Aquatic macroinvertebrate communities and diversity patterns in the Northern Prairie Pothole Region

by

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Author’s Declaration

I hereby declare that I am the sole author of this thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners.

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Abstract

The Northern Prairie Pothole Region (NPPR) of Alberta, Canada contains numerous shallow marshes that serve as important habitat for wildlife and provide many essential ecosystem services. Many of these pothole wetlands have been destroyed or degraded by agricultural activity, prompting research into their condition and management. Aquatic macroinvertebrates are frequently used as indicators of environmental condition in rivers and lakes, but their effectiveness as indicators in prairie pothole marshes is not clear. I discovered that, contrary to my predictions, macroinvertebrate richness and community composition at family-level resolution do not respond to land use. Instead, macroinvertebrate community composition in pothole marshes is structured primarily by hydroperiod, which ranges from temporary, through seasonal and semi-permanent, to permanent marsh classes. I discovered that the macroinvertebrate abundance, diversity and community composition differed significantly among wetland permanence classes, and that macroinvertebrates exhibited a nested community composition along this hydrological gradient. In other words, macroinvertebrates in temporary wetlands were not unique, but rather subsets of the taxa occupying more permanent wetlands. I also looked at macroinvertebrate functional groups (desiccation strategies, functional feeding groups and behavioural guilds). I discovered that the subset of taxa occupying temporary marshes were those that possess strategies for surviving the drawdown period, such as drought resistant stages or the ability to disperse to larger water bodies. Most functional feeding groups and behavioural guilds were more abundant in permanent wetlands; however, variation existed that was unrelated to hydroperiod and might be due to differences in aquatic vegetation. Like abundance, both alpha and gamma diversity were highest in permanent marshes; however, beta diversity was highest in temporary mashes. This suggests that alpha and gamma diversities are constrained in pothole marshes by the tolerance of taxa to periodic desiccation, in keeping with the species-sorting model of community assembly. However, in temporary marshes the assembly process is reinitiated frequently, and is therefore more strongly influenced by the stochastic aspects of dispersal. This yields a higher beta diversity or taxon turnover among temporary marshes and is in line with neutral theory. This stresses the importance of both local and regional factors in shaping biodiversity and provides insight into the community ecology of wetland macroinvertebrates and their associations with environmental variables.

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List of Abbreviations

ANOVA – Analysis of variance

CABIN – Canadian Aquatic Biomonitoring Network

MRPP – Multi-response permutation procedure

NMDS – Non-metric multidimensional scaling

NPPR – Northern Prairie Pothole Region

RMSE – Root-mean-square error

SAV – Submerged aquatic vegetation

1. Introduction and literature review

The Northern Prairie Pothole Region (NPPR) of Alberta, Canada is home to numerous shallow marshes that serve as important habitat for wildlife and provide many essential ecosystem services (Wrubleski and Ross 2011). A significant proportion of these wetlands have been drained and many remaining wetlands occur in landscapes affected by agriculture and cattle grazing (Dahl 1990, Wrubleski and Ross 2011). Alberta has recently implemented a new wetland policy to conserve, restore, protect and manage wetlands “to sustain the benefits they provide to the environment, society and economy” (Government of Alberta, 2013). Yet despite recognition that the agriculture sector is a major driver of wetland loss and degradation (e.g., Schindler and Donahue 2006, Johnston 2013, Clare and Creed 2014), there has been limited research on the effect of agriculture on the biotic communities of NPPR wetlands and few regionally-calibrated monitoring tools are available for tracking wetland condition across the NPPR of Alberta. Aquatic macroinvertebrates are frequently used as indicators of environmental condition in rivers and lakes (Cairns and Pratt 1993), but their effectiveness as indicators of agricultural disturbance in wetlands is unknown. Indeed, the major drivers of macroinvertebrate community structure in these marshes are not well understood. In this thesis, I aim to identify the environmental factors impacting aquatic macroinvertebrate community composition and diversity patterns, as well as evaluate their usefulness as an indicator group for biomonitoring.

1.1 Importance of Northern Prairie Pothole Region marshes

Marshes in the NPPR are responsible for many provisioning, sustaining, regulating and cultural ecosystem services. For example, they are recognized for providing important hydrological functions, such as water filtration, groundwater recharge, flood mitigation and water storage (Stewart and Kantrud 1971, Martin and Hartman 1987, LaBaugh et al. 1998, van der Kamp and Hayashi 1998, Zedler and Kercher 2005, Gleason et al. 2008). These wetlands also sustain wildlife by providing integral habitat for many wetland dependant plants and animals, including birds, invertebrates and amphibians (Cronk and Fennessey 2001, Wrubleski and Ross 2011). The wetlands of the NPPR are of critical importance for waterfowl as they provide necessary breeding and feeding habitat to the majority of migrating duck populations of North America (Beyersbergen et al. 2004). Some of the important regulating services of these marshes are often neglected, including the control of microclimate through evaporative cooling, the sequestration and storage of carbon, and nutrient cycling (Zedler and Kercher 2005, Gleason et al. 2008). Lastly, they provide cultural benefits in the form of aesthetic appeal and opportunity for recreational activities (Gleason et al. 2008). These wetlands are therefore of significant value and contribute to the unique landscape of Alberta.

1.2 NPPR and Alberta's Natural Regions

The marshes characteristic of the NPPR are located in the Parkland and Grassland Natural Regions of Alberta (Wrubleski and Ross 2011). A Natural Region is a geographic region with distinct vegetation communities, soil types and landscape features (Downing and Pettapiece 2006). Together, these two regions are referred to as the White Zone of Alberta and are typically managed together, despite distinctions in their climate and characteristic flora and fauna (Downing and Pettapiece 2006, Government of Alberta 2013). The Natural Regions of Alberta are described in detail by Downing and Pettapiece (2006) as part of the Natural Regions Committee and I have summarized the information presented on both the Parkland and Grassland regions below.

The Grassland Natural Region is a semi-arid prairie landscape situated in southern Alberta that spans 95,564 km^2 or 14.4% of the province. The wetlands here dry earlier than the rest of the province due to increased evaporation rates and low recharge from rainfall. The land is primarily used by humans for cattle grazing and irrigation-based cropping. The landscape is characterized by a distinct lack of trees with shrubs only present in wetter regions. The Parkland region is a transitional zone in central Alberta, located between the Grassland and Boreal Natural Regions, and covers 60,747km^2 or 9% of the province. It is the most densely populated Natural Region in Alberta and is heavily affected by agriculture; primarily row crops such as barley and canola. The natural vegetation characteristic of this region includes aspen forests and willow shrubs.

The average temperature and rainfall of a Natural Region is important in characterizing its overall features and biotic communities (see Table 1-1). The Grassland is the warmest and driest region with the hottest summers and longest growing season in Alberta. Most vegetation in the Grassland is drought tolerant as precipitation is usually less than potential evapotranspiration, yielding a moisture deficit. The Parkland has a cooler temperature, which reduces the potential evapotranspiration and thus the moisture deficit is less extreme, though the region is still semi-arid with a continental climate (see Table 1-1).

1.3 Hydrology and permanence classes

In the NPPR, marshes occur in shallow depressions caused by the retreat of glaciers (Beyersbergen et al. 2004, Wrubleski and Ross 2011). During the early spring thaw, the soil in this region is still frozen, which allows water from the snowmelt to accumulate in depressions (Crumpton and Goldsborough 1998, Hayashi et al. 2016). Most pothole wetlands are isolated from any inflow or outflow channels and the major components of their water balance are the overland input of water from snowmelt and rainfall and the output of water via evaporation and transpiration (Stewart and Kantrud 1971, Winter and Rosenberry 1995, van der Kamp and

Hayashi 2009). Pothole wetlands fill in spring and typically drawdown throughout the summer, many drying out entirely before fall. The resulting variability in hydroperiod, or water retention time, across seasons and years is important to the dynamic nature of these wetlands, whose biota have evolved to rely on the regular fluctuation of water levels (Euliss and Mushet 1996, Euliss et al. 2004, van der Valk 2005). Due to the ecological importance of hydroperiod on the function and structure of marshes in the NPPR, these ecosystems are classified into different permanence classes based on the length of their hydroperiod (Table 1-2; Stewart and Kantrud 1971). The vegetation in NPPR marshes is dependant on these wet-dry cycles (LaBaugh et al. 1998, van der Valk 2005). Plants vary in their tolerance to soil saturation which results in different plant groups (e.g., wet meadow, emergent or submersed aquatic vegetation) establishing in different areas of a wetland (van der Valk and Davies 1980, van der Valk 2005). Consequently, wetlands of different permanence classes are characterized by different combinations of vegetation zones that reflect differences in the permeability of the soil and the permanence of the surface water (Table 1-2; Stewart and Kantrud 1971). Such variation in wetland vegetation has a strong influence on the invertebrate ecology of NPPR marshes.

Wet-dry cycles of the NPPR marshes have both indirect and direct effects on macroinvertebrate ecology. For example, wetlands that dry out annually cannot support fish, and given typical isolation from surface water flows, they are rarely colonized by fish, even during their wet-phases. This frees macroinvertebrates from fish predation, which results in higher macroinvertebrate abundance, biomass and diversity (Cobbaert et al. 2010, Bischof et al. 2013). Aquatic macroinvertebrates will vary in relative abundance throughout the season, as different taxa emerge and hatch at different times (Miller et al. 2008, Bischof et al. 2013). Macroinvertebrates can also take advantage of the variability in water levels for reproduction purposes. In some groups of odonates (e.g., Lestidae), adult females will oviposit eggs directly into standing stalks of vegetation during lower water levels at the end of the summer (Thorp and Covich, 1991). The eggs are drought resistant and hatch the following spring in response to higher water levels when conditions are ideal for the aquatic nymphs (Thorp and Covich, 1991). Thus, the dynamic hydroperiod of NPPR marshes is an important component of macroinvertebrate ecology.

1.4 Agricultural effects

Before European settlement in North America, most of the NPPR was a prairie landscape comprising short and tall grasses with numerous pothole wetlands (Gleason et al. 2008). The glacial till that gave rise to these wetlands is nutrient rich and the last two centuries have seen a rapid expansion of agriculture (Dahl 1990, Dahl and Johnson 1991). Wetlands are under greater agriculture pressure than any other aquatic system (Leitch and Fridgen 1998, Reece and McIntyre 2009) and anthropogenic effects on wetlands may be greater and more damaging than on running water systems as contaminants accumulate over time in the isolated depressions (Wrubleski and Ross 2011).

A drastic number of wetlands have been lost via drainage to allow for increased crop yield (Martin and Hartman 1987, Dahl 1990). In the North Dakota pothole region, it is estimated that 50% of wetlands have been lost over the past two centuries (Dahl 1990, Beyersbergen et al. 2004), while other sources estimate that as much as 70% of Canada’s prairie wetlands have been lost (Alberta Wilderness Association, 2014). Using high-precision mapping to compare the total number of wetlands lost versus the wetland area lost, recent research in Alberta has discovered that small, shorter hydroperiod wetlands are preferentially lost due to cropping and drainage (Serran and Creed 2016). The destruction of small temporary wetlands leads to wetland consolidation, whereby the snowmelt that would originally have been held in numerous small wetlands is instead redirected to larger remnant wetlands in the catchment, causing them to grow even larger (Euliss and Mushet 1996, Anteau 2012). Consolidation drainage alters the volume of water as well as the timing of water input into remnant wetlands (Euliss and Mushet 1996, Anteau 2012). Wetlands which remain in agricultural landscapes can also be subjected to increased sedimentation, nutrient loading, pesticide inputs (Martin and Hartman 1987, Zedler and Kercher 2005, Gleason et al. 2008) and exposure to invasive weedy plant species (Green and Galatowitsch 2001), resulting in altered vegetation communities (Mushet et al. 2002) .

Land containing marshes is also converted into pasture for cattle, which often focus their grazing in and around wetlands because of their high forage quality (Foote and Rice Hornung 2005). This severely compacts the soil, which leads to decreases in soil infiltration, the capacity of the soil to hold water and the organic content of the soil (Wrubleski and Ross 2011). Cattle will also alter the vegetation communities in wetlands by selectively grazing on aquatic plants, which in turn eliminates emergent vegetation that is required habitat by many aquatic invertebrates and waterbirds (Beyersbergen et al. 2004, Foote and Rice Hornung 2005, Wrubleski and Ross 2011).

1.5 Resource management

It is important to properly manage wetland resources to avoid the further loss and deterioration of pothole wetlands. The Government of Alberta has recently implemented a policy that aims to assess the value of wetlands so that “wetlands of the highest value are protected for the long-term benefit of Albertans” (Government of Alberta 2013). As part of this policy implementation, the government requires scientifically created and validated tools to assess wetland condition. There are currently no evaluation protocols to assess the condition of non-permanent marshes in the NPPR.

Field-based rapid assessment tools that assign wetlands a value based on the functions they provide (such as the Alberta Wetland Rapid Evaluation Tool – ABWRET-A) are increasingly popular due to their low cost and comprehensive estimates of wetland value (Government of Alberta 2015), but these tools lack any evaluation of overall wetland condition or ecological integrity. A habitat has ecology integrity if it possess a biotic community of similar taxonomic and functional diversity as a natural, undisturbed system (Karr and Dudley 1981, Karr 1991, Wurtzebach and Schultz 2016). In contrast, ecological functions are processes that occur within a habitat (whether beneficial to humans or not) and ecological value refers to the benefits a system provides to society (McPherson et al. 1997, de Groot et al. 2002). For wetland assessment tools and policies to be effective, a baseline must be set for what undisturbed or 'reference' wetlands are like. The degree of anthropogenic disturbance affecting a wetland can be expressed in comparison to the reference condition benchmark to properly evaluate a wetland's condition in addition to the functions it provides.

1.6 Aquatic macroinvertebrates as bioindicators

When examining the effect of environmental disturbance on habitats, researchers often make use of bioindicators to inform them about the state of the system (Niemi and Mcdonald 2004). A bioindicator is a biological variable, such as a species or a group of organisms, which responds predictably to environmental changes and disturbances (Cairns and Pratt 1993). A bioindicator can therefore be used to monitor anthropogenic disturbances, including both agriculture and cattle grazing (Steinman et al. 2003, Bonada et al. 2006). For a bioindicator to be successful at providing an accurate indication of ecosystem condition, it must be responsive to stress and environmental change (Niemi and Mcdonald 2004, Bonada et al. 2006). If the indicator is sensitive to a narrow range of stressors, it may be diagnostic of the cause of impairment. If it responds to multiple stressors, then it may act as an indication of the overall environmental and biological condition of its habitat (Rooney and Bayley 2012a, 2012b).

Macroinvertebrates are the most commonly used bioindicator of environmental status in aquatic systems (Resh et al. 1995, Bonada et al. 2006, Stewart and Downing 2008), possessing numerous traits that make them excellent bioindicators (Table 1-3). However, despite their popularity and usefulness in river and lake assessments, macroinvertebrates are not well represented in wetland evaluations. The responses of wetland aquatic macroinvertebrates to environmental disturbance have not been well studied and publications often offer conflicting results (review in Batzer 2013). Aquatic macroinvertebrates are a crucial part of wetland ecosystems and their potential as bioindicators merits future study. However, to be a successful bioindicator, macroinvertebrates must be sensitive to land use at a taxonomic scale appropriate for use in biomonitoring programs. The level of identification (family, genus or species) required for the effective use of macroinvertebrates as indicators of environmental disturbance is often debated (Bailey et al. 2001). While species-level resolution provides the most accurate depiction of a community, the constraints (time, resource and level of expertise) associated with providing species-level identifications makes such a protocol unlikely to be adopted by a regional monitoring program with limited resources.

1.7 Aquatic macroinvertebrate ecology

The marshes of the NPPR are an important habitat for aquatic macroinvertebrates, including aquatic insects and their larvae, annelid worms, small crustaceans and gastropods. Many of the macroinvertebrates which live in non-permanent marshes are ecological generalists which can tolerate the fluctuating conditions typical of shallow aquatic habitats, such as seasonal flooding and drying, as well as differences in water levels between years (Euliss and Mushet 1999, Wrubleski and Ross 2011). The macroinvertebrates in these marshes possess adaptations to tolerate these extremes in water level, including drought resistant eggs, diapause stages, or dispersal via flight or passive means (e.g., water birds) when a wetland becomes uninhabitable (Wiggins et al. 1980, Gleason et al. 2004, Wrubleski and Ross 2011). Macroinvertebrates living in non-permanent marshes do not necessarily benefit directly from periodic drawdowns. Rather, they may benefit indirectly from predation or competition release where predators and competitors less tolerant of drought and desiccation are excluded (Wrubleski and Ross 2011, Silver et al. 2012b).

In addition to being categorized by desiccation resistance strategy, aquatic macroinvertebrates are placed into functional feeding groups and behavioural guilds in ecological studies. Guilds or functional groups are broadly used for many groups organisms, such as bird foraging strategies, to facilitate the comparisons of ecological communities based on their functional similarities (review in Simberloff and Dayan 1991). Functional feeding groups do not necessarily dictate the exact type of material consumed by an organism, but rather the strategies they use to obtain food (Lancaster and Downes 2013). In general, macroinvertebrates as a group consume other animals, macrophytes, plankton, biofilms and detritus, although some are parasitic (Thorp and Covich 1991, Merrit et al. 2008, Lancaster and Downes 2013). Some of the methods for obtaining food includes different styles of predation, filter feeding, grazing or scraping and shredding large vegetation pieces (Thorp and Covich 1991, Merrit et al. 2008, Lancaster and Downes 2013). In this context, a behavioural guild refers to the preferred microhabitat within an aquatic system that an organism prefers. This ranges from skaters, which skim the top of the water's surface, to burrowers, which are within the benthic layer, as well as organisms which make use of open water spaces and different types of vegetation (Cummins and Merritt 2001).

1.8 Community assembly

Since the snowmelt fills the basin each spring, many of these wetlands (particularly the temporary systems) must recolonize with macroinvertebrates every year. This means the local population is annually replenished by a combination of the resting egg bank (analogous to the resting seed bank of plants, see Gleason et al. 2004) and by new colonists arriving by passive or active immigration (Bilton et al. 2001). The repeated extirpation and recolonization of NPPR wetlands affords a unique opportunity to examine the applicability of niche-based and neutral community assembly models. Niche or species-sorting models of community assembly suggest that local processes, such as biological interactions, environmental filters, and interspecific trade-offs, are the primary determinants of species composition and diversity (Wiens 2011). In contrast, the unified neutral theory of community assembly, first proposed by Hubbell (2001), emphasizes the role of stochastic colonization, random extinction and ecological drift. Under the neutral model, it is assumed that taxa capable of inhabiting a given habitat will be ecologically similar, and thus differences among taxa are unimportant in community assembly (Rosindell et al. 2011). In the last two decades, ecologists have debated the relative merits of these seemingly conflicting theories (reviews in Mikkelson 2005, Wennekes et al. 2012)

More recently, conciliatory efforts have noted the need to explore the effects of both niche and neutral theories (e.g., Thompson and Townsend 2006, Chase and Myers 2011, Weiher et al. 2011, Mendes et al. 2015). For example, Chase et al. (2011) stress the importance of examining variation in community composition (beta diversity) along both local (among sites along an environmental gradient) and regional (among biogeographic regions) scales. The authors conclude that the importance of stochastic factors does not result in an associated decline in the effect of niche-based processes, but rather both work simultaneously (Chase and Myers 2011). The relative importance of niche and neutral models are affected not only by biogeographic and temporal scales, but also along environmental or stressor gradients (Weiher et al. 2011). Weiher et al. (2011) propose the example of a community with a low alpha diversity that is likely structured by a limiting environmental variable (niche), whereas a community with high alpha diversity has fewer constraints and is likely more influenced by stochastic (neutral) processes of community assembly. In addition to tying together stochastic and environmental processes, modern research suggests the relevance of considering these two models alongside of coexistence theory. While environmental filters can certainly limit which taxa can successfully colonize a habitat, competitive interactions on the local scale can also drive community assembly (HilleRisLambers et al. 2012). After dispersal and environmental constraints have been addressed, the coexistence of taxa within a habitat is dependent on both within-site niche differences and fitness differences (review in HilleRisLambers et al. 2012).

1.9 Thesis objectives

In summary, the unique and valuable non-permanent marshes of the NPPR have undergone extensive drainage and destruction and continue to face degradation by human activities. The loss of these valuable systems can have long-term environmental consequences for both humans and the biota inhabiting NPPR marshes. The Alberta Wetland Policy (Government of Alberta 2013) aims to prevent further loss of wetlands as well as implement mitigation strategies that benefit both landowners and the environment, but a thorough examination of how biological integrity is compromised by disturbance is needed for this policy to be effective.

NPPR wetlands provide habitat to abundant and diverse groups of aquatic macroinvertebrates, which are commonly used in bioassessment of rivers and lakes but have been neglected in marsh assessments. **In Chapter 2, I evaluate the association between aquatic macroinvertebrate community composition and agricultural disturbance in pothole marshes in Alberta's NPPR**. I expect that the community composition, richness and abundance of aquatic macroinvertebrates in wetlands affected by agricultural activity will deviate from the values in natural, undisturbed systems (reference wetlands), and that this deviation will be in proportion to the extent of agricultural activity in the surrounding uplands. I test for differences in community composition among wetlands situated in landscapes with varying extents of agricultural activity. I further test for differences in community that I can attribute to biogeography, as the Parkland and Grassland may support different macroinvertebrate species pools. I find no correlation between community composition and the extent of agricultural activity in the surrounding upland area and conclude that macroinvertebrates at family-level resolution do not respond predictably to land use. While genus or species-level identifications may demonstrate sensitivities to agriculture, the time and resource constraints involved in achieving this level of resolution makes macroinvertebrates unlikely to be adopted as bioindicators in the NPPR when less time-consuming candidates exist (birds and plants).

In Chapter 3, I investigate what abiotic factors (hydrology and water chemistry) structure macroinvertebrate community composition in the NPPR and explore these relationships with three functional group classification methods. In many wetlands, fish predation is an important driver of macroinvertebrate community composition; however, the potholes in Alberta are largely fishless and the primary determinants of community composition are unclear. I discovered that macroinvertebrates exhibit no relationship to land use, and I hypothesize that this is because of the overwhelming influence of hydroperiod on these communities. In Chapter 3, I test for differences in community composition among wetlands of differing permanence classes. I also characterize macroinvertebrates by functional groups to test for associations between hydroperiod and desiccation strategies, feeding groups or behavioural guilds. I find differences in community composition and macroinvertebrate diversity between wetlands of different permanence classes, which appears to be the driving force behind aquatic macroinvertebrate composition in marshes of the NPPR. Macroinvertebrate community composition displayed a nested pattern along the permanence gradient, rather than exhibiting turnover. Based on the distribution of macroinvertebrate functional groups in these wetlands, I also suspect that the physical structure and composition of aquatic vegetation is important to these communities. Surprisingly, the other environmental variables I measured (including dominant cations, turbidity and conductivity) were not strongly associated with macroinvertebrate community composition. Consequently, a significant portion of the variation in macroinvertebrate community composition within non-permanent wetlands of the NPPR remains unexplained.

In my fourth chapter, I characterize **patterns in abundance as well as diversity across wetland permanence classes and discuss their significance in terms of community assembly**. I explore not only taxa richness or alpha diversity (*sensu* Whittaker 1972) but also patterns in gamma and beta diversity across the hydroperiod gradient. If species-sorting processes dominate along a hydrological gradient, then I expect that both alpha and beta diversity will be lowest in temporary wetlands due to the constraints desiccation imposes upon macroinvertebrate taxa.

While both abundance and taxa richness were positively associated with hydroperiod (more permanent marshes support more individuals and more taxa than temporary ones), I detected no difference in community evenness across permanence classes. Unlike average alpha and gamma diversity, I discovered that beta diversity was negatively associated with hydroperiod. In other words, temporary wetlands exhibited significantly more taxonomic turnover than permanent and semi-permanent marshes. I discuss these findings in the context of community assembly, contrasting neutral with niche-based models. I suggest that while species-sorting is important in structuring taxa along a hydrological gradient, the high beta diversity in temporary wetlands (which reassemble each spring) suggests the input of stochastic dispersal processes and provides support for the neutral model of community assembly.

Finally, in Chapter 5, I present a synthesis of my findings and comment on the implications and significance of this research in the context of macroinvertebrate and wetland ecology, as well as environmental management. In closing, I touch upon remaining gaps in the literature and my recommendations for future research in this field.

1.10 Tables

Table 1-1 Mean temperature and precipitation records for the Grassland and Parkland Natural Regions of Alberta (Downing and Pettapiece 2006).

Natural Region	Average maximum daily temperature (Cº; June-August)	Average temperature during hottest months (Cº; July/August)	Average temperature during coldest months (Cº; December/January)	Average annual precipitation (mm)	Average growing season precipitation (mm; June-August)
Parkland	22.5	15.7	-13.4	469.5	335.7
Grassland	24.6	17.4	-11.4	395.4	285.7

Table 1-2 Permanence classes of prairie pothole wetlands and their typical water retention periods after the spring snow melt as per Stewart and Kantrud (1971). The vegetation zone that characterizes the most saturated part of the wetland classes is listed, although higher permanence classes typically also contain patches or borders of vegetation types characterizing less saturated zones.

Class	Name	Permanence	Water retention period	Vegetation zone in most saturated part of wetland	Typical plants in wettest vegetation zone
I	Ephemeral	Non-permanent	Water or saturated soil for first week or two of spring	Wetland-low prairie zone	Grasses
II	Temporary	Non-permanent	First month of spring	Wet meadow	Grasses and sedges
III	Seasonal	Non-permanent	Water present in spring and early summer	Shallow marsh	Emergent plants (sedges, cattails, rushes)
IV	Semi-Permanent	Non-permanent	Only draws down completely in drought years	Deep marsh	Submerged and floating aquatic vegetation
V	Permanent	Permanent	Contains open water though out entire year	Deep marsh and open water	Submerged and floating aquatic vegetation

Table 1-3 Description of traits that make aquatic macroinvertebrates excellent bioindicators in many aquatic ecosystems

Trait	Explanation
Sensitivity	There is a history of literature on the sensitivities of commonly occurring aquatic species to anthropogenic disturbances (Bonada et al. 2006).
Integrate multiple stressors	Aquatic invertebrates are directly exposed to multiple environmental stressors (biological, chemical, physical) and therefore provide a cumulative view of both the abiotic and biotic factors in a system (USA EPA 2002).
Integrate over time	Aquatic invertebrates experience these stressors throughout their life span in the wetland and therefore when selected as bioindicators allow us to assess the cumulative or average effects of environmental stress in a wetland over time
Ease of sampling	Relatively easy and inexpensive to collect as invertebrates are abundant, widespread and sampling does not require any specialized equipment, making aquatic invertebrates an ideal candidate for monitoring aquatic ecosystems with rapid assessment tools (Resh et al. 1995, Kenney et al. 2009)
Established taxonomy	Reliable identification due to established taxonomy (USA EPA 2002, Bonada et al. 2006)
Resolution	The high diversity of invertebrates also allows for the potential of many intermediate responses to environmental impairment (Merritt et al. 2008).
Ecological importance	Invertebrates are an important trophic link between primary producers and other wetland dependant species, such as waterfowl, and so provide an important indication of the status of the overall biotic community (Meyer et al. 2015). For example, invertebrates are an important source of protein and calcium to nesting ducks (Wrubleski and Ross 2011, Silver and Vamosi 2012).

2. Aquatic macroinvertebrates are poor indicators of agriculture in NPPR wetlands

2.1 Introduction

Aquatic macroinvertebrates are the most commonly used bioindicator of environmental condition in both lakes and rivers (Resh et al. 1995, Bonada et al. 2006, Jones et al. 2007, Environment Canada 2014). They have numerous traits that make them excellent bioindicators in many aquatic ecosystems (Table 1-3). Macroinvertebrates are sensitive to multiple environmental stressors and can be indicators of the overall condition of an ecosystem (e.g., Jones et al. 2007), although they are often used specifically to diagnose nutrient pollution (e.g., Johnson et al. 2013b). Despite their popularity and usefulness in river and lake assessments, macroinvertebrates are not well represented in wetland bioassessment or biomonitoring techniques. The sensitivity of wetland macroinvertebrates to environmental stressors has been relatively poorly studied and the published literature offers conflicting results on their potential to serve as bioindicators in wetland ecosystems (review in Batzer 2013). However, research into the concordance between macroinvertebrates and other useful wetland bioindicator taxa (e.g., wetland birds and aquatic macrophytes) in shallow open water marshes of the NPPR concluded that all the bioindicators were correlated with variation in the same subset of environmental variables (Rooney and Bayley 2012a), suggesting that aquatic macroinvertebrates could be as useful in wetland monitoring as they are in other freshwater habitats.

Generally, macroinvertebrates in lentic ecosystems appear strongly influenced by the abundance and nature of top predators and the permanence of ponded water (review in Wellborn et al. 1996), although studies of wetlands across both the American and Canadian prairie pothole region are often in contradiction about the relative importance of other factors, such as surrounding land use. In the Northern Prairie Pothole Region (NPPR; in Alberta), researchers have suggested that wetland macroinvertebrates could be used in biomonitoring programs to assess agricultural impact. For example, both adult and larval odonate genera were indicators of grazing intensity (Hornung and Rice 2003, Foote and Rice Hornung 2005) and macroinvertebrate taxa richness and abundance decreased with increased grazing pressure (Silver and Vamosi 2012).

However, conflict regarding the efficacity of wetland macroinvertebrates as bioindicators emerges if we consider North America more broadly. For example, macroinvertebrates were used to monitor wetland condition in newly constructed wetlands in Iowa, and their diversity decreased with turbidity (Stewart and Downing 2008), which can be related to human activities in the surrounding landscape (e.g., Bayley et al. 2013). In coastal marshes along the Laurentian Great Lakes, aquatic macroinvertebrates responded reliably to the amount of anthropogenic disturbance in the contributing watershed (Kovalenko et al. 2014). In contrast, in the pothole wetlands of Minnesota, the presence of fathead minnows was the primary driver of aquatic invertebrate community composition and diversity (Zimmer et al. 2000). Similarly, the presence of fish was the only significant factor in structuring invertebrate communities in pothole wetlands of North Dakota, with land use having no discernable effect on invertebrate communities (Tangen et al. 2003). In Oklahoma, surrounding land use was also unrelated to the composition of invertebrate communities (Meyer et al. 2015).

It is possible that the signature of land use cannot be observed because macroinvertebrates communities vary drastically in response to other variables. Globally, there have been successful invertebrate indexes created for distinguishing between high and low quality wetlands in the flatland ponds of Spain (Trigal et al. 2009), yet disagreement remains over the reliability of aquatic macroinvertebrates as indicators of human disturbance in wetland ecosystems (review in Batzer 2013). The conflicting reports on the response of invertebrates to anthropogenic activity indicate that our understanding of what drives macroinvertebrate community composition in wetland ecosystems is incomplete and we must be cautious in relying on macroinvertebrate bioassessment tools where regional validation has not been undertaken.

I am interested in the effects of agricultural disturbance on marshes in the NPPR because of high rates of historic wetland loss. A drastic number of wetlands in the prairie region of North America have been lost via drainage and suburban and agricultural expansion (Martin and Hartman 1987, Dahl 1990). The estimates for loss of wetlands in the Canadian prairies reach as high as 70% (Alberta Wilderness Association 2014), and it is estimated that 80% of wetlands lost in the past ten years were drained without permission from the provincial government (Clare and Creed 2014). NPPR marshes that remain are largely located in agricultural landscapes, where they are exposed to soil compaction through livestock activity and farming equipment (Wrubleski and Ross 2011), increased sedimentation and nutrient loading, (Bayley et al. 2013), pesticide contamination (Main et al. 2014), altered vegetation communities (Mushet et al. 2002), increased exposure to invasive species (Green and Galatowitsch 2001), and changes to their et awater budget (Hayashi et al. 2016). In addition to degrading the ecological integrity of prairie potholes, the environmental changes associated with agricultural activities likely affect wetland macroinvertebrate communities as aquatic macroinvertebrates are highly sensitive to changes in water and sediment quality (e.g., Foote and Rice Hornung 2005, Silver and Vamosi 2012, Baker et al. 2014).

2.1.1 Objectives and hypothesis

The province of Alberta recently passed a wetland policy that will require wetland evaluation and monitoring tools to support its implementation (Government of Alberta 2013). Since aquatic macroinvertebrates are effectively used as bioindicators in other aquatic systems and are known to be sensitive to the environmental stressors associated with agricultural activity, they may serve as excellent bioindicators of ecological integrity in marshes in the NPPR. I tested the indicator potential of macroinvertebrates at family-level resolution by examining the relationship between community composition and the extent of agricultural disturbance surrounding the wetland. If aquatic macroinvertebrates are sensitive indicators of agricultural disturbance in the NPPR, I should detect a difference in the diversity or community composition of macroinvertebrates between wetlands in agriculturally dominated landscapes and relatively intact wetlands that are surrounded by natural land covers.

2.2 Methods

2.2.1 Field collection and sample preparation

My study was situated in the NPPR in Alberta (Figure 2-1), where I collected aquatic macroinvertebrates from 64 marshes spanning a gradient of wetland permanence classes (Table 1-2; *sensu* Stewart and Kantrud, 1971). The selected wetlands also spanned an orthogonal gradient (i.e., statistically independent) in the extent of agricultural disturbance. I determined disturbance level based on the extent of non-natural land cover classes (i.e., crops and cattle pasture) within a 500 m radius buffer around the perimeter of each wetland, using the Agriculture and Agri-food Canada crop inventory dataset from 2014 (AAFC 2015). On this basis, I categorized the 64 marshes in disturbance bins as either low (< 25% non-natural land cover), medium (25-75% non-natural land cover), or high (>75% non-natural land cover) agricultural disturbance (low n = 28, medium n = 14, high n = 22). I expected communities to differ most between the extremes (high and low), and so my site selection contained fewer medium wetlands which spanned a larger range in agricultural land cover (25-75%).

At each marsh, I employed the quadrat-column-core (Q-C-C) sampling method as described in Meyer et al. (2013), which provides higher estimates of abundance and biomass for most invertebrate taxa than D-net sampling and has the advantage of being quantitative, enabling comparisons of macroinvertebrate density among wetlands (Meyer et al. 2013). Where wetlands possessed an open water zone (i.e., an area of ponded water with no emergent vegetation but where submersed aquatic and floating vegetation may grow), I collected and composited three replicate quadrat-column-core samples from each of the open water and emergent vegetation zones separately (Figure 2-2), as different macroinvertebrate species could reside in these different microhabitats (Merrit et al. 2008). In wetlands lacking an open water zone, I collected and composited three replicate samples from the emergent vegetation only. Each wetland was sampled between one and three times (based on the availability of standing water) between May, June and early July (each visit approximately three weeks apart). Averaging across multiple sampling events improves the seasonal representation of the aquatic macroinvertebrate community.

My macroinvertebrate sorting, identification and data quality control procedures are based on a modified version of the Canadian Aquatic Biomonitoring Network (CABIN) laboratory protocol (Environment Canada 2014), using 500 micron mesh sieves to separate macroinvertebrates from residue. The abundance of aquatic macroinvertebrates in the sediment core component of each Q-C-C sample to be low in abundance and diversity relative to the water column and vegetation samples (Appendix 10), and the taxa observed in the sediment cores were not novel to the community. Consequently, I excluded the sediment cores from further analysis. The macroinvertebrates were identified to family level (see Appendix 2 for taxa list), following Clifford (1991) and Merrit et al. (2008). The total number of individuals were recorded for each taxon. Family-level identifications were judged appropriate for this study, as my goal was to develop a cost-effective and efficient biomonitoring tool for use in the NPPR. Macroinvertebrate genus and species-level resolution was deemed impractical to be adopted for a regional monitoring program when considering time, labour and resource constraints.

2.2.2 Statistical analysis

All statistical analysis was performed using R (R Core Team 2016). Prior to multivariate analysis, I removed rare taxa (present in fewer than five wetlands) from the community dataset to reduce sparsity (Peck 2010). Counts of taxa from the vegetation quadrat and water column were converted to density on an area-basis (1 m^2) before I summed the counts across sample components. I averaged these densities between open water and emergent vegetation zones, and finally I averaged across wetland visits, such that my sample unit was the individual wetland and community composition was represented by the count of individuals of each taxon per meter-squared at the wetland level. Taxon density (number of individuals of a particular taxa per m^2) was relativized by the maximum density observed among the 64 wetlands. Finally, non-metric multidimensional scaling (NMDS) ordination was performed using a Bray-Curtis dissimilarity matrix with the ‘metaMDS’ function in the *vegan* package (Oksanen et al. 2016). Based on a scree-plot of stress versus dimensionality, a three dimensional NMDS solution was selected (Appendix 8). Data were explored visually using the NMDS plot, with sites symbolized by disturbance level. Ninety percent confidence ellipses were delineated to help identify significant differences in aquatic macroinvertebrate community composition among disturbance levels. All graphing was performed using the R package *ggplot2* (Wickham 2009).

To test the statistical significance of any apparent differences among disturbance levels, I conducted a multi-response permutation test (MRPP; 999 iterations) on a Bray-Curtis dissimilarity matrix, using the *vegan* package. I performed a MRPP analysis to determine if there were differences in community composition between Natural Regions.

To test whether there was a statistically significant difference in macroinvertebrate abundance or taxa richness among disturbance levels, I employed a one-way analysis of variance (ANOVA), assessing the assumptions of homogeneity of variance and normality of the residuals using plots of residuals against fitted values (Appendix 9).

I used Simpson's Index of Dominance: $D = \sum \left(\frac{n}{N}\right)^2$ where *n* is the number of a particular taxon and *N* is the total number of all taxa in the pool (Magurran 2004) as a measure of community evenness. I performed a two-sample t-test to compare evenness between high and low disturbance categories.

Finally, to assess if specific taxa that are considered high potential candidate bioindicators were indicative of a low or high disturbed condition, I performed linear regressions for the total abundances of Chironomidae and odonates, as well as the number of odonate families present, and the percentage of non-natural land cover in a 500 m buffer around the wetland. Chironomids were selected as candidates due to their ubiquity and diversity (Armitage et al. 1995, Liu 2016) and odonates were selected due to their effective use as indicators of grazing intensity in NPPR wetlands by Foote and Rice Hornung (2005).

2.3 Results

The NMDS ordination revealed tremendous overlap in community composition among high, medium and low disturbance wetlands along all three ordination axes (Figure 2-3; NMDS stress = 18.49 after 133 iterations; Procrustes: RMSE = 0.006, max residual = 0.042). Further, there was no statistically significant difference in macroinvertebrate community composition among the three disturbance levels (MRPP: $p = 0.404$) and the chance-corrected within-group agreement was very low ($A < 0.0006$), indicating that community composition within these three disturbance classes was no more homogenous than to be expected from random chance. There was no significant difference in macroinvertebrate abundance among wetland disturbance bins (ANOVA: $F_{2,61} = 0.642$, $p = 0.53$; Figure 2-4A). There was no significant difference in Simpson's Index of Dominance (a measure of evenness) between the high and low disturbance levels (t-test: $t_{43} = 0.301$, $p = 0.748$; Figure 2-4B). Similarly, there was no significant difference in taxa richness among disturbance levels (ANOVA: $F_{2,61} = 0.563$, $p = 0.572$; Figure 2-4C), revealing that aquatic macroinvertebrate diversity at family-level resolution is robust to the influence of agricultural activity.

I performed linear regressions on the abundance of chironomids and odonates, as well as the number of odonate families present to determine if these taxa were predictive of wetland disturbance, but neither taxon had a significant relationship with the extent of agricultural disturbance (odonates: $t = -0.428$, $p = 0.6701$, $R^2 = 0.0029$; odonate families: $t = 0.861$, $p = 0.392$, $R^2 = -0.04$; chironomids: $t = 1.953$, $p = 0.051$, $R^2 = 0.042$). Finally, there was a significant difference in macroinvertebrate communities between the Parkland and Grassland Natural Regions (Appendix 1; MRPP: A = 0.0098, p = 0.003).

2.4 Discussion

I began by listing seven traits that make aquatic macroinvertebrates excellent bioindicators in most freshwater environments (Table 1-3), and although they meet many of these criteria in wetland ecosystems (e.g., ease of sampling, established taxonomy, ecological importance), my results reveal that they do not meet the most important criteria for bioindicator development: aquatic macroinvertebrates at family-level resolution do not respond predictably to agricultural disturbance in NPPR marshes. It is possible that genus or species-level assemblage data might reveal a relationship to disturbance not evident at family-level resolution, as several studies of taxonomic sufficiency have noted that the sensitivity of macroinvertebrates as bioindicators increases with taxonomic precision (e.g., Bowman and Bailey 1997, King and Richardson 2002, Waite et al. 2004). However, in each of these studies, some relationship to disturbance was still evident at the family-level. The topic of taxonomic sufficiency has been debated for over 40 years (e.g., Resh and Unzicker 1975). However, the additional expense and time required to achieve more precise identifications exceeds not only the capacity of most large-scale monitoring programs (review in Bailey et al. 2001), but also far exceeds the investment necessary to achieve species-level identifications in other bioindicator groups like wetland dependent birds and vegetation, which have already proven sensitive to agricultural disturbance in our study region (Wilson et al. 2013, Polan 2016, Anderson 2017).

Despite a weak family-level assemblage relationship to disturbance, I thought that the abundance or richness of individual taxa could vary with agricultural disturbance. I was particularly optimistic about chironomids and odonates, but I discerned no relationship between these taxa and land use. For Odonata, these results are contrary to both my predictions and previous research from Alberta’s NPPR (e.g., Hornung and Rice 2003, Silver and Vamosi 2012).

One explanation for this discrepancy may be that these studies identified larval odonates to genus, but as mentioned this was beyond the scope of my goal to develop a time efficient biomonitoring protocol for the NPPR. Odonates are likely a suitable candidate for biomonitoring in the NPPR but greater taxonomic resolution must be achieved to detect the signature of land use. Chironomidae were considered another strong candidate given their ubiquity, diversity and abundance in wetland habitats (Euliss et al. 1991, Armitage et al. 1995). Again, a finer taxonomic resolution might reveal a stronger relationship to land use, but this is not guaranteed. In fact, a recent study of Chironomidae genera in Albertan wetlands found no strong relationship between the extent of human activity surrounding wetlands and the composition of chironomid genera (Liu 2016).

My results are in general agreement with research in American pothole wetlands, which typically find no consistent response of macroinvertebrates to agricultural activity. These studies usually identify fish predation and water depth as the dominant factors structuring aquatic macroinvertebrate communities, suggesting that predator control overrides any influence of surrounding land use (Tangen et al. 2003) or restoration (Zimmer et al. 2000). However, fish predation cannot explain the variation in macroinvertebrate community observed among the 64 study wetlands, as due to their isolation from surface water connections and their ephemeral nature, the marshes I studied were all fishless. This begs the question, what is controlling the community composition of aquatic macroinvertebrates in NPPR wetlands?

Macroinvertebrate communities in NPPR wetlands likely respond to agricultural disturbance, but this relationship was completely masked by family-level resolution and environmental factors influencing community composition. I observed that communities differed between the Parkland and Grassland Natural Regions (Appendix 1), and I expect this is due to differences in temperature and rainfall, as well as the distribution of wetland permanence classes differing between regions. Liu (2016) also noted that three Natural Regions in Alberta had differing assemblages of chironomids. Pond permanence (or hydroperiod) should affect macroinvertebrates directly by determining how long aquatic stages have to mature or how essential a desiccation-tolerant life stage is for survival in ephemeral environments and influences invertebrate abundance and diversity in wetlands (Wellborn et al. 1996, Batzer et al. 2004, Bischof et al. 2013). The abundance of macrophytes may also play an important role in structuring macroinvertebrate communities in marshes (Zimmer et al. 2000). However, additional exploration of environmental and biological factors driving the diversity and distribution of aquatic macroinvertebrates in NPPR wetlands is warranted.

To my knowledge, this is the most expansive study of non-permanent pothole wetland macroinvertebrates in the NPPR to date, encompassing 64 wetlands in two Natural Regions and a wide range of agricultural disturbance (0-100% agricultural land cover), as well as a statistically independent gradient in wetland permanence class. I observed substantial variation in macroinvertebrate community composition, richness and abundance among these 64 wetlands, but the extent of agricultural activity surrounding each wetland did not explain a significant portion of that variation in community composition and was unrelated to macroinvertebrate abundance, richness or dominance at the family-level. I consequently conclude that further efforts to develop biomonitoring tools using aquatic macroinvertebrates in prairie potholes of Alberta are not warranted. My findings contradict decades of research into the effectiveness of invertebrates as bioindicators in other aquatic systems (e.g., Bonada et al. 2006, Environment Canada 2014, Jones et al. 2007, Rosenberg and Resh, 1993) but support several studies that detected only weak relationships between invertebrates and surrounding land use in prairie potholes (e.g., Batzer 2013, Liu 2016, Tangen et al. 2003). Efforts in biomonitoring and bioassessment tool development for NPPR marshes should be redirected at taxa less effortful to identify to species that have been proven sensitive to agricultural activities, such as waterbirds (Polan 2016, Anderson 2017) or wetland plants (Wilson et al. 2013). I hope that this work will prompt future studies exploring the ecological drivers of macroinvertebrate community structure in NPPR marshes, where most are fishless and thus other factors must be responsible for the observed variation in community composition.

2.5 Figures

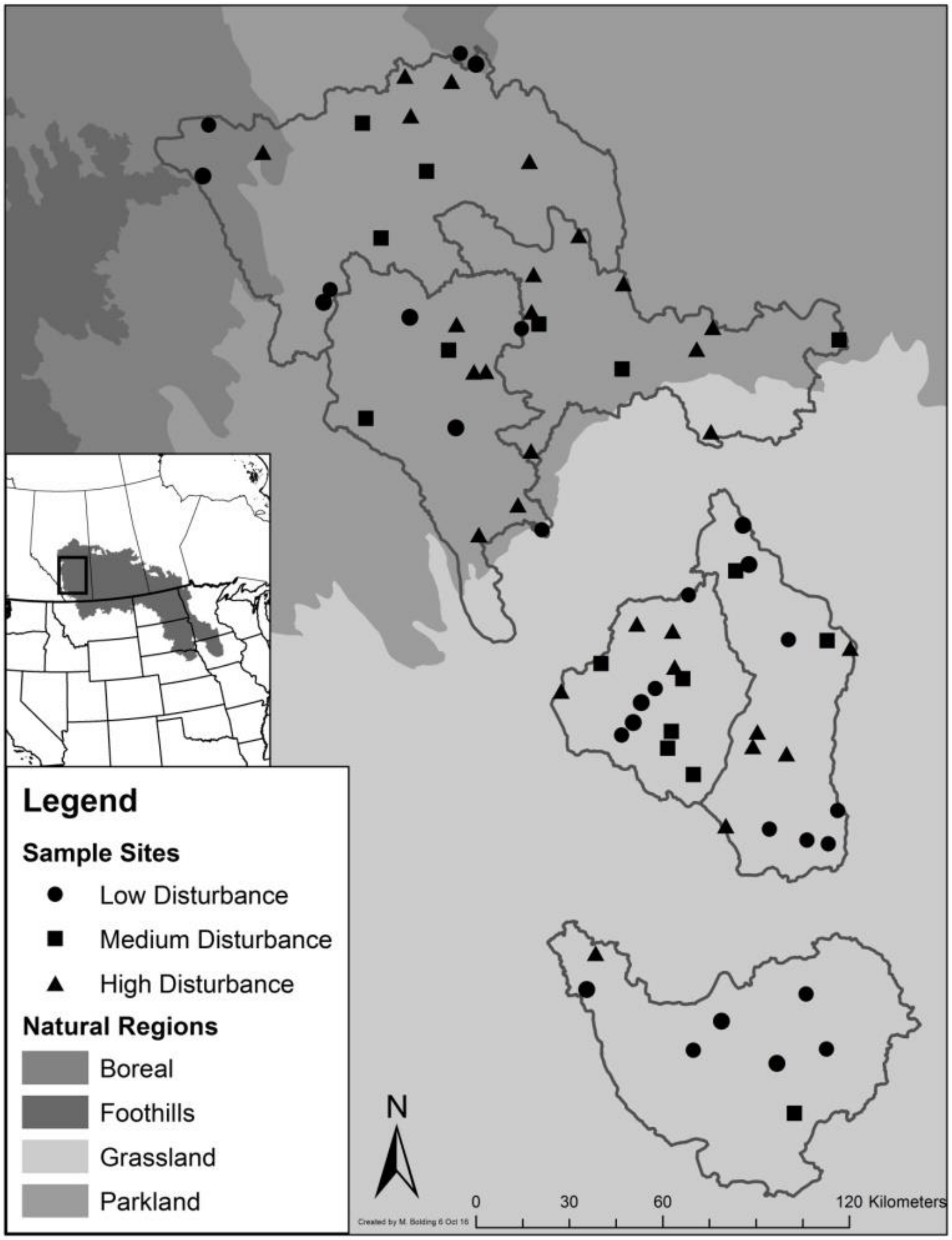

Figure 2-1 A map of the NPPR with 64 wetland sites with varying land use intensity. The study area encompasses six sub-watersheds, two Natural Regions and a range of agricultural disturbance separated into disturbance category bins (low = 28, medium = 14, high = 22).

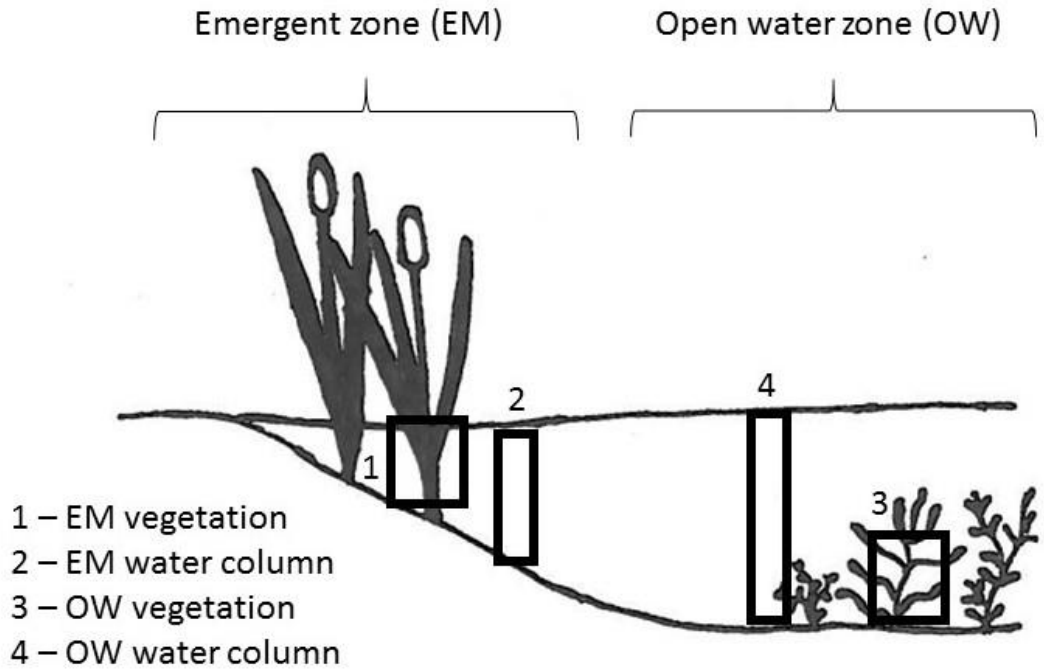

Figure 2-2 A diagram displaying the two major zones sampled in a wetland (if both were present): the emergent zone and the open water zone. The emergent zone typically consists of grasses, sedges and robust emergent. The open water zone contains no emergent vegetation, but typically has floating or submerged aquatic vegetation. In each zone, a water column and a vegetation quadrat were employed to collect macroinvertebrates. This process was repeated three times in each zone, and resulted in a maximum of four composite samples (EM vegetation, EM water column, OW vegetation, OW water column).

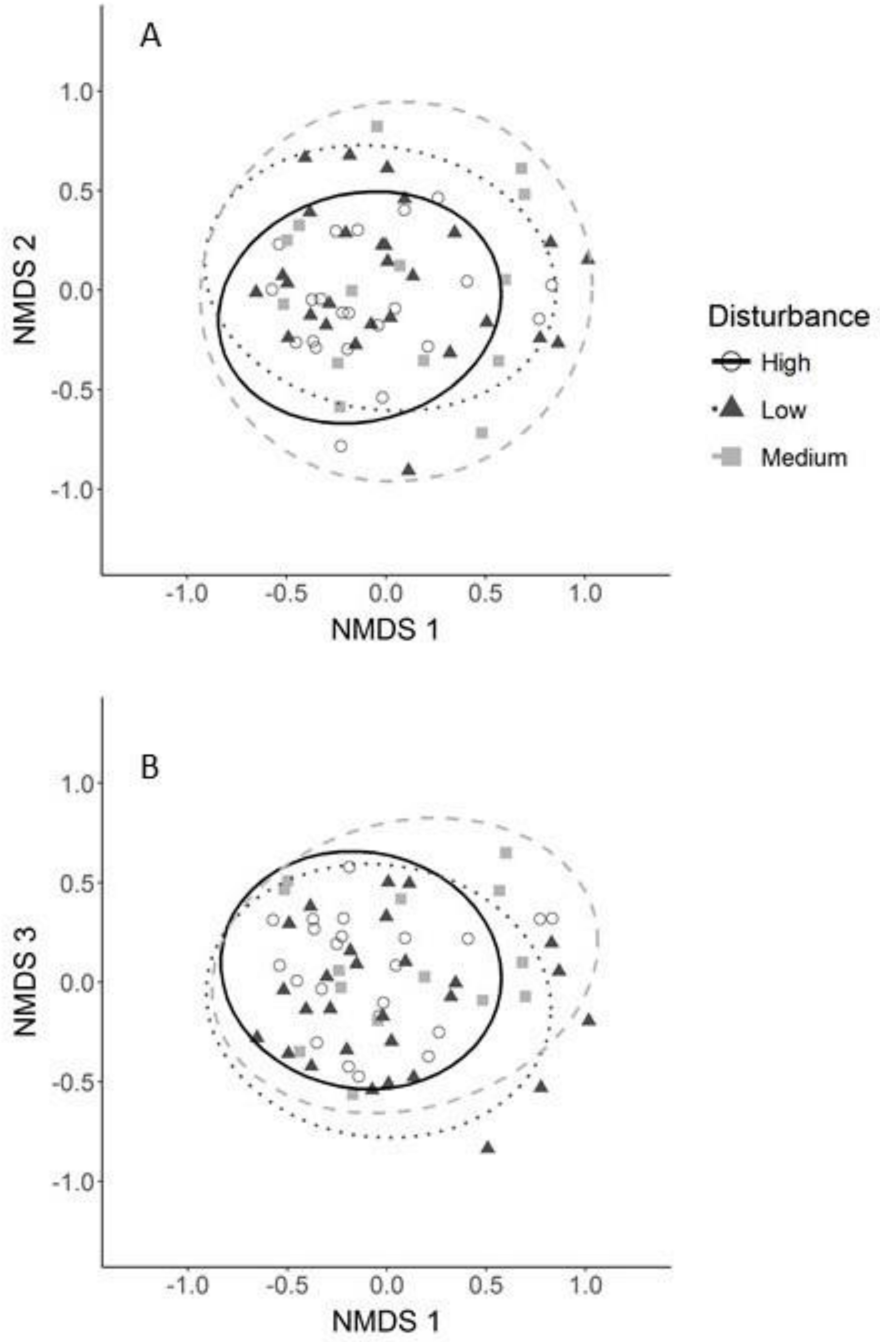

Figure 2-3 NMDS ordination of 64 NPPR wetlands in taxa space with sites symbolized by disturbance category (white circles = low, grey circles = medium, black circles = high) and 90% confidence ellipses overlaid. The optimal solution had three axes (2A = axes 1 and 2; 2B = axes 1 and 3). There is no obvious grouping between disturbance categories and all categories strongly overlap on all three axes.

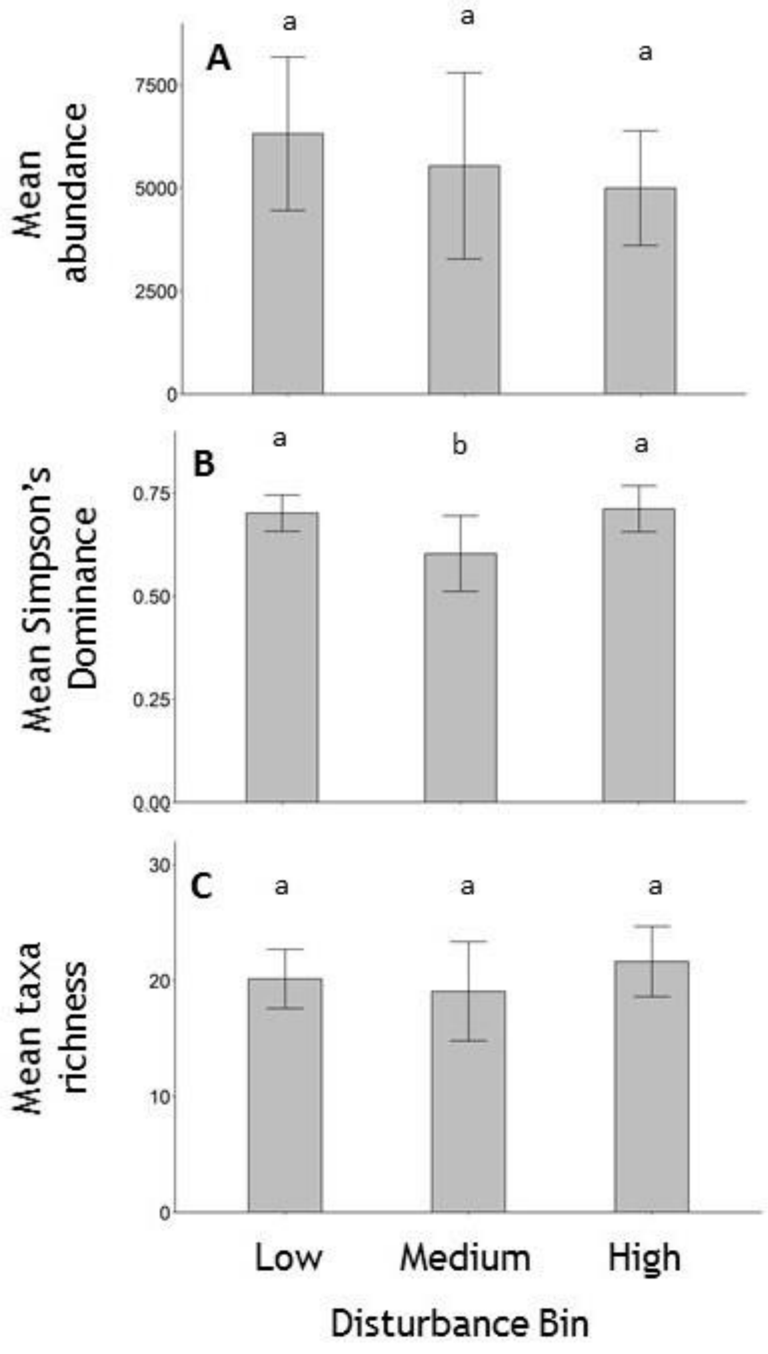

Figure 2-4 Bar charts displayed a) average macroinvertebrate abundance; b) average Simpson's Dominance and c) average taxa richness for each disturbance bin (based of the extent of non-natural land cover in a 500 m buffer surrounding each wetland). Error bars are standard error. Bars with the same letters are not significantly different (*post-hoc* Tukey's multiple comparisons tests, alpha = 0.05).

3. Cyclic drying determines macroinvertebrate community structure in Northern Prairie Potholes

3.1 Introduction

The Northern Prairie Pothole Region (NPPR) is a unique landscape composed of marshes that range in size and hydroperiod (Davis and Bidwell 2008, Wrubleski and Ross 2011). Because they fill with snowmelt, these non-permanent marshes contain saturated soil and ponded water earlier than more permanent wetlands, which may still be frozen. They are a valuable habitat for many aquatic species, as the early availability of open water in these basins promotes early-spring productivity (Euliss and Mushet 2004, Johnson et al. 2010) and contributes to the biodiversity of the landscape (Semlitsch and Bodie 1998). Wetlands in the NPPR span a range in hydroperiod reflecting natural variation in wet and dry phases (Euliss et al. 2004). These wetlands are hydrologically isolated from one another except during flood-related fill-and-spill events, meaning that there is rarely any inflow or outflow in these systems (Marton et al. 2015, Hayashi et al. 2016). Most potholes are non-permanent, drying via evapotranspiration and groundwater recharge over the course of the summer (van der Kamp and Hayashi 1998, Hayashi et al. 2016) and are assigned to categories called permanence classes (Table 1-2; Stewart and Kantrud 1971). I refer to all marshes that experience periodic drying as non-permanent, as the terms ephemeral or temporary are associated with specific permanence classes (Table 1-2).

In addition to supporting waterbirds and wetland vegetation, NPPR marshes are home to diverse and abundant communities of macroinvertebrates. They are important trophic links between primary producers (aquatic vegetation and algae) and higher order consumers, such as nesting waterfowl (Wrubleski and Ross 2011). Aquatic macroinvertebrates are the most common bioindicators in rivers, streams and lakes with a history of effective use (Lenat 1988, Cairns and Pratt 1993, Rosenberg and Resh 1993, Resh et al. 1995, Bonada et al. 2006, Jones et al. 2007, Stewart and Downing 2008); however, their response to land use and their effectiveness as bioindicators in wetlands has yielded conflicting results (review in Batzer 2013). Many NPPR wetlands exist in human modified landscapes composed of cropland or cattle pasture, which has prompted research into bioindicator potential of wetland macroinvertebrates. In Alberta, odonates respond negatively to grazing pressure (Foote and Rice Hornung 2005, Silver and Vamosi 2012), and there is evidence that crop production may affect macroinvertebrates indirectly by increasing the concentration of phosphorus in wetlands (Silver et al. 2012a). Similar research in North Dakota wetlands determined that agriculture negatively impacts the resting egg bank of pothole wetlands (Euliss and Mushet 1999). However, the largest sampling effort of aquatic macroinvertebrates across Alberta's non-permanent marshes to date revealed no association to the extent of surrounding agriculture or grazing intensity (see Chapter 2). Conclusions that invertebrates are only weakly related to surrounding land use are broadly supported across the NPPR. For example, Tangen et al. (2003) studying invertebrates in North Dakota and Liu (2016) looking at Chironomidae across all of Alberta, both discovered only weak associations with land use.

If wetland invertebrates are sensitive to land use in the NPPR, the relationship is likely masked by other, more influential factors. Prior studies have commonly concluded that fish presence is an important driver of invertebrate community composition and diversity in wetlands (Zimmer et al. 2000, Tangen et al. 2003, Hanson et al. 2005, Rennie and Jackson 2005, Hornung and Foote 2006, McParland and Paszkowski 2006, Hentges and Stewart 2010, Chester and Robson 2013). For example, a study of 19 semi-permanent prairie wetlands in Minnesota observed that the presence or absence of fathead minnows was the most important factor in structuring aquatic invertebrate communities (Zimmer et al. 2000). Wetlands with fish supported less diverse and less abundant invertebrate communities that were dominated by Corixidae (Zimmer et al. 2000). A study of larger, more permanent wetlands in the prairie pothole region of North Dakota similarly determined that fish predation structured aquatic macroinvertebrate communities and lowered taxa richness (McLean et al. 2016a). Fish affect macroinvertebrate communities indirectly by increasing turbidity and decreasing vegetation density (Sundberg et al. 2016). Climate can also structure these communities: increased rainfall in North Dakota's pothole region has resulted in formerly fishless systems now containing fathead minnows and other fish species, resulting in a decline in macroinvertebrate diversity with potential negative impacts on waterfowl (McLean et al. 2016b).

However, most prairie pothole wetlands at the northernmost extent of the NPPR (in Alberta, Canada) do not support fish populations or large predaceous amphibians that might fill a similar ecological role (e.g., Benoy 2008). As NPPR wetlands are fishless systems, aquatic macroinvertebrates can be the top predators as well as primary consumers. Zimmer et al. (2000) identified two secondary factors (besides fish predation) that influenced invertebrate community composition: the abundance of aquatic plants and average wetland depth. In the absence of fish predation, these may be the primary determinants of invertebrate community composition; however, a causal interpretation of Zimmer et al.'s (2000) results is challenging because aquatic plant abundance was negatively correlated with both fish presence and water depth. Using path analysis, Maurer et al. (2014) assessed the direct and indirect relationships between fish and invertebrates in 34 permanent marshes in Iowa. They concluded that fish indirectly reduced invertebrate diversity by increasing turbidity, which caused a reduction in plant abundance, suggesting that predation was not the main mechanism of effect. Further, they discovered that deeper wetlands had a higher probability of supporting fish, suggesting that the relationship Zimmer et al. (2000) observed between invertebrates and water depth might even be spurious; the result of depth being confounded with fish presence.

The salinity of ponded water also influences macroinvertebrate composition, though results in pothole wetlands are conflicted. For example, salinity was important in structuring macroinvertebrate communities in Alberta (Silver et al. 2012a); however, a study from North Dakota discerned that macroinvertebrates were not responsive to salinity (Tangen et al. 2003). Globally, studies frequently conclude that macroinvertebrate communities are primarily influenced by both salinity and hydroperiod. The macroinvertebrates inhabiting Spain's temporary wetlands are structured by first conductivity (a proxy for salinity) and then maximum water depth (Florencio et al. 2014). In Ireland, macroinvertebrate taxa richness in temporary ponds declined as salinity increased (Porst et al. 2012). Salinity also had a negative impact on taxa richness in France, though longer hydroperiods increased taxa richness (Waterkeyn et al. 2008). Similarly, research in southern Brazil concluded that hydroperiod affected macroinvertebrate richness, abundance and composition (Moraes et al. 2014). Salinity is often influenced by hydroperiod in non-permanent wetlands: as water evaporates, the salts are conserved leading to increased concentrations (Euliss et al. 1991). However, this is complicated by groundwater recharge and discharge (van der Kamp and Hayashi 2009, Euliss et al. 2014) and run-off events (Hayashi et al. 2016) which makes it difficult to predict salinity from water depth or hydroperiod.

In the North America, there is some debate regarding the mechanism by which hydroperiod affects macroinvertebrates. In Ohio wetlands, canopy cover was the structuring factor of macroinvertebrate communities and there was little influence of either hydroperiod or water chemistry (Plenzler and Michaels 2015), though most research from the NPPR argue the importance of hydroperiod (Batzer and Wissinger 1996, Euliss and Mushet 2004) and large woody vegetation is usually sparse here. Hydroperiod likely does affect the canopy cover of emergent vegetation, as the taxonomic composition and physical structure of the macrophyte community is dependent on hydroperiod (van der Valk and Davies 1980, van der Valk 2005). Macroinvertebrates are affected by the community composition and physical structure of aquatic vegetation, which acts as a food source, refuge, egg laying substrate and an emergence platform (Batzer and Wissinger 1996, Foote and Rice Hornung 2005, Mabry and Dettman 2010, Florencio et al. 2014).

Macroinvertebrates are also directly affected by variation in hydroperiod as it determines how long aquatic stages have to mature or how essential active dispersal or a desiccation-tolerant life stage is for survival in ephemeral systems (Wiggins et al. 1980, Thorp and Covich 1991, Bischof et al. 2013). To be successful in non-permanent marshes, macroinvertebrates must have a life history that allows them to survive periodic drying. Options include either dispersing to more permanent waters if the wetland draws down or entering a desiccation resistant phase to pass the time between wet periods. All such organisms likely possess a rapid rate of development during the wet phase to allow them to complete the life stages that are incapable of dispersing or tolerating desiccation before time runs out. Wiggins et al. (1980) devised a framework for classifying macroinvertebrates based on their survival strategies in non-permanent marshes. He proposed four different strategies: 1) year-round residents which are incapable of active dispersal and can tolerate the drawdown period (tolerators), 2) early recruits which must oviposit on water (wet layers), 3) late recruits which can oviposit in the dry basin (dry layers), and finally 4) active dispersers which move to a more permanent water body during draw down (dispersers; Table 3-1). Whereas desiccation resistant taxa and late recruits (dry layers) likely experience no difficulty surviving in non-permanent marshes, early recruits (wet layers) are likely excluded from wetlands with very brief hydroperiods.

Other popular frameworks for categorizing aquatic macroinvertebrates include those based on food acquisition (functional feeding groups e.g., Table 3-2; Merrit et al. 2008) or microhabitat preference (behavioural guilds e.g., Table 3-3; Lancaster and Downes 2013). These functional traits are used in community ecology to describe aquatic invertebrate assemblages (e.g., Poepperl 1999, Rawer-Jost et al. 2000, Cummins et al. 2005, Ruhí et al. 2013a, Kovalenko et al. 2014). In harsh environments (such as short hydroperiods), there is typically a higher overlap of functional groups (Ruhí et al. 2013a) in addition to lower taxa richness (Zokan and Drake 2015). Rather than supporting specialists unique to non-permanent marshes, I expect that wetlands with briefer hydroperiods will be occupied by generalist macroinvertebrates, because of their ability to tolerate a wide range of conditions and their flexibility in resource needs. This likely assists them in surviving periodic drying (Batzer and Wissinger 1996, Wrubleski and Ross 2011, Silver et al. 2012b). They may also find non-permanent marshes a refuge from predation, as these habitats exclude large predators (Collinson et al. 1995) and are rich in nutrients (Euliss and Mushet 2004). Thus, I expect that it is advantageous for aquatic macroinvertebrates capable of persisting in non-permanent marshes to colonize these habitats.

3.1.1 Objectives and hypotheses

I aim to characterize the aquatic macroinvertebrate communities for each wetland permanence class based on their behavioural guilds and functional feeding groups, as well as their desiccation and dispersal strategies. If hydroperiod is driving macroinvertebrate distribution, I expect aquatic macroinvertebrate community composition will differ among the four marsh permanence classes (temporary, seasonal, semi-permanent and permanent). I should observe distinct communities based on functional groups and behaviours in each wetland class. In more temporary waters, taxa that can oviposit in dry basins or survive desiccation will dominate. Similarly, I should observe more climbers, burrowers, sprawlers and clingers in these wetlands, as their preferred microhabitats remain available despite brief hydroperiods. In contrast, the skater, swimmer and diver behavioural guilds should be more abundant in wetlands with longer hydroperiods where open water is persistent. Finally, I predict that there will be fewer functional feeding groups present in temporary wetlands than permanent, as there is typically a greater overlap of taxa with similar functional groups in harsher environments.

3.2 Methods

3.2.1 Study region and wetland selection

Aquatic macroinvertebrate sampling and environmental covariate collection occurred during the spring and summer of 2014 and 2015 in the NPPR of Alberta. The wetlands sampled spanned two major Natural Regions: the Parkland and the Grassland (Figure 3-1; Downing and Pettapiece 2006). Within each Natural Region, three sub-watersheds were selected based on their shared post-glacial geomorphology and because they were each largely contained within a single Natural Region. The wetlands were initially surveyed via satellite imagery and aerial photography, as well as the provincial merged wetland inventory geospatial data layer (Government of Alberta, 2014). The sites were verified in the field and site selection occurred at the beginning of May each year, based on field confirmation of size and permanence class. In total, 87 wetlands were sampled covering four permanence classes (Table 1-2; temporary n = 21, seasonal n = 35, semi-permanent n = 17, permanent n = 14). The frequency distribution of different permanence classes in the sample was proportional to their frequency distribution in the population of wetlands in our study sub-watersheds, as determined from the Government of Alberta's provincial wetland inventory (Government of Alberta, 2014).

3.2.2 Macroinvertebrate sampling

To capture seasonal changes in the macroinvertebrate community, sampling occurred in mid-May, early June and late June. In wetlands possessing both an open water and an emergent vegetation zone, I collected aquatic macroinvertebrates from both habitats. I collected three replicate quantitative macroinvertebrate samples from each zone if present (Figure 2-2). The emergent zone typically consisted of sedges, cattails or other hydrophytes which emerge from shallow standing water. The open water zone was characterized by ponded water without emergent vegetation and typically contained submerged aquatic vegetation (SAV). Open water was often lacking in wetlands with brief hydroperiods, in which case only the emergent zone was sampled. In some cases, the wetlands dried partially or completely between site visits.

Each quantitative macroinvertebrate sample comprised two sub-sample components: a water column and either a submerged or emergent vegetation sample. This sampling method is a modified version of the Meyer et al. (2013) quadrat-column-core method (Q-C-C) which provides higher estimates of abundance and biomass for most taxonomic groups than D-net sampling. I collected benthic core samples, but do not report on them, as the macroinvertebrate abundance in these was extremely low and they contributed no novel taxa to the list obtained by processing the water column and vegetation quadrat components (see Chapter 2, Appendix 10). Water column sub-samples were collected using an acrylic tube (10 cm in diameter) submerged until just above benthic layer. I emptied the resulting water column sample into a 500 µm sieve to collect macroinvertebrates. For the vegetation sub-sample, I placed a 0.25 m^2 floating quadrat on the surface of the water. In the emergent zone, I clipped and collected all emergent vegetation in this quadrat within 2 cm of the substrate. For the open water zone, I used a rake to collect any SAV within the water bounded by the floating quadrat. I rinsed the clipped or raked vegetation to dislodge clinging macroinvertebrates before draining the rinse water through a 500 µm sieve. This rinsing and sieving procedure was repeated until all the vegetation had been processed. The three replicate water column samples and the three replicate vegetation quadrat samples were composited separately to preserve distinctions between microhabitats. I preserved these composite samples in 95% ethanol. This yielded as many as four samples from each wetland on each sampling occasion: 1) a water column from the open water zone, 2) a water column from the emergent zone, 3) a vegetation quadrat from the open water zone, and 4) a vegetation quadrat from the emergent zone (Figure 2-2).

3.2.3 Hydroperiod and water chemistry

I installed a staff gauge at the deepest point of each wetland in early May to monitor changes in water depth. Each wetland was visited seven times throughout the summer (May through August) and I recorded the water depth at the staff gauge on each visit as well as the date the wetland went dry (if applicable). The average maximum water depth was 0.51 m ± 0.23 (standard deviation). I also took *in situ* readings of water conductivity (DiST 5 EC/TDS/Temperature Tester – HI98311, Hanna Instruments) and turbidity (AquaFluor Handheld Fluorometer and Turbidimeter, Turner Designs) during each site visit. In May, I collected bulk water samples to measure nutrients (nitrogen, phosphorus, carbon) and dominant cations (calcium, magnesium, potassium, sodium). The bulk water samples were analysed at the University of Alberta’s Biogeochemistry Lab. A list of all abiotic variables collected can be found in Appendix 4.

3.2.4 Vegetation area

I categorized the dominant vegetation types in each wetland to the following categories: broad-leaved emergent, narrow-leaved emergent, robust emergent and woody vegetation. In July, I delineated the vegetation groups using a high-precision GPS (SX Blue II receiver, Genq Inc., Montreal, Quebec) to determine the total area of each group per wetland. I then calculated the percent area of each vegetation group based on the total wetland area.

3.2.5 Macroinvertebrate sorting and identification

My macroinvertebrate sorting, identification and data quality control procedures are based on a modified version of the Canadian Aquatic Biomonitoring Network (CABIN) laboratory protocol (Environment Canada 2014). I identified macroinvertebrates to family-level (Appendix 2 for taxa list) following Clifford 1991, Jones et al. 2007, Merrit et al. 2008. I recorded the total number of individuals of each taxon in the sample. Water column samples were sorted in their entirety, but vegetation samples were analyzed using a Marchant box (Marchant 1989) to an enumeration total of 300, following the method recommended by Environment Canada (2014). Marchant box sampling was coupled with a timed (two minute) search for large, rare individuals.

3.2.6 Functional groups

Based on a review of relevant literature (e.g., Cummins and Klug 1979, Wiggins et al. 1980, Clifford 1991, Thorp and Covich 1991, Williams 1998, Merritt et al 2002, Cummins et al. 2005, Merrit et al. 2008, Oliveira and Nessimian 2010, Lancaster and Downes 2013), I assigned each macroinvertebrate taxon observed to a desiccation strategy (Table 3-1), functional feeding group (Table 3-2), and behavioral guild (Table 3-3; see Appendix 2). In some cases, there were within-taxon discrepancies (e.g., most chironomids are gathering collectors but some are predaceous) and in these instances, I selected the most common functional group for that family. I then created three trait-based matrices by tallying the number of individuals of each strategy, group, or guild present in each wetland.

3.2.7 Statistical analysis

All my statistical analysis was performed using R (R Core Team 2016). Multivariate analyses were all based on macroinvertebrate density data or functional trait (strategy, guild or group) density data. The sample unit was the individual wetland. My samples from different microhabitats were standardized to the per m^2 unit and then summed. Samples from different vegetation zones and different sampling dates were averaged. This data reduction process resulted in a single count for each taxon at each wetland. My functional trait matrices were created by summing the counts of all taxa belonging to the same desiccation strategy, functional feeding group, or behavioral guild. For multivariate analysis of macroinvertebrate density, I removed rare taxa (observed at fewer than five sites) to reduce sparsity (Peck 2010). I then relativized the data by the maximum value for that taxon or group to reduce the influence of highly abundant taxa. Finally, these counts were converted to a distance matrix using the Bray-Curtis coefficient.

I used non-metric multi-dimensional scaling (NMDS) ordination to visualize trends in the macroinvertebrate community data and environmental covariates. NMDS was performed on the distance matrices (Bray-Curtis) for the taxa-level data and the three functional group level data (four separate ordinations in total) using the function ‘metaMDS’ in the *vegan* package (Oksanen et al. 2016). The optimal number of dimensions for each NMDS solution was selected based on observations of the scree plot and final stress scores (see Appendix 8). In the NMDS plots, sites were symbolized by permanence class and ninety percent confidence ellipses were delineated to help visualize differences in community composition. To visualize the structure of community composition (or functional traits) and its relationship to environmental covariates, I created joint plots using the ‘envfit’ function in *vegan* (Oksanen et al. 2016). Those covariates or taxa strongly correlated with at least one NMDS axis were overlayed as vectors (at $r^2 > 0.20$ for taxa or groups and at $r^2 > 0.10$ for environmental covariates). All graphing was performed using the R package *ggplot2* (Wickham 2009).

I used multi-response permutation procedures (MRPP) on the taxa abundance and the functional trait Bray-Curtis distance matrices using the ‘mrpp’ function in *vegan* (Oksanen et al. 2016) to determine if community composition differed significantly among permanence classes. Group size was used to weight groups ($C_{i=}{}^{n_i}/_{N}$) as recommended by McCune and Grace (2002). Afterward, pairwise comparisons using MRPP were performed and a Bonferroni adjusted p-value was applied to determine which permanence classes differed from one another.

3.3 Results

I identified macroinvertebrates from over 600 samples collected from 87 wetlands, finding 62 taxa and over 2,250,000 individuals (Appendix 2). The average taxa richness and abundance per site (± standard deviation) were 22.31 ± 7.61 taxa and 6776.19 ± 5617.31 individuals per m^2 respectively. The most common and abundant macroinvertebrates were chironomids, which were present in every wetland with a total abundance double that of the second most abundant taxon (Ostracoda). Other abundant taxa included oligochaetes, nematodes and two gastropod families (Planorbidae and Lymnaeidae). After chironomids, the most abundant insect families were Ceratopogonidae, Dytiscidae, Lestidae and Culicidae.

3.3.1 Macroinvertebrate community composition

The optimal NMDS solution for the macroinvertebrate abundance matrix had three axes and a final stress of 18.08 after 87 iterations (Figure 3-2; Procrustes: RMSE = 0.0003, max residual = 0.0022). The related ($r^2 > 0.10$) hydrologic variables were: 1) the day of year the wetland dried (Julian calendar day), 2) the maximum water depth, 3) the percentage of open water present and 4) amplitude of water depth change expressed as a percentage of the maximum depth. These variables were related to axes one and three, resulting in a clear segregation of permanence classes along both axes (Figure 3-2). A visual analysis of the plots reveals permanent wetlands clustering tightly together. In contrast, temporary wetlands exhibit much larger variability in community composition. Unexpectedly, most water chemistry variables were either unrelated or only weakly associated with this ordination. The only exception was the concentration of sodium cations (Na; $r^2 > 0.10$). The percent area of vegetation groups (robust emergent, narrow leaved emergent, woody vegetation, ground cover) were not strongly associated with any ordination axis (see Appendix 5 for all joint plot scores). To visualize which taxa covaried with the significant NMDS axes, taxa which were strongly related to the NMDS solution ($r^2 > 20$) were overlayed as vectors on the same ordination solution (Figure 3-2).

Macroinvertebrate community composition differed significantly among wetland permanence classes (MRPP: $A = 0.019$, $p < 0.0001$). Post-hoc pairwise comparison tests with Bonferroni corrected p-values suggest that the macroinvertebrate community composition in temporary wetlands was statistically distinct from semi-permanent and permanent marshes and that the community composition in seasonal wetlands was significantly distinct from the communities in permanent wetlands. In other words, the most ephemeral and most permanent wetlands support distinct assemblages of aquatic macroinvertebrates, but there is a gradual transition in community composition between these extremes.

3.3.2 Functional traits

I performed three separate NMDS ordinations and MRPP analyses, one on each distance matrix: 1) desiccation strategies, 2) functional feeding group and 3) behavioural guild.

The desiccation strategies ordination had an optimal NMDS solution of three dimensions and a final stress of 9.96 after 31 iterations (Figure 3-3; Procrustes: RMSE = 0.0005, max residual = 0.004). Hydroperiod was related to axes one and three, resulting in a segregation of permanence classes. Axis one was related to groups more associated with longer hydroperiods (wet layers and dispersers). The wetland permanence classes had distinctly different macroinvertebrate communities based on desiccation strategies (MRPP: $A = 0.025$, $p = 0.01$) although *post-hoc* Bonferroni adjusted comparisons suggested that this difference was only significant between temporary/seasonal wetlands and permanent wetlands.

The optimal NMDS solution for the Bray-Curtis dissimilarity matrix based on the abundance of different functional feeding groups had two dimensions, with a final stress of 15.1 after 63 iterations (Figure 3-4; Procrustes: RMSE < 0.0001, max residual = 0.0001). As with the taxonomic community ordination, there was a segregation of permanence classes along axis one (which was associated with the dry date and maximum water depth at $\mathrm{r}^2 > 0.10$). Functional feeding groups with a strong association ($r^2 > 0.20$) were overlayed as vectors on the ordination. Different wetland permanence classes did support statistically different composition of functional feeding groups (MRPP: $A = 0.034$; $p = 0.001$) and *post-hoc* Bonferroni adjusted comparisons revealed that temporary and permanent wetlands differed (significantly different: temporary versus semi-permanent and permanent; seasonal versus permanent).

For the behavioural guilds, the NMDS ordination had a final stress of 12.3 after 81 iterations and three axes (Figure 3-5; Procrustes: RMSE = 0.0007, max residual = 0.006) and axis one was associated with a gradient of water depth ($r^2 > 0.10$). The MRPP revealed that permanence classes differed significantly in their behavioural guild composition ($A = 0.017$, $p = 0.016$); however, *post-hoc* pairwise Bonferroni adjusted comparisons suggest that the source of this difference is that the assemblage of behavior guilds inhabiting temporary marshes differs from that in semi-permanent marshes.

3.4 Discussion

My goal was to explore the community ecology of aquatic macroinvertebrates in NPPR marshes to assess what environmental covariates drive community composition. I discovered that community composition of macroinvertebrates differs significantly among wetland permanence classes. The differences in macroinvertebrate communities are primarily reflected between the extremes (temporary and permanent classes) with a transition in community composition along a gradient in hydroperiod. All measures of hydrology were strongly associated with variation in community composition: dry date, maximum water depth, open water area and the amplitude of water depth change (see Appendix 4 for all variables). This research complements other studies of aquatic macroinvertebrate communities that stress the importance of hydroperiod and pond depth in structuring aquatic invertebrate communities (e.g., Brooks 2000, Tarr et al. 2005, Waterkeyn et al. 2008, Porst et al. 2012, Schriever and Williams 2013, Bischof et al. 2013, Moraes et al. 2014).

Water quality, measured by conductivity, turbidity, dominant cations and nutrients (phosphorus, nitrogen and carbon) was not strongly associated with the major gradients in community composition. Similar results were detected by Plenzler and Michaels (2015), yet this finding remains surprising. Other wetland studies have cited the importance of salinity (e.g., Preston and Ray 2016), turbidity (Stewart and Downing 2008, Wyss et al. 2013, Maurer et al. 2014) and phosphorus (McCormick et al. 2004, Silver et al. 2012a) to macroinvertebrates. There was an association between sodium concentration and community composition, but conductivity (my measure of salinity) was not related to community composition. I suspect that the lack of response to salinity in these wetlands may be due to the relatively low range in conductivities I observed in my freshwater wetlands (average conductivity: 0.52 ± 0.62 mS/cm; Appendix 4) and the overwhelming influence of hydroperiod. For the other water quality parameters to have so little influence on macroinvertebrate community composition, I conclude that water quantity and the duration of inundation (i.e., hydroperiod) imposes a much stronger constraint on macroinvertebrates in these NPPR marshes than water quality. I also observed no effect of wetland size on macroinvertebrate community composition, while Ren et al. (2016) concluded that macroinvertebrates were structured by the area of temporary rock pools, in addition to depth and water volume. While wetland size can be indicative of hydrology in some systems (Tarr et al. 2005) and result in higher macroinvertebrate taxa richness (Schriever and Williams 2013), I suspect the area of NPPR wetlands is often unrelated to maximum depth and hydroperiod and does not impose restrictions upon macroinvertebrate communities (e.g., Snodgrass et al. 2000). In the 87 wetlands in my study, I determined that the area of the wetland did not predict the maximum depth (linear regression: $R^2 = 0.006$).

3.4.1 Differences in community composition among permanence classes

Most taxa present in temporary wetlands were more abundant in wetlands with longer hydroperiods, suggesting that temporary wetlands support the subset of taxa that are freed from the constraint of hydroperiod by behavioral or life history adaptations. This supports my hypothesis that generalist taxa would occupy all marshes, but sensitive taxa, lacking adaptations to periodic drying, would be excluded from ephemeral wetlands due to the constraints placed on their development time and reproductive strategies. My results support prior work which determined that shorter hydroperiods support fewer macroinvertebrate taxa (Zokan and Drake 2015). Other studies of aquatic macroinvertebrate communities have also discovered the same nested taxonomic pattern (as opposed to turnover) along a gradient of hydroperiod (Baber et al. 2004, Wissinger et al. 2009, Silver et al. 2012b, Ruhí et al. 2013b). In addition to shorter hydroperiods having lower richness due to the exclusion of taxa which cannot survive frequent drawdown (Batzer and Wissinger 1996, Silver et al. 2012b), Baber et al. (2004) suggested that this nested pattern was a result of increased colonization rates and decreased extinction rates in permanent wetlands. The influx of new taxa and a lack of local extinction leads to a nested pattern along a hydrological gradient, rather than a replacement or turnover of taxa.

Only two taxonomic groups were more abundant in temporary wetlands when compared with their abundance in permanent wetlands: Culicidae and Anostraca. These groups have fast development times and desiccation resistant eggs, and Anostraca require a drought phase for eggs to complete development (Thorp and Covich 1991, Merrit et al. 2008). Both groups were also associated with short hydroperiods in Wisconsin wetlands (Lillie 2003). What remains to be explored in future work are the patterns of diversity among permanence classes and whether the same generalist taxa are found consistently across all temporary wetlands, or whether there is substantial turnover among temporary wetlands.

The differences in the behavior and habitat preferences of the taxa that varied in abundance along axis two suggest that it reflects differences in the extent or structure of emergent vegetation versus open water. For example, corixids were positively associated with axis two and these swimmers are usually in the water column. Experimental studies involving habitat manipulation in wetlands have observed that corixids, in addition to chironomids and hydrophilids, increase in number in response to the mowing of wetland vegetation (Batzer and Resh 1992, de Szalay and Resh 2000). The taxa negatively associated with this axis were Pyralidae and Tipulidae, neither of which are swimmers. Pyralids are aquatic lepidopterans which spend their larval stage feeding on hydrophytic vegetation and some mine into plant stalks and leaves (Clifford 1991). Tipulids are typically benthic dwellers and are important detrivores that feed on decomposing plant matter (Merrit et al. 2008). I determined that the spatial extent of the dominant vegetation groups was not related to the ordination solution, but I suspect that this area measurement is not an appropriate surrogate for vegetation stem density or physical structure, nor did it account for submerged aquatic vegetation. The structure, density and composition of aquatic vegetation are drivers of macroinvertebrate community composition (Batzer and Wissinger 1996), as well as functional group composition (Hornung and Foote 2006) and taxa richness (Remsburg and Turner 2009).

The area of open water habitat within the wetland and the maximum depth were the covariates most strongly related to axis three. I observed Libellulidae to be strongly associated with deeper wetlands, and these predacious taxa are common in permanent wetlands without fish (Tarr et al. 2005). The behaviours characteristic of the taxa most strongly differentiated on this axis again suggest that vegetation structure could be an important covariate. Hydrophilids increase in abundance in less vegetated habitats (de Szalay and Resh 2000), whereas the odonates associated with this axis belong to the climber and sprawler behavioural guilds, meaning they climb submerged vegetation stalks or rest on the benthic layer. In Wisconsin wetlands, odonate taxa from climber and sprawler guilds were associated with an increase in submerged vegetation (Remsburg and Turner 2009). Greater study is required to confirm the association of wetland vegetation with variance in macroinvertebrate community composition along the gradient in water depth. A challenge will be that wetland vegetation is also sensitive to water depth (e.g., Zimmer et al. 2000), and separating the influence of hydroperiod from the influence of vegetation could be problematic.

3.4.2 Desiccation strategies and functional groups

There has been extensive study of how aquatic macroinvertebrates persist in non-permanent wetlands in North America (e.g., Wiggins et al. 1980, Bataille and Baldassarre 1993, Williams 1998, Lillie 2003, Silver and Vamosi 2012, Bayley et al. 2013, Schriever and Williams 2013, Leslie and Lamp 2016) and globally (Waterkeyn et al. 2008, Florencio et al. 2016, Ren et al. 2016, Strachan et al. 2016). As expected, the abundance of wet layers, which require ponded water to lay eggs, and dispersers, which can relocate to permanent habitats, were both positively associated with increasing hydroperiod (Figure 3-3), revealing that these two strategies are particularly sensitive to marsh permanence. Although I anticipated that macroinvertebrate taxa possessing suitable desiccation strategies might benefit from predator release (e.g., Collinson et al. 1995) or perhaps competition release due to the exclusion of sensitive taxa from more ephemeral wetlands (e.g., Culcidae in Meyabeme Elono et al. 2010), I did not observe any strategy that was more abundant in less permanent wetlands. The abundance of ‘generalist’ tolerators, which cannot actively disperse and possess a desiccation resistant stage, and dry layers, which can oviposit into dry basins, are both largely independent of hydroperiod (Figure 3-3). Hydroperiod acts as a constraint on taxa lacking appropriate adaptations to survive periodic drying while species possessing appropriate adaptations are freed from the constraint of hydroperiod, resulting in the pattern of nestedness observed in this and other research (Baber et al. 2004, Wissinger et al. 2009). Clearly, water quality is not constraining the abundance of tolerators and dry layers, but perhaps the structure of wetland vegetation plays a role as, in addition to providing both a refuge and a food source (Foote and Rice Hornung 2005, Plenzler and Michaels 2015), it is important to have vegetation appropriate for dry layers to oviposit into (Batzer and Wissinger 1996).

Most functional feeding groups were more abundant in more permanent wetlands. Piercers were strongly correlated with open water area and water depth, indicating that these predators (including Corixidae) are restricted to larger, more permanent marshes. Corixids are diving hemipterans that must disperse when the water draws down in non-permanent marshes (Wiggins et al. 1980) so it is not their predatory behavior that explains their exclusion from temporary marshes. The filterer group proves an exception, with variation in the abundance of filter feeders being slightly negatively correlated with permanence (Figure 3-4). Culicidae were the most abundant filter feeders collected, and as described above, this taxon possesses a rapid larval and pupal development as well as desiccation resistant eggs. Its resistance to periodic drying and association with more ephemeral wetlands is therefore not related to its method of feeding. The abundance of other filter feeders, such as Hydrazoa, were positively associated with wetland hydroperiod. Thus, I conclude that the apparent associations between functional feeding groups and water permanence are likely spurious, and more a reflection of other traits possessed by the taxa dominating the feeding groups.

No macroinvertebrate behavioural guild was associated with temporary wetlands, but other research has concluded that wetland macroinvertebrates typically have high functional group overlaps (i.e., taxa in constrained or 'filtered' habits share the same traits; Ferreira et al. 2012, Ruhí et al. 2013a, Schriever and Lytle 2016). Again, there is a separation of groups along the axes which were not correlated with any environmental variable measured here which may suggest a difference in vegetation structure (e.g., climber taxa versus divers and burrowers).

3.4.3 Conclusions and future work

This research encompasses the most comprehensive dataset set of macroinvertebrates from the non-permanent wetlands of the NPPR to date. The use of multivariate analyses allows us to examine the effect of periodic drying on aquatic macroinvertebrate communities. Temporary and permanent wetlands supported distinct macroinvertebrate communities, but less permanent wetlands did not support novel taxa. Rather, the taxa occupying temporary marshes are a nested subset of those occupying more permanent marshes, where they typically reached higher abundances. In other words, I observed nestedness in community composition across the hydroperiod gradient, not turnover. Taxa with no desiccation resistant stage or which require water to lay eggs were strongly associated with permanent wetlands. The subset of taxa not excluded in temporary marshes possess adaptations that allow them to survive the periodic drying of temporary and seasonal marshes. These adaptations alleviate the constraints on abundance imposed by periodic drying, but most of these taxa are not achieving greater abundances in less permanent marshes. Instead, other factors must constrain their abundances, but my hypotheses that land use (Chapter 2) or water quality (Chapter 3) might be responsible for variation in macroinvertebrate taxon abundance are not supported by my data. Although hydroperiod is clearly a strong predictor of macroinvertebrate community composition, a significant proportion of variation in community composition remains unexplained.

The abundance of vegetation was identified as an important factor in structuring communities of macroinvertebrates in shallow prairie lakes (Paukert and Willis 2003), and the abundance of both plants and course organic particulate matter in the water column is positively related to both macroinvertebrate abundance and diversity (Hentges and Stewart 2010). Further research is recommended to explore the role of vegetation in shaping macroinvertebrate communities in fishless non-permanent marshes of the NPPR. While local factors such as hydroperiod undoubtedly affect macroinvertebrate community composition, other regional factors might include wetland position in the landscape and the spatial configuration of wetland habitat. Groups of macroinvertebrates with the ability to disperse may be more likely to inhabit temporary wetlands if there is a larger water body nearby which can act as a source of refuge during the drawdown period (Davis et al. 2013). This also raises questions about the initial colonization of temporary wetlands each spring. Colonization rates may differ between different taxonomic groups, based on their dispersal strategies (review in Bilton et al. 2001) and the surrounding landscape. For example, active dispersers such as Chironomidae and Coleoptera are often the first taxa to colonize newly created ponds (Coccia et al. 2016). Temporary wetlands in close proximity to permanent marshes or lakes may experience more immigration than isolated temporary wetlands (e.g., Hall et al. 2004).

However, one of the advantages of using temporary wetlands is that they fill more quickly in the spring from snow melt while permanent bodies of water remain frozen. Taking advantage of the early availability of aquatic habitat in temporary wetlands is enabled by the resting egg bank (analogous to the plant seed bank; Gleason et al. 2004). The resting egg bank is critical to replenish macroinvertebrates populations in temporary and seasonal marshes each spring (Gleason et al. 2004). The relative contributions of the resting egg bank and immigration from proximate permanent waters may be responsible for the large degree of variation in community composition I observed in temporary wetlands. Regarding these wetlands in the context of metacommunities (e.g., Leibold et al. 2004) connected via dispersal and landscape factors, in addition to local factors (such as hydroperiod and vegetation structure) may provide insight into the drivers of macroinvertebrate community composition. This would shed light on both wetland and invertebrate ecology, and highlight how environmental variables affect these complex communities.

3.5 Figures

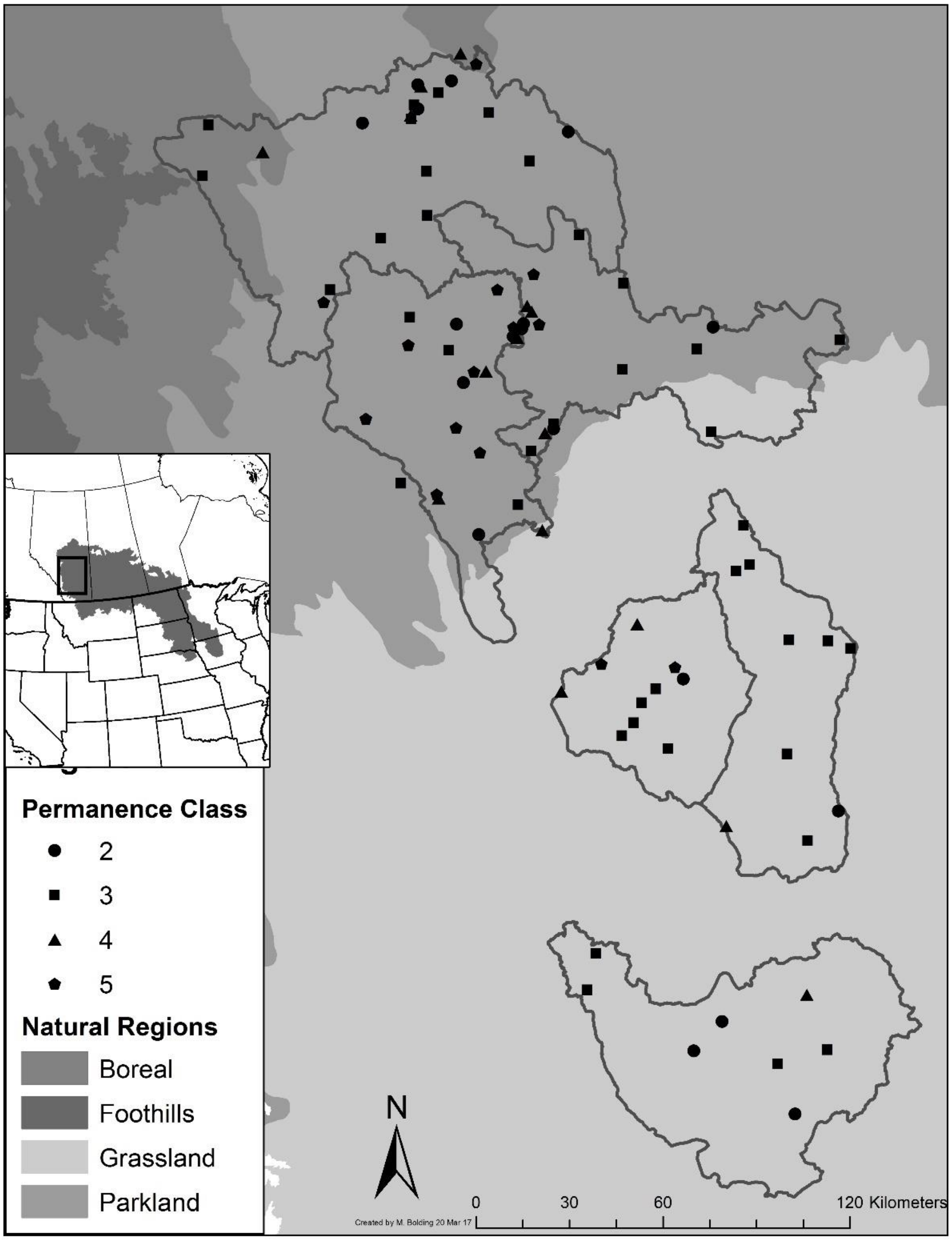

Figure 3-1 A map of the NPPR with 87 wetland sites with varying hydroperiods. Sites are shape coded by wetland permanence class (total n = 87; temporary n = 21, seasonal n = 35, semi-permanent n = 17, permanent n = 14) based on Stewart and Kantrud's classifications (1971). The study area encompasses six sub-watersheds and two Natural Regions.

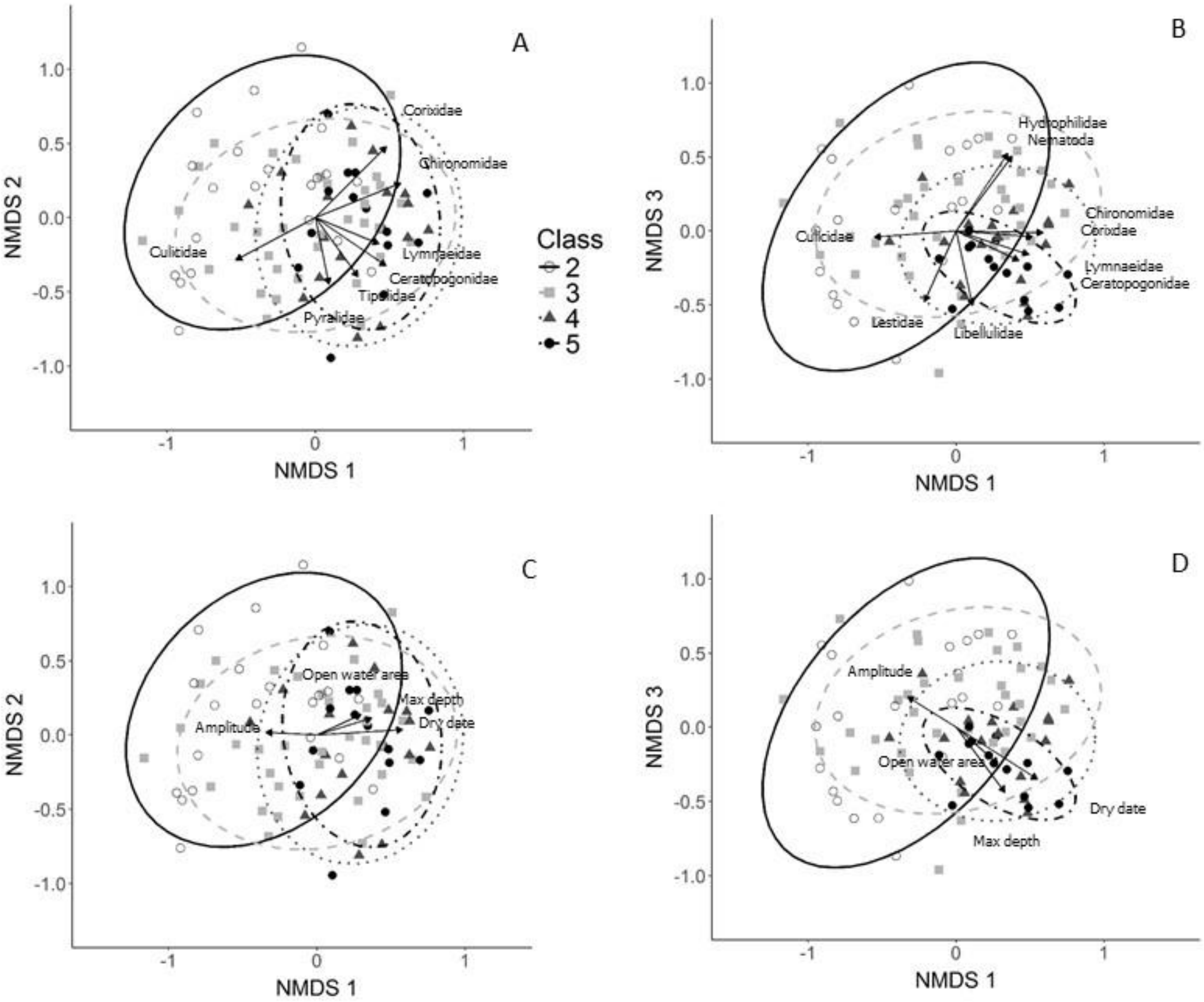
A
NMDS 2
NMDS 1
Corixidae
Chironomidae
Culicidae
Lymnaeidae
Ceratopogonidae
Tipulidae
Pyralidae
Class
2
3
4
5
B
NMDS 3
NMDS 1
Hydrophilidae
Nematoda
Chironomidae
Corixidae
Culicidae
Lymnaeidae
Ceratopogonidae
Lestidae
Libellulidae
C
NMDS 2
NMDS 1
Open water area
Max depth
Dry date
Amplitude
D
NMDS 3
NMDS 1
Amplitude
Open water area
Dry date
Max depth

Figure 3-2 Non-metric multidimensional scaling (NMDS) ordinations of macroinvertebrate community composition in 87 wetlands in the Northern Prairie Pothole Region of Alberta. Symbols represent individual wetlands arranged in ‘species space,’ with point shape and colour representing wetland permanence class. Ninety percent confidence ellipses around the sites belonging to each permanence class help illustrate differences in community composition among classes. For each set of axes, strongly related taxa ($r^2 > 0.20$; 3A and 3B) were overlayed as vectors. The identical ordination solutions were then overlayed with related hydrologic factors below ($r^2 > 0.10$; 3C and 3D).

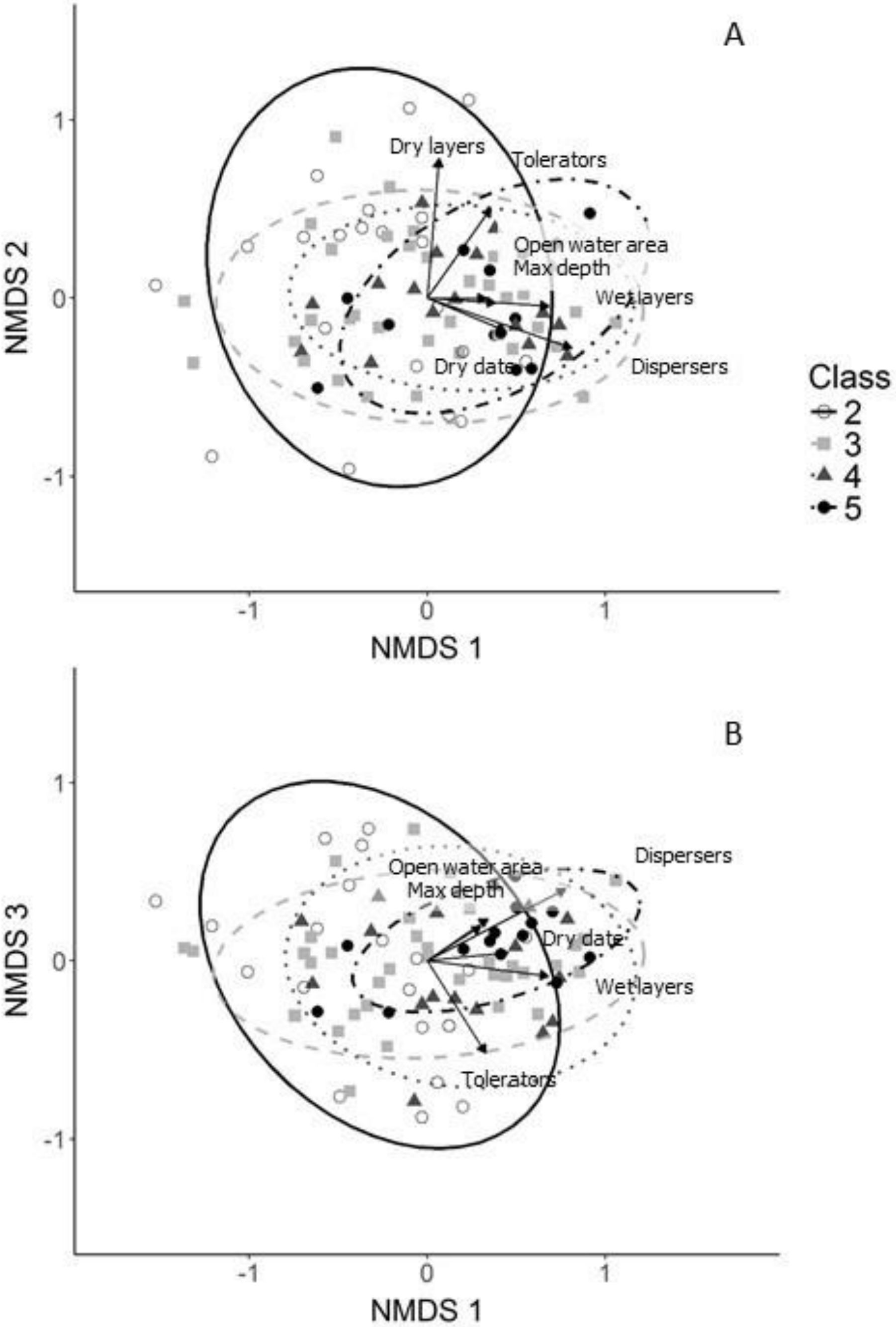

Figure 3-3 Non-metric multidimensional scaling (NMDS) ordinations of Wiggins et al. (1980) macroinvertebrate life history strategies in 87 wetlands in the Northern Prairie Pothole Region of Alberta. Symbols reflect wetland permanence class; ninety percent confidence ellipses depict groupings of each permanence. Related hydrologic factors ($r^2 > 0.10$) and strongly related behavioural guilds (all $r^2 > 0.35$) are overlayed as vectors.

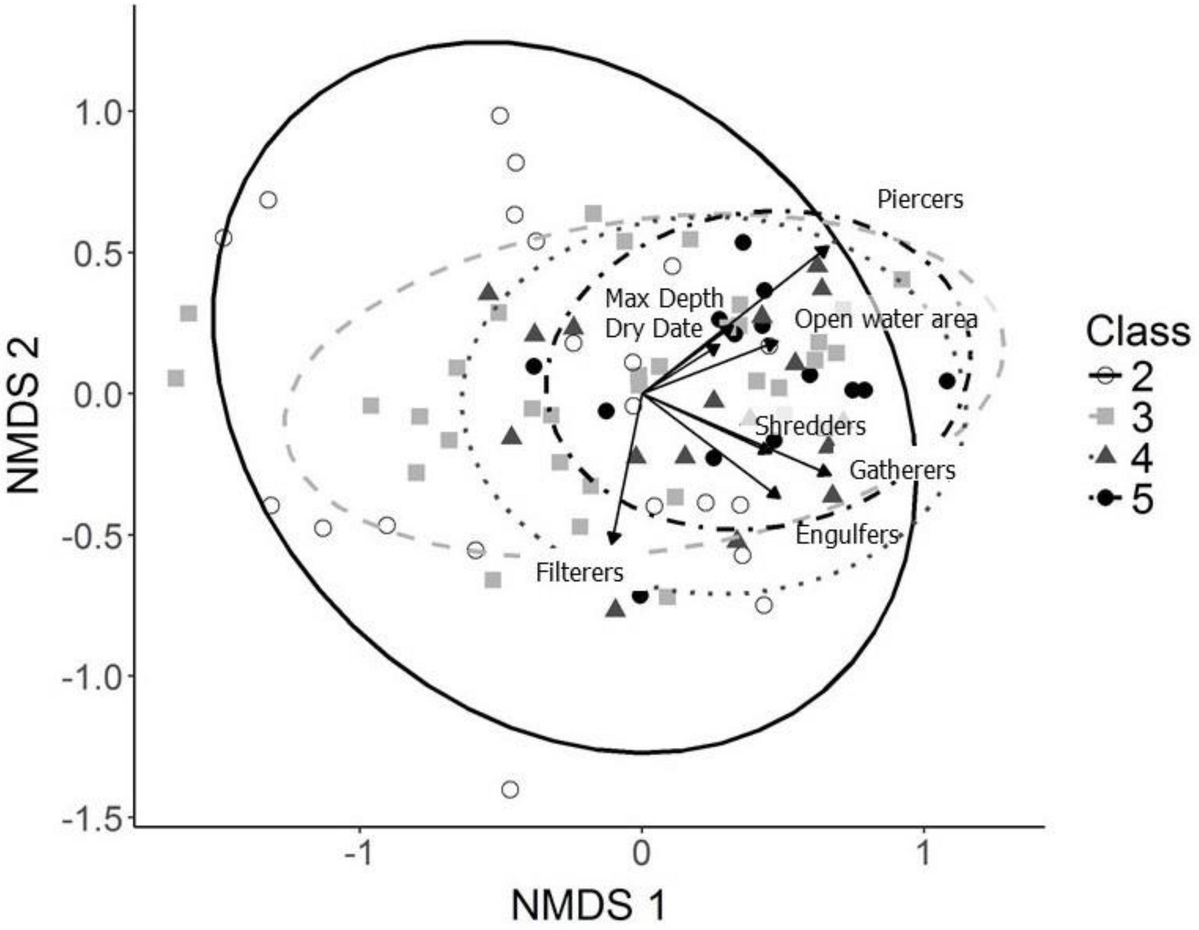

Figure 3-4 Non-metric multidimensional scaling (NMDS) ordination of macroinvertebrate functional feeding groups in 87 wetlands in the Northern Prairie Pothole Region of Alberta. Symbols represent individual wetlands arranged in ‘functional group space’, with point shape and colour representing wetland permanence class or hydroperiod. Ninety percent confidence ellipses have been delineated to depict groupings of each permanence class. Related hydrologic factors ($r^2 > 0.10$) and strongly related functional feeding groups ($r^2 > 0.20$) are overlayed as vectors.

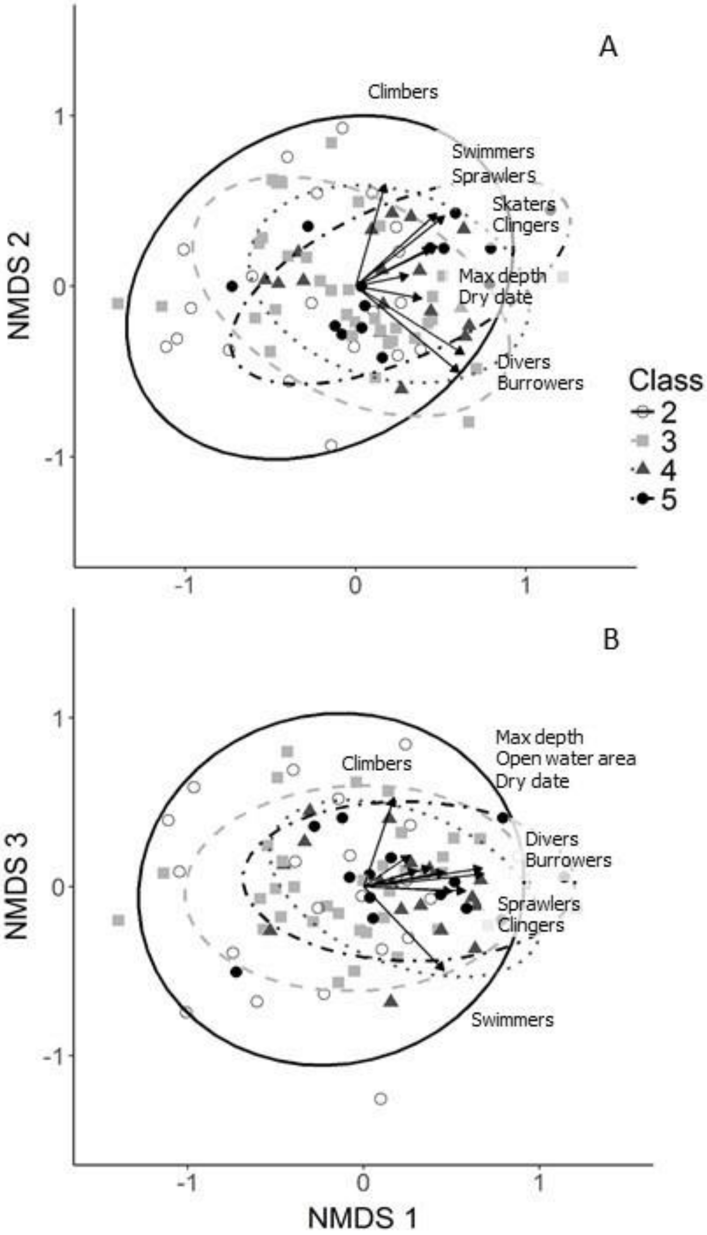

Figure 3-5 Non-metric multidimensional scaling (NMDS) ordinations of macroinvertebrate behavioural guilds in 87 wetlands in the Northern Prairie Pothole Region of Alberta. Symbols represent individual wetlands arranged in 'behavioural guild space', with point shape and colour representing wetland permanence class. Ninety percent confidence ellipses have been delineated to depict groupings of each permanence class. Related hydrologic factors ($r^2 > 0.10$) and strongly related behavioural guilds ($r^2 > 0.20$) are overlayed as vectors.

3.6 Tables

Table 3-1 A description of the life history strategy groups described by Wiggins et al. (1980) . These groups summarize the desiccation strategies of macroinvertebrates capable of inhabiting temporary waters. I named these groups for ease of reference.

Wiggins' group	Name	Description	Examples
1	Tolerators	Possess desiccation resistant stage at some point in life cycle, no active dispersal	Anostraca
2	Wet layers	Require some standing water to oviposit	Ceratopogonidae
3	Dry layers	Can oviposit in the dry basin or vegetation	Lestidae
4	Dispersers	Strong fliers which can actively disperse to larger water bodies, no desiccation tolerance	Corixidae

Table 3-2 A description of the main functional feeding groups of aquatic macroinvertebrates as they are used in this study, based on descriptions by Lancaster and Downes (2013).

Functional feeding group	Description	Examples
Filtering collectors	Collect small particles of food (plant, animal or detritus) floating in the water column using specialized feeding appendages	Amphipoda, Culicidae
Gathering collectors	Actively seek out vegetation or decomposing organic matter	Ephemeroptera, Chironomidae
Grazers/scrapers	Scrape layer of biofilm (algae and bacteria) from rocks and plant stems	Lymnaeidae, Planorbidae
Shredders	Feed on course plant matter floating or on the bottom, shredding mouthparts sends fine plant matter into the water column	Trichoptera
Engulfers	Actively hunt and consume prey by engulfing them	Lestidae, Libellulidae
Piercers	Actively hunt and consume prey using specialized piercing mouthparts	Corixidae, Gerridae
Parasites	Ecto-parasites of other aquatic organisms	Hydrachnida

Table 3-3 A description of the behavioural guilds of aquatic macroinvertebrates observed in the NPPR, after Merrit et al. (2008). Behavioural guilds are typically reflective of preferred microhabitats within a system.

Behavioural guild	Description	Example
Burrowers	Burrow under fine benthic sediments or into plant stems and roots	Oligochaetes, many Chironomidae
Climbers	Move vertically submerged vegetation stalks or other debris	Aeshnidae, Lestidae
Clingers	Maintain position by clinging to substrates using morphological adaptions (claws, silk, mucus)	Limnephilidae, Planorbidae
Divers	Move throughout the water column but come to the surface/meniscus for air and dive to feed/avoid predation	Dytiscidae, Culicidae
Skaters	Skate on the surface film of ponded water	Veliidae, Gerridae
Sprawlers	Rest on the surface of the benthic layer or the surface of submerged leaves	Caenidae, Libellulidae
Swimmers	Actively swim throughout the water column	Anostraca, Amphipoda

4. Local and regional diversity patterns of aquatic macroinvertebrates in temporary and permanent wetlands

4.1 Introduction

Community assembly describes how organisms from a larger regional species pool colonize and persist in novel habitats. The factors that influence community assembly and succession will ultimately affect the composition of that community (Connell and Slatyer 1977). The first step of community ecology is typically described as an abiotic ‘filter’ (any environmental stressor such as salinity or soil saturation) that eliminates taxa based on their specific tolerances (Kraft and Ackerly 2014). Once taxa have established in a local habitat, the community will also be shaped by biotic interactions (e.g., predation, competition), which are thought to promote the coexistence of taxa which make use of different resources or niches (Kraft and Ackerly 2014). The most prevalent models for explaining the patterns of assembly and diversity of a community are 1) the species-sorting or niche model, where the local environment and biotic interactions are the most important factors and any difference between local communities is due to environmental heterogeneity (Leibold et al. 2004); 2) the mass effect model, which suggests a distance-decay relationship where remote communities will encounter less immigration (i.e., the theory of island biogeography; MacArthur and Wilson 1967); and 3) the neutral model, which predicts that organisms in a community are ecologically similar and the community is structured largely by random effects relating to immigration, emigration, local extinctions and ‘ecological drift’ (see Shmida and Wilson 1985, Holyoak and Ray 1999, Hubbel 2001, Chave 2004).

Non-permanent wetlands undergo regular community disassembly at drawdown, whereby all macroinvertebrate taxa either disperse or enter a desiccation resistant stage, followed by community reassembly with the spring snowmelt and rainfall (O'Neill 2016). The Northern Prairie Pothole Region (NPPR) of Alberta, Canada contains many small, depressional wetlands which are responsible for numerous ecological services, including maintaining biodiversity (Semlitsch and Bodie 1998, Zedler and Kercher 2005, Wrubleski and Ross 2011). These wetlands are hydrologically isolated and fill each year with the spring snowmelt runoff and then progressively dry out during the summer via evapotranspiration (LaBaugh et al. 1998, Hayashi et al. 2016). A defining hydrological characteristic of these wetlands is the hydroperiod, or duration of ponded water, which can vary from a few weeks to permanently present. Prairie marshes are classified into permanence classes determined by their hydroperiod and identified by the typical vegetation zone in the most saturated region of the wetland (Table 1-2; Stewart and Kantrud 1971).

The wetlands of the NPPR can be viewed as isolated aquatic 'islands' in a sea of terrestrial habitat which aquatic organisms must cross to establish local populations (e.g., Brooks 2000, Figuerola and Green 2002), but due to their ephemeral nature, these habitats periodically desiccate and cease being usable from the perspective of aquatic macroinvertebrates. Aquatic macroinvertebrate communities in temporary wetlands thus provide a unique opportunity to examine metacommunity dynamics and patterns of diversity. A metacommunity is a collection of communities across a landscape that are connected via the dispersal of multiple interacting taxa (Leibold et al. 2004, Logue et al. 2011, Winegardner et al. 2012). Due to regular desiccation, non-permanent wetlands are entirely reliant on the resting egg bank (analogous to the resting seed bank of vegetation; Gleason et al. 2004), active dispersal from nearby ponds where organisms move among habitats, or passive dispersal where organisms are transferred from one patch to another (e.g., vectored by surface flows, transport by waterfowl; Swanson 1984; Brooks 2000). The regular desiccation and extirpation of these communities means that a new community must assemble each year, which may include a turnover of species and result in novel community compositions from year to year. For example, seminal research of taxa colonization of island habitats with high local extinction and immigration resulted in a high degree of taxonomic turnover (Simberloff 1976, Brown and Kodric-Brown 1977).

While local species richness (or alpha diversity; *sensu* Whittaker 1972) is a common measurement of diversity in community ecology, regional patterns of community composition can differ from those present in individual habitats (Crist et al. 2003). Beta diversity, the degree of turnover in community composition between habitat patches, provides an estimate of how variable community composition is within a region (Whittaker 1972, Chao et al. 2016). Typically, a greater regional species pool (i.e., larger gamma diversity; *sensu* Whittaker 1972) allows for more turnover among habitats (Rooney and Azeria 2014); however, this is not always the case. Although previous studies on aquatic macroinvertebrates in both North American (Brooks 2000, Silver and Vamosi 2012, Schriever and Williams 2013) and Western European (Collinson et al. 1995, Waterkeyn et al. 2008, Porst et al. 2012) wetlands have concluded that systems with longer hydroperiods have a higher alpha diversity relative to systems with short hydroperiods; studies examining beta diversity amongst wetlands of differing hydroperiod do not find the same pattern. In a large meta-analysis of wetlands across the Nearctic and Palearctic regions, Ruhí and Batzer (2014) reported that macroinvertebrate beta diversity may be equivalent in both short and long hydroperiod regimes, suggesting no relationship between community turnover and permanence class. In both streams and ponds, Schriever and Lytle (2016) observed a negative relationship between beta diversity and hydroperiod. In contrast, Zokan and Drake (2015) detected a non-linear relationship between the beta diversity of zooplankton and hydroperiod, which peaked in ponds of mid-range hydroperiod (Zokan and Drake 2015). Therefore, despite consensus that hydroperiod is positively associated with alpha diversity, there remains uncertainty around its relationship to beta diversity.

4.1.1 Objectives and hypotheses

Aquatic macroinvertebrates in wetlands are diverse with complex community relationships to environmental factors (review in Batzer 2013). In Chapter 3, I determined that hydroperiod is an important predictor of macroinvertebrate community composition and functional traits in marshes of the NPPR. I examined how community composition differed among permanence classes and observed low turnover across a gradient of hydroperiod, with the taxa present in temporary marshes comprising a subset of those present in permanent wetlands. However, I have yet to examine how macroinvertebrate diversity is influenced by hydroperiod in detail. In this chapter, I quantify macroinvertebrate abundance and evenness (the relative abundances of taxa), as well as alpha, beta, and gamma diversity and determine how these diversity measures vary among permanence classes. I place my findings within the context of the niche versus neutral debate and discuss the implications for community assembly of macroinvertebrates in non-permanent wetlands. I expect that average alpha diversity will be lowest in temporary wetlands and highest in permanent marshes, in keeping with other published studies that suggest briefer hydroperiods exclude sensitive taxa. However, there is greater uncertainty around how beta diversity might differ among permanence classes. There may be no relationship between taxa turnover and hydroperiod if all wetland classes are equally subject to the stochastic processes of immigration and extirpation, as was reported by Ruhí and Batzer

(2014). However, beta diversity may also decrease with wetland permanence, if a longer period between desiccation events provides greater opportunity for biological interactions to structure or homogenize the community and more time for succession to take place. This pattern was observed by Schriever and Lytle (2016) in both streams and ponds, but was attributed to high habitat heterogeneity in temporary systems. Lastly, it is possible that I will observe a unimodal relationship between hydroperiod and beta diversity, as was observed by Zokan and Drake (2015), who suggest that this is due to intermediate hydroperiods being less constrainted by deterministic processes (hydroperiod or predation) and therefore being more subject to stochastic influences.

4.2 Methods

4.2.1 Macroinvertebrate collection and identification

I collected macroinvertebrates from 87 wetlands in the NPPR of Alberta, Canada, between May-June in the summers of 2014 and 2015 (Figure 3-1). These wetlands spanned a range of hydroperiod and were assigned a permanence classes using Stewart and Kantrud's (1971) criteria for classifying prairie marshes as either temporary (n = 21), seasonal (n = 35), semi-permanent (n = 17), or permanent (n = 14). Most of these wetlands included both zones of emergent vascular plants and zones of open water. I collected macroinvertebrates from both the emergent vegetation and the open water zones (when present). I used both water columns and emergent vegetation clippings/submerged vegetation raking to collect macroinvertebrates making use of these different microhabitats (Figure 2-2). This protocol is based on the quadrat-column-core method, which yields higher counts of abundance and biomass for most invertebrate taxa than D-net sweeps (Meyer et al. 2013). For details on macroinvertebrate collection methods, refer to Chapter 3 (Section 3.2.2 Macroinvertebrate sampling).

I sorted macroinvertebrates to family-level and based my sorting and sub-sampling protocol on a modified version of the Canadian Aquatic Biomonitoring Network's laboratory methods (Environment Canada 2014). A list of all identified macroinvertebrates and their taxonomic resolution can be found in Appendix 2. The final matrix of macroinvertebrate identification resulted in an abundance value per m^2 (averaged across wetland visits) for each taxon per wetland. For a complete description of this protocol, refer to Chapter 3 (Section 3.2.5 *Macroinvertebrate sorting and identification*).

4.2.2 Data analysis

To determine if alpha diversity, abundance or evenness differed among wetlands of differing permanence class, I performed one-way analyses of variance (ANOVAs). I calculated alpha diversity using Jost's formula (Jost 2007) in the R package *vegetarian* with *q* set to taxa richness (Charney and Record 2012). I calculated Simpson's Index of Dominance (my measure of evenness) using the 'diversity' function in the R package *vegan* (Oksanen et al. 2016). It is expressed as the probability that two random individuals drawn from the group will belong to the same taxonomic group and is represented by the equation $D = \sum \left(\frac{n}{N}\right)^2$, where *D* is Simpson's Index of Dominance, *n* is the number of a particular taxon and *N* is the total number of all taxa in the pool (Magurran 2004). In this expression, if $D = 1$, all individuals would belong to the same taxon. Prior to each ANOVA, the assumption of normality of the residuals was visually assessed using plots of residuals against fitted values (Appendix 9) while homogeneity of variance was evaluated using Levene's test using the *car* package (Fox and Weisberg, 2011). Abundance data were square-root transformed prior to ANOVA to better approximate a normal distribution. Evenness values were squared prior to ANOVA to meet the assumptions of normality. After each ANOVA where a significant difference was detected among wetland permanence classes (alpha = 0.05), a Tukey's multiple comparison *post-hoc* test was performed.

Gamma diversity and the multiplicative beta diversity ($\beta = \gamma/\alpha$) were calculated for each permanence class separately as well as all wetlands together using Jost's diversity formulas (Jost 2007) in the R package *vegetarian* with *q* set to taxa richness (Charney and Record 2012). The decomposition approach to measuring beta diversity (Chao et al. 2016) is advantageous because it meets the constraints initially described by Whittaker (1972). Another advantage to this approach is that the formulas described by Jost (2007) make use of Hill numbers (or effective species numbers). The effective species number is the number of equally occurring species necessary to give the same value of S for a given diversity measure (species richness, Shannon diversity, Simpson diversity) which allow results to be directly compared among communities or across studies (Jost 2006, Chao et al. 2014). A disadvantage, however, is that this approach generates a single beta diversity value for each set (i.e., one value for each permanence class) that is calculated from the measured average alpha diversity and gamma diversity of the set. Because only a single diversity value is calculated per set there is no replication within sets and the statistical significance of differences in diversity among permanence classes cannot be assessed. They can, however, be compared qualitatively.

Beta diversity can also be measured in a pair-wise fashion by calculating the Bray-Curtis dissimilarity between each pair of wetlands sampled (Bray and Curtis 1957). If all pair-wise comparisons of wetlands of a single permanence class are considered as replicates, an average beta diversity and associated standard error can be calculated for each wetland permanence class. This replication permits statistical tests of significance on any differences in calculated beta diversity among permanence classes. (see Chao et al. 2016). I produced a Bray-Curtis dissimilarity matrix for each wetland permanence class using PC-ORD v. 6.0 (McCune and Mefford 2011) and then performed an ANOVA to assess whether beta diversity differed significantly among permanence classes. All statistical tests were performed using R (R Core Team 2016).

4.3 Results

The total macroinvertebrate abundance differed among wetland permanence classes (ANOVA $F_{2,83} = 3.053$, $p = 0.033$), due to abundance being significantly lower in temporary (mean ± standard error: 4838.67 ± 910.07) wetlands compared with semi-permanent ones (7749.58 ± 1105.75; Tukey's Multiple Comparisons, $p = 0.035$; Figure 4-1A). The evenness of macroinvertebrate communities was equivalent among the four permanence classes of NPPR wetlands (ANOVA $F_{3,83} = 1.975$, $p = 0.124$; Figure 4-1B). Finally, average alpha diversity was strongly and significantly different among wetland permanence classes (ANOVA $F_{2,83} = 18.97$, $p < 0.0001$), with all classes differing from one another except for semi-permanent and permanent marshes (Tukey's Multiple Comparison $p = 0.94$; Figure 4-1C). As expected, taxa richness increased with increasing permanence class.

Gamma diversity was the lowest in temporary wetlands and plateaued among seasonal, semi-permanent and permanent wetlands (Figure 4-2). However, differences in gamma diversity cannot be tested statistically because of the lack of replication. I performed two analyses of beta diversity for each wetland permanence class. The first was a traditional decomposition approach (Whittaker 1972) which displayed a negative relationship with hydroperiod. The second was based on a Bray-Curtis dissimilarity matrix. The average distance between sites in each permanence class was significantly different (ANOVA $F_{3,1028} = 73.37$, $p < 0.0001$). The results were analogous to the other approach with beta diversity exhibiting a negative relationship with hydroperiod (Figure 4-2). Only semi-permanent and permanent wetlands were not significantly different (Tukey's Multiple Comparisons, $p = 0.935$).

4.4 Discussion

My goal was to examine the patterns in diversity of aquatic macroinvertebrates along a gradient of hydroperiod and put my findings within the context of stochastic and species-sorting models for community assembly. I observed that permanent wetlands support a relatively taxa-rich community, indicated by higher average alpha diversity, but that the community present in permanent marshes is relatively predictable with low turnover in taxa from one permanent marsh to another. In contrast, the wetlands that experience the most rapid drawdown and typically dry out entirely each summer each support a relatively unique assemblage of macroinvertebrate taxa (higher beta diversity), even though these taxa are drawn from a smaller pool, as indicated by the lower gamma diversity in temporary marshes. This supports my hypothesis that hydroperiod is a major driver of community composition in wetlands in the NPPR, likely because periodic drying destabilizes the macroinvertebrate community and prevents succession to a more consistent assemblage.

4.4.1 Measures of diversity

Gamma diversity is the regional species pool, which is all the taxa in a specific region that could possibly immigrate into local site (Whittaker 1972, Kraft et al. 2015). This includes taxa which are well suited to the local environment, as well as taxa supported by other habitats in the region which may not be able to persist at a given site (Kraft and Ackerly 2014). Here, the regional species pool is all taxa present in the NPPR, while the within class gamma diversity values are the total number of taxa present in a particular class of wetland. The total gamma diversity for the NPPR wetlands in my study was higher (62) than the gamma diversity calculated for each wetland class (temporary = 44, seasonal = 56, semi-permanent = 54, permanent = 53), suggesting that the regional species pool is broader than that supported by each wetland class individually. Permanent aquatic habitats are typically associated with higher gamma diversity (Wellborn et al. 1996), whereas temporary wetlands should have a smaller gamma diversity because they will exclude taxa which do not possess drought-resistant strategies (i.e., Wiggins et al. 1980). I therefore believe this within class gamma value is a product of species-sorting by hydroperiod. Many ecological communities are structured by species-sorting effects, where environmental filtering is the first constraint on where taxa can live (Cottenie 2005). A caveat is that I observed that gamma diversity to be similar in seasonal, semi-permanent and permanent wetlands. Seasonal wetlands go dry by the end of the summer but contain ponded water for longer than temporary wetlands (Stewart and Kantrud 1971). I expected seasonal wetlands to possess an intermediate gamma diversity between temporary and permanent wetlands, and is unclear why alpha and gamma diversity don't follow the same pattern along a gradient of hydroperiod. However, I cannot assess whether the difference in gamma diversity among wetland classes is significant given the lack of replication.

The alpha diversity, or taxa richness, of macroinvertebrates increased with hydroperiod before plateauing at semi-permanent and permanent wetlands. This is in keeping with other studies relating macroinvertebrate diversity in aquatic systems to a gradient of hydroperiod (e.g., Wellborn et al. 1996, Brooks 2000, Tarr et al. 2005, Waterkeyn et al. 2008, Porst et al. 2012, Schriever and Williams 2013, Zokan and Drake 2015), although in floodplain wetlands, macroinvertebrate richness was highest in sites with intermediate hydroperiods (Whiles and Goldowitz 2005). Habitat connectivity is often an important factor determining alpha diversity in aquatic systems (Johnson et al. 2013a), as this dictates the likelihood of immigration of new species. However, NPPR wetlands are hydrologically isolated, which can limit the means of active and passive dispersal available to macroinvertebrates. Furthermore, the resting egg bank allows for some carry over of invertebrate taxa between wet cycles, regardless of habitat proximity or connectivity. The alpha diversity in a site is a product of the resting egg bank, active dispersal from other water sources and chance passive dispersal, followed by biotic interactions between the taxa which have established in the wetland (Wiggins et al. 1980). The distance-decay or island biogeography theory is therefore often difficult to apply to temporary aquatic habitats (Angeler and Alvarez-Cobelas 2005).

I attribute the lower alpha diversity that I observed in temporary wetlands instead to the exclusion of taxa that cannot withstand short hydroperiods. I discovered that the taxa present in temporary wetlands were not unique to this permanence class, but rather a subset of those present in other permanence classes (e.g., the nested pattern observed in Chapter 3). This finding is in agreement with work by Silver et al. (2012b), who compared temporary wetlands to permanent wetlands in Alberta, and reported that most of the macroinvertebrate taxa inhabiting temporary wetlands were also present in permanent wetlands. The nested pattern in macroinvertebrate community along a hydroperiod gradient suggests that macroinvertebrate establishment in temporary wetlands is strongly influenced by environmental filtering that excludes desiccation intolerant taxa. Unstable environments typically have subsets of taxa from stable habitats (Brendonck et al. 2015), which emphasizes the role of environmental filtering (i.e., the species-sorting model) in structuring communities. In contrast, a wider pool of macroinvertebrate taxa is capable of surviving the environmental conditions characteristic of permanent wetlands, leaving a greater number of taxa to interact via competition and predation. Because environmental filtering in permanent marshes is less severe, the ultimate structure of macroinvertebrate communities of permanent marshes is more influenced by biological interactions than by environmental filtering alone.

The consequence is that, despite having a greater alpha diversity, permanent wetlands have lower beta diversity, as these habitats are subject to the stabilizing influences of biological interactions over a much longer period of time. Whereas the composition of macroinvertebrates in temporary wetlands, though ultimately governed by the environmental filter of hydroperiod, retain more of a signal of the stochastic processes tied to colonization, such as immigration and dispersal. In support of this, I discovered that both measures of beta diversity (Whittaker's decomposition beta and a Bray-Curtis distance measure beta) were highest in temporary wetlands. My results thus disagree with the lack of pattern between beta diversity and hydroperiod observed by Ruhí and Batzer (2014) and the unimodal pattern reported by Zokan and Drake (2015). If community assembly were governed by purely by random processes, I would expect the beta diversity of temporary wetlands to be lower than in permanent wetlands due to the smaller species pool capable of colonizing and persisting in temporary sites. In other words, random draws with replacement from a smaller pool of taxa should more commonly yield equivalent assemblages than random draws with replacement from a larger pool of taxa. This theory has been related to metaphors about rolling dice; a 20-sided die should result in more unique number combinations than a six-sided die for a given set of rolls (see Shipley 2010). My results contradict this expectation, suggesting that although they may have some influence on the initial colonization of a marsh, stochastic processes are not governing community assembly in permanent wetlands.

My results are consistent with other studies examining the effect of hydroperiod on aquatic macroinvertebrate communities, which suggest a negative relationship between beta diversity and hydroperiod length. For example, in both Arizona streams and ponds in Ontario, beta diversity was higher in temporary habitats than permanent ones despite alpha diversity being lower in temporary aquatic systems (Schriever and Lytle 2016). The high beta diversity in both rivers and ponds with short hydroperiods was attributed to high habitat heterogeneity between sites (Schriever and Lytle 2016). However, in a large meta-analysis, Ruhí and Batzer (2014) observed that macroinvertebrates demonstrated high turnover of taxa (and thus high beta diversity) in both temporary and permanent wetlands. Ruhí and Batzer (2014) calculated beta diversity from a dissimilarity matrix and both permanent and non-permanent wetlands had values approaching one (e.g., infinite diversity). The beta diversity value reported by Ruhí and Batzer (2014) is higher than the beta observed in my dataset likely due to their study achieving greater taxonomic resolution and comprising a broader regional comparison (a continent versus a single region).

Non-permanent wetlands have been suggested to support high macroinvertebrate beta diversity due to increased habitat heterogeneity (Florencio et al. 2014). Habitat heterogeneity has been cited as an important factor in supporting high biodiversity in other wetland systems such as bogs (Kato et al. 2009) and floodplains (Zilli et al. 2008). However, in the NPPR, temporary wetlands are likely to be more environmentally similar to each other as they typically only contain one main vegetation zone (wet prairie/meadow zone), while wetlands with longer hydroperiods can have a variety of vegetation zones (wet meadow, emergent vegetation, open water, etc.; see Stewart and Kantrud 1971). The presence of fish or other vertebrate predators can result in homogenous communities (i.e., low beta diversity) of prey organisms such as macroinvertebrates (Chase et al. 2009) and could potentially explain low beta diversity values in other permanent aquatic systems, but the NPPR wetlands in this study did not contain fish. It is therefore unclear what mechanisms are driving this pattern, but I expect it is related to the repeated succession of these communities.

4.4.2 Community assembly

The opposing theories of niche and neutral community assembly shaped early community ecology and prompted numerous discussions in the decades which followed. These theories are still relevant today, particularly with a recent shift towards metacommunity analyses (Leibold et al. 2004) and research examining the relative importance of stochastic effects versus environmental filtering on community structuring (e.g., Logue et al. 2011; Adams et al. 2014; Mendes et al. 2015; Brown et al. 2016; Stoll et al. 2016). The periodic desiccation of non-permanent wetlands resets the assembly process in these habitats, and thus they remain in a non-equilibrium state. The communities in non-permanent habitats disassemble each year and the colonization process must occur again. Colonization (dispersal processes and establishment) is the first step in many ecological models, followed by biotic interactions (Hargeby 1990), yet it would appear that the same taxa do not colonize or persist in each non-permanent habitat (suggested by a high beta diversity value). The high beta diversity in these communities suggests a large turnover in taxa present between environmentally similar habitats.

I suggest that species-sorting is the most important factor determining community assembly in marshes in the NPPR, as the taxa that cannot withstand periodic desiccation are excluded from the local habitat. However, in temporary wetlands, the stochastic immigration and local extinction processes invoked by the neutral model of community assembly are also in evidence, as there is an extremely high turnover in taxonomic composition of these ‘tolerant’ taxa among temporary marshes. In more stable permanent marshes, biological interactions among macroinvertebrate taxa might be responsible for the homogenization of the community.

In contrast, the stochastic signature of immigration and local extinction are more important community assembly determinants in the less stable temporary wetlands that have briefer periods of inundation between periods of desiccation. Looking at the relative importance of neutral versus niche theory in aquatic odonate nymph communities, Mendes et al. (2015) detected that environmental (niche) effects were the most important structuring factor. However, generalist or tolerant species, were not constrained by filtering processes and more subject to stochastic effects (Mendes et al. 2015). This is in accordance with my results, where species-sorting processes were responsible for structuring communities with respect to hydroperiod, yet the desiccation tolerant taxa were less restricted by the deterministic constraints of frequent droughts and were more subject to chance effects. It is likely both deterministic and stochastic processes interact to form macroinvertebrate communities across the NPPR. Similarly, species-sorting and neutral theories were both stressed as important for structuring macroinvertebrate communities in New Zealand streams (Thompson and Townsend 2006), indicating further research may find ways to reconcile the two theories (e.g., Gewin 2006, Chase and Myers 2011).

4.4.3 Macroinvertebrate abundance and evenness

Macroinvertebrate abundance was highest in permanent wetlands with a gradual increase along the permanence gradient. This is consistent with previous work comparing macroinvertebrate communities between non-permanent and permanent ponds in Alberta (Silver et al. 2012b) and Massachusetts, USA (Brooks 2000). I suspect that deeper, more permanent wetlands can support more macroinvertebrates because of the increased water volume. Evenness was low across all the wetlands due to high abundances of certain taxa, regardless of wetland permanence class. These abundant taxa included chironomids, ostractods, oligochaetes and snails, which agrees with prior characterizations of marsh macroinvertebrates (Hentges and Stewart 2010). Thus, I detected no difference in evenness among permanence classes.

4.4.4 Implications for conservation

Land use can decrease aquatic insect beta diversity by increasing habitat homogeneity (Sueyoshi et al. 2016). Despite the fact that temporary and seasonal wetlands support high macroinvertebrate diversity, these systems are preferentially lost compared with larger, permanent wetlands due to agricultural activity (Semlitsch and Bodie 1998, Serran and Creed 2016). When small wetlands are plowed over or drained, the water in catchments pools in any remaining wetlands. This results in wetland consolidation, where the natural hydroperiod of remaining wetlands are altered and they become deeper and more permanent (McCauley et al. 2015, Wiltermuth and Anteau 2016). Since permanent wetlands largely support the same taxa, this results in a loss of diversity in the landscape, even if the alpha diversity in permanent wetlands is higher than in temporary ones.

When planning conservation efforts, it is important to consider diversity across multiple scales (see Soininen 2010, Socolar et al. 2016) because the loss of a few seemingly ‘unimportant’ small wetlands could drastically reduce gamma diversity and alter the natural hydroperiod of nearby wetlands. It is also important to address the influence of climate change on temporary communities across the landscape as these habitats are especially vulnerable (i.e., Davis et al. 2016). Finally, this research could provide insight into the importance of maintaining variable hydroperiods when restoring wetlands. For example, Anderson (2017) observed that restored wetlands in the NPPR were mostly deep, permanent wetlands which did not support the same waterbird communities present in natural wetlands. I expect macroinvertebrate communities would exhibit the same response based on the low beta diversity values observed here. The restoration or creation of wetlands with briefer hydroperiods could allow for the colonization of macroinvertebrates which assist the maintenance of regional diversity (Coccia et al. 2016), especially since macroinvertebrate communities in wetlands with short hydroperiods could be more susceptible to the effects of climate change (Sim et al. 2013). It is essential to conserve natural hydroperiods and habitat heterogeneity when mitigating wetland loss in order to promote high biodiversity at multiple scales.

4.4.5 Conclusions and future directions

I observed that macroinvertebrate abundance and alpha diversity increased along a gradient of hydroperiod, but that beta diversity was highest in temporary wetlands and decreased with permanence class. This provides insight into the influence of hydroperiod on macroinvertebrate communities and diversity patterns in the NPPR, but also raises questions for future work. It is possible that beta diversity was being underestimated at the family-level of taxa identification (Bringloe et al. 2016) and future work could focus on genus or even species-level identification. It is likely that macroinvertebrate dispersal capabilities play a role in beta diversity (Curry and Baird 2015) and it would be interesting to evaluate beta diversity from a functional group perspective. While this work examined spatial diversity across a large region of Alberta, I did not address the temporal component of beta diversity analysis. Aquatic invertebrate beta diversity patterns could differ between years (Korhonen et al. 2010), or even across a season (Florencio et al. 2009, 2016), stressing the importance of long-term monitoring. Finally, future work should address whether taxa abundance and richness in non-permanent wetlands are influenced by the proximity of a permanent water body. I believe non-permanent habitats can be used as effective case studies for examining the process of community assembly and ultimately in reconciling neutral and niche theories.

4.5 Figures

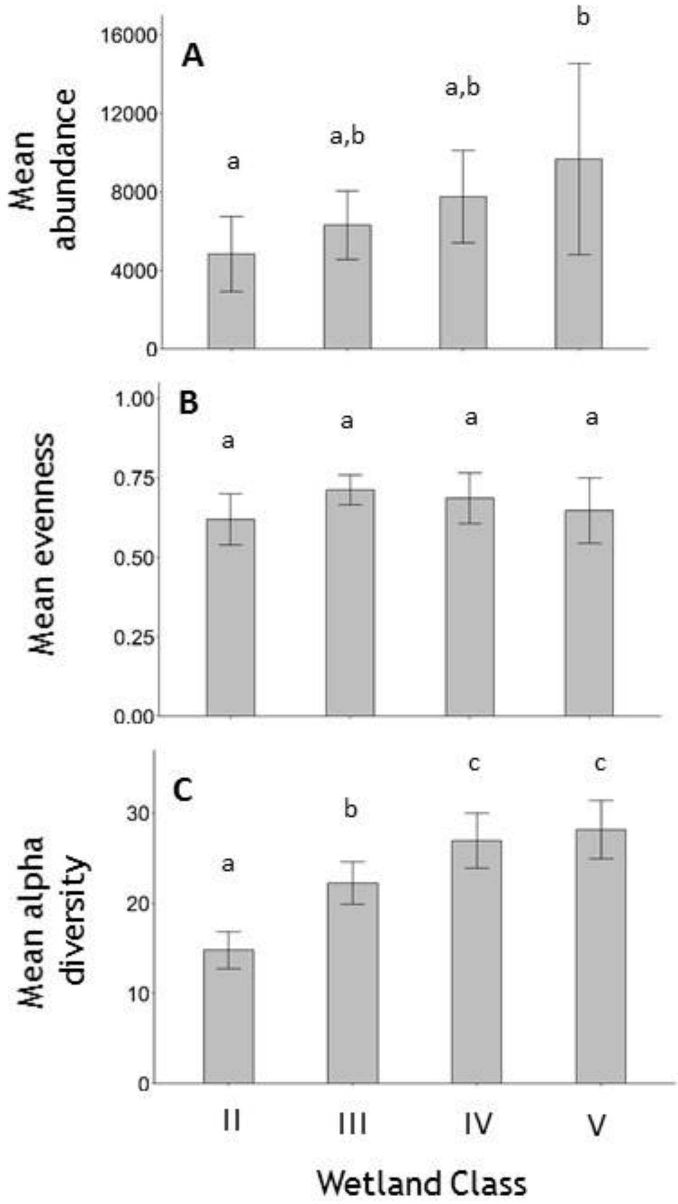

Figure 4-1 Bar charts displaying average a) average total abundance per m^2 of macroinvertebrates; b) average community evenness (measured as Simpson's diversity) and c) average alpha diversity for each permanence class. Error bars are standard error. Bars with the same letters are not significantly different (*post-hoc* Tukey's multiple comparisons tests, alpha = 0.05).

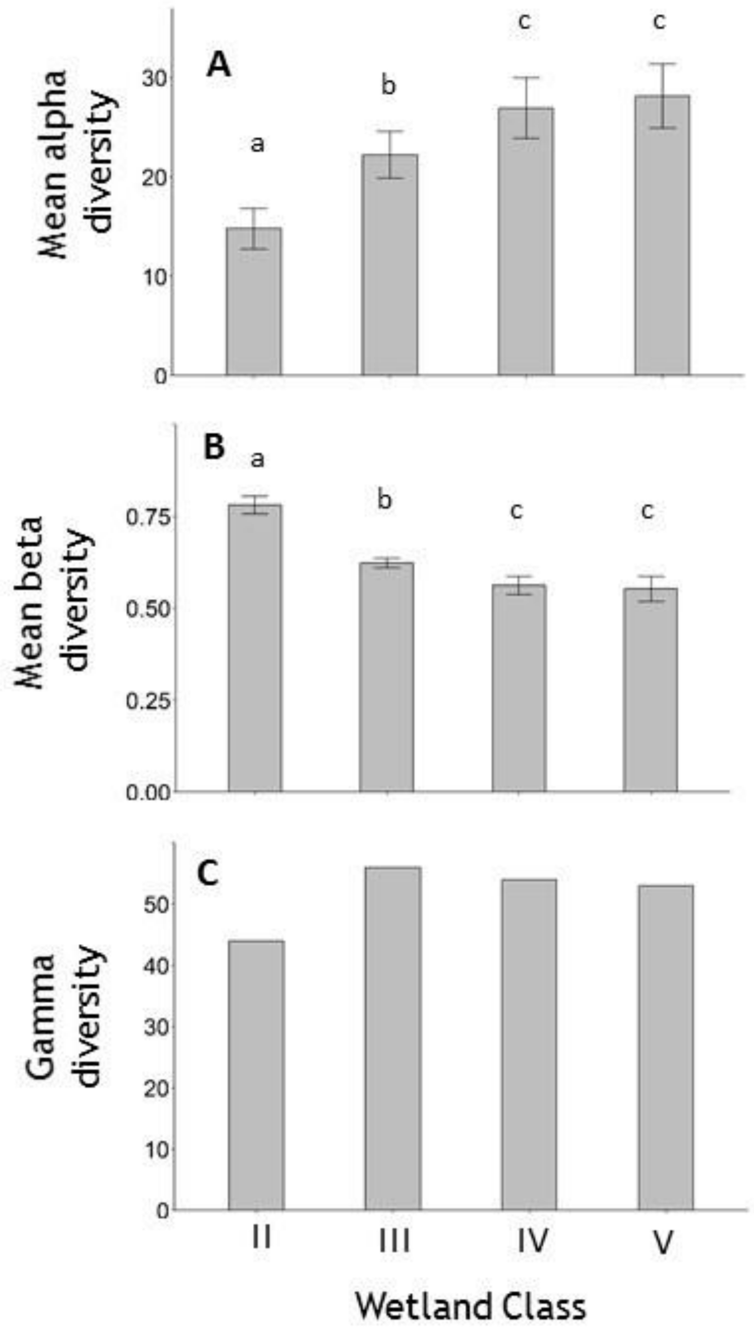

Figure 4-2 Bar charts displayed a) average alpha diversity; b) average beta diversity (determined using a Bray-Curtis dissimilarity matrix) and c) gamma diversity for each permanence class. Error bars are standard error. Bars with the same letters are not significantly different (*post-hoc* Tukey's multiple comparisons tests, alpha = 0.05). Gamma diversity is only a single value per wetland class and thus has no error bars nor could be statistically assessed for differences among groups.

5. Synthesis and conclusions

The wetlands of the Northern Prairie Pothole Region (NPPR) are dynamic habitats which provide numerous hydrological and ecosystem functions (Zedler and Kercher 2005) and support diverse communities of macroinvertebrates (Wrubleski and Ross 2011). Since human settlement in this region, many of these productive habitats have been drained for agricultural purposes and most that remain exist in unnatural landscapes of cropping or cattle pasture. The Government of Alberta has recently implemented a Wetland Policy (2013) that promotes the conservation and mitigation of pothole wetlands, and calls for scientifically validated tools to assess wetland condition. This research was initially prompted by the need for wetland management strategies in the NPPR and the effectiveness of aquatic macroinvertebrates as bioindicators in other systems, such as streams and lakes (e.g., Cairns and Pratt 1993).

However, the community ecology of wetland macroinvertebrates and their responses to environmental variables is poorly understood and research often yields contradictory results (review in Batzer 2013). The lack of consensus regarding the community structure of wetland macroinvertebrates prompted this work to explore the environmental drivers of community composition. Since many wetlands in this region draw down by the end of the summer, the macroinvertebrates which live here must be able to withstand regular fluctuation of water levels and the complete drying of the basin. In addition to this, macroinvertebrates must be able re-establish communities each spring when the wetland refills. This regular community reassembly and subsequent succession allows for a unique perspective of the relative roles of species-sorting and stochastic processes in community assembly.

5.1 Research findings

The goal of my thesis was to evaluate the potential of macroinvertebrates to serve as bioindicators in the NPPR, and to explore patterns of community composition and diversity in relation to wetland hydroperiod. In chapter one, I provided background information about the wetlands in the NPPR and the need for management strategies in the face of historic wetland loss and continued degradation. I also discussed the ecology of aquatic macroinvertebrates, and highlighted the knowledge gaps present in wetland community ecology.

In chapter two, I assessed the association of macroinvertebrates and agricultural land use surrounding wetlands. I observed that, at family-level resolution, there was no change in macroinvertebrate community composition, abundance or taxa richness to the degree of non-natural land cover surrounding the wetland. I conclude that macroinvertebrates are not good candidates for developing biomonitoring tools (e.g., an index of biotic integrity) in the NPPR. Macroinvertebrates likely do respond to land use, but this result is masked by stronger environmental drivers or requires better taxonomic resolution to detect.

In chapter three, I explored the environmental factors that drive macroinvertebrate community composition in the NPPR. Unexpectedly, I observed no strong associations between macroinvertebrates and any of the water chemistry variables I collected (conductivity, turbidity, dominant cations, nutrients). Macroinvertebrates communities were strongly driven by measures of hydrology, including maximum water depth, percentage of open water present, dry date and the amplitude of water depth change. This was reflected in macroinvertebrate communities being structured along a gradient in wetland permanence class (temporary, seasonal, semi-permanent, and permanent; *sensu* Stewart and Kantrud 1971). The range in community composition was greater among temporary wetlands than semi-permanent and permanent wetlands, which were more similar in their community composition. I determined that desiccation strategies suited to longer hydroperiods (active dispersers and wet layers) were associated with permanent wetlands while tolerant taxa (desiccation resistant taxa and groups that can lay eggs in the dry basin) were not constrained by wetland permanence class. Macroinvertebrates exhibited a nested community pattern along a gradient of hydroperiod, where permanent wetlands contained the taxa present in temporary wetlands in addition to novel taxa. I also categorized macroinvertebrates into functional feeding groups and behavioural guilds. The arrangement of these groups suggested a difference in emergent and submerged aquatic vegetation.

In chapter four, I addressed the differences in alpha, beta and gamma diversity among wetland permanence classes and used these results as a case study for theories in community assembly. I observed that alpha and gamma diversity increased with wetland permanence class, likely because more taxa are capable of colonizing and persisting in permanent marshes since no special adaptations to desiccation are needed. This supports the theory of species-sorting in community assembly, whereby the local environment acts as a ‘filter’ for those taxa that cannot persist in a given set of conditions. Alternatively, I observed that beta diversity had a negative relationship with hydroperiod and was highest in temporary wetlands. This suggests that temporary wetlands have a higher degree of taxonomic turnover between wetlands, while permanent wetlands generally consist of the same taxa. These results suggest the initial importance of stochastic dispersal processes in shaping communities (i.e., the neutral theory of community assembly). However, since temporary wetlands disassemble each year, these communities must establish again each spring. With more time between desiccation periods, macroinvertebrate communities in wetlands with longer hydroperiods have more time for biological interactions to lead to local extinctions. Thus, these more permanent wetland classes may reach closer to equilibrium conditions and be less influenced by the stochastic processes governing colonization from the regional species pool.

5.2 Taxonomic resolution

The taxonomic resolution necessary for macroinvertebrates to be effective bioindicators has often been debated by researchers (review in Bailey et al 2001). While species-level data would provide the most accurate response to environmental variables (USA EPA 2002), an effective bioindicator must be able to be identified reliably and within time and resource constraints. The Canadian Aquatic Biomonitoring Network (CABIN) suggests a minimum of family-level resolution for indicator taxa (Environment Canada 2014). While I acknowledge that genus or species-level identifications may have exhibited an association with land use, this level of identification is often beyond the scope of province-wide wetland monitoring programs. I suggest that future efforts should be redirected towards other wetland taxa in the NPPR. For example, waterbirds in the NPPR are responsive to land use (Polan 2016) and a successful index of biotic integrity has been created using waterbird metrics for this region (Anderson 2017).

While some birds, such as sparrows, may be difficult to identify, the majority of birds in the NPPR can be identified to species on site with perhaps some post-field audio analysis (e.g., Polan 2016, Anderson 2017) with the aid of computer software such as Audacity (Audacity Team 2014). Similarly, wetland vegetation in NPPR wetlands can be identified in the field with difficult or rare species collected as vouchers for later verification in a herbarium (e.g., Kraft 2016). In contrast, sorting and identifying macroinvertebrate samples even to family-level requires intensive time after collection, making them impractical to identify further when other sensitive and validated indicators already exist. For example, the macroinvertebrate samples in this study were very high in abundance and required the use of subsampling procedures. Even with subsampling, each sample took approximately four to eight hours to sort and identify macroinvertebrates to family-level resolution. In contrast, Polan (2016) and Anderson (2017) were able to complete bird surveys to species-level resolution within a site visit (10-minute point count, 8-minute auditory survey) in NPPR wetlands.

While time and resource constraints may not make it practical to identify macroinvertebrates to genus or species from a wetland management perspective, this resolution could provide better insights into their community ecology. There were contradictions within the functional groups that I assigned to each family (for example, not all Chironomidae are collector-gatherers). Greater taxonomic resolution would have allowed for more precise group assignments. Feeding groups and behavioural guilds can vary more drastically within groups so this only provided a course overview (USA EPA 2002). However, desiccation strategies can often be assigned at higher levels of taxonomic resolution (e.g., Wiggins et al. 1980), and thus my conclusions from Chapters 3 and 4 regarding the importance of desiccation strategies in tolerating briefer hydroperiods are robust to the low taxonomic level of my identifications.

5.3 Implications and future work

My research contributes to the field of wetland macroinvertebrate community, as well as provides suggestions into the management of NPPR wetlands. My results stress the importance of conserving wetlands across a range of permanence classes in order to preserve macroinvertebrate diversity. If the beta diversity in permanent marshes is lower than in temporary ones, it suggests that any two permanent marshes are more likely to be similar in terms of their macroinvertebrate community composition, whereas any two temporary marshes are unlikely to be equivalent or exchangeable. Unfortunately, small and temporary wetlands are preferentially lost in the landscape by draining (Serran and Creed 2016). This results in wetland consolidation, whereby snowmelt run off that would formerly have been retained in small temporary basins instead consolidates in the few remaining large wetlands in the catchment. These large wetlands consequently become larger and more permanent, changing their natural hydrology (McCauley et al. 2015). Based on my results, I expect that wetland consolidation will lead to the homogenization of macroinvertebrate communities because of the relatively lower beta diversity observed in more permanent wetlands. In addition, climate change can alter the hydroperiod and water temperature of aquatic systems, and pothole wetlands are especially susceptible (Meyer et al. 1999) as they rely on the snowpack melt to refill them each spring (Hayashi et al. 2016). Alternatively, Johnson et al. (2010) predict that temporary wetlands will be more resilient to climate change as they will have naturally dried out before evapotranspiration rates peak in the summer. While there is uncertainty over how water budgets will be affected by changes in precipitation and temperature, the maintenance of natural hydroperiods remains important. I observed that communities of macroinvertebrates significantly differed among wetland permanence classes, and the high beta diversity of temporary wetlands also implies that wetlands with short hydroperiods support different taxa and their loss could have a significant effect on the regional diversity of temporary systems. I also suggest that future restoration efforts in the NPPR work to maintain dynamic hydroperiods and wetlands of all permanence classes in order to best mimic the condition of natural systems.

My results provide insight into the complex community ecology of wetland macroinvertebrates, but raises several questions for future research. The variation in both feeding groups and behavioural guilds suggested differences in emergent and submerged aquatic vegetation may be an important factor in structuring macroinvertebrate communities. While I measured the percent area of dominant vegetation groups, this was not strongly associated to any of the ordination solutions. I conclude that the percent area of wetland vegetation is not an effective measure of the actual stem density and physical structure of wetland vegetation, which are likely to be more influential of habitat quality from a macroinvertebrate perspective. An in-depth analysis of vegetation and macroinvertebrate communities in these wetlands would provide further insight into community structure.

I acknowledge above that family-level identification of macroinvertebrates may not be sufficient to observe more complex patterns in community dynamics. I suggest that future work endeavor to provide genus or species-level identifications, even just in select taxonomic groups. For example, both larval and adult odonates have been used as indicators of habitat condition around the world in many river systems (Clark and Samways 1996, de paiva Silva et al. 2010, Bush et al. 2013, Dutra and De Marco 2015, Kietzka et al. 2015, Elio Rodrigues et al. 2016, Golfieri et al. 2016), wetland complexes (Reece and McIntyre 2009), marshes (Kutcher and Bried 2014) and peatlands (Elo et al. 2015). I detected no response of odonates to agricultural disturbance at family-level, but previous research in the NPPR reported that odonates identified to genus showed community differences in different grazing regimes (Hornung and Rice 2003, Foote and Rice Hornung 2005). A vast meta-analysis by Ruhí and Batzer (2014) concluded that the taxonomic richness of Mollusca, Hemiptera, Coleoptera (called a MHC index) was highly congruent with the richness of other wetland taxa and could be used as a proxy in future macroinvertebrate analysis. I suggest species-level identifications may be more obtainable in terms of time and skill restraints if they are focused on a narrow range of taxonomic groups rather than the entire macroinvertebrate community.

5.4 Significance and conclusions

In this thesis, I have demonstrated that macroinvertebrates in NPPR wetlands do not respond to surrounding land use, be it cropping or cattle grazing at a taxonomic resolution effective for biomonitoring. The strongest driver of macroinvertebrate community composition in these fishless wetlands is permanence class, as all hydrological variables I measured were strongly related to ordination solutions. The dynamic nature of the hydroperiod in NPPR wetlands is a characterizing feature of these systems, and results in a nested pattern of taxonomic composition along a gradient of permanence class. I have also demonstrated that alpha and gamma diversity display a positive relationship with hydroperiod, which I attribute to the constraints it places on taxa with no desiccation resistant phase. Finally, I observed that beta diversity is highest in temporary wetlands, stressing the importance of conserving these habitats. I believe this work provides important contributions to the field of biomonitoring in the NPPR, and gives insight into the community ecology and assembly patterns of wetland macroinvertebrates along a gradient of hydroperiod.

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7. Appendices

7.1 Appendix 1 – Natural Regions ordination

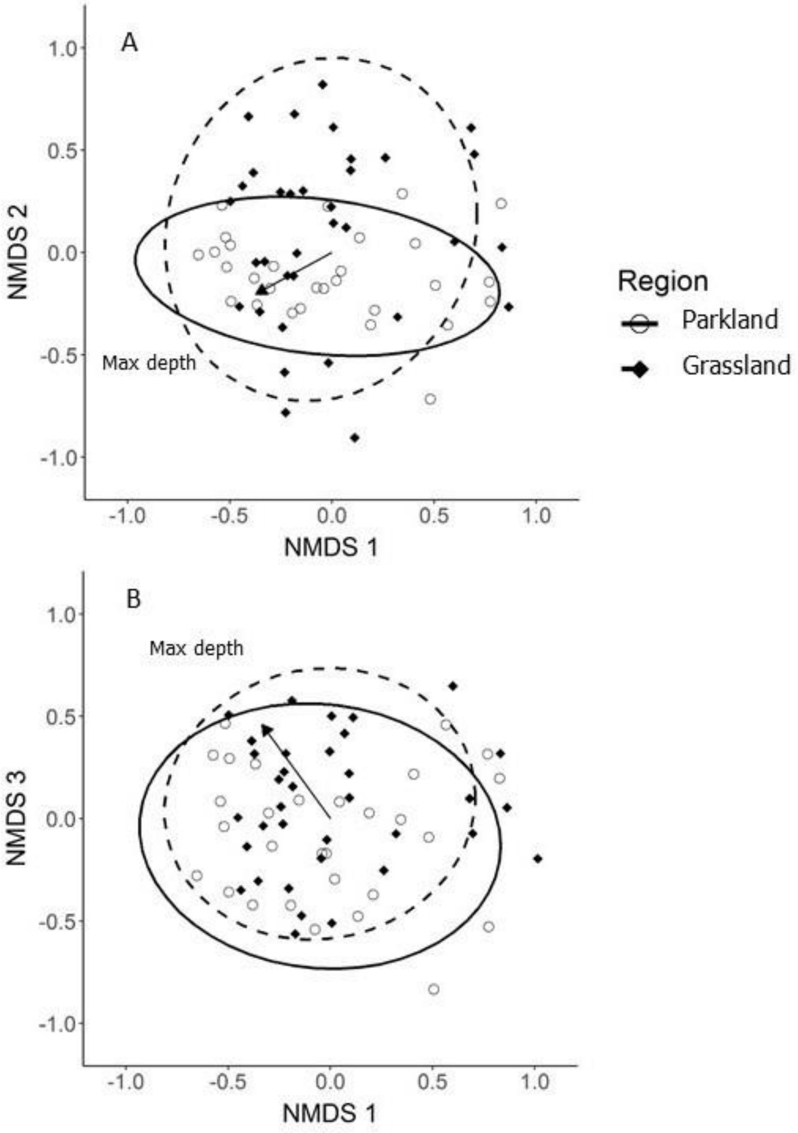

Figure 7-1 NMDS ordination of 64 NPPR wetlands in species space with sites symbolized by Natural Region (Grassland or Parkland). There is a split between regions on axis 2 which appears to be driven by the maximum depth of wetlands. In general, the climate of the Grassland region is hotter and dryer, and so supports more wetlands of lower permanence classes (shorter hydroperiods).

7.2 Appendix 2 – Taxa and functional group list

Table 7-1 A summary list of all macroinvertebrate taxa present in wetland sites across the NPPR with their assigned functional groups. See below for group code legend.

Class	Order	Family	Desiccation Strategy Group	Functional Feeding Group	Behavioural Guild
Insecta	Coleoptera	**Curculionidae**	3	SHRED	CLING
		Chrysomelidae	3	SHRED	CLIMB
		Dytiscidae	2	ENGULF	DIVER
		Elmidae	4	GCOLL	CLING
		Gyrinidae	4	ENGULF	SKATE
		Haliplidae	2	SHRED	DIVER
		Hydraenidae	3	ENGULF	CLIMB
		Hydrophilidae	2	ENGULF	DIVER
		Phalacridae	3	GCOLL	CLIMB
		Ptiliidae	--	--	--
		Salpingidae	--	--	--
		Scirtidae	4	GCOLL	CLING
		Staphylinidae	3	ENGULF	CLING
	Diptera	Anthomyiidae	2	ENGULF	SWIM
		Ceratopogonidae	2	ENGULF	SWIM
		Chaoboridae	3	ENGULF	SWIM
		Chironomidae	2	GCOLL	BUR
		Culicidae	3	FCOLL	SWIM
		Dixidae	2	FCOLL	DIVER
		Dolichopodidae	2	ENGULF	SPRAWL
		Empididae	2	ENGULF	SPRAWL
		Ephydridae	4	GCOLL	BUR
		Psychodidae	2	GCOLL	BUR
		Sciomyzidae	3	ENGULF	BUR
		Stratiomyidae	2	GCOLL	SPRAWL
		Syrphidae	2	GCOLL	BUR
		Tabanidae	2	ENGULF	SPRAWL
		Tipulidae	2	SHRED	BUR
	Ephemeroptera	Baetidae	3	SCRAPE	SWIM
		Caenidae	2	GCOLL	SPRAWL
		Siphlonuridae	2	SCRAPE	SWIM
	Hemiptera	**Corixidae**	4	PIERCE	DIVER
		Gerridae	4	PIERCE	SKATE
		Hebridae	4	PIERCE	SPRAWL
		Mesoveliidae	4	PIERCE	SKATE
		Notonectidae	4	PIERCE	DIVER

		Saldidae	4	PIERCE	CLIMB
		Veliidae	4	PIERCE	SKATE
	Lepidoptera	Noctuidae	2	SHRED	CLIMB
		Pyralidae	2	SHRED	CLIMB
	Odonata	**Aeshnidae**	4	ENGULF	CLIMB
		Coenagrionidae	3	ENGULF	CLIMB
		Lestidae	3	ENGULF	CLIMB
		Libellulidae	3	ENGULF	SPRAWL
	Trichoptera	Brachycentridae	2	GCOLL	SPRAWL
		Leptoceridae	2	SHRED	CLING
		Limnephilidae	3	SHRED	SPRAWL
Entognatha	**Collembola***		1	GCOLL	SWIM
Arachnida	Trombidiformes	**Hydrachnidia***	2	PARA	SWIM
Branchipoda	**Anostraca***		1	FCOLL	SWIM
	Conchostraca*		1	FCOLL	SWIM
	Notostraca	Triopsidae	1	SCRAPE	BUR
Malacostraca	**Amphipoda**		1	GCOLL	SWIM
Ostracoda*			1	GCOLL	SWIM
Bivalvia	Veneroida	**Sphaeriidae**	1	FCOLL	BUR
Gastropoda	Basommatophora	**Lymnaeidae**	1	SCRAPE	CLING
		Planorbidae	1	SCRAPE	CLING
Clitellata	**Hirudinea***		1	ENGULF	SPRAWL
Oligochaeta*			1	GCOLL	BUR
Hydrazoa*			1	FCOLL	CLING
Nematoda**			1	ENGULF	SWIM
Tardigrada			1	SHRED	CLING

Desiccation Strategy Groups: 1 = tolerators, 2 = wet layers, 3 = dry layers, 4 = dispersers; Functional Feeding Groups: ENGULF = engulfing predators, FCOLL = filtering collectors, GCOLL = gathering collectors, SCRAPE = scrapers, SHRED = shredders, PARA = ectoparasites, PIERCE = piercing predators; Behavioural Guilds: BUR = burrowers, CLIMB = climber, CLING = clinger, DIVER = diver, SKATE = skater SPRAWL = sprawler, SWIM = swimmer (see tables 3.2-3.4 for definitions of all traits). Bolded taxa were included in community ordination, not bolded taxa are rare and occurred less than five times. A dashed line (--) indicates no information could be found for this group.
* Not identified to family level
** Phylum level

7.3 Appendix 3 – Site information

Table 7-2 A list of all 87 wetland sites sampled in the NPPR with their region, disturbance bin assignments and permanence classes. A dashed line (--) indicates that these sites were not assigned a disturbance bin and were not included in Chapter 2.

Site ID	Year	Region	Northing	Westing	Disturbance bin	Permanence Class
10	2015	Parkland	52.51477	112.6479	High	Permanent
13	2014	Parkland	52.33939	112.2282	Medium	Seasonal
18	2014	Parkland	52.58656	112.2081	High	Seasonal
25	2014	Parkland	52.14848	111.8227	High	Seasonal
30	2014	Parkland	52.38929	111.8738	High	Temporary
31	2014	Parkland	52.73904	113.3523	High	Seasonal
32	2015	Parkland	52.59304	113.5987	Low	Temporary
35	2014	Parkland	53.07183	113.4282	Medium	Temporary
56	2014	Parkland	52.94941	112.6346	High	Semi-permanent
67	2015	Parkland	52.46586	112.6971	Low	Temporary
89	2014	Parkland	52.34631	112.9285	High	Permanent
90	2014	Parkland	52.34705	112.8723	High	Semi-permanent
98	2014	Grassland	51.90165	111.6973	Low	Seasonal
101	2014	Grassland	51.0377	111.318	Low	Seasonal
109	2014	Grassland	51.01003	111.8337	High	Semi-permanent
110	2015	Grassland	51.53763	111.5058	Low	Seasonal
115	2015	Grassland	51.50547	111.2228	High	Seasonal
117	2014	Grassland	51.19809	111.5391	High	Seasonal
124	2014	Grassland	51.31596	112.2354	Low	Seasonal
131	2014	Grassland	51.28267	112.2946	Low	Temporary
133	2014	Grassland	51.37129	112.1821	Low	Seasonal
135	2014	Grassland	51.49276	112.382	Medium	Semi-permanent
142	2015	Grassland	51.4136	112.1314	Low	Seasonal
145	2015	Grassland	51.60363	112.2061	High	Semi-permanent
149	2014	Grassland	51.47503	112.0392	High	Permanent
152	2014	Grassland	50.36122	111.4242	Low	Temporary
153	2014	Grassland	50.51392	111.5009	Low	Semi-permanent
158	2014	Grassland	50.55512	112.4954	Low	Seasonal
165	2014	Grassland	50.31696	111.6562	Low	Seasonal
173	2015	Grassland	50.16459	111.5389	Medium	Seasonal
182	2014	Parkland	52.73056	112.4106	High	Temporary
184	2014	Grassland	51.41749	112.5684	High	Semi-permanent
186	2014	Grassland	51.83351	111.7223	Low	Semi-permanent
187	2014	Parkland	52.62288	112.6322	High	Permanent
188	2014	Grassland	51.52895	111.328	High	Seasonal
190	2015	Parkland	53.09104	113.197	High	Permanent

194	2014	Parkland	52.21956	113.4428	Medium	Permanent
195	2014	Parkland	52.41014	113.044	Medium	Semi-permanent
200	2014	Parkland	52.47809	112.6137	Medium	Permanent
202	2014	Grassland	50.36549	112.0232	Low	Temporary
203	2014	Grassland	50.65714	112.4499	High	Temporary
301	2015	Parkland	51.87547	112.928	High	Temporary
312	2015	Grassland	51.4394	112.0031	Medium	Temporary
317	2015	Parkland	53.18687	112.9959	Medium	Temporary
321	2015	Parkland	52.44961	111.7938	Medium	Temporary
333	2015	Parkland	53.26561	112.9496	Low	Semi-permanent
338	2015	Grassland	51.27651	111.6697	Medium	Temporary
344	2015	Parkland	52.11278	112.6716	Low	Seasonal
346	2015	Grassland	51.24029	112.085	Low	Seasonal
360	2015	Grassland	51.74384	111.7361	High	Seasonal
365	2015	Parkland	52.92827	113.1265	Medium	Seasonal
368	2015	Parkland	52.39511	111.1994	Medium	Seasonal
377	2015	Parkland	52.4848	113.0046	Medium	Temporary
388	2015	Grassland	50.95792	111.4656	Low	Seasonal
395	2015	Parkland	51.95862	112.7409	High	Seasonal
396	2015	Parkland	53.07396	114.1662	Low	Seasonal
398	2015	Parkland	52.99462	113.9092	Low	Semi-permanent
BARON01	2015	Parkland	52.44455	112.7391	--	Temporary
BATL	2014	Parkland	52.92772	114.1974	Low	Permanent
BELTZ03	2015	Parkland	52.17432	113.5629	--	Semi-permanent
BERGQ07	2015	Parkland	53.17455	113.1446	--	Semi-permanent
BUSEN01	2015	Parkland	53.15369	113.0611	--	Temporary
CAINE01	2015	Parkland	52.4808	112.6881	--	Temporary
COLLI02	2015	Parkland	52.03028	113.2853	--	Seasonal
FORBS10	2015	Parkland	53.08031	113.1942	--	Seasonal
GAD1	2014	Parkland	52.50925	113.2243	Low	Seasonal
GILBE02	2015	Parkland	52.44124	112.72	--	Semi-permanent
GRAND07	2015	Parkland	52.16313	112.6041	--	Permanent
GREEN03	2015	Parkland	52.5316	112.6689	--	Semi-permanent
HEBER03	2015	Parkland	52.18951	112.5604	--	Seasonal
HILLE03	2015	Parkland	52.47155	112.647	--	Permanent
HOLT04	2015	Parkland	52.8012	113.131	--	Seasonal
HWY5302	2015	Parkland	52.58151	112.8063	--	Permanent
JJCOL	2014	Parkland	52.55746	113.6309	Low	Seasonal
KERBE02	2015	Parkland	52.11289	112.9109	--	Permanent
KIN1	2014	Grassland	50.44742	111.89	Low	Temporary
KINVI03	2015	Parkland	51.99566	113.1183	--	Permanent
KINVI06	2015	Parkland	51.98447	113.1109	--	Seasonal
LABRY56	2015	Parkland	53.12063	113.1794	--	Seasonal

MIKA10	2015	Parkland	52.31523	112.9802	--	Semi-permanent
MIQ2	2014	Parkland	53.23397	112.8745	Low	Semi-permanent
OZMEN05	2015	Parkland	53.09171	112.8208	--	Seasonal
PARLB01	2015	Parkland	52.42853	113.2345	--	Permanent
PEARL06	2015	Parkland	53.02945	112.4406	--	Temporary
RETTA09	2015	Parkland	53.17859	113.1595	--	Seasonal
RUM4	2015	Parkland	51.88395	112.6318	Low	Seasonal
TOL3	2014	Parkland	52.18618	113.0198	Low	Temporary

7.4 Appendix 4 – Environmental variables in NPPR wetlands

Table 7-3 A summary of all the abiotic data (including water chemistry and hydrology measures) and percent area cover of the dominant vegetation groups measured in the 87 wetland sites. This data was used primarily in Chapter 3 to determine which environmental factors were correlated with aquatic macroinvertebrate community composition.

Variable	**Units**	**Average**	**± Standard deviation**
Size	m^2	6933.63	7799.66
Amplitude	%	0.79	0.29
Dry date	Julien calendar date	136.53	150.21
Maximum depth	m	0.51	0.23
Open water	%	0.11	0.22
Turbidity	NTU	5.25	6.32
Conductivity	mS/cm	0.52	0.62
Total nitrogen	µg/L	276.34	152.91
Total phosphorus	µg/L	2219.17	445.66
Total carbon	µg/L	2375.27	1588.72
Na (sodium)	mg/L	48.01	60.36
K (potassium)	mg/L	27.29	15.24
Ca (calcium)	mg/L	32.51	29.73
Mg (magnesium)	mg/L	22.42	31.40
TSS (total suspended solids)	mg/L	8.89	11.19
B_emergent (broad leaved emergents)	%	0.01	0.09
N_emergent (narrow leaved emergents)	%	0.64	0.33
R_emergent (robust emergents)	%	0.06	0.13
Woody vegetation	%	0.08	0.21
Permanence class	Factor (II, III, IV, V)	n/a	n/a
Region	Factor (Grassland, Parkland)	n/a	n/a
Disturbance group	Factor (Low, Medium, High)	n/a	n/a

7.5 Appendix 5 – NMDS joint plot scores for environmental variables

Table 7-4A The following tables contain all environmental variables measured for the 87 wetland sites. The scores were generated using the ‘envfit’ function in the R package *vegan* (Oksanen et al. 2016). All scores are associated with the community composition non-metric multidimensional scaling (NMDS) ordination (in taxa space) created in Chapter 3 (see Figure 3-2). The first table is associated with NMDS axes one and two and the second table is associated with axes one and three. For variable codes or units, refer to Appendix 4. The NMDS scores reported are correspond to coordinates within the ordination. This is followed by a measure of goodness-of-fit (squared correlation coefficient: r^2) and the associated p-value. Significant p-values (at a = 0.05) are bolded. Variables with an asterisk (*) are factorial variables.

Variable	**NMDS1**	**NMDS2**	**r^2**	**p**
Size	0.84045	-0.54189	0.0369	0.204
Amplitude	-0.9986	-0.05286	0.1184	**0.002**
Dry date	0.99789	-0.06493	0.3364	**0.001**
Max depth	0.95467	-0.29765	0.1497	**0.001**
Open water	0.90599	-0.42329	0.109	**0.006**
Turbidity	-0.15081	-0.98856	0.0492	0.127
Conductivity	0.36092	-0.9326	0.0628	0.076
Total nitrogen	-0.59003	-0.80738	0.0429	0.142
Total phosphorus	0.53943	0.84203	0.0007	0.978
Total carbon	-0.63882	-0.76936	0.0225	0.401
Na	0.22276	-0.97487	0.1391	**0.002**
K	-0.41377	-0.91038	0.047	0.121
Ca	-0.25139	0.96789	0.001	0.963
Mg	0.68553	-0.72805	0.0362	0.211
TTS	-0.50728	-0.86178	0.0743	**0.036**
B_emergent	0.51765	-0.85559	0.0126	0.589
N_emergent	0.37646	-0.92643	0.0101	0.619
R_emergent	0.66989	0.74246	0.0363	0.211
Woody veg	0.60609	0.79539	0.005	0.808
Permanence class*	n/a	n/a	0.1737	**0.001**
Region*	n/a	n/a	0.0386	0.159
Disturbance group*	n/a	n/a	0.0189	0.786

Table 7-4B

Variable	**NMDS1**	**NMDS3**	**r^2**	**p**
Latitude	-0.36077	0.93265	0.1188	**0.008**
Longitude	-0.28798	0.95764	0.1454	**0.002**
Size	0.99816	-0.06071	0.0284	0.273
Amplitude	-0.84796	-0.53006	0.1487	**0.002**
Dry date	0.84362	0.53694	0.4252	**0.001**
Max depth	0.60362	0.79728	0.3012	**0.001**
Open water	0.75599	0.65458	0.1408	**0.003**
Turbidity	-0.14508	0.98942	0.0487	0.103
Conductivity	0.32702	0.94502	0.0701	0.052
Total nitrogen	-0.94144	0.33719	0.0197	0.44
Total phosphorus	0.11779	0.99304	0.0121	0.591
Total carbon	-0.74929	0.66224	0.0167	0.504
Na	0.41798	0.90846	0.0385	0.221
K	-0.75463	-0.65615	0.0156	0.531
Ca	-0.02778	0.99961	0.0731	**0.041**
Mg	0.46092	0.88744	0.0687	**0.05**
TSS	-0.73827	0.6745	0.0373	0.204
B_emergent	0.73354	-0.67964	0.0066	0.771
N_emergent	0.34826	-0.9374	0.0109	0.605
R_emergent	0.45327	0.89137	0.0684	**0.042**
Woody veg	0.70877	-0.70544	0.0036	0.868
Permanence class*	n/a	n/a	0.212	0.001
Region*	n/a	n/a	0.0321	0.226
Disturbance group*	n/a	n/a	0.0486	0.207

7.6 Appendix 6 – Wetland sites by Natural Region and permanence class

Table 7-5 The distribution of wetland permanence classes (Stewart and Kantrud, 1971) in both Natural Regions sampled, along with the total numbers of wetlands in each permanence class and Natural Region. The parkland contains a higher proportion of permanent wetlands, resulting in a segregation between Natural Regions.

Region	Temporary	Seasonal	Semi-permanent	Permanent	Total
Grassland	7	15	6	1	29
Parkland	14	20	11	13	58
Total	21	35	17	14	87

7.7 Appendix 7 – Alpha, beta and gamma diversity

Table 7-6 The alpha, beta, and gamma diversity of all permanence class groups, as well as all the study wetlands combined. Alpha diversity is a mean value across all wetlands in that group whereas beta and gamma diversity are single values. Diversity values were calculated according to Jost's formulae, which allows for direct comparisons between groups (Jost 2007).

Permanence Class	Mean alpha diversity	Beta diversity	Gamma diversity
II	14.81	2.97	44
III	22.23	2.52	56
IV	26.94	2.00	54
V	28.14	1.88	53
All sites	22.31	2.77	62

7.8 Appendix 8 – Scree plot example

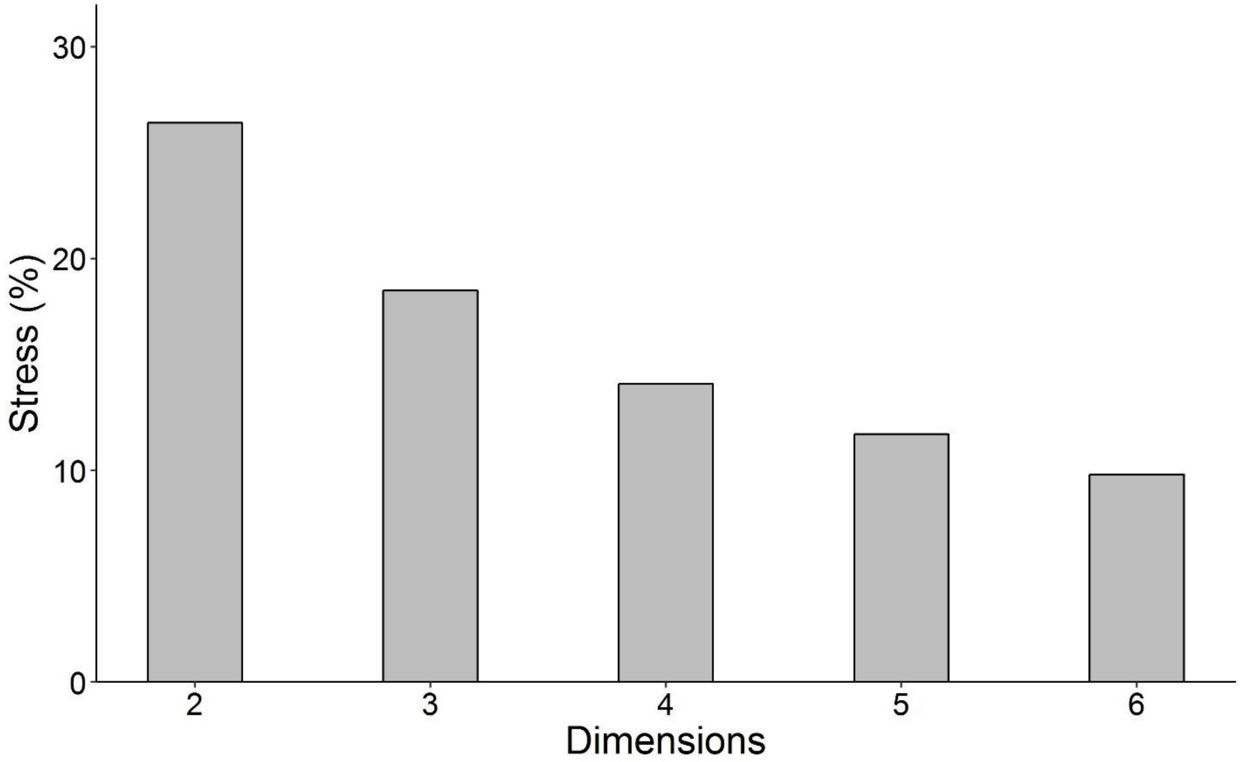

Figure 7-2 A scree plot depicting dimensionality versus NMDS ordination stress. Ideally, both stress and number of dimensions should be minimized to find the optimal ordination solution. Typically, a reduction of at least 5% in stress is required to justify an additional axis. In this case, an ordination with three axes is optimal. A scree plot was generated for each ordination in this work to determine dimensionality.

7.9 Appendix 9 – Residual plot example

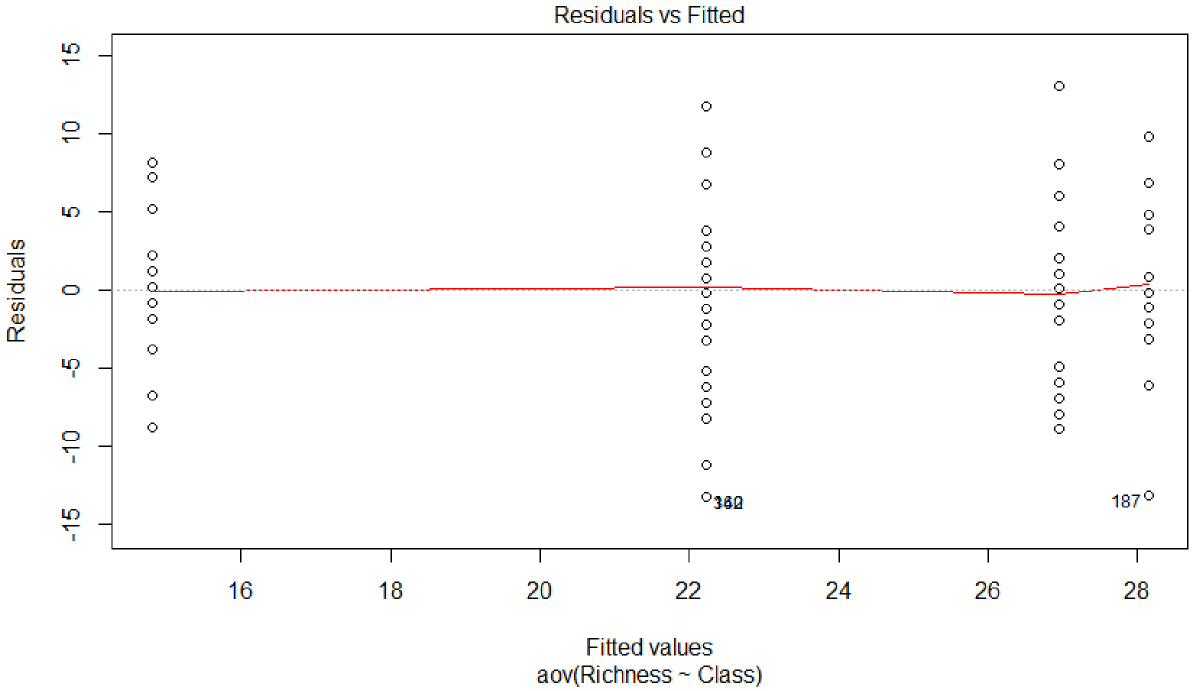

Figure 7-3 An example plot of residuals against fitted values to assess the assumptions of homogeneity of variance and normality of the residuals for a one-way ANOVA analysis.

7.10 Appendix 10 – Benthic core data

Table 7-7 Taxa abundance matrix for 45 benthic core samples sorted. Habitat refers to where the sample was taken within a wetland: the emergent zone (EM) or the open water zone (OW). Counts are number of individuals of a particular taxa present in each core sample, followed by the total number of individuals (abundance) per sample. This was converted to a density basis (m^2) to compare to the larger dataset (water column and vegetation samples).

Site ID	Habitat	Chironomidae	Ceratopogonidae	Tipulidae	Dytiscidae	Ostracoda	Conchostraca	Oligochaeta	Abundance (sample)	Density (m^2)	Taxa richness
13	EM	5	0	0	0	0	0	5	10	1325.6	2
18	EM	0	0	0	0	1	0	0	1	132.56	1
25	EM	0	0	0	0	0	1	3	4	530.24	2
31	EM	1	0	0	0	5	0	1	7	927.92	3
35	EM	0	0	0	0	0	0	0	0	0	0
56	EM	19	0	0	0	0	0	29	48	6362.88	2
67	EM	0	0	0	0	1	0	3	4	530.24	2
89	EM	0	1	1	1	0	0	11	14	1855.84	4
89	OW	13	0	0	0	2	0	0	15	1988.4	2
90	EM	0	0	0	0	2	3	1	6	795.36	3
90	OW	0	0	0	0	0	3	1	4	530.24	2
101	EM	0	0	0	0	0	0	0	0	0	0
109	EM	10	0	0	0	0	0	12	22	2916.32	2
109	OW	4	1	0	0	0	0	18	23	3048.88	3
110	EM	0	0	1	0	0	0	4	5	662.8	2
110	OW	8	1	0	0	0	3	0	12	1590.72	3
117	EM	4	0	0	0	0	0	1	5	662.8	2
117	OW	7	0	0	2	0	0	8	17	2253.52	3
133	EM	6	3	2	0	1	0	1	13	1723.28	5
135	EM	4	1	0	1	1	0	0	7	927.92	4
135	OW	11	0	0	0	0	0	0	11	1458.16	1
142	EM	1	0	0	0	9	3	2	15	1988.4	4
145	EM	0	0	0	0	3	0	0	3	397.68	1
145	OW	1	0	0	0	0	0	1	2	265.12	2

153	EM	4	0	0	0	0	0	4	8	1060.48	2
165	EM	1	0	0	0	0	0	0	1	132.56	1
173	EM	2	0	0	0	0	0	0	2	265.12	1
184	EM	1	0	0	0	0	0	4	5	662.8	2
184	OW	1	0	0	0	0	0	7	8	1060.48	2
186	EM	0	0	0	0	1	0	15	16	2120.96	2
187	EM	12	0	0	0	0	0	0	12	1590.72	1
188	EM	5	0	0	1	0	0	1	7	927.92	3
190	EM	0	0	0	0	0	0	0	0	0	0
194	EM	1	0	0	0	0	0	0	1	132.56	1
194	OW	4	0	0	0	1	0	0	5	662.8	2
195	EM	0	0	0	0	1	0	0	1	132.56	1
200	EM	1	0	0	0	0	0	0	1	132.56	1
200	OW	1	3	0	0	0	0	0	4	530.24	2
202	EM	10	0	0	2	0	0	0	12	1590.72	2
203	EM	3	0	0	0	0	0	4	7	927.92	2
203	OW	2	1	0	0	0	0	1	4	530.24	3
BATL	EM	0	0	0	0	0	0	0	0	0	0
JJCOL	EM	1	0	0	0	0	0	0	1	132.56	1
JJCOL	OW	2	0	0	0	13	0	0	15	1988.4	2
MIQ2	EM	1	0	0	0	0	0	0	1	132.56	1
RUM4	EM	0	0	0	0	0	0	0	0	0	0