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Managing Forest Disturbances: Effects on Mule Deer and Plant Communities in Montana's Northern Forests

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MANAGING FOREST DISTURBANCES:
EFFECTS ON MULE DEER AND PLANT COMMUNITIES
IN MONTANA'S NORTHERN FORESTS

By

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MANAGING FOREST DISTURBANCES: EFFECTS ON MULE DEER AND PLANT COMMUNITIES IN MONTANA'S NORTHERN FORESTS

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Mule deer (*Odocoileus hemionus*) are frequently the focus of population and habitat management in the western United States. Land and wildlife managers use disturbance to reset forests to earlier successional stages and improve the quality and quantity of forage available to mule deer. However, the effects of management practices on nutrition and selection vary widely, so the implementation of management practices raises ecological as well as management-related concerns. This work investigated how disturbance from wildfire, prescribed fire, and timber harvest influences the spatial and temporal distribution of nutritional resources in mule deer summer range, and therefore, how the nutritional landscape influences mule deer selection of disturbance. We studied changes in vegetation and habitat selection by mule deer in three areas with differing disturbance regimes during 2017–2019. We found differences in forage nutrition response to disturbance that was specific to study areas, suggesting that targeted forest management within disturbance regimes would provide nutritional benefits to mule deer populations in the northern Rocky Mountains. Other vegetative responses revealed trade-offs specific to forest and disturbance types. Despite substantial variation in selection among individuals and among study areas, we found some common effects of forage nutrition and disturbance type on selection at population scales. As we predicted, deer selection within home ranges was not explained well within these constraints, suggesting that deer selection may be influenced more by other factors, such as security or cover within home ranges. The age and type of disturbance also influence selection at a population scale, but do not predict selection within home ranges, where the availability of disturbances is irregular. In all study areas, we documented similar selection for more recent disturbance and avoidance of open woodland at the population scale, suggesting that these responses can be generalized to deer in other populations in the Rocky Mountains because we observed them in multiple sites under widely differing conditions. Managers accounting for local and regional frequency and availability of disturbance can identify management actions that are accessible and beneficial for mule deer. Furthermore, consideration of the likely outcomes of forest-specific vegetative responses can help managers balance potential tradeoffs of management alternatives.

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Introduction and Overview

Management practices intended to benefit wildlife populations often alter the abundance and composition of nutritional resources on the landscape (Kie et al. 2002). Mule deer (*Odocoileus hemionus*) are frequently the focus of population and habitat management in the western United States (Mackie et al. 1998, Pierce et al. 2012, Bergman et al. 2015), particularly during periods of declining population estimates and hunter harvests. Numerous studies in western states reveal the importance of bottom-up effects of nutritional resources on dynamics of mule deer populations, which may be combined with top-down forces from predation (Clements and Young 1997, Pierce et al. 2012). In the northern Rocky Mountains, strategies to improve nutritional resources in forested ecosystems often focus on creating and managing disturbance, but nutritional benefits to mule deer vary based on the spatial and temporal distribution of disturbance. While managers have some control over both, the complexity and uncertainty surrounding efficacy of management options present barriers to management decisions.

Establishing a clear link between management practices and vegetative responses can help to inform management decisions for mule deer (Edge et al. 1990, Bergman et al. 2014). Managers can use a complex array of vegetation metrics to measure responses to disturbance, including plant community composition, vegetation productivity, quantity and quality of forage plant species (Lehmkuhl et al. 2001), invasive plant species (Beck 1993, Alba et al. 2015), and overgrazing and –browsing metrics (Morellet et al. 2007, Bergman et al. 2014), but the best approach to measuring disturbance on local scales may not be evident. Managers often seek to fulfill multiple objectives at once, which complicates the interpretation of potential management effects of disturbance on mule deer. In addition, management of vegetation and wildlife are often led by different agencies and even different levels of government. Therefore, conflicts in meeting multiple objectives can arise not only when objectives differ, but also when goals of management agencies differ. Ideally, decisions that aim to improve the nutritional landscape for deer link favorable vegetative responses to enhanced mule deer nutrition, with the ultimate goal of increasing reproduction and survival (Montieth et al 2014, Bergman et al. 2015). Although multiple studies have evaluated effects of mule deer habitat enhancement in more arid systems in Colorado, eastern Oregon, and eastern California (Bergman et al. 2014, Monteith et al. 2014, Hull et a. 2019), studies that incorporate behavioral and vegetative responses to disturbance are needed in the northern Rocky Mountains to better inform mule deer habitat management.

The overarching goal of this thesis was to advance the understanding of mule deer behavioral and nutritional ecology while providing land and wildlife managers with information about the implications of forest management for deer. However, the diversity of habitat and disturbance regimes in the northern forest ecoregion have been largely overlooked (Hayden et al. 2008). The objectives of my research were to determine how disturbance from wildfire, prescribed fire, and timber harvest influences the spatial and temporal distribution of nutritional resources in mule deer summer range, and therefore, how the nutritional landscape influences mule deer selection of disturbance.

In Chapter 1, I investigated how metrics of mule deer habitat respond to disturbance from management practices. I quantified vegetative responses to disturbance that are of interest to many managers: biomass of shrubs, invasive species, and forage species for mule deer; species richness; and habitat condition. I evaluated changes in mule deer forage nutrition and found that although responses were variable, both disturbance regime and disturbance type influenced the availability of forage after disturbance. I found important differences in forage nutrition response to disturbance that was specific to study areas, suggesting that targeted forest management within disturbance regimes would provide nutritional benefits to mule deer populations in the northern Rocky Mountains. Other vegetative responses revealed trade-offs specific to disturbance types within study areas.

In Chapter 2, I asked which of 4 non-exclusive hypotheses best explained selection of disturbance by mule deer during summer, because nutritional intake during this season has implications on reproduction and survival of adult female mule deer. I found support for the prediction that nutrition may be a limiting factor in conifer forests of the northern Rocky Mountains. As predicted, deer selection within home ranges was not explained well within these constraints, suggesting that deer selection may be influenced more by other factors, such as security or cover within home ranges. The age and type of disturbance also influence selection at a population scale, but do not predict selection within home ranges, where the availability of disturbances is irregular.

In summary, my work reveals that disturbances create vegetation responses that vary depending on the type of disturbance and type of forest in which management occurred. The response of vegetation to disturbance provides information about the distribution and quality of mule deer forage, and the choices that deer make to manage costs and benefits associated with accessing forage. In forests where nutrition is limiting, mule deer may benefit from a mosaic of successional stages within both population and individual home ranges (Grumbine 1994). Ecosystem-based forest management that increases availability of infrequent disturbance types may prove particularly beneficial to mule deer. Disturbance does not guarantee improved forage for mule deer if it is localized in small areas or inaccessible (e.g. in wildfires with heavy downfall). Managers accounting for local and regional frequency and availability of disturbance can identify management actions that are accessible and beneficial for mule deer. Furthermore, consideration of the likely outcomes of forest-specific vegetative responses can help managers balance potential tradeoffs of management alternatives.

Because this work represents collaboration during all stages of planning, logistics, and analysis, and because these chapters were designed for publication in scientific journals, I use the collective "we" through the remainder of this thesis.

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Chapter 1 : Habitat Management with Multiple Objectives: Applying Decision Analysis to Mule Deer (*Odocoileus hemionus*) and Forage in Montana's Northern Forests

INTRODUCTION

Conservation of natural resources requires effective management strategies. Such strategies for management of forested lands must balance consideration of wildlife habitat (the resources and conditions that allow a species to survive and reproduce [Hall et al. 1997]), biodiversity conservation, ecosystem functioning, and economic productivity (Lindenmayer et al. 2006). In the western United States, forest managers are also faced with increased prevalence of late seral forests outside of the historical ranges of variability as the result of more than a century of fire suppression (Hessburg et al. 2000, Keane et al. 2002). Long periods of fuel accumulation and climate change put these forests at greater risk of high-severity fire and reduced tree regeneration after fire (Davis et al. 2019). Thus, increasing the prevalence of early successional stands is a potential management strategy, yet such forest treatments might have a variety of specific goals, such as improving wildlife habitat (Noss et al. 2006, Hebblewhite et al. 2009, Allred et al. 2011, Rowland et al. 2018) or managing the prevalence and spread of exotic species (US Forest Service 2013). Managers can use a suite of forest management techniques, including prescribed fire, timber harvest, and wildfire management, to reset forests to earlier stages of succession (Lehmkuhl et al. 2001), yet one technique may not best suit all of the targeted outcomes.

A variety of forest management practices share common goals of reducing tree canopy cover and subsequently allowing more light into the understory, generally altering plant communities through an increased abundance of understory grasses, forbs, and shrubs (Lezberg et al. 1999). However, each management technique has unique effects on forest plant communities based on the manner of tree removal as well as the frequency, severity, intensity, size, and timing of disturbance. Site-specific factors, including forest type (Sachro et al. 2005), time since disturbance, and tree regeneration and composition after disturbance (Van Dyke and Darragh 2006, Romme et al. 2016), further influence the response of understory vegetation. Abundance of herbaceous species often increases in harvest, prescribed fire, and combined harvest and prescribed fire. In contrast, shrub abundance generally decreases after disturbance, particularly in prescribed fire and combined harvest and prescribed fire treatments (Abella and Springer 2015, Willms et al. 2017). In forests of the northern Rocky Mountains, wildfire severity determines which existing plants survive at or below ground level and thus mediates the response of herbaceous and shrub species (Stickney and Campbell 2000).

Differences in the process of canopy removal between forest management alternatives may be particularly important for ungulate species that use the resulting vegetation for forage and cover (Irwin and Peek 1983, Lehmkuhl et al. 2001). Mule deer (*Odocoileus hemionus*) have long been the focus of management, especially during several periods of population decline in the last few decades (Mackie et al. 1998, Pierce et al. 2012, Bergman et al. 2015). Previous investigations identified several factors contributing to declines, including habitat loss or degradation and a resulting loss of nutritional resources (Gill et al. 2001, Heffelfinger and Messmer 2003). Nutritional resources available to ungulates are linked to their subsequent body size and condition, which in turn affects survival and reproduction (Robbins 1994, Parker et al. 2009, Cook et al. 2004, 2013). Access to nutritional resources during summer is particularly important for female mule deer to meet increased metabolic demands of lactation and gestation while increasing body mass to offset energy deficit during winter (Wallmo 1981). Recognizing this link, many state and federal agencies in the western United States have adopted habitat guidelines with treatment recommendations to improve mule deer forage quality and quantity (Hayden et al. 2008). Although forest disturbance has been established as an important way for managers to redistribute and enhance nutritional resources for mule deer (Hayden et al. 2008, Lehmkuhl et al. 2001), the effects of different disturbance types and subsequent succession on nutritional resources remain less clear.

Studies on plant community responses to disturbance document a range of potential effects for mule deer, based on the frequency, severity, size, and timing of disturbance. Disturbance from wildfires can create a mosaic of vegetation that benefit mule deer (Patton and Gordon 1995). Prescribed fire had minimal effect on forage quality in some studies (Wood 1988) or a short-term increase in others (Dills 1970, Keay and Peek 1980, Hobbs and Spowart 1984, Carlson et al. 1993). Studies on forest thinning reported minimal effects or a slight reduction in forage species preferred by mule deer (Long et al. 2008, Kramer et al. 2015). Responses of understory plant communities vary based on forest type (Sachro et al. 2005), disturbance severity and intensity (Lord and Kielland 2015), time since disturbance, and forest regeneration after disturbance (Van Dyke and Darragh 2006, Romme et al. 2016). Mule deer rely heavily on forage from forbs and shrubs (Beck and Peek 2005), and most of the nutritional resources in forests occur in open canopies and transitory habitats that follow disturbance (Kayes et al. 2010). Yet, the period of increased plant diversity and productivity following disturbance can be short, typically less than ten years (Hebblewhite et al. 2009, Vavra and Riggs 2010).

Vegetative responses may also introduce management costs. Disturbances also have a strong role in determining which plant species are able to compete or even to survive in a particular site (Went 1952, Willms et al. 2017), and are often considered a contributing factor to successful invasion by exotic plant species and to a concomitant decline in biodiversity (Parks et al. 2005). The establishment of invasive species after disturbance has long been a concern for land and wildlife managers in the western U.S. (Cox et al. 2009), as research has shown that invasive species can alter the function and character of plant communities (Beck 1993). Although invasive species responses vary across disturbance and forest types, common invaders after disturbance are annual grasses, including cheatgrass (*Bromus tectorum*) and Japanese brome (*B. japonicus*), and long-distance, dispersing forbs including Canada thistle (*Cirsium arvense)* and prickly lettuce (*Lactuca serriola*). Studies have found an increase in non-native species after wildfire (Rew and Johnson 2010) and a greater increase following forest thinning compared to prescribed fire (Willms et al. 2017).

Managers have used the concept of natural variability to interpret disturbance regimes and guide management actions within the range of ecological conditions appropriate for an area (Landres et al. 1999). The intermediate disturbance hypothesis posits that local species diversity and richness is maximized when ecological disturbance occurs with intermediate frequency (Grime 1973). Under this hypothesis, a plant community subject to disturbance frequency above its natural range of disturbance would result in a decline in diversity and ecological condition (LaPaix et al. 2009). Therefore, plant community composition can serve as an indicator of the ecological condition of mule deer habitat (habitat condition), the availability and quality of forage (Taft et al. 1997, U.S. EPA 2002), and spatial and temporal changes in a landscape over time. Managers thus encounter considerable uncertainty when making decisions that bridge conservation objectives with detailed and often specific information concerning vegetation responses at a local scale. There is a need, then, to understand and compare the likely effects of forest management actions across a range of mule deer habitats to make informed management decisions for complex and dynamic landscapes.

We studied the effects of disturbances in 3 regions with divergent disturbance regimes occupied by mule deer in northwest Montana. We compared the effects of disturbance from wildfire, prescribed fire, and timber harvest during the last 35 years on habitat condition, plant community composition, and forage availability for mule deer. Study areas differed in terms of their predominant disturbance regimes, including one area characterized by a recent history of large wildfires, another with widespread timber harvest, and a third with relatively minimal disturbance from either fire or harvest. Based on previous research, we expected that plant communities after disturbance would be a function of the biophysical environment (Mackie et al. 1998, Powell et al. 2000, Lehmkuhl et al. 2013), pre-treatment forest and plant community composition (Mackie et al. 1998, Powell et al. 2000, Lehmkuhl et al. 2013), and the time since disturbances occurred (Abella and Springer 2015, Willms et al. 2017, Roerick et al. 2019). We hypothesized that disturbance from wildfire and forest management techniques have differing effects on understory plants that influence mule deer summer nutrition. Thus, we predicted that forest management actions would: 1) alter habitat condition and plant community composition based on the disturbance regime of the study area in which a management action occurred and 2) improve forage nutrition for mule deer in all study areas based on disturbance type.

For each study area, we used plant composition field surveys combined with remotely-sensed data to quantify plant responses to disturbance and evaluated differences in forage and habitat condition between disturbance types and disturbance regimes. We tested our predictions using general linear models of a habitat condition index as a measure of native and invasive species composition (Swink and Wilhelm 1979, 1994), between-class analysis of plant community composition between disturbance types and study areas (Thioulouse et al. 2018), and analysis of forage nutrition (Pastor 2011, Cook et al. 2016, Rowland et al. 2018).

Finally, we used management outcomes, measured as mean vegetative responses to disturbance, to conduct a decision analysis (Beinat and Nijkamp 1998, Linkov and Moberg 2012) to illustrate a potential approach for managers to evaluate multiple natural resource objectives in the face of tradeoffs between different habitat response metrics. Decision analysis is an approach for selecting among actions that have uncertain outcomes (Beinat and Nijkamp 1998). It can be used to evaluate consequences and trade-offs among alternatives and identify the most optimal decision while accounting for the priorities of the decision-maker. We included five management objectives in our analysis to represent potential consequences for mule deer nutrition (forage nutrition and shrub biomass), native and invasive species management (species richness and invasive species biomass), and overall habitat condition (quality assessment index). Our analyses and subsequent decision analysis provide information on the likely outcomes of wildfire, harvest, and harvest followed by prescribed fire in western Montana, allowing decision-makers to evaluate the relative merits of these management alternatives.

METHODS

Study areas

The study was conducted in northwest Montana and included the ranges of 3 mule deer populations in the Rocky Mountain Front, the Cabinet-Salish Mountains, and the Whitefish Range. Study areas broadly differed in the composition of disturbance types, especially differences in the proportion of fire and harvest (Fig. 1.2).

The Rocky Mountain Front study area included portions of the Bob Marshall and Scapegoat Wilderness areas as well as public and private lands extending eastward. Elevation in the Rocky Mountain Front ranges from about 1,200 to 2,750 m, and yearly average temperatures range from –10° C to 28° C. East of the continental divide, lower-elevation areas include riparian areas, agricultural land, and mixed-grass prairie dominated by bunchgrasses (*Pseudoroegneria spicata*) and fescues (*Festuca campestris, F. idahoensis*). Moving west, the foothills give way to shrub- and conifer-dominated ecosystems, then to a diverse mosaic of meadows, alpine steppe, and subalpine conifer areas at higher elevations. Forest stands are generally mixed and composed of lodgepole pine (*Pinus contorta*), Douglas fir (*Pseudotsuga menziesii*), spruce (*Picea* sp.), and sub-alpine fir (*Abies lasiocarpa*). Much of this region experiences a stand-replacement fire regime with fire intervals of 150 to 250 years (Arno et al. 2000).

The Cabinet-Salish Mountains study area was centered within the Fisher River drainage, and extends westward into the Cabinet Range and eastward to the Salish Mountains. Elevation ranges from 600 m to 2100 m. Yearly average temperatures range from 0° C to 31° C. The study area offers dense- to open-conifer forest with interspersed shrubland and grassland areas. Forests are comprised mainly of western larch (*Larix occidentalis*), Douglas fir, lodgepole pine, and Engelmann spruce (*P. engelmannii*). Smaller areas of western hemlock (*Tsuga heterophylla*) and western red cedar (*Thuja plicata*) occur on some aspects. This region has received consistent and widespread timber harvest activity for decades from timber companies and Forest Service harvests. Wildfires are dispersed, though larger, more frequent burns tend to occur in the drier Salish Mountains.

The Whitefish Range is bordered to the east by Glacier National Park and extends norward into the East Kootenay region of by British Columbia, Canada. Elevations range from 790 m in the Tobacco Valley to around 2440 m in the Whitefish Range. Yearly average temperatures range from –8° C to 30° C. Forests are generally comprised of western larch, Engelmann spruce, Douglas fir, lodgepole pine, and western red cedar. Disturbance includes some areas of small U.S. Forest Service forest thinning projects, and wildfires tend to be relatively small and dispersed.

Data collection

Forest disturbance data.—We identified three types of forest disturbance (wildfire, prescribed fire, and harvest) using a combination of LANDFIRE (LF; LANDFIRE 2012) and global forest change (GFC; Hansen et al. 2013) remotely-sensed data. LF raster spatial products and GFC data have 30-m resolution, though the scale at which disturbance is applied is typically much larger than 30 meters (LANDFIRE 2012). Global forest change uses algorithms to identify reductions in forest canopy using remote-sensed data. GFC defined tree cover as all vegetation greater than 5 meters in height, and tree cover loss indicates the complete removal of tree cover canopy in a 30-meter Landsat pixel. LF captures landscape scale changes in forests due to management activities and natural disturbance reported by the U.S. Forest Service and other users. Whereas LF classifies timber harvest data into three categories (clearcuts, harvests, and thins), we found they were not useful for characterizing canopy removal, and we therefore combined them into a single harvest category.

We calculated time since disturbance as the difference between the disturbance event and the final year of the survey (2019) or the survey year for sites where we conducted vegetation surveys. GIS disturbance data were consistently available from 1999, LF data began in 1999, and GFC data captured canopy cover changes beginning in 2000.

Vegetation sampling.—Within each study area, we conducted vegetation surveys at random points within 4 disturbance types (wildfire, prescribed fire, harvest, and harvest followed by prescribed fire). We defined a disturbance patch using LANDFIRE polygons or a group of more than 10 contiguous pixels (i.e. ≥ 900 m^2) from GFC data. Selected patches ranged from 1 – 25 years since disturbance, and we stratified sampling of patches by time since disturbance (in years): 0 – 5, 6 – 10, 11 – 15, and >16. To account for difficulty of access, we restricted sampling to points within 1.5 km of a road or trail. Forest types were assigned using Environmental Site Potential (ESP) data from LANDFIRE, which categorizes the potential natural vegetation (PNV) type that could be supported based on the biophysical characteristics. ESP forest types represent the natural plant communities likely to establish at late or climax stages of successional development in the absence of disturbance (LANDFIRE 2012). We classified ESP forest types into four broader categories: mesic forest, dry montane-mixed conifer forest, open woodland, and montane riparian (Proffitt et al. 2019).

Concurrent with field sampling, we also surveyed a nearby point in undisturbed forest to capture vegetative differences between disturbed and undisturbed forest. Reference points are not before-after controls and therefore do not represent a true control. This distinction was demonstrated by the finding that many reference and disturbance points were later classified to different ESP forest types after sampling. We used one of the two following methods to assign each reference point with similar slope, aspect, and elevation. During the first year of vegetation sampling, we searched for reference points on the ground that matched biophysical characteristics of the sampled disturbance point. In subsequent years, we first assigned a likely reference point before sampling, using GIS data to find a location with similar site characteristics. In the field, we confirmed the appropriate placement of sampling locations or adjusted point locations using visible cues to achieve the most similar and efficient placement of disturbance and matched reference points. When possible, reference points were located in forest directly adjacent to disturbance patches, but some reference points were located up to 1.5 km from the disturbance patch to find a reference location with similar site characteristics. We required reference points to have no evidence of disturbance in LF or GFC data and visually confirmed that reference points had full canopy cover before these dates using Google Earth imagery. We delineated disturbed and undisturbed patches in the field using evidence of disturbance (burned vegetation or perturbation from mechanical treatments), differences in understory vegetation or canopy cover, and topographic barriers. To avoid edge effects on plant responses (Ries et al. 2004), all points were at least 100 m from the nearest disturbance and points within disturbances were at least 100 meters from the disturbance boundary.

Vegetation surveys were conducted between June 1 and August 31 in 2017, 2018, and 2019. At each point, we surveyed three equally-spaced 1–m^2 quadrats along a 40 m transect. We recorded an ocular estimate of the percent cover of all plant species less than 2 m high in each quadrat. Cover estimates were independent of each other, allowing total cover to exceed 100%. Within each quadrat, we established a 0.5–m^2 clip plot and collected current year's growth of the above ground (>2 cm) biomass of graminoids, forbs, and shrubs within the clip plot. Biomass from each plant form and each sub-quadrat was stored in paper bags. We dried bags in a 50º C oven and weighed the contents with a scale to the nearest 0.1 g. Species-specific biomass for forbs, graminoids, and shrubs at a point was considered proportional to the observed species composition, estimated from quadrats. We then averaged all quadrats from a point to estimate a mean value for each point.

We used coefficient of conservatism (C) values for all plant species to estimate habitat condition at all surveyed points. A value of C for a particular species reflects its response to environmental conditions, tolerance to natural and human disturbance, and restriction to certain habitat types (Taft et al. 1997, Andreas et al. 2004). Values of C range from 0 to 10, representing a spectrum where plants with a value of 0 are habitat generalists that respond positively to disturbance, and plants assigned a value of 10 occur in very specialized habitats and are intolerant of disturbance (Supplementary Material Appendix A). A panel of botanical and ecological experts assigned C values to 1,623 plant taxa that grow in Montana (Pipp 2016). We then used C values from all plants at each surveyed point to estimate overall habitat condition with the floristic quality assessment index (FQAI; Swink and Wilhelm 1979, 1994).

Diet sampling.—To evaluate the composition of mule deer diet, we first collected mule deer fecal pellets in each study area and then identified important forage species found in diets using DNA metabarcoding (Taberlet et al. 2007). We captured 136 female adult (>1.5 years of age) mule deer in winters 2017–2019 using helicopter net-gunning, clover trapping, and chemical immobilization in compliance with the University of Montana IACUC policy # 001-17CBWB-011017 and Montana Fish, Wildlife and Parks ACUC protocol #FWP03-2016. We radiocollared mule deer with Lotek LifeCycle 330 Global Positioning System (GPS) collars programmed to upload one location every 13 hours to GlobalStar satellites. We radiocollared 42 deer in the Cabinet-Salish, 49 in the Rocky Mountain Front, and 45 in the Whitefish Range and distributed capture efforts geographically across the winter ranges of study areas.

To identify forage species selected by mule deer, we collected fecal pellets from radiocollared and uncollared mule deer between June 1 and August 31, 2017–2019. We distributed sampling effort across the full spatial extent of each study area and collected 160 samples: 53 from Cabinet-Salish Mountains, 64 from Rocky Mountain Front, and 43 from the Whitefish Range. One sample consisted of 5-10 pellets collected from a single pellet group. To ensure that pellets came from mule deer and not white-tailed deer, we collected pellets only if fresh pellets came from deer that were observed defecating, fresh pellets were found within 100 m of mule deer that were observed in the past 30 minutes, or pellets were located within 500 m of clusters of GPS collar locations and within 1 week of the time of collection. We generally collected moist, fresh pellets, but occasionally collected dry, dark pellets with a pliable consistency and strong odor when there were not fresh pellets within the search area.

We estimated diet composition using fecal DNA-metabarcoding (Taberlet et al. 2007; Jonah Ventures, Boulder, CO). This method isolates a standardized region (or barcode) from DNA in fecal samples, compares it to a reference database for identification, and returns the relative quantities of plant species in mule deer diets. Most DNA barcodes matched with an existing plant in the database at 98% or greater similarity across the barcode length. However, some species have nearly identical DNA in a given barcode region, making it difficult to distinguish just one species match from the database. In these cases, we used a hierarchical approach to identify the species, genus, or family with the closest match (up to 95% similarity). We filtered plant biomass to include only species that made up >2% of the total diet of deer in each study area (Fig. 1.3; Supplementary Material Appendix B, Table B-1).

Forage nutrition.—To evaluate summer forage nutrition in different disturbance types and disturbance regimes, we combined digestibility and biomass of forage plants to develop a landscape model of nutritional resources available to mule deer (kcal/m^2, hereafter forage nutrition). First, we estimated the digestible energy (DE) of forage species samples in each of 4 phenological phases (emergent, flowering, fruiting, and cured). We combined 5 different plants into a composite sample for each species in each phenophase. We estimated mean DE for plants we collected using sequential fiber analysis (Mould and Robbins 1982, Van Soest 1982, Cook 2002) from the Wildlife Habitat Nutrition Lab (Washington State University, Pullman, Washington) and Dairy One Cooperative, Inc. (Ithaca, NY). For forage plants that were not collected in the field during our study, we used DE values reported in previous studies in Montana, Washington, and Oregon (Wagoner 2011, Proffitt et al. 2016, Hull 2018) (Supplementary Material Appendix B, Table B-2). We were unable to obtain DE values for all forage species, though all of these plants made up less than 5% of deer diets by study area. For forb and shrub species known to be high in tannins, we corrected DE for tannins using a bovine serum assay (BSA) during analysis or with BSA literature values (Robbins 1994, Robbins et al. 1987). With these values, we calculated DE for each phenological stage and then averaged all phenophases to estimate mean DE in summer for each known forage species. We considered species-specific dry biomass for forbs, graminoids, and shrubs proportional to the observed species composition we estimated from quadrats. Then, we summed the biomass of forage species in mule deer diets in each quadrat and averaged all quadrats to estimate mean biomass of forage species (g/m^2) for each sampling point. We then calculated forage nutrition as the mean DE of forage plants per unit area ($kcal/m^2$).

Statistical analyses

Habitat condition model.—To investigate the relationship between disturbance type and habitat condition, we first calculated the floristic quality assessment index (FQAI) using the coefficient of conservation (C) values of plants species from vegetation surveys. We then calculated FQAI as (Swink and Wilhelm 1979, 1994):

$$FQAI = \bar{C}\ (\sqrt{N})$$

where $\bar{C}$ represents the average coefficient of conservatism for native species, and N is the total number of native plant species. Next, we used generalized linear regression to predict habitat condition (measured as FQAI) as a function of spatial covariates. Values of FQAI were square-root transformed to meet assumptions of normality for linear modeling. We restricted *a priori* the candidate set of models to include 4 sets of variables known to influence plant communities composition and forest succession: (1) biophysical environment (elevation and aspect); (2) forest type; (3) disturbance and succession (disturbance type and canopy cover, and invasive species); and (4) a full model containing all variables. To account for non-linear effects of elevation on plant communities, we tested elevation with a linear effect and a quadratic effect. We compared candidate models quantitatively using Akaike information criterion (AIC). We screened covariates for multicollinearity and included only covariates with a Pearson's correlation coefficient < 0.6 and a variance inflation factor < 3.0 (Zuur et al. 2010).

Comparison of plant community composition.—To investigate differences in plant responses to wildfire, prescribed fire, harvest, and harvest with prescribed fire in differing disturbance regimes, we compared the occurrence of invasive species of management concern as well as important forage species in each disturbance type and conducted between-class analyses (BCA; Thioulouse et al. 2018). For each plant species, we first identified survey points in which the species was present. We then calculated the proportion of points where the species was recorded in relation to the total number of surveyed points for each disturbance type.

To further evaluate plant community differences between disturbance types and disturbance regimes, we then performed a between-class analysis (BCA) in R library ade4 (Chessel et al. 2004) based on plant cover data collected at sampling locations. We filtered vegetation survey data to include only species identified in deer diets in any study area so that 159 of 497 total taxa remained during analysis. We partitioned the total variance into groups for comparison. We tested for differences in plant composition in three ways: 1) between study areas (3 groups), 2) between disturbance types (5 groups), and 3) between study areas and disturbance types (15 groups). The third comparison combined factors of five disturbance types (wildfire, prescribed fire, harvest, harvest with prescribed fire, and reference forest) and three study areas (Cabinet-Salish, Rocky Mountain Front, Whitefish Range) for a total of 15 groups. A BCA is carried out by ordination of these groups and projecting individual sampled locations onto the resulting axes. This allowed us to identify species that maximize the difference between disturbances and study areas. We used permutation tests with 999 permutations to assess the statistical significance of the BCA.

Forage nutrition.—We developed summer forage nutrition models using mixed-effects generalized linear models to predict forage nutrition (kcal/m^2) as a function of spatial covariates. Forage nutrition was log transformed to meet assumptions of normality for linear modeling. We evaluated 9 standardized covariates shown to influence forage nutrition in previous studies (Peek et al. 2001, Sachro et al. 2005, Van Dyke and Darragh 2006, Romme et al. 2016, Davis et al. 2019): canopy cover, elevation, climatic water deficit (hereafter deficit), aspect, time since disturbance, proportion of invasive species, disturbance type, and forest type, and included study area as a random effect to account for differences in disturbance regimes. We used likelihood ratio tests to assess whether the random effect of study area improved model fit to a degree that merited the increased model complexity. Deficit is the potential evapotranspiration of a site minus the actual evapotranspiration of a site, and it accounts for the effects of both evaporative demand and water availability on a site's water balance (Stephenson 1998). We obtained estimates of deficit at a 30-m^2 resolution based on a model from Holden (2017).

We identified the best-supported model using Akaike information criterion corrected for small sample size (AICc) using backwards-stepwise model selection from the MASS R package (Venables and Ripley 2002) and considered models with ΔAICc ≤ 2 to be supported (Burnham and Anderson 2004). We then screened for multicollinearity and included only covariates with a variance inflation factor < 6.0 (Zuur et al. 2010). We also included a quadratic function for time since disturbance to represent our prediction of vegetative response over time. We assumed all covariates were measured without error, so estimates of regression coefficients are more precise than they would be if we accounted for uncertainty in predictor variables.

We used unstandardized coefficient estimates from the top ranked model to develop spatially-explicit predictions of forage nutrition across all study areas. We used R^2 values from the top model to assess model fit. Analyses were conducted using R version 3.6.1 (R Core Team 2018).

Decision analysis.— We conducted multi-criteria decision analysis (Beinat and Nijkamp 1998, Linkov and Moberg 2012) to explore management decisions as a function of multiple potential management actions, disturbance regimes (study areas), and metrics of vegetative response. We first quantified mean vegetative responses to disturbances within study areas using 5 metrics: i) forage nutrition for mule deer, ii) biomass of shrubs and iii) invasive species (Table 1.1), iv) species richness, and v) habitat condition. We used mean differences in each of these 5 metrics between disturbance and reference sites to represent the predicted consequences of future forest management actions. We pooled all ages within each disturbance type. We then calculated for each of these 5 metrics the difference between the group mean of each disturbance and the group mean of disturbance controls rather than using the difference between a paired disturbance and reference point.

Next, we used the simple multi-attribute rating technique (SMART; Edwards and Barron 1994, Goodwin and Wright 2004) to compare vegetative responses to forest management options. The SMART technique can quantitatively illustrate potential trade-offs and evaluate overall support for alternative disturbances within study areas. Our decision analysis was based on our 5 metrics for all disturbances in each study area. We populated a consequence table to list possible management objectives, here measured as vegetation metrics, and alternative actions in a SMART spreadsheet (Runge et al. 2011). Then, we illustrated trade-offs in relative performance of harvest, harvest followed by prescribed fire and prescribed fire compared with wildfire using normalized scores (von Winterfeldt and Edwards 1986, Edwards and Barron 1994, Mitchell et al. 2013, Runge et al. 2013). We multiplied values by the probability of each outcome under a management alternative and normalized them to a 0-1 scale relative to other objectives within a study area. Alternatives with higher scores were more likely to achieve a desired outcome than alternatives with lower scores. The total for a single management action indicated the best-supported action within a study area.

RESULTS

We conducted 683 forest vegetation surveys: 190 in the Rocky Mountain Front, 269 in the Cabinet-Salish Mountains, and 225 in the Whitefish Range. Surveyed points included 333 conifer, 61 harvest followed by prescribed fire, 131 harvests, 33 prescribed fire, and 125 wildfire points.

Habitat condition

The best-supported model of habitat condition was the disturbance model (ΔAICc = 0, ω_i = 0.81, log(L) = -163.00), which included the effects of disturbance type, proportion of invasive species, canopy cover, and study area (Table 1.2). Habitat condition values for surveyed locations ranged from 4.0 to 60.9, with a mean value of 25.8. Mean habitat condition values were greater in harvests compared to reference conifer forests. Overall, the Rocky Mountain Front had the greatest mean and largest variability in habitat condition (30.1, SD = 8.8), followed by the Whitefish Mountains (25.2, SD = 7.4), with the lowest and most consistent values in the reference area, the Cabinet-Salish Mountains (23.4, SD = 6.1). The highest habitat condition scores were predicted in harvests (β = 0.06, SE = 0.04), but did not differ strongly between disturbance types (Fig. 1.4). Habitat condition also decreased with increasing tree canopy cover and proportion of invasive species.

Comparison of plant community composition

We investigated vegetative differences between disturbance types and study areas through the lens of mule deer forage. Because non-native species may exert negative influences on native vegetation and forage species, we also examined the occurrence of invasive plant species across disturbance types and study areas. We compared occurrence of 12 important forage species in mule deer diets in each disturbance type across all study areas. Generally, top diet species tended to occur less frequently in reference conifer forests (Fig. 1.6) and study areas showed similar trends for many diet species. Alder (*Alnus spp.*) was an exception. In the Cabinet-Salish Range, alder comprised more than 2% of total deer diets but was minimal in other study areas, and it was more common in disturbances than in other study areas. Wildfire were more likely to contain fireweed (*Chamerion angustifolium*), currant (*Ribes spp.*), raspberry (*Rubus spp.*) and willow (Salix spp.) and less likely to contain serviceberry (*Amemlanchier alnifolia*) and spiraea (*Spiraea betulifolia*). The only non-native diet species within top summer diet composition was cheatgrass (*Bromus tectorum*). Cheatgrass was found most frequently in prescribed fires and wildfires in the Cabinet-Salish and Rocky Mountain Front areas.

We also compared the occurrence of other invasive species that were not important forage species but are of high concern for land and wildlife managers (Fig. 1.7). We combined annual brome species (*Bromus spp.*) and the same response to fire (prescribed and wildfire) we found for cheatgrass due to the limited occurrence of other annual bromes in comparison to cheatgrass. Knapweed (*Centaurea stoebe*), thistle (*Cirsium spp.*), hawkweed (*Hieracium spp.*), and mullein (*Verbascum thapsus*) tended to be most common in harvests, harvests followed by prescribed fire, and prescribed fire alone, with intermediate occurrence in wildfires.

Between-class analyses showed statistically significant differences between study areas (Fig. 1.8; Supplementary Material Appendix C, Table C-1; BCA-test, *p* = 0.001). The plant species that separated study areas on Axis 1 were meadowrue (*Thalictrum occidentalis*) and bedstraw (*Galium boreale*), which were both associated with the Rocky Mountain Front. The second axis revealed separation from the other two study areas, separated by Woods' rose (*Rosa woodsii*), blue wild rye *(Elymus glaucus*), and red fescue (*Festuca rubra*) associated with the Cabinet-Salish Mountains. Pinegrass (*Calamagrostis rubescens*), desert parsley (*Lomatium triternatum*), and spreading dogbane (*Apocynum androsaemifolium*) were mainly associated with the Whitefish area. The first axis explained 68.2% and the second axis 31.8% of the total inertia, which can be roughly interpreted as the percent variance explained by each individual axis.

Between-class analyses also showed statistically significant differences between disturbance types (Fig. 1.9; Supplementary Material Appendix C, Table C-2; BCA-test, *p* = 0.001). *Chamerion angustifolium* separated wildfire from all other disturbance types. Harvest followed by prescribed fire was separated by bearberry (*Arctostaphylos uva-ursi*), *Calamagrostis rubescens*, western larch (*Larix occidentalis*), sedges (*Carex spp*.), and yarrow (*Achillea millefolium*). Reference conifer forests were separated from harvest followed by prescribed fire by pipsissewa (*Chimaphila umbellate*), wintergreen (*Orthilia secunda*), and *Thalictrum* *occidentalis*. Reference forests were most separated from wildfire by twinflower (*Linnea borealis*). In general, harvest and prescribed fire alone did not differ from other disturbance types based on forage species composition. The first axis explained 44.8% and the second axis 26.5% of the total inertia, with cumulative inertia 71.2%.

Finally, we found statistically significant differences between disturbance types and study areas (Fig. 1.10; Supplementary Material Appendix C, Table C-3; BCA-test, $p = 0.001$). Disturbances clustered most closely by study area, showing different composition of forage species by disturbance type within study area groups.

Cabinet-Salish Mountains.—In the Cabinet-Salish area, wildfire was separated from all other disturbances, primarily by *Chamerion angustifolium*, willows (*Salix spp*.) and *Bromus tectorum* on Axis 1. Prescribed fire and harvest followed by prescribed fire clustered closely, where prescribed fire was separated by *Larix occidentalis* and *Achillea millefolium* and harvest followed by prescribed fire most separated by *Carex* spp. and *Arctostaphylos uva-ursi*. Reference conifer forest was separated by *Chimaphila umbellata* and *Linnea borealis*. Harvests were not distinctly separated from any disturbance type. The first axis explained 37.6% and the second axis 28.0% of the total inertia, with cumulative inertia 65.6%.

Rocky Mountain Front.—In the Rocky Mountain Front, prescribed fire was most separated from all other disturbances and also had the smallest number of sampled sites ($n = 11$) which reflected the low prevalence of prescribed fire in this study area. The first axis revealed that prescribed fire was mostly separated by wildrye (*Elymus spp*.) and cinquefoil (*Potentilla spp*). On the second axis, wildfire was separated by *Chamerion angustifolium* and mountain brome (*Bromus carinatus*), where harvest followed by prescribed fire was more associated with *Xerophyllum* *tenax*. In comparison, the main forage species that separated conifer forests were Douglas fir (*Pseudotsuga menziesii*), twisted stalk (*Streptopus amplexifolius*), and *Orthilia secunda*. Harvest was not distinctly separated from any disturbance type. The first axis explained 40.1% and the second axis 26.2% of the total inertia, with cumulative inertia 66.3%.

Whitefish Range.—In the Whitefish area, the forage species that separated wildfire compared to other disturbances (Axis 1) were *Salix* spp., lodgepole pine (*Pinus contorta*), quaking aspen (*Populus tremuloides*), *Chamerion angustifolium*, Alberta penstemon (*Penstemon albertinus*), and *Bromus inermis*. Harvest and harvest followed by prescribed fire were associated with (*Penstemon confertus)*, *Achillea millefolium*, and *Festuca rubra*. The species that separated these disturbances on Axis 2 were *Arctostaphylos uva-ursi* and *Calamagrostis rubescens*, associated with harvest, and *Larix occidentalis*, associated with harvest followed by prescribed fire. Reference conifer forest was separated by *Chimaphila umbellata* and *Thalictrum occidentalis*. The first axis explained 43.4% and the second axis 30.4% of the total inertia, with cumulative inertia 73.8%.

Forage nutrition

The best-supported model of forage nutrition ($R^2 = 0.20$, Table 1.3) included fixed effects of canopy cover, deficit, disturbance type, forest type, and time since disturbance and a fixed effect of study area (Table 1.4). The second-best-supported model (ΔAICc = 0.64, log(L) = -2042.12) included the same effects and included the effect of proportion of invasive species (Table 1.3). In comparison with mesic forest, the effect of dry forest on forage nutrition was strongly positive ($\beta = 1.30$, SE = 0.50). Montane riparian supported lower mean forage nutrition and greater variability (β = -1.06, SE = 1.01). Forage nutrition increased in wildfires compared to reference forests (β = 0.93, SE = 1.42) and was greatest in wildfires and prescribed fires. Forage nutrition was predicted to decline with increasing time since disturbance in all study areas (Fig. 1.5) and with greater canopy cover. Deficit had a strongly positive effect on forage nutrition. We lacked evidence of variation in forage nutrition between sampling months (June, July, and August) either for all points combined ($p = 0.15$) or for each disturbance type analyzed separately (harvest: $p = 0.55$, prescribed fire: $p = 0.93$, harvest with prescribed fire: $p = 0.08$, wildfire: $p = 0.08$, and reference conifer: $p = 0.61$).

Decision analysis for management actions

Mean effects of wildfire in the Cabinet-Salish Mountains (row 1, Table 1.8) indicated an average increase in forage nutrition of 3.22 kcal/m^2 (SE = 1.37), 3.11 g (SE = 1.02) shrub biomass, and 0.94 g (SE = 0.48) invasive species biomass. Species richness increased by an average of 1.93 species (SE = 1.00), and habitat condition increased slightly (FQAI = 0.60; SE = 1.01). Mean responses in the Rocky Mountain Front were smaller and indicated a greater increase in habitat condition despite comparatively greater invasive species biomass and lower species richness. We found a large increase in forage nutrition in wildfires in the Whitefish Range, but weaker or negative effects on other vegetative responses. All disturbances in the Whitefish Range were associated with a reduction in habitat condition. In harvests, the largest increase of forage nutrition (14.66 kcal/m^2; SE = 7.19) occurred in the Whitefish range in conjunction with declines in species richness (-1.2; SE = 0.99) and invasive species biomass (0.34; SE = 0.29). The largest increase in shrub biomass occurred in harvest followed by prescribed fire in the Cabinet-Salish, prescribed fire in the Whitefish Range, and wildfire in the Rocky Mountain Front. In the Rocky Mountain Front, invasive species biomass showed the greatest increase after harvest and harvest followed by prescribed fire. Notably, species richness and habitat condition also increased strongly (although variably). We found that invasive species biomass did not necessarily correspond with lower habitat condition scores.

Comparison of normalized vegetative responses (Table 1.9) further revealed differences in the outcomes of disturbance types between study areas. We did not observe strong patterns among disturbance types between study areas, as each disturbance was associated with a range of vegetative responses. In all study areas, harvests received the highest total scores when all vegetative response objectives were weighted equally.

DISCUSSION

Our results suggest that different mechanisms are likely driving forage availability and habitat condition: 1) the composition of plant communities present before disturbance, and 2) disturbance-specific effects on plant functional groups. We found that habitat condition declined with increasing dominance of invasive species, whereas forage nutrition increased. Species richness and productivity generally increase for several years after disturbance from fire or timber harvest, typically leveling off or declining in the subsequent years (Hebblewhite et al. 2009, Halpern and Lutz 2013, Romme et al. 2016). The increase in species diversity consists of native early-successional pioneer species as well as invasive species. We found that an increase in invasive species did not necessarily decrease the amount of forage nutrition available in post-disturbance forests. Our results support previous work by Alba and others (2015) showing functional groups of plants respond differentially to both forest and disturbance types. Their meta-analysis also reported short-term benefits of prescribed fire for native species and minimal effects on non-native plant composition. In contrast, they found wildfire increased non-native composition and performance over all time scales, with no effect on native species composition. Our results suggest that the type of disturbance may be particularly important in conifer forests, but more research is needed to fully understand how native and invasive species composition change over time. Familiarity with the composition of plants pre- and post-disturbance will help to determine whether disturbance has transported invasive species to a new area or changed the abundance of existing invasive species.

Phenology is an important component of the relationship between native and exotic forage for elk (Kohl et al. 2012), as invasive species can comprise sizable proportion of elk diets during winter and spring. We found that cheatgrass and prickly lettuce were both components of mule deer diets, but both species were consumed earlier in the growing season, as they provide fewer nutritional benefits as summer progresses. After disturbance, invaders generally include annual grasses and long-distance, dispersing forbs more associated with fire (Rew and Johnson 2010). Our results also show that harvest and harvest followed by prescribed fire also appear to increase the prevalence of less mobile invaders (e.g. knapweed and hawkweed).

Whether disturbance comes from natural or anthropogenic sources, the amount of canopy cover removed and the frequency of disturbance have important effects on forage availability (Peek et al. 2001). Surveyed sites in the Cabinet-Salish Mountains tended to produce less forage nutrition overall. In the lodgepole pine forests of Alberta, Canada, Visscher and Merrill (2009) showed that after 30 years of harvest managed for a steady flow of timber, vegetation remained relatively stable without other major disturbances. Under sustained, consistent cutting regimes, plant communities shifted toward more herbaceous plants and shrubs considered palatable forage for elk (Visscher and Merrill 2009). However, our model suggests that mule deer forage does not respond in the same way in the Salish Mountains, where plant communities have been shaped by a legacy of sustained timber harvest since the early 20th century. Disturbance on the Rocky Mountain Front is dominated by wildfires with limited fire suppression, particularly in wilderness areas. On the Rocky Mountain Front, forage production was intermediate between the three study areas, but habitat condition was substantially higher than in the others. Conversely, the Whitefish area receives an intermediate level of disturbance from natural and anthropogenic sources. Here, forage nutrition was greater, and habitat condition scores were intermediate.

Frequency of disturbance, as posited in the intermediate disturbance hypothesis, may partly explain differences in average habitat condition between study areas. The Cabinet-Salish Mountains tended to have lower ecological condition scores. This study area experiences the most widespread and highest-frequency disturbance, especially in comparison with historical disturbance regimes of each area. Assessing habitat condition can also be useful in detecting homogenization of plant communities over time. Homogenization often results from increases in invasive and generalist species combined with concurrent declines of native species. The decline we documented in habitat condition with increasing proportion of invasive species is consistent with the phenomenon of homogenization. Management objectives that prioritize ecological condition may focus on sites that support plants with greater fidelity for particular habitat conditions. Plants that require particular conditions are be more susceptible to extirpation due to changes in the environment (Carignan and Villard 2002). However, this study does not suggest that the type of disturbance differentially influences habitat condition. Rather our results align more with a growing body of work showing that forest disturbances generally do not eliminate species from the understory, and instead typically benefit species absent or uncommon in untreated forest (Abella and Springer 2015).

Studies posit that deer may benefit from increased forage diversity and abundance if fire is used regularly (e.g. every 4–10 years) and creates a mosaic habitat pattern (Roccafort et al. 2010, Horncastle et al. 2013). However, we found that the composition of forage species resulting from harvest followed by prescribed fire and prescribed fire alone differed between disturbance. These disturbances were strongly associated with increases in multiple species of grasses and sedges, several forbs, and bearberry, a sub-shrub. Although many of these species were consumed by deer, they tended to be consumed in low quantities overall or only by a small number of individuals. Considering composition of forage in the context of disturbance regimes can help to predict where forage is likely to be limited and, therefore, which type of forest disturbance may be most beneficial for mule deer.

MANAGEMENT IMPLICATIONS

SMART analysis reveals tradeoffs in management objectives that are specific to forest and disturbance types and helps managers see explicit differences among their choices, across disturbance practices and ecosystems. The benefits of both management actions come with less optimal outcomes for other objectives, including the responses of shrubs, invasive species,

species richness, and habitat condition. Managers can define their own priorities to weigh the relative merits of management actions in each of three disturbance regimes. The use of decision analysis provides managers more information to develop strategies for land management and to identify treatments to balance objectives for management of mule deer.

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FIGURES

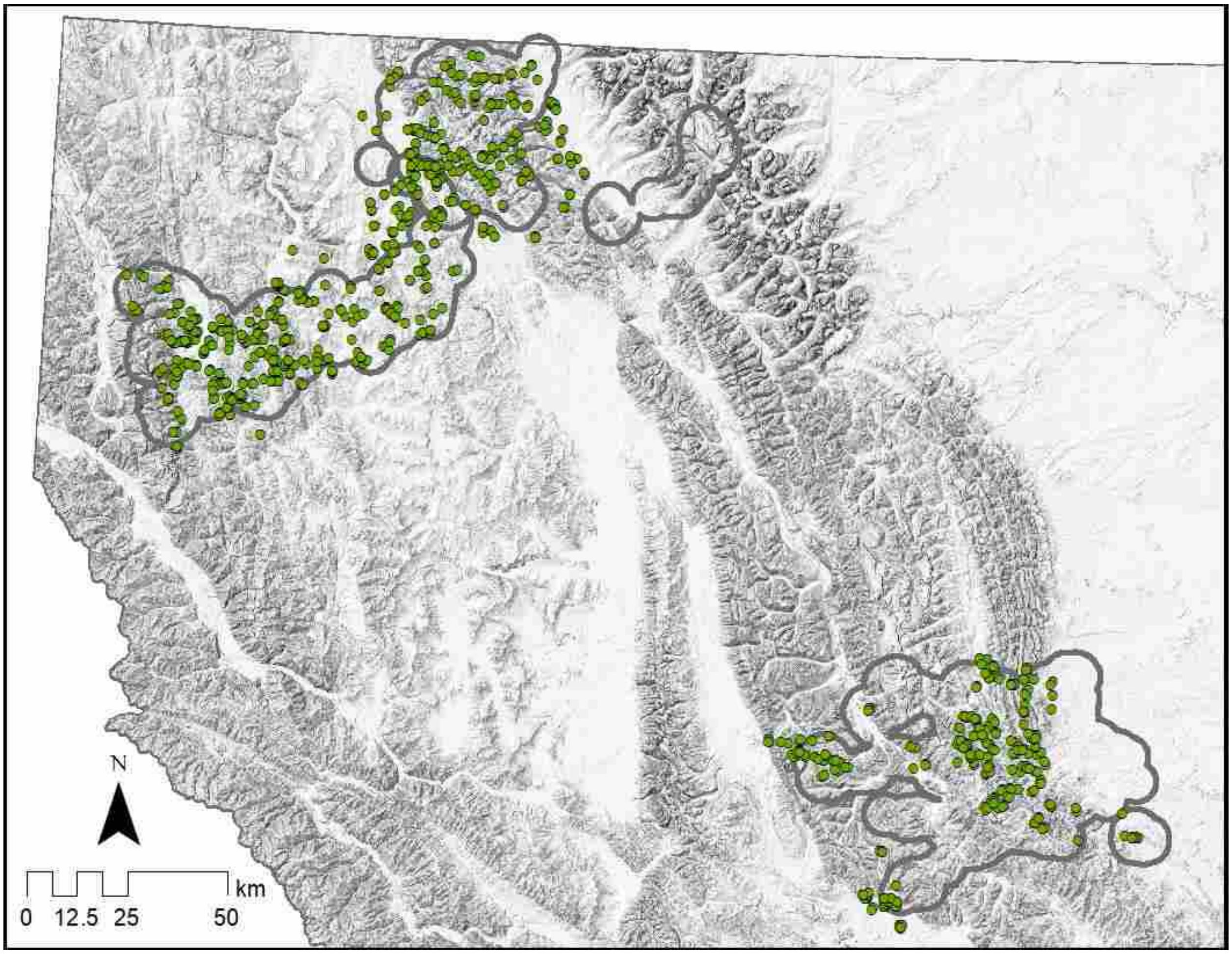


Figure 1.1. The Cabinet-Salish, Rocky Mountain Front, and Whitefish Range mule deer population annual ranges in northwest Montana, USA. Green points represent locations of forest vegetation surveys conducted between June 1 – August 31, 2017–2019.

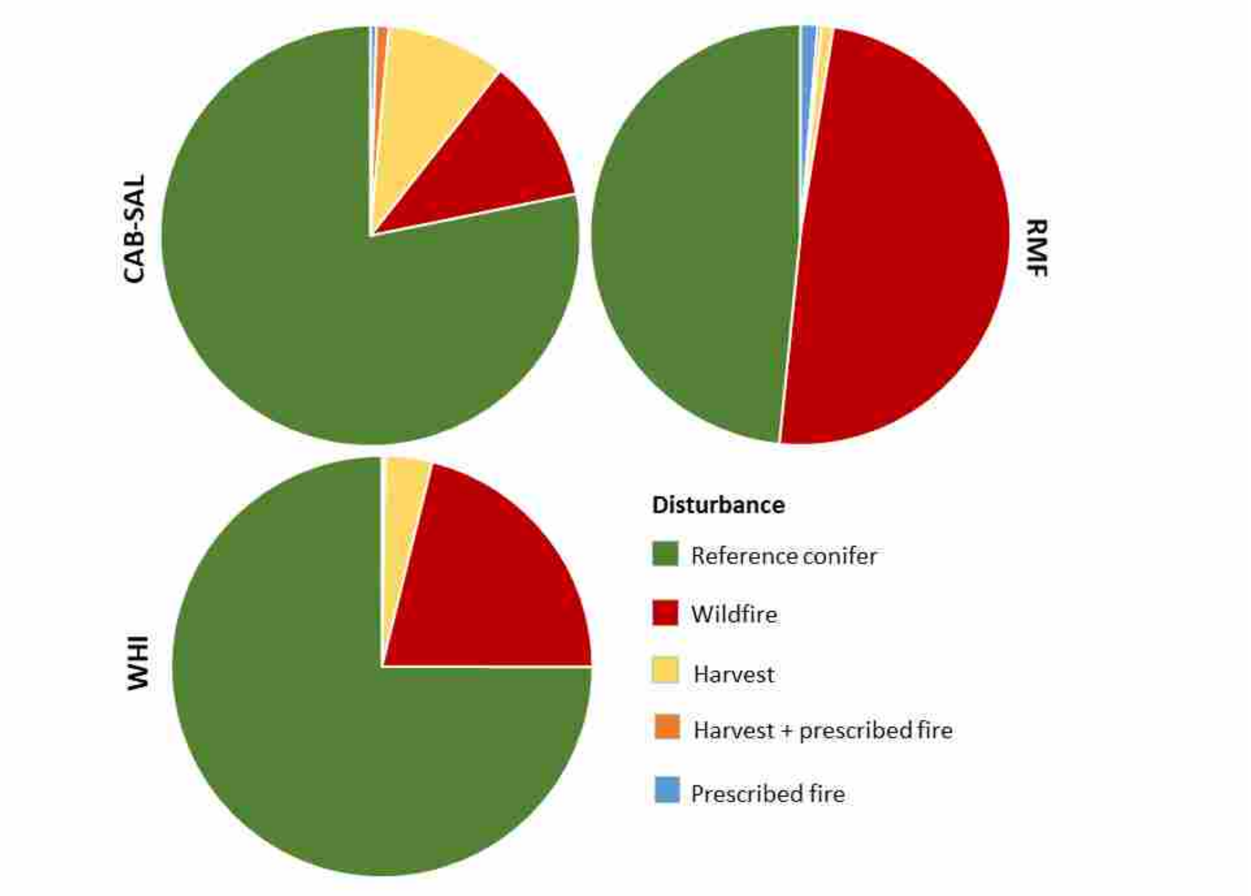


Figure 1.2. Proportion of disturbance within home ranges of mule deer calculated from 95% kernel density estimates (KDE) of GPS radiocollar locations during summer 2017 – 2019.

Table 1.1. **S**pecies name, life history, and form of non-native species identified in 683 forest vegetation surveys during 2017–2019 in three study areas: the Rocky Mountain Front, the Cabinet-Salish Mountains, and the Whitefish Range.

Scientific name	Life history	Form
Agrostis stolonifera	perennial	graminoid
Alyssum alyssoides	annual	forb
Bromus inermis	perennial	graminoid
Bromus japonicus	annual	graminoid
Bromus tectorum	annual	graminoid
Centaurea stoebe	annual	forb
Cirsium arvense	perennial	forb
Cirsium vulgare	perennial	forb
Cynoglossum officinale	annual	forb
Dactylis glomerata	perennial	graminoid
Descurainia sophia	annual	forb
Hieracium aurantiacum	perennial	forb
Hieracium caespitosum	perennial	forb
Hieracium pratense	perennial	forb
Holosteum umbellatum	annual	forb
Hypericum perforatum	perennial	forb
Lactuca serriola	annual	forb
Leucanthemum vulgare	perennial	forb
Medicago lupulina	annual	forb
Myosotis stricta	annual	forb

Phalaris arundinacea	perennial	graminoid
Phleum pratense	perennial	graminoid
Poa compressa	perennial	graminoid
Poa pratensis	perennial	graminoid
Potentilla recta	perennial	forb
Prunella vulgaris	perennial	forb
Schedonorus arundinaceus	perennial	graminoid
Tanacetum vulgare	perennial	forb
Taraxacum erythrospermum	perennial	forb
Taraxacum officinale	perennial	forb
Tragopogon dubius	annual	forb
Trifolium pratense	perennial	forb
Trifolium repens	perennial	forb
Verbascum thapsus	annual	forb
Veronica arvensis	annual	forb

Table 1.2. Akaike model selection criterion (AICc), number of estimable parameters (K), AICc weight (ω_i), and maximized log-likelihood (log(*L*)) for 4 *a priori* models used to test relative support for predictions explaining habitat condition in northwestern Montana, USA. Models were estimated using data from 683 forest vegetation surveys during 2017–2019 in three study areas: the Rocky Mountain Front, the Cabinet-Salish Mountains, and the Whitefish Range.

Model	**Parameters**	**K**	**ΔAICc**	**ω_i**	**Log(*L*)**
Disturbance	DisturbType + StudyArea	10	0	0.81	-163.00
Forest	ForestType + StudyArea	7	4.22	0.1	-168.18
Full	$Elev^2$ + Aspect + ForestType + DisturbType + PropInvasive + CanCov + StudyArea	16	4.76	0.07	-159.13
Environmental	$Elev^2$ + Aspect	7	7.21	0.02	-169.68

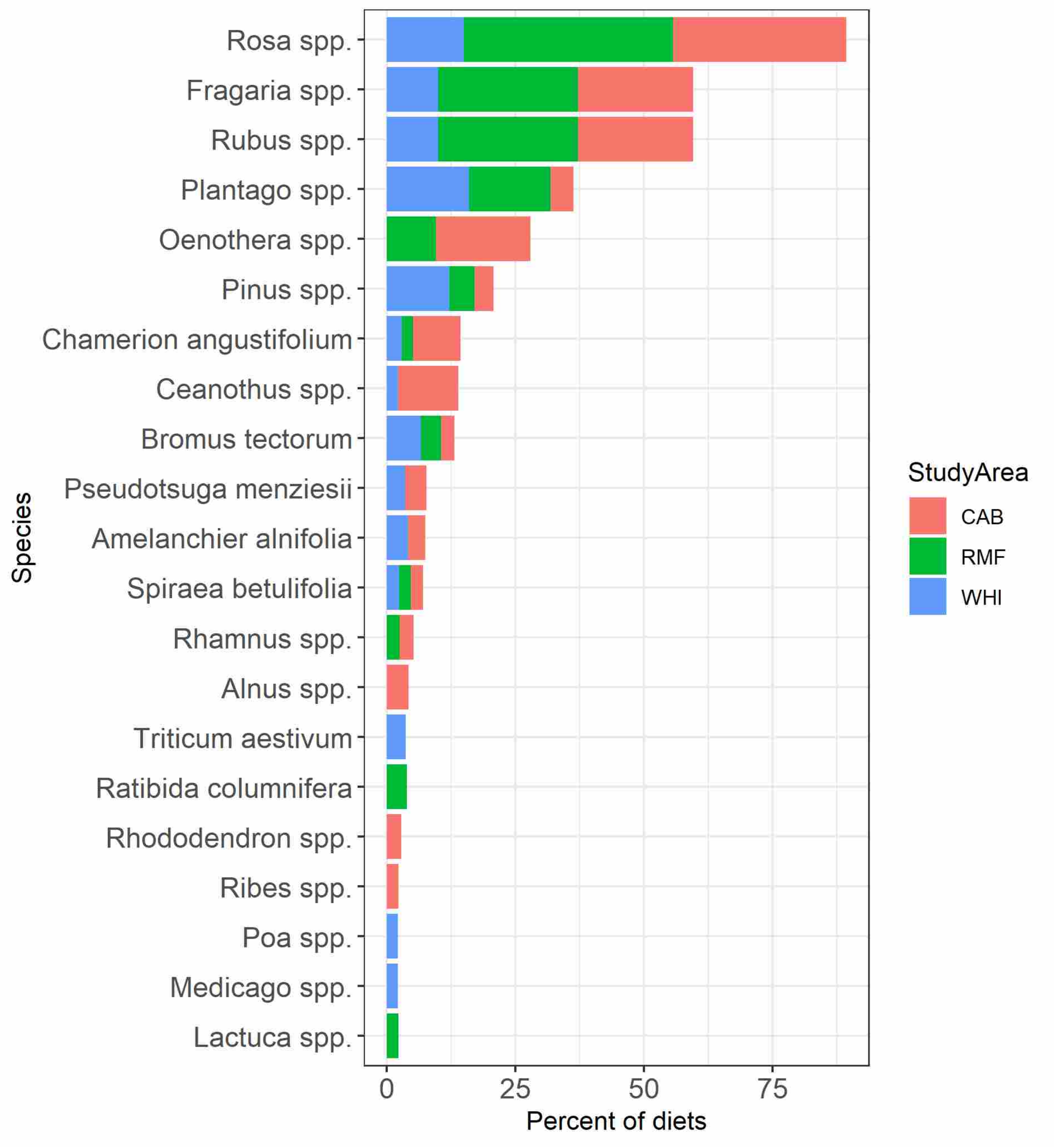


Figure 1.3. Forage species that comprise >2% of total mule deer summer diets from fecal collections during 2017–2019. Values represent the cumulative proportion of individual diets for a given study area.

Figure 1.4. Parameter estimates (centered and scaled) ± 95% CI from the top model of habitat condition, using the floristic quality assessment index (FQAI) in 3 study areas in northwest Montana: the Rocky Mountain Front, the Whitefish Range, and the Cabinet-Salish Mountains, the reference area for the effect of study area, 2017–2019. The vertical line marks the levels of neutral effect at 0.

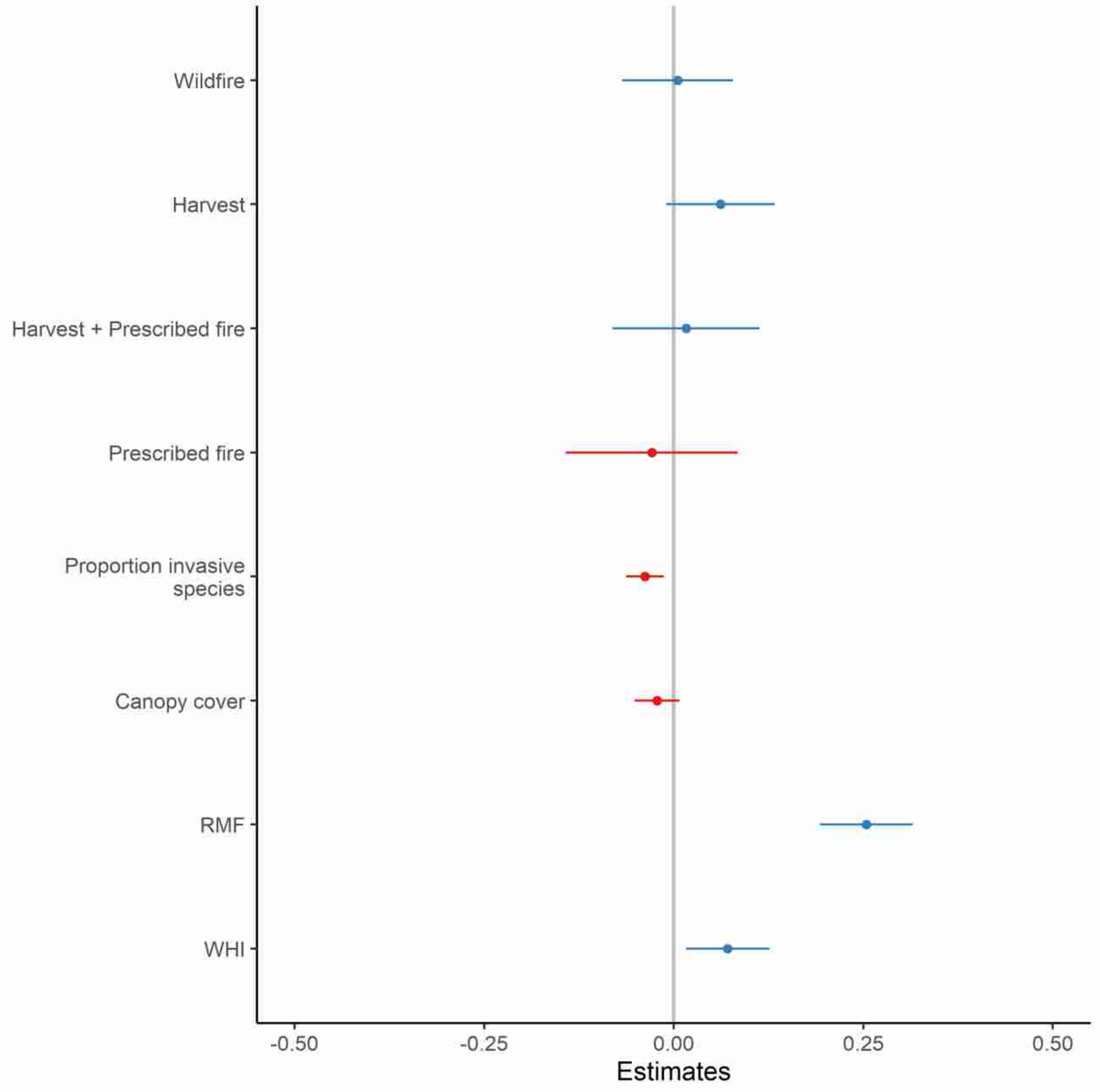


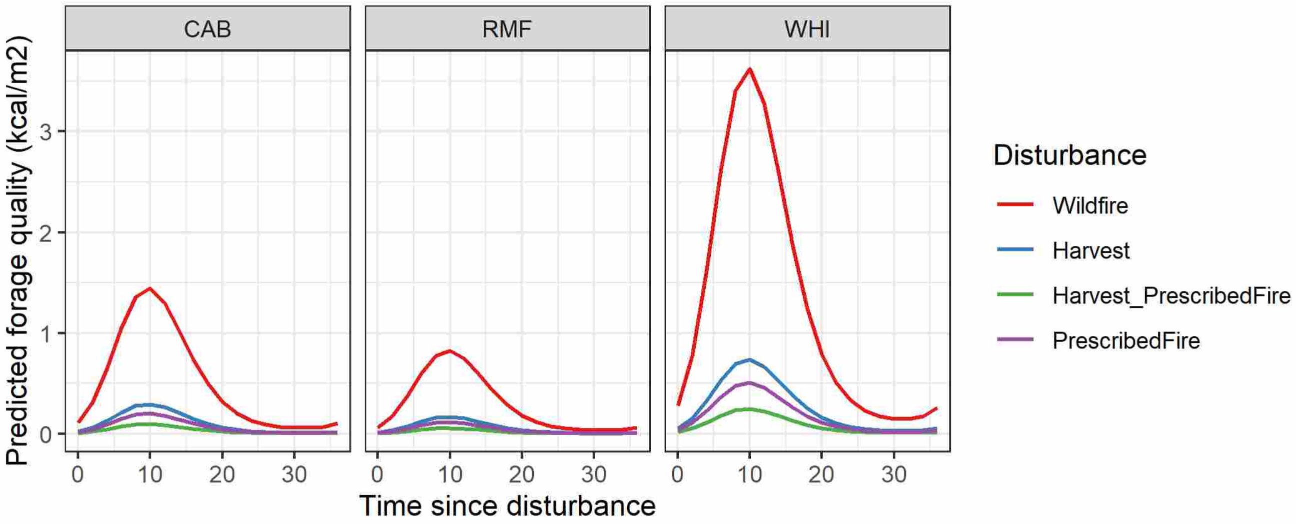
Table 1.3. Akaike model selection criterion (AICc), number of estimable parameters (K), AICc weight (ω_i), and maximized log-likelihood (log(*L*)) for the mixed effects model used to estimate forage nutrition. All models included a random effect of study area, and models were estimated using vegetation survey data from 683 forest vegetation surveys in northwestern Montana, USA, 2017–2019. We considered models with ΔAICc ≤ 2 to be supported (Burnham and Anderson 2004).

Model covariates	**K**	**ΔAICc**	**Log(*L*)**
CanCov^2 + Deficit + DisturbType + ForestType + Time^3	16	0.00	-2042.85
CanCov^2 + Deficit + DisturbType + ForestType + Time^3 + PropInv	17	0.64	-2042.12

Table 1.4. Model structure for the best-supported model of forage nutrition for mule deer during summer in 3 study areas in northwestern Montana, USA: the Rocky Mountain Front, the Whitefish Range, and the Cabinet-Salish Mountains, 2017–2019. Standardized coefficient estimates and standard errors for fixed effects.

Parameter	**Coefficient**	**S. E.**	***p***
(Intercept)	-2.69	1.56	0.08
Canopy cover	-1.06	0.24	0.00
Canopy cover^2	-0.62	0.21	0.00
Deficit	1.11	0.23	0.00
Wildfire	0.93	1.42	0.52
Harvest	-0.67	1.44	0.64
Harvest + prescribed fire	-1.76	1.58	0.27
Prescribed fire	-1.04	1.65	0.53
Open woodland	0.09	0.70	0.90
Dry forest	1.30	0.50	0.01
Montane riparian	-1.06	1.01	0.29
Time	-2.63	0.83	0.00
Time^2	0.90	1.04	0.39
Time^3	1.30	0.66	0.05

Figure 1.5. Predicted mean forage nutrition (kcal/m^2) in wildfire, harvest, harvest with prescribed fire, and prescribed fire in northwest Montana, USA, during summer (June–Aug) 2017–2019.



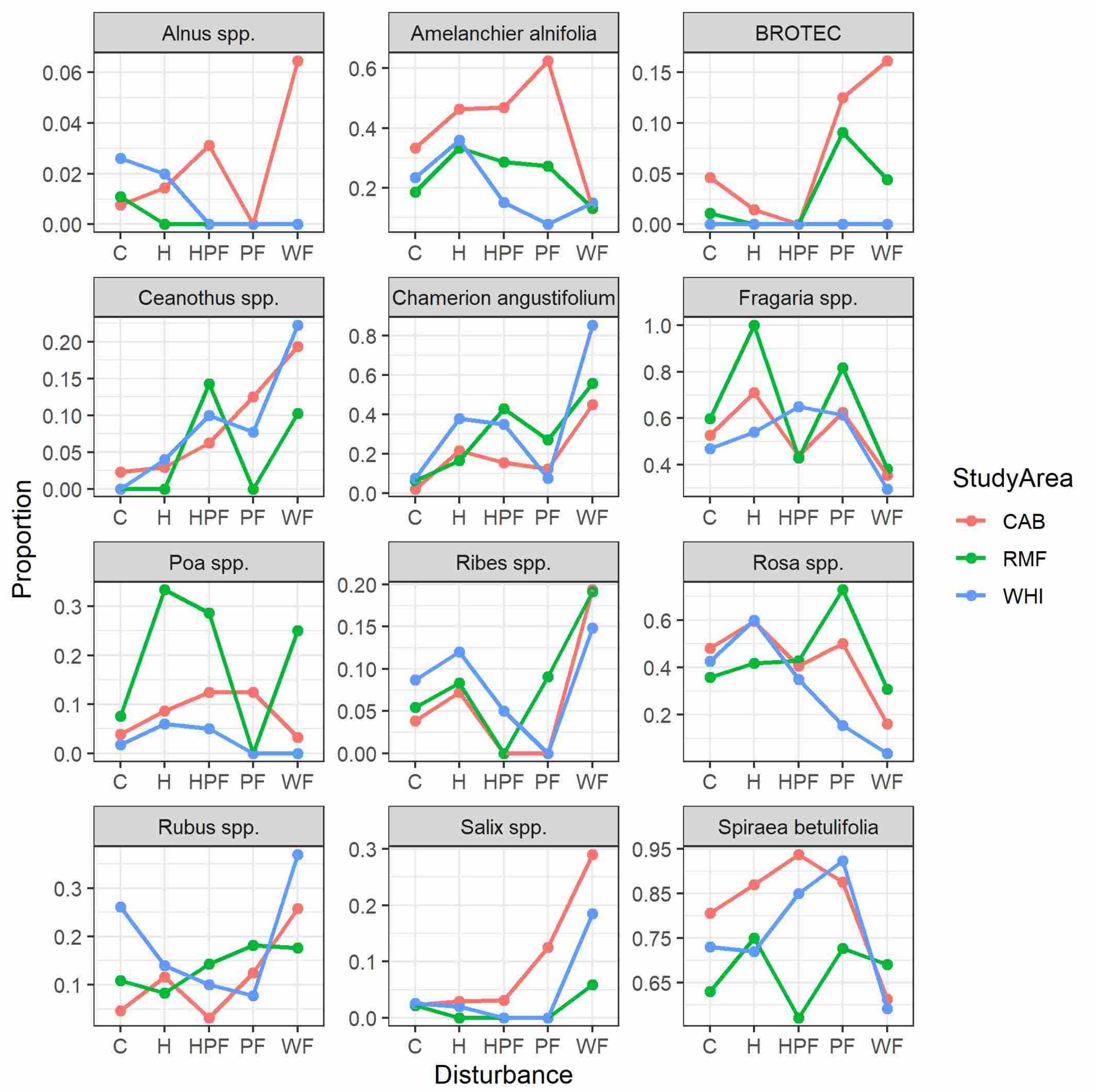


Figure 1.6. Proportion of vegetation points where top species from mule deer diets were recorded in reference conifer forest (C) and 4 disturbance types: harvest (H), harvest + prescribed fire (HPF), prescribed fire (PF), and wildfire (WF). Species occurrence was from 683 forest

vegetation surveys during 2017–2019 in three study areas: the Rocky Mountain Front, the Cabinet-Salish Mountains, and the Whitefish Range.

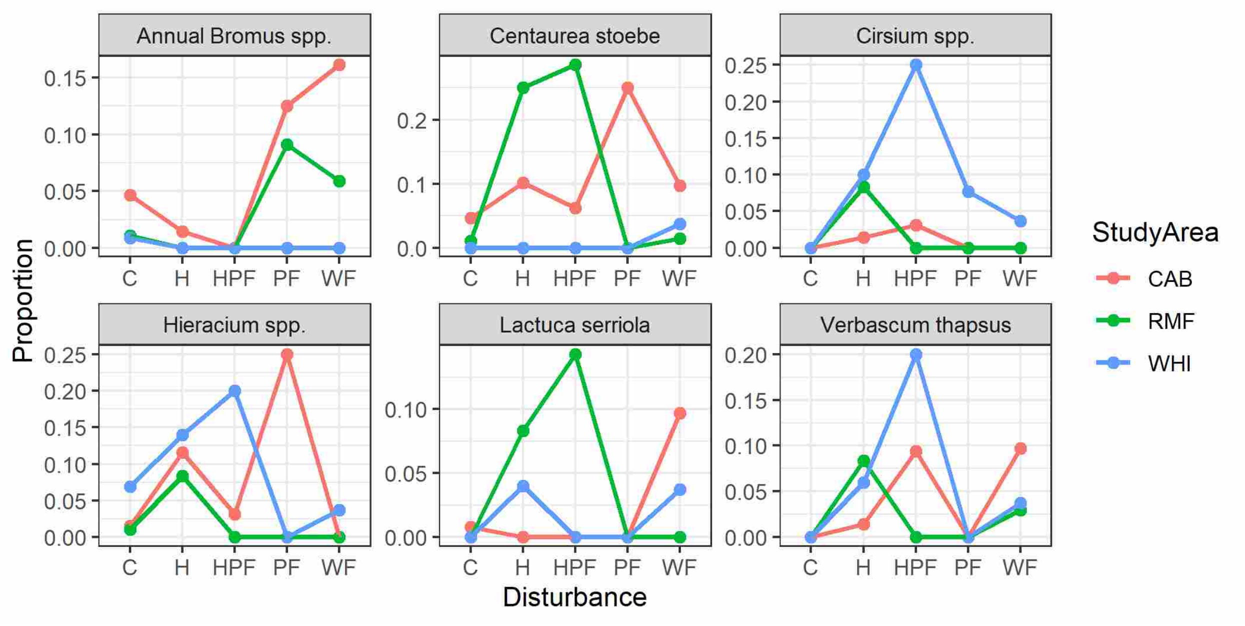


Figure 1.7. Proportion of vegetation points where the most prevalent invasive species were recorded in reference conifer forest (C) and 4 disturbance types: harvest (H), harvest + prescribed fire (HPF), prescribed fire (PF), and wildfire (WF). Species occurrence was from 683 forest vegetation surveys during 2017–2019 in three study areas: the Rocky Mountain Front, the Cabinet-Salish Mountains, and the Whitefish Range.

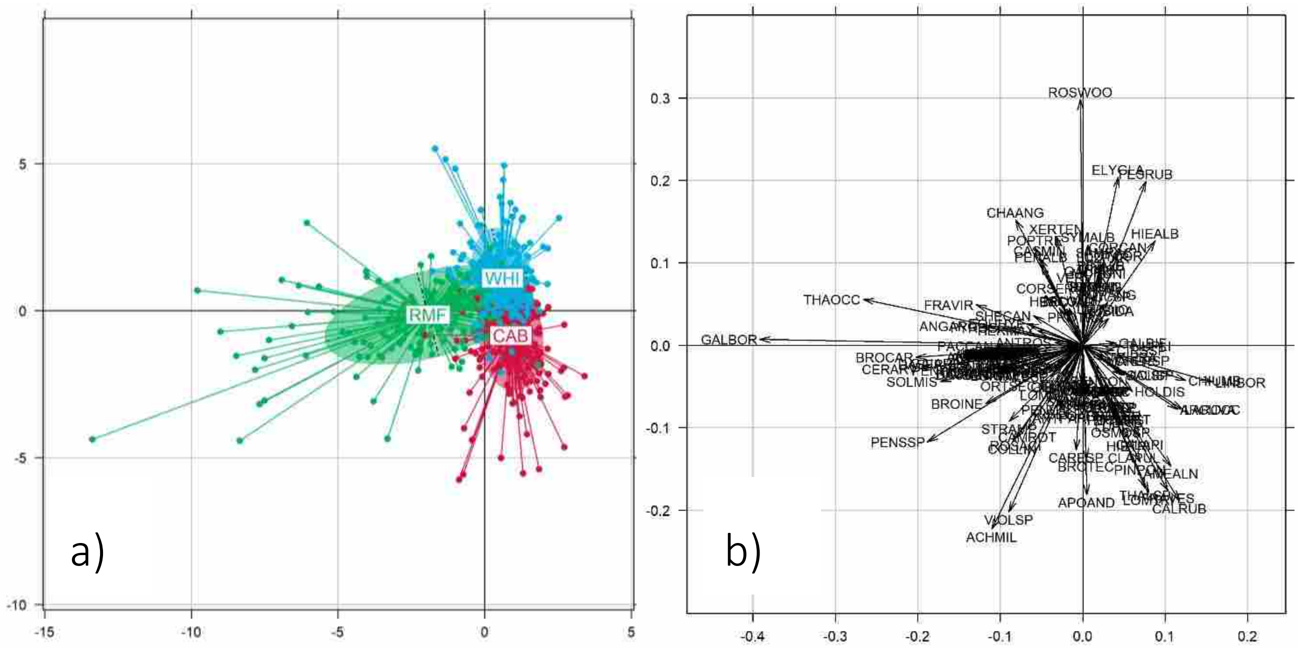


Figure 1.8. Multivariate differences in understory vegetation composition between three study area with different disturbance regimes: Cabinet-Salish Mountains (*n*=269), Rocky Mountain Front (*n*=190) and Whitefish Range (*n*=255) in summers 2017-2019. Normed scores of the two axes from a Hill-Smith (HS) between-class analysis (BCA) based on a) forage plant composition at individual surveyed sites, and b) vegetation cover (%) of forage plant species measured in 1-m^2 quadrats by study area.

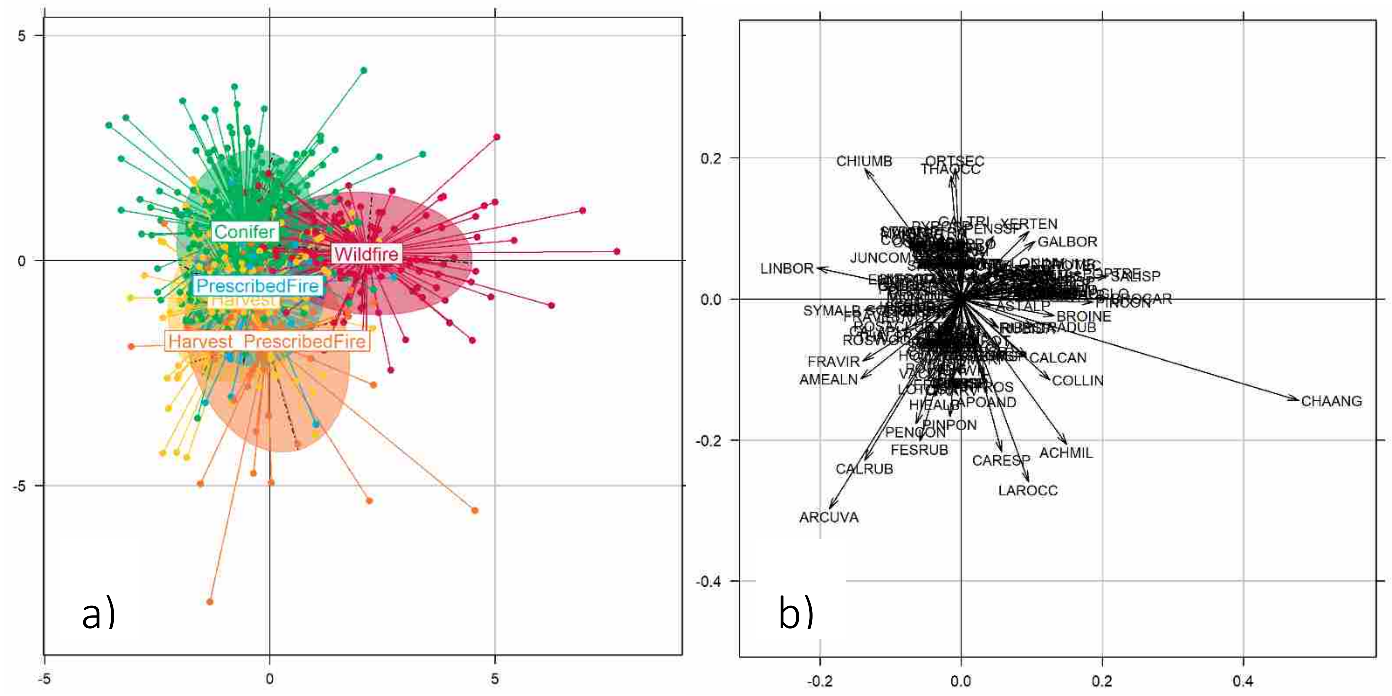


Figure 1.9. Multivariate differences in understory vegetation composition between disturbance types: wildfire (*n*=125), harvest (*n*=131), harvest followed by prescribed fire (*n*=61), prescribed fire (*n*=33), and reference forest (*n*=333) in summers 2017-2019. Normed scores of the two axes from a Hill-Smith (HS)-between class analysis (BCA) based on a) forage plant composition at individual surveyed sites, and b) vegetation cover (%) of forage plant species measured in 1-m^2 quadrats by study area.

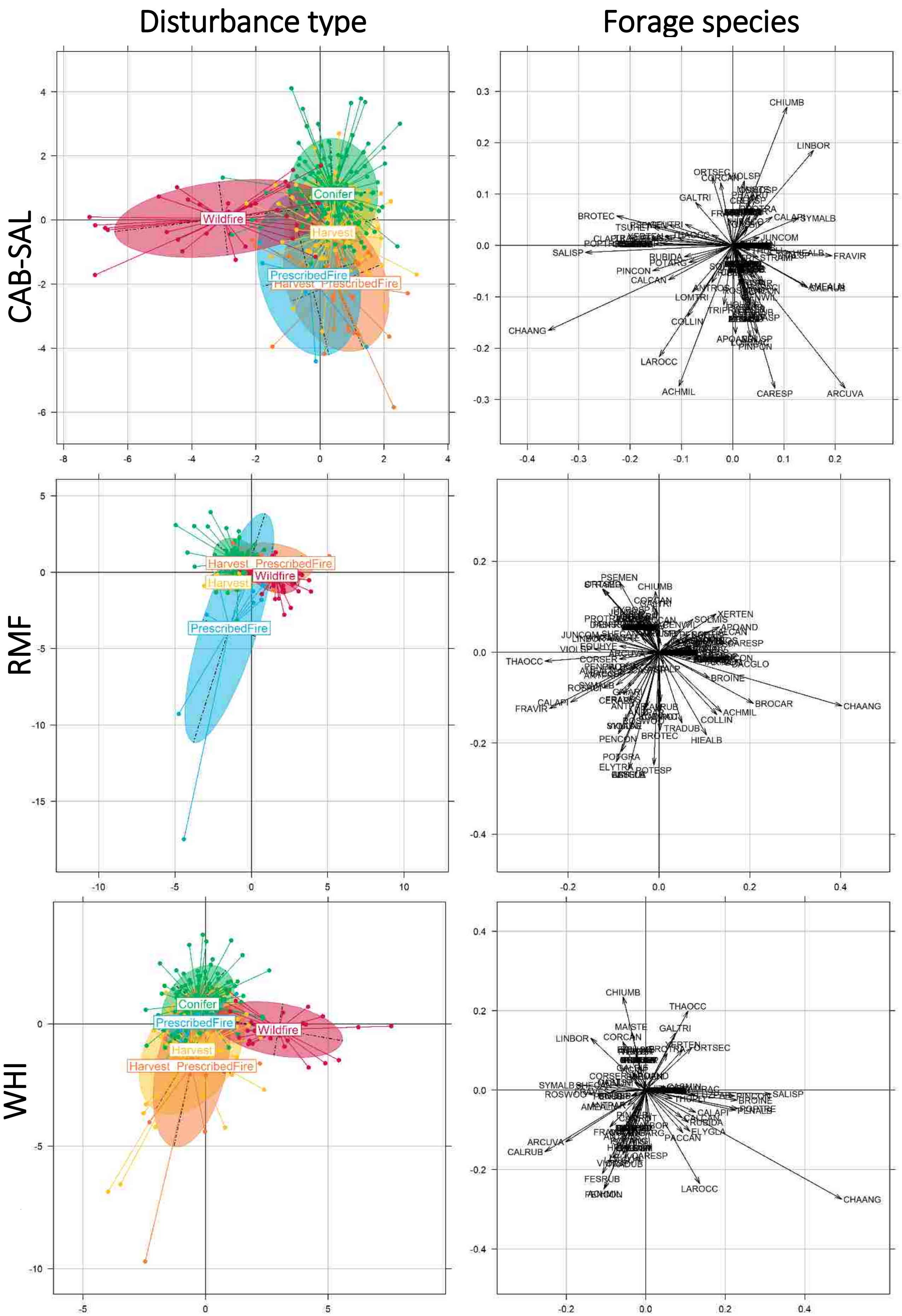

Disturbance type
Forage species
CAB-SAL
RMF
WHI
Conifer
Wildfire
Harvest
PrescribedFire
Harvest_PrescribedFire
CHIUMB
LINBOR
ORTSEC
CORCAN
GALTRI
BROTEC
CALAPI
SYMALB
JUNCOM
SALISP
FRAVIR
PINCON
CALCAN
CHAANG
LOMTRI
COLLIN
LAROCC
ACHMIL
CARESP
ARCUVA
AMEALN
CALRUB
PINPON
PSEMEN
XERTEN
SOLMIS
APOAND
THAOCC
BROINE
BROCAR
HIEALB
TRADUB
POTESP
ELYTRA
POAGRA
PENCON
FESRUB
MAISTE
ELYGLA
PACCAN
ROSWOO
RUBIDA
SYMALB
LINBOR

Figure 1.10. Multivariate differences in understory vegetation composition between disturbance types: wildfire (*n*=125), harvest (*n*=131), harvest followed by prescribed fire (*n*=61), prescribed fire (*n*=33), and reference (*n*=333) in three study areas: Cabinet-Salish Mountains (*n*=269), Rocky Mountain Front (*n*=190) and Whitefish Range (*n*=255) in summers 2017-2019. Normed scores of the two axes from a Hill-Smith (HS)-between class analysis (BCA) of disturbance types based on forage plant composition at individual surveyed sites and forage species cover (%) measured in 1-m^2 quadrats by study area.

Table 1.5. Mean vegetative outcomes of forest management alternatives followed by standard errors. Values represent the mean response to disturbance compared to reference forest, with standard error of the difference. Management options are grouped by study area in the first column. Expected management objectives (quantified by the change in vegetation metrics) are shown in columns across the top row, followed by the desired direction of change, specified as maximize (max) or minimize (min).

			Δ Forage nutrition, kcal/m^2 (S.E.)	Δ Shrub biomass, g (S.E.)	Δ Invasive sp. Biomass, g (S.E.)	Δ Species richness (S.E.)	Δ Habitat condition, FQAI (S.E.)
	Disturbance type	*n*	(max)	(max)	(min)	(max)	(max)
CAB-SAL	Wildfire	31	3.22 (1.37)	3.11 (1.02)	0.94 (0.48)	1.93 (1.00)	0.60 (1.01)
	Harvest	69	1.62 (0.66)	2.77 (0.89)	0.26 (0.17)	3.89 (0.76)	2.34 (0.86)
	Harvest + Prescribed fire	32	1.18 (0.76)	4.12 (3.71)	0.03 (0.16)	0.33 (0.71)	0.52 (1.35)
	Prescribed fire	8	4.23 (3.23)	2.09 (1.86)	0.55 (0.37)	4.39 (1.95)	1.53 (1.69)
RMF	Wildfire	68	2.01 (0.89)	3.30 (1.36)	1.26 (0.43)	0.93 (1.16)	2.04 (1.35)
	Harvest	12	2.41 (1.38)	1.78 (1.55)	3.03 (1.40)	3.15 (1.8)	5.48 (1.78)
	Harvest + Prescribed fire	7	1.54 (1.65)	-0.37 (1.58)	2.35 (2.73)	3.87 (2.88)	7.64 (4.35)
	Prescribed fire	11	3.28 (2.36)	0.93 (3.13)	0.58 (0.78)	0.70 (2.51)	1.76 (3.47)
WHI	Wildfire	27	7.40 (3.09)	1.31 (1.66)	0.34 (0.29)	-1.2 (0.99)	-3.39 (1.94)
	Harvest	50	14.66 (7.19)	2.00 (1.06)	0.61 (0.25)	0.93 (0.80)	-2.33 (1.08)

Harvest + Prescribed fire	20	6.2 (2.53)	3.31 (1.67)	1.06 (0.50)	1.67 (1.00)	-2.78 (1.17)
Prescribed fire	13	2.5 (2.69)	4.30 (4.84)	-0.01 (0.09)	-1.82 (1.51)	-5.01 (1.67)

Table 1.6. Comparison of management alternatives using SMART analysis of mean vegetation responses shown in Table 1.8. Management options are grouped by study area in the first column. Metrics of management outcomes are shown in columns across the top row. Colors represent management outcomes relative to other values in each combination of disturbance and study area. The most desirable outcomes are green and the least desirable are red, with intermediate outcomes shown in yellow and orange colors. Values have been normalized on a 0-1 scale within each study area. The final column shows the outcomes of each management action summed by row, with the highest score indicating the best-supported alternative within a given study area.

	Disturbance type	Forage nutrition	Shrub biomass	Invasive sp. biomass	Species richness	Habitat condition	**Total**
CAB-SAL	Wildfire	0.67	0.50	0.00	0.39	0.04	**1.61**
	Harvest	0.14	0.34	0.74	0.88	1.00	**3.10**
	Harvest + prescribed fire	0.00	1.00	1.00	0.00	0.00	**2.00**
	Prescribed fire	1.00	0.00	0.43	1.00	0.55	**2.98**
RMF	Wildfire	0.27	1.00	0.72	0.07	0.05	**2.11**
	Harvest	0.50	0.59	0.00	0.77	0.63	**2.49**
	Harvest + prescribed fire	0.00	0.00	0.28	1.00	1.00	**2.28**
	Prescribed fire	1.00	0.35	1.00	0.00	0.00	**2.35**
WHI	Wildfire	0.40	0.00	0.67	0.18	0.60	**1.86**
	Harvest	1.00	0.23	0.42	0.79	1.00	**3.44**
	Harvest + prescribed fire	0.30	0.67	0.00	1.00	0.83	**2.81**
	Prescribed fire	0.00	1.00	1.00	0.00	0.00	**2.00**

Chapter 2 : Mule Deer (*Odocoileus hemionus*) Resource Selection in Divergent Disturbance Regimes in Conifer Forests of Northwest Montana

INTRODUCTION

Forest management practices, including prescribed fire, timber harvest, and management of wildfires, have a range of effects on plant communities. These vegetation responses to forest disturbance drive the composition, abundance, and quality of nutritional resources for wildlife (Noss et al. 2006, Hebblewhite et al. 2009, Allred et al. 2011, Rowland et al. 2018). During the last few decades, declines in mule deer population estimates and hunter harvests have magnified the focus on habitat management for this species in particular (Mackie et al. 1998, Pierce et al. 2012, Bergman et al. 2015). Nutritional resources have been linked to mule deer body size and condition, which in turn affects survival and reproduction (Parker et al. 2009, Cook et al. 2004, 2013, Robbins 1994). Nutrition on summer ranges is particularly important for female ungulates to meet increased metabolic demands of lactation and gestation. Summer is also a critical time for mule deer to increase fat and muscle reserves to sustain them later in the year when energy expenditures exceed daily caloric intake (Wallmo 1981). Whereas management practices can be used to create disturbances that improve nutrition for mule deer (Lezberg et al. 1999), the benefits of disturbance change over time (Peek et al. 2001).

Vegetation responses to different management practices influence when and how mule deer use forest disturbances (Carlson et al. 1993). Although some studies reported no effect of prescribed fire on forage quality (Wood 1988) nor mule deer habitat use (Long et al. 2008), others reported an increase in forage quality for several years after prescribed fire (Dills 1970, Keay and Peek 1980, Hobbs and Spowart 1984, Carlson et al. 1993). Results from research on the effects of thinning treatments are also variable. Some have reported increased mule deer use of thinned areas (Germaine et al. 2004, Horncastle et al. 2013, Bergman et al. 2014a, 2014b) whereas other documented little change in mule deer habitat use or forage availability following thinning treatments (Bergman et al. 2014a, Kramer et al. 2015). Although density of mule deer was variable following canopy removal in Pinyon pine (*Pinus edulis*) - Utah juniper (*Juniperus osteosperma*) ecosystems (Bergman et al. 2014 c), the body condition of adults and overwinter survival of fawns both increased after treatments (Bergman et al. 2014a, 2014b). Consequences of wildfire on forage and habitat selection are also variable. Wildfires set back forest succession and often create a diverse mosaic of vegetation that benefit mule deer (Patton and Gordon 1995). Studies have also shown that mule deer avoid post-fire areas associated with larger, more homogeneous fires that create barriers to movement, among other factors (Taber 1973, Severson 1983, Roerick et al. 2019). Responses of understory plant communities vary based on forest type (Sachro et al. 2005), disturbance severity and intensity (Lord and Kielland 2015), time since disturbance, and forest regeneration after disturbance (van Dyke and Darragh 2006, Romme et al. 2016).

The ability of deer to benefit from increased forage is also contingent upon what is available and accessible, and a change in the intake rate of a resource with its availability is described as a functional response (Holling 1959). Faison and others (2016) documented a functional response in browsing selection by moose and white-tailed deer, where browse consumption shifted at different stages of forest stand recovery after disturbance and in different types of disturbance. Management actions can have an important influence on both short-term increases in nutritional resources as well as the longer-term redistribution of nutrition available to mule deer. Understanding habitat selection by mule deer in relation to forest management practices helps to inform the management of nutritional resources over time for healthy deer populations and ecosystems. However, the implications of forest disturbances for mule deer forage and foraging behavior remain largely unexplored in the diverse habitats of the northern forest ecoregion (Hayden et al. 2008).

We assessed effects of forest disturbances on mule deer forage and habitat selection in three areas with differing disturbance regimes in northwestern Montana. This design allowed us to examine broader patterns in forage and selection by mule deer at multiple scales. We hypothesized that 1) forage is the most limiting factor in conifer forests of the Rocky Mountains and 2) use of forest disturbance by mule deer is driven by forage benefits when it is available. Therefore, at the population scale (the second order of Johnson [1980]), we predicted mule deer would select for disturbances to maximize nutrition. We expected deer selection for disturbance would be weaker within summer home ranges (the third order of Johnson [1980]). If disturbance within home ranges is also limited, we predicted that mule deer would select strongly for disturbance at both scales. Alternatively, if forage is not the most limiting resource, we would expect weak selection for disturbance at the study-area scale and stronger selection for disturbance within home ranges.

To test these predictions, we conducted a retrospective study of vegetation in disturbed and reference forests and mule deer resource selection with respect to predicted nutrition of key forage species in 3 study areas. We used a previously developed model of forage nutrition during summer in northern conifer forests to compare nutrition in disturbances (Chapter 1). We then quantified mule deer selection of disturbance using resource-selection functions (RSF; Manly et al. 2004) by contrasting landscape attributes of used and available locations across multiple spatial scales. To understand the underlying mechanisms driving selection of disturbance and the roles of forage nutrition and forest characteristics, we developed models to test *a priori* hypotheses about the relative roles of forage nutrition, forest type, and disturbance type in resource selection (Table 2.1). Finally, we tested whether diets of mule deer differed between study areas.

STUDY AREAS

The study encompassed three areas in northwest Montana, including the Rocky Mountain Front, the Cabinet-Salish Mountains, and the Whitefish Range that broadly differed in the composition of disturbance types (Fig. 2.1). In each area, differences in the frequency, severity, size, and timing of disturbance created unique changes in affected plant communities. As disturbances were repeated over time and space, different disturbance regimes were established, creating persistent, cumulative effects, or legacies, of past events (Franklin et al. 2000, Seidl et al. 2014). Study area extents were determined by the summer range of mule deer in each area, as defined by Global Positioning System (GPS) locations from radiocollared deer.

The Cabinet-Salish Mountains study area encompassed 2,600 km^2, with elevation ranging from 600 m along the Kootenai River to 2,100 m. The study area was centered within the Fisher River drainage, extending westward into the Cabinet Range and eastward to the Salish Mountains. Mean annual temperatures range from 0° C to 31° C. The Salish Mountains are comprised of dense- to open-conifer forest with interspersed shrubland and grassland areas. Forests are comprised mainly of western larch (*Larix occidentalis*), Douglas fir, lodgepole pine, and Engelmann spruce (*P. engelmannii*). The Cabinet Mountains contain moist montane forest transitioning to higher elevation subalpine forest, interspersed with western hemlock (*Tsuga heterophylla*) and western red cedar (*Thuja plicata*) on some aspects. This region has received consistent and widespread timber harvest activity for decades from timber companies and Forest Service harvests. Harvest comprised 9.17% of the study area, 0.47% prescribed fire, and 0.96% harvest followed by prescribed fire. Wildfires are distributed throughout and comprised 11.16% of the study area. Larger, more frequent burns tend to occur in the drier Salish Mountains.

The Rocky Mountain Front study area encompassed 2,100 km^2, with elevation ranging from 1,200 to 2,750 m. The study area included portions of the Bob Marshall and Scapegoat Wilderness areas to the west and a combination of public and private lands extending east of the continental divide. Mean annual temperatures range from –10° C to 28° C. In the eastern portion, lower-elevation foothills and grasslands of the Great Plains include riparian areas, agricultural land, and mixed-grass prairie dominated by bunchgrasses (*Pseudoroegneria spicata*) and fescues (*Festuca campestris, F. idahoensis*). Moving west, foothills transition to shrubland and conifer forest, and then to the complex terrain of the Rocky Mountains, including meadows, alpine steppe, and subalpine conifer. Forests are dominated by lodgepole pine (*Pinus contorta*), Douglas fir (*Pseudotsuga menziesii*), spruce (*Picea* sp.), and sub-alpine fir (*Abies lasiocarpa*). Wildfire comprised 4% of the study area, with stand-replacement fires at intervals between 150 to 250 years (Arno et al. 2000). Disturbance due to forestry practices was limited within the study area, with 0.91% harvest, 0.28% harvest followed by prescribed fire, and 1.33% prescribed fire alone.

The Whitefish Range study area encompassed 1,500 km^2, with elevation ranging from 790 m in the Tobacco Valley to around 2,440 m in the Whitefish Range. The study area was bordered to the east by Glacier National Park and extended norward into the Rocky Mountains of British Columbia, Canada. Mean annual temperatures range from –8° C to 30° C. Forests are comprised of wet and mesic forests comprised of western larch, Engelmann spruce, Douglas fir, lodgepole pine, and western red cedar. Forest thinning and harvest from U.S. Forest Service projects and few private activities comprised 3.61% of the study area, with 0.013% of the study area from harvest followed by prescribed fire and 0.12% from prescribed fire. Wildfires were dispersed, comprising 21.18% of the study area.

Elk (*Cervus elaphus*), white-tailed deer (*Odocoileus virginianus*), bighorn sheep (*Ovis canadensis*), and moose (*Alces alces*) are sympatric with mule deer in all study areas. Pronghorn (*Antilocapra americana*) are also present on Rocky Mountain Front foothills, and mountain goats (*Oreamnos americanus*) are rare in the Rocky Mountain Front and Cabinet Mountains. Carnivore species in all study areas include mountain lion (*Puma concolor*), bobcat (*Lynx rufus*), gray wolf (*Canis lupus*), coyote (*C. latrans*), American black bear (*Ursus americanus*), and grizzly bear (*Ursus arctos*).

METHODS

Overview

We used a combined ground and remote-sensing based approach described previously in Chapter 1 to develop a landscape-scale model of summer forage nutrition for northwestern Montana (e.g. Cook et al. 2016, Rowland et al. 2018, Proffitt et al. 2016). We first determined dominant forage species in summer diets of mule deer in the Cabinet-Salish Mountains, Rocky Mountain Front, and Whitefish Range. Then, we sampled vegetation at locations across a gradient of disturbance types in each study area to evaluate spatial and temporal effects of harvest, harvest with prescribed fire, prescribed fire, and wildfire on forage biomass. Next, we filtered available biomass to include only the plant species that were strongly represented in diet analysis estimated differences in the availability of forage biomass between study areas. In addition to measuring forage biomass, we also sampled forage plants to estimate the mean digestible energy (DE) across phenological stages over the summer. Finally, we combined forage digestibility and forage biomass availability in a landscape model of nutritional forage available to mule deer in summer (kcal/m^2), as described in Chapter 1. We used this model to test for the effect of forest disturbances on the availability of summer nutrition and resource selection by mule deer in each study area. We used mule deer location data collected from collared adult female mule deer to estimate population and individual ranges during summer, combined with remotely-sensed environmental data and estimates of nutrition from the landscape forage nutrition model to investigate whether the differences between disturbance types influenced resource selection by mule deer.

Data collection

Vegetation sampling.—To test the hypothesis that forage is limited for mule deer in 3 study areas, we conducted vegetation sampling to develop a predictive landscape nutrition model. Within each study area, we conducted vegetation surveys in 4 disturbance types (wildfire, prescribed fire, harvest, and harvest followed by prescribed fire). We defined disturbances using a combination of LANDFIRE (LF) data (LANDFIRE 2012), global forest change (GFC) data from Hansen et al. (2013), and Google Earth imagery, as described in Chapter 1.We sampled within disturbances ranging from 1–25 years since disturbance, and we stratified patches by time since disturbance using 0–5, 6–10, 11–15, and >16 years.

We conducted vegetation surveys at random point locations within each disturbance type and surveyed a nearby point in undisturbed forest to capture vegetative differences between disturbed and undisturbed forest following methods described earlier. We conducted vegetation surveys between June 1 and August 31, 2017–2019. At each point, we surveyed three equally-spaced 1–m^2 quadrats along a 40 m transect. We recorded species composition and percent cover of all species in each quadrat, allowing total cover to exceed 100%. We established a 0.5–m^2 clip plot within each quadrat and collected current year's growth of the above ground biomass of graminoids, forbs, and shrubs within the clip plot. Biomass from each plant form and each sub-quadrat was stored in paper bags. We dried bags of plant biomass in a 50º C oven and measured dry weight. We apportioned the dry weight to plant lifeform (forb, graminoid and shrub) based on the percent cover of each lifeform. We then averaged all quadrats from a point to estimate a mean value for each point.

Diet sampling.—We deployed GPS collars (Lotek LifeCycle 330) on 136 female adult (>1.5 years of age) mule deer in winters 2017–2019. We captured deer using helicopter net-gunning, clover trapping, and chemical immobilization in compliance with the University of Montana IACUC policy # 001-17CBWB-011017 and Montana Fish, Wildlife and Parks ACUC protocol #FWP03-2016. Collars were programmed to upload one location every 13 hours to GlobalStar satellites. Upload rates to Globalstar satellites ranged from 29.98 – 100%, with a mean fix rate of 72%. We radiocollared 42 deer in the Cabinet-Salish, 49 in the Rocky Mountain Front, and 45 in the Whitefish Range and distributed capture efforts geographically across the winter ranges of study areas.

We identified forage species selected by mule deer using previously developed methods (Chapter 1). We collected fecal pellets from radiocollared and uncollared mule deer between June 1 and August 31, 2017–2019 and distributed sampling effort across the full spatial extent of each study area. We then estimated diet composition analysis using fecal DNA-metabarcoding (Taberlet et al. 2007; Jonah Ventures, Boulder, CO). We filtered plant biomass to include only species that made up >2% of the total diet of deer in each study area (Fig. 2.2; Supplementary Material Appendix B, Table B-1). We considered species-specific dry biomass for forbs, graminoids, and shrubs proportional to the observed species composition we estimated from quadrats. We then summed the biomass of forage species in mule deer diets in each quadrat and averaged all quadrats to estimate mean biomass of forage species (g/m^2) for each sampling point.

Data analysis

Forage nutrition comparison.—To evaluate forage nutrition in different disturbance types and disturbance regimes, we combined digestibility and biomass of forage plants in a model of summer forage nutrition for mule deer (kcal/m^2). We used mixed-effects generalized linear models to predict forage quality as a function of spatial covariates. To assess overall differences in forage nutrition by disturbance type, we used generalized linear models for each study area in which digestible energy was the response variable and disturbance was a categorical explanatory variable.

Resource selection modeling.—We tested the hypothesis that nutritional differences between forest disturbances may drive mule deer use of disturbance. We estimated resource selection by mule deer at two scales: within the combined (population) summer ranges for all deer in a given study area and within individual summer ranges. Deer location data from May 1 to August 31, 2017–2019 represent summer home ranges in each study area. We estimated summer ranges with a 95% kernel density estimate (KDE) using the R package adehabitatHR (Calenge 2018). KDEs encompassed 95% of telemetry locations within the combined (population) summer ranges for all collared deer in a given study area, and 95% of locations within an individual's summer range in a given study area. Because canopy closure and terrain influence the precision of GPS collars (Frair et al. 2010), we corrected for potential habitat-biased data loss in uploaded location data. We used a spatial model of the probability of successfully acquiring a fix (P_{fix}) to estimate frequency weights ($1/ P_{\mathrm{fix}}$). We included these weights in RSF models, so that hard-to-acquire locations have greater influence on model results (Frair et al. 2010). We developed a logistic regression model to estimate P_{fix} as a function of landscape covariates known to influence GPS fix success. Covariates in the full model included slope, aspect, topographic position index (TPI), terrain ruggedness index (TRI), time of day, and study area (Peterson 2020). Using backwards step selection, we retained the model with the lowest value of Akaike information criterion (AIC).

We sampled 10 available points for every used location at each scale (Northrup et al. 2013). We described used and available locations according to a suite of covariates, falling into three groups of predictions: 1) nutrition included a covariate based on our forage nutrition model; 2) disturbance characteristics included canopy height, time since disturbance, distance to nearest harvest, and categorical disturbance type (harvest, harvest followed by prescribed fire, and wildfire); and 3) forest included categorical forest types (mesic forest, dry forest, open woodland, and montane riparian). We considered linear and quadratic terms for canopy height, time since disturbance and distance to nearest harvest to allow for selection for intermediate levels of these covariates. Continuous covariates were centered on their mean and scaled by standard deviation units. We limited the maximum age since disturbance to 35 years, after which disturbance information was limited or inconsistent. Distance to harvest was transformed with an exponential decay so the effects of harvests eroded precipitously beyond a few hundred meters, and exerting almost no influence at large distances (e.g., >1500 m). We used the decay function (1-$\exp^{-\alpha d}$), where *d* was the distance in meters to the nearest harvest, with α set at 0.002 (Nielsen et al. 2009). To estimate forage nutrition at each location, we used the predictive forage models described earlier.

To evaluate resource selection at the population scale, we used the use-available design of Manly et al. (2002) to approximate the exponential RSF model based on the ratio of used to available resources (Manly et al. 2002). We developed families of models of resource selection functions to test our hypotheses with the following *a priori* framework:

1) Base

$$\hat{w}(x) = \exp(\beta_0 + \beta_1 Elev + \beta_2 Aspect + \beta_3 Slope)$$

2) Nutrition

$$\hat{w}(x) = \exp(\beta_0 + \beta_1 Elev + \beta_2 Aspect + \beta_3 Slope + \beta_4 ForageNutrition)$$

3) Forest

$$\hat{w}(x) = \exp(\beta_0 + \beta_1 Elev + \beta_2 Aspect + \beta_3 Slope + \beta_5 ForestType)$$

4) Disturbance

$$\hat{w}(x) = \exp(\beta_0 + \beta_1 Elev + \beta_2 Aspect + \beta_3 Slope + \beta_6 DisturbType + \beta_7 CanopyHt + \beta_8 TimeSinceDisturb + \beta_9 DistanceHarvest)$$

5) Full

$$\hat{w}(x) = \exp(\beta_0 + \beta_1 Elev + \beta_2 Aspect + \beta_3 Slope + \beta_4 ForageNutrition + \beta_5 ForestType + \beta_6 DisturbType + \beta_7 CanopyHt + \beta_8 TimeSinceDisturb + \beta_9 DistanceHarvest)$$

where $\hat{w}(x)$ is the relative probability of use as a function of multiple coefficients $\hat{\beta}$ representing selection coefficients for hypothesized variables. We then screened each model family for multicollinearity using variance inflation factor (VIF) threshold < 5.0 (Zuur et al. 2010).

To model resource selection at the population scale, we used a case-control design to restrict availability in space (Compton et al. 2002, Johnson et al. 2002, Boyce et al. 2003). We estimated conditional fixed-effects logistic models for each study area using the R package survival (Therneau 2015) to pair each used location with 10 random locations drawn from within each collared deer’s home range (Hosmer and Lemeshow 2000). Using the conditional logit model, the conditional fixed-effects logistic regression, $\hat{w}(x_{ij})$, was estimated following

$$\hat{w}(x_{ij}) = \exp(\hat{\beta}_1 x_{ij1} + \hat{\beta}_2 x_{ij2} + \cdots + \hat{\beta}_n x_{ijn})$$

where $\hat{w}$ is the relative probability of the *j*th resource unit being selected at the *i*th group for covariates x_n, and where $\hat{\beta}_{1\ldots n}$ are the coefficient estimates for each covariate and *n* is the number of groups of matched locations for model selection (Pendergast et al. 1996). Each used GPS location represents the *i*th group, at which a deer makes one of *j* choices from the 11 (10 random and 1 used) options. We used tested the same family of *a priori* models for both population- and home range-RSFs.

Within each study area and spatial scale, we compared each family of models (base, nutrition, forest, disturbance, and full; Table 2.2) using Akaike information criterion (ΔAIC; Anderson and Burnham 2002) to select the best-supported models. We kept only non-collinear ($|r| \leq 0.5$) variables in our best-supported models. We used leave-one-out (LOO) cross-validation based on Matthiopoulos et al. (2011) to compare the results and to quantify model predictive abilities. To evaluate variation in mule deer use of disturbance types with availability, we plotted the proportion of used locations as a function of the proportion of available locations in wildfire and harvest for individual mule deer.

Comparison of diet composition.—To investigate differences in composition of mule deer diet between study areas, we conducted a between-class analysis (BCA; Thioulouse et al. 2018) in R library ade4 (Chessel et al. 2004). We filtered diets to include only those taxa that comprised more than 2% of the total diet of deer in each study area. In a BCA, individual mule deer are projected according to their diet composition, and individuals in the same study area are grouped. The resulting dispersion shows standard deviation within the study area. We then used permutation tests with 999 permutations to assess the statistical significance of the BCA

(Thioulouse et al. 2018). All analyses were performed using R version 3.6.1 (R Core Team 2018).

RESULTS

Forage nutrition

On average, harvest provided the highest forage nutrition for mule deer (6.47 ± 1.27 kcal/m^2), and reference conifer forests provided the lowest forage nutrition (1.67 ± 0.79 kcal/m^2). Forage nutrition did not strongly differ between harvest and harvest followed by prescribed fire, and vegetative responses were also the most variable in these disturbances.

Resource selection function

To examine the roles of forage nutrition, forest type and disturbance, we considered each family of models in the context of best-supported models, and we report standardized coefficients, standard error, and *p*-values from top models in Table 2.3. In all study areas, the best-supported model for population-scale selection was the full model, which included effects from all model families: nutrition, forest type, and disturbance type. Model selection for the population scale model showed clear separation from the full model to the nesx model (ΔAIC > 100) in all 3 study areas. In the Cabinet-Salish and Rocky Mountain Front areas, the best-supported model for home range-scale selection was also the full model, whereas the best-supported model for home-range selection in the Whitefish area was the nutrition-only model.

Mule deer showed strong, consistent selection for low to moderate elevation (represented by the quadratic of elevation in our models; Table 2.3) and higher slope angles (β_{CAB} = 0.55, SE

= 0.024, β_{RMF} = 0.05, SE = 0.017, β_{WHI} = 0.35, SE = 0.020), and avoidance of north-facing aspects (β_{CAB} = -0.34, SE = 0.018, β_{RMF} = -0.32, SE = 0.014, β_{WHI} = -0.18, SE = 0.018). However, in the Rocky Mountain Front and Whitefish areas, individual deer selected for higher elevation (β_{RMF} = 1.94, SE = 0.359; β_{WHI} = 0.14, SE = 0.175) within their home ranges as well as lower-angle slopes (β = -0.25, SE = 0.082) in the Rocky Mountain Front.

Selection for forage nutrition varied by study area, though it generally remained consistent between scales. In the Rocky Mountain Front, mule deer selected for higher forage nutrition at the population-scale (β = 1.19, SE = 0.0.96) and within home range-scale (β = 1.22, SE = 0.456). Deer in the Whitefish area showed neutral selection or weak avoidance of forage nutrition on both scales. The availability of forest types within home ranges varied, and selection of uncommon forest types was highly variable. On average, individual home ranges included 3.1% open woodland 5.4% montane riparian. No difference between selection among forest types emerged within home ranges. However, mule deer selection for forest types was strong at the population scale. At this scale, selection for montane riparian was weakly (β_{RMF} = -0.02, SE = 0.058; β_{WHI} = -0.34, SE = 0.087) to strongly negative across study areas. Dry forest was selected in the Cabinet-Salish (β = 0.45, SE = 0.042) and Whitefish areas (β = 0.86, SE = 0.067). Open woodland was selected in the Rocky Mountain Front (β = 0.14, SE = 0.044) and Whitefish (β = 0.47, SE = 0.189) areas and strongly avoided in the Cabinet-Salish area (β = -0.39, SE = 0.108).

Mule deer had relatively consistent responses to disturbance attributes within scales and mixed responses to disturbance types. Across study areas, deer generally avoided increasing tree canopy height (β_{CAB} = -0.20, SE = 0.017, β_{RMF} = -0.12, SE = 0.026, β_{WHI} = -0.46, SE = 0.028) and avoided older disturbances (β_{CAB} = -0.18, SE = 0.115, β_{RMF} = -0.19, SE = 0.059, β_{WHI} = -1.11, SE = 0.380) at the population scale. Within home ranges, deer in the Cabinet-Salish and Rocky Mountain Front areas showed neutral selection to weak avoidance of canopy cover (β_{CAB} = 0.05, SE = 0.122, β_{RMF} = -0.23, SE = 0.121) and increased selection for older disturbances (β_{CAB} = 3.33, SE = 3.067, β_{RMF} = 1.64, SE = 0.414). At the population scale, mule deer in the Cabinet-Salish and Whitefish areas selected areas farther from harvest (β_{CAB} = 0.35, SE = 0.042, β_{WHI} = 0.41, SE = 0.044), whereas deer in the Rocky Mountain Front selected areas closer to harvest (β = -0.38, SE = 0.058).

Deer use of disturbance types varied between individuals and among populations as a function of availability (Fig. 2.3). At the population scale, mule deer generally showed avoidance or weak selection of disturbances. Exceptions to this trend included selection for wildfire in the Cabinet-Salish area (β = 0.64, SE = 0.140) and selection for harvest in the Rocky Mountain Front (β = 0.32, SE = 0.142). Within home ranges, harvest followed by prescribed fire was only available to a small subset of deer, with the exception of the Cabinet-Salish area. This disturbance was available for 7 of 47 deer in the Whitefish area and 6 of 54 deer in the Rocky Mountain Front, making up a maximum of 4% (and often less) of individual home ranges. Deer tended to avoid disturbance from harvest followed by prescribed fire, but limited availability within home ranges in the Cabinet-Salish and Whitefish areas prevented accurate assessment of selection at that scale.

Disturbance from harvest was inconsistently available to mule deer in all study areas. In the Cabinet-Salish, harvest comprised 15% percent of individual home ranges, but availability ranged from less than 1% to 53.4% for individuals. Average availability of harvest was lower in the Rocky Mountain Front (4.3%) and Whitefish (2.8%) areas. Within home ranges, deer in the Cabinet-Salish and Rocky Mountain Front showed neutral to positive selection for harvest and wildfire. At the population range, deer selected for wildfire in the Cabinet-Salish ($\beta = 0.64$, SE = 0.140) but variable selection within individual home ranges. In the Rocky Mountain Front where large-area wildfires are common, deer avoided wildfire at the population scale ($\beta = -0.19$, SE = 0.072) but selected for wildfire within home ranges ($\beta = 1.16$, SE = 0.572).

Comparison of diet composition

We found statistically significant differences in mule deer diets between study areas (Fig. 2.4; Supplementary Material Appendix D, Table D-1; BCA-test: $p = 0.001$). The plant species that separated study areas on Axis 1 were bluegrass species (*Poa*), alder (*Alnus*), rhododendron (*Rhododendron*), Oregon grape (*Berberis repens*), currant (*Ribes*), and fireweed (*Chamerion angustifolium*) which were associated with diets of mule deer in the Cabinet-Salish Mountains. Diet species associated with the Rocky Mountain Front included evening primrose (*Oenothera*), strawberry (*Fragaria*), prickly lettuce (*Lactuca*), globemallow (*Spaeralcea coccinea*), coneflower (*Ratibida columnifera*), buckwheat (*Eriogonum*), and sweetvetch (*Hedysarum*). Diets of deer in the Whitefish Range were separated by wheat (*Triticum aestivum*), elderberry (*Sambucus*), honeysuckle (*Lonicera*), and huckleberry (*Vaccinium*). The first axis explained 51.8% and the second axis 48.2% of the total inertia.

DISCUSSION

We found support for our prediction that nutrition may be a limiting factor in undisturbed conifer forests of the northern Rocky Mountains and that disturbances generally increase forage nutrition for mule deer. Despite substantial variation in selection among individuals and among study areas, we found common effects of forage nutrition and disturbance type at population scales. As we predicted, deer selection within home ranges was not explained well within these constraints, suggesting that deer selection is closely related to availability of forage and disturbance at smaller scales.

Across all areas, we found that deer avoided areas with increasing time since disturbance, a behavior that was reversed within home ranges. As the spectrum of benefits and costs associated with disturbance changes over time, mule deer individuals experience a small shift in nutritional resources within a given home range, but long-term trends are reflected in populations. Because mule deer show high fidelity to seasonal ranges (Mackie et al. 1998, McClure et al. 2005, Monteith et al. 2014), selection within home ranges is constrained by the availability of nutritional resources. In areas like the Whitefish Range, the abundance of disturbance is limited in space and also tends to be clustered. Although clustering harvest activity saves time and costs across larger scales (Smaltschinski et al. 2015), the potential nutritional benefits will also be concentrated for a small number of deer.

The dominant disturbance in each study area determines the availability of resources and ultimately has lasting effects on the landscape. Over longer periods, cumulative effects of disturbances regulate system dynamics (Spies et al. 1994). Foster and others (2002) showed that these spatial legacies can persist from decades to millennia. The disturbance regime determines the plant communities best adapted for the frequency and intensity of disturbance and may influence the availability and distribution of forage on a landscape scale. The importance of shrubs for mule deer has been well-established in literature (Collins and Urness 1983, Wickstrom et al. 1984, Beck and Peek 2005). In western forests, shrubs are most abundant in open canopies and recently disturbed early successional habitats (Kayes et al. 2010). However, historical widespread suppression of wildfires has increased the prevalence of late successional stages and reduced understory productivity in many conifer forests in the northwestern U.S. (Peek et al. 2001). The shrubs that do grow in mid- and late-seral stages consist mainly of shade-tolerant evergreen shrubs, conifers, and evergreen ferns, which are generally avoided by mule deer (Rowland et al. 2018).

Diets of mule deer in the Whitefish Range, where disturbance was most limited, contained smaller proportions of the top forage species found in other study areas, suggesting that mule deer may need to supplement their diets with less abundant species or consume more species that offer reduced nutritional quality. As discussed in the previous chapter, the response of forage species to disturbance differs between disturbance regimes. We predicted the greatest increase in forage after wildfire, with the greatest effects on overall forage nutrition in the Whitefish Range. The large effect of disturbance and the prediction of greater forage nutrition in the Whitefish Range may have been driven by the high occurrence of the forage species snowbrush (*Ceanothus velutinus*) reported in Chapter 1, particularly in wildfires as well as harvest and harvest followed by prescribed fire to a lesser degree.

Studies have shown that mule deer avoid post-fire areas associated with larger, more homogeneous fires which also pose barriers to movement and accessibility of resources in the interior (Taber 1973, Severson 1983, Roerick et al. 2019). However, we found that mule deer selected for fire at the within-home range scale in the Rocky Mountain Front, where large-scale and high-severity burns have defined the landscape. Additional work to incorporate disturbance severity could clarify difference in plant communities and forage nutrition after disturbance. For deer in the Cabinet-Salish and Whitefish ranges, study areas that do not regularly experience large wildfires, population-level selection for wildfire suggests that palatable, nutritious shrubs and forage associated with fire may be limited on the larger landscape, providing partial support for our prediction that mule deer selection would maximize nutrition on the scales at which it is limiting. However, mule deer avoided wildfire on the population scale, suggesting that forage nutrition benefits may not be accessible.

Despite potential nutritional benefits for mule deer, there may also be costs associated with wildfire. Burned forests can increase spatial overlap between predators and prey (Robinson et al. 2012, Northfield et al. 2017) while reducing the vertical structure of vegetation that provides refuge from heat stress and coursing predators (Long et al. 2014, Lone et al. 2017). Therefore, we would expect that mule deer may need to balance the benefits of nutrition and costs of security when selecting resources. If nutrition is a limiting factor for mule deer in areas with limited or infrequent disturbance (Cox et al. 2009), deer may choose nutrition over security. As nutritional resources vary in space, however, tradeoffs between costs and benefits of using disturbances may also change (Hebblewhite and Merrill 2011).

MANAGEMENT IMPLICATIONS

Differences between disturbance types are linked to the dominant disturbance regime. In areas dominated by wildfire, as in the Rocky Mountain Front, an increase in disturbance may not provide much additional benefit for mule deer. Conversely, in the Whitefish Range and other similar areas with limited disturbance, our research suggests that allowing for more wildfire is likely to benefit mule deer. Management that is applied at a rate that maintains growth of early to mid-seral stage vegetation can help offset declining forage in late-seral forests and aging disturbances. In areas with a greater volume and frequency of disturbance from harvest like the Salish Mountains, the greatest benefit to mule deer may come from invasive species management, especially after additional disturbance from wildfire. Given the high degree of mule deer fidelity to home ranges, management will have greater benefits for a greater number of deer when forest management techniques are spatially and temporally distributed.

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FIGURES

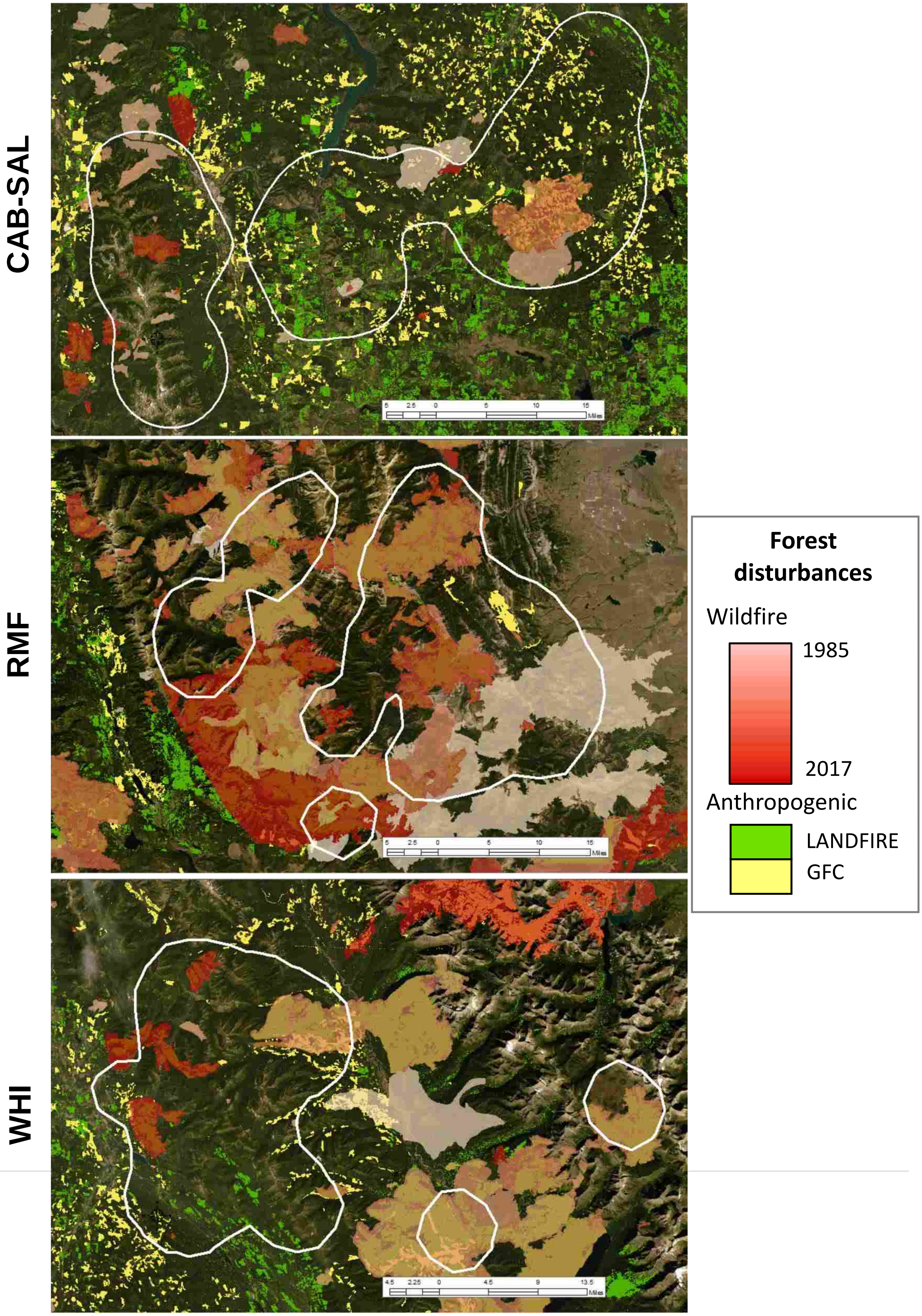
CAB-SAL
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Figure 2.1. The Cabinet-Salish, Rocky Mountain Front, and Whitefish Range mule deer population annual ranges in northwest Montana, USA. Polygons are 95% kernel density estimates (KDE) of adult female mule deer collar locations during summers 2017–2019. Wildfires from 1985-2017 are shown in red, with lighter colors representing older fires. Anthropogenic disturbances reported from LANDFIRE from 1999-2016 (green) and Global Forest Change (GFC) data from 2000-2018 (yellow) represent disturbance from harvest, and prescribed fire, harvest followed by prescribed fire.

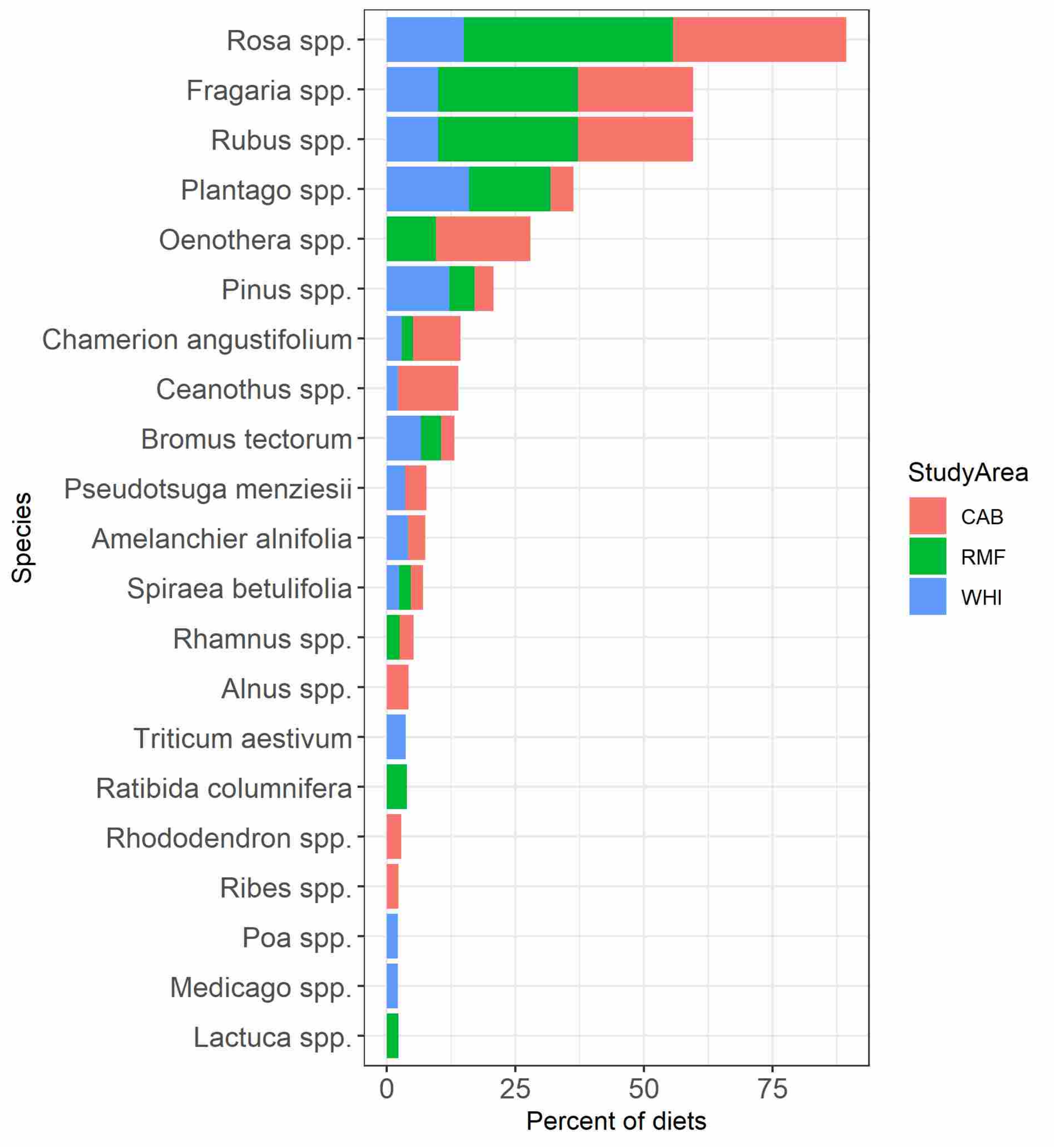


Figure 2.2. Forage species that comprise >2% of total mule deer summer diets from fecal collections during 2017–2019. Values represent the cumulative proportion of individual diets for a given study area.

Table 2.1. Hypothesized explanations for mule deer selection for disturbance. Predictions were tested using a resource selection function to explain selection by 134 adult female mule deer (*Odocoileus hemionus*) in 3 study areas across northwestern Montana, 2017–2019.

Hypothesis	**Predictions**	**References**
FORAGE		
Habitat selection of ungulates is driven primarily by availability of forage	Mule deer will select home ranges to maximize the amount of predicted nutrition from forage plants.	Parker et al. 2009, Pierce et al. 2012
FOREST		
Vegetative resources available to ungulates varies by forest type	Mule deer will select forest types that best balance predation risk and forage benefits	Mackie et al. 1998, Powell et al. 2000, Lehmkuhl et al. 2013
DISTURBANCE		
The type of disturbance differentially influences the responses of vegetative resources for ungulates	Mule deer will select disturbances that best balance predation risk and forage benefits	Lautenschlager et al. 1997, Hebblewhite et al. 2009, Rowland et al. 2018

Table 2.2. Comparison of models of summer resource selection function of mule deer based on forage nutrition, forest type, and disturbance type, in northwestern Montana, 2017–2019. Models in bold were best-supported in explaining variation in selection of mule deer. Separate models were developed at a population scale and home-range scale for each of 3 study areas: the Cabinet-Salish Mountains, the Rocky Mountain Front, and the Whitefish Range.

CAB	**Variables**	**Population scale ΔAIC**	**Home range scale ΔAIC**
Full	ForageQuality + Forest + DisturbType + CanopyHt + CanopyHt^2 + TimeSinceDisturb + TimeSinceDisturb^2 + DistanceHarvest + DistanceHarvest^2 + Base	**0.0**	**0.00**
Disturbance	DisturbType + CanopyHt + CanopyHt^2 + TimeSinceDistur + TimeSinceDisturb^2 + DistanceHarvest + DistanceHarvest^2 + Base	103.09	1.35
Nutrition	ForageQuality + Base	2995.61	25.19
Forest	Forest + Base	3466.82	31.97
Base	Elev + Elev^2 + Aspect + Slope + Slope^2	3557.28	23.66
RMF			
Full	ForageQuality + Forest + DisturbType + CanopyHt + CanopyHt^2 + TimeSinceDisturb + TimeSinceDisturb^2 + DistanceHarvest + DistanceHarvest^2 + Base	**0.0**	**0.0**
Disturbance	DisturbType + CanopyHt + CanopyHt^2 + TimeSinceDisturb + TimeSinceDisturb^2 + DistanceHarvest + DistanceHarvest^2 + Base	118.16	12.7
Forest	Forest + Base	1641.3	43.6
Base	Elev + Elev^2 + Aspect + Slope + Slope^2	1651.56	39.8
Nutrition	ForageQuality + Base	1473.33	39.3
WHI			

Full	ForageQuality + Forest + DisturbType + CanopyHt + CanopyHt^2 + TimeSinceDisturb + TimeSinceDisturb^2 + DistanceHarvest + DistanceHarvest^2 + Base	**0.0**	9.16
Disturbance	DisturbType + CanopyHt + CanopyHt^2 + TimeSinceDisturb + TimeSinceDisturb^2 + DistanceHarvest + DistanceHarvest^2 + Base	181.58	10.73
Forest	Forest + Base	1,296.36	8.79
Nutrition	ForageQuality + Base	1,388.24	**0.00**
Base	Elev + Elev^2 + Aspect + Slope + Slope^2	1,399.13	4.82

Table 2.3. Model structure for top-ranked resource selection functions (RSF) for the relative probability of use by mule deer (*Odocoileus hemionus*) in northwest Montana during 2017–2019. Standardized coefficient estimates and standard errors for models of population and home range scales for each of three study areas: Cabinet-Salish Mountains (CAB), Rocky Mountain Front (RMF), and Whitefish Range (WHI).

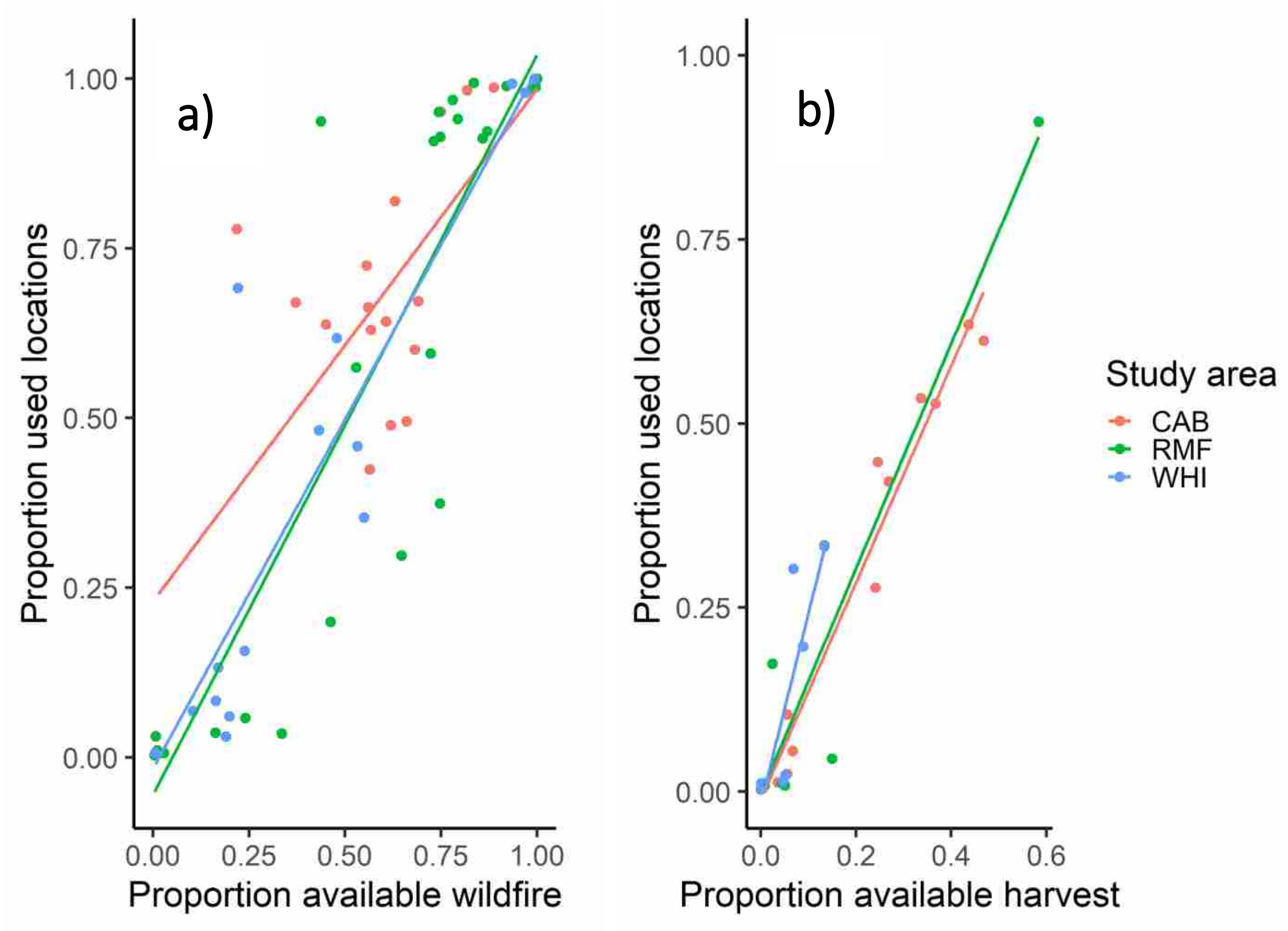
	CAB				**RMF**				**WHI**			
	Population		**Home range**		**Population**		**Home range**		**Population**		**Home range**	
Parameter	Coefficient (S.E.)	*p*	Coefficient (S.E.)	*p*	Coefficient (S.E.)	*p*	Coefficient (S.E.)	*p*	Coefficient (S.E.)	*p*	Coefficient (S.E.)	*p*
Intercept	-2.66 (0.101)	< 0.001	—	—	-2.28 (0.074)	< 0.001	—	—	-1.17 (0.306)	< 0.001	—	—
Elevation	0.41 (0.038)	< 0.001	-0.69 (0.450)	0.128	1.68 (0.069)	< 0.001	1.94 (0.359)	< 0.001	0.26 (0.028)	< 0.001	0.14 (0.175)	0.410
Elevation^2	-0.22 (0.024)	< 0.001	-0.67 (0.257)	0.009	-0.88 (0.037)	< 0.001	-0.99 (0.187)	< 0.001	-0.21 (0.027)	< 0.001	-0.52 (0.168)	0.002
Aspect (north)	-0.34 (0.018)	< 0.001	-0.27 (0.144)	0.062	-0.32 (0.014)	< 0.001	-0.46 (0.086)	< 0.001	-0.19 (0.018)	< 0.001	-0.39 (0.104)	< 0.001
Slope	0.55 (0.024)	< 0.001	0.51 (0.195)	0.009	0.05 (0.017)	0.006	-0.25 (0.082)	0.002	0.35 (0.020)	< 0.001	-0.03 (0.105)	0.781
Slope^2	-0.45 (0.019)	< 0.001	-0.17 (0.147)	0.249	-0.05 (0.014)	< 0.001	0.11 (0.063)	0.084	-0.10 (0.014)	< 0.001	0.13 (0.072)	0.061

NUTRITION												
Forage nutrition	0.08 (0.175)	0.645	1.28 (1.091)	0.240	1.19 (0.096)	< 0.001	1.22 (0.456)	0.008	0.03 (0.013)	0.02	-0.61 (0.544)	0.040
FOREST												
Dry forest	0.45 (0.042)	< 0.001	-0.29 (0.348)	0.399	-0.08 (0.055)	0.129	-0.42 (0.351)	0.231	0.86 (0.067)	< 0.001		
Montane riparian	-0.10(0.100)	0.323	-0.79 (0.758)	0.296	-0.02 (0.058)	0.702	0.43 (0.270)	0.113	-0.34 (0.087)	< 0.001		
Open woodland	-0.39 (0.108)	< 0.001	-15.70 (1109.821)	0.989	0.14 (0.044)	0.001	0.30 (0.270)	0.271	0.47 (0.189)	0.013		
DISTURBANCE												
Harvest	-1.11 (0.160)	< 0.001	6.36 (5.327)	0.232	0.32 (0.142)	0.027	1.44 (1.001)	0.152	-0.95 (0.585)	0.104		
Harvest + Rx fire	-2.15 (0.236)	< 0.001	-10.10 (2918.659)	0.997	0.06 (0.201)	0.748	-1.46 (1.267)	0.249	-14.20 (102.010)	0.890		
Rx fire	-1.63 (0.456)	< 0.001	-		-2.80 (0.357)	< 0.001	-12.92 (1010.191)	0.990	-14.39 (118.819)	0.903		
Wildfire	0.64 (0.140)	< 0.001	5.89 (5.533)	0.287	-0.19 (0.072)	0.009	1.16 (0.572)	0.043	-1.18 (0.553)	0.032		
Canopy height	-0.20 (0.017)	< 0.001	0.05 (0.122)	0.659	-0.12 (0.026)	0.005	-0.23 (0.121)	0.059	-0.46 (0.028)	< 0.001		

Canopy height^2	0.09 (0.011)	< 0.001	0.17 (0.094)	0.065	-0.01 (0.019)	0.479	-0.04 (0.131)	0.777	0.01 (0.020)	0.767
Time since disturbance	-0.18 (0.115)	0.117	3.33 (3.067)	0.377	-0.19 (0.059)	< 0.001	1.64 (0.414)	< 0.001	-1.18 (0.381)	0.002
Time since disturbance^2	0.22 (0.053)	< 0.001	2.21 (1.423)	0.120	0.06 (0.028)	0.028	1.18 (0.353)	0.001	-0.71 (0.128)	< 0.001
Distance to harvest	0.35 (0.042)	< 0.001	0.98 (0.623)	0.116	-0.38 (0.058)	< 0.001	0.43 (0.648)	0.509	0.41 (0.044)	< 0.001
Distance to harvest^2	0.44 (0.018)	< 0.001	0.72 (0.332)	0.029	-0.03 (0.035)	0.393	1.03 (0.543)	0.058	0.26 (0.022)	< 0.001

Effects of forest type are in relation to the reference (intercept) type Mesic forest. Effects of disturbance are in relation to Reference (undisturbed) conifer.

Figure 2.3. Mule deer (*Odocoileus hemionus*) use of disturbance for a) wildfire and b) harvest in relation to availability on summer ranges in northwestern Montana, 2017–2019. Each symbol represents use and availability for an individual within their home range for each of three study areas: the Cabinet-Salish Mountains, the Rocky Mountain Front, and the Whitefish Range.



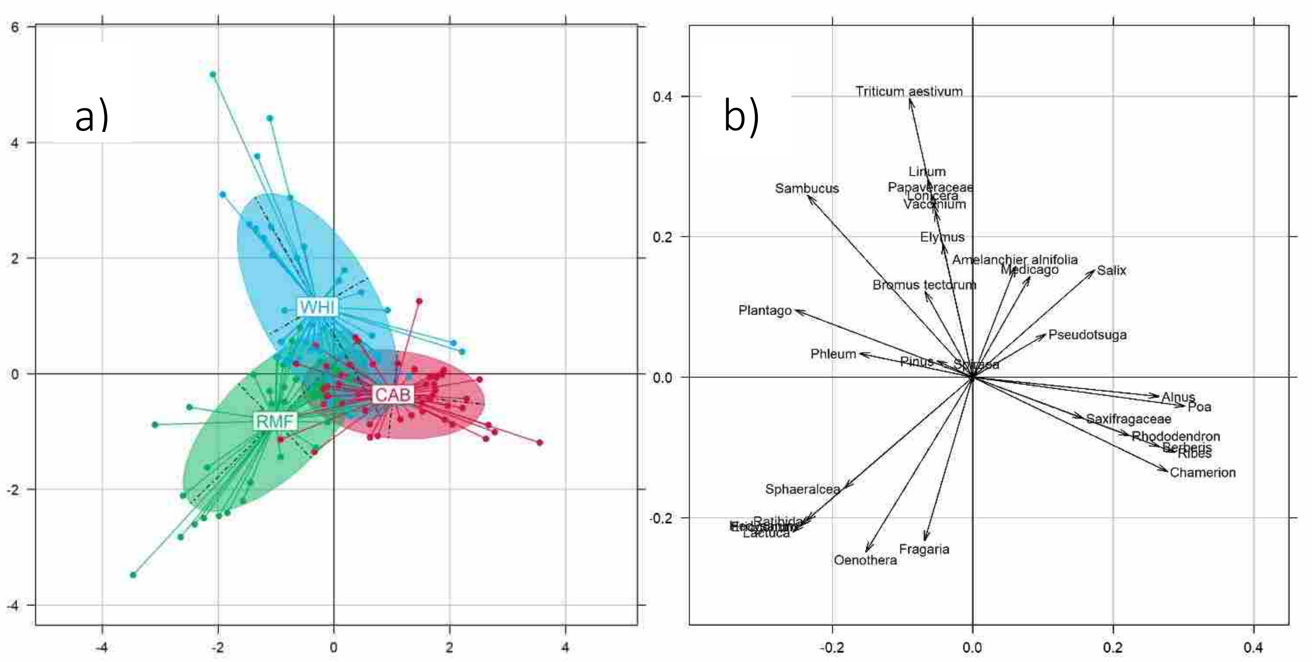


Figure 2.4. Multivariate differences in understory vegetation composition between three study area with different disturbance regimes: Cabinet-Salish Mountains (*n*=269), Rocky Mountain Front (*n*=190) and Whitefish Range (*n*=255) in summers 2017-2019. Normed scores of the two axes from a Hill-Smith (HS) between-class analysis (BCA) based on a) forage plant composition at individual surveyed sites and b) vegetation cover (%) of forage plant species measured in 1-m^2 quadrats by study area.

Supplementary material

Appendix A – Site condition scoring

Table A-1. Definitions for coefficient of conservatism (C) values used in calculating average site conditions through the floristic quality assessment index (FQAI). C values are assigned to every species present at a site to reflect the species' response to environmental conditions, tolerance to natural and human disturbance, and restriction to certain habitat types. Montana-specific panels used these definitions to assign C values, adapted from Zomlefer et al. 2013.

NON-NATIVE MONTANA SPECIES	
0	invasive
1	relatively benign
NATIVE MONTANA SPECIES	
	Non-Opportunistic, Intermediate Ecological Tolerance
2	exhibits a broad range of ecological tolerance and is more or less restricted to areas of human disturbance
	Non-Opportunistic, Intermediate Ecological Tolerance
3	exhibits an intermediate range of ecological tolerance, typifies a stable phase of a native community, and thrives and/or persists under natural or human disturbance
4	exhibits an intermediate range of ecological tolerance, typifies a stable phase of a native community, and persists but does not thrive with some natural or human disturbance
5	exhibits an intermediate range of ecological tolerance, typifies a stable phase of a native community, and persists but does not thrive with a little natural or human disturbance
	Non-Opportunistic, Narrow Ecological Tolerance

6	exhibits a moderate fidelity to a more or less narrow range of ecological tolerance, typifies a stable or near climax community, and tolerates limited natural or human disturbance (unless surrogate for fire or other natural disturbance)
7	exhibits a moderate fidelity to a somewhat narrow range of ecological tolerance, typifies a stable or near climax community, and does not tolerate disturbance
8	exhibits a moderate fidelity to a narrow range of ecological tolerance, typifies a stable or near climax community, and does not tolerate disturbance
9	exhibits a high fidelity to a narrow range of ecological tolerance, typifies a stable or near climax community, and does not tolerate disturbance
10	exhibits a very high fidelity to a very narrow range of ecological tolerance that typifies a stable or near climax community and does not tolerate disturbance

Appendix B – Mule deer diet species

Table B-1. Summer forage taxa in mule deer (*Odocoileus hemionus*) diets, % diet composition of each taxa by study area, and cumulative % diet composition. We considered summer forage plants to include species that comprised >2% of total diets of each study area.

Study area	Species name	Form	Mean % diet	Cumulative % diet
Cabinet-Salish	*Fragaria vesca* [b]	forb	12.73	24.55
Cabinet-Salish	*Ceanothus spp.*[b]	shrub	11.78	11.78
Cabinet-Salish	*Rubus spp.*[a,b]	shrub	11.23	24.55
Cabinet-Salish	*Rosa spp.*[a,b]	shrub	11.23	24.55
Cabinet-Salish	*Fragaria virginiana* [b]	forb	11.23	24.55
Cabinet-Salish	*Chamerion angustifolium* [b]	forb	9.21	32.21
Cabinet-Salish	*Oenothera spp.*	forb	6.2	52.96
Cabinet-Salish	*Pinus spp.*[b]	conifer	5.27	71.49
Cabinet-Salish	*Plantago spp.*	forb	4.45	36.66
Cabinet-Salish	*Alnus spp.*[b]	deciduous tree	4.16	40.82
Cabinet-Salish	*Pseudotsuga menziesii*	conifer	4.11	44.93
Cabinet-Salish	*Amelanchier alnifolia* [b]	shrub	3.28	51.92
Cabinet-Salish	*Rhamnus spp.*	shrub	2.7	57.36
Cabinet-Salish	*Bromus tectorum* [b]	graminoid	2.63	60
Cabinet-Salish	*Spiraea spp.*[b]	shrub	2.44	62.44
Cabinet-Salish	*Ribes spp.*[b]	shrub	2.19	64.63
Cabinet-Salish	*Salix spp.*[b]	shrub	1.84	68.34

Cabinet-Salish	*Mahonia spp.*[b]	shrub	1.6	69.94
Cabinet-Salish	*Medicago spp.*	forb	1.38	74.37
Cabinet-Salish	*Thuja plicata*	conifer	1.34	75.71
Cabinet-Salish	*Poa spp.*[b]	graminoid	1.32	77.03
Cabinet-Salish	*Paxistima spp.*	shrub	1.21	78.23
Cabinet-Salish	*Ratibida columnifera*	forb	1.12	84.86
Cabinet-Salish	*Heuchera spp.*	forb	1.06	79.3
Cabinet-Salish	*Eriogonum umbellatum* [b]	forb	0.92	82.15
Cabinet-Salish	*Abies spp.*	conifer	0.91	83.07
Cabinet-Salish	*Potentilla spp.*	shrub	0.77	89.91
Cabinet-Salish	*Phleum spp.*[b]	graminoid	0.69	85.55
Cabinet-Salish	*Atriplex spp.*	shrub	0.69	86.23
Cabinet-Salish	*Prunus spp.*	shrub	0.68	86.91
Cabinet-Salish	*Acer spp.*[b]	shrub	0.45	87.96
Cabinet-Salish	*Dasiphora fruticosa* [a,b]	shrub	0.41	88.37
Cabinet-Salish	*Drymocallis spp.*[a]	forb	0.41	88.37
Cabinet-Salish	*Comarum spp.*[a]	forb	0.41	88.37
Cabinet-Salish	*Rhus trilobata*	shrub	0.4	88.77
Cabinet-Salish	*Oxalis spp.*	forb	0.4	89.17
Cabinet-Salish	*Gilia spp.*	forb	0.38	89.55
Cabinet-Salish	*Salsola spp.*	forb	0.34	90.25
Cabinet-Salish	*Apocynum spp.*	forb	0.33	90.58
Cabinet-Salish	*Arctostaphylos uva-ursib*	sub-shrub	0.32	91.22
Cabinet-Salish	*Streptanthella spp.*	forb	0.31	91.53

Cabinet-Salish	*Epilobium spp.*[b]	forb	0.28	91.81
Cabinet-Salish	*Purshia tridentata*	shrub	0.27	92.08
Cabinet-Salish	*Taraxacum spp.*[a]	forb	0.23	92.78
Cabinet-Salish	*Lygodesmia spp.*[a]	forb	0.23	92.78
Cabinet-Salish	*Helianthus spp.*[a]	forb	0.23	92.78
Cabinet-Salish	*Echinacea spp.*[a]	forb	0.23	92.78
Cabinet-Salish	*Ambrosia spp.*[a]	forb	0.23	92.78
Cabinet-Salish	*Bromus japonicus*	graminoid	0.22	93.22
Cabinet-Salish	*Chrysosplenium spp.*	forb	0.22	93.44
Cabinet-Salish	*Symphoricarpos spp.*[b]	shrub	0.22	93.66
Cabinet-Salish	*Euphorbia spp.*	forb	0.21	93.43
Cabinet-Salish	*Gutierrezia sarothrae* [a]	shrub	0.21	93.87
Cabinet-Salish	*Oreostemma spp.*[a]	forb	0.21	93.87
Cabinet-Salish	*Chrysothamnus spp.*[a]	shrub	0.21	93.87
Cabinet-Salish	*Symphyotrichum spp.*[a]	forb	0.21	93.87
Cabinet-Salish	*Solidago spp.*[a]	forb	0.21	93.87
Cabinet-Salish	*Eurybia spp.*[a]	forb	0.21	93.87
Cabinet-Salish	*Penstemon spp.*	forb	0.2	94.26
Cabinet-Salish	*Populus spp.*	shrub	0.19	94.65
Cabinet-Salish	*Avena fatua*	graminoid	0.17	95
Cabinet-Salish	*Picea spp.*	conifer	0.17	95.16
Cabinet-Salish	*Solanum spp.*	forb	0.16	95.47
Rocky Mtn. Front	*Plantago spp.*	forb	15.89	15.89
Rocky Mtn. Front	*Fragaria vesca* [a,b]	forb	14.39	29.45

Rocky Mtn. Front	*Rosa spp.*[a,b]	shrub	13.56	29.45
Rocky Mtn. Front	*Fragaria virginiana* [a,b]	forb	13.56	29.45
Rocky Mtn. Front	*Rubus spp.*[b]	shrub	9.1	51.07
Rocky Mtn. Front	*Pinus spp.*[b]	conifer	6.22	71.84
Rocky Mtn. Front	*Ratibida columnifera*	forb	4.39	60.88
Rocky Mtn. Front	*Bromus tectorum* [b]	graminoid	3.83	43.39
Rocky Mtn. Front	*Oenothera spp.*	forb	2.62	55.94
Rocky Mtn. Front	*Rhamnus spp.*	shrub	2.43	45.82
Rocky Mtn. Front	*Lactuca spp.*	forb	2.28	48.1
Rocky Mtn. Front	*Spiraea spp.*[b]	shrub	2.23	54.79
Rocky Mtn. Front	*Chamerion angustifolium* [b]	forb	2.16	56.96
Rocky Mtn. Front	*Poa spp.*[b]	graminoid	1.89	62.76
Rocky Mtn. Front	*Sphaeralcea coccinea*	forb	1.72	64.49
Rocky Mtn. Front	*Amelanchier alnifolia* [b]	shrub	1.69	66.17
Rocky Mtn. Front	*Hedysarum spp.*	forb	1.5	69.26
Rocky Mtn. Front	*Eriogonum umbellatum* [b]	forb	1.29	70.56
Rocky Mtn. Front	*Phleum spp.*[b]	graminoid	1.25	73.09
Rocky Mtn. Front	*Pseudotsuga menziesii*	conifer	1.14	74.23
Rocky Mtn. Front	*Trisetum spp.*[a]	graminoid	1.08	91.15
Rocky Mtn. Front	*Rumex spp.*	forb	0.98	76.2
Rocky Mtn. Front	*Malva spp.*	forb	0.95	79.68
Rocky Mtn. Front	*Salix spp.*[b]	shrub	0.94	77.14
Rocky Mtn. Front	*Prunus spp.*	shrub	0.81	78.79
Rocky Mtn. Front	*Bromus japonicus* [b]	graminoid	0.74	80.3

Rocky Mtn. Front	*Amsinckia spp.*	forb	0.69	81.73
Rocky Mtn. Front	*Potentilla spp.*	shrub	0.68	87.68
Rocky Mtn. Front	*Mahonia spp.*[b]	shrub	0.67	83.08
Rocky Mtn. Front	*Medicago spp.*	forb	0.64	83.72
Rocky Mtn. Front	*Gutierrezia sarothrae* [a]	shrub	0.62	84.34
Rocky Mtn. Front	*Oreostemma spp.*[a]	forb	0.62	84.34
Rocky Mtn. Front	*Chrysothamnus spp.*[a]	shrub	0.62	84.34
Rocky Mtn. Front	*Symphyotrichum spp.*[a]	forb	0.62	84.34
Rocky Mtn. Front	*Solidago spp.*[a]	forb	0.62	84.34
Rocky Mtn. Front	*Eurybia spp.*[a]	forb	0.62	84.34
Rocky Mtn. Front	*Picea spp.*	conifer	0.59	84.93
Rocky Mtn. Front	*Purshia tridentata*	shrub	0.55	87.19
Rocky Mtn. Front	*Ambrosia spp.*	forb	0.5	87.5
Rocky Mtn. Front	*Taraxacum spp.*[a]	forb	0.47	88.16
Rocky Mtn. Front	*Lygodesmia spp.*[a]	forb	0.47	88.16
Rocky Mtn. Front	*Helianthus spp.*[a]	forb	0.47	88.16
Rocky Mtn. Front	*Echinacea spp.*[a]	forb	0.47	88.16
Rocky Mtn. Front	*Avena fatua*	graminoid	0.41	89.01
Rocky Mtn. Front	*Ribes spp.*	shrub	0.41	89.41
Rocky Mtn. Front	*Euphorbia spp.*	forb	0.37	90.07
Rocky Mtn. Front	*Atriplex spp.*	shrub	0.33	90.53
Rocky Mtn. Front	*Sparganium spp.*	forb	0.31	90.84
Rocky Mtn. Front	*Sphenopholis spp.*[a]	forb	0.31	91.15
Rocky Mtn. Front	*Koeleria macrantha* [a,b]	graminoid	0.31	91.15

Rocky Mtn. Front	*Geum triflorum*	forb	0.29	91.43
Rocky Mtn. Front	*Ericameria spp.*	forb	0.27	91.71
Rocky Mtn. Front	*Ceanothus spp.*[b]	shrub	0.26	92.24
Rocky Mtn. Front	*Abies spp.*	conifer	0.25	92.49
Rocky Mtn. Front	*Crataegus spp.*	shrub	0.21	92.94
Rocky Mtn. Front	*Linum spp.*	forb	0.21	93.15
Rocky Mtn. Front	*Pascopyrum smithii* [a]	graminoid	0.21	93.36
Rocky Mtn. Front	*Elymus spp.*[a]	graminoid	0.21	93.36
Rocky Mtn. Front	*Sanguisorba spp.*	forb	0.2	93.56
Rocky Mtn. Front	*Hordeum jubatum*	graminoid	0.19	94.14
Rocky Mtn. Front	*Leucanthemum vulgare* [a]	forb	0.18	94.69
Rocky Mtn. Front	*Artemisia spp.*[a]	forb	0.18	94.69
Rocky Mtn. Front	*Achillea millefolium* [a,b]	forb	0.18	94.69
Rocky Mtn. Front	*Thalictrum spp.*	forb	0.15	95.19
Whitefish Range	*Plantago spp.*	forb	15.97	15.97
Whitefish Range	*Bromus tectorum* [b]	graminoid	6.62	22.59
Whitefish Range	*Pinus spp.*[b]	conifer	6.18	49.31
Whitefish Range	*Fragaria vesca* [b]	forb	5.7	27.59
Whitefish Range	*Triticum aestivum* [b]	graminoid	5.04	39.58
Whitefish Range	*Rubus spp.*[a,b]	shrub	5	27.59
Whitefish Range	*Rosa spp.*[a,b]	shrub	5	27.59
Whitefish Range	*Fragaria virginiana* [b]	forb	5	27.59
Whitefish Range	*Amelanchier alnifolia* [b]	shrub	4.14	35.89
Whitefish Range	*Pseudotsuga menziesii*	conifer	3.55	43.13

Whitefish Range	*Chamerion angustifolium*[b]	forb	2.92	64.55
Whitefish Range	*Spiraea spp.*[b]	shrub	2.39	51.7
Whitefish Range	*Ceanothus spp.*[b]	shrub	2.13	53.83
Whitefish Range	*Medicago spp.*	forb	2.1	55.92
Whitefish Range	*Poa spp.*[b]	graminoid	2.09	58.01
Whitefish Range	*Rhamnus spp.*	shrub	1.91	59.92
Whitefish Range	*Salix spp.*[b]	shrub	1.7	61.62
Whitefish Range	*Pascopyrum smithii*[a]	graminoid	1.36	67.35
Whitefish Range	*Elymus spp.*[a]	graminoid	1.36	67.35
Whitefish Range	*Lonicera spp.*	shrub	1.25	69.93
Whitefish Range	*Linum spp.*	forb	1.18	72.35
Whitefish Range	*Alnus spp.*[b]	deciduous tree	1.1	73.44
Whitefish Range	*Phleum spp.*[b]	graminoid	1.04	74.49
Whitefish Range	*Atriplex spp.*	shrub	0.98	75.46
Whitefish Range	*Avena fatua*	graminoid	0.92	77.35
Whitefish Range	*Eriogonum umbellatum*[b]	forb	0.91	78.27
Whitefish Range	*Ribes spp.*[b]	shrub	0.91	79.18
Whitefish Range	*Oenothera spp.*	forb	0.67	82.63
Whitefish Range	*Bromus japonicus*[b]	graminoid	0.67	83.3
Whitefish Range	*Fraxinus spp.*	deciduous tree	0.6	83.89
Whitefish Range	*Taraxacum spp.*[a]	forb	0.57	84.46
Whitefish Range	*Lygodesmia spp.*[a]	forb	0.57	84.46
Whitefish Range	*Helianthus spp.*[a]	forb	0.57	84.46
Whitefish Range	*Euphorbia spp.*[a]	forb	0.57	84.46

Whitefish Range	*Echinacea spp.*[a]	forb	0.57	84.46
Whitefish Range	*Ratibida columnifera* [a]	forb	0.57	84.46
Whitefish Range	*Sanguisorba spp.*	forb	0.57	85.03
Whitefish Range	*Mahonia spp.*[b]	shrub	0.52	85.56
Whitefish Range	*Purshia tridentata*	shrub	0.5	86.06
Whitefish Range	*Picea spp.*	conifer	0.49	86.55
Whitefish Range	*Ambrosia spp.*	forb	0.49	86.72
Whitefish Range	*Crepis spp.*	forb	0.48	87.03
Whitefish Range	*Sphaeralcea coccinea*	forb	0.42	87.45
Whitefish Range	*Gilia spp.*	forb	0.39	87.84
Whitefish Range	*Crataegus spp.*	shrub	0.39	88.23
Whitefish Range	*Epilobium spp.*[b]	forb	0.38	88.99
Whitefish Range	*Trifolium spp.*	forb	0.38	89.36
Whitefish Range	*Quercus spp.*	deciduous tree	0.37	89.73
Whitefish Range	*Vahlodea spp.*[a]	graminoid	0.37	90.1
Whitefish Range	*Festuca spp.*[a,b]	graminoid	0.37	90.1
Whitefish Range	*Hordeum jubatum*	graminoid	0.37	90.47
Whitefish Range	*Acer spp.*[b]	shrub	0.36	90.83
Whitefish Range	*Heuchera spp.*	forb	0.34	91.17
Whitefish Range	*Malva spp.*	forb	0.34	90.22
Whitefish Range	*Erigeron spp.*	forb	0.33	91.5
Whitefish Range	*Thuja plicata*	conifer	0.33	91.83
Whitefish Range	*Abies spp.*	conifer	0.31	92.45
Whitefish Range	*Zizia spp.*[a]	forb	0.28	92.73

Whitefish Range	*Shoshonea spp.*[a]	forb	0.28	92.73
Whitefish Range	*Orogenia spp.*[a]	forb	0.28	92.73
Whitefish Range	*Musineon spp.*[a]	forb	0.28	92.73
Whitefish Range	*Cymopterus spp.*[a]	forb	0.28	92.73
Whitefish Range	*Lomatium spp.*[a,b]	forb	0.28	92.73
Whitefish Range	*Heracleum maximum*	forb	0.28	92.73
Whitefish Range	*Angelica spp.*[a]	forb	0.28	92.73
Whitefish Range	*Ericameria spp.*	shrub	0.25	93.17
Whitefish Range	*Viola spp.*	forb	0.24	93.23
Whitefish Range	*Gutierrezia sarothraea*	shrub	0.22	93.7
Whitefish Range	*Oreostemma spp.*[a]	forb	0.22	93.7
Whitefish Range	*Chrysothamnus spp.*[a]	shrub	0.22	93.7
Whitefish Range	*Symphyotrichum spp.*[a]	forb	0.22	93.7
Whitefish Range	*Solidago spp.*[a]	forb	0.22	93.7
Whitefish Range	*Eurybia spp.*[a]	forb	0.22	93.7
Whitefish Range	*Lactuca spp.*	forb	0.21	93.91
Whitefish Range	*Apocynum androsaemifolium*	forb	0.2	94.1
Whitefish Range	*Rumex spp.*	forb	0.16	94.98
Whitefish Range	*Juniperus communis* [b]	shrub	0.15	95.14
Whitefish Range	*Streptanthella spp.*	forb	0.14	95.28

[a] DNA barcodes from ESV sequencing correspond with multiple forage taxa, resulting in duplicate estimates of % diet.

[b] DE estimates from samples collected in our study areas.

Table B2. Digestible energy (DE) values in kcal/g for phenological stages of mule deer summer forage taxa, average DE values across phenological stages, and the source of calculated values.

Taxa name	Lifeform	Emergent	Flowering	Fruiting	Mature seed	Senesced	Average	Data source
Pinus spp.	conifer	3.21					3.21	Proffitt et al. (2016)
Alnus spp.	deciduous tree	1.93		1.91			1.92	This study
Chamerion angustifolium	forb	2.22	2.38	2.78			2.54	This study
Fragaria vesca	forb						2.7	Hull (2018)
Bromus spp.	graminoid	3.01	2.98	2.94	2.59	2.67	2.84	Proffitt et al. (2016)
Poa spp.	graminoid	3.02	2.81	2.61	2.92	2.59	2.79	Proffitt et al. (2016)
Triticum aestivum	graminoid	3.29	3.1	3.32		3.12	3.21	Proffitt et al. (2016)
Amelanchier alnifolia	shrub	2.14		2.05			2.08	This study
Ceanothus spp.	shrub						3.26	Hull (2018)
Ribes spp.	shrub	2.58		2.73			2.65	This study
Rosa woodsii	shrub						2.74	Hull (2018)
Rubus spp.	shrub	1.63	1.9	2.51			2.01	This study
Spiraea spp.	shrub						3.17	Hull (2018)

Appendix C – Between-class analyses of plant composition

Table C-1. Normed scores of the two axes from a Hill-Smith (HS) between-class analysis (BCA) describing differences in vegetation communities in three study areas based on vegetation cover (%). Study areas include Cabinet-Salish Mountains (*n*=269), Rocky Mountain Front (*n*=190) and Whitefish Range (*n*=255). Vegetation data were collected between June 1 and August 31, 2017 – 2019.

		Axis 1	**Axis 2**
Group normed scores			
CAB		0.728	-1.014
RMF		-1.595	-0.159
WHI		0.494	1.340
Column normed scores			
Achillea millefolium	ACHMIL	-0.110	**-0.223**
Allium sp	ALLISP	-0.064	-0.009
Alnus incana	ALNINC	-0.050	-0.007
Alnus sp	ALNUSP	0.023	-0.047
Amelanchier alnifolia	AMEALN	0.107	-0.147
Anemone parviflora	ANEPAR	-0.095	-0.014
Angelica arguta	ANGARG	-0.124	0.023
Antennaria alpina	ANTALP	-0.081	-0.012
Antennaria microphylla	ANTMIC	-0.050	-0.007
Antennaria parvifolia	ANTPAR	-0.028	-0.079

Antennaria rosea	ANTROS	-0.034	0.004
Apocynum androsaemifolium	APOAND	0.005	**-0.182**
Arctostaphylos uva-ursi	ARCUVA	0.115	-0.078
Arnica mollis	ARNMOL	-0.050	-0.007
Artemisia frigida	ARTFRI	-0.098	-0.014
Artemisia ludoviciana	ARTLUD	-0.071	-0.010
Aster alpigenus	ASTALP	-0.081	-0.012
Astragalus flexuosus	ASTFLE	-0.050	-0.007
Astragalus sp	ASTRSP	-0.087	-0.013
Avena fatua	AVEFAT	0.023	-0.047
Brassica rapa	BRARAP	-0.050	-0.007
Bromus carinatus	BROCAR	**-0.202**	-0.015
Bromus inermis	BROINE	-0.118	-0.071
Bromus japonicus	BROJAP	-0.019	0.044
Bromus tectorum	BROTEC	0.004	-0.138
Calochortus apiculatus	CALAPI	0.069	-0.111
Calamagrostis canadensis	CALCAN	-0.059	-0.023
Calamagrostis purpurascens	CALPUR	0.023	-0.047
Calamagrostis rubescens	CALRUB	0.117	**-0.189**
Campanula rotundifolia	CAMROT	-0.067	-0.102
Carex sp	CARESP	-0.008	-0.127
Castilleja cusickii	CASCUS	-0.050	-0.007
Castilleja lutescens	CASLUT	-0.050	-0.007

Castilleja miniata	CASMIN	-0.052	0.106
Castilleja occidentalis	CASOCC	0.023	-0.047
Castilleja sp	CASTSP	-0.032	-0.028
Cerastium arvense	CERARV	**-0.197**	-0.029
Chamerion angustifolium	CHAANG	-0.082	0.152
Chimaphila umbellata	CHIUMB	0.125	-0.043
Cirsium arvense	CIRARV	0.032	-0.065
Cirsium sp	CIRSSP	0.038	-0.006
Clarkia pulchella	CLAPUL	0.062	-0.127
Claytonia sp	CLAYSP	-0.019	-0.038
Clematis sp	CLEMSP	0.033	-0.066
Collomia linearis	COLLIN	-0.085	-0.116
Comandra umbellata	COMUMB	-0.095	-0.032
Cornus canadensis	CORCAN	0.042	0.110
Cornus sericea	CORSER	-0.045	0.060
Crepis sp	CREPSP	0.036	-0.018
Dactylis glomerata	DACGLO	-0.106	-0.035
Dasiphora fruticosa	DASFRU	**-0.154**	-0.022
Elymus glaucus	ELYGLA	0.043	**0.204**
Elymus sp	ELYMSP	-0.019	-0.038
Elymus trachycaulus	ELYTRA	-0.061	-0.022
Epilobium sp	EPILSP	0.041	-0.081
Equisetum hyemale	EQUHYE	-0.067	0.026

Eremogone capillaris	ERECAP	-0.050	-0.007
Erigeron compositus	ERICOM	-0.050	-0.007
Erigeron glacialis	ERIGLA	-0.061	-0.022
Erigeron philadelphicus	ERIPHI	0.016	0.062
Eriogonum umbellatum	ERIUMB	-0.069	-0.010
Festuca rubra	FESRUB	0.076	**0.199**
Fragaria vesca	FRAVES	0.103	**-0.176**
Fragaria virginiana	FRAVIR	-0.130	0.049
Gaillardia aristata	GAIARI	**-0.151**	-0.022
Galium bifolium	GALBIF	0.041	0.003
Galium boreale	GALBOR	**-0.392**	0.007
Galium trifidum	GALTRI	0.007	0.081
Geum triflorum	GEUTRI	-0.032	-0.041
Glycyrrhiza lepidota	GLYLEP	0.032	-0.066
Glyceria striata	GLYSTR	-0.059	-0.009
Hedysarum sp	HEDYSP	-0.002	-0.045
Heracleum maximum	HERMAX	-0.055	0.018
Hesperostipa comata	HESCOM	-0.028	0.045
Hieracium albiflorum	HIEALB	0.088	0.127
Hieracium scouleri	HIESCO	0.003	-0.059
Hieracium triste	HIETRI	0.055	-0.113
Hieracium umbellatum	HIEUMB	-0.022	-0.044
Holodiscus discolor	HOLDIS	0.060	-0.056

Hordeum jubatum	HORJUB	-0.050	-0.007
Hypericum perforatum	HYPPER	0.038	-0.077
Juniperus communis	JUNCOM	-0.089	-0.024
Juniperus horizontalis	JUNHOR	-0.071	-0.010
Juniperus scopulorum	JUNSCO	-0.087	-0.013
Koeleria macrantha	KOEMAC	-0.104	-0.033
Larix occidentalis	LAROCC	0.121	-0.078
Leucanthemum vulgare	LEUVUL	-0.016	0.045
Linnaea borealis	LINBOR	**0.158**	-0.045
Lomatium macrocarpum	LOMMAC	-0.040	-0.051
Lomatium triternatum	LOMTRI	0.080	**-0.178**
Lonicera involucrata	LONINV	-0.072	-0.037
Lotus corniculatus	LOTCOR	0.038	0.100
Lupinus sp	LUPISP	0.044	-0.089
Luzula parviflora	LUZPAR	0.025	0.098
Maianthemum stellatum	MAISTE	0.025	-0.019
Microsteris sp	MICRSP	0.023	-0.047
Monotropa uniflora	MONUNI	0.020	0.079
Orthilia secunda	ORTSEC	-0.053	-0.049
Osmorhiza sp	OSMOSP	0.046	-0.097
Packera cana	PACCAN	-0.106	0.000
Pascopyrum smithii	PASSMI	-0.082	-0.012
Pedicularis sp	PEDISP	-0.035	-0.028

Penstemon albertinus	PENALB	-0.051	0.098
Penstemon confertus	PENCON	0.020	-0.035
Penstemon procerus	PENPRO	**-0.136**	-0.031
Penstemon sp	PENSSP	**-0.188**	-0.117
Penstemon wilcoxii	PENWIL	-0.042	-0.069
Phalaris arundinacea	PHAARU	0.037	-0.076
Pinus albicaulis	PINALB	0.022	0.088
Pinus contorta	PINCON	-0.047	-0.029
Pinus flexilis	PINFLE	-0.081	-0.012
Pinus ponderosa	PINPON	0.069	-0.142
Plantago lanceolata	PLALAN	0.016	0.062
Poa sp	POASP	-0.002	-0.076
Populus angustifolia	POPANG	0.030	0.053
Populus balsamifera	POPBAL	-0.042	-0.033
Populus tremuloides	POPTRE	-0.058	0.118
Potentilla argentea	POTARG	0.040	-0.081
Potentilla sp	POTESP	-0.050	-0.036
Potentilla gracilis	POTGRA	-0.072	-0.011
Potentilla pennsylvanica	POTPEN	-0.068	-0.010
Prosartes trachycarpa	PROTRA	-0.009	0.025
Pseudotsuga menziesii	PSEMEN	0.001	-0.062
Pyrola sp	PYROSP	-0.090	0.021
Rhododendron albiflorum	RHOALB	-0.050	-0.007

Ribes sp	RIBESP	-0.030	-0.074
Rosa acicularis	ROSACI	-0.081	-0.112
Rosa woodsii	ROSWOO	-0.003	**0.298**
Rubus idaeus	RUBIDA	0.031	0.033
Salix sp	SALISP	0.050	-0.036
Sambucus nigra	SAMNIG	0.016	0.062
Sambucus racemosa	SAMRAC	0.026	0.104
Sedum sp	SEDUSP	-0.050	-0.007
Senecio integerrimus	SENINT	-0.084	-0.036
Shepherdia canadensis	SHECAN	-0.060	0.036
Solidago missouriensis	SOLMIS	**-0.173**	-0.044
Solidago multiradiata	SOLMUL	-0.050	-0.007
Spiraea sp	SPIRSP	0.023	-0.047
Stipa sp	STIPSP	-0.071	-0.010
Streptopus amplexifolius	STRAMP	-0.089	-0.092
Symphoricarpos albus	SYMALB	0.006	0.122
Symphyotrichum laeve	SYMLAE	-0.012	-0.059
Thalictrum sp	THALSP	0.076	**-0.173**
Thalictrum occidentale	THAOCC	**-0.266**	0.056
Thuja plicata	THUPLI	0.046	-0.001
Tragopogon dubius	TRADUB	-0.097	-0.027
Trifolium sp	TRIFSP	0.021	0.083
Trifolium pratense	TRIPRA	0.028	-0.014

Trisetum spicatum	TRISPI	-0.003	-0.063
Tsuga heterophylla	TSUHET	0.050	-0.081
Urtica dioica	URTDIO	0.024	0.035
Vaccinium sp	VACCSP	0.025	0.050
Valeriana sp	VALESP	-0.039	-0.038
Veratrum viride	VERVIR	-0.001	0.073
Vicia sp	VICISP	0.048	-0.036
Vicia villosa	VICVIL	0.016	0.062
Viola adunca	VIOADU	-0.071	-0.010
Viola sp	VIOLSP	-0.090	**-0.202**
Xerophyllum tenax	XERTEN	-0.032	0.132

Table C-2. Normed scores of the two axes from a Hill-Smith (HS) between-class analysis (BCA) describing differences in vegetation communities between forest disturbances based on vegetation cover (%). Vegetation data were collected between June 1 and August 31, 2017 – 2019.

		Axis 1	**Axis 2**
Group normed scores			
Conifer		-0.533	0.811
Harvest		-0.565	-1.059
Harvest & prescribed fire		-0.054	-2.232
Prescribed fire		-0.251	-0.691
Wildfire		2.071	0.198
Column normed scores			
Achillea millefolium	ACHMIL	**0.150**	**-0.206**
Allium sp	ALLISP	0.067	0.021
Alnus incana	ALNINC	-0.020	0.039
Alnus sp	ALNUSP	-0.002	-0.108
Amelanchier alnifolia	AMEALN	**-0.142**	-0.114
Anemone parviflora	ANEPAR	0.023	0.016
Angelica arguta	ANGARG	-0.001	0.016
Antennaria alpina	ANTALP	0.101	0.022
Antennaria microphylla	ANTMIC	0.077	0.010
Antennaria parvifolia	ANTPAR	-0.027	-0.056
Antennaria rosea	ANTROS	0.033	-0.113
Apocynum androsaemifolium	APOAND	0.036	-0.135

Arctostaphylos uva-ursi	ARCUVA	**-0.187**	**-0.298**
Arnica mollis	ARNMOL	-0.020	0.039
Artemisia frigida	ARTFRI	-0.034	0.043
Artemisia ludoviciana	ARTLUD	0.109	0.013
Aster alpigenus	ASTALP	0.045	-0.009
Astragalus flexuosus	ASTFLE	-0.009	-0.033
Astragalus sp	ASTRSP	0.105	0.025
Avena fatua	AVEFAT	-0.021	-0.051
Brassica rapa	BRARAP	0.077	0.010
Bromus carinatus	BROCAR	**0.209**	0.001
Bromus inermis	BROINE	0.132	-0.024
Bromus japonicus	BROJAP	0.033	0.036
Bromus tectorum	BROTEC	0.111	0.048
Calochortus apiculatus	CALAPI	-0.083	-0.046
Calamagrostis canadensis	CALCAN	0.093	-0.083
Calamagrostis purpurascens	CALPUR	0.077	0.010
Calamagrostis rubescens	CALRUB	-0.137	**-0.229**
Campanula rotundifolia	CAMROT	0.027	-0.048
Carex sp	CARESP	0.057	**-0.217**
Castilleja cusickii	CASCUS	0.077	0.010
Castilleja lutescens	CASLUT	-0.009	-0.033
Castilleja miniata	CASMIN	0.069	0.031
Castilleja occidentalis	CASOCC	-0.021	-0.051

Castilleja sp	CASTSP	0.033	0.026
Cerastium arvense	CERARV	-0.015	0.018
Chamerion angustifolium	CHAANG	**0.479**	-0.144
Chimaphila umbellata	CHIUMB	-0.137	**0.185**
Cirsium arvense	CIRARV	-0.013	-0.118
Cirsium sp	CIRSSP	-0.039	-0.062
Clarkia pulchella	CLAPUL	0.087	0.018
Claytonia sp	CLAYSP	0.040	0.034
Clematis sp	CLEMSP	-0.028	0.055
Collomia linearis	COLLIN	0.126	-0.115
Comandra umbellata	COMUMB	0.096	0.050
Cornus canadensis	CORCAN	-0.070	0.073
Cornus sericea	CORSER	-0.045	-0.015
Crepis sp	CREPSP	-0.024	-0.017
Dactylis glomerata	DACGLO	**0.148**	0.008
Dasiphora fruticosa	DASFRU	-0.001	0.062
Elymus glaucus	ELYGLA	0.036	-0.056
Elymus sp	ELYMSP	0.053	-0.069
Elymus trachycaulus	ELYTRA	-0.024	-0.044
Epilobium sp	EPILSP	-0.032	-0.110
Equisetum hyemale	EQUHYE	-0.042	0.028
Eremogone capillaris	ERECAP	0.077	0.010
Erigeron compositus	ERICOM	-0.020	0.039

Erigeron glacialis	ERIGLA	-0.006	0.055
Erigeron philadelphicus	ERIPHI	-0.021	-0.051
Eriogonum umbellatum	ERIUMB	0.023	0.038
Festuca rubra	FESRUB	-0.059	**-0.202**
Fragaria vesca	FRAVES	-0.083	-0.024
Fragaria virginiana	FRAVIR	-0.140	-0.088
Gaillardia aristata	GAIARI	0.006	0.057
Galium bifolium	GALBIF	-0.042	0.019
Galium boreale	GALBOR	0.105	0.082
Galium trifidum	GALTRI	0.004	0.099
Geum triflorum	GEUTRI	0.020	0.039
Glycyrrhiza lepidota	GLYLEP	-0.029	-0.071
Glyceria striata	GLYSTR	-0.004	0.040
Hedysarum sp	HEDYSP	0.017	0.039
Heracleum maximum	HERMAX	0.043	0.042
Hesperostipa comata	HESCOM	0.022	-0.068
Hieracium albiflorum	HIEALB	-0.038	-0.138
Hieracium scouleri	HIESCO	-0.033	0.029
Hieracium triste	HIETRI	-0.019	-0.036
Hieracium umbellatum	HIEUMB	-0.033	-0.010
Holodiscus discolor	HOLDIS	-0.050	-0.068
Hordeum jubatum	HORJUB	-0.020	0.039
Hypericum perforatum	HYPPER	-0.033	0.027

Juniperus communis	JUNCOM	-0.067	0.059
Juniperus horizontalis	JUNHOR	-0.028	0.055
Juniperus scopulorum	JUNSCO	-0.034	0.067
Koeleria macrantha	KOEMAC	0.042	0.035
Larix occidentalis	LAROCC	0.096	**-0.260**
Leucanthemum vulgare	LEUVUL	-0.036	-0.026
Linnaea borealis	LINBOR	**-0.205**	0.044
Lomatium macrocarpum	LOMMAC	0.003	-0.059
Lomatium triternatum	LOMTRI	0.020	-0.074
Lonicera involucrata	LONINV	0.067	0.051
Lotus corniculatus	LOTCOR	-0.048	-0.116
Lupinus sp	LUPISP	-0.029	0.019
Luzula parviflora	LUZPAR	0.051	0.010
Maianthemum stellatum	MAISTE	-0.077	0.082
Microsteris sp	MICRSP	-0.002	-0.108
Monotropa uniflora	MONUNI	-0.019	0.003
Orthilia secunda	ORTSEC	-0.009	**0.185**
Osmorhiza sp	OSMOSP	-0.053	0.070
Packera cana	PACCAN	0.045	0.035
Pascopyrum smithii	PASSMI	0.047	0.040
Pedicularis sp	PEDISP	-0.027	0.012
Penstemon albertinus	PENALB	0.121	0.006
Penstemon confertus	PENCON	-0.064	**-0.177**

Penstemon procerus	PENPRO	0.007	0.067
Penstemon sp	PENSSP	0.046	0.089
Penstemon wilcoxii	PENWIL	0.000	-0.089
Phalaris arundinacea	PHAARU	-0.032	0.063
Pinus albicaulis	PINALB	-0.015	-0.048
Pinus contorta	PINCON	**0.187**	-0.005
Pinus flexilis	PINFLE	-0.032	0.063
Pinus ponderosa	PINPON	-0.016	-0.167
Plantago lanceolata	PLALAN	-0.020	0.039
Poa sp	POASP	-0.036	-0.052
Populus angustifolia	POPANG	-0.036	-0.087
Populus balsamifera	POPBAL	-0.032	0.015
Populus tremuloides	POPTRE	**0.169**	0.036
Potentilla argentea	POTARG	0.028	0.009
Potentilla sp	POTESP	0.025	-0.063
Potentilla gracilis	POTGRA	-0.018	-0.012
Potentilla pennsylvanica	POTPEN	0.103	0.013
Prosartes trachycarpa	PROTRA	-0.034	0.084
Pseudotsuga menziesii	PSEMEN	-0.022	0.065
Pyrola sp	PYROSP	-0.028	0.092
Rhododendron albiflorum	RHOALB	0.077	0.010
Ribes sp	RIBESP	0.051	-0.040
Rosa acicularis	ROSACI	-0.070	-0.038

Rosa woodsii	ROSWOO	-0.068	-0.058
Rubus idaeus	RUBIDA	0.053	-0.041
Salix sp	SALISP	**0.208**	0.033
Sambucus nigra	SAMNIG	-0.021	-0.051
Sambucus racemosa	SAMRAC	0.031	0.015
Sedum sp	SEDUSP	0.077	0.010
Senecio integerrimus	SENINT	0.095	0.004
Shepherdia canadensis	SHECAN	-0.034	0.037
Solidago missouriensis	SOLMIS	0.092	0.033
Solidago multiradiata	SOLMUL	-0.020	0.039
Spiraea sp	SPIRSP	-0.002	-0.108
Stipa sp	STIPSP	0.053	-0.069
Streptopus amplexifolius	STRAMP	-0.073	0.085
Symphoricarpos albus	SYMALB	-0.138	-0.016
Symphyotrichum laeve	SYMLAE	-0.035	-0.056
Thalictrum sp	THALSP	-0.065	-0.053
Thalictrum occidentale	THAOCC	-0.014	**0.174**
Thuja plicata	THUPLI	-0.016	-0.039
Tragopogon dubius	TRADUB	0.105	-0.040
Trifolium sp	TRIFSP	-0.026	0.052
Trifolium pratense	TRIPRA	-0.017	-0.012
Trisetum spicatum	TRISPI	-0.026	-0.018
Tsuga heterophylla	TSUHET	0.064	0.034

Urtica dioica	URTDIO	-0.028	-0.028
Vaccinium sp	VACCSP	-0.047	-0.094
Valeriana sp	VALESP	-0.034	0.067
Veratrum viride	VERVIR	-0.032	0.064
Vicia sp	VICISP	-0.027	-0.080
Vicia villosa	VICVIL	-0.002	-0.108
Viola adunca	VIOADU	-0.021	0.004
Viola sp	VIOLSP	-0.062	0.081
Xerophyllum tenax	XERTEN	0.096	0.096

Table C-3. Normed scores of the two axes from a Hill-Smith (HS) between-class analysis (BCA) describing differences in vegetation communities between forest disturbances (harvest, harvest followed by prescribed fire, prescribed fire, wildfire, and reference conifer) based on vegetation cover (%). Study areas include Cabinet-Salish Mountains (*n*=269), Rocky Mountain Front (*n*=190) and Whitefish Range (*n*=255). Vegetation data were collected between June 1 and August 31, 2017 – 2019.

		CAB-SAL		**RMF**		**WHI**	
Group normed scores							
		Axis 1	**Axis 2**	**Axis 1**	**Axis 2**	**Axis 1**	**Axis 2**
Conifer		0.376	0.855	-0.703	0.631	-0.287	0.883
Harvest		0.365	-0.405	-1.200	-0.657	-0.491	-1.141
Harvest & prescribed fire		0.462	-2.064	0.997	0.581	-0.513	-1.846
Prescribed fire		-0.309	-1.798	-1.150	-3.602	-0.403	0.071
Wildfire		-2.727	0.047	1.247	-0.215	2.683	-0.248
Column normed scores							
Achillea millefolium	ACHMIL	-0.105	**-0.275**	**0.137**	-0.132	-0.105	**-0.247**
Allium sp	ALLISP	0.000	0.000	0.056	0.000	0.000	0.000
Alnus incana	ALNINC	0.000	0.000	-0.041	0.045	0.000	0.000
Alnus sp	ALNUSP	0.026	-0.133	0.000	0.000	0.000	0.000
Amelanchier alnifolia	AMEALN	0.145	-0.080	-0.091	-0.040	-0.068	-0.041
Anemone parviflora	ANEPAR	0.000	0.000	-0.028	-0.122	0.000	0.000
Angelica arguta	ANGARG	0.021	0.055	-0.069	0.033	-0.001	-0.095
Antennaria alpina	ANTALP	0.000	0.000	0.090	-0.011	0.000	0.000
Antennaria microphylla	ANTMIC	0.000	0.000	0.072	-0.015	0.000	0.000

Antennaria parvifolia	ANTPAR	0.043	-0.064	-0.066	-0.108	-0.046	-0.038
Antennaria rosea	ANTROS	-0.041	-0.073	0.090	0.026	-0.060	-0.103
Apocynum androsaemifolium	APOAND	0.006	**-0.172**	**0.133**	0.055	0.011	0.024
Arctostaphylos uva-ursi	ARCUVA	**0.219**	**-0.279**	-0.026	-0.002	**-0.202**	-0.130
Arnica mollis	ARNMOL	0.000	0.000	-0.041	0.045	0.000	0.000
Artemisia frigida	ARTFRI	0.000	0.000	-0.091	-0.051	0.000	0.000
Artemisia ludoviciana	ARTLUD	0.000	0.000	0.102	-0.022	0.000	0.000
Aster alpigenus	ASTALP	0.000	0.000	0.010	-0.026	0.000	0.000
Astragalus flexuosus	ASTFLE	0.000	0.000	-0.067	**-0.258**	0.000	0.000
Astragalus sp	ASTRSP	0.000	0.000	0.093	-0.009	0.000	0.000
Avena fatua	AVEFAT	0.020	-0.026	0.000	0.000	0.000	0.000
Brassica rapa	BRARAP	0.000	0.000	0.072	-0.015	0.000	0.000
Bromus carinatus	BROCAR	0.021	0.055	**0.208**	-0.113	-0.030	-0.082
Bromus inermis	BROINE	0.032	-0.125	0.111	-0.057	**0.230**	-0.025
Bromus japonicus	BROJAP	0.000	0.000	0.072	-0.015	-0.017	0.064
Bromus tectorum	BROTEC	**-0.226**	0.058	0.002	**-0.172**	0.000	0.000
Calochortus apiculatus	CALAPI	0.078	0.056	**-0.195**	-0.110	0.126	-0.056
Calamagrostis canadensis	CALCAN	-0.125	-0.067	0.112	0.045	0.091	-0.069
Calamagrostis purpurascens	CALPUR	-0.152	0.003	0.000	0.000	0.000	0.000
Calamagrostis rubescens	CALRUB	0.147	-0.083	0.003	-0.109	**-0.254**	-0.155
Campanula rotundifolia	CAMROT	0.013	-0.042	0.003	-0.131	-0.019	-0.058
Carex sp	CARESP	0.082	**-0.278**	**0.147**	0.021	0.010	-0.152
Castilleja cusickii	CASCUS	0.000	0.000	0.072	-0.015	0.000	0.000

Castilleja lutescens	CASLUT	0.000	0.000	-0.067	**-0.258**	0.000	0.000
Castilleja miniata	CASMIN	0.020	-0.026	0.065	0.026	0.050	0.010
Castilleja occidentalis	CASOCC	0.020	-0.026	0.000	0.000	0.000	0.000
Castilleja sp	CASTSP	-0.140	0.004	-0.022	-0.028	-0.029	0.020
Cerastium arvense	CERARV	0.000	0.000	-0.092	-0.095	0.000	0.000
Chamerion angustifolium	CHAANG	**-0.360**	-0.166	**0.403**	-0.118	**0.493**	**-0.274**
Chimaphila umbellata	CHIUMB	0.106	**0.270**	-0.008	0.134	-0.057	**0.235**
Cirsium arvense	CIRARV	0.033	-0.126	0.000	0.000	0.000	0.000
Cirsium sp	CIRSSP	0.027	-0.035	0.000	0.000	-0.033	-0.013
Clarkia pulchella	CLAPUL	**-0.201**	0.014	0.000	0.000	0.000	0.000
Claytonia sp	CLAYSP	-0.152	0.003	-0.041	0.045	0.000	0.000
Clematis sp	CLEMSP	0.030	0.078	0.000	0.000	0.000	0.000
Collomia linearis	COLLIN	-0.088	-0.138	0.127	-0.137	-0.052	-0.094
Comandra umbellata	COMUMB	-0.152	0.003	0.048	0.026	0.000	0.000
Cornus canadensis	CORCAN	-0.023	0.123	-0.013	0.104	-0.059	0.123
Cornus sericea	CORSER	0.000	0.000	-0.088	-0.015	-0.043	0.036
Crepis sp	CREPSP	0.030	0.078	0.000	0.000	-0.031	-0.133
Dactylis glomerata	DACGLO	0.020	-0.026	**0.157**	-0.026	0.000	0.000
Dasiphora fruticosa	DASFRU	0.000	0.000	-0.069	0.061	0.000	0.000
Elymus glaucus	ELYGLA	0.000	0.000	-0.067	**-0.258**	0.111	-0.103
Elymus sp	ELYMSP	0.026	-0.133	0.072	-0.015	0.000	0.000
Elymus trachycaulus	ELYTRA	0.021	0.055	-0.094	**-0.241**	0.000	0.000
Epilobium sp	EPILSP	0.048	**-0.172**	0.002	0.031	-0.025	0.090

Equisetum hyemale	EQUHYE	0.000	0.000	-0.087	0.014	-0.025	0.090
Eremogone capillaris	ERECAP	0.000	0.000	0.072	-0.015	0.000	0.000
Erigeron compositus	ERICOM	0.000	0.000	-0.041	0.045	0.000	0.000
Erigeron glacialis	ERIGLA	-0.152	0.003	-0.057	0.063	0.000	0.000
Erigeron philadelphicus	ERIPHI	0.000	0.000	0.000	0.000	-0.030	-0.082
Eriogonum umbellatum	ERIUMB	0.000	0.000	0.002	0.031	0.000	0.000
Festuca rubra	FESRUB	0.045	-0.120	0.000	0.000	-0.110	**-0.210**
Fragaria vesca	FRAVES	-0.008	0.053	-0.079	-0.093	-0.087	-0.004
Fragaria virginiana	FRAVIR	**0.194**	-0.020	**-0.241**	-0.124	-0.091	-0.093
Gaillardia aristata	GAIARI	0.000	0.000	-0.069	-0.076	0.000	0.000
Galium bifolium	GALBIF	0.029	0.032	0.000	0.000	-0.034	0.045
Galium boreale	GALBOR	0.000	0.000	-0.040	-0.031	0.011	-0.076
Galium trifidum	GALTRI	-0.072	0.084	-0.007	0.096	0.074	0.144
Geum triflorum	GEUTRI	-0.093	0.041	-0.048	0.068	-0.031	-0.133
Glycyrrhiza lepidota	GLYLEP	0.029	-0.037	0.000	0.000	0.000	0.000
Glyceria striata	GLYSTR	0.000	0.000	-0.026	0.041	0.000	0.000
Hedysarum sp	HEDYSP	0.021	0.055	0.072	-0.015	0.000	0.000
Heracleum maximum	HERMAX	0.000	0.000	0.043	0.009	-0.017	0.064
Hesperostipa comata	HESCOM	0.000	0.000	0.022	0.021	-0.031	-0.133
Hieracium albiflorum	HIEALB	0.114	-0.014	0.104	**-0.182**	-0.058	-0.132
Hieracium scouleri	HIESCO	0.028	0.038	-0.041	0.045	0.000	0.000
Hieracium triste	HIETRI	0.014	-0.014	0.000	0.000	0.000	0.000
Hieracium umbellatum	HIEUMB	0.029	-0.037	-0.041	0.045	0.000	0.000

Holodiscus discolor	HOLDIS	0.020	-0.105	0.000	0.000	-0.033	-0.013
Hordeum jubatum	HORJUB	0.000	0.000	-0.041	0.045	0.000	0.000
Hypericum perforatum	HYPPER	0.034	0.057	0.000	0.000	0.000	0.000
Juniperus communis	JUNCOM	0.052	0.016	-0.129	0.038	0.010	0.005
Juniperus horizontalis	JUNHOR	0.000	0.000	-0.058	0.064	0.000	0.000
Juniperus scopulorum	JUNSCO	0.000	0.000	-0.070	0.078	0.000	0.000
Koeleria macrantha	KOEMAC	0.021	0.055	-0.002	-0.130	0.000	0.000
Larix occidentalis	LAROCC	-0.143	**-0.217**	0.000	0.000	0.136	**-0.235**
Leucanthemum vulgare	LEUVUL	0.021	0.055	-0.041	0.045	-0.049	-0.156
Linnaea borealis	LINBOR	**0.158**	**0.185**	-0.115	0.030	-0.139	0.131
Lomatium macrocarpum	LOMMAC	0.035	**-0.179**	-0.020	0.049	0.000	0.000
Lomatium triternatum	LOMTRI	-0.079	-0.091	-0.041	0.045	0.000	0.000
Lonicera involucrata	LONINV	0.021	0.055	0.072	0.007	0.000	0.000
Lotus corniculatus	LOTCOR	0.029	-0.037	0.000	0.000	-0.059	**-0.163**
Lupinus sp	LUPISP	0.011	-0.025	0.000	0.000	0.000	0.000
Luzula parviflora	LUZPAR	0.000	0.000	0.000	0.000	0.124	-0.012
Maianthemum stellatum	MAISTE	0.040	0.100	-0.038	0.032	-0.037	0.148
Microsteris sp	MICRSP	0.026	-0.133	0.000	0.000	0.000	0.000
Monotropa uniflora	MONUNI	0.000	0.000	0.000	0.000	-0.026	0.018
Orthilia secunda	ORTSEC	-0.040	0.134	-0.123	0.139	0.116	0.108
Osmorhiza sp	OSMOSP	0.049	0.099	-0.041	0.045	-0.017	0.064
Packera cana	PACCAN	0.020	-0.026	-0.003	0.060	0.093	-0.107
Pascopyrum smithii	PASSMI	0.000	0.000	0.026	0.024	0.000	0.000

Pedicularis sp	PEDISP	0.020	-0.026	-0.041	0.045	0.000	0.000
Penstemon albertinus	PENALB	0.026	-0.133	0.041	0.039	**0.226**	-0.051
Penstemon confertus	PENCON	0.056	-0.078	-0.090	**-0.180**	-0.105	**-0.249**
Penstemon procerus	PENPRO	-0.152	0.003	-0.079	-0.031	0.000	0.000
Penstemon sp	PENSSP	-0.107	0.015	-0.064	0.061	-0.039	-0.015
Penstemon wilcoxii	PENWIL	0.054	-0.091	0.047	0.051	0.000	0.000
Phalaris arundinacea	PHAARU	0.034	0.089	0.000	0.000	0.000	0.000
Pinus albicaulis	PINALB	0.000	0.000	0.000	0.000	-0.034	-0.049
Pinus contorta	PINCON	-0.156	-0.049	0.128	-0.012	**0.224**	-0.015
Pinus flexilis	PINFLE	0.000	0.000	-0.066	0.073	0.000	0.000
Pinus ponderosa	PINPON	0.044	**-0.187**	0.000	0.000	0.000	0.000
Plantago lanceolata	PLALAN	0.000	0.000	0.000	0.000	-0.017	0.064
Poa sp	POASP	0.062	-0.131	-0.036	0.068	-0.017	0.064
Populus angustifolia	POPANG	0.020	-0.026	0.000	0.000	-0.041	-0.115
Populus balsamifera	POPBAL	0.020	-0.026	-0.052	0.057	0.000	0.000
Populus tremuloides	POPTRE	**-0.215**	0.004	0.068	0.039	**0.233**	-0.047
Potentilla argentea	POTARG	-0.086	-0.034	0.000	0.000	0.000	0.000
Potentilla sp	POTESP	0.025	-0.111	-0.011	**-0.248**	-0.030	-0.082
Potentilla gracilis	POTGRA	0.000	0.000	-0.083	**-0.219**	0.000	0.000
Potentilla pennsylvanica	POTPEN	0.000	0.000	0.097	-0.021	0.000	0.000
Prosartes trachycarpa	PROTRA	0.050	0.062	-0.079	0.074	0.054	0.092
Pseudotsuga menziesii	PSEMEN	-0.125	0.040	-0.087	0.154	-0.003	0.022
Pyrola sp	PYROSP	0.000	0.000	-0.060	0.083	-0.023	0.086

Rhododendron albiflorum	RHOALB	0.000	0.000	0.072	-0.015	0.000	0.000
Ribes sp	RIBESP	0.002	-0.043	0.079	0.000	0.000	0.000
Rosa acicularis	ROSACI	0.061	-0.072	-0.122	-0.078	0.000	0.000
Rosa woodsii	ROSWOO	0.022	-0.078	-0.034	-0.139	**-0.145**	-0.010
Rubus idaeus	RUBIDA	-0.094	-0.022	-0.041	0.045	0.107	-0.081
Salix sp	SALISP	**-0.287**	-0.014	0.070	0.012	**0.315**	-0.010
Sambucus nigra	SAMNIG	0.000	0.000	0.000	0.000	-0.030	-0.082
Sambucus racemosa	SAMRAC	0.000	0.000	0.000	0.000	0.087	0.003
Sedum sp	SEDUSP	0.000	0.000	0.072	-0.015	0.000	0.000
Senecio integerrimus	SENINT	-0.152	0.003	0.069	0.031	0.000	0.000
Shepherdia canadensis	SHECAN	0.010	0.003	-0.043	0.041	-0.080	0.013
Solidago missouriensis	SOLMIS	-0.012	-0.031	0.075	0.073	-0.042	-0.117
Solidago multiradiata	SOLMUL	0.000	0.000	-0.041	0.045	0.000	0.000
Spiraea sp	SPIRSP	0.026	-0.133	0.000	0.000	0.000	0.000
Stipa sp	STIPSP	0.000	0.000	0.092	0.019	0.000	0.000
Streptopus amplexifolius	STRAMP	0.050	-0.023	-0.124	0.138	0.000	0.000
Symphoricarpos albus	SYMALB	0.128	0.054	-0.094	-0.072	**-0.175**	0.013
Symphyotrichum laeve	SYMLAE	0.027	-0.035	-0.076	-0.151	0.000	0.000
Thalictrum sp	THALSP	0.081	-0.019	-0.041	0.045	0.000	0.000
Thalictrum occidentale	THAOCC	-0.041	0.021	**-0.251**	-0.020	0.106	**0.199**
Thuja plicata	THUPLI	0.034	-0.010	0.000	0.000	0.067	-0.021
Tragopogon dubius	TRADUB	**-0.157**	0.014	0.050	**-0.156**	-0.052	**-0.173**
Trifolium sp	TRIFSP	0.000	0.000	0.000	0.000	-0.023	0.086

Trifolium pratense	TRIPRA	-0.017	-0.116	0.000	0.000	-0.017	0.064
Trisetum spicatum	TRISPI	0.038	-0.063	-0.041	0.045	0.000	0.000
Tsuga heterophylla	TSUHET	**-0.156**	0.036	0.000	0.000	-0.017	0.064
Urtica dioica	URTDIO	0.021	0.055	0.000	0.000	-0.030	-0.082
Vaccinium sp	VACCSP	0.027	-0.035	-0.070	-0.047	-0.045	-0.093
Valeriana sp	VALESP	0.021	0.055	-0.057	0.063	0.000	0.000
Veratrum viride	VERVIR	0.000	0.000	-0.041	0.045	-0.023	0.086
Vicia sp	VICISP	0.035	-0.114	0.072	-0.015	-0.030	0.040
Vicia villosa	VICVIL	0.000	0.000	0.000	0.000	-0.031	-0.133
Viola adunca	VIOADU	0.000	0.000	-0.076	-0.151	0.000	0.000
Viola sp	VIOLSP	0.022	0.126	**-0.144**	0.007	-0.083	**-0.171**
Xerophyllum tenax	XERTEN	-0.132	0.018	0.126	0.084	0.093	0.103

Appendix D – Between-class analyses of mule deer diet

Table D-1. Column normed scores and class normed scores of the two axes from a Hill-Smith (HS) between-class analysis (BCA) describing differences in mule deer diets based on forage plant species identified in fecal pellets. Fecal samples were collected in three study areas (Cabinet-Salish Mountains, Rocky Mountain Front, and Whitefish Range) during 2017–2019.

Group normed scores	**Axis 1**	**Axis 2**
CAB	1.196	-0.430
RMF	-1.192	-0.990
WHI	-0.330	1.408
Column normed scores		
Alnus spp.	0.265	-0.027
Chamerion	0.278	-0.134
Pinus spp.	-0.051	0.024
Salix spp.	0.173	0.153
Spiraea betulifolia	0.005	0.009
Fragaria spp.	-0.069	-0.233
Poa spp.	0.303	-0.041
Amelanchier alnifolia	0.061	0.158
Ribes spp.	0.288	-0.107
Bromus tectorum	-0.068	0.122
Oenothera spp.	-0.153	-0.249
Saxifragaceae spp.	0.157	-0.059
Rhododendron albiflorum	0.223	-0.083

Plantago spp.	-0.254	0.096
Pseudotsuga menziesii	0.104	0.062
Berberis spp.	0.266	-0.099
Medicago spp.	0.081	0.144
Hedysarum spp.	-0.245	-0.211
Lactuca spp.	-0.256	-0.221
Eriogonum umbellatum	-0.247	-0.212
Sambucus spp.	-0.236	0.259
Ratibida columnifera	-0.238	-0.205
Phleum spp.	-0.162	0.034
Sphaeralcea coccinea	-0.184	-0.158
Vaccinium spp.	-0.054	0.237
Linum spp.	-0.064	0.283
Triticum aestivum	-0.090	0.397
Papaveraceae spp.	-0.059	0.261
Lonicera spp.	-0.056	0.249
Elymus spp.	-0.043	0.190