Modelling British Columbia’s Ecosystems and Avian Richness Using Landscape-Scale Indirect Indicators of Biodiversity

by

Jessica Laura Fitterer
B.Sc., University of Victoria, 2009

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ABSTRACT

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Developing consistent and repeatable broad-scale methods for biodiversity modelling is an important goal to address as habitat loss, fragmentation and environmental degradation threaten our ability to maintain ecosystem and species diversity levels. Geospatial reviews of biodiversity monitoring have identified ecological indicators for the indirect mapping of species richness and ecosystem components modelling the processes controlling species distribution gradients. The goal of our research is to advance broad-scale biomonitoring by demonstrating how landscape-scale environmental indices can be used to model regional ecosystem and species diversity of British Columbia (BC), Canada.

We meet our ecosystem-modelling goal by selecting and developing suitable ecological indicators from Earth observation data and terrain indices to represent the structure, composition and function of the environment, displaying both static and dynamic landscape processes of BC's ecosystems. We regionalize the selected indirect indicators of biodiversity using a two-step clustering algorithm. The results display 16 ecologically distinct terrestrial ecosystems, 10 of which characterize the northern Boreal, coastal and Southern Interior mountain regions, and six represent the coastal lowlands, interior, Georgia Depression, Boreal and Taiga Plains of British

Columbia. Comparing our classification to BC Ministry of Forests biogeoclimatic zone mapping, we find spatial similarity in the coastal, Taiga and Boreal Plains. Overall, our classification distinguishes a greater diversity of ecosystems in the mountainous regions of the province and greater homogeneity in the Central Interior where our landscape characteristics represent current productivity conditions. Our approach to ecosystem modelling supports legacy mapping by providing ecological information in under-sampled regions of BC and offers a method for consistent repeat modelling of ecosystem diversity to identify landscape change.

To meet our species-modelling goal we employ a flexible non-parametric regression tree model (Random Forests) to establish the power of landscape-scale indicators (productivity, ambient energy, and heterogeneity) to predict the spatial distribution of breeding bird richness and establish the dominant landscape processes controlling vertebrate richness throughout BC. Our models explain approximately 40% of the variation in survey effort stratified breeding bird species richness levels and distinguish ambient energy as the top ranked environmental predictors of breeding richness. Using our modelled relationships, we forecast breeding richness levels for the regions of BC not currently surveyed to support conservation management of birds and vertebrate species. The results identify the lowland, warm and dry regions of the Boreal, Taiga, South and Central Interior and the Georgia Depression to be species rich. These results have implications for conservation managers, as high breeding richness is also concentrated in the areas favourable to human settlement. Additionally, by connecting breeding bird data derived from remotely sensed data and continuously collected climate data, we provide an approach for monitoring ecological indicators as surrogates of vertebrate population levels over broad spatial scales.

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DEDICATION

I dedicate my thesis to my stepson Logan Matthew Andres. I hope, throughout your life you make the short-term sacrifices to follow your dreams. I will be there to support your journey in every way that I can. Thank you for bringing so much joy to my life.

CO-AUTHORSHIP STATEMENT

This thesis is the combination of two scientific manuscripts for which I am the lead author. Together Dr. Trisalyn Nelson, Dr. Nicholas Coops, and Dr. Michael Wulder developed the project structure, where biological modelling using indirect indicators of biodiversity was identified as a key area for broadening the scientific knowledge of large-scale ecosystem and species dynamics. For these two scientific manuscripts, I led all research, data preparation, data analysis, result interpretations and writing. Dr. Nicholas Coops and Dr. Michael Wulder provided guidance in developing research questions and contextualizing research results. Dr. Trisalyn Nelson provided assistance with research structure and methodological considerations. Dr. Trisalyn Nelson, Dr. Nicholas Coops and Dr. Michael Wulder supplied editorial comments and suggestions incorporated into the final manuscripts.

1.0 INTRODUCTION

1.1 Research context

Preserving biodiversity has received considerable attention in the last two decades spurring both political and scientific conservation initiatives including The Global Biodiversity Assessment, The Global Biodiversity Information Facility, The Integrated Taxonomic Information System, Species 2000, Millennium Ecosystem Assessment and The International Union for the Conservation of Nature. The plethora of actions taken emphasizes society's response and commitment to reducing biodiversity loss. Canada's documented commitment began after signing the Convention on Biological Diversity in 1992, with a key dedication to identify and monitor components of biodiversity (Barton, 1992). The breadth of environmental compotents represented by the biodiversity concept often complicates setting management priorties for preserving biological diversity (Wallington et al. 2005). The term encompasses all natural variation across a range of scales (genes, species and ecosystems) (DeLong et al., 1996; Hyde et al., 2010). Given the variety of perspectives (e.g., scientific, resource management and policy), it can be challenging to assess the effectiveness of biodiversity conservation (Failing and Gregory, 2003).

Despite the variety of perspectives and measures of conservation success, generally, anthropogenic activities continue to stress natural processes (Vitousek et al., 1997). For instance, biodiversity is threatened by habitat loss, fragmentation and environmental degradation (Gaston, 2005) and future threats to biodiversity have been identified as land-use pressures, climate change in the northern latitudes, and shifts in the atmospheric CO_2 exchange and nitrogen decomposition (Sala et al., 2000) among others. While researchers predict the future scenarios of biodiversity loss, current scenarios lead to future conditions with reduced biodiversity (Sala et al., 2000). The potential species loss, climatic and ecocystem shifts could have significant effects on the function of the atmospheric balance or biogeochemical cycles (Ehrlich and Ehrlich, 1992). Given the breadth of phenomena represented by the biodiversity concept, and the importance to biodiversity to environmental health, research has suggested focusing on broad-scale models to monitor ecosystem patterns, species richness and change rather than single species or ecosystem components (Franklin, 1993; Duro et al., 2007; Wallington et al., 2005). A broad perspective can provide strategic level information for targeting field-based studies of biodiversity in vulnerable areas (Coops et al., 2009c; Fitterer et al., 2012).

Spatial data and remotely sensed imagery present two important data sources for the advancement of broad-scale biodiversity monitoring (biomonitoring) strategies (Foody et al., 2008). Remote sensing reviews of biodiversity modelling have broken down geospatial datasets into two categories of biodiversity representation. These categories are referred to as direct and indirect indicators (Nagendra, 2001; Kerr and Ostrovsky, 2003; Turner et al., 2003; Duro et al., 2007; Gillespie et al., 2008). Direct indicators are a first order representation of diversity such as individual species or intricate details of land-cover types (Turner et al., 2003). Conversely, indirect indicators, represent broad-scale patterns of the physical environment (structure), vegetation production (composition) and available energy (function) understood to control the spatial distribution of species through resource availability (Turner et al., 2003, Duro et al., 2007, Gillespie et al., 2008). Together indirect indicators of biodiversity can be used to represent ecosystem dynamics (e.g., Coops et al., 2009c; Andrew et al., 2011; Fitterer et al., 2012), or study the broad-scale drivers of species richness (e.g., Currie, 1991; Coops et al. 2009d, 2009b; Andrews et al., 2012).

Across levels of biodiversity, linking broad-scale dynamics of ecosystems or components of species richness is an important task for understanding the environmental conditions which promote biological richness, and is central for predicting the response of species diversity to landscape disturbance and change (Orme et al., 2005). The success of modelling species distributions using consistently collected information for the development of ecological indicators has been noted (Coops et al., 2009d and Andrews et al., 2012) and organizations such as NatureServe Canada have suggested more studies focus on linking biodiversity to remotely sensed data for biomonitoring application (Hyde et al., 2010). In our research we build upon existing ecosystem modelling framewoks (e.g., Nagendra, 2001; Duro et al., 2007; Boutin et al., 2009; Coops et al., 2008, 2009b, 2009c) to model regional ecosystem and species diversity to identify indirect indicators important for the consistent and repeatable monitoring of biodiversity health.

1.2 Research focus

British Columbia is a highly diverse mountainous province with a variety of biophysical processes. Its landscape experienced a wide spread pine beetle epidemic (Robertson, et al., 2009), forest harvesting and climate changes (Gayton, 2008). To understand the ramifications of such landscape changes to ecosystem and species diversity levels it is vital to develop robust and repeatable biodiversity monitoring practices. Given the extent and heterogeneous nature of BC, lack of access limits sampling in mountainous areas (e.g., BC Breeding Bird Atlas observed distribution) and inconsistency of most field collected data restricts its ability for broad-scale biodiversity modelling and monitoring (Haeussler, 2011).

Recently published literature highlighted the limitations of BC’s existing broad-scale ecosystem modelling framework (Haeussler, 2011). These gaps arise from the differences between the original intent of broad-scale ecosystem mapping projects and current biomonitoring objectives. For example, the BC Ministry of Forests developed the biogeoclimatic classification for forest management, and as such, the classification focuses on climate and climax vegetation characteristics using field collected plant associations, plant sub-associations, and topographic constraints to understand where tree species thrive and map ecosystem diversity (Haeussler, 2011). The static temporal representation of characteristics can be used for forest practice in the current time; however, the in situ sampling techniques are problematic for monitoring landscape change, as field samples are unable to provide a uniform spatial coverage of data, or provide seasonal climate and vegetation information given topographic access restrictions and limited resources (Haeussler, 2011). Consequently, an opportunity is available to develop a temporally repeatable broad-scale method for modelling ecosystem diversity and species richness to supplement legacy ecosystem mapping techniques and field assessments of biodiversity by using systematically collected Earth observation data and topographically adjusted climate data.

Additionally, the popular gridded atlas structure of species surveys offers consistently collected data over larger areas to study the relationship between species richness and the ecological indicators suggested for biomonitoring (e.g., Būhning-Gaese, 1997; Hurlbert and Haskell, 2003; Luoto et al., 2004; Coops et al. 2009d, 2009a). Understanding the predictors of species richness over broad spatial scales can support conservation initiatives as species richness is considered an important tool for measuring biodiversity (Pearman and Weber, 2007). Birds are also indicators of landscape-scale habitat condition (Hurlbert and Haskell, 2003) and vertebrate population levels (Gregory et al., 2003) displaying suitable surrogate species characteristics for monitoring vertebrate population diversity as a whole. As such, the recently development of the

BC Breeding Bird Atlas offers a unique opportunity to study the environmental structure and processes controlling regional species richness.

1.3 Research goals and objectives

Our goal is to advance broad-scale modelling of regional diversity and to demonstrate how landscape-scale environmental indices can be used to model biological diversity in the form of ecosystem and species diversity. To meet our goal we address two objectives and use robust and flexible modelling approaches applicable for adaptation around the world.

Our first objective (Chapter 2) is to display methods to characterise BC's ecosystem diversity using surrogates of biodiversity derived from Earth observation data and topographic information. To meet our objective we employ indirect indicators of biodiversity, which overcome some of the limitations of field data collection when mapping over broad scales (Franklin, 1993). We draw upon existing biomonitoring literature to identify fundamental ecosystem characteristics to include functional, compositional and structural components of each ecosystem and regionalize our independent environmental indices using a two-step clustering method developed for large databases and mixed type attributes (SPSS, 2001) with the results creating an ecosystem map maximizing variance between ecosystem characteristics. To establish how our ecosystem delineation can integrate with existing ecosystem-mapping techniques we quantify dominant land cover and forest ecosystem types within each of the ecoregions and discuss the additional information provided by the dynamic ecosystem attributes (annual maximum and seasonal production, seasonal change in snow cover, and annual solar insolation). We also highlight the contributions of our approach to systematic biomonitoring by focusing on the temporal repeatability of our methods and the seasonal information offered by our remotely sensed vegetation and snow cover dynamics.

Our second objective (Chapter 3) is to investigate the landscape-scale relationships between breeding bird richness and environmental indicators to explore the potential of monitoring landscape indicators as a surrogate for vertebrate diversity. We use the BC Breeding Bird Atlas to evaluate the significance of food resources (productivity), thermoregulatory needs (ambient energy) and niche habitat (heterogeneity) on breeding habitat selection of birds. We develop relationships using non-parametric regression trees implemented in the Random Forests algorithm (Breiman, 2001) as a flexible means to discover the important predictors of breeding richness while allowing for interaction effects between indicators. Given that, the BC Breeding Bird Atlas is a newly available dataset we quantify the effects of survey effort and observation bias on breeding bird richness levels to develop indices independent of sampling bias. We also provide suggestions to improve species atlases for conservation and scientific research to understand the processes influencing species richness gradients.

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2.0 MODELLING THE ECOSYSTEM INDICATORS OF BRITISH COLUMBIA USING EARTH OBSERVATION DATA AND TERRAIN INDICES

2.1 Abstract

Remotely sensed data plays a critical role by acquiring data on ecological conditions over broad spatial scales, providing important information for mapping landscape-scale ecosystem characteristics. The goal of our research is to employ a robust clustering algorithm to provide a transparent method of integrating remotely sensed datasets into homogeneous ecosystem units for conservation planning and monitoring ecosystem condition and change. Using a suite of ecosystem characteristics derived from digital elevation and remotely sensed data at 1km spatial resolution, we classify the 94 million ha within the province of British Columbia (BC), Canada, into 16 terrestrial ecosystem regions (and a water category) using a two-step clustering approach. Initially, 10 metrics representing the physical environment (elevation and soil wetness potential), available energy (solar insolation and snow melt) and vegetation production (fraction of photosynthetically active radiation) were considered for ecosystem classification, which were reduced to six after analyzing variable inter-correlations. The results provide ecologically unique terrestrial regions: ten of which describe the Northern Boreal, Coastal Mountains and Southern Interior Mountains, and six the coastal lowlands, Georgia Depression, interior, Boreal Plains and Taiga Plains. Analyzing the spatial interaction between the cluster categories revealed that highly dispersed ecosystem types occur most often in the intermediate elevation zone, moderate dispersion at the highest elevations, and homogeneity in the lowland areas where elevation remains relatively constant. When overlaid with BC's standard biogeoclimatic ecosystem classification zones the newly developed regions represent similar ecosystem ranges in the coastal, Taiga and Boreal Plains. However, overall our delineation exhibits a greater level of

diversity in the alpine environment, and greater homogeneity in the central and southern interior. The quantitative regionalization approach we present offers a broad-scale assessment of British Columbia’s ecosystem diversity that can be used as a supplement to traditional in situ biodiversity assessments to provide detail in under-sampled regions of BC or areas experiencing landscape change.

2.2 Introduction

Globally, anthropogenic activities have increased habitat loss and environmental degradation (Gaston, 2000); fragmenting or removing large areas of temperate, broadleaf and mixed type forests (Wade et al., 2003). As a response to this, and similar degradation, vertebrate populations have decreased on average 31% since 1970 (see Butchart et al., 2010). In Canada, habitat loss caused by agricultural activity and urbanization is thought to be the most prominent threat to endangered species (Venter et al., 2006). In the province of British Columbia (BC), landscape change is occurring due, in part, to extended growing season (Gayton, 2008) and widespread tree mortality created by the range expansion of mountain pine beetle populations (Robertson et al., 2009), with the ramifications of these impacts not yet known. Changes to BC's climate are projected to continue leading to marked shifts in the biogeoclimatic ecosystem classification (BEC) zones (Hamann and Wang, 2006).

To mitigate environmental degradation, management agencies need to consider both tree growth and ecosystem management, creating a need for scientifically rigorous and unbiased broad-scale biodiversity monitoring systems (Boutin et al., 2009). However, species-specific objectives, limited spatial and temporal scales, and inconsistent data collection and reporting beset current biomonitoring practices (Franklin, 1993; Boutin et al., 2009; Hyde et al., 2010). For example, BC's biogeoclimatic zones, established in the 1970's, have a forest management and climax equilibrium focus (Haeussler, 2011). Consequently, there is an opportunity to develop more comprehensive monitoring systems by building on Earth observation data for broad-scale ecosystem and biodiversity assessments (e.g., Nagendra, 2001; Duro et al., 2007; Boutin et al., 2009; Coops et al., 2009a) to supplement existing classification systems. Earth observation data provides spatially consistent, repeatable datasets considered appropriate for broad-scale, annual modelling of ecosystem diversity (Nagendra, 2001; Kerr and Ostrovsky, 2003; Turner et al., 2003; Duro et al., 2007; Gillespie et al., 2008). If Earth observation ecosystem modelling is repeated on a systematic time step, methods can ensure a cost effective, non-subjective regionalization approach (Hargrove and Hoffman, 2004) with sufficient spatial detail and consistency to identify potential changes or shifts in ecosystem diversity (Duro et al., 2007; Coops et al., 2008, 2009a).

Recent reviews have synthesized geospatial biomonitoring into two main categories of data, direct and indirect indicators, and three environmental features, the physical environment, vegetation productivity, and available energy (Turner et al., 2003; Duro et al., 2007; Gillespie et al., 2008). In a biomonitoring context, direct indicators capture information on individual species and land cover types, while indirect indicators often represent broad-scale landscape patterns understood to affect biodiversity (Turner et al., 2003). Such as, digital terrain data, satellite derived estimates of landscape productivity, and cover types, which have been used to predict avian species richness (Coops et al., 2009b). Significant positive correlations have also been found between Landsat-derived Normalized Difference Vegetation Index (NDVI) and in situ sampled vascular plant richness (Levin et al., 2007).

At the ecosystem level, biodiversity indicators can be represented in the form of landscape patterns, types, and/or process (Noss, 1990). For instance, digital elevation models capture landscape structural patterns (physical environment) in the form of topographic indices (Franklin, 1995). Remotely derived vegetation indices provide data appropriate for modelling landscape types and seasonal variations in landscape greenness (vegetation productivity) (Coops et al., 2008). Furthermore, biophysical ecosystem processes (available energy) can be represented by monitoring snow cover changes (Farmer et al., 2010), modelling annual average incoming solar radiation (i.e., insolation) (Kumar et al., 1997), and estimating moisture availability using topographic wetness indices (Franklin, 1995).

The goal of our research is to demonstrate methods to characterize BC's ecosystem diversity using indirect indicators of biodiversity derived from Earth observation data. To meet our goal, we will address the following objectives. First, we provide background on biodiversity indicators suitable for application over large areas. Second, we assess the monotonic correlation between variables to reduce redundancy and apply a two-step multivariate clustering method to delineate BC's ecosystems at a 1 km spatial resolution. Third, we analyze the potential to hierarchically aggregate our regionalization by assessing spatial pattern of the clustered pixels. Fourth, we compare and contrast our ecosystem regions to the established static BC biogeoclimatic zones to demonstrate how our approach can integrate with legacy ecosystem mapping schemes. Last, we discuss the contributions of our model to the broader objective of systematically monitoring ecosystem diversity over broad spatial scales.

2.3 Biodiversity indicators

Ecosystem characteristics are both static (i.e., at decadal time scales or longer) and dynamic. Static ecosystem components represent the landscapes potential to sustain species (Wright et al., 1998), while dynamic characteristics relate the effects of climatic variation and anthropogenic impacts on the landscape (Wallington et al., 2005).

Topography is a relatively static structural ecosystem component, with elevation gradients determining species distributions (Sarr et al., 2005), vegetation productivity (Franklin, 1995) and patterns of disturbance (Dorner et al., 2002). Elevation correlates with soil moisture, where productivity levels peak on low, cool, and moist slopes or high, warm, and dry slopes (Allen et al., 1991). Together, elevation and latitude play a critical role in temperature and moisture dynamics and thus shape vegetation composition and function (Franklin, 1995; Duro et al., 2007).

Elevation data can also be used to represent biophysical ecosystem processes. For instance, Rich et al. (1994) developed a hemispherical viewshed algorithm to model direct and diffuse solar radiation from topographic data, which provides information on a sites microclimate including soil, surface and air temperatures, the sensible heat flux, and evapotranspiration (Kumar et al., 1997), all of which can ultimately influence plant growth. Similarly, studies have found that solar radiation correlates well with forest vegetation patterns (Davis and Goetz, 1990) and provides predictive power for modelling the spatial distribution of vegetative species in alpine environments (Guisan et al., 1998). In addition to solar radiation models, elevation data also provides an opportunity to estimate potential steady state topographic wetness. Topographic wetness indices (TWI) consider the surrounding topography to describe a location's ability to become saturated (Sørensen et al., 2006), and correlate well with soil attributes including horizon depth, silt percentage, and organic matter (Moore et al., 1993). TWI has also been used as a predictor variable of forest health conditions (Zirlewagen et al., 2007).

Snow distribution at the landscape-scale is also an important variable controlling patterns of ecosystem diversity from limiting species establishment and occurrence to driving vegetation seasonality (Walker et al., 1999; Wipf et al., 2009). The presence or absence of snow has either positive or negative effects on evaporation and run-off regimes respectively (Karl et al., 1993). Within the alpine environment, vegetation has adapted to rely on snow cover for protection from extreme weather and provide moisture in the summer (Billings and Bliss, 1959). Therefore, variations in plant diversity and abundance are largely governed by snow presence and melt rate

(Kudo, 1991; Walker et al., 1999), making it a critical ecosystem characteristic in mountainous regions such as BC.

Mapping coarse scale vegetation diversity is also important for ecosystem monitoring because highly productive areas provide more resources to distribute between species and are theorized to support higher levels species richness (Walker et al., 1992). Research also indicates that productive ecosystems are more resilient and recover faster from disturbance (Stone et al., 1996). Studies have effectively integrated annual Moderate Resolution Imaging Spectroradiometer (MODIS) fraction of photosynthetically active radiation (fPAR) metrics representative of annual minimum vegetation, annual cumulative growth and annual vegetation seasonality to characterize broad scale ecosystems characteristics (Mackey et al., 2004;Coops et al., 2008, 2009a). By integrating vegetation dynamics with physical structure and available energy, ecosystem regions can be displayed over broad spatial scale and topographically complex rugged environments (Duro et al., 2007).

2.4 Methods

2.4.1 Study area

British Columbia covers over 940,000 km^2 and is a highly diverse mountainous environment subject to a variety of disturbance regimes (e.g., Masek et al. 2011; Safranyik et al. 2010). The physiography and climate are largely controlled by the Pacific Ocean to the west, continental air masses in the interior plateaus, and Rocky Mountains to the east (Austin et al., 2008). The central interior is composed predominantly of lodgepole pine forests. BC is experiencing an epidemic infestation of mountain pine beetle, due to factors including fire suppression and changing climate (Safranyik et al. 2010). The on-going infestation has contributed to an increase in forest fragmentation (through increased harvesting aimed at mitigation) and effects vegetation productivity (Coops and Wulder, 2010). Rapidly changing landscapes such as those in BC require robust techniques for large-area ecosystem mapping.

2.4.2 Datasets

Ten variables were considered to represent BC's ecosystems including topographic wetness, elevation, average solar radiation, three spring snow cover dynamics and four vegetation indices (Table 2.1). We selected to analyze remotely sensed data on productivity and snow cover characteristics using 2006 acquisition, post the annual peak tree mortality caused by mountain pine beetle infestations (Province of British Columbia, 2011) and representing average growing conditions with the provincial average temperature lying close to the 17 year median and the precipitation amount falling between the 25th and 50th percentile (only 89.5 mm lower than the provincial 17 year median) (Figure 2.1). Therefore, 2006 can be taken as representative of current ecological conditions in BC, while also representing wide-area disturbance conditions. Prior to analysis, all raster datasets were converted to the same extent and a 1 km spatial resolution, partitioning the province into a grid of 1 km x 1 km cells.

Elevation

The Canadian Digital Elevation Data Product (CDED), extracted from the National Topographic Database at scales of 1:50,000 and 1:250,000 source data (GeoBase, 2007), was resampled twice using a bilinear technique, once from 25 m to 100 m spatial resolution for topographic modelling purposes and once from 25 m to 1 km spatial resolution for clustering (Figure 2.2).

Topographic Wetness Index

The Topographic Wetness Index (ln (*a*/tanβ)) (Beven and Kirkby, 1979), a well established index for relating soil moisture indices in support of hydrological modelling (Kopecký and Čížková, 2010), was calculated from the 100m elevation product. In pre-processing all sinks and pits were removed from the Digital Elevation Model (DEM). Next, flow direction and flow accumulation (*a)* layers were derived using the D8 flow algorithm and the slope degree (*β)* was calculated and converted to radians. Results were resampled to 1 km spatial resolution and a focal mean filter was applied to smooth linear trends associated with the non-dispersive flow algorithm (for more details on topographic wetness modelling see Tarboton, 1997) (Figure 2.2).

Annual solar insolation

To characterize BC's available energy, a solar radiation model was created using 25 m CDED product and a hemispherical viewshed model developed by Rich et al. (1994) (for details on calculation see Wulder et al., 2010). The algorithm uses a hemispherical viewshed and irradiance lookup tables, from each sky direction, to calculate direct and diffuse radiation (Rich et al., 1994). For each cell, a viewshed model was calculated and stored in the hemispherical coordinate system, then lookup values from all unobstructed sky directions were summed to estimate total irradiance, and a cosine correction accounted for the angle of incidence (Rich et al., 1994). To produce the most accurate results annual insolation calculations were conducted over two hour intervals for a single mid-day each month and monthly values were averaged to create annual solar insolation estimate (see Kumar et al., 1997) (Figure 2.2).

Snow cover

Spring fractional snow cover layers were developed to represent regions experiencing high moisture availability. Source data were collected from 2006 MODIS Terra product (MOD10A1), which uses the normalized difference snow index to provide daily observation of snow cover, snow albedo and fractional snow cover at 500m spatial resolution (Hall et al., 2006). Daily fractional snow cover datasets were downloaded from NASA DAAC for March, April and May 2006 conditions. Imagery was mosaicked and projected from sinusoidal grid to BC Albers Projection and resampled using a bilinear technique to 1 km resolution. Daily fraction snow cover datasets were used to create maximum and minimum fractional snow cover composites. The three month time period was selected to minimize the capture of cloudy winter images and ensure representation of spatial variability in spring snow cover melt as BC snow cover runoff regimes typically reach average flow by May (e.g., Stewart et al., 2004). The average maximum percentage of snow cover derived from the 1 km daily composites was 92% and the average minimum fractional snow cover was 24%. To estimate the spatial variability of snow cover change (i.e., melt) over the province we subtracted the minimum snow cover values from maximum snow cover composite image (Figure 2.2).

Vegetation productivity

Vegetation productivity estimates were derived from 2006 combined MODIS Terra and Aqua 8-day fPAR product (MCD15A2). The fPAR retrieval algorithm takes into account sun angle, background reflectance and view angles using the Bidirectional Reflectance Distribution Function (BRDF) at spectral bands between 400 and 700 nm (Tian et al., 2000). Values range from 0%, signifying barren land or snow cover, to 100%, representing dense vegetation cover (Coops et al., 2008). Images were also mosaicked, projected from sinusoidal grid to BC Albers

Projection, and resampled using a bilinear technique to 1 km spatial resolution. Following the methodology proposed by Mackey et al. (2004) and implemented in Canada by Coops et al. (2008), 24-day fPAR maximums were calculated to help reduce the effects of cloud cover and null values within the 8-day maximum datasets (Coops et al., 2008). Using the calculated 24-day maxima, 2006 annual maximum, minimum, cumulative sum and coefficient of variation layers were developed. Each layer provides an indication of the annual vegetation productive levels. To describe the layers, annual maximum fPAR displays climax productivity conditions and ultimately signify phenological variation (i.e., alpine areas provide a much lower fPAR value than highly productive coastal evergreen forests) (Figure 2.2). In contrast, annual minimum fPAR relates to the landscapes permanent vegetation cover. Vegetation seasonality is modelled by the coefficient of variation (Figure 2.2) and cumulative sum respectively are dictated by topography, species type, and land cover uses (Coops et al., 2009a). High coefficient of variation values are representative of extreme climates or rotational agricultural practices (Coops et al., 2009a). Conversely, sites with low seasonality values represent evergreen forests, barren land or consistently irrigated lands (Coops et al., 2009a).

Ancillary datasets

The 2006 MODIS Terra and Aqua (version 005, University of Maryland) land cover (MCD12Q1) was also acquired to describe the dominant land cover characteristics within the developed ecosystem regions. This land cover product delineates 14 different land cover types from spectral data at 500 m spatial resolution (Friedl and Tan, 2011). Classes include five forest types, two shrub categories, two savannah classes, grassland, cropland, urban, barren or sparsely vegetated, and water.

Existing ecosystem data were obtained from the BC Ministry of Forests version 7 BEC zones, which divides BC into 16 ecosystems using in situ plant associations (and sub-associations) combined with elevation and aspect empirical rules created from ecological plot data (Austin et al., 2008; Delong et al., 2010). The biogeoclimatic zones are well established and have provided BC's ecosystem characterization for the past 20 years by focusing on relatively permanent ecosystem characteristics such as mature vegetation type, soils and topography to represent homogeneous macroclimates and are most often used in a forest management context (Delong et al., 2010).

2.4.3 Statistical analysis

A two-step clustering method was selected to agglomerate the ecosystem metrics into homogeneous regions. The algorithm provides a robust clustering technique, which is able to accommodate large datasets and mixed-type attributes (SPSS, 2001). Two important factors were considered before clustering these data. First, the correlation between variables was assessed to ensure data independence, because although each indicator has been shown to influence ecosystem diversity (Section 2.3) highly correlated variables can dominate cluster results (Parks, 1966). Secondly, data were standardized to z-scores to eliminate the impact of data units on the a-spatial distance measure used in clustering (Bacher et al., 2004).

A Spearman's correlation test was selected to evaluate the monotonic relationship between indirect indicators of ecosystem diversity. After assessment of the correlation matrix, which will be presented in the results, six variables were retained for clustering: annual maximum fPAR (Max. fPAR), annual vegetation seasonality (CV fPAR), the percent change in spring snow cover (Chg. Snow), elevation (Elev.), Topographic Wetness Index (TWI), and annual solar insolation (Solar Rad.).

These remaining indicators were clustered into 17 statistically homogeneous ecosystem regions in two stages (16 terrestrial classes and one water / wetland class). A 17-class system was selected in order to compare our regionalization results to BC's Ministry of Forests (version 7) BEC zones, which describes, at the coarsest scale, 16 ecosystems to describe BC's regional ecosystem diversity (Austin et al., 2008). The first stage of the clustering algorithm developed a cluster tree with a maximum of 585 nodes reducing the datasets into pre-clusters replacing the raw dataset (SPSS, 2001). Once pre-clustering was complete, the pre-clusters were grouped using an agglomerative hierarchical clustering method and a log-likelihood distance measure to monitor the decrease in log-likelihood as one cluster was grouped with another (SPSS, 2001).

The ecological uniqueness of each cluster was assessed by comparing each region's average indicator value using a one-way ANOVA and Dunnett T3 post hoc test. ANOVA provides an empirical method to ensure at least one of the region's variable means is statistically different from the others. Furthermore, because the Levene's test statistic revealed unequal variances (p-value < .001) and the region's samples sizes are unequal, a Dunnett T3 test was selected for post hoc pair wise comparisons (Field, 2009). In addition to the formal statistical evaluation, the variable mean of each region was ranked using a three-class system. Low, medium and high categories were defined using a natural breaks classification (Table 2.2). Following statistical analysis, regionalization results were imported into a geographic information system for display.

In addition to analyzing the separability of the ecosystem clusters, we characterized the spatial interaction of clusters as a means of developing a method for aggregating clusters hierarchically. To characterize the spatial distribution of cells that compose each cluster, we created a Rook's case first order cell contiguity adjacency matrix to assess the percentage of like adjacencies for each cluster category. Adjacencies are converted to a percentage where the number of like adjacencies involving the region category is divided by the total number of cell adjacencies possible for each category. Adjacencies percentages equal 0% when every cell in the cluster is surrounded by cells classified to a different cluster (dispersed) and approach 100% when the cells of a cluster are spatially contiguous (homogeneous). The metric includes edge pixels of each region, but does not include adjacencies located at the provincial extent.

2.4.4 Cluster characterization

We described each ecosystem region by average indicator value, which were ranked into classes of low, medium and high. To provide a more detailed description of the landscape we quantitatively determined the first and second most frequently occurring MODIS land cover classes and BEC zones and populate BC’s BEC zones with our regions. The results of the analysis were also used to qualitatively compare our approach to the BC standard ecosystem units.

2.5 Results

2.5.1 Correlation

Reviewing the correlation matrix (Table 2.3), strong positive relationships were exhibited between annual maximum, minimum and cumulative sum fPAR variables (r_s = .83, .89, .61, p-value < .001). Therefore, maximum annual fPAR was selected to represent vegetation productivity to reduce data redundancy and provide an intuitive measure of landscape greenness. Maximum annual fPAR also provided the maximum separability between the ecosystem indicators values for each region and provided spatial homogeneity when compared to using a combination of fPAR metrics or fPAR cumulative sum. The fPAR coefficient of variation showed moderate to weak associations with other fPAR variables (r_s = -.43, -.11, -.50, p-value <.001) providing additional information regarding vegetation dynamics (seasonality). Spring snow cover matrices also displayed strong negative relationships between minimum snow cover and the change in snow cover (r_s = -.78, p-value < .001), therefore the change in spring snow cover was selected to represent moisture potential. The change in snow cover was selected over the minimum as it provided information on both the capacity of a pixel to retain a snow pack as well as identify which regions experience seasonal snow cover. Together these two factors influence variations in plant diversity and abundance (Kudo, 1991; Walker et al., 1999). Maximum snow cover is uncorrelated with the change in spring snow cover (r_s = -.07, p-value < .001), but strongly correlated with minimum snow cover (r_s = .62, p-value < .001). Despite its low correlation with snow cover change it was not included in the cluster analysis because maximum snow cover was moderately correlated with elevation (r_s =.49, p-value < .001), maximum fPAR (r_s = .47, p-value < .001) and fPAR coefficient of variation (r_s = .44, p-value < .001); thus, most of the variance within the dataset was captured by other ecosystem variables.

2.5.2 Statistical analysis of the ecosystem regionalization

Regionalization results, depicting the distribution of BC’s ecosystem diversity, are shown in Figure 2.3. Reviewing the f-statistic generated from the division of the between group mean squares and within group mean squares it was concluded with greater than 95% confidence that at least one of the regional means for each ecosystem metric are statistically different. Subsequently, the post hoc results (Table 2.4) compare the ecosystem variables between regions, which did not meet statistical significance to deduce a difference between their means (p-value > .05). To summarize, regions 1 and 2 do not exhibit different annual fPAR coefficient of variation and maximum fPAR characteristics. Regions 3 and 10 and regions 11 and 15 do not display different annual maximum fPAR greenness levels. Regions 3 and 6, 4 and 2, and, 11 and 12 represent similar snow cover seasonality and regions 3 and 6 share comparable potentials to hold soil moisture. In all other cases, the region's mean values for each ecosystem diversity variable are significantly different (p-value < .05). Most notably, elevation and solar radiation provide statistically different variable means between each region. Overall, the regions remain dissimilar if evaluated based on the combination of ecosystem variables and therefore successfully maximize between group variance and within group similarity ensuring our regionalization represents a range of ecological diversity found in the province.

The spatial adjacency matrix (Table 2.5) indicates that the regions 3, 5, 6, 7, 10, and 17 (water) are relatively dispersed with less than 50% of their adjacencies similar. In contrast, regions 11, 14 and 16 are highly homogeneous with over 70% of the possible adjacencies corresponding to the same regional category. Regions 1, 2, 4, 9, 12, 13 and 15 are moderately homogeneous with 50% to 70% of their adjacencies matching. Generally, the highly dispersed cluster values occur most often in the intermediate elevation zones, moderate dispersion levels at the highest elevations, and homogeneity is found in central interior, coastal and Taiga Plains areas where elevation remains relatively constant (Figure 2.2). A threshold for aggregating classes can be determined qualitatively depending on the goals of the aggregation. As an example, if we were to use a threshold of 12 percent or higher to combine regions based on adjacency similarity alone region 1 and 2, 5 and 10, 6 and 8, 4 and 7, 12 and 13, and 14 and 15 could be aggregated reducing our 16 terrestrial ecosystems to 10 regions (Table 2.5).

2.5.3 Ecosystem regionalization results

In addition to the statistical analysis, individually comparing the ranks of the ecosystem metrics offers a good indication of landscapes dynamics (Table 2.6). For example, region 17 represents water or highly saturated ground with low elevations and low vegetation characteristics (Table 2.6). Commonly, the coastal alpine ecosystems (regions 1 and 2) are characterized with low vegetation production, wetness potential and snow seasonality (Table 2.6). Region 14 represents the lowland coastal areas of the province displaying highly productive vegetation with low seasonality, moderate snow cover changes, topographic wetness and solar insolation (Table 2.6). Region 16 located in the southern to mid latitude interior exhibits maximum vegetation production with low seasonality, and moderate elevation. The region's change in snow cover, potential topographic wetness, and solar insolation are high (Table 2.6), which contributes to an abundance of available energy for vegetative growth.

Regions 10, 11, 12 and 13 are located in Taiga Plains, Boreal Plains, and Sub-Boreal Interior, all of which have a moderate vegetation seasonality, high maximum productivity and snow cover change, medium to low elevations, and moderate solar radiation conditions (Table 2.6). Soil wetness potential remains high for regions 11, 12 and 13, but low for region 10 (Table 2.6). Region 9 is located in the higher elevation regions of the Southern Interior and Southern Interior Mountains, correspondingly the soil wetness potential is low, vegetation seasonality is moderate, but snow cover change, maximum fPAR, and solar radiation values are high.

Regions 3, 4, 5, 6, 7 and 8 depict the mid to high mountainous ecosystems. Towards the north-west coast region 3 has low seasonality and high maximum vegetation characteristics (Table 2.6). In contrast, regions 4, 5, 6, 7, and 8 exhibit high vegetation seasonality and moderate vegetation greenness (Table 2.6). Regions 3 through 7 all exhibit low topographic wetness potential while region 8 has a moderate reading (Table 2.6). With the exception of region 5, these mountainous ecosystems have little change in their spring snow cover values (Table 2.6). However, regions 3 through 7 have variable average solar insolation values indicative of their latitudinal position and complex topographies. Regions 3, 4, 5, and 8 have moderate solar insolation values, region 6 low and region 7 high (Table 2.6). In summary, regions 1 through 10 characterize high to middle elevation mountainous ecosystems, and regions 11 through 16 represent lowland, interior and coastal areas (Figure 2.3).

2.5.4 Ecosystem characterization

When compared to BC's standard biogeoclimatic ecosystem classification zones, the newly developed regions occupy similar spatial areas in the coastal, Taiga, and Boreal Plains. Region 1, a coastal alpine ecosystem, is characterised by barren land, sparse vegetation and open scrublands. It is dominated by the Coastal Mountain-heather Alpine and Boreal Altai Fescue Alpine BEC zones. Region 2 is a drier coastal alpine region also characterized with low production levels (Table 2.6). Region 2 is dominated by the Coastal Mountain-heather and Interior Mountain-heather Alpine BEC zones (Table 2.6).

Region 3 is considerably more productive mountainous region than 1 and 2. It is characterised by evergreen needleleaf forests and open shrublands and is dominated by the Boreal Altai Fescue Alpine and the Engelmann Spruce-Subalpine Fir BEC zones (Table 2.6). Region 4 has similar elevation, wetness potential and climate characteristics to region 3, but its vegetation contrasts region 3 with high seasonality and open shrublands. However, region 4, like region 3, is dominated by the Boreal Altai Fescue Alpine and the Engelmann Spruce-Subalpine Fir BEC zones (Table 2.6). Region 5 is situated at a lower elevation level than region 4, and as such, has a moderate change in snow cover. Region 5 is dominated by the Spruce-Willow-Birch BEC zone (Table 2.6). Region 6 has less solar exposure than region 4 sitting at a lower average elevation; however, it exhibits similar vegetation characteristics (high vegetation seasonality and moderate production) and is also characterized by the Boreal Altai Fescue Alpine and the Engelmann Spruce-Subalpine Fir BEC zones (Table 2.6).

Regions 7 through 10 representing the moderate to high mountainous zones span high to moderate vegetation seasonality, moderate to high vegetation production levels and low to high snow seasonality respectively. These regions represent evergreen needleleaf forests, open shrublands and woody savannas. Their dominant BEC zone is the Engelmann Spruce-Subalpine Fir. Their secondary dominant zones set regions 7 and 9 apart (Boreal Altai Fescue Alpine and Montane Spruce, respectively) (Table 2.6).

Regions 11, 12 and 13 are highly productive mixed forests with high moisture availability and seasonal snow covers. Region 11 and 13 located in the Taiga and Boreal Plains are dominated by the Boreal White and Black Spruce BEC Zone (Table 2.6). Region 12 is represented by the Sub-Boreal Spruce ecosystem (Table 2.6). Coastal regions 14 and 15 are also highly productive, with low to moderate vegetation seasonality and moderate to high changes in snow cover (Table 2.6). Region 15 is located in land from region 14 which is situated on the coastline. Both regions are dominated by the Coastal Western Hemlock BEC zone; however, their variation in elevation separates their second dominant zones into Interior Cedar-Hemlock (region 14) and Mountain Hemlock (region 15) (Table 2.6). Region 16 represents the southern to central interior contains evergreen and mixed forests dominated by the Interior Douglas-fir BEC zone and the Sub-Boreal Spruce in the northern parts of the region (Table 2.6). Populating the BEC zones with our classification, we can conclude that our regions exhibit a higher level of homogeneity in coastal lowlands, southern and central Interior, but are considerably more heterogeneous in the mountainous areas (Table 2.7).

2.6 Discussion

The uniqueness of our regions can be characterized by simultaneously considering the ecological attributes of each region as well as the spatial distribution and interaction between the ecosystems. For example, though regions 1 and 2 have similar ecological characteristics, based on attributes (seen in Table 2.4), they display a pronounced latitudinal variation, with region 1 separating the south coastal and interior mountains from region 2's north coastal and interior mountains. Regions 3 and 10, and 11 and 15 have similar maximum greenness levels values, (displayed in Table 2.4), but their spatial separation and statistical properties of the other ecological characteristics set them apart.

Regions 3 and 10 have a maximum like adjacency of only 2 % and their vegetation seasonality differs between a low and moderate level respectively, suggesting phenological variations, which are exacerbated by the differences in their change in snow cover with region 3 keeping most of its snow cover into the summer months. Regions 11 and 15 found in the Taiga Plains and in-land south coast areas respectively, share similar vegetation characteristics (presented in Table 2.4), with moderate vegetation seasonality and high greenness values, but differ vastly in soil wetness potential and solar radiation. Differences between region 11 and 15 are expressed in the dominant species, Boreal Black and White Spruce in region 11 and Coastal Western Hemlock in region 15.

Regions 2, 3, 4, 6 exhibit minimal changes to their winter snow pack and regions 11 and 12 share a similar snow melt season, as seen in Table 2.4. Although, snow cover melt is an ecologically important factor for moisture availability we would expect similar rates of change between these regions because the variation is a seasonal response to the temperature rising above freezing. Mountainous areas with cooler climates and thicker snow packs keep their snow cover into the winter months. However, vegetation dynamics set mountains ecosystem regions apart. The vegetation in region 6 is seasonal with lower greenness values while region 3 has stable vegetation growth and high maximum absorption of fPAR. Rarely are regions 3 and 6 spatial adjacent with a maximum of 5% of their adjacencies together. Regions 2 and 4 are both situated at higher elevation and have low soil wetness potential; however, region 4's vegetation is seasonally variable with a green up season, moderate greenness level, and solar exposure, while region 2 is relatively barren of green foliage, and has high solar exposure. It seems the only common element between region 2 and 4 is the change in spring snow cover as their spatial extents remain disjoint with region 2 situated in the coastal mountains predominately to the south and region 4 in the Northern Boreal area.

In contrast, regions 11 and 12 are relatively ecologically similar with moderate vegetation seasonality and high maximum photosynthetic absorption (84% and 80%, respectively) representative of their high soil wetness potential. Similarities in ecological attribution are expressed by their corresponding land covers dominated by spruce forests. However, they are spatial separated with only 1% to 3% of their possible adjacencies found together and are spatial separated by region 13. In addition, their elevation levels differ. Region 11 is situated at the lowest provincial elevation level and region 12 at a moderate elevation. Specifically, they exhibit a 386 meter difference in their mean ground elevations and correspondingly have significantly different solar radiation levels (seen in Section 2.5.2), most likely impacting their species distributions (Franklin, 1995) and patterns of disturbance (Dorner et al., 2002).

In addition to spatial ecological information being useful for describing the uniqueness of regions, we indicate how the spatial pattern/interaction of individual pixels may be used for cluster aggregation. Aggregating clusters can be useful if fewer clusters are desirable. Ideally, aggregation of clusters should be based on a combination of the ecosystem characteristics and spatial proximity of individual pixels, especially given that British Columbia's elevation gradients typically have marked changes in climatic and vegetation conditions over short distances (Austin et al., 2008). As a suggestion, ecosystems differing in more than two ecological characteristics should not be combined. For example, 16% of Region 5's possible adjacencies are found beside region 10; however, their vegetation characteristics differ (Section 2.5.2). Region 5 exhibits a higher level of vegetation production and snow cover melt. These regions also have different dominant BEC zones Spruce-Willow-Birch (region 5) and Engelmann Spruce-Subalpine Fir (region 10). In contrast, regions 12 and 13 are spatially adjacent, and have similar high vegetation productivity levels, change in snow cover and moderate solar exposure. Notably, regions 12 and 13 house different BEC zones, including the Sub-Boreal Spruce and Black and White Spruce respectively and provide significant ecological indicator regional means, but their spatial proximity provides them with similar growth conditions. Therefore, at the spatial scale examined; it may be ecologically and spatially suitable to consider combining regions 1 and 2, 4 and 7, and 12 and 13; however, in-field assessment is advised as we draw upon these results by comparing the regional average of the ecological indicators.

We can further contextualize our regions through comparison with the utilized and standard BEC zones. Areas of discrepancy between our classification and the BEC zones are similar to those found by Hamann and Wang (2006) who predicted BEC zones using climate data and discriminant analysis. Similar to our results, they found significantly higher classification success rates in the regions of low topographic relief than the mountainous areas of BC. The variability found between our regionalization and BEC zones in the mountainous and central interior regions may be a result of remotely sensed imagery and terrain indices providing a uniform amount of detail over the province which is too costly for in situ sampling (Duro et al., 2007) which governs the BEC classification program (Pojar et al., 1987; Delong et al., 2010). Further, the mountainous regions are spatially variable and more complex than the central interior regions, with elevation gradients and different slope aspects leading to both physiographic and vegetation complexity. Within mountainous areas, the selected ecosystem classifiers have the ability to distinguish the natural heterogeneity that characterizes them.

Unlike the BEC ecosystems boundaries which emphasize the patterns of static variables such as landforms, soils and climax vegetation conditions (Pojar et al., 1987) our methods explicit represent temporally dynamic ecosystem characteristics susceptible to anthropogenic effects and climate change by including Earth observation data. For example, the case of the central interior where vegetation greenness has been subjected to wide spread mountain pine beetle infestation (Robertson et al., 2009; Safranyik et al. 2010). Instead of the vegetation dynamics representing the ecosystem's mature vegetation conditions modelled in the BEC zones (Pojar et al., 1987); our regionalization approach includes the current vegetation conditions representing a more homogeneous central interior. By including current conditions we are allowing for the contemporary vegetation status, growth and variability to be represented. In addition by utilising remote sensing datasets which are continuously updated, this proposed approach is potentially useful for monitoring. A variety of remote sensing datasets can be utilised, including long-term means, or layers updated annually allowing a much more dynamic representation of the ecoregionalizations to be created as ongoing datasets become available.

At the same time as recognizing the strengths of our regionalization approach, data limitations must also be acknowledged. For instance, MODIS sensors are sensitive to atmospheric attenuation and spectral mixing (Jensen, 2007); therefore, maximum fPAR and fractional snow cover should be considered best approximations. It is possible that cloud cover has masked maximum values and spectral mixing has had an effect on the true spatial variation of the vegetation and snow cover indices. We also recognize that in the mountainous areas of BC shadowing due to topography and atmospheric interference may be a concern (Huete et al., 2011). To reduce this possible source of error we used MODIS quality assessment information and monthly maximum retrievals to develop the indicators used. However, apart from the vegetation and snow cover characteristics that may be effected, solar insolation and TWI derived from ground elevation data remain ecological separable.

Despite data limitations, representing species richness using indirect indicators of biodiversity derived from remotely sensed imagery makes spatially consistent standardized broad-scale ecosystem diversity modelling possible when resources and time limit in-field assessments (Franklin, 1993). We considered our biodiversity metrics as components of the ecosystem related to species richness and metrics most effectively represent biodiversity when combined into homogeneous regions, rather than being studied in isolation. We are not suggesting that large-area Earth observation ecosystem modelling could replace in-field or species-specific biodiversity assessments; rather, it should be used as a supplement to target resources for detailed ecosystem monitoring in the most vulnerable areas.

2.7 Conclusion

Given the ecosystem indicators selected, our methods ensure a robust regionalization system that maximizes the variance between and homogeneity within each ecosystem unit at 1 km resolution. The metrics build upon well-established environmental relationships and suggested modelling practices (e.g., Franklin, 1995; Mackey et al., 2004; Duro et al., 2007; Coops et al., 2008, 2009a) and provide sufficient detail, accuracy and spatial consistency to recognize changes or shifts in ecosystem regions (Coops et al., 2008, 2009a; Hyde et al., 2010). By monitoring ecosystem dynamics researchers are transforming space-time data into a resource management tool. Additionally, by ranking the average indicator value into classes of low, medium and high we provide an intuitive summary of the spatial variability of BC’s landscape.

By combining the benefits of systematically and repeatedly collected remotely sensed datasets with a quantitative regionalization approach we have created a baseline model for future ecosystem monitoring. We recommend our approach be used as a supplement to traditional in situ biodiversity assessments (e.g., BC’s biogeoclimatic zones) to provide detail in under-sampled regions of BC or areas experiencing landscape change to support adaptive resource management strategies and resource conservation policies aiming to protect the current, and future, biotic diversity present over the province of British Columbia (BC Ministry of Environment, 2011). With anticipated shifts in BC’s ecosystem dynamics (Hamann and Wang, 2006) monitoring should be a central priority of British Columbia’s conservation initiatives.

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Table 2.1 Summary of the freely available geospatial datasets considered for our broad-scale ecosystem regionalization

Biodiversity metric	Source data	Spatial resolution	Ecological relevance
Elevation	Canadian Digital Elevation Data	25 m	Elevation gradients determine species distributions, vegetation production levels and patterns of disturbance (Franklin, 1995; Dorner et al., 2002).
Topographic Wetness Index	Canadian Digital Elevation Data	25 m	Steady state topographic wetness indices correlate well with soil attributes such as horizon depth, silt percentage and organic matter (Moore et al., 1993) and thereby provide a good indication of site productivity (Franklin, 1995).
Solar Insolation	Canadian Digital Elevation Data	25 m	Solar radiation affects microclimatic processes (Kumar et al., 1997), ultimately influencing the growth activity of plants.
Spring Snow Cover (Max, Min, Chg.)	Daily Fractional Snow Cover (MOD10A1)	500 m	Snow distribution dictates species establishment and occurrence (Walker et al., 1999) with snow melt rates influencing vegetation growth patterns and seasonality (Kudo, 1991; Walker et al., 1999).
fPAR Indices (Max, Min, Sum, CV)	8-day Maximum fPAR (MCD15A2)	1000 m	Highly productive vegetated areas provide more resources to partition between species (Walker et al., 1992) and highly productive ecosystems are considered to be more resilient and recover faster from disturbance (Stone et al., 1996).

Table 2.2 Categories used to rank the average ecosystem indicator value per region.

Variables	Categories		
	Low	Medium	High
Max. fPAR (%)	0 - 32	32 - 73	73 – 100
CV fPAR	0 - .34	.34 -.76	.76 - 2.14
Chg. Snow (%)	0 - 35	35 - 76	76 – 100
Elev. (m)	0 - 809	809 - 1437	1437 – 3534
TWI (ln %)	5.4 - 12.1	12.1 - 13.7	13.7 - 23.5
Solar Rad. (Wh/m^2)	41,643 – 857,797	857,797 – 1,040,432	1,040,432 – 1,497,022

Table 2.3 Spearman's correlation matrix, monotonic relationships are significant at p-value < .001.

	TWI ln(%)	Elev. (m)	Solar Rad. (WH/m^2)	Max. Snow (%)	Min. Snow (%)	Chg. Snow (%)	CV fPAR	Sum. fPAR	Max. fPAR	Min. fPAR
TWI	1									
Elevation	-0.43	1								
Solar Rad.	0.04	0.29	1							
Max. Snow	-0.30	0.49	-0.08	1						
Min. Snow	-0.45	0.57	-0.11	0.62	1					
Chg. Snow	0.35	-0.36	0.06	-0.07	-0.78	1				
CV fPAR	-0.08	0.27	-0.12	0.44	0.30	-0.03	1			
Sum. fPAR	0.36	-0.53	0.10	-0.66	-0.68	0.36	-0.43	1		
Max. fPAR	0.29	-0.52	-0.01	-0.47	-0.57	0.38	-0.11	0.83	1	
Min. fPAR	0.37	-0.41	0.17	-0.61	-0.61	0.31	-0.50	0.89	0.61	1

Correlations were assessed to ensure data independence before applying the two-step cluster.

Table 2.4 Dunnett T3 post-hoc test for unequal variances and samples sizes.

Dunnett T3 Post-hoc test for 17 Ecosystem Regions						
					Confidence Interval	
Variable	Regions	Mean Difference	Std. Error	Sig.	Lower bound	Upper bound
CV fPAR	1 and 2	0.000	0.000	1.000	-0.001	0.002
Max. fPAR	1 and 2	-0.052	0.032	1.000	-0.174	0.071
Max. fPAR	3 and 10	-0.056	0.129	1.000	-0.518	0.406
Max. fPAR	11 and 15	0.194	0.072	0.617	-0.070	0.458
Chg. Snow	3 and 6	-0.034	0.149	1.000	-0.593	0.526
Chg. Snow	4 and 2	0.249	0.090	0.548	-0.087	0.586
Chg. Snow	11 and 12	-0.075	0.038	0.998	-0.194	0.044
TWI	3 and 6	-0.003	0.007	1.000	-0.029	0.023

Results conclude that the ecosystem regions provide statistically unique combination of the ecosystem indicators.

Table 2.5 Rook’s case first order cell contiguity matrix, showing the percentage of like adjacencies between the ecosystem categories (excludes background value adjacencies found at the provincial extent).

Regions	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**
1	63	16	8	4	1	5	2	2	0	0	0	0	0	0	1	0	3
2	11	64	5	1	0	0	7	1	0	0	0	0	0	0	0	0	1
3	6	5	24	5	2	4	8	3	1	1	0	0	1	1	1	2	2
4	6	3	11	52	6	13	16	10	1	1	0	0	0	0	0	0	3
5	1	0	4	5	32	14	2	9	2	10	0	3	1	0	4	0	4
6	4	0	5	8	10	36	0	7	0	2	0	0	0	0	4	0	4
7	2	8	9	9	2	0	41	5	4	0	0	0	0	0	0	0	2
8	2	2	8	11	11	13	10	49	4	2	0	2	0	0	0	0	5
9	0	1	3	1	4	1	10	5	65	10	0	2	0	0	0	5	4
10	0	0	2	1	16	4	1	3	9	49	0	6	4	0	4	2	5
11	0	0	0	0	1	0	0	0	0	0	84	3	4	2	6	0	5
12	0	0	1	0	6	2	0	3	3	9	3	58	9	2	3	7	7
13	0	0	3	0	3	0	0	0	0	7	6	12	68	6	8	5	6
14	1	0	3	0	0	0	0	0	0	0	2	1	3	76	21	1	6
15	1	0	1	0	2	4	0	0	0	1	2	1	1	7	43	0	5
16	0	0	11	0	1	0	0	1	10	4	0	10	6	2	0	77	4
17	2	1	3	2	3	4	2	3	1	2	2	2	1	3	6	1	34

Note that because the regions have different spatial shapes order between the percentage of like adjacencies matters (i.e., the percentage of like adjacencies between region 1 and 2 is different from the percentage of like adjacencies between region 2 and 1). Furthermore, while the percentage magnitudes between like adjacencies of the same class differ the values indicate spatial trends (refer to Section 2.5.2).

Table 2.6 A summary of the ranked ecosystem variables, dominant land cover and biogeoclimatic zone.

		Categorized variable rank comparison						Dominant land cover and ecosystem type			
Region	% Area	CV fPAR	Max. fPAR	Chg. Snow	Elev.	TWI	Solar Rad.	Dominant land cover	Second dominant land cover	Dominant BEC Zone	Second dominant BEC zone
1	4	Low	Low	Low	High	Low	Med.	Barren or sparsely vegetated	Open shrublands	Coastal Mountain-heather Alpine	Boreal Altai Fescue Alpine
2	2	Low	Low	Low	High	Low	High	Barren or sparsely vegetated	Open shrublands	Coastal Mountain-heather Alpine	Interior Mountain-heather Alpine
3	2	Low	High	Low	High	Low	Med.	Evergreen Needleleaf Forest	Open shrublands	Boreal Altai Fescue Alpine	Engelmann Spruce - Subalpine Fir
4	5	High	Med.	Low	High	Low	Med.	Open shrublands	Evergreen Needleleaf forest	Boreal Altai Fescue Alpine	Engelmann Spruce - Subalpine Fir
5	4	High	Med.	Med.	Med.	Low	Med.	Evergreen Needleleaf forest	Woody savannas	Spruce - Willow - Birch	Engelmann Spruce - Subalpine Fir
6	3	High	Med.	Low	Med.	Low	Low	Evergreen Needleleaf forest	Woody savannas	Boreal Altai Fescue Alpine	Engelmann Spruce - Subalpine Fir
7	3	High	Med.	Low	High	Low	High	Open shrublands	Evergreen Needleleaf forest	Engelmann Spruce - Subalpine Fir	Boreal Altai Fescue Alpine
8	5	High	Med.	Low	Med.	Med.	Med.	Evergreen Needleleaf forest	Open shrublands	Engelmann Spruce - Subalpine Fir	Spruce - Willow - Birch
9	7	Med.	High	High	High	Low	High	Evergreen Needleleaf forest	Open shrublands	Engelmann Spruce - Subalpine Fir	Montane Spruce
10	6	Med.	High	High	Med.	Low	Med.	Evergreen Needleleaf forest	Woody savannas	Engelmann Spruce - Subalpine Fir	Spruce - Willow - Birch
11	9	Med.	High	High	Low	High	Med.	Evergreen Needleleaf forest	Mixed forest	Boreal White and Black Spruce	Interior Cedar -Hemlock
12	10	Med.	High	High	Med.	High	Med.	Evergreen Needleleaf forest	Mixed forest	Sub-Boreal Spruce	Boreal White and Black Spruce
13	12	Med.	High	High	Med.	High	Med.	Evergreen Needleleaf forest	Mixed forest	Boreal White and Black Spruce	Sub-Boreal Spruce
14	7	Low	High	Med.	Low	Med.	Med.	Evergreen Needleleaf forest	Mixed forest	Coastal Western Hemlock	Interior Cedar -Hemlock
15	3	Med.	High	High	Low	Low	Low	Evergreen Needleleaf forest	Mixed forest	Coastal Western Hemlock	Mountain Hemlock
16	15	Low	High	High	Med.	High	High	Evergreen Needleleaf forest	Mixed forest	Interior Douglas-fir	Sub-Boreal Spruce
17	3	Low	Low	Med.	Low	N/A	Med.	Water	Water	N/A	N/A

The low, medium and high variable ranks were created by utilizing the natural breaks of the ungrouped data. Subsequently, the regional means were described by the appropriate low, medium, or high categories to assist ecological interpretation.

Table 2.7 A summary of the most frequently occurring ecosystems/regions found within each of BC’s biogeoclimatic zones.

BEC Zone	Ecosystems representing more than 2% of each BEC zone	Dominant region	Second dominant region
Boreal Altai Fescue Alpine	**8**	4	1
Bunchgrass	**6**	16	14
Boreal White and Black Spruce	**5**	11	13
Coastal Douglas Fir	**4**	14	15
Coastal Mountain-heather Alpine	**8**	1	2
Coastal Western Hemlock	**6**	14	15
Engelmann Spruce - Subalpine Fir	**11**	9	10
Interior Cedar –Hemlock	**7**	16	13
Interior Douglas-fir	**6**	16	13
Interior Mountain-heather Alpine	**7**	2	7
Mountain Hemlock	**11**	6	8
Montane Spruce	**3**	16	9
Ponderosa Pine	**6**	16	14
Sub-Boreal Pine – Spruce	**3**	16	12
Sub-Boreal Spruce	**4**	12	16
Spruce - Willow – Birch	**7**	10	5

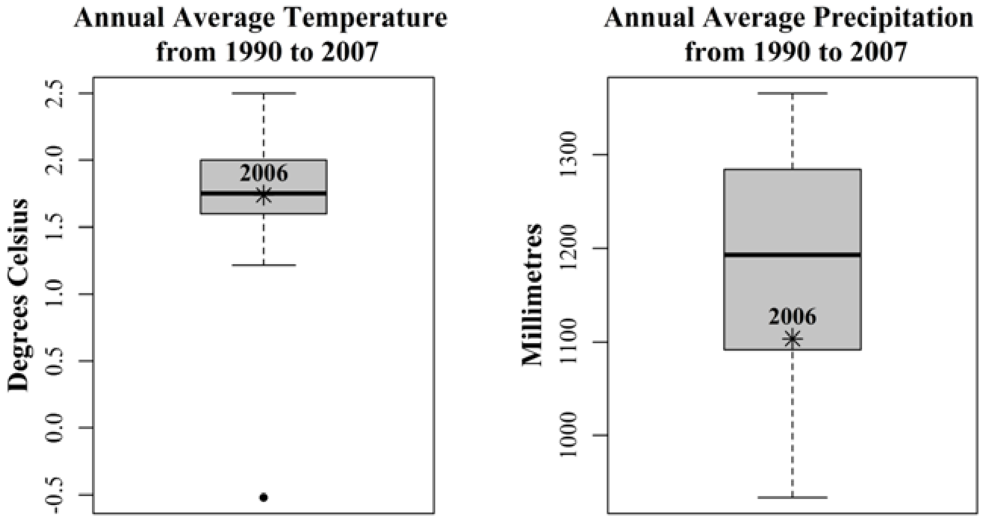

Figure 2.1 British Columbia's annual average temperature and precipitation estimates from 1990 to 2007. Data were derived from Climate Western North America program which provides PRISM modelled climate data, in this case, using the Shuttle Radar Topography Mission 1 km Digital Elevation Model (see Wang et al., 2006 for additional modelling details).

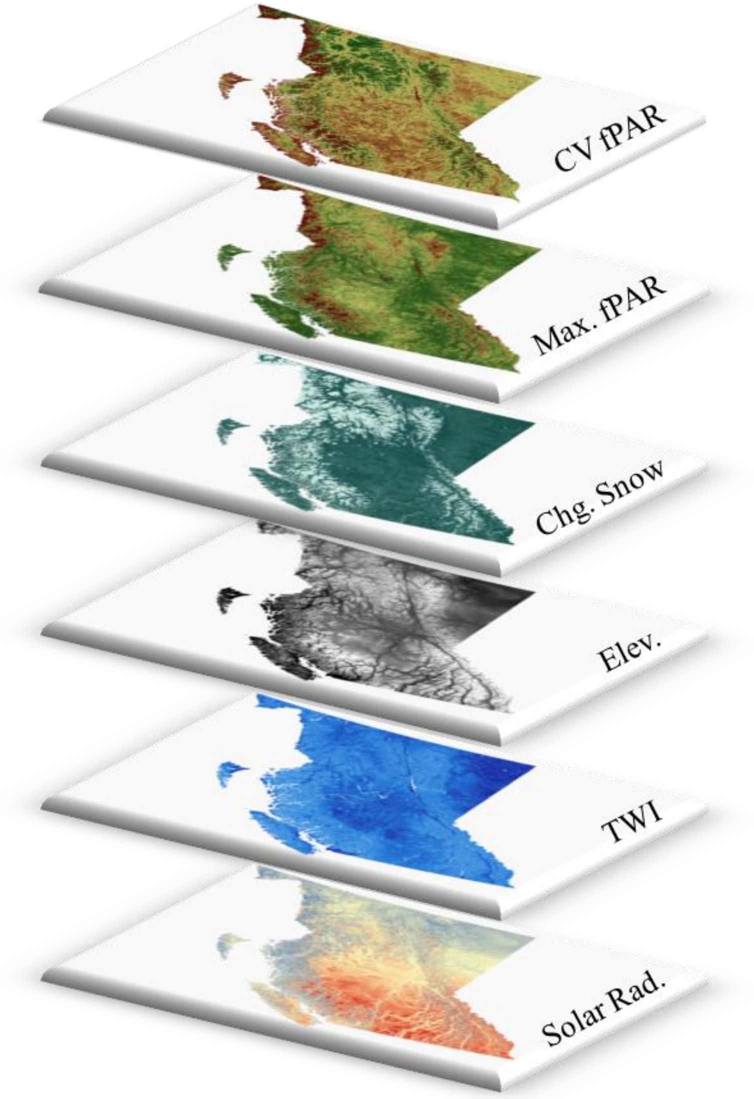

Figure 2.2 Six independent biodiversity indicators used for ecosystem modelling.

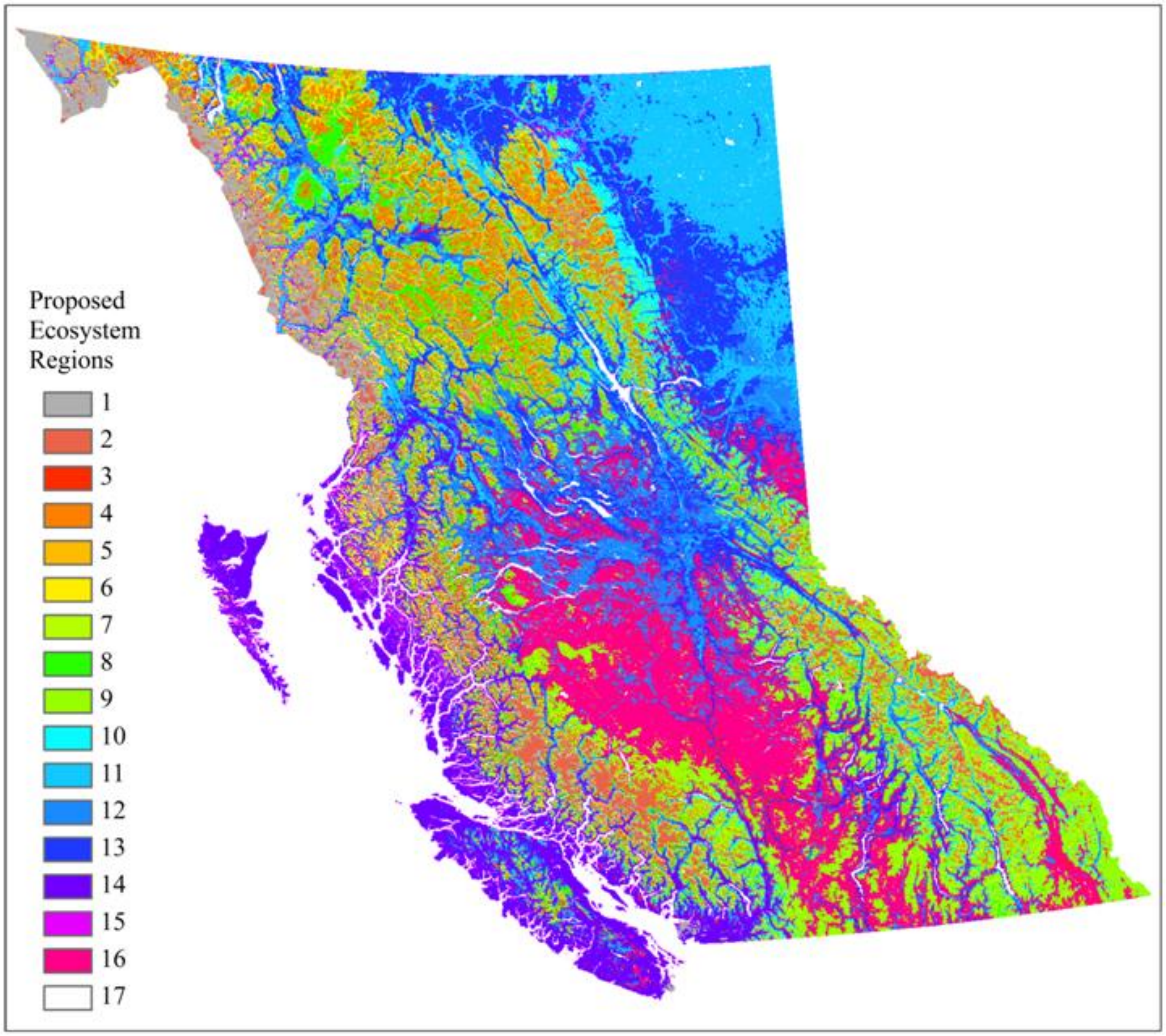

Figure 2.3 Geospatial regionalization of BC’s ecosystem diversity distinguishing 16 terrestrial ecosystem units (regions 1 through 16) and one water class (region 17). Regions 1 through 10 represent mountainous ecosystems and regions 11 through 16 delineate coastal and lowland areas.

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3.0 EXPLORING THE LANDSCAPE-SCALE PROCESSES DRIVING GEOGRAPHICAL PATTERNS OF BREEDING BIRD RICHNESS IN BRITISH COLUMBIA CANADA

3.1 Abstract

By exploring relationships between bird richness and environmental variables, we can better understand landscape conditions, which lead to biological richness and use these relationships to predict the response of vertebrate species to landscape disturbance and change. Breeding bird atlases are an important resource used to map and monitor bird spatial distributions and avian population levels. The spatial extent of bird atlas data provides opportunities to assess the environmental drivers of species richness over large areas. We used data from the British Columbia (BC) Breeding Bird Atlas to examine the influence of productivity, ambient energy and habitat heterogeneity on independently measured breeding bird richness and examine the effects of survey effort and observation biases on the spatial distribution of avian populations. We used non-parametric regression tree analysis to explain the dominant ecological process influencing the variation in breeding bird richness levels. Our results indicate that total breeding richness is significantly correlated ($\alpha < 0.001$) with time spent surveying and the number of surveys collected. By stratifying species richness by survey effort, we observe that ambient energy is the top ranked environmental predictor of breeding bird richness across BC with a combination of environmental variables explaining approximately 40% of the variation in richness. Using our modelled relationships, we predict breeding bird richness in the areas of BC not presently surveyed between three and six hours. The productive Boreal Plains concentrated around Ft. St. John and Dawson Creek, in the southern portion of the Taiga Plains region, the lowlands of the South and Central Interior, along the Rocky Mountain

Trench and the coastal areas of the Georgia Depression are predicted to have the highest categories of breeding richness (35-57 unique species). Our results support ongoing species diversity gradient research, which identifies ambient energy as important factor influencing species diversity distributions in the northern hemisphere. By linking breeding bird richness to environmental data derived from remotely sensed data and systematically collected climate data, we present a possible method of monitoring environmental variables as a surrogate for species diversity health over broad spatial scales. By exploring the influence of survey effort on species richness metrics we also highlight the need to consider consistent collection of additional variables, such as observer experience and breeding season information, to allow greater flexibility for removing survey bias and increasing the utility of atlas data for conservation management and species richness studies.

3.2 Introduction

By exploring relationships between bird richness and environmental variables, we can better understand landscape conditions that lead to biological richness, which is essential for predicting the response of vertebrate species to landscape disturbance and change (Orme et al., 2005). Given that avian species are uniquely able to select for ephemeral resources, birds are considered suitable indicators of habitat condition (Hurlbert and Haskell, 2003) and vertebrate population levels (Blair 1999; Gregory et al., 2003). Therefore, in establishing the ecological processes governing the spatial distribution of the breeding birds we can provide important information for the preservation of habitat conditions know to support high levels vertebrate species richness.

Key environmental drivers of avian richness at regional to global spatial scales include landscape productivity (Wright, 1983; Currie, 1991; Blackburn and Gaston, 1996; Rahbek and Graves, 2001; Hurlbert and Haskell, 2003; Rensburg et al., 2002; Coops et al., 2009a), ambient energy (Currie, 1991; Lennon et al., 2000; Hawkins et al., 2003a), and habitat heterogeneity (Būhning-Gaese, 1997; Kerr and Packer, 1997; Jetz and Rahbek, 2002; Rahbek et al., 2007). Relationships are hypothesized to occur because productivity directly and indirectly limits food resources (Wright, 1983; Hawkins et al., 2003b), ambient energy satisfies the thermoregulatory needs of species (Currie, 1991), and habitat heterogeneity provides niche variety thereby limiting species competition and supporting a diversity of specialist species (Andrén, 1994; Berg, 1997; Farina, 1997).

Breeding Bird Atlas data offers a unique opportunity to assess spatial effects of these ecological processes on species richness over large areas (e.g., Rensburg et al., 2002, Chown et al., 2003). Species atlases generally rely on a large volunteer base to collect data over substantial landscape extents. The main strength of the gridded breeding bird atlas is the organizational structure allowing for spatially consistent repeat assessments of bird distributions and abundance (Donald and Fuller, 1998). Additionally, information gathered from species atlases holds potential to delineate species ranges, monitor species population status, species richness, and species at risk (Donald and Fuller, 1998; Robertson et al., 2010). Assessing the relationship between avian richness and environmental variables also requires environmental data to match the spatial extent of gridded atlases (Donald and Fuller, 1998). Remotely sensed imagery and geospatial datasets play a critical role in this aspect by linking avian richness (e.g., Būhning-Gaese, 1997; Atauri and de Lucio, 2001; Hurlbert and Haskell, 2003; Luoto et al., 2004; Coops et al., 2009a, 2009b) to environmental variables from regional (e.g., Luoto et al., 2004) to continental extents (e.g., Coops et al., 2009b).

For instance, studies have used satellite derived measures of landscape greenness (surrogate for productivity often measured using Normalized Difference Vegetation Index (NDVI) or fraction of absorbed photosynthetically active radiation (fPAR)) to evaluate the relationship between avian species richness and productivity (Hurlbert and Haskell, 2003; Hawkins, 2004; Evans et al., 2006; Coops et al., 2009a, 2009b; St-Louis et al., 2009). Indirectly measured ambient energy (e.g., evapotranspiration or atmospheric temperature) has been mapped from climate records to display a notable effect on variation in avian richness at regional (Lennon et al., 2000), continental (Currie, 1991), and global scales (Hawkins et al., 2003a). Additionally, within grain landscape heterogeneity represented as the number of land cover types per hectare (Autari and De Lucio, 2001; Coops et al., 2009b), elevation standard deviation (Ruggiero and Hawkins, 2008), or texture of NDVI (St-Louis et al., 2009) has been shown to influence the distribution of avian species richness; however, the importance of habitat heterogeneity on the gradient of species richness can vary with study extent and grain size (e.g., Būhning-Gaese, 1997).

Understanding the environmental influences on breeding bird richness over BC can provide important information for conservation managers and help scientists move towards monitoring landscape indices as indicators of potential threats to avian and more generally vertebrate population status. Thus, an important step toward developing robust habitat models able to indicate potential threats to bird species is to investigate if the variation in avian species richness can be predicted with data sets that are collected in a consistent, repeatable manner, over short time intervals.

The British Columbia (BC) Breeding Bird Atlas presents a novel opportunity to assess the spatial effects of habitat patterns on avian species richness. The goal of our study is to explore the relative influence of sampling bias on the observed breeding richness to control survey bias and use the developed richness indices to identify the dominant landscape-scale processes driving the distribution of BC's breeding bird richness. To meet our goal, we demonstrate how systematically collected Earth observation datasets and topographically adjusted climate data can represent fundamental landscape-scale process. Second, we explore the association between survey bias and measures of total breeding richness. Third, we apply non-parametric regression tree analysis to investigate and model relationships between the richness of breeding birds and hypothesized landscape drivers (productivity, ambient energy and landscape heterogeneity). Fourth, we use the modelled relationships relatively unaffected by survey bias to predict breeding richness across the province at uniform survey lengths to provide information for conservation management of avian diversity. We conclude by discussing the contributions of work to regional species diversity studies and indirect mapping of the status of species richness through landscape-scale surrogates.

3.3 Landscape variable background

Productivity both as a permanent and seasonal resource is documented to influence avian species richness (Hurlbert and Haskell, 2004; Hawkins, 2004; Coops et al., 2009b). For instance, it is understood that resident avian richness is limited by the lowest production period and migratory species by the seasonal production pulse (Hurlbert and Haskell, 2003; Hawkins, 2004),while the distribution of total avian species richness responds to cumulative landscape production representing both seasonality and maximum production levels (Coops et al., 2009b). To assess the effects of production on avian richness distribution, remotely derived landscape indices of productivity, surrogates of growth and seasonality, have been developed over broad scales for both annual (Coops et al., 2009a, 2009b) and seasonal (Hurlbert and Haskell, 2003) time scales. However, annual indices of productivity have been hypothesized to obscure landscape relationships leaving one to consider the time scale in which bird distribution and abundance data were collected (Hurlbert and Haskell, 2003; Hawkins, 2004).

Ambient energy, measured in the form of water-energy variables or atmospheric temperature, is documented to influence the variation in vertebrate species richness (e.g., Currie, 1991, Lennon et al., 2000; Hawkins et al., 2003a) particularly in the terrestrial areas of North Hemisphere where thermoregulatory needs of species must be met (Currie,1991; Hawkins et al. 2003a). The relative importance of ambient energy is displayed at both regional (Lennon et al., 2000) and global extents (Hawkins et al., 2003a). For example, summer air temperature is a documented predictor of avian species richness through the geographic extent of the United Kingdom (Lennon et al. 2000) and water-energy variables, such as, potential evapotranspiration account for a significant variation in species diversity in the Northern Hemisphere (Hawkins et al. 2003a). In addition to air temperature and moisture availability, static climate indicators have been shown to influence the gradient of avian species richness. For example, average elevation influences avian species richness at regional extents, with species favouring lower elevations (Farina, 1997). Elevation range, an indirect measure of climate variation (Ruggiero and Hawkins, 2008), has also been identified to enhance the prediction of avian richness (Davies et al., 2007).

The strength of habitat heterogeneity as a predictor of the distribution of avian species richness often depends on the scale of analysis. For example, in the Mediterranean region, habitat heterogeneity has a stronger relationship with species richness than ambient energy (Autari and De Lucio, 2001). Similarly, regional predictive models of richness in Chihuahuan Desert of New Mexico were improved by a combination of productivity and habitat heterogeneity measures (St. Louis et al., 2009). Conversely, at broad spatial scales, Ruggiero and Hawkins (2008) concluded that the climatic gradients influence species richness and must be controlled for before the importance of habitat heterogeneity can be realized. Therefore, we postulate that habitat heterogeneity may be a more influential indicator of avian distributions at regional scales or warmer regions where thermoregulatory needs of species are already satisfied (see Kerr and Packer, 1997, Table 1). Please see Table 3.1 for short summary of notable avian species richness predictors.

3.4 Study area

British Columbia (BC) covers over 940,000km^2 with the land mass physiography and climate controlled by the Pacific Ocean to the west, continental air masses in the interior plateaus, and Rocky Mountains to the east (Austin et al., 2008). BC has highly diverse ecosystem structure comprised of barren and snow covered alpine environments, moderately productive mountainous regions, warm Southern Interior Mountains, moist and productive Taiga and Boreal plains, productive evergreen coastlines and moderately warm and productive interior (Fitterer et al., 2012). The complex landscape structure and ecological processes of BC require predictive breeding bird richness modelling techniques that are able to accommodate non-linear relationships and interaction effects between environmental variables within regions.

3.5 Data and pre-processing

3.5.1 Breeding bird data description

Breeding bird species data used in our analysis were collected as part of the BC Breeding Bird Atlas. The BC breeding bird atlas is a five-year volunteer-based project compiling information on the distribution of all breeding bird species in 10 km by 10 km gridded areas (British Columbia Breeding Bird Atlas, 2011). Breeding evidence information is collected at different confidence levels ranging from observed during the breeding season (with no breeding evidence) to confirmed (displaying visible breeding activities) (British Columbia Breeding Bird Atlas, 2011). For Each observation of a species in a 10 km by 10 km quadrat, the highest level of breeding confirmation is recorded. These levels indicate the likelihood of breeding and 20 different descriptions are available to the bird observer. Nine of the 20 categories are reserved for confirmed breeding activities such as nesting, evidence of bird shells, young present in the nest and adults carrying food to a nest, and three out of the 20 categories are reserved for observed or possible breeding signs such as sightings during the breeding season and breeding calls. The remaining categories exhibit probable breeding characteristics, such as multiple singing males, couple observed in suitable nesting area, among others (British Columbia Breeding Bird Atlas, 2008a). Data used in our study were a compilation of species sightings from 2008-2011. Observer experience ranges from novice to experienced, but no direct attribute of surveying experience is collected. Data provided includes survey effort per sample, observer number, survey number, quadrat identification and taxonomic information.

3.5.2 Breeding richness indices

In order to control for survey effort we represent species richness in a variety of ways. We began by exploring breeding sightings to understand the surveying intensity (number of surveys conducted per grid cell), survey effort (hours spent observing) and spatial extent. We calculated the number of unique species observed within each 10 km by 10 km grid cell (total breeding richness) and recorded maximum survey effort and amount of surveys per grid cell to uncover sampling bias. Using the indices created we quantified the association between breeding richness and maximum survey effort (r_s= .785, α .001) and number of surveys per gird cell (r_s =.718, α .001). Spearman's correlations exhibit strong positive relationships indicating that survey effort and the number of surveys conducted influences the distribution of observed breeding richness.

To understand sampling bias we investigated the skewness and spatial distribution of the Breeding Bird Atlas data up to 2011. Maximum per sample survey effort and total number of surveys data per quadrat exhibit positive skewness (3.9 and 3.4, respectively), with the majority of the province having less than six hours of per survey observational effort, and less than three surveys, with a large portion of grid cells having one to two observation visits. The number of surveys per grid cell limits our ability to apply rarefaction estimates, which require random selection of samples per grid cell (Colwell and Coddington, 1994). Instead, we stratified species richness into survey effort ranges as species richness is expected to increase with survey effort until reaching an asymptote at which all species are observed (Colwell and Coddington, 1994).

To maximize spatial extent of breeding species information over the areal extent of BC we stratified survey effort up to six hours of observation effort (the mean maximum survey length). Categories of survey effort included one to two hours, three to four hours and five to six hours. Breeding bird richness is represented within the stratifications as the maximum number of unique species sighted per survey and 10 km x 10 km grid cell. Once stratified in survey lengths within a two-hour interval (one to two hours, three to four hours, and five to six hours) the quadrats had relatively few completed surveys (average 1.6, 1.3 and 1.2 samples respectively).

3.5.3 Landscape indices

Productivity

Productivity indicators were created from 8-day maximums of Moderate Resolution Imaging Spectroradiometer measured fPAR (MCD15A2) spanning February to September, the same temporal extent as the breeding bird season (British Columbia Breeding Bird Atlas, 2008b). The fraction of absorbed photosynthetically active radiation (fPAR) is measured between 400-700nm (Yuhong et al., 2000) and ranges from 0%, signifying barren land or snow cover, to 100 % for dense vegetation cover (Coops et al., 2008). Monthly maximums were created from the 8-day interval datasets to minimize the effect of cloud cover on the remotely sensed imagery. Subsequent to monthly aggregation, seasonal (February-September) indices from 2008-2011 were derived. Indices included seasonal minimum vegetation cover, maximum vegetation cover, cumulative sum and coefficient of variation representing vegetation seasonality. Productivity indices were then averaged over the 2008-2011 breeding bird data set collection period and re-sampled to 10 km by 10 km resolution using a neighbourhood average to match the spatial resolution at which the avian breeding evidence was collected. Water bodies were masked to avoid skewed productivity values.

Ambient energy

Estimates of ambient energy were produced using MODIS 8-day maximum 1km land surface temperature data (MYA11A2), also aggregated to an approximate monthly maximum. MODIS land surface temperatures (units Kelvin) were calculated from daily conditions represented in the thermal infrared bands during clear sky conditions (Wan et al., 2004). Land surface temperature (LST) is interpreted as the temperature of the canopy top in dense vegetation covers, or soil surface in barren areas (Wan et al., 2004). Subsequent to monthly aggregation, seasonal (February-September) indices from 2008-2011 were derived. Indices include annual seasonal minimum, maximum and range in seasonal LST (February to September) which were averaged over the 2008-2011 time period and re-sampled to 10km by 10km regions using a neighbourhood average.

In addition, to land surface temperature, topographically adjusted climate record data were used to represent atmospheric temperature and moisture availability. Using a re-sampled 1 km digital elevation model created from the Canadian Digital Elevation product (available from www.Geobase.ca) we developed indices representing mean annual temperature, mean summer precipitation, mean annual precipitation, annual climate moisture deficit and annual reference atmospheric evaporative demand over the province of BC from interpolated climate data using the ClimateWNA program. Mean annual temperature, mean annual precipitation, and mean summer precipitation (May to September) are directly calculated from observed monthly weather station data and interpolated across the province (Wang et al., 2012). Both mean annual and summer precipitation were included in our models because the mean summer precipitation did not extend the temporal length of the breeding season for all species in BC (British Columbia Breeding Bird Atlas, 2008b). Reference atmospheric evaporative demand (E_{ref}) and climate moisture deficit (CMD) were derived using Hargreaves equations (see Wang et al., 2012 for equation details). Reference atmospheric evaporative demand is the amount of moisture lost to atmospheric evaporation and climate moisture deficit is interpreted as a drought variable, calculated as the sum of the monthly differences between E_{ref} and precipitation (Wang et al., 2012). Weather data were available for 2008 and 2009. These 1km climate indices were re-sampled from 1km spatial resolution to 10km by 10km using a neighbourhood average. Additionally, to indirectly represent BC's climate we re-sampled 25 m Canadian Digital Elevation Product to 10 km by 10 km using a neighbourhood average and calculated the within pixel range in elevation as a surrogate of climate variation.

Landscape heterogeneity

Habitat heterogeneity was calculated using 25m spatial resolution elevation data provided by the Canadian Digital Elevation Product. Terrain heterogeneity was estimated as the coefficient of variation in elevation within each 10km by 10km grid cell over BC. A second measure of heterogeneity was the complexity of land cover types. The 2009 500m MODIS Terra and Aqua (Version 005, University of Maryland) land cover (MCD12Q1) was used to calculate the number of different land cover types in each 10km by 10km grid cell and also provided land cover information to calculate the queens case percentage of like adjacencies of the nearest-neighbour re-sampled 1km land cover pixels, aggregated to a 10km by 10km using a neighbourhood maximum.

3.6 Methods

3.6.1 Random Forest modelling

Given correlations between survey effort, number of surveys and total breeding richness; maximum species richness per survey and quadrat stratified by one to two hours, three to four hours, and five to six hours of observational effort were used when characterizing the relationships between breeding bird species richness and the landscape indices, representing productivity, ambient energy and landscape heterogeneity. Relationships were modelled using regression trees created in Random Forests R statistical package (described in Breiman, 2001). Regression trees repeatedly partition the selected environmental indices using a hierarchical structure and binary splits based on singular environmental variables that best explain the variation in our breeding bird species richness indices (De’ath and Fabricius, 2000). The “best” split is determined by iteratively examining the landscape indices splits and selecting the environmental variance (split) that maximizes the heterogeneity between the resulting breeding richness groups (ANOVA) (Prasad et al., 2006). Regression trees provide a flexible and robust method for ecological studies when the relationships between dependent and independent variables are non-linear or exhibit interaction effects (De’ath and Fabricius, 2000; Prasad et al., 2006).

We used the Random Forests algorithm to grow 999 regression trees from bootstrapped samples of the original data frame for each survey effort stratification (one to two hours, three to four hours and five to six hours). In addition to the bootstrap sample, the Random Forests algorithm employs a second randomization step where, at each node within the singular tree variables are randomly chosen to determine the best binary split to explain the variation in breeding bird richness (Prasad et al., 2006). Our models randomly selected six environmental variables to choose the best split at each node. Trees are aggregated by averaging the singular tree prediction results to produce the final prediction (Prasad et al., 2006).

Using an ensemble of trees has been shown to significantly improve prediction capabilities by reducing the severity of the boundaries of prediction created by singular trees, which can yield a reduction in prediction variance (Prasad et al., 2006). Additionally, the second randomization step is utilized to decrease the correlation between trees in the forest and reduces the effects of redundant environmental features, thus improving model error rate (see Archer and Kimes, 2008). In addition, by allowing variables that might have been obscured by dominant environmental predictors to be selected, we introduce diversity into the trees that can display interaction effects between variables that may otherwise have been concealed (Strobl et al., 2008). To analyze the residual effect of survey effort on breeding bird species richness we created two Random Forests models for each stratification; one model including and the other excluding survey effort.

To display the environmental variables, which influence the distribution of breeding bird species richness at the 10 km by 10 km scale, we produced variable importance tables for each model. The first variable importance is calculated using the out-of-bag data (data not included in the bootstrap sample) because when 999 trees are grown the error rate is generalized (Prasad et al., 2006). The percentage increase in the mean square error is calculated by randomizing each environmental variable before prediction and comparing the predicted species richness levels to the out-of-bag species richness levels (Breiman, 2001). The increase is then calculated as the difference between the average mean square error before and after randomization for that variable (Prasad et al., 2006; Archer and Kimes, 2008). If the environmental variable does not provide a significant amount of predictive power, when it is randomized the increase in the mean square error value remains low (Archer and Kimes, 2008). The second importance variable signifies the increase in node purity, which is the average reduction in the sum of the squares within the split species richness groups achieved by all splits on the specified environmental variable (Prasad et al., 2006).

3.6.2 Evaluating model performance

Using the modelled relationships derived from the Random Forests we predicted breeding bird species richness within each observed grid cell at each survey effort stratification to assess the differences between predicted and observed levels of breeding bird species richness. We mapped the prediction results of the three to four hour and five to six hour stratification excluding the survey effort covariate to visually assess spatial patterns of error, and report the root mean, minimum and maximum error between observed and predicted breeding bird richness and test if the residuals are normally distributed. We use the three to four and five to six hour models excluding survey effort because the breeding richness stratifications are relatively unaffected by survey effort (see results Section 3.7.1). We also calculated the coefficients of determination to analyze the model’s predictive power.

3.6.3 Prediction of breeding richness

We applied the three to four hour and five to six hour modelled relationships, excluding survey effort covariate, to predict breeding bird richness in the areas not presently surveyed between three to six hours by the BC Breeding Bird Atlas volunteers. To analyze the similarity between breeding richness predictions we compared the difference between the three to four hour model predictions and the five to six hour model’s predictive results and characterize the spatial distributions of the breeding richness predictions using the environmental variables most often selected to reduce the sum of the squares between the breeding richness partitions. Additionally, we describe the spatial location of breeding richness groups using the Ministry of Environment's Ecoprovince classification of British Columbia (Figure 3.1) and highlighted predicted high richness locations as areas where additional field surveying would be warranted to confirm distributions at similar or higher levels of survey effort.

3.6.4 Observation bias

In our final analysis**,** we assessed observer bias, known to obscure the analysis of data collected during volunteer avian breeding surveys (Sauer et al., 1994). We assessed observational bias on a pixel-by-pixel basis determining how species richness changes with survey effort. Where the range in stratified species richness was large between the stratifications and spatially variable (e.g., southern Vancouver Island, South Interior and Ft. St. John area) we created line graphs with survey effort intervals (one to two hours, three to four hours, five to six hours) on the x-axis and maximum species richness (stratified by survey effort) on the y-axis. We expected that breeding bird species richness would increase linearly with observation effort. Deviations outside of a positive linear or asymptotic relationship between additional survey effort and species richness are understood as observer bias. The bias can be attributed to a multitude of affects since breeding richness in each cell is represented by one survey (the maximum observed richness). Examples of the causes of bias may include observation date within the breeding season, observer experience and location within quadrat. We overlaid the range in breeding richness with our predictive errors in the three to four hour model and five to six hour model to explore if a connection exists between maximum residuals and observer bias.

3.7 Results

3.7.1 Drivers of breeding richness

Random Forests variable importance indicators (e.g., Tables 3.2 and 3.3) represent the variables explaining an important portion of breeding richness distribution. The impact of survey effort is evident in the one to two hour model, as survey effort increased the prediction inaccuracy (increased the mean square error) by 61.21% when randomized and was the top ranked node purity variable. Conversely, our three to four hour and five to six hour models were relatively unaffected by survey effort with the covariate increasing the mean square error when their values were randomized and used to predict breeding richness by just 7% and 3.71% respectively. As such, we focussed subsequent analysis on the three to four hour and five to six hour models excluding the survey effort covariate (Tables 3.2 and 3.3).

The three to four hour and five to six hour models are similar in their selection of environmental variables, though variation in ranking is expected given the different spatial extents and frequencies of the data sets (n= 817, n = 492, respectively). However, both the three to four hour and five to six hour models showed that at the spatial resolution (10 km by 10 km) and extent of our analysis, moisture levels, temperature, and elevation were consistently selected as important predictors of breeding bird richness (Tables 3.2 and 3.3). Additionally, the variations in land cover types and percentage of like adjacencies between the dominant land cover types have the lowest ranks for increasing prediction inaccuracy when their values were randomized and used for prediction. When randomized in the three to four-hour model land cover heterogeneity increases prediction inaccuracy by 3.72% and the percentage of like adjacencies by 5.81%. Similarly, in the five to six hour model, land cover heterogeneity increased the mean square error of prediction accuracy by 3.16% and the percentage of like adjacencies by 5.16%. These results indicate that land cover heterogeneity indices are the least useful predictors of breeding bird richness at our grain of analysis and study area.

Our three to four hour model exhibits that climate moisture deficit is the top ranked variable for increasing both mean square error and node purity (Tables 3.2 and 3.3). Subsequent to climate moisture deficit, average elevation, mean summer precipitation, average fPAR, mean annual precipitation, and mean annual temperature are top ranking variables for increasing the mean square error in breeding richness predictions when randomized, meaning that these six variables contributed the most to the accurate prediction of breeding richness (Table 3.2). The node purity indicates that for all developed trees climate moisture deficit and mean summer precipitation were selected most often to reduce the sum of squares in the breeding richness partitions (Table 3.3), demonstrating that moisture and temperature influence the spatial distribution of breeding richness.

The spatial extent of our five to six hour observed maximum breeding richness is relatively small given there are fewer surveys (Figure 3.2, see observed breeding richness map). Despite the reduction in the number of quadrats surveyed, the top ranking environmental variables for predicting breeding richness are similar to our three to four hour model. The top ranking environmental variables increasing the mean square error when randomized include average elevation, average seasonal land surface temperature, mean annual precipitation, mean summer precipitation, mean annual temperature and average fPAR. The two variables that differ in the top six ranks for the three to four hour and five to six hour models are climate moisture deficit and average seasonal land surface temperature. However, these indicators are akin to displaying the variance between warm and cool areas of BC. Similarly, between the two models, the node purity results indicate that mean summer precipitation and annual evaporative demand are most often selected to reduce the sum of squares in the breeding richness partitions (Table 3.3). These results are consistent with our three to four hour model using moisture and the interaction between air temperature and moisture to explain the variation in the distribution of breeding richness.

3.7.2 Model performance

Visualizing the observed (1 to 82 and 1 to 80 species) and predicted (8 to 60 and 11 to 64 species) ranges of species richness for both the three to four hour and five to six hour models respectively (Figure 3.2), we conclude that ambient energy variables are explaining a dominant proportion of the distribution in breeding richness. The calculated coefficients of determination from the Random Forests models excluding survey effort indicate that environmental variables explain 43.99% (three to four hour model) and 41.89% (five to six hour model) of the variation in breeding bird richness.

Evaluating the residuals, our three to four hour model has a root mean square error of six species with maximum over-prediction of 16 species and under-prediction of 24 species. Our five to six hour model performs similarly with a root mean square error of seven species, maximum over-prediction of 21 species and under-prediction of 22 species. Both models display normal distributions in their prediction errors (One-Sample Kolmogorov-Smirnov Test, α .90 and .95 respectively). Despite the range in the residuals, the model predictions have similar spatial patterns between the observed and predicted breeding bird richness distributions (Figure 3.2). These results provide confidence that the environmental variables are predicting the spatial distribution of breeding richness.

3.7.3 Breeding bird richness predictions

Using our evaluated three to four hour, and five to six hour modelled relationships we predicted breeding bird species richness in the regions of BC not represented by survey lengths between three to six hours. Both stratifications forecasted the highest breeding richness (30 to 50 unique species and 34 to 57 unique species, respectively) to be located in the lowlands of the South and Central Interior, Boreal Plains concentrated around Ft. St. John and Dawson Creek, in the southern portion of the Taiga Plains, the lowland coastal areas along the Strait of Georgia, southern portion of Vancouver Island, and along the valley in the Southern Interior Mountains (Figure 3.3). Conversely, the lowest species richness levels are predicted to occur in our highest elevations in the Northern Boreal Mountains region, coastal mountains and Southern Interior Mountains (Figure 3.3). Overall, the highest breeding bird richness levels are in the warmer, lowland areas with higher evaporative demand and moisture deficits (Figure 3.4).

The spatial distributions are similar between models because the primary variables used to split breeding richness into heterogeneous groups are influenced by ambient energy. For example, both modelled relationships used summer precipitation and the water-energy variables (represented by climate moisture deficit and reference evaporative demand) for their primary and secondary most used splitting indices (Table 3.3). The third and fourth ranked variables for reducing the sum of the squares within breeding partitions are average elevation and indicators of temperatures represented by evaporative demand and average seasonal land surface temperature, respectively (Table 3.3). Similarly, the third and fourth ranking variables for reducing the sum of squares are mean annual temperature and elevation range (Table 3.3). From, the modeled relationships and the predicted richness levels we can conclude that the distribution of bird breeding richness is dependent on moisture and temperature with the highest breeding richness located in the Boreal and Taiga Plains and the South and Central Interior. These regions are characterized by our indices to have high temperatures, low summer and annual precipitation levels, low range in elevation and generally lower elevation than the rest of the mountainous province of BC (Figure 3.4).

For the majority of the province the prediction differences between models are within five unique species of each other (Figure 3.3). Generally, the different predictions are along the north and south coast of BC where the terrain and ecosystems are most complex (Fitterer et al., 2012). Given that the ecosystem dynamics within the 10 km by 10 km grain could encompass many different habitat characteristics such as coastline, rain forests and urban areas we would expect breeding richness to be harder to consistently measure and model. The most pronounced differences in breeding richness (11 to 25 unique species) are located along the Georgia Strait, west coast of Vancouver Island and east coastline of the Queen Charlotte Islands (Figure 3.3). Two factors may be influencing these results. First, the three to four hour model exhibits a more even spatial distribution of samples across Vancouver Island and coast. Second, as the survey effort increases to the five to six hour stratification of breeding richness also increases (Figure 3.2). Therefore, throughout the Coast and Mountains Ecoprovince both survey length and the amount of cells surveyed contributes to predictive differences. Similarly, the predictive differences in the southern Taiga Plains could be attributed to lack of surveys and inconsistent observations of richness (see observed ranges in Figure 3.2), generally, the three to four hour model has more surveys to support the breeding richness prediction in the Taiga Plains. Observational timing and experience as highlighted in (Figure 3.5) could cause predictive differences in the South and Central Interior, particularly the negative differences where the observed data used to create the modelled relationships are less stable (i.e., breeding richness between stratifications does not follow a positive relationship with survey effort). Regardless of the differences, the South and Central Interior are modelled as hot spots of breeding richness and the similarity in spatial distribution of breeding richness between the two predictions supersedes the differences.

3.8 Discussion

3.8.1 Sampling bias

Evaluating raw breeding bird richness and total breeding richness survey effort and the number of completed surveys we highlight an association affecting the total number of unique species observed in the BC Breeding Bird Atlas dataset, meaning the spatial distributions of raw species richness hot spots may signify observer density rather than breeding richness. For shorter sampling times (one to two hours), small increases in the amount of time spent in the cell positively affected the number of species sighted per survey. We observed that when survey periods are longer, three to four hours or five to six hours, breeding richness distributions are indicative of observation experience, observational timing and bird habitat selection rather than survey effort variation from cell to cell.

The important influence of survey effort at intervals shorter than two hours indicates that BC’s common species are sighted in shorter survey times and surveys generated from longer time intervals are more appropriate building relationships within environmental indicators. To improve atlas data for richness modelling it would be useful to implement a minimum observation period (e.g., longer than three hours). We also support previous research by stressing that sampling extent is equally important as survey frequency and length when modeling and predicting breeding richness to provide confidence in the breeding richness observed (Robertson et al., 2010).

Given that species richness indices have become an important information resource for conservation planning (Pearman and Weber, 2007), it is necessary for researchers to uncover sampling bias before analyzing the spatial distribution of species richness and linking these distributions to environmental factors to ensure findings support informed conservation decisions. Observational bias can skew the level of species richness observed per survey (e.g., Figure 3.5), obscuring the positive trajectory expected between species richness and survey effort before an asymptote is reached. Within BC Breeding Bird Atlas data, we have identified observational biases, which may have affected the consistency of the relationships formed between BC's breeding bird richness and environmental variables between our stratified models.

For example, if we visually compare the highest error classes in our three to four hour and five to six hour models (Figure 3.2) with the range in the species richness levels between all stratifications (Figure 3.5), we find that the maximum over and under predictions overlay with the highest ranges in the observed breeding richness. Assessing the breeding richness on a pixel based assessment of how breeding richness changes with survey effort using examples extracted from the southern Vancouver Island, Okanagan region and Peace River area (Figure 3.5) it appears that observational effect could be distorting our ability to accurately predicted species richness. Therefore, confounding factors such as observation timing, experience and location of the observer within the 10 km by 10 km quadrat may influence the breeding richness levels because the relationship between maximum breeding richness observed and survey effort does not follow positive trend. Until more data are collected to control observation bias and enable more advanced correction methods, we found that stratifying data by survey effort served to explore environmental variables associated with species richness. To mitigate observation uncertainties when using singular surveys for analysis for environmental species modelling it would be beneficial to include the date and time of observation and judgement on their personal observational skills (e.g., number of seasons spent surveying) in raw breeding evidence datasets. The addition of these attributes will allow researchers to stratify by observation levels and into peak breeding months, potentially reducing observational bias when more surveys are available.

3.8.2 Important indicators of breeding bird richness

Despite the variability in the spatial coverage of our stratified models we found that the interaction between moisture and temperature modeled as climate moisture deficit and reference evaporative demand were the most important (primary and secondary most selected splitting variables) indicators for explaining the variation in the distribution of breeding bird richness (Table 3.3). Higher levels of breeding bird richness are found in lowlands, valleys and warmer areas of BC; areas, which have the highest evaporation of moisture (see Figure 3.4). Examples of areas with the highest level of breeding bird richness include the heart of the Boreal Plains region, southern Vancouver Island and the South and Central Interior.

Similar to our primary splits of breeding bird richness levels we found that available energy continues to play an important role in predicting the richness of breeding bird as elevation, precipitation, water-energy variables and temperature are within the top ranks for increasing the inaccuracy of our models when their values are randomized. Additionally, average seasonal fPAR represents the importance of productivity on breeding habitat selection and is linked with available energy, as vegetation is dependent on water and sunlight for growth (see Hawkins et al., 2003a). With these findings, we highlight consistent patterns of ambient energy variables in the top six ranking predicative environmental variables emphasizing the importance of climate moisture deficit, reference evaporative demand, precipitation, elevation and average seasonal land surface temperature for explaining breeding richness distributions across BC. We conclude that for the observed extents ambient energy (or rather water and climate) control the distribution of breeding bird richness in BC. Our results are consistent with Currie (1991) study highlighting that broad-scale patterns of species richness are associated with climate and H-Acevedo and Currie (2003) concluding that summer bird richness co-varies with annual temperature and precipitation.

The emergence of a connection between BC's breeding richness and available energy demonstrates the potential to monitor climate shifts as a surrogate for vertebrate habitat condition affecting population levels. Given that collecting species information requires a significant amount of resources, time and organization, linking bird richness to continuously and systematically collected environmental data, is advantageous for conservation management (Franklin, 1993). After field surveying is complete, monitoring changes to vertebrate populations, predicted by environmental indices is theorized to provide an indication of biodiversity status (Nagendra, 2001; Duro, 2007; Gillespie et al., 2008). However, there are processes outside of the provincial extent such as habitat and climate change in the migration areas and wintering habitats of BC's migratory breeding birds, which may also influence breeding population levels and would require analysis of bird ranges and larger spatial scales to quantify and predict.

Contrary to the theory that niche variety increases species richness (Andrén, 1994; Berg 1997) we observed landscape heterogeneity indices ranked low in predicting breeding bird richness. Given our spatial extent and resolution, modelled heterogeneity did not increase performance. However, quite possibly heterogeneity may influence BC's breeding bird richness at smaller spatial extents where the energy gradient is uniform, or at different grid cell resolutions. Our study was conducted using a spatial resolution of 10km by 10km and heterogeneity metrics have been observed to have a weakened relationship with species richness as grid cell resolutions decrease from 4 km to 16 km (Būhning-Gaese, 1997). Additionally, our results support Kerr and Packer's (1997) indicating that in the northern latitudes available energy is a more important indicator of species richness than habitat heterogeneity, suggesting that breeding habitats must first meet the thermoregulatory needs of species.

The spatial distribution of the error terms and residual ranges show that our models explain a portion of the variation in breeding bird richness over the province (Section 3.7.2). We theorize that landscape processes operating at a finer scale than the 10km by 10km spatial grain of our study also influence breeding richness. Substantial variations in the landscape composition and structure are expected within a 10km by 10km area as BC has a dynamic habitat structure, exhibiting distinct ecosystem characteristics at smaller spatial resolutions (e.g., Fitterer et al., 2012). Following theory described by the modifiable unit areal problem (MAUP), the variance of the environmental and landscape characteristics will be relatively high within each cell and low between cells (Wiens, 1989; Jelinski and Wu 1996). The decrease in modelled landscape variance may be masking landscape structure and process occurring within grain resolution (Wiens, 1989; Jelinski and Wu 1996). Thus, larger grain sizes will affect the emergence of relationships between species richness and environmental variables, which function at smaller scales. To improve the ability of scientists to link or validate environmental processes with BC breeding bird data it would advantageous for volunteers to consistently record habitat descriptions with species observations and the distance travelled within a gridded location.

3.8.3 Predictions of breeding bird species richness

Our predictions of BC's breeding bird richness in the cell not currently represented by three to six hours of survey effort display similar trends between models increasing our confidence in the extrapolation of our predictions. The similar spatial trends occur despite the limited range of species richness values surveyed within the three to four and five to six hour stratifications and dissimilar spatial extent between the two models influencing the relationship between our environmental indicators and species richness (see Figure 3.2). Analyzing the distribution of our predicted breeding bird richness, we note that high breeding bird richness levels are located in the warmer more inhabitable regions of BC presenting a long-standing conservation issue of provisioning land for conservation in areas favourable to human settlement (Freemark, 2006). Historically, reserve planning has been opportunistic, without key objectives for preserving species richness (Pressey, 1994; Margules and Pressey, 2000), resulting in larger reserves located in the colder, and species poor regions of BC. Our study supports existing research (e.g., Freemark, 2006) indicating BC’s avian richness peaks in the south, particularly the south central areas of the province and southern Vancouver Island, where conservation lands are limited (Freemark, 2006). Considering birds as indicators of vertebrate species richness, our predictions highlight a potential gap in the protection of vertebrate diversity.

However, extrapolating predictions outside of the spatial range of your model introduces inaccuracies; therefore, as a caveat we note the breeding richness levels predicted in the Northern Boreal Mountains, coastal mountains and northern coast were support by a limited number of surveys. While gridded atlases seek to optimize the spatial extent of data collected (Donald and Fuller, 2010), human access to observation areas still plays a major role in data collection and is evident in the spatial distribution of the BC Breeding Atlas surveyed grid cells. When additional resources are available for data collection efforts should focus on gathering breeding information outside the ranges easily accessible by roadways to support our knowledge of the selection of remote areas as breeding habitat. Similarly, the areas of BC predicted to have high species richness, such as South and Central Interior regions, Boreal and Taiga Plains, the coastal areas along the Strait of Georgia, southern portion of Vancouver Island, and valley in the Southern Interior Mountains, are ideal targets for future field surveying.

Breeding bird atlas data are a unique data source for studying broad scale environmental interactions between vertebrates and habitat compositions and structures. For example, atlas data have been successful used to assess the effects of afforestation of invasive tree species on grassland avifauna communities in Mpumalanga Province, South Africa (Allan et al., 1997). Abundance data have been integrated with atlas data to study the large-scale movements of birds across Australia (Griffioen and Clarke, 2002) and important breeding bird areas used to discuss the creation of species protected areas in North England were identified through north England atlas data (Brown et al., 1995). Additionally, gridded bird data displays considerable promise for linking environmental data derived from remotely sensed imagery to vertebrate diversity (e.g., Coops et al., 2009b). These studies, and our own, provide insights into the potential information breeding bird atlas data can supply for monitoring vertebrate populations and guiding conservation and management.

3.9 Conclusion

Our research expands upon ecological studies examining the significance of food resources (productivity), thermoregulatory needs (ambient energy) and niche habitat (heterogeneity) on vertebrate habitat selection. From our models, we have concluded that precipitation levels and climate drive the distribution of breeding bird richness across the province of BC. Our findings support a large body of research supporting water-energy as the fundamental driver of species diversity (see Hawkins et al., 2003a).

By presenting suitable indices for modelling environmental factors and by utilizing a flexible predictive model able to accommodate non-linear relationships, interaction affects and predictor correlations we present transferable methodology for species richness modelling. We believe model performance could be improved as more breeding bird data are collected. Notably, we model and analyze the predictive power of environmental indicators derived from freely available data to encourage the extension of our findings to be used as a stepping-stone for landscape monitoring of vertebrate health.

The benefit of making atlas data freely available throughout project time period will encourage scientists to undertake analysis to uncover potential data bias or quality issues that can be corrected before data collection is complete to optimize data collection efforts. Fostering a connection between atlas organizers and analyzers could enhance the breadth of atlas use for conservation initiatives and provide observers with an understanding of the variety of scientific uses atlas data hold. A few simple additions to attribute data collection could increase the flexibility in how survey data can be utilized by scientists. Examples of these attributes include consistently recording survey time and date, approximate area covered within the quadrat, breeding habitat types, and observer experience such as number of seasons spent surveying. Future field work should target areas of inconsistent breeding richness forecasts (Coast and Mountains, Taiga Plains regions) and areas not currently surveyed but expected to support high levels of species richness (Central and South Interior, productive Boreal Plains and valley of Southern Interior Mountains). To reach these goals, resources are needed to assist volunteers in the collection of species information in the inaccessible areas of BC. Undoubtedly, the richness of gridded bird data makes it a unique data sources for scientist to investigate the large-scale relationships between birds and environmental factors and would not be possible without the generous efforts of the volunteers.

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Table 3.1 A sample of the ecological processes identified to influence the distribution of bird richness.

Study area	**Primary Variable**	**Reference**
Continental (North America)	Seasonal Productivity (NDVI)	Hurlbert and Haskell, 2003
Regional (Ontario)	Cumulative Productivity (fPAR)	Coops et al., 2009b
Continental (North America)	Summer Global Vegetation Index (NDVI)	Hawkins, 2004
Global	Actual evapotranspiration	Hawkins et al., 2003b
Continental (northern latitudes)	Potential evapotranspiration, mean annual temperature	Hawkins et al., 2003b
Continental (North America)	Potential evapotranspiration	Currie, 1991
Regional (Britain)	Seasonal temperature and precipitation	Lennon et al., 2000
Global (Northern Hemisphere)	Potential evapotranspiration	Hawkins et al., 2003a
Regional (sub-Mediterranean)	Elevation	Farina, 1997
Regional (Mediterranean)	Number of land cover types per hectare	Autari and De Lucio, 2001
Regional (Chihuahuan Desert)	Texture of NDVI	St. Louis et al., 2009

Table 3.2 Top six variable performances for predicting breeding bird richness for each model. The percentage increase in the mean square error is the calculated average prediction error rate if the covariate of interest is randomized and used to predict breeding richness. Large increases in the mean square error indicate the variable is important for accurately predicting breeding richness.

Predictor Performance in our Breeding Bird Richness Models			
3 to 4 hr Model		5 to 6 hr Model	
Percent Increase in Mean Square Error			
Climate moisture deficit	20.57	Average elevation	18.08
Average elevation	20.11	Average land surface temperature	14.76
Mean summer precipitation	18.27	Mean annual precipitation	14.36
Average fPAR	17.50	Mean summer precipitation	13.24
Mean annual precipitation	16.5	Mean annual temperature	13.17
Mean annual temperature	15.79	Average fPAR	12.47

Table 3.3 Top six variable performances for reducing the sum of the squares within the breeding bird richness partitions. Larger node purity values indicate variables selected most often to predict the distribution in breeding bird richness.

Top Ranked Predictor Performance in our Breeding Bird Richness Models			
3 to 4 hr Model		5 to 6 hr Model	
Increase in Node Purity			
Climate moisture deficit	17080	Mean summer precipitation	10702
Mean summer precipitation	14605	Evaporative demand	10528
Evaporative demand	14557	Average elevation	10247
Average elevation	13252	Average land surface temperature	8738
Mean annual precipitation	12370	Mean annual precipitation	8953
Elevation range	11518	Elevation range	8080

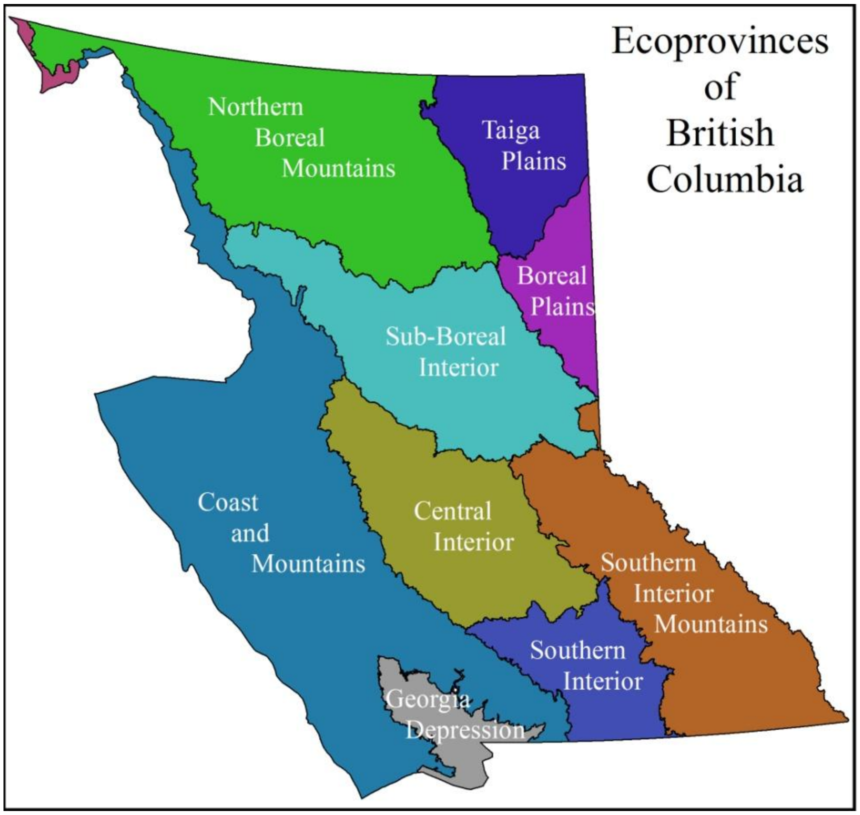

Figure 3.1 Ecoprovince Ecosystem Classification of British Columbia, data accessed from government of British Columbia’s DataBC warehouse.

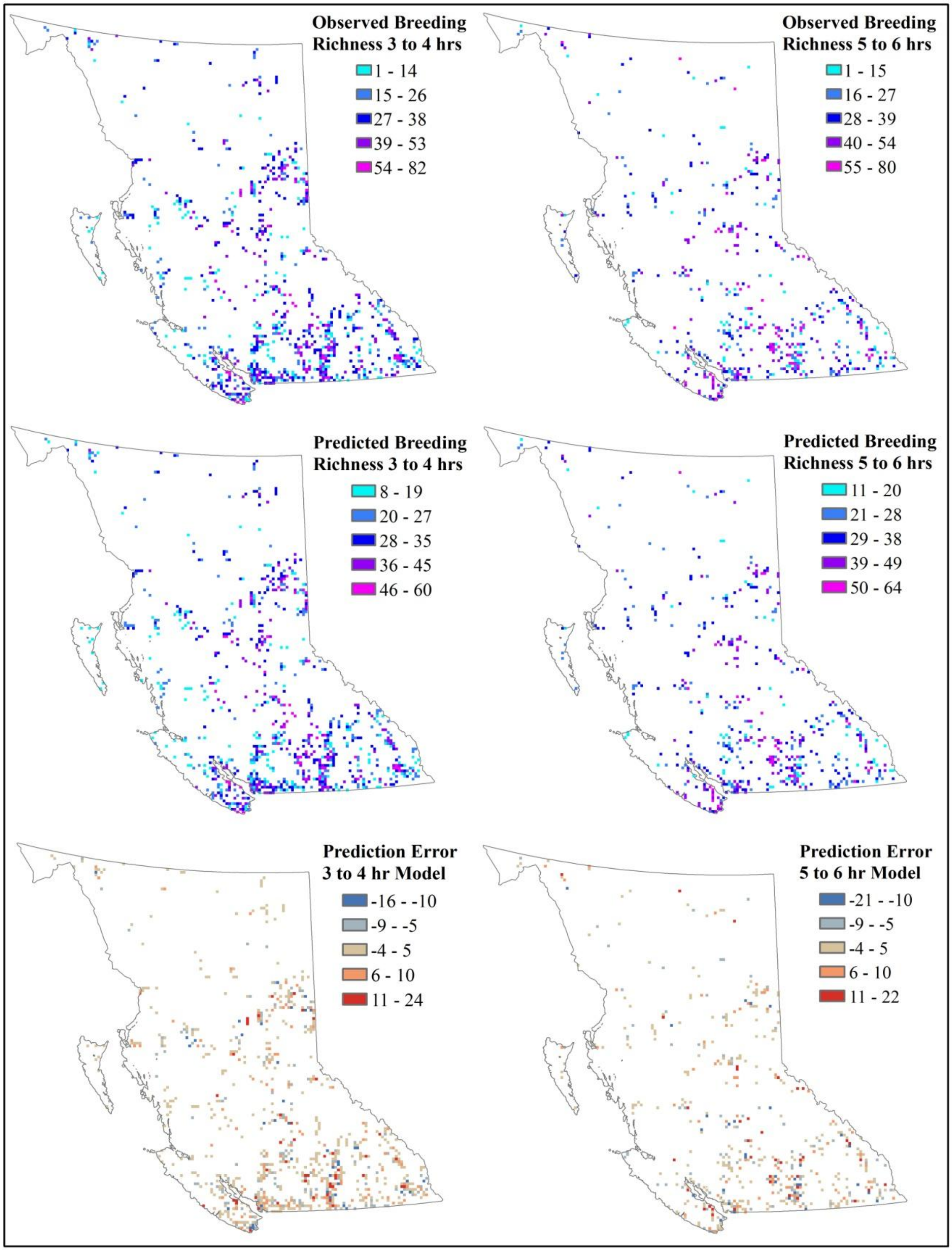

Figure 3.2 Random Forests model performance, three to four and five to six hour breeding richness stratification models.

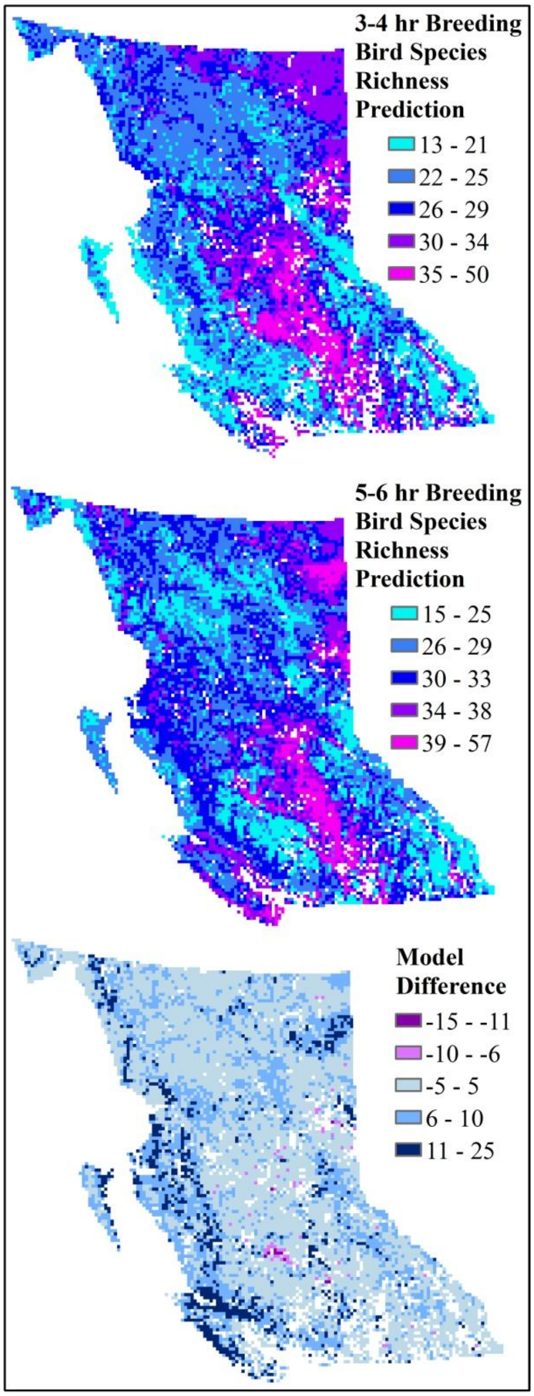

Figure 3.3 Predicted distributions (categorized using Jenks Natural Breaks) of breeding bird richness regions of BC not presently surveyed between 3 to 6 hours. These maps predict richness based on uniform three to four hour and five to six hour survey effort in each 10 km by 10 km quadrat across BC. The final map, model difference, is the breeding richness prediction difference between the five to six hour and three to four hour models.

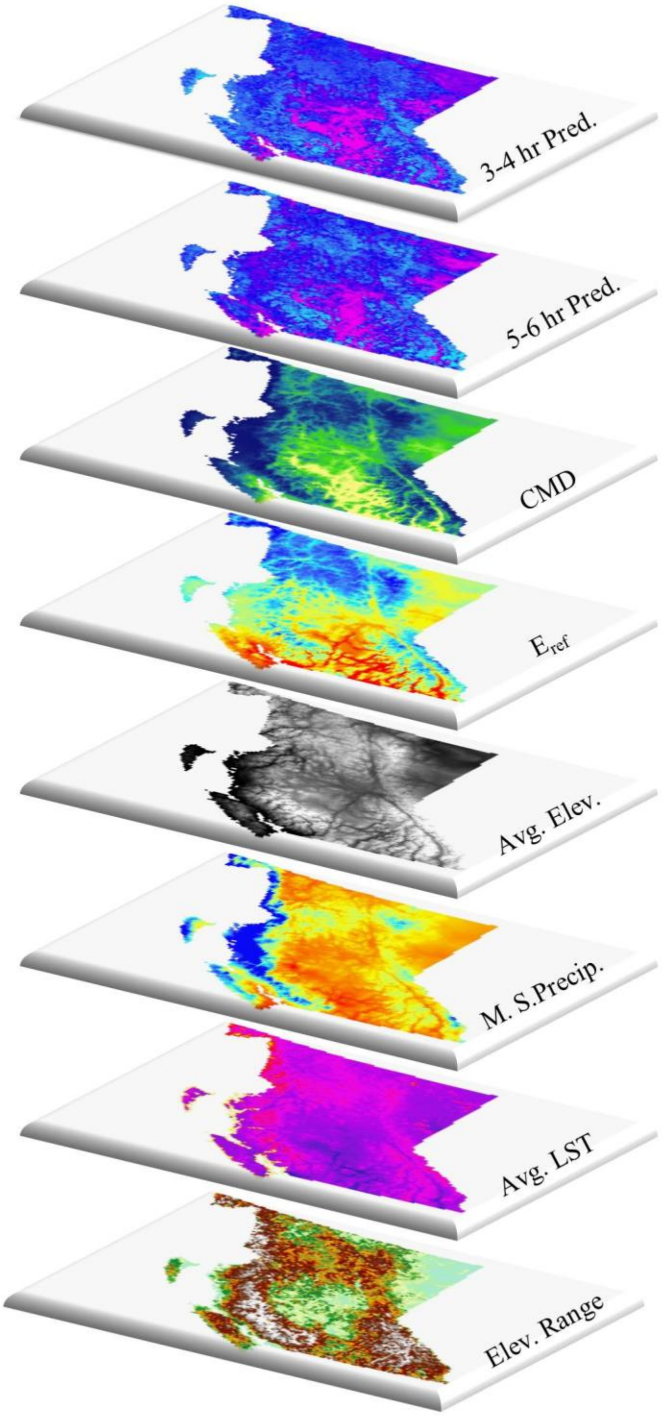

Figure 3.4 Selection of the top ranked splitting predictors of breeding bird richness. The variables represented are a climate moisture deficit, reference evaporative demand, average elevation, mean summer precipitation, average land surface temperature and elevation range.

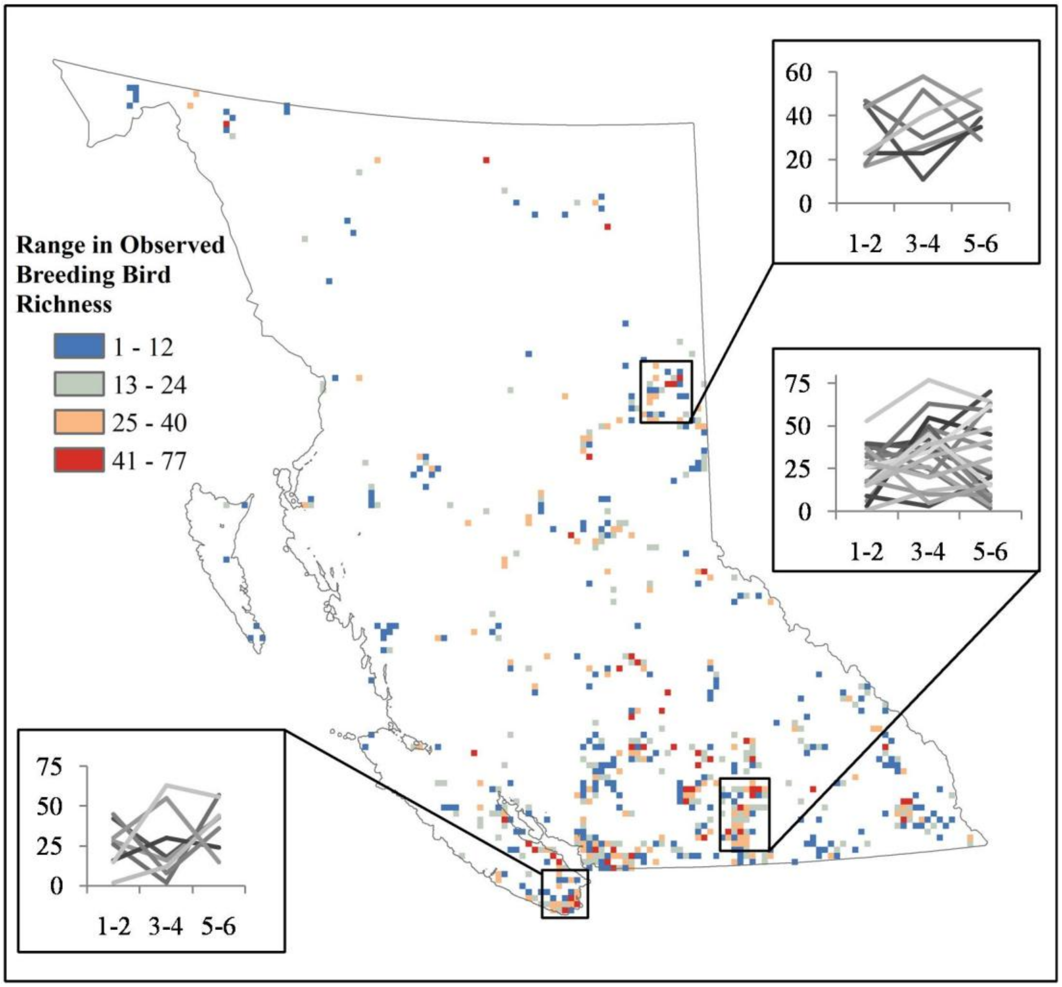

Figure 3.5 Display of the range in the observed breeding richness over the two-hour intervals and graphs depict the relationship between breeding richness and survey effort within the range. These results, highlight observational bias in the stratified (one to two hour, three to four hour, five to six hour) maximum observed species richness indices as we would expect the graphs to display a positive trend as survey effort (hours) increase.

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4.0 CONCLUSIONS

4.1 Discussion and conclusions

Consistent large area biodiversity monitoring is needed due to impending threats to biodiversity loss (Hyde et al., 2010) such as habitat fragmentation, degradation (Gaston, 2000) and ecosystem shifts due to climate change (Hamann and Wang 2006). Research has highlighted gaps in BC's traditional in-field ecosystem mapping processes, which stem from lack of funding for continued monitoring and knowledge transfer, climax ecosystem focus and outdated modelling methods (Haeussler, 2011). Researchers suggest that to reduce potential threats an ecosystem management perspective and scientifically rigorous, unbiased biodiversity modelling practices need to be developed (Boutin et al., 2009). To meet this goal researchers and organizations have reviewed and suggested using indirect indicators of biodiversity as surrogates for ecosystem and species diversity (Nagendra, 2001; Kerr and Ostrovsky, 2003; Turner et al., 2003; Duro et al., 2007; Gillespie et al., 2008). We built upon these suggestions and reviews to developed new approaches for BC's biodiversity modelling. First, we developed an ecosystem model using Earth observation data and terrain indices to provide BC with a repeatable method for monitoring ecosystem diversity and seasonal dynamics. Secondly, we explore the landscape-scale processes influencing geographical patterns of breeding bird richness to establish the possibility of using landscape-scale environmental indices as surrogates for monitoring potential changes in the ecological processes that influence species distributions.

In Chapter 2, we use Moderate Resolution Imaging Spectroradiometer (MODIS) satellite collected data to model BC's maximum vegetation production and annual seasonal vegetative growth and spring snow cover melt at 1 km by 1 km resolution. By analyzing latitudinal positions and changes in elevation, we derived models of potential solar radiation and soil moisture, integrating independent compositional, functional and structural characteristics into an ecosystem classification using a robust clustering method. The results delineate BC into 16 terrestrial ecosystem regions. By analyzing regional characteristics of ecological indicators selected, we ensure our model maximizes the variance between, and homogeneity within, each ecosystem. Comparing our ecosystem model to legacy biogeoclimatic mapping, we are able to delineate a greater level of ecosystem diversity in the under-sampled mountainous regions of BC (Fitterer et al., 2012), while displaying greater homogeneity in the Central interior where the mountain pine beetle affected forest production (Robertson et al., 2009). Overall, our ecosystem model is able to partition intricate details of the environment, such as barren mountainous peaks in the coastal mountains, to desert like conditions with meandering water ways in the South Interior region. Therefore, by building upon spatial ecosystem modelling theory (e.g., Noss, 1990; Duro et al., 2007 and Coops et al., 2009) we are able to represent current and seasonal ecological dynamics into ecosystem classifications and provide continuous ecological information to complement existing ecosystem classifications with data freely available to the public.

In Chapter 3, taking a species modelling approach to diversity modelling we establish how environmental indicators can link to species richness for continued monitoring of vertebrate health through environmental surrogates. We select environmental indicators which represent productivity (food resources), ambient energy (water and temperature), and landscape heterogeneity (niche variety) and assess the effect on the spatial distribution of breeding richness. We use a flexible non-parametric regression tree model (Random Forests) implemented in R statistical software (Breiman, 2001) to demonstrate a modelling approach which is robust to large databases, non-linear relationships, interaction effects between variables, and is able to identify the performance of individual covariates (Breiman et al., 2001; Prasad et al., 2006). Our results reveal that ambient energy, measured in the form of water-energy (i.e., climate moisture deficit, evaporative demand) relationships, and moisture (i.e., precipitation) are the dominant indicators of breeding richness with avian species favouring productive, lowland, warm, and dry areas of BC. Through our development of breeding richness indices, we establish that survey effort (amount of hours spent surveying) and surveying intensity (amount of surveys per quadrat) effects the spatial distribution of breeding richness and that shorter surveys (one to two hours) are less stable for analyzing breeding richness. Therefore, we suggest a more uniform survey effort strategy and consistent recording of survey locations, date, time, and experience (e.g., number of seasons spent surveying) of each observer could improve the use of Bird Atlas data for species richness modelling and potential use in conservation management.

4.2 Research contributions

Our ecosystem diversity study contributes to both the reviews (Nagendra, 2001; Kerr and Ostrovsky, 2003; Turner et al., 2003; Duro et al., 2007; Gillespie et al., 2008) and research (Coops et al., 2008, 2009c, 2009d; Andrew et al., 2011a) on broad-scale environmental modelling by demonstrating how existing ecological indicators can integrate into a regional ecosystem model to develop an approach for modelling and monitoring BC’s dynamic environment. As Earth observation data are readily updatable, our approach provides information for monitoring changes in vegetation production and climate seasonality. By combining information on dynamic ecosystem processes (productivity and climate) with relatively static structural landscape information, we provide a viable approach for monitoring the broad-scale effects of climate change and landscape disturbance on ecosystem health. For instance, coupling freely available Earth observation data and Canadian Digital Elevation Data with a robust clustering algorithm displays a step towards an automated ecosystem classification system with the possibility of saving time and resources usually needed for broad-scale field based assessment of ecosystems (e.g., Pojar et al., 1987 methods). The ecosystem diversity results readily provide information for evaluating the effectiveness of BC's conservation network for protecting the diversity of BC's ecosystems. The monitoring applicability also presents the possibility to identify areas vulnerable to change. Identifying protected area gaps and vulnerable ecosystems enables resource managers to target conservation resources where they are needed most. The ecosystem delineation approach can also be adapted to regions around the world with the availability of Earth observation data (e.g., MODIS) and remotely sensed topographic information (e.g., Shuttle Radar Topography Mission), by which we have transformed geospatial datasets into a resource management information source (Fitterer et al., 2012).

The BC Breeding Bird atlas presented a novel opportunity to study the spatial effects of habitat resources on species richness. Our results contribute to ecological science, which focuses on exploring how landscape processes and structure influence the species diversity gradients. The controls on the distribution of avian species are identified to include composition (productivity), structure (heterogeneity) and energy (ambient energy) over a variety of spatial scales (see Hawkins et al., 2003a, 2003b). Deriving indices representing these three main components and identifying the dominant driver of breeding richness as ambient energy in BC we contribute to a growing body of research which recognizes available energy as the limiting factor of species richness in the northern hemisphere (e.g., Kerr and Packer 1997; Hawkins et al., 2003a). Additionally, we identify habitat heterogeneity as the least informative regional predictor of breeding richness, postulating breeding richness may be influenced by habitat heterogeneity within the 10 km by 10 km grain as studies display a decreasing influence of niche heterogeneity on species richness as the grain of analysis increases from 4 km to 16 km (Būhning-Gaese, 1997).

By contributing to the ecological understanding of the processes driving species distribution over regional scales, we highlight the possibility of monitoring water-energy indicators such as average land surface temperature and precipitation as surrogates of avian diversity health in BC. We also illuminate the utility of participatory data collection for broad-scale assessment of species richness by identifying approaches to remove bias in volunteer data during early stages of data acquisition. By using a variety of data sources (e.g., Canadian Digital Elevation Data, Moderate Resolution Imaging Spectroradiometer imagery, and topographically interpolated weather station data from ClimateWNA) our geospatial modelling approach demonstrates how data sets with varying spatial and temporal resolutions can be used to study the landscape-scale process controlling the distribution of species richness over regional scales further confirming the strength of geospatial science for broad-scale monitoring of biodiversity (Foody et al., 2008). Also, by exploring the relative performance of the Random Forests (Breiman, 2001) non-parametric predictive model, we demonstrate a flexible and transferable method for analyzing complex ecological studies which need to select important predictor variables from a suite of indicators that may exhibit interactive effects and non-linear relationships with the dependent variable (Prasad et al., 2006).

Given that birds present suitable vertebrate indicator species (Gregory et al., 2003), our results also hold important information for conservation management. For instance, the spatial distributions of our modelled and predicted breeding bird richness identify breeding richness to be concentrated in the warmer more inhabitable regions of BC highlighting an enduring conservation issue of protecting habitat where humans are also present (Freemark, 2006). These results identify a potential conflict in the preservation of vertebrate diversity.

4.3 Research opportunities

The landscape indicators modelled and methods explored in our research are fundamental to developing broad-scale systems for monitoring biodiversity at the ecosystem and species levels. There are several opportunities to extend this research. For example, our ecosystem model represents 2006 ecosystem characteristics, data are available from MODIS archives to repeat our modelling structure over different time-periods to assess shifts and changes in dynamic ecosystem characteristics (e.g., productivity and snow cover) or repeat clustering to identify pixel-by-pixel changes in ecosystem structure (e.g., Coppin et al., 1996).

We compared our regionalization to the zone level of the BC Ministry of Forests biogeoclimatic classification. There is an opportunity to derive more clusters, detailing finer spatial scale differences in ecosystem dynamics, to assess the integration of these classification systems at the sub-zone level. Additionally, future analysis could explore how our ecosystem delineation compares to the Ministry of Environment’s Ecoregion Classification systems such as the Ecodomains and Ecoprovinces to establish if the indicators selected for modelling are able to delineate ecosystem characteristics at a variety of scales. In addition, confirmation of our ecosystem delineation using field-based data would be beneficial.

The indicators we selected to represent compositional, functional and structural characteristics of BC’s ecosystems are a sample of the ecological indicators available for environmental modelling. Research results indicate a link between the normalized difference vegetation index and species richness (Evans et al., 2006). Delong et al. (2010) was able to discriminate ecosystem regions using interpolated climate data, and Canada-wide classifications have included categorical land cover information (Coops et al., 2009). Therefore, there is room to explore the addition of independent ecosystem characteristics such as land cover information freely available from MODIS classified imagery (e.g., Hansen et al., 2000), interpolated climate data representing temperature, water-energy variables and growth conditions available from climateWNA program (Wang et al., 2012), or more detailed spatial information on the heterogeneity of land cover types to represent niche variety or landscape composition (e.g., Long et al., 2010).

We also see potential in using finer spatial resolution remotely sensed data for repeatable ecosystem modelling. For example, research has used Landsat Enhanced Thematic Mapper data to develop 25 m land cover maps over the extent of Canada (Wulder et al., 2009). IKONOS and QuickBird sensors offer considerably smaller spatial resolution at pixel sizes from 2.88 to 4.00 m and coupled with Hyperion satellite's multi-spectral resolution of 196 bands can provide extremely detailed information for environmental modelling (see Nagendra and Rocchini, 2008). Additionally, Light Detection and Ranging (LiDAR) technology offers the fine topographic detail needed for smaller scale environmental modelling (e.g., Vierling et al., 2008). However, the cost of smaller spatial and detailed spectral information limits fine grain imagery's use in current broad-scale ecosystem assessments over broad scales (Gillespie et al., 2008).

The current coarse grained resolution of freely available remotely sensed imagery (1 km) effectively delineates ecosystems diversity, and these classifications have been useful for evaluating the parks and protected areas ability to preserve Canada's biodiversity (e.g., Andrew et al., 2011a). A similar gap analysis is possible for BC, using our regional ecosystem diversity model as we also use indirect indicators of species richness and identify the productive regions hypothesized to support higher levels of biological diversity (see Fitterer et al., 2012).

Researchers have also evaluated the effectiveness of current Canada wide ecosystem and land cover classifications to represent species assemblages using broad-scale butterfly datasets (Andrew et al., 2011b). This type of research is important for assessing the use of ecosystem classifications for conservation management of biological diversity. Our regional breeding richness indices or predictions of richness in the areas not currently surveyed could be used in a similar manner to address the effectiveness of our ecosystem model or current BC classifications to represent vertebrate diversity. Data collected during the BC Breeding Bird Atlas 2012 survey season may be employed as validation a data source for both our breeding richness predictions and survey stratified breeding richness indices. There is also an opportunity to explore breeding richness predictions as an indicator of all species using species assemblages such as the high priority species count dataset available from Hectares BC (http://www.hectaresbc.org/app/habc/HaBC.html).

With the datasets available, we present flexible and repeatable methods for modelling ecosystem and species diversity that have potential biomonitoring applications to provide conservation information for BC’s resource managers. Generally, more surveys, longer survey times, and data collection further from roads could improve the BC Breeding Bird Atlas data for use as vertebrate richness surrogate and will improve the performance of our models in linking breeding richness to ecosystem components readily available for repeat monitoring of vertebrate habitat conditions. However, resources must be made available to assist the volunteers in accessing areas with harsh climates and topography. The potential research and validation opportunities are immense with continued observation of breeding birds and upgrades to dynamic ecosystem models as finer spatial resolution remotely sensed data become available, such as, monitoring habitat characteristics and landscape disturbance at finer than 1 km resolution and creating nested ecosystem regionalizations.

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