

Conservation of forest genetic resources in Alberta: gap analysis and future reserve selection

By

Jill Terese Sekely

A thesis submitted in partial fulfillment of the requirements for the following dual degrees:

Master of Forestry
at University of Alberta, Edmonton, Canada

&

Master of Science in Forest Ecology and Management
at University of Freiburg, Germany

© Jill Terese Sekely

Winter 2018

Freiburg im Breisgau, Germany

The author reserves all publication and other rights in association with the copyright in the thesis and neither the thesis nor any substantial portion thereof may be printed or otherwise reproduced in any material form without the author's prior written consent

Acknowledgement

On the wave-beaten shores of Lake Superior, there stands a most remarkable and improbable white pine. Two hundred years ago, a tiny seed landed high upon a barren sea stack at the edge of the world, where against all odds it took root and grew. Today the tree stands as a formidable evergreen giant, clinging to the cliffside with ironclad roots. But this tree would never have survived without the perfect storm of nutrients, light, and hydration – and a healthy dose of good fortune. I tell you now about this magnificent organism because it was under similar conditions that this thesis came to life.

This project began with the seed of an idea, sown by my advisor Dr. Andreas Hamann. His patient encouragement and guidance were invaluable to the growth and completion of this thesis, during both my overseas TRANSFOR-M program and the endless question-and-answer-and-wait-I-have-another-question process that is so crucial to the environment of science.

The light of inspiration has always come from my family. From my parents, who constantly raise the bar higher, but never hesitate to offer me a leg up when it seem just out of reach. From my father, whose constant counsel helps me find my inner strength. From my mother, for encouraging my dreams but also showing me how to balance them with reality. From my little brother, my oldest and best friend, for occasionally conspiring with me to lower the bar my parents set. If we stand on the shoulders of giants, then I know of none taller than you three.

The soothing hydration came from my friends, especially my Freiburg pseudo-family, without whom I would have been adrift during my thesis experience. Angela. Anna. Ata. Cara. Emma. Lorenza. Marion. Simon. In truth the entire list of people and peers who have supported me over the years would fill pages. I thank you most for the long nights of laughter, and for stopping to pick me up whenever I stumbled.

Finally, the luck comes from the countless chance meetings with wonderful people who helped place me on this path: my enthusiastic German language teacher Herr Pankratz, Dr. Heinrich Spiecker and Marianne Stadler for their guidance through the TRANSFOR-M program, and my colleagues in the University of Alberta research lab, to name but a few. It has truly been privilege to walk this academic road and to grow alongside my thesis, with help from so many of you along the way.



*Chapel Rock in Munising, Michigan, USA

Abstract

Genetic diversity is the basis of biodiversity, and the adequate availability of diverse genetic resources can help species adapt to ecosystem change such as climate change. The protection of genetic resources is therefore an important aspect of biodiversity conservation. One of the most widely-used methods for protecting species and their genetic diversity is the use of *in situ* reserves; however, such reserve systems are not typically designed to capture the full genetic diversity of species. In this study, I perform a conservation gap analysis on 14 native tree species in the Canadian province of Alberta, to identify the genetic populations of each species and to determine which of these populations are inadequately protected by the current reserve network. I synthesize forest inventory data, high resolution satellite data, and distribution modeling to infer missing species distribution data, then identify locally-adapted genetic populations using ecological sub-regions as proxy. To improve long-term species adaptation potential, my conservation goal is to reduce the number of unprotected populations by expanding Alberta's reserve network. I use the conservation software Zonation to identify potential new reserve locations for filling the identified conservation gaps. Approximately 14.7% of Alberta's trees are currently located within protected areas. However, 10 of the 14 studied native tree species have at least one genetic population that is inadequately protected. In total, I identified 97 genetic populations, of which 13 are high priority gaps that are not adequately protected in the reserve network. In the design of future reserves, I recommend placing priority on species with low representation, high vulnerability to ecosystem change, or high numbers of unprotected genetic populations. I suggest 10 potential new reserve locations to increase representation for the 13 gap populations, which may help increase native tree species and ecosystem resiliency to environmental change.

Contents

1	Introduction	1
1.1	Why conserve genetic diversity?.....	1
1.2	Protecting common species.....	1
1.3	Genetic diversity and adaptation of trees	2
1.4	The practical value of conserving forest genetic diversity.....	3
1.5	How to protect the invisible	5
1.6	Implementing gene conservation (<i>in situ</i> vs <i>ex situ</i>)	7
1.7	Gap analysis and systematic reserve design.....	9
1.8	Study goals and research questions.....	11
2	Methods	11
2.1	Study area and data sources	11
2.2	Conservation gap analysis methods	16
2.3	Analytical conservation planning with Zonation	17
3	Results.....	18
3.1	Genetic population gaps	18
3.2	Determination of true conservation gaps	32
3.3	Comparative analysis among species.....	35
3.4	Conservation gaps by NSR	37
3.5	Zonation results and comparison of filters.....	39
3.6	Reserve design <i>de novo</i> versus existing reserve system	43
3.7	Options for filling gaps	44
4	Discussion	47
4.1	Conservation gap analysis.....	47
4.2	Future reserve size.....	48
4.3	Potential new reserve locations	49
4.4	Caveats of analysis.....	51
4.5	Further notes: climate change	52
5	Conclusion	56
6	Referenced Literature	57

List of Tables

Table 1. Names and definitions of IUCN protected areas classifications.....	8
Table 2. Latin name, common name, and species code for each of the fourteen native tree species included in this study.....	15
Table 3. All conservation gaps according to individual species graphs.....	33
Table 4. High priority conservation gaps that are not fringe populations, model artifacts, or otherwise already protected.	35

List of Figures

Figure 1. Map of the 5 Natural Regions and 14 Natural Subregions as used in this study.....	13
Figure 2. Delineations of Alberta’s 90 seed zones.....	14
Figure 3. Alberta’s reserve system including IUCN classifications.	16
Figure 4. Cumulative cover and protection level of individual genetic populations of <i>Abies lasiocarpa</i>	19
Figure 5. Cumulative cover and protection level of individual genetic populations of <i>Betula papyrifera</i>	20
Figure 6. Cumulative cover and protection level of individual genetic populations of <i>Juniperus scopulorum</i>	21
Figure 7. Cumulative cover and protection level of individual genetic populations of <i>Larix laricina</i>	22
Figure 8. Cumulative cover and protection level of individual genetic populations of <i>Larix lyallii</i>	23
Figure 9. Cumulative cover and protection level of individual genetic populations of <i>Picea engelmannii</i>	24
Figure 10. Cumulative cover and protection level of individual genetic populations of <i>Picea glauca</i>	25
Figure 11. Cumulative cover and protection level of individual genetic populations of <i>Picea mariana</i>	26
Figure 12. Cumulative cover and protection level of individual genetic populations of <i>Pinus albicaulis</i>	27

Figure 13. Cumulative cover and protection level of individual genetic populations of <i>Pinus banksiana</i>	28
Figure 14. Cumulative cover and protection level of individual genetic populations of <i>Pinus contorta</i>	29
Figure 15. Cumulative cover and protection level of individual genetic populations of <i>Pinus flexilis</i>	30
Figure 16. Cumulative cover and protection level of individual genetic populations of <i>Populus tremuloides</i>	31
Figure 17. Cumulative cover and protection level of individual genetic populations of <i>Pseudotsuga menziesii</i>	32
Figure 18. Comparing number of genetic populations with total cumulative cover.....	36
Figure 19. Proportion of protected and unprotected genetic populations within individual species.....	37
Figure 20. Number of protected and unprotected populations per NSR.....	38
Figure 21. Total and protected area comparison for individual natural sub-regions.....	39
Figure 22. Graphical results of coarse filter Zonation analysis.....	41
Figure 23. Zonation performance curves for coarse filter result.....	41
Figure 24. Graphical results of fine-filter Zonation analysis.....	42
Figure 25. Zonation performance curve for fine-filter result.....	42
Figure 26. Graphical results of superfine filter Zonation analysis.....	43
Figure 27. Zonation performance curve for superfine filter result.....	43
Figure 28. Comparison of existing reserve system with the top priority of fine-filter Zonation results.....	44
Figure 29. Potential options for new reserve selection using superfine Zonation analysis.....	46
Figure 30. Superfine filter Zonation results using gap populations only, combined with multivariate forward and reverse velocity calculations.....	55

1 Introduction

1.1 Why conserve genetic diversity?

Genes provide organisms with the raw materials necessary for adaptation and evolution, and therefore they may be considered the most fundamental component of biodiversity (Srgo *et al* 2011, Ledig *et al* 1998). Species must have an adequate supply of diverse genetic resources in order to adapt to ecosystem change such as disease outbreak, competition, and climate change (Ledig 1986, Menges 1991, Lande 1998). The pressure exerted by ongoing environmental variation directly affects the survival rates of organisms and species, and over time these forces drive evolution and create biodiversity (Pressey *et al* 2003, Sgro *et al* 2011).

High genetic diversity can provide species with increased resiliency to ecosystem change, while reduced genetic variation may make a species more susceptible to change and thereby increase its extinction risk (Ledig 1986, Reusch *et al* 2005, Young *et al* 1996). Genetic diversity increases through mutation or migration of genes from nearby populations. Decreased genetic variation occurs through genetic erosion, which happens when natural selection favors certain genes or when genes are lost by chance if individuals die or do not reproduce, i.e. genetic drift. Reduced genetic variation may lead to inbreeding depression, which lowers evolutionary fitness and increases extinction risk (Spielman *et al* 2004, Young *et al* 1996). Genetic erosion is an especially acute problem for species with small populations, because they may already have depressed genetic diversity. However, the same principles also apply to abundant species (Gaston *et al* 2000).

1.2 Protecting common species

Common species are often perceived as having low extinction risk, but historical evidence shows that common species can decline rapidly and without warning in response to environmental change. For example, the introduction of a nonnative chestnut blight (*Cryphonectria parasitica*) in the 1900s caused precipitous decline in the then-abundant and commercially valuable American chestnut (*Castanea dentate*), which suffered widespread die-offs and altered physical structure in the few surviving trees (Ellison *et al* 2005). Reduced vitality of common tree species can have widespread impacts on overall forest health, and ecosystem deterioration may begin after a relatively low amount of species decline (Ellison *et al* 2005, Gaston and Fuller 2008).

This is because common species are often foundation species in forests, meaning they perform a disproportionately high amount of ecosystem processes in relation to their biomass (Dayton 1972).

Foundation species create the physical structure of a forest, maintain ecosystem processes such as water cycling, and stabilize local environmental conditions, which may help protect smaller plant and animal species (Dayton 1972, Gaston and Fuller 2008, Ellison *et al* 2005, Aycrigg *et al* 2013). In forest ecosystems that only contain one or two foundation species, there is little functional redundancy, so the loss or reduction of one species will likely cause rapid ecosystem shifts (Ebenman and Jonsson 2005). In addition, foundation species loss can also cause many secondary extinctions among interdependent organisms, and in some extreme cases can lead to community collapse (Ebenman and Jonsson 2005, Koh *et al* 2004). In the case of American chestnut, while some individuals still exist in parts of its former range, the diminished population size and altered physical structure mean chestnut is unable to perform its foundation species role. It is therefore considered functionally extinct (Ellison *et al* 2005).

In general, there are far fewer common species than rare species (Isbell *et al* 2011). Biodiversity conservation has been a popular scientific and political goal for many years, but traditionally it has focused on saving already-rare species from extinction rather than preventing the decline of common species (Scott *et al* 1993, Sgro *et al* 2011). Conservation of rare species helps maintain high species diversity, but it is important to also conserve common species to promote high ecosystem health and functioning (Gaston and Fuller 2008, Isbell *et al* 2011). Therefore, conservation efforts should focus on proactively protecting common species in addition to saving rare species.

1.3 Genetic diversity and adaptation of trees

Canada encompasses a wide range of environmental conditions, from the warm, fertile prairies in the south central to cold boreal forests in the north. This natural variation drives individuals to evolve adaptive characteristics which allow them to survive under different environmental conditions. Adaptations in tree species may be morphological traits, such as leaf shape or xylem structure, or physiological traits, such as carbon allocation (Howe *et al* 2003, Montwé *et al* 2015, Landhüsser and Lieffers 2001). Trees have an especially high level of individual genetic

variation in comparison to other plants (Hamrick and Godt 1990). This allows temperate species to be widely distributed (Morgenstern 2011); for example, trembling aspen can grow as far north as the Arctic Circle and as far south as Mexico.

Because trees are sessile and cannot move away from adverse environmental conditions, individuals tend to be adapted to their immediate microclimate in an especially fine-scale manner (Menges 1991). Minute differences in temperature, light levels, elevation, and nutrient availability affect how genes are expressed by individuals. Over time, site-specific natural selection pressures can create groups of genetically distinct local populations that are specifically adapted to their immediate climates (Morgenstern 2011, Savolainen 2007). For example, a study in Oregon found that a single 6100-hectare watershed could have up to six microclimates, and that individual Douglas-fir seedlings were unlikely to survive if they were moved just 670 m higher or lower on the same slope on which they were found (Campbell 1979). In Alberta, cold hardiness in white spruce (*Picea glauca*) is strongly influenced by a seed's original latitude and climate (Sebastian-Azcona *et al* 2018).

An additional type of adaptation is phenotypic plasticity, or the extent to which an individual's genotype can be modified by environmental conditions during its lifespan (Bradshaw 1965). Phenotypic plasticity helps individuals survive the climatic fluctuations that occur on a short temporal scale. For example, a drought in southern Sweden prompted Norway spruce (*Picea abies*) to grow thicker-walled hydraulic systems that were more resistant to cavitation (Montwé *et al* 2015). Different genetic populations within a species may also exhibit higher phenotypic plasticity, as was demonstrated in a study by Schreiber *et al* (2015) that compared provenance trials on aspen and noted that certain populations were better able to alter xylem diameters in response to summer moisture availability. Furthermore, within-population genotypic variation can be quite high due to gene flow; in a recent study on interior spruce and lodgepole pine, growth and cold hardiness varied widely among individuals within the same population (Liepe *et al* 2016, Kremer *et al.* 2012, Yeaman and Jarvis 2006).

1.4 The practical value of conserving forest genetic diversity

Canada's extensive forests cover 347 million hectares, which account for 9% of the world's forest cover and 30% of the global boreal forest (NRC 2017, FAO 2010). These forests contain roughly 66% of the roughly 140,000 species found within Canada. The forestry industry creates

1.2% of the country's gross domestic product, and it is the fourth-largest exporter of forest products in the world (NRC 2017). As the global human population increases, the demand for raw forest products and forest ecosystem services such as clean air and recreation will continue to grow (FAO 2010). Following harvest on Crown lands, sustainable forest management laws require reforestation to ensure ongoing timber production and high ecosystem service functioning. Regeneration may be performed using natural or artificial regeneration methods, e.g. seedling planting and seeding. In 2015, over 500 million seedlings were planted in Canadian forests (NRC 2017).

To maximize growth in planted stands, seedlings must be appropriately adapted to the climate of a new planting site. Finding a good transfer match allows a seedling to grow to its full genetic potential within a new environment, while moving a seedling to a poor match location may result in maladaptation such as cold injury or drought susceptibility (Ying and Yanchuk 2006). One method for determining appropriate matches is provenance studies, which are common garden experiments that test the potential of various wild seed genotypes across multiple planting locations. Additionally, tree breeding programs create genetically improved seed for replanting by selectively choosing appropriate strains of parental genotypes from seed orchards, most commonly for important commercial species such as lodgepole pine (*Pinus contorta*) and white spruce (*Picea glauca*) (MacLachlan *et al* 2017). In addition to increasing stand productivity, tree improvement programs may also increase genetic diversity in natural stands faster than would normally occur, because artificial regeneration methods may move seedlings and their genetic materials much further than they could migrate on their own (Ledig 1986).

In terms of both commercial forestry and biodiversity conservation, wild genetic resources should be conserved because of their potential future value (Ledig 1986). Wild populations benefit by having increased adaptation potential and resilience, and commercial operations benefit because tree breeders have a larger selection from which to choose in case of new industry demand or environmental pressure (Chourmouzis *et al* 2009). For example, climate change is predicted to negatively affect the productivity of lodgepole pine stands in Alberta's Foothills region, and protecting the future productivity in regional planted and wild stands may depend upon the availability of an appropriate genetic variant that is able to withstand the new conditions (Chhin *et al* 2008, Ledig 1986). However, it is impossible to know which exact

genotypes will be most valuable in the future, so the most prudent approach is to systematically protect samples of all genetic variants (Ledig 1986).

Alberta is nearly 60% forested by land area (38 million ha), and its annual harvest of approximately 82,000 ha is worth \$8.4 billion to the provincial economy (Government of Alberta 2017a). In 2015, 26% of Alberta's harvested land was naturally regenerated using *in situ* seed and fostering of vegetative reproduction in aspen (Government of Alberta 2017b). On the remaining 73% of harvested land, artificial regeneration was performed using pre-germinated seedlings (72.2%) as well as a limited amount of seeding (0.8%). Approximately 80 million seedlings are planted annually in Alberta (Government of Alberta 2017b).

The Forestry Division of Alberta Sustainable Resource Development (ASRD) published its "Gene Conservation Plan for the Native Trees of Alberta" in 2009. The stated goal is to adequately conserve *in situ* genetic forest resources for Alberta's native tree species, in order to promote sustainable forest management and protect natural heritage resources. The conservation effort for Alberta's genetic resources began in 1975, but for many years the concepts were only applied to a select few commercial tree species (ASRD 2009). More recently, Alberta forestry practices have shifted towards compulsory use of genetically improved seed whenever available (Alberta Forest Genetic Resources Council 2015). Additionally, two native at-risk species were recently listed as endangered under *Alberta Wildlife Act*: whitebark pine (*Pinus albicaulis*) and limber pine (*Pinus flexilis*). Protective legislature and individual conservation programs are now in place to protect the genetic resources of these species (Alberta Whitebark and Limber Pine Recovery Team 2014). However, the remaining non-commercial and non-endangered native species are underrepresented in the provincial genetic conservation effort.

1.5 How to protect the invisible

The first step towards protecting genetic resources is to determine the number and location of distinct genetic populations, which can be a challenging task. Procurement of exact genetic information is costly and time consuming, because it involves decades-long provenance trials to observe phenotypes or individual DNA analysis to get exact information (Iriando *et al* 2008, Vogel *et al* 2004). Genetic population information is therefore lacking for the vast majority of

species, including Alberta's native trees (Hamann *et al* 2004). However, because tree genotypes are highly adapted to their local climates and physiographic features, a common solution for determining distinct genetic populations is to use environmental factors as proxy (Ledig 1986, Groves *et al* 2002, Margules and Pressey 2000).

Plant ecologists have long recognized the link between physical location and intraspecific vegetation variation (e.g. Cornelius and Johnston 1941), and have developed systems for classifying ecoregions. Ecoregions are categorized by unique plant assemblages and soil groups, which are indicators of a region's climate (Downing and Pettapiece 2006, Vogel *et al* 2004). Alberta has an existing ecoregion delineation system that divides the province into natural regions (NR) and natural sub-regions (NSR) (Downing and Pettapiece 2006). Natural regions are large areas that can be climatically diverse; for example, one of Alberta's Natural Regions, the Boreal Forest, has a 5 degree (C) difference in average temperatures between its northern and southern edges. All individuals of a species that are found within a single Natural Region are not typically genetically uniform across the entire region, but rather are stratified by elevational or latitudinal gradients and are adapted to a specific area within the NR (Vogel *et al* 2004). Thus, natural regions are too coarse to be used as proxy for genetic populations. Each natural region is further divided into natural sub-regions, which are smaller and more homogenous units of land with similar patterns of vegetation, climate, elevation, and physiography. The Boreal Forest NR is divided into six NSR. The homogeneity of these land units is sufficient to use as proxy for locally adapted genetic populations (Groves *et al* 2002). I assume that each NSR contains unique locally adapted genetic resources, and I define a genetic population as all individuals of a species that occupy a single NSR.

There is also a finer habitat delineation category called seed zones, which is used in provincial tree improvement programs to determine appropriate seed transfer matches (Ying and Yanchuk 2006). Seed zones are even finer divisions of NSR, and are initially based on the same environmental factors that separate natural regions from natural sub-regions, then refined using data from provenance trials as it becomes available (Mátyás 1994). However, there is some evidence that seed zones are too spatially fine for use as genetic population proxy, since high gene flow can cause high within-population diversity, i.e. there may not be sufficient environmental differences between adjacent seed zones to create genetically distinct populations

(Liepe *et al* 2016, Hamrick 2004). Therefore in this study, seed zones are used only for comparative analysis.

Once genetic populations have been identified, they can then be protected. In order to systematically preserve genetic samples of all possible genotypes, it is important to protect samples from both representative and unusual habitats. Representative habitats are used in the assumption that the majority of the species' available genetic resources will be contained within them, while the unusual habitats are valuable because they may contain individuals adapted to unique or extreme conditions on the edge of species' range (Ledig 1986).

1.6 Implementing gene conservation (*in situ* vs *ex situ*)

The most effective method for genetic protection is a contested subject. The two prevailing methods are *in situ* protection using reserves, or protected areas, and *ex situ* protection using seed banks and gardens (Pressey *et al* 1993, Ledig 1986). Both methods have merit, but also contain inherent risks. Conservation *in situ* tends to be less expensive and includes additional benefits such as continuing ecological functions and recreation opportunities (Ledig 1986, Possingham *et al* 2006). This method is also considered to be more effective and realistic, since leaving populations in the wild allows them to continue evolving under real-world conditions with other organisms (Frankel 1970). However, the greatest risk associated with *in situ* reserves is the potential loss of genetic resources through human activities or natural disturbance such as fire (Ledig *et al* 1998). Conservation *ex situ* explicitly focuses on preserving genetic resources by removing seeds and storing them off-site, but these methods face problems with long-term funding and the effective cessation of evolutionary adaptation (Ledig 1988). Thus, *in situ* conservation using reserves is typically considered the preferred method for protecting forest ecosystems, although supplemental *ex situ* methods may also be used (Ledig 1988).

There is a wide range of *in situ* protection types, including wild stands protected within reserves and regenerated forests that are managed through monitoring or silviculture practices (Iriondo *et al* 2008, Skrøppa 2003). There are also myriad definitions for "protected area," but here I use the definition from the IUCN: "A clearly defined geographical space, recognized, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values." The global protected areas network has

experienced explosive growth in the last 50 years, a change that is considered by some to be the largest intentional change of human land use management in history (Chape *et al* 2005). Protected areas now rank among the most significant forms of global land use (Dudley 2008). Approximately 14% of the global terrestrial area is already protected within reserves, but the International Union for Conservation of Nature (IUCN) has proposed an increased target of 17% to be protected by 2020 (Dudley 2008). In Alberta, approximately 12.7% of the terrestrial area is currently protected within 477 *in situ* reserves, which are managed by either the federal or provincial government.

Protected areas encompass a highly diverse range of management goals and protection levels, which prompted the IUCN to create a framework of management categories. This framework has become a widely-accepted global standard for the creation and management of reserves (Dudley 2008). The relevant IUCN categories in Alberta include IA – Strict nature reserve, IB – Wilderness area, II – Ecosystem conservation and protection, III – Conservation of natural features, and IV – Conservation through active management (Table 1).

Table 1. Names and definitions of IUCN protected areas classifications (Dudley 2008). Includes examples found within Alberta.

Category	Name	Definition	Examples in Alberta
IA	Strict nature reserve	Strictly protected for biodiversity and/or geological features, where human use and impacts are limited and controlled	White Goat Wilderness Area, Dinosaur Provincial Park
IB	Wilderness area	Large unmodified areas, retaining their natural character and influence	Caribou Mountains Wildland Provincial Park, Willmore Wilderness Park
II	Ecosystem conservation and protection	Large natural areas protecting large-scale ecological processes with characteristic species and ecosystems	Jasper National Park, Castle Provincial Park
III	Conservation of natural features	Protect a specific natural monument (landform, geological feature, or living feature)	Douglas Fir Natural Area, Harper Creek Natural Area
IV	Conservation through active management	Protect particular species or habitats	Twin River Heritage Rangeland Natural Area, Black Creek Heritage Rangeland

Although reserves are a very common conservation tool, much of the global reserve network was not purposefully designed to efficiently represent all species or to capture all genetic variation. Instead, many parks were established to protect a small number of highly valuable species or to preserve otherwise important cultural or geological features. Still others were created *ad hoc* when land became opportunistically available for conservation (Lemieux *et al* 2011, Possingham *et al* 2006, Pressey and Tully 1994). Despite the high percentage of land already set aside in reserves, the global reserve system is still considered incomplete because many species and genetic populations are not adequately protected (Hannah *et al* 2007, Margules and Pressey 2000, Brooks *et al* 2004).

1.7 Gap analysis and systematic reserve design

Incomplete representation can be solved with systematic conservation planning, which aims to fill gaps in the reserve network by identifying the best areas for comprehensively protecting representative samples of diversity (Pressey and Cowling 2001, Margules and Pressey 2000, Possingham *et al* 2006). Conservation planning relies upon the “three R’s”: representation, redundancy, and resilience (after Shaffer and Stein 2000). Representation assumes that by protecting a small amount of all representative species, in this case native tree species, then most biodiversity is also likely to be protected (Tear *et al* 2005, Groves *et al* 2002). Ecosystem representation is already a cornerstone principle of conservation planning practices in all Canadian provinces (Lemieux and Scott 2005). Adequate *in situ* representation requires that sufficiently large population sizes be protected, in order to provide a lasting reservoir of the locally adapted genetic material, to allow for ongoing evolution, and to ensure normal functioning of mating systems (Aitken *et al* 2008, Ledig 1986, Sgro *et al* 2011). This population size is called minimum viable population (MVP) and is an important consideration when deciding quantitative representation goals.

Redundancy is a hedging strategy, intended to safeguard against gene loss by protecting each genetic population within multiple reserves. This ensures continued protection within the overall population even if a portion of the population is lost (Lemieux *et al* 2011). Additionally, since no two genetic populations are ever truly identical, redundancy can provide a supplementary source of representation (West *et al* 2009). The final concept, resilience, is the ability of a species to

persist through adverse environmental conditions, which is directly related to the availability of adequately diverse genetic resources (Sgro *et al* 2011, Shaffer and Stein 2000).

The first part of systematic conservation planning is a conservation gap analysis, which consists of four steps (after Burley 1988). First, target biodiversity features must be identified and their distributions mapped. Since my focus is on conserving genetic diversity, the relevant target biodiversity feature is genetic populations at the NSR level (Iriondo *et al* 2008). Second, the size and location of existing reserves must also be identified. Third, appropriate quantitative goals for representation and redundancy are chosen. Finally, these three pieces of information are compared, i.e. the distribution of target biodiversity features are compared with existing reserve locations in regards to the set quantitative goals. This identifies the conservation features that lack adequate protection within the existing reserve network (Dudley 2008).

After completing the gap analysis, the subsequent step of conservation planning is to fill the identified gaps in a comprehensive manner. There are myriad options for filling gaps, ranging from creation of new *in situ* reserves or changing land management practices in areas that contain target species, to incorporating harvested lands that are dedicated for natural regeneration (ASRD 2009, Scott *et al* 1993, Margules and Pressey 2000). Criteria for the creation of new reserves are likewise dependent upon myriad factors, including exact conservation goals and availability of land and financial resources. Percentage-based conservation targets, such as the 17% goal suggested by IUCN, are useful for raising public awareness about the need for conservation; however, they tend to oversimplify the conservation process, in part because species and genetic diversity is not evenly distributed across landscapes (Svancara *et al* 2005, Carwardine *et al* 2009, Tear *et al* 2005, Hubbell 1979). The connection between extinction risk and representation is also unclear, since the exact minimum conservation target requirements for most species and ecosystems remain unknown (Moilanen *et al* 2005, Tear *et al* 2005). Therefore, in this project I did not set percentage or area-based targets, and instead aim to relevant conservation gaps through a maximum coverage solution to ensure that all gaps are filled.

1.8 Study goals and research questions

The goals of this project are threefold: to identify the genetic populations of Alberta's native tree species, to assess the current protection level of each population within the existing protected areas network, and to investigate one potential method for choosing new reserve locations.

The specific research questions for this project are as follows:

- 1) Where are the existing conservation gaps? Which subregions and species are the least represented within the protected areas network?
- 2) How many genetic populations exist, and how well-protected is each?
- 3) Based on the location and number of gap populations, which areas of the landscape would be ideal locations for potential new reserves?

2 Methods

2.1 Study area and data sources

The study area is the province of Alberta, which lies in southwestern Canada and covers approximately 662,000 km². It shares borders with the Canadian provinces of Saskatchewan, British Columbia, the Northwest Territories, and the U.S. state of Montana. Alberta contains a wide elevational gradient, from 210 m to 3747 m above sea level, and a large latitudinal range, from the 49th to 60th parallel, and therefore encompasses a diverse range of climates and ecosystem types. The Natural Regions Committee has created a vector dataset of its delineations of Alberta, which includes 6 Natural Regions and 21 Natural Subregions (Downing and Pettapiece 2006). These areas were modified slightly for this study based on tree species presence, and were reduced to 5 natural regions and 14 natural sub-regions. The five natural regions used in this study are Boreal Forest, Rocky Mountain, Foothills, Parkland, and Grassland (Fig 1).

Boreal Forest Natural Region encompasses over half of the province and is dominated by wetlands and forests, wherein the most common tree species are lodgepole pine, jack pine, spruce, and aspen (Downing and Pettapiece 2006). It is divided into 6 NSR: Boreal Subarctic

(BSA), Central Mixedwood (CM), Dry Mixedwood (DM), Northern Mixedwood (NM), Upper Boreal Highlands (UBH), and Lower Boreal Highlands (LBH). The Rocky Mountain Natural Region encompasses the high-altitude regions along the southwestern border, where Engelmann spruce, subalpine fir, lodgepole pine, and white spruce dominate below the treeline. It is divided into 3 NSR: Alpine (A), Subalpine (SA), and Montane (M). The Foothills NR is mixed deciduous and coniferous forests lying between the Rocky Mountain NR and the Boreal Forest NR, and is largely a transitional biological mix of the species found within these two regions, e.g. lodgepole pine, aspen, and white spruce. It is divided into 2 NSR: Upper Foothills (UFH) and Lower Foothills (LFH). The Parkland NSR lies south of the Boreal Forest NR and has an overall low abundance of trees besides small pockets of aspen-dominated forests. It is divided into two NSR: Parkland (PKL) and Peace River Parkland (PRP). Finally, the Grassland NR is a warm and dry prairie habitat in the southeast, which contains few trees. It is therefore not divided into multiple NSR; however for analysis purposes it is called the Mixedgrass (MG) NSR. The latter two natural regions are characterized by fertile soils and mild climates, and today they are intensively farmed and ranched, so little of the native vegetation remains. A final NSR that was not used in this study, Canadian Shield, is characterized by exposed bedrock and lakes and also has little vegetation. This area was assimilated into the Northern Mixedwood NSR in the Boreal Forest NR.

Finally, the seed zone vector dataset was created by the Forest Management Branch of the Alberta Sustainable Resource Development (2005). There are 90 seed zones within Alberta, which remain unchanged for this study (Fig 2).

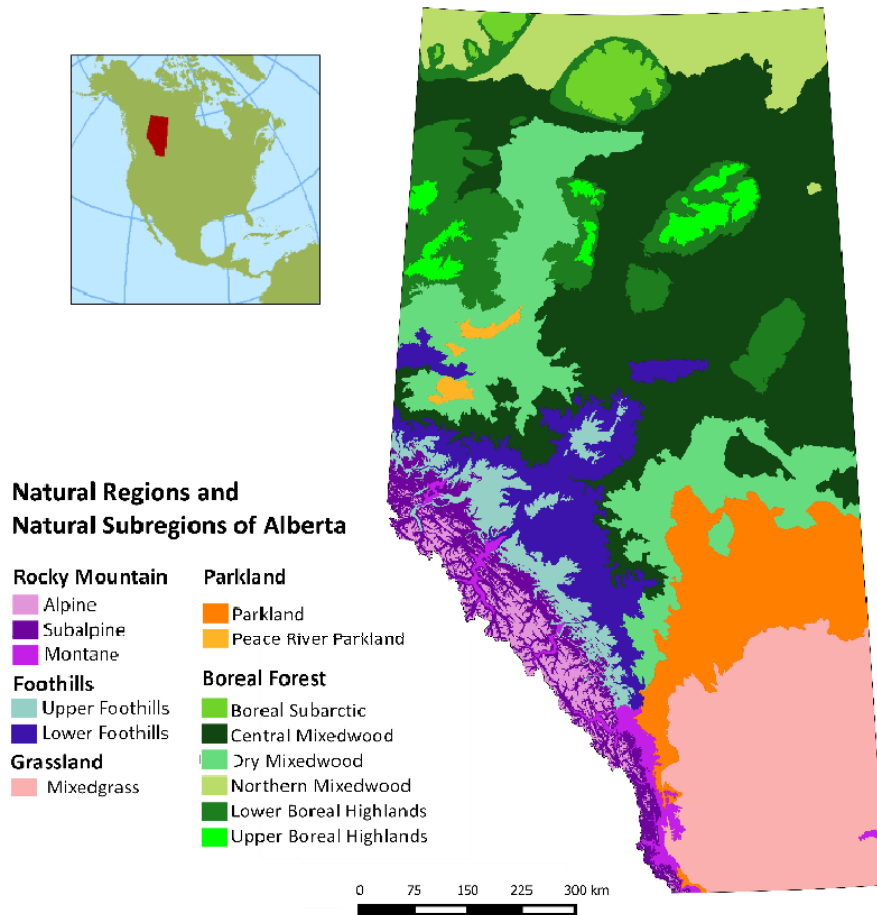


Figure 1. Map of the 5 Natural Regions and 14 Natural Subregions as used in this study. Delineations modified slightly from Natural Regions Committee (Downing and Pettapiece 2006).

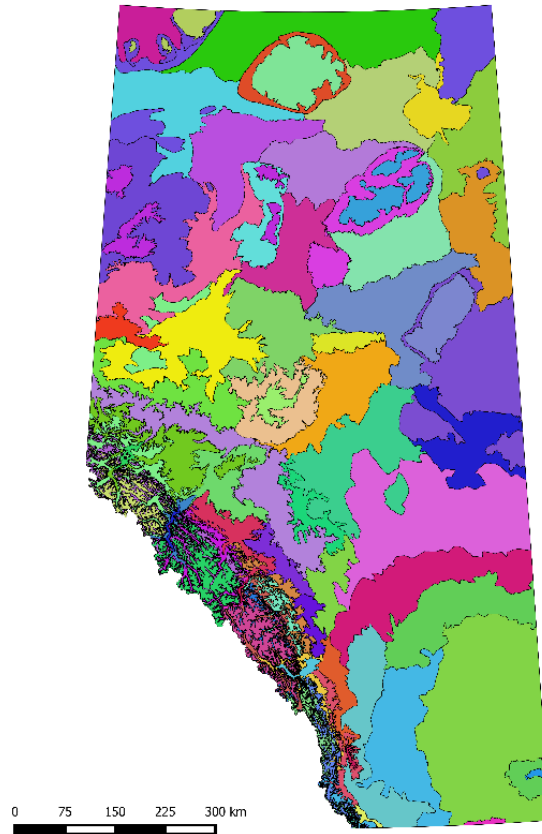


Figure 2. Delineations of Alberta’s 90 seed zones. Seed zones are not labeled individually, as names are irrelevant to this study.

I analyzed a total of 14 native tree species (Table 2). Since species distribution information for Alberta is incomplete, I used species distribution models that were created by Gray and Hamann (2013). First, they collected species-level forest inventory data for a small proportion of Alberta using remote sensing. These real data were then compared with ecosystem delineation data, to establish statistical relationships between environmental predictor variables and percent crown cover of individual tree species. Using these environmental conditions as proxy, they extrapolated their statistical models to create full-province species distribution models in raster dataset form. Distribution models include location as well as frequency information.

Table 2. Latin name, common name, and species code for each of the fourteen native tree species included in this study.

Latin name	Common name	Species code
<i>Abies lasiocarpa</i> (Hook.) Nutt.	Subalpine fir	ABIELAS
<i>Betula papyrifera</i> Marshall	Paper birch	BETUPAP
<i>Juniperus scopulorum</i> Sarg.	Rocky Mountain juniper	JUNISCO
<i>Larix laricina</i> (Du Roi) K. Koch	Tamarack	LARILAR
<i>Larix lyallii</i> Parl.	Subalpine larch	LARILYA
<i>Picea engelmannii</i> Parry ex Engelm.	Engelmann spruce	PICEENG
<i>Picea glauca</i> (Moench) Voss	White spruce	PICEGLA
<i>Picea mariana</i> (Mill.) Britton	Black spruce	PICEMAR
<i>Pinus albicaulis</i> Engelm.	Whitebark pine	PINUALB
<i>Pinus banksiana</i> Lamb.	Jack pine	PINUBAN
<i>Pinus contorta</i> Douglas	Lodgepole pine	PINUCON
<i>Pinus flexilis</i> E. James	Limber pine	PINUFLE
<i>Populus tremuloides</i> Michx.	Trembling aspen	POPUTRE
<i>Pseudotsuga menziesii</i> Mirb. Franco	Douglas-fir	PSEUMEN

The protected areas vector dataset was created by Alberta Parks (2017). The existing reserve network of Alberta includes 477 federally and provincially managed reserves (Fig 3). However, only 260 of these reserves meet IUCN classification criteria IA-V. The remaining 217 “unclassified reserves” do not receive legal protection from future land use change, and I considered these areas to be unprotected land during analysis.

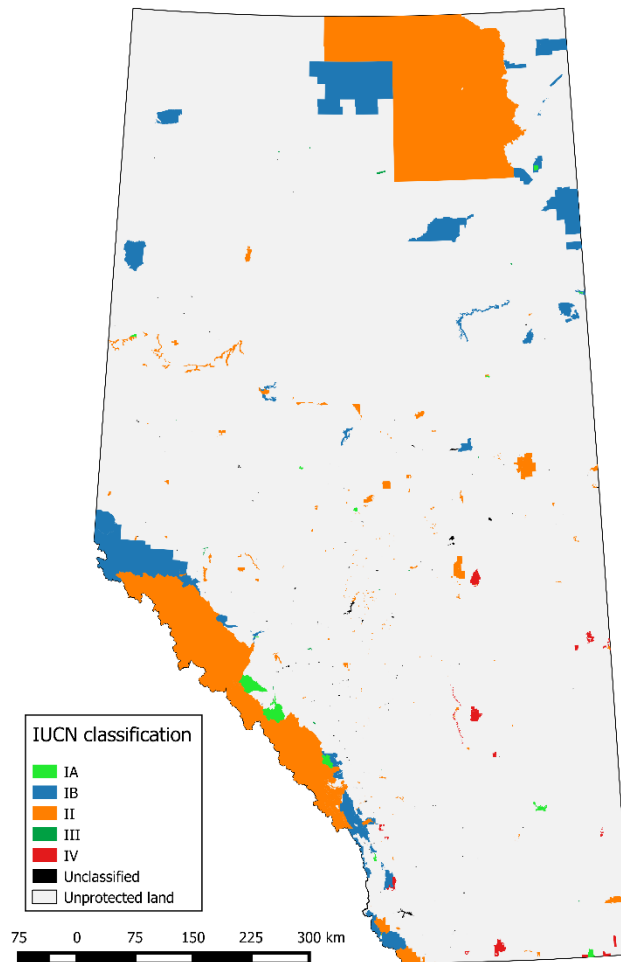


Figure 3. Alberta’s reserve system including IUCN classifications. There are a total of 477 existing federal or provincial reserves.

2.2 Conservation gap analysis methods

This thesis uses similar methods to Hamann and Wang (2006), who focused on protecting commercial tree species in British Columbia. It is also a finer-scale analysis of research initiated by Russell (2014), who analyzed the native tree species population gaps for the entire western half of North America. The conservation gap analysis was conducted using GIS software (Esri’s ArcGIS version 10.4.1 and QGIS 2.12) and R software. Since detailed information regarding distinct genetic populations is not available, populations were determined using environmental proxy, specifically by overlaying NSR vector data with raster species distribution models (Gray and Hamann 2013).

I set specific minimum protection goals for each population, based on the principles of representation and redundancy. I initially use the same criteria for all populations, regardless of rarity. The minimum viable population for trees is at least 5000 mature individuals, which can typically be found within an area of 10 hectares of cumulative cover (Aitken 2000). Therefore, my representation criterion states that each individual reserve must encompass at least 10 hectares of cumulative cover of a given population in order to be considered a viable form of protection. My redundancy criterion is set at 3 separate reserves per population. Populations that are currently found within zero reserves are considered unprotected, while populations found within one or two sufficiently-sized reserves are considered insufficiently protected. Once the populations were mapped and the quantitative goals set, I conducted the conservation gap analysis by comparing the created genetic population dataset with the existing protected areas network in ArcGIS.

2.3 Analytical conservation planning with Zonation

Rather than placing a minimum area target or percent target for this project, I aim towards a maximum coverage situation. This target type maximizes the number of conservation targets met by locating the areas with highest species representation and landscape connectivity (Moilanen 2007). I used an algorithm-based computer software called Zonation, which calculates a nested hierarchy of priority for future conservation areas (Moilanen *et al* 2005). The hierarchy is created by the iterative removal of landscape units, based on the principle of least marginal loss of conservation value. Zonation can assess any type of user-chosen conservation feature, whether it is full-province species distributions or smaller genetic population distributions.

For comparative purposes, three different levels of analysis were run in Zonation: coarse filter, fine filter, and superfine filter. The coarse filter used full-province species distributions as the conservation feature. For the fine-filter analysis, each genetic population was treated as its own conservation feature. For the superfine filter analysis, I further divide each species distribution map by seed zone, effectively treating all individuals within each seed zone as a genetically distinct population. The superfine filter was used only for theoretical analysis in Zonation, and was not used for the conservation gap analysis.

In the initial analysis, large water features were masked to ensure that results were chosen from terrestrial areas. In the future conservation planning analysis, existing reserves were also masked to ensure that results were chosen from unprotected areas. The resolution of my raster species distribution maps is one square kilometer, which is also the size of the selection units, or cells, used in the Zonation analysis. Core-area Zonation (CAZ) settings were used, which emphasizes the highest occurrence levels for each conservation feature individually and ensures that features in species-poor regions are given equal importance to those in a species-rich areas. This makes the CAZ setting especially useful for widespread species.

3 Results

3.1 Genetic population gaps

Alberta's current reserve system protects 14.7% of the total cumulative cover (area*frequency) of all native tree species. The protection status of each species' genetic populations were individually analyzed (Figs 4-17). These individual species graphs indicate the percentage of the total species cumulative cover found within each population, i.e. how the species and its genetic resources are distributed across the landscape. Since there are 14 NSR, each species can have a maximum of 14 genetic populations. I identified a total of 97 genetic populations for the 14 native tree species.

Some species are quite localized and exist in only a few NSR (e.g. Rocky Mountain juniper, Fig 7), while others are widely adapted and found in diverse habitats all across the province (e.g. white spruce, Fig 11). Some genetic populations have highly redundant protection, such as the CM population of white spruce, which is conserved within 78 protected areas (Fig 11). However, a number of locally adapted populations do not have any form of representation or redundancy within the reserve network, e.g. subalpine fir in CM (Fig 4). The latter population type constitutes some of the highest priority conservation gaps.

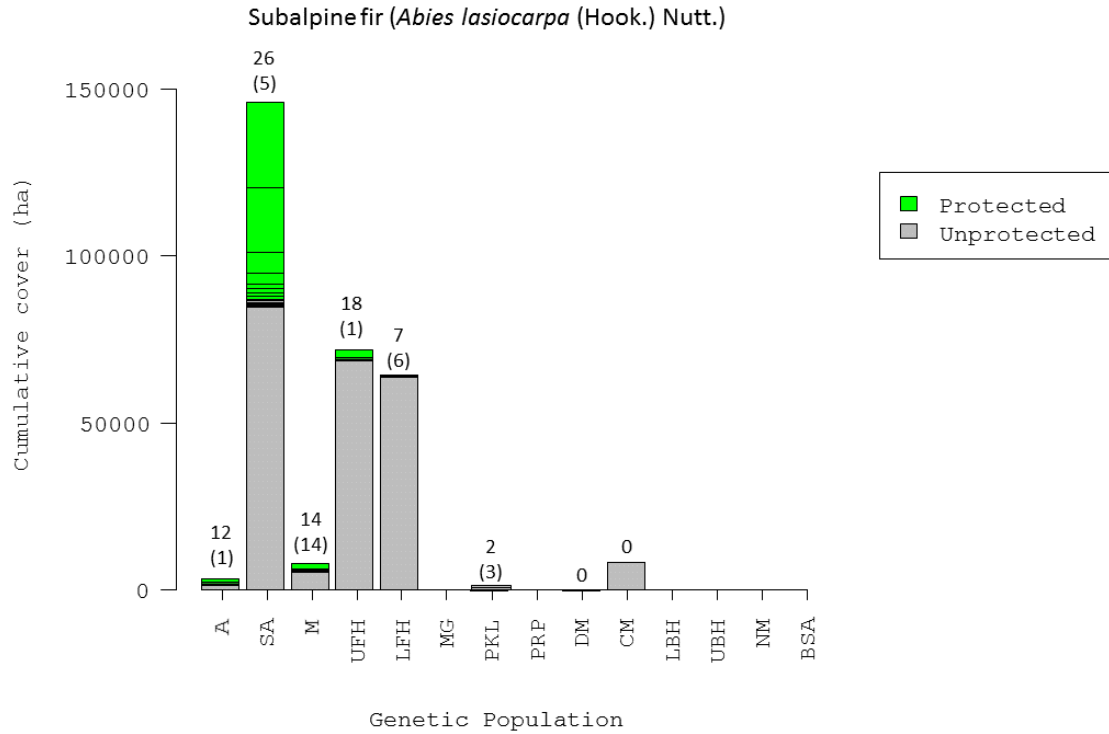


Figure 4. Cumulative cover and protection level of individual genetic populations of *Abies lasiocarpa*. Plain number above each bar indicates number of protected areas of sufficient size, and number in parentheses indicates number of reserves that are not of sufficient size. Green rectangles represent the size of individual protected areas, in descending order by cumulative cover. Black sections are incidental (created by the presence of many small reserves).

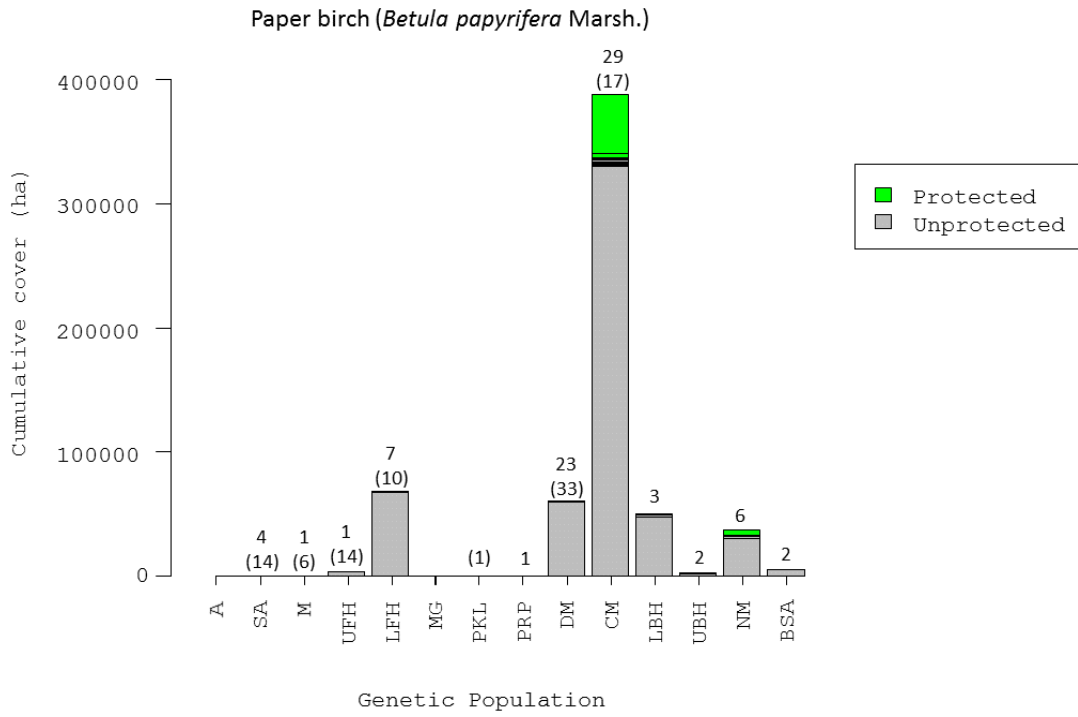


Figure 5. Cumulative cover and protection level of individual genetic populations of *Betula papyrifera*.

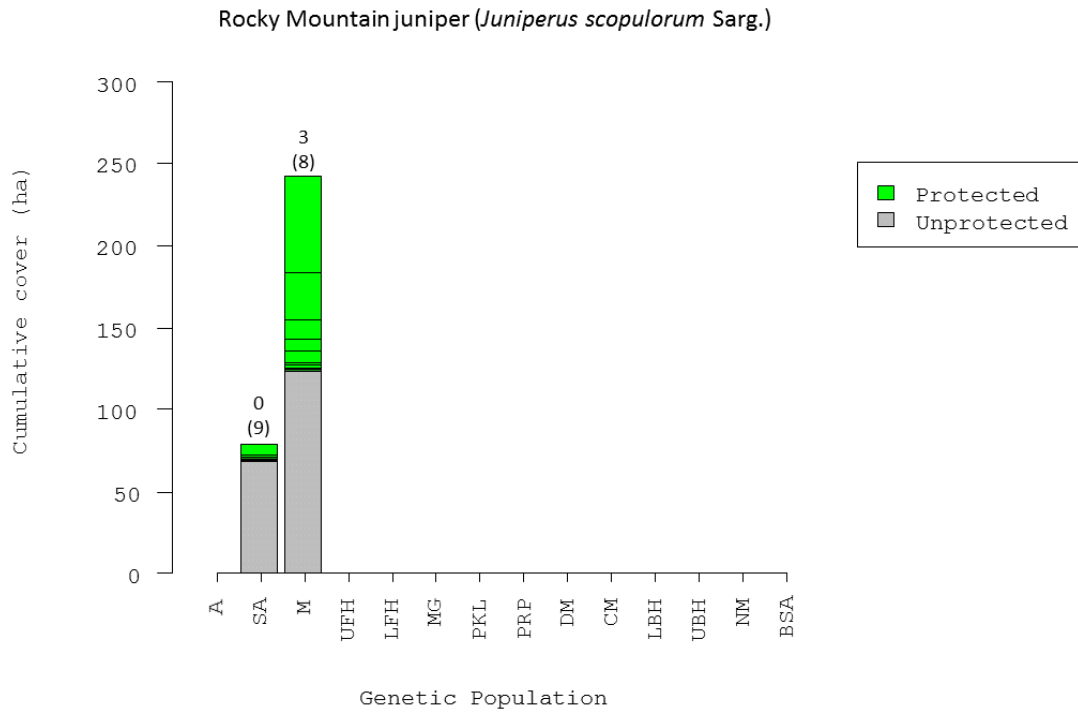


Figure 6. Cumulative cover and protection level of individual genetic populations of *Juniperus scopulorum*

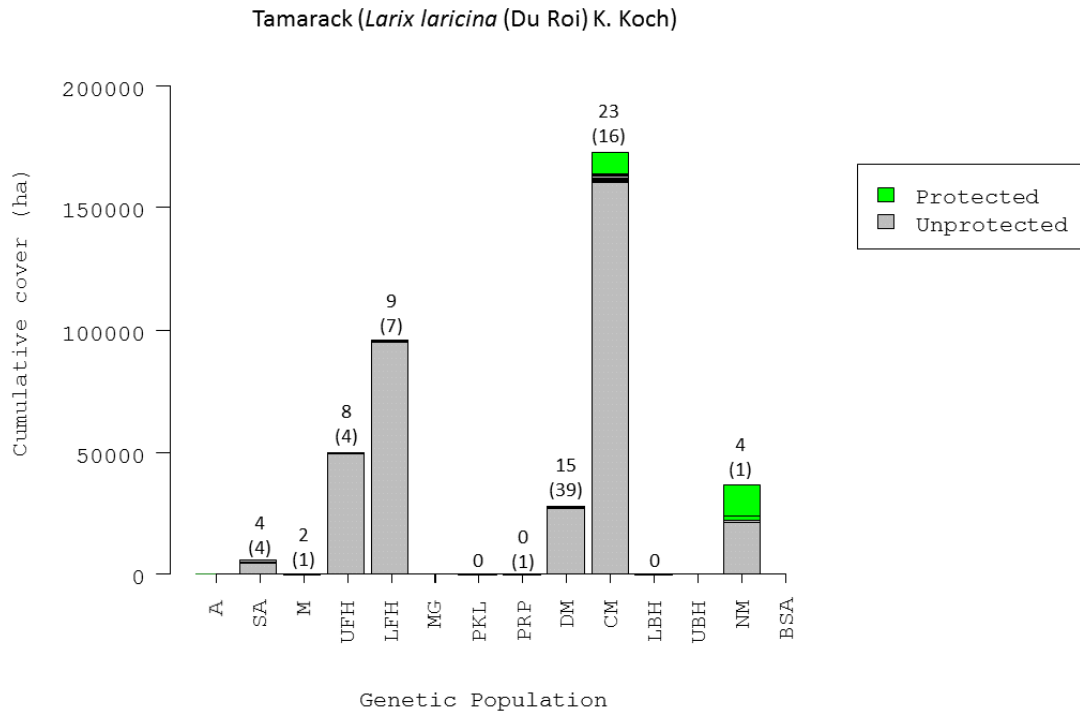


Figure 7. Cumulative cover and protection level of individual genetic populations of *Larix laricina*.

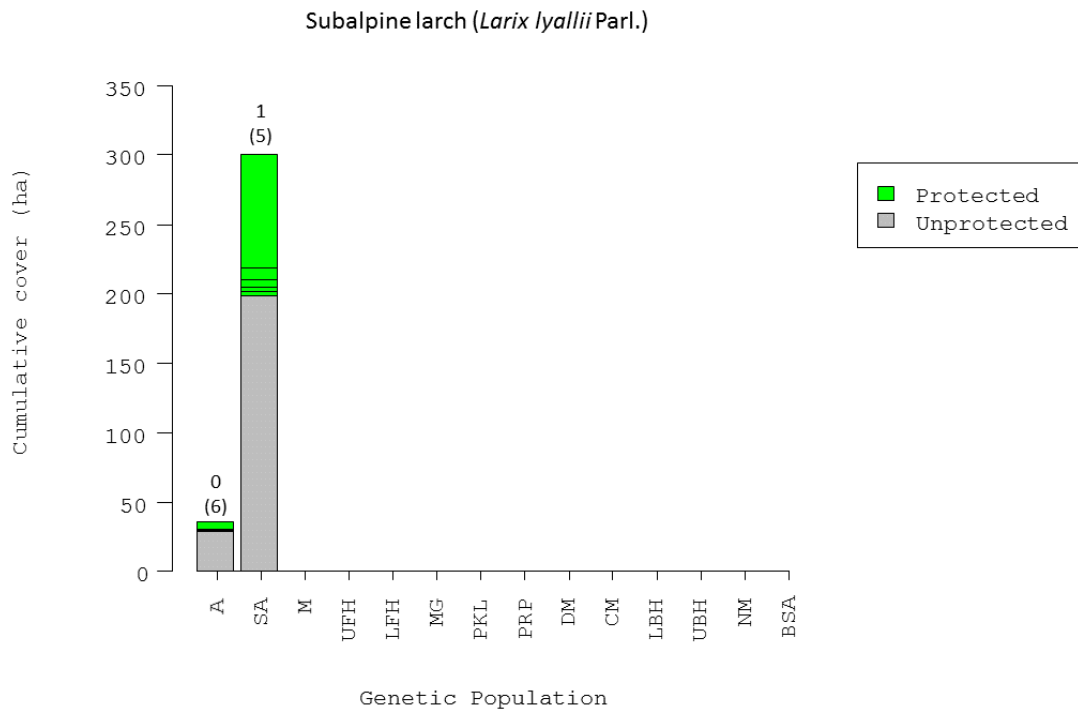


Figure 8. Cumulative cover and protection level of individual genetic populations of *Larix lyallii*.

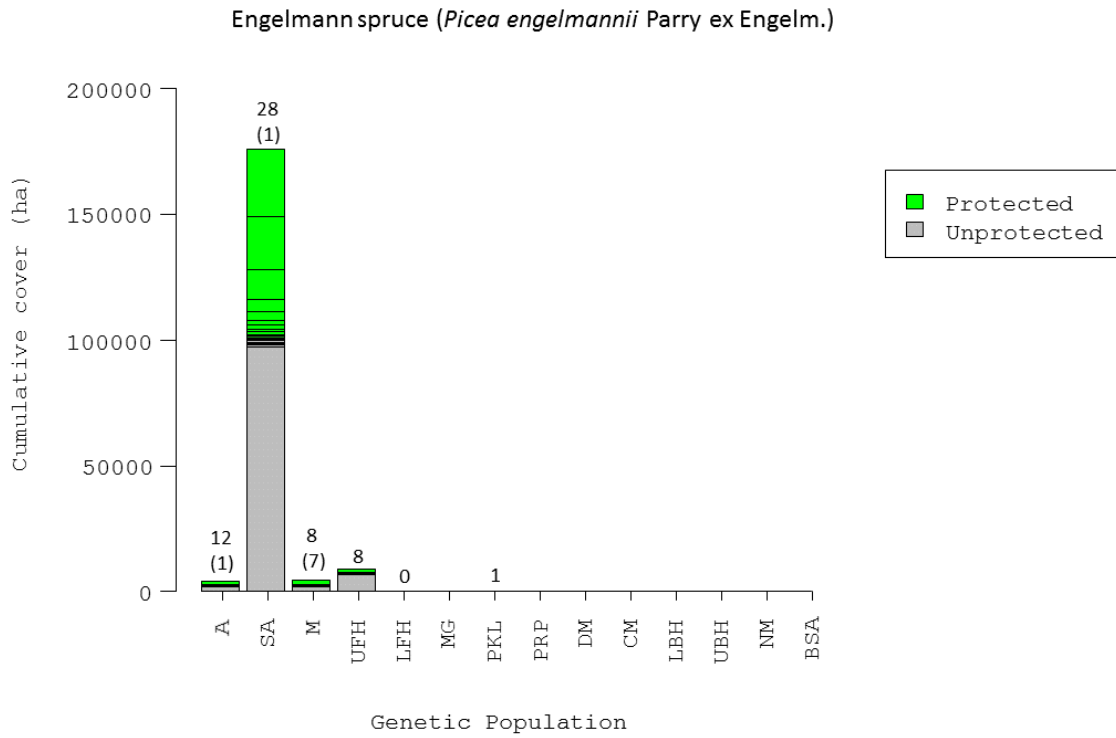


Figure 9. Cumulative cover and protection level of individual genetic populations of *Picea engelmannii*.

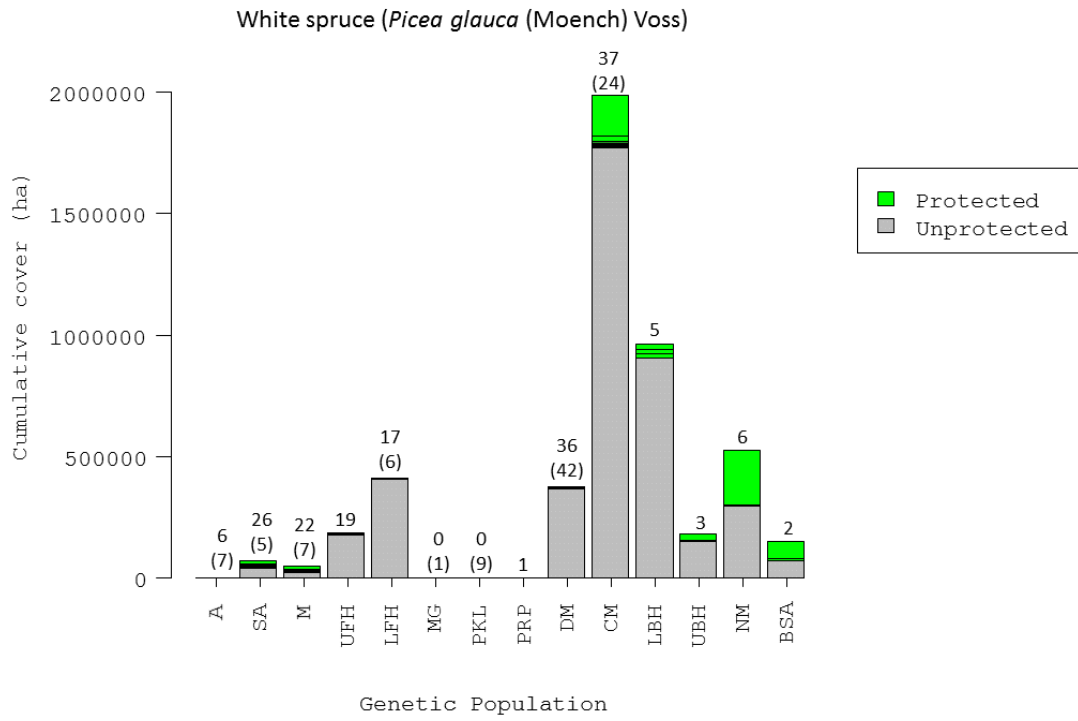


Figure 10. Cumulative cover and protection level of individual genetic populations of *Picea glauca*.

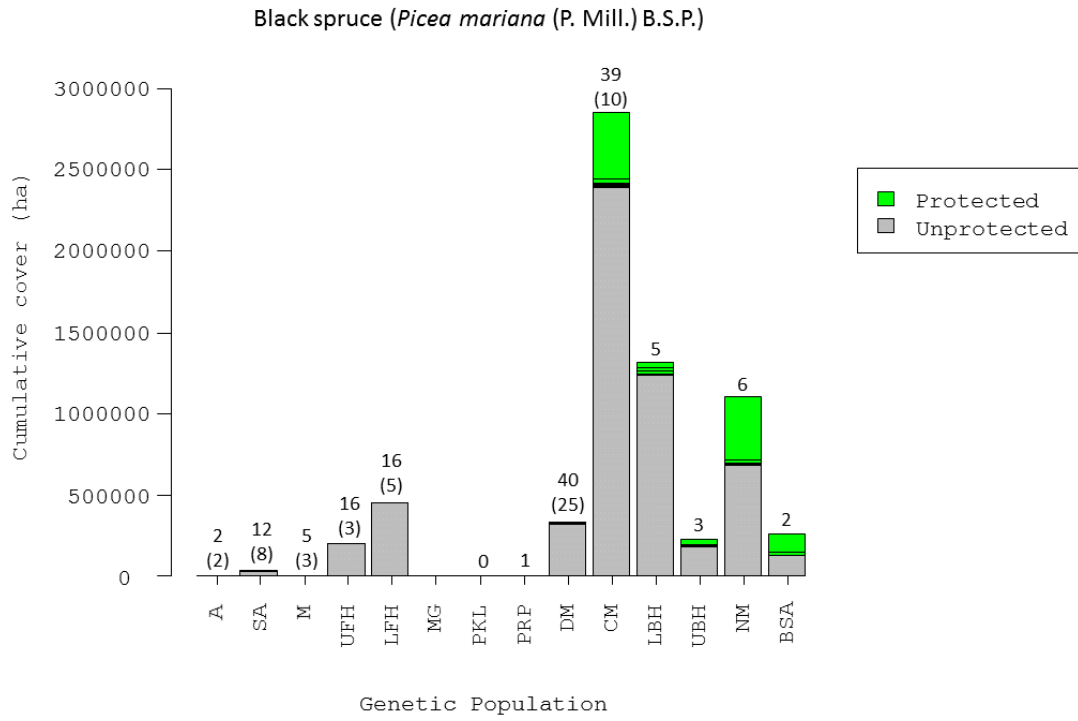


Figure 11. Cumulative cover and protection level of individual genetic populations of *Picea mariana*.

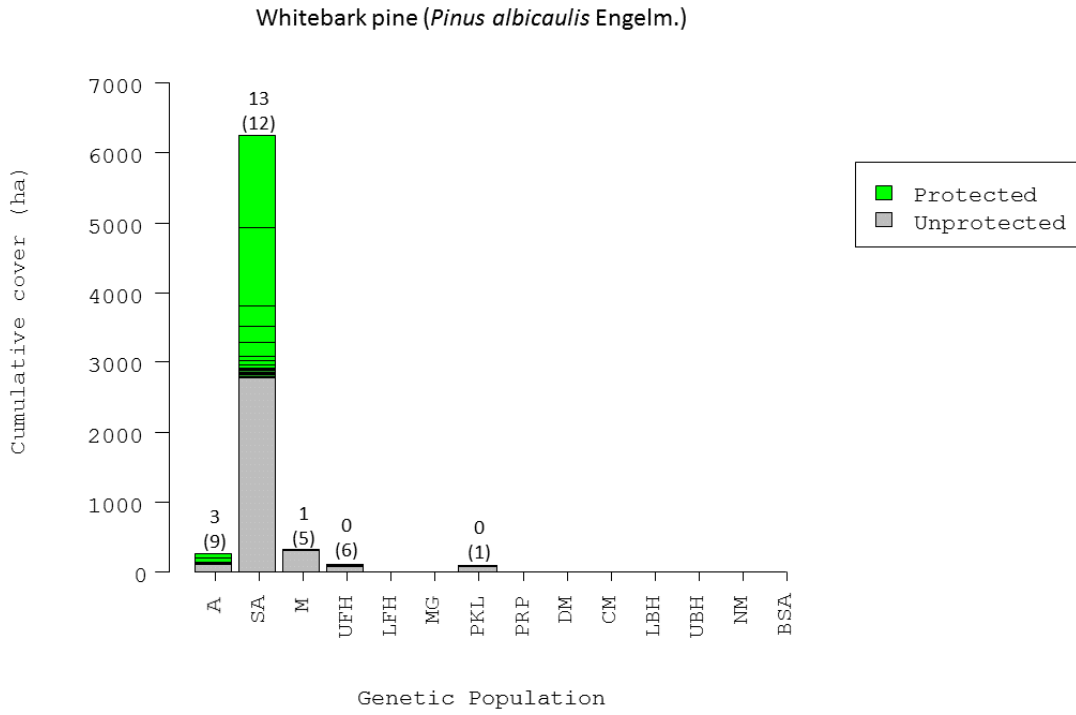


Figure 12. Cumulative cover and protection level of individual genetic populations of *Pinus albicaulis*.

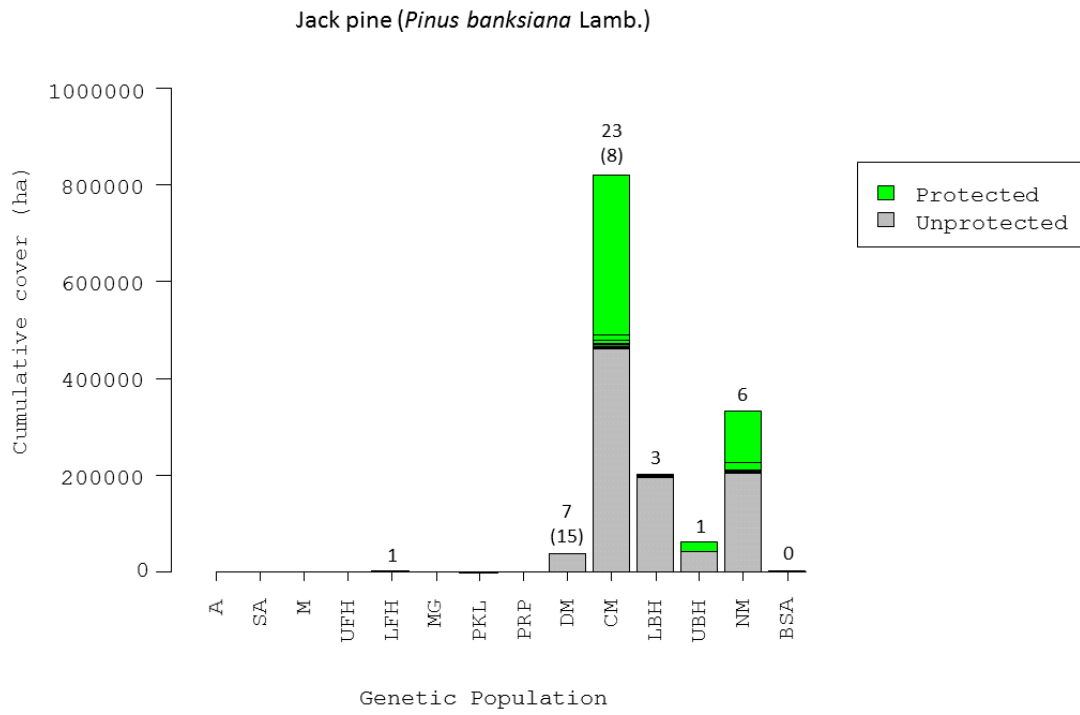


Figure 13. Cumulative cover and protection level of individual genetic populations of *Pinus banksiana*.

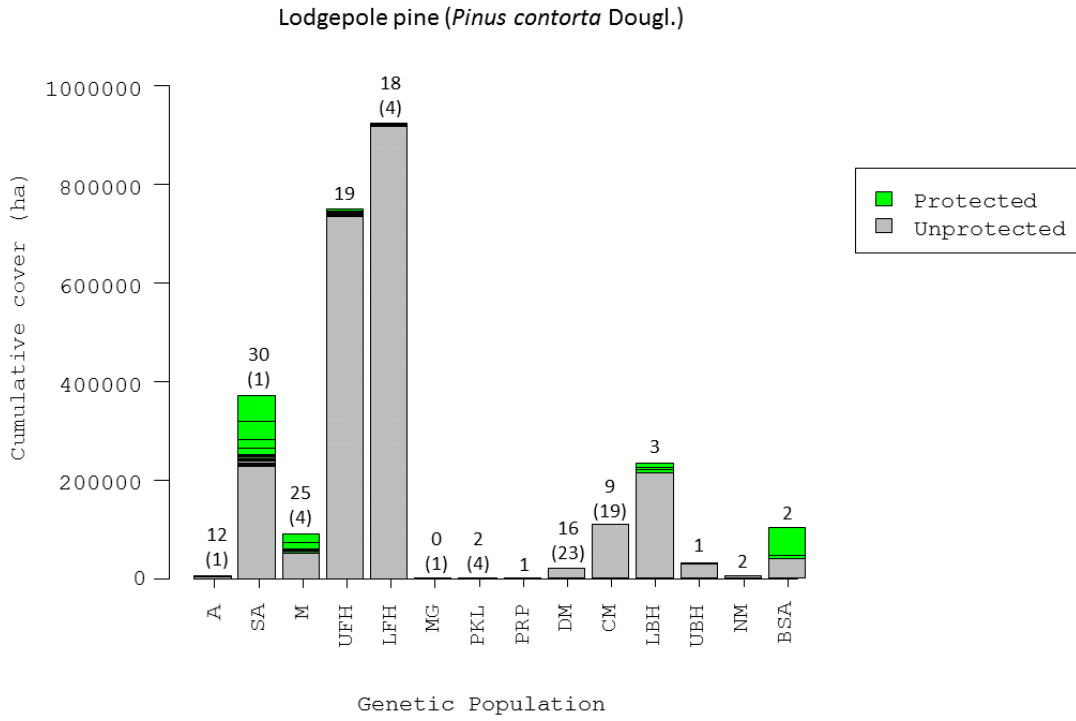


Figure 14. Cumulative cover and protection level of individual genetic populations of *Pinus contorta*.

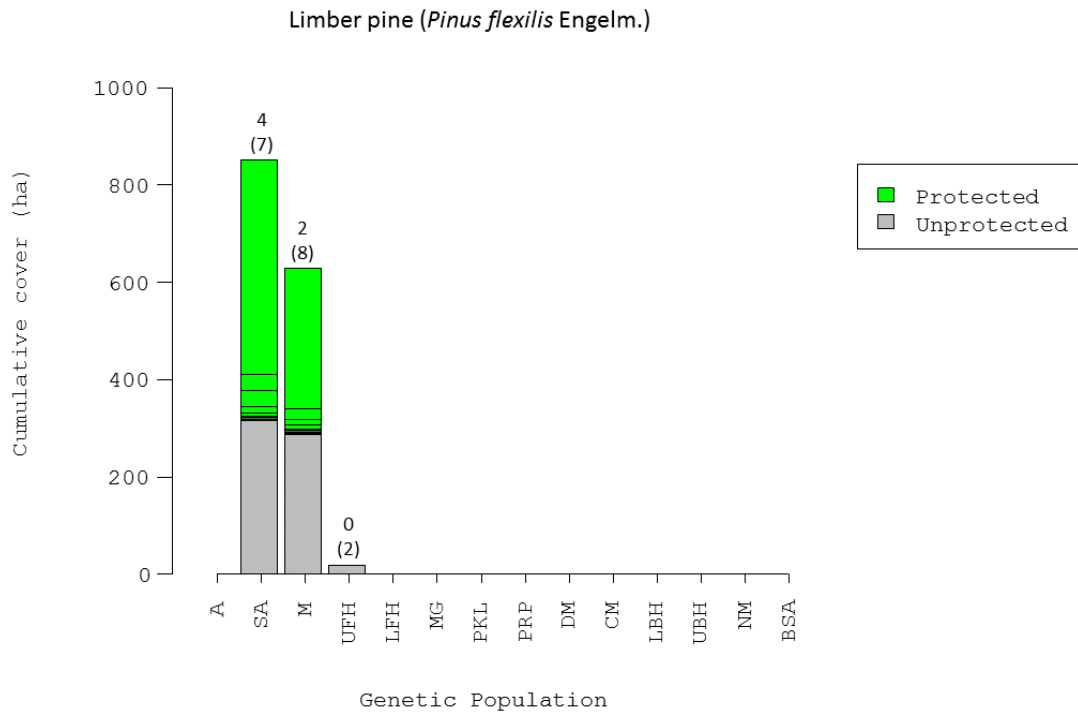


Figure 15. Cumulative cover and protection level of individual genetic populations of *Pinus flexilis*.

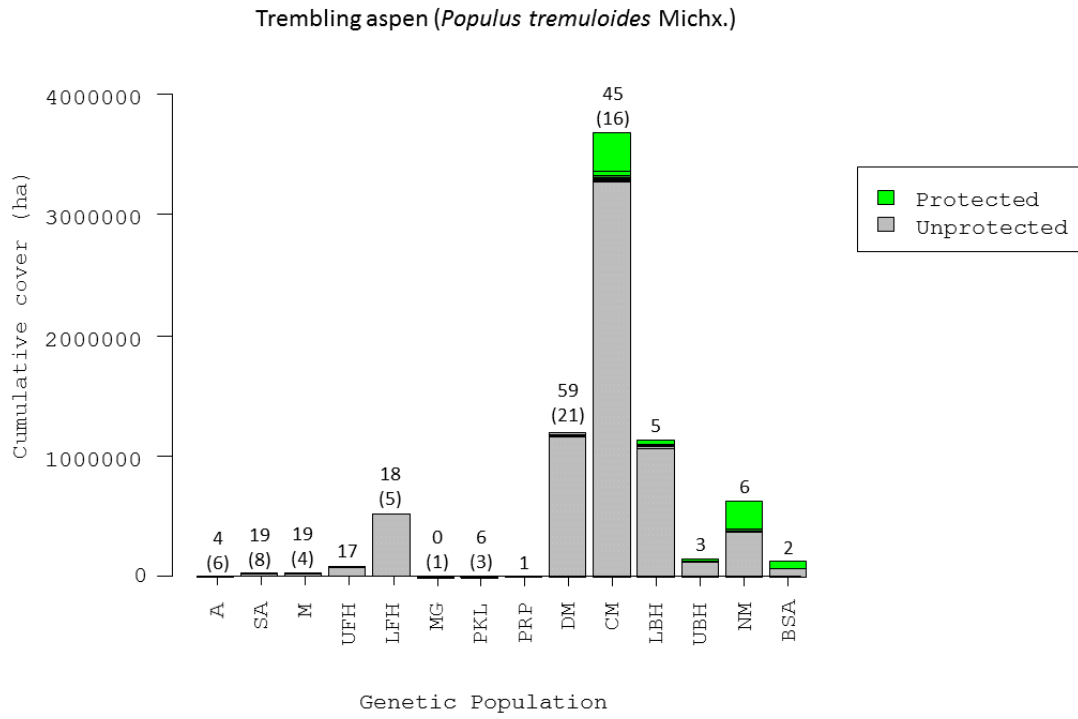


Figure 16. Cumulative cover and protection level of individual genetic populations of *Populus tremuloides*.

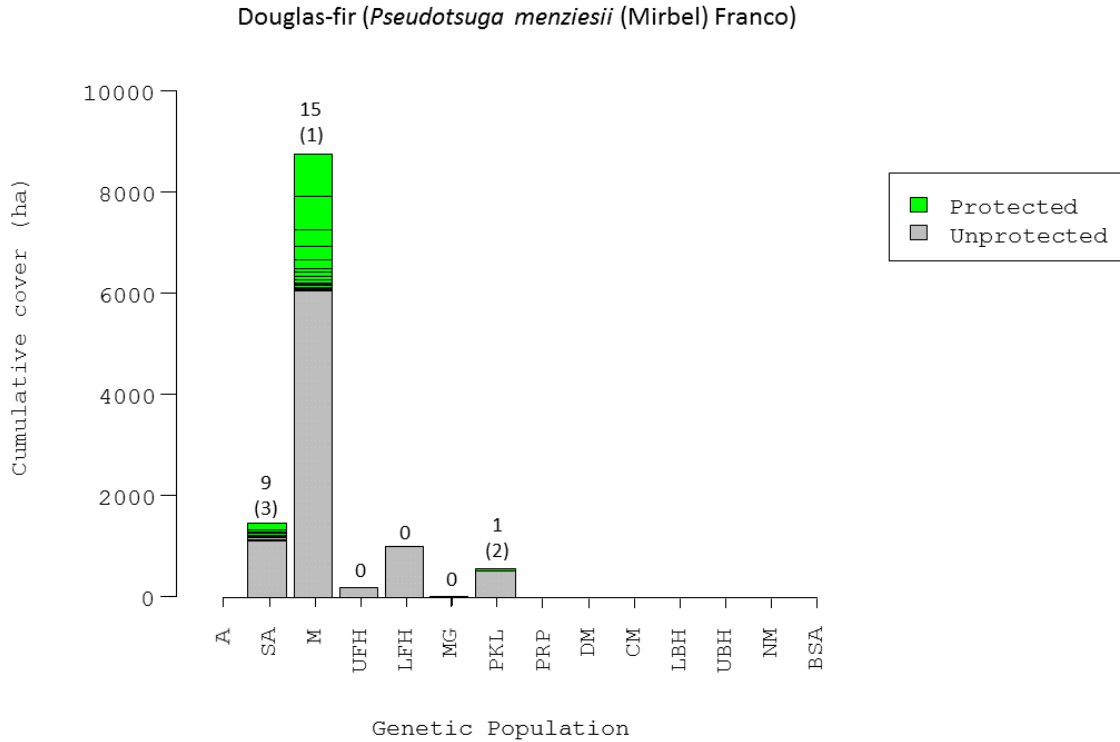


Figure 17. Cumulative cover and protection level of individual genetic populations of *Pseudotsuga menziesii*.

3.2 Determination of true conservation gaps

Individual species graphs show a total of 46 gap populations (Table 3). However, these gap populations had to be manually inspected to ensure that all are legitimate gap populations, and to determine which populations are the highest priority for future conservation. There are three main reasons populations may not actually be gaps or high priority. First, unprotected populations that contain a very small percentage of the overall species cumulative cover, usually less than 1%, may be considered low-priority fringe populations. Second, some populations that do not meet either the redundancy or representation conservation targets may nonetheless be highly protected in terms of percent cumulative cover. Finally, the species distribution models are based on statistical predictions, and some areas with low percentages of cumulative cover may be artifacts of the climate envelope model. Gap populations that meet any of these three criteria were removed from the list of conservation gaps, which resulted in a more accurate list of high priority gaps that will be used in future conservation planning (Table 4).

Table 3. All conservation gaps according to individual species graphs in Section 3.1. Numbers beneath species names indicate number of missing reserves, which are then totaled under Reserves needed. Dashes indicate that a population does not exist or is already adequately protected.

Natural Sub-region	Reserves needed	<i>Abies lasiocarpa</i>	<i>Betula papyrifera</i>	<i>Juniperus scopulorum</i>	<i>Larix laricina</i>	<i>Larix lyallii</i>	<i>Picea engelmannii</i>	<i>Picea glauca</i>	<i>Picea mariana</i>	<i>Pinus albicaulis</i>	<i>Pinus banksiana</i>	<i>Pinus contorta</i>	<i>Pinus flexilis</i>	<i>Populus tremuloides</i>	<i>Pseudotsuga menziesii</i>
PKL	21	1	3	-	3	-	2	3	3	3	-	1	-	-	2
PRP	13	-	2	-	3	-	-	2	2	-	-	2	-	2	-
UFH	11	-	2	-	-	-	-	-	-	3	-	-	3	-	3
MG	9	-	-	-	-	-	-	-	-	-	-	3	-	3	3
BSA	8	-	1	-	-	-	-	1	1	-	3	1	-	1	-
LFH	8	-	-	-	-	-	3	-	-	-	2	-	-	-	3
M	6	-	2	-	1	-	-	-	-	2	-	-	1	-	-
UBH	5	-	1	-	-	-	-	-	-	-	2	2	-	-	-
SA	5	-	-	3	-	2	-	-	-	-	-	-	-	-	-
A	4	-	-	-	-	3	-	-	1	-	-	-	-	-	-
DM	3	3	-	-	-	-	-	-	-	-	-	-	-	-	-
LBH	3	-	-	-	3	-	-	-	-	-	-	-	-	-	-
CM	3	3	-	-	-	-	-	-	-	-	-	-	-	-	-
NM	1	-	-	-	-	-	-	-	-	-	-	1	-	-	-

As a detailed example, the species graph for paper birch shows six gap populations: PKL, PRP, UFH, BSA, M, and UBH (Fig 5, Table 3). However, paper birch is a very widespread species with high provincial cumulative cover, and all of its large populations are well protected, while only the very small populations show as gaps. The first five populations are fringe populations that do not need to be addressed due to their very small size. Many of these fringe populations already have some degree of protection; for example, the M population is over 70% protected by land area, and the UBH population is already protected in two reserves of sufficient size. Thus the only true gap population is BSA, which requires one additional reserve (Table 4).

BSA has many additional gap populations; since there are only two reserves in this region, the redundancy criterion can never be met. However, these two reserves are among the largest in the

province, so some of these gap populations are highly protected by percent cumulative cover. White spruce, black spruce, lodgepole pine, and trembling aspen each have a gap population in BSA (Figs 10, 11, 14, 16). However, all four of these populations are at least 50% protected by the two existing reserves, so all four gaps were removed in Table 4.

Some species have very small distributions within Alberta, which means even small gap populations must be addressed. The cumulative cover of Rocky Mountain juniper is 307 hectares, and its SA population (73 ha) is a gap with zero reserves (Fig 6). While this population is much smaller in size than gap populations in other species that are considered low priority, e.g. the subalpine fir UBH population, the SA population contains 24% of Alberta's overall juniper distribution. Therefore this gap is still considered high priority. Subalpine larch likewise has a small provincial distribution with two populations (Fig 8). The SA population of subalpine larch does not meet the redundancy criterion; however, it is 36% protected and is therefore not a high priority. The very small A population of subalpine larch (30 ha) has zero reserves, which is a higher priority. Because this population is so small, just one further reserve could provide the required protection.

The two at-risk species, which also have very small distributions, will likely be high priority for future conservation in practice. Whitebark pine has two gap populations of possible concern, M and UFH (Fig 12), while its PKL population is a model artifact. In limber pine, the M population is also technically a gap population, since 8 of its 10 reserves are too small, although they protect more than 50% of the population (Fig 15). Limber pine's UFH population is very small, but represents 1.4% of the overall cumulative cover and could be considered a gap that needs to be addressed.

Jack pine has just one gap population, in UBH, which is protected by a single reserve that protects 27% of the population's cumulative cover (Fig 13). Additional reserves may be necessary. Another UBH gap population is lodgepole pine, which is also protected by a single reserve; however, in this case the reserve only protects a small percentage of the population (2%) (Fig 14). Additional reserves for the lodgepole pine population are therefore of higher priority than the jack pine gap. Lodgepole pine has two additional gap populations, PKL, which is a gap, and NM, which is nearly 80% protected within two reserves and may be considered already protected.

The remaining species have either high numbers of artifacts or fringe populations. Subalpine fir shows populations in DM and PKL, which are outside of its expected actual range and were removed from analysis, leaving only the CM population as a true gap. Douglas-fir likewise shows four gap populations, however all are likely model overpredictions (Fig 17). Finally, all gap populations listed for tamarack and Engelmann spruce are fringe populations, and neither of these species have true gaps (Fig 7 and Fig 9, respectively). In total, there are 33 populations in Table 3 that were removed because they are fringe populations, are already highly protected by percent cumulative cover, or are model artifacts. These removals mean there are 13 high priority conservation gaps remaining (Table 4).

Table 4. High priority conservation gaps that are not fringe populations, model artifacts, or otherwise already protected. Numbers beneath species indicate number of missing reserves, which are totaled under Reserves needed. Dashes indicate that a population does not exist or is already adequately protected. Reference number is used in Figure X in section X below.

Ref No	NSR	Reserves needed	<i>Abies lasiocarpa</i>	<i>Betula papyrifera</i>	<i>Juniperus scopulorum</i>	<i>Larix lyallii</i>	<i>Picea glauca</i>	<i>Pinus albicaulis</i>	<i>Pinus banksiana</i>	<i>Pinus contorta</i>	<i>Pinus flexilis</i>	<i>Populus tremulooides</i>
1	UFH	5	-	-	-	-	-	3	-	-	2	-
2	PKL	4	-	-	-	-	3	-	-	1	-	-
3	UBH	4	-	-	-	-	-	-	2	2	-	-
4	CM	3	3	-	-	-	-	-	-	-	-	-
5	M	3	-	-	-	-	-	2	-	-	1	-
6	SA	3	-	-	3	-	-	-	-	-	-	-
7	A	2	-	-	-	2	-	-	-	-	-	-
8	PRP	2	-	-	-	-	-	-	-	-	-	2
9	BSA	1	-	1	-	-	-	-	-	-	-	-

3.3 Comparative analysis among species

The four most abundant species by cumulative cover are trembling aspen, black spruce, white spruce, and lodgepole pine. The three least abundant species, each with less than 13,000 hectares of cumulative cover, are limber pine, subalpine larch, and Rocky Mountain juniper (Fig 18). In general, the more abundant a species is, the more genetic populations it has. For example, each

of the four most abundant species have 12 or 13 populations, with aspen and white spruce having the greatest number of populations. Meanwhile, the three least abundant species have just two or three populations each. Two notable exceptions are jack pine and Douglas-fir, which have fewer populations than other similarly-sized species.

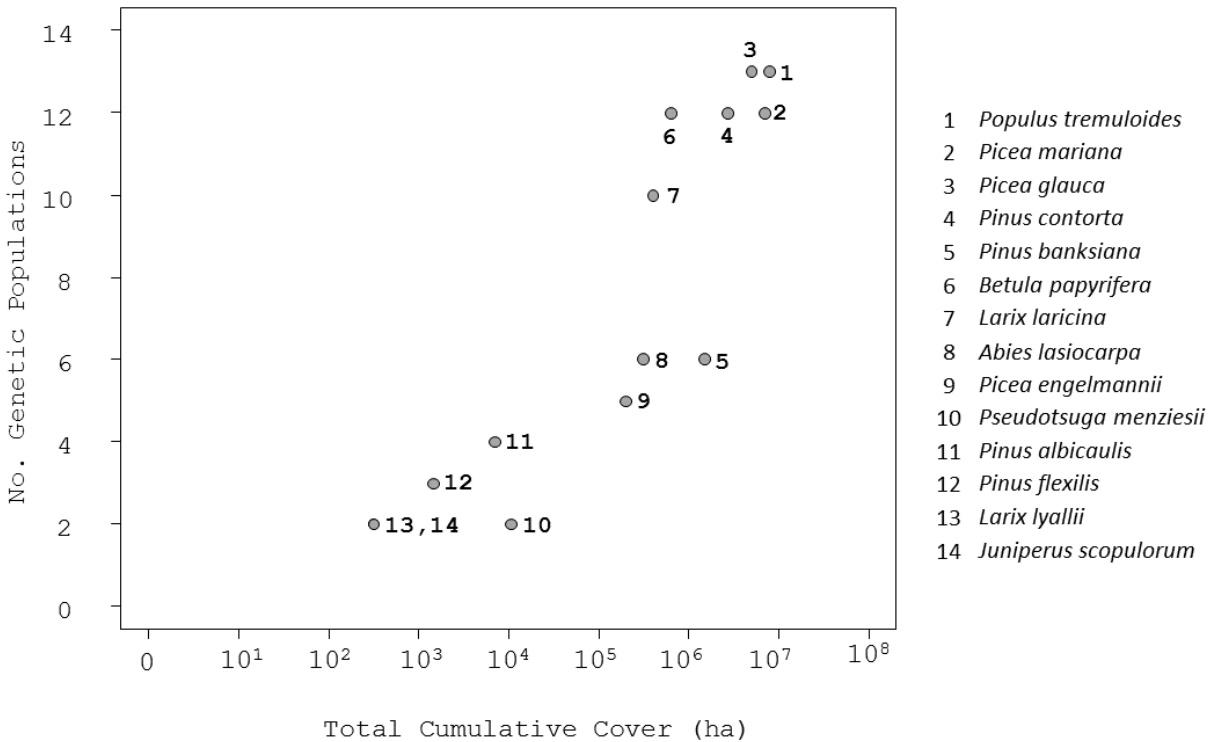


Figure 18. Comparing number of genetic populations with total cumulative cover (shown in logarithmic scale) per individual species. Genetic populations are defined as all individuals of a species living in a single NSR. Number of populations was calculated after determining true populations, including fringe populations (see Section 3.2). Species are listed in descending order of total cumulative cover.

After removal of false conservation gaps, I found that four species are fully protected: black spruce, tamarack, Engelmann spruce, and Douglas-fir. The remaining 10 species all have at least one population that requires further protection. The majority of species have at least 75% of their populations protected, but the four least-abundant species are each only 50-66% protected (Fig 19).

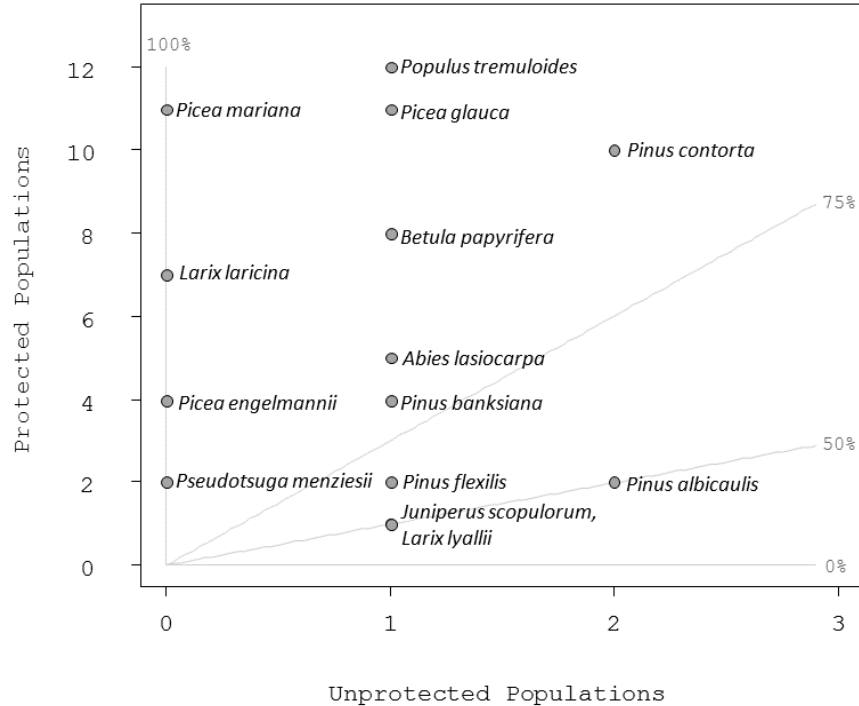


Figure 19. Proportion of protected and unprotected genetic populations within individual species. Genetic populations are defined as all individuals of a species living in a single NSR. Number of populations was calculated after determining true populations and does not include fringe populations (see Section 3.2).

3.4 Conservation gaps by NSR

The NSR with the highest species diversities are SA and M (n= 12 and 11 respectively, Fig 20). Mixedgrass (MG) does not have any sustained tree populations and is omitted from further analysis. There are large differences in percentage of land protected among the NSR (Fig 21). The two highest protected NSR by land area are A and SA (85% and 53% respectively). Seven NSR have less than 7% protection by land area, and many of these poorly protected NSR still have gaps; for example, UFH has 21 reserves protecting 3% of its land area, but two of its populations remain unprotected. However, a low percentage of protected land does not necessarily mean poor species protection. For example, Dry Mixedwood has 91 reserves that protect just 1.6% of its land area, and all of its genetic populations are adequately protected.

There are five NSR with fewer than ten reserves each: NM, LBH, BSA, UBH, and PRP. The first two NSR nonetheless protect all genetic populations, while the latter three have gap populations. Some of these NSR have reserves that are quite large, e.g. the aforementioned BSA which has two reserves protecting 49% of its land area. In total, there are four NSR that do not require any new reserves: DM, LFH, NM, and LBH.

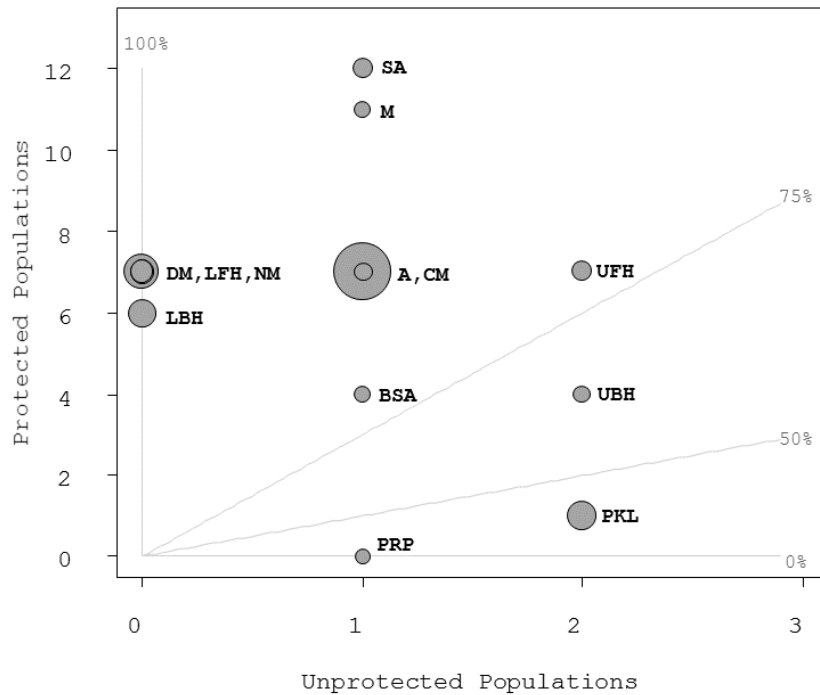


Figure 20. Number of protected and unprotected populations per NSR. Datapoint size is proportional to the total size of NSR in cumulative cover (ha). MG not shown, as it does not have any populations.

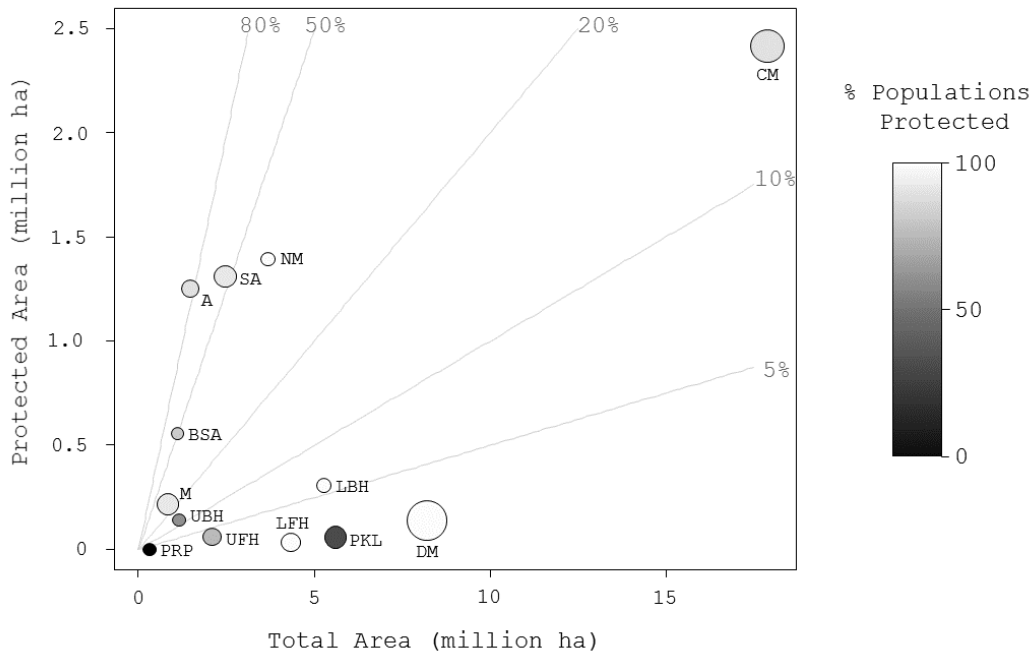


Figure 21. Total and protected area comparison for individual natural sub-regions. Datapoint size is proportional to the number of reserves in each NSR. Datapoint color indicates the percentage of populations protected. MG not shown.

3.5 Zonation results and comparison of filters

The initial Zonation assessment included all fourteen species, regardless of gap status, and included analysis at the coarse, fine, and superfine filter levels. This shows the distribution differences that arise when varying sizes of conservation features are chosen (Figs 22, 24, 26). Additional graphs created during each run of Zonation are the species performance curves (Figs 23, 25, 27), which show the amount of conservation feature distribution remaining after a given proportion of the landscape is removed. Typical outputs show only the values for worst-off and average species (e.g. Fig 25); however, individual values are calculated for each conservation feature used (Fig 23).

The coarse filter result, analyzing the 14 full-province distributions, shows large and densely clustered patches of high priority, with the UFH, LBH, CM and NM being the most favored NSR. Certain NSR have an overall low priority ranking in this analysis, including PKL and PRP. The fine filter result, which used genetic populations based on NSR proxy as conservation features, divided the highest priority rankings into a more evenly distributed result with smaller

patches. UFH and NM remained favored NSR, but other areas increased in rank, such as BSA and UBH. Some NSR that did not have any cells with high priority in the coarse filter result had higher priority results in the fine filter result, most notably PKL in the southeast. Finally, the superfine filter further decreased the clump size and increased the distribution of highly-ranked cells. In this result, high priority rankings are generally small hotspots that are relatively evenly distributed across the province. The greatest differences between fine and superfine filters can be seen in the center of the province, e.g. NM and CM, UFH and LFH. High priority cells show up in all 13 relevant NSR in the superfine filter result. Since a reserve network with fairly even distribution across the province is most likely to capture the greatest range of genetic diversity, I will use the superfine filter results to advise my choices for future additions to the reserve network.

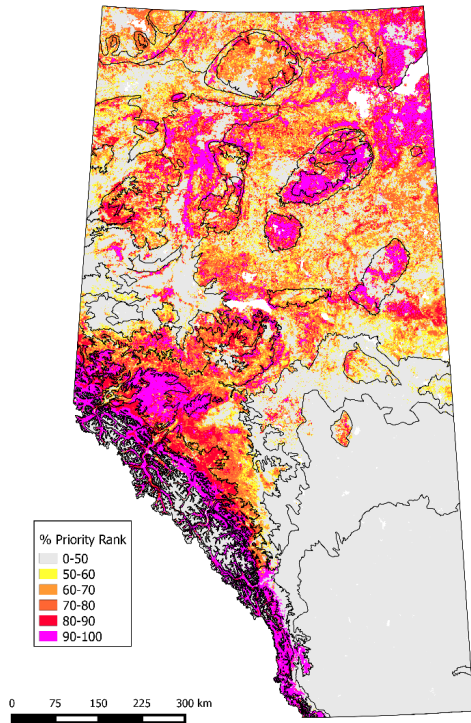


Figure 22. Graphical results of coarse filter Zonation analysis, with large water features masked from analysis (shown in white). Zonation results provide nested hierarchies of priority, with discrete colors outlined in 10% increments. Everything ranked below 50% priority is shown in grey, a section that also includes landscapes unforested by the species of concern.

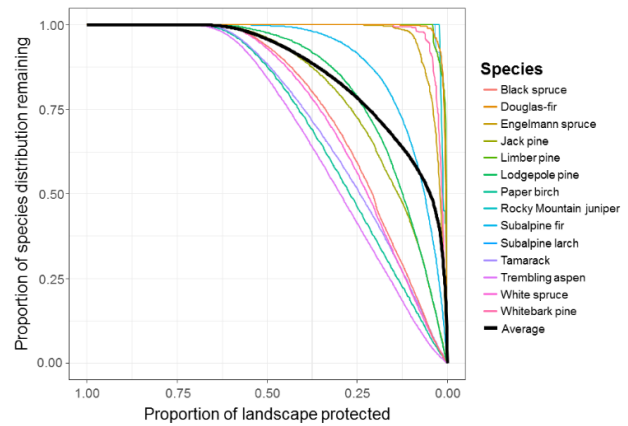


Figure 23. Zonation performance curves for coarse filter result, which shows the amount of land required to protect a given amount of a species' distribution. This particular graph shows each species individually, as well as the average for all species.

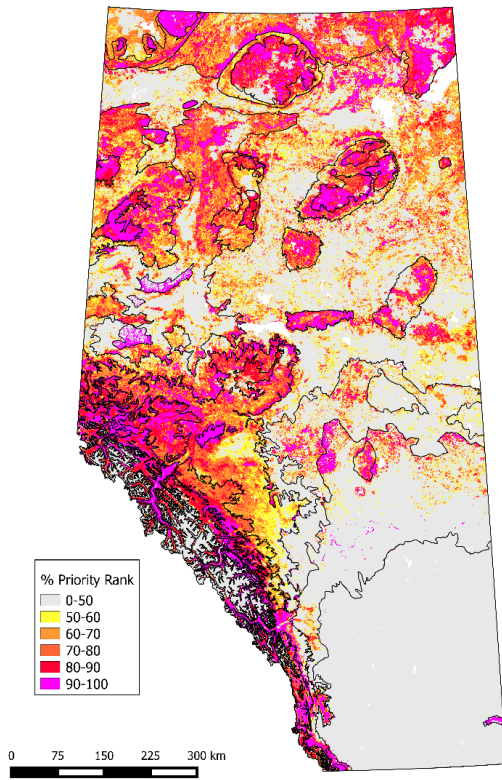


Figure 24. Graphical results of fine-filter

Zonation analysis.

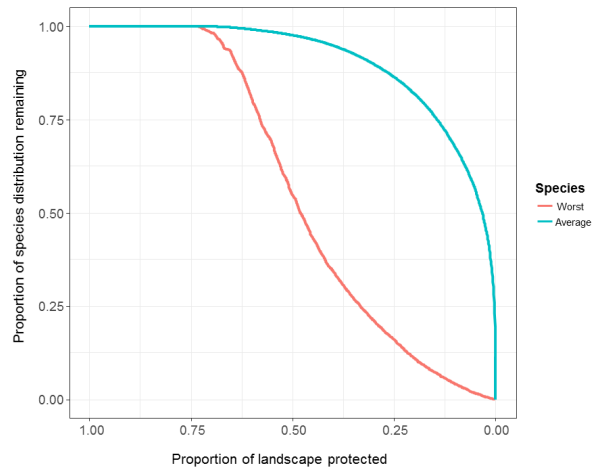


Figure 25. Zonation performance curve for fine-filter result, showing the amount of land required to protect a given amount of the average (blue) and worst-off (red) species.

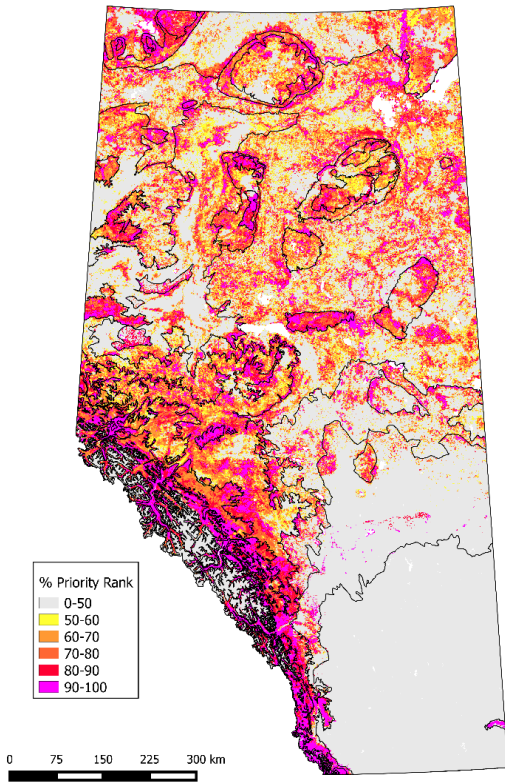


Figure 26. Graphical results of superfine filter Zonation analysis.

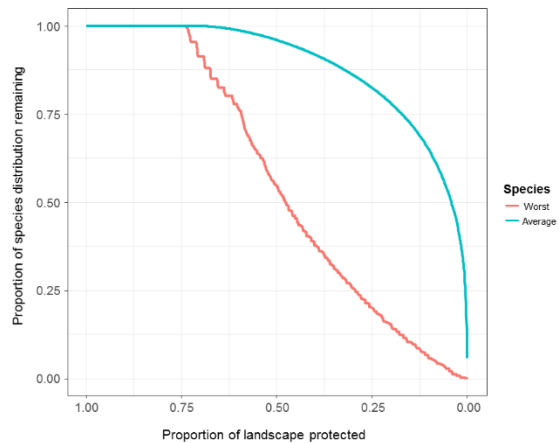


Figure 27. Zonation performance curve for superfine filter result, showing the amount of land required to protect a given amount of the average (blue) and worst-off (red) species.

3.6 Reserve design *de novo* versus existing reserve system

Comparison of Zonation results with existing reserve locations shows the effectiveness of the current reserve system in terms of genetic conservation (Fig 28). Some priority hotspot areas are adequately covered, e.g. Wood Buffalo National Park and the adjacent Caribou Mountains Wildland in the northeast collectively cover many high-priority areas across five NSR. However, in other areas, the existing reserve network and conservation priority areas are not aligned. The high concentration of reserves in the Rocky Mountain Natural Region means this area is well-protected, although Zonation results suggest that much of this region is not necessarily high priority for genetic conservation since much of the high altitude area is unforested. Many high-priority areas lie entirely outside the reserve network, including concentrated hotspots along the lower-altitude regions near the Rocky Mountains and the boreal forests in the northwestern quadrant of the province. These small and scattered hotspot gaps outside the reserve network are the areas where I will concentrate my suggestions for future reserve selection.

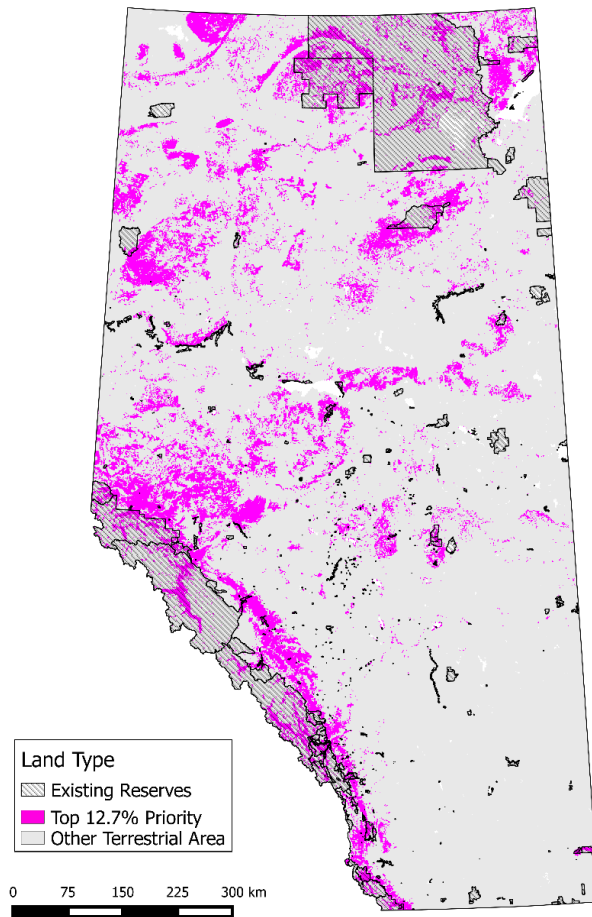


Figure 28. Comparison of existing reserve system, shown in black hashed polygons, superimposed over the top priority of fine-filter Zonation results, shown in magenta. Existing reserve system protects 12.7% of total land area, therefore the top 12.7% of Zonation results are shown. Remaining grey areas are either unforested or fall below the 12.7% priority threshold.

3.7 Options for filling gaps

Once I chose the superfine filter for future reserve design, I performed a second Zonation analysis wherein I used only the true gap populations and masked the existing IUCN-ranked reserves from analysis (Fig 29). Removing existing reserves reassigned the high-priority areas that are already protected (Fig 26) to unprotected areas outside the reserve system, which allows for more accurate selection of future reserve locations. This Zonation analysis was used to identify potential future reserve areas for filling the most urgent gap locations (Table 4).

The five natural sub-regions with only one gap species are most straightforward for future reserve selection, because any high priority cell in Zonation must contain that gap population. Examples include CM (reference number 4 in Table 4 and Fig 29) and SA (6). The four NSR with two gap populations provide more of a challenge, since the distributions of both gap populations must be considered. When both species are found in the same locations, filling gaps is simpler, because a single new reserve could protect both gap species and fewer total new reserves may be required, e.g. PKL and M. In situations where the two species distributions do not overlap, separate reserves must be chosen to protect each species individually. For example, the two at-risk species both have conservation gaps in UFH (1), but their ranges do not overlap according to the model predictions. Two suggestions for future reserve locations are indicated: the northerly selection shows a possible reserve location for whitebark pine, while the southerly selection is a possible reserve location for limber pine. A similar situation occurs in UBH (3), in which jack pine (3a) and lodgepole pine (3b) distributions are completely isolated. In this type of NSR with non-overlapping gap population distributions, a greater number of reserves will need to be created (n=5 for UFH and n=4 for UBH, Table 4).

Tree distribution and abundance also play a role in the creation of new reserves. BSA has just one gap population, paper birch, which is a widespread species that is found across nearly the entire sub-region. A new reserve may be chosen from nearly any location in this region; if the chosen area is not available for conservation use, another nearby area may be substituted. A contrasting example is PKL, in which tree distributions occur in very small patches. PKL has two gap populations, white spruce and lodgepole pine, and some of their distributions do overlap according to model predictions, including the high-priority cells shown in the PKL inset graph (Fig 29). However, these cells are much more fragmented and scattered across the landscape. In this area, if a chosen location is not available for conservation use, there may not be a suitable alternative.

There are also situations where only part of the gap species populations overlap, for example in M (5). The indicated new reserve location shows the only area where whitebark pine and limber pine distributions are predicted to overlap. Placing a reserve in this location would fill the one reserve requirement for limber pine, but a second reserve is required to fill the whitebark pine

gap. Correct placement of reserves could mean only two new reserves are needed instead of three (Table 4).

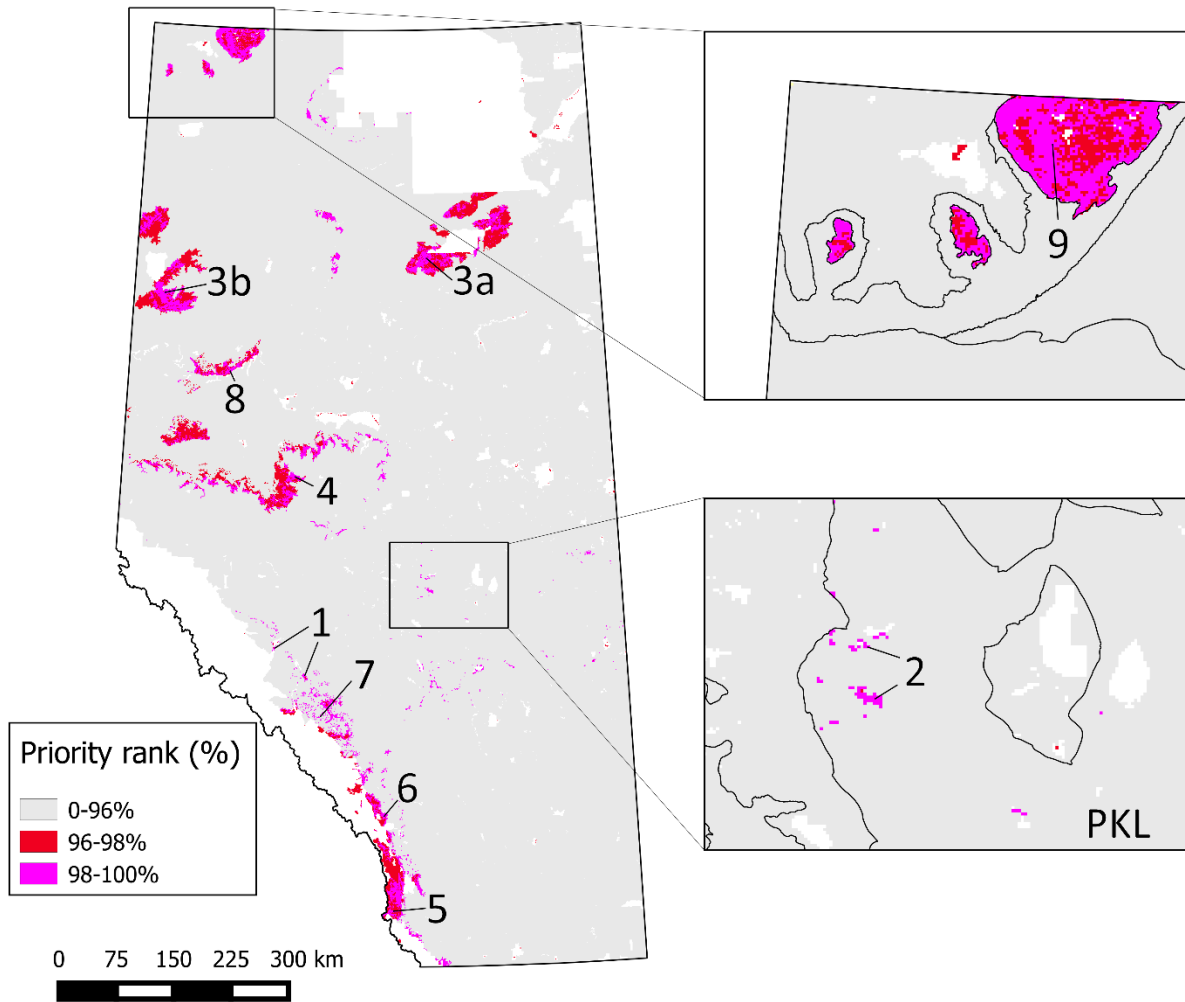


Figure 29. Potential options for new reserve selection using superfine Zonation analysis, which includes only gap populations excludes all IUCN-ranked reserves (shown in white). Numbers indicate specific NSR-based gaps that must be filled, in correlation with reference number in Table 4: UFH (1), PKL (2), UBH (3), CM (4), M (5), SA (6), A (7), PRP (8), BSA (9) . NSR lines not shown in overview map to increase clarity of Zonation result locations. Priority rank colors differ from other Zonation results due to low percentage of land covered by gap populations.

4 Discussion

4.1 Conservation gap analysis

This relationship between abundance and level of genetic diversity depends upon a species' distribution. The four most common species have the highest numbers of genetic populations due to their widespread distributions. These species are found in a vast range of environmental conditions, suggesting that these species have a broad array of available genetic resources that allowed many locally-adapted populations to form (e.g. Silen 1978). However, three of the four species have at least one gap population, and these gaps must be filled in order to retain high genetic richness and ecosystem resilience (Whitham *et al* 2006, Reusch *et al* 2005). In contrast, the four least-abundant species with small range size and few populations are whitebark pine, limber pine, subalpine larch, and Rocky Mountain juniper. These species have very restricted geographical ranges, which may be a sign of already reduced genetic variation. All conservation gaps for these species must be addressed, no matter how small, because species with both a small range and low regional abundance are likely at the highest risk for extinction (Johnson 1998). There is some evidence that most species become extinct before reduction in genetic resources can have a negative impact (Lande 1998); however, further studies have found that genetic diversity is typically lower in threatened species than closely related non-threatened species, indicating that the latter have lower evolutionary potential and reproductive fitness (e.g. Spielman *et al* 2004).

An interesting case regarding abundance is that of jack pine, which is the fifth most abundant species but has just 6 genetic populations, as compared to the 12 or 13 populations found within the four more abundant species. According to my analysis jack pine has the same number of genetic populations as subalpine fir, which is notable since jack pine has 1.47 million ha of cumulative cover while subalpine fir has 314,000 ha. Thus, while subalpine fir could be considered only a semi-abundant species and jack pine abundant, my results suggest that these species may have comparable levels of genetic diversity, meaning they may be at equal risk of extinction. Range size and abundance may play an equally important role in the amount of intraspecific genetic diversity and extinction risk.

Globally, protected areas are commonly located in marginal habitats which have the least value for commercial land uses (e.g. production or resource extraction), such as high alpine areas and those with low-production soils (Aycrigg *et al* 2013). Canada's first four national parks were placed in the high-altitude regions of the Rocky Mountains, including in Alberta, and today its Rocky Mountain NSR are highly protected (Alberta Parks 2017). However, Zonation results indicate that the high-altitude sections of these national parks may not be valuable reservoirs of genetic variation (Fig 26). Protecting populations on marginal sites means that their gene pool may not include all the alleles characteristic of populations that live on the best sites, so it is necessary to ensure that sample populations on land of high site quality are also protected (Ledig 1986). In contrast, the mild climate and fertile soils of the Grassland and Parkland natural regions have led to intensive land use and low percentages of protected land, which is detrimental to the ecosystems that were once abundant in these regions (Lemieux *et al* 2011). In areas such as these it may be more difficult to locate available land that contains target native tree species, but from a genetic variation standpoint it is important to ensure that these areas are protected.

4.2 Future reserve size

Conservation planning often aims towards creating large and widely-spaced reserves, to accommodate endangered faunal species that have large spatial requirements (Franklin 1993). However, trees have different spatial requirements due to their sessile nature and typically short-range reproduction and dispersal mechanisms, which include wind-dispersed pollen and seeds that fall close to the parent plant (Howe and Smallwood 1982). Populations are also highly susceptible to disturbance, and post-disturbance ecosystems depend upon recolonization from other nearby populations. Isolated tree populations generally have lower survival rates than partially connected populations, and if there is no adjacent source of immigrants, species collapse can be rapid (Fahrig and Merriam 1985, Wilcox and Murphy 1985). Thus, trees may be better protected by a network of smaller and more closely-spaced reserves than by larger, more isolated reserves. Smaller protected areas are also useful for fulfilling representation gaps in highly developed areas, where opportunities to establish large protected areas are limited, e.g. the intensively-farmed land in the Parkland region (Lemieux *et al* 2011).

One general argument against the use of small protected areas is that they protect small populations, which are considered to be more vulnerable to extinction due to environmental stochasticity or detrimental effects from increased genetic drift (Shaffer 1981, Frankham 1996). The effects of habitat fragmentation are well documented, including possible disruption of ecological and evolutionary processes, reduction in biodiversity, and exposure to edge effects (Hamrick 2004, Wilcox *et al* 1985, Murcia 1995). However, temperate tree species are thought to be fairly resilient to habitat fragmentation due to their broad distributions and dispersal abilities that allow for quick recolonization following disturbance (Wilcove *et al* 1986, Brown and Kodric-Brown, 1977). Trees are not as vulnerable to edge effects as other plants, and are capable of persisting in very small areas such as residential lawns and city parks as long as the environmental conditions are suitable (Wilcove *et al* 1986). Therefore the negative effects of protecting small populations may be countered by the benefits of having increased numbers of nearby populations.

A final important note is that the biodiversity of smaller forest taxa may still be negatively impacted by the increased edge effects of the small reserve strategy, and larger reserves may be the most beneficial solution for the health of forest ecosystems as a whole. Some existing reserves are quite large, e.g. Wood Buffalo National Park, which at 3.6 million hectares is larger than half of all individual natural sub-regions. Some large parks were created before the 1920s (Jasper, Banff, Wood Buffalo National Parks); however, many others were created in the 1990s and 2000s, with the most recent being established in early 2017 (Castle Provincial Park; 25,500 ha)(Alberta Parks 2017). While creation of large reserves may be more difficult and costly, it is still a possibility that may need to be considered in natural sub-regions that have low overall protection such as PKL.

4.3 Potential new reserve locations

The NSR gap analysis shows that there are many options for filling Alberta's conservation gaps and completing the reserve network, and that many factors should be considered when creating new reserves (Figs 21, 29). A small number of large reserves can be effective as long as they are appropriately placed; for example, NM has just six large reserves that protect all seven populations. If creation of large reserves is not feasible, for example in locations with sparse tree distributions or reduced availability of land for conservation use, it may be just as effective to

use numerous small reserves. DM has 91 reserves that protect 2% of its land area and all of its genetic populations. However, when using small reserves, accurate placement is critical. The detrimental effects of improper reserve placement can be seen in PKL, which has 33 reserves protecting 1% of its land area but still has two gap populations.

Spacing is also a key component for genetic conservation in trees. Encompassing a broad range of physical characteristics within a reserve network helps increase the resilience of the entire system, and this is most likely to succeed if new reserves are widely and evenly distributed across the landscape (Lemieux *et al* 2011). Future reserve selection should be based on gap population distributions, but they should also be carefully placed at appropriate distances from each other to maintain gene flow and recolonization capabilities between adjacent populations both within and among NSR. This is where the superfine filter analysis in Zonation is relevant. Although the seed zones used in the superfine filter are too fine to be used as a genetic proxy (Liepe *et al* 2016), seed zones divide the landscape into many evenly-distributed parcels.

The most urgent conservation gaps are the 13 species listed in Table 4, which should be addressed first. The highest priority should be given to “core” areas wherein a population is most abundant (ASRD 2009). It is also important to conserve populations on the edges of the species or population range (Ledig 1986, ASRD 2009). Once the 13 high priority gaps have been addressed, there are a number of lower-priority fringe populations that could also be considered for further protection, as shown in Results Section 3.2. In widespread populations that require more than one reserve, it may also be prudent to protect edge populations in addition to high abundance areas. The paper birch BSA population is one such area where this approach could work.

The potential reserve locations shown in Figure 30 are just a few of the myriad possibilities for future reserve placement. An additional option could be to use the superfine Zonation analysis that includes all species regardless of gap population status (Fig 26), which may improve representation for non-gap genetic populations. Increased representation is the ideal situation even if the minimum conservation criteria have already been met. One common cost-effective strategy for creation of new reserves is to place high priority on protecting biodiversity hotspots, or regions with high overall diversity (Myers *et al* 2000). This approach is useful for filling

multiple conservation gaps at once, while also potentially increasing representation for other already adequately protected species. However, the hotspot method may ignore gap species that exist in species-poor areas, which is the case in almost half of the NSR with gap populations (Scott *et al* 1993). Therefore I recommended employing the biodiversity hotspot method where possible and appropriate, but it is also critical to ensure that gap species in areas with low species richness are not overlooked (Fig 29).

A specific suggestion for future conservation could be to utilize the 217 protected areas that are not IUCN-classified, i.e. by changing the laws and land management practices. Assigning legal protection against future land use change would increase the likelihood of longer-term population protection. Another possibility to increase representation is to encourage management of multiple-use land, in which the land is permanently protected and has emphasis on maintaining biodiversity, but also allows for resource extraction such as logging and mining (Aycrigg *et al* 2013). Gene conservation can also be incorporated into timber harvesting practices, for example by regeneration with seed from *in situ* populations or through tree improvement programs (Ledig 1988). Finally, it is possible to use existing reserves as a focal point around which additional reserves may be placed, or even to expand the existing reserves themselves (Margules and Pressey 2000).

4.4 Caveats of analysis

Analyzing populations on a case-by-case shows that while the minimum conservation targets are adequate for most populations, other populations may require different criteria. A clear example is Boreal Subarctic, where the two extremely large reserves adequately protect four of its five populations even though the redundancy criterion cannot be met. However, other population classifications were less clear, especially among very small or very large populations. Jack pine's UBH population is considered a gap even though it constitutes a small percentage of the overall species distribution (4%) and is 27% protected by one reserve. A potential solution is to use scaled requirements, i.e. basing the minimum conservation criteria on the size of a population. For example, the ASRD (2009) recommends using two reserves in seed zones that are smaller than 0.5 million ha, which could be adapted for use in this project.

Another analysis caveat is that species distribution models are predictions, and largely have not been ground-truthed. Therefore, some of the gap species that were removed from the list of high priority due to being presumed model artifacts or fringe populations may actually be legitimate gap populations (Table 3, Table 4). The Mixedgrass NSR is a relevant example, since it was the fourth highest NSR gap in Table 3 but was entirely absent from Table 4 after all of its populations were labeled as fringe populations or model artifacts. The same may be true at the species level, e.g. Douglas-fir. This exclusion is important when considering the potential value of preserving samples from the edges of a species' range, since unusual habitats may contain individuals adapted to unique or extreme environmental conditions (Ledig 1986).

Populations in the parkland NSR (PKL and PRP) typically represent a very small percentage of the overall cumulative cover, especially for widespread species such as paper birch, and were considered fringe populations that were omitted from the list of high priority gaps. However, the warm and dry Parkland regions may represent a unique genotype among these species that should be conserved for future use. This is especially critical for the small pockets of aspen-dominated boreal forests found in the Canadian prairies, including in Alberta's Parkland region, which have declined in recent years due to land use change and environmental change including drought (Young *et al* 2006, Hogg *et al* 2008). The Parkland area may benefit from ground-truthing or further finer-scale analysis, especially since this NSR is among the province's least-protected in terms of percent land area.

A final note is that Alberta does not exist in a biological vacuum, but is rather a landlocked province surrounded on all sides by dynamic tree populations, including many of the same species. These populations have the potential to migrate into Alberta or to share genetic material. It is also possible that populations existing on the edges of the province may be listed as rare or gap populations, when in fact that genetic population receives adequate protection in a different state or province (e.g. Russell 2014). These satellite populations should be kept in mind while prioritizing the most urgent conservation gaps.

4.5 Further notes: climate change

This project does not address the effect that anthropogenic climate change will have on Alberta's native tree species, but it is another important consideration when choosing new reserve

locations. In Canada, populations of black spruce, white spruce, aspen, and tamarack are among the species that will be most heavily affected by climate variation, as well as jack pine in Alberta (Gray and Hamann 2013, Russel 2014). While high genetic diversity may not always be critical for maintaining ecosystem processes under relatively stable environmental conditions, the ability to adapt becomes much more important when populations face pressure from rapid climate change (Loreau *et al* 2001). Changing climates also cause range shifts, meaning species may migrate out of protected areas, which reduces the effectiveness of fixed existing reserves (Araújo *et al* 2004). Additionally, creating a new reserve to fill a conservation gap will not be effective if the local environmental conditions will soon shift to become an inhospitable habitat for the targeted population. This creates an additional step for conservation planning, since it is more cost-effective and timely to account for the possibility of shifting ranges before creating new protected areas (Hannah 2007).

Climate change prediction models are one method for testing the effectiveness of new reserves before they are created. In a brief example, I apply the VelocityWNA climate data from Hamann *et al* (2015) to my Zonation results. I use mean annual temperature result for 2050s, which is based on the A1B emissions scenario. Climate change velocity determines how fast organisms must migrate to keep pace with a changing climate. Two types of climate change velocity are forward velocity, or the minimum distance an organism must migrate to maintain similar climactic conditions, and reverse velocity, which identifies the distance from which appropriate genetic variants may be sourced to allow a population to survive under future conditions. High forward velocity is typical of flat areas, especially those at high elevation, and indicates that trees have no suitable climate refuges nearby (Loarie *et al* 2009). High reverse velocity occurs in geographically isolated regions, such as valley floors between mountains, where organisms would have to migrate long distances to reach analogous habitat conditions (Hamann *et al* 2015). Therefore both types of velocity have value for conservation planning: forward helps determine suitable reserve locations under future ecosystem change, and reverse may be useful in assisted migration for rare species (Richardson *et al* 2009).

An example from this analysis is the transitional mid- to high-altitude region of the Foothills and Rocky Mountain natural regions (Fig 30). The eastern portion of this region lies in the southern foothills, which has gradual elevational changes between the flat grasslands and the mountains,

while the Rocky Mountain region to the west is characterized by steep elevational gradients that are associated with large temperature change gradients (Loarie *et al* 2009). Superfine Zonation results overlaid with both forward and reverse velocity predictions may help conservation planners choose locations that will remain effective conservation areas under climate change, i.e. which locations may serve as climate refugia and provide trees with relatively stable conditions. The populations currently located in the foothills region have greater forward velocities and face greater difficulty adapting to new conditions than those in the mountainous region, which have smaller forward velocities and little difficulty adapting to new climate conditions (Hamann *et al* 2015).

Placing new reserves at higher elevations, possibly even above the current distributions of target species, would be a potential solution that would allow for future conservation as populations migrate upslope. However, mountain or hill peaks provide the same challenges as flat regions, namely that once populations reach the tops of mountain peaks, they may no longer have anywhere else to migrate, e.g. the darkest regions in the forward velocity scenario (Fig 30 A, Hamann *et al* 2015). If trees no longer have any nearby suitable climate matches, *in situ* reserves become an ineffective conservation method, and seed collection for *ex situ* conservation is the more worthwhile effort (Ledig 1988).

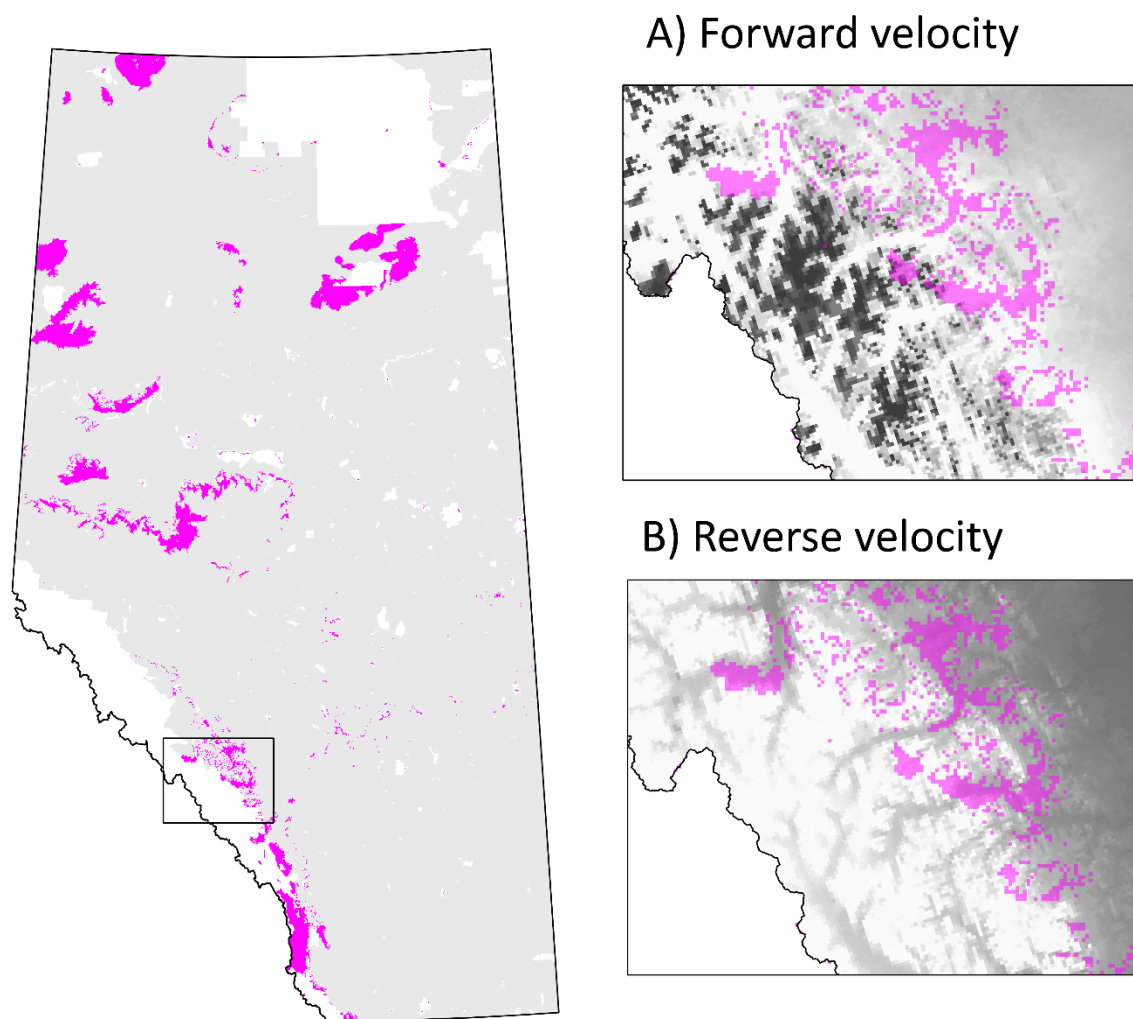


Figure 30. Superfine filter Zonation results using gap populations only (left), combined with multivariate forward (A) and reverse (B) velocity calculations, from current to projected climate change conditions and vice versa (from Hamann *et al* 2015). Forward climate change velocity indicates how far a population must migrate to keep pace with climate change, with darker areas requiring greater migration distance. Reverse climate change velocity indicates the difficulty for immigrating plant populations to colonize and adapt to new climate conditions *in situ*, with darker areas indicating greater difficulty.

Climate change may actually cause some species currently not found in Canada to migrate north, bringing an influx of new genetic variants or tree species from the continental United States that could increase Alberta's biodiversity (Malcolm *et al* 2004, McKenney *et al* 2007). Climate change will likely change the representation within the existing reserve network, and is an

important consideration when planning a systematic reserve system. However, starting with high representation of Alberta's native tree species will help provide a genetic foundation for climate change adaptation. Physiological characteristics of the land such as geology and surficial substrates will remain largely stable despite climate change, so basing representation upon ecological delineations will remain a cornerstone method for the design of protected area networks (Lemieux *et al* 2011).

5 Conclusion

Comprehensively conserving the genetic resources of Alberta's native tree species may provide species with inherent resilience to anthropogenic and environmental stochasticity, thereby reducing their extinction risk. In this study, I focus on protecting the genetic diversity found within native tree species of Alberta. I place equal importance on both common and rare species, because common species promote ecosystem functioning while rare species may promote species richness. Both common and rare species are susceptible to extinction, especially those with already low genetic diversity. Protecting the resilience of trees may also help protect the forest ecosystem as a whole, including the smaller faunal and vegetative species biodiversity found within.

This project provides a baseline understanding of the conservation status of Alberta's native tree species and their genetic diversity, by conducting a conservation gap analysis to identify the genetic populations that are inadequately protected by Alberta's current reserve network. Out of 97 genetic populations, there are 13 populations that are high priority for future conservation. Analysis using the conservation planning software Zonation provides a possible starting point for filling the conservation gaps in the provincial reserve network, by identifying the highest priority locations for future reserves based on tree distributions and gap populations. Many factors must be considered when filling conservation gaps, including population size and range distribution of target species, appropriate spacing between reserves, ideal size of reserves based on tree life histories, and climate change.

The forces driving biodiversity loss are continuous, so it is imperative to design and implement expansions to the reserve system with as much haste as possible (Pressey and Cowling 2001). By quickly identifying and filling conservation gaps for Alberta's genetic resources, we may be able to improve both the individual species' and overall forest ecosystem's inherent resilience against ecosystem change.

6 Referenced Literature

- Aitken, S.N. 2000. Conserving adaptive variation in forest ecosystems. *Journal of Sustainable Forestry*, **10**: 1–12.
- Aitken, S. N., Yeaman, S., Holliday, J. A., Wang, T., and Curtis-McLane, S. 2008. Adaptation, migration or extirpation: climate change outcomes for tree populations. *Evolutionary Applications*, **1**(1): 95-111.
- Alberta Forest Genetic Resources Council. 2015. Alberta Forest Genetic Resources Council 2014–2015 Annual Report. Alberta Forest Genetic Resources Council, Alberta, Canada.
- Alberta Parks. 2017. <https://www.albertaparks.ca/albertaparksca/library/downloadable-data-sets/>
- Alberta Whitebark and Limber Pine Recovery Team. 2014. Alberta Whitebark Pine Recovery Plan 2013-2018. Alberta Environment and Sustainable Resource Development, Alberta Species at Risk Recovery Plan No. 34. Edmonton, AB.
- Araújo, 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.
- ASRD (Alberta Sustainable Resource Development). 2009. Gene Conservation Plan for Native Trees of Alberta. Working Group on Native Tree Gene Conservation in Alberta (Alberta Sustainable Resource Development and Alberta Tourism, Parks and Recreation). Pub No. T/141.
- Aycrigg, J.L., Davidson, A., Svancara, L.K., Gergely, K.J., McKerrow, A., and Scott, J.M. 2013. Representation of ecological systems within the protected areas network of the continental United States. *PLoS One*, **8**(1): e54689.

- Bradshaw, A. D. 1965. Evolutionary significance of phenotypic plasticity in plants. In *Advances in genetics*: 115-155. Academic Press.
- Brooks, T.M., Bakarr, M.I., Boucher, T., Da Fonseca, G.A., Hilton-Taylor, C., Hoekstra, J.M., Moritz, T., Olivieri, S., Parrish, J., Pressey, R.L., and Rodrigues, A.S. 2004. Coverage provided by the global protected-area system: is it enough?. *AIBS Bulletin*, **54**(12): 1081-1091.
- Brown, J. H., and Kodric-Brown, A. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology*, **58**(2): 445-449.
- Burley, F. W. 1988. Monitoring biological diversity for setting priorities in conservation. In *Biodiversity*. National Academy Press, Washington, DC, 227-230.
- Campbell, R. K. 1979. Genecology of douglas-fir in a watershed in the Oregon cascades. *Ecology*, **60**(5): 1036-1050.
- Carwardine, J., Klein, C.J., Wilson, K.A., Pressey, R.L., and H.P. Possingham. 2009. Hitting the target and missing the point: target-based conservation planning in context. *Conservation Letters*, **2**(1): 4-11.
- Chape, S., Harrison, J., Spalding, M., and Lysenko, I. 2005. Measuring the extent and effectiveness of protected areas as an indicator for meeting global biodiversity targets. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, **360**(1454): 443-455.
- Chhin, S., Hogg, E. H., Lieffers, V. J., and Huang, S. 2008. Influences of climate on the radial growth of lodgepole pine in Alberta. *Botany*, **86**(2): 167-178.
- Chourmouzis, C., A. D. Yanchuk, A. Hamann, P. Smets, and S. N. Aitken. 2009. *Forest tree genetic conservation status report 1: In situ conservation status of all indigenous British Columbia species*. B.C. Min. For. Range, Victoria, B.C. Tech. Rep. 53.
- Cornelius, D. R., and Johnston, C. O. 1941. Differences in plant type and reaction to rust among several collections of *Panicum virgatum* L. *Journal of the American Society of Agronomy*.
- Dayton, P.K. 1972. Toward an understanding of community resilience and the potential effects of enrichments to the benthos at McMurdo Sound, Antarctica. In *Proceedings of the colloquium on conservation problems in Antarctica*: 81-96. Allen Press, Lawrence, KS, USA.
- Downing, D.J. and Pettapiece, W.W. 2006. Natural Regions and Subregions of Alberta. Publ.
- Dudley, N. (Ed.). 2008. Guidelines for applying protected area management categories. IUCN.

- Ebenman, B. and Jonsson, T. 2005. Using community viability analysis to identify fragile systems and keystone species. *Trends in Ecology and Evolution*, **20**(10): 568-575.
- Ellison, A.M., Bank, M.S., Clinton, B.D., Colburn, E.A., Elliott, K., Ford, C.R., Foster, D.R., Kloeppel, B.D., Knoepp, J.D., Lovett, G.M. and Mohan, J. 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology and the Environment*, **3**(9): 479-486.
- Fahrig, L., and Merriam, G. 1985. Habitat patch connectivity and population survival. *Ecology*, **66**(6): 1762-1768.
- FAO. 2010. Global Forest Resources Assessment 2010.
- Forest Management Branch of Alberta Sustainable Resource Development. 2005. Seed Zones of Alberta. <http://aep.alberta.ca/forms-maps-services/maps/resource-data-product-catalogue/biophysical.aspx>. Accessed August 2017.
- Frankel, O.H. 1970. Genetic conservation in perspective. In *Genetic resources in plants - their exploration and conservation*: 469-489.
- Frankham, R. 1996. Relationship of genetic variation to population size in wildlife. *Conservation Biology*, **10**(6): 1500-1508.
- Franklin, J.F. 1993. Preserving biodiversity: species, ecosystems, or landscapes?. *Ecological applications*, **3**(2): 202-205.
- Gaston, K.J., Blackburn, T.M., Greenwood, J.J., Gregory, R.D., Quinn, R.M. and Lawton, J.H. 2000. Abundance–occupancy relationships. *Journal of Applied Ecology*, **37**(s1): 39-59.
- Gaston, K.J. and Fuller, R.A. 2008. Commonness, population depletion and conservation biology. *Trends in Ecology and Evolution*, **23**(1): 14-19.
- Government of Alberta. 2017a. Sustainable Forest Management: 2015 Facts and Statistics.
- Government of Alberta. 2017b. Annual Status of Reforestation in Alberta Report.
- Gray, L. K., and Hamann, A. 2013. Tracking suitable habitat for tree populations under climate change in western North America. *Climatic Change*, **117**(1-2): 289-303.
- Groves, C.R., Jensen, D.B., Valutis, L.L., Redford, K.H., Shaffer, M.L., Scott, J.M., Baumgartner, J.V., Higgins, J.V., Beck, M.W., and Anderson, M.G. 2002. Planning for Biodiversity Conservation: Putting Conservation Science into Practice: A seven-step framework for developing regional plans to conserve biological diversity, based upon principles of conservation biology and ecology, is being used extensively by the nature conservancy to identify priority areas for conservation. *AIBS Bulletin*, **52**(6): 499-512.

- Hamann, A., Aitken, S.N., and Yanchuk, A.D. 2004. Cataloguing in situ protection of genetic resources for major commercial forest trees in British Columbia. *Forest ecology and management*, **197**(1): 295-305.
- Hamann, A., and T. L. Wang. 2006. Potential effects of climate change on tree species and ecosystem distribution in British Columbia. *Ecology*, **87**: 2773-2786.
- Hamann, A., Roberts, D.R., Barber, Q.E., Carroll, C. and Nielsen, S.E. 2015. Velocity of climate change algorithms for guiding conservation and management. *Global Change Biology*, **21**: 997–1004.
- Hamrick, J.L., and Godt, M.W. 1990. Allozyme diversity in plant species. In *Plant population genetics, breeding, and genetic resources*: 43-63. Sinauer Associates, Sunderland, MA, USA.
- Hamrick, J. L. 2004. Response of forest trees to global environmental changes. *Forest ecology and management*, **197**(1): 323-335.
- Hannah, L., Midgley, G., Andelman, S., Araújo, M., Hughes, G., Martinez-Meyer, E., Pearson, R. and P. Williams. 2007. Protected area needs in a changing climate. *Frontiers in Ecology and the Environment*, **5**(3): 131-138.
- 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**(6): 1373-1384.
- Howe, G. T., Aitken, S. N., Neale, D. B., Jermstad, K. D., Wheeler, N. C., and Chen, T. H. 2003. From genotype to phenotype: unraveling the complexities of cold adaptation in forest trees. *Canadian Journal of Botany*, **81**(12): 1247-1266.
- Howe, H. F. and Smallwood, J. 1982. Ecology of seed dispersal. *Annual review of ecology and systematics*, **13**(1): 201-228.
- Hubbell, S. P. 1979. Tree dispersion, abundance, and diversity in a tropical dry forest. *Science*, **203**(4387): 1299-1309.
- Iriondo, J. M., Maxted, N., and Dulloo, M. E. (Eds.). 2008. *Conserving plant genetic diversity in protected areas: population management of crop wild relatives*. CABI.
- Isbell, F., Calcagno, V., Hector, A., Connolly, J., Harpole, W.S., Reich, P.B., Scherer-Lorenzen, M., Schmid, B., Tilman, D., van Ruijven, J. and Weigelt, A. 2011. High plant diversity is needed to maintain ecosystem services. *Nature*, **477**(7363): 199-202.
- Johnson, C.N. 1998. Species extinction and the relationship between distribution and abundance. *Nature*, **394**(6690): 272-274.

- Koh, L.P., Dunn, R.R., Sodhi, N.S., Colwell, R.K., Proctor, H.C. and Smith, V.S. 2004. Species coextinctions and the biodiversity crisis. *Science*, **305**(5690): 1632-1634.
- Kremer, A., Ronce, O., Robledo-Arnuncio, J. J., Guillaume, F., Bohrer, G., Nathan, R. and Kuparinen, A. 2012. Long-distance gene flow and adaptation of forest trees to rapid climate change. *Ecology letters*, **15**(4): 378-392.
- Lande, R. 1998. Anthropogenic, ecological and genetic factors in extinction and conservation. *Researches on population ecology*, **40**(3): 259-269.
- Landhäuser, S. M., and Lieffers, V. J. 2001. Photosynthesis and carbon allocation of six boreal tree species grown in understory and open conditions. *Tree physiology*, **21**(4): 243-250.
- Ledig, F.T. 1986. Conservation strategies for forest gene resources. *Forest Ecology and Management*, **14**(2): 77-90.
- Ledig, F.T. 1988. The conservation of diversity in forest trees: why and how should genes be conserved?. *BioScience*, **38**(7): 471-479.
- Ledig, F.T., Vargas-Hernández, J. and Johnsen, K. 1998. The Conservation of Forest Genetic Resources: Case Histories from Canada, Mexico, and the United States. *Journal of Forestry*, **96**(1): 32-41.
- Lemieux, C.J. and Scott, D.J. 2005. Climate change, biodiversity conservation and protected area planning in Canada. *The Canadian Geographer/Le Géographe canadien*, **49**(4): 384-397.
- Lemieux, C.J., Beechey, T.J., and Gray, P.A. 2011. Prospects for Canada's protected areas in an era of rapid climate change. *Land Use Policy*, **28**(4): 928-941.
- Liepe, K. J., Hamann, A., Smets, P., Fitzpatrick, C.R. and Aitken, S.N. 2016. Adaptation of lodgepole pine and interior spruce to climate: implications for reforestation in a warming world. *Evolutionary Applications*, **9**: 409–419.
- Loarie, S. R., Duffy, P. B., Hamilton, H., Asner, G. P., Field, C. B., and Ackerly, D. D. 2009. The velocity of climate change. *Nature*, **462**(7276): 1052.
- Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., Hooper, D.U., Huston, M.A., Raffaelli, D., Schmid, B., and Tilman, D. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science*, **294**(5543): 804-808.
- MacLachlan, I.R., Wang, T., **Hamann, A.**, Smets, P., Aitken, S.N. 2017. Selective breeding of lodgepole pine increases growth and maintains climatic adaptation. *Forest Ecology and Management* **391**: 404–416.

- Malcolm, J. R., Liu, C., Neilson, R. P., Hansen, L., and Hannah, L. E. E. 2006. Global warming and extinctions of endemic species from biodiversity hotspots. *Conservation biology*, **20**(2): 538-548.
- Margules, C.R. and Pressey, R.L. 2000. Systematic conservation planning. *Nature*, **405**(6783): 243-253.
- Mátyás, C. 1994. Modeling climate change effects with provenance test data. *Tree physiology*, **14**(7-8-9): 797-804.
- McKenney, D.W., Pedlar, J.H., Lawrence, K., Campbell, K., and Hutchinson, M.F. 2007. Potential impacts of climate change on the distribution of North American trees. *AIBS Bulletin*, **57**(11): 939-948.
- Menges, E.S. 1991. The application of minimum viable population theory to plants. In *Genetics and conservation of rare plants*: 45-61. Oxford University Press, New York, USA.
- Moilanen, A., Franco, A.M., Early, R.I., Fox, R., Wintle, B., and Thomas, C.D. 2005. Prioritizing multiple-use landscapes for conservation: methods for large multi-species planning problems. *Proceedings of the Royal Society of London B: Biological Sciences*, **272**(1575): 1885-1891.
- Moilanen, A. 2007. Landscape zonation, benefit functions and target-based planning: unifying reserve selection strategies. *Biological Conservation*, **134**(4): 571-579.
- Montwé, D., Spiecker, H. and Hamann, A. 2015. Five decades of growth in a genetic field trial of Douglas-fir reveal trade-offs between productivity and drought tolerance. *Tree Genetics and Genomes* **11**: 29, DOI 10.1007/s11295-015-0854-1.
- Morgenstern, M. 2011. *Geographic variation in forest trees: genetic basis and application of knowledge in silviculture*. University of British Columbia Press, Vancouver, Canada.
- Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. *Trends in ecology and evolution*, **10**(2): 58-62.
- Myers, N., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A., and Kent, J. 2000. Biodiversity hotspots for conservation priorities. *Nature*, **403**(6772): 853-858.
- NRC. 2016. The State of Canada's Forests: Annual Report 2016.
- Possingham, H., Wilson, K.A., Andelman, S.J. and Vynne, C.H. 2006. Protected areas: goals, limitations, and design. In Groom, M.J., Meffe G.K., and Carroll, C.R. (eds)., *Principles of Conservation Biology*, 3rd Edition. Sinauer Associates, Inc. , Sunderland, MA. p. 509-533.

- Pressey, R. L., Humphries, C. J., Margules, C. R., Vane-Wright, R. I., and Williams, P. H. 1993. Beyond opportunism: key principles for systematic reserve selection. *Trends in ecology and evolution*, **8**(4): 124-128.
- Pressey, R.L. and Tully, S.L. 1994. The cost of ad hoc reservation: a case study in western New South Wales. *Australian Ecology*, **19**(4): 375-384.
- Pressey, R.L., and Cowling, R.M. 2001. Reserve selection algorithms and the real world. *Conservation Biology*, **15**(1): 275-277.
- Pressey, R.L., Cowling, R.M. and Rouget, M. 2003. Formulating conservation targets for biodiversity pattern and process in the Cape Floristic Region, South Africa. *Biological Conservation*, **112**(1): 99-127.
- Reusch, T.B., Ehlers, A., Hämmerli, A. and Worm, B. 2005. Ecosystem recovery after climatic extremes enhanced by genotypic diversity. *Proceedings of the National Academy of Sciences of the United States of America*, **102**(8): 2826-2831.
- Richardson, D. M., Hellmann, J. J., McLachlan, J. S., Sax, D. F., Schwartz, M. W., Gonzalez, P., and Schneider, S. H. 2009. Multidimensional evaluation of managed relocation. *Proceedings of the National Academy of Sciences*, **106**(24): 9721-9724.
- Russell, E. J. 2014. Conservation planning for forests, tree species, and their genetic populations under climate change: a case study for western North America (master's thesis). University of Alberta, Edmonton, Canada.
- Savolainen, O., Pyhäjärvi, T. and Knürr, T. 2007. Gene flow and local adaptation in trees. *Annual Review of Ecology, Evolution, and Systematics*, **38**: 595–619.
- Schreiber, S.G., Hacke, U.G. and Hamann, A. 2015. Variation of xylem vessel diameters across a climate gradient: insight from a reciprocal transplant experiment with a widespread boreal tree. *Functional Ecology*, **29**: 1392-1401.
- Scott, J.M., Davis, F., Csuti, B., Noss, R., Butterfield, B., Groves, C., Anderson, H., Caicco, S., D'Erchia, F., Edwards Jr, T.C. and Ulliman, J. 1993. Gap analysis: a geographic approach to protection of biological diversity. *Wildlife monographs*, 3-41.
- Sebastian-Azcona, J., Hacke, U.G., Hamann, A. 2018. Adaptations of white spruce to climate: strong intraspecific differences in cold hardiness linked to survival. *Ecology and Evolution*, **8**: 1758–1768.
- Sgro, C.M., Lowe, A.J. and Hoffmann, A.A., 2011. Building evolutionary resilience for conserving biodiversity under climate change. *Evolutionary Applications*, **4**(2): 326-337.

- Shaffer, M. L. 1981. Minimum population sizes for species conservation. *BioScience*, **31**(2): 131-134.
- Shaffer, M.L. and Stein, B.A., 2000. Safeguarding our precious heritage. *Precious heritage: the status of biodiversity in the United States*: 301-321. Oxford University Press, New York, USA.
- Silen, R.R. 1978. Genetics of Douglas-fir.
- Skårøppa, T. 2003. *EUFORGEN Technical Guidelines for genetic conservation and use for Norway spruce (Picea abies)*. Biodiversity International.
- Spielman, D., Brook, B.W. and Frankham, R., 2004. Most species are not driven to extinction before genetic factors impact them. *Proceedings of the National Academy of Sciences of the United States of America*, **101**(42): 15261-15264.
- Svancara, L.K., Brannon J., Scott, M., Groves, C.R., Noss, R.F., and Pressey, R.L. 2005. Policy-driven versus evidence-based conservation: a review of political targets and biological needs. *BioScience*, **55**(11): 989-995.
- Tear, T.H., Kareiva, P., Angermeier, P.L., Comer, P., Czech, B., Kautz, R., Landon, L., Mehlman, D., Murphy, K., Ruckelshaus, M. and Scott, J.M. 2005. How much is enough? The recurrent problem of setting measurable objectives in conservation. *AIBS Bulletin*, **55**(10): 835-849.
- Vogel, K. P., Schmer, M. R., and Mitchell, R. B. 2005. Plant adaptation regions: ecological and climatic classification of plant materials. *Rangeland ecology & management*, **58**(3): 315-319.
- West, J.M., Julius, S.H., Kareiva, P., Enquist, C., Lawler, J.J., Petersen, B., Johnson, A.E. and Shaw, M.R. 2009. U.S. Natural Resources and Climate Change: Concepts and Approaches for Management Adaptation. *Environmental Management*, **44**(6): 1001–1021.
- Whitham, T.G., Bailey, J.K., Schweitzer, J.A., Shuster, S.M., Bangert, R.K., LeRoy, C.J., Lonsdorf, E.V., Allan, G.J., DiFazio, S.P., Potts, B.M. and Fischer, D.G. 2006. A framework for community and ecosystem genetics: from genes to ecosystems. *Nature Reviews Genetics*, **7**(7): 510-523.
- Wilcove, D. S., McLellan, C. H., and Dobson, A. P. 1986. Habitat fragmentation in the temperate zone. *Conservation biology*, **6**: 237-256.
- Wilcox, B.A. and Murphy, D.D. 1985. Conservation strategy: the effects of fragmentation on extinction. *The American Naturalist*, **125**(6): 879-887.

- Yeaman, S., and Jarvis, A. 2006. Regional heterogeneity and gene flow maintain variance in a quantitative trait within populations of lodgepole pine. *Proceedings of the Royal Society of London B: Biological Sciences*, **273**(1594): 1587-1593.
- 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): 1-13.
- Young, A., Boyle, T., and Brown, T. 1996. The population genetic consequences of habitat fragmentation for plants. *Trends in Ecology and Evolution*, **11**(10): 413-418.
- Young, J. E., Sánchez-Azofeifa, G. A., Hannon, S. J., and Chapman, R. 2006. Trends in land cover change and isolation of protected areas at the interface of the southern boreal mixedwood and aspen parkland in Alberta, Canada. *Forest Ecology and Management*, **230**(1-3): 151-161.