# CHARACTERISING MOOSE HABITAT, ABUNDANCE AND ECOSYSTEM VARIABILITY USING SATELLITE-DERIVED INDICATORS

by

Jean-Simon Michaud

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# Abstract

Natural variability and disturbance events drive spatial and temporal variation in ecosystem processes and play key roles in ecosystem variety and the maintenance of species diversity. As a result, an improved understanding of the links between natural environmental variability and species diversity is needed to guide prioritisation of conservation and management actions. Ontario, the second largest province in Canada, covering approximately 1 million $km^2$, is environmentally diverse and is subject to a large amount of natural and anthropogenic disturbances. Remote sensing is uniquely capable of monitoring dynamic ecosystems over large areas in a repeatable and cost effective manner and has been shown to provide considerable benefit to assess species distribution and biodiversity.

This thesis (1) examines an approach for detecting natural variability and disturbances of vegetation productivity from a remote sensing time-series and (2) demonstrates the use of satellite-derived indicators for the characterisation of moose habitat across Ontario.

First, an approach was developed to assess temporal trends in vegetation productivity which utilised a Theil-Sen's non-parametric statistical trend test over a 6-year period (2003-2008) of ten-day composites of Medium Resolution Imaging Spectroradiometer (MERIS) fraction of Photosynthetically Active Radiation (fPAR). Results indicated that this novel remote sensing approach can be used to characterise trends in landscape productivity patterns over large areas and can aid in provincial and national monitoring activities.

Second, the research investigated the application of remotely sensed indicators such as vegetation productivity, land cover, topography, snow cover and natural and anthropogenic disturbances to predict moose occurrence and abundance. Results indicated that remotely sensed indicators were significantly correlated to moose habitat suitability with moose distribution being more accurately estimated than moose abundance. In addition to providing insights into the relative importance of the predictor covariates for moose occurrence and abundance, this study creates opportunities for further development of spatial models that closely examine the occurrence/abundance-habitat relationships which are highly valuable for habitat management decisions.

# Preface

This thesis is the combination of two scientific papers of which I am the lead author.
I performed the primary research, data analysis, interpretation of the results and prepared the final manuscripts. Dr. Nicholas Coops provided project oversight as well as editorial assistance. Dr. Margaret Andrew provided considerable guidance on ecological principles and statistical approaches throughout my graduate program. Dr. Glen Brown provided project oversight in terms of moose ecology and data specific to Ontario and Dr. Michael Wulder provided suggestions and editorial comments.

Publication arising from this thesis so far include (reprinted with the permission from the publishers):

- Chapter 2: Coops, N.C., **Michaud, J.S.**, Andrew, M.E., Wulder, M.A., (2011). Comparison of a regional-level habitat index derived from MERIS and MODIS estimates of canopy light absorbance. *Remote Sensing Letters*. 2, 327-336.

- Chapter 3: **Michaud, J.-S.**, Coops, N.C., Andrew, M.E., Wulder, M.A. (2011). Characterising spatiotemporal environmental and natural variation using a dynamic habitat index throughout the province of Ontario. *Ecological Indicators*. doi:10.1016/j.ecolind.2011.11.027

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# 1. INTRODUCTION

## 1.1 Biodiversity and natural variability

Maintenance of biodiversity is essential for the provision of ecosystem services such as pure air and water, waste decontamination and decomposition, soil fertility, and climate regulation (Daily et al., 1997). There is a scientific consensus that diversity of life is being lost at a rapid and accelerating rate on Earth (United Nations Environmental Programme (UNEP), 2002, Duraiappah et al., 2005, Groves et al., 2002), which has resulted in commitments from over 175 countries to significantly reduce the rate of loss of biodiversity by 2010 (Secretariat of the Convention on Biological Diversity, 2000). Increases in natural and anthropogenic disturbances, coupled with a rising trend in climate variability across Canada, will make management of ecosystems and the species herein increasingly challenging over the next few decades (Flannigan et al., 2005, Kerr and Packer, 1997, Kurz et al., 2008). Natural variability and disturbance events drive spatial and temporal variation in ecosystem processes and play a key role in ecosystem variety and the maintenance of species diversity (Landres et al., 1999, Petraitis et al., 1989). In a context of global changes, links between natural environmental variability and species diversity needs to be fully understood in order to guide prioritisation of conservation and management actions.

## 1.2 Vegetation trend detection

Ecosystem natural variability is defined by Landres et al. (1999) as "the ecological conditions, and the spatial and temporal variation in these conditions, that are relatively unaffected by people, within a period of time and geographical area appropriate to an expressed goal". Natural variability can be driven by changes in the inherent land cover, topography, seasonality, and natural variations in climate of an ecosystem. Variability can also extend beyond the natural range due to disturbances such as fire, harvesting, land conversion, and increasingly due to extremes in climate (snow storms, flooding, drought, increased temperature, etc) (Coops et al., 2009a) (Figure 1.1).

Disturbances occur at a range of spatial scales, frequencies, and intensities, yielding distinct changes in ecosystem composition and organisation. Within forested ecosystems, low-severity disturbances, occurring over long periods, often favour competitive tree species whereas high-severity disturbances (i.e., stand replacement) often favour colonising species (Frelich, 2002). As a result, natural and human induced disturbance regimes exert a strong control on forest-stand composition and indirectly impact the spatial patterns and the existence of wildlife habitat by regulating forest structure and tree and plant species (Coops et al., 2009a, Morrison et al., 2006).

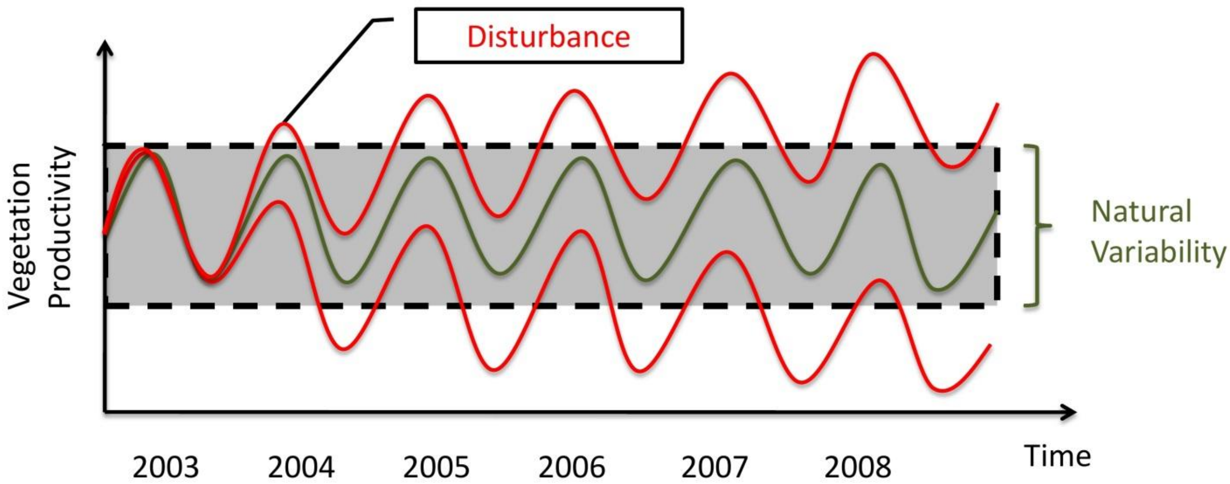



**Figure 1.1. Outline of temporal disturbance influences on vegetation productivity: the variability extend beyond the natural range.**

Characterising broad scale vegetation condition, which relates directly to detecting patterns of natural variability, is the first step towards identifying the drivers of the variability and better understanding the underlying mechanisms. Accurate maps of vegetation change patterns are key elements to predict ecosystem recovery, depletion, and provide insights into wildlife dynamics. Spatiotemporal variation of vegetation productivity can also explain the occurrence and distribution of fauna, and indirectly being an indicator of species richness (Evans et al., 2005, Harestad and Bunnel, 1979). As a result, this information is important for studies on biodiversity as well as contributing valuable insights for monitoring climate change and prioritisation of ecosystem conservation and management actions.

## 1.3 Remote sensing

Remote sensing has been found to be a valuable technology to monitor environmental condition as it allows to synoptically characterising broad scale environments in a timely and repetitive manner (Potter et al., 2003). Earth observation satellites observed Earth's surface with a range of spatial, temporal, and spectral resolutions, which provides the ability to distinguish unique characteristics of the land surface. Advantages of remote sensing for monitoring include the ability to regularly acquire data over an area to provide temporally frequent updates on changes occurring across the landscape. As Earth observation programs mature, there will be increased free access to satellite images for environmental applications which, coupled to ecological models, can help understand fundamentals of biodiversity patterns at relatively low cost (Turner et al., 2003).

Over the past two decades, scientists have demonstrated that satellite imagery provides considerable benefit to assess species distribution and biodiversity (Franklin et al., 1991, Gillespie et al., 2008, Nagendra, 2001). Turner et al. (2003) classified biodiversity monitoring approaches using remote sensing into "direct" and "indirect" techniques. The direct approach involves explicitly mapping species whereas the indirect approach links biodiversity to remote sensed environmental indicators which are known to influence species occurrence. These indicators, summarised by Duro et al. (2007), include (i) measures of the physical environment (i.e. climate, topography), (ii) vegetation productivity, (iii) habitat suitability (i.e. spatial arrangement and structure) and (iv) metrics of disturbances. Climate is a well-established driver of biodiversity at both regional and global scale (Currie and Paquin, 1987, Gaston, 2000, O'Brien, 1998) and in climatic analyses, temperature and moisture are the two variables often utilised (Duro et al., 2007). Topography is a more static indicator than climate; however it has also been well correlated to gradients in species such as in the tropics where higher diversity was found at average elevation (Rosenzweig, 1995). Vegetation productivity has been linked to biodiversity as high productivity zones are more likely to have less competition between species and sustain more individuals (Evans et al., 2005, Skidmore et al., 2003). While climate and vegetation productivity are known to influence species patterns at a broader scale (Gaston, 2000, Willig et al., 2003), spatial patterns governed by land cover and forest structure can be used to investigate species diversity at a finer scale (Fahrig, 2003).

Remote sensing has also been shown to successfully detect rapid changes in dynamic ecosystems. For example, fire, clear cut harvesting, blowdown, and other disturbances that result in stand replacement are particularly effectively detected (Coppin et al., 2004). However, slower changes resulting from shifting climate, likely to impact the boreal forest (Stocks et al., 1998), are harder to detect using remote sensing (Donoghue, 2002). These changes, yet slow, are still of major concern as they alter the ecosystems and indirectly impact the species herein. Studies have been conducted on detecting these changes (Beurs and Henebry, 2005, Donohue et al., 2009, Zhang et al., 2008), however, it is of critical importance to conduct further research on techniques to identify trends in vegetation productivity and understanding the implications of these trends on biodiversity.

## 1.4 Ontario and moose

Ontario, the most populated province of Canada, is environmentally diverse (Baldwin et al., 2000) with three broad ecozones defining the distinctiveness of the physical geography, climate, land-use patterns, and forest types of each region (Rowe and Sheard, 1981). Ontario is characterised by large ecological diversity, including both rare and endangered flora and fauna species (Thompson, 2000, SARA (Species at Risk Act), 2002). In addition to climate change influences, Ontario ecosystems are responding to a large amount of natural disturbances and increasing anthropogenic pressure such as detailed in section 2.1. These disturbance regimes make Ontario a key area for monitoring environmental changes and examining the complex interactions between environmental variability and species distribution.

Moose (*Alces alces*) provide good candidates to evaluate the link between environmental variability and species distribution considering their relatively large home range (i.e. up to 700km$^2$ (Ballard et al., 1991). This large area requirement makes them sensitive to changes in broad-scale spatial arrangements such as habitat fragmentation and forest succession (Voigt et al., 2000). Moose have also been used as focal species for protected area planning due to their fundamental ecological role in the structure and function of boreal forests (Crichton, 1998, Snaith and Beazley, 2002). Moose are long lived, slow to reproduce, and are highly sensitive to habitat alteration and contamination which makes them a good indicator of environmental quality change. In addition, moose are large, charismatic, and of high economic and social values, resulting in significant concern for the management of its habitat. As a result, the need to effectively manage moose habitat combined with the significant environmental variation occurring across Ontario makes this province an ideal study area for this thesis.

## 1.5 Research objectives

The objective of this thesis was to examine if remote sensing derived indicators of biodiversity can be used to assess ecosystem variability and monitor moose habitat and abundance across Ontario. To meet this objective, two specific research questions were posed:

1. Can vegetation productivity predicted by remote sensing be used to assess ecosystem variability throughout Ontario?
2. Can satellite-derived productivity, land cover, terrain and disturbance indicators characterise moose habitat and abundance?

Chapter 2 describes the Ontario physical environment, including the regional climate, soil characteristics, disturbance regimes, and the vegetation found across the province. In addition, we detailed the various spatial datasets derived from remote sensing imagery that are used throughout this study.

Chapter 3 investigates the application of vegetation productivity indicators derived from remote sensing to better understand trends in ecosystem variability. We distilled remote sensing productivity time-series into a three-part dynamic habitat index (DHI; Coops et al. 2008), identified trends in these indices, followed by an assessment of the potential implication for species richness.

Chapter 4 demonstrates the uses of a statistical model which combined remote sensing derived vegetation productivity, forest land cover types, terrain and distance from landscape features to estimate moose habitat and abundance across Ontario. We assessed the relative contribution of the environmental drivers to moose occurrence and abundance and evaluated the implications for moose habitat management.

Finally, Chapter 5 discussed the overall findings and conclusions, in addition to recommendations for future work.

# 2. ONTARIO AND PREDICTOR COVARIATES[1]

## 2.1 Study area

Ontario is the second largest province in Canada, covering approximately 1 million km$^2$, extending over 15 degrees of latitude and 20 degrees of longitude. Ontario's climate is humid continental with the exception of the Northern Hudson Bay region, which has a maritime character (Baldwin et al., 2000). Ontario is characterised by an increasing gradient of temperature from north to south, a precipitation trend increasing from northwest to southeast and snow accumulations that are highly variable across the province. In addition, precipitation and temperature trends are also significantly influenced by the presence of lakes (e.g., Lake Superior and Lake Huron) and by local topographic relief (Baldwin et al., 2000). At the higher latitudes, the Hudson Plains have significant snow cover over an extended period of the year, relatively flat topography, and poor drainage with deep organic soils typified by bogs, fens, lichens and small conifer stands (Rowe, 1972). In central Ontario, the growing season is longer with a more pronounced terrain, a relatively good drainage, and coarse-textured soil on bedrock and as a result coniferous and evergreen forests dominate (Baldwin et al., 2000). Ontario's boreal forest is also naturally disturbed by wildfires, and in addition to anthropogenic activity (e.g., timber harvesting activity, hydroelectricity dams, and mineral exploration), insect infestations, blowdowns, floods, droughts and ice storms also shape its landscape (Thompson, 2000, Perera and Baldwin, 2000, Rosenberg et al., 1995). Southern Ontario is highly urbanised, resulting in a heterogeneous mosaic of urban areas, roads, mixed forests, and agricultural areas and experiences milder weather in comparison to more northerly locations. Within the study area, the major tree species include jack pine (*Pinus banksiana*), black spruce (*Picea mariana*), white spruce (*Picea glauca*), balsam fir (*Abies balsamea*), white birch (*Betula papyrifera*) and trembling aspen (*Populus tremuloides*) (Brandt, 2009).

## 2.2 Data description

We examined three types of variables in this research: biophysical, climatic, and natural and anthropogenic disturbances. These datasets are detailed below and Table 1 is provided to summarise the spatial and temporal resolution and source.

[1] Part of this chapter has been published. Coops, N.C., Michaud, J.S., Andrew, M.E., Wulder, M.A., (2011). Comparison of a regional-level habitat index derived from MERIS and MODIS estimates of canopy light absorbance. *Remote Sensing Letters*. 2, 327-336.

**Table 2.1. Variables used to estimate vegetation productivity trends and/or occurrence and abundance of moose across the province of Ontario.**

| Data layer name | Spatial resolution (km) | Time period | Source |
|---|---|---|---|
| MERIS vegetation productivity (fPAR) | 1.0 x 1.0 | 2003-2008 | European Space Agency, MERIS |
| MODIS vegetation productivity (fPAR) | 1.0 x 1.0 | 2000-2006 | National Aeronautics and Space Administration, MODIS |
| Land cover classification | 0.025 x 0.025 | Circa 2000 | Government of Canada, Canadian Forest Service and Canadian Space Agency, EOSD |
| Topography | 1.0 x 1.0 | 2000 | United States Geological Survey's, EROS Data Center, SRTM |
| Snow cover | 4.0 x 4.0 | 2000-2010 | National Snow and Ice Data Center, MODIS |
| Fire history | Polygon data | 1970-2008 | Government of Canada, Canadian Forest Service, Large Fire Database |
| Distance to nearest road | 1.0 x 1.0 | 2010 | Government of Canada, Statistics Canada and Ontario Ministry of Natural Resources |
| Distance to nearest Human settlement | 1.0 x 1.0 | 2006 | NOAA's National Geophysical Data Center |

### 2.2.1 Fraction of Photosynthetically Active Radiation

The fraction of Photosynthetically Active Radiation absorbed by vegetation (fPAR) is derived from a physically based model of the propagation of light in plant canopies (Tian et al., 2000) and unlike the Normalised Difference Vegetation Index (NDVI), which use a ratio of two spectral bands, utilises multiple bands and knowledge of land cover, seasonal and locational solar conditions to derive the amount of solar irradiance captured by the vegetation (Gobron et al., 1999, Govaerts et al., 1999, Gobron et al., 2007, Knyazikhin et al., 1998). As a result, we derived fPAR metrics from the Medium Resolution Imaging Spectroradiometer (MERIS) and the MODerate resolution Imaging Spectroradiometer (MODIS) sensors.

#### *2.2.1.1 MERIS*

MERIS is a nadir-looking sensor on board of ENVISAT operating in a push-broom mode that measures the solar reflected radiation from 390 – 1040 nm (Bezy et al., 2000). The MERIS sensor has dual spatial resolutions: a full-resolution mode (300m) and a reduced-resolution (1200m) (Bezy et al., 2000, Louet, 2001). MERIS completes a global coverage every 3 days due to its 68.5° field of view and 1150 km wide swath, a key advantage for landscape-scale studies (Baret et al., 2006, Gobron et al., 2007). Since 2002, the MERIS Global Vegetation Index (MGVI), which is analogous to fPAR has been acquired (Gobron et al., 1999). MGVI is calculated using the blue, red and near-infrared top-of-atmosphere reflectance (Gobron et al., 1999) from a physically based algorithm which utilises radiative transfer models to account for overlying atmospheric and underlying soil perturbing factors and angular effects (Gobron et al., 2007). We used the time composite product which selects the most representative valid value over a 10 days sequence to provide a more spatially uniform and complete coverage (Pinty et al., 2002). Six year of data (2003-2008) were provided by the European Space Agency (ESA). The original 1.2 x 1.2 km spatial resolution fPAR data was resampled using a nearest neighbour routine to 1.0 x 1.0 km and was used as basis for computation of the habitat index.

#### *2.2.1.2 MODIS*

The MODIS sensor onboard of TERRA and AQUA provides a suite of geo-registered, composited, atmospherically corrected, data products, calculated from daily surface reflectances including fPAR (Justice et al., 2002, Tian et al., 2000). Information on fPAR is obtained from up to seven spectral bands and is derived from a physically based model which describes the propagation of light in plant canopies taking into account sun angle, background reflectance, and view angle influences (Tian et al. 2000). MODIS provides near daily coverage of Earth's surface at 1-km spatial resolution (Justice et al. 2002) and is combined into monthly fPAR products by selecting the maximum value across each 8-day period, which, similar to the MGVI, minimises the influence of cloud cover and other unfavorable environmental conditions (Yang et al., 2006). MODIS fPAR values were obtained from 2000-2006.

#### *2.2.1.3 Dynamic Habitat Index*

The Dynamic Habitat Index (DHI), first developed by Mackey et al. (2004) and then adapted for Canada by (Coops et al., 2008), is an indirect approach of characterising ecosystem productivity from fPAR measurements. This index is composed of three indicators that estimate the annual productivity, the minimum cover, and the seasonality of the photosynthetic activity at each pixel. The annual productivity is of biological interest since it drives resources availability and indirectly can explain species distribution and abundance (Evans et al., 2005, Skidmore et al., 2003). This indicator is estimated by summing all the fPAR value throughout the year. Minimum cover refers to the lowest (minimum value) level of vegetative cover over the snow free period (June 11$^{th}$ – September 31$^{st}$) which can be an indicator of the capacity of the landscape to sustain adequate level of food and habitat resource during this period. Seasonal variation in productivity, i.e., seasonality, accounts for annual changes in vegetation productivity. Seasonality is a surrogate of habitat quality as it affects essential resources (e.g., food, water and nutrients) and is expected to exert selective pressure on life history traits (Mcloughlin et al., 2000). To evaluate the variation of the vegetation cover throughout the year, we calculated the mean and standard deviation of the yearly fPAR composite and calculated the annual coefficient of variation.

### 2.2.2 Land cover classification

Land cover is recognised as a critical driver of environmental productivity (Mildrexler et al., 2007) and is an important component when interpreting landscape productivity variations and DHI behaviour at a broad scale (Coops et al., 2009b). Land cover information was extracted from the Canadian Forest Service (CFS) and Canadian Space Agency (CSA) Earth Observation for Sustainable Development of forests (EOSD) product which classified circa 2000 Landsat Enhanced Thematic Mapper Plus (ETM+) imagery using an unsupervised classification, followed by a manual labelling of the 23 land cover classes (Wulder and Nelson, 2003) resampled at 25 x 25 m spatial resolution (Wulder et al., 2008). In order to retrieve land cover information over agricultural areas, we utilised the National Land and Water Information Service (NLWIS), an Agriculture and Agri-Food Canada (AAFC) product which is also derived from ETM+ imagery circa 2000 (Fisette et al., 2006).

### 2.2.3 Topography

Topographic information was derived from the Shuttle Radar Topography Mission (SRTM) which provides global elevation data at a spatial resolution of 90 m and a vertical resolution of ~ 5m (Farr et al., 2007, Farr and Kobrick, 2000).

### 2.2.4 Snow cover

Remote sensing estimates of snow cover fraction were provided by MODerate resolution Imaging Spectroradiometer (MODIS) /Terra Snow Cover Monthly L3 Global (MOD10CM) at 0.05 deg spatial resolution from 2000-2006 (Hall and Riggs, 2007). Average fractional monthly snow cover was retrieved from September to June.

### 2.2.5 Fire history

Extensive fire history data for Ontario was retrieved from the Large Fire Database (LFDB) which is a dataset aggregated by the CFS using provincial and territorial fire management agencies data. This geographic collection of vector polygons represents the extent for all fire events larger than 200 ha recorded by satellite and aerial imagery, aerial observation or on the ground using global positioning system (GPS) data from 1959-1997. This information was coupled to burned polygons derived from the annual national burned forests maps prepared by the CFS and Canadian Centre for Remote Sensing (CCRS) for the 1995-2008 period. This data was computed from annual hotspot map from the Advanced Very High Resolution Radiometer (AVHRR) or MODIS which is combined with observed annual changes in vegetation indices from AVHRR (1.1 km resolution), Satellite Pour l'Observation de la Terre(SPOT) Vegetation (VGT) sensor (1.0 km resolution) or MODIS high resolution (0.25 km) imagery. This annual mapping technique is intended to document spatial and temporal distribution of large burns (> 1000 ha) over the boreal forest (Fraser et al., 2000).

### 2.2.6 Distance to nearest road and human settlement

To identify potential anthropogenic drivers of changes in vegetation productivity we derived distance measures from anthropogenic activity which were calculated as the either distance from the nearest road or human settlement. We estimated the nearest distance from road using the 2006 Road Network File (RNF) compiled by Statistics Canada (Statistics Canada, 2006); and the nearest distance from human settlement using the circa 2006 Version 4 DMSP-OLS Nighttime Lights Time Series processed by the NOAA National Geophysical Data Center (NOAA, 2006). For additional information on distance to metrics, see (Wulder et al., 2011).

# 3. CHARACTERISING SPATIOTEMPORAL ENVIRONMENTAL AND NATURAL VARIATION THROUGHOUT THE PROVINCE OF ONTARIO[2]

## 3.1 Introduction

Understanding the natural variability of landscapes has become a critically important issue for land managers charged with maintaining ecosystem function and the protection of species diversity (Landres et al., 1999, Petraitis et al., 1989). Landres et al. (1999) defines ecosystem natural variability as the ecological conditions, and the spatial and temporal variation in these conditions, that are relatively unaffected by people, within a period of time and geographical area appropriate to an expressed goal. Understanding the range of natural variability is also critical when assessing the current and potential impact of climate variation and disturbances on ecosystems (Landres et al., 1999).

Satellite imagery is uniquely capable of monitoring vegetation productivity over large areas in a repeatable and cost effective manner and therefore is a critical tool when assessing changes in environmental conditions (Goward et al., 1985, Balmford et al., 2005). A number of studies have utilised remote sensing data to characterise ecosystem productivity and functioning (Box et al., 1989, Defries and Townshend, 1994, Goward et al., 1985, Kerr and Ostrovsky, 2003), and to predict changes in key vegetation characteristics (Wulder, 1998). To do so, one of the most common methods is to utilise the Normalised Difference Vegetation Index (NDVI) which is a ratio of the near infrared and visible regions of the electromagnetic spectrum. Multi-year NDVI time-series, which are becoming increasingly available, have successfully been used to understand the temporal dynamics of terrestrial vegetation (Alcaraz et al., 2006, Paruelo et al., 2001, Pettorelli et al., 2005, Reed et al., 1994, Wessels et al., 2010). In addition, researchers have also used this temporal information to depict trends in vegetation productivity and monitor environmental landscape scale changes (Alcaraz-Segura et al., 2009, Alcaraz-Segura et al., 2010, Donohue et al., 2009, Vicente-Serrano and Heredia-Laclaustra, 2004).

In addition to NDVI however, there are a number of other remote sensing indices which more directly capture vegetation biophysical attributes. These indices utilise knowledge of land cover, seasonal and locational solar conditions to derive the amount of solar irradiance captured by the

[2] A version of this chapter has been published. Michaud, J.-S., Coops, N.C., Andrew, M.E., Wulder, M.A. (2011). Characterising spatiotemporal environmental and natural variation using a dynamic habitat index throughout the province of Ontario. *Ecological Indicators*. doi:10.1016/j.ecolind.2011.11.027

vegetation (Knyazikhin et al., 1998). For example, the fraction of Photosynthetically Active Radiation absorbed by vegetation (fPAR) is derived from a physically based model of the propagation of light in plant canopies (Tian et al., 2000) and unlike the NDVI, which use a ratio of two spectral bands, utilises multiple bands (Gobron et al., 1999, Gobron et al., 2007, Govaerts et al., 1999).

The dynamic habitat index (DHI) (Coops et al., 2008, Berry et al., 2007), a composite index derived from fPAR time series data, is composed of three indicators of the underlying vegetation dynamics; the cumulative annual productivity, the minimum apparent cover and the variation of the photosynthetic activity all of which have been demonstrated to be of biological significance (Coops et al., 2009c, Andrew et al., 2011). Relationships between DHI and species abundance has been demonstrated in a number of studies. Changes in DHI productivity were significantly correlated to avian species richness across different functional groups (Coops et al., 2009c) in the United States and in Ontario, grassland bird species richness was found to be highly correlated with the minimum cover and seasonality (Coops et al., 2009b). Andrew et al. (2011) found that beta diversity of Canadian butterfly communities was positively correlated with DHI minimum and cumulative annual productivity.

In this paper, we ask whether this type of composite remote sensing indicator can be used to characterise the natural variability of vegetation over a six year period for the province of Ontario, Canada. Our approach was as follows. First we transformed 10-day composites of fPAR data into the DHI habitat index. A non-parametric statistical test was then used to define the level of observed natural variability and highlight those areas which fall within, and beyond, the variability thresholds. Once these areas were defined, we utilised a number of environmental variables to investigate if the observed patterns can be linked to specific natural and anthropogenic conditions. We conclude with an assessment of the approach and its use as an ecological indicator of natural ecosystem variability.

## 3.2 Methods

### 3.2.1 Study site

For a complete study area description, please consult section 3.1. Ontario landscape is highly diverse, resulting from a wide variability of climate, geology, terrain, soils, and hydrology. Ontario's ecosystems are naturally variable principally due to the latitudinal climatic gradient, natural disturbances, and the physical environment. Across Ontario, ecosystems have highly different seasonality effect with growing-degree-days over 5°C ranging from 2,500 in southern Ontario to less than 800 in northern Ontario (Baldwin et al., 2000). Natural variability patterns are complex, and with the rising trend in climate variability across Ontario, we would gain in utilising remote sensing indicators to provide valuable insights to land managers in order to guide prioritisation of conservation and management actions.

### 3.2.2 Data

Vegetation productivity derived from MERIS sensor, land cover, topography, snow cover, fire history, as well as the distance to the nearest road and human settlement were used for this chapter. For complete description of these datasets, please consult section 2.2

### 3.2.3 Ecological classification

To obtain an initial stratification of Ontario's biomes we utilised Canada's hierarchical classification of ecosystems which provide information on terrestrial ecozones and their ecological distinctiveness (Rowe and Sheard, 1981).

### 3.2.4 Trend characterisation and analysis

The Theil Sen's non-parametric test was used to assess variability in the three annual DHI components (annual productivity, minimum cover and seasonality) from 2003-2008 (n=18). The Theil Sen's test is a rank-based test which is robust against non-normality of the distribution and missing values (Theil, 1950), and unlike the Mann-Kendall test, detects not only if a trend exists, but also provides the amplitude of that trend (Sen, 1968). The Theil Sen's test calculates individual slope estimates for each data pair and then computes the median slope (Q) of the time-series (Gilbert, 1987). To capture broad trends, and to reduce spatial misregistration in the fPAR data, we removed the fPAR values within two kilometres of water bodies (as defined from a national coverage available from the CanMap Water v2006.3 compiled by DMTI Spatial) and we averaged the DHI and resampled spatial data layers into a 10 x 10 km grid. For each cell, we normalised the slope value by its six year mean, in order to express the trends as a percent of the mean cell which allowed all three indicators to be compared. To determine which 10 x 10 km cells had a notable trend we used a fixed threshold, similar to the approach used by Wulder et al. (2007), i.e., 20%, based on the entire distribution of trend values for each DHI component.

Our approach was then as follows: we first assessed the overall observed trends for each component of the DHI across the study area. To assess the effect of land cover on the amplitude of the observed trends, we applied a generalised least square modelling approach. To do so we stratified all pixels (n = 8477), into positive and negative trends similar to the approach of Alcaraz-Segura et al. (2010a) to ensure regional trends are maintained for each of the three DHI indicators. We then tested the effect of land cover on the trend values using one-way ANOVAs, which account for spatial autocorrelation of the residuals with a spherical error term (Pinheiro and Bates 2000). Sequential Bonferroni post hoc test (Rice, 1989) ($p < 0.05$) of the ANOVAs were used for multiple comparisons of land cover types. We used generalised least square models to test the effects of environmental, anthropogenic drivers and their interactions, on trend values. Again, each positive and negative trends was modeled individually by DHI component and spatial autocorrelation of the residuals was modeled using a spherical error term.

Second, we focused on those cells which were deemed to be exhibiting a notable trend using the pre-defined, 20%, threshold. To assess if the proportion of cells with a notable trend was different than the proportion of land cover types, a chi-square analysis was used. To evaluate the impact of fire on the largest observed trends historical fire were grouped by burn date, i.e., 1970-1986, 1987-2003 and 2004-2008. We then examined to what extent these fire burn areas had a notable trend over the 6 year period again assessed using a chi-squared test.

All trend computation and analysis were performed using the zyp (Bronaugh and Werner, 2009), nlme (Pinheiro et al., 2010) and tree package (Ripley, 2010) in the R programming environment (R Development Core Team, 2010).

## 3.3 Results

### 3.3.1 Overall observed trends

Figure 3.1 shows the three averaged DHI components for 2003 – 2008 and as expected shows lower annual productivity in the northern plains, increasing in the central uplands and the southern latitudes. A similar pattern is found in the minimum cover component, except in the northern plains where minimum cover is higher. Seasonality also shows higher values in the north, but in contrast to the two other indicators, was higher in the central uplands and lower in the southeast. After normalisation, trend values across the three indicators also varied (Figure 3.2). The Hudson Plains are characterised by decreasing and increasing trends for annual productivity and seasonality, respectively. The central upland region is dominated by a decreasing trend in minimum cover, whereas in the south a combination of decreasing trends in annual productivity and increasing trends in seasonality is found.

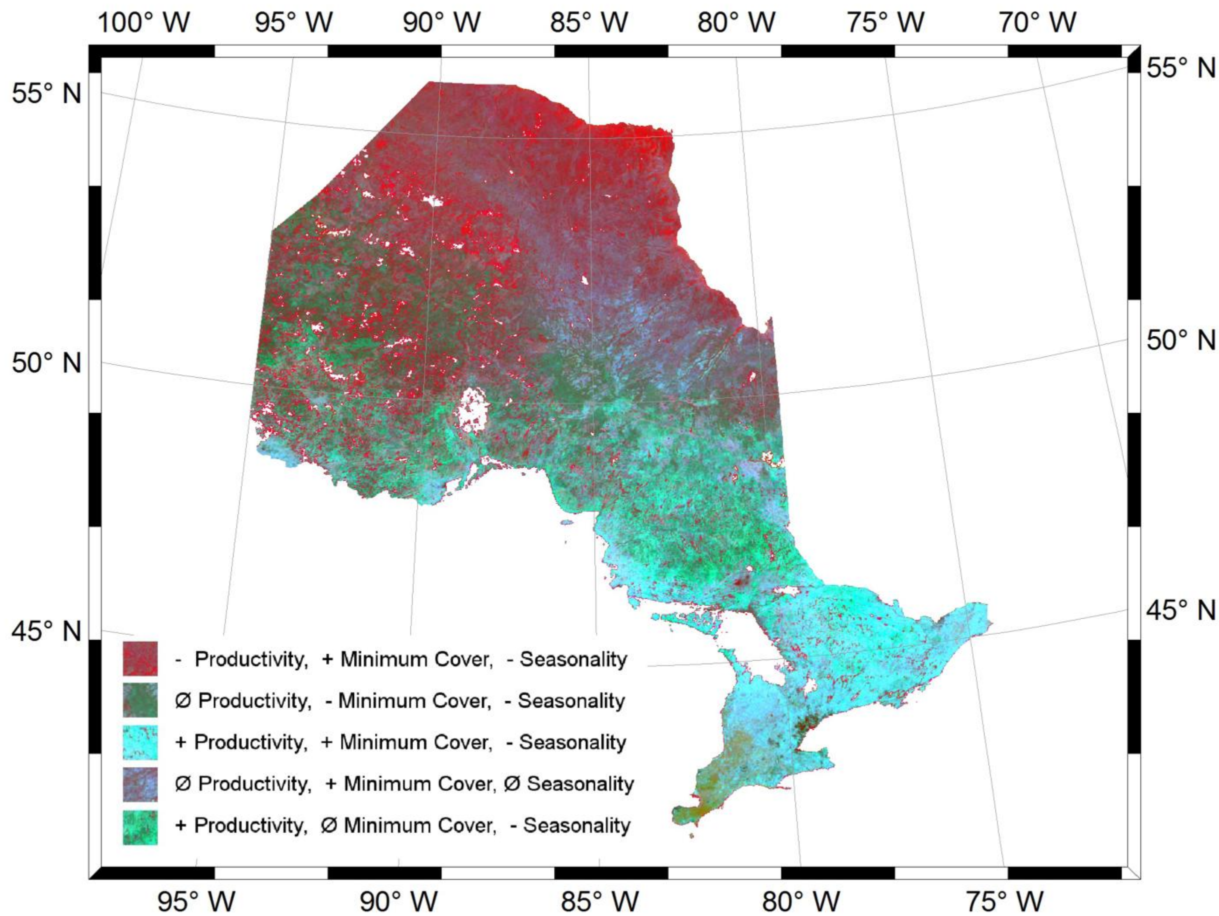



**Figure 3.1. Combined components of the dynamic habitat index averaged over the 6 years of observations (2003-2008). This colour composite is elaborated by assigning the red band to seasonality, the green band to overall greenness and the blue band to minimum cover.**

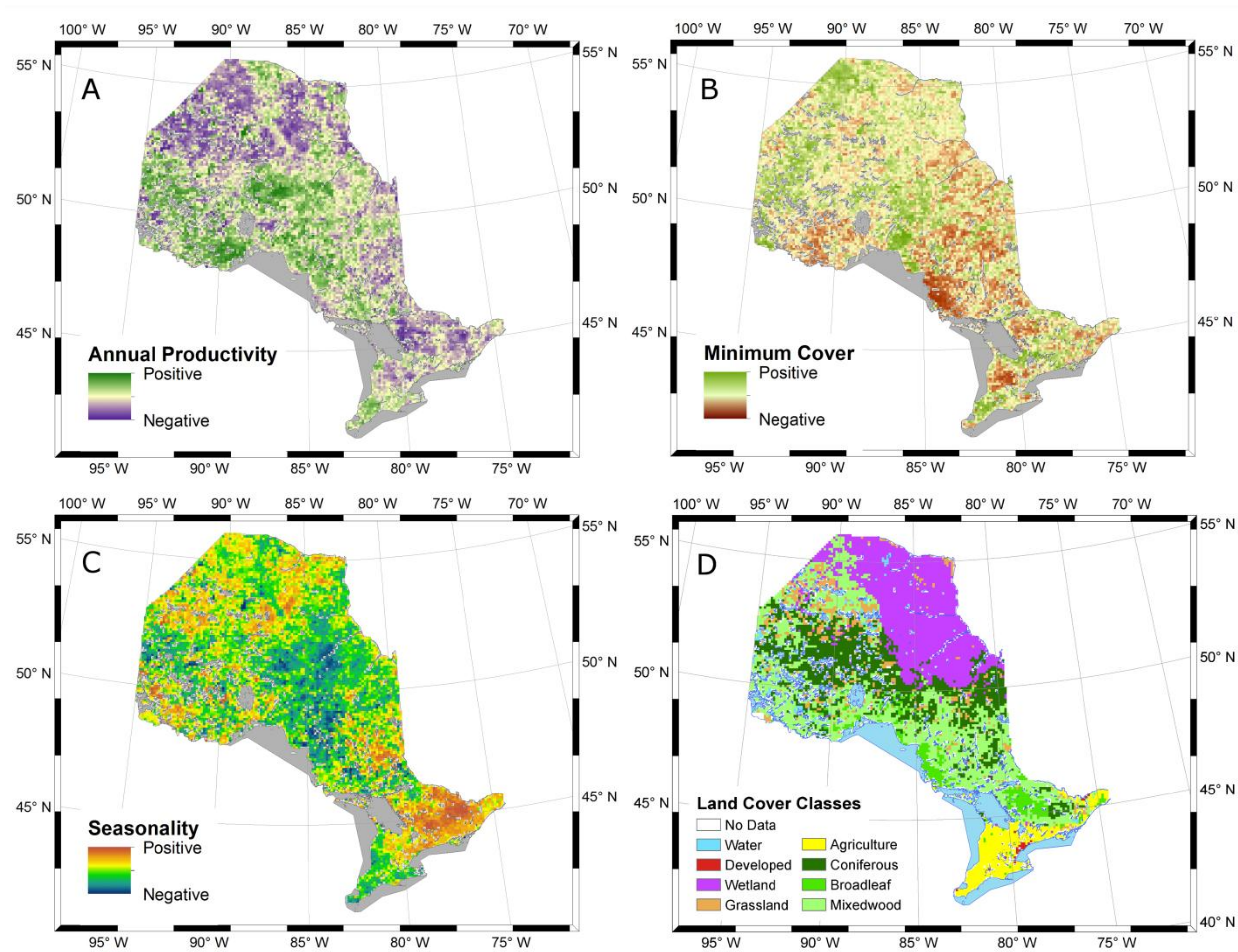



**Figure 3.2. Ontario overall observed Theil-Sen's trend recorded over the 2003-08 period for each of the individual component of the Dynamic Habitat Index (DHI): (A) Annual productivity, (B) Vegetative Cover, (C) Seasonality. Also shown is the EOSD land cover classification resampled to a 10 x 10 km grid (D).**

### 3.3.2 Overall observed trends by land cover

Trends were highly variable between land cover classes (ANOVA, $p<0.001$; Bonferroni post hoc $p < 0.05$) (Figure 3.3). Of the three DHI indicators, the trend variability by land cover type was least for DHI seasonality and greatest for annual productivity and minimum cover. Across all land cover types, grasslands on average had the strongest increasing trend for annual productivity and minimum cover as well as the steepest decreasing trend for seasonality. Broadleaf forest, in contrast, exhibited on average the largest decreasing trend for annual productivity and minimum cover.

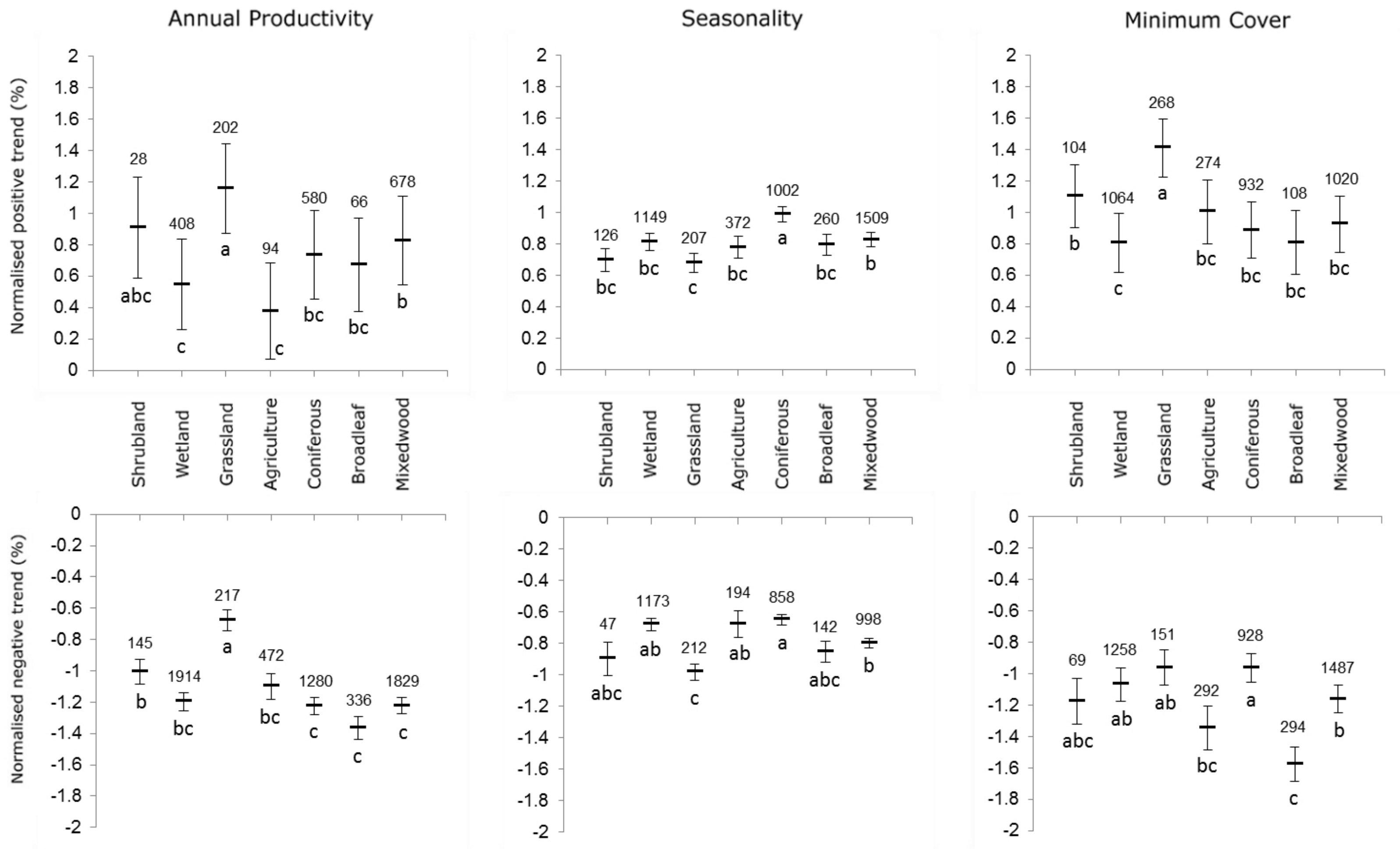



**Figure 3.3. Increasing and decreasing overall observed trend per land cover type. Whisker shows the standard error. Data labels above the whisker indicate the sample size (no. of pixels). The same letter on different classes designates non-significantly different means as informed by a Bonferroni post hoc ($p < 0.05$) test of the ANOVA. For example, for annual productivity, with positive trends (top left figure), shrubland (abc) is not significantly different than any other land cover types, whereas wetland (c) is significantly different to classes with an "a" or a "b" designation.**

### 3.3.3 Overall observed trends by environmental and anthropogenic drivers

Table 3.1 shows the slope of the regression line between the DHI component trends and the log-transformed distance from the nearest road, distance from nearest human settlement, elevation and their interactions. Again increasing and decreasing trend values were assessed for each DHI indicator and only absolute slopes significantly different from zero (p-value < 0.05) are displayed (Table 3.1). Results show significant relationships between the DHI trends and the three drivers, with elevation being the most significant driver for five out of six models. Regression analysis for the anthropogenic drivers indicated that average distance from roads had a negative slope with increasing seasonality and decreasing minimum cover. Average distance from human settlement exhibited a positive slope with decreasing annual productivity and negative with increasing seasonality. The interaction terms demonstrated some expected strong trends with distance to human settlement, and roads, interacting with elevation and positive trends in productivity. Less strong trends were found between the interaction of distance to roads and human settlement with decreasing trends in productivity. The distance to roads and human settlement interaction term was highly significant for decreasing minimum cover.

**Table 3.1. Slope of the regression line between the absolute trend values of the DHI components and the log-transformed average distance from the nearest road, distance from the nearest human settlement, average elevation and their interactions.**

| | Road dist. | | Human settlement dist. | | Elevation | |
|---|---|---|---|---|---|---|
| Annual Productivity + | NS | | NS | | 0.202 | *** |
| Annual Productivity - | NS | | 0.031 | * | -0.109 | * |
| Seasonality + | -0.237 | * | -0.023 | * | -0.024 | * |
| Seasonality - | NS | | NS | | 0.106 | *** |
| Minimum Cover + | NS | | NS | | NS | |
| Minimum Cover - | -0.055 | ** | NS | | 0.205 | ** |
| | **Road dist. x human settlement dist.** | | **Human settlement dist. x elevation** | | **Road dist. x elevation** | |
| Annual Productivity + | NS | | 0.015 | *** | 0.010 | *** |
| Annual Productivity - | 0.002 | * | NS | | NS | |
| Seasonality + | -0.002 | ** | NS | | NS | |
| Seasonality - | NS | | 0.005 | ** | NS | |
| Minimum Cover + | NS | | NS | | NS | |
| Minimum Cover - | -0.005 | *** | NS | | NS | |

***,** and ***, P<0.05, P<0.01, P<0.001, respectively indicate if the values are significantly different than zero.**
**NS, not significant.**

## 3.4 Notable trends

The second component of the analysis focused on those cells which observed a notable trend using the pre-defined, 20%, threshold. Figure 3.4 shows the areas with the largest 20% trend for each DHI component. In the case of annual productivity 89% of the notable area showed a decreasing trend occurring principally north of the 52nd parallel (Table 3.2). In the case of minimum cover, decreasing trends were observed principally in the central uplands and accounted for 63% of the notable trends in this component. In contrast, an increasing trend in seasonality was observed for 62% of the cells sparsely distributed around the 45th parallel.

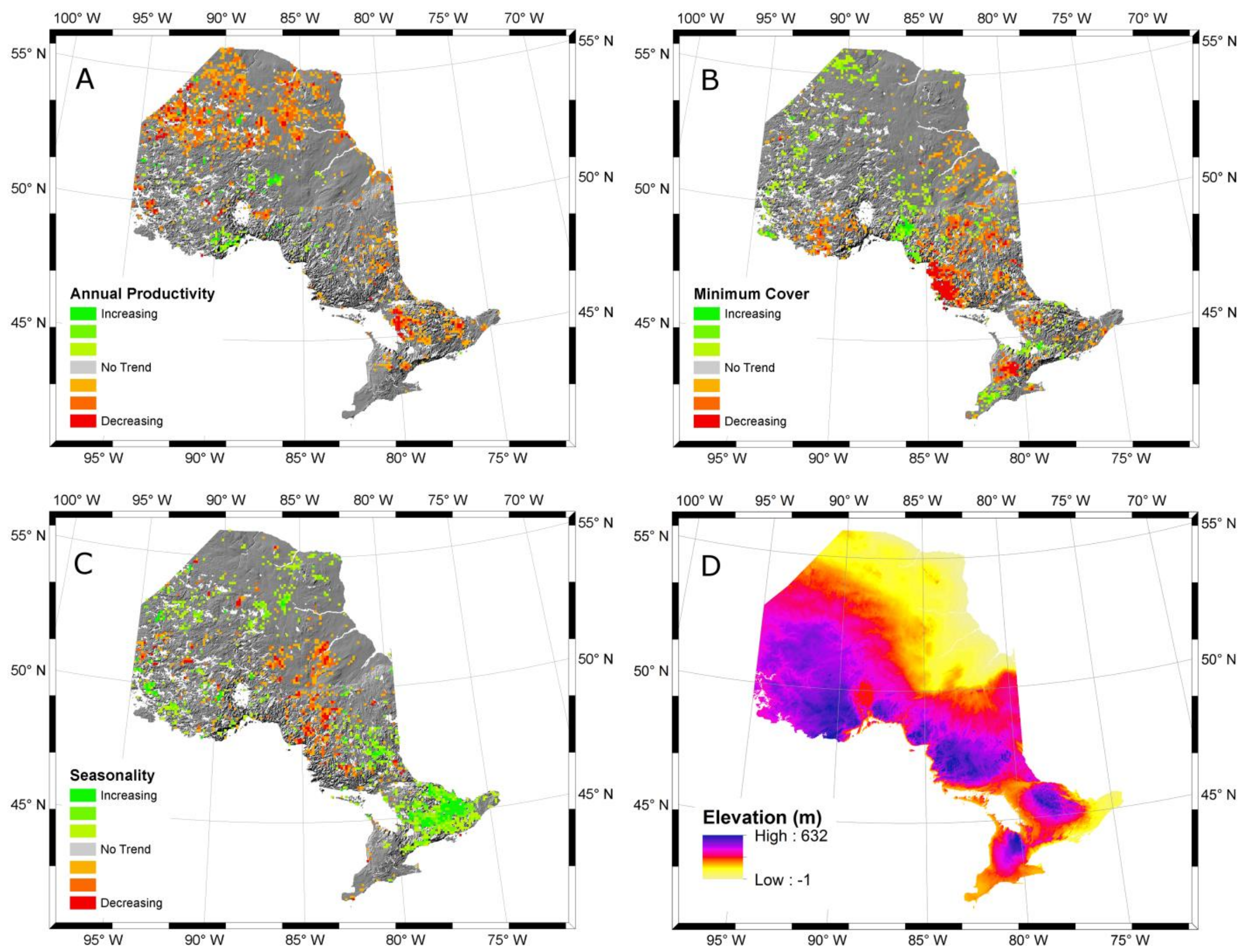



**Figure 3.4. Areas of notable trends, using the 20% threshold, from 2003-08 for each of the components of the Dynamic Habitat Index (DHI): (A) Annual productivity, (B) Vegetative Cover, (C) Seasonality. Also shown is the SRTM elevation map (D).**

Table 3.2. **Area in km2 for each DHI indicator with a notable trend, using the 20% threshold, over the province of Ontario.**

| Trend | Annual Productivity + | Annual Productivity - | Minimum cover + | Minimum cover - | Seasonality + | Seasonality - |
|---|---|---|---|---|---|---|
| Area in ($km^2$) | 19,100 | 150,400 | 62,900 | 106,600 | 105,900 | 63,600 |

Land cover had a significant effect on the observed trends occurrence according to the chi-square test ($X^2 = 1188.62$, df = 50, $p<0.001$), with a number of cells per cover type differing significantly from the expected proportion in the landscape (Figure 3.5).

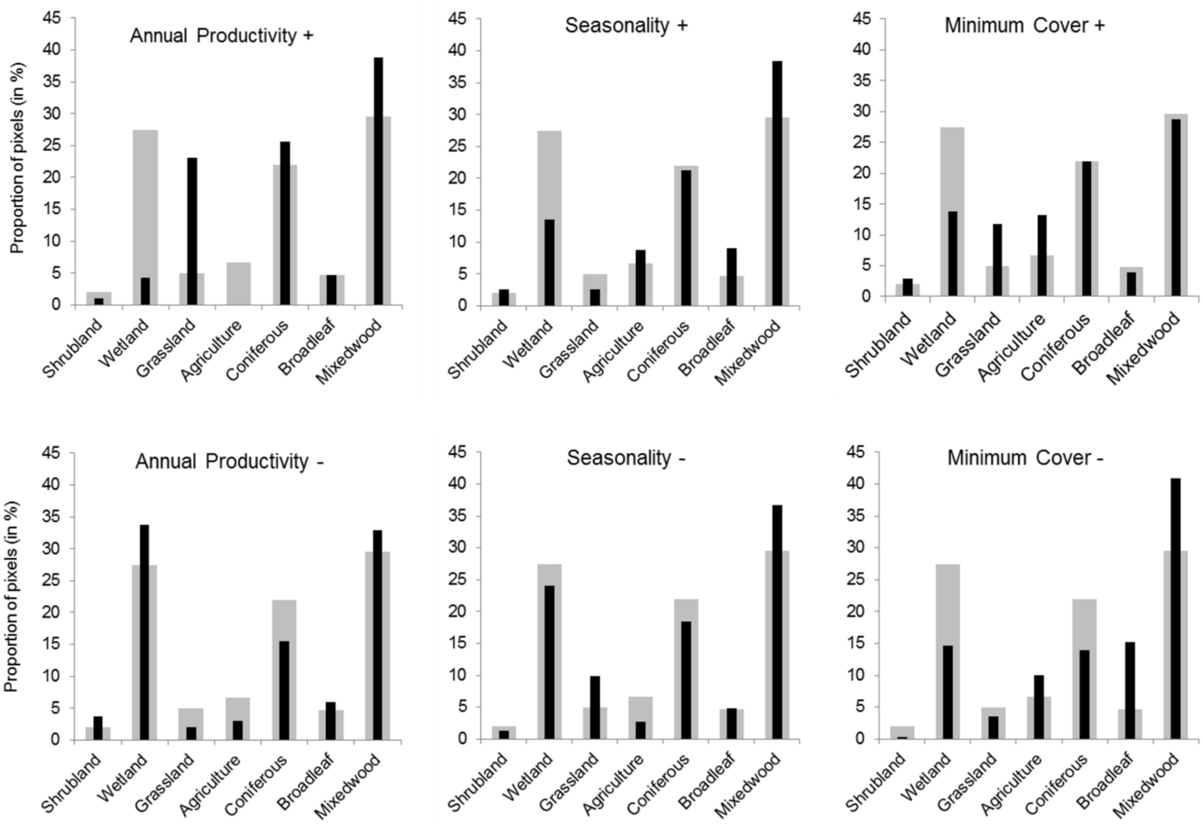



**Figure 3.5. Bar plots show the proportion of pixels by land cover types for each of the DHI component. Pixels observing a notable trend are shown in thin black bars and all pixels in wide grey bars ((+) positive trend; (-) negative trend).**

### 3.4.1 Notable trend by fire history classes

Figure 3.6 shows that across the three fire classes, trends varied by DHI indicator. A decreasing trend in annual productivity was observed for cells in the earliest fire class (1970-1986). Those 10 x 10 km cells experiencing fire from 1987 to 2003 exhibited an increasing trend in annual productivity (128% increase) and minimum cover (32% increase). Lastly, recent burned areas (2004-2008) exhibited a decreasing trend for annual productivity (42% increase) and minimum cover (60% increase).

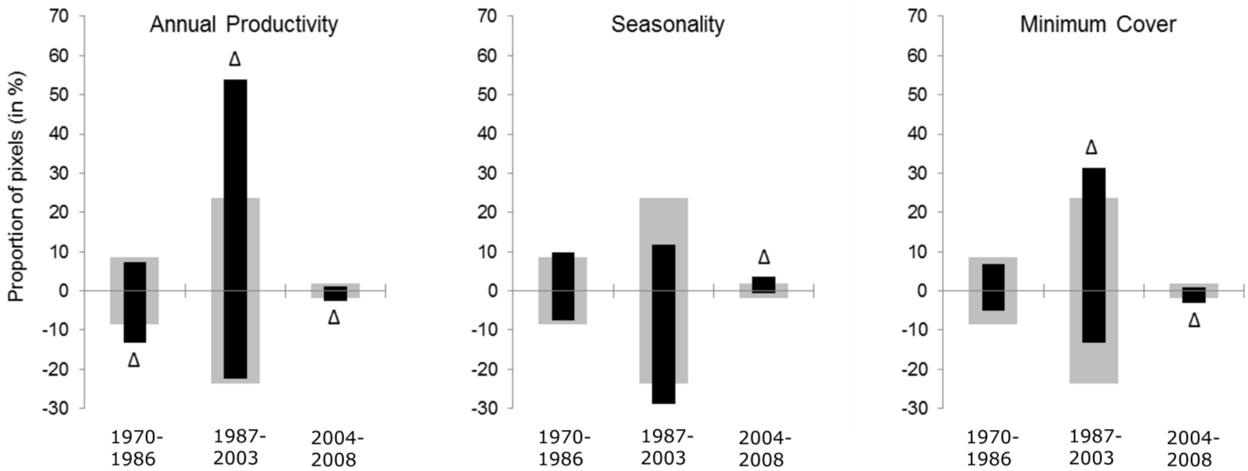



**Figure 3.6. Bar plots show the proportion of pixels by fire years for each DHI component. Pixels observing a notable trend are shown in thin black bars and all pixels in wide grey bars. *Delta* (Δ) indicates if the proportions of pixel are greater than 30% of what is observed in the overall landscape.**

## 3.5 Discussion

## 3.6 Overall observed trend

In this research, we applied a novel remote sensing method to detect trends in vegetation productivity using MERIS fPAR time-series data. Our results indicate that across Ontario there is an increasing trend in seasonality and a decreasing trend in both annual productivity and minimum cover over the 6-year period, which suggest an overall decrease in vegetation productivity that could be, in part, caused by a combination of the North Atlantic Oscillation (NAO) and El Niño/ Southern Oscillation (ENSO) (Hurrell and Deser 2009, Seager 2010). NAO is a source of interannual variability in atmospheric circulation and is determined by change in sea-level pressure over the North Atlantic (Hurrel 1995). ENSO describes the interaction of the ocean and atmosphere in the tropical Pacific and governs the air exchange between the eastern and western hemispheres at tropical and subtropical latitudes (Stenset et al. 2003) ENSO has been found to directly influence precipitation and temperature patterns in Canada (Ropelewski and Halpert 1986). A negative event recorded in 2007 for ENSO is likely to have lowered the temperature over winter (Shabbar and

Khandekar 1996) and may have contributed to the recorded decreasing trend in vegetation productivity.

In northern latitudes, direct anthropogenic pressure is unlikely to be a main driver of observed trends, especially in Hudson Bay ecozone, where the organic soil with poor drainage results in a lack of trees and valuable minerals, and subsequently lacks harvesting and mining activity (Baldwin et al., 2000). As a result, climatic factors are more likely to be driving these observed decreases in vegetation productivity. Climatic factors are also likely to be contributing to the negative trends detected in productivity in central uplands as discussed by Barber et al. (2000) who found that under recent climate warming, increases in temperature have restricted growth for a large portion of the North American boreal forest, due to drought stress. Conversely, we also detected positive productivity trends (i.e., increases in minimum cover and decreases in seasonality) north of Lake Superior, which have previously been recognized by NDVI time-series based on AVHRR in Canada (1985-2006) (Pouliot et al., 2009).

### 3.6.1 Land cover responses

Grassland patches, mostly located in the northwest boreal forests of Ontario, are mostly often associated with regenerating forest from old fire burns. These areas exhibit increasing trend in productivity and minimum cover and the decreasing trend in seasonality likely related to succession with reinvasion of woody plants following fire (Weber and Stocks, 1998).

In contrast, broadleaf forest followed by mixedwood forest land cover types, mainly located on the uplands following a SE-NW axis, observed the largest decreasing trend in annual productivity. Goetz et al. (2005) noted similar decreasing trends in photosynthetic activity across North America boreal forest between 1981-2003 and using a global circulation model, Bunn et al. (2005) predicted that this trend is likely to continue across this region until 2050. Summer droughts have also been recorded by Zhang et al. (2008) across most of the boreal forest region since the late-1990s and are likely to continue as the rate of warming also increases across Ontario's northern plains (Chapin III et al., 2005, Chapman and Walsh, 1993). Thus, our results correspond well with the observations of Zhang et al. (2008), Goetz et al. (2005) and predictions of Bunn et al. (2005) in that, despite the relatively short time period, significant decreasing trends in productivity were found for mixedwood and broadleaf forests.

### 3.6.2 Environmental and anthropogenic drivers

Elevation, average distance from roads and distance from human settlements show significant relationships with the DHI component trends. The most significant relationship was for elevation which was a significant driver for most of the three DHI indicators. In some situations elevation can be considered a surrogate to environmental conditions such as climate. However, this surrogate capacity may be distorted as climate in Ontario is principally driven by air sources which have a different impact on temperature and precipitation depending on the latitude, proximity to large water bodies, and to a lesser extent, topography (Baldwin et al., 2000). Thus, we believe that trends reported to be linked to the elevation gradient are, to some extent more likely to be land cover related. For example, most of the low elevation terrain that occurs in the Hudson Plains is dominated by wetlands which exhibits fewer trends when compared to other land cover types occurring in the uplands (i.e., broadleaf, mixedwood).

Of the anthropogenic indicators, cells closer to roads were predicted to observe an increase in seasonality and a decrease in minimum cover. Further distances to human settlements resulted in decreases in annual productivity. Conversely, cells closer from human settlements were predicted to observe increases in seasonality. As discussed by others, at broad spatial resolutions (1km or greater) forest harvesting and land clearing activities are difficult to capture due to smaller harvesting compartments, partial cuts, and selective harvesting management regimes all which minimise broad scale vegetation removal (Coops et al., 2009b, Fraser et al., 2005). As a result, relationships between the observed DHI trends and these anthropogenic drivers are limited at this spatial scale.

The interaction between elevation and the anthropogenic drivers observed for increasing annual productivity was highly significant confirming the observation that at higher elevations annual productivity increased over the time period. The distance to road interaction with distance to human settlement also exhibited high significance with decreasing minimum cover, suggesting that the variation in decreasing minimum cover with distance from road may be driven by variation in distance from human settlement along this same gradient.

### 3.6.3 Fire history classes

Overall, the pixels observing the highest 20% trend followed fire disturbance, as expected, with areas burnt from 1987 to 2003 exhibiting a higher proportion of increasing productivity cells, versus areas most recently burnt (2004-2008) showing a higher proportion of annual decreasing productivity based on their proportion in the landscape. The only exception was for areas burnt in the earliest fire class (1970-1986) which experienced a higher proportion of decreasing annual productivity trends than expected.

### 3.6.4 Practicality of the approach

Monitoring vegetation productivity using remote sensing time-series has been examined in numerous studies. The majority of the studies have utilised NDVI however recent studies have moved towards the use of physically based indices, such as fPAR (Donohue et al., 2009, Garbulsky et al., 2010, Potter et al., 2007, Paruelo et al., 2005, Zhao and Running, 2010). Based on fPAR metrics, the DHI has the potential to be used as an indicator of environmental changes as, in addition to providing physically based information on vegetation productivity, it can provide biological insights on species richness and abundance (Coops et al., 2008). When coupled with the non-parametric Theil-Sen's test, which is robust against non-normality of the distribution, missing values, and outliers (Theil, 1950), the DHI allows for both the detection of trends in natural variability as well as the magnitude of those trends. Such trend test has already been applied over similar temporal remote sensing datasets and has shown to be well suited to capture long-term environmental change (Alcaraz-Segura et al., 2009, Alcaraz-Segura et al., 2010a, Olthof and Pouliot, 2009).

Whereas previous work have mainly focused on trend validation using single datasets, (e.g., Fang et al. (2004) climate dataset, Alcaraz et al. (2006) land cover types, Alcaraz-Segura et al. (2010b) fire history), we found that a range of datasets provided additional insight on the underlying processes explaining the observed patterns for the studied time-series. In addition, the developed method presented in this paper is easily transferable to other datasets and has been applied to the long term historical AVHRR data over Canada (Fontana et al. (in review)).

## 3.7 Conclusions

The MERIS fPAR time-series, utilised in this study, provided metrics of photosynthetic activity over Ontario for a 6-year period. The aim of this study was to assess if indicators derived from the fPAR time-series allow the characterisation of broad scale vegetation condition across Ontario. Results indicate that time-series of fPAR, expressed as DHI indicators, are useful for effective assessment of the observed natural variability of vegetation, and highlighting areas which fall within, and beyond, the variability thresholds. The Theil-Sen's non-parametric statistical trend test provides valuable data to effectively track depletion and regrowth of vegetation which can aid in provincial or national monitoring activities and also can be used to focus more detailed analysis to local regions of specific interest. Trends in the DHI indicators imply that there is an overall decrease in vegetation productivity over the time period which aligns well with recent studies. We also found that the trend responses are likely to be specific to fire history, plant functional types and topography, which is a surrogate for natural vegetation productivity drivers.

We acknowledge the limits imposed by the length of the 6 year time-series for establishing the natural variability baseline, however we believe that the approach is suitable to remote sensing data and can be applied to longer term datasets as these become available. Continuing efforts to monitor vegetation change over time at a broad scale is critical for management of ecosystems, biodiversity, and monitoring climate change.

# 4. ESTIMATING MOOSE OCCURRENCE AND ABUNDANCE FROM SATELLITE-DERIVED INDICATORS

## 4.1 Introduction

Moose (*Alces alces*) are predominantly found in boreal forests globally, with their range principally limited by food and vegetation cover at the northern extreme (Kelsall and Telfer, 1974) and less suitable climate in the south (Renecker and Hudson, 1986). In recent years their distribution and density in North America has become increasingly variable (Karns, 2007). In Newfoundland, Canada, for example, moose are overabundant and have significantly altered plant composition (McLaren et al., 2004), whereas in southern Ontario the species is no longer present (Karns, 2007, Kelsall, 1987). In the case of southern Ontario, moose distribution has been negatively impacted by development and agricultural land clearing, whereas in the north the distribution has gradually expanded over thousands of years in response to postglacial dispersal (De Vos, 1964).

In 1980, the Government of Ontario developed a *Moose management policy* to ensure the preservation of the species and, as a result, moose populations increased throughout much of Ontario (Karns, 2007, McKenney et al., 1998) despite pressure from hunting, transportation, predation and disease. The key strategies of the current moose management policy (Ontario Ministry of Natural Resources, 1988, Ontario Ministry of Natural Resources, 2009) include maintaining suitable moose habitat, accommodating aboriginal harvesting and hunting, considering management objectives of other predator species (e.g., wolves, bears), limiting the influence of disease, and adapting management actions to mitigate climate change impacts. As a fundamental component of the management plan, the Ontario Ministry of Natural Resources (OMNR) annually undertakes extensive moose aerial surveys to understand population dynamics (McLaren, 2006). However, surveys of ungulate populations are expensive and, as a result, mapping and monitoring key habitat attributes and understanding how they vary through space and time have the potential to help manage the population.

Remote sensing, through its regular data acquisition, offers a data source uniquely suitable to monitor environmental conditions at a range of spatial and temporal scales in a cost effective manner. Satellite imagery has been utilised for more than three decades to monitor environmental conditions (Balmford et al., 2005, Goward et al., 1985). Indicators derived from satellite imagery have the potential to characterise species distributions and biodiversity patterns. For example, species diversity can be modelled using a suite of indirect remotely sensed indicators such as topography, land cover fragmentation, disturbance, and vegetation productivity (Duro et al., 2007). Estimates of vegetation production from satellite imagery include the Normalized Difference Vegetation Index (NDVI) and the fraction of Photosynthetically Active Radiation absorbed by vegetation (fPAR) (Baret and Guyot, 1991, Tucker, 1979). Unlike the NDVI, which is the normalised difference in the red and near infrared region, the fPAR algorithm is derived from a physically-based light propagation canopy algorithm which utilises multiple bands (up to 7) and is designed to minimise atmospheric, underlying soil and bi-directional reflectance effects (Knyazikhin et al., 1998, Myneni et al., 2002, Yang et al., 2006). Metrics from fPAR time-series have been used to derived a number of indicators which have been linked to species abundance and richness, such as avian species across different functional groups in the United States (Coops et al., 2009c), breeding birds throughout the province of Ontario (Coops et al., 2009b), and butterflies across Canada (Andrew et al., 2011).

In this chapter, we (1) examine the usefulness of remotely sensed indicators to characterise moose habitat throughout the Ontario moose range and (2) evaluate and test competing hypotheses of the relative importance of explanatory covariates for the prediction of moose occurrence and abundance.

### 4.1.1 Moose habitat relationships

Animals respond to a large number of limiting factors when selecting habitat, involving complex behavioral decisions made at multiple spatial scales (Johnson et al. 2001, Herfindal et al. 2009). Table 4.1 provides an overview of the range of covariates used to predict moose abundance and occurrence across its range. The table demonstrates that land cover is the most used covariate, which can be derived by remote sensing data or measured in the field. The most second commonly utilised covariate was information on landscape organisation, snow cover, terrain, fire/harvest and human impact which were used in six of the documented studies. In this study, we hypothesised that bottom-up drivers influencing food and reproduction may be more important at the distribution/occurrence level, whereas top-down limitations which govern survival, would influence habitat quality and restrict the abundance (Hunter and Price 1992). We considered the impacts of the limiting factors through a series of hypotheses based on current knowledge of moose-habitat relationships:

**Table 4.3. Covariates used in moose population model in various areas across the boreal forest.**

| Location | Vegetation productivity | Land cover / water | Landscape organisation | Snow | Terrain | Fire / harvest | Human impacts | Predation / hunting | Reference |
|---|---|---|---|---|---|---|---|---|---|
| South-central Alaska | | ■ | | ■ | ■ | | | ■ | Ballard et al., 1991 |
| Ontario | | ■ | | ■ | | | ■ | ■ | Brown 2011 |
| Northwest Québec | | ■ | ■ | | | ■ | | | Courtois et al., 2002 |
| Sweden | | ■ | | | ■ | | ■ | | Dettki et al., 2003 |
| South-central Québec | | ■ | ■ | ■ | | | | ■ | Dussault et al., 2005, 2006b |
| British Columbia | ■ | ■ | | | ■ | | | ■ | Gillingham and Parker 2008 |
| South-central Ontario | | ■ | ■ | | | ■ | | | Hamilton et al., 1980 |
| Norway | | ■ | | | | | | | Herfindal et al., 2009 |
| Northeastern China | ■ | ■ | ■ | | ■ | ■ | ■ | | Jiang et al., 2009 |
| Eastern Ontario | | ■ | | | | | | | Kearny and Gilbert 1976 |
| Central Ontario | | ■ | | ■ | ■ | | ■ | ■ | Kittle et al., 2008 |
| Alaska | | ■ | ■ | | ■ | ■ | ■ | | Maier et al., 2005 |
| South-central Norway | ■ | ■ | ■ | ■ | | | | | Månsson et al., 2007, 2009 |
| Central-west Finland | | ■ | | | | | ■ | | Nikula et al., 2004 |
| Northeastern Alberta | | ■ | | | | ■ | | | Osko et al., 2004 |
| Northeast Minnesota | | ■ | | | | | | | Peek et al., 1976 |
| Algonquin Park, Ontario | | ■ | | ■ | | | | | Puttock et al., 1996 |
| Western Ontario | | ■ | | | | ■ | | | Rempel et al., 1997 |
| Nova Scotia | | ■ | | | | | | | Snaith et al., 2002 |

*Food availability hypothesis*.

Moose distribution and fitness, as with other large herbivores, varies as a function of bottom-up drivers such as food quality, diversity and availability (Johnson et al. 2001, Maier et al. 2005, Månsson et al. 2007). Close proximity to high quality forage greatly impacts herbivores as it decreases the energy required for foraging and digestion, thus maximising energy intake (White 1983). At broad scales, it is hypothesised that absolute consumption will be proportional to forage availability (Senft et al. 1987) and that the site productivity will positively drive habitat selection (Månsson et al. 2007). Alternatively, high quality forage generally offers limited thermal, snow (Puttock et al. 1996) and predation protection (Dussault et al. 2005), often constraining moose to select habitats that provide both access to quality forage and shelter from these limiting environmental and predator factors (Courtois et al. 2002, Dussault et al. 2006a). In addition, moose require access to fresh water for thermoregulation and aquatic forage during summer (Maier et al. 2005).

*Protection hypothesis*

Habitat also provides cover which protects moose from heat stress when ambient temperature exceeds optimal levels (Schwab and Pitt 1991). As winter progresses, dense coniferous cover becomes a key refuge against substantial snow depth which restricts moose movement and access to forage (Thompson and Steward 2007). Conifers also provide protection from top-down limitations such as predation from timber wolves (*Canis lupus*), eastern wolves (*Canis lycaon*) and black bears (*Ursus americanus*), which are the principal predators of moose in Ontario (Bergerud et al. 1983). Wolf predation impacts all age classes of moose year-round, whereas bears only hunt calves for a short period of the summer (Ballard et al. 1991). The spatial pattern between stands which provide forage and protection, known as the cover-food edge, is critical for moose habitat selection (Courtois et al. 2002, Dussault et al. 2005, Dussault et al. 2006b). Moose also prefer habitat closer to human infrastructure when predation risk is high as carnivores generally avoid human contact (Kaartinen et al. 2005). For example, Berger (2007) found that moose birth sites shifted towards roads when predation risk from bears was present. As a result, we hypothesised that moose will select habitat with intermediate level of coniferous cover, high proportion of cover-food edge, and close proximity to anthropogenic features.

*Snow impediment hypothesis.*

At broad scales, moose avoid predation by selecting areas with greater snowfall as they are morphologically better adapted than wolves to increased snow depth (Telfer and Kelsall 1984).

However, long and severe winters can result in increased snow accumulation, and adversely impact moose mobility and food intake, as well as impact moose fecundity, fetal development and weight, and survival of offspring (Mech et al. 1987, Cederlund et al. 1991, Post and Stenseth 1998). Therefore, it is expected that for areas with high predation risk by wolves, moose will favor habitats with intermediate snow cover.

*Disturbance hypothesis.*

Fire is the major natural disturbance in the boreal forest (Johnson 1996) and, combined with harvesting, insect defoliation, and weather events, contributes to habitat heterogeneity. The selection by moose of recently disturbed, early successional stage forest stands is widely documented (Allen et al. 1987, Peek 2007). We expect that as shrub communities develop (e.g., after fire disturbance), prime forage becomes available year-round, thus increasing populations (Rempel et al. 1997). In contrast to the protection hypothesis, some studies have shown that human disturbance, indicated by the proximity of human infrastructure (i.e., distance to nearest road and human settlement), disrupts moose through the creation of barriers, habitat loss or fragmentation, noise, and direct mortality (Nikula et al. 2004, Laurian et al. 2008).

*Land cover variability hypothesis.*

An extensive study conducted by Peek et al. (1976) showed that habitat-use patterns change seasonally. In early summer, moose select areas of aquatic forage and more open stands with younger trees. As summer progresses, more densely populated stands with mature trees are favoured. Similarly, in early winter, open stands are preferred, but as winter progresses, moose move towards closed, dense, coniferous canopies (Peek 2007). Thus, considering the year-round moose habitat requirements, it is expected that higher diversity of land cover types represent the best habitat for moose.

## 4.2 Methods

### 4.2.1 Study site

For a complete study area description, please consult section 3.1. For this chapter, the area of interest corresponds to the mixed and boreal forest of central Ontario and extends from approximately 45°N to 52°N and from 76°W to 95°W, over 580 000 km$^2$ in size. This area is where moose population data was collected by the OMNR within defined wildlife management units (WMU) where moose density is known to be greater than 0.007 moose/km$^2$ (McLaren, 2006).

### 4.2.2 Moose aerial survey

The OMNR conducts moose aerial inventories within the WMUs to estimate the population size, trends and the moose population age and sex composition (McLaren, 2006). The inventory follows a stratified random sampling design with sample plot stratification based on existing knowledge of moose density. A range of variables were measured by the moose aerial inventory, but we solely used the number of moose recorded per plot. Each population survey plots is 2.5 x 10 km with 5,040 plots surveyed by helicopter from December to early February over 11 years (2000-2010) (Oswald, 1997). In this study, we restricted use of the moose aerial survey data to a subset that match the time frame of the environmental covariates used for habitat prediction, i.e., 2004-2007, totalling 1873 plots.

### 4.2.3 Explanatory covariates

In order to summarise the information from the suite of selected environmental covariates (Table 4.2, Figure 4.1) and from the aerial moose survey, we overlaid a continuous coverage of 4,269 non-overlapping 100 $km^2$ hexagons, covering the study area. These analysis units are similar in size to the 93$km^2$ evaluation units used in both Peek et al. (1976) and Allen et al. (1987). Moose home range is variable seasonally, however, south of 60 degrees, sizes of annual home range remain relatively stable and do not exceed 50$km^2$ (Hundertmark 2007). In addition, features far outside of the home range can also influence habitat selection of large herbivores (Kie et al. 2002). The hexagons, which are 12.41 km wide, were utilised for training and validating the competing hypotheses (Table 4.3) as well as for predicting moose occurrence and abundance.

#### *4.2.3.1 Snow*

Remote sensing estimates of snow cover fraction were collected according to specifications in section 2.2.4. Average fractional monthly snow cover was retrieved for each hexagon sample unit from September to June. These values were then averaged over the three winters prior to the moose survey at that location to provide a generalised representation of the potential influence of snow cover on moose habitat suitability. Snow accumulation of the three previous winters has been related to various moose population characteristics such as the calf/cow ratio, the percentage of

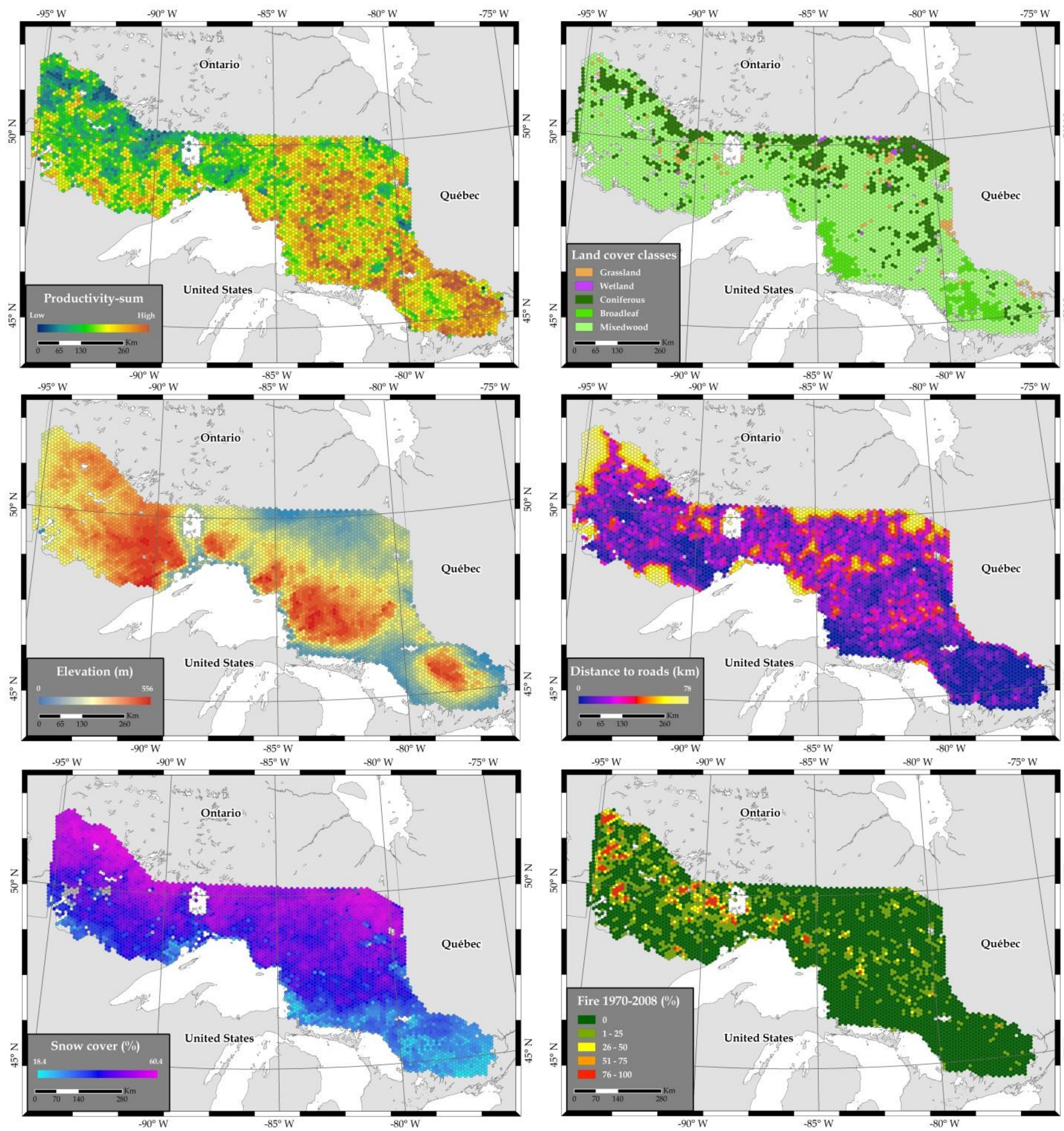



**Figure 4.1. Covariates over the hexagon evaluation units, from top left to bottom right: average productivity-sum, dominant land cover type, average elevation, average distance to nearest road, average snow cover (2000-2010), fire history (1970-2008).**

**Table 4.2. Covariates used to estimate moose occurrence and abundance across the Ontario moose range**

| Covariate group | Covariate name | Description | Res. (km) | Units | Data range |
|---|---|---|---|---|---|
| Landcover | | | | | |
| | Grass-Shrub | % Cover of shrubland, grassland, herbs and any sparse forest | 0.1 | Percent | 0-1 |
| | Mixed | % Dense or open mixedwood canopy cover | 0.1 | Percent | 0-1 |
| | Broad | % Dense or open broadleaf canopy cover | 0.1 | Percent | 0-1 |
| | Wetland | % Cover of wetland | 0.1 | Percent | 0-1 |
| | Coniferous | % Coniferous canopy cover | 0.1 | Percent | 0-1 |
| | LC-Diversity | Shannon Diversity index of land cover types | 0.1 | Unitless | 0.33-1.81 |
| | Btw-Edge | Average density of between-stands cover-food edge | 0.1 | Unitless | 0-0.45 |
| | Dist-Water | Average distance from water features | 0.1 | km | 0.25-8.3 |
| Terrain | | | | | |
| | Elevation | Elevation average | 0.1 | m | 69-556 |
| Disturbance | | | | | |
| | Fire-X_Y | % survey unit impacted by fire from X-Y years prior to survey (which include 0-10, 10-20, 20-30 and 0-30) | 1 | Percent | 0-100 |
| | Depletion-T1_4 | % survey unit impacted by disturbances (harvesting, fire, natural depletion (e.g., blow down, insect)) four years prior to survey | 1 | Percent | 0-44 |
| | Dist-Road | Average distance from nearest road | 0.1 | km | 0-78 |
| | Dist-Urban | Average distance from nearest human settlement | 0.1 | km | 0-121 |
| Productivity | | | | | |
| | Sum-T1 | Annual productivity of year prior to survey over Grass-Shrub, Mixed and Broad | 1 | fPAR | 401.63-678.69 |
| | Sum-Av | Annual productivity average over Grass-Shrub, Mixed and Broad | 1 | fPAR | 403.84-647.26 |
| | Seas-STD-T1 | Seasonality standard deviation of one year prior to survey | 1 | fPAR | 0.07-10.23 |
| | Seas-STD-Av | Seasonality standard deviation average | 1 | fPAR | 0.41-8.58 |
| | Seas-T1_4 | Seasonality sum of four years prior to survey | 1 | fPAR | 2.50-67.33 |
| | Min-T1 | Minimum cover of year prior to survey | 1 | fPAR | 1.95-68.44 |
| Climate | | | | | |
| | SnowCover | Average monthly % snow cover of three years prior to survey | ~4.0 | Scaled Percent | 3.07-6.60 |

moose twins and the percentage of change in moose populations (McRoberts et al., 1995, Mech et al., 1987).

#### *4.2.3.2 Land cover*

Land cover data was extracted from the EOSD product which is detailed in section 2.2.2. Land cover is recognised as a useful means of characterising moose habitat (Allen et al., 1987, Dussault et al., 2006b). Two components were considered for this chapter, the percentage of land cover types providing substantial forage (i.e., grassland, shrubland, wetland, deciduous and sparse forests) and the percentage of land cover types providing protection (i.e., dense and open coniferous) within the hexagon sample unit (Allen et al., 1987). Each land cover type was rendered as the proportion of the area covered compared to the total available land area within each hexagon. As moose are known to trade-off between forage and protection availability, I computed a cover-food edge index which was calculated as the area of land cover suitable for forage within 200 m of land cover suitable for protection. A distance of 200 m was selected based on studies which indicated that moose avoid foraging in large open areas exceeding 80 - 200m from protection (Hamilton et al., 1980, Tomm et al., 1981). Once calculated, the edge index was summed and compared to the total land area within each hexagon. I also calculated a metric of simple land cover diversity based on the Shannon Diversity index (Shannon, 2001) within each hexagon.

#### *4.2.3.3 Dynamic Habitat Index*

The MODIS sensor provided the fPAR layers according to specifications outlined in section 2.2.1. For this study, the annual productivity was calculated exclusively over the forage land cover types as a surrogate for forage quality and availability. Minimum cover refers to the lowest (minimum value) level of vegetative cover through the snow-free period and is an indicator of the landscape's capacity to sustain appropriate levels of protection cover (Schwartz et al., 2006). Seasonal variation in productivity, i.e., seasonality, accounts for annual changes in vegetation productivity and has been shown to be indicative of the underlying phenological characteristics of the site. Within each hexagon, we calculated the standard deviation of the coefficient of variation to obtain insights on the spatial variability of the different seasonal vegetation productivity regimes.

The vegetation productivity indicators were calculated using fPAR data acquired from March to October to avoid fPAR values influenced by low sun angle, clouds, and snow cover, which can bias the responses. By excluding winter months yet including March, April, September and October we reduced biases but still captured the transition of the landscape from the dormant to the active state. The annual productivity and the standard deviation of seasonality were averaged over the 7 years period (2000-2006) to characterise the general vegetation productivity rate and spatial variability, respectively. Seasonality of the four years prior to each survey date provides insight into recent variability in vegetation productivity. In order to assess the previous year's productivity we included the annual productivity, minimum cover, and standard deviation of seasonality for the year before each moose record. All the pixel level productivity information was averaged to the hexagon sample unit for analysis.

#### *4.2.3.4 Disturbances*

The CFS Large Fire Database (LFDB) coupled to the national burned forests maps prepared by the CFS and CCRS were used in this chapter. For complete details on the fire history data acquisition, consult section 2.2.5. Additional information on natural and anthropogenic disturbances across Ontario was also provided by the OMNR. This layer contains information on timber harvesting, insect defoliation, blow down and fire from 2000-2007. The area burnt was accumulated for all fires occurring in the past 30 years as these have been shown to influence moose density (Allen et al., 1987, Peek, 2007) and divided into 10 year increments. All other disturbances were averaged over the prior four years due to the limited records in the OMNR database.

#### *4.2.3.5 Distance to features*

To account for human influence on moose populations, we estimated the nearest Euclidean distance to roads and from human settlement as detailed in section 2.2.6. Additionally, Euclidean distance to the nearest water feature (i.e., lake, river, wetland) was calculated from the EOSD land cover product. Distances to features were averaged over the hexagon sample unit for analysis.

#### *4.2.3.6 Elevation*

The elevation provided by the Shuttle Radar Topography Mission (SRTM) was averaged by hexagon sample unit for this analysis. For further details on the dataset, the reader should consult section 2.2.3.

### 4.2.4 Hypothesis composition

We utilised a range of environmental covariates (Table 4.2) to determine whether moose habitat selection responded to the mechanisms detailed in the five candidate hypotheses (Table 4.3). While some covariates can be found in more than one model, we omitted covariates from the analysis that

**Table 4.3. A priori candidate models used for moose occurrence and abundance modeling. Model name, structure and total parameters (K) including constant are provided. Covariates are described in Table 4.2.**

| Model name | Model structure | K |
|---|---|---|
| Snow impediment | SnowPres-T1_3 + SnowPres-T1_3$^2$ + Elevation + Min-T1 | 5 |
| Food availability | Grass-Shrub + Grass-Shrub$^2$ + Mixed + Mixed$^2$ + Broad + Broad$^2$ + Wetland + Wetland$^2$ + Sum-T1 + Sum-Av + Dist-Water | 12 |
| Protection | Coniferous + Coniferous$^2$ + Mixed + Mixed$^2$ + Btw-Edge + Min-T1 + Dist-Road + Dist-Road$^2$ + Dist-Urban + Dist-Urban$^2$ | 11 |
| Disturbance | Fire-0_10 + Fire-10_20 + Fire-20_30 + Fire-0_30 + Fire-0_30$^2$ + Depletion-T1_4 + Depletion-T1_4$^2$ + Dist-Road + Dist-Road$^2$ + Dist-Urban + Dist-Urban$^2$ | 12 |
| Habitat diversity | LC-Diversity + Elevation + Seas-T1_4 + Seas-T1_4$^2$ + Seas-STD-Av + Seas-STD-T1 + Dist-Water | 8 |

*Quadratic terms have been applied to covariates with "$^2$"

had a Pearson correlation coefficient greater than 0.70. Quadratic terms were computed for covariates where a non-linear relationship was expected. The rationale for the selected covariates for each hypothesis is provided below:

- *Food availability*: Land cover types with suitable forage for moose included grassland-shrubland, mixedwood, broadleaf, and wetland. Annual productivity of these land cover types, minimum cover, and proximity to fresh water were also included as covariates.
- *Protection:* Land cover types with effective protection, i.e., coniferous and mixedwood, and the cover-food edge index, distances to nearest road and human settlement, and minimum cover provided covariates for the protection hypothesis.
- *Snow impediment:* Average fractional snow cover, elevation and the minimum cover provided indication of snow impediment.
- *Disturbance:* We included both the total burned area over 30 years as well as in 10 year increments, the distances to nearest road and human settlement, and the cumulative four year OMNR disturbance layer as indicators of disturbances.
- *Land cover variability:* Spatial layers of land cover diversity, elevation, distance to water, and seasonality provided indicators of land cover variability.

### 4.2.5 Model fitting and selection

Three sets of models were developed to predict moose habitat suitability. We developed suites of models for moose occurrence (presence or absence) and for moose abundance. These two sets of models were used for hypothesis testing and for selecting covariates. Assuming success of the two models we then developed a final model that combined the two models to predict both the presence/absence and abundance of moose within a single model framework.

First, we applied logistic regression to develop a suite of models to predict moose presence and absence for each of the five hypotheses (n = 1873; Table 4.3). The best subset of covariates within each model was assessed using the corrected Akaike information criterion ($AIC_c$). Models with the lowest $\Delta AIC_c$ were considered the most parsimonious. In situations where the lowest AIC models had a $\Delta AIC_c < 2$ then we selected the model with the fewest parameters (Burnham and Anderson, 2002). Based on the resulting modelled predictions, (ranging from 0-1), we categorise whether moose was present in a hexagon unit following a similar approach as Meynard and Quinn (2007). We drew random numbers from a uniform distribution for each unit and if the random number was smaller than the modeled probability of occurrence for that unit, moose was considered to be present.

Second, truncated negative binomial regression was used to model the abundance of moose at locations where moose were present (n=1549) for each of the five competing models (hypotheses) in Table 4.3. The best subset of covariates within each model was assessed following a similar $AIC_c$ approach as for the presence/absence models.
Once the best model for each hypothesis was selected we followed a similar stepwise AICc approach to assess the best overall combination of hypotheses. The best overall occurrence and abundance models were then assessed with a confusion matrix and Pearson's coefficient of correlation, respectively.

Lastly, as a large number of zero counts occurred within the moose dataset, we undertook a Vuong test (Vuong, 1989) to assess if a zero-inflated model response was likely. If confirmed we then computed a two-step Hurdle model which accounts for large numbers of zeros by first predicting the probability of occurrence with a zero count model and if the prediction is positive, proceeds to predict the abundance with a truncated count component. Hurdle models are an alternative class of mixture models commonly used in econometrics (Cameron and Trivedi, 1998) and gaining popularity in other fields such as ecology (Cazau et al., 2011, Stark et al., 2009). The main difference between hurdle and mixed-models is that the zero and non-zero counts are separated (Loeys et al., 2011), allowing for investigation of mechanisms influencing occurrence and abundance separately.

All models were developed using cross-validation by randomly dividing the dataset in a model development subset for training (2/3) with the reminder for validation (1/3). All model selections and analyses were performed using the MuMIn (Barton, 2011), MASS (Venables and Ripley, 2002) and pscl (Zeileis et al., 2008) packages, in the R programming environment (R Development Core Team, 2010).

## 4.3 Results

### 4.3.1 Occurrence model

The protection hypothesis received the highest relative probability of being the best hypothesis explaining moose occurrence with an Akaike weight close to 1 (Table 4.4). All the other hypotheses had relatively lower levels of support. Following the stepwise AICc approach on the combination of all hypotheses, the habitat diversity as well as disturbance and protection hypotheses were selected (Table 4.5). The best model contained seven covariates and predicted presence of moose in 81.6% of the plots compared to an observed presence of 83.7% from the aerial survey. A confusion matrix using the validation dataset confirmed a true positive rate of 82.8% (proportion of plots correctly identified as presence), a true negative rate of 25.0% (proportion of plots correctly identified as absence) and an overall accuracy of the model of 73.44% (Table 4.6).

### 4.3.2 Abundance model

The abundance model revealed that snow impediment was the best single hypothesis (Table 4.4), with the second best model being food availability. The overall abundance model included four of the five hypotheses, with all except the protection hypothesis providing statistically significant improvement of the model fit (Table 4.5). Different hypotheses were selected when compared to the occurrence model, suggesting that the mechanisms influencing abundance differed from those driving occurrence. The combined abundance model fitted to the validation data contained 12 covariates and yield a Pearson's coefficient of correlation of 0.15.

### 4.3.3 Hurdle model

As the Vuong test confirmed the dataset had a zero-inflated model response, we utilised a hurdle negative binomial (Hurdle-NB) model. Surprisingly, many of the variables that were found to be important correlates of moose occurrence in the logistic regression models testing our mechanistic hypotheses did not make significant contributions to predicting moose occurrence in the hurdle model. The logistic portion of the combined Hurdle-NB model indicated that only two of the original covariates were statistically significant. A non-linear relationship was demonstrated for conifer, with the quadratic term of percentage of coniferous cover (Coniferous$^2$) and the percentage of coniferous cover (Coniferous) positively and negatively related to moose occurrence, respectively.

The negative binomial portion of the model indicated that four hypotheses were involved in predicting abundance (snow impediment, food availability, disturbance, and habitat diversity), with 8 significant covariates. The most significant covariates were from the food availability hypothesis: percentage of grassland/shrubland (Grass-Shrub), mixedwood (Mixed), and broadleaf (Broad) all displayed a positive coefficient, and annual productivity average (Sum-Av) a negative coefficient. The snow impediment hypothesis included the minimum cover of the year prior to the survey (Min-T1) which exhibited a significant negative coefficient. The disturbance hypothesis showed positive and negative relationships for the linear and the quadratic terms of average distance to the nearest road (Dist-Road, Dist-Road$^2$) respectively. The habitat diversity hypothesis exhibited a positive relationship for average elevation (Elevation).

Predicted values of moose abundance calculated from the final hurdle model over the period of 2004-2007 varied spatially across the province, reflecting a wide variation in snow cover, food and protection availability, and disturbance regime (Figure 4.2). Occurrence of moose was predicted throughout much of Ontario, with higher occurrence in central Ontario (Figure 4.3). When we compared the predictions to the observed moose data for the 2004-2007 period, we found a strong agreement across the province with a slight divergence in the southeast part of Ontario. Abundance was predicted to be high in central Ontario whereas lower densities occurred in the southeast (Figure 4.4). This lower abundance was ubiquitous in the southeast except for the region of Algonquian Park where a cluster of high abundance was predicted. This local discrepancy may be driven by reduced productivity-sum, reduced proportion of coniferous cover, and higher elevations here relative to the rest of the southeast (Figure 4.1).

**Table 4.4. Results from logistic regression (occurrence) and truncated negative binomial regression (abundance) model selection for each *a priori* candidate model. Covariates are described in Table 4.2. Hypotheses in grey shading indicate the most parsimonious hypothesis for occurrence and abundance, respectively. ΔAICc indicates the delta Akaike Information Criterion corrected for small sample sizes; w, Akaike weight; K, total number of parameters including constant; Accuracy, overall accuracy from a confusion matrix; r, Pearson coefficient of correlation.**

| **Occurrence** | | | | | | |
|---|---|---|---|---|---|---|
| Hypothesis | Covariates | AICc | ΔAICc | w | K | Accuracy |
| Snow impediment | SnowCover + $SnowCover^2$ | 1019.227 | 41.437 | < 0.001 | 3 | 73.17% |
| Food availability | Grass-Shrub + $Grass\text{-}Shrub^2$ + Mixed + $Mixed^2$ + Sum-T1 + Sum-Av | 1004.131 | 26.341 | < 0.001 | 7 | 75.07% |
| Protection | Coniferous + $Coniferous^2$ + Dist-Urban + $Dist\text{-}Urban^2$ | 977.791 | 0.000 | 1.000 | 5 | 75.07% |
| Disturbance | Fire-0_10 + Fire-10_20 + Dist-Urban + $Dist\text{-}Urban^2$ | 997.964 | 20.173 | < 0.001 | 5 | 74.25% |
| Habitat diversity | Elevation | 1001.654 | 23.863 | < 0.001 | 2 | 73.44% |
| **Abundance** | Covariates | AICc | ΔAICc | w | K | r |
| Snow impediment | SnowCover + Min-T1 | 5609.029 | 0.000 | 0.983 | 3 | 0.112 |
| Food availability | Grass-Shrub + Mixed + Broad + Sum-Av | 5617.268 | 8.239 | 0.016 | 5 | 0.172 |
| Protection | Coniferous + Min-T1 + D-Road + $D\text{-}Road^2$ | 5622.219 | 13.189 | 0.001 | 5 | 0.121 |
| Disturbance | Fire-0_10 + Fire-0_30 + $Fire\text{-}0\_30^2$ + Dist-Road+ $Dist\text{-}Road^2$ | 5642.561 | 33.532 | < 0.001 | 6 | 0.058 |
| Habitat diversity | Elevation | 5638.755 | 29.725 | < 0.001 | 2 | 0.116 |

**Table 4.5. Results from logistic regression (occurrence) and truncated negative binomial regression (abundance) model selection of combinations of candidate hypotheses (Table 4.4). Hypotheses in grey shading indicate the most parsimonious hypothesis for occurrence and abundance, respectively.; ΔAICc indicates the delta Akaike Information Criterion corrected for small sample sizes; w, Akaike weight; K, total number of parameters including constant; Accuracy, overall accuracy from a confusion matrix; r, Pearson coefficient of correlation.**

| **Occurrence** | | | | | |
|---|---|---|---|---|---|
| Hypotheses | AICc | ΔAICc | w | K | Accuracy |
| Food availability + Habitat diversity + Snow impediment + Disturbance + Cover protection | 956.785 | 0.000 | 0.430 | 16 | 71.82% |
| Food availability + Habitat diversity + Disturbance + Cover protection | 958.000 | 1.215 | 0.234 | 14 | 76.96% |
| Habitat diversity + Disturbance + Protection | 957.719 | 0.934 | 0.270 | 8 | 73.44% |
| Habitat diversity + Snow impediment + Disturbance + Cover protection | 961.330 | 4.545 | 0.044 | 10 | 72.63% |
| Food availability + Habitat diversity + Snow impediment + Cover protection | 962.823 | 6.038 | 0.021 | 14 | 75.34% |
| **Abundance** | AICc | ΔAICc | w | K | r |
| Food availability + Habitat diversity + Snow impediment + Disturbance | 5574.141 | 0.000 | 0.663 | 13 | 0.151 |
| Food availability + Habitat diversity + Snow impediment + Disturbance + Cover protection | 5575.893 | 1.752 | 0.237 | 14 | 0.113 |
| Habitat diversity + Snow impediment + Disturbance + Cover protection | 5577.161 | 3.020 | 0.088 | 10 | 0.169 |
| Habitat diversity + Snow impediment + Cover protection | 5583.025 | 8.884 | 0.008 | 7 | 0.155 |
| Food availability + Habitat diversity + Snow impediment + Cover protection | 5582.369 | 8.228 | 0.003 | 11 | 0.169 |

**Table 4.6. Confusion matrix and measurements of accuracy (overall accuracy = 73.44%) of the best logistic regression (occurrence) model (Table 4.5) including habitat diversity, disturbance and protection hypotheses (Table 4.4).**

| | Observed absence | Observed presence | Total |
|---|---|---|---|
| Predicted absence | 15 (4.1%) | 53 (14.4%) | 62 (18.4%) |
| Predicted presence | 45 (12.2%) | 256 (69.4%) | 301 (81.6%) |
| Total | 60 (16.3%) | 309 (83.7%) | 369 (100%) |
| True positive rate | 0.828 | | |
| True negative rate | 0.250 | | |

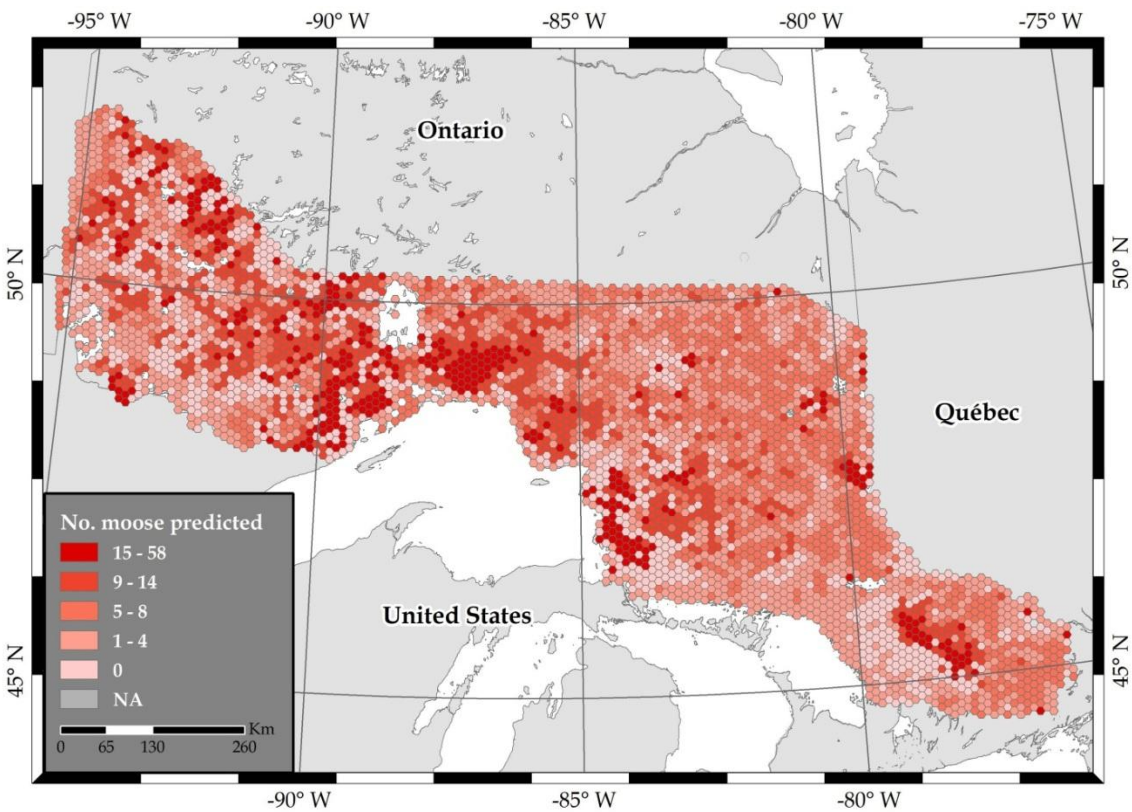
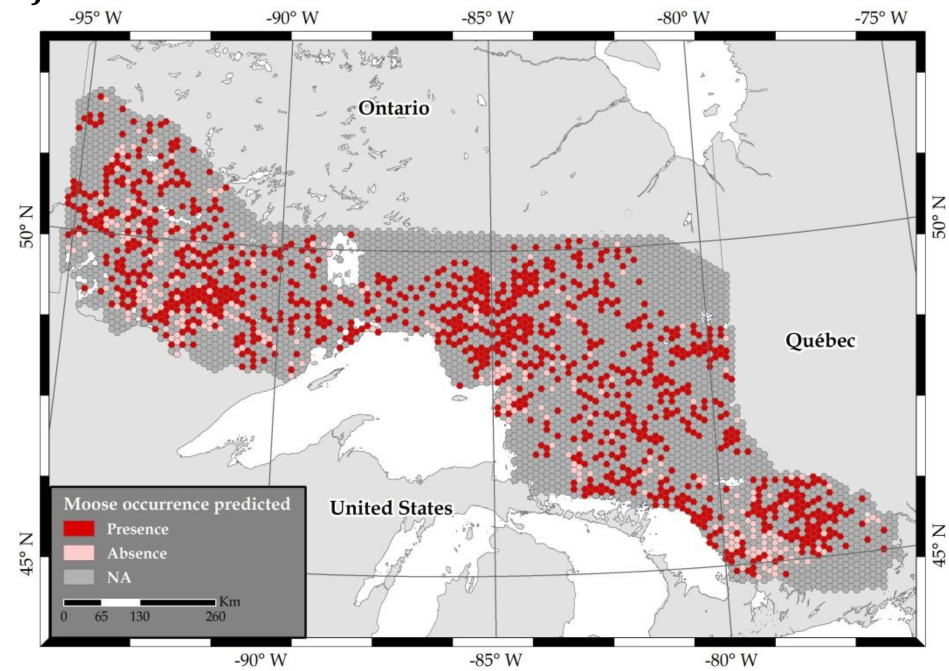



**Figure 4.2. Moose abundance predicted by the final hurdle model. The underlying data is continuous, but for presentation, densities were grouped in five classes based on quantiles of all predicted values. Dark red colours indicate where density is higher and light red colours indicate lower densities.**

**A)**




**B)**

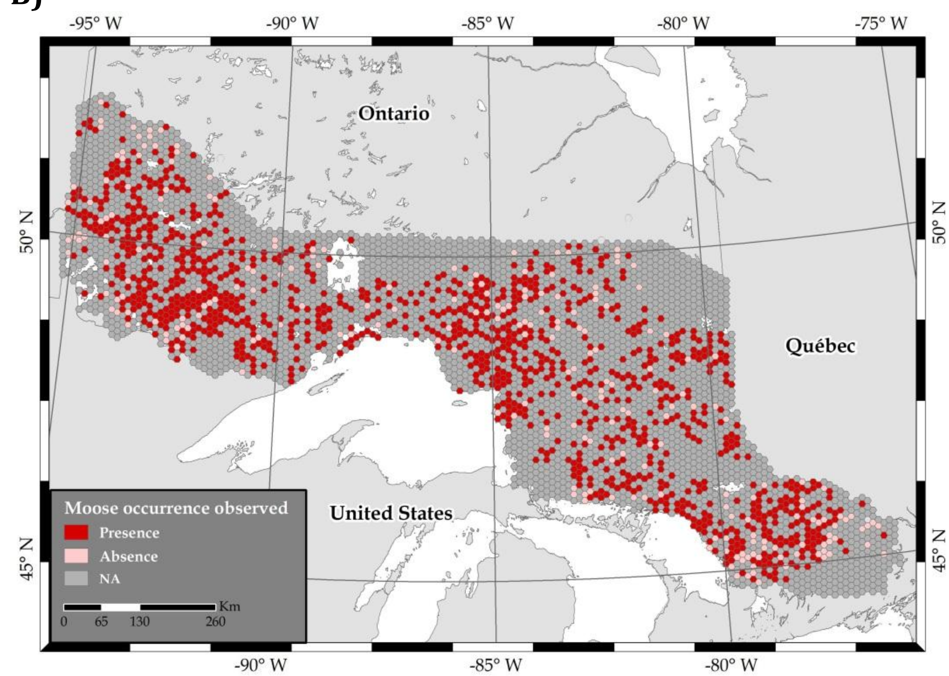
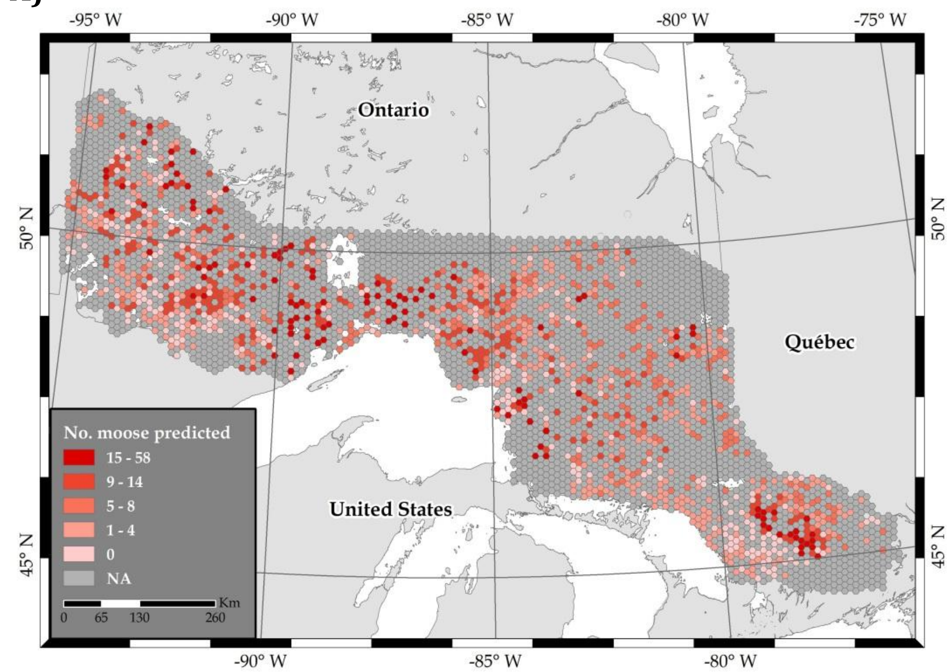



**Figure 4.3. Moose occurrence in Ontario A) predicted by the final hurdle model over the plots that were surveyed from 2004-2007 B) observed by aerial survey from 2004-2007. Dark red colour indicates presence and light red indicates absence.**

**A)**




**B)**

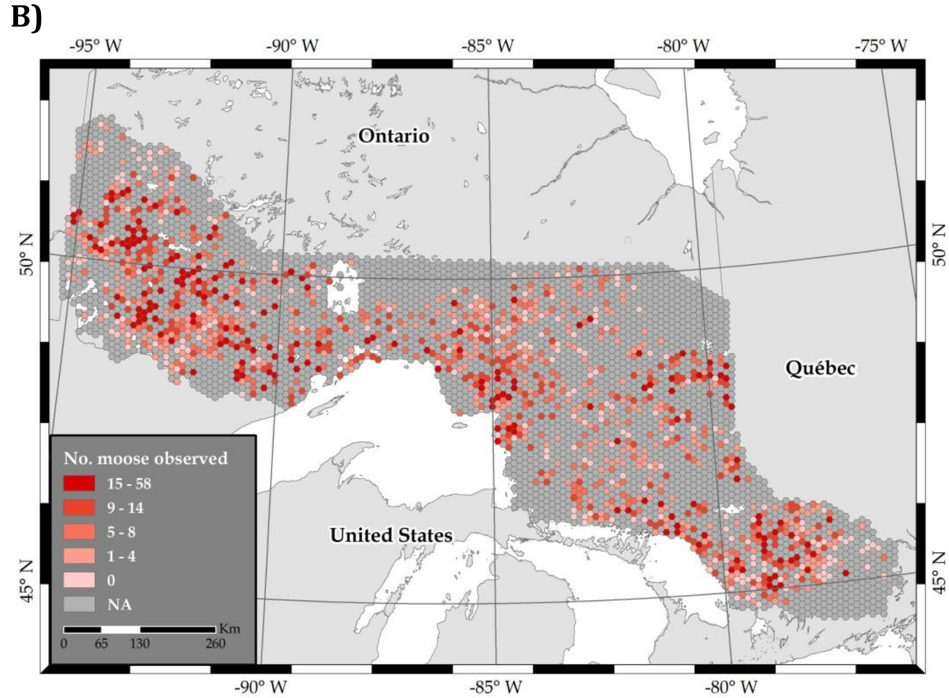



**Figure 4.4. Moose abundance in Ontario A) predicted by the final hurdle model over the plots that were surveyed from 2004-2007 B) observed by aerial survey from 2004-2007. The underlying data is continuous, but for presentation, densities were grouped in five classes based on quantiles of all predicted values. Dark red colours indicate where density is higher and light red colours indicate lower densities.**

## 4.4 Discussion

In this study, we evaluated the use of remotely sensed indicators as predictors of moose habitat. The results suggest that remote sensing indicators provide valuable information for both occurrence and abundance predictions of moose habitat. The occurrence model had relatively good overall accuracy (73.44%), however, the model had a better ability to predict the presence (82.8% of accuracy) than the absence (25.0%). Overall, the moose occurrence was predicted more accurately than abundance, suggesting that abundance is driven by a more complex combination of environmental covariates. This correlates well with other studies that found that abundance prediction across the species range is often challenging (Pearce and Ferrier 2001). In addition, the selection of hypotheses and significance of covariates for the occurrence model differed from the abundance model. Our findings are consistent with Nielsen et al. (2005) and suggest that moose distribution and abundance are driven by different mechanisms.

### 4.4.1 Hypotheses

This research confirmed the assumption that certain competing hypotheses are more significant than others for the prediction of moose occurrence or abundance. The protection hypothesis, including proportion of coniferous (Coniferous, Coniferous$^2$), distance to human settlements (Dist-Urban, Dist-Urban$^2$) was the most parsimonious hypothesis to explain moose occurrence. The snow impediment hypothesis, encompassing the average monthly percentage of snow cover of three years prior to survey (SnowCover$^2$) and the minimum cover during the antecedent year (Min-T1) had the highest relative support in the moose abundance model. Snow cover is known to be a key driver of ungulate habitat selection (Kittle et al., 2008). For example, Månsson (2009) found that the numbers of days with snow cover deeper than 0.1m was statistically significant in predicting moose abundance in certain habitat types.

Hypothesis selection and combination for the best abundance model indicated that both snow impediment and food availability were exclusively important for the prediction of abundance, suggesting that these factors are crucial for habitat quality but less important for explaining moose occurrence. Overall, abundance was driven by all hypotheses, except the protective cover, which is similar to findings of Brown (2011) who found that the coniferous cover was not statistically significant in predicting population growth rate, calves per 100 cows, and the bull / cow ratio.

### 4.4.2 Relative contribution of covariates

The zero-inflated hurdle approach enabled us to assess the relative importance of the selected covariates. Overall for moose occurrence the most significant covariates were protection related, which supports the original contention that moose distribution is highly influenced by climate and other fundamental bottom-up drivers such as conifer cover distribution which are largely driven by climate and landform. Alternatively, the coniferous cover can also be considered a top-down driver since it provides protection from predators. The effect of a positive relationship for the percentage of coniferous forest and a negative relationship for its quadratic equivalent (Table 4.7) suggests that the maximum probability of occurrence occurs at intermediate proportions of coniferous cover. This may reflect the importance of coniferous forest as providing shelter from predators, and providing shelter from extreme climate yet being poor for forage. The minimum cover during the antecedent year was positively correlated to moose abundance, suggesting that when protection cover, i.e., coniferous cover, is sustained over the year, higher moose abundance can be expected. The use of a static land cover assessment of the percentage of coniferous cover combined with the annual monitoring of minimum cover in the antecedent year allowed us to capture both the temporal and spatial variation of the vegetation available for moose protection.

The food availability hypothesis integrates cover types of high quality forage and annual productivity. Similar to snow impediment, moose trade-off between habitats of high quality forage, which often have a higher risk of predation, and protection habitats where the risk of predation is lower but forage availability is often reduced. For cover types which have high quality forage, such as grassland/shrubland, mixedwood, and broadleaf, we found a positive relationship with moose density which matches well with previous studies in the southern Boreal Forest. For example, Dussault et al. (2006b) found that cover types of high quality forage were preferred by moose and Brown (2011) found a positive relationship between moose population growth rates and percentage of mixed-deciduous forest. For vegetation productivity, we found a statistically significant correlation between the

**Table 4.7. Slope parameter estimates and standard error (SE) for explanatory covariates of the final hurdle model. Covariates are described in Table 4.2. Associated levels of significance are reported: • p <0.1, * p< 0.05, ** p<0.01, *** p<0.001, n.i. not included in the model.**

| Explanatory variables | Occurrence Estimate | SE | | Abundance Estimate | SE | |
|---|---|---|---|---|---|---|
| ***Snow impediment*** | | | | | | |
| Min-T1 | n.i. | | | 0.0070 | 0.0029 | * |
| ***Food availability*** | | | | | | |
| Grass-Shrub | n.i. | | | 1.5750 | 0.2552 | *** |
| Mixed | n.i. | | | 1.1300 | 0.2415 | *** |
| Broad | n.i. | | | 1.0424 | 0.2184 | *** |
| Sum-Av | n.i. | | | -0.0046 | 0.0015 | ** |
| ***Cover protection*** | | | | | | |
| Coniferous | 4.6860 | 1.3387 | *** | n.i. | | |
| Coniferous2 | -9.6467 | 2.1549 | *** | n.i. | | |
| ***Disturbance*** | | | | | | |
| Dist-Road | n.i. | | | 0.0252 | 0.0139 | • |
| Dist-Road2 | n.i. | | | -0.0009 | 0.0004 | * |
| ***Habitat diversity*** | | | | | | |
| Elevation | n.i. | | | 0.0014 | 0.0004 | *** |
| ***Regression*** | | | | | | |
| (Intercept) | 1.2664 | 0.1507 | *** | 3.0334 | 0.8550 | *** |

annual productivity and moose abundance. Productivity –sum provides an index of the integrated productive capacity of a landscape, yet exhibited a negative relationship with moose abundance. This contrast with Jiang et al. (2009) who found that measure of reflectance of green vegetation correlated positively with moose occurrence.

The role of disturbances, specifically proximity to anthropogenic features, was found to be statistically significant for the prediction of moose abundance which corresponds with our expectations that top-down limitations (i.e., governing survival) are important for moose abundance. The linear and quadratic average distance to the nearest road was positively and negatively correlated, respectively, with moose density, providing evidence that moose select habitat at intermediate distance from roads. Even though Brown (2011) reported that road density may increase hunter's pressure on moose populations, the competing view is that greater moose abundance is due to prominence of early forest succession closer to roads. In most of northern Ontario, roads are primarily associated with forest harvesting activities, which is prime forage for moose. For the rest of the study area, depending on the condition of use of the roads, a negative effect on wolf use may be expected, thus increasing moose abundance.

Elevation had a positive influence on moose abundance in this study. This result is different than that found by Dettki et al. (2003) who predicted moose prefer low-elevation flat areas. However, that study was conducted exclusively on female moose in winter and it is known that a high proportion of moose in that population migrate between summer and winter ranges (Ball et al., 2001) which may partly explain why our year-round study of cows, bulls and calves would lead to different conclusions.

When applying the global hurdle model over the study area, we found that the predicted moose occurrence and abundance was spatially variable. Occurrence was predicted for most of Ontario and did correspond to the observed occurrence, but under-predicted in southeast Ontario. This predicted absence appears to be related to a lower percentage of coniferous cover here, which was a statistically significant driver for moose occurrence in the model. While conifer cover may generally be lower in the southern extent of the moose range, we recognise that finer scale habitat indicators other than that measured in this study could drive occurrence in regions under-predicted by the model. The highest predicted moose density was recorded in western Ontario whereas relatively lower abundance was located in southeast. Over most of the study area, the predicted abundance model did on average represent the observed abundance patterns, but tended to under-predict moose abundance. For example, the hurdle model under-predicted moose abundance by 17.4% compared to the observed abundance.

In addition to the covariates included in our models, other factors such as interaction with other species (predation, competition), parasites, diseases, aboriginal and license hunting, variation in forage within stands, the age structure of the forest (Price et al. 1988, Rempel et al. 1997,Dettki et al. 2003, Dussault et al. 2005, Dussault et al. 2006b) as well as the size of the calving areas and mineral licks (Ontario Ministry of Natural Resources 1988) have all been shown to impact moose habitat. However, many of these factors cannot be easily predicted over the landscape, limiting our capacity to include them in model development. For example, there is evidence that predation and hunting can regulate moose populations (Messier and Crête 1985, Ballard et al. 1991, Solberg et al. 1999). In contrast to remotely sensed indicators, wolf density data would generally not be available in most jurisdictions for long term monitoring. While variable predation should affect variation in abundance, it should not be a prominent driver of distribution (occurrence), for which bottom-up drivers (i.e., climate and food) should be more important. Furthermore, relationships between moose habitat and environmental covariates, such as disturbance and habitat heterogeneity may occur at relatively finer spatial scales than observed in this study; however our analysis was limited with respect to the spatial resolution of the moose aerial survey (25 $km^2$).

While moose habitat models often necessitate extensive field survey and generally assumed a static environment, the modelling approach applied in this paper utilises exclusively freely available data, existing moose survey data as well as the capacity to be updated with temporal variation in a number of the covariates. In addition, in comparison to some current moose habitat models, the analysis was conducted at a population scale and utilised a novel approaches for tracking both short and long term vegetation productivity patterns (Chapter 3). The methodology and remotely sensed indicators used in this study should provide a useful framework with broad application to a diverse range of systems and species where populations are expected to respond to broad scale variation in land cover and productivity. The generation of predictive maps from this analysis can provide wildlife managers with a greater understanding of variations in moose distribution and their habitat use as inferred from occurrence and abundance: For example,

- Land management decisions can be directed by detailed information on the habitat characteristics as well as knowledge on the relative contribution of the environmental drivers to moose populations.
- In order to minimise the uncertainty and risk in management decision-making, recent environmental information can be integrated in the moose habitat model to assess the habitat supply under current and future situations.
- The relative importance of the predictor covariates and the resulting mechanisms influencing moose habitat selection can aid in provincial monitoring activities, such as moose aerial survey planning, and also can be used to focus more detailed analysis to regions of specific interest.

## 4.5 Conclusion

Remote sensing observations parameterising environmental hypotheses provided statistically significant predictive power when estimating both moose occurrence and abundance across the landscape. We found that environmental hypotheses/covariates influencing occurrence may differ from those limiting abundance, thus providing additional evidence that mechanisms driving moose occurrence and abundance differ. The most important mechanisms for predicting occurrence were protective cover and habitat diversity, whereas snow impediment, food availability, disturbance, and habitat diversity were most statistically significant for abundance. Findings also contrasted with some moose and other ungulates studies which indicate that habitat selection can differ for the same species in broadly different landscapes with different stressors and availability of community types. Besides providing insights on the relative importance of the predictor covariates for moose occurrence and abundance, this study creates opportunities for further development of spatial models that closely examine the occurrence/abundance-habitat relationships which are highly valuable for habitat management decisions.

# 5. CONCLUSION

The overall objective of the research was divided into two main questions. First, my work assessed if vegetation productivity data derived from remote sensing could be used to assess ecosystem variability throughout Ontario and second I and collaborators investigated the contribution of satellite-derived indicators to characterise moose occurrence and abundance. In addition to these two main questions, insights into the environmental variability patterns and drivers of this variability were gained, while a novel approach was developed to detect trends from time series of remote sensing fPAR measurements. The method developed in this research is useful to detect changes in vegetation productivity patterns which can aid in provincial monitoring activities and also can be used to focus more detailed analysis to specific regions of interest. Furthermore, we improved our understanding of the mechanisms affecting moose habitat suitability and we demonstrated that the use of a remote sensing driven model is beneficial to the characterisation of the occurrence/abundance-habitat relationships. For example, this information can be utilised for moose aerial survey planning, minimising the risk in management decision-making by modelling habitat supply for current and future situation, and guiding future research on moose habitat relationships.

## 5.1 Key findings

Results from Chapter 3 indicate that DHI composites of MERIS fPAR time-series allowed the characterisation of broad scale vegetation condition across Ontario. The developed method was shown to be useful for the assessment of the natural variability of vegetation, and highlighting areas which fall within, and beyond, the variability thresholds. We demonstrated that across Ontario there is an overall decrease in vegetation productivity characterised by an increasing trend in seasonality and a decreasing trend in both annual productivity and minimum cover from 2003 to 2008. Similar to the proposition of Barber et al. (2000), we believe that these finding are related to recent climate change which has restricted growth in the North American boreal forest, due to drought stress. Despite the relatively short time-series of the remote sensing data used in this study (six years), our results corresponded well with other studies. As observed by Zhang et al. (2008), Goetz et al. (2005) and predicted by Bunn et al. (2005), our study found negative productivity trends over the boreal forest of the Ontario uplands. This trend was largest for broadleaf forest, followed by mixedwood forest land cover types. Elevation was the prominent environmental driver with relationships that were statistically significant for all three DHI component trends. As expected, DHI trends also responded to fire disturbances with areas most recently burnt (2004-

2008) exhibiting a significantly higher proportion of decreasing trend in productivity (42% increase) and areas burnt from 1987 to 2003 exhibiting an increasing trend in productivity (128% increase). The only exception was areas in the earliest fire class (1970-1986) which observed a decreasing trend in annual productivity. Based on the results of Chapter 3, it can be inferred that broad resolution fPAR time-series coupled to the Theil-Sen's test is a valuable approach for detecting changes in vegetation patterns.

The results from Chapter 4 indicate that remote sensing indicators provided considerable benefit when characterising moose occurrence and abundance. Results indicated that the predicted moose occurrence was more accurate when compared to moose abundance where habitat relationships comprised a more complex assemblage of covariates. This correlates well with Scott et al. (2002) who argue that species occurrence is often more accurately predicted than abundance. Previous studies have demonstrated that different processes govern species distribution and abundance (Meynard and Quinn, 2007,Nielsen et al., 2005,Ridout et al., 1998). Chapter 4 supports this finding by demonstrating a different selection of hypotheses and covariates for the prediction of moose occurrence and density. The protection hypothesis had the highest relative support for moose distribution whereas the snow hypothesis, followed by the food hypothesis, was selected for moose abundance prediction. Moose occurrence was more likely at sites with a moderate proportion of coniferous, which is supported by Courtois et al. (2002) and Dussault et al. (2006b) who argue that moose often trade-off between coniferous protection cover and more open stands providing access to quality forage. Moose abundance was found to be positively driven by abundant high quality forage, such as grassland/shrubland, mixedwood, and broadleaf. This also matches well with previous studies in the southern Boreal Forest, where Dussault et al. (2006b) and Brown (2011) found that cover types of high quality forage were preferred by moose. The approach utilised in Chapter 4 is innovative as it demonstrates the use of freely available remote sensing datasets and the importance of tracking the temporal variation of covariates for monitoring moose habitat quality at landscape scales.

## 5.2 Future work and recommendations

The increasing availability of remotely sensed imagery associated with the rapid advancement of Earth observation technology is expanding the opportunities for monitoring a suite of environmental indicators. Imagery from various satellite sensors with specific spatial and spectral resolutions is available for monitoring different environmental indicators, including snow cover, vegetation disturbances, topography, and vegetation productivity. The approach developed in this research for detecting vegetation productivity trends based on broad scale fPAR time-series is easily transferable to other sensors. MODIS with more than a 10 year archive and long term historical AVHRR which has over 30 years of records are examples of datasets that are available for capturing vegetation variability over extended periods of time. With increased access to a wider range of satellites providing long term time series data, we can expect an increased use of remote sensing for vegetation change tracking, and as Goetz et al. (2005) discussed, there is growing interest in this technology for research on climate and carbon system models. It is hypothesised that, as climate change and anthropogenic pressure intensify, vegetation changes patterns will become more dynamics leading to an increased need for monitoring.

The moose habitat model developed in this research provides evidence that occurrence and abundance respond differently to environmental covariates, which stresses the importance of considering separately these mechanisms when assessing moose habitat. In addition to the covariates considered in our model, many other factors such as wolf predation, deer density, parasites, diseases, aboriginal and license hunting, variation in forage within stands, and other factors detailed in section 4.4.2, have all been proposed to impact moose habitat and were not considered in this study. Thus, improved access to province-wide information of such additional datasets would likely improve the current moose model accuracy.

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