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Species co-occurrence shapes spatial variability in plant diversity–biomass relationships in natural rangelands under different grazing intensities

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Abstract

Grazing can alter plant species interactions in natural rangelands, which in turn might influence the productivity of the ecosystem but we do not fully understand how spatial variability in plant diversity-biomass relationships are modulated by grazing intensity. Here, we hypothesized that plant species co-occurrence in rangelands is mainly driven by niche segregation due to grazing and heterogeneity in local resources, and that grazing therefore modulates diversity–biomass relationships. We tested our hypothesis across 35 rangeland sites in Iran, using a species co-occurrence index to assess plant spatial aggregation within each site. At each site, we measured aboveground biomass, plant diversity, topography, soil nutrients and three levels of grazing intensity. High spatial segregation of plant communities (low species co-occurrence) was found at heavily grazed sites, whereas greater spatial aggregation (high species co-occurrence) was found on low and moderate grazed sites, showing varied associational patterns of species with grazing intensity. Soil nutrients increased with grazing intensity and spatial segregation of plant communities was greater at sites with high soil nutrient concentrations, indicating that grazing intensity influences the spatial heterogeneity of plant communities via nutrients deposited in urine and faeces. Declining plant biomass with grazing intensity was related to a strong decline in graminoid species diversity, which suggests that the diversity-biomass relationship is influenced by selective grazing of palatable species. The relationships between species co-occurrence and biomass or plant diversity suggest non-random patterns in species co-occurrences with grazing intensity, which could be the result of competition driven by high livestock grazing intensity. We therefore suggest that rangeland stocking rates should be managed properly to maintain rangeland production while promoting plant diversity.

Keywords: Diversity-biomass relationships, Species competition, Facilitation, Grazing intensity, Spatial segregation of plant communities

1. Introduction

Plant species diversity and productivity are important for the potential of natural ecosystems to provide goods and services (Grace et al., 2016). Experimental and observational studies support the assumption that plant species richness generally increases aboveground biomass or productivity (Grace et al., 2016; Tilman et al., 2001) and enhances ecosystem functioning (Balvanera et al., 2006; Isbell et al., 2011). The link between plant biodiversity and biomass production is particularly important in systems such as arid and semi-arid rangelands, where the native vegetation is a crucial source of forage for livestock as well as wild animals (Ellison, 1960), and provides an important source of income to support local livelihoods (Martin, Müller, Linstädter, & Frank, 2014). Rangelands in arid and semi-arid regions are structurally complex, species-rich plant communities (Gaitán et al., 2018; Sanaei, Ali, Ahmadaali, & Jahantab, 2018) and recent studies demonstrate that plant species diversity enhances aboveground biomass in semi-arid rangeland (Gaitán et al., 2014; Sanaei, Ali, Chahouki, & Jafari, 2018). Rangelands are increasingly exposed to multiple pressures due to human activities, including overgrazing (Eldridge, Poore, Ruiz-Colmenero, Letnic, & Soliveres, 2016) and climate changes (Ding, Travers, Delgado-Baquerizo, & Eldridge, 2020; Gaitán et al., 2018), which may alter plant diversity and associated ecosystem functions. To assess how these pressures will influence rangeland productivity, we first need to better understand how the relationship between species diversity and aboveground biomass is influenced by other factors such as biotic interactions and spatial heterogeneity.

Plant-plant and plant-soil interactions are important for the biodiversity and functioning of natural ecosystems at different scales (Figure 1; Eldridge & Delgado-Baquerizo, 2017; Gaitán et al., 2018; Wardle et al., 2004). High plant diversity depends on the ability of species to coexist within a community. Species coexistence has been attributed to niche theory, in which species with similar ecological niches compete more strongly with each other, whereas species with different resource requirements tend to compete less (Macarthur & Levins, 1967; Tilman, 1982). As less competitive species may struggle to coexist with superior competitors in natural communities (Chesson, 2000; Tilman et al., 1997), competitive exclusion can shape community assembly and function (Grime, 1973). More specifically, competitive interactions can create spatial segregation, which results in low species co-occurrences (Reitalu et al., 2008). By contrast, niche differentiation, in which species with distinct functional traits are able to use the available resources more efficiently, can improve ecosystem functioning (Tilman et al., 2001). Facilitation can also occur through niche differentiation, when some species modify the local environment in such a way that promotes the persistence of other species (Loreau & Hector, 2001; Vandermeer, 1989). Collectively, niche differentiation and facilitation produce niche complementarity, which increases biodiversity and ecosystem functioning (Loreau & Hector, 2001). Environmental heterogeneity can strengthen the effect of biodiversity on ecosystem functioning (Tylianakis et al., 2008), for example by increasing plant biodiversity through niche partitioning and niche complementarity (Fuhlendorf, Engle, Elmore, Limb, & Bidwell, 2012; Yang et al., 2015). However, we do not fully understand the combined effects of environmental heterogeneity and species co-occurrence on the species diversity–biomass relationships in natural plant communities (see Figure 1).

In rangelands, livestock grazing is one of the most crucial factors in shaping plant community assembly (Eldridge et al., 2016; Saiz & Alados, 2012; Sanaei, Ali, Chahouki, et al., 2018). Grazing has a strong influence on species diversity, plant species distribution and spatial heterogeneity by reducing competition and promoting colonization by new species (Adler, Raff, & Lauenroth, 2001). First, grazing selectively removes palatable species (Díaz et al., 2007), which alters plant community composition and may reduce competition. Second, urine and faeces from livestock create nutrient hotspots (Lezama & Paruelo, 2016), which increase aboveground biomass through rapid plant growth (Quesada et al., 2012), but also promote species competition, mortality and turnover rates (Malhi et al., 2006), resulting in lower plant species diversity (Borer et al., 2014; Huston, 1979). Finally, grazing animals facilitate seed dispersal, which could increase species coexistence (Shea, Roxburgh, & Rauschert, 2004). Consequently, grazing can both enhance or reduce plant diversity and species coexistence through a variety of direct and indirect effects, and the impacts vary strongly with the extent of grazing pressure (Bakker, Ritchie, Olff, Milchunas, & Knops, 2006; Bello, Leqa, & Sebastià, 2006). According to the intermediate disturbance hypothesis, species diversity should be highest at intermediate grazing intensities and decline at low or high levels of disturbance (Connell, 1978). However, the intermediate diversity hypothesis does not always apply to systems with harsh environmental conditions, such as arid and semi-arid rangelands (Gao & Carmel, 2020; Sasaki et al., 2009). Hence, grazing interacts with other drivers of plant community assembly at different scales, which are likely to modify biodiversity-biomass relationships in rangelands.

Given that grazing pressure is intensifying in many rangelands worldwide, we aimed to determine how the combined influence of spatial heterogeneity and grazing modulates biodiversity and biomass by quantifying the extent to which species co-occurrence is driven by niche segregation due to grazing and heterogeneity in local resources. To this end, we studied 35 semi-steppe rangeland sites along a gradient of grazing intensity. We focused on Iranian rangelands, because of their national economic importance and long history of utilization for grazing by livestock (Hosseininia, Azadi, Zarafshani, Samari, & Witlox, 2013). Substantial degradation of these valuable natural ecosystems is occurring due to overpopulation, overexploitation and unsustainable development (United Nations Development Program, 2006). Furthermore, the unsustainable use of rangelands is being intensified by climate change (Rahmanian et al., 2020).

The aim of the present study was to assess the impacts of grazing intensity on plant diversity, species co-occurrence and aboveground biomass across whole plant communities and within three distinct plant growth forms. We addressed three main questions: First, are plant diversity and aboveground biomass associated with species co-occurrence? Second, does grazing intensity explain plant species co-occurrence or differences in diversity and aboveground biomass among sites? Third, do topography and soil nutrients modify the relationships between plant species co-occurrence, diversity, and aboveground biomass? .

2. Materials and Methods

2.1. Study sites and design

The research was undertaken in 2014 in the semi-steppe rangelands located in the center of the Taleghan region (36º08'10''N, 50º43'10''E) in Alborz Province, Iran (Figure S1 in Supplementary Material). The altitude ranges from 1900 to 2500 m above sea level, and the slope ranges between 1° and 23º. The mean annual temperature is 7.5 °C, and the annual rainfall is 460-600 mm (Sanaei, Ali, & Chahouki, 2018). The predominant soil types are Regosols and Cambisols (World Reference Base for Soil Resources, 2006) and for this study, 35 sites with varying abiotic and biotic conditions were selected (Table S1 in Supplementary Material). At each site, we established 21 quadrats measuring 1 m × 1 m (735 quadrats in total) according to a random-stratified sampling design (Hirzel & Guisan, 2002). The 1 m^2 quadrat size was deemed suitable for semi-steppe vegetation comprising graminoids, forbs, and small shrubs, where the size of the quadrat clearly exceeded the size of individual plants (e.g. Lundholm, 2009). We classified all study sites into three grazing intensity levels: 1) low grazing intensity (n = 9 sites), 2) moderate grazing intensity (n = 13 sites), and 3) high grazing intensity (n = 13 sites). As the studied rangelands were freely grazed, it was not possible to define grazing intensity based on stocking density. Instead, grazing intensity at each site was estimated based on recent observations and past grazing pressure, including signs of grazed vegetation, evidence of trampling, as well as local expert knowledge, based on general recommendations for assessing rangeland condition (Mannetje & Jones, 2000; Parker, 1954). The coordinates of each quadrat were recorded by hand-held GPS, and elevation and slope were subsequently derived from digital elevation models.

Within each quadrat, we identified all plants and estimated the percentage cover of each species. We assigned each species to one of three plant growth forms: shrubs, forbs or graminoids (Sanaei, Ali, & Chahouki, 2018). To measure annual aboveground biomass, all individual forbs and graminoids within each quadrat were clipped to ground level during peak biomass growth (between May and June). For shrub species, we collected the current year's branch growth and leaves. All samples were weighed after drying for 24 hours at 70 °C (Sanaei, Ali, & Chahouki, 2018).

To investigate how abiotic factors (soil nutrients) influence plant species co-occurrence, diversity, and biomass, we collected one soil sample at 0-30 cm depth (5-cm diameter) within each quadrat, then the soil samples were dried and sieved (2 mm) in the laboratory. We measured total soil phosphorus (P), nitrogen (N) and potassium (K), where P was extracted in 0.5 M $NaHCO_3$ and measured by colorimetry (Murphy & Riley, 1962), N was analyzed using the Kjeldahl method (Bremner, 1996), and K was analysed by the ammonium acetate and Na^2-EDTA method using flame photometry (Warncke & Brown, 1998). A summary of descriptive statistics for all variables is given in Table S1.

2.2. Data analyses

All data analyses were carried out in R 3.6.1 (R Development Core Team, 2019). For each quadrat, we calculated species richness (S = total number of observed species), Shannon diversity (Hs, based on plant species richness and the abundance of a given species relative to the total species in each quadrat), and Pielou's evenness [$J=Hs/\log(S)$] using the *vegan* package (Oksanen et al., 2015). To compare ecosystem variability across the 35 sites, we used the data from the 21 quadrats per site to calculate mean Shannon's diversity, species richness, evenness and aboveground biomass of all plants and for each growth form individually (shrubs, forbs, and graminoids).

2.2.1. Species co-occurrence

We assessed patterns of species co-occurrence within each site (35 sites) using the *EcoSimR* package (Gotelli, Hart, & Ellison, 2015). First, we calculated the co-occurrence index using the checkerboard score (C-score; Stone & Roberts, 1992) based on a presence-absence matrix for each site (35 matrices in total), where rows corresponded to species and columns to quadrats, indicating the presence (1) or absence (0) of a given species within a particular quadrat (Gotelli & Graves, 1996). Then, for each unique pair of species, the C-score was calculated as:

$\mathrm{C_{ij}} = (\mathrm{R_i} - \mathrm{S})(\mathrm{R_j} - \mathrm{S})$ (Equation 1)

where R_i and R_j are the row sums for species i and j, and S is the number of shared quadrats in which both species i and species j were present (Stone & Roberts, 1992). The C-score for each site was then calculated as the mean C_{ij} of all possible species pairs present at each site. Thus, a high C-score indicates a spatially segregated community characterized by low species co-occurrence whereas a low C-score indicates a spatially aggregated community characterized by high species co-occurrence (Tirado, Pugnaire, & Eriksson, 2005). Subsequently, to account for differences in species' frequency distributions among sites, we created a null model (random species distribution) for each site: for each presence/absence matrix, an expected C-score was calculated based on 5000 simulated matrices, built by randomizing the presences of the species within quadrats, while keeping the sum of rows and columns constant, i.e. the presence of each species across quadrats and the number of species within each quadrat are kept constant (Gotelli, 2000). Finally, we compared C-scores among sites, while accounting for differences in species richness, by calculating the standardized effect size (C_{STD}) for each matrix (Bowker, Soliveres, & Maestre, 2010; Gotelli & Entsminger, 2006) as:

$$C_{STD} = \frac{(\text{observed C}-\text{score} - \text{mean simulated C}-\text{score})}{\text{standard deviation of simulated C}-\text{scores}} \qquad \text{(Equation 2)}$$

Where positive C_{STD}-scores indicate low co-occurrence or high spatial segregation (Observed C-score > Simulated C-score), whereas negative C_{STD}-scores show greater species co-occurrence or high spatial aggregation (Observed C-score < Simulated C-score; Bowker et al., 2010).

2.2.2. Assessing the influence of soil nutrients

To assess the influence of soil nutrients on species co-occurrence, diversity and biomass, we first reduced collinearity among soil nutrients (Figure S2) using Principal Component Analyses (PCA) based on the soil chemical properties (Table S2). In all subsequent statistical analyses, we used the first axis (PC1) of the PCA to represent differences in soil nutrients among sites, whereby higher PC1 values for soil nutrients represent higher soil N and P but lower soil K concentrations.

2.3. Statistical analyses

To assess how grazing intensity influences the patterns of soil nutrients, species co-occurrence, diversity and biomass across the 35 sites, we performed one-way analysis of variance for all plants and for each plant growth form separately. Where the overall effects of grazing intensity were significant ($P<0.05$), we subsequently performed Tukey's post-hoc tests to assess differences among the three levels of grazing intensity. For all ANOVAs, we checked the assumptions of data normality and assessed homogeneity of variances using the Levene test ($P>0.05$ in all cases).

To test the direct and indirect relationships among species co-occurrence, species diversity, and biomass across all plants and for each of the three plant growth forms, we constructed structural equation models (SEMs) in the *lavaan* package (Rosseel, 2012). All variables were log-transformed and then standardized by their mean and standard deviation before analysis (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). The overall goodness of fit of each SEM was assessed by a χ^2-test and associated p-value, the standardized root mean square residual (SRMR), root mean square error of approximation (RMSEA), comparative fit index (CFI), Tucker-Lewis Index (TLI), and goodness-of-fit index (GFI). The best fit model included all pathways from the *a priori model* except for the non-significant direct pathway between C-score and slope. In addition, we calculated the relative contribution of tested predictors on aboveground biomass. Bivariate regression relationships and Pearson correlation coefficients amongst all tested variables were assessed to visually complement the results from SEMs (Supplementary Figures S2-S7). We performed additional SEMs based on species richness and evenness following the same procedures, which provided strikingly similar results to the SEMs based on Shannon's Diversity (Supplementary Figures S8-S9). We thus only present the results for the SEMs based on Shannon's diversity.

Finally, we assessed site-level differences in plant species composition using multivariate analyses in the *vegan* package (Oksanen et al., 2015). The effects of grazing intensity on plant community composition were examined by permutational multivariate analysis of variance (PerMANOVA; *adonis* function) with 999 permutations. To visualize differences among plant communities, we performed non-metric multidimensional scaling (NMDS) ordination based on the relative cover of individual species and Bray-Curtis dissimilarities (*metaMDS* function), achieving a stable two-dimensional solution (stress score < 0.2 and $r^2 > 0.95$). We then used vector-fitting to the NMDS ordinations (*envfit* function) to determine whether the distribution of quadrats in ordination space was explained by soil nutrients, elevation, slope, or the relative proportions of each plant growth forms, using 999 random permutations to generate significance values, and included significant (P<0.05) explanatory variables as arrows in the ordination plot.

3. Results

The highest species diversity was found at moderately grazed sites for all plants (Figure 2a; P=0.065), shrubs (Figure 2d; P=0.016) and forbs (Figure 2f; P<0.001) but not graminoids (Figure 2h; P=0.174). Plant biomass was generally reduced at sites with high grazing intensity compared to sites with moderate or low grazing for all plants (Figure 2b; P<0.001), and within shrubs (Figure 2e; P=0.004) and graminoids (Figure 2i; P<0.001) but not forbs (Figure 2g; P=0.457). Greater spatial segregation (higher C_{STD}) of plant communities was observed at sites with high grazing intensity, whereas greater spatial aggregation of plant communities (lower C_{STD}) was observed at sites with low and moderate grazing intensities (Figure 2c; P=0.005).

Plant biomass was strongly negatively associated with grazing intensity (Figure 3a,b,d), as was the biomass of shrubs and graminoids, whereas the negative association with forb biomass was not significant (Figure 3c). There was no significant relationship between plant diversity and grazing intensity for all plants, or within shrubs and forbs (Figure 3a,b,c), but graminoid species diversity declined significantly with increasing grazing intensity (Figure 3d). In addition, soil nutrients increased with grazing intensity (Figure 3) and species segregation substantially increased with increasing soil nutrients; consequently, species segregation also increased markedly with grazing intensity (Figure 3). The biomass of all plants and graminoids increased with elevation (Figure 3a,d) but only the diversity of forbs increased with elevation (Figure 3c).

The weak indirect relationship between grazing intensity and plant biomass was mediated by species diversity and co-occurrences (Figure 4a,b,c.d, and Table S3). The biomass of all plants declined significantly with increasing species segregation (Figure 3a), the biomass of graminoids declined moderately (Figure 3d), whereas the biomass of shrubs and forbs increased moderately (Figure 3b,c). Finally, biomass generally increased with increasing plant species diversity. The biomass of all plants increased slightly with increasing diversity (Figure 3a), which was explained by a strong increase in the biomass of shrubs and forbs (Figure 3b,c), but a small decline in the biomass of graminoids (Figure 3d).

Plant species composition at the site level was strongly influenced by grazing intensity (PERMANOVA, $F_{2,32} = 4.31$, $p < 0.001$) and NMDS ordination showed a clear separation between sites with low and high grazing intensities (Figure 5). Vector fitting to the NMDS ordination revealed that plant community composition changed markedly with slope ($r^2 = 0.45$, $p = 0.001$) and elevation ($r^2 = 0.81$, $p = 0.001$) but that soil nutrients contributed to the separation of sites with low or high grazing intensity ($r^2 = 0.25$, $p = 0.014$). Overall variation in plant communities was strongly associated with differences in the relative cover of grasses ($r^2 = 0.63$, $p = 0.001$) and forbs ($r^2 = 0.35$, $p = 0.002$; Figure 5).

4. Discussion

Despite intense grazing pressures on aboveground biomass, our study demonstrates that species co-occurrence nonetheless plays an important role in shaping plant diversity and biomass production. We revealed a strong association between grazing and species segregation, which suggests that grazing creates spatial heterogeneity in plant communities by affecting the mechanisms of species coexistence. Although there was no overall relationship between plant diversity and aboveground biomass, the strong positive relationship between the diversity and biomass of shrubs and forbs indicates that niche differentiation may explain the relationships between grazing and species co-occurrence at our study sites. Niche differentiation as a control of species coexistence is further indicated by the relationship between soil nutrients and species segregation, but not between soil nutrients and plant diversity. Finally, niche differentiation is also supported by the separation of plant communities at different levels of grazing intensity, which was related to differences in nutrient availability.

Livestock grazing is recognized as one of the main factors shaping plant-plant interactions and ecosystem functions (Saiz & Alados, 2012; Sanaei, Ali, Chahouki, et al., 2018; Smit, Rietkerk, & Wassen, 2009) as well as soil properties (Wei, Hai-Zhou, Zhi-Nan, & Gao-Lin, 2011) in rangelands. Biomass consumption is one of the major direct effects of grazing (Olff & Ritchie, 1998), but herbivores have distinct feeding preferences depending on plant species (Hiernaux, 1998). Given the differences in grazing pressures among plants of different growth forms, it is perhaps unsurprising that we found no overall relationship between plant diversity and aboveground biomass, as biomass-diversity relationships differed among plant growth forms, depending largely on the extent of biomass removal by grazing. Graminoids are the main source of fodder for livestock in rangelands (Bosco, Bertiller, & Carrera, 2018; Larreguy, Carrera, & Bertiller, 2017; Sanaei, Ali, & Chahouki, 2018), and the marked decline in graminoid biomass and diversity with heavy grazing (Figure .2h and 3d) indicates high palatability of most graminoid species at our study sites (Khojasteh, Chahouki, Azarnivand, & Kikvidze, 2013; Sanaei, Ali, & Chahouki, 2018), which has also been observed in other semi-arid ecosystems (Saiz & Alados, 2012). Biomass removal by livestock thus explains the weak diversity-biomass relationship for graminoids (Figure 3d). By contrast, forb diversity increased with both moderate and heavy grazing (Figure 2f), which could indicate that some forb species benefitted from reduced competition with graminoids and shrubs, or were able to colonize disturbed areas (Dickson & Busby, 2009). Consequently, although the increase in forb biomass with grazing intensity was not significant (Figure 2g), forbs showed the strongest biomass-diversity relationship (Figure 3c).

Livestock selection for more palatable species created a heterogeneous landscape of segregated plant communities with varying aboveground productivity, indicated by higher species segregation (higher C-scores) with increasing grazing intensity (Figure 2c) and distinct plant community composition at high vs. low levels of grazing (Figure 5). We measured the highest plant diversity at moderately grazed sites, which is consistent with the intermediate disturbance hypothesis (Connell, 1978). By contrast, overgrazing in arid plant communities can result in the collapse of vegetation patches that act as fertility islands, which reduces the overall spatial aggregation of the community (Kéfi et al., 2007). Thus, the decline in species co-occurrence we observed in response to heavy grazing likely results from local dominance of grazing-tolerant plants (Saiz & Alados, 2012). Hence, although grazing explained most of the variance in overall aboveground plant biomass in our study, the co-occurrence of species of different plant growth forms also played an important role (Figure 3), indicating that grazing influenced plant productivity not only directly via biomass removal, but also indirectly by altering plant community composition and species co-occurrences at our study sites (Figure 5; Haddad et al., 2008; Reitalu et al., 2008; Sanaei, Li, & Ali, 2019).

Previous studies have found that biodiversity alone is not enough to explain spatial variability in plant biomass because functional niche complementarity plays a key role in BEF relationships (Weigelt, Schumacher, Roscher, & Schmid, 2008). In our study, functional niche complementarity conceivably explains the strong influence of soil nutrients on species co-occurrence. Nutrient enrichment is a major driver of community competition in grasslands (Harpole et al., 2016) and accordingly, we found that spatial segregation increased with soil nutrient concentrations (in our case N and P), and that differences in soil nutrients contributed to the distinct plant communities in sites with high vs. low grazing intensity (Figure 5). The direct relationship between soil nutrients and species co-occurrence indicates that species competition and environmental variables are important drivers in shaping vegetation spatial assemblages (Ulrich, Sewerniak, Puchałka, & Piwczyński, 2017; Vaz, Macedo, Alves, Honrado, & Lomba, 2015). Biomass growth in nutrient-rich soils can promote intense competition, resulting in lower diversity (Quesada et al., 2012). Although we did not find strong evidence to support a negative effect of soil nutrients on plant diversity, community composition was clearly related to differences in soil nutrients (Figure 5) and the relationship between soil nutrients and aboveground biomass differed among plant growth forms. Plants with distinct growth forms have different responses to soil nutrients, especially N (He et al., 2016). Hence, a greater relative influence of soil nutrients on the aboveground biomass of shrubs compared to forbs and graminoids in our study suggests that grazing pressure and soil nutrients might interact to promote niche differentiation, while also increasing competition among plants with the same growth form, which would result in the spatial segregation we observed at our study sites.

The effects of grazing persisted despite the marked topographical gradients across our study sites. Increased diversity of forbs with elevation likely reflects the increasingly specialized plant communities in harsh conditions (Moody & Meentemeyer, 2001; Wehn, Lundemo, & Holten, 2014), whereas greater biomass of all plants and graminoids with elevation could be the result of greater water availability at altitude (Carlyle, Fraser, & Turkington, 2014). Indeed, the distinct responses of different plant growth forms to the environmental conditions determined by elevation and slope explained much of the variation in plant community composition among sites across all grazing intensities (Figure 5). Thus, our study demonstrates that species co-occurrence varies strongly according to grazing pressure, nutrient availability, and topography at our semi-arid rangeland sites. Importantly, the differences in species co-occurrence largely explain variation in aboveground biomass, highlighting the importance of niche segregation for species coexistence (Silvertown, 2004), even in disturbed systems with harsh environmental conditions.

5. Conclusions

Species co-occurrences were strongly associated with grazing and nutrient inputs from livestock and played an important role in shaping overall plant biodiversity and biomass. Despite substantial biomass removal by livestock, we nonetheless demonstrate strong biodiversity-biomass relationships for shrubs and forbs, although the distinct effects of grazing and niche differentiation among plants of different growth forms obscured the overall diversity–biomass relationship in these rangelands. Hence, high grazing intensity resulted in distinct, spatially segregated plant communities and altered plant community structure by differentially affecting shrubs, forbs and graminoids. Consequently, low to moderate stocking rates could help maintain rangeland productivity while promoting plant diversity.

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Data Accessibility

We will publish the data used in this study on Dryad upon acceptance.

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Figure 1.

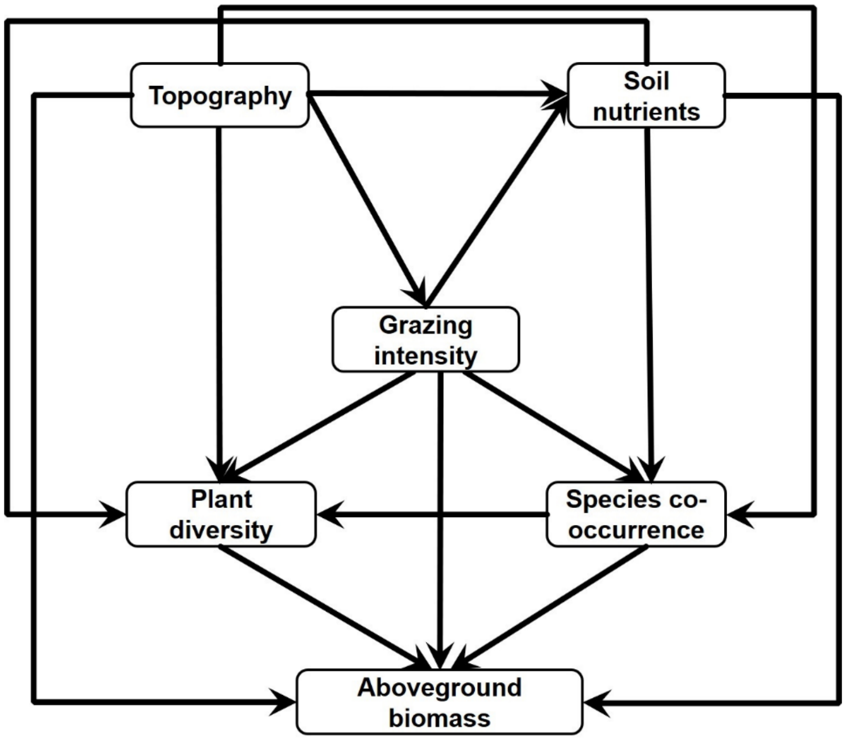

Figure 1. A conceptual model representing the links between plant species co-occurrences, species diversity and aboveground biomass in semi-steppe rangelands, considering the effects of topography, soil nutrient availability and grazing intensity.

Figure 2.

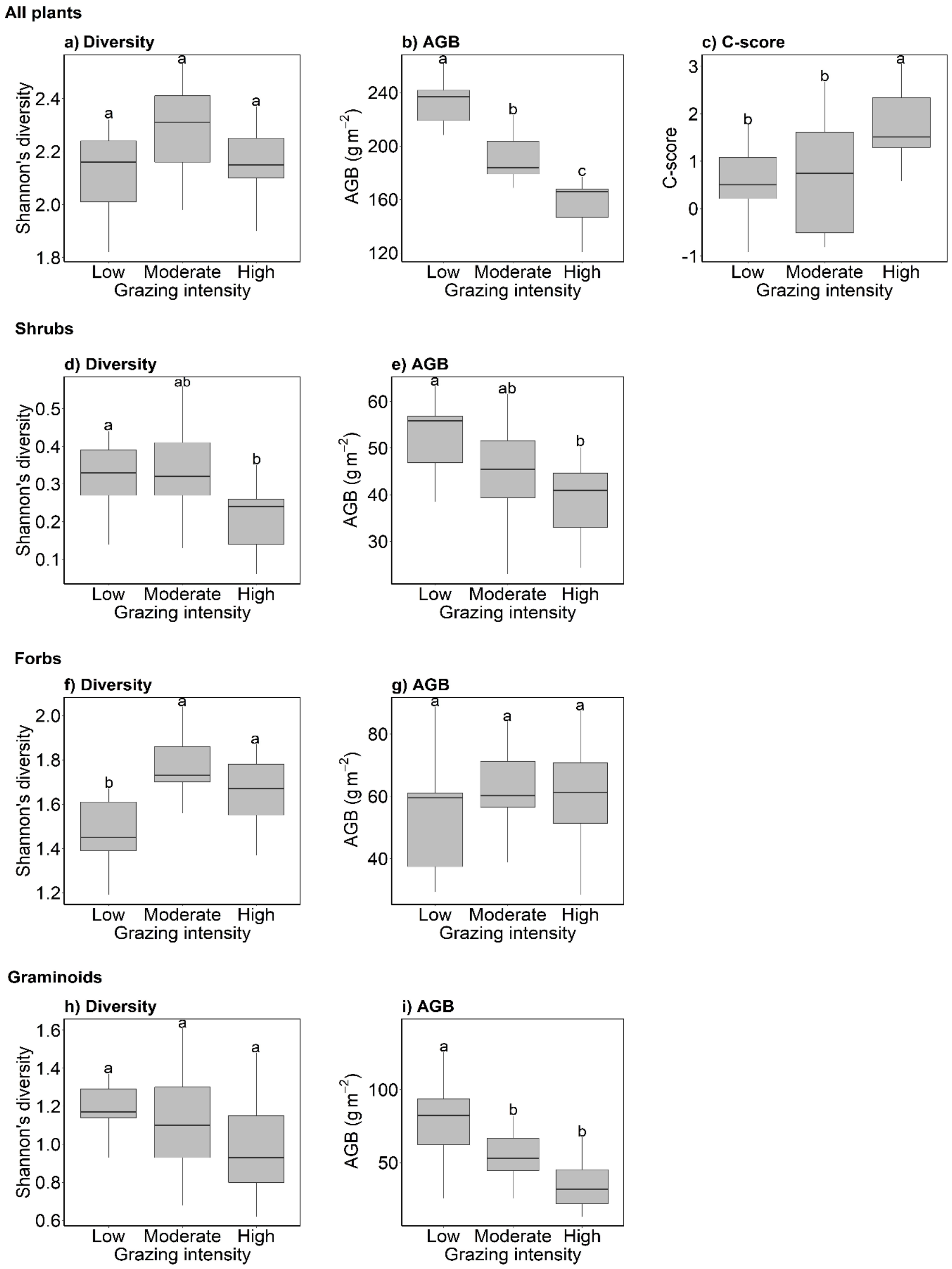

Figure 2. Changes in plant diversity (a,d,f,h), aboveground biomass (AGB; b,e,g,i), and species C-score index (c) for all plants(a-c), shrubs (d,e), forbs (f,g) and graminoids (h,i) at three levels of grazing intensity in a semi-steppe rangeland in Iran. Different letters above boxes represent significant differences among grazing intensities (*P*<0.05; Tukey's test). Boxes and whiskers indicate interquartile ranges, and median lines are given for *n* = 9, *n* = 13, and *n* = 13 sites with low, moderate and high grazing intensity, respectively.

Figure 3.

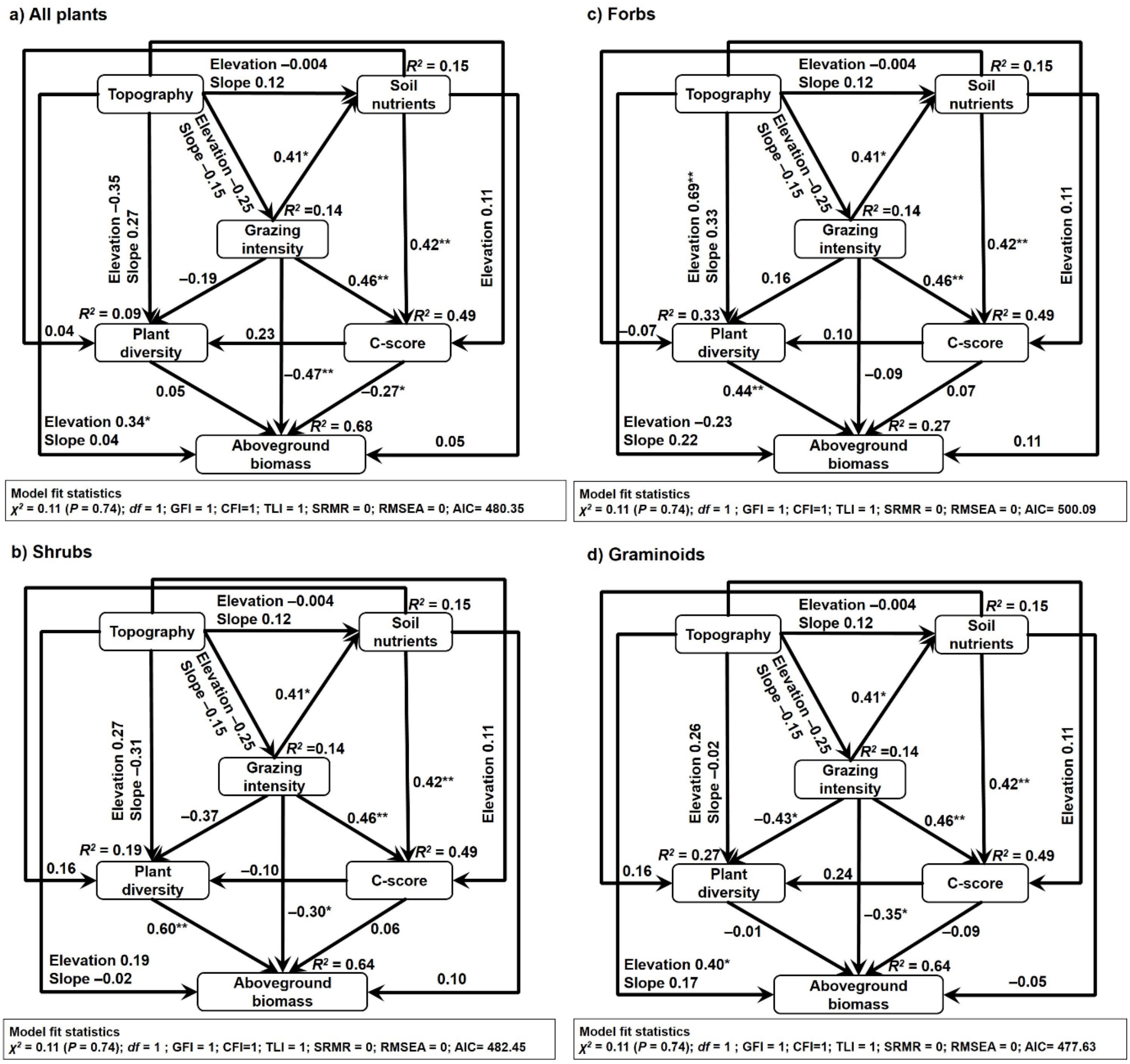

Figure 3. Final structural equation models (SEMs) showing relationships among plant species C-scores (all plants), diversity, grazing intensity, topography (elevation and slope) and soil nutrient for all plants (a), shrubs (b), forbs (c) and graminoids (d). Significance levels are shown as ***P* < 0.01, **P* < 0.05 and pathways without asterisks are not significant. The variance explained by the model (R^2) is shown for each response variable. See Table S3 for details.

Figure 4.

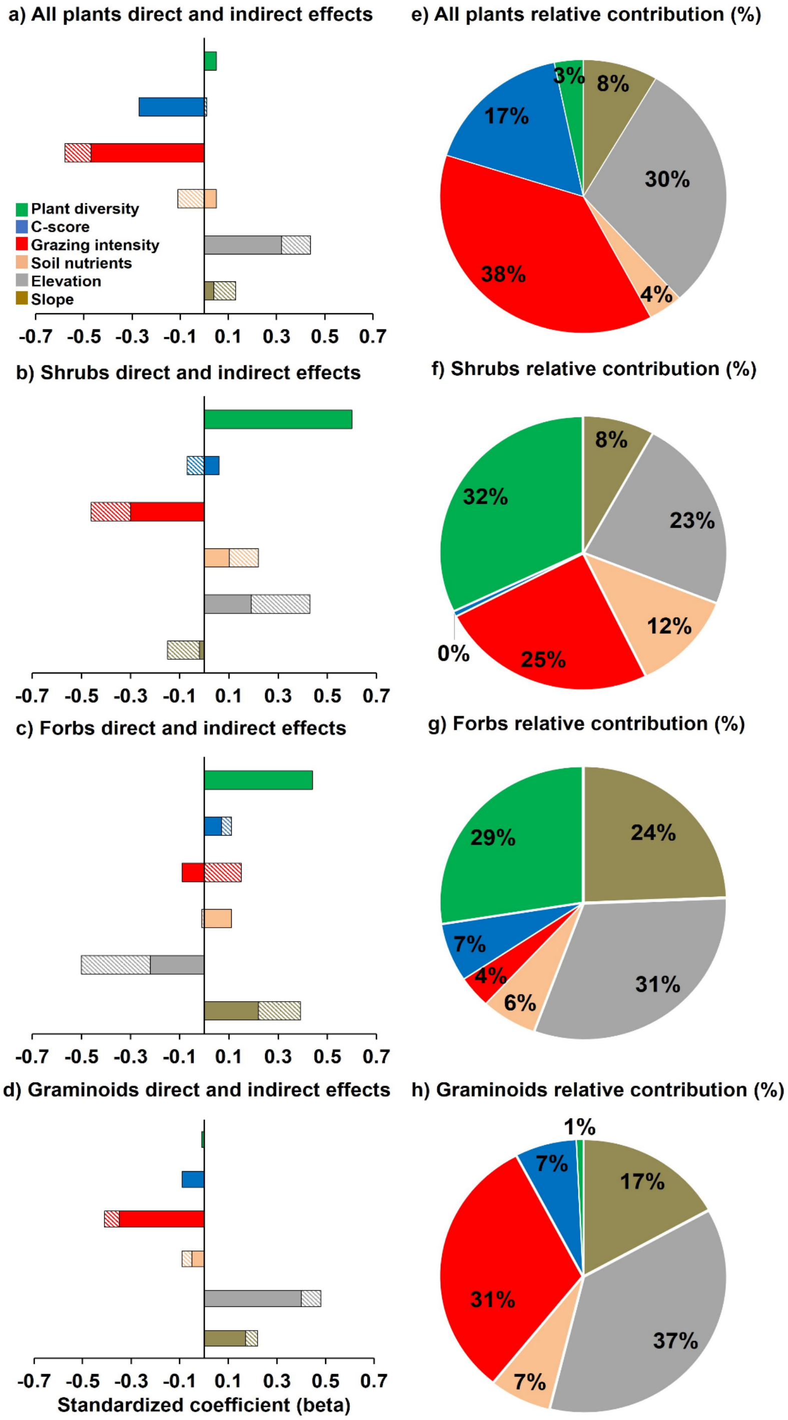

Figure 4. The direct and indirect effects (bar charts) and relative contributions (pie-charts) of plant species C-scores, diversity, grazing intensity, topography (elevation and slope) and soil nutrients on aboveground biomass for all plants (a,e), shrubs (b,f), forbs (c,g) and graminoids (d,h). Bar charts (a-d) show direct (solid colour) and indirect effects (striped) on aboveground biomass, and pie-charts (e-h) show the relative contributions of each variable to aboveground biomass.

Figure 5.

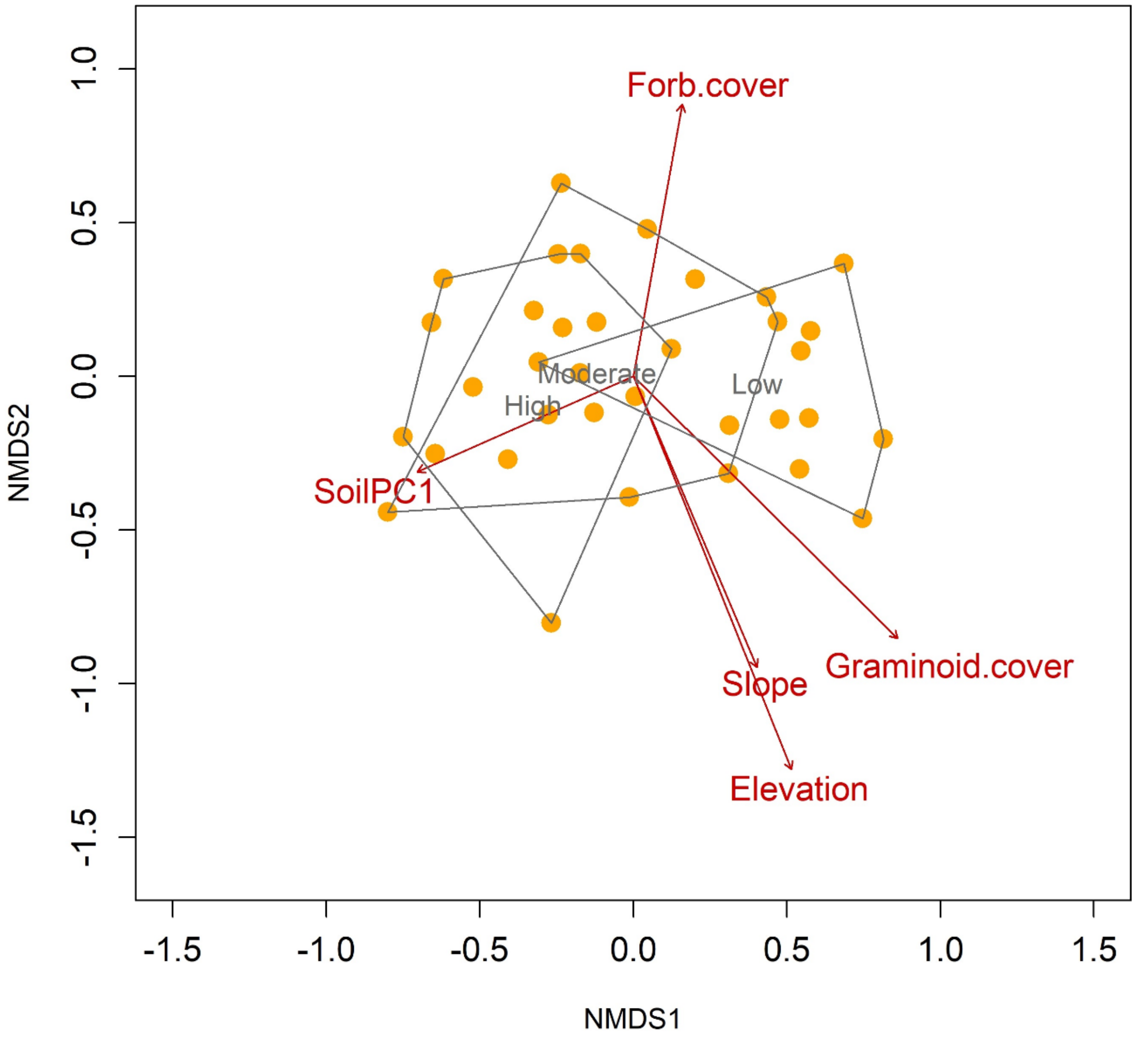

Figure 5. Ordination plot of plant community composition from non-metric multidimensional scaling analysis of relative plant cover based on Bray-Curtis dissimilarities. Points indicate individual sites, and hulls represent grazing intensity levels (high, moderate, low); significant correlations of topography (slope and elevation), soil nutrients (Soil.PC1), or the relative cover of plant growth forms (Graminoid.cover and Forb.cover) with ordination axes are shown as arrows.