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Novel Fire and Herbivory Regime Impacts on Forest Regeneration and Plant Community Assembly

Devri A. Tanner

A dissertation submitted to the faculty of
Brigham Young University
in partial fulfillment of the requirement for the degree of

Doctor of Philosophy

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ABSTRACT

Novel Fire and Herbivory Regime Impacts on Forest
Regeneration and Plant Community Assembly

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Doctor of Philosophy

Human activities are increasing the occurrence of megafires that have the potential to alter the ecology of forest ecosystems. The objective of this study was to understand the impact of a 610-km^2 megafire on patterns of forest regeneration and herbivory of three forest types (aspen/fir, oak/maple, and pinyon/juniper) within the burn scar. Sapling density, meristem removal, and height were measured across a transect network spanning the area of the burn scar over three years from 2019-2021. The network consisted of 17 burned/unburned transect pairs in adjacent burned/unburned forest stands (6 aspen/fir, 5 oak/maple, and 6 pinyon/juniper). Species that regenerated through sprouting generally responded positively to fire while regeneration from seed showed very little post-fire response. Browse pressure was concentrated on deciduous tree species and tended to be greater in burned areas but the effect diminished over time. Meristem removal of sprouting species was below the critical threshold resulting in positive vertical growth across years. Our results indicate that forest regeneration within the megafire scar was generally positive and experienced sustainable levels of ungulate browsing that are likely to result in forest recruitment success.

Novel fire regimes are becoming increasingly common and megafires have burned across ecotonal boundaries across multiple forest types. Plant community structure and composition may be critically affected by changing fire regimes. Our objective was to investigate how a megafire that burned across multiple forest types impacted understory plant community assembly and biodiversity. Paired vegetation transects were installed in burned and unburned areas across aspen/fir, oak/maple, and pinyon/juniper forests within the 2018 Pole Creek Megafire burn scar. Percent cover of understory plants was measured in the summer of 2022 and plants were identified to the species level. Richness and diversity indices were then calculated and analyzed using mixed effects models. Fire decreased species richness of the aspen/fir forest understory and increased plant cover in pinyon/juniper forests, while not significantly impacting oak/maple understories. The significant effects of fire were largely driven by changes in forb species. Fire decreased the richness of native plants in aspen/fir forests but increased the richness of non-native plants in oak/maple and pinyon/juniper forests. Non-native plant abundance also increased in post-fire pinyon/juniper forests. Our results suggest that forest understory communities show variable responses to megafires that burn across multiple forest types with important implications for post-fire plant community structure, diversity, and invasibility.

Large mammal herbivores (ungulates) are increasing in number and spreading into novel habitats throughout the world. Their impact on forest understory plant communities is strong and varies by herbivore, plant growth form, and season. The objective of this study was to determine the individual and collective herbivory impacts of native versus domestic ungulates on the understory plant community composition of post-fire aspen forests. Four-way fencing treatments were installed in 2012 to separate ungulate species, and Daubenmire frames were used to collect percent cover estimates for each understory plant species. Vegetation data were later used to calculate richness and diversity indices. Total understory plant cover, richness, and diversity were not significantly impacted by the herbivory fencing treatment. However, woody plant species' percent cover was 90% greater in full ungulate exclusion plots than in the fenceless controls. Herbivores likely targeted woody plant species due to their high nutrient levels that last longer into the winter than those of forb or graminoid species. Herbivory treatment did not affect non-native species. Our results indicate that herbivore fencing can protect forest understory plant communities, particularly the woody species. Successful regeneration of woody species can benefit the diversity of the entire understory plant community and preserve forest structure.

Keywords: wildfire, novel fire regime, disturbance, sapling, forest recruitment, ungulate browse ungulate herbivory, exclosures, forest understory, woody plants, aspen, megafire, native plants, non-native species, forbs, fir, oak, maple, pinyon, juniper

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CHAPTER 1

Novel Fire and Herbivory Regime Impacts on Forest Regeneration and Plant Community Assembly

Impacts of changing ungulate populations and behaviors on habitat and plant communities

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INTRODUCTION

Plant and Ungulate Coevolution

Plants and animals have strong, and often long-term, coevolutionary histories (Hobbs, 1996). The coevolution of ungulates and plants (i.e. the foraging history) in a landscape is often characterized by plant diversity shifting to favor plants that can either tolerate or avoid foraging by the resident herbivores (Boavista et al., 2019; Eldridge et al., 2018). The coevolution of plants and herbivores has created an enhanced capacity for plants to avoid or tolerate defoliation by evolving to be prostrate or decumbent, have deciduous leaves or high shoot density, grow from stolons or rhizomes or underground nutrient reserves, or have faster rates of transpiration and photosynthesis (Boavista et al., 2019; Briske, 1996; Hobbs, 1996; Milchunas & Lauenroth, 1993). Plant regrowth capacity after herbivory damage is increased with longer histories of foraging by the same herbivore (B. V. Li & Jiang, 2021; Milchunas & Lauenroth, 1993). Plants with a long foraging history have higher growth responses to nitrogen in the form of urea and ammonium (which largely come from dung and feces) as compared to other soil nitrogen, especially when they are damaged by defoliation (Hobbs, 1996). Foraging history can affect habitats and plant communities by modulating the effects of novel ungulate herbivory in concert with ecosystem productivity and herbivory intensity (Milchunas & Lauenroth, 1993). Although long foraging histories are less common in deserts, uneaten, drought-tolerant plants are less affected by novel foraging because adaptations for plant tissue loss to drought are similar to those for herbivory damage (Milchunas & Lauenroth, 1993). The co-evolution of ungulates and plant communities is integral to understanding how biomes will shift when the historic herbivory regime is altered (Eldridge et al., 2018).

Disrupting the coevolutionary history between large mammal herbivores and the plant community leads to novel herbivory regimes (B. V. Li & Jiang, 2021; Milchunas & Lauenroth, 1993; Whitehead et al., 2014; Yan et al., 2015). Altered foraging histories are often perceived as the introduction of novel herbivores (Salgado-Luarte et al., 2018); however, foraging histories can be disturbed through novel ungulate abundances, different temporal dynamics, new behaviors, altered forage selectivity or strategy, or any combination thereof (Figure 1) (Eldridge et al., 2018; Milchunas & Lauenroth, 1993). While areas with long grazing histories and high productivity are often more resilient and reap benefits from moderate herbivory (Boavista et al., 2019; Salgado-Luarte et al., 2018), increasing herbivory intensity past the historic thresholds of any ecosystem can alter primary productivity and nutrient cycling (Díaz et al., 2007; B. V. Li & Jiang, 2021), decrease plant diversity, functional diversity, canopy height and coverage (Côté et al., 2004; Egelkraut et al., 2018; Yan et al., 2015), and ultimately diminish habitat and conservation value (Bernes et al., 2018). Unaltered herbivory regimes resist invasion (A. K. Knapp et al., 1999); however, novel grazing can reduce biotic resistance and give herbivory-resistant plants a competitive advantage (Briske, 1996; Olofsson & Post, 2018; Ward et al., 2013). Adding domestic ungulates to ecosystems with no history of grazing can greatly impact biodiversity (Whitehead et al., 2014), though ecosystems that have evolved with livestock are less impacted by modern-day livestock grazing (B. V. Li & Jiang, 2021). When foraging histories are disrupted in the short term, such as when livestock are added and then removed, biomes can either revert to pre-herbivory status or be invaded by exotics (Whitehead et al., 2014). Future research must take foraging history into account as it can help explain variation between biome responses and possible adaptations that have come from their histories and may influence future herbivory regimes (B. V. Li & Jiang, 2021; Milchunas & Lauenroth, 1993).

HERBIVORY INTENSITY

Ungulate Abundance

Biodiversity Changing ungulate abundance alters plant diversity by affecting niche space and plant regeneration (Connell, 1978; Pruszenski & Hernández, 2020; Schütz et al., 2003). As suggested by the intermediate disturbance hypothesis, moderate levels of herbivory create high plant diversity by opening niche space and stimulating regeneration (Connell, 1978; A. K. Knapp et al., 1999; Pruszenski & Hernández, 2020; Schütz et al., 2003). Moderate levels of herbivory often increase the diversity of both woody and herbaceous species by reducing plant-plant competition and opening niche space (Faison et al., 2016); but at consistently high levels of herbivory, species richness declines because growth rates may not be fast enough for successful plant regeneration (Adey & Loveland, 2007; A. K. Knapp et al., 1999; Rhodes, Larsen, & St. Clair, 2018). Chronic overgrazing as a result of increasing ungulate abundance thus favors browse-tolerant species and low plant diversity (Adey & Loveland, 2007; Frank, 2005; X. lai Li et al., 2013; Royo & Carson, 2006). Decreasing ungulate abundances offers fewer disturbances, which allows the best plant-plant competitors to dominate and reduce plant diversity in the ecosystem (Bernes et al., 2018; Faison et al., 2016).

Structure & Function Changing ungulate abundance alters plant structure and function by affecting plant growth and productivity (Lloyd et al., 2010; Manier & Hobbs, 2007; Rhodes, Larsen, Maxwell, et al., 2018). Moderate herbivory levels create microsites with increased bare ground, light, and soil water availability, which increases seedling emergence and regulates competition among plants (Bernes et al., 2018; Manier & Hobbs, 2007; Martin & Wilsey, 2006). Increased herbivory levels can alter the structure of an ecosystem by changing the composition of plants to mainly consist of grazing-avoidant species that are short or flat, graze-tolerant, stoloniferous, or annuals (Lloyd et al., 2010; Royo & Carson, 2006). Unsustainably high browsing can prevent woody species from reaching canopy levels, which creates stunted, bush-like growth forms of tree species (Milne-Rostkowska et al., 2020; Royo & Carson, 2006). Increasing ungulate abundances can also alter plant productivity by increasing decomposition and nutrient cycling at foraging and defecation sites (Staver et al., 2021); however, if ungulate populations rise or fall too dramatically, increased plant productivity will be lost due to inhibited plant regeneration.

Invasion Increased ungulate abundance can leave ecosystems more susceptible to invasion by increasing plant resource availability, reducing biotic resistance, and increasing dispersal rates (Baltzinger et al., 2019; Kuebbing et al., 2013; MacLaren et al., 2014; Parker et al., 2006). Greater plant resource availability due to increased herbivory rates can weaken resistance to invasion by increasing the amount of light, space, and soil nutrients available for invasive plants (Davis et al., 2000; Kuebbing et al., 2013). Additionally, reduced plant diversity due to ungulate overabundance can decrease plant community resistance to invasion (Kuebbing et al., 2013). Invasion depends heavily on the dispersal of diaspores to susceptible landscapes, and dispersal rates increase alongside increases in ungulate abundance (Kalisz et al., 2014;

Myers et al., 2004). In biomes where ungulate populations are shrinking, invasion rates will be lower as resource availability and dispersal decrease while biotic resistance will increase. The longer a site remains undisturbed by herbivory the more difficult invasion becomes due to a lack of available resources, niche space, and dispersal for new species (Olofsson & Post, 2018).

Biome Trends in Ungulate Abundance Ungulate abundances are changing worldwide, with forest and grassland biomes typically increasing in abundance, and tundra biomes typically stabilizing or decreasing in abundance. Overabundant ungulates in forest biomes throughout the world are increasing invasion rates (Kalisz et al., 2014; Ward et al., 2013), reducing biotic resistance and resilience (Katona et al., 2013; Meier et al., 2017), suppressing plant recruitment (Mason et al., 2010; Rhodes et al., 2017; Shelton et al., 2014), and threatening conversion to alternative stable states (Royo & Carson, 2006). Increased deer density specifically decreases species richness in forests (Vavra et al., 2007). In the Great Smoky Mountains National Park, USA, the invasive grass *Microstegium vimineum* increased as ungulate browsing created more available space and light by decreasing woody plant cover and richness (Kuebbing et al., 2013). A study of overabundant ungulates in British Columbian forests found a positive effect on bryophyte diversity due to ungulates reducing their competition with vascular plants (Chollet et al., 2013). Increasing ungulate populations in grasslands worldwide are changing plant diversity by promoting herbivory tolerant communities (Schütz et al., 2003) and reducing native grasses which increases invasive grass abundance (Berger et al., 2020). Ungulate population sizes in the arctic tundra naturally fluctuate due to forage quality and availability, weather, insects, and human influences (Egelkraut et al., 2018; Jandt et al., 2017; Zamin & Grogan, 2012). While current Alaskan caribou populations are relatively stable (Jandt et al., 2017), herds in Canada and elsewhere are in decline (Zamin & Grogan, 2012). Novel increases in ungulate abundance can shift plant communities to be graminoid-dominated in the space of a few years, lasting up to a decade without grazing (Egelkraut et al., 2018), while novel decreases can encourage shrub encroachment (Olofsson & Post, 2018). Ungulate herbivory can cause shifts in tundra vegetation by increasing soil temperatures and nutrient turnover, and by favoring plants that can tolerate repetitive herbivory and trampling (Egelkraut et al., 2018; Meier et al., 2017; Zamin & Grogan, 2012).

Temporality

Ungulate temporality refers to movements such as migration, grazing rotations, seasonal shifts, and diurnal patterns.

Biodiversity Temporal ungulate movement can increase plant species richness and abundance through seasonal shifts, rotational grazing, and migration that allow plants to regenerate during a resting period (Augustine & McNaughton, 1998; Boavista et al., 2019; Kauffman et al., 2021). In ecosystems that experience seasonal winters, ungulate diets vary temporally due to exclusion from preferred foraging sites that become inaccessible in the snow or ice (Bee et al., 2010; Rhodes, Larsen, & St. Clair, 2018). Many ecosystems are experiencing shorter winters due to climate change, which means ungulates will spend more time foraging in those areas to the potential detriment of plant diversity (Kauffman et al., 2021; Rhodes, Larsen, & St. Clair, 2018). Rotational grazing can increase species richness by decreasing competition and increasing facilitation of grazing-sensitive species (Boavista et al., 2019). In contrast, continuous grazing can decrease species richness by altering palatable species' spread and abundance (Boavista et al., 2019). Decreased migratory behavior in ungulates due to habitat fragmentation leaves less time for browsed plants to regenerate, and plant diversity may be lost (Vavra et al., 2007).

Structure & Function Ungulate temporality is an important yet diminishing component of global herbivory regimes because it affects ecosystem structure and function by altering productivity and resource availability (Boavista et al., 2019; Munyati, 2018; Vavra et al., 2007). Temporal fluctuations in herbivore pressure (e.g., migration, sustainable livestock rotations) relieve top-down pressures long enough to allow plant community regeneration (Aikens et al., 2020; Boavista et al., 2019; Rhodes, Larsen, Maxwell, et al., 2018). Temporal ungulate movement can increase productivity by increasing the biomass of dominant plant species and allowing the growth of new species that were excluded under continuous herbivory (Boavista et al., 2019). Continuous grazing can lead to differentially grazed patches due to herbivore preferences, while rotational grazing encourages less selective herbivory which improves ecosystem resilience and diverse resource use (Boavista et al., 2019). Regeneration through temporal herbivory relief will be more challenging to maintain as ungulate population densities increase (Augustine & McNaughton, 1998). Ungulate communities are migrating less due to human infrastructure, which increases the concentration of grazing, nutrient cycling, and soil compaction or erosion, leading to a homogenization of the plant community (Munyati, 2018; Vavra et al., 2007).

Invasion Altered ungulate temporality can increase plant invasion by increasing dispersal rates and resource availability (Boavista et al., 2019; Dorrough et al., 2007; Vavra et al., 2007). Increased livestock movement and transportation can promote invasion via dispersal across even broader ranges (Dorrough et al., 2007). Invasion potential is also increased as heightened herbivore pressure increases resource availability due to declining migration rates (Vavra et al., 2007). Constant herbivory creates many open soil patches that are highly susceptible to invasion (Boavista et al., 2019).

Biome Trends in Temporality Ungulate temporality is globally shifting, with most biomes experiencing decreased ungulate temporality due to habitat fragmentation and climate change (Kauffman et al., 2021; Vavra et al., 2007). In forests, decreased migration rates can harm plant diversity and plant reproduction by decreasing dispersal and colonization rates, and by increasing temporal overlap between herbivory and plant flowering times (Frank, 2005). Forest biomes may experience winters that create seasonal variation in ungulate movements (Bee et al., 2010; Rhodes, Larsen, & St. Clair, 2018), though climate change is decreasing snowfall in some biomes (Kauffman et al., 2021). Grassland biomes are experiencing less migratory behavior across the board (Geremia et al., 2019; Kauffman et al., 2021) and increased grazing rotations in productive grasslands (Boavista et al., 2019; Dorrough et al., 2007) which both affect productivity, diversity, and invasibility (Boavista et al., 2019; Dorrough et al., 2007; Geremia et al., 2019; Kauffman et al., 2021). An African rangeland study found that browser and most grazer distributions changed seasonally, but mixed feeders and one grazer changed diurnally (Schuette et al., 2016). In tundra biomes, snow governs ungulate temporality by making it more difficult for them to move and obtain food, thus expending more energy if they remain in snowy areas rather than leaving to more desirable locations (Kauffman et al., 2021; Olofsson et al., 2009). Across biomes, large populations can be supported if they are migratory but habitat fragmentation, climate change, and barriers to movement are threatening and disrupting migrations of many biomes (Kauffman et al., 2021).

Behavior

For the purposes of this section, ungulate behavior refers to activities such as rooting, trampling, vigilance, and the animals' tendency to be solitary or in a herd (Fortin et al., 2005; Vavra et al., 2007). These behaviors are relevant in a discussion of global herbivory regimes because they accentuate the effect that herbivores have on habitat and plant communities (Vavra et al., 2007).

Biodiversity Ungulate behavior affects plant species richness and abundance through altered soil quality and biomass removal (Lima & Dill, 1990; Mishra & Upadhyay, 2021; J. Ignacio Ramirez et al., 2018). Ungulate trampling causes soil compaction that can alter plant abundance by reducing seedling emergence (J. Ignacio Ramirez et al., 2018). Body size further accentuates the impact of trampling, as larger ungulates like cattle trample more area because they typically have shorter legs and thus shorter strides (Cumming & Cumming, 2003). The amount of forage that ungulates eat affects plant abundance, and the "landscape of fear" caused by predators keeps the herbivores from overeating (Mishra & Upadhyay, 2021). Herbivores often have to balance tradeoffs between optimal forage and predation risks (Lima & Dill, 1990) but as predation risks change due to predator losses herbivore vigilance may decrease, leading to higher herbivory levels (Berger et al., 2020; Bernes et al., 2018)

Structure & Function Ungulate behavior alters structure and function by affecting plant cover, nutrient cycling, and soil quality (Calkoen et al., 2021; J. Ignacio Ramirez et al., 2018; Vavra et al., 2007). Herbivores must balance plant toxin levels with predator threats, which can indirectly help plant survival and thus plant cover (McArthur et al., 2012). Even the perceived presence of large carnivores reduces the browse intensity and visitation time of large herbivores (Calkoen et al., 2021). Nutrient cycling within an ecosystem can be altered when ungulates eat lower-quality diets because they think they are at risk of predation (Calkoen et al., 2021). Waste deposition from lower-quality diets can lead to plants with decreased digestible content, yet higher protein content (Dorrough et al., 2007; Hamel & Côté, 2007). Altered ungulate populations may also lead to novel behaviors of rooting and trampling that can affect structure and function by exposing soil, increasing erosion, and slowing decomposition rates (Muñoz et al., 2009; Vavra et al., 2007). Trampling will affect the ecosystem functions of soil compaction and water infiltration, which in turn will affect seedling survival and regeneration (Cumming & Cumming, 2003; J. Ignacio Ramirez et al., 2018). Trampling effects can be cumulative in the long term and difficult to reverse (Cumming & Cumming, 2003).

Invasion Ungulate behavior can enhance invasion potential by altering biotic resistance and resource availability (Roberts & Johnson, 2021; Vavra et al., 2007). Increased trampling negatively affects biotic resistance by elevating runoff and erosion rates, and by disrupting soil through compaction or detachment (Vavra et al., 2007). Large herbivores can also disrupt soil on wet slopes through displacement (solifluction), which creates large patches of bare ground that can be readily invaded (Vavra et al., 2007). Disruption of the soil and loss of plant cover will also increase the amount of resources available for invasive plants to use (Shen et al., 2016).

Biome Trends in Behavior Ungulate behavior is changing across biomes, with behavioral effects on plant communities typically being elevated or diminished by changing ungulate abundance or species of ungulate. Forests are seeing increases in behavioral effects of ungulates such as trampling that can be beneficial to stands with low ungulate abundance (Hancock et al., 2010) but detrimental to overpopulated stands (J. Ignacio Ramirez et al., 2018). Heightened ungulate vigilance in forests due to increased predator abundance can reduce herbivory stress on preferred forage (Calkoen et al., 2021; Fortin et al., 2005). Some behavior is based on ungulate population size, such as when larger herds lead to more daytime herbivory caused by either safety in numbers or intraspecific competition (Juan Ignacio Ramirez et al., 2021). Non-native ungulates suppress valuable plant species in Hawaii through rooting and trampling to the point that the plants must be actively recolonized to maintain the community structure (Cole & Litton, 2014). Lichen is an important forage source in tundra biomes and reindeer can trample a year's worth of lichen forage in one week; however, humid lichen shows moderate to insignificant damage following ungulate trampling while dry lichen is severely damaged (Heggenes et al., 2017). In alpine tundra and subalpine forests, female mountain goats traded better forage for safety from predation while they had young offspring, which led to a vegetation pattern with more digestible plants farther from safety (Hamel & Côté, 2007). Humans can alter ungulate behavior by creating a landscape of fear, which is more apparent in open spaces where it is easier to detect ungulates and harder for them to escape (Mols et al., 2022).

PLANT TISSUE TARGETED

Grazer vs Browser

Ungulate forage strategies include that of browsers, grazers, and intermediate feeders (Hofmann, 1989; Rhodes, Larsen, & St. Clair, 2018). Browsers primarily eat high-quality forage from woody plants or forbs while grazers tend to eat lower-quality graminoids (Rhodes, Larsen, & St. Clair, 2018; Sankey et al., 2006). Intermediate or mixed feeders will eat a combination of graminoids, forbs, and woody plant tissue, according to what is most available (Rhodes, Larsen, & St. Clair, 2018). Different forage strategies exist because of morphophysiological differences such as body size and digestive system (Hanley, 1982; Rhodes, Larsen, & St. Clair, 2018).

Biodiversity Ungulate forage strategy alters plant species richness and abundance by changing ratios of woody to herbaceous plant matter (Box et al., 2016; Kuebbing et al., 2013). Browsing can have both negative and positive effects on plant diversity, as it can decrease woody species richness while indirectly increasing graminoid richness (Kuebbing et al., 2013). Grazers can also increase species richness locally, particularly as ecosystems become increasingly productive (Frank, 2005). Plant diversity will be affected when one foraging strategy becomes more prevalent than the other has been historically, such as when grazers take the place of browsers, which typically leads to an increase of woody plants due to herbivory release from browsers (Box et al., 2016).

Structure & Function Changes in ungulate forage strategy alter plant composition, productivity, and nutrient cycling (Box et al., 2016; Hofmann, 1989; Sitters et al., 2017; Staver et al., 2021). Furthermore, when changing ungulate populations alters the ratio of woody to herbaceous plants, the ecosystem will no longer support the same herbivore community (Espunyes et al., 2019). Browsing allows grasses to grow easier than trees because browsing inhibits sapling growth and recruitment, which reduces canopy biomass (Box et al., 2016). Grazing, on the other hand, indirectly increases woody plants by decreasing fire frequency through consuming continuous fine fuel loads (Staver et al., 2009). Thus, increasing grazer-to-browser ratios (often by increasing cattle livestock) leads to woody plant encroachment (Burke, 2004). Unlike grazers or browsers, mixed feeders are much more flexible in their diet and can adjust their foraging behavior to changes in the plant community structure (Espunyes et al., 2019; Sankey et al., 2006). Grazing can increase plant productivity by increasing decomposition rates and nutrient cycling through defecation and urination, and by increasing light availability (Sitters et al., 2017; Staver et al., 2021). However, it is important to note that the biggest increases in productivity come when grazing is either constant and intermediate, or episodic and intense (Staver et al., 2021). Both graminoids and woody plants benefit from grazing-induced improvements in nutrient cycling rates (Staver et al., 2021).

Invasion Ungulate forage strategy can change invasion potential by altering biotic resistance, nutrient availability, and soil quality (Beever et al., 2006; Dorrough et al., 2007; Nilar et al., 2019). All forage strategies modulate plant-plant competition, which can dampen the competitive advantage of invasive plants (Nilar et al., 2019; Royo & Stanovick, 2019). Browsers may decrease biotic resistance and impede ecosystem regeneration by preventing native seedling establishment due to leaf and stem damage (Nilar et al., 2019). Occasionally, browsers can help recover biotic resistance through targeted herbivory that reduces woody invasive plants, and in turn improves the quality of the herbaceous understory (Mundahl & Walsh, 2022). While grazing typically opens niche space for invasion by unpalatable plants, invasion brought on by heavy grazing can also help native plants grow when unpalatable species exhibit a nursing effect for grazing-sensitive plants (Dorrough et al., 2007; Oduor et al., 2018). Increased grazing pressure often harms native species richness and redistributes an increased amount of nutrients to the benefit of invasive plants (Beever et al., 2006; Dorrough et al., 2007). Grazing can disturb soils by increasing bare patches, and thus erosion probability, which creates space for invasive species to take hold and begin to thrive (Beever et al., 2006).

Biome Trends in Forage Strategy Grazer-to-browser ratios are shifting, with forest, grassland, and desert biomes typically increasing in grazer abundance (Fleischner, 1994) and forest biomes typically increasing in browser abundance as well (Côté et al., 2004). In forests, grazer abundance is becoming unsustainably high due to woody plant expansion (Espunyes et al., 2019), although ungulate browsers can suppress woody biomass by limiting sapling recruitment and thinning mature tree canopies (Box et al., 2016). Browsers can prevent forest recovery if saplings are not protected through recruitment (Nilar et al., 2019). Goats can be used as managed browsers to significantly reduce invasive woody plants, but only with consistent management over many years, and may result in a reduction of only some of the invasive plants rather than a complete eradication (Mundahl & Walsh, 2022). Grasslands are experiencing woody plant encroachment due to an increase of grazers (Burke, 2004) or mixed feeders (Manier & Hobbs, 2007; Pruszenski & Hernández, 2020; Staver et al., 2021), which reduces forage and habitat for native grassland ungulates (Schreiner-McGraw et al., 2020) if the woody plants become dominant (A. K. Knapp et al., 1999; Manier & Hobbs, 2007). The Taylor Grazing Act of 1934 was created to protect lands from being overutilized, but overgrazing still occurs in deserts and other biomes (Beever et al., 2006). Removal of grazers in the Mojave desert led to increases in non-native and ruderal plants that could outcompete native perennials (Beever et al., 2006).

Specialist vs Generalist

Whether an ungulate is a specialist (i.e. selective) forager or a generalist is not determined by the same morphophysiological characteristics that sort ungulates into grazers, browsers, or mixed feeders (Codron et al., 2019). However, the behavioral and morphophysiological differences in ungulates may create different preferences and prevent the overlap of desired forage (Hofmann, 1989; Rhodes, Larsen, & St. Clair, 2018; Sankey et al., 2006; Schuette et al., 2016). Lastly, selective foraging effectively disappears under high densities of ungulates which leads to feeding competition (Katona et al., 2013).

Biodiversity Ungulate selectivity affects plant biodiversity by altering both species richness and abundance (Augustine & McNaughton, 1998; Weng et al., 2017). Selective herbivory affects plant diversity through the mechanism of negative-density-dependence, where the consumption of one species allows space for others to grow (Weng et al., 2017); however, selective herbivory can lead to decreased biodiversity when foraging rates become unsustainably high (Augustine & McNaughton, 1998; Côté et al., 2004). Plant diversity is especially altered when selective foragers drastically increase in abundance (Olsen & Hansen, 1977). At high levels of herbivory species richness typically declines and ungulate forage strategy determines which functional groups of vegetation are most affected (i.e. grazers alter herbaceous understory plants while browsers impact forest regeneration) (Hofmann, 1989; Rhodes, Larsen, & St. Clair, 2018). At unsustainably high ungulate densities, plant abundance is at risk as forage competition outweighs foraging selectivity (Katona et al., 2013; Olsen & Hansen, 1977). Increasing herbivore pressure and selective foraging can alter the composition of plant communities by decreasing the relative abundance of more palatable plants (Augustine & McNaughton, 1998; Endress et al., 2012). Generalist herbivores also affect species diversity, but they browse multiple species which often allows for a constant fluctuation of diversity (Weng et al., 2017).

Structure & Function Ungulate selectivity alters plant structure and function by changing the abundance of palatable plants, decomposition, and nutrient cycling (Boulanger et al., 2015; Codron et al., 2019; Olsen & Hansen, 1977). Selective herbivores spend more time and energy looking for palatable, preferred forage that will give them more energy in return (Olsen & Hansen, 1977). When selective herbivory increases past sustainable levels, no matter if the herbivores are browsers or grazers, palatable plants may be eradicated from the ecosystem (Codron et al., 2019). The highest quality of forage for ungulates is found in newly sprouted plants, which can put plant recruitment at risk if the sprouts are overexploited (Aikens et al., 2020; Dorrough et al., 2007). Palatable species often have higher productivity, lower C:N ratios, and lower lignin content that allow them to decompose faster (Kasahara et al., 2016), which means that increasing the abundance of unpalatable plants through selective herbivory will alter the microbial community and decrease productivity, nutrient cycling, and decomposition rates (Hobbs, 1996; Lloyd et al., 2010). Selective grazing can also alter ecosystem growth rates and nutrient cycling by changing the plant community composition (Augustine & McNaughton, 1998; Endress et al., 2012). Consuming more nutritious, palatable plants leads to faster nutrient cycling, where ungulate waste deposition can increase plant growth by improving nutrient availability (Murray et al., 2013).

Invasion Ungulate selectivity can enhance invasion rates by increasing resource availability and decreasing biotic resistance (Olson et al., 1997; Shen et al., 2016; Vavra et al., 2007). Selective herbivory can alter nutrient cycling to increase resource availability when ungulates deposit higher concentrations of nitrogen in their waste, which may allow invasives to dominate as strong competitors under high nutrient availability (Vavra et al., 2007). Declining biodiversity, which decreases biotic resistance, naturally accompanies invasion (Vavra et al., 2007). Selective browsing that targets non-native species can prevent invasion (Katona et al., 2013); however, ungulates often selectively forage on familiar (native) plants and disturb the vegetation through trampling and soil compaction which increases the chance of invasion (Shen et al., 2016).

Biome Trends in Selectivity Ungulate selectivity is changing in biomes worldwide, with grassland biomes typically increasing in selective ungulate abundance while forest biomes have high levels of both generalist (i.e. deer, moose) (Faison et al., 2016) and selective (i.e. cattle) (de Luca & Pardini, 2017; Kuijper et al., 2009; Veblen & Young, 2010) ungulates. Many ungulate species (e.g., Lowland tapirs in Brazil's Atlantic Forest, moose in boreal forests, and ungulates in temperate European forests) can alter forest succession by preferentially foraging for young, palatable plants that have less defense chemistry, higher primary productivity rates, and are within grazing height (de Luca & Pardini, 2017; Kuijper et al., 2009). A study in Austrian forests found that high levels of selective browsing can notably reduce palatable woody plant species and increase browse-tolerant grasses, which decreases the ecosystem's protection against climate change and pest outbreaks by homogenizing and delaying forest regeneration (Meier et al., 2017). Kuijper et al. (2016) found moose to increase their preferred forage by accelerating the nutrient cycling where they feed, which they theorize offsets the otherwise negative effects of selective herbivory. Few papers have discussed the possibility of such trophic rebounding, which could be vital in maintaining plant community structure as ungulate populations expand. Grassland plant diversity decreases as elevated grazing by selective ungulates locally excludes preferred forage (Boavista et al., 2019), and herbivory by multiple selective ungulate species have additive effects on changing plant nutrient content and soil processes despite their foraging differences (Lloyd et al., 2010). In Kenyan savannas, plant diversity was maintained by native, non-selective wildlife that suppressed an invasive grass, while cattle and mega-herbivores reduced positive herbivory effects by selectively overgrazing the most palatable plant (Mandlate & Rodrigues, 2020; Veblen & Young, 2010). Unpalatable plants can have positive effects on habitat and plant communities when they protect neighboring palatable plants from selective herbivory by creating an unpalatable patch (Oduor et al., 2018).

Novel vs Native

Ungulate origin defines the status of an ungulate as native, non-native, introduced, or domestic.

Biodiversity Ungulate origin alters the richness and abundance of plant species due to differences in foraging history (Fleischner, 1994; Parker et al., 2006). Ungulate species favored for domestication and hunting are often added to the landscape without regard to their effect on plant diversity (Spear & Chown, 2009; Vavra et al., 2007) even though introduced ungulates can cause deleterious effects according to the species of herbivore and their co-evolution with plants (Eldridge et al., 2018; Fleischner, 1994). Introduced ungulates significantly reduce plant density and lead to losses of plant biodiversity, specifically of native plants (Fleischner, 1994; Spear & Chown, 2009; Travers et al., 2018). Novel herbivores often eat native plants that are not adapted to foraging, which affects plant diversity by allowing non-native plants that have co-evolved with grazing to outcompete the natives (Fleischner, 1994; Schlierenzauer et al., 2021). It is important to note that native herbivores suppress exotic plants, but exotic herbivores increase the biodiversity of exotic plants (Parker et al., 2006). Altered nutrient cycling will change plant diversity when novel ungulates exhibit differences from native ungulates in their grazing selection, movement, and amount of forage consumed (Endress et al., 2012; Hobbs, 1996). Decreases in biodiversity can decrease nutrient uptake, biomass production, tourism value, beauty, spiritual value, and more (Allen et al., 2010; Isbell et al., 2011). Much work is still needed to more precisely differentiate the ecosystem impacts of non-native, native, and domestic ungulates (Schlierenzauer et al., 2021).

Structure & Function Changes in ungulate origin can alter structure and function by modifying plant cover, forage availability, and ecohydrological processes (Bhattacharya & Sathyakumar, 2011; Fleischner, 1994; Fortini et al., 2021; Schieltz & Rubenstein, 2016). Non-native ungulates are problematic for the conservation of ecosystem structure and function by threatening biodiversity even if they are socially or economically valuable (Spear & Chown, 2009). Simultaneous increases in native and domestic ungulates threaten plant regeneration (Bernes et al., 2018; Côté et al., 2004; Sankey et al., 2006). Domestic livestock are commonly introduced into many biomes, and their heavy impact on plant structure and cover has been found to negatively affect species that require dense cover while positively affecting species that require open spaces (Schieltz & Rubenstein, 2016). Expanding populations of both indigenous and introduced ungulates over the same or decreased habitat sizes leads to a greater likelihood of interference competition and behavioral changes, which can be detrimental to native species (Carusi et al., 2017; Côté et al., 2004; Gooch et al., 2017; Kiffner et al., 2020). Increasing non-native ungulate populations, such as livestock or other economically desirable species, has led to competition with native ungulates for both forage quantity and quality (Bernes et al., 2018; Olsen & Hansen, 1977; Sankey et al., 2006; Schieltz & Rubenstein, 2016). Grazing rotations that provide livestock with optimal forage can leave the wild ungulates in poor habitats with poor forage and the need to expend more energy to escape disturbances (Bhattacharya & Sathyakumar, 2011). Ecosystem functions have been altered to be either dependent on or inhibited by ungulates, dependent on ungulate species and biome (de Groot et al., 2002; Gawel et al., 2018). Invasive ungulates can negatively affect soil infiltration, water quality, and other ecohydrological functions (Fleischner, 1994; Fortini et al., 2021). Novel herbivores themselves can drive tipping points through differences in their abundance, behavior, or morphophysiology (Olofsson & Post, 2018).

Invasion Ungulate invasions are often followed by plant invasions (Cole & Litton, 2014) by altering the mechanisms of dispersal and biotic resistance (Baltzinger et al., 2019; Fleischner, 1994; Parker et al., 2006). It is increasingly common for native, introduced, and domestic ungulates to live in the same ecosystem, with all of them contributing to long-distance seed dispersal of both native and exotic plants (Baltzinger et al., 2019; Fleischner, 1994). Ungulates can disperse diaspores through both endozoochory and epizoochory, meaning that increased ungulate activity from the addition of non-native ungulates elevates potential invasion from many plants across expansive grazing ranges (Baltzinger et al., 2019). The invasibility of an ecosystem also changes with novel ungulate populations, as new herbivores open niche space and increase long-range dispersal rates (Baltzinger et al., 2019; Spear & Chown, 2009; Vavra et al., 2007). A meta-analysis revealed that native herbivores provide biotic resistance to invasion by eating exotic plants across a majority of biomes, while non-native herbivores eat native plants that did not evolve to resist them (Parker et al., 2006).

Biome Trends in Ungulate Origin Ungulate origins are shifting worldwide, with forest, grassland, and desert biomes typically increasing in non-native ungulate abundance. Forest biomes are typically affected by the conversion to pastoral lands for non-native ungulate grazing that changes the structure of the remaining forest (MacLaren et al., 2014) or by increased invasion of exotic, non-palatable species through dispersal and novel grazing behavior (Questad et al., 2018; Spear & Chown, 2009). In Guam forests, however, novel ungulates negatively and positively affect biodiversity and ecosystem function: non-native deer are decreasing seedling and vine abundance while non-native pigs are increasing seed dispersal in dung, a function that was previously lost (Gawel et al., 2018). The creation of short-term corrals for cattle in African savannas increased nutrient inputs, leading to hotspots of novel plant diversity vastly different from the surrounding vegetation (Veblen & Young, 2010). Introduced cattle in the Mojave Desert have increased the spread of an invasive grass by improving nutrient and water availability through defecation (St. Clair, 2021). Introducing livestock negatively impacts native ecosystems, and their grazing damage is magnified in semiarid and arid biomes where livestock preferentially graze in riparian areas (Fleischner, 1994). Novel browsers are threatening ecosystem health in arid Australia by suppressing structurally important woody biomass (Box et al., 2016).

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FIGURES

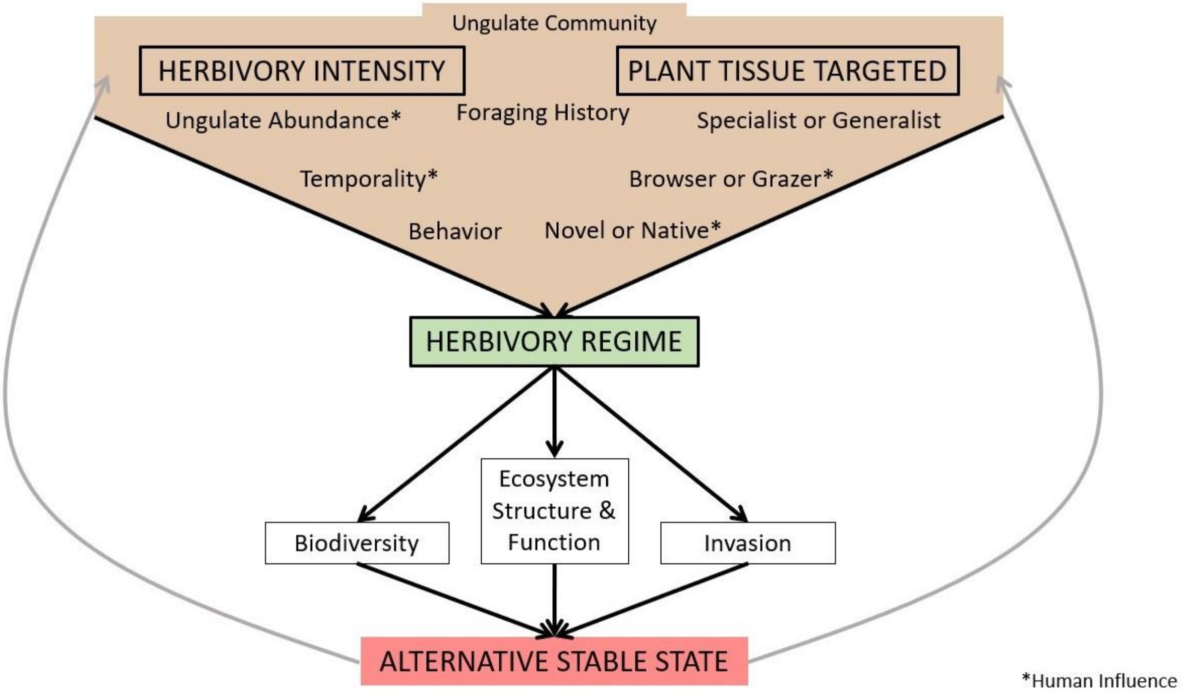

Figure 1-1. Herbivory intensity and the type of plant tissue herbivores target are the two main factors that shape an ungulate herbivory regime. Foraging history ties the two components together through the co-evolution of plants and ungulates. Altered herbivory regimes can shift biodiversity, ecosystem structure & function, and plant invasions to the point of creating an alternative stable state that may reshape the ungulate community in a cyclical process.

CHAPTER 2

Novel Fire and Herbivory Regime Impacts on Forest Regeneration and Plant Community Assembly

Megafire impacts on forest regeneration and herbivory across multiple forest systems

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ABSTRACT

Human activities are increasing the occurrence of megafires that have the potential to alter the ecology of forest ecosystems. The objective of this study was to understand the impact of a 610-km^2 megafire on patterns of forest regeneration and herbivory of three forest types (aspen/fir, oak/maple, and pinyon/juniper) within the burn scar. Sapling density, meristem removal, and height were measured across a transect network spanning the area of the burn scar over three years from 2019-2021. The network consisted of 17 burned/unburned transect pairs in adjacent burned/unburned forest stands (6 aspen/fir, 5 oak/maple, and 6 pinyon/juniper). Species that regenerated through sprouting generally responded positively to fire while regeneration from seed showed very little post-fire response. Browse pressure was concentrated on deciduous tree species and tended to be greater in burned areas but the effect diminished over time. Meristem removal of sprouting species was below the critical threshold resulting in positive vertical growth across years. Our results indicate that forest regeneration within the megafire scar was generally positive and experienced sustainable levels of ungulate browsing that are likely to result in forest recruitment success.

INTRODUCTION

The size, frequency, severity, and timing of wildfires in many ecosystems are changing due to human activity resulting in novel fire regimes that are likely to affect forest regeneration and ecosystem stability (Abatzoglou & Williams, 2016; Allen et al., 2010; Bowman et al., 2009). Megafires are becoming more common and are classified as being expansive (greater than 40,000 hectares) and having a uniquely large ecological and societal impact (Geographic, 2020; Linley et al., 2022). Megafire probability varies by season and increases during warmer and drier periods, which are increasing due to climate change (Allen et al., 2010; Westerling et al., 2003). Extreme drought brought on by climate change makes large, high-severity fires more frequent and extreme (Allen et al., 2010; Westerling et al., 2006). A comprehensive analysis of large fires conducted by Westerling et al. (2006) found regional temperature to explain 66% of annual variation in fire frequency, with fires burning more often in warmer than cooler years. Early spring snowmelt due to warming temperatures also increases wildfire activity (Westerling, 2016), and because snowpack melts earlier in burned areas (Maxwell, Call, et al., 2019), fires are creating a self-perpetuating cycle. Fire suppression in forests leads to increased fuel loads which increases wildfire extent and severity (García-Llamas et al., 2019). Megafires create burn mosaics across the landscape, which may significantly alter the vegetation structure, productivity, and successional pathways in forest ecosystems that likely have strong habitat feedbacks on the wildlife communities (Arroyo-Vargas et al., 2019; Carlson et al., 2011; Commander & White, 2019; Fang et al., 2019; Keane et al., 2008; Stevens-Rumann & Morgan, 2019; H. Y. Wan, Olson, et al., 2014). However, more studies are needed to understand the novel effect of megafires on forest communities and wildlife.

Megafires are burning across broad elevation gradients and multiple plant communities, which may lead to dramatic changes in ecological processes that operate at landscape scales. Species are differentially adapted to elevation, meaning that when a megafire burns, it will have different effects on plant species based on their diverse natural histories (Abutaha et al., 2019; Tanaka & Sato, 2013). A natural history of fire disturbance promotes post-fire regeneration tactics, such as root and stem suckering, which is common in aspen, oak, and maple species (Aubin et al., 2005; Del Tredici, 2001; Harper et al., 1985; H. Y. Wan, Olson, et al., 2014). In contrast, other species such as fir, pinyon, and juniper trees regenerate almost exclusively by seed, making re-establishment success more precarious in post-fire environments (Keane et al., 2008). Large fires can lengthen the timetable of ecosystem recovery by increasing the dispersal distances of propagules (Gill et al., 2022; Kunzler & Harper, 1980; Meng et al., 2015; Noble & Slatyer, 1980; Sparks et al., 2018; Van Lear et al., 2000). Sparks et al. (2018) found that forests containing fire-adapted species have the lowest reduction in net primary production one year post-fire, though persistent differences in productivity between burned and unburned temperate forests lasted up to twelve years. Megafires can elicit even longer recovery timetables when they burn multiple forest types, especially when the forests are not fire-resilient. The ecological effect of megafires that cross multiple forest types on forest regeneration is not well understood.

Burn severity mosaics within megafires leave a spectrum of conditions that differentially affect forest regeneration and wildlife habitat conditions. Low to moderately severe fire in resilient forests may stimulate vegetative growth that provides beneficial ecosystem services or improved rangelands (Kunzler & Harper, 1980; H. Y. Wan, Rhodes, et al., 2014). For example, Kunzler & Harper (1980) found that Gambel oak becomes sparser when moderately burned and provides better forage and habitat for deer. However, regeneration fails if the fire is severe enough to kill the reproductively mature individuals and their root systems (Fang et al., 2019; Van Lear et al., 2000). Further, high-severity fires often create moonscapes with elevated temperatures and scarce shelter that may displace wildlife habitat (Lamont et al., 2019). The mosaic of contiguous burn severities within a megafire has the potential to create novel conditions that have yet to be studied in depth.

Herbivores are attracted to highly visible and nutritious new growth, and burn mosaics within megafires may influence browsing pressure (Arroyo-Vargas et al., 2019; D. S. Smith et al., 2016). Wan, Olson, et al. (2014) found that increasing fire size and severity reduced ungulate herbivory impact on aspen regeneration through bottom-up and top-down regulation. In contrast, Smith et al. (2016) found that elevated populations of *Cervus elaphus* (Rocky Mountain elk) inhibited regeneration of aspen forests due to high levels of herbivory in a megafire burn scar. Arroyo-Vargas et al. (2019) found that native plants failed to regenerate due to overgrazing following burns of variable severity, and unpalatable species invaded the open habitat. The legacy of megafire burn characteristics on ungulate herbivory needs further research as there is no clear consensus in the literature on its impacts on forest recruitment success.

Few long-term data sets exist to address pressing questions of post-megafire regeneration patterns (Arroyo-Vargas et al., 2019; Gustafsson et al., 2019; Swanson et al., 2011), yet the 2018 Pole Creek megafire in central Utah provides an ideal study system for looking at the long-term legacy effects of megafires and novel fire regimes. The mixed deciduous forests that were burned across a wide elevational gradient in this montane system include *Populus tremuloides* (quaking aspen) and *Abies lasiocarpa, Abies concolor* (subalpine fir, white fir) referred to as aspen/fir forests, *Quercus gambelii* (Gambel's oak) and *Acer glabrum, Acer grandidentatum* (mountain maple, bigtooth maple) referred to as oak/maple forests, and *Pinus edulis, Pinus* *monophyla* (pinyon, single-leaf pinyon) and *Juniperus osteosperma* (Utah juniper) referred to as pinyon/juniper forests. Megafire effects on forest regeneration can be more objectively measured in our study area because the ecological response will not be limited to one forest type or variable fire events. Further, our study system is ideal for testing herbivory's effect on forest regeneration because the megafire burned major wildlife food sources: quaking aspen, Gambel oak, and maples (Flagel et al., 2016; Harper et al., 1985; Kunzler & Harper, 1980; H. Y. Wan, Rhodes, et al., 2014). No previous studies that we are aware of have been conducted to analyze the effect of megafire burn characteristics on the regeneration success of multiple forest types.

The objective of this study is to examine how burn conditions and herbivory impact the regeneration of three forest types within a megafire. This study addressed the following questions: 1) Do megafires differentially influence patterns of multi-forest regeneration and does the response vary depending on tree regeneration strategy (vegetative suckering vs. seed regeneration)? and 2) How do patterns of ungulate herbivory vary across multiple forest types and burn conditions?

MATERIALS AND METHODS

Study Area

The study was conducted in the Pole Creek megafire complex located within the Uinta-Wasatch-Cache and Manti-La Sal National Forests in northern Utah (40.0838° N, 111.5960° W). Elevation ranged from 1622 to 2693 meters and slope was held constant across sites. The Coal Hollow fire, Bald Mountain fire, and Pole Creek fire were all lightning-ignited fires beginning on August 4, 24 and September 6, 2018. The three fires converged to create a 610-km^2 burn scar referred to as the Pole Creek megafire that ended on October 6, 2018.

Dominant vegetation was characterized by three distinct forest types that varied along an ecotonal elevational gradient. Aspen/fir forests were dominant at the highest elevation, oak/maple forests at mid-elevation, and pinyon/juniper forests at low elevations of the fires' extent. Of the key species in this study, aspen, maple, and oak saplings regenerate via clonal or vegetative regeneration, while the fir, pinyon, and juniper species regenerate via seeds. Ungulates common to the area include *Cervus canadensis* (elk) and *Odocoileus spp.* (deer). *Bos taurus* (domestic cattle) and *Ovis aries* (domestic sheep) grazing allotments exist within the study area as well.

Study Design

Study plots were chosen within each forest type by pairing proximate burned and unburned patches of comparable size to control for topographic variation. Burn severity maps were created in ArcGIS Pro using differenced normalized difference of vegetation indices (dNDVI) derived from Landsat-8 imagery courtesy of the United States Geological Survey (USGS). The derived maps were then used to identify patches of high burn severity, which we later ground-verified by visiting each location. Six transect pairs were identified for aspen/fir and pinyon/juniper forest types, and five pairs for oak/maple forests (Fig. 1) (Esri, 2012; Esri, 2013). Transects were installed across the entire megafire to the extent that species distribution, burn severity, and human access allowed.

Stand Characterization and Field Measurements

Stand composition and structure of both burned and unburned stands were characterized using estimates of stand density and by identifying tree species. Forest regeneration responses were measured yearly from 2019 to 2021 in late July when ungulate browsing was heaviest (Rhodes, Larsen, Maxwell, et al., 2018). Sapling density, browse, and height of key tree species (quaking aspen and *Abies spp.* in aspen/fir forests, Gambel oak and *Acer spp.* in oak/maple forests, Utah juniper and pinyon species in pinyon/juniper forests) were measured along 50x2 meter belt transects at each of the 34 study sites (Fig. 1). Sapling density was measured by counting all saplings of each key species within the belt transect. Clumped individuals were treated as a single organism for density measurements because they self-thin over time (Keyser et al., 2019). The height of each sapling within the transect was determined using a measuring stick. The browse percentage of saplings was calculated by counting the missing and intact apical meristems after the manner of Rhodes, Larsen, & St. Clair (2018). The average slope and aspect of sites were determined using topographical analysis of USGS Landsat data in ArcGIS Pro.

Statistical Analysis

Data exploration was conducted according to the methods of (Zuur et al. 2010) to test that all model assumptions were met. All response variables met equal variance assumptions. To assess the data, we compared the average density, browse percentage, and height for each tree species and year using a repeated measures analysis of variance (ANOVA) using JMP software (SAS Institute Inc., 2021). Tukey's HSD was used to test pairwise comparisons to test across year burn effects.

RESULTS

Fire Effects on Regeneration by Species

The density of stand sapling regeneration exhibited variable responses depending on species and year. Oak sapling density increased by 99% in burned areas compared to unburned areas when averaged across years ($P \leq 0.05$) (Fig. 2). In contrast, maple, pinyon, and fir densities were reduced by 133%, 200% and 200% along burned transects compared to unburned transects when averaged across years ($P \leq 0.1$) (Fig. 2). Fire did not significantly affect aspen or juniper densities ($P = 0.20$ and $P = 0.27$). Oak sapling density decreased by 19% from 2019 to 2021 while maple and fir sapling densities increased by 32% and 125% during the same three-year period when averaged across burn levels ($P \leq 0.1$) (Fig. 2). Year did not significantly affect aspen, juniper, or pinyon densities ($P = 0.30$, $P = 0.39$, $P = 0.36$). The fire-by-year interaction term was only significant for fir sapling density ($P \leq 0.1$) (Fig. 2).

Fire Effects on Browse Pressure on Deciduous Species

Deciduous saplings were browsed 66% more in burned areas compared to unburned areas when averaged across years ($P \leq 0.05$) (Fig. 3). In 2019, deciduous sapling browse was 94% greater in burned areas than unburned areas ($P \leq 0.1$) (Fig. 3). The main effect of year and the fire by year interaction term did not significantly affect browsing of deciduous species collectively or individually (Figs. 3 and 4). Maple saplings were browsed 117% more in burned areas than in unburned areas when averaged across years ($P \leq 0.05$) (Fig. 4). Fire did not significantly affect the browse of oak and aspen saplings ($P = 0.3$ and $P = 0.5$) (Fig. 4). Coniferous species showed essentially no evidence browsing.

Fire Effects on Recruitment Potential

Sapling height increased by 48% over the three years from 2019 to 2021 ($P \leq 0.001$) (Fig. 5). The main effect of fire and the fire-by-year interaction term did not significantly affect sapling height throughout the study ($P = 0.30$ and $P = 0.11$) (Figure 5).

DISCUSSION

Assessing the regeneration responses of multiple forest types in the Pole Creek Fire provided insights into landscape-scale forest regeneration responses in the boundaries of a megafire scar. The results demonstrated that post-fire environments elicited highly variable forest regeneration responses depending on tree species (Fig. 2). Ungulate herbivory that has been implicated in forest regeneration failure (Rhodes et al., 2017; Rhodes, Larsen, & St. Clair, 2018) was widespread across the forest landscape (Figs. 3 and 4). There was support for our first hypothesis that post-fire regeneration varied by species with quicker responses from root sprouting species (Fig. 2). Ungulate browsing was moderately greater in post-fire environments and varied by tree species (Figs. 3 and 4). While ungulate browsing was widespread across the study area, meristem removal was not chronically high even in burned areas and attenuated over time indicating that forest recruitment is likely to be successful over time (Bristow et al., 2014; Harper et al., 1985; Kulakowski et al., 2006; H. Y. Wan, Olson, et al., 2014).

Fire Effects on Regeneration by Species

Regeneration densities tended to show strong positive or negative responses to fire, which may be partially tied to regeneration strategy (Fig. 2). Sprouting species such as aspen and oak showed strong positive responses to fire, which is in line with previous research (Harper et al., 1985; E. A. Smith et al., 2011; H. Y. Wan, Olson, et al., 2014). High-severity fires have been found to trigger strong suckering responses due to increased light availability, nutrient pulses, and reduced competition (Ficken & Wright, 2017; H. Y. Wan, Rhodes, et al., 2014; X. Wan et al., 2006). Tree species that primarily reproduce by seed, including maple, fir, pinyon, and juniper, showed strong negative responses to fire in our study (Fig. 2), which is consistent with previous studies (Bristow et al., 2014; Christensen & Nixon, 1964; Lee Molinari et al., 2022). Post-fire seed regeneration is often slower than sprouting due to the added barriers of seed dormancy (Kildisheva et al., 2020), reduction in nurse plants (Bristow et al., 2014; Buck & St. Clair, 2014; Calder & St. Clair, 2012), and long distances to seed sources (Gill et al., 2022; Stevens-Rumann & Morgan, 2019). Bigtooth maple can regenerate through sprouting but is also heavily reliant on seed regeneration following high-severity fires (Christensen & Nixon, 1964). Post-fire fir regeneration is primed by aspen facilitation that can take several decades after a fire (Buck & St. Clair, 2014; Calder & St. Clair, 2012; Lee Molinari et al., 2022). As long as mature seed source trees exist within 5-10 kilometers junipers can regenerate from seed relatively quickly under ideal weather conditions, while pinyon trees are more reliant on protective cover and can take much longer to establish (Bristow et al., 2014; Harris & Taylor, 2020).

Fire Effects on Browse

Browse pressure was greater in burned areas than in unburned areas for sprouting species but the effect diminished over time (Fig. 3). Ungulate herbivores can favor foraging in burned areas (Allred et al., 2011; Lewis et al., 2022) because fire instigates sapling regeneration (Rhodes, Larsen, & St. Clair, 2018; Rhodes, Larsen, Maxwell, et al., 2018; X. Wan et al., 2006) with high nutrient and protein content (Allred et al., 2011; Anderson et al., 2007; Chard et al., 2022; Lloyd et al., 2010; Sardans et al., 2005). However, high burn severity can elevate foliar defense chemistry (Rhodes, Larsen, Maxwell, et al., 2018; H. Y. Wan, Rhodes, et al., 2014) that deters ungulate herbivory (Wooley et al., 2008). Selective herbivory of palatable post-fire saplings can lead to an increase in unpalatable saplings (Chard et al., 2022), which may partially explain the decrease in browse pressure over time (Fig. 3). Furthermore, increasing time since fire is inversely related to plant tissue nutrient concentrations that can affect ungulate herbivore browsing preferences (Allred et al., 2011; Sardans et al., 2005). As the vegetation regenerates, the burn scar "magnet effect” on herbivores diminishes (Allred et al., 2011; Archibald et al., 2005) and the animals likely return to pre-fire foraging behavior (Fig. 3) (Cherry et al., 2018).

Fire Effects on Recruitment Potential (in the context of browsing)

Sapling height increased with time since fire showing progression toward stand recruitment (Fig. 5). Large fires remove plant-plant competition and can accelerate the vertical growth rate of saplings (H. Y. Wan, Olson, et al., 2014). Large fires can also widely disperse ungulate herbivores that would otherwise suppress vertical growth through selective overgrazing (H. Y. Wan, Olson, et al., 2014). When herbivory levels drop below 30-40% meristem removal, vertical growth and recruitment potential increase (Rhodes, Larsen, & St. Clair, 2018; Strand et al., 2009). The average meristem removal in burned areas in this study remained below the critical browse threshold one year post-fire and dropped even lower in years two and three (Figs. 3 and 4). Maintaining apical meristems which drive vertical sapling growth (Rhodes, Larsen, & St. Clair, 2018; Strand et al., 2009) likely explains the increased sapling height over time (Fig. 5). Relatively low levels of meristem removal in this study are likely explained by the large size and high burn severity of the Pole Creek Megafire. Both fire size and high burn severity are known to reduce meristem removal by ungulate herbivores by stimulating aspen regeneration vigor and defense and by changing animal foraging behavior (H. Y. Wan, Olson, et al., 2014; H. Y. Wan, Rhodes, et al., 2014).

Conclusions

Our results show that tree species burned within the same megafire event respond differently to fire, likely due to growth strategy, abiotic conditions, and palatability. Wildfires strongly influence regeneration in aspen/fir, oak/maple, and pinyon/juniper forest regeneration with strong potential implications for herbivory (Harper et al. 1985, Wan et al. 2014). Understanding the effect of megafires on forest ecosystems in North America is important because they are becoming more common due to climate change (Abatzoglou & Williams 2016). Our results provide insight into how forest regeneration strategies (seed vs. sprouting) may affect post-fire regeneration responses, but more research is needed to better understand these responses. Further research on how forest regeneration and recruitment respond to novel fires would aid in understanding the simultaneous recovery of multiple forest types and form a more complete picture of the resilience of forest ecosystems in a changing world.

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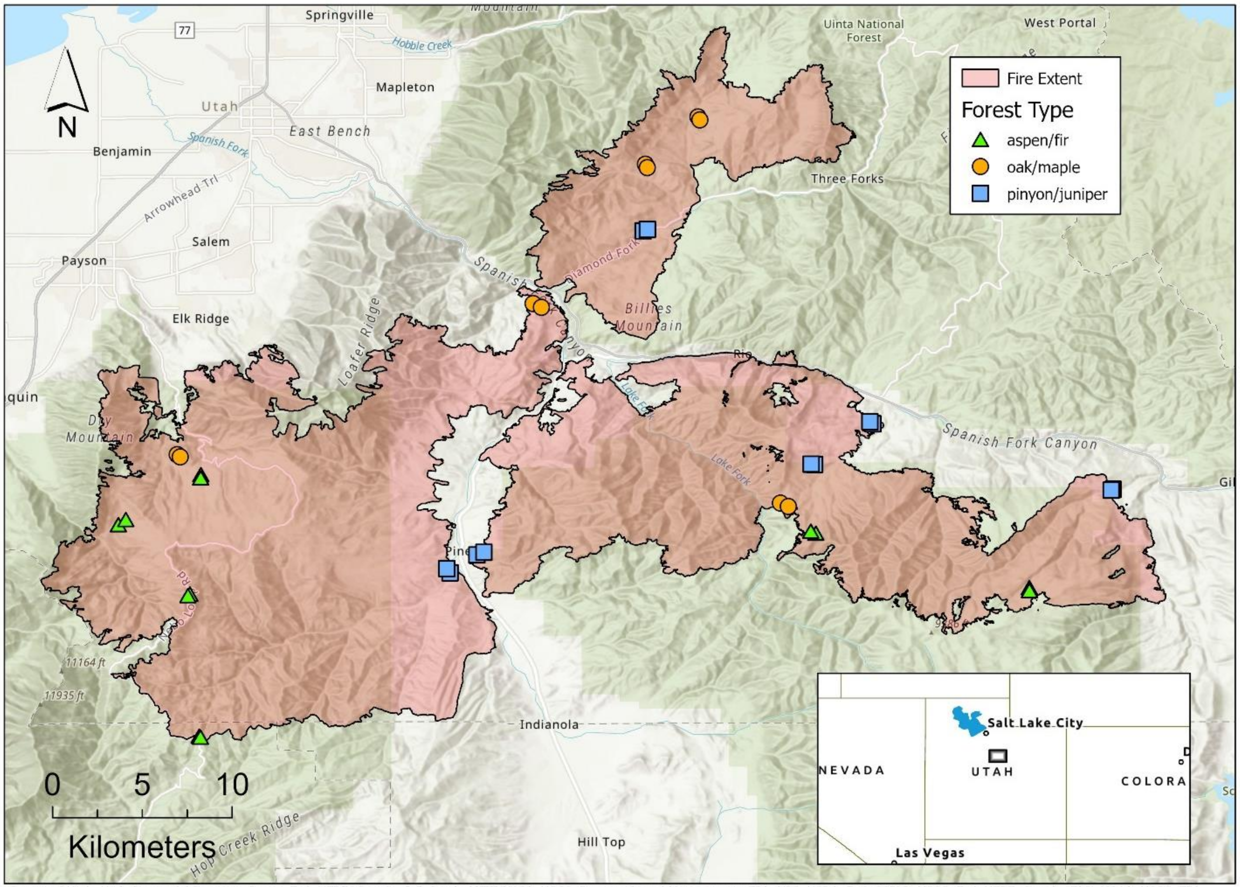
FIGURES



County of Utah, Utah Geospatial Resource Center, Esri, HERE, Garmin, SafeGraph, METI/NASA, USGS, Bureau of Land Management, EPA, NPS, USDA, Esri, CGIAR, USGS, Esri, HERE, Garmin, FAO, NOAA, USGS, EPA

Figure 2-1. Transect locations of aspen/fir, oak/maple, and pinyon/juniper forest types within the Pole Creek Megafire burn scar in northern Utah, USA.

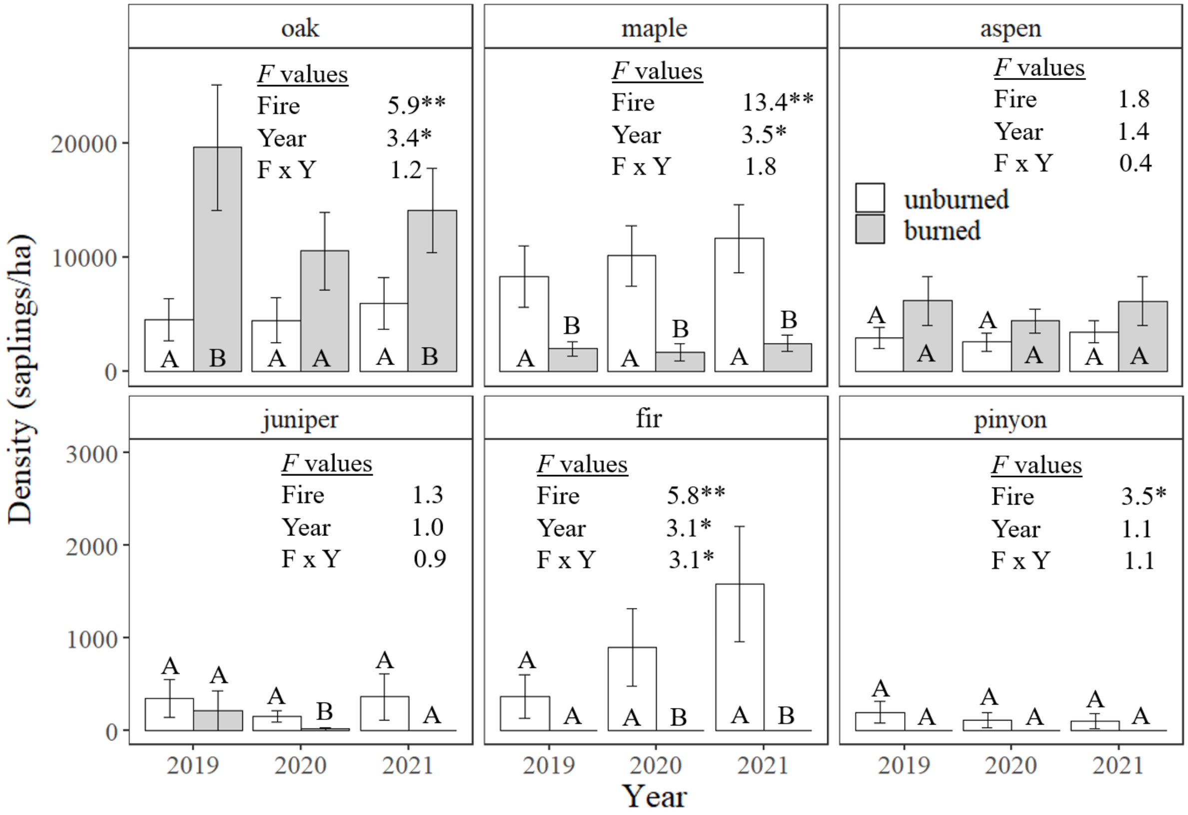


Figure 2-2. Effect of fire on the density of aspen, fir, oak, maple, pinyon, and juniper saplings across years. Asterisks represent p-value significance: * $P \leq 0.1$, ** $P \leq 0.05$, *** $P \leq 0.001$. Letters that are different between bars (within each year, for each species) indicate a significant difference between burned and unburned ($P \leq 0.1$).

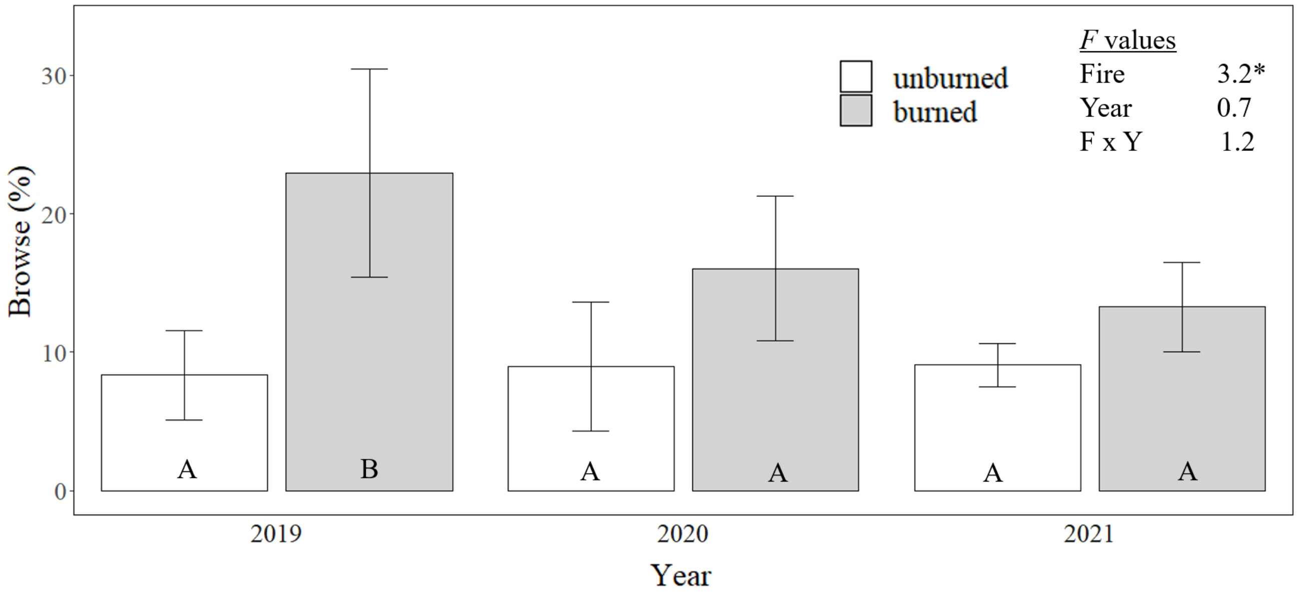


Figure 2-3. Effect of fire on browse levels of aspen, oak, and maple saplings across years. Asterisks represent p-value significance: * P ≤ 0.1, ** P ≤ 0.05, *** P ≤ 0.001. Letters that are different between bars (within each year) indicate a significant difference between burned and unburned (P ≤ 0.1).

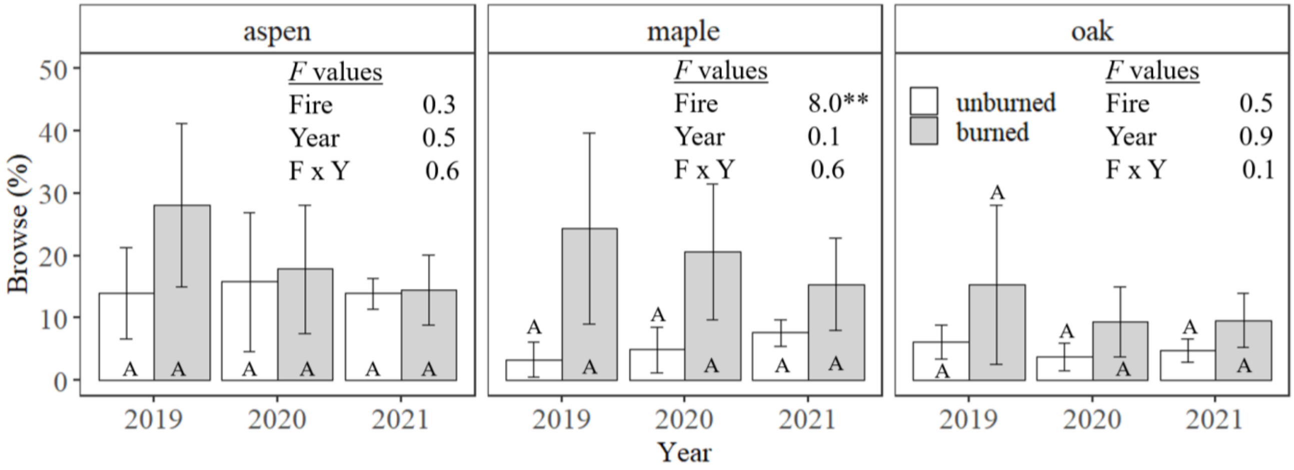


Figure 2-4. Effect of fire on browse levels of aspen, oak, and maple saplings across years. Asterisks represent p-value significance: * P ≤ 0.1, ** P ≤ 0.05, *** P ≤ 0.001. Letters that are different between bars (within each year, for each species) indicate a significant difference between burned and unburned (P ≤ 0.1).

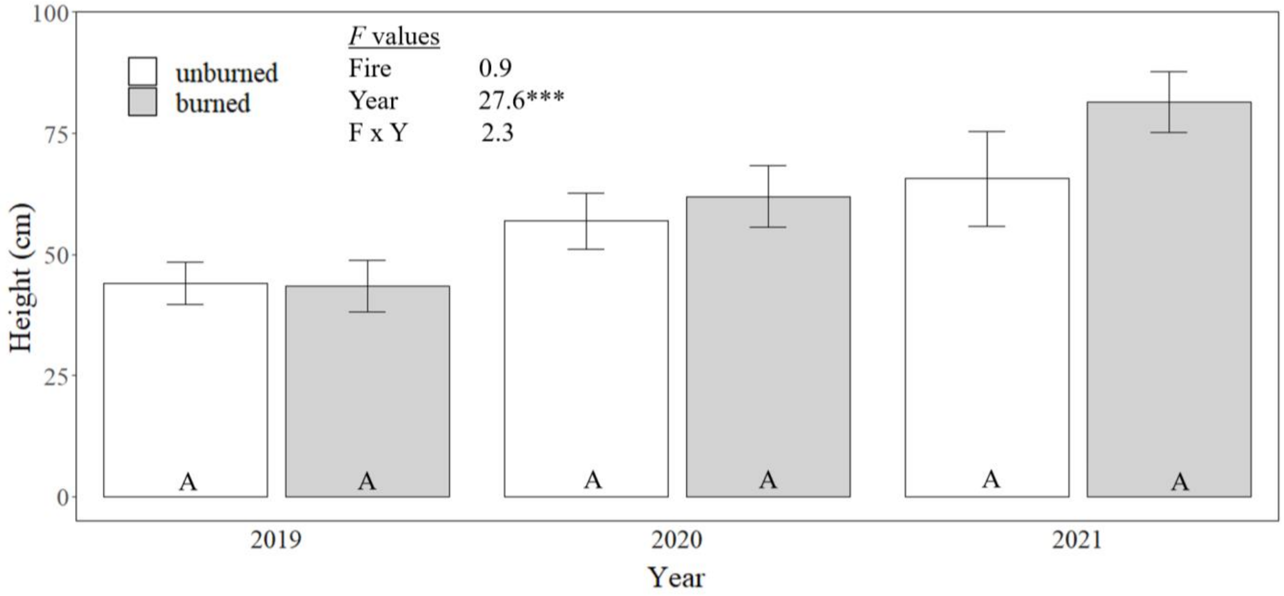


Figure 2-5. Effect of fire on the height of aspen, fir, oak, maple, pinyon, and juniper saplings across years. Asterisks represent p-value significance: * $P \leq 0.1$, ** $P \leq 0.05$, *** $P \leq 0.001$. Letters that are different between bars (within each year) indicate a significant difference between burned and unburned ($P \leq 0.1$).

CHAPTER 3

Novel Fire and Herbivory Regime Impacts on Forest Regeneration and Plant Community Assembly

Effects of a megafire on plant community assembly across multiple forest types

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ABSTRACT

Novel fire regimes are becoming increasingly common and megafires have burned across ecotonal boundaries across multiple forest types. Plant community structure and composition may be critically affected by changing fire regimes. Our objective was to investigate how a megafire that burned across multiple forest types impacted understory plant community assembly and biodiversity. Paired vegetation transects were installed in burned and unburned areas across aspen/fir, oak/maple, and pinyon/juniper forests within the 2018 Pole Creek Megafire burn scar. Percent cover of understory plants was measured in the summer of 2022 and plants were identified to the species level. Richness and diversity indices were then calculated and analyzed using mixed effects models. Fire decreased species richness of the aspen/fir forest understory and increased plant cover in pinyon/juniper forests, while not significantly impacting oak/maple understories. The significant effects of fire were largely driven by changes in forb species. Fire decreased the richness of native plants in aspen/fir forests but increased the richness of non-native plants in oak/maple and pinyon/juniper forests. Non-native plant abundance also increased in post-fire pinyon/juniper forests. Our results suggest that forest understory communities show variable responses to megafires that burn across multiple forest

types with important implications for post-fire plant community structure, diversity, and invasibility.

INTRODUCTION

Anthropogenic climate change and fire suppression are increasing the size, frequency, and severity of wildfires (Bowman et al., 2009). The largest of these fires (Harvey et al., 2016) are termed megafires, which have distinct societal and ecological impacts (Adams, 2013). The frequency of megafires has increased dramatically in recent decades, largely due to increased drought frequency (Petropoulos et al., 2011; Westerling et al., 2006). Climatic variability also increases the frequency and severity of fires due to the build-up of fuel loads during wet years between droughts (Newman, 2019; Westerling et al., 2006). Megafires can affect plant regeneration success through plant mortality due to high burn severity or limitations to pollination or seed dispersal across the large burn scars (Adams, 2013; Gill et al., 2022). Additional studies are needed to fully understand the ecological impacts of megafires.

Megafires can cross ecotonal boundaries to burn multiple forest types. This may lead to shifts in tree regeneration success based on fire adaptation of species across forest types (Swetnam et al., 1999). Forrestel et al. (2011) found that the distribution of plant species changed following a large fire, with fire-adapted and drought-tolerant species growing into fire-opened niche spaces that were previously outside their range. Insolation and topographic variables such as elevation and slope were distinguished as key factors in long-term post-fire plant communities (Springer et al., 2018). Insolation and elevation specifically were negatively correlated with plant biodiversity post-fire (Springer et al., 2018). Another effect of large fires burning multiple forest types is the broad-scale reduction of plant cover and habitat, which may lead to significantly elevated temperatures and displaced wildlife. Research is scarce on how multiple forest types are simultaneously affected by a megafire.

Post-fire vegetation community assembly is dependent on the natural history of pre-fire vegetation and burn characteristics. Fire-adapted species are those that either require fire for germination, can grow back to pre-fire conditions before the next fire, or can survive low-severity fires (Station, 2008). While natural histories strongly influence post-fire regeneration and resilience, novel fire regimes are causing changes in post-fire community assembly because organisms are not adapted to the new fire characteristics (Catling, 1991). Frequent fires lead to simplified vegetation structure by reducing canopy layers (Catling, 1991; Robinson et al., 2013). Moradizadeh et al. (2020) found high post-fire heterogeneity of vegetation that decreased over time. Swetnam et al. (1999) further state that disturbance causes a competitive release that opens niche space for new growth. These findings suggest that post-fire benefits of increased heterogeneity decrease with increasing fire frequency. In the case of a California study, post-fire niche spaces were filled with different species that had been adjacent to the areas preceding the large fire (Forrestel et al., 2011). It is unclear how burn conditions affect post-fire plant community assembly across neighboring forest types with different fire histories.

Plant functional types (i.e., shrubs, forbs, and graminoids) and the native status of understory plant species can affect ecosystem function and habitat quality (Hartsell et al., 2020; Isbell et al., 2011). Woody species provide litter that decomposes slower for better nutrient absorption (Lindroth et al., 2002), nursing effects for young plants (Bristow et al., 2014), nutritious year-round forage (Rhodes et al., 2018; Villalba et al., 2014) and shelter for wildlife (Allred et al., 2011). Forb species can improve nutrient uptake and nutrient cycling (Cong & Eriksen, 2018), restore degraded soil (Lambers et al., 2013), and provide highly palatable and nutritious forage for wildlife such as deer and sage grouse (Bates et al., 2017; Hartsell et al., 2020; Pruszenski & Hernández, 2020). Graminoids can be good long-term competitors (Nilar et al., 2019) reducing the spread of invasive species (Egelkraut et al., 2018; Hartsell et al., 2020) while other grasses are the invaders that create novel fire regimes (Archer et al., 2017; Floyd et al., 2008; St. Clair & Bishop, 2019). Graminoids are the preferred forage for grazers such as cattle and bison (A. K. Knapp et al., 1999; Olsen & Hansen, 1977; Reikowski et al., 2022; Sankey et al., 2006). Native plant species can provide biotic resistance to invasions (Floyd et al., 2006; St. Clair et al., 2016) and preferential habitat for wildlife (Berthon et al., 2021). High diversity of native plant species often is correlated with high diversity of non-native plant species (Nielson et al., 2019; Schlierenzauer et al., 2021; Stohlgren et al., 1997). However, non-native plant species can be damaging to an ecosystem by altering nutrient cycling and disturbance patterns (Reilly et al., 2020; Schlierenzauer et al., 2021), and by decreasing forage quality and abundance (Preston, 2015). There are few studies on how megafires alter understory plant functional type and native status across multiple forest types.

Utah's 2018 Pole Creek megafire is an ideal system for studying post-megafire community assembly across multiple forest types. The 610 km^2 megafire burned across an elevational gradient, capturing 3 forest types with different pre-fire vegetation communities. As such, our findings will be more generalizable to different ecosystems. Our objective is to classify how megafire burn characteristics influence plant community assembly and biodiversity (richness and abundance) across a gradient of forest types. We tested the following questions:

1. Does fire differentially impact understory plant richness, cover, and diversity across multiple forest types burned during a megafire?

2. Do different plant functional groups (woody, forb, and graminoid) demonstrate varying sensitivity to fire across forest types?
3. Does fire differentially impact native and non-native understory plant species richness and cover across forest types?

MATERIALS AND METHODS

Study Area

The study area is inside the burn scar of the Pole Creek Megafire within the Uinta-Wasatch-Cache and Manti-La Sal National forests of northern Utah (40.0838° N, 111.5960° W). The Pole Creek megafire started as three separate lightning-ignited fires, the Coal Hollow fire, Bald Mountain fire, and Pole Creek fire, on August 4, 24, and September 6, 2018, respectively. The fires converged and burned until October 6, 2018, at which point it was 610 km2 in size and termed the Pole Creek megafire. Elevation of the study sites ranged from 1622 to 2693 meters.

Three forest types dominate the study area with ecotonal boundaries along an elevational gradient: aspen/fir forests (*Populus tremuloides* and *Abies lasiocarpa, Abies concolor*) at high elevations, oak/maple forests (*Quercus gambelii* and *Acer glabrum, Acer grandidentatum*) at mid-elevations, and pinyon/juniper forests (*Pinus edulis*, *Pinus monophylla,* and *Juniperus osteosperma*) at low elevations. The regenerative strategies of these key species include clonal (aspen), vegetative (oak, maple), and seed dispersal (maple, fir, pinyon, juniper). Measurements were taken in May 2022 which allowed time for the snowpack to melt and ephemeral understory species to grow.

Dominant understory vegetation varies widely across ecotonal boundaries and elevation. At the highest elevations, the prominent species include snowberry (*Symphoricarpos* *oreophilus*), Oregon grape (*Mahonia aquifolium*), woods' rose (*Rosa woodsii*), and lupine (*Lupinus sp.*) (Mueggler, 1985). At mid-elevation sites, the prominent species include sweet cicely (*Osmorhiza berteroi*), elkweed (*Frasera speciosa*), and musk thistle (*Carduus nutans*) (Forest Service, 1994; Harper et al., 1985). Low-elevation sites primarily include species such as rabbitbrush (*Ericameria spp.*), sagebrush (*Artemesia tridentata*), and cheatgrass (*Bromus tectorum*). Wildlife within the study area includes the following major ungulates: native elk (*Cervus canadensis*) and deer (*Odocoileus spp.*), with cattle (*Bos taurus*) and sheep (*Ovis aries*) often present in grazing rotations.

Study Design

Study plots were installed across the megafire burn scar within matched pairs of adjacent burns and control areas (Springer et al., 2018). Each of the pairings was within one of three forest types: aspen/fir, oak/maple, or pinyon/juniper. Each pair was replicated five to six times per forest type for a total of 17 pairs and 34 total plots across the megafire burn scar. Site burn condition was determined using maps created from satellite data in ArcGIS Pro and validated on the ground.

Transects and Field Measurements

Understory field measurements were taken within each study plot along 50-meter belt transects (Springer et al., 2018). The richness and cover of understory species were measured using Daubenmire frames every 2 meters along the belt transect by identifying each plant to the species level and using ocular estimation and reference charts to determine percent cover (St. Clair et al. 2016). Any unfamiliar plant species discovered during measurements were photographed and keyed out to the species level, if possible. These methods were chosen to classify plant species across a large area quickly and accurately. Transects were chosen as the base method of measurement to maintain site consistency and longevity, as they were installed with the intent to last several years.

Field measurements were later used to classify each species by plant functional type and non-native status. The top ten most abundant species for each forest type and burn level were determined using percent cover estimates. Additionally, the collected percent cover and richness data was used to calculate the Shannon diversity index (Equation 1) and Simpson's diversity index (Equation 2) (Chevaux et al., 2022; Morris et al., 2014; St. Clair et al., 2016). In the following equations, S equals the total number of species, and p_i equals the individuals of one species (n) divided by the total number of individuals (N).

Shannon's Diversity Index: $$\mathrm{H}' = -\sum_{i=1}^{S} p_i ln p_i \tag{1}$$

Simpson's Dominance Index: $$D = \frac{1}{\sum_{i=1}^{S} {p_i}^2} \tag{2}$$

Statistical Analysis

The data was analyzed using mixed effect standard least squares models in JMP to look for trends and account for site variability (SAS Institute Inc., 2021). Each model was run with either richness or percent cover as the response variable. Explanatory fixed variables were burn severity, forest type, and their interaction, and the random effect of transect. Subsequent pairwise comparisons were run using student's t-tests for any main effects with p-values less than 0.1. The statistics governed where to calculate percent changes, which were then used to compare the plant community across sites to determine fire's effect on regeneration by forest type.

RESULTS

Effects of Fire and Forest Type on All Species Richness, Cover, and Diversity

Forest understory plant community richness was not significantly affected by the main effects of forest type or burn level. However, the interaction between forest type and burn level was significant (P = 0.01) (Figure 1 and Table 1), which was likely the result of species richness being reduced by 50% in burned aspen/fir forests (P = 0.002) while oak/maple and pinyon/juniper understories showed no negative effects of fire (Figure 1). Similarly, understory plant community cover was not significantly affected by the main effects of burn level or forest type, but the forest type by burn level interaction term was significant (P = 0.05) (Figure 1 and Table 1). This was likely because the percent cover in burned pinyon/juniper forests was 78% greater than in unburned pinyon/juniper forests (P = 0.007) but the cover of aspen/fir and oak/maple understory species showed no significant response to fire (Figure 1).

The Shannon and Simpson diversity indices were not significantly affected by the main effects of forest type, burn level, or the interaction between forest type and burn level (Figure 2 and Table 1). However, the Shannon diversity index in unburned aspen/fir forests was 33% greater than in burned aspen/fir forests (P = 0.02) (Figure 2).

Effects of Fire and Forest Type on Forb Species Richness and Cover

Forb species richness was not significantly affected by the main effects of forest type or burn level. However, forb richness showed a significant forest type by burn level interaction (P = 0.01) (Figure 3 and Table 1) partially due to the richness of forb species in unburned aspen/fir forests being 49% greater than in burned aspen/fir forests (P = 0.005) (Figure 3), and because the richness of forb species in burned pinyon/juniper forests was 46% greater than in unburned pinyon/juniper forests (P = 0.04) while forb richness in oak/maple forests showed no response to fire (Figure 3). Forb species cover was not significantly affected by forest type or burn level, but it was significantly affected by the interaction of forest type and burn level (P = 0.09) (Figure 3 and Table 1). The interaction was likely due to forb species percent cover in burned pinyon/juniper forests being 103% greater than in unburned pinyon/juniper forests (P = 0.006) while forb cover in aspen/fir and oak/maple forests experienced no fire effect (Figure 3).

Native versus Non-Native Species Richness and Cover

Native understory plant species richness was significantly affected by the main effects of forest type (P = 0.03) and burn level (P = 0.06), and the interaction between forest type and burn level (P = 0.03) (Figure 4 and Table 1). Native species richness was 40% greater in aspen/fir forests than in pinyon/juniper forests (P = 0.005) (Figure 4). Native species richness was 24% greater in unburned forests than in burned forests (P = 0.03) (Figure 4). The interaction effect can likely be attributed to native species richness in unburned aspen/fir forests being 55% greater than in burned aspen/fir forests (P = 0.002) while native richness in oak/maple and pinyon/juniper forests showed no response to fire (Figure 4).

Non-native understory plant species richness was significantly affected by the main effects of forest type (P = 0.001) and burn level (P = 0.04) and by the interaction between forest type and burn level (P = 0.03) (Figure 4 and Table 1). Non-native species richness in pinyon/juniper forests was 73% greater than in aspen/fir forests (P = 0.0002) (Figure 4). Non-native species richness in oak/maple forests was 57% greater than in aspen/fir forests (P = 0.006) (Figure 4). Non-native species richness in burned forests was 31% greater than in unburned forests (P = 0.02) (Figure 4). The interaction term was significant due to non-native species richness in burned pinyon/juniper forests being 59% greater than in unburned pinyon/juniper forests (P = 0.002) while fire did not affect non-native species richness in aspen/fir or oak/maple forest understories (Figure 4).

Native understory plant species cover was not significantly affected by the main effect of burn level or by the interaction between forest type and burn level (Figure 5 and Table 1). However, forest type did significantly affect native species cover (P = 0.03) (Figure 5 and Table 1). Native understory plant species percent cover was 73% greater in aspen/fir forests than in pinyon/juniper forests (P = 0.005) (Figure 5).

Non-native understory plant species cover was significantly affected by the main effects of forest type (P = 0.002) and burn level (P = 0.004), and the interaction between forest type and burn level (P = 0.06) (Figure 5 and Table 1). Non-native species percent cover was 165% greater in pinyon/juniper forests than in aspen/fir forests (P = 0.0003) (Figure 5). Non-native species percent cover was 152% greater in oak/maple forests than in aspen/fir forests (P = 0.009) (Figure 5). Burned forests had a 101% greater percent cover of non-native species than unburned forests (P = 0.002) (Figure 5). The interaction term was significant because non-native species percent cover in burned oak/maple forests was 126% greater than in unburned oak/maple forests (P = 0.001) and non-native species percent cover in burned pinyon/juniper forests was 101% greater than in unburned pinyon/juniper forests (P = 0.003) while cover of non-native species in aspen/fir understories saw no fire effect (Figure 5).

Most Abundant Species by Forest Type and Burn Level

The most abundant species in the forest understory plant community for unburned aspen/fir forests were *Symphoricarpos albus* (SYAL), *Hydrophyllum occidentale* (HYOC), *Maianthemum stellatum* (MAST), *Osmorhiza berteroi* (OSBE), and *Symphoricarpos oreophilus* (SYOR) (Figure 6). The most abundant species in the burned aspen/fir forests were *Iliamna rivularis* (ILRI), *Collinsia parviflora* (COPA), *Arnica cordifolia* (ARCO), *Nemophila breviflora* (NEBR), and *Lathyrus eucosmus* (LAEU) (Figure 6). All ten of the most abundant species in aspen/fir forests were native plants (Figure 6). Burn level only significantly affected SYAL, where the average percent cover of SYAL in control aspen/fir forests was 119% greater than in burned aspen/fir forests (P = 0.1) (Figure 6).

The most abundant species in the unburned oak/maple understory plant community were HYOC, *Acer grandidentatum* (ACGR), *Vicia americana* (VIAM), *Phlox longifolia* (PHLO), *Dactylis glomerata* (DAGL), and *Valeriana occidentalis* (VAOC) (Figure 6). In the burned oak/maple forests, the most abundant understory plants were *Carduus nutans* (CANU), *Lactuca serriola* (LASE), *Quercus gambelii* (QUGA), VIAM, *Poa pratensis* (POPR), and HYOC (Figure 6). Four of the most abundant species in oak/maple forests were non-native plant species (Figure 6). The ten most abundant understory plant species in oak/maple forests were not significantly affected by burn level (Figure 6).

The five most abundant species in unburned pinyon/juniper forests were *Bromus tectorum* (BRTE), *Alyssum alyssoides* (ALAL), *Poa secunda* (POSE), *Ceratocephala testiculata* (CETE), and *Bromus inermis* (BRIN) (Figure 6). The most abundant understory plant species in the burned pinyon/juniper forests were BRTE, CANU, *Melilotus officinalis* (MEOF), *Medicago sativa* (MESA), *Descurainia pinnata* (DEPI), and LASE (Figure 6). Eight of the most abundant species in pinyon/juniper forests were non-native plants (Figure 6). Only DEPI was significantly affected by burn level in pinyon/juniper forests, with burned forests having 133% greater DEPI abundance than unburned controls (P = 0.03) (Figure 6).

DISCUSSION

This study shows that fire differentially affected the richness and cover of understory forest communities with responses varying depending on forest type, plant functional type, and native vs non-native status. In response to our first question, the data showed that fire decreased understory plant richness in aspen/fir forests and increased cover in pinyon/juniper forests, while the understory richness and cover of oak/maple forests were not significantly impacted by fire (Figure 1, Table 1). Understory plant diversity was not significantly impacted by fire or forest type (Figure 2, Table 1). Our inquiry about plant functional type responses showed that forb species were most responsive to fire and forest type, with particularly positive effects of forbs in pinyon/juniper forests (Figure 3, Table 1). The data provided insights into our third question by revealing that most of the post-fire pinyon/juniper understory plant richness and cover increases were from non-native species, while post-fire aspen/fir forests saw a decrease in native species richness (Figures 4-5, Table 1).

Differential Forest Understory Responses to Fire

Fire tended to have negative impacts on the understory plant community of aspen/fir forests while positively impacting pinyon/juniper forests. Fire decreased the richness of the aspen/fir forest understory plant community (Figure 1) which may be related to the vigorous post-fire sprouting of aspen suckers to the exclusion of other species (Floyd et al., 2006; E. E. Knapp & Ritchie, 2016). Post-fire increases in light availability can decrease plant richness through a loss of shade-tolerant species (Laughlin & Fulé, 2008). Fire increased the cover of the pinyon/juniper forest understory plant community (Figure 1). *P. monophylla* is known to prevent understory plant growth through allelopathy, so it is possible that fire partially mitigated allelopathic effects although more research would be needed to test this hypothesis (Kato-Noguchi, 2021; Nektarios et al., 2005). Post-fire reduction in overstory competition for resources can also contribute to increased understory plant cover (Hartsell et al., 2020; Urza et al., 2019). Lastly, extreme precipitation from the 2018 Hurricane Rosa remnants may have augmented post-fire plant regeneration in the typically dry, low-elevation pinyon/juniper stands (Crandall et al., 2021; Urza et al., 2019).

Differential Sensitivities of Forb Species to Fire

Forb species that are abundant in forest understories and perform important ecosystem functions demonstrated the greatest sensitivity to fire across forest types (Figure 3). Fire decreased forb richness in aspen/fir forests (Figure 3). This can be the result of direct mortality or reduced seed viability and dispersal (Abella & Springer, 2015; Allen et al., 2008; Turner et al., 1997). Fire increased forb richness and cover in pinyon/juniper forests (Figure 3). Many of the most abundant forbs were annuals (Figure 6), which can respond positively to fire related to reductions in duff thickness (Bates et al., 1998; E. E. Knapp & Ritchie, 2016).

Native versus Non-Native Understory Response to Fire

The establishment and survival of native versus non-native plant species is often governed by abiotic conditions and biotic conditions (St. Clair et al., 2016). Fire decreased native species richness in aspen/fir forests (Figure 4). Native understory species beneath aspen stands are often facilitated by high soil moisture conditions created by the aspen overstory (Buck & St. Clair, 2012; Stohlgren et al., 1997) that is reduced in post-fire conditions (Kuhn et al., 2011; Stohlgren et al., 1997). Fire increased non-native plant cover in oak/maple forests (Figure 5) and non-native plant cover and richness in pinyon/juniper forests (Figures 4 and 5). Mature pinyon/juniper stands typically have few understory species capable of post-fire sprouting and are thus at risk of non-native plant invasion (Floyd et al., 2006). Furthermore, non-native plants can increase their post-fire growth from the seed bank (Allen et al., 2008) and respond positively to nutrient ash inputs and competition release from native vegetation in post-fire environments (Nektarios et al., 2005; St. Clair et al., 2016).

Broader Ecological Implications

This study investigated understory plant community changes across multiple forest types that may become increasingly common with the emergence of novel fire regimes due to human activity and climate change. We found that five years after a megafire event aspen/fir forests generally experience decreases in plant richness while lower elevation oak/maple and pinyon/juniper forests see increased cover and richness, especially of non-native plant species (Figures 1-6). Knowledge of how the understory plant communities of various forest types respond to megafires is valuable to preserving biodiversity that enhances ecosystem functions, wildlife habitat, and cultural value (Hartsell et al., 2020; Isbell et al., 2011). Management efforts should focus on the variable impacts megafires can have across forest types that may alter the structure, diversity, and invasibility of plant communities.

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FIGURES

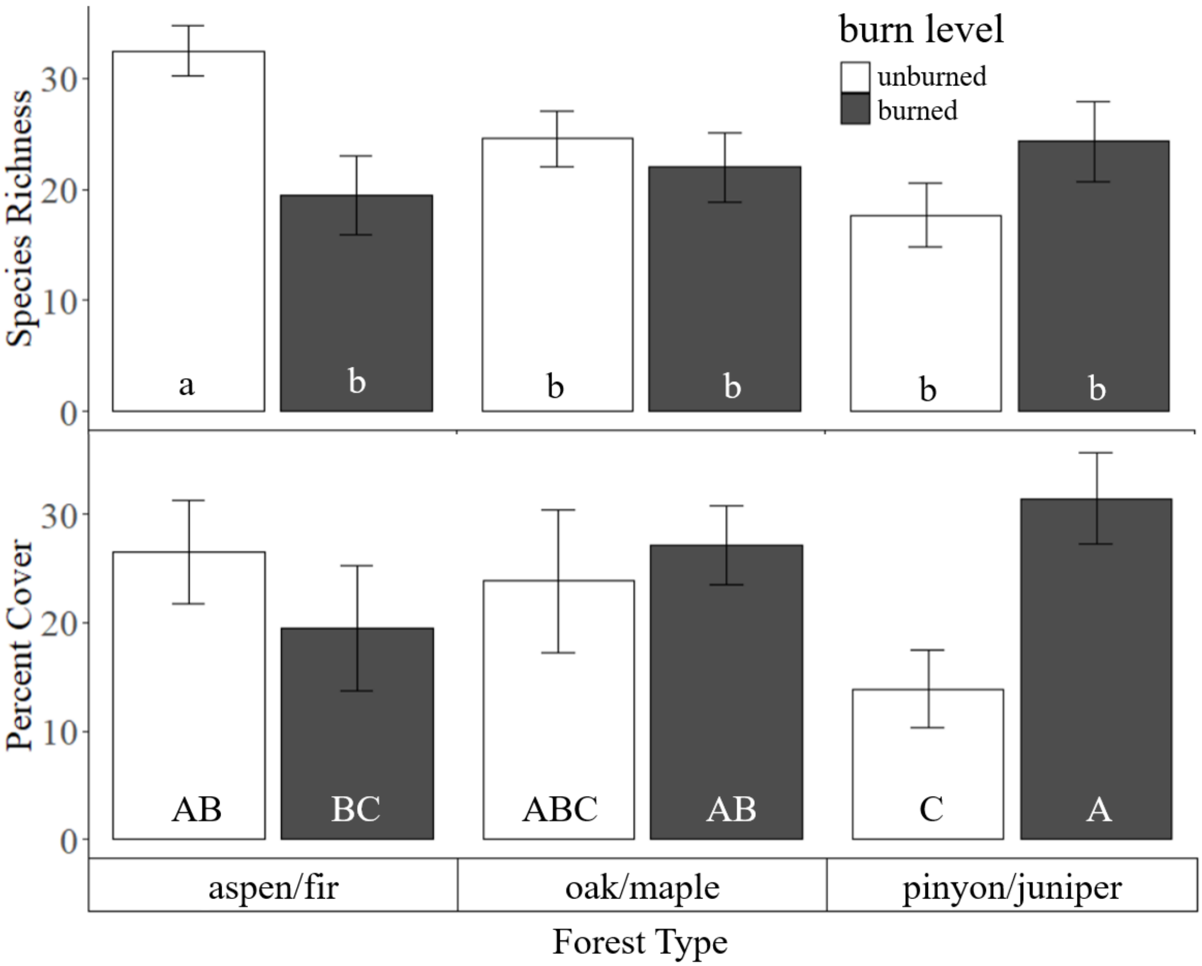

Figure 3-1. Richness and cover for all plant species by forest type and burn level. Letters on bars are compared by case, where bars not connected by the same letter signify P ≤ 0.1.

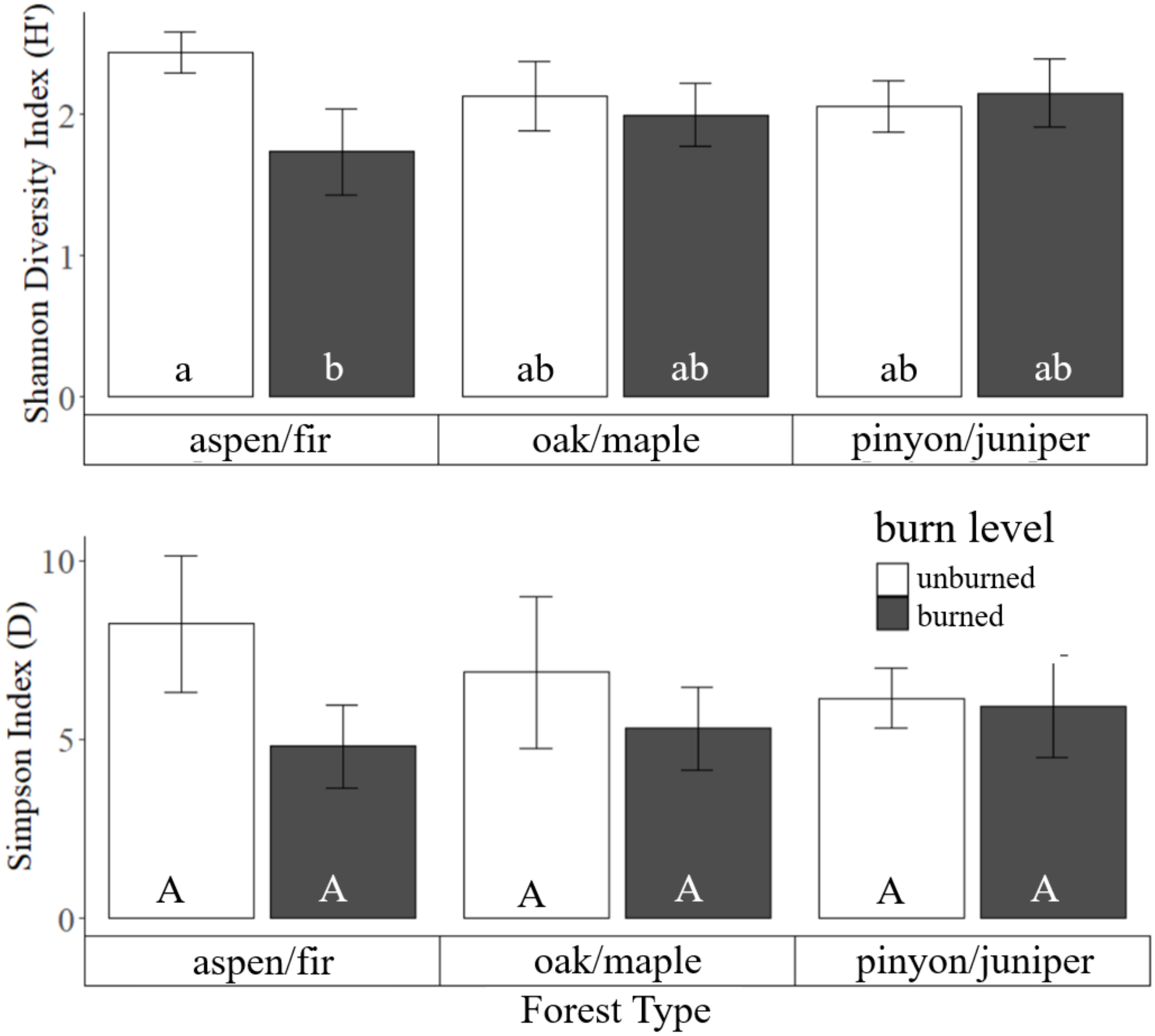

Figure 3-2. Shannon (H’) and Simpson (D) diversity indices for all plant species by forest type and burn level. Letters on bars are compared by case, where different letters signify $P \leq 0.1$.

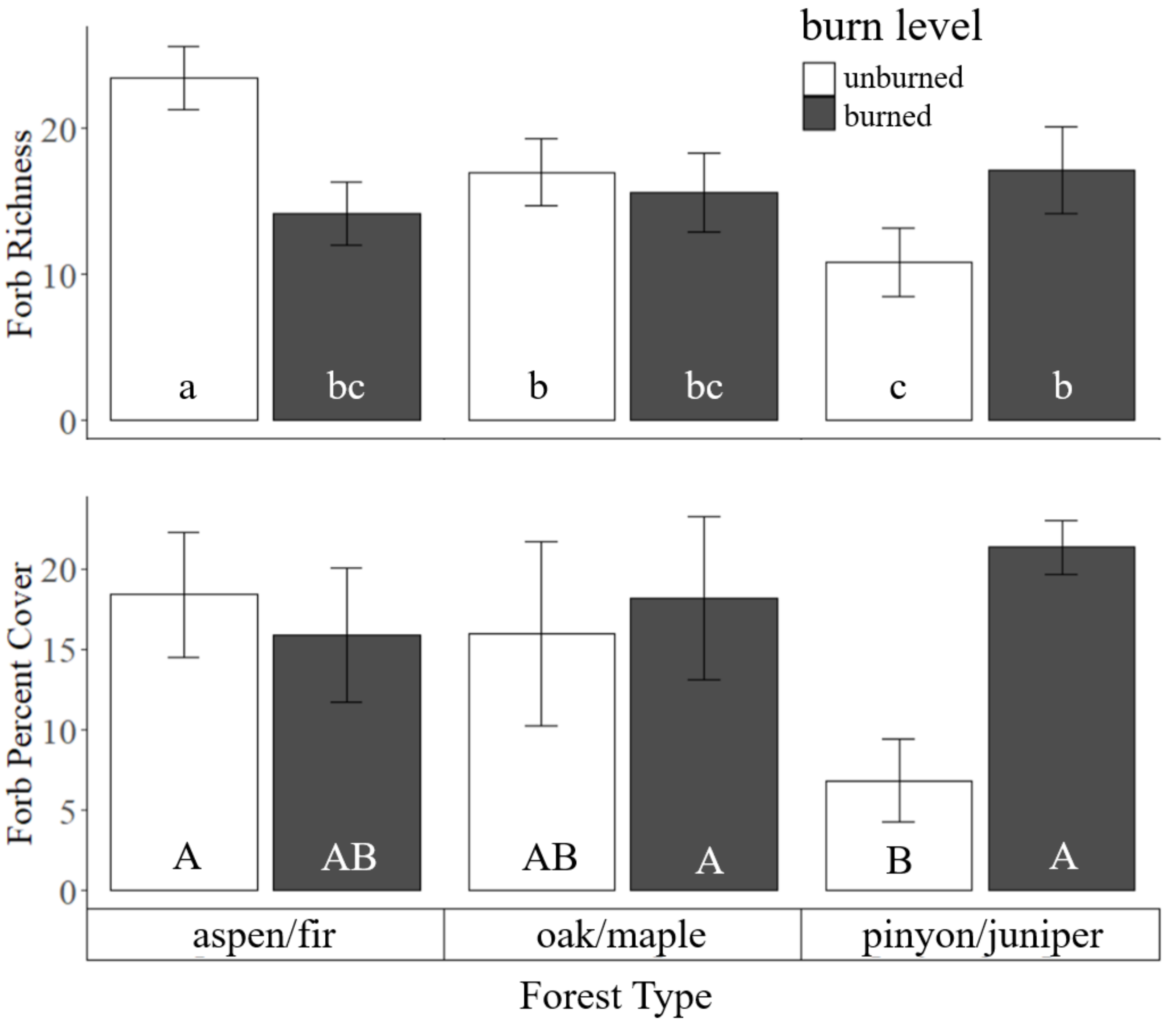

Figure 3-3. Richness and cover of forb species by forest type and burn level. Letters on bars are compared by case, where different letters signify $P \leq 0.1$.

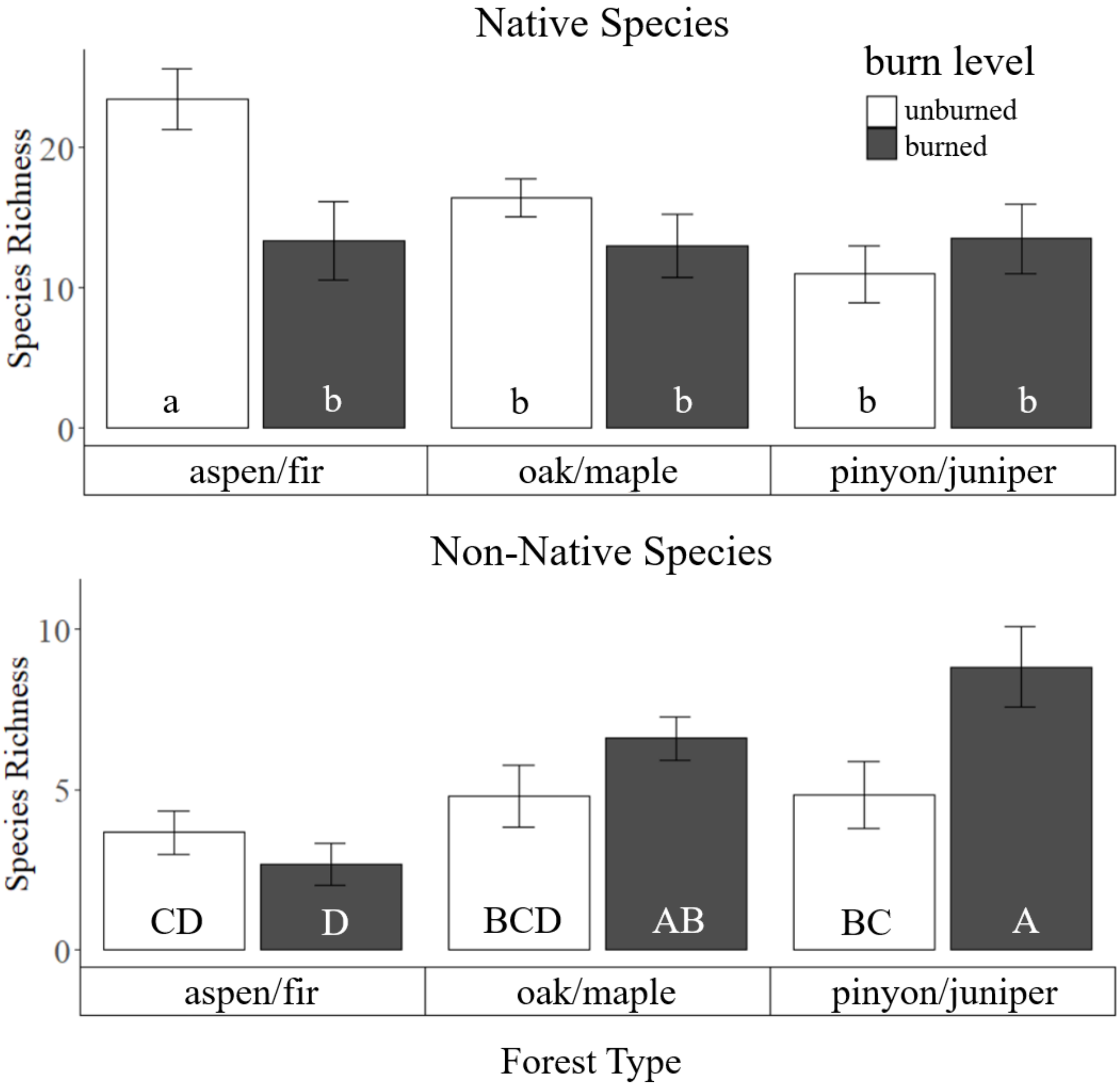

Figure 3-4. Richness of native and non-native plant species by forest type and burn level. Letters on bars are compared by case, where different letters signify $P \leq 0.1$. Note that the y-axis values are not the same and were represented as such to improve legibility.

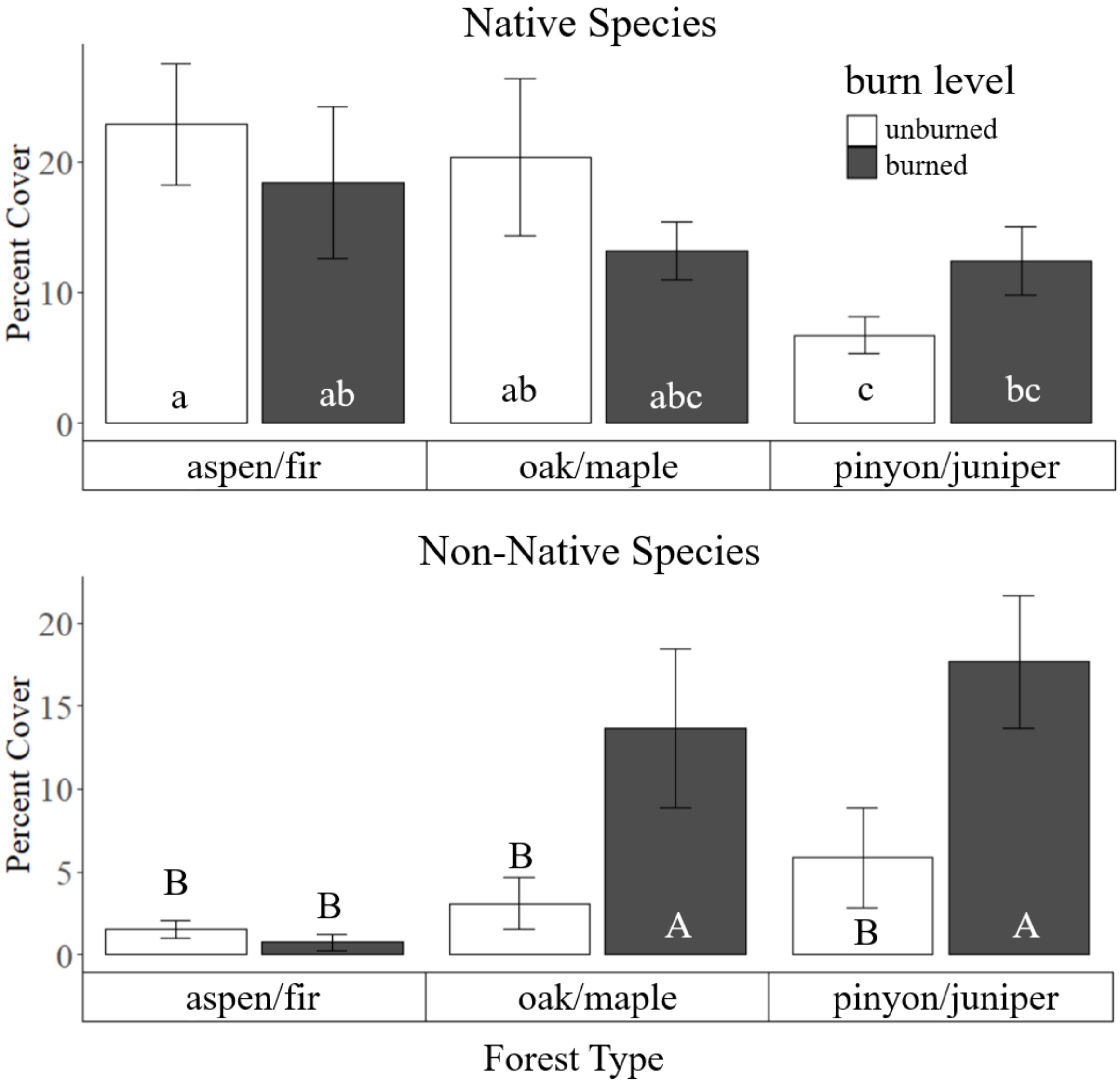

Figure 3-5. Percent cover of native and non-native plant species by forest type and burn level. Letters on bars are compared by case, where different letters signify P ≤ 0.1.

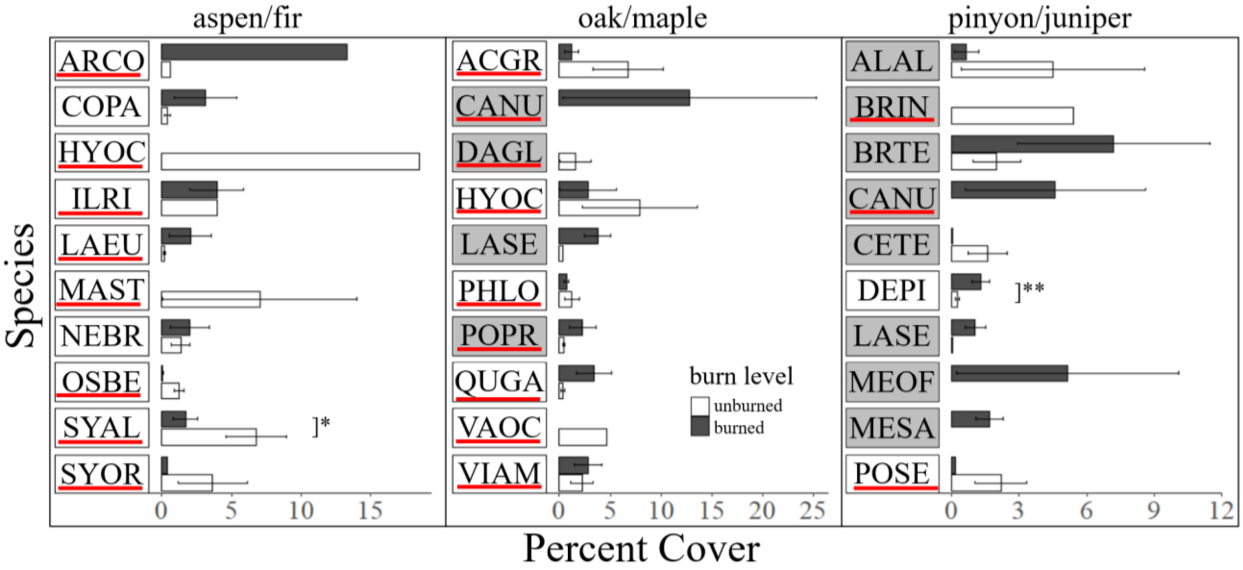

Figure 3-6. Average percent cover of the most abundant species for burned and unburned sites by forest type and burn level. Shaded plant codes indicate that the species is non-native, and a white background indicates the plant is native. Red underline indicates that a species is perennial. Asterisks represent p-value significance at the following levels: *P ≤ 0.1, **P ≤ 0.05.

TABLES

Table 3-1. Statistics of main and interactive effects by forest type (FT), burn level (BL), and the interaction between forest type and burn level (FT x BL). Asterisks represent p-value significance at the following levels: $^*P \leq 0.1$, $^{**}P \leq 0.05$, $^{***}P \leq 0.001$.

			Main Effect	**F-value**
Figure 1	All Species	Richness	FT	1.40
			BL	1.39
			FT x BL	5.41**
		Percent Cover	FT	0.19
			BL	1.35
			FT x BL	3.44**
Figure 2	Diversity Indices	Shannon (H')	FT	0.02
			BL	1.75
			FT x BL	1.68
		Simpson (D)	FT	0.07
			BL	2.04
			FT x BL	0.62
Figure 3	Forb Species	Richness	FT	2.03
			BL	0.53
			FT x BL	5.34**
		Percent Cover	FT	0.41
			BL	2.16
			FT x BL	2.63*
Figure 4	Richness	Native	FT	3.95**
			BL	3.92*
			FT x BL	4.12**
		Non-Native	FT	8.77***
			BL	4.50**
			FT x BL	3.92**
Figure 5	Percent Cover	Native	FT	3.85**
			BL	0.34
			FT x BL	1.33
		Non-Native	FT	7.71**
			BL	9.61**
			FT x BL	3.12*

CHAPTER 4

Novel Fire and Herbivory Regime Impacts on Forest Regeneration and Plant Community Assembly

Ungulate herbivore communities target woody plant species within post-fire forest understory

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ABSTRACT

Large mammal herbivores (ungulates) are increasing in number and spreading into novel habitats throughout the world. Their impact on forest understory plant communities is strong and varies by herbivore, plant growth form, and season. The objective of this study was to determine the individual and collective herbivory impacts of native versus domestic ungulates on the understory plant community composition of post-fire aspen forests. Four-way fencing treatments were installed in 2012 to separate ungulate species, and Daubenmire frames were used to collect percent cover estimates for each understory plant species. Vegetation data were later used to calculate richness and diversity indices. Total understory plant cover, richness, and diversity were not significantly impacted by the herbivory fencing treatment. However, woody plant species' percent cover was 90% greater in full ungulate exclusion plots than in the fenceless controls. Herbivores likely targeted woody plant species due to their high nutrient levels that last longer into the winter than those of forb or graminoid species. Herbivory treatment did not affect non-native species. Our results indicate that herbivore fencing can protect forest understory plant communities, particularly the woody species. Successful regeneration of woody species can benefit the diversity of the entire understory plant community and preserve forest structure.

INTRODUCTION

Ungulate abundance is increasing globally with significant impacts on ecosystems as their populations surpass carrying capacities (Côté et al., 2004; Egelkraut et al., 2018; Manier & Hobbs, 2007; Meier et al., 2017). Deer and elk populations specifically are increasing because of reduced predation and improved forage due to modern land management objectives (Côté et al., 2004; Meier et al., 2017). Domestic ungulates have also been added to the landscape and migration rates have decreased in areas, meaning time spent in one area has increased alongside population counts (Vavra et al., 2007). Ungulate overabundance may cause negative alterations of ecosystems by creating novel herbivory regimes (Côté et al., 2004) that can lead to plant invasions, altered vegetation structure, and forest regeneration failure (Endress et al., 2012; Olsen & Hansen, 1977; Spear & Chown, 2009). However, the potentially negative impacts of ungulates and changing herbivory regimes on plant community structure are not yet fully understood (Spear & Chown, 2009).

Novel herbivory regimes due to altered ungulate communities affect changes in plant community composition and diversity (Côté et al., 2004; D. S. Smith et al., 2016). Novel herbivory regimes can decrease plant biodiversity, increase erosion, and cause forest regeneration failure (Côté et al., 2004; Spear & Chown, 2009). Successional shifts in vegetation due to overgrazing are difficult to reverse and can result in vegetation state changes (Augustine & McNaughton, 1998; Côté et al., 2004; Hobbs, 1996). Ungulate herbivory can affect plant community composition by altering nutrient cycling through selective herbivory and fecal nitrogen addition, which can cause negative changes in plant heterogeneity leading to a trophic cascade (Binkley et al., 2003; Hobbs, 1996; Olsen & Hansen, 1977). The effect of nitrogen changes on plant community diversification is largely governed by plants' ability to recover from herbivory (Augustine & McNaughton, 1998). Plants resilient to herbivory have been found in many ecosystems, and exclosure studies have found that plants will adapt to better resist grazing (Augustine & McNaughton, 1998; Maxwell, Rhodes, et al., 2019). However, large ungulate populations have been found to overwhelm even resilient ecosystems due to the increase in frequency and amount of plant tissue loss, to the point of reaching a state change (Augustine & McNaughton, 1998; Egelkraut et al., 2018). More research is needed to better understand the relationship between increased ungulate populations, plant tolerance to herbivory, and subsequent plant community composition.

Selective ungulate herbivory affects plant community regeneration (Olsen & Hansen, 1977; Rhodes, Larsen, & St. Clair, 2018). Ungulates exhibit different seasonal preferences in browsing selection when foraging due to their anatomy, with two major classes of herbivores being termed as browsers (“concentrate feeders” with smaller mouths) and grazers (“grass and roughage eaters” with larger body sizes) (Olsen & Hansen, 1977; Rhodes, Larsen, & St. Clair, 2018). Plant understory community is likely to be more impacted by grazers such as cattle due to their preference for grasses and other lower-quality forage, while browsers such as deer are more likely to impact the woody species that are higher quality such as aspen trees (Kay & Bartos, 2000; Rhodes, Larsen, & St. Clair, 2018). One study of a mixed aspen-conifer forest found deer foraging behavior to remain constant during the year, while elk browsed aspen mostly during July and August and cattle browsed during the late summer months according to predetermined allotments (Rhodes, Larsen, Maxwell, et al., 2018). Certain ungulates further prefer particular plants. Cattle, for example, will specifically forage for sedges and grasses more than elk would, as cattle want plants with easily digestible tissue due to their slower gut passage rates (Olsen & Hansen, 1977). While all herbivores benefit most from plant tissues high in protein and low in non-digestible fiber, ungulate species that use less energy can forage longer than others to find optimal food sources (Heroy et al., 2017; Olsen & Hansen, 1977). Many ungulate habitats are affected by increased novel fire regimes (Arroyo-Vargas et al., 2019; Hobbs, 1996; H. Y. Wan, Rhodes, et al., 2014), and the ungulates that can thermoregulate better are often able to spend more time foraging due to less energy loss (Long et al., 2014). No previous studies have been conducted to determine the individual and collective impact of elk, deer, and cattle on long-term post-fire plant communities.

Ungulate impact may increase non-native plant richness and abundance by increasing seed dispersal and creating niche opportunities (Fleischner, 1994; Gill et al., 2022). Native and introduced ungulates often co-exist in forest ecosystems, all contributing to long-distance seed dispersal of both native and exotic plants (Baltzinger et al., 2019). Domesticated ungulates such as livestock that are rotated through several grazing allotments may reduce native plant diversity and increase exotic plants by transporting non-native propagules to susceptible landscapes, increasing available niche space, and decreasing plant-plant competition by consuming native vegetation (Fleischner, 1994; Gill et al., 2022; Travers et al., 2018). The permeability and connectivity of the landscape influence colonization rates and can increase invasion by non-native species (Shackelford et al., 2013). Native species richness tends to decrease with increased grazing pressure (Boavista et al., 2019; Dorrough et al., 2007; Nilar et al., 2019). **S**elective browsing that targets non-native species can prevent invasion (Katona et al., 2013), though non-native plants often experience herbivory release due to unfamiliarity (Parker et al., 2006; Shen et al., 2016). Non-native plants may also become invasive due to enemy release and high propagule pressure (Ni et al., 2021; St. Clair & Bishop, 2019). Furthermore, non-native-dominated plant communities are more susceptible to post-fire alterations of landscape structure and composition

(Stephens et al., 2014) and losses of native tree species due to decreased water availability (Reilly et al., 2020). Thus, the collective and individual impacts of ungulates on non-native plant species are likely important but more poorly understood than for native species (Schlierenzauer et al., 2021).

The mixed aspen-conifer forests in central Utah provide an optimal study area to determine the long-term impact of ungulate communities on post-fire plant community composition (Rhodes, Larsen, & St. Clair, 2018). Aspen forests provide preferential habitat for elk and deer, along with cattle during grazing allotments, which allows for the comparison of plant community regeneration across differential ungulate impacts (Rhodes, Larsen, & St. Clair, 2018). A long-term exclosure network was built following fires in 2012 within the Fishlake and Dixie National Forests of Utah, which has allowed for comparison of ungulate impacts on regeneration immediately following disturbance (Rhodes, Larsen, & St. Clair, 2018). Our objective is to classify the individual and collective impacts of elk, deer, and cattle herbivory on post-fire vegetation community assembly. The following questions were investigated:

1. Do elk, cattle, and deer herbivory impact the richness, cover, and diversity of understory plant communities following fire?
2. Do plant functional groups (woody, forb, and graminoids) respond differently to ungulate herbivory pressure?
3. Do ungulate communities differentially affect non-native plant species richness, cover, and diversity?

MATERIALS AND METHODS

Study Area

This study is a follow-up to (Rhodes, Larsen, & St. Clair, 2018) and takes place within 2012 burn scars located in the Fishlake and Dixie National Forests. The Box Creek and Harris Flat fires were 900 and 3,400 ha, respectively. The fires burned between June and July 2012 in mixed aspen-conifer forests. The elevation of exclosure sites placed across these burns ranged from 2430 to 2950 m. Sites had thirty-year averages of precipitation between 25-64 cm (PRISM data, Parameter-elevation Relationships on Independent Slopes Model) (Rhodes, Larsen, & St. Clair, 2018). The dominant vegetation of the Box Creek fire includes aspen (*Populus tremuloides*), subalpine fir (*Abies lasiocarpa*), white fir (*Abies concolor*), big sagebrush (*Artemesia tridentata*), mountain snowberry (*Symphoricarpos oreophilus*), Wood's rose (*Rosa woodsii*), and Ross' sedge (*Carex rossii*). The Harris Flat fire differed only slightly, where the dominant conifer was ponderosa pine (*Pinus ponderosa*), and the understory had higher densities of slender wheatgrass (*Elymus trachycaulus*), western wheatgrass (*Pascopyrum smithii*), and creeping barberry (*Mahonia repens*). Primary ungulates in the study area are cattle (*Bos taurus*), mule deer (*Odocoileus hemionus*), and elk (*Cervus canadensis*).

Sampling Design

Study sites were chosen within the two fires based on an assessment of high-severity burn (100% mortality of overstory) and pre-fire aspen dominance (more than 50% aspen) (Rhodes, Larsen, & St. Clair, 2018). At each site, a four-way ungulate exclosure was randomly assigned for installment in three sites at Box Creek and two at Harris Flat to distinguish ungulates' effect on the post-fire plant community. Each 30 x 30 m plot within the full factorial exclosure design was one of the following: (1) unfenced (cattle, elk, and mule deer access, “control”), (2) native ungulate access (mule deer and elk, “no cattle”), (3) mule deer only access (“no cattle or elk”), and (4) full exclusion (“no ungulates”). The ungulate fencing treatment slowly removed herbivory on a spectrum from grazing to browsing, by first removing grazers (cattle), then mixed feeders (elk), and finally browsers (deer). Fences for each treatment were set up as outlined in (Rhodes, Larsen, & St. Clair, 2018). The fences were viewed as ungulate reduction treatments since ungulates occasionally broke into even the best fences (Reikowski et al., 2022).

Transects and Field Measurements

The plant community was classified along 2 parallel, 24-meter transects within each exclosure level, allowing for a 3-meter buffer to avoid edge effects (Rhodes, Larsen, & St. Clair, 2018). The placement of each transect line was randomly assigned with at least 2 meters in between each transect. The spacing allows for independent measurements along each transect line as well as more systematic plot coverage of vegetation measurements. Along each transect, we recorded the identity and density of each understory species.

Understory plant density was measured with ocular estimates of percent cover using Daubenmire frames (50 x 25 cm quadrats) every 2 meters along the transect lines (St. Clair, O’Connor, Gill, & McMillan, 2016). Plants were identified by their scientific name at the species level. The data was later used to estimate species richness, abundance, Shannon diversity index (Equation 1), and Simpson’s dominance index (Equation 2) (Morris et al., 2014).

Shannon’s Diversity Index: $$\mathrm{H}' = -\sum_{i=1}^{S} p_i \ln p_i \qquad (1)$$

Simpson’s Dominance Index: $$D = \frac{1}{\sum_{i=1}^{S} {p_i}^2} \qquad (2)$$

In the equations above, p_i is equal to the individuals of one species (n) divided by the total number of individuals (N), and S is equal to the total number of species. Plant cover was also assessed by growth form (woody, forb, and graminoid) to estimate the structural complexity of the plant community.

Statistical Analysis

Once model assumptions of variance were met, understory plant richness, cover, and diversity were analyzed by fence treatment and plant growth form using linear mixed-effects modeling in R (Rhodes, Larsen, & St. Clair, 2018). AIC values informed the selection of models where treatment was analyzed as a fixed effect and site as a random effect. The indirect effects of the regenerating aspen were analyzed using linear regressions and F tests within JMP's Graph Builder (SAS Institute Inc., 2021).

RESULTS

Fence Treatment Effects on Understory Plant Community Diversity and Cover

Understory plant community richness was not significantly affected by fence treatments or the fence treatment by growth form interaction term (Figure 2). However, understory plant species richness varied significantly between growth forms in which forb species richness was 100% and 32% greater than woody and graminoid plant species richness, and graminoid species richness was 74% greater than woody species richness when averaged across treatments ($P < 0.0001$) (Figure 2). Pairwise comparisons of growth form mean values revealed that woody plant richness was 67% greater in both no ungulates and no cattle or elk treatments compared to control plots ($P = 0.08$ and $P = 0.08$) (Figure 2).

Understory plant community cover was not significantly affected by fence treatments, but the main effect of growth form and the fence treatment by growth form interaction term were significant ($P = 0.03$ and $P = 0.05$) (Figure 2). The woody cover was 83% and 9% greater than the forb cover and graminoid cover and the graminoid cover was 76% greater than the forb cover when averaged across treatments ($P = 0.03$) (Figure 2). The fence treatment was stronger for woody plant cover ($P = 0.08$) than for forb cover or graminoid cover ($P > 0.1$) (Figure 2). Pairwise comparisons of growth form mean values indicated that cover of woody understory plants was 90%, 127%, and 76% greater in the no ungulates treatment than in the fenceless control, no cattle, and no cattle or elk treatments ($P = 0.05$, $P = 0.02$, and $P = 0.08$) (Figure 2). The graminoid cover was 84% greater in control plots than in the no ungulates treatment plots ($P = 0.08$) (Figure 2).

The main effect of fence treatments was not statistically significant for understory plant community diversity based on Shannon diversity or Simpson dominance indices (Figure 3). However, Simpson's index was 47% and 42% greater in no cattle treatments than in control and no ungulates treatments ($P = 0.06$ and $P = 0.08$) based on pairwise comparison of mean values (Figure 3). Diversity, richness, and cover of the understory plant community were not significantly correlated to the height and density of the regenerating aspen community within each treatment.

Fence Treatment Effects on Non-Native Species Diversity and Cover

Non-native understory richness and cover responses to experimental conditions varied depending on fence treatment and plant growth form. The main effect of ungulate fence treatment and the treatment by growth form interaction term were not significant for non-native understory plant community richness (Figure 4). However, pairwise comparisons of treatment mean values showed that control plots had 55% greater non-native richness than no ungulates treatments (P = 0.06) (Figure 4). The main effect of non-native understory plant growth form richness was significant, with graminoid richness being 30% greater than forb richness when averaged across treatments (P < 0.0001) (Figure 4). Pairwise comparisons of growth form mean values showed that non-native forb richness was 67% greater in control plots than in the no ungulates treatments (P = 0.07) (Figure 4). Non-native understory plant cover was not significantly affected by ungulate fence treatment or the treatment by growth form interaction term (Figure 4). However, pairwise comparisons of treatment mean values showed that total non-native plant community cover was 69% and 78% greater in control plots than in no cattle and no ungulates treatments (P = 0.05 and P = 0.03) (Figure 4). The main effect of ungulate fence treatment was significant for non-native forb cover (P = 0.04). The main effect of growth form was significant for the percent cover of non-native plants, where graminoid cover was 63% greater than forb cover when averaged across treatments (P < 0.0001) (Figure 4). Pairwise comparisons of growth form mean values indicated that cover of non-native forbs in control plots was 72%, 70%, and 107% greater than no cattle, no cattle or elk, and no ungulates treatments (P = 0.03, P = 0.03, and P = 0.007) (Figure 4).

DISCUSSION

The objective of this study was to characterize the individual and collective impacts of elk, cattle, and deer on the composition of understory forest plant communities in post-fire environments. In response to our first question, total understory plant community cover and richness did not vary significantly between fencing treatments (Figures 2 & 3). However, the results of our second question about plant growth forms did show that woody, graminoid, and forb communities had different sensitivities to ungulate browsing as evidenced by significant treatment by growth form interactions (Figure 2). Finally, non-native species did not exhibit significant differences by fencing treatment as posed in our third question (Figure 4).

Ungulate Herbivory Did Not Affect Total Understory Plant Community Diversity and Cover

Ungulate herbivory is a key factor in shaping forest understory plant communities. Despite the importance of herbivory on forest understory communities, we found no significant correlations between fencing treatment and total plant richness and cover (Figure 2) or diversity (Figure 3). Understory composition can be resilient or slow to respond to environmental impacts like herbivory (Coop et al., 2014; Reikowski et al., 2022; Turkington et al., 2014). The total understory plant community richness and cover may also still be responding to post-fire effects that can overshadow more recent ungulate herbivory effects (Reikowski et al., 2022; Springer et al., 2022). It is also possible that the total diversity of the understory plant community may have had no net change due to the compensatory growth of one species when another was lost (Figure 3) (Coop et al., 2014).

Woody Plant Species Showed Greater Sensitivity to Ungulate Herbivory than Forbs and Graminoid Species

Plant growth form can be an important factor in surviving, or being targeted by, herbivores (Kay & Bartos, 2000; Rhodes, Larsen, Maxwell, et al., 2018; Sharp Bowman et al., 2017; Villalba et al., 2014). Our results show that woody species are more sensitive to ungulate herbivory than forb or graminoid species (Figure 2). Ungulates likely targeted woody species

(Figure 2) because they selectively eat plants with the highest protein and foliar nutrient content (Heroy et al., 2018; Lloyd et al., 2010), and woody species maintain their nutritional value longer than forb and graminoid species do (McWilliams, 2000; Rhodes, Larsen, Maxwell, et al., 2018; Villalba et al., 2014). Although woody species may have unpalatable defense chemistry, towards the end of the growing season the defenses fade while the forb and graminoid species simultaneously begin to senesce and ungulates become more selective for the protein and digestible nutrients that woody species have to offer (Holechek et al., 1987; McWilliams, 2000; Villalba et al., 2014). Late-season browsing reduces plant carbohydrate supply and regeneration time (Villalba et al., 2014) and graminoid species have fast growth rates that may allow them to take advantage of herbivory-opened niche space before the browsed woody species can (Figure 2) (A. K. Knapp et al., 1999; Staver et al., 2021). Furthermore, high silica content in grasses may make herbivores avoid graminoid species in favor of more palatable forage (Hartley & DeGabriel, 2016; Johnson et al., 2019; Sharp Bowman et al., 2017).

Non-Native Species are Negligibly Influenced by Ungulate Herbivory

Ungulate herbivory can target native plant species which increases the growth of unfamiliar, less palatable non-native species through herbivory release and by increasing available niche space (Gonzales & Clements, 2010; Nielson et al., 2019; Schlierenzauer et al., 2021). However, our results showed no significant effects of ungulate herbivory on the non-native plant community (Figure 4). Herbivory effects on non-native species can vary greatly at both local and landscape scales (Kie & Lehmkuhl, 2001; Lee & Kotanen, 2017) and by individual species (L. B. Knapp et al., 2008). Furthermore, generalist herbivores such as deer and cattle may still forage on non-native plant species, especially when they closely resemble native plant species (Lee & Kotanen, 2017; Pearse & Hipp, 2014; Sun et al., 2023). Thus, non-native species may not display an herbivory treatment effect if they are not avoided in favor of native species.

Broader Ecological Implications

This study quantified the effect of ungulate herbivory on post-fire forest understory regeneration. Our results show that ungulate herbivory differentially affected the post-fire aspen understory plant community by growth form, likely due to the high and long-lasting nutrient content of woody species. These findings are in line with other studies showing similar patterns of ungulate herbivory targeting woody plant species within multiple different forest types (Kuebbing et al., 2013; Meier et al., 2017). Selective herbivory of the woody species can alter nutrient cycling and overall plant diversity which has potential implications for valuable wildlife habitat and plant succession (Augustine & McNaughton, 1998; Chard et al., 2022; Endress et al., 2012; Garibaldi et al., 2007; Reikowski et al., 2022). Understanding ungulate herbivory's effect on forest understory plant communities is critical as novel herbivory regimes expand across forest ecosystems (Bernes et al., 2018; Faison et al., 2016; Olofsson & Post, 2018; Salgado-Luarte et al., 2018). Fencing that reduces ungulate herbivory can significantly improve woody plant growth, which may facilitate and strengthen forest recruitment and biodiversity in light of ungulate expansion.

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FIGURES

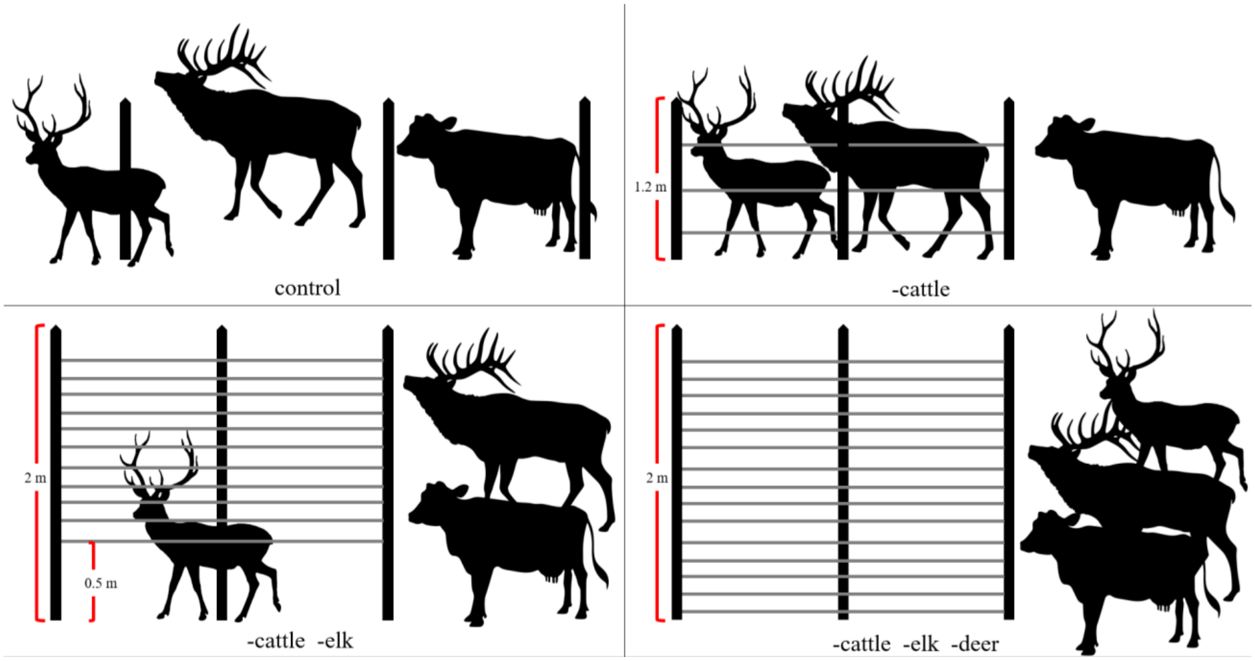
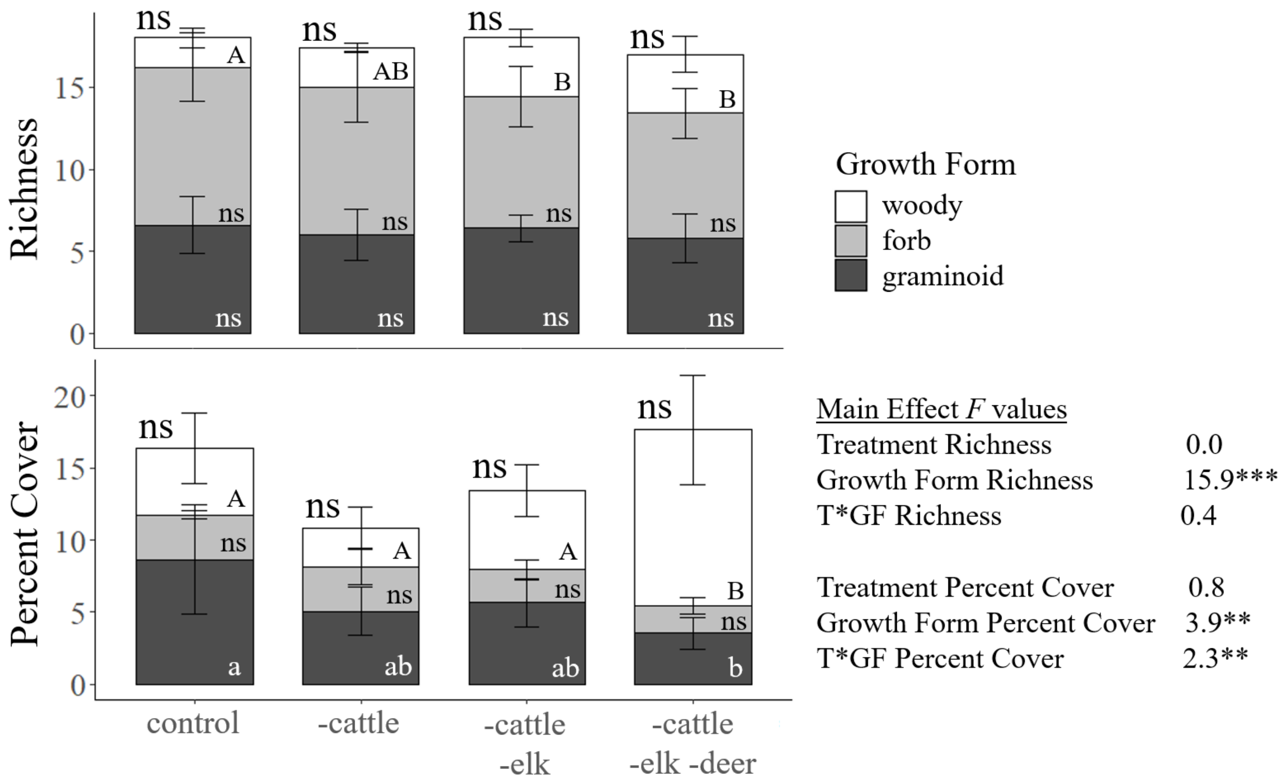


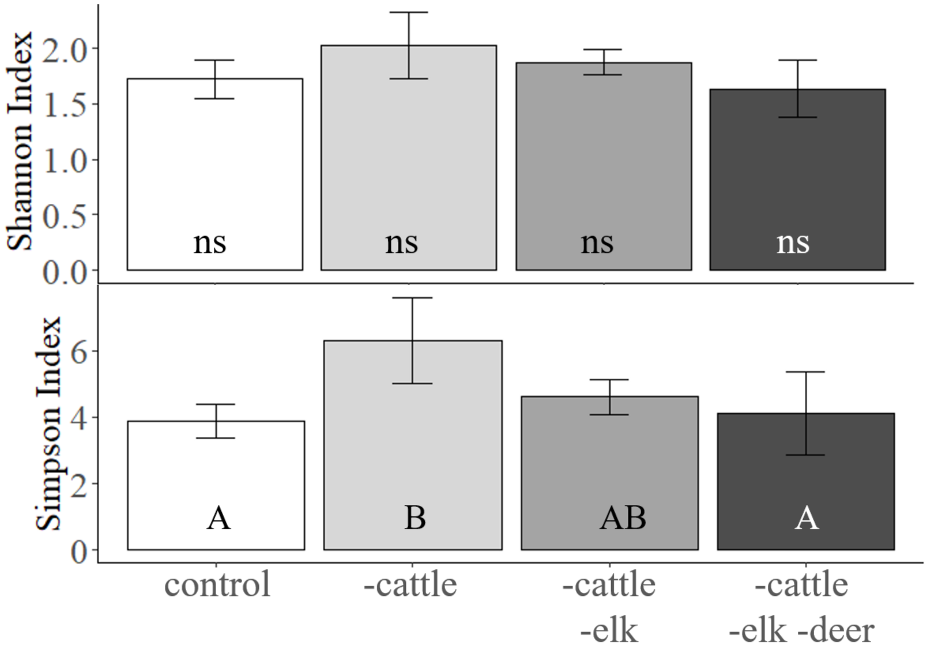
Figure 4-1. Diagram of ungulate exclosure fence treatments. Control sites have no fence to allow access for all large herbivores, -cattle treatments are referred to as “no cattle,” -cattle -elk treatments are referred to as “no cattle or elk,” and -cattle -elk -deer treatments are referred to as “no ungulates.”



<u>Main Effect *F* values</u>

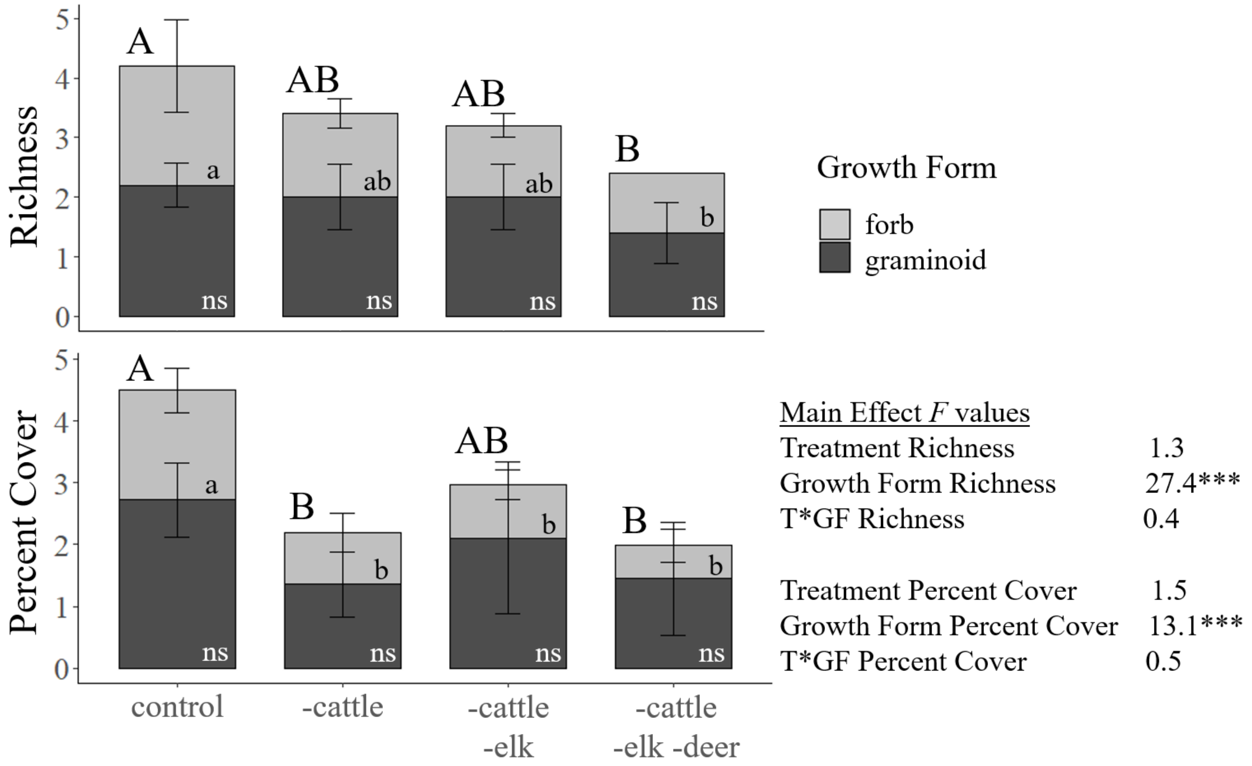
Treatment Richness	0.0
Growth Form Richness	15.9***
T*GF Richness	0.4
Treatment Percent Cover	0.8
Growth Form Percent Cover	3.9**
T*GF Percent Cover	2.3**

Figure 4-2. Richness and cover for all plant species by fence treatment and plant growth form types (woody, forb, graminoid). T*GF signifies the treatment by growth form interaction term. Letters on top of bars are for treatment comparisons. Letters inside of bars are to compare within plant growth form types, across treatments. Different letters signify P ≤ 0.1. Asterisks represent p-value significance at the following levels: *P ≤ 0.1, **P ≤ 0.05, ***P ≤ 0.001.



Treatment *F* values	
Shannon Index	1.0
Simpson Index	1.8

Figure 4-3. Shannon diversity index (H’) and Simpson’s index (D) by fence treatment. Letters within bars are for treatment comparisons. Different letters signify P ≤ 0.1.



Main Effect *F* values	
Treatment Richness	1.3
Growth Form Richness	27.4***
T*GF Richness	0.4
Treatment Percent Cover	1.5
Growth Form Percent Cover	13.1***
T*GF Percent Cover	0.5

Figure 4-4. Richness and cover for non-native plant species by fence treatment and plant growth form types (woody, forb, graminoid). T*GF signifies the treatment by growth form interaction term. Letters on top of bars are for treatment comparisons. Letters inside of bars are to compare within plant growth form types, across treatments. Different letters signify P ≤ 0.1. Asterisks represent p-value significance at the following levels: *P ≤ 0.1, **P ≤ 0.05, ***P ≤ 0.001.