

**EFFECTS OF TOPOGRAPHY ON THE SPATIAL VARIATION OF
LANDCOVER DIVERSITY AND DISTRIBUTION IN A PRAIRIE SANDHILL
ECOSYSTEM**

TAYLER KAYLEN HAMILTON
B.Sc. Environmental Science
University of Lethbridge, 2010

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ABSTRACT

This thesis investigates whether topography has a quantifiable effect on the spatial distribution of landcover within an inland sand dune ecosystem. To accomplish this, an investigation was undertaken to compare the associations between various topographic characteristics and landcover distribution within the Great Sand Hills (GSH), Saskatchewan. The methodology comprised a spatial analysis of digital topographic and landcover data. In terms of landcover diversity, results shows that there is a moderate association between topography and landcover diversity in the GSH, and that results vary with spatial scale. Similarly, results show modest predictability for one particular community type (trees) thought to be strongly related to topographic position in this region. Several environmental factors are proposed that might overprint the topography-landcover association. Overall, this thesis expands the geographic context of the link between topography and landcover, while also demonstrating the utility of high resolution topographic and landcover data and the importance of spatial scale.

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LIST OF ABBREVIATIONS

AUC	Area under the curve
DEM	Digital elevation model
<i>FN</i>	False negative
<i>FP</i>	False positive
GSH	Great Sand Hills
IQR	Interquartile Range
LiDAR	Light detecting and ranging
ROC	Receiver operating characteristic
RU	Topographic ruggedness
SDI	Simpson's diversity index
<i>TN</i>	True negative
<i>TP</i>	True positive
VRM	Vector ruggedness measure
WI	Topographic wetness index
YBP	Years before present

CHAPTER 1: INTRODUCTION AND BACKGROUND

1.1 Motivation

Different ecological regions exist throughout the world and are shaped by their geographic location, climate and topographic gradients. Climate influences broad-scale variations of vegetation, most notably regulating the distribution of world biomes. At a different, higher spatial resolution, topography also influences the distribution of vegetation by creating spatial variations of microclimates, which, in turn, can influence the growth and type of vegetation. In mountainous regions, for example, variations of elevation and aspect encourage spatial variations of solar radiation, moisture and temperature (Oke, 1987). This can create marked differences in the type and pattern of vegetation present (e.g., Hoersch *et al.*, 2002; Coblenz & Riitters, 2004; Deng *et al.*, 2007). Additionally, landcover patterns in arid and semi-arid regions are often attributed to topographic effects (e.g., Coblenz & Riitters, 2004; Liu *et al.*, 2007; Istanbuluoglu *et al.*, 2008). Although the number of physiographic settings where the topography-vegetation association has been tested continues to expand, there are still many different types of vegetated landscapes with distinct signatures of topographic variability that have yet to be examined.

In the context of this thesis research it is important to note that few studies have examined whether the unique topographic characteristics of vegetation-stabilized aeolian dune fields have a quantifiable effect on vegetation patterns. This is particularly relevant based on research published in *Nature Geoscience* showing that aeolian dune field dynamics and boundary-layer processes drive gradients in vegetation that, in turn, trigger eco-hydrological effects that create feedbacks to reinforce vegetation patterning (Jerolmack *et al.*,

2012). To date, however, a quantifiable link between dune field topography and vegetation patterning has yet to be tested or established.

In the Canadian Prairies there are 120 major dune fields stabilized by vegetation, which makes this region ideal for testing and quantifying topography-vegetation linkages. In particular, the Great Sand Hills in southwestern Saskatchewan is the largest contiguous tract of stabilized dunes, and is also the largest undisturbed region of native grassland in Saskatchewan (Koenig, 2012). This unique aeolian landscape serves as a biological hotspot and provides habitat for several specialized and threatened or endangered species, such as Ord's kangaroo rat (*Dipodomys ordii*), slender mouse-ear-cress (*Halimolobos virgata*) and smooth arid goosefoot (*Chenopodium subglabrum*) (Nielsen, 2007). The region has undergone cycles of activity and stability in response to changes in climate during the Holocene, with a steady trend towards stabilization in the past 200 years, effectively transforming the region into a verdant ecosystem of stabilized parabolic sand dunes (Wolfe & Hugenholtz, 2009). Less than 1% of the dunes remain active today (Wolfe *et al.*, 2001; Wolfe & Hugenholtz, 2009), and this is expected to decrease with time (Koenig, 2012). Dunes create topographic variability that is distinctly different from the adjacent glaciogenic landscape, with differences in dune slopes encouraging different edaphic and hydrological conditions (Koenig, 2012). The climate of the region is dry-subhumid on average, and semi-arid in times of severe drought (Wolfe *et al.*, 2001; Hugenholtz & Wolfe, 2005; Wolfe & Hugenholtz, 2009; Hugenholtz *et al.*, 2010). The combination of a dry-subhumid climate, geographic latitude and topographic variability creates the potential for microclimatic gradients to exist within the region, thus potentially influencing the spatial distribution of landcover throughout the region.

This thesis investigates the impact of topography on the spatial distribution of landcover within a Canadian Prairie sandhill ecosystem; in effect, increasing the

physiographic perspective on topography-vegetation associations, as well as the quantitative evidence. The objective of this research is to quantify the extent to which topographic variability has influenced the spatial distribution of vegetation in a stabilized inland dune field. To accomplish this, an investigation was undertaken to compare the associations between various topographic characteristics and landcover. The main methodological approach consisted of spatial analysis of digital topographic and landcover data; this provides a regional perspective of the topography-vegetation association. In Chapter 2, landcover diversity is compared to topographic indices in order to ascertain whether regions of high diversity correspond to greater topographic complexity. In Chapter 3, the spatial predictability of a particular landcover community type (i.e., trees) was tested based on topographic indices. In Chapter 4, the main conclusions of this research are outlined. However, before examining the details of the studies, necessary background information and context is provided so as to place these chapters within the framework of topography-landcover associations.

1.2 Literature review

Several different types of landscapes show strong associations between topographic variability and landcover characteristics (e.g., Hulett *et al.*, 1966; Liu *et al.*, 2007; Istanbuluoglu *et al.*, 2008; Jerolmack *et al.*, 2012). Qualitative interpretation suggests that increased ruggedness, or variability, in topography creates a wider range of microclimates within a region, thus promoting increased landcover diversity (e.g., Brown & Gibson, 1983; Whittaker *et al.*, 2001; Istanbuluoglu *et al.*, 2008). Additionally, life strategies of different vegetation types affect their distribution among specific microclimates, or habitats, throughout a region (e.g., Hulett *et al.*, 1966; Acosta *et al.*, 2007; Liu *et al.*, 2007;

Acosta *et al.*, 2009; McCulloch & Kabzems, 2009; Lowe *et al.*, 2012). This literature review will begin by discussing topographic effects on landcover. Following this, I will discuss the use of digital data and the importance of addressing spatial scale in an ecosystem study. Next, I will review several different ecosystems that have shown an association between topography and vegetation. I will then discuss the topographic influence on landcover within coastal and inland dune field settings. Finally, I will summarize my research hypothesis and thesis outline.

1.2.1 Topographic and non-topographic influences on landcover

Understanding and explaining the spatial distribution of vegetation communities has been of paramount importance in ecology (Guisan & Zimmerman, 2000; Coblenz & Keating, 2008). Vegetation communities are immobile and require specific environmental conditions; thus, the spatial structure of vegetation communities exists through specific habitat preferences or niches (Lowe *et al.*, 2012). The combination of climate and other environmental factors, such as topography, are widely used to explain the spatial distribution of vegetation communities (Guisan & Zimmerman, 2000; Coblenz & Keating, 2008; Zhao *et al.*, 2010; Lowe *et al.*, 2012).

Studies concerning the association between topography and vegetation have focused on the effects of the former on vegetation type, distribution, and diversity (e.g., Coblenz & Riitters, 2004; Deng *et al.*, 2007; Coblenz & Keating, 2008; Hofer *et al.*, 2008; Pérez *et al.*, 2008). Variability in relief and topographic variables such as elevation, slope, and aspect are considered to be key factors influencing landcover in some settings due to their effect on site-specific microclimates (Coblenz & Riitters, 2004; Coblenz & Keating, 2008; Zhao *et al.*, 2010). Topography is an indirect variable governing

different habitat conditions, which are created by the influence of topography on incoming solar radiation, or through elevation changes influencing temperature (Austin, 2002; Coblenz & Riitters, 2004). Solar radiation can affect the success of vegetation by influencing near-surface air temperature, soil temperature and soil moisture (Coblenz & Riitters, 2004; Bennie *et al.*, 2008). The influence of topography on incoming solar radiation indirectly influences microclimates within a region, thus influencing vegetation pattern, distribution and growth (Bennie *et al.*, 2008; Hoersch *et al.*, 2002; Hofer *et al.*, 2008; Zhao *et al.*, 2010). Different life strategies can constrain the distribution of vegetation to specific habitat types (Riley *et al.*, 1999). For example, at the community level, woody plant species (i.e., shrubs, trees) rely heavily on soil moisture during the initial stages of establishment and thus typically occur in regions with greater soil moisture availability (Mitton *et al.*, 1980; McCulloch & Kabzems, 2009). Unlike woody species, herbaceous species (i.e., grasses) are opportunistic and can survive in a multitude of different habitat conditions (Potvin, 1993; Koenig, 2012). Spatial variability in the distribution of different habitat niches, or microclimatic conditions, can therefore result in a corresponding spatial heterogeneity in the distribution of different landcover communities (Burnett *et al.*, 1998; Riley *et al.*, 1999; Maestre *et al.*, 2003). Further, an increase in the ruggedness (i.e., horizontal variability of elevation fluctuations) of topography results in a patch-like distribution of habitat types, potentially allowing for an increase in landcover diversity due to the corresponding increase in richness of landcover types (Coblenz & Riitters, 2004; Pérez *et al.*, 2008).

Primary topographic factors (e.g., slope, aspect, elevation) alter microclimate conditions and indirectly affect the growth and distribution of landcover. Aspect is a critical factor in the distribution and growth of vegetation because it determines the insolation of a surface (McCune & Kean, 2002). Surfaces receiving less insolation generally experience

cooler and, therefore, moister microclimates, whereas surfaces receiving more incoming solar radiation generally experience warmer, and correspondingly dryer conditions (Miller *et al.*, 1983; Ahrens, 2008). Additionally, slope may act as an important input for microclimatic conditions affecting the growth and distribution of vegetation. Steeper slopes generally receive greater concentrations of incoming solar radiation and therefore experience warmer, dryer climates than slopes with decreased steepness (Bennie *et al.*, 2008). Slope also affects soil moisture through downslope drainage, with greater rates of drainage occurring on steeper slopes (Maestre *et al.*, 2003; Koenig, 2012). Furthermore, the influence of spatial gradients and topographic variability on microclimates become exaggerated at mid-to-high latitudes due to the increasingly uneven distribution of incoming solar radiation; which can lead to highly contrasting microclimates in moderate topography (Coblentz & Riitters, 2004; Bennie *et al.*, 2008).

Primary topographic variables can be combined to produce secondary or compound topographic variables (e.g., ruggedness, wetness index, solar radiation) (Moore *et al.*, 1991). Generally, secondary topographic variables explain landcover patterns better than primary topographic variables because they directly parameterize influential factors on landcover from topographic measurements (Moore *et al.*, 1991; Franklin *et al.*, 2000; Hoersch *et al.*, 2002; Hofer *et al.*, 2008).

In addition to topography, the distribution of landcover may also be a result of the complex interactions between the landcover and other environmental conditions, such as historical and current land use, biological interactions, and stochastic environmental events (Grubb, 1977; Lichter, 2000; Rey & Alcántara, 2000; Hoersch *et al.*, 2002; Bennie *et al.*, 2006). The association between topography and landcover also becomes convoluted in landscapes that have been altered due to natural disturbances (e.g., fires, drought) or anthropogenic

activities (e.g., agriculture, ranching), as these alterations disrupt the topographic-induced patterns of landcover (Hoersch *et al.*, 2002). Furthermore, random distributions of vegetation are possible, but evidence suggests that in landscapes with topographic variability, especially in mid-to-high latitudes, the distribution of vegetation can be attributed to the topography (e.g., Burnett *et al.*, 1998; Riley *et al.*, 1999; Hoersch *et al.*, 2002; Coblenz & Riitters, 2004; Hofer *et al.*, 2008; Pérez *et al.*, 2008; Lowe *et al.*, 2012).

1.2.2 The association of topography to landcover distribution and diversity

Understanding and explaining the ecological function and spatial arrangement of vegetation within an ecosystem has been a long-standing question for ecologists (Turner, 1990; Coblenz & Keating, 2008). Patterns of landcover distribution and landcover diversity can be important for understanding the associations between landcover and various ecological functions. For example, landcover patterns can influence the distribution and persistence of wildlife populations (Turner, 1990; Archibold, 1996; McCulluoch & Kabzems, 2009), health and success of migrating wildlife and bird populations (Archibold, 1996; McCulluoch & Kabzems, 2009), and biophysical processes such as net primary production (Turner, 1990; Tilman, 1996). The geomorphometry (i.e., topographic metrics) of a region has also been found to be of paramount importance in influencing the distribution of vegetation and biodiversity in several landscape settings; therefore, topography is an important factor in landcover studies (Coblenz & Riitters, 2004; Coblenz & Keating, 2008).

Topographic variability supports a wide range of microclimatic conditions and can support high vegetation diversity (Whittaker, 1960; Brown & Gibson, 1983; Hoersch *et al.*, 2002; Coblenz & Riitters, 2004; Deng *et al.*, 2007; Coblenz & Keating, 2008).

Regions with greater topographic variability can correspond to greater diversity measures (e.g., Coblenz & Riitters, 2004). Landcover diversity is important because it serves as a surrogate for regional biodiversity, indicating areas with high and low expected biodiversity (Coblenz & Riitters, 2004; Pérez *et al.*, 2008). A greater variety of landcover types can support the existence of a greater variety of associated wildlife species, thus extending landcover diversity to a measure of potential biodiversity within a region (Coblenz & Riitters, 2004; Pérez *et al.*, 2008). Additionally, the functioning of an ecosystem may depend on its biological diversity, with ecosystems of greater diversity resulting in greater stability and productivity (Tilman, 1996; Hector *et al.*, 1999; Tilman *et al.*, 2001; Foster & Dickson, 2004).

Landcover is often distributed according to suitable habitat conditions created by the topography (Hoersch *et al.*, 2002; Coblenz & Riitters, 2004; Hofer *et al.*, 2008; Pérez *et al.*, 2008; Lowe *et al.*, 2012). Different vegetation types occur in habitats that have been selected due to the evolutionary history and development of the species, and according to environmental factors (Bazzaz, 1991). Further, the distribution of landcover tends to favour habitat conditions that allow improved functionality and success of certain species (Bazzaz, 1991). The distribution of plant communities can be important for understanding their associations with wildlife and although the existence of a specific landcover type may not guarantee the occurrence of a specific wildlife species, the absence of the landcover type usually implies the absence of that species (Coblenz & Riitters, 2004). In this context understanding the topographic variability and its influence on the distribution of landcover is valuable for conservation planning, and habitat or species management (Franklin, 1995; Guisan & Zimmerman, 2000; Austin, 2002; Pérez *et al.*, 2008).

1.2.3 Use of digital data and the issue of spatial resolution

Topography-landcover studies have traditionally relied on field data (e.g., Hulett *et al.*, 1966; Zhao *et al.*, 2010), which have a limited spatial resolution, but the availability of digital topographic and landcover data, and the rapid innovations of digital frameworks and processing, have expanded research involving topography-vegetation associations (e.g., Turner, 1990; Franklin, 1995; Coblenz & Riitters, 2004; Coblenz & Keating, 2008; Pérez *et al.*, 2008). There has also been a corresponding increase in the use of quantitative methods and models as a means of identifying and understanding associations between topography and landcover, especially for regional studies (e.g., Coblenz & Riitters, 2004; Pérez *et al.*, 2008).

Digital geospatial data have several advantages over field data. Advances in analyses involving digital terrain and landcover data allow for quantitative comparisons, where previous studies have been restricted to comparison via qualitative analyses using field data or quantitative analyses of sample areas within the overall region (Coblenz & Riitters, 2004; Deng *et al.*, 2007; Zhao *et al.*, 2010). Direct field measurements of environmental factors affecting the spatial distribution of vegetation may be preferred, but due to the time-consuming processes of field studies and large or inaccessible study areas, field data may not be desirable or available. The use of digital data allows for fast and efficient evaluation of the association between topography and landcover over large regions (Hoersch *et al.*, 2002; Coblenz & Riitters, 2004).

Quantifiable topographic variables can be measured with a digital elevation model (DEM), which is a grid of data with each cell containing an elevation value. These data have proven to be powerful for evaluating regional eco-geomorphic characteristics (Coblenz & Riitters, 2004; Coblenz & Keating, 2008; Pérez *et al.*, 2008). Primary topographic variables

such as slope, aspect and elevation can be derived from DEMs and are often used to characterize and model landcover distributions. In turn, these variables may be combined into compound topographic variables, such as topographic wetness index and solar radiation, to better represent direct environmental influences on landcover (Moore *et al.*, 1991; Bennie *et al.*, 2008).

Vegetation distributions can be predicted from various topographic variables within a region using digital data (Franklin, 1995). Predictive landcover mapping relies on the premise that vegetation is associated with the topography (i.e., ecological niche theory) to the extent that the spatial distribution of landcover can be predicted from topographic parameters (Franklin, 1995; Guisan & Zimmerman, 2000; Parolo, 2008). Furthermore, to ensure the use of proper data and reliable results, one of the major issues that must be addressed in an eco-geomorphological study is spatial scale (Levin, 1992; Brosfoske *et al.*, 1999; Scott *et al.*, 2002). The spatial scale of the digital data must be appropriate for the study to represent key landcover and topographic characteristics. If the resolution of the DEM is too coarse it will result in inaccurate representations of the topography that might influence vegetation (Franklin *et al.*, 2000). For example, if the dominant topographic features are smaller than the grid cells of the DEM, with several features contained in each pixel, the results will not reflect the effects of those individual topographic features on the landcover, but rather a blend or average of those features. Therefore, the scale at which the topography-landcover association is analyzed should reflect the overall goal of the study. Additionally, the incorporation of several kernel sizes can allow insight into the topography-landcover association and enable an understanding of how associations may change with spatial scale (Deng *et al.*, 2007; Pérez *et al.*, 2008).

Using digital data to predict and model the characteristics of the landcover from various topographic parameters is meaningless without validation of the results; therefore, models must be tested (Loehle, 1983; Austin, 2002; Lee, 2004). Predictive topography-landcover models can never provide absolute results because the ecosystem is an open system, with other external factors such as disturbance, stochastic environmental events and biological factors influencing landcover (Franklin *et al.*, 2000; Oreskes *et al.*, 1994). Because of this, predictive models are mainly heuristic and can only be evaluated in relative terms and the predictive value of these models is not absolute (Oreskes *et al.*, 1994; Franklin *et al.*, 2000). The most common methods of model evaluation and validation involve a comparison between the results and real-world observations. Model evaluation will determine if the predictions are sufficiently accurate based on comparisons with observed data, and are considered valid when results are similar to the observed data (Loehle, 1983; Oreskes *et al.*, 1994). Quantifying the similarity between models and observed data remains an open research question.

1.2.4 Topography-landcover studies of non-dune landscapes

Studies of the topography-landcover association have been conducted across a multitude of different ecosystems and the effects of topography on the distribution of landcover are especially apparent in mountainous and arid regions.

Mountainous regions are home to some of the most dramatic examples of topographic variability and several studies have demonstrated a correlation between these characteristics (e.g., Hoersch *et al.*, 2002; Coblenz & Riitters, 2004; Pérez *et al.*, 2008; Zhao *et al.*, 2010). The high degree of topographic relief in alpine regions leads to corresponding heterogeneity of microclimatic conditions due to variability in topographic indices such as

elevation, slope aspect, and slope angle (Hoersch *et al.*, 2002; Coblenz & Riitters, 2004; Coblenz & Keating, 2008). As stated previously, differences in the topographic characteristics of a region result in different rates of incoming solar radiation and elevation-dependent temperature, thereby influencing factors such as near surface air temperature, soil temperature, and soil moisture, for example (Hoersch *et al.*, 2002; Coblenz & Riitters, 2008; Coblenz & Keating, 2008). The distribution of landcover is predictable in mountainous regions due to the different habitat conditions created by topography (e.g., Guisan & Zimmerman, 2000; Coblenz & Riitters, 2004; Pérez *et al.*, 2008). In addition to the microclimatic conditions created by the high degree of topographic relief, elevation plays a crucial role in the distribution of vegetation in mountainous regions via vertical stacking of different habitat niches, thus increasing the richness of landcover and therefore further increasing landcover diversity (Coblenz & Riitters, 2004).

Topography also plays a role in the vegetation patterns in arid regions. Typically, arid regions are defined as those that experience an extended dry season and lose more water to evapotranspiration than is gained through precipitation (Rietkerk *et al.*, 2002). Thus, in arid regions the limiting factor on the growth and distribution of landcover is water availability (Burke *et al.*, 1989; Rietkerk *et al.*, 2002). Coblenz & Riitters (2004) suggested that the role of topography on the distribution of landcover and landcover diversity was particularly profound in arid regions of the south-western USA and northern Mexico. Variations in topography create variability in edaphic conditions and various landcover patterns evolve as a direct result of this (Burke *et al.*, 1989; Rietkerk *et al.*, 2002). These patterns depend on the slope gradient and elevation-dependent rainfall, with differences in slope steepness determining the patterns of landcover due to the distribution of soil moisture as regulated by topography (Rietkerk *et al.*, 2002).

Not only is the distribution of landcover affected by topography, but landcover diversity is also affected by heterogeneity in topographic characteristics. A thorough evaluation of this association is critical to understanding long-term biogeographical and geomorphological processes (Pérez *et al.*, 2008). By understanding these processes, topography and landcover can be used to create predictive models that inform ecosystem management and planning.

1.2.5 Topography-landcover studies of coastal dune systems

The topography-landcover association has been widely studied in coastal dune settings with similar findings from disparate locations (e.g., Doing, 1985; Maun & Perumal, 1999; Lichter, 2000; Dech & Maun, 2005; Acosta *et al.*, 2007). Vegetation zonation occurs in coastal dune ecosystems and is found to be closely associated to the geomorphology and sediment characteristics of the dunes (Acosta *et al.*, 2007).

Coastal sand dune ecosystems represent spatial gradients affecting the distribution of landcover. The two most common factors governing the distribution of landcover are sand burial and salt spray (Maun & Perumal, 1999; Lichter, 2000; Dech & Maun, 2005). In addition to sand burial and salt spray, other environmental variables, such as slope and aspect, are also important in coastal dune systems (Maun & Perumal, 1999; Lichter, 2000). Sand dunes provide spatial variability in topography and result in different microsites due to variability of slope and aspect, as seen in other geographic settings. Different aspects and slopes, along with the distance from the shoreline, provide different niche habitats suitable for different landcover types and a wider range in these topographic variations can result in increased landcover diversity (Coblentz & Riitters, 2004). Vegetation becomes dispersed among the coastal dunes as if a filter determines landcover placement. Sand burial and salt

spray effectively distribute landcover according to their tolerances to both factors, with less specificity and patterning occurring further away from the coastline (Dech & Maun, 2005). As a result, the occurrence of woody species gradually increases with the distance from the coastline, whereas species tolerant of sand burial and salt spray are more frequent with decreasing distance from the coastline (Dech & Maun, 2005).

1.2.6 Topography-landcover studies of inland dune systems

Although inland aeolian dune landscapes (dune fields) often contrast their surrounding ecosystems and provide habitat for a variety of unique and specialized flora and fauna, there exists a dearth of information regarding their association in these settings.

Across different inland dune ecosystems, soil moisture is the most common mechanism that creates spatial patterns of vegetation (Hulett *et al.*, 1966; Barnes & Harrison, 1982; Potvin, 1993; Liu *et al.*, 2007). The individual life strategies of plants during the initial stages of establishment determine patterns observed in adult populations (Hulett *et al.*, 1966; Potvin, 1993). The topographic variability associated with the irregular distribution of dunes results in a heterogeneous mosaic of microclimates and habitat conditions, leading to a spatially-heterogeneous distribution of landcover types throughout (Hulett *et al.*, 1966; Liu *et al.*, 2007). For example, areas between dunes (i.e., interdunes) tend to have relatively high soil moisture conditions, which affect vegetation patterns at both the species and community levels (Liu *et al.*, 2007). These areas are typically populated by tree and shrub communities as they provide a constant source of water during the establishment of seedlings (Hulett *et al.*, 1966; Liu *et al.*, 2007). Quantification of the association between topography, landcover diversity and vegetation distribution is rare in inland aeolian sandhills relative to their coastal dune counterparts (Liu *et al.*, 2007).

In Canada, the Great Sand Hills of Saskatchewan is one of the most-studied inland aeolian dune fields. The GSH are also one of the largest contiguous grassland regions in Western Canada and located near the most northern portion of the North American Great Plains. Hulett *et al.*, (1966) studied the distributions of various plant species within the GSH and found consistent patterns of vegetation distributions. Given that the GSH reside in a semiarid to dry subhumid climate, Hulett *et al.*, (1966) proposed that it is reasonable to assume one of the most important factors governing vegetation distributions was micro-environmental differences associated with the terrain.

1.3 Thesis outline

The GSH region is a biological hotspot within the cultivated region of the Canadian prairies because it provides rare habitat for specialized species that occur less frequently in the surrounding prairie grassland, such as Ord's kangaroo rat (*Dipodomys ordii*), slender mouse-ear-crec (*Halimolobos virgata*) and smooth arid goosefoot (*Chenopodium subglabrum*) (Nielsen, 2007). The influence of topographic variability on the regional distribution and diversity of landcover in the GSH is largely unknown. As part of this thesis research preliminary tests for spatial autocorrelation of each landcover community type were undertaken. Results were inconsistent, suggesting non-random vegetation distributions. Therefore, this thesis seeks to elucidate the topography-landcover association within this stabilized dune field ecosystem. The objective was to determine how the topographic relief and topographically-induced microclimates dictate landcover diversity and distribution patterns at the community level within the GSH. This thesis used digital data and attempted to determine how the spatial scale of analysis affects the associations. Therefore, this thesis

expands upon previous small-scale field studies within the GSH to determine the association of landcover and topography at the regional, community scale.

First, following the work of Coblenz & Riitters (2004) and Pérez *et al.*, (2008), this thesis investigated the regional landcover diversity of the GSH (Chapter 2). The predictability and quantitative association of topography and landcover diversity is largely undocumented in inland dune field ecosystems. Using digital topographic data and digital landcover data, regional landcover diversity was calculated at several spatial scales using Simpson's diversity index and compared to a suite of topographic indices derived from a digital elevation model. The results from Chapter 2 show that there is a moderate association between topography and landcover diversity in the GSH, and that results vary with kernel size. It is proposed that other, non-topographic factors also influence the distribution of landcover within this region.

The second study examined the predictability of a specific landcover community type (i.e., trees) based on five topographic indices (i.e., wetness index, elevation, northness, eastness, and curvature) at two study sites in the GSH (Chapter 3). Results suggested that the establishment of tree communities within both study sites was similar and that tree habitat suitability was predicted with an accuracy of 71.9% using a binary logistic regression model. However, although moderate predictability was demonstrated, other non-topographic factors may play a role and account for the other 28.1% in influencing the distribution of trees within the GSH.

Finally, Chapter 4 summarizes the findings of this thesis and makes recommendations on potential areas for future research.

Overall, this thesis provides several interesting contributions. Although several geomorphological studies have suggested that landcover is strongly associated to

topography, this thesis is the first to examine this association in an inland dune field with digital topographic and landcover data. Overall, this thesis adds to the knowledge of topographic-landcover associations.

CHAPTER 2: IS THERE A TOPOGRAPHIC INFLUENCE ON THE LANDCOVER DIVERSITY OF THE GREAT SAND HILLS, SASKATCHEWAN, CANADA?

2.1 Abstract

Topography is a key geophysical attribute that contains information about the geological, geomorphological and climatic history of a region. In many settings it also controls the distribution of landcover through its effect on microclimatic variability and related processes. This study examines the degree to which topography explains the regional distribution of landcover diversity in the Great Sand Hills (GSH) region of southwestern Saskatchewan. This area is dominated by large tracts of stabilized sand dunes, which appear to enhance landcover diversity compared to the surrounding glaciogenic terrain. By quantitatively assessing the association between these attributes through geospatial analysis, this study attempts to broaden the geographic and geomorphic context of topographic influence on ecosystems. The research approach begins with a quantification of GSH topography through calculation of wetness index (WI) and topographic ruggedness (RU). These are compared to the observed landcover diversity calculated with classified satellite data. In this study, diversity is represented by Simpson's diversity index (SDI). The effect of resolution was examined by calculating SDI with different radii (i.e., 50 m, 100 m, 300 m, 500 m, and 1000 m circular radii). Quantitative comparisons between SDI and the topographic metrics were undertaken to determine how well the former was estimated by the latter. To do this, a simplified approach was adopted that involved a calculation of the difference between the dependent (SDI) and independent variables (WI, RU). Results of the differencing show spatial variability in the association of topography and SDI throughout the GSH; RU predicted 62.1% of the distribution of landcover diversity at the smallest kernel

radius (50 m) and was a better predictor of landcover diversity compared to WI. In the most topographically-rough areas of the GSH, which coincide with sand dunes, RU over-predicts landcover diversity, while closer agreement occurs in the smoother areas where diversity is lower. It appears, therefore, that the magnitude of roughness associated with dunes is insufficient to influence landcover diversity in the GSH. However, it is acknowledged that using topography as a predictor of landcover diversity is a first-order measure, as many other eco-geomorphological and anthropogenic factors influence landcover patterns. As such, the potential role of several factors that might explain the spatial variability in the association observed in this study is discussed.

2.2 Introduction

Topographic characteristics of the landscape (e.g., ruggedness, wetness, elevation, slope, and aspect) can be readily measured from digital terrain data and in many settings they influence the distribution of landcover and landcover diversity (e.g., Gosz & Sharpe, 1989; Burke *et al.*, 1989; Franklin, 1995; Kerr & Packer, 1997; Maun & Perumal, 1999; Guisan & Zimmerman, 2000; Hoersch *et al.*, 2002; Rietkerk *et al.*, 2002; Coblenz & Riitters, 2004; Deng *et al.*, 2007; Liu *et al.*, 2007; Coblenz & Keating, 2008; Istanbuluoglu *et al.*, 2008; Zhao *et al.*, 2010). One of the main explanations put forward is that topography creates spatial variability of insolation, which in turn generates variation in microclimate conditions such as soil moisture, air and ground temperature, and snow cover (Oke, 1987). In some settings distinct vegetation patterns arise because microclimatic conditions favor certain species or functional groups (e.g., Brown & Gibson, 1983; Coblenz & Riitters, 2004; Coblenz & Keating, 2008). These effects become greater with a shift from low to high latitudes due to greater insolation contrasts between north- and

south-facing slopes with increasing latitude (Oke, 1987). Similar effects are apparent in many mountainous regions; however, in these settings altitudinal gradients in temperature are also prominent controls on landcover patterns (Whittaker, 1960; Hoersch *et al.*, 2002; Deng *et al.*, 2007). Large changes in elevation and slope allow for vertical stacking of vegetation communities (Coblentz & Riitters, 2004), thus further increasing landcover diversity within some mountainous regions. Landcover in many arid ecosystems also shows a dependency on the microclimatic variations due to topography (e.g., Brown & Gibson, 1983; Burke *et al.*, 1989; Rietkerk *et al.*, 2002). Arid regions can be defined as those where potential evaporation exceeds yearly rainfall (Rietkerk *et al.*, 2002), thus small changes in topography can influence the soil moisture conditions, which is a limiting factor for certain vegetation species in this type of region (e.g., Brown & Gibson, 1983; Burke *et al.*, 1989; Berndtsson *et al.*, 1996; Rietkerk *et al.*, 2002).

In aeolian landscapes (e.g., dune fields, sand seas, draa) the role of topography on vegetation is also particularly profound (e.g., Maun & Perumal, 1999; Acosta *et al.*, 2007; Acosta *et al.*, 2009; Jerolmack *et al.*, 2012). Coastal dunes have demonstrated that sand dune topography can play a significant role in determining the growth and distribution of vegetation communities, with vegetation distribution reflecting a gradient according to the distance from the water (Doing, 1985; Dech & Maun, 2005; Acosta *et al.*, 2007). Additional ecological factors such as distance from salt spray, sand burial and flooding are also important on coastal dunes (Acosta *et al.*, 2007; Acosta *et al.*, 2009). Although less studied than other settings, the landcover of many inland dune fields can also be influenced by topography (e.g., Hulett *et al.*, 1966; Liu *et al.*, 2007). In interdune spaces, increased water availability relative to surrounding dunes allows woody species, such as shrubs and trees, to increase the diversity of these areas (Liu *et al.*, 2007; Koenig, 2012). Additionally, topographic

gradients in dune fields modify airflow and subsequently sediment transport, leading to a corresponding gradient of vegetation distribution (Jerolmack *et al.*, 2012).

Despite the important link between topography and landcover diversity, studies of the association have been primarily limited to small-scale (i.e., microcosms), field-based studies (e.g., Whittaker, 1960; Hulett *et al.*, 1966; Brown & Gibson, 1983) and qualitative studies (e.g., Brown & Gibson, 1983; Whittaker *et al.*, 2001; Istanbuluoglu *et al.*, 2008). Increasing availability of digital topographic and landcover data encourages quantitative, regional-scale analyses to test these associations, especially in large, inaccessible areas (Kerr *et al.*, 2001; Coblenz & Riitters, 2004). To date, this type of approach has yet to be applied to inland dune fields.

This study presents a quantitative geospatial analysis of topographic control on landcover diversity in an inland dune field. The goal is to determine the degree to which topographic variables can be used as indicators of regional landcover diversity and to test the hypothesis that *within the GSH, there is a quantifiable relation between topographic variability and regional landcover diversity such that the former can be used to predict the latter*. In Canada, the only inland dune field with readily available topographic and landcover data at a resolution suitable for quantitatively assessing the influence of topography is the GSH, which is located in southwestern Saskatchewan. Previous research has suggested a link between topography and habitat diversity in the GSH (Nielsen, 2007); however, an objective quantitative assessment has yet to confirm this interpretation. A primary control on the biodiversity of this region is the presence of a variety of post-glacial landforms, which create variations in topographic relief throughout the region. Relic melt-water channels, moraines, as well as clearly defined parabolic dunes, hummocky dune terrain and blowouts are among the main landforms that serve as the topographic template (Hulett *et al.*, 1966; Hugenholtz & Wolfe,

2005; Hugenholtz *et al.*, 2007; Hugenholtz *et al.*, 2010; Fox *et al.*, 2012). From a qualitative interpretation, the variability of topography appears to be linked to the distribution of landcover types throughout the region (Fig. 2.1). Comparisons of topographic relief with landcover community distributions suggest that more landcover community types occur in areas with greater topographic relief, and that topographically-smooth areas tend to be dominated by one landcover type: grassland. Additionally, areas with greater topographic relief and a greater variety of landcover types appear to be associated to dune relief (Fig. 2.1). Thus, the motivation for this study is to evaluate the degree to which topography explains the regional distribution of landcover diversity in the GSH, and to explore whether the resolution of data influences this association. Understanding the influence of topography on landcover diversity in inland dune fields like the GSH may also clarify regional patterns of biological diversity (e.g., Nielsen, 2007), which play a role in land use planning and management.

The methods used here present a way to evaluate landcover diversity at the regional scale. It is important to note that spatial patterns of landcover diversity are not only conditioned by topography; other factors may be involved (e.g., Brown & Gibson, 1983; Coblenz & Riitters, 2004; Nielsen, 2007; Pérez *et al.*, 2008; Fox *et al.*, 2012). However, by testing the degree to which topography relates to landcover diversity we can infer whether the spatial pattern of landcover is conditioned by the underlying geomorphological template, which is important in the context of predictive modeling of dune-vegetation feedbacks (Barchyn & Hugenholtz, 2012a, b).

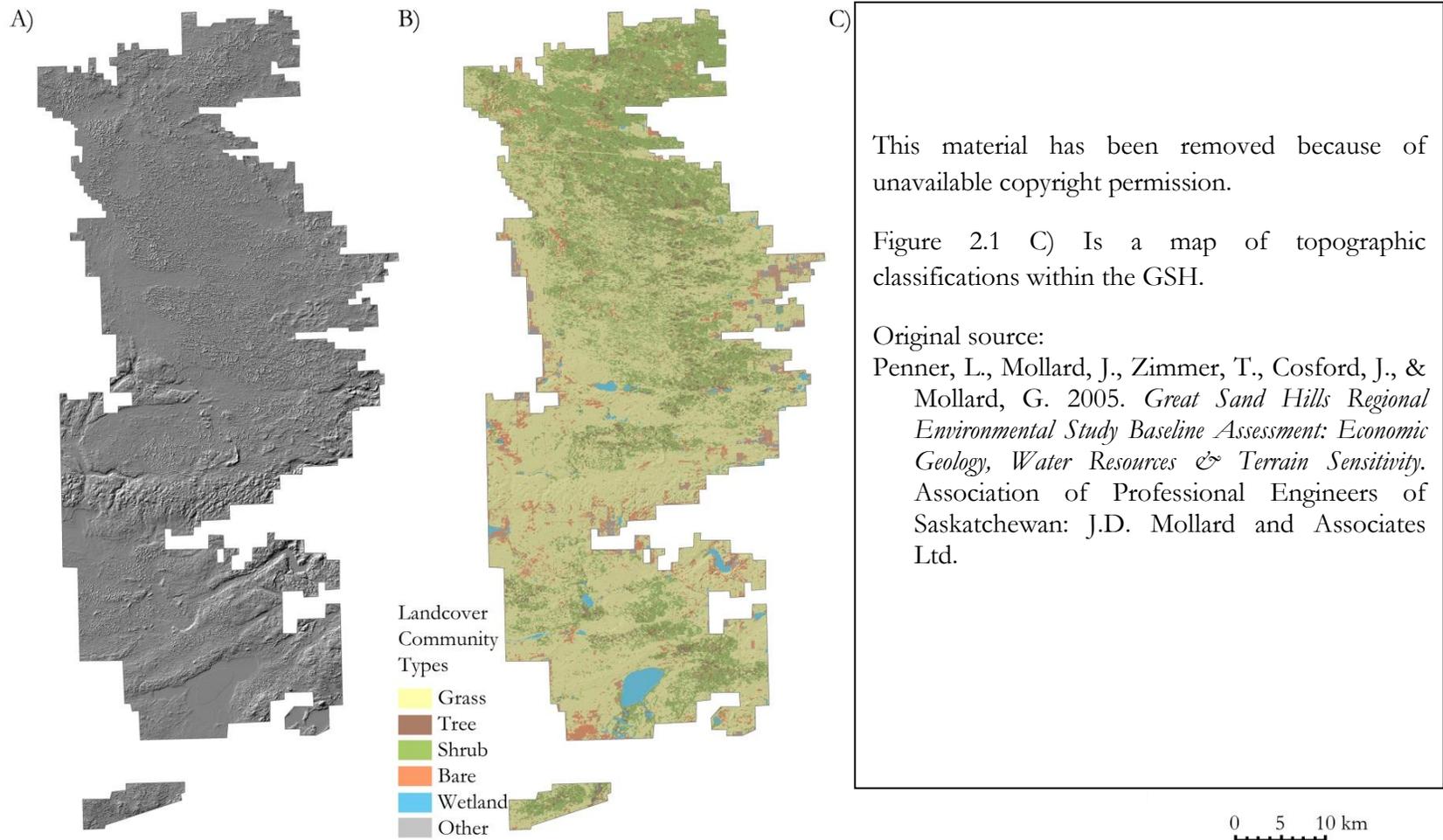


Figure 2.1. A) A hillshade of the GSH. B) Corresponding landcover communities. C) Topographic classifications (source: Penner *et al.*, 2005). It is hypothesized that areas with greater topographic relief result in greater diversity of landcover community types and that this association can be quantitatively linked. Qualitatively, it appears as though a greater variety of landcover communities coincides with the dune relief category in C), whereas a smaller variety of landcover communities coincides with flat, or undulating topographic categories.

2.3 Study area

The GSH cover an area of approximately 2000 km² (Wolfe *et al.*, 2001; Noble, 2008) and is located north of Maple Creek, Saskatchewan, between 50°N and 51°N (Fig. 2.2). This region comprises the largest contiguous dune field on the Canadian prairies (Hugenholtz & Wolfe, 2005). The climate of the region is dry-subhumid, turning to semi-arid in times of severe drought, with short but warm summers and long, cold winters (Wolfe *et al.*, 2001; Hugenholtz & Wolfe, 2005; Wolfe & Hugenholtz, 2009; Hugenholtz *et al.*, 2010). The combined influence of the climate and high latitude creates the potential for microclimatic gradients to exist within the region (e.g., Hugenholtz & Wolfe, 2006; Koenig, 2012).

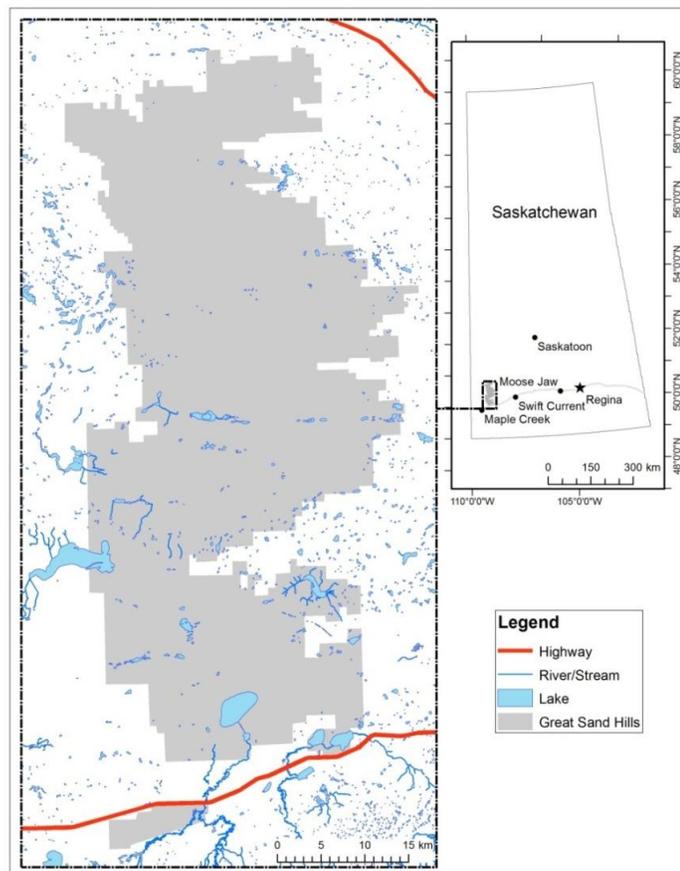


Figure 2.2. Location of the GSH, Saskatchewan.

2.3.1 Aeolian evolution of the GSH

Many of the observable topographic features of the GSH are the result of aeolian activity; Figure 2.1C indicates that sand dunes are the dominant landform. After the retreat of the Laurentide Ice Sheet 13 000 YBP, water levels receded in ice-marginal lakes and vast glaciofluvial and glaciolacustrine sedimentary deposits were exposed to wind, ultimately forming an extensive dune field (Hulett *et al.*, 1966; Wolfe *et al.*, 2001; 2004; Hugenholtz & Wolfe, 2005; Hugenholtz *et al.*, 2010). In the past 200 years, the GSH have effectively transformed from desert-like conditions to a relatively verdant ecosystem due to a change in climate towards warmer and less arid conditions (Wolfe & Hugenholtz, 2009). During this transition, dunes evolved from bare barchan dunes with arms extending downwind, to vegetated parabolic dunes with arms extending upwind (Wolfe & Hugenholtz, 2009). The predominant wind direction during dune formation was westerly, thus the topographic grain of the dunes is in a west to east direction (Hulett *et al.*, 1966). It is anticipated that different microclimatic environments were created due to topographic variability, thus explaining the spatial distribution of vegetation today (Fig. 2.3). The examples in Figure 2.3 show the topographic relief of two contrasting landforms and the overlying pattern of landcover. These examples show a higher diversity of landcover types in the region dominated by hummocky dunes (Fig. 2.3B; D) and lower diversity in the region dominated by a moraine (Fig. 2.3C; E).

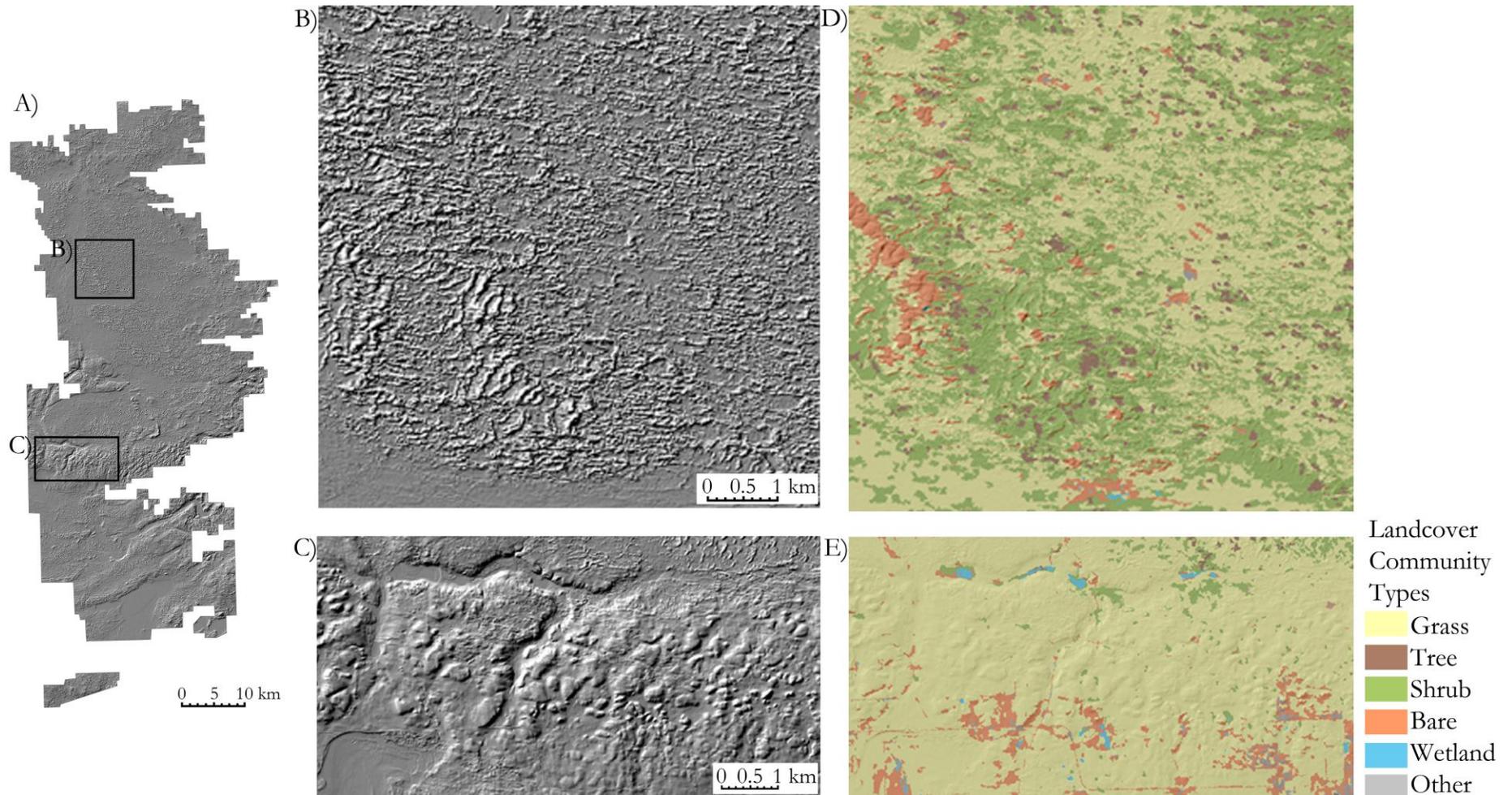


Figure 2.3. The GSH is shown in A), with B) and C) representing areas with different high and low topographic relief, respectively. Rugged topographic relief is represented by B), with corresponding landcover, D), showing a wide variety of landcover community types. Smoother topographic relief is represented by C), with corresponding landcover, E), showing a decreased variety of landcover community types when compared with its rugged counterpart.

2.3.2 Present-day geomorphology of the GSH

Today, the GSH are a relatively verdant, mixed grassland ecosystem that is largely undisturbed by crop agriculture (Noble, 2008; Fig. 2.1C). The GSH contain several different landforms: moraines, parabolic dunes, hummocky dune terrain, blowouts and relic melt-water channels. Each of these landforms adds to the topographic relief of the region and are readily distinguishable in a shaded relief map (Fig. 2.4). A brief description on each of the landforms follows.

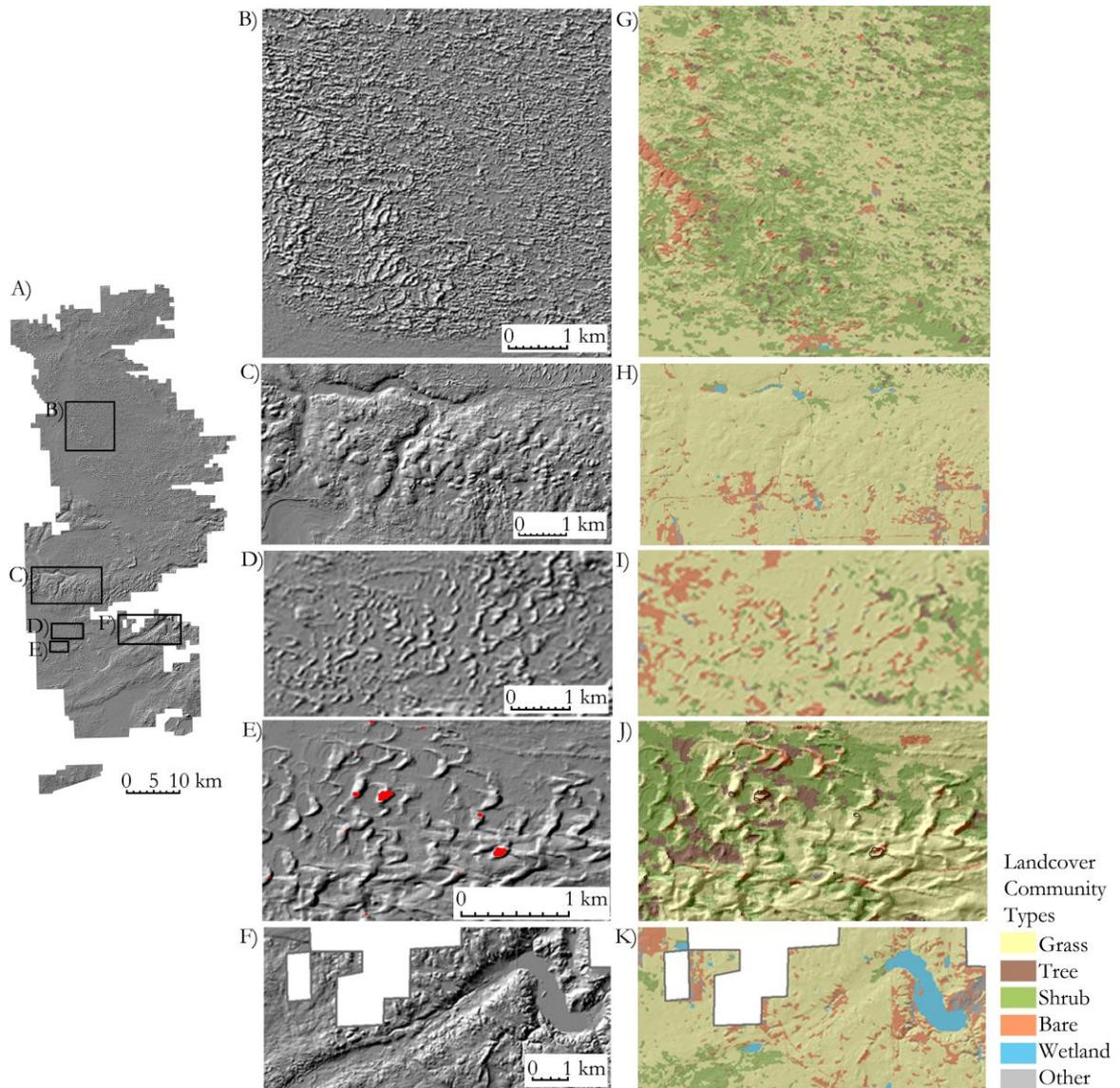


Figure 2.4. The GSH is shown in A), with B) to F) corresponding to hummocky dune terrain, moraine, parabolic dunes, blowouts and relic melt water channel topographic features, respectively. Corresponding landcover images are shown in G) to K). Blowouts in E) are represented by red markers.

Moraines are topographic features formed in terrestrial, subaquatic or ice-marginal environments (Slaymaker & Kelly, 2007). They are typically characterized by smooth, rolling topography consisting of glacial till (Fig. 2.1C) and are primarily dominated by grassland community types in the GSH (Fig. 2.4C; H). The recession of ice sheets and glaciers also releases meltwater that can erode sub-glacial drainage channels (Slaymaker & Kelly, 2007). In

the GSH, meltwater evacuation during recession of the Laurentide Ice Sheet formed large sub-glacial channels (Fig. 2.1C; Fig. 2.4F; K). Once proglacial lakes drained the sandy substrate was exposed to westerly wind, forming barchan dunes that later converted to parabolic dunes with the introduction of vegetation (Wolfe & Hugenholtz, 2009). The north and south slope aspects of the dunes create different microclimates that lead to contrasting aeolian processes, as well as different hydrological and edaphic conditions (Hugenholtz & Wolfe, 2006; Koenig, 2012). Parabolic dunes in the GSH are typically 6 m tall, 300 m long and 250 m wide, with interdune areas ranging from 10-1000 m² (Fig. 2.4D; I; Saskatchewan Environment, 2007). Another important aeolian feature found in the region is hummocky dune terrain. Based on numerical modeling, Barchyn & Hugenholtz (2012b) suggest this type of terrain was formed by the collisions of small, fast-moving dunes during the process of stabilization. Hummocky dune terrain is unorganized, or chaotic, which makes it difficult to discern individual dunes (Fig. 2.4B). Landcover corresponding to hummocky dune terrain is a heterogeneous mixture of different community types (Fig. 2.4G). Blowouts are also present within the region and are created by disturbances on stabilized dunes. They are depressions that are maintained or grow in response to further perturbations by wind (Wolfe & Nickling, 1996; Hugenholtz & Wolfe, 2006; Fox *et al.*, 2012). In the GSH, the majority of blowouts are smaller than 200 m³ (Fig. 2.4E) and offer active sand habitat for uncommon, specialized species, many of which are at risk of extirpation or extinction (Fox *et al.*, 2012).

In summary, a variety of landforms and topographic features exist within the GSH, adding to the overall topographic relief of the region. Furthermore, dunes and blowouts create topographic variability that is distinctly different from the adjacent glaciogenic landscape, which tends to be less rugged overall.

2.3.3 Landcover characteristics

Differences in dune morphology lead to different rates of stabilization (Barchyn & Hugenholtz, 2012a), which subsequently lead to variability in successional stages across the entire landscape. When vegetation expands and stabilizes an aeolian landscape, interdune regions tend to be the first to stabilize (Barchyn & Hugenholtz, 2012b). Although less than 1% of the dunes in the GSH are active today (Wolfe *et al.*, 2001; Wolfe & Hugenholtz, 2009), they provide unique habitat for many specialized and endangered species (Hugenholtz *et al.*, 2010).

Relative to the surrounding cultivated prairie, the GSH are native prairie grassland. Due to the presence of sandy substrate cattle grazing is the primary sustainable land-use activity, followed by the natural gas industry (Noble, 2008). These activities influence the landscape and the associated landcover at the local level; however, at the larger regional level, landcover represents a heterogeneous ecosystem of native landcover. Landcover types within the GSH are typical of prairie vegetation and include grass, trees, shrub, bare ground and wetland. Dominant plant species include, but are not limited to: *Psoralea lanceolata* (lance-leaved psoralea), *Agropyron dasystachyum* (northern wheat grass), *Hesperotipa comata* (spear grass), *Artemesia frigida* (pasture sage), *Elaeagnus commutate* (wolf willow), *Rosa woodsii* (woods' rose), and *Populus tremuloides* (trembling aspen) (Hulett *et al.*, 1966). The GSH are also home to several rare and endangered plants, such as *Botrychium campestre* (prairie dunewort), *Lupinus pusillus* (rusty lupine), *Lygodesmia rostrata* (beaked annual skeleton-weed) (Hulett *et al.*, 1966), as well as rare and endangered animals, such as *Dipodomys ordii* (Ord's kangaroo rat), *Athene cunicularia* (burrowing owl) and *Bufo cognatus* (Great Plains toad). Hulett *et al.*, (1966) studied the distribution of vegetation at the species level within the GSH and determined that the

distributions reflected adaptive characteristics related to microsites. This suggests that regional patterns may arise due to topographically-induced microsite variation.

2.4 Methods

Landcover diversity provides a first-order approximation of biodiversity (Coblentz & Riitters, 2004). For example, the presence of a specific landcover type may not guarantee the corresponding presence of a species, but the absence of a specific landcover type can generally lead to the assumption of the absence of a species (Coblentz & Riitters, 2004). Simultaneously, measuring the diversity of the topography can provide insight about the spatial pattern of landcover and whether a relation between the two exists (Kerr & Packer, 1997; Coblentz & Riitters, 2004; Pérez *et al.*, 2008).

2.4.1 Landcover diversity

High resolution (10 m) classified landcover data were acquired through a Regional Environmental Study of the GSH conducted in 2005 by the Saskatchewan government (Saskatchewan Environment, 2007). For this study, landcover was mapped at the community level; therefore, the initial 17 unique landcover types were grouped into 6 community types (Table 2.1). Grouping at the community level addresses inconsistencies in the original data; some community types were segregated into separate landcover classes, while other landcover types were combined at the community level. For example, grassland, sagebrush and silvery grassland are similar at the community level, but were classified as different vegetation types, whereas all different shrub types were already classified as the same vegetation type.

Table 2.1. Reclassification of landcover data into 6 community types.

Landcover Community Type	Original Classifications	Reasons for Placement in Community Type
Bare	Bare Sand (GSH) 25% Revegetated 50% Revegetated	Bare community type represents all land with active sand. Both the 25% and 50% revegetated classifications represent areas with bare sand and primary succession species, e.g., <i>Psoralea lanceolata</i> (lance-leaved psoralia) and <i>Rumex venosus</i> (wild begonia).
Wetland	Alkali Flat Hay/Alfalfa Shallow Alkaline Water Vegetated Wetland Open Water Wet Meadow	Wetland community type represents open water and the peripheral landcover types. Hay/Alfalfa fits this community type due to its presence in moist, rich soils typical of wetlands in the region.
Grass	Grassland Sagebrush Silvery Grassland	Grass community type contains species typical of grassland communities. Both sagebrush and silvery grassland occur in areas associated mostly with grasses.
Shrub	Mixed Shrub	All shrubs of the region – e.g., <i>Rosa woodsii</i> (Woods' rose), <i>Symphoricarpus occidentalis</i> (western snowberry), <i>Prunus virginiana</i> (chokecherry), <i>Juniperus horizonatlis</i> (creeping juniper).
Tree	Trees	All tree types – e.g., <i>Populus tremuloides</i> (trembling aspen), <i>Populus balsamifera</i> (balsam poplar) and <i>Populus deltoids</i> (cottonwood).
Other	Cultivated Bare Sand (Cultivated) Bare Soil	This community type contains all non-natural landcover types from the original classifications – typically associated with agriculture. Mostly on the edge of the GSH.

Landcover diversity was calculated from the classified landcover data using Simpson's diversity index (Simpson, 1949):

$$SDI = 1 - \sum P_i^2 \quad (2.1)$$

where SDI is Simpson's diversity index; and P represents the proportion of each landcover type, i . Simpson's diversity index provides a measure of heterogeneity by combining community richness and evenness. Richness is the number of community types present, and evenness is their relative abundance. The resulting index values range from 0 to 1, with a larger value indicative of greater landcover diversity. Simpson's diversity index was measured using a pixel-based approach, whereby a moving circular kernel was centred upon each cell of the landcover raster and SDI was calculated within the kernel and applied to the centre cell. Because this is a scale-dependent process, landcover diversity was calculated with multiple kernel sizes in order to allow for an assessment of resolution effects on the results. Kernel radii of 50 m, 100 m, 300 m, 500 m, and 1000 m were analyzed in this study (hereafter referred to as SDI₅₀, SDI₁₀₀, SDI₃₀₀, SDI₅₀₀ and SDI₁₀₀₀). Simpson's diversity index is typically used to determine species-level diversity and although other diversity indices exist, SDI remains one of the most meaningful and rigorous diversity measures available and is less sensitive to classification errors (Magurran, 2003; Pérez *et al.*, 2008). Because of this, SDI provides a first-order measure of diversity that can be used as a surrogate, or proxy, for estimating regional biodiversity (Coblentz & Riitters, 2004; Pérez *et al.*, 2008). Other landcover diversity studies (e.g., Coblentz & Riitters, 2004; Pérez *et al.*, 2008) have shown that SDI is useful in establishing an association between landcover diversity and topographic characteristics over large regions.

2.4.2 Topographic indices

If topography is a major control of the distribution of landcover diversity throughout the GSH, then the former should be able to predict the latter with some level of confidence. In order to evaluate the association between topography and SDI, quantitative

measurements were derived from the topographic data. A DEM was obtained from LiDAR data and was rescaled to 10 m (original resolution was 2 m) in order to match the resolution of landcover data. Following the approach of Coblenz & Riitters (2004) and Pérez *et al.* (2008) several topographic indices were used to represent the regional landcover diversity. This is a straightforward approach that uses standardized topographic variables that can be compared to the SDI maps (Coblenz & Riitters, 2004). Indices used in this study are described as follows.

2.4.2.1 Wetness index

Wetness index (WI) was chosen because it takes into account the local slope geometry and represents relative soil moisture and microclimatic variability at the dune scale. The idea is that wetter areas should be more prone to hosting trees and shrubs, whereas drier locations should favour grass. Wetness index is calculated by:

$$WI = \ln\left(\frac{A_s}{\tan B}\right) \quad (2.2)$$

where A_s is the specific catchment area and $\tan B$ is the percent slope. Specific catchment area is calculated by deriving flow accumulation from a DEM and dividing it by the width of the grid cell. For example, if the water flows diagonally across the cell, the width is 1.41 times the cell width; otherwise it is equal to the cell width. Wetness index has potential for characterizing vegetation distributions and diversities (Moore *et al.*, 1991) and has been used to predict the presence of vegetation in other studies (e.g., Lowe *et al.*, 2012; Melo *et al.*, 2012). Having a mix of both dry and wet relative wetness within the same area

should enhance landcover diversity by allowing a mosaic of different landcover types to coexist. In order to compare WI to SDI, the data values were rescaled to the range 0-1.

2.4.2.2 Topographic ruggedness

Ruggedness (RU) was chosen because of its inclusion of both slope and aspect within a kernel (Fig. 2.5; Sappington *et al.*, 2007). Slope and aspect are anticipated to be major factors contributing to landcover variability associated with dune topography due to their effects on the incoming solar radiation and microclimates. As ruggedness increases it is expected there will be a greater diversity of landcover types due to variability of microclimates associated with different slopes and aspects.

This material has been removed because of unavailable copyright permission.

Figure 2.5 is a graphic showing how ruggedness is calculated.

Original source:

Sappington, J.M., Longshore, K.M., Thompson, D.B. 2007. Quantifying landscape ruggedness for animal habitat analysis: A case study using bighorn sheep in the Mojave desert. *Journal of Wildlife Management*, 71(5), 1419-1426.

Figure 2.5. Ruggedness is calculated from a raster-based DEM. A) Vectors orthogonal to each grid cell in the DEM are broken down into their x, y and z components using standard trigonometric operators and the slope (α) and aspect (β) of each cell. B) A moving kernel calculated the magnitude of the resultant vector ($|r|$) for a given kernel size centred on each grid cell. The resultant vector is standardized (i.e., divided by the number of grid cells within the kernel) and is subtracted from 1 to give a measure of ruggedness in the landscape for the selected kernel size (source: Sappington *et al.*, 2007, Fig. 2).

Ruggedness was calculated using the vector ruggedness measure (VRM), which quantifies RU by measuring the dispersion of vectors perpendicular to the topographic surface (Fig. 2.6; Sappington *et al.*, 2007). Other roughness indices (e.g., land surface

ruggedness index and terrain ruggedness index) do not differentiate between steep slopes and steep slopes with changes in aspect direction. Therefore, the VRM method was chosen as a measure of RU due to its ability to account for both of these factors.

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Figure 2.6 is a graphic demonstrating different combinations of slope steepness and aspect, and the resulting ruggedness values.

Original source:

Sappington, J.M., Longshore, K.M., Thompson, D.B. 2007. Quantifying landscape ruggedness for animal habitat analysis: A case study using bighorn sheep in the Mojave desert. *Journal of Wildlife Management*, 71(5), 1419-1426.

Figure 2.6. Ruggedness calculated using the vector ruggedness measure. Both A) and B) would have lower RU values than C), which demonstrates the greatest RU here (source: Sappington *et al.*, 2007, Fig. 1).

An open source script (Sappington *et al.*, 2007) was used to calculate RU. This tool delineates the kernel size by the number of cells along the edge of a square kernel. The length of the kernel edge used to calculate ruggedness in this study was 990 m (i.e., 99 cells) due to its capability of capturing several dunes within the kernel. Choosing a resolution appropriate to the processes and landscape features of a region is important; if effects of resolution are not considered, analysis results may be meaningless or mask true results (Turner *et al.*, 1989; Moore *et al.*, 1991; Levin, 1992). Thus, RU was calculated at a resolution that would include a periphery large enough to include at least 3 dunes within the kernel. Using a smaller resolution reduces the periphery included within the kernel, and does not include as many dunes; thus, resulting in local RU measures that are less representative of

regional topographic variability. In contrast, using a spatial resolution that is too large begins to include different landscape features in the periphery, resulting in a smoothing effect. Similar to WI the RU values were rescaled to match SDI values (i.e., 0-1).

2.4.3 Differencing

Following the methodology of Coblenz & Rüttgers (2004) and Pérez *et al.* (2008), the difference between the SDI maps and each of the rescaled topographic maps (i.e., WI, RU) was used to assess the association between topography and landcover diversity. Differences (D) are calculated by,

$$D = \text{SDI} - \text{TI} \quad (2.3)$$

where TI is the topographic index (i.e., WI, RU) that is subtracted from the SDI maps. Differencing gives the relative strength of agreement between SDI and topographic indices and allows for a quantitative spatial analysis over the entire region. This method is best suited to the identification of regional variability of the association between landcover diversity and topography.

2.5 Results

2.5.1 SDI maps

SDI maps (Fig. 2.7) show that diversity increases with decreasing resolution. This is expected because large kernels used to calculate diversity (e.g., SDI_{1000} , Fig. 2.7E) have a higher probability of encountering more landcover types, since SDI takes into account the number of vegetation community types present and the relative abundance of each

community (Coblentz & Riitters, 2004; Pérez *et al.*, 2008). However, despite this resolution-dependency, there appears to be a qualitative link between diversity and the geomorphology of the region (Fig. 2.1; Fig. 2.4). For example, low SDI values are observed at moraines, which are dominated by grass (Fig. 2.4C;H), and where there is also less pronounced topographic relief relative to dune terrain. Conversely, high SDI values are observed in regions of high topographic relief especially with hummocky dune terrain and parabolic dunes, where a mix of landcover types coexist (Fig. 2.4B, G; D, I).

Histograms in Figure 2.7 show that the proportion of cells with low SDI values decreases with increasing kernel size. As the kernel size increases the mean SDI value increases and standard deviation decreases, indicating a shift towards larger SDI values, as is also supported by increasingly negative skewness (Fig. 2.7F-J; Table 2.2). Kurtosis values become closer to 0 as the resolution decreases, indicating the distributions become closer to resembling a normal distribution, although distributions are asymmetric (Fig. 2.7F-J; Table 2.2). Furthermore, the median value increases with decreasing resolution, indicating larger SDI values occur in greater proportions with coarser resolutions. In summary, coarser resolution produced higher SDI values.

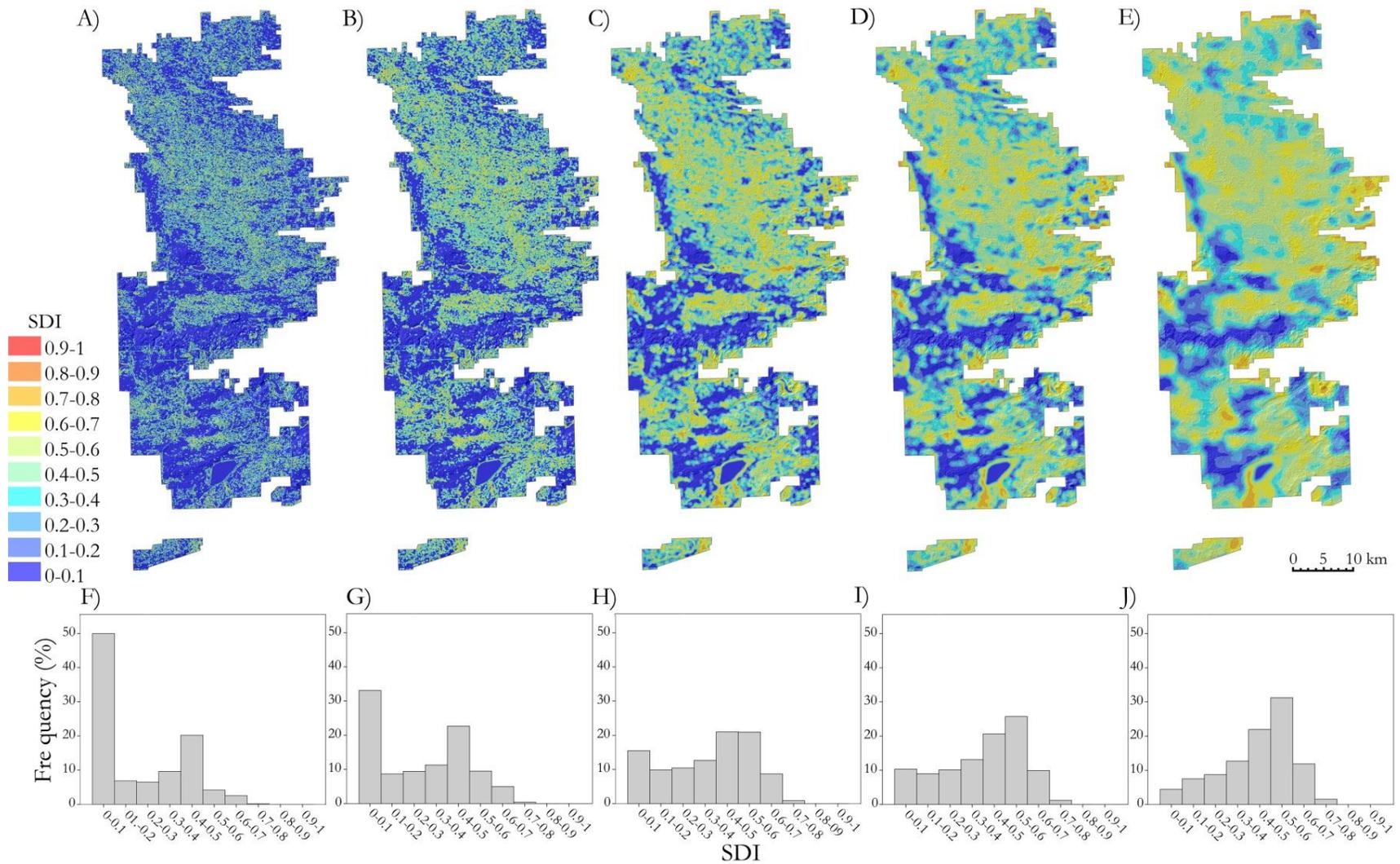


Figure 2.7. SDI maps: A) SDI_{50} ; B) SDI_{100} ; C) SDI_{300} ; D) SDI_{500} ; E) SDI_{1000} . Corresponding histograms (F-J) show distributions of SDI maps.

Table 2.2. Descriptive statistics of SDI maps of the GSH.

Radius	Max.	Mean	Stdev.	Skewness	Kurtosis	Median
SDI ₅₀	0.820	0.199	0.214	0.494	-1.33	0.116
SDI ₁₀₀	0.827	0.272	0.219	0.0500	-1.43	0.289
SDI ₃₀₀	0.811	0.363	0.199	-0.373	-1.04	0.410
SDI ₅₀₀	0.809	0.396	0.187	-0.519	-0.765	0.444
SDI ₁₀₀₀	0.799	0.439	0.165	-0.710	-0.288	0.480

2.5.2 Topographic indices

High WI values occur in low-lying areas, which generally correspond to the positions of lakes, ephemeral water bodies, and wetlands. However, over broad regions WI values are generally low (Table 2.3; Fig. 2.8A) as indicated by low mean (0.217 ± 0.105) and median (0.189) values with positively skewed distribution (Fig. 2.8D; Table 2.3). When using RU, values are higher in areas with greater topographic relief such as hummocky dune terrain and parabolic dunes (Fig. 2.8B). However, values are generally low as indicated by low mean (0.171 ± 0.105) and median (0.112) values with a positively skewed distribution (Fig. 2.8E; Table 2.3).

Table 2.3. Descriptive statistics of topographic maps.

Topographic Index	Max.	Mean	Stdev.	Skewness	Kurtosis	Median
WI	1.00	0.217	0.105	1.18	1.43	0.189
RU	1.00	0.171	0.164	1.59	2.25	0.112

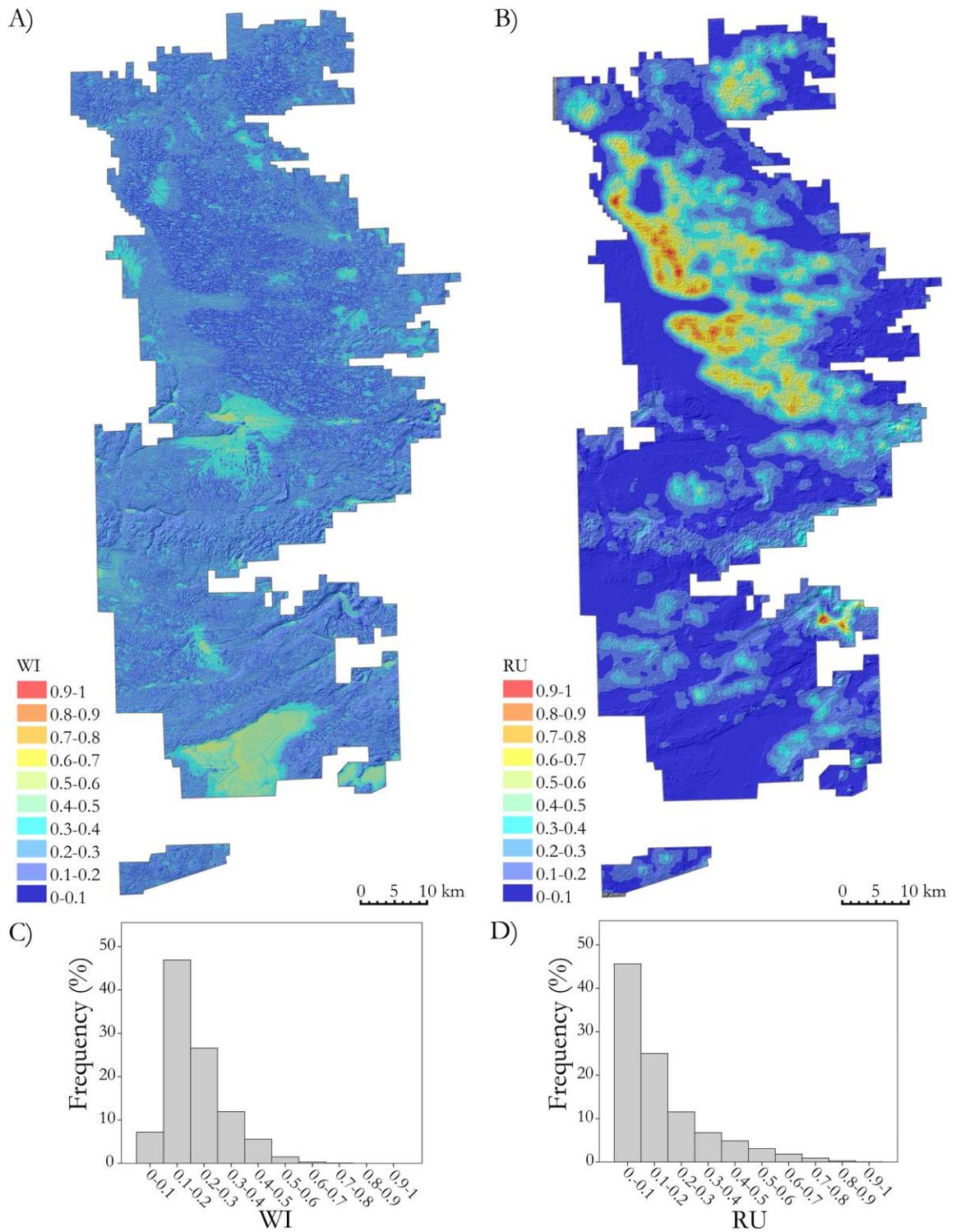


Figure 2.8. Spatial distributions of topographic indices: A) WI, and B) RU, and corresponding histograms (C, D).

2.5.3 Differencing

Assuming a 1:1 association between SDI and topographic indices suggests that high SDI values should coincide with high topographic values and low SDI values should coincide with low topographic values. The spatial variation of the difference between SDI and topographic indices, shown in Figures 2.9 and 2.10, reveals that a 1:1 association does not exist. Regions of positive and negative difference correspond to under- and over-predicted landcover diversity, respectively, whereas values near 0 indicate minimal difference and good agreement between the two. More specifically, cells with values between -0.2 and +0.2 are considered to have strong agreement between the topographic index and SDI, whereas values from +1.0 to +0.2 and from -0.2 to -1.0 are considered to under- and over-predict, respectively.

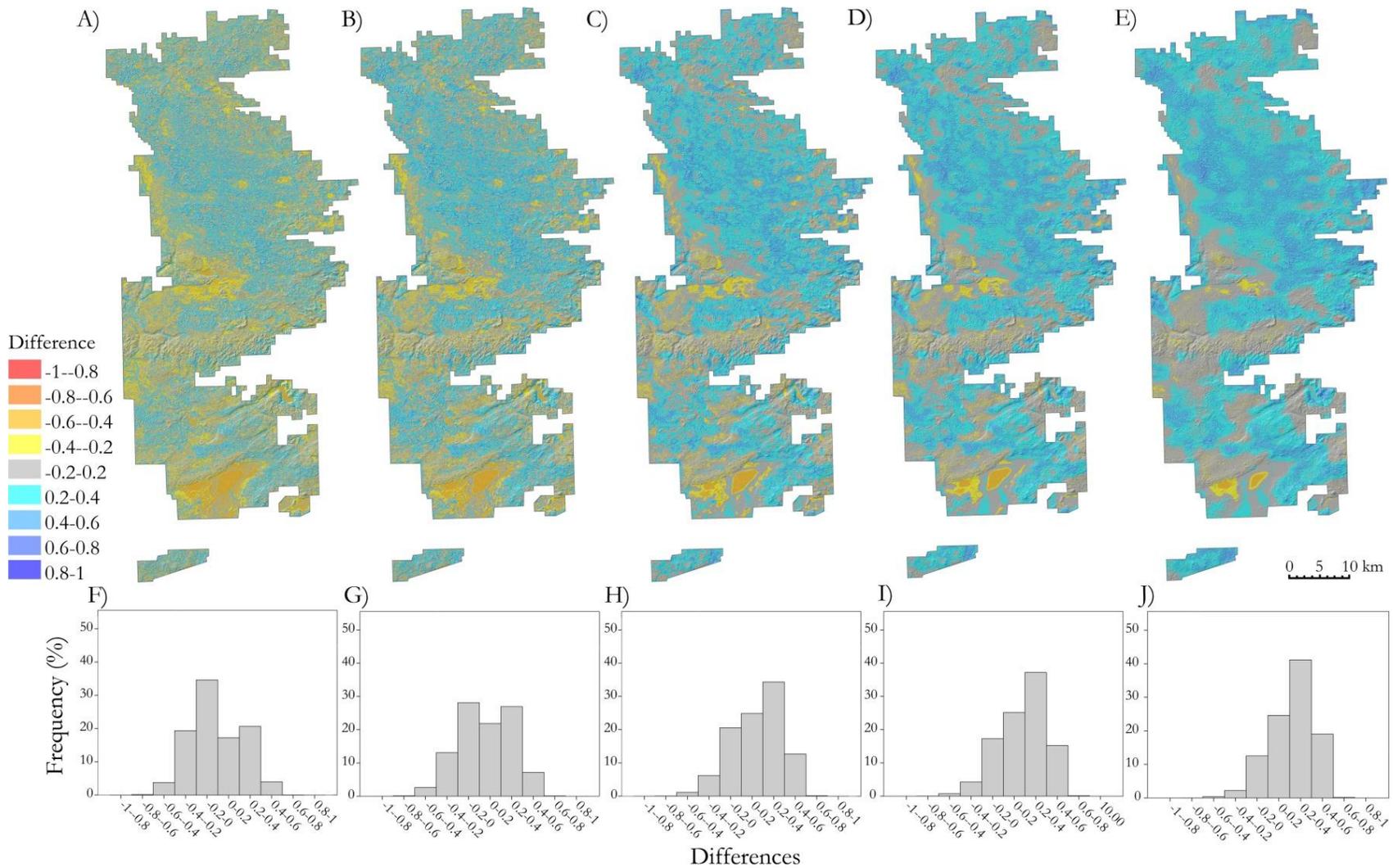


Figure 2.9. Maps of the differences between WI and A) SDI₅₀; B) SDI₁₀₀; C) SDI₃₀₀; D) SDI₅₀₀; E) SDI₁₀₀₀. Corresponding histograms show distributions of the differences at each scale.

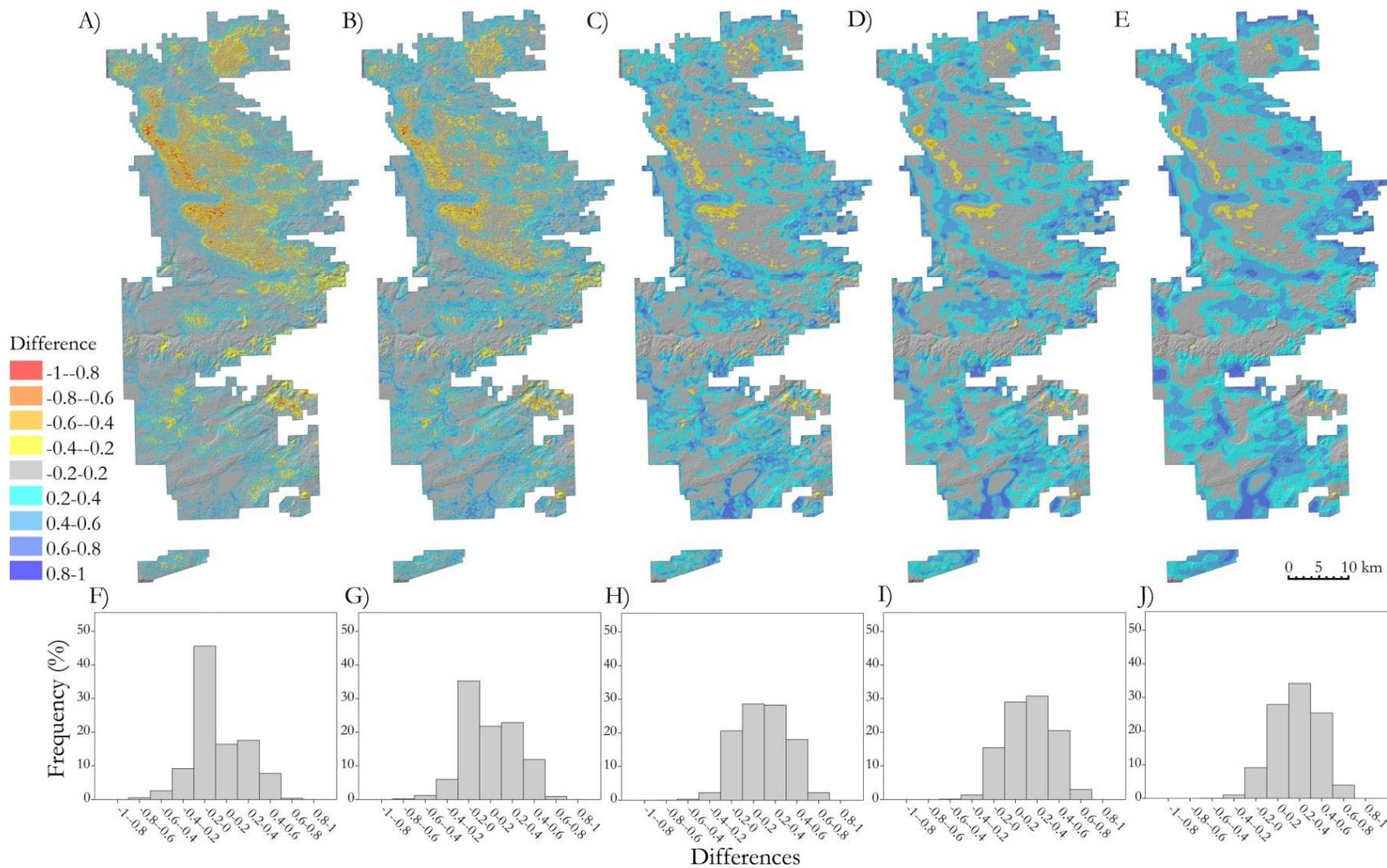


Figure 2.10. Maps of the differences between RU and A) SDI₅₀; B) SDI₁₀₀; C) SDI₃₀₀; D) SDI₅₀₀; E) SDI₁₀₀₀. Corresponding histograms show distributions of the differences at each scale.

Examination of the difference maps in Figure 2.9 shows that a portion of the area has a strong agreement between WI and SDI, but as the resolution of SDI decreases the proportion of cells with strong agreement decreases (Table 2.4). From a landform perspective it seems that the agreement is strongest outside major dune areas. In particular, the large east-west trending moraine clearly stands out in Figure 2.9 as an area with strong agreement. In regions with parabolic dunes and hummocky dune terrain differences indicate diversity values are largely under-predicted. For high-resolution SDI (i.e., SDI_{50}) the majority of cells have values similar to those in the WI map (52%), implying strong agreement over a large area (1057 km²); however, as the SDI resolution decreased the proportion of cells in this category decreased to a minimum of 37.1% (756 km²) at SDI_{1000} . The number of under-predicted cells increased from 24.7% (503 km²) at SDI_{50m} to 60.3% (1227 km²) at SDI_{1000m} , while the reverse trend occurred for over-predicted cells. Very few cells are over-predicted at SDI_{1000} . Overall, these results are consistent with the fact that diversity increases with the kernel size used to calculate SDI, while WI values remain low throughout the GSH region (i.e., WI mean = 0.217).

Table 2.4. Proportions (%) of under- and over-predictions.

		Over-predicted	Strong Agreement	Under-predicted
		(-1 - -0.2)	(-0.2 – 0.2)	(0.2 – 1)
WI	SDI ₅₀	23.3	52.0	24.7
	SDI ₁₀₀	15.8	50.0	34.2
	SDI ₃₀₀	7.42	45.4	47.2
	SDI ₅₀₀	5.02	42.4	52.3
	SDI ₁₀₀₀	2.57	37.1	60.3
RU	SDI ₅₀	12.3	62.1	25.6
	SDI ₁₀₀	7.37	57.0	35.6
	SDI ₃₀₀	2.45	49.1	48.4
	SDI ₅₀₀	1.43	44.4	54.2
	SDI ₁₀₀₀	1.04	36.5	62.5

NB: The sum of over-predictions, strong agreements and under-predictions may not add up to 100% due to rounding.

The difference maps for SDI₅₀ - RU (Fig. 2.10) show that the total number of cells exhibiting a strong agreement is higher (62.1%, 1260 km²) than for SDI₅₀ - WI (52%, 1057 km²). Table 2.4 shows that the proportion of cells exhibiting strong agreement decreased as the resolution of SDI decreased, which is similar to SDI - WI. However, from a visual interpretation of Figure 2.10 there are clear differences in the spatial distribution of cells with strong agreement. The moraine stands out as one commonality, but one notable distinction is that a greater proportion of the area covered by dunes falls in this category, particularly as the resolution of SDI decreases. For SDI₅₀ there is a large region of dunes (380 km²) where RU over-predicts landcover diversity, however, as resolution decreases the agreement between SDI and RU become stronger. This indicates that as diversity values increase with larger SDI kernel sizes, RU, particularly in areas with parabolic dunes and hummocky dune terrain, is better at representing landcover diversity.

The distributions of the difference values between SDI and the topographic indices are non-normal with mean values very close to 0 (Table 2.5). Distributions become

increasingly negative skewed with decreases in resolution, using WI and RU (Figs. 2.9-2.10; Table 2.5). This indicates a trend towards increasing proportions of under-predictions. Although spatial variability in the difference values occurs across the GSH using WI, and RU, a trend towards under-predictions with lower resolution is caused by larger SDI values with decreasing resolution, whereas topographic indices remain constant. The differences show low kurtosis values, indicating a sharp peak in the distribution of differences around the mean. It is noted, however, that a weak linear correlation exists between SDI maps and all topographic indices (median: $r^2 < 0.10$, $p < 0.0001$; mode: $r^2 < 0.02$, $p < 0.0001$). This may be the result of a nonlinear association between SDI and topographic indices, or may reflect that spatially, large areas of poor association between landcover and topography result in low r^2 values.

Table 2.5. Descriptive statistics of differences between SDI maps and topographic indices.

		Min.	Max.	Range	Mean	Stdev.	Median	Skewness	Kurtosis
WI	SDI ₅₀	-1.00	0.725	1.73	-0.174	0.245	-0.0930	0.261	-0.830
	SDI ₁₀₀	-1.00	0.737	1.74	0.0558	0.248	0.0623	-0.0820	-0.913
	SDI ₃₀₀	-0.944	0.724	1.67	0.146	0.228	0.181	-0.434	-0.531
	SDI ₅₀₀	-0.874	0.723	1.60	0.180	0.216	0.216	-0.546	-0.305
	SDI ₁₀₀₀	-0.810	0.724	1.53	0.223	0.196	0.256	-0.671	0.0570
RU	SDI ₅₀	-1.00	0.786	1.79	0.0279	0.237	-0.0283	0.121	-0.0500
	SDI ₁₀₀	-0.994	0.800	1.79	0.101	0.236	0.0671	0.0570	-0.484
	SDI ₃₀₀	-0.673	0.792	1.47	0.192	0.219	0.188	-0.0120	-0.666
	SDI ₅₀₀	-0.627	0.794	1.42	0.225	0.212	0.228	-0.0560	-0.642
	SDI ₁₀₀₀	-0.567	0.762	1.33	0.268	0.202	0.279	-0.197	-0.489

2.6 Discussion

The hypothesis tested as part of this investigation is that *within the GSH, there is a quantifiable relation between topographic variability and regional landcover diversity such that the former can*

be used to predict the latter. Based on a GIS analysis of digital landcover data and topographic indices the main finding is that the best predictor of landcover diversity is topographic ruggedness (RU). RU predicts up to 62.1% (1260 km²) of the landcover diversity in the GSH, which appears to be higher than the association obtained with a similar method by Coblenz & Riitters (2004) for a region encompassing the southwestern USA and northern Mexico. The difference between SDI₅₀ and RU shows that in the most topographically-rough areas of the GSH, RU over-predicts landcover diversity, while closer agreement occurs in the smoother areas where diversity is lower (Figure 2.10A). This suggests that the degree of roughness associated with dunes is insufficient to influence landcover diversity. As the SDI resolution decreases, the topographically-rough areas show better agreement and thus indicate RU is a stronger representation for dune terrain with larger SDI scales.

It is recognized that landcover diversity patterns can be altered by other attributes of topography, as well as other biotic and abiotic influences such as wind, fire and mammals (Gardner *et al.*, 1987). Therefore, in this study WI and RU are first-order estimates for explaining landcover diversity. Other biological and ecological factors not addressed in this study may affect landcover and were not accurately represented by the chosen topographic indices. As a result, many areas throughout the GSH region are under- or over-predicted.

Topographic parameters can be used to predict landcover diversity if microclimate gradients are the key driver of landcover patterns (Coblenz & Riitters, 2004). However, exclusively using topographic parameters to predict diversity is a simplified approach (Coblenz & Riitters, 2004) because topography does not account for the ecological or biological imprints left on landcover. While the relation between topography and diversity has been demonstrated in many environments (e.g., Coblenz & Riitters, 2004; Liu *et al.*, 2007; Pérez *et al.*, 2008), and was a key motivating factor for this investigation,

results show that topography explains diversity with moderate confidence, but overall, it is not the only determinant of diversity in the GSH.

Ecological factors can increase or decrease landcover diversity (Gardner *et al.*, 1987; Olf & Ritchie, 1998; Fox *et al.*, 2012). In the GSH, the historical presence of bison and wildfires are interpreted as key forcings that sustained bare landcover and created mosaics of different successional stages (Fox *et al.*, 2012), thereby increasing regional landcover diversity. Today, much of the GSH is subject to cattle ranching and a dichotomy exists regarding the effects of grazing on landcover diversity; in some settings it enhances landcover diversity, while in others it has the opposite effect (Hartnett *et al.*, 1996; Olf & Ritchie, 1998). Additionally, the change of land use towards cattle grazing and the switch toward a warm, moist climate enable tree and shrub communities to spread (Van Auken, 2000; Wilcox & Thurow, 2005; Ravi *et al.*, 2009). Although there is no proven evidence of tree or shrub encroachment occurring in the GSH historically, the combined effects of replacing native bison with domesticated cattle, decreasing wildfire frequency and a transition toward a warm, moist climate could theoretically encourage this phenomenon (e.g., Campbell *et al.*, 1994; Van Auken, 2000; Wilcox & Thurow, 2005; Ravi *et al.*, 2009). Ecological influences become engrained in landcover but not typically in topography (Dietrich & Perron, 2006), thus calculation of SDI from classified landcover imagery can include these factors, while topographic indices are unable to account for them. Therefore, spatial variability of landcover diversity that arises or reinforces due to ecological factors could account for spatial variations in the strength of associations, as well as over- and under-predictions of landcover diversity based on RU and WI. Further investigation is needed to confirm the effects of disturbance history and current land use patterns on the SDI and related effects on the association between topography and SDI.

When analyzing the landcover diversity and patterns in the GSH it is also important to consider how the present-day topography evolved, and whether it evolved contemporaneously. The region was covered by the Laurentide ice sheet, which strongly influenced several different processes that formed the landscape as it is today, including various topographic features such as relic subglacial drainage channels and moraines. As the ice sheet receded and water levels in ice-dammed and proglacial lakes lowered, glaciofluvial and glaciolacustrine sediments were exposed to aeolian processes (Wolfe *et al.*, 2001), forming sand dunes. Approximately 200 years ago there was a major transition as vegetation expanded dramatically across the region, transforming desert-like barchan dunes into vegetation-stabilized parabolic dunes (Wolfe & Hugenholtz, 2009). According to numerical models (Barchyn & Hugenholtz, 2012a; b) the varieties of dune sizes and vegetation expansion rates may have created variability in the stabilization rates, resulting in different succession pathways. Numerical models show that different types and sizes of dunes can create spatial variations of stabilization. When vegetation stabilization occurs in a dune field, interdune regions tend to be the first to stabilize (Barchyn & Hugenholtz, 2012a; b). Small, immature dunes tend to move faster than larger dunes, and during the stabilization stages they collide and produce hummocky dune terrain. The roughest portions of the GSH coincide with hummocky dune terrain. Medium-sized dunes take the longest to stabilize, while large dunes stabilize quickly because they migrate more slowly, which allows vegetation to out-compete sand transport. This suggests that large dunes in the GSH have been stable the longest, giving them opportunities to host different landcover types. Small dunes are next, followed by medium sized dunes, which have had the least amount of time for vegetation succession.

The magnitude of topographic relief might also account for the variability in the association between topography and landcover diversity. More pronounced topography (i.e. mountains) is capable of exhibiting vertical stacking of landcover communities, thereby increasing diversity due to greater topographic relief (Coblentz & Riitters, 2004). It is possible that dunes in this landscape are not tall enough to create large microclimatic gradients and, as a result, topographic indices do not show strong associations to landcover diversity. Many previous studies that have established a link between topography and landcover diversity have occurred in regions with greater topographic relief, such as mountains (e.g., Hoersch *et al.*, 2002; Coblentz & Riitters, 2004; Pérez *et al.*, 2008). Additionally, landcover was addressed at the community level, which could filter out topography-landcover interactions at higher resolutions. It is speculative that different results may be observed at the species level due to the first-order estimate at the community level using Simpson's diversity index, perhaps allowing stronger representations of individual species. Additionally, Hulett *et al.*, (1966) found associations between the spatial distribution of specific vegetation species and their microsite conditions in a small, field-based study of the GSH.

Data quality is another factor that could contribute to the outcome. SDI maps were calculated using satellite imagery at a 10 m resolution, which was originally classified to an accuracy of 77% (Saskatchewan Environment, 2007). Because of this, the maximum attainable accuracy for SDI is likely to be close to 77%. This could have an unknown influence on the associations between SDI maps and the topographic indices, perhaps accounting for spatial variability in over- and under-predictions.

It is unknown whether climatic gradients across the region are large enough to cause an effect on the spatial distribution of landcover diversity throughout the GSH. The GSH

span ~90 km north to south and undergoes a ~130 m rise in elevation north to south (Saskatchewan Environment, 2007). At the species level, there is an absence of *Juniperus horizontalis* (creeping juniper) south of the east-west trending moraine. It is unclear what external influence allows for this difference and further investigation into the existence and influence of a climatic gradient across the region is needed to resolve any influence it may have on the landcover diversity, independent of any variability of topographic features.

This study shows similarities to previous studies in different geographic locations. Similar to Coblenz & Riitters (2004) and Pérez *et al.*, (2008), the differencing method used in this study also resulted in spatial variability in under- and over-predictions of landcover diversity based on topographic indices. Coblenz & Riitters (2004) used this method in the North American Cordillera region, and as such were able to test this method on more pronounced mountainous topography. In addition to under- and over-predictions, their findings also indicated weak linear correlations ($r^2 < 0.15$) throughout the entire region analyzed. Pérez *et al.* (2008) concluded that this method was capable in predicting >74% of landcover diversity based on topographic indices throughout Mexico, whereas the current study was able to predict 62.1% of landcover diversity in the GSH. Coblenz & Riitters (2004) and Pérez *et al.*, (2008) determined that although many other factors in addition to topography can explain landcover diversity, topography plays a primary role in the distribution of landcover diversity at the regional to continental resolution. Therefore, the current method is valuable as a first-order estimate of landcover diversity for large and inaccessible areas where digital data is easily attainable.

2.7 Conclusion

Topography provides an indirect control on the distribution and diversity of landcover in some ecosystems and contains valuable information about the geomorphology and climatic history of a region (Coblentz & Rütters, 2004; Pérez *et al.*, 2008). The GSH are an island of diversity within the cultivated prairies and contain unique habitat relative to the surrounding glaciogenic terrain. In regions with vast ranges in topographic relief, such as the GSH, high landcover diversity values can occur due to the large range of microclimates corresponding to topographic gradients. To this end, the aim of this study was to understand the distribution of landcover diversity and its spatial association to topography at the regional, community level.

The main findings of this study indicate that using topography as a predictor of diversity can be a useful first-order method for understanding if the distribution of landcover throughout the region. RU predicted 62.1% of the distribution of landcover diversity for local estimates of diversity (i.e., SDI_{50}) and proved to be a better predictor of landcover diversity compared to WI. RU typically over-predicted landcover diversity in areas with dunes in the GSH, while in less rugged areas there was closer agreement. This suggests that the topographic relief created by dunes does not necessarily increase landcover diversity. However, results also show that the association between landcover diversity and roughness varied according to the kernel size used to calculate SDI. For example, the topographically-rough areas (dunes) showed stronger agreements to SDI calculated with larger kernels, thus indicating RU better represents dune terrain with larger-scale landcover diversity, although the difference between SDI_{50} and RU provided the strongest agreement regionally. This suggests that the resolution of landcover diversity may be important in reflecting landscape features throughout the region.

Several discrepancies could account for imperfect results in the association between topography and landcover diversity. Ecological and biological factors that influence landcover remain undetected by topographic indices and could therefore account for imperfect associations. Landcover data was originally classified to an accuracy of 77% (Saskatchewan Environment, 2007), which could pose limitations on the accuracy of any subsequent analyses. Additionally, the GSH likely stabilized at various rates of succession due to geomorphological differences throughout the region, which could account for spatial variability in under- and over-predictions of landcover diversity.

Overall, this study provides evidence that although topography influences the landcover diversity in the GSH, it is not the sole determining factor of the landcover diversity in this region.

CHAPTER 3: THE PREDICTABILITY OF POPLAR WITHIN THE GREAT SAND HILLS USING TOPOGRAPHIC INDICES

3.1 Abstract

This Chapter examines whether the topographic variability of the GSH controls the distribution of one particular landcover type: trees. The hypothesis motivating this research is that *within the GSH, trees (P. tremuloides) are found preferentially in low-lying areas*. More specifically, this study tests whether *Populus* spp. preferentially establishes in interdunes. The rationale for this hypothesis is twofold: *i)* interdune surfaces are closer to the water table, and *ii)* interdunes have been stable longer than the adjacent dunes because vegetation established first in these areas before spreading and stabilizing the dunes. To test the hypothesis, two topographically-similar study sites were selected (one for training and one for validation) and logistic regression was used to determine if trees are located preferentially in the interdunes. Five topographic indices (i.e., WI, elevation, northness, eastness, and curvature) were derived from a DEM and stepwise logistic regression determined the relative strength and importance of each index. Topographic indices were used as independent variables in logistic regression from the training site, with the distribution of trees as the dependent variable for the model. The logistic regression equation was subsequently used to predict suitable and unsuitable tree habitat based on the probability of occupancy, with Cohen's Kappa (*K*) determining an appropriate threshold of 0.30. This threshold level was selected to maximize model accuracy. Suitable habitat is represented by values equal to or greater than 0.30, whereas, unsuitable habitat is represented by values less than 0.30. Stepwise logistic regression determined that WI had the strongest influence on tree distributions with suitable habitat favouring greater WI values, lower elevation values and concave curvature; thus supporting the hypothesis *that trees occur preferentially in low-lying areas or interdunes within two study*

areas in the GSH. The accuracy of the model was tested by applying the logistic regression equation to both sites, resulting in receiver operating characteristic (ROC) curves, from which the area under the curve (AUC) values of 0.756 (training) and 0.721 (validation) were obtained. These AUC values indicate relatively similar performance at both sites, with moderate model accuracy overall. A habitat suitability map was created for the validation site and revealed that 71.9% of the map was correctly predicted, with 25.4% of predictions as false positives and 45.1% of predictions as false negatives. Environmental and biological factors that may overprint the role of topography and account for the other 27.8% of the influence on the tree distribution are also discussed.

3.2 Introduction

On the Canadian prairies the GSH are a unique topographic region dominated by aeolian landforms. Perhaps due to its distinct topography, the GSH region is a biodiversity hotspot among the Canadian prairies, including native grassland and several specialized, disturbance-evolved species (Nielsen, 2007). This region is important in providing a refuge of contiguous native mixed-grassland habitat relative to the surrounding non-native agricultural land (Nielsen, 2007). Given these characteristics, this chapter examines the link between topography and the distribution of tree (i.e., *Populus* spp.) communities, as they have more specific habitat requirements than the other major prairie vegetation communities observed in the GSH (i.e., grasses and shrubs). Anecdotal evidence suggests that tree communities occur more commonly in low-lying areas or interdunes within the GSH. By testing whether topography influences tree distribution this chapter compliments and expands the analysis presented in Chapter 2.

Studies on coastal dunes have demonstrated that sand dune topography can play a significant role in determining the growth and distribution of vegetation communities, with vegetation distribution reflecting a gradient according to the distance from the water (Doing, 1985; Dech & Maun, 2005; Acosta *et al.*, 2007). In inland prairie sandhill ecosystems, however, the effect of topography on vegetation patterns is largely unknown. It is expected that with the absence of coastal processes in inland dune fields, patterns will be different than coastal counterparts. In arid dune fields soil moisture is often cited as a limiting factor for plant growth, and in some regions topography can considerably influence soil moisture distribution (Lee & Lauenroth, 1994; Liu *et al.*, 2007; Koenig, 2012). Variability of topographic indices, such as slope aspect, considerably modifies the amount of incoming solar radiation received on different slopes, which modifies microclimatic and edaphic conditions affecting soil moisture (Koenig, 2012). Hulett *et al.*, (1966) suggested that vegetation patterns in the GSH are the result of variability in the environment associated with the terrain, and that the topography-vegetation association within this inland dune field has not been fully interpreted (Hulett *et al.*, 1966). Based on this context it is anticipated that the distribution of tree communities in the GSH will depend on the relative soil moisture as dictated by the topography.

Populus spp. (particularly *Populus tremuloides*) is the most widespread deciduous species of North America (Mitton & Grant, 1980; McCulloch & Kabzems, 2009). They are most productive on nutrient rich, moist but well-drained sites (Mitton & Grant, 1980; McCulloch & Kabzems, 2009). In the GSH, *P. tremuloides* exists in small clusters (< 1 km²; Saskatchewan Environment, 2007) and almost exclusively in interdune regions. Interdunes are relatively smooth, flat, and low-lying surfaces between dunes. In these areas the groundwater table is often close to the surface (Hulett *et al.*, 1966; Koenig, 2012).

The distribution of tree communities is a direct response to the early growth stages of tree seedlings and the environmental constraints placed upon them (Grubb, 1977; Lichter, 2000; Rey & Alcántara, 2000). Once a seedling successfully germinates, it relies heavily upon a consistent source of water, as drought is the most common cause of low seedling survival in arid and dryland regions (Mitton & Grant, 1980; Lichter, 2000; Rey & Alcántara, 2000; McCulloch & Kabzems, 2009). The shallow ground water table in the GSH can provide tree seedlings with a constant source of water in interdune areas. Additionally, asexual reproduction of *P. tremuloides* relies on a network of roots and shoots, which may be hindered by the overlying sheet of aeolian sand, as dry, sandy soils such as those beneath the stabilized aeolian landscape of the GSH (Koenig, 2012) can act as a barrier to the regeneration of *P. tremuloides* (McCulloch & Kabzems, 2009).

Koenig (2012) investigated soil moisture dynamics between stabilized and active sand dunes in the GSH. His findings indicate that stabilized dunes have drier soil conditions than active dunes, as vegetation requires soil moisture for transpiration, thus drying out the sand below the surface. This would suggest that soil moisture conditions would be more desirable for tree seedlings on active dunes; however, trees are later successional species that do not have the ability to combat seed burial, as early-successional species do (Dech & Maun, 2005). Thus, the dynamics between the dune topography and environmental conditions likely constrain the distribution of trees to interdune areas throughout the region. A few exceptions of tree occurrences are associated with dunes that have migrated into trees, burying the trees and ultimately destroying the community in the process. Therefore, evidence suggests that *P. tremuloides* are constrained to interdune areas due to *i*) proximity to groundwater, and *ii*) thick sand deposits of dunes acting as a barrier to the groundwater.

Aspen stands can provide valuable habitat for wildlife and increase the biodiversity of the prairies (Archibold, 1996; McCulluoch & Kabzems, 2009). During breeding season, aspen stands provide habitat for short- and long-distance migrating birds (Archibold, 1996). Stands also act as refuges to ungulate mammals during the summer and winter extremes on the prairies (Archibold, 1996). They regulate the air temperature and provide a cool escape during the summer, reducing the risk of heat stress; and a warm shelter with food supplies during the winter, increasing the chance of winter survival (Archibold, 1996). Although tree communities are important in maintaining biodiversity of the prairies, they continue to be cleared for agricultural purposes (Archibold, 1996), thus stressing the importance of the natural tree communities within the GSH.

The GSH are relatively unaltered by anthropogenic influences compared to the surrounding cultivated prairie. This study will determine the association between topography and tree community distributions. The presence of dunes in the study sites is anticipated to more strongly influence the distribution of trees than would occur in areas without dunes present. Within this context, the purpose of this study is to test the hypothesis *that trees occur preferentially in low-lying areas or interdunes within two study areas in the GSH.*

3.3 Study site

The GSH is a broad region of mostly stabilized sand dunes located in southwestern Saskatchewan (Fig. 2.2). Background on the geomorphology and ecology of the GSH are provided in Chapter 2. Two study sites were selected for this investigation based on their stage of succession and topographic similarities. One site was used to develop the predictive model of tree distribution based on topographic variables (Site 1), while the other was used to test, or validate, the model (Site 2). Both sites are located within hummocky dune terrain

that is almost completely stabilized (Fig. 3.1). A description of hummocky dune terrain is given by Barchyn & Hugenholtz (2012c). Anecdotal evidence indicates that trees frequently occur in the interdune areas (Fig. 3.2). Being elevated relative to the surrounding interdune terrain, the dunes project away from the water table; thus, tree-covered dunes are rare in this setting. In other settings where moisture is less of a constraint on tree growth, dunes may be covered by forests, but in the GSH moisture is a limiting factor.

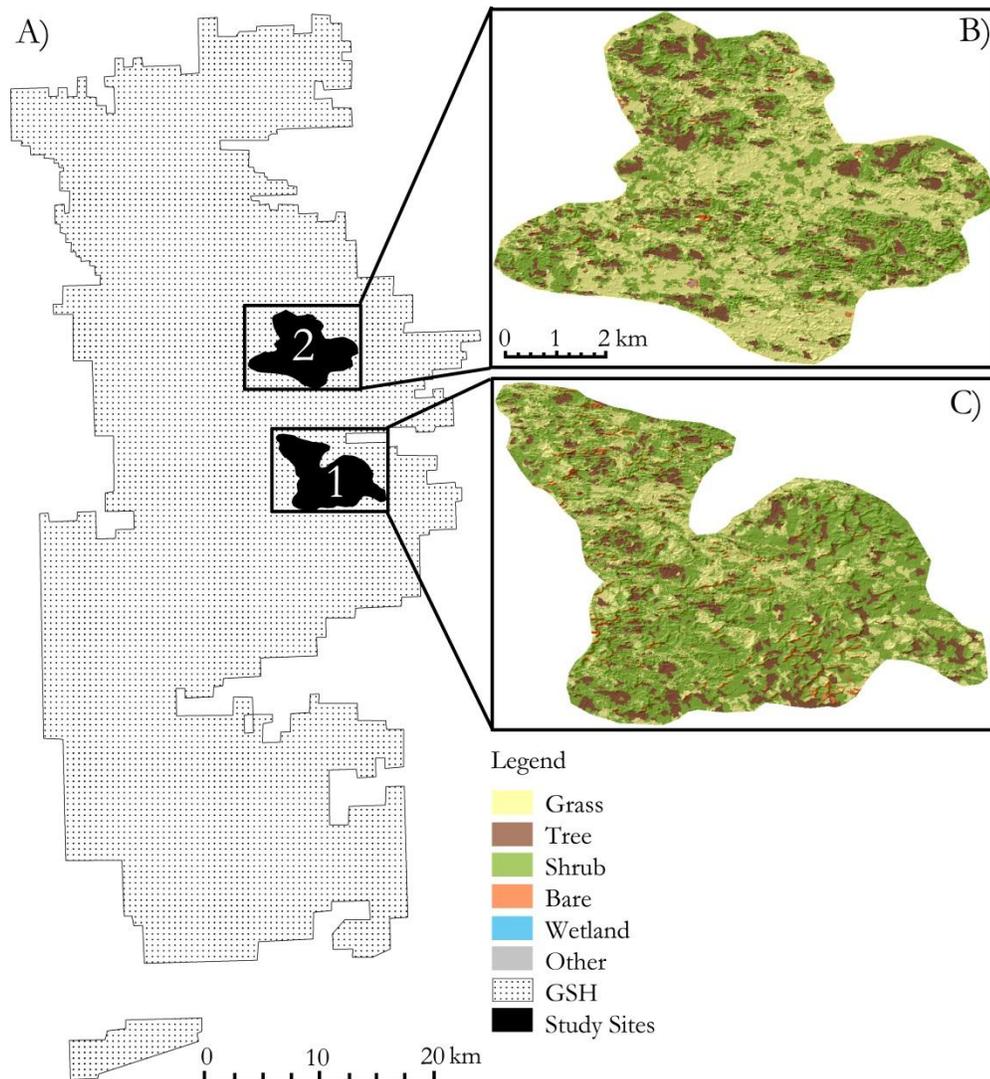


Figure 3.1. Study sites 1 and 2 are located in the northern half of the GSH, A). The distributions of landcover types for both sites are shown in B) and C).

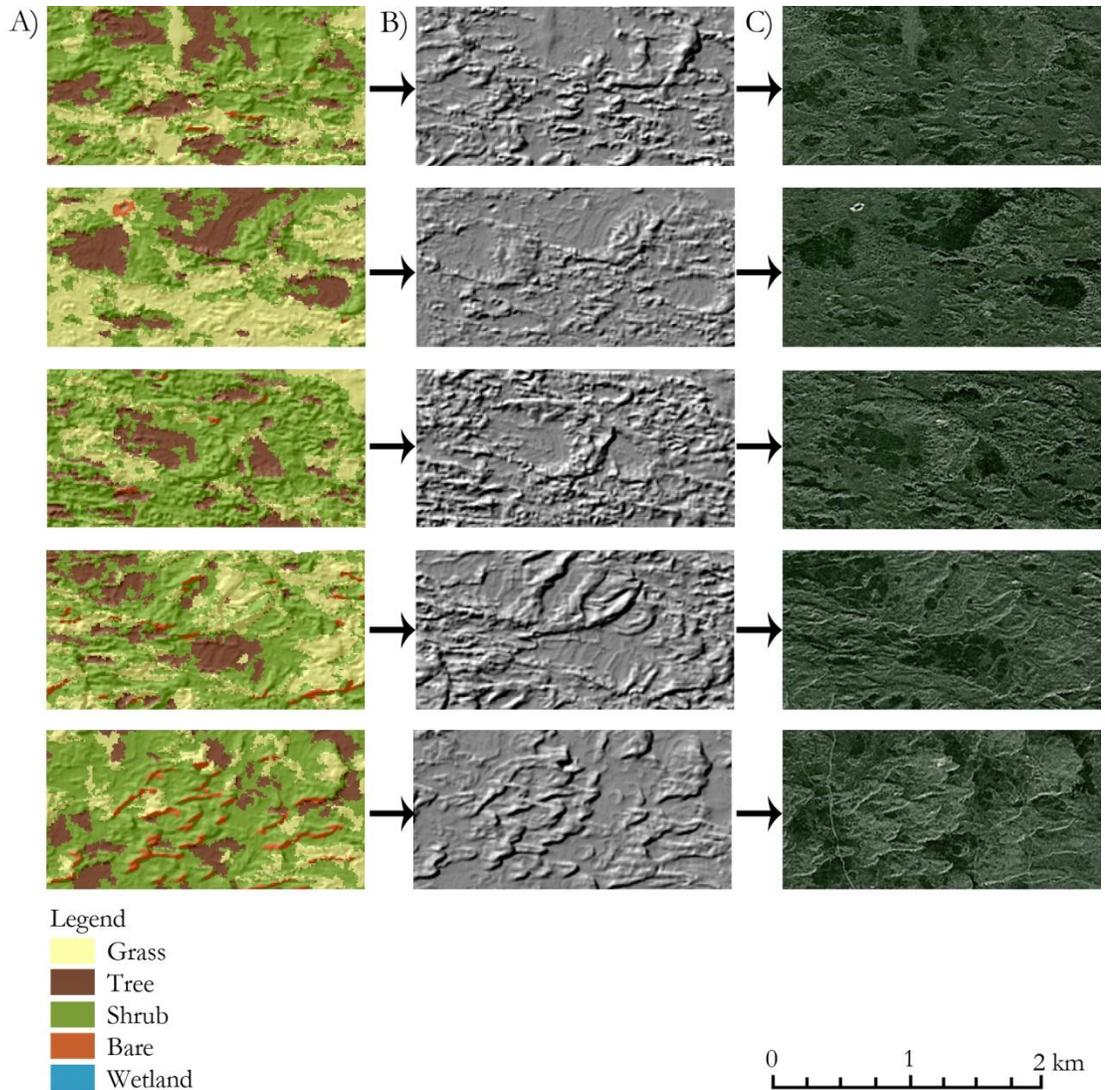


Figure 3.2. Comparisons of the two study sites: A) landcover and B) topographic relief. Tree communities typically occur in interdunes, where topographic relief is smooth in relation to hummocky dune features. Satellite imagery, C), shows corresponding occurrences of dark landcover patches within these interdunes, indicating that the spatial distribution of trees is constrained to interdunes due to dune features.

Trees within the GSH typically belong to the *Populus* genus, with the most common types being *Populus tremuloides* and *Populus deltoides*; the former being the more prevalent of the two. *Populus* trees can reproduce in two ways: *i*) a network of roots that travel underground and produce shoots that grow into clone communities, and *ii*) seed dispersal (Mitton & Grant, 1980). Both of these methods require specific environmental conditions to successfully germinate and produce a new community of trees. Thick layers of aeolian sand

often prevent tree seedlings from accessing a consistent source of groundwater and sand can also act as a barrier to upward growing shoots (McCulloch & Kabzems, 2009). Furthermore, trees die if the rate of sediment deposition exceeds their depositional tolerance (Barchyn & Hugenholtz, 2012c). Therefore, in most Great Plains dune fields trees are limited to growing in interdune areas due to environmental and life-strategy restrictions.

3.4 Methods

3.4.1 Data

Two different high resolution (10 m) data sources were used for this project. They were *i*) a classified landcover raster image acquired in 2005 (Fig. 2.1; Saskatchewan Environment, 2007), and *ii*) a digital elevation model derived from LiDAR data of the GSH acquired in 2005 (Saskatchewan Environment, 2007), rescaled to 10 m from the original 2 m resolution in order to match the resolution of the landcover data.

Topographic descriptors of the following five indices were derived from the DEM of the study areas: wetness index (WI; see Chapter 2), elevation, northness, eastness, and curvature (Fig. 3.3). Wetness index indicates the relative soil moisture based on surrounding slope steepness and drainage accumulation. It is hypothesized that WI highly influences the distribution of trees, as the highest wetness values most often occur within interdune areas, where tree communities occur. Similarly, elevation might also provide information about the distribution of trees within the GSH because as elevation increases, the likelihood of tree communities occurring decreases due to their inability to occur on top of dunes. Northness and eastness were used instead of aspect and are calculated as the cosine or sine of aspect, respectively (McDermid & Smith, 2008). For northness, a value of 1 indicates the aspect is generally northward, and a value of -1 is southward with 0 representing east or west.

Similarly for eastness, a value of 1 indicates the aspect is generally eastward, and a value of -1 is westward with 0 representing north or south. Both northness and eastness affect the microclimatic conditions of the slopes, with greater soil moisture typical to north- and east-facing slopes (Koenig, 2012). North-facing slopes receive less incoming solar radiation than south-facing slopes, thus experience cool and moist environmental conditions. Because of the dominant westerly winds, exposure to wind on west-facing slopes is likely to create harsher evaporation conditions than is experienced on east-facing slopes, thus creating more desirable edaphic conditions for tree communities on east facing slopes. Curvature represents the contours of the topography, with positive values representing convex curves and negative values representing concave curves. Dunes typically exhibit convex curvature, whereas interdunes exhibit flat to concave curvature; therefore, it is expected that negative curvature values will have greater influence on the occurrence of tree communities. Additionally, boxplots of the topographic variables were created to compare the differences and similarities between the presence and absence of trees.

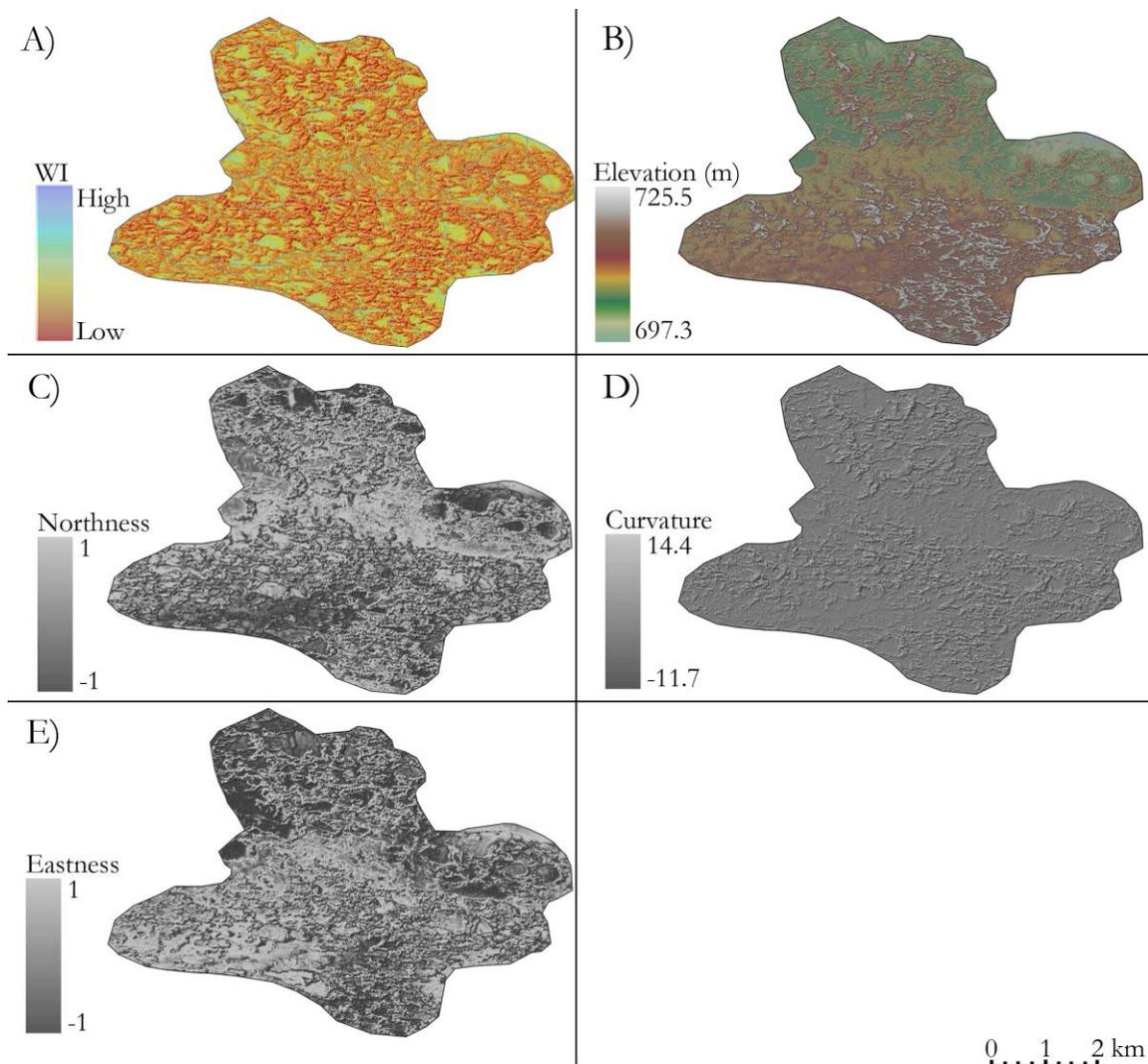


Figure 3.3. Topographic descriptors for Site 2: A) wetness index; B) elevation; C) northness; D) curvature; and, E) eastness.

The distribution of trees across both study sites was characterized by presence and absence in an indicator map obtained from the classified landcover SPOT5 satellite image (Fig. 2.1). The proportions of tree presences and absences are similar for each study site (Table 3.1).

Table 3.1. Proportions (%) of presence and absence of trees for both study sites.

Study Site	Presence	Absence
1	13.06	86.94
2	13.45	86.55

3.4.2 Habitat suitability predictions and model validation

Binary logistic regression based on independent (i.e., topographic) and dependent (i.e., tree presence/absence) variables was used to determine the probability of tree occurrences. Two different study sites were used: one for training (Site 1) and one for validating the model (Site 2; Fig. 3.1). Logistic regression variables were obtained from the training dataset and applied to both datasets to allow a comparison of the model performance at both sites. Binary logistic regression shows how independent variables related to the presence of trees are associated to the occurrence of trees in the GSH (Lowe *et al.*, 2012). Classified landcover data were used for accuracy assessment of model predictions.

The logistic regression equation was used to calculate the probability of occupancy for trees. Probability of occupancy (P) was calculated as:

$$P = \frac{Odds}{(1 + Odds)} \quad (3.1)$$

where odds is defined as:

$$Odds = e^{a + \beta_x + \dots + \beta_n} \quad (3.2)$$

with $a + \beta_x + \dots + \beta_n$ being the logistic regression equation. Stepwise algorithms can be used for determining the best combination of variables for the logistic regression model (e.g., Lowe *et al.*, 2012; Parolo *et al.*, 2008). At each step the predictor variable with the largest score statistic and significance value less than 0.05 is added to the model. The score statistic

and significance value test whether or not an independent predictor variable is important in the model and the outcome of predicting the dependent variable. The largest score statistic indicates the most influential predictor variable on the dependent variable. Independent predictor variables in the model included WI, elevation, northness, eastness, and curvature.

The interaction between the independent topographic variables was included in the model. An interaction is used when the independent variables may interact with each other to affect the outcome of the logistic regression model (Jaccard, 2001). The outcome of the logistic regression model is dependent not only on each topographic variable on its own, but also on how the topographic variables operate together (Jaccard, 2001). For this study, it was believed that wetness index is influenced by both elevation and curvature; therefore, the interactions between wetness and elevation, as well as wetness and curvature, were included.

Once the model was calculated, it was applied spatially in ArcGIS to generate a continuous probability surface ranging between 0 and 1. Probabilities were thresholded at intervals of 0.01 (Table 3.2) and actual tree occurrences were overlaid with probabilities to obtain proportions of model predictions (predicted suitable/unsuitable) against actual observations (observed presence/absence) (Table 3.3). Based on true negative, false positive, true positive and false negative values (*TN*, *FP*, *TP* and *FN*, respectively; Table 3.3) at each threshold level, Cohen's Kappa index was used to determine the Kappa (*K*) value at each threshold interval (Cohen, 1960; Lowe *et al.*, 2012). The threshold level with the largest *K* value indicates the most accurate model of predicted suitable/unsuitable habitat when compared to actual tree occurrences (McDermid & Smith, 2008; Lowe *et al.*, 2012).

Table 3.2. Prediction of suitable and unsuitable tree habitat based on probability (P) of occupancy for threshold values varying between 0 and 1.

Threshold Value	Suitable Habitat	Unsuitable Habitat
0.01	$P \geq 0.01$	$P < 0.01$
0.02	$P \geq 0.02$	$P < 0.02$
0.03	$P \geq 0.03$	$P < 0.03$
...
0.99	$P \geq 0.99$	$P < 0.99$

Table 3.3. Contingency table for calculation of K , sensitivity, and specificity.

	Predicted Unsuitable (0)	Predicted Suitable (1)	Sum
Observed Absence (0)	TN	FP	$TN+FP$
Observed Presence (1)	FN	TP	$FN+TP$
Sum	$TN+FN$	$FP+TP$	N

Cohen's K (Cohen, 1960) was calculated for each threshold value as:

$$K = \frac{Pr_{(a)} - Pr_{(e)}}{1 - Pr_{(e)}} \quad (3.3)$$

where $Pr_{(a)}$ is:

$$Pr_{(a)} = \frac{TP+TN}{N} \quad (3.4)$$

and $Pr_{(e)}$ is:

$$Pr_{(e)} = \left[\left(\frac{TP+FP}{N} \right) \times \left(\frac{TP+FN}{N} \right) \right] + \left[\left(\frac{FN+TN}{N} \right) \times \left(\frac{FP+TN}{N} \right) \right] \quad (3.5)$$

where TP , FP , FN , TN and N are described in Table 3.3. The sensitivity is percentage of presences correctly predicted (also known as the true positive rate) and was calculated as:

$$Sensitivity = \frac{\sum TP}{\sum TP + \sum FN} \times 100 \quad (3.6)$$

where TP and FN are defined in Table 3.3. Specificity is the percentage of absences correctly predicted and was calculated as:

$$Specificity = \frac{\sum TN}{\sum TN + \sum FP} \times 100 \quad (3.7)$$

where TN and FP are defined in Table 3.3.

The receiver operating characteristic (ROC) curve was created by plotting the false positive rate (1-specificity) against the true positive rate (sensitivity) (Hanley, 1989; Hirzel *et al.*, 2006; Lowe *et al.*, 2012). The area under curve (AUC) is one of the most common threshold-independent methods for evaluating habitat suitability models and ranges between 0 and 1 (Elith *et al.*, 2006; Hirzel *et al.*, 2006; Lowe *et al.*, 2012). An AUC value of 0.5 represents no discrimination of the model, thus predictions could be made by chance alone (Swets, 1988; Elith *et al.*, 2006; Hirzel *et al.*, 2006; Lowe *et al.*, 2012). When the value ranges between 0.5 and 0.7, the model has low predictive accuracy because the TP proportion is not much greater than the FN proportion (Swets, 1988). Values ranging between 0.7 and 0.9 represent moderate model accuracy and values between 0.9 and 1.0 represent high accuracy (Swets, 1988; Elith *et al.*, 2006; Hirzel *et al.*, 2006; Lowe *et al.*, 2012). An AUC of 1.0

represents perfect model performance (Swets, 1988; Elith *et al.*, 2006; Hirzel *et al.*, 2006; Lowe *et al.*, 2012).

3.5 Results

Boxplots of the topographic variables were developed to examine differences between the presence and absence of trees (Fig. 3.4; Table 3.4). From a qualitative interpretation of these plots there appears to be little difference between sites with or without trees according to the selected topographic parameters. This suggests that, individually, each index has little discriminatory power in predicting where trees occur and where they are absent; however, by using logistic regression it may be possible to elucidate differences through combinations of topographic indices.

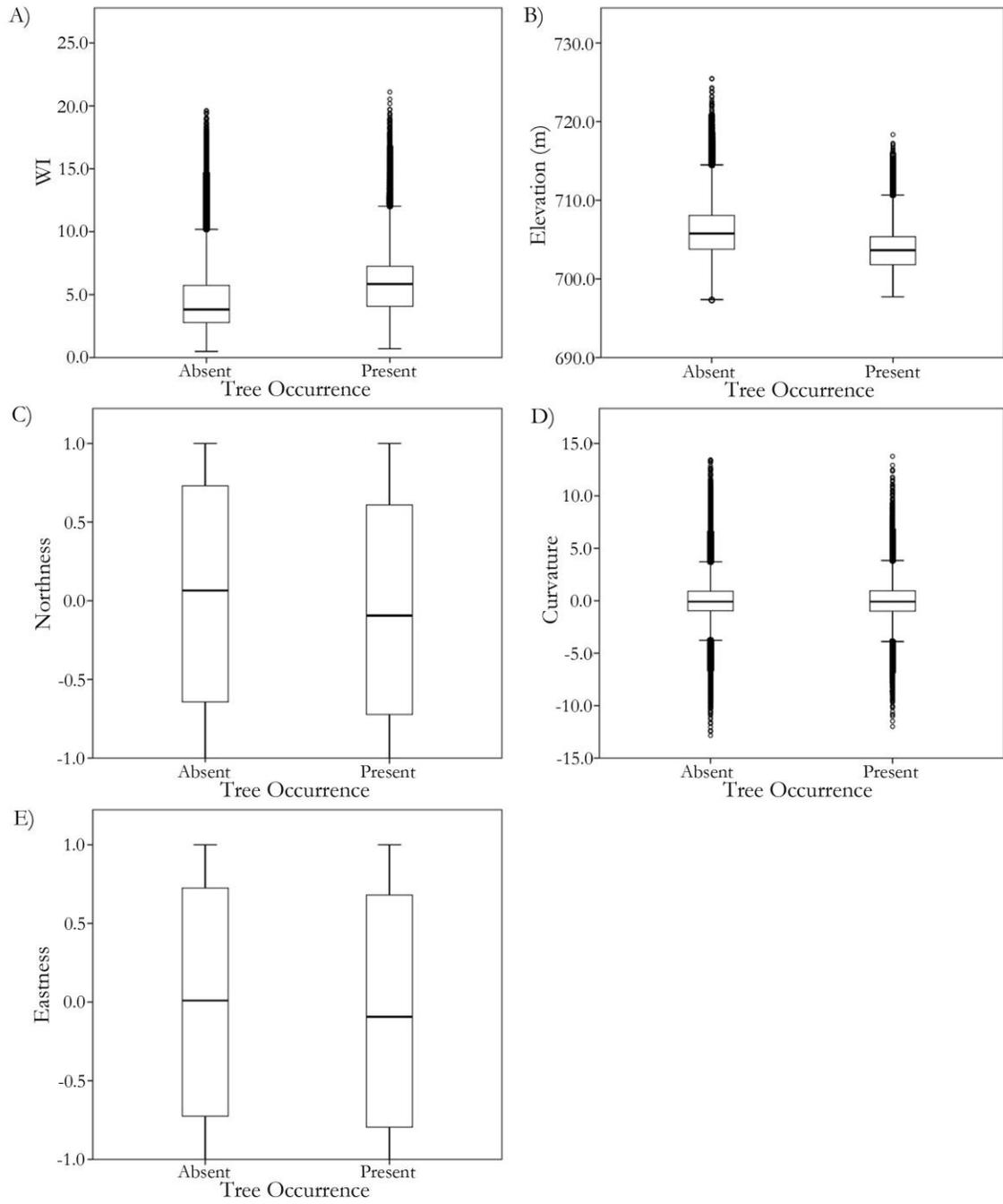


Figure 3.4. Boxplot comparisons of topographic variables in the absence and presence of trees. Descriptive statistics can be found in Table 3.4.

Table 3.4. Descriptive statistics of topographic variables between the presence and absence of trees in Study Site 2.

	Curvature		Elevation (m)		Eastness		Northness		Wetness Index	
	Absent	Present	Absent	Present	Absent	Present	Absent	Present	Absent	Present
Minimum	-11.75	-10.26	697.30	697.72	-1.00	-1.00	-1.00	-1.00	0.49	0.71
Maximum	14.38	11.45	718.34	725.48	1.00	1.00	1.00	1.00	19.63	21.10
Median	-0.06	-0.28	705.77	703.65	-0.09	0.01	0.06	-0.09	3.82	5.83
Std. Dev.	2.03	1.66	3.17	2.50	0.72	0.72	0.70	0.69	2.30	2.36
Q ₁	-0.95	-1.03	725.48	701.81	-0.73	-0.79	-0.64	-0.72	2.78	4.07
Q ₂	-0.06	-0.28	705.77	703.65	0.01	-0.09	0.06	-0.09	3.82	5.83
Q ₃	0.96	0.30	708.07	705.35	0.72	0.68	0.73	0.61	5.75	7.24

Stepwise binary logistic regression resulted in the following logistic regression equation:

$$\ln(\text{odds}) = 84.55 + (-0.142 \times \text{curvature}) + (-0.123 \times \text{elevation}) + (0.186 \times \text{eastness}) + (0.243 \times \text{northness}) + (-4.017 \times \text{WI}) + (0.026 \times (\text{WI} \times \text{curvature})) + (0.006 \times (\text{WI} \times \text{elevation})) \quad (3.8)$$

The most influential predictor variable on the distribution of trees is WI (). As aforementioned, the predictor variable with the largest score statistic and significance value less than 0.05 is added to the model at each step. The score statistic and significance value test whether or not an independent predictor variable is significant in the model. The variable with the largest score statistic indicates the most influential topographic parameter on the distribution of trees in the study areas. Based on the model, the topographic-landcover association suggests greater probability of tree occurrence at lower elevation and in concave slopes, where WI values are typically greater. The positive coefficients for northness and eastness indicate that tree presence is more prevalent on north- and east-facing slopes.

Table 3.5. Predictor variable score statistics and significance levels.

Predictor Variables	Score	Sig.
WI	19966.308	$p < 0.0001$
Elevation	19936.353	$p < 0.0001$
WI x Elevation	19397.641	$p < 0.0001$
Northness	3098.370	$p < 0.0001$
Curvature	1263.176	$p < 0.0001$
Eastness	1137.613	$p < 0.0001$
WI x Curvature	850.608	$p < 0.0001$

The 0.30 threshold for predicted probabilities provided the most accurate map in this study, as determined using Cohen's K method (Cohen, 1960; Fig. 3.5). At this suitability threshold values greater than 0.30 represent suitable habitat for *Populus* spp, whereas values less than 0.30 represent unsuitable habitat.

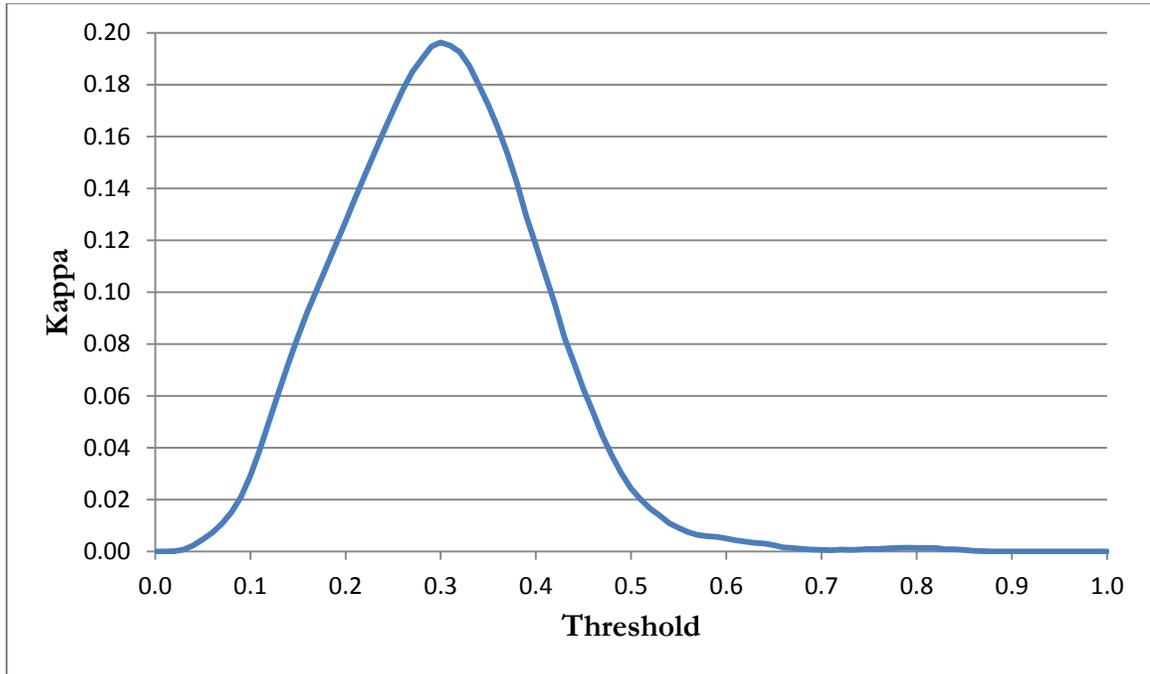


Figure 3.5. Accuracy assessment of habitat suitability predictions using Cohen's Kappa method (Cohen, 1960). The 0.30 threshold provides the largest Kappa value (0.196), indicating a fair level of agreement between the model predictions of tree occurrence and the actual occurrence of trees from classified landcover data.

The final tree habitat suitability map predicted for Site 2 by the best logistic regression model is shown in Figure 3.6. Approximately 71.9% of the model correctly predicts suitable and unsuitable habitat; with 54.9% of the occurrences predicted correctly and 74.6% of the absences predicted correctly.

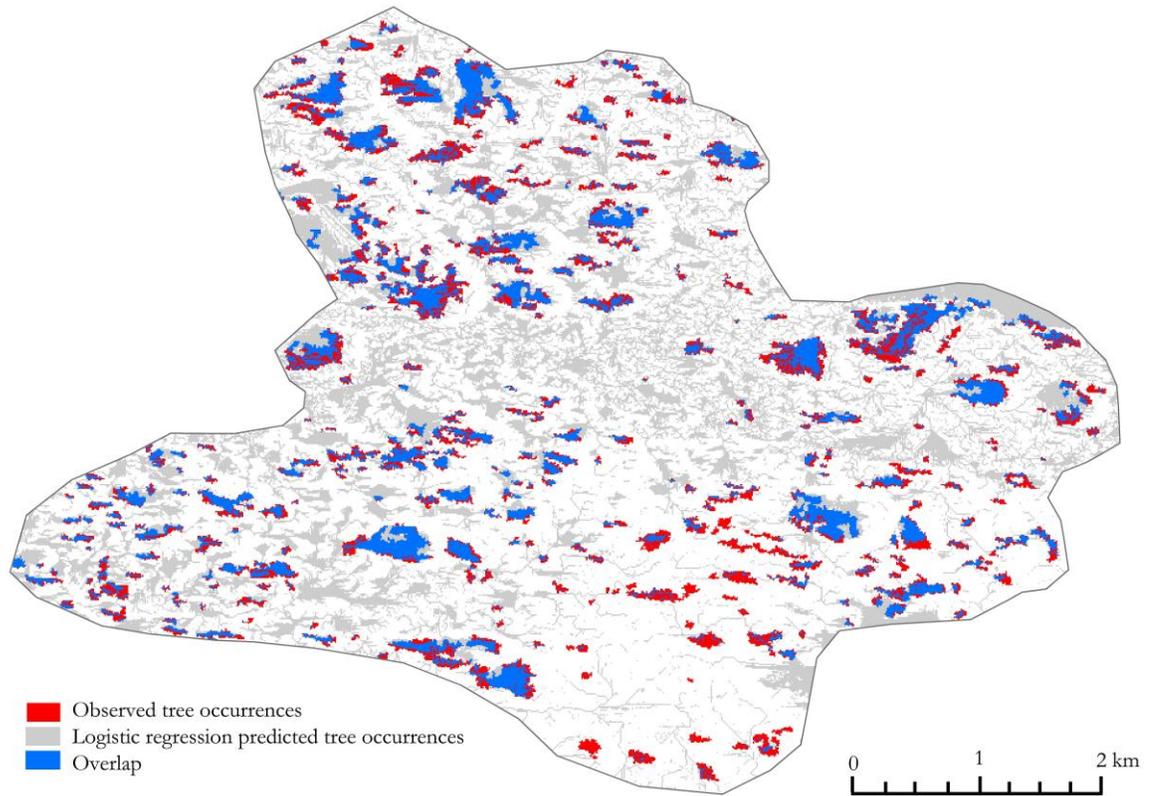


Figure 3.6. Comparison of tree habitat suitability as predicted using logistic regression (grey) to observed tree occurrences (red) at Site 2. The overlap between observed occurrences and predicted suitable habitat is represented by blue. A threshold of 0.30 was used (based on the maximum K value) for the logistic regression probabilities to create a binary suitable-unsuitable map.

The area under the ROC curve (AUC) values were 0.756 and 0.721 for the training (Site 1) and validation (Site 2) datasets, respectively (Fig. 3.7).

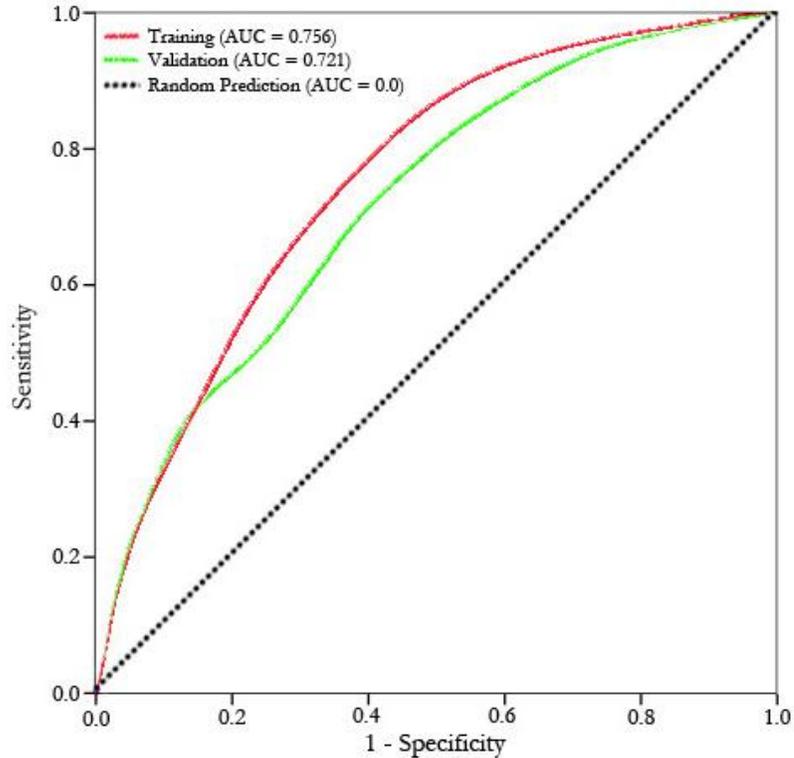


Figure 3.7. ROC curves of binary logistic regression for training (AUC = 0.756) and validation (AUC = 0.721) sites. The dotted diagonal line represents an AUC value of 0.5, where a curve above would represent a model with predictive power better than random chance and a curve below would represent a model with predictive power less than random chance.

Study sites were chosen based on their similar geomorphology and terrain configuration, and similar AUC values indicate comparable distributions of *Populus* spp. within the study sites. As stated, AUC values ranging from 0 to 0.5 represent a worse than random model, and values ranging from 0.5 to 1 indicate a better than random model. Values ranging between 0.5 and 0.7 represent low predictive accuracy, whereas moderate to excellent model accuracy is indicated by values greater than 0.7 (Swets, 1988; Elith *et al.*, 2006; Hirzel *et al.*, 2006; Lowe *et al.*, 2012). Therefore, this model can predict the presence of *Populus* spp. within the study sites with moderate predictive accuracy. This supports the hypothesis of this study, *that trees occur preferentially in low-lying areas or depressions*. However, since moderate predictive accuracy is less than perfect, the model resulted in *FP*

and *FN* results. *FP* results indicate that not all suitable areas are inhabited by *Populus* spp., as 25.4% of habitat predicted as suitable occurred where trees were absent. Additionally, 45.1% of habitat was predicted as unsuitable where trees were present, yielding *FN* results. This indicates that some unsuitable habitat is inhabited by *Populus* spp, and that some suitable habitat is not occupied by *Populus* spp. Therefore, other external influences may have an effect on the distribution of trees, additional to the topographic influences examined.

3.6 Discussion

This investigation used topographic variables (WI, elevation, northness, eastness, and curvature) in a logistic regression model to predict habitat suitability of trees within the study sites. Comparisons between logistic regression habitat suitability results and observed tree occurrences indicate 71.9% of tree occurrences were correctly predicted. AUC values of 0.756 (training) and 0.721 (validation) indicate moderate model performance in predicting the presence of trees. Score statistics in Table 3.5 show that WI is the most influential variable on the distribution of trees, with elevation as the second most influential variable. The α coefficients in the logistic regression equation (Eqn. 3.8) indicated that greater WI values, lower elevation values and concave curvature created suitable habitats for trees to occur. Since greater WI values, lower elevation values and concave curvature are observed more often between dunes (Fig. 3.3), these results support the hypothesis *that trees occur preferentially in low-lying areas or interdunes within two study areas in the GSH.*

Results revealed *FP* at a rate of 25.4% and *FN* at a rate of 45.1%. This indicates that not all suitable habitat is occupied by trees, and that some unsuitable habitat is occupied by trees. This suggests, therefore, that other non-topographic influences not included in the model may have an effect on the distribution of tree communities.

The GSH have undergone stabilization relatively recently, transforming from desert-like conditions to a relatively verdant ecosystem within the past 200 years (Wolfe & Hugenholtz, 2009; Chapt. 2). During the process of stabilization, different landcover communities appear at different times throughout the transition, with shrubs and trees occurring as later successional species than grasses (Dech & Maun, 2005). As such, it is possible that false positive results in this study are an indicator that the transition toward later successional stages is not complete, yielding suitable habitat conditions for tree communities where trees have not yet been recruited.

Additionally, the establishment and distribution of trees can be influenced by stochastic environmental constraints, preventing occurrences in suitable habitat or allowing occurrences in otherwise unsuitable habitat (Grubb, 1977; Lichter, 2000; Rey & Alcántara, 2000). For example, intermittent seed dispersal, weather events such as drought or above average precipitation, and fluctuating populations of rodent seed predators can negatively or positively affect the establishment and growth of tree communities (Grubb, 1977; Lichter, 2000; Rey & Alcántara, 2000). Furthermore, competition from other landcover community types occupying habitats suitable for trees can hinder the establishment of tree communities in some areas, providing insight into suitable habitat predictions occurring in the absence of observed trees (i.e., *FP* results). *Populus* spp. are shade intolerant, thus competition with other shade-tolerant landcover communities may hinder the establishment of trees where habitat conditions appear to be otherwise suitable (McCulloch & Kabzems, 2009).

The landcover data used for this study (Fig. 2.1) was classified to an accuracy of 77%, with some confusion occurring between shrubs and trees (Saskatchewan Environment, 2007). Thus, it is possible to speculate that this confusion may have affected the *FN* results

of the model. Areas which were predicted as unsuitable for trees but had trees present may have been a direct result of poor landcover classifications. For example, shrub communities can occur on the top of dunes, whereas it is extremely unlikely to find tree communities present in these locations of the GSH. Therefore, incorrect classifications of shrubs as trees may have contributed to the model's *FN* results.

This study shows that topographic variables can be used to predict the distribution of trees within these study sites of the GSH with moderate prediction accuracy. Logistic regression showed that tree communities tend to occur in low-lying interdune areas where greater WI values are observed. Although topography can partly explain the distribution of trees within the study sites, overall accuracy of the predictive model could be negatively affected by poorly classified landcover data, the fact that the GSH region has not yet reached the end of stabilization, or other non-topographic factors.

3.7 Conclusion

Topography provides an indirect control on the distribution of tree communities within the GSH. The hummocky dune terrain of the study sites used in this chapter provides a unique topographic template relative to the surrounding cultivated prairies. The dunes create an elevation gap between landcover and groundwater, thus constraining the distribution of tree communities to interdune areas. The aim of this study was to understand the distribution of *Populus* stands and its spatial association to the hummocky dune topography.

The main findings of this study indicate that tree habitat suitability can be predicted to an accuracy of 71.9% when using topographic variables WI, elevation, northness, eastness, and curvature with the threshold was 0.30. Wetness index had the greatest

influence on tree habitat suitability, indicating the strong influence of soil moisture on tree communities in this region. The logistic regression model indicates that trees preferentially occur in low-lying areas where soil moisture is easier to access. However, moderate model accuracy resulted in *FP* and *FN* results, leading to speculation about whether other non-topographic variables, the stage of succession, or the accuracy of landcover classifications had an impact on the habitat suitability model. This study provides evidence that topography alone can provide moderate predictions about the habitat suitability of trees within the hummocky dune terrain of the GSH, but it is also likely that other factors influence their distributions.

CHAPTER 4: CONCLUSIONS AND FUTURE DIRECTIONS

4.1 Summary of conclusions and contributions

Vegetation distribution and diversity are often signatures of the topographic characteristics within a region. Topographic variability, climate and geomorphometry vary across different ecosystems; therefore, it is necessary to study topography-landcover associations in individual ecosystems in order to elucidate connections. This thesis examined the topographic influence on landcover in an inland sand dune ecosystem known as the Great Sand Hills (GSH). The GSH have undergone vegetation stabilization within the past 200 years and are a diverse ecosystem home to several specialized and endangered species today (Wolfe & Hugenholtz, 2009; Nielsen, 2007). Previous field studies in the GSH (i.e., Hulett *et al.*, 1966) have suggested that local vegetation patterns are the result of variability in the environment associated with the topography and that the topography-landcover association has not been fully interpreted. This thesis used high resolution (i.e., 10 m) topographic data and classified satellite imagery to examine associations between topography and *i)* landcover diversity at several different spatial scales, and *ii)* the the spatial distribution of *Populus* spp. Overall, I have several key conclusions:

- 1) Chapter 2 used a simplified approach to determine the association between topography and landcover diversity in the GSH. It involved a calculation of the difference between the dependent (SDI) and independent variables (WI, and RU). Results of the differencing show spatial variability in the association of topography and SDI throughout the GSH; at best, RU predicted 62.1% of the distribution of landcover diversity at the small scale (i.e., SDI₅₀) and was a better predictor of landcover diversity than WI. RU typically over-predicted landcover diversity in areas with dunes, while in

- less rugged areas there was closer agreement. This suggests that the topographic relief created by dunes does not necessarily increase landcover diversity. Several biotic and abiotic factors may overprint the effects of topography on landcover diversity in the GSH.
- 2) Results from Chapter 3 suggest that WI had the strongest influence on tree distributions when using stepwise logistic regression. Results also suggested that suitable habitat favoured greater WI values, lower elevation values and concave curvature; thus supporting the hypothesis *that trees occur preferentially in low-lying areas or interdunes within two study areas in the GSH*. Results of the logistic regression model showed moderate accuracy, with 71.9% of predictions being correct. However, given 25.4% and 45.1% of predictions as *FP* and *FN* results, respectively, it is likely that other environmental and biological factors may slightly filter the role of topography on the distribution of trees in the GSH.
 - 3) It is acknowledged that using topography as a predictor of landcover diversity (Chapter 2) and tree community distribution (Chapter 3) is a first-order approximation. Many other eco-geomorphological and anthropogenic factors can influence landcover patterns and may provide an explanation for imperfect model results, but were beyond the scope of this thesis. Additionally, the young age of the ecosystem could imply that it has not completed the stabilization process, therefore spatially disrupting the topography-landcover association.
 - 4) This study attempted to quantify the association between landcover and topography by means of digital data. Spatial variability in associations and imperfect model predictions could be a consequence of using satellite imagery, and could be a trade-off to using direct field measurements and qualitative methods. Therefore, the current methods may

be valuable as first-order estimates of topography-landcover associations for large or inaccessible areas where digital data are easily attainable.

4.2 Future research directions

The studies in this thesis were designed to quantify topography-landcover associations and the following are future directions that could be taken from these studies. First, both of these studies used data collected in 2005 and were limited to landcover data classified to an accuracy of 77% at a resolution of 10 m. It would be interesting to conduct the same study using, *i*) more accurate and higher resolution data, or *ii*) time series data of the GSH collected at different years. Increased accuracy and higher resolution could improve the associations found between landcover diversity and topography (Chapter 2), whereas analyzing the association over a temporal data series could provide real-world insight into the patterns of stabilization for different landcover communities, as associated to their surrounding terrain (Chapter 3).

Acquiring field measurements from various sites within the GSH would complement this research and may serve to improve associations found between topography and landcover. For example, understanding the source of water for different landcover communities could clarify the reliance of some species on deep ground water versus near-surface soil moisture. This would ultimately determine the restrictions on the distribution of landcover due to sand dunes acting as barriers against the groundwater table. Additionally, analyzing the soil thermal regime at several different locations could provide insight into microclimatic differences and how these correspond to different landcover types and, therefore, their distributions throughout the region. Due to time limitations, these were not included in the scope of work for this thesis.

4.3 Concluding remarks

Throughout this thesis, I have reflected upon what I hoped to add to the existing body of scientific knowledge through my research. I will begin by stating that the topography of different landscapes, such as coastal dunes, mountains, and arid regions, have been shown to be a fundamental influence on the diversity and distributions of landcover (e.g., Gosz & Sharpe, 1989; Burke *et al.*, 1989; Franklin, 1995; Maun & Perumal, 1999; Guisan & Zimmerman, 2000; Hoersch *et al.*, 2002; Rietkerk *et al.*, 2002; Coblenz & Rütters, 2004; Deng *et al.*, 2007; Liu *et al.*, 2007; Coblenz & Keating, 2008; Istanbuluoglu *et al.*, 2008; Zhao *et al.*, 2010). The GSH demonstrate ingredients of a spatially-heterogeneous landscape consisting of relic melt-water channels, moraines, clearly defined parabolic dunes, hummocky dune terrain, and blowouts, along with landcover that, from a qualitative interpretation, appears to coincide with topography to a certain degree. This thesis attempted to quantify that association. Hulett *et al.*, (1966) stated, that “the wide range of differences in patterns [of landcover] is the result of ... variations in the environment that are usually associated with the terrain of an irregular surface” and that “[the GSH region] has provided another illustration of the characteristics of vegetation to be governed in its development and spatial distributions by continuously varying habitat gradients as have been observed elsewhere.”

The GSH region is of ecological importance and is a biological hotspot within the Canadian prairies; it has also undergone recent stabilization from desert-like conditions to the verdant mixed grassland ecosystem it is today (Nielsen, 2007; Wolfe & Hugenholtz, 2009). Research about the topography-landcover association is scarce in inland dune field ecosystems, and the GSH are one of the largest contiguous inland dune fields in Canada that

remain relatively unaltered by anthropogenic activities. Therefore, this study location provided ideal conditions for investigating whether there is a quantifiable association between topography and landcover. With moderate associations and predictability between topography and landcover, I view the future of quantitative studies as promising and sincerely hope this thesis has made a contribution (although small) that will allow future researchers to further analyze the association. I believe that as technology advances, quantitative analyses will become more accurate and could possibly lead to stronger quantifications of the topography-landcover association across different ecosystems. Additionally, understanding the spatial distributions and patterning of landcover within the GSH are of great importance. This is especially true given that anthropogenic activities have been increasing in the area and are potentially disrupting the diversity and distribution of landcover (Noble, 2008). Understanding how the topography influences the landcover diversity and distribution could help us better manage wildlife habitat and thus promote ecosystem sustainability within this prairie sandhill ecosystem.

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