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Evaluating restoration success by tracking the structural and functional recovery of restored, drained, and intact wetlands

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Abstract and Keywords

Wetland restoration efforts have increased on the Canadian prairies to compensate for widespread loss of wetland area, form, and function. Restoration activity presumes a direct replacement for natural wetlands, where restored wetlands provide equivalent ecological functions and services. However, restoration projects often show limited recovery success in biological structure and biogeochemical function. Using plant functional traits is an emerging approach to assessing ecological process and may provide a better indicator of wetland functional recovery than vegetation structural indicators alone. Here, I tracked vegetation structural metrics (i.e., species richness, composition, and cover) and plant functional traits over a chronosequence of restored wetlands to compare structural and functional recovery and evaluate restoration success. Results suggest rapid structural recovery (within five years of restoration) and similar functional diversity among drained, restored, and natural wetlands. The approach taken towards wetland restoration, combined with a heavily impacted agricultural landscape, may be limiting the recovery potential of wetlands, thereby creating a homogenization of wetland form and function.

Keywords: wetland, restoration, recovery, plant functional traits, chronosequence, vegetation, ecosystem process, Prairie Pothole Region

Co-Authorship Statement

Chapter 2 is a manuscript based on data and analysis presented in a manuscript accepted as: Salaria, S., **Howard, R.**, Clare, S., & Creed, I. F. 2018. Incomplete recovery of plant diversity in restored prairie wetlands on agricultural landscapes. *Restoration Ecology*. DOI: 10.1111/rec.12890. Contributions of co-authors: R. Howard and S. Salaria designed the research project, collected and analyzed the data, and contributed to the writing and editing of the manuscript. Additionally, R. Howard conducted an additional year of data collection, analysis, and included a climate analysis as part of this chapter. S. Clare conceived the research project and contributed to writing and editing of the manuscript. I.F. Creed conceived and designed the research project, assisted in the analysis and interpretation of results, and helped to write and edit the manuscript.

Chapter 3 is a manuscript that will be submitted to a peer-reviewed journal with S. Clare and I.F. Creed as co-authors. R. Howard will be lead author as she conceived the research project, completed the collection of data, analysis, and interpretation of results, and will lead the writing of the manuscript. S. Clare and I.F. Creed contributed to the conceptual design, interpretation of results, and will provide assistance in the writing and editing of the manuscript.

Finally, data from Chapters 2 and 3 will be included in another publication that compares structural and plant functional recovery, as permitted by copyright law. R.Howard will be a co-author since she collected the data, will conduct the analysis and will assist in the writing and editing of the manuscript. S. Clare and I.F. Creed will also be co-authors as they will be involved in writing and editing of the manuscript.

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'Make a splash, take time to reflect, listen to nature, reed more, be green, don't get bogged down, and what's the rush?'

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1 Chapter 1. Introduction

1.1 Problem Statement

Wetlands have historically sustained major impacts and high rates of loss on prairie landscapes as a result of the encroachment of development and/or drainage for crop production (Golden et al. 2017). With this wetland loss is an associated loss of wetland functions and ecosystem services (Creed at al. 2017). In the Canadian prairies, wetland restoration is increasingly being used as a tool to return wetland functions and ecosystem services back to the landscape, and the implication is often that ecosystem functions and services provided by the lost natural wetlands have been repaired. Creating wetland habitat (i.e., more wetland area) is easy and relatively successful when hydrologic conditions are restored (Zedler & Kercher 2005). However, ecological processes and functioning take longer to develop than vegetation diversity and structure, and require more time and resources to measures (Meli et al. 2014). Ultimately, return of ecosystem function and services of wetlands post-restoration are required to provide resilient habitats, regulate hydrology, and maintain multi-functional landscapes. Finding a reliable method for assessing and monitoring the recovery of wetland functions is required given that wetland policies and restoration guidelines across North America include functional equivalence as a primary goal or desired outcome (e.g., Alberta's Wetland Policy, Government of Alberta 2013).

1.2 Scientific Justification

1.2.1 Wetlands and Consequences of Their Loss

Wetlands are some of the most diverse and ecologically important habitats in the world, and yet, wetlands are among the most threatened ecosystems (Erwin 2009). Found worldwide in both inland and coastal forms, wetlands cover five to eight percent of the land surface of the Earth (Mitsch & Gosselink 2007) and can be classified based on plant community structure, wetland form, and wetland function. Inland wetlands take four forms; peatlands (i.e., bogs and fens), marshes, swamps, and riparian systems. While class, type, permanence, and definitions may vary in different parts of the world, three conditions must be satisfied for a habitat to be classified as wetland. These include the presence of

water at or near the ground surface of the soil for all or varying periods of the year, the development of hydric soils (further discussed in Chapter 2) that distinguish wetland soils from adjacent uplands, and finally, the presence of biota and vegetation adapted to wet conditions. Despite being variable in character, wetlands have been valued and depended upon for centuries as a source of food, trade, material, and for other products and services (Mitsch and Gosselink 2007).

Wetland habitats have long been threatened by urban expansion, agricultural intensification, and land development, resulting in widespread, global loss in number and area (Davidson 2014). Globally, up to 50% of wetlands have been lost, though these estimates may be conservative and are dated (from the early 1990s) (Davidson 2014). Further, estimates of wetland loss increase significantly (to 80 or 90%) in some areas where wetlands feature (or historically featured) prominently on the landscape; for example, in the Prairie Pothole Region (PPR) where wetlands historically covered ~20% of the landscape. (Mulhouse and Galatowitsch 2003). The PPR is located in the northern Great Plains states of the USA and much of the southern portion of the Prairie Provinces (i.e., Alberta, Saskatchewan, and Manitoba) of Canada (Figure 2.1, inset), and is named after the pothole wetlands that characterize the region. Pothole wetlands are small, shallow wetlands formed following the retreat of the Laurentide ice sheet at the end of the Wisconsinan glaciation (Dyke and Prest 1987). While often considered geographically isolated from one another, in fact, prairie pothole wetlands are hydrologically connected through groundwater, and form one of the largest wetland complexes in North America (Tiner 2003; Van de Valk 2005). The main cause of wetland loss in the PPR has been the conversion of natural landscapes into agriculture (Tiner 1984).

Wetlands have hydrological, biological, and biogeochemical influence on the landscape. These critical landscape features regulate water quantity (Kennedy and Mayer 2002) and water quality (Marton et al. 2015). Wetlands are important for climate regulation and climate change control as they sequester some of the largest stores of carbon on the planet (Finlayson et al. 2005). For example,

globally wetlands represent three percent of total land area, but sequester 30 percent of all soil carbon (Zedler & Kercher 2005). Wetlands store carbon in their vegetation and soils, thus when natural wetlands are drained for cultivation, large quantities of stored organic carbon decompose and are lost to the atmosphere as carbon dioxide (Zedler & Kercher 2005). Further, wetland habitats are an interface between terrestrial and aquatic habitats, supporting a high diversity of plants and wildlife species and contributing disproportionately to primary productivity on the landscape (Kennedy and Mayer 2002).

When wetlands are removed for agricultural, industrial, or other land developmental purposes, the functions and ecosystem services that wetlands provide are lost. The impacts of wetland loss on the Canadian Prairies include increased flooding events (Acreman and Holden 2013), increased frequency of nuisance algal blooms (Davis and Froend 1999), and shifts in landscape level hydrology (Cohen et al. 2016). The Millennium Ecosystem Assessment conducted an economic valuation of wetland ecosystem services and determined that the total economic value of natural wetlands was far greater than the economic value of wetlands converted to agriculture ($5,800 per hectare compared to $2,400 per hectare when drained and used for agricultural purposes) (MEA 2005). Yet, despite the intrinsic and economic values provided by wetland habitats, wetland drainage and deterioration activities are widespread in the interest of economic development (Davidson 2014).

1.2.2 Wetland Management in Canada and on the Prairies

Great efforts have gone into implementing policy to conserve and protect remaining wetlands, and into wetland restoration initiatives to improve landscape function and provisioning of ecosystem services. In Canada, wetland policy implementation, development, and enforcement are a consolidated effort among the federal government, provincial governments, and other wetland management programs (e.g., Ducks Unlimited Canada, North American Waterfowl Management Plan, and the Canadian Habitat Joint Venture programs). The Federal Policy on Wetland Conservation (Government of Canada 1991) advocates for 29% of Canadian wetlands that are located within federal lands

(situated within National Parks, military reserves, National Wildlife Areas, and much of the land in the northern territories) (Rubec & Hanson 2009). The federal policy outlines a 'mitigation hierarchy', which includes steps, in order of preference, for mitigating impacts to wetlands (Government of Canada 1991; Rubec & Hanson 2009). Separately, provincial governments manage most of the country's wetlands and associated functions. While each province has a set of regulations, policies, and practices concerning wetland policy, many operate under a similar mitigation hierarchy (Rubec & Hanson 2009; Clare et al. 2011). Under this hierarchy, both federally and provincially, wetland conservation and avoiding impacts to wetlands are prioritized, then if avoidance of impacts is not practicable then the process progresses through to minimization. Finally, compensation is mandated when impacts to wetlands are unavoidable, usually through restoration, enhancement, or creation activities.

In Alberta, a new wetland policy was implemented in 2013; it is among a wave of policy updates and new policy developments that take a functional approach to wetland management. The Alberta Wetland Policy places a higher value on wetlands that contribute to water quality improvements, hydrology, biodiversity, and human use functions (Government of Alberta 2013). As with the federal policy, Alberta follows a three-stage hierarchy to guide management of wetlands and impacts. Avoidance of wetlands is the preferred response for managing wetlands, followed by an expectation to minimize impacts, and then finally wetland replacement, as opposed to compensation, as a last resort requirement when wetland impacts cannot be avoided or minimized. This policy provides an assessment of the contributions of a specific wetland to the ecosystem and uses wetland relative value to establish restoration requirements if wetland impacts are unavoidable (Government of Alberta 2013).

1.2.3 Wetland Replacement by Restorative Action

Wetland loss in the Prairie Pothole Region has been caused by an extensive network of surface drainage ditches, which have drained wet areas to expand crop production on the prairies (Galatowitsch & van der Valk 1996a). However, increasingly, wetlands are being restored in an effort to recover lost

wetland functions and services. Restoration is defined as the practice of renewing or recovering function to a degraded, damaged, or destroyed ecosystem (SER 2002). Wetland restoration has been shown to mitigate the effects of wetland drainage and loss, but some damages are more difficult to restore, most notably, the loss of ecosystem services (Zedler & Kercher 2005). Ditch-drained wetlands typical of the Prairie Pothole Region are deemed to be among the simplest systems to restore. By constructing a ditch plug (or earthen berm) within the drainage ditch that previously drained the wetland, hydrology of the wetland basin is restored. It is expected that natural re-colonization of wetland plant species will follow (Galatowitsch & van der Valk 1996a). This idea of natural re-colonization, was termed the "efficient community hypothesis" and formed the leading conceptual model for wetland restoration in the 1980s. However, rather than following the anticipated predictable pattern of recovery for wetlands, research suggests that restored wetlands deviate from their expected recovery path (Galatowitsch & van der Valk 1996b; Suding 2011; Moreno-Mateos et al. 2012). An emerging consensus is that the wetland vegetation structure and diversity does not recover to the condition of nearby, undisturbed natural wetlands of similar class, size, and condition. There is a critical need to understand the recovery of wetlands following restoration in an effort to more effectively manage these systems and the provisioning of functions and services they provide.

1.2.4 The Conceptual Basis behind Restoration

The principles of restoration are rooted in community ecology theory, because restoration begins with a disturbance to a degraded system, which initiates a response in the species, biotic interactions, energy transformations within a community. Community ecology describes the processes that underlie the assembly, maintenance of diversity, and functioning of ecology communities (Wainwright et al. 2017). Most restoration activities, assessment, and monitoring approaches are directed towards the plant species that comprise a restored community, so concepts related to coexistence among plants will be discussed (Wainwright et al. 2017). Models of succession, state-transition, and assembly

are fundamental components to understanding and achieving restoration success.

Successional theories describe an orderly predictable return of communities after a disturbance, until a climax community has been achieved (Clements 1916). This theory suggests that the species living in a particular place will gradually change over time as the physical and chemical environment in an area changes. Primary succession describes the changing community that occurs on an entirely new habitat that has not previously been colonized (Gorham et al. 1979). Secondary succession follows, where the community composition changes as the dynamics within the community change (e.g., competition, nutrient conditions, environmental factors) (Horn 1974). Finally, climax communities are achieved when the species in a community are stable and are no longer undergoing change in composition under a set of environmental conditions (Horn 1974).

State and transition models are another framework that can explain community assembly following restoration (Young 2005). State transitions are described as discrete communities that exist under a set of conditions (i.e., climate, soil, topographic) (Westoby et al. 1989). A state is defined as long-term persistence of a new plant community or a new range of variation within a community that previously did not exist (Bestelmeyer et al. 2017). State transitions can be driven by internal mechanisms such as competitive interactions, or by external drivers such as change in climate. Further, changes can be gradual such as by periodic grazing activity, or abrupt such as by an extreme drought (Bestelmeyer et al. 2017). State and transition models were developed to allow for flexibility and nonlinearity otherwise not observed with succession models (Zweig et al. 2009).

Succession and state transition models suggest that a pathway towards a desired state or condition exists. In contrast, assembly theory dictates that a community is determined by a series of hierarchical filters (abiotic or biotic) that control which species can co-exist at a given time (Diamond 1975). Early assembly theorists observed unique species composition in spatially isolated

communities hypothesized to be due to random differences in colonization, establishment, and priority effects (Johnson 2005). Specifically, assembly theory suggests that from a pool of available species in a region, various filters work to limit the species that comprise the community. Some important filters that control wetland species composition may include water levels, fertility, disturbance, competition or other interactions (Keddy 1999).

These models of community development do not work in isolation. Instead, in combination, these evolving theories try to explain differences, change, and/or patterns in community assembly (Chang et al. 2016). Further, increasingly, the concept of alternative stable states is being used to describe community assembly in restored systems (Lewontin 1969). A concept that incorporates aspects of succession, state and transition models, and assembly filters, alternate stable states describes stable ecosystems that exist under different sets of unique biotic and abiotic conditions. The theory suggests that ecological thresholds separate discrete states, but under significant perturbations, shifts between states are possible and can be catastrophic (Scheffer et al. 2001). Stability of an ecosystem determines how significant a perturbation has to be in order to shift states, and theoretically, the resistance and resilience of the system determine ecosystem stability (Mitchell et al. 2000). Ecosystem resilience is the ability of a system to return to normal following a disturbance or stress (Leps et al. 1982), whereas resistance is the ability of a system to avoid being displaces during a disturbance. Stability is an essential determinant of healthy communities and an important concept for ecological restoration (Leps et al. 1982).

Further, alternative stable states have been used to describe the wetland restoration process, where a degraded ecosystem (drained wetland) exists in a stable state and will not transition until a significant perturbation occurs to shift the ecosystem into a new stable state. Hydrologic restoration of drained basins acts as the perturbation, transitioning the community from degraded through to a restored community. However, following restoration, restored communities are subject to a multitude of environmental or biotic conditions that could cause stress and test the stability of a restored community.

Concurrent and related to community assembly, the mechanisms behind the coexistence of species in a community and ecosystem functioning are central to ecological restoration. Several theories exist to explain the occupation of a community by multiple species. To start, niche theory describes the general ecological requirements of a species given the physiological and biotic limits that restrict where they can thrive (Young et al. 2005). Competition for resources was considered the driver for the development of niche space in a community, such that the theory suggests no two species can occupy the exact same niche (competitive exclusion) (Palmer et al. 2006). Consumer differences in resource use determine the outcome of competition (survival, coexistence, or extinction).

Equalizing and/or stabilizing mechanisms are also used to explain the coexistence of species (Chesson et al. 2000). This idea suggests that heterogeneity in an environment results in trade-offs among species, which enables species co-existence. Stabilizing mechanisms increase intraspecific interactions relative to interspecific interactions (such as in relation to resource partitioning) thereby reducing competition since segregation of strategies ensure that species persist through time (Chesson et al. 2000). Whereas equalizing mechanisms minimize fitness differences between species, which increases competition thereby excluding those species unable to compete, which contributes to stable coexistence of a few competitive species (Chesson et al. 2000). Similarly, resource based theories of competition explain coexistence through differential resource requirements and uptake strategies among co-occurring species.

Finally, life-history strategy and trade-off concepts enable coexistence since species exhibit trade-offs in their response to competition, stress, and disturbances (e.g., C-S-R model (Grime 1977)). The CSR model (one example of strategy or trade-off concepts) suggest that species are classified according to a life history strategy related to three factors – growth (as it related to competition for resources), stress (as it related to environmental stress), and ruderality (a species tolerance to environmental disturbance). Grime suggests that species will associate along a continuum of each strategy resulting in a community where life

history traits differ among species allowing coexistence (Grime 1977). Of the theories presented, no one concept explains species coexistence in every community, but rather these concepts should be used by restoration practitioners to explain patterns of community development, species persistence through time, and change in community composition.

Generally, a community with many persistent and coexisting species is a common objective of habitat restoration projects (Palmer et al. 2006), where high diversity is traditionally the main focus (Cadotte et al. 2011). Diversity – function (or biodiversity - ecosystem function (BEF)) relationships are widely studied and continue to feature prominently in ecological research, increasingly so in the field of restoration ecological (Benayas 2009). The theory suggests that biodiversity is a key factor in ecosystem functioning. Ecosystems contain an assemblage of species whose individuals cycle material between organic and inorganic forms referred to as ecosystem processes (Naeem 2006). Ecosystem processes are generally measured as rates of flux among pools of dead, living, or inorganic matter (Naeem 2006). These fluxes can be compared among ecosystems in order to understand ecosystem response to change, such as addition of loss of species, land modification, or restoration efforts (Naeem 2006).

Further, species diversity is hypothesized to play a major in ecosystem stability. Four hypotheses are said to describe the role of species diversity on ecosystem stability (Mitchell et al 2000). First, the diversity - stability hypothesis predicts that ecosystem stability increases as species diversity increases (MacArthur 1955). The rivet hypothesis suggests that an ecosystem will continue to function normally if there are only a few extinctions, but the loss of a critical species or number of species may cause instability within an ecosystem (Ehrlich & Erlich 1981). The redundancy hypothesis suggests that certain species are able to expand their hold in the ecosystem to compensate when neighbouring species are lost (Walker 1992). And finally, the idiosyncratic hypothesis proposes that although ecosystem function changes when diversity changes, the magnitude of and direction of the change is unpredictable because of the

complexity of ecosystems and the varied responses of the species (Lawton 1994).

The ecological concepts and theories described above provide a glimpse of the deep ecological roots that restoration is built upon. Without a doubt, understanding theses concepts of community ecology will help contribute to re-establishing compositionally and functionally diverse communities to the landscape.

1.2.5 A Trait-based Approach to Functional Recovery

Trait-based ecology has recently emerged as a promising approach to evaluate ecosystem function and community dynamics (Laughlin 2014; Zirbel et al. 2017). As described above, communities result from the influence of biotic and abiotic filters that act to constrain species from a regionally available pool. Trait-based ecology predicts that these filters (biotic and abiotic) should also act on the traits of the species that persist in a community. A functional trait is defined as any morphological, physiological, or phenological feature that is measurable at an individual level and is linked to species fitness and performance (e.g., canopy size, seed mass, or flower density) (Violle et al. 2017). Changes in the value, range, and relative abundance of functional traits in an ecosystem provide insight into ecosystem processes (Diaz et al. 2007a). Relationships between plant functional traits and their effect on ecosystem processes and services have been documented for a range of organisms and ecosystems (de Bello et al. 2010). In terrestrial systems, plant functional traits have been shown to influence primary productivity, litter decomposition, cycling of nitrogen and other nutrients, and levels of soil moisture and sediment retention (de Bello et al. 2010; Diaz et al. 2004; Eviner & Chapin 2003). While the trait - ecosystem process relationship in wetlands is understudied, the patterns between traits and function in wetland systems have been found to overlap those found in terrestrial systems; therefore, these relationships can be generalized for wetland systems (Moor et al. 2017). Functional trait research in increasingly being used to understand the field of restoration ecology. For example, trait-based approaches have been used to study species assemblages that most effectively achieve functional outcomes

(e.g., limiting invasion, maximize survival, achieving desired functions) (Laughlin 2014), to evaluate the performance of species for establishment and persistence following restoration (Pywell et al. 2003), and to further describe and understand the diversity - ecosystem function relationship (Cadotte, Carscadden, & Mirotchnick 2011).

1.3   Research goals, hypothesis, and predictions

This observational study evaluated the vegetation communities of 42 prairie pothole wetlands, which included drained, natural, and restored wetlands ranging from one year through 24 years since restoration. The goal of this research project was to track, analyze, and compare structural and functional recovery of vegetation in restored wetlands in an effort to identify indicators of success, infer return to function, and evaluate trajectories of recovery between structural and functional approaches. This research project tested two hypotheses.

1) Structural diversity of restored wetlands recovers rapidly but is dependent on wetland morphometry.

I predict that plant species diversity, community composition, and cover estimates of restored wetlands will be comparable to natural wetlands within a few growing seasons, and that larger wetland area, smaller perimeter to area ratios, and gentler slopes will support vegetation communities that more closely resemble those of natural wetlands.

2) Functional recovery of restored wetlands is slow to recover and will be reflected in plant functional traits and wetland functional diversity.

I predict that newly restored wetlands will be dominated by species that are shorter and have more conservative nutrient acquisition strategies (i.e., low specific leaf area, high leaf dry matter content, low leaf nitrogen content) and have lower functional diversity when compared to natural wetlands, which will be dominated by plant communities with high nutrient acquisition and quick turnover strategies and where wetland functional diversity will be high.

1.4   Thesis organization

This thesis is organized in an integrated article format. Chapter 1 introduces wetland loss, wetland restoration, and the theoretical basis behind restoration ecology. In Chapter 2, I present the results from the assessment of structural metrics for a series of restored wetlands over two years. Here, in addition to restored wetland, two classes of natural wetlands were considered - natural agricultural and natural reserve, which represent different natural wetland disturbance conditions found in central Alberta. These two classes of natural wetlands provided a useful comparison when considering reference condition. In Chapter 3, I assessed the plant functional traits of the dominant species found within the series of restored wetlands. Trait values were compared within species, at the community level, and were combined to compare functional trait diversity among wetland age classes and with drained and natural wetlands. Finally, Chapter 4 compares structural versus functional recovery, discusses the influence of annual variability on results, and provides a general discussion on the significance of integrating structural and functional metrics into assessments of ecosystem recovery.

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2   Chapter 2. Incomplete Recovery of Plant Diversity in Restored Prairie Wetlands on Agricultural Landscapes

2.1   Introduction

Wetlands provide many important ecosystem services, such as carbon sequestration (Mitsch et al. 2013), flood and drought control (Rains et al. 2016), and water quality improvement (Marton et al. 2015). Furthermore, wetlands are biodiversity hotspots and support many species at risk (Calhoun et al. 2017) as well as half of North America's waterfowl population (Junk et al. 2013). Yet, wetlands are at risk of degradation and loss from land conversion activities, with recent global estimates of wetland area loss ranging between 54-57% (Davidson 2014). While these vulnerable waters continue to be threatened (Creed et al. 2017), habitat restoration is increasingly being used as a strategy to reverse historical and on-going wetland losses and degradation.

The practice of wetland restoration has grown rapidly in response to increasing land development, natural habitat degradation, and understanding of the ecological importance of these systems. The recovery of wetland vegetation follows a complex successional trajectory, where rather than expecting to see predictable plant community development characterized by annuals dominating first, followed by herbaceous perennials, and eventual colonization of woody perennials (trees and shrubs) (Noon 1996), it is anticipated that the plant community will be determined by the seeds and propagules present in the remnant seedbank (Galatowitsch & Van der Valk 1996), and the dispersal and colonization abilities of incoming species (Zedler 2000).

Evidence suggests that it is not uncommon for a restored wetland to deviate from its expected recovery path (Suding 2011; Moreno-Mateos et al. 2012). Once a system is degraded, new abiotic and biotic conditions can develop where strong positive feedbacks and interactions among conditions inhibit the ability of a wetland to return to its pre-disturbance state (Suding et al. 2004). For example, in a meta-analysis of 621 restored and created wetland sites worldwide, Moreno-Mateos et al. (2012) observed that biological structure (composed of abundance, density, richness, occupancy, cover, and/or biomass of vertebrates,

macroinvertebrates, and plant assemblages, though mostly driven by the latter) was on average 26% lower in restored wetlands than natural wetlands, even a century post-restoration. This shows that while a number of ecological theories interplay in the restoration of a wetland system (including successional theories, dispersal limitation, and disturbance theory to name a few, see Zedler 2000), restored wetlands are not reaching their natural state equivalent.

The goal of most wetland restoration efforts is to return the degraded ecosystem back to its 'pre-disturbed' state (Hobbs & Harris 2001); however, in most cases, restored wetlands are unlikely to reach a natural reference condition (Moreno-Mateos et al. 2012). This has led to a need to view restored wetlands as novel ecosystems that have been driven and influenced by human action and environmental change, resulting in ecosystems that are characterized by species in combinations or relative abundances not previously observed within natural reference systems (Hobbs et al. 2006). While controversy exists over the utility and management implications of novel ecosystems (Miller & Bestelmeyer 2016), many researchers think that the novel ecosystem concept provides a way forward for managing wetland ecosystems in a landscape fraught with environmental and anthropogenic change and associated legacy effects. Nevertheless, most restoration efforts are still focused on achieving similarity to a given reference state (Hallet et al. 2013), and many restoration practitioners use history as a guide to select reference benchmarks for restoration (Hallet et al. 2013; Higgs et al. 2014). Consideration must be given to the natural history of the surrounding landscapes and historic impacts on reference and restoration sites because they can have major implications on determining restoration success.

Given the need to evaluate restoration efforts within a rapidly changing environment, this study was conducted to determine the recovery success of plant diversity in restored prairie wetlands. Recovery was assessed by comparing restored sites with contemporary examples of natural reference wetlands using plant structural diversity metrics commonly used to evaluate restoration success. I had two hypotheses. The first hypothesis was that plant diversity of restored wetlands increases with time since restoration, and further, that the recovery of

plant structural diversity in restored prairie wetlands is rapid (i.e., equivalence between restored and natural reference is achieved within a few growing seasons). The second hypothesis was that wetland morphology (i.e., area, shape, slope, and perimeter to area ratio) influences plant structural diversity potential. These hypotheses were tested within the Prairie Pothole Region, an area that has been traditionally agriculturally intensive, heavily impacted by wetland loss, and where wetlands are predicted to be profoundly affected by climate change (Rashford et al. 2016).

2.2 Methods

2.2.1 Study area

The study was conducted on geographically isolated wetlands (wetlands surrounded completely by upland with no obvious surficial connection to another wetland) in the Central Parkland ecoregion of Alberta, Canada (Figure 2.1). The mean annual temperature of the region is 2.6 °C and the climate is characterized by warm summers and cold winters based on Canadian Climate Normals (Environment Canada 2016). Mean annual precipitation is 446.1 mm, of which 50% falls from June to August (Environment Canada 2016). The landscape comprises mainly glacial till plains, hummocky uplands, and many shallow prairie pothole wetlands formed by the Wisconsin glaciation. Typical soils found in study wetlands include humic and orthic gleysols (Natural Regions Committee 2006). The dominant native vegetation in the ecoregion is a mix of aspen parkland and prairie plant communities (Natural Regions Committee 2006).
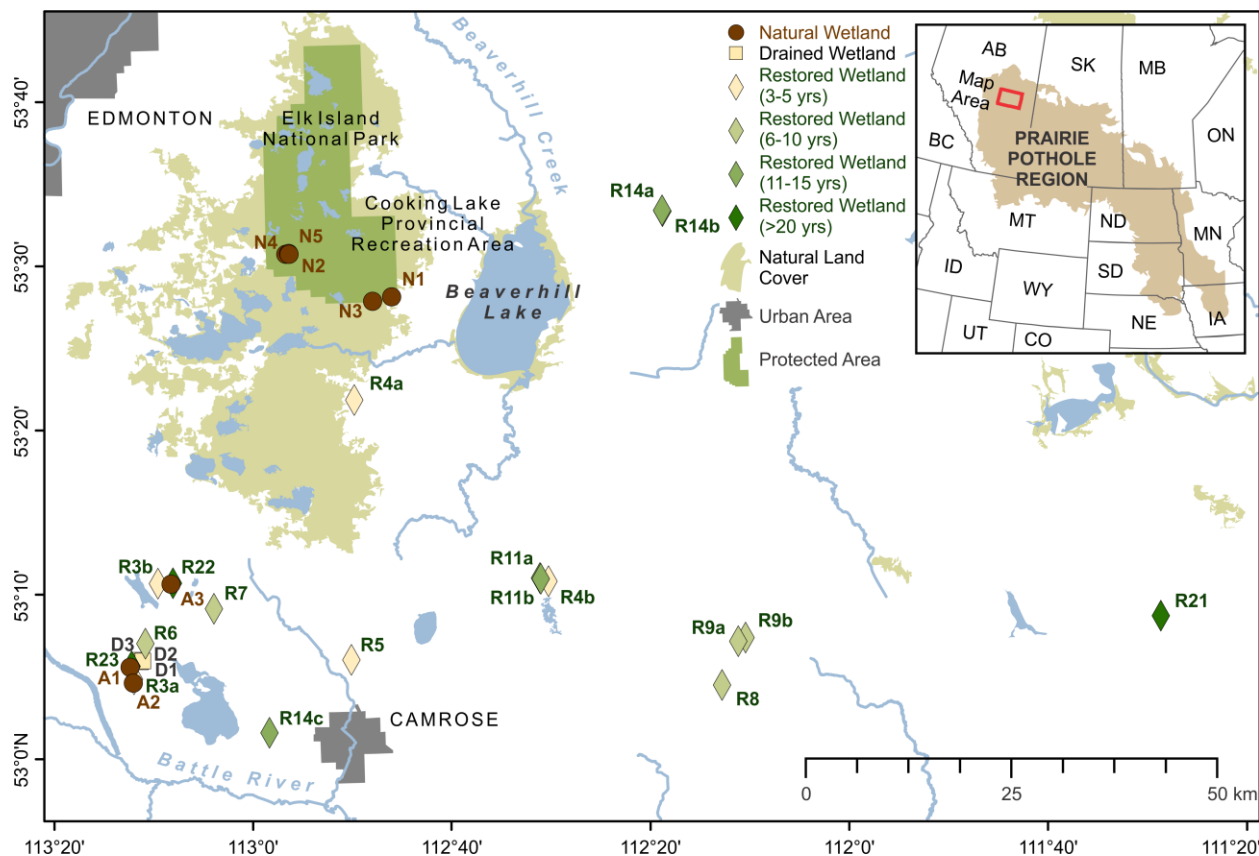
Figure 2.1. Location of study sites used to assess structural recovery in restored wetlands. The study area includes 18 restored wetlands, 8 natural wetlands, and 3 drained wetlands located in Alberta, Canada.

In the Prairie Pothole Region, wetlands can be classified by the vegetation occupying the central or deepest part of the wetland. Temporary wetlands are characterized by a central zone represented by fine stemmed grasses and sedges whereas seasonal wetlands are defined by a central zone dominated by coarse grasses, sedges, and associated forbs (Stewart & Kantrud 1971). Restored temporary and seasonal wetlands were selected from properties owned by Ducks Unlimited Canada (DUC), and ranged in size from 0.06 to 1.06 ha (Table B1). This range in sizes reflected the dominant size class of wetlands in this prairie region (Serran & Creed 2016), as well as the dominant size class of restored wetlands in the Parkland ecoregion (DUC 2016). The chronosequence approach, where study sites are selected that have similar attributes but are of different ages, is a reliable method to study temporal dynamics of plant succession (Cowles 1899; Pickett 1989; Walker 2010), thus making it a suitable

approach for tracking vegetation recovery within restored wetlands. This study included a chronosequence of 29 wetlands that included drained, restored (ranging between 3 and 24 years since restoration), and natural reference wetlands. Drained wetlands (n=3) were actively being cultivated at the time of sampling, and included two wetlands that were completely drained and one wetland with incomplete drainage. The restored wetlands were further categorized into age classes: 3-5 years since restoration (5 wetlands), 6-10 years since restoration (5 wetlands), 11-15 years since restoration (5 wetlands), and >20 years since restoration (3 wetlands). Additionally, the natural reference wetlands were further classified as "natural agriculture" (Nat(Ag), n=3) and "natural reserve" (Nat(Res), n=5). The natural agriculture wetlands had not been impacted by historical drainage and were located within the same parcels as one of the restored wetlands. Land use surrounding the natural agriculture wetlands has historically included cultivation and livestock grazing, and given the proximity between the Nat(Ag) and the restored wetlands, land management practices adjacent to these wetlands was assumed to be comparable. The natural reserve wetlands were situated within the Cooking Lake – Blackfoot Provincial Recreation Area where surrounding land use has historically included recreation such as hiking, horseback riding, and cycling, as well as livestock grazing. These natural reserve wetlands and the surrounding landscape may have been subjected to other historical and contemporary disturbances, including weed control measures and other management activities; however, specifics are unknown.

Wetlands were restored by DUC via construction of an earthen berm across drainage ditches to restore the hydrology of the wetland basin. No hydrophytes or aquatic plants were planted or seeded within restored wetland basins, and as such, the flora reflected natural colonization from seed banks or dispersal. However, following construction, earthen berms were often seeded with an equal portion of grass seed mix containing *Bromus riparius* (meadow brome), *Medicago sativa* (alfalfa), *Schedonorus arundinaceus* (tall fescue), and *Elymus trachycaulus* (slender wheatgrass), and *Hordeum vulgare* (barley) at a rate of 34 kg per hectacre to provide stability during flooding events and to suppress the growth of

weeds (R. Hunka, DUC, personal communication, 3 January 2017). Glyphosate spot treatment and periodic mowing were conducted in uplands surrounding restored wetlands to control the spread of weeds, particularly *Cirsium arvense* (Canada thistle). While land use practices surrounding restored wetlands varied among grazing, haying, or left idle based on DUC's land management goals and objectives, these differences were not considered as part of this study, since these activities were scheduled for later in the season and after field sampling was completed.

2.2.2 Sampling

In 2016, wetlands were delineated in the field based on hydrophytic vegetation and hydric soil indicators. While boundary delineations can often be easily determined using vegetation indicators, soil indicators can identify seasonally saturated conditions and provide a better determinant of soil saturation and wetland conditions than vegetation alone (Government of Alberta 2015). Hydric soil indicators common of the soils in the study area can include a deep organic soil layer, redoximorphic features such a depletion of color of the soil (gleying) within 30cm of the surface, and/or oxidized rhizospheres, identified as a red color located within plant root pores resulting from oxidation of reduced iron when soil moisture drops (Government of Alberta 2015).

In both 2016 and 2017, each wetland was visited and sampled once between June and August. This timeframe corresponds to peak growing season in the region. In 2016, the majority (25) of wetlands were sampled between June 1 and July 1, including all drained, all restored, all Nat(Ag) and one Nat(Res) wetland. The remaining four Nat(Res) wetlands were sampled between July 10 and Aug 10 due to permitting and access constraints. In 2017, all wetlands were sampled between June 19 and August 15, with the majority of sampling (21 sites) conducted in July, as a result of significant standing water present in wetlands at the beginning of the sampling season.

A similar vegetation sampling protocol was employed between sampling years. Stratified random sampling was used to capture vegetation heterogeneity across the hydrologic gradient of the wetland, as represented by different

vegetation zones (Little 2013). Wetland zonation is typical of prairie wetlands, where rings of distinct vegetation communities are observed resultant from the hydrologic gradient found within wetlands (Stewart & Kantrud 1971). Square meter quadrats were randomly placed along four transects that were oriented at 90° from each other, and within each quadrat all herbaceous vegetation was sampled. Following a species accumulation analysis, eight quadrats per vegetation zone was determined to be the optimum sampling effort for a variety of wetland size classes assessed in this study. As such, total number of quadrats sampled per wetland ranged from 6 – 30 quadrats depending on the size of wetland and number of vegetation zones present. All species within a quadrat were identified and percent cover was estimated using an 8-point cover classification system (Mueller-Dembois & Ellenberg 1974). A random walk through was also conducted within each wetland to record any rare species, species occurring in patches, or species not previously identified through quadrat sampling (Mueller-Dembois & Ellenberg 1974).

2.2.3 Plant Diversity

Wetland plant diversity was measured in several ways. First, the average percent cover of hydrophytes, native species, and non-native species were calculated for each wetland by taking the midpoint value of each cover class range for each quadrat sampled. All species detected were assigned a wetland indicator status (WIS) based upon the National Wetland Plant List (Lichvar et al. 2016; U.S. Army Corps of Engineers 2016). All species designated as facultative, facultative wetland, and obligate wetland species were classified as hydrophytes. Native status was assigned as per the Alberta Conservation Information Management System List of Vascular Plants (ACIMS 2015). Plants that could not be identified to species were not assigned a WIS or native status and could not be analyzed as per the metrics. Between both sampling years, 34 out of the total 216 species observed (16%) could not be identified to the species level (Table A1). Second, given the uneven sampling effort within wetlands, species richness was estimated in EstimateS, version 9.1 (Colwell 2013) using rarefaction curves for restored and natural wetlands and extrapolation curves for drained wetlands,

following methods by Colwell et al. (2012). Rarefaction allows for the interpolation of species richness estimates at a lower effort than was conducted in the field, whereas extrapolation allows the estimation of species richness beyond the original sampling intensity. Species richness within each wetland was estimated for 12 quadrats per wetland, and species data collected during quadrat sampling was used to calculate richness estimates using either rarefaction or extrapolation curves. Finally, all species identified within a wetland (i.e., species observed during quadrat sampling and the random walk through) were used in for a community composition analysis. The Sørensen Index was used to estimate similarity in community composition as a distance measure between wetlands (Sørensen 1948). Sensitive species identified as plants with relatively small distributional ranges, small population sizes, or occurrences of ≤100 in Alberta (ACIMS 2015) were excluded from the analysis to remove unnecessary variability in the data (McCune & Grace 2002).

2.2.4 Morphology

Wetland morphometries were derived from the wetland field delineations conducted in 2016 and included area, slope, perimeter-to-area ratio, and shape. Slope was estimated as the mode within each wetland determined from a hydrologically corrected 25 m digital elevation model (Alberta Environment and Parks 2008) that was resampled to generate a 5 m grid in ArcGIS Desktop 10.4 (ESRI, Redlands, CA). Shape was measured as the departure from a circular shape (McGarigal & Marks 1995).

2.2.5 Statistical Analysis

Analysis of variance (ANOVA) was used to compare structural metrics. Where wetland area was correlated to plant diversity metrics, analysis of covariance (ANCOVA) was used to control for wetland area (i.e., for percent cover of hydrophytes and native species, as well as species richness). All figures present estimated marginal means at a constant wetland area of 0.378 ha, in an effort to remove the influence of wetland area on metric results. This wetland area represents the average size of wetlands assessed in the study. Assumptions of ANOVA/ANCOVA models were tested and confirmed by a way of

QQ plots, the Shapiro-Wilk normality test, Bartlett's test, and two-way ANOVA with an interaction term to ensure homogeneity of variance, normality of residuals, and homogeneity of regression slopes. Spearman rank correlation was used to assess the relationship between plant diversity metrics and wetland morphometrics. Pairwise comparisons were conducted using the Sidak test. ANCOVA was performed in SPSS version 24 (IBM Corp, Armonk, NY, U.S.A.) at a significance level of 0.05.

A nonmetric multidimensional scaling (NMDS) was performed using the Sørensen Index to assess differences in community composition, as the data were nonlinear. NMDS was run iteratively until a stable solution was achieved with a recommended goodness of fit below 0.2 (Clarke 1993; McCune & Grace 2002). Wetland area, perimeter-to-area ratio, shape, slope, and wetland age classes were fitted on the ordination to determine correlation with community composition. Morphometric variables were standardized prior to running the ordination to ensure a mean of 0 and standard deviation of 1. NMDS analysis and variable fitting were performed in R using *metaMDS()* and *envfit()* functions in the vegan package (Oksanen et al. 2017; RStudio, Boston, MA, U.S.A.). Significant differences in community composition were tested using PERMANOVA in Primer Version 7 (Clarke & Gorley 2015).

2.2.6 Precipitation and Climate
An analysis of precipitation across sampling years was conducted in an effort to explain some variability among years. Spatial climate models derived for North America were used to interpolate daily precipitation values from October 2015 through September 2017 (McKenney et al. 2011). Further, 30-yr climate normal (1987 - 2017) for a centralized point within the study area (township 49, range 20, W4M) was determined from data retrieved from the Alberta Climate Information Service (ACIS 2018).

2.3 Results
Over two years of quadrat sampling, a total of 216 species were observed within 29 study wetlands (Table A1). After removing unidentified species, 33% of

species were only observed in 2016, whereas an additional 10% of species were only identified in 2017. 90 species were observed in 5 wetlands or less whereas 42 species were observed in at least 50% of all study sites. The species most frequently observed across wetlands include *Cirsium arvense* (observed in 29 wetlands), *Poa palustris* (28 wetlands), *Poa pratensis* (27 wetlands), *Taraxacum officinale* (27 wetlands), *Sonchus arvensis* (26 wetlands), *Carex atherodes* (26 wetlands), and *Eleocharis palustris* (26 wetlands).

2.3.1 Effect of Age on Wetland Recovery

ANCOVA revealed a significant difference in percent cover of hydrophytic species among wetland age groups in 2016 ($F_{(6,21)}$ = 2.741, p = 0.040, partial η^2 = 0.439, observed power = 0.753) (Table 2.1; Figure 2.2A). Given a constant wetland size of 0.378 ha, drained wetlands had a lower percent cover of hydrophytic species (13.23 ± 10.44) when compared with wetlands restored 3-5 years (45.06 ± 7.85), 6-10 years (57.55 ± 8.23), 11-15 years (33.67 ± 7.65), 20-30 years (34.75 ± 9.92), agricultural natural wetlands (26.92 ± 11.25), and natural reserve wetlands (47.23 ± 8.19). Pairwise comparisons suggested that drained wetlands have significantly lower hydrophytic cover than wetlands restored 6-10 years (p = 0.0268), otherwise no significant differences were observed in percent cover of hydrophytic species. Similarly, there was a significant difference in percent cover of native species among age groups in 2016 as determined by ANCOVA ($F_{(6,21)}$ = 3.293, p = 0.019, partial η^2 = 0.485, observed power = 0.838) (Table 2.1; Figure 2.2B). Drained wetlands had a lower percent cover of native species (9.07 ± 9.99) when compared with wetlands restored 3-5 years (44.66 ± 7.51), 6-10 years (58.47 ± 7.88), 11-15 years (36.78 ± 7.33), 20-30 years (36.80 ± 9.50), agricultural natural wetlands (34.04 ± 10.77), and natural reserve wetlands (49.55 ± 7.84). Pairwise comparisons suggested that drained wetlands have a significantly lower native cover than wetlands restored 6-10 years (p = 0.007), otherwise no significant differences were observed in percent cover of native species. ANOVA found no significant difference in percent cover of non-native species among age groups in 2016 ($F_{(6,22)}$ = 0.275, p = 0.951, partial η^2 = 0.066, observed power = 0.103) (Table 2.1; Figure 2.2C). It should be noted that

there was a high cover of bare ground in all drained wetlands as a result of recent and regular cultivation activities, which accounts for low total (hydrophytes, native, and non-native species) cover observed within these wetlands.

Table 2.1. Raw mean values ±SE of structural metrics in 2016, represented by age class. Cover values represent mean cover within a wetland based on quadrat sampling. Species richness is an estimate at 12 quadrats sampled. Nat(Ag) represents natural wetlands on agricultural landscapes and Nat(Res) represents wetlands located within a natural reserve.

	Average Size (ha)	Sample Size	Cover Hydrophytes		Cover Natives		Cover Non-natives		Estimated Species Richness	
			Mean	SE	Mean	SE	Mean	SE	Mean	SE
Drained	0.12	3	6.11	6.07	2.39	2.35	16.89	1.08	12.33	1.67
Age 3-5	0.25	5	41.40	5.26	41.23	4.75	13.99	6.02	28.60	1.66
Age 6-10	0.15	5	51.16	8.13	52.47	8.00	11.56	3.53	24.60	1.86
Age 11-15	0.38	5	33.83	10.59	36.93	10.07	12.29	3.11	21.00	5.36
Age 20-30	0.45	3	36.71	12.95	38.64	13.58	13.66	4.27	22.00	0.58
Nat(Ag)	0.60	3	38.31	15.03	44.73	13.78	9.89	4.78	28.33	3.48
Nat(Res)	0.79	5	53.39	6.15	55.33	6.13	14.99	2.81	44.00	2.39
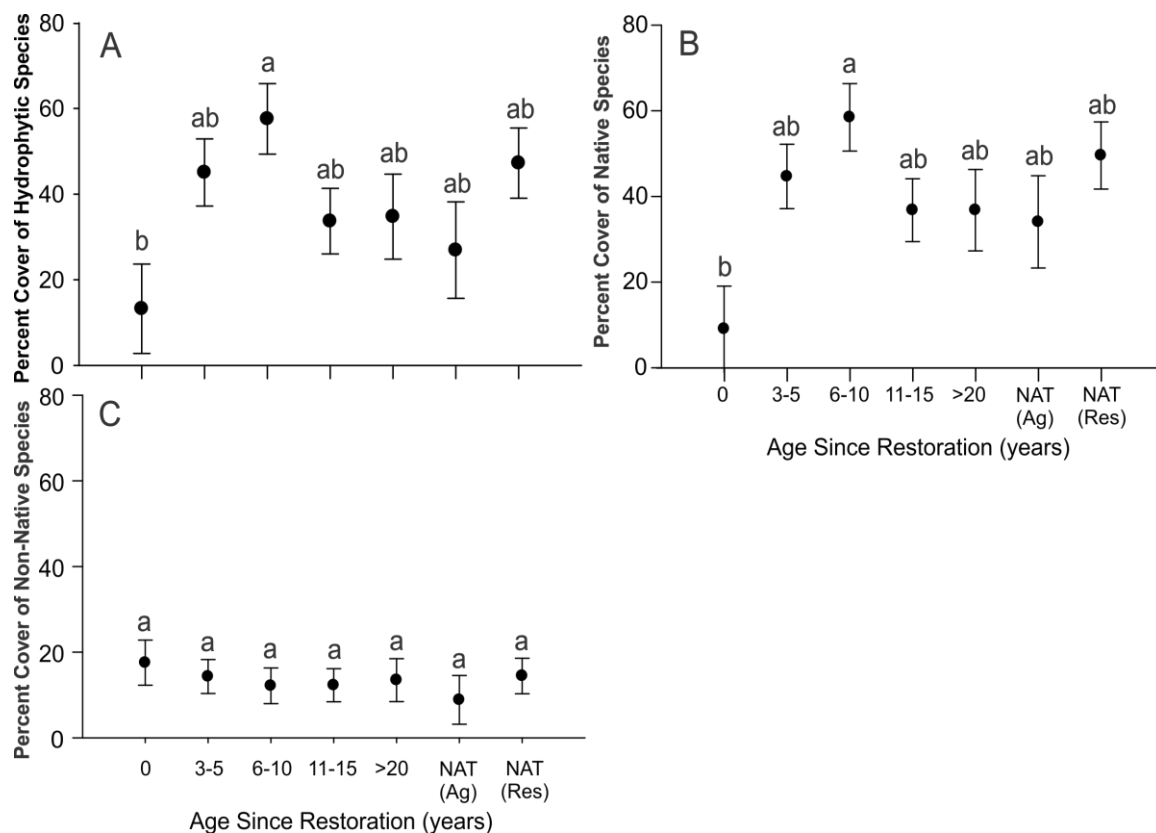
Figure 2.2. Estimated marginal means (± SE) of (A) percent cover of hydrophytes, (B) percent cover of native species, and (C) percent cover of non-native species across a chronosequence of restored wetlands at a standard wetland size of 0.378 ha as observed in 2016. Age 0 represents drained wetlands, Nat(Ag) represents natural wetlands on agricultural landscapes, and Nat(Res) represents wetlands located within a natural reserve. Different letters indicate significant differences.

ANCOVA indicated species richness in 2016 was significantly different among wetland age groups ($F_{(6,21)}$ = 8.386, p < 0.0001, partial η^2 = 0.706, observed power = 0.999). Drained wetlands supported the lowest estimated species richness (14.9 ± 3.60), when compared with wetlands restored 3-5 years (29.92 ± 2.71), 6-10 years (26.91 ± 2.84), 11-15 years (20.94 ± 2.64), 20-30 years (21.29 ± 3.43), agricultural natural wetlands (24.22 ± 3.89) and natural reserve wetlands (41.78 ± 2.83). Pairwise comparisons revealed that drained wetlands had significantly lower species richness than newly restored wetlands (3-5 years; p = 0.0328) and natural reserve wetlands (p = 0.0003). As well, natural reserve wetlands had significantly higher species richness than restored

age classes 6-10 years (p = 0.0303), 11-15 years (p = 0.0004), 20-30 years (p = 0.0021), and agricultural natural wetlands (p = 0.010) (Table 2.1; Figure 2.3).
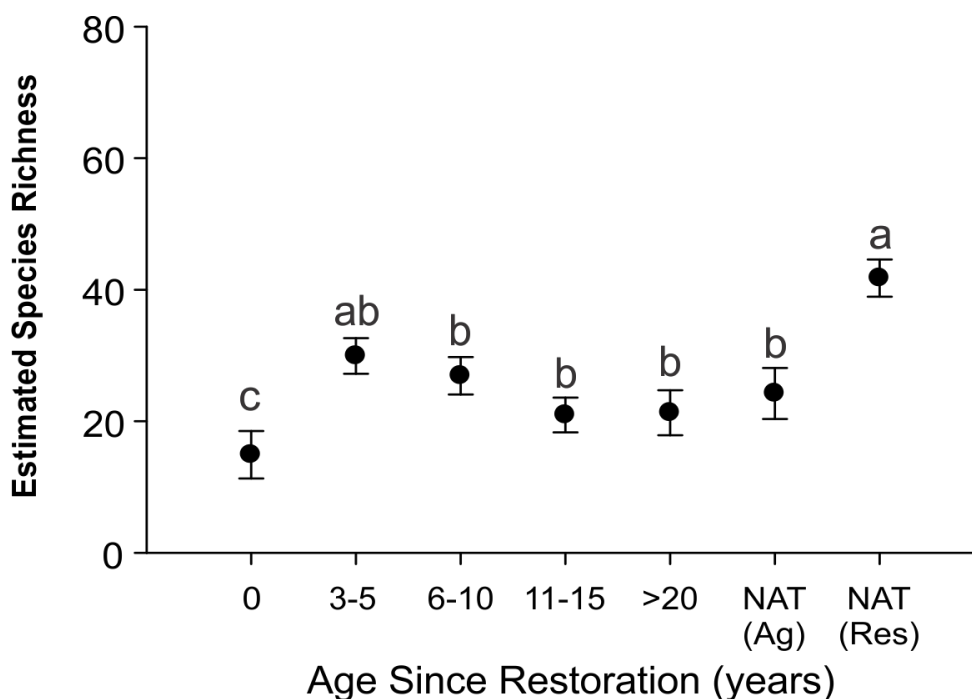
Figure 2.3. Estimate species richness (+/- SE; estimated marginal means at a constant wetland size of 0.378 ha) across a chronosequence of restored wetlands assessed in 2016. Age 0 represents drained wetlands, Nat(Ag) represents natural wetlands on agricultural landscapes, and Nat(Res) represents wetlands located within a natural reserve. Different letters indicate significant differences.

The NMDS ordination of community composition in 2016 revealed three community clusters (Figuer 2.3). Drained wetlands separated from the other wetland classes along the first axis, natural reserve wetlands separated along the second axis, and restored wetlands showed convergence in community composition with agricultural natural wetlands as indicated by close proximity and overlapping clusters. PERMANOVA further confirmed differences in community composition (pseudo-$F_{(6,22)}$ = 3.63, p = 0.0001). Pairwise comparisons suggested that drained wetlands were significantly different from wetlands restored 3-5 years (p = 0.004), 6-10 years (p = 0.003), 11-15 years (p = 0.005), 20-30 years (p = 0.016), agricultural natural wetlands (p = 0.014), and natural reserve wetlands (p < 0.001). Likewise, natural reserve wetlands were also significantly different from wetlands restored 3-5 years (p = 0.018), 6-10 years (p = 0.004), 11-15 years

(p = 0.007), 20-30 years (p = 0.013), and agricultural natural wetlands (p = 0.045). The NMDS iterative algorithm stopped after 20 random starts and provided a solution with a stress of 0.15 indicating a good representation of the underlying structure.
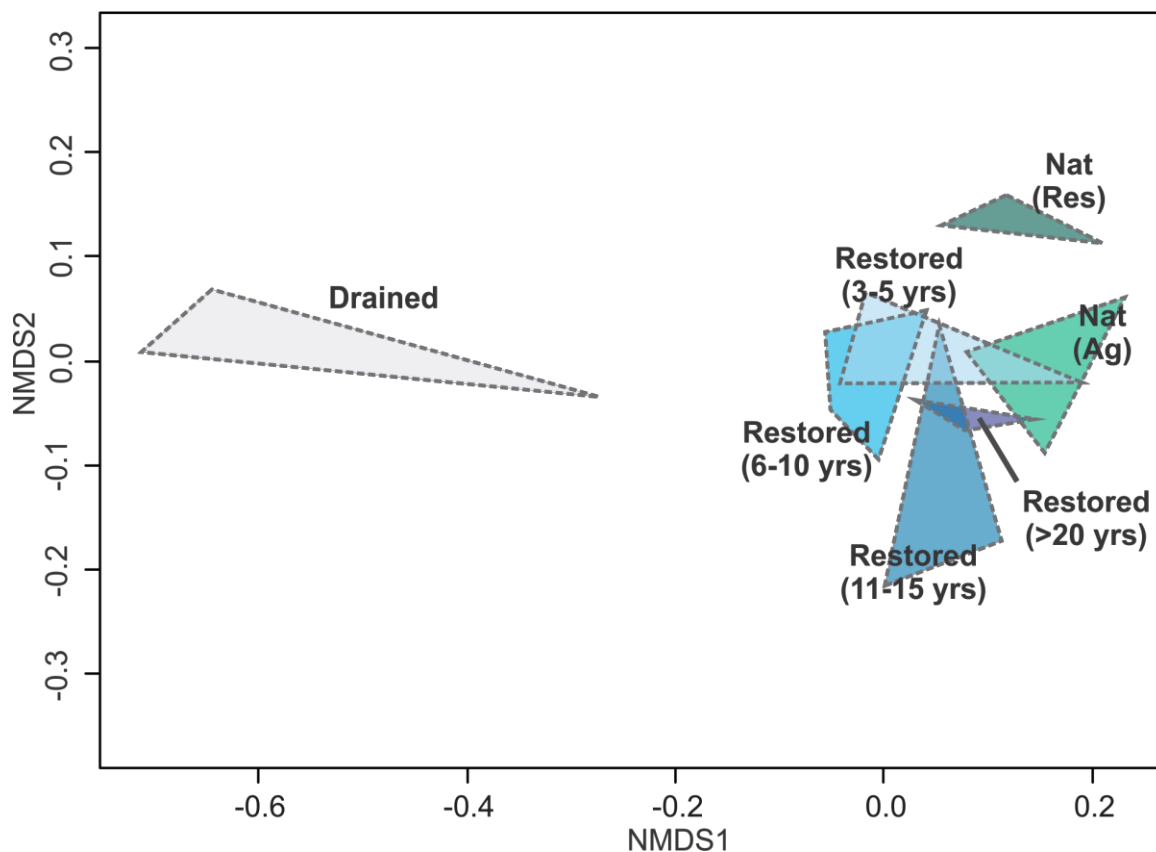
Figure 2.4 NMDS of community composition observed in 2016 grouped by wetland restoration age classes (represented by triangles). Nat(Ag) represents natural wetlands on agricultural landscapes, and Nat(Res) represents wetlands located within a natural reserve (stress = 0.15).

2.3.2 Effect of Morphology on Recovery

In 2016, wetland size and slope had a significant effect on wetland recovery (Table 2.2). Wetland area was positively correlated with species richness (r = 0.474, p = 0.009), percent cover of hydrophytes (r = 0.414, p = 0.025) and natives (r = 0.429, p = 0.020), but not percent cover of non-native species (r = 0.099, p= 0.608). On the other hand, wetland slope was positively correlated with percent cover of non-native species (r = 0.456, p = 0.013) (Table 2.2). Wetland perimeter-to-area ratio and shape had no significant association with structural diversity metrics in 2016 (Table 2.2).

Table 2.2. Spearman rank correlation values between wetland morphometrics and plant structural diversity metrics in 2016. Significant (α =0.05) correlations are bolded and p-values are provided in parentheses.

Plant Diversity Metrics	Area (ha)	Perimeter-to-area Ratio (m^{-1})	Shape	Slope (% rise)
Species Richness	**0.474** **(0.009)**	-0.335 (0.0751)	0.190 (0.321)	0.094 (0.624)
Percent cover Hydrophytes	**0.414** **(0.025)**	-0.258 (0.175)	0.349 (0.063)	-0.014 (0.942)
Percent cover Natives	**0.429** **(0.020)**	-0.272 (0.151)	0.345 (0.066)	-0.069 (0.720)
Percent cover Non-natives	0.099 (0.608)	0.001 (0.995)	0.054 (0.780)	**0.456** **(0.013)**

Wetland area (r^2 = 0.287, p = 0.013) and perimeter-to-area ratio (r^2 = 0.248, p = 0.022) significantly (but weakly) explained dissimilarity in community composition among sites. Perimeter to area ratio fitted on the NMDS of community composition provides further support of that morphometric variability in wetlands types (Figure 2.5).
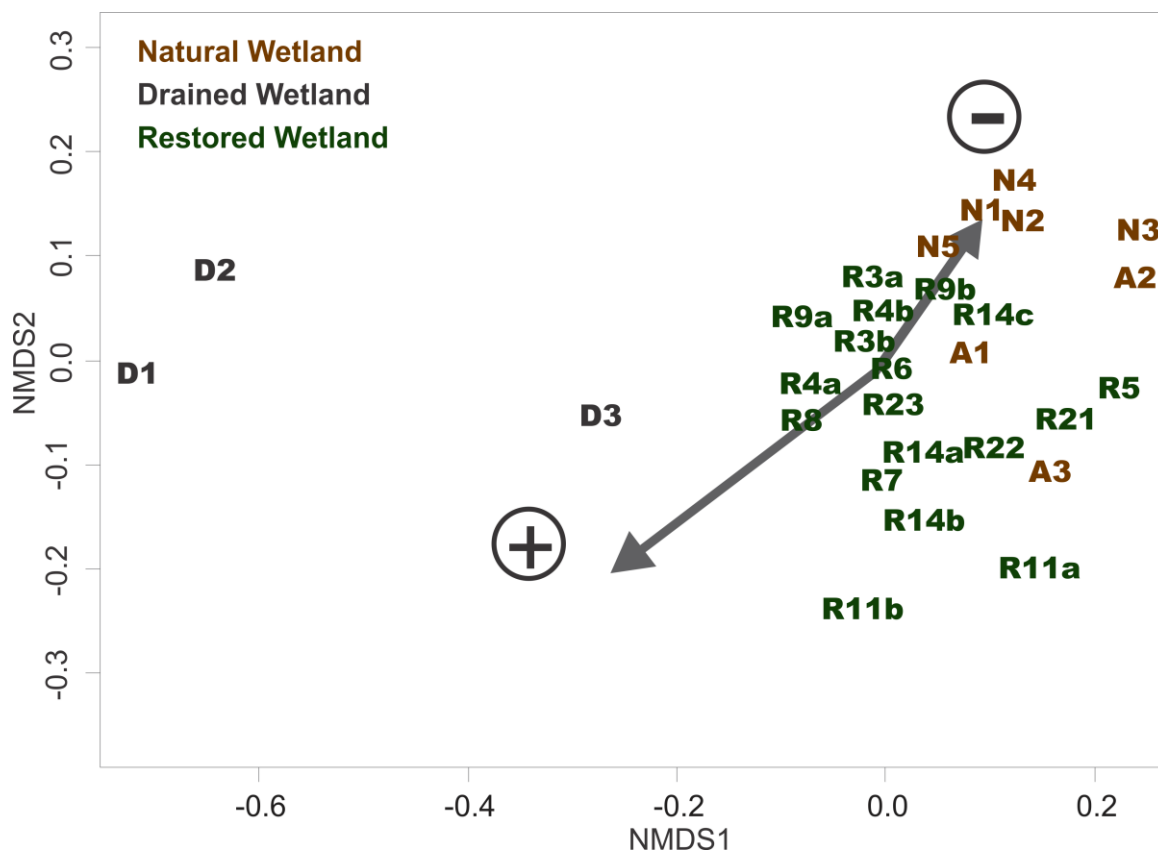
Figure 2.5. Perimeter to area ratio (P:A) fitted on NMDS ordination of community composition in 2016.The centre point of arrows represent the mean P:A of wetlands, and the direction of arrows represent general morphometries of wetlands, where natural wetlands were associated with smaller P:A ratios and drained wetlands were associated with larger perimeter to area ratios.

Wetland points were plotted against perimeter to area ratio as a function of wetland area to better understand the distribution of wetland morphometries within the study. Results suggest most natural wetlands (in agriculture settings and natural reserves) are characterized by low P:A ratios (between 425 - 1250 m/m^2) and had wetland areas on the larger end (all >0.45 ha), whereas drained wetlands in this study had high P:A ratios (all >1900 m/m$^{2)}$ and were small in size (<0.25 ha). Restored wetlands varied from having low to high P:A ratios (422 – 1686 m/m^2) and ranged from small (0.05 ha) to large (1.0 ha) (Figure 2.6).
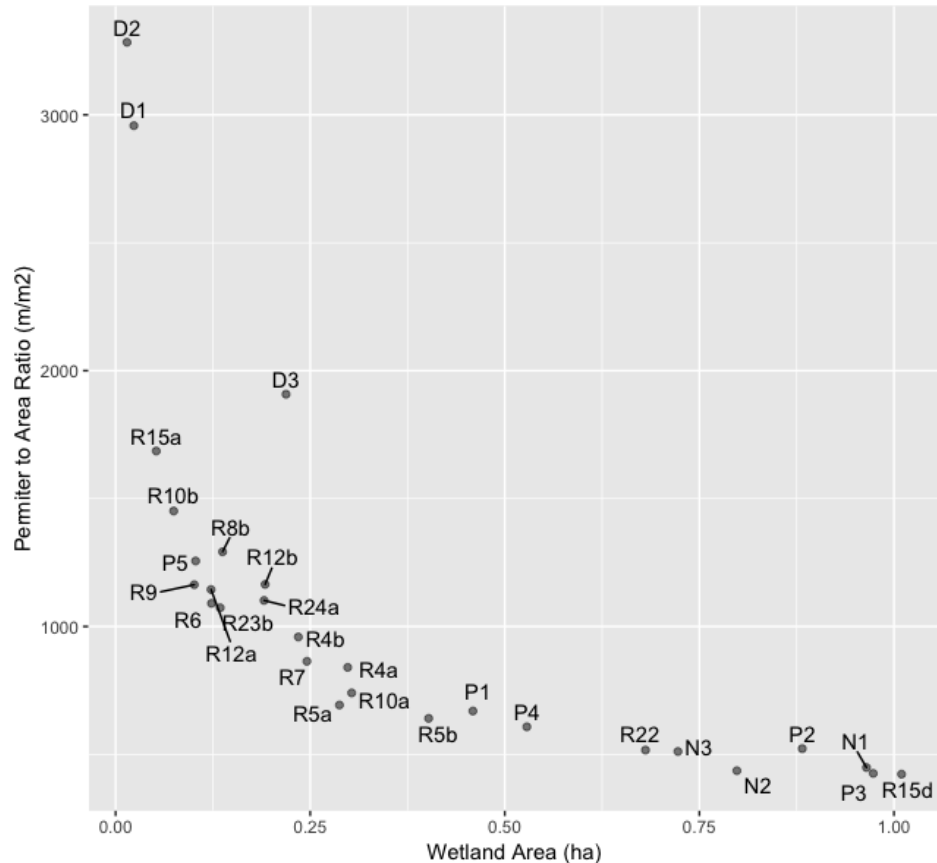
Figure 2.6. Morphometries of study wetlands. Wetlands are identified by a letter representing type of wetlands (R= restored, D = drained, N = Nat(Ag), and P = Nat(Res)) and a number representing wetland number (in the case of drained and all natural sites) or age (in the case of restored wetlands). When more than one restored wetlands were of the same age they were further distinguished by a lower case letter (a – d).

2.3.3 Effect of Annual Variability on Structural Metrics

All wetlands were re-assessed in 2017, and structural metrics were analyzed. Results suggest, in general, native cover and hydrophyte cover were higher in 2017 when compared to 2016 (Figure 2.7A and 2.7B, respectively). All restored and natural wetlands contained average native and hydrophyte covers between approximately 60% and 80% cover. Drained wetlands had lower average native and hydrophyte covers (26% and 27%, respectively). Non-native cover was low across all wetland age classes and was similar between 2016 and 2017 (Figure 2.7C). Drained wetlands, the exception, had an average non-native cover of 42% in 2017 compared to 17% in 2016. ANOVA suggests that in 2017, drained wetlands had significantly higher cover of non-native species when

compared to wetlands Age 3-5 (10 %), Age 11-15 (4.5 %), Age >20 (6.2 %), and Nat(Ag) wetlands (6.2 %) ($F_{(6,21)}$ = 3.0891, p = 0.02501). No significant differences were observed across the chronosequence when analyzing cover of natives ($F_{(6,21)}$ = 2.3003, p = 0.073) or cover hydrophytes ($F_{(6,21)}$ = 2.2836, p = 0.075).

When comparing species richness between years, 2017 had higher estimated species richness in every age class, with the exception of Nat(Res) wetlands (Figure 2.7D). Nat(Res) had 38 species in 2017 compared to 42 species in 2016. ANOVA suggests that in 2017, no significant differences were observed in estimated species richness at 12 quadrats across wetland age classes ($F_{(6,21)}$ = 2.0254, p = 0.1073).
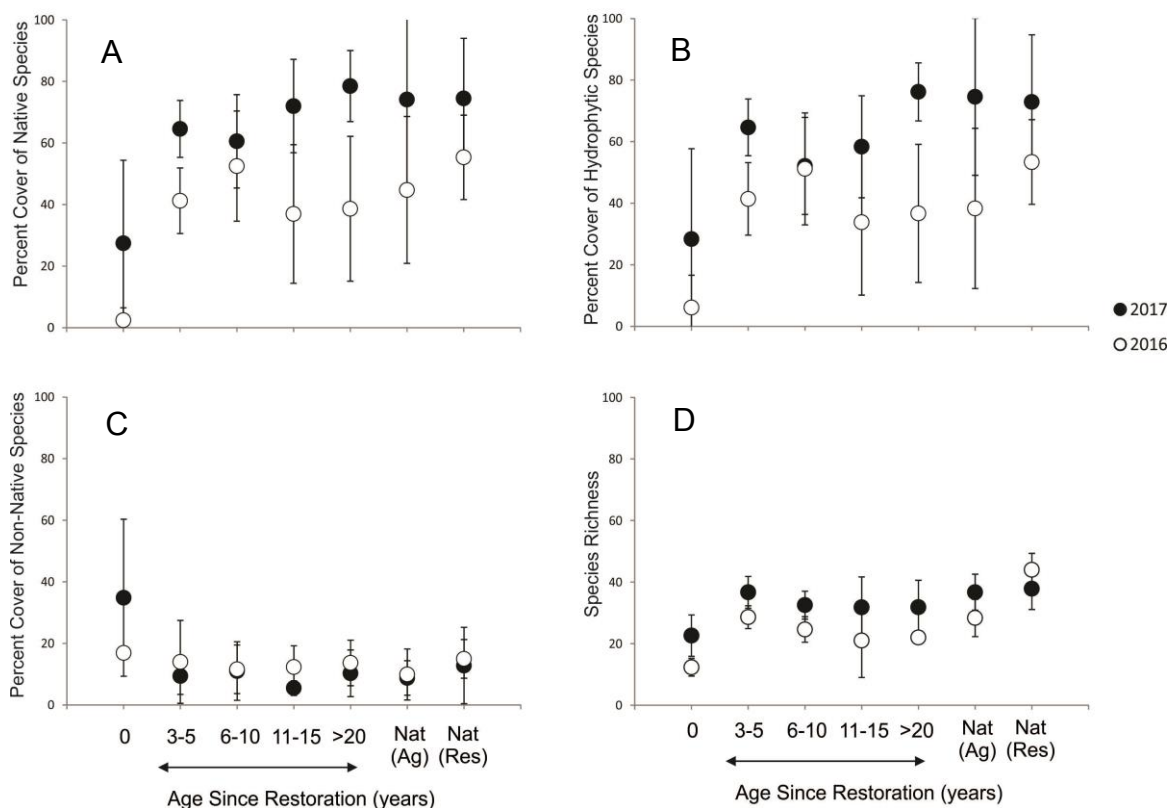
Figure 2.7. Structural diversity metrics (± SE) compared between 2016 and 2017. 2016 values are estimated marginal means, whereas 2017 values are raw values. (A) percent cover of native species, (B) percent cover of hydrophytes, (C) percent cover of non-native species and (D) estimated species richness at 12 quadrats. Age 0 represents drained wetlands, Nat(Ag) represents natural wetlands on agricultural landscapes, and Nat(Res) represents wetlands located within a natural reserve.

When analyzing community composition among wetlands in 2017, a similar differentiation of the species that comprise drained wetlands was observed. Drained wetlands separate along the x-axis from restored and natural wetlands as was observed in 2016. However, the community composition of natural wetlands in natural reserves was not distinctly different from restored and Nat(Ag) wetlands, as was the case in 2016 (Figure 2.8). PERMANOVA confirmed differences in community composition among wetlands (pseudo-$F_{(6,21)}$ = 2.90, p = 0.001).
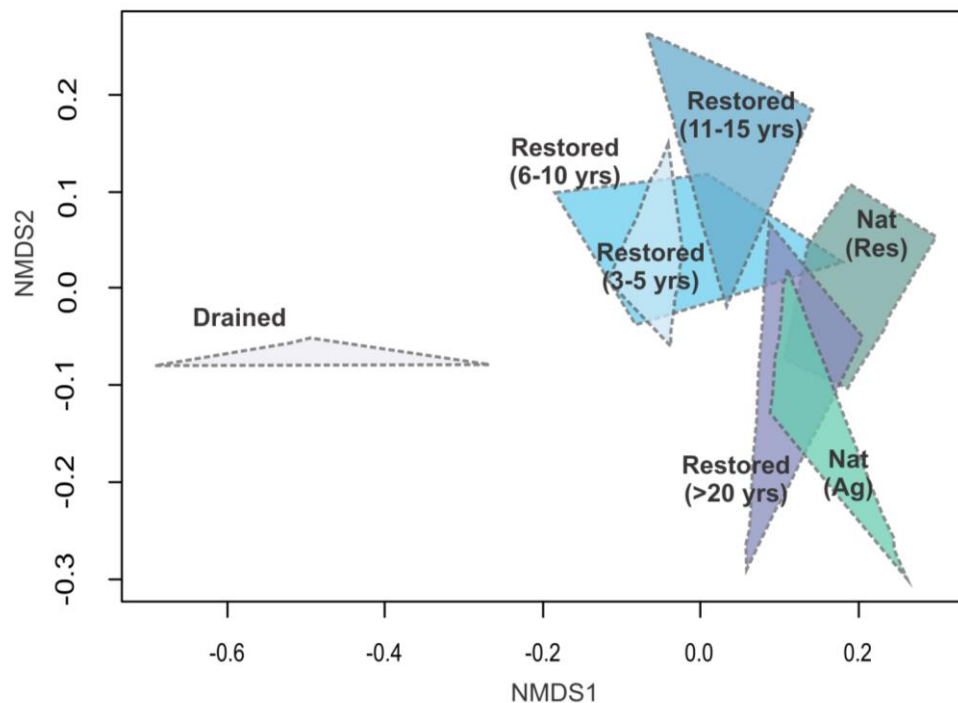
Figure 2.8. NMDS of community composition as assessed in 2017. Wetlands are grouped by restoration age classes represented by polygons. Nat(Res) represents natural wetlands in natural reserves and Nat(Ag) represent natural wetlands on agricultural landscapes (stress = 0.16).

2.3.4 Comparison Precipitation Between Sampling Years

Cumulative daily precipitation values for a centrally located point within the study area suggests that through most of the growing season (May – August), precipitation was consistently higher in 2016 than in 2017, resulting in an accumulation of 347 mm and 234 mm of precipitation respectively (Figure 2.9). When compared to the 30-year precipitation normal for the area, 2016 received

approximately 80 mm more precipitation than average. The cumulative precipitation in 2017 was slightly higher than the 30-yr normal for the first half of the growing season (early July), after which cumulative precipitation values were slightly less than the 30-yr normal.
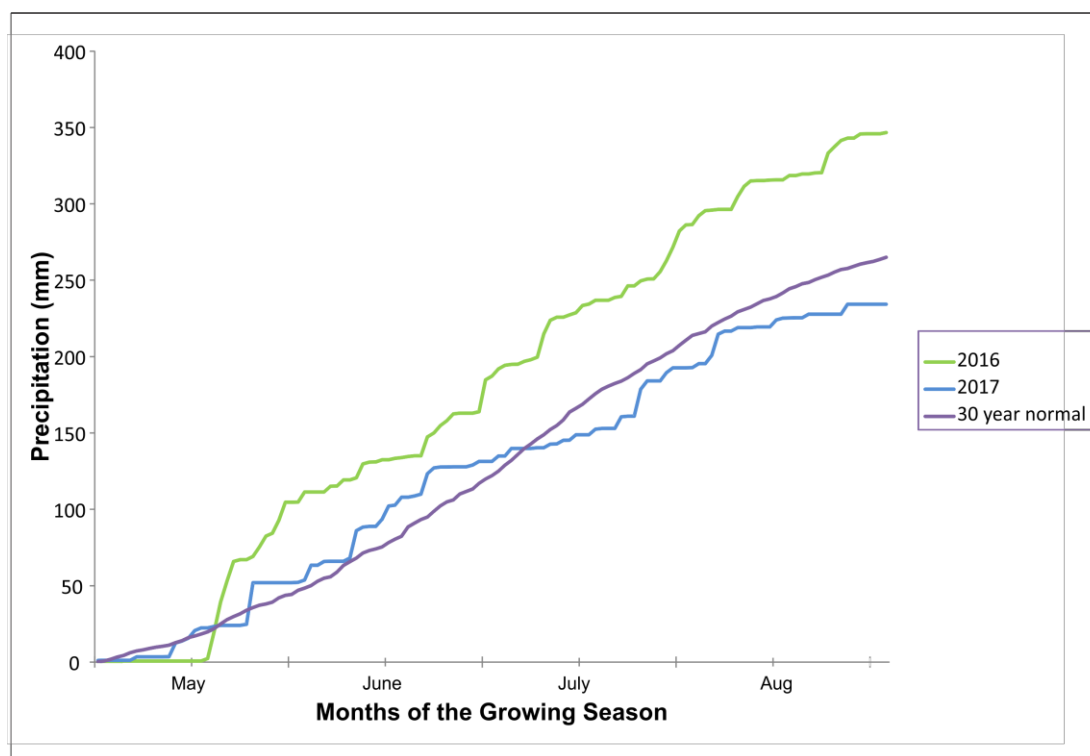
Figure 2.9. Comparison of cumulative precipitation in 2016, 2017, and to the 30-year precipitation normal over the growing season for a centrally located point within the study area.

An analysis of precipitation from the winters prior to field sampling revealed that the snow pack prior to the 2017 field season was nearly three times that of the winter season prior to 2016 (Table 2.3). Nearly 30% of the total precipitation from the 2017 water year (Oct 2016 through Sept 2017) was accumulated in the winter, compared to 13% accumulated in the winter of 2015/2016.

Table 2.3. Monthly water year precipitation compared between 2016 and 2017. Water year is defined from October through September of the following year.

2016 Field Season	Precipitation (mm)	2017 Field Season	Precipitation (mm)
10/2015	6.62	10/2016	61.73
11/2015	11.40	11/2016	40.48
12/2015	5.48	12/2016	15.65
1/2016	11.31	1/2017	10.12
2/2016	8.59	2/2017	14.23
3/2016	15.45	3/2017	21.73
4/2016	13.36	4/2017	57.03
5/2016	104.63	5/2017	51.95
6/2016	80.12	6/2017	79.48
7/2016	101.44	7/2017	61.29
8/2016	60.54	8/2017	41.56
9/2016	27.57	9/2017	48.10
Total Summer (Apr - Sept):	**387.67**		**339.41**
Total Winter (Oct - Mar):	**58.86**		**163.94**
Combined Total:	**446.52 (2016)**		**503.35 (2017)**

2.4   Discussion

2.4.1 Assessment of Degraded Conditions Prior to Wetland Recovery

On the Canadian prairies, wetland drainage for agricultural production has historically been the main cause of wetland loss (Zedler & Kercher 2005). Thus, assessing the condition of drained wetlands allows for the quantification and characterization of the degraded state of these impacted habitats prior to restoration. Typically, wetlands are drained through a ditch that is constructed to convey water away from the wetland basin. The duration that a wetland has been drained and completeness of drainage are factors that can influence species richness and community composition of a site (Weinhold & van der Valk 1989).

In my study, drained wetlands differed significantly from restored and natural wetlands in vegetation community composition and species richness; however, when very simple metrics of plant diversity were compared (i.e., percent cover of hydrophytic, native, and non-native species), I found that the drained

wetlands were not statistically different from restored or natural reference wetlands when the estimated marginal means for a constant wetland area were compared. These results are despite the fact that the drained wetlands included in this study were heavily impacted by agricultural activity, contained few hydrological indicators typical of a wetland ecosystem, and were generally characterized by low species richness and high percent cover of bare ground.

The lack of statistically significant differences in the cover of hydrophytes and native species between drained and restored/natural wetlands may be partially explained by the incomplete drainage of one of the "drained" wetlands. In this wetland, the drainage ditch contained water at the time of sampling, and hydrophytic species were found in patches that were proximal to the drainage ditch. This resulted in relatively high native and hydrophytic species cover estimates, as compared to the two other completely drained wetlands that were included in this age class. The presence of hydrophytes in this drained wetland suggests that this basin holds water for sufficiently long periods so as to allow for the persistence of water-loving plants to develop and persist, both within and between years. This circumstance is not unique to the drained wetland included in this study; in fact, incomplete drainage of prairie pothole wetlands is a fairly common occurrence across central and southern Alberta, and as a result, many drained wetlands continue to support substantial patches of native wetland plants within the drained basin. This is particularly true for drained wetlands that had large basins that were more permanently inundated prior to the initiation of the drainage activity, as these wetlands are generally more difficult to completely drain with a ditch.

While the simple plant diversity metrics included in this study suggest little difference between drained, restored, and natural wetlands, it should be noted that the significant difference measured in species richness and plant community composition suggest that there may be more nuanced differences between wetland age classes than can be captured using these metrics alone. For example, this study did not examine the effect of age class on the spatial arrangement or functional traits of the plant species and communities present. It

is possible that an examination of more complex plant community metrics may reveal important differences in drained and restored wetlands, as compared to natural reference conditions.

2.4.2 Effect of Age on Wetland Recovery

These results showed that at a normalized wetland size of 0.378 ha, species richness is lowest in drained wetlands, increases rapidly within five years of restoration, and appears to stabilize within six to ten years of restoration. Though restored wetlands maintain a similar number of species to Nat(Ag) wetlands, species richness in Nat(Res) wetlands is significantly higher than all restored and Nat(Ag) wetlands, with the exception of newly restored wetlands (Age 3-5). Similarly, cover of hydrophytic and native species increases substantially within 3-5 years of restoration with peak cover of hydrophytic and native species at 6 to 10 years since restoration. As well, though cover estimates can be dependant on timing of field sampling, all cover indicators (i.e., cover of hydrophytes, natives, and non-natives) seem to stabilize within 5 years, suggesting that the rate of recovery within restored wetlands occurs rapidly. Once restored, wetlands generally undergo a period of "self-design" (Mitsch & Wilson 1996) and "self-organization" (Odum 1989) during which succession and community assembly takes place. Prairie wetlands like those observed in the study (i.e., temporary and seasonal wetlands) often experience rapid species accumulation and extinction rates due to a variable hydroperiod (Aronson & Galatowitsch 2008). After the initial increase in species, community composition and species diversity tend to stabilize (Zedler & Callaway 1999). These results are comparable to other studies conducted in the Parkland ecoregion of the prairies where it has been shown that vegetation communities, bird and amphibian assemblages, biotic communities (phytoplankton, zooplankton, and macroinvertebrates), and abiotic conditions (pH, specific conductance, total phosphorus, and dissolved carbon dioxide) within wetlands will recover post restoration and resemble natural wetland communities within approximately a decade (Aronson & Galatowitsch 2008; Puchniak 2002; Bortolotti et al. 2016). While exact recovery rates and conditions of these research studies varied,

combined, these results suggest that wetland restoration does lead to recovery of important biological and chemical conditions, and that this recovery can occur rapidly after the re-establishment of hydrologic function.

While these results are promising, it is clear from this and other studies that restored wetlands do not achieve a natural reference condition for many important biological metrics, even within several decades of recovery. In fact, despite the rapid recovery seen within the first five years of restoration, there appeared to be a plateau in the recovery of the metrics Iassessed between 6-10 years, and in some cases, a decline through time. For example, species richness and community composition of restored wetlands are not comparable to wetlands in natural reserves, even >20 years following restoration. These differences suggest restored wetlands are failing to achieve their maximum restoration potential.

This lack of complete recovery may be partially explained by the influence of the surrounding land use on the assembly and recovery of wetland plant communities (Boughton et al. 2010). Natural re-colonization of wetlands on agricultural landscapes is often impeded because the large-scale loss of wetlands from these landscapes has resulted in scarce or depauperate native seed banks and plant propagules (Galatowitsch 2006). Furthermore, differences in plant communities can be explained by limitations of establishment and dispersal. For example, sedge meadow, wet prairie, and woody perennial species are considered to be low efficiency colonizers due to limited propagule availability or an absence of reliable dispersal vectors (Galatowitsch & van der Valk 1996; Aronson & Galatowitsch 2008). Sedge meadow communities, in particular, are invaluable in wetland systems as they provide micro-topographic variation that promotes high species richness in wetlands (Werner & Zedler 2002). Yet, these communities are frequently absent from restored wetlands (Galatowitsch & Van der Valk 1996) and are hard to restore (van der Valk et al. 1999). In addition, the prominence of non-native perennial species, particularly *Bromus inermis* (smooth brome), *Cirsium arvense* (Canada thistle), *Sonchus arvensis* (perennial sow-thistle), and *Taraxacum officinale* (common dandelion) in restored sites suggests

invasion theory is an important driver in explaining the differences in species composition between wetlands. Key features of invasive species, such as vegetative reproduction (colonial species) and/or the production of many, small, light seeds provide an advantage in newly disturbed habitats for these species to establish quickly and efficiently, thereby impeding establishment of native hydrophytes (Sakai et al. 2001). Further, these features provide not only an advantage during establishment post-restoration but are equally as integral to the pervasiveness of invasive species through time given their prominence across all wetland age classes.

2.4.3 *Effect of Morphology on Wetland Recovery*

Wetlands vary in size and complexity, and as such, it was hypothesized that wetland morphometrics would influence the potential success of a restoration. These results suggest that wetland size influences plant diversity, with wetland area being positively correlated with species richness and cover of hydrophytic and native species. These results are consistent with previous studies that show larger wetlands typically provide increased habitat heterogeneity and support a wider variety of plant species (Mulhouse & Galatowitsch 2003), and that larger wetlands have a higher likelihood of receiving plant propagules and seeds from nearby sources and within site dispersal, thereby increasing both species richness and cover (Cook et al. 2005). While the results of this study are consistent with the literature and provide support for a restoration strategy that targets larger basins, particularly if the goal is to maximize plant diversity within restored sites, is important to note that the wetlands in this study ranged between 0.06 and 1.06 ha. While this size range is representative of temporary and seasonal wetlands in the Canadian prairies and is consistent with the majority of wetlands restored in Alberta, it is at that smaller end of the size range that has been previously studied. Further, the distribution of wetland size across age groups in the study is regrettably uneven, with drained and younger restorations being relatively small (<0.3 ha), and Nat(Ag) wetlands being at the higher end of the size range (0.74 ha – 0.84 ha).

Perimeter to area ratio and shape were not found to influence the diversity or cover of native, non-native, or hydrophytic species; however, perimeter-to-area ratio explained some dissimilarity in community composition, where natural reserve wetlands were associated with smaller perimeter to area ratios. High perimeter-to-area ratio exposes wetland species to edge effects where non-native and other opportunistic species from adjacent uplands can prevent the establishment of native and/or hydrophytic species, thereby altering community composition within a restored wetland (Harker et al. 2009; Young et al. 2001). Steeper slopes (>2% rise) were associated with higher cover of non-native species. Steep slopes in a wetland generally undergo rapid changes in soil moisture conditions during the variable hydroperiods that are typical of temporary and seasonal pothole wetlands, and this increases the susceptibility of a wetland to invasion by non-native species (Zampella & Laidig 2003) and decreases the width of vegetation zones, thereby reducing species richness (Forrest 2010). Overall, the results suggest that larger wetlands with gently sloping basins should be prioritized for restoration and management if the primarily goal of restoration activity is to maximize vegetation community recovery.

Wetland size, perimeter to area ratio, and natural condition are somewhat confounded in this study. The distribution of wetland size across the age groups is regrettably uneven, where drained and younger restorations are all on the small side (<0.3 ha) and older restoration sites and natural wetlands more evenly cover the range previously mentioned. Most Nat(Ag) and several Nat(Res) wetlands, however, are all located the high end of the size range (0.74 ha – 0.84 ha) and lower end of the range in perimeter to area ratios. This is in contrast to drained wetlands, which were situated at the low end of wetland size range and at the end of perimeter to area ratios. Disentangling wetland area from wetland age is important, and I have tried to address this concern by presenting estimated marginal means of hydrophyte, native, non-native cover, and estimated species richness using a constant wetland area of 0.378 ha. This wetland area value represents the average size of wetlands sampled in this study. Further, analysis of covariance tests were used to control for the impact of wetland area on

species diversity metrics. The results presented still show significant differences across the chronosequence after all efforts were made to control for wetland area.

Finally, the distribution of wetland size within this study is representative of the distribution of wetland size on the landscape and is an artifact of a long history of wetland drainage in the area. Typically, wetlands that are easy to drain and tend to be selected for drainage are smaller and less permanent features. This results in a small size of restoration sites as well given that restored wetlands are selected from the drained wetland inventory. Finally, wetlands that are less likely to be drained and thus retained on the landscape are those that are more difficult to be drain given their size or permanence. As such, finding large drained wetlands and/or small natural wetlands was a difficult endeavor. NatPr wetlands represent a wider range of size classes (0.107 – 0.974 ha) given that these wetlands are not typically subjected to drainage given their location in a natural reserve.

2.4.4 Benchmarks for Measuring Restoration Success

Defining and evaluating restoration success is a difficult endeavor and there is currently no standard practice for doing so amongst restoration practitioners. Often, restoration success is determined by specifications outlined in wetland policies. For example, the Alberta Wetland Policy, applicable to the restored wetlands in this study, considers restoration success to be "re-establishment of natural hydrology, vegetation, and wetland processes within a previously drained wetland" (Government of Alberta 2016). This definition, however, fails to provide a target or means of comparison that can serve as a model for planning a restoration project. The Society of Ecological Restoration (SER) Primer on Ecological Restoration (SER 2002) suggests that a historic condition is an ideal starting point for restoration design, while acknowledging that a severely impacted or highly degraded system may never attain the target or even a trajectory towards a natural reference state. Regardless, a comparable intact system can be used to define targets for biological metrics, as well as provide measurable and achievable goals for restoration success.

When comparing the two classes of natural reference wetlands in this study, I found significant differences in species richness and community composition. These results suggest that while "natural" wetlands in an agricultural landscape are not subject to drainage, they are still impacted by disturbances that ultimately influence plant community composition. In contrast, wetlands situated within the Cooking Lake-Blackfoot Provincial Recreation Area represent a "least disturbed" wetland condition, where human influence and management is less intensive. The wetlands contained within these reserve lands contained high species richness and high cover of native species and hydrophytes. They contained 32 species that were otherwise absent from wetlands found within the agricultural landscape, of which 23 were native hydrophytes. These results suggest that continued loss of reserve or protected areas that conserve natural landscapes may result in a depletion of native seed sources and habitats, thereby affecting the vegetation recovery potential of future wetland restorations. This, in addition to the anthropogenic impacts resulting from land-use and climate change, will likely result in increased disparity between the actual (i.e., on the ground) and potential (i.e., reference condition) recovery of restored wetland habitat.

This observational study highlights the critical importance of thoughtfully selecting a reference condition for evaluating wetland restoration success, given that important differences can exist between natural reference conditions depending upon the surrounding landscape context. The conclusions drawn in this study would have been markedly different had I selected a single natural reference condition for comparison, rather than considering natural wetlands embedded within both an agricultural and reserve landscape. Similarly, This study highlights the importance of carefully selecting "drained" wetland sites, as the degree of hydrological disruption related to a drainage activity can greatly influence the presence or absence of hydrophytic and native plant species. Classifying the degree of hydrological disruption, and accounting for this in the sampling design and data analysis, will allow for more precisely measuring differences between restoration age classes and the overall effectiveness of restoration through time. Ultimately, this study has identified a need for the

examination of more complex plant community metrics, functional traits, and/or functional diversity, which may help tease apart additional differences among wetland age classes, in an effort to help restoration agents and land managers better manage wetlands on the landscape.

2.4.5 Variability in Wetlands and the Influence of Precipitation

The differences observed in structural diversity metrics between years suggest that climate and in particular precipitation can have a significant influence on wetlands vegetation communities. At the wetland scale, the effects of change in precipitation can be described by a correlation in number of wetland ponds on a landscape to precipitation of the previous year (Withey & van Kooten 2011). Specifically, wetland numbers are low in the year following a drought event (Bethke & Nudds 1995; Adams 1988; Withey & van Kooten 2011).

Related, the Wetland Continuum describes variability in wetlands as a function of hydrology related to atmospheric inputs (drought versus deluge) and hydrology related to groundwater (recharge versus discharge) (Euliss et al. 2004). The authors predict that the framework can be used to determine community composition (plants, invertebrates, amphibians, and/or birds) expected to occur within the unique positions along the wetland continuum. Generally, drought conditions may result in extensive cover of emergent species and a shrinkage of open water area, whereas periods of deluge and flooding conditions may result in the opposite effect, large areas of open water and limited emergent or deep marsh species cover (Euliss et al. 2004; Johnson et al. 2005).

Wetlands systems are highly variable hydrologically, temporally, and spatially. Despite the two-year monitoring period of this research project, the results demonstrate the importance of considering climate and precipitation in evaluations of wetland condition and vegetation assesments. Prairie Pothole wetlands are sensitive to changes in hydrology and water levels, thus interpreting community assembly and composition should consider the climate record.

This information is particularly relevant when considering the predicted impacts of climate change on the Prairie Pothole Region. Climate change is expected to increase temperatures, change precipitation patterns, increase

length of growing seasons, and produce milder winters and hotter summers in the Prairie Pothole Region (Johnson et al. 2005). These extreme changes in temperatures and precipitation may push wetland systems outside the natural range of variability (e.g., hydrological, biological, structural, etc.). Understanding this variability is critical for managing restored wetlands and ensuring these systems are resilient in the face of change.

2.5   Conclusions and Lessons for Wetland Managers

To maximize restoration success, management of restored wetlands is required. Wetland restoration planning should begin with prioritization of restoration sites with larger basins (>1 ha), where wetland basins have naturally gentle and gradual slopes. However, both small and large restorations are important to maintain representative distributions of wetland size and complexity on the landscape. Second, management should adopt measures that control the spread of non-native species such as *C. arvense* and *S. arvensis* (i.e., weeding) and promote the establishment of native hydrophytes (i.e., sowing or plantings). Finally, it is important to understand and recognize that global drivers may continue to shift biotic and abiotic conditions in both reference and restored wetlands, which could potentially increase the difference in vegetation community composition between these habitats. Restored wetlands, especially under a changing climate, are unlikely to reach reference condition state; therefore, an alternate approach to wetland restoration and management may be required. For example, restoration strategies could be modified to meet a specific purpose such as the provision of an ecological function and/or biological structure. With that said, natural wetlands should be protected from landscape fragmentation and land conversion activities given the important ecosystem functions, seed sources, and frame of reference they provide.

2.6   References

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3 Chapter 3. A Functional Approach to Evaluating Wetland Restoration Success

3.1 Introduction

Wetland habitats have experienced widespread global loss (Davidson 2014). The Prairie Pothole Region of North America, home to one of the world's largest wetlandscapes (landscapes with multiple wetlands) (Thorslund et al. 2017), has experienced extensive land use changes, resulting in significant wetland loss over the last century that varies regionally from 40-90% (Mushet 2016; Keddy et al. 2009; Tiner 1984; Anteau et al. 2016). With this loss comes an associated loss of wetland function and ecosystem services. Ecological restoration has become an increasingly common practice to recover lost habitat and ecosystem function associated with development activities, industrialization, and agricultural intensification (Dobson et al. 1997). As the importance wetland systems for landscape health is increasingly being recognized, wetland loss has slowed and restoration activities have increased (Davidson 2014). While to the best my knowledge there are no existing estimates of wetland area restored, Ducks Unlimited Canada (DUC) has more than 2000 projects covering 2.3 million acres in Alberta alone, representing DUC's largest concentration of habitat projects (DUC 2018). These restoration projects have the potential to provide essential wildlife habitat, support areas of groundwater recharge, act as nutrient and sediment sinks, as well as provide flood control, carbon sequestration, and other environmental and socio-economic benefits (Zedler and Kercher 2005). Wetland restoration is returning wetland number and area back to the prairies but restored wetlands are often of lower quality in terms of biodiversity (Hansen and Gibson 2014), ecosystem functioning (Moreno-Mateos et al. 2012), and sustainability and persistence through time when compared to natural wetlands (Zedler 2003).

The loss of wetland habitat decreases the biodiversity of a landscape. Wetlands provide aquatic habitat for plants, wildlife, invertebrates, and other organisms that would otherwise not be present within the surrounding upland. Worldwide loss of biological diversity, referring to genetic, species, population, or

ecosystem diversity, is an on-going global problem (Hooper et al 2012) and the [biodiversity × ecosystem function] relationship is a central issue in ecological and environmental sciences. Increasing evidence suggests biodiversity loss can decrease ecosystem functioning and services (Loreau et al. 2001; Cardinale et al. 2006; Isbell et al. 2011). Further, research suggests that biodiversity increases the stability of ecosystem functions through time (Cardinale et al. 2012) and provides resilience to communities in the face of disturbance (Carvalho 2013). Both ecosystem stability and resilience in the face of disturbance are key processes when considering recovery following restoration given the natural inherent variability (i.e., hydrologic) that defines prairie pothole wetlands.

Functional diversity is an important component of biodiversity and recent research shows it plays a role in ecosystem functioning (Song et al. 2014). Trait-based ecology and functional diversity, defined as the value, variation, and distribution of traits in a community assembly, provides a link between plant diversity and ecosystem function. The variation in plant traits and plant strategies across flora, taxa, and/or environmental conditions and the trade-offs to individuals associated with these strategies can affect ecosystem processes and services. Plant functional traits (PFTs) reflect the acquisition of resources for growth, reproduction, or survival at the species level, and the assumption of trait-based ecology is that these same processes scale up to the ecosystem functioning level (Lavorel &Garnier 2002). Increasingly, the link between individual plant functional traits and their effect on various ecosystem properties are being studied (Table 3.1) A further benefit to trait-based ecology is that it moves away from taxonomy towards a more generalizable approach focused on traits of organisms, such that comparisons and predictions can be made across scales of biological organization and geographic location (Shipley et al. 2016).

Understanding how biodiversity in wetlands recovers post-restoration is important for evaluating the effectiveness of wetland restoration. Structural attributes (i.e., species cover, species richness, floristic quality index (FQI)) of plant communities are typically used to assess the quality of wetland restoration (Matthews & Endress 2008). However, research shows that wetland structural

recovery fails to recover to pre-disturbance levels (Suding 2011; Moreno-Mateos et al. 2012). An alternate approach to evaluating restoration success is to consider functional composition and diversity. Functional diversity and species richness are often positively correlated (Song et al. 2014), but functional diversity considers the ecological role of the species found in a community based on plant functional traits. Functional diversity can be higher or lower than species diversity due to niche overlap between species and functional redundancies (Song et al. 2014). It is anticipated that high functional diversity can allow for more complete use of resources among species, thereby increasing ecosystem function (e.g., biomass production or nutrient retention) of a system (Loreau 2000; Díaz & Cabido 2001; Villéger et al. 2008; Mouchet et al. 2010).

In this study, I assessed ecosystem functional recovery by analysing the plant functional traits and functional diversity of vegetation within a chronosequence of restored wetlands. I hypothesized that functional recovery of restored wetlands is sensitive to draining and subsequent restoration, so plant functional traits and functional trait diversity will reflect a lower condition than natural wetlands. I predict that newly restored wetlands will be dominated by species that have more conservative nutrient strategies (i.e., low height, low specific leaf area, high leaf dry matter content, low leaf nitrogen content) when compared to older restored and natural wetlands, which will be dominated by plant communities with high nutrient acquisition and quick turnover strategies (i.e., tall, high specific leaf area, low leaf dry matter content, high leaf nitrogen content). With respect to functional trait diversity, I predict that functional diversity will be low in drained wetlands, and be consistently lower across the chronosequence of restored wetlands than when compared to natural wetlands.

Table 3.1. Common plant functional traits used to evaluate ecosystem process and function as established in the literature.

Plant Functional Trait	Link to ecosystem process	Relationship to ecosystem services provisioning	Source
Phenology	Carbon sequestration; Evapotranspiration; Heat exchange	Climate regulation, Water regulation	Diaz et al. 2006
Height	Heat exchange; Primary productivity; Carbon dynamics and storage	Climate regulation; Carbon sequestration	Butterfield & Suding 2013; Diaz et al. 2006
Lignin Content	Decomposition and mineralization; Nutrient mobilization; Herbivory control; Soil formation	Soil fertility and nutrient cycling; Biocontrol; Soil formation	Taylor et al. 1989
Relative Growth Rate	Carbon sequestration; Nutrient/ sediment retention; Oxygen regulation in water	Climate regulation; Water purification	Butterfield & Suding 2013
Leaf Nitrogen Content	Decomposition and mineralization; nutrient mobilization; Herbivory control	Soil fertility and nutrient cycling; Biocontrol	Hodgson et al. 2011
Specific Leaf Area	Decomposition and mineralization; Nutrient mobilization; Herbivory control; Sediment retention	Soil fertility and nutrient cycling; Biocontrol; Water purification; Fodder provisioning	Hodgson et al. 2011, Diaz et al 2004
Leaf Area	Decomposition and mineralization; Nutrient mobilization; Evapotranspiration; Sediment retention	Soil fertility and nutrient cycling; Water regulation; Fodder provisioning	Diaz et al 2004
Density/Depth/Size of Rooting System	Erosion prevention; Decomposition and mineralization; Nutrient mobilization; Evapotranspiration; Soil formation	Soil stability; Natural hazard prevent; Soil fertility and nutrient cycling; Water regulation; Soil formation	Butterfield & Suding 2013; Diaz et al. 2006
Leaf Dry Matter Content	Decomposition/mineralization; Primary productivity; Carbon dynamics and storage; Nutrient mobilization; Sediment retention	Carbon sequestration; Soil fertility and nutrient cycling; Biocontrol; Water purification; Fodder provision	Diaz et al. 2004; Funk et al. 2008; Messier et al. 2016

3.2 Methods

3.2.1 Study area and sample sites

This research was conducted within the Prairie Pothole Region (PPR). The PPR is named for the characteristic landscape of pothole wetlands, which historically covered ~20% of the landscape. These shallow depressional wetlands are a remnant from the retreat of the Wisconsinan glaciation, which left behind low permeability glacial till. Wetlands that make up this study are found within the Central Parkland and the Dry Mixedwood Natural Subregions, where temperatures, precipitation, and growing season conditions are intermediate between the dry, warm grasslands located to the south, and cooler, wetter boreal forest conditions to the north (Natural Regions Committee 2006). The study area receives an average annual precipitation of 426 mm based on daily climate values from 1987 – 2016 (McKenney et al. 2011). Precipitation is greatest in July, averaging 94 mm, and lowest in February averaging 12 mm, and most precipitation falls from June to August. The average annual temperature is approximately 3°C, with extreme temperatures ranging from -43 °C to +34 °C. The annual water balance is typically negative, where potential evapotranspiration exceeds precipitation in most years. In 2017, mean annual temperature and cumulative precipitation for the water year (Oct 2016 through Sept 2017) was 3.5 °C and 455 mm, respectively.

Study wetlands include most wetlands assessed as part of Chapter 2, however additional sites were included for functional trait analysis (Table B1). All wetlands were selected from a database of restored wetlands provided by Ducks Unlimited Canada (DUC) and the Canadian Wetland Inventory (Ducks Unlimited Canada 2016). Wetlands were restored by DUC by constructing an earthen berm across drainage ditches that previously drained each wetland. Twenty-eight restored wetlands were selected that ranged in age from newly restored to 24 years since restoration. In addition to restored wetlands, the experimental design included five drained wetlands to represent pre-restoration conditions, and four natural wetlands, representative of undisturbed, natural reference conditions. The drained and natural wetlands were located proximal to restored wetlands, within a

similar agricultural (cropping and pasture) landscape, and were expected to have been subjected to the same influences and environmental conditions as restored wetlands. Combined, all wetlands form a chronosequence of wetland restoration, defined as a series of spatially distinct sites that vary in age, to represent a temporal sequence of wetland recovery following restoration. Chronosequences are often used to study trajectories of succession and rely on the assumption that all sites are influenced by the same abiotic and/or biotic conditions (Foster & Tilman 2000).

Wetlands sampled as part of this research project were limited to temporary, seasonal, and semi-permanent marsh wetlands. Marsh wetlands, typical of the prairie landscape, have mineral soil, naturally fluctuating water levels, and receive water inputs from groundwater, surface flows, and/or precipitation. Marsh wetlands are classified into permanence classes (e.g., temporary, seasonal, and semi-permanent) based on hydroperiod and vegetation occupying the deepest or central part of a wetland. Marsh wetland vegetation naturally separates into a zonation pattern, where concentric rings of vegetation adapted to varying levels of soil moisture exist around a central, deepest point (Stewart & Kantrud 1971). Given the natural variability of wetland systems, it can be difficult to distinguish among these wetland classes. Seasonal wetlands, in particular, depending on yearly precipitation can be easily mistaken for temporary or semi-permanent in dry and wet years, respectively. Wetland class was included in regression models to understand if effect of restoration age varied by class, and it was determined that wetland class was not a significant factor in the community weighted mean (CWM) models, and as such, all wetlands were combined for subsequent analysis.

3.2.2 Wetland sampling and vegetation dominance

Wetlands were visited twice during the summer of 2017. The first visit focused on inventorying and assessing community composition, occurred between June 21 and Aug 11, and followed the sampling procedures outlined in Chapter 2. This time period was chosen to capture peak standing biomass as the majority of species were sufficiently mature and flowering, which helped facilitate

the identification and differentiation of species. Vegetation was systematically sampled within quadrats located along transects. Four evenly spaced transects (situated at 90° from each other) were established within each wetland from the centre of the wetland to the upland. Two quadrats per vegetation zone, per transect were randomly selected and assessed. Given that wetlands support different vegetation zones dependent on their classification, quadrat sampling varied from 8 (wetlands with only a wet meadow zone) to 32 (large semi-permanent wetlands with three vegetation zones). All vegetation within a quadrat was identified to the species level and a percent cover class was assigned to each species (i.e., <1%, 1-5%, 6-10%, 11-25%, 26-33%, 34-50%, 51-75%, >75% cover as per Mueller-Dombois & Ellenberg 1974). Cover classes were used in an effort to minimize observer bias and increase repeatability across years (Little 2013). For analysis, each species was assigned a value equal to the median of the cover class determined in the field. Species data collected at the quadrat level were combined and averaged across the wetland resulting in an average cover per species per wetland. These data were used to determine the dominant species in each wetland, which informed the second field visit. The second field visit occurred between Aug 15 and Aug 31 and was focused on measuring and collecting plant functional traits of the dominant species. Dominant species were defined as all vascular plant species that together make up at least 70% cover. The mass ratio hypothesis, supported by theory and empirical evidence (Diaz et al. 2007a; Bílá et al. 2014), suggests that the dominant species in a community exert the most influence on ecological function of a system (Grime 1998). While Grime developed the theory in reference to plant productivity, the theory can be (and has been) expanded to state that ecosystem functioning is mainly determined by the trait values of the dominant contributors to plant biomass (i.e., the dominant species) (Diaz et al. 2007a)

3.2.3 Sample handling and processing

Plant functional traits (PFTs) of the dominant species were sampled following standardized protocols outlined in (Perez-Harguindeguy et al. 2013) in late August to ensure species were at or near maximum growth. These protocols

were compiled by a group of researchers to provide step-by-step methods and procedures for sampling many different traits to ensure consistency in information collected by researchers (Perez-Harguindeguy et al. 2013). PFTs selected for this study included: maximum plant height, leaf area (LA), specific leaf area (SLA), leaf dry matter content (LDMC), and leaf nitrogen content (LNC). These traits are among the most commonly assessed in the literature, are fundamentally important to the success and survival of a species, are representative of morphological, physiological and biochemical traits, and provide a good spread of associated ecosystem functions (Perez-Harguindeguy et al. 2013; Weiher et al. 1999; Diaz et al. 2007b; Lavorel and Garnier 2002). Height is an important determinant of competitive ability for light and is an important component for heat exchange (Perez-Harguindeguy 2013; Diaz et al 2016). Leaf area is implicated in leaf energy and water balance (Cornelissen et al. 2003), and relates to environmental stress (Ackerly & Reich 1999). SLA, defined as leaf area over dry weight, captures the trade-offs between growth rate, stress tolerance, and resource acquisition (Garnier et al. 2004; Wright 2004). Species with high SLA values are faster growing, less stress tolerant, and less competitive in nutrient and resource poor environments (Reich et al. 2003). LDMC, defined as leaf dry weight over leaf wet weight, provides an indication of leaf tissue density, which relates to nutrient and water retention in a plant (Ryser & Urbas 2000), as well as resistance to physical stress (Perez-Harguindeguy et al. 2013). Finally, LNC provides information on photosynthetic assimilation and nutrient content, since leaf nitrogen is integral in the mechanisms of photosynthesis (Westoby et al. 2002).

Plant height was determined as the distance from the base of the stem to the tallest point of the main photosynthetic organ (excluding inflorescence) of a species. Ten, fully-grown, healthy, shade-free individuals of each dominant species were randomly selected from within each wetland and measured for height in situ. To get adequate representation, an additional ten individuals per dominant species per wetland were collected for further processing of LA, SLA, LDMC, and LNC. Once collected, whole fresh plant samples were rolled in damp

paper towel, sealed in Ziploc® plastic bags, and kept at 4° C until later processing. This method aims to minimize transpirational water loss from sampled plants and leaves, which may influence leaf area and weight of measured leaves (Garnier et al. 2001). All samples were processed within three weeks of sampling. In total, traits of 2006 individuals were measured.

LA was measured using a LI-3100C area meter (LI-COR, Lincoln, NE, USA). When possible, fresh leaves were passed directly through the leaf area meter. When equipment was unavailable (for approximately half the samples due to equipment access constraints while in the field), leaves were traced on paper, cut out, and then passed through the leaf area meter once equipment became available. A correction factor was applied to the traced LA values after observing that traced LA values were larger than the same fresh LA measured. Correction factors were derived by dividing LA (traced leaves) by LA (fresh leaves) of all individuals sampled. Corrections factors were standardized to a species when available (i.e., both traced LA and fresh LA were measured), but when both traced and fresh LA values were not available for a species (approximately 11 of 41 species), instead, the correction factor used was standardized to thin (i.e., grasses and thin leaved forbs) or large leaved species. Next, individual leaves were dried at 60° C for 48 - 72 hours until dry weight was constant. Of the ten individuals per dominant species dried, three were randomly selected for further processing for leaf nitrogen content. Dried samples were ground into a fine powder using a Wiley mill grinder (Wiley® Mini-Mill, Thomas Scientific, Swedesboro, NJ, USA) followed by ball and mill grinding using a Spex CertiPrep 2000 Geno/Grinder (SPEX CertiPrep, Metuchen, NJ, USA). Dried leaf samples were processed for total nitrogen using the dry combustion method (AOAC International 2000), where a Thermal Conductivity Detector (Costech International Strumatzione, Florence, Italy) quantitatively detected combusted nitrogen elements.

3.2.4 Statistical Analyses

To explore general patterns in the functional recovery of wetlands following restoration, study sites were grouped into seven restoration age classes. Classes

included newly restored sites (Age 1 to 5, n=7), young sites (Age 6 to 10, n=7), moderately aged sites (Age 11 to 15, n=6), moderately old sites (Age 16 to 20, n=2), and old restorations (Age 20 to 25, n=6). Drained (n=5) and natural wetlands (n=4) comprised their own classes. These classes were used to draw ecological distinctions between the successional stages of vegetation development in wetlands (Noon 1996). They assume a similar recovery within an age class and are reflective of age class groupings typical of wetland chronosequence analyses (e.g., DeBerry & Perry 2012; Brown & Norris 2018; Yu et al. 2017).

Functional trait data from ten individuals of each dominant species per wetland were averaged to get an average trait value per species per wetland. First, trait data were analyzed within species by one-way analysis of variance (ANOVA) to assess intraspecific trait variation across the chronosequence for each PFT. Next, species trait values were combined to characterize the wetland community by obtaining a community-weighted mean (CWM). CWMs were calculated per trait by wetland as the sum of mean trait values weighted by relative abundance of each dominant species. Differences in CWMs of traits across age classes were assessed by one-way ANOVA. Homoscedasticity was assessed with Bartlett's test, and normality was determined by Shapiro-Wilk normality test. When variances were not homogeneous or did not approximate a normal distribution, data were transformed (as in LA for *C. rostrata*, height in *T. latifolia*, LDMC in *C. rostrata* and *T. latifolia*, SLA in *P. palustris*, *C. atherodes*, *T. latifolia*, all species for LNC, and CWM Height). After an evaluation of Cooks distance and careful consideration, one outlier (D2) was removed from CWM SLA dataset to ensure homoscedasticity and a normal distribution of variances.

In order to quantify the relationship between community trait values and restoration age, simple linear regressions were conducted by dummy coding wetland age classes. Non-linear regressions were considered for analysis, but did not improve the model fit. Statistical analysis (ANOVA and regressions) on individual species and CWMs were conducted in R using the 'car', 'multcomp',

and 'faraway' packages (R Core Team 2018). Statistical significance was determined when $p < 0.05$.

Functional diversity of each wetland was assessed using multiple functional diversity indices. These indices capture different aspects of functional diversity and are multi-trait metrics, where some indices are weighted by species abundance (Table 3.2). The software package, FDiversity (Casanoves et al. 2010) was used to determine functional diversity, which allows the calculation of a comprehensive list of functional diversity indices and statistical analysis tools (Casanoves et al. 2010). FDiversity runs on an R platform, and requires packages 'proxy', 'mvtnorm', 'geometry', 'vegan', 'FD', 'ade4', 'ape', 'gee', 'lattice', 'nlme', and 'rscproxy' for analysis of functional diversity indices.

Table 3.2. Metrics used to assess functional diversity in a chronosequence of restored wetlands. Analyses were performed using the FDiversity software (Casanoves et al. 2010).

Functional Diversity metric	Code	Abundance Weighted?	Description	Source
Functional Attribute Diversity	FAD	No	Number of different combinations of trait values that occur in a community.	Walker, Kinzig, & Langridge 1999
Community-based functional diversity	FDc	No	Constructs a dendrogram of the species that make up a regional community of species, functional diversity is the sum of all branches in the dendrogram that correspond to the subset of species that make up a wetland.	Petchey & Gaston 2002; Petchey & Gaston 2006; Petchey & Gaston 2007
Plot-based functional diversity	FDp	No	Constructs a dendrogram of species at the plot scale (wetland), sums the branches, and compares among wetland	Petchey & Gaston 2002; Podani & Schmera 2006
Convex hull hypervolume	Chull	No	Using the volume of the 'convex hull' defined by the relative position of species in the trait space to summarize the dispersion of species in the space.	Cornwell, Schwilk, & Ackerly 2006
Rao's quadratic entropy	Rao	Yes	Sum of all species distances based on a dissimilarity matrix, weighted by the product of the species relative abundances	Rao 1982; Pavoine, Ollier, & Pontier 2005
Weighted FDc	wFDc	Yes	Calculated based on the community scale dendrogram approach, but incorporates relative abundance of each species in the calculation	Pla et al. 2008
Weighted FDp	wFDp	Yes	Calculated based on the plot scale dendrogram approach, but incorporates relative abundance of each species.	Pla et al. 2008
Functional Richness	FRic	No	Represents the trait space filled by the community	Villeger, Mason, & Mouillot 2008
Functional Evenness	FEve	Yes	Measures the regularity of spacing between species in trait space and evenness of the distribution of relative abundances	Villeger, Mason, & Mouillot 2008
Functional Divergence	FDiv	Yes	Quantifies how trait values are spread along a range of trait space, sum of the Euclidean distance of each species to a central point.	Villeger, Mason, & Mouillot 2008
Functional Dispersion	FDis	Yes	Average distance of individual species to a weighted centroid of all species in the community trait space, which takes into account species relative abundances	Laliberte & Legendre 2010

3.3 Results

3.3.1 Trait response by species

In total, 41 dominant species were observed across the chronosequence; an average of 5.4 species dominated a wetland. Wetlands in this study had one to ten dominant species.

While traits of all species were assessed, only results from four species (*Poa palustris, Carex atherodes, Carex rostrata, and Typha latifolia)* are included for inter and intra-specific comparisons (Figure 3.1). These species are characteristic of natural wetlands in the area, were considered dominant species in enough wetlands to be represented in most of the age classes that make up the chronosequence and exhibited trends in trait response across the chronosequence. *Poa palustris* was the only species that dominated wetlands in each age class and is therefore the only species whose traits could be tracked across the whole chronosequence. *Carex atherodes* and *C. rostrata* were dominant in at least one wetland within each age class, with the exception of drained wetlands. *Typha latifolia* was a dominant species in at least one wetland in classes: Age 1-5, 6-10, 11-15, 16-20, and natural wetlands. Tables A1 and A2 provide an overview of all dominant species observed within the wetlands.

For *P. palustris*, significant differences were observed across the chronosequence in leaf area ($F_{(6,153)}$ = 5.5022, p< 0.001), height ($F_{(6,153)}$ = 21.743, p< 0.001), specific leaf area ($F_{(6,151)}$ = 6.9618, p< 0.001), and leaf nitrogen content ($F_{(6,38)}$ = 7.3825, p< 0.001) (Figure 3.1A). No differences were observed in LDMC across the chronosequence. Height was the only trait that showed a positive linear trend with increasing time since restoration. Height of *P. palustris* in drained wetlands was significantly lower (29 cm +/- 4.66 SE) than Age 1-5 (62.89 cm +/- 2.69), Age 6-10 (64.98 cm +/- 2.69), Age 11-15 (62.09 cm +/- 2.33), Age 16-20 (67.30 cm +/- 4.66), Age >20 (79.77 cm +/- 2.69), and natural wetlands (94.65 cm +/ 4.65). LA, SLA, and LNC had variable trends across the chronosequence. For LA and SLA, generally, low values were observed in drained wetlands (45.00 +/- 12.38 cm^2 and 10.56 +/- 1.21 cm^2/mg for LA and SLA respectively), followed by high values and high variability observed in newly

restored and young wetlands (104.03 +/- 7.15 cm^2 and 14.76 +/- 1.12 cm^2/mg for LA and SLA in wetlands Age 1-5 respectively, and 90.83 +/- 7.15 cm^2 and 29.47 +/- 1.12 cm^2/mg for and SLA in wetlands Age 6-10 respectively). LA and SLA values tended to stabilize or increase as time since restoration increased (77.21 +/- 7.15 cm^2 and 15.31 +/- 1.12 cm^2/mg, respectively, for Age >20). Mean LA of natural wetlands was low (65.5 +/- 12.38 cm^2) compared to most restoration age classes but was highly variable (ranged from 23 to 153 cm^2). In contrast, SLA of *P. palustris* was significantly higher in natural wetlands than in most of the other restoration age classes. When considering leaf nitrogen content, values were highest (1.53 +/- 0.04 %) and significantly different in Age 6-10 wetlands compared to the other age classes. Otherwise, all other age classes averaged approximately 1.2 % (range from 1.04 % in Age 16-20 to 1.38 % in natural wetlands).

Trait responses of the other species were variable (Figure 3.1 B. – D.). Generally, species were tallest in natural wetlands when compared across the chronosequence. *C. atherodes* and *T. latifolia* were significantly taller in natural wetlands than many of the restoration age classes. Height of *C. rostrata* showed minimal differences across the chronosequence (ranged from an average of 105.93 cm in Age 11-15 to 121.18 cm in Age 1-5 wetlands). Minimal differences or no differences were observed across the chronosequence for SLA, LDMC, or LNC of *C. atherodes* (Figure 3.1B)*, C. rostrata* (Figure 3.1C), and *T. latifolia* (Figure 3.1D).
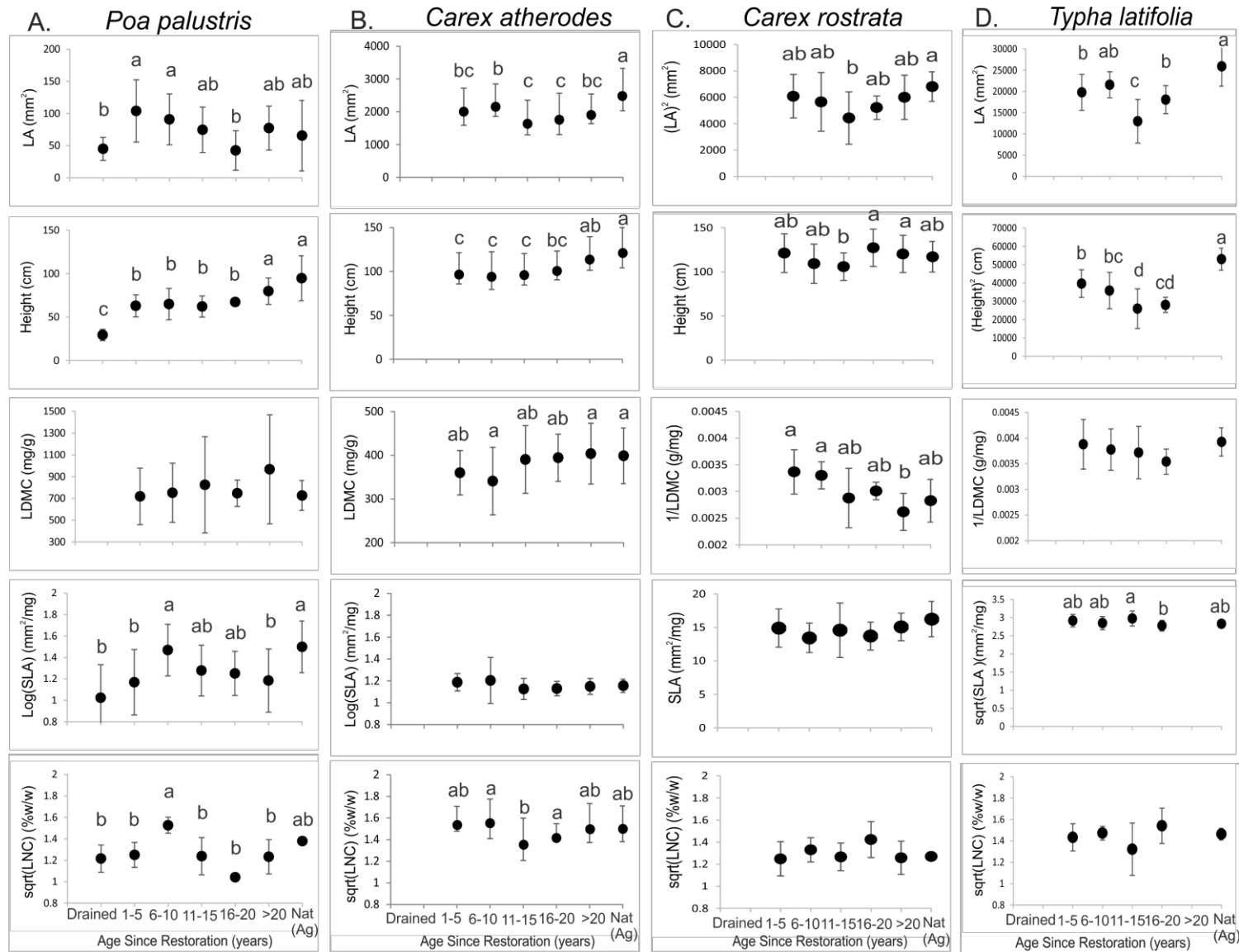
Figure 3.1. Mean (+/- SE) plant functional trait values as a function of time since restoration. Figure allows for comparison of trait values within a species (viewed vertically), within a trait (viewed horizontally), and response by trait within a species (viewed individually). The species selected represent the most common dominant species present within the chronosequence. A) *Poa palustris*, B) *Carex atherodes*, C) *Carex rostrata*, D) *Typha latifolia*. Letters distinguish significant differences

3.3.2 Community level trait response

When considering Community Weighted Means, the response of PFTs were variable (Figure 3.2). CWM leaf area (CWM LA) was low in drained wetlands (1057 +/- 660 cm^2), was significantly higher (albeit with high variability) in newly restored wetlands (Age 1-5: 4822 +/- 558 cm^2), and was followed by a drop in leaf area size, which stayed consistently low across the older age classes of the chronosequence (2991 +/- 558 cm^2, 2051 +/- 660 cm^2, 3139 +/- 603 cm^2, and 2589 +/- 603 cm^2 for Age 6-10, Age 11-15, Age 16-20, and Age >20, respectively). CWM LA in natural wetlands was highest but was highly variable (5035 +/- 738 cm^2). Significant differences in CWM LA were observed between drained and natural wetlands as well as newly restored wetlands (Age 1-5) and Age 11-15 wetlands only (Figure 3.2A).

A similar trend was observed with CWM Height. Height in drained wetlands (62.9 +/-38.6 cm) was significantly lower than newly restored wetlands (Age 1-5: 107.7 +/- 35.5 cm). Height in the subsequent age classes was low (Age 6-10: 96.4 +/- 35.5 cm, Age 11-15: 93.9 +/- 38.6 cm, and Age 16-20: 105 +/- 48.6 cm), prior to increasing in Age >20 (114.6 +/- 36.9 cm) and natural wetlands (122.3 +/- 40.8 cm) (Figure 3.2E).

CWM of leaf nitrogen content (CWM LNC) was highest (2.83 +/- 0.24 %), but highly variable (ranged from 1.67 to 4.53%) in drained wetlands, when compared to newly restored (1.89 +/- 0.2 %), Age 6-10 (2.03 +/- 0.2 %), Age 11-15 (1.56 +/- 0.24 %), Age 16-20 (1.86 +/- 0.38 %), Age >20 (2.08 +/- 0.22 %), and natural wetlands (2.06 +/- 0.27 %). Significant differences were only observed between drained wetlands and Age 11-15 wetlands (Figure 3.2B).

No significant differences were observed across the chronosequence for CWM of SLA, and CWM LDMC. However, drained wetlands were observed to have higher SLA and lower LDMC than the rest of the chronosequence (Figure 3.2D an Figure 3.2C, respectively).

By further qualifying the relationships of CWMs across the chronosequence using linear regressions, significant positive linear relationships were observed in CWM LA ($F_{(6,29)}$ = 4.87, R2 = 0.50 p< 0.01) and CWM Height ($F_{(6,29)}$ = 6.774, R2

= 0.58, p< 0.001). No linear relationships were observed when examining CWM SLA ($F_{(6,28)}$ = 1.364, R2 = 0.23 p= 0.2635), CWM LDMC ($F_{(6,29)}$ = 1.258, R2 = 0.21, p= 0.3069), and CWM LNC ($F_{(6,28)}$ = 1.792, R2 = 0.28, p= 0.1371) (data not shown).
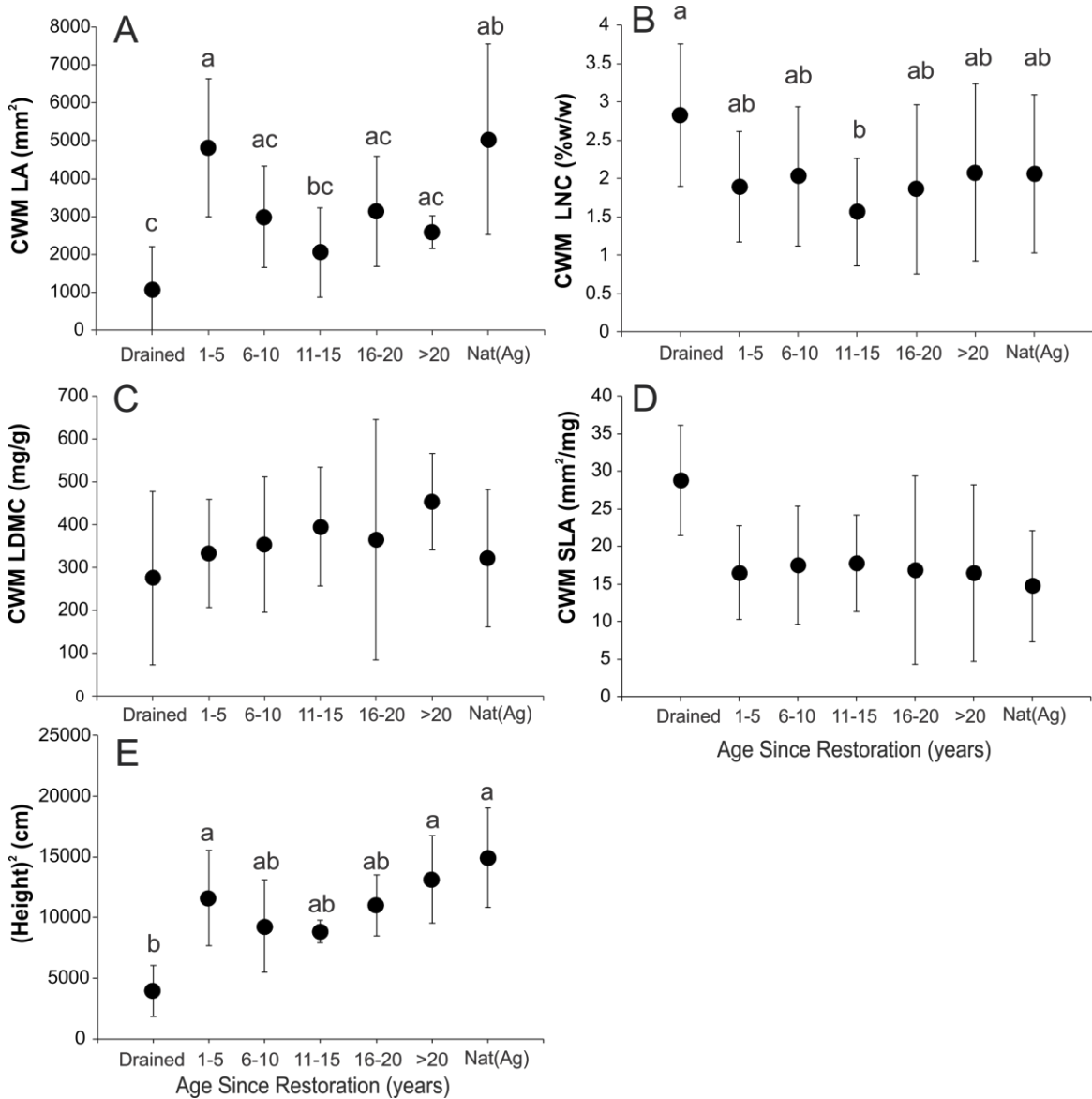
Figure 3.2. Community weighted mean (CWM) trait values (+ SE) in restored wetlands as a function of time since restoration. A) CWM leaf area, B) CWM leaf nitrogen content, C) CWM leaf dry matter content, D) CWM specific leaf area, and E) CWM height. Different letters represent significant differences in trait values across age classes

3.3.3 Functional diversity

No significant differences were observed across the chronosequence in any functional diversity (FD) metric assessed. However, when focusing on four metrics (FRichness, FEvenness, FDivergence, and FDispersion), these indices identify important potential trends across the chronosequence, and provide a multi-dimensional look at functional diversity (Figure 3.3). FRichness appears to be highest in drained, newly restored (Age 1-5), and natural wetlands. FDispersion follows a similar trend and is highest in newly restored (Age 1-5), but is also high in drained, natural, and Age 11-15 wetlands. FEveness and FDivergence were consistent across the chronosequence. Table 3.3 provides an overview of scores for all FD metrics assessed.
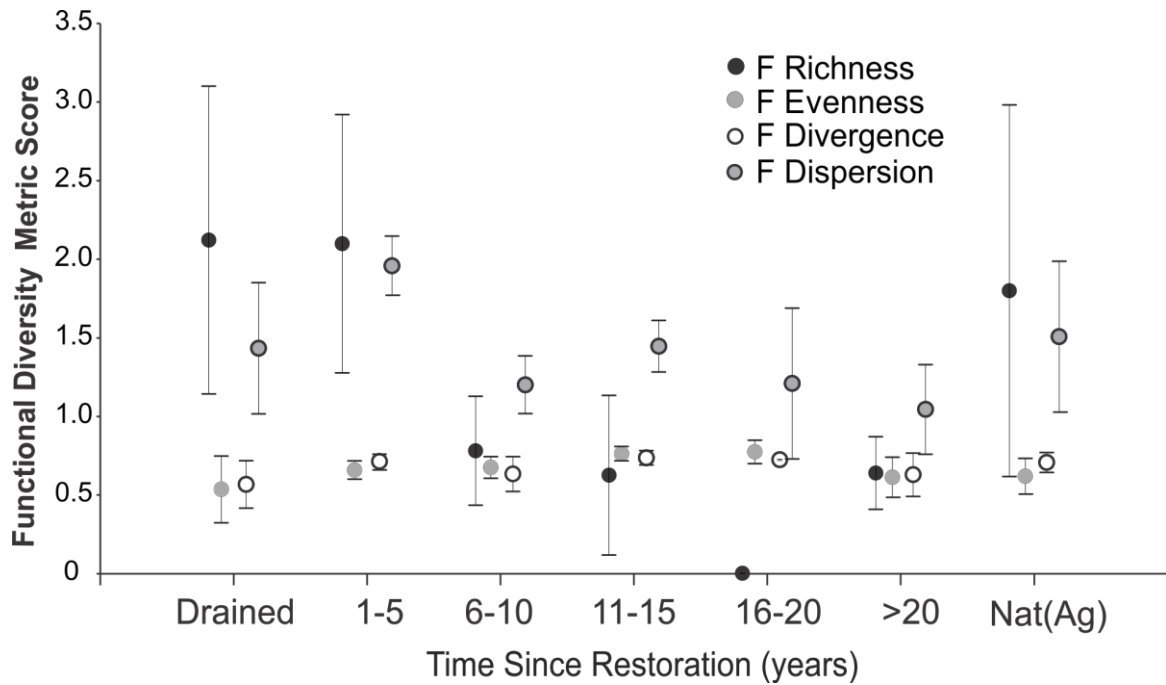
Figure 3.3. Functional diversity as presented by four different Functional Diversity metrics (+ SE) as a function of time since restoration. No significant differences were observed across the age classes for any of the FD metrics, however each metric provides insight into different properties of an ecosystem, and by comparing among metrics, patterns can be observed that may identify nuanced differences across the chronosequence.

Table 3.3. Functional diversity (FD) metric values (raw) by wetland. See Table 3.2 for a description of each metric. No significant differences were observed across age classes for any FD metrics. Blank values reflect an insufficient number of dominant species to calculate an FD, and zero values represent low functional diversity.

Age Class	Wetland	FAD2	FDp	FDc	wFDp	wFDc	rRao	CHull	FRic	FEve	FDiv	FDis
Drained	D1	-	-	-	-	-	-	-	-	-	0.84	-
Drained	D2	5.12	10.24	12.81	10.23	12.79	1.00		5.12		0.78	2.55
Drained	D3	48.00	16.40	15.16	14.62	13.60	0.58	0.08	0.08	0.71	0.69	1.78
Drained	D4	3.35	6.70	6.91	6.52	6.72	0.95		3.35		0.53	1.59
Drained	D5	6.82	6.82	8.97	6.60	8.51	0.86		2.06	0.90	0.00	1.25
Age 1-5	R1a	30.24	14.11	14.40	9.49	9.62	0.31		0.28	0.66	0.52	1.15
Age 1-5	R1b	24.68	11.58	14.40	10.32	12.90	0.65		0.17	0.73	0.70	1.40
Age 1-5	R3	12.97	12.97	11.60	12.98	11.63	0.73		4.45	0.82	0.73	2.45
Age 1-5	R4a	23.95	15.43	15.54	13.45	13.12	0.74		3.08	0.53	0.70	2.25
Age 1-5	R4b	12.47	12.47	12.09	10.38	9.73	0.64		5.28	0.39	0.90	1.92
Age 1-5	R5a	128.50	27.43	24.46	24.52	22.17	0.53	1.38	1.38	0.76	0.78	2.24
Age 1-5	R5b	98.49	24.56	26.48	24.66	26.67	0.45	0.05	0.05	0.72	0.67	2.30
Age 6-10	R6	1.43	2.86	2.53	2.84	2.52	0.98		1.43		0.00	0.70
Age 6-10	R7	27.60	13.14	13.93	12.53	13.48	0.65		0.21	0.72	0.67	1.69
Age 6-10	R8a	32.26	11.83	11.44	11.97	11.48	0.69	0.01	0.01	0.78	0.70	1.49
Age 6-10	R8b	100.50	22.20	22.22	18.50	18.72	0.37	0.96	0.96	0.67	0.67	1.58
Age 6-10	R9	2.48	4.97	4.06	4.95	4.05	0.99		2.48		0.92	1.23
Age 6-10	R10a	27.79	10.27	13.60	10.60	13.56	0.76	0.00	0.00	0.84	0.78	1.34
Age 6-10	R10b	3.09	3.09	6.15	2.27	4.51	0.51		0.38	0.37	0.70	0.38
Age 11-15	R11	21.71	14.08	14.15	13.41	13.74	0.71		3.16	0.93	0.72	2.18
Age 11-15	R12a	16.08	7.83	10.59	7.36	9.38	0.67		0.06	0.85	0.84	1.09
Age 11-15	R12b	24.11	11.37	10.12	9.91	8.46	0.54		0.12	0.76	0.86	1.46
Age 11-15	R15a	79.15	17.33	19.67	15.45	17.36	0.41	0.16	0.16	0.66	0.64	1.25
Age 11-15	R15b	64.30	16.06	18.72	15.70	17.79	0.46	0.03	0.03	0.68	0.66	1.55
Age 11-15	R15c	92.31	16.81	19.47	14.93	16.94	0.53	0.23	0.23	0.70	0.70	1.15
Age 16-20	R17a	21.02	7.59	10.10	6.07	8.46	0.54	0.00	0.00	0.70	0.73	0.73
Age 16-20	R17b	39.08	14.33	17.99	14.07	17.43	0.57	0.00	0.00	0.85	0.72	1.69
Age >20	R22	5.39	5.39	5.52	4.29	4.33	0.70		1.26	0.60	0.95	0.78
Age >20	R23a	28.88	9.24	12.57	8.54	11.09	0.72	0.00	0.00	0.87	0.84	1.34
Age >20	R23b	102.09	18.83	18.55	16.23	16.71	0.54	0.47	0.47	0.77	0.79	1.39
Age >20	R23c	113.32	30.30	31.77	24.38	25.50	0.31	1.18	1.18	0.67	0.59	2.03
Age >20	R24a	-	-	-	-	-	-	-	-	-	-	-
Age >20	R24b	5.39	5.39	5.65	4.57	5.03	0.51		0.93	0.77	0.61	0.73
NatAg	N1	1.35	2.69	3.18	2.67	3.15	0.99		1.35		0.61	0.66
NatAg	N2	14.18	14.18	12.72	14.10	12.44	0.77		5.25	0.88	0.84	2.88
NatAg	N3	33.75	12.32	13.25	10.83	11.94	0.62	0.01	0.01	0.53	0.79	1.36
NatAg	N4	35.80	17.20	15.69	10.64	10.87	0.22		0.59	0.45	0.59	1.13

3.4   Discussion

This study was conducted to evaluate wetland functional recovery following restoration. It has long been assumed that, given enough time, the recovery of wetlands progresses reliably through time following restoration and eventually converges towards a stable climax community, which resembles a natural wetland (Matthews & Spyreas 2010). However, research has shown that structural metrics of vegetation (e.g., species richness, plant cover, diversity) and ecosystem functional processes (e.g., plant productivity or biomass) may not recover to reference/natural site conditions (Aronson & Galatowitsch 2008). Instead, vegetation communities tend to converge towards a more degraded state as a result of invasion by exotics or diverge over time towards a plant community composition that differs from the reference state (Matthews & Spyreas 2010). While monitoring and evaluating vegetation species recovery is useful for understanding succession and managing resources, ultimately, the return to function of wetland ecosystem processes is an important goal to ensure provisioning of ecosystem services and multi-functional landscapes. Understanding how wetlands return function to the landscape following restoration can help plan for and manage against mono-functional landscapes.

When considering the composition of dominant species for functional trait assessment, only one species, *Poa palustris*, was present in all age classes of the chronosequence. Further, of the three additional species for which comprehensive trait analysis were conducted, none were dominant in drained wetlands resulting in a lack of trait values for this 'age' class. These results suggest a marked change in species composition between drained wetlands and the restoration chronosequence, likely resulting from agricultural activity within drained wetlands (i.e., drained wetlands were cultivated and cropped through at the time of assessment). While no formal community composition analysis was conducted given that trait assessment was limited to dominant species in a community, it is important to keep in mind that species ultimately underpin trait values.

An analysis of trait values of the common dominant species found across the restoration chronosequence suggests high intra- and interspecific variation. Generally, all species had high variability across the chronosequence as evidenced by high standard error surrounding mean trait values. In particular, *P. palustris*, which had a mean leaf area of 79 mm^2 (ranged from 8 mm^2 to 193 mm^2) and mean height of 66 cm (ranged from 18 cm to 162 cm), which reflects the small size and plasticity of the species. Further, traits of each species responded differently across the chronosequence. Generally, height of a species increased as restoration age increased and was tallest in natural wetlands. Similarly, leaf area of a species was largest in natural wetlands when compared to restored wetlands. SLA and LDMC had variable responses across the chronosequence, but generally, no differences between trait means by species were observed. Finally, leaf nitrogen content in *P. palustris* and *C. atherodes* was highest and lowest in wetlands Age 6-10 and Age 11-15, respectively, but otherwise no differences were observed across the chronosequence.

While all attempts were made to select representative individuals in a wetland (i.e., mature, unshaded, and healthy individuals), trait values may vary depending on environmental gradients, microclimatic factors, and genetic adaptations (Shipley et al. 2016). The contribution of intraspecific variation in functional trait analysis is poorly understood, especially since most studies use a single, fixed trait value (often acquired from plant trait databases like TRY Plant Trait Database (Kattge et al. 2011) or LEDA-traitbase (Kleyer et al. 2008; Siefert et al. 2014). The common thought is that interspecific variation in traits is much greater than intraspecific variation in traits and that any intraspecific differences would not obscure broader trends observed when comparing among species (Grime 1979; Shipley et al. 2016). This assumption has some empirical support in certain [trait × environment] relationships (Meziane & Shipley 1999 a and b; Garnier et al. 2001) and as such, intraspecific variation was not used for further analysis in this study as the goal was to compare functional traits across communities. However, intraspecific variation could be an important factor to consider in future studies if the intent is to identify trait predictors of performance

(for restoration projects or other habitats) as in Pywell et al. (2003). Further, variation within a trait could be considered a plant functional trait in and of itself, especially in this era of rapid global change (Violle et al. 2012; Shipley 2016).

While species-specific trait responses have previously been used to select high performing species and predict restoration success (Pywell et al. 2003; Martinez-Garza et al. 2013), often the composition of a community is assessed to determine ecosystem functionality. An accumulation of evidence suggests that changes in trait composition of communities are a determinant of change in ecosystem process (Larsen et al. 2005; Barnes et al. 2014; de Bello et al. 2010). My results show that there are changes in CWM LA, CWM Height, and CWM LNC, but no changes in CWM SLA, or CWM LDMC over the wetland chronosequence. CWM Height showed the most obvious linear trajectory of recovery following restoration. A significant positive correlation has been shown between CWM Height and primary productivity (Li et al. 2016). Further, height has been shown to have significant effects on the nitrogen use efficiency of a community (Zuo et al. 2016).

Leaf area on the other hand, had a more variable recovery where values were low in drained wetlands, increased significantly in newly restored wetlands, which was followed by a drop and then stabilization at mid-range CWM LA values in older restoration age classes. In comparison, natural wetlands had high CWM LA values. This trend, where values peak in newly restored wetlands before decreasing in moderate to moderately old restorations, was not only observed in the response of CWM Height to restoration age, but also in many species-specific traits (e.g., SLA of *P. palustris* and *C. atherodes*, as well as LA of *P. palustris*, and *T. latifolia*). While this pattern could be explained by the length of the chronosequence, (e.g., perhaps 24 years is too short a time frame for recovery of leaf area), this 'overshoot' pattern has frequently been observed in the recovery of species diversity and richness in restored freshwater systems (Meyer et al. 2010) and is likely due to an initial colonization of annuals and perennials. Once colonial perennials establish and expand in restoration systems, species richness tends to decline (Baldwin 2004). This same idea likely explains the patterns

observed in plant functional traits, whereby the initial colonization of species results in a wide range of functional trait values (i.e., height and LA) after which the trait values decline and settle to a lower value and/or become representative of natural systems.

Functional trait diversity metrics are increasingly being used as an approach to community ecology, including to understand how functional trait diversity relates to abiotic limitations, to understand species interactions, and more recently to predict community diversity in the face of environmental change (Laughlin 2014). Generally, functional diversity relates to diversity of traits in a community but serves to represent the diversity of species niches or functions (Cadotte et al. 2011). No significant differences were observed among age classes when functional diversity across a chronosequence of restored wetlands was assessed. The FD metrics assessed considered dendrogram distances, metrics weighted and not weighted by species abundance, dissimilarity matrices, as well as total space, evenness, and spread of trait values in a wetland. Each functional diversity metric describes different aspects of functional diversity, but when combined, can provide complementary information to better understand functional composition and response (Mouchet et al. 2010).

Though not significantly different, functional diversity can change across the chronosequence. For example, Functional Richness (FRichness) refers to volume of functional space occupied by a community. High FRichness indicates high resource utilization since a large functional space is occupied (Villéger et al. 2008). FRichness values were highly variable across the chronosequence, but were highest in drained, newly restored, and natural wetlands. In drained wetlands, this may suggest that despite being cultivated with agronomic species, additional species with various trait combinations are growing in drained wetland basins resulting in a high resource use efficiency. A similar trend in newly restored wetlands was also observed, likely as a result of the influx of annuals prior to the stabilization of the restored wetland community. When FRichness of restored wetlands is compared to natural wetlands, all age classes, save newly restored, have lower values suggesting that resources are more efficiently being

used in natural wetlands given a larger functional space occupied by species within the communities. Functional Evenness (FEveness) refers to the distribution and abundance of traits, whereas Function Divergence (FDivergence) provides insight into the level of differentiation of niches in a community (Villéger et al. 2008; Qin et al. 2016; Mason et al. 2005). FEveness and FDivergence were mostly consistent and highest across the chronosequence, possibly indicating that resource use is high as a result of low competition for resources. Finally, Functional Dispersion (FDispersion), represents the average spread of traits to a community centroid by considering evenness and abundance (Laliberte & Legendre 2010), and can provide an indication of the functional redundancy of a community. High evenness of species traits located at larger distances from a centroid provide increased resilience and stability to a system in the face of a disturbance. Contrarily, small values of FDispersion may provide indication of a community with similar traits and higher competition for specific resources (Laliberte et al. 2010). FDispersion values were highest in newly restored and natural wetlands but were relatively consistent throughout.

Environmental filtering and/or niche stabilization likely explain the lack of variation observed across the age classes. First, generally only species adapted to wet conditions and soils will regenerate within a wetland following restoration, second, wetlands are typically highly productive environments, and species with high resource acquisition related traits can be associated with resource-rich environments (Asefa et al. 2017). While this research project was not focused on testing the processes underlying community assembly, niche-based assembly processes have been shown to structure wetland plant communities and influence functional diversity metrics (Fu et al. 2014). Further, trade-offs in the trait responses of species to restoration may be creating equal functional performance among communities. For example, the data show that drained wetlands are dominated by short species with high SLA values whereas natural wetlands tend to be dominated by tall species with low SLA values. When these trait combinations are combined into a functional diversity metric, FD values equilibrate to present similar functional diversity across the chronosequence.

Results from other studies provide support for the idea of trade-offs in trait variation resulting in stable FD values. Spasojevic and Suding (2012) found no difference in multi-variate functional diversity (FDispersion) along a strong stress and resource gradient in the alpine tundra owing to opposite plant strategies driven by plant stature and leaf and resource acquisition traits. Further, Li et al. (2017) show that despite a change in community composition and soil properties in response to wetland drying, no change in functional diversity metrics (FRichness, FEvenness, and FDivergence) were observed in their sites. These authors suggest that community level traits, rather than functional diversity are a stronger influence on ecosystem processes following successional changes to wetland systems.

Functional diversity has been shown to be one of the best predictors of ecosystem function available (Cadotte et al. 2011). Greater functional diversity results in ecosystem stability provided by multiple functional traits and helps to buffer ecosystems against abiotic variation (Walker et al. 1999). However, negative relationships between functional diversity and ecosystem process are also observed, though are often not reported (Fu et al. 2014). The results obtained in this study are inconsistent with my hypothesis that suggests that functional diversity would be lower in drained and restored wetlands due to cultivation and modification of wetland basins, which would reduce the ecological functioning of these sites. With that said, community level trait means can and do provide important insights into ecosystem function. Community level SLA, LDMC, and LNC have been shown to positively correlate with photosynthesis and transpiration rates (Reich et al. 1999; Westoby et al. 2002). Further, leaf area and plant height can affect a number of processes including heat exchange, carbon dynamics and storage, and decomposition rates (Diaz et al. 2004; DeBello et al. 2016; Zirbel et al. 2017; Funk et al. 2016). In one study, when considering traits related to the leaf economic spectrum, including SLA, LDMC, and height, within five years of floodplain meadow restoration, restored sites resembled reference sites (Engst et al. 2016). In contrast, this same study reported that traits related to pollination or plant strategy types were not fully restored, reflecting the complexity

of restoring plant communities and multi-trophic interactions (Engst et al. 2016). In addition, considering plant functional traits that act simultaneously on ecosystem processes further complicates the understanding of community composition and ecosystem process. The idea of considering trait - service clusters, defined as combinations of traits that are simultaneously involved in the control of multiple ecosystem processes, further illustrate the usefulness and applicability of trait-based research and may help manage ecosystems (de Bello et al. 2010).

Overall, these results emphasize the importance of selecting relevant traits for functional analysis. Undoubtedly, the traits selected for analysis strongly influence the outcomes and conclusions derived from the results. This is supported by a large body of literature, which identifies, instructs, and discusses the importance of selecting and standardizing the collection of functional traits (Violle et al. 2007; Petchey & Gaston 2006; Cornelissen et al. 2003; Perez-Harguindeguy et al. 2013). For example, plant functional traits that align along the leaf economic spectrum, known to predict nutrient cycling and productivity (Shipley et al. 2006) can covary with one another, therefore selecting several of these traits in an analysis may bias results and associated inferences. Further, the number of traits used to determine functional diversity can also influence results. A higher number of (uncorrelated) traits used to determine functional diversity can increase the ability to detect functional differences among species or communities while decreasing the chance for functional redundancies given that a larger 'trait space' emerges from more traits (Petchey & Gaston 2002).

Finally, inferring ecosystem recovery from functional traits and functional diversity has its limitations. The mechanisms behind community assembly, functional diversity, trait interactions, and ecosystem function are complex and multifaceted (Cadotte et al. 2011). Further, the strength, magnitude, and direction of correlations observed among traits and ecosystem processes can vary by ecosystem studied. As it relates to wetland ecosystems, limited work has been done, especially in prairie pothole wetlands. As such, functional traits specific to wetland plants, wetland specific processes, and the [trait × ecosystem] process

associations observed in wetlands are understudied (Moor et al. 2017). With that said, the field of restoration ecology is increasingly using functional traits as a promising approach to predicting restoration success (Martinez-Garza et al. 2013), resisting invasion of exotic species (Funk et al. 2008), and defining targets to achieve restoration goals (Laughlin 2014), all of which will help advance the understanding and utility of using plant functional traits to understand ecosystem processes and functional recovery in wetland ecosystems.

3.5   Conclusion

Trait-based ecology is a relatively new field of research often used to describe community assembly and ecosystem function. This observational study aimed to analyze the functional traits and diversity within a chronosequence of restored wetlands to track the trajectory of ecosystem process recovery. While functional diversity did not vary across the chronosequence, community level traits and species-specific analysis did identify differences among age classes. Specifically, height and leaf area were two traits that showed variability among age classes, suggesting that these restored wetlands are not equivalent to nearby natural wetland systems. These results may indicate that ecosystem processes related to productivity, nutrient mobilization, and carbon dynamics are not fully recovered even 24 years post restoration. Trait-based analysis should be considered as a method to assess ecosystem functional recovery; however, selection of traits should be carefully considered in combination with desired outcomes.

3.6   References

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4   Chapter 4. Conclusions

4.1   Research Findings

Historically, wetland losses have been widespread and wetlands remain under the threat of loss and degradation worldwide due to land development, agricultural production, and industrial expansion. As a result, impacts to the landscape where wetlands have been lost have been high. However, over the last 20 years, great efforts have gone into implementing policy to conserve and protect remaining wetlands, as well as into wetland restoration initiatives to mitigate the impacts of wetland loss. This study aimed to provide a comprehensive analysis of vegetation recovery in restored wetlands that were created with the expectation that they function like the natural systems they replace. This study asked two questions: (1) do restored wetland plant communities resemble natural wetlands? and (2) are restored wetlands functioning like natural wetlands?

The answers to these questions were obtained by comparing vegetation structure (i.e. species richness, as well as cover hydrophytes, native species, and non-native species) and plant functional traits from a chronosequence of up to 37 wetlands, which included drained, restored, and natural wetlands. This project provided a unique opportunity to critically evaluate restorations intended to restore wetland area and function. This research is timely and is directly applicable to policy development in Alberta given the recent implementation of the Alberta Wetland Policy (Government of Alberta 2013). This policy is among a wave of updates and new developments with respect to wetland policies that aim to take a functional approach at wetland management (valuing wetlands for the different functions they provide). Commonly, wetland policies take an area-based approach to compensating for wetland impacts, where impacts to one hectare of wetland are replaced by the same area of restored wetland habitat. However, replacement of wetland habitat does not guarantee replacement of wetland function and ecological processes. The implementation and management of function-based policies are in their infancy and are labour-intensive, expensive to administer, and difficult to assess. The Government of Alberta has recently

released a restoration directive that provides guidance to wetland restoration practitioners, but this guide lacks direction on how to assess and evaluate return to function or ecological lift following restoration (Government of Alberta 2016). Now, more than ever, there is a need for functional, resilient wetland ecosystems and multi-functional landscapes as these systems are increasingly faced with changing climate regimes (Renton et al. 2015).

In general, the results of this research suggest little differentiation in vegetation structure or plant functional traits between restored and natural wetlands. Vegetation cover, species richness, and community composition recover quickly and are comparable to nearby natural wetlands within five years of restoration. It is only when comparing results to wetlands located within natural reserves, where differences in species richness and community composition can be observed. In this respect, structural metrics proved to be more sensitive indicators of vegetation recovery following restoration than when compared with functional traits. With plant functional traits, I observed several species that had no differences in plant functional trait values across the wetland chronosequence, I observed only minor differences in community level trait values among wetland age classes, and I observed consistent functional diversity across all wetlands. However, plant functional traits did identify a trend that is supported by structural metrics that suggests a rapid increase in condition (whether species richness, trait values, or cover estimates) similar to natural wetlands, followed by decline within 10-15 years of restoration, after which values incrementally increase as a wetland gets older and condition values approach natural wetland levels. Plant height and leaf area proved to be the traits with the most potential to provide insight into ecosystem functional recovery given the trends observed at both the species and community levels.

These results suggest that management actions prior to and following restoration, as well as of the surrounding landscape may determine wetland restoration success. In Chapter 2, I identified morphometrics of wetlands that may improve restoration success, and start to approximate conditions in natural wetlands. These included prioritizing restoration sites with large (larger than one

hectare) basins, ensuring gradual slopes when grading restoration sites, and managing for the establishment of hydrophytes and native species, while controlling the spread of invasive species. Further, in Chapter 3, I identified minimal differences in functional traits and functional diversity among drained, restored, and natural wetlands, might also be explained by the surrounding. In Chapter 3, analysis were limited to wetlands situated within a landscape driven by a history of disturbance and agricultural pressure, including the natural wetlands (Nat(Ag)). This is in contrast to wetlands located in natural reserves as assessed in Chapter 2, where differences in species richness and community composition were observed when compared to restored and Nat(Ag) wetlands. While management actions may influence recovery following restoration, these results also suggest that condition of reference sites must be considered and is an important component when evaluating restoration success.

Finally, an important contribution of this research was in understanding the natural range of variation of wetlands. Wetlands are highly variable systems that are sensitive to changes in temperature and precipitation (Renton et al. 2015). Even the two-year duration of this research project presented differences in cover estimates, species richness, and community composition among field seasons. Further, high variability was observed across metrics, both structural and functional, as well as across age classes, which contributed to a lack of significant differences across the chronosequence. Variability in a system, particularly wetlands, may be associated with stability and resilience of an ecosystem (Colloff & Baldwin 2010). Species with a wide range of plant functional trait values may be considered more adaptable to a range of environmental conditions, and therefore able to withstand fluctuations in precipitation and climate. Natural ranges in wetland condition, whether from a species, community, or functional perspective, are difficult to determine; however, understanding the natural range of variation found within natural and restored wetlands may help predict restoration success and better manage wetlandscapes.

4.2 Research Significance

Ecological theories and concepts underlie and should help to explain and predict the recovery of and processes occurring in wetlands following restoration. However, the practice of wetland restoration (and other forms of restoration activity) is often carried out in isolation from the science of restoration (Cabin et al. 2010). While restoration practitioners are likely intuitively familiar with principles of community assembly, disturbance, and/or competition, many restoration projects rely on logistical, cultural, or experiential knowledge rather than testing or incorporating scientific concepts (Wainwright et al. 2017). Research shows that restoration programs developed in concert with scientific principles are more successful than restorations carried out following a more trial and error approach (Giardina et al. 2007). In this final section, I aim to situate the results of my research into the general ecological context of community development and ecosystem function.

The patterns observed in structural and functional recovery can be explained by classic community ecological concepts. Following a disturbance (plugging of a drainage ditch) the wetland communities were inundated with new species (mostly annual species) with a wide variety of trait values as expected under a typical successional trajectory (Suding et al. 2004). Within the first five years following restoration, I saw peak species richness and high variability in traits resulting from a plant community comprised of annuals, perennials, and woody species. This influx in species also provides evidence of a transition towards an alternative stable state, where hydrologic restoration provided a significant perturbation enough to surmount the ecological threshold distinguishing drained and natural sites (Suding 2004). The stable state identified following restoration is characterized by high hydrophyte and native species cover, where competition for resources and/or life history strategies may explain the consistency and similarity in structural and functional metrics across restored wetlands. Interestingly, wetlands located within agricultural landscapes exhibit similar conditions (i.e., species richness, percent covers, and trait values) to restored sites. As Bedford (1999) suggests, cumulative effects from widespread

historical wetland loss have implications on the remaining wetlands on a landscape. The disparity observed between the natural wetland classes (Nat(Ag) and Nat(Res)) provide strong evidence that landscape context was a significant factor limiting the recovery following restoration and suggest there exists a second ecological threshold to overcome when considering wetland recovery. Although natural wetlands retained within a landscape otherwise devoid of wetlands (agricultural) are critical elements of habitat mosaics, these isolated systems experience reduced dispersal vectors, decrease in average area over time, and increasing loading of suspended solids (Cohen et al. 2016; Johnston 1994). Restored wetlands and natural wetlands located within agricultural areas are limited in their recovery potential given the barriers presented by landscape isolation. Management actions or additional restoration efforts (i.e., seeding and plantings) will likely help a restored wetland to overcome some of the limitations of existing within an isolated landscape.

Finally, while tracking structural recovery and understanding community assembly and development following restoration is important for management of these systems, ultimately return to function or functional recovery should be the goal. Ecological theory as proposed by the biodiversity - ecosystem function (BEF) relationship predicts higher functioning with increased diversity (e.g., species, genetic, functional diversity (FD)). The results of this research were deficient with regards to functional recovery as evaluated through functional traits. My results suggest no functional differences exist among drained, restored, or natural systems. While the results found in this study can be explained by a number of factors, the BEF does have support in the restoration literature (Mayer 2001; Doherty et al. 2011; Cadotte et al. 2011). Trait based approaches offer an emerging method for assessing ecological function through plant functional trait values and functional diversity (Reiss et al. 2009). These applications are in their infancy and should continue to be incorporated into restoration assessment and management in an effort to reconstruct healthy, functioning ecosystems.

4.3   Recommendations for Future Research

There exist many opportunities for research that explores wetland restoration, studies rates of recovery, and manages for the provisioning of ecosystem functions and services. To begin at a local scale, small changes to the way wetland restorations are currently conducted and/or managed in Alberta could greatly improve ecosystem recovery and landscape function. For example, one approach could be to follow modelling conducted by White and Fennessy (2005), which identified locations on a landscape where high likelihood of restoration success was predicted based on criteria including long-term sustainability, hydric soils, land use, and topography. Further, the importance of a strong initial restoration effort (i.e., plantings, soil transport, contouring, etc.) for healthier wetland ecosystems has been stressed (Gutrich et al. 2008). By combining site suitability modelling with increased on-the-ground effort, the success of wetland restorations could be greatly improved, not just in comparison to a reference condition but also at the landscape level.

Next, a comparison of restoration methods (e.g., passive versus active restoration) and the influence on vegetation recovery would be a directly applicable and valuable contribution towards policy development in Alberta and internationally. Additionally, evaluating or directing restoration approaches towards specific functional outcomes (e.g., increased biodiversity or improve habitat connectivity) could help sustain multi-functional landscapes. The feasibility of these approaches and their implications should be studied further.

Finally, additional work is required to identify reliable indicators of wetland condition following restoration. Given the variability found in wetland systems, the similarity among wetlands on the prairie landscape, and the predicted shifts in climate, it is increasingly important to be able to identify and predict change and effects to wetlands and other natural features. A functional approach to monitoring and evaluating wetland condition is a promising approach towards maintaining landscape functionality, but additional research should be invested to better understand variability in plant functional traits, to explore the trait -

ecosystem function relationship, and identify meaningful traits indicative of healthy wetland systems.

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5   Appendices

Appendix A. Complete lists of species observed within wetlands

Table A4. Species observed in Drained (D), Nat(Ag) (N), and Nat(Res) P wetlands. 'A' represents a species that was observed only in 2016, 'B' represents a species only observed in 2017, and 'C' represents a species that was observed in both 2016 and 2017.

Species	D1	D2	D3	D4[2,3]	D5[2]	N1	N2	N3	N4[2]	P1[4]	P2[4]	P3[4]	P4[4]	P5[4]
Achillea millefolium						A		A		A	A	C	A	A
Achillea sibirica						A	A	C	B	C		A	B	
Actaea rubra							A							
Agoseris glauca														
Agrimonia striata											B	A	C	
Agropyron dasystachyum			C			C		C	B	C				C
Agropyron repens														
Agrostis scabra											A			
Alisma plantago-aquatica														
Alopecurus aequalis	A					A	A			A	C	A	A	A
Alopecurus pratensis										B		B	B	B
Anemone canadensis							A					A		
Antennaria sp.	B	B		B	B									
Aralia nudicaulis							A		B					
Arctium minus														
Artemisia absinthium														
Artemisia sp.											A		A	
Aster borealis			A			A	A	A			A			
Aster ciliolatus														
Aster puniceus						B	B	C	B	C	A	B	C	A
Beckmannia syzigachne	B		B*	B	B	A	A	B		C	C	A	A	C
Bidens cernua								B			C			
Brassica napus	C	C	C	B	B*					A				
Bromus ciliatus										A			A	
Bromus inermis						C	A	A	B*	C	C	C	C	C
Bromus sp.														
Bromus tectorum										B				
Calamagrostis canadensis									B	B	B	B	B	B
Calamagrostis stricta						B	C	B	B	C	B	C	B	
Callitriche verna							B				B			
Capsella bursa-pastoris			C	B	B									
Cardamine pensylvanica													A	A
Carex aquatilis								B			B	C		
Carex atherodes						C*	C*	C*	B*	C	C	C	C	C

Continued….

* Identifies a dominant species used to collect, process, and analyze plant functional traits and functional diversity
[1] Wetland was only assessed in 2016
[2] Wetland was only assessed in 2017
[3] Wetland only used in functional trait analysis
[4] Wetland not used in functional trait analysis

Table A4. Species observed in Drained (D), Nat(Ag) (N), and Nat(Res) P wetlands. 'A' represents a species that was observed only in 2016, 'B' represents a species only observed in 2017, and 'C' represents a species that was observed in both 2016 and 2017.

Species	D1	D2	D3	D4^{2,3}	D5^2	N1	N2	N3	N4^2	P1	P2	P3	P4	P5
Carex aurea									B					
Carex bebbii													A	A
Carex crawfordii							B					B		
Carex diandra													A	A
Carex disperma														A
Carex lanuginosa							B				B			B
Carex rostrata							C*	B		C	C	C	A	C
Carex sartwellii													B	B
Carex sp.							A	C				A		B
Carex sychnocephala			C*	B		A	A			A				
Castilleja miniata												A		
Cerastium nutans														
Ceratophyllum demersum						B						A		
Chenopodium album	C	A	C		B									A
Christmas weed		A	B	B	B									
Cicuta maculata						B	C	B	B		C			
Cirsium arvense	A	A	C		B	C	C*	C	B	C	C	C	C	C
Cornus canadensis							A					B		
Cornus stolonifera								A						
Corylus cornuta												A		
Crepis tectorum														
Dactylis glomerata										A	C		C	C
Deschampsia cespitosa			B											
Descurainia sophia											A			
Eleocharis acicularis														
Eleocharis palustris			C*			C	B	B		C	B	A		A
Epilobium angustifolium							A			A				
Epilobium glandulosum		B	B	B			B	B	B		B	B	B	
Epilobium latifolium					B	A	C			B	A	A		
Equisetum palustre							A	A						
Equisetum pratense		A			B		A	B	B	A	C	C	B	B
Equisetum sylvaticum													A	
Erigeron acris						A								
Erigeron philadelphicus							A	B		C	B	C	A	

Continued…

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Species	D1	D2	D3	D4^{2,3}	D5^2	N1	N2	N3	N4^2	P1	P2	P3	P4	P5
Erigeron sp.														
Erucastrum gallicum	B	C	C	B	B*	A	A			A	A		A	A
Erysimum cheiranthoides							C						A	
Fallopia convolvulus	C	C	A		B									
Festuca elatior														
Festuca pratense														
Festuca saximontana											B			B
Fragaria virginiana								A		A	C	C	C	A
Galeopsis tetrahit	A					A	C	C	B	C			B	
Galium aparine	C	A												
Galium boreale									B		B	A	A	A
Galium labradoricum										A	A			A
Galium sp.														
Galium trifidum			B					B	B		B			B
Galium triflorum							A							
Geranium sp												A		
Geum aleppicum						B	A	C	B	B	B	C		B
Geum macrophyllum										A	A		A	A
Geum rivale										A				
Geum sp.							B							
Glyceria grandis			B				B	B		C	B		A	C
Potamogeton sp.							B					A		
Heracleum maximum							C						A	
Hieracium umbellatum			B											
Hippuris vulgaris						B	C*			A		C		
Hordeum jubatum	B		B*	B	B*					C	A		A	A
Hordeum vulgare	B*	B*		B*										
Juncus balticus					B	B		C	B		C			
Juncus bufonius						B					C			
Lathyrus ochroleucus								A					C	
Lathyrus venosus								B	B		B	B	B	
Lemna minor						B	B	C	B	C	B	C		C
Lemna trisulca							B			C	B	C		
Linaria vulgaris						A								
Juncus sp.							B							

Continued…

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Table A4. Species observed in Drained (D), Nat(Ag) (N), and Nat(Res) P wetlands. 'A' represents a species that was observed only in 2016, 'B' represents a species only observed in 2017, and 'C' represents a species that was observed in both 2016 and 2017.

Species	D1	D2	D3	D4[2,3]	D5[2]	N1	N2	N3	N4[2]	P1	P2	P3	P4	P5
Lycopus asper							B			B				
Lysimachia ciliata														A
Lysimachia thyrsiflora							A							B
Matricaria discoidea														
Matricaria perforata								B						
Medicago sativa			A					A			A			
Melilotus officinalis											A			
Mentha arvensis			C		B	C	C*	C*	B	C	C	C	C	C
Mertensia paniculata							A				A			
Osmorhiza depauperata							A							
Penstemon procerus														
Petasites sagittatus							C*	C*	B*	A	C	A	A	
Phalaris arundinacea						C*	C	C	B	A		C		
Phleum pratense									B	C	C	A	C	C
Plantago major	B	B	C*	B	B	B				C	C			
Poa palustris	B		C	B*		C	C	B	B*	C	C	C	C	C
Poa pratensis	B	B				C	A	C*	B	C	C	C	C	C
Poa sp.														
Polygonum amphibium								B	B					
Polygonum aviculare	B		B	B							C			
Polygonum lapathifolium	B	B	C	B	B	B		A				B	B	
Polygonum sp.		A	A							A		A	A	A
Populus balsamifera						A	C		B			C		
Populus tremuloides							C	A	B			A	A	
Potentilla anserina						C	A	C	B					
Potentilla gracilis														
Potentilla norvegica						C	C			C	A	C	A	A
Potentilla palustris											A			
Prunus virginiana													A	
Ranunculus gmelinii								A						
Ranunculus macounii								B				C	C	A
Ranunculus sceleratus						C	C			C	C	C		C
Ribes glandulosum							B					B	A	
Ribes hudsonianum													A	
Ribes oxyacanthoides							A			A	A			

Continued…

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Species	D1	D2	D3	D4^{2,3}	D5^{2}	N1	N2	N3	N4^{2}	P1	P2	P3	P4	P5
Ribes sp.						A		A						
Ricciocarpos natans							B							
Rosa acicularis							A	A	B		C	A	A	
Rubus idaeus							C		B		A	A		
Rumex maritimus		B	B	B	B	C	A			A	B	C	A	A
Rumex occidentalis					B	A	A	C	B		C		C	A
Rumex sp.														
Salix bebbiana									B		B		B	
Salix exigua														
Salix maccalliana														
Salix petiolaris						C		C	B	C	C	C	C	C
Salix sp.						A	A	A	B	A	C	C	A	A
Schoenoplectus tabernaemontani			C*		B	C	C			C		A		
Scirpus microcarpus							A							
Scirpus paludosus														
Scirpus pungens			B											
Scolochloa festucacea						B	B	B*	B*	B		B		
Scutellaria galericulata						C	C	C	B	C	C	A	C	C
Senecio congestus												A		
Silene campestris					B									
Sisyrinchium montanum								A						
Sium suave						C	A	B	B	C	C	B	A	C
Smilacina stellata							A							
Solidago canadensis						C	A		B	C		C		
Sonchus arvensis	B		C	B	B	C	C*	C	B	C	C	C	C	C
Sparganium eurycarpum							B			A				B
Sphenopholis intermedia										A				
Stachys palustris						B		B	B	C	A	B	A	A
Stellaria crassifolia										A	A	A	A	A
Stellaria longifolia														
Stellaria longipes													B	B
Stellaria media	C	C*	C	B*										
Symphoricarpos albus								A				A		
Tanacetum vulgare			C		B	A				A			A	
Taraxacum officinale	B	C	C	B		C	A	A		C	C	C	C	C

Continued…

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Species	D1	D2	D3	D4[2,3]	D5[2]	N1	N2	N3	N4[2]	P1	P2	P3	P4	P5
Thalictrum venulosum												A		
Thlaspi arvense			B			B		A						
Trifolium hybridum										A	A		A	A
Trifolium pratense														
Trifolium repens			B			B		B	B	C	C	C	C	A
Triglochin palustris											A			
Triticum sp.	A	A	C	B										
Typha latifolia	B		B	B	B	C	C*	C			B	C		
Urtica dioica						A	C		B	C	A	C	C	
Utricularia vulgaris														
Veronica peregrina													A	
Viburnum edule							A							
Vicia americana						A	A	A			A	A	A	A
Viola canadensis							A							
Viola renifolia											A			
Unknown Graminoid 1														
Unknown Graminoid 2						A	A			A	A	A		A
Unknown Graminoid 3														
Unknown Graminoid 4														
Unknown Graminoid 5												A		
Unknown Graminoid 6														
Unknown Graminoid 8												A		
Unknown Graminoid 9														
Unknown Graminoid 10														
Unknown Graminoid 11														
Unknown Graminoid 12														
Unknown Graminoid 13						A								
Unknown Graminoid 14														
Unknown Graminoid 15							A							
Unknown Graminoid 16								A						
Unknown Graminoid 17														
Unknown Forb 1														
Unknown Forb 2												A		
Unknown Forb 3							B							
Unknown Forb 4														

Continued…

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Table A4. Species observed in Drained (D), Nat(Ag) (N), and Nat(Res) P wetlands. 'A' represents a species that was observed only in 2016, 'B' represents a species only observed in 2017, and 'C' represents a species that was observed in both 2016 and 2017.

Species	D1	D2	D3	D4[2,3]	D5[2]	N1	N2	N3	N4[2]	P1	P2	P3	P4	P5
Unknown Forb 5	B	B												
Unknown Forb 6														
Unknown Forb 7														
Unknown Forb 8														
Unknown Forb 9											B			
Unknown Forb 10														
Unknown Forb 11														
Unknown Forb 12								A						
Unknown Forb 13														
Unknown Forb 14							B				B			B
Unknown Forb 15														
Unknown Forb 16							B		B				B	
Unknown Forb 17														
Unknown Forb 18							A							
Unknown Forb 19							A							
Unknown Forb 20							A							
Unknown Forb 21										A				
Unknown Forb 22									B					

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Table A2. Species observed in restored wetlands. Wetlands are identified by type ('R' = restored), followed by years since restoration, and where wetlands were restored in the same year, these are further distinguishes by a lower case letter (a – d). 'A' represents a species that was observed only in 2016, 'B' represents a species only observed in 2017, and 'C' represents a species that was observed in both 2016 and 2017.

Species	R1a[2,3]	R1b[2,3]	R3[3]	R4a	R4b	R5a	R5b	R6	R7	R8a[3]	R8b	R9	R10a	R10b	R11[3]	R12a	R12b	R15a	R15b[1]	R15c[2]	R15d	R17a[3]	R17b[3]	R22	R23a[3]	R23b	R23c[2]	R24a	R24b[2]
Achillea millefolium					A			A	A				A	A	A	A	B	A	A	B				A	C	A	B		
Achillea sibirica	B	B		A				C													C				C	C	C	B	
Actaea rubra																													
Agoseris glauca																									B				
Agrimonia striata																												B	
Agropyron dasystachyum	B	B	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	A	B	C	C	C	C	C	C	B	C	B
Agropyron repens																	B	B											
Agrostis scabra	B											B														B	B		
Alisma plantago-aquatica	B					A	C														C								
Alopecurus aequalis	B	B	A	C	C	B	C		A	B		C	C	A	A		B	B			C	C	C		C		B	A	B
Alopecurus pratensis				A						C								A	C										
Anemone canadensis								A																					
Antennaria sp.						B	B				B	B	A	B							B		B	A					B
Aralia nudicaulis																													
Arctium minus								A			A																		
Artemisia absinthium																						A							
Artemisia sp.																					B								
Aster borealis				A	A		A	A	A			A			A	A	A	A			A			A	A	A		A	
Aster ciliolatus																										A			
Aster puniceus		B	B		B			B	B					B		B		B		B	B		B	C		B	B		B
Beckmannia syzigachne	B	B	C	C	C	C*	C*		C	C	C	C	C	C	A		B*	B*			B	C*	C	C		C	B	A	B
Bidens cernua					B						B						B				B					B	B		

Continued…

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Species	R1a[2,3]	R1b[2,3]	R3[3]	R4a	R4b	R5a	R5b	R6	R7	R8a[3]	R8b	R9	R10a	R10b	R11[3]	R12a	R12b	R15a	R15b[1]	R15c[2]	R15d	R17a[3]	R17b[3]	R22	R23a[3]	R23b	R23c[2]	R24a	R24b[2]
Brassica napus				C												A													
Bromus ciliatus				A	A	A			A		A	A					A	A					A			A		A	
Bromus inermis		B	A	A	A	A	C	C	A	B	C	A		C	A	C	A	A		B	C	C	B	C*	B	C	B	C	
Bromus sp.			B																										
Bromus tectorum			B	B	B	B					B	B														B			B
Calamagrostis canadensis								B			A										B								
Calamagrostis stricta	B*	B					B*	B			B		B			B		B		B*		B*			C	C	B	B		B
Callitriche verna	B	B						B	B	A				B			B						A					B	B
Capsella bursa-pastoris							A														B								
Cardamine pensylvanica																													
Carex aquatilis					B	A							B				B*	B		B	A							B*	
Carex atherodes	B*	B*	B	C	C	C	C*	C*	C*	C*	C*	C*	C	C*	C*	C*	C*	C*	A	B*	C*	C*	C*	C*	C	C*	B*	C*	B*
Carex aurea																													
Carex bebbii					A	A				A			A								A							A	
Carex crawfordii					B	B			B												B		B					B	
Carex diandra																													
Carex disperma																													
Carex lanuginosa		B					B		C		B	B	B*	B*		B*	B	B			B*				A	C			
Carex rostrata	B		B	B	B	B*	B*	B	B	C*	B*	B	B*	C*	B	B*	C*	A		B*	C*		B*	C*		C*	C*	B*	B
Carex sartwellii					B	B	B				B		B	B	B						B					B	B		B
Carex sp.			A		A			C		A	A	B	C	B	A			A		B	A				C	B	A		

Continued…

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Species	R1a[2,3]	R1b[2,3]	R3[3]	R4a	R4b	R5a	R5b	R6	R7	R8a[3]	R8b	R9	R10a	R10b	R11[3]	R12a	R12b	R15a	R15b[1]	R15c[2]	R15d	R17a[3]	R17b[3]	R22	R23a[3]	R23b	R23c[2]	R24a	R24b[2]
Carex sychnocephala			C*	C*	C	C	C			B	B	A		A	A	A					C		B	B	B	A	B	A	
Castilleja miniata																													
Cerastium nutans				A														A						A					
Ceratophyllum demersum	B		C							C					C									C					
Chenopodium album			A				A				C		A			A					A			A				A	
Christmas weed																													
Cicuta maculata																									B	B	B		B
Cirsium arvense	B	B*	C	C	C	C	C	C	C*	C	C*	C	A	C		C	C	A	A	B	C	C*	C	C	C	C*	B*	A	B*
Cornus canadensis																													
Cornus stolonifera																													
Corylus cornuta																													
Crepis tectorum				A																									
Dactylis glomerata																													
Deschampsia cespitosa							B							A		B			A	B									
Descurainia sophia																													
Eleocharis acicularis							B							B															
Eleocharis palustris	B	B	C	C	C*	C	C*	C	C	C	C*	C	C*	A	C*	B*	B	C	A	B	C*	C	C	A	C	C		C	B
Epilobium angustifolium																													

Continued…

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Epilobium glandulosum		B	B			B	B		B	B	B					B					B*	B	B				B		B
Epilobium latifolium			A	C			A															A	A	A					
Equisetum palustre				A	A	A		A			A					A						A	A					A	
Equisetum pratense	B	B		C	B	B	C	C			B		A	C		B	C					C	B		B	B	B	A	
Equisetum sylvaticum																													
Erigeron acris																													
Erigeron philadelphicus			C	A			B														B					C			B
Erigeron sp.																					A								
Erucastrum gallicum	B		B	C	A	C	C		C	C	B	C	A	C							C	A	A		B				B
Erysimum cheiranthoides							A						A	A					B		A						C		
Fallopia convolvulus			A	A			A		A	A	A	B		B								A							
Festuca elatior			C*	B	B	B*	B		B*		B*	B			B														
Festuca pratense				A																									
Festuca saximontana																						B				B*	B		
Fragaria virginiana								A						A															
Galeopsis tetrahit		B	B		B	C*		A			C							A	B	A	B				B	C	B	C	B
Galium aparine			B	A			B																						
Galium boreale								A																					

Continued…

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Galium labradoricum				A	A	A	A	A	A				A									A	A						
Galium sp.								A																					
Galium trifidum	B					B	B	B	B	B			B			B					B	B			B	B	B		B
Galium triflorum																													
Geranium sp																													
Geum aleppicum	B	B			B			A													A		B		C	C	B		
Geum macrophyllum																													
Geum rivale																													
Geum sp.																													
Glyceria grandis	B*	B	C	B	C*	C*	C	C	C*	C*	C	B	B	B		B	B	B	A	B	C*	C*	C*	B	C*	B*	B*		B
Potamogeton sp.	B	B	C							C					C							C	C						
Heracleum maximum																													
Hieracium umbellatum			C	C	A	B	C					C	A									A							
Hippuris vulgaris																													
Hordeum jubatum		B	B	C		B	C			B	B	B	B		C		B	B	A	B	C				B		B		
Hordeum vulgare																													
Juncus balticus		B	B	C			A	C	C		C	A	B		B			C*	A	B	C				C*	C	C	B	
Juncus bufonius			C																										
Lathyrus ochroleucus																								A					

Continued…

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Species	R1a[2,3]	R1b[2,3]	R3[3]	R4a	R4b	R5a	R5b	R6	R7	R8a[3]	R8b	R9	R10a	R10b	R11[1]	R12a	R12b	R15a	R15b[1]	R15c[2]	R15d	R17a[3]	R17b[3]	R22	R23a[3]	R23b	R23c[2]	R24a	R24b[2]
Lathyrus venosus			B	B			B	B								B					B	B	B	B		B			B
Lemna minor	B	B	C		C	B	C	B	B	C		B	B	B	C		B	B		B	B	C	C	C	C	B	B	B	
Lemna trisulca		B	C							C					B									B					
Linaria vulgaris				A							C			A							A								B
Juncus sp.				B	A		C					B	B	B											B	B	B		
Lycopus asper																													
Lysimachia ciliata																													
Lysimachia thyrsiflora								C																	A				
Matricaria discoidea						B																							
Matricaria perforata						A				C		C			A			A	A										
Medicago sativa			C	A	A	C			C		A	C	A		A			A			A			A		A		A	
Melilotus officinalis																													
Mentha arvensis	B		C	C	A	C	C*	C	C		C		C	C		B	A			C	C	C	C				B	C	B
Mertensia paniculata																													
Osmorhiza depauperata																													
Penstemon procerus													A			A	A	A											
Petasites sagittatus								B													B				C	C	B*		
Phalaris arundinacea			B		C	C		C		C*		C			C							B	A		C*	C*	B*	C	B*
Phleum pratense			B	C	B	B	A			C*		B						B			A	B	C	B	C				

Continued…

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Species	R1a[2,3]	R1b[2,3]	R3[3]	R4a	R4b	R5a	R5b	R6	R7	R8a[3]	R8b	R9	R10a	R10b	R11[1]	R12a	R12b	R15a	R15b[1]	R15c[2]	R15d	R17a[3]	R17b[3]	R22	R23a[3]	R23b	R23c[2]	R24a	R24b[2]
Plantago major			C	C	A	A	A		C	B	B			C	A		B	A		B	A		B						
Poa palustris	B	B	C	C*	C*	C*	C	C	C	C*	C*	C	C*	C	C*	C	C	C*	A	B*	C*	C	C*	C	C*	C*	B*	C	B
Poa pratensis	B	B	B	B	C	B	A	C		B	B	B	C	C	C	C	C	A	A	B	C			C	C*	C*	B*	C	B
Poa sp.				B																									
Polygonum amphibium							B	B			B		B	B			B				B					B			
Polygonum aviculare				B		A				B	B	B		B										A	B	B			
Polygonum lapathifolium			C	B	B	B	C			C			C	C		C*	A			B	C		C			C			
Polygonum sp.				A			A	A		A											A								
Populus balsamifera	B		A					A								A	A												
Populus tremuloides	B		C			A	A	A			A							A						A				B	
Potentilla anserina								A												C					C			A	
Potentilla gracilis				A																					A				
Potentilla norvegica	B		C	A	A	B	A		A	C	C	C		A					B	C	C			B		C	B	A	B
Potentilla palustris																													
Prunus virginiana																													
Ranunculus gmelinii							A		A																A				
Ranunculus macounii					C	A		A				A	C	A			C				C		A				A	B	
Ranunculus sceleratus	B	B	C			B			A	C											C	A	C	B				B	B

Continued…

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Ribes glandulosum								B																					
Ribes hudsonianum																													
Ribes oxyacanthoides								A																					
Ribes sp.																													
Ricciocarpos natans					B					B			B							B			B						
Rosa acicularis								C						B		A				B				A					
Rubus idaeus								A																					
Rumex maritimus	B	B	C	A			A		A	C			C		C	B						B	C	C					
Rumex occidentalis	B			A			C	C	C	C	C	C	C	C	C	C	C*	A	A		C			A	C	C	B	A	B
Rumex sp.																A	A												
Salix bebbiana						B	B				B															B	B		
Salix exigua																		B											
Salix maccalliana																					B								
Salix petiolaris	B		B	C		C*	C*	C	C		C	C	C	C		C	C*	A*	A*	B	C		B	C	C	C	B	A	
Salix sp.			B	C		C	C	C	C		C	C				C	A	C			A		B		C	A			
Schoenoplectus tabernaemontani	B	B*	C	C	C	B	C			C	C	C			C			C	A	B	C	C		A					
Scirpus microcarpus																													
Scirpus paludosus							A								A														
Scirpus pungens		B	B	B			B																						

Continued…

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Species	R1a[2,3]	R1b[2,3]	R3[3]	R4a	R4b	R5a	R5b	R6	R7	R8a[3]	R8b	R9	R10a	R10b	R11[3]	R12a	R12b	R15a	R15b[1]	R15c[2]	R15d	R17a[3]	R17b[3]	R22	R23a[3]	R23b	R23c[2]	R24a	R24b[2]
Scolochloa festucacea	B*	B*						B*											B	B*	B*			B					B
Scutellaria galericulata	B			A		B	A	A		A						A	A			B	B	A		A				A	
Senecio congestus									A												A								
Silene campestris																													
Sisyrinchium montanum				A	A			A										A										A	
Sium suave	B		B	A	C	A	C	C		B			C	C		B	C		B	C	C*	C		C	C	B	B	B	B
Smilacina stellata				A																									
Solidago canadensis		B		A				A																	A	B		A	
Sonchus arvensis	B	B	C	C		C	C	C	C	C*		C	C	A	C	C	A	A	B	C	B	C	C	C	A	C	B	C	B
Sparganium eurycarpum			B																					B					
Sphenopholis intermedia																													
Stachys palustris	B	B		B		B	B	B			C					B	B			B	B	B		B				B	B
Stellaria crassifolia								A						A							A					A	A		
Stellaria longifolia																										B			
Stellaria longipes	B					B																			B		B		
Stellaria media			B						B		B	B												B					
Symphoricarpos albus								A																A					

Continued…

* Identifies a dominant species used to collect, process, and analyze plant functional traits and functional diversity
[1] Wetland was only assessed in 2016
[2] Wetland was only assessed in 2017
[3] Wetland only used in functional trait analysis
[4] Wetland not used in functional trait analysis

Table A2. Species observed in restored wetlands. Wetlands are identified by type ('R' = restored), followed by years since restoration, and where wetlands were restored in the same year, these are further distinguishes by a lower case letter (a – d). 'A' represents a species that was observed only in 2016, 'B' represents a species only observed in 2017, and 'C' represents a species that was observed in both 2016 and 2017.

Species	R1a[2,3]	R1b[2,3]	R3[3]	R4a	R4b	R5a	R5b	R6	R7	R8a[3]	R8b	R9	R10a	R10b	R11[3]	R12a	R12b	R15a	R15b[1]	R15c[2]	R15d	R17a[3]	R17b[3]	R22	R23a[3]	R23b	R23c[2]	R24a	R24b[2]
Tanacetum vulgare							A	B	A	C	C	B		A							C			A				A	B
Taraxacum officinale		B	C	C*	C	C	C		C	C	C	C	C	A	A		B	C	A		C	B	C	A	C	A	B	A	B
Thalictrum venulosum																													
Thlaspi arvense			B	A		C	A	A	A	A	C					A		A	B	A	C	C	A	A				C	B
Trifolium hybridum				A	A	A			A	A			A	A		A		A				A		A	A	A		A	
Trifolium pratense																		B											
Trifolium repens			B	B*	B	B*	B			B	B		B	B			B		B				B		B	B	B		B
Triglochin palustris																													
Triticum sp.																													
Typha latifolia	B*	B*	C*	C*	C*	C*	C*		C*	C	C*	C	B		C*		B	C*	A	B	C	B	C*	C	C	C	B		B
Urtica dioica	B	B				C		A			C						A							A				A	B
Utricularia vulgaris		B													C														
Veronica peregrina							A																						
Viburnum edule																													
Vicia americana				A		A			C		A		A			A						A		A	A			A	
Viola canadensis																													
Viola renifolia																													
Unknown Graminoid 1				A																		A							
Unknown Graminoid 2						A	A	A						A								A		A					

Continued…

* Identifies a dominant species used to collect, process, and analyze plant functional traits and functional diversity
[1] Wetland was only assessed in 2016
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[4] Wetland not used in functional trait analysis

Table A2. Species observed in restored wetlands. Wetlands are identified by type ('R' = restored), followed by years since restoration, and where wetlands were restored in the same year, these are further distinguishes by a lower case letter (a – d). 'A' represents a species that was observed only in 2016, 'B' represents a species only observed in 2017, and 'C' represents a species that was observed in both 2016 and 2017.

Species	R1a[2,3]	R1b[2,3]	R3[3]	R4a	R4b	R5a	R5b	R6	R7	R8a[3]	R8b	R9	R10a	R10b	R11[3]	R12a	R12b	R15a	R15b[1]	R15c[2]	R15d	R17a[3]	R17b[3]	R22	R23a[3]	R23b	R23c[2]	R24a	R24b[2]
Unknown Graminoid 3																		B											
Unknown Graminoid 4													B																
Unknown Graminoid 5																													
Unknown Graminoid 6				A																									
Unknown Graminoid 8																													
Unknown Graminoid 9											A																		
Unknown Graminoid 10		B																											
Unknown Graminoid 11						A																							
Unknown Graminoid 12																		A										A	
Unknown Graminoid 13					A																					A			
Unknown Graminoid 14									B																				
Unknown Graminoid 15																													
Unknown Graminoid 16						A			A			A						A					A					A	
Unknown Graminiod 17						A																							
Unknown Forb 1									A																				
Unknown Forb 2																													
Unknown Forb 3		B																											
Unknown Forb 4																					A								
Unknown Forb 5																													

Continued…

* Identifies a dominant species used to collect, process, and analyze plant functional traits and functional diversity
[1] Wetland was only assessed in 2016
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Table A2. Species observed in restored wetlands. Wetlands are identified by type ('R' = restored), followed by years since restoration, and where wetlands were restored in the same year, these are further distinguishes by a lower case letter (a – d). 'A' represents a species that was observed only in 2016, 'B' represents a species only observed in 2017, and 'C' represents a species that was observed in both 2016 and 2017.

Species	R1a[2,3]	R1b[2,3]	R3[3]	R4a	R4b	R5a	R5b	R6	R7	R8a[3]	R8b	R9	R10a	R10b	R11[3]	R12a	R12b	R15a	R15b[1]	R15c[2]	R15d	R17a[3]	R17b[3]	R22	R23a[3]	R23b	R23c[2]	R24a	R24b[2]
Unknown Forb 6																						B							
Unknown Forb 7														B															
Unknown Forb 8														A															
Unknown Forb 9																													
Unknown Forb 10																					B								
Unknown Forb 11														B															
Unknown Forb 12																													
Unknown Forb 13										B																			
Unknown Forb 14		B																		B						B			
Unknown Forb 15													B																
Unknown Forb 16																B		B		B					B		B	B	
Unknown Forb 17																		A										A	
Unknown Forb 18																													
Unknown Forb 19																													
Unknown Forb 20																													
Unknown Forb 21																													
Unknown Forb 22																													

* Identifies a dominant species used to collect, process, and analyze plant functional traits and functional diversity
[1] Wetland was only assessed in 2016
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[3] Wetland only used in functional trait analysis
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Appendix B. Study sites used to assess structural and functional recovery of restored wetlands

Table B1. Name and description of study sites in this project that were used to assess recovery of wetlands following restoration.

Wetland Name	ID	Area (ha)	Wetland Age	Age Class	Wetland Class	Incl. in Str. Analysis (Ch 2) (Y/N)	Incl. in Func. Analysis (Ch 3) (Y/N)
CUR1	D1	0.02	Drained	Drained	Drained	Y	Y
CUR2	D2	0.01	Drained	Drained	Drained	Y	Y
CUR3	D3	0.22	Drained	Drained	Drained	Y	Y
CUR4	D4	0.06	Drained	Drained	Drained	N	Y
CUR5	D5	0.28	Drained	Drained	Drained	N	Y
DEN1	R1a	0.35	1	Age 1-5	Seasonal	N	Y
DEN5	R1b	0.21	1	Age 1-5	Seasonal	N	Y
FOR2	R3	1.59	3	Age 1-5	Semi-perm	N	Y
FOR1	R4a	0.30	4	Age 1-5	Seasonal	Y	Y
ROP1	R4b	0.23	4	Age 1-5	Seasonal	Y	Y
ABB1	R5a	0.29	5	Age 1-5	Seasonal	Y	Y
BOW1	R5b	0.40	5	Age 1-5	Seasonal	Y	Y
OZM1	R6	0.12	6	Age 6-10	Seasonal	Y	Y
LAB1	R7	0.25	7	Age 6-10	Seasonal	Y	Y
BER1	R8a	1.73	8	Age 6-10	Semi-perm	N	Y
BUS1	R8b	0.14	8	Age 6-10	Seasonal	Y	Y
NAS1	R9	0.10	9	Age 6-10	Seasonal	Y	Y
HEN1	R10a	0.30	10	Age 6-10	Seasonal	Y	Y
REU1	R10b	0.07	10	Age 6-10	Seasonal	Y	Y
CHR1	R11	0.87	11	Age 11-15	Semi-perm	N	Y
BOW2	R12a	0.12	12	Age 11-15	Seasonal	Y	Y
BOW3	R12b	0.19	12	Age 11-15	Seasonal	Y	Y
FER1	R15a	0.05	15	Age 11-15	Seasonal	Y	Y
FER2	R15b	0.53	15	Age 11-15	Seasonal	Y	N
FER3	R15c	0.67	15	Age 11-15	Seasonal	N	Y
MCN1	R15d	1.01	15	Age 11-15	Seasonal	Y	Y
KEM1	R17a	0.15	17	Age 16-20	Semi-perm	N	Y
KEM2	R17b	0.21	17	Age 16-20	Semi-perm	N	Y
RAU1	R22	0.68	22	Age >20	Seasonal	Y	Y
MAR1	R23a	0.13	23	Age >20	Semi-perm	N	Y
MIT1	R23b	0.13	23	Age >20	Seasonal	Y	Y
MIT3	R23c	0.14	23	Age >20	Seasonal	N	Y
AMB1	R24a	0.19	24	Age >20	Seasonal	Y	Y
AMB2	R24b	0.14	24	Age >20	Seasonal	N	Y
INT1	N1	0.96	Natural - Ag	Nat(Ag)	Seasonal	Y	Y
INT2	N2	0.80	Natural - Ag	Nat(Ag)	Seasonal	Y	Y
INT3	N3	0.72	Natural - Ag	Nat(Ag)	Seasonal	Y	Y
NewNat1	N4	0.35	Natural - Ag	Nat(Ag)	Seasonal	N	Y
CLBCD1	P1	0.46	Natural - Reserve	Nat(Res)	Seasonal	Y	N
CLBID8	P2	0.88	Natural - Reserve	Nat(Res)	Seasonal	Y	N
CLBIM1	P3	0.97	Natural - Reserve	Nat(Res)	Seasonal	Y	N
CLBRD2	P4	0.53	Natural - Reserve	Nat(Res)	Temporary	Y	N
CLBRD3	P5	0.10	Natural - Reserve	Nat(Res)	Seasonal	Y	N

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Presentations:

Howard R., Creed IF. 2018. Evaluating wetland restoration success by tracking recovery of plant functional traits. Poster Presentation. Ontario Ecology, Ethology, and Evolution Colloquium (OE3C), Western University, London, ON. May 10-12.

Howard, R., Salaria, S., Creed, IF. 2017. Evaluating wetland restoration success by tracking recovery of plant functional traits. Lightning Talk Presentation. Biology Graduate Research Forum, Western University, London, ON. Oct 20.