Abiotic and biotic drivers of aboveground biomass in semi-steppe rangelands

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HIGHLIGHTS
• Aboveground biomass was driven by the niche complementarity and/or selection effects.
• Biotic factors best predicted aboveground biomass across plant growth forms and at whole-community level.
• Aboveground biomass increased with species richness and plant coverage.
• The negative relationship between species evenness and aboveground biomass indicates few dominant species in whole-community.

GRAPHICAL ABSTRACT

ABSTRACT
Rangelands play an important role in the biodiversity conservation and ecosystem functions. Yet, few studies have assessed the effects of biotic and abiotic factors on aboveground biomass across plant growth forms and at whole-community level in rangelands. Here, we hypothesized that aboveground biomass is driven by both biotic (plant coverage, species richness and evenness) and abiotic factors (soil textural properties and topographic factors) but biotic factors may best predict aboveground biomass, probably due to small spatial scale. To test this hypothesis, we performed multiple linear mixed model by including biotic and biotic factors as fixed effects while sites aspects and plant community types across sites, and disturbance intensities as random effects, using data from 735 quadrats across 35 sites in semi-steppe rangelands in Iran. The optimal model for shrubs showed that aboveground biomass was positively related to plant coverage, species richness, elevation, sand, silt and clay. Aboveground biomass of forbs and grasses was positively related to plant coverage, species richness, elevation and slope. Whole-community aboveground biomass was positively related to plant cover, species richness and elevation, but negatively to species evenness and slope. We conclude that higher aboveground biomass is related to high species richness and plant cover, and located on high elevation and/or slope across plant growth forms while having medium-coarse-textured to fine-textured soils for adaptation of shrubs only. Few dominant species or niche overlap in whole-community may also drive high aboveground biomass, and located on high elevation with gentle slope. Therefore, we found support for both the niche complementarity and

Keywords:
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Biodiversity
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Plant coverage
Plant growth forms

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selection effects across plant growth forms and at whole-community. In addition, this study shows that plant coverage is the best proxy for aboveground biomass in the studied rangelands.

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1. Introduction

Rangeland is a natural ecosystem supporting indigenous vegetation consisting of grasses, forbs and shrubs, and predominantly occurs in arid and semi-arid regions (Allen et al., 2011). Rangelands, which compose nearly 25% of the world’s land area, include grasslands, scrublands, woodlands, wetlands, and deserts (Alkemade et al., 2013). Rangelands deliver numerous supporting and regulating ecosystem services such as forage production, carbon sequestration, water quantity and quality, and biodiversity conservation (Havstad et al., 2007). The abilities of ecosystem functions (i.e. aboveground biomass or productivity) of rangelands to provide essential ecosystem services are interactively driven by biotic and abiotic factors such as biodiversity, climate, topographic factors and land management (Díaz et al., 2007; Ruppert et al., 2012).

Biodiversity can quantify both by species richness (the number of plant species in a given area) and species evenness (a measure of how equitably species abundances are distributed in a given area) (Polley et al., 2003). Several ecological hypotheses have been put forward to explain the relationships between biotic (e.g. biodiversity) factors and aboveground biomass or productivity (Grime, 1998). The most prominent relationships between biodiversity and aboveground biomass or productivity are: 1) the humped-back shape relationship, and 2) the positive relationship through niche complementarity. Under the humped-back relationship, species richness and productivity are positively related with increasing resources and environmental favourability until limits to species coexistence are reached at high productivity and species richness decreases (Grace et al., 2016; Grime, 1973). Therefore, it is also plausible that the negative relationships between species richness and aboveground biomass arise from the effects of environmental factors. For instance, soil fertility may enhance aboveground biomass but species richness may peak at intermediate soil fertility, producing a classic unimodal or humped-back relationship (Fraser et al., 2015; Grime, 1979). The niche complementarity hypothesis postulates that species having different niches are able to use available resources more efficiently or facilitate each other within a community, and thus enhancing aboveground biomass or productivity (Tilman et al., 2001). The selection hypothesis assumes that increased productivity is due to the by chance occurrence of a very productive species in the community (Loreau and Hector, 2001). Taken together, the mix of negative and positive relationships are also possible due to the variation in the species pool between sites and other random factors (Rahbek, 2005). Generally, the negative or positive relationships between species richness and aboveground biomass or productivity are scale-dependent in natural communities (Bai et al., 2007; Chisholm et al., 2013; Scheiner and Jones, 2002). For instance, biotic factors are expected to drive aboveground biomass due to the niche complementarity and/or selection effects at small scales, while abiotic factors (e.g. environmental gradients) are expected to drive patterns at large scales (Chisholm et al., 2013; Waide et al., 1999). Moreover, species richness is generally positively related to aboveground biomass and productivity at small scales, whereas mixed with negative relationships are becoming more common at large scales in natural communities (Bai et al., 2007; Chisholm et al., 2013; Zhang et al., 2011).

Besides species richness and evenness, the plant coverage may also be important for aboveground biomass or productivity because it strongly determines the structure and growth potential of rangeland or grassland vegetation (Grytnes, 2008; Ji et al., 2009). Heterogeneity in vegetation density (hence plant coverage) has been theorized to increase the capture and efficient utilization of light (Grace et al., 2016). For instance, plant coverage may positively affect aboveground biomass because a dense vegetation is associated with both more diversity and more biomass or productivity, and hence may positively contribute to vegetation growth through efficient utilization of resources among component species having different niches through the niche complementarity effect (e.g. Ji et al., 2009). In contrast, dense vegetation (high plant coverage) may explain less variation in aboveground biomass but high variation in species richness within a community, probably due to the effects of light and soil resources (Grytnes, 2000). Therefore, we anticipate that change in aboveground biomass in relation to abiotic and biotic factors may be the result of different plant growth forms within a community (Jennings et al., 2005; Ji et al., 2009). For instance, shrubs and some of perennial forbs are mostly dominating the upper layers while grasses and annual forbs are dominating the bottom layers in natural rangelands, since light limits plant performance in different vertical layers (Craine and Dybzinski, 2013; Hautier et al., 2009). Hence, aboveground biomass of different plant functional types should be analyzed individually to better understand changes in aboveground biomass, as different biotic and abiotic factors may have differential effects on them.

The abiotic factors that affect plant growth and productivity include topography (e.g. elevation and slope), soil, and climatic factors (Jiao et al., 2017; Sun et al., 2013). The elevation of the land affects plant growth and productivity primarily through temperature effect (Xu et al., 2017), while the steepness of a slope affects plant growth through solar radiation, wind velocity and soil type (Moeslund et al., 2013). Generally, the relationship between topography and climate variability is dominant in mountainous regions where elevations are moderate, i.e. <2500 m or so. Consequently, in mountainous regions, temperature and precipitation are increased in some regions while decreased in others. However, the interactions between topography and climate variability (including temperature and precipitation) can produce other patterns as well, and the spatial scales of these patterns vary from orogens to valley and ridges (Lookingbill and Urban, 2003; Vuille, 2011). Therefore, it is possible that dominance of certain plant growth forms may varies with topographic factors (Moeslund et al., 2013; Xu et al., 2017). As such, topographic factors (e.g. elevation and slope) are well-known to regulate soil and atmospheric moisture distribution and affect soil water availability, which in turn may affect aboveground biomass (Fisk et al., 1998).

In addition, physical and chemical properties (i.e. edaphic factors) of the soil have pronounced direct effects on plant growth and productivity (Jiao et al., 2017). The physical properties (i.e. soil texture and bulk density) affect the water holding capacity and supply to the plants while the chemical properties (i.e. soil pH and cation exchange capacity) determine its capacity to supply nutrients (Schoonoover and Crim, 2015). As such, soil textural properties have profound influences on soil nutrients, and water flow and availability (Sperry and Hacke, 2002), and as a consequent may influence aboveground biomass. One of the hypotheses related to the soil textural properties and productivity is the inverse-texture hypothesis which predicts that coarse-textured soils are expected to have greater productivity than fine-textured soils by reducing evaporation in arid regions, while fine-textured soils with higher water-holding capacities are expected to have more productivity in humid regions (Noy-Meir, 1973; Sala et al., 1988).

Beside the effects of abiotic and biotic factors, anthropogenic disturbances such as pasturing and local grazing disturbances such as livestock feeding may have strong influences on aboveground biomass...
productivity and species richness (Grace et al., 2016). A popular hypothesis explaining the relationship between species diversity and disturbance, the intermediate disturbance hypothesis, suggests the humped-back shape relationship such that intermediate levels of disturbance maintain the highest diversity (Connell, 1978). In addition, it has been suggested that variation in the aspect of sites may cause a variability in the distribution and composition of plant communities (Gong et al., 2008). Therefore, we tested our proposed hypothesis using multiple linear mixed model by including biotic and abiotic factors as fixed effects, while plant community types and aspect of sites across studied sites, and disturbance intensities as random effects (Fig. 1). In this study, we addressed the following two main questions: 1) how is aboveground biomass related with biotic and abiotic factors across plant growth forms and whole community while accounting for random factors? 2) What are the relative effect (measured in term of standardized coefficient) of biotic and abiotic factors for explaining variation in aboveground biomass across plant growth forms and whole-community, while accounting for random factors. We hypothesize that aboveground biomass is driven by both biotic and abiotic factors but biotic factors may best predict aboveground biomass, probably due to the small spatial scale, across plant growth forms and at whole-community level in semi-steppe rangelands. Our proposed hypothesis leads to the following three main predictions: 1) species richness, species evenness and plant coverage would have positive effects on aboveground biomass; 2) aboveground biomass would increase with increasing elevation and slope; and 3) coarse-textured soils would have higher aboveground biomass than fine-textured soils.

2. Materials and methods

2.1. Description of study area

This study was conducted in the middle section of Taleghan region (36°08′10″N 50°43′10″E) located in Alborz province in Iran (Fig. 2a). The elevation is ranges between 1900 and 2500 m a.s.l., and slope is ranges between 1 and 23°. The study sites are located within the central agroecological zone in Iran, where the soils are predominately Regosols and Cambisols (World Reference Base for Soil Resources, 2006). Lithology of the region is characterized by volcanic rocks, resistant sandstone, limestone conglomerate, fine-grained calcareous, low to moderate mineral gypsum and salt marls. The region has a semi-arid climate with a distinct dry season between June and October. The mean annual temperature is 7.5 °C, where minimum temperature is 4 °C during growing season in March while the maximum temperature in June is 26 °C. The annual precipitation is ranges between 460 and 600 mm, most of which falls between March and April, and in autumn (November) (Khojasteh et al., 2013).

2.2. Random factors used in the analyses

In this study, size of the 35 sites (varies from 1.5 to 57 ha) was randomly selected in semi-steppe rangelands, by following a type of random-systematic sampling method. As such, 21 quadrats within each study site (i.e. 735 quadrats in total) were established where first quadrat within each site was randomly selected and then other following quadrats were established at 10 to 600 m apart, depending on the area of the site (Fig. 2b). Each quadrat size was 1 m × 1 m. More specifically, we established 35 sites within the roughly 3 × 2.5 km study area based on the plant community structure and composition, slope, aspect, soil type, elevation, and disturbance regime. Therefore, the individual sites would be rather homogenous physiognomically. Each site was then assigned to one of the 18 different plant community types based on their floristic composition and relative abundance of dominant species (Table S1). The dominant species in different plant community types were shrubs such as Astragalus ascedens, Astragalus verus, Thymus kotschyanus and Acanthophyllum microcephalum; forbs such as Hypericum scabrum, Stachys lavandulifolia and Pterocephalus canus; and also grasses such as Agropyron intermedium, Agropyron trichophorum, Sipha barbata, and Heteranthelium piliferum.

The aspect of each quadrat was assessed through the digital elevation model using ArcGIS (version 9.3) spatial analyst tool (ESRI, 2008). In our studied area, we classified the aspects of quadrats based on eight geographic aspects such as North, North-East, North-West, West, South, South-West, South-East and East (Table S2). Studied sites were ascribed to five disturbance and stress levels (hereafter simply referred to ‘disturbance intensity’ or ‘disturbance levels’) based on the grazing intensities of livestock (i.e. low, moderate and high grazing), and soil conditions such as erosion, soil depth, percentage of gravel stone and rangeland condition (Table S3). Free grazing system was found as one of the common grazing practices in the study area.

2.3. Fixed factors used in the analyses

2.3.1. Biotic factors

In each quadrat, most of the plants were identified to species level in the field while some unidentified plants were collected, pressed and sent back to the Botanical Herbarium at university of Tehran in Iran for identification through the support of expert taxonomists. Plant species were classified into three major plant growth form, i.e., shrubs (chamaephytes and nanophanerophytes), forbs (hereafter simply referred to “forbs”) including herbaceous annual, biennial and perennial

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**Fig. 1.** Conceptual framework for the abiotic and biotic drivers of aboveground biomass in semi-steppe rangelands. Framework showing hypothesized relationships of how biotic factors (plant coverage, species richness and evenness) and abiotic factors (soil textural properties and topographic factors) affect aboveground biomass while accounting for random factors across plant growth forms and whole-community level.
forbs (geophytes/cryptophytes and hemicryptophytes), and grasses and sedges (graminoids, hereafter simply referred as “grasses”). Between May and June 2014, a time of peak biomass, plant coverage for each specific species was measured in each 1 m × 1 m quadrat (Ji et al., 2009). Plant coverage of each species was represented by the ratio of the shady area of a specific species to the total area of a quadrat (Ji et al., 2009). More specifically, each quadrat was further subdivided into four parts (e.g. 0.25 m² × 4 = 1 m²) by string for more precise estimation of the plant coverage. The calculation on the species richness and species evenness (Eq. (1)) for each quadrat was performed using the “vegan” package for the R 3.2.2 (Oksanen et al., 2015; R Development Core Team, 2015). Species richness is the number of species per plant growth form or whole-community within each quadrat.

\[
SE = \frac{-H_s}{\ln(s)}
\]  

(1)

where \( SE \) is species evenness, \( H_s \) is Shannon’s species diversity, \( H_s = -\sum_{i=1}^{s} p_i \times \ln(p_i) \), \( s \) is the total number of species while \( p_i \) is the proportion of plant coverage of \( i \)th species in a quadrat or per plant growth form within each quadrat.

The summary of plant coverage and aboveground biomass of the studied plant species across 735 quadrats of 35 sites is provided in Appendix S1.

2.3.2. Abiotic factors

To assess the effects of abiotic factors on aboveground biomass, we measured the soil texture properties including sand, silt, clay and gravel (particles > 2 mm in diameter); and topographic factors including elevation and slope.

In May and June 2014, 450 g of soils were collected from 0 to 30 cm depth within each quadrat. Soil samples were collected using a bulk density corer with a known volume. Thus, soil samples were collected from a total of 735 points to capture fine scale variation in soil properties in the study region. The soil samples were immediately transported to the laboratory in sealed plastic bags, where they were sieved (<2 mm) to homogenize the soil samples and to remove visible roots and small stones. In the laboratory, soil textural properties were measured through hydrometer Buoycous method (Gee and Bauder, 1986). The geographical coordinates and elevation of each plot were determined using a handheld Garmin Geographic Positioning System (GPS) (Garmin, 2007), and slope (in degrees) of each quadrat was assessed through the digital elevation model using ArcGIS (version 9.3) spatial analyst tool (ESRI, 2008). Summary of abiotic factors of 735 quadrats across 35 sites is provided in Appendix S1.

2.4. Response variable; measurement of aboveground biomass

We destructively measured aboveground biomass of each plant functional type and whole community (including standing dead plants, i.e. litters) by clipping method. In the field, all plants were harvested at the ground level within each quadrat and then the harvested materials of each plant species were putted in to the separate boxes for further experiments in the laboratory (Fraser et al., 2015). After that the harvested plant materials were oven-dried at 70 °C for 24 h and weighed to the nearest 0.01 g, for the measurement of aboveground biomass (Ashouri et al., 2016). The summary of aboveground biomass of studied species of 735 quadrats across 35 sites is provided in Appendix S1.

2.5. Statistical analyses

We first used simple linear regression analysis to test for bivariate relationships between aboveground biomass and fixed factors within each random factor. We then performed multiple linear mixed model in order to evaluate that how change in aboveground biomass is determined by biotic (plant coverage, species richness and evenness) and abiotic factors (clay, sand, silt, gravel, elevation and slope) across plant growth forms and at whole-community level. More specifically, we used four series of models (i.e. shrubs, grasses, forbs, and whole-community) by including biotic and biotic factors as fixed effects while sites aspects and disturbance intensities as random effects (Ali et al., 2016). We used all subsets regression analysis and selected the optimal model that had lowest AICc (i.e. Akaike Information Criterion adjusted for small sample sizes) for each of the series (Prado-Junior et al., 2016). Models within in each series were considered to be equally supported if the difference in AICc was less than two units (Bartoň, 2016). When models were equally support- ed, we selected the most parsimonious model by considering the lowest number of predictors (Table S8). We calculated the conditional (c) and marginal (m) \( R^2 \) for the each multiple linear mixed model following...
(Nakagawa and Schielzeth, 2013). Conditional \( R^2 (R^2_c) \) indicates the variance explained by both fixed and random factors, whereas marginal \( R^2 (R^2_m) \) indicates the variance explained by fixed factors only (Ali et al., 2016; Prado-Junior et al., 2016). Multiple linear mixed models were conducted using the “nlme” package, and subsets were analyzed with the dredge function of “MuMIn” package (Bartoń, 2016).

Prior to the statistical analyses, aboveground biomass and all explanatory variables were natural-logarithm transformed and standardized. Transformations of the variables were conducted for the purpose to meet the assumptions of normality and linearity in ecological data (Ali and Mattsson, 2017), and to allow comparisons among multiple predictors and models (Zuur et al., 2009). The complementary Pearson’s correlations between pairs of predictors across plant growth forms and at whole-community level are shown in Tables S1–S4. All statistical analyses were conducted in R 3.2.2 (R Development Core Team, 2015). Summary of variables used in the analyses is provided in Appendix S2.

3. Results

3.1. Bivariate relationships of aboveground biomass with biotic and abiotic factors within random factors

Bivariate relationships showed that aboveground biomass was significantly increased with increasing plant coverage and species richness whereas significantly decreased with increasing species evenness across all plant growth forms and at whole-community within each random factor (i.e. all regression lines in red color). Aboveground biomass of shrubs, grasses and whole-community were significantly increased with increasing elevation, whereas aboveground biomass of forbs was decreased within each random factor. Significant increasing trend between aboveground biomass and slope was found for forbs, grasses and whole-community but not for shrubs within each random factor (Figs. 3, 4, 5 and 6; and also see Figs. S1–S4). Aboveground biomass of shrubs was significantly decreased with increasing gravel proportion only, whereas aboveground biomass of forbs was significantly decreased with increasing clay proportion only (Figs. 3 and 4; and also see Figs. S1–S4). High aboveground biomass of grasses and whole-community level were significantly related with decreasing sand and gravel proportions but with increasing clay and slit proportions within each random factor (Figs. 5 and 6; and also see Figs. S1–S4).

With respect to the sub-relationships within each random factor (i.e., sub-regression lines in black color), mixed relationships (positive, negative and/or non-significant) were observed for aboveground biomass with biotic and abiotic factors across plant growth forms and at whole-community level (Figs. 3, 4, 5 and 6; and also see Figs. S1–S4). However, most of the sub-regressions relationships for aboveground biomass with plant coverage and species richness were significantly positive. Markedly, aboveground biomass of shrubs was significantly decreased with increasing species evenness, and aboveground biomass of grasses was increased with increasing elevation within all 5 levels of disturbance intensity (Figs. 3 and 5).

Descriptive statistics of the aboveground biomass, and abiotic and biotic factors across plant growth forms and at whole-community level are shown in Table 1.

3.2. Multiple linear mixed model; what are the main drivers of aboveground biomass?

The optimal linear mixed model for shrubs showed that aboveground biomass was best predicted by plant coverage, species richness,
Aboveground biomass of forbs was best predicted by plant coverage, species richness, elevation and slope. When testing the effects of abiotic and biotic factors on aboveground biomass at whole-community level, the optimal model showed that it was best predicted by plant coverage, species richness, species evenness, elevation and slope (Table 2).

These results showed that high aboveground biomass was mainly driven by biotic factors as compared to abiotic factors across plant growth forms and at whole-community level. Topographic factors (elevation and/or slope) were also important for driving aboveground biomass. We found poor evidence for the effects of soil textural properties (sand, clay, silt and gravel) on aboveground biomass with exception for shrubs in the studied rangelands, while accounting for the effects of random factors. We also found that random factors compared to fixed factors had explained relatively less variation (i.e. 2 to 8%) in aboveground biomass across plant growth forms and at whole-community level.

4. Discussion

We assessed how biotic factors (plant coverage, species richness and species evenness) and abiotic factors (topographic factors and soil textural properties) drive aboveground biomass in rangelands, while accounting for the random effects of sites aspects and plant community types across studied sites, and disturbance intensities. To better understand changes in aboveground biomass we disentangle the effects of biotic and abiotic factors on aboveground across plant growth forms (i.e. shrubs, forbs and grasses) and at whole-community level.

4.1. Effects of biotic factors on aboveground biomass

The optimal models of this study showed that aboveground biomass was positively related to plant coverage and species richness but not to species evenness across plant growth forms. More specifically, the strong positive relationship between plant coverage and aboveground biomass may be attributable to the efficient utilization of resources by component species having high coverage rather than those having low coverage (Ji et al., 2009; Zhang et al., 2016). In addition, this study also showed that plant coverage is a best proxy or predictor for aboveground biomass across plant growth forms and whole-community in semi-arid regions, as shown previously in arid and alpine plant communities (Flombaum and Sala, 2009; Ji et al., 2009).

We found varied effects of species richness on aboveground biomass across plant growth forms. This result may be happened due to the different patterns of light interception by plant species because component species belonging to different plant growth forms are not similarly occupying the canopies and hence they have different patterns of biomass allocation (Duursma and Falster, 2015). In combination, the positive effects of species richness and plant coverage but no effect of species evenness on aboveground biomass may be happened due to strong light competition among and within different plant growth forms (Wilson and Tilman, 1993), and hence reduced the strength of the relationship between biodiversity and aboveground biomass at each plant growth form. Interestingly, at the whole-community level, optimal model suggested that aboveground biomass was also
significantly positively related to plant coverage and species richness but negatively related to species evenness. The negative relationship between species evenness and aboveground biomass indicates that aboveground biomass tends to be high under high dominance at whole-community level, contrary to predictions by the niche complementarity hypothesis. Indeed, the few productive species dominating the whole-community contribute to most of the aboveground biomass in the natural rangelands or grasslands, as shown previously (Drobner et al., 1998; Polley et al., 2003). Although species evenness had a negative effect on aboveground biomass at the whole-community level, still species richness and plant coverage had the positive effects under the niche complementarity effect, in line with most of the previous studies conducted in natural rangelands or grasslands (Ji et al., 2009; Zhang et al., 2017). Similarly, the bivariate analyses showed negative relationship between species evenness and aboveground biomass across plant growth forms at each of the random factors level analyses. Although aboveground biomass may increase with species richness and evenness under the niche complementarity effect (Tilman et al., 2001; Wilsey and Potvin, 2000), the lack of positive effect of species evenness on aboveground biomass might be attributable to competitive exclusion within each plant growth form (Grace et al., 2016; Grime, 1973). Alternatively, the dominance of productive species has a strong effect on aboveground biomass in natural communities (Cardinale et al., 2011; Prado-Junior et al., 2016; Tobner et al., 2016). Therefore, we found support for both the niche complementarity and selection effects across plant growth forms and at whole-community.

The selection effect hypothesis postulates that dominant species or traits drive aboveground biomass or productivity, and that the positive relationship between species richness and biomass are due to the high-functioning species and traits within diverse plant communities (Cardinale et al., 2007; Loreau and Hector, 2001). It is also the actual underlying mechanism linking biodiversity and ecosystem function that plant communities will contain more productive and functionally-similar species which allow greater resource utilization in the site, including promoting the likelihood of positive complementarity and facilitation interactions (Hooper et al., 2005; Loreau and Hector, 2001). Although we did not test the effects of functional trait diversity, the fact that aboveground biomass increased with species richness while decreasing with species evenness confirms that few dominant species may be functionally-similar and can be also explained as niche overlap (species redundancy) for driving aboveground biomass (Mason et al., 2011).

4.2. Effects of abiotic factors on aboveground biomass

We found that the effects of soil textural properties and topographic factors on aboveground biomass varied in magnitude and strength, depending on the plant growth forms and whole-community level in the studied rangelands. Our result showed that aboveground biomass increased with increasing elevation across plant growth forms and whole-community level. Actually, topographic factors regulate moisture distribution and influence soil water availability, which in turn affect aboveground biomass (Fisk et al., 1998). Moreover, it is plausible...
that elevation gradient is associated with changes in precipitation, temperature, productivity and plant community type. For instance, grasslands at high elevations are more productive and hence high aboveground biomass, likely due to an increase in the ratio of precipitation to evaporation, i.e. rainfall increases with elevation while temperature decreases (Carlyle et al., 2014). It has been reported that aboveground biomass increases with increasing elevation until 4400 m, and after aboveground biomass decreases with further increase in elevation (Namgail et al., 2012). In consistent with our finding, Sun et al. (2013) showed that latitude has a positive correlation with aboveground biomass in the alpine steppe. Similarly, Ensslin et al. (2015) reported an increase in biomass with elevation did not extend higher than 2500 m. As such, we also found an increase in aboveground biomass with elevation because our study area falls between 1900 and 2500 m.

We also found that aboveground biomass of forbs and grasses but not shrubs increased with increasing slope of the sites in the studied rangelands, whereas the whole-community aboveground biomass decreased. It is important to be mention here that the average slope of

![Fig. 6](image_url)

**Fig. 6.** The response of aboveground biomass of whole-community to abiotic and biotic factors across disturbance intensities. All solid regression lines are significant at $P < 0.05$ and dashed lines are non-significant at $P > 0.05$. Red lines indicate all regression across each random factor. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

![Table 1](table_url)

**Table 1**

Descriptive statistics for biotic, abiotic and response variables, used for analysis of aboveground biomass across plant growth forms and at whole-community level in semi-steppe rangelands. Summary of these factors across random factors is provided in Tables S1–S3.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Unit</th>
<th>Shrubs (n = 628) Mean</th>
<th>S.E.</th>
<th>Min.</th>
<th>Max.</th>
<th>Forbs (n = 734) Mean</th>
<th>S.E.</th>
<th>Min.</th>
<th>Max.</th>
<th>Grasses (n = 730) Mean</th>
<th>S.E.</th>
<th>Min.</th>
<th>Max.</th>
<th>Whole-community (n = 735) Mean</th>
<th>S.E.</th>
<th>Min.</th>
<th>Max.</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Biotic factors</strong></td>
<td></td>
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</tr>
<tr>
<td>Plant coverage</td>
<td>%</td>
<td>10.75</td>
<td>0.31</td>
<td>0.25</td>
<td>54.00</td>
<td>17.03</td>
<td>0.31</td>
<td>1.00</td>
<td>53.00</td>
<td>15.08</td>
<td>0.39</td>
<td>0.37</td>
<td>75.50</td>
<td>55.94</td>
<td>0.54</td>
<td>13.75</td>
<td>99.70</td>
</tr>
<tr>
<td>Species richness</td>
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<td>1.00</td>
<td>5.00</td>
<td>7.91</td>
<td>0.11</td>
<td>1.00</td>
<td>19.00</td>
<td>4.41</td>
<td>0.06</td>
<td>1.00</td>
<td>9.00</td>
<td>14.52</td>
<td>0.13</td>
<td>5.00</td>
<td>27.00</td>
</tr>
<tr>
<td>Species evenness</td>
<td>Unitless</td>
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Table 2
The optimal models for plant growth forms and whole-community, obtained from a series of multiple regression analyses for aboveground biomass and 9 predictors (3 biotic factors and 6 abiotic factors axes within each model) using linear mixed model. Standardized regression coefficient (Beta), t-test and P-value are given. The coefficient of determination ($R^2$), F-test, $P$-value and Akaike Information Criterion (AICc) of the model are also given. The blank cells represent that predictor variables were not retained in the selected optimal model.

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