ELK BROWSING INTENSITY IMPACTS ASPEN RECRUITMENT ON MULTIPLE USE LANDSCAPE OVER THREE DECADES

by

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ABSTRACT

Quaking aspen (*Populus tremuloides*) stands are vital to ecosystem health, providing wildlife habitat, water and carbon sequestration, and natural fuel breaks. Aspen stands occupy approximately 1.4% of the Greater Yellowstone Ecosystem, which includes the Northern Yellowstone Winter Range, an important ungulate wintering area. Historically, aspen stands occupied approximately 4-6% of the Northern Yellowstone Winter Range. In 1994, the Northern Yellowstone Winter Range elk population peaked at ~19,000 individuals and aspen coverage on the Northern Yellowstone Winter Range declined to 1% due to overbrowsing by elk. As of 2024, the elk population has decreased 71% since its peak, and 85% of the elk herd now migrates north of Yellowstone National Park (YNP) on the Custer Gallatin National Forest (CGNF) in the winter. Because new stems are vulnerable to ungulate browsing, stand sustainability depends on larger stems that are more resistant to herbivory. Assessing the health of Greater Yellowstone Ecosystem aspen therefore requires monitoring stand size structure. The goal of this study was to prioritize aspen management on the CGNF to sustain aspen stands long-term based on outcomes of repeated measurements of over 300 aspen plots on the CGNF north of YNP that were established in 1990. Previous studies concluded that aspen recruitment was increasing on a local scale in a few surveyed drainages, but was not increasing on a landscape scale. It was hypothesized that more time may be needed for aspen recruitment to increase in response to the decline in elk. Even though overall elk density has declined, elk density, and thus browsing pressure, has increased on the border of YNP due to the Northern Yellowstone Winter Range elk migration shift. I found that aspen stem recruitment is now increasing on a landscape scale, with a 90% increase since 2006, and that 59% of stands are considered sustainable long-term. Stems that have outgrown the upper browse height of elk (2 m) increased the most in aspen stands farther from YNP, at lower browsing pressure, and with greater snow water equivalent. Using this information, I prioritized aspen stands that would benefit from Forest Service management to ensure long-term aspen presence on the CGNF. This study is consistent with the hypothesis that aspen stand recruitment is responsive to shifts in browsing pressure at a local and landscape level, as well as other aspen recruitment studies within YNP that found that elk overbrowsing due to increased elk density, led to aspen decline on the Northern Yellowstone Winter Range. An elk density of 3 elk/km^2 may be the threshold on the border of YNP for aspen recruitment to increase. If elk density rebounds to historic levels, this may result in a reversal of aspen recruitment in the future.

CHAPTER ONE

INTRODUCTION

Quaking aspen (*Populus tremuloides*, hereafter 'aspen') is a clonal deciduous tree species found in all of the 48 lower US states, Canada and Alaska. Aspen mainly regenerates by root sprouting, which produces genetically identical trees from a common root system that may be substantially older than the age of the oldest tree in the stand (DeByle and Winokur 1985). The clone itself may be hundreds or even thousands of years old. It is uncommon for aspen to reproduce through seed; however, seed recruitment does occur on bare soil recently affected by fire (Romme et al. 1995). In Montana and Wyoming, aspen is one of the few upland deciduous tree species in the Greater Yellowstone Ecosystem, occupying only ~1.4% of the landscape (Brown et al. 2006). Aspen stands are vital to ecosystem health, providing forage, wildlife habitat, natural fuel breaks, water and carbon sequestration, and other ecosystem services. Fire suppression, climate change induced droughts, conifer encroachment, and ungulate overbrowsing have been theorized to threaten the future of aspen in this geographic area (Despain et al. 1986, McCullough et al. 2013, Seager et al. 2013, Bell et al. 2014, Wan et al. 2014, Krasnow and Stephens 2015).

Aspen grows in discrete stands on mid-elevation benches, near streams, and along conifer forest/shrub steppe ecotones (Houston 1982). It requires moist soils and occurs mostly in areas with ≥ 38 cm of annual precipitation (Jones and DeByle 1985). Stable stands can provide a fuel break for wildfires due to their high moisture content (Kuhn et al. 2011, Krasnow and Stephens

2015, Carter et al. 2017) and can sequester water and carbon (Woldeselassie et al. 2012, Boča et al. 2020). Although aspen is a minor cover type in the arid portions of its range, it is considered a biodiversity hotspot, providing forage and habitat for a variety of plants and wildlife including migratory birds, small mammals, upland game birds, and megafauna such as bears and ungulates (DeByle 1985, Mueggler 1988). Many ungulate species such as Rocky Mountain elk (*Cervus canadensis*), moose (*Alces alces*), bison (*Bison bison*), cattle (*Bos taurus*), and deer (*Odocoileus spp*.) browse aspen suckers seasonally. During winter, ungulate diets include high amounts of aspen because regenerating aspen suckers are highly palatable, nutritional, and accessible above the snow (Kimble et al. 2011b, Rhodes et al. 2018, Reikowski et al. 2022). Light to moderate browsing encourages recruitment through increased sprouting, but recruitment can be depressed through overbrowsing when several herbivores compete for the same forage material, yielding limited opportunity for stands to recruit new stems (Rhodes 2017, Reikowski et al. 2022). Effects of browsing on aspen stand recruitment increase with ungulate population density (Endress et al. 2012, Brice et al. 2024) and are a contributing factor to aspen decline in the winter season (Kimble et al. 2011a).

The Northern Yellowstone Winter Range, hereafter ‘northern range’, is the wintering ground for the largest elk herd in the Greater Yellowstone Ecosystem. The northern range consists of the Lamar, Gardner, and Yellowstone River drainages within Yellowstone National Park (YNP) and continues north of the park into the Custer Gallatin National Forest (CGNF). Historically, aspen stands occupied approximately 4-6% of the northern range (Wagner 2006). Aspen stands on the northern range are an important resource for elk in the winter when they migrate out of the park to lower elevations in the Gardiner Basin. In 1994, the northern range elk population peaked at approximately 19,000 minimum winter counted elk and aspen coverage on the northern range decreased to 1% due to overbrowsing (Romme et al. 1995, Wagner 2006). During this time, browsing rates averaged 88% (Painter et al. 2014) and the average height of aspen stems on Yellowstone's portion of the northern range was consistently kept below 75 cm by wintering elk (Kay 1992, Barmore 2003). Even though aspen stands continued to produce new sprouts, repeated elk browsing inhibited regeneration by preventing young stems from growing to replace those dying of old age or disease (Kay 1992, Romme et al. 1995, White et al. 1998, Council et al. 2002, Barmore 2003). Such evidence links aspen decline on the northern range with browsing of suckers by wintering elk (Council et al. 2002).

Following the population peak in 1994, total winter minimum elk counts on the northern range decreased 71% to 5,597 counted individuals as of 2024 (Yarnall 2024) (Figure 1 and Table A1). During the same period, the elk distribution changed drastically with over 85% of the northern range elk herd migrating north of the park on the CGNF in Montana Fish, Wildlife, and Parks Hunting District (HD) 313 during winter (Yarnall 2024) (Figure 1 and Table A1). This distribution shift began in 2013, with over 75% of elk migrating north of YNP, and could have been due to a number of reasons, including increased competition with bison, less hunting pressure outside the park, availability of irrigated hayfields north of the park, or increased predation inside the park boundary (Proffitt et al. 2009, White et al. 2012, Smith et al. 2023, Brice et al. 2024, Painter et al. 2025). Browsing rates on aspen inside the park decreased to about 30-60% annually (Painter et al. 2014), and the average height of young aspen exceeded one meter (Ripple and Beschta 2012). Increased aspen height was linked to reduced browsing intensity, which was associated with decreased elk density (Ripple and Beschta 2007, 2012, Kauffman et al. 2010, Peterson et al. 2014, Painter et al. 2018, Peterson et al. 2020, Brice et al. 2024, Painter et al. 2025).

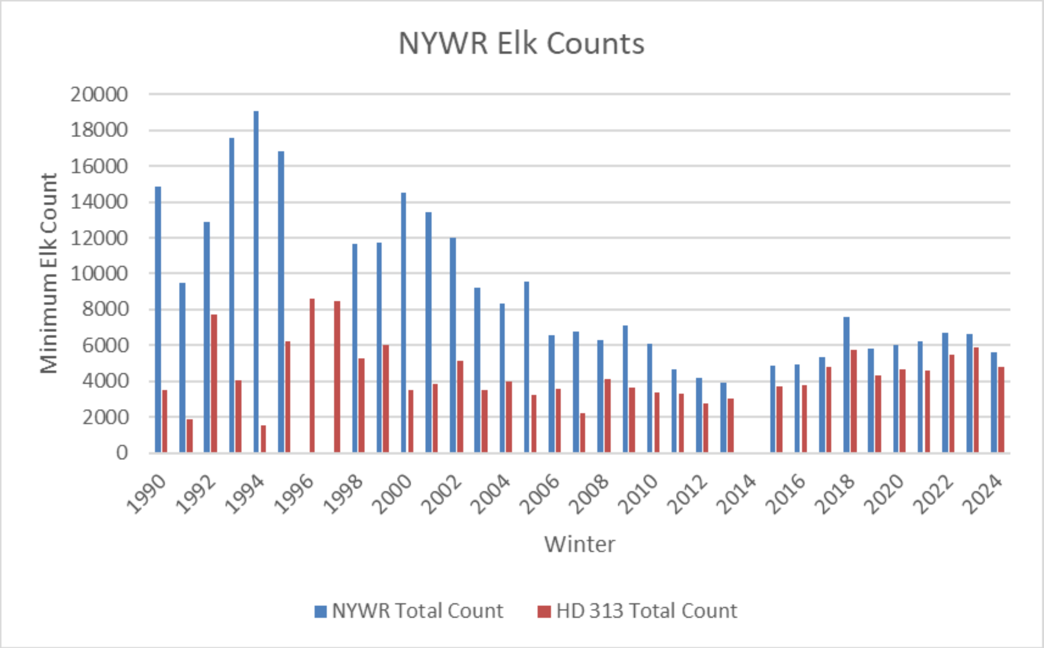

Figure 1. Northern Yellowstone Winter Range (NYWR) winter minimum elk counts (blue), including Montana Fish, Wildlife, and Parks Hunting District 313, and winter minimum elk counts of elk that migrated north of Yellowstone National Park in Hunting District 313 (red) in winter from 1990 to 2024. Fixed-wing flight classification surveys were completed by the Northern Yellowstone Cooperative Wildlife Working Group from December to March.

Elk are not the only ungulates that affect aspen regeneration. Bison pose a threat to aspen recruitment on the northern range due to browsing and trampling (Painter and Ripple 2012, Rose and Cooper 2017). While elk density has decreased on the northern range over the last two decades, bison numbers in the YNP northern bison herd have increased, and bison are now the dominant wintering ungulate on the northern range within YNP (Tallian et al. 2017, Ripple et al. 2010, Beschta et al. 2020, Painter et al. 2023). Historically, bison migrated seasonally over large areas, whereas today they are confined by political and physical boundaries. Even though bison can have a negative impact on aspen, they are predominantly grazers and only occasionally migrate out of the park into CGNF when snowpack levels are high. Cattle can also prevent regeneration or exacerbate wildlife impacts (Kay and Bartos 2000, Kilpatrick et al. 2003). They have a similar effect on aspen as elk and bison, but cattle will primarily feed on aspen stems in the late growing season (late August–mid September). Wild ungulates mainly feed on aspen in the winter, compounding impacts from cattle use earlier in the year (DeByle and Winokur 1985). Even though livestock can impact aspen stands, elk have been found to be the most prevalent ungulate species on the northern range that browse aspen (Houston 1982, Council et al. 2002).

In addition to ungulate impacts, future warming and drying of aspen forests may result in conversion to coniferous forest (Bell et al. 2014) due to shading and crowding by encroaching conifers (McCullough et al. 2013), which can outcompete aspen, especially under drier conditions. Conversion of aspen stands to coniferous forest can lead to a decrease in understory plant diversity, as well as influence soil temperature, moisture retention, and seed germination (McCullough et al. 2013, Krasnow and Stephens 2015).

Aspen Monitoring in the Custer Gallatin National Forest

To inform the discussion on the relationship between ungulate browsing and aspen recruitment, St. John (1995) established an expansive aspen recruitment survey of 342 aspen plots in the CGNF, north of YNP in 1990 and 1991. The CGNF study area contains livestock allotments meaning aspen stems in the region face domestic and wild browsing pressures throughout the year. St. John measured all live aspen stems and ungulate impacts within each aspen plot and considered stems to have recruited successfully to adulthood when they reached two meters in height. Browsing by elk decreases rapidly with stem height above two meters (Kay

1985 and Beschta et al. 2023), and this threshold has functioned well as an indicator of likely recruitment success (Painter et al. 2025). To determine if aspen stands were sustainable, St. John (1995) used Kay's (1985) criterion for stand sustainability. Aspen stands where the number of recruitment stems (≥ 2 m tall and < 5 cm diameter at breast height [DBH]; see also Table 1, below) equals or exceeds the number of non-recruitment stems (≥ 2 m tall and > 5 cm DBH) are theoretically stable or increasing in density (Kay 1985). He found that 47% of the surveyed aspen stands had recently grown at least one stem above elk-browsing height (2 m), but that only 21% of the stands had the requisite 50% or more recruitment stems escaping browsing for the overstories to remain stable or increase in density. Aspen stands with high ungulate impacts had a significantly lower proportion of stems within the recruitment stage structure than stands with low ungulate impacts, 10% and 30% respectively (St. John 1995). Using these metrics, St. John (1995) suggested that browsing by elk and cattle was a major factor preventing recruitment of new stems into the aspen overstory.

To test if a reduction in cattle and elk densities resulted in an increase of aspen recruitment, Kimble et al. (2011b) repeated St. John's (1995) aspen recruitment survey (n = 316 aspen plots) approximately 15 years later (2005–2006). Ungulate impacts and all live aspen stems within each plot were measured. The study area established by St. John (1995) encompassed two elk herds; the portion of the NYWR elk herd that migrates into HD 313, and the Upper Yellowstone West elk herd in Tom Miner basin (HD 314), both of which experienced a decline from 1990 to 2006. Over the 16 years between 1990 and 2006, cattle grazing use declined 38% and the number of Forest Service allotments dropped by 46%. Kimble et al. (2011b) compared cattle grazing impacts on aspen recruitment on CGNF allotments between

1991 and 2006. They found that aspen stem recruitment did not increase in 54% of stands where cattle were removed, indicating that cattle browsing may have had a minor impact on aspen recruitment stems and that elk were the primary ungulate contributing to aspen stem recruitment decline.

Kimble et al. (2011b) assessed conifer encroachment in the study area by classifying stands with conifer encroachment (≥ 10% reproducing conifer canopy cover) and without. They found that sapling, recruitment, and overstory stems were approximately two times greater in stands without conifer encroachment (Kimble et al. 2011b). They reported that 65% of the aspen stands were classified as having medium to high browsing levels in 2006, compared to 80% in 1991, possibly due to the reduced northern range elk population. However, recruitment stem count did not change from 1991 to 2006, and overstory stems (≥ 2 m) declined 12% from 1991 to 2006. They found that aspen recruitment was not increasing on a landscape scale, although it did increase on a local scale in eight of 21 surveyed drainages. They concluded that winter ungulate browsing and conifer encroachment contributed to the decline in overstory stems. In addition to Kay's (1985) criterion, Kimble et al. (2011b) established another measure of individual stand sustainability in which the total number of live aspen stems that have grown above elk-browsing height (2 m) must remain stable or increase over time. By this criterion, they concluded that 63% of the surveyed aspen stands were losing overstory stems more quickly than they were being replaced and therefore were not sustainable. Kimble et al. (2011b) theorized that more time may be needed post-elk population decline for aspen recruitment to increase on a local and landscape level.

Research Objectives

The goal of this study was to prioritize aspen management on the CGNF to sustain aspen stands long-term. This goal was achieved by addressing the following objectives:

1) How aspen stand structure has changed since 2006, and which stands are more vulnerable to threats such as ungulate browsing and conifer encroachment.
2) How aspen stem recruitment and overstory stems have changed since 1991 and 2006, and which factors are influencing this change.
3) Which aspen stands should be prioritized for Forest Service management to improve aspen stand sustainability.

Study Justification

Decades of research have shown that aspen recruitment has increased as ungulate browsing has decreased within YNP (Ripple and Beschta 2007, 2012, Painter et al. 2018, Peterson et al. 2020, Brice et al. 2024, Painter et al. 2025). The long-term monitoring study presented here observes aspen recruitment over 34 years on a landscape scale level outside YNP on actively managed Forest Service lands. This study will provide valuable insight on aspen stand structure over time and how long-term management changes must be in place to attain desired levels of stand recruitment. Long-term data such as these are integral in understanding the cause and effect of ecosystem interactions and will provide context for landscape level management on the CGNF.

CHAPTER TWO

METHODS

Study Area

This study examines over 300 aspen plots established in 1990 and 1991 (St. John 1995) and resampled in 2005 and 2006 (Kimble et al. 2011b). These plots are located in south-central Montana on the CGNF, bordering YNP to the south and the Absaroka-Beartooth Wilderness area to the east (Figure 2). The study area is approximately 560 km^2, and ranges in elevation from 1,571 m to 2,605 m. Vegetation consists of big sagebrush (*Artemisia tridentata*) and grasses (e.g., *Pseudoroegnaria spicata; Festuca idahoensis*) at lower elevations, aspen at forest-grassland boundaries and in riparian areas, Douglas-fir (*Pseudotsuga menziesii*) at mid-elevations, and lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*) at higher elevations (Despain et al. 1986). Aspen stands occupy approximately 7 km^2 of the 560 km^2 study area (St. John 1995). The average (1990–2023) annual precipitation is 537.19 mm and the temperature ranges from –36.61 °C to 34.64 °C with an average of 4.42 °C.

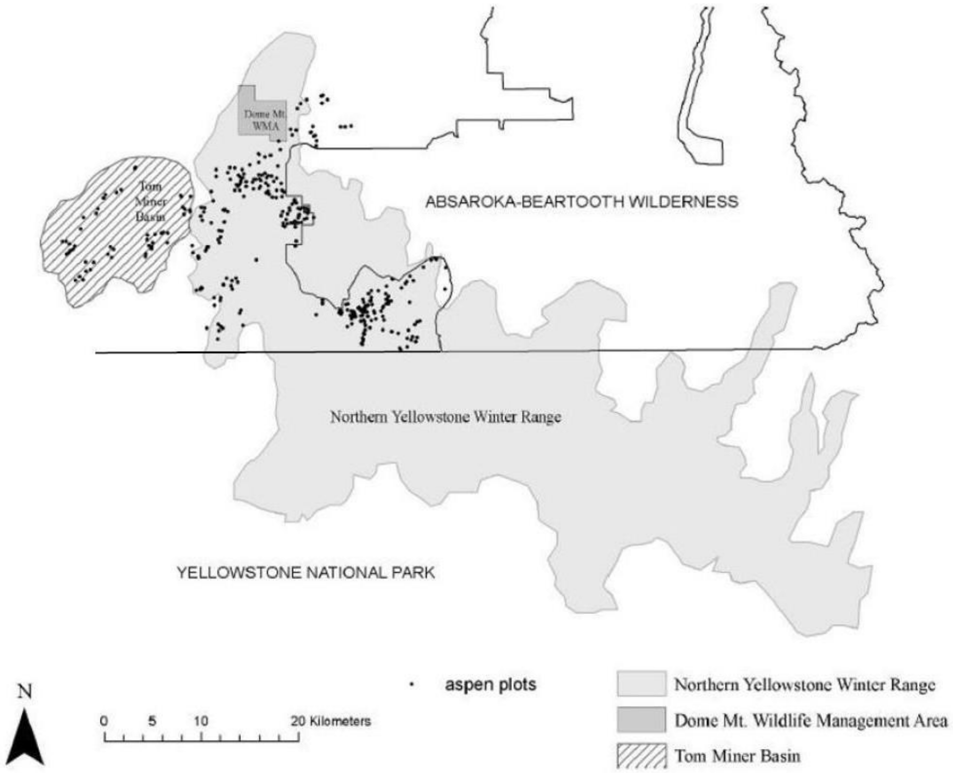

Figure 2. Aspen plot (*n* = 302) locations on the Custer Gallatin National Forest, Montana, north of Yellowstone National Park.

Kimble et al. (2011b) divided the study area into three geographic regions where elk migration patterns, population trends, and cattle grazing differ: the East River, West River, and Tom Miner subunits (Figure 3) to best answer the question of ungulate impacts on aspen stem recruitment. Subunits were identified to encompass Montana Fish, Wildlife, and Parks Hunting Districts and to provide landscape level management areas for the Forest Service. The Tom Miner subunit (*n* = 48 aspen plots) is the smallest at approximately 100 km^2 and consists primarily of private land, checkerboarded with public land (Figure 3). It has three active Forest Service cattle allotments as of 2024. The Tom Miner subunit is the only subunit outside the northern range, located in HD 314, and the Upper Yellowstone West elk herd migrates there in the winter. The East and West River subunits are located in HD 313 and the northern range elk herd migrates there in the winter. The East River (*n* = 207 aspen plots) subunit is located east of the Yellowstone River, and is the largest subunit, at approximately 340 km^2 (Figure 3). The majority of East River is public land and extends from the park boundary north to the Dome Mountain Wildlife Management Area. The East River subunit contains two active Forest Service cattle grazing allotments. West River (*n* = 47 aspen plots) lies on the west side of the Yellowstone River and is approximately 120 km^2 (Figure 3). West River has one active Forest Service cattle grazing allotment.

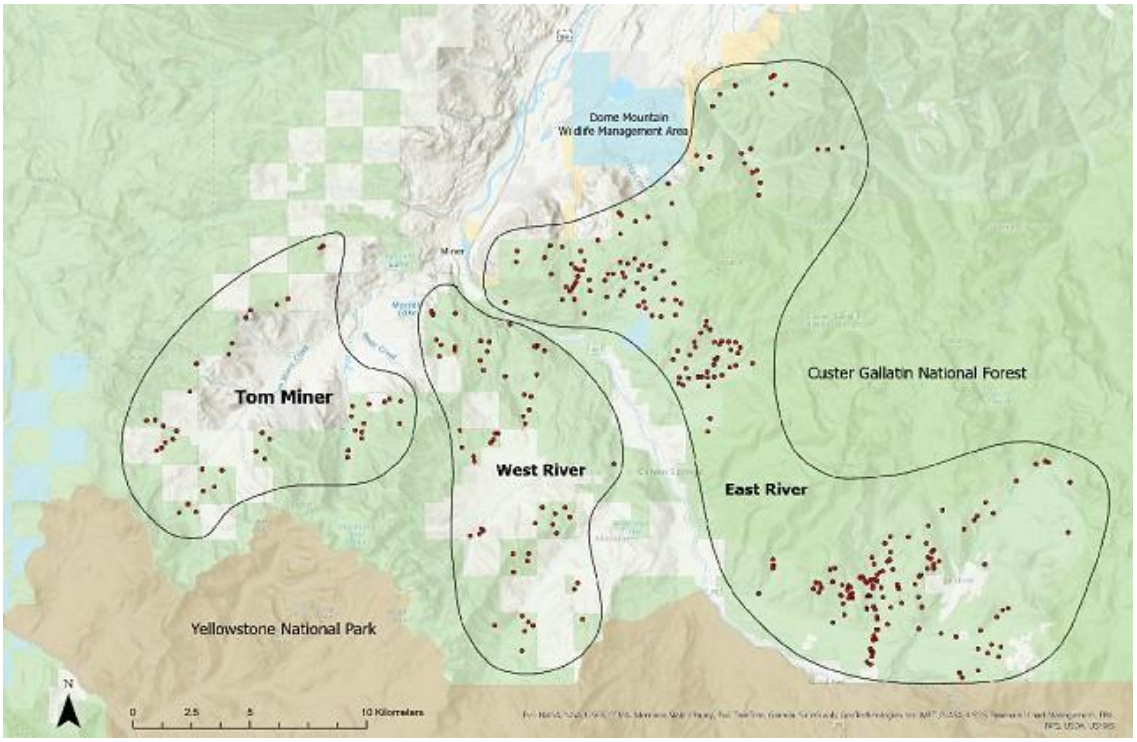

Figure 3. Study area subunits (Tom Miner, West River, and East River) on the Custer Gallatin National Forest, Montana. Subunits include both private and Forest Service land.

There are other ungulate species, besides elk, that occupy the study area that potentially browse or trample aspen. Bison have been shown to have a negative impact on aspen recruitment, but only a small portion (< 10%) of the YNP northern herd migrates out of the park into the West and East River subunits during years of high snowpack, therefore their impact to aspen recruitment within the study area would be minimal (Geremia et al. 2011). Mule deer, white-tailed deer, and moose inhabit the study area and will browse aspen. However, the impact of deer on aspen is minor, since they typically winter below elevations where aspen grow and consume less forage than elk (Houston 1982, DeByle 1985). Moose consume large quantities of forage and winter at elevations where aspen grows, however, moose impact to aspen stands would be minimal, considering it is estimated there are fewer than 200 moose in the entire northern range, and hardly any in the Gardiner Basin (Koitzsch et al. 2022). Even though there are active livestock allotments within the study area, cattle browsing and trampling were found to have a minor impact on aspen recruitment stems and it was theorized that elk are the primary ungulate contributing to aspen recruitment decline on the northern range (Kimble et al. 2011b).

Data Collection

Aspen recruitment data were derived from a repeated survey established by St. John (1995) 1990–1991 (*n* = 342 aspen plots) and resampled by Kimble et al. (2011b) 2005–2006 (*n* = 316 aspen plots). In this study I revisited 302 of the original 342 aspen plots. The number of stands surveyed during each period has decreased over the years due to inaccessibility, fire and beaver damage, and problems relocating some stands. Aspen communities were originally selected on 1:15,840 aerial photos, and portioned by mainstream drainages. Within each drainage, every fourth aspen stand was sampled (St. John 1995). Stands were first located using Universal Transverse Mercator (UTM) coordinates in NAD27 datum with a Geographic Positioning System (GPS) unit (Kimble et al. 2011b). Exact aspen plot stake locations were relocated by: 1) comparison to reference photographs; and 2) comparison to site descriptions including slope, aspect, species of vegetation, and number of mature aspen stems in the plot.

Survey plots were marked with a stake centered on a 202.3 m^2 circular plot, subdivided into four quadrants. Plot longitude, latitude, slope, aspect, elevation, conifer encroachment (≥ 10% canopy cover of reproducing conifers), and active cattle allotments were recorded using ArcGIS Online's *Survey 123* (version 3.19.120) platform. Stem height and diameter at breast height (DBH) of all live aspen stems within the plot were measured and categorized as sprouts (≥ 1 m tall), saplings (1–2 m tall), recruitment (≥ 2 m tall and < 5 cm DBH), non-recruitment (≥ 2 m tall and > 5 cm DBH), or mature (≥ 2 m tall and >10 cm DBH).

To quantify ungulate impacts, the presence or absence of browsing on aspen suckers (sprouts and saplings) were recorded in each plot. Browsing levels were then categorized as having 'very low' (< 10% of suckers browsed), 'low' (10–49% of suckers browsed), 'medium' (50–81% of suckers browsed), or 'high' impacts (> 81% of suckers browsed) (Kimble et al. 2011a). St. John's (1995) ungulate impact methods were not included in this analysis, and therefore browsing impacts are only compared between 2006 and 2024. An aspen stem was considered 'browsed' if its growth from the previous growing season had been eaten, which I identified by a sharp, pruned edge at the base of the current year's growth.

Data Analysis

The first objective of this study is to determine how aspen stand structure has changed since 2006, and which stands are more vulnerable to threats such as conifer encroachment and ungulate browsing. This comparison between 2006 and 2024 included more data than the comparison between 1991, 2006, and 2024, because in 2006 Kimble et al. (2011b) measured additional aspen stage structures (Table 1), conifer encroachment, and browse level to the measurements recorded by St. John (1995). The second objective of this study is to determine how aspen recruitment and overstory stem counts have changed in 34 years, and which factors are influencing this change. Since St. John (1995) only analyzed recruitment (≥ 2 m tall and < 5 cm DBH) and non-recruitment (≥ 2 m tall and > 5 cm DBH), those will be the only two stage structures included in the comparison of 1991, 2006, and 2024 data (Table 1). Aspen stems ≥ 2 m tall (recruitment, non-recruitment, and mature) are referred to as overstory stems to remain consistent with St. John (1995) and Kimble et al. (2011b).

Table 1. Aspen stage structure stem height and diameter at breast height (DBH) data collected by St. John 1995 (1990–1991), Kimble et al. 2011 (2005–2006), and this study (2023–2024). Recruitment non-recruitment, and mature stage structures are considered overstory stems (≥ 2 m).

Stage Category	Sprout	Sapling	Recruitment	Non-recruitment	Mature	Num. Stands
Height	< 1 m	1–2 m	≥ 2m	≥ 2m	≥ 2m	
DBH	any	any	5–10 cm	> 5 cm	> 10 cm	
St. John (1990, 1991)	No	No	Yes	Yes	No	342
Kimble (2005, 2006)	Yes	Yes	Yes	Yes	Yes	316
Keller (2023, 2024)	Yes	Yes	Yes	Yes	Yes	302

Minimum annual winter elk counts were divided by each subunit to calculate elk density within the study area (number of individuals per km^2). The Northern Yellowstone Cooperative Wildlife Working Group completes annual interagency fixed-wing flight classification surveys to count the northern range elk population in winter (December–March). Flight surveys are divided into elk count units and are a conservative, minimum representation of elk numbers (Figure 4).

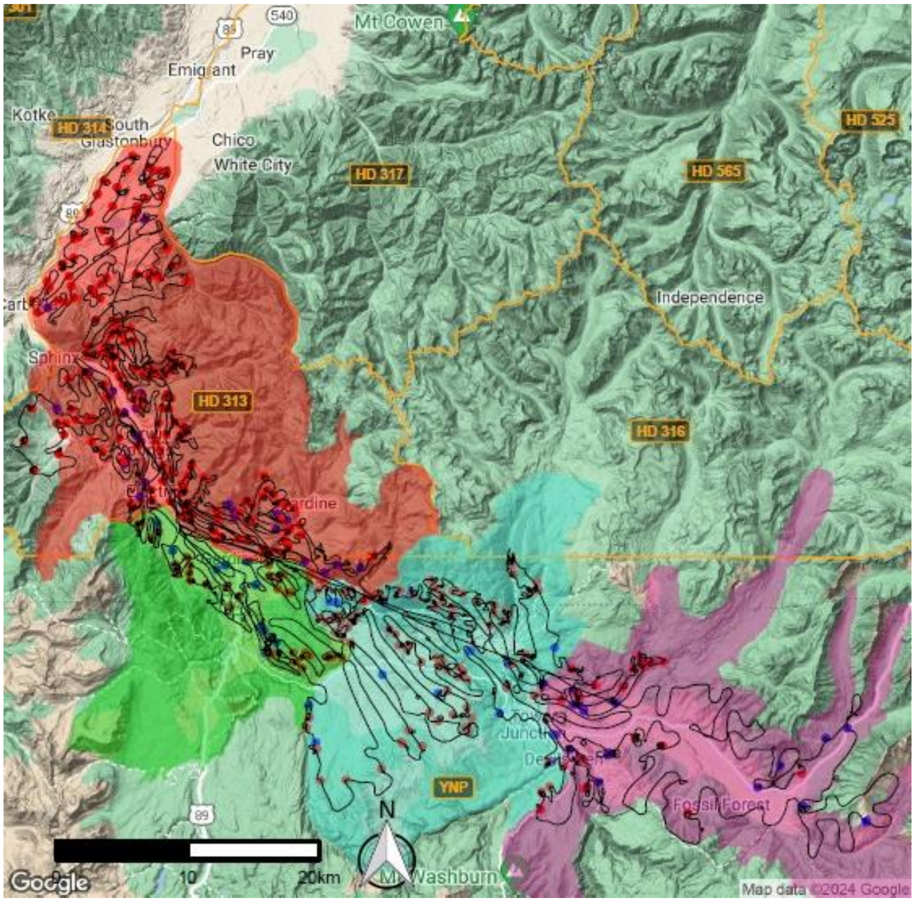

Figure 4. Northern Yellowstone Cooperative Wildlife Working Group winter fixed-wing flight paths and locations of elk groups (red) and incidental observations for other species (blue) during the 2024 classification survey of the Northern Yellowstone Winter Range. Shaded polygons indicate the elevation sectors used to group elk locations: low elevation outside YNP (HD 313, red shading), low elevation inside YNP (green shading), middle elevations (blue shading), and upper elevations (purple shading). Figure is adapted from Yarnall 2024.

Browse level and distance (m) to the nearest border of YNP were used as surrogates for elk density and changes in elk migration within our models. Distance to YNP was collected using ArcGIS Pro's (version 3.3.1) Near (Analysis) Geoprocessing tool. Snow water equivalent (SWE) integrates snowpack depth and density to estimate accumulated snowpack and has been shown to be a primary driver of winter movement and behavior of elk (Proffitt et al. 2011, Brice et al. 2024). Since aspen is a highly drought-sensitive species, spring precipitation is an important driver of aspen growth (Rhodes et al. 2017). These data were acquired via the NASA Daily Surface Weather and Climatological Summaries (DAYMET) at a spatial resolution of 1 km^2 (Thornton et al. 2022). I calculated an aggregated sum of daily precipitation (mm) and SWE (kg/m^2) per year (1990–2024) based on the georeferenced coordinates of each stand. I quantified the spring growing season for aspen as April 1st to July 31st and winter as November 1st to April 30th to encompass the period when ungulates would be browsing aspen (Proffitt et al. 2011, Brice et al. 2024). To account for interannual variability I averaged winter SWE and spring precipitation 10 years prior to each period of interest (1980–1990, 1996–2005, 2013–2023).

To determine how 2006 conditions influenced 2024 stage structure, I created models with 2006 stage structure as predictors and the 2024 number of stems in a given stage structure (sapling, recruitment, or mature) as the response variable. Models were fit as generalized linear models with a Poisson distribution and canonical link function. The 2006 and 2024 data sets included additional stage structures (sprouts, saplings, and mature) (Table 1) that were not measured in 1991; and additional covariates such as conifer encroachment (≥ 10% reproducing conifer canopy cover) and browse level ('very low', 'low', 'medium', and 'high'). In these models, predictors included subunit, distance to YNP, 2006 SWE, 2006 browse level, 2006 conifer encroachment; and 2006 saplings plus sprouts, 2006 recruitment stems, and 2006 mature stems. I included an interaction between browse level and every numeric predictor. Sapling and sprout counts were summed because separately these were multicollinear with other predictors, but these problems were solved when they were summed together. Response variables were the log-transformed counts of 2024 mature, recruitment and sapling stems. I tested planned contrasts of marginal effects of distance to park, SWE, and subunit, all within browse level. Additional tests of effects of previous stage class on current stage class were conducted *post hoc*. A Pearson's χ^2 test was used to compare the difference in number of stands in each browse level for 2006 and 2024.

To determine what factors affected stage structure changes over the 34-year survey period, I fit linear mixed effect models of the effects of landscape and climatic variables on the proportion of stems in the recruitment category in each survey year. Covariates included aspect, subunit (Tom Miner, West River, East River), distance to nearest border of YNP, SWE, elevation, springtime average annual precipitation, and recruitment and non-recruitment aspen stage structures. Year was a fixed predictor and aspen plot (n = 302) was a random effect variable in each model. I included interactions between year and every numeric predictor. The response variable was the arcsine-square root transformed relative proportion of recruitment stems (out of the total number of recruitment and non-recruitment stems, *per* Table 1). To test predictor effects on the response variables, I completed planned contrasts of estimated marginal effects of aspen stage structure, aspect, distance to YNP, subunit, SWE, precipitation, elevation, conifer encroachment, and browse level between years.

Prior to all analysis, I centered and scaled all numeric explanatory variables (mean = 0, s.d. = 1). For each response variable in each comparison, I used AIC-based model selection to choose the model with the highest information quality among all possible candidate models with any combination of predictors in the full model, except that I excluded combinations of variables that were highly correlated ($r > 0.6$) to one another (Figure A1). Assumptions of linearity and normality of variables were evaluated by observing plots of the model standard residuals for the general linear models. All statistical analyses were completed in R version 4.2.3 (R Core Team, 2023).

CHAPTER THREE

RESULTS

Elk Density

The Upper Yellowstone West elk herd (Rock Creek to Tom Miner Basin count unit; HD 314) 9-year average (1990–1999) minimum winter elk count decreased from 787 individuals to a 6-year average of 519 individuals (2000–2006), to an 11-year average of 210 (2013–2024) individuals (Figure 5 and Table A1). This resulted in a decreased elk density in the Tom Miner subunit over time from an average 8 elk/km^2 (1989–1999) to 5 elk/km^2 (2000–2006) to 2 elk/km^2 (2013–2024). The northern range elk herd migrates through the East and West River subunits, but ~60% (2013–2024) of the herd winters north of Dome Mountain, outside the study area (Yarnall 2024). Even though these elk are transient through our study area, average minimum winter elk counts were adjusted to remove the portion of elk that migrate north of Dome Mountain. The HD 313 10-year average (1989–1999) elk winter minimum count decreased from 2,748 individuals to a 6-year average of 1,336 individuals (2000–2006). The 11-year average (2013–2024) winter minimum count increased to 1,850 due to the shift in the northern range elk distribution (Figure 5 and Table A1). Thus, average elk density in the East and West River subunits decreased from 6 elk/km^2 (1989–1999) to 3 elk/km2 (2000–2006) but has since increased to 4 elk/km^2 (2013–2024).

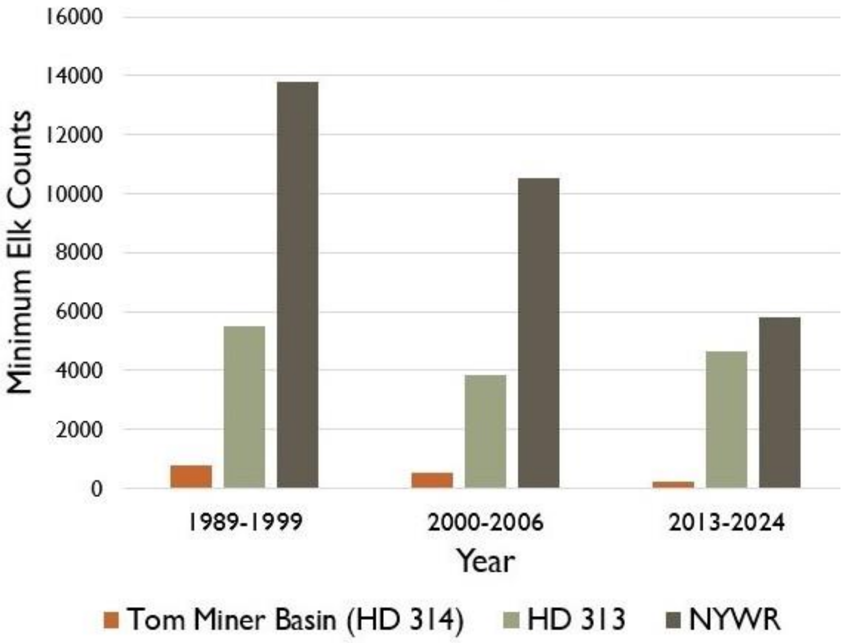

Figure 5. Average minimum winter counted elk by count unit and year (1989–1999, 2000–2006, and 2013–2024). Orange is Rock Creek to Tom Miner Basin (Hunting District 314), which encompasses the Tom Miner subunit. Green is the northern portion of the Northern Yellowstone Winter Range (NYWR) in Hunting District 313 (adjusted to remove elk counts north of Dome Mountain), which encompasses the West and East River subunits. Brown is the entire Northern Yellowstone Winter Range including Hunting District 313 and the portion in Yellowstone National Park. Fixed-wing flight classification surveys were completed by the Northern Yellowstone Cooperative Wildlife Working Group from December to March.

Browse Level

Browsed aspen stands in the study area experienced a decline in every browse level except for ‘high’ browsing pressure, which had a 40% increase from 2006 to 2024 (Table 2). The percentage of browsed aspen stands in the ‘very low’, ‘low’, and ‘medium’ categories decreased from 2006 to 2024, 1%, 20%, and 19% respectively (Table 2).

Table 2. Number and percentage of aspen stands (n =302) with winter browsing impacts categorized as ‘very low’ (< 10% suckers [sprouts and saplings] browsed), ‘low’ (10–49% suckers browsed), ‘medium’ (50–81% suckers browsed), and ‘high’ (> 81% suckers browsed) in 2006 and 2024.

	Very Low	Low	Medium	High
Number of aspen stands – 2006	30	85	114	73
Percentage browsed	10%	28%	38%	24%
Number of aspen stands – 2024	27	24	58	192
Percentage browsed	9%	8%	19%	64%

[1] Distributions differ based on Pearson’s χ^2 test ($p < 0.0001$).

Browsed aspen stands in the East River, Tom Miner, and West River subunits had a decline in every browse level except for ‘high’ browsing pressure. The East River subunit had a 79% increase in ‘high’ browsing pressure, while the Tom Miner subunit had a 145% increase, and the West River subunit had a 99% increase from 2006 to 2024 (Table 3). Collectively, the East and West River subunits had a 178% increase in ‘high’ browse from 2006 to 2024 (Table 3).

Table 3. Number and percentage of aspen stands in the East River subunit (n =207), Tom Miner (n = 48), and West River (n = 47) subunits with winter browsing impacts categorized as ‘very low’ (< 10% suckers [sprouts and saplings] browsed), ‘low’ (10–49% suckers browsed), ‘medium’ (50–81% suckers browsed), and ‘high’ (> 81% suckers browsed) in 2006 and 2024.

	East River $n = 207$	Tom Miner $n = 48$	West River $n = 47$
Number of aspen stands - 2006			
Very Low	20 (10%)	5 (10%)	4 (9%)
Low	61 (29%)	15 (31%)	9 (19%)
Medium	66 (32%)	24 (50%)	24 (51%)
High	60 (29%)	4 (8%)	10 (21%)
Number of aspen stands - 2024			
Very Low	19 (9%)	5 (10%)	4 (9%)
Low	16 (8%)	6 (13%)	2 (4%)
Medium	33 (16%)	13 (27%)	12 (25%)
High	139 (67%)	24 (50%)	29 (62%)

Comparison between 2006 and 2024

The highest-ranking ‘count’ sapling model with 2024 sapling aspen counts as the response variable included the following predictors: 2006 mature, recruitment, and sapling/sprout aspen counts; 2006 browse level; 2006 conifer encroachment; subunit; distance to YNP; 2006 SWE; and interactions between 2006 browse level and 2006 recruitment, sapling/sprout, mature aspen stem counts, 2006 conifer encroachment, subunit, distance to YNP, and 2006 SWE (Tables 4 and A2). The top ‘count’ mature model with 2024 mature aspen counts as the response variable included all the above predictors and interactions except for the interaction between 2006 browse level and 2006 mature aspen stems (Tables 4 and A2). The top ‘count’ recruitment model with 2024 counts of recruitment aspen stems as the response variable included all the above predictors and interactions except for the interaction between 2006 browse level and 2006 conifer encroachment (Tables 4 and A2).

Table 4. Predictors included in the final ‘count models’ with 2024 mature, recruitment, and sapling stem counts as the response variables. An X indicates that the predictor was included in the model.

Predictor	2024 Mature Stems	2024 Recruitment Stems	2024 Sapling Stems
2006 Browse Level	X	X	X
2006 Mature Stems	X	X	X
2006 Recruitment Stems	X	X	X
2006 Sapling/Sprout Stems	X	X	X
2006 Conifer Encroachment	X	X	X
Subunit	X	X	X
Distance to YNP	X	X	X
2006 SWE	X	X	X
2006 Browse Level:2006 Mature Stems		X	X
2006 Browse Level:2006 Recruitment Stems	X	X	X
2006 Browse Level:2006 Sapling/Sprout Stems	X	X	X
2006 Browse Level:2006 Conifer Encroachment	X		X
2006 Browse Level:Subunit	X	X	X
2006 Browse Level:Distance to YNP	X	X	X
2006 Browse Level:2006 SWE	X	X	X

The analysis of deviance table for the top ‘count’ 2024 mature model indicated that every predictor significantly contributed to model fit except for 2006 SWE, 2006 sapling/sprout counts, and the interaction between 2006 browse level and saplings/sprouts (Table A4). The analysis of deviance tables for the top ‘count’ 2024 recruitment and sapling models indicated that every predictor significantly contributed to model fit (Table A4). Planned contrasts were performed on the top models to test effects of encroachment, distance to YNP, subunit, and browse level on the response variables. A *post hoc* contrast testing effects of 2006 recruitment stems on 2024 mature stems was added.

2006 Stand Conditions by 2024 Stem Counts

The predictive models indicated that the highest number of 2024 recruitment aspen stems occurred in stands that experienced ‘very low’ browse in 2006, compared to all other browse levels. Sapling aspen stem count did not significantly differ across browse levels from 2006 (Tables A6 and A7; Figure 6).

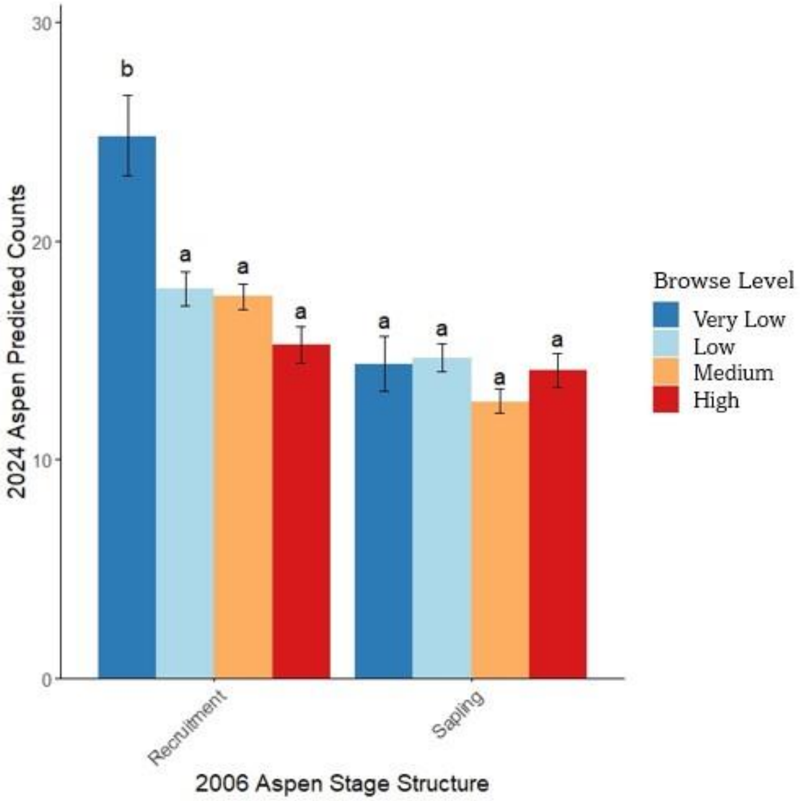

Figure 6. Predicted counts of 2024 recruitment and sapling aspen stems by 2006 recruitment and sapling stems and 2006 browse level (very low, low, medium, high). This figure includes standard error bars and compact letter display. Different letters indicate significant differences in contrasts between browse levels (*p* < 0.05).

2006 Stand Conditions by 2024 Stem Counts and Subunit

In the East River subunit, 2024 recruitment aspen stem count was highest in stands that experienced ‘very low’ and ‘low’ browse in 2006, followed by ‘medium’, and lowest at ‘high’ browse. 2024 sapling aspen stems were highest in stands that experienced ‘low’ browse in 2006, followed by ‘high’ and ‘very low’; there was no significant effect at ‘medium’ browse (Tables A8 and A9; Figure 7). In the Tom Miner subunit, 2024 recruitment stems were highest in stands that had ‘very low’ browse in 2006, followed by ‘medium’ browse; there was no significant effect at ‘high’ or ‘low’ browse. 2024 sapling aspen stems only increased in stands that had ‘medium’ browse in 2006; there was no significant effect at other browse levels (Tables A8 and A9; Figure 7). In the West River subunit, 2024 recruitment stems were highest in stands that experienced ‘low’ browse in 2006, followed by ‘very low’ and ‘high’ browse; there was no significant effect at ‘medium’ browse. 2024 sapling stems were highest in stands with ‘very low’ browse in 2006, followed by ‘high’ and ‘low’ browse, and lowest at ‘medium’ browse (Tables A8 and A9; Figure 7).

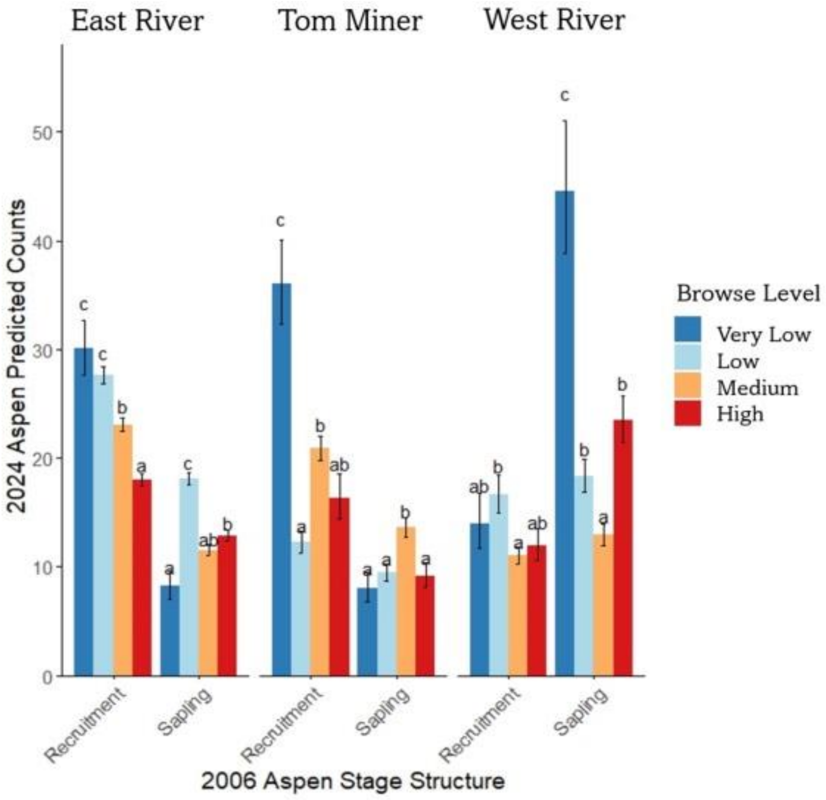

Figure 7. Predicted counts of 2024 recruitment and sapling aspen stems by 2006 browse level (very low, low, medium, high) for each subunit (East River, Tom Miner, and West River). This figure includes standard error bars and compact letter display. Different letters indicate significant differences in contrasts between browse levels ($p < 0.05$).

2006 Recruitment Stems by 2024 Mature Stems

2024 mature aspen stems were higher with more recruitment stems in 2006, especially in stands that experienced ‘high’ browse in 2006 (Tables A10 and A11; Figure 8). The models predicted that higher recruitment counts in 2006 were needed to replace 2024 mature stems in stands that experienced ‘medium’ and ‘high’ browse compared to ‘very low’ and ‘low’ browse levels (Figure 9). Roughly 30 recruitment stems in 2006 were needed to replace six mature trees in 2024 in stands with 2006 ‘medium’ and ‘high’ browse, compared to fewer than 10 recruitment stems at ‘very low’ and ‘low’ browse (Figure 9).

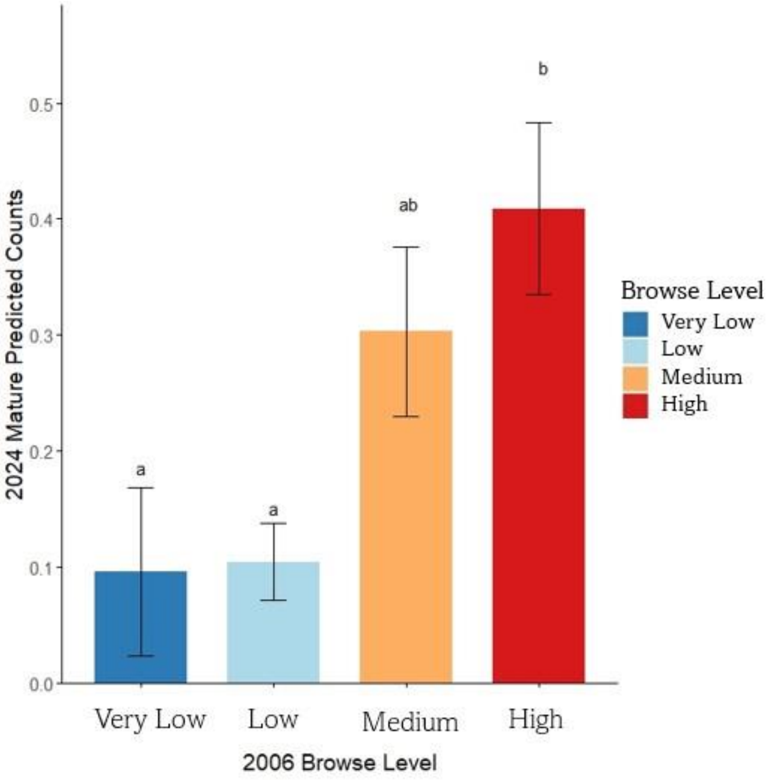

Figure 8. Modeled effects of 2006 recruitment stem predicted counts on 2024 mature predicted stem counts by 2006 browse level (very low, low, medium, high). This figure includes standard error bars and compact letter display. Different letters indicate significant differences in contrasts between browse levels ($p < 0.05$).

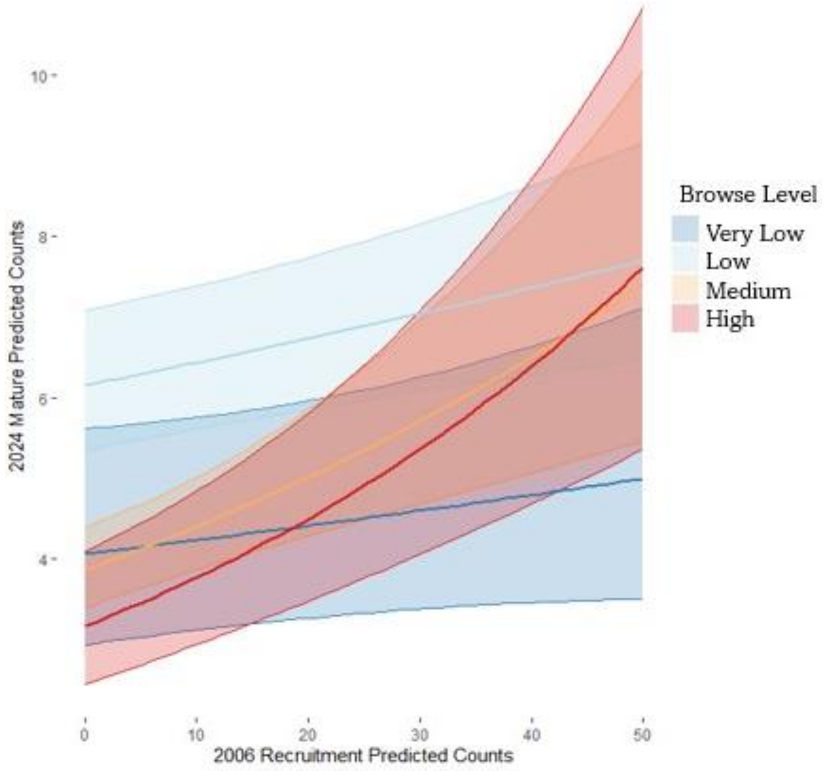

Figure 9. 2006 recruitment stem predicted counts by 2024 mature predicted counts and 2006 browse level (very low, low, medium, high).

<u>2006 Snow Water Equivalent by 2024 Stem Counts</u>

Overall, SWE had a positive effect on aspen regeneration. The strongest positive effect of SWE on mature aspen stem count was in stands that experienced ‘very low’ browse in 2006, followed by ‘medium’ browse. There was no effect of SWE in stands with ‘high’ or ‘low’ browse on 2024 mature aspen stems. In sharp contrast, SWE had a positive effect on recruitment stems in stands that experienced ‘high’ and ‘low’ browse in 2006, but it was the strongest at ‘high’ browse, with more recruitment stems with higher SWE at ‘high’ browse. There was no effect of SWE in stands with ‘medium’ and ‘very low’ browse levels on 2024 recruitment stems. Sapling aspen stems increased across all browse levels at high SWE, with the greatest increase in stands that experienced 'high' browse in 2006 relative to 'low' browse (Tables A12 and A13; Figure 10).

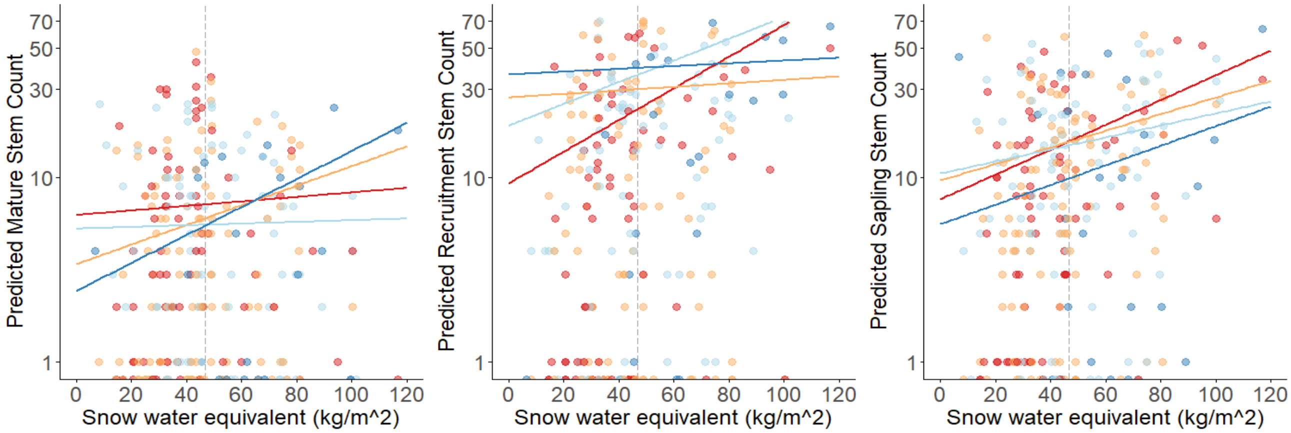

Figure 10. 2024 mature, recruitment, and sapling aspen stem predicted counts by 10-year average annual snow water equivalent (SWE) (kg/m^2) prior to 2006 with 2006 browse level (very low = dark blue, low = light blue, medium = yellow, high = red).

Distance to YNP by 2024 Stem Counts

Mature aspen stems increased farther from YNP in stands that experienced 'low' browse in 2006 but decreased farther from the park across every other browse level. Recruitment aspen stems in the study area were highest in stands with 'very low' browse in 2006 and increased farther from YNP across all browse levels, except for 'low' browse where there was no effect. Sapling aspen stems increased farther from YNP in stands with 'very low' and 'medium' browse levels only (Tables A14 and A15; Figure 11).

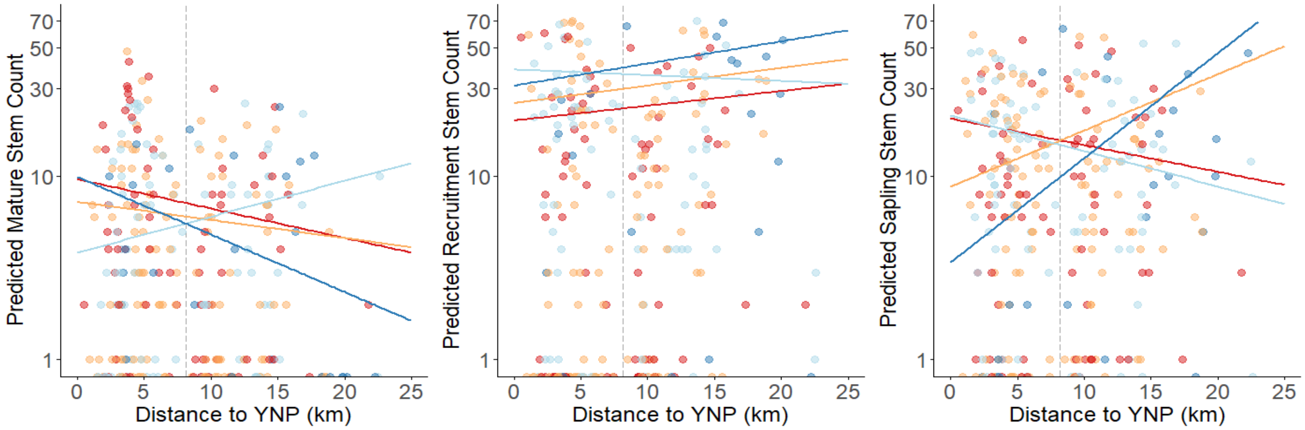

Figure 11. 2024 mature, recruitment, and sapling aspen stem predicted counts by distance to Yellowstone National Park (YNP) (km) with 2006 browse level (very low = dark blue, low = light blue, medium = yellow, high = red).

2006 Conifer Encroachment by 2024 Stem Counts

Conifer encroachment had a positive effect on sapling stem counts in stands with ‘low’ browse in 2006. Conifer encroachment had a significantly negative effect on mature stems in stands that experienced ‘high’ and ‘medium’ browse in 2006, even though the effects were not significantly different from one another. The effect of conifer encroachment was neutral across all other browse levels (Tables A16 and A17; Figure 12). Even though conifer encroachment benefited younger aspen stage structures temporarily, it harmed older stage structures over time.

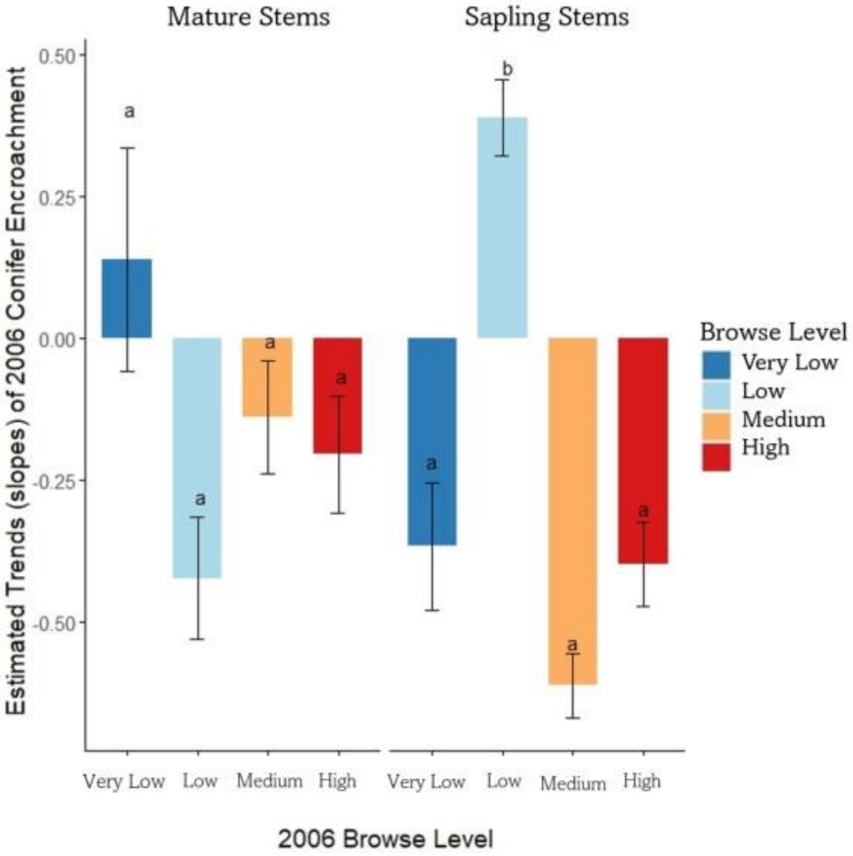

Figure 12. Estimated trends (slopes) of conifer encroachment on 2024 mature and sapling predicted stem counts by 2006 browse level (very low, low, medium, and high). A positive value indicates conifer encroachment increased stem counts, and a negative value indicates conifer encroachment lowered stem counts. This figure includes standard error bars and compact letter display. Different letters indicate significant differences in contrasts between browse levels ($p <$ 0.05).

Comparison between 1991, 2006, and 2024

Precipitation, elevation, and SWE were tightly correlated and were not permitted to be together in the same model. The 'SWE' models had lower AICc than the 'precipitation' or 'elevation' models and were therefore chosen for further analysis (Table A3). The highest-ranking model with the most predictors within 2 ΔAICc included the recruitment proportion (recruitment stems/overstory stems) as the response variable and predictors year, aspect, subunit, distance to YNP, SWE; and the interactions between subunit, distance to YNP, and SWE between years (Table 5). Omnibus tests of predictor effects in the top 'SWE' model indicated that there was a significant effect of year, subunit, distance to YNP, SWE; and the interaction between year and distance to YNP on the proportion of recruitment aspen stems (Table A5).

Table 5. Predictors included in the final 'SWE' model with the proportion of recruitment stems as the response variable. An X indicates that the predictor was included in the model.

Predictor	Proportion Recruitment Stems
Aspect	X
Subunit	X
Year	X
Distance to YNP	X
SWE	X
Year:Aspect	
Year:Subunit	X
Year:Distance to YNP	X
Year:SWE	X

<u>Proportion of Recruitment Stems</u>

The proportion (recruitment/overstory) of aspen recruitment stems was 17% higher in 2006 than 1991, approximately 90% higher in 2024 than 2006, and 122% higher in 2024 than 1991 (Tables A18 and A19; Figure 13). The proportion of aspen recruitment stems in each subunit did not change from 1991 to 2006, but had increased by 2024, with the most dramatic increase observed in the Tom Miner subunit (Tables A20 and A21; Figure 14).

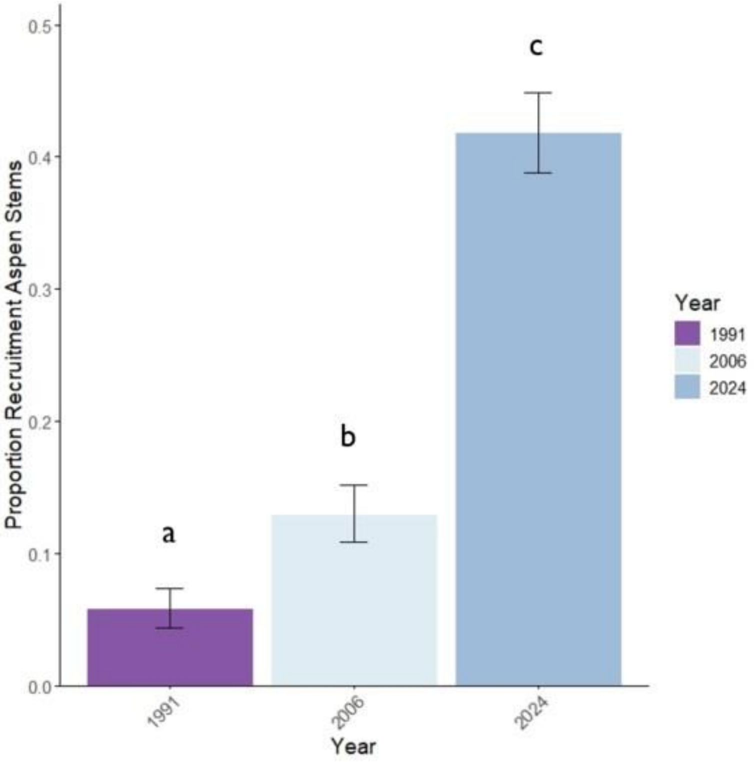

Figure 13. Proportion of aspen recruitment stems out of total overstory stems by year between 1991, 2006, and 2024. This figure includes standard error bars and compact letter display. Different letters indicate significant differences in contrasts between years ($p < 0.05$).

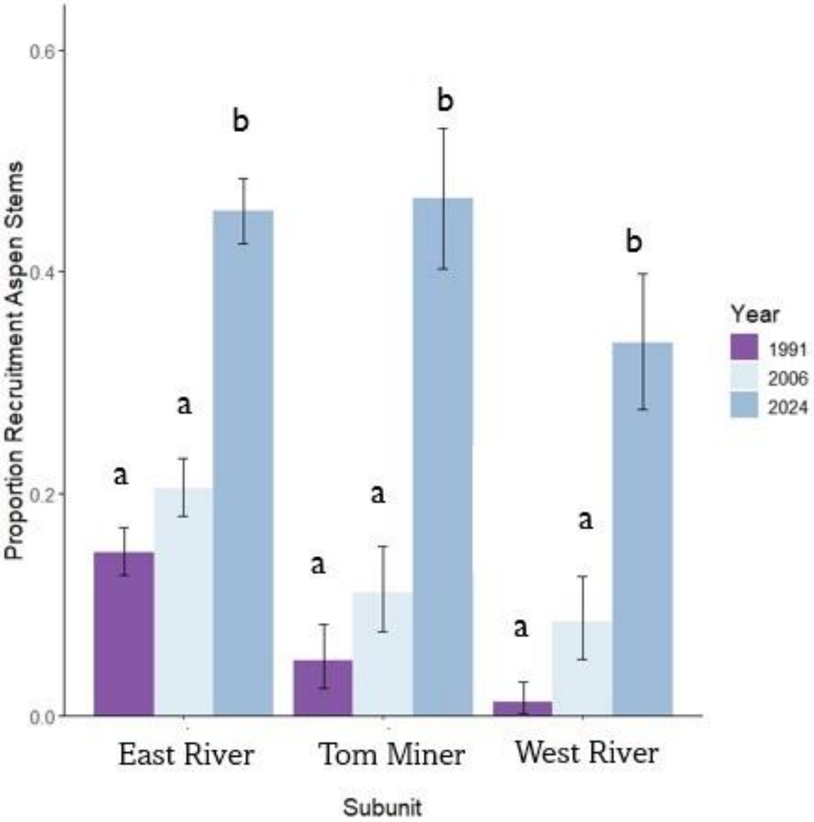

Figure 14. Proportion of aspen recruitment stems out of total overstory stems by subunits; Tom Miner, West River, and East River between 1991, 2006, and 2024. This figure includes standard error bars and compact letter display. Different letters indicate significant differences in contrasts between years ($p < 0.05$).

SWE had a significantly positive effect on the proportion of recruitment aspen stems that did not vary among years (Tables A22 and A23; Figure 15). Distance to YNP had a positive effect on the proportion of recruitment aspen stems in 2006 and 2024, but not 1991 (Tables A24 and A25 and Figure 16). The effect of aspect on the proportion of recruitment aspen stems was marginally significant ($p = 0.0516$) only when comparing east and west-facing slopes.

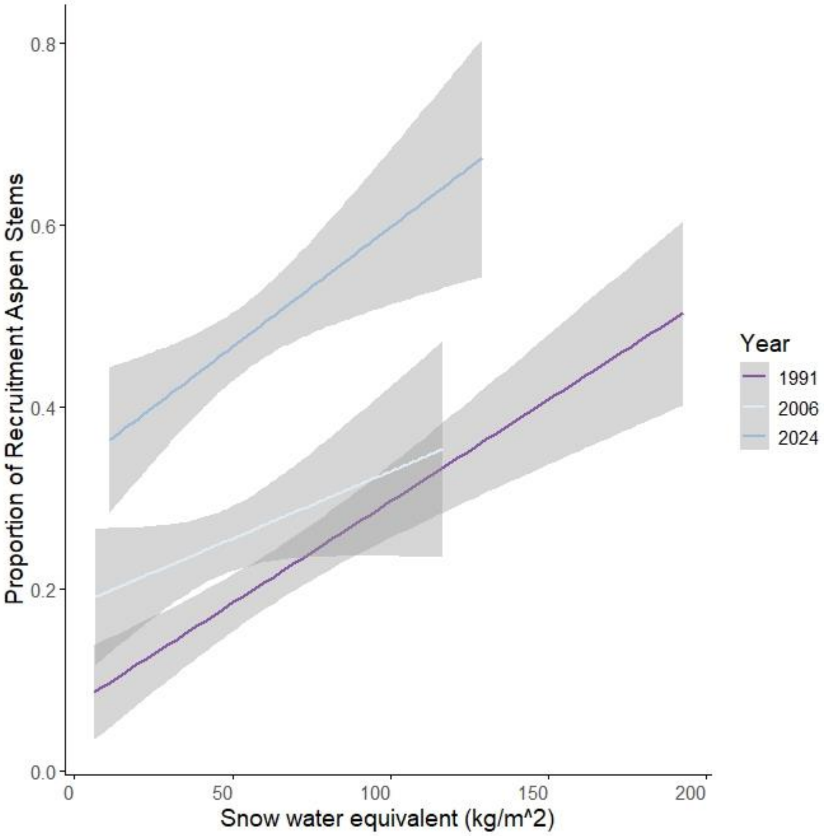

Figure 15. Proportion of aspen recruitment stems out of total overstory stems by the average annual snow water equivalent (SWE) (kg/m^2) for the 10 years prior to 1991, 2006, and 2024.

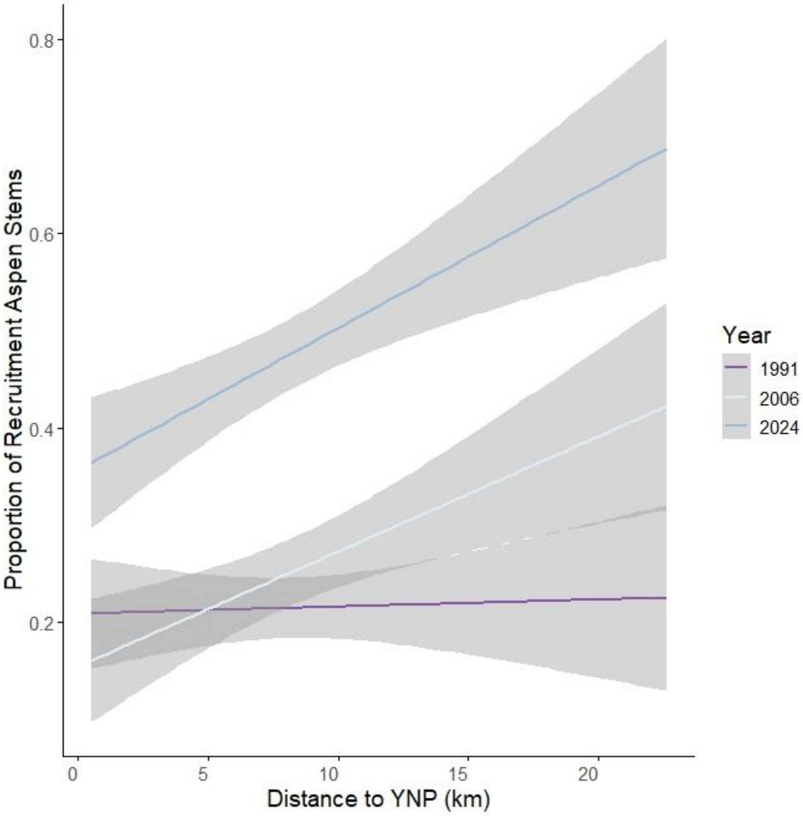

Figure 16. Proportion of aspen recruitment stems out of total overstory stems by distance to Yellowstone National Park (km) between 1991, 2006, and 2024.

<u>Mean Recruitment and Mean Overstory Stems</u>

Mean recruitment stems significantly increased 142% from 2006 to 2024, compared to 0% from 1991 to 2006. Overstory stems (≥ 2 m) significantly increased 66% from 2006 to 2024, compared to a 9% decrease from 1991 to 2006 (Table 6). Mean recruitment and overstory stems (≥ 2 m) in the East River subunit had a 142% and 68% increase 2006–2024 respectively, compared to 0% and a 9% decrease 1991–2006 respectively (Table 7). Mean recruitment and overstory stems in the Tom Miner subunit had a 78% and 97% increase 2006–2024 respectively, compared to a 14% and 29% decrease 1991–2006 respectively (Table 7). Mean recruitment and overstory stems in the West River subunit had a 237% and 71% increase 2006–2024 respectively, compared to a 16% and 20% decrease 1991–2006 respectively (Table 7).

Table 6. Mean recruitment (≥ 2 m and 5 cm DBH), mean overstory stems (≥ 2 m), and percentage of proportion recruitment stems from 302 aspen stands sampled in 1991, 2006, and 2024. P-values are derived from estimated marginal mean tests on the proportion of recruitment aspen stems between years.

	1991	2006	2024	1991–2006 p-value	2006–2024 p-value	1991–2024 p-value
Mean recruitment stems	9.3 (22%)	9.8 (25%)	23.7 (48%)	0.0061	< 0.0001	< 0.0001
Mean overstory stems	12.6	11.6	19.2			

Table 7. Mean recruitment (≥ 2 m and 5 cm DBH) and mean overstory stems (≥ 2 m) for the East River (*n* = 207), Tom Miner (*n* = 48), and West River (*n* = 47) subunits sampled in 1991, 2006, and 2024.

	East River *n* = 207	Tom Miner *n* =48	West River *n* = 47
1991 Mean recruitment stems	9.3	11.8	7.7
1991 Mean overstory stems	25.2	23.4	25.3
2006 Mean recruitment stems	9.8	10.2	6.5
2006 Mean overstory stems	22.9	16.6	20.2
2024 Mean recruitment stems	23.7	18.2	21.9
2024 Mean overstory stems	38.5	32.7	34.6

Sustainable Aspen Stands

The percentage of stands with ≥ 1 recruitment stem increased 23% from 2006 to 2024, compared to a 6% increase from 1991 to 2006, while the percentage of stands with a recruitment ratio ≥ 1 (Kay 1985) increased 24% from 2006 to 2024, compared to a 4% increase from 1991 to 2006 (Table 8). The number of aspen stands that are considered sustainable by the Kimble et al.

(2011b) sustainability criterion increased from 116 in 2006 to 178 stands in 2024, a 21% increase, with 59% of stands considered sustainable (Table 8). The West River subunit had the highest percentage of unsustainable stands, followed by the Tom Miner subunit and the East River subunit, with 47%, 42%, and 40% unsustainable respectively (Table 9).

Table 8. Number and percentage of stands with recruitment stems (≥ 2 m tall and < 5 cm DBH), number and percentage of stands with recruitment ratio (recruitment/non-recruitment) ≥ 1.0 sampled in 1991, 2006, and 2024, and number and percentage of stands that are sustainable in 2024 (2024 overstory stems – 2006 overstory stems ≥ 0) and 2006 (2006 overstory stems – 1991 overstory stems ≥ 0). Overstory stems are all stems ≥ 2 m tall (recruitment + non-recruitment).

n = 302	1991	2006	2024
Number of stands with ≥ 1 recruitment stem	147	165	235
Percentage of stands with ≥ 1 recruitment stem	49%	55%	78%
Kay's sustainability criterion			
Number of sustainable stands	62	72	145
Percentage of sustainable stands	20%	24%	48%
Kimble's sustainability criterion			
Number of sustainable stands		116	178
Percentage of sustainable stands		38%	59%

Table 9. Number and percentage of stands that are unsustainable in 2024 (2024 overstory stems – 2006 overstory stems ≤ 0) for each subunit (East River, Tom Miner, and West River).

	East River (*n* = 207)	Tom Miner (*n* = 48)	West River (*n* = 47)
Number of unsustainable stands	82	20	22
Percentage of unsustainable stands	40%	42%	47%

CHAPTER FOUR

DISCUSSION

The first objective of this study is to determine how aspen stand structure has changed since 2006, and which stands are more vulnerable to threats such as ungulate browsing and conifer encroachment. I found that aspen stands that experienced high browsing pressure in 2006, less SWE in the past 10 years, are closer to YNP, and have fewer recruitment stems are more vulnerable to aspen threats and may disappear on the landscape without active management. Throughout the study area, SWE had a positive effect on aspen regeneration. Because snow has been found to be a primary driver of winter movement and behavior of elk (Proffitt et al. 2011, Brice et al. 2024), higher SWE, and thus a greater snowpack, act as a physical barrier, reducing elk visits to aspen stands, as well as the amount of aspen height lost to winter browsing (Brodie et al. 2012, Martin and Maron 2012). Indirectly, a greater snowpack may have played a role in promoting continued aspen stem growth by deterring ungulate browsing within aspen stands. This was especially seen on 2024 sapling stems where SWE had the greatest positive effect in stands that had experienced high browsing pressure in 2006, most likely due to sprouts and saplings being inaccessible for browsing under the snow. More snowpack can also increase aspen regeneration through increased moisture in the soil throughout the growing season (Harpold et al. 2014). However, some of the effect attributed to snowpack in my models may have also been due to correlated effects of spring precipitation and elevation, which may have created better conditions for aspen growth.

Conifer encroachment had negative or neutral effects on most size categories in 2024, but there were more saplings in encroached stands with low browsing than stands with the same browsing pressure but without conifers. Conifer encroached stands have a higher canopy cover, resulting in microclimates with reduced wind, cooler temperatures, and increased soil moisture (De Frenne et al. 2021). These stand conditions could have positively affected aspen sapling and sprout growth in 2006, resulting in more saplings in 2024. Indirectly, conifers may have shielded aspen sprouts and saplings through increased cover and higher amounts of snowpack, making saplings and sprouts less accessible for browsing in the years leading up to 2024. Even though conifer encroachment was found to benefit sprout and sapling growth, my results suggest that this may not necessarily translate to improved growth of larger size classes. Long-lived and shade-tolerant conifers can eventually outcompete aspens (Kaye et al. 2005), and seem to have had a negative effect on mature aspen stems. These mature trees were most likely recruitment stems in 2006, and the negative effect of conifer encroachment was greater in stands that experienced higher browsing pressure in 2006, indicating that a combination of conifer encroachment and high elk browsing pressure led to fewer mature trees over time. In general, stands with a higher count of recruitment stems in 2006 resulted in more mature trees in 2024. To buffer the negative impacts of browsing on stem growth, stands that experienced high browsing pressure in 2006 needed more recruitment stems to replace mature trees in 2024 than stands with low browsing pressure. These results demonstrate how important it is that recruitment stems escape browsing to maintain the stand long-term.

As a result of the northern range elk migration shift, recruitment, sapling, and mature stem counts were higher farther from YNP in stands that experienced lower browsing pressure in

2006. These results could be a legacy effect from when there were fewer elk migrating out of the park in 2006, in which recruitment, sprout, and sapling stems experienced lower browsing and were able to grow into older stage structures by 2024. In comparison to Tom Miner, both the East River and West River subunits had the lowest counts of recruitment aspen stems at higher browsing pressures. Collectively, the East and West River subunits had a 178% increase in high browsing pressure, indicating that a higher elk density had a greater negative impact on aspen stand regeneration on the border of YNP. Since elk density in the Tom Miner subunit has stayed low since 2006 (2 elk/km^2), the Tom Miner subunit had the greatest counts of recruitment stems in stands that had 'very low' browsing pressure in 2006 and sapling aspen stems were highest in stands that experienced 'medium' browsing pressure in 2006. Aspen stands that have not been affected by high-stress episodes (*i.e.* wildfire) have been found to positively benefit from moderate levels of herbivory (Endress et al. 2012), indicating that moderate browsing may have benefited sprouts and saplings in 2006 in the Tom Miner subunit by initiating more sprouting within the stand.

The second objective of this study is to determine how aspen stem recruitment and overstory stems have changed in the past 34 years, and which factors are influencing this change. In contrast to St. John (1995) and Kimble et al. (2011b), aspen recruitment is now increasing on a local and landscape scale on the northern range outside YNP, indicating that enough time has passed for aspen recruitment to increase post elk population decline. The proportion of recruitment aspen stems (*i.e.*, heights above 2 m and < 5 cm dbh) across the study area is 90% higher in 2024 than 2006, and 122% higher than 1991. Compared to a decline from 1991 to 2006, aspen stem recruitment and overstory stems (≥ 2 m) have dramatically increased since

2006 across all subunits. The Upper Yellowstone West elk herd density in the Tom Miner subunit has decreased to an average of 2 elk/km^2 since 2006 (5 elk/km^2). This decline in elk browsing since 2006 allowed stems to recruit into the overstory and resulted in the Tom Miner subunit having the greatest increase in overstory stems in 2024, as well as the greatest increase in the proportion of recruitment stems in the study area.

Research on aspen recruitment has been ongoing for decades on the northern range within YNP. Most of these studies (Ripple and Beschta 2007, 2012, Kauffman et al. 2010, Painter et al. 2018, Peterson et al. 2020, Brice et al. 2024, Painter et al. 2025) found that aspen recruitment increased on the northern range within YNP as elk density and browsing decreased. Painter et al. (2025) compared aspen recruitment on 87 aspen stands on the northern range within YNP in 1997–1998, 2012, and 2020–2021. Similar to my study, they found that aspen recruitment was not increasing in the 1990s or early 2000s, but had begun to increase after 2012 (Painter et al. 2025), coinciding with the northern elk migration shift. Average elk density (2013–2024) has increased in the East and West River subunits (4 elk/km^2) since 2006 (3 elk/km^2) due to 85% of the northern elk herd now migrating outside of the park in winter. This migration shift could have been due to a number of reasons, including increased competition with bison, less hunting pressure outside the park, availability of irrigated hayfields north of the park, or increased predation inside the park boundary (Proffitt et al. 2009, White et al. 2012, Smith et al. 2023, Brice et al. 2024, Painter et al. 2025). As a result of this migration shift, the proportion of recruitment stems had the greatest increase farther from YNP after 2006 and browsing pressure increased in aspen stands closer to the park boundary. Even though browsing pressure has increased on the border of YNP, the northern range elk migration shift did not result in decreased aspen stem recruitment on a landscape scale in the study area, but rather elk density played an important role (Figure 17). In 2006 Kimble et al. (2011b) was beginning to see increased aspen recruitment in select drainages as elk density was declining. Aspen recruitment within the East and West River subunits has increased post elk population decline as Kimble et al. (2011b) predicted, however, since the elk distribution has changed, aspen recruitment within the migration corridor may decline in the future. Aspen recruitment is a long-term process and there may be a lag effect where recruitment may decrease in the future with increasing elk density. An elk density of 3 elk/km^2 in 2006 allowed aspen recruitment to increase on a landscape scale by 2024. Therefore, an elk density of 3 elk/km^2 may be the threshold in which aspen recruitment can increase on the border of YNP. Since the elk density in the East and West River subunits is increasing (average 4 elk/km^2 2013–2024) due to the northern range migration shift, if it rebounds to historic levels (average 6 elk/km^2 1989–1999) within these subunits, this may result in a reversal of aspen recruitment in the future. These results are consistent with other studies that found that increased elk density led to increased browsing, which resulted in aspen decline on the northern range (Wagner 2006, Kauffman et al. 2010, Brice et al. 2024, Painter et al. 2025).

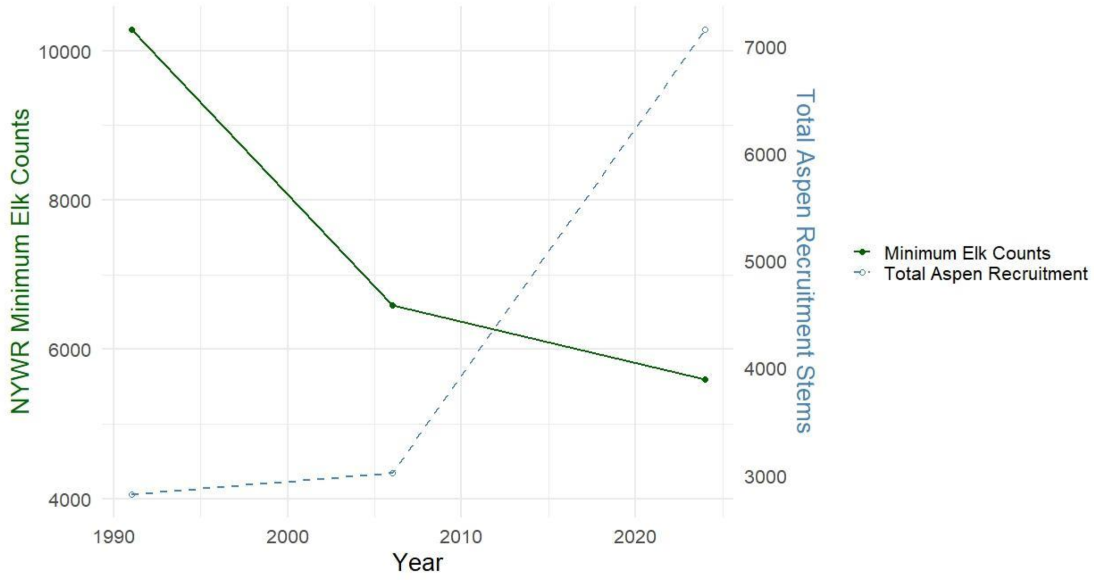

Figure 17. Total aspen recruitment stem counts on the Northern Yellowstone Winter Range (NYWR) outside YNP by NYWR minimum winter elk counts from 1990 to 2024. Aspen recruitment data derived from 1990–1991 (St. John 1995), 2005–2006 (Kimble et al. 2011b), and 2023–2024 (this study). Fixed- wing flight classification surveys were completed by the Northern Yellowstone Cooperative Wildlife Working Group from December to March.

Aspen Stand Sustainability

Even though the overall proportion of aspen recruitment is increasing, this does not represent individual stand recruitment success. Stems taller than two meters have grown beyond the height of typical elk browsing, and their presence in a stand is an important indicator of potential to continue recruiting new stems. Even though newer research has indicated that elk may sometimes browse higher than two meters (Brice et al. 2022), this threshold has functioned well as an indicator of likely recruitment success in previous aspen studies on the northern range (Painter et al. 2025) and is used in this study to remain consistent with St. John (1995) and Kimble et al. (2011).

Stands with more tall trees have more potential for recruitment, and those with at least 50% of trees taller than two meters meet Kay’s (1985) criterion for stand sustainability. However, Kay’s criterion is calculated as a ratio of old to young stems and does not reflect the fact that sustainability may be possible in stands with a low recruitment ratio but a high number of stems. Therefore, Kimble et al. (2011b) created a new stand sustainability definition in which the total number of live aspen stems that have grown above browsing height (2 m; *i.e.* overstory stems) must remain stable or increase over time for a stand to be sustainable. From 2006 to 2024, the percentage of stands with at least one recruitment stem increased 23%, the recruitment ratio increased 24%, and the percentage of stands that are sustainable according to Kimble et al.’s (2011b) criterion increased 21%, with 59% of stands in the study area now considered sustainable. These sustainable stands will most likely persist on the landscape long-term and are not in need of management, as long as elk density remains at or below the identified threshold (3 elk/km^2).

Other Factors Influencing Aspen Recruitment

Climate change and fire suppression have also been theorized to influence aspen recruitment (Houston 1982, Despain et al. 1986, Romme et al. 1995, Barmore 2003). There is evidence of a multi-year drought on the northern range between 2000 and 2007 (McMenamin et al. 2008, Painter et al. 2014, Peterson et al. 2014), and during that period aspen stem height began to increase during the drought, contrary to what would be expected if moisture was the ultimate limiting factor (Painter et al. 2014). Median heights for aspen increased the most after the drought ended in 2007, although that is also when elk counts on the northern range continued to decline. Ripple and Beschta (2007) and Painter et al. (2014, 2015) found no support for the hypothesis that differences in plant productivity explained differences in young aspen heights. Rather, they determined that browsing intensity from elk is the dominant factor. Ungulate exclosures within YNP created in the 1950s and 1960s confirmed that woody plants, despite climate trends or fluctuations, were able to grow once protected from browsing (Kay and Bartos 2000, Painter et al. 2014, Beschta and Ripple 2016). Although climate change has not had a major impact on aspen recruitment today, long-term trends leading to a drier and warmer climate could potentially limit aspen stand expansion on the northern range in the future.

Fire suppression and increased risk of wildfire due to a warmer and drier climate could also be influencing individual aspen stand density (Despain et al. 1986). After the 1988 Yellowstone wildfires, aspen sprouts increased in areas burned. However, few of them survived or reached two meters in height on the northern range because they were consumed by elk (Romme et al. 1995, Hansen et al. 2016). Burned areas have forage that is more attractive to ungulates because they contain higher amounts of crude protein, biomass, and available digestible protein than unburned areas (Sittler et al. 2019). Some aspen saplings survived in areas of the park where elk densities and browsing were relatively low (Halofsky et al. 2008). Durham and Marlow (2010) found a similar relationship in southwest Montana where aspen sucker height and density increased following prescribed burning, especially in plots where ungulate presence was low enough (< 1 elk/km^2) to allow aspen regeneration.

Conclusion

St. John (1995) and Kimble et al. (2011b) reported that aspen stem recruitment was not increasing on a landscape scale within the study area in 1991 or 2006, although Kimble et al. (2011b) did identify a few drainages with recruitment in scattered stands where St. John (1995) did not. My results show that this trend has changed, with a 90% increase in aspen stem recruitment since 2006, and 59% of aspen stands considered sustainable long-term compared to 38% in 2006. Aspen recruitment was consistently lowest at high browsing pressure across the study area. Snow depth inferred from SWE benefited aspen regeneration through increased soil moisture and may have played a role in promoting aspen stem growth by deterring ungulate browsing within aspen stands. Conifer encroachment may have had a temporary positive effect on younger aspen stems by creating a microclimate beneficial for growth and by limiting browsing pressure through increased cover and snowpack, however, increased competition with conifers coupled with higher browsing levels had a negative effect long-term. Increased aspen stem recruitment farther from YNP in areas with lower browsing pressure could be directly tied to the northern range elk herd migration shift that has occurred since 2013, with more than 85% of the elk herd spending their winter outside the park. An average elk density of 3 elk/km^2 may be the threshold on the border of YNP for aspen recruitment to increase. If elk density rebounds to historic levels, this may result in a reversal of aspen recruitment in the future. In contrast, if average elk density remains low as in the Tom Miner subunit, aspen recruitment may continue to increase. My study is consistent with previous studies on the northern range within YNP that found that increased elk density, and thus increased elk browsing, led to aspen decline on the northern range (Wagner 2006, Brice et al. 2024, Painter et al. 2025). This long-term study documents aspen recruitment over 34 years on a landscape scale on the northern portion of the northern range outside YNP. Long-term data such as these are integral in understanding the cause and effect of ecosystem interactions and will provide context for landscape level management on the CGNF.

Management Implications

Aspen coverage on the northern range has been reduced from 4-6% historically to 1% due to overbrowsing (Wagner 2006). To halt this decline and retain vital ecosystem services, management is needed to maintain the remaining aspen stands on the landscape. The third objective of this study is to determine which aspen stands should be prioritized for Forest Service management to improve aspen stand sustainability. Even though aspen recruitment is increasing on a landscape scale in the study area, 124 out of 302 (41%) aspen stands were found to be unsustainable long-term (*i.e.* overstory stems were not stable or increasing over time). The subunit with the highest percentage of unsustainable stands was the West River subunit (47%), followed by Tom Miner (42%) and East River subunits (40%). Management is recommended to ensure long-term presence of these aspen stands on the CGNF, with the caveat that management treatments may only be successful if elk density remains low.

Even though management treatments would occur on a stand-by-stand basis, the following recommendations are intended to allow managers to prioritize management actions on a landscape level. If the goal is to maintain current recruitment and overstory stems, no management actions need to be taken. However, if elk density continues to increase in the West and East River subunits, land managers can expect to see aspen recruitment and sapling stage structures decrease as browsing pressure increases.

If the goal is to increase aspen recruitment and overstory stems, management treatments should be focused on the listed 124 unsustainable stands. For a stand to recover from high browsing pressure, at least 30 recruitment stems must be maintained to replace six mature trees in the future, compared to a stand that is experiencing low browsing pressure, where fewer than 10 recruitment stems are necessary to replace six mature trees. There are 20 stands, 13 in East River and seven in West River, that currently experience high browsing pressure (> 81%), have conifer encroachment (> 10% reproducing conifer canopy cover), have fewer than 30 recruitment stems, have experienced less SWE (< 40 kg/m^2) in the past 10 years, and that are closer (< 10 km) to the border of YNP. These stands are in severe decline and may not be cost-effective to manage. Therefore, management treatments should focus on the remaining 104 unsustainable stands that are prioritized by distance to YNP, conifer encroachment, and browse level (Table 10).

Table 10. Number of aspen stands (*n* = 104) prioritized for Forest Service management by subunit (East River, West River, and Tom Miner).

Priority Criteria	East River *n* = 69	West River *n* = 15	Tom Miner *n* = 20
Very high priority (< 10 km, 'high' browse, conifer encroachment)	6	5	10
High priority ('high' browse, conifer encroachment)	16	3	0
Medium priority ('high' browse)	18	1	0
Low priority ('medium' browse)	16	3	5
Very low priority ('low' and 'very low' browse)	13	3	5

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APPENDIX

APPENDIX: SUPPLEMENTARY TABLES AND FIGURES

Table A1. Northern Yellowstone Cooperative Wildlife Working Group aerial minimum winter elk counts for the Northern Yellowstone Winter Range, Hunting District (HD) 313, and HD 314 (Rock Creek to Tom Miner Basin) from 1990 to 2024.

NYWR		Migration Count (HD 313)		HD 314 (Rock Creek to Tom Miner Basin)	
Winter	Minimum Elk	Winter	Minimum Elk	Winter	Minimum Elk
1990	14829	1990	3529	1990	640
1991	9456	1991	1846	1991	972
1992	12859	1992	7687	1992	581
1993	17585	1993	4013	1993	324
1994	19045	1994	1533	1994	1183
1995	16791	1995	6216	1995	1088
1996		1996	8626	1996	1468
1997		1997	8445	1997	483
1998	11692	1998	5296	1998	493
1999	11742	1999	6030	1999	639
2000	14538	2000	3500	2000	719
2001	13400	2001	3833	2001	651
2002	11969	2002	5104	2002	572
2003	9215	2003	3494	2003	191
2004	8335	2004	3990	2004	190
2005	9545	2005	3243	2005	733
2006	6588	2006	3549	2006	577
2007	6738	2007	2219	2007	
2008	6279	2008	4088	2008	480
2009	7109	2009	3638	2009	312
2010	6070	2010	3359	2010	450
2011	4635	2011	3266	2011	217
2012	4174	2012	2734	2012	283
2013	3915	2013	3000	2013	282
2014		2014		2014	131
2015	4844	2015	3714	2015	268
2016	4912	2016	3804	2016	153
2017	5349	2017	4776	2017	
2018	7579	2018	5738	2018	178
2019	5800	2019	4352	2019	109
2020	6019	2020	4687	2020	
2021	6246	2021	4609	2021	272
2022	6673	2022	5473	2022	311
2023	6651	2023	5906	2023	91

2024	5597	2024	4789	2024	310

Figure A1. Correlations between all candidate predictor variables. Subset models were not considered that had any predictors with |*r*| > 0.6.

Table A2. Combined ‘count’ top 10 model rankings with 2024 counts of mature, recruitment, and sapling aspen predicted counts as the response variables and 2006 counts of mature, recruitment and sapling aspen stems as the predictors. For each model, we report degrees of freedom (df), log likelihood (logLik), Akaike Information Criterion (AICc), ΔAICc, and model weight.

	Intercept	2006 Browse Level	2006 Mature Stems	2006 Recruitment Stems	2006 Conifer Encroachment	2006 Sapling/Sprouts	Subunit	Distance to YNP	2006 SWE	2006 Browselevel:2006 Mature	2006 Browselevel:2006 Recruitment	2006 Browselevel:2006 Conifer Encroachment	2006 Browselevel:2006 Sapling/Sprouts	2006 Browselevel:Subunit	2006 Browselevel:Distance to YNP	2006 Browselevel:2006 SWE	df	logLik	AICc	delta	weight
2024 mature stem count	1.78	+	0.54	0.59	-0.07	-0.082	+	-0.01	0.11		+	+	+	+	+	+	33	-1031	2136.70	0	0.44932
	1.77	+	0.53	0.56	-0.04		+	0.001	0.11		+	+		+	+	+	29	-1036	2137.03	0.33	0.38046
	1.77	+	0.53	0.56	-0.04	0.0008	+	0.001	0.11		+	+		+	+	+	30	-1036	2139.51	2.81	0.11007
	1.77	+	0.54	0.56	-0.04		+	0.003	0.11	+	+	+		+	+	+	32	-1035	2142.88	6.18	0.02048
	1.78	+	0.55	0.59	-0.06	-0.083	+	-0	0.11	+	+	+	+	+	+	+	36	-1031	2143.38	6.67	0.01596
	1.85	+	0.54	0.59	-0.2	-0.092	+	0.021	0.11		+		+	+	+	+	30	-1039	2144.18	7.48	0.01069
	1.77	+	0.54	0.56	-0.04	0.0131	+	0.005	0.11	+	+	+		+	+	+	33	-1035	2145.22	8.52	0.00633
	1.85	+	0.53	0.55	-0.19		+	0.035	0.11		+			+	+	+	26	-1044	2145.78	9.07	0.00481
	1.85	+	0.53	0.55	-0.19	0.0069	+	0.036	0.11		+			+	+	+	27	-1044	2148.14	11.4	0.00147
	1.85	+	0.54	0.59	-0.21	-0.094	+	0.025	0.11	+	+		+	+	+	+	33	-1038	2150.72	14	0.00041
2024 recruitment stem count	3.45	+	0.01	0.19	-0.56	0.4457	+	-0.15	0.44	+	+		+	+	+	+	33	-3391	6855.74	0	0.83872
	3.49	+	0	0.19	-0.63	0.4395	+	-0.14	0.44	+	+	+	+	+	+	+	36	-3388	6859.24	3.49	0.14626
	3.44	+	0.05	0.2	-0.56	0.4378	+	-0.14	0.46		+		+	+	+	+	30	-3398	6863.88	8.14	0.01433
	3.46	+	0.05	0.2	-0.6	0.4334	+	-0.14	0.46		+	+	+	+	+	+	33	-3398	6870.02	14.3	0.00067

	3.47	+		0.19	-0.58	0.4452	+	-0.15	0.43		+		+	+	+	+	29	-3406	6876.69	20.9	2.37E-05
	3.49	+		0.19	-0.63	0.4398	+	-0.14	0.44		+	+	+	+	+	+	32	-3405	6882.74	27	1.15E-06
	3.47	+	-0.04	0.15	-0.57	0.4571	+	-0.18	0.27	+	+		+	+	+		30	-3417	6900.97	45.2	1.27E-10
	3.51	+	-0.05	0.15	-0.65	0.4498	+	-0.17	0.27	+	+	+	+	+	+		33	-3414	6902.68	46.9	5.40E-11
	3.43	+	0		-0.57	0.4537	+	-0.14	0.43	+			+	+	+	+	29	-3425	6915.22	59.5	1.02E-13
	3.43	+	0	0.01	-0.57	0.4533	+	-0.14	0.43	+			+	+	+	+	30	-3425	6916.92	61.2	4.36E-14
2024 sapling stem count	2.75	+	0.1	-0.5	0.007	-0.045	+	-0.22	0.33	+	+	+	+	+	+	+	36	-3112	6305.86	0	0.95337
	2.76	+	0.08	-0.5	0.004	-0.042	+	-0.24	0.26	+	+	+	+	+	+		33	-3119	6312.11	6.25	0.04196
	2.8	+	0.1	-0.2	0.025	-0.052	+	-0.23	0.33	+		+	+	+	+	+	33	-3121	6317.18	11.3	0.00333
	2.8	+	0.09	-0.2	0.022	-0.049	+	-0.24	0.26	+		+	+	+	+		30	-3127	6320.5	14.6	0.00063
	2.78	+	0.04	-0.5	-0.03	-0.043	+	-0.23	0.32		+	+	+	+	+	+	33	-3123	6320.98	15.1	0.0005
	2.78	+	0.04	-0.5	-0.03	-0.04	+	-0.24	0.26		+	+	+	+	+		30	-3128	6323.65	17.8	0.00013
	2.8	+		-0.5	-0.06	-0.041	+	-0.24	0.3		+	+	+	+	+	+	32	-3127	6325.22	19.4	5.98E-05
	2.8	+		-0.5	-0.05	-0.038	+	-0.24	0.26		+	+	+	+	+		29	-3131	6327.26	21.4	2.15E-05
	2.84	+	0.04	-0.2	-0.01	-0.05	+	-0.24	0.31			+	+	+	+	+	30	-3133	6333.25	27.4	1.08E-06
	2.83	+	0.04	-0.2	-0.01	-0.047	+	-0.25	0.27			+	+	+	+		27	-3137	6333.42	27.6	9.90E-07

Table A3. Top 10 ‘SWE’ model rankings with the proportion (recruitment/overstory) of recruitment stems for 1991, 2006, and 2024 as the response variable. For each model, we report degrees of freedom (df), log likelihood (logLik), Akaike Information Criterion (AICc), ΔAICc, and model weight. Model chosen was the model with the most predictors within 2 ΔAICc. The AICc for the top ‘precipitation’ model was 976.09 and the AICc for the top ‘elevation’ model was 985.76.

	Intercept	Aspect	Subunit	Year	Distance to YNP	SWE	Aspect:Year	Subunit:Year	Distance to YNP:Year	SWE:Year	df	logLik	AICc	delta	weight
Proportion	0.43	+	+	+	-0.017	0.079			+	+	16	-470	972.64	0	0.43412
Recruitment	0.46	+	+	+	-0.028	0.08		+	+	+	20	-466.5	973.93	1.29	0.2282
Stems	0.37		+	+	-0.022	0.081			+	+	13	-473.9	974.13	1.49	0.20645
	0.39		+	+	-0.033	0.082		+	+	+	17	-470.3	975.27	2.63	0.11681
	0.42	+	+	+	-0.018	0.079	+		+	+	22	-467.5	980.21	7.57	0.00984
	0.44	+	+	+	-0.029	0.082	+	+	+	+	26	-464.6	982.74	10.1	0.00278
	0.39	+		+	0.002	0.081			+	+	14	-477.9	984.21	11.6	0.00134
	0.32			+	-0.004	0.085			+	+	11	-482.8	987.93	15.3	0.00021
	0.43	+	+	+	0.0554	0.074				+	14	-479.9	988.3	15.7	0.00017
	0.37		+	+	0.0502	0.077				+	11	-483.6	989.57	16.9	9.16E-05

Table A4. Analysis of deviance table from the final 'count models' with 2024 counts of mature, recruitment, and sapling aspen stems as the response variables and 2006 counts of recruitment, sapling/sprout, and mature aspen stems as the predictors. Model results include the likelihood ratio Chi-square (LR Chisq), degrees of freedom (df), and p-value for each term.

		LR Chisq	Df	P
2024 mature stem count	2006 SWE	0.940685	1	0.3321
	Distance to YNP	9.487601	1	0.0021
	2006 Conifer Encoachment	3.954386	1	0.0467
	Subunit	40.65563	2	< 0.0001
	2006 Sapling/Sprout	5.75E-05	1	0.994
	2006 Mature	648.0549	1	< 0.0001
	2006 Recruitment	26.77989	1	< 0.0001
	2006 Browse Level	7.862085	3	0.0489
	2006 SWE:2006 Browse Level	18.11558	3	0.0004
	Distance to YNP:2006 Browse Level	42.91647	3	< 0.0001
	Subunit:2006 Browse Level	95.90779	6	< 0.0001
	Sapling/Sprout:2006 Browse Level	0.627155	3	0.8902
	Conifer Encroachment:2006 Browse Level	7.733476	3	0.0519
	2006 Recruitment:2006 Browse Level	17.80828	3	0.0005
2024 recruitment stem count	2006 SWE	156.9676	1	< 0.0001
	Distance to YNP	7.255564	1	0.0071
	Subunit	12.33137	2	0.0021
	2006 Conifer Encroachment	326.6531	1	< 0.0001
	2006 Sapling/Sprout	307.4385	1	< 0.0001
	2006 Mature	20.83351	1	< 0.0001
	2006 Recruitment	44.6486	1	< 0.0001
	2006 Browse Level	115.4235	3	< 0.0001
	2006 SWE:2006 Browse Level	109.5381	3	< 0.0001
	Distance to YNP:2006 Browse Level	27.37145	3	< 0.0001
	2006 Sapling/Sprout:2006 Browse Level	220.5662	3	< 0.0001
	Subunit:2006 Browse Level	87.76237	6	< 0.0001
	2006 Mature:2006 Browse Level	219.4974	3	< 0.0001
	2006 Recruitment:2006 Browselevel	121.664	3	< 0.0001
2024 sapling stem count	2006 SWE	104.5314	1	< 0.0001
	Distance to YNP	21.23739	1	< 0.0001
	Subunit	49.42088	2	< 0.0001
	2006 Conifer Encroachment	28.68438	1	< 0.0001
	2006 Sapling/Sprout	12.93618	1	0.0003
	2006 Mature	116.4751	1	< 0.0001
	2006 Recruitment	53.44893	1	< 0.0001
	2006 Browse Level	7.588142	3	0.0553
	2006 SWE:2006 Browse Level	16.8333	3	0.0008
	Distance to YNP:2006 Browse Level	309.5202	3	< 0.0001
	2006 Sapling/Sprout:2006 Browse Level	112.0016	3	< 0.0001
	Subunit:2006 Browse Level	123.1313	6	< 0.0001
	Conifer Encroachment:2006 Browse Level	138.7206	3	< 0.0001
	2006 Mature:2006 Browse Level	310.6314	3	< 0.0001
	2006 Recruitment:2006 Browse Level	91.03163	3	< 0.0001

Table A5. ANOVA results from the final chosen 'snow water equivalent (SWE)' model. Model results include the sum of squares, mean of squares, numerator and denominator of degrees of freedom, f-values, and p-values for each term.

	Sum Sq	Mean Sq	NumDF	DenDF	F	P
Year	20.1478	10.0739	2	632.8613	73.5939	< 0.0001
Aspect	1.0229	0.3410	3	306.1927	2.4911	0.0603
Subunit	2.1638	1.0818	2	294.4794	7.9036	0.0005
Distance to YNP	1.3723	1.3723	1	294.4774	10.0258	0.0017
SWE	2.2039	2.2039	1	330.4974	16.1006	< 0.0001
Year:Subunit	0.9545	0.2386	4	592.5359	1.7433	0.1389
Year:Distance to YNP	3.3521	1.6760	2	602.1707	12.2442	< 0.0001
Year:SWE	0.1583	0.0791	2	668.2156	0.5784	0.5611

Table A6. Predicted 2024 recruitment and sapling stem counts as the response variables and 2006 mature, recruitment, and predicted stem counts as the predictors by 2006 browse level. Estimated values are back transformed from the log counts used in the model. Results include the mean, mean plus and minus standard errors, and compact letter display (CLD).

Response Variable	Browse Level	Mean	Mean - SE	Mean + SE	CLD
2024 recruitment stem count	High	15.2	14.4	16.1	a
	Medium	17.4	16.9	18.0	a
	Low	17.8	17.0	18.6	a
	Very low	24.8	23.0	26.7	b
2024 sapling stem count	High	12.7	12.1	13.2	a
	Medium	14.1	13.3	14.8	a
	Low	14.3	13.1	15.6	a
	Very low	14.7	14.0	15.3	a

Table A7**.** Results of estimated marginal means tests comparing differences in contrasts of 2006 browse level for 2024 predicted counts of recruitment and sapling aspen stems. Results include the β estimates, standard errors, degrees of freedom, z-ratios, and p-values.

Response Variable	Contrast	Estimate	SE	df	z	P
2024 recruitment stem count	High – Low	-0.1566	0.071	Inf	-2.2	0.1231
	High – Medium	-0.1365	0.065	Inf	-2.097	0.1539
	High – Very Low	-0.4864	0.093	Inf	-5.239	< 0.0001
	Low – Medium	0.0201	0.054	Inf	0.3731	0.9823
	Low – Very Low	-0.3298	0.085	Inf	-3.872	< 0.0001
	Medium – Very Low	-0.3499	0.08	Inf	-4.352	< 0.0001
2024 sapling stem count	High – Low	-0.0417	0.07	Inf	-0.592	0.9344
	High – Medium	0.1052	0.07	Inf	1.4991	0.4380
	High – Very Low	-0.019	0.103	Inf	-0.184	0.9978
	Low – Medium	0.1469	0.063	Inf	2.3356	0.0901

	Low – Very Low	0.0227	0.099	Inf	0.2305	0.9957
	Medium – Very Low	-0.1242	0.098	Inf	-1.263	0.5869

Table A8. Results of estimated marginal means tests of 2024 mature, recruitment, and sapling predicted stem counts by 2006 browse level and subunit. Results include the emmean, and compact letter display (CLD).

Response Variable	Browse Level	Subunit	emmean	CLD
2024 mature stem count	High	East River	1.864	b
	Medium	East River	1.726	b
	Low	East River	1.501	a
	Very Low	East River	1.775	ab
	High	Tom Miner	1.445	a
	Medium	Tom Miner	1.178	a
	Low	Tom Miner	2.400	b
	Very Low	Tom Miner	0.644	a
	High	West River	0.640	a
	Medium	West River	1.516	b
	Low	West River	1.676	b
	Very Low	West River	1.903	b
2024 recruitment stem count	High	East River	2.890	a
	Medium	East River	3.138	b
	Low	East River	3.319	c
	Very Low	East River	3.403	c
	High	Tom Miner	2.795	ab
	Medium	Tom Miner	3.040	b
	Low	Tom Miner	2.506	a
	Very Low	Tom Miner	3.584	c
	High	West River	2.484	ab
	Medium	West River	2.399	a
	Low	West River	2.812	b
	Very Low	West River	2.639	ab
2024 sapling stem count	High	East River	2.555	b
	Medium	East River	2.443	ab
	Low	East River	2.896	c
	Very Low	East River	2.109	a
	High	Tom Miner	2.217	a
	Medium	Tom Miner	2.609	b
	Low	Tom Miner	2.247	a
	Very Low	Tom Miner	2.082	a
	High	West River	3.157	b
	Medium	West River	2.562	a
	Low	West River	2.911	b

	Very Low	West River	3.796	c

Table A9. Results of estimated marginal means tests comparing differences in contrasts of 2024 mature, recruitment, and sapling aspen stems by 2006 browse level and subunit. Results include the β estimates, standard errors, degrees of freedoms, z-ratios, and p-values.

Response Variable	Contrast	Subunit	Estimate	SE	df	z	P
2024 mature stem count	High – Low	East River	0.3628	0.079	Inf	4.6191	< 0.0001
	High – Medium	East River	0.1376	0.072	Inf	1.9141	0.2220
	High – Very Low	East River	0.0891	0.191	Inf	0.4671	0.9663
	Low – Medium	East River	-0.225	0.078	Inf	-2.9019	0.0194
	Low – Very Low	East River	-0.274	0.193	Inf	-1.4174	0.4884
	Medium – Very Low	East River	-0.048	0.19	Inf	-0.2545	0.9942
	High – Low	Tom Miner	-0.955	0.339	Inf	-2.8169	0.0250
	High – Medium	Tom Miner	0.2668	0.337	Inf	0.7917	0.8583
	High – Very Low	Tom Miner	0.8004	0.437	Inf	1.8323	0.2581
	Low – Medium	Tom Miner	1.2218	0.18	Inf	6.7987	< 0.0001
	Low – Very Low	Tom Miner	1.7554	0.332	Inf	5.2844	< 0.0001
	Medium – Very Low	Tom Miner	0.5336	0.33	Inf	1.6179	0.3684
	High – Low	West River	-1.036	0.284	Inf	-3.6507	0.0015
	High – Medium	West River	-0.877	0.273	Inf	-3.2158	0.0071
	High – Very Low	West River	-1.263	0.327	Inf	-3.8614	< 0.001
	Low – Medium	West River	0.1594	0.209	Inf	0.7635	0.8709
	Low – Very Low	West River	-0.227	0.276	Inf	-0.8232	0.8435
	Medium – Very Low	West River	-0.387	0.263	Inf	-1.468	0.4570
2024 recruitment stem count	High – Low	East River	-0.43	0.042	Inf	-10.18	< 0.0001
	High – Medium	East River	-0.248	0.042	Inf	-5.8573	< 0.0001
	High – Very Low	East River	-0.514	0.09	Inf	-5.7024	< 0.0001
	Low – Medium	East River	0.1814	0.038	Inf	4.7393	< 0.0001
	Low – Very Low	East River	-0.084	0.088	Inf	-0.9556	0.7746
	Medium – Very Low	East River	-0.265	0.088	Inf	-3.0057	0.0141
	High – Low	Tom Miner	0.2881	0.151	Inf	1.9107	0.2234
	High – Medium	Tom Miner	-0.246	0.14	Inf	-1.755	0.2953
	High – Very Low	Tom Miner	-0.79	0.168	Inf	-4.7099	< 0.0001
	Low – Medium	Tom Miner	-0.534	0.093	Inf	-5.7257	< 0.0001
	Low – Very Low	Tom Miner	-1.078	0.131	Inf	-8.2481	< 0.0001
	Medium – Very Low	Tom Miner	-0.544	0.119	Inf	-4.5745	< 0.0001
	High – Low	West River	-0.328	0.158	Inf	-2.0801	0.1596
	High – Medium	West River	0.0846	0.141	Inf	0.5984	0.9326
	High – Very Low	West River	-0.156	0.217	Inf	-0.7184	0.8898
	Low – Medium	West River	0.4128	0.124	Inf	3.3306	0.0048
	Low – Very Low	West River	0.1726	0.206	Inf	0.8395	0.8356
	Medium – Very Low	West River	-0.24	0.193	Inf	-1.2433	0.5992

2024 sapling stem count	High – Low	East River	-0.341	0.053	Inf	-6.466	< 0.0001
	High – Medium	East River	0.1125	0.06	Inf	1.8756	0.2386
	High – Very Low	East River	0.4467	0.158	Inf	2.8289	0.0242
	Low – Medium	East River	0.4531	0.055	Inf	8.249	< 0.0001
	Low – Very Low	East River	0.7874	0.156	Inf	5.0451	< 0.0001
	Medium – Very Low	East River	0.3342	0.159	Inf	2.1065	0.151
	High – Low	Tom Miner	-0.031	0.149	Inf	-0.2059	0.9969
	High – Medium	Tom Miner	-0.392	0.14	Inf	-2.8018	0.0261
	High – Very Low	Tom Miner	0.1346	0.206	Inf	0.6535	0.9144
	Low – Medium	Tom Miner	-0.362	0.106	Inf	-3.4014	0.0037
	Low – Very Low	Tom Miner	0.1652	0.185	Inf	0.8944	0.8078
	Medium – Very Low	Tom Miner	0.5269	0.178	Inf	2.9641	0.0161
	High – Low	West River	0.2461	0.121	Inf	2.0295	0.1771
	High – Medium	West River	0.5954	0.119	Inf	4.9927	< 0.0001
	High – Very Low	West River	-0.638	0.164	Inf	-3.9025	< 0.001
	Low – Medium	West River	0.3493	0.113	Inf	3.0817	0.0111
	Low – Very Low	West River	-0.884	0.159	Inf	-5.552	< 0.0001
	Medium – Very Low	West River	-1.234	0.158	Inf	-7.8199	< 0.0001

Table A10. Modeled effects of 2006 recruitment predicted counts on 2024 mature predicted counts by 2006 browse level. Results include the browse level, recruitment trends, standard errors, degrees of freedom, z-ratios, and p-values.

Response Variable	Browse Level	Recruitment.trend	SE	df	z	P	CLD
2024 mature stem count	High	0.4090	0.0741	Inf	5.516	< 0.0001	b
	Medium	0.1045	0.0331	Inf	3.152	0.0016	ab
	Low	0.3030	0.0733	Inf	4.132	< 0.0001	a
	Very low	0.0959	0.0729	Inf	1.315	0.1884	a

Table A11. Results of estimated marginal trends comparing differences in contrasts of 2006 recruitment predicted counts on 2024 mature predicted counts by 2006 browse level. Results include the β estimates, standard errors, degrees of freedom, z-ratios, and p-values.

Response Variable	Contrast	Estimate	SE	df	z	P
2024 mature stem count	High – Low	0.30455	0.0807	Inf	3.775	0.0009
	High – Medium	0.10604	0.1030	Inf	1.026	0.7344
	High – Very Low	0.31311	0.1040	Inf	-3.006	0.0141
	Low – Medium	-0.19851	0.0799	Inf	-2.484	0.0625
	Low – Very Low	0.00856	0.0802	Inf	0.107	0.9996
	Medium – Very Low	0.20707	0.1040	Inf	1.999	0.1883

Table A12. Results of estimated marginal means tests comparing differences in trends of z-scaled 10-year average 2006 snow water equivalent (SWE) for 2024 predicted counts of mature, recruitment, and sapling stems by 2006 browse level. Results include SWE trends, standard errors, degrees of freedom, z-ratios, p-values, and compact letter display (CLD).

Response Variable	Browse Level	z.SWE trend	SE	df	z	P	CLD
2024 mature stem count	High	0.0593	0.0607	Inf	0.9771	0.3285	ab
	Medium	0.2581	0.0526	Inf	4.9051	< 0.0001	bc
	Low	0.0222	0.052	Inf	0.4261	0.6700	a
	Very Low	0.3686	0.0924	Inf	3.9874	< 0.0001	c
2024 recruitment stem count	High	0.4169	0.0322	Inf	12.961	< 0.0001	c
	Medium	0.0463	0.0273	Inf	1.6979	0.0895	a
	Low	0.2855	0.0216	Inf	13.215	< 0.0001	b
	Very Low	0.0366	0.0382	Inf	0.9573	0.3384	a
2024 sapling stem count	High	0.3266	0.031	Inf	10.546	< 0.0001	b
	Medium	0.2188	0.0328	Inf	6.6644	< 0.0001	ab
	Low	0.1581	0.0276	Inf	5.7246	< 0.0001	a
	Very Low	0.2582	0.0505	Inf	5.1115	< 0.0001	ab

Table A13. Results of estimated marginal means tests comparing differences in contrasts of z-scaled 10-year average 2006 snow water equivalent (SWE) for 2024 predicted counts of mature, recruitment, and sapling aspen stems by 2006 browse level. Results include the β estimates, standard errors, degrees of freedom, z-ratios, and p-values.

Response Variable	Contrast	Estimate	SE	df	z	P
2024 mature stem count	High – Low	0.0372	0.0798	Inf	0.4657	0.9665
	High – Medium	-0.199	0.0803	Inf	-2.475	0.0638
	High – Very Low	-0.309	0.1106	Inf	-2.795	0.0266
	Low – Medium	-0.236	0.0736	Inf	-3.207	0.0073
	Low – Very Low	-0.346	0.1065	Inf	-3.253	0.0063
	Medium – Very Low	-0.111	0.1065	Inf	-1.037	0.7275
2024 recruitment stem count	High – Low	0.1314	0.0387	Inf	3.3914	0.0039
	High – Medium	0.3707	0.0421	Inf	8.8034	< 0.0001
	High – Very Low	0.3804	0.0502	Inf	7.5817	< 0.0001
	Low – Medium	0.2393	0.0348	Inf	6.8816	< 0.0001
	Low – Very Low	0.249	0.0439	Inf	5.6681	< 0.0001
	Medium – Very Low	0.0097	0.0472	Inf	0.2053	0.9969
2024 sapling stem count	High – Low	0.1686	0.0415	Inf	4.0622	< 0.001
	High – Medium	0.1079	0.0451	Inf	2.3904	0.0789
	High – Very Low	0.0684	0.0593	Inf	1.1548	0.6554
	Low – Medium	-0.061	0.0429	Inf	-1.415	0.4901
	Low – Very Low	-0.100	0.0576	Inf	-1.739	0.3033
	Medium – Very Low	-0.039	0.0602	Inf	-0.655	0.9139

Table A14. Results of estimated marginal means tests comparing differences in trends of 2024 mature, recruitment, and sapling predicted counts by z-scaled distance to Yellowstone National Park (YNP) and 2006 browse level. Results include distance to YNP trends, standard errors, degrees of freedom, z-ratios, p-values, and compact letter display (CLD).

Response Variable	Browse Level	z.dist trend	SE	df	z	P	CLD
2024 mature stem count	High	-0.1844	0.0609	Inf	-3.0284	0.0025	a
	Medium	-0.1137	0.0496	Inf	-2.2912	< 0.0001	a
	Low	0.22514	0.0506	Inf	4.4535	0.0220	b
	Very Low	-0.3607	0.1164	Inf	-3.0992	0.0019	a
2024 recruitment stem count	High	0.09242	0.0341	Inf	2.7137	0.0067	b
	Medium	0.11015	0.0238	Inf	4.6339	0.1035	b
	Low	-0.036	0.0221	Inf	-1.6283	< 0.0001	a
	Very Low	0.13874	0.0476	Inf	2.9167	0.0035	b
2024 sapling stem count	High	-0.1671	0.0368	Inf	-4.5383	< 0.0001	a
	Medium	0.35258	0.0294	Inf	12.01	< 0.0001	b
	Low	-0.2221	0.0291	Inf	-7.6288	< 0.0001	a
	Very Low	0.65592	0.0746	Inf	8.7888	< 0.0001	c

Table A15. Results of estimated marginal means tests comparing differences in contrasts of 2024 mature, recruitment, and sapling predicted counts by z-scaled distance to Yellowstone National Park (YNP) and 2006 browse level. Results include the β estimates, standard errors, degrees of freedom, z-ratios, and p-values.

Response Variable	Contrast	Estimate	SE	df	z	P
2024 mature stem count	High – Low	-0.4095	0.0787	Inf	-5.204	< 0.0001
	High – Medium	-0.0707	0.0782	Inf	-0.904	0.8029
	High – Very Low	0.1763	0.1312	Inf	1.343	0.5352
	Low – Medium	0.3388	0.0705	Inf	4.805	< 0.0001
	Low – Very Low	0.5858	0.1268	Inf	4.620	< 0.0001
	Medium – Very Low	0.2470	0.1264	Inf	1.953	0.2061
2024 recruitment stem count	High – Low	0.1285	0.0402	Inf	3.198	0.0076
	High – Medium	-0.0177	0.0412	Inf	-0.430	0.9734
	High – Very Low	-0.0463	0.0583	Inf	-0.795	0.8567
	Low – Medium	-0.1462	0.0321	Inf	-4.549	< 0.0001
	Low – Very Low	-0.1748	0.0522	Inf	-3.347	0.0045
	Medium – Very Low	-0.0286	0.053	Inf	-0.539	0.9494
2024 sapling stem count	High – Low	0.055	0.0469	Inf	1.170	0.6450
	High – Medium	-0.5197	0.0471	Inf	-11.036	< 0.0001
	High – Very Low	-0.823	0.0832	Inf	-9.890	< 0.0001
	Low – Medium	-0.5747	0.0413	Inf	-13.90	< 0.0001
	Low – Very Low	-0.878	0.0801	Inf	-10.96	< 0.0001

	Medium – Very Low	-0.3033	0.0802	Inf	-3.782	0.0009

Table A16. Results of estimated marginal means tests comparing differences in trends of 2024 mature, recruitment, and sapling predicted counts with 2006 conifer encroachment (≥ 10% reproducing conifer canopy cover) by 2006 browse level. Results include conifer encroachment trends, standard errors, degrees of freedom, z-ratios, p-values, and compact letter display (CLD).

Response Variable	Browse Level	Conifer trend	SE	df	z	P	CLD
2024 mature stem count	High	-0.2034	0.103	Inf	-1.973	0.0484	a
	Medium	-0.1383	0.101	Inf	-1.376	0.0001	a
	Low	-0.4223	0.108	Inf	-3.914	0.1688	a
	Very Low	0.1387	0.197	Inf	0.7036	0.4817	a
2024 sapling stem count	High	-0.3976	0.074	Inf	-5.357	< 0.0001	a
	Medium	-0.6114	0.057	Inf	-10.66	< 0.0001	a
	Low	0.3883	0.067	Inf	5.7838	< 0.0001	b
	Very Low	-0.3664	0.113	Inf	-3.252	< 0.0001	a

Table A17. Results of estimated marginal means tests comparing differences in contrasts in 2024 predicted counts of mature and sapling aspen stems by 2006 browse level and 2006 conifer encroachment (≥ 10% reproducing conifer canopy cover). Results include the β estimates, standard errors, degrees of freedoms, z-ratios, and p-values.

Response Variable	Browse Level	Estimate	SE	df	z	P
2024 mature stem count	High – Low	0.2189	0.148	Inf	1.47	0.4528
	High – Medium	-0.0651	0.143	Inf	-0.46	0.9685
	High – Very Low	-0.3422	0.222	Inf	-1.54	0.4147
	Low – Medium	-0.2840	0.145	Inf	-1.95	0.2065
	Low – Very Low	-0.5610	0.225	Inf	-2.50	0.0604
	Medium – Very Low	-0.2771	0.221	Inf	-1.25	0.5934
2024 sapling stem count	High – Low	-0.7859	0.100	Inf	-7.85	< 0.0001
	High – Medium	0.2139	0.094	Inf	2.28	0.1026
	High – Very Low	-0.0312	0.135	Inf	-0.231	0.9956
	Low – Medium	0.9998	0.088	Inf	11.323	< 0.0001
	Low – Very Low	0.7547	0.131	Inf	5.755	< 0.0001
	Medium – Very Low	-0.2451	0.126	Inf	-1.939	0.2118

Table A18. Estimated proportion recruitment aspen stems observed per year. Estimated values are back transformed from the log counts used in the model. Results include the mean, mean plus and minus standard errors, and compact letter display (CLD).

Year	Mean	Mean - SE	Mean + SE	CLD
1991	0.0579	0.0277	0.0983	a
2006	0.1292	0.0822	0.1848	b
2024	0.3465	0.3465	0.4912	c

Table A19. Results of an estimated marginal means test comparing differences in contrasts of the proportion of aspen recruitment stems observed per year. Results include the β estimates, standard errors, degrees of freedom, t-ratios, and p-values. A positive estimate indicates an increase over time.

Contrast	Estimate	SE	df	t	P
1991 – 2006	0.125	0.0405	685	-1.3.080	0.0061
1991 – 2024	0.460	0.0392	620	-11.747	< 0.0001
2006 – 2024	0.335	0.0394	621	-8.516	< 0.0001

Table A20. Estimated proportion recruitment aspen stems observed per year for each subunit. Estimated values are back transformed from the log counts used in the model. Results include the mean, mean plus and minus standard errors, and compact letter display (CLD).

Year	Subunit	Mean	Mean - SE	Mean + SE	CLD
1991	East River	0.1469	0.09970	0.2015	a
2006	East River	0.2048	0.14671	0.2697	a
2024	East River	0.4545	0.38361	0.5263	b
1991	Tom Miner	0.1410	0.00402	0.1410	a
2006	Tom Miner	0.2193	0.03617	0.2193	a
2024	Tom Miner	0.6177	0.31689	0.6177	b
1991	West River	0.0684	0.00173	0.0684	a
2006	West River	0.1944	0.01714	0.1944	a
2024	West River	0.4877	0.19942	0.4877	b

Table A21. Results of an estimated marginal means test comparing differences in contrasts of the proportion of aspen recruitment stems observed per year for each subunit. Results include the β estimates, standard errors, degrees of freedom, t-ratios, and p-values. A positive estimate indicates an increase over time.

Contrast	Subunit	Estimate	SE	df	t	P
1991 – 2006	East River	0.0762	0.039	679.49	-1.9585	0.1234
1991 – 2024	East River	0.3465	0.037	610.34	-9.3013	< 0.0001
2006 – 2024	East River	0.2703	0.038	623.13	-7.0634	< 0.0001
1991 – 2006	Tom Miner	0.1152	0.081	622.13	-1.4174	0.3325
1991 – 2024	Tom Miner	0.5269	0.082	603.97	-6.4042	< 0.0001
2006 – 2024	Tom Miner	0.4117	0.079	601.24	-5.2178	< 0.0001
1991 – 2006	West River	0.1824	0.082	613.36	-2.229	0.0672
1991 – 2024	West River	0.5065	0.08	603.46	-6.3539	< 0.0001
2006 – 2024	West River	0.3241	0.082	602.67	-3.9383	< 0.0001

Table A22. Results of an estimated marginal means test comparing differences in trends of the proportion of aspen recruitment stems observed by z-scaled annual average snow water equivalent (SWE) per year. Results include SWE trends, standard errors, degrees of freedom, t-ratios, p-values, and compact letter display (CLD).

Year	z.SWE trend	SE	df	t	P	CLD
1991	0.0797	0.0204	816	3.900	0.0001	a
2006	0.0708	0.0366	810	1.933	0.0536	a
2024	0.1147	0.0361	813	3.178	0.0015	a

Table A23. Results of an estimated marginal means test comparing differences in contrasts of the proportion of aspen recruitment stems observed by annual average snow water equivalent (SWE) between years. Results include the β estimates, standard errors, degrees of freedom, t-ratios, and p-values.

Contrast	Estimate	SE	df	t	P
1991 – 2006	0.00894	0.0375	708	0.238	0.9692
1991 – 2024	-0.03503	0.0372	705	-0.942	0.6136
2006 – 2024	-0.04397	0.0450	596	-0.978	0.5910

Table A24. Results of an estimated marginal means test comparing differences in trends of the proportion of aspen recruitment stems observed by distance to Yellowstone National Park (YNP) (m) per year. Results include z-scaled distance to YNP trends, standard errors, degrees of freedom, t-ratios, p-values, and compact letter display (CLD).

Year	z.dist trend	SE	df	t	P	CLD
1991	-0.0279	0.0254	801	-1.099	0.2720	a
2006	0.0677	0.0253	802	2.671	0.0077	b
2024	0.1286	0.0258	802	4.988	< 0.0001	b

Table A25. Results of an estimated marginal means test comparing differences in contrasts of the proportion of aspen recruitment stems observed by distance to YNP (m) between years. Results include the β estimates, standard errors, degrees of freedoms, t-ratios, and p-values.

Contrast	Estimate	SE	df	t	P
1991 – 2006	-0.0956	0.0315	597	-3.034	0.0071
1991 – 2024	-0.1565	0.0319	617	-4.900	< 0.0001
2006 – 2024	-0.0609	0.0318	602	-1.913	0.1358