University of Alberta

Assisted migration to address climate change: recommendations for reforestation in western Canada

by

Laura Kelsey Gray

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of

> Doctor of Philosophy in Forest Biology and Management

Department of Renewable Resources

© Laura Kelsey Gray Fall 2011 Edmonton, Alberta

Permission is hereby granted to the University of Alberta Libraries to reproduce single copies of this thesis and to lend or sell such copies for private, scholarly or scientific research purposes only. Where the thesis is converted to, or otherwise made available in digital form, the University of Alberta will advise potential users of the thesis of these terms.

The author reserves all other publication and other rights in association with the copyright in the thesis and, except as herein before provided, neither the thesis nor any substantial portion thereof may be printed or otherwise reproduced in any material form whatsoever without the author's prior written permission.

Examining Committee:

- Dr. Andreas Hamann, University of Alberta, Renewable Resources
- Dr. Erin Bayne, University of Alberta, Biological Sciences
- Dr. Scott Nielsen, University of Alberta, Renewable Resource
- Dr. Barbara Thomas, University of Alberta, Renewable Resources
- Dr. Derek MacKenzie, University of Alberta, Renewable Resources
- Dr. Barbara Hawkins, University of Victoria, Centre for Forest Biology

Abstract

A changing climate is the largest threat to forest productivity in western Canada and to the ability of forested landscapes to provide ecological and economic services, both now and in the future. As climate changes, locally adapted tree populations become mismatched with local conditions, leading to mal-adaptation that may result in a reduction in forest health and productivity. This problem can be reduced with interventions that match reforestation stock to anticipated future environments. As such, there is a pressing need to inform such actions by carefully developing and contextualizing scientific information and by applying it to provincial reforestation policies.

Assisted migration is a climate change adaptation strategy used in the forestry sector, where species and seed sources are moved to new locations. The goal of this thesis is to develop a methodological framework to guide assisted migration efforts for forest trees in western Canada, under a comprehensive range of future climate projections. To assist with these management needs I create a new ecosystem-based climate envelope modeling approach for 16 commercially important tree species. Habitat projections show populations already geographically lag behind their optimal climate and the magnitude of this lag is projected to double for the 2020s. The most pronounced habitat shifts are projected to occur in the boreal forests and the Rocky Mountains, predominately affecting black spruce, tamarack, white spruce and aspen populations.

In a case study for Alberta, I find that genotypes of species that are adapted to drier climatic conditions will be the preferred planting stock over much of the commercially managed boreal forest. Interestingly, no alternate non-native species to Alberta that were examined in this study can be recommended with any confidence as planting stock. Finally, I observe high uncertainty in projections of suitable habitat for most species making reforestation planning beyond the 2050s difficult. Using genetic and remote sensing data for aspen populations, I show that habitat projections from climate envelope models under observed climate change conform well to empirical data on loss of aspen productivity and genetic data on sub-optimal growth due to mal-adaptation.

Acknowledgements

The completion of this research would not have been possible without many sources of support, which I am very thankful for.

I am grateful to Alberta-Pacific Forest Industries, Alberta Forest Research Institute, Ainsworth Engineered Canada LP, Canadian Counsel on Ecological Areas, Daishowa-Marubeni International Ltd., Western Boreal Aspen Corporation, and Weyerhaeuser Company Ltd. for their financial and in-kind support.

My largest thank you is to my supervisor, Andreas Hamann. I can adamantly say there has been no bigger influence in my academic life than Andreas. He is a true mentor, both for his guidance in my research (although his "suggestions" sometimes met resistance) as well as his enthusiastic encouragement to share my research with the scientific community. Andreas, I cannot thank you enough for giving me the opportunity to explore tangents in my research. Even though I complained about wasting time, every time you reeled me back in you taught me to refine my process, as well as embrace a more flexible outlook. I feel very lucky to have had you guide me through this journey and I am looking forward to hopefully many collaborations with you in the future.

I would also like to thank the members of my advisory committee, Dr. Barbara Thomas, Dr. Scott Nielsen and Dr. Erin Bayne for all of their insightful suggestions, which have helped guide this research. I feel very fortunate to be a member of the Hamann research lab. It's cliché, but we really are like a mini family. No matter where my career path takes me, I know that I have a long list of diverse colleagues that I can call upon for their expertise. I want to especially thank Tim Gylander, Michael Mbogga, and Pie-Yu Chen for their contributions to the 3rd research chapter of this thesis. Additionally I would like to thank Xianli Wang and David Roberts for their help completing model runs, trouble shooting, and providing technical advice.

For help with data collection, preparation and preliminary analyses, thank you to Jean Brouard, Leonard Bernhardt, Alvin Yanchuk and Evan Miller-Tait.

Last I would like to thank my family and friends whose never-ending support and encouragement has always pushed me to succeed. To my parents, my sister Katie, my uncle Ross, and the rest of my extended family, thank you for listening and providing advice when I was feeling overwhelmed. Your confidence in me is humbling. To all the friends I have made over the duration of my time here, thank you for being a part of this journey with me. Comradery is a powerful tool in graduate school, and I would not have finished this degree without many of you. To Jason and my dear friends back home on the west coast, thank you for being my patient cheerleaders. Your belief in me means more than you could ever know.

Thank you all!!! I would not have made it through this process without you.

Table of Contents

Chapter 1. Introduction and literature review	1
1.1. Observed climate trends and future climate projections	1
1.2. Observed biological impacts of climate change in forest ecosystems	3
1.3. An assisted migration adaptation strategy for climate change	5
1.4. Concepts of bioclimatic envelope modeling	7
1.5. Assumptions and limitations of climate envelope models	9
1.5.1. Issues arising from collinearity of predictor variables	9
1.5.2. Effects of including or excluding topo-edaphic predictor variable	s. 11
1.5.3. Biotic interactions: accounted for, or not?	12
1.5.4. Local genetic adaptation of populations	15
1.5.5. Equilibrium assumptions	16
1.5.6. Niche conservatism at the species level	17
1.5.7. How to best interpret bioclimate envelope model results	18
1.6. Thesis Outline	19
1.6.1. First research chapter	19
1.6.2. Second research chapter	20
1.6.3. Third research chapter	21
1.7. Literature Cited	22

Chapter 2. Tracking suitable habitat for tree populations under climate

change in western North America	. 32
Summary	. 32
2.1. Introduction	. 33

2.2. Materials and methods	35
2.2.1. Climate envelope modeling	36
2.2.2. Baseline climate data and future projections	36
2.2.3. Tree species inventory data	38
2.2.4. Model evaluation	39
2.3. Results	39
2.3.1. Variable importance and model accuracy	39
2.3.2. Habitat projections and uncertainty	40
2.3.3. Elevation versus latitudinal shifts	42
2.3.4. Tracking habitat of populations	43
2.4. Discussion	44
2.4.1. Characteristics of the ecosystem-based modeling approach	44
2.4.2. Adaptational lag implies a need for assisted migration	45
2.4.3. Uncertainty requires short-term adaptation strategies	47
2.5. Literature Cited	49

Chapter 3. Strategies for reforestation under uncertain future climates:

guidelines for Alberta, Canada	61
Summary	61
3.1. Introduction	62
3.2. Materials and methods	64
3.2.1. Climate envelope modeling	64
3.2.2. Climate data and climate projections	65
3.2.3. Species projections and model validation	66
3.2.4. Seed source recommendations	68
3.3. Results	69

3.3.1. Alberta climatology and climate change projections	69
3.3.2. Projections of tree species habitat	70
3.3.3. Projections of appropriate seed sources	72
3.4. Discussion	73
3.4.1. Species choice for reforestation	73
3.4.2. Choice of genotypes for reforestation	74
3.5. Literature Cited	76

Chapter 4. Assisted migration to address climate change: recommendations

for aspen reforestation in western Canada	103
Summary	103
4.1. Introduction	104
4.2. Materials and methods	106
4.2.1. Reciprocal transplant experiments	106
4.2.2. Remote sensing	107
4.2.3. Climate trends and projections	109
4.2.4. Predictive habitat modeling	110
4.3. Results	112
4.3.1. Regional climatology and climate change	112
4.3.2. Genetic differentiation and adaptational lag	113
4.3.3. Drought impacts on aspen populations	114
4.3.4. Bioclimate envelope shifts	115
4.4. Discussion	116
4.4.1. Adaptational lag causes suboptimal growth	116
4.4.2. Indirect indicators of mal-adaptation	119
4.4.3. Climate envelope models should guide seed transfer	120

4.4.4. Recommendations for aspen	121
4.5. Conclusions	124
4.6. Literature Cited	124
Chapter 5. Synthesis and Conclusions	138
Appendix A. Gloassary of terms	155
	100
Annandix B. Projected babitat and uncertainty mans for western North	
America	155
Appendix B1 – Black spruce	156
Appendix B2 – Douglas-fir	160
Appendix B3 – Engelmann spruce	164
Appendix B4 – Lodgepole pine	168
Appendix B5 – Pacific silver fir	172
Appendix B6 – Ponderosa pine	176
Appendix B7 – Sitka spruce	180
Appendix B8 – Tamarack	184
Appendix B9 – Trembling aspen	188
Appendix B10 – Western hemlock	192
Appendix B11 – Western larch	196
Appendix B12 – Western redcedar	200
Appendix B13 – Western white pine	204
Appendix B14 – White spruce	208
Appendix B15 – Yellow cedar	212

List of Tables

Table 2-1. Importance of predictor climate variables in distinguishing ecosystemsof western North America with the RandomForest ensemble classifier
Table 2-2. Sampling and biogeographical information for species, as well as statistics that describe the predictive accuracy of the species distribution model for 15 major forest tree species in western North America
Table 2-3. The geographic regions that were use to summarize shifts in suitable habitat are defined by four ecological classification systems. The table lists the "zone" name for BC (Meidinger and Pojar 1991), the "natural subregion" name for AB (NRC 2006), the "ecoregion" name for SK and MB (Selby and Santry 1996), or the "level III natural region" name for the US (EPA 2007)
Table 2-4. Northward and elevation shift of suitable habitat for populations relative to the 1961-1990 reference projection, averaged over 18 climate change scenarios. I report elevation change for a constant latitude, and latitudinal change for a constant elevation. For seed transfer these values represent maximum limits for a latitudinal <i>or</i> elevation transfer
Table 3-1. Species statistics and model accuracy 80
Table 3-2. Suitable habitat for white spruce expressed as % area of seed zone for observed climate, and expressed as probability of habitat maintenance under climate change projections from 18 general circulation models
Table 3-3. Suitable habitat for ponderosa pine expressed as % area of seed zone for observed climate, and expressed as probability of habitat maintenance under climate change projections from 18 general circulation models
Table 3-4. Suitable habitat for black spruce expressed as % area of seed zone for observed climate, and expressed as probability of habitat maintenance under climate change projections from 18 general circulation models
Table 3-5. Suitable habitat for Douglas-fir expressed as % area of seed zone for observed climate, and expressed as probability of habitat maintenance under climate change projections from 18 general circulation models
Table 3-6. Suitable habitat for lodgepole pine expressed as % area of seed zone for observed climate, and expressed as probability of habitat maintenance under climate change projections from 18 general circulation models
Table 3-7. Suitable habitat for jack pine expressed as % area of seed zone for observed climate, and expressed as probability of habitat maintenance under climate change projections from 18 general circulation models

Table 3-8. Table of best matching seed sources for 1961-1990 climate. Themultivariate Mahalanobis climate distance is given in parenthesis.90
Table 3-9. Table of best matching seed sources for 1997-2006 climate. Themultivariate Mahalanobis climate distance is given in parenthesis.91
Table 3-10. Table of best matching seed sources for 2020s climate. Themultivariate Mahalanobis climate distance is given in parenthesis.92
Table 3-11. Table of best matching seed sources for 2050s climate. Themultivariate Mahalanobis climate distance is given in parenthesis
Table 3-12. Table of best matching seed sources for 2080s climate. Themultivariate Mahalanobis climate distance is given in parenthesis
Table 3-13. Locations of recommended seed choices which originate outside of Alberta. For British Columbia I report the relevant ecological zones (Meidinger and Pojar 1991), and for the United States I report the corresponding state and "level III" ecoregion (EPA 2007)
Table 4-1. Regional climatology based on 1961 to 1990 normal data for fine ecological regions with observed climate change over the last 25 years in parenthesis. Observed change is calculated as the difference between the 1961–1990 reference period and a recent decadal average 1997–2006
Table 4-2. Range of 18 regional climate change projections from five general circulation models (CGCM2, HADCM3, ECHAM4, CSIRO2 and PCM) implementing four SRES emission scenarios (A1FI, A2, B1, B2) for climate variables in four ecological regions over projected future climate. Projected changes are expressed relative to the 1961–1990 reference period
Table 4-3. Probability to match or exceed the performance of local provenances.The lower left table section represents a southward transfer, and the upper rightsection a northward transfer.132
Table 4-4. Seed transfer recommendations for Alberta's seed management unitsof the natural region and subregion system.133

List of Figures

Figure 2-1. Projections of Douglas-fir habitat for the 1961–1990 reference period and under climate scenarios for the 2020s, 2050s and 2080s. The rows of maps show projections of individual populations, average expected frequency based on multiple climate change scenarios, and degree of consensus among projections Figure 2-2. Plot of the projected northward shift verses the shift in mean elevation for all species-region combinations presented in Table 4. A linear regression according to the formula δ Elevation = δ Latitude \times 0.44 describes the Figure 3 -1. Climate of seed zones in Alberta, which are based on a hierarchical ecological classification system. Colors represent Natural Subregions, and points in the scatterplot represent the finest units of forested ecosystems that govern seed transfer in reforestation. The delineations corresponding to the scatterplot are shown on the map. The expected shift of a mean climate point for Alberta (1961-1990) representing the range of 18 climate change scenarios is indicated by Figure 3-2. Seed zones projections and consensus of habitat maintenance under projected climate change for white spruce in Alberta. Colors represent broad seed sources corresponding to Natural Subregions (upper row), and the gray scale represents the consensus that habitat is maintained for white spruce under 18 climate change scenarios for the 2020s, 2050s, 2080s (lower row). Here, I require at least a 70% probability that habitat is maintained to make a seed source

Figure 3-3. Suitable habitat under projected under climate change for ponderosa pine in Alberta. There is very large uncertainty whether this species may become a viable forestry species in Alberta, with extensive areas of suitable habitat projected under some climate change scenarios, and virtually no habitat under other climate change projections. 98

Figure 3-5. Seed zones projections and consensus of habitat maintenance under projected climate change for Douglas-fir in Alberta. Colors represent broad seed sources corresponding to Natural Subregions (upper row), and the gray scale represents the consensus that habitat is maintained for white spruce under 18

Chapter 1. Introduction and literature review

1.1. Observed climate trends and future climate projections

The Intergovernmental Panel on Climate Change reports in their fourth assessment (IPCC 2007) that in the last century the average global surface temperature has increased approximately +0.7°C. Observed warming trends appear to follow a latitudinal gradient, where observed temperature increases are smallest in the tropics (\sim +0.4°C), followed by middle latitudes (\sim +0.6°C), and finally northern latitudes where temperature increases are almost twice the global average (~+1.3°C) (Hansen et al. 2001; Brohan et al. 2006). In the last 50 years the global warming rate has dramatically accelerated with an average increase of approximately +0.13°C per decade, nearly twice the rate of the previous 100 years (IPCC 2007). At northern latitudes, the warming rate has surpassed global averages since the mid 1980s (Hansen et al. 2001; Smith and Reynolds 2005; Brohan et al. 2006). In western Canada, Mbogga et al. (2009) compared climate averages observed between 1961–1990 and 1997–2006 and found mean annual temperature on average increase $+0.8^{\circ}$ C during the 25-year period (approximately 1975 to 2000), with the most pronounce warming occurring in southern British Columbia and the Canadian Prairies (~+2°C). These values mimic national temperature trends studied by Zhang et al. (2000) over the 20th century. Western Canada's mean annual temperature increase is predominantly driven by a higher frequency of warm winter days (Mbogga et al. 2009); however an increase in the rate of summer warming, accelerating from +0.15°C in 1961-1990 to +0.3°C between 1990 and 2005, has also contributed to the observed temperature trends (Chapin et al. 2005).

Precipitation changes over the 20th century have been both spatially and temporally variable. Globally, the frequency of heavy precipitation events has increased most over land, consistent with warming trends and observed increases in atmospheric water vapor (IPCC 2007). In North America over the last century, the mean annual precipitation has increased at mid and high latitudes (Mbogga et al. 2009); however significant decreases have been observed in Mexico and other areas closer to the equator (Dai et al. 1997). These observations correspond to a global decrease in precipitation from the mid 20th century to approximately the 1990s (Trenberth et al. 2007). More intense and longer droughts have also been observed over wider areas since the 1970s. These events are characteristic of the tropics and sub topics (IPCC 2007), but have also occurred at northern latitudes (Allen et al. 2010). Mbogga *et al.* (2009) also found that mean growing season precipitation varied across western Canada. Precipitation between May and September increased by approximately 12% along the northern coast of British Columbia while it also decreased by the same magnitude in the Prairies.

Future climate projections indicate global temperature will likely increase between +0.3°C and +6.4°C by 2090-2099 relative to 1980-1990 values (IPCC 2007). This results in a +0.2°C increase per decade with Canadian forested ecosystems (northern sub-boreal, boreal, and arctic) expected to experience the strongest warming (Zhou et al. 2001). By the end of the 21st century, precipitation increases are expected at high latitudes, while decreases of as much as 20% are projected for most sub-tropic land regions (IPCC 2007). For Canada, projections vary between 20% increase and a 15% decrease in precipitation.

1.2. Observed biological impacts of climate change in forest ecosystems

In North America, there are numerous examples of recent environment-related impacts on tree species and ecosystem that indicate forests are highly sensitive to climate change. On the positive side, there can be benefits associated with the observed warming trend. First, an increase in the number of warm winter days as well as warmer spring and fall temperatures, can lead to longer growing seasons and increased productivity (Bonsal et al. 2001). Beaubien and Freeland (2000) extracted first-bloom dates for aspen in Edmonton, Alberta from historical data and found a linear trend showing a 26-day shift to earlier blooming over the last century. This pattern correlates with the incidence of El Nino events related to Pacific sea-surface temperatures. Similar shifts towards earlier spring bud break of approximately 1 to 3 days per decade have been shown for woody plants in the United States (Wolfe et al. 2005). Second, warmer conditions have also permitted treeline expansion at northern latitudes and higher altitudes (Sturm et al. 2001; Gamache and Payette 2005; Tape et al. 2006).

While warming trends can benefit forest ecosystems, impacts also include significant ecological and economic losses. First, an increase in the intensity and frequency of major fires have been widely documented in Canada (e.g. Gillett et al. 2004) and the United States (e.g. Flannigan et al. 2000; Dale et al. 2001) following closely to the observed warming trends. Second, warming temperatures and higher precipitation has permitted many forest pests and diseases to expand their ranges. Outbreaks of defoliation diseases, such as *Dothistroma* needle blight, and insect species, such as the spruce budworm (*Choristoneura fumiferana* Clem.) and the forest tent caterpillar (*Malacosoma disstria*), have caused sizeable stand volume losses in forest ecosystems in Canada and the southwestern United States (Fleming and Volney 1995; Swetnam and Betancourt 1998; Hogg et al.

2002; Woods et al. 2005; Welsh et al. 2009). Currently in Canada's boreal zone, pest-caused timber losses may be as much as 1.3–2.0 times the average annual loss from forest fires (Volney and Fleming 2000). Given that the processes that lead to stand-replacing outbreaks of many pest species depend on climate, changes in environmental conditions could lead to more substantial timber losses. For example, increased winter temperatures have contributed to an epidemic outbreak of the Mountain Pine Beetle (Dendroctonus ponderosae) that has devastated pine forests in central British Columbia, Alaska and the western United States (Logan and Powell 2001; Berg et al. 2006; Stahl et al. 2006; Raffa et al. 2008). Third, drought-induced mortality has been widely reported for numerous taxa (see Adams et al. 2009; Allen 2009; van Mantgem et al. 2009). For example, McDowell et al. (2010) found that chronic water stress predisposed lowelevation ponderosa pine (*Pinus ponderosa*) to mortality during drought via constrained gas exchange. Aspen (Populus tremuloides) dieback has also been well documented along the southern edge of the Canadian boreal forest and the western United States (Hogg et al. 2002; Hogg et al. 2008; Allen et al. 2010). Along the southern range of aspen in Alberta and Saskatchewan these loses are substantial, estimated at 45Mt, or 20% of the total aboveground aspen biomass (Michaelian et al. 2010).

Given the observed biological impacts associated with warming temperatures and changes to precipitation, natural resource management will be increasingly challenging under climate change projections of the 21st century. Forest management strategies will need to focus on reducing the vulnerability of forest trees to climate change while also taking advantage of potential benefits. For example, forest managers could reduce the risk of drought-related mortality, while also harnessing the benefits of warmer temperatures and higher precipitation through potentially faster growth rates and increased productivity of selected

species (Zhang et al. 2000; Zhou et al. 2001; Spittlehouse 2005; Lawler 2009). In many cases, the vulnerability of forest trees to climate change reflects maladaptation of locally adapted populations outside their optimal climate niches. Forest management objectives may therefore include assisted migration strategies that aim to match locally adapted populations with their optimal climatic environments under a wide range of future climate projections. Additionally, assisted migration strategies could be beneficial in cases when forest vulnerability is not related to a mismatch between species occurrence and their optimal habitat. Species and genotypes that are optimal for anticipated future climates and are better adapted to establish after a major fire event could be favorable planting stock for many areas if the increase intensity and frequency of major fires continues to follow observed warming trends (Flannigan et al. 2000; Dale et al. 2001; Gillett et al. 2004).

1.3. An assisted migration adaptation strategy for climate change

Assisted migration is a proactive strategy where species or their locally adapted populations are translocated from deficient environments to locations more favorable to their long-term productivity and survival. It is important to differentiate between the movement of species outside their range for conservation purposes (generally referred to as *assisted colonization*), and population movement within or just beyond the leading edge of a species range (generally refer to as *assisted migration*). Although there are some exceptions, this choice of terminology broadly conforms to usage in conversation biology (e.g. Hunter 2007; Hoegh-Guldberg et al. 2008; Ricciardi and Simberloff 2009) and forest resource management (e.g. Millar et al. 2007; O'Neill et al. 2008; McKenney et al. 2009), respectively.

Concern over data limitations and unforeseen consequences associated with the mass translocation of species' populations has caused debate over the validity of using assisted migration to alleviate climate-stress on species (see McLachlan et al. 2007; Marris 2009 for details). Well-established forest resource management principles and legislation that restricts the movement of seed sources in reforestation programs also conflict with assisted migration objectives (e.g. Morgenstern 1996; Ying and Yanchuk 2006; McKenney et al. 2009). However, given current forestry practices, assisted migration of common species is a potential climate change adaptation strategy with a good chance of successful implementation since the movement of species' populations is already a wellestablished management practice. Every year millions of hectares of forest are harvested and reforested, often with planting stock that does not originate at the planting site. Choosing alternate planting stock, suitable for anticipated future climates, could offer a potent climate change adaptation strategy at virtually no additional cost. Additionally, most common tree species have a high degree of within population genetic variation in addition to substantial environmental plasticity (Hamrick 2004). Therefore there will be a small range around the optimal climate conditions of a planting stock that will still be appropriate habitat, likely preventing serious unforeseen consequences associated with assisted migration.

In recognizing the promise and potential benefits of implementing assisted migration strategies, the common questions among managers implementing reforestation practices are "Which tree species are the safest choice for reforestation in my area?" or "Where can I plant 'species X' so that it will perform reasonably well under expected future environments?" Despite general research efforts, usable answers to these questions do not exist for any jurisdiction

in Canada at present. My thesis addresses this knowledge gap by delivering a methodological framework for assisted migration and reforestation programs in Alberta. Since I rely on predictive habitat modeling for much of the recommendations (also known as species distribution models, climate envelope models or ecological niche models, (see Guisan and Zimmermann 2000), I will review their inherent advantages and limitations in the following sections.

1.4. Concepts of bioclimatic envelope modeling

Bioclimate envelope models fall within the class of species-specific models that rely on the establishment of statistical or theoretical relationships between environmental predictors (i.e. climate variables) and observed species distributions. The foundations of bioclimate envelope models are deeply rooted in Hutchinson's (1957) fundamental and realized niche concepts. Under Hutchinson's framework, bioclimate envelope models provide a spatial representation of a species realized niche (Austin et al. 1990; Guisan and Zimmermann 2000; Pearson and Dawson 2003) given that they estimate speciesclimate relationships by correlating climatic predictor variables with observed species distributions, which are constrained by non-climate factors (Araujo and Pearson 2005). Statistical and machine-learning techniques are then used to project the modeled niche into novel environmental conditions. By classifying novel environments as within or outside the modeled niche space, bioclimate envelope models are able to predict where suitable species habitat might occur (Guisan and Zimmermann 2000).

The main advantage of bioclimatic envelope models is their relative simplicity. Unlike process-based models, this approach does not require detailed physiological data about individual species (Morin and Thuiller 2009), thus the models can undertake a relatively rapid analysis of numerous species (Iverson and Prasad 1998, 2001, 2002), even when range-limiting physiological factors for individual species are poorly known. This also enables conclusions regarding the potential impacts of climate change on habitat assemblages to be made (Crumpacker et al. 2001; Botkin et al. 2007).

Bioclimate envelope models have been widely used in many applications to predict the potential impacts of climate change. This includes determining the threat of potential species declines (e.g. Thomas et al. 2004; Thuiller et al. 2005a), determining the potential impact of novel climates on ecosystem biodiversity (e.g. Botkin et al. 2007), investigating the adequacy of established reserves to maintain species habitat (e.g. Araujo and Williams 2000; Araujo et al. 2004; Hannah et al. 2007), assessing the potential for invasive species to thrive (e.g. Peterson 2003; Thuiller et al. 2005b) and selecting sites for novel establishment of populations using assisted migration (e.g. Willis et al. 2009; Vitt et al. 2010). However, failing to acknowledge the underlying model assumptions and limitations can result in incorrect inferences and applications. Bioclimate envelope models may have poor spatial and temporal transferability because they inherently make biologically inaccurate assumptions, suffer from collinearity among predictor variables, and ignore key biological and evolutionary processes that contribute to species occurrence (see Hampe 2004; Dormann 2007; Jeschke and Strayer 2008 for details). In the following sections I will review these key limitations and discuss how they can cause problems when model projections are used in the application listed above. While all of the model limitations do not necessarily apply to the work in this thesis, I believe it is important that they are all acknowledged to build a comprehensive summary of this modeling approach. Most importantly, if the model assumptions and limitation are thoroughly understood, bioclimate envelope

models can become a more useful tool for building climate change adaptation strategies.

1.5. Assumptions and limitations of climate envelope models

It is assumed that if a bioclimatic envelope can accurately define a species' distribution under the current climate space, then it is able to capture the underlying species-climate relationship and can be used to predict the species' future distribution (Iverson and Prasad 1998; Lawler et al. 2006). However model accuracy under current climate conditions does not necessarily guarantee accuracy under future climates (Araujo et al. 2005). In these cases, erroneous prediction could be attributed to biological (e.g. biotic interactions) or evolutionary processes (e.g. adaptation or niche conservatism), species characteristics (e.g. migration capacity), such that climate is not the actual mechanism limiting a species distribution. As such the model predicting into non-analog climates can result in errorous conclusions.

1.5.1. Issues arising from collinearity of predictor variables

As for all modeling methods, collinearity among predictor variables can lead to errors in model projections. When determining the adequacy of protected areas (e.g. Araujo et al. 2004), or selecting sites for novel population establishment for conservation purposes (e.g. Araujo and Williams 2000; Willis et al. 2009), habitat projections should be based on the environmental characteristics which drive species occurrence and provide a good measure of environmental suitability. However for most species, knowledge of the environmental variables that are important to species persistence are largely unknown (Araujo and Pearson 2005). Multi-collinearity may cause ecologically important variables to be excluded from the models if other correlated variables explain the variation in species habitat equally well (Mac Nally 2000; Heikkinen et al. 2006). Since correlation does not imply causation, two possible scenarios can occur when implementing bioclimate envelope models with highly correlated variables. First, a model may select and make predictions using the predictor variable which best explains species occurrence. In this case inferences made from model projections would likely be accurate. However in the second case, a model may be parameterized with an ecologically unimportant variable which is highly correlated to a key environmental attribute. This may result in an over- or underestimation of habitat suitability in model projections (depending on how the key variable versus the correlated variable are predicted to change).

Many statistical techniques have been used in bioclimate envelope modeling (see Guisan and Zimmermann 2000; Heikkinen et al. 2006; Austin 2007 for details). Comparative studies show there is an inconsistency in prediction accuracy among techniques (for review see Jeschke and Strayer 2008). For many statistical techniques, such as generalized additive models or logistic regression, multicollinearity among predictor variables is an acknowledged problem, for which data-reduction and partitioning techniques have been proposed as solutions (see Guisan and Zimmermann 2000; Heikkinen et al. 2006 for details). However, statistical techniques like RandomForest can be used to minimize the risk of selecting incorrect variables in model parameterization. Randomforest grows multiple classification trees from bootstrap samples of the predictor variables and determines the predicted class by majority vote over all classification trees (Cutler et al. 2007). As part of this iterative process, all predictor variables, including those which are highly correlated, are incorporated. Thus there is a better chance that habitat projections are based on key environmental attributes. Over-

parameterization can be associated with RandomForest (Breiman 2001), however this technique is still a better approach given the high risk of selecting incorrect variables with other techniques.

1.5.2. Effects of including or excluding topo-edaphic predictor variables

Topo-edaphic variables are a key example of the limitation detailed in the previous section, given they are often excluded as predictor variables because multi-collinearity between static soil or landscape attributes and climate variables can lead to an underestimation of climate change impacts as previously discussed. However, these attributes have been shown to have a constraining effect on model projections under future climate scenarios (e.g. Taverna et al. 2005; Coudun et al. 2006). For example, Luoto and Heikkinen (2008) used a general additive model to predict the current suitable area and the potential size range of 100 European butterfly species for the period 2051-2080. The authors compared predictions from climate-only and climate-topography models and found the projected losses of species habitat were half when topo-edaphic variables were included. Especially in situations of multi-collinearity, we cannot infer causation from correlations, so the inference whether soil factors are important habitat variables that ultimately determine the species' niche space is very weak.

For the development of practical assisted migration strategies for forestry species, whether or not to include topo-edaphic variables is a minor issue. Under current seed zones and seed transfer guidelines, genotypes are broadly matched to macroclimatic environments, and forest managers have to use their silvicultural knowledge to match planting stock to appropriate soil types. This general approach would not change under recommendations derived from bioclimate envelope model projections.

1.5.3. Biotic interactions: accounted for, or not?

Habitat projections from bioclimatic envelope models are most often questioned on the grounds that they do not include non-climate factors. Notably in one of the most recognized publications that questioned the validity of model projections, Davis et al. (1998) identified the importance of biotic interactions between species. The authors used a simple microcosm experiment including three fruit fly species (Drosophila melanogaster Meigen, D. simulans Sturtevant and D. subobscura Collin) and a parasitoid wasp species (Leptopilina boulardi) to illustrate the impact of interspecific competition on both species distributions under simulated climate change. The authors found inter-species interactions in experimental clines caused differences in the distributions of all three fruit fly species compared to single-species clines. Under simulated climate change, dispersal ability and species interactions produce unexpected changes in the range and abundance of the fruit fly species, including inverted relative species abundances at warmer temperatures. They further suggest that in natural systems, interactions and feedbacks are likely to be even more complex, concluding that predictions made solely by extrapolation of a species' climate envelope may be misleading.

A major criticism of Davis *et al.*'s (1998) conclusions is the scaling of the results of a microcosm experiment to a macroecological scale may be inappropriate, since the biological process that determine species occurrence at the local scale (i.e. competition, predation, or herbivory) are considered to not exert the same dominance at the macroecological level (Huston 1999; Whittaker et al. 2001). But, even though it is widely agreed that climate affects species distributions, there is limited evidence that biotic interactions would not play a major role constraining current and future distributions at macroecological scales (Araujo

and Luoto 2007). Pearson and Dawson (2003) present a hierarchical modeling framework of characteristic scale domains within which climate has dominant control over species distribution at continent and regional scales (>200km), and biotic factors control species distribution at the local and site levels (<1km). Using this framework, bioclimate envelope models can be considered appropriate for predicting species distributions at a macro- scale, where biotic factors are less important for determining species distributions. This may be true as there are a number of bioclimate envelope models which have been highly successful at simulating current species distributions at macro-scales (e.g. Beerling et al. 1995; Pearson et al. 2002). For example Huntley et al. (2004) evaluated bioclimatic envelope model performance for species representing three major taxa (higher plants, insects and birds), including species of different life forms and from four trophic levels, and found the models well-represented observed distributions for 96% of the 306 European species used in their study. The authors conclude climate envelope models provide the best approach currently available for reliably evaluating the potential impacts of future climate change upon biodiversity.

While I agree with Davis *et al.'s* (1998) findings that changes in climate conditions may lead to novel or complex changes in biotic interactions among species, I feel this does not amount to a rejection of the bioclimate envelope approach, but rather a shift in the interpretation of model projections. Davis *et al.'s* (1998) findings properly suggest that models cannot predict what is actually going to happen on the landscape. For example, models of invasive species (e.g. Peterson 2003; Thuiller et al. 2005b) developed in their native ranges often miscalculate suitable climate conditions and consequently under or overestimate potential habitat expansions (Urban et al. 2007). If the species' native competitors are not present in the environment where the invasive species is introduced, the species may thrive more than expected and expand its range. Alternately if an

invasive species encounters a new competitor it may not be able to establish regardless of climate suitability. But for assisted migration strategies, the limitations associated with biotic factors are conceptually a minor problem. Habitat projections based on the species' realized niche provide the best risk estimate of whether or not a species will occur. For example, if model projections indicate habitat suitability for black spruce (Picea mariana) is lost over a large currently forested area, this indicates this area is no longer part of the species' realized niche, but it could still be within the species' fundamental niche. Although many biotic factors could prevent black spruce from occurring in the modeled climate space, the presence of competition is the largest difference between a species fundamental niche and its more restricted realized niche (Davis et al. 1998). Black spruce may therefore be able to perform better in its fundamental niche where its competitors are removed. But for reforestation practices, the only concern is whether or not black spruce should be planted at a particular site. Since the environmental limits of a species' fundamental niche are largely unknown, planting species in areas of projected habitat loss that are suspected to be within the species' fundamental niche is precarious, and economically risky.

Qualitative variables or other ecologically relevant variables, such as disturbance responses, fire adaptations, or novel predator-prey relationships, could be considered once habitat projections identify sites as good candidates for species introduction. For example, Willis *et al.* (2009) consulted with local experts to confirm the presence of breeding habitat for the marbled white (*Melanargia galathea*) and small skipper (*Thymelicus sylvestris*) butterflies at sites chosen for assisted migration approximately 65 and 35 km outside their respective ranges in northern England.

1.5.4. Local genetic adaptation of populations

One of the main disadvantages of bioclimate envelope models is they mistakenly treat species as homogenous units (e.g. Pearson and Dawson 2003). Most widespread tree species show adaptation of local populations to different macroclimatic conditions that are frequently observed over latitudinal or elevational gradients (e.g. Morgenstern 1996; Kawecki and Ebert 2004; Savolainen et al. 2007). Hence, we can expect that environmental change will not be limited to the trailing edge of a species range, but rather impact all populations where climate shifts beyond their narrower niche spaces (Davis et al. 2001; Millar et al. 2007). For example, Redfeldt *et al.* (1999) found in a reciprocal transplant experiment that warming temperatures slowed the growth of locally adapted lodgepole pine populations and increased tree mortality, resulting in a 20% loss of productivity. Without distinguishing between individual locally adapted populations, bioclimate envelope models may underestimate the threat of species loss (e.g. Thullier et al. 2005a) or overestimate the adequacy of protected areas (e.g. Araujo et al. 2004; Hannah et al. 2007).

Expanding bioclimate envelope models to characterize how genetically differentiated populations within a species react to climate may also address other model limitations. Local biotic interactions, such as competition or other biotic stressors, might be a primary factor shaping genetic population structure in plants. For example, Wehenkel *et al.* (2007) found fine-scale genetic differentiation within three target species, sycamore maple (*Acer pseudoplatanus*), European beech (*Fagus sylvatica*), and Norway spruce (*Picea abies*) in multiple forest communities, and suggested the differentiation may be the result of biotic interactions between the genetic structure of each species and the species composition of the community. Lastly, projecting suitable habitat at the

population level may also improve overall model performance, as model accuracy has been found to be negatively related to climate niche width (Kadmon et al. 2003). Including genetic information into bioclimate envelope modeling has been proposed (Botkin et al. 2007), but has yet to be developed.

1.5.5. Equilibrium assumptions

Bioclimate envelope models assume where a species is observed it is in equilibrium (or quasi-equilibrium) with its environment and thus a species will become extinct if the environmental conditions in its current distribution shift away from that equilibrium state (Botkin et al. 2007). However, the resilient, long-lived characteristics of some species' populations (e.g. tree populations) contradict this assumption because once established they can persist for a long time in a less-desirable environment. Observations that long-lived species have survived in small areas of unusual habitats (Pearson 2006), or in habitat outside of their well-established geographic range support this argument. For example, Woodward (1990) examined the distribution limits of small leaved lime (Tilia cordata) in the British Isles and estimated that the species reproductive limit is about 200km south of the northern edge of its present day range. The current small leaved lime distribution reflects the northern limit the species reached in the period between 7000 and 5000 BP (Pigott and Huntley 1981). Woodward et al. (1990) conclude that the current northern limit of the species range is a relic of past climates, reflecting the longevity of the species. For reforestation practices, the limitations of the equilibrium assumptions are negligible, given evolutionary processes in tree species generally occur over a very long time. It is safe to say that if forest managers are content with species survival and productivity under climate equilibriums experienced in the last century, they will be equally content with species performance under habitat projections over the next century.

1.5.6. Niche conservatism at the species level

Habitat projections derived from bioclimate envelope models may overestimate habitat or biodiversity losses within a species range (e.g. Thomas et al. 2004; Thuiller et al. 2005a) because the models only refer to a species narrower realized niche, rather than the species' larger fundamental niche. For these applications bioclimate envelope models have a critical flaw, given they assume the rate of adaptation is slower than the climate induced extinction rate (Pearson and Dawson 2003). However, this could be an incorrect assumption given local populations might have the ability to acclimate or adapt to new environments within a single generation, essentially holding on to habitat that projections indicate as lost. For example, Rehfeldt and Gallo (2001) determined that ponderosa pine (Pinus ponderosa) and Douglas-fir (Pseudotsuga menziesii) populations that were introduced to Victoria Island in Nahuel Haupi Lake of northwest Patagonia, Argentina early in the twentieth century likely originate from a low or middle elevation Californian and a mild US coastal populations, respectively. Although the Argentinean environments were not considered optimal for these populations, both species now appear to be highly productive and especially suited to the ecotone between the steppe and Nothofagus forest in northwest Patagonia (Rehfeldt and Gallo 2001). This indicates that both populations have been able to adapt to their new environments within a single generation and a similar genetic evolution within threatened populations could occur over the next century as climate continues to change. This suggests that areas of projected habitat loss should be viewed as areas of high risk, rather than definite loses to a species' distribution or as an indicator that a population is as Thomas et al. (2004) termed 'committed to extinction'. For reforestation prescriptions in assisted migration, niche conservatism is a minor issue given

these applications does not focus on area of projected species extinctions, but rather where species can be safely planted. Projections that indicate suitable species habitat is well maintained provide strong inference for assisted migration efforts. It is in these areas that low risk, long-term targets and planting strategies can be developed.

1.5.7. How to best interpret bioclimate envelope model results

The limitations of bioclimate envelope modeling are not unique to this approach, given that modeling species distributions is a complex process. Along with sufficient data, an intimate knowledge of the species as well as the statistics used in model development is needed to provide useful answers when the models are applied. It is critical that extrapolated ranges are defined as *potential* ranges given they are contingent on the assumption that current limiting factors remain limiting factors in the future (Dormann 2007). Simply put, model projections cannot be used "blindly" without some consideration for the characteristics of the environment and the species being modeled. For example, habitat projections derived from bioclimate envelope models may overestimate habitat gains at the leading edge of a species' range because the models assume there are no dispersal limitations inhibiting species from occurring in all locations where climate is projected to be favorable. Kharouba et al. (2009) constructed historical models for 297 Canadian butterfly species, and when the authors ran the models forward in time, they found the temporal transferability of models for species that are strong dispersers (defined as large-winged species) was higher than for species with limited dispersal ability (small-winged species), presumably because of their enhanced ability to track changing climate. In this case, if the model projections were "blindly" accepted and the dispersal abilities of these butterfly species were ignored, conservation decisions based on model projections for the weak

dispersers would be wrong. In this example, knowledge of estimated dispersal rates could differentiate between potential reserve sites where species could occupy unaided from those which could only become occupied with human intervention (Midgley et al. 2006).

1.6. Thesis Outline

In this thesis I aim to develop a methodological framework to help guide assisted migration of forest trees, considering a comprehensive range of future climate projections. The thesis has a focus on Alberta, and I want to determine which species and locally adapted populations are optimal planting stock for reforestation programs in this province. However, even for a local application, global species distribution models are highly preferable (Sanchez-Fernandez et al. 2011). I therefore built a larger framework that can be used to guide assisted migration efforts across western North America. This thesis is structured into three research chapters. In the first research chapter I develop a species distribution model that allows for tracking populations of tree species in western North America. In the second research chapter, I use the results of this global model to develop practical reforestation applications for Alberta. In the third research chapters, I focus on validating (or at least contextualizing) assisted migration prescriptions with independent empirical or experimental data.

1.6.1. First research chapter

In the first research chapter, I improve the usefulness of bioclimate envelope model projections by illustrating how within-population genetic diversity can be simplistically integrated using an ecosystem-based modeling technique. I use an ensemble classifier (RandomForest) to project climate envelopes for 770 ecosystem units that represent populations of 15 important tree species in western North America under 18 climate projections for the 2020s, 2050s, and 2080s, as well as under observed climate trends. I develop two sets of projections that describe the average shift of habitat, and uncertainties in habitat projections arising from multi-model climate change scenarios. Specifically, I address the following three research questions:

- How does climatically suitable habitat shift throughout the 2020s, 2050s, and 2080s and what are the uncertainties associated with these species habitat projections?
- How far do individual populations of trees lag behind their optimal climate under observed and predicted climate change?
- Given the lag in climate match under observed and projected climate change, can we derive general north and/or elevational seed transfer recommendations?

1.6.2. Second research chapter

The second research chapter builds on the modeling effort of the first chapter to derive seed transfer recommendations tailored towards Alberta's seed zone system. Private and public reforestation programs in Alberta are required by legislation to use planting stock for reforestation that was collected in one of approximately 60 seed zones. In this chapter I develop recommendations to aid transfer of seeds collected in one seed zone for use in another, optimally matching climate conditions under observed and predicted climate change. In this chapter, I address the following applied research questions:

- Is Alberta's seed zone system a useful framework to govern seed transfer under uncertain future climates?
- Do we need to introduce new species or new seed sources from outside the province to maintain well adapted and productive forests of the future?
- What are the species and genotypes that most likely match anticipated future climates of the sub-boreal and boreal forests of Alberta?

1.6.3. Third research chapter

In the third research chapter, I synthesize research that uses independent modeling, experimental, and empirical research approaches, conducted by myself and three colleagues in the Hamann lab, to develop more dependable guidelines for assisted migration for trembling aspen in western Canada. My contributions to this paper include the bioclimate envelope modeling and reforestation recommendations components, as well as a synthesis of information from remote sensing, genetic field trials, and local climate trends. The objective is to validate (or at least to contextualize) predictions from habitat models. In a case study for aspen, I address the following questions or hypotheses:

 Given the mismatch or lag of locally adapted populations in a changing environment, can we identify adaptational lag in reciprocal transplant experiments? Given observed climate trends in western Canada, I hypothesize that using planting stock transferred from warmer and/or drier source environments to a different planting site will lead to better growth compared to local sources.

- Model projections under observed climate change for aspen indicate loss of habitat at the southern fringe of the boreal forest and in other water-limited forest regions of Alberta. Do those habitat projections accurately reflect observed loss of forest productivity and observed dieback of aspen in central Alberta?
- Given model projections, empirical data of observed climate change impacts, and experimental data from transplant experiments, does the risk of changing established management practices outweigh the risk of status-quo management? If yes, what are the criteria that indicate the need for changing established management practices, and on what tools and data should managers rely in developing climate change adaptation strategies?

For reference, a glossary of important terms used throughout this thesis is provided in Appendix A.

1.7. Literature Cited

- Adams, H.D., Guardiola-Claramonte, M., Barron-Gafford, G.A., Villegas, J.C., Breshears, D.D., Zou, C.B., Troch, P.A., and Huxman, T.E. 2009. Temperature sensitivity of drought-induced tree mortality portends increased regional die-off under global-change-type drought. Proceedings of the National Academy of Sciences of the United States of America 106(17): 7063-7066.
- Allen, C.D. 2009. Climate-induced forest dieback: an escalating global phenomenon. Unasylva **231/232**: 43-49.
- Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.H., Allard, G., Running, S.W., Semerci, A., and Cobb, N. 2010. A global overview of drought and heat-induced tree mortality reveals emerging
climate change risks for forests. Forest Ecology and Management **259**(4): 660-684.

- Araujo, M.B., Cabeza, M., Thuiller, W., Hannah, L., and Williams, P.H. 2004. Would climate change drive species out of reserves? An assessment of existing reserve-selection methods. Global Change Biology 10(9): 1618-1626.
- Araujo, M.B., and Luoto, M. 2007. The importance of biotic interactions for modelling species distributions under climate change. Global Ecology and Biogeography 16(6): 743-753.
- Araujo, M.B., and Pearson, R.G. 2005. Equilibrium of species' distributions with climate. Ecography 28(5): 693-695.
- Araujo, M.B., Pearson, R.G., Thuiller, W., and Erhard, M. 2005. Validation of species-climate impact models under climate change. Global Change Biology 11(9): 1504-1513.
- Araujo, M.B., and Williams, P.H. 2000. Selecting areas for species persistence using occurrence data. Biological Conservation 96(3): 331-345.
- Austin, M. 2007. Species distribution models and ecological theory: A critical assessment and some possible new approaches. Ecological Modelling **200**(1-2): 1-19.
- Austin, M.P., Nicholls, A.O., and Margules, C.R. 1990. Measurement of the realized qualitative niche - environmental niches of 5 Eucalyptus species. Ecological Monographs 60(2): 161-177.
- Beaubien, E.G., and Freeland, H.J. 2000. Spring phenology trends in Alberta, Canada: links to ocean temperature. International Journal of Biometeorology 44(2): 53-59.
- Beerling, D.J., Huntley, B., and Bailey, J.P. 1995. Climate and the distribution of *Fallopia-japonica* use of an introduced species to test the predictive capacity of response surfaces. Journal of Vegetation Science 6(2): 269-282.
- Berg, E.E., Henry, J.D., Fastie, C.L., De Volder, A.D., and Matsuoka, S.M. 2006. Spruce beetle outbreaks on the Kenai Peninsula, Alaska, and Kluane National Park and Reserve, Yukon Territory: Relationship to summer temperatures and regional differences in disturbance regimes. Forest Ecology and Management 227(3): 219-232.
- Bonsal, B.R., Zhang, X., Vincent, L.A., and Hogg, W.D. 2001. Characteristics of daily and extreme temperatures over Canada. Journal of Climate 14(9): 1959-1976.

Botkin, D.B., Saxe, H., Araujo, M.B., Betts, R., Bradshaw, R.H.W., Cedhagen, T., Chesson, P., Dawson, T.P., Etterson, J.R., Faith, D.P., Ferrier, S., Guisan, A., Hansen, A.S., Hilbert, D.W., Loehle, C., Margules, C., New, M., Sobel, M.J., and Stockwell, D.R.B. 2007. Forecasting the effects of global warming on biodiversity. BioScience 57(3): 227-236.

Breiman, L. 2001. Random forests. Machine Learning 45(1): 5-32.

- Brohan, P., Kennedy, J.J., Harris, I., Tett, S.F.B., and Jones, P.D. 2006. Uncertainty estimates in regional and global observed temperature changes: A new data set from 1850. Journal of Geophysical Research-Atmospheres **111**(D12106): doi: 10.1029/2005JD006548.
- Chapin, F.S., Sturm, M., Serreze, M.C., McFadden, J.P., Key, J.R., Lloyd, A.H., McGuire, A.D., Rupp, T.S., Lynch, A.H., Schimel, J.P., Beringer, J., Chapman, W.L., Epstein, H.E., Euskirchen, E.S., Hinzman, L.D., Jia, G., Ping, C.L., Tape, K.D., Thompson, C.D.C., Walker, D.A., and Welker, J.M. 2005. Role of land-surface changes in Arctic summer warming. Science **310**(5748): 657-660.
- Coudun, C., Gegout, J.C., Piedallu, C., and Rameau, J.C. 2006. Soil nutritional factors improve models of plant species distribution: an illustration with *Acer campestre* (L.) in France. Journal of Biogeography **33**(10): 1750-1763.
- Crumpacker, D.W., Box, E.O., and Hardin, E.D. 2001. Implications of climatic warming for conservation of native trees and shrubs in Florida. Conservation Biology **15**(4): 1008-1020.
- Cutler, D.R., Edwards, T.C., Beard, K.H., Cutler, A., and Hess, K.T. 2007. Random forests for classification in ecology. Ecology **88**(11): 2783-2792.
- Dai, A., Fung, I.Y., and DelGenio, A.D. 1997. Surface observed global land precipitation variations during 1900-88. Journal of Climate **10**(11): 2943-2962.
- Dale, V.H., Joyce, L.A., McNulty, S., Neilson, R.P., Ayres, M.P., Flannigan, M.D., Hanson, P.J., Irland, L.C., Lugo, A.E., Peterson, C.J., Simberloff, D., Swanson, F.J., Stocks, B.J., and Wotton, B.M. 2001. Climate change and forest disturbances. BioScience 51(9): 723-734.
- Davis, A.J., Jenkinson, L.S., Lawton, J.H., Shorrocks, B., and Wood, S. 1998. Making mistakes when predicting shifts in species range in response to global warming. Nature **391**(6669): 783-786.
- Davis, L., S., Johnson, K.N., Bettinger, P., and Howard, T., E. 2001. Forest Management: To sustain ecological, economic and social values. Fourth ed. Waveland Press Inc., Long Grove, IL, USA.

- Dormann, C.F. 2007. Promising the future? Global change projections of species distributions. Basic and Applied Ecology **8**(5): 387-397.
- Flannigan, M.D., Stocks, B., J, and Wotton, B.M. 2000. Climate change and forest fires. Science of The Total Environment **262**(3): 221-229.
- Fleming, R.A., and Volney, W.J.A. 1995. Effects of climate-change on insect defoliator population processes in Canada boreal forest - some plausible scenarios. Water Air and Soil Pollution 82(1-2): 445-454.
- Gamache, I., and Payette, S. 2005. Latitudinal response of subarctic tree lines to recent climate change in eastern Canada. Journal of Biogeography **32**(5): 849-862.
- Gillett, N.P., Weaver, A.J., Zwiers, F.W., and Flannigan, M.D. 2004. Detecting the effect of climate change on Canadian forest fires. Geophysical Research Letters **31**(L18211): doi: 1029/2004GL020876.
- Guisan, A., and Zimmermann, N.E. 2000. Predictive habitat distribution models in ecology. Ecological Modelling **135**(2-3): 147-186.
- Hampe, A. 2004. Bioclimate envelope models: What they detect and what they hide. Global Ecology and Biogeography **12**(5): 469-471.
- Hamrick, J.L. 2004. Response of forest trees to global environmental changes. Forest Ecology and Management **197**(1-3): 323-335.
- Hannah, L., Midgley, G., Andelman, S., Araujo, M., Hughes, G., Martinez-Meyer, E., Pearson, R., and Williams, P. 2007. Protected area needs in a changing climate. Frontiers in Ecology and the Environment 5(3): 131-138.
- Hansen, J., Ruedy, R., Sato, M., Imhoff, M., Lawrence, W., Easterling, D., Peterson, T., and Karl, T. 2001. A closer look at United States and global surface temperature change. Journal of Geophysical Research-Atmospheres **106**(D20): 23947-23963.
- Heikkinen, R.K., Luoto, M., Araujo, M.B., Virkkala, R., Thuiller, W., and Sykes, M.T. 2006. Methods and uncertainties in bioclimatic envelope modelling under climate change. Progress in Physical Geography 30(6): 751-777.
- Hoegh-Guldberg, O., Hughes, L., McIntyre, S., Lindenmayer, D.B., Parmesan, C., Possingham, H.P., and Thomas, C.D. 2008. Assisted colonization and rapid climate change. Science **321**(5887): 345-346.
- Hogg, E.H., Brandt, J.P., and Kochtubajda, B. 2002. Growth and dieback of aspen forests in northwestern Alberta, Canada, in relation to climate and insects. Canadian Journal of Forest Research 32(5): 823-832.

- Hogg, E.H., Brandt, J.P., and Michaellian, M. 2008. Impacts of a regional drought on the productivity, dieback, and biomass of western Canadian aspen forests. Canadian Journal of Forest Research 38(6): 1373-1384.
- Hunter, M.L. 2007. Climate change and moving species: Furthering the debate on assisted colonization. Conservation Biology **21**(5): 1356-1358.
- Huntley, B., Green, R., E., Collingham, Y., C., Hill, J., K., Willis, S., G., Bartlein, P., J., Cramer, W., Hagemeiger, W., J. M., and Thomas, C., D. 2004. The performance of models relating species geographical distributions to climate is independent of trophic level. Ecology Letters 7: 417-426.
- Huston, M.A. 1999. Local processes and regional patterns: Appropriate scales for understanding variation in the diversity of plants and animals. Oikos 86(3): 393-401.
- Hutchinson, G.E. 1957. Population studies animal ecology and demograpy concluding remarks. Cold Spring Harbor Symp. Quant. Biol. 22: 415-427.
- IPCC. 2007. Climate change 2007: The physical basics (Summary for policymakers). Intergovernmental Panel on Climate Change. ISBN 978 0521 70596-7.
- Iverson, L.R., and Prasad, A.M. 1998. Predicting abundance of 80 tree species following climate change in the eastern United States. Ecological Monographs 68(4): 465-485.
- Iverson, L.R., and Prasad, A.M. 2001. Potential changes in tree species richness and forest community types following climate change. Ecosystems **4**(3): 186-199.
- Iverson, L.R., and Prasad, A.M. 2002. Potential redistribution of tree species habitat under five climate change scenarios in the eastern US. Forest Ecology and Management **155**(1-3): 205-222.
- Jeschke, J.M., and Strayer, D.L. 2008. Usefulness of bioclimatic models for studying climate change and invasive species. Annals of the New York Academy of Sciences **1134**: 1-24.
- Kadmon, R., Farber, O., and Danin, A. 2003. A systematic analysis of factors affecting the performance of climatic envelope models. Ecological Applications 13(3): 853-867.
- Kawecki, T.J., and Ebert, D. 2004. Conceptual issues in local adaptation. Ecology Letters **7**(12): 1225-1241.

- Kharouba, H.M., Algar, A.C., and Kerr, J.T. 2009. Historically calibrated predictions of butterfly species' range shift using global change as a pseudo-experiment. Ecology **90**(8): 2213-2222.
- Lawler, J.J. 2009. Climate Change Adaptation Strategies for Resource Management and Conservation Planning. Annals of the New York Academy of Sciences **1162**: 79-98.
- Lawler, J.J., White, D., Neilson, R.P., and Blaustein, A.R. 2006. Predicting climate-induced range shifts: Model differences and model reliability. Global Change Biology **12**(8): 1568-1584.
- Logan, J., and Powell, J., A. 2001. Ghost forest, gloabl warming, and the mountain pine beetle (*Coleoptera: Scolytidae*). American Entomologist 47: 160-173.
- Luoto, M., and Heikkinen, R.K. 2008. Disregarding topographical heterogeneity biases species turnover assessments based on bioclimatic models. Global Change Biology **14**(3): 483-494.
- Mac Nally, R. 2000. Regression and model-building in conservation biology, biogeography and ecology: The distinction between and reconciliation of 'predictive' and 'explanatory' models. Biodiversity and Conservation **9**(5): 655-671.
- Marris, E. 2009. Planting the forest of the future. Nature 459(7249): 906-908.
- Mbogga, M.S., Hamann, A., and Wang, T.L. 2009. Historical and projected climate data for natural resource management in western Canada. Agricultural and Forest Meteorology **149**(5): 881-890.
- McDowell, N.G., Allen, C.D., and Marshall, L. 2010. Growth, carbon-isotope discrimination, and drought-associated mortality across a *Pinus ponderosa* elevational transect. Global Change Biology **16**(1): 399-415.
- McKenney, D., Pedlar, J., and O'Neill, G. 2009. Climate change and forest seed zones: Past trends, future prospects and challenges to ponder. Forestry Chronicle **85**(2): 258-266.
- McLachlan, J.S., Hellmann, J.J., and Schwartz, M.W. 2007. A frmework for debate of assisted migration in an era of climate change. Conservation Biology 21(2): 297-302.
- Michaelian, M., Hogg, E.H., Hall, R., J., and Arsenault, E. 2010. Massive mortality of aspen following severe drought along the southern edge of the Canadian boreal forest. Global Change Biology: doi: 10.111/j.1365-2486.2010.02357.x.

- Midgley, G.F., Hughes, G.O., Thuiller, W., and Rebelo, A.G. 2006. Migration rate limitations on climate change-induced range shifts in Cape Proteaceae. Diversity and Distributions **12**(5): 555-562.
- Millar, C.I., Stephenson, N.L., and Stephens, S.L. 2007. Climate change and forests of the future: Managing in the face of uncertainty. Ecological Applications **17**(8): 2145-2151.
- Morgenstern, E. 1996. Geographic Variation in Forest Trees. Genetic Basis and Application of Knowledge in Silviculture. University of British Columbia Press, Vancouver, BC, Canada. 208p.
- Morin, X., and Thuiller, W. 2009. Comparing niche- and process-based models to reduce prediction uncertainty in species range shifts under climate change. Ecology **90**(5): 1301-1313.
- O'Neill, G.A., Ukrainetz, N.K., Carlson, M.R., Cartwright, C.V., Jaquish, B.C., King, J.N., Krakowski, J., Russell, J.H., Stoehr, M.U., Xie, C., and Yanchuk, A.D. 2008. Assisted migration to address climate change in British Columbia: recommendations for interim seed transfer standards. . B.C. Min. For. Range, Res. Br., Victoria, B.C. Tech. Rep. 048.
- Pearson, R., G. 2006. Climate change and the migration of capacity of species. TRENDS in Ecology and Evolution **21**(3): 111-113.
- Pearson, R., G., Dawson, T., P., Berry, P., M., and Harrison, P., A. 2002. SPECIES: A spatial evaluation of climate impact on the enevelope of speices. Ecological Modelling 154: (289-300).
- Pearson, R.G., and Dawson, T.P. 2003. Predicting the impacts of climate change on the distribution of species: Are bioclimate envelope models useful? Global Ecology and Biogeography 12(5): 361-371.
- Peterson, A.T. 2003. Predicting the geography of species' invasions via ecological niche modeling. Quarterly Review of Biology **78**(4): 419-433.
- Pigott, C.D., and Huntley, J.P. 1981. Factors controlling the distribution of Tiliacordata at the northern limits of its geographical range. III Nature and causes of seed sterility. New Phytologist 87(4): 817-839.
- Raffa, K.F., Aukema, B.H., Bentz, B.J., Carroll, A.L., Hicke, J.A., Turner, M.G., and Romme, W.H. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: The dynamics of bark beetle eruptions. BioScience 58(6): 501-517.
- Rehfeldt, G.E., and Gallo, L.A. 2001. Introduction of ponderosa pine and Douglas-fir to Argentina using quantitative traits for retrospective

identification and prospective selection of provenances. New Forests **21**(1): 35-44.

- Rehfeldt, G.E., Ying, C.C., Spittlehouse, D.L., and Hamilton, D.A. 1999. Genetic responses to climate in *Pinus contorta*: Niche breadth, climate change, and reforestation. Ecological Monographs 69(3): 375-407.
- Ricciardi, A., and Simberloff, D. 2009. Assisted colonization is not a viable conservation strategy. Trends in Ecology & Evolution 24(5): 248-253.
- Sanchez-Fernandez, D., Lobo, J.M., and Hernandez-Manrique, O.L. 2011. Species distribution models that do not incorporate global data misrepresent potential distributions: a case study using Iberian diving beetles. Diversity and Distribution **17**(1): 163-171.
- Savolainen, O., Pyhajarvi, T., and Knurr, T. 2007. Gene flow and local adaptation in trees. Annual Review of Ecology Evolution and Systematics **38**: 595-619.
- Smith, T.M., and Reynolds, R.W. 2005. A global merged land-air-sea surface temperature reconstruction based on historical observations (1880-1997). Journal of Climate 18(12): 2021-2036.
- Spittlehouse, D.L. 2005. Integrating climate change adaptation into forest management. Forestry Chronicle **81**(5): 691-695.
- Stahl, K., Moore, R.D., and McKendry, I.G. 2006. Climatology of winter cold spells in relation to mountain pine beetle mortality in British Columbia, Canada. Climate Research 32(1): 13-23.
- Sturm, M., Racine, C., and Tape, K. 2001. Climate change increasing shrub abundance in the Arctic. Nature 411(6837): 546-547.
- Swetnam, T.W., and Betancourt, J.L. 1998. Mesoscale disturbance and ecological response to decadal climatic variability in the american southwest. Journal of Climate 11(12): 3128-3147.
- Tape, K., Sturm, M., and Racine, C. 2006. The evidence for shrub expansion in northern Alaska and the Pan-Arctic. Global Change Biology 12(4): 686-702.
- Taverna, K., Urban, D.L., and McDonald, R.I. 2005. Modeling landscape vegetation pattern in response to historic land-use: A hypothesis-driven approach for the North Carolina Piedmont, USA. Landscape Ecology 20(6): 689-702.
- Thomas, C., D., Cameron, A., Green, R., E., Bakkenes, M., Beaumont, L., J., Collingham, Y., C., Erasmus, B., F. N., Ferreira de Slquelra, M., Grainger,

A., Hannah, L., Huges, L., Huntley, B., van Jaarsveld, A., S., Midgley, G., F., Miles, L., Ortega-Huerta, M., A., Townsend Peterson, A., Phillips, O., L., and Williams, S., E. 2004. Extinciton risk from climate change. Nature **427**: 145-148.

- Thuiller, W., Lavorel, S., Araujo, M., Sykes, M.T., and Prentice, I.C. 2005a. Climate change threats to plant diversity in Europe. PNAS **102**(3): 8245-8250.
- Thuiller, W., Richardson, D.M., Pysek, P., Midgley, G.F., Hughes, G.O., and Rouget, M. 2005b. Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale. Global Change Biology **11**(12): 2234-2250.
- Trenberth, K.E., Jones, P.D., Ambenje, P., Bojariu, R., Easterling, D., Klein Tank, A., Parker, D., Rahimzadeh, F., Renwick, J.A., Rusticucci, M., Soden, B., and Zhai, P. 2007. Observations: Surface and atmospheric climate change. *In* Climate change 2007: The physical science basis. Contribution of Working Group I to the Fourth Assessment Report o the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom; New York, NY, USA. pp. 236-336.
- Urban, M.C., Phillips, B.L., Skelly, D.K., and Shine, R. 2007. The cane toad's (*Chaunus [Bufo] marinus*) increasing ability to invade Australia is revealed by a dynamically updated range model. Proceedings of the Royal Society B-Biological Sciences **274**(1616): 1413-1419.
- van Mantgem, P.J., Stephenson, N.L., Byrne, J.C., Daniels, L.D., Franklin, J.F., Fule, P.Z., Harmon, M.E., Larson, A.J., Smith, J.M., Taylor, A.H., and Veblen, T.T. 2009. Widespread increase of tree mortality rates in the western United States. Science **323**(5913): 521-524.
- Vitt, P., Havens, K., Kramer, A.T., Sollenberger, D., and Yates, E. 2010. Assisted migration of plants: Changes in latitudes, changes in attitudes. Biological Conservation 143(1): 18-27.
- Volney, W.J.A., and Fleming, R.A. 2000. Climate change and impacts of boreal forest insects. Agriculture Ecosystems & Environment 82(1-3): 283-294.
- Wehenkel, C., Bergmann, F., and Gregorius, H.R. 2007. Genotype-species interactions in neighbourhoods of forest tree communities. Silvae Genetica 56(3-4): 101-110.
- Welsh, C., Lewis, K., and Woods, A. 2009. The outbreak history of Dothistroma needle blight: An emerging forest disease in northwestern British Columbia, Canada. Canadian Journal of Forest Research 39(12): 2505-2519.

- Whittaker, R.J., Willis, K.J., and Field, R. 2001. Scale and species richness: Towards a general, hierarchical theory of species diversity. Journal of Biogeography 28(4): 453-470.
- Willis, S.G., Hill, J.K., Thomas, C.D., Roy, D.B., Fox, R., Blakeley, D.S., and Huntley, B. 2009. Assisted colonization in a changing climate: A teststudy using two UK butterflies. Conservation Letters 2(1): 45-51.
- Wolfe, D.W., Schwartz, M.D., Lakso, A.N., Otsuki, Y., Pool, R.M., and Shaulis, N.J. 2005. Climate change and shifts in spring phenology of three horticultural woody perennials in northeastern USA. International Journal of Biometeorology 49(5): 303-309.
- Woods, A., Coates, K.D., and Hamann, A. 2005. Is an unprecedented dothistroma needle blight epidemic related to climate change? BioScience **55**(9): 761-769.
- Woodward, F.I. 1990. The impact of low-temperatures in controlling the geographical distribution of plants. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences **326**(1237): 585-593.
- Ying, C.C., and Yanchuk, A.D. 2006. The development of British Columbia's tree seed transfer guidelines: Purpose, concept, methodology, and implementation. Forest Ecology and Management 227(1-2): 1-13.
- Zhang, X.B., Vincent, L.A., Hogg, W.D., and Niitsoo, A. 2000. Temperature and precipitation trends in Canada during the 20th century. Atmosphere-Ocean 38(3): 395-429.
- Zhou, L., M., Tucker, C., J., Kaufmann, R., K., Slayback, D., Shabanov, N., V., and Myneni, R., B. 2001. Variations in nothern vegetation activity inferred from satelliete data of vegetation index during 1981 to 1999. Journal of Geophysical Research-Atmospheres **106**: 20069-20083.

Chapter 2. Tracking suitable habitat for tree populations under climate change in western North America

Summary

An important criticism of bioclimate envelope models is that many wide-ranging species consists of locally adapted populations that may all lag behind their optimal climate habitat and thus should be modeled separately. Here, I apply a bioclimate envelope model that tracks habitat of individual populations of species to estimate adaptational lags for 15 wide-ranging forest tree species in western North America. An ensemble classifier modeling approach (RandomForest) was used to spatially project the climate space of tree populations under observed climate trends (1970s to 2000s) and multi-model projections for the 2020s, 2050s and 2080s. I find that on average populations already lag behind their optimal climate niche by at least 130km in latitude, or 60m in elevation. For the 2020s an average lag of approximately 310km in latitude or 140m in elevation is predicted, with the most pronounced geographic lags in the Rocky Mountains and boreal forest. The 2020s lag of populations behind their optimal climate niche is projected to approximately double under 2050s climate change scenarios. These results have implications for assisted migration of planting stock in reforestation programs. I recommend transfer guidelines based on a general formula where 100 kilometer north shift is equivalent to approximately 44 meter upward shift in elevation. The formula can be applied regionally to move seed among similar forest types to prevent potential mal-adaptation of locally adapted populations under climate change.

2.1. Introduction

Bioclimate envelope models, also referred to as species distribution models, have emerged as a widely used modeling technique to illustrate the discrepancy between current species distributions and their predicted potential habitat under climate change (e.g. Overpeck et al. 1991; Thomas et al. 2004). Bioclimate envelope models correlate species census data with environmental predictor variables using a wide range of statistical and machine-learning methods (e.g. reviewed by Guisan and Zimmermann 2000). The limitations and weaknesses of the bioclimate envelope model approach have been thoroughly discussed and the general consensus is that bioclimate envelope projections should not be literally interpreted as predicted demographic response of species to climate change, and that loss of habitat predicted by bioclimate envelope models does not necessarily entail extirpation of current populations (e.g. Austin 2007; Botkin et al. 2007; Hampe 2004; Thuiller et al. 2008).

Although bioclimate envelope projections do not directly imply ecological and demographic changes, they can still be useful in guiding climate change adaptation strategies for forestry that involve habitat restoration, reforestation, or conservation objectives (Hamann and Wang 2005). For such management applications, the primary task is to match the correct planting stock with anticipated climate conditions, rather than to predict complex demographic processes and biological interactions under changing climate (e.g. Hamann and Wang 2006). Selecting appropriate planting stock not only requires choosing an appropriate species but also genotypes of locally adapted populations that match anticipated planting environments (Ying and Yanchuk 2006). Therefore, we need to include genetic structure of species in bioclimate envelope models (Botkin et al. 2007; Thuiller et al. 2008).

In widespread tree species, genetically differentiated populations are uniquely and often narrowly adapted to their local environments (Morgenstern 1996). Hence, climate change impacts will not be limited to the trailing edge of a species range, but instead may apply to populations throughout the species range. Under climate change, all populations may occupy environments at or beyond the margins of their individual climate niches (Davis and Shaw 2001; Hampe 2004; Millar et al. 2007). This is also supported by empirical evidence suggesting that genetic population structure in widespread forest trees should not be ignored. For example, O'Neill et al (2008) and Wang *et al.* (2006b; 2010) found that when genetic structure was considered the predicted growth and survival of locally adapted lodgepole pine (*Pinus contorta*) populations was reduced. Chen *et al.* (2010) found that northern and high elevation Douglas-fir (*Pseudotsuga meniesii*) populations are more vulnerable to climate change than the populations from the southern end of the species range, presumably due to narrow genetic adaptation of local populations.

In this study I illustrate how within-population genetic diversity can be simplistically integrated in bioclimate envelope modeling, by breaking-up species census data using delineated ecosystems, which serve as proxy for species' populations. For practical applications of seed movement, we can now identify the geographic origin of locally adapted populations that best match the anticipated future climate. I geographically project suitable habitat for populations of 15 wide-ranging tree species in western North America. My objective is to determine how far populations already lag behind their optimal climate habitat and how these adaptational lags of populations are predicted to change in the future. This analysis relies on the assumption that genetic differentiation of tree populations are reflected by ecosystem delineations. I also assume that individual

tree populations are in equilibrium with their local environments (i.e. optimally adapted) under a reference climate that I use for bioclimate envelope modeling. Previously, information on genetic structure and the equilibrium state of populations for two important forestry species has been used to improve or validate results from bioclimate envelope models (Gray et al. 2011; O'Neill et al. 2008). Here, I contribute a discussion why this information is not essential to derive conservative assisted migration prescriptions.

2.2. Materials and methods

To generate future habitat projections for individual populations I build on an ecosystem-based modeling technique developed by Hamann and Wang (2006) and Mbogga *et al.* (2010). This approach uses independent variables, such as climate conditions, topographic indices, and soil variables to characterize habitat within delineated ecosystem polygons. Ecosystem units are the dependent class variable in this modeling approach. Species distributions are subsequently derived by replacing the predicted ecosystem unit with species' probability of presence or frequency values calculated from sample plot data as explained in more detail below. In this study, I extend this approach by using the ecosystem modeling units as a proxy for tree populations. I do not necessarily assume that each ecosystem represents a locally adapted population, but I assume that genetic differentiation within species is largely accounted for by these fine-scale ecosystem delineations.

2.2.1. Climate envelope modeling

Predictions of ecosystem classes were carried out with an ensemble classification tree analysis implemented by the RandomForest software package (Breiman 2001) for the R programming environment (R Development Core Team 2008). RandomForest grows multiple classification trees from bootstrap samples of the training data and determines the predicted class by majority vote over all classification trees (Cutler et al. 2007). Importance values for predictor variables were calculated as the number of times that a climate variable contributed to a correct classification in a bootstrapped cross-validation procedure with different permutations of predictor variables. As ecosystem delineations I used the Biogeoclimatic Ecological Classification system version 4 for British Columbia (Meidinger and Pojar 1991). In Alberta I use the Natural Regions and Subregions System, 2005 release (NRC 2006). In Saskatchewan and Manitoba I used the National Ecological Framework for Canada (Selby and Santry 1996), and for the United States west of 100° longitude I used the Ecoregion System (EPA 2007). In total, this amounts to 770 fine-scale ecosystem delineations. From each ecosystem I randomly sampled 100 1km grid cells, which were climatically characterized, and subsequently used as training data for classification tree analysis.

2.2.2. Baseline climate data and future projections

For climatic characterization of ecosystems I use interpolated climate data that were generated with the Parameter Regression of Independent Slopes Model (Daly et al. 2008). These surfaces were derived from climate normal data observed at weather stations in the United States and Canada for the 1961-1990 period. This database was enhanced with lapse-rate based down-sampling to 1km resolution and an estimation of biologically relevant climate variables (Mbogga et al. 2009). From this dataset of more than 50 monthly, seasonal, and annual climate variables, I chose ten predictor variables that are biologically important and that had relatively low collinearity. These included mean annual temperature, mean warmest month temperature, mean coldest month temperature, continentality (difference between mean January and mean July temperature), mean annual precipitation, growing season precipitation (May to September), the number of frost free days and the number of growing degree days above 5°C. All of these variables are described in detail by Wang *et al.* (2006a). I also included two dryness indices: annual and summer climate-moisture index according to Hogg (1997).

Climate projections for western North America for the 2020s, 2050s, 2080s were generated by overlaying projections from general circulation models expressed as the difference from the 1961-1990 normal period. For each future period, 18 climate projections base on four major Special Report on Emissions Scenarios (SRES) families (AIFI, A2, B1, B2), implemented by five modeling groups (CGCM, Canada; CSIRO2, Australia, HADCM3; United Kingdom; ECHAM4, Europe; and PCM, United States) were used. Model-emission scenario combinations ECHAM4-A1FI and ECHAM4-B1 were unavailable resulting in a total of 18 future projections per time period. To represent recent climate trends I use the 1997–2006 decadal average, which can be interpreted as observed climate change over a 25-year period (the mid-point of the 1961–1990 climate baseline period and the mid-point of the recent decadal average: 1975 to 2000). For more details refer to Mbogga *et al.* (2009).

2.2.3. Tree species inventory data

For species and population level analysis I selected 15 major forest tree species of commercial importance in western North America: pacific silver fir (*Abies amabilis* Douglas ex J. Forbes), Alaska yellow-cedar (*Chamaecyparis nootkatensis* (D. Don) Sudworth), tamarack (*Larix laricina* (Du Roi) K. Koch), western larch (*Larix occidentalis* Nuttall), Engelmann spruce (*Picea engelmannii var. engelmannii* Parry ex Engelmann), white spruce (*Picea glauca* (Moench) Voss), black spruce (*Picea mariana* (Miller) Britton), Sitka spruce (*Picea sitchensis* (Bongard) Carrière), lodgepole pine (*Pinus contorta* Douglas ex Loudon), western white pine (*Pinus monticola* Douglas ex D. Don in Lambert), ponderosa pine (*Pinus ponderosa* Douglas ex Lawson & C. Lawson), Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco), western red-cedar (*Thuja plicata* Donn ex D. Don in Lambert), western hemlock (*Tsuga heterophylla* (Rafinesque) Sargent), and trembling aspen (*Populus tremuloides* Michaux). The scientific names are according to the Flora of North America Editorial Committee (1993+).

Species frequency across western North America was determined with approximately 30,000 forest inventory plots from western Canada (Hamann and Wang 2005) and approximately 18,000 forest inventory plots from the western United States (Bechtold and Patterson 2005). As a common measure of species frequency, I use an estimated percent areal cover of the canopy projected to the ground, scaled by the total canopy cover of the forest inventory plot. Since this measure was not available for data from the western United States, I used percent basal area as a proxy for frequency as in Schroeder *et al.* (2010). Species frequencies for each ecosystem were calculated as average across all sample plots that fall within an ecosystem polygon. I also calculated probability of presence of

a species for each ecosystem unit. This was simply the proportion of inventory plots across all sample points where the species was present.

2.2.4. Model evaluation

A receiver operating characteristics (ROC) curve of the predicted probability of species presence was used to evaluate the statistical accuracy of the bioclimate envelope model for individual species. Overall model performance was evaluated by the area under the ROC curve (AUC), which represents the probability that the model classifier will correctly identify a randomly chosen true species presence (Fawcett 2006; Fielding and Bell 1997). The AUC of the ROC curve balances the ability of the model to detect a species when it is present (sensitivity) against its ability to not predict a species when it is absent (specificity). I further report model sensitivity (calculated as TP/(TP+FN), where TP=true positives and FP=false positives). Sensitivity and specificity values were reported as an average over a full range of thresholds between zero and one. All ROC and AUC calculations were carried out with the ROCR package (Sing et al. 2005) for the R programming environment (R Development Core Team 2008).

2.3. Results

2.3.1. Variable importance and model accuracy

RandomForest importance values indicate that most climate predictors have fairly equal roles in habitat predictions, with growing season precipitation, mean annual precipitation, and continentality being higher contributors to classifications (Table 2-1). Temperature related variables that describe the growing season apparently contribute less to the classification analysis. The most important variable to differentiate among western North American ecosystems in a classification tree analysis was found to be mean growing season precipitation, followed by mean annual precipitation, which is fairly highly correlated (r=0.79).

Model evaluation statistics for species presence/absence predictions are shown in Table 2-2. Except for the wide-ranging tree species, the total error rate of false positives and false negatives is low, in the single digit percentage range. AUC values are consistently high, ranging from 0.81 to 0.95, again with species that have restricted distributions having the best predictive accuracy (e.g. Sitka spruce). For the majority of species, the number of false negative errors is higher than the number of false positive errors, indicating that model prediction error is predominantly driven by omission error, or falsely predicting species absence. Similarly, model sensitivity, or the proportion of true species presences, is low and model specificity is high for all species, indicating that true species absences were well modeled.

2.3.2. Habitat projections and uncertainty

The first row of maps in Figure 2-1 illustrates the shift in projected ecosystem modeling units that contain Douglas-fir. I indicate aggregated modeling units with different colors representing major ecosystem classes. The displayed ecosystem classes are determined by majority vote over 18 habitat projections, implementing various climate change scenarios. The second row represents projections of Douglas-fir frequencies, derived by replacing ecosystem modeling units with known species frequencies. These maps indicate where Douglas-fir would be expected to be a major forest component in the future, again based on an average

of predictions for a variety of climate change scenarios. A low average frequency could therefore represent either a low frequency in most model runs or a higher frequency in few model runs.

The third row of Figure 2-1 quantifies uncertainty in habitat projections for the 2020s, 2050s, and 2080s. Red indicates that all models agree that the species will be absent, and blue indicates that all models agree that the species will be present. Intermediate shades indicate areas of uncertainty, which substantially increase towards the 2080s. In the example for Douglas-fir, by the end of the century uncertainty for the interior distribution appears to be so high that no reliable predictions can be made: over large areas approximately half the models project species presence and half predict absence of suitable species habitat.

Species frequency projections and maps of model uncertainty for all other species are provided in Appendix B (Figures B1 – B15), which also contain habitat projections under climate change trends observed over the last 25 years, represented by a recent decadal average (1997-2006 relative to the 1962-1990 baseline). Notable observations are the projection of substantial loss of habitat for boreal species, such as black spruce (Figure B1a), tamarack (Figure B8a) and trembling aspen (Figure B9a). Losses of projected habitat are particularly pronounced at the southern fringe of the boreal forest, and the dry boreal forest regions in the eastern rain shadow of the Canadian Rocky Mountains. These losses are consistently predicted with high certainty, regardless of the climate change scenario. Habitat of coastal species appears to be generally well maintained at the species level, although yellow cedar and western hemlock are predicted to lose suitable habitat at their southern coastal range limits (Figures B10 and B15 a-d). Habitat projections based on observed climate trends, represented by the 1997-2006 decadal average, are generally in the direction and

magnitude of climate change predictions. Especially at higher latitudes, habitat projections based on observed climate trends appear to approach or exceed those expected for the 2020s, for example black spruce (Figure B1a), aspen (Figure B9a), or white spruce (Figure B14a).

2.3.3. Elevation versus latitudinal shifts

Habitat projections for individual species' populations are summarized by broad geographic regions (Table 2-3), and I report latitudinal and elevation shifts further aggregated over all 18 climate change scenarios. An important observation is that elevation and latitude shifts predicted by climate envelope modeling are not independent over multiple populations or multiple model runs. For example, the new approximate climate match for an ecosystem unit may be associated with a northward latitudinal shift and a downward elevational shift in one model run, while another run leads to the reverse. This leads to strong negative correlations between predicted elevation and predicted latitudinal shifts (Figure 2-2), where symbols represent species–region combinations.

This relationship shown in Figure 2-2 for the consensus projections of multiple populations holds true for individual model runs: while similar climate change scenarios may produce rather different combinations of elevation and latitude shifts for individual ecosystem units (data not shown), elevation and latitudinal shifts can consistently be described by the formula: δ Elevation = δ Latitude × 0.44. In other words, a 100km north shift in latitude with the elevation held constant is equivalent to a 44m upward shift in elevation with the latitude held constant. The standard error estimate for the slope of this relationship (0.44) is 0.06. The linear relationship explains 37, 54, and 56% of the total variance in the predicted elevation versus northward shifts for the 1996-2006, 2020s and 2050s

climates, respectively. Based on this formula I report the average elevation shift given a zero latitudinal change, and the average latitudinal shift, given a zero elevation change (Table 2-4).

To provide a measure of variability of projections given in this table, average standard deviations across all populations for northward shifts are 100km, 180km for the 2020s and 2050s, respectively. Average standard deviations for elevation shifts are 40 and 80m for the 2020s and 2050s, respectively. Standard deviations for the 2080s are very large at the population level and even at the species level (Figure 2-1 and Appendix B Figures B1d-B15d). I have therefore not included the statistics for the 2080s in Figure 2-2 or Table 2-4, as they should not be used for any management applications.

2.3.4. Tracking habitat of populations

Under 1997–2006 climate conditions, representing an approximately 25-year climate change relative to the 1961–1990 reference period, population habitat across western North America has shifted approximately 130 kilometers north or approximately 60 meters up in elevation according to the bioclimate envelope model. The largest habitat shifts due to observed climate trends were identified for the boreal and the Canadian and US Interior Plateau regions. This reflects warming trends of approximately +1.5°C or more in mean annual temperature for these regions, and a reduction of mean annual precipitation by up to 20% for the 1997–2006 average relative to the 1961–1990 reference period (data not shown).

Projected latitudinal or elevation shifts for western North America on average double for the 2020s, and double again for the 2050s compared to habitat shifts calculated based on the 1997-2006 observed climate (Figure 2-2). As observed in

the recent past, the most prominent shifts for the 2020s are predicted for the boreal and the US and Canadian Rockies regions. This primarily affects populations of black spruce, white spruce, aspen, and tamarack. For the 2050s northern coastal populations of tree species are also projected to experience large geographic lags. For example, populations of yellow cedar, Sitka spruce, pacific silver fir, western hemlock and western redcedar would be affected (Table 2-4).

2.4. Discussion

2.4.1. Characteristics of the ecosystem-based modeling approach

Ecosystem-based bioclimate envelope modeling can be used to integrate genetic information about local adaptation of tree populations within a species. In this study, I use ecosystem delineations only as proxy for species' populations for the purpose of tracking their climatic envelopes under climate change. I therefore do not make assumptions about actual genetic adaptation of populations to local climatic environments. This is nevertheless a useful improvement over standard species distribution models that treat species as a homogeneous unit (e.g. Botkin et al. 2007; Hampe 2004). Rather than just informing where habitat is lost, maintained, or gained, this modeling approach provides geographically referenced matches between the projected and baseline climate conditions. Under the assumption that populations are indeed adapted to local climate conditions, my projections suggest that northern and high elevation populations may be as vulnerable to climate change as populations at the trailing edge of the species range. My analysis supports empirical data by Chen et al. (2010), and confirms reservations by Hampe (2004) on the correct interpretation of species distribution model projections.

Compared to other species distribution models, this ecosystem-based approach appears to yield similar levels of predictive accuracy (e.g. Schroeder et al. 2010). I find the best accuracy for coastal species with AUC values above 0.9, which is generally interpreted as excellent predictive accuracy. Species that tend to have large ranges, such as lodgepole pine or trembling aspen, have the lowest AUC values. Presumably factors other than climate have a higher importance in determining the distribution of these species. A notable difference to standard species distribution models is that error rates in this ecosystem-based modeling approach are driven by omission error rather than falsely predicting species presence, which is more prevalent in other species distribution models (e.g. Rehfeldt et al. 2009). My projections of suitable habitat are therefore somewhat conservative, as this approach tends to under-, rather than over-predict species habitat. The reason for this model property is likely that I more narrowly define the environmental climate niche of species by bounding their climate space with adjacent ecosystem units where species are absent. From a management perspective, determining species choice for management applications should therefore be quite safe because I underpredict suitable habitat.

2.4.2. Adaptational lag implies a need for assisted migration

My results suggest that climate change observed over the last 25 years has already resulted in a notable lag of populations behind their optimal climate niches that are in the same direction and approximately half of the magnitude as climate change predictions for the 2020s (Table 2-4, Figure 2-2). According to this analysis, seed could be moved 130km north or 60m up in elevation, although the values vary for different species and different regions in western North America.

This recommendation makes a number of assumptions that I should discuss in more detail.

In most reforestation programs the choice of planting stock is based on the assumption that local seed is best adapted the climate conditions of the planting site. If environmental conditions change faster than local populations are able to adapt through evolutionary processes, the resulting mismatch is referred to as adaptational lag, which can be revealed by reciprocal transplant experiments (e.g. Matyas 1990). Optimality of local populations refers to the same concept as equilibrium assumptions in species distributions modeling. Obviously, I make the assumption that populations were optimally adapted under the 1961-1990 climate normal that I use as reference period for observed and predicted climate change. This is certainly not always true (Matyas 1990), so I have to ask how this compromises reforestation recommendations. My reply to practitioners would be that these recommendations will not result in an improvement in species survival or productivity observed between 1961 and 1990. In effect, these recommendations perpetuate any adaptational lag that pre-existed during the 1961-1990 reference period. Attempting to truly optimize the match of genotypes and environments requires comprehensive reciprocal transplant experiments, and is an endeavor that has its own limitations and pitfalls (Hamann and Wang 2005).

I further want to emphasize that allowable seed transfers are very generally expressed in Table 2-4 and should only be made within similar forest types to minimize the chance of seed being maladapted. Current recommendations of planting stock for reforestation are usually made for seed zones that often represent broad geographic areas. Within these zones exists a wide variety of local site conditions that differ in moisture, exposure, slope position or nutrient regime. Forest managers use silvicultural knowledge to determine which species are best suited for a particular planting site. The same principle will apply under population transfers guided by Table 2-4. Habitat projections, like seed zones, offer guidance as to which planting stock is best for a broad climatic region. Species choice for microsites continues to be at the discretion of forest managers.

2.4.3. Uncertainty requires short-term adaptation strategies

For assisted migration prescription under climate change projections for the future, I recommend caution and careful review of the model agreement maps in the Appendix Figure B1-B15. For example, projected habitat maps show a large portion of southern Alberta will become climatically suitable for ponderosa pine at a relatively high frequency by the 2050s (Figure B6c), but if I consider the model agreement output, only half the models agree this new habitat will be suitable for ponderosa pine in the 2050s. Unless there is high model agreement for a reforestation target area, I recommend that latitudinal and elevation transfers presented in Table 4-4 should be implemented within a species' current range or just beyond species' current distributions.

Secondly I should note that habitat projections were associated with increasing uncertainties toward the end of the coming century. Differences in habitat projections for the 2020s were moderate but dramatically increased towards the 2080s. By the end of the century, I find substantial proportions within the range of most species, where approximately half of the model runs projected presence, whereas the other half predicted absence (Figure 2-1 and Figures B1-B15). This result suggests that the development of climate change adaptation strategies is limited to a short-term planning horizon.

Even though the life span of most tree species included in this study exceeds the 2080s, I think that forest resource managers need to focus on the immediate future when developing seed transfer prescriptions, since trees are likely most vulnerable to climatic factors at the seedling stage (Black and Bliss 1980; Donovan et al. 1988). We could not currently plant genotypes that would be optimally adapted to 2080s climate. Instead we have to focus on survival under environmental conditions at present and in the near future. Seed transfers according to the 1997-2006 and 2020s projections will have the best chance of survival now and will likely be able to better withstand future climate stress as mature trees that are more resilient to climate fluctuations. Although I realize that this will mean that tree populations will continue to lag behind their optimal climate, targeting current and 2020s climate conditions is still a low-risk improvement over status-quo management practices.

Another compelling argument to locally change status-quo management practices are the substantial number of observed climate change impacts on forest heath and productivity (Allen 2009). The decline of aspen and white spruce in western Canada (Allen et al. 2010; Michaelian et al. 2010) coincides with habitat loss at the southern fringe of the boreal forest in my model projections. Other issues observed in forest trees in the study area include unprecedented insect and disease epidemics in many species of the *Pinaceae* family across western North America (Raffa et al. 2008; Welsh et al. 2009; Woods et al. 2005). Additional issues related to warming and reduced precipitation include mortality or growth reductions in white spruce in Alaska (Barber et al. 2000), ponderosa pine in northern New Mexico (McDowell et al. 2010), and yellow cedar in the Pacific Northwest (Hennon et al. 2006). Although the link to changing climate conditions is not always straight forward (e.g. Hennon et al. 2006; Woods et al. 2005), I

think that these observations are compelling arguments to test different species or

different genotypes that may be better adapted to new climatic realities.

2.5. Literature Cited

- Allen, C.D. 2009. Climate-induced forest dieback: an escalating global phenomenon. Unasylva **231/232**: 43-49.
- Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.H., Allard, G., Running, S.W., Semerci, A., and Cobb, N. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecology and Management 259(4): 660-684.
- Austin, M. 2007. Species distribution models and ecological theory: A critical assessment and some possible new approaches. Ecological Modelling **200**(2-2): 2-19.
- Barber, V.A., Juday, G.P., and Finney, B.P. 2000. Reduced growth of Alaskan white spruce in the twentieth century from temperature-induced drought stress. Nature **405**(6787): 668-673.
- Bechtold, W. A., and Patterson, P. L. 2005. The enhanced Forest Inventory and Analysis program- a national sampling design and estimation procedures. USDA Forest Service General Technical Report, SRS-80.
- Black, R.A., and Bliss, L.C. 1980. Reproductive ecology of *Picea mariana* (Mill.)BSP., at tree line near Inuvik, Northwest Territories, Canada. Ecological Monographs **50**: 331-354.
- Botkin, D.B., Saxe, H., Araujo, M.B., Betts, R., Bradshaw, R.H.W., Cedhagen, T., Chesson, P., Dawson, T.P., Etterson, J.R., Faith, D.P., Ferrier, S., Guisan, A., Hansen, A.S., Hilbert, D.W., Loehle, C., Margules, C., New, M., Sobel, M.J., and Stockwell, D.R.B. 2007. Forecasting the effects of global warming on biodiversity. BioScience 57(3): 227-236.

Breiman, L. 2001. Random forests. Machine Learning 45(1): 5-32.

- Chen, P., Welsh, C., and Hamann, A. 2010. Geographic variation in growth response of Douglas-fir to interannual climate variability and projected climate change. Global Change Biology **16**(12): 3374-3385.
- Cutler, D.R., Edwards, T.C., Beard, K.H., Cutler, A., and Hess, K.T. 2007. Random forests for classification in ecology. Ecology **88**(11): 2783-2792.
- Daly, C., Halbleib, M., Smith, J.I., Gibson, W.P., Doggett, M.K., Taylor, G.H., Curtis, J., and Pasteris, P.P. 2008. Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. International Journal of Climatology 28(15): 2032-2064.
- Davis, M.B., and Shaw, R.G. 2001. Range shifts and adaptive responses to Quaternary climate change. Science **292**(5517): 673-679.
- Donovan, L.A, McLeod, K.W., Sherrod, K.C. Jr., and Stumpff, N.J. 1988. Response of woody swamp seedlings to flooding and increased water temperatures (I) Growth, biomass, and survivorship. American Journal of Botony 75: 1181-1190.
- EPA. 2007. Ecoregion Maps and GIS Resources. U.S. Environmental Protection Agency, Western Ecology Division official website, Available online at: http://www.epa.gov/wed, accessed 10 May 2008.
- Fawcett, T. 2006. An introduction to ROC analysis. Pattern Recognition Letters 27(8): 861-874.
- Fielding, A.H., and Bell, J.F. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Envrionmental Conservation 24(1): 38-49.
- Flora of North America Editorial Committee (eds). 1993+. Flora of North America of Mexico. 15 vols., New York and Oxford.
- Guisan, A., and Zimmermann, N.E. 2000. Predictive habitat distribution models in ecology. Ecological Modelling **135**(2-3): 147-186.
- Hamann, A., Gylander, T., and Chen, P. 2011. Developing seed zones and transfer guidelines with multivariate regression trees. Tree Genetics & Genomes 7: 399-408.
- Hamann, A., and Wang, T. 2006. Potential effects of climate change on ecosystem and tree species distribution in British Columbia. Ecology 87(11): 2773-2786.
- Hamann, A., and Wang, T. 2005. Models of climate normals for genecology and cliamte change studies in British Columbia. Agriculture and Forest Meteorology 128: 211-221.

- Hampe, A. 2004. Bioclimate envelope models: What they detect and what they hide. Global Ecology and Biogeography **12**(5): 469-471.
- Hannah, L., Midgley, G., Andelman, S., Araujo, M., Hughes, G., Martinez-Meyer, E., Pearson, R., and Williams, P. 2007. Protected area needs in a changing climate. Frontiers in Ecology and the Environment 5(3): 132-138.
- Hennon, P., D'Amore, D., Wittwer, D., Johnson, A., Schaberg, P., Hawley, G., Beier, C., Sink, S., and Juday, G. 2006. Climate warming, reduced snow, and freezing injury could explain the demise of yellow-cedar in southeast Alaska, USA. World Resource Review 18(2): (427-450).
- Hogg, E.H. 1997. Temporal scaling of moisture and the forest-grassland boundary in western Canada. Agricultural and Forest Meteorology **84**(2-2): 115-122.
- Jackson, S.T., Betancourt, J.L., Booth, R.K., and Gray, S.T. 2009. Ecology and the ratchet of events: Climate variability, niche dimensions, and species distributions. PNAS **16**(2): 19685-19692.
- Matyas, C. 1990. Adaptational lag: a general feature of natural populations. *In* In: Joint Meeting of Western Forest Genetics Association and IUFRO Working Parties, Douglas-fir, Contorta Pine, Sitka Spruce, and Abies Breeding and Genetic Resources. 20-24 August, Olympia, Washington 11 pp.
- Mbogga, M.S., Hamann, A., and Wang, T.L. 2009. Historical and projected climate data for natural resource management in western Canada. Agricultural and Forest Meteorology **149**(5): 881-890.
- Mbogga, M.S., Wang, X.L., and Hamann, A. 2010. Bioclimate envelope model predictions for natural resource management: dealing with uncertainty. Journal of Applied Ecology 47(4): 731-740.
- McDowell, N.G., Allen, C.D., and Marshall, L. 2010. Growth, carbon-isotope discrimination, and drought-associated mortality across a *Pinus ponderosa* elevational transect. Global Change Biology **16**(1): 399-415.
- Meidinger, D., and Pojar, J. 1991. Ecosystems of British Columbia. Special Report Series 6. Research Branch, BC Ministry of Forests and Ranges, Victoria, British Columbia, ISBN 0843-6452.
- Michaelian, M., Hogg, E.H., Hall, R., J., and Arsenault, E. 2010. Massive mortality of aspen following severe drought along the southern edge of the Canadian boreal forest. Global Change Biology: doi: 10.111/j.1365-2486.2010.02357.x.

- Millar, C.I., Stephenson, N.L., and Stephens, S.L. 2007. Climate change and forests of the future: Managing in the face of uncertainty. Ecological Applications **17**(8): 2145-2151.
- Morgenstern, E.K. 1996. Geographic Variation in Forest Trees. Genetic Basis and Application of Knowledge in Silviculture. University of British Columbia Press, Vancouver, BC, Canada, 209 pp.
- NRC. 2006. Natural regions and Subregions of Alberta. Natural Regions Committee, Government of Alberta, Alberta Environment, Edmonton, Alberta, ISBN 0-7785-4572-5.
- O'Neill, G.A., Hamann, A., and Wang, T.L. 2008. Accounting for population variation improves estimates of the impact of climate change on species' growth and distribution. Journal of Applied Ecology **45**(4): 1040-1049.
- Overpeck, J.T., Bartlein, P.J., and Webb, T. 1991. Potential magnitude of future vegetation change in eastern North-America comparisons with the past. Science **254**(5032): 692-695.
- Poorter, L. 2007. Are species adapted to their regeneration niche, adult niche, or both? The American Naturalist **169**(4): 433-442.
- R Development Core Team. 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing, ISBN 3-900051-07-0, Vienna, Austria.
- Raffa, K.F., Aukema, B.H., Bentz, B.J., Carroll, A.L., Hicke, J.A., Turner, M.G., and Romme, W.H. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: The dynamics of bark beetle eruptions. BioScience 58(6): 501-517.
- Rehfeldt GE, Ferguson DE, Crookston NL (2009) Aspen, climate, and sudden decline in western USA. Forest Ecology and Management 258(11):2353-2364
- Schroeder, T.A., Hamann, A., Wang, T.L., and Coops, N.C. 2010. Occurrence and dominance of six Pacific Northwest conifer species. Journal of Vegetation Science 21(3): 586-596.
- Selby, C.J., and Santry, M.J. 1996. A National Ecological Framework for Canada: Data model, Database and Programs. Centre for Land and Biological Resources Research, Research Branch, Agriculture and Agri-Food Canada and State of the Environment Directorate, Environment Canada, ISBN 0-662-24107-X.

- Sing, T., Sander, O., Beerenwinkel, N., and Lengauer, T. 2005. ROCR: visualizing classifier performance in R. Bioinformatics 21(20): 3940-3941.
- Thomas, C., D., Cameron, A., Green, R., E., Bakkenes, M., Beaumont, L., J.,
 Collingham, Y., C., Erasmus, B., F. N., Ferreira de Slquelra, M., Grainger,
 A., Hannah, L., Huges, L., Huntley, B., van Jaarsveld, A., S., Midgley, G.,
 F., Miles, L., Ortega-Huerta, M., A., Townsend Peterson, A., Phillips, O.,
 L., and Williams, S., E. 2004. Extinciton risk from climate change. Nature
 427: 145-148.
- Thuiller, W., Albert, C., Araujo, M.B., Berry, P.M., Cabeza, M., Guisan, A., Hickler, T., Midgely, G.F., Paterson, J., Schurr, F.M., Sykes, M.T., and Zimmermann, N.E. 2008. Predicting global change impacts on plant species' distributions: future challenges. Perspectives in Plant Ecology Evolution and Systematics 9(3-4): 137-152.
- Wang, T., Hamann, A., Spittlehouse, D.L., and Aitken, S.N. 2006a. Development of scale-free climate data for western Canada for use in resource management. International Journal of Climatology 26(3): 383-397.
- Wang, T., Hamann, A., Yanchuk, A., O'Neill, G.A., and Aitken, S.N. 2006b. Use of response functions in selecting lodgepole pine populations for future climates. Global Change Biology 12(12): 2404-2416.
- Wang, T., O'Neill, G.A., and Aitken, S.N. 2010. Integrating environmental and genetic effects to predict responses of tree populations to climate. Ecological Applications 20(1): 153-163.
- Welsh, C., Lewis, K., and Woods, A. 2009. The outbreak history of Dothistroma needle blight: an emerging forest disease in northwestern British Columbia, Canada. Canadian Journal of Forest Research **39**(12): 2505-2519.
- Woods, A., Coates, K.D., and Hamann, A. 2005. Is an unprecedented dothistroma needle blight epidemic related to climate change? BioScience **55**(9): 761-769.
- Ying, C.C., and Yanchuk, A.D. 2006. The development of British Columbia's tree seed transfer guidelines: Purpose, concept, methodology, and implementation. Forest Ecology and Management 227(1-2): 1-13.

Climate Variable	RF Importance
Mean annual temperature (°C)	6424
Mean warmest month temperature (°C)	5835
Mean coldest month temperature (°C)	7974
Continentality (°C)	8463
Mean annual precipitation (mm)	9049
Growing season precipitation (mm)	9825
Climate moisture index (cm)	7134
Growing season climate moisture index (cm)	6352
Degree days $>5^{\circ}C$ (days)	6862
Frost free period (days)	6811

Table 2-1. Importance of predictor climate variables in distinguishing ecosystems of western North America with the RandomForest ensemble classifier.

Species	Present ¹	Range (sq km)	Relative Abundance ²	Error Rate ³	Model Specificity	Model Sensitivity	AUC
Black spruce	4489	710,748	0.14	0.07	0.88	0.58	0.90
Douglas-fir	8808	1,002,592	0.21	0.12	0.86	0.60	0.88
Engelmann spruce	6223	581,058	0.09	0.10	0.86	0.56	0.81
Lodgepole pine	11275	1,016,718	0.13	0.19	0.77	0.61	0.82
Pacific silver fir	1615	172,348	0.16	0.02	0.95	0.64	0.93
Ponderosa pine	3967	591,394	0.23	0.06	0.93	0.59	0.88
Sitka spruce	1016	217,983	0.21	0.02	0.95	0.65	0.95
Tamarack	406	324,392	0.03	0.01	0.91	0.61	0.93
Trembling Aspen	7241	1,135,473	0.14	0.12	0.76	0.64	0.83
Western hemlock	4860	362,021	0.19	0.05	0.94	0.67	0.94
Western larch	821	119,669	0.05	0.01	0.95	0.54	0.86
Western redcedar	3798	305,163	0.08	0.06	0.92	0.68	0.94
Western white pine	820	185,919	0.02	0.01	0.92	0.60	0.89
White spruce	7115	848,866	0.10	0.11	0.84	0.61	0.88

Table 2-2. Sampling and biogeographical information for species, as well as statistics that describe the predictive accuracy of the species distribution model for 15 major forest tree species in western North America.

¹ Out of approximately 54,716 sample plots, including non-forested plots

² Expected percent basal area when present in a sample plot

³ Error Rate = (False Positive + False Negative)/(Total Positive+Total Negative)

Table 2-3. The geographic regions that were use to summarize shifts in suitable habitat are defined by four ecological classification systems. The table lists the "zone" name for BC (Meidinger and Pojar 1991), the "natural subregion" name for AB (NRC 2006), the "ecoregion" name for SK and MB (Selby and Santry 1996), or the "level III natural region" name for the US (EPA 2007).

Region	Ecosystem Polygons
North Coast	BC: Coastal Western Hemlock and Mountain Hemlock north of 51° latitude; US: Alaskan Panhandle
Mid Coast	BC: Coastal Western Hemlock, Coastal Douglas-Fir and Mountain Hemlock south of 51° latitude; US: Coast Range and Puget Lowlands
South Coast	US: Southern and Central California Chaparral and Oak Woodlands
North Coast Mountains	BC: Engelmann Spruce-Subalpine Fir and Interior Cedar-Hemlock north of 51° latitude.
Mid Coast Mountains	BC: Engelmann Spruce-Subalpine Fir, Interior Douglas-Fir, Mountain Spruce south of 51° latitude; US: Cascades and North Cascades
South Coast Mountains	US: Klamath Mountains, Southern California Mountains, Sierra Nevada
Canadian Rockies	BC: Engelmann Spruce-Subalpine Fir, Interior Cedar-Hemlock, Interior Douglas-Fir, Mountain Spruce and Sub-boreal Spruce within the mountain range; AB: Alpine, Subalpine, Montane and Upper Foothills
US Rockies	US: Northern Rockies, Idaho Batholiths, Middle Rockies, Canadian Rockies, Wasatch and Uinta Mountains, and Southern Rockies within mountain range
Boreal	BC: Boreal White and Black Spruce; AB: Athabasca Plain, Boreal Sub-arctic, Northern Mixedwood, Central Mixedwood, Dry Mixedwood, Kazan Uplands, Lower Boreal Hills and Peace- Athabasca Delta; SK/MB: Athabasca Plain, Churchill River Upland, Mid-boreal Upland, Mid-boreal Lowland and Boreal Transition
Sub-boreal Mixedwood	BC: Sub-Boreal Spruce, Sub-Boreal Pine-Spruce and Spruce- Willow-Birch
Canadian Interior Plateau	BC: Ponderosa Pine and adjacent Interior Douglas-Fir
US Interior Plateau	US: dry conifer forest occurring in selected parts of the Blue Mountains, Middle Rockies, North Cascades, and Eastern Cascades Slopes and Foothills

		1997-2006 Shifts		2020s Shifts		2050s Shifts	
Species	Region	North (km)	Elevation (m)	North (km)	Elevation (m)	North (km)	Elevation (m)
Black E spruce C S	Boreal Canadian Rockies Sub-boreal Mixedwood	223 106	98 46	439 317	193 140	834 642	367 283
		143	63	329	145	704	310
Douglas- fir	Canadian Interior Plateau	399	176	287	126	482	212
	Canadian Rockies	133	58	345	152	668	294
	Mid Coast	141	62	242	106	535	235
Mid Coast Mountains South Coast Sub-boreal Mixedwood	Mid Coast Mountains	88	39	164	72	417	183
	South Coast	75	33	380	167	544	239
	Sub-boreal Mixedwood	161	71	348	153	424	317
	US Interior Plateau	193	85	133	58	721	39
	US Rockies	175	77	240	106	407	179
Engelmann Can spruce Mid Mou US I	Canadian Rockies	62	27	344	151	719	317
	Mountains	31	14	195	86	399	176
	US Interior Plateau	51	22	404	178	557	245
	US Rockies	299	132	264	116	379	167
Lodgepole	Boreal	166	73	337	148	709	312
pine	Canadian Rockies Mid Coast Mountains	62	27	322	142	633	278
		113	50	260	114	571	251
	Sub-boreal Mixedwood	75	33	380	167	544	239
	US Interior Plateau	154	68	264	116	786	202
	US Rockies	168	74	309	136	542	238
Pacific	Mid Coast	175	77	267	118	544	239
silver fir	North Coast	215	95	323	142	/39	325

Table 2-4. Northward and elevation shift of suitable habitat for populations relative to the 1961-1990 reference projection, averaged over 18 climate change scenarios. I report elevation change for a constant latitude, and latitudinal change for a constant elevation. For seed transfer these values represent maximum limits for a latitudinal *or* elevation transfer.

		1997-2006 Shifts		2020s Shifts		2050s Shifts	
Species	Region	North (km)	Elevation (m)	North (km)	Elevation (m)	North (km)	Elevation (m)
Ponderosa pine	US Interior Plateau	102	45	392	172	586	258
	US Rockies	231	102	278	122	533	294
Sitka	Mid Coast	75	33	95	42	268	118
spruce	North Coast	157	69	354	156	834	367
Tamarack	Boreal	114	50	337	148	675	297
	Canadian Rockies	10	4	366	161	549	242
Trembling aspen	Boreal	197	87	387	170	735	323
	Canadian Rockies	81	36	334	147	624	275
	Sub-boreal Mixedwood	192	84	360	158	514	226
US Interior Plateau	US Interior Plateau	130	57	133	58	765	39
US Rockies	US Rockies	92	40	137	60	372	164
Western	Canadian Rockies	281	124	411	181	772	339
hemlock	Mid Coast	135	59	182	80	417	184
	North Coast	159	70	366	161	856	377
Western	Canadian Rockies	170	75	404	178	648	285
larch	US Rockies	196	86	532	234	803	353
Western redcedar	Canadian Rockies Mid Coast North Coast	274 155 128	121 68 56	379 254 328	167 112 145	697 568 753	307 250 331
Western white pine	Canadian Rockies Mid Coast Mountains	314 12	138 5	496 147	218 65	749 392	329 172
White spruce	Boreal	207	91	419	184	817	359
	Canadian Rockies	57	25	307	135	627	276
Yellow	Mid Coast	106	47	356	157	685	301
cedar	North Coast	70	31	262	115	515	227

Table 2-4: Continued.


Figure 2-1. Projections of Douglas-fir habitat for the 1961–1990 reference period and under climate scenarios for the 2020s, 2050s and 2080s. The rows of maps show projections of individual populations, average expected frequency based on multiple climate change scenarios, and degree of consensus among projections based on multiple climate change scenarios.



Figure 2-2. Plot of the projected northward shift verses the shift in mean elevation for all species-region combinations presented in Table 4. A linear regression according to the formula δ Elevation = δ Latitude × 0.44 describes the interchangeable relationship of northward and upward seed transfer.

Chapter 3. Strategies for reforestation under uncertain future climates: guidelines for Alberta, Canada¹

Summary

Commercial forestry programs normally use locally collected seed for reforestation under the assumption that tree populations are optimally adapted to local environments. However, in western Canada this assumption is no longer valid based on climate trends that have materialized over the last several decades. The objective of this study is to demonstrate how I can arrive at reforestation recommendations with alternate species and alternate genotypes that are viable under a majority of climate change scenarios. In a case study for commercially important tree species of Alberta, I use an ecosystem-based bioclimate envelope modeling approach for western North America to project habitat for locally adapted populations of tree species using multi-model climate projections for the 2020s, 2050s and 2080s. I find that genotypes of species that are adapted to drier climatic conditions will be the preferred planting stock over much of the boreal forest that is commercially managed. Interestingly, no alternative species that are currently not present in Alberta can be recommended with any confidence. Finally, I observe very large uncertainties in projections of suitable habitat that make reforestation planning beyond the 2050s difficult for most species. Millions of hectares of forests are commercially harvested and reforested every year in Alberta. Choosing alternative planting stock, suitable for anticipated future climates, could therefore offer a potent climate change adaptation strategy at virtually no additional cost. Habitat projections for locally adapted tree populations under observed climate change conforms generally well with projections for the 2020s, which suggests that it is a safe strategy to change current reforestation practices and adapt to new climatic realities through assisted migration prescriptions.

¹ A version of this chapter has been published as: Gray, L. K. and Hamann, A. 2011.Strategies for reforestation under climate change: guidelines of Alberta, Canada. PLoS One (accepted 01-07-2011)

3.1. Introduction

Reforestation with planting stock that is grown in nurseries is a widely used practice in western Canada and elsewhere. Forest companies and provincial agencies in Alberta plant approximately 80 million seedlings to reforest more than 50,000 hectares annually. For successful reforestation programs, planting stock must be both genetically well adapted to the target environment and contain a sufficient amount of genetic diversity. Generally, two decisions have to be made when selecting planting stock. First, an appropriate species has to be chosen for a planting site. Usually, forest sites can support a variety of tree species, allowing forest managers to choose which species best fit their economic or ecological objectives. The second choice concerns the genetic makeup of reforestation stock. Most widespread tree species show adaptation of local populations to different macroclimatic conditions that are frequently observed over latitudinal or elevational gradients (Morgenstern 1996). To minimize the risk of mal adaptation most jurisdictions legislate seed transfer guidelines or seed zones, which restrict how far seed may be moved from a collection location to a planting site (Ying and Yanchuk 2006; Hamann et al. 2011). Under the assumption that local populations are optimally adapted to the environments in which they occur, prescribing reforestation with species and genotypes collected near the planting site can reduce the risk of mal-adaptation.

In Alberta, movement of seed is regulated with seed zones, a system of approximately 60 geographic delineations for forested areas of the province (Figure 1, map inset). These seed zones are based on an ecological classification system of Natural Regions and Subregions of Alberta (NRC 2006). Seed can be freely moved within the seed zone or origin, but transferring seed outside seed zone boundaries is usually prohibited (SRD 2005). Using fine scale ecosystem classifications as a proxy for the genetic structure of tree species is a common practice when lacking genetic information. As genetic data become available from long-term field experiments, fine scale seed zones are usually consolidated into larger units if no genetic differentiation between adjacent zones is found (Ying and Yanchuk 2006; Hamann et al. 2011).

Although this system of governing seed movement has been successfully used in many parts of the world, the key assumption, that local tree populations are optimally adapted to the environments in which they occur, may no longer be valid. For example, Alberta has experienced a warming trend of 0.8°C and a decrease of about 10% in precipitation over the last 25 years (Mbogga et al. 2009). Large-scale dieback of forest trees related to drought stress has been observed along the southern edge of the boreal forest (Hogg et al. 2002; Hogg et al. 2008; Michaelian et al. 2010). The latter study estimates that drought-related dieback of forest over the last decade has resulted in 45 Megatons of dead biomass in central Alberta, representing 20% of the total aboveground biomass.

Recognizing that management interventions are necessary to maintain forest health and productivity in the face of climate change, the Alberta government released interim seed transfer guidelines in 2009, allowing upward and northward transfers across adjacent seed zone boundaries within the natural subregion of origin (SRD 2009). Larger distance seed transfers may be allowed, but require case-by-case approval from the Alberta Tree Improvement and Seed Center (SRD 2009). I think that this policy framework can be developed into an effective climate change adaptation strategy for the forestry sector, and this study is meant to support decision making by the provincial government of Alberta for selection of species and genotypes that are well adapted to expected future environments.

This study builds on a larger modeling effort that covers 15 commercially important forestry species of western North America, which was presented in Chapter 2. Here, I present a detailed regional analysis that can be used to guide the reforestation activities in Alberta, and that may serve as a template for other jurisdictions. I use multi-model projections of species habitat for the 2020s, 2050s and 2080s to aid species choice for reforestation. The goal is to arrive at species recommendations that are viable under most climate change scenarios. As a second step, I determine suitable genotypes for a given planting site. Given the considerable uncertainty in climate change projections, I provide multiple seed source recommendations that approximately match expected future environments. Multiple seed sources could be prescribed to enhance genetic diversity in the landscape to hedge against uncertainty. I also provide multiple choices of seed sources to allow flexible implementation of assisted migration prescriptions in the face logistical constraints in seed supply that forest companies and provincial agencies face.

3.2. Materials and methods

3.2.1. Climate envelope modeling

This study builds on an ecosystem-based modeling effort, where habitat of populations for 15 commercially important forestry species of western North America are tracked under observed and projected climate change, which was presented in Chapter 2. The modeling approach characterizes the climate space of delineated ecosystem polygons, which represent habitat for individual species' populations. The ecosystem units are then predicted as a dependent class variable using climate conditions under various future scenarios as predictor. Predictions

were performed with an ensemble classification tree analysis implemented by the RandomForest software package (Breiman 2001) for the R programming environment (R Development Core Team 2008). RandomForest grows multiple dichotomous decision trees from bootstrap samples to predict a dependent class variable (Cutler et al. 2007). In this stuyd 200 trees were used and the final predicted ecosystem was determined by majority vote over all classification trees. As dependent variable, the "seedzone" delineation of the Natural Regions and Subregions of Alberta (NRC 2006) were used. To determine whether new species or seed sources from outside Alberta should be introduced under climate change scenarios, this study relied on habitat projections derived in Chapter 2. Thus, additional ecosystem units include the "variant" level of the Biogeoclimatic Ecological Classification system for British Columbia (Meidinger and Polar 1991). For other Canadian provinces and the United States the "ecodistrict" level of the National Ecological Framework for Canada (Selby and Santry 1996), and "level IV" classification of the Ecoregion System (EPA 2007) was used respectively. From each of these ecosystem classes 100 grid cells were randomly sampled at 1km resolution, then climatically characterized, and subsequently used as training data for classification tree analysis.

3.2.2. Climate data and climate projections

I used interpolated climate data for the 1961-1990 normal period, covering the United States and Canada west of 100° latitude. Interpolation of weather station data was performed with the Parameter Regression of Independent Slopes Model (Daly et al. 2008) for monthly minimum temperature, maximum temperature and precipitation. I enhanced this data with lapse-rate based down-scaling to 1km resolution and an estimation of biologically relevant climate variables with a software package that is freely available at

http://www.ualberta.ca/~ahamann/climate.html (Mbogga et al. 2009; 2010). Ten predictor variables with relatively low collinearity were chosen, representing both seasonal and annual climate variables. This includes mean annual temperature, mean warmest month temperature, mean coldest month temperature, continenality (difference between mean January and mean July temperature), mean annual precipitation, growing season precipitation (May to September), the number of frost free days, the number of growing degree days above 5°C, described in more detail by Wang *et al.* (2006). I also included two dryness indices: annual and summer climate-moisture index according to Hogg (1997).

To generate future climate projections for the 2020s, 2050s and 2080s I overlaid projections from general circulation models expressed as the difference from the 1961-1990 normal using the same software package as above. For each future period, climate projections were based on four major SRES emission and population growth scenario families (A1FI, A2, B1, B2), implemented by five modeling groups (CGCM, Canada; CSIRO2. Australia; HADCM3, United Kingdom; ECHAM4, Europe; and PCM, United States). Two model-emission scenario combinations (ECHAM4-A1FI and ECHAM4-B1) were unavailable, resulting in 18 climate projections per time period. Climate projections for the 1997-2006 decadal average were used to represent observed climate change over a 25-year period (the mid-point of the 1961-1990 climate baseline period and the mid-point of the recent decadal average: 1975 to 2000).

3.2.3. Species projections and model validation

Here projected ecosystem units were used to represent populations of tree species and to derive predictions of species habitat. The frequency and probability of presence of major forest tree species in ecosystem units was calculated from 54,716 forest inventory plots covering western North America. This includes provincial databases from British Columbia previously described in Hamann et al. (Hamann et al. 2005). For Alberta I used permanent and temporary forest inventory plots as well as the Ecological Site Information System (ESIS) database provided by the Government of Alberta (Government of Alberta 2008). For all the sample plots in western Canada, an estimated percent areal cover of the canopy projected to the ground, scaled by the total canopy of the forest inventory plot was used for species frequency. In the western United States I rely on the Forest Inventory and Analysis database (Bechtold and Patterson 2005), where the percent basal area was used as a proxy for frequency because the percent areal cover of the canopy was unavailable. Species frequency for each ecosystem unit was calculated as the average across all sample plots that fall within an ecosystem polygon. The probability of presence of a species was simply calculated as the proportion of the inventory plots within the ecosystem polygon where the species was present.

To assess the predictive accuracy of bioclimate envelope models for individual species, the area under the curve (AUC) of the receiver operating characteristics (ROC) curve of the probability of species presence was calculated. The AUC value measures the ability of the model to detect a species where it is known to be present against its ability to correctly predict where the species is known to be absent (Fielding and Bell 1997; Fawcett 2006). All ROC and AUC calculations were carried out with the ROCR package (Sing et al. 2005)for the R programming environment (R Development Core Team 2008).

Five commercially important conifer tree species occur in Alberta: black spruce (*Picea mariana* (Miller) Britton), Douglas-fir (*Pseudotsuga menziesii* (Mirbel)

Franco), lodgepole pine (*Pinus contorta* Douglas ex Loudon), jack pine (*Pinus banksiana* Lambert, Descr.), and white spruce (*Picea glauca* (Moench) Voss). Habitat projections derived in Chapter 2 show ponderosa pine (*Pinus ponderosa* Douglas ex Lawson & C. Lawson) is projected to gain suitable habitat in Alberta in the future and was therefore also included in this analysis. The scientific names are according to the Flora of North America Editorial Committee (Flora of North America Editorial Committee (eds) 1993+).

3.2.4. Seed source recommendations

Multiple options of seed sources for reforestation under current and future climates were derived with a multivariate measure of climate similarity. The objective was to find seed sources that best match a target region under observed and projected climate change. To quantify this match, I use the squared Mahalanobis distance, calculated with the Ecodist package (Goslee and Urban 2007) for the R programming environment (R Development Core Team 2008). Mahalanobis distances matrices were calculated for 10 climate predictor variables described above, and are reported for seed zone units characterized under current climate and under ensemble scenarios for the 2020s, 2050s, and 2080s. The Mahalanobis distance is a normalized Euclidean distance that weighs individual variables according to their collinearity with all other variables (Mahalanobis 1936). Variables that are perfectly correlated are weighted as a single variable in distance calculations, while the Mahalanobis distance for completely independent variables would equal the Euclidean distance. All climate variables were transformed individually to conform to a normal distribution before distance calculations. The Ecodist package further transforms all variables into units of standard deviations around a variable mean of zero prior distance calculations, so that the weight of climate variables is independent of their units of measurement.

3.3. Results

3.3.1. Alberta climatology and climate change projections

The climatology of Alberta's ecological regions and seed zones is primarily driven by a latitudinal temperature gradient, and precipitation patterns that are related to the regional topography. The Rocky Mountain Foothill and Montane ecosystems receive the largest amounts of precipitation (500-700mm) with mean annual temperatures around 2°C (Figure 3-1, blue shades). Note that the outlying Montane ecosystem represents the Cypress Hill region, a forest island in the southeast of the province's grasslands (yellow). Parklands (orange) represent a transitional zone between grasslands and the boreal forest. Ecosystems of the boreal forest (Figure 3-1, green shades) span a diagonal from approximately 400mm precipitation and -4°C temperature to 500mm precipitation and 2°C temperature. The diagonal arrangement of Natural Subregion classes (shades of green) suggests that the precipitation/evaporation balance distinguishes these major ecosystem classes.

To visualize projected climate change relative to the 1961-1990 normal climatology, the current climatology and projections for a central boreal forest location, an area centered around 56° latitude and 115° longitude (Figure 3-1, open circle) was added. The range of uncertainty in predicted temperature and precipitation values is represented by ellipses. The range of projected climate change varies for different locations in Alberta and cannot be comprehensively visualized in this plot. It is clear however, that the uncertainty in climate change projections stands in strong contrast to the precision with which reforestation is managed trough seed zones at present. Even for the 2020s, similar ellipses drawn at other locations may easily encompass several seed zones as possible

alternatives for obtaining reforestation material under climate change. At least in this simple, two-dimensional visualization, it appears challenging to pinpoint seed zone recommendations for the 2050s and 2080s, where similar ellipses drawn at various locations may regularly span several ecological subregions, indicated by different colors in Figure 3-1.

3.3.2. Projections of tree species habitat

Area Under the Curve (AUC) statistics suggest that the predictive accuracy of the ecosystem-based climate envelope model for Alberta is satisfactory (Table 3-1). Local AUC statistics for Alberta are similar to those for the global species range predictions. In general terms, AUC values above 0.9 indicate excellent predictive accuracy and AUC values above 0.8 indicate good accuracy. An AUC value of 0.8 means that 80% of the time a random sample from presence predictions will have a score greater than a random selection from absence predictions across all available probability thresholds to define a presence prediction. An AUC value of 0.5 therefore indicates a random predictor and values between 0.5 and 0.6 are generally considered a failed model (Fielding and Bell 1997).

Habitat projections under future climate change scenarios are shown in Figure 3-2 for white spruce. Projections for other important forestry species in Alberta are provided as Supporting Information Figure 3-4 (black spruce), Figure 3-5 (Douglas-fir), Figure 3-6 (lodgepole pine), Figure 3-7 (jack pine). In these figures, the black-and-white maps represent the consensus of projections for 18 climate change scenarios. Black indicates that all models agree that climate conditions will be suitable for a species, and white indicates that all models agree that suitable habitat is not available under any scenario. Grey shades represent varying levels of uncertainty in future habitat availability. The results for white spruce are

numerically summarized in Table 3-2.Summaries for other important forestry species in Alberta are provided in Table 3-4 (black spruce), Table 3-5 (Douglasfir), Table 3-6 (lodgepole pine) and Table 3-7 (jack pine).

For white spruce (Figure 2, Table 3-2), habitat is generally well maintained into the future except for some of the current Dry Mixedwood and transitional Parkland ecosystems. The ecosystem-based habitat projections also convey where appropriate seed sources for expected future climates may be found. For white spruce I observe that seed sources adapted to drier and warmer conditions (Parkland, Dry Mixedwood) should be suitable for an increasing land base in Alberta in the future. In contrast, black spruce is predicted to lose much of its habitat in Alberta, especially in low elevation regions (Figure 3-4, Table 3-4). Douglas-fir is only a commercially viable forestry species in Montane ecosystems in the southeast corner of the province. However, habitat projections for Douglasfir come with large uncertainties (Figure 3-5, Table 3-5). Climate scenarios that project substantially increased temperature and precipitation for southwestern Alberta, such as the CGCM-A1F1 scenario, result in largely extended habitat for Douglas-fir throughout the Foothill ecosystems of Alberta. On average, however, suitable habitat remains constant or is slightly reduced. The current distribution of lodgepole pine in the foothills of Alberta appears to be well maintained with reasonable certainty (Figure 3-6, Table 3-6). Lastly, habitat for jack pine, currently concentrated at lower elevations in the northeast of the province, is predicted to rapidly decline under most climate change scenarios (Figure 3-7, Table 3-7).

Notably, no alternative species that are currently not present in Alberta can be recommended with confidence, meaning that suitable habitat is predicted under a clear majority of climate change scenarios. Ponderosa pine (Figure 3-3, Table 3-

3) comes closest in gaining habitat with sufficient confidence across multiple climate change scenarios. By the 2050s, the most southern Montane ecosystems of Alberta may become suitable according to approximately half the 18 climate change scenarios I used.

3.3.3. Projections of appropriate seed sources

If habitat for a species is maintained under at least 70% of the climate change scenarios, I also provide projections of suitable seed sources. These projections are visualized in the series of color maps in Figure 3-2 and Figures 3-4 to 3-7 at the broad Natural Subregion level rather than individual seed zones for the purpose of better visualizing shifts in climate habitat. For white spruce, it is apparent that much of the land base of Alberta will require reforestation stock that is adapted to the warmer and drier ecosystems of the current Dry Mixedwood and Parkland ecosystems. In Table 3-8 to 3-12, more detailed information is provided for individual seed zones. This table provides alternative seed sources according to the climate match under current and expected future climates. For example, by the 2020s the Central Mixedwood seedzone CM 1.1 is predicted to closely match current Dry Mixedwood climate of the seed zone DM 1.1, or the more southern Central Mixedwood seed zones CM 1.2 and CM 1.3. These seed zones are also close matches under observed climate change, represented by the 1997-2006 average climate, and might therefore be recommended as source for planting material under a climate change adaptation strategy. Locations of recommended seed choices originating outside of Alberta are provided in Table 3-13.

3.4. Discussion

3.4.1. Species choice for reforestation

To minimize the probability of plantation failure in the face of uncertain future climates, I think that the best strategy is to ensure that species habitat is maintained under a wide range of potential climate change scenarios. In this study I restrict the reporting to a threshold of at least 70% of the models to agreeing that species habitat will be maintained. Practitioners may want to set higher thresholds for implementing large-scale reforestation programs to minimize risks of plantation failure. On the other hand, it should be noted that predicted loss of habitat does not necessarily mean dieback or failure to reproduce for tree species. Like most species distribution models, this approach predicts the realized niche (that is the climate space where the species is found to occur naturally) and not the larger fundamental niche space (namely, all climate conditions that a species can tolerate).

By their nature, the predictions of the realized niche space are more conservative as they account for biotic interactions. For example, a tree species may be predicted to lose habitat because it will be out-competed by other species that are better adapted to the predicted environment. However, in a planting environment with site preparation, controlled spacing, and removal of competing vegetation, natural competition would be limited. Secondly, the realized niche of trees may be determined by the ability of seedlings to germinate under favorable conditions and saplings to get established. Mature trees that have access to water through a large root system tend to have a much larger fundamental niche space than their offspring. Again, forest managers can literally "push the envelope" of where a

tree species can be successfully grown by cultural treatments, such as planting sturdy seedlings that were grown to a relatively large size in a forest nursery.

Biotic interactions that are implicitly included in realized niche models also include insect pests and diseases. A tree species might be excluded from an area not because the environmental conditions are unfavorable, but because the abiotic conditions are also favorable for a forest pest to which the species is susceptible. This mechanism might be particularly relevant to this study area, as many insects and diseases are excluded from boreal environments due to extreme cold in winter (Volney and Fleming 2000). Species choice in large-scale reforestation programs should be determined by the maintenance of the realized niche under most climate change scenarios, avoiding potential exposure of forest trees to pests and diseases under a continued warming trend (Tables 3-2 to 3-7 describe where realized niche space is maintained).

3.4.2. Choice of genotypes for reforestation

Matching genotypes to abiotic environments with the precision of Alberta's current system of seed zones is unlikely to be a sensible strategy in the face of uncertain future climates. In fact, the current level of precision may not even be necessary under constant climate conditions. Forest trees are normally adapted to broad environmental gradients with substantial within-population genetic diversity (Hamrick 2004). Recent data from genetic provenance experiments suggests that genetic differentiation of tree populations in Alberta would occur at a much broader scale than the current seed zone delineations (Rweyongeza et al. 2007; Rweyongeza et al. 2010; Hamann et al. 2011). As such data from long-term trials become available for more species, general seed zones could be consolidated into larger units to ease the administrative and logistical burden of

maintaining many separate seed collections for reforestation needs. For this decision process, which should synthesize genetic differentiation of tree populations, topo-edaphic characteristics of seed zones, and climatic information, I contribute a matrix of climatic similarity for current seed zones in Tables 3-8.

For the development of reforestation strategies under climate change, I encourage practitioners to consult Tables 3-8 and 3-9 that provide multiple choices of appropriate seed sources for climate conditions observed over a recent decade and projections for the 2020s. Ideally, seed sources should be used that appear as options under the 1961-1990 reference climate, under 1997-2006 climate, and under 2020s climate projections. Multiple, consistently suitable choices can usually be found. Making recommendations for the 2050s and 2080s becomes problematic because of the large uncertainties associated with climate projections in the more distant future. I propose that this information might be used for long-term planning, but not for guidance of seed sources in the near future. Planting trees for 2050s and 2080s climate is obviously not sensible as seedlings will likely not survive current planting environments. Secondly, we ultimately do not need to adapt to a "median climate change scenario" but to climate trends that eventually materialize in Alberta. At this point, we do not know with any reasonable amount of certainty what those conditions will be by the end of the century.

In choosing seed sources for the immediate future, I should further discuss the meaning of the Mahalanobis distances provided in Tables S6-S10. The values provide a measure of climatic similarity (smaller = more similar) between seed zones under 1961-1990 reference climate and future climate conditions expected for these seed zones. The measure does not have an interpretable dimension, and may not have biological meaning in a sense that a larger distance always means mal-adaptation of tree populations. While this could be the case, it should be

noted that I do not have biological and genetic data that demonstrates reduced fitness of productivity as a function of any particular climate variable that is used for the Mahalanobis distance calculation. Therefore, I encourage a portfolio strategy of adaptation to climate change that should include a diverse selection of seed sources and a framework for tracking reforestation success, growth, and forest health of plantations and allows for recursive improvements (Millar et al. 2007).

Finally, I should note that importing seed and species from other jurisdictions does not promise to be an important element of a climate change adaptation strategy for the forestry sector in Alberta. Only in small areas of the southern Rocky Mountain Montane and Foothill ecosystem, habitat is projected to be best suited to populations originating from montane ecosystems of British Columbia, and the dry conifer forests in Montana, South Dakota, and Wyoming (Table 3-13). Of approximately 50 western North American tree species that I investigated in a larger modeling effort, no alternative species that are currently not present in Alberta can be recommended with any confidence for reforestation under projected climate change.

3.5. Literature Cited

- Bechtold, W. A., and Patterson, P. L. 2005. The enhanced Forest Inventory and Analysis program- a national sampling design and estimation procedures. USDA Forest Service General Technical Report, SRS-80.
- Breiman, L. 2001. Random forests. Machine Learning 45(1): 5-32.
- Cutler, D.R., Edwards, T.C., Beard, K.H., Cutler, A., and Hess, K.T. 2007. Random forests for classification in ecology. Ecology **88**(11): 2783-2792.

- Daly, C., Halbleib, M., Smith, J.I., Gibson, W.P., Doggett, M.K., Taylor, G.H., Curtis, J., and Pasteris, P.P. 2008. Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. International Journal of Climatology 28(15): 2031-2064.
- EPA. 2007. Ecoregion Maps and GIS Resources. U.S. Environmental Protection Agency, Western Ecology Division official website, Available online at: http://www.epa.gov/wed, accessed 10 May 2008.
- Fawcett, T. 2006. An introduction to ROC analysis. Pattern Recognition Letters 27(8): 861-874.
- Fielding, A.H., and Bell, J.F. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation **24**(1): 38-49.
- Flora of North America Editorial Committee (eds). 1993+. Flora of North America of Mexico. 15 vols., New York and Oxford.
- Goslee, S.C., and Urban, D.L. 2007. The ecodist package for dissimilarity-based analysis of ecological data. Journal of Statistical Software **22**(7): 1-19.
- Government of Alberta. 2008. Ecological Site Information System (ESIS) electronic database. Available online at: http://www.srd.alberta.ca/MapsFormsPublications/Maps/ResourceDataPro ductCatalogue/Ecological.aspx, accessed 10 May 2008.
- Hamann, A., Gylander, T., and Chen, P. 2011. Developing seed zones and transfer guidelines with multivariate regression trees. Tree Genetics & Genomes 7: 399-408.
- Hamann, A., and Wang, T. 2005. Models of climate normals for genecology and cliamte change studies in British Columbia. Agriculture and Forest Meteorology 128: 211-221.
- Hamann, A., and Wang, T.L. 2006. Potential effects of climate change on ecosystem and tree species distribution in British Columbia. Ecology **87**(11): 2773-2786.
- Hamrick, J.L. 2004. Response of forest trees to global environmental changes. Forest Ecology and Management **197**(1-3): 323-335.
- Hogg, E.H. 1997. Temporal scaling of moisture and the forest-grassland boundary in western Canada. Agricultural and Forest Meteorology **84**(1-2): 115-122.
- Hogg, E.H., Brandt, J.P., and Kochtubajda, B. 2002. Growth and dieback of aspen forests in northwestern Alberta, Canada, in relation to climate and insects. Canadian Journal of Forest Research 32(5): 823-832.

- Hogg, E.H., Brandt, J.P., and Michaellian, M. 2008. Impacts of a regional drought on the productivity, dieback, and biomass of western Canadian aspen forests. Canadian Journal of Forest Research 38(6): 1373-1384.
- Mahalanobis, P.C. 1936. On the generalised distance in statistics. Proceedings of the National Institute of Science of India **12**: 49-55.
- Mbogga, M.S., Hamann, A., and Wang, T.L. 2009. Historical and projected climate data for natural resource management in western Canada. Agricultural and Forest Meteorology **149**(5): 881-890.
- Mbogga M, Hansen C, Wang T, Hamann A. 2010. A Comprehensive Set of Interpolated Climate Data for Alberta. Government of Alberta, Publication Number: Ref. T/235. ISBN: 978-0-7785-9184-9 (on-line edition), 978-0-7785-9183-2 (print edition).
- Meidinger, D., and Pojar, J. 1991. Ecosystems of British Columbia. Special Report Series 6. Research Branch, BC Ministry of Forests and Ranges, Victoria, British Columbia, ISBN 0843-6452.
- Michaelian, M., Hogg, E.H., Hall, R., J., and Arsenault, E. 2010. Massive mortality of aspen following severe drought along the southern edge of the Canadian boreal forest. Global Change Biology: doi: 10.111/j.1365-2486.2010.02357.x.
- Millar, C.I., Stephenson, N.L., and Stephens, S.L. 2007. Climate change and forests of the future: Managing in the face of uncertainty. Ecological Applications **17**(8): 2145-2151.
- Morgenstern, E. 1996. Geographic Variation in Forest Trees. Genetic Basis and Application of Knowledge in Silviculture. University of British Columbia Press, Vancouver, BC, Canada. 208p.
- NRC. 2006. Natural regions and Subregions of Alberta. Natural Regions Committee, Government of Alberta, Alberta Environment, Edmonton, Alberta, ISBN 0-7785-4572-5.
- R Development Core Team. 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing, ISBN 3-900051-07-0, Vienna, Austria.
- Rweyongeza, D., M., Barnhardt, L., K., Dhir, N., K., and Hansen, C. 2010. Population differentiation and climatic adaptation for growth potential of white spruce (*Picea glauca*) in Alberta, Canada. Silvae Genetica 59(4): 158-169.
- Rweyongeza, D., M., Dhir, N., K., Barnhardt, L., K., Hansen, C., and Yang, R., C. 2007. Population differentiation of the lodgepole pine (*Pinus contorta*)

and jack pine (*Pinus banksiana*) complex in Alberta: growth, survival, and response to climate. Canadian Journal of Botany **85**(6): 545-556.

- Selby, C.J., and Santry, M.J. 1996. A National Ecological Framework for Canada: Data model, Database and Programs. Centre for Land and Biological Resources Research, Research Branch, Agriculture and Agri-Food Canada and State of the Environment Directorate, Environment Canada, ISBN 0-662-24107-X.
- Sing, T., Sander, O., Beerenwinkel, N., and Lengauer, T. 2005. ROCR: visualizing classifier performance in R. Bioinformatics 21(20): 3940-3941.
- SRD. 2005. Standards for Tree Improvement in Alberta (STIA). Alberta Sustainable Resource Development, ISBN 0-7785-4082-0.
- SRD. 2009. Alberta Forest Genetic Resource Management and Conservation Standards (FGRMS). Alberta Sustainable Resource Development, ISBN 978-0-7785-8467-4.
- Volney, W.J.A., and Fleming, R.A. 2000. Climate change and impacts of boreal forest insects. Agriculture Ecosystems & Environment 82(1-3): 283-294.
- Wang, T., Hamann, A., Spittlehouse, D.L., and Aitken, S.N. 2006. Development of scale-free climate data for western Canada for use in resource management. International Journal of Climatology 26(3): 383-397.
- Ying, C.C., and Yanchuk, A.D. 2006. The development of British Columbia's tree seed transfer guidelines: purpose, concept, methodology, and implementation. Forest Ecology and Management 227(1-2): 1-13.

	Glo	bal Statistics	5	Alberta Statistics			
Species	Presence Samples ¹	Range Size	AUC	Presence Samples ²	Range Size	AUC	
Black spruce	4,489	710,748	0.90	1,750	385,708	0.85	
White spruce	7,115	848,866	0.88	3,606	438,013	0.79	
Douglas-fir	8,808	1,002,592	0.88	269	9,952	0.91	
Lodgepole pine	11,275	1,016,718	0.82	3,813	219,364	0.79	
Ponderosa pine	3,967	591,394	0.88	0	0	NA	
Jack pine	325	229,194	0.99	322	201,255	0.97	

Table 3-1. Species statistics and model accuracy

¹ Out of 54,716 sample plots, including non-forested plots ² Out of 16,391 sample plots, including non-forested plots

White spruce	Observed	climate	Projected climate				
seedzones*	1961-1990	1997-2006	2020s	2050s	2080s		
BSA 1.1	98%	77%	96%	98%	90%		
BSA 1.2	99%	100%	100%	100%	91%		
CM 1.1	100%	100%	100%	98%	75%		
CM 1.2	100%	100%	100%	92%	67%		
CM 1.3	100%	100%	100%	98%	71%		
CM 2.1	100%	100%	100%	88%	79%		
CM 2.2	100%	100%	100%	92%	80%		
CM 2.3	100%	100%	100%	82%	69%		
CM 2.4	100%	99%	96%	85%	77%		
CM 3.1	99%	91%	85%	83%	77%		
CM 3.2	100%	97%	84%	81%	77%		
CM 3.3	100%	100%	98%	88%	74%		
CM 3.4	100%	100%	95%	95%	78%		
CM 3.5	100%	100%	100%	91%	71%		
DM 1.1	100%	100%	99%	85%	56%		
DM 1.2	99%	98%	88%	66%	50%		
DM 1.3	100%	100%	74%	74%	59%		
DM 2.1	73%	95%	74%	88%	57%		
DM 2.2	99%	99%	67%	87%	69%		
DM 2.3	100%	85%	87%	71%	58%		
LBH 1.1	100%	100%	100%	99%	76%		
LBH 1.2	98%	88%	100%	100%	86%		
LBH 1.3	100%	98%	100%	99%	82%		
LBH 1.4	100%	100%	100%	89%	69%		
LBH 1.5	100%	100%	100%	79%	81%		
LBH 1.6	100%	100%	99%	88%	69%		
LBH 2.1	100%	99%	100%	100%	86%		

Table 3-2. Suitable habitat for white spruce expressed as % area of seed zone for observed climate, and expressed as probability of habitat maintenance under climate change projections from 18 general circulation models.

White spruce	Observed	Proj	Projected climate			
seedzones*	1961-1990	1997-2006	2020s	2050s	2080s	
LF 1.1	92%	100%	100%	98%	89%	
LF 1.2	100%	100%	95%	95%	74%	
LF 1.3	100%	99%	100%	100%	88%	
LF 1.4	100%	100%	100%	98%	80%	
LF 1.5	100%	100%	100%	98%	79%	
LF 2.1	100%	99%	100%	99%	80%	
LF 2.2	100%	100%	100%	100%	76%	
LF 2.3	100%	100%	78%	70%	50%	
M 1.1	100%	52%	25%	3%	1%	
M 2.1	100%	100%	92%	54%	33%	
M 2.2	100%	49%	69%	56%	30%	
M 3.2	100%	57%	80%	67%	41%	
M 4.1	100%	52%	83%	71%	42%	
M 4.2	100%	100%	100%	97%	68%	
M 4.3	98%	66%	54%	41%	30%	
M 5.1	98%	34%	74%	59%	36%	
M 5.3	98%	64%	85%	67%	44%	
M 5.4	47%	77%	95%	69%	51%	
NM 1.1	100%	100%	100%	100%	87%	
NM 2.1	99%	100%	100%	100%	85%	
UBH 1.1	99%	98%	99%	100%	82%	
UBH 1.2	100%	100%	100%	96%	80%	
UBH 1.3	94%	100%	100%	97%	86%	
UF 1.1	100%	100%	100%	93%	65%	
UF 1.2	100%	100%	100%	100%	89%	
UF 1.3	100%	83%	98%	79%	54%	
UF 1.4	100%	100%	100%	99%	77%	
UF 1.5	100%	100%	97%	87%	63%	
UF 2.4	100%	100%	100%	100%	80%	
UF 2.5	99%	96%	100%	94%	67%	

Table 3-2. Continued.

Ponderoda pine	Observed	climate	Projected climate			
seed zones*	1961-1990	1997-2006	2020s	2050s	2080s	
CM 3.5	0%	0%	0%	11%	43%	
DM 2.3	0%	3%	0%	40%	66%	
LF 2.3	0%	3%	1%	42%	67%	
M 1.1	0%	0%	7%	33%	30%	
M 2.1	0%	0%	0%	13%	58%	
M 2.2	0%	1%	2%	19%	44%	
M 3.2	0%	1%	0%	11%	36%	
M 4.3	0%	0%	4%	30%	46%	
M 4.4	0%	0%	4%	49%	67%	
M 4.5	0%	25%	19%	54%	51%	
M 5.6	0%	1%	10%	46%	60%	

Table 3-3. Suitable habitat for ponderosa pine expressed as % area of seed zone for observed climate, and expressed as probability of habitat maintenance under climate change projections from 18 general circulation models.

Black spruce	Observed	climate	Projected climate			
seed zones*	1961-1990	1997-2006	2020s	2050s	2080s	
BSA 1.1	98%	77%	96%	98%	89%	
BSA 1.2	100%	100%	100%	100%	90%	
CM 1.1	100%	100%	100%	94%	52%	
CM 1.2	100%	100%	100%	75%	34%	
CM 1.3	100%	100%	100%	95%	46%	
CM 2.1	100%	99%	98%	58%	29%	
CM 2.2	100%	100%	97%	60%	30%	
CM 2.3	100%	100%	97%	47%	22%	
CM 2.4	100%	100%	87%	52%	30%	
CM 3.1	99%	82%	59%	29%	17%	
CM 3.2	100%	64%	75%	42%	23%	
CM 3.3	100%	100%	96%	56%	33%	
CM 3.4	100%	100%	76%	36%	27%	
CM 3.5	68%	99%	15%	38%	21%	
DM 1.1	100%	100%	99%	62%	29%	
DM 1.2	99%	83%	73%	22%	7%	
DM 1.3	100%	95%	40%	11%	4%	
DM 2.2	99%	26%	24%	19%	14%	
DM 2.3	100%	87%	62%	28%	8%	
LBH 1.1	100%	100%	100%	98%	60%	
LBH 1.2	98%	88%	100%	100%	76%	
LBH 1.3	100%	94%	100%	97%	61%	
LBH 1.4	100%	100%	100%	77%	40%	
LBH 1.5	100%	100%	99%	71%	45%	
LBH 1.6	100%	100%	98%	70%	39%	
LBH 2.1	100%	100%	100%	100%	83%	

Table 3-4. Suitable habitat for black spruce expressed as % area of seed zone for observed climate, and expressed as probability of habitat maintenance under climate change projections from 18 general circulation models.

Black spruce	Observed	climate	Proje	Projected climate		
seed zones*	1961-1990	1961-1990 1997-2006		2050s	2080s	
LF 1.1	95%	100%	100%	94%	65%	
LF 1.2	95%	100%	82%	25%	20%	
LF 1.3	100%	81%	84%	77%	65%	
LF 1.4	100%	57%	88%	78%	59%	
LF 1.5	100%	99%	43%	57%	40%	
LF 2.1	100%	67%	83%	77%	57%	
LF 2.2	100%	87%	74%	61%	32%	
LF 2.3	81%	21%	72%	37%	14%	
NM 1.1	100%	100%	100%	100%	71%	
NM 2.1	99%	100%	100%	100%	81%	
UBH 1.1	99%	97%	99%	100%	77%	
UBH 1.2	100%	100%	100%	95%	62%	
UBH 1.3	94%	100%	100%	91%	61%	
UF 1.1	100%	81%	100%	93%	58%	
UF 1.2	100%	57%	100%	95%	77%	
UF 1.3	93%	36%	98%	79%	44%	
UF 1.4	98%	72%	99%	88%	60%	
UF 1.5	77%	63%	78%	68%	29%	
UF 2.4	100%	99%	96%	93%	67%	
UF 2.5	65%	90%	86%	86%	53%	

Table 3-4. Continued.

Douglas-fir	Observed	climate	Proj	Projected climate			
seed zones*	1961-1990	1997-2006	2020s	2050s	2080s		
M 2.2	91%	70%	55%	57%	64%		
M 4.3	97%	56%	39%	53%	50%		
M 4.5	100%	100%	78%	73%	51%		
M 5.3	77%	38%	49%	50%	57%		
M 5.5	100%	100%	88%	71%	56%		
M 5.6	85%	87%	85%	78%	72%		

Table 3-5. Suitable habitat for Douglas-fir expressed as % area of seed zone for observed climate, and expressed as probability of habitat maintenance under climate change projections from 18 general circulation models.

Lodgepole pine	Observed	climate	Projected climate			
seed zones*	1961-1990	1997-2006	2020s	2050s	2080s	
BSA 1.1	98%	59%	67%	61%	47%	
CM 3.2	48%	15%	70%	55%	45%	
CM 3.3	21%	71%	74%	68%	58%	
CM 3.4	100%	86%	87%	72%	69%	
CM 3.5	95%	7%	94%	76%	49%	
LBH 1.2	96%	20%	46%	34%	17%	
LBH 1.5	99%	44%	42%	40%	24%	
LBH 2.1	100%	89%	65%	49%	24%	
LF 1.2	100%	100%	88%	59%	66%	
LF 1.3	100%	75%	100%	99%	87%	
LF 1.4	100%	96%	99%	98%	85%	
LF 1.5	100%	54%	99%	91%	69%	
LF 2.1	100%	99%	98%	98%	88%	
LF 2.2	100%	99%	89%	86%	61%	
LF 2.3	100%	100%	65%	51%	51%	
M 1.1	99%	75%	27%	23%	11%	
M 2.1	100%	100%	99%	93%	67%	
M 2.2	100%	89%	70%	63%	61%	
M 3.2	100%	98%	79%	80%	76%	
M 4.1	100%	100%	86%	85%	78%	
M 4.2	100%	100%	99%	87%	91%	
M 4.3	100%	100%	55%	57%	51%	
M 4.4	100%	100%	60%	58%	48%	
M 4.5	98%	98%	78%	73%	51%	

Table 3-6. Suitable habitat for lodgepole pine expressed as % area of seed zone for observed climate, and expressed as probability of habitat maintenance under climate change projections from 18 general circulation models.

Lodgepole pine	Observed	climate	Proje	Projected climate		
seed zones*	1961-1990	1997-2006	2020s	2050s	2080s	
M 5.1	100%	95%	85%	80%	79%	
M 5.3	100%	100%	89%	81%	71%	
M 5.4	100%	100%	96%	75%	63%	
M 5.5	100%	100%	88%	72%	56%	
M 5.6	96%	86%	90%	82%	71%	
UBH 1.2	87%	97%	54%	43%	39%	
UBH 1.3	93%	100%	80%	76%	64%	
UF 1.1	100%	100%	100%	93%	67%	
UF 1.2	100%	100%	100%	100%	89%	
UF 1.3	100%	91%	98%	84%	56%	
UF 1.4	100%	100%	97%	95%	85%	
UF 1.5	100%	100%	91%	77%	61%	
UF 2.4	100%	100%	99%	92%	90%	
UF 2.5	100%	100%	100%	90%	86%	

Table 3-6. Continued.

Jack pine	Observed	climate	Projected climate			
seed zones*	1961-1990	1997-2006	2020s	2050s	2080s	
CM 1.1	99%	100%	89%	52%	31%	
CM 1.3	94%	87%	71%	32%	15%	
CM 2.1	100%	36%	69%	55%	22%	
CM 2.2	100%	10%	84%	71%	33%	
CM 3.1	97%	20%	72%	31%	14%	
CM 3.2	96%	16%	73%	37%	16%	
CM 3.3	88%	37%	67%	42%	21%	
DM 1.1	89%	41%	38%	10%	3%	
LBH 1.5	100%	54%	97%	70%	38%	
LF 1.1	81%	41%	86%	73%	47%	
NM 1.1	98%	91%	85%	69%	43%	
NM 2.1	93%	42%	57%	74%	42%	
UBH 1.2	78%	17%	23%	44%	34%	

Table 3-7. Suitable habitat for jack pine expressed as % area of seed zone for observed climate, and expressed as probability of habitat maintenance under climate change projections from 18 general circulation models.

Table 3-8. Table of best matching seed sources for 1961-1990 climate. The multivariate Mahalanobis climate distance is given in parenthesis.

Seed Zone	Choice 1	Choice 2	Choice 3	Choice 4	Choice 5	Choice 6	Choice 7	Choice 8	Choice 9	Choice 10
Northern Mi	xedwood									
NM11	NM11(0)	KU11(0.5)	LBH12(1.2)	NM21(2.3)	LBH21(2.6)	PAD11(2.9)	CM11(3.2)			
NM21	NM21(0)	LBH21(0.3)	BSA12(0.8)	LBH12(1)	KU11(1.7)	NM11(2.3)	LBH11(3.2)			
Central Mixe	edwood									
CM11	CM11(0)	PAD11(0)	AP11(0.1)	CM13(0.6)	LBH11(0.8)	CM12(1.7)	DM11(2)	LBH12(2.6)	CM21(2.9)	KU11(2.9)
CM12	CM12(0)	CM21(0.4)	DM11(0.4)	CM22(1.2)	UBH12(1.2)	AP11(1.4)	CM13(1.4)	LBH14(1.4)	CM11(1.7)	
CM13 CM21	CM13(0)	CM12(0.4)	AP11(0.6) CM22(0.5)	CM11(0.6)	PADI1(0.6)	CM21(2)	DM11(1) CM22(1,2)	CM12(1.4)	UBH12(2)	LBH14(2.9)
CM21 CM22	CM21(0) CM22(0)	CM12(0.4)	CM22(0.5)	LBH14(0.5)	CM24(1)	LBH13(1)	CM23(1.2) CM12(1.2)	UBH12(1.2)	DM11(1.7)	LBH15 (1.7)
CM23	CM23(0)	CM22(0.4)	CM24(0.8)	LBH14(0.8)	CM21(1.2)	LBH13(1.7)	CM12(2)	UBH12(2)	DM11(2.6)	LBH15(2.6)
CM24	CM24(0)	CM23(0.8)	LBH15(0.8)	LF11(0.8)	CM22(1)	CM21(1.4)	CM31(1.7)	LBH14(1.7)		
CM31	CM31(0)	CM33(0.5)	LBH15(0.6)	DM21(0.8)	LF11(1)	CM32(1.2)	DM13(1.2)	DM12(1.4)	PRP11(1.4)	
CM32	CM32(0)	DM22(0.5)	CM33(0.8)	CM34(0.8)	CP11(0.8)	DM21(0.8)	CM31(1.2)	CP12(2)	DM13(2)	LF12(2)
CM33	CM33(0)	CM31(0.5)	DM13(0.6)	LF11(0.6)	CM32(0.8)	CM34(0.8)	DM21(0.8)	PRP11(1.2)	CP11(1.7)	CP12(1.7)
CM34	CM34(0)	CM32(0.8)	CM33(0.8)	CP11(1)	CP12(1)	DM22(1)	DM21(1.2)	LF12(1.2)	DM13(1.4)	DM23(1.7)
CM35	CM35(0)	LF15(0.2)	LF14(0.5)	LF13(1)	DM22(1.2)	DM23(1.4)	LF21(1.4)	UF12(1.7)	LF22(2)	
Dry Mixedw	vood	CN 112(0,4)	CM2 1(0, ()	CN(12(1)			A D11(1.7)	(1) (22(1.7)	CM11(2)	
DM11 DM12	DM11(0) DM12(0)	DM12(0.4)	LBH16(0.8)	CM13(1) PRP11(0.8)	CM31(1.4)	UBH12(1.4) I BH15(1.7)	APTI(1.7) CM33(2)	UBH13(2)	CM11(2) CM24(2,3)	DM21(2 3)
DM12 DM13	DM12(0)	PRP11(0.3)	CM33(0.6)	DM12(0.8)	DM21(1)	CM31(1.2)	CP12(1.2)	CM34(1.4)	CP11(1.7)	LF12(17)
DM21	DM21(0)	CP11(0.4)	CM31(0.8)	CM32(0.8)	CM33(0.8)	CP12(0.8)	DM13(1)	DM22(1)	PRP11(1)	
DM22	DM22(0)	CP11(0.4)	CM32(0.5)	CM34(1)	DM21(1)	CM35(1.2)	CP12(1.4)	LF12(1.7)	LF14(1.7)	LF15(1.7)
DM23	DM23(0)	LF21(0.5)	LF22(0.5)	LF15(0.8)	LF14(1)	CM35(1.4)	UF14(1.4)	CM34(1.7)		
Boreal High	lands									
BSA11	BSA11(0)	BSA12(2.6)	LBH12(2.6)	LBH21(2.6)						
BSA12	BSA12(0)	LBH21(0.6)	NM21(0.8)	LBH12(2)	BSA11(2.6)	KU11(2.9)				
LBH11	LBH11(0)	CM13(0.5)	AP11(0.8)	CM11(0.8)	PAD11(1)	UBH12(2)	CM12(2.3)	DM11(2.3)		
LBH12	LBH12(0)	LBH21(0.6)	KU11(1)	NM21(1)	NM11(1.2)	BSA12(2)	CM22(1)	CN (12(2.2)	1.0111/2.0)	
LBH13 LBH14	LBH13(0)	UBH11(0.8)	CM22(0.5)	OBH12(1.2) CM21(0.8)	CM21(1.7)	UM23(1.7)	CM22(1)	DM11(1.4)	LBH11(3.2)	
LBH15	LBH15(0)	CM31(0.6)	CM24(0.8)	LF11(1)	LBH16(1.2)	CM21(1.7)	CM33(1.7)	DM11(1.4) DM12(1.7)	CM22(2)	LBH14(2)
LBH16	LBH16(0)	DM12(0.8)	UBH13(1)	LBH15(1.2)	LBH14(1.4)	UBH12(1.4)	CM31(2)	DM11(2)	CM21(2.3)	CM24(2.3)
LBH21	LBH21(0)	NM21(0.3)	BSA12(0.6)	LBH12(0.6)	KU11(2)	BSA11(2.6)	NM11(2.6)	LBH11(3.2)	. ,	
UBH11	UBH11(0)	LBH13(0.8)	UBH12(1.7)	LBH11(2.6)	LBH14(2.6)	CM21(3.2)	CM22(3.2)	CM12(3.6)		
UBH12	UBH12(0)	LBH14(0.4)	CM21(1)	CM12(1.2)	CM22(1.2)	LBH13(1.2)	DM11(1.4)	LBH16(1.4)	UBH11(1.7)	
UBH13	UBH13(0)	LBH16(1)	DM12(2)	LBH15(2.3)	PRP11(2.3)	CM31(2.6)	LF12(2.6)	DM13(2.9)	DM21(3.2)	
Lower Footh	nills									
LF11	LF11(0)	CM33(0.6)	CM24(0.8)	CM31(1)	LBH15(1)	DM13(2)	CM32(2.3)	CM34(2.6)	DM12(2.6)	
LF12	LF12(0)	CP11(1)	CP12(1)	CM34(1.2)	DM21(1.2)	PRP11(1.2)	BWBSmw1(1.7)	DM13(1.7)	DM22(1.7)	NF11(1.7)
LF13 LE14	LF13(0)	CM35(1)	UF12(1) CM25(0.5)	LF14(1.2)	LF15(1.4)	BWBSWK1(2.6)	DM22(2.9)	LF21(2.9) LF22(1.4)	UF13(2.9) UF14(1.4)	DM22(17)
LF14 LF15	LF14(0) LF15(0)	CM35(0.2)	LF14(0.4)	LF21(0.5)	DM23(0.8)	$L E^{22}(1)$	LF13(1.2) LIF12(1.2)	LF22(1.4) LF13(1.4)	0114(1.4)	DM22(1.7)
LF21	LF21(0)	LF22(0.3)	DM23(0.5)	LF15(0.5)	LF14(0.6)	UF14(0.8)	UF12(1.2)	CM35(1.4)	UF13(2.3)	
LF22	LF22(0)	LF21(0.3)	DM23(0.5)	LF15(1)	UF14(1.2)	LF14(1.4)	CM35(2)	LF23(2.3)	CM34(2.6)	UF12(2.6)
LF23	LF23(0)	UF15(0.3)	FP11(1)	M44(1.4)	M43(1.7)	LF22(2.3)	M53(2.3)	UF25(2.3)	M32(2.6)	
Montane										
M11	M11(0)	MG13(2.3)								
M21	M21(0)	UF13(0.8)	UF14(2)	UF24(2)	SA11(2.6)	UF12(2.6)	LF14(3.6)			
M22	M22(0)	M32(0.5)	FF11(1)	M41(1.2)	M45(1.2)	FP11(1.4)	M51(1.7)	M55(1.7)	MG11(1.7)	LF12(2.3)
M32	M32(0)	M22(0.5)	M41(0.8)	M45(1)	UF25(1.2)	FF11(1.4)	FP11(1.4)	M51(1.4)	M55(1.4)	
M41 M42	M41(0)	M32(0.8)	M51(0.8)	UF25(0.8)	M53(1)	M54(1)	M22(1.2)	M45(1.2)	M55(1.4)	M44(1.7)
M42 M43	M42(0) M43(0)	M44(0.1)	OF25(2) FP11(0.5)	M53(2.6) M53(0.5)	M54(2.9) M54(0.6)	UF15(2.9) UF15(1)	M41(3.2) L E23(1.7)	SA41(5.6) FE11(2)	M41(2)	LIE25(2)
M44	M45(0)	M43(0.1)	FP11(0.5)	M53(0.5)	M54(0.5)	UF15(0.8)	LF23(1.4)	M41(1.7)	UF25(1.7)	EF11(2)
M45	M45(0)	M55(0.4)	M51(1)	M32(1)	FF11(1.2)	M22(1.2)	M41(1.2)	M54(1.2)	FP12(1.4)	M56(1.4)
M51	M51(0)	M55(0.6)	M41(0.8)	M45(1)	M54(1.2)	M32(1.4)	M53(1.4)	SA32(1.4)	M22(1.7)	UF25(1.7)
M53	M53(0)	M54(0.2)	M43(0.5)	M44(0.5)	UF25(0.8)	M41(1)	UF15(1)	FP11(1.2)	M51(1.4)	M45(1.7)
M54	M54(0)	M53(0.2)	M44(0.5)	M43(0.6)	M41(1)	M45(1.2)	M51(1.2)	UF25(1.2)	FP11(1.4)	UF15(1.7)
M55	M55(0)	M45(0.4)	M51(0.6)	M56(1)	M32(1.4)	M41(1.4)	M22(1.7)	MSdk(1.7)	SA32(1.7)	
M56	M56(0)	SA33(0.8)	M55(1)	FP12(1.4)	M45(1.4)					
Upper Footh	ulls LIELLON									
UFII LIF12	UF11(0) UF12(0)	L F14(0.6)	UE13(0.8)	L F13(1)	L F15(1.2)	L F21(1-2)	LIF14(1.4)	CM35(1.7)	DM23(2.3)	
UF12 UF13	UF13(0)	M21(0.8)	UF12(0.8)	UF14(1)	UF24(1.4)	LF14(1.2)	LF21(2.3)	SA11(2.3)	DM23(2.3)	
UF14	UF14(0)	LF21(0.8)	UF24(0.8)	UF13(1)	LF22(1.2)	DM23(1.4)	LF14(1.4)	UF12(1.4)	LF15(1.7)	
UF15	UF15(0)	LF23(0.3)	FP11(0.8)	M44(0.8)	M43(1)	M53(1)	UF25(1.2)	M54(1.7)	M32(2)	
UF24	UF24(0)	UF14(0.8)	SA11(1.4)	UF13(1.4)	UF25(1.4)	M32(1.7)	SA12(1.7)	M21(2)	M41(2)	LF21(2.6)
UF25	UF25(0)	M41(0.8)	M53(0.8)	M32(1.2)	M54(1.2)	UF15(1.2)	SA31(1.4)	UF24(1.4)		

Table 3-9. Table of best matching seed sources for 1997-2006 climate. The multivariate Mahalanobis climate distance is given in parenthesis.

Seed Zone	Choice 1	Choice 2	Choice 3	Choice 4	Choice 5	Choice 6	Choice 7	Choice 8	Choice 9	Choice 10
Northern Mi	ixedwood									
NM11	CM11(4.4)	PAD11(4.4)	AP11(4.8)							
NM21	AP11(0.6)	CM11(0.6)	PAD11(0.8)	LBH11(1.4)	CM13(1.7)	CM12(2)	CM21(2.6)	UBH12(2.6)	LBH12(2.6)	
Central Mix	edwood									
CM11	CM12(3.6)	DM11(4)	CM21(4.8)							
CM12	CM12(3.2)	CM24(3.2)	CM21(3.6)	CM23(3.6)	DM11(4)	CM31(4)	LBH15(4)	CM22(4)	LBH16(4.4)	DM12(4.4)
CM13	CM12(1.2)	DM11(1.4)	CM21(1.4)	CM22(2)	CM23(2)	LBH14(2.3)	CM24(2.3)	LBH16(2.6)	UBH12(2.6)	LBH15(2.6)
CM21	CM31(2.6)	LBH15(2.9)	CM24(2.9)	LF11(3.6)	CM21(4)	DM12(4)	CM33(4)	CM12(4.4)	DM11(4.4)	LBH16(4.4)
CM22	CM24(2)	LBH15(2.6)	CM23(2.6)	CM31(2.9)	LF11(2.9)	CM21(3.2)	CM22(3.2)	CM12(3.6)	LBH16(3.6)	DM12(3.6)
CM23	CM24(2.6)	CM23(2.6)	CM22(3.6)	LBH15(4)	LF11(4)	CM21(4.4)	LBH14(4.4)	DM12(4.4)	CM12(4.8)	LBH16(4.8)
CM24	LF11(2.3)	CM31(2.6)	CM24(2.6)	CM33(2.9)	LBH15(3.2)	DM12(3.6)	DM21(3.6)	DM13(3.6)	PRP11(4)	CM32(4)
CM31	DM21(1.7) DM21(1.7)	CM31(2.3) CM32(1.7)	CM33(2.3)	DM22(2.3)	CPT1(2.3) CM24(2)	PKP11(2.9) CM22(2.2)	DM13(2.9) CP12(2.3)	DM12(2.9)	DM22(2.9)	LF11(3.2) LF12(2.0)
CM32 CM32	DM21(1.7) CM22(2)	DM12(2)	LF11(2.6)	DM22(1.7) DM21(2.6)	CM34(2) PP P11(2.6)	CM33(2.3)	CP12(2.5) CM24(2.6)	CM21(2.0)	CM32(2.9)	LF12(2.9) NF11(2.9)
CM34	CM34(1.4)	CP12(1.7)	DM13(2.3)	M22(2,3)	M32(2,3)	MG11(2,3)	CM33(2.6)	PRP11(2.6)	LE12(2.6)	NF11(2.5)
CM35	CM35(0.8)	LF15(0.8)	LF14(1)	LF21(1.2)	LF13(1.2)	DM23(1.7)	DM22(2)	LF22(2)	UF14(2.3)	UF13(2.6)
Dry Mixedy	vood	Li 10(0.0)	2111(1)	2121(1.2)	LI 15(1.2)	5	5	51 ==(=)	011 ((2.5)	0110(2.0)
DM11	CM24(2.3)	CM23(2.6)	CM12(2.9)	DM11(3.2)	CM21(3.2)	LBH15(3.2)	CM31(3.2)	CM22(3.2)	DM12(3.2)	LBH16(3.6)
DM12	DM12(2.3)	PRP11(2.6)	DM13(2.6)	CM31(3.6)	CM33(3.6)	NF11(3.6)	LBH16(4)	CM24(4)	LF11(4)	DM21(4)
DM13	PRP11(2)	DM13(2)	NF11(2.3)	MG11(2.3)	CP12(2.6)	DM12(2.9)	CM33(2.9)	DMG11(2.9)	M22(2.9)	()
DM21	CP11(1.4)	DM21(1.7)	CP12(2)	DM22(2)	CM32(2.3)	NF11(2.3)	CM34(2.6)	CM33(2.9)	PRP11(2.9)	DM13(2.9)
DM22	DM22(1.2)	CP11(1.4)	CP12(2)	CM34(2)	DM21(2.3)	CM32(2.3)	LF14(2.3)	CM35(2.3)	LF12(2.6)	LF15(2.6)
DM23	LF21(0.8)	DM23(1)	LF15(1)	UF14(1.2)	LF22(1.2)	LF14(1.4)	CM35(1.4)	UF12(1.4)	UF13(2)	LF13(2.6)
Boreal High	lands									
BSA11	BSA11(4.4)	UBH11(4.8)								
BSA12	LBH12(1.2)	UBH12(4)	CM11(2.3)	KU11(2.3)	PAD11(2.3)	LBH11(2.6)	LBH21(2.9)	NM11(2.9)	UBH11(3.2)	BSA11(3.6)
LBH11	CM12(0.8)	CM21(1)	UBH12(1.2)	LBH14(1.2)	CM22(1.2)	CM23(1.4)	DM11(1.7)	LBH13(2)		
LBH12	CM11(2.9)	PAD11(3.2)	CM12(4)	UBH12(4)	CM13(4)	LBH11(4.4)	LBH12(4.4)	DM11(4.8)	CM21(4.8)	NM11(4.8)
LBH13	CM23(2.3)	CM22(2.6)	CM21(2.9)	UBH12(2.9)	LBH14(2.9)	CM24(2.9)	CM12(3.2)	LBH13(3.2)	LBH15(3.6)	
LBH14	CM23(1.7)	CM24(2.3)	LBH14(2.6)	LBH16(2.9)	CM22(2.9)	CM21(3.2)	UBH12(3.2)	LBH15(3.2)	CM12(3.6)	DM12(3.6)
LBH15	CM31(1.7)	LBH15(2.6)	LF11(2.6)	DM21(2.6)	CM33(2.6)	DM13(2.9)	CM24(3.2)	DM12(3.2)	PRP11(3.2)	CM32(3.2)
LBH16	DM12(2.3)	LBH16(2.6)	CM24(2.9)	CM31(3.2)	UBH13(3.2)	LF11(3.2)	DM13(3.2)	LBH15(3.6)	CM23(3.6)	PRP11(3.6)
	UPH12(2.0)	PADII(1.4)	CM12(4)	CM12(2.5) CM21(4)	UBH12(2.5)	UBH11(4)	UBH11(2.3)	CM22(4.4)	CM23(4 4)	I DU15(4 8)
UBH12	CM23(2,3)	UBH12(2.6)	L BH14(2.6)	CM22(2.9)	CM21(3.2)	UBH16(3.2)	CM24(3,2)	L BH13(3 2)	CM123(4.4)	LBH15(4.8)
UBH13	UBH13(2.6)	DM12(2.9)	LBH16(3.2)	LF11(3.2)	PRP11(3.2)	M41(3.2)	M51(3.2)	DM13(3.6)	M22(3.6)	M32(3.6)
Lower Foot	hills	5		DI I ((0.2)	1 nu n(0.2)			200000		=(0.0)
LF11	LF11(2)	CM33(2.3)	CM31(2.6)	DM13(2.9)	CM24(3 2)	DM21(3.2)	LBH15(3.6)	PRP11(3.6)	CM32(3.6)	CM34(3.6)
LF12	PRP11(2)	NF11(2)	LF12(2)	CP12(2)	DM13(2.3)	CM34(2.3)	M32(2.3)	MG11(2.3)	CP11(2.9)	FF11(2.9)
LF13	UF12(1)	LF14(1.2)	LF13(1.4)	LF21(2)	UF13(2)	LF15(2)	CM35(2.3)	DM23(2.9)	UF14(2.9)	DM22(3.2)
LF14	LF21(0.8)	LF14(1.2)	UF12(1.2)	DM23(1.4)	UF14(1.4)	UF13(1.4)	LF22(1.7)	M32(2)	LF15(2)	CM34(2.3)
LF15	LF21(0.6)	LF15(0.6)	LF14(0.8)	CM35(1)	UF12(1)	DM23(1.2)	LF22(1.4)	LF13(1.4)	UF14(1.7)	UF13(2)
LF21	LF21(0.6)	UF14(1)	LF22(1.2)	DM23(1.4)	LF14(1.7)	UF13(1.7)	UF12(1.7)	LF15(2)	M32(2.3)	UF24(2.3)
LF22	LF21(0.5)	LF22(0.6)	UF14(0.8)	DM23(1.2)	LF15(1.2)	LF14(1.7)	CM35(2)	UF12(2)	UF13(2.3)	UF24(2.9)
LF23	LF23(1.2)	UF15(1.7)	UF14(2)	LF22(2.3)	UF24(2.9)	LF21(2.9)	FP11(2.9)	DM23(3.2)	UF25(3.2)	M32(3.6)
Montane										
M11	M11(4.4)	M21(4.4)								
M21	M21(0.6)	UF24(2)	UF13(2)	UF14(2.6)	SA11(2.9)	M32(3.2)	M22(4)	M41(4)	UF12(4)	
M22	M22(0.5)	M32(0.8)	M41(1.7)	FF11(1.7)	M45(2)	FP11(2)	M55(2.3)	UF24(2.3)	M21(2.3)	M51(2.6)
M32	M32(0.4)	M22(0.8)	UF24(1)	M41(1.2)	M21(1.4)	UF25(1.7)	UF14(1.7)	M51(2)	FP11(2)	UF13(2)
M41	M41(1)	UF24(1)	M32(1.2)	M22(1.7)	M51(1.7)	UF25(1.7)	M21(2)	M55(2.3)	M45(2.3)	
M42 M42	UF24(1.4) UF15(1.2)	SA12(2.3)	UF14(2.3) EP11(1.4)	UF25(2.6) M41(1.7)	SATI(2.9)	UF13(2.9) M44(1.7)	M32(3.2) M32(2)	M41(3.6) M52(2)	M51(3.6) M42(2)	11E24(2)
M44	UF15(1.2) UF24(1.7)	LF25(1.2) UF15(1.7)	I = I = I = I = I = I = I = I = I = I =	IIF14(2)	UF25(1.7) UF25(2.3)	M44(1.7) M41(2.6)	M32(2) M32(2.6)	M44(2.6)	FP11(2.6)	M53(2.9)
M45	UF24(2)	M21(2 3)	SA12(2.6)	M41(2.6)	M32(2.6)	M55(2.6)	M32(2.6) M45(2.6)	SA11(2.6)	1111(2.0)	10155(2.5)
M51	ESSEdc1(0.8)	M21(2:5)	M51(1)	M32(1.2)	UF24(1.2)	SA12(1.4)	M55(1.7)	UF25(1.7)	SA11(2)	M45(2)
M53	UF24(0.8)	UF25(1.4)	UF14(1.4)	M41(1.7)	M32(1.7)	UF15(2)	M53(2.3)	LF23(2.3)	M21(2.6)	M51(2.9)
M54	UF24(1)	UF25(1.7)	UF14(1.7)	M41(2)	M32(2.3)	UF15(2.6)	M21(2.6)	SA12(2.9)	M45(2.9)	M53(2.9)
M55	UF24(2)	SA12(2.3)	SA11(2.3)	M55(2.6)	M21(2.6)	M32(2.9)	UF13(2.9)	M41(3.2)	M51(3.2)	M45(3.2)
M56	ESSFmv2(2.3)	ESSFwk2(2.6)	SBSwk2(2.9)	ESSFwc1(2.9)	ESSFmm1(3.2)	ESSFdc1(3.2)	SA33(3.2)	SA12(3.6)	ESSFdk(3.6)	ESSFwc4(3.6)
Upper Footh	nills									
UF11	UF11(1.4)	LF13(4.4)								
UF12	UF13(0.8)	UF12(1.2)	UF14(1.4)	LF21(1.7)	UF24(2)	M21(2)	LF14(2.3)	LF22(2.9)	DM23(3.2)	LF15(3.2)
UF13	UF13(0.8)	M21(1.2)	UF24(1.4)	UF14(1.7)	SA11(1.7)	UF12(2.3)	M32(2.6)	LF21(2.9)	UF25(3.2)	LF14(3.6)
UF14	UF14(0.5)	UF24(1.2)	UF13(1.2)	M21(1.2)	LF21(1.4)	LF22(2)	UF12(2)	DM23(2.3)	M32(2.6)	LF14(2.6)
UF15	LF23(0.8)	UF15(1)	UF14(1.4)	UF24(1.7)	UF25(1.7)	M32(2.3)	LF22(2.3)	FP11(2.3)	M41(2.6)	M53(2.6)
UF24 UF25	UF24(0.5)	UF14(1.2)	M21(1.2)	UF13(1.4)	SATI(1.7)	M32(2.3)	UF25(2.3)	SA12(2.6)	M41(2.9)	OF12(2.9)
UF25	UF24(0.6)	UF25(1)	M41(2)	UF14(2)	UF15(2)	M32(2.3)	5A11(2.3)	SA12(2.0)	MD3(2.6)	

Table 3-10. Table of best matching seed sources for 2020s climate. The multivariateMahalanobis climate distance is given in parenthesis.

NameN	Seed Zone	Choice 1	Choice 2	Choice 3	Choice 4	Choice 5	Choice 6	Choice 7	Choice 8	Choice 9	Choice 10	
NMI NMI(2) NMI(2) <td colspan="10">Northern Mixedwood</td>	Northern Mixedwood											
NNEL NULL CMULCI CMULCI CMULCI BAULCIO LBBUCO LBBUCO <td>NM11</td> <td>NM11(2.5)</td> <td>PAD11(3.9)</td> <td>CM11(4.2)</td> <td></td> <td></td> <td></td> <td></td> <td></td> <td></td> <td></td>	NM11	NM11(2.5)	PAD11(3.9)	CM11(4.2)								
Carrel Name <	NM21	NM11(1.2)	PAD11(1.3)	CM11(1.5)	CM13(1.7)	LBH12(1.7)	AP11(1.9)	LBH11(2)	KU11(2.1)	NM21(2.6)	LBH21(2.8)	
Chill DMIIIC10 CHI221 CMIR231	Central Mixedwood											
Chill DMIII(13) CMIR[23] CMR[23] LBBI(22) CCMP231 DBI(14) LBBI(24) CARDAL CARDAL <t< td=""><td>CM11</td><td>DM11(1.6)</td><td>CM12(2.1)</td><td>CM13(2.1)</td><td>PAD11(2.2)</td><td>CM11(2.3)</td><td>AP11(2.4)</td><td>CM21(3.3)</td><td>LBH11(4.3)</td><td></td><td></td></t<>	CM11	DM11(1.6)	CM12(2.1)	CM13(2.1)	PAD11(2.2)	CM11(2.3)	AP11(2.4)	CM21(3.3)	LBH11(4.3)			
Chilo DMU(16) CMU(18)	CM12	DM11(1.5)	CM12(2)	CM21(2.3)	CM31(2.4)	LBH15(2.9)	CM24(3.1)	DM12(3.1)	LBH16(3.2)	CM22(3.8)	LBH14(4.1)	
$ \begin{array}{c} \mbox{Lab} (1.5) & \mbox{Lab} (2.5) & \mbox$	CM13	DM11(0.8)	CM13(1.8)	CM12(1.9)	CM21(2.5)	LBH16(2.7)	AP11(3.1)	PAD11(3.1)	CM11(3.2)	LBH15(3.4)	1 E11(2)	
NMA CUR2407 CUR3415 DITUL 3 CUR3415 DITUL 3 DITUL 3 <thditul 3<="" th=""> <thditu 3<="" th=""> <thditul< td=""><td>CM21 CM22</td><td>CM31(1.3) CM24(0.6)</td><td>DM11(1.8) CM21(1.4)</td><td>LBH15(1.8)</td><td>CM24(1.9) CM21(1.7)</td><td>CM22(1.7)</td><td>LE11(1.8)</td><td>DM12(2,7) CM22(1,0)</td><td>CM33(2.9) DM12(2.1)</td><td>CM22(2,2)</td><td>DM11(2,2)</td></thditul<></thditu></thditul>	CM21 CM22	CM31(1.3) CM24(0.6)	DM11(1.8) CM21(1.4)	LBH15(1.8)	CM24(1.9) CM21(1.7)	CM22(1.7)	LE11(1.8)	DM12(2,7) CM22(1,0)	CM33(2.9) DM12(2.1)	CM22(2,2)	DM11(2,2)	
CN36 CN3608 CN31010 LU1123 CN3210 CN3210 LU3123 PSP1120 CN31 DA12105 CN1010 CU11410 CN4211 CN1012 CN3112 CN3110 CU1210 DM1220 CN3210 CU1210 DM1210 CN3110 CU1210 DM1210 CN3112 CN3110 CU1202 CN3110 CU1202 DM1210 CN3110	CM23	CM24(0.0)	CM23(1.5)	LBIII5(1.4) LE11(1.7)	CM31(1.8)	DM12(1.8)	LFH(1.8) LBH15(1.9)	CM22(1.3) CM22(2.2)	CM33(2,2)	LBH16(2.5)	DWI1(2.3)	
CM10 DM2(0.5) CM32(0) CM32(1) CM31(2) CM31(2) CM31(2) CM32(2) CM32(3) CM32(3) <thcm33(3)< th=""> <thcm33(3)< th=""> <thcm3< td=""><td>CM24</td><td>CM33(0.8)</td><td>CM31(1)</td><td>LF11(1.2)</td><td>CM24(1.5)</td><td>DM12(1.6)</td><td>CM32(1.7)</td><td>DM21(2)</td><td>LBH15(2.1)</td><td>DM12(2.3)</td><td>PRP11(2.6)</td></thcm3<></thcm33(3)<></thcm33(3)<>	CM24	CM33(0.8)	CM31(1)	LF11(1.2)	CM24(1.5)	DM12(1.6)	CM32(1.7)	DM21(2)	LBH15(2.1)	DM12(2.3)	PRP11(2.6)	
CM32DM2209CM3210CM1410CM3410CM3410CM14210LM1221LM14210CM12410LM14210CM34CM340CM3410CM2410CM2410CM2410CM24210DM24221DM24221LF1222LF1222CM34CM3403CM3410CM2410CM2410CM2410DM24230LF1221LF1221LF1221CM3403DM110CM3112CM1121CM2121DM2121DM2121DM2121CM2131CM3113DM130DM3060CM4900PM2110CM3113CM3113CM31123CM1121LF12121LF12121CM21218PM1123DM12PM2103DM1210CM2113CM1121CM1123CM11232LF1214LF12131CM1123CM3133CM3138CM3133DM22DM2208PM1101CM1125LF1211LF1211LF1211LF1213LF1133CM3133LM1133LM1133LM1133DM22DM2208PM1125CM1123AM1123LF11411CM1133AM1133LM1133LM1133LM1133LM1133DM32CM3103CM1125LH1143AM1123LH11133LM1133LM1133LM1133LM1133LM1133LM1133DM32CM3104CM1125LH1123LH1113LH1113LH1133L	CM31	DM21(0.5)	CM32(0.6)	CP11(0.9)	DM22(1.1)	CM31(1.2)	CM33(1.2)	CM34(1.7)	CP12(1.8)	DM13(1.8)	PRP11(2)	
CMSCMS200CMS400, CMS400,CMS400, CMS40,CMS40, 	CM32	DM22(0.6)	CM32(1)	CP11(1.4)	CM34(1.9)	CM35(2)	DM21(2)	LF15(2.6)	CM33(2.8)	CP12(2.8)	LF14(2.8)	
CMAGeCMAGeCMAGECMAGECPREAT </td <td>CM33</td> <td>CM32(0.6)</td> <td>CM34(0.7)</td> <td>DM22(0.9)</td> <td>CM33(1)</td> <td>CP11(1)</td> <td>DM21(1)</td> <td>CP12(1.6)</td> <td>DM13(1.6)</td> <td>LF12(2)</td> <td>CM31(2.1)</td>	CM33	CM32(0.6)	CM34(0.7)	DM22(0.9)	CM33(1)	CP11(1)	DM21(1)	CP12(1.6)	DM13(1.6)	LF12(2)	CM31(2.1)	
CM35EF18(1)CH35(1)EF18(2.1)DM2(2.7) <td>CM34</td> <td>CM34(0.5)</td> <td>DM22(1.1)</td> <td>CP11(1.4)</td> <td>CM32(1.6)</td> <td>CP12(1.7)</td> <td>LF14(1.8)</td> <td>DM21(2.2)</td> <td>DM23(2.2)</td> <td>LF12(2.2)</td> <td>LF15(2.2)</td>	CM34	CM34(0.5)	DM22(1.1)	CP11(1.4)	CM32(1.6)	CP12(1.7)	LF14(1.8)	DM21(2.2)	DM23(2.2)	LF12(2.2)	LF15(2.2)	
Dx MaccolarDy MargenDy Margen </td <td>CM35</td> <td>LF13(1)</td> <td>CM35(1.3)</td> <td>LF15(2.1)</td> <td>LF14(2.7)</td> <td>DM22(3.4)</td> <td>UF12(3.5)</td> <td>LF21(4.4)</td> <td></td> <td></td> <td></td>	CM35	LF13(1)	CM35(1.3)	LF15(2.1)	LF14(2.7)	DM22(3.4)	UF12(3.5)	LF21(4.4)				
DM11 DM11(17) CMB12(2) DM12(2) DM12(2) DM12(2) CMB12(2) CMB12(3) CMB12(4) CMB12(4) <thcm< td=""><td>Dry Mixedw</td><td>vood</td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td></thcm<>	Dry Mixedw	vood										
DM13 DM140 DM12(1) DM2(1) CM2(1) CM2(1) CM2(1) CM2(1) CM2(1) CM2(1) CM2(1) CM2(1) CM3(1) DM1(1) CM2(1) CM3(1) DM22 DM2(1) CM3(1) CM3(2) DM2(1) CM3(2) DM2(1) CM3(2) CM3(2) DM2(1) CM3(2) DM2(2) DM3(2)	DM11	DM11(1.7)	CM31(2.2)	DM12(2.3)	CM12(2.9)	LBH16(2.9)	LBH15(3)	CM21(3.1)	DM21(3.4)	CM24(3.6)	PRP11(3.7)	
DM13 DM1400 CMA409 PMP1109 DM210 CPU210 CMA4023 CPU210 CPU210 <thcpu210< th=""> <thcpu210< th=""> <thcpu210< td="" tht<=""><td>DM12</td><td>PRP11(0.4)</td><td>DM13(0.6)</td><td>DM12(1)</td><td>DM21(1.3)</td><td>CM33(1.8)</td><td>CM31(1.9)</td><td>CP12(1.9)</td><td>NF11(2)</td><td>LF12(2.1)</td><td>CP11(2.3)</td></thcpu210<></thcpu210<></thcpu210<>	DM12	PRP11(0.4)	DM13(0.6)	DM12(1)	DM21(1.3)	CM33(1.8)	CM31(1.9)	CP12(1.9)	NF11(2)	LF12(2.1)	CP11(2.3)	
DAL2 DAL2 <thdal2< th=""> DAL2 DAL2 <thd< td=""><td>DM13</td><td>DM13(0.6)</td><td>CM34(0.9)</td><td>PRP11(0.9)</td><td>DM21(1)</td><td>CP12(1.1)</td><td>CM33(1.2)</td><td>CP11(1.2)</td><td>LF12(1.7)</td><td>CM32(1.8)</td><td>NF11(2)</td></thd<></thdal2<>	DM13	DM13(0.6)	CM34(0.9)	PRP11(0.9)	DM21(1)	CP12(1.1)	CM33(1.2)	CP11(1.2)	LF12(1.7)	CM32(1.8)	NF11(2)	
Data Data< Data< Data <	DM21 DM22	DM22(1,1)	DM22(0.8) CM25(1.5)	DM21(1.1) CP11(2.1)	LE12(2, 1)	CP12(1.6) LF15(2.4)	NF11(2.1) CM22(2.6)	LE14(2.3)	LF12(2.0) DM21(2.5)	CM33(3)	CM35(3.1) CP12(2.7)	
Date Display Display <thdisplay< th=""> <thdisplay< th=""> <thdisp< td=""><td>DM22 DM23</td><td>CM35(0.3)</td><td>LF15(0.4)</td><td>LF14(0.8)</td><td>DM23(1 1)</td><td>LF13(2.4)</td><td>LF21(1.4)</td><td>LF14(2.7) LF22(1.8)</td><td>UF12(1.8)</td><td>DM22(2)</td><td>UF12(3.7) UF14(2.4)</td></thdisp<></thdisplay<></thdisplay<>	DM22 DM23	CM35(0.3)	LF15(0.4)	LF14(0.8)	DM23(1 1)	LF13(2.4)	LF21(1.4)	LF14(2.7) LF22(1.8)	UF12(1.8)	DM22(2)	UF12(3.7) UF14(2.4)	
Instrumentation Instrumentatinstrumentatinstrumentation Instrumentation <td>Boreal High</td> <td>lands</td> <td>EI 15(0.1)</td> <td>EI 1 ((0.0)</td> <td>Din125(111)</td> <td>EI 15(1.5)</td> <td>LI 21(1.1)</td> <td>EI 22(1.0)</td> <td>0112(1.0)</td> <td>DN122(2)</td> <td>0111(2.1)</td>	Boreal High	lands	EI 15(0.1)	EI 1 ((0.0)	Din125(111)	EI 15(1.5)	LI 21(1.1)	EI 22(1.0)	0112(1.0)	DN122(2)	0111(2.1)	
BX12 BX11007 BBH12(1) KU1107 BX120	BSA11	I BH12(1.1)	NM11(1.8)	KU11(2.5)	I BH21(3.2)	PAD11(3.2)	CM11(3.3)	AP11(3.7)	CM13(3.8)	LBH11(3.8)	NM21(4.2)	
BHR1 DM110(4) CM12(7) CM12(1) CM12(1) CM12(1) CM12(1) DM12(2) DM11(1) DM11(1,1) DM11(1,2) DM11(1,3) DM11(1,3) DM11(1,4) DM11(1,4) DM11(1,2) DM13(1,3) DM13(1,3) DM13(1,3) CM32(1,4) CM32(1,3) CM32(1,3) CM32(1,4) CM32(1,4) CM32(1,4) DM12(1,4) DM11(1,1) DM11(1,3) DM13(1,3) CM32(1,4) DM12(1,3) CM32(1,4) CM32(1,4) CM32(1,4) CM32(1,4) CM32(1,4) CM32(1,4) CM32(1,4) DM32(2,4) DM12(1,3) CM32(1,4) DM32(1,2) DM13(1,3) CM31(1,4) DM32(1,3) DM12(1,4) DM32(1,4) DM32(1,4) </td <td>BSA12</td> <td>NM11(0.7)</td> <td>LBH12(1.2)</td> <td>KU11(1.6)</td> <td>NM21(2)</td> <td>LBH21(2.1)</td> <td>PAD11(3.1)</td> <td>CM11(3.3)</td> <td>BSA12(3.7)</td> <td>LBH11(3.7)</td> <td>CM13(3.8)</td>	BSA12	NM11(0.7)	LBH12(1.2)	KU11(1.6)	NM21(2)	LBH21(2.1)	PAD11(3.1)	CM11(3.3)	BSA12(3.7)	LBH11(3.7)	CM13(3.8)	
LBH12 NM10(15) PAD1(2.5) CM13(2.5) LBH12(2.5) AP11(2.9) KU11(2.5) LBH12(7.5) CM13(2.5) LBH13 CM10(2.0) LBH16(7.1) LBH12(1.1) CM24(1.3) CM31(1.3) LBH14(1.1) CM21(2.1) CM22(2.1) LBH11(1.1) CM11(1.5) DM11(1.2) CM32(1.1) CM31(2.1) CM31(2.1) CM31(2.1) CM31(2.1) CM31(2.1) CM31(2.1) CM32(2.1) LBH12(1.5) CM31(2.1) CM32(2.1) CM32(2.1) LBH12(1.5) CM31(2.1) CM32(2.1) LBH12(1.5) CM31(2.1) CM32(2.1) CM32(2	LBH11	DM11(0.4)	CM13(0.7)	CM12(1.1)	CM21(1.6)	AP11(1.8)	CM11(1.9)	LBH11(2)	PAD11(2)	UBH12(2)	LBH16(2.4)	
LBH18CM210.0CM20.0.5LBH140,07CM20.0.5CM20.0.5CM210.1.0LBH15(1.1)CM110.1.0UB10.1.2.1CH110.1.0CM210.0.5CM220.0.5CM220.1.5CM210.5CM210.5CM220.7CM210.5CM220.7CM210.5CM210.5CM220.7CM210.5CM210.5CM220.7CM210.5CM210.5CM220.7CM210.5CM210.5CM220.7CM210.7 </td <td>LBH12</td> <td>NM11(1.8)</td> <td>PAD11(2.3)</td> <td>CM11(2.5)</td> <td>CM13(2.5)</td> <td>LBH12(2.8)</td> <td>AP11(2.9)</td> <td>KU11(3.2)</td> <td>LBH11(3.7)</td> <td></td> <td></td>	LBH12	NM11(1.8)	PAD11(2.3)	CM11(2.5)	CM13(2.5)	LBH12(2.8)	AP11(2.9)	KU11(3.2)	LBH11(3.7)			
LBH14 LBH15DM1207 DM1206LBH15(.1)CM24(1.3)CM3(1.3)DM11(1.6)LBH14(.7)CM2(1.9)CM2(1.9)CM2(1.9)CM2(1.9)CM2(1.9)CM2(1.9)DM12(1.	LBH13	CM21(0.4)	CM22(0.5)	LBH14(0.7)	CM23(0.8)	CM24(0.8)	CM12(1.1)	LBH15(1.1)	DM11(1.2)	UBH12(1.2)	LBH16(1.5)	
LBH15CM3102CM3009PM2108DM2103CM3103CM3105DF111.60LF11(7)PM1107.7DM1107.9LBH16DM10206PM1108CM1307PAD1107.10CM1101.30CM3105.5DM211.63CM320.4LBF12.07LBF12.07LBF12.07LBF12.07LBF12.07LBF12.07CM12.07LBF12.07CM12.07 <td< td=""><td>LBH14</td><td>DM12(0.7)</td><td>LBH16(0.7)</td><td>LBH15(1.1)</td><td>CM24(1.3)</td><td>CM31(1.3)</td><td>DM11(1.6)</td><td>LBH14(1.7)</td><td>CM21(1.9)</td><td>CM23(2.1)</td><td>CM22(2.3)</td></td<>	LBH14	DM12(0.7)	LBH16(0.7)	LBH15(1.1)	CM24(1.3)	CM31(1.3)	DM11(1.6)	LBH14(1.7)	CM21(1.9)	CM23(2.1)	CM22(2.3)	
LBH16 M112(0.5) PEP11(0.8) M13(1.2) LBH16(1.3) M13(1.2) LBH12(1.5) M13(1.7) PAD1(1.7) M11(1.8) BH11(1.9) M13(1.2) LBH12(2.5) M13(1.2) M13(1.2) M13(1.2) M13(1.2) M13(1.2) M13(1.2) M13(1.2) M11(1.2) M11(1.2) M11(1.2) M11(1.2) M11(1.2) M11(1.2) M11(2.1) M11(2.2) M11(2.1) M11(2.2) M112(2.2) M112(2.2) M112(2.2) </td <td>LBH15</td> <td>CM31(0.2)</td> <td>CM33(0.6)</td> <td>DM21(0.6)</td> <td>CM32(0.7)</td> <td>DM13(1.3)</td> <td>LBH15(1.5)</td> <td>CP11(1.6)</td> <td>LF11(1.7)</td> <td>PRP11(1.7)</td> <td>DM12(1.9)</td>	LBH15	CM31(0.2)	CM33(0.6)	DM21(0.6)	CM32(0.7)	DM13(1.3)	LBH15(1.5)	CP11(1.6)	LF11(1.7)	PRP11(1.7)	DM12(1.9)	
LBH2 NM1(1.4) LBH12(1.5) CM15(1.7) PAD1(1.7.) CM11(1.8) LBH11(1.2) AP11(2.2) KU11(2.4) LBH12(2.7) NM21(2.8) UBH11 UBH12(0.4) CK10(0.7) LBH14(0.8) CM12(1.3) UBH13(1.5) CM21(1.6) CM31(1.6) CM13(1.7) CM12(1.9) UBH13 LF12(0.5) UBH13(1.1) PM11(1.5) DM21(2.3) UBH13(2.4) CM21(6.6) CM31(1.6) CM31(2.7) CM32(7) LF14 CM320.60 CM31(1.4) LF11(1.4) DM21(1.5) DM13(2.6) DM22(1.8) PH1(2.3) LF14.2 CM32(7) LF13 LF13(0.8) CM52(5.5) UF12(2.7) LF14.3 LF13(0.8) PM1(2.3) LF14.4 CM32(3.7) LF14 LF14(0.5) LF13(0.7) CM53(0.9) LF16(0.9) LF12(1.1) LF21(1.4) LF21(1.5) DM23(1.3) DM12(2.3) DM23(2.1) DM23(2.1) UF14(7.7) LF12(7.7) LF22(7.5) LF14 LF14(0.5) LF13(0.7) LF13(0.5) LF14(1.5) LF12(1.1) LF12(1.5) LF12(1	LBH16	DM12(0.6)	PRP11(0.8)	DM13(1.2)	LBH16(1.3)	UBH13(1.3)	CM31(1.5)	DM21(1.8)	CM33(2.1)	LF12(2.1)	LBH15(2.6)	
CBR11 OBR12(0.4) CM2(1.7) CBR12(1.4) CM12(1.5) C	LBH21	NM11(1.4)	LBH12(1.5)	CM13(1.7)	PAD11(1.7)	CM11(1.8)	LBH11(1.9)	AP11(2.2)	KU11(2.4)	LBH21(2.7)	NM21(2.8)	
	UBHII	UBH12(0.4)	CM21(0.7)	DM11(1.2)	CM12(1)	DMI1(1.1)	LBH10(1.2)	CM22(1.4)	LBH15(1.0)	UM13(1.9)	CM25(2.1)	
Data Description Description <thdescription< th=""> <thde< td=""><td>UBH13</td><td>LBII10(0.5) L F12(0.9)</td><td>UBH13(1.1)</td><td>PRP11(1.2)</td><td>DM12(1.3) DM21(2)</td><td>DM12(2.4)</td><td>DM13(2.4)</td><td>CP12(2.5)</td><td>NF11(2.5)</td><td>CM31(2.6)</td><td>CP11(2.6)</td></thde<></thdescription<>	UBH13	LBII10(0.5) L F12(0.9)	UBH13(1.1)	PRP11(1.2)	DM12(1.3) DM21(2)	DM12(2.4)	DM13(2.4)	CP12(2.5)	NF11(2.5)	CM31(2.6)	CP11(2.6)	
Instructional Instrument Inst	Lower Footh	hills	obiiio(iii)	114 11(1.5)	5	52(2.1)	5	0112(2.5)		0.000 (2.0)	0111(2.0)	
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	LF11	CM33(0.4)	CM32(0.6)	CM31(1.4)	LF11(1.4)	DM21(1.5)	DM13(1.6)	DM22(1.8)	CP11(2)	PRP11(2.6)	CP12(2.7)	
	LF12	LF12(0.7)	CP11(1)	CP12(1.1)	CM34(1.4)	DM22(1.5)	DM21(1.8)	NF11(1.8)	PRP11(2.3)	LF14(2.4)	CM32(2.7)	
IF14IF140;IF130,7)CM350,9)IF18(0,9)IF12(1,8)IDM23(2,3)DM23(2,6)UF13(2,7)IF22(2,9)LF15CM350,7)LF130,7)LF15(1,1)LF14(1,6)UF12(2,6)DM23(1,6)DM23(2,6)LF22(3,5)UF14(3,6)LF21LF15(0,5)CH540,60)LF21(0,8)UF12(0,8)UF12(2,6)DM23(1,6)LF21(1,8)UF13(2,7)LF21(2,8)UF13(1,8)UF12(1,8)UF13(2,8)UF13(1,8) <td< td=""><td>LF13</td><td>LF13(0.8)</td><td>CM35(2.5)</td><td>UF12(2.9)</td><td>LF14(3.2)</td><td>LF15(3.2)</td><td></td><td></td><td></td><td></td><td></td></td<>	LF13	LF13(0.8)	CM35(2.5)	UF12(2.9)	LF14(3.2)	LF15(3.2)						
LF15CM3307LF1307LF15(1.1)LF14(1.6)UF12(2.1)LF21(2.6)DM22(3.1)DM22(3.1)DM22(3.1)LF23(3.1)LF23(3.1)UF14(3.8)UF14(3.8)UF14(3.9)LF21LF15(0.5)CM35(0.6)LF21(0.8)LF14(1.1)LF22(1.1)DM232(1.3)LF13(1.3)LF13(1.8)UF14(.8)UF14(.9)DM22(2.9)DM23(2.9)DM23(2.9)DM23(2.9)DM23(2.9)DM23(2.9)DM23(2.9)DM23(2.9)DM23(2.9)DM23(2.9)DM23(2.9)DM23(2.9)DM23(2.9)LF14(.9)DM23(2.9)LF14(.9)DM23(2.9)DM23(2.9)LF14(.9)DM23(2.9)LF14(.9)DM23(2.9)LF14(.9)DM23(2.9)LF14(.9)LF14	LF14	LF14(0.5)	LF13(0.7)	CM35(0.9)	LF15(0.9)	UF12(1)	LF21(1.8)	DM23(2.3)	DM22(2.6)	UF13(2.7)	LF22(2.9)	
	LF15	CM35(0.7)	LF13(0.7)	LF15(1.1)	LF14(1.6)	UF12(2.1)	LF21(2.6)	DM22(3.1)	DM23(3.2)	LF22(3.5)	UF14(3.9)	
$ \begin{array}{c c c c c c c c c c c c c c c c c c c $	LF21	LF15(0.5)	LF14(0.7)	LF21(0.8)	UF12(0.8)	CM35(0.9)	LF13(1.1)	LF22(1.6)	DM23(1.8)	UF14(1.8)	UF13(2.4)	
LF23 LF23(0.5) LF23(0.5) DM23(1.2) LF21(1.2) UF14(1.5) UF15(1.5) PF11(2.1) M32(2.4) LF15(2.6) LF14(2.5) Montane M11 M110(7) MG13(2.3) LF14(3.7) LF13(4.2) SA11(4.2) LF21(4.4) MG12(2.2) M22 M22(1.1) FF11(1.2) MG11(1.2) LF12(1.5) M32(1.5) CP12(1.6) M55(1.6) M45(1.7) NF11(2.) MG12(2.2) M32 M32(0.9) CP11(3) DM23(1.3) LF14(1.3) UF14(1.4) M22(1.6) M45(1.6) LF12(1.6) F11(1.5) F11(1.5) MG12(2.2) MG12(2.3) LF2(3.5)	LF22	LF15(0.3)	CM35(0.6)	LF21(0.8)	LF14(1)	LF22(1)	DM23(1.3)	LF13(1.8)	UF12(1.8)	UF14(1.9)	DM22(2.9)	
Minime Million MG3C3 M11 M110,0 MG3C3 LF14(3.7) LF13(4.2) SA11(4.2) LF21(4.4) M22 M22(1.1) FF11(1.2) MG11(1.2) LF12(1.5) M32(1.5) CP12(1.6) M55(1.6) M45(1.7) NF11(2) MG12(2.2) M32 M32(0.5) CP11(3) DM23(1.3) LF14(1.3) UF14(1.4) M22(1.6) M45(1.6) UF13(1.6) LF12(1.7) LF2(1.7) M41 M32(0.5) M45(0.7) M55(0.8) M41(1) M22(1.2) M51(1.5) FP11(1.5) LF2(3.5) LF2(3.5) M43 FP11(0.8) UF4(1.4) M41(1.8) M51(1.7) M54(1.8) M51(1.7) M54(1.8) M54(1.1) M5	LF23	LF22(0.6)	LF23(0.9)	DM23(1.2)	LF21(1.2)	UF14(1.5)	UF15(1.5)	FP11(2.1)	M32(2.4)	LF15(2.6)	LF14(2.9)	
M11 M11(0.7) M11(0.7) M11(0.7) M11(0.7) UF13(1) UF13(1) UF14(2.5) UF24(3.7) LF13(4.7) SA11(4.2) LF21(4.4) M22 M22(1.1) FF11(1.2) MG11(1.2) LF12(1.5) M32(1.5) CP12(1.6) M55(1.6) M45(1.7) NF11(2) MG12(2.2) M32 M32(0.9) CP11(3) DM23(1.3) LF14(1.3) UF14(2.2) W24(1.2) M45(1.6) UF13(1.6) LF12(1.7) LF21(1.7) M41 M32(0.5) M45(0.7) M55(0.8) M41(1) M22(1.2) W124(1.2) M51(1.5) FP12(1.6) FF11(1.8) M42 UF24(1.4) UF14(1.8) FP12(2.5) M42(2.8) SA12(2.9) M32(1.1) M45(1.1) LF22(3.5) M43 FP11(0.8) M44(0.9) FF11(1.1) M45(1.1) M32(1.2) UF15(1.3) FP12(1.4) M53(1.4) M53(1.1) M45(1.4) M45(1.4) M45(1.4) M43(1.4) M45(1.4) M45(1.4) M45(1.4) M45(1.4) M45(1.4) M45(1.4) M45(1.4) M45(1.4) <td>Montane</td> <td>N(11(0.7)</td> <td></td> <td></td> <td></td> <td></td> <td></td> <td></td> <td></td> <td></td> <td></td>	Montane	N(11(0.7)										
M21 M2(0.5) OF12(1.2) OF12(2.3) OF12(2.3) DF14(2.5) DF12(1.6) M55(1.6) M45(1.7) NF11(2) M612(2.2) M32 M32(0.5) M45(0.7) M55(0.8) M41(1) M22(2.1) UF24(1.2) M51(1.5) FP12(1.6) M51(1.5) FP12(1.6) M53(1.6) LF21(3.5) LF22(3.5) M42 UF24(1.4) UF14(1.8) FP12(2.2) UF25(2.5) M42(2.8) SA12(2.9) M32(1.1) M45(1.1) LF22(3.5) M43 UF14(1.6) M44(0.5) M43(0.7) FF11(1.1) M42(1.8) UF14(1.8) LF21(1.7) LF21(1.7) M53(1.4) M51(1.5) M45(1.4) M53(1.1) M54(1.4) M54(1	M11 M21	M11(0.7) M21(0.5)	MG15(2.5)	LIE12(2.5)	LIE14(2.5)	11524(2.2)	LE14(2.7)	1 E12(4.2)	SA11(4.2)	1 E21(4.4)		
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	M21 M22	M21(0.3) M22(1.1)	OF15(1) FE11(1.2)	MG11(1.2)	UF14(2.5) LF12(1.5)	M32(1.5)	CP12(1.6)	LF13(4.2) M55(1.6)	SATT(4.2) M45(1.7)	LF21(4.4) NF11(2)	MG12(2.2)	
Mail M32(0.5) M45(0.7) M55(0.8) M41(1) M22(1.2) UF24(1.2) M51(1.5) FP12(1.6) FF11(1.8) M42 UF24(1.4) UF14(1.8) FP12(2.2) UF25(2.5) M42(2.8) SA12(2.9) M32(3.2) M41(3.2) LF21(3.5) LF22(3.5) M43 FP11(0.5) M44(0.5) M43(0.7) FF11(1) M54(1) UF15(1) M32(1.1) M45(1.1) M53(1.1) LF23(1.3) M44 FP110.8) M44(0.9) FF11(1.1) M45(1.1) M32(1.2) UF15(1) M32(1.1) M45(1.4) M45(1.4) M45(1.4) M45(1.4) M45(1.4) M45(1.4) M56(1.1) M56(1.1) M51(1.5) FF11(1.6) M41(1.6) M44(1.6) M45 M45(0.7) M32(0.8) FP12(0.9) M55(1.2) M54(1.3) M51(1.5) M51(1.5) M41(1.6) M44(1.6) M54 M45(0.4) FP12(0.8) M55(0.8) M32(1) FF11(1.4) M54(1.4) M51(1.5) M56(1.5) M41(1.6) M42(1.6) M54 M45(0.4) <td>M32</td> <td>M32(0.9)</td> <td>CP11(3)</td> <td>DM23(1.3)</td> <td>LF14(1.3)</td> <td>UF14(1.4)</td> <td>M22(1.6)</td> <td>M45(1.6)</td> <td>UF13(1.6)</td> <td>LF12(1.7)</td> <td>LF21(17)</td>	M32	M32(0.9)	CP11(3)	DM23(1.3)	LF14(1.3)	UF14(1.4)	M22(1.6)	M45(1.6)	UF13(1.6)	LF12(1.7)	LF21(17)	
M42 UF24(1.4) UF14(1.8) FP12(2.2) UF25(2.5) M42(2.8) SA12(2.9) M32(3.2) M4(6.2) LF21(3.5) LF22(3.5) M43 FP11(0.5) M44(0.5) M43(0.7) FF11(1) M54(1) UF15(1) M32(1.1) M45(1.1) M53(1.1) LF22(3.5) M44 FP11(0.8) M44(0.9) FF11(1.1) M45(1.1) M32(1.2) UF15(1.3) FP12(1.4) ICHmk3(1.4) M43(1.4) M54(1.4) M45 M56(1) FP12(1.1) M45(1.2) M55(1.2) UF16(1.3) M51(1.5) M41(1.6) M44(1.6) M53 M45(0.7) M32(0.8) FP12(0.9) M55(1.2) M54(1.3) M51(1.5) M51(1.6) M41(1.6) M44(1.6) M54 M45(0.4) FP12(0.8) M55(1.2) M54(1.4) M51(1.5) M56(1.5) M41(1.6) M45(1.7) M55 M56(0.9) M55(1.1) FP12(1.6) M45(1.6) SA33(2.3) M32(2.7) FF11(3) LF12(3.1) M41(3.6) M22(3.3) M56 M56(1.2)	M41	M32(0.5)	M45(0.7)	M55(0.8)	M41(1)	M22(1.2)	UF24(1.2)	M51(1.5)	FP12(1.6)	FF11(1.8)		
M43FP11(0.5)M44(0.5)M43(0.7)FF11(1)M54(1)UF15(1)M32(1.1)M45(1.1)M53(1.1)LF23(1.3)M44FP11(0.8)M44(0.9)FF11(1.1)M45(1.1)M32(1.2)UF15(1.3)FP12(1.4)ICHms3(1.4)M43(1.4)M54(1.4)M45M56(1)FP12(1.1)M45(1.2)M55(1.2)UF15(1.3)FP12(1.4)ICHms3(1.4)M22(1.9)M51M45(0.7)M55(0.8)FP12(0.9)M55(1.2)M54(1.3)M51(1.2)M41(1.5)M51(1.5)M41(1.6)M44(1.6)M54M45(0.4)FP12(0.8)M55(0.8)M32(1.0)FF11(1.4)M54(1.4)M51(1.5)M56(1.5)M41(1.6)M53(1.7)M55M56(0.9)M55(1.1)FP12(0.6)M45(1.6)SA33(2.3)M32(2.7)FF11(3)LF12(3.1)M11(.6)M32(1.3)M56M56(1.2)FP12(1.9)ICHmk1(1.9)MSdk(1.9)SA32(2)SBSwk2(2.1)ICHwk1(2.2)17x(2.3)ESSFwc4(2.3)SBSvk2(2.4)Upper FootHilsM51(2.2)LF12(3.1)UF14(3.4)M21(4.3)M21(4.3)UF14(1.9)UF11UF11LF14(2.2)LF12(2.2)UF14(2.4)LF14(3.4)M21(3.2)UF24(3.9)UF13UF110.0UF12(0.8)LF14(1.9)CM35(2.2)LF15(2.2)UF13(2.3)LF14(1.4)M21(4.3)UF13UF110UF12(1.3)LF14(1.3)UF13(1.3)LF14(2.4)LF14(2.4)UF14(3.4)M21(3.2)UF24(3.9)UF14UF12(0.8	M42	UF24(1.4)	UF14(1.8)	FP12(2.2)	UF25(2.5)	M42(2.8)	SA12(2.9)	M32(3.2)	M41(3.2)	LF21(3.5)	LF22(3.5)	
M44FP110.8M44(0.9)FF11(1.1)M45(1.1)M32(1.2)UF15(1.3)FP12(1.4)ICHmk3(1.4)M43(1.4)M54(1.4)M45M56(1)FP12(1.1)M45(1.2)M55(1.2)KKKKKM51M45(0.7)M55(0.8)FP12(1.0)M32(1)M56(1.1)M51(1.2)M41(1.3)UF24(1.8)M22(1.9)M44(1.6)M53M45(0.7)M32(0.8)FP12(0.9)M55(1.2)M54(1.4)M51(1.4)M51(1.5)FF11(1.6)M41(1.6)M43(1.7)M54M45(0.4)FP12(0.8)M55(0.8)M32(1.0)FF11(1.4)M54(1.4)M51(1.5)M51(1.5)M41(1.6)M42(3.3)M55M56(1.2)FP12(1.6)M45(1.6)SA33(2.3)M32(2.7)FF11(3)LF12(3.1)M51(3.1)M22(3.3)M56M56(1.2)FP12(1.6)M45(1.6)SA33(2.3)M32(2.7)FF11(3)LF12(3.1)M51(1.2)SBsvk(2.3)Upper FootHilsKKKKKKKKKKUF11UF11(1.1)KKKKKKKKKUF12LF13(0.7)UF12(0.8)LF14(1.9)CM35(2.2)LF15(2.2)UF13(2.3)LF12(3.1)UF14(3.4)M21(4.3)UF24(3.9)UF13UF12(0.8)UF14(1.1)LF13(1.3)LF14(1.3)UF13(1.3)LF13(1.3)LF14(1.3)UF14(2.4)LF13(3.5)LF21(1.2)UF33(1.5)LF21(1.2)UF14(1.2)M32(1.5)LF21(1.7)M44(2.1)<	M43	FP11(0.5)	M44(0.5)	M43(0.7)	FF11(1)	M54(1)	UF15(1)	M32(1.1)	M45(1.1)	M53(1.1)	LF23(1.3)	
M45M56(1)FP12(1.1)M45(1.2)M55(1.2)M50(1.2)M41(1.3)UF24(1.8)M22(1.9)M51M45(0.7)M32(0.8)FP12(1)M32(1)M56(1.1)M51(1.2)M51(1.5)FF11(1.6)M41(1.6)M44(1.6)M53M45(0.7)M32(0.8)FP12(0.9)M55(1.2)M54(1.3)M53(1.4)M51(1.5)FF11(1.6)M41(1.6)M45(1.6)M54M45(0.4)FP12(0.8)M55(0.8)M32(1)FF11(1.4)M54(1.4)M51(1.5)M5(1.5)M41(1.6)M53(1.7)M55M56(0.2)FP12(1.9)ICHmk1(1.9)M5dk(1.6)SA33(2.3)M32(2.7)FF11(3)LF12(3.1)M51(3.1)M22(3.3)M56M56(1.2)FP12(1.9)ICHmk1(1.9)MSdk(1.9)SA33(2.3)M32(2.7)FF11(3)LF12(3.1)M51(3.1)M22(3.3)Upper FootHilsM5dx(1.9)SA33(2.3)M32(2.7)ICHwk1(2.2)17x(2.3)ESSFwe4(2.3)SBsvk(2.4)UF11UF11(1.1)MSdx(1.9)SA33(2.3)M32(2.7)ICHwk1(2.2)17x(2.3)ESSFwe4(2.3)SBsvk(2.4)UF13UF13(0.7)UF12(0.9)LF14(1.9)CM35(2.2)LF15(2.2)UF13(2.3)LF12(3.1)UF14(3.4)M21(4.3)UF13UF13(0.7)UF12(0.9)LF14(1.3)LF14(2.2)UF14(2.4)LF15(3.0)CM35(3.1)LF24(3.9)UF24(3.9)UF14UF12(0.8)LF12(1.3)LF14(1.3)UF13(1.3)LF14(1.2)M32(1.5)FP11(1.7)M44(2.2)UF24(2.9) </td <td>M44</td> <td>FP11(0.8)</td> <td>M44(0.9)</td> <td>FF11(1.1)</td> <td>M45(1.1)</td> <td>M32(1.2)</td> <td>UF15(1.3)</td> <td>FP12(1.4)</td> <td>ICHmk3(1.4)</td> <td>M43(1.4)</td> <td>M54(1.4)</td>	M44	FP11(0.8)	M44(0.9)	FF11(1.1)	M45(1.1)	M32(1.2)	UF15(1.3)	FP12(1.4)	ICHmk3(1.4)	M43(1.4)	M54(1.4)	
M51 M45(0.7) M55(0.8) FP12(1) M32(1) M56(1.1) M51(1.2) M41(1.3) UF24(1.8) M22(1.9) M53 M45(0.7) M32(0.8) FP12(0.9) M55(1.2) M54(1.3) M51(1.4) M51(1.5) FF11(1.6) M41(1.6) M44(1.6) M54 M45(0.4) FP12(0.8) M55(0.8) M32(1) FF11(1.4) M54(1.4) M51(1.5) M51(1.5) M41(1.6) M53(1.7) M55 M56(0.9) M55(1.1) FP12(1.6) M45(1.6) SA32(2.3) M32(2.7) FF11(3) LF12(3.1) M51(3.1) M22(3.3) M56 M56(1.2) FP12(1.9) ICHmk1(1.9) MSdk(1.6) SA32(2.3) M32(2.7) IF14(3.4) M51(3.1) M22(3.3) Upper Foothils U ICHmk1(1.9) MSdk(1.6) SA32(2) SBSwk2(2.1) ICHwk1(2.2) 17x(2.3) ESSFwe4(2.3) SBSvk(2.4) Upper Foothils UF14 UF110 UF14(3.4) M21(4.3) UF14(3.4) M21(4.3) UF24(3.9) UF24(3.9) UF24(3.9)	M45	M56(1)	FP12(1.1)	M45(1.2)	M55(1.2)							
M53 M45(0.7) M32(0.8) FP12(0.9) M55(1.2) M54(1.3) M53(1.4) M51(1.5) FF11(1.6) M41(1.6) M44(1.6) M54 M45(0.4) FP12(0.8) M55(0.8) M32(1) FF11(1.4) M54(1.4) M51(1.5) M56(1.5) M41(1.6) M53(1.7) M55 M56(0.9) M55(1.1) FP12(1.6) M45(1.6) SA33(2.3) M32(2.7) FF11(3) LF12(3.1) M51(3.1) M22(3.3) M56 M56(1.2) FP12(1.9) ICHmk1(1.9) M5d(1.6) SA33(2.3) SBswk2(2.1) ICHwk1(2.2) 17x(2.3) ESSFwc4(2.3) SBsvk2(.4) Upper Foothils UF11 UF11(1.1) UF11 UF11(1.1) UF12(0.9) LF14(1.9) CM35(2.2) LF15(2.2) UF14(2.3) UF14(3.4) M21(4.3) UF24(3.9) UF13 UF12(0.7) UF12(0.8) LF13(1.6) M21(1.8) LF14(2.0) UF14(2.4) LF21(3.1) UF14(3.4) M21(2.4) UF13 UF12(0.8) UF14(1.1) LF13(1.3) LF14(2.0) UF14(2.4) <td< td=""><td>M51</td><td>M45(0.7)</td><td>M55(0.8)</td><td>FP12(1)</td><td>M32(1)</td><td>M56(1.1)</td><td>M51(1.2)</td><td>M41(1.3)</td><td>UF24(1.8)</td><td>M22(1.9)</td><td></td></td<>	M51	M45(0.7)	M55(0.8)	FP12(1)	M32(1)	M56(1.1)	M51(1.2)	M41(1.3)	UF24(1.8)	M22(1.9)		
M54 M45(0.4) FP12(0.8) M55(0.8) M32(1) FF11(1.4) M54(1.4) M51(1.5) M56(1.5) M41(1.6) M53(1.7) M55 M56(0.9) M55(1.1) FP12(1.6) M45(1.6) SA33(2.3) M32(2.7) FF11(3) LF12(3.1) M51(3.1) M22(3.3) M56 M56(1.2) FP12(1.9) ICHmk1(1.9) MSdk(1.9) SA33(2) SBSwk2(2.1) ICHwk1(2.2) 17x(2.3) ESSFwc4(2.3) SBSvk2(2.4) Upper Foothils UF11 UF11 UF11 UF11(1.1) UF12(0.9) LF14(1.9) CM35(2.2) LF15(2.2) UF13(2.3) LF21(3.1) UF14(3.4) M21(4.3) UF13 UF13(0.7) UF12(0.9) LF14(1.9) CM35(2.2) LF14(2.0) UF14(2.1) UF14(3.4) M21(4.3) UF14(2.4) LF16(3.0) CM35(3.1) LF21(3.1) UF14(3.4) M21(2.4) UF14 UF12(0.8) UF14(1.1) LF13(1.3) LF14(2) UF14(2.4) LF21(5.1) DM23(2.4) M21(2.4) UF15 LF22(0.7) LF23(0.9) <t< td=""><td>M53</td><td>M45(0.7)</td><td>M32(0.8)</td><td>FP12(0.9)</td><td>M55(1.2)</td><td>M54(1.3)</td><td>M53(1.4)</td><td>M51(1.5)</td><td>FF11(1.6)</td><td>M41(1.6)</td><td>M44(1.6)</td></t<>	M53	M45(0.7)	M32(0.8)	FP12(0.9)	M55(1.2)	M54(1.3)	M53(1.4)	M51(1.5)	FF11(1.6)	M41(1.6)	M44(1.6)	
M55 M56(0.9) M55(1.1) FP12(1.6) M45(1.6) SA33(2.3) M32(2.7) FP1(3) LF12(3.1) M51(3.1) M22(3.3) M56 M56(1.2) FP12(1.9) ICHmk1(1.9) M3d(2.9) SA33(2) SBSwk2(2.1) ICHwk1(2.2) 17x(2.3) ESSFwc4(2.3) SBSvk(2.4) Upper Foothils UF11 UF11 UF11 UF11 UF12 LF13(0.7) UF12(0.9) LF14(1.9) CM35(2.2) LF15(2.2) UF13(2.3) LF14(3.4) M21(4.3) UF13 UF13(0.7) UF12(0.8) LF13(1.6) M21(1.8) LF14(2) UF14(2.4) LF15(3) CM35(3.1) LF21(3.2) UF24(3.9) UF14 UF12(0.8) UF13(1.3) LF14(1.3) UF13(1.3) LF15(1.4) CM35(1.5) LF21(1.7) DM23(2.4) M21(2.4) UF15 LF22(0.7) LF23(0.9) UF15(1.1) DM23(1.2) LF21(1.2) UF14(1.2) M32(1.5) FP11(1.7) M44(2.2) UF24(2.2) UF24 UF13(0.6) UF14(0.9) UF12(1) M21(1.3) LF14(1	M54	M45(0.4)	FP12(0.8)	M55(0.8)	M32(1)	FF11(1.4)	M54(1.4)	M51(1.5)	M56(1.5)	M41(1.6)	M53(1.7)	
Upper Foothills UF12(1.5) UF14(1.5) Disa(1.5) S755(2) S55W2(2.1) UCHWR1(2.2) UX(2.3) ESSFW04(2.3) S55W2(2.4) Upper Foothills UF11 UF11 UF11 UF11 UF12 LF13(0.7) UF12(0.9) LF14(1.9) CM35(2.2) LF15(2.2) UF13(2.3) LF21(3.1) UF14(3.4) M21(4.3) UF13 UF13(0.7) UF12(0.8) LF13(1.6) M21(1.8) LF14(2) UF14(2.4) LF15(3) CM35(3.1) LF21(3.2) UF24(3.9) UF14 UF12(0.8) UF14(1.1) LF13(1.3) LF14(1.3) UF13(1.3) LF15(1.4) CM35(1.5) LF21(1.7) DM23(2.4) M21(2.4) UF15 LF22(0.7) LF23(0.9) UF15(1.1) DM23(1.2) LF21(1.2) UF14(1.2) M32(1.5) FP11(1.7) M44(2.2) UF24(2.2) UF24 UF13(0.6) UF14(0.9) UF12(1) M21(1.3) LF14(1.6) UF24(1.8) LF13(2) LF12(2.3) CM35(2.4) UF25 UF24(0.6) UF14(0.7) M32(1.1) UF25(1.5)	M55 M56	M56(0.9) M56(1.2)	M33(1.1) FP12(1.0)	rP12(1.6) ICHmk1(1.0)	M45(1.6) MSdk(1.0)	SA33(2.3) SA33(2)	M32(2.7) SBSwk2(2.1)	rF11(3) ICHwk1(22)	LF12(3.1) $17_{x}(2.2)$	MOI(3.1) $ESSEwed(2.2)$	M22(3.3) SBSul(2.4)	
Lepter roomers UF11 UF1 UF12 LF13(0.7) UF12(0.9) LF14(1.9) CM35(2.2) LF15(2.2) UF13(2.3) LF21(3.1) UF14(3.4) M21(4.3) UF13 UF13(0.7) UF12(0.8) LF13(1.6) M21(1.8) LF14(2) UF14(2.4) LF15(3) CM35(3.1) LF21(3.2) UF24(3.9) UF14 UF12(0.8) UF13(1.3) LF14(1.3) UF13(1.3) LF15(1.4) CM35(1.5) LF21(1.7) DM23(2.4) M21(2.4) UF15 LF22(0.7) LF23(0.9) UF15(1.1) DM23(1.2) LF21(1.2) UF14(1.2) M32(1.5) FP11(1.7) M44(2.2) UF24(2.2) UF24 UF13(0.6) UF14(0.9) UF12(1) M21(1.3) LF14(1.6) UF24(1.8) LF13(2) LF12(2.3) CM35(2.4) UF25 UF24(0.6) UF14(0.7) M32(1.1) UF25(1.5) LF21(1.7) UF13(1.7) FP12(1.8) LF22(1.9) DM23(2.1) M41(2.1)	IVIJU	wi30(1.2)	rr12(1.9)	юпшк1(1.9)	wisuk(1.9)	5A33(2)	3D3WK2(2.1)	тспwк1(2.2)	1/X(2.3)	LOOF WC4(2.3)	з д зүк(2.4)	
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$	UF11 UF11(1.1)											
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	UF12	LF13(0.7)	UF12(0.9)	LF14(1.9)	CM35(2.2)	LF15(2.2)	UF13(2.3)	LF21(3.1)	UF14(3.4)	M21(4.3)		
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$	UF13	UF13(0.7)	UF12(0.8)	LF13(1.6)	M21(1.8)	LF14(2)	UF14(2.4)	LF15(3)	CM35(3.1)	LF21(3.2)	UF24(3.9)	
UF15 LF22(0.7) LF23(0.9) UF15(1.1) DM23(1.2) LF21(1.2) UF14(1.2) M32(1.5) FP11(1.7) M44(2.2) UF24(2.2) UF24 UF13(0.6) UF14(0.9) UF12(1) M21(1.3) LF14(1.6) UF24(1.8) LF13(2) LF15(2.3) LF21(2.3) CM35(2.4) UF25 UF24(0.6) UF14(0.7) M32(1.1) UF25(1.5) LF21(1.7) UF13(1.7) FP12(1.8) LF22(1.9) DM23(2.1) M41(2.1)	UF14	UF12(0.8)	UF14(1.1)	LF13(1.3)	LF14(1.3)	UF13(1.3)	LF15(1.4)	CM35(1.5)	LF21(1.7)	DM23(2.4)	M21(2.4)	
UF24 UF13(0.6) UF14(0.9) UF12(1) M21(1.3) LF14(1.6) UF24(1.8) LF13(2) LF15(2.3) LF21(2.3) CM35(2.4) UF25 UF24(0.6) UF14(0.7) M32(1.1) UF25(1.5) LF21(1.7) UF13(1.7) FP12(1.8) LF22(1.9) DM23(2.1) M41(2.1)	UF15	LF22(0.7)	LF23(0.9)	UF15(1.1)	DM23(1.2)	LF21(1.2)	UF14(1.2)	M32(1.5)	FP11(1.7)	M44(2.2)	UF24(2.2)	
UF25 UF24(0.6) UF14(0.7) M32(1.1) UF25(1.5) LF21(1.7) UF13(1.7) FP12(1.8) LF22(1.9) DM23(2.1) M41(2.1)	UF24	UF13(0.6)	UF14(0.9)	UF12(1)	M21(1.3)	LF14(1.6)	UF24(1.8)	LF13(2)	LF15(2.3)	LF21(2.3)	CM35(2.4)	
	UF25	UF24(0.6)	UF14(0.7)	M32(1.1)	UF25(1.5)	LF21(1.7)	UF13(1.7)	FP12(1.8)	LF22(1.9)	DM23(2.1)	M41(2.1)	

Table 3-11	. Table of b	est matching se	eed sources for	2050s climate.	The multivariate
Mahalanobi	s climate d	istance is giver	in parenthesis	5.	

Seed Zone	Choice 1	Choice 2	Choice 3	Choice 4	Choice 5	Choice 6	Choice 7	Choice 8	Choice 9	Choice 10	
Northern Mi	ixedwood										
NM11	BWBSmw2(3.8)										
NM21	CM13(2.1)	PAD11(2.5)	CM11(2.7)	AP11(3.1)	DM11(3.1)	LBH11(3.8)	CM12(4.3)	NM11(4.3)			
Central Mix	edwood										
CM11	DM11(3.9)	CM31(4.8)	DIMAN	() () () () () () () () () () () () () (53 F22 (1 5)	DDD11/// C	53 (10/1 B)	DIMAN			
CM12	CM31(3)	DM21(3.3)	DM12(4.1)	CM32(4.3)	CM33(4.5)	PRP11(4.6)	DM13(4.7)	DM11(4.9)	UDUDALO	D1/12/4.0)	
CM15 CM21	CM31(3)	DM11(3)	DM12(3.2) CM22(2.8)	DM21(3.4)	LBH10(3.8)	PKP11(4.1)	CB11(4)	CM12(4.5)	UBH13(4.0) DM22(4.1)	DM15(4.8)	
CM21 CM22	CM31(2.2)	CM33(1.9)	CM32(2.8) CM32(2.2)	DM21(2.3)	DM13(3.8)	CM24(2.6)	LF11(2.8)	DM12(2.9)	LBH15(3.2)	PRP11(3.3)	
CM22 CM23	CM33(1.8)	CM31(2)	DM13(2)	DM21(2.3)	CM32(2.6)	DM12(2.6)	PRP11(2.6)	LF11(2.9)	CM24(3)	Hu H(5.5)	
CM24	CM32(1.5)	CM33(1.7)	DM21(1.9)	DM13(2.2)	CM31(2.4)	DM22(2.4)	CM34(2.5)	CP11(2.5)	PRP11(3.1)	LF11(3.3)	
СМ31	DM22(1.2)	CP11(1.4)	DM21(1.8)	CM32(1.9)	CP12(2.6)	CM34(2.8)	NF11(3.2)	CM33(3.3)	CM35(3.6)	DM13(3.6)	
CM32	DM22(1.8)	CM35(2.5)	CM32(3)	CP11(3)	LF13(3.3)	LF15(3.4)	CM34(3.9)	LF14(3.9)	DM21(4.2)	CP12(4.5)	
CM33	DM22(1)	CP11(1.6)	CM32(1.7)	CM34(1.8)	DM21(2.3)	CP12(2.5)	CM35(2.6)	CM33(3)	LF14(3.1)	LF15(3.1)	
CM34	DM22(1.6)	CM35(1.8)	CM34(2)	LF15(2.1)	LF14(2.2)	CP11(2.4)	CM32(2.9)	DM23(2.9)	CP12(3)	LF13(3)	
CM35	CM35(3.8)	LF13(3.3)									
Dry Mixedw	vood										
DM11	DM21(2.6)	CM31(2.9)	DM12(3.4)	PRP11(3.5)	DM13(3.9)	CP11(4.1)	CM32(4.2)	CM33(4.3)	NF11(4.9)		
DM12	PRP11(1.2)	DM21(1.4)	CP11(1.5)	DM13(1.5)	CP12(1.6)	NF11(1.7)	LF12(2.2)	CM34(2.5)	DM22(2.6)	CM33(2.7)	
DM13	CP11(1.3)	CP12(1.5)	DM22(1.5)	CM34(1.6)	DM21(1.9)	DM13(2.2)	CM32(2.4)	PRP11(2.4)	NF11(2.5)	LF12(2.7)	
DM21	DM22(2)	CP11(2.3)	CM35(3.4)	CP12(3.4)	DM21(3.4)	NF11(3.7)	CM32(3.8)	LF13(4.2)	CM34(4.5)	LF15(4.7)	
DM22	CM35(2.9)	CP11(4.6)	DM22(3.3)	LF13(3.2)	LF14(4.8)	LF15(4.2)	LIE10(2.7)	DM00(2.0)	1 522(4)	11014/4 7	
DM23	CM35(1.3)	LF13(1.7)	LF15(1.9)	LF14(2.7)	DM23(3.3)	LF21(3.5)	UF12(3.7)	DM22(3.8)	LF22(4)	UF14(4.7)	
<u>Boreal Highlands</u>											
BSA11	BWBSdk2(2.5)	BWBSmw2(3)	NM11(4.7)	CM13(4.8)	I DI LICCI AN	4.D11/1-0	17111// 0				
BSA12	NM11(2.8)	CM13(3.6)	PAD11(3.7)	CM11(4)	LBH12(4.3)	AP11(4.6)	KU11(4.9)	0.000			
LBHIL	DM11(1.6)	LBH16(2.4)	DM12(2.6)	CM12(2.8)	CM31(2.8)	CM21(3.2)	LBH15(3.3)	CM13(3.6)	UBH13(3.6)		
LDH12 LBH13	омватw2(2.5) Смято в	DWD50K2(3.3)	CM24(1-6)	IBHIS(17)	CM33(1-8)	1 BH16(2 1)	1 F11(2-1)	DM13/230	DM21/2-33	CM32(2-7)	
LBH14	DM12(1.2)	CM31(1.3)	PRP11(1.3)	DM13(1.4)	DM21(1.4)	CM33(1.9)	LBH16(2.5)	CM32(2.5)	CP11(2.5)	LBH15(2.9)	
LBH15	DM21(0.7)	CM32(0.8)	DM22(0.9)	CP11(1)	CM33(1.4)	CM31(1.6)	CM34(1.8)	DM13(1.9)	CP12(2)	PRP11(2.1)	
LBH16	PRP11(0.9)	DM21(1.2)	DM13(1.5)	LF12(1.6)	CP11(1.8)	CP12(2)	DM12(2)	NF11(2)	CM31(2.5)	CM33(2.5)	
LBH21	CM13(2.4)	PAD11(3.3)	CM11(3.5)	DM11(3.6)	AP11(3.8)	LBH11(4.2)	NM11(4.7)				
UBH11	CM31(1.1)	LBH16(1.1)	LBH15(1.4)	DM12(1.6)	UBH13(1.8)	DM11(2)	CM24(2.4)	CM21(2.5)	DM21(2.6)	CM33(2.7)	
UBH12	CM31(1.4)	DM12(1.4)	DM21(1.7)	LBH16(1.9)	PRP11(1.9)	UBH13(1.9)	CP12(4)	DM13(2.3)	CM33(2.6)	LBH15(2.6)	
UBH13	LF12(1.2)	NF11(2)	CP11(2.1)	CP12(2.1)	PRP11(2.1)	DM21(2.2)	DM13(3.2)	DM22(3.2)	CM34(3.4)	UBH13(3.4)	
Lower Footh	nills										
LF11	CM32(1.1)	CM34(1.3)	DM22(1.3)	CM33(1.7)	CP11(2.1)	DM21(2.2)	DM13(2.8)	CM35(3.1)	CP12(3.1)	CM31(3.2)	
LF12	CP11(1.5)	DM22(1.6)	CP12(1.7)	LF12(2)	CM34(2.2)	LF14(2.3)	NF11(2.4)	CM35(2.7)	DM21(2.8)	LF13(3)	
LF13	LF13(3.1)	CM35(4.8)									
LF14	LF13(1.2)	CM35(1.6)	LF15(2)	LF14(2.1)	UF12(2.8)	LF21(3.5)	DM23(3.8)	DM22(4.1)	LF22(4.4)	UF13(4.9)	
LF15	LF13(2.6)	CM35(3)	LF15(3.9)	LF14(4.8)							
LF21	LF13(1.4)	CM35(1.8)	LF15(1.9)	LF14(2.4)	UF12(2.5)	LF21(2.9)	LF22(3.8)	DM23(3.9)	UF14(4)	UF13(4.5)	
LF22	CM35(1.5)	LF15(1.7)	LF13(1.8)	LF14(2.6)	LF21(3)	UF12(3.2)	LF22(3.4)	DM23(3.5)	UF14(4.1)	DM22(4.4)	
LF23	LF22(0.8)	DM23(1)	LF15(1)	LF21(1)	CM35(1.6)	LF14(1.6)	UF14(1.6)	UF12(2.5)	LF23(2.7)	LF13(3)	
Montane	12 (2)	MINAC	17 10 0	17 1/2 2	001/0 5	00 (0 5)	12 (2.5	17.1 (2.5)	10.1/0.0	101/0.00	
M11	43x(2)	M11(2.2)	17aj(2.3)	17al(2.3)	80b(2.5)	80c(2.5)	43w(2.6)	17ab(2.7)	18d(2.8)	18b(2.9)	
M21 M22	M21(1.8)	UF13(2.3)	UF12(3.1)	LF13(3.2)	UF14(4.3)	LF14(4.4)	UF11(4.4)	DM22(2.1)	1/22/2 1	MEETOO	
M22	FF11(1.6)	MG11(1.6)	LF14(1.8)	CP12(1.9)	LF12(1.9)	M22(1.9)	M45(1.9)	DM23(2.1)	M32(2.1)	M55(2.2) ED12(1.0)	
1v132 M41	LF14(0.8) ED12(1.8)	0F12(1.4) M55(1.9)	UF13(1.4) UF13(1.9)	CM35(1.6) LE14(1.0)	DM23(1.6) M45(1.0)	LF13(1.6) M56(2)	LF13(1.7) M32(2.1)	UF14(1.7) UF14(2.1)	$L\Gamma 21(1.8)$ M21(2.2)	rr12(1.9) UF24(2.2)	
M42	11F12(1.8) HF12(1.7)	I = F14(1.8)	5F15(1.8) FP12(1.9)	CM35(2.1)	IF15(2.2)	$M_{20}(2)$ LIF12(2.2)	I = F13(2,3)	UF14(2.1) LF21(2.4)	$M \ge 1(2.3)$ UF13(2.5)	UF24(2.3) UF24(2.7)	
M43	FF11(1)	EP12(1)	DM23(1.3)	M45(13)	M32(1.5)	FP11(1.7)	LF22(1.9)	M22(2)	M44(2)	0127(2.7)	
M44	FP12(1)	DM23(1.4)	FF11(1.5)	M45(1.7)	LF22(1.9)	M32(1.9)	FP11(2.1)	LF21(2.1)	UF14(2.1)		
M45	FP12(1.6)	M56(2.1)	M45(2.6)	M55(2.8)	LF14(3.2)	FF11(3.4)	CM35(3.7)	LF12(3.7)	MG11(3.8)	CP12(3.9)	
M51	M56(1.1)	FP12(1.4)	M55(1.7)	M45(1.9)	LF14(2.5)	LF12(2.6)	M32(2.6)	SA33(2.7)	UF13(2.7)	·-·· /	
M53	FP12(0.9)	M45(1.7)	LF14(1.8)	M56(1.8)	DM23(1.9)	M55(2)	M32(2.1)	UF14(2.2)	FF11(2.3)		
M54	FP12(0.7)	M45(1.5)	M56(1.7)	M55(1.9)	LF14(2.2)	M32(2.2)	DM23(2.3)	FF11(2.3)	UF14(2.3)	CM35(2.7)	
M55	FP12(1.9)	M56(2.2)	M45(3)	M55(3)	UF13(3.5)	CM35(3.8)	LF12(3.9)	LF13(3.9)	SA33(3.9)	UF14(3.9)	
M56	ICHmw2(1.9)	ESSFwc1(2.1)	ESSFwk2(2.8)	ICHdw(2.9)	SBSwk2(3)	150(3.2)	BWBSwk1(3.2)	ICHwk1(3.2)	17x(3.3)	80c(3.3)	
Upper Footh	nills										
UF11	UF11(3.8)										
UF12	LF13(2.3)	UF12(3.7)	UF11(4.2)	CM35(4.4)	LF15(4.8)	LF14(4.9)					
UF13	LF13(1.8)	UF12(1.9)	UF13(2.3)	LF14(3.1)	M21(3.2)	CM35(3.6)	LF15(3.8)	UF14(3.8)	UF11(4.2)	LF21(4.4)	
UF14	LF13(1.4)	UF12(2.1)	CM35(2.4)	LF15(2.7)	LF14(2.8)	UF13(2.9)	UF14(3)	LF21(3.6)	M21(4)	DM23(4.5)	
UF15	LF21(0.7)	LF22(0.7)	DM23(0.8)	LF15(0.9)	UF14(1)	LF14(1.1)	CM35(1.4)	UF12(1.9)	FP12(2.3)	LF23(2.5)	
UF24	LF13(1.5)	UF13(1.8)	UF12(1.9)	M21(2.5)	UF14(2.7)	LF14(2.8)	CM35(2.9)	LF15(3.3)	UF24(4)		

Seed Zone	Choice 1	Choice 2	Choice 3	Choice 4	Choice 5	Choice 6	Choice 7	Choice 8	Choice 9	Choice 10
Northern Mixedwood										
NM11	BWBSmw2(5.9)	BWBSdk2(7)	BWBSmw1(8.9)							
NM21	DM11(3.8)	CM13(4.8)	CM12(5.4)							
Central Mixe	edwood									
CM11 CM12	42i(5.2)	421-(4.2)	DM21(4.2)	CM22(5.2)	CD11(5.2)	CM21(5.2)				
CM12 CM12	421(3.8) DM21(2.0)	42K(4.2)	DM21(4.3)	CM32(5.2)	CP11(5.2)	CM31(5.3)	NE11(4.5)	CM22(4.8)	DM22(4.0)	
CM21	DM21(2.9)	CM32(3.8)	DM22(4 2)	CP11(44)	CM31(4.6)	CM33(4.9)	DM13(5.2)	CM32(4.8)	DIVI22(4.9)	
CM22	CM32(2.8)	DM21(3)	CM33(3.4)	DM22(3.4)	CP11(3.6)	DM13(3.6)	CM31(3.7)	PRP11(4.3)	CM34(4.5)	CP12(5)
CM23	DM21(2.8)	CM32(2.9)	DM13(3.1)	CM33(3.2)	CP11(3.2)	DM22(3.3)	PRP11(3.7)	CM31(3.9)	CM34(3.9)	
CM24	DM22(2.6)	CM32(2.7)	CP11(3.1)	DM21(3.3)	CM34(3.5)	CM33(3.7)	DM13(3.9)	CP12(4.2)	PRP11(4.7)	
CM31	DM22(2.4)	CP11(2.8)	CP12(3.7)	DM21(3.7)	CM32(3.8)	CM35(3.9)	CM34(4.2)	NF11(4.3)	LF13(4.8)	LF15(5)
CM32	CM35(3.7)	DM22(3.7)	LF13(4.6)	LF15(4.6)	CP11(5)	CM32(5.2)	1 512(2.0)	1	CD12(4.1)	D (2) (4.4)
CM33 CM34	DM22(2.2)	CM35(2.8)	CP11(3.2) DM23(4)	CM32(3.5)	LF15(3.5)	CM34(3.6)	LF13(3.8) LF13(3.7)	CP11(4.1)	CP12(4.1)	DM21(4.4)
CM34 CM35	17b(3.6)	17a(5.1)	DM23(4)	LI 15(5)	LI 14(5.5)	CM34(3.7)	LI 15(5.7)	CI II(4.1)	CI 12(4.0)	LI 21(4.0)
Dry Mixedw	/ood									
DM11	42i(2.8)	42k(2.9)	DM21(3.4)	CP11(4)	DM22(4.6)	NF11(4.6)	PRP11(4.6)	CM32(4.8)	CM31(4.9)	DM13(4.9)
DM12	CP11(1.7)	CP12(1.9)	NF11(2)	DM22(2.3)	DM21(2.4)	PRP11(2.7)	DMG11(2.9)	DM13(3)	CM34(3.1)	LF12(3.3)
DM13	DM22(2.2)	CP11(2.3)	CP12(2.7)	CM34(2.9)	DM21(3.6)	CM32(3.7)	CM35(3.7)	NF11(3.7)	DM13(4.1)	MG11(4.3)
DM21	DM22(3.7)	CP11(4)	CM35(4.4)	CP12(4.8)	LF13(4.9)	NF11(5.1)				
DM22 DM23	CM35(4.3)	LF13(4.5)	DM22(5.2)	LE14(4.7)	DM22(5.2)	LE21(5.2)				
DWI25	CM35(3)	LI 15(5.5)	$LI^{(3,1)}$	LI 14(4.7)	DM23(3.2)	LI-21(5.5)				
BSA11	BWBSdk2(2.7)	BWBSmw2(2.8)								
BSA12	BWBSmw2(2.2)	BWBSdk2(3.8)	CM13(5.1)							
LBH11	DM21(2.6)	DM12(2.8)	CM31(2.9)	PRP11(3.3)	DM13(3.9)	LBH16(4)	CP11(4.1)	CM32(4.6)	CM33(4.6)	UBH13(4.7)
LBH12	BWBSmw2(3.6)	BWBSdk2(4.6)								
LBH13	DM21(1.7)	CM31(1.9)	CM32(2)	CM33(2)	DM13(2.3)	PRP11(2.6)	CP11(2.7)	DM22(2.8)	DM12(2.9)	LF11(3.4)
LBH14	DM21(1.5)	CP11(1.9)	PRP11(2)	DM13(2.2)	DM22(2.5)	CM32(2.7)	CP12(2.7)	NF11(2.7)	CM31(2.9)	CM33(2.9)
LBH15	DM22(1.3)	CP11(1.5)	CM32(2)	DM21(2)	CP12(2.5)	CM34(2.7)	CM35(3.1)	CM33(3.2)	NF11(3.3)	DM13(3.4)
LBH10 LBH21	$\frac{\text{CPII}(1.5)}{\text{BWBSmu}^2(2.9)}$	DM21(1.7) BWBSdF2(4.3)	DM11(4.5)	NF11(1.8) I BH16(5.2)	UBH13(5.2)	CM13(5.3)	DM22(2.3)	DM13(2.4)	CM34(2.9)	DMGII(3.1)
UBH11	DWB3IIW2(2.5)	CM31(1.4)	PRP11(2)	CM32(2.1)	DM12(2.1)	CM33(2.2)	CP11(2.2)	DM13(2.2)	DM22(2.6)	LF12(2.8)
UBH12	DM21(1.5)	CP11(1.9)	PRP11(2.2)	DM22(2.6)	LF12(2.7)	NF11(2.7)	CM31(2.8)	DM13(2.8)	CP12(2.9)	CM32(3)
UBH13	LF12(1.8)	CP11(2)	NF11(2)	CP12(2.1)	DM22(2.8)	DM21(2.9)	PRP11(3.2)	CM34(3.5)	MG11(3.6)	DMG11(3.7)
Lower Footh	<u>uills</u>									
LF11	DM22(2)	CM32(2.6)	CM34(2.7)	CM35(2.9)	CP11(3.1)	LF15(3.3)	LF14(3.7)	CM33(3.9)	LF13(3.9)	DM21(4)
LF12	DM22(2.2)	CM35(2.4)	CP11(2.5)	CP12(2.7)	LF13(2.7)	LF14(2.7)	LF15(3)	CM34(3.2)	DM23(3.5)	LF12(3.6)
LF13 LF14	17b(5.9) LE13(2.9)	LF13(6.1) CM35(3)	CM35(7.2) LE15(3.4)	UFII(7.2) L E14(3.9)	LF15(8) LF21(4.8)	UE12(4.8)	DM23(5.1)			
LF14 LF15	17b(4)	LF13(5)	CM35(5.4)	LF14(5.9)	LF21(4.8)	0112(4.8)	DIv125(5.1)			
LF21	LF13(3.3)	CM35(3.6)	LF15(3.9)	LF14(4.8)	UF12(5.1)	LF21(5.2)				
LF22	CM35(3.3)	LF13(3.6)	LF15(3.8)	LF14(4.9)	LF21(5.3)					
LF23	LF15(1.7)	CM35(1.8)	LF22(2.2)	DM23(2.3)	LF21(2.3)	LF14(2.7)	LF13(2.9)	UF14(3.1)	UF12(3.7)	
Montane										
M11	43w(1.7)	43x(2)	80c(2.7)	80b(2.9)	430(3.1)	17a(3.2)	17aj(3.2)	18b(3.2)	17al(3.3)	43q(3.3)
M21	17t(1.9)	M21(3.4)	UF11(4)	UF13(4.3)	LF13(4.4)	UF12(4.9)	IDEL 2/2 ()	10110		0.050.0
M22 M32	IDFmw1(1.9) I F13(1.3)	IDFmw2(2) I F14(1.6)	15c(2.2) CM35(1.7)	PPdh2(2.2)	42q(2.3) UE12(2.2)	BWBSwk1(2.3)	IDFdm2(2.4) UE13(2.6)	MG11(2.4) FP12(2.7)	LF14(2.5) LF21(2.9)	UE14(2.9)
M41	BWBSwk1(0.9)	LF14(1.0) LF13(1.9)	UF13(2 3)	LF13(2.1) LF14(2.4)	CM35(2.6)	EP12(2.6)	UF12(2.6)	M21(2.7)	UF14(2.8)	0114(2.9)
M42	LF13(2.2)	CM35(2.7)	LF14(3.1)	LF15(3.4)	UF12(3.4)	FP12(3.5)	UF14(3.5)	UF13(3.8)	LF21(4.4)	M56(4.5)
M43	FP12(1.5)	CM35(1.6)	DM23(1.6)	LF15(1.8)	LF14(1.9)	FF11(2.2)	LF21(2.3)	LF22(2.3)	M45(2.5)	UF14(2.7)
M44	FP12(1.7)	CM35(1.8)	DM23(1.8)	LF15(1.9)	LF14(2.1)	LF21(2.4)	LF22(2.4)	UF14(2.7)	FF11(2.8)	LF13(3)
M45	43v(2.1)	17a(2.4)	ICHmw2(2.6)	BWBSwk1(2.8)	FP12(2.8)	ICHdw(2.9)	15c(3)	43q(3.1)	ICHmk1(3.1)	IDFmw1(3.3)
M51 M52	BWBSwk1(1.1)	SBSwk2(1.8)	ESSFmv2(1.9)	FP12(1.9)	ICHmw2(1.9)	ICHmk1(2.1)	M56(2.1)	ESSFwc1(2.2)	ICHmm(2.2)	MSdk(2.4)
M55 M54	FP12(1.4) FP12(1.7)	CM35(1.7)	LF14(2) LF14(2.5)	LF13(2.1) LF13(2.7)	LF15(2.5) LF15(2.7)	DM23(2.5)	M56(3)	M36(2.8) M45(3.1)	LF21(2.9) UF14(3.2)	M45(2.9)
M55	17a(2.1)	BWBSwk1(2.3)	43v(2.7)	17b(3.1)	17t(3.2)	ICHmw2(3.2)	ESSFmv2(3.3)	43a(3.4)	43d(3.5)	EP 21(3.5) FP12(3.5)
M56	17a(3.6)	ICHmw2(3.6)	150(3.9)	BWBSwk1(4.1)	ESSFwc1(4.1)	80c(4.2)	ICHdw(4.4)	ESSFmv2(4.5)	17b(4.6)	()
Upper Foothills										
UF11	UF11(8.3)	17b(12.1)								
UF12	LF13(5.3)	UF11(5.4)	TELO/4 C	0.000	LTE12/4 C	1.014/4.02	L DI C/C C	101/5.0		
UFI3 UE14	LF13(3.2)	UF11(3.6)	UF12(4.2)	CM35(4.8)	UF13(4.8)	LF14(4.9)	LF15(5.1)	M21(5.2)		
UF14 UF15	CM35(1-1)	UF11(3.9) LF15(1.2)	CN155(4.1) LF14(17)	UF12(4.4) LF21(1.7)	DM23(1.8)	LF14(4.9) LF13(1.8)	UF14(3.1) LF22(1.9)	UF15(5.5) UF14(2.1)	UE12(2.5)	FP12(3-1)
UF24	UF11(2.3)	LF13(2.5)	UF12(3.6)	UF13(3.7)	CM35(4.2)	M21(4.3)	LF14(4.5)	UF14(4.5)	LF15(4.8)	- • • • • • • • • • • • • • • • • • • •
UF25	LF13(1.4)	CM35(1.9)	LF14(2.1)	UF12(2.1)	LF15(2.3)	UF14(2.3)	UF13(2.5)	LF21(3)	DM23(3.3)	FP12(3.3)

Table 3-12. Table of best matching seed sources for 2080s climate. The multivariateMahalanobis climate distance is given in parenthesis.
Table 3-13. Locations of recommended seed choices which originate outside of Alberta. For British Columbia I report the relevant ecological zones (Meidinger and Pojar 1991), and for the United States I report the corresponding state and "level III" ecoregion (EPA 2007).

Recommended seed choice	Zone/Ecoregion
British Columbia	
BWBSdk2, BWBSmw1, BWBSmw2, BWBSwk1	Boreal White and Black Spruce zone
ESSFmv2, ESSFwc1 ESSFwk2	Engelmann Spruce-Subalpine Fir zone
ICHdw, ICHmm, ICHmk1, ICHmw2, ICHwk1	Interior Cedar-Hemlock zone
IDFdm2, IDFmw1, IDFmw2	Interior Douglas-fir zone
MSdk	Montane Spruce zone
PPdh2	Ponderosa Pine zone
SBSwk2	Sub-Boreal Spruce zone
<u>Idaho</u>	
150	Northern Rockies ecoregion
17ab	Middle Rockies ecoregion
80b, 80c	Northern Basin and Range ecoregion
<u>Montana</u>	
15c	Northern Rockies ecoregion
17al, 17aj, 17t, 17x	Middle Rockies ecoregion
42i, 42k, 42q	Northwestern Glaciated Plains ecoregion
43d, 43o, 43v	Northwestern Great Plains ecoregion
South Dakota	
17b	Middle Rockies ecoregion
Wyoming	
17a	Middle Rockies ecoregion
18b, 18d	Wyoming Basin ecoregion
43q, 43x, 43w	Northwestern Great Plains ecoregion



Figure 3 -1. Climate of seed zones in Alberta, which are based on a hierarchical ecological classification system. Colors represent Natural Subregions, and points in the scatterplot represent the finest units of forested ecosystems that govern seed transfer in reforestation. The delineations corresponding to the scatterplot are shown on the map. The expected shift of a mean climate point for Alberta (1961-1990) representing the range of 18 climate change scenarios is indicated by ellipses (2020s, 2050s, 2080s).



Figure 3-2. Seed zones projections and consensus of habitat maintenance under projected climate change for white spruce in Alberta. Colors represent broad seed sources corresponding to Natural Subregions (upper row), and the gray scale represents the consensus that habitat is maintained for white spruce under 18 climate change scenarios for the 2020s, 2050s, 2080s (lower row). Here, I require at least a 70% probability that habitat is maintained to make a seed source recommendation.



Figure 3-3. Suitable habitat under projected under climate change for ponderosa pine in Alberta. There is very large uncertainty whether this species may become a viable forestry species in Alberta, with extensive areas of suitable habitat projected under some climate change scenarios, and virtually no habitat under other climate change projections.



Figure 3-4. Seed zones projections and consensus of habitat maintenance under projected climate change for black spruce in Alberta. Colors represent broad seed sources corresponding to Natural Subregions (upper row), and the gray scale represents the consensus that habitat is maintained for white spruce under 18 climate change scenarios for the 2020s, 2050s, 2080s (lower row). Here, I require at least a 70% probability that habitat is maintained to make a seed source recommendation.



Figure 3-5. Seed zones projections and consensus of habitat maintenance under projected climate change for Douglas-fir in Alberta. Colors represent broad seed sources corresponding to Natural Subregions (upper row), and the gray scale represents the consensus that habitat is maintained for white spruce under 18 climate change scenarios for the 2020s, 2050s, 2080s (lower row). Here, I require at least a 70% probability that habitat is maintained to make a seed source recommendation.



Figure 3-6. Seed zones projections and consensus of habitat maintenance under projected climate change for lodgepole pine in Alberta. Colors represent broad seed sources corresponding to Natural Subregions (upper row), and the gray scale represents the consensus that habitat is maintained for white spruce under 18 climate change scenarios for the 2020s, 2050s, 2080s (lower row). Here, I require at least a 70% probability that habitat is maintained to make a seed source recommendation.



Figure 3-7. Seed zones projections and consensus of habitat maintenance under projected climate change for jack pine in Alberta. Colors represent broad seed sources corresponding to Natural Subregions (upper row), and the gray scale represents the consensus that habitat is maintained for white spruce under 18 climate change scenarios for the 2020s, 2050s, 2080s (lower row). Here, I require at least a 70% probability that habitat is maintained to make a seed source recommendation.

Chapter 4. Assisted migration to address climate change: recommendations for aspen reforestation in western Canada²

Summary

Human-aided movement of species' populations in large scale reforestation programs could be a efficient and cost effective climate change adaptation strategy. Such large-scale management interventions, however, tend to entail the risks of unintended consequences, and I propose that three conditions should be met before implementing assisted migration in reforestation programs: (1) evidence of a climate-related adaptational lag, (2) observed biological impacts, and (3) robust model projections to target assisted migration efforts. In a case study of aspen (Populus tremuloides Michaux.) I use reciprocal transplant experiments to study adaptation of tree populations to local environments. Secondly, I monitor natural aspen populations using the MODIS enhanced vegetation index as a proxy for forest health and productivity. Lastly, I report results from bioclimate envelope models that predict suitable habitat for locally adapted genotypes under observed and predicted climate change. The combined results support assisted migration prescriptions and indicate that the risk of inaction likely exceeds the risk associated with changing established management practices. However, uncertainty in model projections also implies that we are restricted to a relatively short 20-year planning horizon for prescribing seed movement in reforestation programs. I believe that this study exemplifies a safe and realistic climate change adaptation strategy based on multiple sources of information and some understanding of the uncertainty associated with recommendations for assisted migration. Ad hoc migration prescriptions without a similar level of supporting information should be avoided in reforestation programs.

² A version of this chapter has been published as: Gray, L.K., Gylander, T., Mbogga, M.S., Chen, P. and Hamann, A. 2010. Assisted migration to address climate change: recommendations for aspen in western Canada.. Ecological Applications 21: 1591–1603.

I contributed the bioclimate envelope modeling and reforestation recommendations, MSB contributed the climatology work, TG contributed genetic data, and PC contributed the remote sensing analysis. I synthesized the data and wrote the paper.

4.1. Introduction

Climate change is projected to eliminate suitable habitat of many endemic or range-restricted species (e.g. Hannah et al. 2005; Parmesan 2006), which suggests that assisted movement of endangered species outside their historic range may be necessary for conservation purposes (e.g. Millar 2004; McLachlan et al. 2007). However, proactive mass translocation of a wide variety of species to mitigate loss of biodiversity under changing climate is a contentious issue and conflicts with well established conservation principles, such as ensuring translocated species do not become invasive (Hunter 2007; Ricciardi and Simberloff 2009). The concept of assisted migration may also be applied to translocation of populations within a species range. Populations within wide-ranging species are usually adapted to local environmental conditions (e.g. Kawecki and Ebert 2004; Savolainen et al. 2007) and mal-adaptation due to climate change may require population movement to matching habitat in new locations to maintain ecosystem health and productivity. This version of assisted migration also is subject to debate (Marris 2009), and it also conflicts with well established forest resource management principles and legislation that restricts the movement of seed sources in reforestation programs (e.g. Morgenstern 1996; Ying and Yanchuk 2006; McKenney et al. 2009).

It is useful to differentiate between the movement of species far outside their range for conservation purposes (*assisted colonization*), and population movement within a species range or somewhat beyond the leading edge (*assisted migration*). Under this definition, assisted migration would usually apply to common and widespread species for the purpose of maintaining ecosystem health and productivity, whereas assisted colonization aims at conserving endemic or range restricted species. Although there are exceptions, this definition largely

reflects previous usage of terminology in conservation biology (e.g. Hunter 2007; Hoegh-Guldberg et al. 2008; Ricciardi and Simberloff 2009) and forest resource management (e.g. Millar et al. 2007; O'Neill et al. 2008b; McKenney et al. 2009). For both assisted migration and assisted colonization, the contentious issue is the risk of unintended consequences associated with large-scale management interventions as well as a lack of rigorous scientific knowledge to guide the movement of species or genotypes. While predictive habitat modeling and observed biological impacts suggest an obvious general need for assisted migration (e.g. Parks and Bernier 2010 and associated conference papers), we usually do not know if this need applies to a particular species' population and where exactly appropriate target habitat would be under uncertain future climates.

My view is that assisted migration of common species is a promising climate change adaptation strategy with good chances of successful implementation: First, movement of planting stock is already a well established management practice in reforestation programs, although the emphasis has historically been on restricting seed movement (Ying and Yanchuk 2006). Second, there is a substantial body of research on how populations of commercially important tree species are adapted to local environments (Morgenstern 1996), and we can further draw on existing programs for commercial forestry species that monitor forest growth and health to determine the need for assisted migration (Parks and Bernier 2010). Third, robust predictive habitat models to reliably guide assisted migration are far easier to develop for common species than for rare endemics that lack census data for model parameterization (Kadmon et al. 2003). Fourth, most common tree species have a high degree of within population genetic variation in addition to substantial environmental plasticity (Hamrick 2004). Therefore there will be a small range around the optimal climate conditions of a planting stock that will still be appropriate habitat, likely preventing serious unforeseen consequences associated

with assisted migration. Lastly, implementing assisted migration at a large scale requires little or no additional financial resources when put into operation through existing reforestation programs.

Nevertheless, patterns of adaptive genetic variation and response to environmental change can be quite species-specific in trees, thus generic and *ad hoc* assisted migration efforts should be avoided. A moderate research effort is required to determine if assisted migration is necessary and how it should be implemented. Ideally, we should rely on a population-specific case-by-case evaluation if the benefits associated with a management intervention outweigh the potential risks. In a case study for aspen in western Canada, I develop a framework to guide assisted migration that draws on reciprocal transplant experiments to determine adaptational lag of populations, remote sensing to identify populations that are potentially vulnerable to climate change, and predictive habitat modeling to target assisted migration efforts both in terms of species choice and at the level of locally adapted populations within a species. My intention is to develop more dependable guidelines for assisted migration by synthesizing information from a variety of data sources and by drawing on independent modeling, experimental, and empirical research approaches.

4.2. Materials and methods

4.2.1. Reciprocal transplant experiments

Regional genetic differences and adaptational lag of aspen populations were quantified with a provenance trial series established by a forest industry cooperative at five locations in western Canada. The planting locations were

chosen to represent major ecosystem classes including the eastern Rocky Mountain foothills (test site coordinates: 52°50'N, 114°53'W), the southern boreal plains of Alberta (54°45'N, 113°10'W) and of Saskatchewan (53°26'N, 105°35'W), and the northern boreal plains of Alberta (56°46'N, 117°38'W) and of British Columbia (58°34'N, 122°22'W). Three to ten bulked commercial seed lots from collection locations in the broad vicinity of each test site were grown in a forest nursery in 1997 and seedlings representing a total of 38 provenances (seed lots) were planted at all five test locations in the spring of 1998. At each test site, provenances were planted in a randomized complete block design with 6 replications in 5-tree row plots. Tree height at age 9 was recorded in 2006. Means of 5-tree row plots were used as experimental units for analysis of variance implemented with PROC GLM of the SAS statistical software package (SAS Institute 2001). Averages and standard errors of provenances by source location were calculated with the least squares means method, taking advantage of the nested sampling and blocked experimental designs. Subsequently a matrix of probabilities that provenances transferred from different ecoregions (representing assisted migration) match or exceed the growth of provenances collected near the test site (representing local genotypes) was calculated.

4.2.2. Remote sensing

To infer forest health and productivity through remote sensing the Enhanced Vegetation Index (EVI) from the Moderate Resolution Imaging Spectroradiometer (MODIS) of NASA's Terra satellite was used. A 16-day interval 500m grid resolution EVI product (Huete et al. 2002; Gao et al. 2008) was obtained from the MODIS-for-NACP data products website (NASA 2008). MODIS/EVI data for North America was cropped to the study area and filtered for grid cells that primarily contained aspen stands. For the filtering the use of Alberta Vegetation Inventory database (ASRD 2005), and 25m grid resolution land cover data for western Canada (Wulder et al. 2008) was explored. Summarized at 500m grid resolution corresponding to MODIS/EVI data, the deciduous class of 25m land cover data closely reproduce aspen frequency data from Alberta's forest inventory database. This is plausible because aspen is the predominant deciduous forest species throughout the study area (representing 75 to 95% of deciduous trees for boreal ecosystems). Therefore deciduous forest cover was used as a proxy for aspen frequency over the entire study area, since forest inventory data for the study area was regionally incomplete and not available for most parts of Saskatchewan.

To infer potential vulnerability of aspen populations to climate change, I took advantage of a major regional drought that led to dieback of aspen stands in western Canada in 2002 (Bonsal and Wheaton 2005; Hogg and Bernier 2005; Hogg et al. 2008). First, 16-day interval MODIS/EVI data that was available from 2001 to 2006 was processed with the TIMESAT software package, using an adaptive Savitzky–Golay function to fit EVI values as a function of Julian date over the course of each year (Jonsson and Eklundh 2004). The large integral under the Savitzky–Golay function was used to generate remotely sensed proxies of forest productivity. The large integral represents the cumulative amount of green vegetation, measured as EVI, over the course of the growing season. This measure can be used to estimate net primary productivity with additional predictor variables (Huete et al. 2002), but in this study raw integral data was analyzed. Integral values were generated for 700,000 aspen grid cells for six years, and subsequently converted to annual anomalies from the six year average. The anomaly values were mapped to evaluate geographic variation of EVI values integrated over the course of the growing season in response to the 2002 regional drought.

4.2.3. Climate trends and projections

The baseline climate data was derived from monthly precipitation and temperature grids that were generated by Daly *et al.* (2008) using the Parameterelevation Regression of Independent Slopes Model (PRISM) to interpolate climate normal data observed at weather stations for the period 1961–1990 for the United States and Canada. This database was enhanced with lapse-rate based down-sampling to 1km resolution and estimation of biologically relevant climate variables (Hamann and Wang 2005; Wang et al. 2006a; Mbogga et al. 2009). Climate variables were selected to exclude pairs of highly correlated variables and include mean annual temperature. This list includes mean warmest month temperature, mean coldest month temperature, continentality (difference between mean January and mean July temperature), mean annual precipitation, mean growing season precipitation (May to September), the number of frost free days, growing degree days above 5°C, and annual and summer dryness indices according to Hogg (1997). The climate variables are described in more detail by Wang *et al.* (2006a).

A measure of observed climate change was calculated as the difference between the 1961–1990 climate normal and the 1997–2006 decadal average, which corresponds to the period when trees were grown in the reciprocal transplant experiment described above. Climate projections for the sample sites for the 2020s, 2050s, and 2080s were generated by overlaying projections from general circulation models expressed as the difference from the 1961–1990 normal period. I used 18 future projections based on four major SRES emission and population growth scenario families (A1FI, A2, B1, B2) and implementations of these scenarios by five modeling groups (CGCM2, Canada; HADCM3, UK; ECHAM4, Europe; CSIRO2, Australia; and PCM, United States). Two model-

scenario combinations were not available (ECHAM4-A1F1 and ECHAM4-B1). The difference between the 1961–1990 climate normal and the 1997–2006 average can further be interpreted as observed climate change over a 25-year period (approximately 1975 to 2000) and was used for predictive habitat modeling in the same way as projections from general circulation models (Mbogga et al. 2009).

All grid manipulations of climate data, lapse rate elevation adjustments, data extraction from grids for sample locations, overlays of historical anomalies and climate projections described above were carried out with a custom software application that is freely available. The database and software for western Canada has been released (Mbogga et al. 2009)³, while an extension of this database to western North America is available on-line as beta version (Wang et al., unpublished manuscript)⁴.

4.2.4. Predictive habitat modeling

For projections of aspen habitat and aspen seed zones that represent locally adapted aspen populations, an ecosystem based bioclimate envelope modeling technique developed by Hamann and Wang (2006) and Mbogga *et al.* (2010) was used. Predictions were carried out with classification trees implemented by the RandomForest software package (Breiman 2001; Cutler et al. 2007) for the R programming environment (R Development Core Team 2008). RandomForest grows multiple classification trees from bootstrap samples of the training data and

³ Available for download at *http://www.ualberta.ca/~ahamann/climate.html*

⁴ Available for download at

http://www.genetics.forestry.ubc.ca/cfcg/ClimateWNA/ClimateWNA.html

determines the predicted class by majority vote over all classification trees. As dependent class variables, I used mapped ecosystems for western Canada and the United States, rasterized at 1km resolution. From each of 771 mapped ecosystems, 100 grid cells were randomly sampled to be used as training data for classification tree analysis. For British Columbia I use the "Variant" level of the Biogeoclimatic Ecological Classification system version 4 (Meidinger and Pojar 1991). In Alberta, I use the "Seed zone" level of Natural Regions and Subregions System, 2005 release (NRC 2006). "Ecodistricts" of the National Ecological Framework for Canada were used for Saskatchewan and Manitoba (Selby and Santry 1996), and "Level 4" delineation of the United States Ecoregion System were used for the area west of 100° longitude and north of 42° latitude (EPA 2007).

This modeling approach has some disadvantages. For example, spatial autocorrelations in the ecosystem response variables requires a different approach to model validation (Hamann and Wang 2006), and community-based modeling methods may restrict individualistic species response to climate change (Baselga and Araujo 2009). However, there are also important advantages to the approach: species frequencies (in addition to probability of presence) can be inferred by replacing the ecosystems modeling units with known species frequencies (Hamann and Wang 2006), and crucially, can be accounted for genetic structure within wide-ranging species by aggregating modeling units into higher hierarchical groups that represent similarly adapted genotypes. Although accounting for within-species genetic structure in bioclimate envelope modeling has previously been proposed (e.g. Botkin et al. 2007), to my knowledge this is the first study that implements this idea. A final practical advantage is that the ecosystem modeling units are also the framework for current natural resource

management prescriptions, and model projections can therefore be directly linked to a set of applicable management practices under anticipated future climates.

4.3. Results

4.3.1. Regional climatology and climate change

For subsequent interpretation of experimental, empirical, and modeling results, it is instructive to examine the climatology of the study area. The foothills ecosystem (Table 4-1, Figure 4-1) stands out with higher precipitation and a more maritime climate (cooler summers and warmer winters) than all other zones. For the rest of the study area I find a latitudinal temperature gradient and a unimodal precipitation gradient that has a maximum at approximately 56°N latitude, corresponding to the summer position of the polar jet stream storm track that defines the climatology of the Boreal Plains region (Alberta Environment 2005). Precipitation declines both towards the northern boreal ecosystems and the aspen parklands in the south.

The average climate during the decade 1997–2006 when trees of the reciprocal transplant experiment were grown in the field was substantially warmer and drier than the 1961–1990 reference period (Table 4-1). Temperature increases were more pronounced in the north (+1.4°C) than in the south (+0.8°C) with more warming in winter than in summer temperatures. Observed temperature trends approximately correspond to patterns described in the IPCC fourth assessment report (IPCC 2007) and also match regional climate change projections by general circulation models for the 2020s in direction and magnitude (Table 4-2). In contrast, observed precipitation trends are opposite in direction to projections by

most general circulation models. The trend towards drier climate conditions was more pronounced in winter, and together with warmer winter temperatures have resulted in major reductions in precipitation as snow (Table 4-1).

Taking climate trends observed over the last 25 years into account, the Boreal Plains for the 1997–2006 period (MAT=1.6, MAP=444) starts to resemble the 1961–1990 climatology of the Aspen Parkland. The Northern Boreal zone under the 1997–2006 period is very dry, but does not reach the 1961–1990 temperature values of the Aspen Parkland. Similarly, the Taiga Plains under the 1997–2006, does not reach the temperature values of the current Northen Boreal zone, but exceeds it in dryness. This implies a general northward shift of climatically defined habitat conditions for a recent 10-year period, which is driven by reduced precipitation and increased temperatures.

4.3.2. Genetic differentiation and adaptational lag

Growth of aspen provenances that have been subjected to assisted migration in a reciprocal transplant experiment indicate an apparent adaptational lag (Figure 4-1). Provenances from the Taiga region in northeast British Columbia (color code: olive) perform poorly when transferred south with the relatively lowest height growth at the most southern test site (33). The group of five provenances from northern Alberta (dark green) perform somewhat more poorly than local sources at the southern test sites (33, 60, 90), but are the best performer when transferred to the most northern test site (70). The remaining provenances from the Boreal Plains region of central Alberta and Saskachewan (light green) and the Foothills (blue) show similar growth across all test sites. These provenances outperform the local sources when transferred to the Northern Boreal test

site (10). The Rocky Mountain Foothill provenances are weakly distinguished from Boreal Plains provenances by lower performance at several test locations, including their local test site (33).

The probability of provenance groups matching or exceeding the local sources following an assisted migration treatment are listed in Table 4-3. The probability values reflect both the effect size of the provenance transfer and the sample size for each region (i.e. it is essentially a confidence interval calculation). The probabilities of matching or increasing productivity relative to local sources are very pronounced for movement to and from the most northern region (Taiga, Site 70), with northward transfer very likely to be beneficial and southward movements certain to be disadvantageous. However, the results are less clear-cut for the Northern Boreal test location (Site 10). Here, a southward transfer from the region is clearly disadvantageous, but a northward transfer to the region is unlikely to have a benefit. Smaller positive effects associated with a high probability include transfers from the Boreal Plains to the Foothills and transfers from Saskachewan to Alberta. All other probability values are intermediate, indicating either a minor transfer effect size or uncertainty due to low sample sizes.

4.3.3. Drought impacts on aspen populations

Remotely sensed EVI values integrated over the course of the growing season show two main areas of negative anomalies during the 2002 regional drought (Figure 4-2). Within the Northern Boreal zone I find an area of reduced productivity in eastern Alberta that approximately corresponds to the Dry Mixedwood and Peace River Parkland ecological subregions (Figure 4-2, dotted lines). Within the Boreal Plains of Saskachewan and Alberta the southern fringe has negative integral and peak value anomalies (Figure 4-2, dotted lines). The negative anomalies extend further south into the Aspen Parkland ecoregion (not delineated in Figure 4-2) towards the southern range limit of aspen. Another region that showed substantial negative anomalies is the eastern part of the boreal plains in Saskatchewan.

4.3.4. Bioclimate envelope shifts

Composite results of predictive habitat models are shown in Figure 4-3. Predicted species frequencies indicate where aspen is expected to be a major forest component. Counts of predicted presence or absence from multiple bioclimate envelope model projections indicate the risk (or uncertainty) of future habitat loss. Aspen is currently most frequent in the Northern Boreal zone and the western portion of the Boreal Plains of Alberta (Figure 4-3, 1961–1990). A majority of model runs, however, project a complete loss of habitat for aspen over much of this area (Figure 4-3, 2080s). In contrast, the Foothills and the Taiga Plains are projected to maintain aspen habitat. Also, moderately high aspen frequencies and low probability of habitat loss are expected along a band across the Boreal Plains that originates in the Rocky Mountain Foothills and crosses Alberta in a northeast direction. Interestingly, projected habitat shifts for the 1997–2006 decadal average approach model projections for the 2020s quite closely. Notably, aspen appears to have already lost climatically suitable habitat along the southern fringe of its distribution.

In Figure 4-4 I break the same projections down into climate envelopes of seed zones represented by major ecological regions (rather than into aspen frequency classes as in Figure 4-3). In this case, the model consensus maps for future projections reflect confidence in seed zone recommendations. High confidence

(towards 100%), means that all model runs result in the same seed zone recommendation. At the low end of confidence, 6 out of 18 model runs (~30%) project the same seed zone for a grid cell with the remaining 12 model runs comprised of various other seed zone projections. For the 2020s and the 1997– 2006 average, I observed a general north shift of seed zone bioclimate envelopes by 1–2° latitude, and for the 2020s, there is generally high confidence in seed zone projections with areas of uncertainty restricted to boundaries between projected seed zone envelopes. For the 2050s and 2080s, the Northern Boreal and Boreal Plains climate envelopes are primarily replaced by Aspen Parkland climates. However, there is a very high degree of uncertainty associated with these predictions.

4.4. Discussion

4.4.1. Adaptational lag causes suboptimal growth

Adaptational lag refers to a mismatch of genotypes and environments, caused by a relatively fast environmental change and a comparably slow evolutionary response (Matyas 1990). Adaptational lag is not uncommon, and is in fact part of any evolutionary change through directional natural selection. Even if adaptational lag does not pose a threat to a species' overall survival, it is a concern for forest management because it can result in suboptimal growth, poor forest health, and high rates of tree mortality. Even though these impacts could be viewed as a natural part of evolutionary change, proactive climate change adaptation strategies should aim at maximizing forest health and productivity through intervention.

Adaptational lag can be detected with reciprocal transplant experiments if transferred seed sources outperform local seed sources. Given the regional climatology and observed climate trends described in Table 1, we would expect nonoptimality due to temperature changes to be most pronounced in the Taiga plains, where the warming signal was strongest (+1.4°C mean annual temperature). The expectation is that southern sources, adapted to warmer environments, outperform local provenances when transferred north. With respect to precipitation there is a general trend towards drier conditions, which was most pronounced in the Northern Boreal Plains (-9% mean annual precipitation). This means that provenance adapted to drier environments may outperform local sources when transferred to originally wetter sites that now match their conditions of origin.

Results from the reciprocal transplant experiment generally conform to these expectations. For example, local sources at the northern Taiga Plains test site were outperformed by all other provenances that were transferred north to this site (Figure 4-1). The Northern Boreal provenances, which are a very good match in both temperature and precipitation for the new Taiga plains environment, outperform the local sources by a large margin (30% increase in height relative to the local Taiga Plains provenances). Conversely, a transfer of provenances southward generally leads to poor performance, e.g., Northern Boreal and Taiga provenances to any southern test site.

Transfer results with respect to changes in precipitation partially conform to expectations. For example, local Foothills sources were out-performed by Boreal Plains sources, which are adapted to drier environments (Figure 4-1). However, sources from the wet Foothills ecosystem outperform local sources when transferred to the dry Taiga Plains environment. A plausible explanation arises

from the fact that evolutionary fitness is not necessarily reflected by growth measured in short term common garden trials. Some environments require survival adaptations that result in a trade-off with adaptations that maximize growth (Mangold and Libby 1978). Taiga Plains provenances likely have conservative growth strategies that may include late bud break, early bud set, and wood properties to avoid frost damage in harsh northern environments. While such damage did not occur to Foothills provenances at the Taiga Plains site during the testing period, the local provenances may still have a long-term evolutionary advantage in surviving extreme climate events. It would therefore be instructive to evaluate adaptive traits in the common garden experiments before recommending such transfers to non-matching environments.

Another example that indicates more than one climatic factor drives local adaptation of genotypes is the Northern Boreal test site. Here, local sources outperformed all introduced provenances, even though the Boreal Plains provenances would be a good match after a temperature increase of 1.1°C (Table 4-1). However, these sources also came from wetter environments that did not match the test site conditions with respect to precipitation. The transplant experiment did not include provenances from the dry and warm Aspen Parkland region, but I can speculate these sources could outperform local sources because they climatically match the observed 1997–2006 climate of the Northern Boreal region. These results point to the potential value of other approaches to complement limited information from sample-based reciprocal transplant experiments.

4.4.2. Indirect indicators of mal-adaptation

In addition to the reciprocal transplant experiment, bioclimate envelope modeling and remote sensing provide independent data that can guide assisted migration efforts. Negative anomalies in remotely sensed EVI values during a regional drought in 2002 identify two general areas where aspen populations are vulnerable to climate change: the southern fringe of the Boreal Plains and Dry Mixedwood subregion of the Northern Boreal ecosystem (Figure 4-2). Remarkably, the remotely sensed negative anomalies correspond to loss of habitat inferred from bioclimate envelope modeling (Figure 4-3, 1997-2006). In addition, reduced productivity and dieback of aspen forests along the sourthern range limit of aspen in Alberta and Saskachewan has been found in through field observations (Hogg et al. 2002; Hogg and Bernier 2005). For the southern fringe, the realized niche model corresponds to empirical data from fundamental niche observations (negative EVI anomalies), suggesting that the limits of the fundamental and realized niche are the same at the southern range limit of aspen.

Bioclimate envelope model projections for the 1997-2006 period did not show a loss of habitat for the Dry Mixedwood subregion of the Northern Boreal ecosystem, the second region where remotely sensed negative anomalies were observed (Figure 4-2). However, substantial loss of aspen habitat is predicted in this area for the 2050s and 2080s (Figure 4-3). The discrepancy among the realized niche projections for the 1997-2006 period and fundamental niche observations (reduced productivity in the northern Dry Mixedwood subregion) is not surprising. By treating species as homogenous units, bioclimate envelope models essentially allow translocation of climate envelopes within the species range from southern/low elevation populations to northern/high elevation locations. This is equivalent to assuming unlimited migration of genotypes within

a species range, and thereby underestimating potential climate change impacts on northern and high elevation populations (Chen et al. 2010). In Figure 4-4, for the first time, the translocations of populations by a bioclimate envelope model within a species range are visualized. The species-level model (Figure 4-3) could correctly account for climate change impacts at the southern fringe, but failed to account for impacts in the dry mixedwood subregion, where habitat was maintained at the species level, but lost for the Northern Boreal genotype (Figure 4-4).

4.4.3. Climate envelope models should guide seed transfer

Although reciprocal transplant experiments can theoretically be used to determine optimal transfer distances for seed sources (Wang et al. 2006b, O'Neill et al. 2008a), I propose that bioclimate model projections are a better and safer approach to make such inferences. Bioclimate envelope models have many limitations that have been thoroughly discussed (e.g. Hampe 2004; Araujo and Guisan 2006; Botkin et al. 2007). However, many of these limitations do not apply in a reforestation context. For example, management practices can "migrate" as rapidly as bioclimate envelope model results suggest. Also, competition and species interactions are usually controlled through spacing of plantations and choice of planting stock. Perhaps most importantly, the limitation that bioclimate envelope models project the realized niche and not the fundamental niche of tree species turns out to be an advantage in a reforestation context.

For example, consider the results of a reciprocal transplant experiment to determine growth across the fundamental niche of lodgepole pine, *Pinus contorta* (Wang et al. 2006b; O'Neill et al. 2008a). These studies showed that the species

may grow well under projected climate warming in many areas as long as there are no moisture limitations. However, warm and moist growing conditions can also lead to severe needle cast caused by the native fungus *Dothistroma pini* (Woods et al. 2005). This biotic interaction reduces the fundamental niche space of lodgepole pine to a more restricted realized niche. A judicious recommendation for reforestation under climate change should exclude warm and wet climate conditions, i.e., a conservative approach to species choice for reforestation should be guided by projections of the realized niche, not the fundamental niche. While this approach may possibly forgo some potential gains in tree growth due to climate change, it is less risky and corresponds to the widely adopted reforestation policy of not planting species outside their observed range.

Another disadvantage of using data describing the fundamental niche of tree populations from common garden trials has been mentioned before. Long-term evolutionary fitness is not necessarily reflected by growth measured in short-term common garden trials. In contrast, the realized niche inferred from distribution data should be a reasonable approximation of environmental conditions under which a species (or populations of a species) are competitive in the long term.

4.4.4. Recommendations for aspen

Bioclimate envelope projections at the seed zone level for the 2020s and 1997– 2006 period suggest that aspen seed sources may be moved north by 1° to 2° latitude (Figure 4-3). However, we do not need to change seed zone boundaries or other delineations that currently serve as framework for forest resource management. Instead it is more useful to provide general seed source recommendations for established forest management areas or even individual planting sites. In Table 4-4 the most appropriate climatic regions where seed

should be obtained for reforestation is listed. For example, for the Alberta forest management unit NM 1.1 we can see that aspen habitat in this unit is fully maintained until the 2080s (100% of the management unit). The recommended seed source for the 1961–1990 normal period is the Taiga Plains (TP, 100% of the management unit). However, under currently observed climate and 2020s projections, 24% and 32% of this management unit is climatically best suited for seed sources from the Northern Boreal climate region.

In many instances, the recommendations for 2020 projections and the climate observed over the last decade are very similar (Table 4-4, Figure 4-3). However it should be noted that this similarity is based on slightly different climatologies: for the recent decade, precipitation values are lower, but this is compensated by cooler temperatures compared to the 2020s projection. A relatively short-term 25-year trend in observed precipitation cannot be extrapolated into the future, and we should not make the assumption that the trend will continue. Nevertheless, from an applied perspective, the combined information from GCM projections, climate trends that have apparently materialized, and observed biological response make a strong case for implementing adaptation strategies in the southern fringe of the Boreal Plains, and the Dry Mixedwoods of the Northern Boreal region.

Reforestation programs should rely on more drought-tolerant species or genotypes in the future, and aspen forestry should concentrate on the moister and more northern ecosystems. Reforestation with aspen genotypes other than the local sources requires some confidence in the projections of which genotype should be used. Model consensus for seed zones is generally high for the 2020s, but shows dramatic reductions toward the 2050s and 2080s (Figure 4-4). Does this suggest that we should develop relatively "short-sighted" adaptation strategies, i.e., focus on the 2020s projection and dismiss longer-term projections as too uncertain for

practical resource management? I think the answer to this question is "Yes." Despite consideration of their long lifetime, it is important to realize that the most vulnerable phase of trees remains their seedling and sapling stage (Jackson et al. 2009). In a changing environment, we should not focus on optimizing planting stock for maximum growth during midrotation, when this means that seedlings planted today will not survive because climate conditions predicted for the 2050s have yet to materialize. The high degree of uncertainty in longer-term climate projections is an additional argument to develop adaptation strategies for the immediate future with a 10–20 year planning horizon.

While there is a high degree of uncertainty in determining optimal seed sources for deployment by the 2050s and 2080s, I recognize that applied tree improvement programs regularly have planning horizons of several decades or even a century. What can be recommended with respect to developing long-term breeding programs and establishment of seed- and cutting orchards for improved aspen planting stock? It certainly appears that there will be limited future demand for aspen planting stock that is adapted to moist environments of the Rocky Mountain Foothills ecosystems and the adjacent Boreal Plains zone (Figure 4-4, blue and light green). These areas, which currently receive relatively high summer precipitation, are predicted to be more suitable for genotypes adapted to warmer and drier growing conditions by the 2050s and 2080s (Figure 4-4, orange). At the same time the climate envelope of the current Foothills and Boreal Plains regions are predicted to largely disappear from the study area. A breeding program or seed zone corresponding to the parkland ecoregion (Figure 4-4, orange) currently does not exist, and I think that the establishment of a tree improvement programs with genotypes from this region would be a worthwhile consideration.

4.5. Conclusions

In this chapter I advocate assisted migration prescriptions for a common tree species to address climate change within a framework of normal reforestation programs. However, patterns of adaptive genetic variation and response to environmental change can be quite species-specific in trees, and I think that generic and *ad hoc* assisted migration efforts should be avoided. A moderate research effort is required to determine if assisted migration is necessary and how it should be implemented.

To develop dependable, species-specific guidelines for assisted migration we may draw on information from a variety of data sources and use independent modeling, experimental, and empirical research approaches. In a case study for aspen, I evaluated adaptational lag in a transplant experiment, *in situ* productivity anomalies through remote sensing, and population-specific habitat projections from bioclimate envelope models. Additional research approaches may be useful to develop population-specific prescriptions. For example, dendro-climatology approaches can be used to identify tree populations vulnerable to climate change. Monitoring problems such as failure of plantation establishment or pest and disease outbreaks can provide additional information where the risk of inaction likely exceeds the risk associated with changing established management practices.

4.6. Literature Cited

Alberta Environment. 2005. Alberta Climate Model (ACM) to provide climate estimates (1961-1990) for any location in Alberta from its geographic

coordinates. Publication No. T/749. Alberta Environment, Edmonton, Alberta, Canada.

- Araujo, M.B. and Guisan, A. 2006. Five (or so) challenges for species distribution modeling. Journal of Biogeography 33: 1677-1688.
- ASRD. 2005. Alberta Vegetation Inventory, Version 2.1.1, Volume 1. Resource Information Management Branch, Alberta Sustainable Resource Development (ASRD). Available online at http://srd.alberta.ca/forests/researcheducation/vegetationinventory.aspx, accessed 8 September 2009.
- Baselga, A., and Araujo, M.B. 2009. Individualistic vs community modelling of species distributions under climate change. Ecography **32**(1): 55-65.
- Bonsal, B.R., and Wheaton, E.E. 2005. Atmospheric circulation comparisons between the 2001 and 2002 and the 1961 and 1988 Canadian Prairie droughts. Atmosphere-Ocean **43**(2): 163-172.
- Botkin, D.B., Saxe, H., Araujo, M.B., Betts, R., Bradshaw, R.H.W., Cedhagen, T., Chesson, P., Dawson, T.P., Etterson, J.R., Faith, D.P., Ferrier, S., Guisan, A., Hansen, A.S., Hilbert, D.W., Loehle, C., Margules, C., New, M., Sobel, M.J., and Stockwell, D.R.B. 2007. Forecasting the effects of global warming on biodiversity. Bioscience 57(3): 227-236.
- Breiman, L. 2001. Random forests. Machine Learning 45(1): 5-32.
- Chen, P., Welsh, C., and Hamann, A. 2010. Geographic variation in growth response of Douglas-fir to interannual climate variability and projected climate change. Global Change Biology **16**(12): 3374-3385.
- Cutler, D.R., Edwards, T.C., Beard, K.H., Cutler, A., and Hess, K.T. 2007. Random forests for classification in ecology. Ecology **88**(11): 2783-2792.
- Daly, C., Halbleib, M., Smith, J.I., Gibson, W.P., Doggett, M.K., Taylor, G.H., Curtis, J., and Pasteris, P.P. 2008. Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. International Journal of Climatology 28(15): 2032-2064.
- EPA. 2007. Ecoregion Maps and GIS Resources. U.S. Environmental Protection Agency, Western Ecology Division official website, Available online at: http://www.epa.gov/wed, accessed 10 May 2008.
- Gao, F., Morisette, J.T., Wolfe, R.E., Ederer, G., Pedelty, J., Masuoka, E., Myneni, R., Tan, B., and Nightingale, J. 2008. An algorithm to produce temporally and spatially continuous MODIS-LAI time series. Ieee Geosci Remote S 5(1): 60-64.

- Hamann, A. and Wang, T.L. 2005. Models of climatic normals for genecology and climate change studies in British Columbia. Agricultural and Forest Meterology **128**: 211-221.
- Hamann, A., and Wang, T.L. 2006. Potential effects of climate change on ecosystem and tree species distribution in British Columbia. Ecology 87(11): 2773-2786.
- Hampe, A. 2004. Bioclimate envelope models: what they detect and what they hide. Global Ecology and Biogeography **13**: 469-471.
- Hamrick, J.L. 2004. Response of forest trees to global environmental changes. Forest Ecology and Management **197**(1-3): 323-335.
- Hannah, L., Midgley, G., F., Hughes, G., and Bomhard, B. 2005. The view from the Cape: Extinction risk, protected areas, and climate change. BioScience **55**(3): (231-242).
- Hoegh-Guldberg, O., Hughes, L., McIntyre, S., Lindenmayer, D.B., Parmesan, C., Possingham, H.P., and Thomas, C.D. 2008. Assisted colonization and rapid climate change. Science **321**(5887): 345-346.
- Hogg, E.H. 1997. Temporal scaling of moisture and the forest-grassland boundary in western Canada. Agricultural and Forest Meteorology **84**(1-2): 115-122.
- Hogg, E.H., Brandt, J.P., and Kochtubajda, B. 2002. Growth and dieback of aspen forests in northwestern Alberta, Canada, in relation to climate and insects. Canadian Journal of Forest Research 32(5): 823-832.
- Hogg, E.H., Brandt, J.P., and Michaelian, M. 2008. Impacts of a regional drought on the productivity, dieback, and biomass of western Canadian aspen forests. Canadian Journal of Forest Research 38: 1373-1384.
- Hogg, E.H.T., and Bernier, P.Y. 2005. Climate change impacts on drought-prone forests in western Canada. Forestry Chronicle **81**(5): 675-682.
- Huete, A., Didan, K., Miura, T., Rodrigues, E., P., Gao, X., and Ferreira, L., G. 2002. Overview of the radiometric and biophysical performance of MODIS vegetation indices. Remote Sensing of Environment 83(1-2): 195-213.
- Hunter, M.L. 2007. Climate change and moving species: Furthering the debate on assisted colonization. Conservation Biology **21**(5): 1356-1358.
- IPCC. 2007. Climate change 2007: The physical basics (Summary for policymakers). Intergovernmental Panel on Climate Change. ISBN 978 0521 70596-7.

- Jackson, S.T., Betancourt, J.L., Booth, R.K., and Gray, S.T. 2009. Ecology and the ratchet of events: Climate variability, niche dimensions, and species distributions. PNAS 106(2): 19685-19692.
- Jonsson, P., and Eklundh, L. 2004. TIMESAT a program for analyzing timeseries of satellite sensor data. Comput Geosci-Uk **30**(8): 833-845.
- Kadmon, R., Farber, O., and Danin, A. 2003. A systematic analysis of factors affecting the performance of climatic envelope models. Ecological Applications 13(3): 853-867.
- Kawecki, T.J., and Ebert, D. 2004. Conceptual issues in local adaptation. Ecology Letters **7**(12): 1225-1241.
- Mangold, R.D., and Libby, W.J. 1978. Model for reforestation with optimal and suboptimal tree populations. Silvae Genetica **27**(2): 66-68.
- Marris, E. 2009. Planting the forest of the future. Nature 459(7249): 906-908.
- Matyas, C. 1990. Adaptational lag: a general feature of natural populations. *In* In: Joint Meeting of Western Forest Genetics Association and IUFRO Working Parties, Douglas-fir, Contorta Pine, Sitka Spruce, and Abies Breeding and Genetic Resources. 20-24 August, Olympia, Washington 11 pp.
- Mbogga, M.S., Hamann, A., and Wang, T. 2009. Historical and projected climate data for natural resource management in western Canada. Agricultural and Forest Meteorology 149: 881 – 890.
- Mbogga, M.S., Wang, X.L., and Hamann, A. 2010. Bioclimate envelope model predictions for natural resource management: dealing with uncertainty. Journal of Applied Ecology **47**(4): 731-740.
- McKenney, D., Pedlar, J., and O'Neill, G. 2009. Climate change and forest seed zones: Past trends, future prospects and challenges to ponder. Forestry Chronicle **85**(2): 258-266.
- McLachlan, J.S., Hellmann, J.J., and Schwartz, M.W. 2007. A framework for debate of assisted migration in an era of climate change. Conservation Biology 21: 297-302.
- Meidinger, D., and Pojar, J. 1991. Ecosystems of British Columbia. Special Report Series 6. Research Branch, BC Ministry of Forests and Ranges, Victoria, British Columbia, ISBN 0843-6452.
- Miller, C.I. 2004. Climate change as an ecosystem architect: implications to rare plant ecology, conservation, and restroation. Pages 139-157 in M. Brooks, editor. Proceedings of the Conference on Rare Plants of Northern

California. February 6-9, 2002, Arcata, California. California Native Plant Society, Sacramento, CA.

- Millar, C.I., Stephenson, N.L., and Stephens, S.L. 2007. Climate change and forests of the future: Managing in the face of uncertainty. Ecological Applications **17**(8): 2145-2151.
- Morgenstern, E. 1996. Geographic Variation in Forest Trees. Genetic Basis and Application of Knowledge in Silviculture. University of British Columbia Press, Vancouver, BC, Canada. 208p.
- NASA. 2008. MODIS-for-NACP data products. National Aeronautics and Space Administration (NASA). Available online at http://accweb.nascom.nasa.gov/, accessed 8 September 2009.
- NRC. 2006. Natural regions and Subregions of Alberta. Natural Regions Committee, Government of Alberta, Alberta Environment, Edmonton, Alberta, ISBN 0-7785-4572-5.
- O'Neill, G.A., Hamann, A. and Wang. T.L. 2008a. Accounting for population variation improves estimates of the impact of climate change on species' growth and distribution. Journal of Applied Ecology **45**: 1040-1049.
- O'Neill, G., Ukrainetz, N., K., Carlson, M., R., Cartwright, C., V., Jaquish, B., C, King, J., N., Krakowski, J., Russell, J., H., Stoehr, M., U., Xie, C., and Yanchuk, A., D. 2008b. Assisted migration to address climate change in British Columbia: Recommendations for interim seed transfer standards. British Columbia Ministry of Forests, Research Branch, Victoria, British Columbia. Technical Report 048.
- Parks, C.G., and Bernier, P. 2010. Adaptation of forests and forest management to changing climate with emphasis on forest health: A review of science, policies and practices. Forest Ecology and Management **259** 657–659.
- Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology and Systematics **37**: 637-669.
- R Development Core Team. 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing, ISBN 3-900051-07-0, Vienna, Austria.
- Ricciardi, A., and Simberloff, D. 2009. Assisted colonization is not a viable conservation strategy. Trends in Ecology & Evolution 24(5): 248-253.
- SAS Institute. 2001. SAS/STAT user's guide, release 8.2. SAS Institute, Cary, North Carolina, USA.

- Savolainen, O., Pyhajarvi, T., and Knurr, T. 2007. Gene flow and local adaptation in trees. Annual Review of Ecology Evolution and Systematics **38**: 595-619.
- Selby, C.J., and Santry, M.J. 1996. A National Ecological Framework for Canada: Data model, Database and Programs. Centre for Land and Biological Resources Research, Research Branch, Agriculture and Agri-Food Canada and State of the Environment Directorate, Environment Canada, ISBN 0-662-24107-X.
- Wang, T.L, Hamann, A. Spittlehouse, D.L. and Aitken, S.N. 2006a. Development of scale-free climate data for western Canada for use in resource management. International Journal of Climatology 26: 282-397.
- Wang, T.L., Hamann, A. Yanchuk, A. O'Neill, G.A. and Aitken, S.N. 2006b. Use of response functions in selecting lodgepole pine populations for future climates. Global Change Biology 12: 2404-2416.
- Woods, A. Coates, K.D. and Hamann, A. 2005. Is an unprecedented dothistroma needle blight epidemic related to climate change? BioScience **55**: 761-769.
- Wulder, M.A., White, J.C., Cranny, M., Hall, R.J., Luther, J.E., Beaudoin, A., Goodenough, D.G., and Dechka, J.A. 2008. Monitoring Canada's forests. Part 1: Completion of the EOSD land cover project. Canadian Journal of Remote Sensing 34(6): 549-562.
- Ying, C.C., and Yanchuk, A.D. 2006. The development of British Columbia's tree seed transfer guidelines: Purpose, concept, methodology, and implementation. Forest Ecology and Management 227(1-2): 1-13.

Climate	Ecological Regions ²									
Variable ¹	Aspen Parkland		Foothills		Boreal Plains		Northern Boreal		Taiga Plains	
MAT (°C)	1.9	(+0.8)	1.9	(+0.8)	0.5	(+1.1)	-0.6	(+1.1)	-2.5	(+1.4)
MWMT (°C)	17.5	(+0.3)	13.9	(+0.4)	16.5	(+0.6)	15.4	(+0.6)	15.6	(+0.8)
MCMT (°C)	-16.7	(+1.9)	-11.5	(+1.8)	-18.7	(+2.0)	-20.2	(+1.9)	-23.9	(+2.4)
TD (°C)	34.2	(-1.6)	25.4	(-1.4)	35.2	(-1.4)	35.6	(-1.3)	39.5	(-1.6)
MAP (mm)	437	(-3%)	620	(-5%)	472	(-6%)	454	(-9%)	392	(-7%)
MSP (mm)	294	(-1.6%)	395	(-4%)	316	(-4%)	284	(-5%)	238	(+0.2%)
PAS (mm)	106	(-12%)	183	(-13%)	127	(-13%)	145	(-17%)	144	(-16%)
AHM	27.4	(+2.9)	19.5	(+2.5)	22.3	(+3.9)	20.8	(+4.9)	19.3	(+5.5)
SHM	60.1	(+1.9)	35.7	(+2.6)	52.8	(+3.8)	55.9	(+4.9)	67.8	(+3.0)
DD0 (dd)	1776	(-290)	1289	(-252)	2049	(-346)	2233	(-375)	2778	(-466)
DD5 (dd)	1519	(+12)	1028	(+26)	1333	(+479)	1177	(+30)	1129	(+41)
NFFD (days)	164	(-1.0)	144	(+0.4)	156	(+0.1)	148	(+0.1)	142	(+1.5)
FFP (date)	107	(-0.4)	79	(+1.5)	97	(+2.8)	87	(+2.6)	83	(+4.3)
EMT (°C)	-47.4	(+1.2)	-44.2	(+1.9)	-48.4	(+1.0)	-48.6	(+0.8)	-49.6	(+0.6)

Table 4-1. Regional climatology based on 1961 to 1990 normal data for fine ecological regions with observed climate change over the last 25 years in parenthesis. Observed change is calculated as the difference between the 1961–1990 reference period and a recent decadal average 1997–2006.

¹) MAT, mean annual temperature; MWMT, mean July temperature; MCMT, mean January temperature; TD, temperature difference; MAP, mean annual precipitation; MSP, mean summer precipitation; PAS, precipitation as snow; AHM, annual heat-moisture index; SHM, summer heat-moisture index; DD0, chilling degree days below 0°C; DD5°C, growing degree above 5°C; NFFD, number of frost free days; FFP, frost free period; EMT, Extreme minimum temperature.

²) Ecological regions are shown as maps in Figure 1, except the Aspen Parkland which is located south of the boreal plains.
Table 4-2. Range of 18 regional climate change projections from five general circulation models (CGCM2, HADCM3, ECHAM4, CSIRO2 and PCM) implementing four SRES emission scenarios (A1FI, A2, B1, B2) for climate variables in four ecological regions over projected future climate. Projected changes are expressed relative to the 1961–1990 reference period.

Climate	Ecological Regions ²					
Variable ¹	Foothills	Boreal Plains	Northern Boreal	Taiga Plains		
<u>2020s</u>						
MAT (°C)	+0.5 to +1.9	+0.6 to +2.0	+0.5 to +2.1	+0.6 to +2.1		
MAP (%)	+0.3 to +3.2	-0.2 to +3.1	-0.4 to +3.9	-0.1 to +4.2		
SHM	+1.6 to +5.6	+1.0 to +6.0	-0.9 to +5.5	-2.2 to +5.8		
<u>2050s</u>						
MAT (°C)	+1.0 to +3.1	+1.2 to +3.8	+1.1 to +3.4	+1.3 to +3.6		
MAP (%)	+0.5 to +5.8	-0.4 to +5.1	-0.7 to +6.4	-0.3 to +6.9		
SHM	+2.7 to +13.7	+1.9 to +14.5	-0.6 to +13.2	-3.2 to +13.7		
<u>2080s</u>						
MAT (°C)	+1.5 to +5.3	+1.8 to +6.4	+1.9 to +5.6	+1.4 to +5.9		
MAP (%)	+0.8 to +9.6	-0.8 to +7.5	-1.4 to +11	-13 to +11.6		
SHM	+3.5 to +24	+2.0 to +25	+0.7 to +22	-2.6 to +22.4		

MAT, mean annual temperature; MAP, mean annual precipitation; SHM, summer heat-moisture index.
 Ecological regions are shown as maps in Figure 3-1.

	Provenance from:				
Transferred to:	Taiga Plains	Northern Boreal	Boreal Plains (AB)	Boreal Plains (SK)	Foothills
Site 70 – Taiga Plains	_	>0.99	0.91	0.96	0.71
Site 10 – Northern Boreal	< 0.01	_	0.29	0.26	0.41
Site 60 – Boreal Plains (AB)	< 0.01	0.13	_	0.95	0.52
Site 90 – Boreal Plains (SK)	< 0.01	0.21	0.54	_	0.29
Site 33 – Foothills	< 0.01	0.26	0.74	0.91	_

Table 4-3. Probability to match or exceed the performance of local provenances. The lower left table section represents a southward transfer, and the upper right section a northward transfer.

Manage	ment Unit ¹		Asper	n Habita	t (%)		Seed	source Recommen	dation ²
Name	Size (km ²)	Normal	97-06	2020s	2050s	2080s	Normal	97-06	2020s
NM 1.1	23,803	100	100	100	100	100	TP(100)	TP(70), NB(24)	TP(67), NB(32)
CM 1.1	16,756	100	100	100	100	100	TP(99)	NB(98)	NB(98)
CM 1.2	12,098	100	100	100	100	100	TP(55), NB(45)	NB(94)	NB(100)
CM 2.1	12,436	100	100	100	99	74	NB(82), TP(17)	NB(70), BP(15)	NB(64), BP(35)
CM 2.2	13,849	100	100	100	98	85	NB(93)	NB(94)	BP(55), NB(42)
CM 2.3	11,036	100	100	100	100	76	NB(91)	NB(86), BP(14)	BP(53), NB(47)
CM 2.4	17,861	100	100	100	80	55	BP(53), NB(47)	BP(46), NB(41)	BP(76), AP(17)
CM 3.1	25,246	100	92	89	48	29	BP(94)	BP(70), AP(27)	BP(59), AP(41)
CM 3.2	13,015	100	74	89	90	94	BP(99)	BP(60), AP(36)	BP(60), AP(37)
CM 3.3	14,022	100	100	100	99	95	BP(96)	BP(63), AP(22)	BP(95)
CM 3.4	9,928	100	100	98	94	91	BP(86)	BP(39), FH(32)	BP(47), AP(27)
DM 1.1	14,764	100	100	100	100	87	NB(78), TP(22)	NB(87), BP(13)	NB(100)
DM 1.2	17,361	99	94	79	45	17	NB(92)	NB(56), BP(31)	NB(41), AP(34)
DM 1.3	17,042	100	97	76	19	14	BP(67), NB(33)	BP(46), NB(29)	AP(84), BP(10)
DM 2.2	19,512	100	27	51	55	57	BP(96)	AP(75), BP(20)	AP(64), BP(32)
LF 1.4	7,795	100	100	100	100	100	FH(88)	M(56), FH(43)	FH(83), M(14)
LF 1.5	9,996	100	100	100	100	100	FH(99)	FH(85), M(15)	FH(99)
LF 2.1	6,639	100	100	100	100	100	FH(98)	M(61), FH(37)	FH(87), M(13)
LF 2.2	3,352	100	100	100	100	100	FH(100)	M(53), FH(46)	FH(99)
LF 2.3	2,110	100	100	100	96	79	FH(100)	M(97)	FH(59), AP(35)

Table 4-4. Seed transfer recommendations for Alberta's seed management units of the natural region and subregion system.

¹) Seed management units are based on the finest subdivisions of the Alberta Natural Subregion classification.

NM, Northern Mixedwood; CM, Central Mixedwood; DM, Dry Mixedwood, LF, Lower Foothills.

²) Recommended seedsources are based on major ecological regions also shown in Figure 4-1, including TP, Taiga Plains; NB, Northern Boreal; FH, Foothills; M, Montane; BP Boreal Plains; and AP, Aspen Parkland.



Figure 4-1. Bar charts show height of 38 transferred seed lots expressed in percent relative to the local sources from the vicinity of five test sites (\blacktriangle). Each seed source from locations throughout the study area (\bigcirc) is grown in a common garden environment to reveal genetic differences. Within-regional variation among provenances is indicated by standard deviations.



Figure 4-2. Inferred productivity loss of aspen stands during a regional drought event in 2002. The map displays the 2002 anomaly from the 2001-2006 average for the large integral parameter of the adaptive Savitzky–Golay function of TimeSat, fitted to 16 day interval 500m resolution MODIS/EVI data and filtered for deciduous (aspen dominated) grid cells. Areas of the Dry Mixedwood (DM) where pronounced decreases in forest health and productivity were found are defined.







Figure 4-3. Aspen frequency under baseline (1961–1990), recent decade (1997–2006) and projected future climate scenarios for the 2020s, 2050s and 2080s time slices. General circulation model (GCM). Agreement for modeled aspen frequency under future climate is also provided. Outlines of the aspen seed zones are added for orientation.







Figure 4-4. Aspen seed zone climate envelope under baseline (1961–1990), recent decade (1997–2006) and future climate scenarios for the 2020s, 2050s and 2080s, and general circulation model (GCM) consensus for predicted shifts under future climate. Outlines of current aspen seed zones are added for orientation.

Chapter 5. Synthesis and Conclusions

The objective of my thesis was to develop a methodological framework to help guide assisted migration efforts by determining which species and genetically adapted planting stocks are optimal for reforestation programs in Alberta. The answers to the research questions I posed in the introductory chapter provide a broad overview of potentially mal-adapted forest trees in western North America due to uncertain future climate change, and show strong support for practical assisted migration efforts in western Canada to mitigate these affects. Below I describe by each major question what my contributions were.

• How does climatically suitable habitat shift throughout the 2020s, 2050s, and 2080s and what are the uncertainties associated with these species habitat projections?

I predicted a general trend of ecosystem units, representing population habitat, shifting northward and up in elevation under future climate scenarios; however the magnitude of habitat shifts varied for regions across western North America. Losses of projected habitat were pronounced at the southern fringe of the boreal forest, and the dry boreal forest regions in the eastern rain shadow of the Canadian Rocky Mountains. These losses were predicted with high certainty, regardless of the climate change scenario. Habitat shifts in these areas reflects substantial habitat losses for boreal species, such as black spruce, tamarack and trembling aspen. Habitat of coastal species appears to be generally well maintained at the species level, although yellow cedar and western hemlock are predicted to lose suitable habitat at their southern coastal range limits. Habitat

projections based on observed climate trends, represented by the 1997-2006 decadal average, are generally in the direction and magnitude of climate change predictions. Especially at higher latitudes, habitat projections based on observed climate trends appear to be approaching or exceeding those expected for the 2020s.

The uncertainty in habitat projections was quantified by calculating the consensus of species occurrences among models. For all species, habitat projections were associated with increasing uncertainties towards the 2080s. By the end of the century, I found substantial proportions of most species ranges to be lost in approximately half of the model runs. This result suggests that the development of climate change adaptation strategies in reforestation is limited to a relatively short-term planting horizon.

• How far do individual populations of trees lag behind their optimal climate under observed and predicted climate change?

I compared habitat projections for locally adapted populations under the interpolated 1961-1990 climate baseline with habitat projections under the 1997-2006 decadal averages, representing recent climate trends. This comparison can be interpreted as observed climate change over a 25 year period (the mid-point of the 1961-1990 climate baseline period and the mid-point of the recent decadal average: 1975 to 2000). I found that at the ecosystem level across western North America, populations are already lagging behind their optimal climate by 130km in latitude, or 60m in elevation. The most pronounced shifts occurred in the Interior Plateau regions in Canada and the United States. This result is not

surprising, given these regions are characterized by hot dry summers and cool winters with light snow. The habitat shifts likely reflect the observed warming trends of approximately +1.5°C or more in mean annual temperature surrounding these regions and a reduction of mean annual precipitation by up to 20% for the 1997–2006 average relative to the 1961–1990 reference period (data not shown). Compared to habitat shifts calculated based on the 1997-2006 observed climate, the projected latitudinal and elevation shifts for ecosystems in western North America doubled by the 2020s, and doubling again by the 2050s. For locally adapted populations this translates in to an average geographic lag of approximately 310km in latitude or 140m in elevation in the 2020s, and 590km in latitude or 260m in elevation in the 2050s. Due to high uncertainty in model projections the approximate geographic-lag for the 2080s was not reported.

 Given the lag in climate match under observed and projected climate change, can we derive general north and/or elevational seed transfer recommendations?

An important observation from habitat projections is that projected elevation and latitude shifts are not independent over multiple populations or multiple model runs. For example, a large latitudinal shift north to colder climates may be associated with a downward shift in elevation to find a new approximate climate match for an ecosystem unit in one model run, while another model run results in a reversed situation. This leads to strong negative correlations between predicted elevation and predicted latitudinal shifts, which I found can be described by the formula: δ Elevation = δ Latitude × 0.44. In other words, a 100 km north shift in latitude with the elevation held constant is equivalent to a 44m upward shift in

elevation with the latitude held constant. Ideally, the regional latitudinal and elevation transfer distances I presented should be implemented within a species' current range or somewhat beyond species' current distributions. Further, the allowable seed transfers I presented are very generally expressed and therefore should only be made within similar forest types to minimize the chance of seed being mal-adapted.

For the majority of the tree species included in this thesis I found confidence in predicted species habitat up to the 2020s. Although the life span of most of these species exceeds the 2080s, I think that focusing on the immediate future when developing seed transfer prescriptions is the best strategy, given trees are most vulnerable to climatic factors at the seedling stage. If we plant seedlings optimal for climates expected in the 2080s, those seedlings would be mal-adapted to the current climate conditions and likely be unable to establish or suffer from low productivity. Given the uncertainty in future climate projections, seed transfers according to the 1997-2006 and 2020s projections will have the best chance of survival now and will likely be able to better withstand future climate stress as mature trees that are more resilient to climate fluctuations. Ultimately species' populations do not need to be adapted to a "median climate change scenario" but to climate trends that eventually materialize, and at this point, we do not know with any reasonable amount of certainty what those conditions will be by the end of the century. Hence it is better to plan for climate we can confidently expect and use habitat projections for the 2050s and 2080s for long-term planning rather than for guidance of seed sources in the near future.

It is also important to note that in practice the seed transfer recommendations presented in this thesis will be constrained by environmental and ecological factors not included in my climate-based models. For example, tree species are sometimes associated with specific soil types, which will not change at any rate comparable to projected climate change. Given the presented seed transfer recommendations, forest managers still have to match planting stock to appropriate soil types, just as under current seed zone prescriptions. Model projections, which give a framework as to where species and genetically adapted planting will likely match climate conditions, need to be refined with a forest manger's knowledge of non-climate factors that could impact seedling establishment, to compose practical planting decisions.

• Is Alberta's seed zone system a useful framework to govern seed transfer under uncertain future climates?

As part of this chapter, I displayed the 1961-1990 climatology of Alberta's ecological regions and seed zones, represented by the mean annual temperature and mean annual precipitation for each unit. To visualize projected climate change in relation to the displayed values, I added the current climatology and projections for a central boreal forest location centered around 56° latitude and 115° longitude, as well as the range of uncertainty in predicted temperature and precipitation values (represented by ellipses). Based on this simplified analysis, it is clear that the uncertainty in climate change projections is in strong contrast to the precision in which reforestation in Alberta is currently managed. Even for the 2020, if projected temperature and precipitation values are applied to a planting site, multiple locations, each representing a locally adapted population, can be

considered climate matches. Given the increasing uncertainty in climate projections towards the end of the century, the variety of possible seed choices amplifies for the 2050s and 2080s. These results suggest that appropriate genetic planting stock cannot be pinpointed given future climate uncertainty in Alberta, but I think in the long run relying on precise recommendations is a poor strategy. Multiple seed sources, each of which is a close climatic match to the planting site, should be prescribed to enhance genetic diversity in the landscape to hedge against uncertainty. I therefore encourage a portfolio strategy of adaptation to climate change be used, that should include a diverse selection of seed sources and a framework for tracking reforestation success, growth and forest health of plantations and that allows for recursive improvements.

• Do we need to introduce new species or new seed sources from outside the province to maintain well adapted and productive forests of the future?

In western Canada, there is a common belief that importing alternate species and genotypes from other jurisdictions (mainly from the United States) will be a promising forest management strategy to mitigate climate change. However, of approximately 50 western North American tree species that we investigated in a larger modeling effort, no alternative species that are currently not present in Alberta can be recommended with any confidence for reforestation under projected climate change. Habitat projections for western North America show that ponderosa pine (*Pinus ponderosa*) is the closest to gaining habitat with sufficient confidence across multiple climate change scenarios. While most southern Montane ecosystems of Alberta may become suitable according to approximately half of the 18 climate change scenarios we used by the 2050s, the

uncertainty in ponderosa pine occurrence is too high to recommend the species for planting. At the genotype level, while in small areas of the southern Rocky Mountain Montane and Foothill ecosystem, habitat is projected to be best suited to populations originating from montane ecosystems of British Columbia, and the dry conifer forests in Montana, South Dakota, and Wyoming, the majority of recommendations reflect planting stock native to Alberta. These results indicate that in Alberta, importing seed and species from other jurisdictions does not promise to be an important element of a climate change adaptation strategy for the forestry sector.

• What are the species and genotypes that most likely match anticipated future climates of the sub-boreal and boreal forests of Alberta?

To minimize the probability of plantation failure in the face of uncertain future climates, I think that the best strategy is to ensure that species habitat is maintained under a wide range of potential climate change scenarios. In this study I restrict reporting to a threshold of at least 70% of the models to agreeing that species habitat will be maintained. Practitioners may want to set higher thresholds for implementing large-scale reforestation programs to minimize risks of plantation failure. Overall, model projections suggest that species and genotypes better adapted to drier and warmer conditions, typically found in the Parkland and Dry Mixedwood ecosystems should be suitable for an increasing land base in Alberta in the future. This directly applies to recommendations for white spruce in Alberta, for which projections show habitat is generally well maintained into the future with the exception of some of the current Dry Mixedwood and transitional Parkland ecosystems. In contrast, black spruce is predicted to lose much of its

habitat in Alberta, especially in low elevation regions. Although habitat projections for Douglas-fir come with very large uncertainties, on average suitable habitat remains constant or is slightly reduced. The current distribution of lodgepole pine in the foothills of Alberta appears to be fairly well maintained with reasonable certainty, however habitat for jack pine, currently concentrated at lower elevations in the northeast of the province, is predicted to rapidly decline under most climate change scenarios.

 Given the mismatch or lag of locally adapted populations in a changing environment, can we identify adaptational lag in reciprocal transplant experiments? Given observed climate trends in western Canada, I hypothesize that using planting stock transferred from warmer and/or drier source environments to a different planting site will lead to better growth compared to local sources.

A reciprocal transplant experiment was used to test the adaptation of aspen tree populations to their local environments. Observed growth of aspen provenances which were transplanted indicated a pronounced adaptational lag, given local seed sources were commonly outperformed by transferred sources. The probabilities of matching or increasing productivity relative to the local sources are very pronounced from the most northern region studied (Taiga Plains). Northward transfers into this region were found to be beneficial, however transfers south were found to be very disadvantageous. Additionally, smaller positive effects associated with a higher probability of matching or increasing productivity include seed transfers from the drier Boreal Plains to the wetter Foothills, and transfers from Saskatchewan to Alberta. These results indicate that the majority of

aspen populations studied in western Canada are likely mal-adapted to the recent changes in both temperatures and precipitation levels. Further, these results support my hypothesis that using planting stock transferred from warmer and/or drier source environments to a different planting site will lead to better growth compared to local sources.

 Model projections under observed climate change for aspen indicate loss of habitat at the southern fringe of the boreal forest and in other water-limited forest regions of Alberta. Do those habitat projections accurately reflect observed loss of forest productivity and observed dieback of aspen in central Alberta?

Most simply, the answer to this question is yes. Habitat projections for aspen in western North Canada under the 1997-2006 period of recent climate change indicate significant loss of species habitat along the southern fringe of the boreal forest and portions of the Dry Mixedwood subregion in the boreal forest of northwestern Alberta. These locations directly correspond to negative anomalies that indicate areas where aspen populations were found to be vulnerable to climate change, using remotely sensed EVI values during Alberta's regional drought in 2002. Additionally, model projections match observed reductions in productivity and aspen dieback observed along the southern range limit of aspen in Alberta and Saskatchewan.

• Given model projections, empirical data of observed climate change impacts, and experimental data from transplant experiments, does the risk of changing established management practices outweigh the risk of status-quo

management? If yes, what are the criteria that indicate the need for changing established management practices and on what tools and data should managers rely in developing climate change adaptation strategies?

I purpose that assisted migration should only be implemented in a situation where the benefits of its implementation outweigh the negative impacts of climate change. In the case for aspen in western Canada, reciprocal transplant experiments determined that local populations are already mal-adapted to the climate conditions they are currently facing. Empirical data from observed climate change impacts combined with habitat projections under future climate scenarios, suggest that aspen is currently vulnerable, and will likely continue to be vulnerable to climate change in the future. Together all three pieces suggest that if management practices do not change and develop adaptation strategies to mitigate climate change, there is a high risk that aspen populations will continue to suffer from reduced productivity and dieback. I purpose that three criteria should be established before assisted migration is implemented in reforestation practices: (1) there is evidence of a climate-related adaptational lag, (2) climate-change has resulted in observed biological impacts, and finally (3) robust model projections that target assisted migration efforts are developed. Given this criteria, assisted migration of aspen populations appears to be a promising climate change adaption strategy in western Canada.

Appendix A. Glossary of terms

Abiotic factor - a non-living chemical or physical feature in an environment (e.g. temperature, soil pH). *Also see biotic factor*.

Acclimate – become accustomed to new environmental conditions through a physical or behavioral response (e.g. warmer spring temperatures can induce an earlier bud-break among forest trees). This process is not evolutionary (*see Adaptation*) and generally occurs over a short time period (e.g. a season).

Adaptation – the evolutionary process driven by natural selection which results in the evolution of a useful trait for a population or species.

Adaptational lag – the mismatch of genotypes and environments, caused by a relatively fast environmental change and a comparably show evolutionary response. *Also see geographic lag, equilibrium.*

Adaptive trait – a characteristic that is essential for tree survival (e.g. drought tolerance). *Also see adaptation*.

Allele – one member of a pair of genes that controls the same trait. Also see gene.

Assisted colonization - the translocation of species or genotypes from deficient environments to locations far outside their range which are more favorable for their long-term conservation. This definition reflects the previous usage of terminology in conservation biology which permits me to differentiate between assisted colonization and assisted migration. *Also see assisted migration*.

Assisted migration – the translocation of species or genotypes from deficient environments to locations within or just beyond their species range which are more favorable for their long-term survival and productivity. This definition reflects the previous usage of terminology in forest resource management which permits me to differentiate between assisted migration and assisted colonization. *Also see assisted colonization*.

Bioclimate envelope model – a niche model where a species-environment relationship is described by correlating environmental predictor variables with observed species occurrences. This approach does not explicitly incorporate biological processes or physiological knowledge of a species. *Also see mechanistic model.*

Biodiversity – the degree of variation (both in numbers and frequency) of organisms within a given area (e.g. ecosystem, biome, continent, etc.).

Biome – generally the largest-scale ecosystem delineation describing broad types of species assemblages (e.g. temperate forest, grasslands, deserts, etc.). *Also see ecozone, ecoregion, ecological variant.*

Biotic factor – a feature created by a living organism or any living component within an environment that affects another organism (e.g. a predator-prey interaction, competition, disease). *Also see abiotic factor*.

BP – a term used in paleological research standing for "before present".

Climate change – a directional change in observed temperature and/or precipitation levels in excess of natural climate variability, which is attributed directly or indirectly to human activity (e.g. an increase in carbon-dioxide emissions) or a major environmental event (e.g. dust and aerosols being thrust into the atmosphere by a volcanic eruption).

Climatic suitability – a measure of the match between the environmental requirements of a species and climate conditions. *Also see locally adapted population and mal-adapted*.

Cline – a continuous gradient of genetic variation that usually reflects adaptation to an environmental gradient. Populations are not geographically isolated and gene flow among population within the cline prevents speciation (e.g. along an elevational or latitudinal gradient). *Also see ecotype*.

Collinearity – the case when two or more (multi-collinearity) variables are correlated. This often arises if variables are different measurements that are related through a common cause (e.g. soil moisture and mean annual precipitation).

Colonization – the successful establishment of a organism in a new region or environment. *Also see dispersal and migration*.

Common garden experiment, provenance trial – an experiment where individuals of a species are grown with an experimental design in a common environment to reveal genetic differences among the species. If the trial includes seed sources collected from a large part of a species' range it is usually referred to as a provenance trial. *Also see provenance, reciprocal transplant experiment and tree improvement.*

Dispersal – the movement of a species away from an existing population or parent individual. For immobile species (e.g. trees), dispersal requires a natural mechanism (e.g. wind). *Also see colonization and migration*.

Ecological variant – a small-scale ecosystem delineation which is distinguished by small variations in species composition, climate, or soils from similar

ecosystems (in this thesis, ecological variants are modeling units for climate envelope modeling). *Also see biome, ecozone, ecological variant*.

Ecoregion, ecological region – a mid-scale ecosystem delineation with distinct climate, geology, type of soil, water availability and species communities (e.g. Rocky Mountains foothills, Dry Mixedwoods would be examples for Alberta). *Also see biome, ecological variant.*

Ecosystem – a biological environment consisting of all the organisms living in a particular area (applies to delineations of all scales). *Also see biome, ecozone, ecoregion.*

Ecotype – a genetically differentiated population that is at least somewhat geographically isolated (e.g. by distance) resulting in limited exchange through pollen and seed and a distinct genotype. *Also see cline*.

Ecozone – a large-scale ecosystem delineation that describes major forest types (e.g. sub-boreal forest, boreal forest, sub-alpine forest). *Also see biome, ecoregion, ecosystem.*

Equilibrium – the state in which all acting influences, such as climate or biotic interactions, are balanced resulting in a stable system which is optimal for species survival, productivity and reproduction. A species that is in equilibrium with its environment should be optimally adapted. *Also see geographic lag, adaptational lag.*

Environmental plasticity – a broad definition of *phenotypic plasticity* or the adaptability of trees to different environmental conditions by changing it morphology or physiological characteristics without a genetic change through evolution (e.g. a tree may allocate more resources to root growth rather that shoot growth if nutrient conditions are poor). This ability is more important for trees than other organisms given they are unable to relocate to new environments and require the ability to handle environmental variability throughout a long lifetime.

Extrapolate – to extend an application to a novel situation by assuming the existing trends will continue or similar methods will be applicable in the novel situation (e.g. derive climate data for locations beyond the limits of weather stations using known weather characteristics from areas with similar latitude, elevation and aspect). *Also see interpolate*.

Fundamental niche – a set of abiotic factors that allow a species to survive and reproduce. This niche is much wider and encompasses the more restrictive realized and regeneration niches. *Also see realized niche and regeneration niche, abiotic factor*.

Gene – a hereditary unit consisting of a sequence of DNA that occupies a specific location on a chromosome and determines a particular characteristic in a tree (e.g. pathogen resistance). *Also see allele*.

Genetic variation – dissimilarity among alleles of genes which occurs both within and among populations within the natural geographic range of a species. *Also see gene, and allele.*

Genotype – the distinct genetic makeup of an individual or a population. *Also see phenotype*.

Geographic lag – the geographic distance between the geographic location of a population and another location where optimal habitat conditions for the species can be found. *Also see adaptational lag, equilibrium.*

Habitat – the natural environment where a species or a locally adapted population persists.

Interpolate – to extend an application to a novel situation occurring within a given range by combining trends or data from know points (e.g. derive climate data for a location occurring between two points using data from weather stations at each point). *Also see extrapolate*.

Leading edge – the northernmost or highest elevation point within a species range. Species' populations along this edge are often incorrectly inferred to be less impacted by climate change since species habitat is projected to predominantly move northward to up in elevation. *Also see trailing edge*.

Locally adapted population – a group of individuals which are genetically adapted to a local environmental conditions, including biotic and abiotic factors. *Also see cline, ecotype, adaptation.*

Mechanistic model, process based model – in this thesis referred to as a habitat model that predicts the response of an individual or a population to environmental conditions by explicitly incorporating biological processes calibrated with observations on individuals in natural populations. In this approach, a species distribution is defined by a set of functions based on knowledge of the physiology of a species. *Also see bioclimate envelope model*.

Machine learning – the process where an algorithms is developed that allow a computer to evolve behaviors based on empirical data (e.g. using a training data set to develop classification criteria).

Macroecological – the subfield of ecology that deals with species-environment relationships at a larger scale (i.e. continental).

Mal-adapted – when a species is poorly suited to the particular environment which they live in. *Also see climate suitability, and locally adapted population.*

Methodological framework – a concept based on a system of methods.

Migration – the process where a species distribution is shifted or expanded. *Also see dispersal and colonization*.

Model – a mathematical representation of an observed relationship.

Parameterize – to describe a system or a set of operations in terms of numerical or other measurable factors (e.g. tree growth may be predicted with parameters that represent the amount of available water and light resources)

Phenotype – the set of observable characteristics of a tree resulting from the interaction of its genotype with the environment (e.g. observed tree growth is the result of a tree's genetic productive capacity and the climate conditions it is exposed to). *Also see genotype*.

Planting stock – seedlings used in reforestation.

Plantation/Planting site – the location where reforestation is performed.

Population – a broad term that refers to a sub-group of individuals within a species in the same region. Population may be used to describe groups at various geographic scales, where members of a population are more likely to inter-breed than to cross-breed with individuals outside the population. *Also see provenance*.

Productivity – a trait used as an indicator of a trees health and/or economic value that is able to be measured over time (e.g. in this thesis, a tree height is used as a measure of productivity).

Provenance – typically used to describe a geographic source location of seed. Provenance is often interchangeably used with population. Different provenances usually do not represent randomly mating individuals (e.g. collections from adjacent trees are not referred to as different provenances, but collections several kilometers distant may be referred to as a separate provenances) *Also see population*.

Predictor variable, independent variable – a factor that is used to predict the value of another variable (response variable) in a statistical analysis (e.g. in this thesis climate variables are used to predict habitat suitability for a tree species). *Also see response variable.*

Realized Niche – the combination of abiotic and biotic factors that allow a species to survive and reproduce. This niche is represented by the species

observed distribution. The realized niche is within a species wider fundamental niche and in the early stages of a tree's life cycle a narrower version of this niche, referred to as a regeneration niche, often occurs. *Also see fundamental niche and regeneration niche*.

Reciprocal transplant experiment – a series of common garden trials where seed is collected and tested in multiple environments to reveal adaptation and adaptational lag. *Also see common garden trial and tree improvement*.

Reforestation – the process where trees are replanted after a harvest or disturbance.

Regeneration niche – the biotic and abiotic environmental conditions which occur in the early phase in the life cycle of a tree (e.g. the seedling or sapling stage) which allow it to establish. This niche is within a species wider fundamental niche and is often narrower than the realized niche of an adult tree within the same population since juvenile trees have limited root systems, low carbon reserves, and reduced photosynthetic capacity. *Also see realized niche and fundamental niche*.

Response variable – the factor being modeled or predicted through a statistical analysis (e.g. in this thesis the ecosystem class for a location is predicted using the sites climate variables). *Also see predictor variable*.

Seed source – a population or general location where seed used as planting stock originates. *Also see planting stock and seed zone*.

Seed transfer limitations – how seed can be moved in reference to its location of origin. *Also see seed source and seed zone*.

Seed zone – an ecological and genetic unit that is intended to define an area with a locally adapted population. In Alberta a system of approximately 60 legislated seed zones govern seed transfer limitations, where seed can be freely moved within its seed zone of origin, but transfers between seed zones is highly regulated and often prohibited. *Also see seed source and seed transfer limitations*.

Spatial transferability – the ability of a model to correctly predict species habitat in a new geographic space. *Also see temporal transferability*.

Species range – the geographic area within which a species can be found.

Subspecies – geographically isolated populations of a species occurring in different ecozones which show a clearly visible difference in morphology, but are still capable of interbreeding. *Also see ecotype, variety, cline*.

Temporal transferability – the ability of a model to correctly predict species habitat in a novel time period. *Also see spatial transferability*.

Trailing edge – the southernmost or lowest elevation point within a species range. Species' populations will likely be impacted by climate change along this edge since species habitat is projected to predominantly move northward to up in elevation. *Also see leading edge*.

Tree improvement – the practical application of forest genetics where the performance of trees from natural populations are tested on multiple sites to determine which population grow best when planted on specific sites. *Also see common garden trial and reciprocal transplant experiment*.

Varieties – populations of a species that may or may not be geographically isolated but show visible differences in some traits which are less pronounced than for subspecies (e.g. lodgepole pine has been divided geographically into four varieties: shore pine or coast pine on the west coast of North America, Bolander pine in California, Sierra lodgepole pine in Nevada and the Rocky Mountian lodgepole pine in the Rocky Mountains). *Also see subspecies, ecotype, cline.*

Appendix B. Projected habitat and uncertainty maps for western North America

In this appendix I provide the complete habitat distribution maps for 15 major forestry species in western North America under the 1961-1990 climate baseline and observed climate trends (Figure a), as well as under multi-model projections for the 2020s (Figure b), 2050s (Figure c) and 2080s (Figure d).

The 1961-1990 and 1997-2006 maps (Figure a) as well as the left images in Figures b-d, represent projections of species frequencies, derived by replacing ecosystem-modeling units with known species frequencies. These maps indicate where a species would generally be expected to be a major forest component in the future, based on an average of predictions for a variety of climate change scenarios. A low average frequency could represent either a low frequency in most model runs or a higher frequency in few model runs.

The right images in Figures b-d quantify uncertainty in habitat projections for the 2020s, 2050s, and 2080s. Red indicates that all models agree that the species will be absent, and blue indicates that all models agree that the species will be present. Intermediate shades indicate areas of uncertainty, which substantially increase towards the 2080s.

Appendix B1 – Black spruce



Black spruce – Current

Figure B1 a. Projected habitat of black spruce (*Picea mariana* (Miller) Britton). The left image is an expected frequency (% canopy cover projected to the ground) for the 1961-1990 normal period, representing long-term climate condition and model training data. The right image models habitat for the 1997-2006 period, representing a recent (25-year) climate trend.





Figure B1 b. Projected habitat of black spruce for the 2011–2040 normal period according to 18 climate change projections. The left image is an average expected frequency (% canopy cover projected to the ground). The right image represents agreement of species presence/absence projections for 18 general circulation models.





Figure B1 c. Projected habitat of black spruce for the 2041–2070 normal period according to 18 climate change projections. The left image is an average expected frequency (% canopy cover projected to the ground). The right image represents agreement of species presence/absence projections for 18 general circulation models.





Figure B1 d. Projected habitat of black spruce for the 2071–2100 normal period according to 18 climate change projections. The left image is an average expected frequency (% canopy cover projected to the ground). The right image represents agreement of species presence/absence projections for 18 general circulation models.

Appendix B2 – Douglas-fir



Douglas-fir – Current

Figure B2 a. Projected habitat of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). The left image is an expected frequency (% canopy cover projected to the ground) for the 1961-1990 normal period, representing long-term climate condition and model training data. The right image models habitat for the 1997-2006 period, representing a recent (25-year) climate trend.

18 GCMs for 2020s 2020s GCM Agreement Absent 100% Present Frequency < 5 10 15 20 25 35 45 55 65 75% 50% 100%

Douglas-fir – 2020s

Figure B2 b. Projected habitat of Douglas-fir for the 2011–2040 normal period according to 18 climate change projections. The left image is an average expected frequency (% canopy cover projected to the ground). The right image represents agreement of species presence/absence projections for 18 general circulation models.



Douglas-fir – 2050s

Figure B2 c. Projected habitat of Douglas-fir for the 2041–2070 normal period according to 18 climate change projections. The left image is an average expected frequency (% canopy cover projected to the ground). The right image represents agreement of species presence/absence projections for 18 general circulation models.



Douglas-fir – 2080s

Figure B2 d. Projected habitat of Douglas-fir for the 2071–2100 normal period according to 18 climate change projections. The left image is an average expected frequency (% canopy cover projected to the ground). The right image represents agreement of species presence/absence projections for 18 general circulation models.

Appendix B3 – Engelmann spruce



Engelmann spruce – Current

Figure B3 a. Projected habitat of Engelmann spruce ((*Picea engelmannii var. engelmannii* Parry ex Engelmann). The left image is an expected frequency (% canopy cover projected to the ground) for the 1961-1990 normal period, representing long-term climate condition and model training data. The right image models habitat for the 1997-2006 period, representing a recent (25-year) climate trend.

Engelmann spruce – 2020s



Figure B3 b. Projected habitat of Engelmann spruce for the 2011–2040 normal period according to 18 climate change projections. The left image is an average expected frequency (% canopy cover projected to the ground). The right image represents agreement of species presence/absence projections for 18 general circulation models.

Engelmann spruce – 2050s



Figure B3 c. Projected habitat of Engelmann spruce for the 2041–2070 normal period according to 18 climate change projections. The left image is an average expected frequency (% canopy cover projected to the ground). The right image represents agreement of species presence/absence projections for 18 general circulation models.




Figure B3 d. Projected habitat of Engelmann spruce for the 2071–2100 normal period according to 18 climate change projections. The left image is an average expected frequency (% canopy cover projected to the ground). The right image represents agreement of species presence/absence projections for 18 general circulation models.

Appendix B4 – Lodgepole pine



Lodgepole pine – Current

Figure B4 a. Projected habitat of lodgepole pine (*Pinus contorta* Douglas ex Loudon). The left image is an expected frequency (% canopy cover projected to the ground) for the 1961-1990 normal period, representing long-term climate condition and model training data. The right image models habitat for the 1997-2006 period, representing a recent (25-year) climate trend.

Lodgepole pine – 2020s



Figure B4 b. Projected habitat of lodgepole pine for the 2011–2040 normal period according to 18 climate change projections. The left image is an average expected frequency (% canopy cover projected to the ground). The right image represents agreement of species presence/absence projections for 18 general circulation models.





Figure B4 c. Projected habitat of lodgepole pine for the 2041–2070 normal period according to 18 climate change projections. The left image is an average expected frequency (% canopy cover projected to the ground). The right image represents agreement of species presence/absence projections for 18 general circulation models.



Lodgepole pine – 2080s

Figure B4 d. Projected habitat of lodgepole pine for the 2071–2100 normal period according to 18 climate change projections. The left image is an average expected frequency (% canopy cover projected to the ground). The right image represents agreement of species presence/absence projections for 18 general circulation models.

Appendix B5 – Pacific silver fir



Pacific silver fir – Current

Figure B5 a. Projected habitat of pacific silver fir (*Abies amabilis* Douglas ex J. Forbes). The left image is an expected frequency (% canopy cover projected to the ground) for the 1961-1990 normal period, representing long-term climate condition and model training data. The right image models habitat for the 1997-2006 period, representing a recent (25-year) climate trend.



Pacific silver fir – 2020s

Figure B5 b. Projected habitat of pacific silver fir for the 2011–2040 normal period according to 18 climate change projections. The left image is an average expected frequency (% canopy cover projected to the ground). The right image represents agreement of species presence/absence projections for 18 general circulation models.



Pacific silver fir – 2050s

Figure B5 c. Projected habitat of pacific silver fir for the 2041–2070 normal period according to 18 climate change projections. The left image is an average expected frequency (% canopy cover projected to the ground). The right image represents agreement of species presence/absence projections for 18 general circulation models.



Pacific silver fir – 2080s

Figure B5 d. Projected habitat of pacific silver fir for the 2071–2100 normal period according to 18 climate change projections. The left image is an average expected frequency (% canopy cover projected to the ground). The right image represents agreement of species presence/absence projections for 18 general circulation models.

Appendix B6 – Ponderosa pine



Ponderosa pine – Current

Figure B6 a. Projected habitat of ponderosa pine (*Pinus ponderosa* Douglas ex Lawson & C. Lawson). The left image is an expected frequency (% canopy cover projected to the ground) for the 1961-1990 normal period, representing long-term climate condition and model training data. The right image models habitat for the 1997-2006 period, representing a recent (25-year) climate trend.

Ponderosa Pine – 2020s



Figure B6 b. Projected habitat of ponderosa pine for the 2011–2040 normal period according to 18 climate change projections. The left image is an average expected frequency (% canopy cover projected to the ground). The right image represents agreement of species presence/absence projections for 18 general circulation models.

Ponderosa pine – 2050s



Figure B6 c. Projected habitat of ponderosa pine for the 2041–2070 normal period according to 18 climate change projections. The left image is an average expected frequency (% canopy cover projected to the ground). The right image represents agreement of species presence/absence projections for 18 general circulation models.

Ponderosa pine - 2080s



Figure B6 d. Projected habitat of ponderosa pine (*Pinus ponderosa*) for the 2071–2100 normal period according to 18 climate change projections. The left image is an average expected frequency (% canopy cover projected to the ground). The right image represents agreement of species presence/absence projections for 18 general circulation models.

Appendix B7 – Sitka spruce



Sitka spruce – Current

Figure B7 a. Projected habitat of Sitka spruce (*Picea sitchensis* (Bongard) Carrière). The left image is an expected frequency (% canopy cover projected to the ground) for the 1961-1990 normal period, representing long-term climate condition and model training data. The right image models habitat for the 1997-2006 period, representing a recent (25-year) climate trend.



Sitka spruce – 2020s

Figure B7 b. Projected habitat of Sitka spruce for the 2011–2040 normal period according to 18 climate change projections. The left image is an average expected frequency (% canopy cover projected to the ground). The right image represents agreement of species presence/absence projections for 18 general circulation models.



Figure B7 c. Projected habitat of Sitka spruce for the 2041–2070 normal period according to 18 climate change projections. The left image is an average expected frequency (% canopy cover projected to the ground). The right image represents agreement of species presence/absence projections for 18 general circulation models.



Sitka spruce – 2080s

Figure B7 d. Projected habitat of Sitka spruce for the 2071–2100 normal period according to 18 climate change projections. The left image is an average expected frequency (% canopy cover projected to the ground). The right image represents agreement of species presence/absence projections for 18 general circulation models.

Appendix B8 – Tamarack



Tamarack – Current

Figure B8 a. Projected habitat of tamarack (*Larix laricina* (Du Roi) K. Koch). The left image is an expected frequency (% canopy cover projected to the ground) for the 1961-1990 normal period, representing long-term climate condition and model training data. The right image models habitat for the 1997-2006 period, representing a recent (25-year) climate trend.





Figure B8 b. Projected habitat of tamarack for the 2011–2040 normal period according to 18 climate change projections. The left image is an average expected frequency (% canopy cover projected to the ground). The right image represents agreement of species presence/absence projections for 18 general circulation models.





Figure B8 c. Projected habitat of tamarack for the 2041–2070 normal period according to 18 climate change projections. The left image is an average expected frequency (% canopy cover projected to the ground). The right image represents agreement of species presence/absence projections for 18 general circulation models.





Figure B8 d. Projected habitat of tamarack for the 2071–2100 normal period according to 18 climate change projections. The left image is an average expected frequency (% canopy cover projected to the ground). The right image represents agreement of species presence/absence projections for 18 general circulation models.

Appendix B9 – Trembling aspen



Trembling aspen – Current

Figure B9 a. Projected habitat of trembling aspen (*Populus tremuloides* Michaux). The left image is an expected frequency (% canopy cover projected to the ground) for the 1961-1990 normal period, representing long-term climate condition and model training data. The right image models habitat for the 1997-2006 period, representing a recent (25-year) climate trend.

Trembling aspen – 2020s



Figure B9 b. Projected habitat of trembling aspen for the 2011–2040 normal period according to 18 climate change projections. The left image is an average expected frequency (% canopy cover projected to the ground). The right image represents agreement of species presence/absence projections for 18 general circulation models.

Trembling aspen – 2050s



Figure B9 c. Projected habitat of trembling aspen the 2041–2070 normal period according to 18 climate change projections. The left image is an average expected frequency (% canopy cover projected to the ground). The right image represents agreement of species presence/absence projections for 18 general circulation models.

Trembling aspen – 2080s



Figure B9 d. Projected habitat of trembling aspen for the 2071–2100 normal period according to 18 climate change projections. The left image is an average expected frequency (% canopy cover projected to the ground). The right image represents agreement of species presence/absence projections for 18 general circulation models.

Appendix B10 – Western hemlock



Western hemlock – Current

Figure B10 a. Projected habitat of western hemlock (*Tsuga heterophylla* (Rafinesque) Sargent). The left image is an expected frequency (% canopy cover projected to the ground) for the 1961-1990 normal period, representing long-term climate condition and model training data. The right image models habitat for the 1997-2006 period, representing a recent (25-year) climate trend.





Figure B10 b. Projected habitat of western hemlock for the 2011–2040 normal period according to 18 climate change projections. The left image is an average expected frequency (% canopy cover projected to the ground). The right image represents agreement of species presence/absence projections for 18 general circulation models.





Figure B10 c. Projected habitat of western hemlock for the 2041–2070 normal period according to 18 climate change projections. The left image is an average expected frequency (% canopy cover projected to the ground). The right image represents agreement of species presence/absence projections for 18 general circulation models.

Western hemlock - 2080s



Figure B10 d. Projected habitat of western hemlock for the 2071–2100 normal period according to 18 climate change projections. The left image is an average expected frequency (% canopy cover projected to the ground). The right image represents agreement of species presence/absence projections for 18 general circulation models.

Appendix B11 – Western larch



Western larch – Current

Figure B11 a. Projected habitat of western larch (*Larix occidentalis* Nuttall). The left image is an expected frequency (% canopy cover projected to the ground) for the 1961-1990 normal period, representing long-term climate condition and model training data. The right image models habitat for the 1997-2006 period, representing a recent (25-year) climate trend.

Western larch – 2020s



Figure B11 b. Projected habitat of western larch for the 2011–2040 normal period according to 18 climate change projections. The left image is an average expected frequency (% canopy cover projected to the ground). The right image represents agreement of species presence/absence projections for 18 general circulation models.

Western larch – 2050s



Figure B11 c. Projected habitat of western larch for the 2041–2070 normal period according to 18 climate change projections. The left image is an average expected frequency (% canopy cover projected to the ground). The right image represents agreement of species presence/absence projections for 18 general circulation models.



Western larch – 2080s

Figure B11 d. Projected habitat of western larch for the 2071–2100 normal period according to 18 climate change projections. The left image is an average expected frequency (% canopy cover projected to the ground). The right image represents agreement of species presence/absence projections for 18 general circulation models.

Appendix B12 – Western redcedar



Western redcedar – Current

Figure B12 a. Projected habitat of western redcedar (*Thuja plicata* Donn ex D. Don in Lambert). The left image is an expected frequency (% canopy cover projected to the ground) for the 1961-1990 normal period, representing long-term climate condition and model training data. The right image models habitat for the 1997-2006 period, representing a recent (25-year) climate trend.

Western redcedar – 2020s



Figure B12 b. Projected habitat of western redcedar for the 2011–2040 normal period according to 18 climate change projections. The left image is an average expected frequency (% canopy cover projected to the ground). The right image represents agreement of species presence/absence projections for 18 general circulation models.



Western redcedar – 2050s

Figure B12 c. Projected habitat of western redcedar for the 2041–2070 normal period according to 18 climate change projections. The left image is an average expected frequency (% canopy cover projected to the ground). The right image represents agreement of species presence/absence projections for 18 general circulation models.


Western redcedar – 2080s

Figure B12 d. Projected habitat of western red cedar for the 2071–2100 normal period according to 18 climate change projections. The left image is an average expected frequency (% canopy cover projected to the ground). The right image represents agreement of species presence/absence projections for 18 general circulation models.

Appendix B13 – Western white pine



Western white pine – Current

Figure B13 a. Projected habitat of western white pine (*Pinus monticola* Douglas ex D. Don in Lambert). The left image is an expected frequency (% canopy cover projected to the ground) for the 1961-1990 normal period, representing long-term climate condition and model training data. The right image models habitat for the 1997-2006 period, representing a recent (25-year) climate trend.

Western white pine – 2020s



Figure B13 b. Projected habitat of western white pine for the 2011–2040 normal period according to 18 climate change projections. The left image is an average expected frequency (% canopy cover projected to the ground). The right image represents agreement of species presence/absence projections for 18 general circulation models.





Figure B13 c. Projected habitat of western white pine for the 2041–2070 normal period according to 18 climate change projections. The left image is an average expected frequency (% canopy cover projected to the ground). The right image represents agreement of species presence/absence projections for 18 general circulation models.



Western white pine – 2080s

Figure B13 d. Projected habitat of western white pine for the 2071–2100 normal period according to 18 climate change projections. The left image is an average expected frequency (% canopy cover projected to the ground). The right image represents agreement of species presence/absence projections for 18 general circulation models.

Appendix B14 – White spruce



White spruce – Current

Figure B14 a. Projected habitat of white spruce (*Picea glauca* (Moench) Voss). The left image is an expected frequency (% canopy cover projected to the ground) for the 1961-1990 normal period, representing long-term climate condition and model training data. The right image models habitat for the 1997-2006 period, representing a recent (25-year) climate trend.





Figure B14 b. Projected habitat of white spruce for the 2011–2040 normal period according to 18 climate change projections. The left image is an average expected frequency (% canopy cover projected to the ground). The right image represents agreement of species presence/absence projections for 18 general circulation models.





Figure B14 c. Projected habitat of white spruce for the 2041–2070 normal period according to 18 climate change projections. The left image is an average expected frequency (% canopy cover projected to the ground). The right image represents agreement of species presence/absence projections for 18 general circulation models.





Figure B14 d. Projected habitat of white spruce for the 2071–2100 normal period according to 18 climate change projections. The left image is an average expected frequency (% canopy cover projected to the ground). The right image represents agreement of species presence/absence projections for 18 general circulation models.

Appendix B15 – Yellow cedar



Yellow cedar – Current

Figure B15 a. Projected habitat of yellow cedar (*Chamaecyparis nootkatensis* (D. Don) Sudworth). The left image is an expected frequency (% canopy cover projected to the ground) for the 1961-1990 normal period, representing long-term climate condition and model training data. The right image models habitat for the 1997-2006 period, representing a recent (25-year) climate trend.





Figure B15 b. Projected habitat of yellow cedar for the 2011–2040 normal period according to 18 climate change projections. The left image is an average expected frequency (% canopy cover projected to the ground). The right image represents agreement of species presence/absence projections for 18 general circulation models.





Figure B15 c. Projected habitat of yellow cedar for the 2041–2070 normal period according to 18 climate change projections. The left image is an average expected frequency (% canopy cover projected to the ground). The right image represents agreement of species presence/absence projections for 18 general circulation models.

Yellow cedar - 2080s



Figure B15 d. Projected habitat of yellow cedar for the 2071–2100 normal period according to 18 climate change projections. The left image is an average expected frequency (% canopy cover projected to the ground). The right image represents agreement of species presence/absence projections for 18 general circulation models.