

EFFECTS OF CLIMATE CHANGE, VEGETATION AND ROADS ON CARIBOU
DISTRIBUTION IN WESTERN NORTH-AMERICA

by

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ABSTRACT

Caribou (*Rangifer tarandus*) are a vital component of the cultural history and contemporary existence of First Nations and northern communities. However, caribou habitat is increasingly threatened by cumulative effects of climate change and land-use pressures from human settlement, forestry, and energy or mineral exploration. Of notable concern are rapid changes in the boreal region of Canada, which is mostly publicly owned, and supports a quarter of the world's remaining intact forest. I used downscaled climate projections and anthropogenic disturbance data, as inputs to niche models to project potential changes in vegetation and caribou occurrence across western North America, over the next century. This allowed me to compare potential projected changes between climate only, climate +vegetation, and climate+vegetation+roads models for northern and southern mountain, boreal, barren-ground and Grant's caribou distributions. I concurrently identified areas in the Canadian boreal region that met intactness, ecologically-based size, and connectivity requirements for dynamic reserves. Consistent with other studies, vegetation projections show a considerable potential redistribution of vegetation through expansion of grasslands into current boreal forest, concomitant with expansion of temperate ecosystems northward and into higher elevations. Caribou models suggest that human activities are an important driver of current caribou distribution. Future projections suggest that climate change will push caribou niches further northward or upslope. With significant shifts in caribou distribution expected, I identified only a few potential climate refuges, inferring that impact on caribou could be severe. A significant shift in management strategies is needed, including the identification of areas in land-use planning to facilitate caribou

climate adaptation. The scale and inherent uncertainty of climate and caribou data evaluated limit their use to broad-scale conservation. However, the road data I compiled can be used at finer scales, with more detailed caribou location data, to identify potential thresholds at which further development may impede caribou occupancy and survival, and thus support a balance between caribou conservation and economic development.

PREFACE

This thesis is an original work by Yannick Neveux. No part of this thesis has been previously published.

I was responsible for the data collection and analysis as well as the thesis composition. The references and source for the data used are specified within each appropriate chapter. I undertook all original analyses presented in this thesis.

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Finally, I am grateful for being able to work in western Canada in an area and on a project that has been thought provoking and complex, and on such an inspiring study species. The experience has given me a down-to-earth perspective and an even more solid praise for wildlife conservation. I hope that this work will benefit land use planning and environmental mitigation, enabling persistence of caribou and their long-term recovery in North America.

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1. CHAPTER ONE: INTRODUCTION

1.1 Status, trends and threats to caribou (*Rangifer tarandus*) in North America

Caribou (*Rangifer tarandus*) are a vital component of the cultural history and contemporary existence of northern communities, especially to First Nations (Hayes and Couture 2004). However, the species distribution is receding in Canada and worldwide, and some populations are at record low numbers (Environment Canada 2008, Vors and Boyce 2009, Festa-Bianchet et al. 2011). In western Canada, barren-ground caribou (*R. t. groenlandicus*) are listed as of special concern, Peary caribou (*R. t. pearyi*) as endangered, and woodland caribou (*R. t. caribou*) as threatened (boreal population), endangered (central and southern mountain populations), or of special concern (northern mountain population) under the Species at Risk Act (SARA) (COSEWIC 2002, 2014). Due to ongoing negotiation between jurisdictions and a lack of exhaustive phylogenetic studies, I used both SARA and COSEWIC taxonomy (COSEWIC 2002, 2014), with notably nine herds reclassified from SARA's southern to COSEWIC's northern mountain populations (Fig.1.1).

With about one quarter of all woodland caribou in Canada (~45,000 animals distributed in 45 herds across 1,000,000 km² in Yukon, western Northwest Territories, and northern British Columbia; Fig. 1.1), the northern and mountain population contains most of the remaining woodland caribou herds capable of sustaining human harvest (COSEWIC 2014). With seven herds stable, two increasing, and nine decreasing, the status of the northern mountain caribou remains unchanged, although forestry, roads and other developments are beginning to affect some herds, and the trend is unknown for 27 herds (two-thirds of the population) (COSEWIC 2014).

Although considerable research has been undertaken to explain individual factors contributing to the decline of woodland caribou, little is known about the effects of climate change and the cumulative impacts of human activities on caribou habitat (Rohner and Demarchi 2000, Environment Canada 2008). As well, few populations have been studied under human harvest

(Environment Canada 2012). Northern mountain caribou occupy habitats with pronounced elevation gradients, and the northern regions in which they occur are experiencing more rapid climate change effects than other ecotypes of woodland caribou (IPCC 2014). Rapid land-use changes associated with resource development and increased human settlement are also occurring throughout the distribution of the northern mountain caribou.

Given the vulnerability of caribou to these stressors, and a high degree of public interest in this species, there is a pressing need to better understand the potential impacts of these multiple, interacting stressors, and where possible, identify opportunities to mitigate these impacts through pro-active planning. At the core of my research is the attempt to explore at three scales (entire species in western North America, full range of each population, and Yukon winter range of northern mountain caribou) the potential interactive effects of current roads with climate change on future caribou distribution, with additional realism from integrating potential change in vegetation projections and fire size.

1.2 Effects of climate change on boreal ecosystems and caribou in North America

Boreal forest ecosystems contain important habitat for caribou. A third of all boreal forests are found in Canada, and these forests represent 10% of the world's forest cover (Canadian Forest Service 2011). The boreal forest is also an important ecosystem for Canadian resource-based industries, which produce numerous goods, including timber, pulp and fuelwood, as well energy and mineral products. Boreal ecosystems provide important ecological functions, such as regulating climate and floods, nutrient cycling, soil formation and water purification, as well as cultural functions such as educational, recreational and aesthetic values (Canadian Forest Service 2011).

However, climate change is among the threats to the boreal forest (B.C. Ministry of Forests 2010, USDA 2011). Mean temperature and precipitation have already increased in North America, and it is expected to become substantially warmer and drier in the future, especially in northern latitudes (Balshi et al. 2009, Mbogga et al. 2009, Price et al. 2013, Boulanger et al. 2014, IPCC 2014). In the Arctic, melting of glaciers/permafrost and shrub/ tree line expansion in

the tundra and the alpine are already accelerating (Danby and Hik 2007, Lara et al. 2016, Rowland et al. 2016). The effects of climate change-induced increase in drought (Michaelian et al. 2011, Price et al. 2013, Worrall et al. 2013, Montwé et al. 2016), wildfires (Balshi et al. 2009, Boulanger et al. 2014), diseases/ pests (Kurz et al. 2008, Raffa et al. 2013) and thermokarsts (Jorgenson et al. 2006, Osterkamp 2007, Schuur et al. 2015) may add to one another to accelerate vegetation response to climate change (Montwé et al. 2016). The Boreal could turn into a Carbon source before 2050 (Myers-Smith et al. 2008, O'Donnell et al. 2012, Price et al. 2013, Johnston et al. 2014, Lara et al. 2016) although an overall conversion from coniferous stands to deciduous (Johnstone et al. 2010, Mbogga et al. 2010) could reduce forest flammability (Higuera et al. 2009, Schwilk and Caprio 2011, Kelly et al. 2013, Marchal et al. 2017).

Nevertheless, vegetation explains much of caribou habitat selection at the landscape level (Leblond et al. 2011, Beguin et al. 2013, Boan et al. 2014, Poley et al. 2014). Caribou prefer areas of low fire frequency (125-275 years cycle) that are suited for less dense and old coniferous/lichen complexes (Collins et al. 2011, Polfus et al. 2011, Boan et al. 2014, Courbin et al. 2014, Latombe et al. 2014, Leclerc et al. 2014), even avoiding burned areas for up to 10km and 60 years (Joly et al. 2003, Johnson et al. 2015). With burnt areas to increase up to 60% by 2050 in Alaska's Tundra, high quality habitat for caribou may decrease by 30% in winter range, as moose habitat may increase by 64% (Joly et al. 2012).

Food availability may become a limiting factor to caribou in some circumstances (Hébert and Weladji 2013, Avgar et al. 2015). Global warming induced changes in plant or insect phenologies may lead to 'trophic mismatch' of migration or parturition with spring green-up (Ronnegard et al. 2002, Post 2003, Post and Forchhammer 2008), and earlier emergence or increased abundance of hematophage insects (Hagemoen and Reimers 2002, Weladji et al. 2003). However, caribou are especially vulnerable in winter, when niche overlap with wolves is greatest (Latham et al. 2013). More dramatic climate changes are also expected in winter and northern latitudes (Rinke and Dethloff 2008), threatening caribou survival and reproduction, as observed with the Peary caribou (*R. t. pearyi*) (e.g. 98% loss on the Western Queen Elizabeth Islands between 1995-1997; Miller and Gunn 2003), Svalbard reindeer (*R. t. platyrhynchus*) (e.g. 80% loss of the Brøggerhalvøya population in 1993-1994; Solberg et al. 2001, Aanes et al. 2002), and semi-

domestic Scandinavian reindeer (Tveraa et al. 2007). Reduced winter range fidelity in sedentary woodland caribou also shows the need of protecting large blocks of winter habitat rather than calving grounds where they reduce predation on new borns by spreading-out (Schaefer 2008, Faille et al. 2010, Schaefer and Mahoney 2013).

1.3 Effects of human activities on boreal ecosystems and caribou in North America

The industrial footprint in Canada's North is increasing rapidly, particularly in association with hydrocarbon and mining exploration and development (McLoughlin et al. 2003, Vors et al. 2007, Wittmer et al. 2007, Environment Canada 2008); further altering disturbance regimes and fuel patterns (Krawchuk and Cumming 2010, Whitman et al. 2015, Lehsten et al. 2016, Parisien et al. 2016, Nlungu-Kweta et al. 2017). Habitat loss and fragmentation are the indirect but ultimate cause of caribou declines, especially within the southern mountain (McLoughlin et al. 2003, Wittmer et al. 2007) and boreal populations (Sorensen et al. 2008, Environment Canada 2008), where human disturbances are greatest. Caribou are also more likely to avoid and be negatively affected by logged areas than burnt areas (Environment Canada 2008, Beguin et al. 2013, Lesmerises et al. 2013, Beauchesne et al. 2014, Losier et al. 2015), principally because the former is associated with roads/trails development which are linked to expansion of white-tailed deer and associated increases in diseases (e.g. *Parelaphostrongylus tenuis*) and predation (Parmesan and Yohe 2003, (Courtois et al. 2007, Schaefer and Mahoney 2007, Vors et al. 2007, Wittmer et al. 2007, Boan et al. 2014, Rempel 2011, Courbin et al. 2014, Leclerc et al. 2014, Poley et al. 2014, Avgar et al. 2015, Dawe and Boutin 2016). Indeed, low density secondary roads are strongly selected by wolves and bears as their plasticity to anthropogenic food sources and infrastructure give them movement advantages (Lesmerises et al. 2012, McKenzie et al. 2012, Latham et al. 2013, Boan et al. 2014). Concomitantly, undisturbed patches <100km² create concentrations of caribou that are better hunting for predators (Lesmerises et al. 2013, Latombe et al. 2014).

Although distance thresholds may be smaller in highly disturbed areas (Leblond et al. 2014), caribou generally avoid cut-blocks by up to 5km, seismic lines by 100m to over 2km as densities increase (Beauchesne et al. 2013, Johnson et al. 2015), mines by 2-10 km (Polfus et al. 2011,

Leblond et al. 2014, Johnson et al. 2015), primary roads by up to 30km, secondary roads by up to 10km, rural roads by about 1km (Leblond et al. 2014, Johnson et al. 2015), and wellsites and tourist cabin by 1-4km (Polfus et al. 2011, Johnson et al. 2015). Caribou use of habitats decreases (Lesmerises et al. 2013), and calf mortality rates increase, with all disturbances, as well as with increasing amounts of deciduous or mixed forest (Polfus et al. 2011, Lesmerises et al. 2013, Beauchesne et al. 2014, Leclerc et al. 2014, Losier et al. 2015). Barriers to migration and dispersion (e.g. deep snow, burns/cuts, roads/seismic lines) may also impact caribou access to important seasonal forage (Wolfe et al. 2000, Dyer et al. 2001, Johnson et al. 2001, Nellemann et al. 2001, Seip et al. 2007) and refuge from insects, predators and thermal stress (Kuzyk et al. 1999, James and Stuart-Smith 2000).

The Recovery Strategy for the boreal population identifies a minimum of 65% undisturbed habitat in a range as the critical habitat that can aid in recovery or provides a 60% probability for a local population to be self sustaining (Environment Canada 2008). The risk to caribou of an Allee effect at small population sizes (Wittmer et al. 2005, Vors et al. 2007, Wittmer et al. 2007) also underscores the importance of connectivity to metapopulation sustainability (Arlt and Manseau 2011, Courbin et al. 2014, Leblond et al. 2014).

1.4 Niche models

Niche models (also known as Species Distribution Models) rely on the statistical or theoretical relationships between environmental predictors and observed species distributions (reviewed by Elith et al. 2006). Niche models are also known as bioclimatic envelope models when correlating observed species distributions and climate conditions, and have been widely used to predict climate change impacts on: species and community shifts (Thomas et al. 2004, Rose and Burton 2009, Ding et al. 2017), ecosystem biodiversity (Botkin et al. 2007), reserves' effectiveness (Araujo and Williams 2000, Araujo et al. 2004, Hannah et al. 2007, Hole et al. 2009, Carroll et al. 2017) invasive species (Thuiller et al. 2005), and assisted migration (Gray et al. 2016).

While climatic variables often explain most of distributional variance of species and predict well the current distributions (Rowland et al. 2016), vegetation response to climate is usually lagging

and attributed to topo-edaphic conditions, lags in seed dispersal or long-lived tree species that can persist in environment unsuitable for recruitment (Stralberg et al. 2015a, Renwick et al. 2016). This may not matter when using empirical data to predict species distribution, as long as the associations between climate, vegetation, and other drivers remain constant over the modeling domain. However, when extrapolating into new spatial or temporal domains, the costs of using proximate variables are greater, depending on the degree of decoupling that may occur over space or time (Roberts and Hamann 2012).

Furthermore, while the role of human landscape modification is likely to be confounded with current climate conditions at a coarse scale (given the concentration of development activities in more southern regions), it may not be the case at finer scales (such as the one applied here to winter ranges in Yukon) or in the future. Nevertheless, since many northern mountain caribou herds have not been well-studied, an environmental niche model across their entire distribution is the first step in understanding habitat needs (as per boreal caribou; Environment Canada 2008).

1.5 Thesis rationale and overview

The objective of this thesis is to explore the impacts that future climate change may have on caribou distribution, and to integrate caribou conservation and climate change into a dynamic conservation planning framework.

In the *first research chapter*, I use niche models to examine potential response of vegetation to climate change in western North America. The specific chapter objectives are as follows:

- 1) Evaluate vegetation response to current climate and topo-edaphic controls and project potential vegetation changes for the 2020s, 2050s, and 2080s.
- 2) Compare different techniques and model uncertainties for vegetation projections and extrapolation into novel conditions.

To predict potential future distributions of northern mountain caribou and associated vegetation classes, I had to consider ecosystem types potentially affected by boreal forest expansion (taiga

and tundra), or that may expand into the current boreal region (hemi-boreal, prairie/grassland), thus the study area was extended to western North America. I use two modeling techniques: discriminant analysis (Goslee and Urban 2007) and regression tree (RandomForest, Cutler et al. 2007) to predict vegetation classes. I test the predictability of nine vegetation classifications before projecting them in the future, identifying de facto current analogues to future boreal climate conditions and potential shifts in vegetation. To model the climate, I use 18 coarse-scale General Circulation Models (GCM). I use a combination of four digital elevation models at a fine scale in order to downsize general circulation models used to project vegetation response to climate for the baseline year (1961-1990) and to train the dataset in order to project into the future (2020's, 2050s and 2080s).

In my *second research chapter*, I examine key controls of each caribou population and evaluate how they affect their distribution, and how predictions depend on the scale considered. The specific objectives of this chapter are to:

- 1) Incorporate current and potential future vegetation and climate into projections of potential future caribou distribution, in order to identify potential population vulnerability to climate or to roads, and the uncertainty with scales.
- 2) Compare potential shifts in distribution with current population distribution, in order to identify potential climate “refuges”.

I compare niches based on climate only, climate+vegetation, and climate+vegetation+roads using maximum entropy models (MaxENT) (Peterson and Robins 2003). These results were then coupled with climate and vegetation projections, to assess caribou vulnerability to these changes, and identify potential climate change “refuges”. Finally, to assess the importance of scale, the models were developed based on i) the herd ranges for the entire species in western North America (broad scale), ii) the herd ranges for each populations (intermediate scale), ii) then only the key winter areas for northern mountain herds in Yukon (regional scale) (Fig. 1.1).

In my *third research chapter*, I integrate caribou conservation and potential climate-driven changes in fire and vegetation into a dynamic conservation planning framework, with specific objectives to:

- 1) Study the potential effect of changes in climate on the minimum reserve sizes needed.
- 2) Examine how current protected areas correspond with the potential caribou refuges and candidate reserve networks identified.

Although the climate scenarios produced in previous chapters should define the response limits of vegetation and caribou, the reality will most likely lie between these extremes. Where gaps in existing protection for a particular caribou population could be filled by potential climate-change refuges, I generate candidate reserves of minimum intactness, connectivity, and size for resilience to future fire disturbances (Anderson 2009, Krawchuk and Cumming 2010).

The three research chapters form a continuation of one another, and offer valuable information on how potential changes in climate and vegetation may impact already threatened caribou populations in western North America in the future. This research identifies potential conservation areas that are or will be suitable for caribou, taking into account intactness, connectivity and current and future potential vegetation, climate, and fire size. The final chapter of this thesis summarizes the findings, provides management recommendations, and discusses future research direction for caribou conservation.

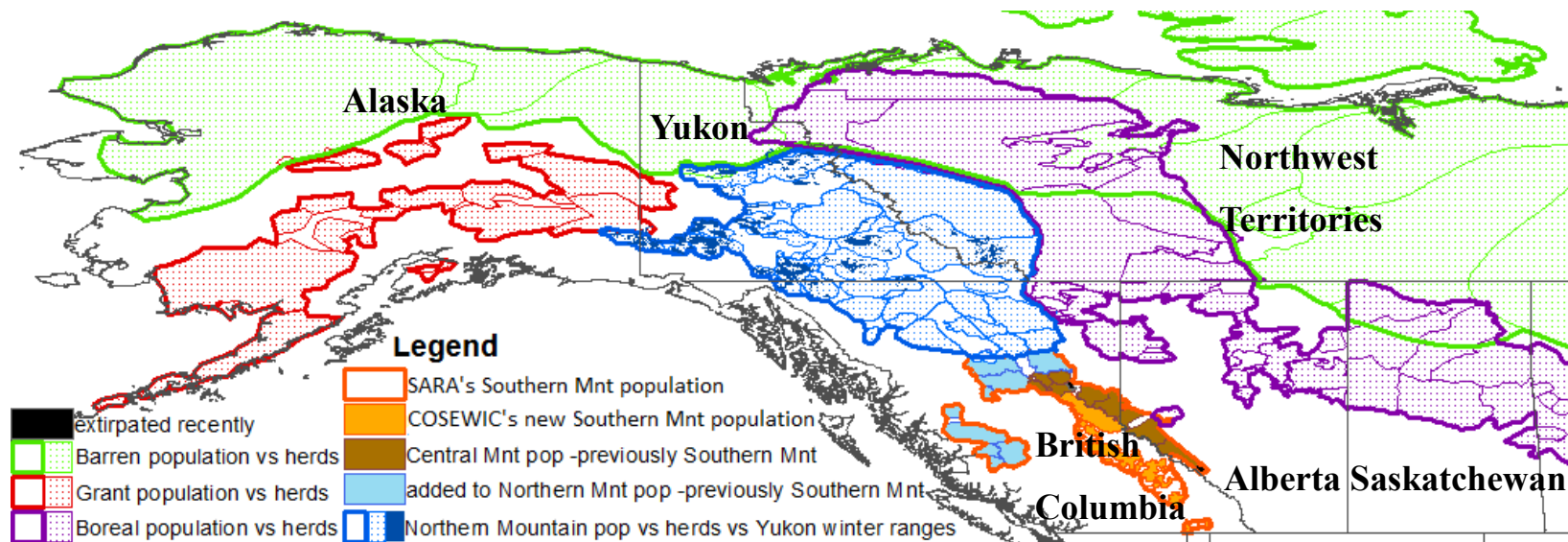


Figure 1.1 Delineation of the broad scale study areas, with ranges for caribou populations and herds, as well as the northern mountain caribou winter ranges in Yukon, displayed in the Geographic Coordinate System WGS 1983.

2. CHAPTER TWO: POTENTIAL EFFECTS OF CLIMATE CHANGE ON VEGETATION IN WESTERN NORTH AMERICA

2.1 Summary

Concerns over declining forest biodiversity due to human development and climate change have increased the use of models to support and evaluate management decisions over large spatial and temporal scales. However, desired thematic and spatial resolution may be lacking in available climatic projections of biomes, ecoregions or tree species ranges. This study addresses the lack of appropriate land cover data for forest conservation and wildlife-habitat modeling by forecasting climate-induced changes in 9 commonly used vegetation products over northwestern North America, using climate envelope models. I applied two ecosystem-based climate envelope modeling techniques - discriminant analysis and classification tree analysis - to evaluate the effect of modeling method on prediction of vegetation class distribution. RandomForest classification tree analysis performed better than discriminant analysis for this purpose. Consistent with studies from southern provinces, model predictions show vast potential redistribution of vegetation associated with expansion of typically temperate classes northward and into higher elevations.

2.2 Introduction

Climate change is one of the main threats to biodiversity worldwide (Thomas et al. 2004, Ceballos et al. 2017). Not only do many species have low adaptability ((Yeaman et al. 2016), but migration will also have to be faster than in previous glaciations (Roberts and Hamann 2016).

Increasing temperatures in western North America of 0.32°C per decade since the 1970s (Kumar 2007) have resulted in drought-induced forest mortality (Breshears et al. 2005, van Mantgem and Stephenson 2007, Hogg et al. 2008, Michaelian et al. 2011, Price et al. 2013), increase in wildfires and reforestation failures (Filmon et al. 2004, Balshi et al. 2009, Price et al. 2013, Boulanger et al. 2014), and epidemics of diseases and pests (Woods et al. 2005, Kurz et al. 2008,

Price et al. 2013, Raffa et al. 2013). Associated climate-induced changes in forest composition and structure are expected to intensify, especially in northern latitudes (Williams and Liebhold 2002, Logan et al. 2003, IPCC 2007, Balshi et al. 2009, Price et al. 2013, Boulanger et al. 2014), as warming accelerates and the expansion of human activities further alter disturbance regimes and fuel patterns (Krawchuk and Cumming 2010, Whitman et al. 2015). These potential negative impacts suggest a continued warming of 0.43 C per decade (A2 scenario; (IPCC 2000)) threatens western North America's forest resources and ecosystems (Price et al. 2013). More frequent and intense disturbances could speed up the conversion of boreal mixedwood forests to transitional aspen parkland along southern margins (Hogg and Bernier 2005, Mbogga et al. 2010), and promote an overall conversion from coniferous stands to deciduous (Johnstone et al. 2010). Observed tree-line shifts to higher elevations and along the western boreal-arctic transition zone are also expected to accelerate (Hansell et al. 1998, Sturm et al. 2001, Danby and Hik 2007, Lara et al. 2016).

Rapid permafrost thawing and associated land surface collapse (i.e. thermokarsts) are also expected to increase with climate change (Jorgenson et al. 2006, Osterkamp 2007, Price et al. 2013, Schuur et al. 2015), causing substantial tree mortality and additional release of methane (Jorgenson et al. 2001, Myers-Smith et al. 2007, Myers-Smith et al. 2008, O'Donnell et al. 2012, Price et al. 2013, Johnston et al. 2014, Lara et al. 2016). Permafrost in birch forests may only be 0.2–0.5 °C from widespread thawing (Osterkamp 2007, O'Donnell et al. 2012, Lara et al. 2016). In spruce forests, mosses and thick organic soils have historically provided resistance to thermokarsting by insulating the ground against summer heat greater than cold penetration during winter (O'Donnell et al. 2009, Jorgenson et al. 2010, Turetsky et al. 2012, Lara et al. 2016); however, this is likely to be destabilised with future increase in warming, droughts and fires (Bergner et al. 2004, Myers-Smith et al. 2008, Jafarov et al. 2013, Lara et al. 2016). Up to a million square kilometres of discontinuous permafrost within the Canadian boreal zone could be degraded by 2100, and the rest by 2200 (Price et al. 2013). Thawing and thermokarsting will cause initial waterlogging of many low-productivity woodlands, and for much of the southern discontinuous permafrost zone, the tipping point from carbon sink to carbon source could occur before 2050 (Price et al. 2013). These effects are already apparent in some regions, with documented changes in Yukon including melting of glaciers, permafrost thaw, alpine tree line

advance, shrub expansion on the arctic tundra, range expansion of some insects, and earlier egg-laying in arctic birds with earlier snow melt (Rowland et al. 2016).

Diversity of forest-associated species is related to the abundance and quality of forest habitats. Quantifying climate-induced vegetation changes is therefore required to predict impacts on forests and to manage changing ecosystems (Millar et al. 2007). Niche models are now widely used to infer which areas will be likely to maintain suitable habitat to proactively mitigate climate change impacts by establishing reserves (Carroll et al. 2017), habitat restoration, or assisted migration programs (Gray et al. 2011, Gray et al. 2016). Such additional sources of information may allow policy makers and practitioners to weigh the risk of changing existing practices against status-quo (e.g. Gray et al. 2011, Gray et al. 2016). However, studies that use the lowest levels of vegetation classification for western Canada still reported their results focusing on broad biomes (Mbogga et al. 2010), or based only on climate without attempting to account for expected time lag in vegetation shifts (Rowland et al. 2016). Other studies focus on productivity (Powers et al. 2016) and specific species (Gray et al. 2011, Gray and Hamann 2013), or complex and stochastic processes such as fire and vegetation dynamics using landscape simulation models (Rupp et al. 2006).

Examining biological responses to environmental trends and variability is valuable for revealing potential changes in species or communities distribution, and to guide management and conservation efforts (Millar et al. 2004, Millar et al. 2007). Empirical and experimental approaches have been used to reveal plant response to climate variability and climate change over large geographic scales, such as long-term provenance trials over many environments (e.g. Matyas 1994, Rehfeldt et al. 1999), analysis of growth and mortality in forest inventory plots (e.g. van Mantgem and Stephenson 2007), net primary productivity (e.g. Boisvenue and Running 2006) and dendro-climatology (e.g. Barber et al. 2000). First used in the 1990s, niche models (also known as species distribution models or bioclimatic envelope models) are the most common approach to project species responses to climate change (Araújo et al. 2005, Hannah et al. 2007, Hole et al. 2009, Rose and Burton 2009, Roberts and Hamann 2016, Rowland et al. 2016, Ding et al. 2017). Niche models predict suitability or occurrence by simply correlating

survey data with environmental predictor variables, using one of many statistical and machine-learning methods (reviewed by Elith et al. 2006).

The choice of modeling technique is a cause of uncertainty in projecting species responses to climate change (Thuiller et al. 2004, Hijmans and Graham 2006, Lawler et al. 2006, Pearson 2006), but this can be reduced with methods like RandomForest or ensemble methods (Stralberg et al. 2015b). Nevertheless, because of substantial uncertainty in projections, there is a need to investigate the relative and interactive effects of selection of a wide set of predictors (e.g. Global Circulation Models (GCM) projections) and modeling techniques to identify inadequacies in methods or data quality (Thuiller 2003, Stralberg et al. 2015b). Dependent variables may also be better explained (show a better model fit) using different data sources or models (Moisen and Frescino 2002, Thuiller et al. 2003).

Thus, in order to develop ecosystem-based climate projections to support species-habitat modelling, my objectives for this chapter are as follows:

- 1) Investigate the uncertainty with identifying the key climatic and topo-edaphic controls for various vegetation products.
- 2) Evaluate vegetation responses to current conditions and project potential vegetation changes for the 2011-2040, 2041-2070, 2071-2100 periods (hereafter referred as 2020s, 2050s, and 2080s), based on a range of GCMs and emission scenarios.
- 3) Compare different techniques for vegetation projections.
- 4) Evaluate variation in model accuracy, and potential shifts in vegetation across classification algorithms and landcover products.

2.3 Materials and methods

2.3.1 Study area

The study focused on western North America, bordered to the north by the Arctic Ocean (72°N), to the west by the Pacific Ocean (168°W), to the south by Mexico (32°N) and to the east by Manitoba and Nunavut (102°W). Shown in Fig. 2.5, the area covers about 10,000,000 square

kilometers of land in United States and Canada. The study area from north to south-east contains the Tundra, the Taiga, the Northern Forest (boreal forest), and the Great Plains ecoregions (CEC 2009). From west to center are the Marine West Coast Forests (or Mediterranean California to the south) and Northwestern Forested Mountains (or North American Deserts to the south) ecoregions.

2.3.2 Data sources

2.3.2.1 Climate baselines and future projections

With coarse-resolution climate grids, temperature variations are obscured, especially in mountainous areas (Hamann and Wang 2006). Therefore, in order to address my first objective, I first used the climate WNA software to downscale (i.e. bilinear interpolation and lapse-rate based elevation adjustment) the 1961-1990 baselines (i.e. monthly precipitation and temperature interpolated with the Parameter-elevation Regression of Independent Slopes Model - PRISM; (Daly et al. 2008) from 2.5 arc-minutes to 0.5 arcmin; the average resolution of four high-resolution Digital Elevation Models (DEM): SRTM, GTOPO30, GMTED, and CA30 (Hamann and Wang 2006) and the resolution of my ensuing models (kept in a Geographic Coordinate System "WGS 1983" except when they had to be otherwise projected in Yukon Albers for analysis of distance and area). ClimateWNA downscaling of GCMs was evaluated by Mbogga et al. (2009), who found that the downscaling algorithms eliminated up to 65% of the unexplained variance in observed monthly temperatures, and reduced standard errors of climate estimates by up to 40%.

Climate WNA was also used to compute 70 seasonal and annual climate variables for each of the desired 30-year periods: 1951-1980, 1961-1990, 1971-2000, and 1981-2009 (Wang et al. 2012). However, only the 1961-1990 period was kept as baseline after a preliminary analysis revealed its slightly greater sensitivity (up to 2.7% with the second best period: 1971-2000) in discriminant analysis and randomForest, despite that most land cover products date approximately from 2000.

Uncertainty in projections partly arises from the variance in Global Circulation Models (GCMs, IPCC 2007) and their implementations of each scenario on CO₂ emissions (Stralberg et al. 2015b). Not only do GCMs predictability of past climates vary by variables, periods, and regions (Knutti 2010, Terando et al. 2012), but historical prediction accuracy does not correlate well with future projections accuracy (Räisänen 2007, Jun et al. 2008, Knutti et al. 2009). Thus, I tested the most dissimilar models from a principle component analysis (PCA) (Abdi and Williams 2010) and a distance matrix using only the selected climate variables for the GCMs' projections of the 2070–2099 period (hereafter called the 2080s). Additionally, I tested various combinations of similar GCMs, as other studies show that multi or ensemble models consistently outperformed individual GCMs in predicting historical climates regardless of the method (Knutti et al. 2009). This was completed using a bootstrap-cluster analysis and ordination with non-linear multidimensional scaling (NMDS), using the packages Ecodist (Goslee and Urban 2007) and pvclust (Suzuki and Shimodaira 2006) in the R programming environment (R Core Team 2014), to test the robustness of the clusters created with "Euclidean", "maximum", and "manhattan" or "Mahalanobis" distances. I used two emission scenarios A2 and A1B from the Special Report on Emissions Scenarios (IPCC 2000) and their implementations for 2020s, 2050s and 2080s by 22 GCMs from the Coupled Model Intercomparison Project (CMIP3) dataset (Meehl et al. 2007)(BCCR_BCM2_0, CCCMA_CGCM3.1, CNRM.CM3, CSIRO.MK3.0, GFDL.CM2.0 & 2.1, GISS.AOM, INMCM3.0, IPSL.CM4, MIROC3.2.MEDRES, MIUB.ECHO.G, MPI.ECHAM5, MRI.CGCM2.3.2A, NCAR.CCSM3.0, NCAR.PCM1, UKMO.HADCM3, and UKMO.HADGEM1), or specific to A2 (GISS.ER), or to A1B (CCCMA.CGCM3.T63, GISS.EH, IAP.FGOALS1.0G, and MIROC3.2.HIRES). In this preliminary analysis, identified clusters of GCMs were not highly distinct and varied greatly depending on climate variables used, region analyzed, distance type, and clustering method. This suggests that there were no clear, stable clusters of similar GCMs and that even selecting a set of most dissimilar single GCMs is challenging. I therefor dropped the A1B scenario, as the variance among GCMs was much greater than among SRES scenarios. Additionally, I averaged across all available models for the A2 scenario to smooth uncertainty, and improve interpretability of vegetation models, recognizing that this may result in unfortunate smoothing of model variability (Knutti et al. 2009).

Most climate variables were highly correlated, especially monthly, seasonal and annual averages of the same variable. Discriminant analysis offered similar canonical functions (Appendix Fig. 2.1) while randomForest classification sensitivity (Table 2.1) decreased by less than 0.8% (versus up to 4% for discriminant analysis) with any subset of 5-8 temperature, precipitation and continentality variables. Thus, I identified the best compromise of predictors for all vegetation classifications using bootstrapped cross-validations with permutations of predictors (Beaumont et al. 2005, Guisan et al. 2007) and identified eight biologically relevant and uncorrelated climate variables ($r < 0.85$): degree-days above 5°C and below 0°C (DD>5 & DD<0), climate moisture index (CMI- the difference between precipitation and Hargreaves climatic moisture deficit according to Hogg (1997), continentality (TD- the difference between mean January and mean July temperature), mean summer and annual precipitation (MSP & MAP), extreme minimum Temperature (EMT), the Julian date on which the frost-free period begins (bFFP) (Fig. 2.1).

2.3.2.2 Topo-edaphic predictors

One hundred thirty seven topo-edaphic variables were also converted to 0.5 arc-minutes before a similar bootstrapped cross-validation selected 10 relatively uncorrelated ($r < 0.6$) variables: soil, wilting point between 0-150cm, nitrogen density between 0-30cm, geology, field capacity between 0-30cm, saturated hydraulic conductivity between 0-150cm, slope, maximum soil moisture, water abundance, and hillshade (Fig. 2.1). The slope and hillshade variables I calculated with the DEM Surface Tools (v. 2.1.375; jennessent.com) were indeed more important to models thus preferred to the HYDRO1k dataset (e.g. slope, aspect etc. Verdin and Verdin 1999). Likewise, the variable “water abundance” was produced by averaging a 5 arc-minutes raster on water percentage ((FAO/IIASA/ISRIC/ISSCAS/JRC 2012), iiasa.ac.at) with a line density raster I produced from Canada (NHN-Level1-Ed1.0 (NRCAN 2016); open.canada.ca) /U.S.A watercourse datasets (Simley and Carswell Jr. 2010, usgs.com) at a search radius of 0.5 arc-minutes (after incremental testing of 0.1 search radius and converting the pixel of maximum watercourse density to a value of 100).

The other 122 variables came from US Geological Survey (www.usgs.gov), Oak Ridge National Laboratory Distributed Active Archive Center (<http://daac.ornl.gov/>), Data Basin

(<http://databasin.org>), and International Institute for Applied Systems Analysis (iiasa.ac.at) (see Appendix Table 2.1 for more details).

Although elevation was omitted to avoid collinearity with climate (e.g. Araújo and Guisan 2006), static topo-edaphic variables were used to constrain projections, as suggested by Luoto et al. (2007).

2.3.2.3 Land cover and ecoregion response variables

In order to evaluate the variation among multiple land cover and ecoregion response variables, as outlined in the second objective, I tested nine products: CEC-L.III ecoregions ((CEC 2009): cec.org), MCD12Q1 ((Friedl et al. 2010): lpdaac.usgs.gov), NALC2005.v2 ((CCRS 2013): cec.org), NA-GLC2000v2 ((Latifovic et al. 2002): forobs.jrc.ec.europa.eu), GLC2000v1.1 ((Fritz et al. 2003): forobs.jrc.ec.europa.eu), Global 1981-94 ((Hansen et al. 2009): glcf.umd.edu), Canadian1988-91 ((Agriculture and Agri-food Canada 2013): open.canada.ca), Globcover2009v2.3 ((Arino et al. 2012): due.esrin.esa.int), and SYNMAP2000 ((Jung et al. 2006): webmap.ornl.gov) (Table 2.1). Land cover classes considered unnatural or less climatically driven, such as wetlands, cropland, and urban areas were not modeled; neither were rare cover types lacking sufficient occurrences.

2.3.3 Analysis

To address the third objective of comparing techniques used for vegetation projections, I used two contrasting techniques: discriminant analysis and classification tree analysis carried out in the R programming environment by the MASS (Venables and Ripley 2002) and randomForest (Breiman 2001) packages, respectively.

2.3.3.1 Sampling of the training dataset

Discriminant analysis and randomForest techniques are able to carry out classification even when the new combination of predictors has no current analogue conditions (Roberts and Hamann 2012), a risk that is high at local scales but low at large, sub-continental scales (Williams and Jackson 2007). I wanted to avoid exacerbating such risk and to address (Roberts and Hamann 2012) concern for an inflated statistical power with autocorrelated observations, while following Breiman's (2001) recommendation that the number of observations within classes are equal. Thus, I used a random sampling of 0.1% of the grid cells, or about 20,000 data points distributed equally between classes for each modeling exercise (Table 2.1). The slight differences in number of data points between each vegetation class are due to the need for all classes of the two categorical predictors (geology and superficial soil types) to be represented by at least 20 data points within each vegetation class. I also confirmed that model accuracy and robustness were consistent between training the models with all 20,000 sampling observations (0.1% of the tiles), or only a random 2/3 subset.

2.3.3.2 Discriminant analysis

Discriminant analysis is a rotation-based technique that maximizes the total variance between groups (vegetation classes in my case) to identify which of the variables differentiates groups best. Discriminant analysis uses a reduced set of independent canonical discriminant functions of the original variables to reduce multicollinearity and over-parameterization (Appendix Fig. 2.1). Therefore, I tested the assumptions of univariate normality and homogeneity of covariance among groups and transformed variables as necessary to conform to a standard normal distribution with the Ecodist package (Goslee and Urban 2007).

2.3.3.3 Classification tree analysis using randomForest

RandomForest is a robust ensemble classifier that runs a subset of variables along many dichotomous decision trees (4 random variables along 500 trees in this study) from bootstrap

samples of the training data, and determines the predicted class by majority vote over all classification trees (Lawler et al. 2006, Cutler et al. 2007). In contrast with discriminant analysis, the scaling of the predictor variables is irrelevant for classification trees.

According to Roberts and Hamann (2012), models that do not consider genetic differentiation within species tend to underestimate the negative effect of climate change on available niche space. Presuming that species genetic variation is mostly accounted for by ecoregion delineations, I also tested an ecosystem-based method that intersect each land cover classification with CEC level II ecoregions (a framework commonly used for research and natural resource management). As the models forecast several hundred fine-scale vegetation classes, I expected a low predictability of such detailed classifications but improved results once combined back into the broader original land cover classifications. However, this preliminary analysis suggested that even once the modeling units were combined back into the broader original vegetation classifications, misclassification error rates with the ecosystem-based method (i.e. Intersect with CEC level II ecoregion) were about a third greater than with land cover alone; therefore abandoned.

2.3.3.4 Model evaluation

As part of my fourth objective, I compared accuracy for each current land cover classification in the following manner: (1) I compared the best set of predictors for each classification and identified a compromise set of predictor variables to model all classifications, as well as ecoregions even if the later were not used to select predictors. (2) I used a random 2/3 of samples for training and 1/3 for evaluation (out-of-bag) to report Cohen Kappa values and the aptitude of the models to identify a vegetation class where it occurs (sensitivity, measured as $TP/(TP+FN)$, with true positives (TP) and false negatives (Lawler et al. 2003). (3) I compared predictability from randomForest with discriminant analysis. (4) I estimated how much of the variance in the predicted elevation versus northward changes is explained by the formula: $\delta \text{ Elevation} = \delta \text{ Latitude} \times \text{slope}$.

2.4 Results

2.4.1 Key climate and topo-edaphic predictors of vegetation

RandomForest importance values suggest the primary vegetation predictors were climatic (mostly $DD > 5$ and $DD < 0$), followed by the edaphic variables (mostly soil), and finally, the topographic variables, that were by far the least important (Fig. 2.1). In fact, I used 18 variables for best predictability but a stepwise elimination procedure revealed that using the most important 14 variables (i.e. without the four topographic variables) resulted in barely any loss in sensitivity. Also, when using only the eight climate variables randomForest classification accuracies suffered only by 2-3% compared with about 6% when using all 10 topo-edaphic variables (Table 2.1).

2.4.2 Accuracy across vegetation products

Model sensitivity across all classifications was much lower than specificity (ability to detect an absence of vegetation, measured as $TN/(TN+FP)$) and, more importantly, positively associated with their spatial homogeneity and latitudinal segregation of classes. Thus, it was not surprising that among the four most predictable classifications were the three most spatially clumped (vs. granulated): CEC level III ecoregions, MCD12Q1 and CA-AVHRR. Thus, it seems reasonable to extrapolate data from Canada to fill CA_AVHRR's missing data for the entire USA territory (Fig. 2.4), especially since projections in USA compared well visually with other classifications despite maybe overestimating coniferous forest in Alaska at the expense of transitional forest (Fig. 2.2-2.5). Although a trade-off had to be found between predictability and complexity, NALC2005 was nevertheless the most interesting classification, with better predictability than CA-AVHRR and MCD12Q1 despite containing more classes (Table 2.1), as well as spatial and latitudinal heterogeneity (Fig. 2.2-2.5). NA-GLC2000, Global-AVHRR and Globcover2009 were the least homogenous and predictable (less than 70% classification sensitivity and 60% Cohen Kappa), thus their results are not discussed and their projections not shown.

2.4.3 Accuracy across modeling techniques

For the discriminant analyses, two orthogonal canonical discriminant functions explained 90% of the variance among CA_AVHRR vegetation classes, 82% for NALC2005, and 70% for MCD12Q1. The first canonical discriminant function for interpolated data (eigenvalue of 6.0, 7.5, and 1.5; and 62%, 64%, and 44% of variance explained for CA-AVHRR, NALC2005, and MCD12Q1, respectively) can be observed along an elevational gradient and shows high correlations with temperature variables, especially when measured during the growing season such as degree-days above 5°C (Appendix Fig. 2.1). Independent from the first, the second canonical discriminant function (eigenvalue of 2.7, 2.0, and 0.8; and 28%, 18%, and 25% of variance explained for CA-AVHRR, NALC2005, and MCD12Q1, respectively) reveals a gradient from continental to maritime climate, with milder winters and more precipitation on the coast due to a strong oceanic influence (Appendix Fig. 2.1). Although a third and fourth functions independent dimensions were respectively required to account for 90% or more of the total variance in NALC2005 and MCD12Q1 vegetation, all other functions could be dropped without affecting the predictions or misclassification error rates. Similar discriminant functions were obtained for similar land cover classes across CA_AVHRR, NALC2005, and MCD12Q1 classifications (Appendix Fig. 2.1).

Nevertheless, my analysis showed that randomForest was more robust, with a sensitivity for the three most predictable land cover classifications (i.e. MCD12Q1, NALC2005, CA-AVHRR) of 21-28%, compared with 37-46% with discriminant analysis (Table 2.1).

2.4.4 Uncertainty and projection of vegetation shifts

Most class-specific sensitivities for MCD12Q1, NALC2005, and CA-AVHRR were above a Kappa of 60% and none were below 40% (Appendix Table 2.2-2.4). When MCD12Q1, NALC2005, and CA-AVHRR products were grouped into classes based on Kappa values (<50, 50-60, and >60), an inverse trend with the standard deviation of their latitude was apparent. In other words, the more specific a land cover was in term of latitude, the better the Kappa value (e.g. the NALC2005 classification where broad temperate/sub-polar classes had on average a

kappa of 55.7 compared to 74.1 for the more localized sub-polar/polar or tropical/sub-tropical classes). I also observed a weaker trend toward higher model accuracies for vegetation classes in higher elevation. Across all three classifications, the vegetation product with higher Kappa such as snow/ice, grassland, and barren were observed at higher elevation compared to the broadleaf, savanna/transitional/shrubland, needleleaf, and mixed forests (Appendix Fig. 3.2).

I found an inverse linear relationship between changes in projected elevation and latitude (Fig. 2.6). Based on the formula: $\delta \text{ Elevation} = \delta \text{ Latitude} \times \text{slope}$, the slope fluctuated from 0.31 for MCD12Q1, to 0.42 for NALC2005, 0.44 for CEC Ecoregions, and 0.51 for CA-AVHRR. Concretely, classes for NALC2005, MCD12Q1, CA-AVHRR and CEC Ecoregions are respectively expected to shift 0.6, 0.9, 1.9 and 1.8 m up slope or 1.6, 3.3, 3.5, and 3.2 km northward yearly. This correlation explained 25, 53, 45 and 22 % of the variance in the predicted elevation versus northward changes for the NALC2005, MCD12Q1, CA-AVHRR and CEC Ecoregions projections, respectively.

Aside from the southern US, for which projections may lack modern analogues within my study area, the biggest increase in mean latitude by 2080 are expected in the Northern Forests (Boreal Plains ecoregion: 528km north; MCD12Q1's Mixed/ broadleaf: 456km north; NALC2005's Temperate or sub-polar broadleaf deciduous: 410km north; NALC2005's Mixed Forest: 500km north; CA-AVHRR's Broadleaf: 595km north; Appendix Fig. 2.2). The models also predicted a large displacement of Taiga vegetation (Taiga Shield ecoregion: 299km north; Taiga Cordillera ecoregion: 321m up slope; Alaska Boreal Interior ecoregion: 208m up slope; MCD12Q1's Woody savannas: 330km north; MCD12Q1's Savannas: 276m up slope; MCD12Q1's Deciduous Needleleaf: 294 km north; NALC2005' Sub-polar taiga Needleleaf: 265km north; NALC2005's Sub-polar or polar barren-lichen-moss: 329km north), and Tundra vegetation (NALC2005's Sub-polar or polar barren-lichen-moss:329km north, CA-AVHRR's Tundra:371 km north) (Appendix Fig. 2.2).

By the 2080s, the Temperate Sierras ecoregion is expected to replace the Mediterranean and semi-arid ecoregions at higher elevations. The Mediterranean and semi-arid ecoregions are in turn predicted to expand west at the expense of North American deserts. North American deserts

are likely to shift northward in parts of the Northwestern Forested Mountains (i.e. South/central BC). The Great Plains ecoregion would also slightly move northward into the Northern Forests, especially around west-central and north-west Alberta. The same vegetation shift is also projected around north-eastern BC, and south-central Yukon. The ecoregions of Northwestern Forested Mountains and especially Marine West Coast Forests are not projected to shift much, other than the former expanding into taiga. Northern Forests (dominated by mixed broadleaves and needleleaves) are also expected to extensively push Alaska and NWT's taiga/transitional forests in higher latitude and elevation at the expense of tundra (open shrubland and barren). Although not discussed, loss and gains for all vegetation projections are also summarized by political regions (Appendix Fig. 2.3).

2.5 Discussion

I addressed the general lack in spatial and thematic resolution by projecting changes in climate suitability for 9 commonly used land cover and one ecoregion classifications using niche models. Based on what I found, the Tundra and Taiga ecoregions may be the most at risk from climate change, with a projected loss of 20-30% and 20-40% respectively by 2050-80s, for the benefits of Deserts/Great plains with a gain of 20-40% by 2050-80s. More surprising, the Northern Forests ecoregion may also expand by 30% by 2050s and over 50% by 2080s but we need to be cautious as a third of the gain expected by 2080s are disconnected in Alaska/Yukon. In addition, the Northern Forests ecoregion may increase the most in latitude with 4 +/- 6 degrees by 2080s (e.g. 528 km north for the Boreal Plains ecoregion) and about 18% of the current distribution is to be lost.

Although the link between climate change and ecological impacts can be complex (e.g. Woods et al. 2005, Hennon et al. 2006), niche models are invaluable for climate change adaptation and conservation planning efforts. As such, this study adds compelling reasons for careful attention to management of natural resources if currently observed climate trends continue or are accelerated. Since the reliability of projections depends on their uncertainty and accuracy associated with modeling approaches and parameters (Beaumont et al. 2005, Coudun et al. 2006, Luoto and Heikkinen 2008), as well as the type and quality of predictor variables and census data

(Taverna et al. 2005, Botkin et al. 2007), I summarize here the identified sources of uncertainty and error, and how they were addressed.

2.5.1 Key climate and topo-edaphic predictors of vegetation

2.5.1.1 Effects of static variables in ecological niche modeling

Evaluation of potential climate change effects on biota usually focus on dynamic climate projections based on GCMs. However, environmental niches also depend on vegetation, soil and land use to increase discriminatory capability for better predictions (Iverson and Prasad 1998, Calmé and Desrochers 2000, Zimmermann et al. 2007, Buermann et al. 2008, Brook et al. 2009). These predictors can be treated as static because soil is imperceptibly changing over geologic time, while vegetation and land use are changing faster but reliable projections are missing.

Combining dynamic climate predictors with static soil or land use data is not trivial (Brook et al. 2009). Some studies have excluded static predictors (e.g. Williams et al. 2003, Thuiller et al. 2005, Araújo et al. 2006, Hole et al. 2009, Carvalho et al. 2010), while others did not in order to improve model performance (Iverson and Prasad 1998, Peterson et al. 2002). It is preferable to exclude predictors that are indirectly biologically relevant (e.g. elevation), as they would otherwise result in an underestimation of climate change (Stanton et al. 2012). However, it is less obvious how to treat them when distributions directly depend on a static variable (e.g. plants and solar radiation; Austin and Van Niel 2011), especially if correlations with climate are not clear (e.g. vegetation; Thuiller et al. 2004).

Topo-edaphic variables contributed less to model accuracy than climate variables, consistent with Mbogga et al. (2010). However, models solely based on climate tend to be too pessimistic at the rear edge of species distributions (Roberts and Hamann 2012), and underestimate species' topo-edaphic adaptation or resilience in micro-sites (Morin and Thuiller 2009, Chen et al. 2010, Gillingham et al. 2012, Stralberg et al. 2015a). Stanton et al. (2012) also suggested that in some

instances, static variables improve performance for present distributions and result in no or only small degradation in the predictive performance for future distributions.

2.5.1.2 Limitations with correlated predictors

Differing opinions exist as to whether and how correlated variables (static or dynamic) should be combined in niche models. Including only climate variables can cause models to be overly sensitive to climate change under future climate scenarios (Iverson and Prasad 1998), but including correlated non-climatic variables could result in models that are over-fitted to current distributions, yet will be insensitive to future climate scenarios because climate variables are down weighted (Taverna et al. 2005, Coudun et al. 2006, Luoto and Heikkinen 2008, Stralberg et al. 2015b). The situation is complicated by possible interactions between static and dynamic variables.

The effects of one variable could also be overestimated in the case of strongly correlated variables (Clavero et al. 2011). While the sensitivity of niche models may inform which variables are most relevant to differentiate ecosystems and their distributions, it does not provide the mechanisms underlying ecological responses (Parmesan et al. 2005). Extreme events such as drought or low temperatures may act as limiting factors (Parmesan et al. 2000). However, annual climate indices, such as mean annual precipitation or temperature, proved to be better predictors, likely because they combine the information from multiple variables or events. The choice of climate predictors may therefore not be important for this type of analysis, unless correlations between unknown mechanistic drivers and variables change in the future (Schar et al. 2004). Stralberg et al. (2015b) found no change in the correlation matrix of climate variables between 1970s and 2080s projections, therefore I had no quantitative basis for modeling under a different assumption.

Vegetation response to climate also tends to lag and vary due to topo-edaphic conditions, lags in seed dispersal (Nathan et al. 2011), long-lived tree species that can persist in environments unsuitable for recruitment (Stralberg et al. 2015a, Renwick et al. 2016), and differences in

species' plasticity and local genetic adaptation (Gray et al. 2016). Lodgepole pine and spruce, for instance, are relatively similar genetically and may be more restricted in their ability to adapt to climate than expected (Yeaman et al. 2016). It is impossible and unnecessary to consider all these factors when doing bioclimate envelope models at a broad scale, as long as the associations between climate, vegetation, and other drivers remain constant over the modeling domain (Thomas et al. 2004, Thuiller et al. 2005, Loarie et al. 2008). However, when extrapolating into new spatial or temporal domains, the costs of using proximate variables are greater, depending on the degree of decoupling that may occur over space or time (Roberts and Hamann 2012).

2.5.1.3 *Issues with correlated dynamic and static predictors*

Including an indirect and static variable (elevation) that is a proxy for, and strongly correlated with, a direct and dynamic variable (temperature) is clearly problematic. Some plants may also occur on some types of soil when precipitation (or water availability) is low, but on others when precipitation is above a certain value. Nevertheless, Stanton et al. (2012) demonstrated that it is especially important when projecting potential future conditions to include variables that interact with climate variables.

I could have used the static variables to mask out areas that are unsuitable for non-climatic factors, but for variables that interact with climate variables (e.g. vegetation or land use), it would make the invalid assumption that their effects on species distributions are independent of climate, whereas including them in the analysis allows Maxent to incorporate dependencies. Another option would have been to create a separate suitability layer based on the static variable (e.g. by assigning a separate suitability value to each soil type or running a separate niche model with the static variables only) and multiplying this map with the probability map that is output from the niche model with the climatic variables (a related approach to Pearson et al. 2004). Although this approach may be a useful way to integrate the large scale effects of climate with the more local effects of land cover (Pearson et al. 2004), as with masking, the multiplication assumes wrongly that the two layers are independent.

2.5.2 Variation among land cover and ecoregion response variables

Like others (Guisan et al. 2007, Dobrowski et al. 2010), my data structure (especially of responses variables) had biogeographic features that affected accuracy. Indeed, land cover variables that were spatially homogeneous and segregated in latitude or higher elevation tended to have higher predictability. This implies that while a trade-off between predictability and complexity (over parameterization) should be considered, I may still have improved predictability (especially for MCD12Q1's barren, woody savanna, and open shrubland classes) by splitting the climate envelope of some vegetation classes between north and south or low and high elevation. Doing so may also have further restrained projected vegetation shifts in ways similar to the ecosystem-based method. My lower success with heterogeneous vegetation products (e.g. SYNMAP) is also most likely due to a combination of disturbance history and unmapped topographic factors. Yet, my best projections may be combined, as was done to produce SYNMAP, to obtain a similarly high thematic resolution.

2.5.3 Using different techniques for vegetation projections

There is growing support for considering the genetic structure when projecting wide-ranging species (Botkin et al. 2007, St Clair and Howe 2007, O'Neill et al. 2008, Thuiller et al. 2008, Chen et al. 2010, Polfus et al. 2017). I intersected vegetation classes with ecoregions as a substitute for complex processes (e.g. frequency/probability of presence, mortality/growth rate, disturbance regime, genotype) (Hamann and Wang 2006, Botkin et al. 2007, Thuiller et al. 2008, Mbogga et al. 2010, Gray and Hamann 2011) and to lessen predicted vegetation shifts (Baselga and Araújo 2009). However, the accuracy of the ecoregion-constrained method was lower than the "land cover only" projections, contrary to Roberts and Hamann (2012) assessment for tree species, because either using ecoregions as proxies is far from the true genotype distributions, or North American trees have repeatedly expanded and receded without many extinctions or losses of genetic diversity (Davis and Shaw 2001, Botkin et al. 2007).

Nevertheless, my subsequent modeling of ecoregions alone was even more successful, and given that the underlying modeling units are also the framework for natural resource management,

predictions can thus be directly linked to a set of applicable prescriptions under anticipated future climates (Gray et al. 2011, Gray and Hamann 2011, Hamann et al. 2011).

2.5.4 Model uncertainty and accuracy, and potential shifts in vegetation.

Climate and topo-edaphic predictors and land cover products are spatially auto-correlated, but a non-independent validation can assess the relative worth of models, though it may be over-optimistic (Araújo et al. 2005, Roberts and Hamann 2012). As similar discriminant functions were obtained for similar classes across land cover products, a visual comparison suggests the CA-AVHRR model was able to predict class distribution beyond original coverage. Also, while similar out-of-sample validations indicate absence of over-parameterization, it is also reassuring that the overall model fits of 70-80% (and over 90% for ecoregions) seem competitive with other climate envelope studies only based on climate parameters, presence/absence data, or more spatially autocorrelated data like broader biomes and species distribution (Roberts and Hamann 2012a, b, Gray and Hamann 2013, Rowland et al. 2016).

Similar to Gray and Hamann (2013), I found that on average a 100 km shift northward corresponds to an upward shift of 42 meters (Fig.2.4), versus 44 meters for Gray and Hamann (2013). This constitutes, on average, an annual 1.28m shift up in elevation or 3.1km north shift, compared with 2.4m and 5km reported by Gray and Hamann (2013).

As climate change is the same for all vegetation products, the differences in latitude and elevation shifts also illustrate the uncertainty with the method. One reason could be that some vegetation products are less closely linked to climate than others, perhaps simply due to mapping inaccuracies (spatial or qualitative). It is also possible that vegetation types that are really massively different get lumped into the same class or fail to track elevation well. Another reason could be related to scales and summaries. Maybe one vegetation product has lots of units in the north where shifts are strongest, and fewer on the coast or in the south, which would bias the regression lines.

Generally, misclassifications of current conditions tend to happen between nearby cover types. However, there are stretches of coniferous (i.e. CA-AVHRR) or deciduous needleleaves (i.e.MCD12Q1) found in the North West Territories arctic in 2080 projections, and closed shrublands on the northern coast of Alaska (i.e. MCD12Q1).The overall patterns of projections tend to follow real tendencies and similar work (Johnstone et al. 2010, Mbogga et al. 2010, Rehfeldt et al. 2012, Price et al. 2013, Johnston et al. 2014, Lara et al. 2016, Rowland et al. 2016). Consistent with other studies, I found that temperate species are projected to expand their range northward and into higher elevations, at the expense of boreal species, while losing suitable habitat at the southern end of their distribution to more tropical species (Talkkari and Hypén 1996, Iverson and Prasad 2002, Stralberg et al. 2015b). Although the lower United States and the arctic state or provinces (AK, YT, NWT/Nunavut, and Arctic Islands) may gain in biodiversity, the lower Canadian provinces are predicted to lose biodiversity (Appendix Fig. 2.3).

My projections for the 2080s change most notably in the higher latitudes, where the warming signal is strongest (Bogaert et al. 2002, Lloyd and Fastie 2003, IPCC 2007), and in flat regions, where climate velocity is higher (Loarie et al. 2009, Hamann et al. 2015). While climate change may result in no net loss of Marine West Coast Forests, the Taiga and Tundra ecoregions are projected to shrink substantially. This suggests that northern and high elevation ecosystems may be as vulnerable to climate change as evergreens in southern provinces or states, especially if considering genetic adaptation of populations to local environments (Hampe 2004).

Among other reasons, these ecosystem shifts are important to understand as they will have an impact on wildlife that depend on them for habitat. For example, the predicted impacts of climate change on boreal forest in western North America will impact threatened caribou populations in these areas. These caribou populations are already being pushed northward by development and human activity (Environment Canada 2008, Vors and Boyce 2009, Festa-Bianchet et al. 2011). My next research chapter will build on the work of this chapter to examine the potential cumulative impacts of human activity, climate change and vegetation shift on caribou populations in western North Canada.

Table 2.1 Description of all products tested for predictability, including source, classification, resolution, number of classes use (number of classes merged) per number of original classes, number of sample points per class, randomForest's accuracy given by the classification sensitivity and the Cohen Kappa per class (per merged class).

Satellite -Sensor	Classifications / source & reference	resol ^o	# used classes/ #original	sample pts /class	randomForest				discrim
					18 clim+topo Kappa	8 climate sensitiv	10 topo sensitiv	18clim.topo sensitivity	
-	CEC-LIIIecoregions /cec.org CEC 2009	-	80(21)/ 182	250	90.58 (90.5)	91.85 (95.5)	89.35	87.42	77.96
TERRA -MODIS	MCD12Q1 /lpdaac.usgs.gov Friedl et al.2010	0.25 arc min	10(7)/17	1600	61.33 (64.7)	72.44 (81.4)	70.73	68.36	54.17
	NALC2005v2/ cec.org CCRS 2013	250m	13(8)/19	1700	65.07 (71.9)	73.40 (86.1)	71.71	69.23	63.04
SPOT- VGT	NA-GLC2000v2 / forobs.jrc.ec.europa.eu Latifovic et al. 2002	0.5arc min	18/35	1000	51.56	57.44	55.86	54.38	43.72
	GLC2000v1.1/ forobs.jrc.ec.europa.eu Fritz et al. 2003	0.5arc min	9/22	2200	53.06	65.56	63.82	62.05	49.56
NOAA - AVHRR	Global 1981-94/ glcf.umd.edu Hansen et al.2009	0.6arc min	10/14	2300	50.52	63.02	61.32	59.63	47.09
	Canadian1988-91/ open.canada.ca AAFC 2013	0.6arc min	8(6)/11	2500	64.35 (66.6)	78.63 (86.6)	76.8	74.13	58.37
ENVISAT -MERIS	Globcover2009v2.3 /due.esrin.esa.int Arino et al. 2012	10arc sec	12/23	1500	48.86	57.95	56.4	54.86	43.68
-	SYNMAP2000 /webmap.ornl.gov Jung et al. 2006	0.5arc min	34/48	600	53.58	56.61	55.09	53.4	42.91

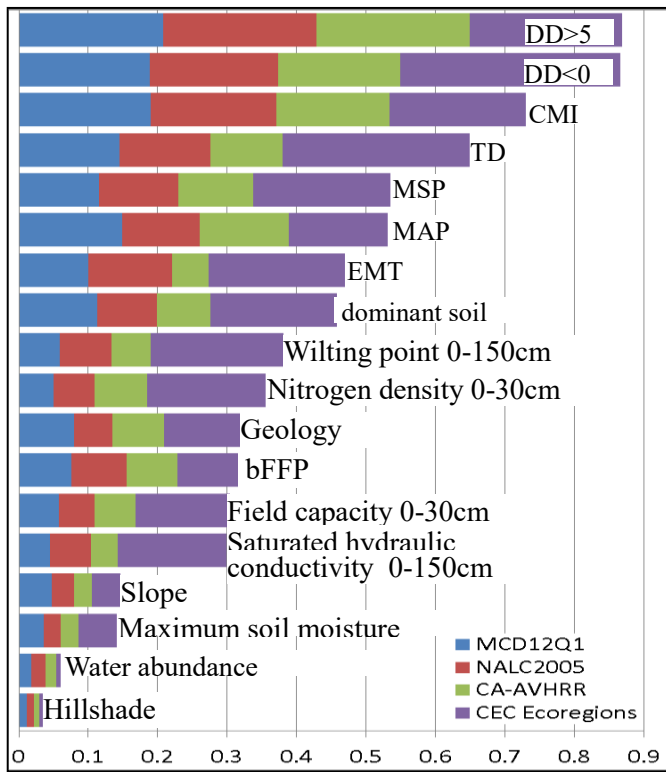


Figure 2.1 Importance of climate and topo-edaphic variables in randomForest models. The figure shows the cumulative importance of each variable across the four most predictable vegetation products (MCD12Q1, NALC2005, CA-AVHRR, and CEC Ecoregions). Importance was measured as the number of times each variable contributed to a correct classification in a bootstrapped cross-validation procedure with different permutations of predictors.

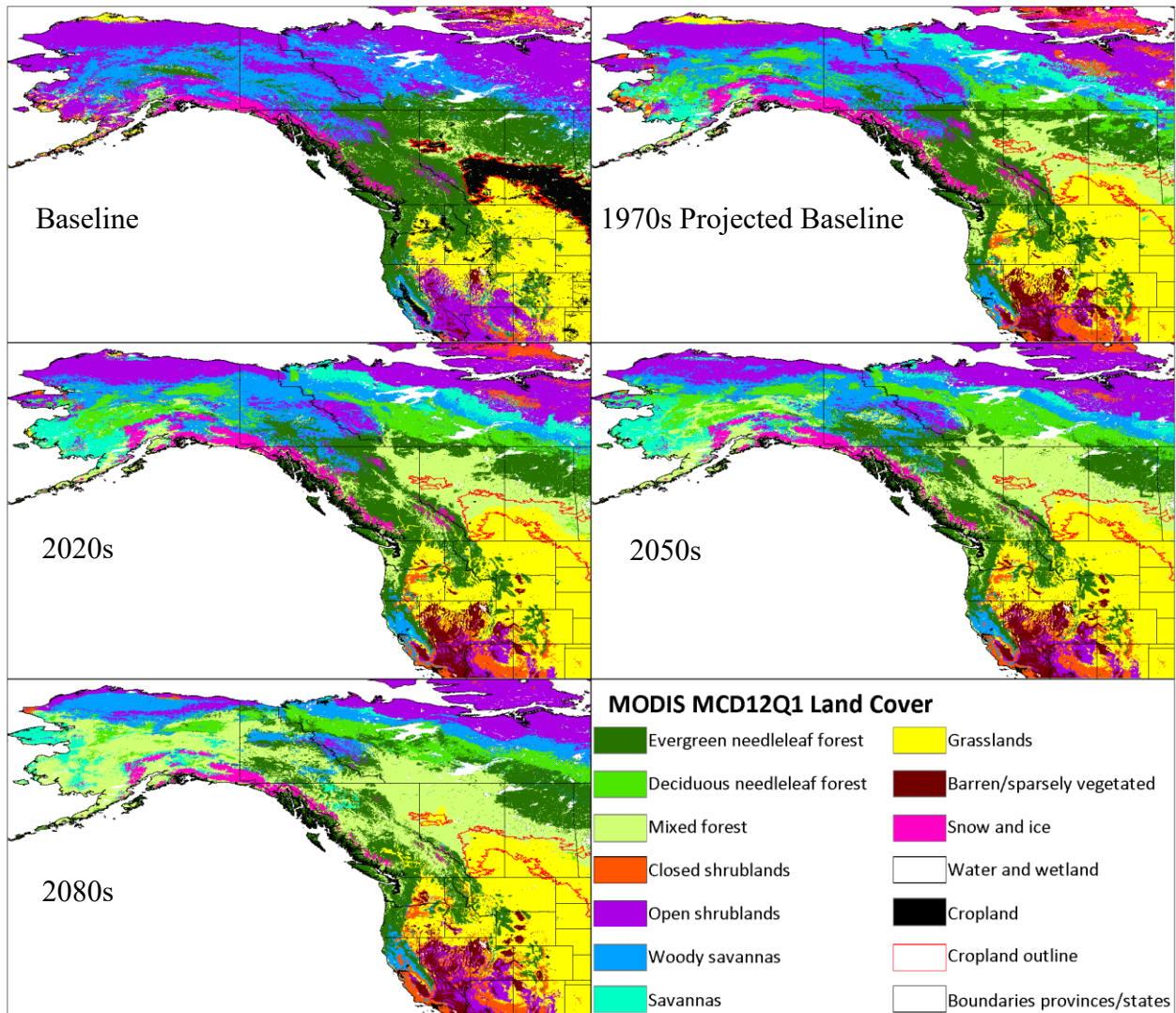


Figure 2.2 Projected changes in distribution of MCD12Q1 vegetation. The maps depict MCD12Q1’s original data for present day and randomForest’s projections for the 1961–1990 reference period, the 2020s, the 2050s, and the 2080s.

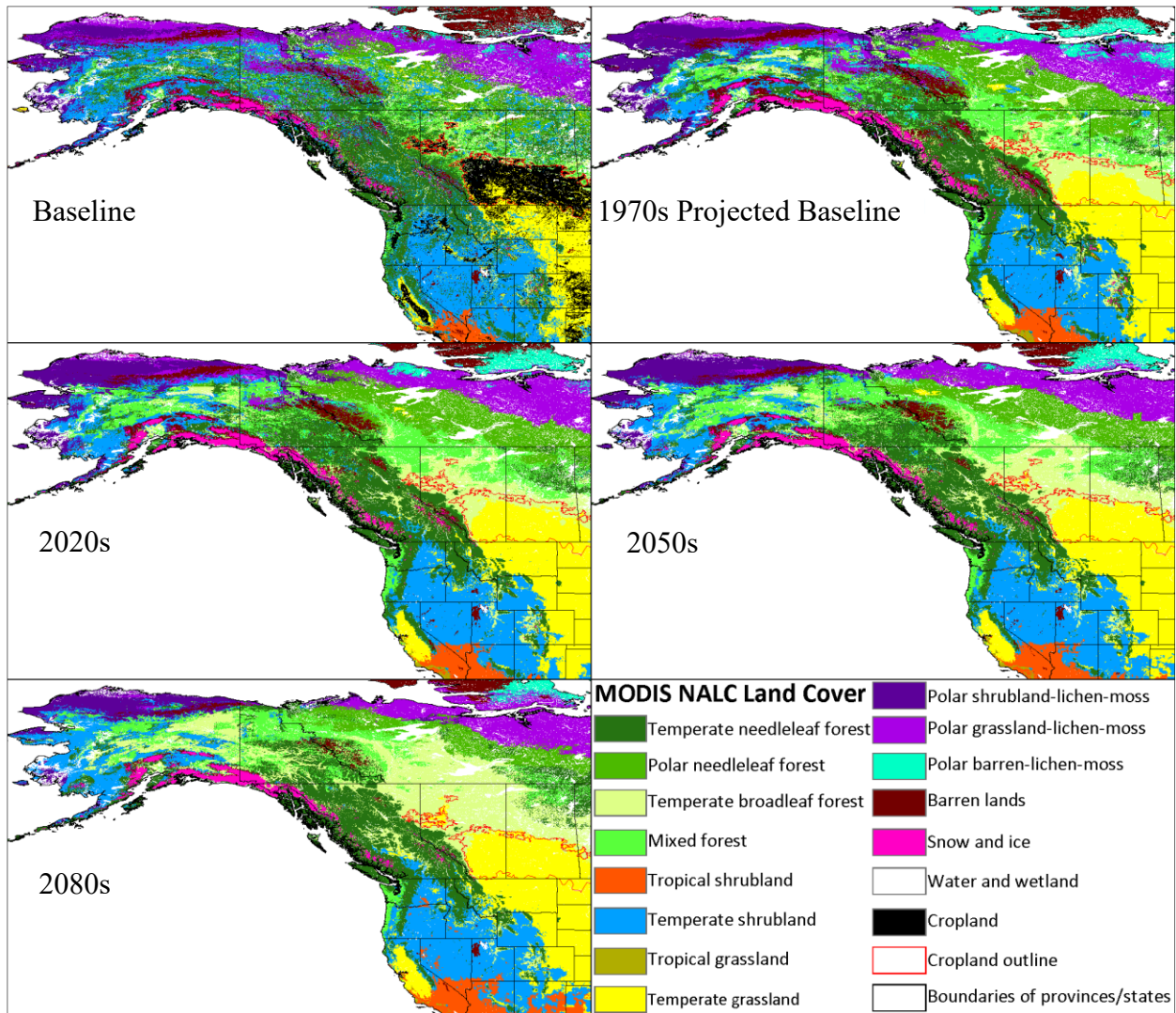


Figure 2.3 Projected changes in distribution of NALC2005 vegetation. The maps depict NALC2005's original data for present day and randomForest's projections for the 1961–1990 reference period, the 2020s, the 2050s, and the 2080s.

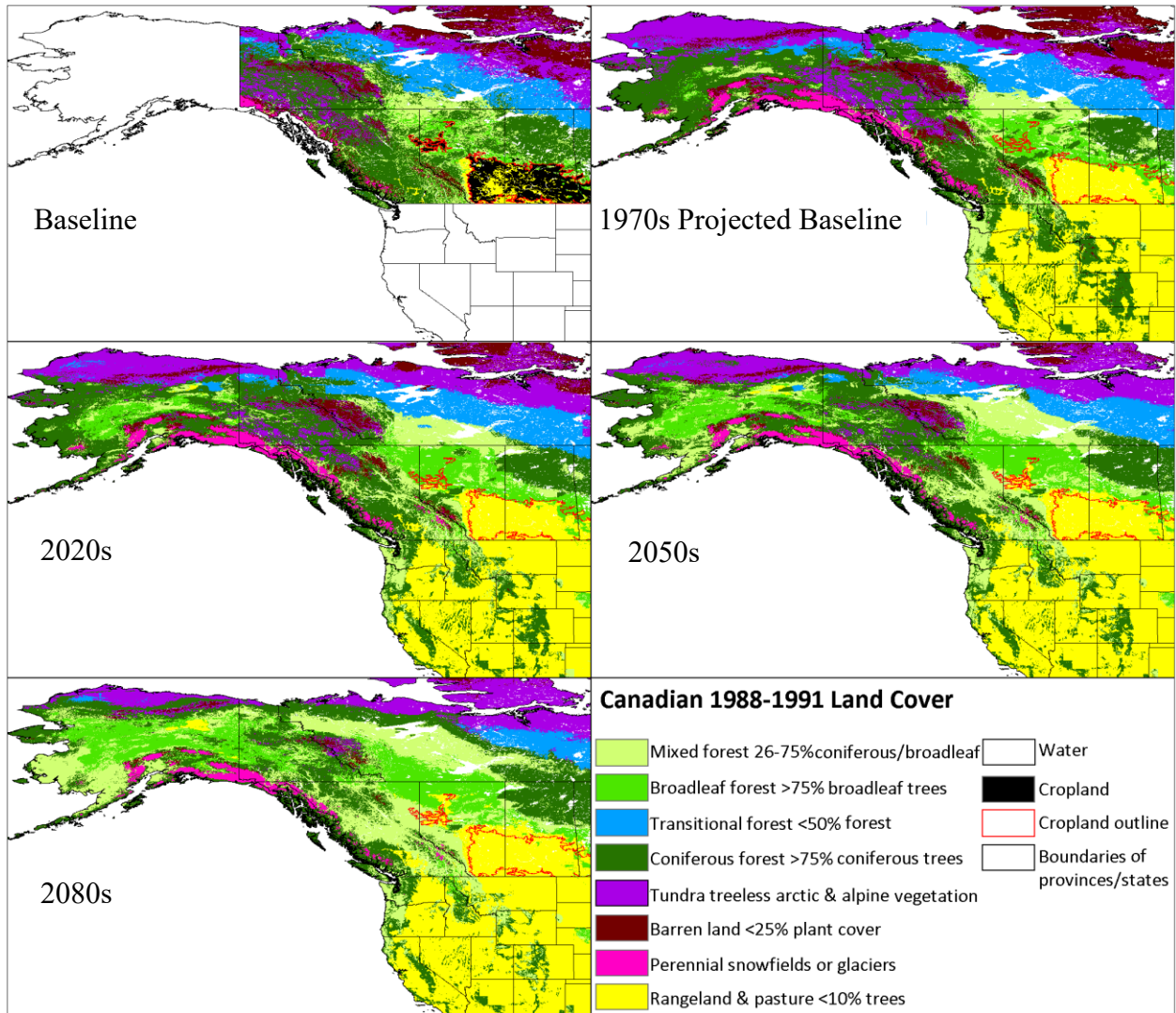


Figure 2.4 Projected changes in distribution of Canadian AVHRR vegetation. The maps depict Canadian AVHRR's original data for present day and randomForest's projections for the 1961–1990 reference period, the 2020s, the 2050s, and the 2080s.

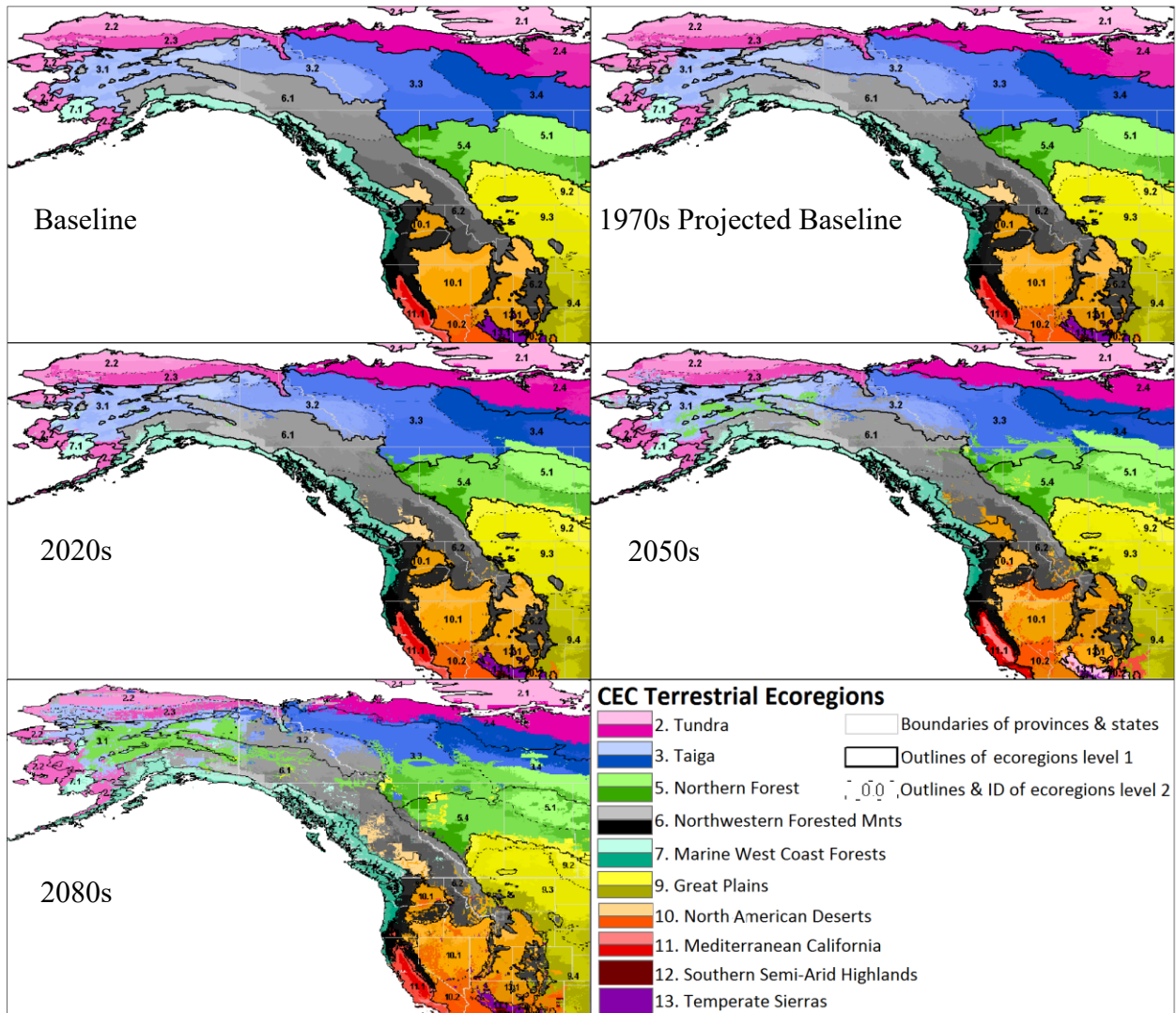


Figure 2.5 Projected changes in distribution of CEC North American ecoregions. The maps depict original data for present day CEC ecoregions and randomForest's projections for the 1961–1990 reference period, the 2020s, the 2050s, and the 2080s.

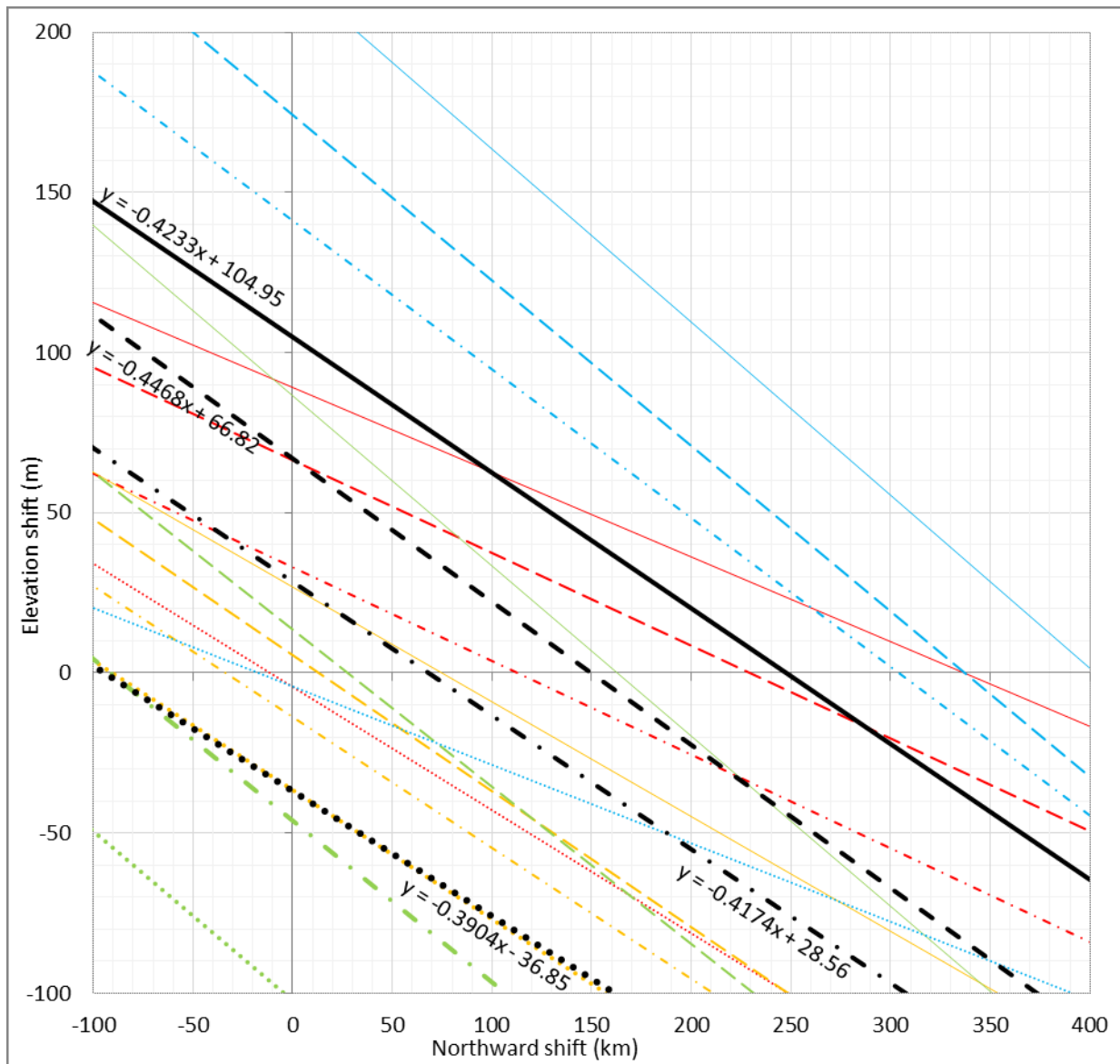


Figure 2.6 Projected shift in mean elevation versus latitude for the four most predictable vegetation products. Linear regression trend lines are provided for the overall trend (Black and Bliss), the three best land cover products (green- CA-AVHRR, orange- NALC2005, red- MCD12Q1) and the CEC ecoregions (blue), for each period (dotted- 1970s, dash/dotted-2020s, dashed-2050s, solid-2080s). The equation is also indicated for the overall trend line of each time period.

3. CHAPTER THREE: EFFECT OF ANTHROPOGENIC AND CLIMATE CHANGES ON CARIBOU DISTRIBUTION IN WESTERN NORTH AMERICA

3.1 Summary

Although considerable research has been undertaken on individual threats to caribou in Canada (*Rangifer tarandus*), less is known about the potential extent and speed of climate change effects, especially when combined with the cumulative impacts of human activities. Forestry, energy and mineral exploration, and rural expansion, are rapid land-use changes occurring throughout the distribution of caribou, threatening their already diminished habitat. Enhanced understanding of how stressors of caribou habitat may be exacerbated by anticipated climate change is urgently needed. Using MaxENT, I test whether adding road density to climate only or climate+vegetation models better explains the present distribution of caribou populations across western Canada and Alaska, and investigate potential future changes in caribou distribution based on vegetation and climate scenarios. I performed cross-validation of models and compared the implication of examining various distributional scales for northern mountain caribou in the Yukon Territory. Results suggest that human activities, and assumed changes in induced biotic factors such predation and competition, have influenced current caribou distribution beyond consideration of climate and vegetation alone. However, projections for the end of the century suggest that potential future effects of climate change on caribou may supersede biotic interactions, especially at the southern range. With significant shifts in caribou distribution to be expected, I identified potential climate refuges for each caribou population.

3.2 Introduction

3.2.1 *Caribou status, threats and importance of winter habitats*

Caribou (*Rangifer tarandus*) are important to the ecology, culture and economy of Canada and Alaska (Hayes and Couture 2004). However, the species distribution is receding in Canada and worldwide, with some populations at record low numbers (Environment Canada 2008, Vors and Boyce 2009, Festa-Bianchet et al. 2011). In Western Canada, barren-ground caribou (*R. t. groenlandicus*) are listed as of special concern, Peary caribou (*R. t. pearyi*) as endangered, and woodland caribou (*R. t. caribou*) as threatened (boreal population), endangered (central and southern mountain populations), or of special concern (northern mountain population) under the Species at Risk Act (SARA) (COSEWIC 2002, 2014).

A northward shift in the distribution of woodland caribou has been observed in conjunction with anthropogenic disturbance (Vors et al. 2007), and the Recovery Strategy for the boreal population identifies a minimum of 65% undisturbed habitat in a range as the critical habitat that can aid in recovery or provides a 60% probability for a local population to be self sustaining (Environment Canada 2008). Climate change may already affect caribou through effects on forage abundance and accessibility (Post and Forchhammer 2008), or predator efficiency (Huggard 1993). However, indirect and cumulative effects of human development are still hypothesized to be the greatest threat to woodland caribou (McLoughlin et al. 2003, Vors et al. 2007, Wittmer et al. 2007, Environment Canada 2008).

3.2.2 *Climate change*

Food availability is important to caribou and can be a limiting factor in some circumstances (Hébert and Weladji 2013, Avgar et al. 2015), with regeneration following overgrazing within 20 years (Collins et al. 2011). Global warming induced changes in plant or insect phenologies may lead to 'trophic mismatch' of migration or parturition with spring green-up (Ronnegard et al. 2002, Post 2003, Post and Forchhammer 2008), and earlier emergence or increased abundance of

hematophage insects (Hagemoen and Reimers 2002, Weladji et al. 2003). With vegetation explaining much of caribou habitat selection at the landscape level (Leblond et al. 2011, Beguin et al. 2013, Boan et al. 2014, Poley et al. 2014), management decisions should consider the dynamic nature of landscapes (Arlt and Manseau 2011).

Climate change could alter vegetation and hence the habitat of all caribou types (Ruckstuhl et al. 2008). First, as discussed in the previous chapter, prolonged growing seasons may result in expanded timber harvest because of a higher tree growth and advancement of the tree line (Ruckstuhl et al. 2008). Second, drought stress without comparable increases in precipitation is expected to cause tree mortality, changes in frequency and intensity of fires or insect outbreaks, reduced forest mean age, and tree species composition (Logan et al. 2003, Page and Jenkins 2007, Flannigan et al. 2009). Caribou tend to select for relatively less dense vegetation, more lichen, and longer periods since fire (125-275 years cycle) that are suited for old coniferous/lichen complexes (Collins et al. 2011, Polfus et al. 2011, Boan et al. 2014, Courbin et al. 2014, Latombe et al. 2014, Leclerc et al. 2014). Further, caribou may avoid burned areas for up to 10km and 60 years (Joly et al. 2003, Johnson et al. 2015). With burnt areas projected to increase up to 30% and 60% by 2053 in Alaska's northwest Arctic and Tundra, respectively, high quality habitat for caribou overall may decrease 6% by 2053, and up to 30% in caribou's core winter range, where moose habitat was projected to increase up to 64% (Joly et al. 2012). Caribou are also more likely to avoid and be negatively affected by logged areas than burnt areas (Beguin et al. 2013, Lesmerises et al. 2013, Beauchesne et al. 2014, Losier et al. 2015), because the former is associated with roads/trails development which are linked to expansion of white-tailed deer and associated increases in predation (Dawe and Boutin 2016).

3.2.3 Anthropogenic disturbances

The industrial footprint in Canada's North is increasing rapidly, particularly in association with hydrocarbon and mining exploration and development (McLoughlin et al. 2003, Vors et al. 2007, Wittmer et al. 2007, Environment Canada 2008); however, the respective effects of different activities on caribou have not been segregated (Vors et al. 2007). Habitat loss, degradation and fragmentation from cumulative effects are the indirect but ultimate cause of caribou declines,

especially at the southern edge of their distribution, where human disturbances are greatest: southern mountain (McLoughlin et al. 2003, Wittmer et al. 2007) and boreal populations (Sorensen et al. 2008, Environment Canada 2008).

Linear features (even winter roads or snowmobile trails, cutlines, hydro-transmission lines, and pipelines), as well as expansion of herb, shrubland and deciduous forest northward or in elevation, brings concomitant changes in the abundance and distribution of alternate prey species like white-tailed deer and moose (Parmesan and Yohe 2003, Schaefer and Mahoney 2007, Vors et al. 2007, Wittmer et al. 2007, Rempel 2011, Courbin et al. 2014, Leclerc et al. 2014, Dawe and Boutin 2016). Transmission of parasites and diseases to caribou (e.g. *Parelaphostrongylus tenuis*) may then also increase, as do the proximate causes of caribou decline: predation and human harvest (James and Stuart-Smith 2000, Courtois et al. 2007, Vors et al. 2007, Boan et al. 2011, Boan et al. 2014, Poley et al. 2014, Avgar et al. 2015). Indeed, wolves and bears are more common in human-disturbed areas than caribou, as their plasticity to anthropogenic food sources and infrastructure give them hunting and movement advantages (Lesmerises et al. 2012, Boan et al. 2014). Predators strongly select for low density secondary roads (Lesmerises et al. 2012), and use seismic lines more than bogs, fens, upland conifer stands, and undisturbed forest interiors, compared to caribou (Latham et al. 2013). As a result, an increase in functional response can result in a more than linear response with respect to prey density, as well as interactions with seismic line density (McKenzie et al. 2012). Concomitantly, undisturbed patches <math><100\text{km}^2</math> create concentrations of caribou that are better hunting for predators (Lesmerises et al. 2013, Latombe et al. 2014).

Although distance thresholds may be smaller in highly disturbed areas (Leblond et al. 2014), caribou generally avoid cut-blocks by up to 5km, seismic lines by 100m to over 2km as densities increase (Beauchesne et al. 2013, Johnson et al. 2015), mines by 2-10 km (Polfus et al. 2011, Leblond et al. 2014, Johnson et al. 2015), primary roads by up to 30km, secondary roads by up to 10km, rural roads by about 1km (Leblond et al. 2014, Johnson et al. 2015), and wellsites and tourist cabin by 1-4km (Polfus et al. 2011, Johnson et al. 2015). Caribou use of habitats decreases (Lesmerises et al. 2013), and calf mortality rates increase, with all disturbances, as well as with increasing amounts of deciduous or mixed forest (Polfus et al. 2011, Lesmerises et

al. 2013, Beauchesne et al. 2014, Leclerc et al. 2014, Losier et al. 2015). Barriers to migration and dispersion (e.g. deep snow, burns/cuts, roads/seismic lines) may also impact caribou access to important seasonal forage (Wolfe et al. 2000, Dyer et al. 2001, Johnson et al. 2001, Nellemann et al. 2001, Seip et al. 2007) and refuge from insects, predators and thermal stress (Kuzyk et al. 1999, James and Stuart-Smith 2000). The associated development of a transportation network may thus partly explain why forestry operations have a greater negative impact on caribou populations than equivalent losses of mature forests by wildfires (Environment Canada 2008).

A resultant conclusion is that human disturbances increase caribou risk to predation, either due to increased hunting efficiency of wolves and other predators around disturbance features (Ehlers et al. 2014), or due to expansion of apparent competitors (Latham et al. 2013). The risk to caribou of an Allee effect at small population sizes (Wittmer et al. 2005, Vors et al. 2007, Wittmer et al. 2007) also underscores the importance of connectivity to metapopulation sustainability (Arlt and Manseau 2011, Courbin et al. 2014, Leblond et al. 2014).

3.2.4 Winter

Caribou are especially vulnerable to additional stressors in winter, as snow depth and hardness influence escape from predators, travel, and access to a highly specialized diet (Arseneault et al. 1997). Niche overlap of wolves and woodland caribou is also greatest in winter (Latham et al. 2013). Changes in winter conditions may thus jeopardize woodland caribou survival and reproduction, as observed in the decline in extreme latitude of insular Peary caribou (*R. t. pearyi*) (e.g. 98% loss on the Western Queen Elizabeth Islands between 1995-1997 (Miller and Gunn 2003) and Svalbard reindeer (*R. t. platyrhynchus*) (e.g. 80% loss of the Brøggerhalvøya population in 1993-1994; (Solberg et al. 2001, Aanes et al. 2002), as well to a lesser extent so far, the more mobile (i.e. continental) and southern semi-domestic Scandinavian reindeer (Tveraa et al. 2007). The more sedentary woodland caribou isolate themselves to reduce predation on new born calves, thus protection of winter habitat rather than calving grounds per se may be more important to population persistence (Schaefer 2008). Reduced winter range fidelity also highlights the necessity of protecting large blocks of preferred forest habitat (Faille et al. 2010, Schaefer and Mahoney 2013). Finally, more dramatic climate changes are expected in winter and

northern latitudes (Rinke and Dethloff 2008), and will likely increasingly impact all aspects of *Rangifer* fitness and hence population dynamics. These considerations, in addition to strong differences in seasonal habitat selection, make winter habitats key to landscape-level conservation of caribou.

3.2.5 The approach: Environmental niches

Studies of the predictive accuracy among numerous species distribution modeling techniques support an important role for presence-only models when absence data are not available (Stockwell and Peterson 2002, Phillips et al. 2009, Elith et al. 2011). MaxEnt (Phillips et al. 2006, Phillips and Dudik 2008) is among the most widely used and best performing of such presence-only modeling approaches (Elith et al. 2006). All niche techniques have limits when it comes to extrapolation to environments not included in model calibration (Pearson 2006), and in dealing with spatial bias in occurrence records (Graham et al. 2008). Maxent is no exception (e.g. Phillips and Dudík 2008, Phillips et al. 2009).

Environmental niche models are particularly useful for studying the distribution of boreal caribou because many populations have not been studied and their distributions are not well mapped. In fact, according to (Environment Canada 2008), an environmental niche model across the entire distribution of boreal caribou populations is an appropriate first step in understanding critical habitat needs.

The ultimate goal of this research was to integrate climate change and anthropogenic disturbance patterns into broad-scale caribou conservation planning. I first incorporated current and future vegetation and climate into projections of potential future caribou distribution, in order to identify potential population vulnerability to climate or to roads, and the uncertainty with scales. I then compared potential shifts in distribution with current population distribution, in order to identify potential climate “refuges”.

3.3 Methods

My purpose was to build on a previous study on boreal woodland caribou (See Appendix 6.4 in Environment Canada 2008) by modeling the impact of climate change and human footprint on potential distribution changes in caribou subspecies and populations in western North America. The absence of rare or threatened species records may often represent false negatives. Thus, I used a species distribution-model based on presence information (presence-only) to express the most uniform distribution (maximum entropy) of suitability over 0.5 arc-minutes grid cells (all models kept in a Geographic Coordinate System "WGS 1983" except when they had to be otherwise projected in Yukon Albers for analysis of distance and area) as a function of environmental variables (MaxEnt v3.1; (Phillips et al. 2006)).

3.3.1 Variables and model parameters

As in Chapter 2, I evaluated 137 topo-edaphic variables (Chapter 2-Table 2.1). Similarly, 70 climate variables were downscaled at 0.5 arcmin by the software Climate WNA (Hamann and Wang 2006, Wang et al. 2012), based on the emission scenario A2 (IPCC 2000), and an average of 18 GCMs (Meehl et al. 2007): BCCR_BCM2_0, CCCMA_CGCM3.1, CNRM.CM3, CSIRO.MK3.0, GFDL.CM2.0 & 2.1, GISS.AOM, INMCM3.0, IPSL.CM4, MIROC3.2.MEDRES, MIUB.ECHO.G, MPI.ECHAM5, MRI.CGCM2.3.2A, NCAR.CCSM3.0, NCAR.PCM1, UKMO.HADCM3, UKMO.HADGEM1, and GISS.ER) for the 1970s (baseline), 2020s, 2050s and 2080s periods. Most variables were highly correlated. Thus, I identified the best compromise set of predictors for all caribou models by training without each one, then using it in isolation (jackknife).

It is difficult to model the distribution of species with large ranges, as their subpopulations inhabit different regions and may be driven by different climate, vegetation and biotic interactions. Thus, I also evaluated response variables at multiple delineations and scales by comparing results for the species all together vs each subspecies, ecotypes (for woodland caribou; referred to as populations by SARA or Designated Units by COSEWIC) and winter ranges (for northern mountain caribou in the Yukon Territory).

A drawback encountered was the lack of comparable telemetry data between jurisdictions and populations, and the reality that many northern caribou herds had no radio-tagged animals. Using limited, available telemetry data would add spatial bias to training data (Johnson and Gillingham 2008, Phillips and Dudik 2008, Environment Canada 2008), even if telemetry data was filtered to fit other input timelines (McKenzie et al. 2009) prior to modeling multiple random (Araújo and New 2007) but stratified samples (Araújo and Guisan 2006); methods that do not address the lack of data for some populations. Thus, I used as the response variable systematic samples from the distribution polygons for the different populations, delineations and scales of interest.

Boreal, SARA's northern and southern mountain populations, and COSEWIC's northern, central and southern mountain populations Designated Units were obtained from COSEWIC (2011), while those for barren/Peary and Grant's populations were respectively from the Circum Arctic Rangifer Monitoring and Assessment Network (CARMA) and the Alaska Department of Fish and Game. Detailed winter ranges for northern mountain caribou in Yukon are from the Wildlife Key Areas (WKA v. 2013) dataset compiled by the Yukon Department of Environment from observed locations of wildlife and various ancillary sources.

Maxent is a probability density estimation method, where the presence data are assumed to be drawn from some probability distribution over the study region (Phillips et al. 2006). Like most methods for modeling species distributions from occurrence records, it requires data representing the range of environmental conditions in the modeled region (background or pseudo-absence data), usually drawn at random from the entire region (Stockwell and Peterson 2002, Phillips et al. 2009, Elith et al. 2011). Special consideration is to be given to niche model sensitivity to sample effort and biases in the geographic distribution of data, especially for comparison of models for different species or populations (Stockwell and Peterson 2002, Phillips et al. 2009, Elith et al. 2011). Therefore, I maintained the sampling intensity across caribou populations with systematic sampling every 10 km, resulting in approximately 400 (for southern DU) to 20,000 (for barren-ground) presence points and 30,000 (for barren-ground) to 50,000 (for southern DU) background points. Backgrounds points were limited to the historical caribou range illustrated in Figure 3.5. (COSEWIC 2002, 2014), and include the presence points from other populations. The sampling intensity for the "entire species model" (when no distinction between populations and all ranges are considered as presence) was reduced to every 20 km for presence points,

resulting in about 10,000 sampling and 15,000 background points. For the “Yukon winter range model”, I examined the influence of different scales by first using the same background points as for SARA’s northern population (all other populations considered as background), then by using all populations (including SARA’s northern population) as background and finally, by defining background as the smallest rectangle around locations.

Sampling population distributions, as opposed to using arbitrary and scarce location data, allowed me to cross-validate five random subsets of points for each population. The probability of presence (or relative suitability) was then estimated as the average logistic distribution over the five replicates, while the distinction between presence and absence was set at the maximum test sensitivity plus specificity logistic threshold. The scaled up “logistic output” (i.e. the exponential of the raw distribution’s uncertainty) although it represents rank order suitability rather than actual probability of occurrence, made for easier interpretation and comparison across populations, delineations and scales. Although Maxent limits over-fitting by limiting the expected value of each environmental variable to match the average over sampling points (Phillips et al. 2006), the risk of over-fitting is increased by using the auto features (a combination of linear, quadratic, product, threshold and hinge features) in order to get the most detailed response to each predictor, as implemented here.

3.3.2 Modeling caribou distributions with climate, topo-edaphic and vegetation predictors

My second objective was to describe the current and future niche of caribou when ignoring anthropogenic influences (Soberon 2007, Hirzel and Le Lay 2008). Thus, I first used only topo-edaphic and climate indices to model caribou distribution, before separating direct from indirect effects by testing current and future importance of several variations of the nine vegetation products I projected in Chapter 2 (Appendix Table 2.2). Preliminary AUC results revealed that the best vegetation predictors for most caribou populations were CEC-L.III ecoregions and NALC2005.v2, once temperate as well as sub-polar woody classes were merged, thus are the two discussed forward. Although vegetation is obviously limited by climate (as well as topo-edaphic conditions), its response to climate change is likely delayed due to the persistence of long-lived tree species even under unsuitable conditions for establishment, and time associated with seed

dispersal (Stralberg et al. 2016). Therefore, to assess caribou vulnerability to climate change in the short-term, separating the influence of vegetation from other climate-related factors may be of critical importance (Huntley 1995).

3.3.3 Modeling caribou distributions by adding roads

My third objective was to model the areas presently occupied by caribou and test whether climate or anthropogenic disturbances best explain their distribution. This niche is related to direct and indirect effects of human disturbances (Guisan and Zimmermann 2000), as young forests attract primary wolf prey species like moose and deer, increasing wolf predation on secondary prey like caribou (Wittmer et al. 2007, Sorensen et al. 2008). I generated various “distance to” layers derived from point, polygon and linear disturbance sources compiled to circa 2010 (e.g. history of mineral claims and fire; (Canadian Forest Service 2011b, a), but later discarded them as adding unnecessary complexity with little influence on the models. This “distance to” scheme was then replaced by density rasters for the linear sources only (Appendix Table 3.1). In an iterative process, I increased the search radius in 10-km increments up to 400 km for primary roads, 150 km for secondary, and 100 km for both rural and trail rasters, when importance on all caribou models leveled off. As primary, secondary and rural road densities are not independent from each other, I started by determining the threshold for primary roads, then secondary, rural and other linear features. This classification seemed to best capture the different types and magnitudes of landscape disturbances. I found these linear feature density layers to be more consistent and relevant than “distance to” metrics, and used them in lieu of the latter.

The linear features assessed include pipelines (~10 m wide), airfields (~100 m), railways (~15 m), transmission lines (~30 m), primary roads (paved, ~60 m), secondary roads (less often paved ~25 m), rural roads (unpaved ~10 m), and trails/cut lines (~2 m). The data sources, the buffers used to avoid duplicates and regions affected by those linear features and buffers are listed in Appendix Table 3.2. The classification used for those linear features, its correspondence with an alternative one I also tested, as well as a description and the order of width expected on the ground are listed in Appendix Table 3.3. A number of tasks were performed to ensure quality data. To eliminate duplicate or differentially classified features between intersected datasets, a

rank-order protocol was followed where the suspected most accurate (often most detailed) was given priority and used to clip the next one and so on. Each feature source was edited separately in each province/region, and clipped by all sources suspected more accurate in the region. Efforts were then made to use and reconcile existing dataset classifications and come up with a common classification that maintained as much detail as possible. This also required investigating inconsistencies in classification between bordering datasets or administrative regions (e.g. a British Columbia secondary road switching to a Yukon primary road). In some cases it was difficult to determine disturbance type, particularly when classified differently by different sources. To minimize error, I applied a knowledge-based approach to develop two classification systems: one focusing on importance /use and the other on whether or not roads were paved and pipelines underground. The best exploratory models across caribou populations included primary road density with a 400-km search radius (improving AUCs by 0.006) and secondary, rural and trails, all at 100-km radius (improving AUCs by 0.002 each) and so preferred to the paved vs unpaved system.

3.3.4 Comparing current and future niches with climate only or concomitantly with vegetation and roads

My fourth objective was to compare current distribution patterns with a population's vulnerability to combinations of climate, vegetation, and human disturbance, before trying to anticipate potential climate change "refuges" (Peterson et al. 2006). I hypothesized that the difference between climate only and climate+vegetation+roads models illustrates the additive effects of competition, predation, and human avoidance. While this approach seems reasonable for current conditions, with up to date climate, vegetation and road data, their respective effects are confounded due to correlation between climatic variables and road density. As a result, Maxent attributes to roads some importance otherwise accounted for by climate, thus artificially reducing model response to future climate when roads are kept static; functionally a reduced "upper bound" of bioclimatic envelope projections. Nevertheless, even partly understanding the respective and cumulative effects of climate change and human disturbance allows exploration of their-potential effects with future scenarios.

3.4 Results

3.4.1 Importance of variables to caribou distribution

As in the previous chapter, from the available suite of measures, I screened seven biologically relevant, and uncorrelated climate variables ($r < 0.7$) (Parra et al. 2004) for inclusion in models: fall, winter and spring precipitation (ppt-at, ppt-wt and ppt-sp), and average temperatures for each seasons (tav-wt, tav-sp, tav-sm, tav-at). Estimates of variable importance using relative model fit (AUC scores) were generated for each population unit using two methods (Fig. 3.1, left – full variable set with one removed; right – each variable in isolation). CEC-L.III ecoregions (CEC 2009) and primary roads (prim400k) had the highest individual AUC scores (all populations combined), and thus appear to have the most useful information by themselves (Fig. 3.1). They are also the variables that decrease the AUC values the most when omitted, with the exception of NALC2005 for the Yukon winter range model, therefore appearing to have the most information not present in the other variables (Fig. 3.1). The decrease in AUC for the other variables was relatively minor.

MaxENT predicted greater probability of caribou occurrence when average winter temperature was between -25 C and -8 C for most populations (Fig. 3.2). However, when modeling the entire species (not shown), the greatest probabilities of occurrence occur from -40 C to -10 C, because the barren population has high probability of occurrence in lower winter temperatures than most other populations (Fig 3.2). Caribou occurrence generally decreased with increased road density, with higher sensitivity to primary, then secondary, then rural roads, and the least sensitivity to trails, although boreal and southern DU caribou seem relatively more sensitive to rural roads and trails, respectively (Fig. 3.2).

3.4.2 Modeling caribou distributions with climate, topo-edaphic and vegetation predictors

In general, climate and vegetation models perform better at predicting current caribou distributions than climate only models, but worse than ecoregions alone (Table 3.1). However,

spatial extrapolations (left column of Figure 3.3) suggest that current climate performed better alone (where better is assessed as the more optimistic model within current range and less optimistic out of it; Environment Canada 2008) not only for boreal caribou in southern Northwest Territories, but also in mountainous parts of Yukon Key Winter Areas and COSEWIC's central mountain DU.

To approach the potential respective effects of climate and vegetation on distributions of each caribou population by 2080, I subtracted projections for the climate+vegetation models (with the compensatory effect of my projected vegetation for 2080 from the previous chapter) from climate only projections (right column of Figure 3.3). Projections for 2080 show climate favorability for most populations declining, especially in relation to elevation for mountainous populations (i.e. Grant's and SARA or COSEWIC's mountain populations, including Yukon Key Winter Areas), or at the southern edge of their distributions (particularly boreal and barren populations).

3.4.3 Modeling caribou distribution when adding roads

Figure 3.4 illustrates the potential cumulative effects of anthropogenic factors, represented as the difference between climate+vegetation models and climate+vegetation+roads models. Adding roads to climate and vegetation improved AUC values, (Table 3.1), although most models were still not as strong as ecoregions alone (except for sCOSEWIC's south and central mountain DUs). Current negative impacts of roads on distribution are visible in Anchorage (AK), Fairbanks (AK), and Eagle Plains (YT) for the Grant's caribou ; in Eagle Plains (YT) and Yellowknife (NWT) for the barren caribou; in Prince-George (BC) and Calgary (AB) for SARA's southern population; in Edmonton, Fort St John (BC), Fort Nelson (BC) and La Crête (AB) for boreal caribou; and in Fort Nelson (BC) and Carmacks/Whitehorse (YT) for SARA's northern population (Fig. 3.4).

The 2080s climate +vegetation models project distribution northward of the climate+vegetation+roads models (Fig.3.4), especially at lower elevations for mountainous populations (i.e. Grant's and SARA's mountain populations, including Yukon Key Winter Areas)

or at southern edge of distributions (particularly boreal and barren populations). Overall, adding roads renders models more optimistic, a counterintuitive result of the reduced climate effect due to inclusion of static roads, which are correlated with current climate ($r < 0.65$).

3.4.4 Comparing current and future niches with climate only or concomitantly with vegetation and roads

Figure 3.5 represents each populations projected losses and gains in distribution by the 2080s based solely on ecoregions. Figure 3.6 shows projected population losses and gains by the 2080s (SARA's and COSEWIC's populations in respectively left and right columns), based on climate (top row), climate and vegetation (middle row with NALC2005 vegetation current and projected) and climate, vegetation and roads (bottom row). Similarly, Fig. 3.7 summarizes the amount (km^2) and percentage of each SARA's and COSEWIC's population distribution that niche models predict by 2080 as losses (red) or refuges (orange) (adding to 100%), as well as predicted refuges (green) and gains (blue) outside those ranges.

Figures 3.5 to 3.7 show smaller losses of potential distribution with additional model complexity (i.e. adding vegetation to climate, then roads), partly because roads are held static, diminishing the effect of climate. A change in correlation structure was not examined as there is no empirical/observed data related to expected future decoupling for alternative scenarios. While all ecoregion based models predict over 40% refuges or gains outside the current distributions, except for barren caribou ($\leq 10\%$; Fig.3.5 and 3.7), the climate +vegetation models for populations other than Grant's, SARA's southern mountain and its finer COSEWIC's central DU, are not as optimistic outside the current distributions, and adding roads makes it even less so, with significant losses of refuges by 2080 (Fig.3.6 and 3.7).

Both SARA and COSEWIC's populations are projected to be better maintained within their current delineations and less superimposed by the 2080s (i.e. less potential for competition between populations) when roads are added to the models. However, Figures 3.5 and 3.6 show either a vacuum space between SARA's southern and northern mountain populations (as the

former is not taking over what is lost in the south by the latter), or COSEWIC's northern mountain DU losing connectivity around the BC/Yukon border.

3.4.5 Population units and scale

Both climate+vegetation and climate+vegetation+roads models performed more poorly at predicting caribou distributions at the broader species scale (all populations combined) compared to more specific population models (Table 3.1). This may be due in part to a functionally reduced background sampling area at the species scale, and resultant reduction in contrast of the variables examined. Similarly, except for the ecoregion models, the models restricted to the scale of the Yukon winter ranges had higher AUC scores than the more general models of SARA's northern mountain population, itself better than the broader COSEWIC's northern mountain DU and woodland caribou models (Table 3.1).

The selection of background points also influenced model results, as using either the smallest window around the known "Yukon winter range" locations or all populations (including SARA's northern population) respectively underpredict within "Yukon winter range" by 6 and 1% and overpredict outside SARA's northern mountain population by 67 and 6%, representing losses in AUCs of 0.001-0.13 compared to using the same background points as for SARA's northern population (all other populations considered as background except SARA's northern population).

Finally, the amount of predicted refuge area within current SARA's northern mountain range was larger than predicted Yukon Winter ranges, which is expected as it is a subset of the first (Fig. 3.8). However, this also represents a much smaller proportion of winter refuge area within current, although greater proportional gains of external refuge and future distribution are predicted (Fig. 3.7).

3.5 Discussion

This is an ambitious study of caribou distribution in terms of geographic extent (Canada and United States), variety of predictors considered (climate, vegetation & anthropogenic); scenarios (climate change, vegetation lag, human cumulative effects), scales (species, population, winter range) and competing population units (SARA's northern and southern mountain populations, COSEWICS's northern, central and southern mountain DU, and boreal, barren and Grant's populations common to both classifications), yet it is only a first step in understanding the conservation needs of this widespread but vulnerable species.

3.5.1 Drivers of caribou distribution in western North America

Probability of occurrence for most caribou populations was higher in areas with average winter temperature below -8 C. Adding vegetation and roads did not dramatically improve climate only models. Yet, all populations were more sensitive to road density than individual climate variables; especially to primary roads, then secondary and rural roads, and finally trails. The vegetation classes in NALC2005 also added more significantly to the finer scale Yukon winter range models. Projections for 2080 suggest climate only models are more dynamic and more favorable at higher latitudes (particularly at the southern edge of boreal and barren distributions) and higher elevation (particularly for Grant's and SARA's mountain populations, including Yukon Key Winter Areas), than when vegetation is included, and even more so compared to projections with roads added. Overall, all models predict little distributional gain and significant potential losses of refuges by 2080, with all populations better maintained within their current delineations and less superimposed on one another (i.e. less competition) when adding roads to the projections. This is likely due to maintenance of static roads (i.e. no projections of future road expansion, or recovery), which reduced the somewhat correlated climate effect under current conditions.

3.5.1.1 *Effects of static variables in ecological niche modeling*

Applications of correlative niche models to forecast changes in species' distributions with climate generally use only climate GCMs' projections, which are 'dynamic' because they change over the time frame being modelled. Yet, other predictors are proven important for estimating present-day species distributions despite often considered 'static' because they change at different rates (e.g. over geologic timescales for soil and delayed vegetation response to climate) or in unpredictable ways (e.g. roads) (Iverson and Prasad 1998, Calmé and Desrochers 2000, Zimmermann et al. 2007, Buermann et al. 2008, Brook et al. 2009).

Combining dynamic and static variables in niche model predictions for future climate projections remains contentious (Brook et al. 2009). While some authors did not include static variables (e.g. Williams et al. 2003, Thuiller et al. 2005, Araújo et al. 2006, Hole et al. 2009, Carvalho et al. 2010), others did concluded that the best models included a mixture of climatic and static predictors (Iverson and Prasad 1998, Peterson et al. 2002). Static variables that only indirectly influence suitability (e.g. elevation) should be excluded as they can otherwise hinder the accuracy of future predictions. Similarly to others, (Stanton et al. 2012) found that some 'down-weighting' of climate variables may be appropriate when distribution directly depends on a static variable (e.g. plants and solar radiation; Austin and Van Niel 2011), especially if correlations with climate are not clear (e.g. vegetation; (e.g. vegetation; Thuiller et al. 2004).

Also, while some consider it better to leave "unpredictable" variables such as roads out of the analysis, the results of Stanton et al. (2012) indicate that if such variables do affect species distributions, including them in the model is better, even if it means making the unrealistic assumption that their values will not change in the future.

3.5.1.2 *Limitations with correlated predictors*

They are risks with using Maxent (e.g. Phillips and Dudík 2008, Phillips et al. 2009), as with other niche techniques, especially when extrapolating to environments not included in model

calibration (Pearson 2006), or dealing with spatial bias in occurrence records (Graham et al. 2008).

Some believe that only including climate would render models overly sensitive to future climate scenarios (Iverson and Prasad 1998), while others state that using non-climatic variables would fit well the current distributions but be insensitive to down weighted future climate scenarios, especially in the case of correlated predictors (Williams et al. 2003, Thuiller et al. 2005, Araújo et al. 2006, Hole et al. 2009, Carvalho et al. 2010).

Time-lag in vegetation response to climate is attributed to topo-edaphic conditions, lags in seed dispersal, or persistence of long-lived tree species in unsuitable environment for recruitment (Stralberg et al. 2015a, Renwick et al. 2016). Using proximate variables may not matter as long as the associations between climate, vegetation, and other drivers remain constant, but could become a problem when extrapolating into new spatial or temporal domains because of the risk for decoupling (Roberts and Hamann 2012).

When variable relationships are strong, the effects of one variable could be overestimated (Clavero et al. 2011), and minimal broadscale decoupling is sufficient for potentially spurious local variations in projections to arise (Stralberg et al. 2015a). For instance, roads are especially biased toward southern climates in the boreal and associated vegetation types (NABCI (North American Bird Conservation Initiative Canada) 2012, Machtans et al. 2014). My extensive road data set, which included data from more remote parts of the boreal region, markedly reduced this bias, as did the use of the full range of populations instead of observational data generally biased toward areas with greater access and warmer climates.

3.5.1.3 *Issues with correlated dynamic and static predictors*

While the role of roads, especially primary roads, is somewhat correlated with current temperatures ($r < 0.7$) and precipitations ($r < 0.4$) at my coarse scales of analysis (given the concentration of development activities in more southern regions), it is not the case at finer scales (such as the one applied here to winter ranges in Yukon; $r < 0.2$). Yet, models that

depend on correlated static and dynamic variables, and perhaps also on how they interact, raise important issues. For instance, as elevation *per se* does not influence species distribution but is correlated with factors that do, such as temperature, precipitation and air pressure, keeping elevation static during future climate scenarios may cause significant inconsistencies due to unstable correlation structure between predictors (Austin 2002). Nonetheless, it is especially important to try to project and use variables that interact with climate variables, as using only the current data layers, in combination with dynamic climate layers, does not fully account for their effect on the potential future habitat suitability for the species (Stanton et al. 2012).

Modelling only with dynamic variables and then using static variables (e.g. vegetation or land use) as a mask would be invalid if their effects on suitability depend on climate, whereas including them in the analysis allows Maxent to incorporate interactions (Stanton et al. 2012). A related approach, which has been used to integrate data at different spatial scales (Pearson et al. 2004), is to combine dynamic climate and static land cover data in a two-step process: (i) a climate-only model is built and shifts under future climate scenarios are predicted; (ii) the output from the climate-only model is used alongside land cover as inputs to a second model. Yet, similarly to the 'mask' method, the local effect of static and large scale effect of dynamic predictors would mistakenly not interact (Pearson et al. 2004).

3.5.2 Scales and population units matter

The importance of biologically relevant variables in models depended to some extent on the scale (resolution and extent) of delineation and populations being modeled. For instance, the relatively fine scale NALC2005 matters more with Yukon winter range than northern population entire range. Similarly, the value of location data is illustrated by models for Yukon winter ranges outperforming the annual ranges of northern caribou, which performed better than the broader woodland caribou and the overall species models. It is not surprising that it is difficult to model distribution of the widespread caribou as a single homogenous species, because of variation in life history characteristics that have contributed to the finer-scale population units, such as

specialized diet in the winter and differences in population seasonal habitat (Arseneault et al. 1997, COSEWIC 2002, 2011, 2014).

3.5.3 Adding potential vegetation response to climate change may delay species distribution shifts

The majority of species distribution models that project species habitat responses to climate change use climatic variables as their sole input. Climate variables often explain a large percentage of the variance in species' probability of occurrence, and produce models with good predictive abilities with respect to current distributions. However, using solely climate proximate variables to extrapolate into new spatial or temporal domains has greater consequences due notably to a tendency toward over projecting, when realistically a decoupling in vegetation response to climate variables is expected (Ichii et al. 2002). I thus combined climate and vegetation data to seek their respective potential effects on projections of species distribution (Peterson et al. 2006). In lieu of modeling of demographic processes, I focus on best-case and worst-case scenarios. Such extreme scenarios are useful for conservation planning to see if there are any threats under the most optimistic scenario or no threats under the worst case scenario. I incorporated dynamic vegetation layers to evaluate two best case scenarios: 1) for caribou plasticity to climate and lag in vegetation response to climate (ecoregions only), and 2) for caribou plasticity to new road development (climate+vegetation+roads, where roads are held static at current conditions). A worst-case scenario that assumes irrelevant or immediate vegetation response to climate (climate only), and an intermediate scenario where climate importance is lessened by vegetation lag response (climate + vegetation), are also added for a comprehensive interpretation of projections (Araújo et al. 2004, Thomas et al. 2004). Although adding vegetation is important to improve models by more realistically slowing response to climate, the topo-edaphically constrained projections from Chapter 2 should not be interpreted as realistic models of plant demographics or future delineation of vegetation distributions but rather as a reduced "upper bound" of bioclimatic envelope projections.

3.5.4 Climate-induced northward shift may add to other threats to caribou

Similarly, I ask whether adding road density to climate only or climate+vegetation models better explains the present distribution of caribou populations across western Canada and Alaska, and investigate potential future changes in caribou distribution based on potential vegetation and climate scenarios. Yet, the simultaneous northward progression of climatic change and other human disturbances render interpretation and prediction of their effects on caribou difficult. Gains in AUC scores with inclusion of roads in the models suggest that anthropogenic disturbances, and inferred induced biotic factors such as changes in predation and competition, were influencing caribou distribution beyond consideration of climate and vegetation alone - at least up to year 2000 (date of the data I used). However, it does not exclude the possibility that climate change effects on caribou may already or in the future supplant other human induced direct and indirect biotic factors. The current relative optimism within distributions and yet expected dramatic erosion by 2080 of climate only models, suggests that climatic factors will become increasingly important as predictors, especially at population southern edges, as suggested for boreal caribou (Environment Canada 2008).

Although it was not emphasized, each of my models can account for uncertainty in genetic/adaptive potential via scenarios on adaptation (homogenous species vs populations) and migration (changes within or out of original ranges): (1) no migration and no adaptation, with population or ecotype's refuges being cells suitable in future projections but within original range; (2) migration only, a scenario similar to the first, but where suitable habitat for each populations can now be projected outside its original range; (3) adaptation only, with caribou not being stratified into populations, but only able to adapt to conditions within the current range of the species; and (4) migration and adaptation, with no restriction to the species projection as a homogenous entity.

These assumptions could be stressed or relaxed for populations with further ecological or genetic data. For instance, the no migration scenario might be appropriate for COSEWIC or SARA's southern populations, as they are isolated, fragmented, and thus susceptible to Allee effect (which also suggests the no adaptation scenario unless there is great phenotypic plasticity).

Conversely, my migration scenarios may be more realistic for the migratory barren caribou. Future conditions probably include some vegetation changes and local adaptations to climate change, but this realistic set of alternative scenarios should adequately define caribou response limits, and support a landscape simulation approach that would allow a more complex analysis.

3.5.5 Few refuges from cumulative effects of climate change and human encroachment

Some climate induced range contraction may have occurred in the Okanagan and Cariboo regions of BC and North Idaho for the southern population, at the southern frontier of Alberta and Saskatchewan for boreal caribou (consistent with Environment Canada 2008), and at the southern limit of the northern and barren populations, subsequent to population delineations. However, the climate only model of Grant's, southern and boreal caribou extend south of the delineations in most other areas. This confirms other studies showing northward recession of caribou in those areas (Schaefer and Mahoney 2007, Vors et al. 2007), attributable to linear disturbances (roads) in my models. Additionally, though to be possibly soon superseded by climate change in Grant's, barren, boreal, SARA's southern and northern mountain populations, and COSEWIC's central and northern DU, this anthropogenic cumulative effect is also expected to grow by 2080, despite my static approach to representation of roads, resulting in very little refuge or gain, as most projected future northward opportunities may never come to fruition due to lack of connectivity.

3.5.6 Finer-scale prediction requires location data

A common use of species distribution models is to answer the questions: What are the key controls on the species being modeled? How do they affect its distribution? However, a few of my results indicate an urgent need for compatible location data between jurisdictions or populations (especially in isolated northern herds). For example, my use of broad caribou population delineation as an alternative to location data failed to capture the importance of fire or mining history, as reported by Environment Canada (2009). Similarly, my work also reveals that without fine scale caribou data, acquiring multi-jurisdictional yet detailed (i.e. exhaustive

classification), precise (e.g. downscaled climate data) and time-specific anthropogenic data, such as road density and forestry or mining activities, is ineffective as only my very broad road density layers were useful.

Multi-jurisdictional efforts for acquisition of comparable GPS location data are all the more necessary as economical and timely availability of high resolution satellite vegetation data is secured for modeling at broad geographic scales (Yang et al. 2006, Environment Canada 2008). Satellite based explanatory and response data (i.e. higher resolution vegetation and GPS animal location data) should improve specificity even further when used concurrently (Peterson and Robins 2003, Parra et al. 2004). My coarse caribou resolution may also explain why the detailed vegetation data (e.g. NALC2005) were generally worse predictors than the coarser ecoregions, though using the latter could risk over-fitted models, as ecoregions are the foundation of SARA's caribou classification (COSEWIC 2014).

Nonetheless, my models offer a predictive form of environmental impact assessment, wherein the zone of influence of different anthropogenic disturbances (Polfus et al. 2011) can be explored relative to multiple scales of caribou response, and in relation to other environmental drivers, including climate and vegetation. While caribou occurrence was overall greater between -40 to -10°C in winter, the probability of occurrence dropped after 0.01km/km² of primary roads and 0.1km/km² of secondary roads.

Table 3.1 MaxENT model results for caribou population distribution in western North America based on climate, vegetation, roads, and ecoregions, including AUC scores, specificity and sensitivity (under/over prediction of original distribution based on maximum test sensitivity and logistic threshold for specificity).

Organizational level	AUC				%pixel under/over prediction			
	Climate	Climate + Veg	Climate +Veg +Roads	Ecoregion	Climate	Climate + Veg	Climate +Veg +Roads	Ecoregion
Species								
Caribou –								
<i>Rangifer tarandus</i>	0.65	0.68	0.69	0.73	12.0/486	11.5/480	8.82/362	9.68/308
Sub-Species								
Barren-ground –								
<i>R. t. groenlandicus</i>	0.82	0.82	0.83	0.91	3.87/112	3.89/112	3.6/107	7.9/109
Grant’s – <i>R. t. granti</i>	0.94	0.94	0.96	0.98	6.45/265	5.89/268	5.4/190	2.99/264
Woodland – <i>R. t. caribou</i>	0.80	0.81	0.81	0.85	9.59/380	8.94/388	6.98/288	7.98/250
Woodland Designated Units								
Boreal	0.90	0.90	0.91	0.96	8.23/156	8.09/159	6.1/112	1.92/171
SARA northern mnt pop	0.94	0.95	0.96	0.98	4.92/164	4.03/174	2.82/146	7.49/125
SARA southern mnt pop	0.97	0.97	0.98	0.97	3.65/378	3.44/383	1.79/262	2.31/38
COSEWIC south mnt DU	0.99	0.99	0.99	0.97	10.2/452	10.3/448	26.7/138	0/720
COSEWIC central mnt DU	0.98	0.99	1.00	0.99	2.97/976	1.3/1469	0.59/324	13.01/507
COSEWIC north mnt DU	0.93	0.93	0.95	0.97	6.41/167	6.99/161	4.1/129	5.02/157
N. Mountain Range								
Yukon Winter Key Areas	0.97	0.98	0.98	0.95	6.8/1332	5.9/1726	5.3/1093	1.12/2297

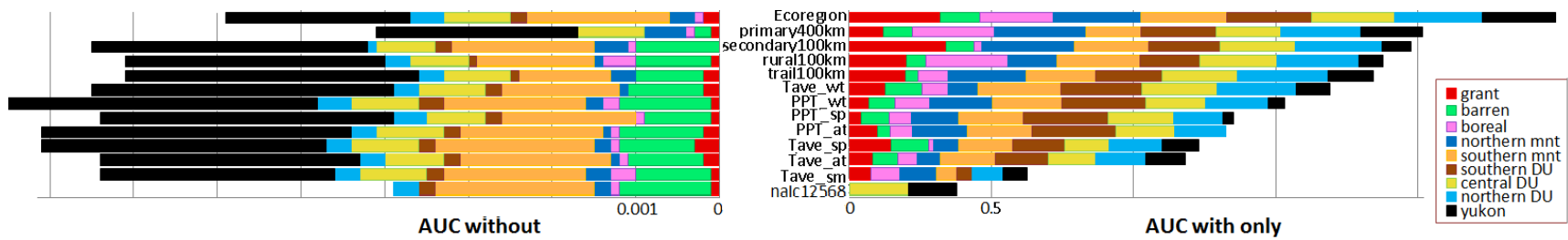


Figure 3.1 Importance of climate, vegetation and roads to caribou distribution in western North America, as measured by relative AUC values for each population (the lowest value, by population, was subtracted from the group, and are thus comparable among the variables, but not among populations). Variables are arranged with highest contribution on top to lowest on bottom, for each variable in isolation on the right, and all variables except one on the left.

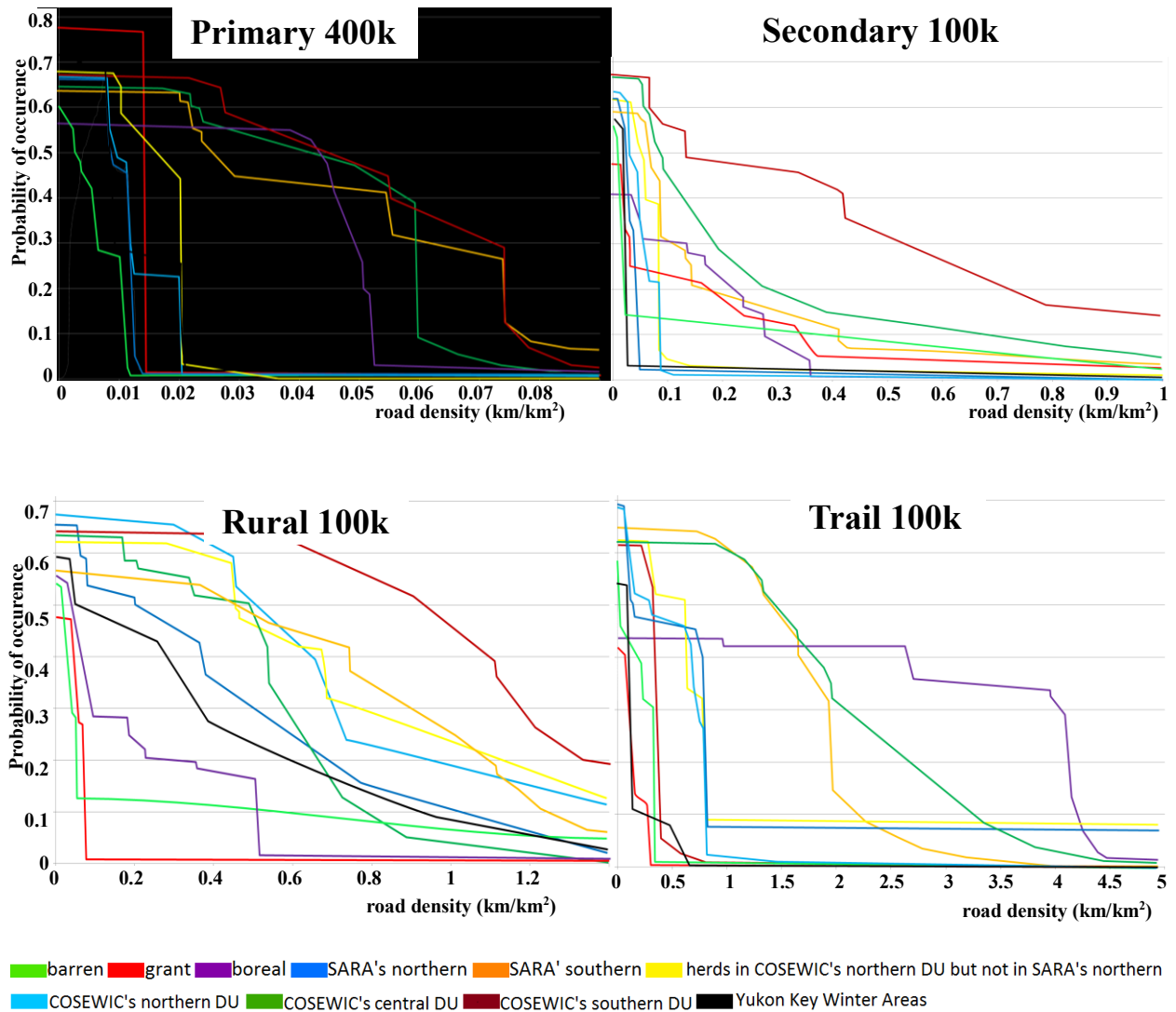


Figure 3.2 Response curves of current caribou probability of occurrence in western North America to road density (km/km^2). Notation following road types indicates the search radius considered

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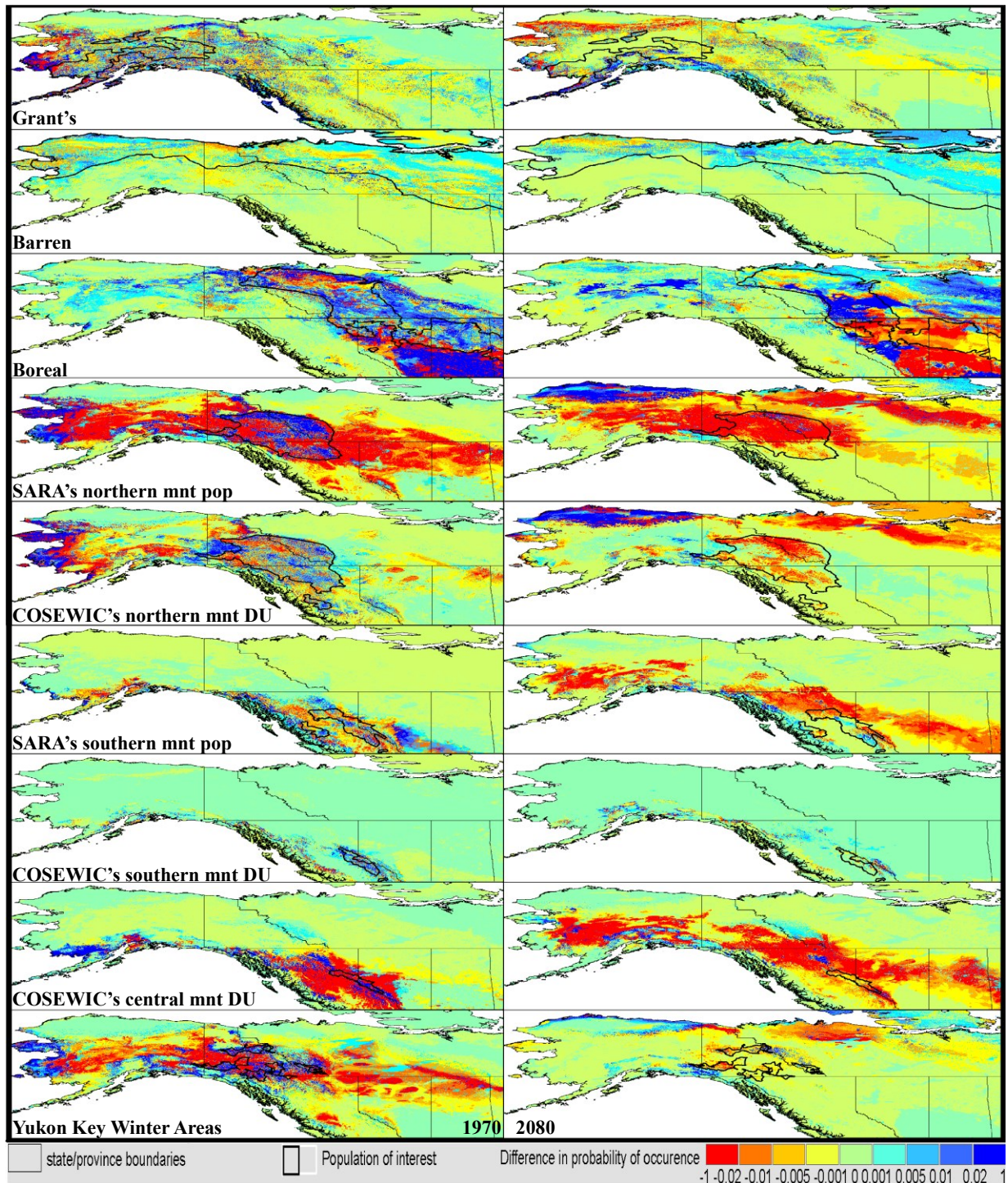


Figure 3.3 Difference between climate only and climate + vegetation models for the baseline (1961-1990; left side) and 2080s projections for caribou populations in western North America..Places where climate only models predict more caribou occurrence are shown in gradient of blue while places where climate and vegetation models predict more caribou occurrence are shown in a gradient of red.

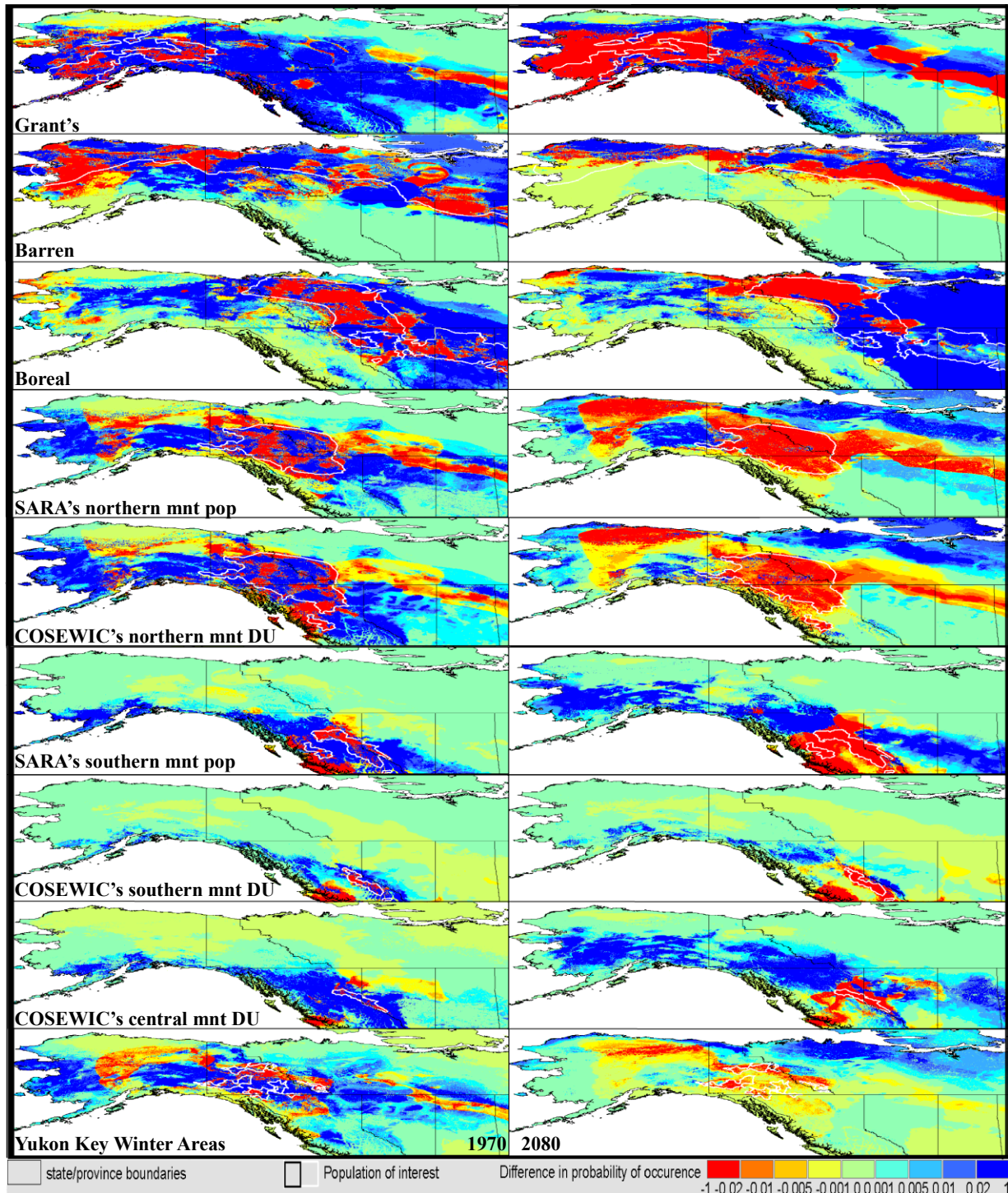


Figure 3.4 Difference between climate only and climate+vegetation+roads models for the baseline (1961-1990; left side) and 2080s climate and vegetation projections for caribou populations in western North America. Places where climate only models predict more caribou occurrence are shown in gradient of blue while places where adding roads to the models predict more caribou occurrence are shown in a gradient of red

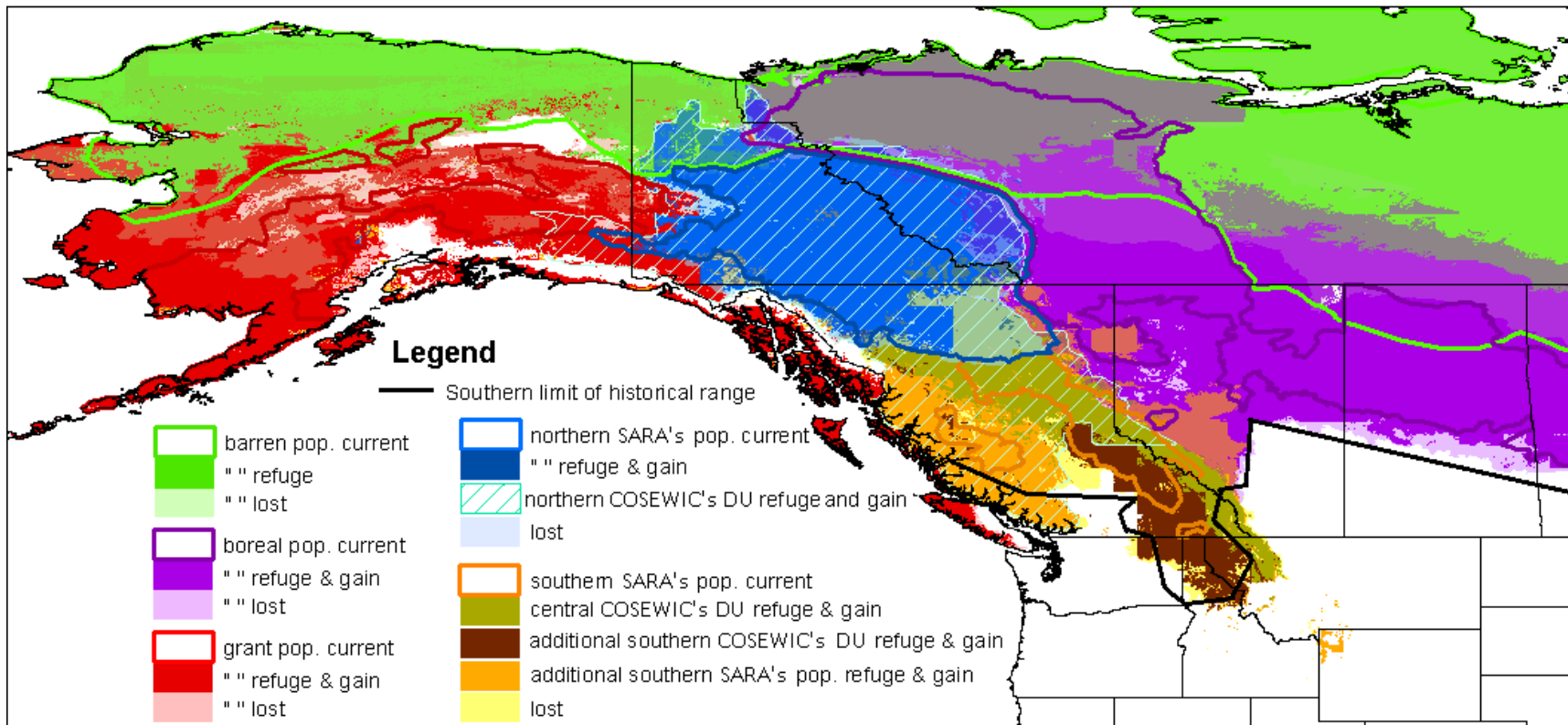


Figure 3.5 Caribou distribution gain, loss and refuge based on ecoregions. The map shows barren (pale green), Grant's (red), boreal (purple), SARA northern (blue) and southern (orange) mountain pop, COSEWIC southern (brown), northern (pale ashed blue) and central (dark green) DU current distributions (outlines), refuge/ gain (areas of habitat unchanged between now and 2080s or currently uninhabitable but to become favourable in 2080s), and loss (lightest shaded color showing habitat areas projected to be lost by the 2080s) based on ecoregions only.

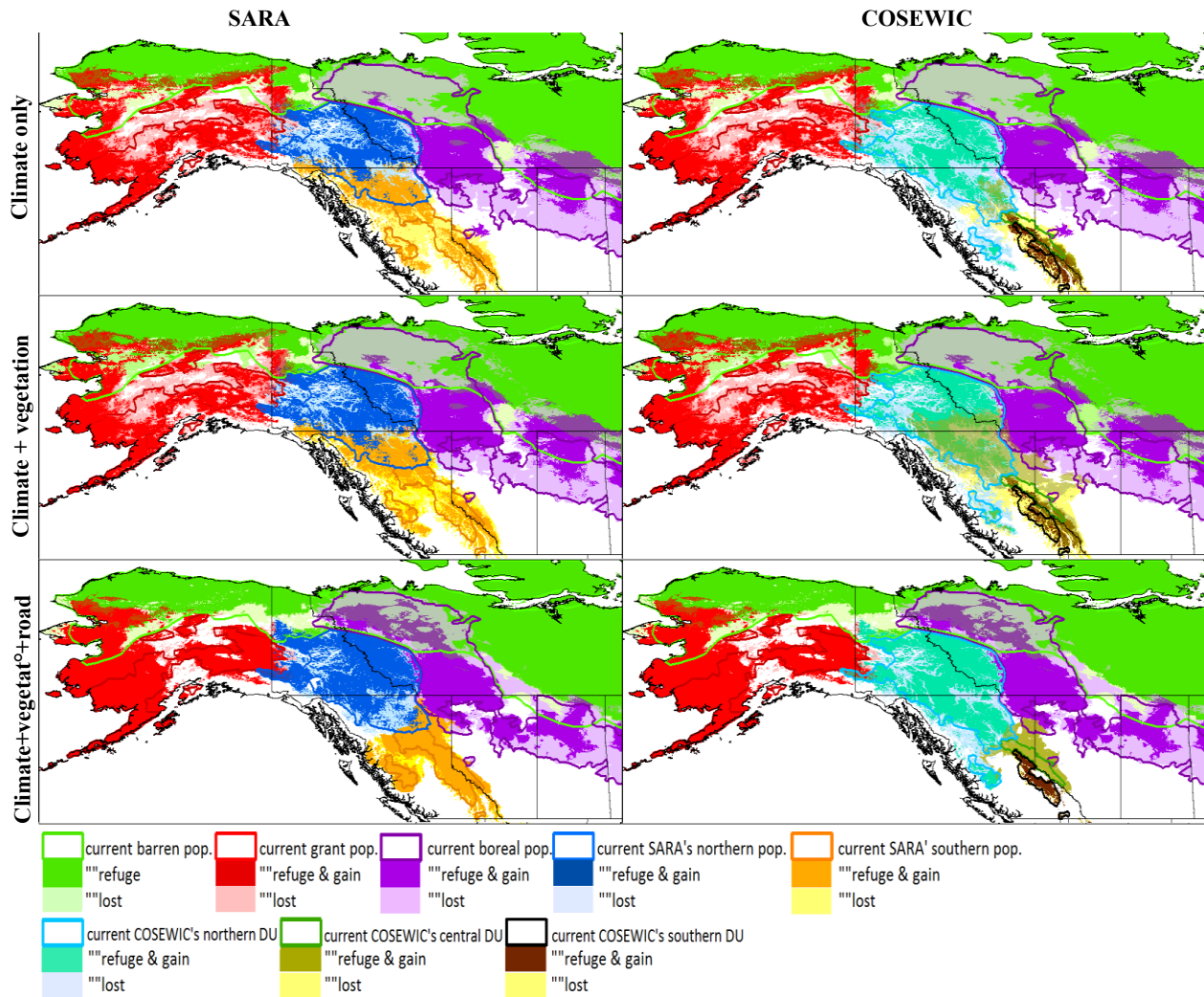


Figure 3.6. Predicted areas of refuge or gain (unchanged suitability between current and 2080s distribution or currently unsuitable but expected to become favourable in 2080s), and loss (suitable areas projected to be lost by the 2080s), based on climate only, climate + vegetation, and climate+vegetation+roads for caribou populations in western North America. The left and right panels are for models built with SARA's and COSEWIC's classifications, respectively.

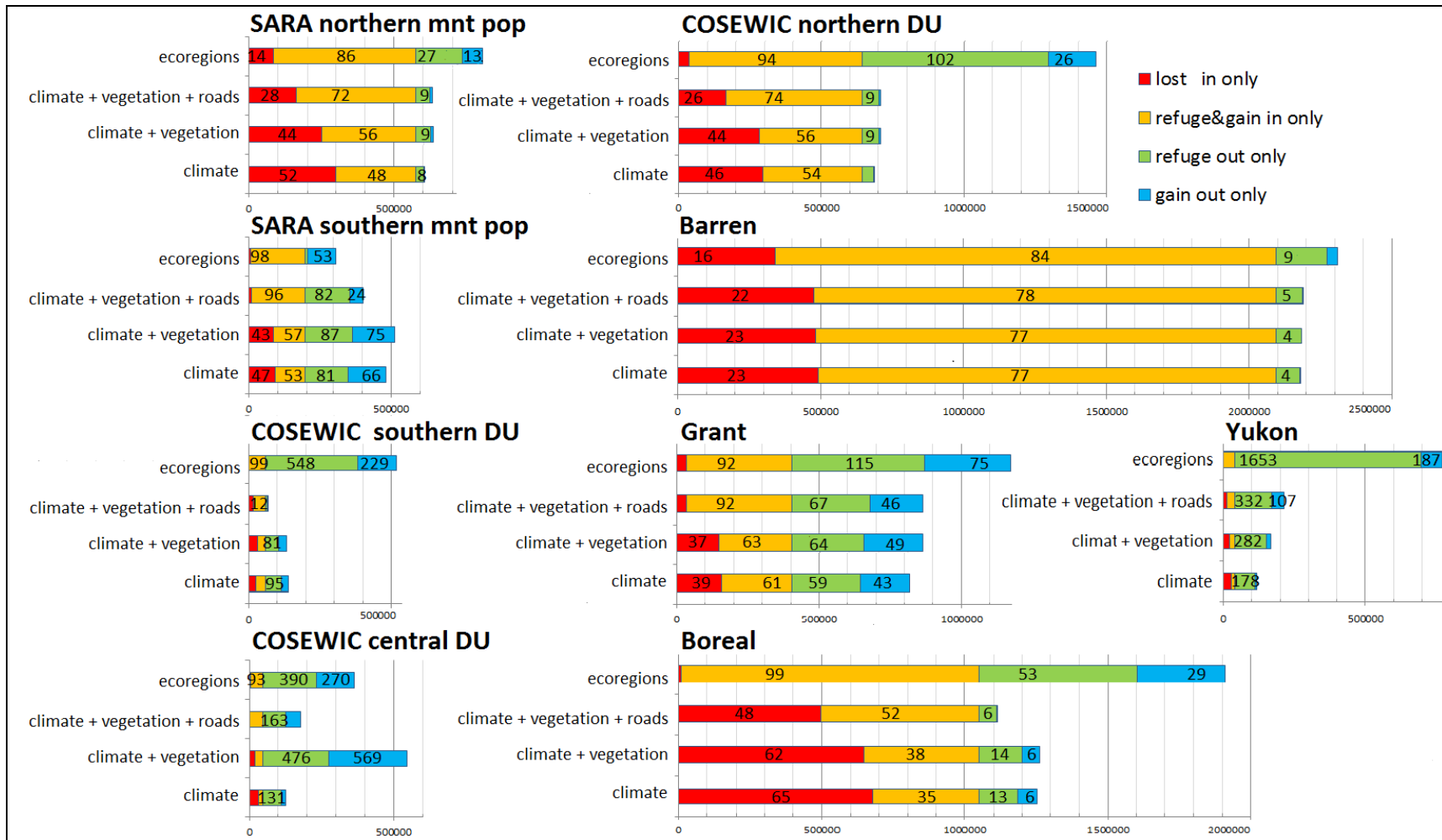


Figure 3.7 Total area (km²) and percent of current distribution (inside the bars) of predicted areas of refuge (unchanged suitability between current and 2080s distribution), gain (areas that are currently unsuitable but will become favourable in 2080s), and loss (distribution projected to be lost by the 2080s) based on climate only, climate + vegetation, and climate+vegetation+roads for caribou populations in western North America (Yukon Albers projection).

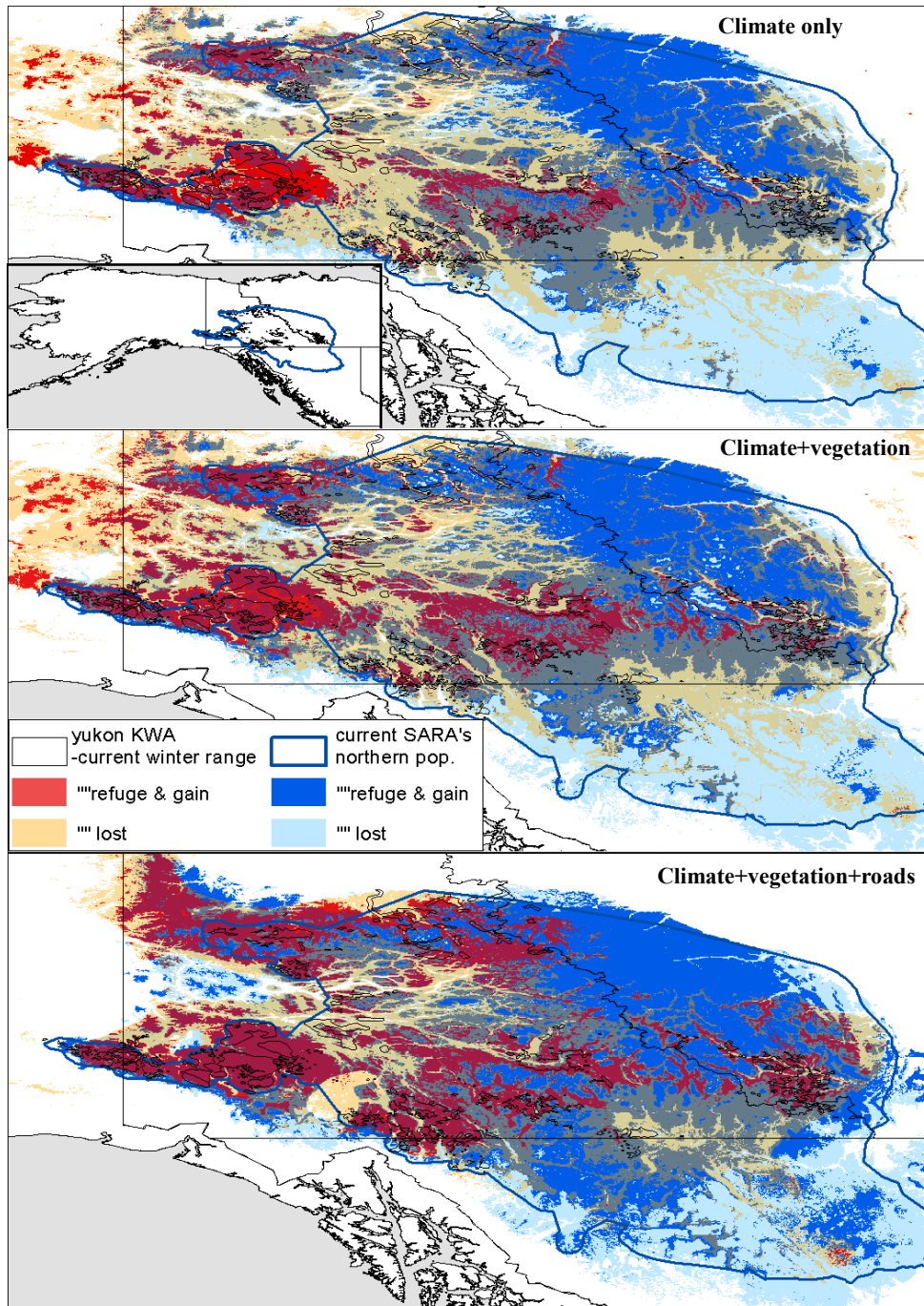


Figure 3.8 Predicted areas of refuge (unchanged suitability between current and 2080s distribution), gain (areas that are currently unsuitable but will become favourable in 2080s), and loss (habitat areas projected to be lost by the 2080s) based on climate only—at the top, climate + vegetation—in the middle, and climate+vegetation+roads—at the bottom for SARA northern caribou population and Yukon Key Winter caribou areas.

4. CHAPTER FOUR. CARIBOU, CLIMATE CHANGE AND CONSERVATION PLANNING IN WESTERN CANADA

4.1 Summary

I used two software tools developed by the BEACONS Project¹ (CONSERV and Benchmark Builder) to identify areas in the western Canadian boreal region) that met minimum intactness, connectivity, and size requirements to increase the probability of biotic resilience to future natural disturbances, and serve as ecological benchmarks for understanding the potential effects of climate change and human activities on these systems. Moreover, with significant shifts in caribou distribution expected, I also identified, for each caribou population in the region, potential climate refuges that met these benchmark requirements.

4.2 Introduction

4.2.1 The boreal region: importance, threats and potential

The Canadian boreal region is important ecologically, economically and socially to Canadians (Anielski and Wilson 2006, Lee et al. 2006). The region is still relatively untouched by human settlement (Lee et al. 2006) and provides many ecological services, including provision of clean water and flood control (Brandt et al. 2013) by regulating temperature and rainfall patterns, while also providing globally significant carbon storage (Betts 2000, Hyvonen et al. 2007). The boreal region also contains a significant portion of the remaining population distributions of large mammals in North America (Laliberte and Ripple 2004).

However, boreal forest ecosystems have experienced significant human alterations in the last few decades due to economic growth and resource exploitation, particularly in association with the

¹ <http://www.beaconsproject.ca/toolbox>

agriculture, logging, mining and energy sectors (CBI 2005, Cardillo et al. 2006, Young et al. 2006). Currently, 11% of western Canada is under permanent protection, while an additional 5% is under interim protection. In addition to concerns about the overall extent of protection, existing reserves are often too small to sustain wildlife populations (Newmark 1995, Wiersma and Nudda 2009, Wiersma and Simonson 2010), biodiversity (Margules and Pressey 2000), and ecological processes such as natural disturbance regimes (Poiani et al. 2000, Rayfield et al. 2008). Small reserves are unlikely to maintain ecological integrity over time (Bengtsson et al. 2003, Meir et al. 2004) and may not represent areas of ecological importance (Danby and Slocombe 2005).

The boreal forest comprises about 30% of remaining wilderness globally (Watson et al. 2016), located mostly on public lands that are largely unprotected but relatively undisturbed (CBI 2005, Lee et al. 2006, Andrew et al. 2012), thus providing an unparalleled conservation opportunity. In particular, there is a unique opportunity to establish ecological benchmarks that enable biodiversity conservation, maintain vital ecological function, and provide economic and ecological benefits to human and animal communities (CBI 2005, Schmiegelow 2008). Conservation of large, dynamic areas, designed as ecological benchmarks to support sustainable natural resource development, is possible through application of systematic conservation planning (e.g. Margules and Pressey 2000, Cabeza and Moilanen 2001, Moritz 2002).

4.2.2 The approach: Conservation planning

Systematic conservation planning is a structured approach to reserve selection that concomitantly fulfills goals for focal species habitat, vegetation communities, or other elements (Cabeza and Moilanen 2001, Noss et al. 2002, Beazley et al. 2005), and improves historical ad hoc protection of discrete sites or reserve networks (Pressey and Tully 1994, Margules and Pressey 2000). A number of reserve selection algorithms and methods have been developed (sensu Margules and Pressey 2000, Possingham et al. 2002, Lawler et al. 2003, Sarkar et al. 2006), including scoring based approaches (Margules and Usher 1981, Pressey and Nicholls 1989), multivariate statistical analysis (Faith and Walker 1996), gap analysis (Scott et al. 1993), and optimization techniques (Vanderkam et al. 2007, Carroll et al. 2010, Lehtomaki and Moilanen 2013). Due to limited

funds or other reasons, not all candidate reserves are likely to be designated and consequently options need to be ranked using various criteria, including their irreplaceability and other *de facto* conservation values (Margules and Pressey 2000, Noss et al. 2002, Drechsler 2005).

However, conventional tools are often derived from existing conditions and assume constant distributions of conservation targets (Pyke and Fischer 2005). Few tools integrate changes in populations (Moilanen and Cabeza 2002), landscapes (Pyke and Fischer 2005, Soares-Filho et al. 2006), and their uncertainty (Cabeza and Moilanen 2001, Moilanen and Cabeza 2002, Halpern et al. 2006). Even fewer evaluate the required size to sustain such processes through time (Pressey et al. 2004, Leroux et al. 2007b). Consequently, protected areas often fail to conserve ecosystem processes and functions such as disturbances and succession (Cabeza and Moilanen 2001, Moilanen and Cabeza 2002, Halpern et al. 2006), predator-prey dynamics (Poiani et al. 2000), water and air quality, carbon storage and biodiversity (Rodrigues et al. 2004) over long periods of time (Margules and Pressey 2000, Halpern et al. 2006, Soares-Filho et al. 2006). This is especially true in highly dynamic systems, such as the boreal forest, that experience extensive natural disturbances such as fire, insect outbreaks, windstorms, and floods.

The concept of minimum dynamic areas (MDA) (Pickett and Thompson 1978) mixes shifting-mosaic (Bormann and Likens 1979), species-area effect (Jaccard 1902), and insurance factor (Allison et al. 2003) approaches to guide the design of reserves that maintain ecological function under the dominant disturbance regime. However, it lacks empirical support due to qualitative and restraining conditions like the requirement for quasi-equilibrium landscapes (absent in boreal or western coniferous forests that require periodic fires to regenerate) (e.g. Baker 1989, Cumming et al. 1996), and the desirability of separate analysis by habitat (Kneeshaw and Gauthier 2003). Consequently, there is an increased need to have practical, quantitative criteria that can guide reserve size to achieve long-term conservation goals (Foley et al. 2005, Cardillo 2006). Dynamic simulation models (Peters et al. 1997) and historical patch dynamic data (Poiani et al. 2000, Bengtsson et al. 2003, Kneeshaw and Gauthier 2003) may palliate the absence of explicit or quantitative criteria for self-sufficient MDAs. The minimum dynamic reserve (MDR) approach further operationalizes the MDA concept by identifying the minimum area required to sustain native ecological communities over long time periods (Leroux et al. 2007a). MDRs can

inform reserve size in the context of landscape dynamics, a core concept in the design of reserve networks.

Consideration of landscape dynamics in reserve design is especially pertinent to the remaining large intact boreal and Amazonian forests (Sanderson et al. 2002, Mittermeier et al. 2003), where natural disturbances, hydrological regimes, and nutrient cycles still shape landscapes pattern and process (Pickett and Thompson 1978, Margules and Pressey 2000, Bengtsson et al. 2003). However, traditional conservation approaches maximize the protection of rare and endangered ecosystems with high biodiversity (e.g. Cabeza and Moilanen 2001, Rodrigues et al. 2004, Groom et al. 2006), or threatened, endemic and umbrella species (Margules and Pressey 2000). Reserves are nevertheless expected to achieve multiple conservation goals (Pyke and Fischer 2005), despite often being located in substantially altered landscapes that restrict their size and location (Bengtsson et al. 2003). Although crucial, these reactive efforts are not sufficient, nor well-suited for large intact landscapes like the boreal region (Powers et al. 2013, Watson et al. 2016), that have relatively low biodiversity and endemism and are shaped by natural disturbances that result in dynamic distributions over large extents (Peres 2005, Pyke and Fischer 2005, Leroux et al. 2007b). It is also increasingly appropriate to focus on dynamic and large scale processes, as the scale and frequency of disturbances are likely to rise with climate change, especially in the boreal region (Chen et al. 2017, Murray et al. 2017). Nevertheless, few studies consider species distributions, biodiversity, or other conservation priorities together with climate change (but see Stralberg et al. 2015a, Stralberg et al. 2015b, Chai et al. 2016, Powers et al. 2016, Turetsky et al. 2017). The wide distribution of most boreal species should allow for climatic refuges, especially at the species' current northern limit or in areas of expected distribution gain.

The ultimate goal of this thesis was to integrate caribou conservation and climate change into a dynamic conservation planning framework. In this final chapter, I anticipated how identified potential climate refuges for caribou, current protected areas, and candidate reserve networks designed to serve as ecological benchmarks interacted with one another.

4.3. Methods

Focusing on western Canada (east of Manitoba and Nunavut, 102°W), this reserve design analysis builds on the 2080s climate and vegetation projections for CEC-L.III ecoregions in Chapter 2. These projections used randomForest (Breiman 2001) and 70 climate variables downscaled at 0.5 arcmin by the software Climate WNA (Hamann and Wang 2006, Wang et al. 2012), based on the emission scenario A2 (IPCC 2000), and an average of 18 GCMs (Meehl et al. 2007): BCCR_BCM2_0, CCCMA_CGCM3.1, CNRM.CM3, CSIRO.MK3.0, GFDL.CM2.0 & 2.1, GISS.AOM, INMCM3.0, IPSL.CM4, MIROC3.2.MEDRES, MIUB.ECHO.G, MPI.ECHAM5, MRI.CGCM2.3.2A, NCAR.CCSM3.0, NCAR.PCM1, UKMO.HADCM3, UKMO.HADGEM1, and GISS.ER). This analysis also integrates the 2080s Maxent projections of caribou from Chapter 3 (current distribution polygons for boreal, SARA's northern and southern mountain populations, and COSEWIC's northern, central and southern mountain Designated Units obtained from COSEWIC 2011, and from the Circum Arctic Rangifer Monitoring and Assessment Network and the Alaska Department of Fish and Game for barren/Peary and Grant's populations), also at a resolution of 0.5 arcmin (models were kept in a Geographic Coordinate System "WGS 1983" except when they had to be otherwise projected in Yukon Albers for analysis of distance and area).

4.3.1 Estimating the Size of Minimum Dynamic Reserves (MDRs)

Wildfires, insect outbreaks (often in fire suppressed areas; (Ogden 2007), flooding, and windstorms are the most common large-scale natural disturbances affecting vegetation dynamics in the boreal region of western Canada (Amiro et al. 2001). We estimated the minimum size requirement for ecological benchmarks using the characteristics of local fire regimes, as fire is the dominant disturbance in the study region. For a given planning region, this approach consists of two broad steps: i) estimating the minimum size required to sustain the largest expected fires within a candidate reserve, referred to as the minimum dynamic reserve (MDR; (Leroux et al. 2007a) and ii) evaluating the resilience of the candidate reserve over time, under anticipated ongoing disturbance by fire. MDR requirements are a key criteria in the selection of system-level

benchmarks, which are designed to be large, intact, hydrologically connected, and of sufficient size to maintain representation of vulnerable habitats given an active natural disturbance regime.

MDR sizes were estimated for 662-10,000 km² hexagons that intersected the boreal region of Canada (see BEACONS 2015). The first step consisted of identifying, for each hexagon, the smallest possible area (i.e., candidate MDR) that contained minimum amounts of each flammable vegetation class. Minimum amounts were defined by rescaling the area of each class so that the maximum area of the most abundant class was equal to the estimated maximum fire size (EMFS) for that hexagon. A GIS moving window with an area equal to the sum of the rescaled vegetation classes was then used to search for a suitable candidate MDR (i.e., a square area that contained all five vegetation types in their minimum required amounts) within the focal hexagon and its six neighbours. If no solution was found, the size of the moving window was increased by one pixel and the process was repeated until a candidate reserve was identified. Further details on methods can be found in BEACONS (2015).

Once a candidate reserve was selected, the second step consisted of assessing its resilience using CONSERV, a dynamic landscape simulation model (Leroux et al. 2007a,b) to determine if specified minimum amounts of each vegetation class could be maintained over a 250-year simulation period. CONSERV consists of a suite of landscape models, including a forest succession model and a fire model. The forest succession model simulates vegetation dynamics using deterministic and/or stochastic succession rules applied to a vegetation and forest age map of Canada. Fire model parameters were estimated for each hexagon within a grid of 10,000 km² hexagons overlaying the boreal region of Canada. Parameters included estimated maximum fire size (EMFS), and ignition, escape and spread probabilities (methods described in BEACONS 2015). All parameters were estimated from the 1980-2013 Canadian National Fire Database (NRCAN 2013). Both the forest succession and fire models require two key datasets to run: a forest age map and vegetation map. The forest age map has a resolution of 1-km² and was developed using a combination of forest inventory data, satellite imagery, and other ancillary datasets (Pan et al. 2011). The vegetation map was based on a 250-m resolution MODIS-based land cover map of Canada (Latifovic et al. 2008) resampled to 1-km². The vegetation map was reclassified to 10 classes, including 5 flammable/successional classes: closed coniferous, open

coniferous, mixedwood, deciduous, and shrubs. Broad-scale succession rules for the 5 flammable classes (Table 4.1) were provided by the BEACONS Project.

Using CONSERV, the evaluation process was repeated 100 times using Monte Carlo simulation. If one or more vegetation class went extinct, even for one year in a single simulation, the candidate reserve was considered to be unsuitable i.e., not resilient. In that case, the size of the candidate reserve was increased to capture additional amounts of each vegetation type, and the Monte Carlo simulation runs were repeated. This process was implemented until a resilient candidate reserve was identified. To avoid inflating MDR size, I did not include the deciduous class in the evaluation of resilience, since it is avoided by caribou (COSEWIC 2011, 2014), and presently rare in my study region, but predicted to be similar to mixedwood forest with respect to drastic expansion in the future (see Chapter 2).

MDR sizes were originally estimated within a grid of 10,000 km² hexagons using the methods developed by Leroux et al. (2007a) and Anderson (2009). However, I also wanted to anticipate the impact of climate change on fire regimes and MDR sizes. To do this, I clipped hexagons using the North American Level 3 sub-ecoregions designated by the Commission for Environmental Cooperation (CEC 2009) and calculated an area weighted average of MDR sizes and EMFS (estimated maximum fire size) for each of them. If less than 50% of an ecoregion was covered by hexagons, I calculated a weighted average of the level 2 ecoregions. Similarly, if less than 50% of a level 2 ecoregion was covered by hexagons, I calculated a weighted average of the level 1 ecoregions. Extracting MDR size and EMFS to ecoregions allowed me to use future projections of the latter (see Chapter 2) to predict future changes in MDR size and EMFS for each 0.5 arc-minutes pixel, before averaging them for each catchment (drainage unit created using the Atlas of Canada 1:1,000,000 Drainage Network Skeleton Version 6 (NRCAN 2009) required for benchmark construction; see below) using either the current or future values, whichever was greater.

4.3.2. Identify candidate benchmarks

Once the minimum size for candidate MDRs under climate change were estimated for each ecoregion, it was still necessary to identify those areas that also met minimum intactness and connectivity requirements. To achieve this, I used custom software (Benchmark Builder v3.3.11) to construct a set of potential benchmarks that met size and intactness criteria, while respecting hydrological connectivity (BEACONS 2015). The Benchmark Builder begins with one or more seed catchments, and selects additional contiguous catchments that are up- or down-stream until the specified size criteria is reached (breaking hydrologic connectivity as last resort). Catchments were developed using the the National Scale Frameworks Hydrology NRCAN (NRCAN 2009). Only catchments that were $\geq 80\%$ intact, as measured from the Global Forest Watch Canada (GFWC) Landscape Fragments data (Lee et al. 2006), were included. Candidate ecological benchmarks were retained if they reached the appropriate ecoregion MDR size and had a benchmark-level intactness of at least 95% (individual catchments could have a minimum intactness value of 80% but their area-weighted average needed to be at least 95%), meeting the average intactness of the strictness category of protected areas in the Canadian boreal region (i.e. Category 1, (IUCN and WCMC 1994)).

The composite coverage of candidate benchmarks areas was subsequently intersected with the potential climatic refuge areas for caribou populations (Chapter 3, Fig. 3.6) to identify priority conservation sites.

4.4. Results

4.4.1 Minimum size of Minimum Dynamic Reserves (MDRs)

Estimated MDR sizes ranged from 1,001 km² for the Marine West Coast Forests ecoregion to 9,354 km² for the Taiga Plains ecoregion (Fig. 4.1). The estimated MDR sizes increased linearly with the size of the largest expected fire event (Leroux et al. 2007b), although the Great Plains and to some extent the Tundra ecoregions had high estimated MDR sizes with low EMFS. As

such, the relatively small EMFSs in the Marine West Coast Forests ecoregion contributed to a relatively small estimated MDR value in that study area.

With climate induced redistribution of ecoregions in Western Canada, mean EMFS and MDR size are expected to increase slightly; on average from 1581 and 4961 km² to 1587 and 5048 km², respectively, by 2080.

4.4.2. Identify candidate benchmarks

Figure 4.2 shows the combined area of all candidate benchmarks with an average intactness value of at least 95%, as derived by the Benchmark Builder software (BEACONS 2015) using catchments that were at least 80% intact. The refuges/gain and loss predicted for each caribou population from the interaction of climate, vegetation and roads (see Chapter 3) are also displayed on Fig. 4.2, along with current protected areas (dark green). The protected areas located within SARA's southern population refugia (and COSEWIC equivalents) match closely the candidate benchmark areas. However, by the 2080s, the population extent is predicted to contract, as connectivity is poor between the few, fragmented protected areas in the south and the potential areas of expansion north. Present and future distributions of northern (SARA or COSEWIC's) and especially barren populations are also located within the potential benchmark areas. However, the existing protected areas within expected refuges for the northern population are very fragmented and limited. The boreal caribou population seems to be the most disadvantaged. Not only is its distribution expected to decline the most, but it is also in areas that are not suitable for benchmark establishment and contain fewer intact protected areas at present. Overall, current protected areas are few, small and fragmented, but the analysis of candidate benchmarks shows large areas that are suitable candidates for protection.

4.5 Discussion

4.5.1 MDR size must be three times the largest expected fire

As the ultimate goal of this research was to integrate caribou conservation and climate change into a dynamic conservation planning framework, I asked how MDR size varied with respect to fire regime and what changes to expect in the future. I estimated mean MDR size in Western Canada as 2.5-3.2 times the estimated maximum fire size (EMFS), depending on whether the trend line is forced to pass by the origin and if the Great Plains are excluded as an outlier, given they are highly disturbed and sparsely forested (high proportion of static grassland). This is similar to the ratios of 2.7 and 2.8 times the EMFS estimated in NWT (Leroux et al. 2007a) and in Yukon (Anderson 2009), as well as the recommendation by Johnson and Gutsell (1994) that dynamic reserves should be at least three times the size of the largest disturbance. If similar empirical relationships are found in areas of even more diverse topology and vegetation than among regions of Western Canada, this could simplify the design of dynamic reserves.

Compared to previous MDR studies where fire was the only natural disturbance modeled (Leroux et al. 2007a, Anderson 2009), this study considers the important additive effect of climate change on fire size (Kurz et al. 2008), as rising temperature and drought expected with climate change are increasing fire size (Soja et al. 2007, Girardin and Mudelsee 2008). This was accomplished by proxy, with use of anticipated shifts in ecoregions and their associated fire regions. The increases in EMFS and MDR seem small because reported on average across all western Canada. While ecoregions are mostly maintained or replaced by others of similar fire regime, it doesn't mean that some regional changes won't be drastic. In addition, one assumption here is that areas where ecoregions are maintained won't change fire regime. This approach could be improved by directly including climate change or other related disturbances such as insect outbreaks (Hogg and Bernier 2005, Danby and Hik 2007, Ogden 2007, Johnstone et al. 2010) in the landscape simulations and benchmark design process. For example, vegetation data could be updated during model runs using the predictions generated in Chapter 2, or by modifying successional trajectories. In fact, this should be part of a broader uncertainty analysis designed to evaluate the responsiveness of these analyses to changes in underlying parameters.

For instance, it may be appropriate to require larger minimum representation of each vegetation type through time by considering minimum areas required for animal species.

4.5.2 Identify candidate benchmarks

I also asked how identified potential climate refuges for caribou, current protected areas, and candidate reserve networks correspond with one another, and if there are potential secure areas remaining for locally adapted caribou populations. The Canadian boreal region contains a quarter of global frontier forests (Bryant et al. 1997) and offers an opportunity to establish large ecological benchmarks to conserve biodiversity and ecological processes (CBI 2005, Schmiegelow et al. 2006, Schmiegelow et al. 2014). Maximizing connectivity, along with maintaining large-scale hydrologic processes and climate refuges, is essential to enable biodiversity resilience to climate change (Heller and Zavaleta 2009, Mawdsley et al. 2009, Schmitz et al. 2015), a major conservation priority (Beier et al. 2006, Kareiva 2006).

The Benchmark Builder software (BEACONS 2015) identifies candidate ecological benchmarks based on size, intactness, and hydrologic connectivity. This study shows that large, intact areas in the Canadian boreal forest support candidates for reserves that incorporate all of these attributes, and thus could function as system-level ecological benchmarks. Present and potential future distributions of barren and both southern and northern mountain caribou are located within these candidate reserve areas. However, the current protected areas within the projected potential future northern mountain range are either limited or fragmented based on SARA or COSEWIC's delineations, respectively (COSEWIC 2002a, 2014). The situation may even be worse for the boreal and COSEWIC's southern mountain delineations, which may encompass few candidate reserves, signaling an urgent need for protection of these areas.

Table 4.1 Dynamic vegetation classes and their succession rules for estimation of minimum dynamic reserves (MDRs) in ecoregions of northwestern Canada. All classes follow deterministic rules except Deciduous, which has a probability of 0.5 of following one of two successional pathways as denoted by (*).

Trajectory	Age class (years)					
	0-2	3-20	21-60	61-80	81-120	121-160
Closed coniferous	Burned	Closed coniferous	Closed coniferous	Closed coniferous	Closed coniferous	Closed coniferous
Open coniferous	Burned	Open coniferous	Open coniferous	Open coniferous	Open coniferous	Open coniferous
Mixedwood	Burned	Deciduous	Mixedwood	Mixedwood	Mixedwood	Mixedwood
Deciduous*	Burned	Deciduous	Mixedwood	Mixedwood	Mixedwood	Open coniferous
Deciduous*	Burned	Deciduous	Deciduous	Deciduous	Deciduous	Deciduous
Shrub	Burned	Shrub	Shrub	Mixedwood	Mixedwood	Closed coniferous

Table 4.2 Range of Estimated Maximum Fire Size (EMFS) and size of Minimum Dynamic Reserves (MDR) for ecoregions in northwestern Canada (current and 2080 projected averages if different). The data used to estimate EMFS and MDR values include ignition, escape and spread probabilities per ecoregion derived from 10,000 km² hexagon data.

Ecoregion	Estimated MDR size (km ²)	EMFS (km ²)
2.1 Northern Arctic	2238	625
2.2 Alaska Tundra	3540	625
2.3 Brooks Range Tundra	7291	1852
2.4 Southern Arctic	5409	1494
2. TUNDRA	4503	1140
3.1 Alaska Boreal Interior	5324	1514
3.2 Taiga Cordillera	3121-3991	1048-1330
3.3 Taiga Plains	8160-10710	2680-4178
3.4 Taiga Shield	6603-6163	2121-2563
3. TAIGA	6490	2220
5.1 Softwood Shield	7738	2469
5.4 Boreal Plains	3708-8115	1071-2338
5. NORTHERN FORESTS	7387	2295
6.1 Boreal Cordillera	3362-7657	1053-1941
6.2 Western Cordillera	887-1671	210-660
6. NW. FORESTED MOUNTAINS	2557	729
7. MARINE W. COAST FORESTS	1001	242
9. GREAT PLAINS	5886	703
10. N. AMERICAN DESERTS	2238	625
MEAN	4961	1581

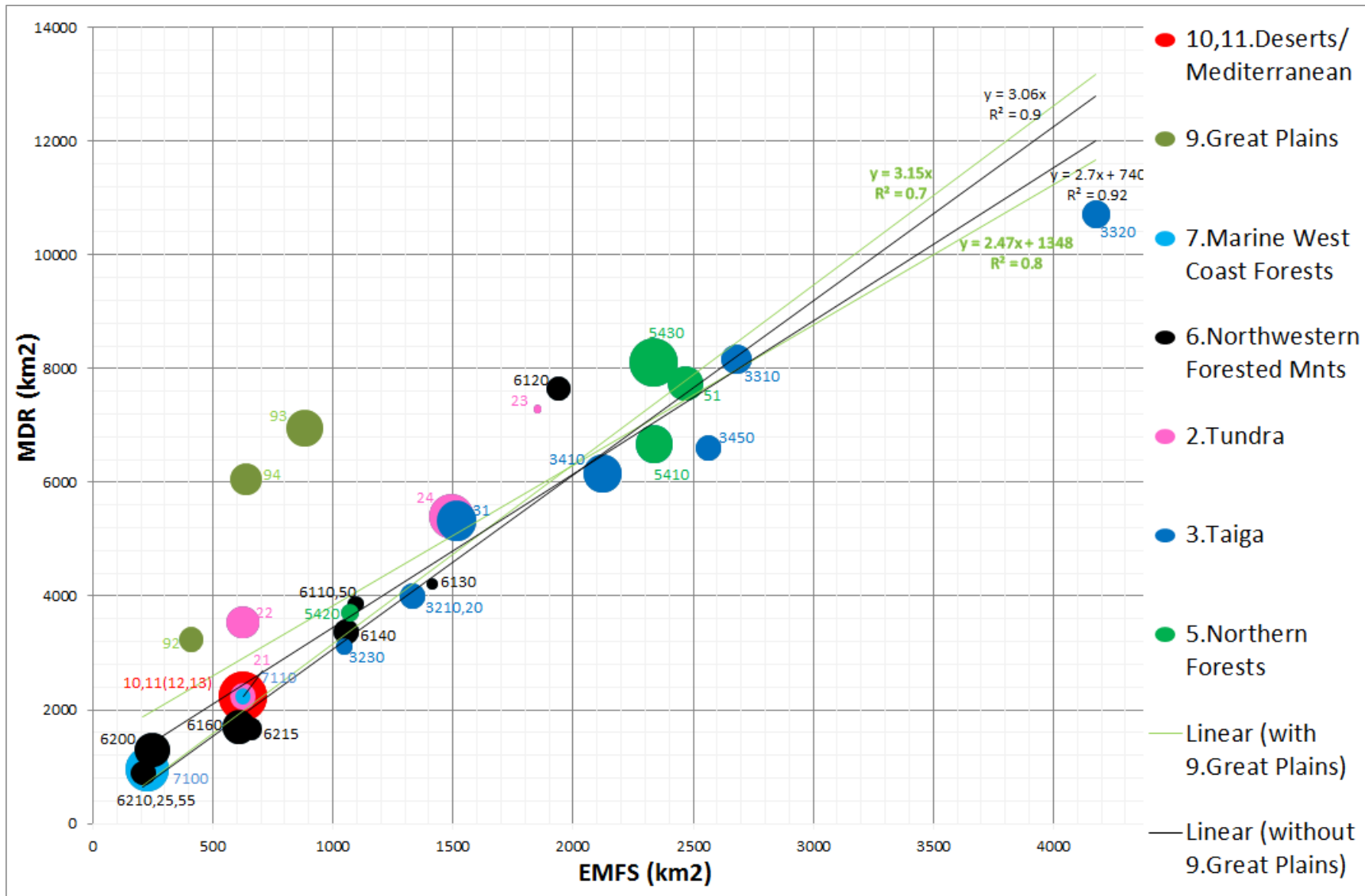


Figure 4.1 Relationship between minimum dynamic reserve (MDR) size and estimated maximum fire size (EMFS) for ecoregions in northwestern Canada.

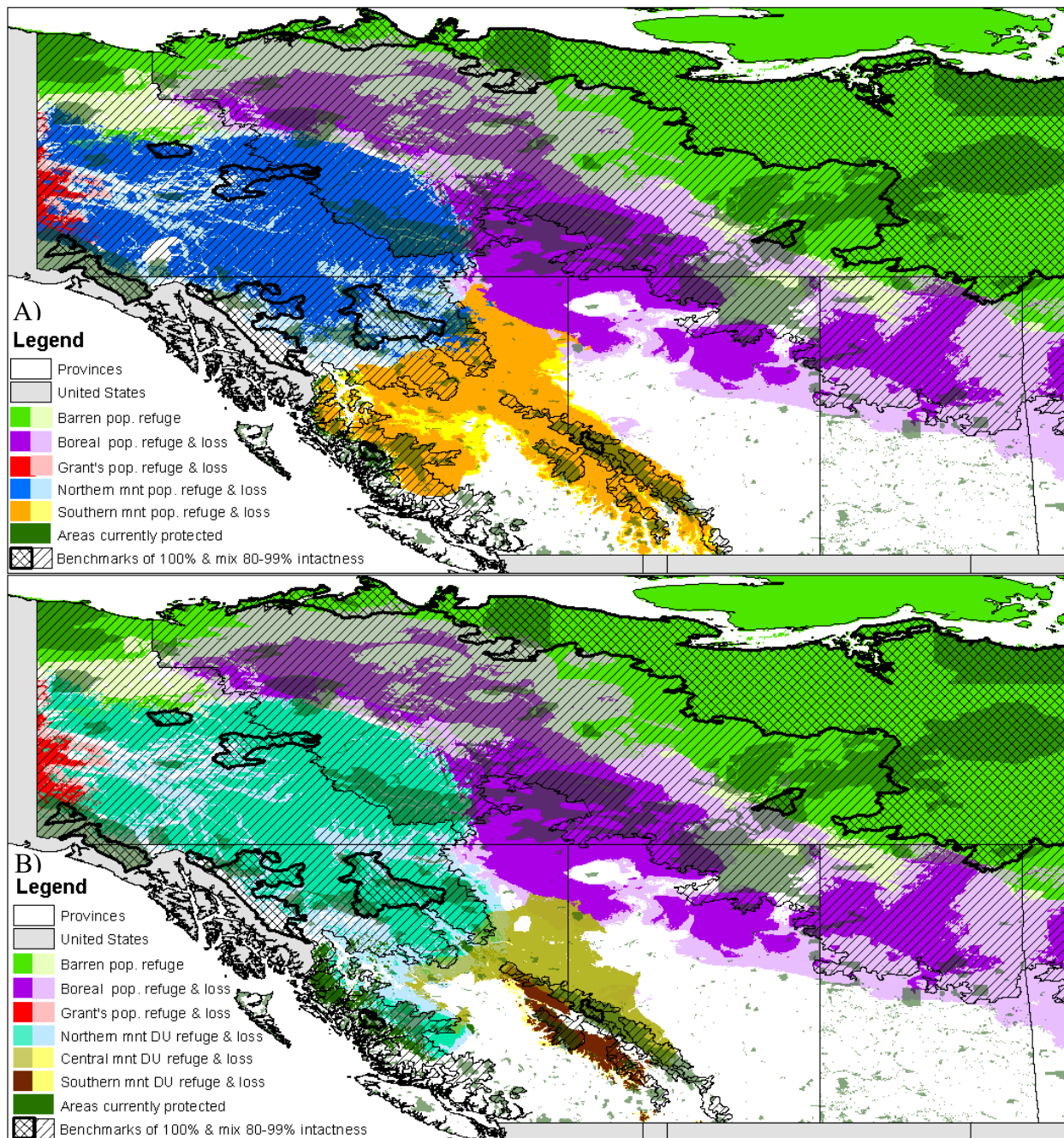


Figure 4.2 Distribution of protected areas (green), potential benchmark areas with $\geq 80-100\%$ intactness, and caribou population refuge/ gain (dark shades) or loss (light shades) in northwestern Canada based on 2080s projections and A) SARA or B) COSEWIC's classifications.

5. CHAPTER FIVE: CONCLUSION

5.1 Summary of results

The objective of this Master's thesis was to evaluate threats to caribou in western North America, and to propose a dynamic reserve design to protect existing and future habitat areas. This was an ambitious study of caribou distribution in terms of geographic extent (Canada and United States), variety of predictors considered (climate, vegetation & anthropogenic), scenarios (climate change, vegetation lag, human cumulative effects), scales (species, population, winter range) and competing population units (SARA's northern and southern mountain populations, COSEWICS's northern, central and southern mountain DU, and boreal, barren and Grant's populations common to both classifications), yet it is only a first step in understanding the conservation needs of this vulnerable species, and a case study of potential effects of rapidly changing conditions.

The major threats to caribou come from anthropogenic and climate changes altering vegetation and species interactions through land-use change and through frequent extreme weather events and forest fires. In this thesis, I identified potential present and future climate impact on western North America's vegetation in the first research chapter. I then examined the potential combined impacts of climate, vegetation and anthropogenic changes on current and projected future caribou distribution in the second research chapter. Finally, in the third research chapter, I integrated caribou conservation and potential climate-driven changes in fire and vegetation to propose areas that may serve as ecological benchmarks for caribou habitat. Ecological benchmarks consider intactness, connectivity and current and potential future vegetation, climate, and fire size when delineating potential suitable areas.

Results suggest that human activities, and induced biotic factors such as changes in predation and competition, had influenced current caribou distribution beyond consideration of climate and vegetation alone. However, projections for the end of the century suggest that future effects of climate change on caribou may supersede biotic interactions, especially at the southern range.

Revisiting my original research questions outlined in the introductory chapter, my thesis work contributed the following knowledge to caribou conservation:

- 1) Evaluate vegetation response to current climate and topo-edaphic controls and project potential vegetation changes for the 2020s, 2050s, and 2080s.

My projections for the 2080s suggest a general northward and upslope move of ecoregions. Aside from the southern US, for which projections may lack modern analogues, the biggest increase in mean latitude or elevation by 2080 are expected in the northern ecosystems. Concomitantly, the models also predicted a possible expansion of the Northern Forests, pushing the Northwestern Forested Mountains up slope, and more dramatically, the Taiga further north at the expense of the Tundra. The general trend is one where low elevation needleleaves may push each adjacent vegetation class higher in latitude and elevation at the expense of open shrubland, barren, and tundra. As shown in previous studies, I found that temperate classes may shift range northward and into higher elevations at the expense of Nordic shrubland and barren tundra, while their southern range may be taken over by more tropical ones (Iverson and Prasad 2002, Loarie et al. 2009, Mbogga et al. 2010, Rehfeldt et al. 2012, Rowland et al. 2016). While the lower United States and the arctic state or provinces (AK, YT, NWT/Nunavut, and Arctic Islands unclear) may experience a related rise in biodiversity, the lower Canadian provinces may see a decrease in biodiversity

This result suggests that vegetation classes found in the north or at high elevations, as well as the evergreen classes in southern areas, may be vulnerable to climate change (Hansell et al. 1998, Sturm et al. 2001, Hampe 2004, Hogg and Bernier 2005, Danby and Hik 2007, Mbogga et al. 2010, Lara et al. 2016). Induced changes in forest composition and structure will intensify as warming accelerates, especially in northern latitudes (Root et al. 2003, Balshi et al. 2009, Price et al. 2013, IPCC 2014). I found that on average a 100 km shift northward may correspond to an upward shift of 42 meters, similar to other studies (Gray and Hamann 2013), that constitutes an annual average of 1.28m shift up in elevation or 3.1km northward shift. I used nine commonly used land cover and ecoregion classifications to forecast potential climate induced changes with

climate envelope models. As a result, this study adds compelling reasons for necessary changes to management of natural resources if currently observed climate trends continue or accelerate.

2) Compare different techniques and model uncertainties for vegetation projections and extrapolation into novel conditions.

The choice of modeling technique is a cause of uncertainty in projecting species responses to climate change (Thuiller et al. 2004, Hijmans and Graham 2006, Lawler et al. 2006, Pearson 2006), but this can be reduced with state of the art methods like RandomForest or ensemble methods (Stralberg et al. 2015b). I compared two contrasting modeling techniques, discriminant analysis and randomForest. I confirmed that randomForest is more robust than discriminant analysis (see also Roberts and Hamann 2012). Variable importance in randomForest showed that climate variables were the primary vegetation-predictors, although they were highly autocorrelated. Edaphic and topographic variables were less important than climate. Further, my analysis showed that randomForest had lower misclassification error rate for the three most predictable land cover classifications compared with discriminant analysis. Despite potential over-parameterisation, model accuracy and robustness were consistent between training models with a percent of the dataset or only a random 2/3 subset of them. Both randomForest and discriminant analysis account for collinearity among predictors and I selected the most uncorrelated. Although topo-edaphic variables are useful to restrain species response to climate change (Taverna et al. 2005, Coudun et al. 2006, Luoto and Heikkinen 2008, Morin and Thuiller 2009, Chen et al. 2010, Gillingham et al. 2012, Roberts and Hamann 2012, Stralberg et al. 2015b), - the topo-edaphically constrained projections that result should not be interpreted as realistic models of plant demographics or future delineation of vegetation distributions. At best they could be rationalized as a reduced “upper bound” of bioclimatic envelope projections.

My response variables had biogeographic features that affected accuracy and I achieved better predictive ability for homogeneous land cover variables that segregated in latitude or higher elevation. I suggest that vegetation responses to climate change lag and vary due to local genetic adaptation (Rehfeldt et al. 1999, Gray et al. 2016), but see (Yeaman et al. 2016), seed dispersal

(Nathan et al. 2011), and perseverance of long-lived tree species in conditions not suitable for recruitment (Hamrick 2004, Botkin et al. 2007, Aitken et al. 2008).

- 3) Incorporate current and potential future vegetation and climate into projecting of potential future caribou distribution in order to identify potential population vulnerability to climate or to roads and the uncertainty with scales.

The simultaneous northward progression of climatic change and other human disturbances render interpretation and prediction of their relative effects on caribou difficult. I thus combine climate, potential vegetation, and linear disturbance data into best (climate + vegetation+roads), intermediate (climate + vegetation) and worst-case (climate only) scenarios, as decoupling vegetation response to climate variables and anthropogenic factors is difficult and a risk for projections into new spatial or temporal domains (Ichii et al. 2002, Araújo et al. 2004, Thomas et al. 2004, Peterson et al. 2006), but explicitly addressing it is extremely challenging. My analysis demonstrates the potential importance of vegetation as a limiting and moderating influence on climate induced changes.

- 4) Compare potential shifts in distribution with current population distribution, in order to identify potential “refuges”.

Overall, my research suggests significant potential losses to caribou current distribution (not considering potential gains), particularly at the southern edges of current distribution or at lower elevations. The climate only models are worse for the northern mountain (especially their winter ranges in Yukon) and boreal caribou, with major losses and little refuges or gains to be expected. Inversely, the climate+vegetation+roads models for southern mountain and Grant’s populations are more optimistic regarding losses, as a result of static roads limiting losses from climate change, although this counterintuitive result is due to the correlation between current roads and climate. Southern mountain and Grant’s populations are predicted to have significant expansion of their current distribution, although most will probably not be realized due to barriers to migration.

My results support those of others (See Appendix 6.4 in Environment Canada 2008), with some potential climate induced range contraction at the southern frontier of Alberta and Saskatchewan for boreal caribou, but also in the Okanagan valley of British Columbia and North Idaho for the southern population, and at the southern limit of the northern and barren populations. However, I also agree with their finding, and of others (Schaefer and Mahoney 2007, Vors et al. 2007), that mostly attribute a northward retraction of Grant's, southern mountain and boreal caribou distribution to linear disturbances, notably at Canada/Montana border and South-East BC (southern mountain population), southwestern Alberta and Saskatchewan/Manitoba border (boreal population) and around Anchorage and Fairbank (Grant's population).

5) Study the potential effect of changes in climate on the minimum reserve size needed.

Similarly to other studies (Johnson and Gutsell 1994, Leroux et al. 2007a, Anderson 2009), I estimate mean MDR size in western Canada as 2.7-3 times the estimated maximum fire size (EMFS), which could simplify the design of dynamic reserves.

Comparative to previous MDR studies where fire was the only natural disturbance modeled (Leroux et al. 2007a, Anderson 2009), mine considers the important additive effect of climate change on fire regimes (Soja et al. 2007, Girardin and Mudelsee 2008, Kurz et al. 2008), as inferred by shifts in ecoregions, showing both estimated maximum fire size (EMFS) and size of Minimum Dynamic Reserves (MDR) increasing over western Canada by 2080.

6) Examine how current protected areas correspond with the potential caribou refuges and candidate reserve networks I identified in research chapters two and three respectively.

In order to design a sustainable reserve, the size of the largest disturbance needs to be considered. My analysis shows that the minimum reserve size should be 2.8 times as large as the largest anticipated wildfire event, supporting other studies (Johnson and Gutsell 1994, Leroux et al. 2007a, Anderson 2009). I identified candidate reserve networks in western North America that have over 95% intactness, and compared them with areas that are currently under protection. The closest match with current protected areas is within the southern population refuges. However,

under projections for the 2080s, the population range is expected to decline in the south and especially in BC, and potential for new reserves is limited and existing ones fragmented. Conversely, northern and barren populations are located in a much more intact matrix, with great candidate reserve potential presently and projected to be suitable habitat in the 2080s, although current reserves there are too fragmented, signaling a need for more protection. Conservation of habitat for the boreal caribou population is a top priority according to my results, as their current and future range is less suitable for reserve establishment, with only few and fragmented protected areas already present. Over the entire caribou distribution, the protected areas are few and fragmented, but my analysis shows large potential for establishment of dynamic reserves in northern parts of western Canada.

5.2 Vegetation shifts and further directions in bioclimatic envelope modeling

Due to the longevity of trees, vegetation shifts in some areas may be delayed for a few decades. Nevertheless, the extent of changes forecasted and impacts already witnessed or presumed (e.g. the mountain pine beetle epidemic) are of concern. For instance, projections pointing to a gain of ecosystem diversity in Alaska greater than that of current British Columbia, may compromise productivity and health of locally adapted ecosystems (Allen et al. 2010, Roberts and Hamann 2012). Although, results from reciprocal transplant experiment suggest that great gains in productivity could be achieved in northern regions by matching genotypes to new environmental conditions through assisted migration (Wang et al. 2006, O'Neill et al. 2008, Gray et al. 2016) but see (Yeaman et al. 2016).

My research also supplements an emergent call for necessary changes to management of natural resources if current tendencies carry on or speed up. Given the large and increasing influence of broad-scale disturbances, which should accelerate vegetation response to climate change, bioclimatic models can be useful to identify trends and zones or species for assisted migration, habitat restoration, or conservation when suitable environment may be preserved (McKenney et al. 2009, Gray et al. 2011, Gray and Hamann 2011, Gray et al. 2016, Carroll et al. 2017).

Considering my models project vegetation classes as homogeneous (unlimited migration and plasticity scenario) may overlook the risk associated with constrained genetic structures or decoupling between interacting species, additional research may be useful to develop complementary scenarios based on ‘No migration or plasticity’.

5.3 Further directions in niche modelling and reserve design

Management of caribou populations is challenging, as they occupy large areas and either extensively migrate (i.e. barren caribou) or exist at low densities (i.e. woodland caribou). Sample stratification could be used with niche based distribution models to increase sampling efficiency, and new data could be used for better predictions (Jiménez-Valverde and Lobo 2006). For example, sink populations should be excluded from environmental niche models since they may represent marginal niche space (resources and conditions) for sustainable populations (Pulliam 2000, Soberon 2007). The extensive land use data I compiled could be used in conjunction with demographic data to address this, and also used for finer-scale habitat analysis than mine, such as resource selection probability functions (RSPFs, Lele and Keim 2006) using radio-collared caribou data not available for this study.

The changes in the new Designatable Units (DU) structure (COSEWIC 2014) from the previous assessment (COSEWIC 2002b) reflect distinction between caribou that are adapted, at least behaviorally, to specific high-elevation forest with deep snow (2-5 m) and feed exclusively on arboreal lichens for 3-4 months of the year (now exclusively southern mountain DU) and the shallow snow/terrestrial lichen feeding caribou (now either central or northern mountain DUs). The Peace River and the Rocky Mountains also separate the central mountain DU from the northern and southern mountain DUs, respectively. Based on limited samples, the northern mountain DU (from the Beringian-Eurasian lineage exclusively) is, however, not only further genetically from the central mountain DU than the southern (both mixed of northern Beringian-Eurasian and southern North American lineages) (McDevitt et al. 2009, Serrouya et al. 2012, Weckworth et al. 2012), but also from the west central BC herds (Zittlau 2004, Serrouya et al. 2012). It is thus recognized that further phylogenetic studies are needed before a revision of the taxonomy (COSEWIC 2014). To complement this, a method similar to mine could evaluate herd

specific niches before further testing whether they are significantly different from one another using techniques such as ENMTools (Warren et al. 2010).

Finally, other than maintaining climate refuges, maximizing connectivity across landscapes has been the most frequent recommendation to enable biodiversity resilience to climate change (Heller and Zavaleta 2009, Mawdsley et al. 2009). Although in my third research chapter I consider hydrological connectivity in reserve design, a connectivity analysis more specific to caribou could confirm whether the populations studied here are likely to be able to track projected shifts in their future niche space.

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APPENDIX

Appendix Table 2.1. Predictors' data source. Information on source, author, scale & layer name.

Source	Authors	Scale	layer names
US Geological Survey usgs.gov	Garrity and Soller 2009	1:5M	Geologic Map of North America (Reed et al., 2005)
Oak Ridge National Laboratory Distributed Active Archive Center ORNL DAAC daac.ornl.gov/	International Geo-Biosphere Program -DIS, GSDTG 2000	5 arc-min	soil-carbon density (kg/m ²), total nitrogen density (g/m ²), field capacity (mm), wilting point (mm), profile available water capacity (mm), thermal capacity (J/m ³ /K), bulk density (g/cm ³)
	International Soil Reference & Information Centre -WISE, Batjes, 2000	30 arc-min	total available water capacity (mm/m soil depth), soil organic carbon density (kg C/m ² for 0-30cm and 0-100cm depth ranges), soil carbonate carbon density (kg C/m ² for 0-100cm depth range), soil pH (at 0-30cm and 0-100cm depth ranges)
	Dunne and Willmott 2000		global distribution of plant extractable water capacity of soil
	International Geosphere-Biosphere Program ISLSCP II, Scholes et al. 2011	60 arc-min	at 0-30 & 0-150 cm depth: bulk density (g/cm ³), clay content (% w/w), field capacity (mm), saturated hydraulic conductivity (cm/day), soil nitrogen (g/m ²), soil carbon (kg/m ²), soil organic carbon (%), profile available water (mm), residual water (cm ³ /cm ³), sand (% w/w), porosity (cm ³ /cm ³), silt (% w/w), wilting point (mm), thermal capacity at 0, 10, 50 and 100% volumetric soil-water fraction (J/m ³ /K), 12 texture classes
	Webb et al. 2000		water-holding capacity (mm), potential storage of water in the soil profile (mm), global map of the potential storage of water in the root zone (mm), global map of potential storage of water derived from soil texture (mm), classification of 106 soil types identified by Zobler (1986) from the FAO/UNESCO World map
	Kleidon 2011		total plant-available water storage capacity of rooting zone
	Schenk and Jackson 2009		ecosystem rooting depths
Data Basin databasin.org	Churkina and Running 1998	30 arc-min	plant available water limitation on plant growth variable
	Vorosmarty et. al., 2005		global annual average Climate Moisture Index and its coefficient of variation for 1950-2000
	Bachelet et al. 2001		1961-1990 average vegetation carbon for US and Canada
International Institute for Applied Systems Analysis iiasa.ac.at	Harmonized World Soil Database v1.2 FAO/IIASA/ISRIC/ISSCAS/JRC 2009	0.5 arc-min	dominant soil map, available water storage & moisture storage capacities (mm/m), drainage, soil depth (Loarie et al.), phase 1&2, other properties (gelic, vertic, petric), topsoil texture, productivity (%)
			at 0-30 cm & 30-100 cm depth: sand, silt, clay, gypsum, organic carbon, calcium carbonate fractions (%weight), gravel (%vol.), texture, bulk and reference bulk (kg/dm ³), pH(-log(H ⁺)), cation exchange capacity for clay & soil, total exchangeable bases (cmol/kg), base saturation and sodicity (%), salinity (%dS/m), carbon pool (kg.m-y), carbon/nitrogen, nitrogen(%)
			nutrient availability, nutrient retention capacity, rooting conditions, oxygen availability, excess salts, toxicity, workability
		5 arc-min	global raster on water bodies' percentage share of total grid-cell

Appendix Table 2.2. Classification and misclassification rate of observed MCD12Q1 vegetation at sampled points for the present day. RandomForest’s classification sensitivity (%) as well as Cohen Kappa (K) is reported. In grey are classes that could be combined.

Observed	Modelled Land covers										n	%	K
	5	6	7	1	3	8	9	10	15	16			
5 Mixed/ broadleaf	1433	3	1	109	33	20	44	2	15	0	1660	86.3	75.2
6 Closed shrublands	15	1081	128	19	33	75	92	84	65	8	1600	67.4	56.3
7 Open shrublands	9	127	1064	22	65	136	169	44	54	90	1780	59.6	48.5
1 Evergreen Needleleaf	221	12	7	1238	171	88	13	34	35	1	1820	67.9	56.8
3 Deciduous Needleleaf	107	19	26	119	967	208	137	3	14	0	1600	60.4	49.3
8 Woody savannas	24	49	89	82	201	974	176	45	20	0	1660	58.7	47.6
9 Savannas	68	64	87	40	112	146	1031	18	33	1	1600	64.4	53.3
10 Grasslands	25	82	25	65	6	13	41	1370	66	47	1740	78.6	67.5
15 Snow & ice	10	33	34	19	6	4	20	19	1462	33	1640	89.0	77.9
16 Barren	1	9	19	0	0	0	2	34	47	1488	1600	93.0	81.9
Total	1913	1479	1480	1713	1594	1664	1725	1653	1811	1668	16700	72.4	61.3
												81.4	64.7

Appendix Table 2.3. Classification and misclassification rate of observed NALC2005 vegetation at sampled points for the present day. RandomForest’s classification sensitivity (%) as well as Cohen Kappa (K) is reported. In grey are classes that could be combined.

Observed	Modelled Land covers													N	%	K
	1	2	5	6	8	19	7	9	10	11	12	13	16			
1 Temperate or sub-polar needleleaf	1122	119	106	293	170	16	2	0	11	11	11	1	18	1880	59.5	51.2
2 Sub-polar taiga Needleleaf	47	1342	15	112	17	0	0	0	6	38	112	10	21	1720	77.9	69.6
5 Temperate or sub-polar broadleaf deciduous	207	23	1065	340	46	17	0	0	19	14	7	2	20	1760	60.5	52.2
6 Mixed Forest	215	154	337	913	70	0	0	0	8	38	15	3	7	1760	51.6	43.3
8 Temperate or sub-polar shrubland	253	106	52	110	953	29	41	3	84	94	45	6	64	1840	51.8	43.5
19 Snow and Ice	18	0	5	0	3	1632	0	0	8	1	3	1	69	1740	93.8	85.5
7 Tropical or sub-tropical shrubland	0	0	0	0	9	0	1575	115	1	0	0	0	0	1700	92.6	84.3
9 Tropical or sub-tropical grassland	0	0	0	0	1	0	8	1691	0	0	0	0	0	1700	99.5	91.1
10 Temperate or sub-polar grassland	49	65	37	20	97	9	6	2	1547	0	1	1	6	1840	84.1	75.8
11 Sub-polar or polar shrubland-lichen-moss	1	64	2	24	31	3	0	0	0	1408	119	0	48	1700	82.8	74.5
12 Sub-polar or polar grassland-lichen-moss	11	89	3	16	35	7	0	0	0	159	1177	205	78	1780	66.2	57.8
13 Sub-polar or polar barren-lichen-moss	2	21	3	4	4	4	0	0	2	1	138	1290	231	1700	75.9	67.5
16 Barren Lands	35	16	8	5	49	181	16	0	14	37	46	275	1118	1800	62.0	53.7
Total	1960	1999	1633	1837	1485	1898	1648	1811	1700	1801	1674	1794	1680	22920	73.4	65.1
															86.1	71.9

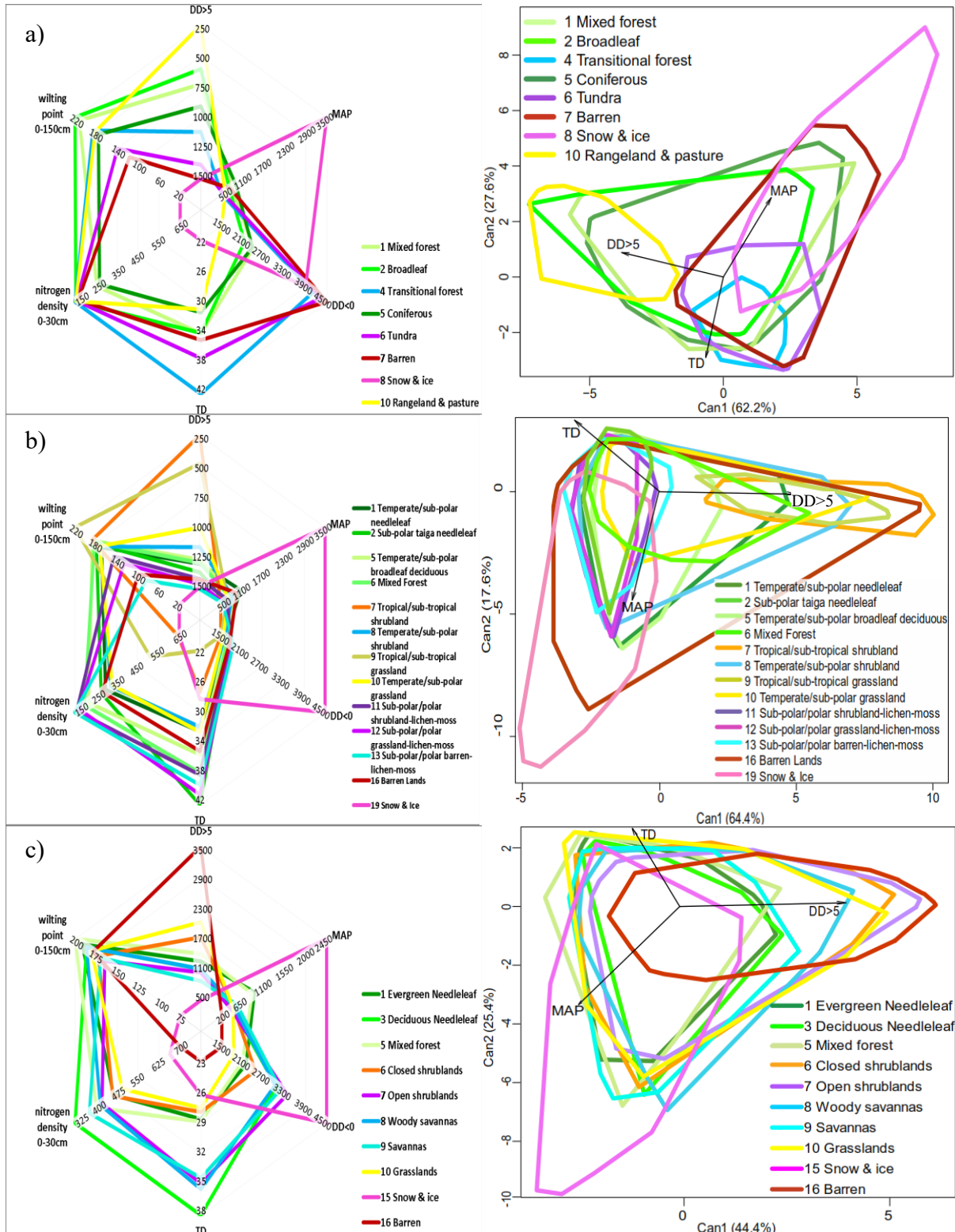
Appendix Table 2.4. Classification and misclassification rate of observed CA-AVHRR vegetation at sampled points for the present day. RandomForest’s classification sensitivity (%) as well as Cohen Kappa (K) is reported. In grey are classes that could be combined.

	Modelled Land covers								n	%	K
	1	2	4	5	6	7	8	10			
1 Mixed forest	1479	514	55	485	26	42	26	33	2660	55.6	41.3
2 Broadleaf	363	2075	2	114	8	22	9	47	2640	78.6	64.3
4 Transitional forest	24	0	2414	57	100	5	0	0	2600	92.8	78.6
5 Coniferous	378	158	119	1826	182	108	34	15	2820	64.8	50.5
6 Tundra	18	2	147	196	1685	468	4	0	2520	66.9	52.6
7 Barren	22	11	2	82	347	1946	170	0	2580	75.4	61.1
8 Snow & ice	9	1	0	19	3	43	2565	0	2640	97.1	82.9
10 Rangeland & pasture	7	24	0	5	0	0	0	2604	2640	98.6	84.4
Total	2300	2785	2739	2784	2351	2634	2808	2699	21100	78.6	64.3
										86.6	66.6

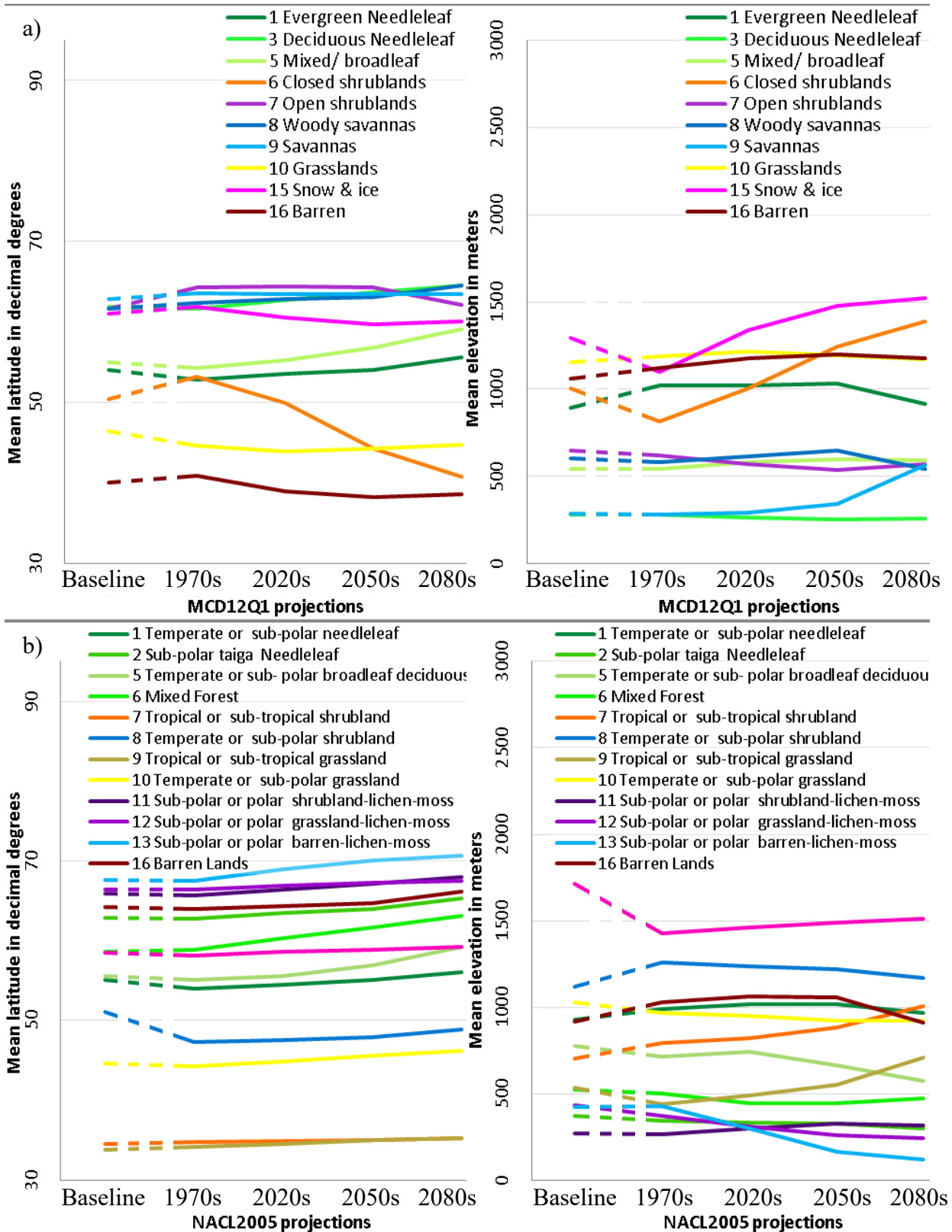
Appendix Table 2.5. Classification and misclassification rate of observed CEC level II ecoregions at sampled points for the present day. RandomForest’s classification sensitivity (%) as well as Cohen Kappa (K) is reported.

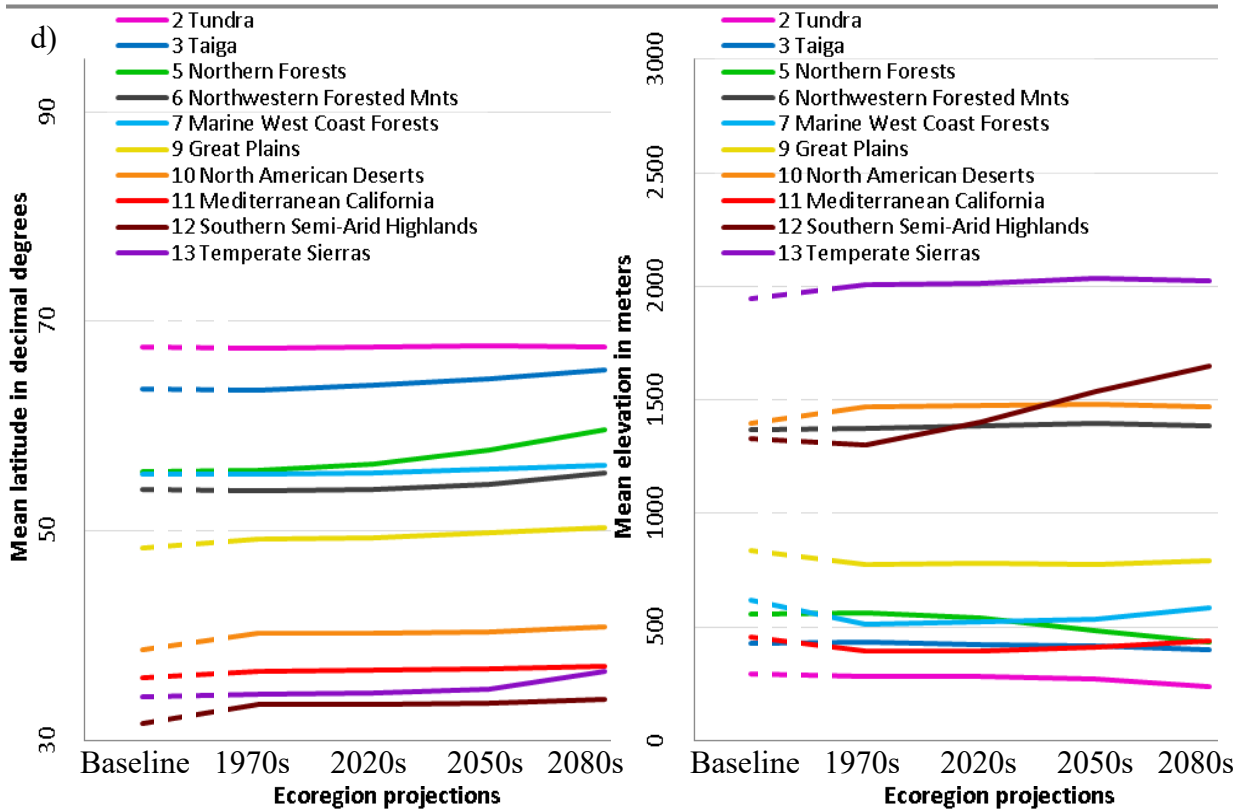
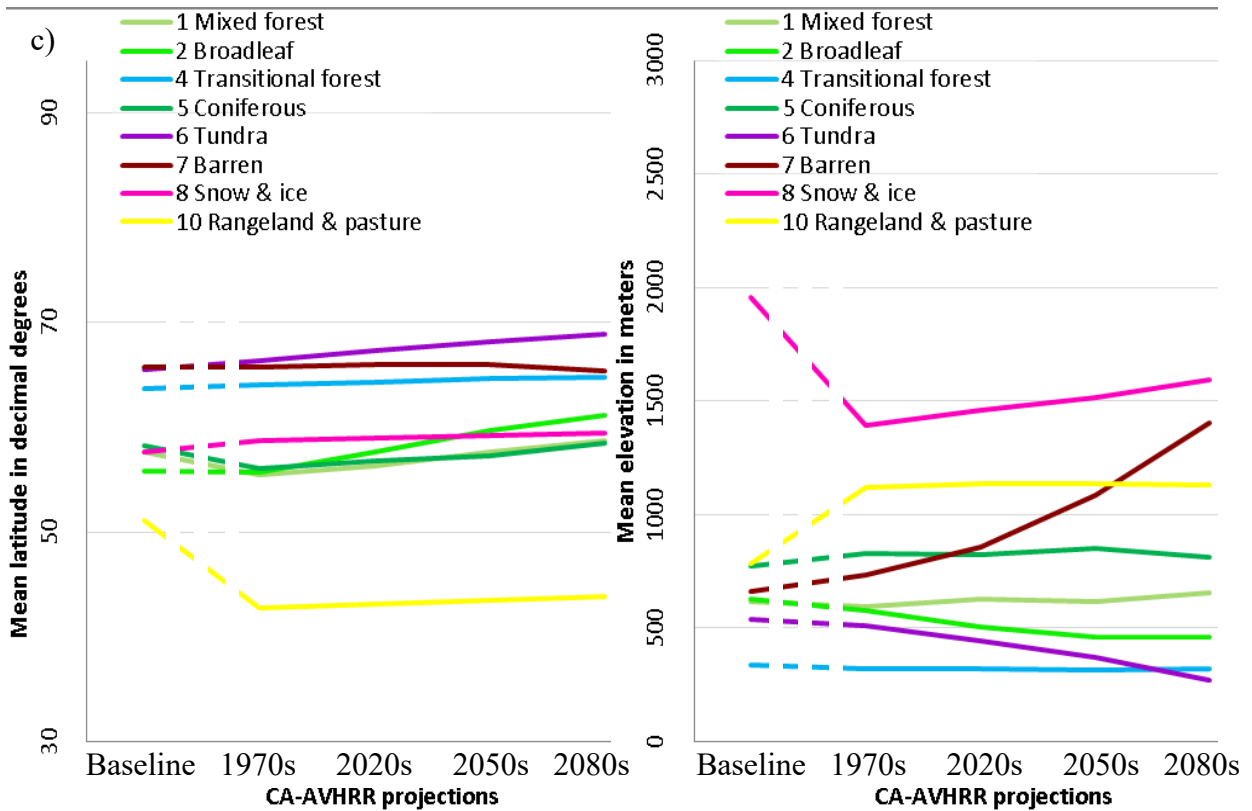
Level II Ecoregions	Modelled Ecoregions													n	%	K									
	2.1	2.2	2.3	2.4	3.1	3.2	3.3	3.4	5.1	5.4	6.1	6.2	7.1				9.2	9.3	9.4	10.1	10.2	11	12	13	
2.1 Northern Arctic	495	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	500	99.0	94.0
2.2 Alaska Tundra	0	1463	12	1	9	0	0	0	0	0	1	0	14	0	0	0	0	0	0	0	0	0	1500	97.5	92.5
2.3 Brooks Range Tundra	0	7	234	0	3	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	250	93.6	88.6
2.4 Southern Arctic	2	0	0	736	0	0	8	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	750	98.1	93.1
3.1 Alaska Boreal Interior	0	21	4	0	691	4	0	0	0	0	25	0	5	0	0	0	0	0	0	0	0	0	750	92.1	87.1
3.2 Taiga Cordillera	0	0	3	0	9	716	13	0	0	0	9	0	0	0	0	0	0	0	0	0	0	0	750	95.5	90.5
3.3 Taiga Plains	0	0	0	10	0	18	458	2	0	10	2	0	0	0	0	0	0	0	0	0	0	0	500	91.6	86.6
3.4 Taiga Shield	0	0	0	5	0	0	4	488	3	0	0	0	0	0	0	0	0	0	0	0	0	0	500	97.6	92.6
5.1 Softwood Shield	0	0	0	0	0	0	4	244	2	0	0	0	0	0	0	0	0	0	0	0	0	0	250	97.6	92.6
5.4 Boreal Plains	0	0	0	0	0	4	0	1	722	0	7	0	16	0	0	0	0	0	0	0	0	0	750	96.3	91.3
6.1 Boreal Cordillera	0	1	6	0	33	10	1	0	0	1	1401	7	40	0	0	0	0	0	0	0	0	0	1500	93.4	88.4
6.2 Western Cordillera	0	0	0	0	0	0	0	0	0	8	12	3579	33	0	3	4	93	0	17	0	1	3750	95.4	90.4	
7.1 Marine West Coast Forests	0	25	0	0	4	0	0	0	0	0	31	33	2152	0	0	0	2	0	3	0	0	2250	95.6	90.6	
9.2 Temperate Prairies	0	0	0	0	0	0	0	0	0	5	0	0	0	492	3	0	0	0	0	0	0	0	500	98.4	93.4
9.3 West Central Semi-Arid Prairies	0	0	0	0	0	0	0	0	0	0	0	18	0	9	711	11	1	0	0	0	0	0	750	94.8	89.8
9.4 South Central Semi-Arid Prairies	0	0	0	0	0	0	0	0	0	0	0	1	0	0	9	738	0	1	0	0	1	750	98.4	93.4	
10.1 Cold Deserts	0	0	0	0	0	0	0	0	0	0	0	86	9	0	3	2	1881	6	0	0	13	2000	94.1	89.1	
10.2 Warm Deserts	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	9	722	6	7	4	750	96.3	91.3	
11.1 Mediterranean California	0	0	0	0	0	0	0	0	0	0	0	12	1	0	0	0	0	0	737	0	0	0	750	98.3	93.3
12.1 Western Sierra Madre Piedmont	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	247	3	250	98.8	93.8	
13.1 Upper Gila Mtns	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	3	26	7	0	15	197	250	78.8	73.8	
Total	497	1517	259	757	749	754	488	498	248	748	1481	3745	2254	517	729	760	2012	736	763	269	219	20000	95.5	90.5	

Appendix Figure 2.1. Ecological niche of land cover classes. Star plots showing means (left) and canonical components of discriminant analysis (Kremen et al.) of predicted land cover classes for CA-AVHRR (a), NALC2005 (b), and MCD12Q1 (c) products.

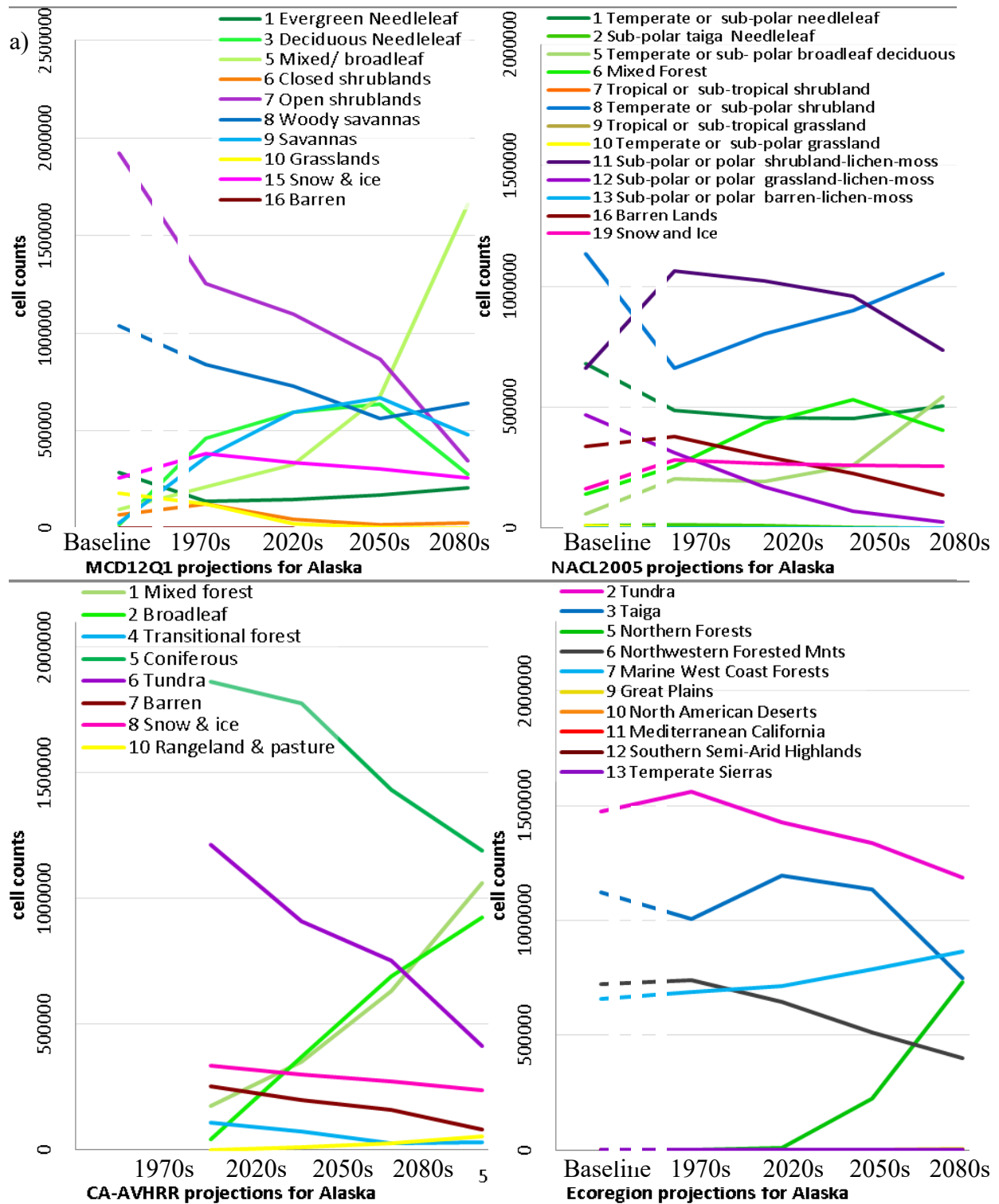


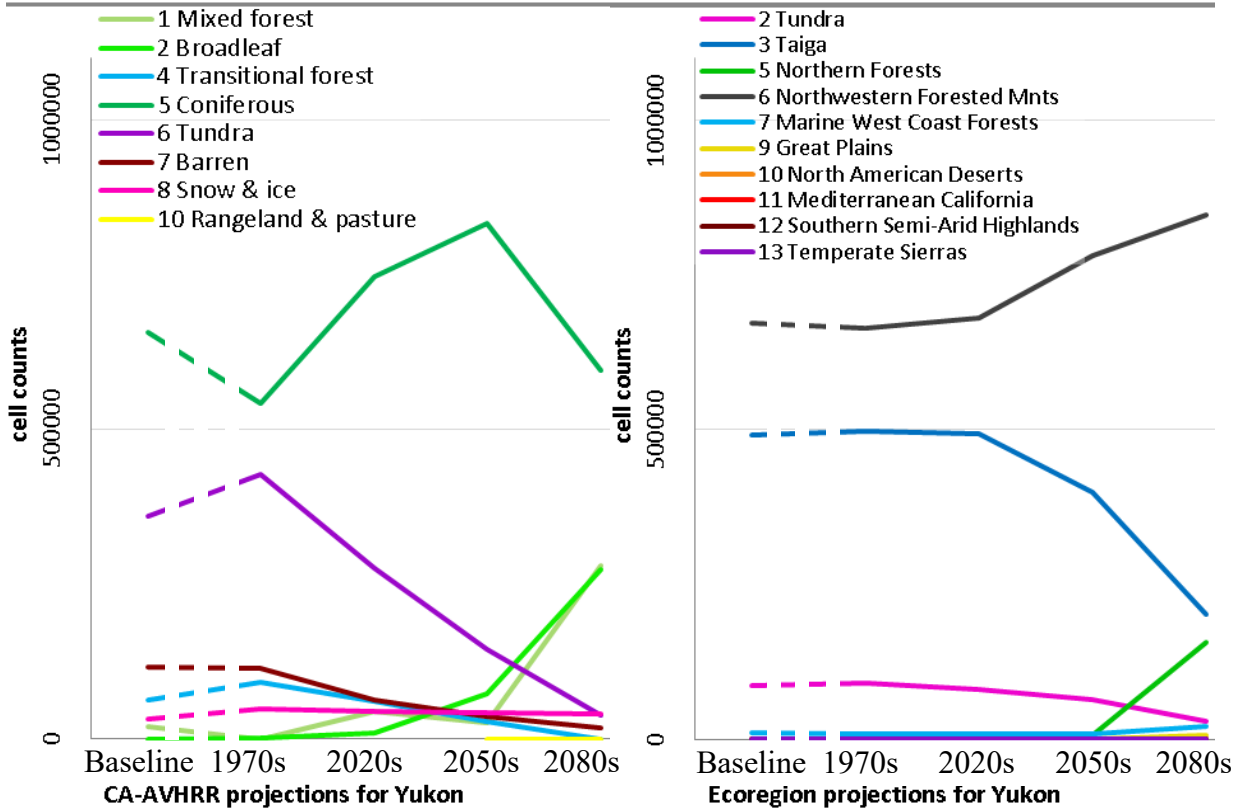
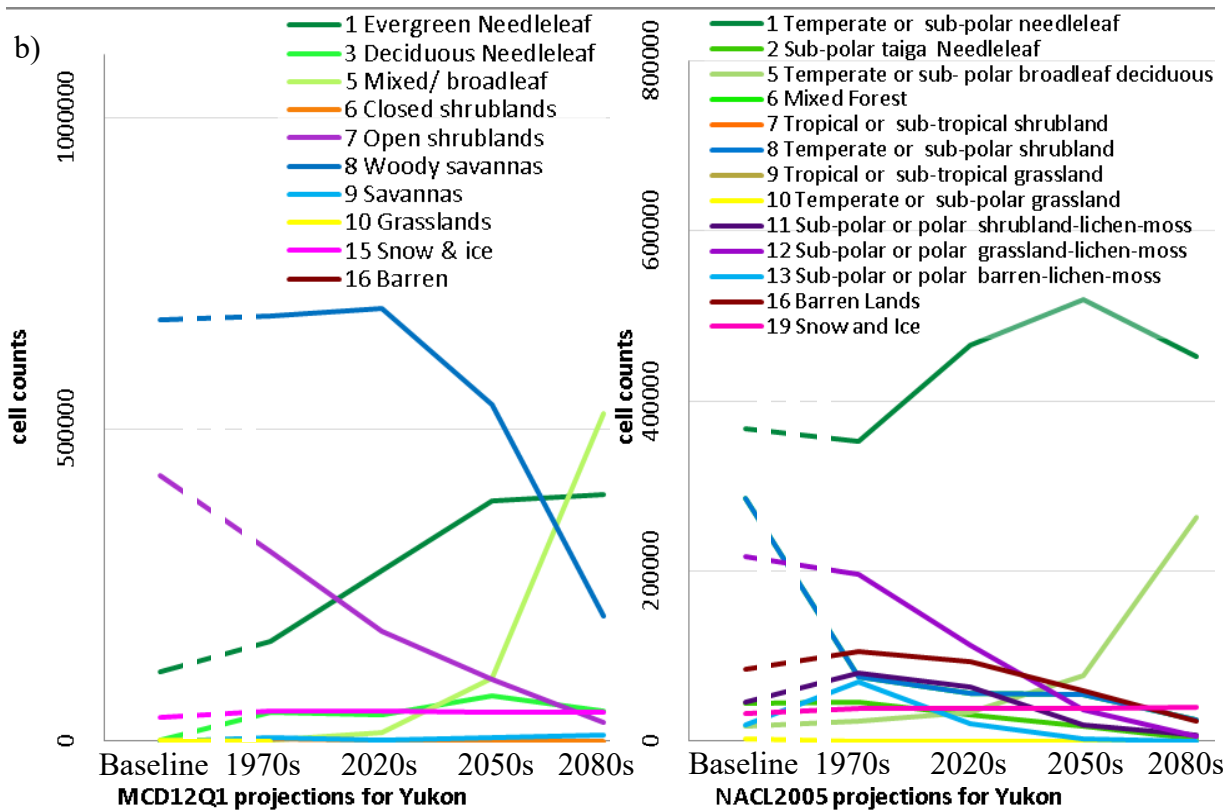
Appendix Figure 2.2. RandomForest’s projected changes in land cover distributions. Classes’ latitude (left) & elevation (right) are given for each time period & land cover product (a, b, c, d).

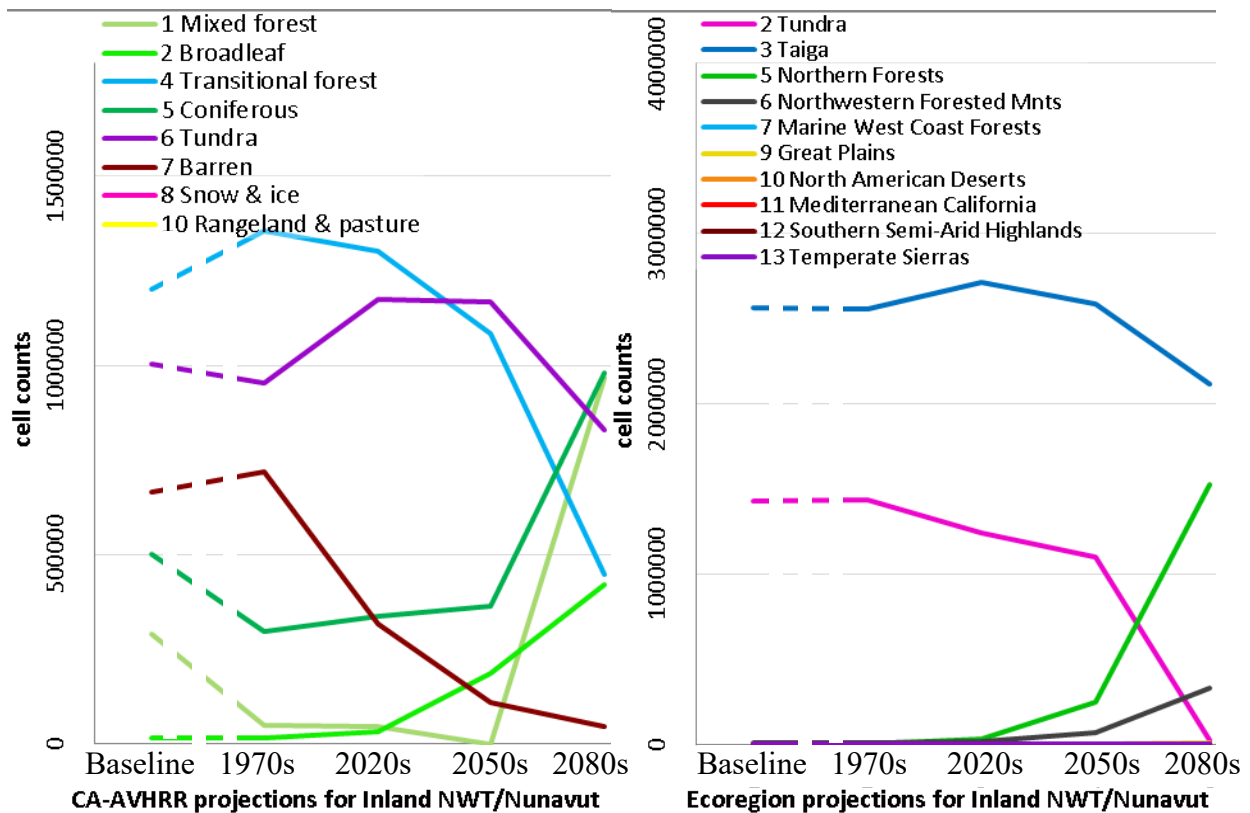
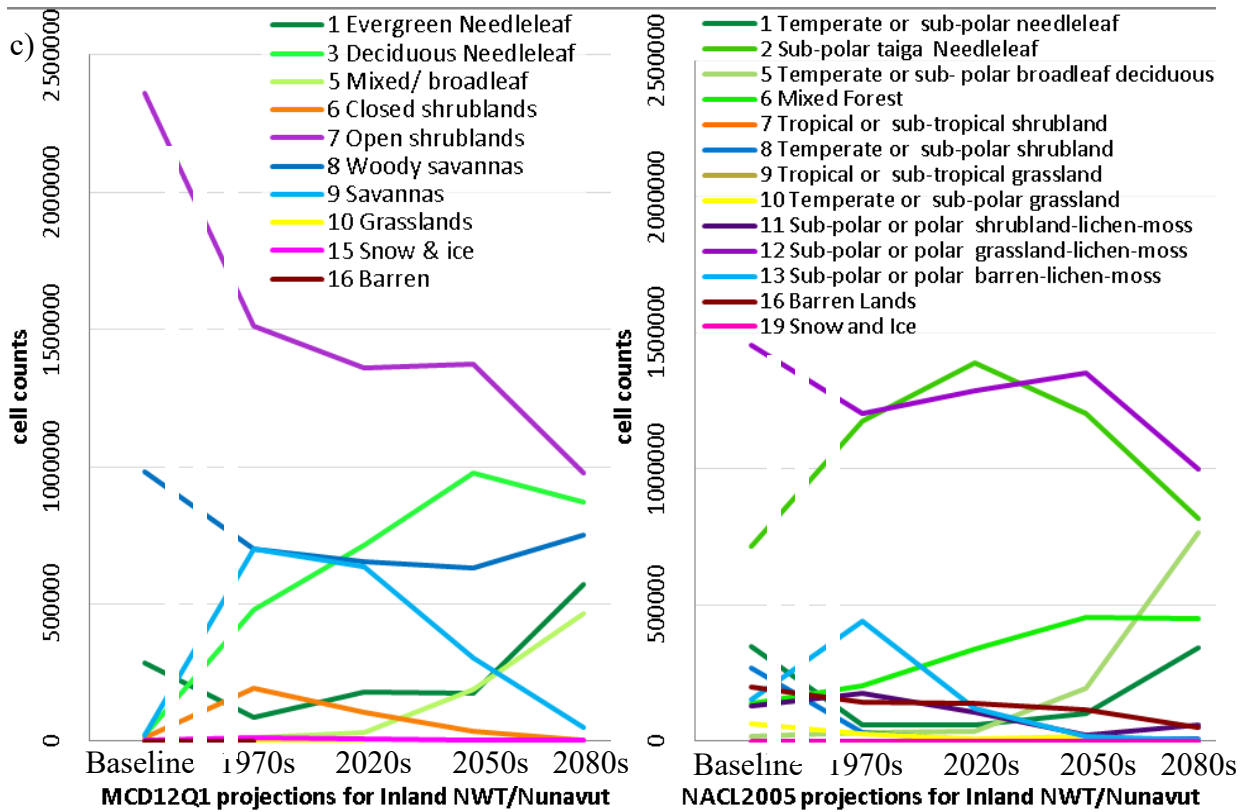


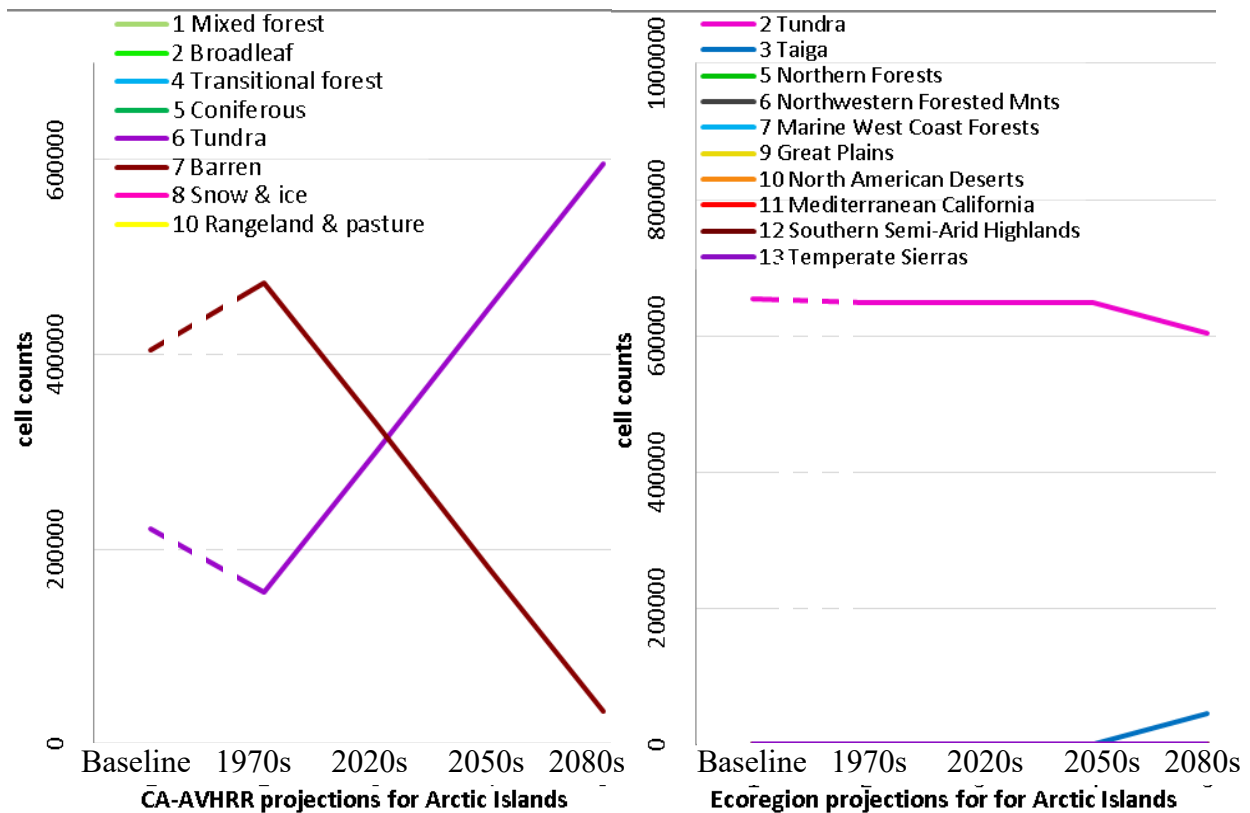
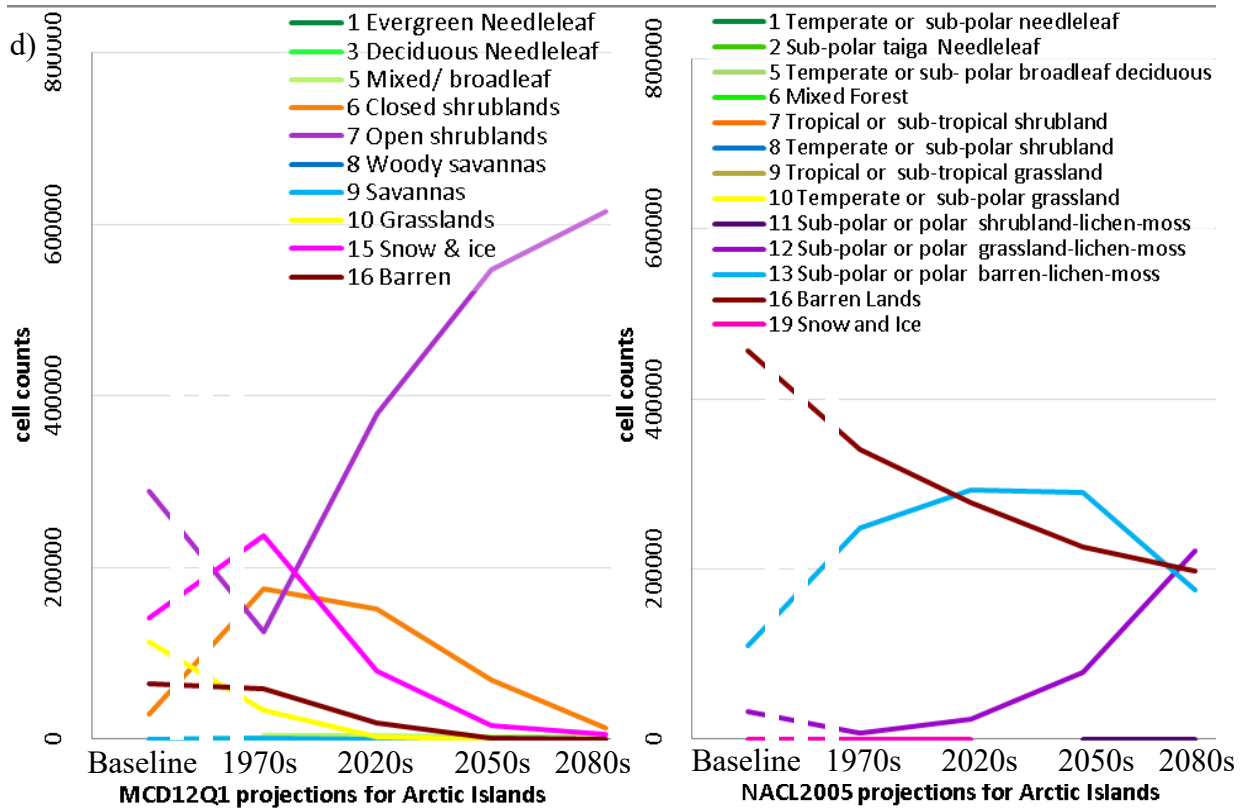


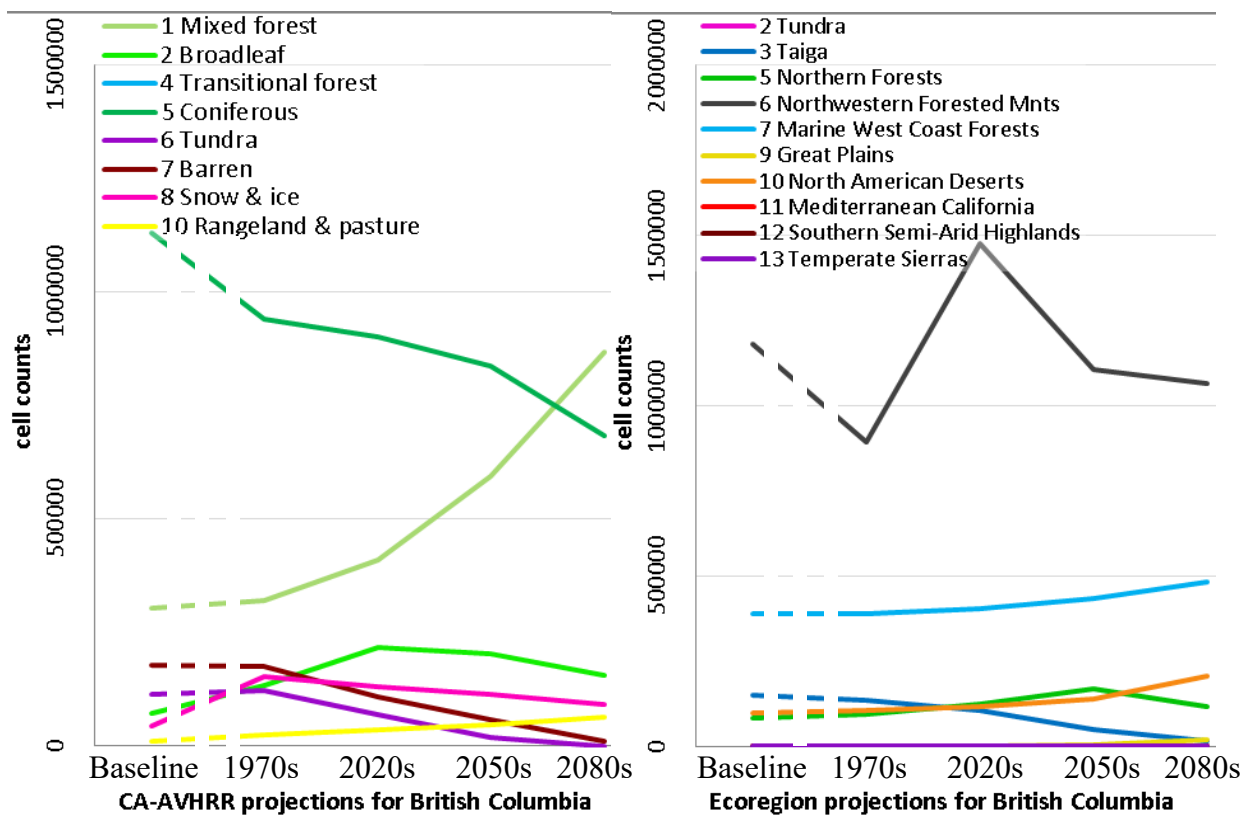
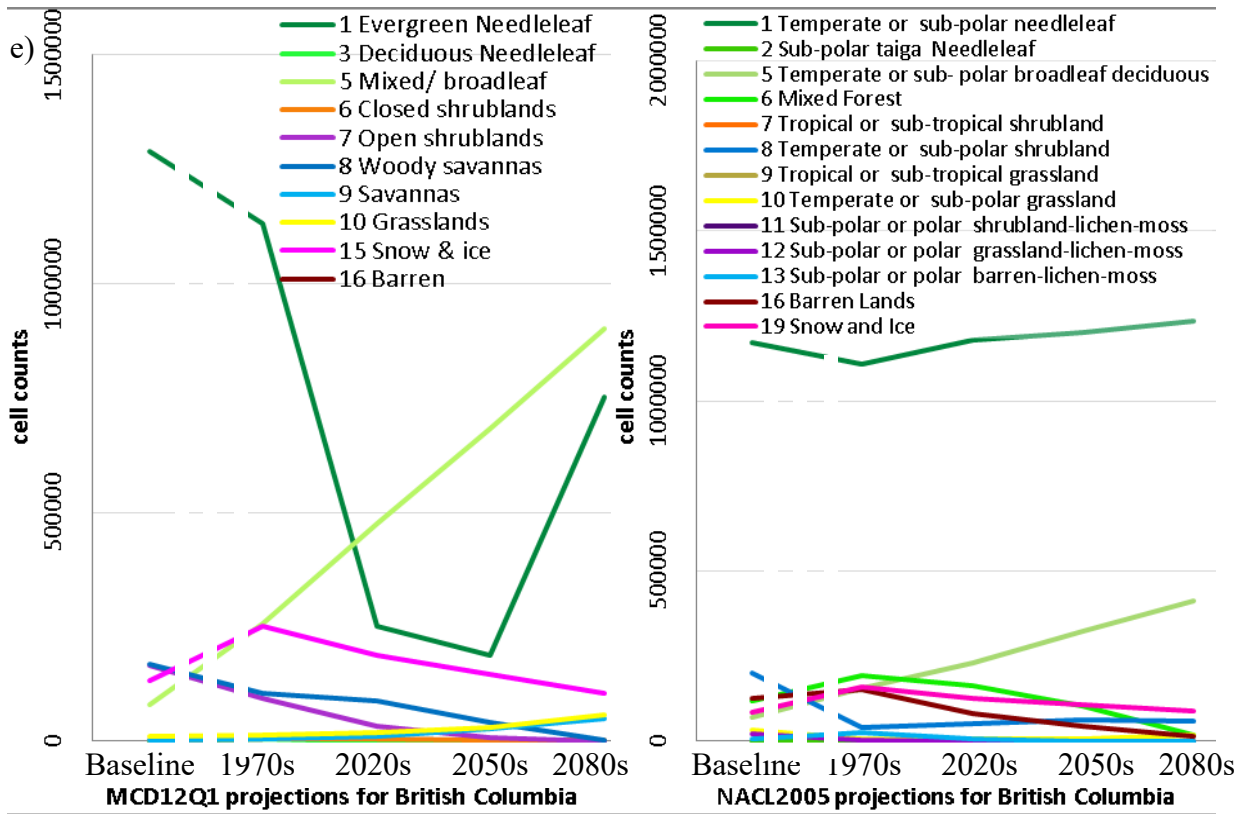
Appendix Figure 2.3. Projected changes in land cover and ecoregions. The number of cells RandomForest predicted overtime is given for each class, product & region: Alaska, Yukon, NWT/Nunavut, Arctic Islands, British Columbia, Alberta, Saskatchewan, & Lower US (a-h).

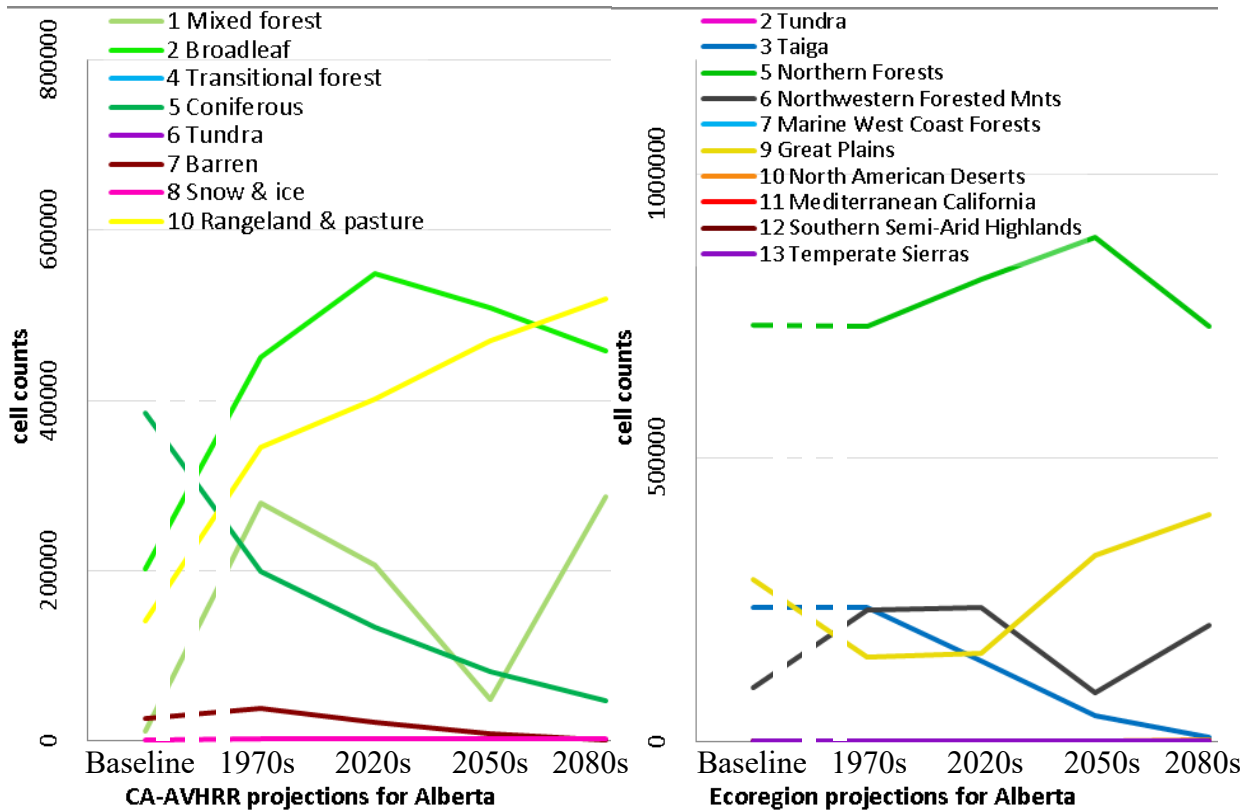
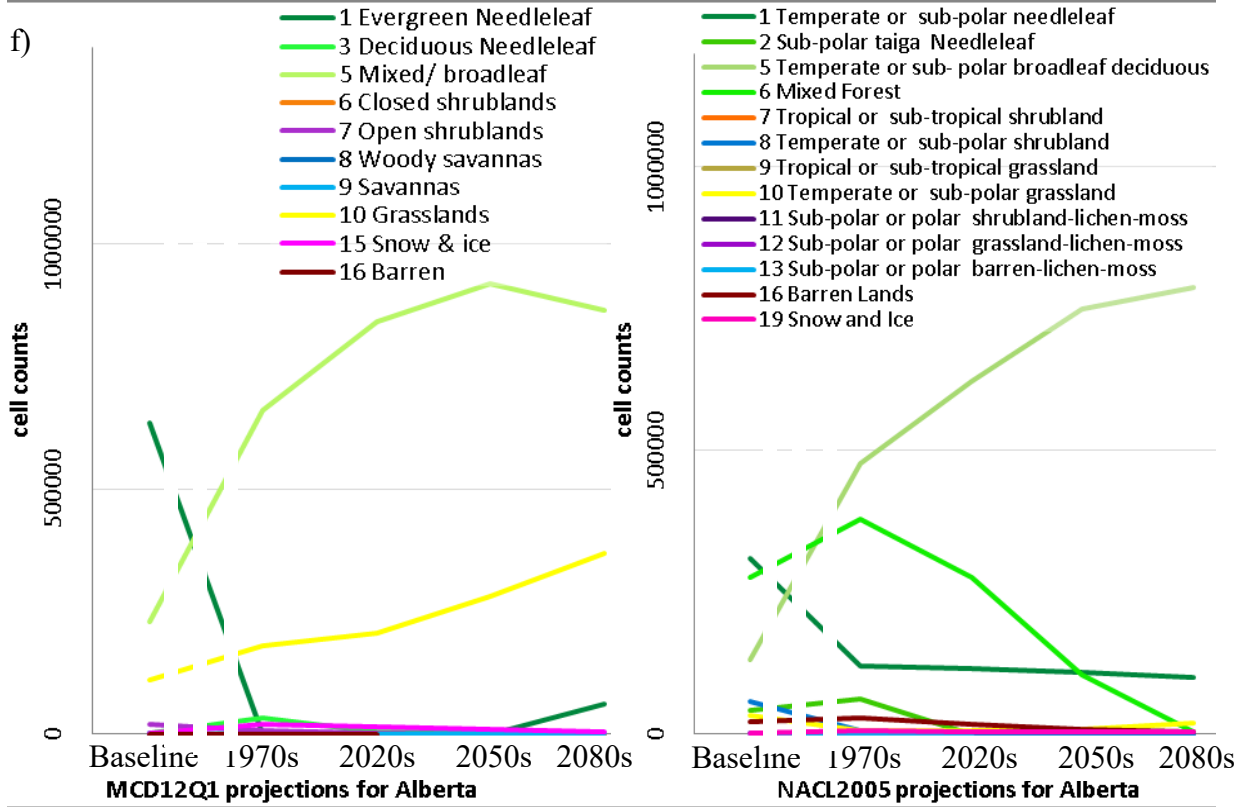


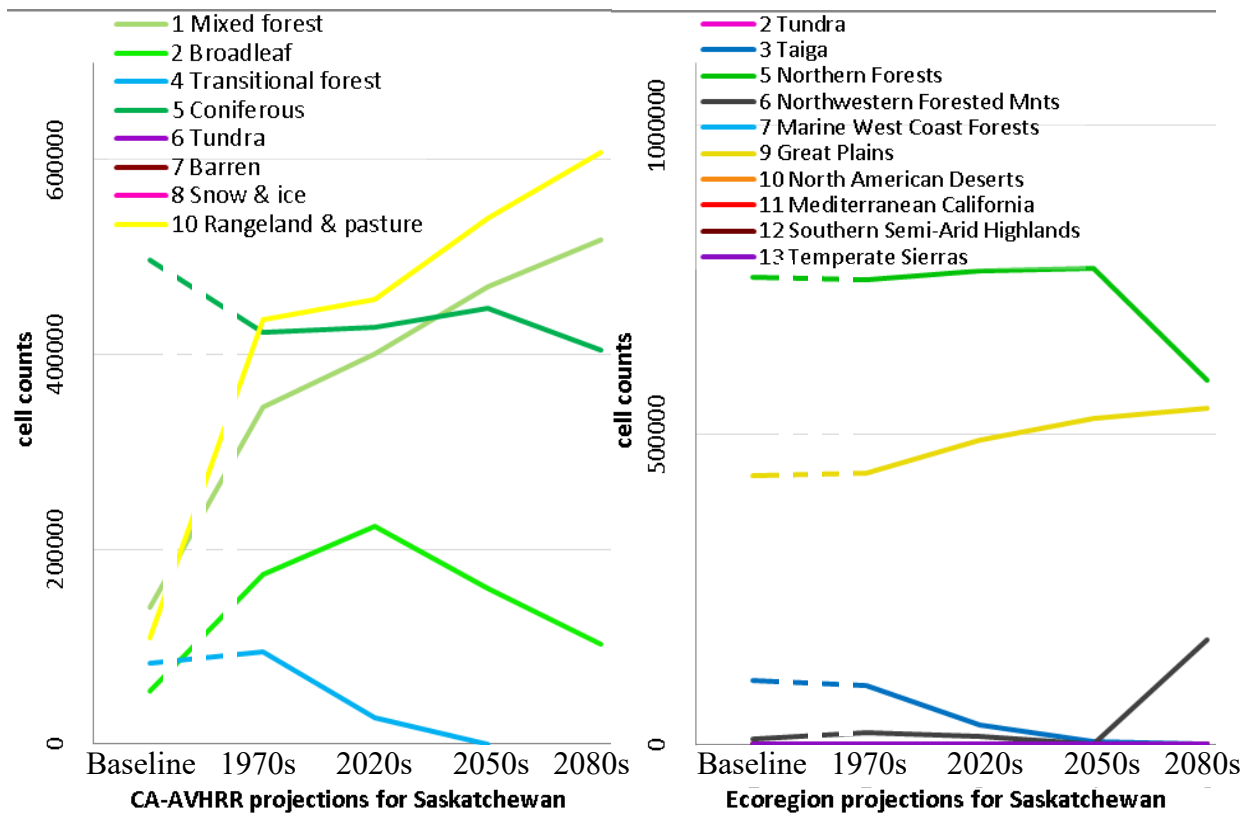
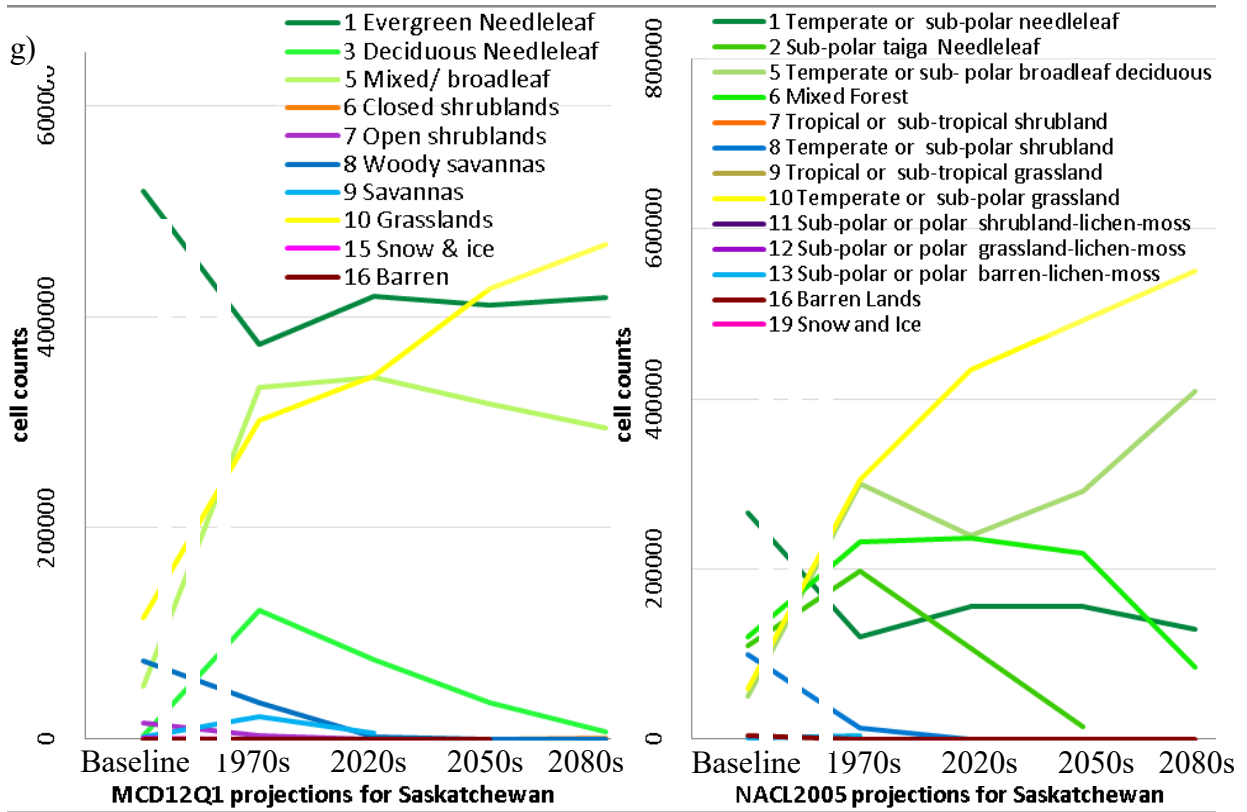


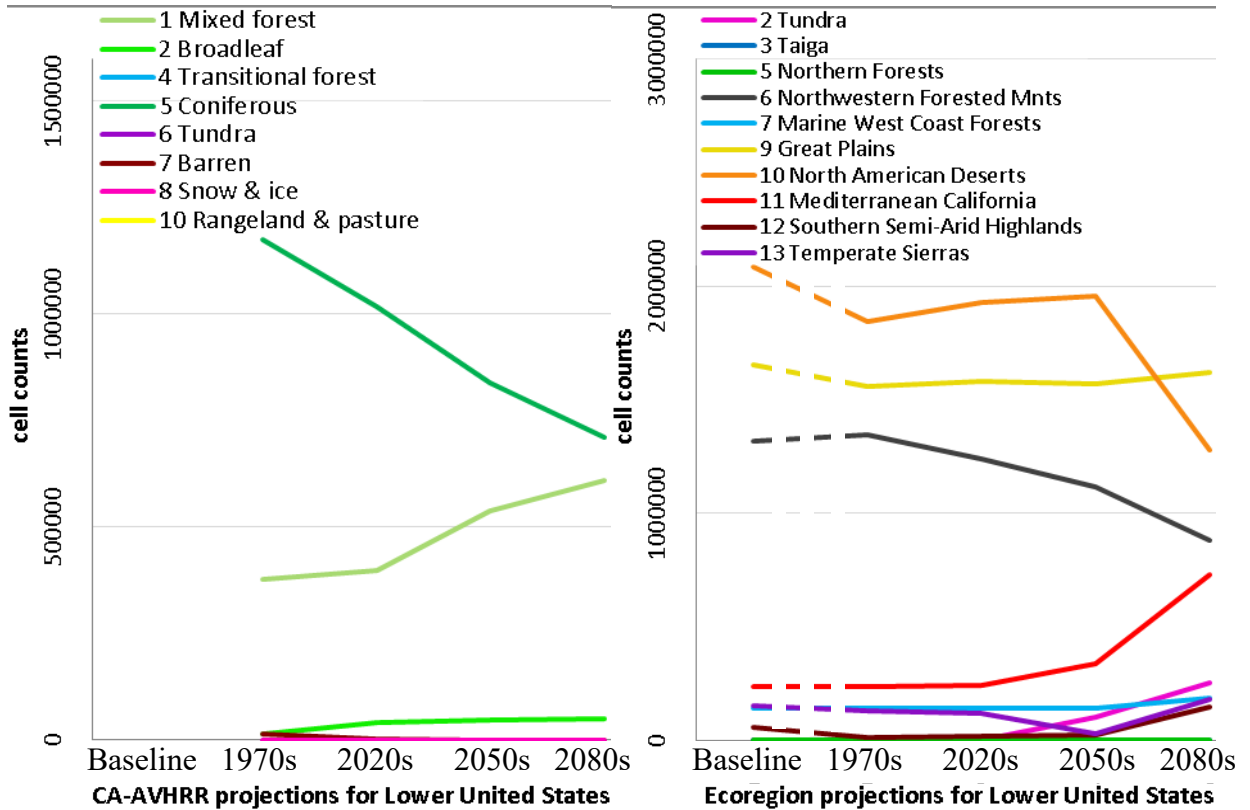
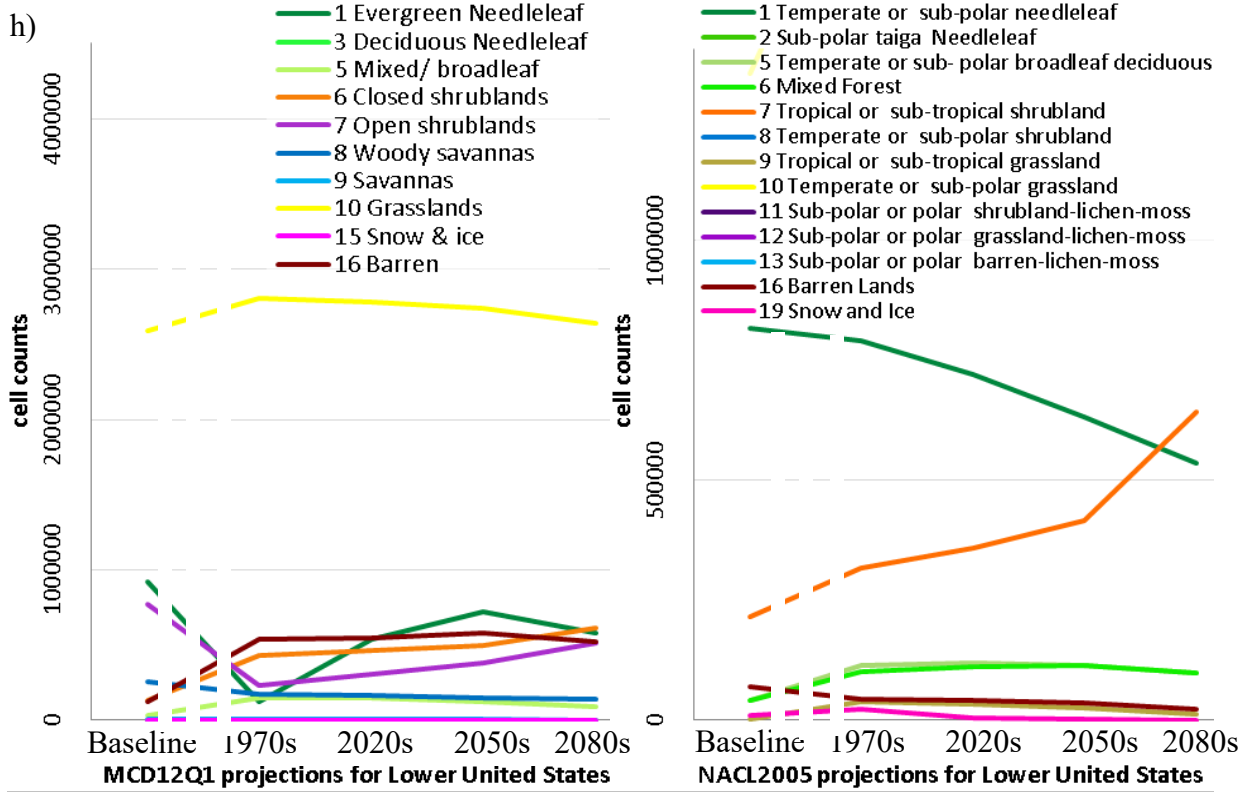












Appendix Table 3.1. Linear disturbances data source

Sources	File
Environnement Yukon	surfacedisturbance_linear
UofA_AltaLIS Ltd	BF CUT TRAIL ARC BF PIPELINE ARC BF POWERLINE ARC BF RAILWAY ARC BF ROAD ARC
Wildlife Conservation Society Canada	CCH range linear FT may2012
data.gov.bc.ca	WHSE_basemapping_DRA_DGTL_road_atlas_MPAR_SP WHSE_forest_tenure.FTEN_road_segment_lines_SVW WHSE_imagery_&_base_maps_mot_road_features_inventory WHSE_mineral_tenure_og_petrlm_dev_Rds_PRE06_pub_SP WHSE_mineral_tenure_OG_petrlm_dev_roads_PUB_SP WHSE_mineral_tenure_OG_petrlm_access_roads_PUB_SP
emr.gov.yk.ca	Seismic Lines
open.canada.ca	canvec11_gdb_CA_BS_2230009_1 canvec11_gdb_CA_EN_1120009_1 canvec11_gdb_CA_EN_1180009_1 canvec11_gdb_CA_LX_2420009_1 canvec11_gdb_CA_TR_1020009_1 canvec11_gdb_CA_TR_1760009_1 canvec11_gdb_CA_VE_2290009_1 secondary roads - 1mln & trails - 1mln
geomaticsyukon.ca	INVENTORY ROAD_40K ROAD LN 1M SVW TRANSPORTATION LN 50K & 250K
dnr.alaska.gov	FAA_Airports_and_Runways_In Pipelines_63360_In Telephone_Lines_63360_In Trails_63360_In Transportation - Power Lines - 63,360_LINE secondary Roads_63360_In,
mli2.gov.mb.ca	Muniroad
www.asgdc.state.ak.us	FS_FSTOPO_Transportation_L RS2477_Trails_In
www2.census.gov/geo/tiger/TIGERrd13	tl_rd13_geographic area_edges (railway not included for lower USstates)

Appendix Table 3.2. Linear disturbances Files and buffer per province

Region affected	File name	Buffer if there is
Pipelines		
Canada	canvec11_gdb_CA_EN_1180009_1	200m in AB
AB	BF PIPELINE ARC	
BC	Utility_LN_250K	
AK	Pipelines_63360_In	
Airfields		
YT	INVENTORY ROAD 40K	
AK	FAA Airports and Runways In	
AK	FS FSTOPO Transportation L	
Railways		
YT	CCH_range_linear_FT_may2012	20m
Canada	canvec11_gdb_CA_TR_1020009_1	200m in AB
AB	BF RAILWAY ARC	
AK	tl_rd13_geographic_area_edges	
AK	FS FSTOPO Transportation L	
Transmission lines		
YT	CCH_range_linear_FT_may2012	20m
Canada	canvec11_gdb_CA_BS_2230009_1	
Canada	canvec11_gdb_CA_EN_1120009_1	200m in AB
YT	INVENTORY ROAD 40K	
AB	BF POWERLINE ARC	
AK	Telephone Lines 63360 In	
AK	Transportation - Power Lines - 63,360 LINE	
All roads and trails		
AK	tl_rd13_geographic_area_edges	
AK	FS FSTOPO Transportation L	1.5km
AK	RS2477 Trails In	1.5km
YT	CCH_range_linear_FT_may2012	20m
YT	surface disturbance linear	
BC	WHSE basemapping DRA DGTL road atlas MPAR SP	100m
BC	WHSE forest tenure.FTEN road segment lines SVW	100m
BC	WHSE imagery & base maps mot road features inventory	100m
BC	WHSE mineral tenure og petrIm dev Rds PRE06 pub SP	100m
BC	WHSE mineral tenure OG petrIm dev roads PUB SP	100m
BC	WHSE mineral tenure OG petrIm access roads PUB SP	100m
Canada	canvec11_gdb_CA_TR_1760009_1	100m
AB	BF ROAD ARC & BF CUT TRAIL ARC	200m
YT	Seismic Lines	200m
Canada	canvec11_gdb_CA_LX_2420009_1	2kmYT
Canada	canvec11_gdb_CA_VE_2290009_1	200m
BC,YT,NT	transportation_LN_50K & 250K	500m,200m in YT
BC,AK,YT,NT	ROAD LN 1M SVW	2km,200m in YT
MB	Secondary muniroad	500m
YT	INVENTORY ROAD 40K	200m
Canada	CA SBM LINE COMPILE	2km,200m inYT,NT
Canada	secondary roads - 1mln & trails - 1mln	
AK	secondary Roads 63360 In & Trails 63360 In	

Appendix Table 3.3. For indication, Linear feature types as described by most sources (AEM 2004).

Feature Classification	Alternative Feature Type	Description	Feature Width (m)
Pipeline			10
Airfield			100
Railway		Railway tracks and associated right-of-way.	15
Transmission line		Cut line with associated above ground structures, i.e., power poles and power lines.	30
Primary Road	80% paved; 60% NT	Highways and associated right-of- ways.	60
Secondary Road	70% paved; 100% US; 50% Canada	All major high use paved and gravel roads and associated right-of-ways.	25
Rural Road	99% unpaved; 70% AK	All other roads (and associated right- of-ways), e.g., roads leading rural residences, agricultural parcels, grazing leases, mine sites / tailings, excavation sites and recreational areas.	10
Trail/ Cut Line		Trails for recreational use and lines cut for purposes of surveying, e.g., survey and possibly seismic lines.	2