

Physicochemical and Vegetative Responses of Prairie Wetlands to Local Land Covers

by

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Author's Declaration

I hereby declare that I am the sole author of this thesis.

This is a true copy of the thesis, including any required final revisions, as accepted by my examiners.

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Abstract

Effective environmental monitoring and biological assessment initiatives require knowledge of the spatial and temporal scales at which human activities most strongly influence ecosystem conditions. I compared the environmental conditions and vegetation communities of 48 non-permanent wetlands in the Prairie Pothole Region of Alberta, Canada, to adjacent land cover measured at ten spatial extents and in four consecutive years. I found that both vegetation community composition and environmental conditions within the wetland were significantly related to variation in land cover across a wide range of spatial extents and the entire time period that I analyzed. Importantly, no spatial extent and year combination yielded land-cover data that was statistically significantly more concordant with environmental conditions or vegetation communities than the others within 1 km of the wetland boundary. Contrary to expectations, the catchments did not yield land cover significantly more concordant with wetland conditions than symmetrical buffers. I therefore conclude that concerns around having the most recent and highest-resolution land cover or most precisely-delineated catchment boundaries should be relaxed. Despite the lack of significant differences among extents and age of land cover data, I did observe consistent trends in concordance. Wetland environmental conditions were more concordant with land cover extracted from either the wetland catchments or from within a 200-500 m buffer around the wetland. The analysis also suggested a time-lag in the relationship of four years or more. Wetland vegetation communities appeared more strongly related to land cover at 500-5,000 m from the wetland and exhibited a one-year time lag; however, when I controlled for spatial autocorrelation, the strength of the concordance between vegetation and land cover from all extents decreased to insignificance. This revealed the same pattern as

observed for environmental conditions, but at weaker concordance levels. Spatial autocorrelation in terms of environmental conditions, wetland vegetation and surrounding land cover may be associated with natural climatic and physiographic gradients in my study region and highlights the need for additional exploration of geographic variability within jurisdictional units. These findings raise interesting questions for science and have important consequences for wetland monitoring, management and conservation.

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Chapter 1: General Introduction and Thesis Overview

1.1 Importance of Scale in Ecological Studies

Landscape ecology is the study of the dynamics between organisms and ecosystems over a broad area and the consequences of spatial heterogeneity and patterning on these relationships (Delcourt and Delcourt 1988; Turner 1990). The study of scale is a major focus within this field due to scale's importance in measuring and understanding the interactions among different environmental and biological properties and processes (Delcourt and Delcourt 1988; Wiens 1989; Turner et al. 1989; Fahrig 1992; Levin 1992; Willis and Whitaker 2002). The selection of which scales will be used in a study can have a considerable bearing on research results and interpretations. Landscape structure (e.g., land cover composition or configuration) is variable across space and time due to both natural and anthropogenic processes (Forman 1995), meaning that the same landscape can be represented differently according to the area and/or time period under consideration (Houlahan and Findlay 2004; Houlahan et al. 2006; Tavernia and Reed 2010; Jackson and Fahrig 2012, 2015).

The same ecological process might show different patterns at different scales of observation owing to the apparent homogeneity at larger scales, which may obscure the patterns and diversity that are evident at finer scales (Turner 1990; Findlay and Zheng 1997; Findlay and Bourdages 2000; King et al. 2005; Rooney and Bayley 2011). Furthermore, because not all aspects of an organism's ecology are observable at a single scale (Wiens 1989; Levin 1992; Wheatley and Johnson 2009; Tavernia and Reed 2010), the spatial and temporal scales used to represent landscape structure can affect the detected and inferred relationships with ecosystem attributes by revealing different patterns across scales. Consequently, if scales are arbitrarily

selected or are not of an appropriate range, the patterns and processes observed may not be the ones relevant to the ecosystem or taxon of interest (Wheatley and Johnson 2009; Jackson and Fahrig 2015). In some circumstances, inappropriate selection of research scale can have negative consequences for natural resource management or wildlife conservation (Schindler 1987; Wiens 1989; Findlay and Zheng 1997; Wheatley and Johnson 2009). For example, the distance at which agricultural intensity affects amphibian habitat quality varies among species (Koumaris and Fahrig 2016), implying that management of agriculture at a single spatial scale would benefit some species but may be inadequate for the survival of others.

There are multiple sources of spatial, temporal, and organizational variation that influence organisms and ecosystems, including those associated with certain scales (Levin 1992; Willis and Whitaker 2002). As such, the optimal spatial and temporal scales for a study must be determined by the study objectives and study organisms or system in order to have meaningful results (Delcourt and Delcourt 1988; Findlay and Zheng 1997; Wheatley and Johnson 2009; Jackson and Fahrig 2012, 2015). Determining the scale(s) that are appropriate for a landscape ecology study is paramount to accurate investigation of the interaction(s) between landscape structure and ecological patterns and processes.

1.2 Definition of Scale

While the importance of scale in ecology is well-recognized, the precise meaning and correct usage of the term can be ambiguous (Dungan et al. 2002; Wheatley and Johnson 2009; Jackson and Fahrig 2015). Many studies that have claimed to examine “scale” (e.g., Galatowitsch et al. 2000; Wheatley and Johnson 2009; Bird and Day 2014; Olker et al. 2016)

have used the term to refer to the spatial component of environmental heterogeneity only, although ecological variability through time is equally important (Delcourt and Delcourt 1988; Turner 1990; Fahrig 1992; Levin 1992). I adopt a general definition of ecological scale as the spatial and/or temporal dimensions and resolution at which ecosystem or landscape heterogeneity is measured (Fahrig 1992; Levin 1992; Dungan et al. 2002; Willis and Whitaker 2002; Wheatley and Johnson 2009). Spatial and temporal scales are conceptually similar in that they are both characterized by research scope and data resolution (Wiens 1989) and can span several orders of magnitude (Delcourt and Delcourt 1988; Willis and Whitaker 2002). However, the two concepts should be considered distinct as they describe different properties of the phenomenon of interest, the sampling units used, and the data analysis employed (Dungan et al. 2002). In this thesis, I address spatial scale in terms of both spatial extent (area considered) and grain (spatial resolution), whereas I define temporal scale in terms of temporal extent (duration considered), lag (frequency of data collection), and data age (time since collection), (see **Table 1.1**).

1.3 Scope of Review

My intent in this review chapter is to summarize the information available on the appropriate spatial and temporal scales of land-use/land-cover data used for wetland assessment and monitoring. Although I present a general survey of ecological scale literature, I focus on the landscape responses of freshwater wetlands and their biological communities, particularly those in non-permanent marshes (**Table 1.2**). Furthermore, I am focusing my discussion of spatial scale around spatial extent, as the decision of what extents are ecologically relevant is more subjective and debated in the literature than grain (which is typically determined more by

technological capacity, funding availability and logistics rather than by the researchers themselves; Dungan et al. 2002).

1.4 Spatial Scale Research

As described above, how a landscape is defined influences how it is measured, and in turn what ecological inferences can be made about the role of the landscape in determining wetland properties or processes. Multiple landscape models exist for the assessment of human-modified landscapes, but in this thesis I have adopted the landscape mosaic model (described in detail by Forman 1995, but also see Delcourt and Delcourt 1988; Turner 1990; Fahrig 2003). The landscape mosaic model is a patch-based approach wherein land-cover polygons or raster cells are classified into bins of homogeneous types. While landscape mosaic approaches are prevalent in the landscape ecology literature, conservation biologists have proposed other frameworks such as the habitat continuum model (McIntyre and Hobbs 1999) or the habitat contours model (Fischer et al. 2004), which acknowledge the heterogeneity of habitat types and the importance of ecotones and gradients. However, as with grain size, the availability of geospatial data often constrains the type of landscape model a researcher can employ. Most widely available land-cover data presents a mosaic of patches assigned to different homogenous cover types, for example in the Albertan Parkland and Grassland Regions this is the only type of data available spanning multiple years. However, even if data following a continuum of land cover were available, adoption of a more sophisticated landscape model would limit the applicability of research findings beyond these regions. One of my thesis goals is to inform wetland management and policy implementation, therefore I will adopt more broadly-applicable landscape mosaic model.

Much spatial scale research has been on contrasting the effect of land cover at different extents (if multiple scales were considered at all) on some ecosystem attribute. Studies that select and contrast multiple spatial extents are known as “focal site multiscale designs” (Brennan et al. 2002; Jackson and Fahrig 2015) or “cross-scalar experimental designs” (Wheatley and Johnson 2009). The purpose of using more than one spatial extent is to determine whether there is an optimal extent at which landscape structure best predicts some ecosystem attribute. The optimal extent – also referred to as the “critical distance” (Houlihan and Findlay 2004) or the “scale of effect” (Jackson and Fahrig 2015) – is typically determined according to the lowest Akaike Information Criterion or highest r or r^2 values of a model describing the relationships between the landscape structure measured at a particular extent and an ecosystem attribute (Jackson and Fahrig 2012, 2015).

Ecosystem attributes can be abiotic (habitat quality variables such as water nitrates or turbidity; e.g., Houlihan and Findlay 2004) or biological (population levels or community composition; e.g., Brazner et al. 2007), and may be examined singly or in tandem with one another. While the types of ecosystem attributes vary widely among and within studies (**Table 1.2**), all are considered to be some property of an ecosystem which responds to landscape structure in a measurable way. Hence, for simplicity’s sake, I will use the term “ecological response” to collectively describe the organisms and processes being examined in multiscale studies.

The number and range of spatial extents considered in a study presents a large constraint on what the optimal extent is determined to be, as the optimal extent must be selected from among these candidates. Ideally, the selected extents reflect ecological properties of the response itself, such as an organism's life span or dispersal capabilities (Jackson and Fahrig 2012). However, spatial extents in ecological studies are often selected arbitrarily and with little biological justification or consideration of what factors might influence the optimal extent. Indeed, recent quantitative reviews of multiscale landscape-wildlife studies (Wheatley and Johnson 2009; Jackson and Fahrig 2015) have shown that over 70% of the spatial extents considered in the studies were selected arbitrarily and had no biological justification. I conducted a similar literature survey using the keywords "scale*", "spatial OR temporal", "landscape* OR land cover* OR land use*" and "wetland* OR marsh*" on the Web of Science database and found 22 multiscale landscape-wetland studies (**Table 1.2**). Of these studies, I found that 55% similarly offered no rationale for the selection of extents that they employed. In most cases, multiscale studies contrasted symmetrical buffers of various radii, assuming that the critical distance is the same in all directions from a focal point.

While buffers are simple to understand and generate using Geographic Information Systems, they may not accurately depict the landscape area of influence, as many environmental and biological processes are anisotropic (Turner 1990; Dungan et al. 2002). Some recent work has advocated for using hydrologic catchments as a more ecologically-relevant spatial extent to measure land cover around freshwater wetlands (McCauley and Anteau 2014; Novikmec et al. 2016); however, no direct comparisons have been made between topographically-delineated catchments and symmetrical buffers of comparable size, possibly because of the difficulty in

obtaining topographic data of consistent resolution and broad spatial coverage (Martinez et al. 2010; McCauley and Anteau 2014; Novikmec et al. 2016; Wu and Lane 2016). Thus, despite the popularity of the multiscale experimental design, the relative importance of anisotropy in freshwater wetland landscape delineation remains untested.

Besides the typical lack of biological rationale in selection of landscape extent, the range of extents considered may be too narrow and further limit detection of the optimal extent. In their review of 71 studies, Jackson and Fahrig (2015) found that the optimal extent for a species was often the largest (23% of cases) or smallest (21% of cases) spatial extent that researchers considered, indicating that in many cases researchers were still under- or over-estimating the optimal extent, respectively. The range of candidate spatial extents may be further constrained by data quality: in some older studies (Mensing et al. 1998; Crosbie and Chow-Fraser 1999; Galatowitsch et al. 2000), the smallest possible extent was determined by minimum data resolution, while the maximum extent was limited by data availability and spatial coverage. When researchers select extents that are too few and/or of an inappropriate range, uncertainty arises as to whether the true optimal extent (if one exists) was among the range of extents considered (Wheatley and Johnson 2009; Jackson and Fahrig 2015). Thus, careful consideration and analysis of prior studies should be used in selecting the range of spatial extents examined in a multiscale experimental design.

The strength and nature of landscape-ecological response relationships are not always constant among spatial extents (e.g., Turner 1990; Findlay and Zheng 1997; Findlay and Bourdages 2000; King et al. 2005; Rooney and Bayley 2011). However, landscape heterogeneity

can also result in considerable variability in these relationships across a geographic area, even when the same spatial extent is used. This phenomenon is known as spatial non-stationarity (Fotheringham et al. 2002; Foody 2004). Non-stationarity has been shown to exist for both abiotic and biotic responses: Tu (2011) found that water pollutant concentrations were positively correlated with anthropogenic land covers in some areas of a watershed and negatively correlated in others, while landscape predictors of avian richness vary spatially across the continents of South America (Rahbek and Graves 2001) and Africa (Foody 2004). Organismal traits such as territory size may be non-stationary and vary according to geographically heterogeneous properties such as landscape fragmentation or population density (Fahrig 2003; Jackson and Fahrig 2012), a factor that may explain why different optimal extent sizes have been identified for the same species (Jackson and Fahrig 2015). Thus, the complexities surrounding geographic heterogeneity and non-stationarity imply that for some responses, there is no universally optimal spatial extent (Levin 1992), further complicating the question of what portion of a landscape should be measured to best predict ecological responses. This knowledge suggests that every study of landscape effects on ecological patterns or processes should commence with an explicit multiscale assessment to identify the appropriate spatial extent of study, as results from other regions or ecosystems will not necessarily hold.

1.5 Temporal Scale Research

Three discrete, but related concepts characterize the discussion of most studies relating landscape structure over time to ecological responses: time lags, legacy effects and extinction debts. Time lags are the phenomenon where a disturbance event occurs and some interval of time passes before the impacts of the event are detectable on an ecosystem, owing to the mechanistic

linkage between effects being produced, transferred to the ecosystem, and detected by monitoring programs (reviewed in Meals et al. 2010). These have been observed in wetlands for both water quantity, where pond hydroperiods were altered six years after local land cover changes (van der Kamp et al. 1999), and for water quality, where nitrogen export from a eutrophied wetland was delayed due to biogeochemical conversions and land cover changes (Van Meter and Basu 2015). In contrast to time lag effects, which reflect the delayed beginning of disturbance effects, legacy effects describe the prolonged ending of disturbance effects. Specifically, they are indirect effects that persist after the activity responsible has ceased or the source of disturbance removed (reviewed in Foster et al. 2003; Cuddington 2012). Examples include the persistent influence of tillage on soil biogeochemistry (McLauchlan 2006) or reduced species richness following afforestation of agricultural land (Flinn and Vellend 2005). In wetlands in South Carolina, Kirkman et al. (1996) observed legacy effects where vegetation community composition was linked to human disturbance from 40 years earlier. The authors concluded that the successional trajectories of affected wetlands were likely to continue to differ from undisturbed wetlands. Finally, extinction debts are a particular form of legacy effect, wherein the total species richness of an ecosystem declines in response to historic habitat loss or degradation, even if no further perturbations occur (Tilman et al. 1994; Hylander and Ehrlén 2013). Extinction debts can take several decades or longer to be “paid off” for plants (e.g., Vellend et al. 2006) or animals (e.g., Hanski and Ovaskainen 2002), and may be the mechanism behind continued loss of wetland biodiversity in historically-modified landscapes (e.g., Jenkins et al. 2003). Given the possible interplay of time lags and legacy effects, the temporal scale of observation can thus make a critical difference to the detected condition of wetlands under study.

Despite the body of research concerning time lags, legacy effects and extinction debts, and the acknowledgement that spatial and temporal scales are of equal importance in ecology (Fahrig 1992; Levin 1992; Findlay and Bourdages 2000; Willis and Whitaker 2002), few researchers have examined what temporal scale is appropriate in wetland research. That is, while ample research has been conducted which explores the optimal spatial extent (e.g., **Table 1.2**) or grain (e.g., Turner et al. 1989; Rahbek and Graves 2001; Dungan et al. 2002) for relating surrounding land cover to habitat conditions at the patch-level, the influences of temporal extent, lag and age on landscape-ecological response relationships are less studied. Indeed, a survey of the multiscale wetland literature reveals that the vast majority of studies contrasted landscape structure at multiple spatial rather than temporal scales. Only two of the 22 studies listed in **Table 1.2** considered more than one temporal scale of data, and these studies draw conflicting conclusions regarding the appropriate temporal scale. Findlay and Bourdages (2000) found that wetland biota exhibited a lagged response to historical road densities, while Tavernia and Reed (2010) found no evidence that historical land covers were more influential on wetland birds than contemporary land cover. This conflict highlights the knowledge gap surrounding temporal scale selection in wetland research; however, in most wetland monitoring and assessment work or studies relating wetland condition to surrounding land cover, emphasis is placed on using recent land-cover data that as narrowly as possible captures the land cover distribution at the time of field work.

A major hurdle in carrying out landscape ecology studies that cover a temporal range is that temporal scale analysis requires multiple land-cover data sets collected at different times that are constructed using consistent methods and are of comparable spatial extent and grain. These

are seldom available (Fahrig 1992), especially as remote sensing technology improves with time, yielding continually finer and finer grain data produced by novel remote sensing and land cover classification methods. Thus, even where comparable data collection or creation methods were used, research into time lags and legacy effects must work with the data quality that was available at the oldest point in the temporal range of interest. In terms of land cover data, this means working with pixel sizes that are often too large to be informative. As discussed above, grain size can severely constrain researchers (Mensing et al. 1998; Crosbie and Chow-Fraser 1999; Galatowitsch et al. 2000), and the degree to which such data limitations impede detection power is unresolved. Consequently, long term data sets of consistent collection methods and quality are uncommon but sought after (Schindler 1987; Hylander and Ehrlén 2013). In assessments of land cover over time, the scarcity is compounded by the expense required to acquire land-cover data, the changes in remote sensing platforms and capabilities over time (Fisette et al. 2014), and the variability in collection dates of aerial photographs over broad study regions (Findlay and Bourdages 2000). Landscape-ecological response relationships may exist at a particular time scale, but the generally limited availability of land-cover data from multiple time periods precludes further investigation into this matter.

Data limitations aside, considering multiple time periods of land cover may be wise not just because time-lagged or legacy effects in landscape-ecological response relationships may exist, but also because these relationships may not be consistent through time (Tavernia and Reed 2010). Non-stationarity exists in the temporal dimension as well (Burt and Worrall 2007) and can confound understandings of landscape-ecological response linkages, particularly when a long time series is considered. For example, climatic cycles such as the North Atlantic

Oscillation, Pacific Decadal Oscillation or the El Niño Southern Oscillation yield dynamic and variable wet-dry cycles that are difficult to predict, which can interact with each other to create inter-annual variability in lake water levels (Pham et al. 2009; Molinos and Donohue 2014). The shifting baselines due to anthropogenic climate change can further confound predictions of aquatic ecosystem responses to landscape factors (Johnson et al. 2016). Similar temporal non-stationarity is exhibited with extinction debts, as landscape effects on current biota may be undetectable in some years and very prominent in others (Tilman et al. 1994; Hylander and Ehrlén 2013).

In the absence of clear guidance on what time period is appropriate for the analysis of relationships between land cover and ecological responses and some evidence that non-stationarity in time may mean that there is no “optimal” time period for such analyses, researchers have generally defaulted to seeking the most recent land-cover data available (e.g., Rooney et al. 2012; Koumaris and Fahrig 2016). This has created great pressure on governments and conservation authorities to invest in renewing their remotely sensed data inventories regularly (e.g., Fiset et al. 2014). In light of finite budgets, it merits consideration whether land-cover data really must be obtained in the same year as field work to detect ecologically meaningful relationships between land cover and ecological conditions.

1.6 Knowledge Gaps Surrounding Scale Selection

Despite the large body of knowledge surrounding the importance of ecological scales, the selection of ecologically-relevant scales remains a challenge. If “optimal” spatial and temporal scales do exist where landscape influence on ecological responses is strongest, recent surveys of

landscape-ecological response literature have revealed that many studies were unlikely to have detected these relationships due to inadequate study design (Wheatley and Johnson 2009; Jackson and Fahrig 2015). Studies that have considered more than one taxon or type of ecological response have found that the optimal spatial (Mensing et al. 1998; Houlahan and Findlay 2004; Houlahan et al. 2006; Brazner et al. 2007; Rooney et al. 2012) and temporal (Findlay and Bourdages 2000) scales differ among the response variables. No single spatial or temporal scale exists that can adequately characterize all population, community or ecosystem variability (Levin 1992), and the appropriateness of a scale depends more on the focal organism or process of interest than what is most convenient or conventional to measure. Consequently, researchers must acknowledge intrinsic properties of their study organisms, environments and landscapes and select candidate scales accordingly. Factors that should influence the selection of both spatial and temporal scales include (but are not limited to): 1) life history traits of the taxa of interest, including dispersal capabilities and migratory status (Jackson and Fahrig 2012), life span (Findlay and Bourdages 2000; Hylander and Ehrlén 2013), or phenology and habitat specificity (Tavernia and Reed 2010; Koumaris and Fahrig 2016); 2) ecosystem traits, such as dominant disturbance type and frequency (Dungan et al. 2002; Hylander and Ehrlén 2013; Olker et al. 2016); 3) variability of the geographic region of interest (unless conditions and relationships are fairly narrowly defined, spatial or temporal non-stationarity may exist (Foody 2004; Burt and Worrall 2007; Tu 2011)); and for aquatic ecosystems, 4) hydrologic regime, including water budget and source (Novikmec et al. 2016; Olker et al. 2016), residence time (Meals et al. 2010) and catchment size (McCauley and Anteau 2014; Wu and Lane 2016).

Even if the four factors described above are taken into consideration when selecting research scales, uncertainty exists as to whether optimal scales exist at all and are detectable (Levin 1992; Willis and Whitaker 2002; Jackson and Fahrig 2015). There remain numerous knowledge gaps concerning the practicalities of research scale selection and usage, which are common to many ecosystems and situations. I list six of these gaps below:

1. What is the relative importance of spatial extent versus grain for spatial scale selection? How do these factors interact?
2. What is the relative importance of temporal extent, lag and data age on temporal scale selection? How do these factors interact?
3. Where different taxa or ecosystem services may have different optimal scales (e.g., Galatowitsch et al. 2000; Houlahan and Findlay 2004; Houlahan et al. 2006; Rooney and Bayley 2011; Rooney et al. 2012), how do we select scales for ecological assessment? Can effective compromises in scale selection be made?
4. To what extent does spatial or temporal data quality and availability restrict detection of ecological responses to landscape structure? Are these concerns warranted (e.g., Martinez et al. 2010), or are the relationships robust enough that they could be detected with both medium- and high-resolution data (e.g., McCauley and Anteau 2014)?
5. To what extent does spatial non-stationarity exist across a study system? Does this need to be controlled for using methods that geographically weight bivariate relationships (e.g., Fotheringham et al. 2002) or by examining alternative models of landscape structure that embrace ecotones (e.g., McIntyre and Hobbs 1999; Fischer et al. 2004)?
6. To what extent does temporal non-stationarity exist in a system? Does an existing study design permit detection of time-lagged or legacy effects or extinction debts? How might

these delayed responses be influenced by long-term, temporally-variable processes such as climate cycles?

1.7 Albertan Prairie Pothole Wetlands and Scale

In this thesis, I will explore the first four of these knowledge gaps, using temporary to semi-permanent marshes in the Prairie Pothole Region (PPR) of Alberta, Canada as my study ecosystem. These small, depressional wetlands are highly influenced by landscape morphology (McCauley and Anteau 2014; Wu and Lane 2016) and surrounding land cover (van der Kamp et al. 1999) due to their geographic and hydrological isolation from other wetlands or water bodies (van der Kamp and Hayashi 2009; Marton et al. 2015). This isolation, coupled with an inter- and intra-annually variable hydroperiod, allows the wetlands to support diverse biological communities (Semlitsch and Bodie 1998; van der Kamp et al. 1999; Galatowitsch et al. 2000; Jenkins et al. 2003) and provide multiple ecological services such as flood abatement and water quality improvement (Zedler 2003; Marton et al. 2015).

However, the linkages between landscape structure and wetland abiotic conditions or biota are not well understood, partly due to considerable loss and degradation of PPR wetlands (Bartzen et al. 2010) and because these ecosystems have received minimal research attention at the northern margin of their distribution. No published literature exists concerning scale for non-permanent wetlands in Alberta: a search of the Web of Science Database using the key words “non-permanent OR temporary OR seasonal”, “marsh* OR wetland* OR pond* OR pothole*”, “scale*”, and “land use* OR land cover*” yielded zero papers from Alberta published in the date range of 1900-2016. Extrapolation of knowledge gleaned from other wetland studies (e.g., those

listed in **Table 1.2**) to Alberta PPR wetlands may not be possible due to inherent differences in hydrology, climate, and biota. Many of the studies described in **Table 1.2**, such as Houlahan and Findlay (2004), examined wetlands with strong groundwater or surface water connectivity which have discrete differences in the importance of upland-wetland hydrologic pathways compared to PPR wetlands (Marton et al. 2015). Furthermore, the studies that considered depressional wetlands (e.g., Alsfeld et al. 2010; Boughton et al. 2010; Tavernia and Reed 2010; Bird and Day 2014) were in regions of different climate and land cover regimes. Alberta's PPR has a semi-arid climate which limits the hydroperiod of wetland ponds (Pham et al. 2009), and the water budgets of these wetlands is much more dependent on spring snowmelt than in other areas with more precipitation (van der Kamp and Hayashi 2009). As such, the spatial and temporal scales of effect on wetland ecological responses here are unlikely to be similar to those in other wetland types or where growing-season precipitation exceeds potential evapotranspiration (e.g., Novikmek et al. 2016). It is currently unknown to what extent PPR wetlands may be influenced by land cover at spatial or temporal scales, but I hypothesize that both spatial and temporal scale selection will have a strong effect on landscape-ecological response relationship detection. The importance of catchment land covers to PPR wetland hydrology (van der Kamp et al. 1999) may imply that the local catchment is the optimal spatial extent (McCauley and Anteau 2014), while the existence of time lags, legacy effects and extinction debts observed in the PPR (e.g., Jenkins et al. 2003; Van Meter and Basu 2015) is likely due to the extensive landscape alterations and wetland destruction in this region (Bartzen et al. 2010).

The identification of appropriate scales is of practical concern for conservation agencies, industry and regulatory bodies who require ecological assessment and monitoring programs that

have been optimized for the systems of interest yet do not involve the unnecessary expense of sampling over a broader area or longer time interval (Findlay and Zheng 1997; Findlay and Bourdages 2000). Small, non-permanent wetlands are ecologically important but their ephemeral nature makes them especially susceptible to human modifications (Bartzen et al. 2010); as a result, they may be considered “expendable” and their conservation not prioritized (Semlitsch and Bodie 1998). Without knowing the appropriate scale at which ecological conditions in these wetlands are affected by adjacent land uses and land covers, we may underestimate the nature and complexity of landscape-ecosystem dynamics and fail to detect human impacts, resulting in wetland degradation (Schindler 1987; Fahrig 2003; Hylander and Ehrlén 2013; Olker et al. 2016). Acknowledgement of the knowledge gaps surrounding ecological scale is a critical first step towards effective ecosystem management and conservation.

1.8 Thesis Objectives and Outline

My objectives are to contribute to the state of knowledge on wetland-landscape linkages and the importance of scale to these relationships, and to provide guidance for future wetland assessment initiatives. In the data analysis chapter of my thesis, I examine the effects of spatial and temporal scale on the concordance between land-cover data and wetland environmental conditions, as well as the concordance between land-cover data and plant community composition in the Grassland and Parkland Natural Regions of Alberta, Canada. Specifically, I address the following research questions: 1) what is the optimal spatial extent for detecting relationships between land cover and wetland conditions, and does extracting land cover from anisotropic catchments delineated from topographic data of different grain sizes yield stronger congruence than extracting land cover from from symmetrical buffers; 2) within a four year

time-span, what is the optimal window for landscape-wetland assessment – recent or current land-cover data?; and 3) do these optima differ for wetland vegetation versus environmental conditions, and if so, what underlying processes may be responsible? In the final chapter of this thesis, I provide a synthesis of my results and my contributions towards future landscape ecology research and bioassessment initiatives, as well as the implications of my conclusions for wetland policy and management in Alberta.

1.9 Figures and Tables

Table 1.1: Types and components of ecological scale. Concepts and definitions were compiled from numerous sources (Turner et al. 1989; Wiens 1989; Fahrig 1992; Levin 1992; Dungan et al. 2002; Willis and Whitaker 2002; Wheatley and Johnson 2009).

Scale Type	Component	Definition	Example
Spatial	Extent	Area of landscape under consideration	Circle of 100 m radius, 2 km radius, or local catchment
	Grain	Minimum resolution or mapping unit size	Cell size of 10 m, 30 m, 1 km, or 10 km
Temporal	Extent	Duration of time period under consideration	Span of one, five, ten or fifty years
	Lag	Frequency of data collection	Collection interval of one month, one year, or ten years
	Age	Date of data collection, relative to some baseline	Data collected in same month, previous year, or ten years ago

Table 1.2: Summary of 22 multiscale studies examining landscape-ecological response relationships in wetlands.

Study	Location	Study System	^a Ecological response(s)	^b Spatial extent(s)	Temporal period(s)	^c Biological rationale?
Roth et al. 1996	Michigan	1st-3rd order streams	F, SQ, WQ	3*	1	Yes
Findlay and Houlihan 1997	Southeastern Ontario	Freshwater coastal marshes, riparian marshes and swamps, depressional marshes, bogs	B, H, M, V	4*	1	No
Mensing et al. 1998	Minnesota	Riparian wetlands	B, F, H, I, V	4	1	No
Crosbie and Chow-Fraser 1999	Ontario Great Lakes Basin	Freshwater coastal wetlands	SQ, WQ	1	1	No
Findlay and Bourdages 2000	Southeastern Ontario	Freshwater coastal marshes, riparian marshes and swamps, depressional marshes, bogs	B, H, V	4*	3	Yes
Galatowitsch et al. 2000	Minnesota	Depressional marshes	V	3*	1	No
Lopez et al. 2002	Ohio	Depressional marshes	V	1*	1	No
DeLuca et al. 2004	Chesapeake Bay, USA	Marine coastal wetlands	B	2*	1	No
Houlihan and Findlay 2004	Southeastern Ontario	Freshwater coastal marshes, riparian marshes and swamps, depressional marshes	SQ, WQ	17*	1	Yes
King et al. 2005	Chesapeake Bay, USA	1st-3rd order streams	I, WQ	6	1	No
Houlihan et al. 2006	Southeastern Ontario	Freshwater coastal marshes, riparian marshes and swamps, depressional marshes	V	16*	1	No
Brazner et al. 2007	USA Great Lakes Basin	Freshwater coastal wetlands	B, D, F, H, I, V	5	1	Yes
Alsfield et al. 2010	Delaware	Constructed depressional marshes	B, I, V	2*	1	Yes
Boughton et al. 2010	Florida	Depressional marshes	V	10*	1	No
Tavernia and Reed 2010	Massachusetts	Depressional marshes	B	10*	3	Yes
Rooney and Bayley 2011	Northern Alberta	Shallow open water wetlands	V	5*	1	Yes
Bayley et al. 2012	Northern Alberta	Shallow open water wetlands	WQ	1*	1	No
Rooney et al. 2012	Central Alberta	Shallow open water wetlands	B, V	7*	1	No

Study	Location	Study System	^a Ecological response(s)	^b Spatial extent(s)	Temporal period(s)	^c Biological rationale?
Bird and Day 2014	South Africa	Depressional marshes	WQ	2*	1	No
Koumaris and Fahrig 2016	Eastern Ontario	Agricultural ponds	H	3*	1	Yes
Novikmec et al. 2016	Slovakia	Agricultural ponds	SQ, WQ	3	1	Yes
Olker et al. 2016	USA Great Lakes Basin	Freshwater coastal wetlands	SQ, V, WQ	3	1	Yes

^a Abbreviations indicate the types and taxa of ecological responses examined: B = birds; D = diatoms; F = fishes; H = herptiles (amphibians and/or reptiles); I = invertebrates; M = mammals; SQ = sediment quality; V = vegetation; WQ = water quality.

^b Asterisks indicate that all spatial extents were symmetrical buffers.

^c Refers to whether some biological justification was offered for the selection of at least one of the spatial extent or temporal periods.

Chapter 2: Time Lag and Scale Dependency in the Relationships Between Land Cover and Wetland Conditions

2.1 Introduction

Bioassessment, the practice of using biological taxa as indicators of anthropogenic impacts on ecosystems, is widely used for environmental assessment and monitoring (reviewed in Bailey et al. 2004). Bioassessment tools such as indices of biotic integrity (Karr 1981) facilitate the management of freshwater wetlands by producing a composite index that integrates multiple stressors and measurements of natural variability (Bailey et al. 2004). Quantifying deviations from the natural range of wetland variability helps inform management decisions because managers are usually trying to detect degradation against a background of hydrologic, vegetative and chemical variation that is driven by natural environmental cycles.

The conceptual model underlying the use of bioassessment is that human activity affects biota directly, but also modifies site-level environmental conditions (e.g., water levels, soil chemistry) and that these environmental conditions affect the biota (e.g., vegetation, birds, or macro-invertebrates) in a quantifiable and predictable manner (**Figure 2.1**). The efficacy of a bioindicator thus depends in part on the reliability and sensitivity with which changes in land use are reflected by changes in its abundance or status (Cairns et al. 1993).

While methods to measure the biotic and environmental (i.e., physicochemical and hydrological) structure and function of wetland ecosystems are well established (e.g., U.S. EPA 2002; Werner and Zedler 2002; Houlihan et al. 2006; Rooney and Bayley 2010; Quesnelle et al. 2013; Olker et al. 2016) there has been less research on the response of wetland biota to changes

in surrounding land cover. Even when the causal links between land cover and wetland-level environmental conditions are known (e.g., Houlihan and Findlay 2004), the extent to which biota are influenced directly by landscape structure versus indirectly through environmental modification is often unknown (Akasaka et al. 2010; Capers et al. 2010; Alahuhta et al. 2013; Mikulyuk et al. 2013; Olker et al. 2016). Furthermore, when data are not a limiting constraint, researchers must still determine the spatial extent and timing of land-cover data that is most appropriate to related to the ecological process or taxon of interest (Rooney et al. 2012). The issue is that there is heterogeneity in the spatial extent and timing of different ecological processes acting in wetlands (e.g., Houlihan and Findlay 2004 versus Houlihan et al. 2006). Since ecological processes and different wetland taxa also respond differently to local land use, land management, and land cover (e.g., Findlay and Bourdages 2000; Akasaka et al. 2010; Rooney et al. 2012) it is challenging to identify a single spatial extent and timing of land-cover data to evaluate the impacts of land use and land cover on wetland systems (e.g., Tavernia and Reed 2010).

2.1.1 Spatial Extent of Land Cover

Human activity in the landscape surrounding a wetland may influence the wetland and its biota in several ways, such as directly limiting species dispersal (Rooney and Bayley 2011), changing the microclimate (Zhong et al. 2016), and facilitating the spread of invasive species (Werner and Zedler 2002) or predators (Fahrig 2003). As depicted in **Figure 2.1**, landscape composition may influence wetland vegetation communities directly, for example, by isolating the wetland from potential propagule sources (e.g., Boughton et al. 2010; Capers et al. 2010). However, surrounding land use may also influence wetland biota indirectly, mediated by its

influence on environmental conditions in the wetland and the environmental tolerances of different species. For example, land cover within a wetland's catchment may alter the volumes of snowdrift and snowmelt that enter the wetland (van der Kamp et al. 1999) and affect the transport and accumulation of sediments (Martin and Hartman 1987; Werner and Zedler 2002), nutrients (Freeland et al. 1999), salts (Hayashi et al. 1998b) and contaminants (Messing et al. 2011; Main et al. 2016) in runoff.

Yet another factor to consider, however, is that landscape composition may be spuriously related to wetland biota, if it merely reflects the signature of a particular biogeographic region, and thus is correlated with the species pool, soil type(s), or climate available in that region (e.g., Mikulyuk et al. 2013; Rooney and Azeria 2015; **Figure 2.1**). In which case, an apparent association between land cover and wetland conditions would be entirely the result of spatial autocorrelation (King et al. 2005; Rooney et al. 2012). Failing to test for and control spatial autocorrelation can lead researchers to falsely conclude that there are significant associations between their study systems and the adjacent landscape (Legendre et al. 2015) and may interfere with the selection of the most biologically-appropriate spatial extent (Wheatley and Johnson 2009; Jackson and Fahrig 2015).

Most studies investigating the relationship between wetland conditions and surrounding land cover define the landscape of influence using symmetrical buffers (e.g., Galatowitsch et al. 2000; Houlahan and Findlay 2004; Houlahan et al. 2006; Akasaka et al. 2010; Tavernia and Reed 2010; Rooney et al. 2012). Buffers capture the land cover within a specified radius of the wetland perimeter and may be either nested (e.g., all the land cover within a radius of 100, 250,

500, or 1,000 m) or multiple rings, which enable the differentiation of land cover between ranges (e.g., 0-100, 101-250, 251-500 m). While buffers around wetlands can be easily generated and visualized using contemporary Geographical Information Systems, the choice of buffer radius is typically arbitrary and may have little ecological relevance (Levin 1992; Jackson and Fahrig 2015). Moreover, symmetrical buffers presume that the “critical” distance at which land cover affects wetland conditions is isotropic (i.e., the same in all directions) for all study sites. However, as I described above, wetlands are strongly affected by runoff processes. They sit at the bottom of their catchments, not the center (**Figure 2.2**). Thus, the spatial influence of runoff is anisotropic, due to topography and gravity (Maltby and Barker 2009), and thus the influence of surrounding land cover on wetlands is unlikely isotropic.

The reliance of studies relating wetland environmental and biological conditions to surrounding land use on symmetrical buffers is at least in part because delineating catchments is more work (Martinez et al. 2010; Novikmec et al. 2016), especially in areas like the Prairie Pothole Region (PPR) where high-resolution digital elevation models (DEMs) are necessary to delineate catchments due to the low relief topography (van der Kamp and Hayashi 2009; McCauley and Anteau 2014). In such areas, the resolution of the DEM used in delineation may have a significant influence on the catchment size and shape (e.g., **Figure 2.2**), yet the importance of this resolution dependency is unknown.

2.1.2 Timing of Land Cover

The year of land-cover data collection in research on the effects of land use on wetland condition is important because it determines whether wetland conditions are being compared to

contemporary or historical land covers (Tavernia and Reed 2010). Generally, researchers make an effort to obtain the most recent land-cover data available, but it is not clear whether using land-cover data from a few years ago will have a marked influence on the study outcome. In agricultural lands with inter-annual and annual crop rotations, for example, land cover may change substantially year to year. In some studies, the land-cover data being compared to ecosystem conditions predates the field work by several years (e.g., Galatowitsch et al. 2000; Houlihan et al. 2006; Bayley et al. 2012), whereas other studies obtain land-cover data during the same year as field sampling (e.g., Rooney et al. 2012; Qiu and Turner 2015). Because aquatic ecosystems may take years or even decades (e.g., Kirkman et al. 1996; Findlay and Bourdages 2000) to respond to changes in land cover, studies that employ land-cover data from the same year as fieldwork is conducted may actually underestimate the effects of human land use on ecological processes and structure (Tavernia and Reed 2010).

2.1.3 Knowledge Gaps and Objectives

In general, my analyses will help to test my conceptual model that land cover influences environmental conditions directly (through snowmelt runoff processes) which in turn influence what vegetation is observed at a wetland. Further, that land cover can also influence wetland vegetation directly through imposition of dispersal constraints and the connectivity to propagules sources. Lastly, my analyses will test that these causal relationships take place within the confines imposed by regional differences in climate and species pool. In this chapter, I will contrast the concordance of wetland vegetation and environmental variables with land-cover data extracted from symmetrical buffers of varying radius and from wetland catchments defined by digital elevation models of differing resolution to determine whether using catchments

significantly improves the detection of concordance with wetland conditions. Additionally, I will contrast land-cover data extracted in the year of field work with data extracted from the preceding three years to determine whether current land cover data yields a different prediction of wetland condition than data that is a few years out of date. I will thereby identify the spatial scale(s) and temporal period(s) at which land cover composition around wetlands is most strongly predictive of wetland conditions. I hypothesize that both the wetland abiotic and vegetation data will be significantly correlated with adjacent land cover and that the environmental variables will be more responsive to land cover within the delineated catchment than land cover from symmetrical buffers, reflecting the important role of snowmelt runoff. I hypothesize that the plant communities will reflect local environmental conditions and also be strongly linked with catchment land covers, though the concordance between vegetation and land cover will be of lesser magnitude due to the influence of biogeographical processes operating at larger spatial extents. Finally, I hypothesize that, due to the importance of antecedent conditions (i.e. time lag effects), the environmental and vegetation response data will be less responsive to land cover measured during the year of sampling than land-cover data collected in preceding years.

2.2 Methods

2.2.1 Study Region and Sites

My study area included the Grassland and Parkland Natural Regions of Alberta, Canada, within the semi-arid glaciated plains of North America (**Figure 2.3**). Both the Grassland and Parkland have undulating topography, with soils being primarily poorly drained, clay-rich glacial tills (van der Kamp and Hayashi 2009). These Natural Regions are distinct, however, in terms of

climate and dominant natural land covers. The Grassland is a dry mixed-grass prairie ~95,000 km² in area, whereas the Parkland is an ecotone between the Grassland and Boreal Forest ~61,000 km² in area, with small stands of trembling aspen (*Populus tremuloides* Michx.) interspersed among the prairie vegetation (Natural Regions Committee 2006). The dominant land use in both of these areas is agriculture: mainly cereal and oilseed cultivation in the Parkland where mean annual precipitation (MAP) is 441 mm and mean annual temperature (MAT) is 2.3 °C; and a mix of cropping and grazing in the drier Grassland, where MAP and MAT are 371 mm and 4.2 °C, respectively (Natural Regions Committee 2006). Urban areas and oil and gas exploration are also present in both Natural Regions.

In both Natural Regions, graminoid marshes (“prairie potholes”) form in topographic depressions on the landscape (Stewart and Kantrud 1971). These marshes receive the majority of their water from snowmelt (Hayashi et al. 1998a; van der Kamp and Hayashi 2009). The semi-arid climate creates a moisture deficit the rest of the year, which limits the amount of runoff and surface water connectivity between prairie pothole basins except for infrequent summer deluge conditions, in which a “fill-spill” effect may occur between adjacent basins (van der Kamp and Hayashi 2009; Shaw et al. 2012). Wetland water levels draw down gradually over the growing season through evapotranspiration and soil infiltration, resulting in a dominance of wetlands with non-permanent ponds known as ephemeral, temporary, seasonal, semi-permanent or permanent, depending on the duration of ponding (Stewart and Kantrud 1971; Zhang et al. 2009). Groundwater recharge occurs at some wetlands, but most infiltrated water is moved by horizontal flow into the uplands (Hayashi et al. 1998a); due to the very low hydraulic conductivity of the glacial tills, there is essentially no inter-wetland hydrologic connectivity via

groundwater flow (van der Kamp and Hayashi 2009). Therefore, these marshes are mainly hydrologically isolated from each other and dependent on water inputs within their catchments.

While both Natural Regions contain marshes whose open water ponds range from ephemeral to permanent, the species composition of these wetlands differs between the Grassland and Parkland. The cooler climate in the Parkland supports more robust emergent vegetation such as cattails (*Typha latifolia* L.) and willow shrubs (*Salix* spp. L.), whereas the drier Grassland wetlands are typically dominated by herbaceous wet meadow species such as foxtail barley (*Hordeum jubatum* L.), slough-grass (*Beckmannia syzigachne* (Steud.) Fernald) and fowl bluegrass (*Poa palustris* L.) (Stewart and Kantrud 1971). Additionally, wetland vegetation communities in the Parkland are augmented by species from neighboring forests, while these landforms are absent in the Grassland and remnant prairies are the only source of native upland vegetation entering wetlands (Natural Regions Committee 2006). The dominant anthropogenic land uses – cultivation and grazing – may also modify the regional species pools (Rooney and Azeria 2015) and have selective effects on wetland community composition (Galatowitsch et al. 2000; Werner and Zedler 2002).

2.2.2 Site Selection

I randomly selected three major sub-watersheds within each of Alberta's Grassland and Parkland Natural Regions, based on the criteria that they did not cross interprovincial or international borders and comprised landforms of glaciolacustrine or glaciofluvial origin to help standardize the influence of surficial geology on wetland density and permanence class. Within each sub-watershed, I queried the Alberta Wetland Inventory (AEP 2014) to identify all non-

permanent marshes (sensu Stewart and Kantrud 1971) and shortlisted a random subset of these. I stratified my sample frame along two orthogonal gradients: one spanning a range of permanence class (seasonal, temporary and semi-permanent marshes) and the second a gradient of human disturbance as measured by the extent of non-natural land cover within a 500 m buffer surrounding each wetland during 2013 (AAFC 2013c). Non-natural cover included developed, cropped and grazed lands, as opposed to natural covers like forest, open water, other wetlands and grassland. Selection of the final sampling sites was subject to property access and ground-level verification of the wetland permanence class (AEP 2014) and disturbance levels (AAFC 2013c). Additionally, I ensured that the size of wetlands selected in each sub-watershed reflected the size frequency distribution within that sub-watershed, and maintained a distance of at least 3.5 km between wetlands to control for spatial independence. Based on these criteria, I selected eight marshes within each sub-watershed for a total of 48 sites within my study region (**Figure 2.3**) and visited each five times at approximately three-week intervals between May and August 2014.

2.2.3 Water Sampling

During the first visit to each wetland, a staff gauge was installed at the deepest point of the basin to allow tracking of water-level change throughout the growing season (May-August 2014). I measured water depth at the staff gauge on each subsequent visit. At the same time, I measured turbidity (AquaFluor, Turner Designs), pH (IQ150, Spectrum Technologies), dissolved oxygen (DO; HQd Portable Meter and LDO101, Hach Company), conductivity and temperature (HQd Portable Meter and CDC401, Hach Company) *in situ* about 30 cm below the water surface within a 1 m radius of the staff gauge.

Also during the first site visit, I collected water samples as this is when water levels are typically highest in prairie potholes (van der Kamp et al. 1999) and matches the sampling protocol timing of Main et al. (2016). My samples were collected into sample bottles that were pre-rinsed with distilled and de-ionized water and pond water, filled with no headspace at the deepest part of the pond basin, kept chilled and in the dark, and received by the analytical labs within 72 hours of collection.

The first water sample collected at each wetland was submitted to the Alberta Innovates Environmental Analytical Services Laboratory in Vegreville, AB for analysis of glyphosate and residues of its derivatives, aminomethylphosphonic acid (AMPA) and glufosinate. These compounds were prepared and derivatized following Tsunoda (1993) and Alferness and Iwata (1994), and then identified and quantified using gas chromatography and ion trap mass spectroscopy. Detection limits were 0.2 µg/L for glyphosate and AMPA, and 1.0 µg/L for glufosinate.

Water samples collected for analysis of neonicotinoids were also submitted to the Alberta Innovates lab, where they were acidified and individual compounds (thiamethoxan, clothianidin and imidacloprid) were extracted using dichloromethane and concentrated. The majority of the extract was run through a gas chromatography ion trap to isolate thiamethoxan, while 100 µL was concentrated to dryness, reconstituted in methanol and run through liquid chromatography and mass spectroscopy to isolate clothianidin and imidacloprid. Detection limits were 0.05 µg/L for thiamethoxan and 0.01 µg/L for clothianidin and imidacloprid.

The third water sample collected from each wetland was submitted to the Agriculture and Agri-Food Canada Lethbridge Research Centre in Lethbridge, AB, and analyzed for a suite of 104 herbicides, insecticides and fungicides, including 2, 4-D, difenoconazole and MCPA. Compounds were first extracted using the Agilent QuEChERS reagent (Anastassiades et al. 2003), then derivatized and analyzed by gas chromatography and mass spectroscopy using an Agilent GC/MS/MS Pesticides Analyser 3.0, following the approaches of Bruns et al. (1991) and Hill et al. (2002). Detection limits were approximately 0.025 µg/L for most pesticides, and all detected compounds are listed in **Appendix A**.

A bulk water sample was also collected for analysis of nutrients, major ions, total suspended solids (TSS) and dissolved organic carbon (DOC) and was submitted to the University of Alberta Biogeochemical Analytical Services Laboratory. Anions (Cl⁻ and SO₄²⁻) were analyzed using a Dionex DX-600 Ion Chromatograph, following U.S. EPA method 300.1 (Pfaff et al. 1997). Cations (Ca²⁺, Mg²⁺, K⁺ and Na⁺) were analyzed using a Thermo Scientific ICAP 6300 Inductively-Coupled Argon Plasma - Optical Emission Spectrometer (ICP-OES), following U.S. EPA method 200.7 (Martin et al. 1994). Total carbon (TC) and DOC were analyzed using a Shimadzu TOC-5000A Total Organic Carbon Analyzer, following U.S. EPA method 415.1 (U.S. EPA 1979). Total nitrogen (TN) and total phosphorus (TP) were analyzed using a Lachat QuickChem QC8500 FIA Automated Ion Analyzer, following standard procedures (AWWA 2012a, b). TSS was determined gravimetrically from residues dried at 180 °C following U.S. EPA method 160.1 (U.S. EPA 1971). All water physical and chemical analytes are listed in **Appendix B**.

2.2.4 Vegetation Sampling

Vegetation sampling occurred from mid-July to mid-August 2014, when most plants were at maturity and peak biomass. I used a handheld GPS receiver with <2.5 m horizontal accuracy (Juno Trimble T41/5 running ArcPad v. 10.0 (ESRI 2011) and SXBlue II GNSS Receiver) to map the wetland-upland boundary and vegetation assemblages within the wetland. This delineation was based on the presence of plants determined to be wetland-facultative or wetland-obligate in the North American Great Plains (sensu Lichvar et al. 2014). Vegetation assemblages were identified according to species (co-)dominance within a patch (>25% cover), and a threshold of 50% cover was used to delineate patch edges along upland or assemblage ecotones. All wetland and assemblage mapping was done by myself to reduce bias associated with multiple observers and to ensure consistency in delineation among wetlands.

Sampling intensity was in proportion to the size of each vegetation assemblage to reflect the complexity and relative composition of the wetland vegetation communities. In assemblages that exceeded a net area of 100 m², I deployed a minimum of five 1 m² quadrats randomly, stratified among multiple patches if more than one was delineated. An additional 1 m² quadrat was added for each 1,000 m² that the assemblage exceeded 5,000 m² in area until no additional species were detected after deploying three consecutive quadrats. *A priori* power analyses found that this sampling intensity was adequate at characterizing plant community composition, a contention which I validated with post-hoc analyses (detailed in **Appendix C**). Within each quadrat, vascular plants were identified to the species-level where possible. The relative abundance of each species within a quadrat was estimated using modified Braun-Blanquet percent-cover classes. Plants were identified following the nomenclature of Moss and Packer (1983) and updated to reflect the current taxonomic status accepted by the Integrated Taxonomic

Information System (<http://www.itis.gov/>; accessed January 2016). Voucher specimens of difficult-to-identify species are housed at the ALTA Vascular Plant Herbarium at the University of Alberta. Among the 48 wetlands, I deployed 792 quadrats within 150 vegetation assemblages and observed a total of 169 plant species, which are listed in **Appendix D**.

2.2.5 Soil Sampling

Wetland soil sampling was concurrent with vegetation surveys. *In situ* measurements of conductivity (HI98331, Hanna Instruments) were taken at all vegetation quadrats; when soil was not saturated with water, a saturation paste was prepared and conductivity was measured in the paste instead of directly from the soil. At three quadrats per vegetation assemblage I used a cylindrical suction corer of 4.9 cm inner diameter to extract three replicate soil cores to a depth of 10 cm. These cores were composited and kept frozen until analysis. In total, I took 450 soil samples and *in situ* measurements from 792 quadrats.

Bulk density and water content were determined gravimetrically after drying soil at 80 °C for 72 h and weighing. Loss-on-ignition was determined following 4 h in a muffle furnace at 550 °C. TC and TN were analyzed using a CE-440 Elemental Analyzer (Exeter Analytical) following U.S. EPA 440.0 (Zimmerman et al. 1997) at the University of Alberta Biogeochemical Analytical Services Laboratory. Additional soil fertility analysis was conducted at the University of Guelph Agriculture and Food Laboratory in Guelph, ON. Soil pH was determined using an electrode in a saturation paste as described by Hendershot et al. (1993). K⁺, Na⁺, Mg²⁺ and Ca²⁺ were extracted using ammonium acetate (Simard 1993), zinc (Zn) was extracted using diethylene triamine pentaacetic acid (Liang and Karamanos 1993), manganese (Mn) was extracted with

phosphoric acid (OMAFRA 1998), and total sulfur (TS) was determined using nitric acid closed vessel microwave digestion (Anderson 1999). Concentrations of extracted K^+ , Na^+ , Mg^{2+} , Ca^{2+} , Zn, Mn and TS were determined using a Varian Vista Pro ICP-OES. P was extracted using the Olsen sodium bicarbonate method (OMAFRA 1998), with concentration determined colorimetrically with a SEAL AutoAnalyzer 3 HR. Lastly, extraction and analysis of soil pesticide residues was also performed at the Agriculture Agri-Food Canada-Lethbridge Research Centre, following the process described above for water samples. All soil physical and chemical analytes are listed in **Appendix B**.

2.2.6 Spatial Analyses

To extract land-cover data for comparison with measured abiotic and vegetation data, I first obtained Agriculture and Agri-Food Canada's (AAFC) Annual Crop Inventory data from 2011, 2012, 2013, and 2014 (AAFC 2013a, b, c, 2015). All subsequent analyses were applied to each of these four datasets. The Annual Crop Inventory classifies and maps land cover in Canada's agricultural regions at a 30 m spatial resolution based on composites of optical- and radar-based satellite imagery (Fisette et al. 2014). It identifies 60 land cover types across Canada, with specific emphasis on crop covers. Due to the increased thematic resolution at which crops were classified relative to other land cover types, consolidation of cover classes was necessary to avoid differences in landscape characterization associated with different levels of classification precision (Buyantuyev and Wu 2007). Land-cover data were reclassified into nine types that represent vegetation types that have similar ecological function (i.e., forests, wetlands, native grassland, shrubland), similar land use and land management activities (i.e., cropland, pasture/hay, developed), water bodies, or exposed/barren land (see **Appendix E**). To derive these

nine classes, I consolidated mixed-wood, deciduous, and coniferous land-cover types into one forest cover bin and consolidated annual crops (e.g., barley, canola, wheat) into a single cropland land-cover bin.

For each of these four datasets, I produced eight nested buffers of varying radii in ArcMap, v. 10.3.1 (ESRI 2015) (radii of 30, 100, 200, 300, 500, 1,000, 2,000, and 5,000 m; **Figure 2.2**). Buffers extended from each wetland's perimeter, as defined during vegetation mapping. In addition, I generated wetland catchments using digital elevation models (DEMs) at 10 m and 25 m resolution for southern Alberta. I contrasted two DEMs to determine whether spatial resolution of the DEM affected the strength of the relationships between land cover and wetland abiotic or vegetation data. My approach to catchment delineation followed McCauley and Anteau (2014). In brief, each DEM was used to create a flow direction raster, from which basins were defined as the area receiving surface water flow. Cells in the raster comprising a basin were converted into a basin polygon representing the boundary and area of the basin. I considered basin polygons that intersected with the mapped wetland polygon to be hydrologically contributing to the wetland, and merged these to create a catchment for each wetland. To check whether a catchment polygon was interrupted by linear features (e.g., **Figure 2.2**), I added road and stream vector files and checked for intersections between these two within each catchment. If no culverts were observed during field work or indicated by road/stream vector overlap, I considered the road to be a hydrologic barrier to the catchment (Shaw et al. 2012) and truncated the catchment polygon along the road.

For each year \times extent polygon combination, I extracted land-cover data from the AAFC Annual Crop Inventory. I then calculated the proportional coverage of land-cover classes within each buffer or catchment. Proportional coverage of land cover was used, rather than absolute area, because it provided a standardized measurement across wetlands with different areal extents (**Table 2.1**). In total, 40 different land-cover datasets were created (10 spatial extents \times 4 time periods). Map production and all spatial analyses were performed in ArcMap, v. 10.3.1 (ESRI 2015).

2.2.7 Statistical Analyses

For comparison purposes, I standardized the 45 environmental variables by relativizing each measurement by its column maximum (McCune and Grace 2002). Repeated *in situ* measurements of water depth, temperature, turbidity, conductivity, dissolved oxygen and pH were each averaged across site visits to provide one value per wetland. I also consolidated the pesticide data by type, yielding the incidence of herbicide, insecticide and fungicide detections in each medium. Vegetation community composition was represented as the relative abundance (percent cover) of each observed plant species at a wetland, and was determined by calculating the site-level average abundance among the quadrats sampled at each site. Similarly, I took the average of soil nutrients, ions and physical parameters across quadrats to provide wetland-level soil data. To reduce dataset sparsity that results from the presence of rare species and can strongly affect dissimilarity matrices, I removed 48 species that were observed in only one of the 150 assemblages, leaving 121 plant species for the analysis (see **Appendix D**).

I used Mantel tests (McCune and Grace 2002; Legendre et al. 2015) to evaluate the concordance between a given land-cover dataset and the wetland environmental or vegetation data (hereafter response matrices). Mantel tests evaluate the correlation between two dissimilarity matrices and describe the extent to which the two dissimilarity matrices exhibit the same pattern of redundancy. Two important assumptions are made about the relationships between these dissimilarity matrices: 1) that the relationships between rank-transformed variables must be monotonic, and 2) that small (large) values in the first dissimilarity matrix correspond with small (large) values in the second, indicating homoscedasticity (equivalent variances) in the distribution (Legendre et al. 2015). Because the Mantel test operates on dissimilarity matrices rather than on raw data, it should only be used to assess hypotheses concerning the agreement between dissimilarity matrices and not hypotheses about the original data (Legendre et al. 2015). However, the Mantel test is perfectly suited to my application in this chapter, because I seek to evaluate the degree of concordance between pairs of dissimilarity matrices, rather than describe the nature of the relationships between individual land cover, abiotic or plant variables. Thus, the Mantel test lets me assess whether there is evidence of association between landscape composition and wetland conditions, without requiring assumptions about how specific chemical or hydrological variables or how individual species will respond to changes in the relative abundance of specific land cover classes. I am testing the hypothesis that sites that are similar in terms of local landscape composition are also similar environmentally or in terms of vegetation composition. The significance of the standardized Mantel statistic (r_M , a correlation coefficient between the two dissimilarity matrices) is determined by repeated randomization of the rows and columns of one matrix, where the resulting p -value represents the proportion of randomized permutations with a correlation score

larger than the observed score. Mantel r_M values are usually much smaller than the Pearson's correlation coefficients produced for the same sample size (Dutilleul et al. 2000; Goslee and Urban 2007): r_M coefficients ≥ 0.1 have been shown to be highly statistically significant and indicate a strong association between the two dissimilarity matrices (e.g., King et al. 2005; Rooney and Azeria 2015).

In the comparison between land cover and abiotic variables, I used Euclidean distances, because these datasets exhibited bivariate linearity and low sparsity. Euclidean distance was inappropriate for calculating the dissimilarity matrix on vegetation data, because vegetation community datasets typically possess high sparsity and because species vary naturally in their maximum abundance such that Euclidean distances lose sensitivity with increasing environmental distance (see McCune and Grace 2002). Consequently, for the comparison between land cover and vegetation dissimilarity matrices, dissimilarity was calculated using the Bray-Curtis distance measure (Bray and Curtis 1957). I ran Mantel tests comparing land-cover dissimilarity matrices calculated from the 10 spatial extents \times the four years (40 total) to both of the environmental and vegetation dissimilarity matrices for a total of 80 Mantel tests. Each Mantel test used 10,000 permutations of a Monte Carlo randomization test to assess the significance of the calculated r_M value (Jackson and Somers 1989). To identify which of the 40 spatial extent \times year combinations of land-cover data yielded the strongest association with the abiotic and vegetation response matrices, I identified which Mantel test yielded the largest r_M and used bootstrapping without replacement to generate 90th percentile confidence intervals around each r_M value, to assess whether differences in r_M were statistically significant (Goslee and

Urban 2007; Rooney and Azeria 2015). Bootstrapping involved 5,000 iterations at a resampling rate of 0.7 without replacement (Rooney and Azeria 2015).

Given the latitudinal gradients in climate and land cover types in my study region (Natural Regions Committee 2006), I suspected that the similarity in land cover and wetland conditions of some sites may be influenced by their geographic position (i.e., spatial autocorrelation; e.g., King et al. 2005). Because spatial autocorrelation among wetlands may artificially inflate r_M values, I used partial Mantel tests (Legendre et al. 2015) to assess the effect of removing the spatial component of variation among sites on the overall congruence between the land-cover and response matrices. Partial Mantel tests measure concordance between two dissimilarity matrices while controlling for the confounding variation associated with a third dissimilarity matrix (King et al. 2005; Goslee and Urban 2007). In my case, this third matrix comprised the geographic coordinates of the wetlands. As with the simple Mantel tests, I compared all 40 land-cover dissimilarity matrices with each of the abiotic and vegetation dissimilarity matrices for a total of 80 partial Mantel tests, using the method described already. Legendre et al. (2015) note that the presence of spatial autocorrelation may violate the Mantel test assumptions of linearity/monotonicity and homoscedasticity between the dissimilarity matrices, resulting in a loss of statistical power. Thus, I am not using the partial Mantel test as a means to quantify the nature and extent of possible spatial autocorrelation among my study wetlands, but to indicate whether the original Mantel test results may have been confounded and inflated by uncontrolled spatial variation. After removing the spatial component of variation with the partial Mantel tests, I considered decreases in r_M values to indicate that spatial

autocorrelation is likely present and may have contributed to some of the land cover × wetland congruence detected by the original Mantel tests.

All Mantel tests and bootstrapping were performed in the statistical platform R, v. 3.2.3 (R Core Team 2015) using the Mantel function of the “ecodist” package (Goslee and Urban 2007).

2.3 Results

2.3.1 Wetland, Catchment, Buffer Delineation and Land Cover Extraction

My study wetlands were generally small (mean area = 0.81 ha, range = 0.04-3.28 ha; **Table 2.1**), which is typical in the PPR where wetlands <1 ha in size are historically the most abundant on the landscape (Hayashi et al. 1998a; Zhang et al. 2009). The geographic distribution of the wetlands ranged from 50.16 °N to 53.23 °N in latitude and from 111.22 °W to 114.20 °W in longitude (**Figure 2.3**). Wetland catchments, having been delineated from topographic data of differing resolutions, varied in size and shape among my study wetlands. Though the catchments delineated from the 10 m DEM were smaller than the 25 m DEM catchments (two-tailed paired sample *t*-test: $t = -3.279$, $df = 47$, $p = 0.002$), the 10 m DEM catchments had a size range (**Table 2.1**). Mean catchment size was twice as large in the Grassland than in the Parkland for catchments delineated from both 10 m and 25 m resolution DEMs. The 10 m DEM catchments were 23.40 ha in the Grassland versus 11.08 ha in the Parkland (on average), whereas the mean 25 m DEM catchment size for the Grassland and Parkland was 29.05 ha and 14.43 ha, respectively). The frequency distributions of catchment sizes were right-skewed, whereas the frequency distributions of the buffer sizes were more normal. The mean catchment area based on

the 10 m DEM and the 25 m DEM were not statistically different from the areas of the 200 m buffers (two-tailed paired sample t -test: $t = -1.487$, $df = 47$, $p = 0.144$ and $t = 0.586$, $df = 47$, $p = 0.561$, respectively), although catchment size was considerably more variable among wetlands (**Table 2.1**). Two-sample t -tests revealed significant differences in landscape composition between the Grassland and Parkland wetlands, with more native prairies in the Grassland ($t = 8.569$, $df = 46$, $p < 0.001$) but more cropland ($t = -4.629$, $df = 46$, $p < 0.001$), developed land ($t = -3.584$, $df = 46$, $p = 0.001$), forests ($t = -3.781$, $df = 46$, $p < 0.001$), pasture ($t = -3.160$, $df = 46$, $p = 0.003$) and shrubland ($t = -6.635$, $df = 46$, $p < 0.001$) surrounding Parkland wetlands based on the 5,000 m buffer extent and 2014 land-cover data (**Appendix E**).

2.3.2 Land Cover × Environment Mantel Test Results

Land cover × environmental r_M values ranged from 0.0390 to 0.2418, with a mean of 0.1523 and standard deviation of 0.0570 (see **Appendix F**). Comparing the different spatial extents, a threshold in Mantel r_M values is evident at 1000 m. Land cover extracted from within 1000 m of study wetlands was significantly concordant with abiotic data (lower confidence interval for r_M does not overlap 0, $\alpha = 0.05$), while land cover extracted from buffers with radii greater than 1000 m were not significantly concordant with abiotic data (r_M values not significantly different from 0; **Figure 2.4**). The average width of the 90% confidence intervals around the r_M values was 0.1778, with a standard deviation of 0.0222 and ranging from 0.1503 to 0.2446. The 90% confidence intervals of all spatial extent × year combinations equal to or less than 1000 m overlapped (**Figure 2.4**), indicating insignificant differences in concordance among land-cover datasets that were significantly concordant with environmental conditions.

2.3.3 Land Cover × Vegetation Mantel Test Results

The r_M values indicating concordance between the land cover and vegetation dissimilarity matrices ranged from 0.0169 to 0.1296, with a mean value of 0.0879 and standard deviation of 0.0260 (see **Appendix G**). Land-cover data extracted from catchments was always concordant with vegetation, but when land cover data was extracted from symmetrical buffers, only buffers with a radius greater than 300 m yielded land cover data significantly concordant with wetland vegetation composition in every sample year ($\alpha = 0.05$). Conversely, land-cover data extracted from buffers less than 300 m in 2014 and from buffers less than 200 m in all four years were not significantly concordant with vegetation composition (**Figure 2.5**). The average width of the bootstrapped 90% confidence intervals constructed around the r_M values was 0.1483, with a standard deviation of 0.0070 and ranging from 0.1264 to 0.1595. All confidence intervals overlapped with one another, resulting in no spatial extent × time period combination with a significantly greater or smaller r_M value than another (**Figure 2.5**).

2.3.4 Comparison of Environmental and Vegetation r_M Values

The catchments were always among the most strongly concordant spatial extent, regardless of whether land cover was compared to environmental conditions or vegetation composition. However, I observed two differences between the patterns of r_M values for the environmental (**Figure 2.4**) and vegetation (**Figure 2.5**) Mantel tests. First, I observed a clear peak in r_M values comparing the environmental dissimilarity matrix with intermediate spatial extents of land cover (i.e., at the 200-500 m buffers; **Figure 2.4**), while the strength of the correlation between the land cover and vegetation dissimilarity matrices appears to increase with spatial extent (**Figure 2.5**). Second, whereas the r_M values increased when comparing environmental data to older land-cover data, I observed a peak in r_M values between the vegetation abundance dissimilarity matrix and

the one-year-old land-cover data, indicative of a one-year time lag between land cover change and vegetation community change. However, these trends should be interpreted with caution because of the overlap in bootstrapped 90% confidence intervals.

2.3.5 Spatial Autocorrelation

Mantel tests conducted between the geographic and response data dissimilarity matrices found significant associations between wetland location and both measures of wetland condition (location \times environment $r_M = 0.1906$, $p = 0.0030$; location \times vegetation $r_M = 0.2027$, $p < 0.0001$). After controlling for geographic position with the partial Mantel tests, I observed decreases in all r_M values and increases in p -values (i.e., lower statistical significance) relative to the simple Mantel test results for environmental (**Figure 2.6; Appendix F**) and vegetation (**Figure 2.7; Appendix G**) response matrices. All land cover \times environment combinations that were significantly concordant based on the simple Mantel tests remained significant after removing the spatial component of the inter-wetland variation ($\alpha = 0.05$), except for the case of land-cover data extracted from 1000 m buffers, which became insignificant once the effect of spatial autocorrelation was removed. Conversely, all land cover \times vegetation r_M values except for the 25 m DEM catchment in 2013 ($p = 0.0433$) became non-significant once geographic position was controlled for.

2.4 Discussion

I sought to determine whether the relationships between adjacent land covers and wetland-level characteristics in marshes in Alberta were spatially-dependent or exhibited time lag effects. Specifically, I used dissimilarity matrices to compare both wetland environmental

and vegetation community measurements to land-cover data collected in four consecutive years and extracted using ten spatial extents. Of the spatial extents tested, I included topographically delineated wetland catchments, which McCauley and Anteau (2014) predicted would be more effective than fixed buffer distances at representing the land covers that influence marshes because they should better reflect the importance of surface water connectivity. Despite arguments in the literature in support of catchment-based land-cover analysis (McCauley and Anteau 2014; Novikmec et al 2016), I found no significant improvement in the association between the composition of land cover and abiotic or vegetation measurements, when the land-cover data was extracted within topographically defined catchments versus when it was extracted from within symmetrical buffers. In fact, the concordance between land cover and wetland conditions was strong enough to be detected at nearly every combination of time period and spatial extent examined. Non-significant trends in my analysis suggest that using land cover composition within catchments may outperform predictions of environmental conditions and vegetation composition over very small (<100 m) or very large (>1 km) radius buffers; however, my results indicate that the associations between land cover and wetland conditions are quite robust to spatial extent. This should allay concerns around reliance on buffers where high resolution DEMs or catchment polygons are not available.

There is much evidence that land use changes can affect wetland biota (Galatowitsch et al. 2000; Lopez et al. 2002; Houlahan et al. 2006; Akasaka et al. 2010; Rooney et al. 2012; Quesnelle et al. 2013), but the effects may not be realized immediately. The mechanism usually called upon to explain time lags in biological response to changes in land cover relates to the concept of extinction debt, whereby populations dwindle slowly once habitat conditions have

deteriorated to unsustainable levels (Hanski and Ovaskainen 2002). For example, Findlay and Bourdages (2000) observed that wetland biodiversity losses were more strongly predicted by historic road density than contemporary road density and concluded that the full effects of existing roads were yet to be felt, and Jenkins et al. (2003) found that prairie pothole crustacean diversity continues to decline following historic wetland drainage. Alternatively, lags in biological response may be related to slow dispersal rates (e.g., Hutsemekers et al. 2008; Helm et al. 2006). In some cases, it may take over a hundred years for populations to come into equilibrium with the altered composition of their landscape (e.g., Jenkins et al. 2003; Paltto et al. 2006; Vellend et al. 2006). In my analysis, I found some support for a brief (one-year) time lag in response of vegetation to surrounding land cover, although the trend was non-significant.

Research around best management practices in agriculture has also found time lags between changes in management or land use and water quality (Meals et al. 2010) or wetland ecosystem states (Zweig and Kitchens 2009). These time lags are in part attributed to the cumulative time required for land use activities to produce an effect (e.g., pulse of nutrients), for the effect to reach an aquatic ecosystem, and for the ecosystem to respond to the effect (Meals et al. 2010). I observed evidence of a time lag between land cover and abiotic conditions in my study system, where the strength of association between abiotic variables and land-cover data at all spatial extents was strongest when the land-cover data was extracted from 2011 and 2012, and sequentially weaker with land-cover data from 2013 and 2014. However, due to large confidence intervals, these trends were not statistically significant. Longer term land-cover datasets (i.e., collected ≥ 5 years ago) are necessary to really investigate time lags in land cover impacts on prairie pothole hydrological (van der Kamp et al. 1999) or biogeochemical (Van Meter and Basu

2015) properties, though the availability and quality of such data may be inferior compared to more recent data.

However, I was not attempting to detect the legacy effects of historic land cover changes. Rather, I sought to address the question of whether researchers really must obtain land cover data from the year in which their field study was conducted, or whether relatively recent (i.e. within the last four years) data on land cover would be adequate to detect a relationship between surrounding land use and wetland condition in both abiotic and biological terms. Given I observed no significant difference in concordance among the four years of land-cover data that I compared, I conclude that reliance on slightly outdated land cover data will not majorly affect the results, and may in fact yield a more predictive relationship to wetland condition than seeking data from the same year as field work. A search for evidence of longer-term lags on my measured environmental and biological variables remains an area for future research and will need to overcome difficulties around changes to classification method and grain size that emerge with older land-cover data.

2.4.1 Spatial Autocorrelation

When land cover types are non-randomly distributed on a landscape, spatial autocorrelation may create the appearance of congruence between dissimilarity matrices (King et al. 2005). This appears to be an important factor in my datasets, as when I controlled for spatial autocorrelation all my r_M values declined, though the comparisons between land-cover data and abiotic variables remained statistically significant at spatial extents less than 1000 m in radius. The spatial effects removed by the partial Mantel tests were likely associated with the latitudinal

climatic and physiographic gradients (e.g., in temperature, precipitation, soil type, dominant vegetation; Natural Regions Committee 2006) that span my broad study area (**Figure 2.3**) and contribute to the different land cover types between the two Natural Regions (**Appendix E**). The comparison of environmental conditions and land-cover data extracted from the catchments and buffers less than and equal to 500 m in radius remained significant, indicating that the concordance between land cover and abiotic conditions detected at those scales could reflect a direct effect of land cover on environmental conditions. However, controlling for geographic location rendered nearly all of the land cover \times vegetation r_M values non-significant, suggesting that the associations between vegetation and land cover are the product of differences in the regional species pools between the Grassland and Parkland (Mikulyuk et al. 2013; Rooney and Azeria 2015). That there are distinct wetland biological communities between Alberta's Natural Regions is supported by previous research (Natural Regions Committee 2006; Rooney and Azeria 2015; Polan 2016) and by visual inspection of an ordination plot of my study wetlands positioned in species space and grouped by Natural Region (see **Appendix H**).

The relatively larger decline in concordance between land cover and vegetation composition, once spatial autocorrelation was accounted for, actually affects my conceptual model (**Figure 2.1**). Once spatial patterning was accounted for, the residual concordance between land cover and vegetation composition closely mirrored the pattern in concordance between land cover and environmental conditions, with the largest r_M values being found in the catchments and echoed in the buffers of 300-500 m radius (**Figure 2.7**). In fact, the environmental and vegetation distance matrices are strongly concordant, even after accounting for spatial patterning (partial Mantel $r_M = 0.1948$, $p = 0.0080$). This suggests that the

environmental conditions themselves are what determine the vegetation composition of the marshes more so than the effect of land cover on propagule dispersal into the marshes. I consequently attribute the non-significant, residual concordance between land cover and vegetation to the effect of environmental conditions on vegetation composition and conclude that land cover composition only indirectly influences the wetland vegetation through its influence on environmental conditions. I also conclude that because the reduction in concordance between land cover and vegetation was so large once spatial autocorrelation was removed, especially at the largest buffer extents, biogeographical factors have a comparatively strong influence on vegetation community composition in these wetlands.

2.4.2 Land Cover × Environment Spatial Patterns

Environmental conditions in wetlands are concordant with adjacent land cover, whether it is defined from the catchment or from buffers 500 m in radius or less. Because of the anisotropic nature of runoff processes and previous research on ponds in Slovakia (Novikmec et al. 2016), I expected that extracting land cover from within catchments would yield stronger concordance with environmental conditions than land use extracted from buffers; however, my data do not support this hypothesis. While the catchments are representative of the hydrologically contributing area around the wetlands (van der Kamp and Hayashi 2009; Shaw et al. 2012; McCauley and Anteau 2014), it is possible that the runoff within the catchments is not the major delivery vector of sediments, nutrients and contaminants to prairie wetlands (though see Main et al. 2016). Due to naturally high infiltration rates in prairie soils (van der Kamp et al. 1999), little overland flow of runoff occurs during the active growing season. Instead, most of the runoff into prairie marshes occurs as snowmelt over frozen soil, when infiltration is low (Hayashi et al.

1998a; van der Kamp and Hayashi 2009; Shaw et al. 2012). Frozen soils not only resist infiltration, but also resist erosion and sediment transport to wetland depressions. Other processes that are not constrained by catchment boundaries, such as aerial deposition of sediments (Martin and Hartman 1987), salts (Hayashi et al. 1998b) or pesticides (Messing et al. 2011) may serve as the major vectors connecting wetland conditions to their surrounding landscape. Regardless, my results suggest that concordance detected between environmental conditions and land cover from more than 500 m away is an artifact of spatial autocorrelation. This contention is supported by previous research (Alahuhta et al. 2013; Mikulyuk et al. 2013; Novikmec et al. 2016; Olker et al. 2016) showing that adjacent land cover may be a poor predictor of wetland environmental conditions when spatial patterning exists but has not been adequately accounted for.

2.4.3 Land Cover × Environment Temporal Patterns

I had expected that land cover from the previous year would have the strongest concordance with abiotic conditions because spring snowmelt runoff would presumably carry the chemical signature of the land cover from the previous summer. As discussed above, however, my results suggest that runoff processes are not the major vector tying the abiotic condition of marshes to their surrounding landscape. Instead, the concordance between environmental conditions and land cover increased with the age of the land-cover data. In some regions, the delayed response of environmental conditions to land cover can be attributed to the slow movement of surficial groundwater transporting nutrients, salts or contaminants from the adjacent uplands (irrespective of catchment boundaries) into the wetland (Tomer and Burkart 2003; Meals et al. 2010). However, this mechanism is unlikely in the PPR, where groundwater

flow is extremely slow and does not make up an important component of the water budget of most wetlands (Hayashi et al. 1998a; van der Kamp and Hayashi 2009). The larger r_M values observed with older land-cover data may instead be associated with soil chemistry, which are modified over a much longer temporal scale (e.g., Freeland et al. 1999; Van Meter and Basu 2015) and provide a more integrative depiction of historical and recent land use activities than water chemistry (Houlahan and Findlay 2004). However, I cannot make inferences based on r_M values concerning which individual environmental analytes may be driving this time lag pattern (Legendre et al. 2015), and note that the differences in r_M values among years were not statistically significant.

2.4.4 Land Cover × Vegetation Spatial Patterns

Wetland vegetation appears to be insensitive to adjacent land cover at all spatial extents, once spatial autocorrelation among wetlands is accounted for. I hypothesized that the vegetation community in a wetland would be influenced both by its abiotic conditions (Mikulyuk et al. 2011; Rooney and Bayley 2011; Alahuhta et al. 2013) and by the direct effects of land cover on species dispersal and propagule sources (Lopez et al. 2002; Houlahan et al. 2006; Capers et al. 2010). However, my results suggest that the apparent association between land cover and vegetation is actually the product of the influence of environmental conditions, which are concordant with land cover, on wetland vegetation composition and the biogeographical differences between Natural Regions that affect the plant species pool. This is reinforced by the observation that the greatest decline in concordance due to removing spatial autocorrelation was evident in the largest buffer sizes. The strong concordance between land cover and wetland vegetation at buffers greater than 500 m in radius was likely driven by the differences in both

land cover and vegetation community composition between the Grassland and Parkland (Natural Regions Committee 2006), such that larger spatial extents provide a more accurate prediction of which Natural Region the wetland is found in, and therefore which species could colonize the site from the regional species pool. This observation supports the warning from Legendre et al. (2015) that the Mantel test could yield inaccurate conclusions when spatial patterning is unaccounted for.

2.4.5 Land Cover × Vegetation Temporal Patterns

I found no quantitative support for temporal effects of land cover on vegetation composition. I had predicted that vegetation would be significantly more responsive to land cover measured before the year of field sampling due to the time lags observed in other wetland studies (e.g., Kirkman et al. 1996; Findlay and Bourdages 2000), but there were no significant differences in vegetation concordance with land cover among years considered. This indicates a relative insensitivity of vegetation to different measures of landscape composition over this time interval, possibly due to the aforementioned spatial autocorrelation obscuring any time lag effects. The four-year time series considered in this study may be of inadequate duration to detect temporal responses of wetland biota to landscape changes: previous research has shown that the full effects of land cover change and disturbance on vegetation may not be detectable for several decades after the initial disturbance (Kirkman et al. 1996; Findlay and Bourdages 2000; Helm et al. 2006; Cuddington 2012). While the particular mechanisms relating wetland vegetation to the adjacent landscape are little understood in the PPR and warrant further investigation, future studies will likely find land-cover data extracted from any of the years I considered to be equally useful. I conclude that concerns around using recent land-cover data in

place of collecting land-cover data at the same time as field work is conducted are most often unwarranted, and the older data may even yield stronger associations with wetland conditions in some cases.

2.4.6 Geospatial Data Quality

I delineated wetland catchments using two topographic datasets of differing spatial grain (10 m and 25 m pixel DEMs). Catchments defined using the higher resolution DEM were typically smaller, but I found no significant difference between the r_M values based on DEM resolution when comparing land cover to either wetland environmental or vegetation dissimilarity matrices (**Figure 2.4, Figure 2.5**). The similarity in observed land cover composition between the two catchment types, despite their difference in area, was likely due to the resolution of the land-cover data (i.e., 30 m) being greater than both DEM resolutions (i.e., 10 and 25 m). The result of this spatial mismatch is that on average the same land cover cells were included in both 10 m and 25 m catchments (e.g., **Figure 2.2**). High concordance between the land cover extracted from the two catchment types supports this contention (Mantel tests by year, averaged across the four years: mean $r_M = 0.8720$, mean $p < 0.0001$).

For other applications involving delineated catchments (e.g., hydrologic modelling), previous work suggests that while using high resolution DEMs (<10 m resolution) can improve fine-scale topographical detail (Martinez et al. 2010), they do not produce catchments that considerably differ in size or shape from those delineated at moderate resolutions (McCauley and Anteau 2014). Thus, I conclude that both of the DEMs used in this study were adequate for prairie pothole catchment delineation. Furthermore, the acquisition of higher resolution

topographic data for similar studies may not be a justifiable expense unless the geospatial data describing landscape features (e.g., land cover) are also represented at a very high spatial resolution (Novikmec et al. 2016).

I found that the land cover classifications offered by the AAFC data generally agreed with my field observations and supported the claim of >87% classification accuracy in Alberta (Fisette et al. 2014) for the years of data I examined (AAFC 2013a, b, c, 2015). However, I note a misclassification of known grazing lands as native prairie, which may have led to an underestimation of disturbed land around several sites. Although many wetlands and prairies in the Grassland Natural Region are actively grazed by cattle (Natural Regions Committee 2006), the majority of the land cover around wetlands in the Grassland Natural Region was classified as “Native Grassland” (see **Appendix E**), with the “Pasture and Forages” cover class being apparently reserved for the confined feeding operations and hayed lands more common in the Parkland. While this misclassification may have limited my ability to distinguish between grazed versus ungrazed wetland conditions using the Mantel tests, the discrepancy was common to all spatial extent \times time period combinations, and so I do not consider it to have strongly influenced my results.

2.4.7 Land Cover Configuration

I extracted land-cover data based on composition (type and proportion) only and did not measure the spatial configuration of patches within the spatial extents. Evidence from other studies (e.g., Fahrig 2003; Quesnelle et al. 2013) indicates that the spatial arrangement and connectivity of land covers can have important implications for wetland biota, and linear

disturbances such as roads can have disproportionately large impacts (relative to their area) on wetland environments (e.g., Houlihan and Findlay 2004; Shaw et al. 2012) and biota (e.g., Findlay and Bourdages 2000; Houlihan et al. 2006; Rooney et al. 2012). Land cover configuration around wetlands may be important to consider in complex agricultural landscapes such as the PPR, where there are many sources of non-point nutrient and contaminant pollution that may impact aquatic ecosystems (Gergel 2005; Qiu and Turner 2015). Thus, I recommend that further work in this area considers whether measuring land cover configuration around wetlands yields greater insight into the mechanisms by which land cover influences wetland conditions and helps to distinguish among sites with similar adjacent land cover composition but different configurations.

2.4.8 Conclusions

My study demonstrates that significant associations between adjacent land cover and environmental conditions in marshes of the Prairie Pothole Region are robust to the manner and spatial scale of land cover extraction and the age of land cover data, within a four-year window preceding field work. Concerns around access to catchment polygons or selection of an appropriate buffer size when relating land cover to environmental conditions or vegetation in marshes may be unnecessary.

Though catchments may provide a more meaningful basis for comparing environmental conditions with land cover due to the role of hydrologic connections in vectoring contaminants, nutrients, particles and propagules into the wetland from the surrounding landscape, symmetrical buffers between 200 and 500 m in radius yielded equally strong associations between land cover

and environmental conditions. I suspect my results differ from those of studies conducted in moister climates because of the limited growing season runoff generated in Alberta's moisture-deficit climate. At larger spatial extents I found that the observed association of environmental conditions with land cover was merely the product of spatial autocorrelation, rather than a direct influence of land cover on environmental conditions in the marsh.

Once I accounted for spatial patterning, I detected no consistent significant concordance between land cover and wetland vegetation composition, though vegetation remained significantly concordant with environmental conditions. I therefore conclude that the apparent association between land cover and vegetation composition is actually an echo of the association between land cover and environmental conditions combined with the effects of species pool differences between natural regions.

For future researchers, if catchment-level land cover data from the year preceding field work is not available, I recommend using land cover from any year within the last five and extracting it using a 500 m symmetrical buffer. Rather than putting exhaustive effort and resources into acquiring higher resolution DEMs or more recent geospatial data, I conclude that researchers should focus their efforts towards increasing their study sample size to improve statistical power and better represent the variability of their study ecosystems. This study demonstrates that the relationships of both abiotic and biotic wetland conditions to adjacent land cover are robust to the selection of spatial and temporal scales of land-cover data. However, in large study areas, spatial autocorrelation should be tested for and controlled to avoid drawing spurious conclusions on the nature of landscape-environment-biota relationships.

2.5 Figures and Tables

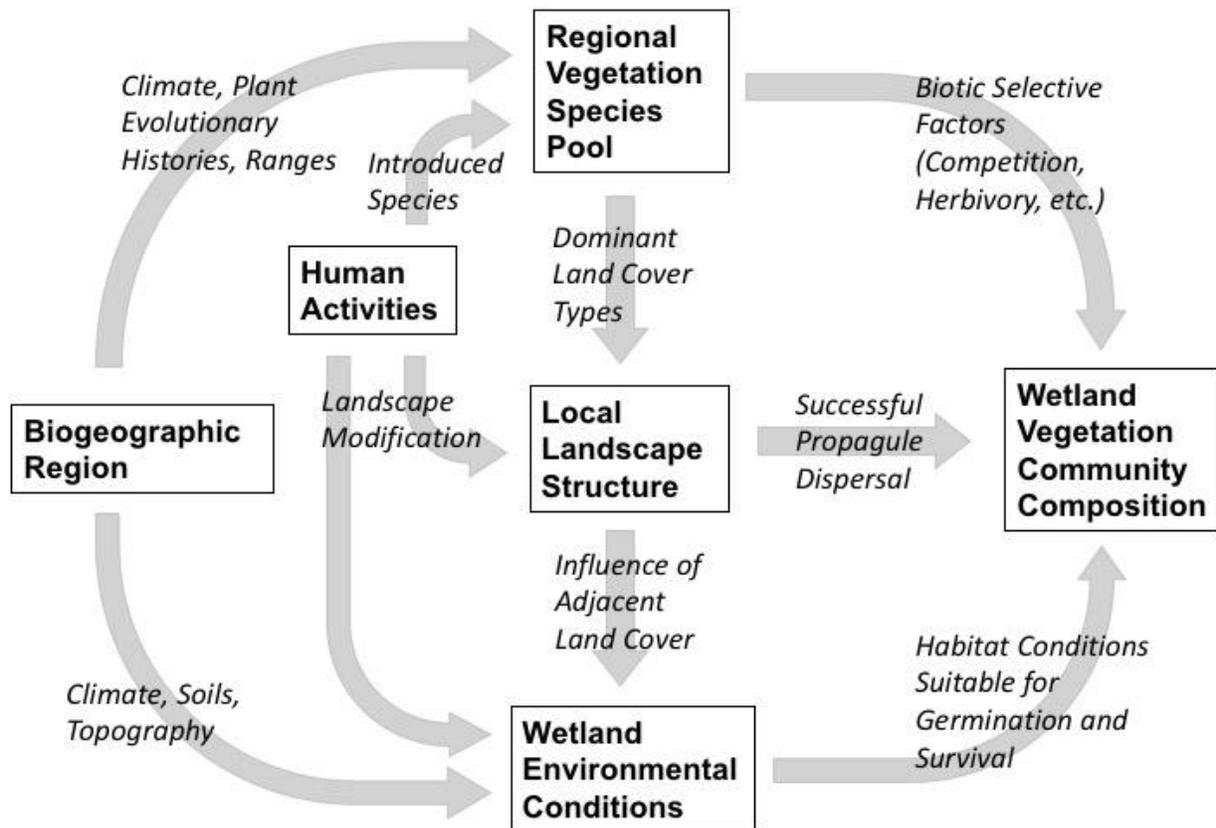


Figure 2.1: Conceptual model illustrating the various controls and filters on wetland vegetation community assembly. Items in boxes represent major components of the system while arrows represent the major mechanisms or processes linking the components. While model components are arranged according to the order in which they are perceived regulate vegetation community composition, no attempt has been made to distinguish the relative importance of individual processes from one another, nor are all possible controls depicted. Similar pathways may exist for other wetland biota, though with emphasis on different mechanisms or processes.

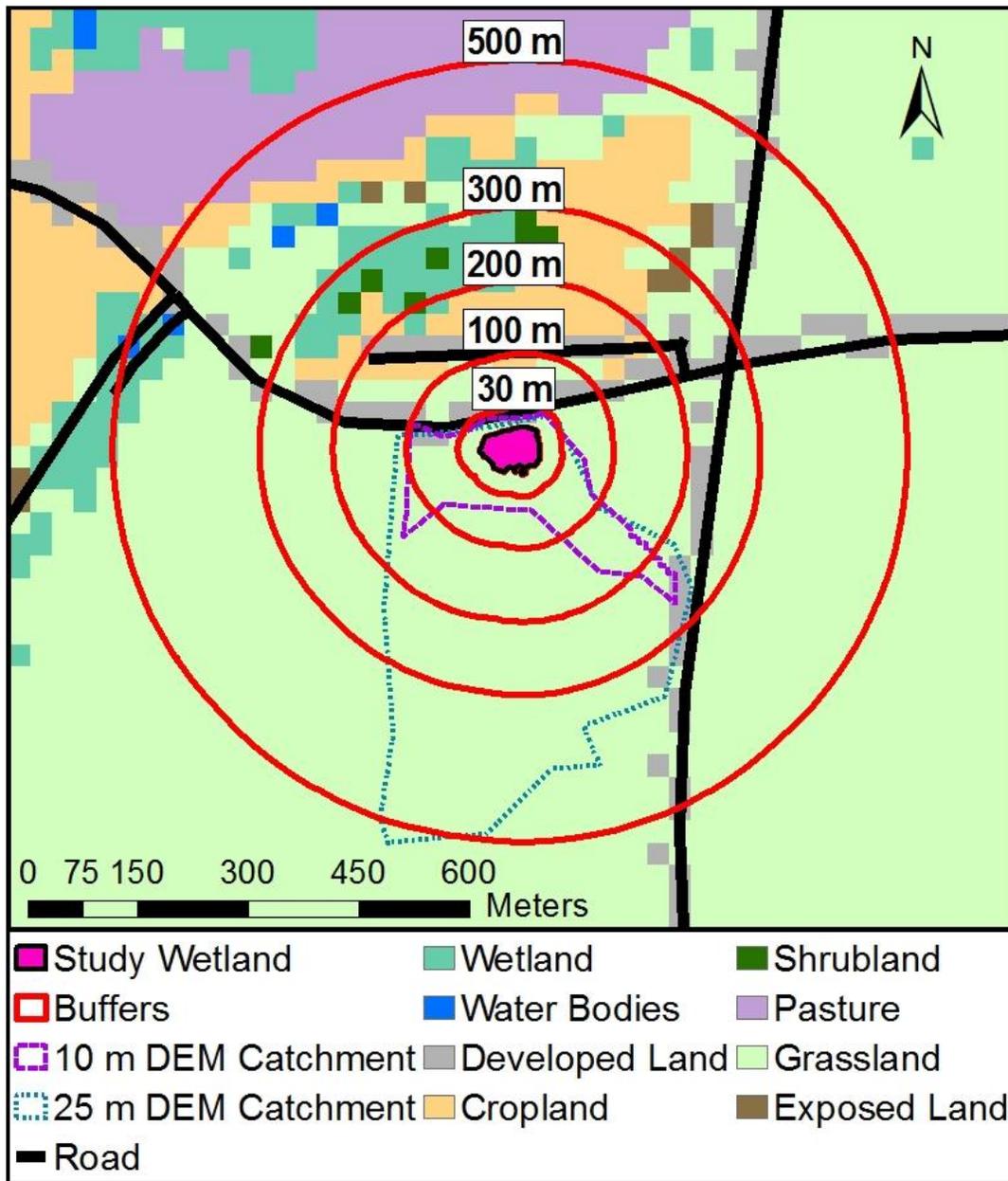


Figure 2.2: The difference among landscape extents used to characterize landscape composition around a study wetland. Depicted is a 0.37 ha wetland situated in the Grassland Natural Region of Alberta. Although only buffers extending up to 500 m from the wetland boundary are included, I considered ten landscape extents: eight nested buffers (30, 100, 200, 300, 500, 1,000, 2,000, and 5,000 m) and two catchments delineated from digital elevation models (DEMs) of 10 and 25 m spatial resolution. Where culverts were lacking, catchments were truncated along linear road features, whereas buffers were not constrained by road networks and may extend beyond hydrologic boundaries.

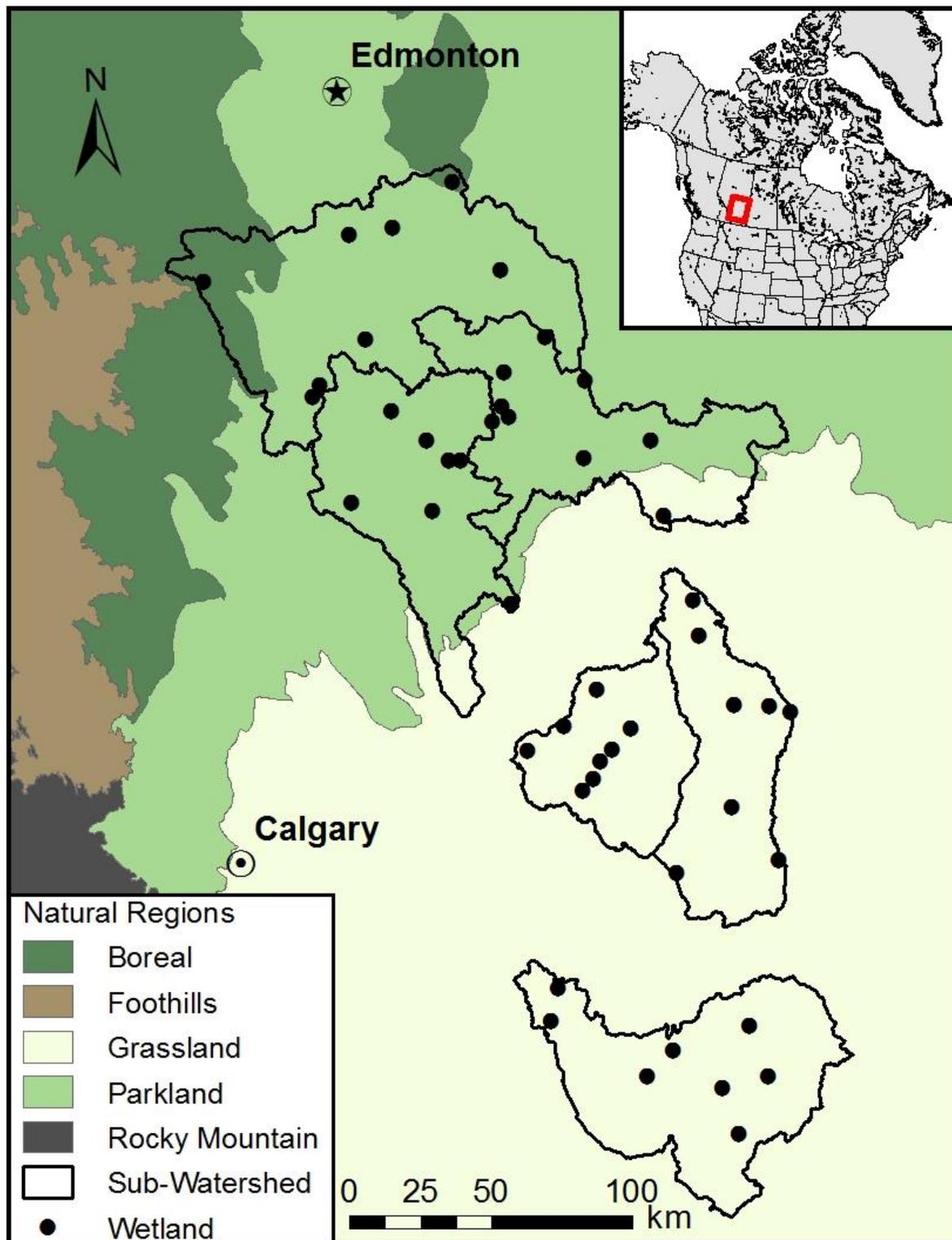


Figure 2.3: Map depicting the distribution of wetlands sampled in 2014 within six major sub-watersheds in the Grassland and Parkland Natural Regions of southern Alberta, Canada ($n = 48$).

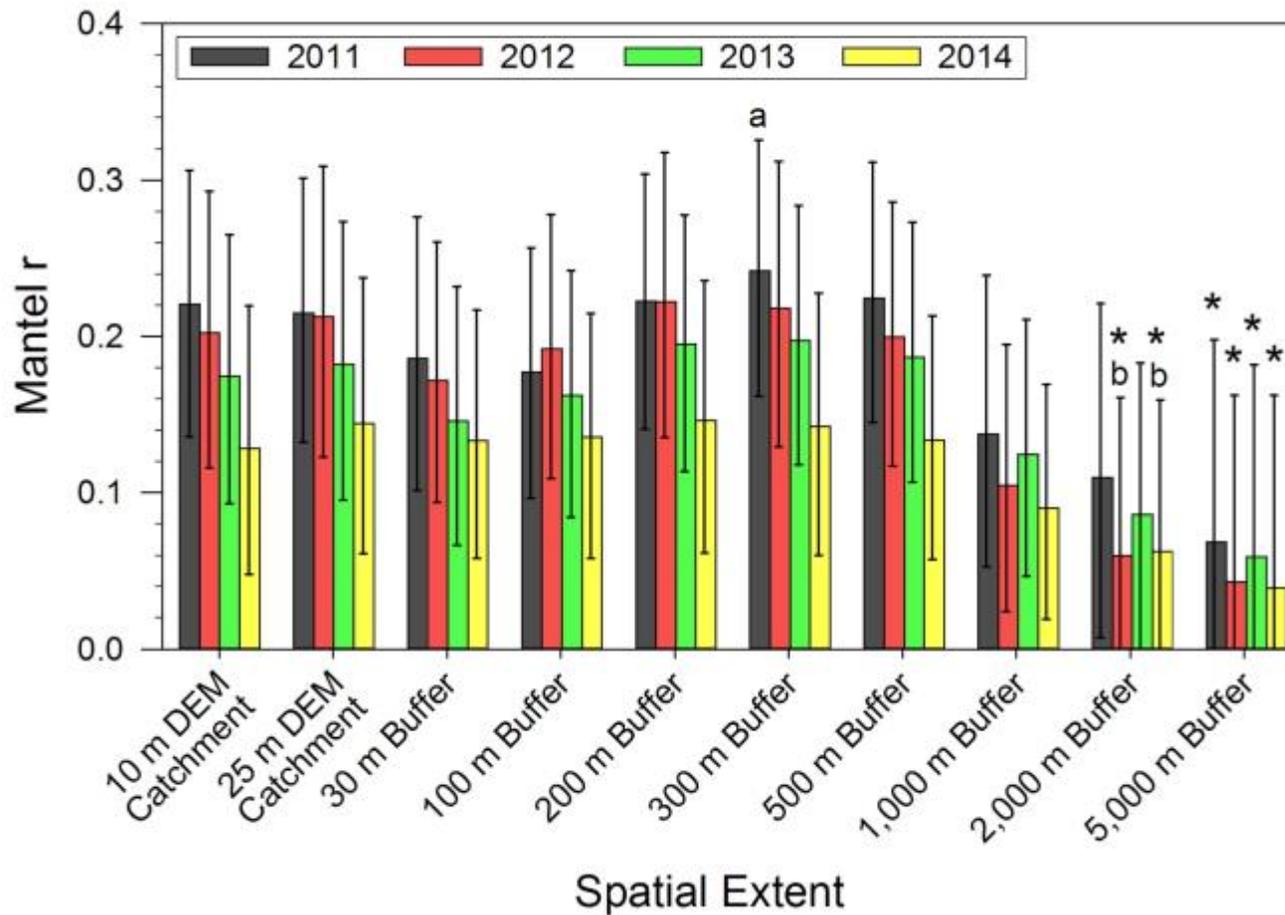


Figure 2.4: Results of Mantel tests comparing land cover to environmental conditions of 48 non-permanent wetlands. Land cover was calculated as the percent cover of nine land cover types within ten spatial extents around the wetlands for each of four years. Bars represent bootstrapped 90% confidence intervals around the Mantel r_M values. All confidence intervals overlap except for the 2011 \times 300 m buffer r_M value (letter “a”), which was significantly higher than the 2012 \times 2,000 m and 2014 \times 2,000 m buffer r_M values (letter “b”). Asterisks indicate r_M values that were non-significant at $\alpha = 0.05$, i.e., the 90% confidence intervals overlap 0.

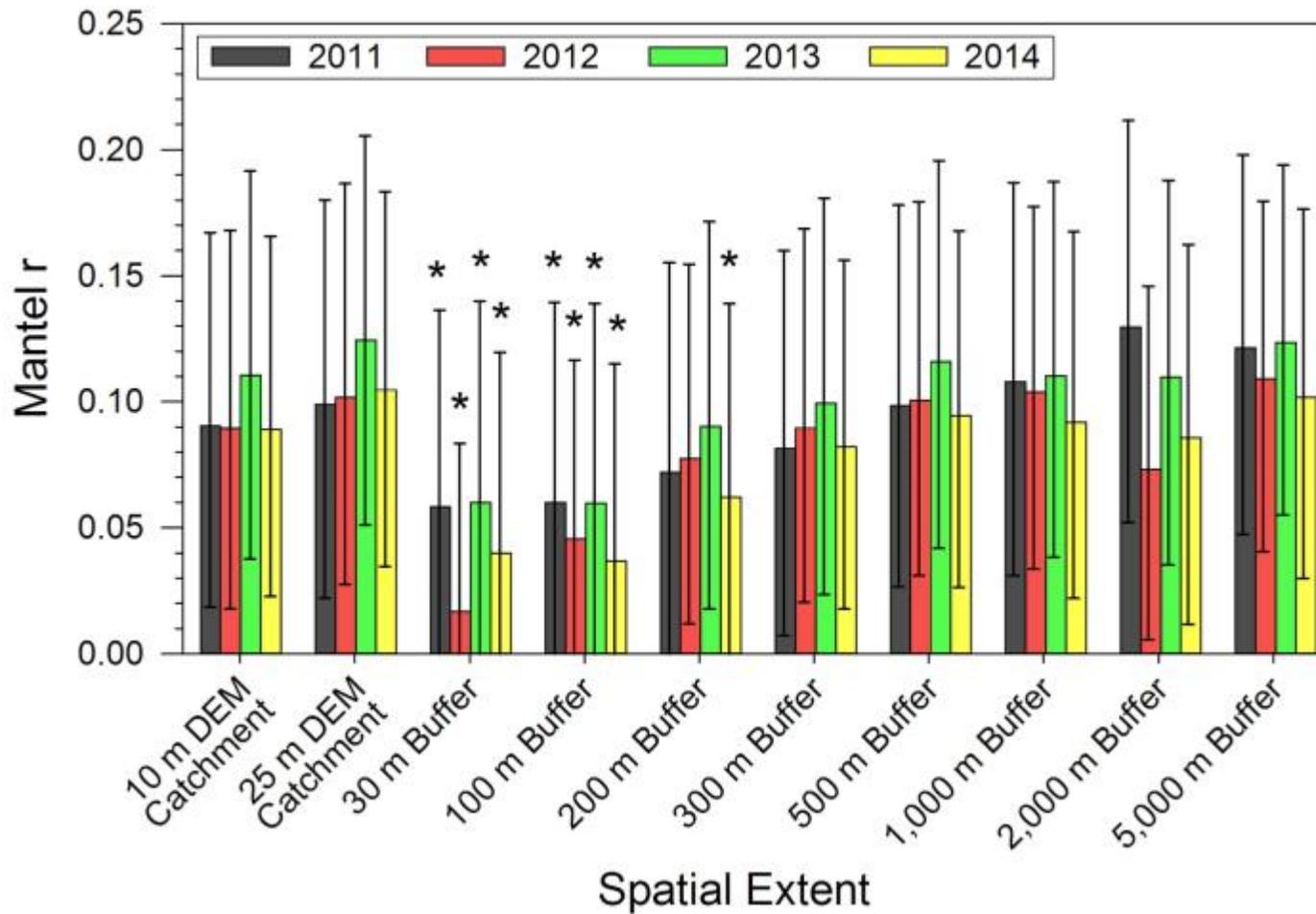


Figure 2.5: Results of Mantel tests comparing land cover to vegetation community composition of 48 non-permanent wetlands. Land cover was calculated as the percent cover of nine land cover types within ten spatial extents for each of four years. Bars represent bootstrapped 90% confidence intervals around the Mantel r_M values, revealing no significant difference among the Mantel test results. Asterisks indicate r_M values that were non-significant at $\alpha = 0.05$, i.e., the 90% confidence intervals overlap 0.

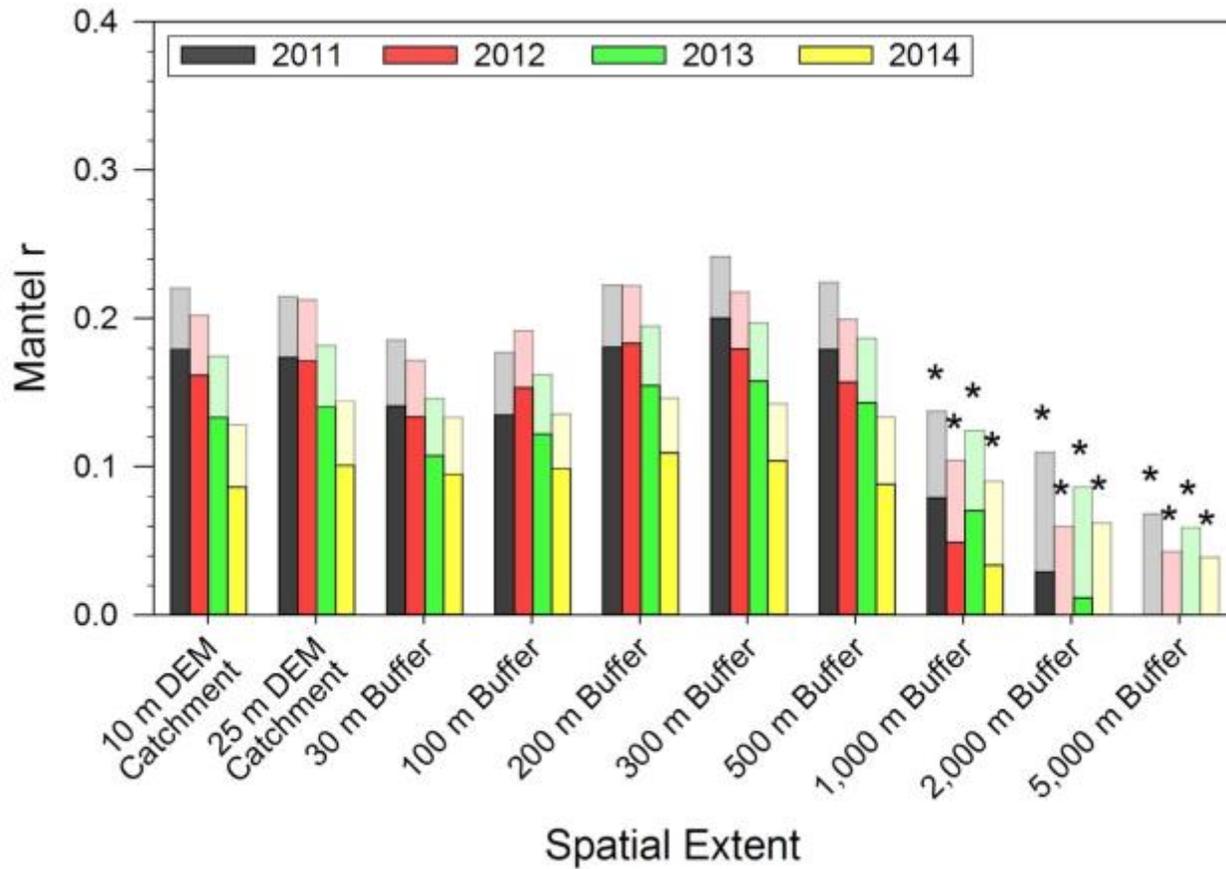


Figure 2.6: Comparison of standard (faded bars) and partial (darker-coloured bars) Mantel test results examining congruence of wetland environmental conditions and land cover measured at ten spatial extents and four years for 48 non-permanent wetlands. The partial Mantel test r_M values represent the remaining congruence between the environmental and land cover data after removing the spatial component of variation from these dissimilarity matrices. Asterisks indicate partial Mantel r_M values that were non-significant at $\alpha = 0.05$ once spatial autocorrelation was corrected for.

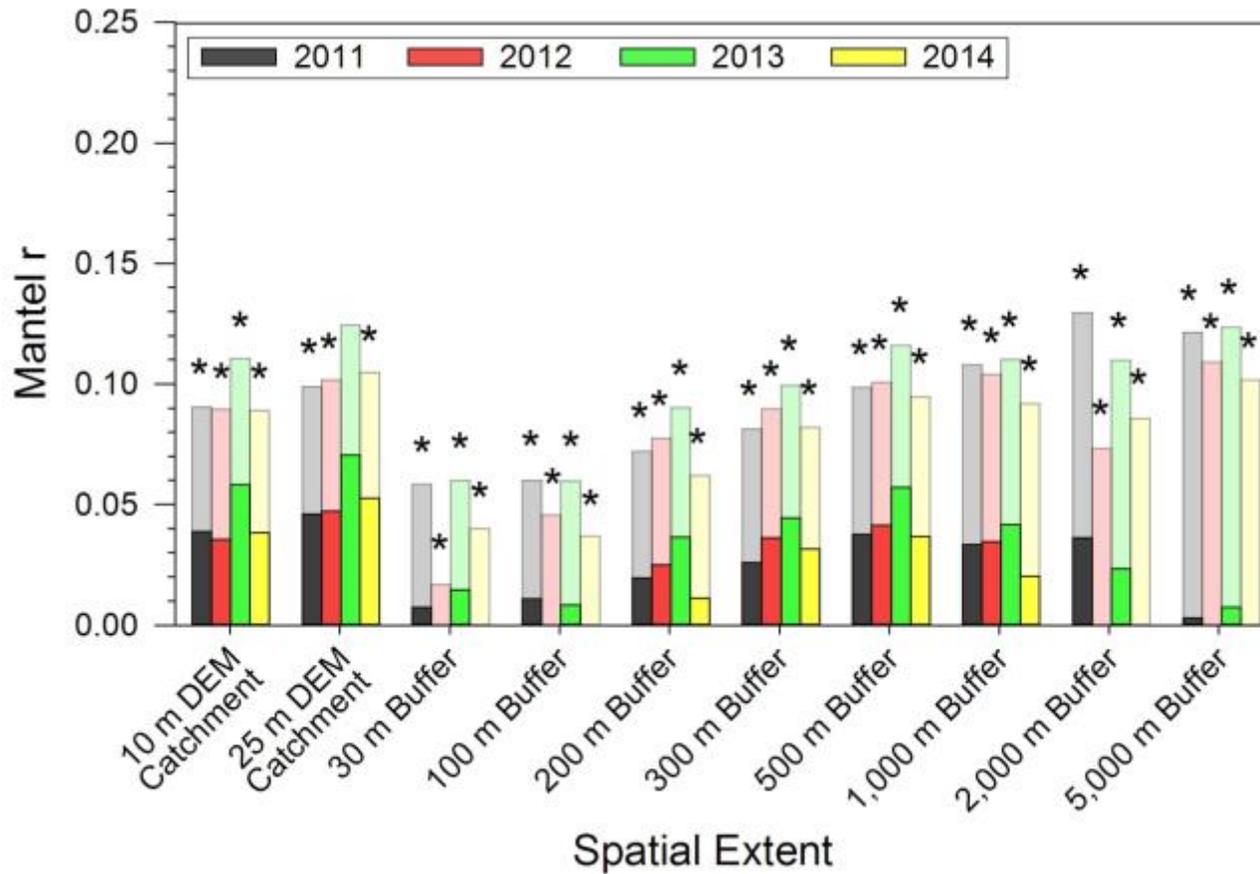


Figure 2.7: Comparison of standard (faded bars) and partial (darker-coloured bars) Mantel test results examining congruence of wetland vegetation community composition and land cover measured at ten spatial extents and four years for 48 non-permanent wetlands. The partial Mantel test r_M values represent the remaining congruence between the vegetation and land cover data after removing the spatial component of variation from these dissimilarity matrices. Asterisks indicate partial Mantel r_M values that were non-significant at $\alpha = 0.05$ after accounting for spatial autocorrelation.

Table 2.1: Summary statistics of the size of wetlands and the ten landscape extents used to extract land-cover data around each wetland ($n = 48$). Landscape extents include catchments delineated using 10 and 25 m digital elevation models (DEMs) and eight nested symmetrical buffers of various radii. Units for all values are in hectares.

Spatial Extent	Mean	Median	Standard Deviation	Range
Wetland	0.81	0.50	0.81	0.04 - 3.28
10 m DEM Catchment	17.24	12.42	16.79	2.51 - 76.01
25 m DEM Catchment	21.74	18.03	17.37	2.95 - 72.94
30 m Buffer	1.55	1.25	0.83	0.52 - 3.92
100 m Buffer	7.13	6.26	2.48	3.93 - 13.74
200 m Buffer	20.38	18.74	4.74	14.13 - 32.61
300 m Buffer	39.88	37.50	6.97	30.61 - 57.68
500 m Buffer	97.72	93.84	11.41	82.41 - 126.58
1,000 m Buffer	352.18	344.58	22.46	321.78 - 408.60
2,000 m Buffer	1332.01	1317.01	44.54	1271.47 - 1443.43
5,000 m Buffer	8039.11	8000.97	110.84	7888.01 - 8315.38

Chapter 3: Implications and Further Research

3.1 General Discussion

Non-permanent marshes of the Prairie Pothole Region (PPR) are unique and dynamic ecosystems (Stewart and Kantrud 1971), and provide numerous functions of considerable ecological and societal importance (Murkin 1998; Zedler 2003; Marton et al. 2015). However, agricultural and urban development in the PPR have resulted in extensive wetland loss and degradation (Zedler and Kercher 2005; Bartzen et al. 2010) and these trends are currently ongoing (Johnston 2013). To establish a foundation for wetland management and conservation, there is a growing need to monitor these wetlands to identify the extent of human impacts and to determine the pathways between human activities and wetland conditions (Bailey et al. 2004). Effective wetland monitoring and impact assessment first requires determination of the most ecologically-relevant scales to relate measurements of disturbance, such as adjacent land covers, to wetland conditions (Houlahan and Findlay 2004; Houlahan et al. 2006; Rooney et al. 2012).

The first chapter of this thesis provided a background overview of the importance of spatial and temporal scale selection in ecology. Generally, research scales are not selected with a biological rationale, which may limit our ability to identify key interactions between ecological processes and the surrounding landscape. In the Prairie Pothole Region of Alberta, Canada, no research has yet attempted to determine the appropriate scale to characterize landscape-wetland relationships for temporary, seasonal and semi-permanent marshes.

The objective of my thesis was to examine the effects of the spatial and temporal scale at which land-cover data is extracted on the strength of the relationship between land cover and wetland conditions in temporary, seasonal and semi-permanent marshes of Alberta, Canada. The specific wetland conditions I considered included abiotic variables related to water and soil chemistry and hydrology, as well as the community composition of vegetation growing in the wetlands. In my second chapter, I compared wetland environmental conditions and vegetation community composition to adjacent land cover measured at ten spatial extents and from four consecutive years. I found that both vegetation community composition and environmental conditions within the wetland were significantly related to variation in land cover across a wide range of spatial extents and sample years, though these relationships were influenced by spatial autocorrelation. Consequently, concerns around having the most recent and highest resolution land-cover data possible should likely be relaxed. Further, though the case can be made that using elevation data to delineate catchments may yield land-cover data more directly responsible for environmental conditions, symmetrical buffers yielded land-cover data just as predictive of vegetation and environmental conditions as did catchments, but with less effort. However, I also found that the scale at which the strength of the relationship to land cover was greatest differed between wetland physicochemical conditions and wetland vegetation communities, suggesting different mechanisms of action may relate environmental conditions to land cover from those determining the relationship between wetland vegetation and land cover. These findings raise interesting questions for science and have important consequences for wetland management.

In this final chapter, I discuss my findings in the context of current wetland management and policy in Alberta and suggest future research directions around bioassessment tool

development and on landscape influences on wetland plant communities. My hope is that the findings of this research will help advance our scientific understanding of temporary, seasonal and semi-permanent wetlands in Alberta and guide their management and conservation amidst increasing natural and anthropogenic pressures.

3.2 Alberta Wetland Policy

The Alberta Wetland Policy (AWP; ESRD 2013) was released in 2013 and has been fully implemented across the province of Alberta as of June 2016. It seeks to minimize further wetland loss and degradation while accommodating economic development by managing wetlands on the basis of their “relative wetland value”. Relative wetland value refers to the capacity of a wetland to provide ecological services (namely biodiversity support, water quality improvement, hydrologic functioning, and social values). Though avoidance or minimization of impacts to wetlands is prioritized under the policy, when a wetland loss is deemed unavoidable, its loss must be mitigated through restoration, creation or enhancement to offset the loss of ecosystem services that the wetland provided. The estimated relative value of a wetland slated for drainage or infilling is used to establish the area-ratio for restoration, enhancement or creation. Variation in replacement ratios allows developers to be penalized more severely for disturbing or destroying high value wetlands, while permitting development of relatively lower value wetlands. Further, because restored and created wetlands are known to underperform relative to natural wetlands (e.g., Moreno-Mateos et al. 2012), variation in replacement ratios is intended to prevent the net loss of relative wetland values on the landscape.

A major policy gap is that the AWP concerns the physical area of the wetland itself, but does not regulate any of the land surrounding the wetland. Effectively, a wetland may be replaced but there are no restrictions on what sorts of land uses may occupy the immediately adjacent area, despite arguments that some natural buffer between wetlands and human activities are needed (e.g., Findlay and Houlihan 1997; Rickerl et al. 2000; Houlihan and Findlay 2004; Houlihan et al. 2006; Skagen et al. 2008). My work has shown that there are significant connections between wetland conditions and surrounding land cover, at least 5 km away. These landscape features contribute to the environmental conditions and biotic communities in the wetlands and likely influence the quality and quantity of ecosystem services provided by a wetland (Zedler 2005). If the restoration goal is to create a wetland that provides comparable ecological services as the wetland it is replacing, then my results suggest that restoration outcomes could be improved by considering the surrounding landscape context when prioritizing land parcels for acquisition. Even if the replacement wetland has the same area and features of the original wetland, the replacement wetland may not provide the same ecological services as its natural analogue if it is embedded in different type of landscape, such as an agricultural rather than forested landscape. Where larger scale reclamation is being undertaken, reclaimed wetlands will be more likely to resemble natural ones if the landscape more closely mimics a natural composition and configuration of land covers (Rooney and Bayley 2011; Rooney et al. 2015). For smaller wetland-focused restoration or reclamation efforts, success could be improved by pairing wetland restoration projects with upland restoration in the same catchment. This would promote similar upland-wetland interactions as what originally existed, and may “shield” the restored or reclaimed wetland from human activities in adjacent lands (Rickerl et al. 2000; Detenbeck et al. 2002; Houlihan et al. 2006; Skagen et al. 2008).

I recommend that wetland restoration agencies in Alberta make an effort to situate restoration projects in catchments with more natural landscape composition and configuration, with the wetland catchment being the most ecologically appropriate spatial extent to do this in. However, if catchments have not been delineated, then a buffer of 500 m radius is equally predictive of wetland conditions. Decision makers should consider these wetlands and their catchments as inseparable units and a policy focused on conserving wetland values should aim to protect not only the wetland per se, but also its adjacent lands.

3.3 Bioassessment Tool Development

For its effective implementation, the AWP identifies the need for “wetland value assessment tools [that] incorporate ground-level data (e.g., species composition, water quality information, etc.) into the decision-making process.” (ESRD 2013, pp. 21) to help evaluate wetlands and determine restoration success. I found that both environmental conditions and vegetation are sensitive to landscape structure at many spatial and temporal scales, and vegetation in particular may be a good candidate for bioassessment tool development (e.g., an index of biotic integrity; Karr 1981). Plants have many traits of a good bioindicator, including being sensitive to environmental stressors, biological and societal relevance, and having easy, non-destructive sampling methods associated with them (Cairns et al. 1993). For temporary, seasonal and semi-permanent marshes in the PPR, plants may be the optimal taxon for bioassessment, as the ephemeral nature of the standing water in wetland ponds may limit the reliability of aquatic taxa such as fish or macroinvertebrates as bio-indicators during naturally

dryer periods. Furthermore, plants, as immobile organisms, will remain at a site despite conditions which cause other organisms to emigrate; thus, through their persistence, plant communities are integrative of the environmental and biological dynamics of a system (U.S. EPA 2002). Indeed, previous research on depressional marshes in Montana's PPR (Borth 1998) and shallow open-water wetlands in Alberta's Parkland (Wilson and Bayley 2012) found that vascular plants show high potential to serve as reliable indicators of wetland condition, though their potential to represent the biological integrity of temporary, seasonal, and semi-permanent marshes in the Parkland or in any wetland type in the Grassland remains an area for future research.

The significant relationships between wetland physicochemical conditions and land cover at multiple scales suggests the suitability of using these abiotic measurements for ecosystem monitoring (e.g., Rooney and Bayley 2010). However, because these features have different spatiotemporal relations to surrounding land cover than the vegetation community, they may provide a different signal around disturbance in the landscape than would be observed by examining vegetation alone. Thus, including both environmental and vegetation indicators may integrate more information about the wetland and its surroundings and make for a more robust multi-metric assessment tool than considering vegetation or physicochemical variables alone. While previous work in Alberta's Parkland (Wilson and Bayley 2012) found that bioassessment tools developed from different wetland taxa are equally sensitive to disturbance and can be considered surrogates for each other, I expect that abiotic conditions and measures of the vegetation community will be relatively poor surrogates for each other due to the differences I observed in the scale of their associated landscapes. Additionally, cross-taxon congruence has

been shown to vary with disturbance level and Natural Regions in Alberta (Rooney and Azeria 2015), raising further doubt that a single taxon such as vegetation could represent all the ecological variability of a wetland.

I recommend that future research on non-permanent marshes in Alberta's PPR focuses on exploring the suitability of vegetation and environmental conditions as metrics for ecological assessment tools. However, these initiatives will likely require larger sample sizes than I considered in this thesis, so that the Grassland and Parkland Natural Regions may be treated separately without compromising statistical power. I found evidence for spatial autocorrelation among my study wetlands which likely reflected the natural variability of land cover types, environmental conditions and vegetation communities across Alberta's PPR (Natural Regions Committee 2006). By considering a more narrowly-defined region within which ecological assessment tools are developed, we may be able to limit the confounding variation of those natural gradients and increase the efficacy of bioassessment tools (Bailey et al. 2004). Developing wetland assessment tools for the Grassland and Parkland separately also has implications for policy. In the AWP, both Natural Regions are currently managed as the same jurisdictional unit: the settled, agricultural portion of the province known as the "White Zone" (ESRD 2013). If the natural gradients in the PPR the Grassland and Parkland have different relationships between land cover and wetland conditions, generalizations about the scales and mechanisms at which human activities affect wetlands may be falsely made if this spatial non-stationarity is not acknowledged. To avoid wetlands in one Natural Region being inappropriately compared to wetlands in the other Natural Region, I recommend that wetland assessment tools

and restoration targets for temporary, seasonal and semi-permanent marshes be developed for the Grassland and Parkland separately.

3.4 Landscape Influences on Wetland Vegetation Communities

My study found that while wetland vegetation was highly sensitive to local land cover composition, the trends in concordance with land use across spatial and temporal scales appear to be driven by the spatial position of the wetlands within the study region. Qualitative inspection of the land cover \times vegetation congruence remaining after removing spatial variation revealed similar influential spatial extents as with the environmental conditions, including the hydrologic catchments. Although prairie wetland water and sediment conditions have strong selective effects on vegetation community composition (van der Valk and Davis 1978; van der Valk 1981), these site-level conditions and biological pressures such as herbivory or competition are not the first determinant of plant assembly at a wetland. Rather, the inclusion of a plant species in the community occupying a wetland first requires the presence of the species in the regional species pool *and* for propagules to have successfully dispersed from a source to the wetland (Weiher and Keddy 1995). The difference in optimal scales for observing the relationship between land cover and wetland plants versus the relationship between land cover and environmental conditions may indicate the influence of biogeographical or dispersal constraints on the vegetation, thereby producing different pathways in which the landscape affects these wetland components. In chapter 2, I had explored some potential explanations for these pathways, though the mechanisms behind the unique response of the vegetation to land cover, including the apparent one-year time lag, warrant further investigation.

The vegetation community composition of PPR wetlands may have been affected by changes to the regional species pool associated with the extensive agricultural activity in this region. It is possible that increasing amounts of agriculture in a landscape contributes to changing the wetland species pool in two ways: 1) by eradicating sources of natural wetland propagules such as *Carex* spp. L. (sedges) through wetland drainage and modification (Werner and Zedler 2002), and 2) by contributing propagules of non-native annual species which outcompete native vegetation (Galatowitsch et al. 2000). Thus, due to these direct and indirect changes, agricultural wetlands may have considerably different vegetation communities than wetlands in landscapes with greater amounts of native vegetation cover. I have anecdotal evidence (based on site observations and unpublished data) that species such as *Sonchus arvensis* L. (Perennial Sow-Thistle), *Cirsium arvense* (L.) Scop. (Canada Thistle), and *Rumex crispus* L. (Curly Dock) were typically associated with wetlands in highly agricultural areas. These plants are not native to Alberta (Moss and Packer 1983) and are known to be aggressive colonizers of open and disturbed areas, such as the drawdown mudflat areas of wetland fringes (Dix and Smeins 1967; Stewart and Kantrud 1971; van der Valk 1981). However, the associations between these weedy species and non-natural land covers require more rigorous investigation. Reciprocal transplant experiments, wherein native species are introduced into a disturbed wetland and weedy species into a natural wetland, may reveal the relative importance of propagule source and biological competition in determining the assemblage of plants in wetlands exposed to agricultural disturbance.

Examination of wetland seed and propagule banks would provide a long-term record of which plant species were able to successfully disperse to the wetlands (van der Valk and Davis

1976), though not all of these propagules may actually germinate under wetland field conditions (van der Valk and Davis 1978; Weiher and Keddy 1995). Similarly, artificially introducing propagules of different dispersal types into a mesocosm, as with the transplant experiments detailed above, would permit examination of differences in competitive abilities among dispersal types (e.g., Weiher and Keddy 1995). If propagule dispersal ability is limiting the abundance of native species in wetlands in disturbed landscapes, seeding and/or planting may help restored and reclaimed wetlands in agricultural landscapes achieve vegetation-community based targets.

Experiments could also be devised to test the relative importance of different dispersal mechanisms for species found missing from wetlands in disturbed landscapes. For example, a possible line of inquiry is to determine whether the presence of hydrochorous species in a wetland, such as *Carex* spp. L. or *Schoenoplectus* spp. (Rchb.) Palla (bulrushes) depends on whether the propagule sources are within the wetland's catchment, rather than simply in the surrounding buffer. A strong association between the presence of hydrochorous plants and catchment land covers would indicate that wetland community composition is likely structured by dispersal limitations. Conversely, if land cover within the catchment does not predict vegetation community composition better than land cover in a symmetrical buffer, as my findings suggested, then the immigration of propagules may be isotropic and dependent on other vectors such as waterfowl dispersal (Mueller and van der Valk 2002). In this case, the configuration of propagule sources in the adjacent landscape may be a large constraint to whether a propagule reaches the wetland (May et al. 2013).

Finally, I advise further exploration of the landscape/environment/biota relationships for prairie wetlands by identifying which land covers (or other features such as road density) are driving the distribution and abundances of individual plant species, and to what extent. Although the Mantel test is not appropriate to address these questions (Legendre et al. 2015), methods such as structural equation modelling (Riseng et al. 2011) or constrained ordination approaches such as canonical correspondence analysis or redundancy analysis (McCune and Grace 2002) have been effectively used in the past (e.g., Houlahan et al. 2006; Bird and Day 2014), and may be appropriate to use with my data. Such approaches may also be employed to determine the relationships between land cover types and individual environmental variables (e.g., Houlahan and Findlay 2004), or the relative contribution of land cover and environmental conditions on plant community composition (e.g., Capers et al. 2010; Alahuhta et al. 2013; Mikulyuk et al. 2013).

3.5 Conclusion

My thesis work determined that both environmental and vegetative components of temporary, seasonal and semi-permanent marshes in Alberta are sensitive to land cover across many spatial and temporal scales, with unique patterns of landscape association between the two wetland indicator types. Herein, I have noted the implications for wetland policy in Alberta, namely that for wetland conservation to be effective and for restoration and reclamation to be more successful, we must consider the landscape context around wetlands, not just wetlands in isolation. In addition, I have raised two new avenues for inquiry. The sensitivity of both environmental variables and vegetation community composition to landscape composition indicates that they may provide useful assessment tools that could be used in wetland monitoring

and evaluation. Future research should explore what individual metrics are most representative of wetland conditions. Another fruitful line of inquiry would be to explore how abiotic metrics could be combined with vegetation-derived ones to yield a more integrative assessment tool, owing to the differences in scale at which abiotic variables and vegetation community composition are sensitive to surrounding land cover. Lastly, my research raises novel questions about the mechanisms by which vegetation community composition is responding to changes in the surrounding landscape. My original hypothesis - that land cover within the wetland's catchment would influence environmental conditions in the wetland through run-off processes, and that these in turn would control what plant species were present in a wetland and in what proportions - has been revealed to be incomplete. Land cover may also influence wetland vegetation through other, as yet undetermined, processes. Identifying and quantifying these other mechanisms would yield great insight into the processes by which plant communities assemble in relatively natural and disturbed landscapes.

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Appendices

Appendix A: List of pesticide compounds detected in water and soil samples

All compound measurements and detection limits are in µg/L. Registration status refers to whether the compound is currently actively registered for use in Canada versus having been deregistered or being a persisting “legacy” compound or degradation product of another compound. Deregistration dates are provided where possible. Note that while samples were analyzed for the presence of over 150 compounds, only compounds with positive detections are listed below.

Compound	Type	Minimum Detection Limit	Registration Status	Medium
2,4-Dichlorophenoxyacetic acid	Herbicide	0.02507	Active	Both
Aminomethylphosphonic acid	Herbicide	0.2	Degradation Product	^a Water
Azinphos-methyl	Insecticide	0.63717	Deregistered (2012)	Soil
Azoxystrobin	Fungicide	0.02529	Active	Soil
Bentazon	Herbicide	0.02508	Active	Water
Boscalid	Fungicide	0.02546	Active	Soil
<i>cis</i> -Chlordane	Insecticide	0.02668	Deregistered	Soil
<i>t</i> -Chlordane	Insecticide	0.02543	Deregistered	Soil
Chlorothalonil	Fungicide	0.0247	Active	Soil
Clopyralid	Herbicide	0.02559	Active	Both
Diazinon	Insecticide	0.02491	Active	Soil
<i>p,p</i> -Dichlorodiphenyldichloroethylene	Insecticide	0.02535	Legacy	Soil
Diclofop	Herbicide	0.02512	Active	Soil
Dieldrin	Insecticide	0.02502	Deregistered	Soil
Difenoconazole	Fungicide	0.02484	Active	Soil
Ethalfuralin	Herbicide	0.1168	Active	Soil
Fluroxypyr	Herbicide	0.02489	Active	Both
Glyphosate	Herbicide	0.2	Active	^a Water
<i>tr</i> -Heptachlor Epoxide	Insecticide	0.06973	Legacy	Soil
Imidacloprid	Insecticide	0.01	Active	^a Water
Iprodione	Fungicide	0.02542	Active	Soil
Lindane (Hexachlorocyclohexane-gamma)	Insecticide	0.02557	Legacy	Soil
MCPA (2-methyl-4-chlorophenoxyacetic acid)	Herbicide	0.02511	Active	Both
Pirimicarb	Insecticide	0.02592	Deregistered (2010)	Soil
Prothioconazole-Desthio	Fungicide	0.02547	Active	Soil
Propiconazole	Fungicide	0.07398	Active	Soil

Compound	Type	Minimum Detection Limit	Registration Status	Medium
Prometon	Herbicide	0.02493	Deregistered (2000)	Water
Sulprophos	Insecticide	0.02442	Deregistered	Soil
Tebuconazole	Fungicide	0.2506	Active	Soil
Thiamethoxam	Insecticide	0.05	Active	^a Water
Triallate	Herbicide	0.02506	Active	Soil
Trifluralin	Herbicide	0.02537	Active	Soil
Triticonazole	Fungicide	0.02495	Active	Soil

^a Compound was analyzed for in water samples only.

Appendix B: Summary of physicochemical and hydrological measurements taken from study wetlands

Summary of the 45 water and soil analytes measured at the wetlands in 2014 used to construct the environmental dissimilarity matrix. Averages are presented for all 48 study wetlands combined and for the Grassland and Parkland Natural Regions separately ($n = 24$ each). To illustrate the variability in environmental conditions as non-natural land cover increases, sites are also binned according to the extent of cropland, developed land and pasture surrounding the site within a 500 m buffer in 2013: low disturbance ($n = 22$) represents sites with 0-25% non-natural cover; medium disturbance ($n = 8$) represents sites with 25-75% non-natural cover; and high disturbance ($n = 18$) represents sites with 75-100% non-natural cover. Sampling methods are described in detail beginning on **page 30**.

Variable	^a Location Measured	Units	Total Average (SD)	Grassland Sites	Parkland Sites	Low Disturb.	Medium Disturb.	High Disturb.
Amplitude:Maximum Depth Ratio	Field	---	0.70 (0.34)	0.77	0.63	0.77	0.68	0.62
Bulk Density	UW-RL	g/cm ³	1.04 (0.24)	1.20	0.88	1.03	1.00	1.08
Calcium (soil)	UG-AFL	mg/kg	4160.61 (2990.02)	2713.59	5607.64	4384.46	3924.47	3991.98
Calcium (water)	UA-BASL	mg/L	31.37 (38.01)	21.36	41.38	22.56	26.26	44.42
Carbon:Nitrogen Ratio (soil)	UA-BASL	---	12.50 (1.53)	12.45	12.54	12.22	12.40	12.88
Carbon:Nitrogen Ratio (water)	UA-BASL	---	11.54 (12.35)	12.87	10.22	14.62	8.68	9.05
Chloride (water)	UA-BASL	mg/L	5.46 (5.04)	5.03	5.90	4.53	3.85	7.31
Dissolved Organic Carbon (water)	UA-BASL	mg/L	29.84 (11.81)	27.90	31.78	30.62	33.21	27.38
Dissolved Oxygen (<i>in situ</i> average, water)	Field	mg/L	8.48 (2.80)	9.29	7.67	8.98	8.19	7.99
Electrical Conductivity (<i>in situ</i> average, water)	Field	mS/cm	2.56 (0.47)	2.42	2.69	2.41	2.71	2.67
Electrical Conductivity (soil)	Field	mS/cm	0.92 (1.20)	0.80	1.05	0.86	1.20	0.88
Gravimetric Water Content	UW-RL	% soil wet	40.93 (12.78)	33.03	48.83	41.35	40.29	40.70

Variable	^a Location Measured	Units	Total Average (SD)	Grassland Sites	Parkland Sites	Low Disturb.	Medium Disturb.	High Disturb.
Loss-On-Ignition	UW-RL	weight % soil dry weight	17.70 (12.87)	11.50	23.90	20.44	16.33	14.97
Magnesium (soil)	UG-AFL	mg/kg	978.39 (722.82)	731.61	1225.17	840.25	1349.57	982.25
Magnesium (water)	UA-BASL	mg/L	23.73 (48.59)	10.27	37.17	9.25	41.23	33.63
Manganese (soil)	UG-AFL	mg/kg	57.79 (26.81)	66.98	48.60	58.40	50.13	60.45
Maximum Pond Depth	Field	m	0.51 (0.24)	0.50	0.52	0.45	0.52	0.58
Olsen Phosphorous (soil)	UG-AFL	mg/kg	58.56 (21.78)	54.83	62.28	61.19	50.16	59.07
pH (<i>in situ</i> average, water)	Field	---	7.35 (0.81)	7.49	7.21	7.44	7.18	7.32
pH (soil)	UG-AFL	---	6.00 (0.89)	5.71	6.29	5.86	6.28	6.05
Pond Amplitude	Field	m	0.30 (0.15)	0.34	0.26	0.31	0.23	0.33
Pond Depth (<i>in situ</i> average, water)	Field	m	0.36 (0.24)	0.33	0.40	0.31	0.38	0.42
Pond Dry Date	Field	day of year	297.42 (82.01)	304.33	290.50	274.77	280.75	332.50
Potassium (soil)	UG-AFL	mg/kg	794.44 (324.26)	941.50	647.38	783.79	824.22	794.23
Potassium (water)	UA-BASL	mg/L	25.28 (13.95)	22.78	27.79	19.05	26.02	32.58
Sodium (soil)	UG-AFL	mg/kg	631.67 (1224.87)	556.64	706.70	707.91	757.40	482.60
Sodium (water)	UA-BASL	mg/L	61.46 (130.29)	28.00	94.93	45.06	84.86	71.11
Sodium Adsorption Ratio (soil)	UG-AFL	---	12.74 (26.37)	13.07	12.41	15.95	14.03	8.24
Sodium Adsorption Ratio (water)	UA-BASL	---	11.46 (24.03)	7.98	14.95	13.65	13.16	8.03
Sulfate (water)	UA-BASL	mg/L	161.17 (404.18)	54.56	267.78	51.31	231.61	264.13
Temperature (<i>in situ</i> average, water)	Field	°C	18.21 (2.73)	18.51	17.91	18.39	18.58	17.82
Total Carbon (soil)	UA-BASL	µg/L	9.40 (7.41)	5.67	13.12	10.86	8.57	7.98
Total Carbon (water)	UA-BASL	µg/L	2060.18 (2096.46)	1686.44	2433.91	1949.95	2628.25	1942.42
Total Detected Fungicides (soil)	AAFC-LRC	count	0.57 (0.78)	0.51	0.63	0.32	0.50	0.90
Total Detected Herbicides (soil)	AAFC-LRC	count	1.07 (1.10)	1.18	0.97	0.74	1.00	1.52

Variable	^a Location Measured	Units	Total Average (SD)	Grassland Sites	Parkland Sites	Low Disturb.	Medium Disturb.	High Disturb.
Total Detected Herbicides (water)	AAFC-LRC, AITF-EAS	count	0.69 (1.29)	0.79	0.58	0.14	0.63	1.39
Total Detected Insecticides (soil)	AAFC-LRC	count	0.68 (0.98)	0.93	0.43	0.56	1.13	0.63
Total Detected Insecticides (water)	AAFC-LRC, AITF-EAS	count	0.04 (0.20)	0.00	0.08	0.00	0.00	0.11
Total Nitrogen (soil)	UA-BASL	µg/L	0.77 (0.90)	0.48	1.06	0.90	0.69	0.65
Total Nitrogen (water)	UA-BASL	µg/L	251.52 (250.85)	179.39	323.65	219.39	349.60	247.20
Total Phosphorous (water)	UA-BASL	µg/L	548.06 (867.46)	596.79	499.33	588.14	344.50	589.56
Total Sulphur (soil)	UG-AFL	mg/kg	1929.04 (2292.94)	1003.80	2854.28	2055.00	1845.40	1812.26
Total Suspended Solids	UA-BASL	mg/L	8.11 (15.31)	4.15	12.08	7.32	10.69	7.94
Turbidity (<i>in situ</i> average)	Field	NTU	0.68 (0.47)	0.64	0.73	0.59	0.97	0.67
Zinc (soil)	UG-AFL	mg/kg	9.68 (6.88)	6.84	12.52	10.82	7.71	9.17

^a Acronyms refer to the following laboratories: AAFC-LRC = Agriculture and Agri-Food Canada Lethbridge Research Centre; AITF-EAS = Alberta Innovates Technology Futures Environmental Analytical Services Laboratory; UA-BASL = University of Alberta Biogeochemical Analytical Services Laboratory; UG-AFL = University of Guelph Agricultural and Food Laboratory; UW-RL = University of Waterloo Rooney Laboratory.

Appendix C: Power analysis to assess adequacy of vegetation sampling intensity with species rarefaction curves

To determine whether the area-based vegetation sampling intensity in 2014 was adequate to characterize general patterns of assemblage composition and could be implemented in the 2015 vegetation sampling, I constructed sample-based rarefaction curves as a form of power analysis (Colwell et al. 2012). Rarefaction curves are a form of species-area/accumulation curves, where the number of new species detected with each additional sampling unit decreases until an asymptote is reached (i.e., the detection of additional species is unlikely even with further sampling effort). Rarefaction uses the empirical observations of site-level richness as a reference to interpolate or extrapolate expected richness if the number of sampling units decreased or increased, respectively (Colwell et al. 2012). Because my sampling was intended to represent broad patterns of species dominance among the assemblages, not to detect all possible rare species at a wetland, I de-emphasized the role of rare species (those detected at only one vegetation assemblage) in the rarefaction analyses. I removed 48 rare species from the data matrix (see **Appendix D**), as well as 4 genus- and 2 family-level identifications and 8 non-vascular plant cover types such as bare ground, litter and open water. Quadrat-level abundance data for the remaining 121 plant species was converted into presence/absence data and imported into the statistical package EstimateS, v. 9.1.0 (Colwell 2013). I ran the diversity analysis for each of the 48 study sites using 100 runs of randomizing the sample units without replacement, extrapolating to a total of 50 samples (the largest number of quadrats deployed at a given site was 35). Rarefaction curves were constructed for each site by plotting the estimated richness by the number of sampling units. Grassland sites are those with a name beginning with BN, CG, or CH, while Parkland sites have names beginning with CD, FA, or FC.

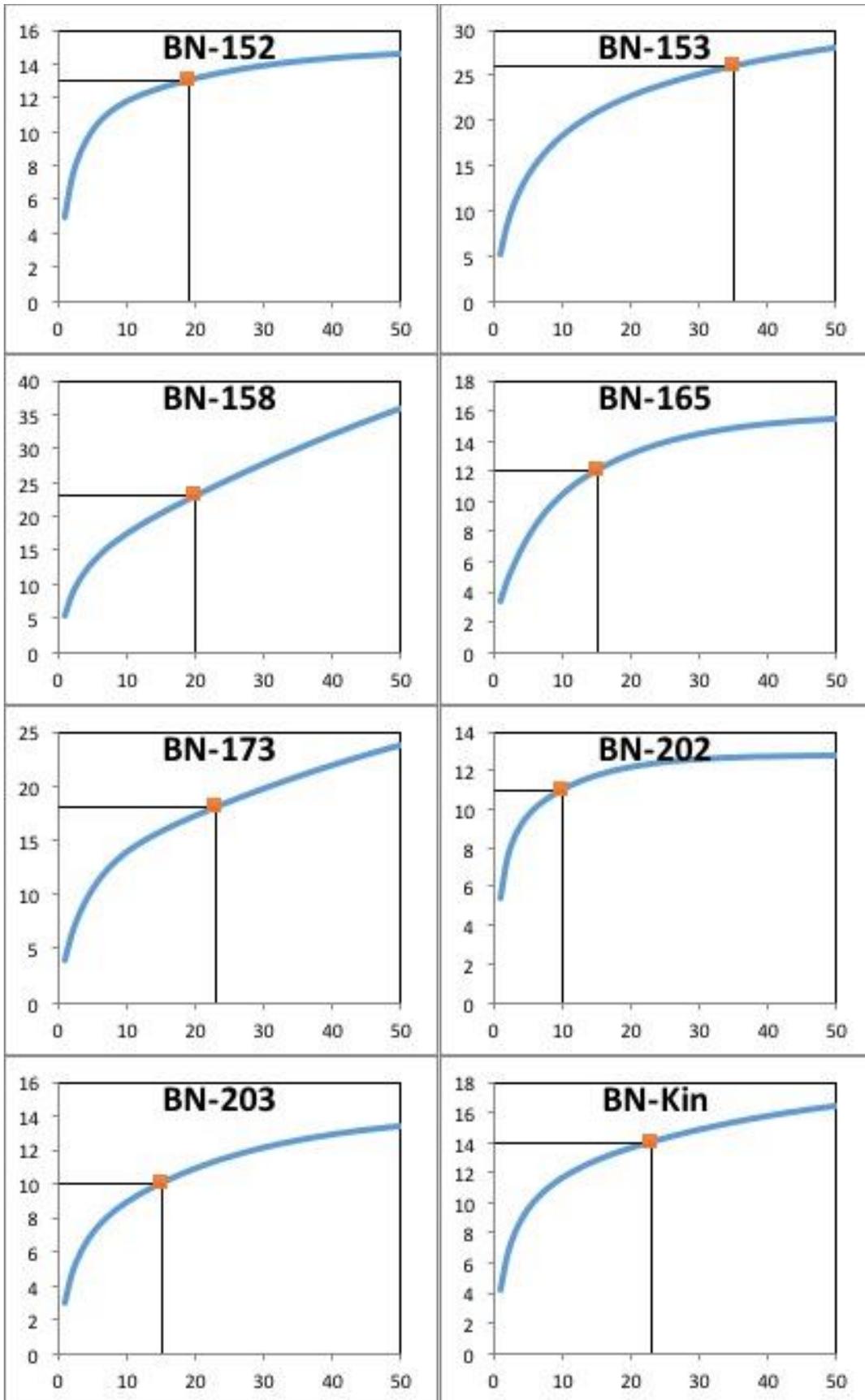
For all figures, the horizontal axis represents the number of sampling units (1 m² quadrats) deployed and the vertical axis represents the number of plant species detected. The actual sampling intensity and number of species detected is shown in orange (point “S”). The efficacy of sampling for a given site can be assessed by examining whether the rarefaction curve asymptotes before or after *S*: if before, this indicates that the sampling was likely adequate to characterize vegetation diversity and a further increase in detected species is unlikely with the addition of extra sample units. Conversely, if the curve continues to rise after *S* (indicating that additional species continued to be detected with the addition of sample units), richness may have been underestimated at that site. While there are some study sites where estimated richness continued to increase after *S* (i.e., BN-158, CG-142, CG-184, CH-117, CD-89, CD-Gad, FA-31, FA-JJColl, FC-200) the majority of the plots show that the rarefaction curve asymptotes around *S*. This indicates that the sampling intensity used in 2014 was largely adequate to represent vegetation richness, supporting the use of this sampling protocol for wetland vegetation surveys in non-permanent prairie wetlands.

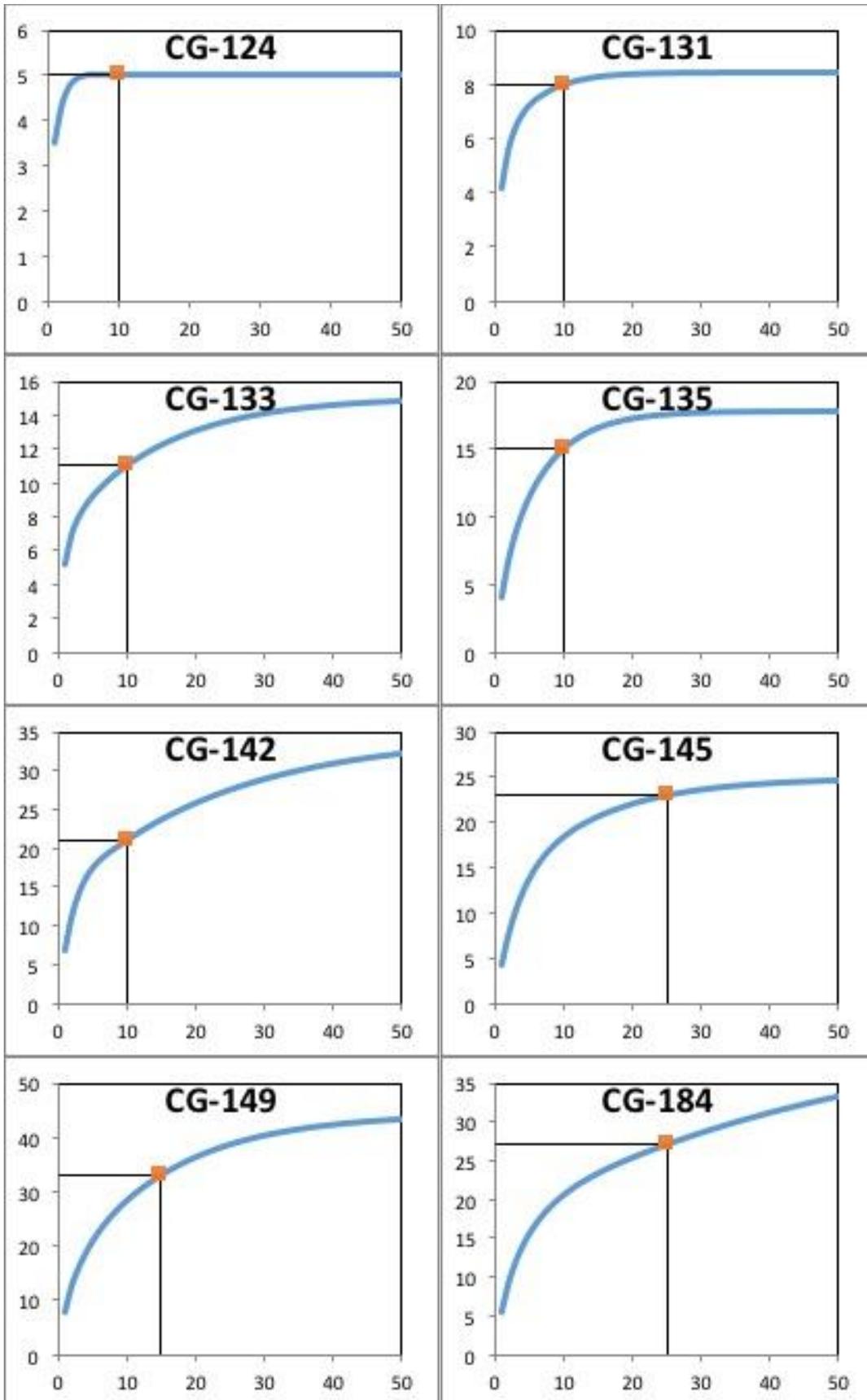
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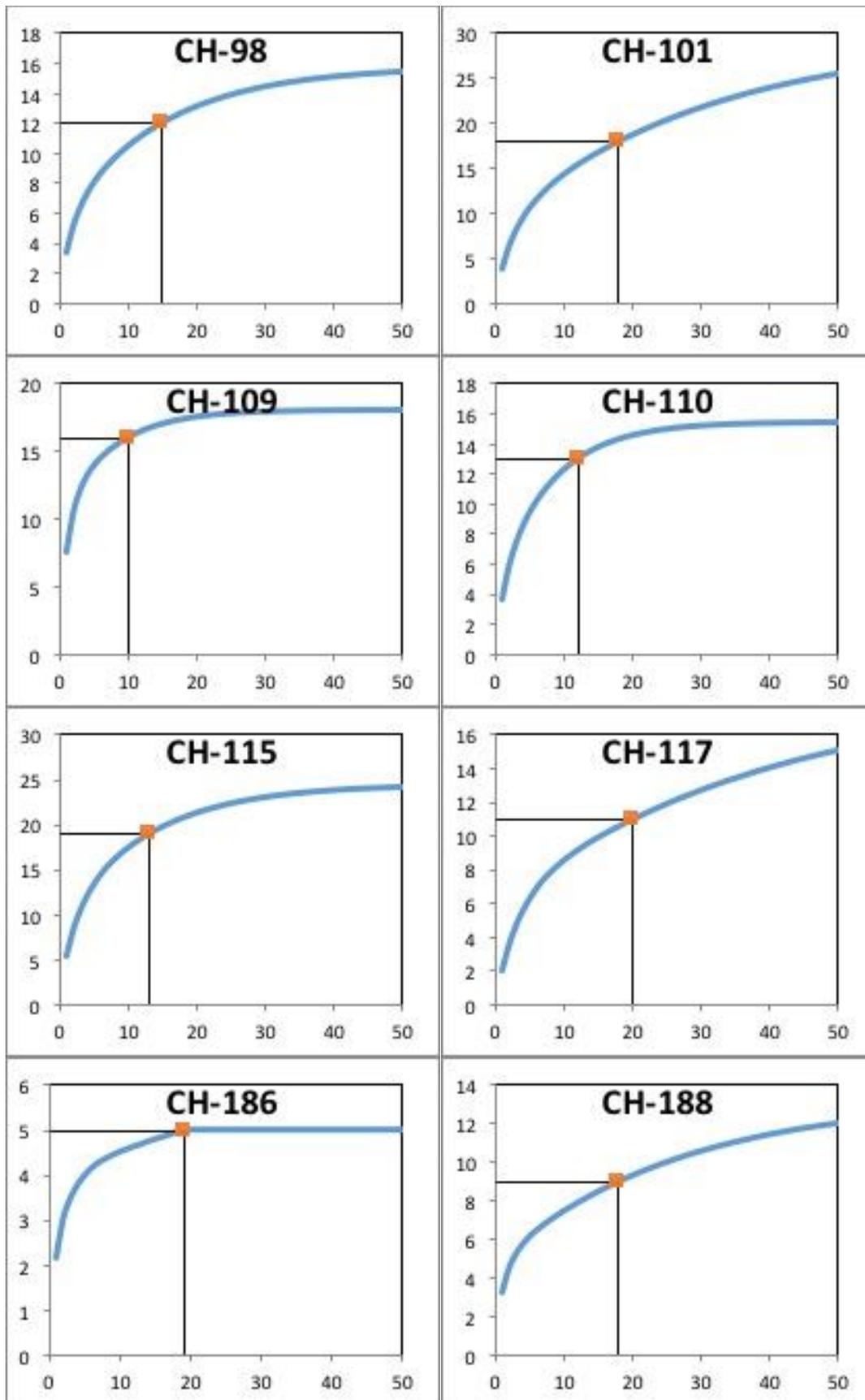
Colwell RK, Chao A, Gotelli NJ, et al (2012) Models and estimators linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. *J Plant Ecol* 5:3–21. doi: 10.1093/jpe/rtr044

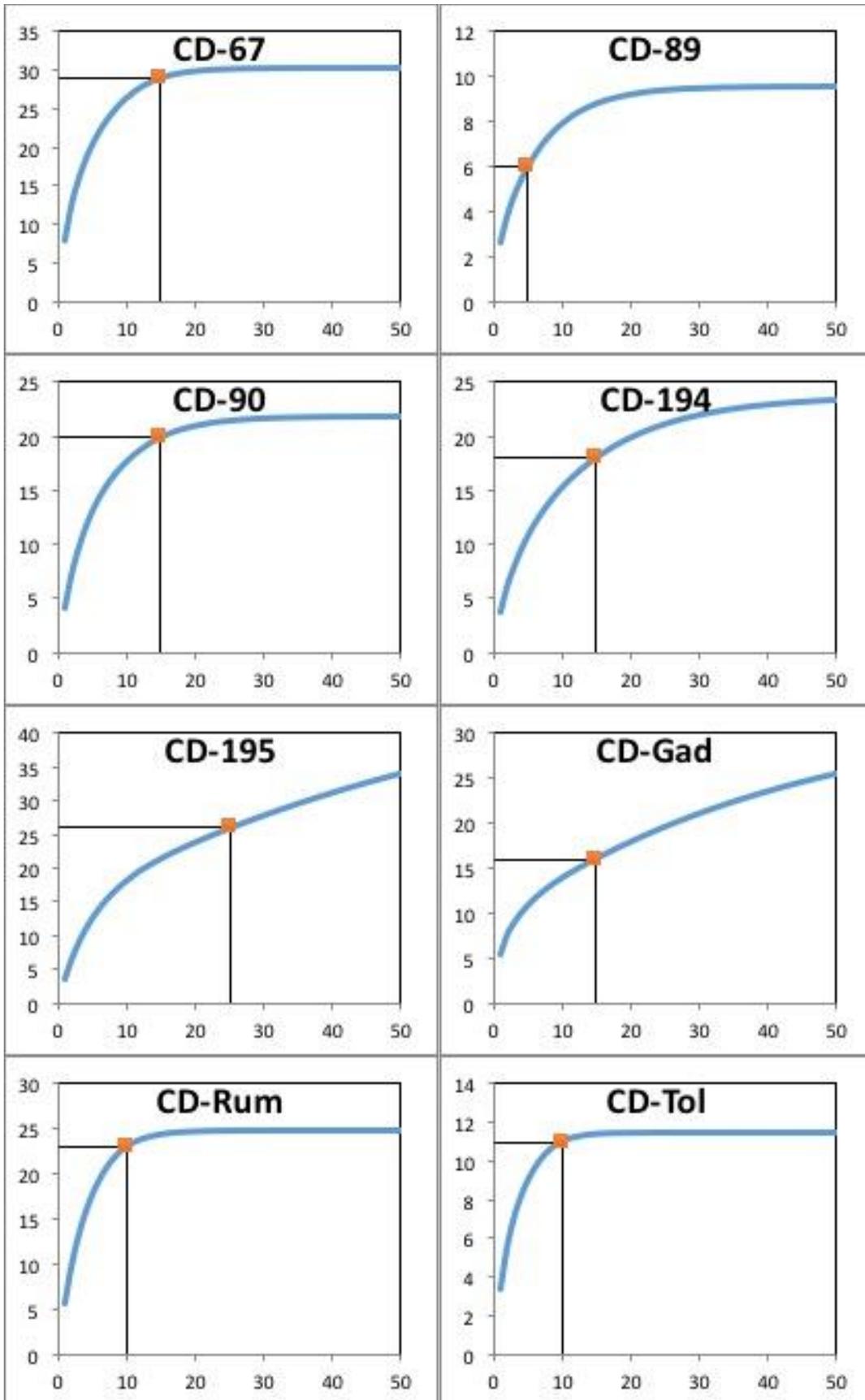
Colwell RK (2013) EstimateS: Statistical estimation of species richness and shared species from samples. Version 9.1.0. User's Guide and application published at:

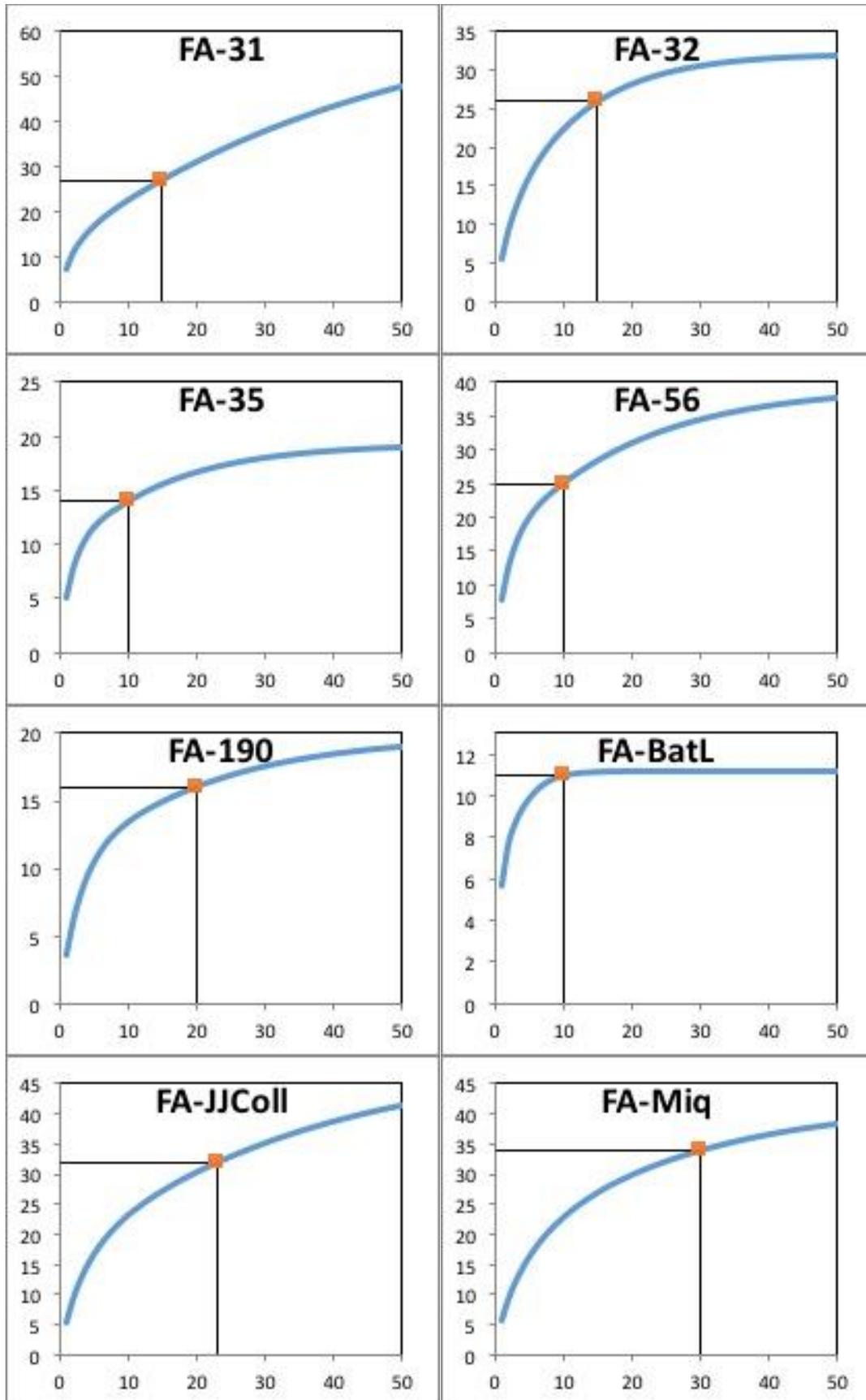
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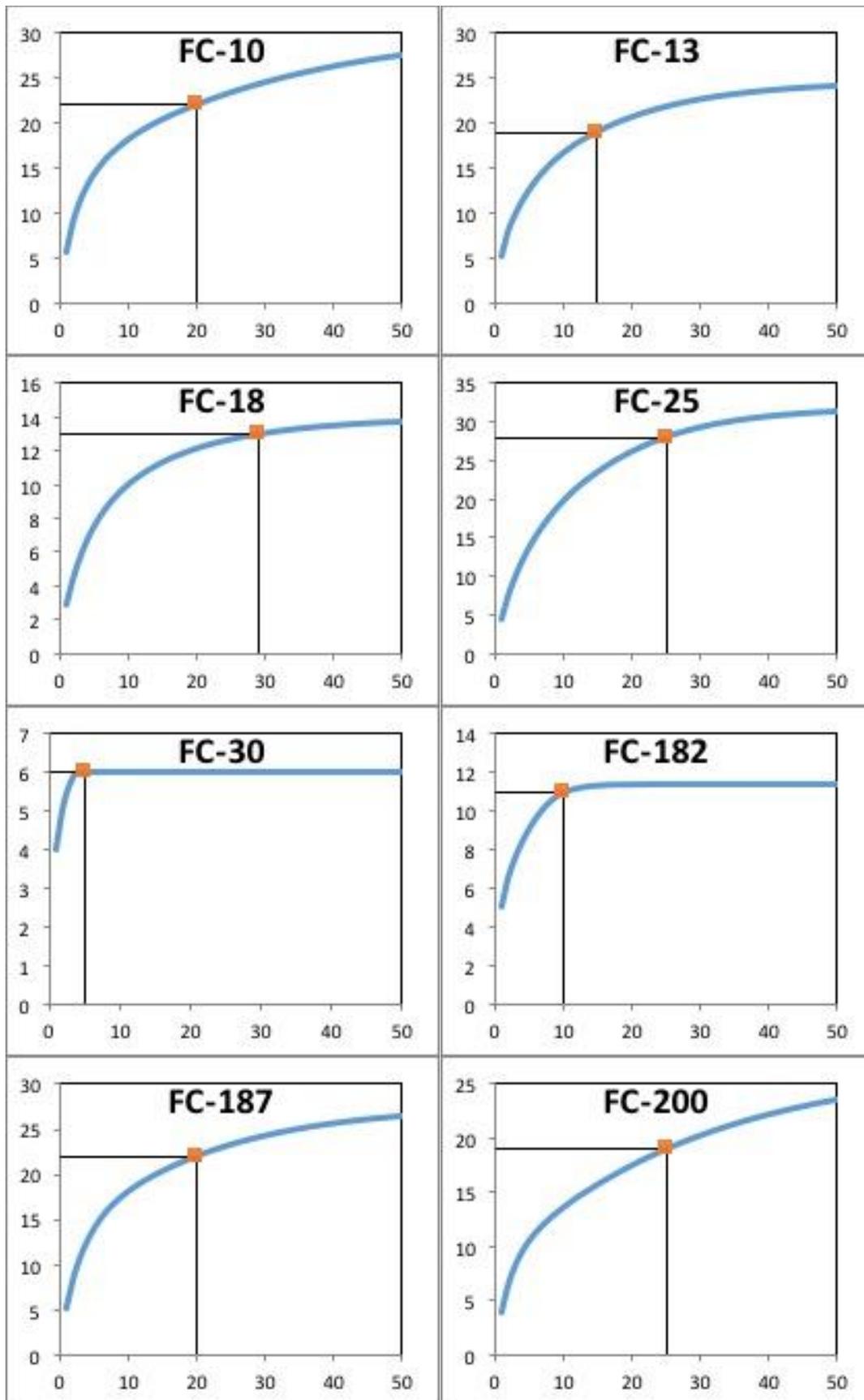












Appendix D: List of plant species observed at study wetlands

Summary of the plant species observed, the abundance data for which was used to construct the vegetation dissimilarity matrix in my Mantel analyses. Species richness was $n = 113$ in the Grassland and $n = 128$ in the Parkland, with 169 species observed in total between the two Natural Regions. Nomenclature reflects the current taxonomic status of each plant as recognized by the Integrated Taxonomic Information System (ITIS 2016), though initial species identification was done using the Flora of Alberta (Moss and Packer 1983). Bolded entries indicate that a voucher specimen was deposited at the ALTA Vascular Plants Herbarium at the University of Alberta in Edmonton, Alberta, Canada. An asterisk indicates that the plant was observed in one vegetation assemblage only, and was therefore deemed rare and excluded from my Mantel analyses.

Botanical Name	Common Name	Family	Region
<i>Achillea alpina</i> L. *	Siberian Yarrow	Asteraceae	Parkland
<i>Achillea millefolium</i> L.	Common Yarrow	Asteraceae	Both
<i>Acorus calamus</i> L. *	Sweet-Flag	Acoraceae	Parkland
<i>Agrimonia striata</i> Michx.	Roadside Agrimony	Rosaceae	Parkland
<i>Agrostis scabra</i> Willd.	Ticklegrass	Poaceae	Parkland
<i>Alisma triviale</i> Pursh	Northern Water Plantain	Alismataceae	Both
<i>Alopecurus aequalis</i> Sobol.	Short-Awn Meadow-Foxtail	Poaceae	Both
<i>Amaranthus retroflexus</i> L. *	Redroot Pigweed	Amaranthaceae	Grassland
<i>Anagalilis minima</i> (L.) E.H.L. Krause *	Chaffweed	Primulaceae	Grassland
<i>Anemone canadensis</i> L.	Canada Anemone	Ranunculaceae	Grassland
<i>Antennaria parvifolia</i> Nutt. *	Small-Leaf Pussytoes	Asteraceae	Parkland
<i>Artemisia biennis</i> Willd.	Biennial Sagewort	Asteraceae	Both
<i>Artemisia longifolia</i> Nutt.	Longleaf Sagebrush	Asteraceae	Both
<i>Artemisia ludoviciana</i> Nutt.	Gray Sagewort	Asteraceae	Grassland
<i>Atriplex prostrata</i> Boucher ex DC. *	Triangle Orache	Amaranthaceae	Grassland
<i>Avena fatua</i> L. *	Wild Oats	Poaceae	Grassland
<i>Beckmannia syzigachne</i> ssp. <i>syzigachne</i> (Steud.) Fernald	American Sloughgrass	Poaceae	Both
<i>Bidens cernua</i> L.	Nodding Beggarticks	Asteraceae	Both
<i>Brassica napus</i> L. *	Argentine Canola	Brassicaceae	Grassland
<i>Bromus inermis</i> Leyss.	Smooth Brome	Poaceae	Both
<i>Calamagrostis canadensis</i> var. <i>canadensis</i> (Michx.) P. Beauv.	Bluejoint	Poaceae	Both
<i>Calamagrostis stricta</i> ssp. <i>inexpansa</i> (A. Gray) C.W. Greene	Slimstem Reedgrass	Poaceae	Both
<i>Calla palustris</i> L.	Water Arum	Araceae	Parkland
<i>Callitriche palustris</i> L.	Vernal Water-Starwort	Plantaginaceae	Both
<i>Caltha palustris</i> L.	Yellow Marsh Marigold	Ranunculaceae	Parkland

Botanical Name	Common Name	Family	Region
<i>Capsella bursa-pastoris</i> (L.) Medik.	Shepherd's Purse	Brassicaceae	Grassland
<i>Carex aquatilis</i> Wahlenb.	Water Sedge	Cyperaceae	Both
<i>Carex atherodes</i> Spreng.	Awned Sedge	Cyperaceae	Both
<i>Carex bebbii</i> Olney ex Fernald	Bebb's Sedge	Cyperaceae	Both
<i>Carex lacustris</i> Willd. *	Lakebank Sedge	Cyperaceae	Parkland
<i>Carex pellita</i> Muhl. ex Willd.	Woolly Sedge	Cyperaceae	Both
<i>Carex praegracilis</i> W. Boott	Clustered Field Sedge	Cyperaceae	Both
<i>Carex retrorsa</i> Schwein.	Knotsheath Sedge	Cyperaceae	Grassland
<i>Carex sychnocephala</i> J. Carey *	Many-Headed Sedge	Cyperaceae	Parkland
<i>Carex utriculata</i> Boott	Northwest Territory Sedge	Cyperaceae	Both
<i>Carum carvi</i> L. *	Wild Caraway	Apiaceae	Parkland
<i>Cerastium arvense</i> L. *	Field Chickweed	Caryophyllaceae	Parkland
<i>Chamerion angustifolium</i> ssp. <i>angustifolium</i> (L.) Holub	Fireweed	Onagraceae	Parkland
<i>Chenopodium album</i> L.	Common Lamb's Quarters	Amaranthaceae	Both
<i>Chenopodium capitatum</i> (L.) Ambrosi	Strawberry Blite	Amaranthaceae	Both
<i>Cicuta maculata</i> var. <i>angustifolia</i> L. *	Spotted Water Hemlock	Apiaceae	Parkland
<i>Cirsium arvense</i> (L.) Scop.	Canada Thistle	Asteraceae	Both
<i>Cirsium vulgare</i> (Savi) Ten. *	Bull Thistle	Asteraceae	Grassland
<i>Collomia linearis</i> Nutt. *	Narrow-Leaf Mountain Trumpet	Polemoniaceae	Grassland
<i>Comarum palustre</i> L.	Purple Marshlocks	Rosaceae	Parkland
<i>Cornus sericea</i> ssp. <i>sericea</i> L.	Red Osier Dogwood	Cornaceae	Parkland
<i>Crepis tectorum</i> L.	Narrow-Leaf Hawk's Beard	Asteraceae	Grassland
<i>Deschampsia cespitosa</i> ssp. <i>cespitosa</i> (L.) P. Beauv.	Tufted Hairgrass	Poaceae	Both
<i>Descurainia sophia</i> (L.) Webb ex Prantl	Flaxweed	Brassicaceae	Grassland
<i>Echinochloa crus-galli</i> (L.) P. Beauv.	Tansymustard		
	Barnyard Grass	Poaceae	Both
<i>Eleocharis acicularis</i> (L.) Roem. & Schult.	Needle Spikerush	Cyperaceae	Both
<i>Eleocharis palustris</i> (L.) Roem. & Schult.	Creeping Spikerush	Cyperaceae	Both
<i>Elymus repens</i> (L.) Gould *	Quackgrass	Poaceae	Parkland
<i>Elymus trachycaulus</i> (Link) Gould ex Shinners	Slender Wheatgrass	Poaceae	Both
<i>Epilobium ciliatum</i> ssp. <i>glandulosum</i> (Lehm.) Hoch & P.H. Raven	Fringed Willow-Herb	Onagraceae	Both
<i>Epilobium leptophyllum</i> Raf. *	Bog Willow-Herb	Onagraceae	Grassland
<i>Epilobium palustre</i> L.	Marsh Willow-Herb	Onagraceae	Parkland
<i>Equisetum arvense</i> L.	Common Horsetail	Equisetaceae	Parkland
<i>Equisetum hyemale</i> ssp. <i>affine</i> (Engelm.) Calder & Roy L. Taylor *	Scouring Horsetail	Equisetaceae	Grassland
<i>Equisetum pratense</i> Ehrh.	Meadow Horsetail	Equisetaceae	Both
<i>Erigeron lonchophyllus</i> Hook. *	Low-Meadow Fleabane	Asteraceae	Grassland
<i>Erigeron philadelphicus</i> L. *	Philadelphia Fleabane	Asteraceae	Parkland
<i>Erysimum cheiranthoides</i> L.	Wallflower Mustard	Brassicaceae	Both
<i>Fallopia convolvulus</i> (L.) Á. Löve	Black Bindweed	Polygonaceae	Both
<i>Fallopia scandens</i> (L.) Holub *	Climbing False	Polygonaceae	Grassland

Botanical Name	Common Name	Family	Region
	Buckwheat		
<i>Festuca saximontana</i> Rydb. *	Rocky Mountain Fescue	Poaceae	Parkland
<i>Fragaria vesca</i> L.	Woodland Strawberry	Rosaceae	Parkland
<i>Fragaria virginiana</i> ssp. <i>glauca</i> (S. Watson) Staudt	Wild Strawberry	Rosaceae	Parkland
<i>Galeopsis tetrahit</i> L.	Brittle-Stem Hedge-Nettle	Lamiaceae	Parkland
<i>Galium trifidum</i> L.	Small Bedstraw	Rubiaceae	Parkland
<i>Galium triflorum</i> Michx.	Sweet Bedstraw	Rubiaceae	Parkland
<i>Geum aleppicum</i> Jacq.	Yellow Avens	Rosaceae	Both
<i>Geum macrophyllum</i> var. <i>princisum</i> (Rydb.) Raup	Large-Leaf Avens	Rosaceae	Parkland
<i>Geum rivale</i> L.	Purple Avens	Rosaceae	Parkland
<i>Glyceria borealis</i> (Nash) Batch.	Northern Manna Grass	Poaceae	Grassland
<i>Glyceria grandis</i> S. Watson	American Manna Grass	Poaceae	Both
<i>Glyceria striata</i> (Lam.) Hitchc.	Fowl Manna Grass	Poaceae	Parkland
<i>Gratiola neglecta</i> Torr.	Clammy Hedge-Hyssop	Plantaginaceae	Parkland
<i>Grindelia squarrosa</i> (Pursh) Dunal *	Curlytop Gumweed	Asteraceae	Grassland
<i>Hippuris vulgaris</i> L.	Common Mare's Tail	Plantaginaceae	Grassland
<i>Hordeum jubatum</i> L.	Foxtail Barley	Poaceae	Both
<i>Juncus balticus</i> ssp. <i>ater</i> Willd.	Baltic Rush	Juncaceae	Both
<i>Juncus longistylus</i> Torr. *	Long-Style Rush	Juncaceae	Parkland
<i>Juncus nodosus</i> L. *	Jointed Rush	Juncaceae	Parkland
<i>Juncus vaseyi</i> Engelm. *	Vasey's Rush	Juncaceae	Parkland
<i>Krascheninnikovia lanata</i> (Pursh) A. Meeuse & A. Smit *	Winterfat	Amaranthaceae	Grassland
<i>Lactuca serriola</i> L.	Prickly Lettuce	Asteraceae	Grassland
<i>Lathyrus othroleucus</i> Hook. *	Cream Peavine	Fabaceae	Parkland
<i>Lemna minor</i> L.	Common Duckweed	Araceae	Both
<i>Linum usitatissimum</i> L. *	Common Flax	Linaceae	Grassland
<i>Lycopus asper</i> Greene	Rough Water Hore-Hound	Lamiaceae	Parkland
<i>Lysimachia maritima</i> (L.) Galasso, Banfi & Soldano *	Sea Milkwort	Primulaceae	Parkland
<i>Lysimachia thyrsoflora</i> L. *	Tufted Yellow Loosestrife	Primulaceae	Grassland
<i>Maianthemum stellatum</i> (L.) Link	False Solomon's Seal	Asparagaceae	Both
<i>Malva neglecta</i> Wallr. *	Roundleaf Mallow	Malvaceae	Grassland
<i>Medicago sativa</i> L. *	Alfalfa	Fabaceae	Grassland
<i>Melilotus albus</i> Medik. *	White Sweet-Clover	Fabaceae	Parkland
<i>Mentha arvensis</i> L.	Wild Mint	Lamiaceae	Both
<i>Persicaria amphibia</i> (L.) Delarbre	Water Knotweed	Polygonaceae	Both
<i>Persicaria lapathifolia</i> (L.) Gray	Curlytop Knotweed	Polygonaceae	Both
<i>Petasites frigidus</i> var. <i>sagittatus</i> (Banks ex Pursh) Chern	Arctic Sweet Colt's-Foot	Asteraceae	Parkland
<i>Phalaris arundinacea</i> L.	Reed Canary Grass	Poaceae	Both
<i>Phleum pratense</i> L.	Common Timothy	Poaceae	Both
<i>Plagiobothrys scouleri</i> (Hook & Arn.) I.M. Johnst.	Scouler's Popcornflower	Boraginaceae	Both
<i>Plantago major</i> L.	Broadleaf Plantain	Plantaginaceae	Parkland

Botanical Name	Common Name	Family	Region
<i>Platanthera hyperborea</i> (L.) Lindl. *	Northern Bog Orchid	Orchidaceae	Parkland
<i>Poa palustris</i> L.	Fowl Bluegrass	Poaceae	Both
<i>Poa pratensis</i> L.	Kentucky Bluegrass	Poaceae	Both
<i>Polygonum aviculare</i> ssp. <i>depressum</i> (Meisn.) Arcang.	Prostrate Knotweed	Polygonaceae	Grassland
<i>Polygonum ramosissimum</i> Michx.	Bushy Knotweed	Polygonaceae	Grassland
<i>Populus tremuloides</i> Michx. *	Trembling Aspen	Salicaceae	Parkland
<i>Potamogeton gramineus</i> L.	Variable-Leaf Pondweed	Potamogetonaceae	Grassland
<i>Potamogeton richardsonii</i> (A. Benn.) Rydb. *	Richardson's Pondweed	Potamogetonaceae	Grassland
<i>Potentilla anserina</i> L.	Silverweed Cinquefoil	Rosaceae	Both
<i>Potentilla norvegica</i> L.	Norwegian Cinquefoil	Rosaceae	Both
<i>Ranunculus aquatilis</i> var. <i>diffusus</i> With.	Water Buttercup	Ranunculaceae	Both
<i>Ranunculus cymbalaria</i> Pursh	Alkali Buttercup	Ranunculaceae	Both
<i>Ranunculus gmelinii</i> DC.	Gmelin's Buttercup	Ranunculaceae	Both
<i>Ranunculus sceleratus</i> var. <i>multifidus</i> (Nutt.) Hultén	Celeryleaf Buttercup	Ranunculaceae	Both
<i>Ribes oxycanthoides</i> L.	Canadian Gooseberry	Grossulariaceae	Parkland
<i>Rorippa palustris</i> (L.) Besser	Marsh Yellowcress	Brassicaceae	Both
<i>Rosa acicularis</i> ssp. <i>sayi</i> (Schwein.) W.H. Lewis	Prickly Rose	Rosaceae	Both
<i>Rubus pubescens</i> Raf. *	Dwarf Red Raspberry	Rosaceae	Parkland
<i>Rubus sachalinensis</i> var. <i>sachalinensis</i> H. Lév.	Common Red Raspberry	Rosaceae	Parkland
<i>Rumex britannica</i> L. *	Greater Water Dock	Polygonaceae	Grassland
<i>Rumex crispus</i> L.	Curly Dock	Polygonaceae	Both
<i>Rumex fueginus</i> Phil.	Golden Dock	Polygonaceae	Both
<i>Rumex occidentalis</i> S. Watson	Western Dock	Polygonaceae	Both
<i>Rumex salicifolius</i> Weinm.	Willow Dock	Polygonaceae	Grassland
<i>Sagittaria cuneata</i> E. Sheld.	Arum-Leaf Arrowhead	Alismataceae	Both
<i>Salicornia rubra</i> A. Nelson	Red Samphire	Amaranthaceae	Grassland
<i>Salix discolor</i> Muhl.	Pussy Willow	Salicaceae	Parkland
<i>Salix exigua</i> Nutt.	Sandbar Willow	Salicaceae	Parkland
<i>Salix lasiandra</i> var. <i>lasiandra</i> Benth.	Pacific Willow	Salicaceae	Both
<i>Salix lucida</i> Muhl.	Shining Willow	Salicaceae	Parkland
<i>Salix planifolia</i> Pursh *	Plain-Leaf Willow	Salicaceae	Parkland
<i>Salix pseudomonticola</i> C.R. Ball *	False Mountain Willow	Salicaceae	Parkland
<i>Salix serissima</i> (L.H. Bailey) Fernald *	Autumn Willow	Salicaceae	Parkland
<i>Schoenoplectus acutus</i> var. <i>acutus</i> (Muhl. ex Bigelow) Á. Löve & D. Löve	Hard-Stem Bulrush	Cyperaceae	Grassland
<i>Schoenoplectus pungens</i> var. <i>pungens</i> (Vahl) Palla	Common Three-Square Bulrush	Cyperaceae	Parkland
<i>Schoenoplectus tabernaemontani</i> (C.C. Gmel.) Palla	Soft-Stem Bulrush	Cyperaceae	Both
<i>Scolochloa festucacea</i> (Willd.) Link	Common Rivergrass	Poaceae	Both
<i>Scutellaria galericulata</i> L.	Marsh Skullcap	Lamiaceae	Both
<i>Senecio vulgaris</i> L. *	Common Groundsel	Asteraceae	Grassland
<i>Sium suave</i> Walter	Common Water Parsnip	Apiaceae	Both
<i>Solidago altissima</i> ssp. <i>gilvocanescens</i> (Rydb.) Semple	Canada Goldenrod	Asteraceae	Both
<i>Sonchus arvensis</i> L.	Perennial Sow-Thistle	Asteraceae	Both
<i>Sonchus asper</i> (L.) Hill	Prickly Sow-Thistle	Asteraceae	Both

Botanical Name	Common Name	Family	Region
<i>Sonchus oleraceus</i> L. *	Annual Sow-Thistle	Asteraceae	Grassland
<i>Spergularia salina</i> J. Presl & C. Presl	Salt Sandspurry	Caryophyllaceae	Grassland
<i>Stachys pilosa</i> var. <i>pilosa</i> Nutt.	Hairy Hedgenettle	Lamiaceae	Both
<i>Stellaria longifolia</i> Muhl. ex Willd. *	Long-Leag Starwort	Caryophyllaceae	Parkland
<i>Suaeda calceoliformis</i> (Hook.) Moq.	Paiuteweed	Amaranthaceae	Grassland
<i>Symphoricarpos occidentalis</i> Hook.	Western Snowberry	Caprifoliaceae	Grassland
<i>Symphotrichum boreale</i> (Torr. & A. Gray) Á. Löve & D. Löve *	Northern Bog Aster	Asteraceae	Both
<i>Symphotrichum ericoides</i> var. <i>pansum</i> (S.F. Blake) G.L. Nesom	White Heath Aster	Asteraceae	Grassland
<i>Symphotrichum lanceolatum</i> var. <i>hesperium</i> (A. Gray) G.L. Nesom	White Panicle Aster	Asteraceae	Both
<i>Symphotrichum puniceum</i> var. <i>puniceum</i> (L.) Á. Löve & D. Löve	Purplestem Aster	Asteraceae	Parkland
<i>Taraxacum officinale</i> F.H. Wigg.	Common Dandelion	Asteraceae	Both
<i>Thlaspi arvense</i> L.	Field Pennycress	Brassicaceae	Both
<i>Trifolium hybridum</i> L.	Alsike Clover	Fabaceae	Parkland
<i>Triglochin maritima</i> L.	Seaside Arrow-Grass	Juncaginaceae	Both
<i>Typha latifolia</i> L.	Common Cattail	Typhaceae	Both
<i>Urtica dioica</i> ssp. <i>gracilis</i> L.	Stinging Nettle	Urticaceae	Parkland
<i>Utricularia vulgaris</i> ssp. <i>macrorrhiza</i> (Leconte) R.T. Clausen	Common Bladderwort	Lentibulariaceae	Grassland
<i>Veronica peregrina</i> L. *	Purslane Speedwell	Plantaginaceae	Parkland
<i>Veronica scutellata</i> L.	Marsh Speedwell	Plantaginaceae	Both
<i>Vicia americana</i> Muhl. ex Willd.	American Vetch	Fabaceae	Parkland
<i>Viola adunca</i> Sm. *	Early Blue Violet	Violaceae	Parkland

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Appendix E: Average landscape composition surrounding study sites, 2011-2014

Values are calculated as the percentage of a 5,000 m buffer around the perimeter of the wetlands occupied by each of nine land cover types, using publically available land-cover data at 30 m resolution (AAFC 2013a, b, c, 2015). A 5,000 m buffer was selected as this spatial extent encompasses the smaller buffers and catchments; however, it did not yield the strongest concordance values in comparing wetland conditions to land cover. Land cover values are presented as averaged across all study sites ($n = 48$) and separated into the Grassland and Parkland Natural Regions ($n = 24$ each).

Year	Sites	Land Cover Type (% of 5,000 m buffer)								
		Cropland	Developed Areas	Exposed Land	Forest	Native Grassland	Pasture and Forages	Shrubland	Water Bodies	Wetland
2011	All	30.07	0.73	0.89	4.56	34.48	19.22	4.65	2.69	2.71
	Grassland	15.01	0.52	1.67	0.18	63.87	11.83	0.98	2.88	3.07
	Parkland	45.14	0.94	0.11	8.95	5.09	26.61	8.31	2.49	2.36
2012	All	31.23	0.87	1.58	5.14	31.95	16.30	6.30	2.80	3.83
	Grassland	16.34	0.55	2.81	0.20	59.55	12.19	1.46	3.30	3.62
	Parkland	46.12	1.20	0.35	10.09	4.35	20.40	11.15	2.31	4.04
2013	All	30.00	0.89	1.45	5.33	32.59	17.75	5.29	2.80	3.90
	Grassland	16.37	0.58	2.48	0.31	60.42	12.16	0.73	3.30	3.66
	Parkland	43.64	1.19	0.43	10.35	4.75	23.35	9.86	2.30	4.13
2014	All	30.21	2.11	0.87	4.42	31.80	16.11	6.17	2.95	5.36
	Grassland	16.85	1.37	1.52	0.34	58.50	11.25	1.60	3.03	5.55
	Parkland	43.57	2.85	0.22	8.51	5.10	20.98	10.75	2.87	5.17

References:

AAFC (2013a) Annual Crop Inventory 2011. Earth Observation Team, Science and Technology Branch, Agriculture and Agri-Food Canada. Available from: <http://open.canada.ca/data/en/dataset/58ca7629-4f6d-465a-88eb-ad7fd3a847e3>.

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AAFC (2013c) Annual Crop Inventory 2013. Earth Observation Team, Science and Technology Branch, Agriculture and Agri-Food Canada. Available from: <http://open.canada.ca/data/en/dataset/4b1d45b0-5bfe-4c6d-bcd3-96c9d821ad3b>.

AAFC (2015) Annual Crop Inventory 2014. Earth Observation Team, Science and Technology Branch, Agriculture and Agri-Food Canada. Available from: <http://open.canada.ca/data/en/dataset/ae61f47e-8bcb-47c1-b438-8081601fa8fe>.

Appendix F: Results of 40 Mantel and partial Mantel tests comparing land cover to wetland environmental conditions

Land cover was calculated as the percent cover of nine land cover types within ten landscape extents around the wetlands for each of four years. 90% confidence intervals (CIs) were calculated around the Mantel r_M values (coefficients indicating the level of similarity between two dissimilarity matrices), while partial Mantel test results represent the remaining land cover \times environmental congruence after controlling for wetland spatial position. The significance of r_M values was determined at $\alpha = 0.05$.

Spatial Extent	Year	<i>Mantel Test</i>					<i>Partial Mantel Test</i>		r_M Change ^a
		r_M	Lower CI	Upper CI	CI width	p -value	r_M	p -value	
10 m DEM Catchment	2011	0.2205	0.1358	0.3063	0.1705	0.0001	0.1792	0.0003	-0.0413
	2012	0.2021	0.1158	0.2928	0.1770	0.0001	0.1614	0.0003	-0.0407
	2013	0.1744	0.0929	0.2651	0.1722	0.0002	0.1331	0.0020	-0.0414
	2014	0.1281	0.0479	0.2194	0.1716	0.0025	0.0861	0.0317	-0.0421
25 m DEM Catchment	2011	0.2147	0.1323	0.3013	0.1690	0.0001	0.1734	0.0007	-0.0413
	2012	0.2127	0.1228	0.3087	0.1859	0.0001	0.1714	0.0007	-0.0413
	2013	0.1818	0.0953	0.2735	0.1782	0.0001	0.1403	0.0026	-0.0416
	2014	0.1441	0.0611	0.2376	0.1765	0.0012	0.1009	0.0150	-0.0432
30 m Buffer	2011	0.1856	0.1013	0.2764	0.1751	0.0002	0.1408	0.0030	-0.0449
	2012	0.1717	0.0937	0.2605	0.1669	0.0008	0.1337	0.0060	-0.0381
	2013	0.1457	0.0663	0.2319	0.1656	0.0037	0.1075	0.0172	-0.0382
	2014	0.1333	0.0579	0.2167	0.1588	0.0036	0.0948	0.0293	-0.0384
100 m Buffer	2011	0.1771	0.0966	0.2566	0.1600	0.0001	0.1349	0.0023	-0.0422
	2012	0.1918	0.1090	0.2778	0.1689	0.0001	0.1530	0.0011	-0.0388
	2013	0.1620	0.0843	0.2422	0.1579	0.0006	0.1220	0.0055	-0.0401
	2014	0.1355	0.0578	0.2145	0.1568	0.0030	0.0988	0.0290	-0.0368
200 m Buffer	2011	0.2226	0.1406	0.3039	0.1633	0.0001	0.1806	0.0005	-0.0420
	2012	0.2221	0.1353	0.3174	0.1822	0.0001	0.1834	0.0005	-0.0387
	2013	0.1948	0.1137	0.2777	0.1640	0.0001	0.1548	0.0011	-0.0400
	2014	0.1463	0.0614	0.2358	0.1744	0.0017	0.1095	0.0180	-0.0368

Spatial Extent	Year	<i>Mantel Test</i>					<i>Partial Mantel Test</i>		r_M Change ^a
		r_M	Lower CI	Upper CI	CI width	p -value	r_M	p -value	
300 m Buffer	2011	0.2418	0.1616	0.3256	0.1640	0.0001	0.2002	0.0003	-0.0416
	2012	0.2180	0.1291	0.3120	0.1829	0.0001	0.1793	0.0004	-0.0387
	2013	0.1971	0.1180	0.2837	0.1657	0.0001	0.1576	0.0013	-0.0395
	2014	0.1424	0.0600	0.2278	0.1678	0.0006	0.1040	0.0165	-0.0384
500 m Buffer	2011	0.2243	0.1447	0.3113	0.1665	0.0001	0.1791	0.0007	-0.0452
	2012	0.1996	0.1172	0.2861	0.1690	0.0001	0.1570	0.0006	-0.0426
	2013	0.1867	0.1069	0.2732	0.1663	0.0001	0.1430	0.0021	-0.0437
	2014	0.1334	0.0572	0.2131	0.1559	0.0016	0.0882	0.0256	-0.0452
1,000 m Buffer	2011	0.1374	0.0527	0.2390	0.1864	0.0029	0.0790	0.0725	-0.0584
	2012	0.1045	0.0238	0.1948	0.1709	0.0135	0.0490	0.1614	-0.0555
	2013	0.1245	0.0465	0.2106	0.1641	0.0048	0.0705	0.0770	-0.0540
	2014	0.0903	0.0190	0.1694	0.1503	0.0278	0.0335	0.2387	-0.0568
2,000 m Buffer	2011	0.1097	0.0072	0.2210	0.2138	0.0095	0.0288	0.3060	-0.0809
	2012	0.0598	-0.0314	0.1607	0.1921	0.1092	-0.0264	0.6760	-0.0862
	2013	0.0860	-0.0006	0.1829	0.1835	0.0452	0.0116	0.4100	-0.0744
	2014	0.0621	-0.0217	0.1592	0.1809	0.1194	-0.0181	0.6244	-0.0802
5,000 m Buffer	2011	0.0682	-0.0468	0.1979	0.2446	0.0657	-0.0814	0.8129	-0.1496
	2012	0.0427	-0.0650	0.1622	0.2272	0.1957	-0.0814	0.9163	-0.1241
	2013	0.0589	-0.0519	0.1818	0.2337	0.1201	-0.0590	0.8362	-0.1179
	2014	0.0390	-0.0679	0.1622	0.2301	0.2216	-0.0827	0.9108	-0.1217

^a r_M Change = decrease in r_M after controlling for geographic position (Mantel r_M – partial Mantel r_M).

Appendix G: Results of 40 Mantel and partial Mantel tests comparing land cover to wetland vegetation community composition

Land cover was calculated as the percent cover of nine land cover types within ten landscape extents around the wetlands for each of four years. 90% confidence intervals (CIs) were calculated around the Mantel r_M values (coefficients indicating the level of similarity between two dissimilarity matrices), while partial Mantel test results represent the remaining land cover \times vegetation congruence after controlling for wetland spatial position. The significance of r_M values was determined at $\alpha = 0.05$.

Spatial Extent	Year	<i>Mantel Test</i>					<i>Partial Mantel Test</i>		r_M Change ^a
		r_M	Lower CI	Upper CI	CI width	p -value	r_M	p -value	
10 m DEM Catchment	2011	0.0904	0.0185	0.1671	0.1487	0.0172	0.0387	0.1777	-0.0517
	2012	0.0895	0.0177	0.1679	0.1502	0.0170	0.0356	0.1907	-0.0539
	2013	0.1105	0.0376	0.1915	0.1539	0.0040	0.0583	0.0652	-0.0522
	2014	0.0889	0.0227	0.1657	0.1429	0.0140	0.0384	0.1528	-0.0505
25 m DEM Catchment	2011	0.0989	0.0220	0.1800	0.1579	0.0097	0.0461	0.1284	-0.0528
	2012	0.1016	0.0275	0.1865	0.1590	0.0101	0.0473	0.1376	-0.0543
	2013	0.1244	0.0511	0.2055	0.1544	0.0022	0.0705	0.0433	-0.0539
	2014	0.1047	0.0347	0.1834	0.1487	0.0057	0.0527	0.0872	-0.0521
30 m Buffer	2011	0.0584	-0.0102	0.1364	0.1465	0.0870	0.0074	0.4178	-0.0510
	2012	0.0169	-0.0431	0.0834	0.1264	0.3329	-0.0299	0.7361	-0.0468
	2013	0.0599	-0.0116	0.1399	0.1515	0.0806	0.0147	0.3403	-0.0452
	2014	0.0400	-0.0332	0.1196	0.1528	0.1530	-0.0029	0.5127	-0.0429
100 m Buffer	2011	0.0599	-0.0096	0.1395	0.1491	0.0762	0.0108	0.3787	-0.0491
	2012	0.0457	-0.0171	0.1165	0.1337	0.1322	-0.0058	0.5396	-0.0515
	2013	0.0597	-0.0110	0.1390	0.1500	0.0718	0.0084	0.3986	-0.0513
	2014	0.0369	-0.0297	0.1150	0.1447	0.1654	-0.0112	0.5868	-0.0480
200 m Buffer	2011	0.0721	-0.0002	0.1552	0.1553	0.0409	0.0196	0.3087	-0.0525
	2012	0.0774	0.0119	0.1546	0.1427	0.0311	0.0250	0.2792	-0.0524

Spatial Extent	Year	<i>Mantel Test</i>					<i>Partial Mantel Test</i>		r_M Change ^a
		r_M	Lower CI	Upper CI	CI width	p -value	r_M	p -value	
300 m Buffer	2013	0.0902	0.0178	0.1715	0.1537	0.0170	0.0365	0.1808	-0.0537
	2014	0.0621	-0.0078	0.1390	0.1468	0.0668	0.0112	0.3810	-0.0509
	2011	0.0813	0.0073	0.1600	0.1527	0.0274	0.0260	0.2643	-0.0553
	2012	0.0896	0.0204	0.1686	0.1482	0.0197	0.0363	0.1936	-0.0532
500 m Buffer	2013	0.0994	0.0235	0.1808	0.1573	0.0078	0.0445	0.1334	-0.0548
	2014	0.0821	0.0177	0.1561	0.1384	0.0209	0.0315	0.2078	-0.0506
	2011	0.0985	0.0265	0.1781	0.1516	0.0093	0.0376	0.1852	-0.0610
	2012	0.1006	0.0311	0.1794	0.1483	0.0059	0.0414	0.1455	-0.0592
1,000 m Buffer	2013	0.1160	0.0419	0.1956	0.1538	0.0037	0.0571	0.0782	-0.0588
	2014	0.0945	0.0263	0.1678	0.1415	0.0127	0.0367	0.1634	-0.0578
	2011	0.1078	0.0310	0.1869	0.1560	0.0055	0.0334	0.2273	-0.0745
	2012	0.1039	0.0335	0.1774	0.1439	0.0046	0.0347	0.1851	-0.0692
2,000 m Buffer	2013	0.1102	0.0383	0.1872	0.1489	0.0043	0.0417	0.1595	-0.0685
	2014	0.0918	0.0220	0.1674	0.1455	0.0168	0.0202	0.2935	-0.0716
	2011	0.1296	0.0520	0.2116	0.1595	0.0010	0.0363	0.2302	-0.0933
	2012	0.0732	0.0057	0.1458	0.1401	0.0419	-0.0200	0.6547	-0.0932
5,000 m Buffer	2013	0.1098	0.0353	0.1878	0.1526	0.0071	0.0233	0.2997	-0.0865
	2014	0.0858	0.0117	0.1624	0.1506	0.0303	-0.0105	0.5734	-0.0962
	2011	0.1214	0.0472	0.1980	0.1507	0.0031	0.0029	0.4778	-0.1186
	2012	0.1091	0.0405	0.1796	0.1391	0.0098	-0.0137	0.6032	-0.1228
	2013	0.1234	0.0550	0.1940	0.1391	0.0048	0.0073	0.4551	-0.1161
	2014	0.1017	0.0300	0.1765	0.1466	0.0185	-0.0239	0.6669	-0.1257

^a r_M Change = decrease in r_M after controlling for geographic position (Mantel r_M – partial Mantel r_M).

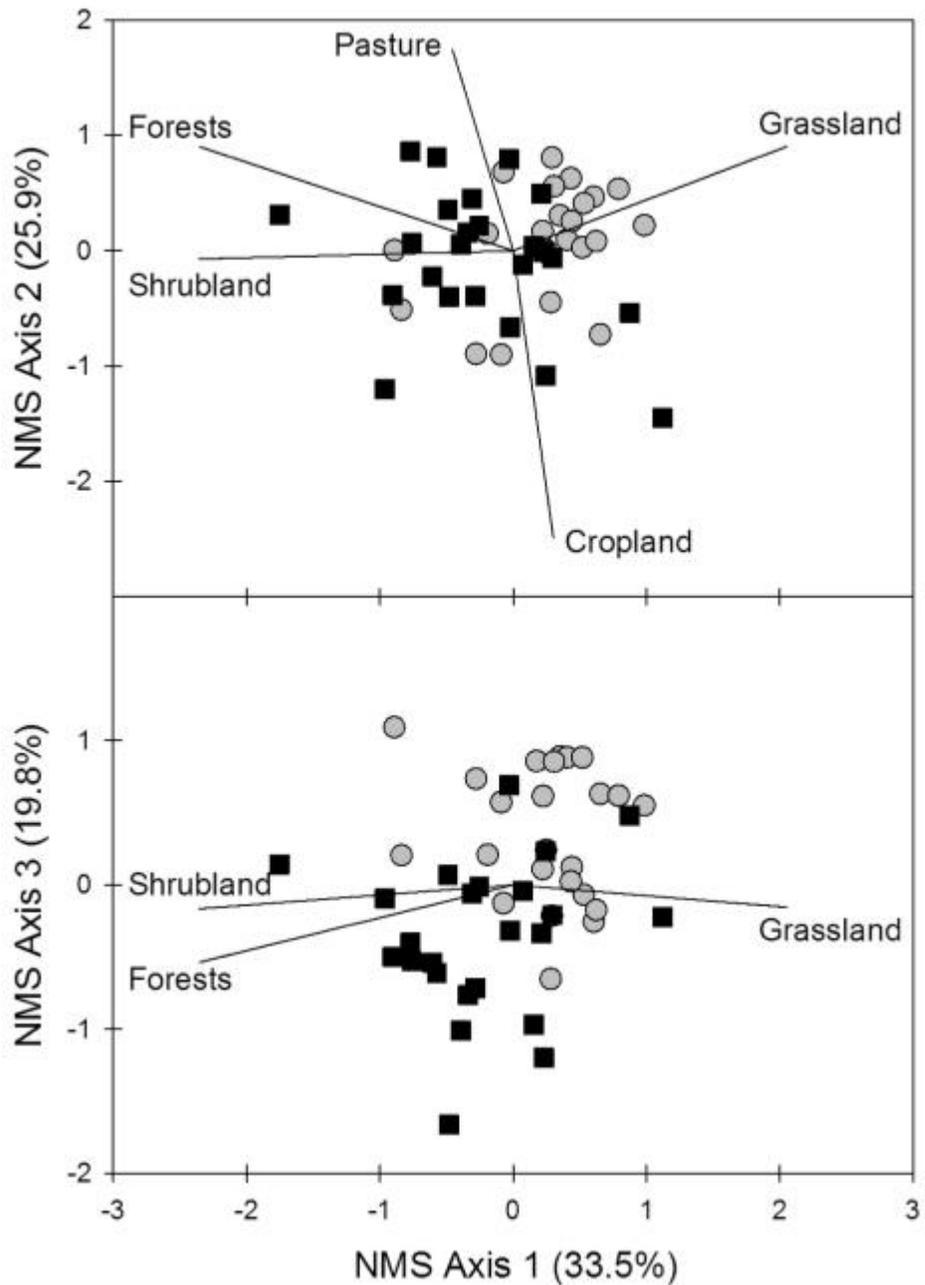
Appendix H: Non-metric multidimensional scaling (NMS) ordination solution depicting 48 non-permanent marshes in the Grassland and Parkland Natural Regions of Alberta, Canada positioned in vegetation species space.

To visualize patterns in vegetation community composition among the 48 non-permanent wetlands that I sampled in 2014, I performed an NMS ordination on a Bray-Curtis dissimilarity matrix created from wetland vegetation percent cover data. Prior to carrying out the ordination, I eliminated 48 rare species to minimize the effects of data sparsity (see **Appendix D**) and applied an arcsine square root transformation to eliminate platykurtosis in the percent cover data (McCune and Grace 2002). The final NMS solution was identified following 250 runs with real data and 250 with randomized data, and a 3-dimensional solution was recommended. The final stress was 14.71 and final instability was <0.00001 based on 75 iterations. I applied a Varimax rotation, which is a rigid rotation that aligns the NMS axis explaining the greatest proportion of variance in the vegetation composition dissimilarity matrix with the first axis (McCune and Grace 2002). The percentages indicated in the axes labels depict the approximate amount of variation in the original dissimilarity matrix that is explained by each axis. I performed this ordination using PC-ORD v. 6.0 (McCune and Mefford 2009).

The Grassland sites (grey circles; $n = 24$) typically had higher NMS axis 1 scores than the Parkland sites (black squares; $n = 24$), indicating that the wetland vegetation communities differ by Natural Region. To further explore the differences in wetlands between the Grassland and Parkland, I overlaid vectors representing correlations of land covers with the NMS axes. Land cover was represented by 2013 percent composition cover extracted within 500 m buffers; vector lengths were increased by a factor of 5 to improve visibility, though only vectors with $R^2 > 0.1$

are shown. Vectors of forest and shrubland cover are negatively loaded on NMS axis 1 versus a positive loading of the grassland cover vector, indicating that these land cover types may be mutually exclusive and are associated with sites in the Parkland and Grassland Natural Regions, respectively.

Partial clustering of sites with others from the same Natural Region indicates some similarities in species composition within Natural Regions but differences in composition between the Grassland and Parkland. This supports my interpretation of my partial Mantel test results, that before controlling for spatial autocorrelation, the larger buffers appeared to better align with wetland vegetation simply because they more consistently reflected which Natural Region the site was located in, not because the land cover from so far away directly influenced what vegetation assembled at a wetland. The differences in species composition between the Grassland and Parkland are likely driven by both the distinct species pools of the two Natural Regions and differences in climatic and physiographic conditions, wherein different land cover types dominate in each of the Grassland and Parkland and thus support distinct wetland vegetation communities.



References:

McCune B, Grace JB (2002) Analysis of Ecological Communities. MjM Software Design, Oregon, U.S.A.

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