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Plant And Arthropod Associations With Environmental Gradients In A Northern Tallgrass Prairie

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PLANT AND ARTHROPOD ASSOCIATIONS WITH ENVIRONMENTAL GRADIENTS IN A NORTHERN TALLGRASS PRAIRIE

by

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This thesis, submitted by Bryon W. Deal in partial fulfillment of the requirements for the Degree of Master of Science from the University of North Dakota, has been read by the Faculty Advisory Committee under whom the work has been done and is hereby approved.

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Bryon W. Deal
August 05, 2016

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ABSTRACT

Plants and arthropods are the base of grassland communities, and their interactions with environmental gradients and each other can determine their composition and spatial structure within a site. The composition and spatial structure of these communities can determine how they contribute to grassland function, yet grassland conservation and restoration efforts typically do not consider both plants and arthropods. As a result, our understanding of how plant and arthropod communities assemble in response to environmental gradients, and each other, in the same space is incomplete. Furthermore, most studies of grassland community assembly do not address assembly across multiple taxonomic levels, and those that do tend to focus on limited groups of taxa. My research expands on this by investigating the response of plants to environmental gradients, and the response of three arthropod functional communities to plant and environmental gradients across a northern tallgrass prairie. Soil abiotic variables and elevation were sampled at 229 plots systematically distributed across UND's Oakville Prairie in 2014 and 2015. Plant species were surveyed at the same plots in late summer of both years and used to describe plant species composition, native and non-native species composition, non-native species cover, functional group composition, and plant community architecture across the site. Arthropods were sampled in mid- and late summer of both years at three locations in the plant community (litter; mid-story; canopy) in a subset of plots (n = 37). Three environmental gradients (elevation, soil moisture, and soil salinity)

most strongly affected plant community composition in both years. The range of zonation across plant community composition metrics was most similar in response to elevation and most variable in response to soil moisture. Plant community architecture, which strongly affects site use by grassland birds, was not directly associated with site environmental gradients. Results show that plant community zonation patterns can vary depending on the ways in which the plant community is described. Litter arthropods responded to salinity in year one and canopy arthropods responded to salinity in year two. Mid-story arthropods responded to plant gradients in both years, and the salinity gradient in year two. Mid-story arthropods were poorly structured along plant cover gradients that responded to environmental variables, but were well-structured along plant architectural gradients that did not respond to environmental variables. Arthropod functional communities were structured over a wider range of salinity than plant communities. These results show that plants and arthropods can co-vary along strong environmental gradients. These results improve our understanding of how grassland plant and arthropod zonation patterns form in the same space, which can help to inform a more holistic approach to grassland restoration.

CHAPTER I

INTRODUCTION

One of the foundational goals of community ecology is to describe how species interact with each other and their environment to assemble into communities along gradients and maintain community structure over time. Assembly in diverse communities and the patterns that emerge can be driven by complex, not easily discernable species interactions with multiple environmental gradients (Snow & Vince 1984; Vince & Snow 1984). Community assembly occurs with the introduction of species to a given area, and is responsible for the maintenance of established communities (Fukami 2010). Assembly within a community is defined by the spatial patterns of species coexistence that emerge within a given area (Dallas & Drake 2014).

Clements (1916) proposed the first formal hypothesis of community assembly, the organismal hypothesis, which is defined by distinct, multi-species zones of association along environmental gradients. Gleason (1926) introduced an alternate hypothesis, the individualistic hypothesis, which predicts that species distributions along environmental gradients occur more independently of one another to form random species associations. In contrast to the organismal hypothesis which predicts that community assembly is driven by species interactions with the abiotic environment, the individualistic hypothesis predicts that community assembly is driven by species abilities to disperse to new areas and compete for limited resources (Weiher et al. 2011).

The debate about the influence of abiotic filters and biotic interactions on community assembly is still relevant to community ecology. Modern hypotheses of community assembly predict a combination of abiotic and biotic species interactions drive community assembly in a given area. Deterministic community assembly hypotheses predict that community assembly occurs in response to environmental conditions and biotic interactions, such that locations that share a species pool and similar environmental conditions will support similar species composition over time (Fukami 2010). Historically contingent community assembly hypotheses predict that community assembly is largely determined by stochastic events (e.g., disturbance events; species dispersals), such that habitat patches with similar environmental conditions can support different species composition depending on the availability of resources and the order of arrival of colonizers (Fukami 2010). These two hypotheses predict that community assembly is driven by fundamentally different processes. Deterministic community assembly is driven by niche-based processes, while historically contingent community assembly is driven by neutral processes and environmental stochasticity.

Niche-based assembly and neutral theory, have been at the forefront of debate about the underlying processes that drive community assembly. Niche-based community assembly processes are rooted in organismal ideas, predicting that assembly is driven by abiotic filters that act as a selecting force on the ability of species from a regional species pool to establish within a community (Weiher et al. 2011). If this is the case, we should see local species composition vary as conditions change along environmental gradients. Neutral theory is based on the assumption that species with similar trophic strategies

(e.g., primary producers) are ecologically equivalent (Hubbell 2001). So, the ability of species to disperse to new sites and stochasticity drive assembly under neutral theory (Chase & Myers 2011). If this is the case, we would expect to see random distribution of species composition along environmental gradients where dispersal is not a limiting factor.

Realistically, both niche-based and neutral processes are likely to influence community assembly. Species need to be able to access available resources in order to establish in a novel environment (Tilman 2004). However, species need to be able to withstand the abiotic conditions present in a site in order to establish (Fattorini & Halle 2004). Once established, species traits can limit potential distribution along environmental gradients (Keddy 1992), which can directly impact the spatial structure of a community through recruitment and exclusion (Seabloom & van der Valk 2003a). The alternative stable states hypothesis (hereafter ASS) incorporates both niche-based and stochastic processes into models of community assembly. ASS predicts that communities are restricted by niche based processes as predicted by the organismal hypothesis, but that there is an element of stochasticity that arises from environmental stochasticity and random species dispersals (Temperton & Hobbs 2004). So, if community assembly is consistent with ASS species composition at environmentally similar habitat patches can vary, but only species that are able to withstand local environmental conditions will be able to establish.

These hypotheses of community assembly have been developed for plant communities without consideration of the associated animal communities. Plant and

arthropod communities are highly interdependent, but our knowledge about how these communities assemble in response to environmental gradients in the same space is incomplete. Research into grassland community assembly typically focuses on more limited taxonomic groupings, such as just plants or a single arthropod functional community. However, this narrow focus is not able to wholly capture community level processes (Drake 1991). My research broadens typical focus to be more inclusive of the plant and arthropod communities that form the base of grassland ecosystems. The results of my study improve our understanding of how grassland plant and arthropod communities assemble in the same space in response to gradients of soil environmental variables and interactions with each other.

My study was conducted at Oakville Prairie Complex (hereafter Oakville), an approximately 453 ha remnant tallgrass prairie. Oakville is located in a largely contiguous 16 × 48 km grassland corridor in Central Grand Forks County, ND. Grasslands in this corridor are typically managed for cattle production (grazing or haying) or enrolled in state or federal conservation programs. Poorly drained soils and a shallow aquifer that results in highly saline soils characterize soil conditions throughout the area (Laird 1944; Sandoval et al. 1964). The accumulation of chloride salts makes salinity in Central Grand Forks County unique among saline soils in the northern Great Plains (Seelig 2000). Previous research at Oakville has shown that salinity transitions from non-saline soils in the upland areas to severely saline soils in the low, wet areas (Redmann 1972). This provides a unique gradient in addition to typical grassland environmental gradients, such as pH, soil moisture, soil texture, and elevation, to

investigate how grassland plant and arthropod communities assemble and over what environmental scales does assembly occur.

My study assesses how community assembly occurs across multiple taxonomic groups (plants and arthropods) in response to grassland environmental gradients. Chapter II assesses the response of plant species and functional group composition and plant community architecture to environmental gradients, and what these responses indicate about plant community assembly. Chapter III assesses the response of arthropod composition across three functional communities (litter; mid-story; canopy) to plant and environmental gradients, and what these responses indicate about community assembly. My study asks the questions: 1) what environmental gradients are influencing plant species and functional group composition and plant community architecture; 2) what environmental scales are these gradients acting on plant species and functional group composition and plant community architecture; 3) what plant and environmental gradients are influencing arthropod functional composition across three functional communities (litter; mid-story; canopy); and 4) what environmental scales are these plant and environmental gradients acting on arthropod functional community composition. The results of my study will show how grassland community assembly can occur across multiple taxonomic levels.

CHAPTER II

PLANT ASSOCIATIONS WITH ENVIRONMENTAL GRADIENTS IN A NORTHERN TALLGRASS PRAIRIE

Abstract

Interactions with soil environmental gradients strongly influence how grassland plant communities assemble and how they are structured within a site. The composition and spatial structure of plant communities within a site contribute to ecosystem function and determine the ecosystem services that are provided to associated animal communities. In diverse ecosystems, such as grasslands, plant species and functional group composition metrics and plant community architecture can respond individually or as a whole to a complex suite of environmental gradients. These responses can determine the spatial structure of a plant community across a site. To determine how plant community composition and architecture respond to environmental gradients, and what this indicates about plant community assembly and over what environmental scales it occurs, I sampled soil environmental variables and plant species composition and plant community architecture at 229 plots distributed across a 453 ha northern tallgrass prairie. From plant species composition I calculated native and non-native species composition, non-native species cover and functional group composition. Plant species and functional group composition consistently responded to three environmental gradients (elevation, soil

moisture, and soil salinity). Plant community architecture describes the physical structure of the plant community at Oakville. Plant community architecture did not respond to any environmental gradients, but did form strong correlations with plant compositional metrics. This shows that plant community architecture is not responding to environmental gradients, but may be influenced by the biological structure of the Oakville plant community. Plant species and functional group composition responded similarly to gradients of elevation, soil moisture, and soil salinity. However, zonation patterns of functional group composition were generally broader along each of these gradients. This shows that interactions with multiple strong environmental gradients can separately influence compositional patterns in grassland plant communities.

Introduction

Ecologists have long been interested in the effects of environmental gradients on plant community composition and assembly (e.g., Cowles 1899; Clements 1916; Gleason 1926; Curtis & McIntosh 1951; Whittaker 1953; Whittaker 1960; Tilman 1986; Lookingbill & Urban 2005). Early debate about assembly polarized around whether plants assemble into communities in unison forming distinct community types in response to abiotic environmental gradients, or whether species assort individually along gradients driven by competition to form communities (Clements 1916; Gleason 1926). Realistically, species assembly into communities can occur both in unison and individually within the same space (Lortie et al. 2004). Regardless of how assembly occurs species must be able to withstand abiotic environmental conditions to establish

and spread through a site (Keddy 1992; Fattorini & Halle 2004; Andersen et al. 2015). My study investigates how environmental gradients influence plant community composition and zonation patterns in a northern tallgrass prairie, and what these patterns indicate about how plant community assembly occurs in the site.

Plant species composition can be strongly influenced by changing environmental conditions within an ecosystem (Whittaker 1956; Nelson & Anderson 1983; Klimek et al. 2007; Zelnik & Carni 2008; McGlinn & Palmer 2011). Changing environmental conditions within an ecosystem can also influence the architectural complexity of plant species (Reinhardt & Kuhlemeier 2002; Silveira & Oliveira 2013). If plant species are responding to the same environmental gradients this will likely influence plant architecture at the community level. In some communities, species composition, patterns of zonation, and changes in plant architectural complexity can be driven by simple interactions with a single environmental gradient, such as wetland plant community response to water depth (Seabloom & van der Valk 2003a). However, in more complex systems species interactions with multiple environmental gradients can strongly affect patterns of species composition within plant communities (Vince & Snow 1984; Snow & Vince 1984).

Species traits determine their ability to withstand changes in conditions along environmental gradients (Savage & Cavender-Bares 2012). Within the past 15 years, research into how plant functional traits and composition respond to environmental gradients (Ackerly & Cornwell 2007; Edwards & Still 2008; Yan & de Beurs 2016) has improved our understanding of how species tolerance to environmental conditions

influence community assembly. For example, Willis et al. (2010) showed that environmental filtering of species based on functional traits occurred differently between the landscape and local scales in a Minnesota oak savanna, a community type that is closely associated with the North American tallgrass prairie. Edwards and Still (2008) found a difference in the distribution of C_3 and C_4 grasses along a precipitation gradient in Hawaii, which they attributed to the increased water use efficiency of the C_4 photosynthetic strategy allowing these species to thrive in drier habitats.

The environmental associations and zonation patterns of non-native species are particularly interesting because they may not respond to the same environmental gradients or assemble over the same scales as native species. Dispersal limits the introduction of non-native species to novel communities. Non-native species are often either intentionally (e.g., *Melilotus sp.*), or inadvertently (e.g., *Euphorbia esula*) introduced into plant communities. Following introduction, there are several impediments to the establishment and spread of non-native species (Theoharides & Dukes 2007). Non-native species need to be able to access resources in order to establish (Tilman 2004), and resources are usually most available following disturbance. In communities that are adapted to frequent disturbances for maintenance of structure and composition, such as grassland communities, suppressing natural disturbance, such as fire, can allow established non-native species to expand their distribution (Lenz et al. 2003; Flory & Clay 2010). Species introductions follow selection for specific traits which likely makes non-native species pools less tolerant of environmental extremes than native species

pools, which may limit the ability of non-native species to distribute along environmental gradients.

Many studies of grassland community response to environmental gradients focus on common gradients such as moisture, pH and soil texture. However, there is increasing concern about how salinity affects grassland plant communities (Bui 2013). Salinity, when present, can strongly influence the composition of grassland communities (Piernik et al. 1996; Zalatnai & Kormoczi 2004; Aschenbach & Kindscher 2006; Valko et al. 2014). Most studies of grassland salinity gradients occur in secondarily salinized sites. Salinity places physiological stress on plant species and this may cause salinity to more strongly affect plant community assembly than elevation and soil moisture. Understanding the effects of salinity on community assembly in semi-natural systems can improve our understanding of plant community response in secondarily salinized grasslands.

The grassland corridor in Central Grand Forks County, ND provides a unique opportunity to study how plant community structure and composition responds to environmental gradients. It is situated in the northern portions of the North American Tallgrass Prairie. In addition to moisture gradients, this grassland corridor experiences natural salinity levels that are greater than the surrounding areas in the Red River Valley, as a result of poorly drained soils and upwelling from the shallow aquifer (Laird 1944; Sandoval et al. 1964). Many of the plants that comprise the native flora of this area of North Dakota are halophytic species (e.g., *Distichlis spicata*), or species that are able to tolerate a wide range of soil salinity (e.g., *Hordeum jubatum*; Seelig 2000). Additionally,

management is infrequently and sporadically implemented in this area. The absence of regular disturbance may allow non-native species to increase their distribution into areas with tolerable environmental conditions. This may provide insight into the limits that stressful environmental conditions, such as high soil salinity, can place on non-native species distributions within tallgrass prairie habitats.

My study investigated the response of plant community composition and architecture to environmental gradients in a remnant tallgrass prairie in this area of North Dakota and how response to these gradients influences community assembly. I ask the questions: 1) what environmental gradients do plant community composition and plant community architecture respond to; 2) how do these responses shape plant community structure at Oakville; 3) is the plant community responding consistently across all levels of composition and architecture. Knowing how plant community assembly occurs in grasslands with strong environmental gradients can help to inform restoration as human activity increases the amount of grassland area subject to strong environmental gradients globally.

Methods

Study Site

The Oakville Prairie Complex (hereafter Oakville) is an approximately 453 ha remnant tallgrass prairie (centroid latitude 47.893, longitude -97.315) in the Central Grand Forks County grassland corridor comprised of the University of North Dakota's Oakville Prairie Field Station and North Dakota Game and Fish's Oakville/Crawford Wildlife

Management Area. The site has a slight elevation gradient (mean slope between adjacent plots = $0.46^{o} \pm 0.05^{o}$) and topographic relief is provided by the Blanchard beach ridges remaining from Glacial Lake Aggasiz (Laird 1944). Soils of the lowland areas are of the Ojata series, which are characterized by high salinity. Soils of the upland areas are primarily of the Antler series, and have moderate to low salinity (Redmann 1972; Whitman & Wali 1975; Soil Survey Staff NRCS). Soil salinity results from localized upwelling of saline ground water (Laird 1944; Whitman & Wali 1975). Prior to the initiation of my study, the most recent prescribed fire occurred in the southern portion of the site in the mid-1990s (Robert Seabloom, unpublished). Following year one of my study prescribed burns were performed in one area in the north (~62.9 ha) and one area in the south (~81.8 ha). Non-native species were sporadically managed with herbicide spraying until the early 2000s (Robert Sheppard, personal communication, 31 December 2015).

Sampling Scheme

Permanent 10 × 10 m sample plots were established in a systematic grid (100 m spacing, n = 229 plots) across eight management units at Oakville (ArcGIS 10.1; ESRI; Redlands, CA; **Figure 1**). Sample plots were positioned ≥ 150 m from management unit borders (to minimize edge effects) and marked with a metal stake at their centroid. Relative plot elevation (m above ellipsoid; hereafter elevation) was measured at each plot's centroid with a Trimble GeoExplorer 2008 (Trimble Navigation Limited; Westminster, CO) held at waist height.

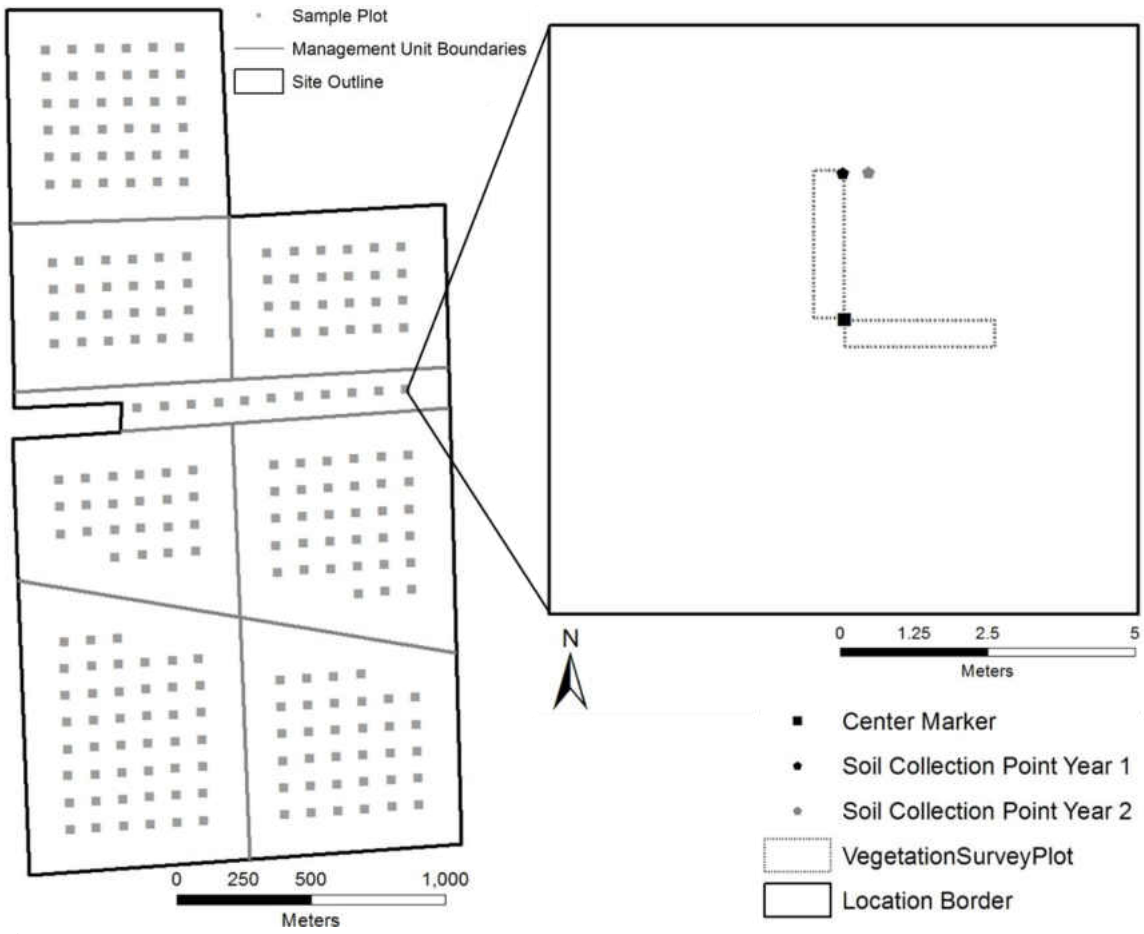

Figure 1. Oakville and plant community sampling locations. Inset map depicts plant sample plot design.

Soil Sampling

In 2014 and 2015 soil moisture (% Volumetric Wet Content to 20 cm; %VWC) was measured at each plot's centroid (Spectrum Field Scout TDR soil moisture probe; Spectrum Technologies, Inc.; Aurora, IL) twice per month following subsidence of standing water (early July 2014, mid-April 2015). Volumetric water content measures the ratio of the volume of water in a given volume of soil to the total soil volume, so that at saturation %VWC will be equal to the percent of soil pore space in a given volume of soil. Soil temperature (Specmeters; Spectrum Technologies, Inc.; Aurora, IL; ^{o}C; to 20

cm depth) was measured twice per month from mid-April to mid-August 2015. Soil cores (1 cm diameter × approximately 20 cm depth) were collected once from mid-July to mid-August 2 m north of the center point of each plot (0.5 m spacing between years; **Figure 1**). Soil cores were assessed for soil texture by soil particle size analysis, following the modified pipette method of Gavlak et al. (2005), and were measured for pH (Oakton acorn pH 5+ meter; Oakton Instruments; Vernon Hills, IL) and salinity (electrical conductivity; EC; $\mu S \cdot cm^{-1}$; Oakton Acorn Conductivity 6+ meter; Oakton Instruments; Vernon Hills, IL).

Vegetation Sampling

Two 0.5 × 2 m quadrats (one in a N-S orientation, one in an E-W orientation; **Figure 1**) were surveyed for plant species composition within each of the 10 × 10 m plots over a two-week period in late July 2014 and 2015. Species were recorded in each quadrat and the aerial percent cover (p_i) of each species was estimated to the nearest 5 percent. Each species was individually assessed and species canopies could overlap, so total coverage could exceed 100% for a quadrat. Rare species (e.g., < 5% coverage) were assigned a value of 1 percent (modified from Seabloom & van der Valk 2003b). Aerial coverage values per species were summed to calculate functional group (cool season (C_3) grass; warm season (C_4) grass; non-grass graminoid; legume; non-leguminous forb; and woody) and native and non-native cover. Additionally, percentage bare ground was recorded in 2015. Coverage values and total species (S) and functional group richness values were averaged across quadrats to generate a plot value for each year.

Plant community architecture was measured as vegetation height density (cm), vegetation live height (cm), vegetation dead height (cm), and in 2015 photosynthetically active radiation (PAR; $\mu mol \cdot m^{-1} \cdot s^{-1}$) and percent bare ground. Vegetation height density (cm) was estimated with a Robel pole with methods adapted from Robel et al. (1970), Vermeire and Gillen (2001) and Vermeire et al. (2002). A Robel pole was placed with its bottom edge flush with soil level at plot centroid. An observer at 4 m distance from plot centroid, with eye line at 1 m height from soil level, measured the lowest band on the Robel pole that was not completely obscured by vegetation. Measurements were taken in each of the four cardinal directions, and these values were averaged to provide a plot value. A meter stick was placed perpendicular to the soil surface to measure vegetation live height (position of the tallest stem in cm) and vegetation dead height (position of tallest dead vegetation $\leq 45^{o}$ angle with the ground surface in cm). Live height and dead height were measured at 2.5 m from plot centroid in each of the four ordinal directions. These measures were averaged to generate a single live height and a single dead height value for each plot.

In year two above and below canopy PAR was measured monthly from early June through early August (Accupar LP-80 ceptometer; Decagon Devices; Pullman, WA). Measurements were taken between 1100 and 1600 CST. Two readings were taken at each plot's centroid with the sensor bar in offset orientations (N-S and E-W). Above and below canopy values were used to calculate plot average percent intercepted PAR.

Data Analysis

Distance matrices were constructed in R 3.2.0 using the *ecodist* package function *distance*() for each plant and environmental variable using distance measures appropriate for the type of data in each matrix (R Core Team 2015; Goslee & Urban 2007; **Table 1**). Euclidean distance is based on Pythagoras' formula (Legendre & Legendre 2008) which makes it appropriate for data that tends to vary in a straight-line manner, such as environmental variables or spatial coordinates (Goslee & Urban 2007). Sorensen distance is calculated in city-block space, and is useful for proportional data, such as plant species relative abundance (McCune & Grace 2002). Sorensen distance can accurately measure the absolute difference between two samples in city-block space (Cha 2007). Distance matrices consisted of a single or suite of variables depending on the compositional metric of interest. For example, I used a composite functional group composition matrix

Table 1. Distance matrices included in Mantel tests between plant community and environmental variables. Matrices were created separately for year one and year two except for Soil Texture and Elevation, which did not change between years.

Matrix	Included Variables	Distance
Plant		
Species Composition	Percent cover per species	Sorensen
Native Composition	Percent native species cover	Sorensen
Non-Native Composition	Percent non-native species cover	Sorensen
Non-Native Cover	Sum non-native species cover	Sorensen
Functional Composition	Percent cover of C3 Grass, C4 Grass, Non-Grass Graminoid, Forb, Legume and Woody species	Sorensen
Architectural Structure	Height density (cm); live height (cm); dead height (cm); % exposed ground♦; % intercepted PAR ($\mu mol \cdot m^{-1} \cdot s^{-1}$)♦	Euclidean
Environmental		
pH	pH	Euclidean
Salinity	electrical conductivity ($\mu S \cdot cm^{-1}$)	Euclidean
Soil Texture	% sand, clay, silt	Euclidean
Soil Moisture	Mean across season soil moisture (% VWC)	Euclidean
Elevation	Height above ellipsoid (m)	Euclidean

♦Exposed ground and PAR were not available in year one architectural Structure matrix.

(simultaneously assessing cover of all functional groups) and assessed cover of each functional group separately.

Following Seabloom & van der Valk (2003a), Mantel tests (10000 permutations) performed in R 3.2.0 using the *ecodist* package function *mantel*() were used to assess correlations between the plant and environmental distance matrices within each sample year (R Core Team 2015; Goslee & Urban 2007; **Table 1**). Positive correlation of plant matrices with environmental matrices indicates that sites with similar composition of environmental variables also have similar composition of plant variables (Seabloom & van der Valk 2003a; Goslee 2007). All Mantel tests were repeated as partial Mantel tests with the inclusion of a control matrix of plot centroid UTM coordinates to control for spatial autocorrelation, but doing so did not affect the results and this matrix was not retained in the final analyses.

Mantel correlograms (1000 permutations) were constructed in R 3.2.0 using the *ecodist* package function *mgram*() for plant matrices which met a minimum correlation criterion ($r_M \geq 0.2$ and $p \leq 0.01$) with environmental matrices (R Core Team 2015; Goslee & Urban 2007). The minimum correlation criterion was determined from Mantel test results that indicated a natural break in the correlations of plant matrices with environmental matrices. Mantel correlograms were used to determine over what distances in environmental explanatory matrices changes occurred within corresponding plant matrices. The number of bins in each correlogram was determined by Sturge's rule, which gives similar results to alternative methods for choosing bin number when sample sizes are moderate or low (~ 200 or fewer; Dogan & Dogan 2010). Bin ranges were

calculated from the range of values along each environmental gradient and the number of bins, providing even bin size across each correlogram.

Empirical Bayesian Kriging models (EBK) were constructed in ArcGIS 10.3 (ESRI; Redlands, CA) with power semivariograms (100 iterations) to generate prediction surfaces for all environmental gradients that met the minimum correlation criteria with at least one plant matrix. EBK estimates a semivariogram from known data points, simulating new values at known data points from this semivariogram, estimates a new semivariogram from these new values and then estimates the likelihood that the new semivariograms could be produced from the original data (Krivoruchko 2012). This is an iterative process that reduces the error from traditional kriging models built on a single semivariogram. However, since predicted values are influenced by known values at all neighboring data points the predicted values may not reach the extreme values from the range of values at known data points. The prediction surfaces created with EBK models show how the environmental variables that influence assembly in plant communities and patterns of plant species composition are distributed across Oakville to form gradients. To show sufficient detail in each prediction surface six classes were chosen. Bin size for each class was determined with Jenks natural breaks. Jenks natural breaks provide a way of breaking up continuous data into discrete classes in choropleth maps which minimize the sum of absolute deviation from class means by repeatedly transferring values from class boundaries to adjacent classes until the sum of absolute deviation from class means is minimized (Coulson 1987; Brewer & Pickle 2002).

Results

Environmental conditions varied between years and among management units. The number of monthly precipitation events and the mean accumulation (mm) per event differed between years (**Appendix A; Table A.1**). Across field season precipitation (1 May – 15 August) was 54.4 mm greater in year one than in year two (Wunderground.com 2016). Weather data were collected from the weather station at the Grand Forks Air Force Base which is approximately 7 km NW of Oakville. Soil salinity more strongly varied among management units in the second year than in the first year (**Table 2**; **Figure 2**). Soil moisture differences among management units were consistent between sample years (**Table 2**; **Figure 3**). Monthly mean daily temperature (^{o}C) and wind speed ($km \cdot h^{-1}$) were similar between years (**Appendix A; Table A.1**).

In year one, 72 native and 22 non-native species were encountered. In year two, 85 native and 14 non-native species were encountered. Typically, the most frequently encountered species were less abundant within plots (mean plot cover < 20%; **Table 3**).

Table 2. F-values from two-way ANOVAs (n = 229) of effects of management unit and sample year on Oakville soil salinity and soil moisture. ANOVA models were built on type III sums of squares due to unequal sample sizes among management units.

Model	df	F	p
Soil Salinity			
Unit	7	18.2534	<0.0001
Year	1	12.2208	0.0005
Unit × Year	7	5.6378	<0.0001
Residuals	442		
Soil Moisture			
Unit	7	12.8304	< 0.0001
Year	1	0.1486	0.7000
Unit × Year	7	0.4886	0.8429
Residuals	442		

Among the most frequently encountered species, two native grasses (*H. jubatum* and *Spartina pectinata*) and two non-native grasses (*Bromus inermis* and *Poa pratensis*) tended to be dominant species within plots (mean plot cover ≥ 45%; **Table 3**). There were notable changes in the frequency (≥ 10%) of three native grasses (*S. pectinata*; *Muhlenbergia asperifolia*; *Pascopyrum smithii*) and four non-native species (*B. inermis*; *Melilotus officinalis*, a legume; *P. pratensis*; *Lappula squarrosa*, a forb) between sample years. In addition, *P. smithii* and *P. pratensis* notably declined between years (> 10%), and *B. inermis* and *M. officinalis* cover notably increased between years. plant species typically comprised a low percentage (< 20%) of plot cover (**Table 3**).

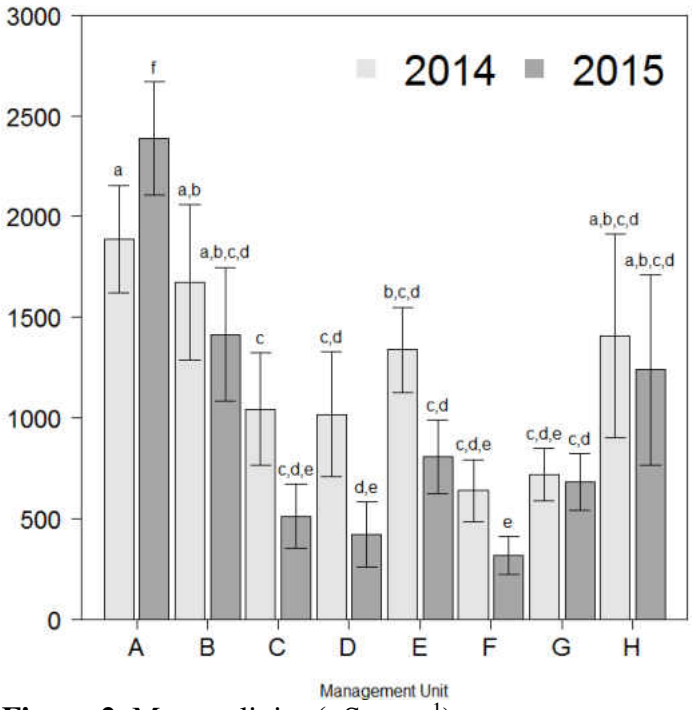

Figure 2. Mean salinity ($\mu S \cdot cm^{-1}$) across management units and between sample years. Management Units A and F were burned between sample years. Error bars represent 95% confidence intervals. Significant differences across management units and between years, determined with a Tukey's post-hoc test, are indicated by different letters.

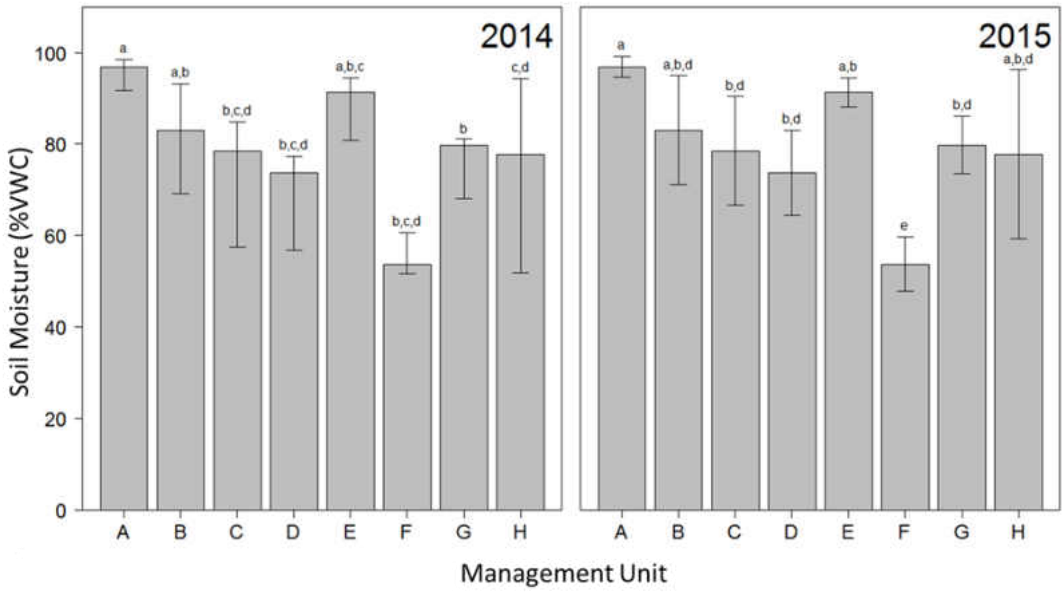

Figure 3. Mean soil moisture within management units in year one and year two. Error bars represent 95% confidence intervals. Significant differences, determined with a Tukey's post-hoc test, are indicated by different letters.

Table 3. Frequency of occurrence (n = 229 plots) and mean (± se) percent plot cover of the ten most commonly encountered native and non-native species at Oakville.

Species	Functional Group♦	Frequency (%)		Cover (%)	
		2014	**2015**	**2014**	**2015**
Native					
Ambrosia artemisiifolia	F	43.7	49.3	14.8 (1.6)	18.8 (1.8)
Hordeum jubatum	C_3	40.6	51.1	66.7 (3.6)	61.4 (3.3)
Helianthus maximiliani	F	34.1	42.4	10.2 (1.4)	13.8 (1.4)
Oligoneuron rigidum	F	30.6	37.1	11.8 (1.7	14.5 (1.4)
Symphoricarpos occidentalis	W	31.9	31.0	20.6 (2.2)	22.8 (1.8)
Symphyotrichum lanceolatum	F	28.8	31.0	6.5 (0.7)	5.0 (1.1)
Spartina pectinata	C_4	26.6	46.0	49.2 (4.8)	57 (5.3)
Muhlenbergia asperifolia	C_4	12.2	37.6	6.7 (1.5)	8.7 (1.0)
Pascopyrum smithii	C_3	10.9	37.6	30.7 (6.5)	15.5 (1.6)
Glycyrrhiza lepidota	L	21.8	24.0	11.3 (1.9)	18.1 (2.2)
Non-Native					
Cirsium arvense	F	47.6	52.0	8.3 (0.9)	8.4 (0.7)
Sonchus arvensis	F	45.4	50.7	11.8 (1.3)	12.3 (1.3)
Bromus inermis	C_3	38.0	55.5	58.3 (4.0)	72.1 (3.2)
Melilotus officinalis	L	14.0	42.7	6.5 (1.8)	15.0 (1.7)
Poa pratensis	C_3	30.6	22.2	63.2 (3.9)	47.8 (5.4)
Sonchus oleraceus	F	19.7	25.3	19.7 (2.6)	20.3 (2.2)
Lappula squarrosa	F	0	37.6	-	7.6 (1.0)
Plantago lanceolate	F	3.5	8.7	7.5 (3.3)	4.1 (1.9)
Euphorbia esula	F	4.8	6.1	10.6 (6.6)	18.7 (7.2)
Taraxacum laevigatum	F	5.2	3.9	6.4 (1.8)	10 (2.8)

♦F = Forb; C_3 = C_3 grass; C_4 = C_4 grass; W = Woody; L = Legume

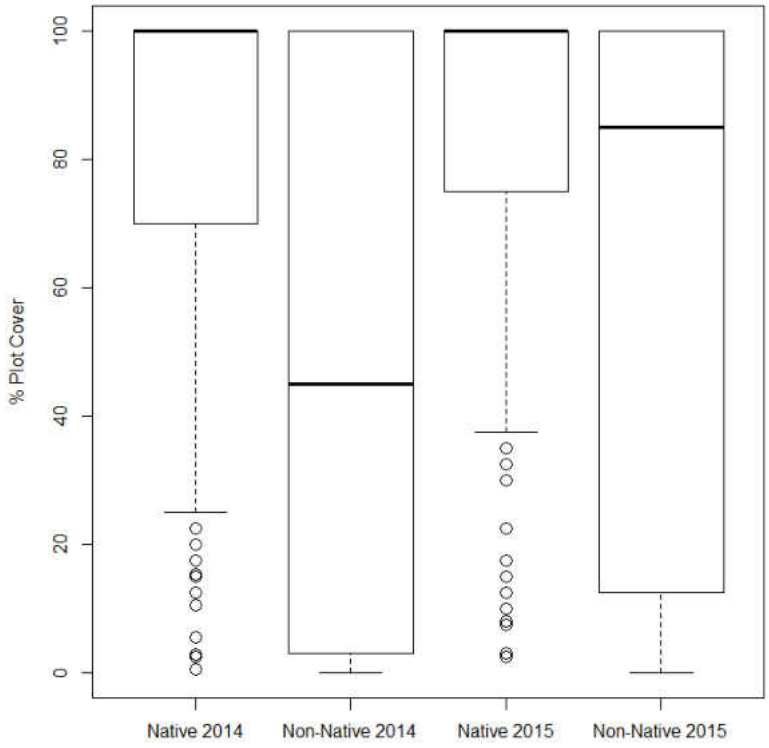

Figure 4. Native and non-native species cover across Oakville in year one and year two.

Native species were present at 100% of plots in both years. Non-native species were present within 86% of the plots in year one and 93% in year two. Native cover (year one median = 100%, Q_1 = 70.0%, Q_3 = 100%; year two median = 100%, Q_1 = 75.0%, Q_3 = 100%) was greater than non-native cover (year one median = 45.0%, Q_1 = 3.0%, Q_3 = 100%; year two median = 85.0%, Q_1 = 12.5%, Q_3 = 100%) in year one ($U = 32568$, $p < 0.0001$) and year two ($U = 38075$, $p < 0.0001$; **Figure 4**).

Plant matrices differed in their correlation with environmental matrices (**Appendix A**; **Table A.2**). C_3 grass cover was the only plant variable that was not correlated with environmental matrices. C_4 grass, non-grass graminoid and native cover and plant architectural structure were weakly ($r_M < 0.10$, $p \leq 0.05$) correlated with

Table 4. Plant matrices that were strongly correlated with at least one environmental matrix in either year one or year two. Correlation (r_M) was determined by simple Mantel tests between matrices. Values that meet the criterion of strong correlation ($r_M \geq 0.2$ and $p \leq 0.01$) are listed in bold text.

Plant Matrix	Soil Salinity		Soil Moisture		Elevation	
	2014	2015	2014	2015	2014	2015
Species Composition	**0.265*** **	**0.322*** **	**0.323*** **	**0.383*** **	**0.244*** **	**0.346*** **
Native Composition	0.154***	0.167***	0.095**	0.188***	0.147***	**0.225*** **
Non-Native Composition	0.003	0.028	**0.278*** **	**0.305*** **	0.062**	0.189***
Non-Native Cover	0.128***	**0.293*** **	**0.215*** **	0.190***	0.125***	**0.264*** **
Functional Composition	0.173***	0.172***	**0.238*** **	**0.313*** **	**0.226*** **	0.120***
Forb Cover	0.084***	0.199***	0.051*	0.037	0.034	0.094***
Legume Cover	0.052‡	-0.021	**0.422*** **	**0.478*** **	0.091**	0.163***
Woody Cover	0.056‡	-0.018	**0.327*** **	**0.520*** **	0.194***	**0.218*** **

*** < 0.001; ** < 0.01; * < 0.05; ‡ < 0.1

environmental matrices. C_4 grass cover was weakly correlated with elevation in both years, and non-grass graminoid cover was weakly correlated with elevation in year two. In year one, native cover was weakly correlated to pH and soil moisture, but was not correlated to any environmental gradient in year two. In year two, architectural structure was correlated with salinity and weakly correlated with elevation, but in year one was not correlated with any environmental gradient.

In both years, select plant matrix correlations with salinity, soil moisture and elevation met the minimum criterion to be considered strong ($r_M \geq 0.20$ and $p < 0.01$; **Table 4**). Species composition was strongly correlated with these gradients and weakly correlated with pH and soil texture in both years. Native species composition was most strongly correlated with elevation in year two. Non-native species composition was consistently strongly correlated with soil moisture in both years. Non-native cover was most strongly correlated with soil moisture in year one, and salinity and elevation in the year two (**Figure 5**).

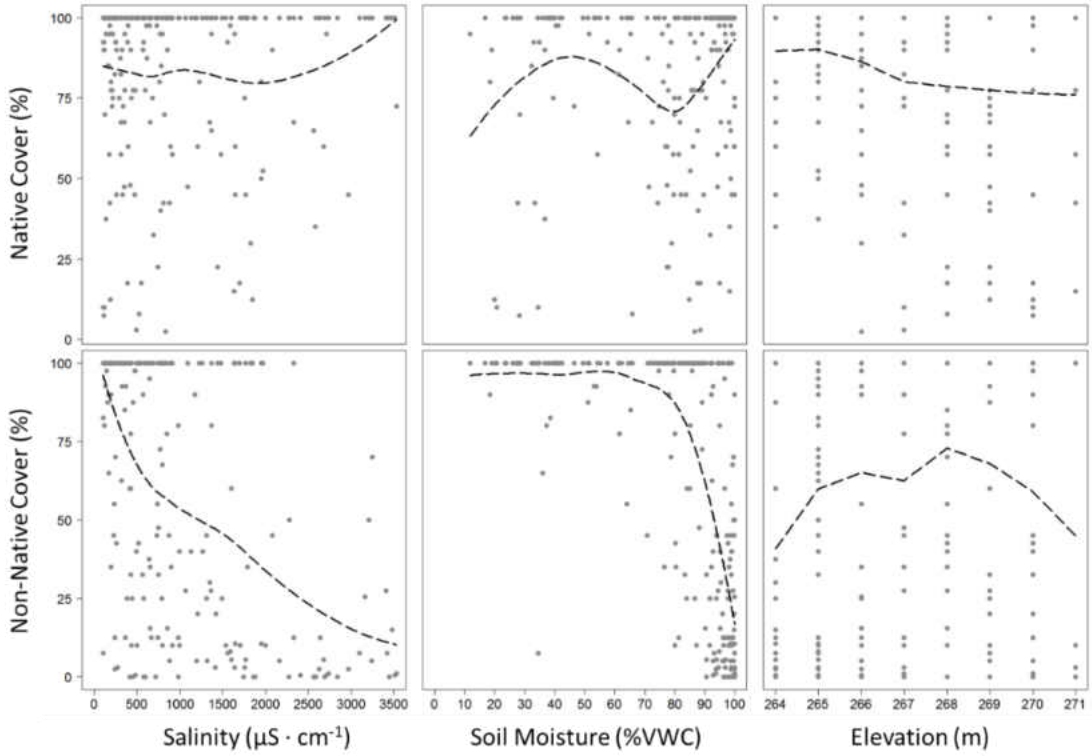

Figure 5. Scatterplot of year two native and non-native cover along salinity, soil moisture and elevation gradients. Lines added for illustrative purposes are locally weighted polynomial regression curves of plot cover along each gradient.

Forb cover was most strongly correlated ($r_M = 0.199$, $p = 0.0001$) with salinity in the second year (**Figure 6**). Legume and woody cover were consistently and strongly correlated with soil moisture (**Table 4**; **Figure 6**). Woody cover was also strongly correlated with elevation in year two (**Figure 6**).

The environmental gradients that were strongly correlated with at least one plant matrix (elevation, soil moisture, and soil salinity) occurred in SW-NE gradients across Oakville (**Figure 7**). Salinity was strongly positively correlated with soil moisture and strongly negatively correlated with elevation in both years, and soil moisture was strongly negatively correlated with elevation in both years (**Appendix A; Tables A.3-A.4**). The scale of change in soil moisture closely resembles that of elevation across

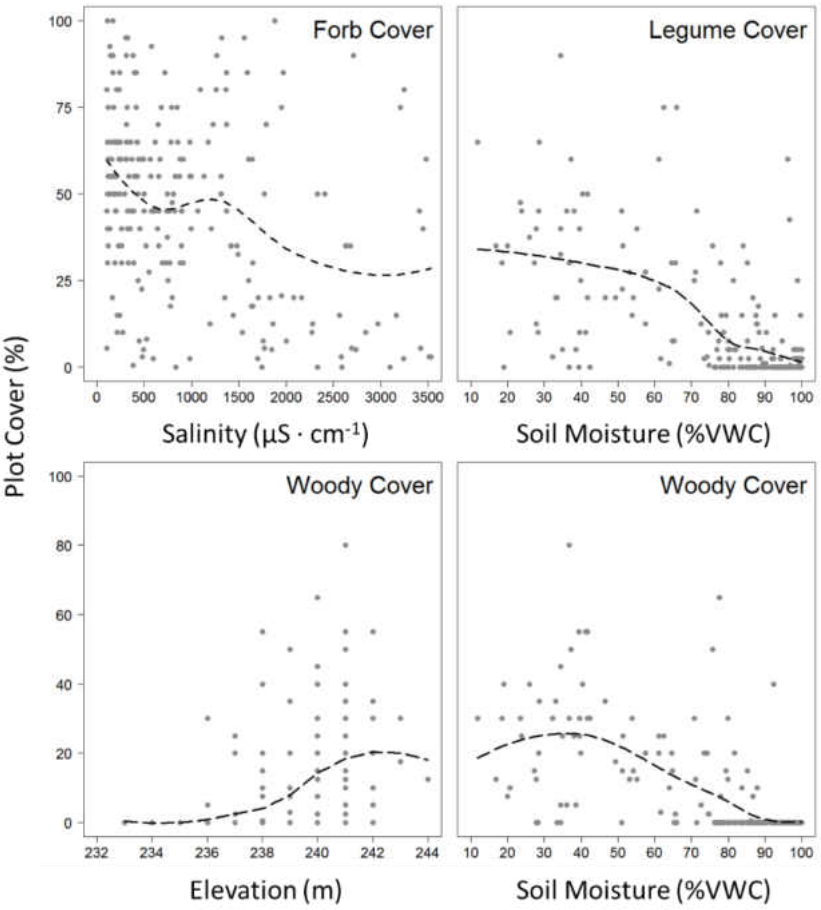

Figure 6. Forb, legume, and woody cover along strongly associated environmental gradients in year two. Locally weighted polynomial regression curves showing plot cover trends along environmental gradients added for illustrative purposes.

Oakville, with generally increasing moisture as elevation decreases. However, the scale of change in soil salinity does not resemble elevation or soil moisture. At upland positions across the site soil salinity was generally low (≤ 500 µS · cm^{-1}). Throughout the low, wet areas in the more southerly parts of Oakville salinity was moderate (≤ 1390 µS · cm^{-1}). Soils were only strongly saline in the low, wet areas of the northern most management unit.

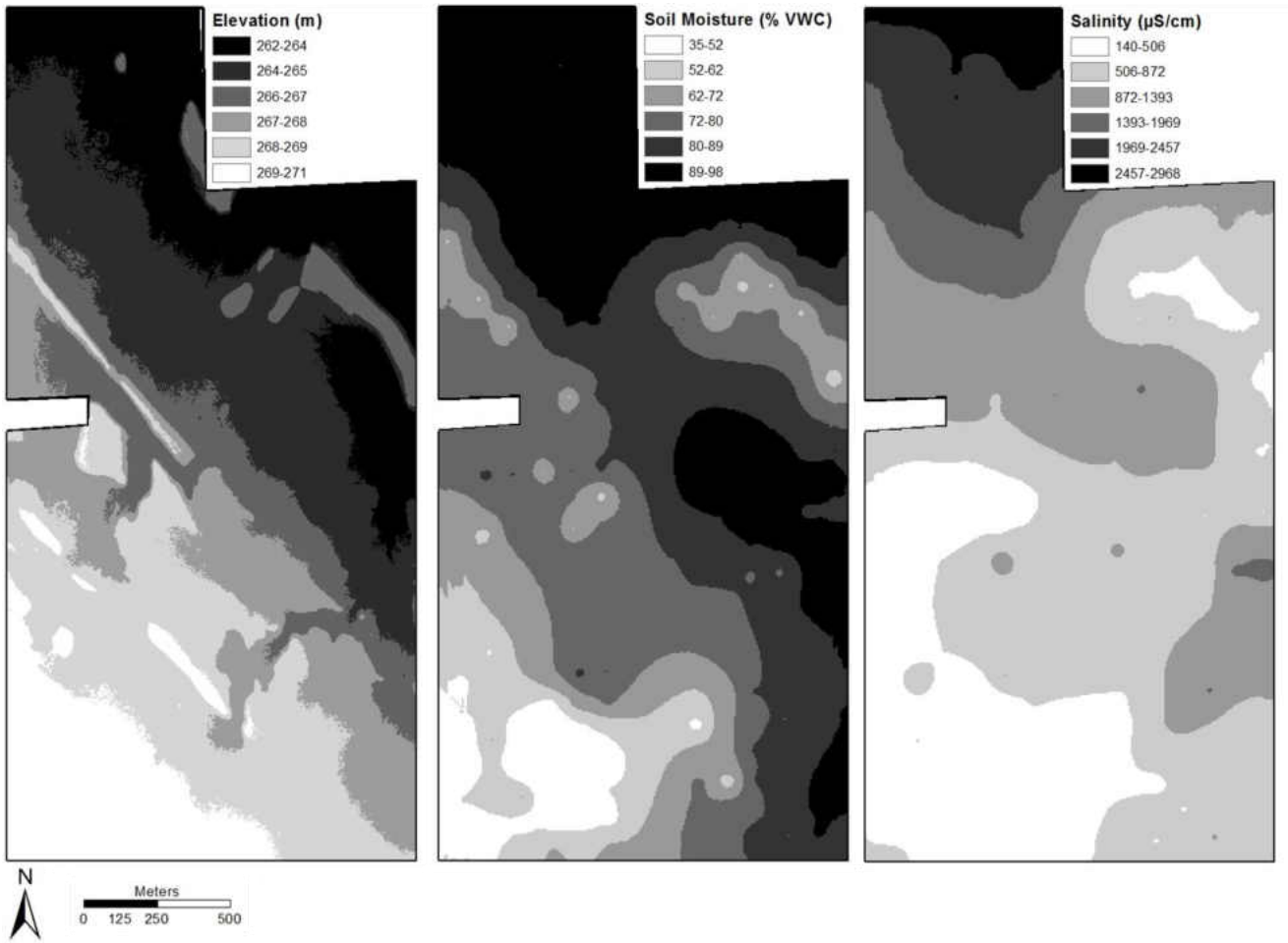

Figure 7. Elevation, soil moisture, and soil salinity gradients across Oakville. Salinity and soil moisture gradients determined with Empirical Bayesian Kriging models with year two values. Elevation gradient determined by a digital elevation model (DEM) from the USGS, available from: http://viewer.nationalmap.gov/basic/.

Table 5. Environmental distances (bin centroid value) over which plant matrices were positively and negatively correlated with site environmental gradients in year two as determined with Mantel correlograms.

Plant Matrix	Salinity (µS · cm^{-1})		Soil Moisture (%VWC)		Elevation (m)	
	Positive	Negative	Positive	Negative	Positive	Negative
Species Composition	107.1-535.5	1178-3319.9	2.8-13.8	24.8; 35.8-85.4	1-1.7	3.1-10.0
Native Composition	-	-	-	-	1-1.7	3.8-9.3
Non-Native Composition	-	-	2.8-8.3	13.8-79.9	-	-
Non-Native Cover	107.1-535.5	1178-3319.9	2.8-8.3; 30.3; 52.3	19.3-24.8; 57.8-85.4	1-1.7	3.8-10.7
Functional Composition	-	-	2.8 – 19.3	35.8 – 85.4	-	-
Forb Cover	107.1-749.7	1392.2-2891.5; 3319.9	-	-	-	-
Legume Cover	-	-	2.8-19.3	30.3-74.4; 85.4	-	-
Woody Cover	-	-	2.8-19.3	35.8-79.9	1-1.7	3.8-7.2

Plant species composition and non-native species cover responded similarly to soil salinity (**Figure 8**). Plant species composition and non-native cover were positively correlated among plots within 535.5 µS · cm^{-1} of one another (**Table 5; Figure 8**). However, plant species composition and non-native species cover differed among plots

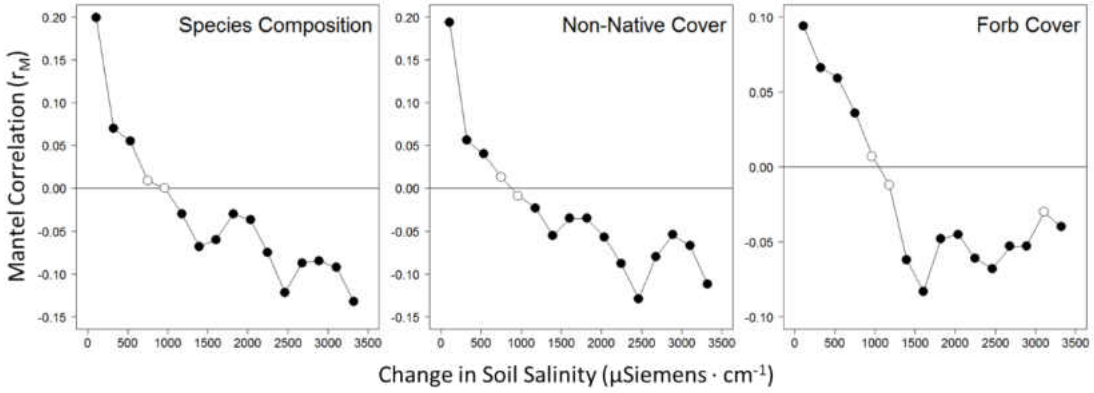

Figure 8. Mantel correlograms of plant species composition, non-native species cover and forb species cover in response to changing soil salinity. Solid circles represent significant correlations.

that differed in soil salinity by greater than 1178 $\mu S \cdot cm^{-1}$(**Table 5; Figure 8**). Forb cover was positively correlated over a longer range, and differences in forb cover began at a greater distance along the salinity gradient (**Figure 8**). Forb cover was similar among plots within 749.7 $\mu S \cdot cm^{-1}$ of one another (**Table 5; Figure 8**). Forb cover differed among plots that differed by greater than 1392.2 $\mu S \cdot cm^{-1}$ of one another (**Table 5; Figure 8**).

There were more differences in patterns of positive and negative correlation among plant community metrics that were strongly correlated with the soil moisture gradient than the salinity gradient. Plant species composition was positively correlated among plots that were within 13.8% VWC of one another (**Table 5; Figure 9**). Plant species composition was different among plots that differed by 24.8% VWC and greater than 35.8% VWC (**Table 5; Figure 9**). Positive correlation occurred over the same range along the soil moisture gradient in functional group composition, legume cover and woody cover (**Figure 9**). Functional group composition, legume cover, and woody cover were similar among plots that were within 19.3% VWC of one another (**Table 5; Figure 9**). However, negative correlation occurred over different ranges in each of these plant community metrics (**Figure 9**). Functional group composition differed among plots that differed by greater than 41.3% VWC (**Table 5; Figure 9**). Legume cover differed among plots that differed by 30.3-74.4 %, and 85.4% VWC (**Table 5; Figure 9**). Woody cover differed among plots that differed by 35.8-79.9% VWC (**Table 5; Figure 9**). The correlation patterns of non-native species cover along the soil moisture gradient differed from correlation patterns of non-native species composition. Positive correlation was

present over the same soil moisture range (**Figure 9**). Non-native species composition and non-native species cover were similar among plots that were within 8.3% VWC of one another. However, non-native species cover was additionally similar among plots that were 30.3% and 52.3% apart. The ranges of negative correlation of non-native species composition and non-native species cover differed (**Figure 9**). Non-native species composition differed among plots that differed by greater than 13.8% VWC (**Table 5; Figure 9**). Non-native species cover differed among plots that differed by 19.3-24.8% and greater than 57.8% VWC.

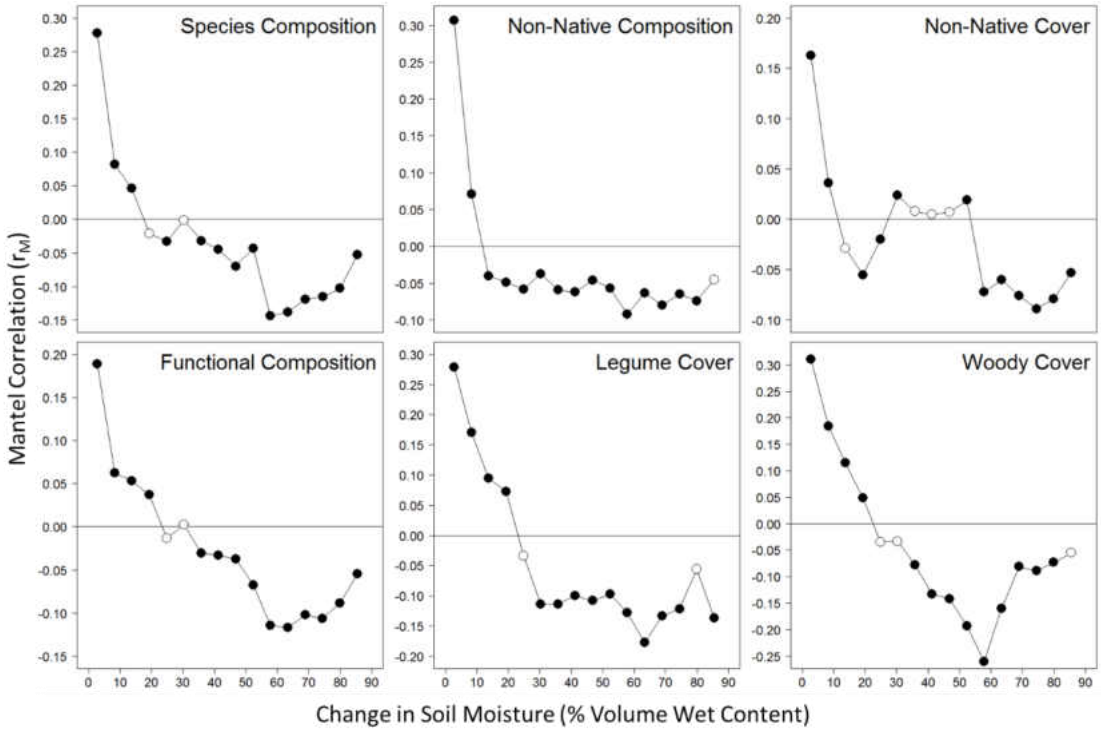

Figure 9. Mantel correlograms of plant species composition, non-native cover, non-native composition, functional group composition, legume cover and woody cover in response to changing soil moisture. Solid circles represent significant relationships.

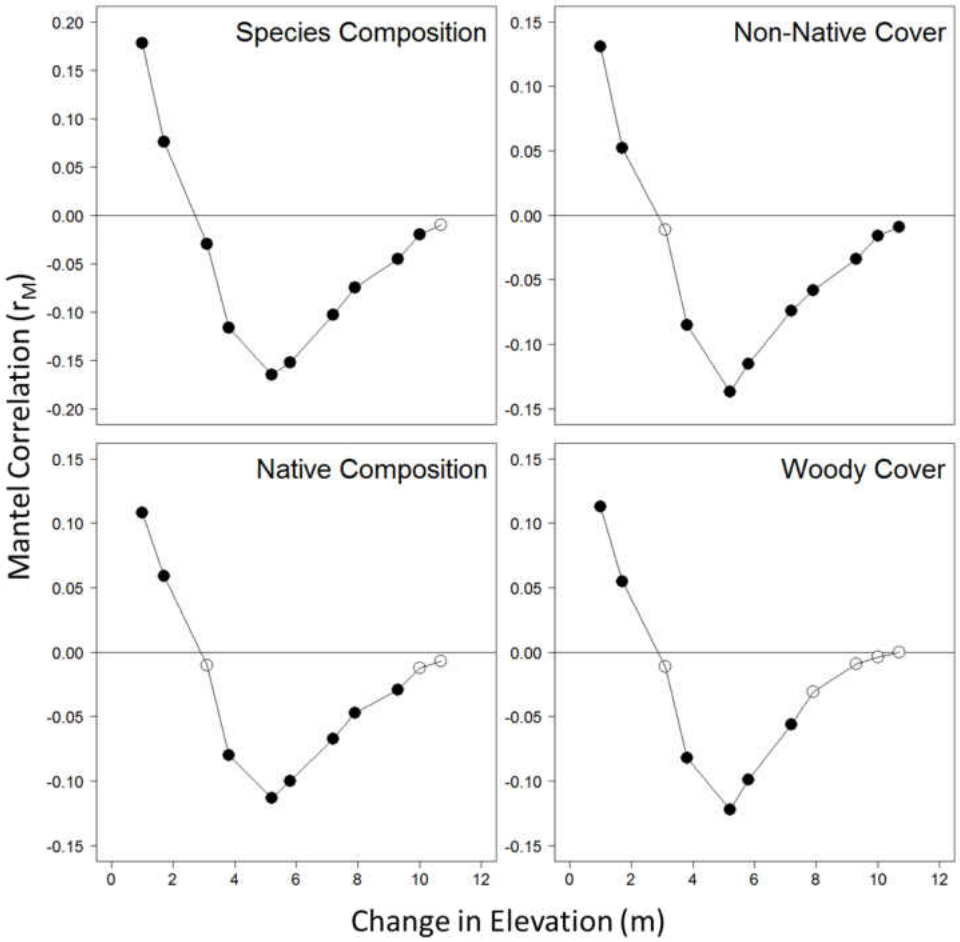

Figure 10. Mantel correlograms of species composition, non-native cover, native composition, and woody cover in response to changing elevation. Solid circles represent significant relationships.

All plant metrics that were strongly correlated with elevation correlated positively with elevation over the same range (**Table 5; Figure 10**). Plant species composition, native species composition, non-native species cover, and woody cover were similar among plots within 1.7 m of one another (**Table 5; Figure 10**). However, the ranges of negative correlation differed among all plant metrics (**Figure 10**). Plant species composition differed among plots that differed by 3.1-10 m (**Table 5; Figure 10**). Native species composition differed among plots that differed by 3.8-9.3 m (**Table 5; Figure**

10). Non-native species cover differed among plots that differed by greater than 3.8 m (**Table 5; Figure 10**). Woody cover differed among plots that differed by 3.8-7.2 m (**Table 5; Figure 10**).

Discussion

My study assessed how plant community composition metrics and plant community architecture responded to multiple grassland environmental gradients. Overall, elevation, soil moisture, and soil salinity strongly affected plant structure and composition. However, the strength of correlation and the scales of response varied depending on the way in which community was characterized. Mainly, the strength of the relationship declined with coarser plant taxonomic and structural resolution. This is likely driven by changes in plant species pools and availability within more extreme environmental conditions, such as high salinity. Previous research has demonstrated that changes in plant species composition (Alhamad et al. 2007; Klimek et al. 2007; Seabloom & van der Valk 2003a), functional traits (Schwilk & Ackerley 2005; Yan & de Beurs 2016), and non-native species composition (Andersen et al. 2015; Uddin et al. 2013) can occur in response to environmental gradients and landscape position. The results of my study expand on this by showing how plant species, functional group, native species and non-native species composition within the same plant community respond to environmental gradients.

Approximately five decades ago several investigators described the Oakville plant community correlation with environmental conditions across the site (Redmann & Hulett

1964; Hadley & Buccos 1967; Hadley 1970; Redmann 1972; Whitman & Wali 1975). Since this time, there have been some notable changes in plant community composition within the site. Several species that had formed dominant community types in the mid-1960s (Hadley & Buccos 1967; Redmann 1972) have become minor components of species composition at Oakville, most likely as a result of fire cessation. By the mid-1980s *Andropogon gerrardii* and *Schyzachyrium scoparium* had become limited in their distribution across the site, no longer defining a major community type as described in the mid-1960s (Heidel 1986). *Muhlenbergia* formed a dominant community type in the mid-1960s, but in the current study *M. richardsonis* was not encountered and *M. asperifolia* was a frequently encountered subordinate species. *A. gerardii*, *S. scoparium* and *M. asperifolia* are all typical of drier, lower saline areas within the site. Hadley & Buccos (1967) described *B. inermis* as being restricted to dry, upland mounds in the southern portions of the site which had been frequently mowed prior to their survey (Redmann 1972). Since this time *B. inermis* has increased its distribution, becoming one of the most frequently encountered dominant species. This increase in presence of *B. inermis* may have influenced the decline of other dominant warm season grasses.

Redmann's (1972) description of the plant community across Oakville was based on surveys at 36 randomly distributed locations across the site, and then mapping the distribution of community types by comparison with aerial photographs. Redmann took soil samples from four widely distributed pits to describe the site's soil conditions. My study takes a more thorough approach by systematically surveying the entire site to describe site-wide soil conditions and plant community in the same plots. Redmann used

polar ordination techniques to plot the distribution of major plant species along soil moisture and salinity gradients, so he was limited to determining correlation between plant community composition and environmental conditions. I used Mantel tests which are a more direct way to assess the correlation of plant community composition with changing environmental conditions between plots. Additionally, Mantel correlograms allowed me to determine over what range of change in environmental gradients plant community composition was positively or negatively correlated. Redmann showed broad scale change of community types across Oakville. The methods employed in my study were able to show finer scale change of species composition as a whole along the site, and tie these changes directly to environmental gradients. However, the findings of my study are generally in-line with the findings of Redmann's study.

Plant community species and functional group composition metrics formed well defined groups in response to elevation, soil moisture, and soil salinity. This suggests that niche-based processes are driving deterministic community assembly at Oakville (Chase & Myers 2011). Elevation, soil moisture, and soil salinity act as filters causing turnover in species and functional group composition across the site. These filters are acting more strongly on plant species composition metrics than functional group composition metrics. Plant species composition and non-native species cover responded strongly to each of these three gradients, but functional group composition metrics only responded strongly to subsets of these gradients. Zonation patterns of species composition metrics show that they are typically more well-structured in response to elevation, soil moisture, and soil salinity than functional group composition metrics. Turnover of species composition

metrics occurred at finer environmental scales in response to soil moisture and soil salinity than turnover of functional group composition metrics. Also, species composition metrics were negatively correlated over broader distances than functional group composition metrics in response to all three gradients. This suggests that these environmental filters are acting more strongly at the species composition level.

Plant species turnover across fine environmental scales will create distinct, localized plant species groupings. However, if functional group composition is changing over broader environmental scales changes in functional group composition along environmental gradients will be less predictable. This can have implications for grassland ecosystem services within a site. For example, Orford et al. (2016) have shown that pollinator diversity increases with grassland plant species diversity. However, many wildlife species, such as generalist arthropod herbivores and grassland birds, use of grassland habitats are affected by plant functional group composition (Joern 1982; Coppedge 2001). This may make it harder to predict how wildlife habitat can change within a site with strong environmental gradients than to predict how pollinator services will be provided.

Functional group response to environmental gradients is driven by less dominant functional groups. Forb, legume, and woody functional groups were the only functional groups that responded to environmental gradients in either year at Oakville. Forb cover correlation with soil salinity in year two was just below the minimum correlation criterion. Legume and woody cover correlations with environmental gradients met the minimum correlation criterion. Legume composition consisted overwhelmingly of two

species (*Melilotus officinalis* and *Glycyrrhiza lepidota*) and woody composition consisted overwhelmingly of one species (*Symphoricarpos occidentalis*). C_3 and C_4 grasses did not respond to any environmental gradients. The response of legume and woody functional groups being driven by just a few species likely accounts for environmental filters acting less strongly at plant functional group level composition than species level composition.

Plant community response to elevation was the most consistent across species and functional group composition metrics. Species composition, native species composition, non-native species cover, and woody cover were all positively correlated among plots within 1.7 m elevation of one another. The slight elevation gradient at Oakville means that elevation changes very little over long distances, so there should be little spatial variation in these metrics across the site. Species composition was negatively correlated over a wider distance along the elevation gradient than any other metric. However, the presence of beach ridges that provide relief on the landscape which can see a change in elevation of 2-3 m over a distance of less than 20 meters. So, change in species composition can occur over a short range when moving to a beach ridge from surrounding plains. Otherwise change in species composition is likely to occur over greater distances when moving from lowland areas to upland areas across Oakville. Native species composition and non-native species cover were negatively correlated over a wider distance than woody cover, showing that composition is more structured at the species level.

There was more variation among plant responses to the soil moisture gradient at Oakville than there was to the salinity gradient. Functional composition, and in particular,

legume and woody cover remained positively correlated over a wider range along the soil moisture gradient than plant species composition, and negative correlation began at a greater distance along this gradient. This shows that more well defined distinct groupings are present in species composition along the soil moisture gradient, but that functional group composition and individual functional groups are also forming distinct groups along this gradient at broader environmental scales.

Soil moisture is more influential of zonation patterns of non-native species composition and non-native species cover than it is of zonation patterns of species composition as a whole. Non-native species may be more restricted in their distribution along the soil moisture gradient than native species as a result of a more limited species pool (Andersen et al. 2015). Non-native species composition and non-native species cover remained positively correlated for a shorter range than plant species composition, and negative correlation began in these plant metrics at a shorter distance along the soil moisture gradient than in the plant species composition matrix. These areas are frequently inundated in the spring and early summer and non-native species may not be able to withstand seasonal flooding.

Legumes and woody species were the only functional groups to respond to the soil moisture gradient and these functional groups were less well represented than grasses and forbs. There were two legume species (*Glycyrrhiza lepidota* and *Melilotus officinalis*) and one woody species (*Symphoricarpos occidentalis*) among the twenty species in the most frequently encountered native and non-native plant species. This reflects the limited species pool in these two functional groups compared to grasses and

forbs. So, it is likely the response of a few dominant species within the legume and woody functional groups are driving the response of functional group composition to soil moisture. The limited representation of legumes and woody species could explain why the response of functional group composition metrics to soil moisture was less well defined than the response of species composition metrics. Even though functional group composition is less well defined than species composition it is important to understand how functional group composition assembles and distributes across grasslands because this can alter the suitability of grassland habitat for desirable wildlife populations (Joern 1982; Coppedge et al. 2001).

Change in soil moisture occurred over approximately the same spatial scale as elevation and over a finer spatial scale than soil salinity across most of Oakville. Response to soil moisture was also more well defined than response to elevation. So, soil moisture will have led to more spatial variability in plant species and functional composition than elevation or soil salinity. The exception is the northern most management unit which ranges from highly saline to severely saline soils. In this unit there is little variation in soil moisture, but salinity and elevation do change across this unit.

The responses of plant species composition, non-native species cover and forb cover to salinity were similar. Zonation patterns of plant species composition and non-native species cover occurred over the same ranges in response to the salinity gradient. Structure in zonation patterns of forb cover in response to salinity was not as well-structured. However, zonation patterns of all three of these plant metrics show that they

form distinct groups among plots that have similar levels of salinity and differ among plots that have more different salinity levels. Salinity places plant species under osmotic stress and can cause ion toxicity (Seelig 2000). Halophytes have evolved physiological and biochemical mechanisms to cope with high ion concentrations resulting from salinity without damage (Flowers & Colmer 2008). Several species native to Grand Forks County, ND, such as *H. jubatum* and *S. pectinata*, are halophytic or salt tolerant (Tesky 1992; Howard 1996; Seelig 2000).

Spatial variability of saline conditions is minimal across the southern portions of Oakville (**Figure 7**). Throughout the southern portions of the site salinity remains low or moderate and only becomes high or severe in the northern most unit of the site. If change of species composition, non-native species cover, and forb cover occur tightly with changes in soil salinity this could potentially result in low spatial variability of these plant composition metrics across the southern portions of Oakville.

Despite strong correlations with species and functional group composition (**Appendix A; Tables A.5-A.6**), plant community architecture did not respond strongly to any environmental gradients. Plant community architecture only correlated with salinity and elevation in year two. This suggests that there is only a weak relationship between plant community architecture and the soil environment at Oakville, and this relationship does not the determining factor that causes change in plant community architecture across the site. Strong correlations with species and functional group composition suggest that plant community architecture is responding to changes in plant community composition across Oakville. These correlations show that plots with similar

species and functional group composition also had similar architectural structure. Many wildlife species, such as grassland birds and arthropods, select habitat based on plant community architecture or functional composition (Joern 1982; Hovick et al. 2014). So, maintaining architectural heterogeneity is important to sustain a diversity of wildlife populations (Tews et al. 2004). The response at Oakville shows that changes in plant species and functional composition can lead to changes in plant community architecture which will ultimately create architectural heterogeneity across grassland habitats.

My study shows that community assembly processes are occurring similarly across different plant scales of plant species and functional composition at Oakville. Along each strongly correlated environmental gradient plant metrics form distinct groups among plots with similar environmental conditions and differ among plots that have greater difference of environmental conditions. This structure in response to environmental gradients shows that deterministic community assembly is occurring in the plant community at Oakville. The presence of three strong environmental gradients act as abiotic filters influencing plant species and functional composition. Demonstrating how plant communities can assemble and form patterns in response to strong environmental gradients in remnant communities can help to inform restoration practices that can improve restoration success in the Red River Valley of North Dakota where these strong environmental gradients are present on the landscape. Restoring these environmental gradients can increase the likelihood that a desirable plant community will be able to establish in restored sites.

CHAPTER III

ARTHROPOD ASSOCIATIONS WITH PLANT AND ENVIRONMENTAL GRADIENTS IN A NORTHERN TALLGRASS PRAIRIE

Abstract

Arthropods comprise a large portion of grassland biodiversity, and provide decomposition, wildlife forage and pollination services within grasslands. Arthropod community composition, and the services they provide, can be spatially variable within grasslands and strongly influenced by plant and environmental gradients. However, the influence of plant and environmental gradients on the spatial variability of arthropod community composition is not well understood. To investigate these relationships, arthropods were collected at three locations within the plant community (litter; mid-story; canopy) across a structurally diverse northern tallgrass prairie during mid- and late summer 2014 and 2015. There were no plant or environmental gradients with which arthropods consistently correlated across functional community or across year. Litter arthropods correlated with plant and environmental gradients in both years, but not consistently. Litter arthropods responded strongly to soil salinity in year one and did not respond strongly to any gradients in year two. Mid-story arthropods responded strongly to grass cover and plant architectural gradients in year one and plant species composition, non-native species cover, and salinity gradients in year two. Mid-story arthropod composition did not become structured in response to any plant cover gradients

until becoming negatively correlated over a large change in plant cover occurred. Mid-story arthropod composition was positive correlated among plots with similar plant community architecture and negatively correlated among plots in which plant community architecture differed more widely. This shows that mid-story arthropods are more well-structured along plant community architecture gradients than plant cover gradients. Mid-story arthropod zonation patterns in response to salinity were more well-structured than litter arthropods. Canopy arthropods did not respond to any gradients in year one, and did not respond strongly with any gradients in year two. These results suggest that plant gradients may not strongly affect litter and canopy arthropods and environmental gradients may not be affecting canopy arthropods at the site-scale. Mid-story arthropod response to environmental gradients can be stronger than litter arthropods. Mid-story arthropod community assembly can be driven by complex interactions with plant and environmental gradients that influence spatial structure of morphospecies composition differently. There is clear stratification of arthropod communities (litter; mid-story; canopy) within the plant community at Oakville. This can influence the plant and environmental gradients that affect community assembly and formation of zonal patterns in each arthropod functional community

Introduction

Plant community assembly in response to gradients of environmental variables has been a major focus of research within community ecology since its inception. We have a good understanding of how community assembly processes in plant communities

determine species composition, and patterns within plant communities (Cowles 1899; Clements 1916; Gleason 1926; Curtis & McIntosh 1951; Whittaker 1956; Whittaker 1960; Piernik et al. 1996; Solon et al. 2007). However, we have an incomplete understanding of how arthropod communities assemble in response to plant and environmental gradients. Changes in arthropod species composition along gradients will affect how arthropods contribute to ecosystem function within a site. Research that addresses arthropod community response to plant and environmental gradients usually has a narrow focus, such as on a single taxonomic group (Rypstra et al. 1999) or among arthropods at a single location within the plant community (Garcia et al. 2010; Pan et al. 2015). Research to determine how community assembly processes act on arthropods at different locations within the plant community, and whether the same drivers are responsible for assembly and patterns of species composition is needed to better understand how grassland arthropod communities form. My study assesses to what extent three grassland arthropod functional communities (litter; mid-story; canopy), as determined by location within the plant community, are correlated with northern tallgrass prairie plant and environmental gradients, and what this tells us about assembly in these functional communities.

Tallgrass prairies support diverse arthropod communities which provide essential services within these grassland habitats that maintain healthy grassland ecosystem function (Fox-Dobbs et al. 2010). Arthropods affect decomposition, soil health, pollination, and serve as a source of prey within the habitats they occupy (Landis et al. 2008; Del Toro et al. 2012). Arthropod contributions to ecosystem function will vary

with location in the plant community. For example, detrivores can comprise a large portion of litter arthropod communities. Detrivores (e.g., *Cylisticus convexus*) in litter arthropod communities aid in nutrient cycling by breaking down dead plant matter (Miller 1993; Rapp 2001). Mound building arthropods that are also common components of grassland litter arthropod communities (e.g., ants and termites) can ameliorate stressful environmental conditions, creating habitat that supports species across a range of taxonomic levels (Wali & Kannowski 1975; Pringle et al. 2010). Mid-story arthropod herbivores can play a suppressive role on forb abundance within grasslands, influencing species composition and helping to maintain a high grass to forb ratio (La Pierre et al. 2015). Grassland arthropods, such as aerial predators, also provide natural pest control (Cox et al. 2014). Pollinators typical of canopy arthropod communities provide valuable pollination services within agricultural landscapes (Isaacs et al. 2009).

Arthropod interactions with plant and environmental gradients can determine composition, and zonation patterns in arthropod communities within a site (Potts & Willmer 1997; Siemann 1998; Pan et al. 2015; Lengyel et al. 2016). Arthropods respond to plant species composition, plant functional group composition, plant community architecture and soil abiotic environment (Crist et al. 2006; Mormul et al. 2011; Koricheva et al. 2000; Kwon et al. 2016). The location of arthropods within the plant community should determine how plant and environmental gradients affect composition and zonation patterns within arthropod functional communities (Bestelmeyer & Wiens 2001; Johnson & Agrawal 2005; Pasquet et al. 2008; Pan et al. 2015; Kwon et al. 2016).

Vertical stratification is more clearly understood in woody ecosystems, as are its effects on stratification within associated animal communities. In grasslands vertical stratification has received little attention, yet heterogeneous grassland plant communities are clearly vertically stratified (Liira et al. 2002). We do not fully understand how arthropod communities fully exploit the architectural resources made available at different locations within grassland plant communities because most research focuses on a single location within grassland plant communities (e.g., Bestelmeyer & Wiens 2001; Johnson & Agrawal 2005; Pan et al. 2015) or limited representation of arthropod taxa from multiple strata within grasslands (Rypstra et al. 1999; Schaffers et al. 2008).

Litter arthropods occupy a ground level position, so interactions with plant litter should most strongly affect their composition. Increased architectural complexity of plant litter can provide greater habitat (Nemec et al. 2014; Horvath et al. 2015) and provide protection from daily and seasonal soil temperature fluctuations (Rypstra et al. 1999; Mazia et al. 2006). Mid-story arthropod communities are commonly comprised of herbivores, and so mid-story arthropods should be directly associated with plant resources (Borror et al. 1981; Simons et al. 2016). Plant species composition can determine mid-story herbivore and predator diversity (Torma et al. 2014). Mid-story arthropods rely on plant community architecture to provide essential habitat (Rypstra et al. 199). Canopy arthropod communities are commonly comprised of highly mobile arthropods, such as pollinators, that often have wide foraging distance (Bidlingmayer & Hem 1981; Borror et al. 1981; Pasquet et al. 2008). Canopy arthropod abundance and

richness can be determined by floral resources and plant canopy cover (Matteson et al. 2013).

Arthropod response to environmental gradients can be mediated through interactions with the plant community. It is well documented that plant community composition and structure are directly influenced by interactions with abiotic environmental gradients (Cowles 1899; Clements 1916; Gleason 1926; Curtis & McIntosh 1951; Whittaker 1956; Whittaker 1960; van der Valk 1981; Weiher & Keddy 1995; Seabloom & van der Valk 2003a; Aronson & Galatowitsch 2008). Recruitment and exclusion of plant species based on their environmental tolerance can determine plant community structure (Fattorini & Halle 2004). The structure of plant communities can determine how arthropods use them, ultimately influencing arthropod community composition (Voigt & Perner 2004). Plant interactions with environmental gradients can determine plant phenotypic expression, and expressed plant phenotypes will influence arthropod community composition (Johnson & Agrawal 2005). Soil chemistry can alter plant tissue chemistry and plant morphology, thus influencing how arthropods use plants (Meindl et al. 2013). Plant mediated response to environmental gradients can determine arthropod community composition, but direct arthropod interactions with environmental gradients can also influence arthropod composition.

Arthropods can also be directly influenced by environmental gradients through their exposure to and use of the abiotic environment. As adults, litter arthropods are more directly exposed to the soil environment than mid-story and canopy arthropods. It is likely because of this that the direct effects of environmental gradients have been better

documented in litter arthropods than mid-story or canopy arthropods. It has been shown that litter arthropod abundance and diversity can be influenced by soil salinity (Pan et al. 2015; Kwon et al. 2016) and soil texture (Bestelmeyer & Wiens 2001). Soil salinity can also affect litter arthropod survival, reproduction and feeding behavior (Owojori et al. 2009; Skarkova et al. 2016). As adults, mid-story and canopy arthropods will likely be less directly exposed to soil environments, so environmental influence on these communities should most often be mediated through interactions with plants.

The different ways that arthropod functional communities can respond to plant and environmental gradients makes it necessary to determine how these gradients influence arthropod composition and zonation patterns. My study investigated how morphospecies composition of three arthropod functional communities (litter; mid-story; canopy) change in response to plant composition and plant community architecture gradients and soil abiotic environmental gradients, and how response to plant and environmental gradients cause zonation patterns within arthropod functional communities in a northern tallgrass prairie. I asked the questions: 1) do arthropod functional communities differ in their response to plant and environmental gradients; 2) does arthropod community assembly occur similarly across each arthropod functional community; and 3) do plant and environmental gradients act on arthropod functional communities over the same environmental scales? I test the hypothesis that different arthropod functional communities respond to different environmental and plant gradients. The results of my study will improve our understanding of how interactions with plant and environmental gradients influence assembly and the patterns within arthropod

functional communities. Knowing how community assembly occurs across multiple arthropod functional communities and the environmental scales over which assembly occurs within a site will improve our ability to restore grassland arthropods and the services they provide.

Methods

Study Site

The Oakville Prairie Complex is an approximately 453 ha remnant tallgrass prairie (centroid latitude 47.893, longitude -97.315) in the Central Grand Forks County grassland corridor comprised of the University of North Dakota's Oakville Prairie Field Station and North Dakota Game and Fish's Oakville/Crawford Wildlife Management Area. The site has a slight elevation gradient (mean slope between adjacent plots = $0.46^{o} \pm 0.05^{o}$) and topographic relief is provided by the Blanchard beach ridges remaining from Glacial Lake Aggasiz (Laird 1944). Soils of the lowland areas are of the Ojata series, which are characterized by high salinity. Soils of the upland areas are primarily of the Antler series, and have moderate to low salinity (Redmann 1972; Whitman & Wali 1975; Soil Survey Staff NRCS). Soil salinity results from localized upwelling of saline ground water (Laird 1944; Whitman & Wali 1975). Prior to the initiation of my study, the most recent prescribed fire occurred in the southern portion of the site in the mid-1990s (Robert Seabloom, unpublished). Following year one of my study prescribed burns were performed in one area in the north (~62.9 ha) and one area in the south (~81.8 ha). Non-

native species were sporadically managed with herbicide spraying until the early 2000s (Robert Sheppard, personal communication, 31 December 2015).

Sampling Scheme

A subset of sample plots (n = 37) across eight management units were selected for arthropod sample collection from the systematic grid of sample plots (n = 229) described in Chapter II (ArcGIS 10.1; ESRI; Redlands, CA; **Figure 11**). Arthropod sample plots were spaced ≥ 200 m apart to minimize influence on specimen collection between adjacent arthropod sample plots.

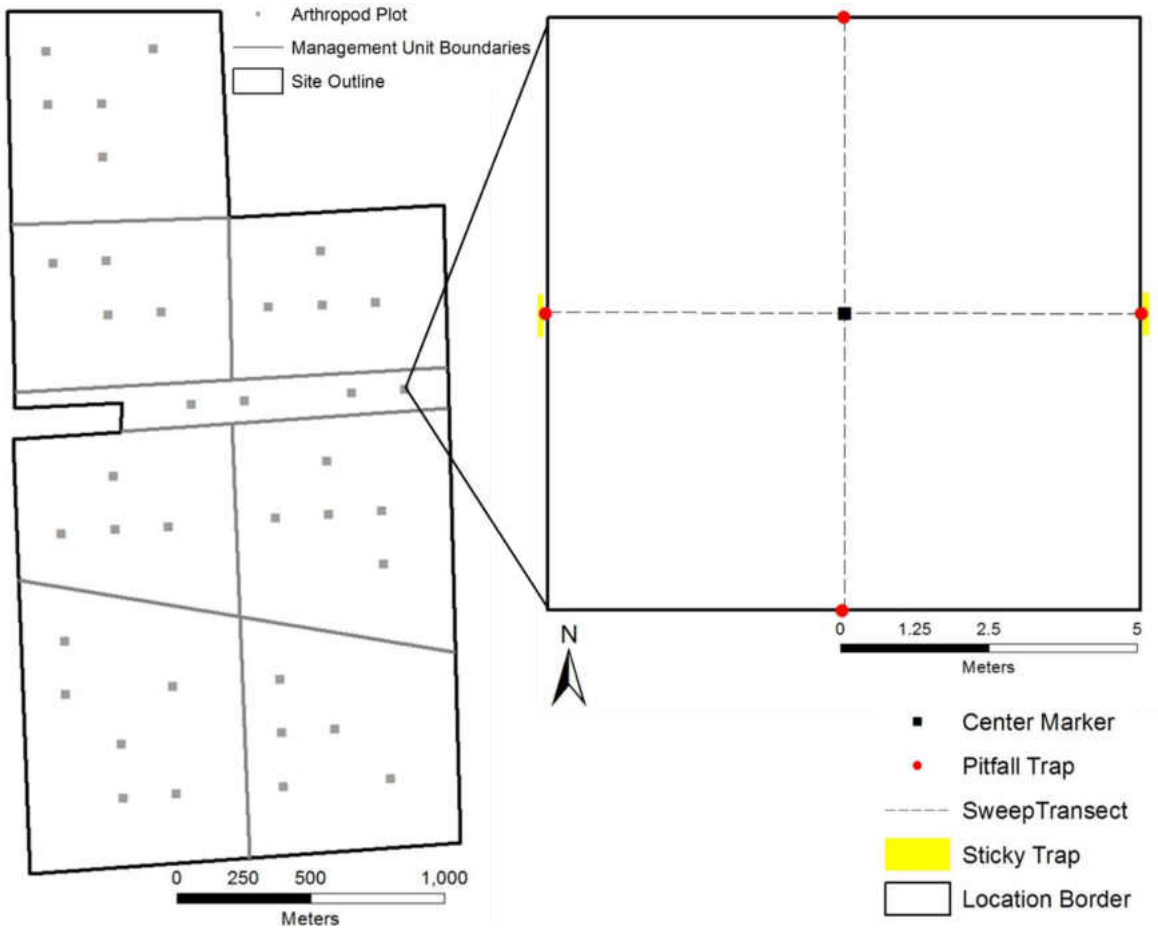

Figure 11. Oakville arthropod functional community sampling locations. Inset map depicts arthropod sample plot design.

Soil Sampling

Soil moisture (% volumetric wet content; VWC), texture (% content sand, silt, clay), pH and salinity (electrical conductivity; $\mu S \cdot cm^{-1}$) were measured as described in Chapter II. Environmental matrices were constructed from these measures taken at arthropod sample plots to describe environmental gradients in analysis of arthropod correlations.

Vegetation Sampling

The vegetation was surveyed as described in Chapter II to determine plant community composition and architecture. Plant species composition was recorded as aerial percent cover (p_i) of each species encountered in a sample plot. Aerial coverage values per species were used to calculate native, non-native and functional cover. Plant community architecture was measured as height density (cm), vegetation live height (cm) and vegetation dead height (cm). Additionally, percentage bare ground and percent intercepted photosynthetically active radiation (PAR; $\mu mol \cdot m^{-1} \cdot s^{-1}$) were measured in 2015. Plant community composition and architecture matrices were constructed from these measures.

Arthropod Sampling

Arthropods were collected twice (mid-June and mid-July) in year one and year two. Three arthropod functional communities (litter; mid-story; canopy) were described based on the location within the plant community in which specimens were collected. These three arthropod functional communities were analyzed separately for correlation with plant and environmental gradients within Oakville.

Litter dwelling arthropods were collected with pitfall traps placed flush with soil level at the midpoint of each of the four arthropod sample plot borders during a three-day collection period (N_{2014} = 228, N_{2015} = 256; **Figure 11**). The specimens collected in each pitfall trap were stored separately following collection, so that four litter arthropod samples were collected per arthropod sample plot during each collection period. Sample sizes were reduced in year one and year two due to standing water (17 plots mid-June year one; 10 plots mid-July year two).

Mid-story arthropods were collected by sweep net. Sweep net sampling was done along two orthogonal 10 m transects during each collection period (N_{2014} = 146, N_{2015} =148; **Figure 11**). One sweep net sample consisted of three passes along one transect with 10 sweeps through the mid-story of the plant community per pass (3 × 10 = 30 sweeps per sample). Following collection along each transect the contents of the sweep net were transferred to a one-gallon plastic sealable bag and placed on ice, so that two mid-story arthropod samples were collected per arthropod sample plot during each collection period. During the mid-July year one collection period, weather conditions preventing sampling at one plot. Sweep net sampling was completed within two days of pitfall and sticky trap collection

Canopy arthropods were collected with two-way sticky traps. Sticky traps were made by applying Tangle Trap™ Sticky Coating (Contech Enterprises, Inc.; Grand Rapids, MI) to an approximately 25.4 × 17.8 cm area on a yellow plastic card. Yellow was chosen to maximize the number of individuals and arthropod families collected (Hobeck et al. 1999). Sticky traps were unbaited to prevent favorably attracting any

arthropod group. One two-way sticky trap was hung with its bottom edge at canopy level on the east and west borders of each arthropod sample plot, with trap faces perpendicular to plot borders, during each three-day collection period (N = 148; **Figure 11**). One face of each sticky trap was considered one sample, so four samples per sticky trap effort were collected at each plot.

Following collection, all samples were returned to University of North Dakota's campus for storage until identification. Litter arthropods were stored in 70% ethanol and mid-story and canopy arthropods were stored in a -20ºC freezer. Limited worker hours prevented identification of all collected samples. So, a random number generator was used to select one sample from each arthropod sample plot during each collection period for identification to prevent bias in sample selection. Litter ($n_{2014} = 57$, $n_{2015} = 64$) and mid-story ($n_{2014} = 73$, $n_{2015} = 74$) arthropods were identified to family. Canopy (n = 74) arthropods were identified to order because specimens collected with sticky traps were covered with sticky trap coating which prevented ability to identify them beyond order. Following taxonomic identification, specimens were grouped into unique morphospecies based on similarity of morphological characters, and the number of representative individuals of a morphospecies in each sample was counted. Morphospecies identification provides a conservative estimate of true arthropod taxa richness, and can be an adequate, quick assessment of arthropod community composition (Obrist & Duelli 2010). Litter and mid-story specimens were categorized within the same morphospecies system. Because canopy specimens could only be accurately identified to order, these specimens were classified with a separate morphospecies system. Each unique

morphospecies was photographed and intact voucher specimens (litter; mid-story) were deposited in the Grand Forks County Prairie Project morphospecies collection in the UND Landscape Ecology Lab. Morphospecies counts for each plot were pooled across collection period in each year and used in analysis of arthropod correlations.

Data Analysis

Arthropod trapping efficacy was tested with species accumulation curves constructed in R 3.2.0 using the *vegan* package function *specaccum*() with Kindt's exact method (Oksanen et al. 2016; R Core Team 2015). Ugland et al. (2003) found that exact methods are able to more accurately predict species richness than traditional methods of constructing species accumulation curves.

Distance matrices were constructed in R 3.2.0 using the *ecodist* package function *distance*() for each arthropod variable, and plant and environmental variables from arthropod sample plots as described in Chapter II (R Core Team 2015; Goslee & Urban 2007; **Table 6**). Plant and environmental values from arthropod plots were used to construct distance matrices because the Mantel test determines correlation of two matrices consisting of different sets of variables from the same plots (Legendre & Legendre 2012). Matrices consisted of a single or suite of variables, and were constructed with distance measures appropriate to the type of data (**Table 6**).

Correlations between arthropod composition matrices and plant or environmental matrices were assessed separately by year with Mantel tests (10000 permutations)

Table 6. Distance matrices included in Mantel tests between arthropod and plant or environmental variables. Matrices were created separately for year one and year two except for Soil Texture and Elevation, which did not change between years.

Matrix	Included Variables	Distance
Arthropod		
Litter Composition	Morphospecies counts	Euclidean
Mid-Story Composition	Morphospecies counts	Euclidean
Canopy Composition	Morphospecies counts	Euclidean
Plant		
Species Composition	Percent species cover	Sorensen
Native Composition	Native percent species cover	Sorensen
Non-Native Composition	Non-native percent species cover	Sorensen
Non-Native Cover	Sum non-native species cover	Sorensen
Functional Composition	Sum cover of C_3 grass, C_4 grass, Graminoid, Forb, Legume and Woody species	Sorensen
Plant Architecture	Height density (cm); live height (cm); dead height (cm); % bare ground♦; % intercepted PAR ($\mu mol \cdot m^{-1} \cdot s^{-1}$)♦	Euclidean
Environmental		
pH	pH	Euclidean
Salinity	electrical conductivity ($\mu S \cdot cm^{-1}$)	Euclidean
Soil Texture	% sand, clay, silt	Euclidean
Soil Moisture	Mean across season soil moisture (% VWC)	Euclidean
Elevation	Height above ellipsoid (m)	Euclidean

♦Bare ground and PAR were not available in year one Plant Architecture matrix.

performed in R 3.2.0 using the *ecodist* package function *mantel*() as described in Chapter II (Goslee & Urban 2007, R Core Team 2015; **Table 6**). Positive correlation of arthropod matrices with plant or environmental matrices indicates that sites with similar composition of plant or environmental variables also have similar arthropod composition (Seabloom & van der Valk 2003a; Goslee 2007). All Mantel tests were repeated as partial Mantel tests with the inclusion of a matrix of plot centroid UTM coordinates to control for spatial autocorrelation, doing so did not affect the results and this matrix was not retained in the final analyses.

Mantel correlograms were constructed in R 3.2.0 using the *ecodist* package function *mgram*() for arthropod matrices which met a minimum correlation criterion ($r_M \geq 0.30$ and $p \leq 0.05$) with plant or environmental matrices (Goslee & Urban 2007, R Core Team 2015). The minimum correlation criterion was determined from Mantel test results

that indicated a natural break in the correlations of arthropod matrices with plant and environmental matrices. Mantel correlograms were used to determine over what distances in plant or environmental explanatory matrices changes occurred within corresponding arthropod matrices. It is difficult to meaningfully interpret correlograms in response to composite variables because the resulting units of change in a composite variable do not correspond to measurable change along gradients of the composite variable, and for this reason Mantel correlograms were not constructed for these variables. The number of bins in each correlogram was determined by Sturge's rule, which gives similar results to alternative methods for choosing bin number when sample sizes are moderate or low (~ 200 or fewer; Dogan & Dogan 2010). Bin ranges were calculated from the range of values along each environmental gradient and the number of bins, providing even bin size across each correlogram.

Empirical Bayesian Kriging models (EBK) were constructed in ArcGIS 10.3 (ESRI; Redlands, CA) with power semivariograms (100 simulations) to generate prediction surfaces for all plant and environmental variables that were included in Mantel correlogram analysis. The prediction surfaces created with EBK models show how the plant and environmental gradients that influence assembly in arthropod functional communities and patterns of arthropod composition are distributed across Oakville to form gradients. To show sufficient detail in each prediction surface six classes were chosen. Bin size for each class was determined with Jenks natural breaks. Jenks natural breaks provide a way of breaking up continuous data into discrete classes in choropleth maps which minimize the sum of absolute deviation from class means by repeatedly

transferring values from class boundaries to adjacent classes until the sum of absolute deviation from class means is minimized (Coulson 1987; Brewer & Pickle 2002).

Results

Precipitation, management and plant community composition differed between sample years. Monthly precipitation was greater in year one than in year two (**Appendix A; Table A.1**), and there were 54.4 mm more precipitation accumulation across the year one field season (1 May-15 August) than in year two (Wunderground.com 2016). Two management units (containing 29.7% of arthropod sample plots) were burned in the Fall of year one. Non-native species richness was greater in year one than in year two, though median non-native species cover increased in year two. In year one of my study 23.4% of encountered plant species (22 species) were non-native, which decreased to 14.1% of encountered plant species (14 species) in year two. Site-wide median non-native cover, vegetation live height (cm) and vegetation dead height (cm); increased from year one to year two (**Appendix A; Figure A.1**).

The number of orders identified within each arthropod community was similar between years, but the number of families identified increased in the litter and mid-story communities in year two (**Appendix A; Table A.7**). Five arthropod orders (Araneae, Coleoptera, Diptera, Hemiptera and Hymenoptera) consistently contained the greatest number of families and morphospecies across arthropod functional communities. Diptera was the dominant order across all arthropod functional communities. Diptera was represented by more families and morphospecies than any other order in each arthropod

functional community in both years, except the litter arthropod community in year one (**Appendix A; Table A.8**). In the year one litter arthropod community Diptera, Coleoptera and Hemiptera were represented by the same number of morphospecies (**Appendix A; Table A.8**).

Species accumulation curves show that trapping efforts did not capture true morphospecies richness in any arthropod functional community at Oakville (**Figure 12**). However, trapping more closely approximated true morphospecies richness in the year two mid-story arthropod community and the canopy arthropod community in both years than the remaining arthropod communities. The species accumulation curves for the litter arthropod community both years and the mid-story arthropod community in year were far from reaching the asymptote of the curves (**Figure 12)**. The species accumulation curves for the mid-story arthropod community in year two and the canopy community in both years were close to reaching the asymptote of the curves (**Figure 12)**.

When viewed at the resolution of morphospecies, arthropod community composition differed within and among functional communities, and between years. The number of specimens collected and the number of identified morphospecies differed within each arthropod functional community between years (**Appendix A; Table A.7**). The average number of morphospecies per sample was similar in both years in the litter arthropod community (year one: 18.0 ± 0.6 morphospecies; year two: 20.3 ± 1.6 morphospecies), but increased by over 10 morphospecies per sample in the mid-story (year one: 25.0 ± 1.1 morphospecies; year two: 41.1 ± 1.5 morphospecies) and canopy (year one: 33.2 ± 1.0 morphospecies; year two: 45.1 ± 1.0 morphospecies) arthropod

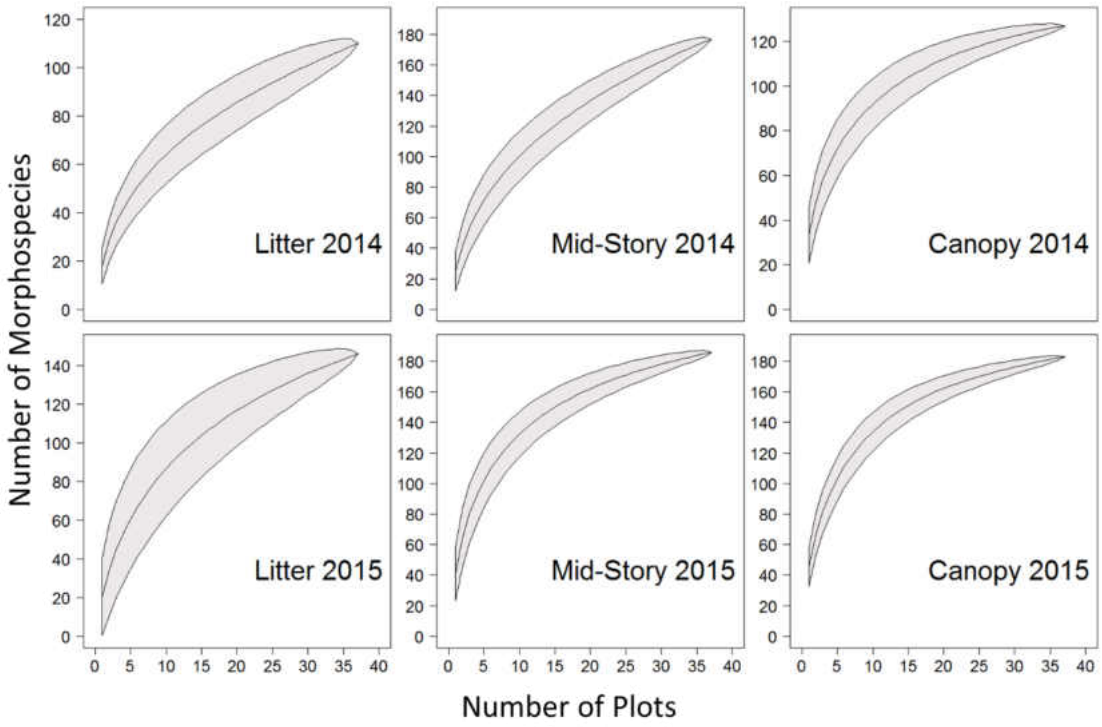

Figure 12. Species accumulation curves for year one and year two litter, mid-story and canopy arthropod communities constructed with Kindt's exact method.

communities in year two. The five most frequently collected morphospecies differed between litter and mid-story communities (**Table 7**). It was not possible to identify all specimens collected by sticky trap to family, so comparison of the morphospecies present that composed canopy arthropod composition with other functional communities was not possible. Within each arthropod functional community, only two of the top five most frequently collected morphospecies were common across years (**Table 7**).

Arthropod functional community composition matrices were not correlated with each other within either year (**Appendix A; Tables A.9-A.10**) and composition was not correlated between years within any arthropod functional community (Litter: $r_M = -0.123$, $p = 0.8518$; Mid-story: $r_M = 0.214$, $p = 0.0645$; Canopy: $r_M = -0.036$, $p = 0.6077$). Arthropod functional community composition matrices differed in their correlations with

Table 7. Morphospecies ID, order, family, presence (measured as the percent of plots collected at; n = 37) and mean count per sample of the five most frequently collected morphospecies (determined by presence) from each arthropod functional community in year one and year two.

Order	Family▼	Morphospecies ID♦	Presence (%)	Mean Count	Order	Family▼	Morphospecies ID♦	Presence (%)	Mean Count
2014					2015				
Litter					*Litter*				
Entomobryomorpha	Tomoceridae	ENTO.001	97.3	19.8	Entomobryomorpha	Tomoceridae	ENTO.001	86.5	21.2
Hymenoptera	Pteromalidae	HYME.076	78.4	2.2	Araneae	Salticidae	ARAN.005	86.5	14.6
Araneae	Salticidae	ARAN.017	73.0	8.4	Diptera	Stratiomyidae	DIPT.087	81.1	7.1
Entomobryomorpha	Isotomidae	ENTO.002	70.3	22.9	Coleoptera	Carabidae	COLE.046	59.5	2.6
Isopoda	Cylisticidae	ISOP.001	67.6	11.6	Entomobryomorpha	Isotomidae	ENTO.002	56.8	9.2
Mid-Story					*Mid-Story*				
Diptera	Muscidae	DIPT.009	100	16.9	Thysanoptera	Thripidae	THYS.001	97.3	14.9
Diptera	Anthomyiidae	DIPT.053	81.1	7.12	Diptera	Diastatidae	DIPT.067	94.6	16.9
Thysanoptera	Thripidae	THYS.001	78.4	32.2	Diptera	Tachinidae	DIPT.058	89.2	9.0
Ixodida	Argasidae	IXOD.002	62.2	5.5	Hemiptera	Cicadellidae	HEMI.052	83.8	5.5
Trichoptera	Hydropsychidae	TRIC.002	62.2	3.4	Diptera	Muscidae	DIPT.009	81.1	8.0
Canopy					*Canopy*				
Thysanoptera	-	THYS.001C	100	413.9	Thysanoptera	-	THYS.001C	100	358.7
Diptera	-	DIPT.004C	100	52.8	Diptera	-	DIPT.004C	100	153.7
Diptera	-	DIPT.002C	100	29.5	Diptera	-	DIPT.006C	100	57.6
Diptera	-	DIPT.001C	100	20.8	Thysanoptera	-	THYS.002C	100	27.8
Hymenoptera	-	HYME.001C	100	7.6	Diptera	-	DIPT.014C	100	24.5

▼Canopy specimens were not identified past Order prior to grouping into morphospecies.

♦Canopy specimens were assigned morphospecies identifiers separately from litter and mid-story specimens as indicated by the addition of C to the end of the morphospecies ID.

Table 8. Arthropod morphospecies composition matrix correlations with plant and environmental matrices. Correlation (r_M) was determined with simple Mantel tests.

Explanatory Matrix	Litter Composition		Mid-Story Composition		Canopy Composition	
	2014	**2015**	**2014**	**2015**	**2014**	**2015**
Plant						
Species Composition	0.204*	-0.032	0.197*	0.441***	-0.063	0.179*
Non-Native Composition	-0.055	0.210*	-0.143	0.022	0.044	0.112‡
Non-Native Cover	0.027	-0.053	-0.003	0.353***	-0.025	0.169*
Functional Composition	0.281*	0.003	0.304*	0.155*	0.065	0.159*
C_3 Grass Cover	-0.046	-0.083	0.372***	0.037	-0.085	-0.110
C_4 Grass Cover	-0.079	-0.150	0.422**	0.049	-0.101	-0.099
Plant Architecture	0.044	-0.132	0.507***	0.166‡	-0.144	0.104
Height Density (cm)	0.079	-0.112	0.452***	0.092	-0.164	0.063
Dead Height (cm)	-0.081	-0.074	0.337*	0.130	-0.037	-0.069
% Intercepted PAR	-	-0.053	-	0.073	-	0.148*
Environmental						
pH	-0.017	0.238*	-0.052	0.207‡	-0.067	-0.066
Salinity	0.433*	-0.068	0.015	0.727***	0.042	0.204*
Elevation	0.053	0.171*	0.077	0.091	0.088‡	0.087‡

*** < 0.0001; ** < 0.01; * <0.05; ‡ <0.1

plant and environmental matrices within year, and within arthropod functional community correlations differed between years (**Table 8**). No arthropod functional community composition matrix ever correlated with native plant composition, native plant cover, non-grass graminoid cover, forb cover, legume cover, woody cover, bare ground, soil moisture or soil texture.

There were no plant or environmental matrices with which litter arthropod composition correlated with consistently. In year one, litter arthropod composition correlated with plant species composition, functional composition and salinity (**Table 8**). In year two, litter composition correlated with non-native plant species composition, pH and elevation (**Table 8**). Litter composition correlation with salinity in year one met the minimum criterion ($r_M \geq 0.30$ and $p \leq 0.05$) for constructing Mantel correlograms.

There were two plant matrices (plant species and functional composition) with which mid-story arthropods consistently correlated, and the only correlation with an environmental matrix occurred in year two (**Table 8**). In year one, mid-story arthropod correlations with C_3 and C_4 grass cover, height density, and dead height (cm) met the criterion ($r_M \geq 0.30$ and $p \leq 0.05$) for constructing Mantel correlograms (**Table 8**). In year two, mid-story arthropod correlations with plant non-native species cover and salinity met the criterion ($r_M \geq 0.30$ and $p \leq 0.05$) for constructing Mantel correlograms (**Table 8**).

In year one, canopy arthropod composition did not correlate with any plant or environmental matrices (**Table 8**). In year two, canopy arthropods correlated with plant species composition, non-native species cover, functional composition, percent intercepted PAR and salinity (**Table 8).** None of the canopy arthropod correlations with plant and environmental gradients met the minimum criterion ($r_M \geq 0.30$ and $p \leq 0.05$) for constructing a Mantel correlogram.

In year one, the major univariate plant composition gradients the mid-story arthropod functional community composition responded to were defined by C_3 and C_4 grass cover (**Figure 13**), and the major univariate plant community architecture gradients were defined by plant height density and dead height (cm) (**Figure 14**). In year one, salinity defined the major environmental gradient to which mid-story arthropod functional community composition responded (**Figure 14**). Each of these gradients occur in a similar N-S direction across the Oakville. Areas of higher salinity tended to have higher C_3 grass cover and lower C_4 grass cover. Height density was greatest through the

middle of Oakville. Salinity, pH, and non-native species cover define the major univariate gradients in year two (**Figure 15**). Each of these gradients occur in a similar SW-NE direction across the Oakville. Areas of higher salinity tended to have lower pH and lower non-native species cover.

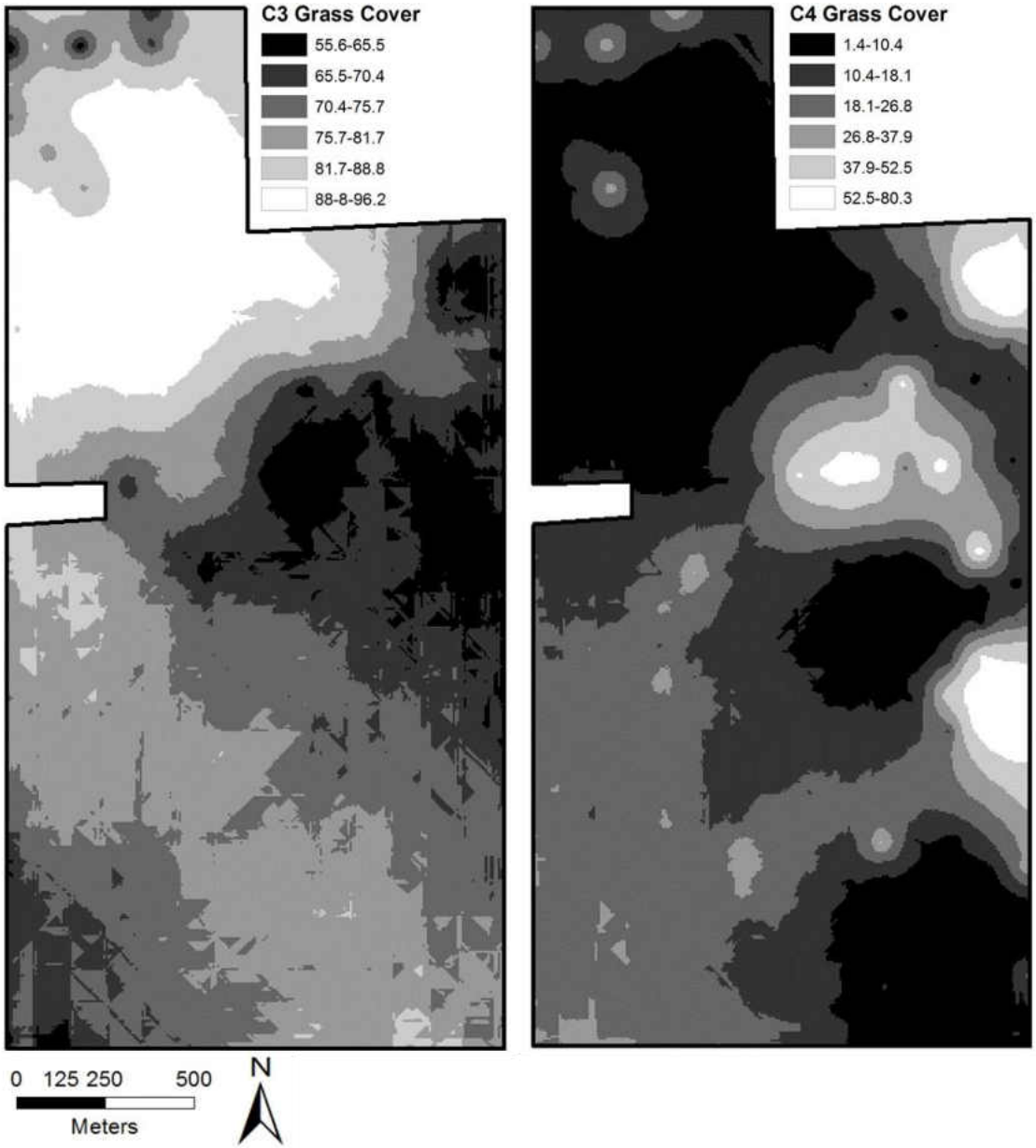

Figure 13. Year one C_3 and C_4 grass cover gradients across Oakville. Gradients determined with Empirical Bayesian Kriging models with year one values.

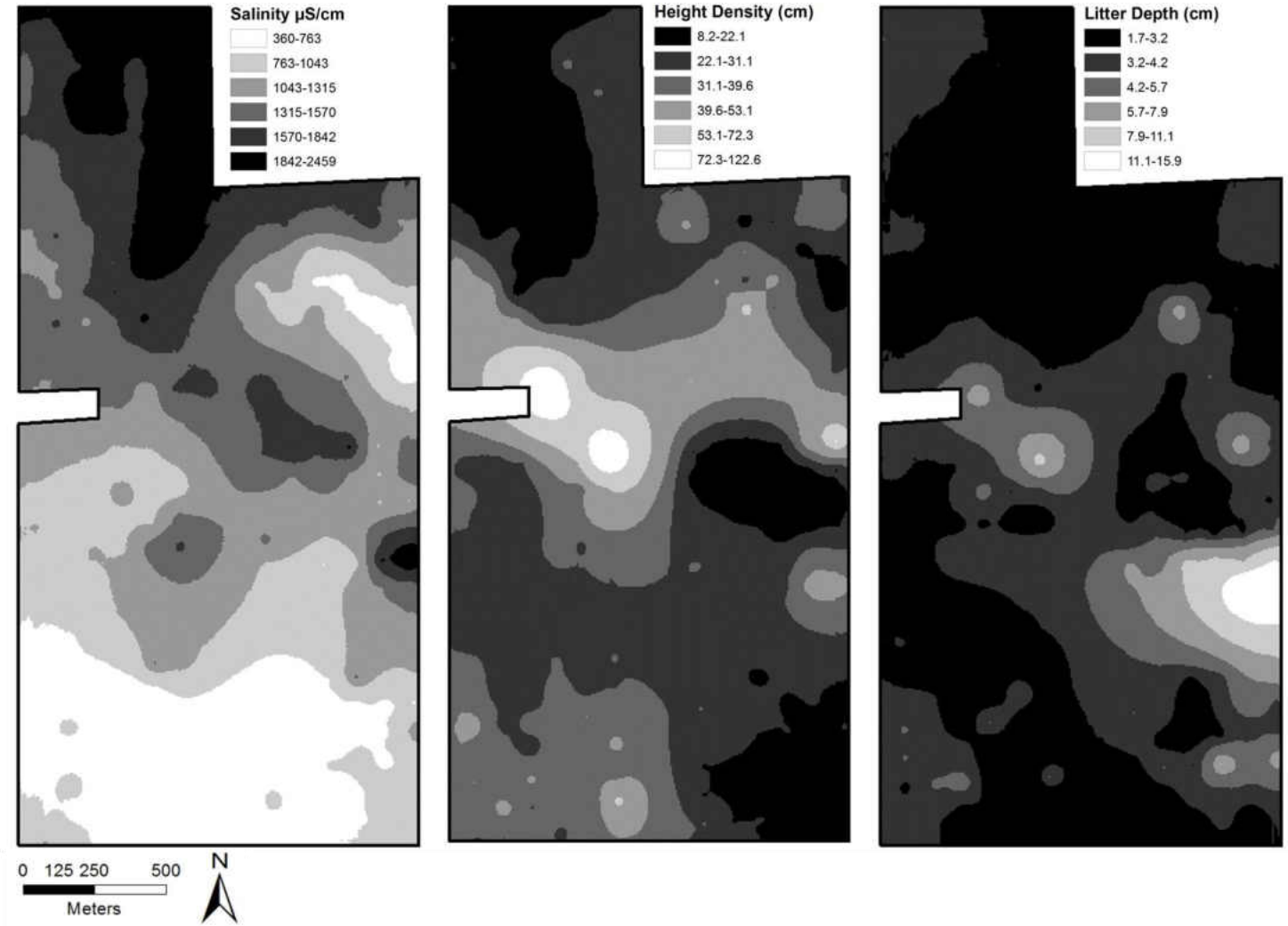

Figure 14. Year one salinity, height density, and vegetation dead height gradients across Oakville. Gradients determined with Empirical Bayesian Kriging models with year one values.

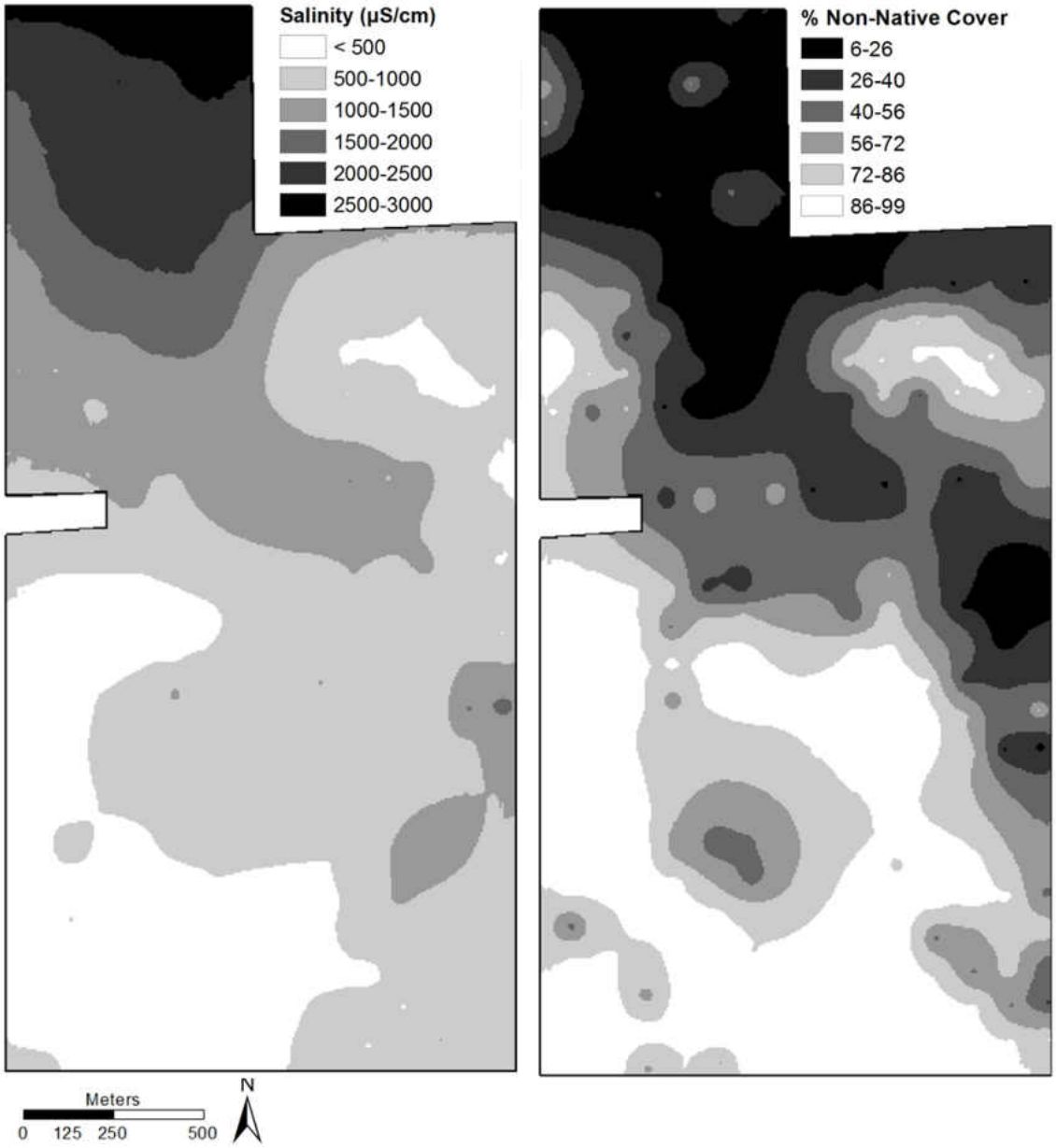

Figure 15. Year two salinity and non-native cover gradients across Oakville. Gradients determined with Empirical Bayesian Kriging models with year two values.

In year one, litter arthropod composition was structured in response to salinity. Year one litter arthropod composition was positively correlated among plots that were within 162.6 $\mu S \cdot cm^{-1}$ of one another, and negatively correlated among plots that differed by greater than 2438.5 $\mu S \cdot cm^{-1}$ (**Figure 16**).

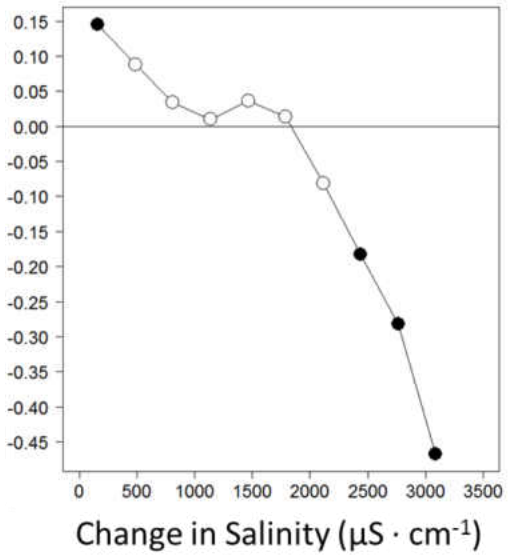

Figure 16. Mantel correlogram of year one litter arthropod composition in response to changing pH, and year two litter arthropod composition in response to changing salinity ($\mu S \cdot cm^{-1}$). Solid symbols represent values that are significantly different from zero.

Despite a strong response to the C_3 and C_4 cover gradients in year one, mid-story arthropod composition only differed among plots at the extremes of these variables. Mid-story arthropod composition was negatively correlated among plots that differed by greater than 85% C_3 cover (**Figure 17**). Mid-story arthropod composition was also negatively correlated among plots that differed by 95 % C_4 cover. Mid-story arthropod composition was more structured along the height density gradient. Mid-story composition was positively correlated among plots that were within 11.6 cm height density from one another and negatively correlated among plots that differed by more than 30.1 cm in height density (**Figure 17**).

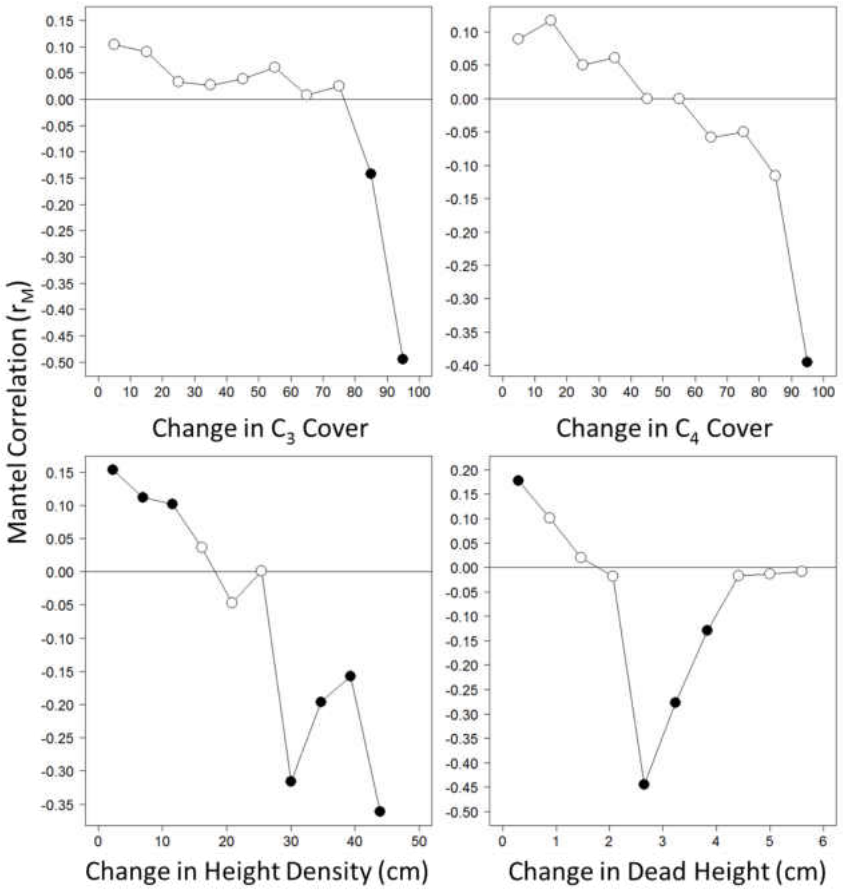

Figure 17. Mantel correlogram of year one mid-story arthropod composition in response to changing C_3 and C_4 grass cover, height density (cm), and dead height (cm). Solid symbols represent values that are significantly different from zero.

In year two, mid-story arthropod composition was negatively correlated among plots that differed by 95% non-native species cover (**Figure 18**). Mid-story arthropod composition was more structured along the salinity gradient. Mid-story composition was positively correlated among plots within 512.9 $\mu S \cdot cm^{-1}$ of one another, and negatively correlated among plots that differed by greater than 1880.5 $\mu S \cdot cm^{-1}$ (**Figure 18**).

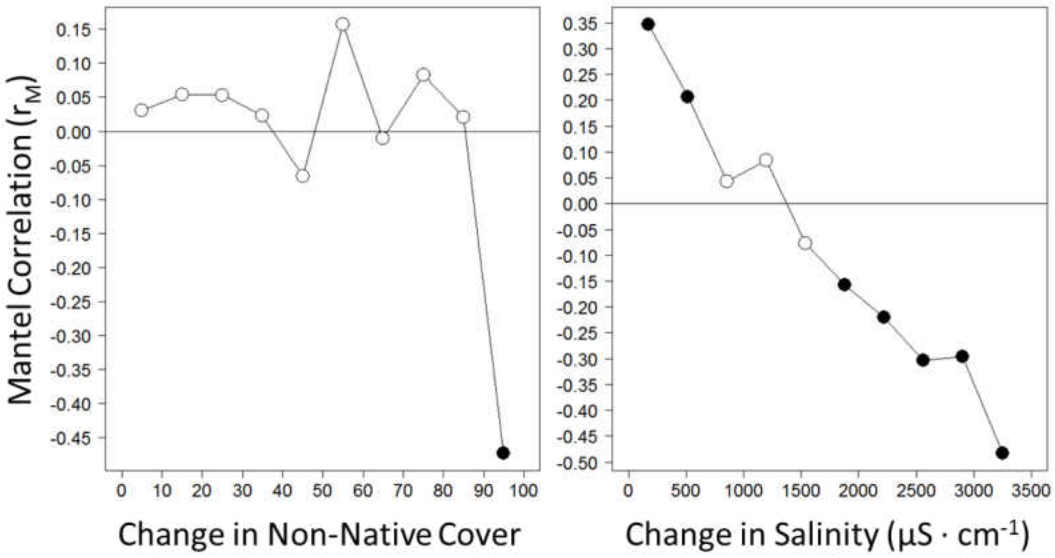

Figure 18. Mantel correlogram of year two mid-story arthropod morphospecies composition in response to changing non-native plant species cover and changing salinity (µS · cm^{-1}). Solid circles represent values that are significantly different from zero.

Discussion

Previous research has shown that grassland arthropod community composition can vary in response to plant architectural gradients (Nemec et al. 2014; Mazia et al. 2006; Horvath et al. 2015), plant compositional gradients (Torma et al. 2014; Farrell et al. 2015), and environmental gradients (Bestelmeyer & Wiens 2001; Pan et al. 2015). Several studies have shown that response to plant and environmental gradients can affect arthropod community assembly, and zonation patterns of arthropod morphospecies composition within a site (Schaffers et al. 2008; Matteson et al. 2013; Nemec et al. 2014; Torma et al. 2014; Farrell et al. 2015; Horvath et al. 2015). However, these studies tend to focus on a single functional community or include a limited number of representatives from each functional community. My study took a more complete approach, including all

collected arthropods from three functional communities (litter; mid-story; canopy). My results show that arthropod, delineated by position within the plant community, response to plant and environmental gradients differs among functional communities.

Litter arthropod composition can be affected by plant community composition (Rypstra et al. 1999; Wolkovich et al. 2009) and soil environmental variables (Pan et al. 2015; Kwon et al. 2016). The correlations of litter arthropods with plant gradients show that its relationship with plant composition was not a strong influencer of litter arthropod composition at Oakville. The trapping method used to collect litter specimens may have skewed the characterization of this community. Pitfall traps are more effective for trapping arthropods that are more active at ground level (Parsifka et al. 2007). This likely under sampled litter arthropods that are more active in the plant litter level, which may have resulted in lack of detection of a strong response to any plant gradients.

Litter arthropods did respond strongly to soil salinity in year one. Unique groupings of litter arthropod composition occurred over a short distance of change along the soil salinity gradient. Litter arthropod composition does not become distinctly different until transitioning from one extreme of salinity to the other. This means that the litter arthropod composition in the most severely saline areas are different from litter arthropod composition in the least saline areas of Oakville. This shows that salinity did affect year one litter arthropod community assembly, but that zonation occurred at broad scales along the salinity gradient.

Mid-story arthropods are dependent on plant community structure (Rypstra et al. 1999), and mid-story arthropod community composition will vary with changes in plant

community structure (Johnson & Agrawal 2005). Mid-story arthropods did respond to plant community composition and plant community architecture at Oakville. The scale of plant community composition that mid-story arthropods responded to was different between years. Mid-story arthropods responded to functional composition and C_3 and C_4 grass cover in year one and species composition and non-native cover in year two. Zonal patterns of mid-story arthropod composition in response to plant cover gradients (C_3 and C_4 grass and non-native plant species) show that mid-story arthropods only differ among plots that vary substantially in cover of these plant species. In year one, mid-story arthropods responded to plant community architecture, height density, and dead height, but did not respond to these gradients in year two. Mid-story arthropods were more well-structured in response to plant community architecture gradients than to plant composition gradients. Mid-story arthropods form distinct groups among areas that have similar height density and dead height and differ among plots that have less similar height density and dead height. The differences in response to plant composition and plant community architecture suggest physical resources provided by the plant community are more important to patterns in mid-story arthropods than the actual species or functional groups that are present.

In year two, mid-story arthropods responded strongly to salinity. There was a steeper salinity gradient in year two (**Chapter II; Figure 2**) which may have influenced nutrient content and morphology of plants along the salinity gradient (Hester 2001; Johnson & Agrawal 2005). Changes in plant morphology and nutrient content will affect herbivore community composition which will have cascading effects on the composition

of their predators (Johnson & Agrawal 2005). This may have led to the well-structured zonation patterns of mid-story arthropods in response to salinity, and may explain why they were more well-structured in their response to salinity than litter arthropods in year one.

The canopy community did not form correlations with any plant or environmental gradients in year one, but did form correlations with plant and environmental gradients in year two. Canopy arthropod correlations with plant and environmental gradients in year two may show increased use of the site in favorable years. There were fewer precipitation events in the months in which arthropod collection occurred in year two, which may have affected the abundance of aerial arthropods at the site (Gruebler et al. 2008). Oakville is an open grassland which does not provide much protection from wind and rain to aerial arthropods, and this may have an effect on how it is used by the canopy community (Gruebler et al. 2008). However, canopy arthropods did not respond strongly to any plant or environmental gradients which suggests that site-scale gradients may not influence canopy community assembly. This may be due to the highly mobile nature of this community.

Each arthropod functional community was structure along plant and environmental gradients with which they strongly responded. This shows that there are niche-based assembly processes acting on each arthropod functional community. However, if arthropod community assembly were driven solely by niche-based processes, as is predicted with deterministic assembly, they would have responded to the same gradients in each year. The inconsistent response to plant and environmental gradients in

each arthropod functional community suggest that there are also stochastic processes acting on arthropod community assembly in each functional community. The presence of niche-based and stochastic processes suggest that Oakville arthropod community assembly is in accordance with the alternative stable states theory of community assembly.

Arthropod communities, and their relationship with the plant community, form the base of grassland food-webs. Interactions with plant and environmental gradients can determine how arthropod communities assemble and form patterns of community composition. Arthropod community composition and patterns within a site can influence how arthropods function in grassland habitats (Fox-Dobbs et al. 2010; Pringle et al. 2010). Yet our understanding of how arthropod communities assemble and form zonation patterns of composition in response to plant and environmental gradients is limited. This study shows that arthropod response to plant and environmental gradients can vary based on location within the plant community. Understanding how arthropod community assembly occurs in remnant grasslands may inform our understanding of how community assembly will occur in grassland restorations (Wodika & Baer 2015). This can help restoration efforts, which typically solely focus restoration of plant communities, to better plan restorations that will include grassland arthropods.

CHAPTER IV

CONCLUSIONS

Soil environmental variables can function as abiotic filters that influence assembly and distribution within plant and arthropod communities (Nelson & Anderson 1983; Potts & Wilmer 1997; Fattorini & Halle 2004; Klimek et al. 2007; Pan et al. 2015; Kwon et al. 2016). Additionally, arthropod interactions with plant community can function as biotic filters that influence assembly and distribution within arthropod communities (Siemann 1998; Fantinato et al. 2016; Lengyel et al. 2016). However, we do not have a good understanding of how assembly processes act across multiple taxonomic levels to influence grassland plant and arthropod community structure. The associations among plants, arthropods and environmental gradients can show how assembly occurs in plant and arthropod communities to maintain patterns of community composition.

Seabloom & van der Valk (2003a) used Mantel tests to show that prairie wetland plant species composition responds directly to environmental gradients, and Mantel correlograms to show how zonation patterns form in the plant community in response to these environmental gradients. They showed that plant species composition in natural and restored prairie wetlands respond to a single environmental gradient (water depth). My study expands on this by using Mantel tests to show direct response across multiple taxonomic groups (plants and arthropods) to environmental gradients and each

other in a more complex system than prairie wetlands. I also employed Mantel correlograms to show how zonation patterns form in response to the gradients that strongly influenced plant and arthropod community composition.

There were three environmental gradients (elevation, soil moisture, and soil salinity) that plant community composition consistently responded to in both years of the study. Change in elevation has been shown to influence plant community composition (Andersen et al. 2015), and soil salinity and soil moisture can function as abiotic filters that can determine spatial patterns in plant communities (Smith et al. 2015). Elevation changed from upland to lowland along a SW to NE gradient, and change in soil moisture and soil salinity occurred in this same direction (**Chapter II; Figure 7**). However, the extent of change along each of these gradients differed. Soil moisture was the most heterogeneous and soil salinity was the least heterogeneous over geographic space.

Overall, community assembly in response to elevation, soil moisture, and soil salinity was occurring deterministically across plant species and functional composition metrics. Even though community assembly was occurring in the same ways across plant species and functional composition metrics responses varied between them. Response of functional composition was driven by three functional groups: forb, legume, and woody. C_3 and C_4 grass composition did not respond to any environmental gradients. Zonation patterns of functional composition metrics were less well defined than zonation patterns of plant species composition metrics. Zonation patterns also varied depending on the environmental gradient that was driving response in the plant community.

Zonation patterns were most similar along the elevation gradient (**Figure 19**). Distinct groupings occurred over the same range in species composition, native species composition, non-native species cover, and woody cover. Zonation patterns in response to soil moisture were more variable than in response elevation or soil salinity (**Figure 19**). This creates more spatial heterogeneity of species and functional composition metrics in response to soil moisture than the other gradients because soil moisture is more geographically heterogeneous and plant composition responses are more variable. Zonation patterns of plant species composition and non-native species cover were similar in response to soil salinity, and they were defined than over shorter ranges of salinity than the response of forb cover. Responses to soil salinity will create less spatial heterogeneity in plant species and functional composition across Oakville. Soil salinity is less geographically heterogeneous than elevation and soil moisture. Even the more well defined groupings of plant species composition and non-native species cover will remain similar over wider geographic distances across Oakville because of the broader extent of change across the site in response to salinity.

Arthropod response to plant gradients was more complex than the responses of the plant community to environmental gradients. Arthropod functional communities (litter; mid-story; canopy) did not consistently correlate with any plant gradients, showing a different response of these three functional communities. Within each arthropod functional community response to environmental gradients between years was inconsistent. The inconsistencies in response to indicate that there is some stochasticity acting on arthropod community assembly. However, non-random distribution along plant

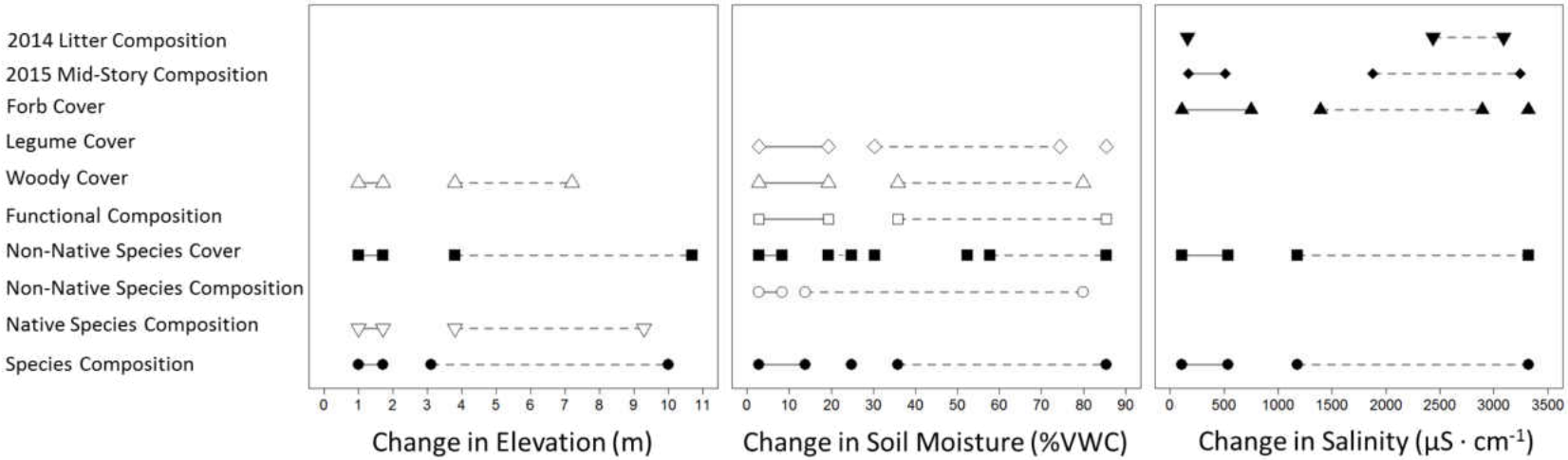

Figure 19. Response of plant and arthropod metrics to changes of elevation (m), soil moisture (% VWC), and salinity ($\mu S \cdot cm^{-1}$) as determined with Mantel correlograms in Chapters II and III. Solid lines represent range of positive correlation, and dashed lines represent range of negative correlation.

and environmental gradients indicates that there are some niche-based processes also acting on arthropod community assembly.

Litter arthropods responded strongly to soil salinity in year one, but did not respond strongly to plant gradients which suggests that litter community assembly is most strongly influenced by salinity at Oakville. Mid-story arthropods responded to soil salinity in year two, and were more well-structured along this gradient than litter arthropods were in year one (**Figure 19**). The salinity gradient was steeper in year two than it was in year one which may account for the differences in structure along the salinity gradient between these two arthropod functional communities (**Chapter II; Figure 2**). Zonation patterns of mid-story arthropods in response to salinity were similar to plant species composition and non-native species cover (**Figure 19**). However, mid-story patterns were less well defined. Mid-story arthropod community response to soil salinity was assessed with data from 37 plots that were widely distributed across Oakville, while the plant community response to soil salinity was assessed with data from 229 plots that were more evenly distributed across Oakville. The differences in sample size and distribution of data collection points may be causing the differences seen in zonation patterns between plants and mid-story arthropods.

The mid-story arthropod functional community was the only arthropod functional community to respond strongly to plant gradients. Mid-story arthropod response to plant gradients was not influenced by plant gradient response to environmental gradients. In year one mid-story arthropod community composition responded to plant gradients (C_3 and C_4 grass cover) that did not respond to any environmental gradients. In year two,

mid-story arthropods responded to plant species composition and non-native species cover, but patterns of mid-story arthropod composition in response to non-native species cover were not similar to patterns of non-native species cover in response to environmental gradients. Mid-story arthropod composition did not become structured until reaching extreme differences in non-native species cover. In year one, mid-story arthropods also responded to plant community architecture, height density, and dead height. None of these plant gradients responded to environmental gradients.

Canopy arthropods did not correlate with any gradients in year one and did not respond strongly to any plant or environmental gradients in year two. This suggests that site-scale gradients may not be strongly influencing assembly or zonation patterns in canopy arthropods, and is not able to provide much insight into how they used Oakville.

My results show how assembly occurs in grassland plant communities in response to strong environmental gradients, and how assembly occurs in grassland arthropod communities in response to plant and environmental gradients in the same space. Environmental gradients (elevation, soil moisture, and soil salinity) strongly influence plant community assembly similarly across all resolutions of community in response to these gradients. Though, patterns of plant species and functional composition varied in response to environmental gradients. Arthropod functional community response to plant and environmental gradients differs with location in the plant community, and mid-story arthropods was the only community that responded to plant and environmental gradients. Mid-story arthropod community assembly along plant gradients was not similar to plant community assembly along environmental gradients. However, mid-story arthropod

community assembly in response to salinity was very similar to plant community assembly in response to salinity.

APPENDIX A:
ADDITIONAL FIGURES AND TABLES

Table A.1. Mean year one and year two daily temperature (°C), daily wind speed (km · h^{-1}) and per precipitation event accumulation (mm) summary for field season by month in year one and year two. Mean values calculated from data collected at the Grand Forks Air Force Base, ND weather station. Data were retrieved from http://www.wunderground.com.

Weather Metric		May		June		July		August	
		2014	**2015**	**2014**	**2015**	**2014**	**2015**	**2014**	**2015**
Mean Daily Temperature (°C)	High (se)	18.2 (1.4)	18.2 (1.3)	23.3 (0.6)	24.4 (0.7)	25.5 (0.6)	27.0 (0.5)	25.1 (0.5)	26.5 (0.7)
	Average (se)	12.3 (1.1)	11.4 (0.9)	18.1 (0.4)	18.2 (0.5)	19.4 (0.6)	21.1 (0.5)	19.5 (0.4)	19.4 (0.7)
	Low (se)	6.6 (1.1)	4.7 (0.8)	13.0 (0.5)	12.0 (0.5)	13.4 (0.5	15.4 (0.6)	13.9 (0.6)	12.2 (0.7)
Mean Daily Wind Speed (km · h^{-1})	High (se)	27.3 (1.6)	30.0 (2.2)	29.5 (1.7)	26.9 (1.7)	27.5 (2.2)	27.1 (2.1)	22.9 (1.9)	25.1 (1.6)
	Average (se)	14.8 (1.9)	16.1 (1.5)	15.1 (1.0)	12.4 (0.9)	13.6 (1.1)	13.1 (1.2)	10.5 (0.8)	11.9 (1.0)
Mean Gusting Wind Speed (km · h^{-1})	Days with Gusts	20	25	25	21	19	17	14	15
	Mean Gusts (se)	44.2 (1.9)	44.7 (3.2)	47.1 (3.8)	44.6 (2.4)	45.5 (2.8)	46.9 (3.9)	42.4 (5.5)	44.1 (2.9)
Per Event Precipitation (mm)	Events	15	14	16	14	8	10	8	3
	Accumulation (se)	5.1 (1.5)	9.0 (3.8)	9.9 (3.8)	6.5 (2.1)	16.6 (14.1)	10.9 (2.9)	8.8 (2.5)	19.6 (10.3)

Table A.2. Correlations of year one and year two plant community matrices with environmental matrices. Values represent Mantel correlation (r_M; 9999 permutations). Values that meet the criteria for strong correlation ($r_M \geq 0.20$ and $p < 0.01$) are listed in bold text.

Plant Matrix	pH		Soil Salinity		Soil Texture		Soil Moisture		Elevation	
	2014	**2015**	**2014**	**2015**	**2014**	**2015**	**2014**	**2015**	**2014**	**2015**
Species Composition	0.064**	0.071**	**0.265*** **	**0.322*** **	0.059**	0.124***	**0.323*** **	**0.383*** **	**0.244*** **	**0.346*** **
Native Species Composition	-0.015	0.046‡	0.154***	0.167***	0.0001	0.028	0.095**	0.188***	0.147***	**0.225*** **
Non-Native Species Composition	0.062*	0.050‡	0.003	0.028	0.111***	0.091**	**0.278*** **	**0.305*** **	0.062**	0.189***
Non-Native Percent Cover	0.030**	0.051*	0.128***	**0.293*** **	0.068***	0.073***	**0.215*** **	0.190***	0.125***	**0.264*** **
Functional Group Composition	0.042‡	0.045‡	0.173***	0.172***	0.061*	0.093*	**0.238*** **	**0.313*** **	**0.226*** **	0.120***
C3 Grass Cover	-0.031	0.02	-0.050	-0.008	-0.025	-0.041	-0.050	-0.030	0.038	0.048‡
C4 Grass Cover	-0.004	-0.051	-0.045	-0.059	-0.035	-0.055	-0.070	-0.052	0.075**	0.062*
Graminoid Cover	-0.036	0.088‡	0.052‡	0.067‡	0.019	0.033	-0.061	-0.05	0.016	0.076*
Forb Cover	0.001	-0.002	0.084***	0.199***	0.049	0.03	0.051*	0.037	0.034	0.094***
Legume Cover	0.022	0.064‡	0.052‡	-0.021	0.049	-0.007	**0.422*** **	**0.478*** **	0.091**	0.163***
Woody Cover	0.042	-0.024	0.056‡	-0.018	0.064‡	0.024	**0.327*** **	**0.520*** **	0.194***	0.022***
Plant Architecture	0.072‡	0.010	0.0004	0.163***	-0.049	-0.007	0.005	0.25	-0.004	0.074**
Height Density	0.070‡	0.020	0.005	0.027	-0.049	-0.017	0.044	0.057‡	0.006	0.072*
Dead Height	0.006	0.002	-0.025	0.005	-0.005	-0.040	-0.049	-0.052	-0.060	-0.006
Bare Ground	-	-0.063	-	**0.211*** **	-	0.002	-	-0.056	-	0.022
PAR	-	-0.066	-	**0.283*** **	-	0.038	-	0.113**	-	0.129***

*** < 0.001; ** < 0.01; * < 0.05; ‡ < 0.1

Table A.3. Correlations among year one environmental variables. Values represent Pearson's correlation coefficient (r). Significant values ($p < 0.05$) have been marked with an asterisk.

Environmental Variables	pH	Salinity	Sand Content	Clay Content	Silt Content	Seasonal Moisture
pH	1					
Salinity	-0.362*	1				
Sand Content	0.177*	-0.415*	1			
Clay Content	-0.055	-0.243*	-0.187*	1		
Silt Content	-0.075	0.496*	-0.530*	-0.734*	1	
Seasonal Moisture	-0.222*	0.704*	-0.543*	0.013	0.364*	1
Elevation	0.016	-0.489*	0.524*	0.262*	-0.587*	-0.561*

Table A.4. Correlations among year two environmental variables. Values represent Pearson's correlation coefficient (r). Significant values ($p < 0.05$) have been marked with an asterisk.

Environmental Variables	pH	Salinity	Sand Content	Clay Content	Silt Content	Seasonal Moisture
pH	1					
Salinity	-0.498*	1				
Sand Content	0.251*	-0.403*	1			
Clay Content	-0.020	-0.278*	-0.187*	1		
Silt Content	-0.156*	0.519*	-0.530*	-0.734*	1	
Seasonal Moisture	-0.401*	0.564*	-0.538*	0.014	0.360*	1
Elevation	0.196*	-0.511*	0.524*	0.262*	-0.587*	-0.607*

Table A.5. Correlations among year one plant community matrices. Values represent Mantel correlation (r_M).

	Species Composition	Functional Composition	C3 Cover	C4 Cover	Graminoid Cover	Forb Cover	Legume Cover	Woody Cover	Native Composition	Non-Native Composition	Non-Native Cover
Functional Composition	0.441***	1									
C3 Cover	0.177***	0.245***	1								
C4 Cover	0.137***	0.258***	0.648***	1							
Graminoid Cover	0.093**	0.108**	0.091*	-0.012	1						
Forb Cover	0.140***	0.101***	0.056*	-0.022	0.003	1					
Legume Cover	0.025	0.104**	-0.067	-0.094	-0.064	0.003	1				
Woody Cover	0.123***	0.169***	0.007	-0.062	-0.059	-0.069	0.213**	1			
Native Composition	0.433***	0.257***	0.263***	0.340***	0.172***	0.125***	-0.046	0.066*	1		
Non-Native Composition	0.157***	0.058*	-0.077	-0.13	-0.051	0.025	0.199***	0.136**	-0.151	1	
Non-Native Cover	0.325***	0.162***	0.019*	0.017‡	-0.004	0.095***	0.071***	0.047***	0.246***	0.492***	1
Plant Architecture	0.291***	0.228***	0.310***	0.119*	0.023	0.189***	-0.03	0.028	0.229***	-0.076	0.016‡

*** < 0.001; ** < 0.01; * < 0.05; ‡ < 0.1

Table A.6. Correlations among year two plant community matrices. Values represent Mantel correlation (r_M).

	Species Composition	Functional Composition	C3 Cover	C4 Cover	Graminoid Cover	Forb Cover	Legume Cover	Woody Cover	Native Composition	Non-Native Composition	Non-Native Cover
Functional Composition	0.501***	1									
C3 Cover	0.242***	0.145**	1								
C4 Cover	0.149***	0.092*	0.672***	1							
Graminoid Cover	0.073*	0.192***	0.090‡	0.105*	1						
Forb Cover	0.247***	0.192***	0.103**	0.012	0.065‡	1					
Legume Cover	0.125***	0.176***	-0.028	-0.052	-0.067	0.033	1				
Woody Cover	0.176***	0.254***	-0.012	-0.012	-0.066	-0.017	0.349***	1			
Native Composition	0.485***	0.260***	0.344***	0.425***	0.177***	0.161***	0.078*	0.098**	1		
Non-Native Composition	0.284***	0.182***	0.002	-0.053	-0.081	0.046*	0.279***	0.225***	0.174***	1	
Non-Native Cover	0.490***	0.322***	0.131***	0.082***	-0.075	0.168***	0.052*	0.037*	0.518***	0.463***	1
Plant Architecture	0.376***	0.196***	0.428***	0.135**	-0.022	0.150***	-0.022	0.053	0.260**	-0.046	0.193***

*** < 0.001; ** < 0.01; * < 0.05; ‡ < 0.1

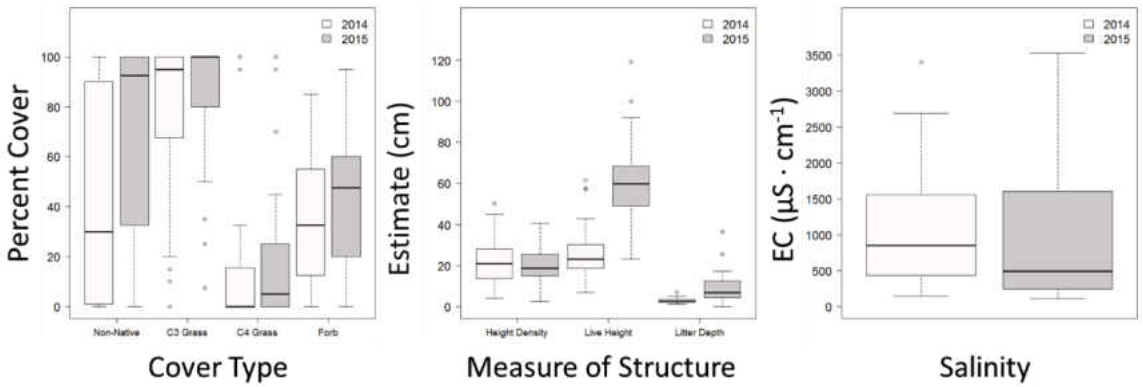

Figure A.1. Plant and environmental variables which were strongly correlated with at least one arthropod matrix in one but not both years of the study. Boxplots represent data collected at arthropod sample locations.

Table A.7. Specimen count and number of orders, families and morphospecies represented in each arthropod functional community at Oakville in year one and year two.

Functional Community	Number of specimens		Number of Orders		Number of Families		Number of Morphospecies	
	2014	2015	2014	2015	2014	2015	2014	2015
Litter	4092	3686	20	19	79	95	110	146
Mid-Story	4480	8231	17	14	94	113	177	186
Canopy	23411	31137	14	16	-	-	127	183

Table A.8. Number of families and morphospecies identified in the five most frequently collected orders in each arthropod functional community across years.

Functional	Litter				Mid-Story				Canopy	
	2014		2015		2014		2015		2014	2015
Community	Families	Morphospecies	Families	Morphospecies	Families	Morphospecies	Families	Morphospecies	Morphospecies	Morphospecies
Araneae	8	15	9	16	9	15	10	19	11	13
Coleoptera	11	17	13	22	15	25	17	32	22	22
Diptera	14	17	28	34	34	59	34	55	40	62
Hemiptera	10	17	7	21	18	47	16	48	17	33
Hymenoptera	10	12	11	16	16	24	20	30	19	32

Table A.9. Correlations among year one Oakville arthropod functional community composition and diversity matrices. Values represent Mantel correlation (r_M).

	Litter Composition	**Mid-story Composition**	**Canopy Composition**
Litter Composition	1		
Mid-story Composition	0.137‡	1	
Canopy Composition	0.096	-0.087	1

*** < 0.001; ** < 0.01; * < 0.05; ‡ < 0.1

Table A.10. Correlations among year two Oakville arthropod functional community composition and diversity matrices. Values represent Mantel correlation (r_M).

	Litter Composition	**Mid-story Composition**	**Canopy Composition**
Litter Composition	1		
Mid-story Composition	-0.080	1	
Canopy Composition	0.026	0.114	1

*** < 0.001; ** < 0.01; * < 0.05; ‡ < 0.1

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