plant productivity, and a vast array of heterogeneous habitats attracts high numbers of animals and animal species, many of which depend entirely on wetlands (Zedler & Kercher, 2005).

1.2. Water level fluctuations and species distribution

Many biotic and abiotic variables can influence the distribution and dynamics of wetland vegetation. One of the most dominant variables explaining their distribution at the local scale is water level fluctuation. Wetlands occupy a unique transitional position between the aquatic and terrestrial environment providing a diverse gradient of abiotic conditions for plant species. Some species can tolerate a range of environmental conditions, while others have a very narrow niche. This assemblage of different plant species occupying narrow niches along the water level continuum defines what is called "**hydrosere**" or "**toposequence**" (Figure 1.1). Water-level fluctuation is a natural phenomenon and is mostly induced by climatic variability. Wetland communities have evolved to adapt to a range of water depths and water level changes (Albert et al., 2005; Wilcox, 2004; Mortsch, 1998; Mayer, Edsall & Munawar, 2004) and researchers have long documented the effects of water level fluctuations on wetland community dynamics, productivity and function (Mortsch, 1998; Nilsson & Svedmark, 2002; Mayer, Edsall & Munawar, 2004).

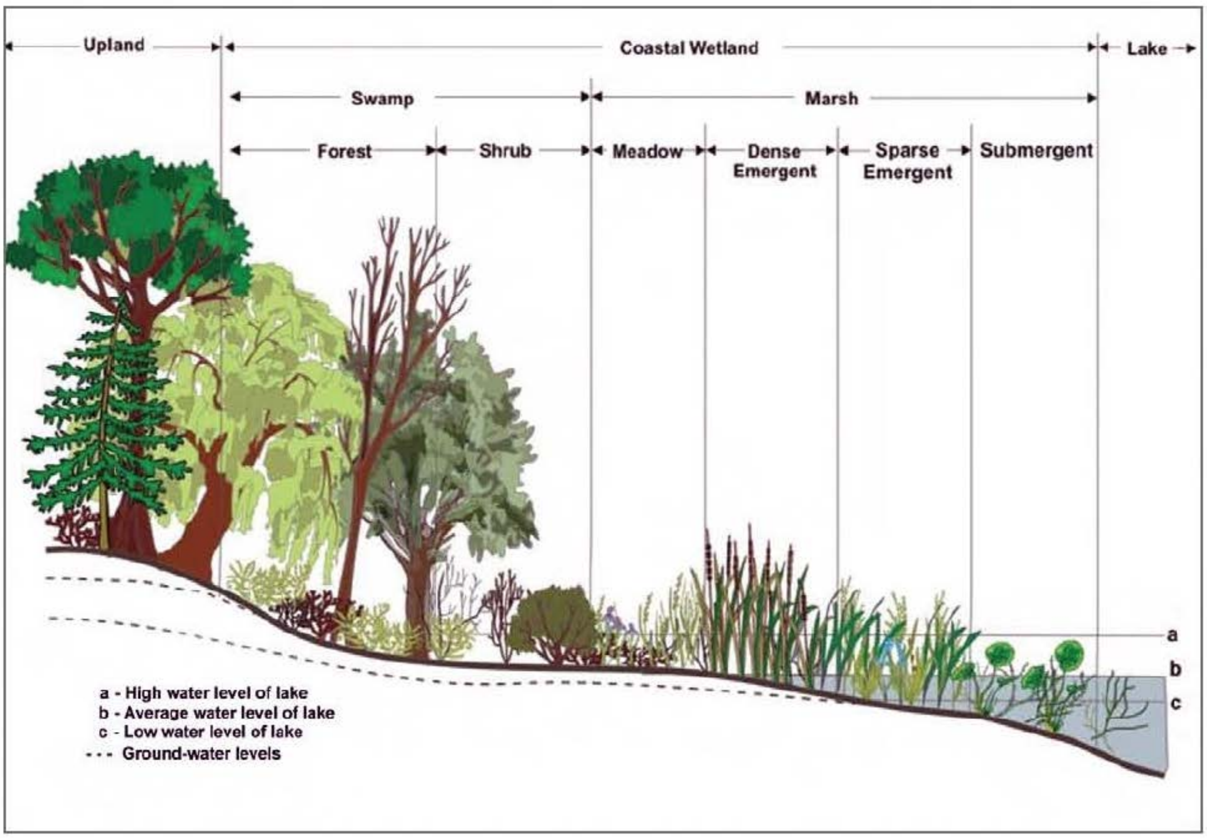

Figure 1.1. Hydrosere or toposequence of a typical coastal wetland from lake to upland showing changes in plant communities related to lake water level history (from Environment Canada, 2002)

Regular water level fluctuations are crucial for wetlands. They provide a disturbance regime by fluctuating in seasonal, annual and inter-annual cycles (Keddy & Reznicek, 1986; Wilcox, 2004). These physical and chemical disturbances at the interface between water and land expose wetlands to continuous cyclical succession, preventing them from ever reaching climax communities (Keddy & Reznicek, 1986; Wilcox, 2004). These water level fluctuations increase shoreline vegetation area as well as the diversity of vegetation types and species (Keddy and Reznicek, 1986). High water levels change the chemistry of soils (Tiner, 2016). Diffusion is 10,000 times slower in saturated soils than it is in aerated soils. When a soil is flooded, respiration by aerobic bacteria and other organisms (aerobes) consume the remaining oxygen in the soil within hours or days and turn soils from oxic to anoxic (Tiner, 2016). High water level periods also inhibit woody vegetation and other terrestrial species from occupying areas close to the water and temporally change the vegetation from wet meadow to emergent species, or from emergent species to floating-leaved and submerged species. High water levels furthermore eliminate dominant species such as *Typha* sp. and *Phragmites australis* which would otherwise form extensive monocultures. On the other hand, low water level periods eliminate vegetation intolerant to drying and allow many mud flat annuals, meadow and emergent marsh species to regenerate from buried seeds (Tiner, 2016).

Water-level stabilization disrupts the historical cycle and converts formerly diverse, structurally complex wetlands to large areas of only a few species by promoting aggressive species (Keddy and Reznicek 1986; Frieswyk and Zedler, 2007). Water level stabilisation eliminates the highest and lowest water levels that are important to wetland regeneration and alters competitive interactions among species as well as increase phosphorus availability (Frieswyk et Zedler, 2007). Wilcox et al., (2004) have shown that regulation of long-term water-level fluctuations of Lake Ontario creates hydrologic conditions that support the expansion of dominant emergent and submergend plant species which reduces plant species richness and emergent marsh habitat quality.

1.3. Wetlands classification

There are several classification systems for wetland types (*e.g.*, Cowardin, 1979; Brinson, 1993; Zoltai et Vitt, 1995; Warner and Rubec 1997; Brinson et Malvárez, 2002; Albert et al. 2005; Brooks et al.,2011) that are mostly based on three components: 1) hydrology or hydrogeomorphology, 2) soil characteristics and 3) vegetation species. Classifications based on hydrogeomorphology are on a larger scale (Brinson 1993; Albert et al. 2005; Brooks et al. 2011; *e.g.*, Lacustrine, Riverine and Barrier-enclosed systems) while classification based on vegetation having similar needs are on a smaller scale (Zoltai et Vitt, 1995; Turgeon et al. 2006; Hudon et al. 2006; *e.g.*, *Sphagnum*-dominated bogs, non-peat-forming marshes). The great diversity and especially the hydrogeomorphological particularities of the wetlands of the Great Lakes (**GL**; significant interannual and intra-annual variations in water levels, high exposure to currents and waves due to strong winds and the presence of seiche) led to the development of unique classification of *coastal* *wetlands* (Keough et al., 1999; Albert et al., 2005). In this study, we used Albert et al. (2005) classification at a larger scale to describe wetlands based on hydrogeomorphology (see Appendix 1), and a vegetation species classification to describe the different wetland classes along the hydrosere (See Table 1) for each wetland site.

1.4. Wetlands of the Great Lakes

The GL watershed spans over 500,000 km^2 and over 250,000 km^2 of open water area (Figure 1.2). The GL and their connecting channels hold approximately one-fifth of the world's freshwater (Mayer *et al.*, 2004). They are part of an extensive interconnected waterway, making their wetlands among the most dynamic in the world. Water flows from Lake Superior into Lake Huron and Lake Michigan, then into Lake Erie and finally into Lake Ontario. The lakes drain through two outflows, the St. Lawrence River at the East, and the Chicago Sanitary and Ship Canal at the West. Outflow from the GL is relatively small (less than 1% per year of their volume) (Mayer et al., 2004). Fluctuating water levels in the GL directly affect plant community structure and drive vegetation cycles (Keddy & Reznicek, 1986). The interconnection between GL affects hydrologic circulation patterns, nutrient dynamics, climate variation, and disturbance regimes (Keough *et al.*, 1999).

Coastal wetlands of the GL region have essential ecological, economic and social roles. Their importance stems from providing coastal protection, water purification, regulate watershed hydrology and essential habitat for many species of fauna and flora (Mayer *et al.*, 2004; Midwood & Chow-Fraser, 2010). The GL region holds 46 unique species and 279 rare plants and animals (Niemi, Kelly & Danz, 2007). Over 35 million inhabitants occupy the GL watershed. While industry in the GL accounts for a major part of the economy for the United States and Canada (Niemi, Kelly & Danz, 2007), coastal wetlands are under threat due to increasing agriculture, urbanization, land cover changes, hydrological modifications, point source pollution, atmospheric deposition, climate change, and invasive species (Keough *et al.*, 1999; Johnston, Zedler & Tulbure, 2010; Lemein, Albert & Del Giudice Tuttle, 2017).

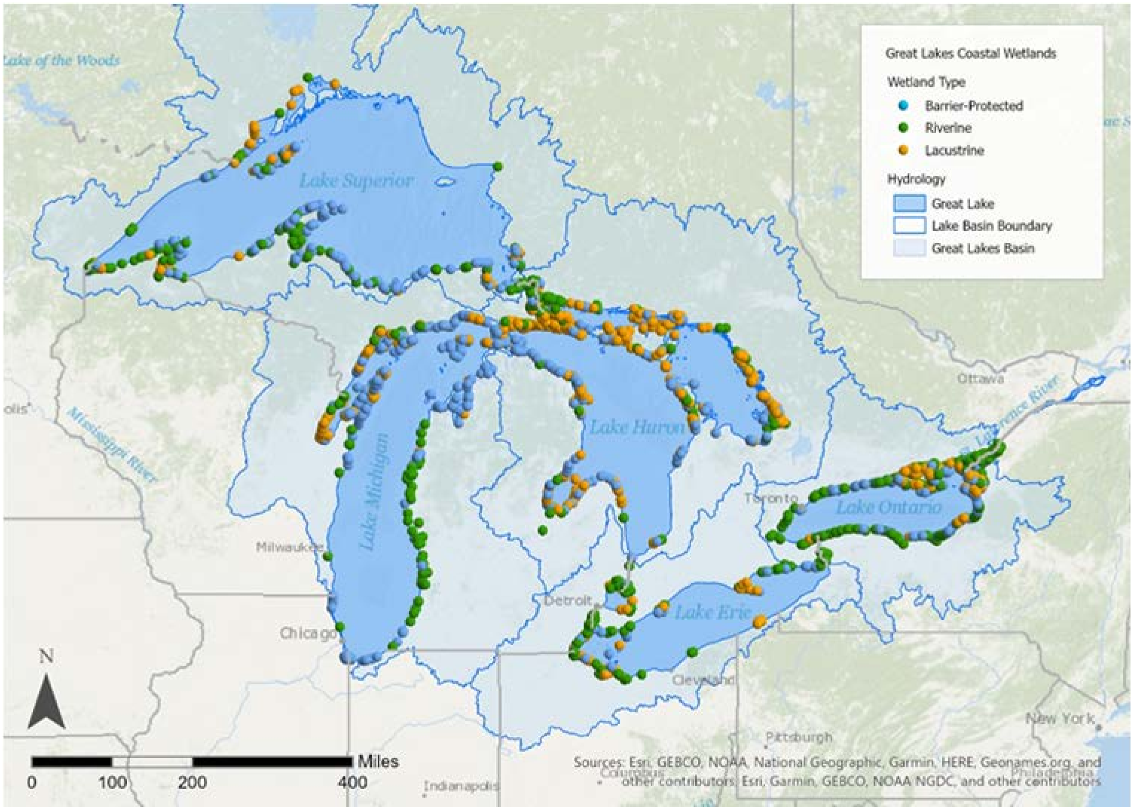

Figure 1.2. The Great Lakes Basin and the distribution of coastal wetlands selected in 2010 for long-term monitoring by the Coastal Wetland Monitoring Program (CWMP), including wetlands selected by the stratified-random sampling design and for other research purposes. Colored circles represent wetland locations and wetland type for each Great Lake: barrier-protected (blue), riverine (green) and lacustrine (orange). Source: CWMP (ESRI, GEBCO NOAA. National Geographic database)

1.5. Characteristics and status of the Great Lakes

Lake Superior is located at the top of the chain of GL and is the world's largest freshwater lake by area (Figure 1.2). It is also the coldest and deepest of the GL, with a maximum depth of 406 m (LAMP, 2013). Because of its massive size, Lake Superior has a retention period of 191 years and rarely completely freezes over due to the enormous mass of water, even in the coldest winters (LAMP 2013). According to a study of the water quality index (**WQI**), 70% of Lake Superior marshes are minimally impacted (Cvetkovic & Chow-Fraser, 2011). During the late 1800s, serious encroachments were made on the natural water regime of its outflow through St. Marys River. It is thought that 1887 was the last year of the natural flow regime of Lake Superior.

Lake Huron is actually four separate interacting water bodies (Figure 1.2): the North Channel, Georgian Bay, Saginaw Bay, and Lake Huron (Taylor, Derosier & Dinse, 2010). The average water depth of Lake

Huron is 59 m with a maximum of 229 m (Derosier et al., 2015). Lake Huron has a retention period of 27 years and its outlet is the St. Clair River, which flows into Lake Erie (Derosier et al., 2015). Erosion-resistant igneous and metamorphic bedrock form much of the northern coast and Georgian Bay. This region contains extensive high-quality coastal wetlands as well as heavily forested habitats. The Georgian Bay has the highest proportion of wetlands in very good and excellent condition and the least number of wetlands in a degraded state in the GL region (Cvetkovic & Chow-Fraser, 2011). Lake Huron also contains more islands than any other GL. The isolated nature of islands allows them to harbor unique ecosystems as well as insulate them from threats common to connected shorelines.

Lake Michigan is the second largest GL by volume and fifth largest lake by area in the world (Figure 1.2). Connected to Lake Huron through the Straits of Mackinac, the two lakes technically behave like one big water body. The average water depth of Lake Michigan is 85 with a maximum of 281 m. Lake Michigan has a retention period of 62 years and its outlet is the Straits of Mackinac, which flows into Lake Huron (Derosier et al., 2015). In certain areas of Lake Michigan, excess nutrients create blooms of algae that die off and decompose, creating oxygen-deprived "dead zones" (Derosier et al., 2015). Green Bay is particularly vulnerable to these events. According to the WQI from Cvetkovic & Chow-Fraser (2011), over 50% of marshes in Lake Michigan

Lake Erie's shallow waters and southern location (Figure 1.2) make it the most productive of the GL (Pearsall *et al.*, 2012). Lake Erie has an average water depth of 19 m and a maximum of 64 m (Derosier et al., 2015). Lake Erie has a retention period of 2.7 years and its outlets are the Niagara River and Welland Canal (Derosier et al., 2015). Lake Erie also has the most altered basin and suffers from invasive species, increased nutrient concentrations, pollution and habitat destruction. Anthropogenic changes have caused wildlife and plant populations to decline and, in some locations, disappear, changing Lake Erie's natural biological diversity and diminishing many of its ecological services (Pearsall et al., 2012). Harmful algal blooms regularly plague Lake Erie (Derosier et al., 2015). The western basin's warm, shallow water and nutrient-rich agricultural runoff create perfect conditions for toxin-producing blue-green algae. Over 50% of Lake Erie's wetlands is in a degraded state while 11% is in a highly degraded state (Cvetkovic & Chow-Fraser, 2011).

Lake Ontario is the last lake in the chain of Laurentian GL (Figure 1.2). It is the smallest of the GL but has the highest ratio of watershed area to lake surface area (Lake Ontario LaMP, 2011). It is a deepwater system, with an average depth of 86 m and a maximum depth of 244 m, second only to Lake Superior. Approximately 80% of the water flowing into Lake Ontario comes from Lake Erie through the Niagara River. The remaining flow comes from Lake Ontario basin tributaries (14%) and precipitation (7%) (Lake Ontario LaMP, 2011). six years and its outlet is the St. Lawrence River, which flows into the Atlantic Ocean (Derosier et al., 2015). The completion of the Robert Moses-Saunders Power Dam in 1960 was the start of water-level regulation in Lake Ontario and the upper St. Lawrence River (Farrell et al., 2010). Belonging to Canada and the United States, dam operations are controlled by the International Joint Commission (IJC) formed by the Boundary Water Treaty Act of 1909. Under the current (Plan 2014 with deviations) and past (Plan 1958 DD with deviations) regulation plan, high lake levels normally experienced during high water-supply periods have been lowered and low lake levels during low water supply periods raised (Wilcox & Xie, 2007). The lake-level range has been compressed from approximately 1.5 m to 0.7 m, or half of what it was prior to regulation or would have been without regulation (Wilcox & Xie, 2008; Wilcox & Xie, 2007). According to Cvetkovic & Chow-Fraser (2011), 50% Lake Ontario's wetlands is in a degraded state and over 7% is in a highly degraded state.

1.6. Regional differences between Great Lakes

The GL watershed is highly variable in geology, climate, vegetation and land use (Mayer *et al.*, 2004; Johnston *et al.*, 2010). The Great Lakes watershed extends over three physiographic provinces: Canadian Shield, Central Lowlands and the St-Lawrence Lowlands (Mayer *et al.*, 2004). First, the GLs region varies in its geology and possesses three types of bedrock, namely igneous, metamorphic and sedimentary rock. The bedrock underlying the northern coasts of Lakes Superior and Huron consist of igneous and metamorphic rock. This is believed to generate a substrate of lower fertility than those of the southern GLs consisting of sedimentary bedrock (Johnston *et al.*, 2010). The type of bedrock affects the weathering process and so influences the water chemistry (Mayer et al., 2004). For example, Lake Superior with its granitic bedrock, is much less alkaline and contains fewer ions than Lake Michigan and Lake Erie which are both surrounded by sedimentary bedrock and glacial deposits (Keough *et al.*, 1999). The low alkalinity of Lake Superior results in the acidification of sediments and the establishment of poor fen and bog plants such as *Sphagnum* spp. (Vitt, 1994; Albert & Minc, 2004). The establishment of such plants reduces the productivity of agricultural crops and thus limits the amount of agricultural development within most Lake Superior watersheds (Albert & Minc, 2004).

Second, the GLs region is exposed to a range of climatic conditions from subarctic in the north, to humid continental warm in the south (Edsall, 1998). Three factors influence the weather in the GLs basin (Trebitz & Taylor, 2007; Edsall, 1998): 1) air masses from other regions, 2) location of the basin within a large continental land mass and 3) the moderating influence of the lakes themselves. Humid air masses from the Gulf of Mexico influence the southern part of the basin while cold dry air masses from the Arctic and northwest are received at the northern region. The lakes are slower to warm and slower to cool than the land, therefore act as heat sinks during the summer and heat sources during the winter (Edsall, 1998). This phenomenon combined with the large size of the GLs are responsible for their moderating effect on the regional climate (Mayer et al., 2004). The GLs also influence the climatic conditions by increasing the amount of precipitation and snow. Air masses moving across the GLs accumulate moisture from the lake surface and drop it downwind mainly off the eastern and southern shores (Mayer et al., 2004). Climate as well as precipitation patterns influences wetland evolution, including their plant assemblages (Mayer et al., 2004). There is a large latitudinal difference in plant growth across the GLs. Coastal wetlands along Lake Erie have a 60% longer growing season than the coastal wetlands along Lake Huron (Johnston et al., 2010). A longer growing season in the south attracts more anthropogenic agricultural activities. A study by Lemein et al. (2017), has found that latitude and agriculture are the strongest indicators of community distribution in both meadow and emergent wetland plant communities and were inversely proportional to each other.

Third, anthropogenic stress is another important factor that causes regional differences in vegetation. Johnston et al., (2010) stipulated that a latitudinal gradient in wetland plant species distribution has probably always existed along GLs coasts due to natural variations, but human activities concentrated in the southern portion of the basin have undoubtedly steepened that gradient. Lower lakes possess warmer waters and higher levels of nutrients and disturbance (Trebitz & Taylor, 2007; Johnston, Zedler & Tulbure, 2010).

1.7. Great Lakes stressors and their impacts on wetlands

1.7.1. Climate change

Climate is a key factor in determining the distribution, productivity and functioning of a wetland ecosystem. Increases in concentrations of atmospheric greenhouse gases are projected to cause many changes to the climate, the most certain outcome being an increase in global air temperature while precipitation changes are more uncertain (Mortsch et al., 2006).

An increase in air temperature will also bring about an increase in water temperature which can have significant impact on shallow, near shore areas and affect dissolved oxygen concentrations. Furthermore, warmer temperatures will shift thawing events, causing an earlier spring melt and alter seasonal water level cycles (Mortsch et al., 2006). A new established baseline temperature conditions can extend the length of growing seasons and increase evapotranspiration. Climate change effects on wetland ecosystems will be determined by how rapidly climate changes and its resulting effects on water levels. If changes occur rapidly, the adaptive capacity of many wetland species may be exceeded and species will not have the opportunity to adapt quickly enough to these changes (Albert et al., 2005; Wilcox & Xie, 2007; Wilcox, 2004; Mortsch et al., 2006).

Climate change is expected to increase the frequency and intensity of extreme weather events such as storms and hurricanes. Such events can increase the risk of flooding and increase soil erosion (Mortsch et al., 2006). Droughts are also expected to increase in frequency and duration with climate change. Environmental stochasticity brought on by climate change, such as extreme weather events or increased drought and flooding can drastically change areas with species with low populations because of a greater risk of extinction (Fujiwara & Takada, 2017; Mortsch et al., 2006). Many wetlands are already critically affected by the many stressors brought on by urbanization, agricultural runoff, and fragmentation and may have little resilience to respond to the new pressures of climate change (Allan et al., 2012; Mortsch et al., 2006).

1.7.2. Anthropogenic stressors

Different land uses impose different environmental stresses on natural plant and animal communities. Land use changes can have consequent implications to water quality, ecosystem services, economic welfare, and human health (Allan et al., 2013; Wolter and Johnson 2006). Land use changes such as increased urbanization and agricultural land can cause hydrological changes, increase nutrient inputs from both aqueous and atmospheric sources, eliminate natural spaces, increase fragmentation of the landscape, increase the presence of pesticide and/or herbicide, increase erosion of sediment, increase introduction and dispersal of exotic species (Lougheed and al., 2008). These consequences can have quick and long-lasting effects on the biodiversity of wetlands.

The types of adjacent land use (residential, commercial and industrial), road density and human population density in the surrounding region all affect water flow into and through the wetland (Booth & Jackson, 1997; Ehrenfeld, 2008). These factors also influence water quality through nutrient and pollutant inputs. Increasing urbanization increases the amount of impervious surface area which in turn increases the volume of storm runoff. Higher amounts of impervious surface area decrease storm water retention time. A study by Schueler (1994) demonstrated that stream quality often begins to degrade when impervious surface area within the contributing watershed exceeds 10%.

Other direct impacts that alter hydrological regimes such as dredging of channels and ditches, building dikes or dams within or near a wetland can affect the local flora of that environment. Alterations of natural habitats enables species to become established into areas where they previously would not have succeeded (Farwell 1916).

1.7.3.Exotic and invasive species

One of the most pervasive and alarming anthropogenic effects on the world's aquatic ecosystems is the global transfer of exotic organisms (Mills et al. 1993). A study by Ehrenfeld in 2008 has shown that patterns of invasion appear to reflect a combination of particular environmental conditions and human influences at individual sites and the ecological characteristics of individual species.

Exotic and invasive species can negatively affect biodiversity (Rojas and Zedler, 2015), food webs and ecosystem functioning (Trebitz and Taylor, 2007). In the United-States alone, exotic species have caused major environmental damages and losses estimated between $1.1 billion per year (OTA, 1997) to $120 billion per year (Pimentel et al., 2004). Introduced or exotic species can be defined as successfully reproducing organisms transported by humans into regions where they did not previously exist. With increasing globalization, foreign species are finding their way into even the most remote areas of the world. Some introduced species can be very successful and wreak havoc on the established flora and fauna of the region which has not evolved to deal with this new arrival. Such a specie is considered invasive and can lead to biotic homogenization. The term “biotic homogenization” often refers to the process whereby diverse native communities are gradually replaced by a few, often exotic, species (McKinney & Lockwood, 1999).

Exotic species can arrive in a variety of ways through deliberate or unintentional releases, migration through and along canals, railroads, and highways (Mills and al., 1993). Invasive species are are not necessarily exotic although many are (Rojas and Zedler, 2015). For some invasive species, their origins are uncertain. The success of exotic species depends on many factors, including their survivability in unfavorable conditions, adaptability to new environments, high reproductive capability, competitiveness for resources, and their ability to disperse rapidly (Mills and al., 1993). Often, invasive plant species will exert dominance through their abundance, height, shade, belowground biomass, and chemistry (Rojas and Zedler, 2015). Understanding the consequences of introduced species on different ecosystems is critical because successful exotics may render previously stable ecosystems unbalanced and unpredictable.

Some exotic plant species form monospecific stands that displace native species, reducing plant biodiversity and the habitat available for associated fauna (Tulbure and al., 2007; Trebitz and Taylor, 2007). Variations in climatic conditions, alteration of the hydrologic regime, changes in land use, and nutrient increase can help competitive invasive species to dominate an area. Wetlands that occur in sinks are particularly vulnerable to invasions as they accumulate runoff, nutrients and sediments, and propagules of potential invaders. Successful invasive species can exert strong influence on productivity, canopy strata, nutrient cycling, and soil properties of a community (Rojas and Zedler, 2015).

1.8. Most problematic plant species in the Great Lakes' wetlands

The success of exotic species depends on many factors, including their survivability in unfavorable conditions, adaptability to new environments, high reproductive capability, competitiveness for resources, and their ability to disperse rapidly (Mills and al., 1993). Often, invasive species will exert dominance through their abundance, height, shade, belowground biomass, and chemistry (Rojas and Zedler, 2015). The adverse effects of exotic plants on wetlands can include reduced flora richness, degradation of faunal habitat (overly dense growth, reduced structural diversity, loss of sediment microtopography), decline in forage value (plants less desirable as food for waterfowl, support fewer macro-invertebrates), and alteration in ecosystem functions such as nutrient cycling (Zedler and Kercher 2005; Lishawa et al., 2014).

1.8.1. Phragmite

Phragmites australis (Cav.) Trin. ex Steud., also known as Phragmite, is an invasive wetland grass species native to Eurasia and North America (Carlsen et al., 2014). It forms large stands of vegetation that displace native species and reduce biodiversity in GL wetlands, as well as other areas around the world (Carlsen et al., 2014; Trebitz and Taylor, 2007; Lougheed et al., 2008). Phragmite is one of the most aggressive invasive species in GL wetlands, outcompeting native plants due to its rapid growth and deep root systems (Tulbure and al., 2007). It creates dense stands which make it difficult for other plants to grow, leading to a decrease in biodiversity and a reduction in the habitat available for associated fauna (Carlsen et al., 2014; Trebitz and Taylor, 2007; Tulbure and al., 2007). The spread of *Phragmites australis* into GLs wetlands can also be attributed to various environmental factors such as climate change, hydrologic changes, altered land use and increased nutrient levels (Carlsen et al., 2014). Climate predictions have indicated that there will be an increase in suitable habitat for Phragmites in coastal Lakes Huron and Michigan in particular (Carlsen et al., 2014). In addition, prolonged periods of below-average water levels can expose unvegetated lagoon bottoms as mud flats which provide an ideal substrate for new plant colonization by this invasive species. Control methods currently employed include combinations of cutting, flooding, burning and herbicide application; however, treatments must be repeated annually or biannually to maintain desired effects due to the resilient nature of Phragmite. The cost associated with controlling established Phragmite stands is substantial; therefore it is important that conservationists take proactive measures to understand the underlying causes of its expansion so they can better manage GL coastal wetlands against future invasions.

1.8.2. *Typha* sp.

Typha, also commonly referred to as Cattail, is an invasive perennial wetland plant. This genus comprises nearly 40 species and hybrids are found across wetland ecosystems throughout the world (Bansal et al., 2019). North America's GLs have three dominant species of Typha: the native *Typha latifolia* (broadleaf cattail), the exotic *Typha angustifolia* (narrowleaf cattail), and a hybrid taxon *Typha × glauca* (a cross of T. latifolia and T. angustifolia) (Bansal et al., 2019). These species have become a major problem for local biodiversity due to its quick growth rate, impressive adaptability, and ability to rapidly spread throughout the GLs region due to an abundance of wind-dispersed seeds (Bansal et al., 2019; Trebitz and Taylor, 2007; Herrick and Wolf, 2005). Typha plants tend to grow rapidly and form dense stands which is particularly evident in the GLs wetlands where invasive Typha stands dominate the landscape in many areas (Trebitz and Taylor, 2007; Lishawa et al., 2014). Another successful trait for Typha is its high tolerance to a wide range of water levels (Bansal et al., 2019). Furthermore, Typha have been shown to display an adaptation for rapid nutrient uptake when exposed to nutrient-rich environments (Lishawa et al., 2014). Anthropogenic stressors such as increased nutrient inputs from surrounding sources have been linked with promoting the spread of invasive Typha within GLs habitats (Bansal et al., 2019). Various control methods exist including physical removal or burning along with chemical treatments or drastic hydrologic alterations; however, results are inconsistent between locations and multiple treatments may be necessary before successful management takes place (Bansal et al., 2019).

1.8.3. Hydrocharis morsus-ranae

Hydrocharis morsus-ranae, commonly known as European frog-bit, is a floating aquatic plant native to wetlands in Europe and parts of Asia (Mills et al., 1993). It has become an invasive species in many other countries due to its ability to spread quickly and outcompete native vegetation. It was first introduced to Canada in the 1930s and has since spread into the GLs region (Mills et al., 1993). *Hydrocharis morsus-ranae* forms dense mats on the surface of still or slow-moving waters which can block light from reaching deeper water plants, disrupt ecosystems and threaten wetland habitats around the world (Simkovic, 2020). When these dense mats die back, they decrease oxygen levels in the water which can be fatal to fish and other aquatic organisms. They also impede recreational activities such as swimming, boating and fishing. *Hydrocharis morsus-ranae* is able to reproduce both sexually through pollen transfer between flowers and asexually through fragmentation of stems or stolons budding off from parent plants (Simkovic, 2020). This species' rapid adaptation to different environmental conditions has allowed it to spread rapidly across multiple continents causing significant damage to native aquatic ecosystems. *Hydrocharis morsus-ranae*'s growth rate depends on many factors including water temperature, nutrient availability, light intensity and pH levels. However lack of competition is often the most important factor for its growth rates in newly invaded areas (Simkovic, 2020). This species has been classified as one of the top 100 worst invasive alien species in the world due to its wide distribution and potential for ecological disruption. In order to control *Hydrocharis morsus-ranae*'s spread there are several management strategies that should be implemented depending on the size of the affected area; these include physical removal (with nets or hand picking), chemical treatments such as herbicides, mechanical disturbance (such as dredging), biological controls (such as introducing predators), and finally education programs aimed at raising public awareness about this invasive species. All approaches must be adapted according to local environmental conditions and should be assessed regularly to ensure their effectiveness over time.

1.9. Objectives of this study

A better understanding of the current GL coastal wetland plant biodiversity and its response to well known stressors will allow for proactive wetland conservation planning and management. Incorporating biodiversity analysis into decision-making for future wetland conservation, restoration, and management will help protect important GL coastal wetland functions and values. To do so, Environment and Climate Change Canada (**ECCC**) acted through the Great Lakes Protection Initiative (**GLPI**) to address the most significant environmental challenges affecting Great Lakes water quality and ecosystem health. Using data acquired by the GLPI in 2018 and 2019, the purpose of this study was to get an up-to-date status of plant biodiversity of the GL wetlands and to propose a conceptual framework to initiate a discussion to prioritize sites for conservation and restoration. More specifically, this study 1) used several biodiversity metrics (species richness, Shannon-Weaver diversity, Pielou evenness, and beta-diversity) to describe the biodiversity of plants in GL coastal wetlands at multiple scales (lake, wetland site and wetland class), 2) examined the relationships between biodiversity metrics, the prevalence of exotics and invasive species and land use cover variables, and finally 3) suggested a framework to identify sites to conserved, protected and/or restored based on biodiversity data and land use variables.

CHAPTER II: CHARACTERIZING BODIVERSITY PATTERNS ACROSS CANADIAN GREAT LAKES WETLANDS: IMPACTS OF LAND USE AND EXOTIC SPECIES

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Abstract

The Great Lakes wetlands are degrating rapidly as a result of invasive species and anthropogenic stressors. In this study, we utilized data from 2018 and 2019 from the Great Lakes Protection Initiative funded by Environment and Climate Change Canada to assess the current state of plant biodiversity in the Great Lakes wetlands. Specifically, we employed various biodiversity metrics (species richness, Shannon-Weaver diversity, Pielou evenness, and beta-diversity) to describe plant biodiversity in the coastal wetlands of Great Lakes at different scales (lake, wetland site, and wetland class). Additionally, we investigated the relationships between biodiversity metrics, the prevalence of exotic and invasive species, and land use cover variables. We suggested a framework using Principal Component Analysis (PCA) to identify sites that should be conserved, protected, and/or restored based on biodiversity data and land use variables. By analyzing this comprehensive dataset, we aim to contribute to the conservation and restoration efforts in the GL wetlands and facilitate decision-making processes.

2.1. Introduction

Coastal wetlands of the Great Lakes (**GL**) are highly productive and diverse ecosystems that have essential ecological, economic and social roles. Home to over 35 million inhabitants from the United-States and Canada, their importance stems from providing numerous ecosystem services and functions such as coastal protection, water purification and essential habitat for a large variety of species of fauna and flora (Mayer, Edsall & Munawar, 2004; Midwood & Chow-Fraser, 2010, Cvetkovic & Chow-Fraser, 2011). They also play a significant role to mitigate climate change by sequestering carbon. Many ecosystem functions provided by these wetlands are driven by the biodiversity, distribution, and abundance of the plants inhabiting the area. A rich wetland plants biodiversity provides high levels of primary productivity as the foundation for complex food webs, and provide habitat for many invertebrates, fish, amphibians, reptiles, birds, and mammals (Albert & Minc, 2004; Cvetkovic & Chow-Fraser, 2011).

Coastal wetlands of the GL occupy a transitional position between aquatic and terrestrial environments, which provides a variety of abiotic conditions for plant germination, and growth (Farrell *et al.*, 2010; Bedford, 1992). Most plants species have unique characteristics and adaptations that enable their survival in a narrow niche along the wetlands water level continuum; this succession of plants is called the **hydrosere** (Tiner, 2016). Wetland plant species that possess similar tolerances generally grow at comparable elevations and moisture conditions (Tiner, 2016). Based on those tolerances, wetlands have been classified into different types (*e.g.*, marsh, swamp, peatland) based on their vegetal communities that are influenced by hydrogeomorphological characteristics as well as water level fluctuations, slope, water depth, wave exposure, substrate properties (Hudon et al., 2006; Wilcox and Nichols, 2008; Lemein et al., 2017; Weller and Chow-Fraser, 2019). Classification systems can provide important information on wetland biodiversity, functions, and services (Mitsch and Goselink, 2000; Bridgham et al., 2006).

Despite their importance, wetlands of the GLs have been experiencing rapid degradation from increasing agriculture, urbanization, land cover changes, hydrological modifications, point source pollution, atmospheric deposition and climate change (Booth & Jackson, 1997; Keough et al., 1999; Crosbie & Chow-Fraser, 1999; Frieswyk & Zedler, 2007). Apart from these abiotic factors, biotic factors such as the establishment and expansion of exotic and invasive plant species have been responsible for a multitude of ecosystem changes in the GLs. These biotic and abiotic stressors can act individually, additionally or synergistically to change the distribution and the composition of plant species in the wetlands (Allan et al., 2013; Frieswyk & Zedler, 2007). Ecosystem alterations caused by exotic and invasive species are of major concern and include the reduction of plant species diversity and the alteration of community composition, changes in light conditions, nutrient cycling, litter accumulation, a modification in established competitive relationships and a greater community homogenization at the wetland scale (Keddy & Reznicek, 1986; Mills et al., 1993; Lishawa, Albert & Tuchman, 2010).

In recent years concerns regarding wetland loss and degradation have led to the adoption of several conventions, directives, laws, and a range of conservation actions to protect them (*e.g.*, Natura 2000 sites in the Europe, Ramsar Convention). Wetland restoration is also increasingly viewed as an important element of conservation management (Young, 2000, Harris et al., 2006). Therefore, systematic conservation planning (**SCP;** Margules & Pressey, 2000) is gaining attention to identify cost-efficient networks of conservation (protected area and reserves), restoration and production sites on a given landscape to achieve greater benefits for all parties (landscape multifunctionality; Bennett, Peterson & Gordon, 2009). The SCP approach offers a decision support framework that can support landscape multifunctionality by indicating where efforts should be implemented based on indicators (e.g., ecosystems services and functions).

A better understanding of the current GL coastal wetland plant biodiversity, as a metric of ecological functions, and its response to well known stressors will allow for proactive wetland conservation planning and management. Incorporating biodiversity analysis into decision-making for future wetland conservation, restoration, and management will help protect important GL coastal wetland functions and values. To do so, Environment and Climate Change Canada (**ECCC**) acted through the Great Lakes Protection Initiative (**GLPI**) to address the most significant environmental challenges affecting Great Lakes water quality and ecosystem health. Using data acquired by the GLPI in 2018 and 2019, the purpose of this study was to get an up-to-date status of plant biodiversity of the GL wetlands and to propose a conceptual framework to initiate a discussion to prioritize sites for conservation and restoration. More specifically, this study 1) used several biodiversity metrics (species richness, Shannon-Weaver diversity, Pielou evenness, and beta-diversity) to describe the biodiversity of plants in GL coastal wetlands at multiple scales (lake, wetland site and wetland class), 2) examined the relationships between biodiversity metrics, the prevalence of exotics and invasive species and land use cover variables, and finally 3) suggested a framework using a PCA to identify sites to be conserved, protected and/or restored based on biodiversity data and land use variables.

2.2. Methodology

2.2.1 Study sites

The GLPI selected a total of 26 sentinel coastal wetlands representative of the dominant hydrogeomorphological systems found in the Canadian part of the Great Lakes region (Annex A). The 26 wetlands sites were studied from seven different lakes or rivers. Sites were distributed as follows: nine in Lake Huron (Baie Du Doré, Collingwood Shores, Hay Bay, Coffin Rock Wetland, Francis Point Marsh, Hog Bay, Key River Wetland, Treasure Bay and Whiskey Harbour Wetland), six in Lake Erie (Selkirk Provincial Park, Fox Creek/Dolson's Creek, Grand River Mouth Wetlands, Long Point, Rondeau Bay and Detroit River Marshes), five in Lake Ontario (Airport Creek Marsh, Jordan Station, Lynde Creek, South Bay Marsh and Wesleyville Marsh), two in Lake Superior (Hurkett Cove and Mission Marsh), two in Lake St. Clair (Lake St. Clair Marshes and St. Anne's Marsh of Walpole Island), one in St. Mary's River (Anderson Creek), and one site in the Saint-Lawrence River (Hill Island East Marsh). See Annex A for a description of the sites.

2.2.2 Vegetation survey and cover estimates

For each wetland site, vegetation surveys have been performed in 150-200 sampling quadrats distributed among 15-20 transects. The number of transects and quadrats per site was determined by the size of the wetland (see Annex A). The locations of the transects were predetermined by ECCC to capture a variety of habitats along the hydrosere. If a certain transect needed to be shortened to fit with the site, additional transects were produced for a maximum of 20 transects per site. The orientation and length of transects were pre-determined to capture elevation points in each vegetation community present. Sampling quadrats were uniformly distributed along each transects with a general rule of 10 quadrats by transects.

Sampling was carried out during the summer of 2018 and 2019 between the end of July and the beginning of September, when plant growth is at its maximum and before fall senescence commences. Vegetation surveys were performed by the Canadian Wildlife Service, Natural Resource Solutions Inc. and Dillon Consulting in 2018 and 2019 for the benefit of ECCC. Quadrats of 1.0 m x 0.5 m were distributed along transects. Each quadrat was carefully placed along the elevation gradient to have the longer side of the rectangular quadrat perpendicular to the elevation gradient. In each quadrat, the total percentage of vegetation cover was estimated, as well as the percentage of cover for each species present. For plants that were difficult to identify to the species level (*e.g.*, Characeae), they were identified at the genus. Species cover percentage was estimated by vertical projection from 0 to 5% by increments of 5%. The total cumulative cover percentage for all taxa in a quadrat may surpass 100% due to the superposition of the different vegetation strata. Vegetation cover was estimated by two surveyors to minimize sampling error and species misidentification. If the quadrat was in deep water and the vegetation cover could not be accurately estimated, surveyors used a rake device to identify the taxa in the quadrat and estimated cover from the raked vegetation. Positioning and elevation data (X, Y and Z) were recorded for each quadrat using high precision topographic survey technique with a d-GPS.

2.2.3 Categorizing native and exotic species

All species sampled were classified into two groups: Native or Exotic. In order to classify each species into these groups, extensive research of the current literature was performed as well as a comparison with the data provided by the United States Department of Agriculture (**USDA**). If the species in a quadrat was identified to its genus level (i.e., *Epilobium* sp.), then it was categorized as "unspecified" as one genus can hold multiple native (ex.: *Epilobium leptophyllum*) and exotic species (ex.: *Epilobium hirsutum*).

2.2.4 Land-use

In order to support the biodiversity analyses, land use data at each wetland site were compiled from the Annual Crop Inventory (**ACI**) map available on Agriculture Canada website that can be access with this link (https://www.agr.gc.ca/atlas/apps/metrics/index-en.html?appid=aci-iac). This crop inventory provides fundamental information on the state and changes in Canada's agricultural landscape year by year. This map possesses a spatial resolution of 30m based on a Decision Tree (**DT**) based methodology that was applied using optical (Landsat-8, Sentinel-2) and radar (RADARSAT-2) based satellite images. Buffer areas at a centroid point of each site was created to summarise the information of the ACI land use map. Buffers of 2.5 km, 5 km and 10 km diameter were used and were extracted using "Grid classes Areas for polygons" in the System for Automated Geoscientific Analyses (SAGA GIS) version 7.2.0.

2.2.5 Statistical analyses

2.2.5.1 Determination of large wetland classes

The first step was using an accurate elevation model, crucial for wetland plant succession models, using the Coastal Wetland Response Model (CWRM). This model predicts the distribution of large wetland classes based on hydrodynamic factors and wave time series. It connects broad dynamics, like Great Lakes climate and hydrodynamics, to smaller processes that influence changes in wetland class distribution. The elevation model is created through high-definition Digital Elevation Models (DEMs), which represent the topography of an area at a specific scale determined by its cell size in a regular grid setup. Various data sources, including the International Great Lakes Datum 1985, the Canadian Geodetic Vertical Datum 1928, and the Canadian Geodetic Vertical Datum 2013, were used to create the vertical coordinate reference system. The datasets were interpolated to the DEM grid using Ordinary Kringing interpolation in Python, with a spatial resolution of 2 m. Elevation data for 300 to 600 survey points per study site were collected and used to validate the DEM. With this DEM, primary terrain attributes like elevation and slope could be extracted for quadrat of the vegetation survey. The DEM is important because wetland classes are structured along a topographical gradient, and the elevation range (relative to water level) in which certain species can persist is often narrow (<1 m). Between open water (**OW**) and upland (**UPL**), the typical wetland classes of the hydrosere are the submerged aquatic vegetation (**SAV**) below the surface of the water, persistent emergent marshes (**EM**), non-persistent emergent marshes (**NPE**) in shallow water or inundated substrate, wet meadows (**WM**) above the shoreline, followed by swamps (**SS**) at the inland limit of the wetland (Thériault et al. 2022). The different types of models are based on the same assumption: the distribution of hydrophilic species and wetland classes is strongly influenced by hydrological processes (Nilsson & Keddy, 2011; Toner & Keddy, 1997). In order to assign a wetland class to each vegetation survey point, clustering analysis were performed for each lake independently. The clustering analysis allows associating a large wetland class to vegetation species occurrences. To minimize the bias induced by rare species, only species with a frequency higher than 3% in each lake were included in the analyses. Forb and graminoid species with a frequency lower than 3% were grouped based on the combination of their growth form and wetness index (Thériault et al. 2022). Clustering analyses were performed for each lake independently in order to assign a wetland class to each quadrat surveyed. Only species with a frequency higher than 3% in each lake were included in these analyses to reduce bias induced by rare species. The clValid package v.0.7 in R (Brock et al 2008) was used to determine the best clustering method between Ward's Hierarchical or K-means and the optimal number of clusters according to the Connectivity, Silhouette and Dunn Indexes (Thériault et al. 2022). Clusters were then grouped into 5 classes (Table 1.1).

Table 2.1. Number of quadrats by large wetland class and the dominant species found in each class in decreasing percentage of cover for that class

Wetland classes	Number of quadrats	Dominant species
Submerged aquatic vegetation (SAV)	1825	*Ceratophyllum demersum* *Chara sp.* *Lemna minor* *Vallisneria americana* *Nymphaea Odorata ssp. odorata*
Non persistent emergent	650	*Chara sp.*

(NPE)		*Sparganium eurycarpum* *Zizania palustris*
Emergent marsh (EM)	1526	*Typha x Glauca* *Phragmites australis* *Hydrocharis morsus-ranae* *Lemna minor*
Wet meadow (WM)	1459	*Calamagrotis canadensis* *Phalaris arundinacea* *Carex lacustris* *Carex aquatilis*
Swamp (SS)	710	*Cornus Stolonifera* *Alnus incana* *Vitis riparia* *Calamagrotis canadensis*

2.2.5.2 Biodiversity analysis

To study the taxonomic diversity of plants, we calculated the alpha-, beta-, and gamma-diversity at multiple scales (quadrat, transect, large wetland class, site and lake levels). Alpha and gamma diversity indices were species richness (at the quadrat or transect scale for the alpha and at the site level for the gamma), Shannon diversity index and Pielou's evenness index. Beta diversity was partitioned into 2 statistics: the degree of variation of individual species across the study area given by the relative Species Contribution to Beta Diversity (SCBD; Legendre et al., 2013) and an indicator of the ecological uniqueness of the sites described by the Local Contribution to Beta Diversity (LCBD; Legendre et al., 2013). LCBD values were obtained using the beta.div() function from the adespatial package v.0.3-20 (Dray et al., 2018). Shannon diversity index was calculated with the diversity() function from the vegan package version 2.4-2. Species richness and Pielou index of evenness were obtained through simple calculations performed in R. We used linear regression to test the relationship between biodiversity metrics and latitude and biodiversity metrics and land use cover variables. All statistical analyses were performed using the R software (version 3.4.3; R Core Team, Vienna, Austria).

To develop the conceptual framework for prioritization of sites for conservation and restauration, a principal component analysis (**PCA**) was also performed in R. A PCA is a statistical ordination technique and involves transforming variables related to each other ("correlated") into new variables decorrelated from each other (orthogonal). These new variables are called principal components (**PC**), or principal axes. A PCA makes it possible to reduce the number of variables, to summarize them, and to make the information less redundant. A PCA biplot (see Figure 2.5) shows both principal components scores of samples (dots) and loadings of variables (vectors). The further away these vectors are from a PC origin, the more influence they have on that PC. We used richness, diversity, evenness, LCBD and cover of exotic species for biodiversity variables, as well as land use variables (percentage of agricultural land, natural and urban area) at the site level in the PCA.

2.3. Results

2.3.1. Biodiversity metrics across sites and lakes

Four biodiversity metrics were used to characterize the wetlands (species richness, Shannon-Weaver index, Pielou index and the local contribution to local diversity; LCBD). These metrics varied greatly across sites and lakes in the Great Lakes but not between years (2018 – 2019; Appendix C, figure A1). Across the 26 wetland sites, species richness varied between only 26 species (Lake St. Clair marsh in 2018) to more than 197 species (South Bay Marsh in Lake Ontario in 2019; Figure 2.1a). A similar pattern was observed for the Shannon-Weaver diversity index (Figure 2.1b) and for the evenness Pielou index (Figure 2.1c). The LCBD, which can be interpreted as an index of uniqueness of the site, varied from 0.0098 to 0.0280 (Figure 2.1d). Exotic species cover also varied greatly among wetlands. The site with the least exotic species cover was Anderson Creek (St. Mary's River) with less than 1% exotic species cover, and the site with the highest exotic species cover is Lynde Creek Marsh (Lake Ontario) with 49.6% of its total cover being exotic species (Figure 2.1e). For figures, and to compute the correlation matrix between biodiversity metrics, we combined years (2018-2019) as they did not show any significant differences (ANOVA; $p > 0.51$ for all metrics; Appendix C, figure A1). Species richness was strongly correlated with Shannon-Weaver (Pearson = 0.80) but moderately with Evenness (Pearson = 0.34). Furthermore, the percentage of exotic species cover was negatively correlated with species richness (Pearson = -0.38), Shannon-Weaver (Pearson = -0.49) and Evenness (Pearson = -0.35).

2.3.2. Land use metrics across sites and lakes

Land use data extracted from the Annual Crop Inventory (ACI) map demonstrated a large difference between wetlands sites from the North to South (Figure 2.2). The examination of the largest buffer area around the site (10 km radius) showed that the percentage of agricultural land cover around the site varied from 0 % (Coffin Rock Wetland, Francis Point Marsh and Key River Wetland from Lake Huron; Figure

2.2 a) to 88.1% (Lake St. Clair Marsh; Figure 2.2 a) with an average agricultural land cover of 35% across all wetland sites. Unsurprisingly, the percentage of natural land is inversely correlated with agricultural land cover (Pearson = -87.9) and cover varied between 8% (Lake St. Clair Marsh; figure 2.2 b) to 99.9% (Key River Wetland from Lake Huron; Figure 2.2 b) with an average of 54.1%. The percentage of Urban land cover varies between 0% and 69.8% (Lynde Creek Marsh from Lake Ontario; Figure 2.2 c) with an average of 10.9%. Land use averages at the lake level varied greatly between the North and the South. Lakes in the south are strongly dominated by agriculture (Erie and Ontario; 60.4 % and 42.1 % of agricultural cover respectively), whereas lakes in the North are in a more natural state (Huron and Superior; 77.5% and 74.7% of natural cover respectively).

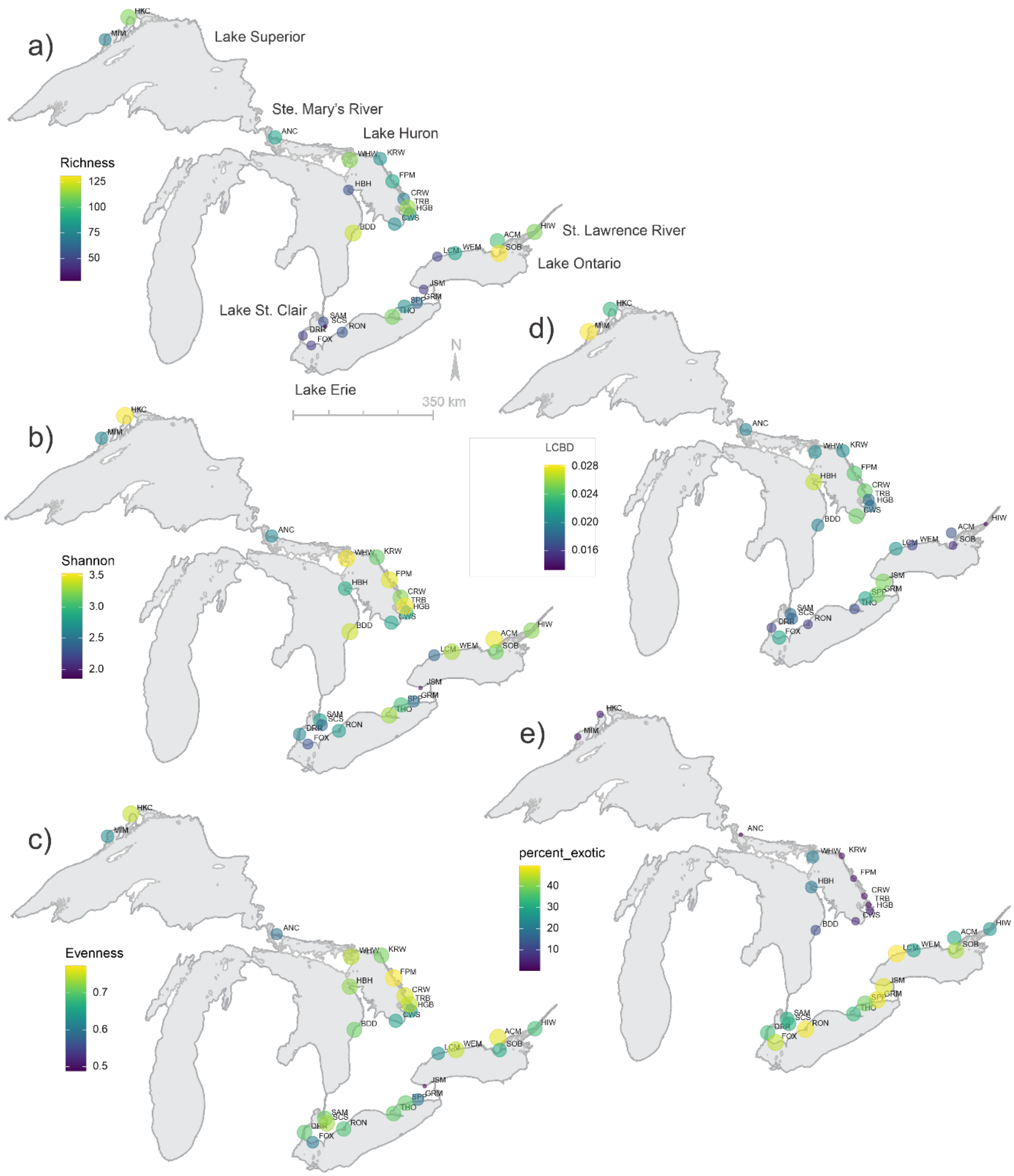

Figure 2.1. Maps of biodiversity metrics across the Great Lakes at the site level, metric results are an average between year 2018 and 2019 for a) species richness, b) Shannon Weaver diversity index, c) Evenness Pielou index (varying from 0 to 1), and d) local contribution to beta diversity (LCBD) of each site. LCBD values represent the degree of uniqueness of each site in terms of community composition and the size of the symbol and its color gradient reflects the magnitude of the metrics at that site. Figure 1 e) represents the percentage of exotic species cover at each wetland site.

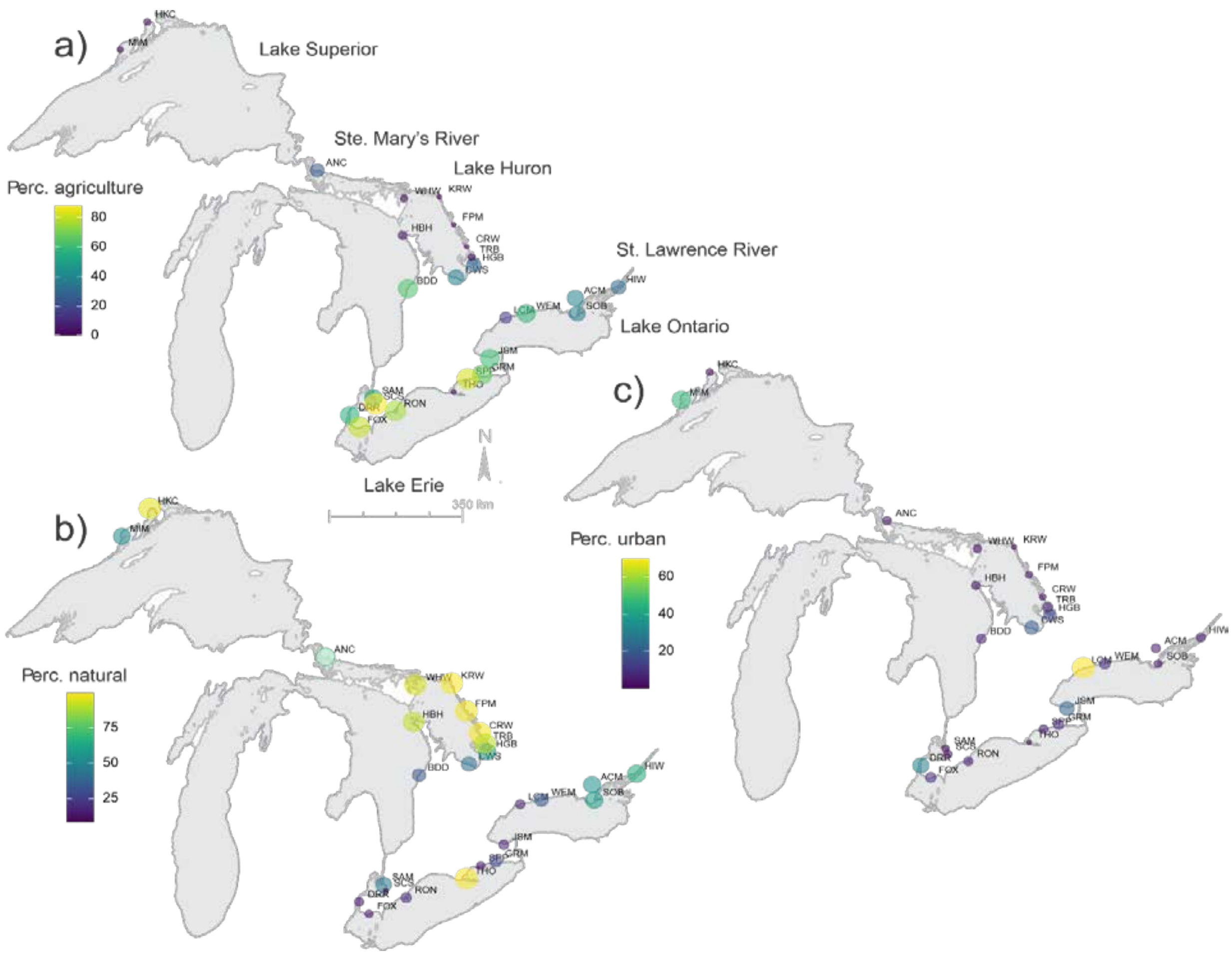

Figure 2.2. Maps of land use across the Great Lakes at the site level, years combined for a) percent agricultural cover, b) percent natural cover and c) percent urban cover. The size of each point and its color gradient reflects the magnitude of the metric at that site. Each point represents a percent average of land use in a 10km buffer around a centroid point at each site.

2.2.2 Patterns of biodiversity in relation to latitude and land use

Contrary to the assumption that a higher plant richness and diversity thrive in the south versus the north due to a longer growing season, warmer climate and milder winters, we observed a positive relationship between biodiversity and latitude. In other words, we observed a higher biodiversity in the North. Species richness (Figure 2.1a and Figure 2.3a; linear regression; t-value = 2.979, p-value = 0.005), Shannon-Weaver diversity (Figure 2.1b and Figure S2a; t-value = 2.093, p-value = 0.047) and LCBD (Figure 2.1d and Figure S2c, t-value = 2.262, p-value = 0.033) increased with increasing latitude, but not evenness (Figure 2.1c and Figure S2b, t-value = 0.818, p-value = 0.422). Sites in lower latitudes (Lake Erie and Lake Ontario) also showed a greater cover of exotic species than sites in the north (Figure 1d and Figure S2d; t-value = -5.677, p-value < 0.001). For example, the percentage of cover of exotic species in Lake Erie varies from 33.2 to

48.5% with an average of 41.3%. The dominant exotic or invasive species consisted of *Typha x Glauca* and *Phragmites australis* (Appendix 3, Table S1). On the other hand, exotic species cover in wetland sites in Lake Huron varied between 2.1% and 21% with an average of 7.6%.

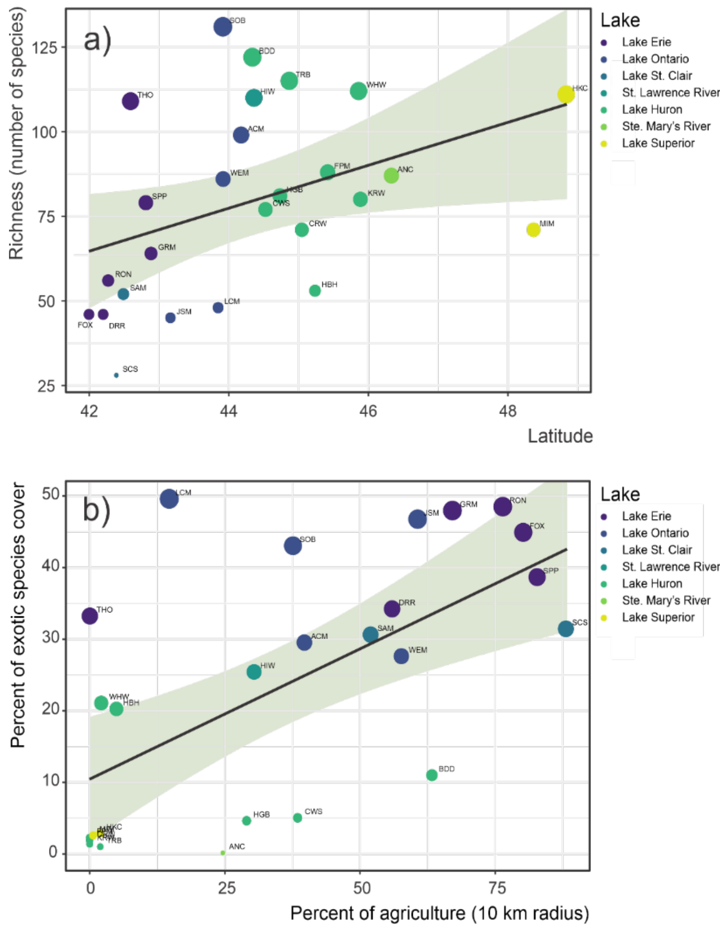

Figure 2.3. Linear regression between a) species richness and latitude and b) percentage of exotic species cover at each wetland site and its corresponding percentage of agricultural land use in a 10 km radius. The size of each point reflects a) species richness and b) percentage of total exotic species cover at each site.

The percentage of exotic species cover across our 26 sites was strongly and positively related to the percentage of agricultural land use (Figure 2.3b; t-value = 3.995, p-value < 0.001). Wetland sites from Lake Erie, Lake Ontario and Lake St-Clair were characterized by a high percentage of agricultural land and had the highest percentage of exotic species cover (Figures 2.1e, and 2.2a). The Longpoint site (THO; Lake Erie) seems to be an exception to this pattern and has little agricultural land use around the site and a high percentage of exotic species cover (Figure 2.3b). This site, however, was located on a narrow piece of land protruding into Lake Erie and the 10 km buffer from the centroid point mostly captured water. Lynde Creek Marsh (LCM; Lake Ontario) has a high 49.6% exotic species cover with a relatively low agricultural cover (14.7%; Figure 2.3b), however 69.7% of LCM's cover was classified as Urban land use which is also a strongly anthropized ecosystem (Figure 2.3c). The other biodiversity indices (Richness, Shannon-Weaver, Evenness and LCBD) were all negatively related to the percentage of agriculture in the 10 km radius buffer surrounding our wetland sites (Figure S3).

2.2.3 Biodiversity patterns within large wetland classes

The clustering exercise of plant species in large wetland classes revealed that the sampling effort was efficient in capturing all wetland classes (Table 2.1). The non persistent emergent class (NPE) was the least abundant class with 650 quadrats, followed by the swamp wetland class (SS) with 710 quadrats (Table 1). The most sampled wetland class was the submerged aquatic vegetation class (SAV) with 1825 quadrats. The dominant species identified in the SAV class were *Ceratophyllum demersum*, *Chara* sp., *Lemna minor* and *Vallisneria americana* (Table 2.1). The dominant species in the NPE, was *Chara* sp. followed by *Sparganium eurycarpum* and *Zizania palustris* (Table 2.1). Emergent marshes (EM) and Wet meadows (WM) both have comparable numbers of total quadrats (1526 and 1459 quadrats respectively; Table 1.1). In the EM class, *Typha x Glauca*, *Phragmites australis* and *Hydrocharis morsus-ranae* were the dominant species (Table 2.1). The dominant species of the WM class were *Calamagrostis canadensis*, *Phalaris arundinacea* and *Carex lacustris* (Table 2.1). The SS class was dominated by *Cornus Stolonifera, Alnus incana and Vitis riparia.*

The EM class had the most exotic and/or invasive species cover (Figure 2.4a; ANOVA; F-value = 61.9, p-value < 0.001). On average across all sites, this class had 52.7% more exotic species cover than in any other wetland class (Figure 2.4a). The emergent marsh class was also the most uneven wetland class as demonstrated in (Figure 2.4b, Pielou index; F-value = 62.45, p-value < 0.001) suggesting that few species dominate the community in EM. The EM class is mostly dominated by *Typha x Glauca* and *Phragmites australis* which are exotic and strongly invasive species.

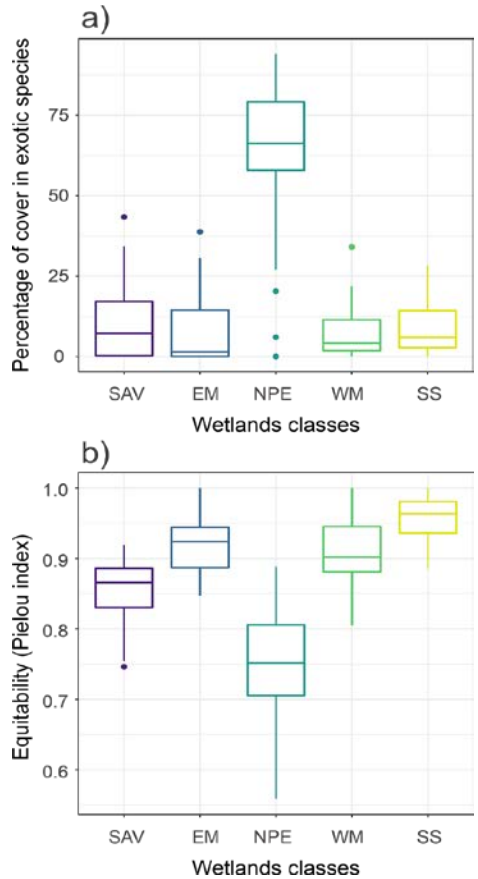

Figure 2.4. Boxplot of a) the percentage of exotic cover in relation to wetland classes and b) Evenness (pielou index) in relation to wetland classes. SAV = Submerged aquatic vegetation, EM = Emergent marsh, NPE = Non persistent emergent, WM = wet meadows, and SS = Shruby and treed swamp.

2.2.4 Conceptual framework to prioritize conservation and/or restoration

We used a PCA to generate the conceptual framework to suggest which sites should be conserved and/or restored based on the biodiversity metrics (species richness, Shannon-Weaver index of diversity, Pielou's index of Evenness, LCBD, exotic species cover) and land use (percentage of agricultural land, natural environment or urban environment; Figures 5 and 6). The PCA resulted in two main axes (Figure 5, Table 2). Axis 1 explained 50.5% of the variation and represents a biodiversity gradient (Figure 5, Table 2). The left panels of the PCA are characterized by a high species richness, a high Shannon-Weaver diversity, a high evenness (Pielou index) and a strong dominance of natural environments adjacent to the sites. The right panels are the opposite (Figure 2.5, Table 2). Axis 2, explained 20.6% of the variation and represented a gradient of human impacts. The upper panels of the PCA are characterized by a strong dominance of agriculture adjacent to the site, a high cover of exotic and invasive species and by sites that meet a low degree of uniqueness (LCBD; Figure 5, Table 2).

Based on PCA scores of each site, we classified them in four categories corresponding to the four quadrants of the PCA (Figure 6a). The first category is characterized by sites to conserve in priority (green quadrant; bottom-left panel) which are sites represented by a very high biodiversity, low exotic species cover and presence, low human impact and a high degree of uniqueness (Figure 6a). Those sites were mainly distributed in Lakes Superior and Huron (Figure 6b). The second category are sites that should be conserved because they are still characterized by a high biodiversity but demonstrated some degree of anthropic impacts (presence of exotic species and high cover of agriculture; blue top-left panel; Figure 6a). Those sites are distributed across lakes (Huron, Ontario and Erie; Figure 6b). The third category is characterized by sites that should be restored in priority (yellow, bottom-right panel; Figure 6a). Those sites are degraded and have low biodiversity but they still have a low cover of exotic species so they might be easier to restore. Those sites are in the four Great Lakes (Figure 6b). Finally, the fourth quadrant represent sites that are strongly degraded, with a high cover of exotic species and low biodiversity (dark-orange, top-right panel; Figure 6a). Those sites are all located in lakes St-Clair and Erie (Figure 6b).

Table 2.2: *Values (component loadings) of variables in both PCA main axes of the conceptual framework*

Variables	**Axe 1**	**Axe 2**
Richness	-0.759	0.237
Shannon-Weaver	-0.918	0.279
Evenness	-0.711	0.325
LCBD	0.107	-0.826
Exotic species cover	0.702	0.456
Percentage agriculture	0.715	0.579
Percentage natural	-0.893	-0.297
Percentage urban	0.504	-0.485

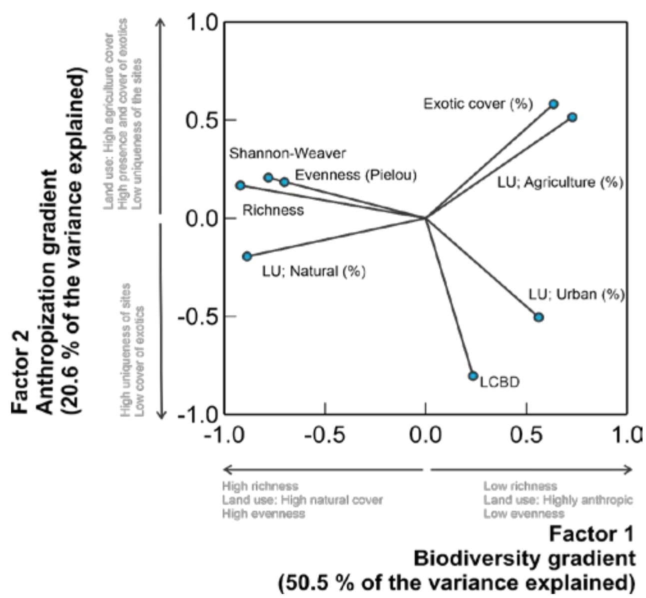

Figure 2.5. A principal component analysis (PCA) used to classify sites based on biodiversity indices and land use cover variables. Axis 1 explains 50.5% of the variation and represents a biodiversity gradient. Axis 2 explains 20.6% of the variation and represents an anthropic gradient. See Table 2 for the component loadings.

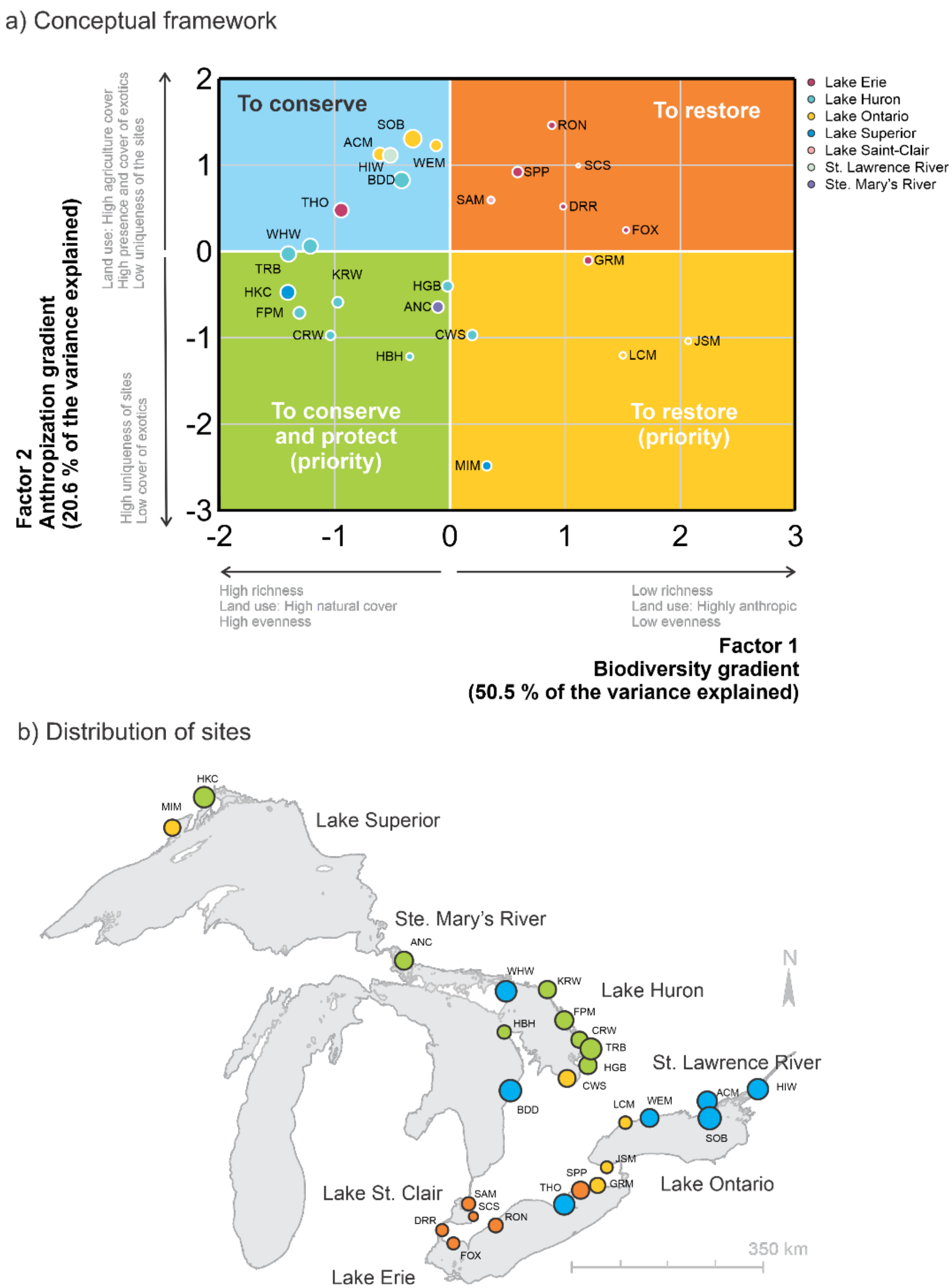

Figure 2.6. Conceptual framework showing a) PCA scores for each of the 26 sites along the two PCA axis and distributed in four quadrants that represent categories to conserve and restore sites based on biodiversity indices and land use variables, b) distribution of the sites across the Great Lakes region with a color-code that represent their suggested status in terms of conservation and restoration based on our conceptual framework.

2.3 Discussion

2.3.1. Updated status of biodiversity coastal wetland vegetation of the GL

Little was known about the current state of the Canadian Great Lakes wetlands plant biodiversity (Mayer et al., 2004). Previous studies have either an incomplete spatial coverage of the Great Lakes (Johnston and al., 2010; Lougheed and al., 2008; Munawar et al., 2005), focused on too few wetland classes (Trebitz and Taylor, 2007; Angradi and al., 2013; Lougheed and al., 2011) or tried to incorporate too many taxonomic groups of the wetland biota (Lougheed and al., 2008; Mills and al., 1993). An updated status of the biodiversity of coastal wetland vegetation of the GL was timely given the nature of wetland plant succession and its rapidly changing state with increasing anthropogenic stresses and the spread of exotic and invasive species (Wilcox & Nichols, 2008; Munawar and al., 2005; Lougheed and al., 2008). Here, using the impressive and extensive dataset acquired by the GLPI funded by the ECCC, covering 26 wetlands sites (8498 quadrats among 1028 transects from 2018-2019), this study aims to fill this gap. We offer an up-to-date analysis of plant biodiversity in GL wetlands within a context of invasive species and land use. This study shows a clear latitudinal gradient with species richness across the Great lakes in relation to anthropogenic stressors. Furthermore, the results show that the wetland class most affected by invasive species is the emergent marsh class. Finally, this study offers a conceptual framework based on various biodiversity metrics and land cover uses to help wetland managers to determine and prioritize which sites should be conserved and/or restored.

Contrary to the expected notion of the latitudinal diversity gradient (LDG), in which the number of species increases from the poles to the Equator (Hillebrand, 2004; Johnston et al., 2010), we found an increasing biodiversity (richness) with increasing latitude. This pattern relates to the positive relationships between the percent cover of invasive species and the percent cover of agricultural land use (Figure 4b). Wetland sites in the south (Lake Erie and Ontario) are heavily populated and developed which can change plant communities (Trebitz & Taylor, 2007; Mayer et al., 2004). An abundance of agricultural lands in the surrounding areas (Figure 2.2a) can cause high amounts of nutrients to accumulate in the wetlands through runoff (Lishawa and al., 2014). These conditions create opportunities that are well matched by wetland opportunists such as exotic and invasive species (Henrick and Wolf, 2005; Bansal and al., 2019). The differential response by individual species creates a changing mosaic of plant communities that needs to be closely monitored (Gathman et al., 2005). This finding underlines the importance of the effects of anthropogenic stressors and invasive species, working in synergy, to impact wetland biodiversity and species composition (Allan and al., 2013).

When comparing previous studies of exotic species cover in the GL, our study shows a more advanced stage of dominance by exotic and invasive species. A study by Munawar et al. in 2005 observed that invasive plants cover represented around 10% to 30% of the local flora in Lake Erie, comparatively to our findings of around 33.2% to 48.5% with an average of 41.3% in this same Lake (Figure 2.2e).

Furthermore, this study takes on a multiscale approach in order to observe differences that might be masked at larger scales due to natural variability between lakes, sites, or wetland classes. The multiscale approach is effective in analysing the invasive species as it helps uncover where we should prioritize conservation and restoration efforts. When comparing all wetland classes, our results show that the emergent marsh class is the most invaded by exotic plant species (Figure 2.4a). Phragmite and *Typha x glauca* are the main cause for this as they dominate the emergent marsh class. Both plants grow quickly and form dense stands that prevent other species from gaining a foothold in the environment thus reducing species richness and biodiversity values considerably (Figure 1a,b). Both plants also have high nutrient-uptake abilities which makes them capable of outcompeting native plants especially with increased nutrient inputs from neighboring agricultural lands. Previous studies have shown that Phragmites and Typha plants were more likely to be present and dominant as agricultural intensity increased and were associated with elevated emergent cover and decreased emergent richness (Trebitz and Taylor, 2007). The results from this project support the same findings (Figure 2.4b) as exotic species cover increased as agricultural lands increased in a 10km radius around the site.

2.3.2. Suggesting a conceptual framework to orient conservation and restoration efforts

Systematic conservation planning (**SCP;** Margules & Pressey, 2000) need robust indicators and metrics to indicate where efforts should be implemented. Biodiversity is usually strongly correlated with ecosystems functions and services. The results of this study, using several diversity metrics and land use covers, will provide valuable information that is currently lacking or outdated and will help guide resource managers and restoration practitioners to target and prioritize areas at risk (to restore) and areas to protect. This study proposed a conceptual framework that identifies sites that need to be prioritized for conservation and restoration efforts. Axis 1 of the framework represents a gradient of biodiversity where the green and blue quadrants represent areas where the sites are very rich in biodiversity (richness and diversity) and good evenness (there is no extremely dominant species in the community; Figure 2.6 a,b). The yellow quadrant represents areas where sites are poorly diversified and have lower evenness, suggesting that some species are very dominant (Figure 2.6 a,b). Axis 2 represents an anthropization gradient; the blue and dark orange quadrants represent anthropized sites where exotic species are abundant and where the most homogeneous sites are found in areas dominated by agriculture (Figure 2.6 a,b). Based on these characteristics, green and blue symbols represent sites that should be conserved and protected because their biodiversity is high and would allow these sites to be resilient and have a good capacity for adaptation in a context of climate change (Figure 2.6 a,b). The orange symbols represent the sites that could be restored because we believe that the reduced biodiversity and the homogenization of the communities by a strong presence of exotic and invasive species can cause a loss of resilience and a decreased ability to adapt to stresses and climate change (Figure 2.6 a,b).

The main findings from the conceptual framework are that several sites found in Lake Huron and Lake Superior are still characterized by excellent biodiversity and do not suffer from too many disturbances (i.e., presence of natural environments). If we must prioritize the protection and conservation of wetlands in the GL, we suggest the sites in green (priority) and blue (Figure 2.6b). The wetlands of Lake Erie are particularly degraded (low biodiversity, many invasive and exotic species and high anthropization). These sites would be good candidates for restoration if not too strongly regulated. The sites in yellow are characterized by low biodiversity but are not yet invaded by excessive exotic and invasive species. These sites therefore represent excellent candidates for restoration (Figure 6b). Dark orange sites will be more difficult to restore because they are heavily invaded by exotic species and the control of invasive species in wetlands is expensive and difficult to maintain (Dia and al., 2020; Blossey and al., 2001).

2.3.3. Limitations of the study

This study is limited to a 2-year period of robust data and therefore doesn't demonstrate biodiversity changes over the years. Sampling over several years to generate a time series would be needed in order to get an accurate assessment of the wetlands health over time. Moreover, 2018 and 2019 were years with high water levels which can underestimate the upper wetlands classes such as wet meadows and swamps. Finally, the conceptual framework is based only on vegetation biodiversity. To be more robust and useful for managers, the framework should also incorporate other measures of biodiversity (fish, birds, insects) and should also integrate proxies of ecosystems services.

2.4 Conclusion

Our analysis of wetlands biodiversity in the Great Lakes region has revealed a clear pattern of dominance by exotic and/or invasive species in some sites and particular position in the hydrosere (emergent marsh). The emergent marsh class was found to be most invaded, with Phragmites and *Typha x glauca* as the main culprits for this decrease in diversity. We have also identified areas that should be prioritized for conservation and restoration efforts based on their relative levels of anthropogenic disturbance and invasive species presence. These findings provide valuable insight into how wetlands can best be managed so that we may protect them from further degradation due to human activities or invasive species introductions. With careful management, these wetlands can remain viable habitats for native flora and fauna while providing important ecosystem services such as water filtration, fish habitat, flood control and carbon sequestration.

APPENDIX A: Description of the 26 wetlands site used in the study

Coastal Wetland			Dominant hydrogeomorphology	First Nation Site	Park/ NWA	
Site	**Acronym**	**Region**			**Nat.**	**Prov.**
Airport Creek	ACM	LKO	Open Drowned River-mouth	X		
Jordan Station	JSM	LKO	Barred Drowned River-mouth			
Lynde Creek	LCM	LKO	Barred Drowned River-mouth			
South Bay	SOB	LKO	Open Embayment			
Wesleyville Marsh	WEM	LKO	Barrier Beach Lagoon			
Detroit River Marshes	DRR	LKE	Open Shoreline			
Fox Creek	FOX	LKE	Barred Drowned River-mouth			
Grand River Mouth Wetlands	GRM	LKE	Barred Drowned River-mouth		X	
Long Point National Wildlife Area	THO	LKE	Open Embayment		X	
Rondeau Provincial Park	RON	LKE	Sand-spit Embayment			X
Selkirk Provincial Park	SPP	LKE	Barred Drowned River-mouth			
Baie Du Doré	BDD	LKH	Open Embayment			
Collingwood Shores Wetlands	CWS	LKH	Open Shoreline		X	
Hay Bay Wetland	HBH	LKH	Protected Embayment		X	
Hog Bay	HGB	LKH	Protected Embayment			
Key River Wetland	KRW	LKH	Protected Embayment		X	
Whiskey Harbour Wetland	WHW	LKH	Protected Embayment	X		
Francis Point Marsh	FPM	LKH	Protected Embayment			
Coffin Rock Wetland	CRW	LKH	Protected Embayment			
Treasure Bay	TRB	LKH	Protected Embayment			
Anderson Creek	ANC	SMR	Open Drowned River-mouth			
Lake St. Clair Marshes	SCS	LSC	Open Shoreline			
St. Anne's Marsh - Walpole Island	SAM	LSC	Delta	X		
Hurkett Cove	HKC	LKS	Protected Embayment			
Mission Marsh	MIM	LKS	Open Shorline			
Hill Island East Marsh	HIW	SLR	Protected Embayment		X	

APPENDIX B: Additional criteria used to classify sites into large wetland classes and examples of plants species

Wetland class	Criteria	Example of communities
Upland	Dominated by FACU and UPL species	Goldenrod prairies Agricultural wastelands dominated by ruderal species Oak forest
Treed swamp	>25% of hydrophyte tree species	Eastern white cedar forest Red ash forest Tamarack forest
Shrubby swamp	>25% of hydrophyte shrub species	
Wet meadow	>25% emergent macrophytes	Alder swamp Willow swamp Dogwood thickets
Emergent marsh	25% of Typha or Phragmites spp. Submerged aquatic plants are often present	Bluejoint meadow marsh Sedge meadow marsh Reed canary grass meadow marsh
Non persistent emergent marsh	25% of of NPE indicator species Except for bulrushes if: bulrush cover > 0 bulrush cover > EM species bulrush cover > MM species	Phragmites australis marsh Typha marsh
Submerged aquatic vegetation	> 25% of aquatic plants	Bur-reed marsh Wild rice marsh Arrowhead marsh
Open Water	< 25% of aquatic plants Dominated by open water	Eelgrass beds Pondweed beds Algeae beds

APPENDIX C: Comparison of biodiversity indices between 2018 and 2019

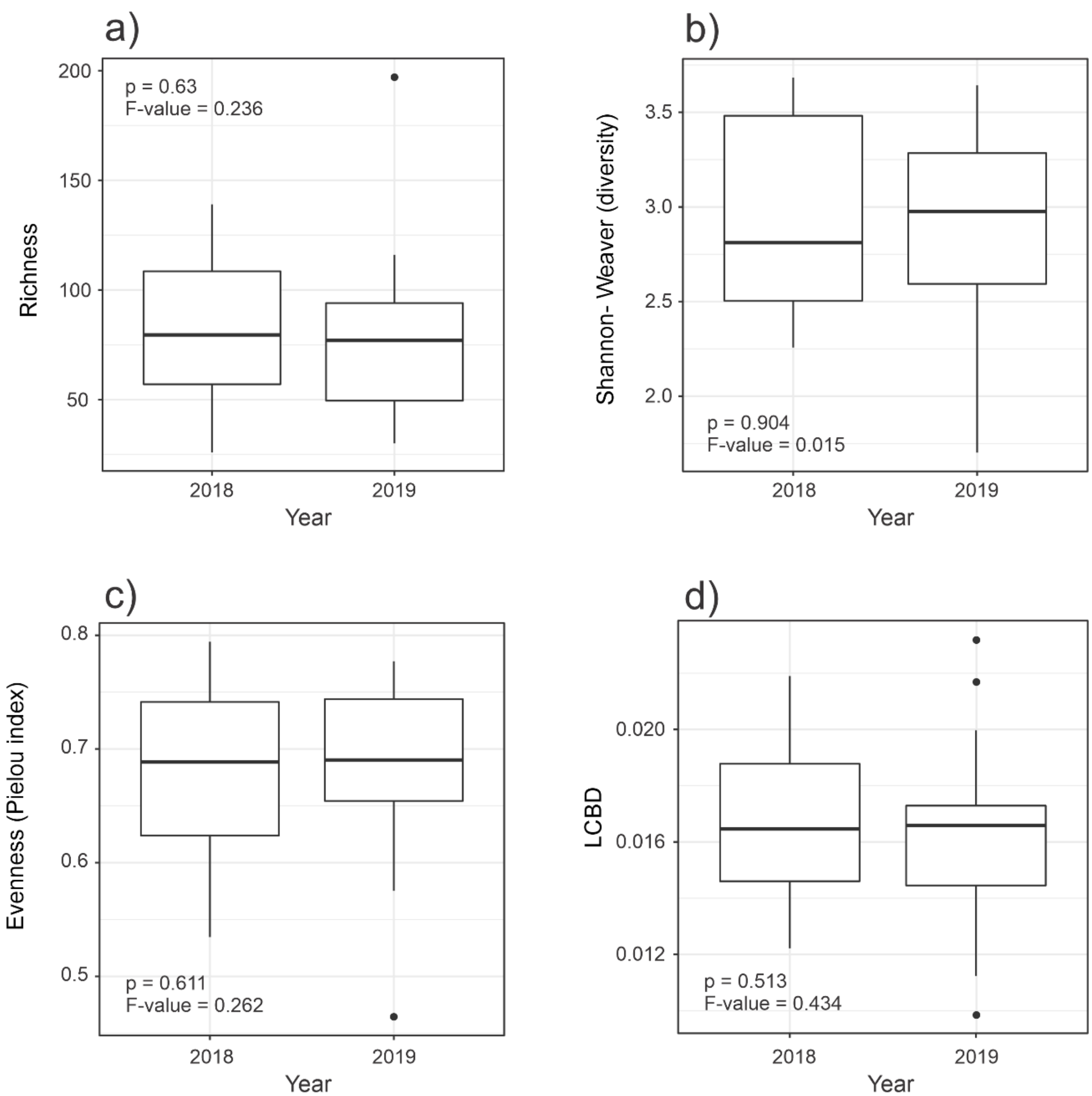

Figure C.1. Comparison of a) richness, b) Shannon-Weaver diversity index, c) evenness (Pielou index) and d) LCBD between 2018 and 2019.

APPENDIX D: Linear regression between biodiversity indices and latitude

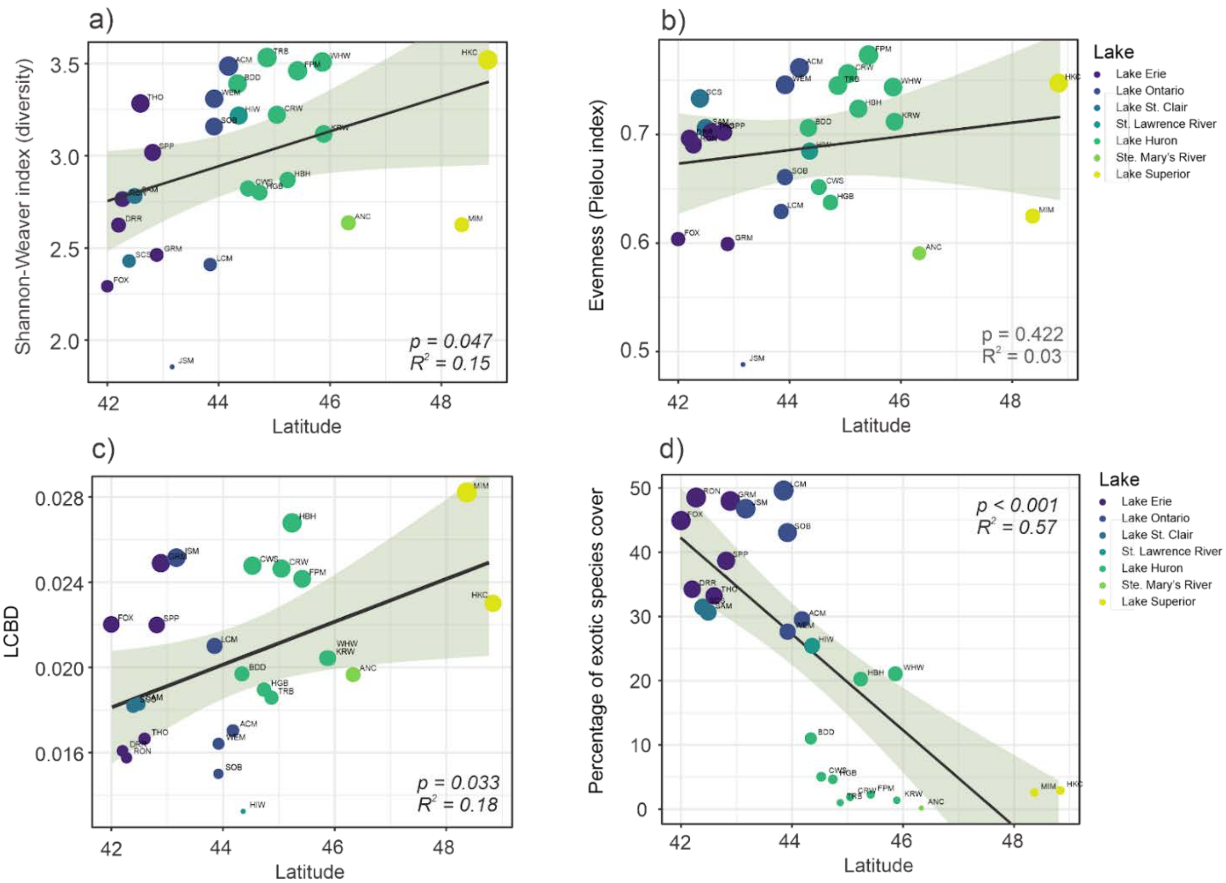

Figure D1. Linear regression between a) Shannon-Weaver diversity index and latitude, b) evenness (Pielou index) and latitude, c) LCBD and latitude and d) the percentage of exotic species cover and latitude. The size of each point reflects the magnitude of the biodiversity indices, and the colors correspond to the different lakes and rivers.

APPENDIX E: Linear regression between biodiversity indices and percentage of agriculture

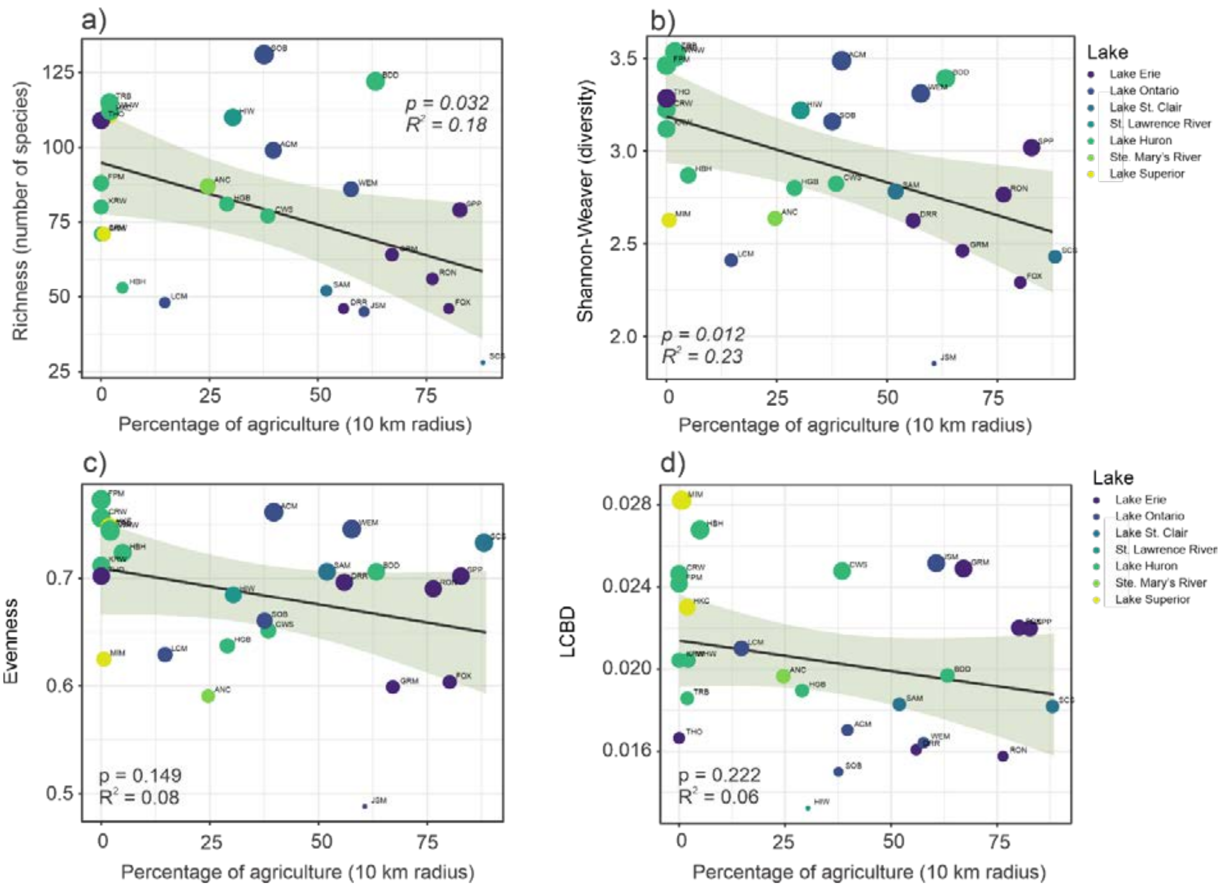

Figure D2. Linear regression between a) Shannon-Weaver diversity index and latitude and b) evenness (Pielou index) and latitude. The size of each point reflects the magnitude of the biodiversity indices.

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