AQUATIC MACROINVERTEBRATE RESPONSE TO SHIFTS IN HYDROCLIMATIC VARIABILITY AND ECOHYDROLOGICAL CONDITIONS IN PRAIRIE-POTHOLE WETLANDS: IMPLICATIONS FOR BIODIVERSITY CONSERVATION

A Dissertation
Submitted to the Graduate Faculty
of the
North Dakota State University
of Agriculture and Applied Science

By

Kyle Ian McLean

In Partial Fulfillment of the Requirements
for the Degree of
DOCTOR OF PHILOSOPHY

Major Program:
Environmental and Conservation Sciences

August 2020

Fargo, North Dakota

North Dakota State University
Graduate School

Title

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The Supervisory Committee certifies that this ***disquisition*** complies with North Dakota State University's regulations and meets the accepted standards for the degree of

DOCTOR OF PHILOSOPHY

SUPERVISORY COMMITTEE:

Jon N. Sweetman, PhD
Chair

David M. Mushet, PhD

Craig A. Stockwell, PhD

E. Shawn DeKeyser, PhD

Approved:

8/14/2020	Craig A. Stockwell, PhD
Date	Program Chair

ABSTRACT

Ecosystem degradation and subsequent biodiversity loss has plagued freshwater environments globally. Wetland ecosystems, such as the depressional wetlands found in the Prairie Pothole Region of North America, have been heavily impacted by historical land-use change and continue to be vulnerable to continued landscape modifications and climate change. Using existing literature, I summarized how recent shifts in climate coupled with historic and contemporary landscape modifications have driven a shift in wetland ecohydrological variability. However, clear trends in biodiversity were often limited by the spatial and temporal resolution of published research.

I used 24 years (1992–2015) of hydrologic and aquatic-macroinvertebrate data from a complex of 16 prairie-pothole wetlands located in North Dakota to relate wetland ecohydrological variability to biodiversity. I used structural equation modeling techniques to test a set of causal hypotheses linking a wetland's hydrogeologic setting and local climate conditions (i.e., the Wetland Continuum) to changes in hydrology, water chemistry, and biology, with an emphasis on aquatic-macroinvertebrate community response. I then examined the temporal synchrony of aquatic-macroinvertebrate populations to examine the relative importance of landscape-scale controls (e.g., climate, metacommunity dynamics) and wetland-specific controls on community assembly. Using this information, I then quantified among-wetland and among-year changes in aquatic-macroinvertebrate beta diversity to investigate patterns of biotic homogenization.

I found that spatial and temporal variability in aquatic-macroinvertebrate composition was strongly influenced by ponded-water dynamics. In addition to hydrologic controls, the high levels of temporal coherence of aquatic-macroinvertebrate compositional turnover supported the hypothesis that wetland biodiversity is also dependent on metacommunity dynamics. Analyses of spatio-temporal patterns in beta diversity did not reveal climate driven homogenization of aquatic-macroinvertebrate taxa among wetlands. However, shifts towards more permanently ponded water regimes corresponded with lasting shifts in aquatic-macroinvertebrate community composition. The communities of temporarily ponded wetlands maintained high levels of both temporal and spatial beta diversity. My collective findings indicate that the conservation of aquatic-macroinvertebrate diversity is dependent on the conservation of heterogenous, well-connected, wetland complexes.

ACKNOWLEDGMENTS

This work has greatly benefited from the support and previous efforts of numerous individuals and agencies. Without their support none of the work presented here would be possible. I thank North Dakota State University (NDSU) Graduate School, the Department of Biological Sciences, and the Environmental and Conservation Sciences (ECS) graduate program for the opportunity to pursue a PhD and for their continued support and assistance during my time as a graduate student. I especially thank my advisor Dr. Jon N. Sweetman for his guidance, patience, and willingness to accommodate my occasionally hectic schedule.

I thank the US Geological Survey's (USGS) Northern Prairie Wildlife Research Center (NPWRC) for their financial and logistical support, especially my acceptance into the USGS Pathways Internship Program. I am especially grateful for the years of guidance and mentorship given to me by my NPWRC supervisor, Dr. David M. Mushet. His direction has been critical in helping me navigate life as both a graduate student and USGS Ecologist.

In addition to Dr. Mushet and Dr. Sweetman, I also thank Dr. Craig A. Stockwell and Dr. E. Shawn DeKeyser for serving on my graduate committee, challenging me to think about my research in different ways, and their willingness to help whenever needed. I additionally thank Dr. Stockwell for his support as ECS program director and his previous years of guidance as my master's advisor.

I am indebted to the efforts of George Swanson (deceased) and Dr. Ned Euliss, Jr. (USGS retired) for starting and maintaining the long-term data collection efforts at the Cottonwood Lake Study Area, which provided the source data for my analysis. The pioneering research of these scientists also provide a solid foundation for my dissertation work to expand upon. I also thank the numerous field technicians and ecologists who have worked hard over the years to collect

and catalogue the Study Area's data assets. I especially thank Matt Solensky who manages, coordinates, and actively participates in the collecting, formatting, and cataloging of Cottonwood Lake Study Area data. Matt's efforts have provided a great resource for me and numerous other scientists.

I thank my colleagues at NPWRC for their support over the years and their part in making NPWRC a great place to work. I additionally thank Dr. Owen McKenna for the many brainstorming sessions over the last few years. I thank my current and former NDSU labmates Nate Williams, Kui Hu, and Christine Cornish for their support, scientific discussion, and familiarizing me with diatoms, pesticides, and many other once unfamiliar aspects of wetland ecology.

I thank my friends and family for their love and support. I thank my mother Lilli McLean and father Scott McLean for always being there for me. I especially thank my wife Emily for her love, support, patience, and additional patience. Finally, I thank my daughter Cheltzie and son Ira for all the love and smiles they bring to my life every day. They have been and will continue to be that constant reminder to challenge myself to always do better.

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CHAPTER 1. INTRODUCTION

Biodiversity refers to the biological heterogeneity distributed across space. The maintenance of this heterogeneity can have many environmental and economic benefits (Pimentel et al., 1997). Generally, more biodiverse systems have greater ecosystem stability, resiliency, and multifunctionality (Tilman, 1996; Hooper et al., 2012; Sandifer et al., 2015). However, biodiversity has been declining worldwide (Gaston, 2000; Butchart et al., 2010), and subsequently, so has ecosystem stability, resiliency, and multifunctionality (Worm et al., 2006; Allan et al., 2015; Oliver et al., 2015). The rates of loss have been spatially variable. For example, freshwater ecosystems have among the highest rates of biodiversity loss, mostly due to widespread ecosystem degradation (Ricciardi and Rasmussen, 2001; Dudgeon et al., 2006; Reid et al., 2019). Freshwater wetlands are ecosystems that have been heavily modified and continue to be vulnerable to human alterations and climate change (Brinson and Malvárez, 2002; Creed et al., 2017). Freshwater wetlands not only support diverse plant and animal communities rarely found in other ecosystem types, but they also provide shelter, food, and water for numerous terrestrial species found in the surrounding landscapes. Thus, the continued destruction of these wetlands would likely exacerbate biodiversity losses.

Historically, wetlands have been viewed as costly wastelands (Mitsche and Gosselink, 1986). This negative view of wetlands contributed to the estimated 50% loss of wetlands globally (Davidson et al., 2014) and their becoming one of the most degraded ecosystems on earth (Dudgeon et al., 2006; Reid et al., 2019). In the conterminous United States, an estimated 53% of wetlands were drained or filled between the 1780s and 1980s (Dahl, 1990). The historical and continued loss of wetlands, and their accompanying ecological functions, can have cascading effects that alter hydrologic stability and ecological processes in surrounding landscapes (Gibbs, 2000; Blann et al., 2009; Acreman and Holden 2013; Cohen et al., 2016; Verheijen et al., 2020).

Compared to other ecosystems, our understanding of biodiversity loss in freshwater wetlands is limited (Kingsford et al., 2016). The limited historical records detailing wetland biological communities along with the naturally high temporal variability exhibited by these systems have made it difficult to measure biodiversity losses. In the once wetland-rich Great Plains of the United States, the widespread draining and filling of wetland habitats mostly occurred prior to the ecological study of wetlands in the region. Therefore, very little is known about how historical land-use change has impacted wetland biodiversity (Jenkins et al., 2003). An increased understanding of the mechanisms governing biological assembly in "naturally" functioning wetlands can provide insight into what past wetland communities might have looked like and inform future wetland-conservation practices.

1.1. Thesis Objectives

The overall goal of my dissertation is to increase our understanding of the relative importance of spatial and temporal variability of ponded-water dynamics in determining biological community structure in freshwater wetland ecosystems and their implications for biodiversity conservation. My research specifically focused on prairie-pothole wetland ecosystems and their aquatic-macroinvertebrate communities. I developed four objectives that are pertinent to the overall goal of the dissertation. My first objective was to identify relevant threats to aquatic-macroinvertebrates by reviewing prairie-pothole wetland literature on historical, contemporary, and predicted (future) changes in prairie-pothole ecosystem variability. My second objective was to develop a causal model to test hypothesized relationships linking a wetland's unique hydrogeologic setting and climate to aquatic-macroinvertebrate community structure. My third objective was to assess the degree of spatial synchrony of aquatic-macroinvertebrate communities to better understand the relative importance of local and landscape controls on aquatic-macroinvertebrate community assembly in freshwater wetlands. My fourth and final objective was to explore decreased hydrologic variability as a potential mechanism for the biotic homogenization of invertebrate communities, i.e., causes temporal and/or spatial reduction in beta diversity.

1.2. Thesis Approach

I used a unique set of 24 years of environmental monitoring data from a complex of 16 depressional prairie-pothole wetlands known as the Cottonwood Lake Study Area (CLSA) to quantify and assess aquatic-macroinvertebrate community responses to shifting hydrologic dynamics. The CLSA is within a U.S. Fish and Wildlife Service managed Waterfowl Production Area located in Stutsman County, North Dakota, near the center of the U.S. portion of the Prairie Pothole Region (PPR, Fig 1.1.). The wetlands monitored within the CLSA are among the most intensively studied wetlands in the world. Continuous observations of wetland hydrology began in 1979, and additional monitoring incorporating biological communities began in 1992. The wetlands are embedded within a prairie-grassland landscape that has remained relatively isolated from direct anthropogenic modifications, making this complex of wetlands a unique study system to conduct wetland research.

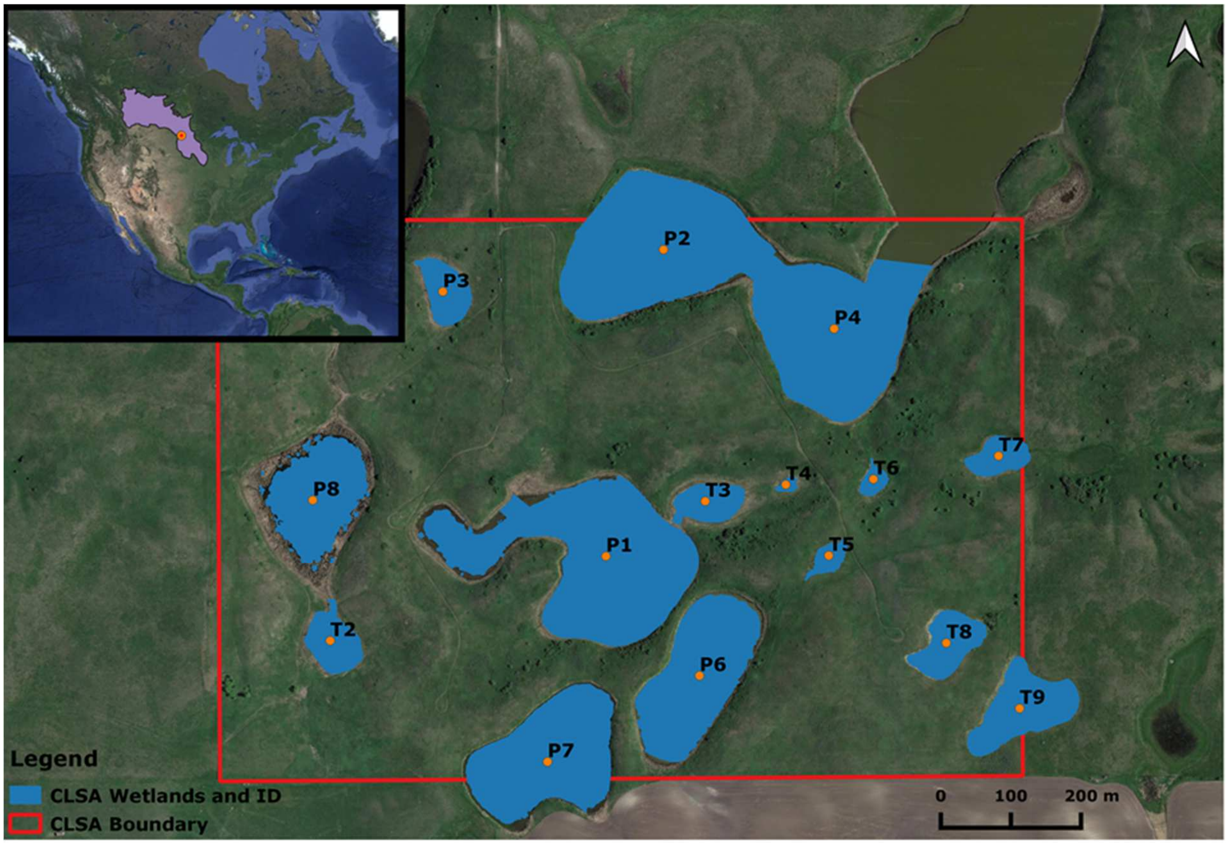

Figure 1.1. Map of the Cottonwood Lake Study Area in Stutsman County, ND, USA; and the Prairie Pothole Region of North America, shown in purple in the inset. Wetland P-11 (not shown) is located approximately 3-km west of the core study area depicted here.

The CLSA wetlands exhibit high among-wetland and among-year variability in ponded water dynamics. This is because, like most depressional wetlands (Hayashi et al., 2016), ponded-water dynamics of the CLSA wetlands are primarily driven by precipitation inputs and evaporative losses. The CLSA wetlands also occur along a recharge to discharge gradient of groundwater flow that includes wetlands that lose water to local groundwater flows, wetlands that both lose water to local groundwater and periodically receive groundwater, and wetlands that primarily receive groundwater and rarely lose water (Winter, 2003). While groundwater losses can alter ponded-water levels, especially in smaller wetlands, groundwater inputs have minimal impact on any one wetland's overall water budget (van der Kamp and Hayashi, 2009) but can greatly influence their water chemistry (Euliss et al., 2004, 2014). The among wetland heterogeneity and temporal breadth of hydrological, chemical, and biological dynamics provided by the CLSA's extensive data assets provide a unique opportunity to evaluate temporal processes in freshwater wetland ecosystems.

For the analyses presented here, I used CLSA wetland monitoring data collected between 1992 and 2015, which coincides with the start of aquatic-macroinvertebrate sampling and ends with the most recent CLSA data releases. I used wetland surface-water elevation (Mushet et al., 2016a), wetland vegetation-zone delineations (Mushet et al., 2017a), surface-water electrical conductivity (Mushet et al., 2016b), and wetland bathymetry (Mushet et al., 2017b) data to characterize each wetland's hydrogeologic characteristics and climate conditions. Metrics of aquatic-macroinvertebrate community composition were derived from both counts by taxa (Mushet et al., 2017c) and biomass by taxa (Mushet et al., 2018) data sets. Tiger salamander (*Ambystoma mavortium*) abundance data (Mushet and Solensky 2018) were used to characterize predation pressure. Full descriptions of the data collection methodology and specific summarizations of the data can be found in the following chapters. All data sets used are openly available from the U.S. Geological Survey through the Missouri Coteau Wetland Ecosystem Observatory at: https://www.sciencebase.gov/catalog/item/52f0ffd9e4b0f941aa181fc6.

1.3. Thesis Structure

In Chapter 2, I reviewed prairie-pothole wetland ecosystem response to historical and contemporary changes in climate and land use. I developed a conceptual model linking the direct, additive, and synergistic effects of wetland loss, surrounding land-use change, and climate shifts to the homogenization of wetland ecosystems. This review ties together several observational studies indicating shifts in prairie-pothole wetland hydrologic variability and identifies informational gaps that require further study.

In Chapter 3, I developed a structural equation model that incorporated relationships outlined in the Wetland Continuum Concept (see Euliss et al., 2004) linking a wetland's relationship to local surface and groundwater flows and climate to ponded-water dynamics and ultimately aquatic-macroinvertebrate community composition. Structural equation models are well suited for testing causal hypothesis using large observational datasets (Grace, 2008). The results indicated ponded-water characteristics are strong determinants of aquatic-macroinvertebrate composition, especially in comparison to measures of competition and predation.

In Chapter 4, I quantified among-wetland spatial synchrony, i.e., temporal coherence, of aquatic macroinvertebrates from 1992 to 2015. Temporal coherence was used to estimate the relative importance of wetland heterogeneity and landscape processes (i.e., climate) in determining aquatic-macroinvertebrate community dynamics. If wetlands are responding similarly across a landscape, it would suggest regional or landscape processes may be more important. My results indicated that both among-wetland environmental heterogeneity and between-wetland landscape linkages influence macroinvertebrate composition. I discuss the findings in the context of wetland conservation.

In Chapter 5, I examined spatial, temporal, and spatio-temporal patterns of aquatic-macroinvertebrate beta-diversity using different metrics of taxonomic turnover. Overall, my analyses suggested that among-wetland beta diversity has not decreased over time, which would indicate increased biotic homogenization. However, I found that larger, more permanently ponded wetlands experienced an aquatic-macroinvertebrate community shift in response to increased ponded-water volumes and stability.

In my final chapter, Chapter 6, I summarized general conclusions and synthesized my findings in the context of wetland and biodiversity conservation. I found that spatial connectivity and among-wetland heterogeneity are important aspects of aquatic-macroinvertebrate biodiversity maintenance. Smaller, more temporarily ponded wetlands disproportionately contributed to among-wetland and among-year beta diversity, and the presence or rare aquatic-macroinvertebrate taxa on the landscape.

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CHAPTER 2. CLIMATE AND LAND USE DRIVEN ECOSYSTEM HOMOGENIZATION IN THE PRAIRIE POTHOLE REGION

2.1. Abstract

The homogenization of freshwater ecosystems and their biological communities has emerged as a prevalent and concerning observation in recent decades. The loss of environmental variability has been linked to loss of ecosystem multifunctionality. The millions of prairie-pothole wetlands scattered across the Prairie Pothole Region (hereafter PPR) provide critical ecosystem functions at local, regional, and even continental scales. However, an estimated loss of 50% of historical wetlands and the widespread conversion of grasslands to row-crop agriculture make the PPR a heavily modified landscape. Therefore, it is essential to understand the current and potential future stressors affecting prairie-pothole wetland ecosystems in order to conserve and restore their important functions. Here I describe a conceptual model that illustrates how (a) historical wetland losses, (b) anthropogenic landscape modifications, and (c) climate change interact and have altered the variability among remaining depressional-wetland ecosystems (i.e., ecosystem homogenization) in the PPR. I reviewed existing literature to provide examples of wetland-ecosystem homogenization, potential implications for wetland management, and informational gaps that require further study. I found evidence for spatial, hydrological, and chemical homogenization of prairie-pothole wetlands, especially in the U.S. portion of the PPR. Evidence for biotic homogenization in the PPR was limited by the availability of long-term observations of wetland biodiversity. My findings indicate that the maintenance of wetland ecosystem multifunctionality is dependent on the preservation and restoration of heterogenous wetland complexes, especially the restoration of small wetland basins.

2.2. Introduction

Globally, freshwater ecosystems are experiencing widespread habitat degradation and biodiversity loss (Dudgeon et al., 2006; Reid et al., 2019). An increasingly observed trend in freshwater ecosystems is the homogenization of both physical habitats and biological communities (Rahel, 2002; Poff et al., 2007). The decreasing variability in both physical habitats and biotic communities contribute to losses of ecosystem multifunctionality (Bedford, 1999; Zedler and Kercher, 2005; Otte et al., 2007; Mouillot et al., 2007)). This loss of multifunctionality due to decreased variability in habitat characteristics has been referred to as ecosystem homogenization (Houghton, 2007). For freshwater ecosystems, evidence for ecosystem homogenization has been demonstrated in lakes and rivers, many of which have been highly modified through damming and streambed channelization (Houghton, 2007; Moyle and Mount, 2007; Poff et al., 2007; Rahel, 2007; Zeni and Cassatti, 2014). There has been considerably less attention focused on the homogenization of freshwater wetlands. However, freshwater-wetland ecosystems are among the most vulnerable to habitat degradation and provide critical functions in maintaining local and downstream ecosystem functions (Creed et al., 2017).

Wetlands are perhaps one of the most important and often overlooked components of our freshwater systems and cover an area greater than 1.2-million hectares worldwide (Finlayson et al., 2005). These temporally and spatially variable ecosystems provide numerous functions that are important for the health of the landscape (Cohen et al., 2016). Wetlands embedded entirely within upland landscapes are particularly sensitive to anthropogenic modifications and climate change (Frayer, 1983; Tiner, 1984; Brinson and Malvárez, 2002). This sensitivity to climate and land-use change make wetlands especially vulnerable to decreased hydrologic variability, increased biotic homogenization, and loss of ecosystem function, i.e., ecosystem homogenization (Bedford, 1999; Zedler and Kercher, 2004; Price et al., 2020). Ecosystem functions provided by freshwater wetlands, e.g., nutrient cycling, groundwater recharge, and biodiversity reservoirs, often vary depending on a wetland's geographic location (i.e., forested vs non-forested), hydro-period, and hydrogeologic setting (Richardson, 1994; Euliss et al., 2004; Bam et al., 2020). Bedford (1999) hypothesized that the non-random loss, degradation, and restoration of wetland ecosystems in the United States and Canada has likely resulted in a shift in the relative proportion of different types of wetlands on the landscape, which in turn has likely resulted in a net loss of wetland ecosystem multifunctionality. This prediction was based on the interactions between local climate, a wetland's hydrogeologic setting, i.e., a wetland's relationship to local groundwater and surface water flows, and wetland-upland linkages (Winter, 1988; Bedford, 1999), which is now commonly known as the Wetland Continuum Concept (Euliss et al., 2004). Based on the hypothesis of Bedford (1999), I developed a conceptual model for wetland ecosystem homogenization (Fig 2.1). This framework incorporates how independent, interactive, and synergistic processes caused by directional shifts in climate, land-use change, and historical wetland loss can lead to ecosystem homogenization. In this chapter, I use depressional wetlands located in the Prairie-Pothole Region (PPR) of the United States as a case study of wetland ecosystem homogenization.

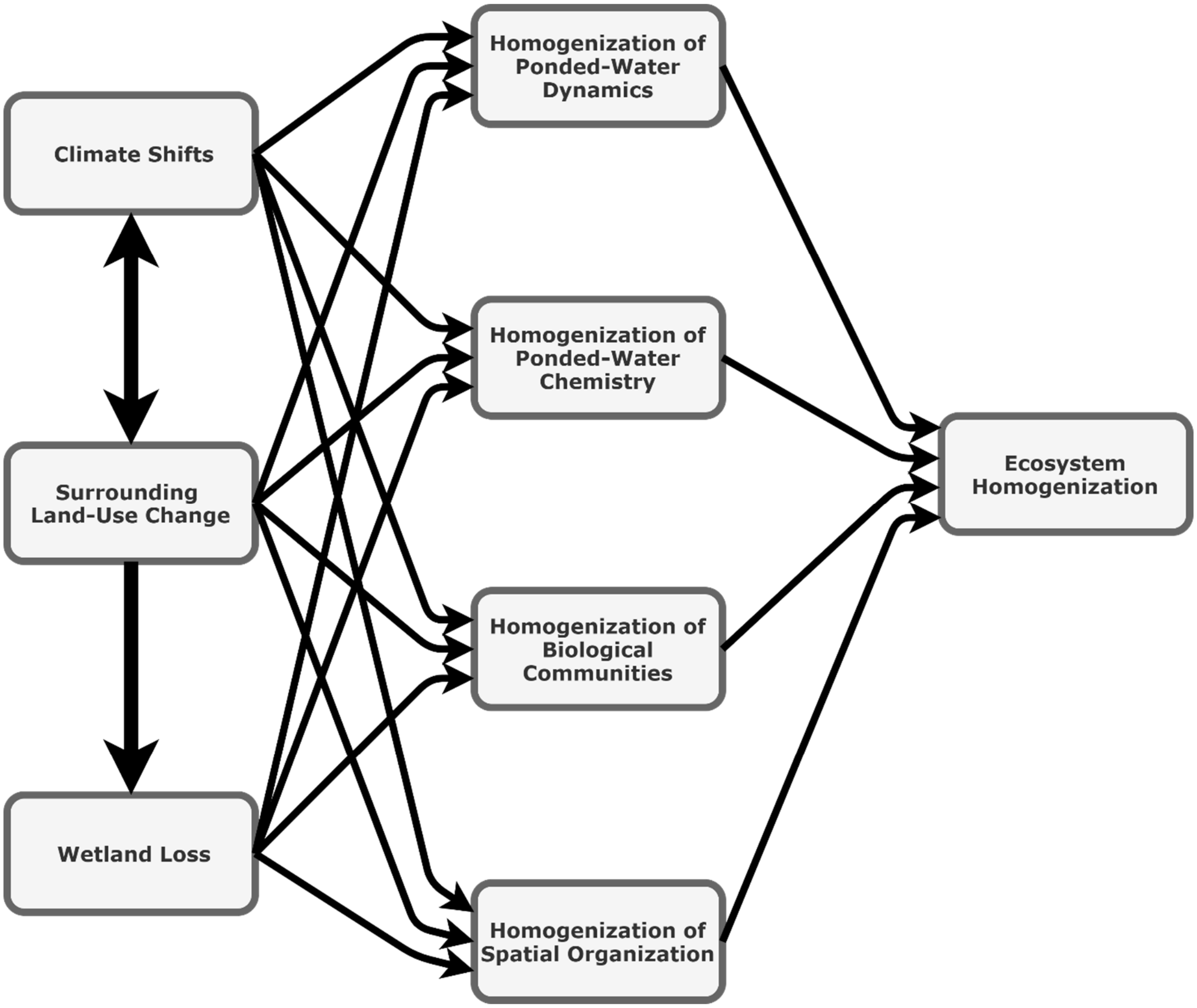

Figure 2.1. Conceptual model indicating hypothesized connections between climate shifts, land-use change, wetland losses, and components of wetland ecosystem variability, leading ultimately to ecosystem-level homogenization.

2.2.1. Prairie-pothole Wetland Ecosystem Variability and Function

Prairie-pothole wetlands are the predominant wetland type that occurs in the PPR. The PPR is one of the largest and most-modified, wetlands-dominated regions on earth. The PPR covers approximately 777,000 km^2, spanning north and west from northwest Iowa through the Dakotas and into central Alberta (Fig 2.2; Smith et al., 1964). As such, it forms the largest wetland complex in North America (van der Valk et al., 2005). Within the PPR, there are millions of individual wetland basins that can exhibit variable ponded-water dynamics (Gleason et al., 2011). The high spatial and temporal variability exhibited by prairie-pothole wetlands is a reflection of the high spatial and temporal variability in climate across the region (Winter, 2003; Liu and Schwartz, 2012). The entire PPR's climate is highly variable within and among years.

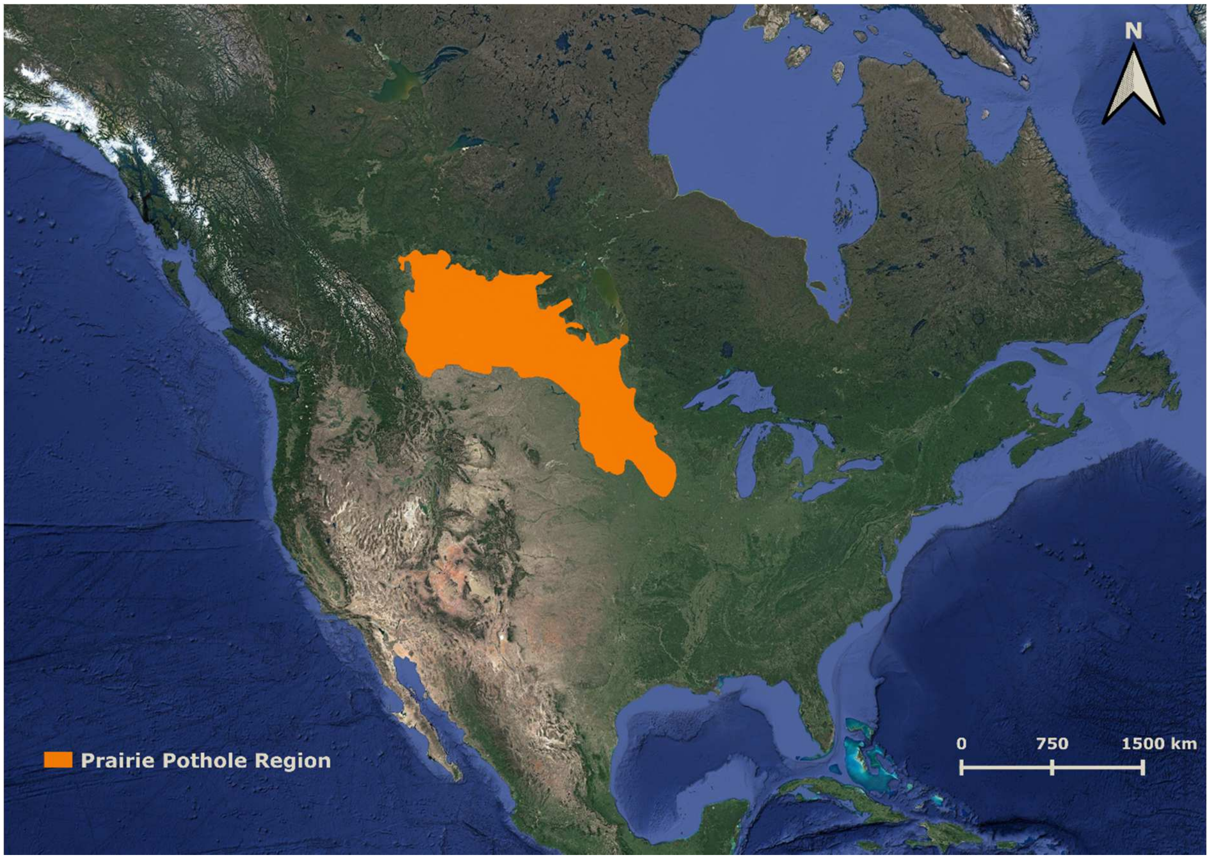

Figure 2.2. The Prairie Pothole Region of North America.

Annual maximum and minimum temperatures can range between 40 °C in the summer and -40 °C in the winter and mean annual precipitation can range from 30 cm/year to 90 cm/year. Typically, the northern portion of the PPR is cooler than the southern, and the eastern portion is wetter than the western. Precipitation can also exhibit both interannual variability and decadal oscillations in the form of wet-dry cycles (Winter and Rosenberry, 1998). These wet-dry cycles can influence the distribution of ponded-water area among wetlands, especially during times of drought or extreme deluge (Fig. 2.3). The typically closed-basin morphology and low-permeability substrates of prairie-pothole wetlands make them highly responsive to changes in surface-water inputs. However, they also accumulate or lose water to or from subsurface flows depending on a basin's relationship to the local groundwater table (Hayashi et al., 2016). Wetlands above the water table can recharge groundwater, are typically small, accumulate less salt, and have short hydroperiods; while wetlands below the water table receive groundwater discharge, are typically larger, accumulate more salts (through groundwater), and have longer hydroperiods (Euliss et al., 2004; Hayashi et al., 2016). Losses and accumulations of salts through the groundwater system, combined with climate-driven dilution and concentration effects, result in substantial variation in hydrogeochemistry (LaBaugh et al., 1987) among prairie-pothole wetlands. For example, the temporal and spatial variability in their ponded-water salinity can range from extremely fresh (<0.8 mS/cm) to hypersaline (>60 mS/cm), *i.e.* saltier than sea water (~50,*000 uS;* Cowardin et al., 1979; Swanson 1988).

The hydroecological variability of prairie-pothole wetlands contributes to the variety of ecosystem functions they perform (Euliss et al., 2004; Gleason et al., 2011; Euliss et al., 2014). Some of the more important functions include groundwater recharge, nutrient cycling, carbon sequestration, and stormwater retention (Crumpton et al.,1998; van der Kamp and Hayashi, 1998; Euliss et al., 2006; Huang et al., 2011). Prairie-pothole wetlands also uniquely contribute to regional aquatic, semiaquatic, and terrestrial biodiversity through the habitat and resources they provide (Euliss et al., 1999; Gleason et al., 2008; Johnson et al., 2008). For example. the PPR typically hosts around 50% of the continental breeding-duck population, making it a globally important area for wildlife management (Batt et al., 1989; Sørensen et al., 1998). Many of these ecosystem functions are maintained through the aforementioned spatial and temporal variability exhibited by the wetlands. However, historical and contemporary changes in climate, landcover, and wetland drainage have altered this natural variability.

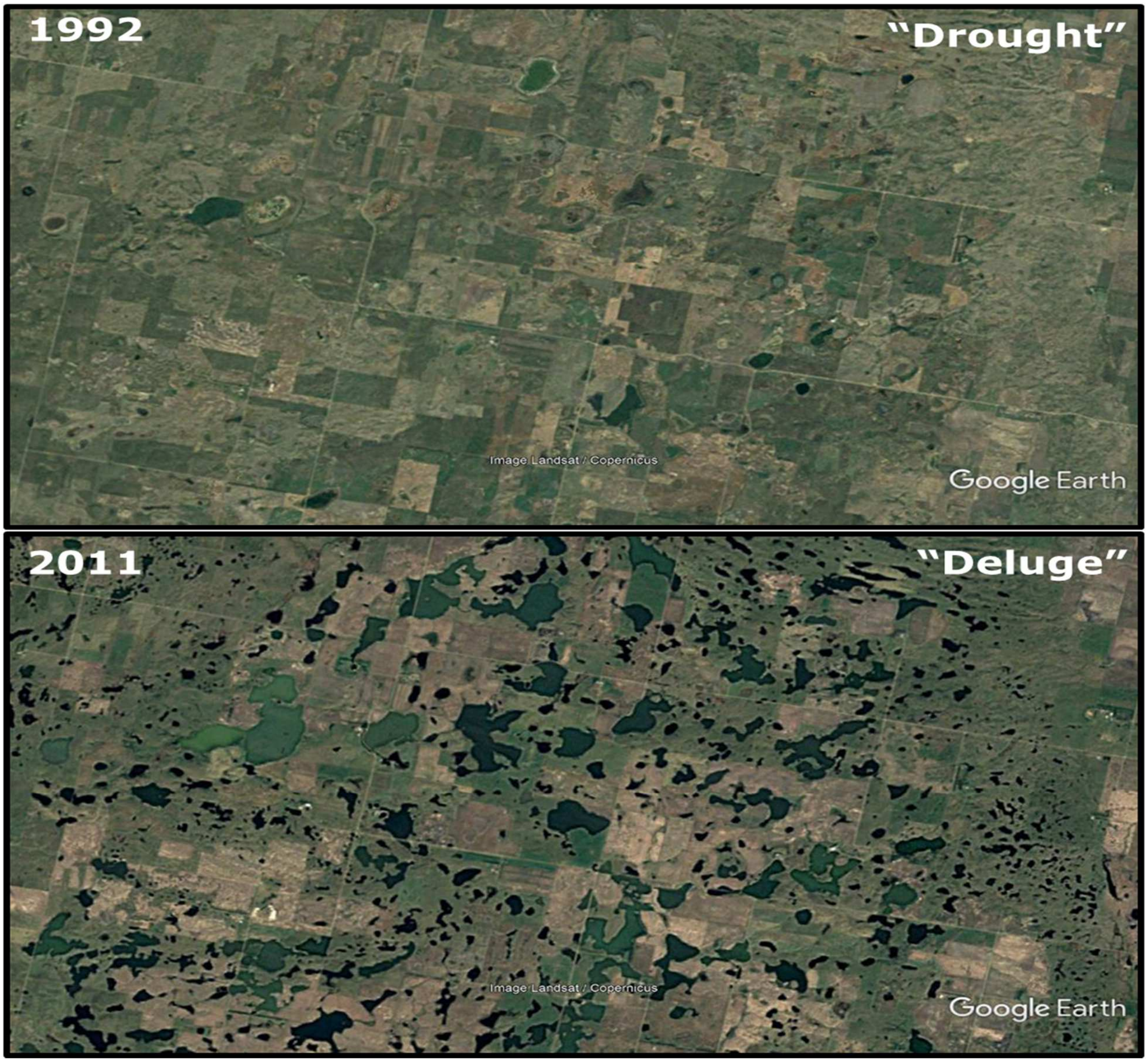

Figure 2.3. Landsat satellite imagery obtained from Google Earth depicting wetland surface-water changes during a period of drought (1992) and deluge (2011) in Stutsman County, North Dakota, USA.

2.3. Ecosystem Homogenization

Variability of prairie-pothole ecosystems is driven by an individual wetland’s hydrogeologic setting, local climate, and surrounding landscape characteristics. A wetland basin’s setting is defined as a basin’s topographic elevation, size, geomorphology, and underlying substrate, which in turn influence its relationship with local surface-water and groundwater flows, and subsequently contribute to a wetland’s capacity to pond and store water

(Hayashi et al., 2016). However, even wetlands with very similar hydrogeologic characteristics can exhibit high among-wetland variability due to spatial variation in climate and surrounding land use (van der Kamp et al., 2003; Renton et al., 2015). Wetlands and their functions are linked through landscape connections that determine how water, nutrients, and biota move through the landscape (Thiere et al., 2009; Shook and Pomeroy, 2011; McIntyre et al., 2014; Anteau et al., 2016; Martin et al., 2019). Alterations of wetland-to-wetland landscape linkages, i.e., the uplands that connect wetlands, and the geographic distance between wetlands can, in turn, influence the hydrologic and biotic variability of nearby wetlands (Bedford, 1999; Gibbs, 2000; Thiere et al., 2009; Hayashi et al., 2016). Many wetland ecosystem functions, e.g., biodiversity maintenance, groundwater recharge, and stormwater retention, are maximized in complexes of wetlands with heterogenous water regimes (McLean et al., 2019; Bam et al., 2020; Elliot et al., 2020). Therefore, the loss of variability in water regimes, altered spatial organization of wetland landscapes, and corresponding changes in functions can lead to ecosystem homogenization.

2.3.1. Conceptual Model for Ecosystem Homogenization

Natural landscape and climate variability are essential to maintaining heterogenous complexes of wetlands. However, large-scale landscape alterations and long-term or severe changes in regional climate can have additive and often synergistic effects on wetland ecosystem functions (Anteau et al., 2016; McKenna et al., 2017; Mushet et al., 2018; Mckenna et al., 2019). My conceptual model for wetland ecosystem homogenization (Fig 2.1) depicts how shifts in climate cause directional changes in wetland hydrology that, in turn, can cause a directional change in water and soil chemistry, and subsequently modified biotic communities. In addition to being a primary driver of wetland ponding; directional shifts in climate can influence wetland ecosystems by driving changes in surrounding land use, such as a change from pasture to crop production, which in turn impact wetlands through water-management decisions that can result in the movement of water off the landscape (Coote and Gregorich 2000; McKenna et al., 2017). The wetland loss category refers to the deliberate draining, ditching, and filling of wetland basins. The loss of functioning wetlands not only simplifies the geographic configuration of remaining wetlands, but their displacement changes local surface-water flows, which in turn can alter the temporal and spatial dynamics of remaining wetlands on the landscape (Bedford, 1999 Rains et al., 2016; Calhoun et al., 2017).

2.3.2. Mechanisms for Ecosystem Homogenization in the PPR

The landcover of the pre-European settlement PPR was primarily a mix of native grassland with embedded depressional wetlands. These relatively small, prairie-pothole wetlands covered an estimated 20% of the region's land area (Euliss et al., 2006). However, the interplay between European settlement, local topography, local climate, and agricultural production have led to spatial simplification of prairie-pothole wetland distributions (Bedford 1999; Van Meter and Basu, 2015; Serran and Creed, 2016; Creed et al., 2017). This simplification was predominately driven by the conversion of wetlands and their native uplands (native prairie) to cropland. It has been estimated that 65% of the historical wetland basins in the PPR were lost due to anthropogenic influences (Euliss et al. 2006). This loss is spatially variable, ranging from 35% in South Dakota to >90% in the Des Moines lobe ecoregion of Iowa (Dahl, 1990, van Meter and Basu 2015). Since wetland losses in the PPR were primarily a result of the draining and filling of wetland basins for agriculture (Dahl, 2014), losses were concentrated in the most heavily farmed areas (Johnston 2013). In addition, a disproportionate number of wetlands that were drained or filled were the small, most temporarily ponded wetlands (Bedford 1999; Serran and Creed 2016; van Meter and Basu, 2015). The preferential loss of these smaller wetlands not only decreased the hydrologic variability on the landscape but also led to the loss of spatial connectivity and ecosystem homogenization (Gibbs, 2000; Jenkins et al., 2003; Rains et al., 2016; Vanderhoof et al, 2017).

In addition to the loss of many historical wetlands, the conversion of uplands to farmland and consolidation of runoff from wetland-drainage networks further altered the ecohydrological variability of remaining wetlands (Anteau, 2012; McCauley et al., 2015; McKenna et al., 2019). Most of the historical wetland drainage in the PPR occurs in the form of surface ditching, which works by moving water from numerous small wetlands into a single, larger, terminal waterbody, i.e., wetland consolidation (McCauley et al., 2015). The increased water inputs to the terminal wetland results in increased ponded-water extent and duration (Anteau, 2012) in the terminal wetland. Along with consolidation, runoff rates have also increased in the region due to the conversion of native uplands to cropland (Hayashi et al., 2016; Rains et al., 2016). An estimated 90% of native grasslands in the PPR have been converted to other landcover types, typically cropland (Mac et al., 1998). By contrast, widespread establishment of monotypic stands of invasive grasses in grassland-covered uplands surrounding wetlands can reduce runoff rates resulting in increased drying of wetland ponds (Gleason et al., 2011). Non-native grasses, primarily *Bromus inermis* and *Poa pratensis,* have invaded many remaining grasslands in the region (DeKeyser et al., 2013; Toledo et al., 2014; Dixon et al., 2019).

In the absence of prairie buffers, agricultural runoff into wetlands is associated with greater rates of sedimentation, nutrient loads, and pesticide pollution (Gleason and Euliss 1998; Main et al., 2014; Martin et al., 2019; Williams and Sweetman 2019), which in turn can alter the chemical and biotic composition of affected wetlands. The loss of surrounding grasslands also becomes a loss of habitat and inter-wetland connectivity for species that require grasslands in addition to ponded wetlands to complete their lifecycle (Euliss and Mushet 2004; Mushet et al., 2014; McIntyre et al., 2019). The cumulative effects of wetland loss and the conversion of prairie to cropland in the PPR have simplified the spatial distribution of wetland basins and the upland landscapes in which they are embedded, and reduced ponded-water variability in remaining wetlands. In the context of my ecosystem-homogenization conceptual model, these changes also influence the sensitivity to climate of the remaining wetlands within this altered landscape (Fig 2.1).

Beginning in 1993, parts of the PPR experienced an extended multi-decadal wet period (Ballard et al., 2014; McKenna et al., 2017). Even in the absence of anthropogenic land-use change, the magnitude of precipitation increases has resulted in cascading effects. The combination of rising groundwater tables and increased soil moisture in the region has resulted in increased surface-water runoff and reduced groundwater losses from wetlands (Mushet et al., 2015; McKenna et al., 2017). However, most of the PPR is not absent from anthropogenic change, and the timing of this wet period coincided with a loss of grasslands, an increase in row-crop agriculture, and an increase in tile drainage (Johnston 2013; Johnston and McIntyre 2019; McKenna et al., 2017). This observed directional shift in climate, land-use change, and non-random wetland loss has led to a shift towards reduced ecohydrological variability for much of the US PPR (Kahara et al., 2009; McKenna et al., 2017, Mushet et al., 2018).

2.4. Evidence for Ecosystem Homogenization

The response of prairie-pothole wetland ecosystems to increased precipitation has been highly variable and spatially dependent (Liu and Schwartz, 2012; Cressey et al., 2016). Based on our conceptual model, these patterns are intuitive considering that wetland loss, land-use change, and relative climates are regionally variable (Kahara et al., 2009; Millet et al., 2009; van Meter and Basu, 2015; Serran and Creed, 2016). While some areas might experience greater change than others, most long-term studies in the PPR of the U.S. have indicated increases in hydroperiod, ponded-water surface area, depth, and connectivity over the last 15 to 30 years (Kahara et al., 2009; Mushet et al., 2015; Van Meter and Basu, 2015; Wiltermuth, 2014; Cressey et al., 2016; McKenna et al., 2017; Vanderhoof et al., 2017). These observed hydrological shifts often resulted in decreased variability of ponded-water regimes, homogenized water chemistries, and altered biotic communities (McCauley et al., 2015; Mushet et al., 2015; Cressey, 2016; LaBaugh et al., 2018; McLean et al., 2019).

Even though many, especially smaller, prairie-pothole wetlands have been drained or filled, in more contemporary time periods (i.e., the last 50 years) the mean number of wetland ponds and ponded-water surface area in the US PPR has increased over the last 15 to 30 years in response to wetter climate conditions (Neimuth et al., 2010; Vanderhoof et al., 2016, 2017). This greater ponded-water area is predominately driven by an increased distribution of large ponded basins (Kahara et al., 2009). This is in part due to the extreme saturation of wetlands on the landscape. As wetland basins become increasingly ponded, they fill until water spills into the next wetland basin. This dynamic is called “fill-and-spill” (Shaw et al., 2011). In the case where a larger lower-elevation basin increases in surface area and engulfs higher-elevation wetlands (Kahara et al., 2009; van Meter and Basu, 2015; Vanderhoof and Alexander, 2016), it is called “fill-and-merge” (Leibowitz et al., 2016). Cressey et al., (2016) compared ponded-water surface area, depth, and salinity for 80 prairie-pothole wetlands between two periods (1961–1966 and 2013–2014) and found that even at relatively small spatial scales (i.e., central ND) wetland complexes responded differently to changing hydroclimatic conditions. For example, wetland areas with low topographic relief and an absence of defined outlets typically had greater area for ponded water to expand and merge with nearby wetlands, and therefore exhibited the greatest hydrologic changes (Cressey et al., 2016). In contrast, wetlands with high topographic relief and defined outlets often exhibit less surface-water variability (Cressey et al., 2016; McLean et al., 2019). Vanderhoof and Alexander (2016) found through Landsat-derived surface-water maps from 1990 to 2011 that lake expansion in the PPR caused increased surface-water connectivity to nearby wetlands and sometime the inundation of wetlands tens of kms away by the expanding lake. At a smaller scale, long-term monitoring beginning in 1979 at the Cottonwood Lake Study Area in south central North Dakota indicated that after 1993 the 16 wetlands monitored had increased in surface-water depth, permanency, and connectivity compared to the previous two-decade averages (Leibowitz et al., 2016; McKenna et al., 2017; LaBaugh et al., 2018). Both climate driven fill-and-spill/fill-and-merge dynamics and consolidation of wetlands through drainage networks not only influence associated wetland ponded-water regimes but can also homogenize the composition and concentration of dissolved ions, nutrients levels, and biota found in the newly merged wetlands (Whigham and Jordan, 2003; Mushet et al., 2015; Wiltermuth et al., 2016; Cressey, 2016; McLean et al., 2016).

Increased atmospheric water inputs into wetlands and the merging of previously separate basins can have profound influences on the water chemistry of a wetland. Water chemistry, specifically dissolved-ion concentrations, in prairie-pothole wetlands is highly variable in space and time (Nachshon et al., 2015; Mushet et al., 2015; Labaugh et al., 2018). As dissolved-ion concentrations increase, biotic communities often shift to more salt tolerant taxa (Swanson et al., 1988; Euliss et al., 1999). The increases in surface-water runoff and connectivity observed throughout much of the PPR have reduced the salinity gradient length and among wetland variability (Nachshon et al., 2014, Mushet et al., 2015).

Dissolved-ion concentrations in wetlands are driven by salt inputs and losses, combined with dilution and concentration effects. Typically, wetlands situated above local groundwater flows lose ponded water and dissolved salts to the soil, recharging the groundwater. By contrast, wetlands located at or below groundwater flows receive salts through groundwater discharge (Euliss et al., 2014). Atmospheric-water inputs (i.e., direct precipitation or precipitation driven runoff inputs) dilute the concentration of dissolved ions within a wetland, while evaporation and transpiration result in increased ion concentrations. When fill-and-spill or fill-and-merge dynamics are incorporated, dissolved ions mix, typically resulting in the saltier of the newly connected wetlands becoming fresher and the fresher wetland becoming more saline (Mushet et al., 2015; Cressey et al., 2016; Leibowitz et al., 2016). Two separate multi-county studies in central North Dakota found that since the 1960s and 1970s, saline wetlands have become significantly fresher and fresh wetlands have either remained static or slightly increased in salinity, resulting in less variability in salinity and a more homogenous salinity gradient (Mushet et al., 2015; Cressey et al., 2016). Mushet et al., (2015) found that for 167 large central North Dakota prairie-potholes sampled in the 1960s and 1970s, and resampled in 2012 and 2013, the specific conductance range between wetlands was 365 µS/cm to 70,300 µS/cm with a mean of 8,376 µS/cm in the earlier time period and decreased to a range of 449 to 40,350 µS/cm with a mean of 2,*897* µS/cm in the more recent sampling. Similarly Cressey et al., (2016) found that for 80 central North Dakota wetlands with variable ponded-water regimes, wetlands that were saline in the 1961 to 1966 sampling period were much fresher during the 2013 to 2014 sampling period, and many of the smaller, historically fresher wetlands increased in salinity, which resulted in a much narrower and more homogenous salinity gradient in the later period. The cumulative changes in ponded water; volume, duration, extent, and chemistry have already started to alter species assemblages in the region (Maurer et al., 2015; Mushet et al., 2015; Cressey 2016; McLean et al., 2019).

The concept of biotic homogenization has a rich and still growing literature base in the aquatic sciences (Lockwood and McKinney 2001; Olden 2006; Petsch 2016). The dominant mechanisms that drive biotic homogenization are habitat simplification due to anthropogenic modification and the spread of invasive species (Lockwood and McKinney 2001; Petsch 2016). These two mechanisms work hand in hand since habitat simplification can result in a loss of specialist taxa which provide an opportunity for non-endemic or other generalist taxa to replace them (Olden 2006). While habitat simplification of wetland ecosystems has occurred in the PPR, investigations of biotic responses in the context of biotic homogenization are limited (McLean et al., 2019). The research that has indicated evidence for biotic homogenization in the PPR are mostly observations of decreased-beta diversity in wetland plant communities (Aronson and Galatowitsch 2008; Cressey 2016; Price et al., 2020). The potential homogenization of wetland animal communities, e.g., invertebrates and amphibians, is likely less understood due to the limited availability of long-term monitoring data (McLean et al., 2016a).

Prairie-wetland vegetation dynamics and diversity are highly dependent on hydrologic dynamics (Aronson and Galatowitsch, 2008). Contemporary shifts towards larger, deeper, more connected wetland ponds in the PPR and the conversion of many uplands to cropland can simplify both the structure and taxonomical composition of wetland plant communities. Depending on a wetlands ponded-water regime, prairie-pothole wetlands can have open-water, deep-marsh, shallow-marsh, and wet-meadow vegetation zones (Stewart and Kantrud, 1971). Vegetation structure is different in each zone. For example, open-water zones in wetlands contain submergent vegetation, deep-marsh zones contain tall emergent species, shallow-marsh zones contain mid-height emergent vegetation, and wet-meadow zones contain shorter sedges (Kantrud et al., 1989). When multiple vegetation zones are present, even minor changes in surface water can significantly change a wetlands vegetation structure (van der Valk and Mushet, 2016). The shift towards larger, deeper, more permanently ponded wetlands can lead to the loss of shallow marsh and wet meadow zones, which results with most of the wetland being in open-water or deep-marsh vegetation (McLean et al., 2019). Another widespread mechanism for loss in wetland vegetation structure has been the cultivation of wetland edges (Glooschenko et al., 1993; Johnston and McIntyre, 2019). The simplification of vegetative structure through loss of vegetation zones, can in turn result in a loss of plant (and animal) species unique to the specific vegetation zones.

The stabilization of ponded-water regimes can result in a loss of plant communities that prefer dynamic surface-water fluctuations, which in turn can facilitate their replacement with exotic plants (Wiltermuth et al., 2016; Price et al., 2018; Bansal et al., 2019). Increased sedimentation and nutrient transport into wetlands from surrounding croplands has also been attributed to the establishment of invasive wetland plants such as hybrid cattail (*Typha* ×*glauca*), reed canarygrass (*Phalarus arundinacaea*), and common reed (*Phragmites australis*), which are known to spread rapidly and can choke out entire wetland basins (Bansal et al., 2019; Price et al., 2020). For restored wetlands in the southeastern portion of the PPR, Aronson and Galatoswitch (2008) found that beta diversity began to decrease after 12-years post reflooding when extinction rates began to exceeded colonization rates. A major mechanism in these losses was the invasion of reed canary grass and hybrid cattails. The rise of invasive cattails and reed canary grass in shallow-marsh and wet-meadow zones has been observed in other studies within the region as well (Cressey, 2016; Wiltermuth et al., 2016). While the observed loss of vegetation structure and native species and increases in invasive species in prairie-pothole wetland plant communities appears to be a common pattern, the response of aquatic animal communities to habitat simplification has been less predictable (McLean et al., 2019), although shifts in aquatic plant communities would impact other organisms within these wetlands.

McLean et al., (2019) used long-term monitoring data from 16 wetlands in the PPR of North Dakota to investigate the simplification of ponded-water regimes observed through a shift towards more permanently ponded wetlands, and to determine if the shifts were correlated with decreases in aquatic-macroinvertebrate beta diversity. Overall, among-wetland beta diversity did not change over time (1992 to 2015). However, for the wetlands that shifted to more lake-like ponded-water regimes, they observed a clear shift towards a more novel and less dynamic invertebrate community composition (McLean et al., 2019). Unfortunately, for the sites included in McLean et al (2019), aquatic-macroinvertebrate sampling did not begin until the start of an extended wet period, and consequently, their study was not able to quantify community composition that occurred in the more hydrologically dynamic periods that occurred before the start of the current wet period (i.e., pre 1993). The temporal limitations of this study can be expanded across the PPR, where there are very few, if any, aquatic-invertebrate studies that capture the taxonomic variability observed before and after 1993 (McLean et al., 2016a).

Under contemporary ecohydrological conditions in the PPR, most wetland studies aimed at identifying environmental and surrounding land-use predictors of aquatic macroinvertebrates and or amphibians have been inconclusive in their findings (Batzer, 2013). However, using the information available, we can put together the pieces and generate hypotheses as to how climate and land use driven simplification of wetland ecohydrological variability influences regional biodiversity. The preferential loss of small, temporarily ponded wetlands have likely resulted in localized or even regional loss of plant and animal communities that are specially adapted to these systems (Bedford, 1999; Calhoun et al., 2017). For example, many fairy shrimp (Anostraca) species require periodic drying of wetlands in order to complete their lifecycle. In regions outside the PPR, the loss of ephemeral wetland habitats has resulted in the regional loss or in some cases extinction of specific species (King et al., 1998; Jenkins et al., 2002). However, for the PPR, there is very little literature that documents wetland macroinvertebrate communities present prior to the large-scale drainage of wetlands. While some invertebrates leave behind a record of their occur in wetland sediments, many leave behind no recalcitrant remains. Therefore, we will likely never know the actual extent of the pre-European-settlement species lost (Belk, 1996). Another group of specialist wetland taxa that have likely become less abundant on the landscape are the saline tolerant invertebrates (i.e., brine shrimp, brine flies) and plants (Mushet et al., 2015; McLean et al., 2016a). The observed decreases in highly saline habitats and the loss of temporarily ponded wetlands have likely resulted in a loss of these specialist taxa. The current, fresher and larger wetland ponds have become suitable for a wider range of generalist taxa, and many can now support taxa that require permanent ponds to persist, e.g., fish that were not historically associated with prairie-pothole wetlands (McLean et al. 2016b). The increased presence of these fish communities has been identified as a major threat to aquatic-macroinvertebrate and amphibian communities (Zimmer et al., 2000; Hanson et al., 2005; Batzer, 2013; McLean et al., 2016b).

For the most part, prairie-pothole wetlands have not been subjected to many exotic and invasive aquatic animals that have plagued other nearby aquatic ecosystems (e.g., zebra mussels, rusty crayfish, and faucet snails). The exception is the increased prevalence of fish communities. While most of the fish taxa associated with prairie-potholes are native to the region, they would historically be absent from most prairie-pothole wetlands (Peterka, 1989). Prior to 1993, most wetlands in the PPR were likely not deep or fresh enough to support these fish (McLean et al., 2016b). It is likely that infrequent colonization of fish into prairie-pothole wetlands has naturally occurred. However, long-term persistence in these systems would be rare considering that even some of the largest potholes periodically dry or become too shallow to overwinter fishes (Peterka, 1989; Mushet et al., 2015). In addition to historically being unsuitable for fish population persistence, the lack of surface-water connections would have limited fish dispersal from adjacent lakes and rivers. The cumulative effect of decreased ponded-water salinity, increased ponded-water volume and duration, and increased surface-water connectivity currently prevalent in the PPR has likely facilitated the colonization of fish into prairie-potholes (McLean et al., 2016b). The most prevalent fish species observed in prairie-pothole wetlands is the fathead minnow (*Pimephales promelas*). Gamefish, e.g., yellow perch (*Perca flavescens*), have also become increasingly prevalent in many wetlands in the U.S. portion of the PPR. In addition to dispersal through surface-water connections, the commercial and recreational value of baitfish such as minnows and gamefish such as perch has led to an increase in stocking previously fishless habitats. Since prairie-pothole wetland ecosystems did not evolve with fish, their presence in a wetland can lead to rapid changes to the native species that live and/or feed in wetlands (Zimmer et al., 2000, 2001; Hanson et al., 2005). For example, fathead minnow presence is correlated with decreased macroinvertebrate alpha diversity and biomass (McLean et al., 2016a). The presence of fish is also correlated with decreases in native amphibian abundance, particularly for barred tiger salamanders (*Ambystoma mavortium*) and northern leopard frogs (*Lithobates pipiens*), which both compete with and become prey to some fish species (Zimmer et al., 2000; McLean et al., 2016b).

In addition to their negative impacts on aquatic-macroinvertebrate and amphibian species distributions, the increased presence of fathead minnows also simplifies trophic networks and results in ecosystem degradation (Hanson et al., 2005; Sundberg et al., 2016). For example, fathead minnows can deplete small, herbivorous, zooplankton populations, which can often result in a trophic cascade if algal blooms arise. These algal blooms, in turn, reduce submergent vegetation by blocking sunlight (Hanson and Riggs, 1995; Zimmer et al., 2001; Hanson et al., 2005). As another example, when in competition with fathead minnows, brooding ducklings have reduced growth and survival rates (Cox et al., 1998).

2.5. Consequences of Ecosystem Homogenization

While the distribution and variability of ecosystem functions provided by prairie-pothole wetlands has likely decreased due to historical wetland losses and shifting (wetter) ecohydrological conditions, remaining prairie-potholes still provide valuable habitat for regional biodiversity and perform critical ecosystem services. The selective losses of small wetlands and saline wetlands has likely resulted in a loss on the landscape of the unique taxa associate with these wetland types. However, the larger, more permanently ponded wetlands remaining on the landscape often have higher aquatic-macroinvertebrate taxon richness (Gleason and Rooney, 2018; Daniel et al., 2019). The increased presence of water on the landscape has also boosted local duck and fish populations (Niemuth and Solberg, 2003). The increased duck populations and fishing opportunities in prairie-pothole wetlands have also benefited outdoor recreation in the region. However, the functional roles of prairie-pothole wetlands extend beyond wildlife conservation. Homogenization of other prairie-pothole ecosystem attributes threaten their important landscape functions and the societal benefits they provide.

The smaller, temporarily ponded wetlands that were once much more common in the PPR landscape provide many important ecosystem services due to their unique properties (Calhoun et al., 2017). For example, these smaller wetlands are the primary contributors to groundwater recharge to the aquifer (Ameli and Creed, 2019; Bam et al., 2020) because they store and quickly lose water to the groundwater. They can also capture a disproportionate amount of stormwater runoff compared to larger discharge wetlands, which helps alleviate flooding (Zhang et al., 2009; Huang et al., 2011; Liu and Schwartz, 2012). This is especially important under current climate conditions when many larger wetlands have remained at or near their spill point which limits their water-storage capacity. In addition to water storage, smaller wetlands are disproportionately important for their geochemical functions as well (Calhoun et al., 2017). For example, smaller wetland basins have proportionally larger reactive zones, which make them more efficient in biogeochemical cycling (Cohen et al., 2016).

2.6. Potential Impacts of Continued Climate Change

While ecohydrological conditions of wetlands for most of the US PPR over the most recent 15 to 25 years have been wetter and resulted in larger wetland ponds than historical averages (Mushet et al., 2015; McKenna et al., 2017), these conditions are likely to change under future climate scenarios (Liu et al., 2016; Muhammad et al., 2018). However, there is still much uncertainty as to the magnitude of seasonal and annual temperature and precipitation changes in the PPR, and how wetland ecosystems will respond to these changes (Hawkins and Sutton, 2011; Sofaer et al., 2016; Steen et al., 2018). One commonality in future climate predictions is that temperatures will continue to increase, and average ponded-wetland densities will decrease (Sofaer et al., 2016). With increases in temperatures come increases in evaporation rates of wetland ponds. If evaporation and transpiration water losses exceed precipitation inputs into wetlands, then ponded wetland area will decrease, which could result in a loss of wetland network connectivity (Liu et al., 2016). Considering that evaporation and transpiration rates decrease as the volume to surface-area ratio increases, and that smaller recharge wetlands lose more water to the soil during dry periods, short-term droughts could have a disproportionate influence on the smaller wetland ponds (van der Kamp and Hayashi 1998; Zhang et al., 2009; Hayashi et al., 2016). LaBaugh et al., (2016) found that even though salt concentrations in the more permanently ponded wetlands were decreasing due to dilution, the accumulation of salts has continued to increase over time in some wetland ponds. This could have serious consequences for local biota if these larger ponds begin to dry and concentrate these salt additions. Land-use change has also been a continuous process in the region that can either help or harm wetland ecosystems depending on our future management decisions.

2.7. Conclusions

Depressional wetlands, such as prairie-pothole wetlands are highly sensitive to adjacent landscape modifications and climate shifts (Brinson and Malvárez, 2002). Through my review of the prairie-pothole wetland literature, I found consistent patterns indicating climate and land use driven shifts in wetland hydroecological variability. The synergistic effects of climate and land use are working to pull wetland ecosystems towards one of two stable states, a dry state or a permanently ponded state (Mushet et al., 2020). Over the last few decades, many larger wetlands have shifted towards being more permanently ponded lakes. However, in the future, climate warming will likely shift wetlands towards a dry state, which will disproportionately impact smaller wetlands. Currently, the smaller temporarily ponded wetlands continue to be the most vulnerable to future losses and are perhaps the most valuable for maintaining wetland landscape multifunctionality (Cohen et al., 2016; Calhoun et al., 2017; Creed et al., 2017: Bam et al., 2019).

2.8. References

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CHAPTER 3. LONG-TERM MULTIDECADAL DATA FROM A PRAIRIE-POTHOLE WETLAND COMPLEX REVEAL CONTROLS ON AQUATIC-MACROINVERTEBRATE COMMUNITIES[1]

3.1. Abstract

Interactions between climate and hydrogeologic setting contribute to the hydrologic variability among depressional wetlands, which influences their aquatic communities. These interactions and resulting variability have led to inconsistent results in terms of identifying reliable predictors of aquatic-macroinvertebrates community composition for depressional wetlands. This is especially true in the Prairie Pothole Region of North America where, in addition to pronounced climate variability, studies are often confounded by fish introductions. We used environmental monitoring data collected over a 24-year period from a complex of seventeen, depressional wetlands, and structural equation modeling techniques that incorporated theoretical and empirical relationships outlined in the Wetland Continuum to identify key environmental (climate and hydrogeologic setting) and biotic (competition and predation) drivers of aquatic-macroinvertebrate community composition for prairie-pothole wetlands. Uplands in the study area were primarily native prairie, thus, embedded wetlands were impacted minimally by agricultural influences. Additionally, study wetlands were predominately fishless. We found variables related to the placement of wetlands along axes of the Wetland Continuum, e.g., salinity (as related to hydrogeologic setting) and the proportion of open-water habitat in a

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[1] The material in this chapter was co-authored by Kyle I Mclean, David M. Mushet, Wesley Newton, and Jon N Sweetman. Kyle I McLean had the primary responsibility of data analysis, developing conclusions, and drafting the manuscript. David M. Mushet and Wesley Newton were instrumental in developing the initial study design. David M. Mushet, Wesley Newton, and Jon N. Sweetman served as proofreaders and supplied constructive comments on the interpretation of the findings of this study.

wetland (as related to climate), to be influential drivers of macroinvertebrate community assemblages. Biotic interactions (i.e., predation and competition) further influenced macroinvertebrate compositions. In the absence of the overwhelming influence of fishes, major drivers influencing aquatic-macroinvertebrate communities were revealed through the use of data spanning multidecadal-long climate cycles.

3.2. Introduction

Despite the importance of depressional wetlands as inland-water ecosystems, our understanding of processes influencing their biotic communities is lacking compared to other lentic ecosystems (NRC, 1996; Murkin, 1998). Depressional-wetland ecosystems are highly variable in both space and time. The aquatic invertebrates inhabiting these systems are necessarily adapted to this high spatial and temporal variability (Brinson, 1993; Batzer et al., 2004). However, the full range of environmental variability in depressional wetlands is typically not captured in studies of these complex ecosystems (Batzer, 2013; McLean et al., 2016a). Therefore, the ability to identify and quantify the influence of environmental drivers of wetland communities are hindered. For example, increased hydroperiods (i.e., the length of time a wetland contains ponded water) and decreased salinities during wet periods can mask key processes influencing aquatic communities by reducing strong environmental filters such as pond drying and the co-occurring concentration of salts. Disentangling the potential impacts of hydroclimatic variability is important in effectively managing prairie-pothole wetlands.

The high, natural, spatio-temporal variability in depressional-wetland ecosystems can be attributed to their placement along continua defined by each wetland's unique relationship with groundwater and atmospheric-water inputs and losses, i.e., the Wetland Continuum as originally described by Euliss et al., (2004) and later modified by Hayashi et al., (2016). The Wetland

Continuum conceptual model provides an indication of the hydrologic function of a particular wetland, as mediated by its local topographic position in the landscape, configuration of the associated water table, type and structure of underlying geological substrates, and climate-driven variation in atmospheric inputs and losses. The unique hydrology and climate of a region have a profound influence on the water chemistry and ponded-water permanence of wetlands, thereby influencing biota at different hydrological stages. The placement of wetlands along spatial and temporal continua that represent their unique hydrogeologic setting has been identified as a framework to integrate ecological studies (Bedford, 1999; Euliss et al., 2014) and provides hypothesized relationships that can be empirically tested.

Few studies have integrated hydrogeologic processes of prairie-pothole wetlands into biological investigations (Hanson et al., 2005). Thus, we used the Wetland Continuum framework to provide insights into hydrogeochemical influences on aquatic invertebrate communities inhabiting depressional wetlands. Those that have were largely inconsistent in identifying reliable predictors of aquatic-macroinvertebrate community composition (reviewed in Batzer, 2013). However, one consistent predictor of invertebrate assemblages has been the presence of introduced fish (McLean et al., 2016b). Fish introductions have been found to decrease invertebrate abundance and taxonomic heterogeneity (Hanson and Riggs, 1995; Zimmer et al., 2000; Tangen et al., 2003; Hanson et al., 2005; Anteau and Afton, 2008; Maurer et al., 2014; McLean et al., 2016a), and the marked influence of fishes on aquatic-invertebrate communities of wetlands might mask other important drivers of community composition (Anteau, 2012; McLean et al., 2016a).

Using ideas and concepts presented in the Wetland Continuum, we developed a conceptual model that captured the major drivers of aquatic-macroinvertebrate community composition: 1) a wetland's specific position along the spatial and temporal Wetland Continuum axes, and 2) biotic interactions, including competition and predation. These drivers were hypothesized to work together to shape the taxonomic composition of invertebrate communities (Fig. 3.1). We then used 24 years of aquatic-macroinvertebrate, amphibian, hydrology, and water-chemistry data from a complex of depressional wetlands, and hierarchical hypothesized relationships linking ponded-water dynamics with wetland biota, to develop a structural equation model that incorporated the theoretical and empirical relationships outlined in the Wetland Continuum framework. From the resultant model, we obtained significant insight into the drivers shaping aquatic-macroinvertebrate communities of depressional-wetland ecosystems.

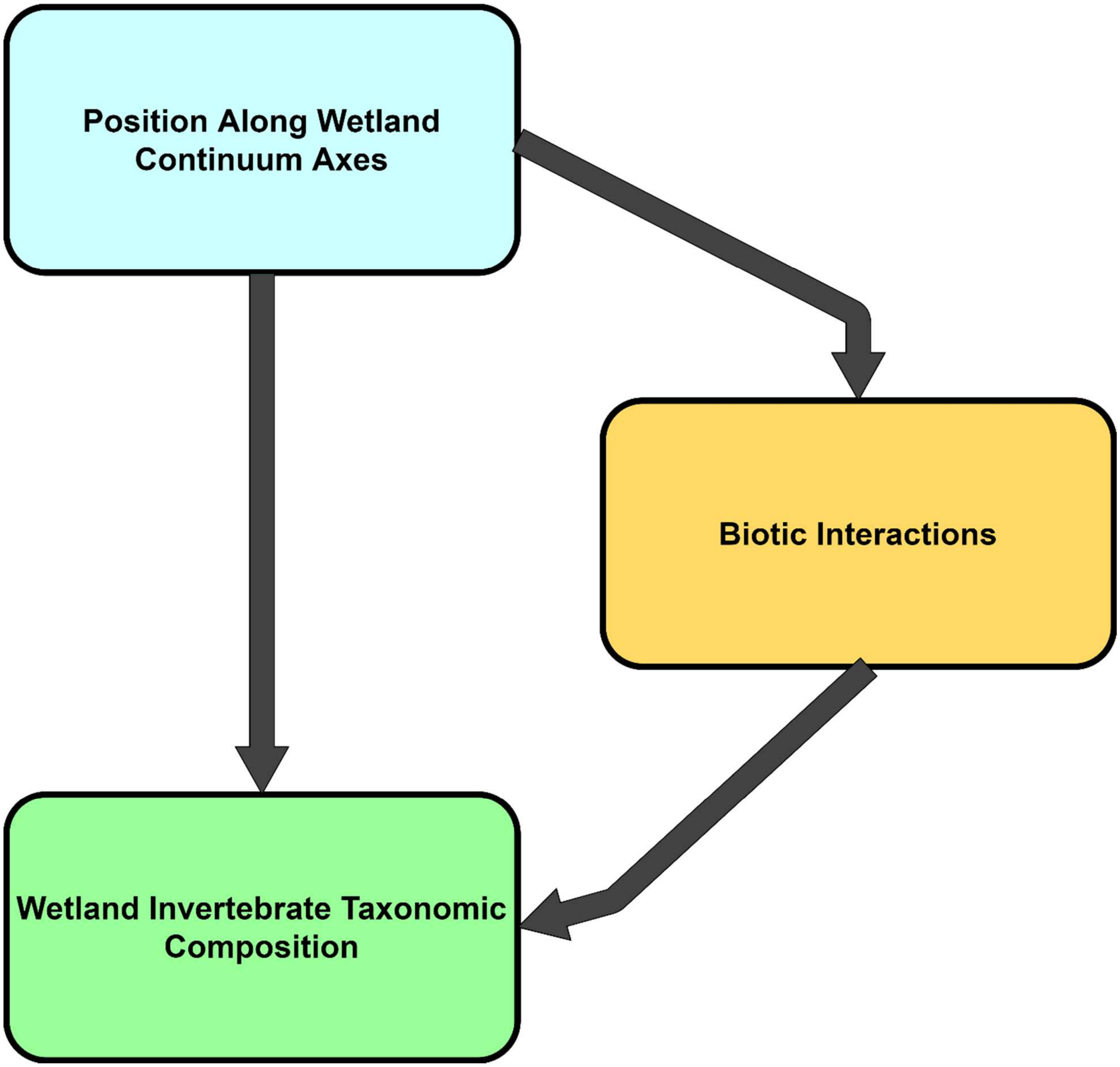

Figure 3.1. Conceptual model of direct and indirect deterministic controls of aquatic invertebrate community assemblages.

3.3. Methods

3.3.1. Study Area

With over 2.5 million individual wetland basins (Dahl, 2014), the landscape of the Prairie Pothole Region (PPR), possesses the greatest density of naturally formed, depressional wetlands in North America (Reynolds et al., 2006), and forms one of Earth's largest wetland complexes (van der Valk, 2005). Not only are wetlands a ubiquitous feature on the PPR landscape, they provide numerous ecological and economic benefits by serving as breeding habitat for approximately 70% of the continental duck population, mitigating overland flooding, facilitating the recharge of groundwater, sequestering carbon, and maintaining local, regional, and global biodiversity (Batzer and Wissinger, 1996; Murkin, 1998; Tiner, 2003; Gleason et al., 2011).

The ubiquitous depressional wetlands of the PPR (hereafter referred to as prairie-pothole wetlands) are diverse in size, and each can exhibit great intra- and inter-annual variation in surface-water extent (Larson, 1995; Niemuth et al., 2010; Ballard, 2014). Much of this variation can be attributed to the PPR's variable climate. In combination with climate variability and spatial setting, the closed-basin nature of many prairie-pothole wetlands contributes to high temporal and spatial variability in dissolved ion-concentrations from dilution and concentration effects resulting from changing water volumes. Given the important influence of climate on hydrological properties of prairie-pothole wetlands and, in turn, the great temporal and spatial range of variation expressed in these systems, they can be useful study systems to disentangle the influences of abiotic and biotic drivers on aquatic-macroinvertebrate community composition.

The Cottonwood Lake Study Area (CLSA) is part of a complex of U.S Fish and Wildlife Service managed Waterfowl Production Areas located in Stutsman County, North Dakota along the eastern edge of the PPR's Missouri Coteau (Fig. 3.2). The CLSA is located in a regional groundwater-recharge area but, at the local scale, contains wetlands that function as groundwater recharge, flow-through, and discharge systems (LaBaugh et al., 1987). Many abiotic and biotic components of the 16 prairie-pothole wetlands forming the CLSA complex have been continually monitored since 1979. The wetlands forming the CLSA wetland complex were initially classified in 1967 with "P" and "T" designations that separated the wetlands with the longer hydroperiods (P wetlands) from those that typically dried during a normal summer (T wetlands) The CLSA wetlands designated as P wetlands consist of semi-permanently and permanently ponded wetlands (Class IV and V, respectively; Stewart and Kantrud, 1971). The T wetlands consist of temporarily and seasonally ponded wetlands (Class II and III, respectively; Stewart and Kantrud, 1971).

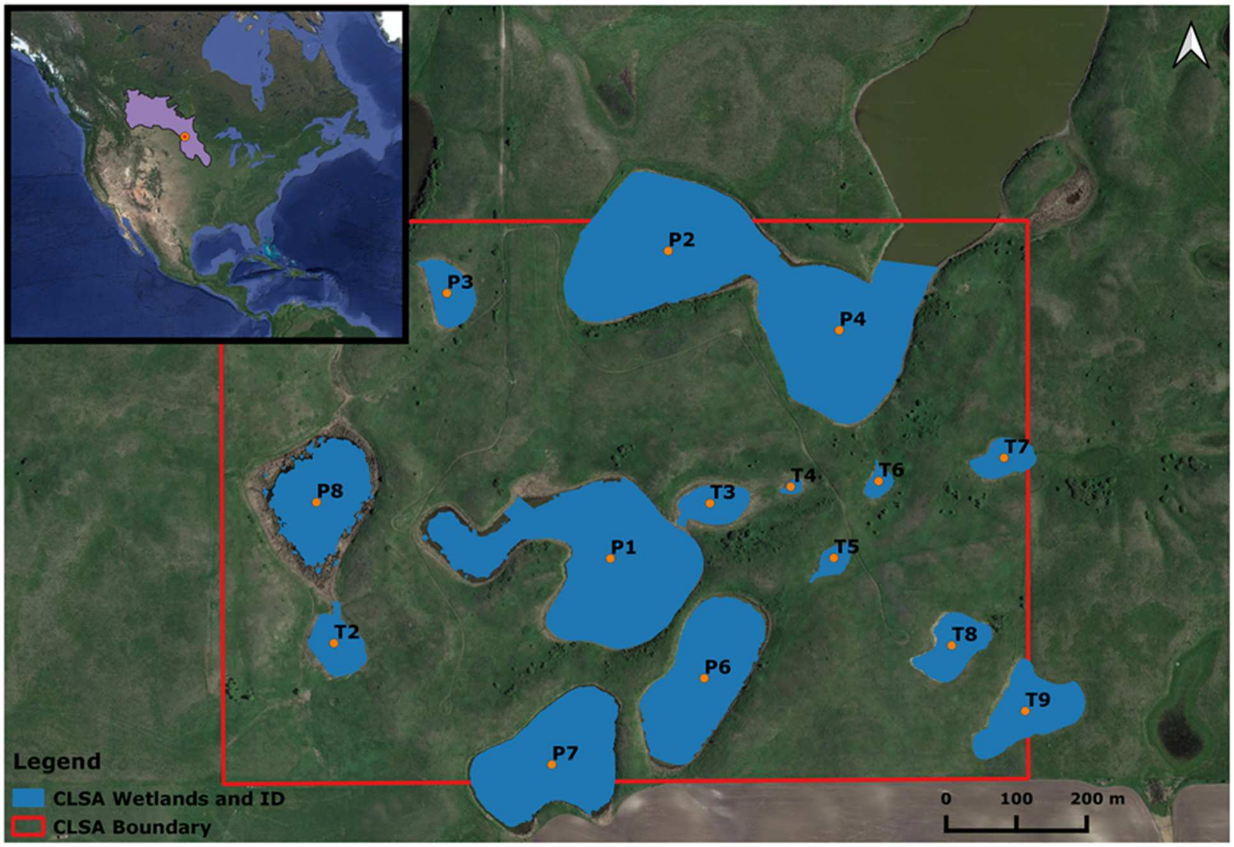

Figure 3.2. Map of the Cottonwood Lake Study Area in Stutsman County, ND, USA, and the Prairie Pothole Region of North America, shown in purple in the inset. Wetland P-11 (not shown) is located approximately 3 km west of the core study area depicted here.

Although several of the data sets from CLSA have been collected since 1979, we restricted our analyses to data collected from 1992 to 2015, the period that coincided with the availability of aquatic-macroinvertebrate data. All long-term, wetland-monitoring data from the CLSA are openly available from the U.S. Geological Survey at: https://www.sciencebase.gov/catalog/item/52f0ffd9e4b0f941aa181fc6. In our exploration into the drivers shaping the aquatic-macroinvertebrate communities of depressional wetlands, we used data from all 17 CLSA wetlands and eight variables: 1) wetland-elevation, 2) electrical conductivity (EC) of ponded water, 3) proportion of wetland ponded, 4) proportion of open-water area in a wetland, 5) salamander abundance, 6) predatory-macroinvertebrate biomass, 7) nonpredatory-macroinvertebrate biomass, and 8) macroinvertebrate counts by taxa. The first two variables (1 and 2) are related to a wetland's unique position along the groundwater axis of the Wetland Continuum. Variable 3 and 4 are related to a wetland's position along the atmospheric-water axis. The next three variables are related to the biotic interactions of predation (5 and 6) and competition (7). Variable 8, aquatic-macroinvertebrate counts by taxa, was used to define the dependent variable in our analyses, i.e., aquatic macro-invertebrate community composition. We used non-metric multidimensional scaling (hereafter NMDS) on the Bray-Curtis dissimilarities of our macroinvertebrate abundance data to reduce all taxa by wetland by year observations into two meaningful axes, which were then used to represent community composition (see Appendix A)[2]. We then used the taxon by NMDS Axis pairwise correlations (r) to characterize what macroinvertebrate taxa were strongly associated with each NMDS axis.

3.3.2. Statistical Design

We used structural equation modeling to explore relationships among biotic and abiotic factors and their influence on aquatic macroinvertebrate communities using R statistical and computing software (R Development Core Team, 2011). Structural equation modeling (SEM) is a multivariate statistical technique that can combine multiple predictor and response variables into a single causal network (Lefcheck, 2016). Structural equation modeling is well suited for large observational datasets involving multiple direct, indirect, and cascading interactions

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[2] *A detailed description of all variables used in the structural equation modeling are provided in Appendix A.*

between variables (Grace et al., 2007; Grace, 2008). The process of structural equation modeling involves the development of a theoretical model using hypothesized causal relationships graphically modelled as pathways between predictor and dependent variables. The modeled pathways are analyzed in the form of structured equations representing a sequence of causal relationships, which can be examined simultaneously (global estimation) or individually (local estimation), while also accounting for correlation between multiple response variables (Bollen, 1989; Shipley, 2000; Lefcheck, 2016).

We developed our theoretical model from relationships that were outlined in Euliss et al. (2004) and supported by relevant literature (Appendix A). For the model design we took the hierarchical structure from our conceptual model (Fig. 3.1) and populated the "Position Along Wetland Continuum Axes", "Biotic-Interactions", and "Wetland Invertebrate Taxonomic Composition" components with measured variables from the CLSA wetlands data (Fig. 3.3). Using the original relationships described in Euliss et al. (2004) and expanded upon in Hayashi et al. (2016), we predicted a wetlands hydrogeologic setting, which we measured using wetland basin elevation, would influence each wetland's relative groundwater and surface-water inflows, driving among wetland hydrologic variability. We used EC to indicate relative groundwater inputs among wetlands and proportion of open-water area in a wetland basin to estimate differences in surface-water inputs. We used proportion of wetland ponded as our measure of atmospheric-water inputs. As hypothesized in the Wetland Continuum concept, the amount of ponded water, associated ponded-water habitats (open-water or vegetated), and salinity are important drivers of invertebrate communities, quantified by our NMDS axes. The environmental filters also were predicted to influence the strength of biotic filters such as competition and predation, i.e., nonpredatory-invertebrate biomass, predatory-invertebrate biomass, and salamander abundance, which, in turn, would influence invertebrate community composition (Fig. 3.3).

We then evaluated our measurement model using local-estimation methods, in which we examined model fit of hypothesized relationships (modeled pathways) using field data collected over 24 years (1992–2015) at the CLSA (Fig. 3.3; Appendix A, Table A.1). Using localized estimations increased our flexibility in fitting data with different distributions and accounting for non-independence due to repeated sampling. We used Shipley's test of d-separation to assess overall model fit (Shipley, 2009). The Shipley's test of d-separation tests the assumption of conditional independence among variables, which we used to identify pathways between variables missing from the model and the strength of existing pathways (Lefcheck, 2016). In some cases, we also calculated indirect effects by multiplying the effect (i.e., standardized path coefficient) variable x has on variable y by the effect variable y has on variable z (Grace et al., 2012).

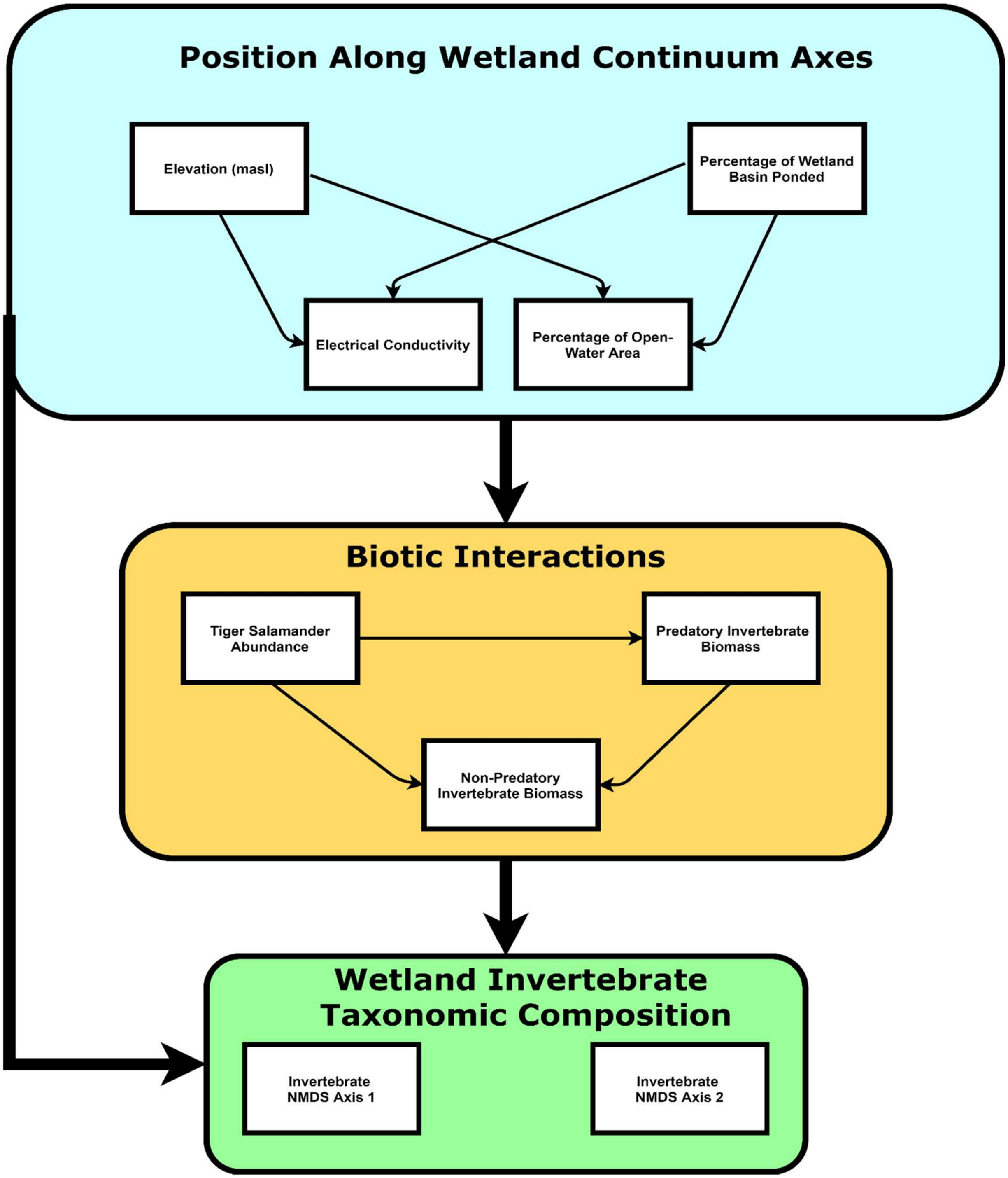

Figure 3.3. Path diagram of observed variable measurement model linking hypothesized causal relationships between a wetland's position along the wetland continuum (measured variables = wetland elevation, electrical conductivity, proportion ponded, and proportion open-water area), biotic interactions (measured variables = tiger salamander abundances, predatory and non-predatory invertebrate biomass) to invertebrate taxonomical variation.

3.3.3. Statistical Analysis

Prior to SEM analyses, we screened the data for normality and heteroscedasticity using the R package *MVN* (Korkmaz et al., 2014). We evaluated univariate skewness, kurtosis, and multivariate normality using Mardia's Test of multivariate kurtosis (Mardia, 1974). Highly skewed and homoscedastic data can become problematic for fitting structural equation models (Arhonditsis et al., 2006; Grace, 2008). We square-root transformed EC, log transformed (log +1) tiger salamander abundance, predatory-invertebrate biomass, and invertebrate biomass, and arcsine square root transformed proportion of wetland basin that is ponded and proportion of a wetland basin that is open water to increase linearity.

To test our measurement models, we used the *psem* function from the "Piecewise" package in R (Lefcheck et al., 2016). In addition to our modeled pathways, we also modeled the correlation among years for each wetland using a continuous autoregressive 1 autocorrelation structure with the *CAR1* function from the "NLME" package (Pinheiro et al., 2013). This allowed us to address non-independence issues of temporally correlated data (Lefcheck, 2016). After the initial model was evaluated, we went through a process of adding/removing pathways and variables by evaluating significance of pathway loadings (coefficients) and tests of d-seperation until we found the best-fitting, ecologically plausible model. The removal of non-significant pathways was accomplished by iteratively removing the modeled pathway with the greatest non-significant p-value, re-assessing model fit, and repeating the process until either no non-significant pathways remained or until the overall model fit started to decrease.

3.4. Results

3.4.1. Aquatic Invertebrate Communities

We identified several unique gradients of aquatic-macroinvertebrate community composition from our NMDS analysis. The NMDS results indicated that two axes were adequate in reducing the dimensionality of CLSA aquatic invertebrate count data using an arbitrary reduction criterion of five in the stress score as prescribed by Peck (2011). Taxa with correlations greater than r = 0.25 or less than r = -0.25 are provided in Table 3.1. The taxa positively correlated with NMDS Axis 1 consisted of taxa common to wetlands with longer hydroperiods and abundant open-water (Mahoney et al., 1990; Tarr et al., 2005; Stenert and Maltchik, 2007; Schilling et al., 2009; Silver et al., 2012). Taxa with a negative correlation to NMDS Axis 1 are widely distributed among wetland ecosystems (Whiles and Goldwitz, 2005; Silver et al., 2012; MacLean, 2013). However, many of the taxa negatively correlated with Axis 1 (Table 3.1) are typical of wetlands with seasonally drying ponds (Gaiser and Lang, 1998; Dietz-Brantley, 2002; Florencio et al., 2011; Silver et al., 2012; McLean et al., 2019) and well-vegetated, shallow-water areas (Swanson et al., 2003; MacLean, 2013).

Table 3.1. Correlations (r) of NMDS ordination axes with aquatic invertebrate counts for n=363 wetland by year combinations. Only correlations with an r > 0.25 are listed. Note: diving beetle = predaceous diving beetle; scavenger beetle = water scavenger beetle; crawling beetle = crawling water beetle.

Taxa	Common Name	NMDS Axis 1	NMDS Axis 2
Calanoida	Copepod	0.76	
Gammarus lacustris	Lake amphipod	0.75	
Notonecta	Backswimmer	0.69	
Hydrachnidae	Water mite	0.66	-0.33
Dasycorixa rawsonii	Water boatman	0.54	
Hyallela azteca	Amphipod	0.52	-0.28
Cenocorixa	Water boatman	0.51	
Erpobdella	Leach	0.42	
Buenoa	Backswimmer	0.28	
Daphnia	Water flea	0.28	
Simocephalus	Water flea	-0.68	-0.27
Rhantus	Diving beetle	-0.53	-0.31
Chaoborus	Phantom midge	-0.47	-0.42
Hygrotus	Diving beetle	-0.47	
Callicorixa	Water boatman	-0.40	-0.37
Colymbetes	Diving beetle	-0.38	-0.28
Cyclopoida	Copepod	-0.38	0.26
Graphoderus	Diving beetle		-0.34
Stagnicola elodes	Pond snail	-0.33	
Promenetus umbilicatellus	Sprite snail	-0.33	
Liodessus affinis	Diving beetle	-0.32	
Ostracoda	Seed shrimp	-0.31	
Aedes	Mosquito	-0.29	0.30
Hesperocorixa	Damselfly	-0.28	-0.32
Oligochaeta	Aquatic worm	-0.28	
Ceriodaphnia	Water Flea	-0.28	
Armiger crista	Ramshorn snail	-0.25	
Culiseta	Mosquito	-0.25	0.32
Culex	Mosquito		0.25
Haliplus	Crawling beetle		-0.47
Callibaetis	Small minnow mayfly		-0.37
Enallagma	Damselfly		-0.36
Cymatia	Water boatman		-0.31
Caenis	Small squaregill mayfly		-0.31
Ilybius fraterculus	Diving Beetle		-0.30
Chironominae	Midge		-0.28
Peltodytes	Crawling beetle		-0.26

Cyclopoid copepods and mosquito taxa, e.g., *Aedes, Culiseta,* and *Culex* had the strongest positive correlations to NMDS Axis 2. Mosquito taxa are often associated with in temporarily ponded habitats (Batzer and Wissinger, 1996). Aquatic-macroinvertebrate taxa negatively correlated with NMDS Axis 2, e.g., predaceous diving beetles, crawling beetles, phantom-midges, damselflies, water boatmen, and mayflies, are all flying insects that mostly belong to the predator or gatherer collector functional feeding groups (Merritt and Cummins, 1996). These taxa are also found in a variety of wetland habitats with variable hydrologic regimes (Silver et al., 2012; Table 3.1).

3.4.2. Structural Equation Modeling

Our final data set contained 363 observations for each variable in the model. Transforming our indicator variable to the log scale greatly improved data normality. Our initial measurement had a poor global model fit indicated by a Fisher's C Statistic of 16.685 on 4-degrees of freedom and a P-Value of 0.01. The poor model fit was likely a result of the model being over fit and having unspecified correlated errors between variables. The tests of d-separation indicated that a significant pathway linking the NMDS Axis 1 and NMDS Axis 2 was missing. We decided to treat the bivariate correlation in the model as a correlated error since we did not have a plausible explanation for the relationship being causal. We found and removed a total of eight non-significant pathways from the model, which included removing the non-predatory invertebrate biomass variable from the model since it did not provide any influential pathways. Even though we found four additional non-significant pathways, we retained them in the model as their inclusion improved overall model fit. After non-influential pathways were removed, we obtained a final model (Fig. 3.4) with a Fisher's C-Statistic of 11.012 on 14 degrees of freedom (P-Value 0.685). The final model explained 80% of the variation along NMDS Axis 1 (R^2=0.8) and 18% of the variation along Axis 2 (R^2=0.18).

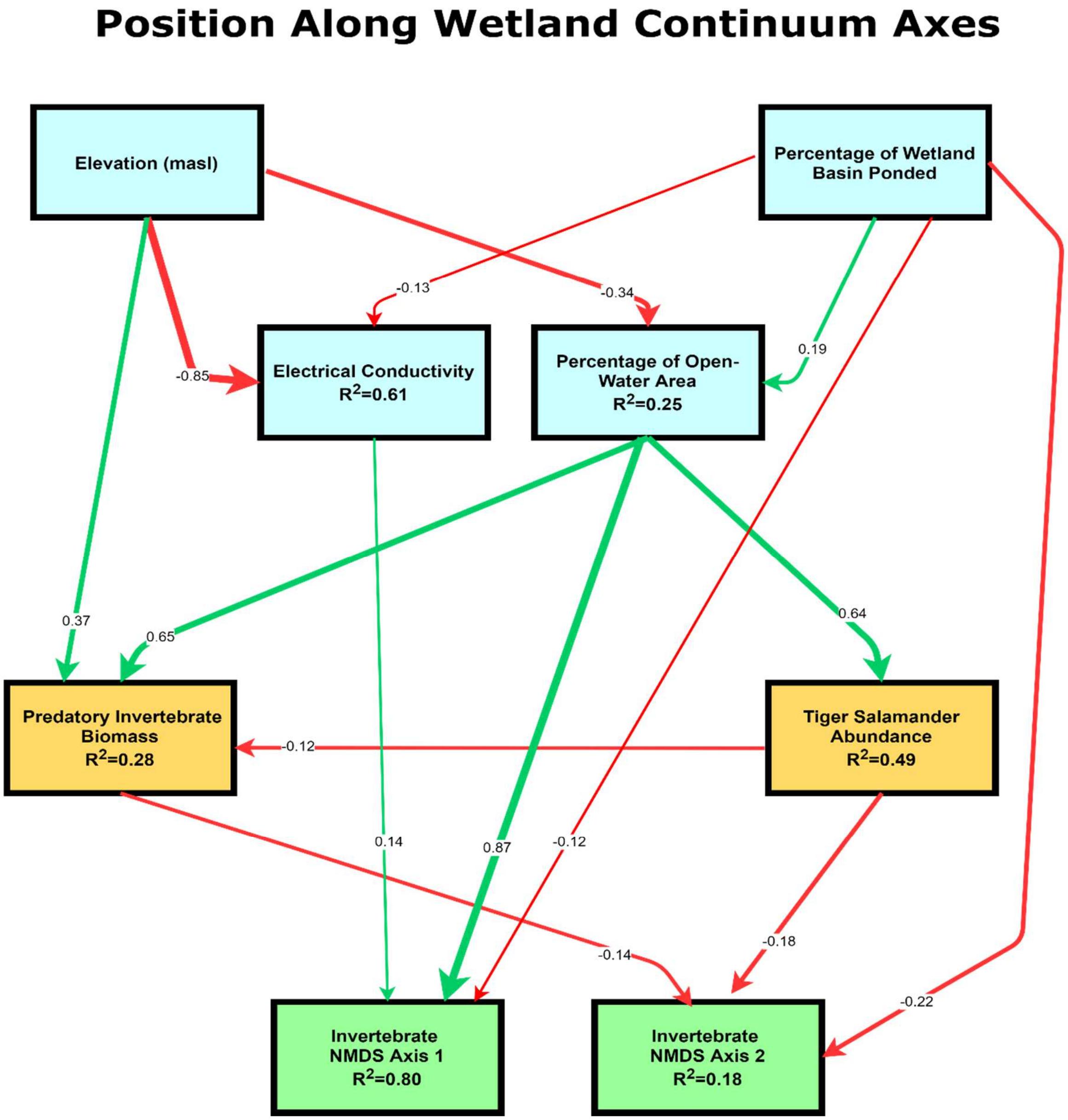

Figure 3.4. Path diagram of final, best-fitting, structural equation model (Fisher's C Statistic = 11.012, 14 degrees of freedom, P-Value = 0.685) of causal relationships linking a wetlands elevation, electrical conductivity, proportion ponded area, proportion open-water area, tiger salamander abundance, and predatory and non-predatory invertebrate biomass to invertebrate community compositions. Green arrows represent positive correlations, red arrows represent negative correlations, dotted black lines represent non-significant modeled pathways, and the numbers along each arrow represent standardized path coefficient. Arrow width increases with the strength of the relationship.

The two, main variables representing a wetland's hydrogeologic were elevation of the wetland basin, which is directly related to positioning along groundwater axis of the Wetland Continuum (Hayashi et al., 2016), and the proportion of the wetland ponded, which is directly affected by climate, i.e., positioning along the atmospheric-water axis of the Wetland Continuum. These two observed variables were direct casual indicators of salinity (i.e., EC) of ponded water and the proportion of open-water area in a wetland, other measures tied to the positioning of wetlands along the axes of the Wetland Continuum (Fig. 3.4).

As expected, causal pathways linking wetland elevation and the proportion of a wetland ponded to ponded-water salinity and proportion of open-water area were statistically significant (P-Value < 0.05). Consistent with Wetland Continuum concepts, the direct effect of wetland elevation on proportion of open-water area was negative (standardized path coefficient, -0.85), i.e., wetlands at higher elevations had lower salinity ponds than wetlands at lower elevations, and therefore groundwater flow positions in the local landscape (Hayashi et al., 2016). The proportion of open-water area in a wetland also was negatively influenced by elevation (standardized path coefficient, -0.34). Thus, at higher elevations, the proportion of open water in wetlands relative to wetlands at lower elevations decreased. The proportion of a wetland basin ponded had a significant effect on ponded water salinity (standardized path coefficient = -0.14), and a positive effect on the proportion of open-water area (standardized path coefficient = 0.19).

Ecohydrological variables influenced aquatic-macroinvertebrate composition predominately through direct effects (Fig. 3.4). The proportion of open-water area in a wetland had a positive, direct effect on aquatic-macroinvertebrate communities associated with more permanently ponded wetlands (i.e., taxa positively correlated with NMDS Axis 1) and a negative effect on taxa typical of seasonally ponded and well-vegetated wetlands (i.e., taxa negatively correlated with NMDS Axis 1). The proportion of a wetland ponded, and wetland elevation had an indirect effect on NMDS Axis 1 by modifying the proportion of open-water area in wetlands (indirect pathway coefficients,0.17 & -0.30, respectively). Proportion of a wetland ponded, and salinity had a significant but lesser direct effect on NMDS Axis 1 (standardized path coefficients = -0.13 & 0.14, respectively), but pathways linking biotic interactions to NMDS Axis 1 were all non-significant (P-Value > 0.05). However, the non-significant pathways linking predatory-invertebrate biomass and salamander abundance to NMDS Axis 1 were determined to be influential in maintaining model fit.

The explained variation in NMDS Axis 2 was a result of significant direct effects from the proportion of wetland ponded, salamander abundance, and predatory-invertebrate biomass (standardized path coefficients = -0.23, -0.19, -0.15, respectively). While proportion of open-water area did not have a significant direct effect on NMDS Axis 2, tests of mediation revealed that open-water area indirectly influenced NMDS Axis 2 by modifying the influence of salamander abundance and predatory-invertebrate biomass (indirect pathway coefficients= 0.12 and -0.10, respectively).

3.5. Discussion

Using 24 years of environmental monitoring data from a complex of 17, prairie-pothole wetlands, we found substantial effects of a wetland’s hydrogeologic setting and local climate conditions on aquatic-macroinvertebrate communities. These results are consistent with the idea promulgated by Euliss et al., (2004) that both axes of the Wetland Continuum work together to influence biotic communities of wetlands. The ecohydrological conditions (e.g., proportion of wetland ponded, relative elevation, EC, and proportion of open-water area) had the strongest direct effects on aquatic-macroinvertebrate community composition and significantly modified the effect of our predation variables (e.g., salamander abundance and predatory-invertebrate biomass) in these systems.

While we did not measure a wetland's direct relationship to local groundwater flows or atmospheric-water inputs, for wetlands within a localized area, the use of relative elevation and proportion of a wetland basin that is ponded were useful for describing the positioning in the Wetland Continuum. Interestingly, we did not expect a wetland's relative elevation to have a greater effect on the proportion of open-water area in a wetland than proportion of a wetland ponded. The observed relationship was likely due to reduced climate variability during our study period. The study coincided with multidecadal increases in mean annual precipitation that shifted hydrologic regimes in the P-Wetlands to more permanent, lake-like conditions (McKenna et al., 2017; Mushet et al., 2018). Open-water area and the proportion of a wetland basin that was ponded in these larger wetlands were likely less responsive to annual climate patterns, and therefore they were influenced more by temporal autocorrelation. Smaller, shallow wetlands are more sensitive to annual weather patterns (Hayashi et al., 2016), but the open-water area in these wetlands are also less sensitive to the proportion ponded due to the shallow nature of wetlands (McLean et al., 2019). Our results are consistent with the hypothesis that wetlands at higher elevations on a local landscape have smaller pond volumes, shallower depths, and, thus, more fully vegetated areas with less open water than wetlands at lower elevations (Euliss et al., 2004; Hayashi et al., 2016).

Considering the habitat preferences of the taxa strongly correlated with NMDS Axis 1 (Table 3.1), it was not surprising that the proportion of open-water area in a wetland had the strongest effect of the modeled variables. Many of the positively correlated taxa, e.g., Calanoida, *Gammarus lacustris, Hyallela azteca*, *Notonecta* spp., *Daphnia* spp., and Hydrachnidae are among the most common taxa found in permanently ponded, prairie-pothole wetlands (Mushet et al., 2015). Conversely, many taxa negatively correlated with NMDS Axis 1, e.g., *Simocephalus*, *Rhantus fusca*, *Chaoborus*, and *Colymbetes*, have been shown to be more common in shallow, densely vegetated, and more intermittently ponded wetlands (Dietz-Brantley et al. 2002; Florencio et al. 2011; MacLean, 2013).

The positive association with salinity (EC) with NMDS Axis 1 was consistent with previous research on wetland invertebrate community composition along salinity gradients (McLean et al., 2016a; Lancaster and Scudder, 1987; Waterkeyn et al., 2008). As wetlands become more saline there has been an observed transition from macrophyte-dominated to algae-dominated systems (Wollheim and Lovvorn, 1995), which can also result in invertebrate community shifts towards increased abundance of planktivorous grazers and hemipteran predators (Wollheim and Lovvorn, 1995 & 1996). Fresher and shallower wetlands being dominated by macrophytes is consistent with the habitat preferences for many taxa negatively correlated with NMDS Axis 1, e.g., *Stagnicola elodes*, *Prumentus umbelictus*, *Simocephalus* spp., *Rhantus frontalis*, and *Colymbetes* spp. that are associated with macrophytes and littoral habitats (Cvancara, 1983; Wollheim and Lovvorn, 1995; Gaiser and Lang, 1996; MacLean, 2013). Surprisingly, hydrologic variables had a minimal effect on NMDS Axis 2. The positive correlates of Axis 2 were the *Aedes, Culiseta,* and *Culex* mosquitos which are both associated with short hydroperiods in many wetland systems (Batzer and Wissinger, 1996; Schneider and Frost, 1996; Lillie, 2003), and cyclopoida copepods. However, the relationship between hydroperiods and mosquitos might have more to do with how biotic interactions, i.e., predation and competition, that can be mediated by pond duration (Schneider and Frost, 1996; Knight et al., 2004; Elono et al., 2010). We suspect the direct effect of proportion of wetland ponded on

NMDS Axis 2 (standardized path coefficient = -0.22), captures the relationship of mosquitos and their antagonists (competitors and predators) to hydroperiods, whereas, mosquitos can thrive following drought conditions that limit competition and predation (Chase and Knight, 2003). This hypothesis is supported by the data, i.e., the highest mosquito abundances recorded in the CLSA occurred in 1993 following a significant drought (Mushet et al., 2017). The wetlands that exhibited the highest abundances were also shallow basins located at intermediate relative elevations which would also help explain why elevation had a negative effect (standardized pathway coefficient, -0.22) on NMDS Axis 2.

In almost all respects, biotic interactions had smaller effects than abiotic drivers tied to positioning along the Wetland Continuum. This contrasts with findings of Hanson et al., (2005). In their review of biotic interactions as determinates of prairie-pothole-wetland ecosystem structure, they determined that the influence of biotic drivers was not adequately accounted for in the conceptual framework of the Wetland Continuum. However, there review focused primarily on permanently ponded wetlands containing fishes. Thus, the important influences of abiotic drivers where likely masked by not incorporating the full range of wetland types and by the overwhelmingly dominant influence of fishes, relatively recently introduced ecosystem disruptors historically absent from most prairie-pothole wetlands (McLean et al., 2016a). Since the distribution of fishes has been shown to increase under wet climate conditions and is limited to wetlands that are more permanently ponded and deep enough to allow fish to overwinter (Wiltermuth, 2014; McLean et al., 2016b; Sundberg et al., 2018), a wetlands placement along the Wetland Continuum axes would likely be a strong predictor of fish population persistence. Our structural equation modeling results clearly indicated a dominance of abiotic drivers in the absence of fishes, but also captured the subtler effects of the biotic interactions of predation and competition in shaping aquatic-macroinvertebrate communities.

Our model explained 18% of NMDS Axis 2's variation. The mosquito taxa *Aedes, Culiseta,* and *Culex*, and the Cyclopoida copepods had the strongest positive correlations to Axis 2. A few of the taxa negatively correlated to Axis 2, e.g., predaceous diving beetles, phantom midges, dragon fly larvae, and the *Cymatia* and *Callicorixa* genus of waterboatman are all known predators of mosquito larvae and copepods (James 1966; Schneider and Frost 1996; Vinnersten et al., 2009; Haedicke et al., 2017). Therefore, variation found in this axis could be explained by interaction between wetland hydrology and biotic interactions. While our competition variable (non-predatory invertebrate biomass) did not have a significant effect, mosquito populations have been shown to be sensitive to competition (Elono et al., 2010). Mosquitos are among the most rapid dispersers, and competition and predation increase later in the season as other invertebrates colonize wetlands (Batzer and Wissinger, 1996; Chase and Knight, 2003). The transition from mosquito dominated communities to insect predators and other planktonic invertebrates has been shown to be a temporal process that typically occurs within years (Chase and Knight, 2003). We acknowledge that our use of biomass as a measure of competition likely did not capture its true importance in determining community composition. For example, since competition is typically a reciprocal process, using annual means for measurement variables in the model likely masked some of the key biotic interactions occurring within years.

Although salamanders are often the top, native, aquatic predator in wetlands where they feed predominately on aquatic invertebrates (Benoy et al., 2002; Benoy, 2008), they were comparatively weak predictors of community composition. This pattern, or rather lack of a pattern, has been noted before (e.g., Zimmer et al., 2001, McLean at al., 2016a). Salamander abundance had the strongest direct effect on NMDS Axis 2 (standardized path coefficient, -.19), which is not surprising considering that, when available, mosquitos have been shown to be a preferred prey of salamander larvae (Brodman and Dorton, 2006). We hypothesize that although salamanders can reduce invertebrate biomass (Benoy et al., 2002; Benoy, 2008), by being dependent on hydroperiods lasting 3 to 4 months (Deutschman and Peterka, 1988) their influence on overall community structure is being masked by the stark contrasts of temporarily ponded and permanently ponded wetlands within the CLSA (McLean et al., 2019).

While our modeled biotic interactions only had modest effects on our NMDS Axes representing gradients of invertebrate composition, we did find strong effects of wetland hydrologic variables on salamander abundances and predatory-invertebrate biomass ($R^2 = 0.49$ and 0.28, respectively). Not surprisingly, salamander abundance was highly responsive to increased proportions of open-water area (standardized path coefficient = 0.65). Tiger salamanders in North Dakota require at least 3–4 months of ponded water to develop from larvae (Deutschman and Peterka, 1988). They are also susceptible to waterbird predation in shallow water making deeper habitats ideal during the day (Wiedenheft, 1983). The proportion of open-water area in a wetland also had the strongest effect on predatory-invertebrate biomass (standardized path coefficient = 0.65); elevation had the second strongest effect (0.37). This is consistent with research linking predatory-invertebrate abundance with water permanence (Corti et al., 1996; Wissinger et al., 1999a; Babbitt et al., 2003). Predatory invertebrates often dominate wetlands of intermediate hydroperiods (Whiles and Goldwitz, 2001; Wissinger et al., 1999b). These intermediate-hydroperiod wetlands are likely be higher in elevation than nearby wetlands with more permanent hydroperiods. The lower elevation wetlands with more permanent hydroperiods, in turn, are often dominated by vertebrate predators such as fish or salamanders that eat both predatory and non-predatory invertebrates (Holomuzki et al., 1994; Wissinger et al., 1999b; Benoy et al., 2002).

3.6. Conclusions

The proportion of open-water habitat in a wetland was found to be the most influential driver of biotic interactions and aquatic macro-invertebrate community assembly. Considering that open-water area in a wetland is highly dependent on surface-water inputs from snowmelt and precipitation, climate necessarily plays a major role in structuring the biotic communities of prairie-pothole wetlands. The data used in our analysis started in 1992 following a massive drought and at the beginning of an uncharacteristically wet period (Winter and Rosenberry, 1998; McKenna et al., 2017). Therefore, it is not surprising that most of the taxonomical variation was correlated with increasing water levels. With the increased hydroperiods and concomitant softening of abiotic filters we would predict a reduction of deterministic processes of community assembly (i.e., environmental sorting) and an increase in neutral processes (Chase, 2007; Lepori and Malmqvist, 2009). On a landscape, loss of hydroperiod variation due to persistent and extreme changes in precipitation could result in the loss of niche taxa and beta-diversity. For example, many taxa, including anostracans and most culicidae larvae, are dependent on short-term hydroperiods (Lillie, 2003; Silver et al., 2012; Bischof et al., 2013).

The CLSA is relatively sheltered from anthropogenic influences (i.e., agriculture, hydrological alterations, and fish introductions) over the 24-year period of our study. These factors benefited our ability to identify “natural” influences on aquatic-macroinvertebrate communities. However, most of the PPR landscape is used in agricultural production (Dahl, 1990) and altered by associated land-use practices such as wetland drainage, vegetation removal, and tillage (Gleason et al., 2003; Anteau, 2012; McCauley et al., 2015). On a landscape scale, agricultural use in the PPR has indicated minimal changes in wetland invertebrate communities (Tangen et al., 2003; Gleason and Rooney, 2017). It is likely that land-use influences are also dependent on spatial setting and individual management practices such as wetland drainage. We would predict invertebrates to respond similarly to anthropogenic increases in hydroperiod (consolidation drainage) and open-water (vegetation removal) as they do to hydroperiod and open-water variability uninfluenced by human activities. Additionally, many semipermanently and permanently ponded wetlands in the PPR of North Dakota now contain fish (Wiltermuth, 2014; McLean et al., 2016b). The overwhelming influence of fish in prairie-pothole wetlands (Hanson et al., 2005) can obscure other important drivers of aquatic-macroinvertebrate communities. In addition to their importance to wetland-ecosystem management, a better understanding of the proximate mechanisms that control aquatic-macroinvertebrate communities in the highly spatio-temporal variable PPR may provide unique insights into aquatic-community assembly under changing environmental conditions. Our findings support the idea that depressional wetlands should be treated as units of environmental variability within a hydrologic complex.

3.7. Acknowledgements

Our manuscript would have not been possible if not for the pioneering efforts of George Swanson (deceased) and Ned Euliss, Jr. (USGS retired) in starting and maintaining the long-term data collection efforts at the Cottonwood Lake Study Area. We also thank Ned Euliss, Jr. and Clint R. V. Otto for the significant insights they provided during the early stages of our work. Additionally, we thank Mark Wiltermuth and two anonymous reviewers for their reviews of earlier drafts of this manuscript. Funding for our research was provided through the U.S

Geological Survey's Land Change Science Research and Development Program. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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CHAPTER 4. TEMPORAL COHERENCE PATTERNS OF PRAIRIE-POTHOLE WETLANDS INDICATE THE IMPORTANCE OF LANDSCAPE LINKAGES AND WETLAND HETEROGENEITY IN MAINTAINING BIODIVERSITY[3]

4.1. Abstract

Wetland ecosystems are diverse and productive habitats that are essential reservoirs of biodiversity. Not only are they home to numerous wetland-specialist species, they also provide food, water, and shelter that support terrestrial wildlife populations. However, like observed patterns of biodiversity loss, wetland habitats have experienced widespread loss and degradation. In order to conserve and restore wetlands, and thereby the biodiversity they support, it is important to gain a better understanding of how biodiversity in wetland habitats is maintained. Habitat heterogeneity and connectivity are thought to be predominate drivers of wetland biodiversity. We quantified the spatial synchrony of wetland animal communities using intra-class correlations among 16 depressional wetlands sampled continuously over 24 years to better understand the relative influences heterogeneity (i.e., intrinsic processes specific to individual wetlands and connectivity (i.e., extrinsic processes occurring on the landscape) on wetland biodiversity. We found that while wetlands with different ponded-water regimes (temporarily ponded or permanently ponded) often hosted different invertebrate communities, the directional changes in invertebrate composition were synchronous. We also found the relative importance of intrinsic versus extrinsic forces in determining community assembly vary depending on a

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[3] The material in this chapter was co-authored by Kyle I Mclean, David M. Mushet, and Jon N Sweetman. Kyle I McLean had the primary responsibility of data analysis, developing conclusions, and drafting the manuscript. David M. Mushet and Jon N. Sweetman served as proofreaders and supplied constructive comments on the interpretation of the findings of this study.

wetland’s hydrologic function and climate influences. Our results confirm that heterogeneity and spatial connectivity of wetland landscapes are important drivers of wetland biodiversity.

4.2. Introduction

Biodiversity loss has been occurring at alarming rates worldwide and in many cases is expected to increase with climate warming and resultant land-use changes (Pimm et al., 1995; Sala et al. 2000). The loss of biodiversity has been shown to have global impacts on human wellbeing in addition to ecological stability (Diaz et al., 2006; Cardinale et al., 2012; Hooper et al., 2012). Biodiversity loss in freshwater ecosystems is occurring at rates even greater than in their terrestrial counterparts (Ricciardi and Rasmussen, 1999; Reid et al., 2019). Most global estimates of biodiversity and biodiversity loss for freshwater ecosystems are predominately estimated from large lake and river ecosystem observations (Ricciardi and Rasmussen, 1999; Balian et al., 2007). However, wetland ecosystems have been identified as a major source of unique aquatic diversity and are also key to maintaining biodiversity in many surrounding terrestrial ecosystems (Boylan and MacLean, 1997; Bobbink et al., 2006; Reid et al., 2019). The severity of biodiversity losses and corresponding ecological ramifications magnifies the need to better understand processes that influence biodiversity.

Wetlands are located at the transitional interface between fully terrestrial and fully aquatic habitats (Junk et al., 2014). Their position at this interface contributes to wetlands being among the most productive ecosystems, supporting levels of biodiversity disproportionate to the area they occupy (Dudgeon et al., 2006; Kingsford et al., 2016). The highly dynamic hydrology typical of many wetlands contribute to the diversity of their biotic communities (Gibbs, 1993). The high biotic productivity of wetlands in turn is critical for the persistence of many transitory species such as waterfowl and other migratory water birds (Gibbs, 1993; Haig et al., 2019). The enhanced importance of wetlands to biodiversity at local and landscape scales has been a primary driver of wetland conservation (Zedler and Kercher, 2005).

Numerous studies have revealed the need to conserve and restore the spatial connectivity of wetlands in addition to simply maintaining wetlands on the landscape (e.g. Gibbs, 2000; Calhoun et al., 2017; Verheijen et al., 2018). This reflects an understanding of the importance of landscape linkages in structuring wetland communities, in addition to the unique characteristics intrinsic to wetlands. However, there have been few, if any comparisons detailing the contributions of both intrinsic processes related to habitat heterogeneity and extrinsic processes related to connectivity in structuring wetland communities. One common way to investigate the relative role of intrinsic and extrinsic processes in ecosystems is to assess the spatial synchrony of variables over time (hereafter, temporal coherence; Magnusson et al., 1990).

Temporal coherence, often measured as intra-class correlation (r_i), is an indirect measure of spatial and temporal processes. High among-site correlations indicate that year-specific controls on the landscape (e.g., climate) are predominately driving variability. By contrast, low among-site correlations indicate that internal (within site) processes have greater control over variability (Kratz et al., 1987; Rusak et al., 1999). This estimation of temporal coherence has been commonly used in the aquatic sciences in explorations of spatial and temporal processes, albeit mostly in large, lacustrine ecosystems, (see Huttenen et al., 2014). Temporal coherence has been shown to differ within and among sites with different spatial settings, geologic settings, acidification histories, and climate periods (Magnusson et al., 1990; Webster et al., 2000; Angeler and Johnson, 2012; Huttenen et al., 2014). In lacustrine ecosystems, coherence has been found to be strongest for abiotic variables and generally weaker for biotic variables, with the exception of taxonomic compositional turnover, which is potentially more synchronous (see

Angeler and Johnson, 2012). Huttenen et al. (2014) found that for small, temperate streams that exhibit strong seasonality, measures of macroinvertebrate abundance and diversity are highly synchronous. However, temporal coherence in wetland ecosystems has yet to be assessed and could provide valuable insights into the relative importance of landscape features and wetland attributes in structuring biota.

In recent years, many scientists have postulated that wetlands are units embedded within a larger connected system, and that their biotic characteristics are dependent on among wetland landscape linkages and wetland heterogeneity (Rains et al., 2016; Zamberletti et al., 2016; Mushet et al., 2018a; Smith et al., 2019). We hypothesize that temporal coherence of wetland biota (e.g., invertebrates and amphibians) would be high due to the interaction of intrinsic heterogeneity and extrinsic connectivity in these temporally dynamic systems (Pope et al., 2000; Euliss et al., 2004; Smith et al., 2019). Here we used 24 years of environmental monitoring data from a complex of 16 wetlands with variable hydrologic regimes to investigate temporal coherence of biotic variables relevant to biodiversity conservation.

Our first objective was to quantify the overall temporal coherence of both abundance and diversity-based measures of biotic communities (invertebrates and amphibians) for all wetlands sampled during the duration of the study. The goal of this objective was to better understand the importance of wetland heterogeneity on maintaining diversity. Our second objective was to explore connectivity through comparisons of coherence patterns between more mobile dispersing fauna (insects and amphibians) and less mobile dispersers (non-insect aquatic invertebrates). Our third objective was to quantify and compare temporal coherence patterns of biotic variables by subsets of wetlands with different hydrologic regimes (i.e., temporarily ponded & permanently ponded). Thus, we could better understand the efficacy of making generalizations of prairie-pothole community dynamics regardless of hydrologic regime. Our fourth and final objective was to compare temporal coherence of biotic variables among two hydroclimatic periods, a “filling period” (1993–1999) and the “post-filling period” (2000–2015). These two periods represent a climate-induced hydrologic state shift that was triggered by substantial increases in precipitation (1993–1999). This precipitation increases led to changes in surface and groundwater dynamics. In the ensuing post-filling period, water levels stabilized in the larger wetlands but resumed cycling between ponded and dry for the smaller, higher-elevation wetlands (McKenna et al., 2017; McLean et al., 2019).

4.3. Methods

4.3.1. Study Area

We used long-term, environmental data from the Cottonwood Lakes Study Area (CLSA) centrally located within the Prairie Pothole Region (PPR) of North America (Figure 4.1). The millions of wetlands spanning approximately 777,000 km^2 across the center of the North American continent (Smith et al., 1964; Dahl, 2014) make the PPR one of the largest, wetland-dominated regions on earth (van der Valk, 2005). Prairie-pothole wetlands are upland-embedded, depressional wetlands and make up a majority of the wetland habitats found in the PPR. Prairie-pothole wetlands can exhibit high spatial and temporal variability in ponded-water duration, volume, and chemistry (Euliss et al., 2004; Mushet et al., 2015; Labaugh et al., 2018). This hydrological variability is driven by spatial variability in hydrogeologic setting, e.g., catchment size, relationship to local groundwater flows, surrounding upland characteristics, and spatial and temporal variability in climate (Euliss et al., 2004; Hayashi et al., 2016).

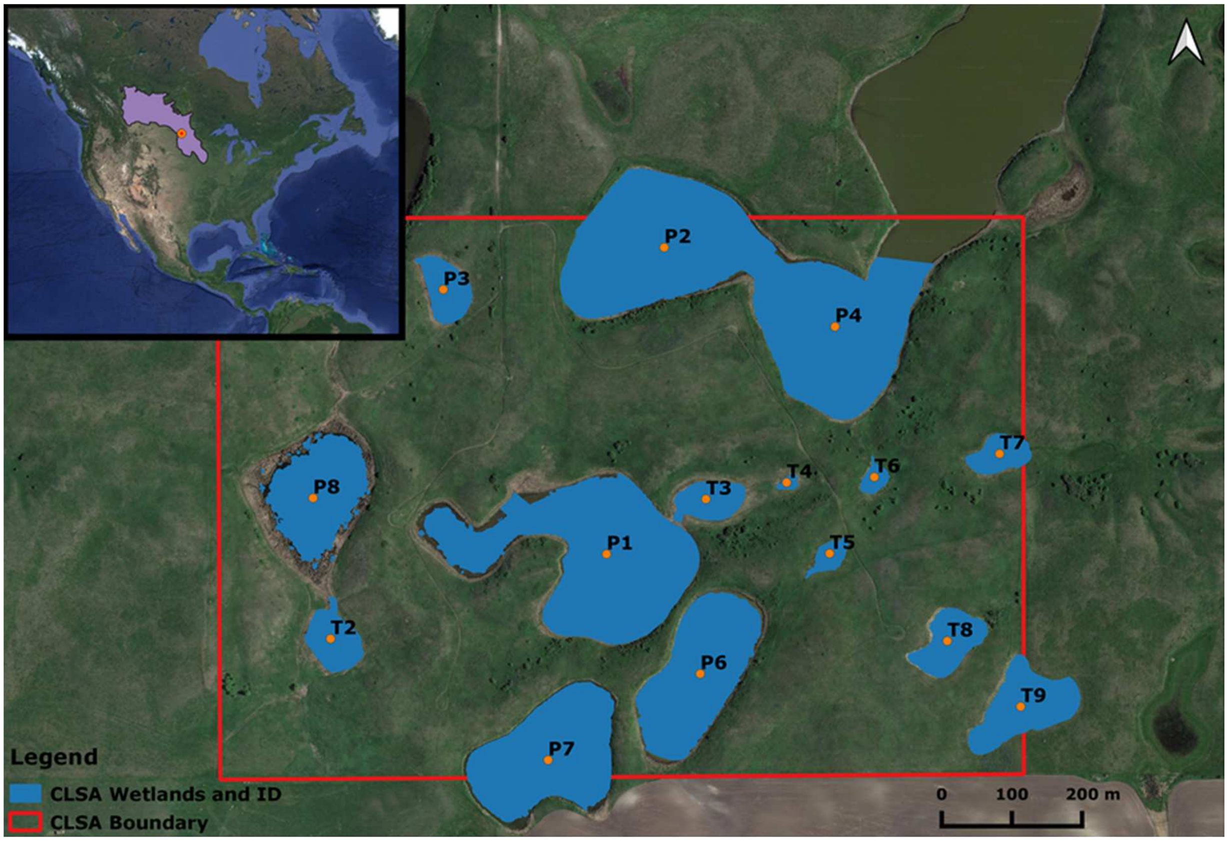

Figure 4.1. Map of the Cottonwood Lake Study Area Located in Stutsman County, ND, USA, and the Prairie Pothole Region of North America, highlighted in purple in the inset. Wetland P-11 (not shown) is located approximately 3-km west of the core study area depicted here.

The flora and fauna found in prairie potholes are diverse and often uniquely adapted to the spatially and temporally variability found in these wetlands (van der Valk and Davis, 1978; Euliss et al., 1999; Euliss et al., 2004). Since prairie-pothole wetlands are the dominant water bodies found in the PPR, they are critical habitats for aquatic fauna, primarily invertebrates and amphibians. The plants, invertebrates, and amphibians found within prairie-pothole wetlands provide critical forage for migrating and nesting waterbirds (Deutschman and Peterka, 1988; Krapu and Reinecke, 1992; Stafford et al., 2016; Ferguson et al., 2019). Protection and restoration of prairie-pothole wetlands has been largely driven by waterbird conservation efforts, specifically ducks (Doherty et al., 2013; Dixon et al., 2019).

The CLSA is a complex of 16 neighboring wetlands located on US Fish and Wildlife Service managed Waterfowl Production Areas located on the eastern edge of the Missouri Coteau in Stutsman County, North Dakota (Figure 4.1). Most of the wetlands in the CLSA (n=15) are embedded within a 92-ha prairie-grassland (i.e., non-cropland) landscape, and are relatively untouched by anthropogenic landscape alterations. One wetland, P-11, is located 3 km from the core study area. All of the CLSA wetlands exhibited a wide range of spatial and temporal variability in ponded-water extent and duration (Table 4.1). Thus, the CLSA wetland complex provides an ideal system to explore the relative influences of intrinsic and extrinsic processes affecting biotic components of naturally functioning, depressional wetlands.

Table 4.1. Summary of observed maximum annual ponded-water area and depth for 16 prairie-pothole wetlands monitored at the Cottonwood Lake Study Area, North Dakota, from 1992 to 2015.

	Ponded Area (ha)			Depth (m)		
Wetland	Minimum	Mean	Maximum	Minimum	Mean	Maximum
P1	0.34	3.82	4.25	0.18	2.03	2.79
P2	0.09	3.95	4.41	0.24	2.3	3.06
P3	0.30	0.46	0.51	0.21	0.77	0.89
P4	0.07	3.64	4.03	0.2	2.1	2.86
P6	0.60	2.53	2.93	0.33	2.11	3.04
P7	0.11	2.39	2.79	0.21	3.21	4.18
P8	0.02	1.99	2.13	0.13	1.13	1.23
P11	15.43	21.21	23.21	0.23	2.91	3.99
T2	0.08	0.25	0.31	0.28	0.61	0.68
T3	0.01	0.24	0.67	0.08	0.57	1.18
T4	<0.01	0.02	0.04	0.14	0.37	0.48
T5	0.0	0.04	0.16	0	0.38	0.66
T6	<0.01	0.04	0.06	0.09	0.37	0.48
T7	0.0	0.10	0.28	0	0.42	0.66
T8	<0.01	0.22	0.75	0.04	0.56	1.09
T9	0.03	0.87	1.36	0.12	0.82	1.47

Wetland communities, e.g., aquatic invertebrates, amphibians, and birds, have been continuously monitored since 1992. In addition to community data, a detailed account of each wetland's hydrologic variability has been documented through long-term monitoring of surface water and vegetation zones (Labaugh et al., 1987; Winter, 2003). Using their original 1967 classification, Stewart & Kantrud (1967) classified half (N = 8) of the CLSA wetlands as permanently ponded and half (N = 8) as temporarily ponded. This classification separates the CLSA wetlands that typically contain water throughout the year (hereafter referred to as P wetlands) from those that annually cycle between ponded and dry (hereafter referred to as T wetlands) (Winter, 2003 and LaBaugh et al., 2018).

4.3.2. Data

We used water-level and aquatic-invertebrate data from the CLSA collected from 1992–2015, the period that coincides with the availability of aquatic-invertebrate monitoring data. All long-term, wetland-monitoring data from the CLSA are openly available from the U.S. Geological Survey through the Missouri Coteau Wetland Ecosystem Observatory at: https://www.sciencebase.gov/catalog/item/52f0ffd9e4b0f941aa181fc6.

McLean et al. (2019) found that three hydrologic-related variables (temporal shifts in the variability of ponded-water depth, the proportion of wetland ponded, and the proportion of open-water area in a wetland) coincided with shifts in aquatic-invertebrate community composition. The shifts in temporal variability indicated two hydrologically distinct time periods, 1992–1999 and 2000–2015 that were referred to as the "filling" and "post-filling" period, respectively. We used the same three hydrologic variables in this study to relate the spatial and temporal shifts in hydrologic variability to potential shifts in temporal coherence of communities.

Wetland ponded-water depths were manually recorded weekly from staff gauges installed within the ponded portion of each CLSA wetland. We used the maximum water-depth recorded each year for our analyses. The proportion of a wetland ponded was calculated by using each wetland's maximum water-surface elevation overlaid as a plane onto a digital elevation model (DEM) of the wetland (Mushet et al., 2016; Mushet et al., 2017a) using ArcGIS (ESRI, 2011). We then calculated area of ponded water from each water-surface-elevation plane overlay. This value was then divided by the maximum surface-water area recorded (1979–2015) for each wetland. Proportion of open-water area was quantified from annual vegetation-zone delineations (Mushet et al., 2017b). Wetland vegetation zones (wet meadow, shallow marsh, deep marsh, and open water) were delineated annually for all CLSA wetlands using aerial photographs of each wetland acquired during mid-summer using a digital camera at altitudes of photography ranging from 300-m to 1,500-m above ground level (AGL). Aerial photographs were georeferenced using computer databases and vegetative zones delineated using ArcMap (ESRI, 2011). From these data, we calculated the proportion of the wetland that was identified as open water, i.e., the total area of open water divided by the total area of all wetland zones combined.

Aquatic invertebrates were sampled monthly at each CLSA wetland. Typically, sampling started in April and ended in September. Aquatic invertebrates were sampled using vertically oriented, funnel traps (Swanson, 1978) that were randomly distributed within each distinct vegetation zone along three transects (Mushet et al., 2017c). Monthly samples were collected and stored in 80% EtOH and subsequently transported to a U.S. Geological Survey laboratory in Jamestown, ND for storage and later processing. Sample processing consisted of sorting to separate invertebrates and debris, identification of invertebrates to the lowest feasible taxonomic resolution (typically genus), drying invertebrates to a constant weight at 60 °C, and weighing to obtain a biomass measurement (Mushet et al., 2017c; Mushet et al., 2018b). We summarized the aquatic-invertebrate data by mean abundance and mean biomass for each sampling season.

4.3.3. Data Analyses

Prior to examining temporal coherence of wetland hydrologic conditions and aquatic-invertebrate communities, we calculated community metrics for each wetland that characterized different aspects of the aquatic-invertebrate communities. We calculated invertebrate taxon richness (number of unique taxa), Shannon's diversity index (Shannon, 1948; hereafter, Shannon diversity), and biomass for each wetland annually. We then calculated the same three metrics separately for matrices containing only insect taxa and non-insect taxa. We used non-metric multidimensional scaling (NMDS) to measure temporal turnover of aquatic-invertebrate community compositions. We assessed compositional turnover for both aquatic-invertebrate abundances and presence-absences. Since aquatic-invertebrate abundances can be highly variable among taxa, we log transformed the aquatic-invertebrate abundances to help reduce the influence of especially abundant taxa in the NMDS model. We used Bray-Curtis based dissimilarities on the abundance data and Sørensen based dissimilarities on the presence-absence data to create the NMDS models using the *metamds* function in the 'vegan' R package (Oksanen et al., 2015). Derivation of final NMDS axes was determined by finding the lowest dimensional model solution with a stress value <0.20 and a stress reduction < 0.50 when an additional dimension is added (Clarke, 1993; Peck, 2011).

We examined the temporal coherence of hydrologic and invertebrate variables for all 16 wetlands sampled annually over the 24-year duration of the study. We then analyzed and compared temporal coherence values within two subsets of wetlands, the T wetlands (n=8) and the P wetlands (n=8). McLean et al. (2019) found that two P wetlands (P-03 and P-08) had more stable water regimes and less turnover than other wetlands as a result of defined surface-water outlets that mediate water depth during high conditions, which made them less responsive to changes in climate. We chose to compare coherence values for P wetlands with and without the two permanently ponded “open-basin” wetlands. We also compared how the levels of temporal coherence correspond to shifts in hydroclimatic variability by grouping wetlands into two hydrologically distinct periods, the filling period (1992–2000) and the post-filling period (2001–2015). We measured temporal coherence using the intra-class correlation coefficient, r_i, as described in Rusak et al., (1999). Using output from a two-way, Type-II ANOVA models without replication we calculated r_i as: $(MS_T\text{-}MS_E)/\ (MS_T + (n\text{-}1\text{-})\ MS_E)$

For this equation, MS_T is the mean sums squared of time (sampling year), MS_E is the mean square of the error, and n is the number of wetlands used in the corresponding ANOVA model. The resulting r_i values range from -1/(n-1) to 1 (Zar, 1984). Values that are closer to one indicate measured variables are more synchronous, and as values decrease the variability between wetlands within years becomes greater than between years (Rusak 1999). As intraclass correlation assumes variables are normally distributed (Zar, 1984), we log(x+1) transformed aquatic-macroinvertebrate biomass data. We then standardized (mean = 0, sd = 1) all variables except the NMDS Axis scores which were already normally distributed. When derived from z-score transformed data the r_i value is analogous to the mean pairwise Pearson’s correlation coefficient for all wetland by year combinations (Haggard, 1958). We used Fisher’s Z-test (Fisher, 1915) to statistically assess whether the synchronicity among wetlands, measured as r_i, for each measured variable was significantly different from the null value 0 (Angeler and Johnson, 2012). We plotted the standardized values of the hydrologic and biotic variables assessed for each wetland over time to provide visual representations of temporal fluctuations among wetlands.

4.4. Results

A total of 355 uniquely identified, wetland-invertebrate taxa were observed during the period of study and used in our analysis. Annual invertebrate richness and mean annual invertebrate biomass measurements for each wetland range from five to 55 uniquely identified taxa and 0.01 to 10.5 grams, respectively (Table 4.2). We obtained a two-dimensional solution for our invertebrate abundance (Bray-Curtis dissimilarities) and presence-absence (Sørensen dissimilarities) derived NMDS models (Stress=0.18 & 0.19, respectively).

Table 4.2. Among wetland annual variability of total invertebrate, insect only, and, non-insect only taxon richness (S), Shannon's Diversity (H), and biomass for 16 wetlands monitored at the Cottonwood Lake Study Area between 1992 and 2015.

	Temporarily Ponded			Permanently Ponded		
Variable	Minimum	Mean	Maximum	Minimum	Mean	Maximum
S	5	34	55	13	36	62
Insect S	3	21	35	7	22	40
Non-Insect S	2	13	25	6	14	25
H	0.29	1.57	2.72	0.26	1.46	2.58
Insect H	0.35	1.88	2.90	0.25	1.81	2.84
Non-Insect H	0.01	1.14	2.26	0.21	1.14	2.04
Biomass	0.01	0.46	6.64	0.05	0.60	10.54
Insect Biomass	0.01	0.24	1.78	0.02	0.28	1.53
Non-Insect Biomass	<0.01	0.21	6.50	<0.01	0.31	10.34

We found that temporal fluctuations in wetland depth (m), proportion-ponded, and proportion of open-water area for all 16 CLSA wetlands exhibited spatially synchronous patterns between 1992 and 2015 (Table 4.3, Figure 4.2). Fisher's Z-test indicated the intraclass correlation values for depth, proportion of wetland ponded, and proportion of open-water area (0.51, 0.52, and 0.65, respectively) were significantly greater than zero (alpha 0.05, Table 4.3). When broken down by hydrologic regime and hydrologic period, we found that ponded water fluctuations in P wetlands were more coherent than in T wetlands. We also found that the among wetland synchrony for all 16 wetlands was greater during the “filling” period than during the “post-filling” period (Table 4.4, Figure 4.2).

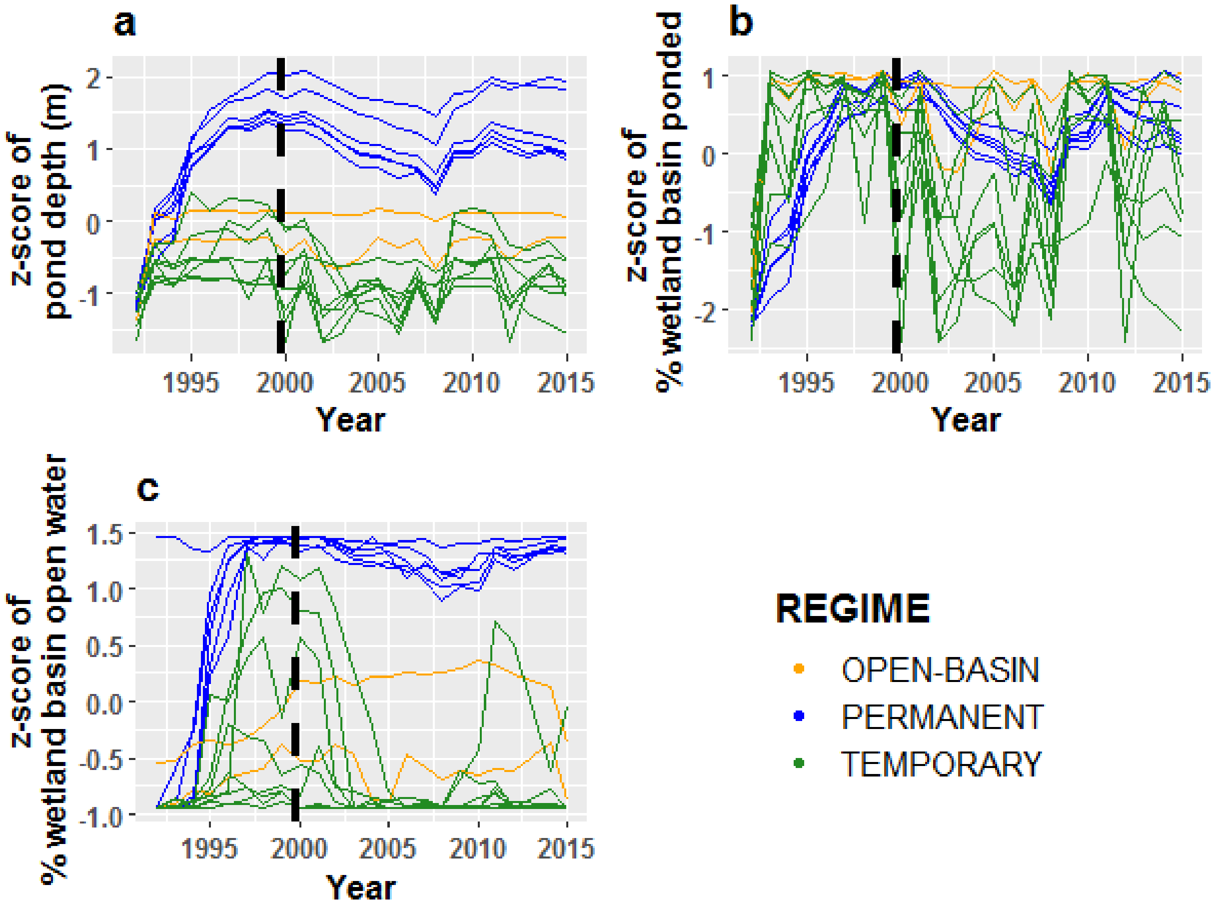

Figure 4.2. Normalized z-scores of a) maximum observed annual ponded-water depths (m), b) maximum ponded-water extent (%), and c) open-water area (%) for sixteen Cottonwood Lake Study Area wetlands sampled from 1992 to 2015. For each plot, green lines represent temporarily ponded wetlands (T-Wetlands), blue lines represent permanently ponded wetlands with closed basins (P-Wetlands), and orange lines represent permanently ponded wetlands with open basins (OB-Wetland). The black dashed lines indicate the transition for the ‘‘filling period’’ (1992–2000), and the ‘‘post-filling period’’ (2001–2015).

Table 4.3. Intraclass Correlation Coefficient (r_i) among all wetlands (n=16), just P-Wetlands (n=8), P-Wetlands excluding OB-Wetlands (n-6), and just T-Wetlands (n=8) sampled annually between 1992–2015 (n=24).

	All Wetlands		P-Wetlands	OB- Wetlands Removed	T-Wetlands
Variables	r_i	P-val	r_i	r_i	r_i
Ponded- Water Depth (m)	0.51	0.02	0.83	0.86	0.19
Percent Ponded	0.52	0.02	0.86	0.88	-0.14
Percent Open Water Area	0.65	0.00	0.91	0.92	0.28
Invertebrate Taxon Richness	0.04	0.46	-0.07	0.46	0.36
Insect Taxon Richness	-0.03	0.46	0.05	0.51	-0.14
Non-Insect Taxon Richness	0.62	0.00	0.03	-0.14	0.80
Invertebrate H	0.06	0.42	-0.07	-0.19	0.06
Insect H	0.08	0.39	0.13	0.04	-0.08
Non-Insect H	0.59	0.01	0.35	0.20	0.70
Invertebrate Biomass(g)	0.01	0.49	0.52	0.60	0.58
Insect Biomass(g)	0.55	0.01	-0.07	0.02	0.81
Non-Insect Biomass(g)	0.53	0.02	0.78	0.77	0.14
Sørensen NMDS Axis 1	0.78	0.00	0.87	0.86	0.58
Sørensen NMDS Axis 2	0.16	0.28	0.55	0.60	-0.13
Bray-Curtis NMDS Axis 1	0.66	0.00	0.91	0.92	-0.12
Bray-Curtis NMDS Axis 2	0.47	0.03	0.51	0.65	0.42

Table 4.4. Intraclass Correlation Coefficient (r_i) among all wetlands (n=16), just P-Wetlands (n=8), P-Wetlands excluding OB-Wetlands (n-6), and just T-Wetlands (n=8) sampled during the filling hydroclimatic period (1992—2000) and the post-filling hydroclimatic period (2001—2015).

	Filling Period				Post-Filling Period			
	All	P	No-OB	T	All	P	No-OB	T
Variables	r_i	r_i	r_i	r_i	r_i	r_i	r_i	r_i
Ponded Water Depth (m)	0.94	0.96	0.97	0.82	-0.03	0.01	0.18	0.14
Percent Ponded	0.94	0.97	0.99	0.87	0.04	0.21	0.52	0.32
Percent Open-Water Area	0.96	0.97	0.98	0.92	0.69	0.52	0.54	0.77
Invertebrate Taxon Richness	0.50	- 0.12	0.44	0.84	0.78	0.92	0.93	0.49
Insect Taxon Richness	0.59	- 0.05	0.15	0.85	0.66	0.86	0.89	0.11
Non-Insect Taxon Richness	0.14	0.26	0.61	0.7	0.82	0.88	0.91	0.75
Invertebrate H	-0.05	0.12	0.26	0.03	0.53	0.45	0.27	0.57
Insect H	0.81	0.77	0.70	0.83	0.2	0.7	0.82	0.02
Non-Insect H	0.1	-0.14	-0.17	0.37	0.57	0.49	0.36	0.62
Invertebrate Biomass(g)	0.58	0.72	0.78	0.35	0.41	0.25	0.33	0.49
Insect Biomass(g)	0.24	0.21	0.17	0.2	0.44	0.48	0.53	0.38
Non-Insect Biomass(g)	0.69	0.76	0.83	0.59	0.12	-0.12	-0.08	0.24
Sørensen NMDS Axis 1	0.97	0.98	0.97	0.93	-0.06	0.68	0.87	-0.14
Sørensen NMDS Axis 2	0.36	0.85	0.23	0.54	0.72	0.86	0.91	0.44
Bray-Curtis NMDS Axis 1	0.93	0.97	0.98	0.78	0.31	0.37	0.49	0.74
Bray-Curtis NMDS Axis 2	0.05	0.38	-0.01	0.27	0.35	0.37	0.54	-0.01

Temporal coherence of biotic variables among CLSA wetlands differed depending on the community assessed and the metric used to characterize it. Using the complete invertebrate data set for all 16 wetlands over the 24-year period we found that turnover of community composition, as measured by our NMDS Axes, was typically synchronous among wetlands (Table 4.4; Figure 4.5). The one exception was NMDS Axis two, derived from presence-absence data, which had a non-significant r_i value of 0.16. However, temporal coherence of invertebrate alpha diversity (richness, Shannon diversity) and mean annual biomass varied by invertebrate guild (Tables 4.3,4.4; Figure. 4.3,4.4). For example, insect richness and Shannon diversity had relatively low, non-significant r_i values, -0.03, 0.08, respectively. Conversely, non-insect taxon richness and Shannon's diversity, and biomass all exhibited significantly different (P-Value <0.05) temporally coherent dynamics ($r_i = 0.62, 0.59$, respectively). Both insect biomass (r_i value = 0.55) and non-insect biomass (r_i value = 0.53) were significantly different (P-Value < 0.05) then a null value of 0.

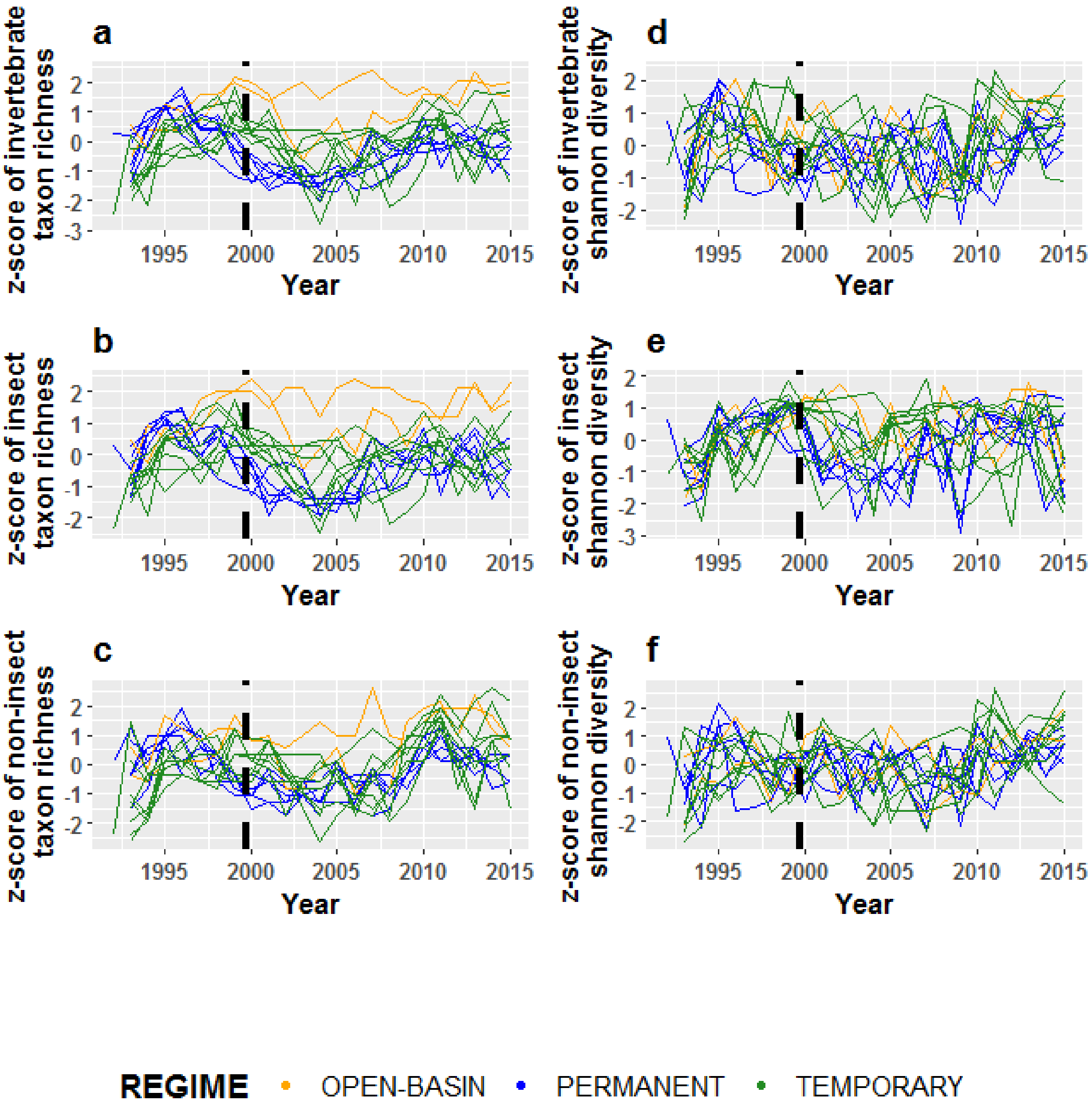

Figure 4.3. Normalized z-scores of **a** total invertebrate taxon richness, **b** insect taxon richness, **c** non-insect taxon richness, **d** total invertebrate Shannon's Diversity**, e** non-insect taxon Shannon's Diversity**, f** and non-insect taxon Shannon's Diversity for sixteen Cottonwood Lake Study Area wetlands sampled from 1992 to 2015. For each plot, green lines represent temporarily ponded wetlands (T-Wetlands), blue lines represent permanently ponded wetlands with closed basins (P-Wetlands), and orange lines represent permanently ponded wetlands with open basins (OB-Wetland). The black dashed lines indicate the transition for the ''filling period'' (1992–2000), and the ''post-filling period'' (2001–2015).

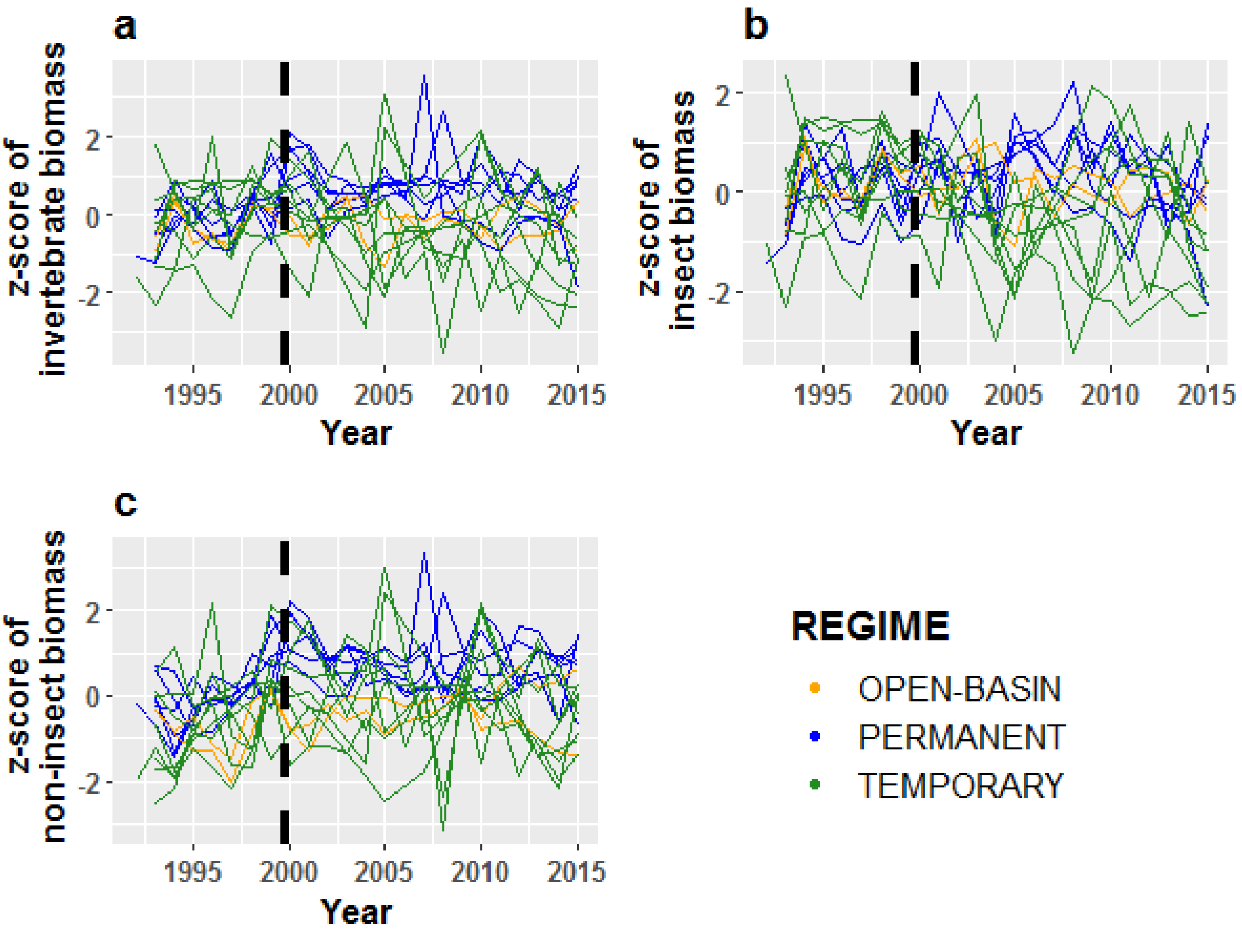

Figure 4.4. Normalized z-scores of log transformed mean annual **a** invertebrate biomass (g), **b** insect biomass(g), **c** and non-insect biomass (g) for sixteen Cottonwood Lake Study Area wetlands sampled from 1992 to 2015. For each plot, green lines represent temporarily ponded wetlands (T-Wetlands), blue lines represent permanently ponded wetlands with closed basins (P-Wetlands), and orange lines represent permanently ponded wetlands with open basins (OB-Wetland). The black dashed lines indicate the transition for the ''filling period'' (1992–2000), and the ''post-filling period'' (2001–2015).

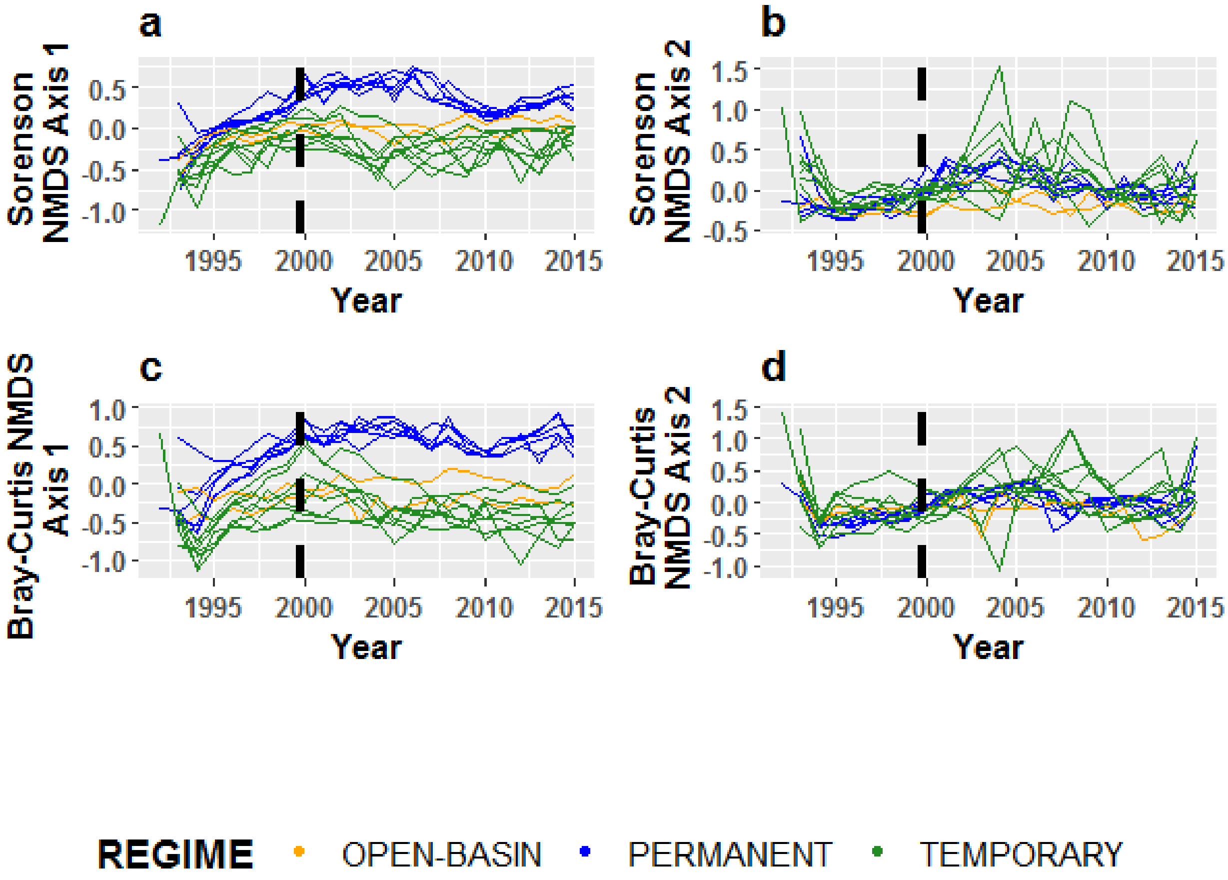

Figure 4.5. a Sørensen dissimilarity based NMDS Axis 1, b Sørensen dissimilarity based NMDS Axis 2, c Bray-Curtis dissimilarity based NMDS Axis 1, d and Bray-Curtis dissimilarity based NMDS Axis 2 scored based on invertebrate taxon presence-absences (Sørensen) and abundances (Bray-Curtis) for sixteen Cottonwood Lake Study Area wetlands sampled from 1992 to 2015. For each plot, green lines represent temporarily ponded wetlands (T-Wetlands), blue lines represent permanently ponded wetlands with closed basins (P-Wetlands), and orange lines represent permanently ponded wetlands with open basins (OB-Wetland). The black dashed lines indicate the transition for the ‘‘filling period’’ (1992–2000), and the ‘‘post-filling period’’ (2001–2015)

In addition to community-specific and metric-specific variability in temporal coherence, we observed both similar and contrasting patterns of coherence when wetlands were grouped by hydrologic regimes. When using the complete invertebrate data sets T wetlands and P wetlands had similar, but relatively low, coherence values (r_i range = -0.07 – 0.36; Table 4.3). When the invertebrate community was broken down into insect and non-insect taxa, we found r_i values were higher for non-insect taxon richness and Shannon diversity (range = 0.03 – 0.8) then insect taxa (range = -0.14 – 0.13), with the highest values found among T wetlands (Table 4.4). For both T wetlands and P wetlands, mean annual biomass measurements among wetlands were similar and relatively synchronous (r_i values = 0.52. and 0.53, respectively). However, T wetlands had high coherence values for insect biomass ($r_i = 0.81$) and low values for non-insect biomass (0.14), while P wetlands had an opposite pattern with higher r_i values for non-insect biomass ($r_i = 0.78$) than for insect biomass ($r_i = -0.07$, Table 4.4).

Our analysis investigating how temporal coherence values have responded to observed shifts in hydroclimatic variability also revealed context-specific patterns. As previously mentioned, the synchrony of among-wetland, ponded-water fluctuations were much higher during the "filling" period than during the "post-filling" period. However, shifts in the temporal coherence of wetland invertebrates did not typically correspond to shifts in ponded-water synchrony. For example, temporal coherence values for most invertebrate diversity metrics indicated that synchrony typically increased during the "post-filling" period (Table 4.4) with the exception of the Shannon diversity of insect taxa, which was much higher during the "filling" period (Table 4.4; Figure 4.3). Mean annual biomass for invertebrate communities had similar levels of coherence for both periods (Table 4.4; Figure 4.4), insect biomass fluctuations were more coherent during the "post-filling" period ($r_i = 0.44$, 0.24), and non-insect biomass was less coherent during the post-filling period ($r_i = 0.69$, 0.12). The greatest observed shift in temporal coherence between periods was invertebrate composition, measured by NMDS Axes (Table 4.4).

4.5. Discussion

Our initial assessment of the degree of temporal coherence exhibited by aquatic-invertebrate communities in a complex of 16, prairie-pothole wetlands spanning over a sampling period of 24 years provides a starting point for further investigations into how to maximize and conserve biodiversity in depressional wetland ecosystems. We found that even at relatively small spatial scales the relative importance of landscape controls in determining wetland characteristics can be dependent on a wetland's hydrologic regime and multi-year changes in hydroclimatic variability. The variable responses observed at different levels of community organization (i.e., community types and metrics) highlight the importance of landscape controls, meta-community processes, and wetland heterogeneity in shaping community assemblages. Our results also provide examples of contrasts and similarity between hydrologically variable, wetland ecosystems and larger, relatively stable, lake ecosystems.

The 16 wetlands used in our analysis were variable in size with maximum observed ponded areas ranging from 0 to 23 hectares. They also exhibited high variability in ponded-water duration, ranging from wetlands that did not pond water every year to ones that were continually ponded for the duration of our study period (Mushet et al., 2016). However, we observed temporally coherent dynamics of ponded-water characteristics, non-insect taxa richness and Shannon diversity, non-insect and insect taxa biomass, and invertebrate compositional turnover. These observations indicated that landscape controls are an important part of community assembly and support the idea that conservation of wetland biodiversity benefits from the preservation and restoration of diverse complexes of grassland embedded wetlands (Whiles and Whiles and Goldwitz, 2001; Gibbs, 2000; Cohen et al., 2016; Verheijen et al., 2018).

Previous research has demonstrated how prairie-pothole wetland hydrology is sensitive to shifts in climate (Winter and Rosenberry, 1998; Cressey et al., 2016; McKenna et al., 2017), which in turn influence community assemblages (Mushet et al., 2015; Haig et al., 2019; McLean et al., 2019). The temporally coherent, ponded-water dynamics at the CLSA were most pronounced in the P wetlands, which had more stable, ponded-water regimes, and for all wetlands during the “filling-period” when precipitation driven shifts in hydrology were strongest. These results are consistent with those of Magnuson et al. (2006) who found that physical parameters (i.e., hydrology) in lakes are typically spatially synchronous, and Huttennen et al. (2014) who found that extreme climate events increase temporal coherence in aquatic ecosystems. Even though smaller, temporarily ponded wetlands are particularly sensitive to changes in climate (Zhang et al., 2009), we found that the ponded-water dynamics in T wetlands at the CLSA over the 24-year period were not temporally coherent. We believe the lack of spatial synchrony among T wetlands was due to non-linear rates of precipitation runoff, evapotranspiration, and sensitivity to fill and spill dynamics (Zhang et al., 2009; Hayashi et al., 2016; Leibowitz et al., 2016). The amount of runoff entering a wetland is primarily dependent on the amount of precipitation, and the slope and area of the catchment (Hayashi et al., 2016). The threshold for the amount of precipitation needed to generate runoff decreases with increased slope and catchment size.

Interestingly, when wetlands with different hydrologic regimes (i.e., P wetlands and T wetlands) were pooled, we found that for many biotic measurements of temporal coherence were similar to, or even greater than, temporal coherence measurements of ponded-water fluctuations. This is a sharp contrast to previous studies that have found physical processes to be more temporally coherent then measurements of biotic change (Magnuson et al., 2006; Huttenen et al., 2014). However, when synchrony is only assessed using the more lake-like P-Wetlands, we found patterns similar to other lacustrine studies. For example, we found that physical properties and invertebrate compositional turnover to be highly synchronous compared to measurements of abundance and alpha diversity (Anneville et al., 2005; Angeler and Johnson, 2012). Climate driven, synchronous changes in ponded-water levels are likely contributing to increased levels temporal coherence for some of our measured variables. However, our results indicate that both intrinsic factors unique to each wetland and extrinsic processes of connectivity at least partially independent of climate are also driving certain aspects of community assembly on the landscape. For example, certain invertebrate-community metrics, i.e., overall taxa alpha diversity and biomass, insect alpha diversity, and invertebrate taxa associated with NMDS Axes (Bray-Curtis and Sorensen), did not exhibit synchronous patterns that would indicate the observed variability in these variables was due to intrinsic processes (i.e., wetland heterogeneity). Further, T wetlands were found to not have coherent ponded-water dynamics, but still had synchronous changes in non-insect diversity, invertebrate biomass, insect biomass, and invertebrate compositional turnover found in Axis 1 of the Bray-Curtis NMDS model. While these results do not rule out climate as a driving force of the observed synchrony, they do suggest the mechanisms extend beyond coherent changes in ponded-water regimes.

Some other extrinsic factors that have been shown to contribute to temporal coherence are synchronous dispersal among populations and the populations responding to trophic interactions with synchronous taxa (Ranta et al., 1997a,b; Liebhold et al., 2004; Heino et al., 2015). These mechanisms can be independent of climate fluctuations or in response to climatic conditions on the landscape (Korhonen et al., 2010; Hillebrand et al., 2010). We predicted that mobile dispersers would exhibit more synchronous patterns because dispersal is partially limited by landscape controls (Cosentino and Schooley, 2018). However, we found that less mobile non-insects to be more synchronous in temporal changes in alpha diversity then their more mobile insect counterparts (Table 3). This pattern has is similar to that observed in Soininen et al., (2007) that beta-diversity was greater among more mobile dispersing taxa then passive dispersers. Another possibility for decreased synchronicity of alpha diversity among wetlands could be attributed to different generational times among taxa grouped into one category (Kratz, 1987; Rusak et al., 1999). Whereas, while many taxa might be highly synchronous among wetlands, when grouped together this pattern disappears.

Batzer (2013), reviewed predictors of wetland invertebrate composition and found very little consistency among studies. The temporal perspective provided by the long-term sampling at CLSA have provided a unique perspective on drivers of wetland-invertebrate alpha and beta diversity (Leibowitz et al., 2016; McLean et al., 2019; Mushet et al., 2019; McLean et al., *in prep*). It has become evident that predictors of wetland-invertebrate community composition are dynamic, much like the wetland ecosystems themselves. Communities in these systems are assembled through environmental sorting, patch dynamics, and mass effects. The relative importance of these processes is temporally and spatially variable. The differences in community composition that are unique to wetlands with different ponded-water regimes, salinities, and vegetation structure are likely the product of sorting effects due to habitat heterogeneity, and the strength of these sorting effects can change shift with changes in climate (McLean et al., 2016a,b; Gleason and Rooney 2018; Gleason et al., 2018; McLean et al., *in prep*). However, there can also be overlap in community composition among wetlands with heterogenous, ponded-water regimes. The increases in average ponded-water levels and number of ponded wetlands observed in North Dakota post 1993 have likely facilitated an increase of dispersal (McLean et al., 2016b). Mass effects are likely important under these conditions, whereas, increased dispersal would allow taxa to colonize habitats that are not suitable for long term persistence. Patch dynamics are also likely important in prairie-pothole wetlands as many of these systems exhibit periodic drying and subsequent ponding. This creates opportunities for taxa such as mosquitoes that are rapid colonizers (Batzer and Wissinger, 1996) but poor competitors

(Knight et al., 2004; Elono et al., 2010) to persist in newly ponded wetlands under reduced threat of competition and predation (Chase and Knight, 2003). While the environmental filters determining wetland community composition are fairly well established, future research is needed to understand the relative roles of mass effects, patch dynamics, and other metacommunity processes in maintain biodiversity.

4.5.1. Conservation Implications

Depressional wetland ecosystems, such as prairie-pothole wetlands have been extensively drained and modified at a landscape level (Dahl,1990; Dahl et al., 2014), which in combination with directional shifts in climate has led to a loss of spatial and hydrologic heterogeneity (Bedford, 1999; Van Meter and Basu, 2015). The strategic preservation and restoration of wetland ecosystems to conserve biodiversity is dependent on our understanding of the importance of intrinsic and extrinsic processes in shaping wetland communities and how these processes might be influenced by climate change. McLean et al. (2019) found that invertebrate taxonomic composition and variability in CLSA wetland differed between permanently and temporarily ponded wetlands. Building upon that finding, we found that even though wetlands with differing hydrological regimes host distinct communities, compositional turnover was synchronous (Table 4.3, Figure 4.6). Our finding that invertebrate composition and biomass within invertebrate guilds exhibited temporally coherent dynamics suggests that metacommunities are indeed an important determinant of wetland assembly. Therefore, the presence of neighboring wetlands with variable hydrologic regimes increases landscape biodiversity through increased habitat heterogeneity and connectivity. Heterogenous complexes of wetlands with high metacommunity connectivity are also likely going to be more resilient to shifts in climate (de Boer et al., 2014; Lowe et al., 2015; Verheijen et al., 2018). Overall, our findings provide long-term evidence that wetland ecosystem functions are dependent on their relationship to local climate conditions and wetland to wetland landscape linkages. Thus, the unique contributions of biodiversity and ecosystem functions provided by wetlands can be maximized through the conservation and restoration of complexes of heterogenous wetlands.

4.6. References

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CHAPTER 5. INVERTEBRATE COMMUNITIES OF PRAIRIE-POTHOLE WETLANDS IN THE AGE OF THE AQUATIC HOMOGENOCENE[4]

5.1. Abstract

Community simplification is a common consequence of anthropogenic modification. However, the prevalence and mechanisms of biotic homogenization among wetland systems require further examination. Biota of wetlands in the North American Prairie Pothole Region are adapted to high spatial and temporal variability in ponded-water duration and salinity. Recent climate changes, however, have resulted in decreased hydrologic variability. Land-use changes have exacerbated this loss of variability. We used aquatic-macroinvertebrate data from 16, prairie-pothole wetlands sampled between 1992 and 2015 to explore the homogenization of wetland communities. Macroinvertebrate communities of small wetlands that continued to cycle between wet and dry phases experienced greater turnover and supported more unique taxa compared to larger wetlands that shifted towards less dynamic, permanently ponded, lake-like regimes. Temporal turnover in beta-diversity was lowest in these permanently ponded wetlands. Additionally, wetlands that shifted to permanently ponded regimes also experienced a shift from palustrine to lacustrine communities. While increased pond permanence can increase species and overall beta diversity in local areas previously lacking lake communities, homogenization of wetland communities at a larger, landscape scale can result in an overall loss of biodiversity as the diverse communities of many wetland systems become increasingly similar to those of lakes.

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[4] The material in this chapter was co-authored by Kyle I Mclean, David M. Mushet, and Jon N Sweetman. Kyle I McLean had the primary responsibility of data analysis, developing conclusions, and drafting the manuscript. David M. Mushet and Jon N. Sweetman served as proofreaders and supplied constructive comments on the interpretation of the findings of this study. This chapter was published in the journal *Hydrobiologia* in 2019.

5.2. Introduction

Globally, freshwater ecosystems are experiencing widespread habitat degradation and biodiversity loss (Dudgeon et al., 2006; Reid et al., 2018). Compared to taxa in surrounding terrestrial communities, freshwater taxa are perhaps the most imperiled biota (Sala, 2000; Reid et al., 2018). Not only are freshwater taxa being lost at alarming rates globally, regionally many aquatic ecosystems and their biotic communities are becoming increasingly similar or homogenous (Rahel, 2002; Petsch, 2016). Olden (2008) defined biotic homogenization as "the process by which species invasions and extinctions increase the genetic, taxonomic or functional similarity of two or more locations over a specified time interval." In many cases, endemic species in an ecosystem are replaced by non-endemic invaders, often as a result of anthropogenic modifications to the environment (McKinney and Lockwood, 1999). Biotic homogenization often results in a loss of ecosystem function and, in turn, ecosystem health (Kinzig et al., 2001; Cardinale et al., 2002; Vaughn, 2010). Since increased similarity implies a decrease in variability, biotic homogenization is often detected as temporal decreases in beta diversity (Olden and Rooney, 2006; Olden et al., 2018). While many of the foundational papers exploring evidence and mechanisms for biotic homogenization have been rooted in the aquatic sciences, these investigations are largely limited to fish and plant communities in riverine and lacustrine environments (Olden, 2006). The prevalence of and mechanisms for biotic homogenization in wetland ecosystems remain relatively unexplored. Therefore, a better understanding of biotic homogenization in wetland ecosystems is needed to contribute to landscape level biodiversity conservation efforts.

In the context of biotic homogenization, previous investigations on the influence of climate and land use driven modifications to wetlands have been limited to examination of plant communities (Houlahan and Findlay, 2004; Aronson and Galatowitsch, 2008; Spyreas et al., 2010). Little is known about how widespread spatial and temporal changes in wetland hydrology influences aquatic animal diversity, especially aquatic macroinvertebrates. One possible explanation for this lack of information is that there are very few studies on aquatic macroinvertebrate communities that both span time periods long enough to detect a biotic homogenization trend and have sufficient taxonomic resolution needed to detect fine-scale community shifts. Another possible explanation is that wetland aquatic macroinvertebrates are highly adaptable to exist in these highly variable environments and are often dominated by generalists, making them resistant to hydrologic and anthropogenic changes (Batzer, 2013; Janke et al., 2019).

Decreased spatial and temporal variability of hydrological regimes and increased ponded-water connectivity are potential mechanisms promoting biotic homogenization. However, increased ponded-water extent, duration, and depth combined with decreased dissolved-ion concentrations can also make systems less deterministic (Daniel et al., 2019). Chase (2007) found that increasing hydroperiod and therefore reducing determinism in aquatic systems leads to increased species diversity, which results in an increase in biotic filtering (competition/predation), stochastic processes and subsequent beta diversity. In such cases, increased biodiversity as a result of greater stochasticity is predicted to increase overall productivity (Chase, 2010). Potentially this shift towards a more stochastic assembly might be the key to understanding why very few aquatic macroinvertebrate studies have identified land use, salinity, or water-depth as a significant driver of species richness or beta-diversity (reviewed in Batzer, 2013). While biotic homogenization in its strictest sense is limited to an overall decrease in beta-diversity over time, it can also be tied to the replacement of endemic taxa with non-endemic taxa. This taxa replacement can at times increase both alpha and beta diversity in individual wetlands (Olden and Rooney, 2006).

We contend that wetland ecosystems provide an opportunity to gain useful insights into mechanisms driving biotic homogenization and the susceptibility and resistance of systems to these drivers. In order to explore biotic homogenization in the context of wetland aquatic macroinvertebrate communities, we developed three hypotheses that relate biotic homogenization to hydrologic variability in prairie-pothole wetlands: (1) reduced spatial variability of wetland hydrologic regimes over time will lead to a decrease in mean annual between-wetland beta diversity, (2) reduced temporal variability in an individual wetland's hydrological regime will decrease mean between-year beta diversity in an individual wetland over time, and (3) a reduction in wetlands that frequently transition from ponded to dry will result in a loss of unique macroinvertebrate communities adapted to these conditions. We examined these hypotheses using hydrologic and aquatic macroinvertebrate data collected over a 24-year period from the Cottonwood Lake Study Area (CLSA), an area of the North American Prairie Pothole Region (PPR) in east central North Dakota. The CLSA is the most extensively studied and monitored wetland complex in the PPR. As typical for the region, wetlands in this complex have shifted in recent decades towards longer-hydroperiods, with the larger wetlands becoming less dynamic and lake-like over the past two decades (McKenna et al., 2017).

5.3. Methods

5.3.1. Study Area

The PPR is a highly cultivated landscape dominated by agriculture making it one of the largest and most human-modified, wetlands-dominated regions on Earth (van der Valk 2005). The PPR consists of approximately 777,000 km^2 of prairie-wetland mosaic spanning north and west from northwest Iowa through the Dakotas and into central Alberta (Smith et al., 1964). Depressional, prairie-pothole wetlands (hereafter referred to simply as “prairie potholes”) are the predominant wetland type occurring in the PPR. Prairie potholes can exhibit high spatial and temporal environmental variation in ponded-water extent, duration, depth, and salinity. The high variation is mostly attributable to the position of wetlands along elevation, groundwater, and geologic spatial gradients; and temporal gradients dominated by high inter-annual variation in precipitation (Euliss et al., 2004). Like many wetland systems, prairie potholes support unique biotic communities due to their hydrologic and geochemical dynamics (Euliss et al., 1999). Historically, biotic variation was maintained through high spatio-temporal variability in precipitation and temperature, in combination with the presence of numerous, heterogenous, wetland basins on the PPR landscape (Winter and Rosenberry 1998, Anteau et al., 2016). However, contemporary changes in regional climate and land use have been shown to alter the spatial and temporal hydrologic variability of these systems (Mushet et al., 2015; Cressey et al., 2016; McKenna et al., 2017)

An estimated 60 to 65% of the historically present wetland basins in the PPR have been lost due to anthropogenic modifications, e.g., ditching, filling (Dahl, 2014). Of these wetlands, the smaller, temporarily and seasonally ponded wetlands have been preferentially lost (Kahara et al., 2009; Serran and Creed, 2015; Van Meter and Basu, 2015). The loss of smaller wetlands on the landscape often consolidates runoff into the remaining wetlands which, in turn, decreases the number of small wetlands on the PPR landscape while simultaneously increasing the pond duration and size of wetlands that remain, resulting in decreased dynamics in their response to climate variability (Anteau, 2012; McCauley et al., 2015). The effect of modified waterflow paths can be exacerbated by shifts in climate, especially during periods of above or below average precipitation. Beginning in 1993, the southern portion of the PPR has experienced an extended, multi-decade, wet period (Ballard et al., 2014; McKenna et al., 2017). These wet conditions extended north into the Canadian portion of the PPR starting in 2005 (Hayashi et al., 2016). The increased precipitation has resulted in cascading effects resulting in a shift towards more permanently ponded, connected, and lake-like wetland hydrological regimes (Mushet et al., 2015; Cressey et al., 2016; Vanderhoof and Alexander, 2016; Vanderhoof et al., 2016; McKenna et al., 2017). Under these conditions ponded-water variability and dissolved-ion concentrations can become homogenized by shifting towards larger and fresher ponds during wet periods (Mushet et al., 2015; Leibowitz et al., 2016; Cressey et al., 2016). The current shift towards more permanently ponded and fresher wetlands in the PPR provides a model to examine how decreased hydrologic variability influences biotic homogenization.

The CLSA is part of a complex of U.S Fish and Wildlife Service managed Waterfowl Production Areas located on the eastern edge of the Missouri Coteau in Stutsman County, North Dakota (Fig. 5.1). Surface and groundwater hydrology of the sixteen wetlands forming the CLSA complex have been continually monitored since 1979. The wetlands forming the CLSA wetland complex were initially classified in 1967 into permanently (P) and temporarily (T) ponded groupings. Using this original 1967 classification (Stewart and Kantrud, 1967), half (N = 8) of the wetlands were identified as permanently ponded and half (N = 8) as temporarily ponded. However, under the later Stewart and Kantrud (1971) classification system, the CLSA wetlands designated as permanently ponded contain both semi-permanently (N = 7) and permanently ponded (N = 1) wetlands (Class IV and V, respectively). Similarly, the wetlands originally classified as temporarily ponded contain both temporarily (N = 2) and seasonally ponded (N = 6) wetlands (Class II and III, respectively). Additionally, inter-annual changes in precipitation have influenced surface-water connections and extent of ponded water, which in turn significantly altered ponded-water permanence (Leibowitz et al., 2016; McKenna et al., 2017).

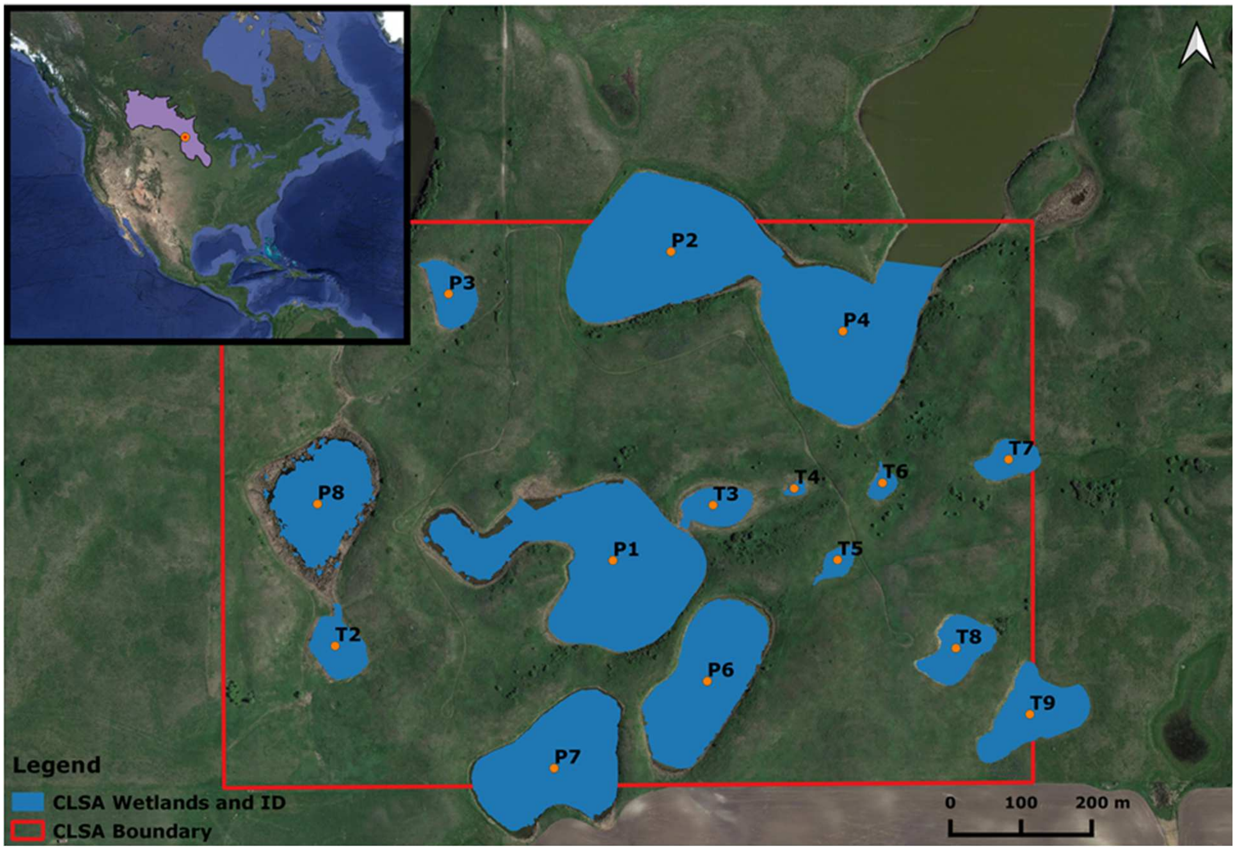

Figure 5.1. Map of prairie-pothole wetlands in the Cottonwood Lake Study Area, Stutsman County, North Dakota. Wetland P-11 (not shown) is located 3-km west of the core study area depicted here. The map in the upper left corner indicates the extent of the Prairie Pothole Region in purple and the orange circle represents the location of the study area.

For this study we used the original temporary (T) and permanent (P) wetland classifications since they separate the wetlands that were permanently ponded throughout the time frame of the study (P-Wetlands) from those that cycled between ponded and dry (T-Wetlands). Two of the wetlands originally classified as P-Wetlands (P-3, P-8) lose water to surface outlets, which limit maximum water depths, so we added in a third classification called open-basin wetland (OB-Wetland). Since the two OB-Wetlands are depth limited, they are typically shallower than other P-Wetlands that have greater ponded-water storage capacity during wet periods that allows for emergent vegetation to occur over a greater proportion of their area compared to other P-Wetlands (Fig. 2). The wetlands in the CLSA are embedded within a prairie-grassland (i.e., non-cropland) landscape and are relatively untouched by anthropogenic landscape alterations. The CLSA wetlands have also remained mostly absent of sustained fish communities during the duration of this study, apart from fathead minnows (*Pimphales promelas*) and yellow perch (*Perca flavescens*) being introduced into “P-11” in 2014 and persisting in subsequent years; and occasional, but temporary, invasions of fathead minnows into wetland P8. Thus, the CLSA wetland complex for the most part provides an ideal system to explore potential environmental mechanisms of biotic homogenization in prairie-potholes without the need to disentangle the influence landscape modifications or fish.

5.3.2. Data

To evaluate temporal patterns in beta diversity and potential drivers of biotic homogenization, we used a combination of available biotic and abiotic CLSA datasets. All long-term wetland monitoring data from the CLSA are openly available from the U.S. Geological Survey through the Missouri Coteau Wetland Ecosystem Observatory at: https://www.sciencebase.gov/catalog/item/52f0ffd9e4b0f941aa181fc6. We used the following datasets for this study: aquatic-macroinvertebrate counts (Mushet et al. 2017a), wetland stage (ponded-water elevation; Mushet et al. 2016), and vegetation-zone area (Mushet et al. 2017b). Although several of the data sets from CLSA have been collected since 1979, we restricted most of our analyses to data from collected from 1992 to 2015, the period that coincides with the availability of aquatic-macroinvertebrate data.

5.3.2.1. Environmental Variables

To provide context to general temporal trends in hydrologic variability observed in CLSA wetlands, we indexed mean annual pond duration in each basin with measured water depths (m), the proportion of the wetland basin that was ponded with water, and the proportion of the wetland that classified as open water. Water depths were manually recorded from staff gauges that were installed within the ponded portion of each CLSA wetland. To quantify the proportion of a wetland basin that was ponded, we used each wetland's maximum water-surface elevation for each year and overlaid the elevation as a plane onto a digital elevation model (DEM) of the wetland complex (Mushet et al., 2017b) using ArcGIS. From this overlay, we calculated the area of the water-surface-elevation plane as a proportion of the area of a water-surface elevation plane from the date when the pond was at its maximum pool level for the period of record (1979–2015). We used wetland vegetation-zone delineations from each CLSA wetland (Mushet et al., 2017b) to quantify the proportion of the basin classified as open-water. Wetland vegetation zones (wet meadow, shallow marsh, deep marsh, and open water) were delineated annually for all CLSA wetlands using aerial photographs of each wetland acquired during mid-summer using a digital camera at altitudes of photography ranging from 300 to 1,500 meters above-ground-level. Aerial photographs were georeferenced using computer databases and major vegetative zones delineated using Mapping and Image Processing Software (MIPS). From these data, we calculated the proportion of the wetland that was identified as open water, i.e., the total area of open water divided by the total area of all wetland zones. We plotted each wetland's depth, the proportion of the basin that was ponded, and proportion of the basin that was open-water over time (1979–2015). We incorporated a smoothing line with shaded 95% confidence intervals through the mean values for wetlands by hydrological regime. Using patterns observed in these plots, we developed a hydroclimatic-period classification highlighting three different periods: (1) the “pre-wetting period” (1979–1992), (2) the “filling-period” (1993–1999), and (3) the “post-filling period” (2000–2015). The classification was based on the observed hydrologic variability. Between 1979 and 1992, CLSA wetlands cycled between being ponded and being dry; from 1993 to 1999, most wetland ponds were in a period of consistent filling until their water levels peaked in 1999; and from 2000 to 2015, the T-Wetlands continued to frequently alternate between ponded and dry while the P-Wetlands and OB-Wetlands maintained high, ponded-water levels (Fig. 5.2).

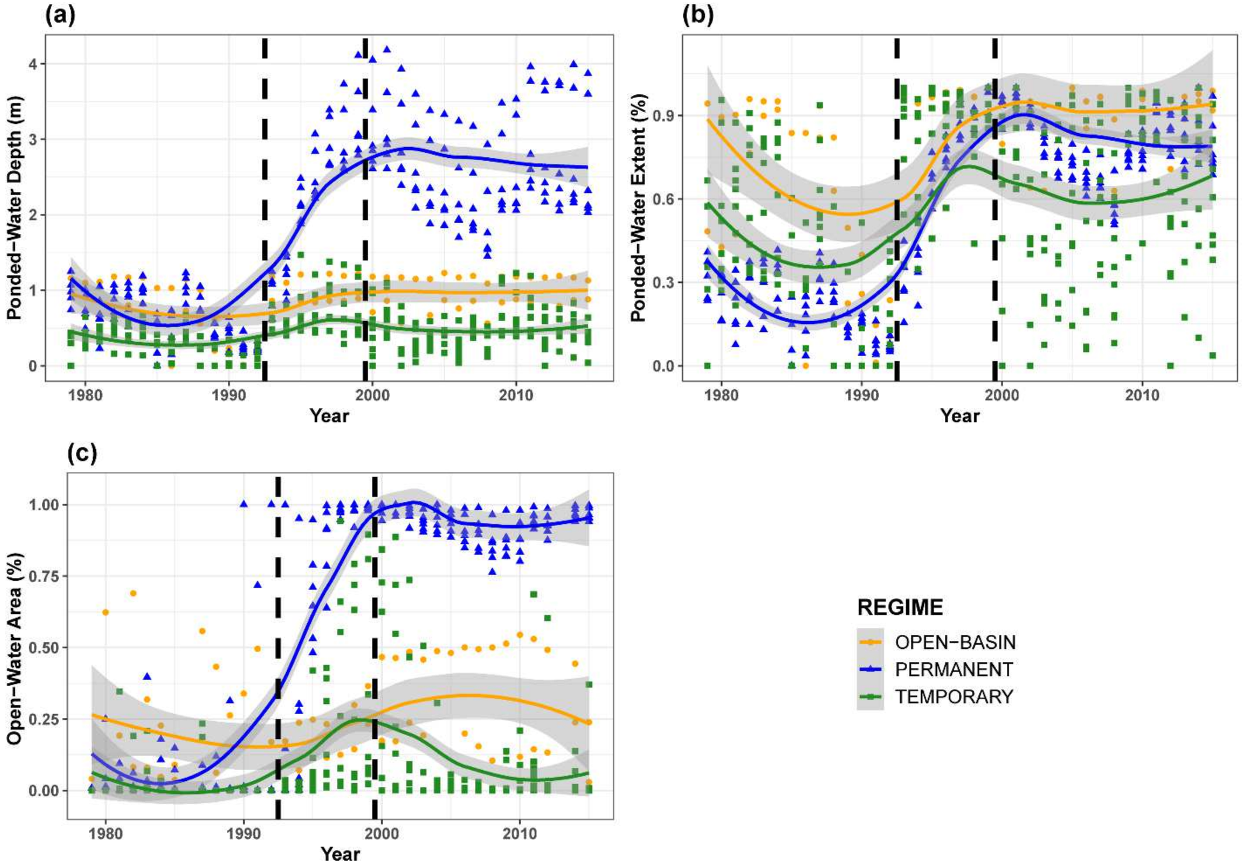

Figure 5.2. (**a**) Maximum observed annual ponded-water depths (m), (**b**) maximum ponded-water extent (%), (**c**) and open-water area (%) for sixteen Cottonwood Lake Study Area wetlands sampled from 1979 to 2015. For each plot, green squares represent temporarily ponded wetlands (T-Wetlands), blue triangles represent permanently ponded wetlands with closed basins (P-Wetlands), and orange circles represent permanently ponded wetlands with open-basins (OB-Wetland). The solid lines represent fitted means for wetlands by hydrological regime. The grey shaded areas surrounding each regression line represent the 95% confidence intervals. The black dashed lines indicate the transition for three different time periods; the “pre-wetting period” (1979–1992), the “filling-period” (1993–1999), and the “post-filling period” (2000–2015).

5.3.2.2. Biotic Variables

We used aquatic macroinvertebrate taxonomic composition and diversity to evaluate biotic homogenization. Compared to other wetland fauna, aquatic macroinvertebrates are abundant and speciose (Batzer and Wissinger, 1996). Aquatic macroinvertebrates have been monitored at CLSA since 1992. Recorded data include counts and biomass by taxa (lowest feasible resolution; typically, genus). Aquatic macroinvertebrates were sampled at CLSA using unbaited, vertically oriented, funnel traps (Swanson, 1978). Samples were collected monthly from random locations within each vegetation zone along three transects in each wetland from April to September. The number of vegetation zones present in a wetland varied by wetland and year, therefore the number of funnel traps used during a sampling occasion also varied by wetland and year. Since we used funnel-type activity traps the more benthic aquatic macroinvertebrates are likely underrepresented in the samples. Collected samples were stored in ethyl alcohol (80%) and processed in a U.S. Geological Survey laboratory in Jamestown, North Dakota. For our analyses, we calculated mean count for each unique taxonomical group for each wetland by year. We summarized the CLSA aquatic-macroinvertebrate data by each unique taxon's mean abundance for each funnel trap used per wetland per year. The resulting dataset consisted of rows identifying the wetland and year sampled and columns indicating the mean abundance of each unique aquatic macroinvertebrate taxon observed during the whole study. We then created a presence-absence matrix from the summarized aquatic-macroinvertebrate count data to reduce the influence of relative abundances that might result from an uneven sampling bias.

5.3.3. Statistical Analysis

All statistical analyses were completed in R v. 3.5.2 (R Developmental Core Team, 2013). To visualize how water depths and vegetation-zone compositions of CLSA wetlands have changed over time (1979–2015) in response to climatological conditions, we plotted water depth (m), proportion of each wetland basin ponded with water, and proportion of each wetland that was in an open-water state. We investigated biotic homogenization of aquatic macroinvertebrates by exploring different measures of beta diversity at different spatial scales over time.

5.3.3.1. Analysis of Aquatic-Macroinvertebrate Biotic Homogenization

The most common way to detect evidence for biotic homogenization is through quantifications of beta-diversity (Olden and Rooney, 2006). As different metrics of beta-diversity may capture different aspects of similarity between communities, we used multiple approaches for assessing beta diversity to evaluate both turnover of aquatic macroinvertebrate communities, total variation, and compositional differences of individual wetlands. We calculated Sorensen Index based measures of beta diversity on our presence/absence matrix to calculate beta diversity. Biotic homogenization has been shown to occur at the local scale (individual wetland) at which beta-diversity in the form of temporal turnover is reduced over time, and at the complex scale at which between site variation is reduced over time (Lambdon et al., 2008; Legendre and Cáceres 2013). For this study, we compared within-wetland beta diversity by comparing mean annual changes in beta diversity between years, and we compared complex-scale beta diversity by comparing mean annual beta diversity between the 16 CLSA wetlands per year over the duration of the study (1992–2015). For each metric quantifying a measure of beta-diversity that could be compared by wetland regime, we ran an ANOVA model to identify differences in beta-diversity among hydroclimatic periods and hydrologic regimes. Hydroclimatic period was a categorical variable that grouped observations into the "filling period" and "post-filling period" periods described above. The "pre-wetting" period was not used as a categorical variable for beta-diversity type analysis since we did not have aquatic-macroinvertebrate data for years prior to 1992.

Our first form of biotic homogenization explored was the simplification of between wetland communities. We analyzed how mean beta diversity varied annually among CLSA wetlands using the *beta.multi* function and Sorensen Index based dissimilarities derived from our presence-absence matrix using the ‘betapart’ package (Baslega et al., 2018). This approach calculates three multi-site dissimilarity coefficients: (1) Sorensen’s coefficient, a measure of overall between wetland beta-diversity per year, which is partitioned to calculate (2) Simpson’s coefficient, a measure of turnover without the influence of richness differences, and (3) the nestedness coefficient, a measure of the nestedness of a site resulting from between wetland richness differences (Baslega, 2010). We compared each year’s mean beta-diversity, turnover, and nestedness using data from all CLSA wetlands. Since overall between wetland beta-diversity would be expected to decrease as the number of wetlands used in the analysis are reduced, we chose not to compare total beta diversity by hydroclimatic period.

Our second form of biotic homogenization explored was within-wetland biotic homogenization over time, i.e., the reduction of between year beta-diversity in aquatic macroinvertebrate communities for each individual wetland. We analyzed within-wetland homogenization using the *beta.temp* function from the ‘betapart’ package (Baslega et al., 2018). Using Sorensen Index based dissimilarities on our presence/absence matrix, we partitioned between year mean annual beta diversity for each sampled wetland into three beta-diversity coefficients: (1) Sorensen’s coefficient for total between-year beta diversity, (2) Simpson’s coefficient, for between-year turnover, and (3) the nestedness coefficient, for the between-year nestedness. For this analysis we removed the sampling period 1992 since only two wetlands contained water during this exceptionally dry year. We plotted total beta-diversity, turnover, and nestedness over the 23-year period. Using an ANOVA, we then compared the average between year total beta-diversity, turnover, and nestedness for all CLSA wetlands by regime (T-Wetlands, P-Wetlands, OB-Wetlands).

To better understand the potential patterns of an individual wetland's contribution to diversity, we portioned our overall spatio-temporal beta-diversity into individual points in time. To do this we used Local Contributions to Beta Diversity (LCBD) analyses (Legendre and De Cáceres, 2013) to identify which wetland-by-year combination contributed significantly to either degraded or enhanced diversity. The indices derived from LCBD analysis are comparative indicators of how compositional uniqueness of taxa of sites by year contribute to overall beta-diversity (Legendre and De Cáceres, 2013). The LCBD values are the squared distances of a site to the data centroid (Legendre, 2014). We used the *beta.div* function in the 'adespatial' package (Dray et al., 2016) using Sorensen Index based dissimilarities to compute LCBD scores for each wetland and used a permutation test based on 1000 permutations to identify which site by year aquatic macroinvertebrates communities were significantly different in taxonomical composition to the mean. We used an ANOVA to test if mean LCBD scores were significantly different depending on hydrologic regime and hydroclimatic period.

One of the common patterns in biotic homogenization is the replacement of specialist or endemic taxa with more ubiquitous, and sometimes, non-native taxa. Even though our understanding of what taxa are generalist or non-native to prairie potholes is limited, the replacement of taxa resulting in differing aquatic-macroinvertebrate communities over time can reveal patterns that are potentially relevant to the process of biotic homogenization. Thus, in addition to analysis of beta-diversity we explored potential compositional shifts of aquatic macroinvertebrate taxa over time by analyzing how specific taxa compositions have changed. We used non-metric multidimensional scaling (NMDS) to graphically display changes in CLSA wetland macroinvertebrate community composition for the different hydrologic regimes and hydroclimatic periods. Our NMDS model was created using the *metamds* function in the 'vegan' package (Oksanen et al., 2015), in which we used Sorensen Index based dissimilarities on our aquatic-macroinvertebrate presence/absence matrix. We plotted each wetland by years' location on the first two NMDS axes and highlighted both the hydrologic regime and hydroclimatic period to visually observe their aquatic-macroinvertebrate communities in two-dimensional space. To evaluate whether aquatic-macroinvertebrate community compositions differed by hydrologic regime or hydroclimatic period, we ran a PERMANOVA using the *Adonis* function in the 'vegan' package (Stevens and Oksanen, 2012).

In addition to the NMDS model we used a hierarchical clustering approach to create groups of sample units (communities) of similar species composition to compare their distributions by wetland regime category over time. Wetlands were clustered by species composition using the Ward clustering technique. We created a distance matrix based on Sorensen Index based dissimilarities with the *vegdist* function in the 'vegan' package using the aquatic macroinvertebrate presence/absence matrix for the years 1992 to 2015 and used the *hclust* function in the 'stats' package to create a cluster dendrogram (Murtagh et al., 2014). The cluster dendrogram was then pruned into groups, with number of groups being selected by the combination of how many sample units a cluster and identifying unique branches from the dendrogram while keeping a limited number of unique clusters. We used the *Indval* function from the 'labdsv' package (Roberts, 2016) to run an indicator species analysis and detect taxa that are significantly associated with the selected clusters. We then plotted the number of wetlands belonging to each wetland by regime category over time.

5.4. Results

5.4.1. Environmental Changes

As previously shown in McKenna et al. (2017), we found CLSA wetlands shifted towards having increased extent, depth, and open water after 1993 compared to the period between 1979 and 1993 (Fig. 5.2). The combination of year, wetland regime, and time period all significantly influenced variation in ponded-water depth, percentage of the wetland basin that was ponded, and the percentage of the wetland delineated as open water (Appendix B, Tables B.1–3). The percentage of a basin that was ponded and the percentage of a basin that was delineated as open water for T- P-, and OB-Wetlands all had dynamic and temporally coherent oscillations of wetting and drying periods (Fig. 5.2). However, post-1993 water levels in T-wetlands continued to cycle between wet and dry, while in P-Wetlands water levels increased and vegetation-zone extent decreased and then remained relatively stable over time, while (Fig. 2). The depth-constrained OB-Wetlands typically had less open-water due to increased area for emergent vegetation to establish and were very stable in the amount of open-water during the "filling period" and "post-filling period" periods compared to both T-and P-Wetlands. The primary difference in hydrologic conditions between the "filling-period" and "post-filling period" was that T-Wetlands continued to cycle between ponded and dry, while P and OB Wetlands remained permanently ponded in more lake-like conditions (Fig. 5.2).

5.4.2. Total Beta Diversity Trends

Our analysis of total Sorensen Index based dissimilarity between each wetland at a given year did not indicate a consistent increase or decrease of mean total beta-diversity over time (Fig. 5.3). The between-wetland dissimilarity values were typically high (>0.7) throughout the duration of the study (Appendix B, Table B.4). Throughout the analyzed time period, most of the beta-diversity was a product of turnover of aquatic-macroinvertebrate taxa between wetlands (Fig 5.3). The "filling-period" between 1993 and 1999 actually had lower mean annual between-wetland beta-diversity when compared to the "post-filling period" period that occurred between 2000 and 2015. This result was unsurprising considering all the wetlands were dry during a portion of the year 1992 and rapidly begin to fill during the following six years (Fig. 5. 2) when they were likely being colonized by the many of the same aquatic macroinvertebrates that were either rapid dispersers or can withstand periodic drying events. During the "post-filling period" period there was greater overall variability in mean total annual beta-diversity as well as the nestedness as turnover components of the overall beta-diversity (Fig. 5.3). While P-Wetlands and OB-Wetlands had reduced hydrologic variability during the "post-filling period" period, they also exhibited very different temporal hydrologic characteristics then the T-Wetlands during this period compared to the "filling-period". Therefore, this greater difference in hydrologic characteristics between hydrologic regimes during the "post-filling period" period could have been a mechanism for overall greater beta-diversity in the CLSA complex.

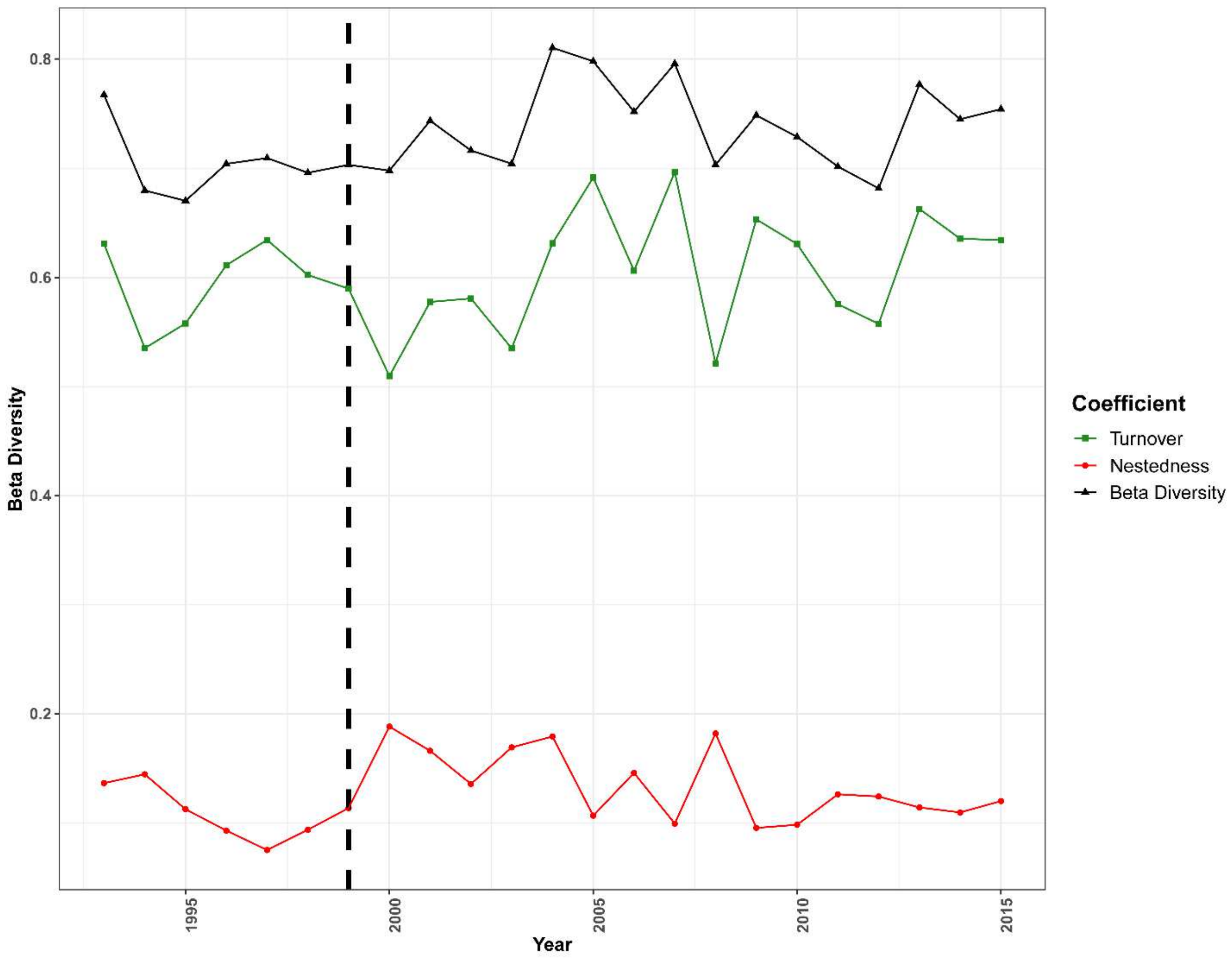

Figure 5.3. Mean annual between-wetland-by-year Sorensen Index based dissimilarities derived from aquatic-macroinvertebrate presences and absences for all 16 sampled Cottonwood Lake Study Area Wetlands beginning in 1993 and ending in 2015. Each unique color by shape combination connected by a solid line represents a different component of beta-diversity; (1) the green squares represent the proportion of mean annual beta diversity that was attributed to turnover (Simpson's Coefficient), (2) the red circles represent the proportion of mean annual beta diversity that was attributed to nestedness (Nestedness Coefficient), and the black triangles represent the mean between-wetland total beta diversity value per year (Sorensen's Coefficient). The vertically oriented black dashed line indicates the transition from the "filling-period" (1993–1999) to the "post-filling period" (2000–2015) on the x-axis.

5.4.3. Temporal Turnover of Beta-Diversity

Overall, our analysis within-wetland, between-year beta-diversity did not reveal any linear patterns of consistent increases or decreases of total-beta-diversity, turnover, or nestedness over time (Fig. 5.4). Like the between-wetland analysis of beta diversity, the within-wetland beta diversity was mostly driven by changes in turnover compared to nestedness (Fig. 5.4a and b).

However, overall variance of total beta diversity was significantly different for wetlands in the “filling-period” and “post-filling period” period (Fig. 5.4c, Table 5.1). The wetlands with the greatest amount of hydrologic variability over time (i.e., T-Wetlands) did have significantly higher amounts of between year beta-diversity (Fig. 4c, Table 5.1). Therefore, we cannot completely reject or support our hypothesis that reduced hydrologic variability in an individual wetland over time would lead to reduce between year beta-diversity in an individual wetland over time.

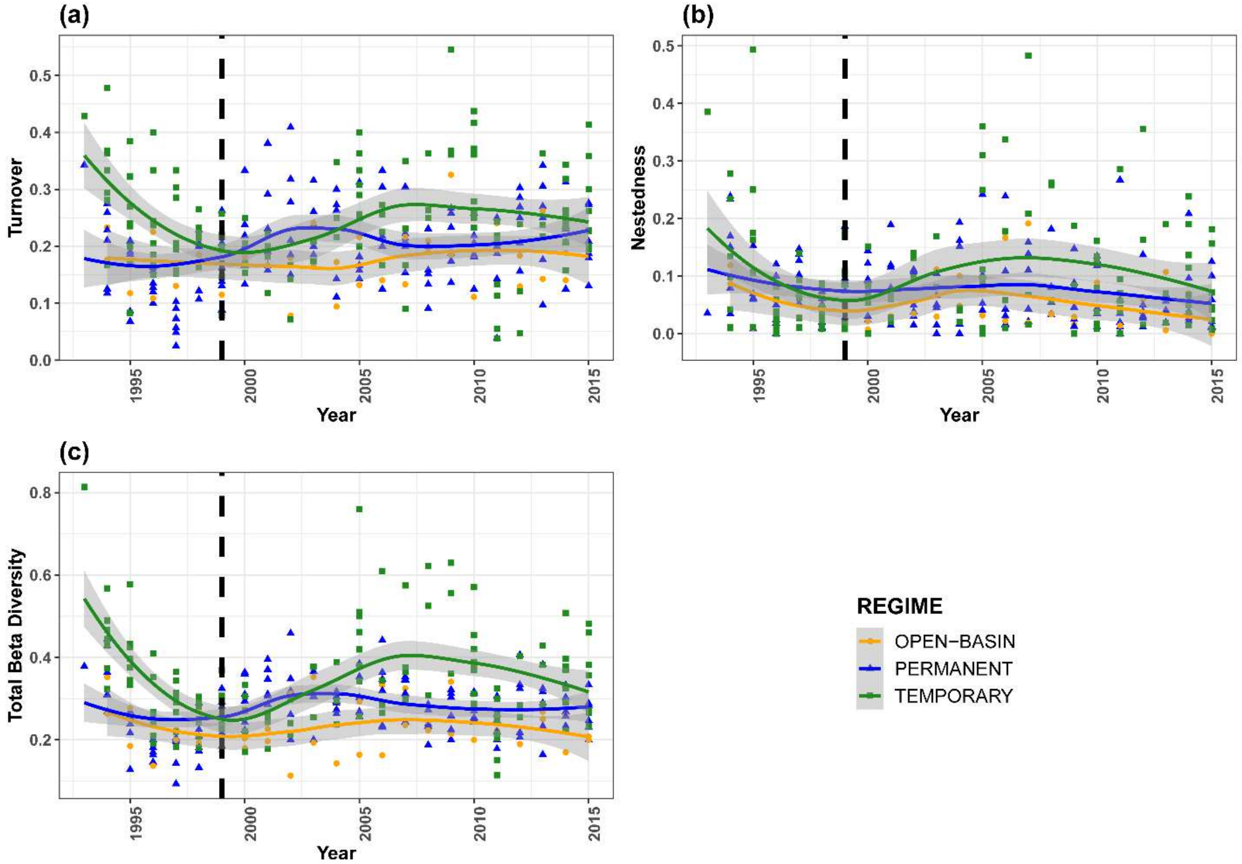

Figure 5.4. Mean annual between-year Sorensen Index based dissimilarities based on aquatic macroinvertebrate presences and absences for all 16 sampled Cottonwood Lake Study Area Wetlands beginning in 1993 and ending in 2015. Each plot represents a different component of between year within-wetland beta-diversity; (a) the proportion of mean annual between-year, within-wetland total-beta diversity that was attributed to turnover (Simpson's Coefficient), (b) the proportion of mean annual between-year, within-wetland total-beta diversity that was attributed to nestedness (Nestedness Coefficient), and (c) the mean annual between-year, within-wetland beta diversity value (Sorensen's Coefficient).The solid lines represent fitted means for wetlands by hydrological regime. The grey shaded areas represent 95% confidence-intervals for each fitted regression line. The black dashed line indicates the transition from the "filling-period" (1993–1999) to the "post-filling period" (2000–2015).

Table 5.1. Results of ANOVA model “Sørensen’s Coefficient~ Regime +Hydroclimatic Period + Regime: Hydroclimatic Period” evaluating the differences in variability of Sørensen’s Index based dissimilarities between wetland hydrological regime (P-Wetland, T-Wetland, and OB-Wetland) and hydroclimatic period (“Filling Period”, “Post Filling Period”) for 16 wetlands in the Cottonwood Lake Study Area in Stutsman, County, North Dakota sampled from 1993 to 2015.

	Degrees of Freedom	Sums Squares	Mean Squares	F-Value	Pr(>F)
Regime	2	0.5321	0.26607	31.283	4.65e-13
Hydroclimatic Period	1	0.0511	0.05112	6.010	0.0148
Regime: Period	2	0.0278	0.01391	1.636	0.1965
Residuals	298	2.5345	0.00851		

Table 5.2. Results of ANOVA model “LCBD~ Regime +Hydrologic Period + Regime: Hydroclimatic Period” evaluating the differences in variability of Sørensen’s Index based local contribution to beta diversity values between wetland hydrological regime (P-Wetland, T-Wetland, and OB-Wetland) and hydroclimatic period (“Filling Period”, “Post Filling Period”) for 16 wetlands in the Cottonwood Lake Study Area in Stutsman, County, North Dakota sampled from 1993 to 2015.

	Degrees of Freedom	Sums Squares	Mean Squares	F-Value	Pr(>F)
Regime	2	1.642e-05	8.212e-06	12.328	6.8e-06
Hydroclimatic Period	1	1.570e-06	1.566e-06	2.351	0.1261
Regime: Period	2	5.730e-06	2.864e-06	4.300	0.0143
Residuals	337	2.245e-04	6.660e-07		

Table 5.3. Results of PERMANOVA model "Sorensen Dissimilarity Matrix~ Regime +Hydroclimatic Period + Regime: Hydroclimatic Period" based on 999 permutations evaluating the differences in variability of Sørensen's Index based dissimilarities between wetland hydrological regime (P-Wetland, T-Wetland, and OB-Wetland) and hydroclimatic period ("Filling Period", "Post Filling Period") for 16 wetlands in the Cottonwood Lake Study Area in Stutsman, County, North Dakota sampled from 1993 to 2015.

	Degrees Freedom	Sums Squares	Mean Squares	F-Value	R^2	Pr(>F)
Regime	2	6.602	3.3012	41.597	0.18	<0.001
Hydroclimatic Period	1	2.955	2.9552	37.237	0.08	<0.001
Regime: Period	2	0.962	0.4808	6.058	0.02	<0.001
Residuals	337	26.745	0.0794		0.72	

5.4.4. Contribution of Individual Wetlands to Beta Diversity

Our analysis of temporal variability of an individual wetland's LCBD was to complement our overall between-wetland mean annual beta-diversity analysis by partitioning the beta-diversity into individual wetlands. The LCBD analysis did reveal temporal patterns in each wetland's unique contribution to beta diversity (Fig. 5.5; Table 5.2; Appendix B, Fig. B.1). During the "filling-period", T-Wetlands declined in mean LCBD scores, while P-Wetland and OB-Wetlands remained fairly constant (Fig. 5.5). Then in the "post-filling period" period T-Wetlands and P-Wetlands showed a hump shaped mean in LCBD scores where the gradually increased and decreased, while the OB-Wetlands remained fairly constant. Our ANOVA model indicated that variation of LCBD scores differed by hydrologic regime, and that hydrologic regimes differed in LCBD score variation in the different hydroclimatic periods (Table 5.2). We found that when ponded, the T-Wetlands were more likely to host significantly unique taxonomical community compositions. Our LCBD values per wetland by year plot revealed that after the year 2000, T-Wetlands were more likely to have LCBD values that were statistically greater than the mean (P-Value <0.05), indicating aquatic-macroinvertebrate communities in these wetlands were more distinct in taxonomical composition relative to the "average" aquatic-macroinvertebrate composition over the duration of the study. The P-Wetlands appear to increase in LCBD values between 1995 and 2005 but decrease from 2005 to 2015 (Fig. 5.5).

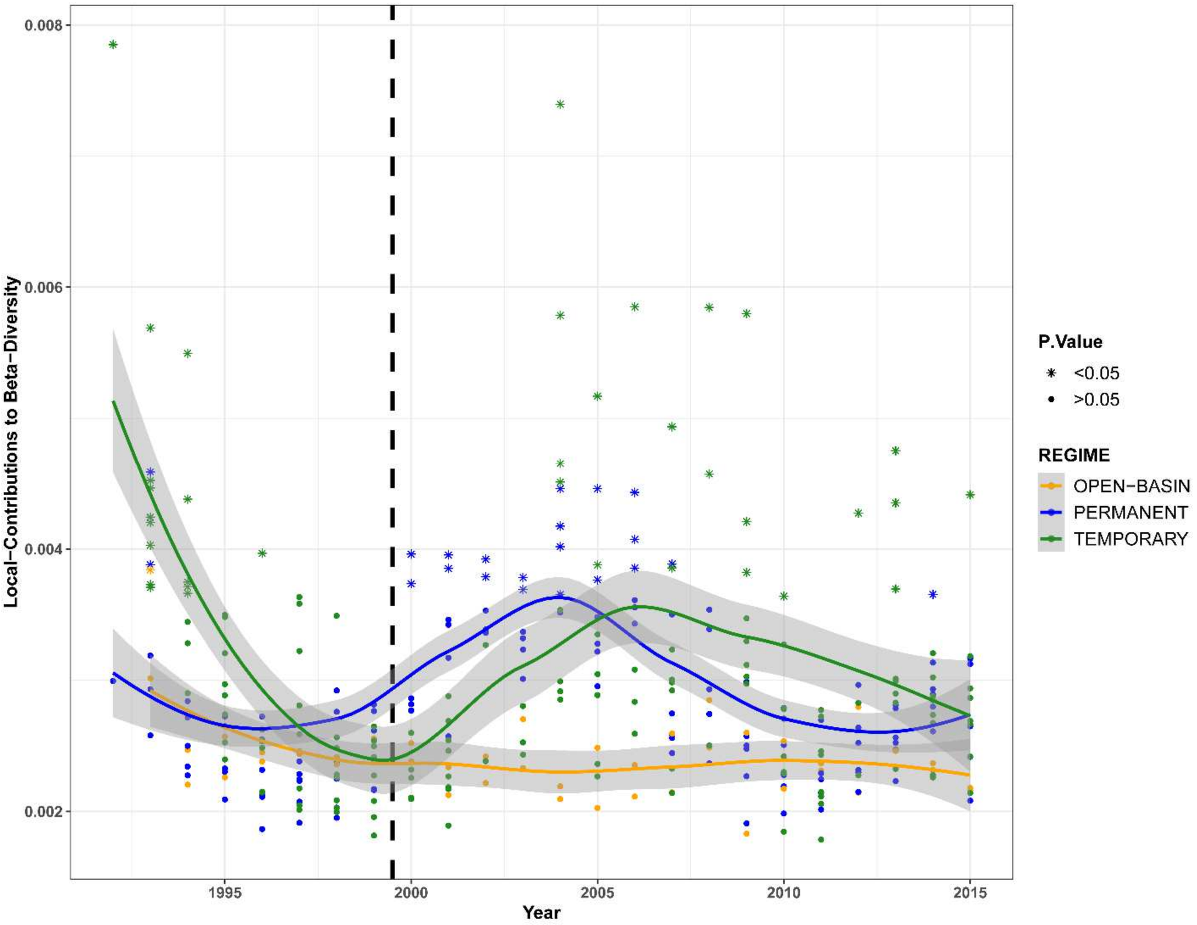

Figure 5.5. Temporal trends of Sorensen Index dissimilarity based Local Contributions to Beta Diversity (LCBD) values derived from the presence/absence-based aquatic-macroinvertebrate compositions for Cottonwood Lake Study Area wetland (n = 16) by year (n = 23) combinations plotted from 1993 to 2015. The y-axis represents the LCBD values, which are the partitioned amount of beta-diversity that a single wetland in a single year contributes to the overall beta-diversity observed in the study. Green points represent temporarily ponded wetlands (T-Wetlands), blue points represent permanently ponded wetlands with closed basins (P-Wetlands), and orange points represent permanently ponded wetlands with an open basin (OB-Wetland). Wetland-by-year combinations with LCBD values that were significantly greater than mean LCBD values (alpha\0.05) are indicated by solid asterisks. Sites with LCBD values not significantly greater than overall mean LCBD values are indicated by solid circles. The solid lines represent fitted mean LCBD values for wetlands by hydrological regime. The gray-shaded areas represent 95% confidence intervals for each fitted regression line. The black dashed line indicates the transition from the ''filling period'' (1993–1999) to the ''postfilling period'' (2000–2015)

5.4.5. Aquatic-Macroinvertebrate Community Shifts Over Time

Our NMDS analysis based on Sorensen's Index based dissimilarities of aquatic macroinvertebrate compositions using our presence-absence matrix yielded a three-dimensional solution with a stress of 0.15. Since most of the variation is found in the first two axis, we only plotted site scores on the first two axis (Fig. 5.6). The NMDS plot and complementary PERMANOVA showed wetlands varied by regime and hydroclimatic period, and that hydrologic regime explained the greatest amount of variation in the Sorensen's Index based dissimilarity matrix (Fig. 5.6, Table 5.3), Typically, T-Wetlands were ordinated towards the left, OB-Wetlands towards the center, and P-Wetlands towards the right on Axis 1. There was a lot of overlap among wetlands of different regime categories during the early "filling period" period, and reduced overlap during the "post-filling" period when a majority of the P-Wetlands shifted to the right side of the Axis 1 and towards the bottom of Axis 2, indicating a shift in aquatic macroinvertebrate composition (Fig. 5.6).

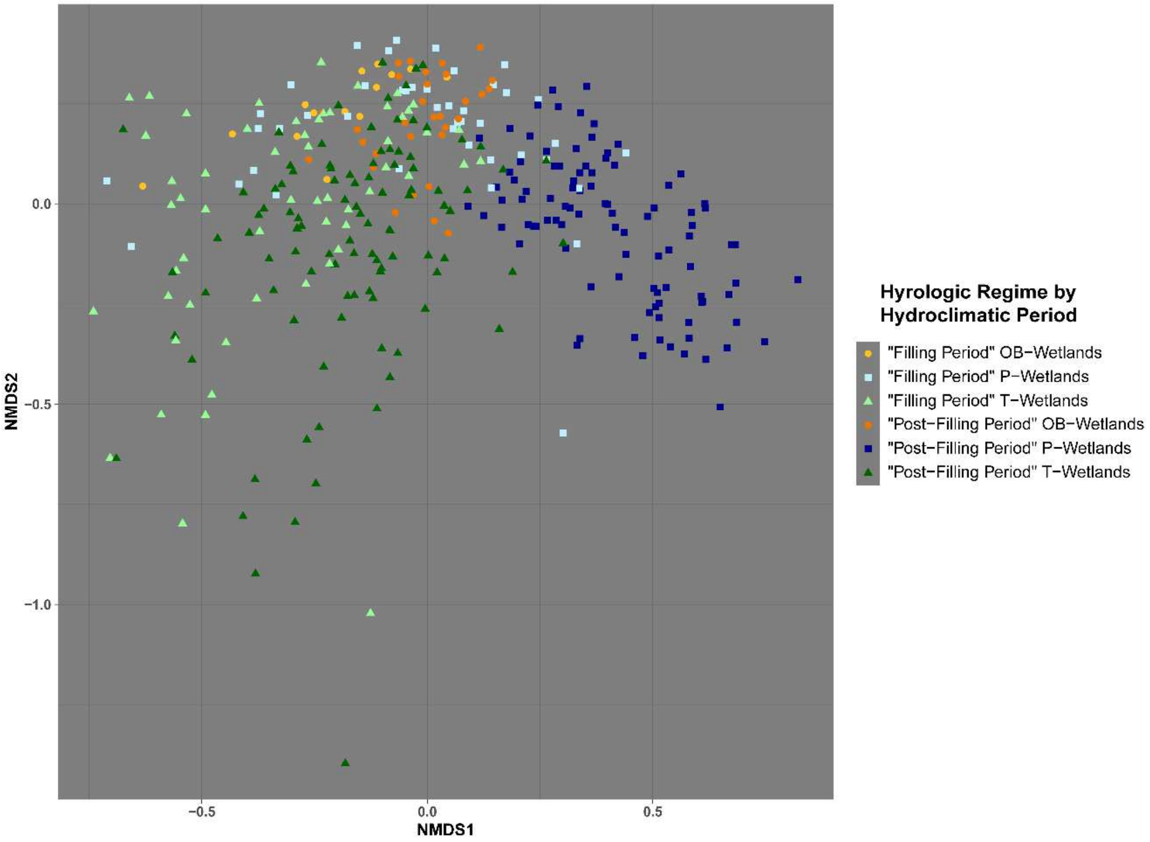

Figure 5.6. Nonmetric multidimensional scaling ordination (k = 3, stress = 0.15) analyzed from Sorensen's Index based dissimilarities of presence/absence based aquatic macroinvertebrate taxonomic compositions for Cottonwood Lake Study Area wetland (n=16) by year (n=23) combinations. Hydrologic regime by hydroclimatic period categories were indicated by unique color by shape combinations. Open basin wetlands (OB-Wetlands) during the "filling period" (1993–1999) are indicated by golden circles, open basin wetlands during the "post-filling period" (2000–2015) are indicated by dark orange circles, permanently ponded wetlands (P-Wetlands) during the "filling period" (1993-1999) are indicated by light-blue squares, permanently ponded wetlands during the "post-filling period" (2000-2015) are indicated by dark blue squares, temporarily ponded wetland (T-Wetlands) during the "filling period" (1993-1999) are indicated by light-green triangles, and temporarily ponded wetlands during the "post-filling period" (2000-2015) are indicated by forest-green triangles.

Our cluster analysis revealed three clusters that were visually divergent in aquatic macroinvertebrate community composition and evenness of sample units (Fig. 5.7, Clusters 1–3, N=163, 84, and 96, respectively). Indicator species analysis revealed that each of the three clusters had unique, statistically significant, indicator taxa with indicator values greater than or equal to 0.4 (0–1 scale, Table 5.4). The indicator values for cluster 1 were highest for the mosquito genera *Culiseta* and *Aedes*, the moss bladder snail (*Aplexa hypnorum*), *Eubranchipus bundyi* (a fairy shrimp), and *Eubranchipus ornatus* (a fairy shrimp), which are all typically associated with wetlands with shorter hydroperiods (Den Hartog and Wolf, 1962 ; Cvancara, 1983; Chase and Knight, 2003; Silver et al., 2011; Libonatti and Ruta, 2018). Cluster number 2 had the greatest number of significant indicator taxa, most of which are indicative of clear, highly vegetated waters (Table 5.4; Cvancara, 1983; Thorp and Covich, 200;). The significant indicator taxa for cluster number 3 were *Dasycorixa rawsoni* (a water boatman), *Physa gyrina* (pond snail), and the family Sphaeriidae (fingernail clams), which are all typically associated with semi-permanent or permanently ponded environments (Cvancara, 1983; Thorp and Covich, 2009).

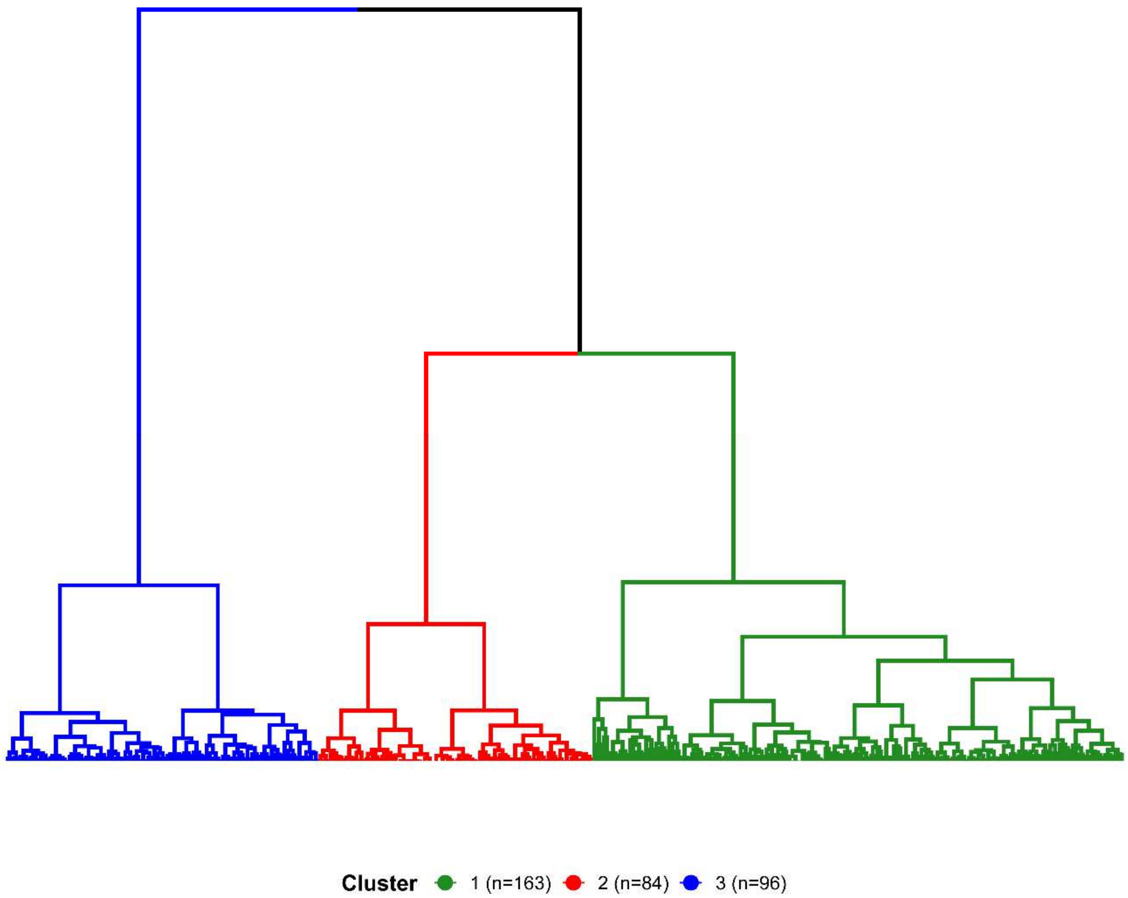

Figure 5.7. Dendrogram representation of Ward's method of cluster analysis of Sorensen's Index dissimilarities of presence/absence based aquatic macroinvertebrate taxonomic compositions for Cottonwood Lake Study Area wetland (n=16) by year (n=23) combinations. The dendrogram was pruned to three unique clusters, that are indicated by differently colored branches. Cluster number 1 (n=163) is represented by green branches, cluster 2 (n=84) by red branches, and cluster 3 (n=96) by blue branches.

Table 5.4. Indicator values of aquatic macroinvertebrate species belonging to cluster-derived aquatic macroinvertebrate species communities from Cottonwood Lake Study Area wetlands between 1992 and 2015. Clusters based on Ward's method of cluster analysis of Sorensen's Index dissimilarities of presence/absence based aquatic macroinvertebrate taxonomic compositions for Cottonwood Lake Study Area wetland (n=16) by year (n=23) combinations.

Taxon	Common Name	Cluster 1 N=118	Cluster 2 N=95	Cluster 3 N=26
Aedes	Mosquito	0.64		
Culiseta	Mosquito	0.61		
Aplexa hypnorum	Moss Bladder Snail	0.52		
Eubranchipus bundyi	Knobbedlip Fairy Shrimp	0.45		
Eubranchipus ornatus	Ornate Fairy Shrimp	0.40		
Cymatia	Water Boatman		0.79	
Peltodytes	Crawling Water Beetle		0.76	
Caenis	Squaregilled Mayfly		0.75	
Ilybius fraterculus	Predaceous Diving Beetle		0.71	
Zygoptera	Damselfly		0.65	
Helisoma trivolvis	Marsh Ram's Horn Snail		0.62	
Aeshna	Mosaic Darners		0.60	
Gyrinus	Whirligig beetle		0.58	
Limnephilidae	Northern Caddisfly		0.49	
Glossiphonia	Leach		0.42	
Anax	Dragonfly		0.41	
Dasycorixa rawsoni	Water Boatman			0.78
Physa gyrina	Pond Snail			0.47
Sphareiidae	Fingernail Clam			0.42

Our plots detailing the number of wetlands by regime belonging to each cluster revealed that the first cluster was associated primarily with T-Wetlands and OB-Wetlands, while cluster two had a high frequency of occurrence in all regime categories until the year 2002, when only T-Wetlands and OB-Wetlands were grouped into the cluster (Fig. 5.8). The P-Wetlands changed in cluster representation over time, during the first two years, most of the P-Wetlands shifted from cluster 1 to cluster 2, and by 2002 all had shifted to cluster 3 and remained there throughout the remainder of the study (Fig. 5.8**)**. The only P-Wetland that occurred in cluster 3 prior to 1999 was P-11, the only CLSA wetland originally classified as a Class V, permanently ponded wetland. The T-Wetlands and OB-Wetlands often cycled between being part of clusters 1 and 2, except from 2002–2004 when one of the T-Wetlands (T-3) belonged to cluster number 3 (Fig.

5.8). This is also the period when ponded water from one of the P-Wetlands (P-1) was merged with T-3. Over time P-Wetlands experienced a shift to more permanent and stable water regimes that was reflected by an increase in their frequency in cluster membership associated with lacustrine communities (Fig. 2, Fig. 8). During the early portion of the study, except for Wetland P-11, P-Wetland aquatic macroinvertebrates communities were grouped into cluster 1 much like the T-Wetlands and OB-Wetlands. However, they shifted from cluster 1 to cluster 2 in 1995 and remained there until 2001, and then shifted to cluster 3 in 2002 (Fig. 5.8).

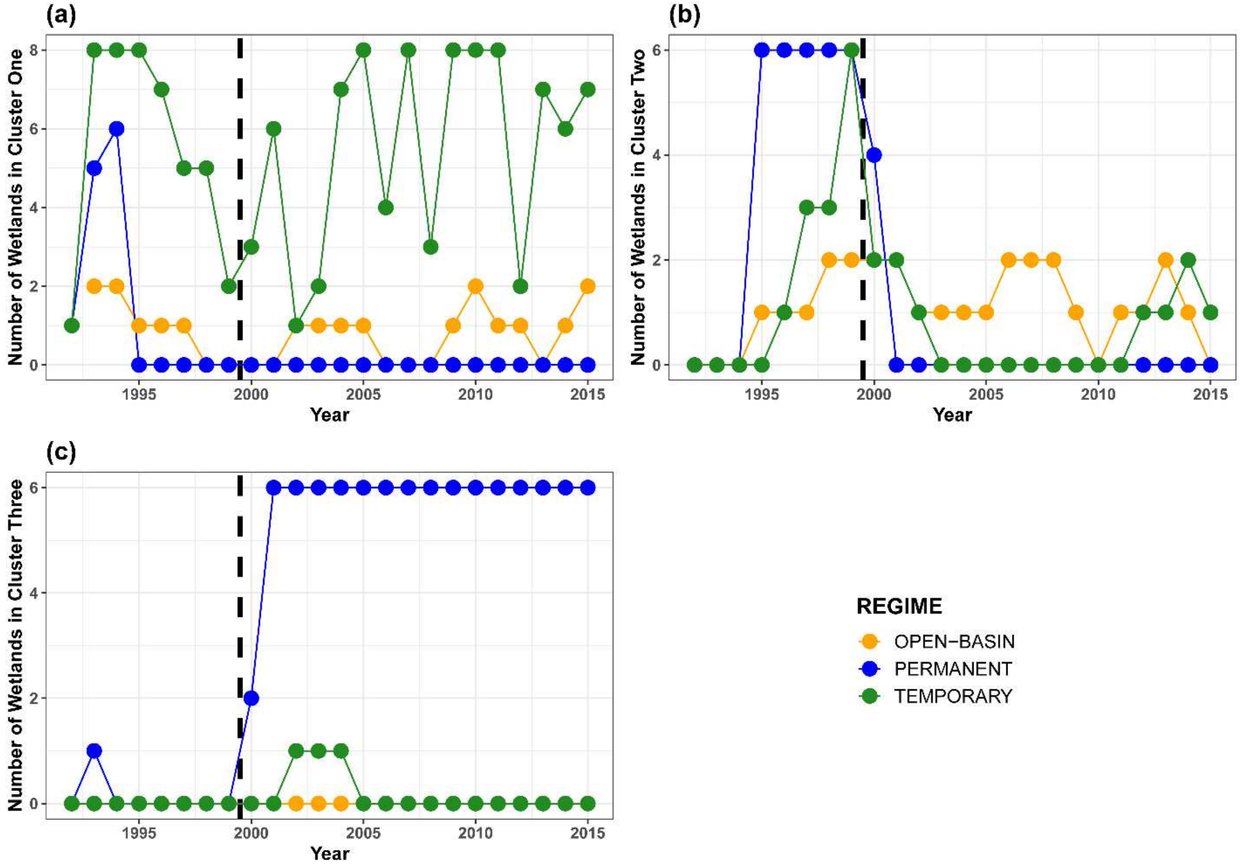

Figure 5.8. Scatterplot indicating the number of Cottonwood Lake Study Area wetland (n=16) by year (n=23) combinations belonging to (**a**) cluster 1, (**b**), cluster 2, and (**c**) cluster 3 of Ward's method of cluster analysis of Sorensen's Index dissimilarities of presence/absence based aquatic macroinvertebrate taxonomic compositions during the years 1992 to 2015. Each unique point by color combination represents the hydrological regime category for each wetland. The black dashed line indicates the transition from the "filling-period" (1993–1999) to the "post-filling period" (2000–2015).

5.5. Discussion

We found that within the relatively undisturbed confines of the CLSA, that hosts a variety of different sized wetland basins, there was no long-term pattern of reduced beta-diversity. However, if beta-diversity and hydrologic variability patterns observed at the CLSA are comparable to the surrounding more modified portions of the prairie-pothole region, there might be a greater concern for biotic homogenization on the landscape. We found that the T-Wetlands had more temporally variable hydrologic regimes, more temporal turnover of beta-diversity, greater contributions to overall beta-diversity during the study and occupied a larger but unique gradient of our NMDS ordination compared to the more hydrologically stable P-Wetlands and OB-Wetlands. Considering that approximately 60–65% of prairie-potholes have been drained (Dahl, 2014), and a disproportionate number of those wetlands are smaller more temporarily ponded basins (Serran and Creed, 2015), then the assumed loss of these smaller wetlands would result in a loss of unique aquatic-macroinvertebrate communities and subsequent decreases in total beta-diversity from portions of the landscape. Since all closed basin P-Wetlands shifted to more lake-like systems during this study and T-Wetlands continued to cycle between ponded and dry, the aquatic-macroinvertebrate community type we categorized as typically associated with temporarily-ponded or shallow, highly-vegetated wetlands were no longer present during the latter portion of the study (Fig. 5.8). In addition to the loss of smaller wetland basins, many PPR studies have also indicated that semi-permanent type wetlands are shifting to deeper, lake-like wetlands throughout a large portion of the PPR (Ballard et al., 2014; Hayashi et al., 2016; Cressey et al., 2016). Our cluster frequency analysis and NMDS analysis indicate that this hydrologic shift towards more lacustrine water regimes could potentially result in a shift in aquatic-macroinvertebrate communities in these wetlands.

Even though the twenty-five-year dataset used to evaluate this temporal trend contains a longer temporal gradient than any other known aquatic macroinvertebrate study conducted in prairie-pothole wetlands, it begins in a year in which most of the wetland ponds were completely dry then immediately transitioned to a period of deluge (Winter and Rosenberry, 1998). The deluge caused the wetlands to rapidly increase in depth in the following five years before stabilizing at higher levels than previously present (Fig. 5.2). This does not capture the historical dynamic temporal variability of hydrological conditions in P-Wetlands, in which there were more frequent hydrological fluctuations. As a result, we cannot conclusively compare aquatic macroinvertebrates during historical, and arguably more "normal," hydrological regimes to their current state.

While we hypothesized that both between-wetland beta diversity and between-year beta diversity in individual wetlands would decrease when hydrologic characteristics between wetlands and between years become less variable, we observed a trend where P-Wetland exhibited the most beta-diversity during the early portion of the "post-filling period" period (2000–2006). We hypothesize that this might indicate a shift towards increases in stochastic assembly processes and biotic interactions that are intrinsic to each wetland and that can increase overall compositional dissimilarity, even in seemingly homogenous habitats. For example, many of the P-Wetlands had high turnover in the years 2001 and 2002 (Fig. 5.4). We hypothesize this change may be due to an iridovirus outbreak that decimated tiger salamander (*Ambystoma mavortium*) populations at CLSA in 2000 (Dooley, 2001). Tiger salamanders are the native top aquatic predators in these more permanently ponded systems and their presence can alter the abundance and composition of aquatic macroinvertebrates (Holomuzki et al., 1994; Benoy, 2008). Their abundances rapidly increased post-1993 and peaked in the year 2000 (Mushet and

Solensky, 2018). When the predatory salamander population collapsed following the viral outbreak in 2000, it allowed many aquatic macroinvertebrate populations to increase. This time frame also coincides with when P-Wetlands had the highest LCBD values (Fig 5; Appendix B, Fig B.1), indicating that beta-diversity in these wetlands was highest during those years.

While we were not surprised by the results of T-Wetlands having typically higher LCBD scores when ponded, the ecological mechanisms behind these results are less understood. When relating the results to hydrologic variability, the continuation of dynamic water regimes and fluctuating environmental conditions have likely made T-Wetland aquatic macroinvertebrate communities less susceptible to biotic homogenization. T-Wetlands did show a mean increase in ponded water, but they continued to fluctuate between wetting and drying phases, which resulted in fluctuations in the amount of the basin that was in open water vs. a vegetated marsh state. The frequent drying of T-Wetlands can result in periodic reshuffling of aquatic macroinvertebrate communities which would result in higher beta-diversity and resulting between wetland differentiation due to ecological drift. Another not mutually exclusive hypothesis is that the more temporally homogenous hydrologic characteristics in P-Wetlands and OB-Wetlands result in different in taxonomic compositions of macroinvertebrate communities between the more permanently ponded hydrologic regimes and the more temporarily ponded regimes. This is because there is likely a subset of taxa that either require period drying to complete their life-cycle so they only occurred in wetlands that periodically dry up and another subset of taxa that cannot tolerate desiccation (Gleason and Rooney, 2018). This is supported by the patterns in our NMDS ordination (Fig 6) and cluster representation (Fig. 5.8, Table 5.4). Using natural history characteristics of indicator taxa from the first cluster, we can arguably categorize this cluster as the temporarily-ponded wetland macroinvertebrate communities. Mosquitos typically have short larval life cycles and flying adults can colonize and disperse to newly ponded wetlands; their survival in wetlands that dry periodically is typically much higher than in those that remain ponded (Chase and Knight 2003). The moss bladder snail (*Aplexa hypnorum*) is typically only found in temporarily ponded wetlands; the eggs and larval stages of this snail are freeze-and-desiccation tolerant (Den Hartog and Wolf, 1962). The knobbedlipped fairy shrimp (*Eubranchipus bundyi*) deposits eggs in dry wetland basins and will rapidly hatch after seven days post-thaw in the spring, allowing them to persist under very limited ponding periods (Dabron, 1976). Cluster number two contains a diverse combination of insects and crustaceans that can occupy a wide gradient of hydrologic regimes, and many of these taxa are associated with emergent or submergent vegetation characteristic of semi-permanent wetlands (Thorp and Covich, 2009). Cluster 3 captures the more permanently ponded or lake-like wetland macroinvertebrate community. The strongest indicator was Dasycorixa *rawsoni* (a water boatman). This species is associated with permanently-ponded waterbodies and were first observed in the CLSA in 1998 and 1999. They subsequently became extremely numerous in relative abundance in the following years (Hanson et al., 2003; Mushet et al., 2018).

5.5.1. Importance of Temporarily Ponded Wetland Contributions to Biodiversity

There has been an observed disproportionate amount of smaller temporarily ponded wetlands that have lost hydrologic function on the landscape (Serran and Creed, 2015; van Meter and Basu, 2015). There has also been a potential loss of the unique aquatic macroinvertebrates associated with these systems. This potential loss of specialist taxa is concerning due to the widespread loss of temporary wetlands on the landscape and their continued susceptibility to climate change, drainage, and filling with sediments (Serran and Creed, 2015; Creed et al., 2017). The loss of temporally ponded wetlands has been an identified threat to fairy shrimp

(Anostraca) in wetland systems across the United States (Angeler et al., 2008). Fairy shrimp are important to breeding waterfowl in the region, especially during early spring since when they are among the first available invertebrates for consumption by arriving migratory waterfowl (Eldridge, 1990). A gadwall (*Mareca strepera*) diet study conducted in central North Dakota found that fairy shrimp comprised 2/3 of the pre-egg-laying diet and 33% of the full breeding-season diet of gadwall hens (Serie and Swanson, 1976). This preference was hypothesized to be a result of the high quantities and diversity of amino acids found in Anostracans (Serie and Swanson 1976).

5.5.2. Importance of Permanently Ponded Wetland Contributions to Biodiversity

When compared to wetlands of different hydrologic regimes, permanently ponded wetlands also contain uniquely adapted aquatic macroinvertebrate community compositions (Fig 6, Fig 8). During drought events that cause smaller wetland basins to dry these systems provide refugia to organisms that are not adapted to desiccation (Mushet et al. 2013). While larger more permanently ponded wetlands are less vulnerable to drainage, outside of protected areas such as the CLSA, many are still vulnerable to anthropogenic degradation such as increased nutrients inputs, chemicals, and sedimentation due to runoff (Gleason and Euliss, 1998; Guntenspergen, 2002; Main et al. 2014). The contemporary hydrologic shift towards deeper and less saline systems (Mushet et al., 2015; Cressey et al., 2016) is believed to have facilitated an increase in the distribution of fish in previously fishless habitats which in turn alter the resident biotic communities (Zimmer et al., 2001; Zimmer et al., 2002; Hansen et al., 2005; Wiltermuth, 2014; McLean et al., 2016a). The invasion of fish into prairie potholes has had a negative impact on aquatic-macroinvertebrates in larger wetlands (Anteau and Afton, 2008, Anteau et al., 2011, Wiltermuth 2014, McLean et al., 2016b). In addition to fish directly altering aquatic macroinvertebrate abundance and distribution through competition and predation, the reduction in macroinvertebrates that feed on algae can promote algal blooms, causing a regime shift from a clear submergent vegetation state to a turbid eutrophic state, thus reducing aquatic macroinvertebrate habitat and trophic complexity (Scheffer and Jeppesen, 2007; Hanson and Butler, 1994). However, our understanding of taxa that were historically present in prairie potholes compared to more lacustrine systems of the PPR is limited by our lack of long-term distributional data for prairie-pothole biota.

5.6. Conclusions

Prairie-pothole wetlands occur in a highly modified landscape and are susceptible to land-use and climate changes. Historically, wetlands in the region were subjected to highly variable environmental conditions. In recent years, land-use modifications and climate change have resulted in less spatial and temporal variation in wetland ecosystems. These characteristics have likely facilitated some form of biotic homogenization; however, our ability to detect homogenization at larger spatial and temporal scales is challenged, as there are few long-term biomonitoring efforts in the region. We provided examples of how aquatic macroinvertebrate dynamics differ by ponded-water regimes. More information is needed to determine which prairie-pothole species are susceptible to replacement and their preferred habitats. It may also be important to understand the resiliency of the native biotic communities if prairie-pothole ponded-water dynamics were to return to their historical state. Since the macroinvertebrate communities of wetlands that typically dry appear to be more resistant to biotic homogenization, long-term maintenance of biodiversity in prairie-pothole complexes would require a priority being placed on the conservation and restoration of wetlands with temporally-ponded and seasonally-ponded water regimes on the PPR landscape.

5.7. Acknowledgements

We thank Darold Batzer and two anonymous individuals for providing their constructive reviews of our manuscript. Data from Cottonwood Lake Study Area wetlands are publicly available through the Missouri Coteau Wetland Ecosystem Observatory (https://www.sciencebase.gov/catalog/item/52f0ffd9e4b0f941aa181fc6) and maintained through funding received from the U.S. Geological Survey's Land Change Science Research and Development Program. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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CHAPTER 6. GENERAL CONCLUSIONS

6.1. Summary

Effective conservation and management of wetland habitats can benefit local and regional biodiversity. Prioritizing wetland conservation efforts that benefit landscape-level diversity is often dependent on our understanding of the influential processes that maintain biodiversity. The primary goal of my dissertation was to provide an increased understanding of the relative importance that spatial and temporal variability of ponded-water dynamics have on shaping community structure in wetland ecosystems.

In Chapter 2., I presented a literature review exploring how the additive and often synergistic effects of historical wetland loss, landcover changes, and climate-variability shifts have altered, and continue to alter, wetland heterogeneity in the Prairie Pothole Region. The preferential loss of smaller, more temporarily-ponded wetlands (van Meter and Basu 2015; Serran and Creed 2016) and a climate-driven ecohydrological state-shift exacerbated by changes in surrounding land use (McKenna et al., 2017, 2019) have resulted in a distributional shift towards larger and deeper wetland ponds (Kahara et al., 2009; Mushet et al., 2015; Cressey et al., 2016). The observed shifts in hydrologic variability in the Prairie Pothole Region have likely altered the distribution and composition of the aquatic-macroinvertebrate communities found in these systems.

For Chapter 3., I modeled environmental and biologic predictors of aquatic-macroinvertebrate community composition and found invertebrate composition to be strongly influenced by ponded-water dynamics. Specifically, the proportion of open water in a wetland had the greatest influence on invertebrate communities. Therefore, the shift toward more lake-like, open-water conditions observed in many larger wetlands in the PPR has likely resulted in a landscape-level shift in the regional composition of wetland macroinvertebrates.

In Chapter 4., I described my quantification of aquatic-macroinvertebrate communities with respect to wetland temporal coherence. My results indicated that the relative coherence of aquatic-macroinvertebrate communities varied by the community metric used, a wetland's hydrological regime, and the hydroclimatic variability of the analyzed time period. The temporal dynamics of the entire aquatic-macroinvertebrate population were dependent on a combination of both landscape-level controls and wetland heterogeneity. The high among-wetland synchrony observed in the compositional turnover of aquatic macroinvertebrates indicated that meta-community processes are especially important in these wetland ecosystems.

In Chapter 5., I quantified temporal changes in among-wetland and among-year, aquatic-macroinvertebrate beta diversity in the context of biotic homogenization. The reduced hydrologic variability over time observed in the larger, more permanently ponded wetlands (P-Wetlands) did not result in reduced beta diversity. However, there was a shift in community composition that differentiated the P-Wetlands from the smaller, more temporarily ponded wetlands (i.e., T-Wetlands). The T-Wetlands also contributed disproportionately to the overall beta diversity observed at the Cottonwood Lake Study Area, likely through the presence of specialist taxa in these smaller, more temporarily ponded wetlands.

6.2. Synthesis and Conservation Implications

Long-term monitoring data for wetland ecosystems is a rare and important resource. As humans continue to exacerbate the rate of environmental change, long-term monitoring data will continue to be an important component of environmental science and our best method for detecting patterns of environmental change, such as biodiversity loss (Lovett et al., 2007). The

Cottonwood Lake Study Area has uniquely contributed to our understanding of wetland hydrology and hydro-geochemistry (e.g., LaBaugh et al., 1987; Winter 2003; LaBaugh et al., 2018). The use of 24 years of aquatic-macroinvertebrate data in my research will further contribute to our understanding of wetland macroinvertebrate dynamics and prairie-pothole wetland ecosystems. The findings presented here also have implications for the conservation of wetland biodiversity.

The historical distributions and composition of communities, such as aquatic-macroinvertebrate communities, that inhabited prairie-pothole wetlands and other wetland systems of the U.S. Midwest are poorly understood (Jenkins et al., 2003). Historical wetland losses have disproportionately affected smaller, more temporarily ponded wetlands (Serran and Creed 2016), which continue to be most vulnerable to degradation (Creed et al., 2017). My findings and the findings of previous studies have indicated that these temporarily ponded wetlands host unique invertebrate communities and exhibit higher, among-wetland and among-year levels of beta diversity (Gleason and Rooney 2018; Daniel et al. 2019; McLean et al. 2019). Considering the importance of endemic communities in maintaining landscape biodiversity (Wilson et al. 2006), these small, vulnerable wetlands are of great conservation value (Calhoun et al., 2017).

The loss of among-wetland heterogeneity and the spatial homogenization of remaining wetlands also poses a risk to the region’s biodiversity (Van Meter Basu 2015; Serran and Creed 2016). The high spatial synchrony of aquatic-macroinvertebrate communities from the heterogenous wetlands observed in Chapter 4., indicate that landscape controls are an essential component of community assembly. It is likely that the metacommunity processes dependent on among-wetland linkages would erode in regions with widespread wetland losses and reduced spatial connectivity, resulting in fewer taxa over time. For example, the loss of smaller wetlands can reduce overall wetland connectivity by eliminating “stepping stones” between larger wetlands, which in turn limits rescue effects typically provided by connected metapopulations (Semlitsch and Bodie 2001). In the context of wetland biodiversity conservation strategies, additional research is needed at larger spatial scales to understand how land-use change influences biological community assembly processes in freshwater wetland ecosystems.

The observed increases in the duration and surface area of wetland ponds for much of the Prairie Pothole Region could also facilitate shifts towards novel ecosystems that might favor non-endemic taxa. Several new observations of more lacustrine invertebrate taxa occurring in the more permanently ponded wetlands have likely been a response to wetter hydroclimatic conditions (McLean et al. 2019). Fathead minnows (*Pimephales promelas*) and Yellow Perch (*Perca flavescens*) have also been introduced across the Prairie Pothole Region, including colonization of one of my studied wetlands, Wetland P-11 (McLean et al. 2019). While the mostly negative effects of fish on aquatic-invertebrate diversity is well established (Hanson et al. 2005), further study of aquatic-invertebrate community response to the simultaneous shift in climate and concurrent fish colonization is essential for evaluating the resiliency of wetland ecosystems. Especially, as the climate continues to shift in response to ever-increasing levels of greenhouse gasses in the atmosphere.

The key findings of my research support an increasingly common theme in wetland conservation, that is, wetland policy and conservation need to work in tandem to prioritize the preservation and restoration of heterogenous and well-connected wetland complexes (Bedford et al., 1999, Verheijen et al., 2018). In addition to among-wetland heterogeneity, conservation efforts should emphasize the preservation and restoration of smaller wetlands, which are often the most vulnerable to degradation and provide unique additions to regional biodiversity (Creed et al. 2017). An increased understanding of how wetland spatial connectivity and landscape linkages relate to meta-community processes would also benefit future conservation and restoration efforts (Gibbs 1993,2000; Semlitsch and Bodie 2001).

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APPENDIX A. LONG-TERM MULTIDECADAL DATA FROM A PRAIRIE-POTHOLE WETLAND COMPLEX REVEAL CONTROLS ON AQUATIC-MACROINVERTEBRATE COMMUNITIES [5]

A.1. Details of Variables Used in Structural Equation Modelling and Hypothesized Causal Relationships

1) *Wetland-basin elevation*

In the water-surface elevation data set from CLSA (Mushet et al., 2016a), the surface elevation of ponded-water in each wetland is recorded weekly during the ice-free portion of the year, typically April–October. In years when a wetland's pond dries completely, the elevation of the lowest point in the dry wetland basin is recorded. This lowest elevation can be subtracted from the water-surface elevation when a wetland is ponded to obtain the maximum water depth. We used these "lowest-point" elevations to define the elevation of each wetland basin relative to that of other wetlands at the site and to relate the wetland to its positioning along the relation-to-groundwater axis (the elevational axis as defined by Hayashi et al., [2016]) of the Wetland Continuum.

2) *Conductivity*

Euliss et al., (2004) also related the relation-to-groundwater axis to the accumulation of dissolved ions, i.e., salts. For prairie-pothole wetlands, conductivity measurements provide an accurate measure of salinity (Euliss et al., 2014). We used data of the electrical conductivity (EC) of ponded water (corrected to 25 °C) in each CLSA wetland (Mushet et al., 2016b) as a measure of salinity. Electrical-conductivity measurements are collected weekly for all wetlands

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[5] The supplementary information provided here is formatted for submission to the journal *Ecosystems* as a supplementary file to Chapter 3.

at CLSA during the ice-free portion of each year concurrent with the measurement of pond-surface elevations. Previous studies have identified EC as a reliable predictor of dissolved-ion concentrations in CLSA wetlands. From 1992–2007, EC measurements were made using an Orion Model 126 meter with an Orion Model 012210 conductivity measuring cell; from 2008–2015 measurements were made with a WTW Model 315i meter with a TetraCon® Model 325 conductivity measuring cell. We used the mean annual electrical-conductivity values for the years 1992–2015 as our measurement of ponded water EC.

3) *Proportion of wetland basin ponded*

To calculate the proportion of a wetland basin that was ponded, we used each wetland's average water-surface elevation (Mushet et al., 2016a) for the month of July and overlaid the elevation as a plane onto a digital elevation model (DEM) of the wetland complex (Mushet et al., 2017a) using ArcGIS. From this overlay, we calculated the area of the water-surface-elevation plane as a proportion of the area of a water-surface elevation plane from a date when the pond was at its maximum pool level for the period of record. Since ponded water in prairie-pothole wetlands comes mainly from runoff of snow-melt and precipitation (both inputs of atmospheric water), and the amount of precipitation that enters a wetland can vary depending on catchment characteristics (size, slope, upland cover), we assumed the proportion of a wetland basin that was ponded to be an indicator of a wetland's unique position along the atmospheric water (i.e., drought to deluge) axis of the Wetland Continuum.

4) *Proportion of open-water*

We used wetland vegetation-zone delineations from each CLSA wetland (Mushet et al., 2017b), 1992–2012, to quantify the percentage of open water in a wetland basin. While the proportion of a wetland basin that is ponded is likely to be correlated with the amount of open-water, depending on wetland basin characteristics (i.e., depth) and antecedent conditions the amount of open water can vary among wetlands. Wetland vegetation zones (wet meadow, shallow marsh, deep marsh, and open water) are delineated annually for all CLSA wetlands using aerial photographs of each wetland acquired during mid-summer using a digital camera at altitudes of photography ranging from 300 to 1,500 meters above-ground-level. Aerial photographs were georeferenced using computer databases and major vegetative zones delineated using ArcMap software (ESRI, 2011). From this data, we calculated the proportion of the wetland that was identified as open water, i.e., the total area of open water divided by the total area of all wetland zones. As with the proportion of a wetland basin ponded, we assumed the proportion of open water to be related to a wetland's position along the atmospheric-water axis of the Wetland Continuum.

5) *Predatory-salamander abundance*

Adult, paedomorphic, and larval tiger salamanders (*Ambystoma mavortium*) are primary predators of aquatic macroinvertebrates in prairie-pothole wetlands. To estimate potential predation pressure from these salamanders, we used July salamander abundance data from the CLSA (Mushet and Solensky, 2017). At the CLSA, all amphibians occurring in wetlands are sampled monthly from May–September using amphibian funnel traps (Mushet et al., 1997) placed in the central zone of each wetlands. Funnel traps are set on Monday mornings and checked each morning, Tuesday through Friday. Data collected consist of numbers of individuals, sex, and developmental stage (larval, paedomorph, adult) of animals caught per sampling effort. However, since salamander abundance peaks in July in these wetlands, we only used abundance data from the July survey as our yearly indicator of predation pressure from salamanders.

6) Predatory-macroinvertebrate biomass

There are many species of aquatic invertebrates inhabiting prairie-pothole wetlands that prey upon other invertebrates. Aquatic invertebrates are sampled monthly at all CLSA ponded wetlands from April–September. Recorded data include counts and biomass by taxa (lowest feasible resolution) and by trophic-function group (Mushet et al., 2017c, 2018). Aquatic invertebrates are sampled at CLSA using vertically oriented, funnel traps (Swanson 1978). Samples are collected from random locations within each vegetation zone along three transects in each wetland and processed in a U.S. Geological Survey laboratory in Jamestown, North Dakota. Processing consists of separating invertebrates from debris, identifying aquatic invertebrates (typically to genus), drying invertebrates to a constant weight at 60° C, and weighing dried invertebrates to obtain a biomass measurement (Mushet et al., 2018). Invertebrate taxa are then categorized into trophic-function groups (Thorp and Covich, 1991; Merritt et al., 1996), including "predators." We calculated the mean annual biomass of all aquatic invertebrates identified as predators per funnel trap for each wetland to obtain a measure of predation pressure from predatory invertebrates.

7) Non-predatory aquatic invertebrate biomass

We used the total biomass of non-predatory aquatic invertebrates in a wetland (Mushet et al., 2018) as a measure of conspecific competition. Thus, we calculated mean annual aquatic invertebrate biomass per funnel trap (see above under "predatory-invertebrate biomass" for collection methodology) by wetland and by year.

8) Aquatic macroinvertebrate counts by taxa

We used the aquatic invertebrate abundance data to perform our analysis of community composition (Mushet et al., 2017c). We summarized the data by calculating the mean annual abundance of aquatic invertebrates by taxa for each wetland. We used nonmetric multidimensional scaling (NMDS) as an ordination technique to reduce the dimensionality of the CLSA aquatic invertebrate abundance data from 155 unique taxa quantified in Mushet et al., (2017c) to a small number of meaningful axes defining communities. Since the distribution of aquatic invertebrate abundance can be highly variable among taxa, we log transformed the aquatic invertebrate data to help reduce the influence of especially abundant taxa in the NMDS model. Using Bray-Curtis based dissimilarities on the abundance data, we created the NMDS model using the *metamds* function in the 'vegan' R package (Oksanen et al., 2015). Derivation of final NMDS axes was determined by finding the lowest dimensional model solution with a usable mode fit which was determined by the model having a stress value <0.20 and a stress reduction < 0.50 when an additional dimension is added (Clarke, 1993; Peck, 2011) We then used the NMDS defined axes as dependent (i.e., endogenous) variables in our structural equation modeling efforts. Using NMDS in this way allowed us to relate aquatic macro-invertebrate measured data to a couple variables representing distinct gradients of community composition.

A.2. Hypothesized Causal Relationships

Past explorations into prairie-pothole wetland invertebrate dynamics indicate that community composition is determined by a combination of direct abiotic controls (i.e., ponded-water availability, salinity), habitat types (i.e., open-water, vegetated marsh), and biotic interactions such as competition for resources and predation (Table A.1). The relative importance of abiotic and biotic determinants can be predicted by interdependent linkages to the larger hydrologic system (i.e., surface water and groundwater flows). We predicted that a wetlands elevation relative to other wetland basins within the same hydrologic system can be used to estimate relative differences in groundwater and atmospheric water inputs and losses. Wetlands at higher elevations above the water table are often referred to as recharge wetland because they lose water through the soil, which recharges the groundwater (Winter and Rosenberry, 1995; Euliss et al., 2004). Wetlands at or below the water table function as discharge wetlands because they receive groundwater discharge. Wetlands near the water table elevation where they either recharge or discharge wetlands in response to change water table elevations function as flow-through wetlands (Euliss et al., 2004). In addition to determining a wetland's relationship to local groundwater tables, a wetland's relative elevation can also be an indicator of basin size, surface-water connectivity to neighboring wetlands, and pond-permanency (Hayashi et al., 2016). Wetlands at higher elevations typically have small basins and when these basins fill, water spills towards lower elevation basins (Leibowitz et al., 2016). Wetlands at lower elevations typically occur within larger basins, have greater surface-water connectivity to other wetlands, and have greater pond-permanency (Hayashi et al., 2016). While hydrogeologic setting can influence a wetlands sensitivity to climate, the temporal variability in water levels exhibited in prairie-pothole wetlands is mainly attributed to changes in precipitation and evaporation (McKenna et al., 2017). A wetland's relationship to atmospheric water is determined by the amount of precipitation falling on the landscape and how much of that water makes it into a wetland basin (Euliss et al., 2004; Hayashi et al., 2016). Precipitation driven runoff inputs can vary depending on catchment size, catchment slope, and surrounding upland cover (i.e., grass, bare soil, cropland), resulting in wetland ponds responding differently to precipitation (Renton et al., 2015; Hayashi et al., 2016). To capture both variability in climate and variability in runoff patterns into wetland basins, we used the proportion of a wetland basin ponded as our measure of a wetland's position along the atmospheric-water axis.

The spatially (elevation) and temporally (climate) driven variability in wetland hydrology can also influence habitat characteristics such as vegetation structure and salinity. For aquatic invertebrates, taxonomic compositional shifts occur between areas within a wetland dominated by emergent vegetation and those dominated by submergent vegetation or open water (Gleason et al., 2018). While the proportion of a wetland basin that is ponded contributes to the proportion of a wetland that is not vegetated (open-water), there are other processes that determine the relative proportion of open water in a wetland basin. As noted previously, wetlands at higher elevations typically have smaller catchments then nearby wetlands at lower elevations (Hayashi et al., 2016), and since water moves down elevation, when ponded; larger, deeper catchments would also have more open-water area and less emergent vegetation. Climate and elevation are also predicted to drive wetland salinity levels (Euliss et al., 2014). Groundwater can contain high amounts dissolved salts, therefore wetlands at lower elevations that receive groundwater also accumulate more salts (Euliss et al., 2004, 2014). While salts are expected to accumulate with increased groundwater flow into a wetland, the concentration of salts (salinity) is also variable depending on atmospheric water inputs or losses (i.e., dilution and concentration). While hydroperiod, salinity, and vegetation structure of a wetland is expected to directly influence aquatic invertebrate composition (Gleason and Rooney, 2018; Gleason et al., 2018; Preston et al., 2016; McLean et al., 2019), these environmental conditions also influence biotic processes such as predation and competition (Table A.1).

Biotic interactions are predicted to shift depending on hydrologic conditions. Typically, increased ponded-water permanence is associated with an increase in predatory invertebrates and vertebrates, such as tiger salamanders (Wissinger, 1999a, b; Chase and Knight, 2003; Swanson et al., 2003; Euliss et al., 2004). Larger more permanent wetland ponds are also expected to have increased competition among aquatic invertebrates (Corti et al., 1996; Chase and Knight, 2003; Whiles and Goldwitz, 2005; Silver et al., 2012). We predicted invertebrate community composition is influenced by ponded-water extent and duration (Silver et al., 2012; Gleason and Rooney, 2018; McLean et al., 2019), the amount of open-water habitat (Gleason et al., 2018), salinity (McLean et al., 2016), predatory invertebrates (Batzer and Wissinger, 1996; Wissinger et al., 1999b), tiger salamander abundance (Holomuzki et al., 1994; Wissinger et al., 1999a; Benoy, 2008), and competition (Williams, 1997; Chase and Knight, 2003; Elono et al., 2010).

Table A.1. Individual pathways examined in structural equation model, expected relationships between modeled variables, and source literature used to inform the expected relationships.

Pathway	Expected Relationship	Supporting Literature
Electrical Conductivity ~Elevation	Wetlands at lower relative elevations will receive more salts through groundwater discharge.	Euliss et al., 2004; Hayashi et al., 2016
Electrical Conductivity ~Proportion of Basin Ponded	The ratio of precipitation to evaporation cause dilution and concentration effects.	Euliss et al., 2004; Hayashi et al., 2016
Proportion of Basin Open Water ~Elevation	Basins at lower relative elevations within a hydrologic complex often have larger and deeper catchments that can limit emergent vegetation area.	Euliss et al., 2004; Hayashi et al., 2016
Proportion of Basin Open Water ~Proportion of Basin Ponded	The proportion of open-water area typically increases with ponded-water levels.	Kantrud et al., 1989; Winter, 2003; Euliss et al., 2004
Tiger Salamander Abundance ~Proportion of Basin Ponded	Tiger salamanders require wetlands ponds with longer hydroperiods (3-4months).	Deutschman and Peterka, 1988; Wissinger et al., 1999a; Winter, 2003; Euliss et al., 2004
Tiger Salamander Abundance ~Proportion of Basin Open Water	Tiger salamanders require wetland ponds with longer hydroperiods which is positively correlated with open-water area.	Deutschman and Peterka, 1988; Wissinger et al., 1999a; Winter, 2003; Euliss et al., 2004
Predatory Invertebrate Biomass ~Proportion of Basin Ponded	Predaceous invertebrate populations fluctuate along a pond-permanence gradient.	Wissinger, 1999a & b; Tarr et al., 2005; Waterkeyn et al., 2008; Silver et al., 2012
Predatory Invertebrate Biomass ~Proportion of Basin Open Water	Predaceous beetle populations are expected to increase in shallow highly vegetated ponds and predaceous hemipterans in more lacustrine open-water habitats.	Tarr et al., 2005; Hart and Lovvorn, 2005; Silver et al., 2012;
Predatory Invertebrate Biomass ~Electrical Conductivity	Predatory invertebrate biomass is expected to increase with salinity as a result of physiological influences and transitions from macrophyte dominated primary production to phytoplankton.	Lancaster and Scudder, 1987; Wollheim and Lovvorn, 1995 & 1996; Hart and Lovvorn, 2005
Predatory Invertebrate Biomass ~Tiger Salamander Abundance	Tiger salamanders are expected to decrease predatory invertebrate biomass through competition and predation.	Holomuzki, 1994; Wissinger et al., 1999a&b
Non-Predatory Invertebrate Biomass ~Proportion of Basin Ponded	Invertebrate biomass is expected to increase during filling periods, especially post drought.	Mahoney et al., 1990; Bataille and Baldassare, 1993; Corti et al., 1996; Chase and Knight, 2003; Euliss et al., 2004; Whiles and Goldwitz, 2005

Table A.1. Individual pathways examined in structural equation model, expected relationships between modeled variables, and source literature used to inform the expected relationships(continued).

Pathway	Expected Relationship	Supporting Literature
Non-Predatory Invertebrate Biomass ~Proportion of Basin Open Water	Non-benthic invertebrate biomass is expected to be positively correlated with open water area.	Mahoney et al., 1990; Batzer and Resh, 1992; Corti et al., 1996; Gaiser and Lang, 1998; Vinnersten et al., 2009; Silver et al., 2012; Gleason et al., 2018
Non-Predatory Invertebrate Biomass ~Electrical Conductivity	Non-benthic invertebrate populations often increase in more saline environments.	Wollheim Lovvorn, 1995; Hart and Lovvorn, 2005; Waterkeyn et al., 2008; McLean et al., 2016
Non-Predatory Invertebrate Biomass ~Tiger Salamander Abundance	Tiger salamanders are expected to have a top down control on invertebrate biomass through predation.	Holomuzki, 1994; Wissinger et al., 1999a; Benoy et al., 2002; Benoy, 2008;
Non-Predatory Invertebrate Biomass ~Predatory Invertebrate Biomass	Predatory invertebrates can exert a top-down control on aquatic invertebrate community composition.	Chase and Knight, 2003; Knight et al., 2004; Cobbaert et al., 2010
NMDS Axes ~Proportion of Basin Ponded	The amount and duration of ponded water in a wetland is predicted to be an important deterministic filter on invertebrate community composition.	Wissinger et al., 1999a; Lillie 2003; Stenert and Maltchik, 2007; Florencio et al., 2011; Gleason and Rooney, 2018
NMDS Axes ~Proportion of Basin Open Water	Invertebrate communities are expected to vary between vegetated and open water habitats.	Gaiser and Lang, 1998; Euliss et al., 2004; Tarr et al., 2005; Gleason et al., 2018
NMDS Axes ~Electrical Conductivity	Invertebrate community composition can shift in response to physiological driven influences of salinity.	Wollheim and Lovvorn, 1995: Waterkeyn et al., 2008; McLean et al., 2016; Preston et al., 2016; Lancaster and Scudder, 1987
NMDS Axes ~Tiger Salamander Abundance	Tiger salamanders are expected to have a top down control on invertebrate presence and abundance at multiple trophic levels.	Holomuzki 1994; Wissinger et al., 1999a; Benoy et al., 2002; Benoy, 2008
NMDS Axes ~Predatory Invertebrate Biomass	Increased biomass of predatory insects can have top down effects on community structure.	Schneider and Frost, 1996; Chase and Knight, 2003; Knight et al., 2004; Hart and Lovvorn, 2005; Cobbaert et al., 2010
NMDS Axes ~Non-Predatory Invertebrate Biomass	High densities of invertebrates can result in increased competitive interactions, which in turn can alter community structure.	Batzer and Wissinger, 1996; Knight et al., 2004; Elono et al., 2010

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APPENDIX B. INVERTEBRATE COMMUNITIES OF PRAIRIE-POTHOLE WETLANDS IN THE AGE OF THE AQUATIC HOMOGENOCENE [6]

This file contains tabulated analysis results to supplement the findings of Chapter 5.

B.1. Supplementary Tables

Table B.1. ANOVA table for regression model "Depth~Year+Regime+Regime*Period"(R^2=.80, P-Value<0.05) evaluating the significance of year sampled, wetland hydrological regime, and hydrological period in explaining variation in maximum annual water depth (m) for 16 wetlands in the Cottonwood Lake Study Area in Stutsman, County, North Dakota sampled from 1992 to 2015.

	Deg Freedom	Sums Squares	Mean Squares	F-Value	Pr(>F)
Year	1	67.48	67.48	354.28	<2e-16
Regime	2	253.22	126.61	664.75	<2e-16
Period	2	34.99	17.49	91.85	<2e-16
Regime: Period	4	86.17	21.54	113.11	<2e-16
Residuals	570	108.56			

Table B.2. ANOVA table for regression model "Percentage of Basin Ponded~Year+Regime+Regime*Period" (R^2=.59, P-Value<0.05) evaluating the significance of year sampled, wetland hydrological regime, and hydrological period in explaining variation in the annual maximum percentage of a wetland basin that was ponded for 16 wetlands in the Cottonwood Lake Study Area in Stutsman, County, North Dakota sampled from 1992 to 2015.

	Deg Freedom	Sums Squares	Mean Squares	F-Value	Pr(>F)
Year	1	12.19	12.186	229.60	<2e-16
Regime	2	3.93	1.965	37.02	6.88e-16
Period	1	14.05	7.025	132.35	<2e-16
Regime: Period	2	4.17	1.043	19.64	3.29e-15
Residuals	602	31.95	0.053		

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[6] The supplementary information was published in *Hydrobiologia* in 2019 as a supplementary file to Chapter 5.

Table B.3. ANOVA table for regression model "Percentage of Basin Open Water~Year+Regime+Regime*Period" (R^2=.74, P-Value<0.05) evaluating the significance of year sampled, wetland hydrological regime, and hydrological period in explaining variation in the annual percentage of a wetland basin that was delineated as open-water for 16 wetlands in the Cottonwood Lake Study Area in Stutsman, County, North Dakota sampled from 1992 to 2015.

	Deg Freedom	Sums Squares	Mean Squares	F-Value	Pr(>F)
Year	1	10.07	10.069	240.87	<2e-16
Regime	2	35.23	17.617	421.44	<2e-16
Period	2	3.48	1.741	41.65	<2e-16
Regime: Period	4	12.53	3.133	74.94	<2e-16
Residuals	524	21.90	0.042		

Table B.4. Mean, minimum, and maximum within year total beta-diversity (Sorensen's Coefficient), partitioned turnover component (Simpson's Coefficient), and partitioned nestedness component (Nestedness Coefficient) derived from aquatic-macroinvertebrate presence-absence data for all 16 wetlands in the Cottonwood Lake Study Area in Stutsman, County, North Dakota sampled from 1993 to 2015.

Coefficient	Mean	Minimum	Maximum
Sorensen's	0.8118	0.7273	0.8596
Simpson's	0.6873	0.6150	0.8468
Nestedness	0.6851	0.5669	0.7658

Table B.5. Results of ANOVA model "Sørensen's Coefficient~ Regime +Hydroclimatic Period + Regime: Hydroclimatic Period" evaluating the differences in variability of Sørensen's Index based dissimilarities between wetland hydrological regime (P-Wetland, T-Wetland, and OB-Wetland) and hydroclimatic period ("Filling Period", "Post Filling Period") for 16 wetlands in the Cottonwood Lake Study Area in Stutsman, County, North Dakota sampled from 1993 to 2015.

	Deg Freedom	Sums Squares	Mean Squares	F-Value	Pr(>F)
Regime	2	0.5321	0.26607	31.283	4.65e-13
Hydroclimatic Period	1	0.0511	0.05112	6.010	0.0148
Regime: Period	2	0.0278	0.01391	1.636	0.1965
Residuals	298	2.5345	0.00851		

Table B.6. Results of ANOVA model “LCBD~ Regime +Hydrologic Period + Regime: Hydroclimatic Period” evaluating the differences in variability of Sørensen’s Index based local contribution to beta diversity values between wetland hydrological regime (P-Wetland, T-Wetland, and OB-Wetland) and hydroclimatic period (“Filling Period”, “Post Filling Period”) for 16 wetlands in the Cottonwood Lake Study Area in Stutsman, County, North Dakota sampled from 1993 to 2015.

	Deg Freedom	Sums Squares	Mean Squares	F-Value	Pr(>F)
Regime	2	1.642e-05	8.212e-06	12.328	6.8e-06
Hydroclimatic Period	1	1.570e-06	1.566e-06	2.351	0.1261
Regime: Hydroclimatic Period	2	5.730e-06	2.864e-06	4.300	0.0143
Residuals	337	2.245e-04	6.660e-07		

Table B.7. Results of PERMANOVA model “Sorensen Dissimilarity Matrix~ Regime +Hydroclimatic Period + Regime: Hydroclimatic Period” based on 999 permutations evaluating the differences in variability of Sørensen’s Index based dissimilarities between wetland hydrological regime (P-Wetland, T-Wetland, and OB-Wetland) and hydroclimatic period (“Filling Period”, “Post Filling Period”) for 16 wetlands in the Cottonwood Lake Study Area in Stutsman, County, North Dakota sampled from 1993 to 2015.

	Deg Freedom	Sums Squares	Mean Squares	F-Value	R^2	Pr(>F)
Regime	2	6.602	3.3012	41.597	0.18	<0.001
Hydroclimatic Period	1	2.955	2.9552	37.237	0.08	<0.001
Regime: Hydroclimatic Period	2	0.962	0.4808	6.058	0.02	<0.001
Residuals	337	26.745	0.0794		0.72	

Table B.8. ANOVA table for regression model “LCBD~Year+Regime+Regime*Period” (R^2=.18, P-Value<0.05) evaluating the significance of year sampled, wetland hydrological regime, and hydrological period in explaining variation LCBD values for 16 wetlands in the Cottonwood Lake Study Area in Stutsman, County, North Dakota sampled from 1992 to 2015.

	Deg Freedom	Sums Squares	Mean Squares	F-Value	Pr(>F)
Year	1	0.0000000	3.000e-08	0.025	0.8741
Regime	2	0.0000671	3.357e-05	30.523	6.6e-13
Period	1	0.0000024	2.380e-06	2.165	0.1422
Regime: Period	2	0.0000098	4.890e-06	4.450	0.0124
Residuals	296	0.0003695	1.100e-06		

B.2. Supplementary Figure

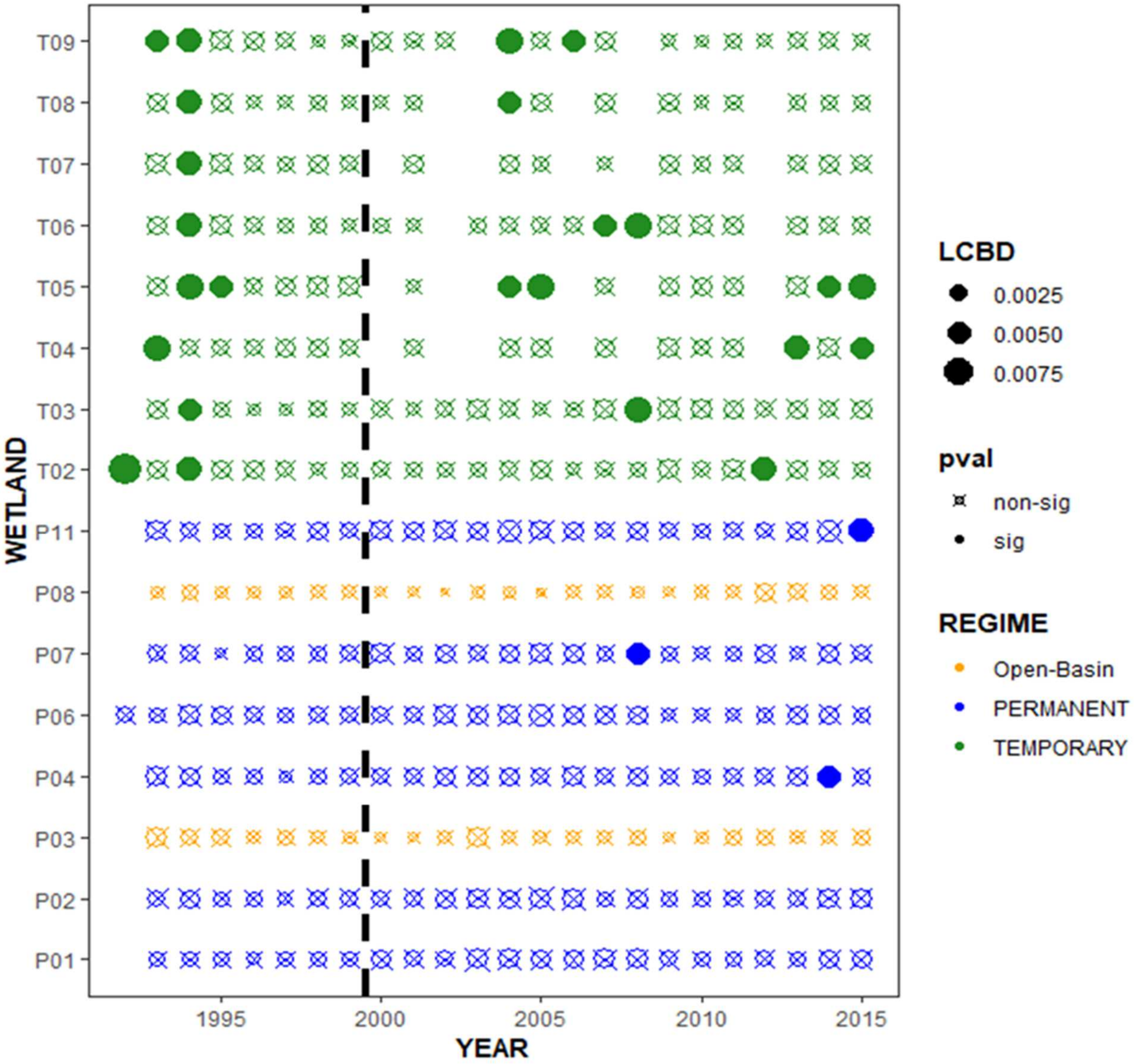

Figure B.1. Space-time plot of Sorensen's Dissimilarity Index based Local Contributions to Beta Diversity values derived from presence/absence-based aquatic-macroinvertebrate compositions for Cottonwood Lake Study Area wetland by year combinations from 1992–2015. The circles represent wetland by year combinations, and circle size indicates proportional increases or decreases in LCBD values. Hydrological regime categories are indicated by the color of each circle. Wetland by year combinations with LCBD values that were significantly greater then mean LCBD values (alpha <0.05) are indicated by solid fill circles. Sites with non-significantly different communities are indicated by crossed out open circles. The black dashed line indicates the transition from the "filling-period" (1993–1999) to the "post-filling period" (2000–2015).