THE BEEF AND THE BEES: HOW LIVESTOCK GRAZING AFFECTS POLLINATOR FEEDING AND NESTING RESOURCES OVER TIME

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A Thesis

Submitted in Partial Fulfillment

of the Requirements for the Degree of

Master of Science

in Environmental Science and Policy

Northern Arizona University

May 2023

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ABSTRACT

THE BEEF AND THE BEES: HOW LIVESTOCK GRAZING AFFECTS POLLINATOR FEEDING AND NESTING RESOURCES OVER TIME

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Livestock grazing is one of the most ubiquitous and ecologically significant disturbances on public lands in the Western U.S., with more than 250 million acres open to grazing on U.S. Forest Service and Bureau of Land Management lands (Beschta et al., 2013; Bureau of Land Management, n.d.; United States Department of Agriculture, 2017). Although numerous studies have investigated the effects of grazing on various ecosystem elements and processes, relatively few address its impacts on pollinators. Animal pollination is critical to the majority of flowering plant reproduction (Ollerton et al., 2011) as well as crop production (Klein et al., 2007). However, insect pollinators are exhibiting declines driven by climate change, pesticide use, and disease (Lebuhn et al., 2013; Pauw & Hawkins, 2011; Potts et al., 2010), with consequences not only for biodiversity but food security as well (Bauer & Sue Wing, 2016; Bauer & Wing, 2010). Leveraging a landscape-scale baseline dataset, this study assessed the effect of low-intensity grazing on pollinators via changes to floral and nesting resources on the Kaibab Plateau in northern Arizona. In July and August of 2022 we resampled selected plots within grassland and pinyon-juniper ecosystems, in both regularly grazed pastures and areas that had not been grazed for nine or more years. Analyses examined differences in vegetation and forb communities, forb abundance and diversity, soil characteristics, and ground cover across time and grazing status. Comparing baseline to current data, we found significant grazing impacts to vegetation and forb community composition as well as increased soil compaction at grazed sites. However, these effects were inconsistent across vegetation types. In addition, forb species diversity declined consistently across time, grazing status, and vegetation type, suggesting climatic shifts and grazing may be affecting pollinator habitat independently or interactively. Climate projections predict increased interannual variability and continued drier, hotter conditions, and grazing will likely continue as a widespread public land use. Implementing adaptive management strategies and pollinator-friendly grazing practices on public lands could mitigate these continued stressors and make a significant contribution to pollinator and rangeland ecosystem conservation.

ACKNOWLEDGEMENTS

Thank you to my committee for their invaluable guidance and assistance through every stage of my project; to my fellow Environmental Sciences & Policy students for their feedback, advice, proofreading, and encouragement; and to my family and friends for their moral support throughout a challenging endeavor. Thank you to Tyler Head for fearless assistance in the field, and to Stephanie Brown for excellent support with soils analysis. Last but not least, thank you to Sarah Colombo, for long hours and many laughs in the meadows of the Kaibab Plateau.

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CHAPTER 1: INTRODUCTION

Rangelands such as grasslands and scrublands cover more than half of earth's terrestrial surface, and livestock grazing is one of the most widespread land use practices in these ecosystems (Alkemade et al., 2013; Thapa-Magar et al., 2022). The ubiquity of grazing makes it one of the most significant disturbances affecting vegetation globally, potentially altering plant communities around the world (Díaz et al., 2007). In North America, European settlers introduced livestock (e.g. cattle, sheep) in the mid-1500s (Beschta et al., 2013). After a significant increase in livestock grazing from the mid-1800s to early 1900s, the federal government implemented regulations to address overgrazing and the consequent deterioration of vegetative cover and soil conditions (Beschta et al., 2013). Subsequently, federal agencies have overseen livestock grazing on most public lands, generally through a permit system authorizing a specific number of animal unit months (AUMs). One AUM represents the amount of forage needed to sustain a cow and calf pair for a month, and current permits allow more than 14 million cattle AUMs on western public lands every year (Kauffman et al., 2022). The U.S. Forest Service (USFS) authorizes grazing on more than 102 million acres and the Bureau of Land Management (BLM) on more than 155 million acres, equaling more than half the lands administered by the two largest federal land management agencies (Bureau of Land Management, n.d.; United States Department of Agriculture, 2017).

While the effects of grazing on plant communities have been extensively studied (Eldridge et al., 2016), few studies have examined impacts on pollinator communities (Thapa-Magar et al., 2020). Grazing may directly impact pollinator population dynamics or may indirectly affect pollinators through alterations to their habitat, particularly vegetation and soils (Buckles & Harmon-Threatt, 2019; Hanberry et al., 2021; Kimoto et al., 2012, Thapa-Magar et al., 2022). The Colorado Plateau, an area with both a long history of cattle grazing and high native bee diversity, may provide insight into the relationship between grazing and pollinators, particularly in arid ecosystems. The manuscript in Chapter 2 describes primary research conducted in the summer of 2022 on the impact of low-intensity cattle grazing on pollinator habitat in two vegetation community-types on the Kaibab Plateau in Northern Arizona. By resurveying research plots originally established in the mid 2000s, this research provided insight into grazing impacts on pollinator forage and nesting resources over a relatively short time (ca. 15 years). In the background section of Chapter 1, I provide a broader historic, and political context for the information presented in Chapter 2.

Ecological Background of Grazing on the Colorado Plateau

Several theoretical models provide context for the effect of grazing on pollinator habitat on the Colorado Plateau. The two most prominent of these models are the MSL model developed by Milchunas et al. (1988), and the state-and-transition (S-T) model presented by Westoby et al. (1989). The MSL model suggests that vegetation reacts to grazing based on environmental moisture and the ecosystem's evolutionary grazing history (Milchunas et al., 1988). The S-T model holds that there are a variety of possible states of vegetation within an ecosystem, and a set of possible transitions between persistent states (Westoby et al., 1989). Transitions are brought about by climate, natural events such as fire, and management actions (Westoby et al., 1989). Cingolani et al. (2005) refine the MSL model to reconcile it with the S-T model by suggesting that systems with a short evolutionary history of ungulate grazing can experience permanent transitions due to a relative lack of resilience to grazing (Cingolani et al., 2005). Studies evaluating the impact of grazing on plant communities are inconclusive, supporting theoretical frameworks in some cases while challenging them in others. Some research has documented negative impacts to plant species richness (Bakker et al., 2006; Floyd et al., 2003; Herrero-Juregui & Oesterheld, 2018) and functional diversity (Carmona et al., 2012). Other studies found no impact of grazing on trends in vegetative cover (Chew, 1982), or a positive influence on species diversity (Beck & Zavaleta, n.d.) and richness (Stohlgren et al., 1999). Often results depend on which metrics the study assesses, grazing intensity, and the specific plant community (Beschta et al., 2013), as well as climate (Herrero-Juregui & Oesterheld, 2018).

Rangelands on the Colorado Plateau are arid or semi-arid, and likely have a short evolutionary history of grazing. The climate of the Colorado Plateau is widely variable depending on elevation, but is often defined by low and inconsistent annual precipitation (Belesky & Malinowski, 2016). The evolutionary history of grazing in Arizona and other southwestern rangelands is still debated. Some authors argue that the area has a long history of mega-herbivorous grazing that has influenced the evolution of local plant communities (J. H. Brown & Mcdonald, 1995). Dung and keratinous remains do provide evidence of megaherbivores in the Colorado Plateau region (Mead & Agenbroad, 1992). However, lack of dung beetles (34 species of which exist east of the Rockies where there is evidence for historical high grazing pressure), and presence of grazing-sensitive grasses and soils indicate this area does not have a long evolutionary history of grazing (Mack & Thompson, 1982). Therefore, in this arid/semi-arid environment presumably lacking a long evolutionary history of herbivory, the MSL model would predict that grazing would negatively impact native plant diversity (Milchunas et al., 1988).

Grazing impacts on vegetation in semi-arid ecosystems and on the Colorado Plateau are variable. Several studies found that grazing reduces plant and functional diversity in dry, low productivity systems (Bakker et al., 2006; Carmona et al., 2012), and that the most extreme negative effects of grazing on species richness appeared in arid environments (Herrero-Juregui & Oesterheld, 2018). On the Colorado Plateau, research has found negative impacts like reduced species richness in grazed areas (Floyd et al., 2003), as well as no effect on plant functional group composition (Duniway et al., 2018), and positive effects of moderate grazing on native plant diversity (Souther et al., 2020). Milchunas et al. (1988) note that adaptations to aridity such as low height, storing resources below the ground, and the ability to grow quickly may also provide partial resistance to grazing, and thereby mitigate its impacts in arid systems. Rangelands may have undergone a state transition in response to grazing practices following the European introduction of livestock altered plant communities in this region. Historical sources indicate that from the mid-1800s onwards, and especially in the late 1800s to early 1900s, many areas of the Southwest were grazed at an intensity likely beyond what local plant communities could tolerate (Milchunas, 2006). On the Colorado Plateau, intensive grazing in combination with low and variable precipitation may have resulted in a permanent state change as theorized by the S-T model or Cingolani et al. (2005) (Bernstein et al., 2014; Wolf et al., 2020). In areas where a state change has occurred, the vegetation community may reflect a novel assemblage shaped by relatively recent grazing pressure rather than evolutionary grazing history (Wolf et al., 2020).

Intensive grazing may also have lasting effects on soil conditions in Colorado Plateau ecosystems. Soils on the Colorado Plateau developed primarily from sedimentary materials such as sandstones, limestones, or shales, and tend to be shallow (Duniway et al., 2016). Research in Northern Arizona found that heavy grazing increased soil compaction while reducing stability and water availability (Roberts et al., 2016). A long-term experiment in Western Colorado utilizing paired grazed and ungrazed sites established in 1953 also found that grazing reduced soil stability and increased compaction (Duniway et al., 2018). In addition, based on comparisons of ground cover at several points between 1953 – 2004 and local grazing history, the researchers concluded that persistent differences between sites suggest the area underwent a state transition due to overgrazing and droughts during the 1950s (Duniway et al., 2018).

Livestock Grazing and Pollinators

The impacts of livestock grazing on pollinator diversity and abundance have only recently received more frequent consideration and are still not thoroughly understood (Thapa-Magar et al., 2020). Climate and co-evolutionary history of vegetation with large ungulates may affect response of pollinators to herbivory. Studies have found both neutral or positive as well as negative effects on pollinators in systems adapted to high grazing pressure (Hanberry et al., 2021), but one meta-analysis found that livestock grazing was associated with lower pollinator richness in semi-arid systems with short evolutionary grazing histories (Thapa-Magar et al., 2022). The timing and duration or intensity of grazing also potentially influences effects on pollinators. For example, livestock grazing when floral resources are at an ebb, or at the height of foraging season, could leave pollinators like bumblebees without sufficient resources and/or change bee foraging behavior (Black et al., 2011; Kimoto et al., 2012). Grazing intensity may also negatively impact bee abundance and species richness (Hatfield & LeBuhn, 2007).

One of the most fundamental mechanisms by which grazing may impact pollinators is alterations to food resources (Shapira et al., 2020). Pollinators consume the nectar and pollen from flowering plants for their survival as well as the survival of their offspring. Diet overlaps with grazers (Debano et al., 2016), grazing-induced changes to vegetation height and density (Kimoto et al., 2012), and decreases in floral richness (Buckles & Harmon-Threatt, 2019) could all affect the visibility and availability of floral resources. Forb response to grazing is likely dependent on associated shifts in competition and ecological conditions rather than specific adaptation to grazing pressure. Grazing can reduce competition for resources from preferred forage such as perennial grasses, as well as create favorable conditions for forbs by increasing bare ground and decreasing litter depth and vegetation height (Hayes & Holl, 2003). Predicting grazing effects on forb species is challenging since forb response to grazing is highly idiosyncratic; some studies document declines, while others have shown no effect or even increases in forb species richness (Hayes & Holl, 2003), relative abundance (Liu et al., 2015), and floral abundance (Shapira et al., 2020) as a function of grazing. Numerous factors may explain the lack of consistency in forb response to grazing, including grassland productivity, grazing intensity, climate, and evolutionary history of grazing.

Grazing impacts vegetative communities directly through herbivory and trampling, and indirectly by altering ground cover, soil structure, and nutrients. Soil properties such as moisture, bulk density (a measure of compaction), penetration resistance (a measure of strength), and stability respond to grazing (Schmalz et al., 2013). One meta-analysis found that grazing at high and moderate levels significantly increased soil bulk density and penetration resistance, with intensive grazing also reducing water content (Lai & Kumar, 2020). Research suggests that grazing can also increase proportions of bare ground (Jones, 2000; Kimoto et al., 2012; Roberts et al., 2016) and reduce herbaceous litter (Kimoto et al., 2012; Schmalz et al., 2013). These changes to soil characteristics and ground cover can also influence processes that impacts plants such as erosion, nutrient cycling, and water infiltration, which in turn limits plant access to water and nutrients (Taboada et al., 2015). Furthermore, vegetation not only responds to soils and ground cover but affects them as well; as a result the relationship between grazing, vegetation, and soils can involve a complicated network of direct and indirect effects as well as feedback loops (Taboada et al., 2015).

Changes to soil characteristics and ground cover due to grazing (Bilotta et al., 2007; Taboada et al., 2015) directly influence pollinator communities. Over 80% of native bees nest in the ground, and herbivores may degrade nesting habitat for ground-dwelling species by compacting or destabilizing soils or altering soil moisture (Buckles & Harmon-Threatt, 2019; Kimoto et al., 2012). Additionally, herbivory and trampling may reduce nesting material such as woody debris or vegetative litter (Hanberry et al., 2021). Pollinators vary in their preferences for nesting conditions (Hanberry et al., 2021); consequently, alterations to these characteristics by livestock grazing may reduce or eliminate suitable nesting habitat depending on species. Trampling by large grazers like cattle may also result in the direct destruction of potential nest sites or existing nests (Sugden, 1985). While there is evidence that grazing negatively impacts nesting conditions (Buckles & Harmon-Threatt, 2019; Kimoto et al., 2012), the extent and importance of these effects is unknown. For instance, grazing could also have no effect on the availability or diversity of nesting resources or may even benefit nesting habitat by increasing areas of bare ground (Shapira et al., 2020).

Colorado Plateau Pollinator Diversity and Knowledge Gaps

The Colorado Plateau hosts an incredible diversity of native bees; one recent study found 660 species in Grand Staircase National Monument, UT, alone (Carril et al., 2018). However, there is a lack of studies examining the effects of livestock grazing on pollinators in this area. Of only three studies in Arizona, Colorado, Utah, or New Mexico, all found decreases in pollinator abundance (Kearns & Oliveras, 2009; Minckley, 2014) or diversity (Debano, 2006) related to grazing. In Southeast Arizona, Debano, (2006) found significant reductions in insect (including pollinators) species richness and/or diversity at grazed sites, and Minckley (2014) found reduced bee abundance at grazed sites. Kearns & Oliveras (2009) sampled grassland plots over five years near Boulder, Colorado, and categorized plots into grazing regimes ranging from ungrazed for 20+ years to grazed throughout the study. They observed decreased bee abundance with increased grazing, although they found no significant difference in species richness.

Historical and Political Context of Livestock Grazing on the Colorado Plateau

Livestock management in the West, including the Colorado Plateau, is rooted in a long history of – until the mid-1900s – largely unregulated grazing practices. Across the West, livestock grazing spread with Euro-American settlement, reaching a peak in the late 1800s (Fleischner, 2010). In Arizona, estimates show an increase from 40,000 to 1.5 million cattle between 1870 and 1891 (Sayre, 1999), and records suggest a similar “cattle boom” in New Mexico (Fredrickson et al., 1998). By the early 1900s, overstocking and climatic variability had resulted in such a dramatic decline in rangeland conditions and ranching viability that members of the ranching community themselves began to consider regulation necessary (Fleischner, 2010; Fredrickson et al., 1998; Sayre, 1999). Despite the ecological and economic rationale for grazing reform, political action was slow, and livestock grazing became the last major land use in the West to be governed by federal law (Fleischner, 2010). The Taylor Grazing Act was passed in 1934, authorizing the Department of the Interior to formalize grazing areas on public lands, issue permits for their use, and collect an associated fee. Since then, the Federal Land Policy Management Act (FLPMA) and Public Rangelands Improvement Act (PRIA) have expanded upon and refined the role of the government in grazing management on public lands, adding greater emphasis to managing lands for multiple uses and improving rangeland conditions (Regan, 2016).The implementation of federal regulation created an enduring source of tension about grazing policy, with two conflicting interpretations: that ranchers have codified rights to public lands, or that ranchers have grazing privileges subject to amendment or withdrawal by the government (Regan, 2016).

Conflicts over rangeland management are exacerbated by the ambiguity and lack of options for resolving disagreements between environmental and ranching interests evident in existing policy. Requirements that permittees actively graze on their allotments and own nearby private properties that can be associated with the permit generally preclude environmental groups from simply purchasing permits for conservation purposes. Instead, environmental advocates utilize the Endangered Species Act and the National Environmental Policy Act to achieve their goals, resulting in greater legal and social conflict (Regan, 2016). The lack of legal clarity about the nature of ranchers' access to public lands also creates conflicts between ranching operations and the government. For example, even though the establishment of Grand Staircase Escalante National Monument (GSENM) specifically included protections for existing grazing permits within the monument, many local ranchers and politicians were bitterly opposed to the designation due to concerns that grazing would be curtailed as a result (Wrabley, 2009).

Despite these challenges, environmentalists, ranchers, government agencies, and politicians have collaborated to find solutions in some cases. There are examples of conservation groups organizing buyouts of grazing permits, wherein ranchers sell their base property and associated permit and the organization requests that the managing government agency retire the allotment (Regan, 2016). The Grand Canyon Trust (GCT) has implemented this strategy in our study area, although they were unsuccessful in permanently retiring permits and instead graze the lowest possible number of cattle allowed by the BLM and USFS. The GCT used this strategy elsewhere in and around GSENM in the early 2000s with some success in retiring permits, although subsequent legal and political challenges highlight the susceptibility of buyouts to regional backlash and changes in government administrations or personnel (Regan, 2016; Wrabley, 2009). There have been political efforts to formalize and protect a buyout strategy, such as the Voluntary Grazing Permit Buyout Act (H.R. 3324), introduced in 2003, which would have allowed permit holders to surrender their grazing privileges for compensation from the federal government and retired associated lands from grazing (Wrabley, 2009). Although H.R. 3324 did not pass, Representative Adam Smith (D-WA) has introduced a similar Voluntary Grazing Permit Retirement Act (H.R. 6935) several times over the past few years. H.R. 6935 would simply allow permittees to voluntarily waive their grazing privileges for the purpose of permanently ceasing livestock grazing, in which case managing agencies would be required to ensure grazing ended and prevented from issuing any new permits for the associated allotment. While some ranchers have been open to negotiated buyouts or relevant legislation, ranching industry associations and many individual ranchers have remained opposed to these efforts, and overall livestock grazing remains a socially and politically contentious issue in the American West (Regan, 2016; Wrabley, 2009).

Management Considerations

Pollinators are essential to the survival of roughly 80% of flowering plant species (Ollerton et al., 2011) and 35% of global crop production (Klein et al., 2007), making them a fundamental component of both functioning ecosystems and food security (Bauer & Sue Wing, 2016; Bauer & Wing, 2010). Alarmingly, scientists have documented declines in pollinators globally across ecosystems and regions; for example, studies have found extirpation or range reductions in half of all Illinois bumble bee species since the mid 1900s (Hanberry et al., 2021), and significant losses in bee species diversity in Britain after 1980 (Potts et al., 2010). Known factors linked to pollinator decline include habitat loss, pesticides, climate change, and disease (Potts et al., 2010), and identifying and minimizing additional stressors could improve trajectories for pollinators (M. J. F. Brown et al., 2016). Acknowledging livestock grazing as a potential stressor connects grazing management and federal policy to biodiversity and food security in novel ways.

Regardless of sociopolitical tensions surrounding livestock management, if grazing has the potential to affect pollinator abundance, diversity, and habitat resources, implementing pollinator-friendly grazing practices will be critical for sustaining rangelands. Despite gaps in scientific understanding of the relationship between grazing and pollinators, there are general grazing management practices that can minimize effects on pollinators. Several studies identify spatial and temporal scales of grazing as particularly important factors to evaluate. Hanberry et al. (2021) suggest that best management practices should address both these factors in the context of historical ungulate grazing patterns, as well as generally avoid grazing over large areas for extended periods of time. For example, applying grazing and burning to create dynamic points of disturbance and produce shifting combinations of habitat patches could enhance biodiversity and enrich wildlife habitat compared to traditional management techniques that result in more uniform utilization (Fuhlendorf & Engle, 2001).

Hayes & Holl (2003) also emphasize the importance of diversifying disturbance regimes and considering an ecosystem's adaptation to grazing, based on their finding that grazing can affect life-history guilds differently within a vegetation community. Black et al. (2011), summarizing science-backed recommendations for rangeland management, reinforce the significance of spatial and temporal scales in grazing regimes and conclude that identifying the right combination of timing and grazing intensity is necessary for grazing to benefit pollinators. In addition, they find that allowing overgrazed sites to regain forb diversity and abundance, weighting time toward recovery periods for vegetation rather than periods of grazing, and low-intensity short-duration grazing in the fall are all important strategies for supporting pollinator habitat in rangelands.

Data-informed and targeted management strategies may also be beneficial. For example, management based on forb utilization rate rather than a set stocking rate and reducing livestock numbers during drought may improve pollinator habitat and increase plant community resilience (Hanberry et al., 2021). A study on the response of pollinator habitat characteristics to management techniques suggested tracking bare ground, the Floristic Quality Index, and floral richness to assess how management strategies affect pollinator resources (Buckles & Harmon-Threatt, 2019). Another study examining the diet overlap between native bees and ungulates concluded that management techniques should begin by identifying grazers' spatial and temporal use of the environment, as well as understanding the main characteristics and phenology of native bee and floral communities. With this information, managers could avoid grazing areas during sensitive periods and/or when a high degree of diet overlap with native bees is likely, as well as consider restoration plantings to provide bees with forage plants (Debano et al., 2016). Finally, management plans that anticipate climatic factors – such as episodic drought in arid rangelands – could improve conservation outcomes for native plant communities (Loeser et al., 2007) and by extension, pollinators.

Livestock grazing is also an area where land managers may consider reconciliation-focused approaches. Fuhlendorf & Engle (2001) note that rangelands encompass large areas of extensive plant communities, yet historically have been, and often still are, managed for livestock production. With most rangeland management techniques developed to increase and sustain livestock production by controlling the natural variability of rangeland ecosystems and grazing itself, opportunities to manage for biodiversity are lost. Alternative management techniques that strive for heterogeneity can balance biological diversity, wildlife habitat, and agricultural objectives Fuhlendorf & Engle (2001).

References

Alkemade, R., Reid, R. S., Van Den Berg, M., De Leeuw, J., & Jeuken, M. (2013). Assessing the impacts of livestock production on biodiversity in rangeland ecosystems. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(52), 20900–20905. https://doi.org/10.1073/pnas.1011013108

Bakker, E. S., Ritchie, M. E., Olff, H., Milchunas, D. G., & Knops, J. M. H. (2006). Herbivore impact on grassland plant diversity depends on habitat productivity and herbivore size. *Ecology Letters*, *9*(7), 780–788. https://doi.org/10.1111/j.1461-0248.2006.00925.x

Bauer, D. M., & Sue Wing, I. (2016). The macroeconomic cost of catastrophic pollinator declines. *Ecological Economics*, *126*, 1–13. https://doi.org/10.1016/J.ECOLECON.2016.01.011

Bauer, D. M., & Wing, I. S. (2010). Economic Consequences of Pollinator Declines: A Synthesis. In *Agricultural and Resource Economics Review* (Vol. 39, Issue 3).

Beck, J. J., & Zavaleta, E. S. (n.d.). *Grazing maintains native plant diversity and promotes community stability in an annual grassland*. https://www.researchgate.net/publication/280042155

Belesky, D. P., & Malinowski, D. P. (2016). Grassland communities in the USA and expected trends associated with climate change. In *Acta Agrobotanica* (Vol. 69, Issue 2). Polish Botanical Society. https://doi.org/10.5586/aa.1673

Bernstein, E. J., Albano, C. M., Sisk, T. D., Crews, T. E., & Rosenstock, S. (2014). Establishing cool-season grasses on a degraded arid rangeland of the Colorado Plateau. *Restoration Ecology*, *22*(1), 57–64. https://doi.org/10.1111/rec.12023

Beschta, R. L., Donahue, D. L., Dellasala, D. A., Rhodes, J. J., Karr, J. R., O’Brien, M. H., Fleischner, T. L., & Deacon Williams, C. (2013). Adapting to climate change on western public lands: Addressing the ecological effects of domestic, wild, and feral ungulates. *Environmental Management*, *51*(2), 474–491. https://doi.org/10.1007/s00267-012-9964-9

Bilotta, G. S., Brazier, R. E., & Haygarth, P. M. (2007). The Impacts of Grazing Animals on the Quality of Soils, Vegetation, and Surface Waters in Intensively Managed Grasslands. In *Advances in Agronomy* (Vol. 94, pp. 237–280).

Black, S. H., Shepherd, M., & Vaughan, M. (2011). Rangeland management for pollinators. *Rangelands*, *33*(3), 9–13. https://doi.org/10.2111/1551-501X-33.3.9

Brown, J. H., & Mcdonald, W. (1995). *Livestock Grazing and Conservation on Southwestern Rangelands* (Vol. 9, Issue 6).

Brown, M. J. F., Dicks, L. v., Paxton, R. J., Baldock, K. C. R., Barron, A. B., Chauzat, M. P., Freitas, B. M., Goulson, D., Jepsen, S., Kremen, C., Li, J., Neumann, P., Pattemore, D. E., Potts, S. G., Schweiger, O., Seymour, C. L., & Stout, J. C. (2016). A horizon scan of future threats and opportunities for pollinators and pollination. *PeerJ*, *2016*(9). https://doi.org/10.7717/PEERJ.2249

Buckles, B. J., & Harmon-Threatt, A. N. (2019). Bee diversity in tallgrass prairies affected by management and its effects on above- and below-ground resources. *Journal of Applied Ecology*, *56*(11), 2443–2453. https://doi.org/10.1111/1365-2664.13479

Bureau of Land Management. (n.d.). *Livestock Grazing on Public Lands*. Retrieved April 12, 2022, from https://www.blm.gov/programs/natural-resources/rangelands-and-grazing/livestock-grazing

Carmona, C. P., Azcárate, F. M., De Bello, F., Ollero, H. S., Lepš, J., & Peco, B. (2012). Taxonomical and functional diversity turnover in Mediterranean grasslands: interactions between grazing, habitat type and rainfall. *Source: Journal of Applied Ecology*, *49*(5), 1084–1093. https://doi.org/10.1111/j.l

Carril, O. M., Griswold, T., Haefner, J., & Wilson, J. S. (2018). Wild bees of grand staircase-escalante national monument: Richness, abundance, and spatio-temporal beta-diversity. *PeerJ*, *2018*(11). https://doi.org/10.7717/peerj.5867

Chew, R. M. (1982). Changes in Herbaceous and Suffrutescent Perennials in Grazed and Ungrazed Desertified Grassland in Southeastern Arizona, 1958-1978. *The American Midland Naturalist*, *108*(1), 159–169. https://about.jstor.org/terms

Cingolani, A. M., Noy-Meir, I., & Díaz, S. (2005). Grazing effects on rangeland diversity: A synthesis of contemporary models. *Ecological Applications*, *15*(2), 757–773. https://doi.org/10.1890/03-5272

Debano, S. J. (2006). Effects of livestock grazing on aboveground insect communities in semi-arid grasslands of southeastern Arizona. *Biodiversity and Conservation*, *15*(8), 2547–2564. https://doi.org/10.1007/s10531-005-2786-9

Debano, S. J., Roof, S. M., Rowland, M. M., & Smith, L. A. (2016). Diet Overlap of Mammalian Herbivores and Native Bees: Implications for Managing Cooccurring Grazers and Pollinators. *Natural Areas Journal*, *36*(4), 458–477. https://doi.org/10.3375/043.036.0412

Díaz, S., Lavorel, S., McIntyre, S., Falczuk, V., Casanoves, F., Milchunas, D. G., Skarpe, C., Rusch, G., Sternberg, M., Noy-Meir, I., Landsberg, J., Zhang, W., Clark, H., & Campbell, B. D. (2007). Plant trait responses to grazing - A global synthesis. *Global Change Biology*, *13*(2), 313–341. https://doi.org/10.1111/j.1365-2486.2006.01288.x

Duniway, M. C., Geiger, E. L., Minnick, T. J., Phillips, S. L., & Belnap, J. (2018). Insights from Long-Term Ungrazed and Grazed Watersheds in a Salt Desert Colorado Plateau Ecosystem ☆. *Rangeland Ecology & Management*, *71*, 492–505. https://doi.org/10.1016/j.rama.2018.02.007

Duniway, M. C., Nauman, T. W., Johanson, J. K., Green, S., Miller, M. E., Williamson, J. C., & Bestelmeyer, B. T. (2016). Generalizing Ecological Site Concepts of the Colorado Plateau for Landscape-Level Applications. *Rangelands*, *38*(6), 342–349. https://doi.org/10.1016/j.rala.2016.10.010

Eldridge, D. J., Poore, A. G. B., Ruiz-Colmenero, M., Letnic, M., Soliveres, S., & Soliveres3, S. (2016). Ecosystem structure, function, and composition in rangelands are negatively affected by livestock grazing. In *Ecological Applications* (Vol. 26, Issue 4).

Fleischner, T. L. (2010). Livestock Grazing and Wildlife Conservation in the American West. In J. du Toit, R. Kock, & J. Deutsch (Eds.), *Wild Rangelands: Conserving Wildlife While Maintaining Livestock i Semi-arid Ecosystems.* (pp. 235–265). Blackwell Publishing.

Floyd, M. L., Fleischner, T. L., Hanna, D., & Whitefield, P. (2003). Effects of Historic Livestock Grazing on Vegetation at Chaco Culture National Historic Park, New Mexico. *Conservation Biology*, *17*(6), 1703–1711.

Fredrickson, E., Avstad, K. M. H., Estell, R., & Yder, P. H. (1998). Perspectives on desertification: south-western United States. *Journal of Arid Environments*, 191–207.

Fuhlendorf, S. D., & Engle, D. M. (2001). Restoring Heterogeneity on Rangelands: Ecosystem Management Based on Evolutionary Grazing Patterns. *BioScience*, *51*(8). https://academic.oup.com/bioscience/article/51/8/625/220557

Hanberry, B. B., DeBano, S. J., Kaye, T. N., Rowland, M. M., Hartway, C. R., & Shorrock, D. (2021). Pollinators of the Great Plains: Disturbances, Stressors, Management, and Research Needs. *Rangeland Ecology and Management*, *78*, 220–234. https://doi.org/10.1016/j.rama.2020.08.006

Hatfield, R. G., & LeBuhn, G. (2007). Patch and landscape factors shape community assemblage of bumble bees, Bombus spp. (Hymenoptera: Apidae), in montane meadows. *Biological Conservation*, *139*(1–2), 150–158. https://doi.org/10.1016/j.biocon.2007.06.019

Hayes, G. F., & Holl, K. D. (2003). Cattle Grazing Impacts on Annual Forbs and Vegetation Composition of Mesic Grasslands in California. In *Conservation Biology* (Vol. 17, Issue 6).

Herrero-Juregui, C., & Oesterheld, M. (2018). Effects of grazing intensity on plant richness and diversity: a meta-analysis. *Oikos*, *127*(6), 757–766. https://doi.org/10.1111/oik.04893

Jones, A. (2000). Effects of Cattle Grazing on North American Arid Ecosystems: A Quantitative Review. In *Source: Western North American Naturalist* (Vol. 60, Issue 2).

Kauffman, J. B., Beschta, R. L., Lacy, P. M., & Liverman, M. (2022). Livestock Use on Public Lands in the Western USA Exacerbates Climate Change: Implications for Climate Change Mitigation and Adaptation. *Environmental Management*, *69*(6), 1137–1152. https://doi.org/10.1007/s00267-022-01633-8

Kearns, C. A., & Oliveras, D. M. (2009). Environmental factors affecting bee diversity in urban and remote grassland plots in Boulder, Colorado. *Journal of Insect Conservation*, *13*(6), 655–665. https://doi.org/10.1007/s10841-009-9215-4

Kimoto, C., Debano, S. J., Thorp, R. W., Taylor, R. V., Schmalz, H., Delcurto, T., Johnson, T., Kennedy, P. L., & Rao, S. (2012). Short-term responses of native bees to livestock and implications for managing ecosystem services in grasslands. *Ecosphere*, *3*(10). https://doi.org/10.1890/ES12-00118.1

Klein, A.-M., Vassiere, B. E., Cane, J. H., Seffan-Dewenter, I., Cunningham, S. A., Kremen, C., & Tscharntke, T. (2007). Importance of pollinators in changing landscapes for world crops _ Enhanced Reader. *Proceedings of the Royal Society B*, *274*, 303–313.

Lai, L., & Kumar, S. (2020). A global meta-analysis of livestock grazing impacts on soil properties. *PLoS ONE*, *15*(8).

Liu, J., Feng, C., Wang, D., Wang, L., Wilsey, B. J., & Zhong, Z. (2015). Impacts of grazing by different large herbivores in grassland depend on plant species. In *Source: Journal of Applied Ecology* (Vol. 52, Issue 4).

Loeser, M. R. R., Sisk, T. D., & Crews, T. E. (2007). Impact of grazing intensity during drought in an Arizona grassland: Contributed papers. *Conservation Biology*, *21*(1), 87–97. https://doi.org/10.1111/j.1523-1739.2006.00606.x

Mack, R. N., & Thompson, J. N. (1982). Evolution in Steppe with Few Large, Hooved Mammals. In *Source: The American Naturalist* (Vol. 119, Issue 6).

Mead, J. I., & Agenbroad, L. D. (1992). Isotope dating of Pleistocene dung deposits from the Colorado Plateau, Arizona and Utah. *Radiocarbon*, *34*(1), 1–19. https://doi.org/10.1017/S0033822200013370

Milchunas, D. G. (2006). *Responses of Plant Communities to Grazing in the Southwestern United States*. http://www.fs.fed.us/rm

Milchunas, D. G., Sala, O. E., & Lauenroth, W. K. (1988). A Generalized Model of the Effects of Grazing by Large Herbivores on Grassland Community Structure. In *Source: The American Naturalist* (Vol. 132, Issue 1). https://about.jstor.org/terms

Minckley, R. L. (2014). Maintenance of richness despite reduced abundance of desert bees (Hymenoptera: Apiformes) to persistent grazing. *Insect Conservation and Diversity*, *7*(3), 263–273. https://doi.org/10.1111/icad.12049

Ollerton, J., Winfree, R., & Tarrant, S. (2011). How many flowering plants are pollinated by animals? *Oikos*, *120*(3), 321–326. https://doi.org/10.1111/j.1600-0706.2010.18644.x

Potts, S. G., Biesmeijer, J. C., Kremen, C., Neumann, P., Schweiger, O., & Kunin, W. E. (2010). Global pollinator declines: Trends, impacts and drivers. In *Trends in Ecology and Evolution* (Vol. 25, Issue 6, pp. 345–353). https://doi.org/10.1016/j.tree.2010.01.007

Regan, S. (2016). *Managing Conflicts over Western Rangelands* (Vol. 54). www.perc.org

Roberts, A. J., Johnson, N. C., Ostergren, D., & Sanford, R. (2016). *The Influence of Grazing Management on Soil Carbon and Mycorrhizae*.

Sayre, N. (1999). The Cattle Boom in Southern Arizona: Towards a Critical Political Ecology. In *Source: Journal of the Southwest* (Vol. 41, Issue 2). https://about.jstor.org/terms

Schmalz, H. J., Taylor, R. V., Johnson, T. N., Kennedy, P. L., Debano, S. J., Newingham, B. A., & McDaniel, P. A. (2013). Soil morphologic properties and cattle stocking rate affect dynamic soil properties. *Rangeland Ecology and Management*, *66*(4), 445–453. https://doi.org/10.2111/REM-D-12-00040.1

Shapira, T., Henkin, Z., Dag, A., & Mandelik, Y. (2020). Rangeland sharing by cattle and bees: moderate grazing does not impair bee communities and resource availability. *Ecological Applications*, *30*(3). https://doi.org/10.1002/eap.2066

Souther, S., Loeser, M., Crews, T. E., & Sisk, T. (2020). Drought exacerbates negative consequences of high-intensity cattle grazing in a semiarid grassland. *Ecological Applications*, *30*(3). https://doi.org/10.1002/eap.2048

Stohlgren, T. J., Schell, L. D., Heuvel, B. vanden, & Vanden, B. (1999). How Grazing and Soil Quality Affect Native and Exotic Plant Diversity in Rocky Mountain Grasslands. In *Ecological Applications* (Vol. 9, Issue 1). D.

Sugden, E. A. (1985). Pollinators of Astragalus monoensis Barneby (Fabaceae): new host records; potential impact of sheep grazing. *Great Basin Naturalist*, *45*(2).

Taboada, M. A., Rubio, G., & Chaneton, E. J. (2015). Grazing Impacts on Soil Physical, Chemical, and Ecological Properties in Forage Production Systems. In *Soil Management: Building a Stable Base for Agriculture* (pp. 301–320). wiley. https://doi.org/10.2136/2011.soilmanagement.c20

Thapa-Magar, K. B., Davis, T. S., & Fernández-Giménez, M. E. (2022). A meta-analysis of the effects of habitat aridity, evolutionary history of grazing and grazing intensity on bee and butterfly communities worldwide. *Ecological Solutions and Evidence*, *3*(2). https://doi.org/10.1002/2688-8319.12141

Thapa-Magar, K. B., Davis, T. S., & Kondratieff, B. (2020). Livestock grazing is associated with seasonal reduction in pollinator biodiversity and functional dispersion but cheatgrass invasion is not Variation in bee assemblages in a multi-use shortgrass prairie _ Enhanced Reader. *PLoS ONE*, *15*(12).

United States Department of Agriculture. (2017). *Grazing Statistical Summary*. https://www.fs.fed.us/rangeland-management/documents/grazing-stats/2010s/GrazingStatisticalSummaryFY2016.pdf

Westoby, M., Walker, B., & Noy-Meir, I. (1989). Opportunistic management for rangelands not at equilibrium. *Journal of Range Management*, *42*(4), 266–274.

Wolf, A. C., Mitchell, R. M., Aslan, C., Butterfield, B., & Souther, S. (2020). *Evidence for State Change in an Arid Grassland-Steppe: Limited Recovery of Vegetation After Intermediate to Long-Term Cattle Exclusion in the Southwestern U.S.*

Wrabley, R. B. (2009). *Managing The Monument: Cows and Conservation In Grand Staircase-Escalante National Monument*. http://www.hcn.org/issues/90/2796.

CHAPTER 2: THE BEEF AND THE BEES: HOW LIVESTOCK GRAZING AFFECTS POLLINATOR FEEDING AND NESTING RESOURCES OVER TIME

Introduction

Roughly half of all terrestrial ecosystems are rangelands, with the majority of these regions dedicated to livestock grazing (Alkemade et al., 2013; Thapa-Magar et al., 2022). The ubiquity of grazing makes it one of the most significant disturbances affecting vegetation globally, potentially altering plant communities on a global scale (Díaz et al., 2007). In North America, European settlers introduced livestock (e.g. cattle, sheep) in the mid-1500s, and a significant increase in livestock grazing followed from the mid-1800s to early 1900s (Beschta et al., 2013). Today the U.S. Forest Service (USFS) and Bureau of Land Management (BLM) authorize grazing on more than 250 million acres combined, an area representing more than half of the lands these agencies administer, and a significant portion of the Western U.S. (Bureau of Land Management, n.d.; United States Department of Agriculture, 2017). The Colorado Plateau is an area with extensive public lands, a long history of cattle grazing, and high native bee diversity, which may provide insight into the relationship between grazing and pollinator habitat, particularly in arid ecosystems.

Several theoretical models provide context for the effect of grazing on pollinator habitat on the Colorado Plateau. Milchunas et al. (1988) suggests that vegetation reacts to grazing based on environmental moisture and the ecosystem’s evolutionary grazing history. Westoby et al. (1989) present the state-and-transition (S-T) model, which holds that there are a variety of possible states of vegetation within an ecosystem, and a set of possible transitions between persistent states. Transitions are brought about by climate, natural events such as fire, and management actions (Westoby et al., 1989). Cingolani et al. (2005) refine the MSL model to reconcile it with the S-T model by suggesting that systems with a short evolutionary history of ungulate grazing can experience permanent transitions due to a relative lack of resilience to grazing. The Colorado Plateau is best categorized as an arid or semi-arid system with a short evolutionary history of grazing. Climate across the plateau is often defined by low and inconsistent annual precipitation (Belesky & Malinowski, 2016), and while the evolutionary history of grazing in Arizona is still debated, lack of dung beetles (which are often associated with high grazing pressure) and presence of grazing-sensitive grasses and soils indicate a short evolutionary history of grazing (Mack & Thompson, 1982).

In this arid/semi-arid environment presumably lacking a long evolutionary history of herbivory, theory predicts that grazing will have a negative impact on plant diversity. Research in semi-arid ecosystems and on the Colorado Plateau specifically has produced mixed results. Studies have found that grazing reduces species and functional diversity in dry, low productivity systems (Bakker et al., 2006; Carmona et al., 2012). Some research shows that the most extreme negative effects of grazing on species richness appears in arid environments (Herrero-Juregui & Oesterheld, 2018). Studies located in Colorado Plateau ecosystems have found negative impacts like reduced species richness in grazed areas (Floyd et al., 2003), as well as no effect on plant functional group composition (Duniway et al., 2018), and positive effects of moderate grazing on native plant diversity (Souther et al., 2020). The history of livestock grazing in this region may explain some of these discrepancies. From the mid-1800s onwards, especially around the turn of the century, many areas of the Southwest were grazed at an intensity likely beyond what local plant communities could tolerate (Milchunas, 2006). In areas where a state change has occurred, the vegetation community may reflect a novel assemblage shaped by relatively recent grazing pressure rather than evolutionary grazing history (Wolf et al., 2020). Intensive grazing may also have lasting effects on soil conditions in Colorado Plateau ecosystems. Research in Northern Arizona found that heavy grazing increased soil compaction while reducing stability and water availability (Roberts et al., 2016). A long-term study in Western Colorado established in 1953 also found that grazing reduced soil stability and increased compaction (Duniway et al., 2018). Duniway et al. (n.d.) also found evidence that the area had undergone a state transition due to overgrazing and drought, after evaluating ground cover over a span of 50 years and finding persistent differences between grazed and ungrazed sites.

While grazing impacts to vegetation have been extensively studied, little is known about the effects on pollinator communities (Thapa-Magar et al., 2020). Grazing may directly impact pollinator population dynamics or may indirectly affect polinators through alterations to habitat, particularly vegetation and soils (Buckles & Harmon-Threatt, 2019; Hanberry et al., 2021; Kimoto et al., 2012; Thapa-Magar et al., 2022). Alterations to food and nesting resources is one of the most fundamental mechanisms by which grazing may affect pollinators (Shapira et al., 2020). Pollinators rely on the nectar and pollen from flowering plants for their survival as well as reproduction. Diet overlaps with grazers (Debano et al., 2016), grazing-induced changes to vegetation height and density (Kimoto et al., 2012), and decreases in floral richness (Buckles

& Harmon-Threatt, 2019) could all affect the visibility and availability of floral resources. Grazing may also indirectly affect vegetation, and pollinator nesting habitat, by changing soil characteristics and ground cover (Bilotta et al., 2007; Schmalz et al., 2013; Taboada et al., 2015). These changes to soil characteristics and ground cover can also influence processes that impact plants such as erosion, nutrient cycling, and water infiltration, which in turn limits plant access to water and nutrients (Taboada et al., 2015). Furthermore, vegetation not only responds to soils and ground cover but affects them as well; as a result the relationship between grazing, vegetation, and soils can involve a complicated network of direct and indirect effects as well as feedback loops (Taboada et al., 2015). Over 80% of native bees nest in the ground, and grazing may degrade the nesting habitat of ground-dwelling species by compacting or destabilizing soils, or altering soil moisture (Buckles & Harmon-Threatt, 2019; Kimoto et al., 2012). Additionally, herbivory and trampling may reduce nesting material such as woody debris (Hanberry et al., 2021). Pollinators vary in their preferences for nesting conditions (Hanberry et al., 2021); consequently, changes to soil characteristics and ground cover may reduce or eliminate suitable nesting habitat depending on species.

To evaluate the impact of cattle grazing on pollinator forage and nesting resources in a semi-arid region with limited adaptation to grazing and a long history of livestock use, we measured differences in vegetation community composition and diversity, ground cover, and soil characteristics over time and across grazing levels. We drew time comparisons between baseline data collected in 2005 and 2007, and current data collected in the summer of 2022; sampling sites were distributed between actively grazed pastures and pastures that have not been grazed for at least nine years. We used two questions to assess the effect of cattle grazing on pollinator habitat: 1) How do pollinator forage resources, including vegetation/forb community composition, forb species diversity, functional diversity of traits related to pollination, and forb cover and relative abundance, differ across time periods and grazing status? 2) How does pollinator nesting habitat, including soil bulk density, water content, stability, and compaction; extent of bare ground; and abundance of woody debris, differ across time periods and grazing status?

Methods

Study Site

The Arizona Strip lies directly north of the Grand Canyon, stretching from Marble Canyon on the east to the border of Arizona and Nevada on the west. The area contains a wide variety of ecoregions; precipitation and climate vary with elevation, but the region is semi-arid and experiences high temperatures at lower elevations during the summer months (Western Regional Climate Center, n.d.). The Arizona Strip has a long history of Indigenous inhabitation, use by European settlers, trappers, and traders, and by the late 1800s, extensive livestock grazing (Trudeau, 2006).

The Grand Canyon Trust (GCT), a non-profit organization dedicated to environmental protection on the Colorado Plateau, holds the permits for two grazing allotments at the eastern end of the Arizona Strip. Known collectively as the North Rim Ranches, these allotments are comprised of 830,000 acres of public lands and encompass much of the Kaibab Plateau, Paria Plateau, and House Rock Valley. A comprehensive grazing history for this landscape is difficult to piece together, although evidence suggests that in some areas historical overgrazing resulted in substantial reductions in vegetation, perhaps to the point of making ranching unviable (Trudeau, 2006). In addition, research conducted on these allotments indicates that grazing may have contributed to a permanent state change in the vegetation community in this region (Bernstein et al., 2014; Wolf et al., 2020). When the GCT acquired the grazing permits for the Kane and Two-Mile allotments in 2005, no livestock had grazed the area since 2003. Starting in 2006 the GCT implemented a rest-rotational grazing system with ~600 cow-calf pairs, which represents a low stocking level relative to most commercial ranching operations. Due to high summer temperatures and relatively temperate winters at lower elevations, the cattle alternate between summer and winter pastures on a rotation schedule wherein each pasture is only grazed every other year. In addition, some pastures are not included in the rotation and are permanently rested.

We measured vegetation and soil characteristics at 57 sites in grassland (29 sites) and pinyon-juniper woodland (28 sites) vegetation types within the USFS allotment on the Kaibab Plateau. Within each vegetation type approximately half of the sites were located in “grazed” pastures, defined as pastures currently included in the rest-rotational schedule managed by the GCT (15 grassland and 13 pinyon-juniper woodland sites). The remaining half were located in “ungrazed” pastures, defined as pastures which have not been grazed for at least nine years (14 grassland and 15 pinyon-juniper woodland sites). All sites were selected from a set of 650 sites included in a baseline assessment conducted by the GCT and NAU, based on their location relative to the focus vegetation types and grazing status, and then by accessibility. Five sites were sampled for the baseline assessment in 2007 instead of 2005, and were included in data collection and analyses due to a relatively low number of accessible ungrazed grassland sites overall. Due to the location of grazed and ungrazed pastures, grazed grassland sites were concentrated in meadows on the top of the plateau while ungrazed grassland sites fell on the western slope. Grazed pinyon-juniper sites were primarily on the eastern slope of the plateau, and ungrazed sites primarily on the western slope (Figure 1).

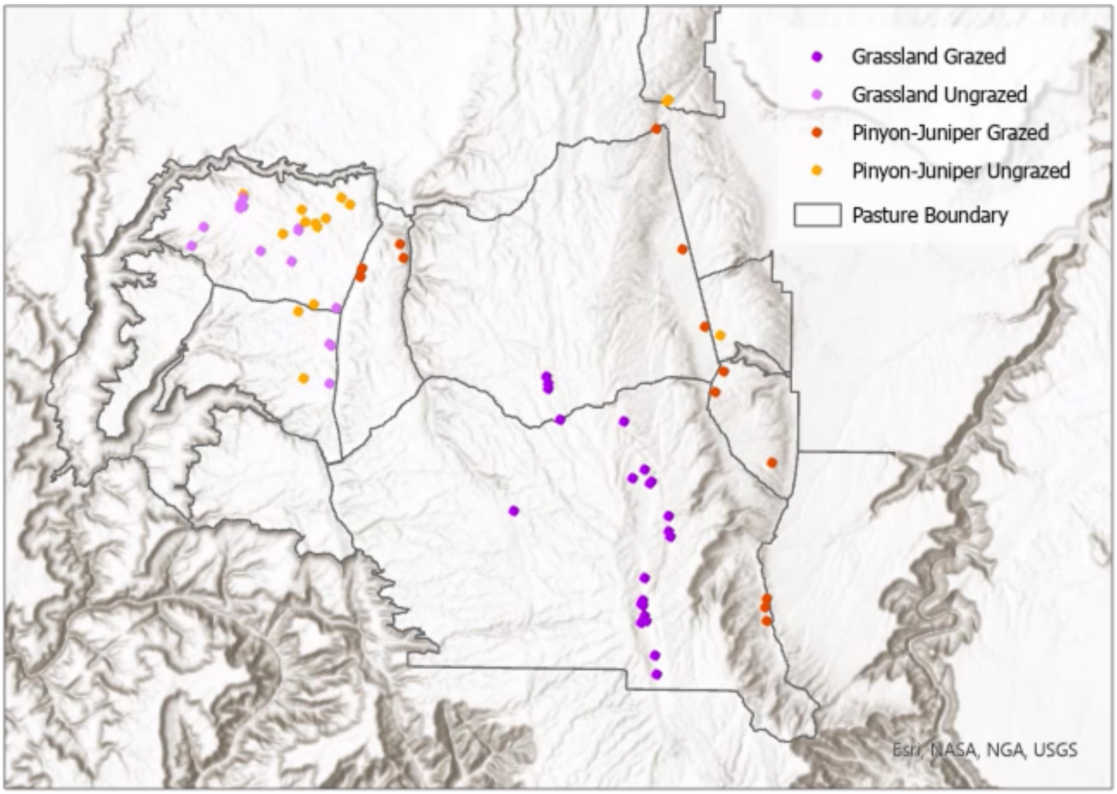


Figure 1: Baseline sites resampled in 2022 with vegetation type and pasture-level grazing status

Vegetation and Soil Measurements

All field measurements were conducted from early July 2022 to late August 2022, following the onset of summer monsoons. We followed the baseline assessment plot survey protocol for vegetation and disturbance characterization, vegetation cover, ground cover, and soil stability to allow for direct comparison between data collected in 2005/2007 and 2022. After locating the center of a site (marked by rebar), we set up three 15 m transects centered on the geographic coordinates of the plot, so that a 7.32m section of transect extended from the center at 30°, 90°, 150°, 210°, 270°, and 330°. Quadrats (1 m2) were placed at 2.44m and 4.57m from the center at 30°, 150°, and 270° degrees, and 6.1m from the center at 90°, 210°, and 330° (Figure 2).

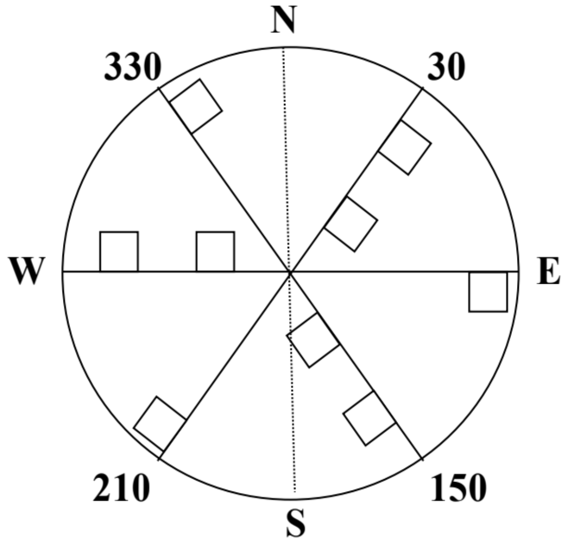


Figure 2: Sampling plot design with three 15 m transects centered on the geographic coordinates of the plot. Squares represent quadrats placed along the transect lines.

Within these quadrats we recorded species-level cover by ocular estimation, and height of the tallest living plant of each species. We also measured non-vegetative ground cover, including soil (soil and rocks < pea sized), rock (> pea sized), wood (>1" diameter), litter (newly fallen plant material), duff (decomposing plant material), moss, lichen, cryptobiotic soil crust (cyanobacteria soil), scat, water, and human trash. Finally, we recorded the overall vegetation type of the site, disturbance (e.g. grazing, fire) evidence at the site, and distance from plot center to water if any water source was located within 50m. If we recorded grazing as a disturbance, we conducted a scat count of the circular plot area and recorded counts by species (cattle, deer, elk, or rabbit/hare).

We collected four soil data points: stability, bulk density, soil water content, and compaction. We used a field test kit and followed the protocol described by Herrick et al. (2001) to measure soil stability, collecting 18 surface samples from within the plot boundary, from interspace areas and underneath plant canopy. We measured compaction at the south, center, and north points of the plot using a pocket penetrometer, and collected soil core samples at the same three locations. Soils were combined into a bulk sample processed at the NAU Arizona Climate and Ecosystems (ACE) Isotope Laboratory for bulk density and soil water content.

Statistical Analyses

Vegetative and forb community response to grazing through time

We examined differences in both overall vegetation community composition and forb community composition as a function of year and grazing status for each of our two principal vegetation types, grasslands and pinyon-juniper woodlands. We conducted community comparisons using permutational multivariate analysis of variance (PERMANOVA) using 1,000 permutations and Bray-Curtis distance as a measure of dissimilarity in the R-package '*vegan*' with the '*adonis2'* function. We used Wisconsin standardized abundance data in all analyses, and visualized the differences in community composition using Nonmetric Multidimensional

Scaling (NMDS) plots. One ungrazed pinyon-juniper site and one ungrazed grassland site appeared as extreme outliers in NMDS plots during the forb community composition analyses, preventing visualization of any other trends within the plot, and were therefore excluded from analyses. We conducted all analyses in R version 4.2.2 (R Core Team, 2022).

Given spatial disaggregation of grazed and ungrazed sites for both vegetation types, we analyzed a subset of grassland sites that occurred in the same high-elevation area, in order to confirm broad-level patterns observed when analyzing the complete dataset. Within these sites, we classified grazing intensity at a granular scale. Based on scat counts and prevalence of browsed plants, we classified sites as “moderately grazed” or “heavily grazed”. We again analyzed community dissimilarity for this subset of high elevation grassland sites, enabling us to explore whether differences between grazed and ungrazed sites were driven by grazing or inherent differences in grassland plant communities driven by elevation.

Forb diversity responses to grazing through time

To examine forb species diversity across time and grazing status, we calculated taxonomic diversity within each year, vegetation type, and grazing status combination as Hill numbers (q = 0, 1, 2, corresponding to richness, Shannon diversity, and Simpson diversity) with the package *‘iNext’* in R (Hsieh et al., 2016). We visualized changes in diversity across time by plotting Rarefaction/Extrapolation (R/E) curves for baseline and current years, grouped by grazing status and vegetation type.

Key traits related to pollination included life history (annual or perennial), flowering period (grouped into pre-monsoon, monsoon, post-monsoon, and possible combinations thereof), flowering duration (in months), plant height (cm), flower color and size (diameter in mm), radial symmetry (yes or no), and inflorescence type (grouped into solitary or many). We determined species traits primarily using SEINet, as well as other online resources when information was not available through SEINet. We excluded three species from the 2022 data and 11 species from the 2005/2007 data due to lack of trait information. For 19 species we were unable to find information on one or more specific traits, in which case values for those traits were left blank. For each trait we determined functional richness (FRic) and evenness (FEve) using the *'dbFD'* function in the R-package *'FD'* with Wisconsin standardized abundance data. We then analyzed the data according to a Before-After-Control-Impact design, using LME models to account for repeated plot measurements. Grazing status, year, and grazing status*year were fixed effects and site was a random effect. We selected the model of best fit using the Akaike Information Criterion (AIC).

Forb and ground cover response to grazing through time

To compare forb cover, forb relative abundance, amount of bare ground, and woody litter abundance (i.e., potential nesting material), we again utilized a Before-After-Control-Impact design and LME models. We calculated forb relative abundance as the proportion of total forb species cover relative to total plant species cover at a plot level. Full models included grazing treatment, year, and grazing treatment*year, with soil type, annual precipitation, and annual mean temperature as covariates, and plot included as a random effect. We selected the model of best fit using the '*AIC*' function. Soil types were derived from the USDA Natural Resources Conservation Service Web Soil Survey (Soil Survey Staff, 2023). Climate variables were extracted from downscaled climate models from WorldClim database (Fick & Hijmans, 2017).

Soil response to grazing status

We calculated soil bulk density (dry weight of soil/volume of soil) and water content ((wet weight - dry weight) / dry weight) at the NAU ACE Isotope Laboratory. Compaction and soil stability were averaged by plot; stability was averaged by category (interspace and under plant canopy). Several soil metrics were not collected during the baseline assessment or baseline data were incomplete, precluding before-after comparisons. Instead, we examined patterns of soil stability, water content, compaction, and bulk density across the landscape by grazing status using Generalized Linear Models (GLMs; *'lm'* function). We used all possible combinations of grazing status, soil type, annual precipitation, and annual mean temperature as fixed additive effects. We used the '*AIC*' function to select the best fit model.

Results

Vegetative and forb community response to grazing through time

Vegetative communities varied significantly through time and by grazing status in both pinyon-juniper woodlands and grasslands (Table 1). Neither pinyon-juniper grazed nor ungrazed sites differed significantly between baseline and current years (Table 2). Community composition at high elevation (grazed) grassland sites changed significantly over time, while year did not have a significant effect for mid-elevation (ungrazed) sites (Table 2). NMDS plots reflect these results, showing distinct baseline and current community compositions at high elevation (grazed) grassland sites while mid-elevation (ungrazed) sites demonstrate an overlap between past and current vegetation communities (Figure 3).

Results for moderately and heavily grazed grassland sites mirrored patterns seen across the complete grassland sample. Although vegetation community composition at both moderately and heavily grazed sites changed significantly over time (Table 2), NMDS plots show more distinct communities between baseline and current years for heavily grazed sites compared to moderately grazed (Figure 4).

Table 1: Results of overall vegetation community composition analyses, at vegetation-type level. Bolding indicates a significant p-value at alpha = .05.

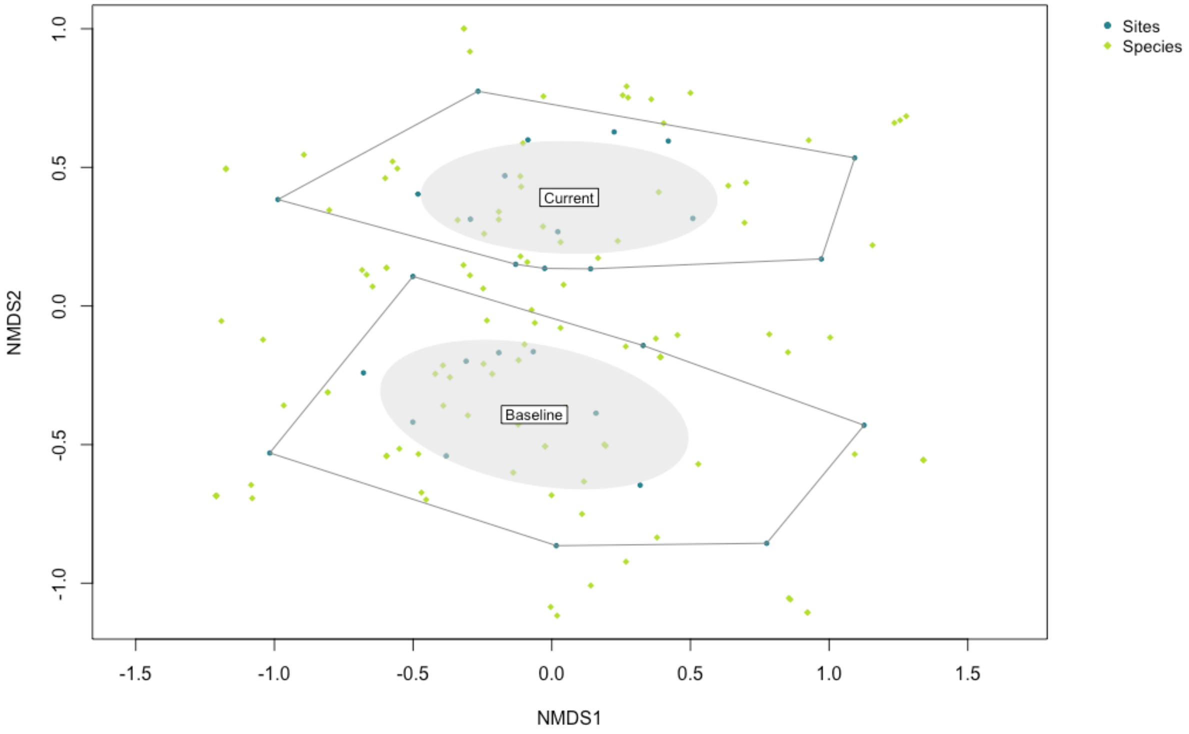
	R2	**F**	**Pr(>F)**
Mid/High Elevation Grassland			
Grazing Status	0.175687	12.46928	**0.001**
Year	0.035228	2.5003	**0.002**
Grazing Status * Year	0.028248	2.004855	**0.02**
Moderate/Heavily Grazed Grassland			
Grazing Status	0.057424	2.212027	**0.003**
Year	0.098988	3.813135	**0.001**
Grazing Status * Year	0.012874	0.495938	0.962
Pinyon-Juniper Woodland			
Grazing Status	0.048971	2.823697	**0.004**
Year	0.035183	2.028699	**0.014**
Grazing Status * Year	0.014017	0.808258	0.656

Table 2: Results of overall vegetation community composition analyses, at vegetation-type/grazing status level. Bolding indicates a significant p-value at alpha = .05.

	R2	**F**	**Pr(>F)**
Mid-elevation (Ungrazed) Grassland			
Year	0.053742	1.476647	0.101
High Elevation (Grazed) Grassland			
Year	0.101169	3.151563	**0.001**
Moderately Grazed Grassland			
Year	0.10162	1.809828	**0.04**
Heavily Grazed Grassland			
Year	0.137134	2.542862	**0.001**
Ungrazed Pinyon-Juniper Woodland			
Year	0.046428	1.363272	0.13
Grazed Pinyon-Juniper Woodland			
Year	0.058959	1.503661	0.15

NMDS represents a condensed version of the position of data in multidimensional space, plotted on two dimensions (axes). Within an NMDS plot, sites are placed to minimize the distance to all species found at the site, and thus the closer sites are to one another the more similar their species compositions. Lines are drawn around the outermost site points of a group, and ellipses represent the standard deviation of the points.

High Elevation (Grazed) Grassland – All Vegetation



Mid-elevation (Ungrazed) Grassland – All Vegetation

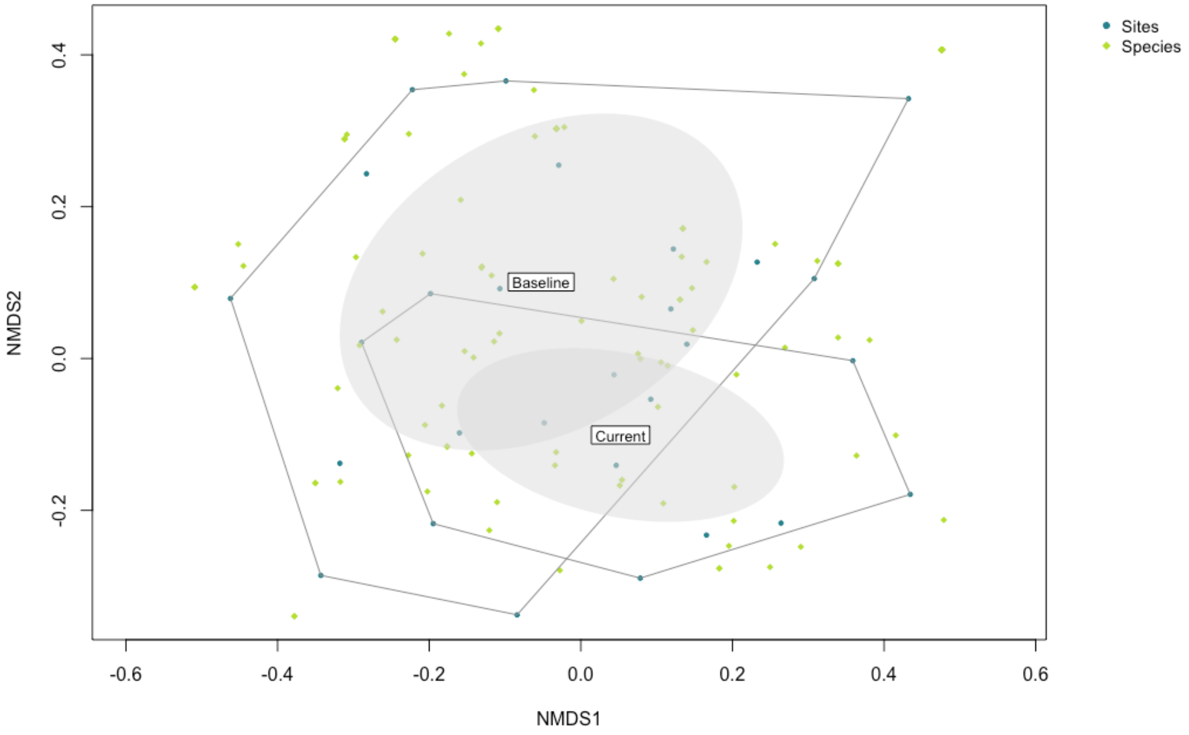
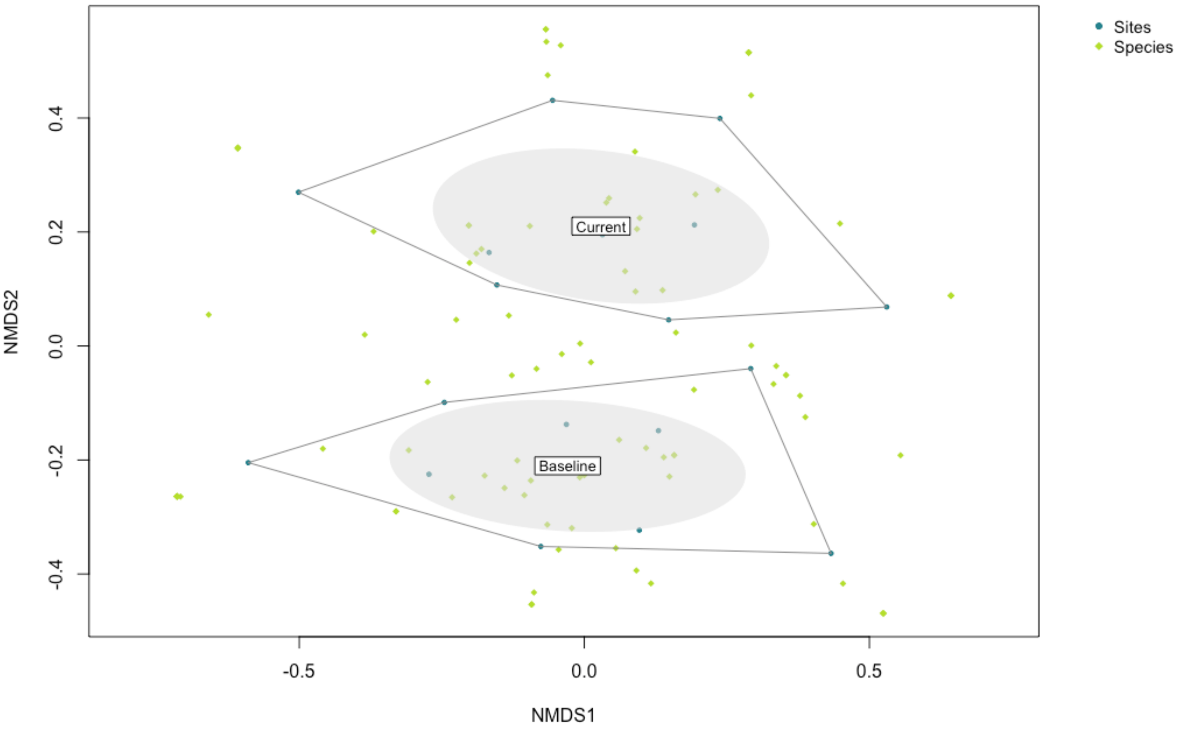


Figure 3: Non-metric multidimensional scaling (NMDS) plots for vegetation community composition at high elevation (grazed) and mid-elevation (ungrazed) grassland sites.

Heavily Grazed Grassland – All Vegetation



Moderately Grazed Grassland – All Vegetation

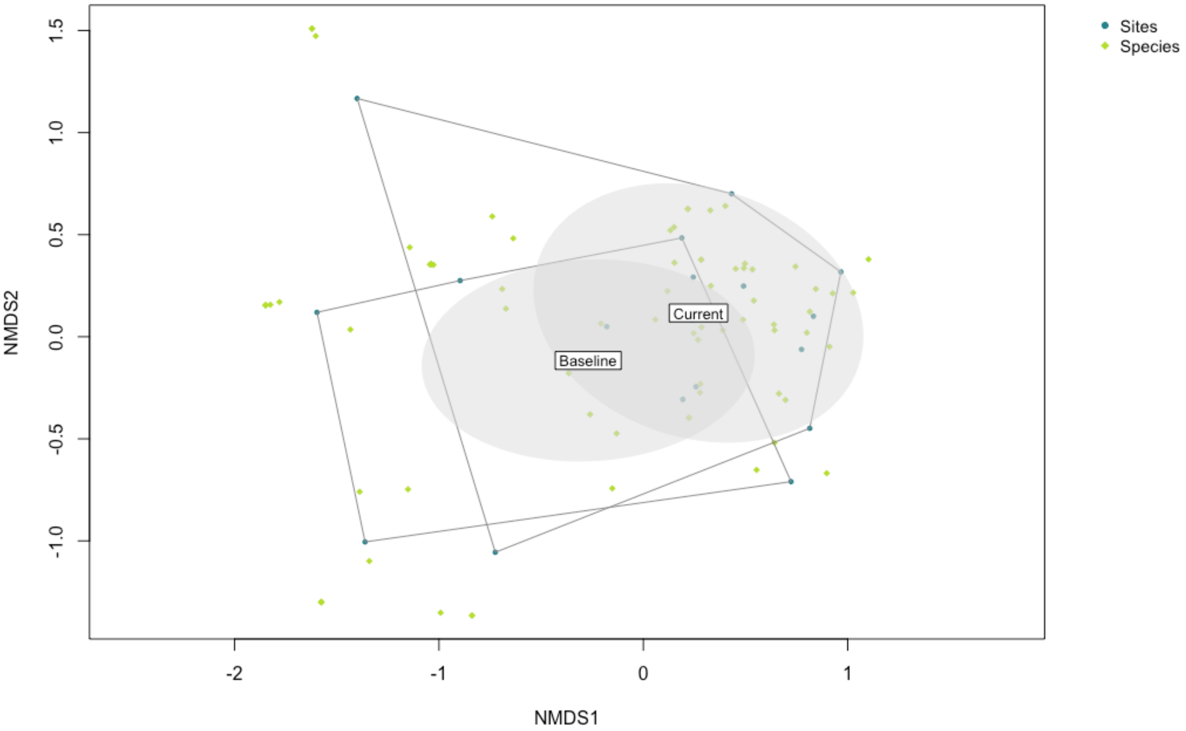


Figure 4: Non-metric multidimensional scaling (NMDS) plots for vegetation community composition at heavily grazed and moderately grazed grassland sites.

Forb community composition showed significant change through time and by grazing status in both vegetation types (Table 3). In pinyon-juniper forb communities, we found significant change from baseline to current years for ungrazed sites, while grazed sites did not differ significantly (Table 4). At grassland sites, baseline forb communities were significantly different from current communities for both high elevation (grazed) and mid-elevation (ungrazed) sites (Table 4). NMDS plots for pinyon-juniper sites show greater overlap between baseline and current forb communities at grazed sites, although ungrazed sites exhibit similarities over time as well despite a statistically significant difference (Table 4; Figure 5). Grassland NMDS plots also don't entirely align with statistically significant findings, with a noticeable separation between forb communities in high elevation (grazed) grassland sites over time and a substantial overlap in community composition at mid-elevation (ungrazed) sites, despite both grazed and ungrazed sites differing significantly by year (Table 4; Figure 6).

Within the moderately/heavily grazed grassland subset, forb communities differed significantly between baseline and current years at heavily grazed sites but not at moderately grazed sites. NMDS plots reflect these results and show similar patterns to plots for the complete grassland sample, with distinct baseline and current communities at heavily grazed sites while moderately grazed sites exhibit greater similarity over time (Figure 7).

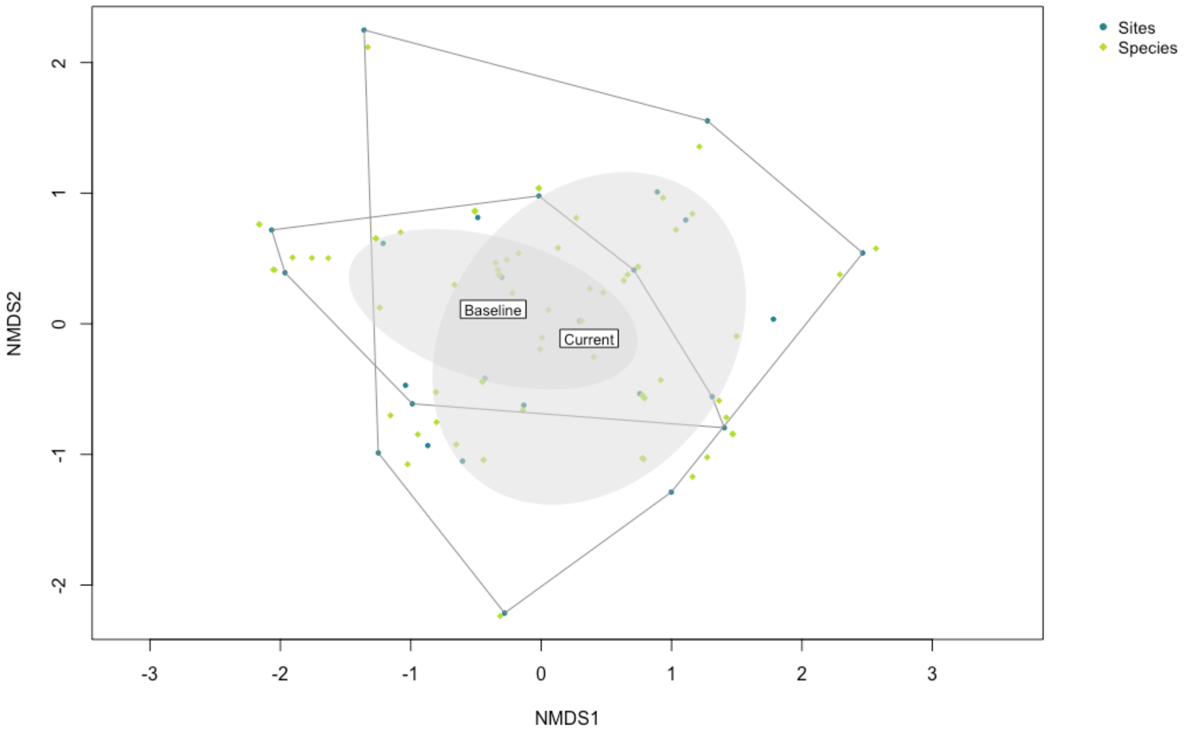
Table 3: Results of forb community composition analyses, at vegetation-type level. Bolding indicates a significant p-value at alpha = .05.

	R2	**F**	**Pr(>F)**
Mid/High Elevation Grassland			
Grazing Status	0.174828	11.95702	**0.001**
Year	0.032975	2.255235	**0.007**
Grazing Status * Year	0.031885	2.180713	**0.009**
Moderate/Heavily Grazed Grassland			
Grazing Status	0.069664	2.637386	**0.001**
Year	0.06526	2.470667	**0.003**
Grazing Status * Year	0.019824	0.75052	0.767
Pinyon-Juniper Woodland			
Grazing Status	0.026165	1.418408	**0.045**
Year	0.034793	1.886147	**0.001**
Grazing Status * Year	0.016711	0.905938	0.627

Table 4: Results of forb community composition analyses, at vegetation-type/grazing status level. Bolding indicates a significant p-value at alpha = .05.

	R2	**F**	**Pr(>F)**
Mid-elevation (Ungrazed) Grassland			
Year	0.066099	1.698642	**0.019**
High Elevation (Grazed) Grassland			
Year	0.093295	2.881043	**0.002**
Moderately Grazed Grassland			
Year	0.086331	1.511803	0.123
Heavily Grazed Grassland			
Year	0.09698	1.718332	**0.05**
Ungrazed Pinyon-Juniper Woodland			
Year	0.060748	1.681593	**0.008**
Grazed Pinyon-Juniper Woodland			
Year	0.044686	1.122618	0.263

Pinyon-juniper Grazed



Pinyon-juniper Ungrazed

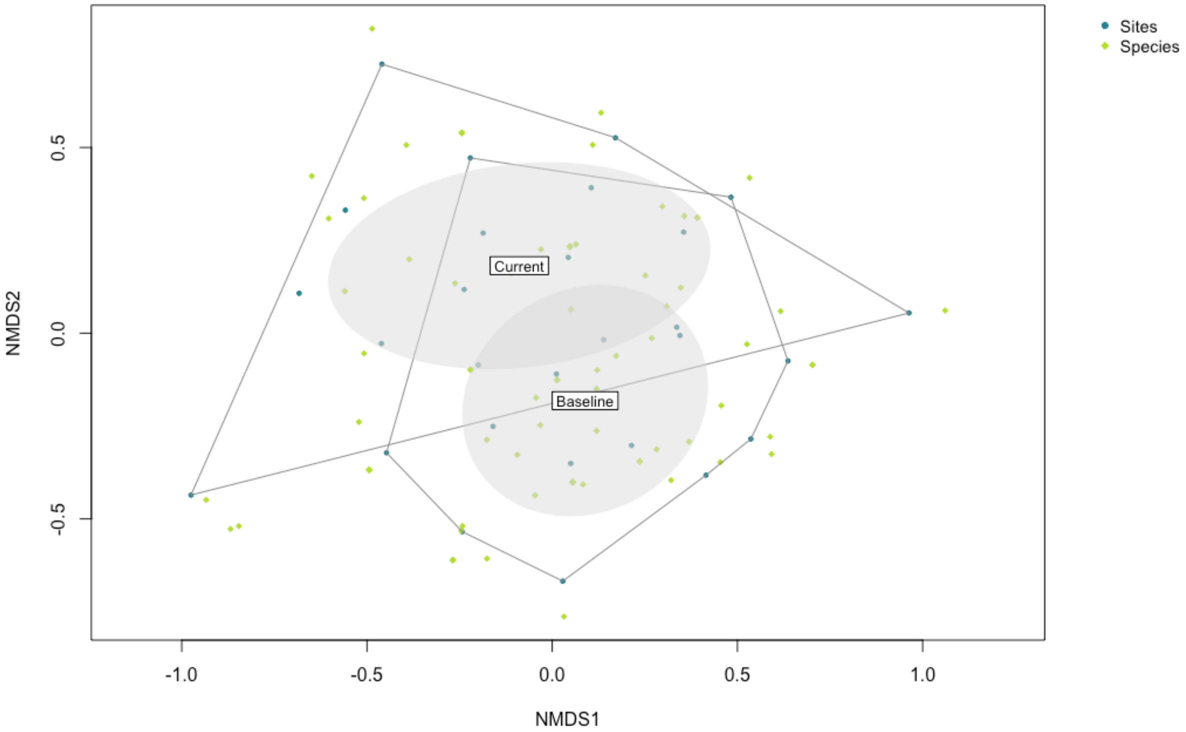
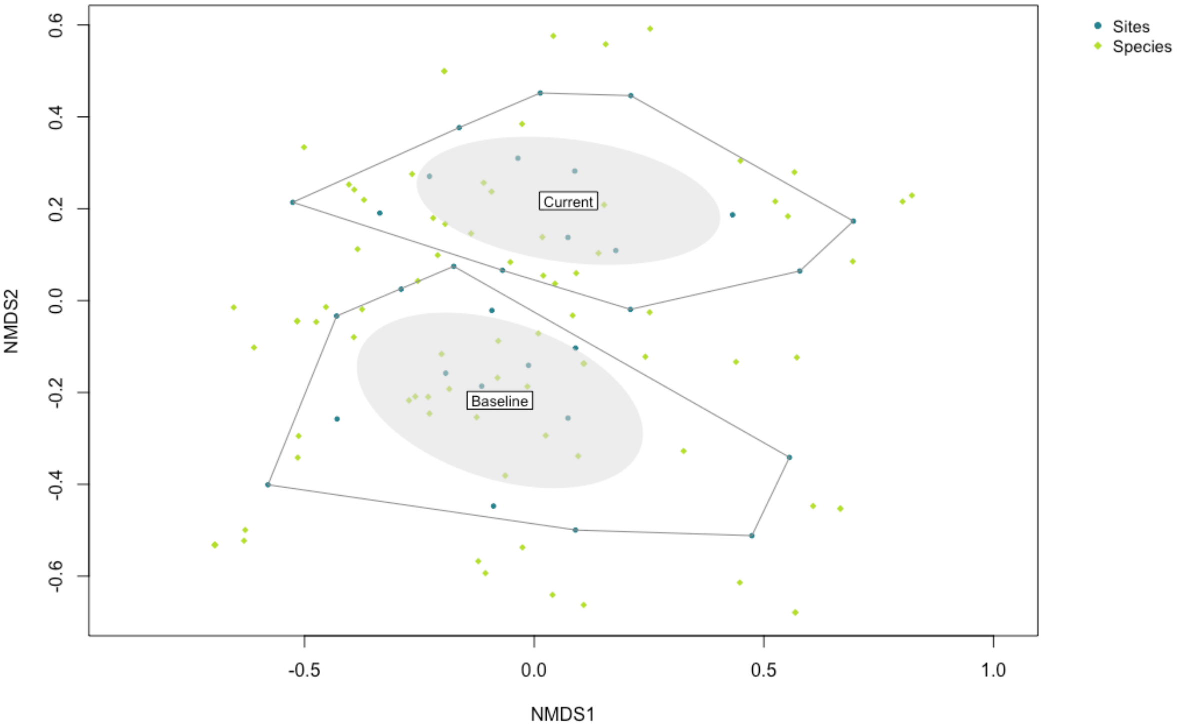


Figure 5: Non-metric multidimensional scaling (NMDS) plots for forb community composition at grazed and ungrazed pinyon-juniper sites.

High Elevation (Grazed) Grassland



Mid-elevation (Ungrazed) Grassland

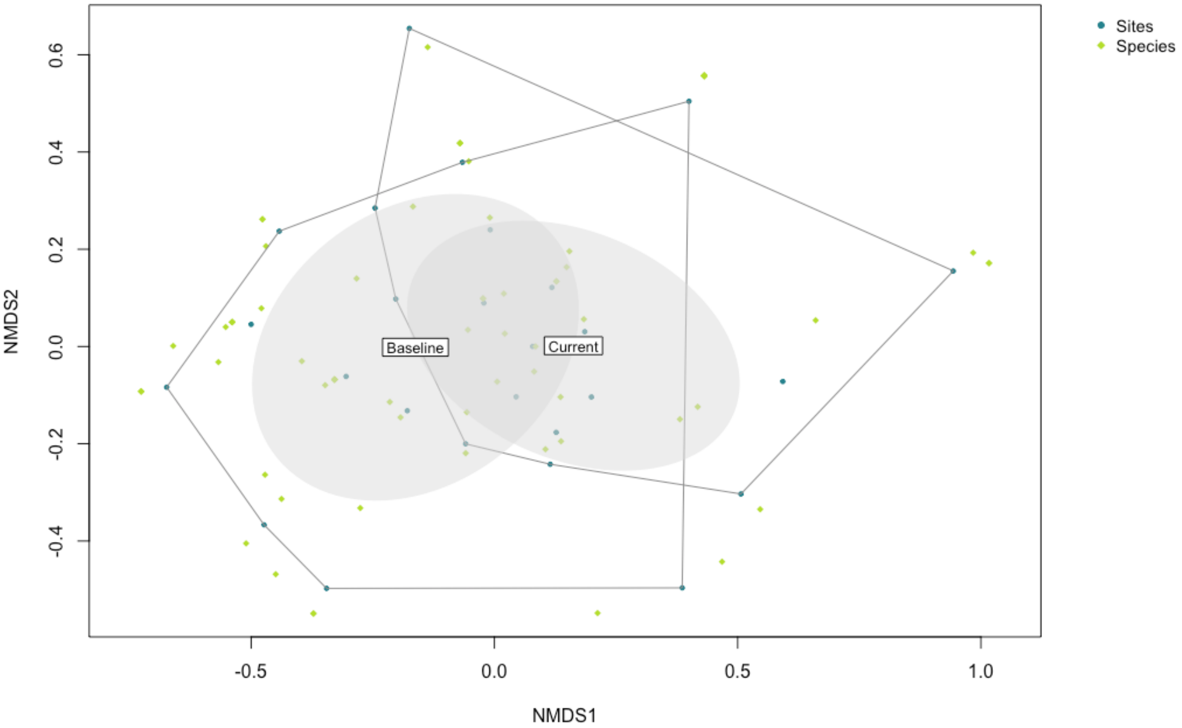
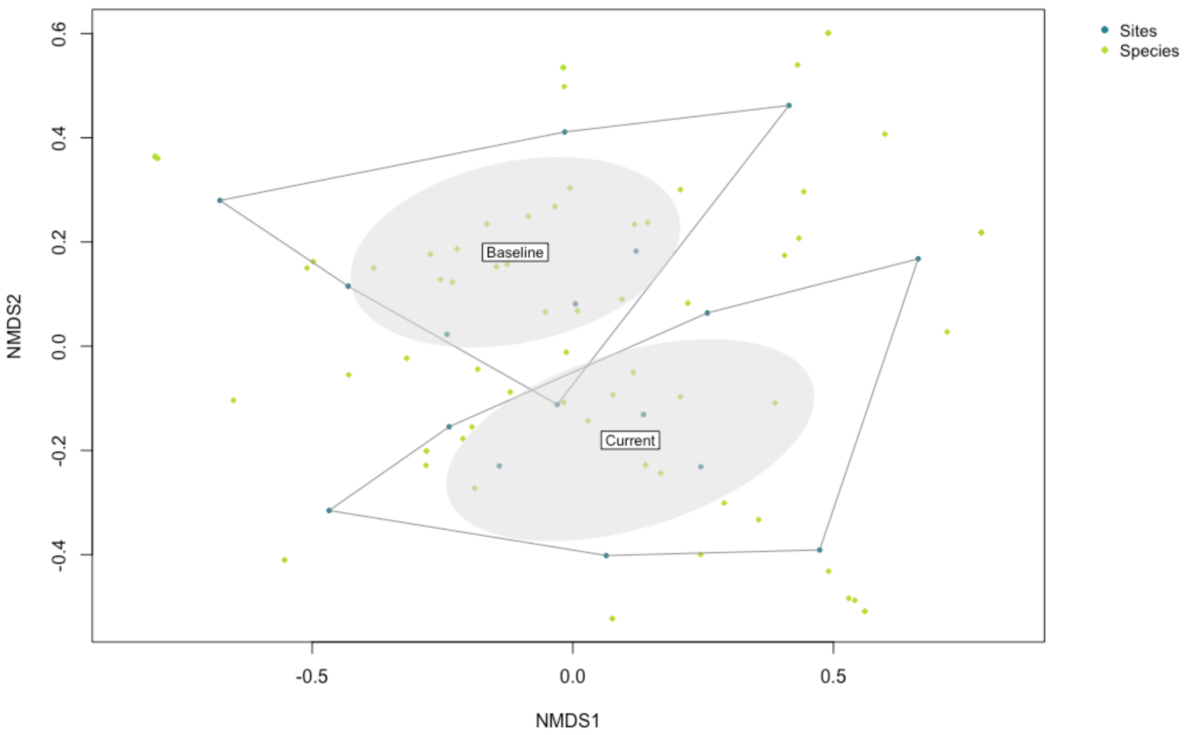


Figure 6: Non-metric multidimensional scaling (NMDS) plots for forb community composition at high elevation (grazed) and mid-elevation (ungrazed) grassland sites.

Heavily Grazed Grassland



Moderately Grazed Grassland

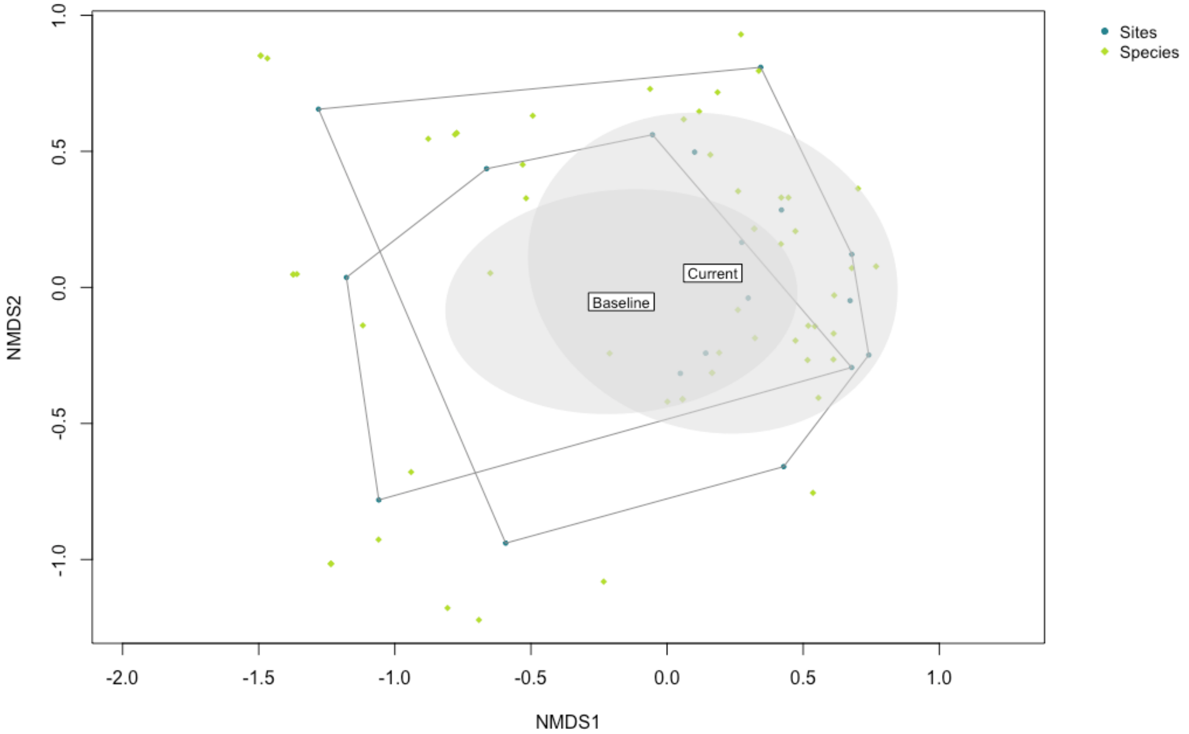


Figure 7: Non-metric multidimensional scaling (NMDS) plots for forb community composition at heavily grazed and moderately grazed grassland sites.

Forb diversity responses to grazing through time – species diversity

Forb species diversity was lower in 2022 than 2005/2007 for both vegetation types across all metrics, including richness (q=0), exponential Shannon entropy (q=1), and inverse Simpson index (q=2) (Table 5 and 10). Pinyon-juniper sites showed similar differences in diversity over time and across grazing status, with both grazed and ungrazed sites exhibiting lower species diversity and a smaller increase in diversity as number of sampling units increased in 2022 compared to 2005/2007 (Figure 7). At ungrazed sites estimator values for richness, Shannon's, and Simpson's diversity declined by 47.8%, 50.5%, and 52.6% respectively, while at grazed sites these metrics declined by 59.3%, 50.5%, and 41.9% between baseline and current years. In grassland sites, species diversity was consistently lower in 2022 than baseline years, but diverged less over time at high elevation (grazed) sites compared to mid elevation (ungrazed) sites (Figure 8). At high elevation (grazed) sites, estimator values for richness, Shannon's, and Simpson's diversity declined by 38.6%, 22.4%, and 20.6% over time, while at ungrazed sites declines were substantially greater (68.8%, 75.1%, and 70.6% respectively).

Table 5: Results of species diversity analyses, by vegetation type and grazing status, for baseline years and 2022.

Mid-elevation (Ungrazed) Grassland	**Observed**	**Estimator**	**s.e.**	**LCL**	**UCL**
Baseline Species richness	69.00	120.19	21.21	78.63	161.75
Baseline Shannon diversity	53.02	86.68	9.30	68.45	104.90
Baseline Simpson diversity	38.82	51.75	6.71	38.60	64.90
2022 Species richness	22.00	37.48	16.85	22.00	70.50
2022 Shannon diversity	16.27	21.58	3.47	14.77	28.38
2022 Simpson diversity	13.01	15.23	2.18	10.95	19.50

	Observed	**Estimator**	**s.e.**	**LCL**	**UCL**
High Elevation (Grazed) Grassland					
Baseline Species richness	70.00	106.59	19.68	70.00	145.15
Baseline Shannon diversity	47.95	57.33	3.30	50.87	63.79
Baseline Simpson diversity	37.69	40.79	2.04	36.78	44.79
2022 Species richness	52.00	65.49	11.03	52.00	87.10
2022 Shannon diversity	37.65	44.49	2.99	38.62	50.36
2022 Simpson diversity	29.19	32.38	1.97	28.51	36.24
Pinyon-Juniper Ungrazed					
Baseline Species richness	68.00	89.86	10.73	68.84	110.89
Baseline Shannon diversity	57.82	80.88	5.81	69.50	92.26
Baseline Simpson diversity	49.93	71.91	6.16	59.84	83.99
2022 Species richness	30.00	46.88	10.36	30.00	67.19
2022 Shannon diversity	25.62	40.05	5.27	29.72	50.37
2022 Simpson diversity	22.08	34.05	4.91	24.42	43.68
Pinyon-Juniper Grazed					
Baseline Species richness	76.00	165.77	24.75	117.27	214.27
Baseline Shannon diversity	58.27	97.33	10.15	77.44	117.22
Baseline Simpson diversity	45.59	60.28	6.39	47.76	72.79
2022 Species richness	38.00	67.40	16.90	38.00	100.53
2022 Shannon diversity	30.66	48.19	6.47	35.51	60.87
2022 Simpson diversity	25.11	35.01	5.06	25.09	44.92

Sample size based Rarefaction/Extrapolation (R/E) sampling curves plot calculated diversity estimates and associated 95% confidence intervals for actual and extrapolated species incidence data. Solid lines represent diversity metrics based on observed data, while dotted lines show extrapolated values (i.e. estimates of diversity at greater sample sizes). Shaded areas around the lines show the confidence interval, and dark blue represents baseline data while current data is light green.

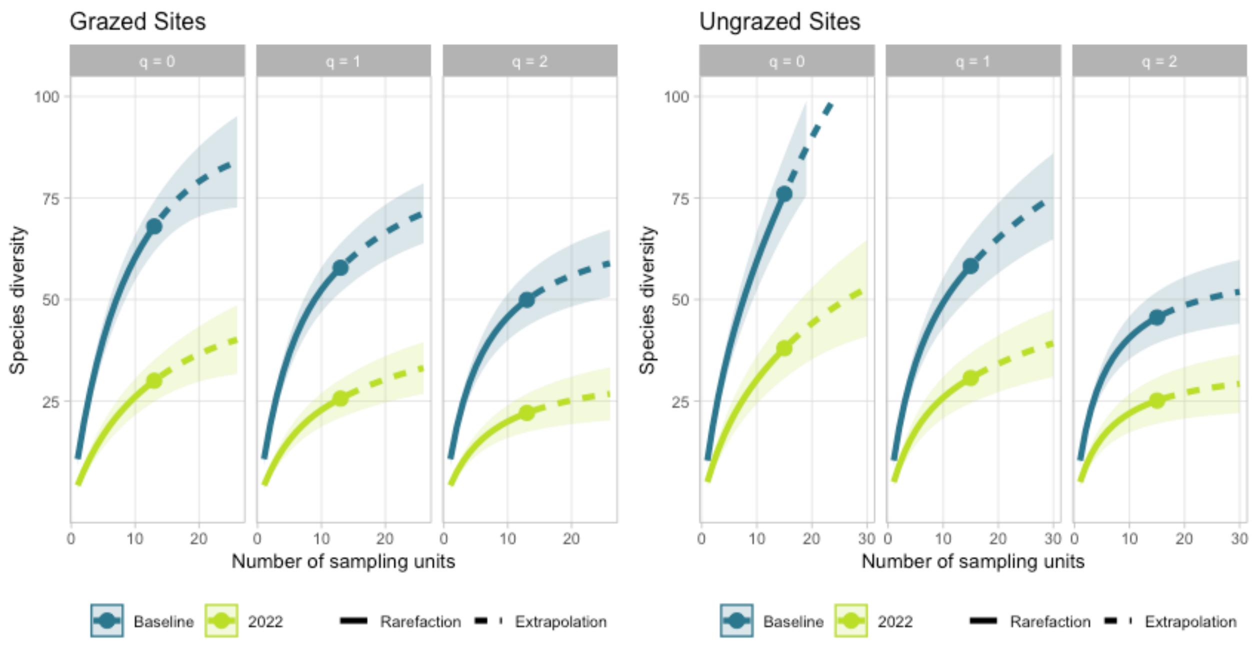


Figure 8: Rarefaction/Extrapolation curves for pinyon-juniper sites in baseline years and 2022, separated by grazing status. Diversity measures are species richness (q=0), exponential Shannon entropy (q=1), and inverse Simpson index (q=2).

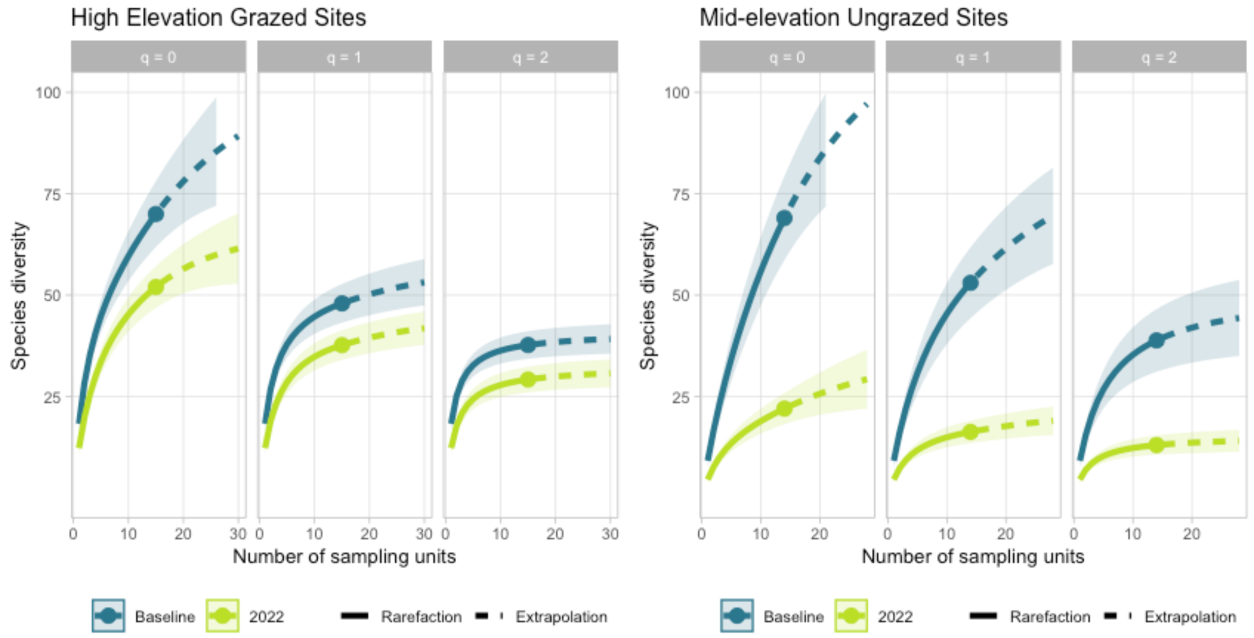


Figure 9: Rarefaction/Extrapolation curves for grassland sites in baseline years and 2022, separated by grazing status. Diversity measures are species richness (q=0), exponential Shannon entropy (q=1), and inverse Simpson index (q=2).

Forb diversity responses to grazing through time – functional diversity of pollination-related traits

Functional richness (FRic) and evenness (FEve) of pollination-related traits varied widely in response to time and grazing status, and responses differed between vegetation types. At grassland sites, grazing status*year had a significant effect on richness of plant height, flowering period richness and evenness, and flower color evenness (Table 6 and 10). Plant height richness increased over time at mid-elevation (ungrazed) sites and decreased at high elevation (grazed) sites, while flowering period richness and evenness decreased at ungrazed sites and increased at grazed sites (Figures 9 – 11). Flower color evenness increased over time at both grazed and ungrazed sites, with the greatest increase at ungrazed sites (Figure 12). Flower color evenness, radial symmetry richness, flower size richness and evenness, inflorescence type richness, and flowering period richness differed significantly by grazing status (Table 6). Flower color and size evenness were higher at ungrazed sites while richness of radial symmetry, flower size, inflorescence type, and flowering period were higher at grazed sites.

Several traits which responded to grazing status or grazing status*year also differed significantly over time alone. Flower color evenness and flower size evenness increased significantly between baseline years and 2022 (Table 6 and 10; Figure 12 and 15). Radial symmetry richness, flower size richness, inflorescence type richness, and flowering period richness decreased significantly over time (Table 6 and 10; Figures 13, 14, 16, and 10 respectively). In the case of life history and flowering duration, grazing status had no effect on trait functional diversity; rather, these traits varied significantly through time (Table 6 and 10).

Table 6: Results of pollination-related trait functional diversity analyses for grasslands. Bolding indicates a significant p-value at alpha=0.05.

Mid/High Elevation Grassland	**Sum Sq**	**Mean Sq**	**F value**	**Pr(>F)**
Plant Height (FRic)				
Grazing Status	0.100825	0.100825	0.039114	0.844704
Year	0.06062	0.06062	0.023517	0.879261
Grazing Status * Year	11.03314	11.03314	4.280205	**0.048256**
Flower Color (FEve)				
Grazing Status	0.405498	0.405498	47.52074	**2.56E-07**
Year	0.101719	0.101719	11.92058	**0.001996**
Grazing Status * Year	0.087965	0.087965	10.3087	**0.003632**
Radial Symmetry (FRic)				
Grazing Status	10.89507	10.89507	13.41732	**0.001072**
Year	6.094523	6.094523	7.505432	**0.010766**
Grazing Status * Year	3.241353	3.241353	3.991741	0.055889
Flower Size (FRic)				
Grazing Status	1.68E+01	1.68E+01	2.67E+01	**1.96E-05**
Year	1.45E+01	1.45E+01	2.30E+01	**5.27E-05**
Grazing Status * Year	3.49E-30	3.49E-30	5.54E-30	1.00
Flower Size (FEve)				
Grazing Status	0.077504	0.077504	12.61429	**0.001469**
Year	0.077147	0.077147	12.55612	**0.001647**
Grazing Status * Year	0.006514	0.006514	1.060212	0.313392
Inflorescence Type (FRic)				
Grazing Status	18.40804	18.40804	14.27013	**0.000397**
Year	8.649305	8.649305	6.705043	**0.012331**
Grazing Status * Year	0.134331	0.134331	0.104135	0.748169
Flowering Period (FRic)				
Grazing Status	28.87102	28.87102	51.03622	**2.40E-09**
Year	4.305501	4.305501	7.610971	**0.007903**
Grazing Status * Year	9.54688	9.54688	16.87632	**0.000136**

Mid/High Elevation Grassland	**Sum Sq**	**Mean Sq**	**F value**	**Pr(>F)**
Flowering Period (FEve)				
Grazing Status	0.001815	0.001815	0.578407	0.452503
Year	0.00338	0.00338	1.077294	0.30703
Grazing Status * Year	0.02632	0.02632	8.38821	**0.006734**
Flowering Duration (FRic)				
Grazing Status	1.605835	1.605835	3.242146	0.082949
Year	8.580902	8.580902	17.32465	**0.000288**
Grazing Status * Year	0.22517	0.22517	0.454612	0.505885
Life History (FRic)				
Grazing Status	0.005192	0.005192	0.025421	0.87451
Year	2.485714	2.485714	12.17098	**0.001682**
Grazing Status * Year	0.002956	0.002956	0.014472	0.905137

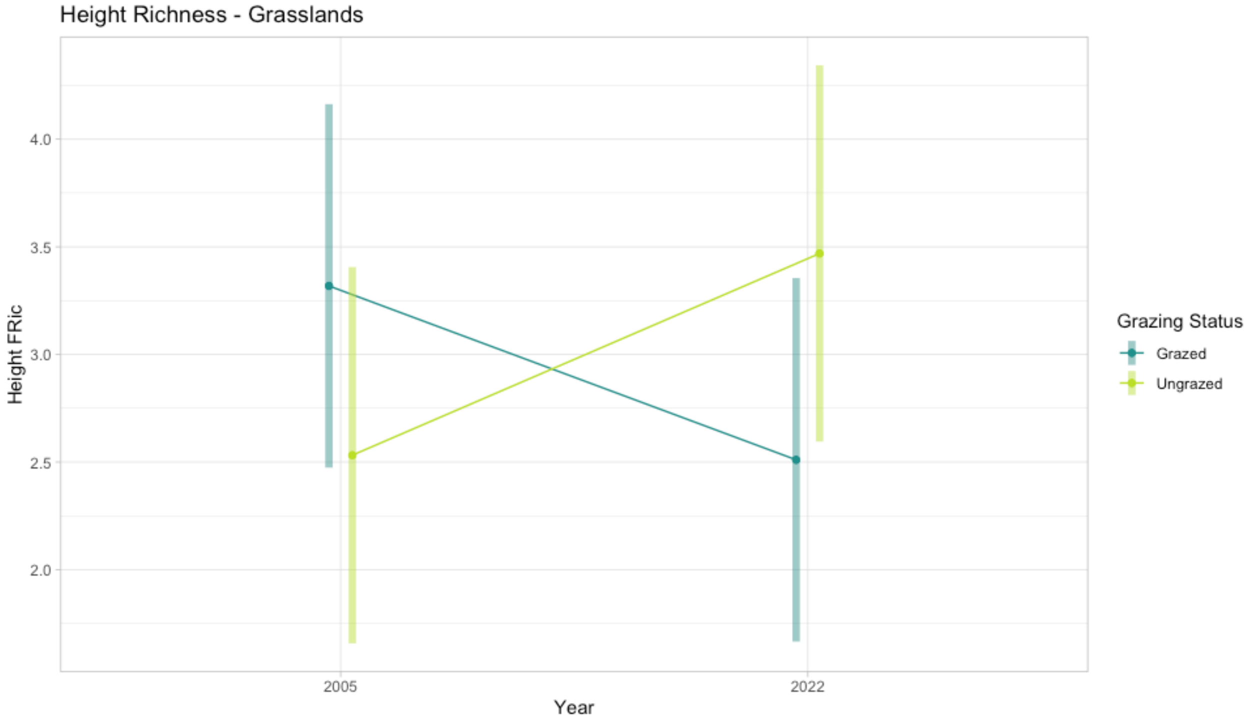


Figure 10: Plant height functional richness across time for high elevation (grazed) and mid-elevation (ungrazed) grassland sites.

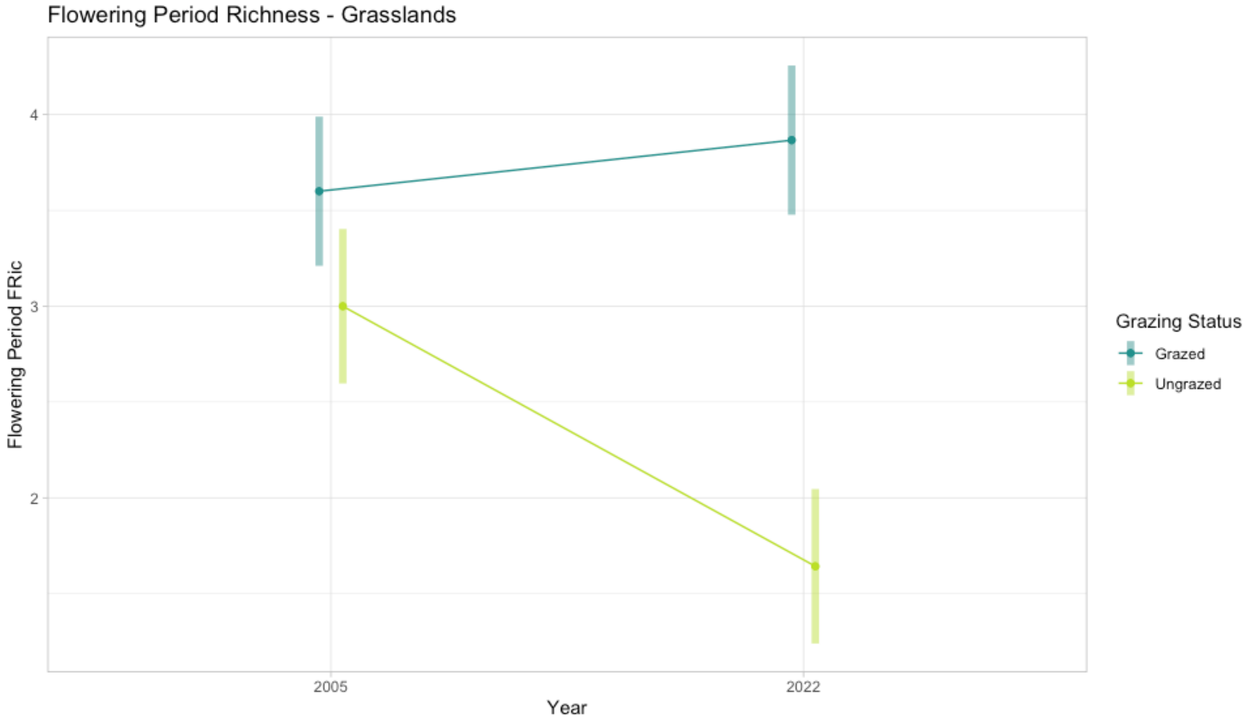


Figure 11: Flowering period functional richness across time for high elevation (grazed) and mid-elevation (ungrazed) grassland sites.

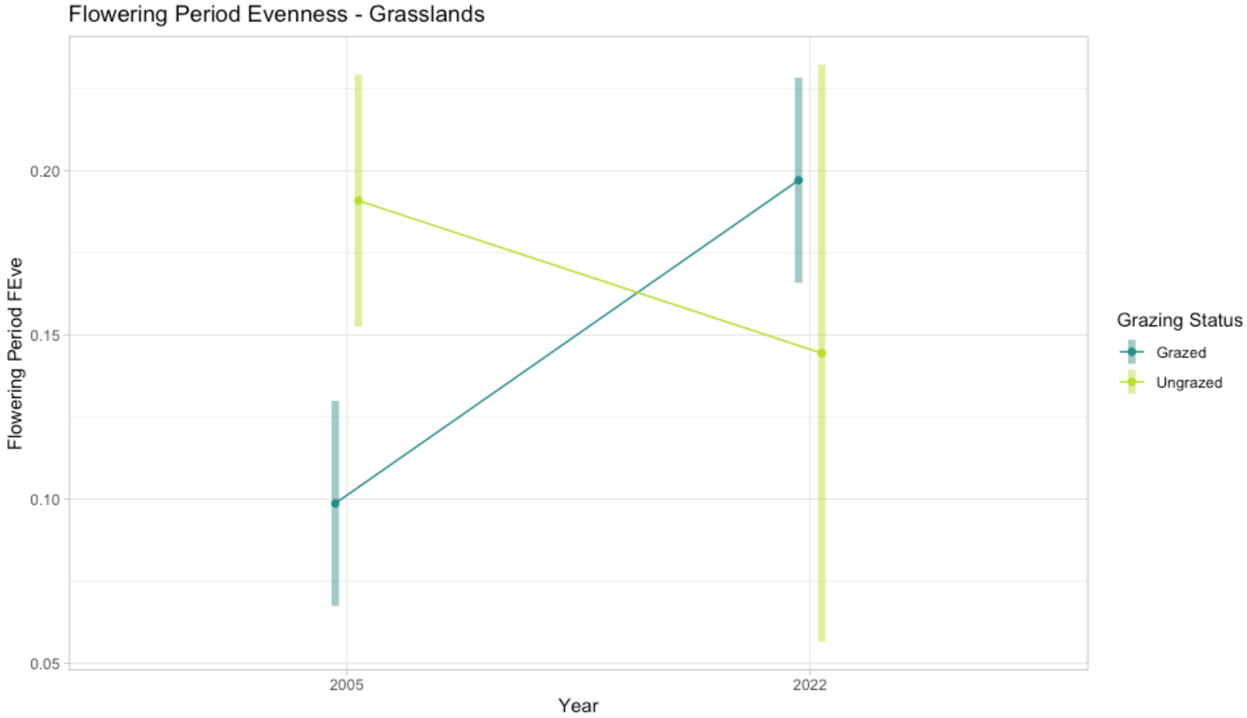


Figure 12: Flowering period functional evenness across time for high elevation (grazed) and mid-elevation (ungrazed) grassland sites.

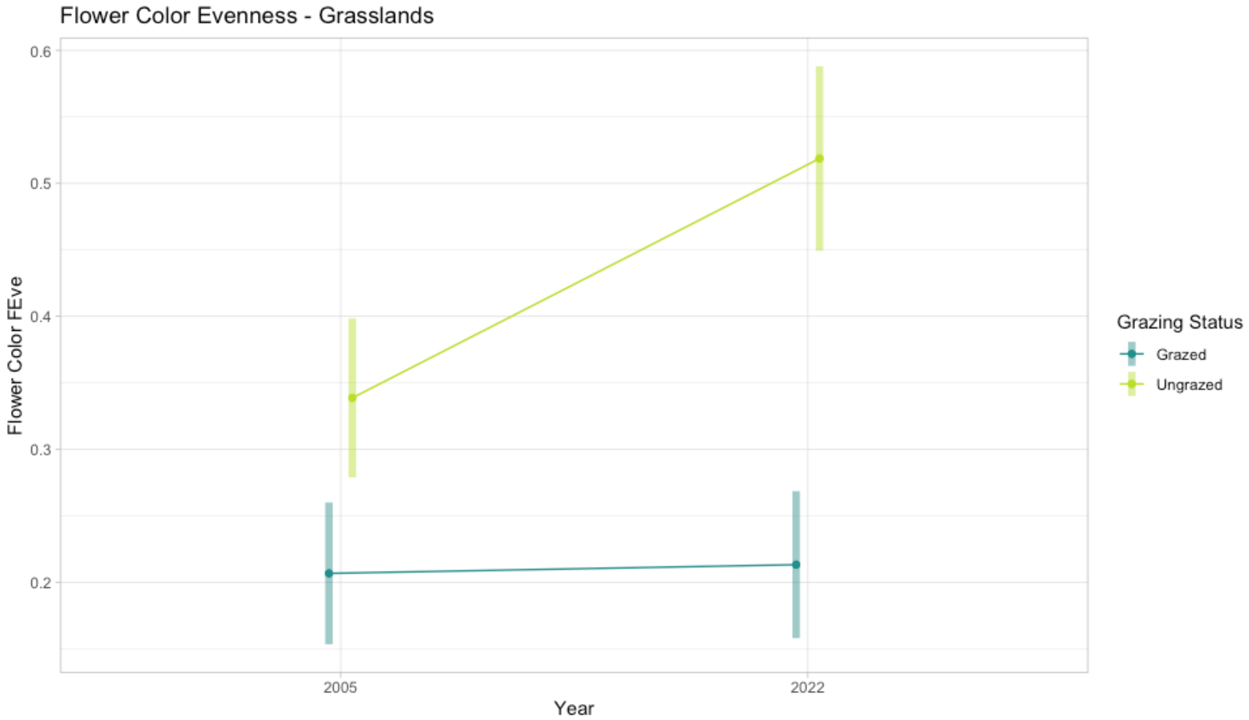


Figure 13: Flower color functional evenness across time for high elevation (grazed) and mid-elevation (ungrazed) grassland sites.

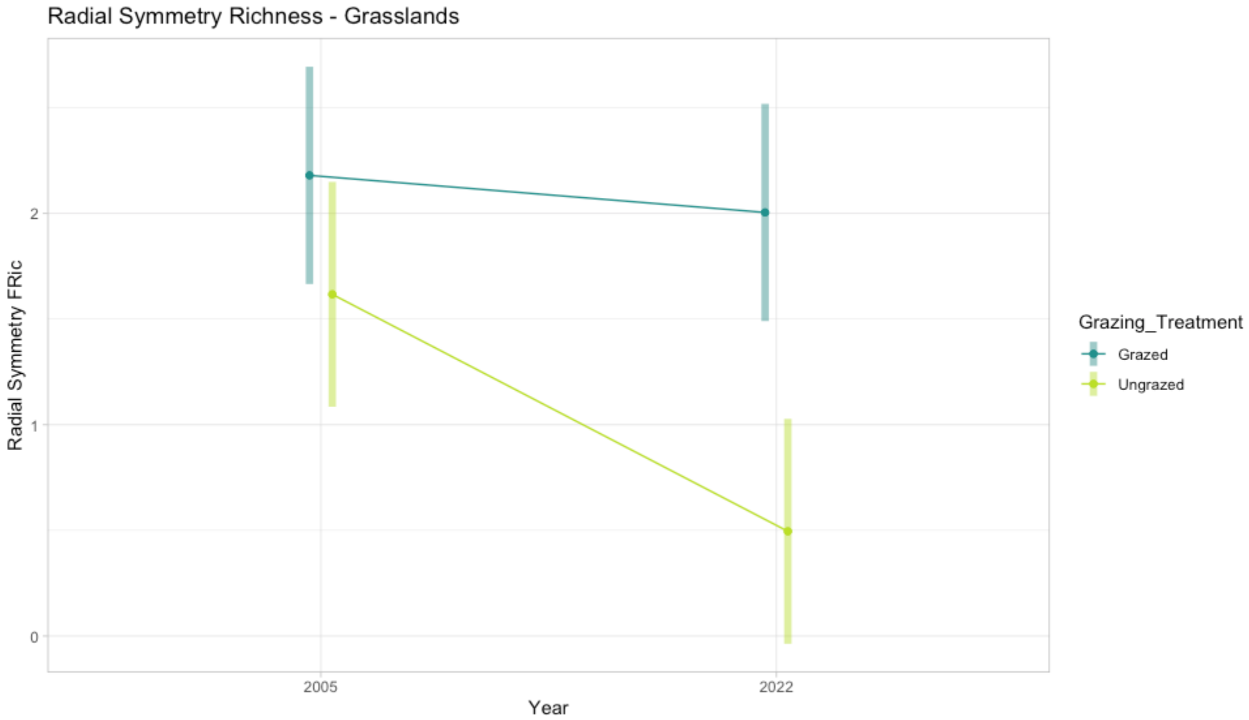


Figure 14: Radial symmetry functional richness across time for high elevation (grazed) and mid-elevation (ungrazed) grassland sites.

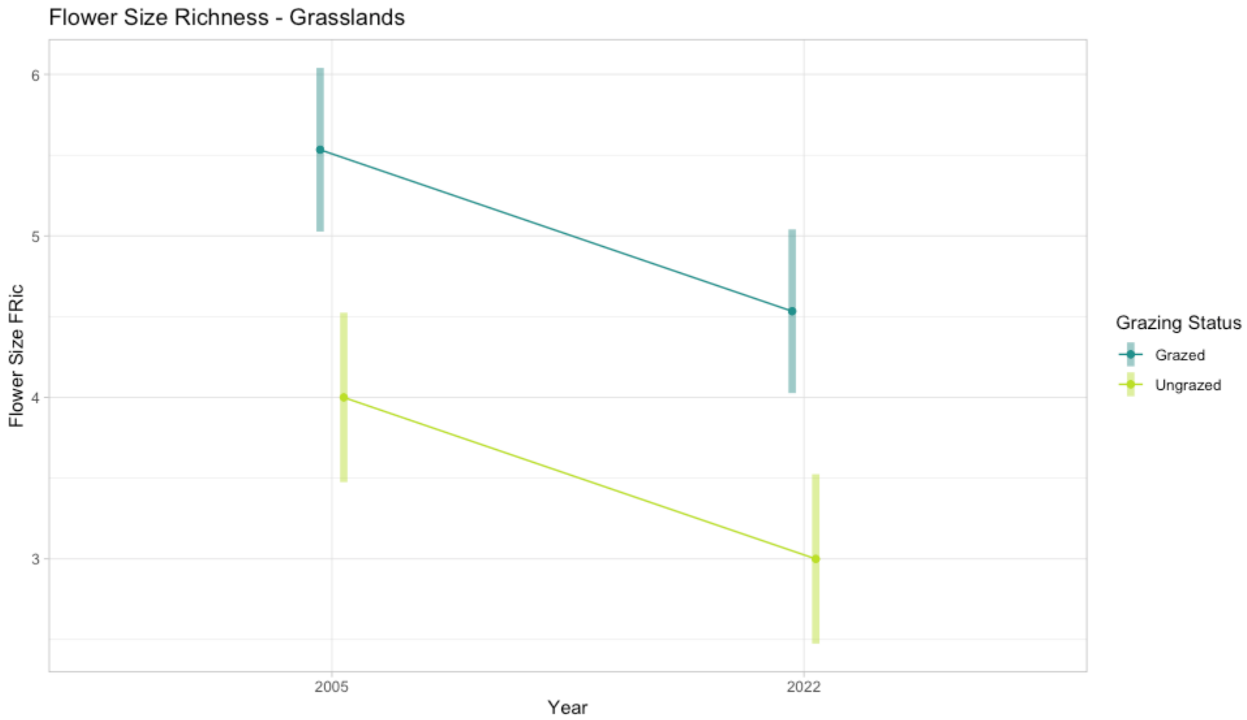


Figure 15: Flower size functional richness across time for high elevation (grazed) and mid-elevation (ungrazed) grassland sites.

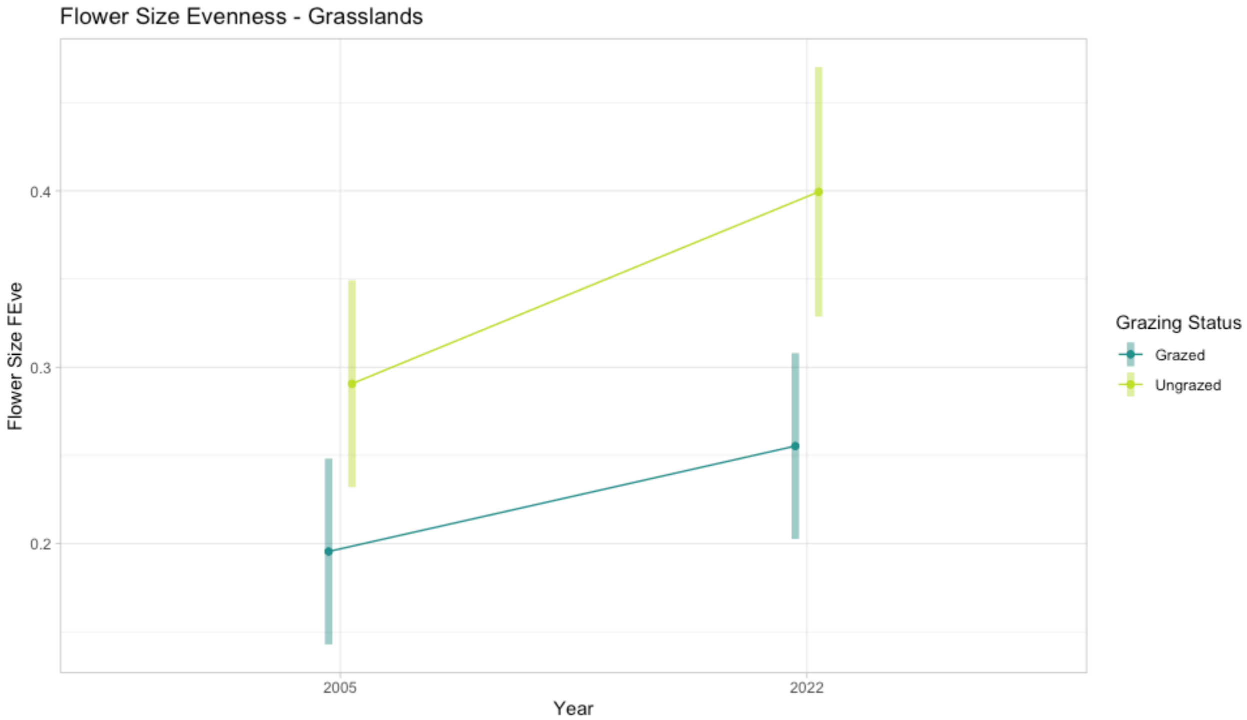


Figure 16: Flower size functional evenness across time for high elevation (grazed) and mid-elevation (ungrazed) grassland sites.

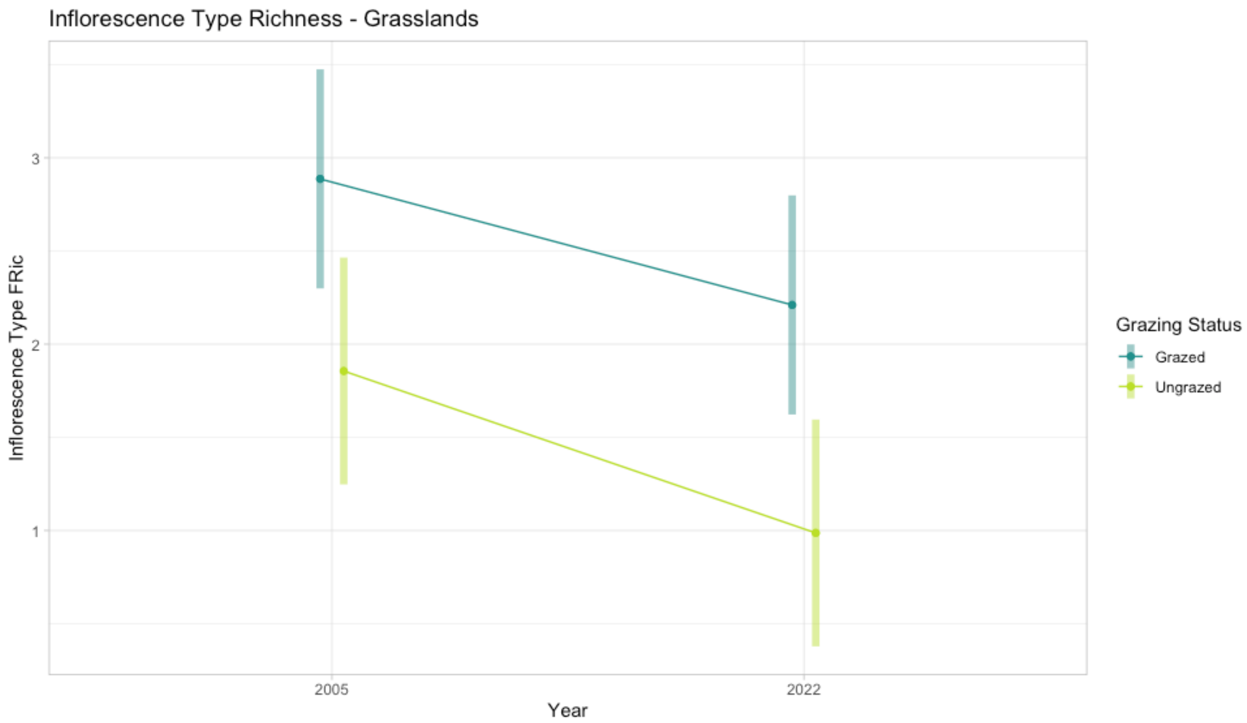


Figure 17: Inflorescence type functional richness across time for high elevation (grazed) and mid-elevation (ungrazed) grassland sites.

Within pinyon-juniper sites, grazing status*year had a significant effect for richness of life history and flower color, both of which declined at grazed and ungrazed sites over time (Table 7 and 10; Figures 17 and 18). Life history and flowering period richness were both significantly higher in ungrazed sites compared to grazed sites, and declined significantly between baseline years and 2022 (Table 7 and 10; Figure 17 and 19). Four traits varied significantly over time only, including height (functional richness and evenness), richness of radial symmetry and flowering duration, and flower size (richness and evenness) (Table 7 and 10). Inflorescence type did not vary significantly by grazing status*year, grazing status, or year.

Table 7: Results of pollination-related trait functional diversity analyses for pinyon-juniper woodlands. Bolding indicates a significant p-value at alpha=0.05.

Pinyon-Juniper Woodland	**Sum Sq**	**Mean Sq**	**F value**	**Pr(>F)**
Life History (FRic)				
Grazing Status	1.340751	1.340751	8.340622	**0.005638**
Year	5.407418	5.407418	33.63878	**3.98E-07**
Grazing Status * Year	0.693132	0.693132	4.311876	**0.042806**
Flower Color (FRic)				
Grazing Status	1.407869	1.407869	1.509388	0.230238
Year	41.23086	41.23086	44.20395	**4.72E-07**
Grazing Status * Year	4.802289	4.802289	5.148574	**0.031798**
Flowering Period (FRic)				
Grazing Status	1.333348	1.333348	4.330605	**0.047424**
Year	25.04844	25.04844	81.35529	**1.74E-09**
Grazing Status * Year	1.048443	1.048443	3.405258	0.076408
Height (FRic)				
Grazing Status	4.411331	4.411331	2.209264	0.149211
Year	19.77698	19.77698	9.904626	**0.004106**
Grazing Status * Year	0.202834	0.202834	0.101583	0.752485
Height (FEve)				
Grazing Status	0.000348	0.000348	0.014604	0.904724
Year	0.350583	0.350583	14.71075	**0.000861**
Grazing Status * Year	0.00072	0.00072	0.030207	0.863561
Radial Symmetry (FRic)				
Grazing Status	8.73E-06	8.73E-06	1.33E-05	0.997123
Year	4.82E+00	4.82E+00	7.31E+00	**0.011921**
Grazing Status * Year	1.92E-01	1.92E-01	2.91E-01	0.593907
Flower Size (FRic)				
Grazing Status	1.616207	1.616207	0.892514	0.353494
Year	19.97152	19.97152	11.02882	**0.002665**
Grazing Status * Year	0.97152	0.97152	0.5365	0.470439

Pinyon-Juniper Woodland	**Sum Sq**	**Mean Sq**	**F value**	**Pr(>F)**
Flower Size (FEve)				
Grazing Status	0.006463	0.006463	0.328877	0.571405
Year	0.390982	0.390982	19.89443	**0.000173**
Grazing Status * Year	0.003033	0.003033	0.154315	0.698004
Flowering Duration (FRic)				
Grazing Status	0.232612	0.232612	0.330714	0.570182
Year	12.46273	12.46273	17.7188	**0.000270**
Grazing Status * Year	1.17656	1.17656	1.672766	0.207262

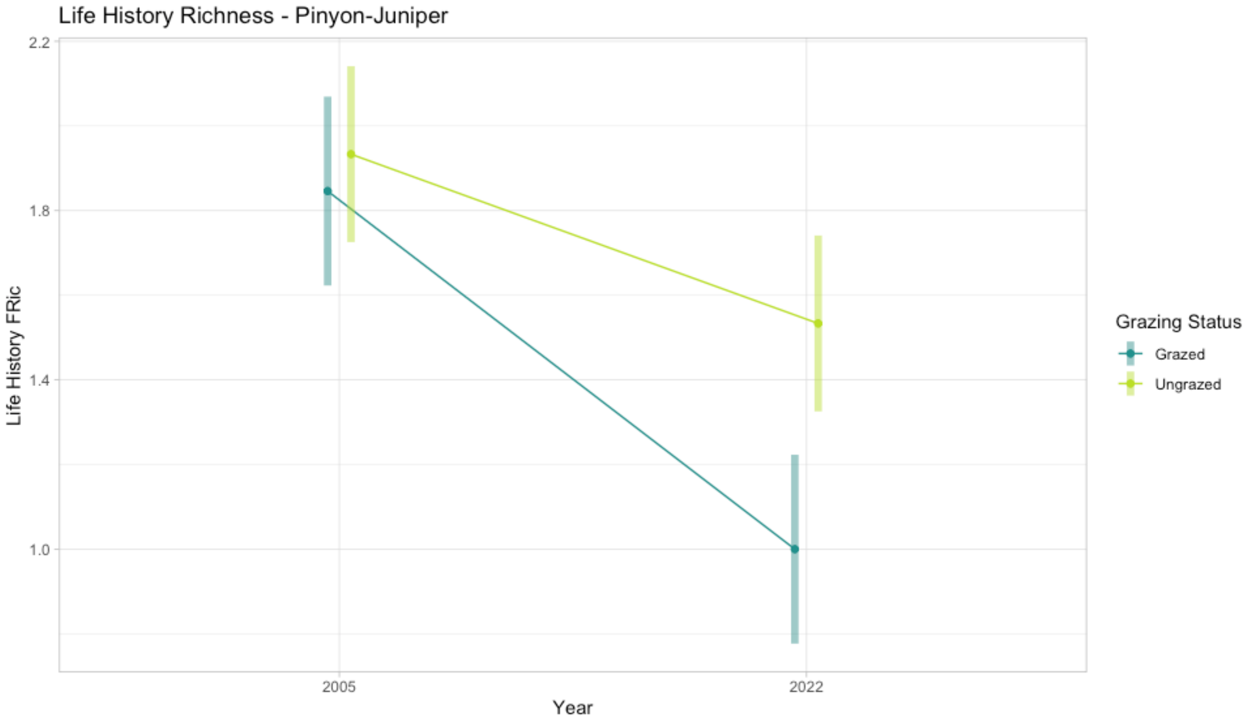


Figure 18: Life history functional richness across time for grazed and ungrazed pinyon-juniper sites.

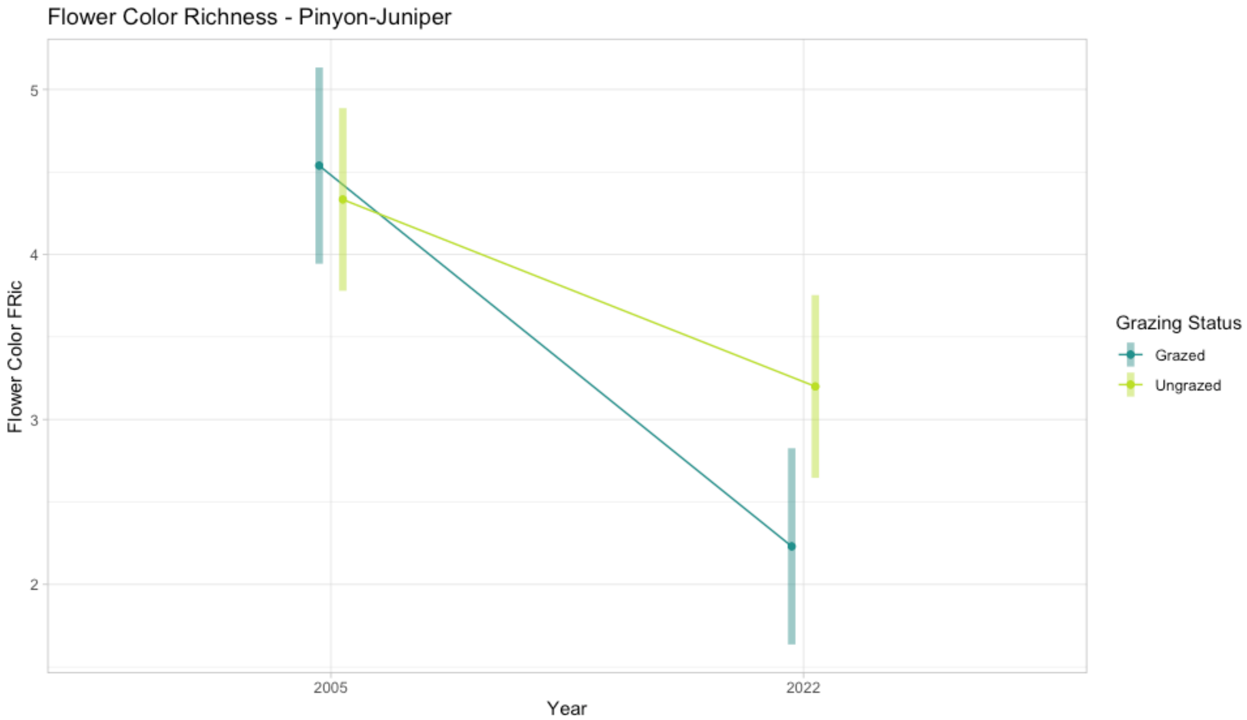


Figure 19: Flower color functional richness across time for grazed and ungrazed pinyon-juniper sites.

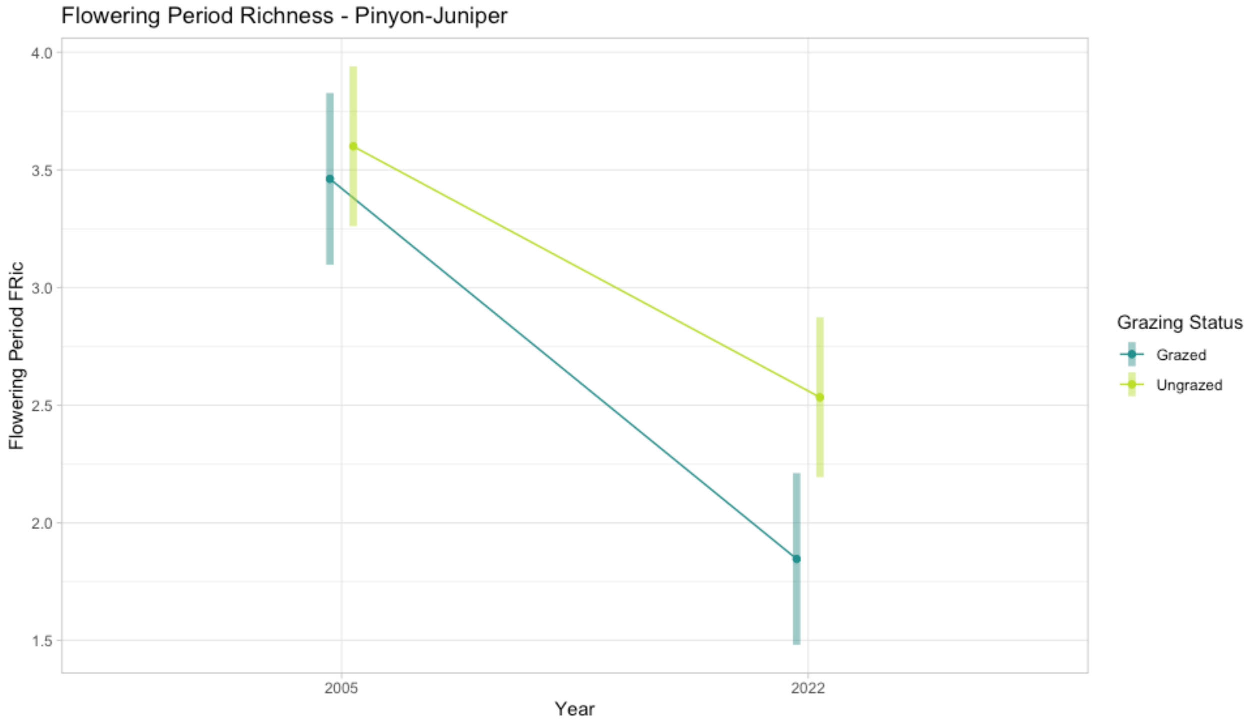


Figure 20: Flowering period functional richness across time for grazed and ungrazed pinyon-juniper sites.

Forb and ground cover response to grazing through time

In grassland sites, forb relative abundance was 95% lower in 2005/7 and 110% lower in 2022 at ungrazed sites compared to grazed sites, a significant difference (Table 8; Figure 21). Forb cover showed no significant response to any explanatory variables. Amount of bare ground and abundance of woody debris did not vary significantly over time or by grazing status; instead, both differed significantly based on soil type (Table 8). At pinyon-juniper sites, forb relative abundance, forb cover, and amount of bare ground did not respond to grazing status, but declined significantly between baseline years and present (Table 9 and 10; Figure 22-24). Forb relative abundance declined by 58%, forb cover by 30%, and bare ground by 40%. No explanatory variables had a significant effect on abundance of woody debris.

Table 8: Results of cover analyses for grassland sites. Only results from the best fit model for each response variable are displayed. Bolding indicates a significant p-value at alpha=0.05.

Mid/High Elevation Grassland	**Sum Sq**	**Mean Sq**	**F value**	**Pr(>F)**
Forb Relative Abundance				
Grazing Status	1.297956	1.297956	86.09949	**6.90E-10**
Year	0.027976	0.027976	1.855806	0.184367
Grazing Status * Year	0.000221	0.000221	0.014668	0.904499
Extent of Bare Ground				
Grazing Status	74.98231	74.98231	0.561164	0.462966
Soil Type	4216.325	602.3322	4.507825	**0.004146**
Annual Mean Temperature	155.9414	155.9414	1.167058	0.293529
Year	234.7994	234.7994	1.757227	0.196078
Grazing Status * Year	336.8535	336.8535	2.520995	0.123983

Mid/High Elevation Grassland	**Sum Sq**	**Mean Sq**	**F value**	**Pr(>F)**
Abundance of Woody Debris				
Grazing Status	4.82078	4.82078	0.602099	0.441750
Soil Type	587.5076	83.92965	10.48253	**8.63E-08**
Annual Mean Temperature	0.135458	0.135458	0.016918	0.897078
Year	8.366406	8.366406	1.044936	0.312022
Grazing Status * Year	15.71081	15.71081	1.962228	0.167985

Table 9: Results of cover analyses for pinyon-juniper sites. Only results from the best fit model for each response variable are displayed. Bolding indicates a significant p-value at alpha=0.05.

Pinyon-juniper Woodland	**Sum Sq**	**Mean Sq**	**F value**	**Pr(>F)**
Forb Relative Abundance				
Grazing Status	0.086455	0.086455	4.178409	0.051194
Year	0.266271	0.266271	12.869	**0.001358**
Grazing Status * Year	0.051315	0.051315	2.48008	0.127388
Forb Cover				
Grazing Status	1.402194	1.402194	0.961991	0.337851
Soil Type	14.55868	2.911736	1.997629	0.120753
Year	7.726981	7.726981	5.301182	**0.02957**
Grazing Status * Year	0.433297	0.433297	0.297268	0.590247
Extent of Bare Ground				
Grazing Status	2.247768	2.247768	0.034745	0.854009
Soil Type	164.1993	32.83985	0.507624	0.767118
Annual Mean Temperature	93.3325	93.3325	1.442693	0.243736
Year	800.0871	800.0871	12.3674	**0.001626**
Grazing Status * Year	231.7537	231.7537	3.582348	0.06958

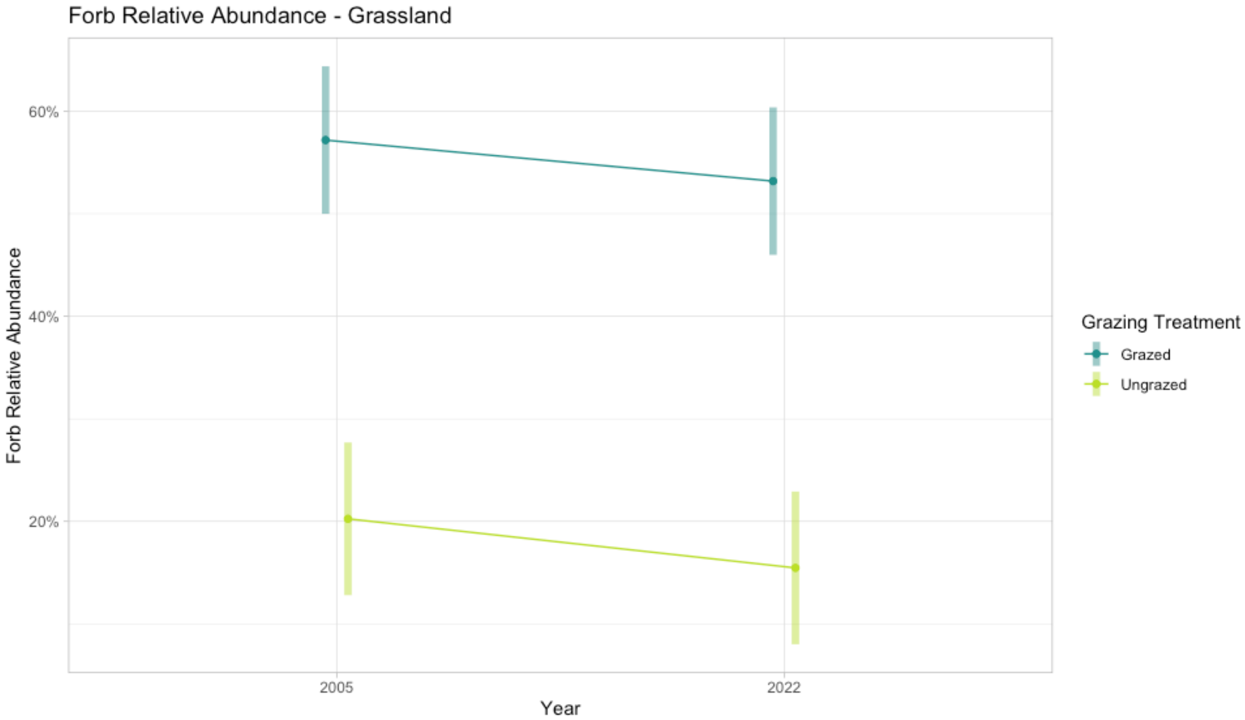


Figure 21: Forb relative abundance for high elevation (grazed) and mid-elevation (ungrazed) grassland sites.

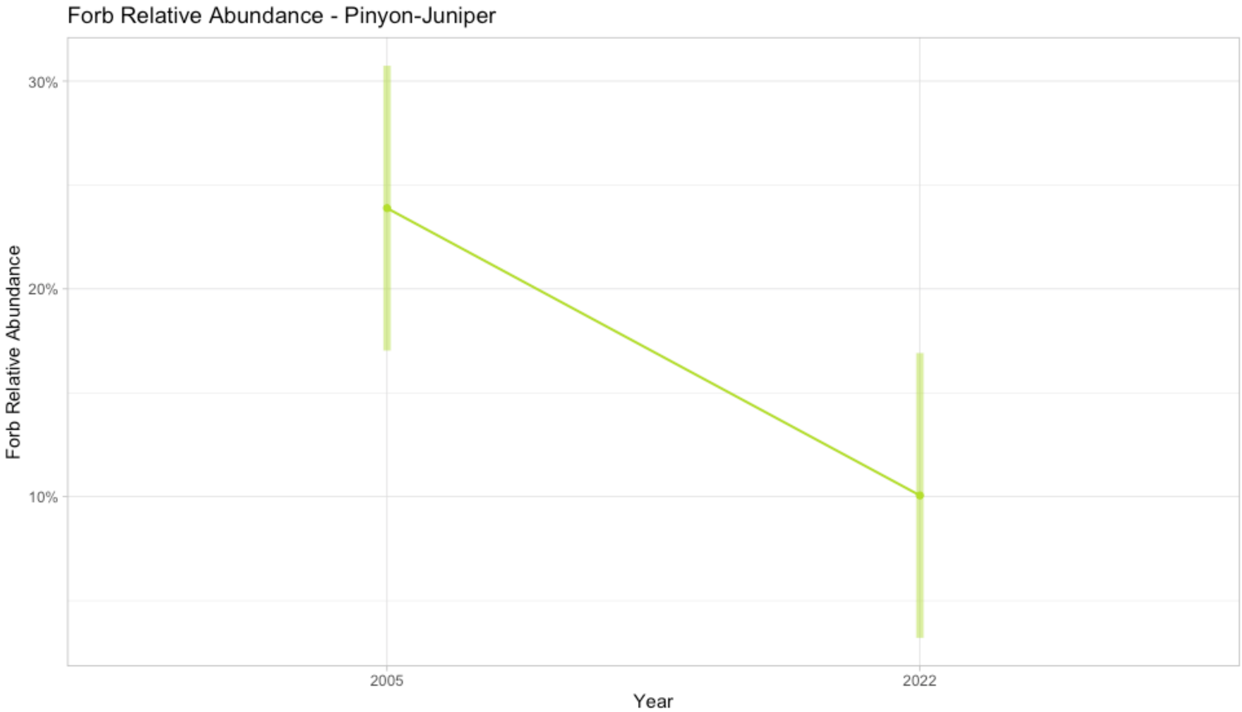


Figure 22: Forb relative abundance across time at pinyon-juniper sites.

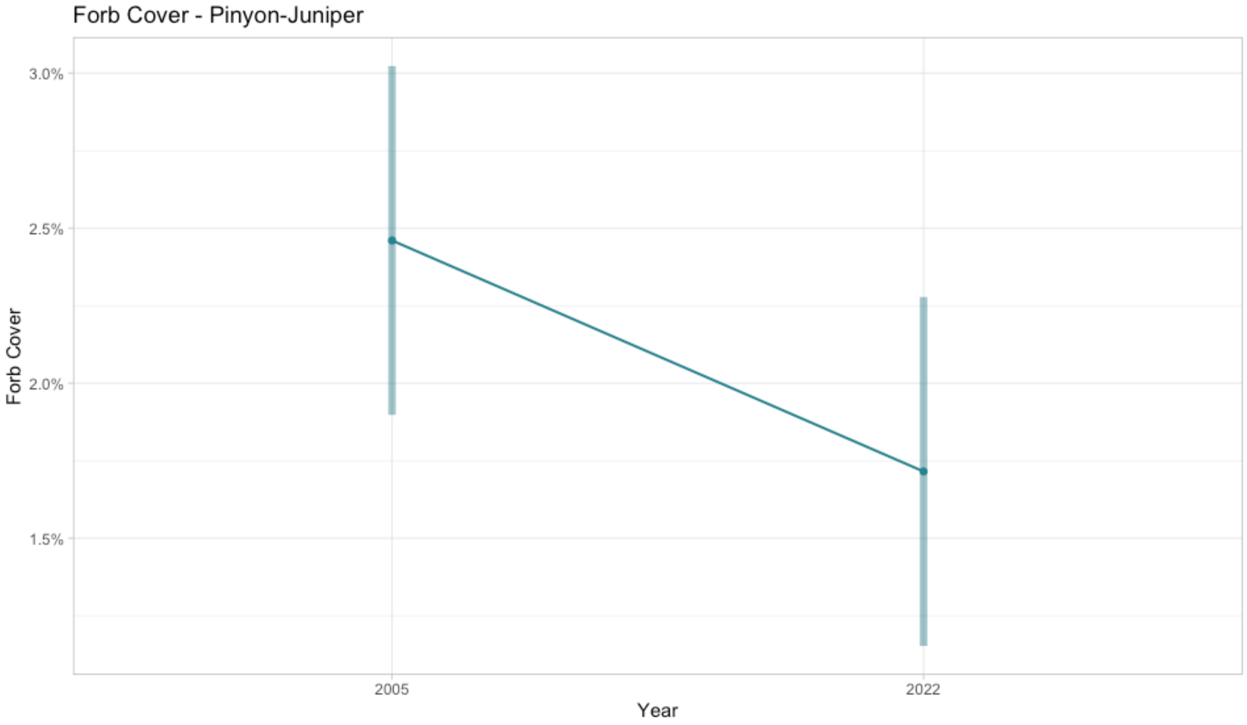


Figure 23: Percent forb cover across time at pinyon-juniper sites.

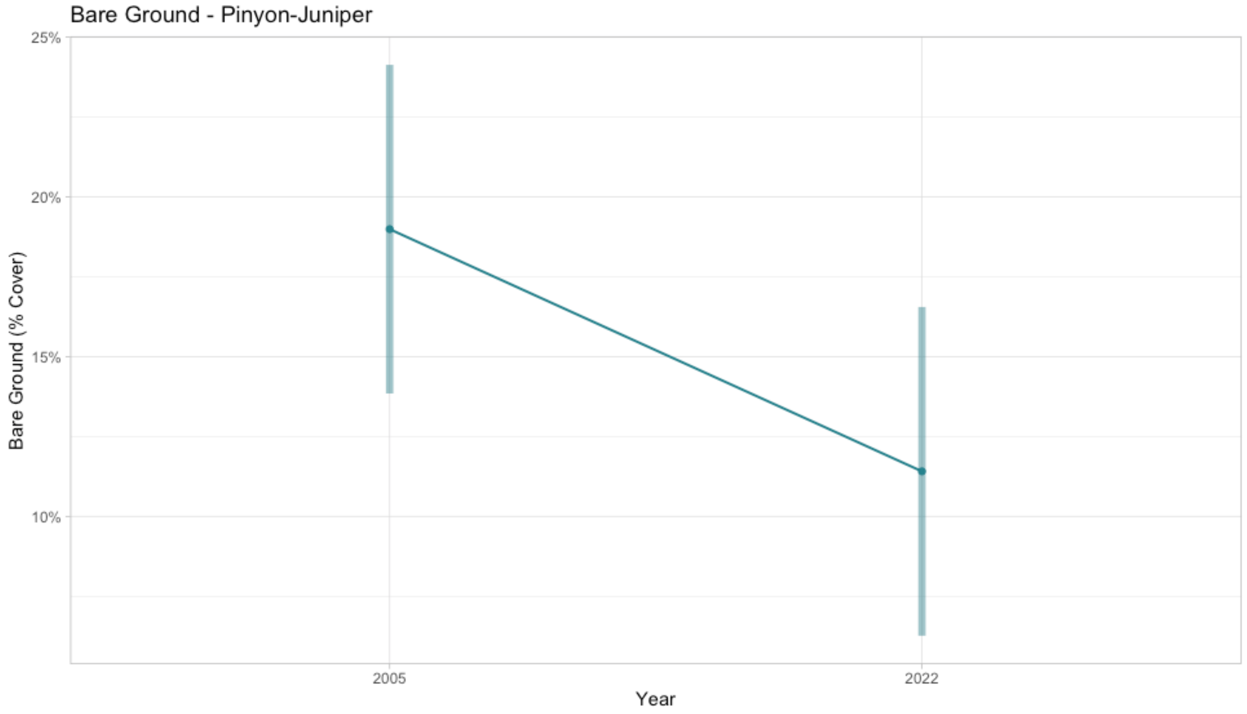


Figure 24: Bare ground across time at pinyon-juniper sites.

Table 10: Summary of change over time for response variables with available baseline data. Only statistically significant differences by year or grazing status*year are represented.*

Response Variable	Grassland		Pinyon-Juniper	
	Grazed	Ungrazed	Grazed	Ungrazed
Forb species diversity				
Richness	↘	↘	↘	↘
Shannon Diversity Index	↘	↘	↘	↘
Simpson Diversity Index	↘	↘	↘	↘
Functional diversity of pollination-related traits (Richness)				
Life History	↘	↘	↘	↘
Height	↘	↗	↘	↘
Flower Color			↘	↘
Radial Symmetry	↘	↘	↘	↘
Flower Size	↘	↘	↘	↘
Inflorescence Type	↘	↘		
Flowering Period	↗	↘	↘	↘
Flowering Duration	↘	↘	↘	↘
Functional diversity of pollination-related traits (Evenness)				
Life History				
Height			↗	↗
Flower Color	→	↗		
Radial Symmetry				
Flower Size	↗	↗	↗	↗
Inflorescence Type				
Flowering Period	↗	↘		
Flowering Duration				

Response Variable	Grassland		Pinyon-Juniper	
	Grazed	Ungrazed	Grazed	Ungrazed
Forb and ground cover				
Forb relative abundance			↘	↘
Forb cover			↘	↘
Extent of bare ground			↘	↘
Abundance of woody debris				

* Except for forb species diversity, which could not be analyzed for statistical significance due to data constraints.

Soil response to grazing status

At grassland sites soil compaction was 64% higher in grazed sites compared to ungrazed, a significant difference (Table 11, Figure 25). There was no effect of grazing status on interspace or canopy soil stability, water content, or bulk density. Soil type significantly affected soil water content and canopy stability; interspace soil stability and bulk density did not have a significant response to any explanatory variables (Table 11). In pinyon-juniper sites there was no effect of grazing status on soil stability, water content, compaction, or bulk density. Instead, these metrics showed significant responses to either annual precipitation, annual mean temperature, or soil type (Table 12).

Table 11: Results of soil analyses for grassland sites. Only results from the best fit model for each response variable are displayed. Bolding indicates a significant p-value at alpha=0.05.

Mid/High Elevation Grassland	**Sum Sq**	**Mean Sq**	**F value**	**Pr(>F)**
Canopy Stability				
Soil Type	5.456614	0.779516	4.379428	**0.004804**
Soil Water Content				
Grazing Status	0.001567	0.001567	1.169703	0.292331
Soil Type	0.078334	0.011191	8.352504	**8.50E-05**
Compaction				
Grazing Status	2.4049	2.4049	6.925977	**0.013872**

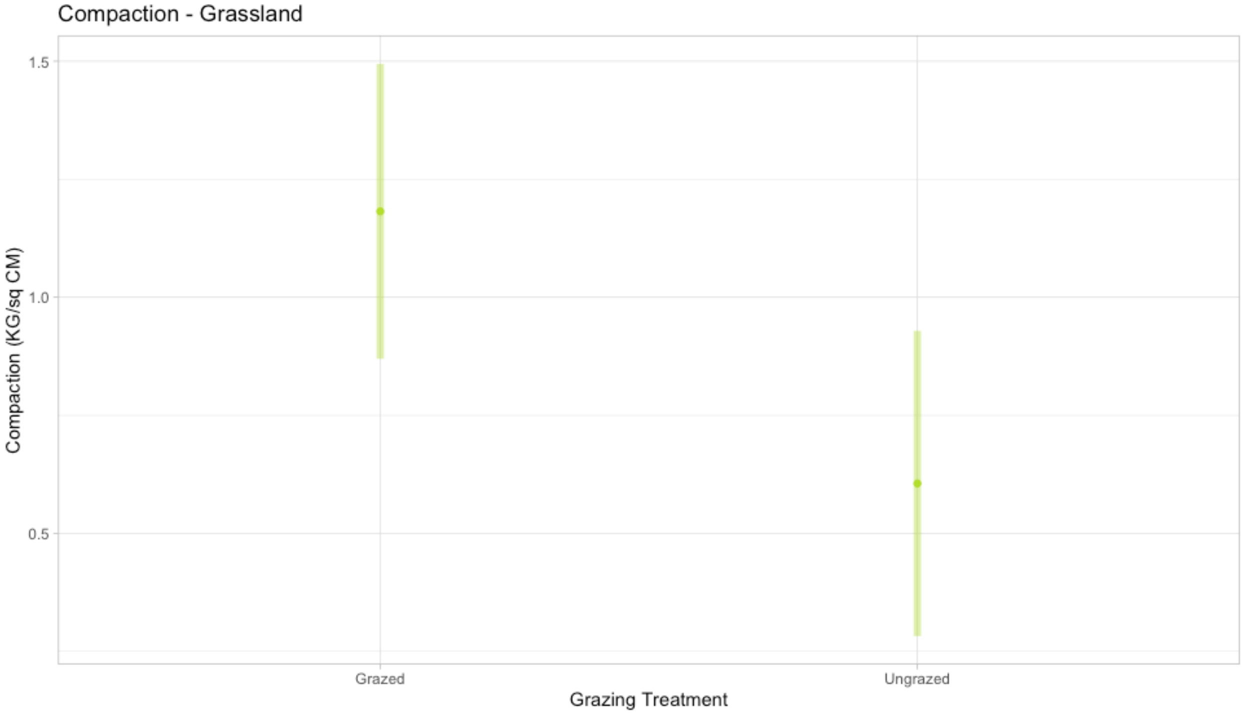


Figure 25: Soil compaction at high elevation (grazed) and mid-elevation (ungrazed) grassland sites.

Table 12: Results of soil analyses for pinyon-juniper sites. Only results from the best fit model for each response variable are displayed. Bolding indicates a significant p-value at alpha=0.05.

Pinyon-juniper Woodland	Sum Sq	Mean Sq	F value	Pr(>F)
Interspace Stability				
Annual Mean Temperature	3.00975	3.00975	5.754167	**0.024231**
Annual Precipitation	3.382428	3.382428	6.466668	**0.017558**
Bulk Density				
Annual Precipitation	0.099122	0.099122	4.893252	**0.035953**
Soil Water Content				
Annual Mean Temperature	0.020511	0.020511	6.530289	**0.0168**
Compaction				
Soil Type	0.800109	0.160022	2.745991	**0.047893**
Annual Mean Temperature	0.031439	0.031439	0.539501	0.471164
Annual Precipitation	0.375054	0.375054	6.435973	**0.01962**

Discussion

This study capitalized on a landscape-level baseline assessment conducted in 2005 to examine differences in pollinator forage and nesting resources in response to livestock grazing. In general, our results show that the impact of grazing on pollinator habitat varies between different vegetation types. Grassland sites responded to grazing status more frequently than pinyon-juniper sites, where year more often had a significant effect, indicating grazing impacts may be mediated by broad vegetation type. The impact of grazing differed among response variables, and vegetation generally appeared more responsive to grazing status than soils. Some metrics, such as forb and vegetation community composition, functional diversity of certain pollination-related traits, and soil compaction show a negative impact from grazing. Others, such as forb species diversity, forb relative abundance, and forb cover showed either no effect or a positive effect of grazing. Alarmingly, we observed consistent declines in pollinator forage species over time regardless of grazing treatment.

Grazing impacts on pollinator forage resources

At grassland sites, grazing was associated with significant vegetation community change over time, while ungrazed sites were not significantly different in baseline and current years. Forb communities at both high elevation grazed and mid-elevation ungrazed grassland sites showed statistically significant changes over time. These results suggest that grazing could have contributed to a shift in vegetation and forb communities at grassland sites over the past 15-17 years, with potentially negative consequences for pollinator forage. Our findings for grassland sites are consistent with evidence that grazing can alter vegetation communities (Bakker et al., 2006; Carmona et al., 2012; Díaz et al., 2007; Floyd et al., 2003; Herrero-Juregui & Oesterheld, 2018), potentially with negative effects on pollinators through changes to vegetation structure or decreases in floral resources (Buckles & Harmon-Threatt, 2019; Kimoto et al., 2012).

At pinyon-juniper sites however, forb communities showed greater change over time at ungrazed sites, which had significantly different community compositions in baseline and current years while grazed sites showed no year effect. This result indicates grazing may have a stabilizing effect on forb community composition in pinyon-juniper ecosystems. In contrast to grassland sites, the results for pinyon-juniper sites support local research done by Souther et al. (2020) that suggests moderate grazing can stabilize plant communities through time. It's possible that the timing of grazing is playing a role in the differences in responses between vegetation communities, as lower elevation pinyon-juniper pastures are likely grazed earlier in the season than higher elevation grassland pastures. Additionally, relatively dense tree cover in pinyon-juniper sites may limit the intensity of grazing compared to more open and accessible grassland sites, as cattle tend to prefer flat, open spaces.

Grassland forb species diversity showed notably greater declines over time at mid-elevation ungrazed sites compared to high elevation grazed sites, while grazed and ungrazed sites showed similar declines between baseline and current years at pinyon-juniper sites. Grassland results support previous findings that grazing can have a positive effect on forb diversity, such as Hayes & Holl (2003), which compared 25 paired grazed and ungrazed sites and found higher annual forb species richness at grazed sites. The smaller loss of diversity at grazed sites is also consistent with Souther et al. (2020), and a potential stabilizing effect of moderate grazing on plant assemblages. Shapira et al. (2020), however, found no effect of grazing on forb species richness, which reflects our results at pinyon-juniper sites.

We found consistent declines in forb species diversity across all sites, irrespective of grazing status. This broad trend suggests climatic shifts may be contributing to the changes we observed over time. Much of the western United States has experienced widespread warming and increased interannual variability combined with overall reduction of precipitation over the past five decades (Zhang et al., 2021). In the southwest, the last two decades have been the driest since at least 800 CE (Williams et al., 2022). Plant communities on the Colorado Plateau have demonstrated sensitivity to climate change, and drought itself may contribute to state changes (Munson et al., 2011). Grazing and climatic shifts may also have interactive effects on vegetation communities. Multiple studies on the Colorado Plateau have documented vegetative drought responses mediated by grazing intensity, including reduced response to precipitation (Munson et al., 2016) and increased non-native invasion (Souther et al., 2020) with intensive grazing. In addition, Colorado Plateau ecosystems can exhibit low recovery capacity even decades after grazing cessation (Bernstein et al., 2014; Miller et al., 2011; Wolf et al., 2020). Consistent long-term monitoring will be crucial to understanding these interactive effects and informing land management practices (Munson et al., 2016; Souther et al., 2020).

Effect of grazing status on functional diversity of pollination-related traits varied widely, with no consistent pattern at grassland sites, and declines both related and unrelated to grazing status at pinyon-juniper sites. In grasslands, some traits showed declines at both high elevation grazed and mid-elevation ungrazed sites (flower size and inflorescence type richness), while others were relatively stable at grazed sites and either increased or decreased more at ungrazed sites (flower color evenness and radial symmetry richness), and still others showed opposite responses over time depending on grazing status (height and flowering period richness, and flowering period evenness). Only flower size evenness increased over time for both grazed and ungrazed sites. Taken together, these results suggest there is no consistent effect of grazing on functional diversity of this suite of pollination-related traits in grasslands. The observed changes are more likely attributable to the varying decreases in forb species diversity and shifts in forb community composition across grazed and ungrazed sites that we found in other analyses. The variety of responses among traits highlights how difficult it may be to predict cascading effects of changes to community composition or diversity on pollination-related traits. Due to the complexity of plant-pollinator networks, any change to diversity, abundance, or composition of pollination-related traits has the potential to negatively affect the local pollinator community.

Pollination-related traits in pinyon-juniper sites showed more consistent trends, where all but one (inflorescence type) showed significant declines in functional richness over time, and only height and flower size functional evenness increased over time. Grazing status did affect life history, flower color, and flowering period functional richness, with grazed sites showing lower values and/or greater decreases over time. There is very little research on the relationship between grazing and pollination-related traits, but these findings complement some studies which found that grazing can reduce diversity of floral traits. Rakosy et al. (2022) found that intensively grazed pastures were significantly more dominated by plants with a particular type of flower structure, and Goulnik et al. (2021) concluded that land-use intensification, including grazing, could select for generalized floral traits (Goulnik et al., 2021; Rakosy et al., 2022). Lower life history functional richness at grazed sites may potentially be due to a tendency for grazing to select for annual rather than perennial species (Díaz et al., 2007). In addition, the significant decline in functional richness over time, regardless of grazing status, for most of the traits we assessed suggests a connection to overall declines in forb species richness at pinyon-juniper sites and possibly a broader change in climate.

We found no evidence for grazing impacts to forb relative abundance or cover. At grassland sites, relative abundance was significantly lower at mid-elevation ungrazed sites, but this was equally true in baseline and current years and both grazed and ungrazed sites showed a similar trend in relative abundance over time. Both forb relative abundance and cover declined significantly over time at pinyon-juniper sites, but we found no effect of grazing status or grazing status by year. Taken together, these results indicate that differences in forb relative abundance in grasslands are driven by existing differences in the vegetation communities at mid- and high elevation sites, while abundance and cover at pinyon-juniper sites are responding to climate change, rather than grazing impacts in either vegetation type. Shapira et al. (2020) report similar results after comparing three grazed/ungrazed paired sites over two years, finding that grazing had no effect on flowering plant abundance.

Grazing impacts on pollinator nesting habitat

We found limited evidence for grazing status impacting pollinator nesting resources in either vegetation type. Our results showed no effect of grazing status or grazing status by year for extent of bare ground or woody debris. Bare ground did decrease significantly over time at pinyon-juniper sites, although this may simply be due to continued accumulation of litter from pinyon and juniper trees. We also found no effect of grazing status on interspace or canopy soil stability, bulk density, or water content in either vegetation type, and no effect for compaction in pinyon-juniper sites. Grazing status significantly affected compaction at grassland sites however, with higher compaction at high elevation grazed sites. Increased compaction associated with grazing is consistent with regional studies on grazing impacts to soils (Duniway et al., 2018; Roberts et al., 2016). Other studies have found that grazing inconsistently increased compaction (Schmalz et al., 2013), or compaction was related to grazing intensity (Kimoto et al., 2012), which may explain the variation in our results across vegetation types. The exact soil characteristic requirements of pollinators are still largely unknown and may vary widely, meaning that changes in compaction observed at grassland sites could negatively affect pollinator nesting habitat (Hanberry et al., 2021).

Drawbacks of this study design

Although it is challenging to conclusively attribute responses to specific factors in an observational study, this type of research allows for documentation of real-world changes in complex ecological systems and can be conducted at large scales. Due to the observational nature of our study, grazed and ungrazed pastures of the same vegetation type could be physically distant from one another, resulting in spatial disaggregation of sites by grazing status. To mitigate this issue, we used a BACI design to compare the response of individual grazed and ungrazed sites over time. We also conducted additional analyses on spatially concentrated high elevation grassland sites to validate results found when comparing spatially distant sites.

The inherent difference between grassland plant communities at mid-elevation ungrazed sites and high elevation sites does potentially confound our results for pollinator forage resource metrics in grasslands. However, to explore the impact of this difference, we applied the same forb and plant community composition analyses to a group of high elevation grassland sites, categorized as either moderately grazed or heavily grazed based on scat counts and prevalence of browsed plants. If the shifts in mid-elevation and high elevation grassland communities were due to inherent differences between these grasslands, we would expect to see different results when restricting analyses to grasslands at one elevation level. However, the results of these additional analyses were similar to those of the complete grassland sample, and we observed greater shifts over time in both forb and vegetation community composition at heavily grazed sites compared to moderately grazed sites.

Conclusion

Cumulatively, our results provide evidence that a combination of climatic shifts and grazing impacts are affecting pollinator habitat on the Kaibab Plateau, and that the nature of these effects is not consistently predictable across vegetation types. We found significant changes in grassland vegetation and forb communities related to grazing, which are potentially driving significant changes to forb pollination-related traits. We also found significant differences in compaction based on grazing status at grassland sites, indicating that grazing is potentially negatively impacting pollinator nesting habitat. However, these trends were not reflected at pinyon-juniper sites. The only variable that showed a consistent response across time, grazing status, and vegetation type was forb species diversity, which declined substantially by all metrics. Such persistent declines point to the role of an increasingly drier, hotter climate.

Our findings highlight the intricacy of relationships between grazing, vegetation, and soils, the variable impact of those relationships on pollinator habitat, and the added complexity of interactive effects with climate change. Climate projections predict increased interannual variability and continued drier, hotter conditions, which has direct connections to livestock grazing on public lands given that cattle can exacerbate the effects of climate change in numerous ways (Kauffman et al., 2022). Ecosystems on the Colorado Plateau have demonstrated sensitivity to climatic shifts (Munson et al., 2011) and limited capacity for recovery after grazing and/or climate-induced state changes (Bernstein et al., 2014; Miller et al., 2011; Wolf et al., 2020). Pollinator populations in the southwest have also responded negatively to grazing (Debano, 2006; Kearns & Oliveras, 2009; Minckley, 2014), and we have found evidence that climate change and grazing may degrade pollinator habitat on the Colorado Plateau.

Modifying grazing management in the West continues to present social and political challenges, but it will be critical to conserving pollinator habitat and rangeland ecosystems in the face of complicated and variable feedbacks between land use, climate change, and ecological conditions. The complexity of plant-pollinator networks and diversity of ecosystem-specific responses to grazing present additional challenges for land managers, and further research including long-term monitoring will be necessary to support adaptive management. However, public agency staffing limitations, and the huge temporal and spatial scale of research necessary to truly inform local management across public lands, are serious practical concerns. The importance of pollinators to ecosystem function and food security warrants a cautionary approach. Existing evidence supports strategic changes to grazing management, such as maintaining habitat heterogeneity in grazed lands, timing grazing to minimize impacts on pollinator forage, managing stocking levels based on utilization rates, and monitoring impacts to pollinator habitat (Black et al., 2011; Buckles & Harmon-Threatt, 2019; Fuhlendorf & Engle, 2001; Hanberry et al., 2021). Implementing these pollinator-friendly grazing practices on public lands could be a significant step toward rangeland conservation that avoids well-worn sociopolitical conflicts over grazing management.

References

Alkemade, R., Reid, R. S., Van Den Berg, M., De Leeuw, J., & Jeuken, M. (2013). Assessing the impacts of livestock production on biodiversity in rangeland ecosystems. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(52), 20900–20905. https://doi.org/10.1073/pnas.1011013108

Bakker, E. S., Ritchie, M. E., Olff, H., Milchunas, D. G., & Knops, J. M. H. (2006). Herbivore impact on grassland plant diversity depends on habitat productivity and herbivore size. *Ecology Letters*, *9*(7), 780–788. https://doi.org/10.1111/j.1461-0248.2006.00925.x

Belesky, D. P., & Malinowski, D. P. (2016). Grassland communities in the USA and expected trends associated with climate change. In *Acta Agrobotanica* (Vol. 69, Issue 2). Polish Botanical Society. https://doi.org/10.5586/aa.1673

Bernstein, E. J., Albano, C. M., Sisk, T. D., Crews, T. E., & Rosenstock, S. (2014). Establishing cool-season grasses on a degraded arid rangeland of the Colorado Plateau. *Restoration Ecology*, *22*(1), 57–64. https://doi.org/10.1111/rec.12023

Beschta, R. L., Donahue, D. L., Dellasala, D. A., Rhodes, J. J., Karr, J. R., O'Brien, M. H., Fleischner, T. L., & Deacon Williams, C. (2013). Adapting to climate change on western public lands: Addressing the ecological effects of domestic, wild, and feral ungulates. *Environmental Management*, *51*(2), 474–491. https://doi.org/10.1007/s00267-012-9964-9

Bilotta, G. S., Brazier, R. E., & Haygarth, P. M. (2007). The Impacts of Grazing Animals on the Quality of Soils, Vegetation, and Surface Waters in Intensively Managed Grasslands. In *Advances in Agronomy* (Vol. 94, pp. 237–280).

Black, S. H., Shepherd, M., & Vaughan, M. (2011). Rangeland management for pollinators. *Rangelands*, *33*(3), 9–13. https://doi.org/10.2111/1551-501X-33.3.9

Buckles, B. J., & Harmon-Threatt, A. N. (2019). Bee diversity in tallgrass prairies affected by management and its effects on above- and below-ground resources. *Journal of Applied Ecology*, *56*(11), 2443–2453. https://doi.org/10.1111/1365-2664.13479

Bureau of Land Management. (n.d.). *Livestock Grazing on Public Lands*. Retrieved April 12, 2022, from https://www.blm.gov/programs/natural-resources/rangelands-and-grazing/livestock-grazing

Carmona, C. P., Azcárate, F. M., De Bello, F., Ollero, H. S., Lepš, J., & Peco, B. (2012). Taxonomical and functional diversity turnover in Mediterranean grasslands: interactions between grazing, habitat type and rainfall. *Source: Journal of Applied Ecology*, *49*(5), 1084–1093. https://doi.org/10.1111/j.l

Cingolani, A. M., Noy-Meir, I., & Díaz, S. (2005). Grazing effects on rangeland diversity: A synthesis of contemporary models. *Ecological Applications*, *15*(2), 757–773. https://doi.org/10.1890/03-5272

Debano, S. J. (2006). Effects of livestock grazing on aboveground insect communities in semi-arid grasslands of southeastern Arizona. *Biodiversity and Conservation*, *15*(8), 2547–2564. https://doi.org/10.1007/s10531-005-2786-9

Debano, S. J., Roof, S. M., Rowland, M. M., & Smith, L. A. (2016). Diet Overlap of Mammalian Herbivores and Native Bees: Implications for Managing Cooccurring Grazers and Pollinators. *Natural Areas Journal*, *36*(4), 458–477. https://doi.org/10.3375/043.036.0412

Díaz, S., Lavorel, S., McIntyre, S., Falczuk, V., Casanoves, F., Milchunas, D. G., Skarpe, C., Rusch, G., Sternberg, M., Noy-Meir, I., Landsberg, J., Zhang, W., Clark, H., & Campbell, B. D. (2007). Plant trait responses to grazing - A global synthesis. *Global Change Biology*, *13*(2), 313–341. https://doi.org/10.1111/j.1365-2486.2006.01288.x

Duniway, M. C., Geiger, E. L., Minnick, T. J., Phillips, S. L., & Belnap, J. (2018). Insights from Long-Term Ungrazed and Grazed Watersheds in a Salt Desert Colorado Plateau Ecosystem ☆. *Rangeland Ecology & Management*, *71*, 492–505. https://doi.org/10.1016/j.rama.2018.02.007

Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, *37*(12), 4302–4315. https://doi.org/10.1002/joc.5086

Floyd, M. L., Fleischner, T. L., Hanna, D., & Whitefield, P. (2003). Effects of Historic Livestock Grazing on Vegetation at Chaco Culture National Historic Park, New Mexico. *Conservation Biology*, *17*(6), 1703–1711.

Fuhlendorf, S. D., & Engle, D. M. (2001). Restoring Heterogeneity on Rangelands: Ecosystem Management Based on Evolutionary Grazing Patterns. *BioScience*, *51*(8). https://academic.oup.com/bioscience/article/51/8/625/220557

Goulnik, J., Plantureux, S., Dajoz, I., & Michelot-Antalik, A. (2021). Using Matching Traits to Study the Impacts of Land-Use Intensification on Plant–Pollinator Interactions in European Grasslands: A Review. *Insects*, *12*(680).

Hanberry, B. B., DeBano, S. J., Kaye, T. N., Rowland, M. M., Hartway, C. R., & Shorrock, D. (2021). Pollinators of the Great Plains: Disturbances, Stressors, Management, and Research Needs. *Rangeland Ecology and Management*, *78*, 220–234. https://doi.org/10.1016/j.rama.2020.08.006

Herrero-Juregui, C., & Oesterheld, M. (2018). Effects of grazing intensity on plant richness and diversity: a meta-analysis. *Oikos*, *127*(6), 757–766. https://doi.org/10.1111/oik.04893

Herrick, J. E., Whitford, W. G., De Soyza, A. G., Van Zee, J. W., Havstad, K. M., Seybold, C. A., & Walton, M. (2001). Field soil aggregate stability kit for soil quality and rangeland health evaluations. In *Catena* (Vol. 44). www.elsevier.comrlocatercatena

Kauffman, J. B., Beschta, R. L., Lacy, P. M., & Liverman, M. (2022). Livestock Use on Public Lands in the Western USA Exacerbates Climate Change: Implications for Climate Change Mitigation and Adaptation. *Environmental Management*, *69*(6), 1137–1152. https://doi.org/10.1007/s00267-022-01633-8

Kearns, C. A., & Oliveras, D. M. (2009). Environmental factors affecting bee diversity in urban and remote grassland plots in Boulder, Colorado. *Journal of Insect Conservation*, *13*(6), 655–665. https://doi.org/10.1007/s10841-009-9215-4

Kimoto, C., Debano, S. J., Thorp, R. W., Taylor, R. V., Schmalz, H., Delcurto, T., Johnson, T., Kennedy, P. L., & Rao, S. (2012). Short-term responses of native bees to livestock and implications for managing ecosystem services in grasslands. *Ecosphere*, *3*(10). https://doi.org/10.1890/ES12-00118.1

Mack, R. N., & Thompson, J. N. (1982). Evolution in Steppe with Few Large, Hooved Mammals. In *Source: The American Naturalist* (Vol. 119, Issue 6).

Milchunas, D. G. (2006). *Responses of Plant Communities to Grazing in the Southwestern United States*. http://www.fs.fed.us/rm

Milchunas, D. G., Sala, O. E., & Lauenroth, W. K. (1988). A Generalized Model of the Effects of Grazing by Large Herbivores on Grassland Community Structure. In *Source: The American Naturalist* (Vol. 132, Issue 1). https://about.jstor.org/terms

Miller, M. E., Belote, R. T., Bowker, M. A., & Garman, S. L. (2011). Alternative states of a semiarid grassland ecosystem: Implications for ecosystem services. *Ecosphere*, *2*(5). https://doi.org/10.1890/ES11-00027.1

Minckley, R. L. (2014). Maintenance of richness despite reduced abundance of desert bees (Hymenoptera: Apiformes) to persistent grazing. *Insect Conservation and Diversity*, *7*(3), 263–273. https://doi.org/10.1111/icad.12049

Munson, S. M., Belnap, J., Schelz, C. D., Moran, M., & Carolin, T. W. (2011). On the brink of change: plant responses to climate on the Colorado Plateau. *Ecosphere*, *2*(6), art68. https://doi.org/10.1890/es11-00059.1

Munson, S. M., Duniway, M. C., & Johanson, J. K. (2016). Rangeland Monitoring Reveals Long-Term Plant Responses to Precipitation and Grazing at the Landscape Scale. *Rangeland Ecology and Management*, *69*(1), 76–83. https://doi.org/10.1016/j.rama.2015.09.004

Rakosy, D., Motivans, E., Ştefan, V., Nowak, A., Świerszcz, S., Feldmann, R., Kühn, E., Geppert, C., Venkataraman, N., Sobieraj-Betlińska, A., Grossmann, A., Rojek, W., Pochrząst, K., Cielniak, M., Gathof, A. K., Baumann, K., & Knight, T. M. (2022). Intensive grazing alters the diversity, composition and structure of plant-pollinator interaction networks in Central European grasslands. *PLoS ONE*, *17*(3 March). https://doi.org/10.1371/journal.pone.0263576

Roberts, A. J., Johnson, N. C., Ostergren, D., & Sanford, R. (2016). *The Influence of Grazing Management on Soil Carbon and Mycorrhizae*.

Schmalz, H. J., Taylor, R. V., Johnson, T. N., Kennedy, P. L., Debano, S. J., Newingham, B. A., & McDaniel, P. A. (2013). Soil morphologic properties and cattle stocking rate affect dynamic soil properties. *Rangeland Ecology and Management*, *66*(4), 445–453. https://doi.org/10.2111/REM-D-12-00040.1

Shapira, T., Henkin, Z., Dag, A., & Mandelik, Y. (2020). Rangeland sharing by cattle and bees: moderate grazing does not impair bee communities and resource availability. *Ecological Applications*, *30*(3). https://doi.org/10.1002/eap.2066

Soil Survey Staff. (2023). *Web Soil Survey*. Natural Resources Conservation Service, United States Department of Agriculture. http://websoilsurvey.sc.egov.usda.gov/

Souther, S., Loeser, M., Crews, T. E., & Sisk, T. (2020). Drought exacerbates negative consequences of high-intensity cattle grazing in a semiarid grassland. *Ecological Applications*, *30*(3). https://doi.org/10.1002/eap.2048

Taboada, M. A., Rubio, G., & Chaneton, E. J. (2015). Grazing Impacts on Soil Physical, Chemical, and Ecological Properties in Forage Production Systems. In *Soil Management: Building a Stable Base for Agriculture* (pp. 301–320). wiley. https://doi.org/10.2136/2011.soilmanagement.c20

Thapa-Magar, K. B., Davis, T. S., & Fernández-Giménez, M. E. (2022). A meta-analysis of the effects of habitat aridity, evolutionary history of grazing and grazing intensity on bee and butterfly communities worldwide. *Ecological Solutions and Evidence*, *3*(2). https://doi.org/10.1002/2688-8319.12141

Thapa-Magar, K. B., Davis, T. S., & Kondratieff, B. (2020). Livestock grazing is associated with seasonal reduction in pollinator biodiversity and functional dispersion but cheatgrass invasion is not Variation in bee assemblages in a multi-use shortgrass prairie _ Enhanced Reader. *PLoS ONE*, *15*(12).

Trudeau, J. M. (2006). *Environmental History of the Kane and Two Mile Ranches in Arizona*.

United States Department of Agriculture. (2017). *Grazing Statistical Summary*. https://www.fs.fed.us/rangeland-management/documents/grazing-stats/2010s/GrazingStatisticalSummaryFY2016.pdf

Western Regional Climate Center. (n.d.). *Climate of Arizona*. Retrieved April 12, 2022, from https://wrcc.dri.edu/climate/narrative_az.php

Westoby, M., Walker, B., & Noy-Meir, I. (1989). Opportunistic management for rangelands not at equilibrium. *Journal of Range Management*, *42*(4), 266–274.

Williams, A. P., Cook, B. I., & Smerdon, J. E. (2022). Rapid intensification of the emerging southwestern North American megadrought in 2020–2021. *Nature Climate Change*, *12*(3), 232–234. https://doi.org/10.1038/s41558-022-01290-z

Wolf, A. C., Mitchell, R. M., Aslan, C., Butterfield, B., & Souther, S. (2020). *Evidence for State Change in an Arid Grassland-Steppe: Limited Recovery of Vegetation After Intermediate to Long-Term Cattle Exclusion in the Southwestern U.S.*

Zhang, F., Biederman, J. A., Dannenberg, M. P., Yan, D., Reed, S. C., & Smith, W. K. (2021). Five Decades of Observed Daily Precipitation Reveal Longer and More Variable Drought Events Across Much of the Western United States. *Geophysical Research Letters*, *48*(7). https://doi.org/10.1029/2020GL092293