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Grazing intensity alters the plant diversity-ecosystem carbon storage relationship in rangelands across topographic and climatic gradients

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Conflict of interest
The authors declare that they do not have any conflict of interest. Emma J. Sayer is a Senior Editor and Hugo Saiz is an Associate Editor of Functional Ecology, but both took no part in the peer review and decision-making processes for this paper**.**

Data Availability
The data that support the findings of this study are openly available on Figshare at: https://doi.org/10.6084/m9.figshare.21835896 (Sanaei et al., 2023)

Abstract

1. Plant diversity supports multiple ecosystem functions, including carbon sequestration. Recent shifts in plant diversity in rangelands due to increased grazing pressure and climate changes have the potential to impact the sequestration of carbon in arid to semi-humid regions worldwide. However, plant diversity, grazing intensity and carbon storage are also influenced by environmental factors such as nutrient availability, climate, and topography. The complexity of these interactions limits our ability to fully assess the impacts of grazing on biodiversity-ecosystem function (BEF) relationships.

2. We assessed how grazing intensity modifies BEF relationships by determining the links between plant diversity and ecosystem carbon stocks (plant and soil carbon) across broad environmental gradients and different plant growth forms. To achieve this, we surveyed 1493 quadrats across 10 rangelands, covering an area of 23,756 ha in northern Iran.

3. We show that aboveground carbon stocks increased with plant diversity across topographic, climatic and soil fertility gradients. The relationship between aboveground carbon stocks and plant diversity was strongest for forbs, followed by shrubs and grasses. Soil carbon stocks increased strongly with soil fertility across sites, but aridity, grazing, plant diversity and topography were also important in explaining variation in soil carbon stocks.

4. Importantly, aboveground and soil carbon stocks declined at high grazing intensity, and grazing modified the relationship between plant diversity and carbon stocks regardless of differences in abiotic conditions across sites.

4. Our study demonstrates that relationships between plant diversity and ecosystem carbon stocks persist across gradients of aridity, topography, and soil fertility, but the relationships are modified by grazing intensity. Our findings suggest that potential losses in plant diversity under grazing intensification could reduce ecosystem carbon storage across wide areas of arid to semi-humid rangelands. We discuss the potential mechanisms underpinning rangeland BEF relationships to stimulate future research.

Keywords: Biodiversity-ecosystem function; carbon storage; climate change; grazing intensity; rangeland plants; soil fertility; topography

1. Introduction

Biodiversity loss associated with climate change, invasive species, and land-use intensification can dramatically affect terrestrial ecosystem functions (Allan *et al.* 2015), including their capacity to store carbon in plants and soils (Yang *et al.* 2019). Understanding biodiversity-ecosystem function (BEF) relationships, such as the links between plant diversity and ecosystem carbon storage, is becoming increasingly important for determining the impacts of global changes (Eisenhauer *et al.* 2016). Several studies have demonstrated a strong relationship between plant diversity and aboveground carbon stocks (Loreau *et al.* 2001; Xu *et al.* 2020), because plant diversity increases biomass through the functional complementarity or asynchronous performance of different species, which enhances overall ecosystem productivity (Tilman *et al*. 2014). In addition, plant diversity can promote soil carbon storage (Maestre *et al.* 2012; Yang *et al.* 2019) by increasing soil microbial activity through biomass production and litter inputs (Eisenhauer *et al.* 2010; Scherber *et al.* 2010; Lange *et al.* 2015). Hence, a positive relationship between plant diversity and soil C stocks might be expected if diversity enhances plant growth and increases the quality and quantity of plant litter inputs, which underpin soil biogeochemical cycles and soil C storage (Wardle *et al.* 2004; Macdonald *et al.* 2018). Moreover, accumulating evidence indicates that the BEF relationship varies considerably with both climate and soil (Grace *et al.* 2016). For example, variation in precipitation and temperature determine water availability and growing season length, which can alter biodiversity (McLaughlin *et al.* 2017) and thereby affect ecosystem functioning (García *et al.* 2018). Soil nutrient availability might be particularly important in shaping the relationship between plant diversity and carbon storage at smaller scales because nutrient availability promotes biomass production and microbial activity (Macdonald *et al.* 2018), and complementary nutrient use by a diverse plant community could enhance overall soil carbon storage (Hobbie 1992; Tilman *et al.* 2001). However, other environmental factors such as soil properties and topography could also play an important role (Hobley *et al.* 2015), because plant species with distinct growth forms and root systems may develop on different soil types (Eckhart *et al.* 2010). Topography further shapes plant communities by influencing water availability, evapotranspiration, and nutrient accumulation (Sebastiá 2004). Hence, to fully understand the impacts of global changes on ecosystem functioning, we first need to characterize BEF relationships and determine how they are influenced by the abiotic environment (van der Plas 2019).

Although recent research suggests that BEF relationships may be stronger in drier climates (Ratcliffe *et al.* 2017), they have been largely explored in temperate grasslands, shrublands and forests (reviewed by van der Plas 2019) but are under-characterized in arid systems (Grace *et al.* 2016). In arid and semi-arid regions, rangelands are one of the dominant ecosystems occupying about half of the total land area (Allen *et al.* 2011). Rangelands play an important role in the livelihoods of millions because they support multiple ecosystem services and functions including water uptake, nutrient cycling, and food production (Lund 2007). However, rangelands are also under great threat from increasing aridity as a result of climate change, and from increased grazing intensity to provide food for a growing global population (Ash *et al.* 2012; McCollum *et al.* 2017). Reduced plant species diversity associated with increased aridity and grazing intensification in arid and semi-arid rangelands might also have a strong negative impact on both plant and soil carbon stocks in these culturally and economically important ecosystems (Sitters *et al.* 2020). Indeed, declining plant diversity with lower water availability is already thought to be reducing the capacity of rangelands to store carbon (Vandandorj *et al.* 2017). Given the potential impact of both climate change and livestock grazing on plant diversity and species composition (Eldridge *et al.* 2016, 2018; Gaitán *et al.* 2018), understanding how changes in plant diversity will influence important ecosystem services such as carbon storage is essential for ensuring that rangeland ecosystems can be managed sustainably.

Grazing of rangelands by livestock provides food and income to millions of people but also dramatically alters plant species diversity and ecosystem carbon storage (Eldridge *et al.* 2018; Sanaei *et al*. 2018; Zhou *et al.* 2019). Livestock grazing can influence plant and soil conditions through biomass consumption, trampling, and addition of nutrients in dung and urine (Hoffmann *et al.* 2016; Lu *et al.* 2017; Sanaei *et al*. 2018), but the extent of the impacts depend upon grazing intensity and frequency, local climate, and the type of plant community (Bai *et al.* 2012; Eldridge *et al.* 2016). Declining plant and soil carbon stocks with grazing can be attributed to the consumption of plant biomass by animals, changes in plant species composition, and reduced carbon allocation to roots (Maestre *et al.* 2016; Zhou *et al.* 2017). Nonetheless, grazing can also promote species competition and, according to the intermediate disturbance hypothesis, the highest plant species diversity might be found at intermediate grazing intensity (Huston 1979), which may promote carbon storage. However, grazing intensity is also linked to abiotic conditions (Mysterud *et al*. 2007; Homburger *et al.* 2015) and topography, because access by livestock can be limited in areas with steep slopes and at higher elevations (Mysterud *et al*. 2007). Hence, although grazing intensity is likely to affect ecosystem carbon storage by altering plant diversity, the impacts could vary considerably over different spatial scales and environmental gradients (Bai *et al.* 2012; Sanaei *et al*. 2019; Souther *et al.* 2019).

Here, we investigated the relationships between plant diversity and ecosystem carbon storage in rangelands by surveying 1493 quadrats across 10 rangeland sites in Northern Iran. Our study aimed to assess 1) whether ecosystem carbon storage is related to plant species diversity, 2) how ecosystem carbon storage differs among sites with distinct abiotic conditions (aridity, topography and soil nitrogen) and 3) whether the relationship between plant diversity and carbon storage is modified by grazing intensity. We hypothesized that (H1) rangeland ecosystem carbon storage (aboveground biomass and soil carbon stocks) would increase with plant species diversity but decline with grazing intensity; (H2) although plant diversity, ecosystem carbon storage and grazing intensity are influenced by abiotic site conditions, the relationship between carbon storage and diversity or grazing would persist across broad environmental gradients; but (H3) differences in the relationship between plant species diversity and carbon storage would be explained by grazing intensity, regardless of site conditions.

2. Materials and Methods

2.1. Study area and vegetation sampling

The study was carried out across 10 natural rangelands in the arid, semi-arid, and semi-humid regions of northern Iran, spanning 33°00´-39°00´ N in latitude, and 45°00´-54°00´ E in longitude (Table 1; Figure S1). No permits were required to conduct fieldwork at the sites. Although small areas within these rangelands have previously been cultivated, most of the land has been freely grazed for at least 20 years. The elevation of the study area ranged between 309 and 3255 m above sea level, and the slope of the sites ranged between 1 and 68%. Mean annual precipitation, mean annual temperature and potential evapotranspiration ranged from 186-796 mm, 3.5-16.5 °C, and 1291-2089 mm, respectively. Thus, the sites spanned a total area of 240 km^2, an elevation gradient of c. 2900 m, a rainfall gradient of almost 800 mm, and were located on several different soil types, including loam, clay loam, sandy loam, silt loam, and sandy clay loam. Soil nitrogen and phosphorus concentrations ranged from 0.01-0.46% and 1-89 mg kg^{-1}, respectively.

We surveyed a total of 1493 quadrats (1 m^2 each) across the 10 rangeland sites during the peak growing seasons of 2014 to 2018 (Table 1). A random-stratified sampling design was used across the study area and within sites, and quadrats within each site were located at least 12 m apart (range: 12-1000 m; Hirzel & Guisan 2002). To identify links between plant diversity, grazing and ecosystem carbon stocks, we identified all plant species occurring in each quadrat to species level and assigned them to one of three growth forms: shrubs, forbs or graminoids (henceforth 'grasses'). We did not subdivide forbs into nitrogen-fixing and non-nitrogen-fixing species because the number of nitrogen-fixing species was very low across all study sites. The studied rangelands included arid (two sites), semi-arid (six sites), and semi-humid (two sites) rangelands based on the United Nations Development Programme classification (UNDP 1993) and the total number of plant species at a given site varied from 29 to 237 (Table 1), and across all sites, we identified 16,283 individuals of 567 plant species. In semi-humid rangelands, the most dominant species were: *Psathyrostachys fragilis* (Boiss.) Nevski, *Festuca ovina* L. and *Bromus tomentellus* Boiss. Semi-arid rangelands were dominated by *Thymus kotschyanus* Boiss. & Hohen., *Bromus tomentellus* Boiss. and *Astragalus* spp. Finally, in arid rangelands the most dominant species were *Salsola laricina*, *Stipa hohenackeriana* Trin. & Rupr. and *Artemisia sieberi* Besser. For each quadrat we calculated the Shannon's diversity of the whole plant community and each plant growth form, based on species richness and relative cover, using the *vegan* package (Oksanen *et al.* 2018) in R 3.6.1 (R Development Core Team 2019).

2.2. Aboveground and soil carbon stocks

To quantify aboveground carbon stocks, aboveground biomass was measured by destructively harvesting all individual plants within each quadrat, oven-drying them to constant mass, and weighing them to obtain dry aboveground biomass. The aboveground biomass of each individual plant was multiplied by average biomass carbon content (0.47; Viglizzo *et al.* 2019), and then summed across all plant individuals within each quadrat to estimate total aboveground carbon stocks in g C m^{-2}. Aboveground carbon stocks were calculated separately for each species and plant growth form (i.e., shrubs, forbs, and grasses).

To estimate soil carbon stocks, we took one soil sample to 0-10 cm depth in each quadrat. The soil samples were weighed, sieved (2-mm mesh) and dried to constant weight at 105 ºC; particles larger than 2-mm diameter were weighed separately for calculation of soil carbon stocks. Soil bulk density was calculated as the mass of oven-dried soil divided by its volume (Blake & Hartge 1986). We measured the soil organic carbon concentration (g kg^{-1}) in each sample using the acidified dichromate ($K_2Cr_2O_7$–H_2SO_4) oxidation method (Lu 1999), and then calculated the soil carbon stock according to Equation 1:

$$SOC_{stock} = (1 - G_i) \times h \times D_i \times C_i / 100 \quad \text{(Equation 1)}$$

Where, SOC_{stock} is the soil organic carbon stock (kg m^{-2}), G_i is the coarse sand (> 2 mm) fraction (%), h is the soil depth (10 cm), D_i is the bulk density (g cm^{-3}), and C_i is the organic carbon content (g kg^{-1}), we then converted soil organic carbon stocks to g C m^{-2}. Finally, as a measure of soil fertility, we analyzed soil nitrogen for each quadrat using the Kjeldahl method (Bremner 1996).

2.3. Topography, aridity, and grazing intensity

For each quadrat, elevation was recorded by handheld GPS and slope was extracted from digital elevation models. To account for climatic variation across the study region, we calculated the aridity index (AI) using mean annual precipitation and potential evapotranspiration data in the CRU TS4.01 database (University of East Anglia Climatic Research Unit; Harris & Jones 2017); we extracted these data at *c.* 1 km^2 spatial resolution to account for differences among quadrats at large sites. The AI was then calculated as the mean annual precipitation divided by potential evapotranspiration, and aridity was expressed for each quadrat as 1-AI, such that high values indicate arid sites and low values indicate humid sites.

Grazing intensity for the area around each quadrat was quantified following general recommendations for assessing rangeland condition (Parker 1954; Mannetje & Jones 2000), which are currently used in freely-grazed rangelands in Iran (Talebi *et al.* 2021). We used multiple visual indices, such as the influence of grazing on plants (removal of biomass by livestock), signs of livestock trampling, distance from watering sources, resting areas or villages, and rangeland conditions, drawing on local experts' knowledge as well as our own observations, to classify all quadrats into three levels of grazing intensity: 1) low grazing intensity; 2) moderate grazing intensity; and 3) high grazing intensity (Table S1). See Table 1 for a summary of the variables for each site.

2.4. Statistical analyses

To explore the potential linkages between plant diversity, ecosystem carbon storage, and grazing across sites differing in aridity, topography, and soil nitrogen (H1 and H2), we tested an initial conceptual model (Figure 1) using piece-wise structural equation modeling in the *piecewiseSEM* package (*psem function;* Lefcheck 2016) in R version 3.6.1 (R Development Core Team 2019). Piecewise SEM provides the means to account for hierarchically structured data (i.e. multiple quadrats sampled within each site) using random effects in mixed-effects models. We fitted separate linear mixed-effects models (LMM) to each of the paths in our conceptual model. We modeled carbon stocks as a function of topography, aridity, soil nitrogen, grazing intensity and plant diversity, with quadrat nested within site as a random intercept effect (1|site/quadrat), using the *lme* function in the *nlme* package (Pinheiro *et al.* 2021). The nested sampling design accounts for potential pseudoreplication (and thus spatial auto-correlation) by pooling the interaction variance with the main effect of variance of the nested factor (Schielzeth & Nakagawa 2013). We then used pSEMs to incorporate multiple hypotheses and mechanisms into a single model, while accounting for differences in the number of sampled quadrats per site by considering the quadrats nested within rangeland sites as a random intercept effect. Thus, the pSEMs join multiple LMMs into a single model to estimate the effects of both random (quadrat nested within site) and fixed (measured variables) factors on the response variables. We also included an error term to account for unexplained variance due to the correlation between aboveground and soil carbon storage.

We constructed a model for the whole plant community (all species), as well as individual models for each plant growth form. We tested pSEMs with the following hypothesized paths: 1) Topography influences aridity, soil nitrogen, grazing intensity, and Shannon's species diversity; 2) Aridity influences soil nitrogen and grazing intensity; 3) Aridity and soil nitrogen influence Shannon's species diversity; 4) Grazing intensity influences soil nitrogen and Shannon's species diversity; and 5) All abiotic and biotic variables together influence carbon storage. We incorporated grazing intensity as an ordinal categorical variable coded as 1 (low), 2 (intermediate) and 3 (high) as recommended by (Rosseel 2012; Grace *et al.* 2016). To aid interpretation, we also constructed individual pSEMs based on the whole plant community for each grazing level separately. We used Fisher's C statistic and the associated P-value to evaluate the model fit to the data, where $P > 0.05$ indicates that the pSEM is an acceptable fit. By joining multiple LMMs into a single model, the pSEM calculates the conditional R^2 (R^2_c), which considers the variance explained by both fixed and random effects, and marginal R^2 (R^2_m), which only considers the variance explained by fixed effects for each response variable (Nakagawa & Schielzeth 2013; Lefcheck 2016). Hence, the difference between R^2_c and R^2_m represents the variance explained by the random factor 'quadrat nested within site' (henceforth 'site') in our models. We used the directional separation test (d-separation test) to determine whether missing paths between measured variables should be included in the pSEM. We then selected the best model based on the lowest Akaike Information Criterion (AIC). To make effect sizes comparable, all continuous variables (i.e., excluding grazing intensity) were standardized (Z-score transformation) before pSEM analysis (Gelman *et al.* 2020). To complement the results from the pSEMs, we subsequently conducted Pearson's correlations to assess bivariate relationships between tested variables (Figure S2) for each hypothesized path (Figures S3-S6).

To infer how each variable contributes to differences in plant diversity or ecosystem carbon stocks, we calculated effect sizes and the proportion of variation explained. As pSEMs do not provide individual values for indirect and total effects, we calculated them manually for each response variable. Indirect effects were calculated by synthesizing all direct pathways that link two variables through a mediator, and total effects were calculated by summing all direct and indirect effects connecting two variables (Grace 2006). We then calculated the relative contribution of each explanatory variable to aboveground or soil carbon stocks from the ratio between the standardized regression coefficient of a given explanatory variable from the LMMs and the sum of all coefficients of all explanatory variables. Finally, to test whether the relationship between plant diversity and carbon stocks differs among levels of grazing intensity (H3), we used linear mixed-effects models including plant diversity, carbon stocks and their interactions with grazing intensity as fixed effects, and quadrat nested within site as a random effect using the *nlme* package (Pinheiro *et al.* 2021). The R^2_m and R^2_c values for each model were calculated using the *MuMIn* package (Bartoń, 2018). A significant interaction term indicates a change in the relationship between plant diversity and carbon stocks with grazing intensity. Thus, the pSEMs and associated correlations reveal the linkages between plant diversity, carbon stocks and grazing intensity (H1), while accounting for the influence of site characteristics on plant diversity, carbon stocks and grazing intensity (H2). Regression analyses then specifically test whether grazing intensity modifies the relationship between plant diversity and carbon stocks across all sites (H3).

We note that differences in the relationships among environmental variables (aridity, topography, and soil fertility) in the final pSEMs for individual plant growth forms were largely due to differences in the number of quadrats in which species of each growth form were present (1120, 1478 and 1307 quadrats for shrubs, forbs and grasses, respectively), and we thus only present the relationships among environmental variables for the whole plant community. As it is not possible to formally compare the paths between individual pSEMs in our study, we use the standardized regression coefficients for a given path to compare the strength of relationships among plant growth forms as an aid to interpretation.

3. Results

All measured variables varied substantially across the 10 rangeland sites. Overall, the sites with the lowest overall plant species diversity also had the lowest aboveground carbon stocks, but sites with intermediate plant species diversity tended to have the highest soil carbon stocks (Table 1). In support of our first hypothesis, carbon stocks in aboveground biomass and soil increased with plant species diversity and declined with grazing intensity across rangelands (Figures 2a and S3).

Aboveground carbon stocks was strongly related to species diversity for all three individual plant growth forms (Figures 2b-d and 3) but the relationship was strongest for forbs (Figures 3 and S4-6). The species diversity of the whole plant community and all plant growth forms was highest at intermediate grazing intensity (Figures S3-S6) and thus the pSEMs showed only decline in species diversity of grasses with grazing intensity (Figure 2). Nonetheless, aboveground carbon stocks declined with grazing intensity for the whole plant community and all plant growth forms (Figures 2 and 3) but the relationship was stronger for grasses than for shrubs and relatively weak for forbs (Figures 2 and 3).

Interestingly, soil carbon stocks were only related to plant diversity across the whole plant community (Figures 2a and S7b) but not within individual plant growth forms (Figures 2c,d and 3). Soil carbon stocks declined with grazing, but the effect was much weaker than for aboveground carbon stocks. Nonetheless, the relationship between grazing and soil carbon stocks was significant for all plant growth forms (Figures 2 and 3).

Influence of climate, topography, and soil fertility

In support of our second hypothesis, differences in plant diversity, aboveground carbon stocks, soil carbon stocks and grazing intensity were associated with aridity, topography, or soil nitrogen. Site (the random factor) explained a large proportion of variation (R^2_c - R^2_m) in the tested hypothesized paths, indicating that the relationships among variables were highly site-specific (Figure 2). Nonetheless, our model accounted for significant variation in soil nitrogen (R^2_m= 0.25-0.35; R^2_c= 0.97-0.99), Shannon's diversity (R^2_m= 0.08-0.15; R^2_c= 0.91-0.95), aboveground carbon stocks (R^2_m= 0.15-0.27; R^2_c= 0.93-0.96) and soil carbon stocks (R^2_m= 0.07-0.39; R^2_c= 0.98-0.99; Figure 2). Across sites, aridity declined with slope but increased with elevation, whereas soil nitrogen increased with both slope and elevation, but declined with aridity. Grazing intensity for the whole plant community and all plant growth forms was lower at steep sites (Figure 2) but increased with increasing elevation (Figure 2a). Grazing intensity also declined with aridity for the whole plant community, but increased with aridity for grasses (Figure 2a,d).

The relationships between species diversity and environmental factors differed strongly among growth forms. The species diversity of all plant growth forms except grasses increased with aridity; the increase was strongest for the whole plant community, followed by forbs and shrubs (Figure 2). The diversity of shrubs and grasses increased with elevation (Figure 2b,d) but the species diversity of forbs declined (Figure 2c). The diversity of the whole plant community and forbs increased with slope (Figure 2a,c), but there was no relationship between slope and the diversity of grasses or shrubs.

The relationships between aboveground carbon stocks and environmental factors also differed markedly among plant growth forms. Aboveground carbon stocks declined with elevation for the whole plant community and shrubs, but increased with elevation for forbs increased (Figures 2a,b,c and 3a). Aboveground carbon stocks also increased significantly with slope for the whole plant community and grasses (Figures 2a,d and 3a), but not for shrubs or forbs. Finally, aboveground carbon stocks were not related to soil nitrogen for the whole plant community (Figures 2a and 3), as aboveground carbon stocks in grasses increased significantly with soil nitrogen but declined in shrubs and forbs (Figures 2b-d and 3a).

The relationships between soil carbon stocks and most environmental factors were consistent across all plant growth forms. Soil carbon stocks increased with slope and soil nitrogen but declined with elevation (Figure 2). However, soil carbon stocks declined with aridity for the whole plant community, but there were no significant relationships between soil carbon stocks and aridity for the individual plant growth forms (Figure 2).

Overall, variation in aboveground carbon stocks was largely explained by plant species diversity, followed by grazing intensity and topography, but the proportion of variation explained differed among plant growth forms (Figure 4). Notably, grazing explained more variation in aboveground carbon stocks in grasses than in shrubs and forbs, but plant diversity alone nonetheless explained 48% of the variation in aboveground carbon stocks in forbs (Figure 4). By contrast, most of the variation in soil carbon stocks across all plant groups was explained by soil nitrogen, grazing and topography. Interestingly, plant diversity explained ≤5% of the variation in soil carbon stocks but grazing explained 22%-34% of the variation (Figure 4). Aridity explained *c*. 26% of the variation in soil carbon stocks for grasses (Figure 4), but only 6% and 10% of the variation in soil carbon stocks for shrubs and forbs, respectively.

Grazing modifies the relationship between plant species diversity and carbon stocks

Linear mixed-effects model regression revealed strong relationships between plant diversity and carbon stocks, which differed among levels of grazing intensity (significant grazing × plant diversity interactions for aboveground and soil carbon at p <0.001; Figure 5). Although site (R^2_c- R^2_m) explained 90-97% of variation in plant and soil carbon stocks, the interaction between plant diversity and grazing (R^2_m) explained 3-14% (Figure 5a,b). Thus, grazing altered the relationship between plant species diversity and carbon stocks across sites.

Aboveground and soil carbon stocks were significantly positively associated with each other (Figure 5c). Site explained 94% of the variation in the relationship between aboveground and soil carbon stocks. However, the relationship between aboveground and soil carbon stocks was nonetheless modified by the interaction between grazing intensity and plant carbon stocks (p <0.001; Figure 5c).

4. Discussion

Our study demonstrates that ecosystem carbon storage increases with plant diversity in natural rangelands across broad climatic and topographic gradients (H1 and H2), and that the relationship between plant diversity and aboveground or soil carbon stocks is modified by grazing intensity (H3; Figure 5). Thus, our findings for rangeland sites add considerably to previous studies demonstrating that ecosystem carbon stocks are related to plant species diversity in natural ecosystems (Steinbeiss *et al.* 2008; Grace *et al.* 2016; Sanaei *et al*. 2018; Yang *et al.* 2019). Importantly, the linkages between plant diversity and carbon stocks, and the impacts of grazing intensity, differed among plant growth forms. Here, we discuss how the relationships among variables measured in our study reveal the potential mechanisms by which biotic and abiotic factors might shape plant diversity and carbon storage in rangelands.

Ecosystem carbon storage is related to plant diversity and modified by grazing

A strong overall relationship between plant diversity and carbon stocks is often attributed to higher plant productivity through temporal, spatial or functional niche complementarity (Tilman *et al.* 2001), which would also enhance inputs of plant-derived carbon to the soil (Caldeira *et al.* 2001; Steinbeiss *et al.* 2008; Yang *et al.* 2019). In support of our first hypothesis, regression analysis revealed that ecosystem carbon stocks generally increased with plant diversity across sites (Figure 5a,b), confirming the pSEM analysis results that revealed strong direct linkages between plant diversity and aboveground or soil carbon stocks (Figure 2a). Differences in species' niches and resource use in diverse plant communities can lead to facilitative interactions and enhance plant growth and aboveground biomass (Tilman *et al.* 2001). Greater productivity of diverse plant communities in turn boosts soil carbon stocks (Chen *et al.* 2018; Yang *et al.* 2019), which is indicated by the clear relationship between aboveground and soil carbon stocks in our study (Figure 5c). Thus, the relationship between plant diversity and soil carbon stocks is mediated by plant productivity (Chen *et al.* 2018; Yang *et al.* 2019).

The relationship between soil carbon stocks and plant diversity can be largely attributed to the high proportion (63%) of perennial species at our study sites. The relationship between soil carbon stocks and the diversity of the whole plant community (Figures 2a and 3b) but not individual plant growth forms (Figure 2b-d), reflects the fact that most quadrats included several plant growth forms. Differences in soil carbon storage therefore cannot be attributed to the species diversity of individual plant functional groups. Nonetheless, our results are supported by experimental work demonstrating that functional diversity may be more important for carbon storage than species diversity *per se* (van der Plas 2019; Chen *et al.* 2020). Functional plant diversity, such as that provided by different plant growth forms, can enhance soil carbon storage through functional complementarity of litter traits, which provides a wider range of resources to support microbial activity (Chen *et al.* 2019a; Chen *et al.* 2020) and greater belowground carbon inputs (Fornara & Tilman 2008). Plant communities with higher species diversity and including different growth forms are likely to have greater productivity, root biomass and litter inputs, resulting in larger soil carbon stocks (van der Plas 2019). Thus, the functional diversity afforded by different plant growth forms likely explains the strong linkage between the diversity of the whole plant community and carbon stocks in our study.

The low plant diversity and carbon stocks in quadrats with high grazing intensity demonstrate the impact of grazing on biodiversity and ecosystem carbon storage (Zhou *et al.* 2019; Sanaei *et al.* 2021). Livestock grazing not only directly influences plant diversity and carbon stocks through removal of aboveground biomass (Milchunas *et al*. 1988; Eldridge *et al.* 2016), but also indirectly through trampling (Schrama *et al.* 2013). Attrition of plant species that are sensitive to grazing or trampling would explain the reduced plant diversity we observed at the highest grazing intensity, as resistant species with better defenses become dominant (Ritchie *et al*. 1998; Bai *et al.* 2012). Our results demonstrating that high grazing intensity substantially reduces plant biomass and soil carbon stocks are consistent with previous findings (Lu *et al.* 2017; Sanaei *et al*. 2019; Zhou *et al.* 2019). However, the differences in overall plant diversity among grazing intensity levels were small (Figure S3). As our study assessed grazing intensity based on observations at a single time-point, the impacts of grazing on plant diversity and aboveground carbon stocks will depend partly on how recently a given quadrat was grazed. Nonetheless, in support of our third hypothesis (H3), we revealed that grazing modifies the relationships between plant diversity and aboveground or soil carbon stocks (Figure 5a,b).

Our regression analyses revealed a significant interaction between grazing and plant diversity, which indicates that selective biomass removal by livestock probably accounts for the shifts in the relationship between plant diversity and aboveground carbon stocks at different grazing intensities (Figure 5a). For example, the strong negative impact of grazing on aboveground carbon stocks in grasses (Figure 3) reflects the importance of grasses as forage plants for livestock in rangelands, whereas the lack of grazing impacts on shrub species diversity (Figure S4) could indicate displacement of highly palatable species by woody plants (Souther *et al.* 2019).

Belowground carbon inputs can vary with both plant diversity and in response to grazing (Caldeira *et al.* 2001; Steinbeiss *et al.* 2008; Wilson *et al.* 2018) but the distinct relationships between plant diversity and soil carbon stocks at different grazing intensities in our study were largely attributed to the impact of grazing on plant diversity (Figure 2b). Soil carbon storage might be inherently lower under plant communities that are resistant to grazing because plant palatability is often related to decomposition rates (Grime *et al.* 1996; Wardle *et al*. 2002). Lower litter production, as well as slower decomposition of unpalatable plant material, could therefore reduce soil carbon storage in heavily grazed areas (Hoffmann *et al.* 2016; Wang *et al.* 2018).

Plant community composition also determines the extent of changes in root growth or exudate production in response to moderate grazing (Bai *et al.* 2012), which could explain the strong relationship between plant diversity and soil carbon stocks at low and intermediate grazing intensities in our study (Figure 2b). By contrast, stimulatory feedbacks such as compensatory growth or increased root exudation cannot be sustained at high grazing intensities (Bai *et al.* 2012). In addition, a weaker relationship between plant diversity and soil carbon stocks would be expected at sites with heavy grazing because over-grazing and trampling reduce plant inputs to the soil and increase soil disturbance (Dunne *et al*. 2011). Hence, lower soil carbon stocks at heavily grazed sites can be attributed to biomass removal and reduced root inputs coupled with greater dominance of slow-growing plant species that are resistant to grazing.

It is important to note that our regression analyses tested whether the relationships between plant diversity and carbon stocks differ among grazing levels regardless of site conditions. By contrast, the pSEMs account for differences in soil nutrients, climate, and topography. Individual pSEMs for each grazing level showed that plant diversity was more strongly related to soil nitrogen and aridity under low or moderate grazing intensity (Figure S8a,b) than under high grazing intensity (Figure S8c), which suggests that the relative influence of livestock on plant diversity increases with grazing intensity. Consequently, the relationships between plant diversity and carbon stocks in the pSEMs were strongest at high grazing intensity when the influence of site characteristics were accounted for (Figure S8). The greater relative importance of grazing on plant diversity is expected in arid, low-productivity systems such as the rangelands in our study (Herrero-Jáuregui & Oesterheld 2018). Our findings demonstrate that the impacts of grazing intensity on plant diversity also modify the relationships between biodiversity and ecosystem functioning.

Site characteristics influence grazing, plant diversity and carbon storage

Consistent with our second hypothesis (H2), plant diversity, carbon stocks, and grazing intensity were all influenced by site characteristics. Plant diversity and ecosystem carbon stocks are often related to nutrient availability (Ziter & MacDougall 2013; Borer *et al.* 2014), and we found clear positive relationships between soil nitrogen, plant diversity, and soil carbon stocks. Surprisingly, although nitrogen availability often limits plant growth in arid and semi-arid rangelands (Hooper & Johnson 1999), aboveground carbon stocks in shrubs and forbs tended to decline with increasing soil nitrogen content in our study (Figures 2b-c and 3a). It is possible that our measurements of total soil nitrogen do not reflect the amount of nitrogen available to plants, or that other nutrients co-limit shrub productivity. However, the distinct relationships between soil nitrogen and aboveground carbon stocks between grasses, shrubs and forbs (Figure 3) suggest that competitive interactions might play an important role in shaping plant carbon stocks in arid grasslands across soil fertility gradients (Yan *et al.* 2016). Greater aboveground carbon stocks in grasses but declining carbon stocks in shrubs and forbs with increasing soil nitrogen (Figure 2b-d) suggest that increased competition from grasses could have reduced the growth of shrubs and forbs in fertile soils (Dwyer 1958). In addition, grazing at sites with high resource availability can stimulate compensatory growth in grazing-tolerant species (Bai *et al.* 2012) or enhance root exudation (Bardgett *et al*. 1998), which would explain the differences in aboveground carbon stocks among plant functional types, as well as the linkages between soil nitrogen, plant diversity and soil carbon stocks in our pSEMs (Figure 2). By contrast, consistent patterns of increasing soil carbon stocks with soil nitrogen concentrations across all plant growth forms likely reflect greater investment of plants in belowground biomass and root exudates, rather than greater aboveground litter inputs, as well as the major role of nitrogen in soil carbon storage and stabilization (Yusuf *et al*. 2015). Thus, the relationships between plant diversity, soil nitrogen, and soil carbon stocks are best explained by biotic interactions resulting in enhanced belowground carbon inputs.

Ecosystem productivity, and thus carbon storage, generally declines with altitude as a result of lower temperatures and shorter growing seasons (Brown *et al.* 2004; Michaletz *et al.* 2014). Changes in the vegetation and soil or climatic conditions with elevation are therefore likely to be more important for plant diversity and carbon storage than grazing (Moeslund *et al.* 2013; Sanaei *et al*. 2019). It is noteworthy that most sites at higher elevation also tended to be drier (Figure 2a) and thus, increased grass and shrub diversity but declining forb diversity with altitude (Figure 2b,c,d) could reflect the increasingly specialized plant communities in the harsh conditions of arid and semi-arid highlands (Moody & Meentemeyer 2001; Wehn *et al*. 2014). The declines in aboveground and soil carbon stocks with elevation in our study (Figures 2a and S3) likely reflect lower plant growth and cooler, drier conditions that limit decomposition.

The distinct responses of plant growth forms to aridity could reflect differences in plant stress tolerance (Grime *et al.* 2008) as shrubs and grasses are often better adapted to withstand drought than forbs (Breshears *et al.* 2016; Tello-García *et al.* 2020). In our study, aboveground carbon stocks declined strongly with increasing aridity for forbs and grasses (Figures 2c-d and 3). Greater sensitivity of forbs to aridity would therefore also contribute to the decline in forb diversity with altitude. Lower aboveground carbon stocks for forbs with increasing aridity demonstrate the importance of water as a growth-limiting resource in arid and semi-arid rangelands (Niu *et al.* 2008; Cheng *et al.* 2011). Greater water availability can increase biomass carbon accumulation by lengthening the growing season (Toledo *et al.* 2012) and improving nutrient availability (Sun *et al.* 2020). Accordingly, our models indicate that declining water availability would greatly reduce aboveground carbon stocks. However, it is notable that soil carbon stocks increased with aridity when the whole plant community was considered (Figure 2). Slower decomposition at arid sites could partly account for greater soil carbon stocks, but it is also likely that deeper root growth to access soil water reserves at dry sites enhances soil carbon storage (Sala *et al.* 1997; Nippert & Knapp 2007). Nonetheless, the recent trends towards decreasing annual precipitation in arid and semi-arid ecosystems in Iran (Mansouri *et al*. 2019) and across Asia (Zhang *et al.* 2018; Chen *et al.* 2019b) are highly concerning, as they could entail substantial regional losses of both biodiversity and aboveground carbon stocks in rangelands. Importantly, the impacts of increasing aridity might be exacerbated by intensified grazing.

The impacts of grazing differ markedly among sites depending on grazing history, climate, and resource availability (Milchunas & Lauenroth 1993; Bai *et al.* 2012). Given that our sites spanned broad environmental gradients, it is likely that the strong influence of climate and topography on plant diversity modifies the impact of grazing, especially as grazing intensity tended to decline with slope and elevation (Figure 2). The decline in grazing intensity with increasing slope likely reflects limited access and reduced movement of livestock at steep sites (Milchunas *et al.* 1989) and reduced grazing at steep sites in turn explains why aboveground carbon stocks in grasses increased with slope (Figures 2d and 3a). The decline in grazing intensity with aridity for the whole plant community in our study is probably partly due to lower aboveground biomass (Figure 2c,d) and reduced palatability of plant material associated with slow-growing stress-tolerant plants (Augustine & McNaughton 1998) at arid sites. Nonetheless, the greater number of quadrats classed as moderately or highly grazed at arid sites in our study could be due to the greater negative impacts of grazing at drier sites (Oñatibia *et al.* 2020), rather than higher cattle stocking density. Indeed, the declines in aboveground biomass with grazing and aridity are consistent with previous work demonstrating that grazing has particularly detrimental effects on the vegetation at dry sites, because aridity constrains the plants' ability to recover from damage (Oñatibia *et al.* 2020). Hence, intensified grazing in combination with increasing aridity is likely to alter plant community composition and ultimately reduce overall rangeland carbon storage in future.

5. Conclusions

Our study demonstrates that ecosystem carbon stocks in natural rangelands are related to plant diversity across environmental gradients, but the relationship is altered by grazing intensity. Although soil carbon stocks were more strongly related to environmental conditions (climate, topography, and soil fertility), plant diversity and community composition nonetheless play a key role in explaining variation in ecosystem carbon stocks. The impact of grazing intensity on plant and soil carbon stocks was apparent across climatic and topographical gradients, but our results indicate that the interplay between climate, topography, grazing pressure, and plant growth forms could shape ecosystem carbon storage in future. Local losses in plant diversity and community composition associated with increasing aridity and intensified grazing could therefore substantially reduce ecosystem carbon storage in arid and semi-arid rangelands across Asia. To fully assess the potential impacts of intensified grazing and climate changes on rangeland carbon storage, future work will need to account for site topography as well as the variable responses of different plant growth forms.

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Figure captions

Figure 1. A conceptual model linking rangeland aboveground and soil carbon stocks to plant species diversity, topography, aridity, soil fertility, and grazing intensity, showing a schematic illustration of potential relationships among variables. Signs (+ or −) indicate direction of relationships based on previous evidence and expectations.

Figure 2. Diagrams of the final piece-wise structural equation models (pSEM) linking aboveground carbon stocks, soil carbon stocks and species diversity (Shannon's H) to topography, climate, soil fertility, and grazing conditions in natural rangelands for (a) all plant species (b), shrubs (c), forbs (d) and grasses. Significance levels are shown as ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$ and pathways without asterisks are not significant. The colour of the arrows corresponds to the colour of the predictor variables and for each exogenous variable, conditional (c) and marginal (m) R^2 values are provided, where R^2_c represents the variance explained by both fixed and random effects, and R^2_m represents the variance explained by fixed effects only. Widths of paths are scaled by standardized path coefficients. Model-fit statistics are given below each model diagram. Details of the full paths are given in Tables S2-S5.

Figure 3. Comparison of standardized beta coefficients of model predictors for (a) aboveground carbon stocks and (b) soil carbon stocks. The coefficients are derived from the piecewise structural equation models (pSEMs) shown in Figure 2 and indicate differences in the strength of predictor variables for the whole plant community and different plant growth forms (PGF). Mean coefficients (symbols) ±1 standard error (error bars) are shown, whereby open symbols indicate non-significant paths, and filled symbols indicate significant paths at $P \leq 0.05$.

Figure 4. Relative contributions (%) of topography, aridity, soil nitrogen, grazing intensity and plant species diversity to variation in aboveground and soil carbon stocks, shown for the whole plant community and different plant growth forms.

Figure 5. Relationships between (a) aboveground carbon stocks and plant species diversity, (b) soil carbon stocks and plant species diversity, and (c) aboveground carbon stocks and soil carbon stocks for three levels of grazing intensity. Lines represent the modelled effects of the interaction between plant species diversity (Hs) and grazing intensity for aboveground carbon stocks (ACS) or soil carbon stocks using the linear mixed-effects model regressions (marginal R^2; R^2_m). Shading represents 95% confidence intervals and conditional (c) and marginal (m) R^2 values are shown, where R^2_c represents the variance explained by both fixed and random effects, and R^2_m represents the variance explained by fixed effects only; P-values are given for fixed effects terms.

Table 1 Characteristics of the 10 rangeland study sites in Iran, showing means and standard errors calculated from the total number of quadrats (No. quadrat) at each site, where C is carbon.

Site	Location	Plant diversity (H)	Plant species richness	Aboveground C stocks (g m^{-2})	Soil C stocks (g m^{-2})	Soil nitrogen (%)	Aridity	Climate	Elevation (m.a.s.l.)	Slope (%)	No. quadrat	Area (ha)
Ardabil	43.60 N 76.01 E	2±0.04	15±0.46	43.1±2.2	62.63±2.06	0.22±0.01	0.38±0.01	Semi-humid	1049±43	11.0±0.46	138	12000
Lasem	39.66 N 61.39 E	1.19±0.02	4±0.09	72.9±1.5	46.89±0.77	0.06±0.01	0.23	Semi-humid	2790±6.51	32.5±0.60	350	5000
Middle Taleghan	40.00 N 47.48 E	2.19±0.01	13±0.13	88.1±0.9	185.17±1.92	0.14±0.01	0.41	Semi-arid	2205±3.98	23.1±0.35	735	750
Hiko	39.91 N 71.25 E	1.33±0.05	9±0.38	110.6±13	173.06±6.23	0.16±0.01	0.79	Semi-arid	2496±38	27.2±1.5	90	6000
Jashloubar	39.62 N 69.63 E	1.37±0.06	6±0.33	39.7±3.9	148±5.44	0.18	0.80	Semi-arid	2485±2.15	24.2±1.8	30	1
Khoshkeroud	39.22 N 46.50 E	1.27±0.06	8±2.29	39.1±3.7	31.30±0.74	0.03	0.90	Arid	1402±0.78	9.8±0.21	30	1
Kordan	39.79 N 48.69 E	1.36±0.06	6±0.38	21.7±2.0	186.48±3.89	0.19±0.01	0.80	Semi-arid	1676±0.93	26.2±0.51	30	1
Lazour	39.70 N 64.64 E	1.54±0.05	7±0.38	79.9±6.5	244.26±4.38	0.27±0.02	0.64	Semi-arid	2801±1.65	7.5±0.51	30	1
Ozine	39.47 N 63.08 E	1.19±0.07	5±0.45	27.4±3.5	122.35±1.15	0.10	0.64	Semi-arid	2280±1.33	8.8±0.05	30	1
Salafchegan	38.20 N 44.49 E	1.59±0.05	8±0.29	44.3±4.3	56.56±3.69	0.06	0.92	Arid	1562±0.53	3.4±0.09	30	1
Total			11±0.15	76.2±1.2	134.23±2	0.13	0.44		2232±14	23.2±0.32	1493	

Figure 1

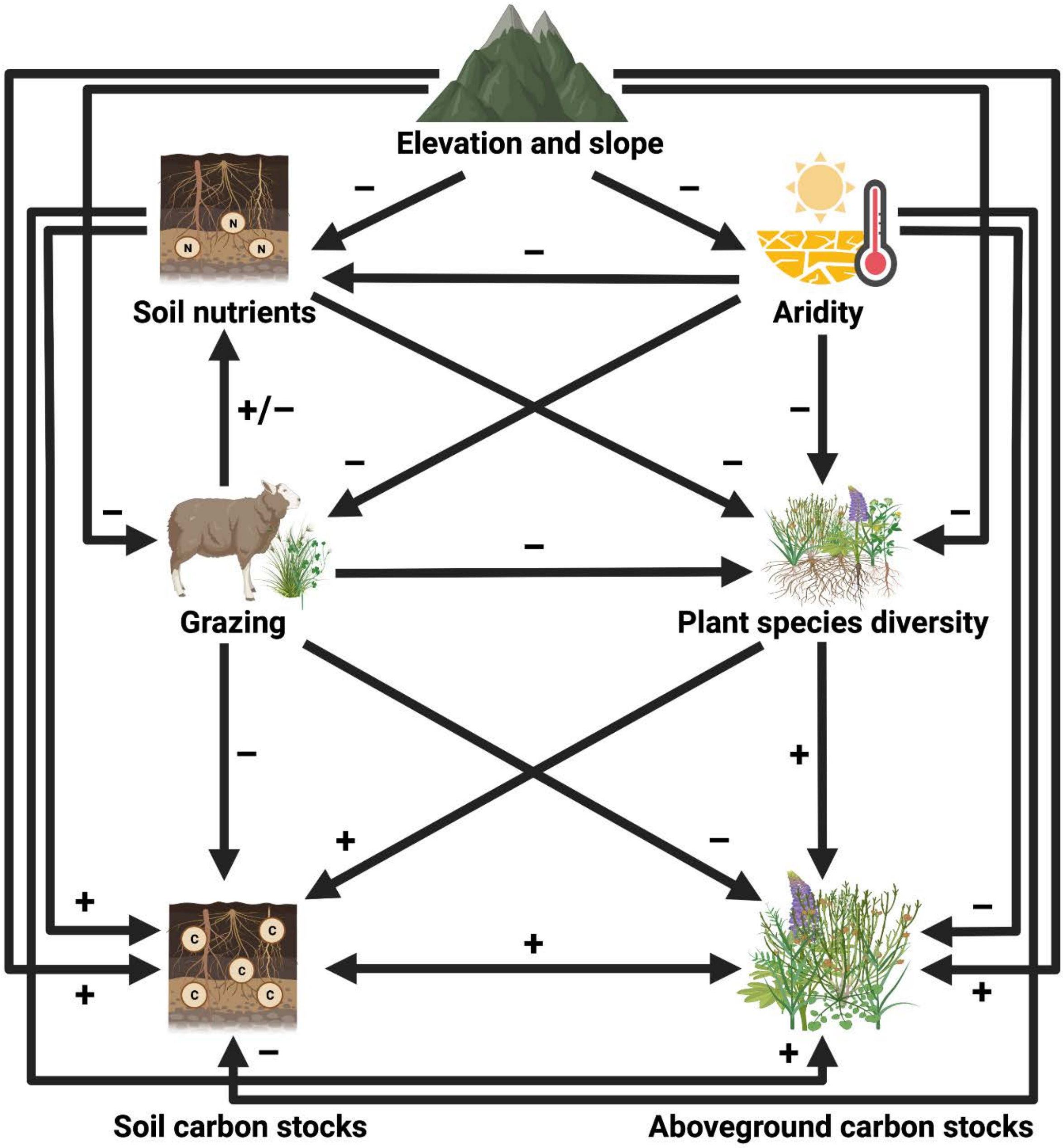

Elevation and slope
Soil nutrients
Aridity
Grazing
Plant species diversity
Soil carbon stocks
Aboveground carbon stocks
+/−
N
C

Figure 2

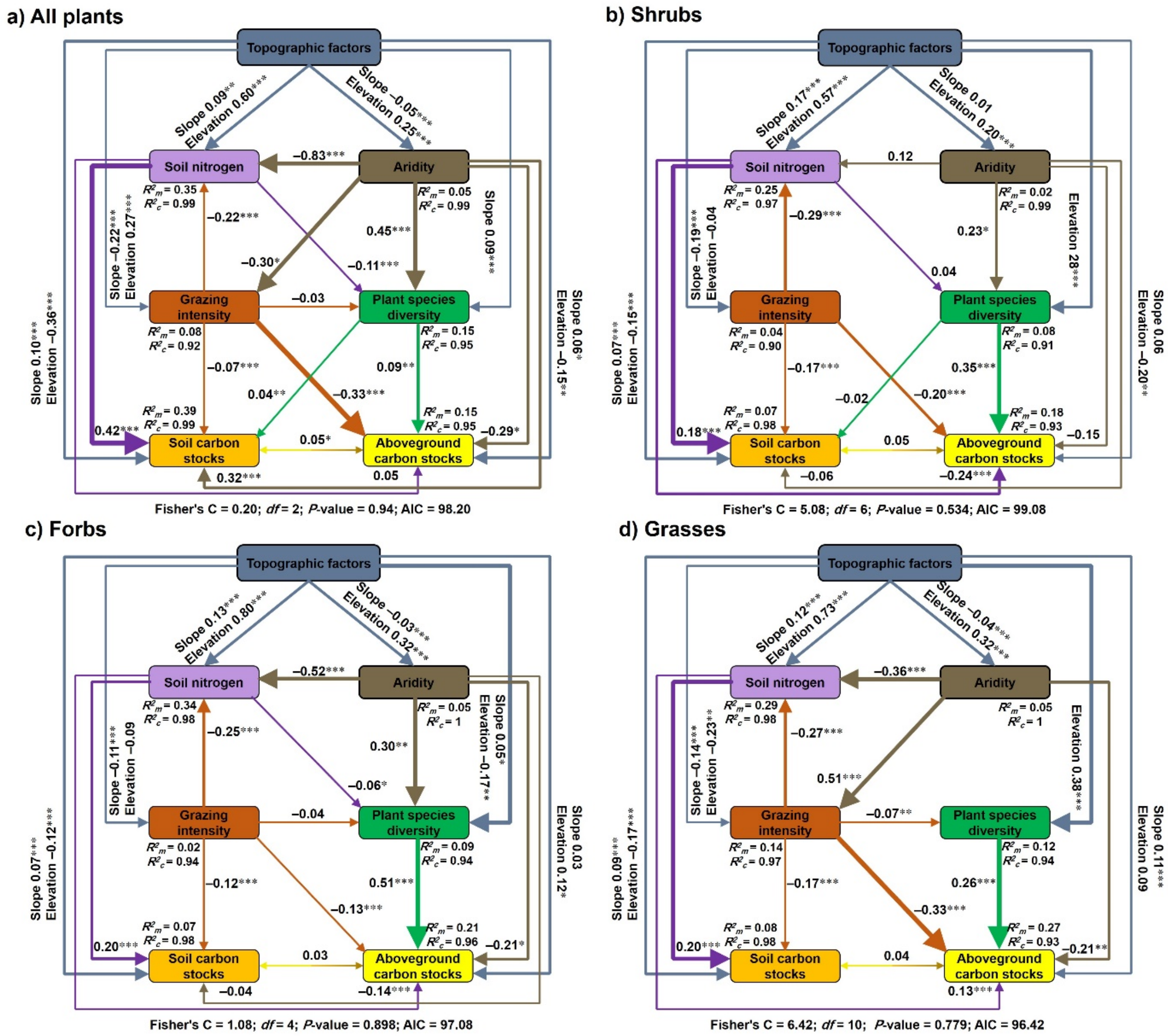

a) All plants
b) Shrubs
c) Forbs
d) Grasses
Topographic factors
Soil nitrogen
Aridity
Grazing intensity
Plant species diversity
Soil carbon stocks
Aboveground carbon stocks
Fisher's C = 0.20; df = 2; P-value = 0.94; AIC = 98.20
Fisher's C = 5.08; df = 6; P-value = 0.534; AIC = 99.08
Fisher's C = 1.08; df = 4; P-value = 0.898; AIC = 97.08
Fisher's C = 6.42; df = 10; P-value = 0.779; AIC = 96.42

Figure 3

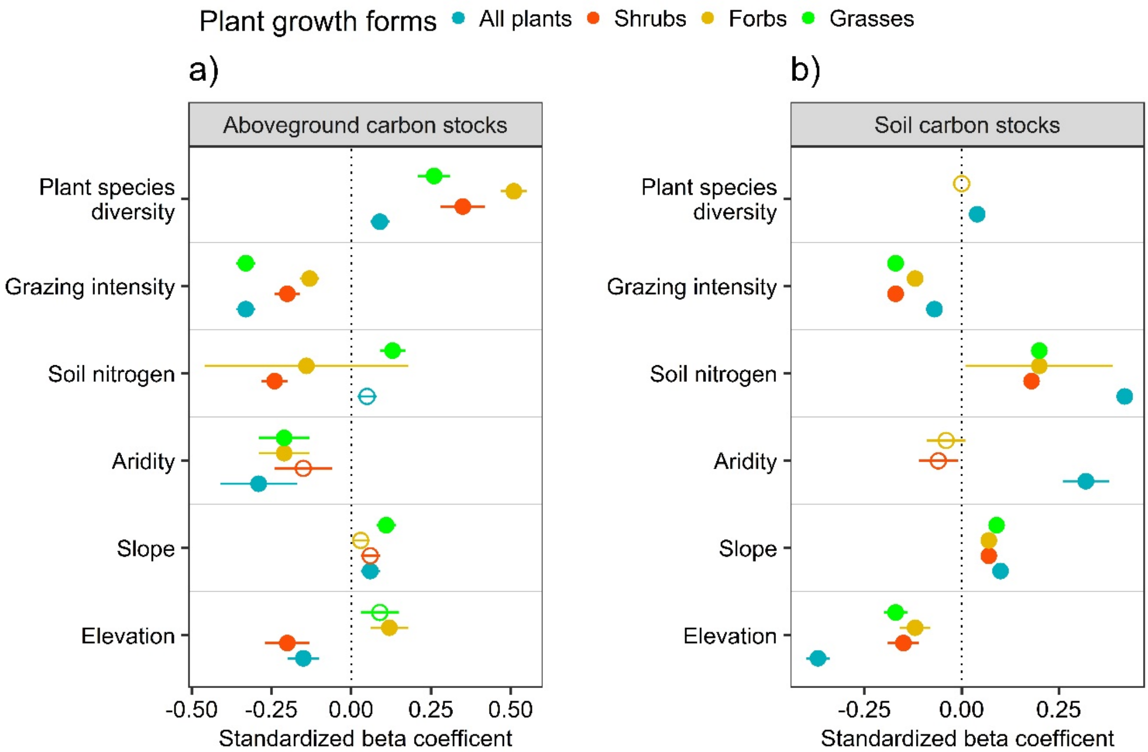

Plant growth forms
All plants
Shrubs
Forbs
Grasses
a)
b)
Aboveground carbon stocks
Soil carbon stocks
Plant species diversity
Grazing intensity
Soil nitrogen
Aridity
Slope
Elevation
-0.50
-0.25
0.00
0.25
0.50
Standardized beta coefficent
-0.25
0.00
0.25
Standardized beta coefficent

Figure 4

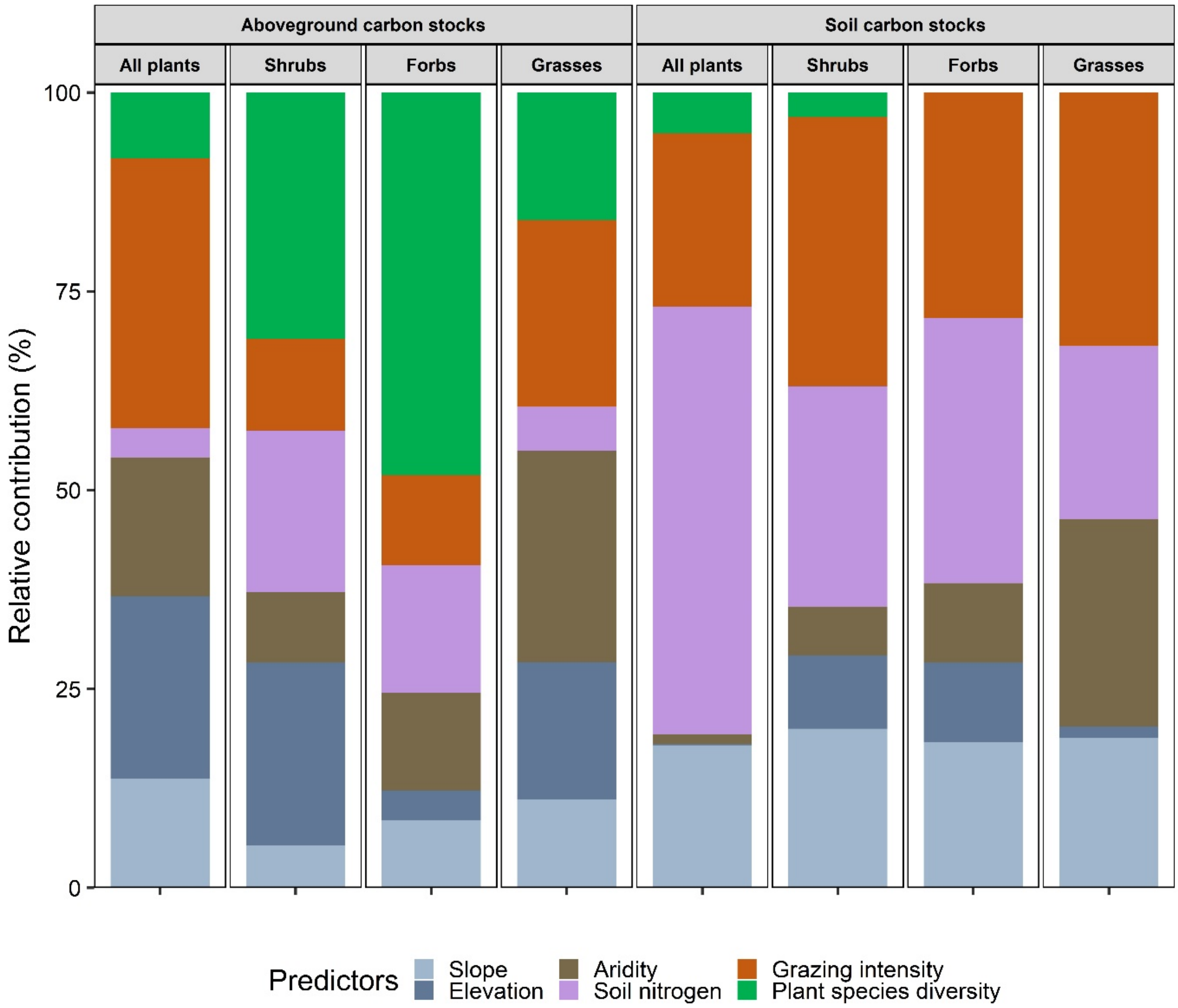
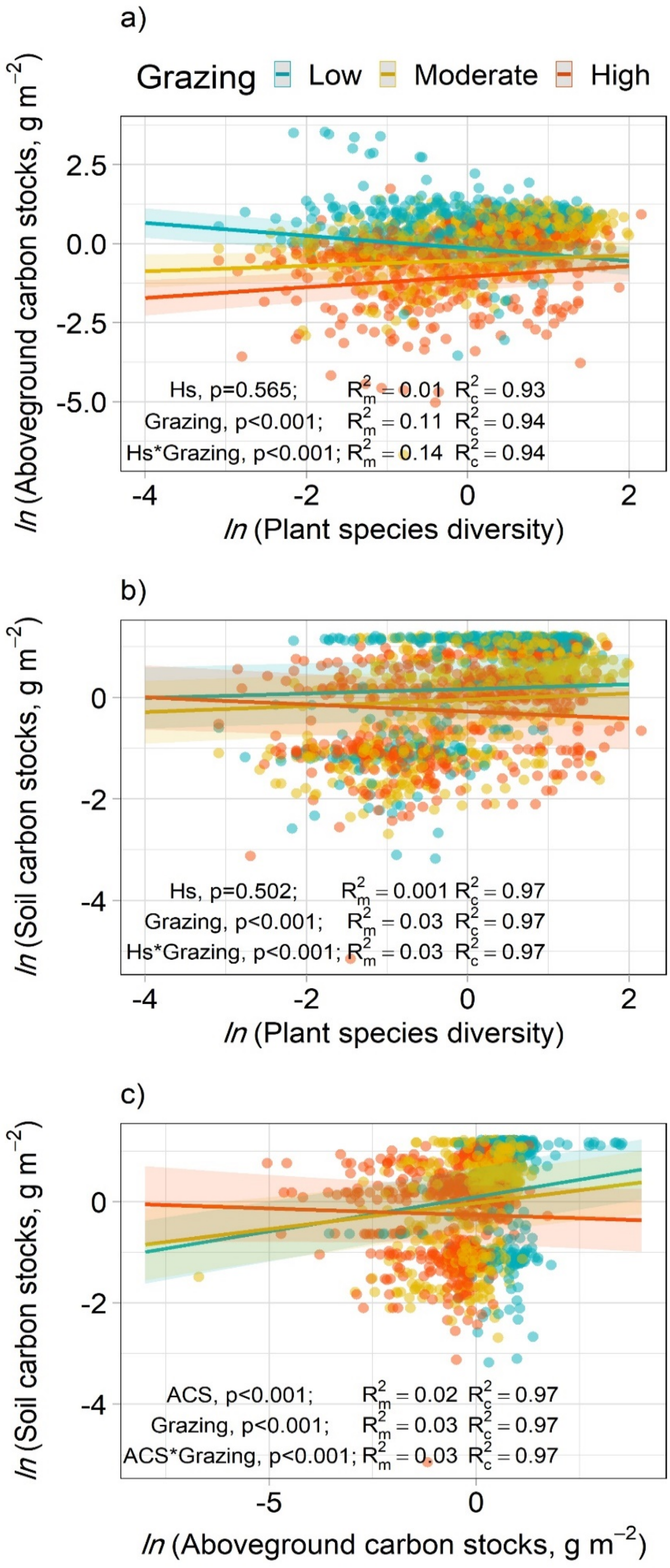


Figure 5



a)
Grazing
Low
Moderate
High
ln (Aboveground carbon stocks, g m−2)
2.5
0.0
-2.5
-5.0
Hs, p=0.565; R2m = 0.01 R2c = 0.93
Grazing, p<0.001; R2m = 0.11 R2c = 0.94
Hs*Grazing, p<0.001; R2m = 0.14 R2c = 0.94
-4
-2
0
2
ln (Plant species diversity)
b)
ln (Soil carbon stocks, g m−2)
0
-2
-4
Hs, p=0.502; R2m = 0.001 R2c = 0.97
Grazing, p<0.001; R2m = 0.03 R2c = 0.97
Hs*Grazing, p<0.001; R2m = 0.03 R2c = 0.97
-4
-2
0
2
ln (Plant species diversity)
c)
ln (Soil carbon stocks, g m−2)
0
-2
-4
ACS, p<0.001; R2m = 0.02 R2c = 0.97
Grazing, p<0.001; R2m = 0.03 R2c = 0.97
ACS*Grazing, p<0.001; R2m = 0.03 R2c = 0.97
-5
0
ln (Aboveground carbon stocks, g m−2)

APPENDIX A: SUPPLEMENTARY INFORMATION

Table S1. Description of grazing intensity levels in the study area

Grazing intensity	Soil trampling	Rangeland condition	Removal of biomass	Distance from watering source	Distance from village	Distance from resting areas
Low	Low evidence	Good	< 30%	> 1 km	> 3 km	> 1 km
Moderate	Moderate evidence	Fair	30-50%	0.5-1 km	1-3 km	0.5-1 km
High	High evidence	Poor	>50%	< 0.5 km	< 1 km	< 0.5 km

Table S2. Summary statistics of the piece-wise structural equation model (pSEM) for the whole plant community, linking aboveground carbon stocks (ACS) and soil carbon stocks (SCS) to topography (elevation and slope), aridity, soil nitrogen, grazing intensity, and Shannon's diversity (Hs) in natural rangelands. Significant effects (P < 0.05) are indicated in bold and the final pSEM diagram is shown in Fig. 2a.

Response	Predictor	Standard error	Critical value	*P*-value	Effect
Hs	Slope	0.02	3.79	**<0.001**	0.09
Hs	Nitrogen	0.03	-4.18	**<0.001**	-0.11
Hs	Aridity	0.08	5.33	**<0.001**	0.45
Hs	Grazing	0.02	-1.92	0.055	-0.03
ACS	Elevation	0.05	-2.96	**0.003**	-0.15
ACS	Slope	0.03	2.10	**0.036**	0.06
ACS	Aridity	0.12	-2.48	**0.013**	-0.29
ACS	Hs	0.03	3.11	**0.002**	0.09
ACS	Grazing	0.03	-16.78	**<0.001**	-0.33
ACS	Nitrogen	0.03	1.75	0.080	0.05
SCS	Elevation	0.03	-14.32	**<0.001**	-0.37
SCS	Slope	0.01	6.60	**<0.001**	0.10
SCS	Aridity	0.06	5.33	**<0.001**	0.32
SCS	Hs	0.01	3.15	**0.002**	0.04
SCS	Grazing	0.01	-7.00	**<0.001**	-0.07
SCS	Nitrogen	0.01	29.10	**<0.001**	0.42
ACS~~SCS	~~	---	2.10	**0.018**	0.05
Nitrogen	Slope	0.03	3.30	**0.001**	0.09
Nitrogen	Elevation	0.04	13.98	**<0.001**	0.60
Nitrogen	Grazing	0.02	-13.43	**<0.001**	-0.22
Nitrogen	Aridity	0.11	-7.95	**<0.001**	-0.83
Grazing	Slope	0.03	-5.06	**<0.001**	-0.21
Grazing	Elevation	0.05	4.19	**<0.001**	0.27
Grazing	Aridity	0.11	-2.17	**0.030**	-0.30
Aridity	Slope	0.01	-8.81	**<0.001**	-0.05
Aridity	Elevation	0.01	29.79	**<0.001**	0.25

Table S3. Summary statistics of the piece-wise structural equation model (pSEM) for shrubs, linking aboveground carbon stocks (ACS) and soil carbon stocks (SCS) to topography (elevation and slope), aridity, soil nitrogen, grazing intensity, and Shannon's diversity (Hs) in natural rangelands. Significant effects ($P < 0.05$) are indicated in bold and the final pSEM diagram is shown in Fig. 2b.

Response	Predictor	Standard error	Critical value	*P*-value	Effect
Hs	Elevation	0.03	3.87	**<0.001**	0.28
Hs	Nitrogen	0.02	1.01	0.311	0.04
Hs	Aridity	0.03	2.45	**0.015**	0.23
ACS	Elevation	0.07	-3.03	**0.003**	-0.20
ACS	Slope	0.03	1.84	0.066	0.06
ACS	Aridity	0.09	-1.75	0.081	-0.15
ACS	Hs	0.07	13.87	**<0.001**	0.35
ACS	Grazing	0.04	-7.39	**<0.001**	-0.20
ACS	Nitrogen	0.04	-6.89	**<0.001**	-0.24
SCS	Elevation	0.04	-4.19	**<0.001**	-0.15
SCS	Slope	0.02	4.03	**<0.001**	0.07
SCS	Aridity	0.05	-1.10	0.273	-0.06
SCS	Hs	0.04	-1.23	0.220	-0.02
SCS	Grazing	0.02	-12.29	**<0.001**	-0.17
SCS	Nitrogen	0.02	10.16	**<0.001**	0.18
ACS~~ SCS	~~	---	1.58	0.057	0.05
Nitrogen	Slope	0.02	6.15	**<0.001**	0.17
Nitrogen	Elevation	0.05	10.00	**<0.001**	0.57
Nitrogen	Grazing	0.02	-13.42	**<0.001**	-0.29
Nitrogen	Aridity	0.07	1.45	0.149	0.12
Grazing	Slope	0.03	-5.10	**<0.001**	-0.19
Grazing	Elevation	0.05	-0.56	0.574	-0.04
Aridity	Slope	0.01	1.22	0.223	0.01
Aridity	Elevation	0.02	10.78	**<0.001**	0.20

Table S4. Summary statistics of the piece-wise structural equation model (pSEM) for forbs, linking aboveground carbon stocks (ACS) and soil carbon stocks (SCS) to topography (elevation and slope), aridity, soil nitrogen, grazing intensity, and Shannon's diversity (Hs) in natural rangelands. Significant effects (P < 0.05) are indicated in bold and the final pSEM diagram is shown in Fig. 2c.

Response	Predictor	Standard error	Critical value	*P*-value	Effect
Hs	Elevation	0.04	-2.63	**0.009**	-0.17
Hs	Slope	0.02	2.01	**0.045**	0.05
Hs	Nitrogen	0.21	-2.13	**0.033**	-0.06
Hs	Aridity	0.05	3.27	**0.001**	0.30
Hs	Grazing	0.02	-1.63	0.104	-0.04
ACS	Elevation	0.06	2.13	**0.033**	0.12
ACS	Slope	0.02	1.30	0.196	0.03
ACS	Aridity	0.08	-2.50	**0.013**	-0.21
ACS	Hs	0.04	22.58	**<0.001**	0.51
ACS	Grazing	0.03	-6.28	**<0.001**	-0.13
ACS	Nitrogen	0.32	-5.42	**<0.001**	-0.14
SCS	Elevation	0.04	-3.37	**0.001**	-0.12
SCS	Slope	0.01	4.82	**<0.001**	0.07
SCS	Aridity	0.05	-0.75	0.451	-0.04
SCS	Grazing	0.02	-10.08	**<0.001**	-0.12
SCS	Nitrogen	0.19	12.47	**<0.001**	0.20
ACS~~SCS	~~	---	1.21	0.112	0.03
Nitrogen	Slope	0.00	5.96	**<0.001**	0.13
Nitrogen	Elevation	0.00	14.82	**<0.001**	0.80
Nitrogen	Grazing	0.00	-13.00	**<0.001**	-0.25
Nitrogen	Aridity	0.01	-6.12	**<0.001**	-0.52
Grazing	Slope	0.03	-3.71	**<0.001**	-0.11
Grazing	Elevation	0.05	-1.36	0.174	-0.09
Aridity	Slope	0.01	-5.03	**<0.001**	-0.03
Aridity	Elevation	0.01	22.21	**<0.001**	0.32

Table S5. Summary statistics of the piece-wise structural equation model (pSEM) for grasses, linking aboveground carbon stocks (ACS) and soil carbon stocks (SCS) to topography (elevation and slope), aridity, soil nitrogen, grazing intensity, and Shannon's diversity (Hs) in natural rangelands. Significant effects (P < 0.05) are indicated in bold and the final pSEM diagram is shown in Fig. 2d.

Response	Predictor	Standard error	Critical value	*P*-value	Effect
Hs	Elevation	0.03	7.65	**<0.001**	0.38
Hs	Grazing	0.02	-3.14	**0.002**	-0.07
ACS	Elevation	0.06	1.47	0.142	0.09
ACS	Slope	0.03	3.68	**<0.001**	0.11
ACS	Aridity	0.08	-2.76	**0.006**	-0.21
ACS	Hs	0.05	9.10	**<0.001**	0.26
ACS	Grazing	0.03	-12.99	**<0.001**	-0.33
ACS	Nitrogen	0.04	4.36	**<0.001**	0.13
SCS	Elevation	0.03	-5.31	**<0.001**	-0.17
SCS	Slope	0.02	5.66	**<0.001**	0.09
SCS	Grazing	0.02	-12.82	**<0.001**	-0.17
SCS	Nitrogen	0.02	12.51	**<0.001**	0.20
ACS~~SCS	~~	---	1.57	0.058	0.04
Nitrogen	Slope	0.02	4.54	**<0.001**	0.12
Nitrogen	Elevation	0.05	12.78	**<0.001**	0.73
Nitrogen	Grazing	0.02	-12.71	**<0.001**	-0.27
Nitrogen	Aridity	0.07	-4.02	**<0.001**	-0.36
Grazing	Slope	0.03	-4.44	**<0.001**	-0.14
Grazing	Elevation	0.06	-3.17	**0.002**	-0.23
Grazing	Aridity	0.09	4.57	**<0.001**	0.51
Aridity	Slope	0.01	-5.87	**<0.001**	-0.04
Aridity	Elevation	0.02	21.59	**<0.001**	0.32

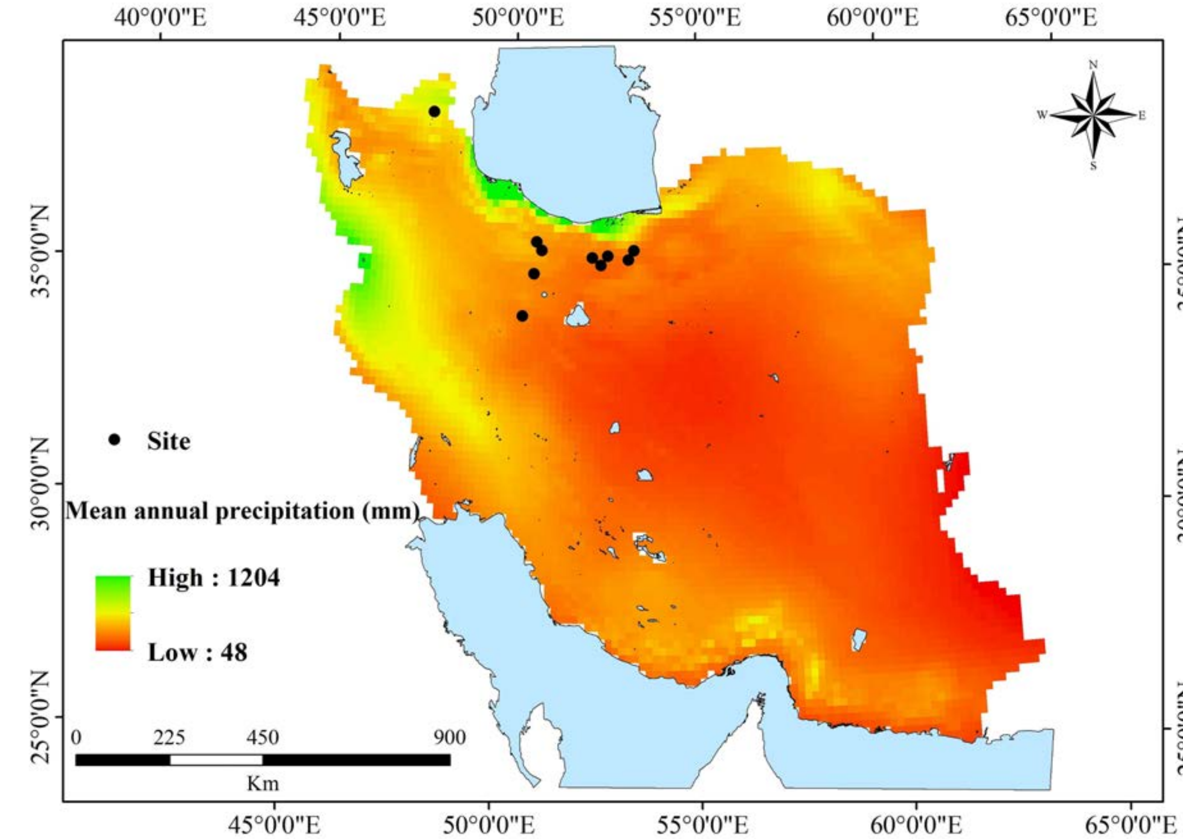


Fig. S1. Locations of the study sites (black circles) in northern Iran. The heatmap shows mean annual precipitation, which ranged from 186 to 796 across study sites.

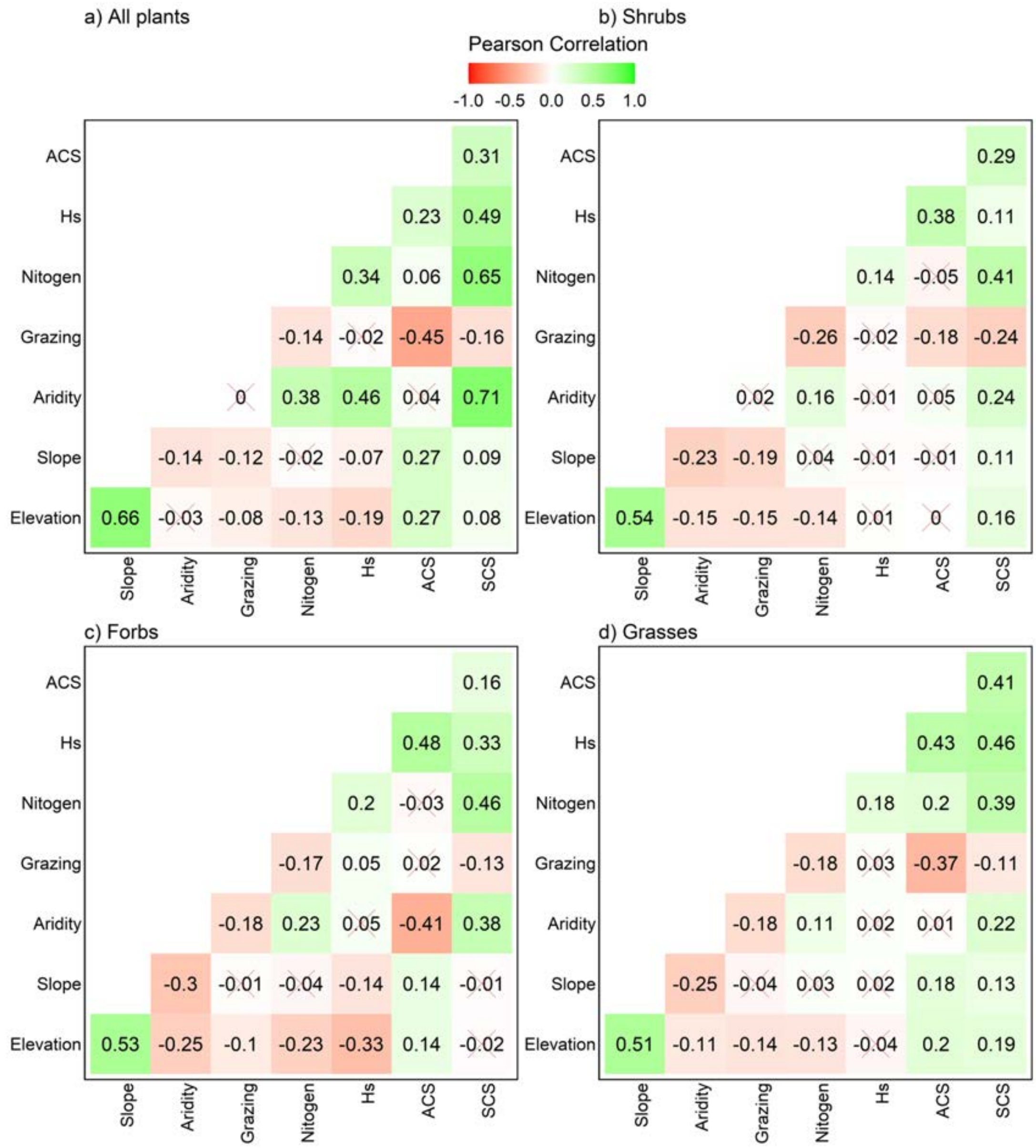


Fig. S2. Pearson's correlation coefficients (r^2) for all pairs of variables used in this study across (a) all plants (b), shrubs (c), forbs (d) and grasses. Red indicates negative relationships; green indicates positive relationships, and the shading indicates the strength of the correlation; white squares with a red cross indicate non-significant correlations ($P > 0.05$). Abbreviations for the variables are given in Table S2.

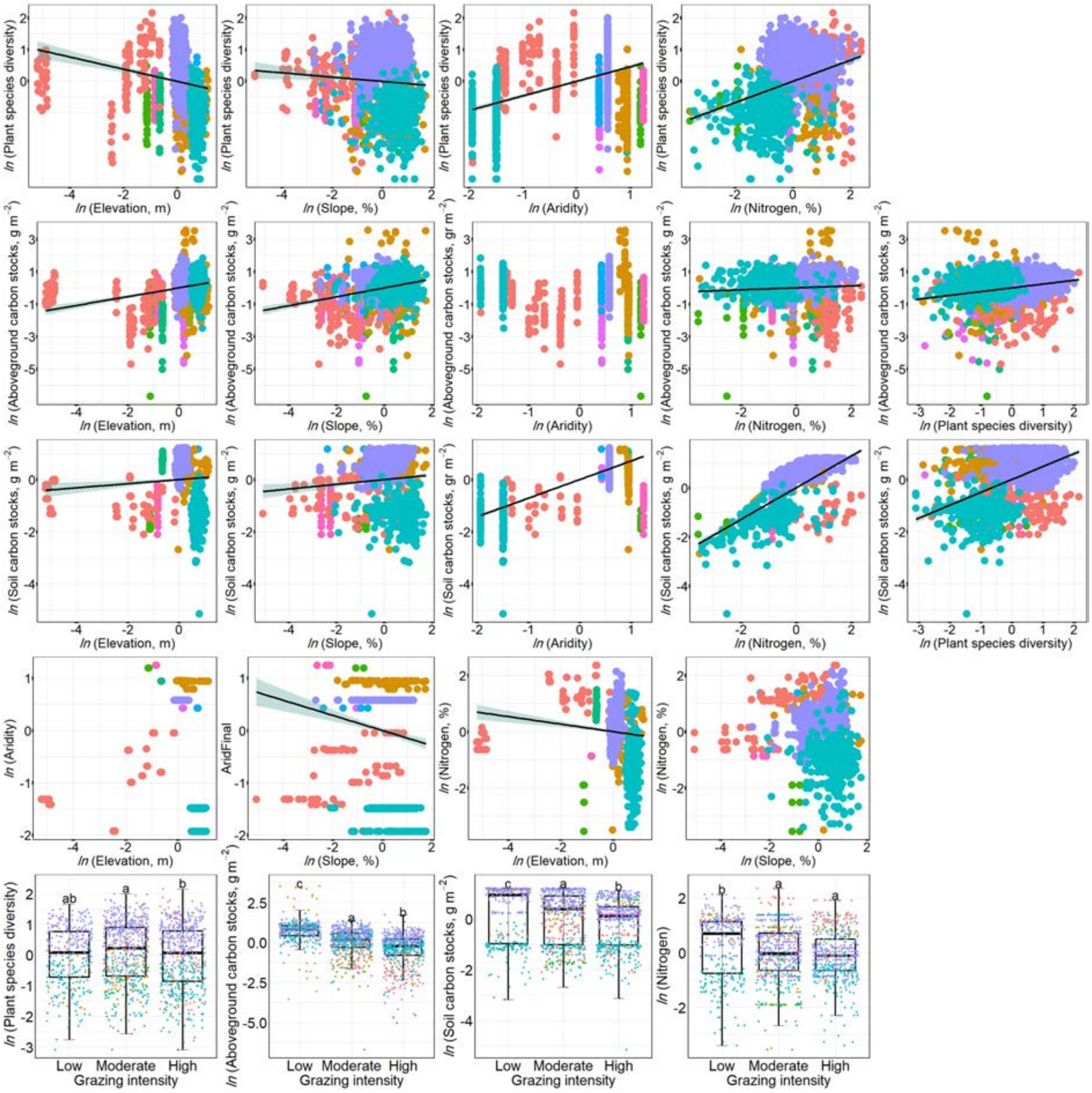


Fig. S3. Bivariate relationships between **plant species diversity** (Shannon's H), aboveground carbon stocks, soil carbon stocks, elevation, slope, aridity, and soil nitrogen, as well as differences in Shannon's diversity, aboveground carbon stocks and soil carbon stocks among levels of grazing intensity in natural rangelands. Regression lines are shown for significant relationships at $P < 0.05$. Boxplots show the 10th to 90th percentiles with median lines; different letters indicate significant differences among grazing intensity levels at $P < 0.05$ (Tukey's test). Different symbol colours correspond to different sites.

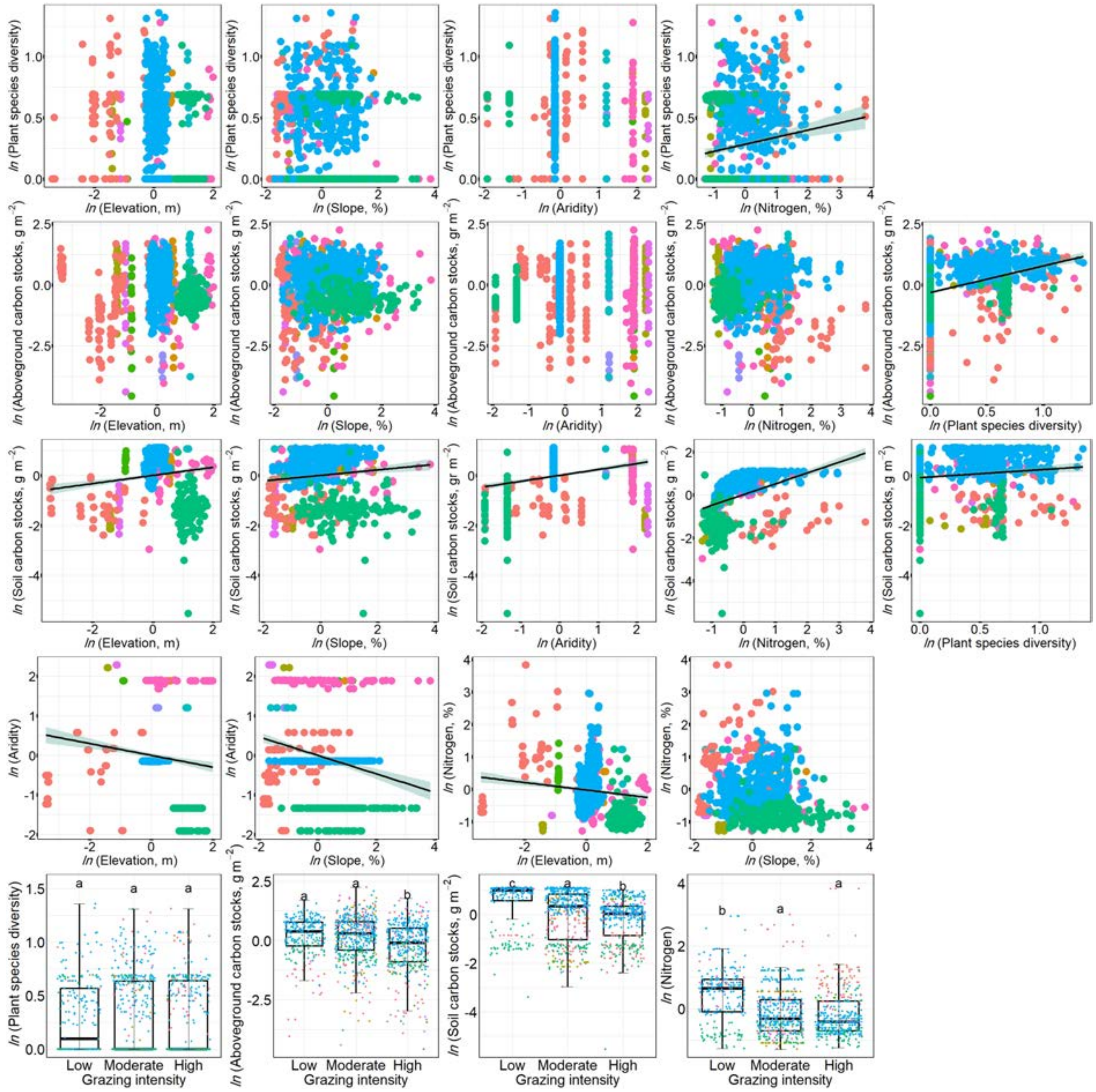


Fig. S4. Bivariate relationships between **shrub species diversity** (Shannon's H), aboveground carbon stocks, soil carbon stocks, elevation, slope, aridity, and soil nitrogen, as well as differences in Shannon's diversity, aboveground carbon stocks and soil carbon stocks among levels of grazing intensity in natural rangelands. Regression lines are shown for significant relationships at *P* < 0.05. Boxplots show the 10th to 90th percentiles with median lines; different letters indicate significant differences among grazing intensity levels at *P* < 0.05 (Tukey's test). Different symbol colours correspond to different sites.

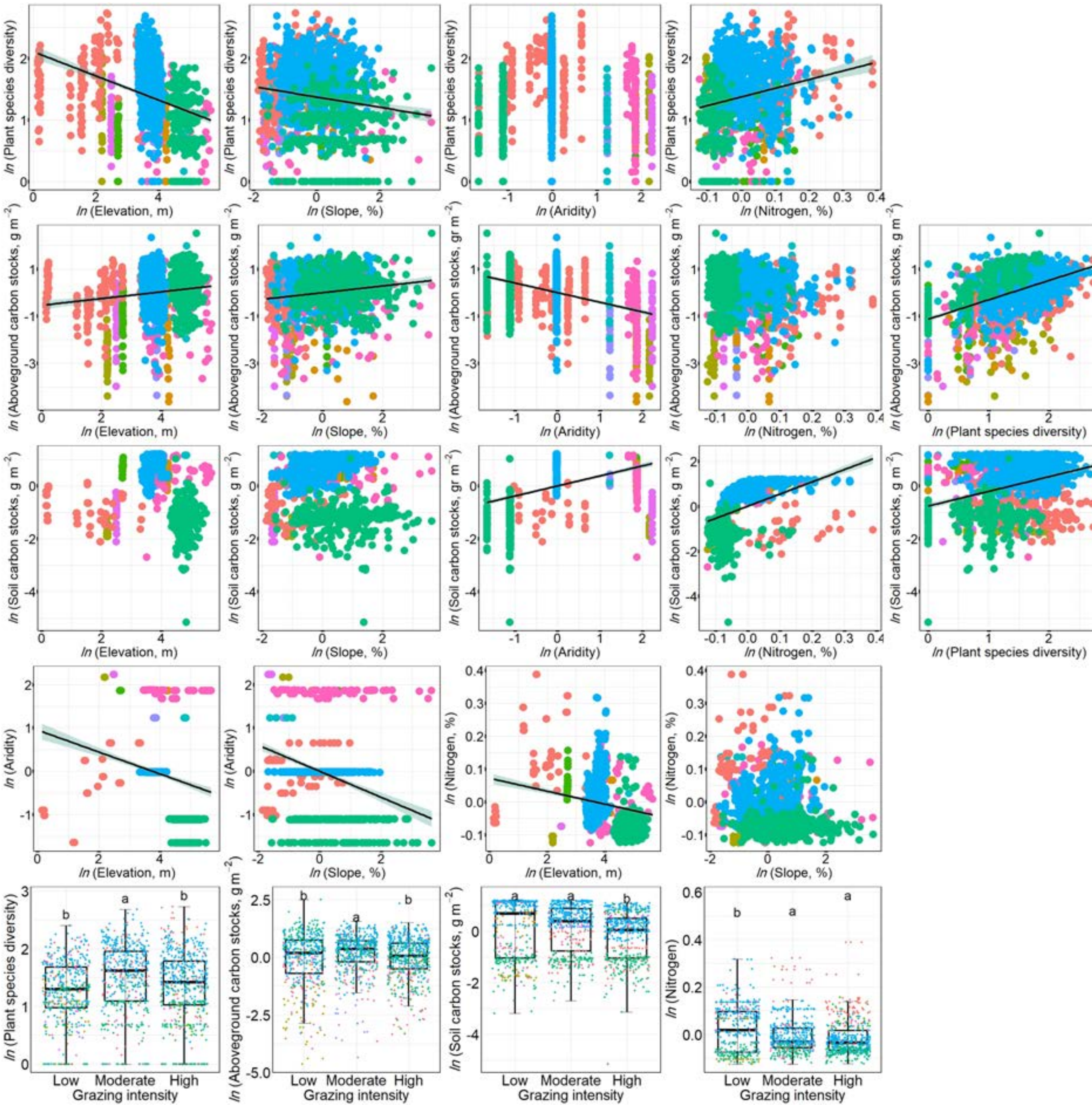


Fig. S5. Bivariate relationships between **forb species diversity** (Shannon's H), aboveground carbon stocks, soil carbon stocks, elevation, slope, aridity, and soil nitrogen, as well as differences in Shannon's diversity, aboveground carbon stocks and soil carbon stocks among levels of grazing intensity in natural rangelands. Regression lines are shown for significant relationships at *P* < 0.05. Boxplots show the 10^{th} to 90^{th} percentiles with median lines; different letters indicate significant differences among grazing intensity levels at *P* < 0.05 (Tukey's test). Different symbol colours correspond to different sites.

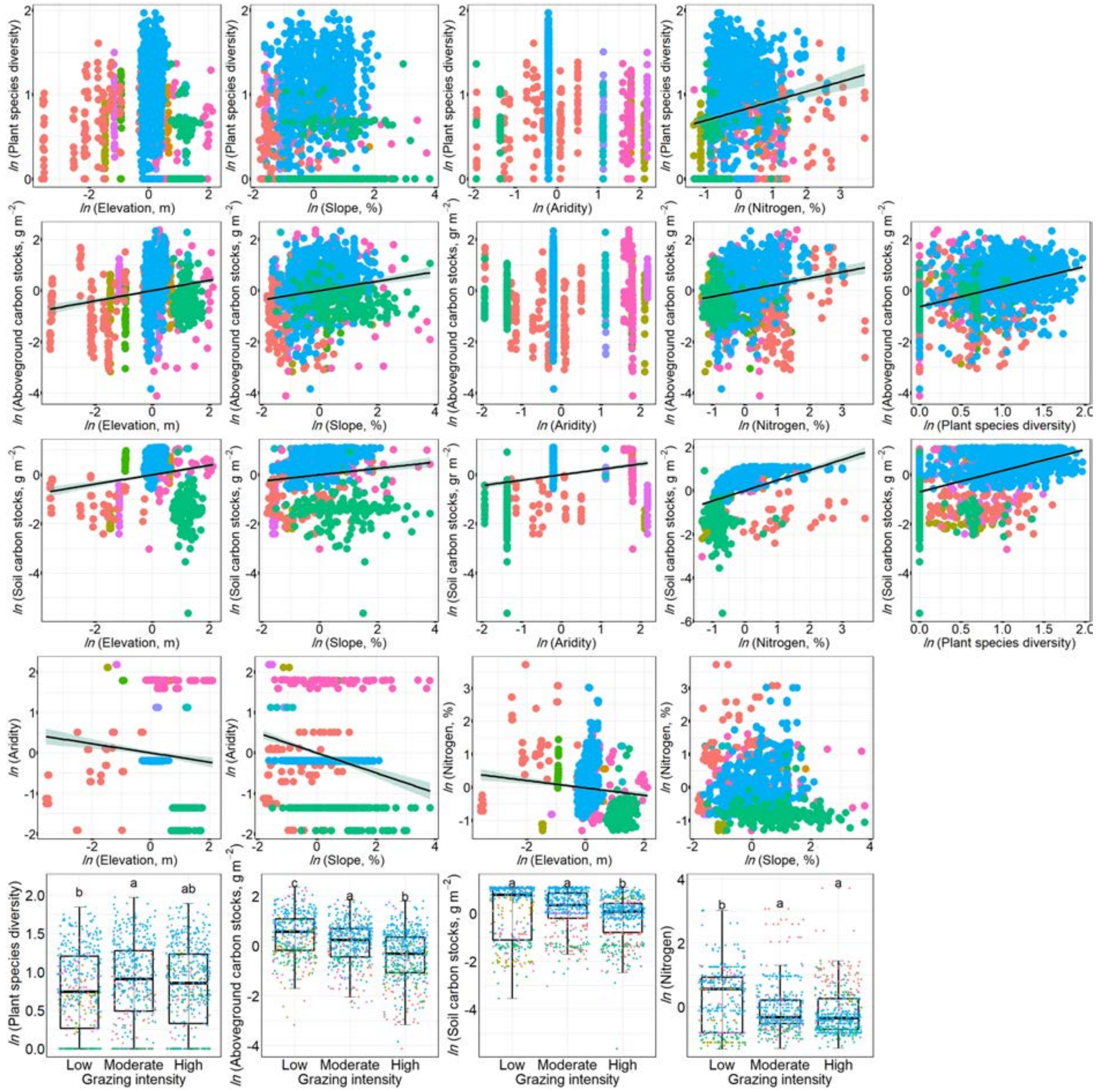


Fig. S6. Bivariate relationships between **grass species diversity** (Shannon's H), aboveground carbon stocks, soil carbon stocks, elevation, slope, aridity, and soil nitrogen, as well as differences in Shannon's diversity, aboveground carbon stocks and soil carbon stocks among levels of grazing intensity in natural rangelands. Regression lines are shown for significant relationships at $P < 0.05$. Boxplots show the 10th to 90th percentiles with median lines; different letters indicate significant differences among grazing intensity levels at $P < 0.05$ (Tukey's test). Different symbol colours correspond to different sites.

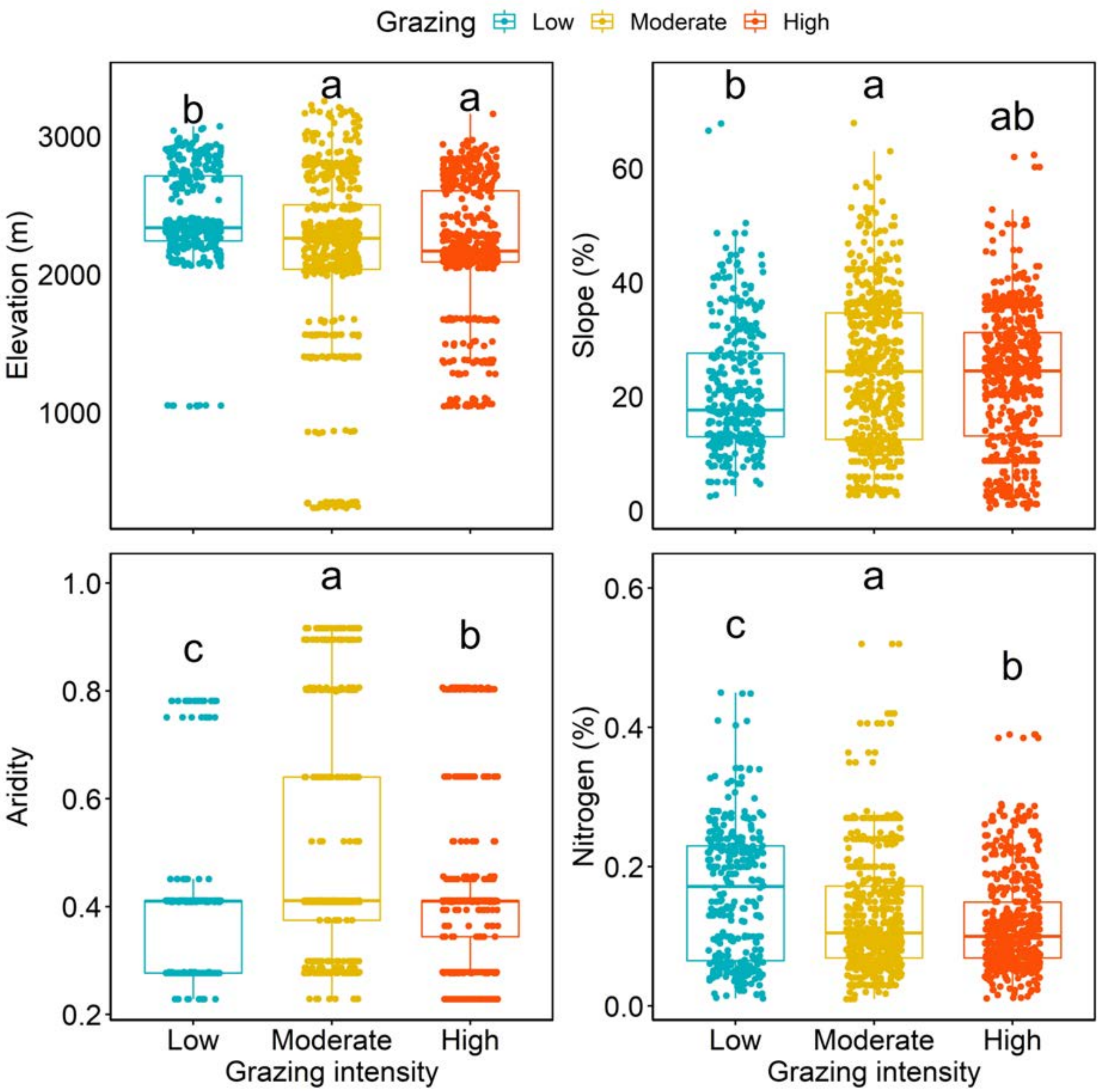


Fig. S7. Range of elevation, slope, aridity, and soil nitrogen for three levels of grazing intensity (low, moderate, high) in natural rangelands. Boxplots show the 10th to 90th percentiles with median lines; different letters indicate significant differences among grazing intensity levels at $P < 0.05$ (Tukey's test). Different symbol colours correspond to different plots in each level of grazing intensity. ANOVA performed on the original data.

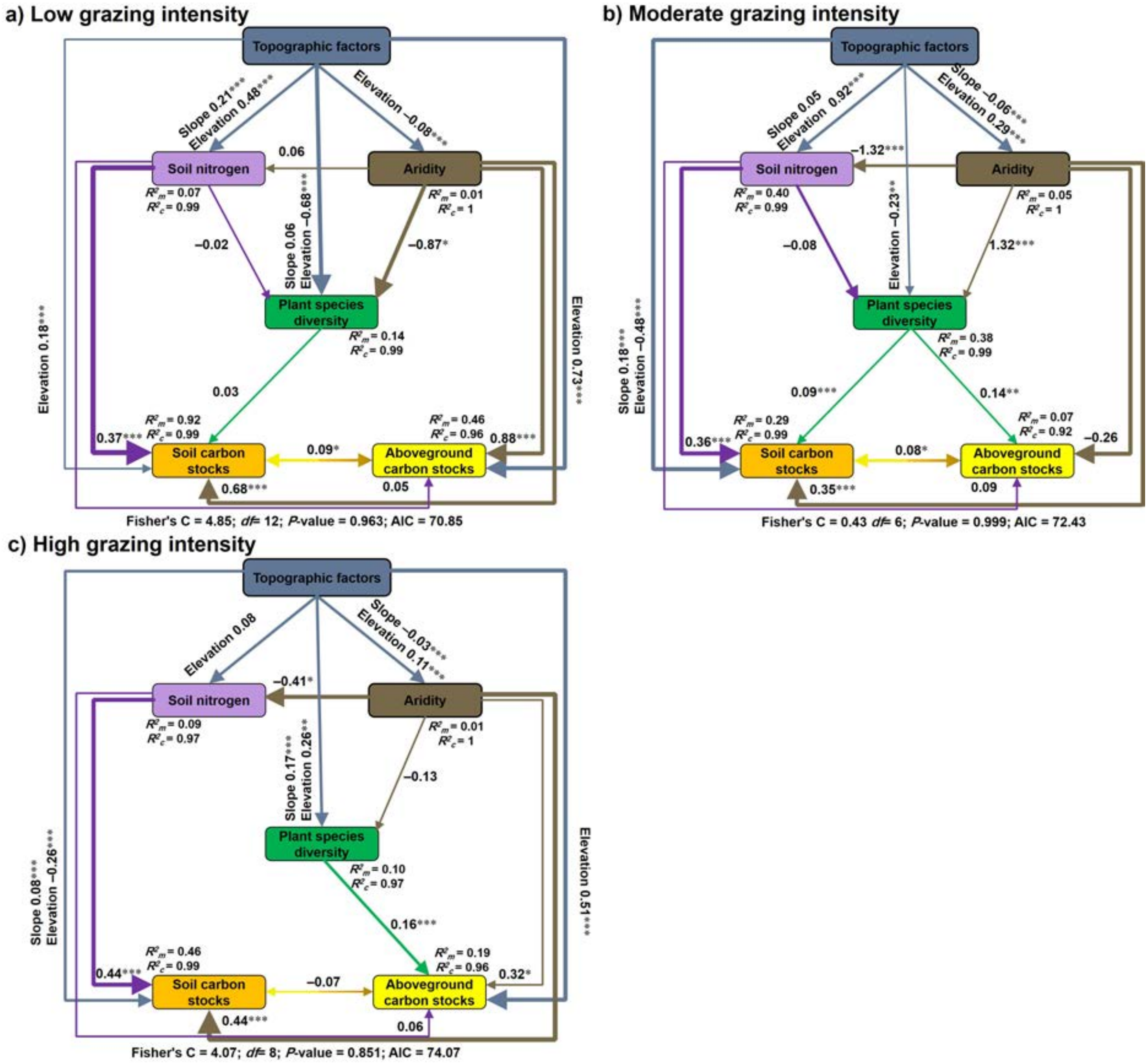


Figure S8. Diagrams of the piece-wise structural equation models (pSEM) linking aboveground carbon stocks, soil carbon stocks and species diversity (Shannon's H) to topography, climate and soil fertility in natural rangelands across (a) low (b), moderate (c) and high grazing intensity. Significance levels are shown as ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$ and pathways without asterisks are not significant. The colour of the arrows corresponds to the colour of the predictor variables and for each exogenous variable, conditional (c) and marginal (m) R^2 values are provided, where R^2_c represents the variance explained by both fixed and random effects, and R^2_m represents the variance explained by fixed effects only. Widths of paths are scaled by standardized path coefficients. Model-fit statistics are given below each model diagram.