

Rainfall increases similarity in plant species composition between grazed and ungrazed sites in a tropical semi-arid grassland

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Abstract

1. In peninsular India, semi-arid grasslands support marginal farmers and rich endemic biodiversity, yet are commonly designated as wastelands, and fragmentation has caused heavy grazing by domestic and wild mammals. The impacts of unmanaged grazing and increasingly variable monsoon rainfall on the plant community are unknown.
2. We studied an ancient tropical semi-arid grassland in a drought year and a subsequent wet year. In replicated grazed and long-term ungrazed sites, we assessed plant community composition, richness, biomass, traits and functional groups, as well as invertebrate herbivory, fungal infection, soil and plant nutrient stoichiometry.
3. We found that grasses dominated over forbs and legumes. The species richness rose from 35 in the dry year to 83 in the wet year, reflecting the grassland's long evolutionary history of high variation of annual rainfall. However, community composition differed greatly between grazed and ungrazed sites, especially in the dry year. Grass *Heteropogon contortus* was abundant in the wet year, while *Chrysopogon fulvus* dominated ungrazed sites in the dry year. *H. contortus* may persist under heavy grazing owing to its low palatability, whereas fast-growing *C. fulvus* may outcompete it given sufficient rain and no grazing. Specific leaf area was unrelated to grazing, but increased in the wet year, probably reflecting more acquisitive species.
4. Most plants had insect damage, which was 10% lower in the wet year despite high community-level plant nitrogen, perhaps because high plant density reduced per capita herbivory. Fungal

disease incidence was high in the wet year, possibly due to rapid pathogen growth in the humid microclimate. Plant and soil C:N ratios were low in the wet year, when greater legume cover may have increased N availability.

5. *Synthesis*. Both grazing and rainfall shaped the plant community. Grazing affected species composition, whereas rainfall affected species richness, herbivory and disease incidence. As climate change makes the Indian monsoon more extreme and land use confines grazers to smaller areas, plant species diversity is likely to decline, even among plants adapted to both aridity and grazing.

Key words:

Peninsular India, unmanaged grassland, community composition, *Heteropogon*, grazing livestock, wild ungulates, savanna grassland

Introduction

Arid and semi-arid grassland cover 30% of Earth's terrestrial surface (Zhan et al., 2007). These grasslands are grazed by both wild mammals and livestock. They are vulnerable to land degradation and desertification. In the semi-arid zones of peninsular India and trans Himalayas, agriculture is not economical and hence livestock grazing is the primary source of livelihood for pastoral communities. Despite their central role in supporting the livelihood of marginal farmers and providing shelter to many endemic flora and fauna, the effects of grazing on the semi-arid grassland plant community is understudied, especially in comparison to mesic grasslands.

Grazers are a natural part of grassland communities and affect plant community directly and indirectly in many ways. They preferentially consume palatable plants which affects grassland plant species composition and can increase (Koerner et al., 2018; Shaheen et al.,

2025) or decrease (Herrero-Juregui & Oesterheld, 2018) plant species richness and diversity, as well as on the morphological plant traits such as height, specific leaf area (SLA) and leaf dry matter content (LDMC) (Vuorinen et al., 2021). Since grazing affects the plant community (Bagchi & Ritchie, 2010; Milchunas et al., 1988) it also affects herbivory by invertebrates (Mysterud et al., 2005) and pathogen infection (Liu et al., 2021). Semi-arid grassland suffers from water scarcity, such that plant biomass and community composition varies strongly depending on the amount of rainfall (Y. Li et al., 2025; Ondier et al., 2019).

Grazers reduce plant biomass and feed selectively on palatable plant species. This affects plant community composition partly by providing space and resources for subordinate species to grow under reduced plant competition. The Intermediate Disturbance Hypothesis (Connell, 1978) predicts that intermediate grazing leads to high grassland diversity. This pattern has been shown in studies of mesic grassland where grazing leads to increased diversity and species richness through reduced plant competition (Koerner et al., 2018). The increase in plant species richness with grazing holds true for productive habitats which have abundant rainfall and soil nutrients. However, in non-productive habitat, grazing has neutral (Milchunas et al., 1998) to negative (Mathewos et al., 2023) effects on plant richness and diversity. Grazing shifts the composition towards annual plants which decreases the stability of grassland community (Rutherford & Powrie, 2013). Grazing can also increase (Adler et al., 2004) or decrease (Huang et al., 2026) plant functional group (such as forb, grass and legumes) richness and diversity. Overgrazing in semi-arid grasslands shifts the plant community from palatable to non-palatable species as widely seen in Central India (Datar, 2016) and North America, Africa and Europe (Augustine & Mcnaughton, 1998). It also reduces perennial grass abundance due to consumption of plant biomass.

Plant species composition can affect insect herbivory and incidence of plant disease and vice versa (Stein et al., 2010). This can be the result of plants in different functional groups experiencing different levels of herbivory. For example, the study conducted in inner Mongolia shows that forbs suffer more severe damage than legumes, at intermediate level of grazing (Wan et al., 2015). Additionally, under heavy grazing plant biomass will be low, leading to high herbivory of remaining plants at least on a short time scale, as the insect community may be large compared to the diminished plant biomass available (Y. Liu et al., 2022).

Grazing may affect disease prevalence in several ways. Low biomass due to grazing can reduce the spread and abundance of fungal pathogens by reducing the amount of host plant available to the pathogen and physical contact between plants, which is crucial in spread of the disease (Parker & Gilbert, 2018). Grazers may also affect disease prevalence by consuming pathogen infected plants, hence reducing overall pathogen load in plant community. For example, in semi-arid grassland of China, grazing decreased the fungal incidence on palatable plant species (Zhang et al., 2020). But grazers may also lead to increase in disease incidence on plants by spreading disease as they move around the habitat or exposing plant parts to infection (Daleo et al., 2009). For instance, a study performed on Qinghai Tibetan plateau found that grazers promoted infection by producing wounds on leaves (Liu et al., 2021).

Plant species' responses to grazers are reflected in plant trait values such as height, specific leaf area (SLA) and leaf dry matter content (LDMC). SLA and LDMC provide information about the photosynthetic area available for light capture and water loss and hence relates to plant physiological processes and productivity (Durak et al., 2025; Gitelson et al., 2014). Traits will vary depending on the productivity of the environment. In a resource rich environment, a plant

species can tolerate herbivory by regrowing after consumption by grazers. This is termed as acquisitive strategy. This has been found in the mesic grassland of Czech Republic (Mládek et al., 2013). In resource poor environments, such as arid and most semi-arid zones, plants lack resources to regrow tissue lost to herbivory, hence they may have low fitness, or conserve resources by being small, and having low SLA and high LDMC, as found in S. African grasslands (te Beest et al. 2021). Acquisitive or conservative trait values are relevant to the tolerance levels of plants growing under different grazing regimes and resource availability in a grassland ecosystem.

Grassland plant communities are highly responsive to the amount of precipitation they receive, and in arid and semi-arid ecosystems above ground productivity is limited by water availability (Knapp & Smith, 2001; Wilcox et al., 2015). Several studies have found high species replacement and a dramatic increase in species richness between dry and wet years in semi-arid grassland (Chen et al., 2018).

Precipitation also affects different plant species and plant functional groups differently. Grasses tend to be resource acquisitive, whereas forbs tend to be resource conservative due to their deeper roots. Thus, it has been found that cover of grasses has increased at the expense of forbs with increasing precipitation in the mesic grasslands of Switzerland (Stampfli et al., 2018). In grasslands under grazing regimes, precipitation and grazing have been found to interactively determine plant species composition and biomass (Y. Li et al., 2025; Ondier et al., 2019).

Grazing also affects soil nitrogen content and availability (Piñeiro et al., 2006) through trampling and deposition of N rich faeces (McNaughton S.J. et al., 1997) which may enhance litter decomposition and increase available N in the soil (Zacheis et al., 2002).

However, grazing can also decrease soil N by decreasing biomass of palatable N fixing plant species (Shan et al., 2011).

Grassland ecosystems store high amounts of carbon in soil (than vegetation, see (Carvalhais et al., 2014)) which contributes to soil aggregation and water holding capacity of grassland soil (Kool et al., 2007). In mesic grasslands, grazing has been found to increase soil carbon stocks (Bork et al., 2023) due to increase in nutrient content and biomass of graminoids which increased grassland litter and mulch, whereas in semi-arid grassland, grazing has been shown to decrease carbon content in top layers of soil due to soil compaction which probably reduces the activity of C fixing soil microbes (Shi et al., 2013). This contradicts to the study performed in India where SOC was higher in semi-arid grassland due to higher root biomass and litter deposition (Kumar et al., 2023). Livestock grazing has also been shown to reduce the carbon of above ground biomass through consumption and inhibit the loss of soil carbon (through reduction in soil respiration) in the semi-arid grassland of Inner Mongolia (Liang et al., 2021).

There are many studies of effects of grazing either on grassland plant community composition (Bagchi & Ritchie, 2010; Milchunas et al., 1988) or disease incidence (M. Liu et al., 2021) or soil nutrients (McNaughton S.J. et al., 1997), primarily in mesic grasslands. None of these studies incorporate all these variables together with respect to grazing. In India much of the grassland is arid or semi-arid, and much of the grassland is classified as wastelands (Madhusudan & Vanak, 2023), which leaves it prone to degradation and land conversion. As the grasslands becoming increasingly fragmented and degraded (Lahiri Sutirtha & Sushma Reddy, 2025), overgrazing occurs. This overgrazing has been shown in reducing plant species diversity (Katewa & Sharma, 1998; Shankarnarayan, 2016) and alters nutrient stoichiometry crucial in supporting plant growth (Craine et al., 2008).

This study was conducted in a natural semi-arid tropical grassland grazed by both wild mammals and domestic livestock. We ask (i) how grazing affects plant community composition and diversity, (ii) what are the (in)direct effects of grazing on insect herbivory, fungal infection, and plant and soil carbon and nitrogen, and (iii) how the effect of grazing on these factors differ at high and low rainfall.

We conducted a vegetation survey for two consecutive years in a semi-arid grassland in replicated grazed and long term-ungrazed sites. These years differed greatly in the amount of rain. The first year, 2023, had lower than average rainfall while the second year, 2024, had higher than average rainfall. The grazed sites contain wild animals and domestic livestock, and ungrazed sites had been fenced and ungrazed for more than 10 years.

We expected that due to grazing, which in semi-arid grassland may reduce rather than increase diversity, and interspecific competition, which also tends to decrease diversity, plant species richness and diversity will not differ between grazed and ungrazed sites. However, plant species composition in grazed and ungrazed sites will differ. Low biomass in the grazed sites will lead to high insect herbivory and fungal disease incidence. Due to animal excreta and plant species composition, we expect high soil and plant C:N ratio in grazed sites. With increase in precipitation, we expected that the plant species composition in grazed sites would become more like in ungrazed sites.

Plants, grazers, insect herbivores, phytopathogens and soil affect one another. Thus, changes in one will alter the community composition of the others. Hence, this study is important as it incorporates these variables in a common yet understudied mixed grazing system. Additionally, with the decrease in grassland globally, the existing grasslands are under pressure of both domestic and wild grazers. Moreover, seasonal rainfall in the semi-arid grasslands plays an important role in determining plant species composition and productivity and is becoming

increasingly variable (Rai & Raveh-Rubin, 2023). Hence knowing their combined effects on the grassland community will be helpful to understand the grassland community in the Anthropocene and guide sustainable management practices.

Materials and Methods

Study area: The study was carried out in Challakere, Karnataka situated in peninsular India (14.25 N, 76.75 E). The study site is in the mostly undeveloped Indian Institute of Science (IISc) campus, spread across 1500 acres characterized by grass, herbs and thorny shrubs. The dominant grass species are *Heteropogon* sp., *Aristida* sp, *Chrysopogon* sp (personal observation), which are native (POWO, 2026). The common shrubs are *Dodonaea viscosa*, *Albizia amara*, *Acacia leucophloea* and *Ziziphus spp* (Chandregowda et al., 2018). The peninsular region of India has been identified to be dominated by grass *Sehima* spp and *Dichanthium* spp (Dabadghao & Shankarnarayan, 1973).

Historically, the region was recognized as Amrit Mahal Kaval spreading across 1,00,000 hectares. It hosts a special breed of cattle named Amrit Mahal which is adapted to dry regions. After India's independence in 1947, the change in land use patterns reduced it to 30,000 hectares of fragmented grazed landscape (Kapuria, 2021) and it is continuing to decline (Aswatha, 2020; NGT 2014). The study area is currently grazed by domestic cows, goats and sheep, as well as wild deer and blackbuck (*Antelope cervicapra*).

Climatic conditions: The mean elevation is 733.9 m. The study region receives precipitation from southwest monsoon from July to September and northeast monsoon from October to December (Khan et al., 2020). The dry period extends from January through April. According to long term meteorological data, the mean maximum temperature is 36.2° C in April averaged

over the last 10 years. The mean minimum temperature recorded is 16.5° C in December. The average annual rainfall is 710 mm. During the growing season, the rainfall is 590.7 mm. (Abatzoglou et al., 2018). The annual variation in rainfall have shaped the land use patterns in these regions (A H Kumar Naik et al., 2026).

Study design: We identified three fenced sites in the study area, which were located at least 1 km apart. Due to the fencing, these sites have been ungrazed for the last 10 years. The fence height was more than 1.5 m at all three ungrazed sites to prevent the entry of large mammals. The region located outside of fenced ungrazed site is grazed by domestic livestock and wild animals, which we refer to as the grazed site.

In each of the grazed and long term fenced sites, we randomly selected 8 plots each of 1 meter square. These plots were separated from each other by at least 10-15 m and were at least 25-30 m from the fence, to reduce the edge effects. In the year 2023, we sampled two pairs of grazed and ungrazed sites, hence 32 plots sampled. In the year 2024, we sampled three pairs of grazed and ungrazed sites, hence 48 plots sampled. We did not have accurate data for the stocking rate and abundance of wild grazers, so we use above ground biomass as a proxy for intensity of grazing (Fulbright et al., 2023).

Data collection: Plant survey and sampling were performed during peak biomass growth season which falls between September and November depending on weather. In 2023 it was in late October and 2024 it was in mid-November. Much of the protocols for the plant survey and sampling and associated insect damage and disease incidences were adapted from Bugnet (Kempel et al., 2025). We have Bugnet plots in the same field site. Data collection was performed from 9:00 AM to 5:00 PM. The year 2023 had exceptionally low rainfall (327.36 mm) during the rainy season, and 2024 has slightly high rainfall (700 mm).

Plant sampling: The vegetation survey began with visual estimation of plant cover (to the nearest 1%) followed by recording the abundance of each plant species present in 1 x 1 m² plot. Plant abundance was noted for each species by manually counting. One individual of each plant species was collected (in a herbarium) for plant identification. In addition, the five plant species from each plot with the highest percent cover were selected in accordance with the protocol of Kempel et al., (2025) 10 individuals of these five abundant plant species were visually inspected for occurrence of invertebrate herbivory and pathogen infection. The invertebrate herbivory was classified as due to chewing, sucking, rasping, or mining. The pathogen incidence was classified as rust, downy mildew, and powdery mildew due to fungal pathogens and “leafspot” which could be due to fungal or other pathogens. Additionally, grazing marks were recorded on the plants in the grazed sites. 5 healthy individuals of the same plant species were used to measure plant traits. Plant height was measured in the field. We avoided plant individuals which were noticeably grazed while measuring height. This was followed by packing each plant in a zip lock bag with wet tissues and bringing them to the lab for further analysis (SLA, LDMC, leaf dry weight). Plants brought from the field were kept at 4°C in the lab and were analyzed within 7 days of collection in 2023. In 2024, the leaf sample was analyzed within 2 days of collection. The difference in analyzing days did not affect the end results. Leaf area, leaf fresh weight and leaf dry weight were measured on five leaves (or leaflets) from each plant individual, following the protocol of (Perez-Harguindeguy & Natalia, 2016). These measurements were used to calculate specific leaf area (SLA) and leaf dry matter content (LDMC) by the formula:

$$SLA = \frac{\text{Leaf surface area (mm}^2\text{)}}{\text{Leaf dry weight (mg)}}$$

$$\text{LDMC} = \frac{\text{Leaf dry weight (mg)}}{\text{Water saturated fresh mass (g)}}$$

Above ground biomass: Above ground biomass was measured by clipping above ground plant part in two strips of 10 x 50 cm each on the two outer sides of each plot. The plant material was collected in paper bags and kept at 70°C for 72 hours in a hot air oven before weighing. These plant samples were further ground to measure carbon (C) and nitrogen (N) using a CHNS analyzer.

Soil sampling: Soil was collected from the top 10 cm in each of the 32 (for the year 2023) and 48 plots (for the year 2024). The top 10 cm was chosen because that depth is most affected by local environment (Meena et al., 2020) and in a recent study by Bhan et al., (2024), no variation was reported in soil organic carbon when dug up to 30 cm deep. A shovel and pic-axe were used to dig down 10 cm deep because the soil was too rocky to use a soil corer. Soil was collected in the zip locks and brought to the lab for C and N analysis using CHNS (Carbon, Hydrogen, Nitrogen, Sulphur) elemental analyzer (TruSpec, Leco, USA till 2019; thereafter Elementar Analysensysteme, Germany). This machine uses high temperature combustion in an oxygen-rich environment and is based on the classical Pregl-Dumas method (Naidu et al., 2022).

Statistical analyses

All the data analysis has been performed using R 4.4.2 version (R Core Team, 2024). Mixed effect models were used where grazing conditions (grazed or ungrazed) and year (2023 or 2024) were fixed effects and site (climate, solar and third site) was a random effect. Data

transformation was performed where needed to meet the assumptions of homogeneity of variance.

Above ground biomass

We used a generalized linear mixed effect model (glmer) to analyze the effect of grazing condition and year (predictor variables) on biomass (log response variable). The predictor and response variable were linked through ‘log’ function. We used gamma error distribution based on the spread of the data and following the assumption of normality of residuals.

Vegetation cover and bare ground

We used generalized linear mixed model with template model builder (glmmTMB) for the analyses of percent cover by vegetation and % bare ground. Vegetation cover is taken independently for every plant species present in the plot and hence in some cases it can exceed 100% because of overlap between plant parts (Kempel et al., 2025). This is also why bare ground is not simply the inverse of cover. The vegetation cover and bare ground data were scaled to range between 0 and 1 to follow the assumption of beta regression. The analysis was performed using ‘beta’ distribution from glmmTMB package (Mollie E. Brooks et al., 2017). We looked at the effect of grazing condition and year (fixed effects) on vegetation cover / bare ground cover (response variables). The response and predictor variables were linked through ‘logit’ function. The same was followed for analysis of cover based on life history and functional group.

Plant community composition

To compare the community composition between grazing conditions and years, we used NMDS (Nonmetric Multi-Dimensional Scaling) plot in the ‘vegan’ R package (Oksanen et al.,

2025). The relative abundance of each species is taken into consideration in this analysis. Each site and treatment is treated as a group; hence there were 4 groups in the year 2023 and 6 groups in the year 2024. To statistically compare plant composition between grazing conditions and years, we carried out permanova analysis using *adonis2* function. For the post hoc analysis, we used Tukey HSD to perform pairwise comparisons.

To account for excess zeroes in the data due to many species only being present in some of the plots, we used the function *decostand* from *vegan* package. We used the Bray Curtis dissimilarity index to calculate the dissimilarity indices between every group. The stress value for the plot was 0.14 which shows that the rank of observed dissimilarity correlates well with the ordination distance.

Plant species richness and diversity

To analyze the overall species richness (response variable) with respect to grazing condition and year (predictor variable), we used a lmer model. An lmer model was also used to measure species richness based on life history (annual and perennial). To analyze species richness among functional groups (forbs, grasses and legume), the two years were analyzed separately because there was a very large difference in species richness between years. We used lmer with functional group and grazing condition as fixed effects in the year 2023. For the year 2024, species richness was square root transformed.

For plant diversity, we analyzed the effects of grazing condition and year on plant diversity (Shannon Weiner index) using lmer with ‘plant diversity’ as response ratio.

Plant traits

The three plant traits, height, LDMC and SLA, were measured. Because 2023 was much drier than 2024 the height, LDMC and SLA were extremely different and the distributions of the data were also different. Thus in order to effectively compare grazing conditions, we analyzed the two years separately for each of the three plant traits.

Height: We attempted to sample only plants without evidence of grazing or feeding damage however for some species we were not able to always find five whole mature individuals. Therefore, plant individuals with grazing incidence, apex of the shoot broken or non-flowering plant individuals, were excluded from the analysis (163 values removed). We also removed outliers from the data to reduce the effect of extreme values (121 values removed). From 3029 data points, we ended up with 2745 data points comprising 1422 in grazed and 1323 in ungrazed sites. For the years 2023, we analyzed the effect of grazing condition on the height of the plant community using the glmer model with 'gamma' distribution. Predictor and response variable were linked through the 'log' function. Post hoc analysis was carried out using the R package *lsmeans* (Russell V. Lenth, 2016). For 2024, the height data were not distributed normally so we used Kruskal Wallis test. A Post hoc test was carried out using the R package *dunn.test* (Alexis Dinno, 2024).

Specific leaf area (SLA): For the analysis we excluded non-mature plant individuals. We also removed outliers from the data to reduce the effect of extreme values. Overall, we used 1670 data points comprising 847 values in grazed and 823 values in ungrazed sites. Since the SLA data were not distributed normally in either year, a Kruskal Wallis test followed by post hoc test was carried out for each.

Leaf Dry Matter Content (LDMC): We have in total 1762 data points. Upon removal of outliers, 1755 data points comprising 891 values in grazed and 864 values in ungrazed were used for the

analysis. Again, the LDMC data were not distributed normally in both years, so a Kruskal Wallis test followed by post hoc test was carried out for each of the years.

Insect herbivore damage incidence

The damage data is binomial data with two values: 0 and 1. We used a glmer model with a binomial distribution. The predictor variables were grazing condition and year, with the response variables insect herbivore damage or disease incidence. The analysis for damage and disease incidence were performed separately.

Predictor and response variable were linked through the ‘logit’ function. To run this model, data was arranged in the required format with the help of function ‘gather’ from *tidyr* package (Hadley Wickham et al., 2024). Post hoc analysis was performed to estimate the pairwise comparison between damage incidences as a response variable and grazing conditions and year as a predictor variable using ‘lsmeans’ function from *lsmeans* package .

Disease incidence

The damage data is binomial data with two values: 0 and 1. We used a glmer model with a binomial distribution. The predictor variables were grazing condition and year, with the response variable disease incidence.

Predictor and response variable were linked through the ‘logit’ function. To run this model, data was arranged in the required format with the help of function ‘gather’ from *tidyr* package. Post hoc analysis was performed to estimate the pairwise comparison between disease incidences as a response variable and grazing conditions and year as a predictor variable using ‘lsmeans’ function from *lsmeans* package.

Nutrient stoichiometry

We analyzed plant C:N ratio using linear mixed effect models (lmer). The response variable C:N ratio was log transformed to follow the assumptions of normality. We also analyzed Carbon and Nitrogen % separately. C value was analyzed using lmer models. Due to a large difference in N value between the years, we analyzed each year separately. For 2023, lmer model was used with log transformation. In 2024, we used lmer models with N percent as response variable and grazing conditions as fixed predictor and site as random predictor.

To analyze the soil C:N ratio, lmer models were used with log transformation. Due to large difference in C:N between two years, we analyzed the data separately. For 2023, linear mixed effect models were used whereas for 2024, glmmTMB model was used with gamma error distribution.

Results

Above ground biomass

Above ground biomass was higher in ungrazed than in grazed sites in both years. In 2023, the above ground biomass was on average 5.33 g /0.1 m² (95% CI: 3.31-8.59) in grazed sites. It was 517% higher (estimate: 32.62, 95% CI: 20.30 - 52.44) in ungrazed sites. In 2024, the average biomass in grazed sites was 20.71/ 0.1 m² (95% CI: 13.38 - 32.06), and 201.54% greater in the ungrazed sites. Biomass also differed greatly between years, with a 257.48% higher biomass in the grazed sites in 2024 than in 2023.

Vegetation cover and bare ground

Plant cover was lower in grazed than in ungrazed sites in both years. In 2023, average plot cover was 0.28 m² (95% CI: 0.19 - 0.38) in grazed sites and 146 % (estimate: 0.692, 95% CI:

0.58 - 0.77) greater in ungrazed sites. In 2024, the cover in grazed site was 0.63 m² (95% CI: 0.52-0.75), and 1.03 m² (95% CI: 0.92 – 1.11) in the ungrazed site. The increase in plant cover between 2023 and 2024 was higher in grazed sites (by 125%) than ungrazed sites (by 49.27%). In 2023, average barren ground cover was 0.80 m² (95% CI: 0.73 – 0.86) in grazed and 0.24 m² (95% CI: 0.17 – 0.33). There was a decrease in barren ground cover in 2024 by 51.85% in grazed sites and 58.3% in ungrazed sites.

The vegetation cover by perennial plants increased between 2023 and 2024 (suppl table R 1.1). This increase was greater in ungrazed than in grazed sites (refer to suppl. Table R1) (Fig. 1).

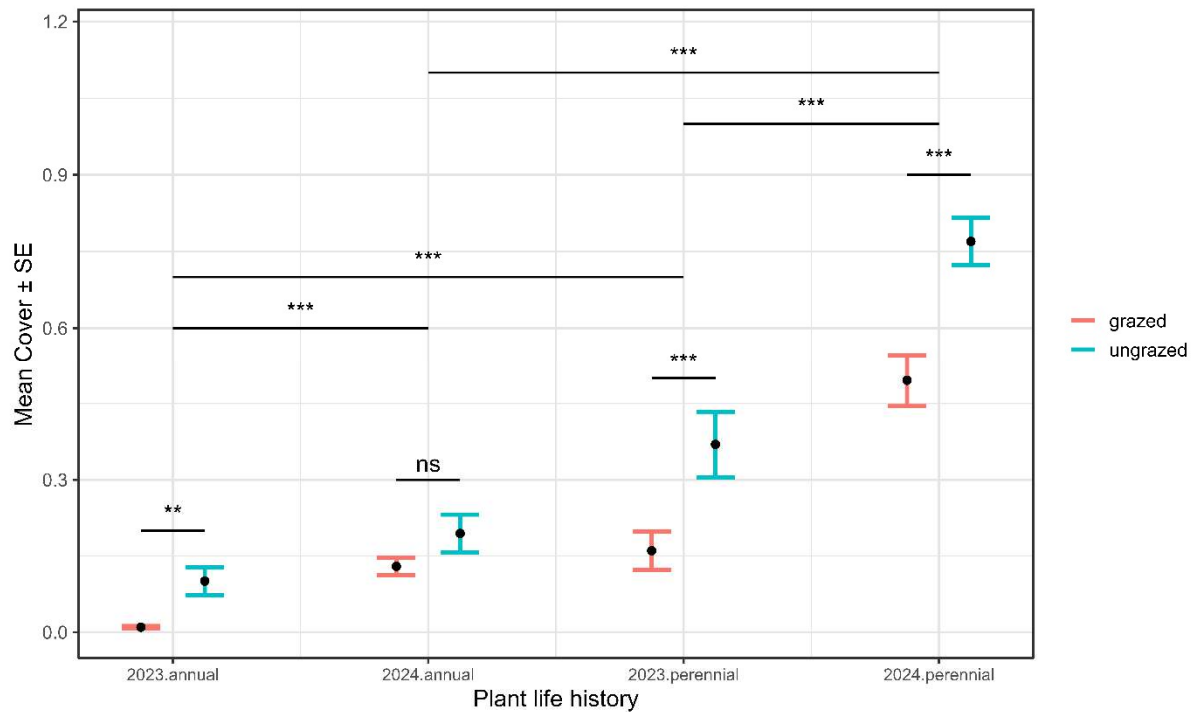


Fig. 1: Mean plant cover per plot plotted against life history of the plant in grazed and ungrazed sites. Mean values are plotted with error bar denoting standard errors. The horizontal bar below the asterisks represents the pairwise comparisons and asterisks denote statistical significance (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$). ns represents non-significant difference.

Grass has the highest cover among the functional groups in both the year 2023 and 2024 irrespective of grazing (suppl. table R 2). In 2023 forbs had the second highest cover of 0.07 (95% CI: 0.04 - 0.11) followed by legumes (cover: 0.04, 95% CI: 0.02 - 0.07) in the ungrazed sites. In 2024, the cover of forbs and legumes were equal (fig. 2).

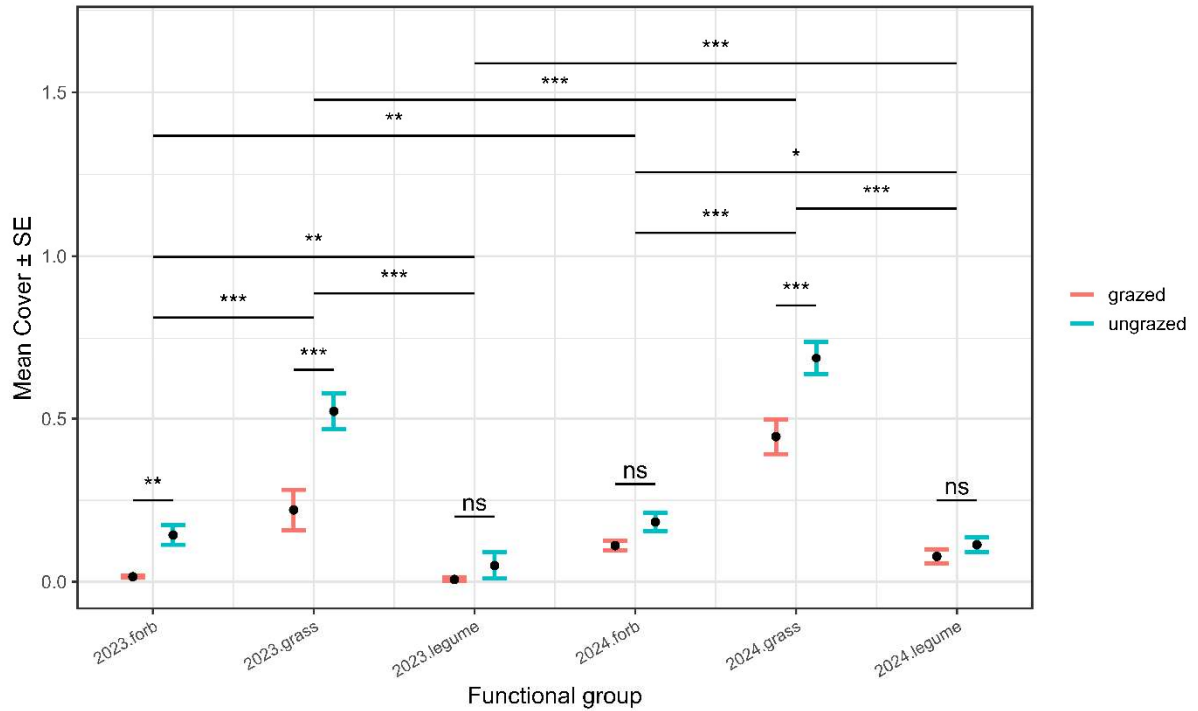


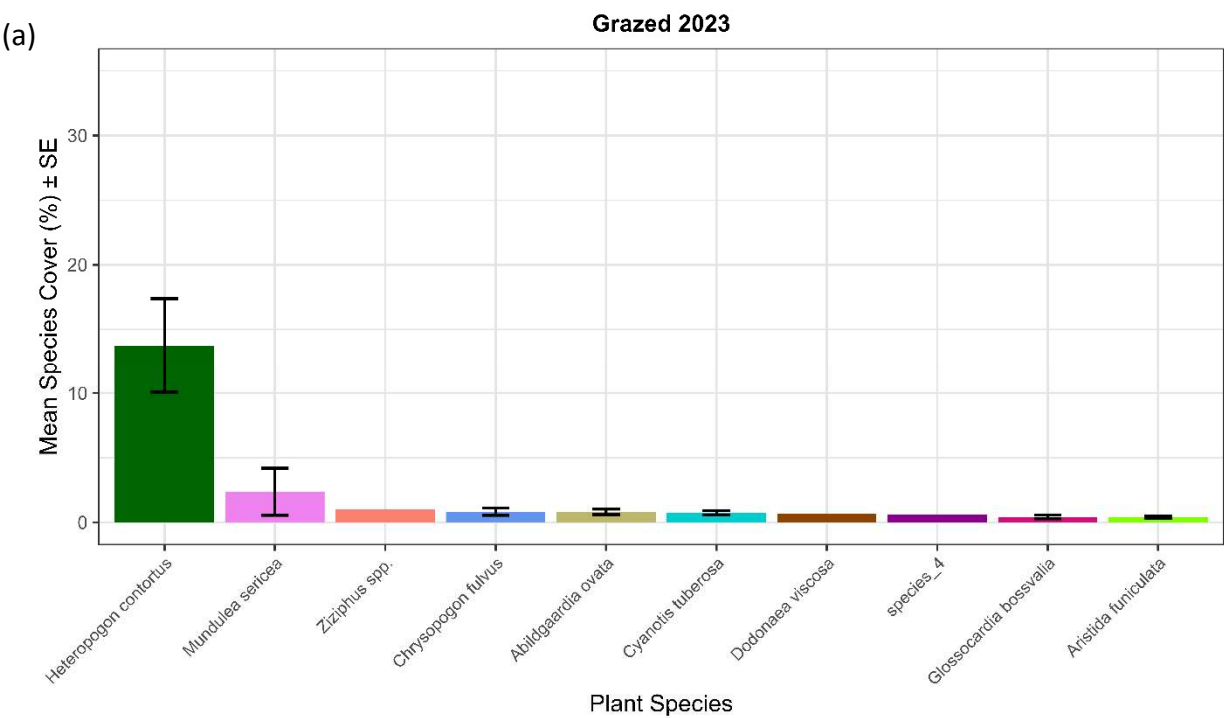
Fig. 2: Mean plant cover per plot plotted against functional group (grass, forb, legume) of the plant in grazed and ungrazed sites. Mean values are plotted with error bar denoting standard errors. The horizontal bar below the asterisks represents the pairwise comparisons and asterisks denote statistical significance (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$). ns represents non-significant difference.

Plant species composition: Species with highest cover

A total of 35 plant species from 14 different families were recorded in the year 2023 and 83 plant species from 25 plant families were recorded in the year 2024 (refer table R3.1, 3.2). The predominant plant family was Poaceae grasses. Of these plants there were only 6 invasive species (*Chromolena odorata* (Asteraceae), *Waltheria indica* (Malvaceae), *Phyllanthus*

amarus (Phyllanthaceae), *Euphorbia hirta* (Euphorbiaceae), *Senna uniflora* (Fabaceae), *Partheium hysteroportous* (Asteraceae)) (POWO, 2026) which were only found in low abundance.

In 2023, the plant species cover differed between grazed and ungrazed sites (Fig. 3a, b). In grazed sites, *Heteropogon contortus* had the highest cover (~13%) followed by shrub *Mundulea sericea* and *Ziziphus* sp covering almost 3%. In ungrazed sites, the grasses *H. contortus* and *Chrysopogon fulvus* had a cover of about 40%. This was followed by a mix of forb and legumes covering almost 30%.



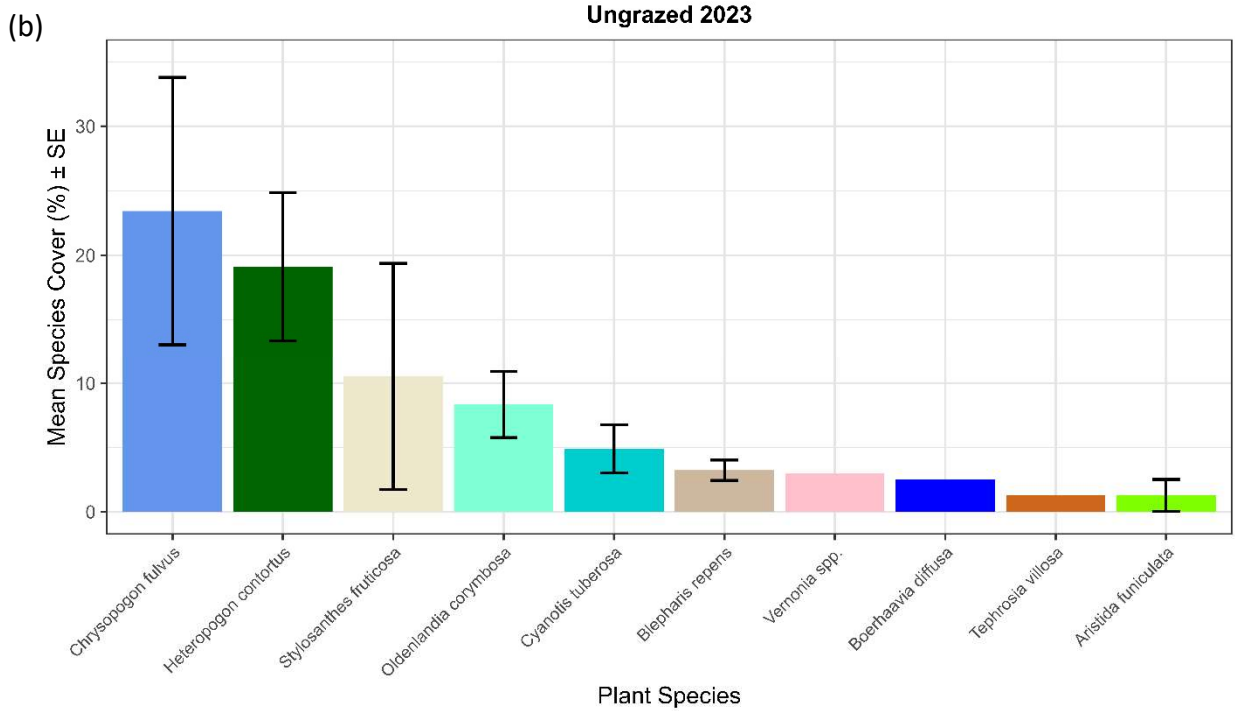


Fig. 3: The top 10 plant species with highest cover in 2023. (a) represents grazed sites. Mean values are plotted with error bar denoting standard errors. The plant species with one data point has no error bar. (b) represents ungrazed sites. Mean values are plotted with error bar denoting standard errors. The plant species with one data point has no error bar.

The cover of dominant plant species differed between grazed and ungrazed sites of the year 2024. (Fig. 4a, b). In grazed sites, the grasses *H. contortus*, *C. fulvus* and *Aristida setacea* have the highest cover (20 – 25%) with a mix of forbs and legumes covering around 5 – 7%. In ungrazed sites, the grasses dominated to a larger degree, with *H. contortus*, *Diectomis fastigiata* and *Dichanthium aristatum* covering 50 – 60%, and other plants covering around 10 – 12%.

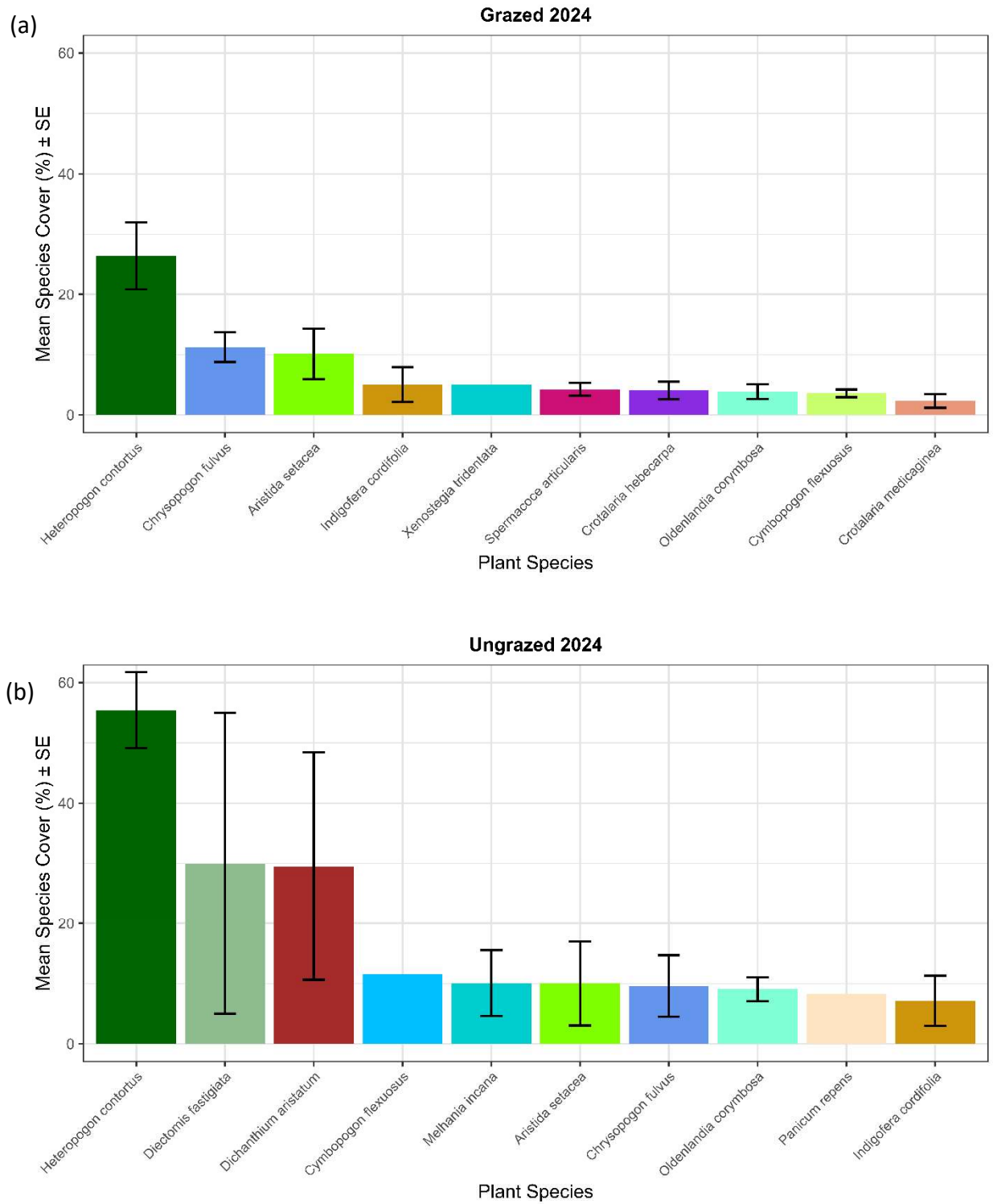


Fig. 4: The top 10 plant species with highest cover in 2024. (a) represents grazed sites. Mean values are plotted with error bar denoting standard errors. The plant species with one data point has no error bar. (b) represents

ungrazed sites. Mean values are plotted with error bar denoting standard errors. The plant species with one data point has no error bar.

Plant species composition: Species showing similarity

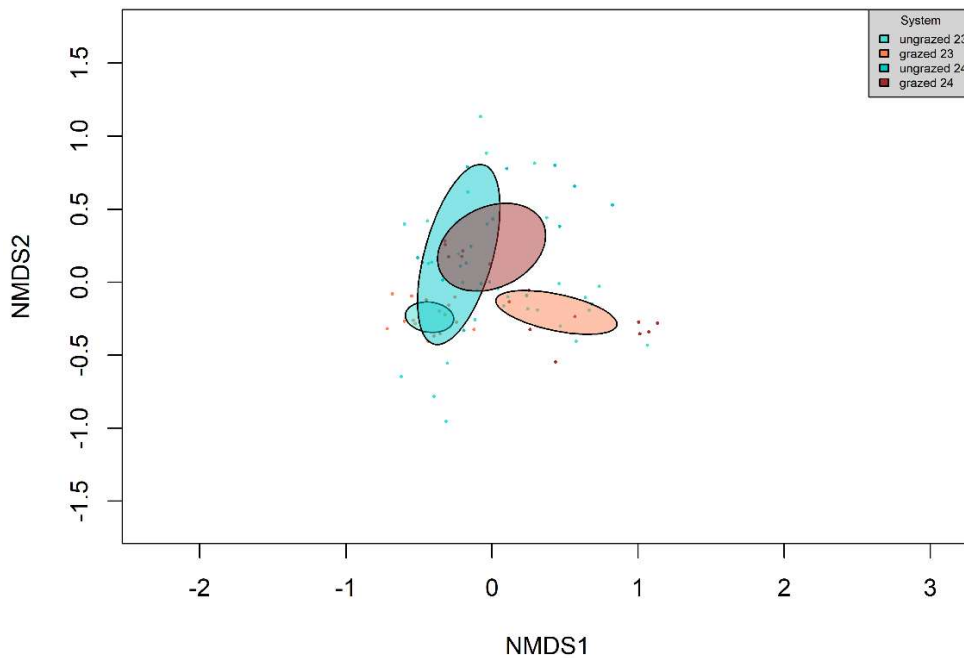


Fig. 5: NMDS plot showing similarity in plant species composition between grazed and ungrazed sites in both the years. Each dot represents plot in grazed and ungrazed sites. The ellipse covers the central spread of the data in both grazed and ungrazed sites in both the years. The closer the ellipse, more similar the plant species composition are. The axis does not hold any biological meaning.

Using multidimensional modeling it is evident that in 2023, species composition differed between grazed and ungrazed sites ($F = 9.315$, $p_{\text{adj}} = 0.03$). However, in 2024, grazed and ungrazed sites were similar ($F = 7.57$, $p_{\text{adj}} = 0.65$). The grazed sites differed between 2023 and 2024 ($F = 13.67$, $p_{\text{adj}} = 0.049$). But ungrazed sites in both years have similar plant species composition ($F = 10.72$, $p_{\text{adj}} = 0.45$; fig. 5).

Plant species richness and diversity

Overall, species richness was higher in 2024 (15.29 ± 0.61) than in 2023 (8.06 ± 0.4) irrespective of grazing (suppl. table R4). In 2023, the average plant species richness per plot was 8 (95% CI: 6.8 - 10.5) in grazed sites which was significantly greater than in the ungrazed sites (species richness: 6.54, 95% CI: 5.1 - 8.2). In 2024 richness increased to 16 in ungrazed sites (estimate: 16.21, 95% CI: 13.6 - 18.9) and 14 (estimate: 14.4, 95% CI: 12.0 - 16.8) in ungrazed sites with no significant difference (fig. 6).

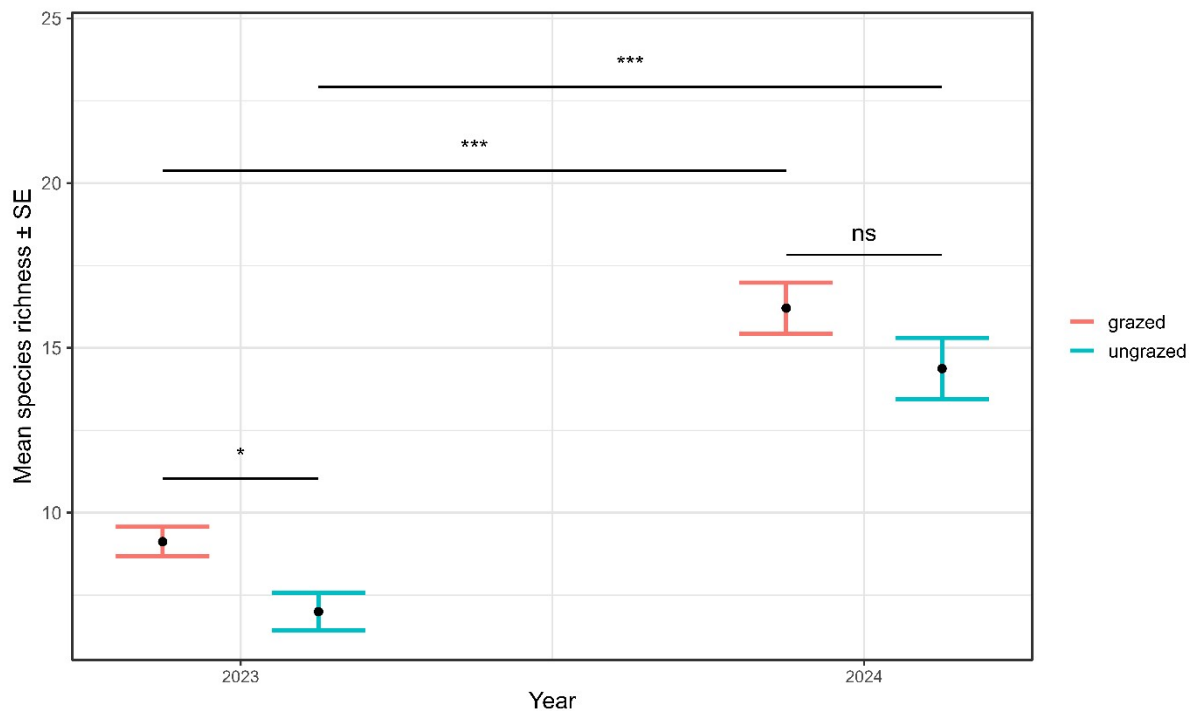


Fig. 6: Mean plant species richness plotted against grazing conditions. Mean values are plotted with error bar denoting standard errors. The horizontal bar below the asterisks represents the pairwise comparisons and asterisks denote statistical significance (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$). ns represents non-significant difference.

Perennials have higher species richness than annuals irrespective of years and grazing conditions. In 2023, annuals have an average of 2.7 (95% CI: 0.8 – 4.5) species richness per plot in grazed and 1.4 (95% CI: -0.3 – 3.25) in ungrazed sites. Perennials have a species richness

of 4.9 (95% CI: 3.1 – 6.7) in grazed and 3.5 (95% CI: 1.7 – 5.4) in ungrazed sites. In 2024, species richness of annuals increased to 6.54 (95% CI: 4.6 – 8.4) in grazed and 5.75 (95% CI: 3.9 – 7.6) in ungrazed sites. Perennials species richness increased to 10.1 (95% CI: 8.2 – 11.9) in grazed and 8.1 (95% CI: 6.3 – 9.9) in ungrazed sites.

The species richness of all three functional groups was higher in 2024 than in 2023 in both grazed and ungrazed sites (suppl table R 4.1, fig.7). Overall, forbs had the highest species richness in the year 2024. The species richness of grass was higher in grazed site by 89% (estimate: 5.2 units, 95% CI: 4.2 - 6.3) than ungrazed (estimate: 2.8 units, 95% CI: 2.2 - 3.7) sites in the year 2024.

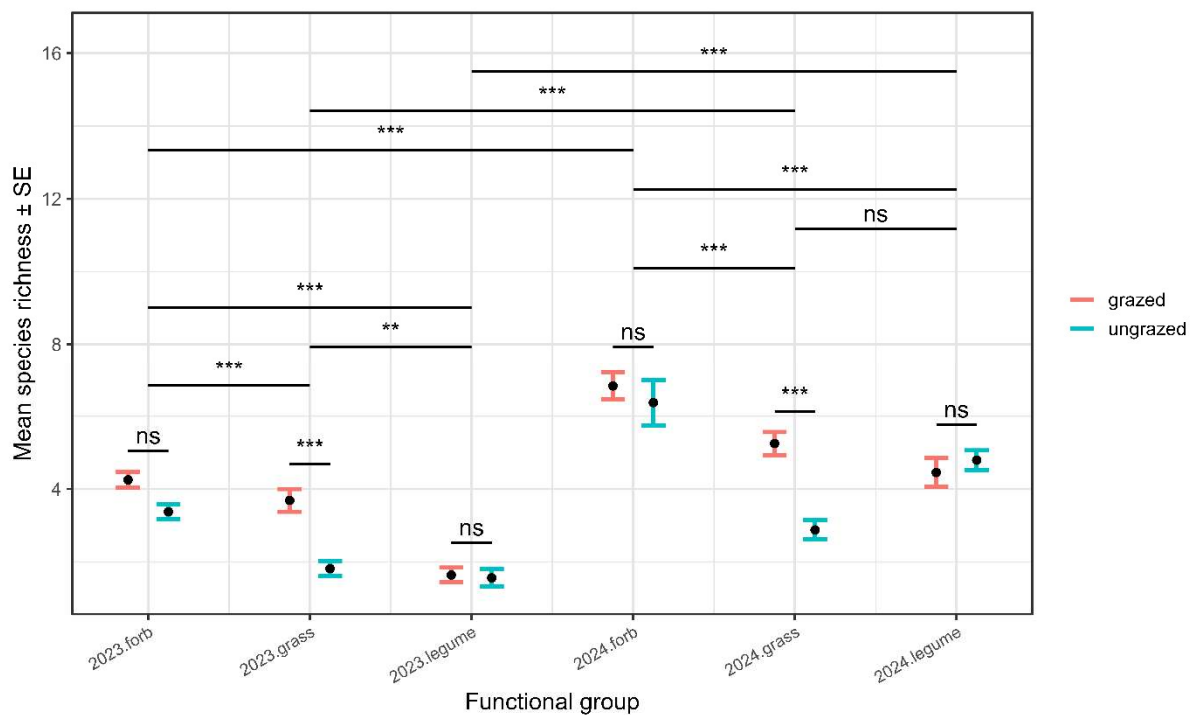


Fig. 7: Mean plant species richness of functional groups (forb, grass and legume) in grazed and ungrazed sites. Mean values are plotted with error bar denoting standard errors. The horizontal bar below the asterisks represents the pairwise comparisons and asterisks denote statistical significance (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$). ns represents non-significant difference.

Plant diversity as measured by Shannon Weiner diversity indices was similar in both years and did not differ between grazed and ungrazed sites. (Refer table R5, supplementary)

Plant traits

The plant traits measured were height, specific leaf area (SLA), and leaf dry matter content (LDMC). Plants were taller in 2024 than in 2023, and in both years the plants were also taller in ungrazed sites than in grazed sites (table R 6.1, 6.2, supplementary). In 2023, the average plant community height was 2.63 cm (95% CI: 2.44 - 2.84) cm and 9.83 cm (95% CI: 9.15 - 10.57) in grazed and ungrazed sites, respectively (fig. 8a). In 2024, the average community height increased by 792.08% in grazed and 221.30% in ungrazed sites (Kruskal Wallis chi-squared: 50.52, $df = 1$, $p = 1.77e-12$).

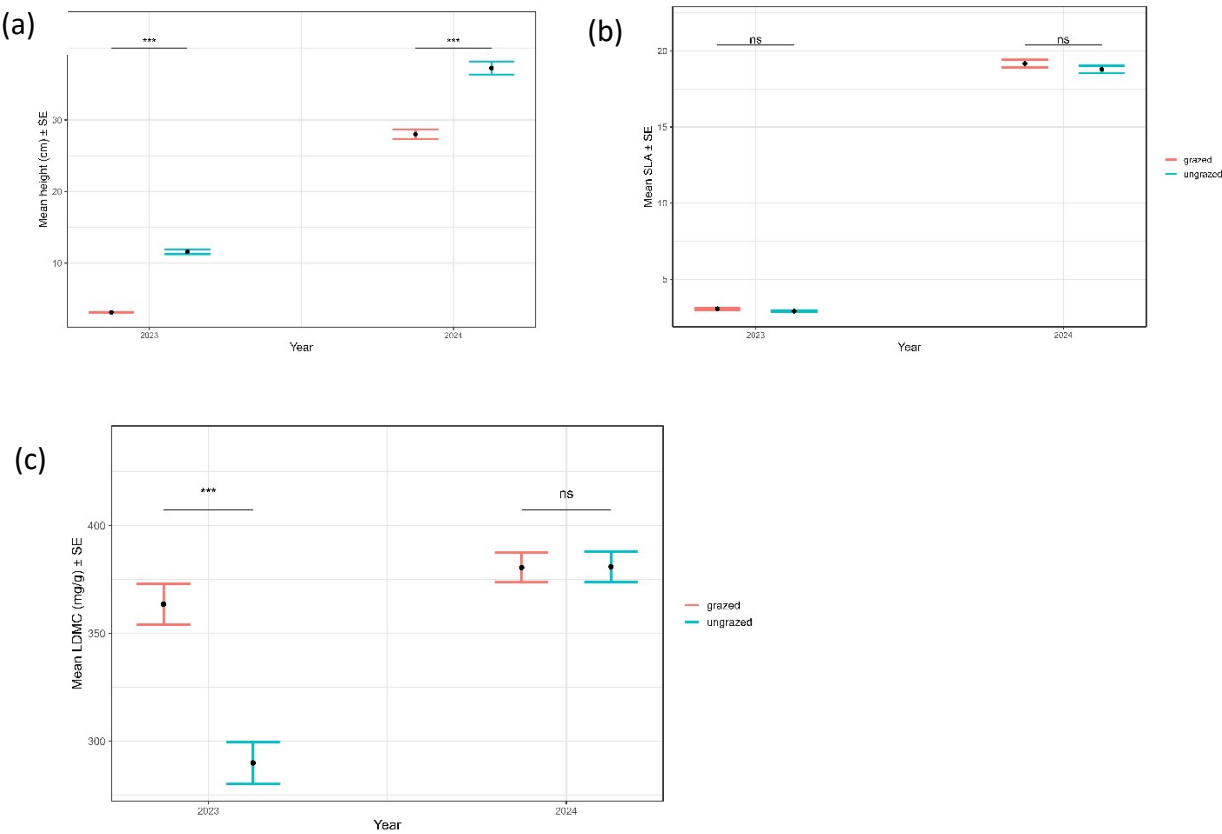


Fig. 8. Plant trait values in the grazed and ungrazed sites in 2023 and 2024. (a) Average plant community height, (b) Average SLA (specific leaf area) and (c) Average LDMC (Leaf Dry Matter Content). Mean values are plotted with error bar denoting standard errors. The horizontal bar below the asterisks represents the pairwise comparisons and asterisks denote statistical significance (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$). ns represents non-significant difference.

Overall, SLA was much higher in 2024 than 2023 but it did not differ between grazed and ungrazed sites (refer table R 6.3, fig. 8b). In 2023, LDMC was higher in grazed sites (Kruskal-Wallis chi-squared = 27.632, $df = 1$, $p = 1.467e-07$). But, in the year 2024, there was no difference between the grazing conditions (Fig. 8c; Kruskal-Wallis chi-squared = 0.019201, $df = 1$, $p = 0.8898$)

Incidence of insect damage on plants

Most of the plants experienced insect herbivory in both 2023 and 2024 (Fig. 9a). Incidence of insect herbivory was higher in 2023 (Grazed = damage: 0.90, 95% CI: 0.86 - 0.93; Ungrazed = 95% CI: 0.9, 95% CI: 0.85 - 0.93) than in 2024 (Grazed = 0.82, 95% CI: 0.76 - 0.87; Ungrazed = 0.85, 95% CI: 0.80 - 0.89) and did not differ between grazed and ungrazed sites.

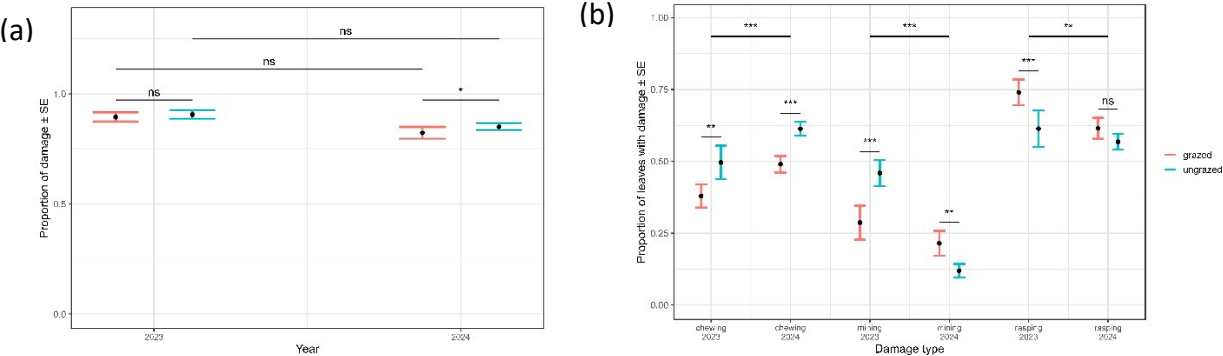


Fig. 9: The average percent of sampled plants in grazed in grazed and ungrazed plots in 2023 and 2024 damaged by (a) all insect herbivores; and (b) insect herbivores in different feeding guilds, chewing, mining and sucking or rasping. Mean values are plotted with error bar denoting standard errors.

Damage by sucking and rasping insects was highest followed by mining and chewing in both grazed and ungrazed sites of the year 2023. In 2024, the damage incidence followed the following pattern: sucking rasping > chewing in grazed sites and chewing > sucking rasping in ungrazed sites (Fig, 9b; table R 7.1, 7.2, supplementary).

Fungal disease incidence on plants

Evidence of fungal disease was found on 42 % of the plants. Disease incidence was much higher in 2024 than 2023 (Fig. 10a). In 2023, disease incidence in grazed sites was 0.04 (95% CI: 0.02 - 0.05). In ungrazed sites it was 200% greater (estimate: 0.09, 95% CI: 0.06 - 0.13). In 2024 about 43% of the plants in both grazed an ungrazed site exhibited disease.

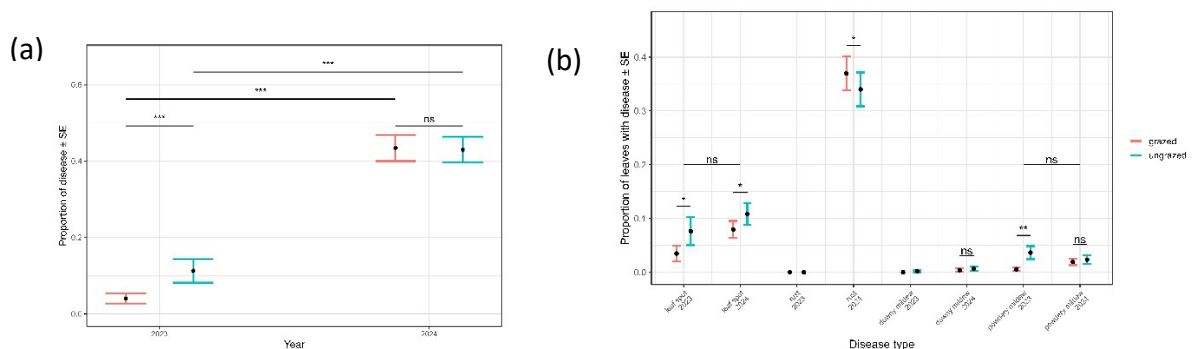


Fig. 10. The disease incidence of each year in grazed and ungrazed sites. (a) The mean percent of plants sampled that had evidence of any disease, and (b) The mean percent of plants sampled showing evidence downy mildew, leaf spot, powdery mildew and rust. Mean values are plotted with error bar denoting standard errors.

Among diseases, leaf spots were higher followed by powdery mildew (in grazed) and downy mildew (in ungrazed) respectively. Rust incidence was not present in grazed and ungrazed sites of 2023. Downy mildew was absent from plants of grazed sites in the year 2023 (Fig. 10b, refer

table R 7.2, supplementary). For the year 2024, the disease incidence followed the following pattern: rust > mining > leafspot > downy mildew and powdery mildew in grazed sites and rust > mining ~ leafspot > downy mildew ~ powdery mildew in ungrazed sites (refer table R 7.2, supplementary).

Plant nutrient stoichiometry

In the year 2023, C content was 2.2 g/kg (95% CI: 1.9 - 2.4) in the grazed and 3.22 g/kg (95% CI: 2.9 – 3.4) in ungrazed sites. In 2024, C content increased to 3.3 g/kg (95% CI: 3.1 – 3.5) in grazed and 3.5 g/kg (95% CI: 3.3 – 3.7) in ungrazed respectively. In 2023, N content was 0.05 g/kg and 0.07 g/kg in grazed and ungrazed sites respectively. In 2024, it increased to 0.17 g/kg in grazed (95% CI: 0.13 – 0.21) and 0.16 g/kg in ungrazed (95% CI: 0.12 – 0.19) sites respectively. N content was higher in the plant samples collected in 2024 than 2023. Consequently, the C:N ratio was higher in 2023 than 2024 under both grazed and ungrazed conditions (refer table 8, supplementary). In 2023, the grazed sites had C:N ratio of 3.83 g/kg (95% CI: 3.42 – 4.28) and the ungrazed sites had 4.26 (95% CI: 3.81 – 4.78). These decreased by 18% in grazed (estimate: 1.94, 95% CI: 1.79 – 2.11) and 16.8% (estimate: 2.26, 95% CI: 2.07 – 2.47) in ungrazed sites in 2024.

Soil nutrient stoichiometry

C content in 2023 was 0.06 g/kg in grazed and 0.05 g / kg in ungrazed respectively. In 2024, it increased to 0.26 g/kg and 0.06 g/kg in grazed and ungrazed sites respectively. N content increased in the year 2024. In 2023, N content was 0.009 g /kg in grazed and 0.011 g/kg in ungrazed sites. In 2024, N content increased to 0.12 g / kg in grazed and 0.04 g /kg in ungrazed sites.

We found that soil C: N ratio was higher in the year 2023 than in 2024 in grazing conditions but did not differ between the sites. In grazed site, 2023 has a C:N ratio of 6.36 (95% CI: 4.9 - 8.16) which decreased by 81% (estimate: 1.2, 95% CI: 0.95 - 1.51) in 2024. In an ungrazed site, 2023 has a C:N ratio of 5.03 (95% CI: 3.9 - 6.4) which decreased to 24.65% (estimate: 1.24, 95% CI: 0.99 - 1.56) in 2024.

Discussion

We investigated a semi-arid grassland plant community under heavy grazing by wild and domesticated animals and in fenced long term ungrazed conditions, over two years that differed in the amount of rainfall. The year 2023 had lower than average rainfall and the year 2024 had higher than average rainfall. We found a total of 99 species of grasses and herbs, with no abundant invasive plants. Grazing by wild ungulates and livestock decreased the above-ground biomass and vegetation cover. The community responses to grazing and rain were different for different functional groups (forb, grass and legume).

We also investigated how grazing and rainfall affected community level plant fungal disease infection and insect herbivory. Disease incidence was low in grazed sites, where plant cover was low, but there was no difference in invertebrate damage incidence between the grazed and ungrazed sites.

Results show that grazing decreases homogeneity in plant species in two years. Homogeneity here refers to the number of plant species that are common between grazing conditions. In the year when rainfall was high, the difference in plant community between grazed and ungrazed sites decreased, which was due to the grazed plant community becoming similar to the ungrazed plant community increasing the homogeneity in plant

species. Chen et al., (2018) found that rainfall increased plant species richness and cover of perennial plants, irrespective of grazing, showing that plant species richness are more dependent on environmental factors than on grazing pressure.

Plant biomass and cover

As expected, grazing decreased above ground plant biomass and cover. While this is not always the case in mesic grasslands where moderate grazing may result in compensatory growth (Penner & Frank, 2021), previous studies of semi-arid grasslands have this pattern (J. Zhang et al., 2017). This was true in both the dry and the rainy years. In both the years, cover by grass was higher than forbs and legumes. This is expected in semi-arid grasslands due to the low water requirement of grasses (Hai et al., 2022), and the long history of grazing, which makes grass species resistant to grazing (Adler et al., 2004). Among the three plant functional groups, in the wet year, cover of forbs was much lower in grazed than in ungrazed sites. This difference may have arisen due to forbs being chosen by grazers (Huang et al., 2026). In the dry year, both forbs and legume had a much lower cover in grazed than ungrazed sites (89% and 85% lower respectively), compared to the grass cover, this could again be due to a higher grazing on forbs and legumes and lower availability of biomass in that year.

Plant community composition

Community composition can differ due to availability of resources such as water and space (Rota et al., 2017) and interspecific competition leading to physical dormancy of some seeds and affecting survival of seeds. It can differ between the grazed and ungrazed sites due to preferential consumption of plants by grazers and interspecific competition in

ungrazed sites as seen in most of the grassland studies (Koerner et al., 2018; Zainelabdeen et al., 2020). Plant species composition strongly differed between grazed and ungrazed sites especially in the low precipitation year. In the dry year, *Sehima spp.* and *Dichanthium spp.* was not recorded in both grazed and ungrazed sites, despite the region being known for the abundance of these two grasses. In the wet year, *Dichanthium aristatum* was present in the top 10 highest covering plant species. *Heteropogon contortus* dominated grazed and ungrazed sites in the year 2024. In 2023 the grazed sites had the most *Heteropogon contortus* whereas ungrazed sites had *Chrysopogon fulvus*. The abundance of these two grasses over *Sehima* and *Dichanthium* suggests the shift in vegetation from more palatable grass to least palatable grass because of overgrazing (Vinay Kumar et al., 2024). *H. contortus* and *C. fulvus* are less palatable grasses due to presence of awns and their abundance over other palatable grasses could also affect the survival of other endangered fauna in the long run (Vinay Kumar et al., 2024). Grazed site also had a significant number of forbs. In ungrazed sites, grass was followed by forbs which were followed by legumes. This could be attributed to selective grazing (Wan et al., 2015), plant competition (Zainelabdeen et al., 2020) and lack of water, which leads to difference in species composition between grazed and ungrazed sites.

With increasing rain, plant species composition in the grazed and ungrazed sites became more similar, mostly due to changes in the grazed plant community. This greater change in the grazed site may be because with higher biomass, grazing pressure declined, and because seeds dormant in the seed bank may have germinated in response to high rainfall, and were able to grow without competition in the relatively open grazed area. While most of the difference was in the grazed sites with rain, the highest cover in the ungrazed sites became the grass *Heteropogon contortus*.

Plant species richness and diversity

Grazing can lead to an increase in plant species co-existence due to reduction of interspecific competition between plants (Koerner et al., 2018). This could have resulted in plant species richness in the low precipitation year (2023) being higher in the grazed than ungrazed site in 2023. Increase in species richness as a response to grazing is prevalent in temperate grasslands of Europe (Dvorský et al., 2022; Schneider & Hering, 2024) and Serengeti ((Anderson et al., 2007). Animal excreta also may serve as small germination hotspots for plants (Gokbulak & Call, 2004).

In the higher precipitation year (2024), species richness was much higher than in 2023 and did not differ between grazing conditions. This could be attributed to germination of physically dormant seeds and low mortality of seeds and seedlings in the year under wetter conditions. This is contradictory to the findings of Fulbright et al., (2023) who found only a weak positive correlation between species richness and precipitation in semi- arid grassland, and is instead more like what occurs in arid grassland where richness responds strongly to annual rainfall (Chen et al., 2018).

With the increase of rainfall and plant species richness, plant diversity also increases (Sun et al., 2019) which is contradictory to our findings. However, in the sites with long evolutionary history of grazing, plant diversity decreases in grazed sites (Price et al., 2022).

Plant species diversity depends on resource availability (water and nutrients) and evolutionary history (Milchunas et al., 1988). In low productive sites such as arid and semi-arid grasslands, grazing herbivores have been found to have neutral to negative effects on plant diversity (Mathewos et al., 2023) due to long evolutionary history of grazing which makes the plants adapted to grazing (Milchunas et al., 1988) similar to what we found. We

did not find any difference in diversity between grazing conditions and years which could be attributed to the above-mentioned reasons.

Plant traits

Grazing often brings heterogeneity to plant community composition, which was also reflected through plant traits because plant community height was smaller in grazed compared to ungrazed sites. In this study, we measured specific leaf area (SLA), leaf dry matter content (LDMC), and height of plants. In the grazing system of arid grassland, plants have previously been found to have high LDMC with low SLA to increase the lifespan of leaves, reduce palatability due to high dry matter (Garnier et al., 2007; te Beest et al., 2021). SLA represents plant investment in leaves, which is positively related to the plants photosynthetic rate, and is expected to have positive relation to water availability (Wilcox et al., 2021) and grazing (Zheng et al., 2015) but see (S. X. Zheng et al., 2010). SLA values for the year 2024 were higher and for 2023, it was lower than those in other studies performed in semi-arid grassland (9.06 mm² /mg in grazed to 13.96 mm² /mg in ungrazed for 10 years, (An et al., 2025), 5.37 mm² /mg to 4.54 mm² /mg from lower to higher grazing intensity, (Bär Lamas et al., 2013)). This suggests that at the community level photosynthetic rate is limited by rainfall in a semi-arid grassland. The difference in SLA between two years could have also arise due to increase in plant species with the acquisitive strategy which could have resulted in higher SLA in rainy year (Díaz et al., 2001).

While at the community level, SLA was much higher in 2024 than 2023, it did not differ between grazed and ungrazed sites in either year, despite the differences in plant species composition, cover, and biomass. The difference in SLA between the years could be related to the difference in plant resource allocation. In high resource environment, such

as mesic grasslands of Europe and N. America, plant species show grazing tolerance, in which they rejuvenate tissue lost to grazing (Zheng et al., 2015) which was also seen in our results when the rainfall was higher. In 2024, plants in arid system may have maintained SLA under grazing because of the high-water availability. However, in low resource environment, which is observed in arid and semi-arid grasslands, plant species also show grazing avoidance mechanism where they develop structural (e.g., thicker leaf, trichomes or hair on leaves) and chemical defense associated with grazing (te Beest et al., 2021). These alternative mechanisms of resource use strategy need further investigation.

As mentioned by M. A. R. K. Westoby (1999), in low grazing conditions, plants with higher SLA are preferred than the plants with lower SLA due to large leaves providing better bite size for grazers and including less stem material compared to plants with lower SLA. However, in highly grazed environment with annual variation in rainfall, grazing intensity and specificity towards any plants is regulated by the available biomass (M. Westoby, 2016) and hence, mostly, every species gets grazed which results in lower SLA which we also found in our field site. Due to lower biomass and lower SLA, grazed plants don't have energy reserves to compensate for the loss of tissue due to grazing which have been found in some other semi-arid regions (te Beest et al., 2021), resulting in lower SLA. At the same time in ungrazed sites, plant species due to aridity would have reduced investment in above ground biomass resulting in lower SLA and altogether no difference in SLA between grazed and ungrazed sites.

LDMC measures density of plant tissue (Gitelson et al., 2014) and hence it serves as an important functional trait for plant resource use strategy (Kurze et al., 2021). Higher LDMC leads to low water and nutrient retention in leaves (Poorter & Markesteijn, 2008).

LDMC values ranged from 289 mg/g in the dry year to 380 mg/g in the wet year. These values were much lower than the values obtained from plants in another semi-arid climate (609 mg/g in ungrazed, 548.3 mg/g in grazed, (Z. Wang et al., 2021). The low dry matter content in the grassland suggests very low investment in leaves, perhaps due to adaptation to the long history of grazing (Vuorinen et al., 2021). Lower LDMC also indicate shift of species from conservative resource use traits to acquisitive traits (Niu et al., 2016) whereas higher LDMC suggests leaves with higher longevity (Garnier et al., 2001) especially seen in low grazed conditions.

In grassland communities, tall herbaceous plant individuals are accessible to grazers, and short stature is associated with lower grazing, favoring short stature plants where grazing is common (Díaz et al., 2007). At the same time, competition among plants for light can lead to the evolution of tall grassland plants (Coley et al., 1985). In 2023, the mature plants in the grazed community were much shorter than in the ungrazed community. This may be the result of both shorter plant species persisting, and low regrowth under heavy grazing, which can be an avoidance mechanism by plant species to avoid consumed by grazers (Díaz et al., 2007). In 2024, plants in both communities were taller, with less difference between grazed and ungrazed sites. The increased height was likely due to water availability. Since biomass was high there was also lower per capita grazing risk.

Overall, we found that in dry year, plant height, SLA and LDMC was lower than what has been observed in other semi-arid grasslands. These findings suggest that plant community due to aridity and grazing switched to conservative resource use strategy where they modified their plant traits to decrease the chances of being grazed. With increase of rain, plant height and SLA was higher and LDMC was lower when compared to other semi-arid grassland studies. The change in plants traits with increase of rainfall suggests that rainfall increased the availability

of water which semi-arid grassland plants always lack of, and it also switched the plant community trait towards acquisitive resource use strategy to obtain maximum resource use which is a characteristic of plants under heavy grazing.

Plant and soil Carbon and Nitrogen

In our study, plant and soil C:N ratio was higher in 2023 than in 2024. This was due to higher nitrogen in both plants and soil in 2024. N fixing plants had significantly higher cover in 2024 than 2023, which may have increased the levels of tissue N hence lowering the community level plant C:N ratio, as found in other grassland studies (Spehn et al., 2002) Plant C:N value reported in our study site was higher than the values reported from another semi-arid climate (3.019 in ungrazed, 6.514 in grazed; X. Gao et al., 2023) but lower than the mesic grassland (23.59 in grazed, 34.26 in ungrazed; Bai et al., 2012).

Grazing has been found to decrease plant and soil C:N ratio through consumption of nutritious plants and altering plant community composition (Bagchi & Ritchie, 2010). We did not find that the soil C:N ratio differed between the grazed and ungrazed sites. This may be due to different processes taking place in each condition. In grazed sites, mineralization of N in the form of dung and urine may increase the availability of N in the soil and be available to the plants (Zacheis et al., 2002). Ungrazed sites have high biomass, and more N was allocated in stems and leaves (Qiu et al., 2013) than roots due to interspecific competition. These two processes may lead to no difference in C:N ratio of plants. No difference in soil C:N ratio could also reflect the long evolutionary history of grazing which could have made the grassland tolerant to grazing. However, we did not find any literature supporting this theory.

The Soil C:N ratio was much lower in our study compared to other arid and semi-arid

regions (6.97 and 6.028 in grazed and ungrazed respectively; (K. Wang et al., 2016), 12.53 in grazed and 17.98 in ungrazed respectively; (Wang et al., 2014) and also from mesic grassland (11.6 in grazed and 11.3 in ungrazed; (Pineiro et al., 2009). This dissimilarity could be due to differences in plant species composition with the change in topography or the difference in microbial community regulating the decomposition processes.

Insects herbivory and fungal disease

Insect herbivores affect grassland plant biomass and community diversity and composition (Stein et al., 2010). Further, grazing can affect insect herbivore community, mostly negatively, through their effects on plant community composition and biomass (Olff & Ritchie, 1998). Finally, the interaction of grassland plant and insect communities is affected by water availability (Tamburini et al., 2018). 75% to 85% of the plants were damaged irrespective of grazing. However, insect damage incidence was higher on legumes in grazed sites and on grass in ungrazed sites in the year 2024. A high damage incidence on legumes could be because of its palatability acting as good N source (Sheaffer et al., 2009). We scored incidence of damage by chewing, mining, galling, and sucking and rasping insects separately. Sucking and rasping type damage was the most prevalent. This type of damage is caused by thrips (Thysanoptera), sucking Heteroptera such as pentatomid bugs, and Homoptera such as leaf hoppers and aphids. Damage incidence on plants was lower in 2024 than 2023 which could be due to increase in biomass due to rain which reduced per capita damage on the plant individuals, especially since the year before (2023) the insect community may have been small since plant biomass was small.

Incidence of plant disease can be affected by grazing through reduction of plant biomass, and its effect on plant community composition (Y. Liu et al., 2022). Rainfall also affects

plant disease, generally increasing its incidence (Hu et al., 2025). We found fungal disease incidence to be greater in the ungrazed than the grazed sites, which could be due to higher plant biomass hence a larger disease population (Termorshuizen, 2016), and potentially more spread of disease due to physical contact (but see (Douma & Noordhoek, 2025)). The similar pattern was also seen by (P. Zhang et al., 2025) in semi-arid grassland. Fungal disease incidence was also higher in the year with higher rainfall, in both grazed and ungrazed sites. This is as expected because rainfall increased plant density, and because the rain and local humidity facilitate spread of fungal disease, and has been shown in semi-arid steppe grassland of China (G. Li et al., 2025).

In 2023, disease incidence was higher on legume than on grass in ungrazed sites. Legumes are rich in nitrogen which increases their preference towards grazing by mammals and invertebrates (Singh et al., 1997). Grazing exposes inner plant cells which also increases the vulnerability towards fungal pathogens, which could increase disease incidence (Daleo et al., 2009). Additionally, high nitrogen plant tissue is often infected by biotrophic pathogens (rusts, powdery mildews) that feed on living cells (Mitchell et al., 2003). In the year 2024, disease incidence was higher on grass followed by legumes and forbs in ungrazed sites which is similar to Yang et al., 2024. This could be due to increase in density of host plants and proximity between them which facilitates the spread (Burdon & Chilvers, 1982), but see (Douma & Noordhoek, 2025).

Our results suggest that rain plays a crucial role in replenishing the adverse effects of grazing as found in other semi-arid regions such as the Serengeti grasslands of S. Africa and Mongolian grasslands in China (Zhong et al., 2019). In these regions, rain serves as a limiting factor for plant growth (Knapp et al., 2001; Wilcox et al., 2015), playing a crucial

role in determining plant community biomass, plant species composition, richness (Chen et al., 2018; Wilcox et al., 2015) and plant traits (M. Liu et al., 2019).

Conclusions

In this study, we found that plant community composition in grazed and long term ungrazed sites are very different, with both equally rich and diverse. Similar results have been seen in other semi-arid rangelands (Milchunas & Lauenroth, 1993). This suggests that ecosystem functioning driven by grazing would be related to the replacement of some species by others with different functional traits (Díaz et al., 2001; Tilman & Downing, 1994) rather than affecting the number of species. Grazing also reduced biomass in grassland which may reduce the spread of fungal pathogens and hence lower disease incidence on plants. We also found that rainfall plays an important role in determining the species richness in these grasslands. This coincides with other findings that changes in species' richness is more dependent on environmental factor (changes in temperature or precipitation) than on grazing pressure (Pizzio et al., 2016). Rainfall also served to make grazed and ungrazed sites more similar. Rainfall also reduced per capita invertebrate damage on plant individuals, perhaps due to increase in productivity and biomass of the grassland.

The semi-arid grassland plant community is extremely dependent on rainfall. In this study we saw a year of low rain and low species richness, with extreme low biomass under grazing conditions. Species richness was brought back by rain, to conditions similar to where grazers were excluded. As climate change alters the Indian monsoon, making more extreme and variable annual conditions (Rai & Raveh-Rubin, 2023), we can expect a loss

of species diversity, even among these plants that are adapted to both an arid environment and grazing, if there are sequential years of low rain when grazing is high.

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