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Macroinvertebrate Communities of Temporary Prairie Pothole Wetlands

by

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ABSTRACT

Macroinvertebrate communities were sampled in rotationally grazed, temporary wetlands in the prairie pothole region. Seven wetlands were grazed when temporary wetlands contained water (early grazed), and six wetlands were grazed when temporary wetlands were dry (late grazed). Late grazed wetlands contained more abundant and diverse macroinvertebrate communities than early grazed wetlands. Phylogenetic comparison of macroinvertebrates from temporary wetlands with those from permanent wetlands suggested the temporary community was influenced by environmental filtering, while the permanent community was influenced by biotic interactions, indicating fewer groups were able to survive the short wet period of temporary wetlands, compared to permanent wetlands. Both taxonomic and functional traits perspectives demonstrated that rotational grazing created two distinct habitats, by allowing late grazed wetlands to escape grazing pressure during the wet season. Given contrasting patterns observed between permanent and temporary wetlands, macroinvertebrate diversity at the landscape level is best served by maintaining wetlands of varying permanence.

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DEDICATION

I dedicate this thesis to my family, for their continuing encouragement to continue along my own, often muddy, path.

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EPIGRAPH

The secret of all victory lies in the organization of the non-obvious.

~ Marcus Aurelius ~

CHAPTER 1: GENERAL INTRODUCTION

A wetland is defined as land that is saturated with water long enough to promote wetland or aquatic processes as indicated by poorly drained soils, hydrophytic vegetation and various kinds of biological activity which are adapted to a wet environment (National Wetlands Working Group 1988). There are a wide variety of wetlands found in numerous diverse ecosystems from coastal estuaries to the bogs and fens of the high arctic. The wetlands function to filter water, reduce the severity of floods and droughts, and provide habitat for a large variety of plants and animals.

The prairie pothole region (PPR) of North America covers approximately 777,000 km² and extends from eastern Alberta, through southern Saskatchewan and down through North and South Dakota to Minnesota and Iowa (Fig. 1.1). The PPR is considered the most important habitat for many species of waterfowl in North America, as between 50-80% of the continent's waterfowl are reared in the PPR (United States Department of the Interior and Environment Canada 1986). Waterfowl thrive in the PPR partially due to the extremely high densities of wetlands (National Wetlands Working Group 1988).

The wetlands of the PPR are also home to diverse macroinvertebrate communities. These communities are composed of a variety of animals including insects, snails, and leeches (Batzler and Wissinger 1996). The macroinvertebrates serve as the primary protein source for waterfowl returning from southern wintering grounds and for ducklings that are born a few weeks later (Murkin and Kadlec 1986, Cox et al. 1998, Pietz et al. 2003). Aquatic macroinvertebrate communities found in freshwater wetlands

are diverse and consist of permanently aquatic taxa (e.g., Amphipoda and Hirudinae), taxa with a terrestrial adult stage (e.g., Diptera and Odonata), and taxa that utilize both the terrestrial and aquatic environments (e.g., adult Coleoptera and Hemiptera; Batzer and Wissinger 1996). The particular macroinvertebrate community present in a given wetland can depend on many factors, including geographic location (e.g., Mihuc and Toetz 1996, Nicolet et al. 2004), wetland depth (Zimmer et al. 2000), turbidity (Anteau and Afton 2009), fish presence (e.g., Cox et al. 1998, McParland and Paszkowski 2006), vegetation density and structure (e.g., deSzalay and Resh 1997, Gardner et al. 2001), human influences (e.g., Richards et al. 1993, Ometo et al. 2000), open water area (Anteau and Afton 2009) and wetland permanence (e.g., Euliss et al. 2002, Lillie 2003). As the number of factors potentially influencing the macroinvertebrate community is quite large, even wetlands located very close to each other can have very different macroinvertebrate communities (e.g., Lindeman and Clark 1999, Fairchild et al. 2000). Furthermore, macroinvertebrate community composition can change within a given wetland throughout the ice-free season (e.g., Lahr et al. 1999, Culioli et al. 2006).

The wetlands of the PPR tend to be small, with many having a surface area less than 0.2 ha (National Wetlands Working Group 1988). Most prairie wetlands form in the numerous ‘potholes’ left on the landscape as the glaciers retreated. The wetlands tend to be isolated from both ground water and permanent overland flows. The wetlands often serve as drainage basins for large parts of the often-flat prairies. The variability in pothole wetland size and depth, combined with weather conditions of the prairies, cause these small wetlands to experience dry periods of varying lengths. Stewart and Kantrud (1971)

created a wetland classification system for prairie wetlands based on water permanence, vegetative structure and water chemistry, categorizing most prairie wetlands into one of seven classes. The first five classes are based on increasing water permanence while classes VI and VII are grouped based on very specific water chemistry parameters (Table 1; Stewart and Kantrud 1971). Although the extreme variability in prairie weather can cause wetlands to 'change' class from year to year, in general, the Stewart and Kantrud system is considered the best prairie wetland classification system.

Class II, temporary wetlands were selected as the focus of the present study. Temporary wetlands were chosen as they present the opportunity to study clearly defined habitats, as each wetland is isolated from the others. The short wet period also allows one to track macroinvertebrate community development from initial wetting through complete drying of the habitat. Temporary wetlands of the PPR represent a significant proportion of the inland water found on the prairies (van der Valk and Pederson 2003). The temporary wetlands are filled by snowmelt and early spring rains (Williams 1987) and typically have standing water from early spring through mid summer. Waterfowl tend use the temporary prairie pothole wetlands immediately upon return to the PPR in the spring (Swanson et al. 1985, Krapu et al. 1997). Temporary wetlands tend to be some of the first ice-free water bodies on the landscape, and the waters are often rich with macroinvertebrates for the waterfowl to feed on before they relocate to more permanent water bodies to mate (Krapu et al. 2006, Niemuth et al. 2006).

The macroinvertebrate communities of temporary wetlands contain a subset of taxa present in more permanent wetlands, combined with a few taxa that are found exclusively

in the temporary wetlands (Jeffries 1994, Collinson et al. 1995). The macroinvertebrates recolonize the temporary wetlands at the beginning of each wet period either from terrestrial habitats, permanent wetlands or from desiccation-resistant stages in the substrate. Mosquitoes and chironomids are typically the most abundant members of temporary wetlands (Bratton 1990, Batzer and Wissinger 1996, Nicolet et al. 2004). The presence or absence of invertebrate predators such as Odonata and Dytiscidae has a large influence on the macroinvertebrate community structure of fishless wetlands (Turner and Chislock 2007, Cobbaert et al. 2010).

A common trait among the taxa found in temporary wetlands is an ability to survive the dry phase (Wiggins et al. 1980). There are several different strategies employed. Most taxa leave the aquatic environment and live as terrestrial adults. Some taxa bury into the substrate and wait for the water to return, and a few taxa have highly mobile adult stages that are able to use both the aquatic and terrestrial habitats. These taxa generally relocate to more permanent wetlands until the temporary wetlands refill in the spring. Occasionally, taxa are sampled from temporary wetlands that do not possess a dry-phase survival strategy (i.e. they must stay wet throughout their lifecycle). Often these taxa are transported from nearby permanent wetlands to the temporary habitats by animal vectors, most often waterfowl (Green et al. 2008). These taxa generally are extirpated from the temporary wetlands during the dry phase.

Despite the abundant and diverse communities associated with temporary wetlands, they are often considered 'wasted land', and expendable especially when they occur in agricultural fields (Semlitsch and Bodie 1998). As a result of this attitude and the lack of

well-enforced wetland conservation legislation, it is estimated that more than 50% of the temporary wetlands once present in the PPR were permanently lost between 1780 and 1980 (National Wetlands Working Group 1988, Dahl 1990). In more recent years, conversion of native prairie to agricultural land has increased as crops have become more drought resistant, and farming techniques and technologies allow for agriculture to occur in areas that were previously inaccessible (Stephens 2010). The loss occurs when these wetlands are either ploughed through to become level with the surrounding land, or they are altered hydrologically, usually through ditching. The loss of these wetlands eliminates habitat for macroinvertebrates, waterfowl, plants and other communities that depend on the temporary wetlands.

Estimates suggest that as much as 95% of remaining wetlands in the PPR, including Alberta, have impacted margins (Turner et al. 1987). Wetlands with impacted margins still hold water, but agricultural practices occur right up to, and often through, the wetland. This results in the loss of the distinctive wetland vegetation usually found in and immediately around these wetlands (Turner et al. 1987). The encroaching agriculture has the potential to alter every aspect of the wetland, leading to increased levels of nitrogen and phosphorus in the water (Carpenter et al. 1998), and decreased diversity of the plant (Mountford et al. 1993, Galatowitsch et al. 2000), macroinvertebrate (Euliss and Musher 1999) and waterfowl (Bethke and Nudds 1995) communities.

Cattle grazing is the primary form of agriculture in Alberta's portion of the PPR. The cattle pastures often contain wetlands of varying permanence, and cattle are generally allowed full access to any wetlands in their pasture. The pasture wetlands serve as

sources of drinking water and high quality forage from spring through fall. Cattle grazing in and around permanent wetlands leads to increased nitrogen (Nader et al. 1998), decreased vegetation height due to grazing and trampling (Hornung and Rice 2003), a decrease in macroinvertebrate community diversity (Scrimgeour and Kendall 2003), and decrease in waterfowl use of the wetlands (Bue et al. 1952).

Because halting agriculture in the PPR is not practical, wetland conservation groups have looked for ways to allow agriculture and wetlands to coexist. Solutions include purchasing critical wetland habitat or providing easements allowing land managers to retain ownership of the land, while protecting the wetland from agricultural encroachment. For cattle ranchers, permanently restricting cattle from wetlands in their pasture is often not practical or desirable, as the wetlands provide water and forage for the cattle. As a compromise, rotational grazing practices are often implemented. Rotational or rest-rotational grazing moves the cattle herd from pasture to pasture throughout the year (Hormay and Talbot 1961). This practice is advantageous as it allows pasture wetlands to be free from direct cattle pressure for a part of each year, while providing cattle with increased access to natural forage for a larger portion of the year.

The benefits of rotational grazing for waterfowl using the permanent wetlands are well documented (e.g., Gjersing 1975, Munding 1976, Lapointe et al. 2000, Carroll et al. 2007). In general, waterfowl prefer to use the permanent wetlands in pastures not grazed during the spring (Munding 1976), with more broods being produced in rotationally grazed pastures than in pastures allowing cattle continual access to all wetlands (Gjersing 1975, Lapointe et al. 2000). The increased success of waterfowl in

rotationally grazed systems is generally linked to increased vegetation cover for the permanent wetlands that are not grazed during nesting (Gjersing 1975, Carroll et al. 2007).

Conversely, the impacts of rotational grazing on the macroinvertebrate community of pasture wetlands are not well studied. Research on macroinvertebrates in rotationally grazed systems has been conducted on benthic invertebrates in freshwater streams that run through cattle pastures (Sovell et al. 2000, Weigel et al. 2000, Braccia and Voshell 2007). Overall, diversity of the benthic invertebrate community is increased for rotationally grazed systems compared to continually grazed systems, but the trend is rarely significant (Sovell et al. 2000, Weigel et al. 2000, Braccia and Voshell 2007). The lack of significance has typically been attributed to watershed-level factors having a stronger influence on the macroinvertebrate community than very local land use (Weigel et al. 2000).

The aim of the present study is to fill in some of the knowledge gap regarding rotational grazing and the macroinvertebrate community. The land manager of the study area located in the PPR approximately 45 km northeast of Calgary, Alberta, grazed the cattle herd on four different pastures throughout the year. The land manager implemented rotational grazing in 1994, and the pastures have been grazed in the same order since that time. The approximate grazing timing for each pasture is: early grazed pasture used May 15 through June 27, mating pasture used June 27 through July 31, late grazed pasture used July 31 through October 15, and the overwintering pasture used October 15 through May 15. Only the early and late grazed pastures were used for this study, because the

land manager did not want sampling to occur in the mating pasture as the presence of bulls made sampling unsafe, and when the cattle are in the overwintering pasture they are fed supplementary food, instead of relying on natural forage. A single fence separates the early and late grazed pastures; thus, local weather and microhabitat differences are not likely to have an undue influence on the results. The study did not include pristine (i.e., ungrazed) or continually grazed pasture wetlands because (i) there were no pastures within a reasonable distance available for study, and (ii) increasing the study area would likely have increased the influence of local weather events and slight habitat differences.

The macroinvertebrate communities of thirteen temporary wetlands were repeatedly sampled throughout the local growing season (May through August) in 2008. Seven wetlands were in the early grazed pasture, and six were found the late grazed pasture. Temporary wetlands were chosen for the study unit for three reasons: 1) they are extremely abundant, yet understudied, in the PPR; 2) they are isolated systems, greatly increasing the chance that local land-use would have an impact; and 3) the wetlands are wet when cattle are grazing the early grazed pasture, but by the time cattle had been moved to the late grazed pasture, the temporary wetlands have usually dried, allowing for the comparison of wetlands grazed when they have water, to wetlands grazed when they are dry. Water depth, wetland area, and nine water chemistry variables were also measured during each sampling period, and the wetland vegetation community was assessed in late June 2008. The initial plan included resampling these wetlands in 2009. However, drought conditions resulted in few of the wetlands being refilled with water in spring, and all wetlands that contained water were dry by June 15, 2009. Because of the

inherent unpredictability of the prairie region and other logistical considerations (e.g., funding), sampling in 2010 was not attempted.

The macroinvertebrate communities in the wetlands were compared in two distinct ways. First, the diversity, abundance and composition of the early and late grazed communities were examined from a traditional taxonomic perspective and also a functional traits perspective to determine how the timing of grazing impacted community membership (Chapter 2). Second, the phylogenetic relatedness of the taxa present in the temporary wetlands was examined and compared to a set of permanent wetlands from central Alberta to determine if environmental filtering or biotic interactions had a stronger influence on shaping the macroinvertebrate communities in each wetland type over the season (Chapter 3).

Table 1.1: Summary of Stewart and Kantrud (1971) wetland classes.

| Class | Typical Wet Period | Defining Vegetation |
|--------------------------|----------------------------|--|
| Class I: Ephemeral | Few days to a week | <i>Poa</i> spp., <i>Solidago</i> spp. |
| Class II: Temporary | Spring through mid summer | <i>Eleocharis</i> spp., <i>Carex</i> spp. |
| Class III: Seasonal | Spring through late summer | <i>Lemna</i> spp., <i>Carex</i> spp. |
| Class IV: Semi-Permanent | Early spring through fall | <i>Typha</i> spp., <i>Scirpus</i> spp. |
| Class V: Permanent | All year | <i>Scolochlora</i> spp., <i>Typha</i> spp. |
| Class VI: Alkali | Varies | <i>Ruppia</i> spp. |
| Class VII: Fen | Varies | <i>Glyceria</i> spp., <i>Phragmites</i> spp. |



Figure 1.1: Prairie pothole region of North America (U.S. Fish and Wildlife Service).

The black box indicates the approximate location of the study site.

CHAPTER 2: MACROINVERTEBRATE COMMUNITY COMPOSITION OF TEMPORARY PRAIRIE POTHOLE WETLANDS IN ROTATIONALLY GRAZED PASTURES

Introduction

Macroinvertebrates found in wetlands are often quite diverse and abundant. They are important members of local food webs, providing much of the protein required by higher trophic level species such as fish and waterfowl. The macroinvertebrate community present in a given wetland depends on many factors, including geographic location (e.g., Mihuc and Toetz 1996, Nicolet et al. 2004), wetland depth (Zimmer et al. 2000), water turbidity (Anteau and Afton 2009), fish presence (e.g., Cox et al. 1998, McParland and Paszkowski 2006), vegetation density and structure (e.g., deSzalay and Resh 1997, Gardner et al. 2001), human influences (e.g., Richards et al. 1993, Ometo et al. 2000), open water area (Anteau and Afton 2009) and wetland permanence (e.g., Euliss et al. 2002, Lillie 2003). Additionally, the macroinvertebrate community composition can change within a given wetland throughout the ice-free season (e.g., Lahr et al. 1999, Culioli et al. 2006).

Temporary wetlands of the prairie pothole region of North America represent a significant proportion of the inland water found on the prairies (van der Valk and Pederson 2003). The temporary wetlands are filled by snowmelt and early spring rains (Williams 1987) and, in the prairies of North America, these wetlands typically have

standing water from early spring through mid- to late summer. When the temporary wetlands contain standing water, they are home to a wide variety of biota including waterfowl and macroinvertebrates.

The challenges faced by macroinvertebrates present in each type of wetland vary greatly. Although permanent wetlands offer a more consistent environment compared to temporary wetlands, permanent wetlands tend to contain more macroinvertebrate predators such as fish (e.g., Diehl 1992, Zimmer et al. 2001) and waterfowl (e.g., Krull 1970, Murkin and Kadlec 1986). Macroinvertebrate diversity is typically higher in permanent wetlands, with communities often being dominated by Diptera, Amphipoda, and Hemiptera (deSzalay and Resh 1997, Zimmer et al. 2001). By their nature, temporary wetlands present a more unpredictable and variable habitat for macroinvertebrates. Taxa found in temporary wetlands must be able to survive or escape the drying wetland, and strategies include relocating to a permanent wetland, possessing a terrestrial adult form, or having a desiccation-resistant stage that can survive in the substrate until the wetland fills with water again.

In addition to the traditional taxonomic community perspective (i.e., using the Linnaean system to categorize individuals), studies examining communities from the functional traits perspective are becoming more common. Most functional trait studies have been conducted on plant communities using traits such as leaf area (Ackerly and Reich 1999), plant growth rate (Cavender-Bares et al. 2004b), and leaf nitrogen content (Kraft et al. 2008). For animals, functional traits are most commonly used on a small subset of aquatic macroinvertebrates to assess and compare water quality and ecosystem

health (e.g., Heino et al. 2004, Doleddec et al. 2006). Few studies have attempted to compare community-wide animal functional traits in systems with different levels of disturbance (e.g., see Usseglio-Polatera et al. 2000, Moretti and Legg 2009). Despite the lack of such studies, it is recognized that functional trait studies can provide new insight into the composition of communities in disturbed systems.

It is estimated that over half of the temporary wetlands in the prairie pothole region (including Alberta) have been converted to agricultural land since the early 1800's (Dahl 1990). Temporary wetlands located in agricultural fields are often tilled, used for crop production or cattle grazing especially after they have dried or during drought years (Euliss et al. 2002). One system proposed to reduce the impact of cattle grazing on wetlands is rotational grazing. Rotational grazing practices have the cattle grazing in one pasture for the early spring through early summer (hereafter, early grazed; i.e., grazed when temporary wetlands contain water), and in another pasture for late summer through fall (hereafter, late grazed; i.e., grazed when temporary wetlands are generally dry). This system has the potential advantage of increasing the amount of year-round forage for the cattle, reducing costs to land managers, and maintaining or increasing cattle productivity.

To my knowledge, the impacts of rotational grazing practices on temporary wetlands and the communities they support in the prairie pothole landscape are yet unstudied. Although it has been found that macroinvertebrate communities can be altered in response to minor changes in water quality (Hämäläinen and Huttunen 1998), such studies have not been conducted on temporary wetlands. By comparing the macroinvertebrate communities in temporary wetlands located in rotationally grazed

pastures, the impact of the timing of grazing on the temporary wetlands and the community composition can be evaluated.

I sampled thirteen temporary wetlands in the prairie region of Alberta, Canada five times during the ice-free season. My goal was to characterize the macroinvertebrate communities present in early and late grazed wetlands using two perspectives: the traditional Linnaean taxonomic perspective and by considering the functional traits possessed by the individuals in the communities. I made four predictions about the macroinvertebrate communities: (1) Late grazed wetlands will contain more abundant and diverse taxa than early grazed wetlands, because cattle grazing is expected to have a negative impact on the early grazed wetland macroinvertebrate community composition. (2) Abundance and diversity will decrease over the season in both wetland types, as the wetlands dry and more species leave the aquatic habitat. (3) Patterns of change over time obtained from both analyses will differ between early and late grazed wetlands. (4) Taxonomic analyses will find a greater difference in the composition of early vs. late grazed wetlands than will functional traits analyses, because the degree of specialization required to inhabit any temporary wetland is expected to be similar for early and late grazed wetlands.

Methods

Data Collection

Thirteen temporary wetlands were sampled from the prairie pothole region (PPR) in an area north of Strathmore, Alberta (“Rosebud Complex”; 51°18' N, 113°27' W). This

region contains numerous temporary, seasonal and permanent wetlands, most of which are surrounded by various forms of agriculture (including large cattle pastures utilizing rotational grazing). Seven wetlands were located in a pasture that was grazed from May through June (early grazed), and six wetlands were located in an adjacent pasture that was grazed from August through October (late grazed). Macroinvertebrates were sampled using a D-sweep net (500 nm mesh size with opening of 650 cm²), which was lowered vertically into the water to the benthic-pelagic boundary and then returned to the surface with a small arching motion to sample the vertical water column. Four samples were taken from random locations throughout the wetland during each sampling date.

A total of five sampling dates were conducted for the temporary wetlands, with macroinvertebrates being collected every three weeks from mid May through early August 2008. Because of wetland drying, the number of wetlands available for sampling declined. All wetlands were sampled in mid-May (sampling date 1) and again in mid June (sampling date 2). In early July (sampling date 3) 12 wetlands remained. For the fourth (late July) and fifth (early August) sampling dates, only four and three wetlands remained, respectively.

Macroinvertebrate samples were stored in 70% ethanol until identified to the lowest taxonomic level possible, mostly genus with occasional subfamily or species when available using Clifford (1991). Genus level identification provides good resolution of macroinvertebrate communities, while still allowing samples to be processed in a timely manner (O'Leary et al. 2004, Waite et al. 2004).

Water samples were collected from just below the water surface from several random locations within each wetland directly into acid washed bottles. Samples were put on ice, filtered within 24 hours and analyzed for total phosphorus (TP), total nitrogen (TN), ammonium (NH_4^+), and dissolved organic carbon (DOC). All water sample analyses were conducted by the Biogeochemical Analytical Laboratory at the University of Alberta (Edmonton, Alberta) using the techniques described in Bayley and Prather (2003).

The plant community for each wetland was assessed during sampling date 3. Each hydrophytic genus present in and around each wetland was identified. For emergent genera, the height of five randomly selected individuals of each genus was recorded.

Field measurements of pH, temperature, electrical conductivity, total dissolved solids (TDS) and salinity were measured from the centre of each wetland *in situ* using a YSI 556MPS handheld multi-parameter field probe. Additionally, three permanent markers were placed in each wetland during the first sampling date: one at the edge of the open water, one in the centre of the wetland, and one midway between the two. Depth measurements at these markers were recorded during each sampling date. The length and width of the open water for each wetland was also determined during each sampling date. These measurements were used to calculate area, treating the wetlands as ovals. Wetland volume (V_w) was subsequently estimated by considering each wetland as half an ellipsoid:

$$V_w = 1/2(3/4\pi((\text{length}/2)*(\text{width}/2)*(\text{depth}/2))) \quad [1]$$

where depth was obtained from the centre of the wetland because it is considered the maximum depth (or widest diameter of the ellipsoid). Because the wetlands tended to be oval-shaped, area of each wetland (A_w) was calculated as:

$$A_w = \pi(\text{length}/2 * \text{width}/2). \quad [2]$$

Functional Traits

To examine functional traits and how they change over the season, each taxon was characterized using seven traits (Table 2.1). The selected traits were variable among taxa, and highlighted differences in desiccation survival strategies. Traits (except body size) were primarily determined using Clifford (1991), Hornung (2005) and Williams (2005). Body size (i.e. volume) of most macroinvertebrate taxa (V_m) was calculated by assuming that their bodies approximate rectangular prisms:

$$V_m = \text{length} * \text{width} * \text{height}. \quad [3]$$

Body size (V_e) for Hemiptera, adult Coleoptera, and Hydrachnidia was calculated assuming that their bodies approximate ellipsoids:

$$V_e = 3/4\pi((\text{length}/2) * (\text{width}/2) * (\text{depth}/2)). \quad [4]$$

Body size (V_c) for Gastropods, with the exception of Planorbidae, was calculated assuming that individuals were cones:

$$V_c = 1/3\pi((\text{length}/2) * (\text{width}/2) * \text{height}). \quad [5]$$

Planorbid snails and Amphipods are more disk-shaped; therefore, body sizes (V_d) were calculated using equations for a cylinder:

$$V_d = \pi((\text{length}/2)*(\text{width}/2))*\text{height}. \quad [6]$$

All Gastropod body sizes include the shell. The body sizes for each taxon collected in each wetland during each sampling date were averaged separately.

The resulting taxon by trait matrix was combined with the taxon abundance by wetland matrix resulting in the traits by sites matrix. The traits by sites matrix was created by combining the site, taxon abundances and trait data (following Garnier et al. 2004, Moretti and Legg 2009):

$$T_m = \sum p_i x_i \quad [7]$$

where T_m is the trait value for each site during each sampling date, p_i is the relative abundance of the i th taxon and x_i is the trait value for the i th taxon. For nominal traits, the trait value is 0 or 1 (Table 2.1).

Analysis

Data analyses were designed to examine trends in macroinvertebrate communities in wetlands over the sampling season. First, I compared taxonomic and trait-based communities present in the early and late grazed wetlands through time. The environmental variables were also compared to the communities found in each grazing treatment as the sampling season progressed.

My analysis utilized three matrices. The first, taxa by sites, contained the $\log(\text{abundance}+1)$ transformed taxonomic data. Taxa appearing in only a single sample were removed prior to analysis, because such rare taxa may have a disproportionately large impact on the analysis (McCune and Grace 2002). The second matrix, traits by sites, contained the $\log(T_m+1)$ transformed trait values. The third matrix, environment by sites, contained the nine water chemistry variables (temperature, conductivity, TDS, salinity, pH, NH_4^+ , TN, TP, and DOC), wetland volume and area, sampling date, and the timing of grazing (early or late). All variables (except grazing and sampling date) were relativized (to base 100) to account for differences in variables with different means, variation and standard deviations. The taxonomic and trait data were subjected to the same analysis to allow for direct comparison of the results.

Early and Late Grazed Communities

Differences between early and late grazed wetlands were visualized using stacked column graphs. For taxon-based communities, the relative abundance of Chironominae, *Aedes*, other Diptera, Odonata, Hemiptera, Coleoptera and remaining taxa were compared for the early and late grazed wetlands during the five sampling dates. For the trait data, the relative proportion of the functional feeding groups (FFG) and the desiccation strategies (listed in Table 2.1) were compared separately for early and late grazed wetlands. Generalized linear mixed models (GLMM) with Poisson error distributions were used to compare the taxon groups between early and late grazed wetlands throughout the sampling season. Repeated measures linear mixed models (LMM) were used to compare the desiccation strategies and FFG T_m values for the early and late

grazed wetlands over the sampling season. Grazing (early or late) and sampling date were treated as fixed effects, while each individual wetland sampled during each sampling date (wetland ID) was considered a random effect. To meet normality assumptions, all T_m values were $\log(x+1)$ transformed prior to analysis.

Indicator species analysis (ISA; Dufrene and Legendre 1997) was applied to examine the differences in early and late grazed communities. A Monte Carlo simulation (1000 permutations) was used to assess the significance of each macroinvertebrate taxon as an indicator (Dufrene and Legendre 1997). The presence of at least one indicator taxon for each cluster indicates that it is a valid group of wetlands with a distinct macroinvertebrate community.

Environmental Correlations

Two-sample *t*-tests on $\log(x+1)$ transformed data were used to compare each environmental variable in early and late grazed wetlands. Because neither the abundance nor trait data displayed a linear response to environmental variables, methods such as principal components analysis (PCA) and redundancy analysis (RDA) were not appropriate. Additionally, constrained correspondence analysis (CCA) can only be used when the response variables are linear combinations of the measured environmental variables (McCune 1997). Accordingly, Nonmetric Multidimensional Scaling (NMDS) ordinations, which arrange the variables in strictly species space with no assumed relation to the environmental variables, were used to compare environmental variables to the macroinvertebrate communities.

The NMDS ordinations were used to determine if early and late grazed communities were distinct, as well as to identify which environmental variables were associated with different community types and species distributions. All NMDS ordinations were run using the Bray-Curtis distance measure (Bray and Curtis 1957), because it remains robust even with non-linear taxon responses (Faith et al. 1987). The start was random and the number of dimensions was determined by examining how much stress (%) each additional dimension accounted for. Dimensionality was determined based on the point of diminishing returns with respect to how much the addition of another dimension decreased the overall stress value. Environmental data were then overlain on the ordination as vectors to help define the environmental context of the wetland distribution.

Vegetative Communities

Plant heights recorded for each emergent genus were averaged for each wetland and log transformed prior to analysis to meet normality assumptions. The heights of the plants in early and late grazed wetlands were compared using a two-sample *t*-test. A generalized linear model (glm), with Poisson-family distribution was used to compare aquatic plant diversity in the early and late grazed wetlands (following Trites and Bayley 2009).

All statistical analysis were conducted in R (R Development Core Team 2009) using the ‘vegan’ (Oksanen et al. 2007) and ‘labdsv’ (Roberts 2006) packages.

Results

A total of 6,351 macroinvertebrates belonging to 65 taxa were collected during this study (see Supplementary Tables 2.1 and 2.2). Of those collected, 6,306 macroinvertebrates

from 47 taxa were present in more than one sample and used in the analysis. Samples from early grazed wetlands contained a total of 1,858 macroinvertebrates from 44 taxa, whereas late grazed wetland samples contained 4,493 individuals from 58 taxa. In general, total abundance and diversity decreased for early and late grazed wetlands over the sampling season (Fig. 2.1). For all sampling dates, the abundance and diversity of macroinvertebrates in early grazed wetlands was lower than that observed in late grazed wetlands (Fig. 2.1).

Early and Late Grazed Communities

Early and late grazed wetlands had markedly different communities throughout the sampling season (Fig. 2.2). Both Chironominae and Odonata abundances changed significantly through the sampling season (GLMM, $p < 0.03$), with Odonata disappearing from the samples after sampling date 3. However, the pattern of change through the sampling season was not equivalent for Chironominae, Odonata and other Diptera in the early and late grazed wetlands (GLMM, $p < 0.046$; Fig. 2.2).

Indicator species analysis also highlighted differences between early and late grazed communities. Two taxa, Empididae and *Mystacides*, were identified as indicator taxa for early grazed wetlands (Table 2.2). Conversely, eleven indicator taxa (*Bakerilymnaea*, *Chaoborus*, Chironominae, *Dytiscus*, *Haliplus*, *Ilybius*, *Notonecta*, *Promenetus*, *Rhantus*, *Sigara*, and Tanypodinae) were identified for late grazed wetlands (Table 2.2).

Functional traits analyses again revealed differences between the communities of early and late grazed wetlands (Fig. 2.3). Early grazed wetlands had significantly more

scrapers (LMM, $t = -2.920$, $p = 0.0139$), whereas late grazed wetlands had more gatherers (LMM, $t = 3.944$, $p = 0.0023$; Fig. 3A and B). The patterns of change for these two FFGs also changed in different ways for early and late grazed wetlands. Scrapers greatly increased in prominence in early grazed wetlands over time (LMM, $t = 3.263$, $p = 0.0027$), whereas their numbers remained more constant in late grazed wetlands (LMM, $t = 1.999$, $p = 0.0618$). Gatherers, on the other hand, were not found in early grazed wetlands after sampling date 3 (LMM, $t = 1.059$, $p = 0.3087$), whereas late grazed wetland communities contained high abundances of gathers throughout the sampling season (LMM, $t = -3.927$, $p = 0.0050$; Fig. 2.3A and B). Filter feeders showed a similar and significant, decrease as the sampling season progressed for both early and late grazed wetlands (LMM, $t = 2.423$, $p = 0.0216$).

Desiccation strategies employed by taxa present in the wetlands throughout the sampling dates also showed some variation between early and late grazed wetland communities (Fig. 2.4A and B). As expected, communities in both wetland types were initially dominated by taxa that remain in the dry substrate as eggs or larvae during the dry phase, with the presence of these taxa decreasing as the sampling season progressed (LMM, $t = 2.408$, $p = 0.0224$). Early wetlands contained more taxa that move to terrestrial habitats (LMM, $t = 4.000$, $p = 0.0021$) and taxa that remain as larvae during the dry phase compared to the late grazed wetlands (LMM, $t = 3.438$, $p = 0.0055$; Fig. 4A and B). The pattern of change through the sampling season varied in significantly different ways in early and late grazed wetlands for taxa that remain as adults (LMM, $t = 2.268$, $p = 0.0307$), for those that move to terrestrial habitats (LMM, $t = 3.355$, $p =$

0.0022) and taxa that remain as larvae (LMM, $t = -3.562$, $p = 0.0013$) during the dry phase (Fig. 2.4A and B).

For the trait data, ISA identified two traits indicative of each wetland type (Table 2). Surface dwelling and filter feeding traits were indicative of early grazed wetland communities, whereas late grazed wetlands had more highly mobile taxa that use a combination of aquatic habitats, and more taxa that utilize permanent wetlands during the dry phase.

Environmental Correlations

Overall, conductivity, TDS, salinity, TN, TP, and DOC decreased as the water dried, whereas temperature and pH increased over the sampling season (Fig. 2.5). When comparing the magnitude and pattern of change over the sampling season for the nine water chemistry variables, early and late grazed wetlands were quite different (Fig. 2.5). Additionally, the variance among early grazed wetlands was higher than among late grazed wetlands. Of the nine water chemistry variables measured, early grazed wetlands had significantly higher values than late grazed wetlands for all but pH (two-sample t -tests, all $p < 0.03$), with pH being only marginally different between early and late grazed wetlands (two-sample t -test, $t = 1.808$, $p = 0.078$).

NMDS ordination of the taxon-based community data resulted in three dimensions with a final stress of 14.6% (Fig. 2.6A). The first axis was defined primarily by sampling date along with grazing treatment (early or late). The second axis separated the wetlands based on pH. Overall, early and late grazed wetlands were only partially separated. Along

with pH, six variables (TN, DOC, TDS, salinity, conductivity, and temperature) were significantly correlated with taxon-based community structure (Fig. 2.6A). For trait data, the final NMDS had two dimensions with a final stress of 12.2%. Trait data were not significantly structured by timing of grazing, with early and late grazed communities being poorly separated (Fig 2.4B). Sampling date, which defined the secondary axis, again played a significant role in community structure. TN, DOC, conductivity, TDS and salinity significantly structured trait-based communities. Post hoc inspection of the data suggests that the primary axis is best defined by wetland area and NH_4^+ (Fig. 2.6B).

Vegetation

A total of six aquatic plant genera (*Eleocharis*, *Scirpus*, *Potamogeton*, *Carex*, *Caltha*, and *Lemna*) were identified in and surrounding the sampled wetlands during the vegetation survey. Three genera (*Eleocharis*, *Scirpus*, and *Lemna*) were present in early grazed wetlands, and all six were found in late grazed wetlands. Diversity was significantly higher in late grazed wetlands than in early grazed wetlands (glm, $Z = 2.26$, $p = 0.034$). Additionally, late grazed wetlands had significantly taller plants around their margins (average $58.7 \text{ cm} \pm 2.3 \text{ cm}$) than early grazed wetlands (average $32.1 \text{ cm} \pm 2.0 \text{ cm}$; two-sample t -test, $t = -3.70$, $p = 0.002$).

Discussion

In this study, I analyzed and compared the macroinvertebrate communities of early and late grazed wetlands located within a rotationally grazed pasture. Despite the close proximity of the focal wetland types, with several early grazed wetlands being within 300

m of some late grazed wetlands, their communities were quite different. As I predicted, late grazed wetlands had more abundant and diverse taxa compared to the early grazed wetlands. Additionally, abundance and diversity decreased for both wetland types as the sampling season progressed and the wetlands dried. Although the composition of early and late grazed wetlands changed over the sampling season, it did not do so in the same way in the two wetland types. Late grazed wetlands were dominated by different taxa with a different set of traits than the early grazed wetlands throughout the sampling season.

Taxon-based analyses revealed clear differences between the communities of the two wetland types. Chironominae dominated late grazed wetlands, whereas early grazed wetlands contained more Dipterans and predaceous Odonata larvae. In addition to the expected loss of vegetation height and diversity, cattle passing through a wetland may mix the water with the substrate, which likely reduces the suitability of the benthic habitat for Chironominae. Conversely, warmer, shallow water serves as suitable habitat for *Aedes* and other Dipterans, which are notorious for inhabiting basically any standing water, with particular preference for highly disturbed temporary wetlands (Schneider and Frost 1996, Lysyk 2010). High abundances of prey species, such as *Aedes* and Dipteran larvae, likely supported the high numbers of predaceous Odonata larvae in early grazed wetlands (Quiroz-Martinez and Rodriguez-Castro 2007). Additionally, the high abundances of Hemiptera in early grazed wetlands towards the end of the sampling season is consistent with previous research showing that Hemiptera, particularly the

highly mobile *Sigara* adults, have an affinity for wetlands surrounded by agriculture (Silver et al. submitted).

Similar to the taxon-based perspective, the trait data revealed the same separation of early and late grazed wetlands. While the same seven FFGs were present in early and late grazed wetlands, the proportions of scrapers and gatherers and how they changed throughout the sampling season differed between early and late grazed wetlands. The increase in scrapers found towards the end of the sampling season in the early grazed wetlands was likely due to increasing algal growth as the wetlands dry (Heino et al. 2004, McCormick et al. 2004). Unlike scrapers, gatherers prefer high amounts of fine organic particulates to be present on the substrate (Wright and Smock 2001, Kreutzweiser et al. 2005). The unmixed substrate of the late grazed wetlands would contain more fine particulates than the heavily perturbed early grazed wetlands.

The proportions of taxa using different desiccation survival strategies were also different for the early and late grazed wetlands. Late grazed wetlands had more taxa remaining as larvae during the dry phase, whereas early grazed wetlands had more taxa utilizing terrestrial environments or surviving the dry phase as adults. Late grazed wetlands also contained more taxa that remain in the wetland substrate during the dry phase than the early grazed wetlands. Trampling of the soil by cattle reduces the number of pores in the soil, while increasing the soil water content (Taboada and Lavado 1993). For macroinvertebrates that have evolved to remain in the substrate during the dry-phase, these changes to the soil could reduce survival. Increased porosity allows more

macroinvertebrates to successfully penetrate the substrate, and has been linked to increased macroinvertebrate diversity (Gayraud and Philippe 2001).

The presence of cattle in and around early grazed wetlands was also associated with significant differences in water chemistry. Nitrogen and phosphorus were significantly higher in early grazed wetlands compared to the late grazed wetlands. High concentrations of nitrogen and phosphorus are the hallmarks of eutrophication, with increased eutrophication typically leading to a decrease in macroinvertebrate abundance and diversity (e.g. Ometo et al. 2000, Steinman et al. 2003, McCormick et al. 2004). I also found that TN, TP, salinity, conductivity and DOC were significantly higher in the early grazed wetlands, and were also key factors associated with macroinvertebrate community structure.

Interestingly, the late grazed wetlands were still quite eutrophic compared to more pristine wetlands found in the prairies (Whigham and Jordan 2003). Although most prairie wetlands are impacted by agriculture or urbanization to some degree, pasture wetlands are often the most eutrophic (Nader et al. 1998, Steinman et al. 2003). For the late grazed wetlands in my study, the residual cattle faeces left in the dry wetlands after the fall grazing date appear to carry over to the following spring. The faeces that were left from the fall grazing in the late grazed pasture led to high initial nitrogen values, but those values drop as the nutrients are diluted and partially removed from the system by biotic processes. Without any new inputs, due to the lack of cattle, the wetlands become increasingly less eutrophic throughout the season.

The unpredictable nature of the temporary wetlands possesses a challenge for the taxa that inhabit them. Many larger taxa such as Odonata and Coleoptera use temporary wetlands as a relatively predator-free and prey-rich habitat for larval development. In a year when the temporary wetlands remain wet through the end of July, these larvae are able to survive and develop into semi-terrestrial adults, which are able to leave the drying wetland and seek out more permanent water for the remainder of the year. But in some years, this bet-hedging strategy can lead to high mortality. Most of the study wetlands contained water through mid-late July in 2008. In the following summer, dry conditions resulted in all study wetlands being completely dry by mid-June (C. Silver personal observation). It is quite likely that many organisms with a longer aquatic stage were not able to effectively utilize the temporary wetlands in 2009, and would have to rely on the populations in the more permanent wetlands to maintain their numbers until another wetter year when the temporary wetlands become viable habitat again. I expect that investigations of meta-population interactions of permanent and temporary wetlands would further increase our understanding of macroinvertebrate communities in prairie environments.

Conclusions

Rotational grazing has been shown to benefit land managers by allowing the cattle access to natural forage for a large part of the year, reducing costs and increasing productivity (Gjersing 1975). In addition to these benefits, I have shown that rotational grazing can create two very different habitats despite having only a fence separating them. When half of the pasture wetlands are provided time free from grazing, diverse and abundant

communities can become established. I note that early grazed wetlands were not devoid of life and, while they had reduced diversity and abundances compared to late grazed wetlands, they served as habitat for many macroinvertebrates. Thus, my study highlights the importance of protecting and maintaining temporary wetlands in the prairie landscape. In much of the prairies, temporary wetlands are ploughed, filled and/or ditched during the dry phase in an effort to make the wetland area useable for crops or pasture. Removing these habitats from the landscape could lead the loss of many taxa that flourish in temporary wetlands, including specialized taxa that add to the overall diversity of the prairie ecosystem.

Table 2.1: Macroinvertebrate traits. Ordinal traits were treated as single variables, with the number of states for each shown in parentheses in Data Type. Nominal traits were coded as dummy variables (number shown in # of Variables) with two states each (present/absent). Trait data (except body size) were determined using Clifford (1991), Hornung (2005) and Williams (2005). Body size was calculated from measurements as described in the text.

| Trait Type | # of Variables | Data Type | Attribute |
|-------------------------------|-----------------------|------------------|--|
| Habitat specificity | 1 | Ordinal (2) | 1 = limited, permanently aquatic with no terrestrial stage; or 2 = wider, with combination of terrestrial and aquatic stages. |
| Dispersal ability | 1 | Ordinal (3) | 1 = no terrestrial stage and/or dispersed by other organisms (e.g. waterfowl or mobile host) only; 2 = moderate flying ability and/or short terrestrial stage; 3 = very mobile flying terrestrial stage and/or long terrestrial stage. |
| Functional feeding group | 7 | Nominal | Filterer feeder; Gatherer/collector; Omnivore, Predator; Saprovore; Scraper; or Shredder. |
| Aquatic stage habitat | 5 | Nominal | Primarily found in: Vegetation = remain in vegetated area; Open = occur in the open water; Substrate = present in benthic substrate; Surface = remain on or just below water's surface; Combination = highly mobile taxa that inhabit multiple aquatic habitats. |
| Oxygen source | 2 | Nominal | Obtain oxygen from: Air or Water. |
| Desiccation survival strategy | 5 | Nominal | Terrestrial = become exclusively terrestrial; Permanent = relocate to permanent wetlands nearby; Egg = desiccation-resistant eggs remain in the substrate; Larvae = desiccation-resistant larvae remain in substrate; or Adult = desiccation-resistant adult remains in substrate. |
| Body size (mm ³) | 1 | Continuous | Average body volume (size) of individual taxa calculated for each wetland and sampling date independently. |

Table 2.2: Indicator species analysis (ISA) results for early and late grazed wetland communities. Communities were analyzed using taxon- and trait-based approaches separately (see Table 2.1 for an explanation of the traits). Only taxa or traits with a p-value ≤ 0.1 are shown.

| Community | Grazing | Taxa or Trait | ISA Value (%) | p-value |
|------------------|----------------|----------------------|----------------------|----------------|
| Taxon-based | Early | Empididae | 19.4 | 0.081 |
| | | <i>Mystacides</i> | 14.3 | 0.089 |
| | Late | <i>Bakerilymnaea</i> | 25.0 | 0.021 |
| | | <i>Chaoborus</i> | 30.5 | 0.018 |
| | | Chironominae | 49.7 | 0.091 |
| | | <i>Dytiscus</i> | 20.8 | 0.068 |
| | | <i>Haliphus</i> | 19.1 | 0.093 |
| | | <i>Ilybius</i> | 33.3 | 0.004 |
| | | <i>Notonecta</i> | 26.1 | 0.032 |
| | | <i>Promenetus</i> | 52.0 | 0.001 |
| | | <i>Rhantus</i> | 34.5 | 0.031 |
| | | <i>Sigara</i> | 46.2 | 0.009 |
| | Tanypodinae | 33.6 | 0.033 | |
| | Trait-based | Early | Surface | 53.4 |
| Filterer | | | 54.8 | 0.095 |
| Late | | Permanent | 59.5 | 0.093 |
| | | Combination | 52.0 | 0.096 |

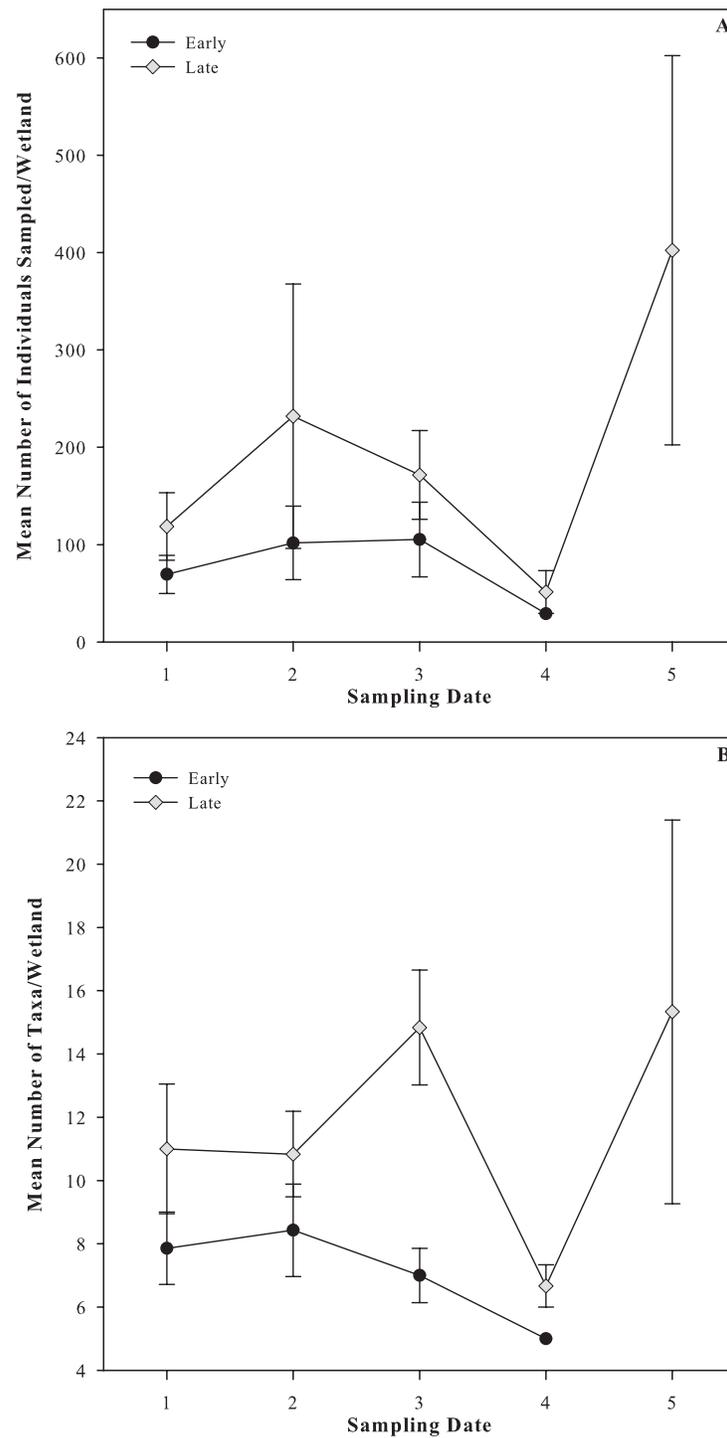


Figure 2.1: Mean abundance (\pm standard error) per wetland (A) and number of taxa per wetland (B) found in early and late grazed wetlands over five sampling dates.

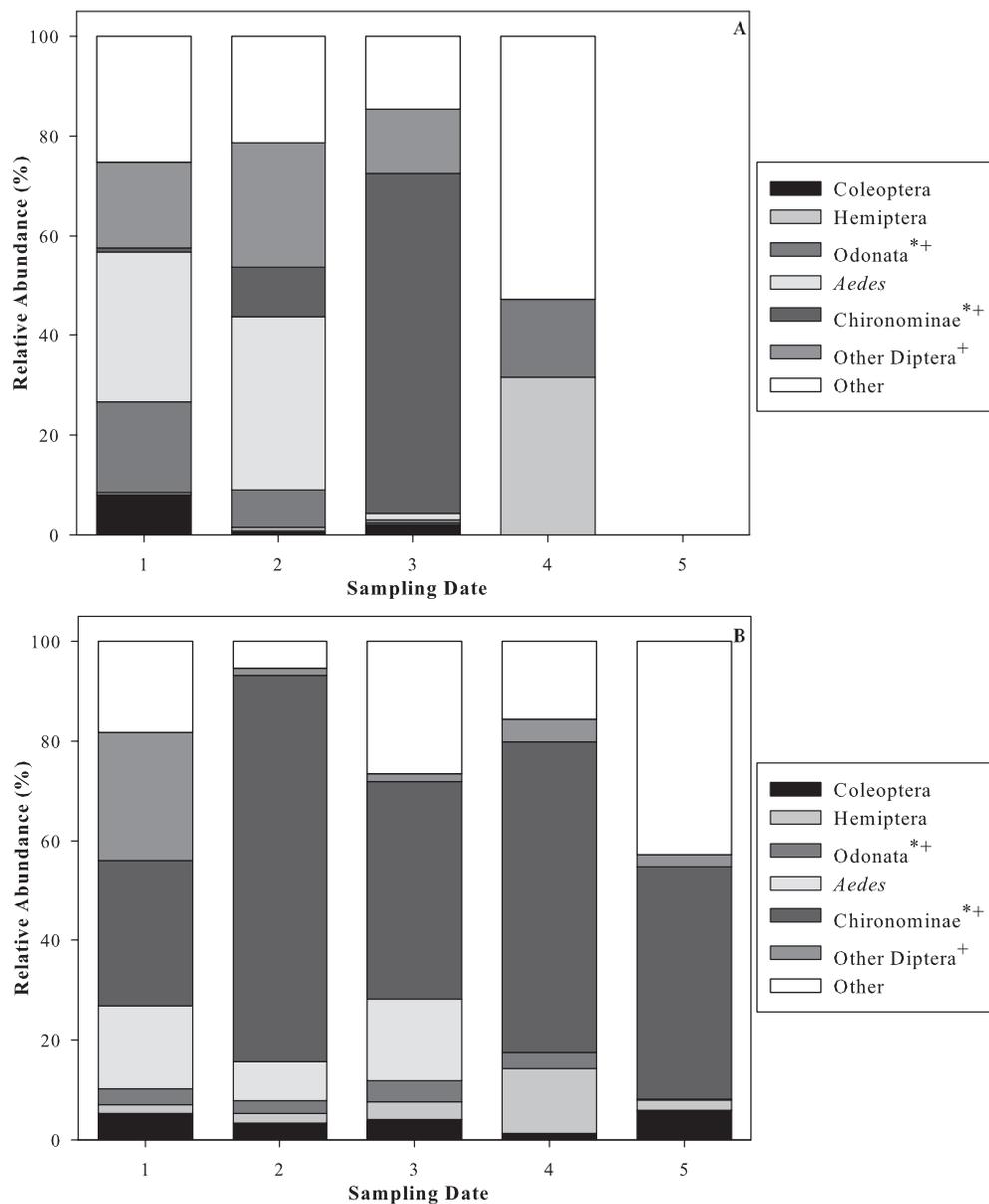


Figure 2.2: Relative abundance of seven groups of macroinvertebrates over five sampling dates in (A) early grazed wetlands and (B) late grazed wetlands. * indicates taxon abundance changed significantly over the sampling season (GLMM, $p < 0.05$), + indicates early and late grazed wetlands had significantly different patterns of abundance for that taxa throughout the sampling season (GLMM, $p < 0.05$).

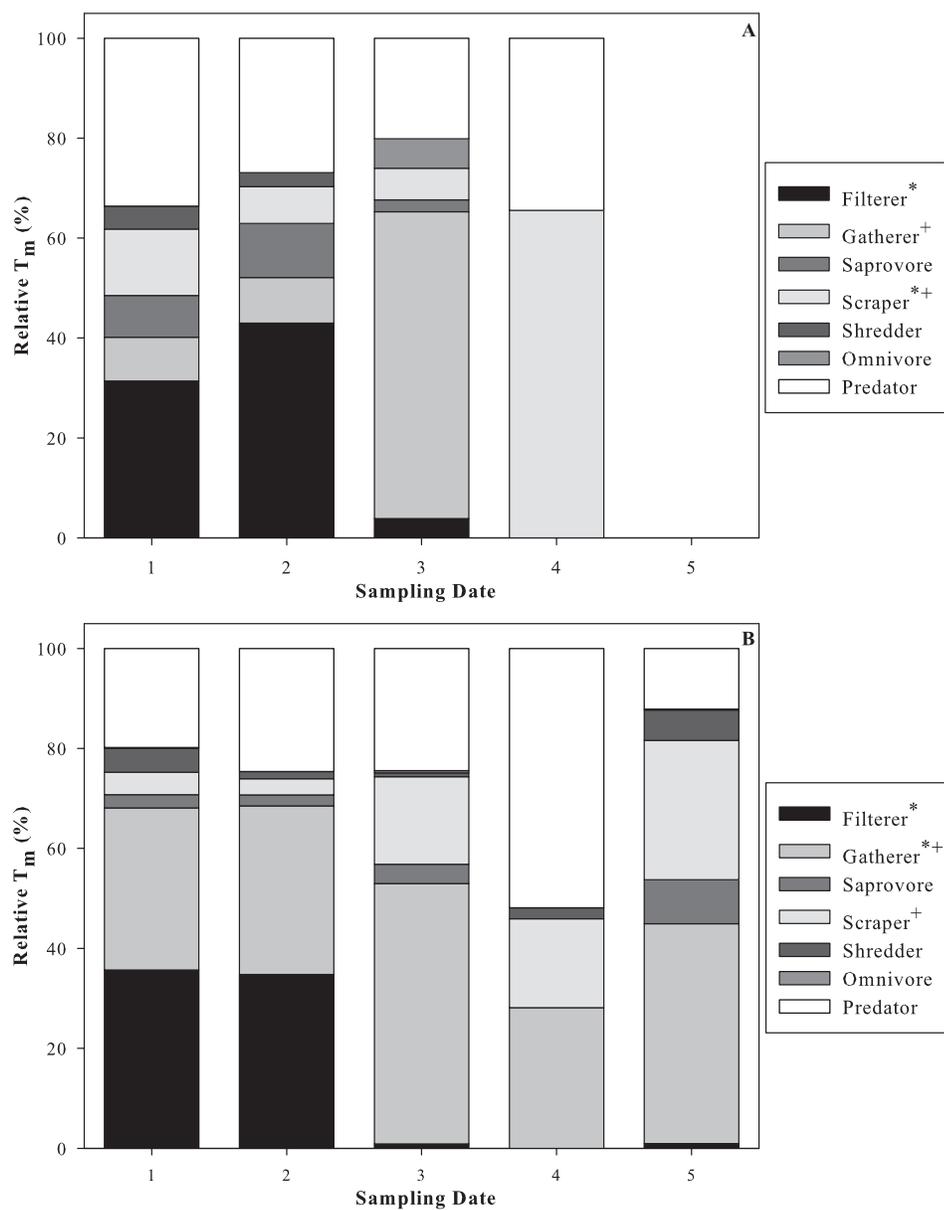


Figure 2.3: Relative trait scores (T_m) over five sampling dates for functional feeding groups (FFG) of (A) early grazed and (B) late grazed wetlands. * indicates FFG abundance changed significantly over the sampling season (LMM, $p < 0.05$), + indicates early and late grazed wetlands had significantly different patterns of abundance for that taxa throughout the sampling season (LMM, $p < 0.05$).

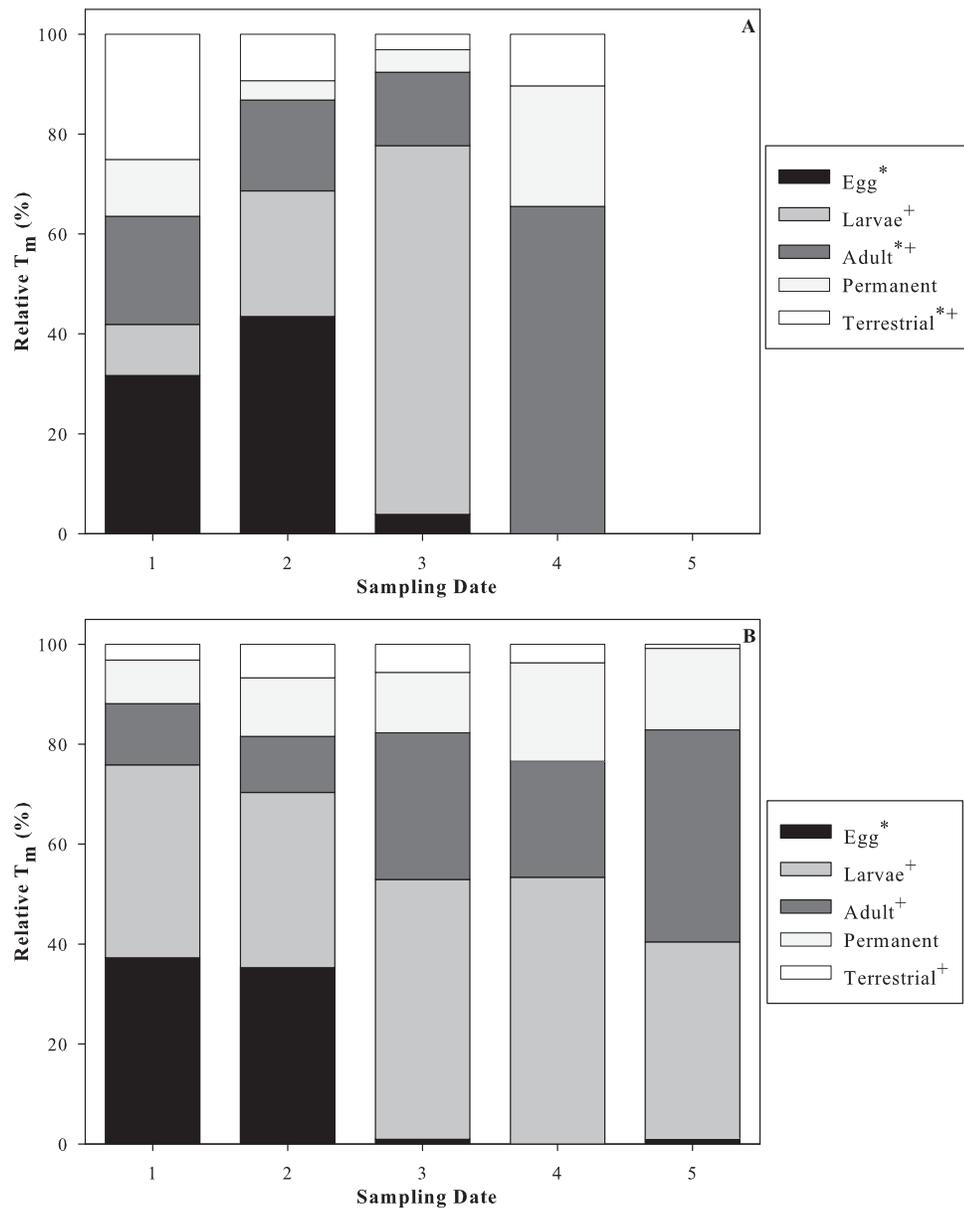


Figure 2.4: Relative trait scores (T_m) over five sampling dates for desiccation strategies of taxa found in (A) early grazed and (B) late grazed wetlands. * indicates desiccation strategy abundance changed significantly over the sampling season (LMM, $p < 0.05$), + indicates early and late grazed wetlands had significantly different patterns of abundance for that taxa throughout the sampling season (LMM, $p < 0.05$).

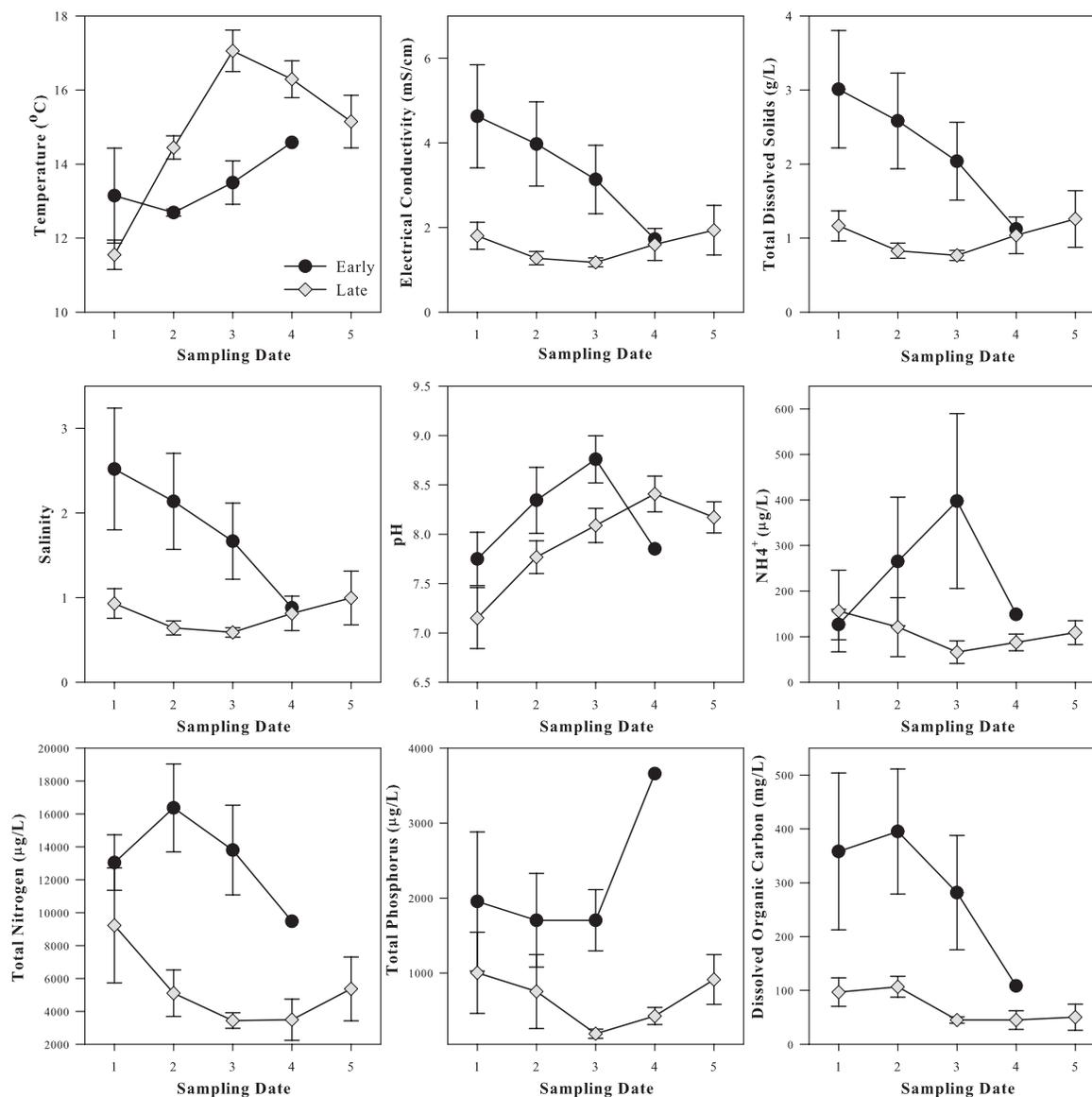


Figure 2.5: Mean values (\pm standard error) of the nine water chemistry variables for the early and late grazed wetlands over the five sampling dates.

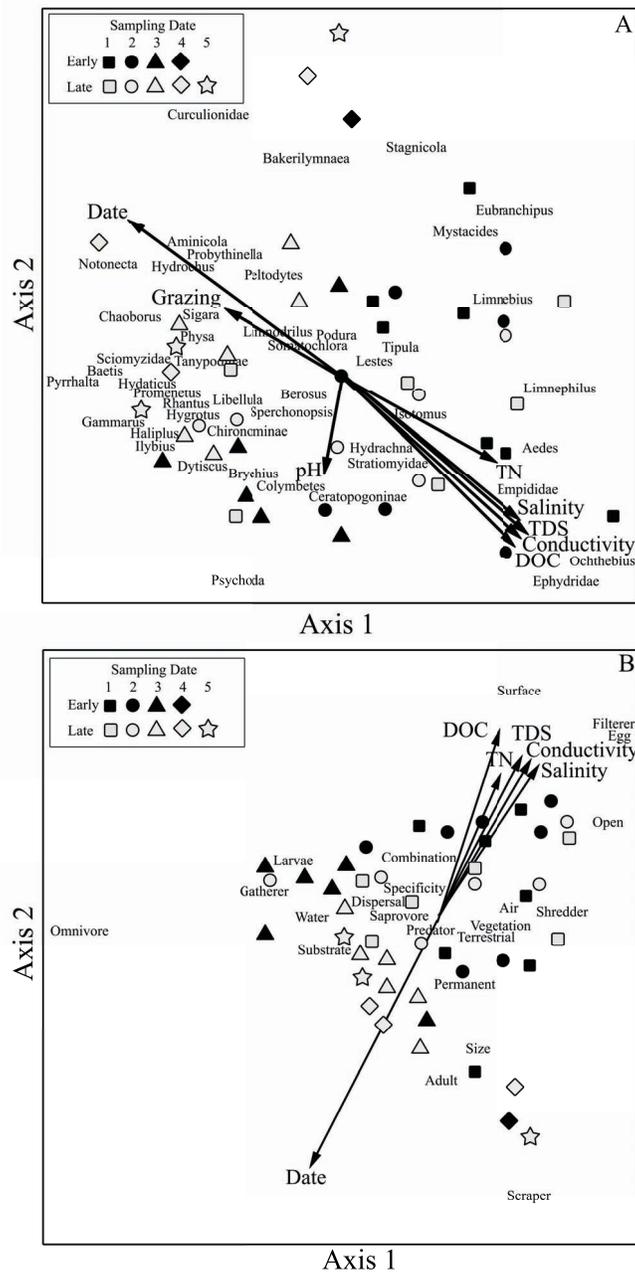


Figure 2.6: NMDS ordination bi-plots for macroinvertebrate communities and environmental variables. The taxon-based community ordination (A) yielded three dimensions with a final stress of 14.6%, and the trait-based community ordination (B) had two dimensions with a final stress of 12.2%. For both ordinations, environmental variables with a p -value ≤ 0.05 are shown.

Supplementary Table 2.1: Number of wetlands sampled, number of taxa, and total number of macroinvertebrates collected during each sampling date.

| Grazing | Sampling Date | Wetlands | Taxa Sampled | Macroinvertebrates Collected |
|----------------|----------------------|-----------------|---------------------|-------------------------------------|
| Early | 1 | 7 | 55 | 486 |
| | 2 | 7 | 59 | 712 |
| | 3 | 6 | 42 | 631 |
| | 4 | 1 | 5 | 29 |
| | 5 | 0 | 0 | 0 |
| Late | 1 | 6 | 66 | 712 |
| | 2 | 6 | 65 | 1391 |
| | 3 | 6 | 89 | 1029 |
| | 4 | 3 | 20 | 154 |
| | 5 | 3 | 46 | 1207 |

Supplementary Table 2.2: All aquatic macroinvertebrate families and genera collected during the present study. Total abundance of each taxon in early and late grazed wetlands is shown.

| Family | Genus [†] | Total Abundance | | Family | Genus [†] | Total Abundance | |
|-----------------|-------------------------|-----------------|------|---------------|----------------------|-----------------|------|
| | | Early | Late | | | Early | Late |
| Anthomyiidae | | 0 | 0 | Haliplidae | <i>Peltodytes</i> | 1 | 9 |
| Athericidae | <i>Atherix</i> | 0 | 0 | Hydrachnidae | <i>Hydrachna</i> | 19 | 31 |
| Baetidae | <i>Baetis</i> | 0 | 3 | Hydraenidae | <i>Limnebius</i> | 5 | 6 |
| Branchinectidae | <i>Branchinecta</i> | 2 | 0 | Hydraenidae | <i>Ochthebius</i> | 33 | 2 |
| Ceratopogonidae | <i>Ceratopogoninae</i> | 251 | 45 | Hydrobiidae | <i>Aminicola</i> | 1 | 104 |
| Chaoboridae | <i>Chaoborus</i> | 1 | 14 | Hydrobiidae | <i>Probythinella</i> | 3 | 58 |
| Chirocephalidae | <i>Eubranchipus</i> | 0 | 2 | Hydrophilidae | <i>Berosus</i> | 3 | 8 |
| Chironomidae | Chironominae | 495 | 2187 | Hydrophilidae | <i>Enochrus</i> | 1 | 0 |
| Chironomidae | Tanypodinae | 11 | 126 | Hydrophilidae | <i>Helophorus</i> | 1 | 0 |
| Chrysomelidae | <i>Pyrrhalta</i> | 0 | 3 | Hydrophilidae | <i>Hydrochus</i> | 0 | 3 |
| Coenagrionidae | <i>Ischnura</i> | 0 | 11 | Hydrophilidae | <i>Hydrophilus</i> | 0 | 3 |
| Corduliidae | <i>Somatochlora</i> | 13 | 14 | Hydrophilidae | <i>Laccobius</i> | 1 | 0 |
| Corixidae | <i>Sigara</i> | 14 | 101 | Hydroptilidae | <i>Agraylea</i> | 0 | 0 |
| Culicidae | <i>Aedes</i> | 401 | 384 | Isotomidae | <i>Isotomus</i> | 2 | 0 |
| Curculionidae | | 0 | 2 | Leptoceridae | <i>Mystacides</i> | 3 | 0 |
| Dytiscidae | <i>Acilius</i> | 0 | 1 | Lestidae | <i>Lestes</i> | 135 | 78 |
| Dytiscidae | <i>Agabus</i> | 0 | 2 | Libellulidae | <i>Libellula</i> | 0 | 2 |
| Dytiscidae | <i>Colymbetes</i> | 1 | 0 | Limnephilidae | <i>Arctopora</i> | 0 | 1 |
| Dytiscidae | <i>Dytiscus</i> | 0 | 11 | Limnephilidae | <i>Limnephilus</i> | 1 | 8 |
| Dytiscidae | <i>Graphoderus</i> | 0 | 3 | Limnephilidae | <i>Nemotaulius</i> | 1 | 0 |
| Dytiscidae | <i>Hydaticus</i> | 2 | 2 | Lymnaeidae | <i>Bakerilymnaea</i> | 0 | 17 |
| Dytiscidae | <i>Hydroporus</i> | 0 | 1 | Lymnaeidae | <i>Lymnaea</i> | 9 | 0 |
| Dytiscidae | <i>Hygrotus</i> | 7 | 8 | Lymnaeidae | <i>Stagnicola</i> | 107 | 83 |
| Dytiscidae | <i>Ilybius</i> | 0 | 32 | Notonectidae | <i>Notonecta</i> | 1 | 13 |
| Dytiscidae | <i>Laccophilus</i> | 0 | 1 | Physidae | <i>Physa</i> | 2 | 8 |
| Dytiscidae | <i>Rhantus</i> | 3 | 22 | Planorbidae | <i>Promenetus</i> | 2 | 250 |
| Empididae | | 48 | 0 | Poduridae | <i>Podura</i> | 76 | 25 |
| Ephydriidae | | 35 | 1 | Psychodidae | <i>Psychoda</i> | 0 | 63 |
| Erpobdellidae | <i>Dina</i> | 0 | 1 | Sciomyzidae | | 2 | 2 |
| Gammaridae | <i>Gammarus</i> | 54 | 8 | Sperchonidae | <i>Sperchonopsis</i> | 2 | 3 |
| Glossiphoniidae | <i>Alboglossiphonia</i> | 0 | 0 | Stratiomyidae | | 3 | 6 |
| Haliplidae | <i>Brychius</i> | 2 | 5 | Tipulidae | <i>Tipula</i> | 1 | 1 |
| Haliplidae | <i>Haliplus</i> | 1 | 35 | Tubificidae | <i>Limnodrilus</i> | 102 | 237 |

[†] In cases where macroinvertebrates could not be identified to genera, the lowest available taxonomic level (usually subfamily) is listed in the 'Genus' column. Blank entries in the 'Genus' column represent taxa for which identification beyond the family level was not possible.

CHAPTER 3: MACROINVERTEBRATE COMMUNITIES IN WETLANDS: DIVERSITY AND PHYLOGENETIC STRUCTURE THROUGH TIME

Introduction

Macroinvertebrates found in wetlands are remarkably diverse and abundant. They are important members of local food webs, providing much of the protein required by higher trophic level species such as fish and waterfowl. The macroinvertebrate community present in a given wetland depends on many factors, including geographic location (e.g., Mihuc and Toetz 1996, Nicolet et al. 2004), wetland depth (Zimmer et al. 2000), water turbidity (Anteau and Afton 2009), fish presence (e.g., Cox et al. 1998, McParland and Paszkowski 2006), vegetation density and structure (e.g., deSzalay and Resh 1997, Gardner et al. 2001), human influences (e.g., Richards et al. 1993, Ometo et al. 2000), open water area (Anteau and Afton 2009) and wetland permanence (e.g., Euliss et al. 2002, Lillie 2003). Additionally, the macroinvertebrate community composition can change within a given wetland throughout the ice-free season (e.g., Lahr et al. 1999, Culioli et al. 2006).

The challenges faced by macroinvertebrates present in each type of wetland vary greatly. Although permanent wetlands offer a more consistent environment compared to temporary wetlands, permanent wetlands tend to contain more macroinvertebrate predators such as fish (e.g., Diehl 1992, Zimmer et al. 2001) and waterfowl (e.g., Krull

1970, Murkin and Kadlec 1986). Macroinvertebrate diversity is typically high in permanent wetlands, with communities often being dominated by Diptera, Amphipoda, and Hemiptera (deSzalay and Resh 1997, Zimmer et al. 2001). By their nature, temporary wetlands present a more unpredictable and variable habitat for macroinvertebrates. Species found in temporary wetlands must be able to survive or escape the drying wetland, and strategies include relocating to a permanent wetland, possessing a terrestrial adult form, or having a desiccation resistant stage that can survive in the substrate until the wetland fills with water again. As a consequence of the specializations required, temporary wetlands tend to be numerically dominated by mosquito larvae (Nicolet et al. 2004). Many predaceous aquatic insects (e.g., diving beetles), which are also found to lesser extents in permanent wetlands, may also reach relatively high abundances in these prey-rich environments (Nicolet et al. 2004).

Previous studies have examined differences in diversity and abundances for wetlands of varying permanence (e.g., Brooks 2000, Urban 2004, Della Bella et al. 2005). These studies all found temporary wetlands to have lower diversity than more permanent wetlands. The lowered diversity was attributed to environmental filtering, as very specific adaptations are required to survive the extreme, and quickly changing conditions present in temporary wetlands. As there seems to be a consensus that macroinvertebrate diversity is reduced in temporary wetlands compared to permanent wetlands, here I investigate how the relatedness of the taxa found in each wetland type changes over the summer months. Examining patterns of phylogenetic relatedness of species in a community can reveal the underlying mechanisms driving community composition (Cavender-Bares et

al. 2009, Vamosi et al. 2009). Phylogenetic data allow community assemblages to be examined by considering taxa in their historical context with the implication that many interactions, both with the environment and other taxa, have been occurring over a long time period (Cavender-Bares et al. 2009). The concept of limiting similarity suggests that there is a balance between shared resources (competition), which limit similar species coexistence, and similar species having similar environmental tolerances (environmental filtering), leading them to occur in the same habitats (Abrams 1983). Because closely related species tend to exhibit phylogenetic signal in relevant functional traits (Harvey and Pagel 1991, Harvey 1996), using phylogenetic data can help distinguish which factor is more strongly driving community assembly. Additionally, as the season progresses the balance of competition and environmental filtering is expected to change (see Dinnage 2009), particularly in the temporary wetlands where environmental disturbance becomes more extreme as the wetlands dry.

A key assumption in the evaluation of phylogenetic patterns is closely related taxa share similar traits, with the implication that those shared traits are used for a similar function (Webb et al. 2002). Comparisons of the phylogenetic conservation of phylogenetic relatedness and functional similarity has found that in most systems there is a high amount of linkage between relatedness and shared functional traits (Perry 1999, Prinzing et al. 2001). While the relationship between phylogenetic relatedness and functional similarity is not always completely consistent, phylogenetic analyses provide a valuable tool when full trait level information on all members of a community is not available.

Like much of interior North America, Alberta, Canada contains thousands of glacially formed freshwater wetlands. These wetlands are home to a wide variety of plants and animals including macroinvertebrates. The aquatic macroinvertebrate communities found in freshwater wetlands are diverse and consist of permanently aquatic taxa (e.g., Amphipoda and Hirudinae), taxa with a terrestrial adult stage (e.g., Diptera and Odonata), and taxa that utilize both the terrestrial and aquatic environments (e.g., adult Coleoptera and Hemiptera; see Batzer and Wissinger 1996). In this study, I focused on how macroinvertebrate communities differed in permanent and temporary wetlands. Permanent wetlands are defined as wetlands that contain standing water throughout the entire year. In Alberta, Canada, permanent wetlands tend to be shallow, productive (Bayley and Prather 2003) and freeze in winter. Although they may experience winterkill events (Greenbank 1945), these wetlands serve as an aquatic overwintering habitat for many macroinvertebrates (Tonn et al. 2004). In contrast to permanent wetlands, temporary wetlands in Alberta are filled by snowmelt and early spring rains (Williams 1987) and typically have standing water from early spring through mid to late summer (Class II and III, Stewart and Kantrud 1971). The length of the wet period (when standing water is present) varies greatly from year to year depending on the daily temperatures and amount and timing of precipitation (Williams 1997). Although temporary wetlands tend to be quite small, they represent a significant proportion of the inland water found on the prairies (van der Valk and Pederson 2003).

I sampled several permanent and temporary wetlands in Alberta multiple times during the ice-free season. Based on the different characteristics of the two wetland types, I

made three predictions about the diversity and phylogenetic structure of their communities: (1) When comparing the relatedness of the taxa in permanent and temporary wetlands, I expected the permanent wetlands to contain more diverse taxa (i.e., less related on average) and exhibit less turnover through the summer than temporary wetlands. (2) Because the extreme nature of temporary wetlands requires very specific adaptations, which will likely be possessed by only a small portion of taxa found in the regional pool, I predicted that taxa present would be more related on average than those in the permanent wetlands. (3) Finally, as the amount of water present decreases in the temporary wetlands as the summer progresses, I predicted that the relatedness of remaining taxa would increase, in response to the rapid drying and loss of habitat.

Materials and Methods

Data Collection

I sampled 13 temporary wetlands and 16 permanent wetlands. The 13 temporary wetlands were sampled from an area north of Strathmore, Alberta (51°18' N, 113°27' W). The wetlands in this region typically have high phosphorus levels due, in part, to the high level of agricultural development present on the prairies (Neely and Baker 1989). The sampled wetlands are no exception, as the average total phosphorus (TP) was 1,228 µg/L, and the average total nitrogen (TN) was 9,589 µg/L (Chapter 2). Samples for the 16 permanent wetlands were taken from wetlands near Lac La Biche, Alberta (54°46' N, 111°58' W). These wetlands had an average depth of 1.3 m and, characteristic of most

wetlands in Boreal Alberta, were eutrophic (Bayley and Prather 2003). In these wetlands, TP averaged 409 $\mu\text{g/L}$, and TN averaged 3,691 $\mu\text{g/L}$ (Silver et al. unpublished results).

For both wetland types, macroinvertebrates were sampled using a D-sweep net (500 nm mesh size with opening of 650 cm^2), which was lowered vertically into the water to the benthic-pelagic boundary and then returned to the surface with a small arching motion to sample the vertical water column. For the temporary wetlands, four samples were taken from random locations throughout the wetland during each sampling date. For the permanent wetlands, which were larger than the temporary wetlands, five samples were collected from random locations in the emergent zone of each wetland during each sampling date.

A total of five sampling dates were conducted for the temporary wetlands, with collections occurring every three weeks from mid May through early August 2008. Because of the drying regime characteristic of these wetlands, the number of wetlands available for sampling declined with time. All 13 wetlands were sampled in mid May (sampling period 1) and early June (sampling period 2), and 12 wetlands were available for sampling for the third sampling period in early July. For the fourth sampling period in late July, only four wetlands remained. During the final sampling round (sampling round 5) in early August only three wetlands remained. For the permanent wetlands, three sampling dates were completed in 2006. In May and July (equivalent to the first and third temporary wetland sampling periods, respectively) 16 wetlands were sampled. In August, equivalent to the fifth sampling period for temporary wetlands, 14 wetlands were sampled as two wetlands had become inaccessible.

Macroinvertebrate samples were stored in 70% ethanol until identified to genus (or species when possible) using Clifford (1991). Genus level identification provides good resolution of macroinvertebrate communities, while still allowing samples to be processed in a timely manner (O'Leary et al. 2004, Waite et al. 2004).

Tree Construction

I created a hypothesized phylogenetic tree for the 121 taxa sampled during my surveys. The tree was constructed using Mesquite (Maddison and Maddison 2009), with reference to several molecular phylogenies (Remigio and Blair 1997, Harbach and Kitching 1998, Light and Siddall 1999, Kjer et al. 2002, Morgan et al. 2002, Siddall 2002, Kjer 2004, Maddison and Schulz 2007, Vamosi and Vamosi 2007, Wethington and Lydeard 2007). The relationships of the *Leptoceridae* (Morse 1981), *Limnephilidae* (Vshivkova 2006) and *Hydrophilinae* (Archangelsky 2004) were further resolved using taxonomy, because taxonomy is considered a reasonable surrogate for phylogeny (Crozier et al. 2005, Vamosi and Vamosi 2007). In the absence of detailed information on the phylogenetic relationships for several groups, I assumed taxa were monophyletic and polytomous.

Branch lengths were assigned to the phylogenetic tree using the BLADJ (branch length adjuster) module of Phylocom (version 4.1 Webb et al. 2008). BLADJ fixes nodes with known ages at their estimated age and the remaining node ages are set by evenly spacing undated nodes between dated nodes to reduce variance in branch lengths. Node ages were compiled using TimeTree (Hedges et al. 2006) and Remigio and Blair's (1997) paper on Lymnaeidae snail systematics. Ages for a total of 21 of the 101 internal nodes

were available. The aged nodes were spread throughout the phylogenetic tree, with good resolution along the backbone (Fig. 3.1). From this tree, two trees (i.e., “regional pools”), one for the permanent wetland taxa, and one for the temporary wetland taxa, were created and used for the phylogenetic analyses.

Phylogenetic Analysis

I calculated several measures of relatedness for each wetland during each sampling date for the macroinvertebrate data. First I calculated the phylogenetic distance (PD; Faith 1992) to determine the proportion of the total evolutionary history represented by the taxa found in each sample. Second, species richness (SR), the average number of taxa found in each wetland, was also calculated. Third, I calculated mean pairwise distance (MPD), which represents the mean phylogenetic distance among all pairwise species combinations present in a community (Webb 2000, Webb et al. 2002). Finally, mean nearest neighbor distance (MNND) was calculated to show the mean phylogenetic distance to the nearest relative for all species found in each wetland sample (Webb 2000, Webb et al. 2002). As with most previous studies, MPD and MNND were calculated using presence-absence data, as opposed to abundance-weighted data. When applied to studies that incorporate multiple trophic levels, weighting by abundance overemphasizes the contribution of small, abundant taxa (e.g., mosquitoes), and deemphasizes the contribution of larger macroinvertebrate predators (e.g., dragonflies and diving beetles), to community structure. By using presence-absence data, MPD and MNND are interpreted as phylogenetic distances between species, not phylogenetic distances between individuals.

Calculated MPD and MNND values were compared to the relative distribution of distances calculated for 999 random null communities to determine whether the phylogenetic structure of the wetland communities differs from the community structure expected by chance. Null models were randomly generated using the independent swap algorithm (Gotelli 2000), which holds the row and column sums of the sample/taxa abundance matrix constant while (1) swapping taxa among samples to randomize taxa co-occurrences and (2) maintaining taxa frequency and sample taxa richness (constrained model, Kembel and Hubbell 2006).

Once MPD and MNND were calculated for the null communities, the values were compared to those found for the actual communities through the use of two indices proposed by Webb (2000). Net relatedness index (NRI) is a measure of the phylogenetic clustering of a given community compared to the total species pool. NRI is calculated as $[-1(\text{MPD}_{\text{obs}} - \text{MPD}_{\text{null}})/\text{SD}(\text{MPD}_{\text{null}})]$, where MPD_{obs} is the MPD calculated for the observed wetland community, MPD_{null} is the mean MPD calculated for the 999 null communities, and $\text{SD}(\text{MPD}_{\text{null}})$ is the standard deviation of the MPD_{null} values (Webb 2000, Webb et al. 2002). Positive NRI values indicate co-occurring taxa are more related than expected by chance. Nearest taxon index (NTI) examines the extent of terminal clustering by measuring the minimum branch length between taxa in a given community. NTI is calculated much like NRI, but compares the MNND values of the observed and null communities. NTI is calculated as $[-1(\text{MNND}_{\text{obs}} - \text{MNND}_{\text{null}})/\text{SD}(\text{MNND}_{\text{null}})]$, where MNND_{obs} is the MNND calculated for the observed wetland community, $\text{MNND}_{\text{null}}$ is the mean MNND value calculated for the 999 null communities, and

$SD(MNND_{null})$ is the standard deviation of the MNND values for the 999 null communities (Webb 2000, Webb et al. 2002). Positive NTI values generally indicate terminal clustering, which occurs when closely related species are present in the sample.

Three repeated measures linear mixed models (LMM) were used to compare the PD, NRI and NTI values for the two regions over the five time periods. A generalized linear mixed model (GLMM) with a Poisson error distribution was specified for SR, as they are count data. Wetland type and sampling date were treated as fixed effects, while each individual wetland sampled during each sampling period (wetland ID) was considered a random effect. Unlike all other analyses, the data used in these analyses was derived from the complete phylogeny (shown in Fig. 3.1), not the wetland specific phylogenies. This was to provide a constant regional pool to allow for comparisons between the wetlands types to look for differences between the wetland types for the four measures of richness and relatedness. To meet normality assumptions, PD and NRI were log-transformed prior to analysis.

Taxonomic Scale

It has been previously shown that communities may become more phylogenetically even (i.e., NRI and NTI closer to or less than zero) as the taxonomic scale becomes finer (Cavender-Bares et al. 2006, Swenson et al. 2006). Given the high diversity of taxa found in my focal wetlands, I compared the NRI and NTI values of two subsets of taxa with those obtained with the full samples. Within each subset, I had three nested taxonomic scales, with the full wetland type pool (Bilateria) constituting the highest-order regional pool in each case. The first comparison contrasted patterns obtained with the wetland

specific phylogeny (denoted as Full for both wetland types) with Class Insecta, and Order Diptera. I was able to carry out this comparison separately for permanent and temporary wetlands. The second comparison contrasted patterns obtained with Superphylum Lophotrochozoa (snails, clams and leeches), and Order Gastropoda. Due to the low abundances and diversity of Lophotrochozoa in temporary wetlands, these analyses were conducted only with permanent wetlands. For both subsets, previous data reveal the potential for strong interspecific interactions among constituent species (e.g., Bronmark 1992, Juliano 1998).

Two-tailed *t*-tests were used to determine if the mean NRI and NTI values found for each wetland type at each taxonomic level for every sampling date were significantly different from random (=zero). Additionally, six repeated measures LMMs were used to investigate if the different taxonomic scales (Full : Insecta : Diptera and Full : Lophotrochozoa : Gastropoda separately) had significantly different NTI or NRI values for either wetland type over the sampling season. For all LMMs, taxonomic scale and sampling date were treated as fixed effects, and wetland ID was treated as a random effect. To meet normality assumptions, NRI was log- transformed prior to analysis.

All statistical analyses were conducted in R version 2.10.0 (R Development Core Team 2009) using the ‘vegan’ (Oksanen et al. 2007), ‘picante’ (Kembel et al. 2009), ‘ape’ (Paradis et al. 2004), ‘MASS’ (Venables and Ripley 2002) and ‘nlme’ (Pinheiro et al. 2009) packages.

Results

Abundance and Diversity

Across all samples, 18,899 macroinvertebrates belonging to 107 taxa were collected (Table 3.1). A total of 41 taxa were common to both wetland types, while 43 taxa were unique to the permanent wetlands, and 23 taxa were unique to the temporary wetlands. *Gammarus* was the most abundant taxon overall (6,563 individuals), followed by Chironominae (3,263 individuals) and *Hyaella* (3,187 individuals). In permanent wetlands, the 12,634 macroinvertebrates collected, belonging to 84 taxa, were numerically dominated by *Gammarus* (6,501 individuals), *Hyaella* (3,187 individuals), and *Chaoborus* (443 individuals). A total of 6,265 macroinvertebrates were collected from the temporary wetlands. Of the 64 taxa collected, Chironominae (2,829 individuals) was numerically dominant, followed by *Aedes* (806 individuals) and Ceratopogoninae (390 individuals).

Phylogenetic Patterns

Overall, there was limited evidence for nonrandom (i.e. different from zero) phylogenetic structure for either wetland type with reference to the full individual wetland type phylogenies. For the permanent wetlands, the communities were significantly clustered, with the taxa being more closely related than expected for sampling period 1 only (Table 3.2). The temporary wetlands showed evidence of phylogenetic clustering in mean NTI for sampling period 4 only (Table 3.2).

Despite the lack of significant phylogenetic structure for most sampling periods, the pattern of change for each wetland type as the season progressed varied (Fig. 3.2). PD was significantly different between wetland types ($p = 0.0009$), although there was no statistical evidence that sampling date had an impact for either wetland type (Fig. 3.2A). Permanent wetlands showed a significant change in SR over the season ($p = 0.0291$), as well as being different from the temporary wetlands ($p = 0.0001$; Fig. 3.2B). The wetlands also showed a different pattern of change in SR throughout the sampling periods (interaction between wetland type and sampling date; $p = 0.0299$). Mean NRI was significantly similar between the wetland types over the season (Fig. 3.2C). However, the permanent wetlands showed a much larger drop in NRI through the sampling season ($p = 0.0385$) compared to the temporary wetlands. Mean NTI decreased significantly over the season for the permanent wetlands ($p = 0.0052$), but the temporary wetlands remained more consistent. Unlike NRI, the change in NTI over the sampling season was different for permanent and temporary wetlands ($p = 0.0654$).

Taxonomic Scale

When communities were examined at different taxonomic scales, each scale revealed different patterns (Table 3.2, Figs. 3.3 and 3.4). The first comparison was between the wetland type specific regional pool (Full), the class Insecta and the order Diptera. For the permanent wetlands, mean NRI was different for the three scales ($p = 0.0318$) with all scales showing different patterns throughout the season ($p = 0.0265$; Fig. 3.3A). For NTI, the permanent wetlands also had different mean NTI values for the three scales ($p = 0.0454$) and had marginally different patterns of change over the sampling season ($p =$

0.0558; Fig. 3.3B). The temporary wetlands had even more disparity in the patterns seen for the three taxonomic scales. Mean NRI changed over the season for all scales ($p = 0.0094$), but the pattern of change was not equivalent for the three scales ($p = 0.0379$; Fig. 3.3C). Mean NTI showed a similar pattern with the three scales being significantly different from each other ($p = 0.0346$), as well as showing significant changes in mean NTI throughout the season, but in ways that were unique for each taxonomic scale ($p = 0.0243$; Fig. 3.3D).

The second taxonomic scale comparison compared the permanent wetland regional pool (Full) with superphylum Lophotrochozoa and order Gastropoda (Table 3.2, Fig. 3.4). Mean NRI patterns were quite similar for all three scales (Fig. 3.4A), with the same significant decrease in mean NRI over the sampling season ($p = 0.0033$). NTI showed a similar trend, with all scales following the same pattern of decrease in mean NTI over the sampling season ($p = 0.0464$).

Discussion

In my study, I found that temporary wetlands contained fewer macroinvertebrates belonging to fewer taxa than permanent wetlands. This finding, which is consistent with other studies (e.g., Brooks 2000, Urban 2004, Della Bella et al. 2005), is likely due to the specific adaptations required to live in a temporary habitat. Of the 64 taxa found in the temporary wetlands, 52 have a terrestrial stage. The remaining taxa included snails, which can survive in the substrate between wet periods (Jensen et al. 1996, Gerard 2001), and two genera of Anostraca, which are only found in temporary wetlands as their eggs

require a dry stage to become viable (Bohonak and Whiteman 1999, Merta 2003). The two genera of leeches and single amphipod species found in temporary wetlands were encountered in small numbers, and were probably transported by waterfowl from permanent wetlands nearby (Charalambidou and Santamaria 2005, Green et al. 2008). Therefore, as predicted, the majority of taxa found in the temporary wetlands possessed an adaptation that allow them to either leave the drying wetland or survive in the substrate until the next wet period.

Overall, I found only limited evidence for strong phylogenetic structuring. Although mean values often appeared to be quite different from zero, considerable variation among wetlands frequently resulted in nonsignificant patterns. To date, the majority of phylogenetic community studies have focused on established plant communities (Vamosi et al. 2009). Whereas plants remain in the same location after germination, most macroinvertebrates sampled here are motile (to varying degrees), being able to move between the numerous wetlands often found in close proximity to each other. Additionally, a large number of macroinvertebrates leave the aquatic system altogether as they complete their terrestrial life cycle, where they are no longer sampled as part of the aquatic community. As more phylogenetic studies on diverse animal communities are completed, I anticipate it may become necessary to adapt the NTI and NRI metrics to account for the increased variation encountered in ecologically heterogeneous communities.

The permanent wetlands appear to have greater higher-level clustering (lower NTI values, and higher NRI values), whereas temporary wetlands were more clustered at the

tips (higher NTI values, and lower NRI values; see Fig. 3.2) for most of the season. Positive NTI indicates the taxa are locally clustered within particular terminal clades, although the relationship among those clades is not accounted for (Webb 2000). Whereas these clumped clades have a positive NTI, the clades can be well spread out on the overall phylogeny, resulting in an NRI value closer to zero. Conversely, when there is less terminal clustering, NTI can be close to zero, but if the higher clades are more clumped, positive NRI values result (Webb 2000). I interpret these patterns to indicate that permanent wetlands contain few closely related terminal taxa (i.e., species and genera), whereas higher-level groups (e.g., families) are clustered. This suggests that competition for resources, or other biotic interactions, is largely driving community assembly. Conversely, in temporary wetlands, closely related terminal taxa occurred together (i.e., congeners were found together), but higher level clustering was not observed. I interpret this pattern to suggest that environmental filtering and the requirements for specialized adaptations are important in community assembly in these temporary habitats.

Although these patterns held overall, the communities did not maintain constant relatedness throughout the summer (Fig. 3.2). Permanent wetlands contained clustered communities (positive NRI and NTI) in the early spring, which became progressively more even (negative NRI and NTI) over the sampling period. That is, taxa in the communities become less related throughout the season, suggesting an increased role for species interactions driving community assembly in these wetlands. Temporary wetlands displayed a slight increase in NRI early in the season, before decreasing as the wetlands

dry. Unlike the pattern seen for the permanent wetlands, mean NTI for the temporary wetlands remained close to or above zero for the entire season. Taken together, the communities in temporary wetlands start out with several higher-level clades (high NRI) with a random assortment of terminal taxa from each of these clades (NTI near zero). Community assembly appears to be driven by environmental filtering, with a limited number of clades being able to inhabit a temporary habitat, with a more stochastic element to the specific taxa found in any given wetland. This may be analogous to the early stages of succession, where initial community assembly is a random selection of the local species pool (Dinnage 2009). With drying, some higher clades leave the system as their members become terrestrial, causing a reduction in NRI values. Competition does not appear to have a large influence on temporary wetland communities.

Examination of communities at different taxonomic scales revealed interesting patterns, although I did not find a predictable/repeated progression towards phylogenetic evenness (Cavender-Bares et al. 2006, Swenson et al. 2006). Insect and Dipteran assemblages became more phylogenetically even towards the middle of the season in permanent wetlands, with more taxa that use the wetlands for only a small part of their yearly life cycle entering the system. In contrast to full wetland communities, which decreased in relatedness through the season, insects and Dipterans became more phylogenetically clustered towards the end of the season, which was likely caused by some closely related taxa either leaving the aquatic system or overwintering as a stage not captured by my sampling (e.g., eggs). Because more closely related species are likely to share the same overwintering strategy, only those taxa that remained in the water column

were being sampled at this time. Conversely, the Lophotrochozoa and Gastropoda found in permanent wetlands experienced a continual decrease in relatedness (both NRI and NTI) as the season progressed. The highly clustered starting point is likely related to two factors: (1) high over-wintering mortality (Ansart and Vernon 2003), causing some taxa to become extirpated from the wetland, and (2) the fact that many of these taxa lose a large amount of body mass over the winter, which may cause smaller taxa to not be sampled early in the spring until they increase in size (Ansart and Vernon 2003). Intra- and inter-clade predation and competition for space and resources likely lead to a reduction in related taxa, lowering NRI and NTI as the season progresses (Bronmark 1992, Turner et al. 2007).

Despite accounting for the majority of the macroinvertebrates collected from temporary wetlands (Insecta = 80.3%; Diptera = 69.8%), patterns for these assemblages were markedly different than for full temporary wetland communities. The influence of environmental filtering appeared to be more pronounced at both scales. When the temporary wetlands are newly refilled with water, insect and Dipteran assemblages are even (i.e., negative NRI and NTI). Increasing clustering observed for Dipteran and, to a lesser extent, insect assemblages, is likely due to a combination of two factors: (1) many insects become terrestrial adults and leave the aquatic system by early/mid summer, and (2) the environmental stresses increase as wetlands start to dry. Both factors likely lead to increased relatedness as the remaining taxa likely have a longer aquatic lifecycle, and are able to survive the changes associated with drying.

Although temporary wetland communities generally showed different phylogenetic patterns than permanent wetland communities, most of the taxa present in the temporary wetlands were also sampled in the permanent wetlands. Individuals inhabiting temporary wetlands risk being caught in an environment that dries out before they can finish (a) particular life stage(s) in standing water. Conversely, they may benefit from reduced predatory risk, which may greatly reduce the abundance of most macroinvertebrates found in permanent wetlands (e.g. Diehl 1992, Paukert and Willis 2003). Whereas temporary wetlands often remain wet into late summer, there are drought years in which the temporary wetlands can be dry by late spring/early summer. Indeed, I attempted to resample the temporary wetlands in 2009, but several of them never filled and all were dry by mid June due to very limited precipitation (Silver and Vamosi unpublished results). In years in which temporary wetlands are present for much of the summer, they serve as valuable habitat for macroinvertebrates possessing the required adaptations to escape high levels of predation pressure. Conversely, in dry years most species rely on permanent wetlands to provide a 'backup' habitat. The metacommunity interactions between permanent and temporary wetlands located in close proximity to one another, and the effects of environmental variation on the resulting "exchange" of phylogenetic diversity, present an interesting and timely avenue for further research.

Conclusions

Temporary and permanent wetlands are routinely lost due to drainage for urbanization and agricultural purposes. The loss of these wetlands has the potential to result in the loss of the rich macroinvertebrate communities found in these wetlands. Macroinvertebrates

are the primary protein source for many fish and waterfowl species, which also depend on the presence of these wetlands. Temporary wetlands are particularly vulnerable as they are not protected by any current legislation and they are often plowed over during dry periods preventing their formation in future years (Collinson et al. 1995, Semlitsch and Bodie 1998, Naugle et al. 2001). By understanding the mechanisms driving the assembly of the macroinvertebrate communities in permanent and temporary wetlands, we stand to gain valuable insights into the importance of maintaining a variety of wetlands with varying hydroperiods.

Table 3.1: Aquatic macroinvertebrate taxa sampled from permanent (PERM), temporary (TEMP) or both (Both) wetland types. Taxon codes are used in Fig 3.1.

| Taxon Code | Full Identification | Wetland Type | Taxon Code | Full Identification | Wetland Type |
|------------|-------------------------------------|--------------|------------|----------------------------------|--------------|
| Aciliu | <i>Acilius</i> | Both | Hydrop | <i>Hydrophilus</i> | TEMP |
| Aedes | <i>Aedes</i> | TEMP | Hygrot | <i>Hygrotus</i> | Both |
| Aeshna | <i>Aeshna</i> | PERM | Ilybiu | <i>Ilybius</i> | Both |
| Agabus | <i>Agabus</i> | Both | Ischur | <i>Ischnura</i> | TEMP |
| Albogl | <i>Alboglossiphonia heteroclita</i> | Both | Isotom | <i>Isotomus</i> | TEMP |
| Aminic | <i>Aminicola limosa</i> | TEMP | Laccob | <i>Laccobius</i> | Both |
| Amioce | <i>Amiocentrus</i> | PERM | Laccop | <i>Laccophilus</i> | Both |
| Anax | <i>Anax</i> | PERM | Lestes | <i>Lestes</i> | Both |
| Arctop | <i>Arctopora</i> | Both | Libell | <i>Libellula</i> | TEMP |
| Armige | <i>Armiger crista</i> | PERM | Limneb | <i>Limnebius</i> | TEMP |
| Baetis | <i>Baetis</i> | Both | Limnep | <i>Limnephilus</i> | Both |
| Bakeri | <i>Bakerilymnaea</i> | Both | Limnod | <i>Limnodrilus</i> | TEMP |
| Banksi | <i>Banksiola</i> | PERM | Limoni | Limoniinae* | PERM |
| Berosu | <i>Berosus</i> | TEMP | Lymnae | <i>Lymnaea stagnalis</i> | Both |
| Branch | <i>Branchinecta</i> | TEMP | Manson | <i>Mansonia</i> | PERM |
| Brychi | <i>Brychius</i> | Both | Menetu | <i>Menetus cooperi</i> | PERM |
| Caenis | <i>Caenis</i> | Both | Mesove | <i>Mesovelia</i> | PERM |
| Centro | <i>Centroptilum</i> | PERM | Mooreo | <i>Mooreobdella</i> | PERM |
| Cerato | <i>Ceratopogoninae</i> | Both | Mystac | <i>Mystacides</i> | Both |
| Chaobo | <i>Chaoborus</i> | Both | Narpus | <i>Narpus</i> | PERM |
| Chiron | Chironominae* | Both | Nemota | <i>Nemotaulius</i> | Both |
| Cloeon | <i>Cloeon</i> | TEMP | Nephel | <i>Nephelopsis obscura</i> | PERM |
| Coenag | <i>Coenagrion</i> | PERM | Notone | <i>Notonecta</i> | Both |
| Colymb | <i>Colymbetes</i> | Both | Ochthe | <i>Ochthebius</i> | Both |
| Culex | <i>Culex</i> | PERM | Pedomo | <i>Pedomoecus</i> | PERM |
| Curcul | Curculionidae* | Both | Peltod | <i>Peltodytes</i> | TEMP |
| Cymati | <i>Cymatia americanus</i> | PERM | Perico | <i>Pericoma</i> | PERM |
| Dina | <i>Dina</i> | Both | Phryga | <i>Phryganea</i> | PERM |
| Dixell | <i>Dixella</i> | PERM | Physa | <i>Physa</i> | Both |
| Dytisc | <i>Dytiscus</i> | Both | Pisidi | <i>Pisidium</i> | PERM |
| Ecclis | <i>Ecclisomyia</i> | PERM | Plaorn | <i>Placobdella ornata</i> | PERM |
| Empidi | Empididae* | Both | Plapap | <i>Placobdella papillifera</i> | PERM |
| Enalla | <i>Enallagma</i> | Both | Plapar | <i>Placobdella parasitica</i> | PERM |
| Enochu | <i>Enochrus</i> | TEMP | Podura | <i>Podura aquatica</i> | TEMP |
| Ephydr | Ephydriidae* | TEMP | Priono | <i>Prionocera</i> | PERM |
| Erista | <i>Eristalis</i> | PERM | Probyt | <i>Probythinella lacustris</i> | TEMP |
| Erpobd | <i>Erpobdella punctata</i> | PERM | Promex | <i>Promenetus exacuus</i> | PERM |
| Eubran | <i>Eubranchipus</i> | TEMP | Promum | <i>Promenetus umbilicatellus</i> | Both |
| Fossar | <i>Fossaria</i> | PERM | Psycho | <i>Psychoda</i> | TEMP |
| Gammar | <i>Gammarus lacustris</i> | Both | Ptilos | <i>Ptilostomis</i> | PERM |
| Gerris | <i>Gerris</i> | PERM | Pyrrha | <i>Pyrrhalta</i> | Both |
| Glossi | <i>Glossiphonia complanata</i> | PERM | Rhantu | <i>Rhantus</i> | Both |
| Glypho | <i>Glyphopsyche</i> | PERM | Sciomy | Sciomyzidae* | TEMP |
| Grapho | <i>Graphoderus</i> | Both | Sigara | <i>Sigara</i> | Both |
| Gyraul | <i>Gyraul</i> | PERM | Somato | <i>Somatochlora</i> | Both |
| Gyrinu | <i>Gyrinus</i> | PERM | Stagni | <i>Stagnicola</i> | Both |
| Halipl | <i>Haliplus</i> | Both | Strati | Stratiomyidae* | Both |
| Heliso | <i>Helisoma</i> | PERM | Sympet | <i>Sympetrum</i> | PERM |
| Helobd | <i>Helobdella stagnalis</i> | PERM | Tanypo | Tanypodinae* | Both |
| Heloph | <i>Helophorus</i> | TEMP | Therom | <i>Theromyzon</i> | PERM |
| Hyalel | <i>Hyalella azteca</i> | PERM | Tipula | <i>Tipula</i> | TEMP |
| Hydati | <i>Hydaticus</i> | Both | Triaen | <i>Triaenodes</i> | PERM |
| Hydroc | <i>Hydrochus</i> | TEMP | Valvat | <i>Valvat sincera</i> | PERM |
| Hydroo | <i>Hydroporus</i> | TEMP | | | |

*Indicates Family or Subfamily was the lowest level of identification possible.

Table 3.2: Phylogenetic structure of macroinvertebrate assemblages at different taxonomic scales for permanent and temporary wetlands repeatedly sampled between May and August; Sampling date: mid May (1), early June (2), early July (3), late July (4), early August (5), all time periods pooled (Overall); Net Relatedness Index (NRI); Nearest Taxon Index (NTI). Two-tailed *t*-tests were used to determine if NRI or NTI values were significantly different from zero, where *indicates $p < 0.05$, and + indicates $p < 0.10$.

| Wetland Type | Sampling Date | Full | | Insecta | | Diptera | | Lophotrochozoa | | Gastropoda | |
|--------------|---------------|-------------------|-------------------|-------------------|--------------------|---------|--------------------|-------------------|-------|------------|-------|
| | | NRI | NTI | NRI | NTI | NRI | NTI | NRI | NTI | NRI | NTI |
| Permanent | Overall | 0.07 | 0.09 | 0.23 | 0.05 | 0.09 | 0.02 | 0.37 | 0.19 | 0.24 | 0.13 |
| | 1 | 0.54 ⁺ | 0.75 [*] | 1.01 [*] | 0.24 | 0.21 | 0.10 | 1.18 [*] | 0.73 | 0.73 | 0.57 |
| | 3 | -0.07 | -0.05 | -0.21 | -0.11 | -0.23 | -0.32 | 0.10 | 0.06 | 0.10 | 0.01 |
| | 5 | -0.32 | -0.50 | -0.20 | 0.02 | 0.36 | 0.36 | -0.32 | -0.35 | -0.63 | -0.60 |
| | Overall | 0.03 | 0.07 | 0.26 | -1.21 [*] | 0.04 | 0.12 | | | | |
| Temporary | 1 | 0.05 | 0.04 | -0.24 | -0.74 [*] | -0.50 | -0.56 ⁺ | | | | |
| | 2 | 0.26 | 0.18 | 0.43 | -1.22 [*] | 0.04 | 0.08 | | | | |
| | 3 | 0.01 | -0.10 | 0.62 | -1.61 [*] | 0.42 | 0.65 [*] | | | | |
| | 4 | -0.28 | 0.54 ⁺ | -0.03 | -1.05 | 1.15 | 1.16 | | | | |
| | 5 | -0.51 | -0.17 | 0.53 | -1.85 | 0.44 | 0.78 | | | | |

Note: A separate “regional” phylogeny was constructed for each wetland type for each taxonomic level.

These phylogenies, labeled as Full, contained only the taxa found in that wetland type, and were used for all analyses of the corresponding wetland type.

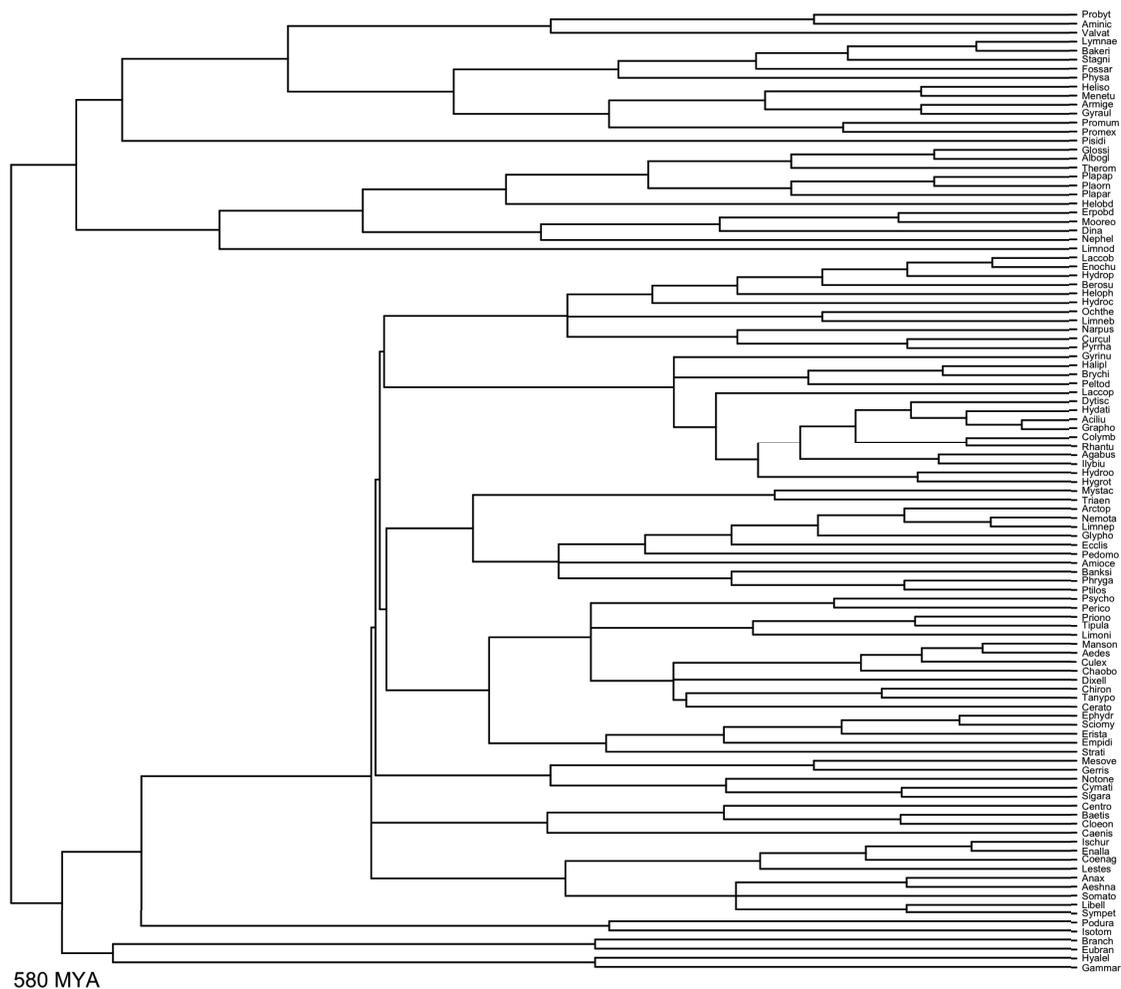


Figure 3.1: Composite phylogeny of relationships among the aquatic macroinvertebrates (see Table 3.1 for taxon codes) sampled from permanent and temporary wetlands.

Undated nodes are evenly spaced between dated nodes to minimize variation in branch length.

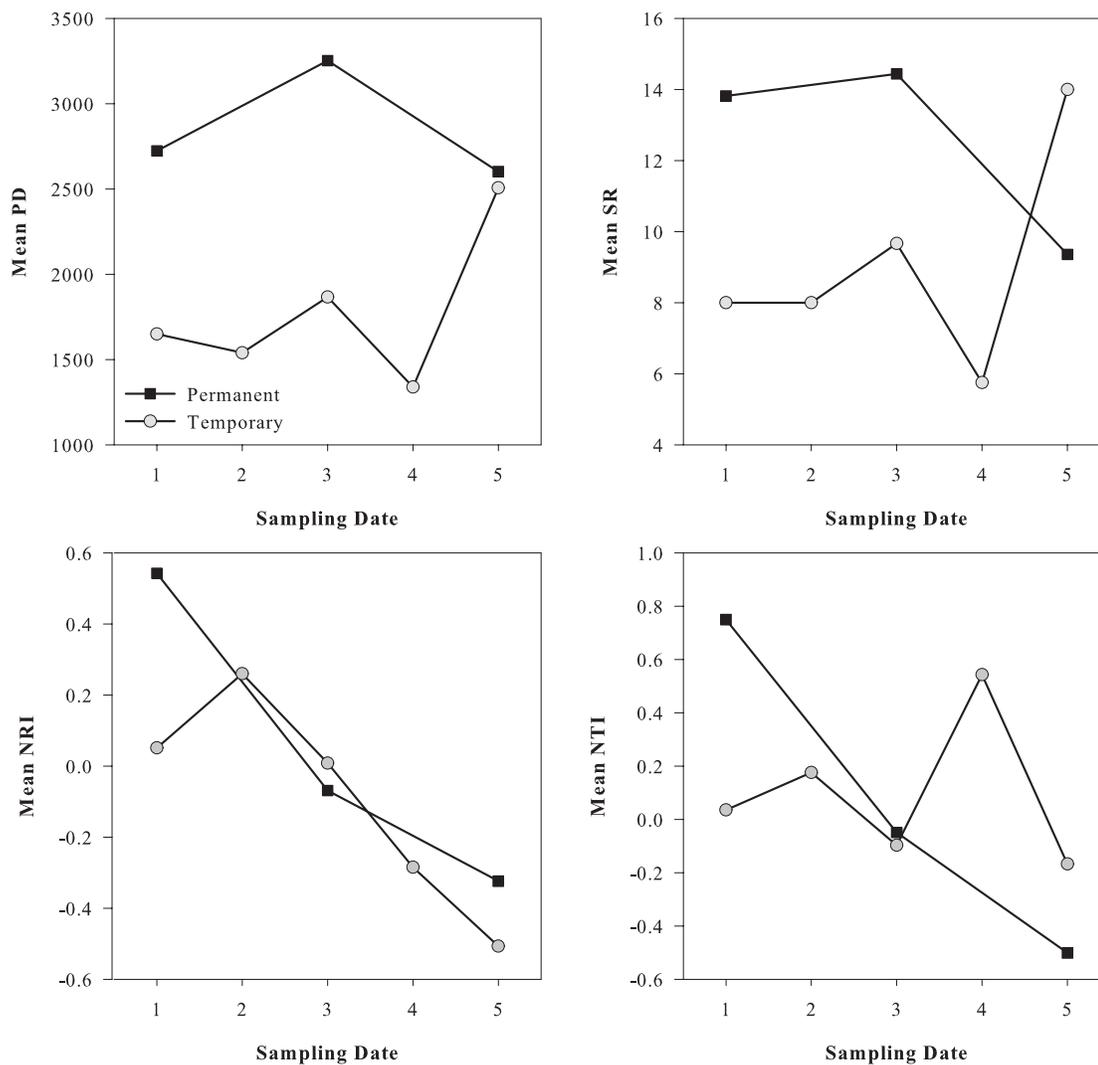


Figure 3.2: Changes in four measures of aquatic macroinvertebrate richness and relatedness for permanent (black lines) and temporary (grey lines) wetlands of Alberta, Canada. Wetlands were repeatedly measured between May and August (1 = mid May, 2 = early June, 3 = early July, 4 = late July and 5 = early August); (A) phylogenetic distance (PD); (B) species richness (SR); (C) Net Relatedness Index (NRI); (D) Net Taxon Index (NTI).

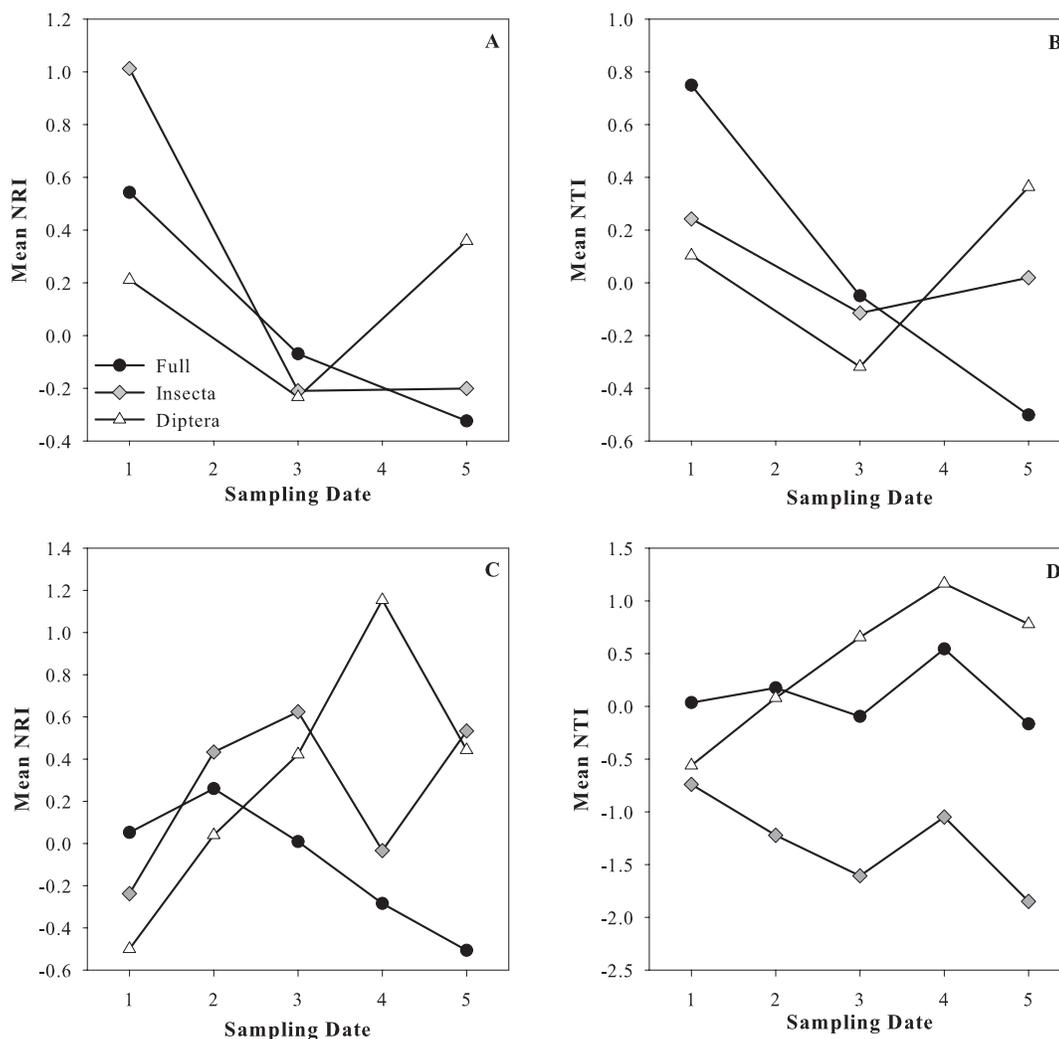


Figure 3.3: Patterns of phylogenetic structure (A, C: NRI; B, D: NTI) in permanent (A, B) and temporary (C, D) wetlands at different taxonomic scales; Full (most diverse), Insecta, and Diptera (least diverse). Full refers to the average values for the corresponding wetland type phylogeny (shown in Fig. 2C and D). Wetlands were repeatedly measured between May and August (1 = mid May, 2 = early June, 3 = early July, 4 = late July and 5 = early August).

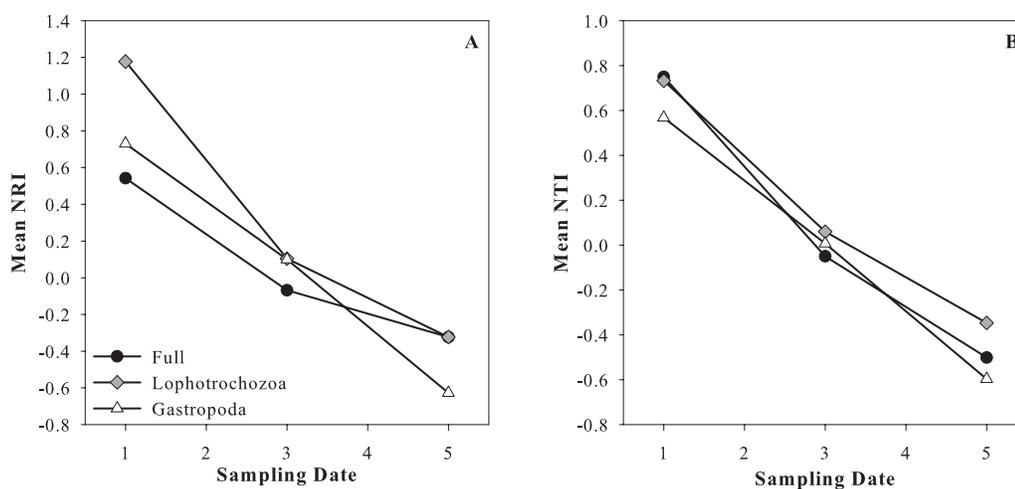


Figure 3.4: Patterns of phylogenetic structure (A: NRI; B: NTI) in permanent wetlands at different taxonomic scales; Full (most diverse), Lophotrochozoa, and Gastropoda (least diverse). Full refers to the average values for the permanent wetland phylogeny (shown in Fig. 2C and D). Wetlands were repeatedly measured between May and August (1 = mid May, 3 = early July, and 5 = early August).

CHAPTER 4: GENERAL CONCLUSIONS

This study revealed that temporary wetlands of the PPR provide habitat for diverse and abundant macroinvertebrate communities, even when the wetlands occur in cattle pastures. The temporary nature of these wetlands appears to be the primary driver in structuring the community composition. Few groups of macroinvertebrates are able to effectively utilize the water present for only a few weeks in these wetlands. Those taxa that are present tend to achieve high abundances, likely due a combination of relaxed predation pressure and reduced competition for resources compared to more permanent water bodies.

The vast majority of the taxa found in the temporary wetlands were also found in permanent wetlands (see Chapter 3), but usually in much smaller numbers (Nicolet et al. 2004; Chapter 3). Individuals from this subset of well-adapted taxa take a risk by inhabiting temporary wetlands to gain the rewards of increased access to resources and reduced predation. But in years when the temporary wetlands dry quickly, such as observed for the study wetlands in 2009, the risk does not pay off. In those drought years, individuals that stayed in more permanent wetlands sustain the taxon's population. This meta-population interaction between temporary and permanent wetlands has been examined in other regions (Jeffries 1994), and it would be interesting question to examine in the PPR.

Temporary wetlands play a vital role in maintaining the populations of many of the macroinverbrates found in the PPR (Semlitsch and Bodie 1998). Temporary wetlands are

typically considered sink habitats as the long-term intrinsic population growth rates in temporary wetlands tends to be negative. While sinks are typically low quality habitats requiring constant immigration to replace individuals lost to mortality, sinks play a vital role in maintaining the overall population (e.g., Long et al. 2007, Matthews and Gonzalez 2007). There is increasing evidence that temporal variation in the habitat quality of sinks may result in periods of positive growth leading to long-term persistence of sink populations (Johnson 2004). Sink habitats, such as temporary wetlands, can support long-term metapopulations in a stochastic environment (Matthews and Gonzalez 2007). The stochastic environment results in years where sink habitats are of higher quality than other years. In “good” years positive population growth often occurs in the traditional sink habitats (Gonzalez and Holt 2002, Matthews and Gonzalez 2007). For the macroinvertebrates in PPR wetlands, this means that if a permanent source wetland is drained or otherwise becomes uninhabitable, the populations of many macroinvertebrate groups could be maintained in the temporary wetlands scattered throughout the landscape.

The rotational grazing schedule examined for this study was successful in creating two distinct habitat types, early grazed and late grazed wetlands. While a single fence separates these pastures, and many of the late grazed wetlands were within 300m of some early grazed wetlands, the macroinvertebrate communities present in each type were quite different, especially when considered from the taxonomic perspective. It appears the late grazed wetlands are able to recover, to a large degree, from fall grazing and support diverse and abundant macroinvertebrate communities when the wetlands again

contain water in spring. By splitting the pasture, the late grazed wetlands can serve as a refuge for taxa that may not be able to exist in the altered vegetation and water chemistry of the early grazed wetlands. If continual grazing was used, those taxa may not be able to inhabit any wetlands in the cattle pasture. This could lead to extirpation or even extinction if intense, continual cattle grazing occurred over its entire range. This study examined the early and late grazed wetlands only, and comparison with pristine and continually grazed wetlands would be desirable for future studies if a suitable study area were found. Based on other studies of macroinvertebrate diversity and cattle stocking densities (e.g., Sovell et al. 2000, Steinman et al. 2003, Braccia and Voshell 2007), it is likely that continually grazed wetlands would have the lowest macroinvertebrate diversity, and early grazed would be expected to have slightly higher diversity as the wetlands, and the bordering terrestrial habitat, are free from grazing for part of the year. There is no clear evidence available to predict if late grazed wetlands would have higher, lower or equivalent diversity to the pristine, ungrazed wetlands.

Rotational grazing is becoming increasingly popular in Alberta, as many land managers have switched from continual grazing to rotational grazing in the last 10-20 years (Chorney and Josephson 2000). The majority of those that switched identified several benefits, including cattle gaining weight more rapidly, increased growth of natural forage on all pastures, and reduced overwintering costs (Chorney and Josephson 2000). The downside to rotational grazing for land managers included increased labour costs to move cattle and maintain fences, as well as increased planning time. But all land managers agreed the benefits more than outweigh the downside, and no land manager

surveyed would return to continual grazing (Chorney and Josephson 2000). For land managers using continual grazing, costs associated with adding new fences and labour as well as a lack of information regarding the benefits of rotational grazing were identified as the primary reasons for not switching to rotational grazing (Chorney and Josephson 2000). Expanding programs providing financial assistance and information to land managers would allow more land managers to switch to rotational grazing.

While awareness regarding the value of wetlands has been increasing, large numbers of temporary wetlands are still being lost each year. Current legislation governing much of the PPR only protects wetlands when they contain water, leaving temporary wetlands vulnerable during the dry phase, or offers protection only to larger wetlands. However, the situation is rapidly improving as more knowledge about the interaction of agriculture and wetlands becomes available. On March 10, 2010 the United States Senate unanimously passed a bill to enhance the North American Wetlands Conservation Act (NAWCA). The enhancement bill allows for Canadian funds to be matched by the program, increasing funding for wetland conservation. In Alberta, a new wetland policy, Water for Life, is expected in the near future and should provide further protection and mitigation measures for wetlands in Alberta. Unfortunately, temporary wetlands are unlikely to be covered under the new legislation as their temporary nature makes it difficult to delineate what is and what is not a wetland.

New legislation is a huge step, but even larger, permanent wetlands that are protected under current legislation are often drained and altered by landowners to make the land more useful for crop production or cattle grazing. The best way to protect PPR wetlands

involves educating the public and landowners about the value of wetlands and working with landowners to implement programs such as rotational grazing to allow wetlands and agriculture to co-exist.

Many groups are working to increase landowner knowledge and working towards successful coexistence of agriculture and wetlands. The largest wetland conservation group in North America's PPR is Duck's Unlimited (DU) and Duck's Unlimited Canada (DUC). DU and DUC work toward the preservation of wetlands through land acquisitions, easements and landowner education regarding more wetland-friendly agricultural practices including rotational grazing. In Alberta, the Riparian Habitat Management Society known as Cows and Fish, and the Alberta Water Council have focused their efforts on maintaining the remaining riparian areas, including wetlands, found in Alberta. Cows and Fish works with landowners to find economically sensible ways for their agricultural practices to continue, while protecting the riparian habitat present on their lands. The Alberta Water Council explores new ideas for furthering Alberta's wetland protection policies.

Demonstrating ecological and economic success of alternate agricultural techniques, such as rotational grazing, that help protect wetlands is the best way to convince landowners to switch. Antelope Creek Ranch, located near Brooks in southern Alberta, works to find techniques that allow for the coexistence of oil and gas production and economically feasible agriculture balanced with conscientious conservation of wetland and native grassland habitat. Antelope Creek has been successfully operating using since 1986, showing that habitat conservation does not preclude successful agriculture.

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APPENDIX A: NULL MODELS IN COMMUNITY ECOLOGY

Introduction

Null models are statistical models that assume no interactions among species (Harvey et al. 1983). They are commonly used in community ecology in an attempt to assess if a community assembly is a random sampling of available species, or if some factor has caused a non-random community to be formed. Null models allow ecologists to test the null hypothesis that communities are assembled randomly, by chance, from non-interacting species (Morin 1999). Statistically determining that a community is non-random (i.e., rejecting the null hypothesis) leads to the conclusion that community assembly may be affected by interactions between the various species, dispersal limitation and/or by abiotic features of the environment (i.e., habitat filtering). Null models are necessary in ecology, because the experiments required to experimentally construct complex communities with appropriate replicates are not always feasible (Colwell and Winkler 1984).

In this review, I describe the history, implementation and extended use (with regard to community phylogenetics) of null models in ecology. I begin with a summary of the (at times heated) debate surrounding the development and implementation of null models for community ecology. After a few decades of debate, null models became widely accepted as a valid technique in community ecology. Following the acceptance of null models by community ecologists, studies were conducted to determine which null model to use for different hypotheses and datasets. The focus of these studies was on reducing Type I and II errors by using null models created by different algorithms, and I describe

the most commonly used ones. Once armed with this information, a subset of community ecologists focusing on relatedness among species in communities fully embraced null models. The null models allowed phylogenetic studies to statistically assess if a community is more or less related than chance, providing a powerful analysis framework that was previously lacking from the field. I describe a few examples of community relatedness hypotheses and how they were addressed using null model techniques. I conclude with a discussion of how to interpret the results of null model analyses because, as with most studies of the processes shaping communities, the answer is rarely straightforward, and a brief examination of experimental approaches and null model use.

Historical Development and Debates

Although null models are now commonplace in community ecology, this was not always the case. Like many statistics, null models were difficult to implement prior to the advent of computers capable of performing the randomizations required to create the null models, and calculating the metrics that allow for comparisons of the null model and observed community. Prior to the 1970's communities were compared in a very qualitative way. For example, many community ecologists compared genus to species ratios between communities to assess if a given community was more closely or distantly related than expected based on the species pool of the region (e.g., Elton 1946, Moreau 1948). This method had widely known drawbacks, including the different results that arose when using different taxonomic systems and divisions and the incompleteness of all community surveys. Elton (1946) was also careful to explain that the different community types could be due to different tolerance ranges and resource utilization of

closely related species, competition between the various taxa, as well as predator/prey dynamics.

Genus to species ratios provided a very qualitative way to compare species associations. With this method, one could conclude that one community had more single-species genera than another, but there was no significance testing to determine if the patterns were truly different from random. For example, Moreau (1948) completed a survey tropical bird communities of 31 different sites in Tanzania. In total, Moreau identified 172 species of birds nested in 92 genera, with 41 genera being represented by more than a single species. For eight of the nine families (all frugivorous or insectivorous), Moreau found 94% of the congeneric species were ecologically isolated from each other. For the ninth family, Ploceidae, the amount of overlap was much higher among congeners. Species in the family Ploceidae feed on temporarily abundant seeds found on flood plains. As the dry season progresses, this resource disappears, and the birds must relocate to find a new food patch, whereas the resources used by the other families remain more consistent. With the available analysis, Moreau concluded by inferring that the factors maintaining ecological isolation of most congeners are highly effective. However, Moreau was unable to comment on whether the distributions for the Ploceidae family were statistically different from each other or from random species distributions. The lack of statistical comparisons also prevented further examination into the specific factors that may be driving the assembly of these bird communities.

Ironically, the publication that sparked the debate on the creation and use of null models in community ecology made no mention of null models at all. Diamond's (1975) paper compared incidence functions of birds on different islands in an archipelago near

New Guinea. Diamond noticed several occurrences of species pairs that were not present, despite the apparent lack of physical barriers such as habitat differences or dispersal ability preventing those species from co-existing. The simplest example results in a checkerboard pattern, where two ecologically similar species occur in the same general region (i.e., are sympatric) but are mutually exclusive in local areas, resulting in a checkerboard like pattern of distribution. Diamond identified several checkerboard patterns ranging from two species of fruit pigeons (*Ptilinopus*), to four honeyeater species (*Myzomela*), to twelve species of white-eyes (*Zosterops*). As a result of his extensive study, Diamond proposed seven rules of community assembly, focusing primarily on “permissible” and “non-permissible” combinations of species forming the observed non-random communities.

The famous response paper by Connor and Simberloff (1979) pointed out several issues with Diamond’s (1975) assembly rules and methodology. Many of their criticisms focused on the lack of statistical evidence provided by Diamond (1975) to support his assembly rules and conclusions. In particular, Connor and Simberloff (1979) were unconvinced of Diamond’s (1975) primary untested assumption that the communities are not assembled by chance. In order to test if the communities are in fact non-randomly assembled, Connor and Simberloff (1979) proposed a null model approach. The null model proposed by Connor and Simberloff (1979) uses the original presence/absence species by site matrix, and randomly rearranges the values while maintaining three features of the original data: (1) Number of species per site (column totals) (2) Number of sites each species is found in (row totals) and (3) Species are only placed in sites with a total number of species consistent with the naturally observed range for that species.

Connor and Simberloff (1979) rearranged the data 10 times (i.e. created 10 different null models) and compared these models to the original data to determine if the communities are non-randomly assembled. They then counted all of the non-existent species pairs present in the actual data and the 10 null models. The number of non-existent pairs was then compared to the observed communities using Chi squared analysis to determine if observed communities were different from random. Although the New Guinea dataset used by Diamond (1975) was not available for Connor and Simberloff (1979) to analyze with their null model, they did compare the other community datasets mentioned by Diamond (1975) as further support for his assembly rules. Connor and Simberloff (1979) found these communities showed no evidence of being different from random.

Perhaps unsurprisingly, the critique by Connor and Simberloff (1979) prompted several response papers. Diamond and Gilpin (1982) was a direct response to the criticisms and null model method presented in Connor and Simberloff (1979), and additionally provided a different null model that contradicted the results in the latter paper. Diamond and Gilpin (1982, p. 64) began their paper by stating that the null models presented by Connor and Simberloff were "...nothing more than one of many possible competing hypotheses, one that is implausible, unparsimonious, and definitely not null..." The primary issue discussed by Diamond and Gilpin (1982) revolved around: (1) the lack of "null-ness" in the Connor and Simberloff null model and (2) the fact that the construction of an appropriate null model is likely much more difficult than Connor and Simberloff indicated. Diamond and Gilpin (1982) argued that the Connor and Simberloff null model is so restricted, because it maintains row and column totals which makes it no longer null. In essence, the Connor and Simberloff's null model incorporates hidden

community structure, resulting in the null model not actually being different from the observed data, and therefore it becomes impossible to find the communities to be non-randomly distributed at all (i.e., not able to reject the null hypothesis). Additionally, Diamond and Gilpin (1982) reported that the Connor and Simberloff model could not detect a full checkerboard distribution, which is arguably the epitome of non-random distributions. The alternate null model presented by Gilpin and Diamond (1982) uses presence/absence data and calculates the probability of each species occurring in a given site, while maintaining row and column totals found in the original data set. The number of non-existent species pairs is counted, and compared to the expected probabilities from the null model with a Chi squared test to assess significance. Gilpin and Diamond's (1982) model successfully detected the checkerboard pattern as non-random and showed the communities shown to be random by Connor and Simberloff (1979) were actually non-randomly distributed. Gilpin and Diamond (1982) also note that their model also likely incorporates some hidden community structure by maintaining row and column totals, but this model uses probabilities, instead of the presence/absence data, making their model superior to Connor and Simberloff's approach.

In addition to the criticisms of the model presented by Connor and Simberloff (1979), further criticism was directed at the data itself (Diamond and Gilpin 1982, Wright and Biehl 1982). Diamond's (1975) original analysis to determine the assembly rules was conducted with ecological guilds, whereas Connor and Simberloff (1979) used species data. Guilds are groups of related species that use similar niches, and are the most likely to be directly interacting (Root 1967). Species in different guilds are much less likely to be interacting to a degree that can alter their distributions (Diamond and Gilpin 1982).

The problem with using species data when trying to find community patterns was termed the dilution effect, where community patterns are buried in a mass of non-interacting species data and are thus not statistically detected (Diamond and Gilpin 1982, Wright and Biehl 1982). As an example, Diamond and Gilpin (1982) explained how owls and hummingbirds may be present in the same habitats but, because they utilize vastly different resources, there is no expectation that one is having an impact on the presence or abundance of the other. When examining all species-pair interactions (like Connor and Simberloff 1979), many comparisons are between species that are not directly (or even indirectly) interacting. This dilutes any non-random pattern that may be found in the much smaller number of comparisons between species of the same guild, making it undetectable by the null model analysis (Diamond and Gilpin 1982).

In response to these criticisms, Connor and Simberloff (1983) were quick to point out that the Gilpin and Diamond (1982) model still included the hidden community structure they criticized in Connor and Simberloff's (1979) model. They argued for the necessity of constraining row and column totals to account for species clustering in larger habitats, because using a completely random model to test for patterns would simply show species aggregation in larger habitats (Connor and Simberloff 1983). The inability of the Connor and Simberloff method to detect the basic checkerboard patterns (Diamond and Gilpin 1982) results from a checkerboard including only a subset of sites, and Connor and Simberloff's method evaluates the entire dataset simultaneously (Connor and Simberloff 1983). Finally, using guilds instead of species requires data on resource use of every species, making it very difficult to correctly define the guilds (Connor and Simberloff 1983), especially given that guild boundaries rarely follow taxonomic boundaries (Root

1967). Connor and Simberloff (1983) also critiqued the null model method proposed by Gilpin and Diamond (1982). They showed the probabilities to actually be expected frequencies, and that a normal distribution is assumed but untested, even though the distribution chosen can have a large impact on the significance test results. Connor and Simberloff (1983) concluded that null models can vary and it is important to be explicit about what facet of the community structure is being tested for, and that the ideal null model must account for species aggregation due to habitat size by restricting row and column totals.

From here, the discussion turned towards the usefulness of null models in community ecology (Gilpin and Diamond 1984). Gilpin and Diamond (1984) suggested that null models are actually not a useful tool for community ecologists, as the null models presented to that point (e.g., Connor and Simberloff 1979, Gilpin and Diamond 1982) had hidden structure making them, by definition, not null at all. Additionally, Gilpin and Diamond (1984) concluded that a proper null model is impossible to construct, and further attempts to do so would only lead to more confusion. Colwell and Winkler (1984) also conceded that constructing an appropriate null model is extremely difficult; at the same time, they acknowledged the impossibilities of conducting the necessary experiments to determine if community assembly is non-random. They concluded that null models are required given that the necessary experiments cannot be undertaken, but the assumptions embedded in the chosen null model need to be carefully considered to prevent misinterpretation of the results. Finally, Connor and Simberloff (1986) emphasized the usefulness of null models constrained by the appropriate assumptions in

community ecology to compare non-experimental community data with theories of community assembly.

Comparing Null Models

Given the emphasis on defining appropriate null models, Lawlor (1980) and Gotelli (2000) developed several different algorithms for rearranging the original community data and compared the results obtained. Lawlor (1980) compared four randomization algorithms (RA) to create four unique null models. All of the models maintained the same number of communities and sites as the original data, but varied in the degree of constraints, with RA1 being the least constrained and RA4 being the most constrained.

The algorithms altered the original data as follows:

RA1: All values, including zeros, replaced with values ranging from 0 to 1 drawn from uniform random numbers.

RA2: Only non-zero values replaced with uniformly distributed random numbers ranging from 0 to 1. This maintains species specialization.

RA3: For each species independently, all values including zeros were randomly shuffled and reassigned. This maintains niche breadth and species specialization.

RA4: For each species independently, only non-zero values were randomly shuffled and reassigned. This maintains niche breadth, and species specialization including unused sites.

The four RAs were then tested with actual data of 10 lizard communities and the stability (minimum eigenvalue of the community matrix) compared between RAs and the original

data (Lawlor 1980). RA1 was found to produce consistently unstable results, while RA2, RA3 and RA4 produced approximately the same number of stable results and consistent significance results (Lawlor 1980). RA3 was later shown to be superior to RA4 for detecting patterns of community structure and RA3 was recommended as the most suitable algorithm for creating null models (Winemiller and Pianka 1990).

Gotelli (2000) compared Type I and II error rates for nine null model randomization algorithms (SIMs), using four indices, on two types of data. To create the algorithms, the rows (species) and columns (sites) are either randomly varied, have the probabilities of species placement proportional to column totals, or fixed. These constraints allow for the creation of nine unique models with SIM1 being the most randomized and SIM9 most closely resembling the actual dataset (Table A.1). Many of these algorithms have been previously presented in the null model literature. For example, SIM2 is equivalent to RA3 (Lawlor 1980), SIM8 is similar to the Gilpin and Diamond (1982) model, and SIM9 was proposed by Connor and Simberloff (1979).

To compare the actual community data and the null models, four indices were also identified:

Checker: Count the number of perfect checkerboard distributions in the data. A non-random community will have a higher checker score than the model. Based on Diamond's (1975) analysis.

C-score: Checkerboard-score is the mean number of checkerboard units per species-pair for each community. A non-random community will have a higher C-score than the model (Stone and Roberts 1990).

V-ratio: Variance ratio is the ratio of the variance in total species number in samples to the sum of the variances of individual species. A non-random community will have a lower V-ratio than the model (Schluter 1984).

Combo: Counts the number of unique species combinations. A non-random community will have a lower number of unique combinations than the model (Pielou and Pielou 1968).

Finally, two types of datasets commonly collected in community ecology were also identified to explore if the results of the null model approach varies for the different types of data. The two data types were:

Island lists: Contain nearly complete species lists from well-defined habitats, such as islands. Degenerative matrices are not present.

Sample lists: Collected from standardized samples (e.g., quadrats, sweep nets, transects) of a relatively homogeneous habitat. These lists are usually incomplete, particularly lacking rare and under sampled species. Sample lists can form degenerative matrices, as some samples may have no species.

Gotelli (2000) began by looking at the Type I and II error rates for each model/index combination for both island lists and sample lists. Type I errors occur when the model/index combination identifies a pattern in a random matrix, concluding the community is non-randomly distributed. To test for this, four different random matrices were created and each model/index combination was run 1000 times for each randomized matrix. The number of times the null hypothesis was rejected, and the index value for each run, was recorded and averaged across the four random matrices. Five series of ten

matrices with an increasing amount of 'noise' obscuring a known pattern were run 1000 times for each model/index combination to test for Type II error rates. Type II errors occur when a model/index combination incorrectly accepts the null hypothesis of the community being randomly distributed. It was found SIM2 and SIM9, and the index Combo had the lowest Type I error rates, while SIM3 and SIM5 and index Checker had the highest Type I errors. For Type II error rates were lowest for SIM2, SIM4 and SIM9 and the C-score index while the other SIMs and Combo and Checker suffered from high Type II error rates.

Gotelli (2000) concluded that SIM9 is the most appropriate algorithm for Island lists to address species clustering on larger islands. SIM2 is preferable for Sample lists because sites are of similar size and quality (which occurs when using quadrat, sweep net, transect, etc. to sample). For sample lists, it is better to randomize the sites (columns), while holding the species occurrences (row totals) constant. For both Island and Sample lists, the C-score index is recommended as it functions better than the other indices when a true pattern is slightly obscured by 'noise' that is likely to be present in community datasets.

Null Models and Community Phylogenetics

Null models are commonly used to examine if the species within a given community (or, ideally, a set of communities) are more or less related than expected to have developed due to random community assembly. Investigations into phylogenetic community composition typically start with the premise that species that are more closely related (congeners) share more of the same traits and, therefore, use more of the same resources.

If these similarities lead to an overlap in the use of limited resources (Lord et al. 1995) and interspecific competition results in one congener being excluded from the site, communities may then be composed of species that are phylogenetically less related than expected by chance (i.e., over dispersed communities; e.g., Cavender-Bares et al. 2004a). Conversely, shared traits may allow (certain sets of) species to access abundant resources that other species are not able to utilize due to some extreme adaptation possessed by those related species. This may result in communities that are more related than expected (i.e., clustered communities; e.g., Weiblen et al. 2006) if species distributions were randomly determined. The conservatism of many species traits during the evolution of a lineage leads to a positive correlation between relatedness and ecological similarities. Therefore, by considering species in their evolutionary context instead of as equivalent and independent units, further insight on the underlying ecological processes organizing the community is gained (Harvey 1996, Webb 2000).

By combining null models and knowledge of phylogenetic relatedness, Webb (2000) and Webb et al. (2002) developed two indices to evaluate the relatedness of a community:

NRI (Net Related Index): a standardized measure of mean pairwise distance (MPD) of the species in a given sample, relative to an appropriate null model. Positive values indicate the community is more related than expected, while negative values indicate the community is less related than expected.

NTI (Nearest Taxon Index): a standardized measure of mean nearest neighbor distance (MNND) of each species in the sample, and quantifies the extent of

clustering compared to an appropriate null model. As with NRI values, positive values indicate the community is more related than expected, while negative values indicate the community is less related than expected

These two indices are often paired with a metric developed by Faith (1992):

PD (Phylogenetic Diversity): is a calculation of the total branch length of a phylogeny represented by the given community. This metric provides a measure to quantify and compare how closely related the species found the communities are. A low PD value indicates the species present are all very closely related, whereas a large PD value indicates the community contains many more distantly related species.

These measures have been used to examine the relatedness of a variety of community types (e.g., Neotropical forest communities, Kembel and Hubbell 2006, dytiscid beetle communities, Vamosi and Vamosi 2007), but have also been applied to other questions, such as determining the phylogenetic patterns of host plant use in tropical insects (Weiblen et al. 2006), and even to examine the relatedness of free-living bacterial communities (Horner-Devine and Bohannan 2006).

In addition to using these measures to answer questions regarding the phylogeny of a community, they can also be applied to functional trait community data (e.g., Petchey and Gaston 2002, Kraft et al. 2008). Functional traits are phenotypic characteristics of species that differentiate them from other species (reviewed by Petchey and Gaston 2006). These include traits like leaf or body size, presences of spots or stripes, locomotive abilities (or lack thereof). Most phylogenies are created from molecular data examining genetic

similarities among species. But genetic similarities or differences do not always correspond exactly with phenotypic differences that may influence the way species interact with each other in a community (e.g., Diaz and Cabido 2001, Ackerly 2003, Petchey 2004). In the same way molecular data is used to create phylogenies, functional traits can be used to create dendograms with species sharing more traits being placed closer together (Petchey and Gaston 2002). These ‘functional dendograms’ are then analyzed using the same measures as phylogenies. NRI is used to assess if the species in a community share more (or fewer) traits than expected, while NTI and PD indicate whether the species in the community are more or less functionally related than expected.

The primary difficulty with using functional traits revolves around the lack of enough information on the specific traits processed by all species in the community. To create a functional dendogram for a given community, information on the trait state of every single species in the community for numerous traits is required. Missing information or a limited number of traits severely reduces the usefulness of analyzing the functional trait data (Lavorel et al. 1997, Podani and Schmera 2006). When a functional dendogram can be created and analyzed for a community, valuable insights into which specific traits and possible environmental factors are driving community assembly can be uncovered (e.g., Ackerly and Reich 1999, Ackerly 2003, Cavender-Bares et al. 2004b, Kraft et al. 2008).

Implementing Null Model Analyses

There are many free programs available to ecologists to help them use null models to analyze community data. One of the most commonly used programs is EcoSim (Gotelli and Entsminger 1999). EcoSim creates null models and compares them to the original

community data. Null models can be created and compared to the original data using any of the nine SIMs and four metrics presented in Gotelli (2000).

EcoSim can be used to address several types of questions including: (1) determining if there is a significant difference in species richness (number of species) or evenness (distribution of individuals among species) in two different habitat types and (2) if there is evidence of temporal segregation of co-occurring species. To answer the first type of question, a matrix of species abundances with the species listed in the first column and the habitat types listed in the first row is analyzed with the Species Diversity module. The vast majority of community surveys are incomplete as it is not possible to know if all species present in the community have been sampled and community boundaries are often difficult to define (Gotelli and Entsminger 1999). Null models are required to provide a baseline comparison to determine if differences in species richness and evenness are due to biological differences between sites or if more sampling would eliminate these differences. The analysis produces null models using a random sampling of species from the habitat type where more individuals were collected to make simulations with the same number of individuals as the other habitat type, but randomly distributed among all species found in the habitat type with the most individuals. The average species diversity and evenness of the simulated communities can then be compared to the diversity and evenness of the habitat type with fewer individuals. Various metrics can be used to statistically assess if the species richness of the simulated and observed habitat types are actually different, when sampling differences are accounted for. For the second question type, one utilizes presence/absence data (EcoSim can automatically convert abundance data to presence/absence if required) with the

species of interest listed in the first column, and the time steps listed as the first row. The Co-occurrence module is used to create an appropriate null model and statistically compare the observed and null model to determine if the data as a whole contains more or less co-occurring species than expected. Additionally, each species pair is independently assessed to allow for identification of specific species pairs that may be temporarily segregated.

To answer phylogenetic questions, such as if different community types show different or non-random patterns in the phylogenetic community structure, community ecologists often use the program Phylocom (Webb et al. 2008). Phylocom is used to calculate the NTI, NRI and PD of phylogenies created for actual and null model communities, allowing for comparisons between the two community types. To begin an analysis in Phylocom, a phylogeny of the sampled species is entered. The phylogeny can be created manually in Phylocom, or by using programs such as Mesquite (Maddison and Maddison 2009). Species data is input with one row per taxon and three columns, usually Sample ID, Species Abundance and Species Name. Once the data are input, an appropriate null model algorithm is selected, and PD, NRI and NTI are calculated. Functional trait dendograms can be analyzed the same way to allow for comparison of phylogenetic and functional trait results. The resulting PD, NRI and NTI values for different habitat types can be compared to show if there are any phylogenetic or functional trait differences that may be linked to biological differences of the habitat types.

Interpretation of Null Model Results

One of the shortcomings of null models compared to rigorous experiments is that even when a community is found to have a non-random distribution, the driving factor or combination of factors causing the non-random assembly cannot be determined.

Although some studies equate detected patterns to competition (either inter- or intra-specific; e.g., Elton 1946, Sale 1974, Wright and Biehl 1982), others emphasize the impossibility of knowing which specific factor or combination of factors has caused the non-random patterns from null model analysis alone (e.g., Schluter 1984, Connor and Simberloff 1986, Morin 1999).

Colwell and Futuyma (1971) suggested the only way to determine if competition is causing the non-random patterns would be to conduct an experiment removing competitors from the community, or exploiting natural situations where a competitor is absent or by artificially increasing resources and comparing the patterns of resource use by the competing species in each situation. Unfortunately, this type of experiment is rarely feasible, particularly with enough replicates to find statistically sound results (Colwell and Futuyma 1971). Based on knowledge of species interactions, the common factors identified as possible drivers of community assembly include: competition (both inter- and intra-specific), dispersal abilities, resource use, overexploitation strategies, predator densities, and chance (e.g., Diamond 1975, Schluter 1984, Connor and Simberloff 1986, Morin 1999).

Additionally, Connor and Simberloff (1986) also emphasized that accepting the null hypothesis (accepting the community to be randomly assembled) does not indicate there is nothing structuring the data. Instead, accepting the null hypothesis may indicate a lack

of a pattern in the data available, while more data may lead to rejection of the null hypothesis (Connor and Simberloff 1986). Furthermore, the lack of detectable patterns may indicate that several factors are working in combination, with both positive and negative species interactions occurring, preventing the formation of a clear pattern (Schluter 1984). While these interpretations may appear to discount null models as useful tools in ecology, because both rejecting and accepting the null model can indicate species interactions are affecting community assembly (Gilpin and Diamond 1984), null models do provide valuable information and when insufficient biological knowledge about a given community is known. Null models can be used to differentiate between competing theories (Schluter 1984), or test observed data with theory, or indicate that a few or one unknown factor is driving community distribution in a very specific direction (Connor and Simberloff 1986).

Null Models and Experimental Approaches

It was once thought that it was not feasible to conduct an experiment showing that competition is causing the non-random patterns in community assembly (Colwell and Futuyma 1971). As the debate regarding the usefulness and interpretation of null models continued through the 1980's, the popularity of field experiments examining competition and community assembly began rapidly increasing (reviewed by Schoener 1983). The vast majority of the competition experiments conducted have found evidence of interspecific competition influencing community composition (Schoener 1983, Gurevitch et al. 1992).

By the time null models became more widely accepted experimental approaches to competition questions had become commonplace. This created two groups of community ecologists: those that use null model approaches, and those that use experimental approaches. Experimental ecologists do not agree with the black and white view (competition or no competition) inherent in null model approaches (Brown 1997). Null model ecologists, on the other hand, take issue with the large number of uncontrolled variables and “noise” integrated into experimental designs (Kareiva 1997). I could find no example of a study using both approaches to examine competition in a single system. Comparing the results of null model approaches and experimental approaches on the same system may shed further light on the biases, assumptions and strengths of each approach. In conclusion, null models are one of the tools available to examine ecological communities, and the results of the null model tests provide further information on the underlying structure, or lack thereof, for the observed communities especially when the required experiments are not possible.

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Table A.1: Randomization algorithms identified and compared by Gotelli (2000).

| Row Totals | Column Totals | | |
|--------------------------|----------------------|--------------------------|--------------|
| | Randomly Vary | Probability Based | Fixed |
| Randomly Vary | SIM1 | SIM6 | SIM3 |
| Probability Based | SIM7 | SIM8 | SIM5 |
| Fixed | SIM2 | SIM4 | SIM9 |