Spatial pattern of the shrub layer across the subarctic landscape of Churchill Manitoba

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ENVS 4902
March 28th, 2014

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Acknowledgements

I would like to thank Dr. Karen Harper for her continual guidance through the stages involved in this research project, as well as Pavel Dodonov for his extensive field advice and continual support in all stages of the project, and Danielle St. Louis for her field assistance and guidance. I also thank Dr. Tarah Wright and Dr. Shannon Sterling for their lessons on writing an effective research proposal and thesis.

Funding and logistical support were provided by the Churchill Northern Studies Centre, the Strategic Cooperative Education Incentive, Natural Sciences and Engineering Research Council of Canada, and the Northern Scientific Training Program.

Abstract

The shrub layer provides important habitat for wildlife throughout the harsh environment of the arctic tundra landscape. Studies have shown that the shrub layer is expanding in tundra landscapes and changing habitat conditions due to climate warming. My research goal was to determine the spatial pattern of the shrub layer across the tundra and forest-tundra ecotone landscapes. Data were collected in 1x1 m contiguous quadrats along two 500 m long transects in open tundra and across the forest-tundra ecotone. Within each quadrat, I identified shrub species, recorded their cover and height, and also sampled explanatory variables (soil pH and microtopography). I used wavelet analysis to determine the locations of significant patches and gaps in the shrub layer. Results indicate that distance to a natural or created edge, and microtopography were the environmental variables that best explained the spatial pattern of shrubs across tundra and forest-tundra ecotone landscapes. Throughout both habitat types, shrub height and diversity increased closer to lakeshore edges. The pattern of the shrub layer in the tundra showed gradual changes with relatively uniform distributions of prostrate shrub species. The ecotone displayed a pattern of abrupt changes in shrub habitat with fine-scale variation in shrub diversity and height. The heterogeneity of the shrub layer in subarctic regions will likely continue to change with further climate change.

1.0 Introduction

Over the past several decades, the distribution of vegetation has been changing across arctic landscapes. Many scientists believe that the northward shift in vegetation is a result of climate change, which has been affecting northern latitudes more intensely than lower latitudes (Serreze et al., 2000; Bret-Harte et al., 2002; Danby & Hik, 2007). Of the several different vegetative life forms, the shrub layer has been observed to move northward first while the other life forms, such as coniferous trees, lichens, and mosses, follow behind (Myers-Smith et al., 2011). Previous studies have focused on tree line advancements in the subarctic due to climate change (Danby & Hik, 2007; Harsch et al., 2009); however, fewer studies have focused on other vegetative layers such as the shrub layer and what influences its spatial distribution on a landscape level. I focused on the spatial pattern and distribution of shrub species across two habitats in the subarctic landscape and examined environmental factors that influence the spatial pattern of shrubs on a landscape level.

Vegetation across the subarctic landscape is highly heterogeneous. The Churchill region in Manitoba is situated in the transition zone between the boreal forest and arctic tundra biomes and, as a result, has an array of vegetative communities that intersect and overlap (Harper et al., 2011). Within the forest-tundra ecotone there is a diverse shrub layer that ranges from dwarf prostrate shrubs to tall dense bushes. The range in shrub growth can be used as habitat by other species to serve as protection from the Arctic climate conditions. Understanding the spatial pattern of the shrub layer across the tundra and ecotone landscapes will be useful fundamental knowledge to infer relationships between shrub distributions and the environmental factors that appear to facilitate shrub growth and patches.

1.1 Background information

The Arctic tundra is an area where the sub-soil layer is permanently frozen at varying depths throughout the landscape, and the layer of topsoil above the permafrost is thin (Schultz, 1969). The dominant vegetation in the Arctic tundra is composed of prostrate shrubs, grasses, lichens, and mosses (Britton, 1966). The boreal forest-tundra ecotone is defined as a transition zone between two adjacent habitats, the area of convergence between the boreal forest and the Arctic tundra (Harper et al., 2011). Vegetation in the forest-tundra ecotone consists of the dominant white spruce (*Picea glauca*), black spruce (*Picea mariana*), and tamarack (*Larix laricina*) trees found in the boreal forest, as well as tall and prostrate shrubs, grasses, lichens, and heath habitat (Johnson & Fairfield, 1987). The ecotone landscape is very heterogeneous with sparse patches of trees interspersed with tundra lichen-heath and permafrost soils.

A shrub is defined as a plant with a woody or semi-woody component that retains some portion of living biological tissues above ground year-round and is low growing in height (Rundell, 1991). Across the subarctic, taller shrubs are 40 cm in height or higher with bases containing multiple stems and shoots. Examples of taller shrub species of northern Manitoba are willows (*Salix* spp.), birches (*Betula* spp.), and alders (*Alnus* spp.). Erect dwarf shrubs of intermediate height are 10-40 cm tall, and dominate in ecotone areas and pockets of tundra. Examples of intermediate shrubs in the arctic are berry species (*Vaccinium* spp.), shorter willows (*Salix* spp.), bearberries (*Arctostaphyolos* spp.), and *Rhododendron* spp. In the open tundra there are prostrate dwarf shrubs that grow between 0 and 10 cm tall, and include common shrubs such as crowberry (*Empetrum nigrum*), mountain-avens (*Dryas intergrifolia*) *Andromeda polifolia*, *Salix reticulata*, and *Vaccinium vitis-idaea*.

1.2 Environmental relevance

In the arctic, the growing season is short and the permafrost layer can range from a few centimeters to several meters in depth (Smith et al., 2010). The shrub layer is often the tallest plant layer present. In the northernmost latitudes of North America, the older, more mature shrubs play a key role in aboveground carbon sequestration (Michaelson et al., 1996). The expansion of the shrub layer across the subarctic tundra will affect the carbon cycle dynamics of the Canadian Arctic by increasing carbon sequestration (Michaelson et al., 1996). In addition, the shrub layer has been known to modify its environment to facilitate warmer climate zones, which would increase the potential for further northward vegetation shifts (Myers-Smith et al., 2011).

The expansion of the shrub layer will also provide more habitat for some species. For example, any increase in plant foliage, abundance and height will result directly in an increase of avian species occupying the area (Willson, 1974). Common avian species occupying the tundra landscape and actively using the shrub layer are snow geese (*Chen caerulescens)*, arctic terns (*Sterna paradisaea*), rock ptarmigans (*Lagopus muta*), tundra swans (*Cygnus columbianus*), and many others (Davidson et al., 2008). In addition to the increase in bird abundance in the tundra landscape, an increase in herbivores could also result from the shrub layer expansion. Arctic herbivores such as the arctic hare (*Lepus arcticus*) and the muskox (*Ovibos moschatus*) depend on the presence of a healthy shrub layer to eat berries, seeds, woody branches, and foliage of many different species of shrubs (Klein & Bay, 1994). As such, shrub species are a fundamental component of the arctic food web; they are a critical primary energy source consumed by herbivores and distributed to higher trophic level organisms.

From an anthropogenic perspective, shrubs have a significant nutritional and medicinal value to humans living in northern areas, in particular the arctic indigenous peoples belonging to the Innu and Métis communities (Karst, 2010). Berry shrubs found in the north such as blueberry, cranberry, crowberry, and cloudberry provide a significant source of vitamins to the human diet. For example, vitamins A and C, fiber, and calcium can be found in all of these species (Porsild, 1953). It is common for members of aboriginal communities to gather berries in the summer months and to store them to eat year-round by making jams or jellies, freezing them, or drying them as methods of preservation (Karst, 2010). Shrubs are also commonly used in traditional herbal healing practices as natural methods of boosting the immune system to increase well-being and to maintain good health (Karst, 2010). Often, scientists and tourists rely on the knowledge of the arctic indigenous people to seek out the locations of the best berry patches and to learn the history of edible shrubs in the area. My study of the spatial pattern and distribution of shrub species in relation to landscape features could add to the existing knowledge on what factors can be related to dense shrub patches. Furthermore, knowing the factors that influence the location of shrub patches will be useful knowledge for researchers or local residents to predict future locations of shrub patches as the subarctic region continues to undergo shrub expansion as a result of climate change.

2.0 Background and literature

2.1 Arctic shrub expansion

Within the past decade, shrub densification has been occurring at many different sites across the Arctic biome (Chapin et al., 2005; Myers-Smith, 2007; Myers-Smith et al., 2011; Blok et al., 2011; Hallinger & Wilmking, 2011). Hallinger et al. (2010) classify three distinct forms of shrub expansion: (1) an increase of shrubs growing between gaps within the landscape known as “infilling”, (2) an increase in vertical and horizontal growth of the shrubs, (3) the colonization of new shrub seedlings beyond the previous range of occurrence. The northward movement of shrub vegetation is a dynamic phenomenon and the ecological impacts and magnitude of the trend remain uncertain. Mechanisms predicted to influence shrub expansion are temperature variations, incoming radiation, growing season length, annual precipitation, soil moisture, nutrient availability, disturbances, and snow pack or soil compression (Myers-Smith et al., 2011). These mechanisms operate as feedback systems that are subject to change as climate and environmental inputs change (Myers-Smith et al., 2011). The expansion of the shrub layer is expected to affect global, local, and regional scale feedback systems in positive, negative, and undeterminable relationships (Figure 1, Myers-Smith et al., 2011).

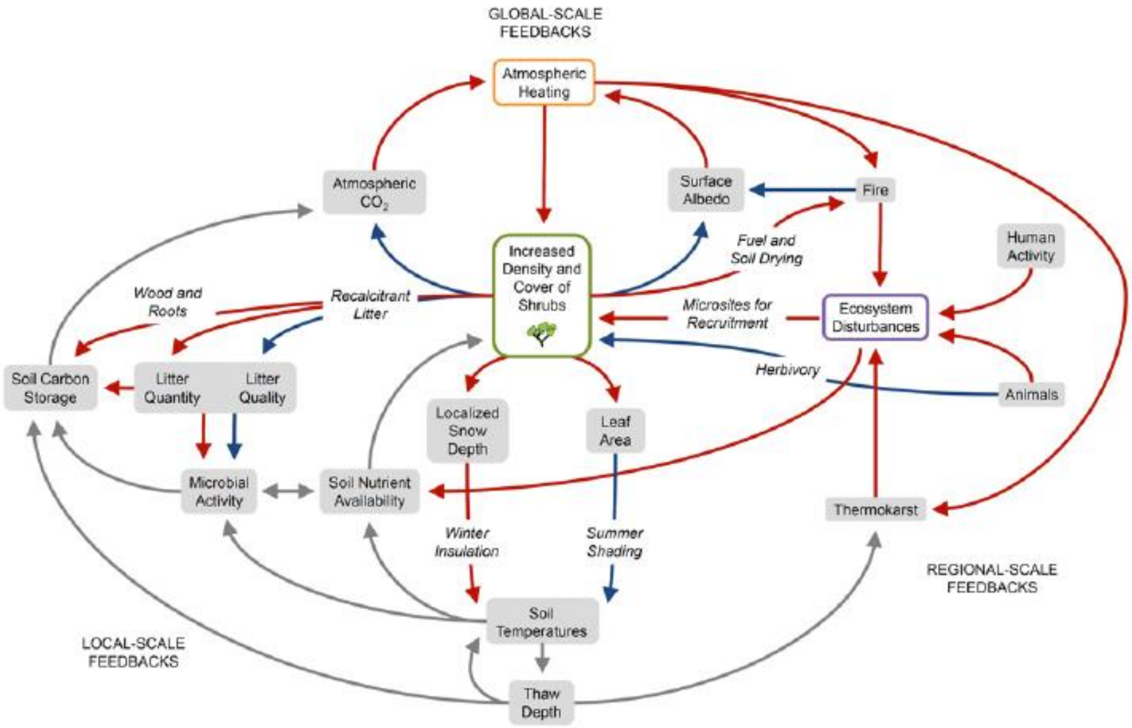

Figure 1. Potential feedback loops resulting from increased shrub density on ecosystem processes and properties in arctic ecosystems. Red arrows indicate positive relationships, blue arrows indicate negative relationships, and the grey arrows indicate undetermined influences on the connected entities. Diagram from Myers-Smith et al. (2011).

Shrub expansion in the subarctic landscape may cause physical environmental changes to ecosystem properties and patterns in the affected area (Hallinger et al., 2010; Myers-Smith et al.; 2011, Sturm et al.; 2005). During the winter a patch of tall dense shrubs creates a snow trap where snow accumulates as a blanket over the shrub canopy. This snow blanket results in a thermal air trap below the snow keeping the soil underneath the shrubs warmer than in neighboring areas with no shrub cover (Sturm et al., 2001). Strum et al. (2001) showed that soil temperature in the winter season below a dense shrub patch was as much as 30 °C warmer then the soil temperature in an adjacent open tundra area. The warmer soils below shrubs may result in the inability of the permafrost to regenerate during the cold winter months, thereby maintaining a lower or decreased proportion of permafrost soil in those affected locations.

During the early spring months the increase in shrub foliage is associated with lower albedo, which is defined as the increase in absorption and decrease in reflection of the incoming shortwave radiation (Blok et al., 2011). The trend of decreasing albedo across the arctic landscapes over the last few decades has been observed to be more significant over shrub covered surface areas than non-shrub covered areas (Blok et al., 2011). The increase in shrub cover and density in the subarctic landscape is projected to reduce albedo in the spring and summer months and reduce the regeneration of permafrost in the winter months. Therefore, shrub expansion can facilitate further climate warming in the tundra and forest-tundra ecotone.

However, contrasting ideologies regarding the role of shrub expansion on facilitating further climate change effects have been published in the recent literature. Shade resulting from taller shrub patches on the landscape is believed to create cooler soil temperatures, which might explain the decrease in permafrost thaw under shrub patches (Blok et al., 2011; Marsh et al., 2010). In addition, shrub shading in the spring can contribute to the delay of snowmelt surrounding shrub patches, which also decreases or delays the degradation of permafrost that may occur in midsummer, temporarily mitigating climate warming (Blok et al., 2011). In the spring, areas under shrub patches are cooler than areas open to full sunlight (open tundra), and in the winter, areas under shrubs are warmer than areas exposed to extreme cold winds (Blok et al., 2011). Changes to the abundance and density of the shrub vegetation in arctic regions may mitigate climate effects, encourage further warming in those regions, or a combination of both processes (Myers-Smith et al., 2011).

2.2 Use of the shrub layer as habitat for avian species

Throughout the tundra biome the shrub layer plays a crucial role as a source of shelter and habitat for songbirds, waterfowl, and game birds in an otherwise barren landscape. Taller shrub species, such as dwarf birch (*Betula glandulosa*) and willow, have been observed to be the most important shrubs for arctic birds (Henden et al., 2013). Willow shrubs have been established as the dominant shrub species at arctic riparian edges (Baril et al., 2011). Determining the spatial patterns and environmental conditions that facilitate growth of willow and birch shrubs is considered important knowledge for understanding the habitat requirements necessary for the arctic breeding songbirds and game birds (Henden et al., 2013). Henden et al. (2013) studied the importance of willow at riparian edges for several arctic breeding birds in northern Norway. They classified bird species based on their affiliation with willows: willow canopy breeding birds, willow related ground breeding bird species, and bird species with a looser connection to the willow shrubs because they are mostly affiliated with the adjacent open tundra (Henden et al., 2013). Results indicated that bird sightings were 10-13 times higher in riparian habitats dominated by willows than riparian habitats without willows (Ims & Henden, 2012). The increase of willow throughout the arctic tundra is expected to have a direct positive effect on the populations of breeding birds in those regions (Henden et al., 2013).

Ehrich et al. (2011) studied the importance of the shrub layer to the arctic population of willow ptarmigan (*Lagopus lagopus*). Their study revealed that willow and dwarf birch are critical habitat components for the ptarmigan because of their wide use of these two shrub species. Willow ptarmigan eat, sleep, nest, and hide from predators within the taller willow and birch shrub patches across the landscape (Ehrich et al., 2011). The common name of the willow ptarmigan comes from the well-known relationship of the game bird species to willow (Ehrich et al., 2011). The diet of the willow ptarmigan changes with the seasons as food availability varies between winter and summer; however, willow and birch remain the majority of their food intake year round (Weeden, 1969). During the winter months, the buds and catkins of willow and birch shrubs account for 95% of the willow ptarmigan's diet, and while other shrubs are fruiting in the summer months, willow and birch account for less then 12% of their diet (Weeden, 1969). Other arctic shrub species that ptarmigan eat in the summer months are berry-producing shrubs such as crowberry, cranberry, and blueberry (Weeden, 1969). Shrub species provide a variety of food, shelter, and nesting options for willow ptarmigan. My research on the patterns of shrubs across the tundra and forest-tundra ecotone landscapes can aid in population monitoring or habitat suitability models for ptarmigans, as well as for other avian species who also rely on patches of shrubs throughout the landscape to survive.

2.3 Vegetation patterns across edges

An edge is defined as the area of convergence between different ecosystems (Harper & Macdonald, 2011). The properties of one habitat, such as a freshwater lake, may impact and influence properties at the edge of an adjacent habitat, such as open tundra. The influence that a particular environment has on the composition or structure of adjacent environments is known as edge influence (Harper et al., 2005). Many studies have focused on anthropogenic forest edges across a landscape; however, few have focused on natural edges and transitions. Thomas et al. (1979) state that some natural edges on a landscape occur because of gradual or steep changes in physical variables such as elevation, topography, geomorphology, or microclimate. These environmental variables likely influence the location of natural edges throughout a landscape.

Many researchers have described the subarctic landscape as a mosaic of vegetation types that occur in patches across the landscape, resulting in a heterogeneous array of habitat types (Payette, et al., 2001; Harper et al., 2011; Ropars & Boudreau, 2012). The array of habitat types implies a higher frequency of edges or transitions throughout the subarctic landscape. It is important to understand the effect that edges and transition zones have on the spatial pattern of vegetation throughout landscapes. A study by Henden et al. (2013) determined that the height and density of willow and birch shrubs were greater at lakeshore edges, which is one example of how a natural edge landscape feature can influence the spatial pattern of shrub vegetation. There are few studies on how other natural edges may affect vegetation patterns. It would be beneficial for future studies to focus on how natural edges throughout the subarctic landscape affect the spatial pattern of the vegetation.

2.4 Knowledge gaps in the shrub literature

Several studies have focused on the Canadian Arctic and its responses to climate change and many of these have narrowed their focus to tree line movement. However, few have narrowed their search to the changing patterns and distributions of the shrub layer or related those patterns to other factors. Myers-Smith et al. (2011) provide knowledge on the degree to which shrub expansion could impact the subarctic ecosystem and landscape dynamics. They also predict how shrub expansion may facilitate or mitigate climate change in the arctic, but there is a knowledge gap on the scale at which shrub patterns occur on the landscape and how the patches relate to physical and environmental factors. The set of environmental conditions present in a given area that will result in either a patch or gap of shrub vegetation is unknown. Although the subarctic landscape has been widely known to be patchy and heterogeneous, the factors causing the landscape mosaic and the relationship of shrub patches to other landscape features appears to remain unstudied.

Ropars & Boudreau (2012) studied shrub expansion across a subarctic landscape in northern Quebec. They state that there is a need to understand the relationship that variables such as elevation, topography, and microtopography have on the spatial distribution of shrubs because no such information has thus far been published. The use of spatial pattern analysis in combination with other quantitative and qualitative data on the landscape features is relatively novel. The spatial pattern of the shrub layer in Canada’s subarctic is not well documented, and my study could serve as baseline knowledge for future studies on changes to the shrub layer across the arctic. In summary, there is limited knowledge on how shrub expansion will continue to spread across subarctic landscapes, how the shrub expansion will change ecosystem dynamics, and how the existing and evolving environmental variables are and will continue to influence the distribution of the shrub layer.

3.0 Research questions

This study focuses on observing the spatial pattern of the shrub layer across two main habitat types throughout Churchill Manitoba: the tundra, and the forest-tundra ecotone. Three research questions are addressed in this study. (1) What is the spatial pattern of the shrub layer throughout the arctic tundra and the forest-tundra ecotone habitats? (2) How do the existing landscape features and sampled explanatory variables relate to the spatial pattern of shrubs? (3) Are there any distinct patterns for shrub species richness and diversity at transition zones or edges?

I predicted that (1) patches of shrubs will be taller and more abundant across the forest-ecotone transect than across the tundra transect; (2) shrub cover will increase as the distance to a water source decreases; (3) both soil pH and microtopography will influence the distribution of shrubs. I assumed that as microtopography variation increases, taller shrub species such as birch and willow will increase in abundance, and prostrate berry-producing shrubs will decrease in abundance.

4.0 Methods

4.1 Study area

The study area was near the Churchill Northern Studies Centre (CNSC) approximately 23 km east of the town of Churchill Manitoba, Canada, along the western side of the Hudson Bay coast (Figure 2). The Churchill area is considered to be subarctic terrain in an area of transition between the boreal forest biome and the arctic tundra biome (Harper et al., 2011). The vegetation has been described as a mosaic of black and white spruce (*P. glauca* and *P. mariana*) with patches of wetlands and dense shrubs (Harper et al., 2011). The average temperature of Churchill is 12 °C in July, and -26.7 °C in January (Government of Manitoba, 2013). Data from Environment Canada (2009) state that between 1971 and 2000, the average annual precipitation was 431.6 mm, of which approximately 40% was snowfall.

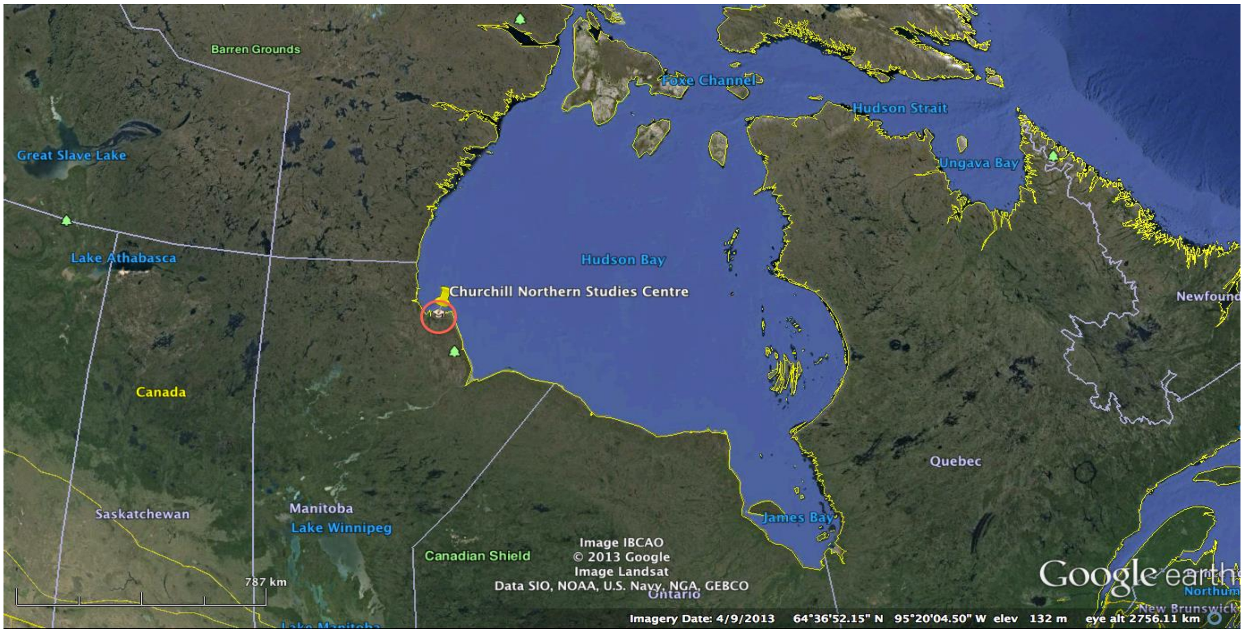

Figure 2. A Google Earth image of the field station Churchill Northern Studies Centre (red circle). The study area is located near the western shore of Hudson Bay. Image retrieved from Google 2013.

I placed one 412 m long transect 1.8 km southeast of the CNSC in open tundra habitat, and another 460 m long transect 1.5 km southwest of the CNSC in forest-tundra ecotone habitat (Figure 3). Both locations were selected purposefully to represent the desired characteristics of tundra and of forest-tundra ecotone. The two transects varied in length because each transect was selected to begin and end at a body of water, a naturally occurring landscape feature free of any shrub cover.

Figure 3. Google Earth satellite image of the Churchill Northern Studies Centre and the locations of the tundra transect (T1-000m to T1-412m) and the forest-tundra ecotone transect (T2-000m to T2-460m). White lines on the map are gravel roads. Image taken from Google, 2013.

4.2 Sampling design

Sampling methods were modified from methods used in Brosofske et al. (1999), who sampled plant species within 1x1 m quadrats every 5 meters along a long linear transect in order to determine the pattern of the vegetation across the landscape. My sampling methods also used 1x1 m quadrats on long linear transects; however, sampling across the transects was spatially contiguous because of the heterogeneity of the Churchill landscape and recommendations by Dale (1999). Dale (1999) recommends that when studying the spatial pattern of vegetation, it is best to sample across the desired landscape contiguously with no gaps in the sampling. Contiguous sampling increases the likeliness of sampling the true spatial pattern of the habitat as no patch or gaps will be missed at finer scales (Dale, 1999).

Sampled response variables were percent cover and height of each shrub species in the 1x1 meter quadrats. Cover of each shrub species was estimated as belonging to one of the following classes: 0-10%, 10-25%, 25-50%, 50-75%, and 75-100%. Shrub height was categorized into one of the following categories: 0-10, 10-40, 40-100, 100-160 and > 160 cm tall. Categories for height and percent cover were based on ones used by previous studies of the forest-tundra ecotone in the Churchill region undertaken by the International Polar Year research group (Hofgaard & Rees, 2008).

Explanatory variables that were collected in order to explain the spatial patterns of the shrubs are microtopography, soil pH, and distance to a water source. Microtopography was estimated by measuring the range in ground height as the difference between the lowest and the highest points within each quadrat. Soil pH was measured at every meter along the transect lines using a pH meter (model pH-707 from Tecpel). The distance to the nearest water source (lake, pond, river, or wetland) was measured in the field and also served as a proxy variable for soil moisture level.

4.3 Data analysis

The response variables were cover and height of *Andromeda polifollia*, *Vaccinium* *uligunosum*, and *Empetrum nigrum*, as well as shrub species richness and diversity per quadrat. I only conducted analysis for the most commonly occurring shrub species along both the tundra and the forest tundra ecotone transects. Only the species that occurred in at least 50% of the vegetated quadrats across both landscapes (*Andromeda polifolia*, *Empetrum nigrum*, and *Vaccinium uligunosum*) were analyzed individually for spatial patterns across the tundra and ecotone landscapes. Analysis of all shrub species was not conducted due to time constraints for analysis of the large data set and numerous variables.

Shrub species richness was determined by counting how many shrub species were found within each quadrat. Estimates of shrub cover and height were converted to the midpoint value of the category (e.g., a cover of 1-10% was assigned a value of 5%). I then used the midpoint values for cover to calculate the Shannon-Wiener diversity index for every quadrat using the formula $H= -\Sigma[(p_i) * \ln(p_i)]$, where p_i is the proportion of cover of shrub species *i* within the quadrat. Spatial pattern analysis was used to determine the spatial pattern of the shrub layer across tundra and forest-tundra ecotone habitats using the program PASSaGE 2.0 (Rosenberg, 2009).

Spatial analysis in plant ecology is the process of assessing the predictability of how plants are arranged in space (Dale & Mah, 1998). To evaluate spatial pattern of shrubs along each transect, wavelet analysis was used to indicate the location of significant patches or gaps in the shrub layer.

Wavelet analysis assesses how well a data series matches a selected wavelet template (Figure 4). A common wavelet template called the Mexican Hat wavelet was used in this study to detect significant patches and gaps of shrubs on the landscape (Dale & Mah, 1998). Wavelet analysis also detects the scale at which the pattern occurs by varying the size of the wavelet template. The scale at which a pattern occurs is defined as the average distance from the center of a patch to the center of a gap (Dale & MacIsaac, 1989).

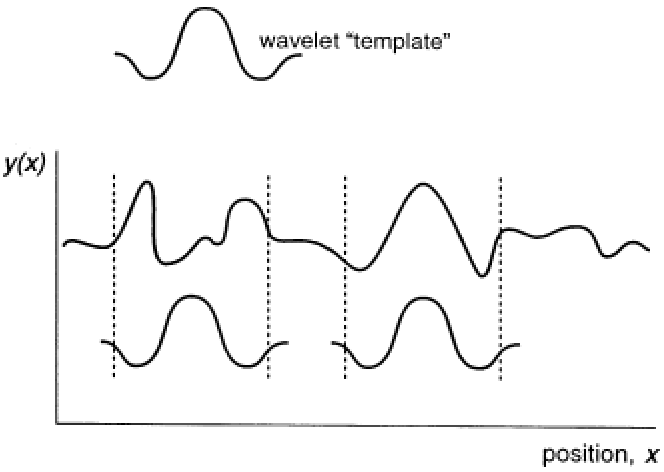

Figure 4. A diagram of the Mexican hat wavelet template used to analyze spatial pattern. In the window (between the vertical dashed lines) on the left, the template matches the data series poorly, indicating that there is no patch at that location; in the right window the data matches the template well, indicating a significant pattern at this scale. Diagram from Dale & Mah (1998).

Wavelet analysis was chosen as the method for data analysis because it provides more detailed and accurate results on plant spatial patterns in comparison to other spatial analysis methods (such as blocked quadrat variance analysis) (Dale & Mah, 1998). For example, wavelet analysis provides information on the positions of patches, gaps, and abrupt changes along the transect.

To determine the significance of shrub patches throughout the landscape I conducted randomization tests on the data within the PASSaGE program. Randomization tests involve shuffling the true data set into a random order and reassessing the randomly ordered data for any positive matches to the wavelet template. Within PASSaGE, 999 randomized permutations were generated for each response variable to come up with the randomization curve for each variable, which represents the 95% confidence interval line for the randomized data. Therefore, any peaks in the observed data that exceed the distribution generated by the randomization tests (expected data) will be determined as significant patterns (Rosenberg, 2009).

The output from wavelet analysis is a variance matrix that explains the variation for each position (quadrat location) at different scales. The position*scale matrix values for the response variables were summed over all scales for each position. The randomization value for each position represents the confidence interval from the randomization tests. The randomization outputs generated from PASSaGE are half of the confidence intervals; however, I wanted to test areas where shrub cover was either higher or lower than expected values for each response variable. Therefore, the randomization outputs were multiplied by two. Summed wavelet variance values and corresponding randomization curves were then visually related to the locations of significant landscape features, such as a transition between tundra or ecotone habitat and a lake or a road, as well as to trends in the explanatory data (soil pH and microtopography).

5.0 Results

The tundra transect had fewer shrub species present overall in comparison to the ecotone transect; however, the average number of shrub species that appeared within each quadrat was similar for both transects (Table 1). The average Shannon-Weiner diversity index was slightly higher in the tundra than the ecotone. Mean soil pH had similar values for both transects and the range from lowest to highest pH value for both transects were almost identical. The tundra had a slightly higher average variation in microtopography than the ecotone, although the standard deviation value was higher for the ecotone transect than the tundra. *Andromeda polifolia* and *Vaccinium uligunosum* covered a greater proportion of the ecotone transect than the tundra transect, but *Empetrum nigrum* was found in a greater proportion of quadrats along the tundra than the ecotone transect.

Table 1. A comparison of characteristics of the tundra and forest-tundra ecotone transects for the explanatory variables and response variables.

Variable	**Tundra (T1)**	**Ecotone (T2)**
Latitude and longitude (0 m)	58°43'36.38"N, 93°47'46.45"W	58°43'27.99"N, 93°49'59.83"W
Latitude and longitude (412 m for T1, 460 m for T2)	58°43'49.32"N, 93°47'41.86"W	58°43'43.94"N, 93°50'5.28"W
Quadrat shrub species richness (average # species +/- sd)	6.63 (+/- 3.64)	6.34 (+/- 3.63)
Total shrub species richness (total # species/transect)	15	21
Shrub diversity (Shannon index per quadrat, average +/- sd)	1.71 (+/- 0.85)	1.63 (+/- 0.81)
Soil pH (average +/- sd)	6.32 (+/- 0.38)	6.20 (+/- 0.30)
Range in microtopography (cm per quadrat, average +/- sd)	5.85 (+/- 3.01)[1]	5.74 (+/- 3.78)
Frequency of *Andromeda polifolia* (% quadrats)	70%	80%
Frequency of *Empetrum nigrum* (% quadrats)	91%	63%
Frequency of *Vaccinium uligunosum* (% quadrats)	63%	68%

[1] Excluding an outlier; the range with the outlier was 6.18 (+/- 4.09) cm.

5.1 Explanatory variables

The most acidic soil conditions were in the middle of the transect far from natural or created edges (Figure 5). pH was less acidic closer to water bodies. The ecotone showed more fine-scale variations in changing pH when compared to the tundra. Other than more acidic conditions around a pond at 400 m along the ecotone transect, pH was higher near water bodies along both transects.

The tundra displayed fine-scale variation in microtopography with the exception of a large hill within the first 5 m that occurred directly after a lake (Figure 5). If this large variation in microtopography is disregarded as an outlier, then the tundra had more consistently occurring smaller height variations within each quadrat in comparison to the ecotone. The tundra had a uniform distribution of peat mounds (hummocks) throughout the transect that created fine-scale variation in microtopography.

The ecotone displayed more abrupt fluctuations in microtopography at the scale of one meter. The ecotone also had regions of peat accumulation in the form of hummocks; however, the hummock regions were dispersed throughout the transect at different locations and were interrupted by various other habitat types such as grasslands, forest patches, and mudflats.

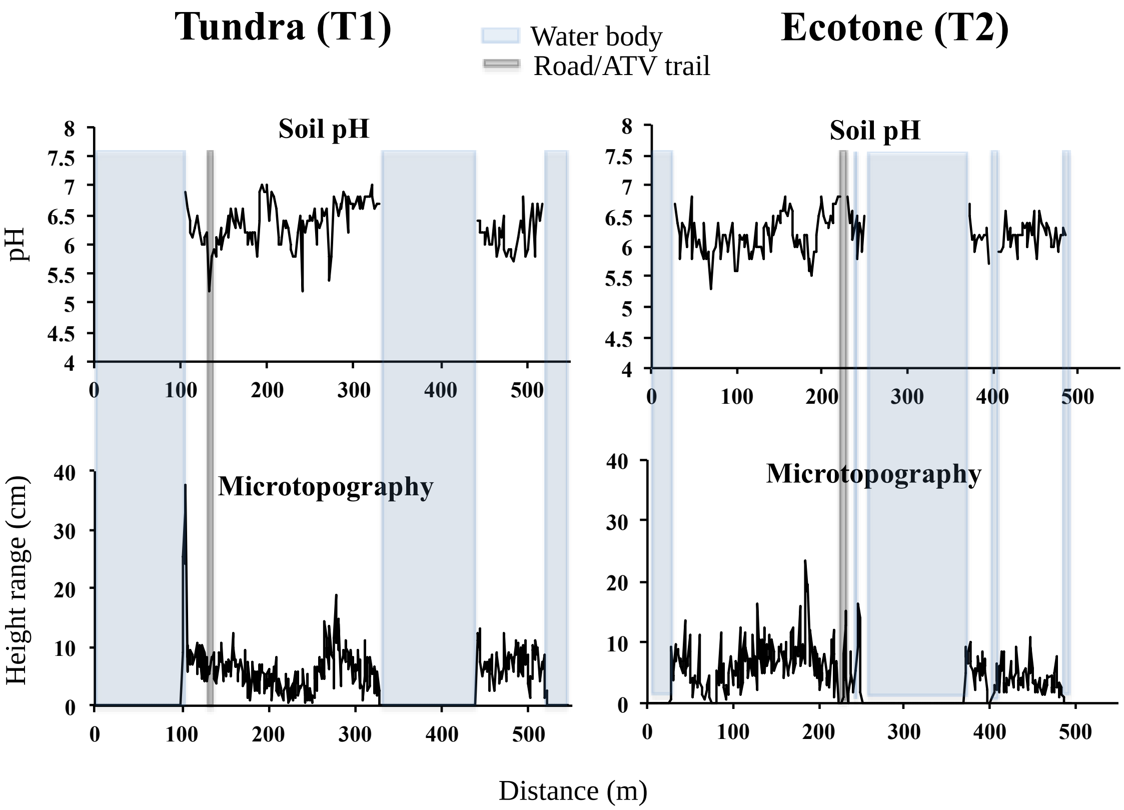

Figure 5. Soil pH and microtopography (range in elevation) across the tundra and ecotone transects. Blue rectangular shaded regions represent the locations of water bodies and the shaded grey rectangles represent the locations of roads or ATV trails.

5.2 Patterns of response variables

Shrub species richness in both the tundra and the forest-tundra ecotone was greater closer to natural edges such as lakeshore edges and pond edges (Figure 6). The tundra had longer significant patches of shrub richness closer to natural edges, and the ecotone had shorter more compact patches of shrub richness closer to water bodies. Shrub richness and diversity presented similar patterns in both transects, they were greater in close proximity to natural edges. The tundra showed longer patches of significantly higher diversity that occurred closer to natural edges on the landscape and the ecotone had shorter and more frequent significant patches of diversity closer to the natural edges.

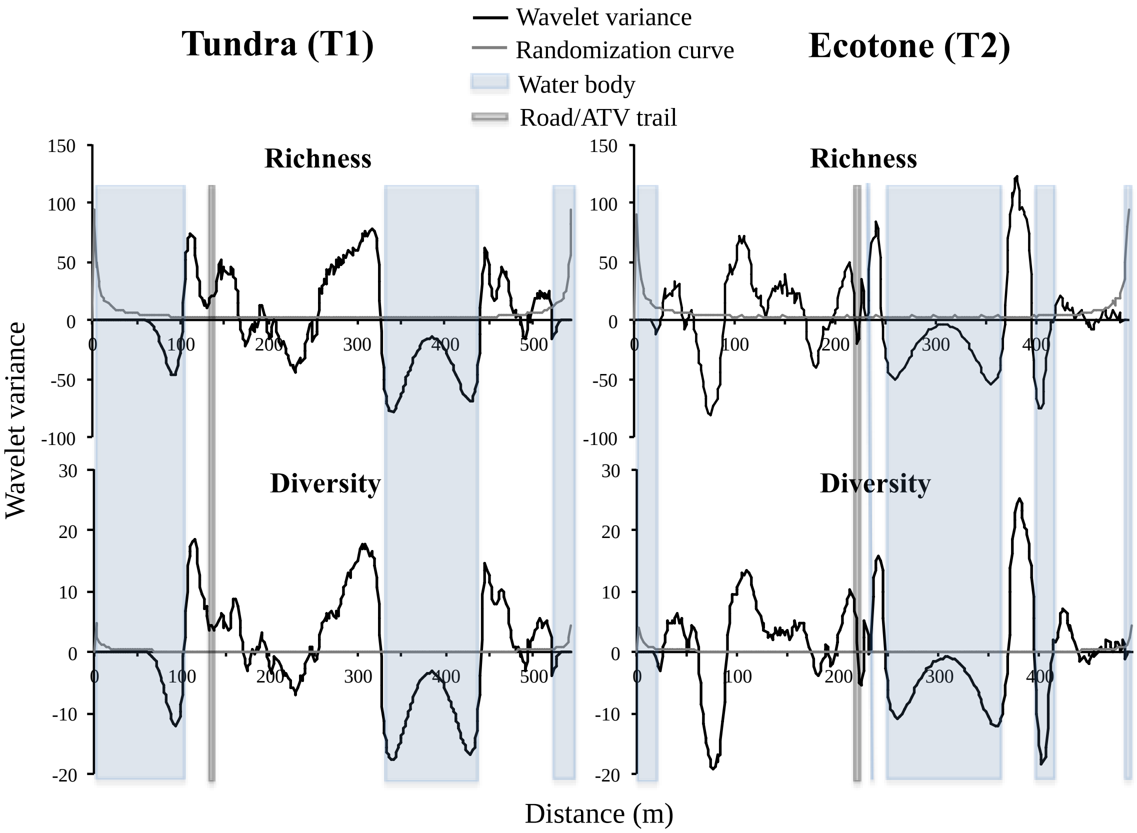

Figure 6. Position variance (black line) and the 95% confidence level from the randomization tests (gray line) from the Mexican hat wavelet analysis of shrub species richness and shrub diversity for the tundra transect (left) and the ecotone transect (right). Distances where wavelet variance is above the randomization curve represent locations of significant patches.

The tundra had fewer but longer significant patches of *A. polifolia* and the ecotone had smaller and more numerous significant patches (Figure 7). *A. polifolia* was distributed widely throughout both habitat types but showed little or no spatial pattern to locations close to a water body or created edge such as a road. The height of *A. polifolia* across the tundra transect did not vary; all quadrats with *A. polifolia* had the same height (< 10 cm). In the ecotone, however, there were variations in height throughout the transect. *A. polifolia* patches closer to a water source were often taller (10- 25 cm) than patches further from the water (<10 cm).

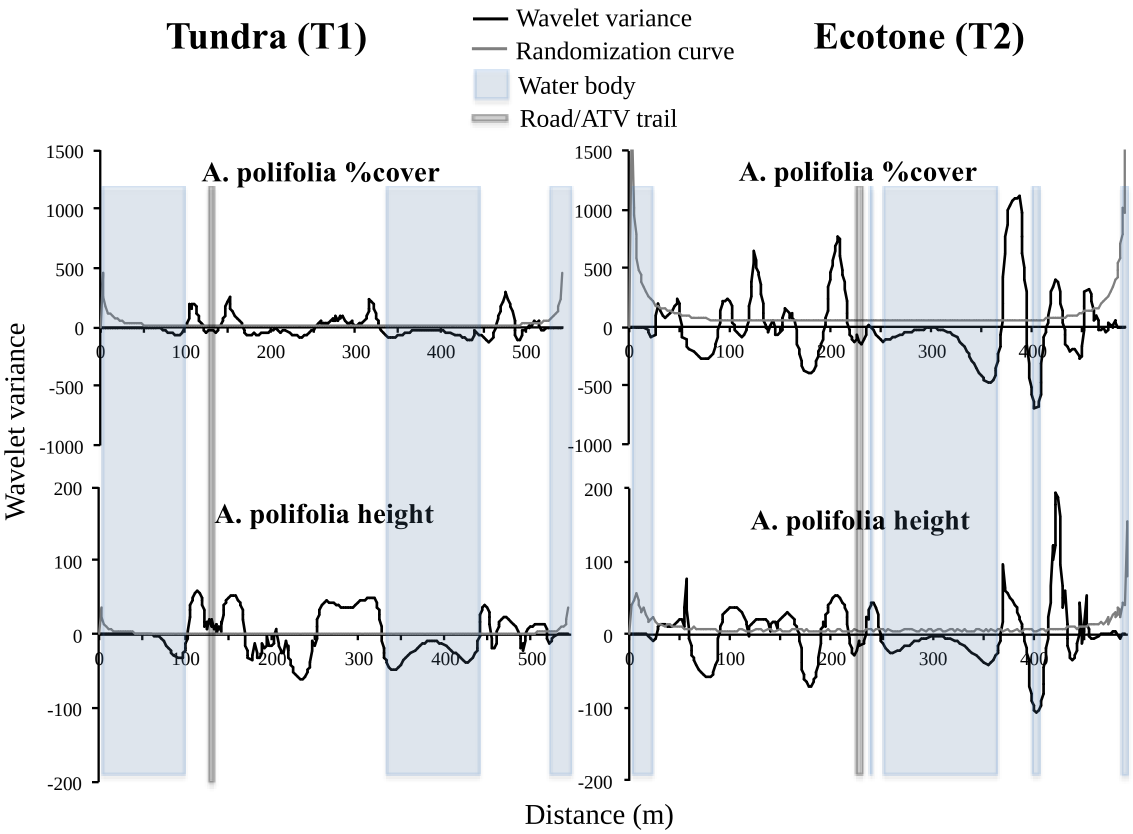

Figure 7. The position variance (black line) and the 95% confidence level from the randomization tests (gray line) from the Mexican hat wavelet analysis of shrub cover and height for the species *Andromeda polifolia* for the tundra transect (left) and the ecotone transect (right). Distances where wavelet variance is above the randomization curve represent locations of significant patches.

Empetrum nigrum displayed an opposite trend to *A. polifolia*; the tundra transect had shorter more frequent significant patches of *E. nigrum* and the ecotone had fewer and slightly longer significant patches (Figure 8). *E. nigrum* was widely distributed throughout both transects. The tundra had *E. nigrum* in 91% of the quadrats and the ecotone had *Empetrum* present in 63% of the quadrats (not including water covered quadrats). Similar to *A. polifolia*, *E. nigrum* did not appear to have any pattern of cover in relation to natural edges or created edges such as a road or an ATV trail (Figure 8). Height of *E. nigrum* across the tundra transect was uniformly low (0-10 cm). Across the ecotone transect the majority of *E. nigrum* shrubs were in the smallest height class (<10 cm) except at the end of the transect where patches were 10-25 cm tall. The change in height class on the ecotone transect occurred close to water bodies.

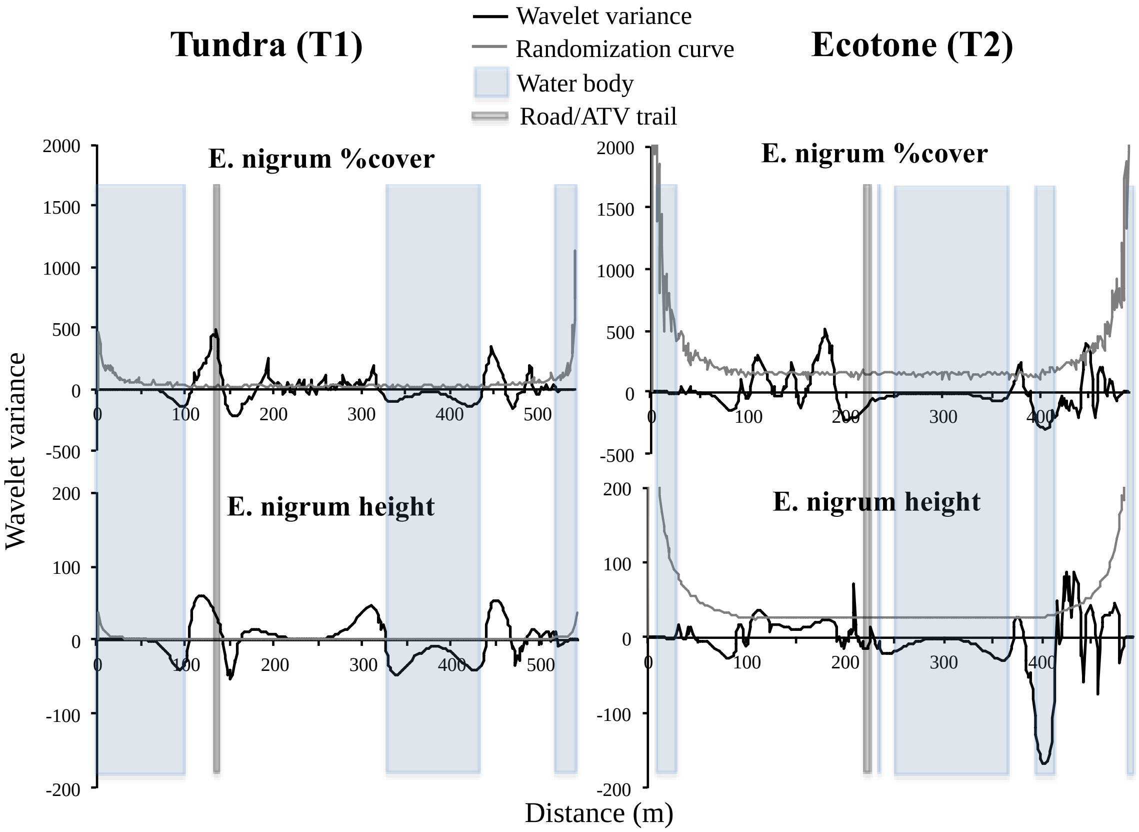

Figure 8. The position variance (black line) and the 95% confidence level from the randomization tests (gray line) from the Mexican hat wavelet analysis of shrub cover and height for the species *Empetrun nigrum* for the tundra transect (left) and the ecotone transect (right). Distances where wavelet variance is above the randomization curve represent locations of significant patches.

In both the tundra and the ecotone cover of *V. uligunosum* was greater at natural edges or created edges (Figure 9). The length of significant patches varied greatly within both transects. Some patches of *V. uligunosum* were longer and sparsely distributed, while others were short and occurred frequently in other sections of the transects. Height of *V. uligunosum* was greater closer to natural and created edges (Figure 9). The patches of *V. uligunosum* were larger when closer to water bodies in the tundra and in the ecotone. Height of *V. uligunosum* in the tundra and forest-tundra ecotone was taller near created edges (ATV trail or road) and natural edges (Lakshore or ponds).

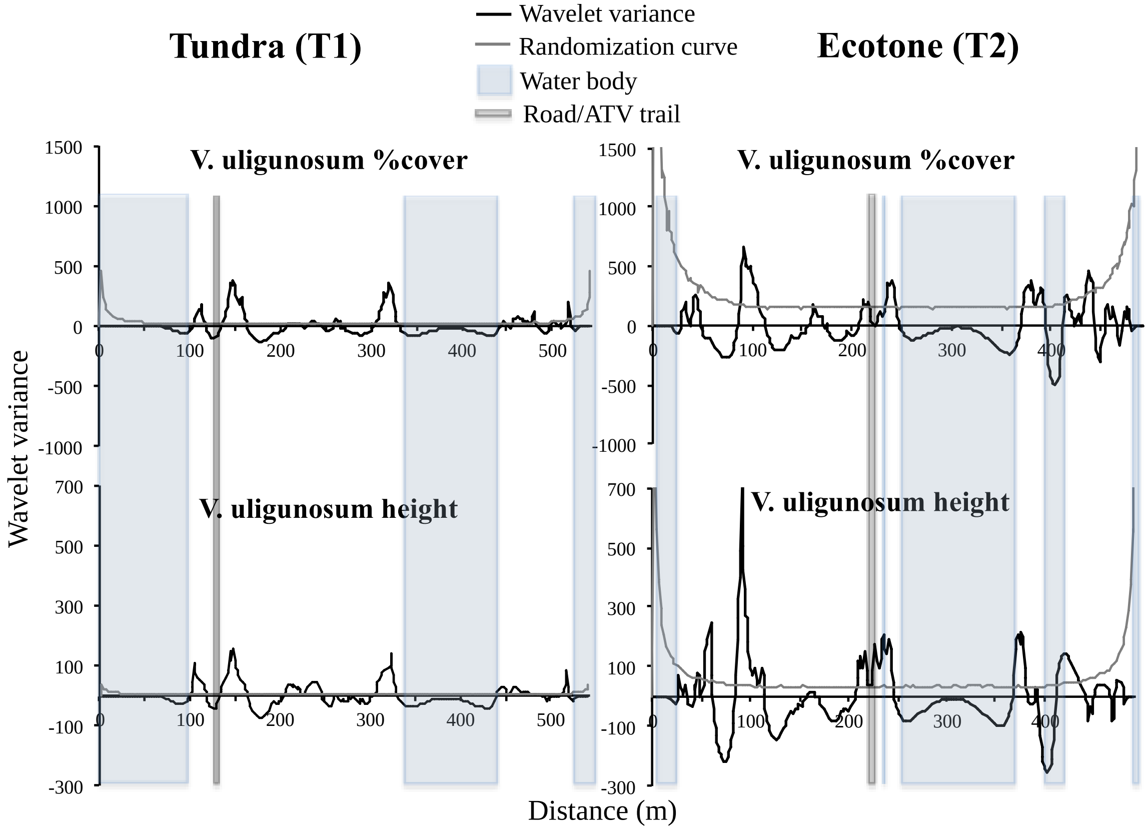

Figure 9. The position variance (black line) and the 95% confidence level from the randomization tests (gray line) from the Mexican hat wavelet analysis of shrub cover and height for the species *Vaccinium uligunosum* for the tundra transect (left) and the ecotone transect (right). Distances where wavelet

variance is above the randomization curve represent locations of significant patches.

6.0 Discussion

6.1 Shrub spatial pattern

The spatial pattern of the shrub layer across the tundra was less heterogeneous in comparison to the ecotone landscape. This result supports my hypothesis that there would be a greater number of taller patches of shrubs in the ecotone than in the tundra. The tundra habitat had a repeated pattern of hummocks around the same size and height across the transect. The pattern of shrub patches and gaps supports the conclusion of Myers-Smith (2007) that tundra vegetation appears to be evenly distributed at predictable scales of distance unless affected by a natural edge, created edge, or disturbance. Greater shrub height, species richness, and diversity close to a water source were also found by Henden et al; (2011), and Ehrich et al. (2011). Total shrub species richness and diversity were greater close to natural and created edges.

For the tundra landscape, *A. polifollia* and *V. uligunosum* showed greater cover and height when in close proximity to a water body, whereas *E. nigrum* appears to increase in cover and stay consistent in height when further way from edges. Therefore, *E. nigrum* showed preference for growing in regions with drier soils away from a water body's edge. Cover of *E. nigrum* appears to be greater in areas with small variation in microtoporgraphy where the ground is more flat. It was unclear as to whether or not *A. polifolia* or *V. uligunosum* had a relationship with microtopography.

The larger hill that occurs at the start of the tundra transect (Figure 5) was created by ice wedging of the soil in winter when strong winds push large detached ice blocks into the lakeshore edge, which upheaves the soil (Fishback, L., pers. comm.). This ice wedge phenomena can be common in arctic regions; however, it was not found on the lakeshore edges of any other lakes I sampled in tundra. It appears as though the presence of the hill corresponded with greater cover and height of the taller woody shrub species such as *Betula glandulosa*, and *Salix planifolia* (pers. obs.). This pattern of taller woody shrubs growing in a dense patch behind the hill is likely due to the combination of higher moisture from the close proximity to the lake, and shelter from the harsh winds blowing across the lake.

The spatial pattern of the shrub layer across the forest-tundra ecotone landscape was highly heterogeneous. The cause of the heterogeneity in vegetation and specifically the shrub layer is difficult to determine. One hypothesis by Payette et al. (2001) states that the heterogeneity of vegetation pattern is a result of past fires where regions severely affected by fire became open tundra patches, and areas less burnt remained forest patches. Although the study by Payette et al. (2001) was done at a much larger landscape scale than mine, the same reasoning may apply to explain the heterogeneity of the Churchill landscape. There are many factors that could contribute to the increased number of natural edges and habitat transitions that occur throughout forest-tundra ecotone habitats. However, I focused on what environmental variables are present on the landscape and appear to influence the growth and distribution of the shrub layer across heterogeneous landscapes.

6.2 Explanatory variables and shrub spatial pattern

The explanatory variable that appeared to be most closely related to the shrub spatial pattern was distance to a habitat transition (edge). The distance away from natural habitat transitions such as lakeshore or pond edges served as a proxy variable for soil moisture level. Intuitively, areas close to a lakeshore or pond edge have higher soil moisture levels, which might explain the increase in shrub diversity, richness, height, and cover in those areas if water is the limiting resource (Valentin et al., 1999). However, the relationship between created edges and an increase in shrub cover and height is less intuitive. On the tundra transect where the created edge was an ATV trail, the ground was repeatedly disturbed as evidenced by the tire marks of the ATVs, so the soil became compact. This area also receives heavy foot traffic from hikers, which further adds to soil compaction and surface depressions (changes in microtopography). The surface depressions fill with rainwater or groundwater fed by the nearby lake. Therefore the soil in the disturbed region would also have increased soil moisture, which could explain the increase in shrub cover and height at that location.

Similar reasons likely apply to the increase in shrub richness, diversity, height, and cover along the road edges across the ecotone transect. The road that crosses the ecotone transect is an unpaved limestone gravel road. Davis & Wilson (2005) conclude that coarse ground gravel has a higher porosity and permeability then organic peat soils. Therefore, the soil on either edge of the road may be holding more runoff water during precipitation events such as rain or snowmelt. The increase in soil moisture from the runoff on the gravel road is likely contributing to the increase in shrub cover and height. However, one side of the road edge on the ecotone transect showed slightly greater shrub richness and diversity than the other side. This result may be attributed to the overall slope and runoff direction of water flowing through that area. For example, there was a small pond (4 m wide) adjacent to the edge of the road with greater shrub species richness and diversity. The pond was 4 m away from the edge of the gravel and may indicate that runoff water is pooling close to the road edge. The pond likely also continues to provide additional soil moisture to the shrubs at that edge of the road, explaining the unique shrub pattern displayed at that location.

Fluctuations in soil pH rarely coincided with locations of significant patches or gaps in shrub cover throughout the tundra or ecotone transect. For the few instances where there was a noticeable increase or decrease in pH at the same location as a patch of shrubs, there were also other phenomena occurring at the same location that could explain changes to shrub height, cover, diversity, or richness. For example, the lowest pH value recorded on the tundra transect (5.2) occurred at the location of the disturbed soil from the ATV trail. The soil compaction and water logged regions on the ATV trail likely caused the acidic soil pH. It is difficult to determine if the changes in shrub diversity and richness on either edge of the ATV trail are attributed to the low pH or the increased soil moisture level.

A similar result but opposite pH trend occurred at the edges of the road on the ecotone transect. The soil pH level increased to the highest point on the pH range throughout the ecotone transect (6.8) at the road edge, which may be associated with the basic properties of the limestone gravel that makes up the road. However, a pH of 6.8 was also reached at other locations further from the road edge where there is not a significant amount of limestone. In addition, there are regions on the tundra transect that have a higher pH (6.9) and are also not near a limestone road. Therefore it is presumed that soil pH plays a more minimal role in the shrub spatial pattern across the tundra and the ecotone landscapes.

Changes in microtopography frequently coincided with the location of significant shrub patches throughout the tundra and ecotone landscapes. Regions with higher variations in ground height had higher shrub species richness and diversity. The combination of low depressions and higher hummocks allows for a variety of shrub species to colonize and grow in those areas (Bergkamp, 1998). Some shrub species prefer to grow on the drier hummocks within the quadrat and other species preferred the lower wetter areas of the landscape based on soil moisture preferences (Bergkamp, 1998). In locations where microtopohraphy variation is low and the ground level is flat the levels of water infiltration into the soil are uniform and fewer species may occupy the landscape (Bergkamp, 1998). Studies have shown that flat land in the arctic and subarctic regions have lower plant species richness because of the harsher environmental conditions that exist in flat open landscapes such as increased wind exposure and soil erosion (Britton, 1966). Therefore, microtopography across arctic and subarctic landscapes appears to play an important role in the shrub spatial patterns and distributions.

6.3 Shrub expansion and implications for climate change

My results may aid in the prediction of how the shrub layer will develop across tundra and ecotone landscapes as climate change continues. In my research one of the most important factors facilitating further shrub growth appears to be soil moisture. Therefore, the trends of shrub expansion could match the trends of soil moisture levels as climate change progresses. As the average temperature over the Churchill region increases, the rate of evapotranspiration may increase resulting in decreased surface areas of ponds or lakes. As the amount of freshwater decreases over arctic and subarctic landscapes it is possible that soil moisture would decrease and shrub expansion would slow or even stop. So far scientists find that predicting changes in hydrology across arctic regions is difficult to determine (White et al., 2007; Serreze at al., 2006).

Currently the common shrub species that reside in drier soil conditions of the tundra are *Andromeda pollifollia*, *Empetriun nigrum*, *Vaccinium uligunosum*, and other prostrate berry species (Johnson & Fairfield, 1987). As temperatures increase and soil moisture decreases it is possible that there will be an overall decline in these prostrate shrub species. The dwarf and prostrate shrubs may, however, continue to expand northward into further permafrost soil regions of even higher latitude. For most arctic regions it has been predicted that there will be an increase of the taller shrub species such as birch and willow species, which may expand and increase their cover throughout the current tundra regions (Block et al., 2011). However, if the soil moisture levels decrease with the warming climate, then the current tundra areas will not be colonized and expanded by the larger shrub species and would become more of a barren landscape. If soil moisture were to increase with warming climates due to increased precipitation, then it would be expected to see birch and willow species expanding at higher rates throughout tundra and ecotone landscapes. The land currently classified as ecotone may first experience more expansion and densification, however trees may also expand and outcompete the taller woody shrubs for resources. The tree line expansion of the boreal forest into subarctic regions like Churchill is expected to increase as climate change progresses (Harper et al., 2011). As trees encroach on the ecotone landscape it is likely that taller woody shrubs such as dwarf birch and various willow species would decrease due to shading by trees and competition for water. Therefore, as temperatures warm in subarctic regions, prostrate and dwarfed shrubs species may decrease in abundance, and taller woody shrub species may increase in most regions unless tree species begin to compete with the taller woody shrubs.

6.4 Shrub expansion and implications for bird habitat

Changes in shrub density and cover will ultimately affect habitat space for arctic birds. As previously mentioned, many bird species are dependent on the presence of taller woody shrubs as well as the prostrate berry producing shrubs for survival and reproduction (Henden et al., 2011). The populations of migratory songbirds will likely increase as birch and willow increase in abundance and cover. However, any obligate open tundra ground-breeding birds will likely decrease in abundance across subarctic landscapes as expansion of the dense woody shrubs continues.

Previous studies have already linked the presence of natural edges such as riparian edges to the presence of taller more woody shrubs (Ehrich et al., 2011, Henden et al., 2011). Therefore, whether or not subarctic regions experience an increase in the percentage of breeding birds also depends on the changes in hydrology. Specifically, willow ptarmigan (*Lagopus lagopus*) would increase in population numbers because they are well known for their dependence on dwarf birch and willows for food, shelter, and nesting grounds (Ehrich et al., 2011). However, as temperatures in Churchill increase, the cover of prostrate and dwarf shrubs, such as berry producing shrubs will likely decrease in abundance, and birds that feed on berries may not increase in population. Additionally, predatory birds such as eagles, falcons, and owls may decrease in population if shrub expansion continues to cover subarctic landscapes because of reduced visibility to catch their prey (lemmings, hares, rabbits, ptarmigans, songbirds and fish) (Warfe & Barmuta, 2004). Overall, it is difficult to predict how the arctic and subarctic bird populations will behave as vegetation and shrub patterns change with climate change.

6.5 Research limitations and opportunities for future research

My study focused on spatial pattern analysis of the most predominant shrub species found on both transects (*A. polifollia*, *E. nigrum*, and *V. uligunosum*) as well as total shrub richness and diversity. However, conducting wavelet analysis for multiple variables is a very time consuming process, therefore, this study was designed to assess the spatial pattern of only the most influential shrub species to the Churchill region. It would be beneficial to assess the spatial trends of the less frequent species that may only occur at edges such as birch and willow species. Further analysis may have uncovered additional patterns that may contribute to insight on shrub expansion predictions related to climate change. Future shrub spatial pattern research could focus on all individual species as well as total richness and diversity.

I determined that one of the primary indicators of shrub distribution is soil moisture, followed by changes in microtopograpgy; however, the inclusion of additional environmental explanatory variables would also be beneficial. Further research that would be valuable to vegetation patterns would be watershed hydrology patterns because of the strong link of soil moisture and vegetation growth. This study used distance to a water body as a proxy for soil moisture; however, it would be beneficial to measure soil moisture directly. It would also be interesting to test the effects of other vegetative life forms such as trees, grasses, sedges, lichens, etc. on the spatial pattern of the shrubs and vice versa. Additional variables such as elevation and soil biogeochemistry could also be interesting to relate to the spatial pattern of the vegetation. Further studies on carbon exchange, hydrology patterns, and climate variability would also be helpful to a wide variety of other arctic researchers that seek to relate their field of study to the climate change.

The spatial pattern of the shrub layer across the tundra and forest-tundra ecotone landscapes in this study is likely to be site specific and may not necessarily apply to other arctic or subarctic regions. Previous vegetation spatial pattern research in Canada’s Arctic has determined that vegetation patterns across different tundra and forest-tundra ecotone regions in Canada varied widely and patterns were site specific (Harper at al., 2011). This study provides only a snap shot of the shrub vegetation patterns throughout Churchill Manitoba as data was collected in one growing season. A more dynamic study of the shrub distribution that continues to assess the changes over time would be useful for determining the shrub changes resulting from climate change. A long-term study that monitored and quantified changes in the shrub distributions throughout the landscape of Churchill would be very beneficial for understanding continuing changes to landscape ecology in Canadian subarctic regions.

7.0 Summary and conclusions

Arctic regions are experiencing changes in vegetation composition due to climate change effects. My study focused on assessing the spatial pattern of the shrub layer across tundra and forest-tundra ecotone landscapes, and related those patterns to environmental variables. The spatial pattern of the shrub layer across subarctic landscapes varied between tundra and forest-tundra ecotone habitats. Overall, species composition did not change much throughout the tundra landscape and the distribution of species was mostly consistent. Across the ecotone transect shrub species composition was more variable. The ecotone had greater shrub diversity than the tundra, and there were fewer patches of shrubs found in the tundra than in the ecotone. Significant patches were found most often near habitat transitions and edges that were either natural or created. Throughout both transects cover and height of shrub species was greater near natural and created edges. Distance to a natural or created edge and microtopography were the environmental variables that corresponded most strongly with the spatial location of significant patches of shrubs. Soil pH did not coincide strongly with the location of significant patches of shrubs. The critical variable that appears to determine the spatial pattern of the shrubs across subarctic landscapes is soil moisture.

Implications of this research may be useful in predicting how the shrub layer will change and evolve across arctic regions as climate warming continues. As temperatures increase the shrub patterns observed in open tundra habitats may decrease as habitat transforms into forest-tundra ecotone. The current forest-tundra ecotone regions will experience shrub densification and expansion until they become out-competed by larger tree species associated with forest habitats. The increase in shrub cover and density may positively or negatively affect the arctic populations of breeding birds depending on the bird species and their habitat requirements and preferences for food, shelter, and nesting.

Further research on soil moisture and hydrology patterns would be useful for improving our understanding of the changing distributions of the shrub layer across arctic and subarctic landscapes. An assessment of the long-term vegetation patterns both spatially and temporally would increase our knowledge of ecosystem responses in our changing climate. Subarctic landscapes as a whole are continuing to undergo vast changes in vegetation compositions as well as ecosystem dynamics as climate change influences environmental patterns. Therefore, increased scientific collaboration to include a variety of environmental disciplines may further improve our understanding of Canadian arctic ecology at a landscape level as climate change continues.

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