**Mitigating the Effects of Human Activity
on Grizzly Bears (*Ursus arctos*) in Southwestern Alberta**

by

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Abstract

Anthropogenic habitat loss and alteration, as well as human-caused mortalities associated with increasing access, threaten grizzly bear populations across much of their North American range. This research investigates strategies for mitigating the negative effects of human activities on grizzly bears in southwestern Alberta. First, an optimization approach was used to prioritize sites for both protection and restoration while also considering landscape composition. Seasonal habitats where bears forage were balanced against proximity to roads, which are associated with mortality risk, to identify priority source- (high quality, low risk) and sink-like (high quality, high risk) habitats. Most sink-like sites (63%) were associated with unimproved roads or truck trails and are the best candidates for decommissioning and restoration efforts. Approximately 75% of priority source-like sites are currently unprotected, and overlap between protected areas and source-like sites was geographically biased. Second, the viability of using wildlife habitat enhancements to increase local food supply in clearcuts for grizzly bears was assessed. Specifically, I conducted planting trials of seedlings (plugs) for three important late-season fruiting shrubs and monitored their survival and growth over two growing seasons. The effects of soil nutrient amendments, exclosures, initial seedling condition, and environmental factors (elevation and terrain) on seedling survival and growth were considered. *A. alnifolia* had the highest survival rate, although may not be as effective as *S. canadensis* and *V. membranaceum* in the long term due to browse preferences. Soil nutrient amendments reduced survival rates, whereas exclosures increased survival rates. Survival rates for *S. canadensis* and *A. alnifolia* along elevation gradients were inconsistent with expected niche spaces for both species, suggesting that knowledge of their natural niche spaces along the elevation gradient alone may not be sufficient to identify sites where they have the greatest chances of success. Management

of sustainable grizzly bear populations should include measures that reduce the negative effects of human activities. Access management will be a critical component of this, and should be prioritized to areas where conflicts are most likely to occur, or to proactively protect secure, high quality habitats. As the prevalence of natural forest openings continues to decline, wildlife habitat enhancements in disturbed areas with open canopies, including forest harvests, have the potential to locally increase late-season food supply for grizzly bears and should be further explored.

Preface

Chapter 2 of this thesis – "Prioritizing Sites for Protection and Restoration for a Species at Risk" – has been submitted for publication by myself and S. E. Nielsen in *Biological Conservation*. S. E. Nielsen was the supervising author and assisted with concept formation, analyses, and manuscript composition. I was responsible for concept formation, data collection, analyses, and manuscript composition.

In dedication to my parents, Robert and Doris.

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CHAPTER 1
General Introduction

1. BACKGROUND

The historical range of grizzly bears (*Ursus arctos*) once included much of western North America and Eurasia (Servheen, 1990; Alberta Grizzly Bear Recovery Team, 2008; COSEWIC, 2012). Today, many populations in Europe and Asia are now small, insular, and under threat (Servheen, 1990; COSEWIC, 2012). In North America, the range of grizzly bears (ca. 1850) extended from the Arctic to Mexico, and from the Pacific coast to the Mississippi River (Servheen, 1990; Mattson and Merril, 2002; Alberta Grizzly Bear Recovery Team, 2008). During the mid-1800s, grizzly bear populations in the United States came into contact with European settlers, which lead to rapid, widespread population declines and extensive range contraction (Mattson and Merril, 2002). Populations in the contiguous United States now occupy only 1% of their historic range, and recovery in many areas is unlikely (Servheen, 1999). In Canada, historical population reductions are largely attributable to the expansion of human settlement (and particularly ranchland) to the foothills of the Rocky Mountains in Alberta, where people perceived grizzly bears as threats to their safety and their livestock (McLellan, 1998). Grizzly bears were able to persist in the more remote, rugged, or densely forested areas of the foothills and the Rocky Mountains where human settlement was rare (McLellan, 1998). Because of this, range contraction due to human activity was far less severe in Canada than it was in the United States. The current Canadian grizzly bear range includes the Yukon, British Columbia, most of mainland Nunavut, as well as parts of Alberta, the Northwest Territories, Manitoba, and potentially far northern Saskatchewan (Servheen, 1990; COSEWIC, 2012). Populations in the Yukon and British Columbia are relatively healthy, but there is particular concern over the persistence of grizzly bears in Alberta (Nielsen et al., 2006; Nielsen et al., 2008; Festa-Bianchet 2010), where the population is comprised of approximately 700 individuals (COSEWIC, 2012).

In 2006, the regulated hunting of grizzly bears (excluding aboriginal subsistence hunting) was prohibited indefinitely in Alberta, and in 2010 they were listed as *threatened* under Alberta's Wildlife Act (COSEWIC, 2012; Linke et al., 2013). Like many other large mammalian

carnivores, grizzly bears are particularly vulnerable to extinction and extirpation because they typically occur at low densities and have low reproductive rates that slow population recovery (Boyce et al. 2001; Nielsen et al., 2004a). Continued expansion of anthropogenic developments for recreation, resource extraction, and other land uses poses a serious threat to the persistence of grizzly bears in the province (Nielsen et al., 2004b). In general, human activities cause increased habitat fragmentation, habitat loss, and habitat alteration, all of which indirectly limit population size by reducing the number of grizzly bears a given area can support (Hilderbrand et al., 1999; Nielsen et al., 2003; 2004a; Munro et al., 2006; Alberta Grizzly Bear Recovery Team, 2008).

Additionally, anthropogenic activity causes increased access (i.e. roads, trails, railways), which is closely linked to human-bear conflicts and human-caused mortalities (McLellan et al., 1999; Benn and Herrero, 2002; Nielsen et al., 2004a; 2004b; Northrup, 2010; Northrup et al., 2012). Human use of access and the associated increases in human-caused mortalities are widely regarded as the most immediate threats to the persistence of grizzly bears in Alberta (Mattson et al., 1996). Benn (1998) found that 89% of human-caused mortalities in Alberta's Central Rockies ecosystem occurred within 500 m of roads on provincial lands. Benn and Herrero (2002) also found that 91% of known mortalities were human-caused in Banff and Yoho National Parks. Of these, all occurred within 500 m of roads or 200 m of trails. Studies of grizzly bear survival in the Greater Yellowstone ecosystem have linked mortality risk to road density and developed sites (Johnson et al., 2004; Schwartz et al., 2010). Females with cubs select areas near roads during the spring and are more likely to cross low-volume roads, both of which can increase the likelihood that they will encounter humans (McLellan and Shackleton, 1988; Northrup, 2010; Graham et al., 2010). Adult females also avoid roads and developments during the fall, which may affect energetic balances, leading to poorer body condition, reduced survival, and lower cohort fecundity (Mattson et al., 1987).

Given the threat that increased access poses to grizzly bear populations, access management has become a core element of recovery plans. Traditionally, managers have proactively limited road access and number (density) in core grizzly bear habitat in an attempt to reduce mortalities (Nielsen et al., 2009; Northrup, 2012). Other forms of access management, including decommissioning of old industry roads and limiting road access with gates (either seasonally or

year-round) have also been employed. The success of such strategies, however, hinges on accurately identifying habitats that confer the greatest chances of survival and reproductive success, and conversely, identifying habitats that pose the greatest threats to survival. Carnivore survival is typically limited by human-caused mortality, while reproductive rates are governed by nutritional states of individual animals (Naves et al., 2003). Resource selection functions are frequently used to estimate habitat quality for grizzly bears, but often fail to consider population processes such as survival, reproduction, or growth that are necessary for predicting realized habitat quality (Ciarniello et al., 2007; Nielsen et al., 2010; Nielsen, 2011). Management actions based on such approaches may exacerbate issues associated with source-sink dynamics by supporting maladaptive habitat selection (Johnson et al., 2004; Nielsen et al., 2006; 2010; Ciarniello et al., 2007; Nielsen, 2011).

To address this shortcoming, two-dimensional frameworks that consider trade-offs between top-down and bottom-up regulators of populations have been used to define habitat states, including source-like and sink-like habitats (Naves et al., 2003; Nielsen et al., 2006; Nielsen, 2011; Northrup et al., 2012). In these frameworks, the top-down dimension is represented by survival or mortality risk, whereas bottom-up effects are represented by occupancy (based on resource selection functions) or indices of habitat productivity, such as the availability of food resources (Naves et al., 2003; Nielsen et al., 2006; Nielsen, 2011; Northrup et al., 2012). Two-dimensional approaches to quantifying habitat states have value for making general access management recommendations and conservation planning decisions, but there is also a growing need to prioritize specific sites to provide a foundation for action and to maximize the utility of limited resources. Methods for objectively prioritizing sites for access management are currently lacking, and seldom consider the landscape context of grizzly bear habitat.

Quite often, the effects of human activity on the landscape are highly conspicuous (as is the case with roads). However, some of the most impactful consequences of anthropogenic development are indirect and less visible. Disturbance plays an important role in determining the availability and productivity of certain critical grizzly bear foods (Nielsen et al., 2004c). Over the past century, aggressive wildfire suppression policies in Alberta, along with long-term climatic cycles, have altered natural disturbance regimes that were historically dominated by fire

(Johnson et al., 2001; Linke et al., 2013). Grizzly bears in Alberta depend heavily on two fire-successional fruiting shrubs, *Shepherdia canadensis* (buffaloberry) and *Vaccinium membranaceum* (mountain huckleberry), during their late summer and autumn hyperphagic period when they attempt to accumulate enough fat to survive winter hibernation (Martin, 1983; Hamer et al., 1991; Hamer, 1996). Fire also plays a key role in establishing successionally-mature open plant communities that are often high quality grizzly bear habitat (Hamer and Herrero, 1987; Stewart et al., 2012). In the absence (or relative absence) of wildfire, critical grizzly bear feeding habitat has been lost, and will continue to be lost if current successional trends continue (Hamer and Herrero, 1987; Stewart et al., 2012). In place of wildfire, forest harvesting has become a dominant source of disturbance in Alberta's forests (Festa-Bianchet, 2010; Stewart et al., 2012). The productivity of some bear foods may be higher in clearcuts, and grizzly bears will utilize them under certain conditions (Nielsen et al., 2004b; Stewart et al., 2012); however, silvicultural practices such as mechanical scarification can adversely affect the recovery of some key fruiting species, including *S. canadensis* and *V. membranaceum* (Anzinger, 2002; Nielsen et al., 2004c). Recovery prior to canopy closure can be limited, which in turn reduces late-season food supply for grizzly bears in these areas (Nielsen et al., 2004c).

Part of the strategy to mitigate the negative effects of forest harvesting on late-season grizzly bear food resources is to limit the use or severity of disruptive site preparation techniques such as mechanical scarification wherever possible (Nielsen et al., 2004c). Another option is to periodically thin regenerating conifer stands to reduce canopy cover and promote fruit production (Nielsen et al., 2004c). Habitat enhancements (wildlife food plots) have also been proposed to accelerate the recovery of critical fruiting shrub species in clearcuts (Nielsen et al., 2004c). Planting fruiting shrubs in clearcuts has the potential to generate significant increases in late-season food supply for grizzly bears. If coupled with access restrictions and periodic forest thinning (once canopy closure occurs), this mitigation strategy could enable conservation planners to create 'safe-harbour' habitats (high habitat quality, low mortality risk). However, it is currently unclear whether planting fruiting shrubs in clearcuts is a feasible option for improving grizzly bear habitat quality, and tests of the effectiveness of planting fruiting shrub seedlings in clearcuts are still needed.

2. OBJECTIVES

The overarching goal of this thesis is to explore management strategies for mitigating the effects of human activity on grizzly bears in southwestern Alberta. It is my hope that the results of these studies will inform management decisions aimed at reducing human-caused grizzly bear mortalities, and provide information that will help form the basis for habitat enhancement programs designed to strategically improve grizzly bear habitat quality.

In Chapter 2, I present an approach for prioritizing sites for conservation in southwestern Alberta that balances late-season grizzly bear food resources (habitat) against threats (access) while considering landscape context (patches of habitat). I first develop habitat quality indices to quantify bottom-up factors (predicted distributions of late-season food resources) as well as top-down population regulators (road-based mortality risk). I then prioritize late-season source-like habitats (i.e., productive sites with low mortality risk) for protection, as well as late-season sink-like habitats (i.e., productive sites with high mortality risk) for restoration. Finally, I provide recommendations for using systematic conservation planning methods that explicitly prioritize conservation actions and consider landscape context (patch size) to inform access management decisions. In Chapter 3, I test the viability of using habitat enhancements (wildlife food plots) to increase grizzly bear food supply in clearcuts. I conducted short-term planting trials for three important late season grizzly bear foods – *S. canadensis*, *V. membranaceum*, and *Amelanchier alnifolia* (saskatoon) – in clearcuts in southwestern Alberta and monitored their survival and growth over two growing seasons. I assess the effects of amendment and exclosure treatments, as well as the effects of initial seedling condition and environment (elevation and terrain [potential solar radiation]), on seedling survival and growth. I then assess the overall viability of using habitat enhancements to increase grizzly bear food supply and make recommendations for possible applications in habitat management. Lastly, in Chapter 4 I provide a summary of my thesis, comment on potential management implications of these studies and possibilities for future research, and provide general concluding remarks.

This thesis is organized as two independent manuscripts, both of which were written and formatted with the intention of submission for publication in *Biological Conservation*. Chapter 2

has been submitted and is currently with reviewers, whereas Chapter 3 has not yet been submitted. Formatting for the rest of the thesis (and wherever conflicts between formatting requirements occurred) follows the minimum thesis formatting requirements set forth by the Faculty of Graduate Studies and Research at the University of Alberta.

CHAPTER 2

Prioritizing Sites for Protection and Restoration for a Species at Risk

1. INTRODUCTION

Applied conservation biology aims to protect undisturbed sites from future degradation, and to restore degraded sites to their former states. For many landscapes, the spectrum of site conditions ranges from pristine to destroyed (Noss et al., 2009). More pristine sites could benefit from future protection, whereas degraded sites require restoration. However, needs for protection and restoration often outstrip the resources available to address them (Carwardine et al., 2009). Conservation actions must therefore be prioritized (Margules et al., 2002). Methods for prioritizing conservation actions frequently fall under the banner of systematic conservation planning, which identifies conservation goals or objectives and optimizes management actions to achieve them (Margules and Pressey, 2000; Brooks et al., 2006; Watson et al., 2011). Although systematic conservation planning has frequently been used to optimize the design of protected area networks, there remains a need to expand these concepts to a wider area of conservation objectives and management actions, including landscape prioritization of sites for restoration (Noss et al., 2009; Watson et al., 2011). The broadening scope of systematic conservation planning reflects the need for prioritization in all facets of applied conservation biology to encompass the full spectrum of site conditions.

Focal species are frequently used for land use and conservation planning because complete inventories of biodiversity are generally not practical (Akçakaya and Sjögren-Gulve, 2000; Fleishman et al., 2000; Margules et al., 2002). They are typically well-studied, charismatic megafauna (flagship species) that often have large area requirements for maintaining viable populations, and are therefore thought to confer umbrella effects to other co-occurring species (Akçakaya and Sjögren-Gulve, 2000; Carroll et al., 2001; Nielsen, 2011). In some cases, focal species may also be considered keystone species if their role in ecosystem functioning is disproportionate relative to their abundance (Fleishman et al., 2000; Watson et al., 2011). Traditionally, single-species conservation planning methods have relied mostly on spatially-explicit species habitat models (i.e., resource selection functions, species distribution models,

and ecological niche models) to predict spatial distributions of species and in some cases to prioritize sites for conservation (Elith and Leathwick, 2009a, 2009b). Examples include conservation planning for Amur tigers (*Panthera tigris altaica*; Xiaofeng et al., 2011), African elephants (*Loxodonta Africana*; Pierce et al., 2005), and grizzly bears (*Ursus arctos*; Nielsen et al., 2009).

Habitat-based approaches to defining species habitat are sometimes replaced by analytical techniques that synthesize information about both habitat and population demographics. These methods acknowledge the need to use estimates of realized habitat quality (i.e., potential habitat quality balanced by information about survival or mortality risk; Nielsen et al., 2010) as the basis for effective conservation planning. Spatial population viability analyses (SPVAs) incorporate demographic and habitat data to predict species decline or recovery and are frequently used in conservation planning (Akçakaya and Sjögren-Gulve, 2000; McCarthy, 2009). Two-dimensional approaches that explicitly consider trade-offs between bottom-up and top-down regulators of populations have also been used to estimate realized habitat quality and to identify areas where habitat restoration efforts are most likely to succeed (Merrill et al., 1999; Naves et al., 2003; Nielsen et al., 2006, 2010).

Two major gaps with using these approaches in conservation planning still remain. First, they generally do not consider landscape context of individual sites, which can undermine the ecological relevance of their outputs (Briers, 2002). And second, they seldom provide explicit prioritizations of sites for the two primary conservation tools of protection and restoration (Margules and Pressey, 2000), thereby limiting their impetus for focusing management actions. Here I present an approach for simultaneously prioritizing sites for protection and restoration in the context of landscape conditions. This process is illustrated for a threatened population of grizzly bears in southwestern Alberta, Canada, by balancing seasonal habitats where bears forage against proximity to roads, which are tied to mortality risk (McLellan et al., 1999; Benn and Herrero, 2002; Neilsen et al. 2004). More specifically, my objectives were to: (1) develop habitat quality indices that consider bottom-up factors (predicted distributions of important food resources) as well as top-down population regulators (road-based mortality risk); and (2) prioritize late-season source-like habitats (highly productive, low risk) for protection, and late-

season sink-like habitats (highly productive, high risk) for restoration (access management), while considering the landscape context of bear habitat.

2. METHODS

2.1 Study area

I sampled bear foods across a 5,065 km^2 study area in southwestern Alberta (Figure 2-1) extending east from the British Columbia border to the edge of the foothills, and north approximately 125 km from the Waterton Lakes National Park boundary. The study area is characterized by mountains, high, rolling foothills, and deeply-cut glacial valleys (Natural Regions Committee, 2006). Elevations in the study area range from 1155 m to 3009 m, with a mean elevation of 1672 m. Summers are short and cool (623 growing degree days > 5°C, mean annual temperature of -0.4°C), and mean annual precipitation is 798 mm (Natural Regions Committee, 2006). Highly variable topography and geography yield a wide variety of plant communities. In general, open *Picea engelmannii* (Englemann spruce) and *Abies lasiocarpa* (subalpine fir) stands and herbaceous meadows occur at the highest elevations, whereas closed *Pinus contorta* (lodgepole pine) stands with *P. engelmannii* and *A. lasiocarpa* occur at moderate elevations (Natural Regions Committee, 2006; Government of Alberta, 2010a). Grasslands, mixed-wood forests, and open forests comprised of *Pseudotsuga menzeisii* (Douglas fir), *P. contorta*, and *Picea glauca* (white spruce) occur at lower elevations (Natural Regions Committee, 2006). Timber harvesting is common to the area, especially north of Highway 3 (Natural Regions Committee, 2006; Government of Alberta, 2010b). Recreational use is prevalent, with the exception of the easternmost portion of the study area where landowners control access (Government of Alberta, 2010b; Northrup et al., 2012).

2.2 Focal species defining grizzly bear habitat

Thirteen fruiting species were selected based on their prevalence in the study area (present at more than 10% of sample locations) and their known importance to regional grizzly bear diets (Hamer et al., 1991; McLellan and Hovey, 1995; Merrill et al., 1999; Nielsen et al., 2003; Munro

et al., 2006). Species included *Shepherdia canadensis* (Canada buffaloberry), *Vaccinium membranceum* (mountain huckleberry), *Amelanchier alinifolia* (saskatoon), *Ribes* spp. (gooseberry), *Arctostaphylos uva-ursi* (bearberry), *Lonicera involucrata* (black twinberry), *Sambucus racemosa* (black elderberry), *Fragaria virginiana* (wild strawberry), *Rubus idaeus* (wild red raspberry), *Rubus parviflorus* (thimbleberry), *Vaccinium caespitosum* (dwarf blueberry), *Vaccinium scoparium* (grouse whortleberry), and *Vaccinium myrtillus* (bilberry). Species were grouped into four categories of importance based on their prevalence in grizzly bear dietary scat analyses (Table 2-1). *S. canadensis* and *V. membranaceum* typically dominate grizzly bear diets in Alberta and interior British Columbia during hyperphagia, a period between late summer and early fall when bears intensify foraging efforts to build body fat reserves for hibernation (Hamer et al., 1991; McLellan and Hovey, 1995, 2001; Hamer, 1996; McLellan et al., 1999, 2011; Nielsen et al., 2003; Munro et al., 2006). *A. alnifolia* has been identified as a significant component of late-season grizzly bear diets in southwestern Alberta, and *A. uva-ursi* is targeted by bears during late spring and early fall (Hamer et al., 1991). *Ribes* spp., *S. racemosa*, and *L. involucrata* are utilized less frequently (Hamer et al., 1991; Merrill et al., 1999; Nielsen et al., 2003), but have the potential to produce significant amounts of fruit. The remaining species occur only to a limited extent in grizzly bear diets (Merill et al., 1999; Nielsen et al., 2003); as such, their consumption is considered incidental to that of other more productive and nutritious species.

2.3 Field plots and data collection

Presence/absence data of grizzly bear foods were collected from 322 stratified field plots in southwestern Alberta (Figure 2-1) in 2012 (early July to mid-August) and 2013 (late May to mid-August) to characterize bottom-up resources with an emphasis on fruiting species. Plots were selected based on a stratification of Alberta Vegetation Inventory (AVI; Government of Alberta, 2005) classes and 100-m elevation zones (strata) using a geographic information system (GIS; Environmental Systems Research Institute, 2013). Plots were placed at centroids of AVI polygons and chosen to be representative of environments in the region, while still being accessible (i.e., within 2.5 km of roads and trails). Sampling effort in each 100-m elevation zone (ranging from 1300 m to 2300 m) was weighted based on the frequency of available elevations in

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the study area. At each site, presence of fruit-producing bear food species, along with their respective reproductive stages (phenophases), were recorded along a 50-m belt transect with a belt width of 10 m (total plot size of 0.05 ha).

2.4 Attractive sink and safe harbour habitats

Species distribution models were developed for each focal species using a purposeful model-building approach with logistic regression (Appendix A; Hosmer et al., 2013). A suite of climate, landcover, terrain, and stand variables were considered during model building (Table A-1). Presence of reproductive structures (flowering or fruiting) was then modeled (Appendix A), again using logistic regression (0 – present, but no sign of reproduction; 1 – present with signs of reproduction), for each fruiting species to define fruiting habitat that would be relevant to bears during hyperphagia. Model estimates were used to create binary rasters (for both presence and fruiting models) for each species in a GIS (Environmental Systems Research Institute, 2013). Because the fruiting model was conditional on presence of the species, binary fruiting rasters were multiplied by the binary presence rasters for each species to produce binary rasters of fruiting given presence. These rasters were then summed across the study area using additive dietary weights (Table 2-1) to generate an index of late-season habitat productivity:

(1) $H_{LS} = [0.30(SCAN + VMEM)] + [0.15(AALN + AUVA)] + [0.10(RIBG + LINV + SRAC)] + [0.025(FVIR + RPAR + RIDA + VSCO + VCAE + VMUS)]$

where H_{LS} represented late-season habitat productivity within any given study area pixel (30-m resolution) with each four-letter species code corresponding to one of the thirteen focal fruiting species (Table 2-1). A road-based mortality risk index (M_R) was calculated using a distance-to-access coefficient from a human-caused grizzly bear mortality risk model by Nielsen et al. (2004):

(2) $M_R = \exp(-1.63d) / [1 + \exp(-1.63d)]$

where *d* was distance in km to the nearest road. Both indices were rescaled to range from 0 to 1. Given the importance of food resources (particularly fruiting species) to grizzly bears during hyperphagia, H_{LS} was used to represent the bottom-up dimension within a two-dimensional habitat framework. M_R was used to represent the top-down dimension, and using a procedure similar to that of Nielsen et al. (2006), attractive sink and safe harbour indices were estimated for the study area. Attractive sinks (also referred to as ecological traps) are areas where both habitat productivity and mortality risk are high, whereas safe harbours (source-like habitats) are areas where habitat productivity is high and mortality risk is low (Nielsen et al., 2006). Thus, I defined our attractive sink and safe harbour indices as:

(3) $\qquad AS = H_{LS} \times M_R$

and

(4) $\qquad SH = H_{LS} \times (1 - M_R)$

where *AS* is an index of a site's potential to be an attractive sink ($0 = $ low, $1 = $ high), and *SH* is an index of a site's potential to be a safe harbour ($0 = $ low, $1 = $ high). These two habitat conditions were assumed to correlate with survival and reproduction (which is closely tied to nutritional state; Naves et al., 2003), both of which are responsible for regulating population growth (Boyce et al., 2001). Knowledge of the spatial distribution of these indices can aid conservation efforts by providing a basis for management actions directed at bolstering grizzly bear populations by mitigating mortality risk and/or fostering reproduction. In spite of this, representations of these indices across large areas can be difficult to translate into management action, creating a need to prioritize sites.

2.5 Optimizing sites using Marxan

Marxan is a spatially-explicit software tool developed to aid in the design of reserve systems (protected areas), and is commonly used to provide decision support for conservation planning (Ball and Possingham, 2000; Sala et al., 2002; Ceballos et al., 2005; Ball et al., 2009; Watts et

al., 2009). Optimization using Marxan requires the definition of planning units – spatial units that summarize conservation features and costs. Marxan optimization algorithms include simulated annealing to identify many near-optimal sets (runs) of planning units that attempt to meet pre-defined conservation targets while minimizing associated costs (Smith et al., 2006). Total cost of any given run is defined as the sum of planning unit, target penalties, and boundary costs (Smith et al., 2006). One output is a summed solution, which summarizes the number of times each planning unit was selected across all runs. The summed solution is frequently used to quantify the relative irreplaceability of planning units (Smith et al., 2006; Carwardine et al., 2007; Nielsen et al., 2011). Within the context of a given optimization framework, planning units selected in many runs likely have higher conservation value than planning units selected less frequently. We used hexagonal planning units to maximize the number of connections, which increases the effectiveness of manipulating the boundary length modifier (BLM). The BLM penalizes solutions with longer boundary lengths (i.e., less compactness), and thereby encourages the selection of planning units with shared boundaries. This reduces the overall fragmentation of solutions, which in turn yields more realistic options for conservation management (Pressey et al., 2007; Ball et al., 2009). The size of hexagonal planning units was set at 9 ha (shortest diagonal = 322.37 m) to maximize the total number of planning units while ensuring that their size was greater than the lowest resolution product that was used for modeling (300-m climate surfaces from Roberts et al., 2014). The value of conservation features (fruiting species) within each planning unit was defined as total pixels of habitat suitable for reproduction (from fruiting models) for each fruiting species within that planning unit. Conservation targets were set for each species using the same additive dietary weights (Table 2-1) that were used to calculate the late-season habitat productivity index (H_{LS}).

2.6 Identifying priority sites for protection and restoration

To identify priority source-like habitats, we first ran an optimization in Marxan that used the mean road-based mortality index (M_R) value of each planning unit as a cost. This encouraged the selection of planning units away from roads (habitats with high H_{LS} values and low M_R values). Sink-like habitats were then identified by running an optimization that used the inverse of the mean road-based mortality index (M_R) value of each planning unit as a cost, which favoured the

selection of planning units close to roads (habitats with high H_{LS} and M_R values). Using the sum of solutions from 100 iterations, priority source- and sink-like habitats were defined as any planning unit selected more than 50 times.

3. RESULTS

3.1 Habitat quality indices

Late-season habitat productivity (H_{LS}) values were highest where there was considerable overlap of fruiting species (particularly critical species, *S. canadensis* and *V. membranaceum*) habitat (Figure 2-2, Figure 2-3a). Mortality risk (M_R) values were highest on or very near to roads ($M_R \approx$ 1.0), but dropped to 0.61 and 0.33 at distances of 500 m and 1000 m from roads, respectively (Figure 2-3b). Attractive sink (*AS*) index values were highest where both H_{LS} and M_R values were high (i.e. productive fruiting habitats close to roads), whereas safe harbour (*SH*) index values were highest in areas with high H_{LS} values and low M_R values (i.e. productive fruiting habitats away from roads; Figures 2-3c and 2-3d, respectively).

3.2 Priority sites for protection and restoration

Optimization analysis in Marxan identified 425.8 km^2 of priority sink-like habitat (Figure 2-4). Of this, 62.7% was attributable to unimproved roads and truck trails, which are primary candidates for permanent or seasonal closure (42.8% and 19.9% respectively). Paved roads accounted for only 6.1% of priority sink-like planning units, whereas gravel roads accounted for 26.0% of sink-like planning units. Mean distance to road for priority sink-like habitats was 341.4 m (SE = 5.3 m). A total of 656.9 km^2 (13.0% of study area) of priority source-like habitat was identified, 24.7% (162.5 km^2) of which is currently protected (Figure 2-4). Of this overlap between priority source-like habitats and current protected areas, 97.8% (158.8 km^2) occurred in two adjacent existing protected areas. Patch sizes for source-like habitats ranged from 0.08 km^2 to 219.6 km^2 (mean patch size 8.01 km^2; SE = 3.37 km^2). Mean distance to road for source-like habitats was 3.54 km (SE = 0.017 km), and minimum distance to road was 957 m.

4. DISCUSSION

4.1 Habitat quality indices

The index of attractive sink habitat was highest where fruiting habitats overlapped for multiple important fruiting species in areas close to roads. Conversely, the index of safe harbour habitat was highest where fruiting species habitats coincided in areas away from roads. These habitat indices provide a measure of the spatial interaction between top-down and bottom-up population factors and can be used to quantify the risk or security of grizzly bear habitat during hyperphagia. Even so, they have limited applicability at a management level unless they are complemented by specific criteria for management action. For example, Nielsen et al. (2006) applied thresholds to habitat quality indices to define relative habitat states, and specifically recommended management strategies, such as protection and restoration. However, even when habitat states are clearly defined, managing all habitats across a large region is not feasible given that conservation resources are limited. There is a need to therefore prioritize sites to provide a stronger basis for focusing management actions.

4.2 Priority sites for protection and restoration

Optimization using Marxan identified priority late-season source- and sink-like sites for protection and restoration. These sites (planning units) were selected in the majority of runs and represented the most valuable habitats for meeting pre-defined conservation targets (focal fruiting species presence) while minimizing costs. Overall, the co-occurrence of both critical fruiting species, or one critical fruiting species and several major or moderate fruiting species, determined the selection of priority sites for conservation (either away from roads for source-like sites, or close to roads for sink-like sites). Mean distance-to-road for priority sink-like sites was 341.4 m (SE = 5.3 m), which is consistent with observed patterns of most bear mortalities occurring within 500 m of roads (Benn and Herrero, 2002). Similarly, minimum distance-to-road for priority source-like sites was 971 m, which is well outside the "high risk" zone for grizzly bears (Benn and Herrero, 2002).

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Mean patch size of priority source-like habitats was 8.01 km^2, and ranged from 0.08 km^2 to 219.6 km^2. The minimum patch size of approximately 8 ha is still relevant to foraging grizzly bears (i.e., large enough to contain a significant quantity of fruit), but is too small to justify individual protection or restoration actions. Larger patches are indicative of Marxan grouping highly valuable planning units that occur in close proximity, including planning units with less value (i.e., conservation features) to establish connectivity between high-value sites. Overlap between protected areas and priority source-like sites was 24.7% (165 km^2), indicating that a large portion of important late-season grizzly bear foraging habitat is not currently protected from future road access. The majority of this overlap (97.8%) occurs in two adjacent protected areas, suggesting that current protection of priority source-like sites is also geographically biased. Only 13.0% of the study area was identified as priority source-like habitat, which highlights the importance of these sites to grizzly bear habitat management in the region. Protection of priority source-like sites must include restrictions on future road development to maintain their security and effectiveness. New access features will also modify the "costs" of planning units if they are closer than existing roads, and may shift subsequent optimization solutions. Where road installation in close proximity to priority source-like sites is necessary for industrial activity, all access points should be decommissioned following resource extraction. Restoration should follow to discourage people from accessing these areas and to maintain the security of nearby priority source-like sites.

The majority of priority sink-like sites (62.7%) were associated with unimproved roads or truck trails. These low-volume roads are used almost exclusively for recreational purposes and would represent the best candidates for permanent closure and restoration. Almost all remaining priority sink-like sites (26.0%) were attributable to gravel roads, which generally see more frequent use from both industry and the public and require significant monetary investments for construction and maintenance. Permanent closure and restoration of gravel roads may be an unattractive management option in most cases. Instead, stakeholders may be more amenable to modified access strategies such as seasonal closures during hyperphagia or gated access to restrict public use of industry roads. Most grizzly bear mortalities occur on or near roads where public access is permitted (Wielgus et al., 2002). Thus, limiting public access could lead to significant reductions of mortality risk; however, relaxing access restrictions following the completion of industrial

activities would require careful consideration since grizzly bears can become habituated to industrial activity on roads (McLellan and Shackleton, 1989a, 1989b; Wielgus et al., 2002).

4.3 Prioritization and landscape patterns in conservation planning

Conservation planning using focal species is rarely systematic, in spite of the growing need to maximize the efficiency of management efforts. Complementing definitions of habitat quality or relative habitat states with prioritizations of candidate sites for conservation provides additional impetus for management action. Prioritization methods such as the one employed in this study can complement measures of habitat quality (i.e., habitat indices) by identifying habitats where the potential utility of conservation actions (both protection and restoration) is highest. A common objective of systematic conservation planning is to design minimum-cost solutions to meet quantitative conservation goals (Carwardine et al., 2009; Watts et al., 2009). As demonstrated here, Marxan achieves this by identifying portfolios of sites (planning units) that have the highest value for meeting conservation feature targets at the lowest 'cost'.

Furthermore, conservation planning approaches that employ the use of a focal species frequently ignore landscape patterns (Briers, 2002), which can complicate their applicability from a management perspective. Particularly for species with large ranges, the quality of a site is dictated not only by bottom-up and top-down factors, but also by the quality of nearby or connected sites (Saunders et al., 1991). Thus, management actions based on fine-scale definitions of habitat quality that do not incorporate the surrounding landscape context may lack ecological relevance. An isolated high quality site may have less ecological value than a group of connected moderate quality sites (Saunders et al., 1991; Taylor et al., 1993). Similarly, low quality sites that join groupings of high quality sites together may have increased ecological value because they promote habitat connectivity (Saunders et al., 1991; Taylor et al., 1993). Connectivity of sites is also appealing from an operational standpoint, because management of a diffuse set of solutions may be logistically impractical (Pressey et al., 2007; Ball et al., 2009). Marxan incorporates such landscape patterns into prioritization solutions via its boundary length modifier (BLM), which encourages the selection of connected (adjacent) planning units (Pressey et al., 2007). While this increases the number of planning units required to meet conservation targets, it promotes the

connectivity of solutions to make them more ecologically relevant and to yield more realistic management options (Pressey et al., 2007).

5. CONCLUSIONS

Systematic conservation planning identifies conservation goals and optimizes management actions to achieve them, but has been used mostly for optimizing the design of protected area networks. The need to also restore sites, though already apparent, will only grow as human environmental impacts continue to intensify. Systematic conservation planning provides an avenue for maximizing the utility of limited conservation resources, but its scope must be expanded to encompass the full spectrum of site conditions. For degraded sites, the aim of restoration efforts must be to mitigate the "costs" associated with them, as this will ultimately drive their selection during prioritization. Similarly, the focus of management strategies for sites prioritized for protection should be to proactively restrict increases in "cost". The optimization method we present here simultaneously prioritizes sites for protection and restoration, addressing the need to protect undisturbed sites from degradation, as well as the need to restore degraded sites to their former states. Systematic approaches to focal species conservation planning should be complemented by measures of habitat quality (i.e., habitat indices) to provide context for management decisions. Habitat indices provide an overall measure of regional habitat quality, whereas prioritizing sites for protection and restoration can form the basis for targeted management actions.

6. ACKNOWLEDGEMENTS

Table 2-1. Categories of fruiting species importance based on prevalence in grizzly bear dietary scat analyses, and associated weights (used to generate an index of late-season habitat productivity, H_{LS}) and conservation feature targets for Marxan optimization.

Species name	Species code	Importance category	Species weight and optimization target
Vaccinium membranaceum	VMEM	Critical	0.300
Shepherdia canadensis	SCAN	Critical	0.300
Amelanchier alnifolia	AALN	Major	0.150
Arctostaphylos uva-ursi	AUVA	Major	0.150
Ribes spp. (Gooseberry)	RIBG	Moderate	0.100
Lonicera involucrata	LINV	Moderate	0.100
Sambucus racemosa	SRAC	Moderate	0.100
Rubus parvifolorus	RPAR	Minor	0.025
Rubus idaeus	RIDA	Minor	0.025
Vaccinium myrtillus	VMUS	Minor	0.025
Vaccinium caespitosum	VCAE	Minor	0.025
Vaccinium scoparium	VSCO	Minor	0.025
Fragaria virginiana	FVIR	Minor	0.025
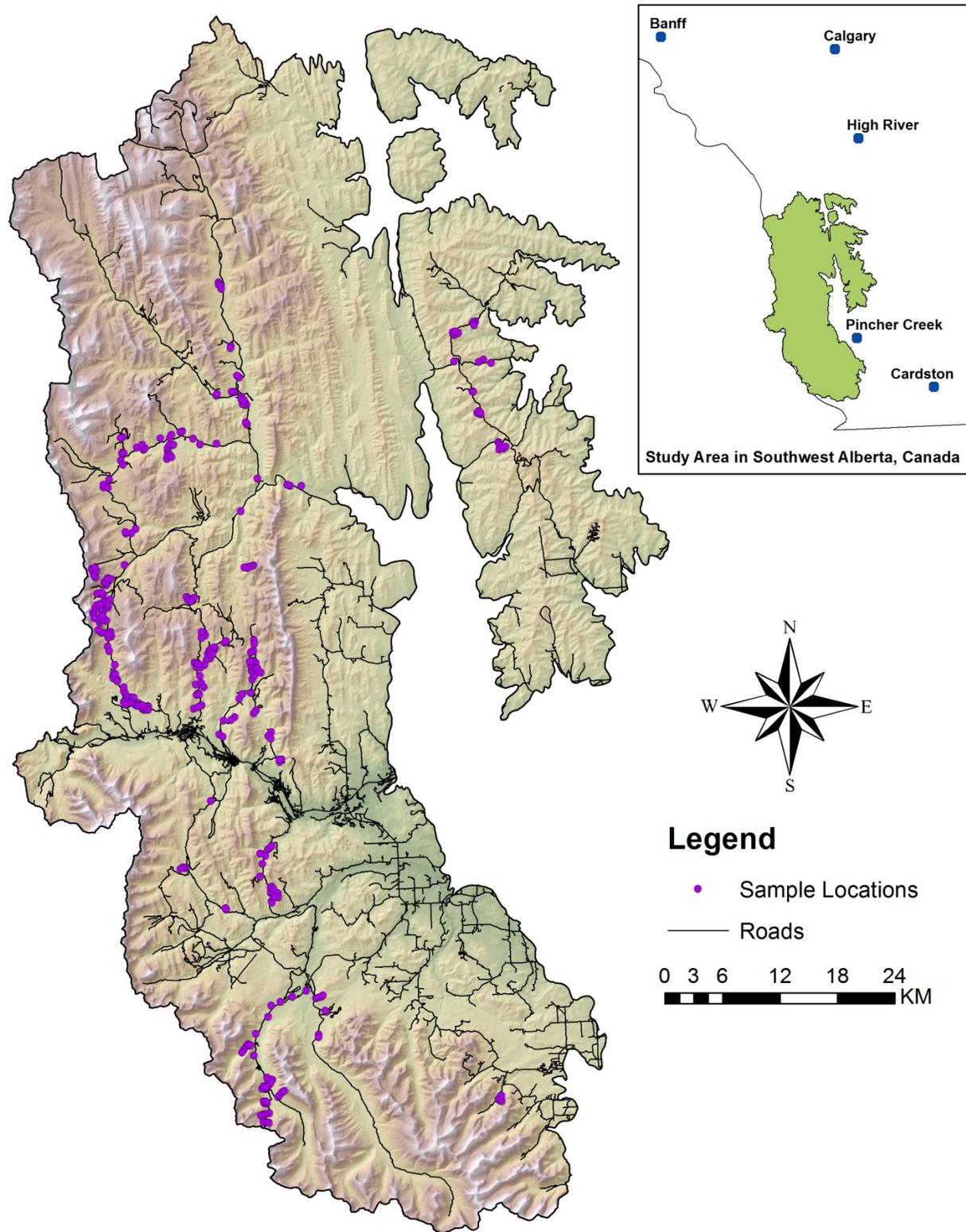
Figure 2-1. Location of the study area in southwestern Alberta, Canada, with field plots indicated.
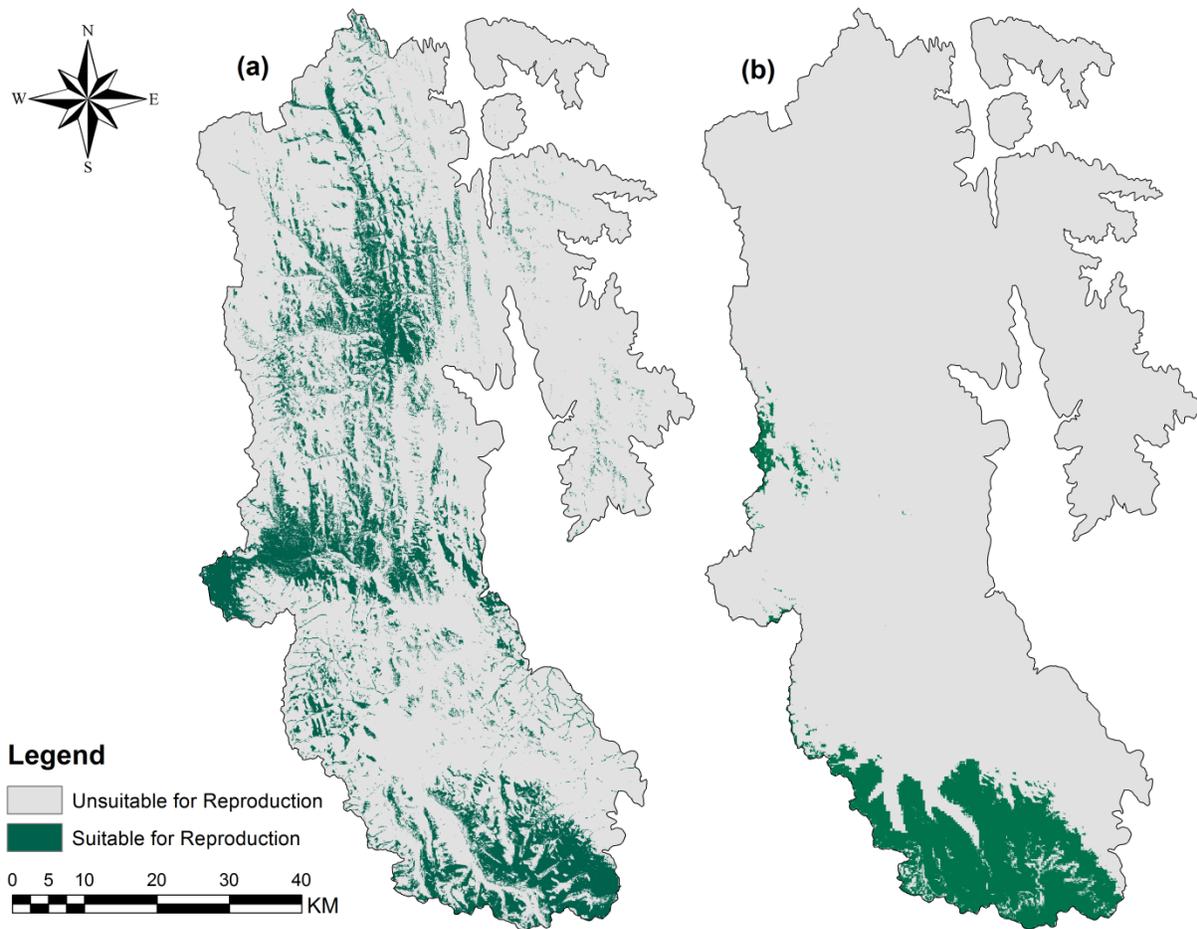
Figure 2-2. Binary fruiting maps for critical fruiting species: (a) *Shepherdia canadensis* and (b) *Vaccinium membranaceum*.
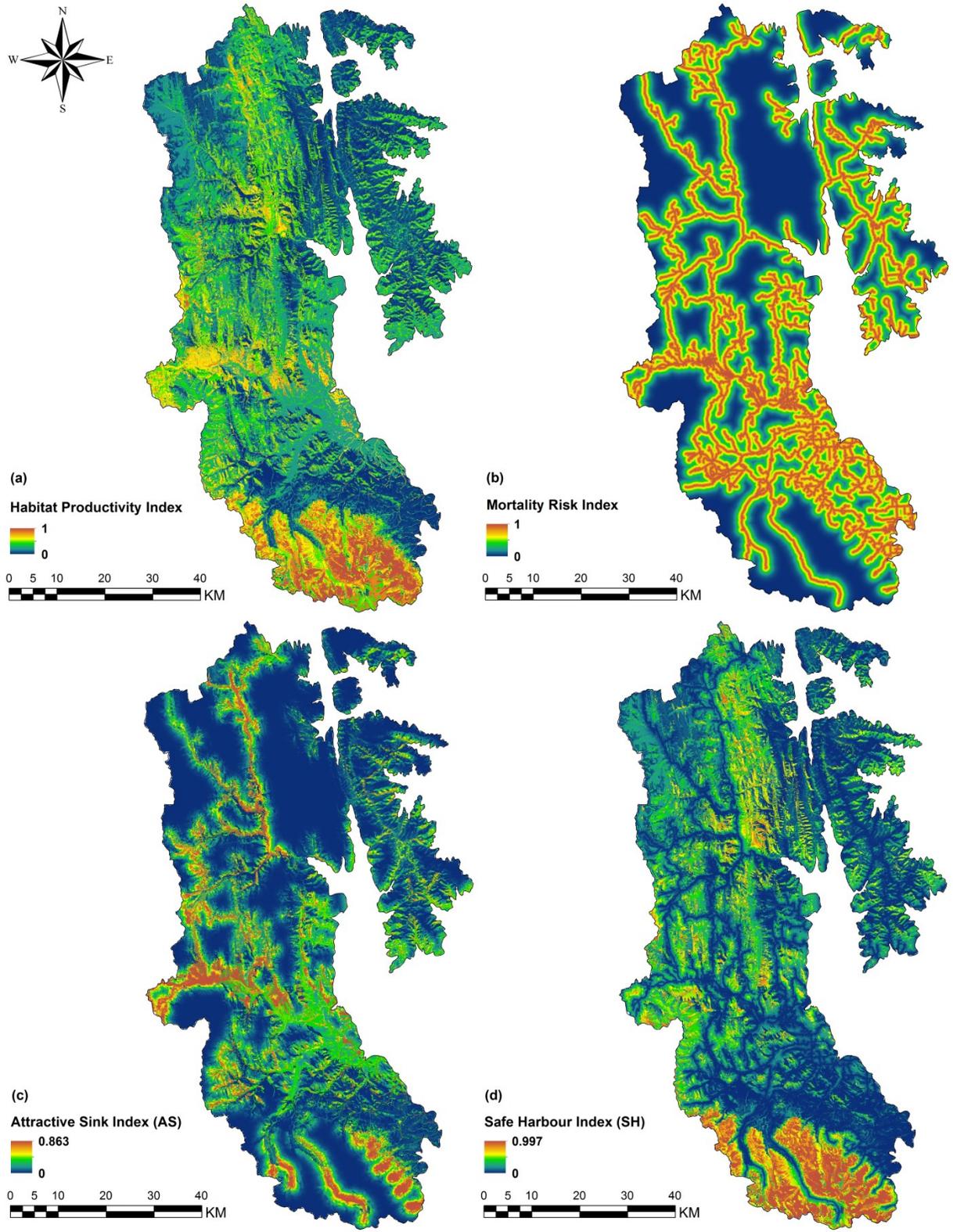
Figure 2-3. Maps of (a) late-season habitat productivity (H_{LS}); (b) road-based mortality risk (M_R); (c) attractive sink (AS); and (d) safe harbour (SH) indices.
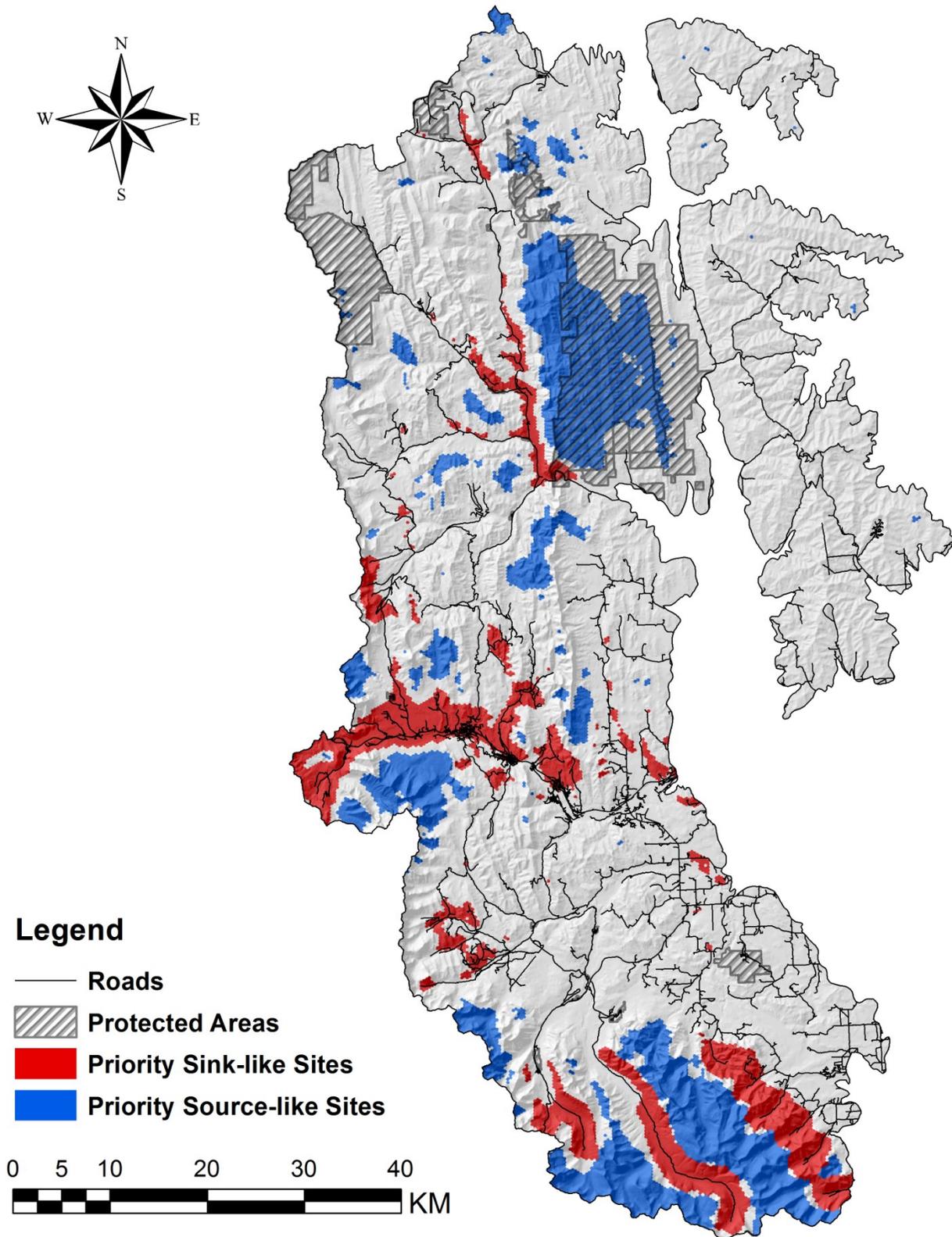
Figure 2-4. Map showing priority source- and sink-like sites in southwestern Alberta.

CHAPTER 3

Using Wildlife Habitat Enhancements to Increase Grizzly Bear (*Ursus arctos*) Food Supply in Clearcuts

1. INTRODUCTION

Grizzly bear (*Ursus arctos*) populations are under threat across much of their North American range, primarily due to anthropogenic habitat loss and alteration, as well as increases in human-caused mortalities associated with increases in human access (Hilderbrand et al., 1999; Nielsen et al., 2003; Nielsen et al., 2004a; Nielsen et al., 2004b; Munro et al., 2006; Linke et al., 2013). Fostering healthy and sustainable grizzly bear populations requires improving our understanding of their ecology, as well as conceptualizing and testing new and innovative conservation management strategies. Current management efforts to recover and sustain populations focus on reducing human-bear conflicts and human-caused mortalities, as well as identifying and maintaining grizzly bear habitats (Alberta Grizzly Bear Recovery Team, 2008). Although these strategies have been effective, complementary strategies should be explored, particularly where traditional approaches are ineffective or impractical. There is a growing need for strategies that create or improve habitat to balance habitat losses and alterations to habitat that are associated with a continually expanding human footprint.

Along with human-caused mortality, food availability is a critical component of grizzly bear habitat quality (Nielsen et al., 2010) and should therefore be a central focus of strategies aimed at creating or improving habitat. Hibernation requires significant stores of energy that must be accumulated during a relatively short foraging season (McLellan and Hovey, 1995; Hilderbrand et al., 1999; Nielsen et al., 2010; McLellan, 2011; Bojarska and Selva, 2012). Food quantity and quality are closely linked with reproductive rates, and may be the ultimate factors limiting some grizzly bear populations (McLellan and Hovey, 1995; Bojarska and Selva, 2012). Mowat et al. (2013) suggest that food supply, even independent of human-caused mortality, may actually be the strongest driver of grizzly bear densities in North America. Grizzly bears are generalist omnivores, and as such have a highly diverse diet that varies both seasonally and spatially (Munro et al., 2006; Bojarska and Selva, 2012). In Alberta, grizzly bears do not have access to

regular sources of protein-rich foods (with the possible exception of late spring when ungulate neonates are consumed), and depend heavily on plant matter throughout much of the foraging season (McLellan and Hovey, 1995; Munro et al., 2006). This is particularly true during hyperphagia (late summer to early fall) when bears forage primarily on fruit-producing species to help accumulate the fat reserves necessary to survive the winter (Martin, 1983; Hamer and Herrero, 1987a; Hamer et al., 1991; Hamer, 1996; Munro et al., 2006; Holden et al., 2012; Mowat et al., 2013). Fruit from *Shepherdia canadensis* (buffaloberry) and *Vaccinium membranceum* (mountain huckleberry) comprise the majority of grizzly bear diets in the Canadian Rockies during hyperphagia (Hamer and Herrero, 1987a; Hamer et al., 1991; McLellan and Hovey, 1995; Munro et al., 2006), although in some cases *Amelanchier alnifolia* (saskatoon) also features prominently in the diet of bears (Hamer et al., 1991).

One of the most important factors regulating the availability and productivity of certain grizzly bear foods is forest disturbance (Nielsen et al., 2004c). In Alberta, natural disturbance regimes that were historically dominated by fire have been largely disrupted in the past century (Johnson et al.; Linke et al., 2013). Fire plays key roles in establishing successionally-mature open plant communities that typically represent high quality grizzly bear habitat (Hamer and Herrero, 1987b; Stewart et al., 2012). Additionally, both *S. canadensis* and *V. membranaceum*, which are critical late-season bear foods, are fire-successional species (Martin, 1983; Hamer et al., 1991; Hamer, 1996). Thus, the absence of recurring wildfires has contributed to losses of important grizzly bear feeding habitat (Hamer and Herrero, 1987b; Stewart et al., 2012).

In place of wildfire, forest harvesting has become the most prevalent source of disturbance within the forested areas of Alberta's grizzly bear range (Nielsen et al., 2008; Festa-Bianchet, 2010; Stewart et al., 2012). Some studies have suggested that forest harvesting has the potential to act as a surrogate for natural disturbance (Hunter, 1993; Nielsen et al., 2004b), while others have demonstrated that successfully emulating the ecological effects of natural disturbances remains challenging (Niemela, 1999; McRae et al., 2001; Nielsen et al., 2008; Lorente et al., 2012). Soil and vegetation characteristics often differ significantly between forest harvests and burns, and these differences can persist for periods in excess of 60 years (Lorente et al., 2012). Forest harvesting can increase local food supply for bears under certain conditions, and bears

may utilize forest harvests in areas where fire suppression activities limit the availability of natural forest openings (Nielsen et al., 2004b; Stewart et al., 2012). However, forest harvests can also negatively affect the recovery of some fruiting species (including *S. canadensis* and *V. membranaceum*) that are important late-season food sources (Anzinger, 2002; Nielsen et al. 2004c). Silvicultural practices such as scarification can disrupt the roots or rhizomes of these species, thereby limiting their vegetative recovery post-harvest (Anzinger, 2002; Nielsen et al. 2004c). Thus, even with the removal of canopy cover, which should promote fruit production (Hamer et al., 1996; Nielsen et al., 2004c), some of these key bear foods may not fully recover before canopy closure occurs. Because of this, the late-season food supply for bears in these areas can be reduced (Nielsen et al., 2004c).

To mitigate this effect of forest harvesting, habitat enhancements (wildlife food plots) have been proposed to accelerate the recovery of fruiting species in clearcuts (Nielsen et al., 2004c). Habitat enhancements have the potential to be a valuable tool for land managers because they provide opportunities for using anthropogenic disturbances to create positive conservation outcomes. Given that clearcuts are one of the most prevalent disturbance features in Alberta's forests (White et al., 2014), it follows that they could be ideal locations for habitat enhancements. Planting fruiting shrubs in clearcuts (or other anthropogenically-created disturbances such as reclaimed mine sites; Cristescu et al., 2012) where there is no canopy cover could generate significant increases in late-season food supply for grizzly bears. This, coupled with access restrictions and silvicultural forest thinning, could enable conservation planners to create 'safe-harbour' habitats, where habitat quality is high, and mortality risk is low (Nielsen et al., 2004c; Nielsen et al., 2006). However, little is known about whether habitat enhancements represent a feasible option for improving grizzly bear habitat quality. In particular, tests of the effectiveness of planting seedlings of different fruiting shrub species in clearcuts are lacking.

In southwestern Alberta, the confluence of extensive forest harvesting with a diverse array of climatic zones presents a unique opportunity to test the viability of habitat enhancements for increasing grizzly bear food supply in clearcuts. In this study, I conducted short-term planting trials for three important late season grizzly bear foods – *V. membranaceum*, *S. canadensis*, and *A. alnifolia* – in clearcuts in southwestern Alberta and monitored their survival and growth over

two growing seasons. Specifically, my objectives were: (1) to test whether a soil nutrient amendment treatment increased seedling survival and growth; (2) to test whether exclosure (fencing) treatments on seedlings increased survival and growth; (3) to test whether more developed seedlings had increased survival and growth; (4) to test whether changes in seedling survival and growth rates along the elevation gradient were consistent with the expected niche spaces of the trial species; and (5) to test whether higher solar radiation decreased seedling survival and growth.

2. METHODS

2.1 Study area

I installed 18 planting trials across a 5,065 km^2 study area in southwestern Alberta (Figure 3-1). The study area is bounded to the west by the British Columbia-Alberta border, and extends to the eastern edge of the Porcupine Hills. It is bounded to the south by the Waterton Lakes National Park boundary, and extends north approximately 125 km (N: 50.307 – 49.155, W: 114.753 – 113.791). Two of Alberta's seven grizzly bear population units (Livingstone and Waterton units) are represented in this study area (Nielsen et al., 2009). The study area is comprised primarily of mountainous and foothill ecosystems, with elevations ranging from 1155 m to 3009 m (mean elevation of 1672 m). At higher elevations (alpine and subalpine zones), summers are short and cool, and precipitation (particularly snow) is relatively high (Natural Regions Committee, 2006; Government of Alberta, 2010b). Lower elevation areas and foothills receive less precipitation and have short, warm summers (Natural Regions Committee, 2006; Government of Alberta, 2010b). Local climatic conditions are highly variable depending on elevation and topographic differences. Similarly, vegetation patterns are complex and correspond to differences in slope, aspect, elevation, latitude, and substrate (Natural Regions Committee, 2006). At the highest elevations, plant communities are generally herbaceous meadows or open conifer stands, whereas closed conifer, mixed-wood, and grassland communities occur at middle to lower elevations (Natural Regions Committee, 2006). Common conifer species include *Pinus contorta* (lodgepole pine), *Pinus flexilis* (limber pine), *Picea engelmannii* (Engelmann spruce), *Picea glauca* (white spruce), *Abies lasiocarpa* (subalpine fir), and *Pseudotsuga menziesii* (Douglas fir).

The most common deciduous species are *Populus tremuloides* (trembling aspen) and *Populus balsamifera* (balsam poplar).

The primary natural source of disturbance in the region is fire. Aggressive fire suppression and prevention, along with long-term climatic cycles, have diminished the presence of wildfire on the landscape (Johnson et al., 2001; Linke et al., 2013). Timber harvesting activities have been prevalent in the region for over a century and have replaced fire as the primary source of forest disturbance (Government of Alberta, 2010a; Stewart et al., 2012). Large amounts of unmerchantable timber can generate significant quantities of logging debris with regeneration of these sites often necessitating the use of scarification treatments to expose mineral soil (Government of Alberta, 2010b). Recreation activities occur throughout the study area, but are mainly concentrated in the Castle area south of highway 3, and in the Atlas road and Dutch creek areas north of highway 3 (Northrup et al., 2012). Cattle grazing is common throughout the study area, especially in native rangelands or disturbed areas, and primarily at low to moderate elevations (Natural Regions Committee, 2006). In general, cattle avoid forested areas (with the exception of forest edges which are used for shade or shelter) and spend most of their time foraging in clearcuts.

2.2 Trial species

Trial species included *S. canadensis*, *V. membranceum*, and *A. alinifolia*, three fruiting shrubs that are important food sources for bears during hyperphagia (late summer to early fall). *V. membranaceum* and *S. canadensis* comprise the majority of grizzly bear diets in Alberta and interior British Columbia during hyperphagia when they forage mostly on fruiting species to help accumulate the fat reserves needed for winter hibernation (Hamer et al., 1991; McLellan and Hovey, 1995, 2001; Hamer, 1996; McLellan et al., 1999, 2011; Nielsen et al., 2003; Munro et al., 2006). *A. alnifolia* has been identified as a significant component of late-season grizzly bear diets in southwestern Alberta (Hamer et al., 1991).

S. canadensis is a nitrogen-fixing shrub species that is able to thrive on nutrient-poor sites (Walkup, 1991). Vegetative reproduction is generally slow (Walkup, 1991). In the Canadian

Rockies, *S. canadensis* is typically found at low to moderate elevations (Walkup, 1991; Nielsen et al., 2003; Nielsen et al., 2004c; Roberts et al., 2014), and fruit production is inversely related to canopy cover (Hamer, 1996; Nielsen et al., 2004c). *V. membranaceum* is an understory shrub species that most often reproduces vegetatively via extensive systems of rhizomes. It typically thrives on cool, mesic sites with fruit production peaking in forest openings (Simonin, 2000). *V. membranaceum* generally occurs at moderate to high elevations in the Canadian Rockies (Hauessler and Coates, 1986; Roberts et al., 2014). Both *S. canadensis* and *V. membranaceum* utilize mycorrhizal symbiosis to help attain essential nutrients (Visser et al., 1991; McCracken, 1999). Finally, *A. alnifolia* is a thicket- or clump-forming shrub species that occurs in a wide variety of habitats, often reproducing vegetatively by sprouting from root crowns and rhizomes (Fryer, 1997; Chai et al., 2013). *A. alnifolia* is limited by moisture availability and will not tolerate prolonged periods of drought (Fryer, 1997). It is shade intolerant and generally grows in forest openings or under moderate levels of canopy cover (Fryer, 1997). In the Canadian Rockies, *A.alnifolia* is found from low to high elevations (Roberts et al., 2014), although it is less common at higher elevations where growth is often limited by temperature.

2.3 Site selection

Planting trials were installed in 18 clearcuts with a minimum of three trials in each of four 100-m elevation zones ranging from 1400 m to 1800 m. Only clearcuts with slopes of less than 10 degrees were used for trials to minimize slope-aspect effects. Site selection was also limited to clearcuts that had been planted within the past five years to limit competition between experimental seedlings and canopy species, including conifer seedlings. Site-specific details for planting trials are summarized in Table 3-1.

2.4 Seedling procurement and handling

Seedlings of *S. canadensis*, *V. membranaceum*, and *A. alnifolia*, were obtained from nearby Cranbrook, British Columbia with similar climates and habitats (~95 km distance). All stock was established from locally-sourced seeds in January 2013 and grown until June 2013. Seedlings were grown in heated greenhouses until they developed a solid root ball, at which point they

were moved outside to harden. Seedlings were moistened and wrapped in cellophane to help keep them moist during shipment. Shipments were staggered during the planting period (June 15 – June 26) to avoid heat or moisture stress prior to planting. Seedlings were kept in a cool, shaded location, misted nightly to prevent them from drying out, and planted within two days of being received. Planting date had no major effect on survival or growth and was therefore not included in any models. Mean temperature and total precipitation were 7.5% and 1.2% higher than normal during the summer of 2013 (June – August), respectively.

2.5 Planting trial design

Species were randomly distributed in each trial site within a 6 × 6 grid (12 m × 12 m, 144 m^2; Figure 3-2). Each species grid square (4 m^2) included four seedlings of that species (one for each of the four experimental treatments) resulting in 12 replicates of each treatment-species combination (n = 216 for each species-treatment combination across all 18 trial sites). Planting trials were designed to incorporate the three trial species (*V. membranaceum, S. canadensis,* and *A. alnifolia*) and four experimental treatments. Specifically, treatments included an exclosure (fencing), a soil nutrient amendment, a combined treatment of amendment and exclosure, and a control (no treatment). The amendment treatment consisted of 10 g of slow-release shrub fertilizer (18-4-6) applied in separate holes approximately 4 inches deep and 1 inch away from each seedling. Newly planted seedlings generally have limited root development and, thus, reduced capacity for water and nutrient uptake (Grossnickle, 2005). For this reason, slow release fertilizers placed near the root system are generally recommended to help overcome planting stress and improve seedling establishment (Grossnickle, 2005). For the exclosure treatment, cylindrical exclosures measuring approximately 12 inches tall and 5 inches in diameter were constructed from 1-inch hexagonal weave chicken wire. Individual exclosures accommodated the randomized plot layout by removing the need to group seedlings within large exclosures at each site, while still discouraging ungulate browsing.

2.6 Measures of seedling shrub survival and growth

Initial seedling heights were measured at time of planting in June 2013. For each species, heights were measured as the length of the longest stem from its base to its terminal bud. First-season survival and growth were measured at the end of the first growing season (September 2013) prior to seedling senescence and snow cover to allow for identification of live shrubs. Overwinter survival was measured at the start of the second growing season (June 2014) following snowmelt and leaf out. Finally, second-season survival and growth were measured at the end of the second growing season in late August 2013.

2.7 Models of seedling shrub survival

Seedling survival was modeled separately for each species as a binary response (0 – died; 1 – survived) using mixed effects logistic regression and separately for the first growing season, overwinter, and second growing season periods. Only seedlings that survived a given period were included in analyses for subsequent periods (i.e., only seedlings that survived the first growing season were included in overwinter survival analyses). Overall survival (i.e., dead seedlings were not censored) was also modeled to assess treatment and non-treatment effects across the full trial period (15 months). A random effect (intercept) for block was used to account for possible survival differences between blocks. The spatial arrangement of seedlings within each trial plot had no significant effect on survival and was therefore not considered in survival models. Binary variables were coded for each treatment and included in initial models to test for treatment effects on seedling survival. Initial seedling height (representative of initial seedling condition) and elevation were then added to treatment models to test for possible non-treatment effects on survival. Initial seedling height was used to represent initial seedling condition, which may affect survival, whereas elevation was used as a proxy for possible climatic effects. Elevation is a complex set of environmental variables that are a surrogate of climate that varies geographically, but is useful for ease of communicating results to land managers. Linear and quadratic forms of the elevation covariate were considered, and the most-supported form (based on p-values) was included in the full model for that species. Finally, potential direct incident radiation (PDIR; McCune and Keon, 2002) derived from a digital

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elevation model was included to account for possible slope and aspect effects on seedling survival despite plots being associated with slopes of less than 10 degrees.

2.8 Models of seedling shrub growth

Similar to survival, seedling growth was modeled separately for each species. Given that growth is conditional on survival, only seedlings that survived the growing season were included in growth models. First-season growth data were not analyzed because seedlings were hardened prior to planting, which can influence growth. Growth data were highly skewed (i.e., many zeros and low growth values), which violated the normality assumptions of linear regression (transformations did not help normality). To overcome this, growth data were analyzed using mixed effects ordered logistic regression models. Growth data were binned into three ordinal growth classes. Seedlings were assigned a value of "0" if they survived a particular growing season but had no measurable growth. Mean growth of the remaining seedlings (i.e., those seedlings that had measurable growth) was used as the threshold for assigning each seedling a value of "1" or "2" (measurable growth less than the mean or measurable growth greater than the mean, respectively). Ordered logistic regression uses an ordinal response variable to estimate multiple equations with separate intercepts for each level (number of growth classes minus one), and each regression equation uses the same set of predictor variable coefficients (Leu et al., 2011). A random effect (intercept) for block was included to account for possible between-block effects on growth. The spatial arrangement of seedlings within trial plots did not significantly affect seedling growth and was not considered in growth models. As with survival analyses, initial models included only binary treatment variables with initial seedling height, elevation and PDIR added to test for non-treatment effects on growth. Ordered logistic regression assumes parallel regression lines (Leu et al., 2011) for each equation (i.e., the relationship between each growth class is the same, which is why only one set of coefficients is needed). To test this assumption, a likelihood-ratio test of proportionality of odds across response categories was performed for each model. A significant result from this test indicates a difference in coefficients between models (i.e. non-parallel slopes), which violates the parallel regression assumption.

3. RESULTS

3.1 Seedling survival

First-season (summer) survival was highest for *A. alnifolia* (80.4%), followed by *V. membranaceum* (57.1%) and *S. canadensis* (45.7%). Treatment effects on first-season survival were consistent across all trials species (Table 3-1, Figure 3-3). Amendment and combined (included both amendment and exclosures) treatments were negatively related to survival, whereas the exclosure treatment increased survival probabilities. First-season survival of *S. canadensis* was positively related to elevation and PDIR. First-season survival for *V. membranaceum* was not related to treatments. First-season survival of *A. alnifolia* was positively related to initial seedling height and PDIR.

Overwinter survival for those seedlings that survived their first summer was higher than first season (summer) survival at 90.5%, 71.4%, and 70.8% for *A. alnifolia*, *S. canadensis*, and *V. membranaceum*, respectively. The exclosure treatment positively affected *S. canadensis* overwinter survival, but no other treatment effects were supported in overwinter survival models (Table 3-1, Figure 3-3). Non-treatment factors were generally not supported in overwinter survival models with the exception of initial seedling height, which was positively related to *A. alnifolia* overwinter survival.

A. alnifolia had the highest second-season (summer) survival rate (85.1%), followed by *V. membraceum* (63.6%) and *S. canadensis* (61.7%). The exclosure treatment increased second-season survival for *V. membranaceum* and *A. alnifolia* (Table 3-1, Figure 3-3). The amendment treatment had a positive effect on second-season survival of *S. canadensis* and a negative effect on second-season survival of *A. alnifolia*. Second-season survival for *S. canadensis* was positively related to elevation. A positive relationship between PDIR and second-season survival was weakly supported for *S. canadensis*, and strongly supported for *A. alnifolia*.

Overall survival was highest for *A. alnifolia* (61.9%), followed by *V. membranaceum* (25.7%) and *S. canadensis* (20.1%). The exclosure treatment positively affected overall survival for all

three trial species, whereas the amendment treatment negatively affected overall survival for *A. alnifolia* and *V. membranaceum* (Table 3-1, Figure 3-3). The combined treatment did not affect overall survival for any trial species. Initial seedling height positively affected overall survival for *A. alnifolia*. Overall survival for *S. canadensis* and *V. membranaceum* increased with elevation, whereas no effect of changing elevation was observed on overall *A. alnifolia* survival. As with first- and second-season survival, PDIR positively affected overall survival for *S. canadensis* and *A. alnifolia*.

3.2 Seedling growth

Mean proportional growth for surviving seedlings (total growth as a percentage of initial seedling height) was highest for *S. canadensis* (16.8%), followed by *A. alnifolia* (7.0%) and *V. membranaceum* (3.4%). Similarly, cumulative proportional growth (total growth as a percentage of initial seedling height) was highest for *S. canadensis* (19.6%), followed by *A. alnifolia* (11.3%), and *V. membranaceum* (6.4%). Treatment effects were not supported in second-season growth models for any trial species (Table 3-2, Figure 3-4). Non-treatment factor effects were also generally not supported in second-season growth models. However, initial seedling height was inversely related to *A. alnifolia* growth, while elevation was positively related to *V. membranaceum* growth.

4. DISCUSSION

4.1 Seedling Survival

Survival rates were lowest during the first growing season for all three trial species, and increased for the overwinter and second-season observation periods. Overall survival was highest for *A. alnifolia* (61.9%), followed by *V. membranaceum* (25.7%) and *S. canadensis* (20.1%). Similar tests of containerized *A. alnifolia* and *S. canadensis* seedling survival have been conducted to assess their potential for use in reclamation because both species generally perform well on nutrient-deprived, disturbed sites (Walkup, 1991; Fryer, 1997; Shaw et al., 2004). Dreesen (2000) obtained a comparable survival rate of 53% for containerized *A. alnifolia*

seedlings planted on mine overburden piles, whereas Fedkenheuer et al. (1980) reported survival rates of between 78% and 100% for *A. alnifolia* seedlings planted on amended oil sand tailings. In the same study, survival rates for containerized *S. canadensis* seedlings ranged from 56% to 100%. Similarly, Visser et al. (1991) reported first-year survival rates for *S. canadensis* seedlings planted on amended oil sand tailings of 53 to 75%, although they noted much lower survival in the second year. The lack of browsing and herbaceous competition may explain the higher survival rates for both species when planted on amended oil sand tailings. Comparable tests of containerized *Vaccinium* spp. seedling survival on disturbed sites are lacking.

Treatment effects were strongest during the first growing season, indicating that although amendments and exclosures may have played significant roles in determining initial seedling establishment (i.e. first-season survival), they did not substantially influence subsequent seedling survival (Table 3-1, Figure 3-3). Low survival rates and strong treatment effects during the first growing season affected overall survival rates, with patterns in overall survival data paralleling first-season patterns (Figure 3-3). The exclosure treatment positively affected overall seedling survival for all trial species, although evidence for browsing was limited. Generally, this suggests that exclosures may have increased survival rates by limiting competition from neighbouring plants and not necessarily by protecting the seedlings from browsing. Contrary to what was predicted, the amendment treatment negatively affected overall survival for both *V. membranaceum* and *A. alnifolia*, and did not significantly affect overall *S. canadensis* survival (Table 3-1, Figure 3-3). This is likely because the addition of soil nutrients increased the competitive ability of neighbouring plants. Limited root development and root-soil contact could have reduced the seedlings' ability to uptake nutrients compared to other plants already established in the clearcut (Grossnickle 2005). The combined treatments negatively affected first-season survival for *V. membranaceum* and *A. alnifolia*, but had no effect on overall survival, perhaps indicating that the initial negative effect of the amendment was balanced by a consistently positive effect of exclosures.

More developed seedlings were predicted to have higher survival rates, but initial seedling height had no significant effect on *S. canadensis* or *V. membranaceum* survival. However, initial height was positively related to survival for *A. alnifolia* (first-season, overwinter, and overall survival),

suggesting that initial seedling condition plays an important role in determining survival rates for *A. alnifolia*, with more developed seedlings having a higher chance of success. Overall survival rates increased with elevation for *V. membranaceum*, which is consistent with the expected niche space for the species (moderate to high elevations; Roberts et al., 2014). Changes in observed occupancy rates of *V. membranaceum* (calculated using presence-absence data from field plots) with elevation were consistent with changes in survival rates along the same gradient (Table 3-4, Figure 3-5). Elevation was also positively related to overall survival for *S. canadensis*, which is unexpected given that *S. canadensis* is typically described as a low to moderate-elevation species in Alberta (Walkup, 1991; Nielsen et al., 2003; Nielsen et al., 2004c). Observed occupancy rates of *S. canadensis* were consistent with the expected niche space of the species and decreased with elevation (Table 3-4, Figure 3-5). This suggests that other factors (potentially site-specific factors, such as soil characteristics) influenced *S. canadensis* survival more strongly than elevation and bolstered survival at higher elevations. Similar to *S. canadensis*, *A. alnifolia* typically occurs at low to moderate elevations in Alberta (Roberts et al., 2014). Observed occupancy rates of *A. alnifolia* corroborated this and decreased with elevation (Table 3-4, Figure 3-5). Conversely, overall *A. alnifolia* survival rates were consistently high across all elevations, which is inconsistent with the expected niche space of the species and suggests that the fundamental niche of the species may be much wider than its realized niche, which is shaped by longer-term processes like interspecific competition for resources (Griesemer, 1992; Pulliam, 2000). Lastly, solar radiation (PDIR) positively affected first-season and overall survival for *S. canadensis* and *A. alnifolia*, suggesting that warmer microsites promoted survival for these species. This suggests that microsite-related increases in growing degree days may be more important than moisture in limiting survival of these two species. However, given that all trial sites had slopes less than 10 degrees, the range of PDIR values was relatively narrow, and thus relationships between PDIR and survival rates are representative of only a portion of possible PDIR values.

4.2 Seedling growth

Mean proportional growth in the second growing season was highest for *S. canadensis* (16.8%). This result is consistent with the findings of Densmore et al. (2000), who reported "vigorous"

growth responses for containerized *S. canadensis* seedlings planted on disturbed areas in Alaska. Similarly, Visser et al. (1991) observed significant growth for containerized *S. canadensis* seedlings after two growing seasons, although they were planted in a markedly different substrate (oil sands tailings amended with peat or a peat-mineral mix). Die back was observed for *A. alnifolia* and *V. membranaceum* seedlings, which may explain why they had lower mean proportional growth values (7.0% and 3.4%, respectively). Densmore et al. (2000) reported similar die back for containerized *Vaccinium uliginosum* and *Vaccinium vitis-idaea* seedlings planted on disturbed sites.

Treatments did not affect second-season growth for any trial species, suggesting that treatments affected survival (and more specifically, initial seedling establishment), but did not significantly influence subsequent growth (Table 3-2, Figure 3-4). *A. alnifolia* growth was negatively related to initial seedling height, which may indicate that while taller *A. alnifolia* seedlings were more likely to survive, they were also more likely to be browsed (thus limiting any measurable growth). An alternative explanation is that taller *A. alnifolia* seedlings may have been less able to sustain their size, leading to stem die back and limiting growth. The growth of *A. alnifolia* seedlings is dependent on soil moisture availability (Shaw et al, 2004), and thus the growth of taller *A. alnifolia* seedlings may have been moisture-limited. *V. membranaceum* growth was greater at higher elevations, which is consistent with the expected niche space for this species (Haeussler and Coates, 1986; Roberts et al., 2014).

4.3 Management recommendations

Overall survival rates were lowest for *S. canadensis* and *V. membranaceum*, at 20% and 26% respectively. This indicates that establishment of these species in clearcuts is feasible, although survival rates can likely be increased by testing alternative growing and outplanting methods. *A. alnifolia* had the highest overall survival rate (62%), but is also preferred browse for ungulates which can limit its long-term productivity (Ferguson, 1983; Kay, 1995; Paschke et al., 2003; Shaw et al., 2004, Straker et al., 2010). Thus, even though *S. canadensis* and *V. membranaceum* may have lower short-term survival rates, they would also have lower long-term browsing pressure and could therefore be more productive than *A. alnifolia* in the long-term.

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Survival rates were lowest for the first growing season, and increased for subsequent observation periods, which highlights the importance of enhancing initial seedling establishment. The addition of soil nutrient amendments was expected to bolster seedling survival and growth, but had the opposite effect with decreased survival rates. Dreesen (2000) observed a similar negative relationship between soil nutrient amendments and seedling survival rates for containerized *A. alnifolia* seedlings, although they applied fertilizer over five successive growing seasons. Conversely, Densmore & Holmes (1987) found that fertilizer treatments had little to no effect on short-term (first-season) containerized seedling survival. The use of soil nutrient amendments in wildlife habitat enhancements should be informed by site-specific soil nutrient assessments and should be applied on a case-by-case basis. Nutrient regimes will differ between sites, and nutrient requirements of candidate shrub species will also vary. For example, *S. canadensis* is a nitrogen-fixing species that can thrive on disturbed, nutrient-poor sites (Walkup, 1991). Because of this, it may not require additional nutrients, and may even be negatively affected by fertilizer treatments if they increase herbaceous competition.

Exclosures increased survival rates but required a significant monetary investment to construct and install. Straker et al. (2010) found that individual physical plant protectors (exclosures) increase survival rates for most deciduous species, but are also costly to install and maintain. For preferred browse species such as *A. alnifolia*, the use of exclosures can help to ensure successful establishment and to protect seedlings until they are sufficiently developed to resist browsing pressure (Straker et al., 2010). Protection from browsing pressure is generally recommended for *A. alnifolia* seedlings during the first 3 to 4 growing seasons because new shoots are highly palatable to ungulates (Paschke et al., 2003; Shaw et al, 2004; Straker et al, 2010). This is especially true for forest grazing leases (which are prevalent in this study area) because young *A. alnifolia* growth is palatable to livestock (Paschke et al., 2003). Conversely, habitat enhancements using less palatable species such as *S. canadensis* or *V. membranaceum* could benefit from simply planting additional seedlings rather than investing in protective measures such as exclosures.

Initial seedling height did not affect survival rates for *S. canadensis* or *V. membranaceum*. This is consistent with the findings of Straker et al. (2010), who found that stock age and size did not significantly affect long-term seedling survival for containerized shrub seedlings used in coal mine reclamation and suggested that younger seedlings are generally more cost-effective. Conversely, initial seedling height positively affected *A. alnifolia* survival, suggesting that larger, more developed seedlings had a better chance of success.

Both *S. canadensis* and *A. alnifolia* typically occur at low to moderate elevations in Alberta (Walkup, 1991; Nielsen et al., 2003; Nielsen et al., 2004c, Roberts et al., 2014), yet the results of these trials indicate the opposite trend for *S. canadensis*, and no effect of elevation was observed on *A. alnifolia* survival. In the case of *S. canadensis*, this suggests that knowledge of its niche space along the elevation gradient alone is not sufficient to identify areas where it will have a higher chance of success as an enhancement species. For *A. alnifolia*, on the other hand, consistently high survival rates across the elevation gradient suggest that its fundamental niche is much wider than its realized niche, which in turn indicates that it is possible to plant the species outside of its expected niche space and still have successful establishment. From a management perspective, knowledge of the relationships between the survival and growth of these species and elevation will be an important component of designing successful wildlife habitat enhancements.

Finally, *A. alnifolia* typically shows adaptations to local conditions (Shaw et al., 2004). It is recommended that seeds used to grow containerized stock are collected in close proximity to eventual planting locations (Paschke et al., 2003; Shaw et al., 2004). While it is unclear whether this also applies to *S. canadensis* and *V. membranaceum*, it is not unreasonable to assume that most shrub species exhibit local optimality to some extent (Chai et al., 2013), and that seedlings may underperform when planted on sites dissimilar to their original seed sources. The closest native plant nursery with sufficient quantities of planting stock for this study was located in Cranbrook, British Columbia at a distance of ~95 km (59 miles). Though they source their seeds locally and the general range of climates between the areas (seed sources and planting locations) is similar, this may have reduced survival rates (Hope et al., 1991; Ketchenson et al., 1991; Coupé et al., 1991; Natural Regions Committee, 2006). Transfer of seedlings between similar biogeoclimatic regions is also consistent with Alberta's native plant revegetation guidelines

(Native Plant Working Group, 2000). Where possible, managers should strive to obtain planting stock from local sources to help maximize survival rates. In some cases (such as in Alberta), use of locally-sourced planting stock for shrubs is becoming a regulatory requirement to limit maladaptation and to maintain genetic integrity (Chai et al., 2013).

5. CONCLUSIONS

Habitat enhancements have the potential to increase grizzly bear food supply in disturbed areas, including forest harvests. *A. alnifolia* had significantly higher survival rates than *S. canadensis* and *V. membranaceum*, but is also preferred browse which may make it less effective in the long-term if unprotected from browsing pressure. Soil nutrient amendments reduced seedling survival rates for all three trial species. Given that these species occur naturally on these soils, such amendments may be unnecessary. Furthermore, addition of soil nutrients may have increased herbaceous competition, which can negatively affect seedling survival and growth (Paschke et al., 2003). Exclosures increased seedling survival rates for all three trial species and may be considered for use in the early stages of habitat enhancements, particularly for highly palatable species such as *A. alnifolia*. Given the investment required to install and maintain exclosures (Straker et al., 2004), it may be more effective cost-wise to simply plant more seedlings. Long-term tests are needed to quantify eventual fruit production for fruiting shrubs. Furthermore, long-term trials would better incorporate the effects of inter-annual climatic variation and interspecific interactions (browsing, competition for resources, etc.), which would likely influence long-term survival, growth, and fruit production (Griesemer, 1992; Pulliam, 2000).

As natural forest openings become less prevalent (Nielsen et al., 2004b; Stewart et al., 2012), anthropogenically-created forest openings, if properly managed, have the potential to provide considerable quantities of late-season food resources (fruit) for grizzly bears (Nielsen et al., 2004b). However, the use of habitat enhancements must be coupled with access restrictions to avoid the development of attractive sinks (high risk, high quality habitats) (Nielsen et al. 2004c; Cristescu et al., 2012). Active management techniques such as planting fruit-producing food items in clear cuts (as suggested by Nielsen et al., 2004b), represent one possible aspect of the

mitigation strategy needed in clear cuts. Use of disruptive post-harvest site preparation methods, such as mechanical scarification, should be avoided where possible, and long-term periodic thinning of planted conifers should be considered. Thinning has the potential to bolster grizzly bear food supply in clearcuts by reducing canopy cover (Nielsen et al., 2004b), and can also increase timber yields by reducing competition between conifer saplings. In the absence of periodic thinning (which may also complicate access restrictions), planting containerized shrub seedlings may be the only viable option for producing significant quantities of fruit in clearcuts before canopy closure limits fruit production.

Table 3-1. Site details for planting trials in southwestern Alberta. Universal transverse Mercator (UTM) coordinates are specific to UTM zone 11. Opening numbers are unique identifiers for clearcuts and are a concatenation of the clearcut's legal land description and a grid cell number (format is MRRTTTSSGG, where M = meridian, RR = range, TTT = township, SS = section, GG = grid cell). Percent cover for trial species was calculated using line intercept data from 50-m line intercept transects conducted within each trial clearcut.

Site Number	UTM Easting	UTM Northing	Elevation (m)	Slope (°)	Aspect (°)	Opening Number	S. canadensis Cover (%)	V. membranaceum Cover (%)	A. alnifolia Cover (%)
1	0674528	5503421	1465	3	164	5050082330	4.2	0.0	3.0
2	0674507	5504120	1476	0	-	5050082340	0.0	0.0	0.4
3	0681535	5508323	1797	3	344	5040090470	0.8	0.0	0.0
4	0683449	5531222	1494	5	190	5040111450	0.0	0.0	0.0
5	0680975	5531778	1518	2	70	5040111510	0.0	0.0	0.0
6	0681651	5531195	1532	2	184	5040111540	0.0	0.0	0.0
7	0672906	5508090	1680	5	262	5050090340	4.0	0.0	2.0
8	0672152	5511278	1757	6	270	5050091500	0.0	0.0	0.0
9	0672624	5506821	1604	7	260	5050083420	-	-	-
10	0673807	5505501	1583	10	225	5050082800	1.2	0.0	0.0
11	0675822	5503785	1485	2	55	5050082410	1.4	0.0	4.4
12	0682026	5503668	1550	8	130	5040082190	1.6	0.0	2.0
13	0681319	5505259	1708	9	120	5040082850	0.0	0.0	1.2
14	0681537	5503651	1592	6	95	5040082160	0.2	0.0	0.0
15	0681384	5503324	1611	7	220	5040082150	0.0	0.0	0.0
16	0673102	5507111	1633	4	200	5050083460	2.6	0.0	1.4
17	0675332	5503769	1478	4	255	5050082380	0.0	0.0	3.0
18	0681319	5505259	1631	7	85	5040082850	0.0	0.0	0.0

Table 3-2. Model coefficients and standard errors for first-season, overwinter, second-season, and overall survival (AE = amendment and exclosure, E = exclosure, A = amendment, PDIR = potential direct incident radiation based on a digital elevation model).

Species	Period	Model[a]	Treatments			Covariates			
			AE	E	A	Initial Height	Elevation	Elevation^2	PDIR
S. canadensis	First	1	-0.36 (0.21)*	0.81 (0.21)***	-0.92 (0.21)***				
		2	-0.36 (0.21)*	0.78 (0.21)***	-0.94 (0.21)***	0.060 (0.037)	5.1^b (1.2^b)***		12 (3.2)***
	Overwinter	1	-0.16 (0.32)	0.77 (0.32)**	-0.38 (0.35)				
		2	-0.18 (0.32)	0.78 (0.32)**	-0.39 (0.35)	0.016 (0.060)	2.5^b (1.9^b)		-3.7 (4.4)
	Second	1	0.69 (0.39)*	0.22 (0.31)	0.99 (0.46)**				
		2	0.65 (0.39)*	0.26 (0.32)	0.98 (0.46) **	-0.96^b (0.061)	4.6^a (1.4^b)***		6.1 (3.5)*
	Overall	1	0.034 (0.26)	0.84 (0.24)***	-0.34 (0.28)				
		2	0.022 (0.26)	0.81 (0.24)***	-0.36 (0.28)	0.053 (0.043)	6.5^b (1.4^b)***		9.0 (3.6)**
V. membranaceum	First	1	-0.59 (0.22)***	0.78 (0.24)***	-0.83 (0.22)***				
		2	-0.59 (0.22)***	0.77(0.24) ***	-0.83 (0.22)***	0.012 (0.015)	0.094 (0.10)	-0.027^b (0.031^b)	11 (8.0)
	Overwinter	1	0.055 (0.30)	0.35 (0.28)	-0.25 (0.30)				
		2	0.055 (0.30)	0.40 (0.28)	-0.25 (0.30)	0.035 (0.019)*	0.089 (0.054)*	-0.026^b (0.017^b)	-3.1 (4.1)
	Second	1	0.20 (0.34)	0.66 (0.32)**	-0.26 (0.35)				
		2	0.17 (0.34)	0.64 (0.32)**	-0.27 (0.35)	-2.8^b (0.021)	-0.13 (0.085)	0.040 (0.026)	3.8 (6.7)
	Overall	1	-0.21 (0.24)	0.78 (0.23)***	-0.72 (0.26)***				
		2	-0.21 (0.24)	0.78 (0.23)***	-0.73 (0.26)***	0.015 (0.015)	6.9^b (2.5^b)***		8.1 (6.3)
A. alnifolia	First	1	-0.60 (0.25)**	0.71 (0.32)**	-0.95 (0.25)***				
		2	-0.60 (0.26)**	0.76 (0.32)**	-0.98 (0.25)***	0.028 (8.3^b)***	-0.026 (0.061)	0.0082^b (0.019^b)	15 (5.3)***
	Overwinter	1	0.37 (0.39)	0.43 (0.38)	-0.39 (0.35)				
		2	0.41 (0.40)	0.52 (0.38)	-0.38 (0.35)	0.032 (0.013)***	-0.092 (0.086)	0.029 (0.027)	4.6 (6.7)
	Second	1	0.58 (0.35)*	0.71 (0.34)**	-0.73 (0.30)**				
		2	0.57 (0.35)	0.69 (0.34)**	-0.70 (0.30)**	-6.6^b (0.012)	3.6^b (1.5^b)**		12 (4.2)***
	Overall	1	0.00 (0.21)	0.73 (0.22)***	-0.89 (0.21)***				
		2	5.4^b (0.21)	0.76 (0.23)***	-0.90 (0.21)***	0.021 (7.1^b)***	1.9^b (1.4^b)		13 (3.8)***

* p-value < 0.1; ** p-value < 0.05; *** p-value < 0.01.

[a] Model 1 included only treatment variables; Model 2 included both treatment and non-treatment variables.

[b] Original value 1,000 times smaller.

Table 3-3. Model coefficients and standard errors for second-season growth (AE = amendment and exclosure, E = exclosure, A = amendment, PDIR = potential direct incident radiation from a digital elevation model).

Species	Model[a]	Covariates						
		AE	E	A	Initial Height	Elevation	Elevation^2	PDIR
S. canadensis	1	0.63 (0.44)	0.64 (0.40)	0.22 (0.47)				
	2	0.77 (0.46)*	0.73 (0.40)*	0.30 (0.47)	-0.093 (0.079)	2.3[b] (1.7[b])		1.8 (4.1)
V. membranaceum	1	-0.73 (0.45)*	-0.55 (0.37)	-0.35 (0.47)				
	2	-0.77 (0.45)*	-0.45 (0.37)	-0.27 (0.47)	0.039 (0.026)	5.4[b] (2.2[b])**		2.5 (4.9)
A. alnifolia	1	-0.065 (0.23)	-0.073 (0.22)	0.20 (0.26)				
	2	-0.11 (0.23)	-0.13 (0.22)	0.19 (0.26)	-0.029 (8.3[b])***	0.068 (0.050)	-0.020[b] (0.015)[b]	1.5 (3.9)

* p-value < 0.1; ** p-value < 0.05; *** p-value < 0.01.

[a] Model 1 included only treatment variables; Model 2 included both treatment and non-treatment variables.

[b] Original value 1,000 times smaller.

Table 3-4. Occupancy rates for trial species and number of field plots in 100-m elevation zones ranging from 1300 m to 2100 m. Occupancy rates for each elevation zone are the number field plots occupied by a given trial species divided by the total number of field plots within that elevation zone.

Elevation Zone (m)	*S. canadensis* Occupancy Rate	*V. membranaceum* Occupancy Rate	*A. alnifolia* Occupancy Rate	Number of Field Plots
1300 – 1400	0.67	0.00	0.83	6
1400 – 1500	0.48	0.18	0.56	62
1500 – 1600	0.41	0.06	0.50	70
1600 – 1700	0.51	0.03	0.40	67
1700 – 1800	0.41	0.02	0.28	64
1800 – 1900	0.25	0.36	0.04	28
1900 – 2000	0.17	0.58	0.17	12
2000 – 2100	0.25	0.38	0.00	8
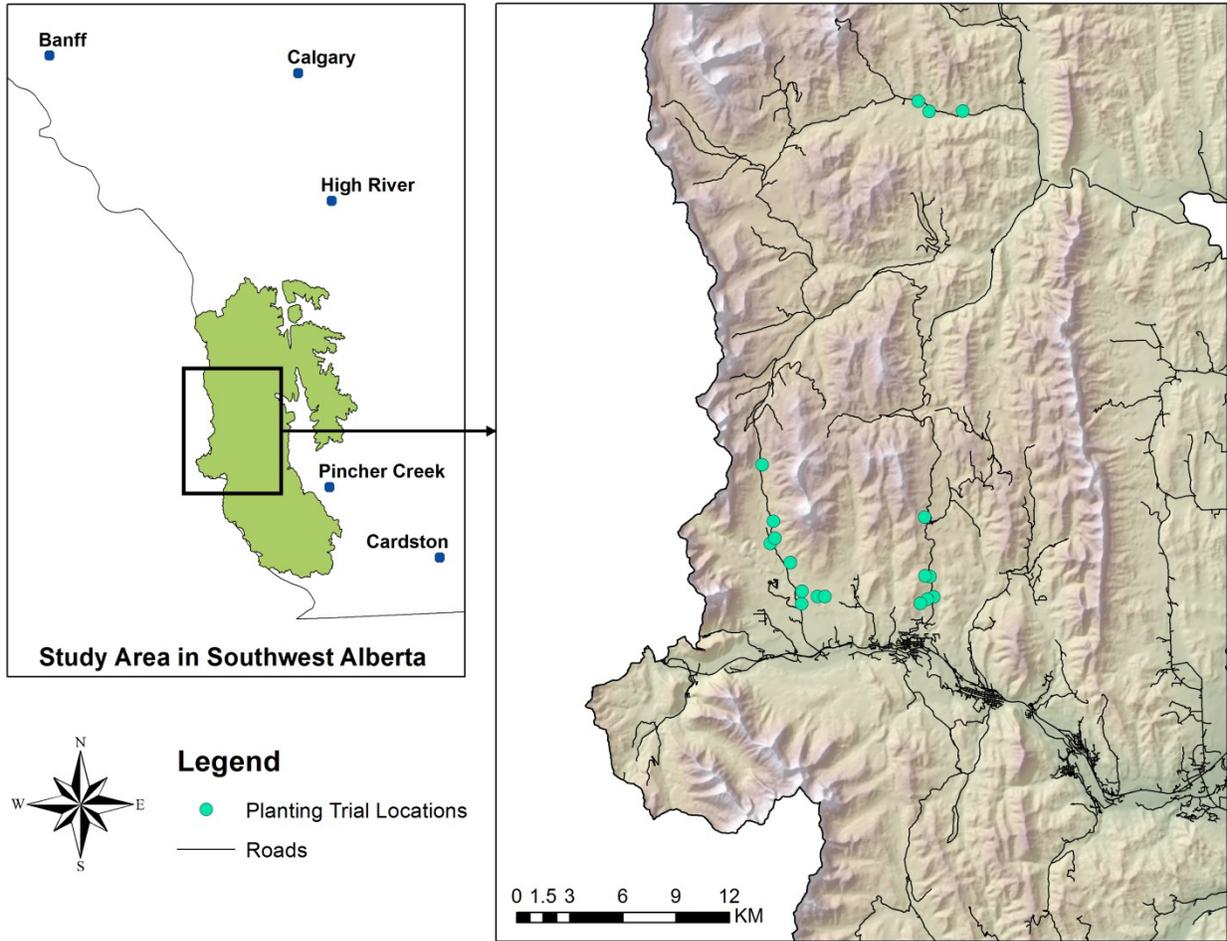
Figure 3-1. Planting trial locations in southwestern Alberta.
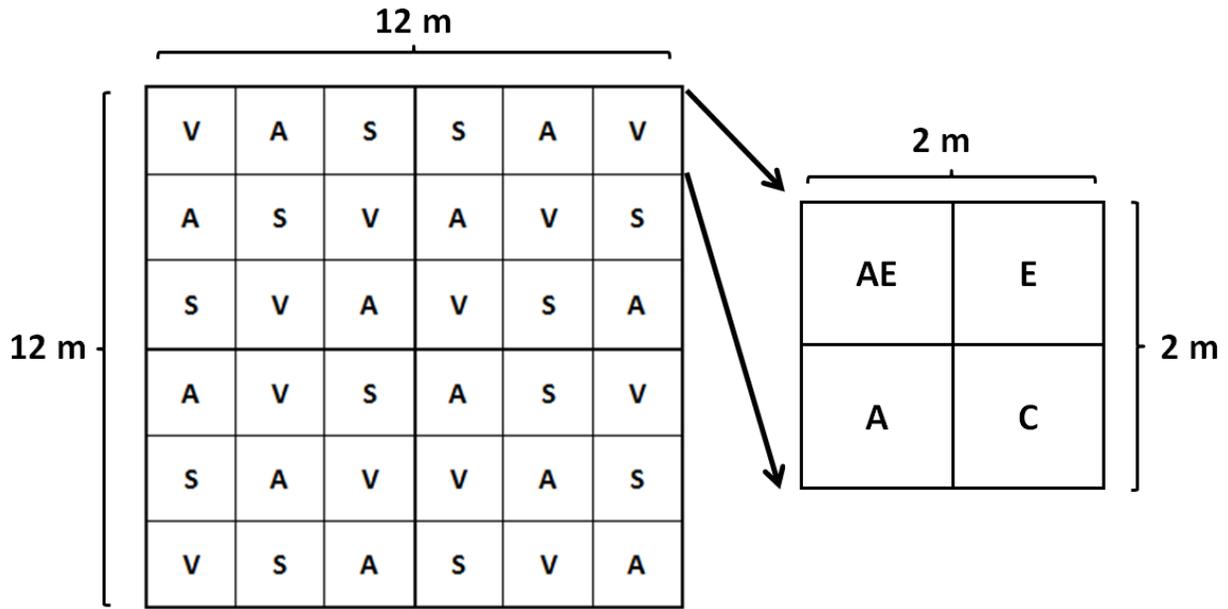
Figure 3-2. Planting trials were 144 m^2 plots consisting of 36 randomized species grid squares (V = *Vaccinium membranaceum,* S = *Shepherdia canadensis,* and A = *Alnifolia alnifolia*). Each 4 m^2 species grid (2 m × 2 m) contained four plugs of that species (one for each experimental treatment; AE = amendment and exclosure, E = exclosure, A = amendment, C = control).
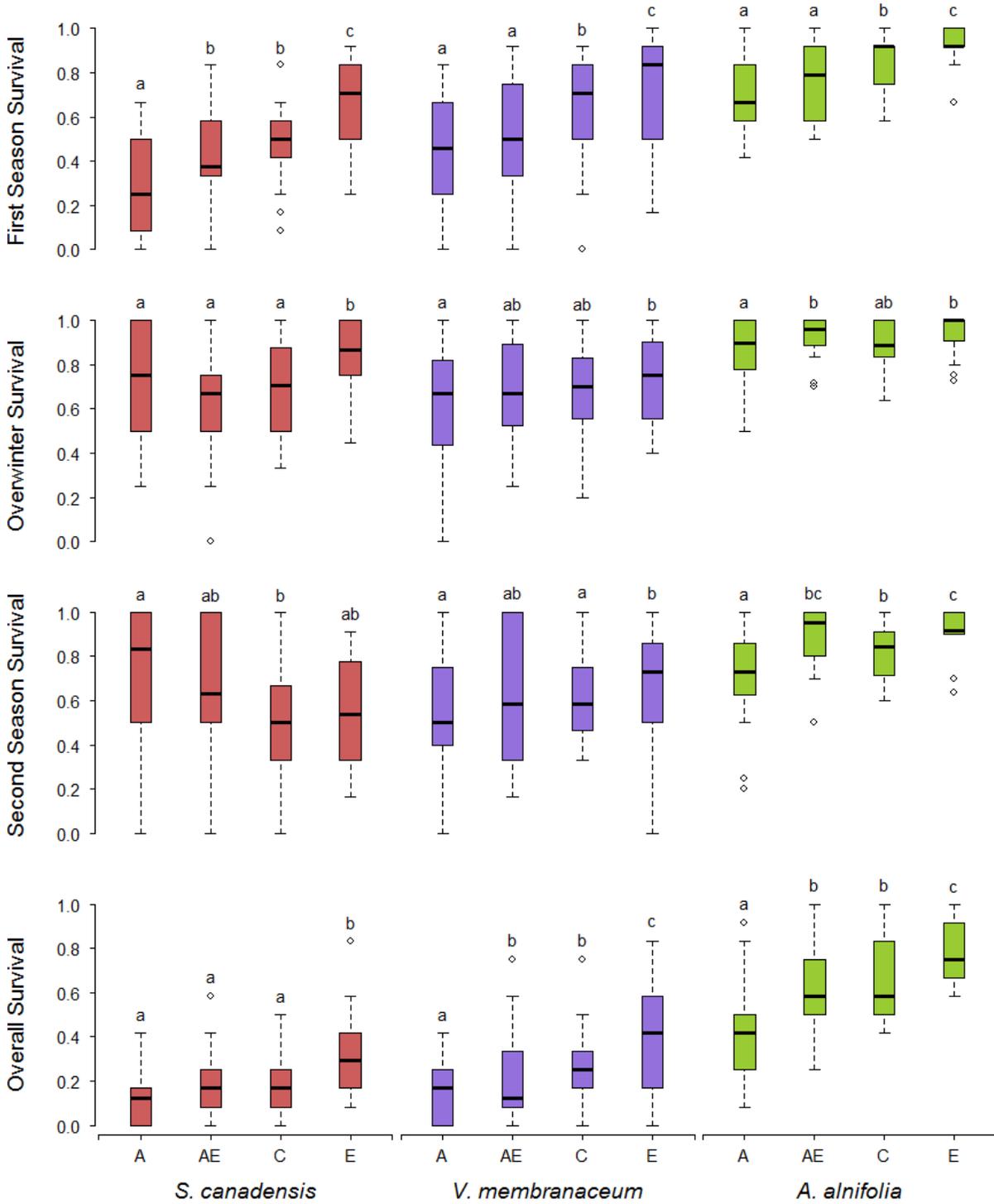
Figure 3-3. Boxplots of first-season, overwinter, second-season, and overall survival (proportion of seedlings survived) by block for each trial species (A = amendment; AE = amendment and exclosure; C = control; E = exclosure). Letters indicate significant differences between treatments (while controlling for effects of solar radiation, elevation, and initial seedling height using logistic regression; $p < 0.05$).
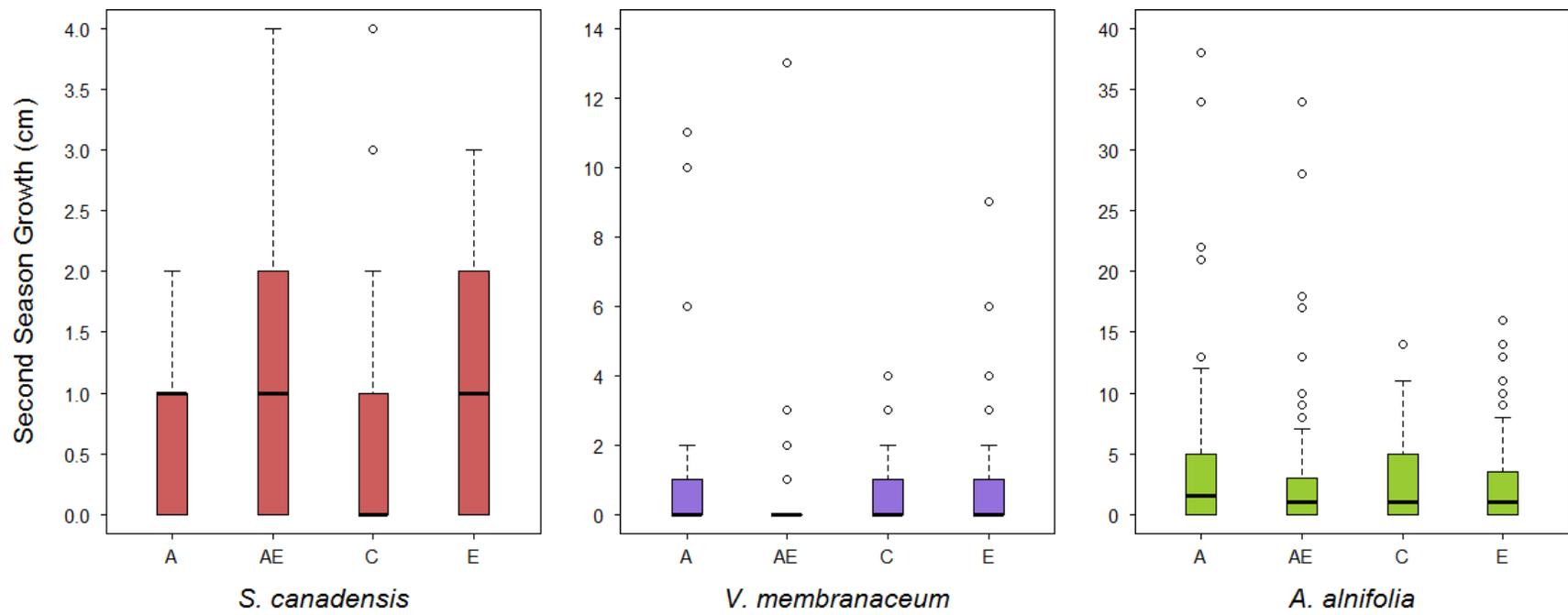
Figure 3-4. Boxplots of second-season growth for each trial species (A = amendment; AE = amendment and exclosure; C = control; E = exclosure).
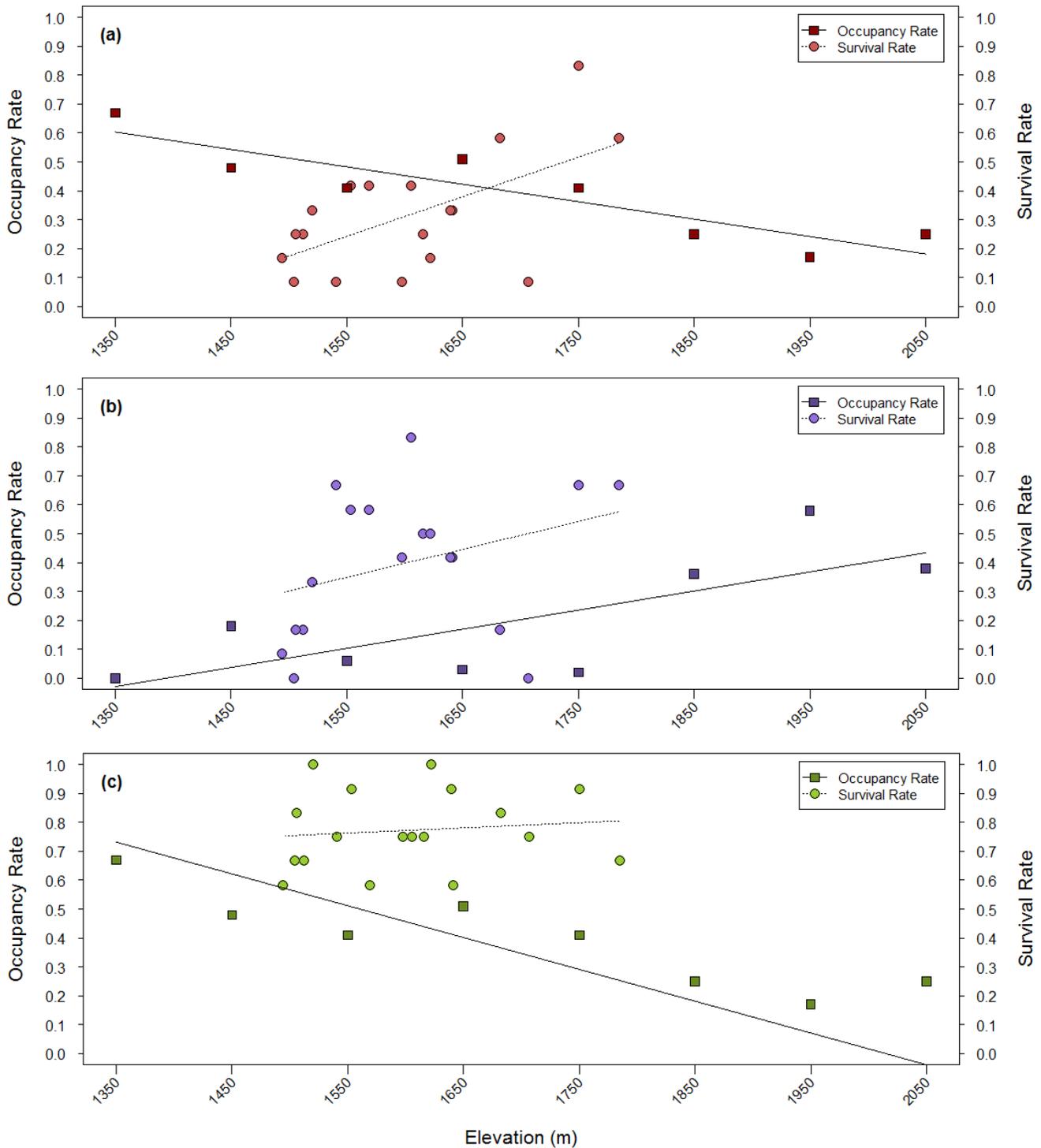
Figure 3-5. Occupancy rates and survival rates for (a) *Shepherdia canadensis*, (b) *Vaccinium membranaceum*, and (c) *Amelanchier alnifolia* along an elevation gradient. Occupancy rates were calculated for 100-m elevation zones ranging from 1300 m to 2100 m using presence-absence data from 322 stratified field plots. Survival rates were calculated for each trial site and plotted against elevation.

CHAPTER 4

General Discussion and Conclusions

1. PRIORITIZING SITES FOR PROTECTION AND RESTORATION

The field of applied conservation biology is frequently tasked with finding solutions to 'wicked problems'. Uncertainty is a diagnostic feature of a wicked problem (Ludwig, 2001). In conservation biology, this uncertainty frequently stems from limited knowledge of how many and what kind of species there are (i.e., the Linnean shortfall), as well as how species are distributed (i.e., the Wallacean shortfall; Watson et al., 2011). Focal species are often used in conservation planning because they enable conservation planners to bypass knowledge shortfalls based on the assumption that conserving one species will confer benefits to other co-occurring species (Akçakaya and Sjögren-Gulve, 2000; Carroll et al., 2001; Nielsen, 2011). Another key feature of wicked problems in conservation biology is that the needs for protection and restoration generally exceed the resources available to implement them (Carwardine et al., 2009). Systematic approaches are becoming more common in conservation planning to maximize the utility of limited conservation resources, but to date have been used primarily to optimize the design of protected area networks (Noss et al., 2009; Watson et al., 2011). In spite of the growing need to prioritize conservation decisions, single-species conservation planning is seldom systematic. Instead, single-species conservation planning has traditionally used spatial habitat models to predict species distributions and identify important areas for conservation (Elith and Leathwick, 2009a, 2009b). These measures of habitat quality or relative habitat states generally ignore landscape patterns and often fail to provide an impetus for targeted management action. In Chapter 2, I presented a novel method for single-species systematic conservation planning that can complement definitions of habitat quality by explicitly identifying sites where the utility of conservation actions (both protection and restoration) is highest while considering the landscape composition.

Habitats far from roads in the Castle River drainages and front range drainages were identified as priority source-like sites because habitat productivity were generally higher in those areas (largely due to co-occurrence of *S. canadensis* and *V. membranaceum* fruiting habitat). Priority

source-like sites in the north (in the vicinity of the Bob Creek Wildland Provincial Park) coincided with *S. canadensis*, *S. racemosa*, and *Ribes* spp. fruiting habitats. Deadman Pass, an important wildlife corridor (especially for carnivores), was identified as priority source-like habitat for grizzly bears, highlighting its importance from a conservation perspective.

As with priority source-like sites, habitat productivity values drove the selection of priority sink-like sites in areas close to roads in the Castle River drainages and front-range drainages. Several of the front range drainages currently have restricted access (gates), which was not considered during optimization. These roads are used infrequently during hyperphagia, and thus sites identified as priority sink-like habitats in these areas may actually have source-like qualities. Priority sink-like sites identified centrally, as well as along the forestry trunk road to the north, coincided with *S. canadensis* fruiting habitat, whereas priority sites identified in the South Racehorse Creek and Window Mountain Lake areas coincided with *V. membranaceum* fruiting habitat. The South Racehorse Creek drainages are productive fruiting habitats, but are also relatively accessible and are frequented for recreational use. Old clear cuts in these areas provide high elevation openings (generally > 2000 m) that receive relatively high amounts of precipitation due to their proximity to the Rocky Mountains. These factors, combined with slow conifer regeneration that limits canopy cover, provide favourable fruiting habitat for *V. membranaceum*, *Ribes* spp., and *S. racemosa*.

The lack of overlap between protected areas and priority source-like sites indicates that a large portion of important late-season grizzly bear foraging habitat is currently unprotected. Furthermore, the majority of this overlap occurs in two adjacent protected areas, suggesting that current protection of priority source-like sites is geographically biased. When human access is granted to unprotected, productive grizzly bear habitats, the likelihood that those sites can be considered secure again is low barring subsequent access removal and restoration. For this reason, access management strategies for source-like sites that are not currently protected should be proactively managed by limiting future road development. If road development occurs for industrial activity, immediate decommissioning and restoration should follow to prevent people from accessing the area.

Access management actions aimed at addressing sites identified as priority sink-like habitats will vary depending on the type of road and traffic volume. Low-volume roads are used almost exclusively for recreational purposes and represent the best candidates for permanent closure and restoration. Given the investment required to construct gravel roads, as well as the amount of use they typically receive from both industry and the public, permanent closure may be an unattractive management option. Instead, modified access strategies such as seasonal closures or gated access could be employed. Gated access is already in place in parts of the Castle River drainages, as well as most of the front range drainages in the southeastern portion of the study area. For higher volume roads such as the forestry trunk road and most paved roads, competing uses (recreation, resource extraction, major highways) may necessitate the use of alternative strategies. Although grizzly bears generally avoid high-volume roads (Northrup et al. 2012), there is also evidence to suggest that this may not be the case in areas where habitat quality is high (Gibeau et al., 2002; Chruszcz et al., 2003).

1.1 Limitations and future work

Unlike many other species of mammalian carnivore, diets of interior grizzly bear populations are comprised primarily of plant matter and have marked variation that parallels seasonal productivity of different food resources (McLellan and Hovey, 1995; Munro et al., 2006). Priority sites identified in this study are specific to the hyperphagic (late summer to early fall) period when grizzly bears in Alberta focus their foraging efforts on fruit (Martin, 1983; Hamer and Herrero, 1987a; Hamer et al., 1991; Hamer, 1996; Munro et al., 2006; Holden et al., 2012). Future work could use an optimization approach to identify priority sites for other parts of the active period, as they may differ from those identified here. Additionally, future work should identify priority source- and sink-like sites based on other forms of access that were not considered in this study (such as hiking trails), which also contribute to human-bear conflicts (Benn and Herrero, 2002). Finally, systematic conservation planning is a powerful tool for optimizing management actions to meet conservation goals, and it does so using representation targets that are set using the best available knowledge (Smith et al., 2006). This is perceived by some as a limitation because of the uncertainty associated with setting targets, and because the outputs of systematic conservation planning approaches will be strongly affected by the targets

that are used (Smith et al., 2006). However, targets are an integral component of systematic conservation planning and will change as knowledge increases and conservation goals change (Smith et al., 2006). Therefore, systematic conservation planning approaches should be viewed as adaptive processes (akin to adaptive management) that will be continue to be strengthened by further research (Smith et al., 2006). Similarly, the outputs of systematic conservation planning are dynamic and will change if components of the optimization framework are modified. In the case of this study, changes in access may alter the set of priority sites. For example, it is possible that road closures resulting from access management will cause nearby sites that were previously marginal (or potentially even priority sink-like sites) to be identified as priority source-like sites in subsequent optimizations.

2. USING WILDLIFE HABITAT ENHANCEMENTS TO INCREASE FOOD SUPPLY

Anthropogenic habitat loss and alteration, along with human-caused mortalities, are threatening grizzly bear populations across much of their North American range. Human activities have disrupted natural disturbance regimes that historically regulated the availability and productivity of critical late-season grizzly bear foods. Fire suppression and long-term climatic cycles have reduced the influence of wildfire on the landscape, which has in turn contributed to losses of important grizzly bear feeding habitat (Johnson et al., 2001; Linke et al., 2013). Disturbance regimes are now largely anthropogenically-driven, and forest harvesting has become the most prevalent source of disturbance in the forested areas of Alberta's grizzly bear range (Nielsen et al., 2008; Festa-Bianchet, 2010; Stewart et al., 2012). Forest harvesting can increase the productivity of some grizzly bear foods (Nielsen et al., 2004b), but silvicultural processes such as mechanical scarification limit post-harvest vegetative recovery of critical fruiting species such as *S. canadensis* and *V. membranaceum* (Anzinger, 2002; Nielsen et al., 2004c). This can lead to significant reductions in late-season food supply for grizzly bears (Nielsen et al., 2004c). Habitat enhancements have been proposed to mitigate this effect of forest harvesting (Nielsen et al., 2004c), yet it remains unclear whether actively planting fruiting shrubs in clearcuts is a viable option for locally increasing food supply for bears. Even initial tests of the effectiveness of planting fruiting shrub seedlings in clearcuts are lacking. I installed short-term planting trials for three important late-season grizzly bear foods (*V. membranaceum*, *S. canadensis*, and *A.*

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alnifolia) and observed seedling survival and growth over two growing seasons to assess the viability of using habitat enhancements to increase food supply for bears in clearcuts.

Overall, *A. alnifolia* had significantly higher survival rates than *S. canadensis* and *V. membranaceum*, and has the potential to be a top candidate for habitat enhancements. However, browsing pressure may limit its long-term effectiveness relative to *S. canadensis* and *V. membranaceum*, which are less palatable to ungulates. In general, soil nutrient amendments reduced seedling survival rates. Given that all three trial species occur naturally on these soils, additional nutrients may be unnecessary and may even increase competition from other species. Exclosures increased seedling survival rates, and should be considered for use in habitat enhancements, particularly for more palatable species such as *A. alnifolia* during the first few years of establishment and growth. However, the prospective benefits of using exclosures to protect seedlings must be balanced by the considerable investment required for their installation and maintenance. In some cases, it may be more economical to invest in additional seedlings of less palatable species such as *S. canadensis* or *V. membranaceum*. Elevation effects (or the lack thereof) on survival were inconsistent with expected niche spaces for *S. canadensis* and *A. alnifolia*. Survival rates of *S. canadensis* increased with elevation, which is the opposite of the expected trend (based on observed occupancy rates over the same gradient), which suggests that other factors influenced survival rates more strongly than elevation. *A. alnifolia* survival rates were high irrespective of changes in elevation, indicating that it has a relatively wide fundamental niche and that establishment outside of its expected niche space may still be successful.

2.1 Limitations and future work

The results from this study provide a critical first step towards determining whether habitat enhancements are a feasible management option, but several limitations must be noted. Firstly, greenhouse trials were not conducted but could have been used to test the overall quality of the seedlings, which may have influenced survival and growth results. Secondly, soil nutrient assessments of the clearcuts used in these trials could have provided greater insight into site-specific differences in survival and growth responses for each trial species. Thirdly, both *S.*

canadensis and *V. membranaceum* utilize mycorrhizal symbiosis to acquire essential nutrients (Visser et al., 1991; McCracken, 1999). *S. canadensis* was found to naturally occur in 44.4% of the clearcuts used in this study, whereas *V. membranaceum* did not naturally occur on any trial site. In both cases, a lack of mycorrhizal symbionts at all (in the case of *V. membranaceum*) or some (in the case of *S. canadensis*) of the trial sites could have contributed to reduced survival and growth rates. If these species (or others with mycorrhizal dependencies) are being considered as candidates for wildlife habitat enhancements on sites where they do not naturally occur, mycorrhizal inoculation could be considered to boost seedling performance. In the case of *S. canadensis* in particular, Danielson and Visser (1990) demonstrated that seedlings seldom form nodules or mycorrhizal associations prior to being shipped to the buyer, and Visser et al. (1991) found that *S. canadensis* containerized seedlings increased significantly when they were inoculated with symbionts prior to planting.

Several important questions also remain that must be answered by long-term studies. Firstly, there is a need to quantify fruit production in experimental plantings since this ultimately determines the potential utility of actively planting fruiting shrubs in clearcuts in order to locally increase food supply for bears. Secondly, long-term studies are needed to incorporate the possible effects of inter-annual climatic variation, which influences fruit production (Holden et al., 2012), and may also affect seedling establishment, survival, and growth. The results from long-term trials would also better incorporate the effects of interannual climatic variation and interspecific interactions (browsing, competition for resources, etc.), both of which likely act on coarser timescales than the one examined in this study and likely influence long-term survival, growth, and fruit production.

3. GRIZZLY BEAR CONSERVATION IN SOUTHWESTERN ALBERTA

Grizzly bears in southwestern Alberta face a unique confluence of anthropogenic threats. Historic range contraction associated with the expansion of human settlements and ranchlands has left remnant populations in more remote, rugged, and densely forested areas of the foothills and the Rocky Mountains. Recent estimates suggest that the Waterton population unit may be growing, which has contributed to increased conflicts between bears and ranchers in the region.

It remains unclear whether the Livingstone population unit just to the north is also expanding, although a population survey is currently underway. Given simultaneously expanding grizzly bear populations and human footprints, it is not unreasonable to suggest that the risk of human-bear conflict in the region is also increasing. Managing for sustainable grizzly bear populations must include measures that aim to reduce human-bear conflicts. Management actions must be prioritized to target accessible, highly productive sites where conflicts are most likely to occur. In these areas, access should be limited to the greatest extent possible, subject to competing stakeholder interests. Similarly, granting access to secure, high quality sites should be avoided.

Strategies for mitigating anthropogenic habitat loss and habitat alteration should also continue to be explored. In particular, attempts to locally increase food supply for bears in anthropogenically created forest openings by planting fruiting shrub seedlings should continue to be tested with longer-term trials to quantify the influence of long-term environmental factors. This is partly due to the prevalence of forest harvesting activities in the region, but also because several new coal mines have been proposed for development in the near future. Conservation offset programs (i.e., no net habitat loss) are one option that may be considered for mitigating the effects of these new mines on wildlife in the region. Wildlife habitat enhancements in clearcuts are one possible approach for offsetting habitat losses resulting from coal mining activities (provided that human access to these enhancements is minimized), and these short-term enhancement trials indicate that establishing seedlings of *S. canadensis*, *V. membranaceum*, and *A. alnifolia* in clearcuts is feasible.

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APPENDIX A

1. MODELING SPECIES DISTRIBUTIONS TO DEFINE GRIZZLY BEAR HABITAT

Species distributions and predicted presence of reproductive structures were modeled using a purposeful model building approach as outlined by and Hosmer et al. (2013). This approach began with univariate logistic regression analysis (0 – absence; 1 – presence) of each covariate (Table A-1). Covariates were then ranked for importance using Akaike information criterion (AIC), and models were built by first including the top-ranked covariate, and then successively adding the next-highest ranked covariate. Highly correlated variables ($r > |0.7|$) were not included in the same model. If a covariate was added to the model and did not have a significant p-value (i.e., $p < 0.1$), it was discarded. This process was iterated until all covariates had been considered. Quadratic forms of each climate covariate and selected terrain variables were also included in the model building process to test for possible non-linear relationships. Following completion of a main effects model, interaction terms were considered on the basis of hypothesized relationships and statistical significance. Model complexity was limited to no more than one variable per 6 observations (Table A-2). Finally, model fit was assessed using the receiver operating characteristic (ROC) area under the curve (AUC), as well as a Hosmer-Lemeshow goodness-of-fit test using 10 groups (Table A-2).

For fruiting models, only field plots where a particular species was observed were included, and observations were restricted to the period where reproductive structures were observed for that species. This allowed separation of sites where the species may be present but not fruiting (such as presence under tree cover). Optimal probability cut-off values were estimated for each species using equalized sensitivity-specificity probability thresholds (i.e., intersection of sensitivity and specificity curves) from ROC calculations (Pearce and Ferrier, 2000; Boyce et al., 2002). These values were used to reclassify original probabilities and generate binary raster layers of predicted presence-absence (for both presence and fruiting models) across the study area (0 – absence; 1 – presence). Binary fruiting rasters were multiplied by binary presence rasters for each species to produce binary rasters of fruiting given presence.

2. SPECIES DISTRIBUTIONS

Predicted presence of fruiting species was influenced mainly by temperature (climate) and terrain-derived variables, while stand (clearcut and canopy cover) and landcover variables were generally less important (Table A-3). Fruiting models, on the other hand, were driven mainly by climate (both temperature- and precipitation-based climate normals), terrain-derived, and stand-level variables (Table A-4). For instance, canopy cover was important for predicting fruiting for seven focal species, with moderate levels of canopy cover favouring fruiting for *S. canadensis*, *L. involucrata*, and *F. virginiana*, and low levels of canopy cover favouring fruiting for *A. uva-ursi*, *R. parviflorus*, *V. myrtillus*, and *V. caespitosum*.

3. ENVIRONMENTAL RESPONSES FOR CRITICAL FRUITING SPECIES

Predicted presence of *S. canadensis* was positively related to moderate frost-free periods, as well as areas of low canopy cover, high soil wetness (CTI), and low heat load values (Table A-3). Interaction effects between canopy cover, soil wetness, and heat load values suggest that *S. canadensis* is more likely to occur when two or more of these conditions are satisfied (i.e. sites with low canopy cover and high soil wetness). *V. membranaceum* was predicted to occur in areas with higher canopy cover, lower heat load index values, and areas that receive more precipitation as snow. *V. membranaceum* occurrence was also predicted to be lower at moderate January minimum temperatures (tmn01). Contrary to its relationship with canopy cover (positive), *V. membranaceum* presence was also associated with clearcuts. Finally, an interaction effect between canopy cover and heat load values indicated that *V. membranceum* was more likely to occur on sites with lower heat loads and lower canopy cover. *S. canadensis* fruiting was negatively associated with moderate January minimum temperatures (tmn01), but positively associated with higher heat load values (Table A-4). *V. membranaceum* fruiting was not significantly related to any terrain-derived or stand-level variables, but instead, was strongly predicted by a summer heat-to-moisture index.

Table A-1. Environmental covariates used to model distributions and habitats suitable for reproduction for thirteen fruiting species in southwestern Alberta.

Variable Group	Model Covariates	Variable Code
Climate	Annual heat-to-moisture Index	ahm
	Beginning of frost-free period	bffp
	Climatic moisture deficit	cmd
	Climate moisture index	cmi
	Climate moisture index for June, July, and August	cmijja
	Degree-days below 0 °C	dd0
	Degree-days above 5 °C	dd5
	Ending of frost-free period	effp
	Estimated extreme minimum temperature, 30-yr normal	emt
	Reference atmospheric evaporative demand	eref
	Frost-free period	ffp
	Mean annual precipitation	map
	Mean annual temperature	mat
	Mean coldest-month temperature	mcmt
	Mean May-to-September precipitation	msp
	Mean warmest temperature	mwmt
	Number of frost-free days	nffd
	Proportion of precipitation as snow	pas
	Summer precipitation	pptsm
	Winter precipitation	pptwt
	Summer heat-to-moisture index	shm
	Average summer temperature	tavsm
	Average winter temperature	tavwt
	Continentality (MWMT – MCMT)	td
	Minimum temperature in January	tmn01
	Maximum temperature in July	tmx07
Landcover	Dense coniferous forest	dcf
	Moderate coniferous forest	mcf
	Open coniferous forest	ocf
	Mixed forest	mxf
	Broadleaf forest	blf
	Shrub	shb
	Herbaceous	hrb
	Agriculture	agr
	Barren	bar
	Water	wat
Terrain	Compound topographic index	cti
	Slope aspect index	sai
	Potential direct incident radiation	pdir
	Heat load index	hli
Disturbance	Clearcut (binary)	cb
Canopy	Canopy cover	cc

Table A-2. Selected statistics for presence and fruiting models. **Prevalence** is the proportion of sites occupied (for presence models) or proportion of sites occupied with presence of reproductive structures (for fruiting models). **Probability threshold** refers to optimal probability cut-off values estimated using equalized sensitivity-specificity probability thresholds from ROC calculations. **H-L GOF** refers to the Hosmer-Lemeshow goodness-of-fit test with 10 groups (probability > Hosmer-Lemeshow χ^2). **Model complexity** is the total number of observations divided by the total number of variables, including the constant.

Model	Species	Prevalence	Probability Threshold	AUC	H-L GOF	Model Complexity
Presence	*Vaccinium membranaceum*	0.121	0.213	0.978	0.999	40.3
	Shepherdia canadensis	0.416	0.424	0.758	0.228	32.2
	Amelanchier alnifolia	0.382	0.414	0.834	0.333	53.7
	Arctostaphylos uva-ursi	0.214	0.234	0.812	0.838	26.8
	Ribes spp. (Gooseberry)	0.472	0.488	0.729	0.702	40.3
	Lonicera involucrata	0.196	0.212	0.800	0.593	29.3
	Sambucus racemosa	0.140	0.147	0.871	0.968	29.3
	Rubus parvifolorus	0.335	0.291	0.802	0.0731	80.5
	Rubus idaeus	0.161	0.155	0.748	0.413	80.5
	Vaccinium myrtillus	0.394	0.445	0.824	0.367	29.3
	Vaccinium caespitosum	0.193	0.189	0.795	0.625	53.7
	Vaccinium scoparium	0.239	0.228	0.843	0.432	53.7
	Fragaria virginiana	0.721	0.696	0.814	0.599	24.8
Fruit	*Vaccinium membranaceum*	0.806	0.636	0.894	0.989	12.0
	Shepherdia canadensis	0.556	0.565	0.777	0.518	19.0
	Amelanchier alnifolia	0.487	0.405	0.855	0.490	17.0
	Arctostaphylos uva-ursi	0.591	0.567	0.849	0.814	11.0
	Ribes spp. (Gooseberry)	0.584	0.573	0.748	0.672	29.8
	Lonicera involucrata	0.762	0.624	0.967	0.639	7.88
	Sambucus racemosa	0.822	0.792	0.878	0.329	7.50
	Rubus parvifolorus	0.752	0.778	0.893	0.118	12.6
	Rubus idaeus	0.689	0.677	0.845	0.427	9.00
	Vaccinium myrtillus	0.758	0.542	0.868	0.184	15.8
	Vaccinium caespitosum	0.682	0.498	0.973	0.442	6.29
	Vaccinium scoparium	0.707	0.760	0.892	0.630	12.5
	Fragaria virginiana	0.420	0.409	0.774	0.136	23.1

Table A-3. Logistic regression models predicting the occurrence of late-season grizzly bear food resources (fruiting species) in Southwestern Alberta.

Species	Final Model
V. membranaceum	$0.048pas - 1.3hli + 0.18cc + 2.3cb - 529tmn01 - 18tmn01^2 - 0.21(hli \times cc) - 3929$
S. canadensis	$-0.25msp + 0.00034msp^2 + 19effp - 0.038effp^2 - 0.044cc + 0.33cti - 3.4hli + 0.15(hli \times cc) - 0.0051(cti \times cc) - 2251$
A. alnifolia	$-0.012dd0 + 0.12ahm + 3.5hli - 3.1sai + 15sai^2 + 9.4$
A. uva-ursi	$-1.9shm + 0.023shm^2 + 33effp - 0.066effp^2 + 2.5ocf - 0.85tmn01 + 63hli - 47hli^2 - 1.6bar + 4.9pdir - 0.24cti - 4144$
Ribes spp. (Gooseberry)	$0.88shm - 0.013shm^2 + 24hli - 19hli^2 - 3.8pdir - 0.72mcf + 0.15cti - 21$
L. involucrata	$5.9cb - 2.9pdir + 0.063pas - 0.000075pas^2 + 2.4cti - 0.11cti^2 + 0.84tmn01 + 1.6ffp - 0.010ffp^2 - 7.3(pdir \times cb) - 73$
S. racemosa	$6.2ahm - 0.23ahm^2 - 0.031cc - 39td + 0.82td^2 + 5.2cb - 5.9pdir + 0.13cti + 0.028cb^2 - 0.63(cti \times cb) + 423$
R. parviflorus	$1.2emt + 0.0050map + 0.50tmx07 + 35$
R. idaeus	$0.26effp + 0.51td - 0.019cc - 77$
V. myrtillus	$-0.17cb + 0.077cmd - 0.00057cmd^2 + 0.082mcmt - 0.0064map + 3.0sai - 20sai^2 - 36td + 0.77td^2 + 5.3(sai \times cb) + 432$
V. caespitosum	$31effp - 0.061effp^2 - 1.2tmn01 - 0.021ppt\_sm - 2.3sai - 3894$
V. scoparium	$-0.47effp + 0.032map - 0.000020map^2 + 1.7bar + 0.58tmn01 + 111$
F. virginiana	$6.3pdir + 2.4mxf - 3.9cb + 0.20cti + 0.044cc - 0.00076cc^2 + 27hli - 22hli^2 - 0.042pptwt + 0.000083pptwt^2 - 1.2bar + 8.2(pdir \times cb) - 8.0$

Table A-4. Models for predicting suitable fruiting habitat for late-season grizzly bear food resources (fruiting species) in Southwestern Alberta.

Species	Final Model
V. membranaceum	$-0.68shm + 26$
S. canadensis	$0.063cc - 0.0012cc^2 + 56tmn01 + 1.8tmn01^2 + 6.7hli + 0.20bffp + 399$
A. alnifolia	$-7.1cti + 0.39cti^2 + 8.2pdir - 0.67cb - 0.040cc + 0.030(cb \times cc) + 25$
A. uva-ursi	$-3.0ppt\_sm + 0.0078ppt\_sm^2 + 15pdir + 0.16mcmt - 0.025cc + 280$
Ribes spp. (Gooseberry)	$-0.76tmx07 + 6.8cb + 3.5hli - 12(hli \times cb) + 14$
L. involucrata	$7.2cb + 0.86cc - 0.013cc^2 - 263tmn01 - 8.6tmn01^2 + 5.0dcf + 3.3mat - 2017$
S. racemosa	$-4.0mwmt + 7.0cti - 0.31cti^2 - 0.21map + 0.00012map^2 + 109$
R. parviflorus	$0.35dd0 - 0.00015dd0^2 - 141hli + 112hli^2 + 0.018ppt\_wt - 5.7sai - 1.9tmn01 - 193$
R. idaeus	$1.0mcmt - 0.050mcmt^2 - 152hli + 119hli^2 + 45$
V. myrtillus	$-0.023cc - 0.70cti - 1.4dcf + 0.64ppt\_sm - 0.0015ppt\_sm^2 - 61$
V. caespitosum	$-398td + 8.1td^2 - 0.71cti + 0.077pas - 0.074cc - 6.8dcf + 4857$
V. scoparium	$-4.6dcf + 0.093msp - 2.0hrb + 157emt + 1.9emt^2 + 3292$
F. virginiana	$-3.8cb + 0.083cc - 0.0013cc^2 - 65emt - 0.77emt^2 + 1.1hrb - 0.11cti + 0.022(cb \times cc) + 0.55(cti \times cb) - 1355.032)$