The positive relationships between biodiversity and aboveground biomass are important for biodiversity conservation and greater ecosystem functioning and services that humans depend on. However, the interaction effects of plant coverage and biodiversity on aboveground biomass across plant growth forms (shrubs, forbs and grasses) in natural rangelands are poorly studied. Here, we hypothesized that, while accounting for environmental factors and disturbance intensities, the positive relationships between plant coverage, biodiversity, and aboveground biomass are ubiquitous across plant growth forms in natural rangelands. We applied structural equation models (SEMs) using data from 735 quadrats across 35 study sites in semi-steppe rangelands in Iran. The combination of plant coverage and species richness rather than Shannon’s diversity or species diversity (a latent variable of species richness and evenness) substantially enhance aboveground biomass across plant growth forms. In all selected SEMs, plant coverage had a strong positive direct effect on aboveground biomass ($\beta = 0.72$ for shrubs, $0.84$ for forbs and $0.80$ for grasses), followed by a positive effect of species richness ($\beta = 0.26$ for shrubs, $0.05$ for forbs and $0.09$ for grasses), and topographic factors. Disturbance intensity had a negative effect on plant coverage, whereas it had a variable effect on species richness across plant growth forms. Plant coverage had a strong positive total effect on aboveground biomass ($\beta = 0.84$ for shrubs, $0.88$ for forbs, and $0.85$ for grasses), followed by a positive effect of species richness, and a negative effect of disturbance intensity across plant growth forms. Our results shed light on the management of rangelands that high plant coverage can significantly improve species richness and aboveground biomass across plant growth forms. We also found that high disturbance intensity due to heavy grazing has a strong negative effect on plant coverage rather than species richness in semi-steppe rangelands. This study suggests that proper grazing systems (e.g. rotational system) based on carrying capacity and stocking rate of a rangeland may be helpful for biodiversity conservation, better grazing of livestock, improvement of plant coverage and enhancement of aboveground biomass.
Empirical studies typically provide evidence for the functional diversity (i.e., number of plant growth forms) and composition (i.e., specific plant growth forms) rather than species diversity (i.e., species richness) are more significant drivers of biomass, productivity and light penetration in experimental grasslands (Tilman et al., 1997). In addition, it is becoming increasingly reported that functional traits of the component species, i.e., the identity, abundance and range of species traits, strongly affect ecosystem functions across different ecosystem types (Ali et al., 2017; Mokany et al., 2008). Given that plant growth forms have greater influence on ecosystem functions, it is therefore insightful to analyze the relationships of plant coverage and biodiversity with aboveground biomass across plant growth forms. As such, natural rangelands are always structurally complex having variety of plant species belonging to different plant growth forms (i.e., shrubs, forbs and grasses) (Allen et al., 2011). Therefore, understanding relationships of aboveground biomass with plant coverage and biodiversity across plant growth forms may provide baseline information for ecological modeling of biodiversity and ecosystem functions (Connolly et al., 2013; Harrison et al., 2014).

Niche complementarity among co-occurring species is one of the prominent ecological mechanisms that contributes to the productivity differences between biodiversity and aboveground biomass (Loreau and Hector, 2001). However, the effects of species or functional diversity on ecosystem functions are expected to increase with the strength of the differences among species or growth forms, which in turn may influence the strength of the effects caused by compositional differences (Tilman et al., 1997). Although species diversity and functional diversity are correlated, species richness within each growth form may provide a useful gauge of ecosystem functions (Tilman et al., 1997). Moreover, species composition within each plant growth form or dominant growth form may also strongly influence aboveground biomass or productivity in a natural ecosystem (Li et al., 2010, 2016). For instance, observational and experimental studies have shown that differences in plant growth forms or dominant growth form are the key drivers of species richness — productivity relationships in natural grasslands (Ji et al., 2009; Li et al., 2016). It is plausible that vertical biomass allocation patterns differ across plant growth forms (Reynolds et al., 1997), and as a result may potentially influence ecosystem functions such as aboveground biomass. Therefore, maintaining species diversity across plant growth forms may be more important to ecological integrity and biodiversity conservation than simply maintaining species diversity of a given area (Hooper and Vitousek, 1997; Tilman et al., 1997).

Plant coverage represents the proportion of community physical space occupied by plants within a given area (Ji et al., 2009). Plant communities with higher coverage are likely to use more environmental resources than those with lower coverage, and hence leading to the positive relationship between plant coverage and aboveground biomass (Ji et al., 2009). For instance, few fast-growing species within a community may explain the larger proportion of variation in aboveground biomass due to occupying more available physical space. As a result, it is reasonable that aboveground biomass does not necessarily increase with increasing species richness (Ji et al., 2009). Also, increasing species richness may increase the physical space for the functional differences among species that strongly affect ecosystem processes (Casano et al., 2011; Petchey et al., 2004). Yet, few studies have explicitly tested the effects of plant coverage in combination with multiple measures of biodiversity on aboveground biomass across plant growth forms in natural rangelands, while accounting for the effects of environmental factors and disturbance intensities (see conceptual models in Fig. 1). Studies on the relationships between biodiversity and aboveground biomass conducted in natural ecosystems have been suggested to account for the effects of environmental factors and disturbance intensities that may be important in influencing functions in natural rangelands (Grace et al., 2016). For instance, livestock grazing has been recognized as one of the most important types of disturbances affecting species persistence and influencing the coverage and composition of plant communities (Olliff and Ritchie, 1998). 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 influence biodiversity, plant coverage and aboveground biomass (Fisk et al., 1998).

In this study, we hypothesize that, while accounting for environmental factors and disturbance intensities, the positive relationships between plant coverage, biodiversity, and aboveground biomass are ubiquitous across plant growth forms in natural rangelands. We predict that the strength of the relationships of aboveground biomass with biodiversity and plant coverage may vary across plant growth forms due to resources (light, water and soil nutrients) availabilities for each growth form. For instance, shrubs and some of perennial forbs are mostly dominating the canopy layers while grasses and annual forbs are dominating the below-canopy layers in natural rangelands, since light and other resources limit plant performance in different vertical layers (Hautier et al., 2009). In order to explicitly test our hypothesis, we employed structural equation model (SEM; Malaebs et al., 2000) to analyze data from 735 quadrats in rangelands in Iran. Specifically, we asked the following three major questions: 1) which combination of plant coverage with each measure of biodiversity (species richness, Shannon’s diversity, or a latent variable of species richness and evenness) best explains variation in aboveground biomass; 2) what are the relative effects (measured as the standardized coefficient, beta) of plant coverage and biodiversity on aboveground biomass; and 3) how environmental factors and disturbance intensities modulate the relationships of aboveground biomass with plant coverage and biodiversity across plant growth forms in natural rangelands?

2. Materials and methods

2.1. Study area, sites, and quadrats

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. S1a). In this study, we randomly selected 35 study sites, where 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 predominantly 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 November (Khojasteh et al., 2013).

In this study, 35 sites (size varies from 1.5 to 57 ha) were 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 10–600 m apart, depending on the area of the site (Fig. S1b). Each quadrat size was...
1 m × 1 m. The studied sites contained between 5 and 27 plant species per quadrat. The summary of relative coverage of the studied plant species across 735 quadrats of 35 study sites are provided in Appendix S1.

2.2. Quantification of biodiversity, and measurements of plant coverage and aboveground biomass

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 Tehran University in Iran for identification through the support of expert taxonomists. Plant species were classified into three major plant growth forms, i.e., shrubs (chamaephytes and nanophanerophytes), forbs including herbaceous annual, biennial and perennial forbs (geophytes/cryptophytes and hemicryptophytes), and grasses and sedges (hereafter simply referred as “grasses”). Shrub species were observed in 628 quadrats, forbs in 734 quadrats, and grasses in 730 quadrats across 735 quadrats. The calculations on the biodiversity indices (i.e. species richness, evenness and Shannon’s diversity) for each plant growth form within each quadrat were performed using the vegan package for the R 3.2.2 (Oksanen et al., 2015; R Development Core Team, 2015). We selected Shannon’s index as a measure of species diversity to account for species richness and evenness, and alternatively we incorporated species richness and species evenness as a latent variable (in SEM) in order to represent species diversity as a whole. Species richness is the number of species per plant growth form within each quadrat. Species richness, evenness and Shannon’s diversity indices were calculated to represent species diversity for each plant growth form with the following equations:

\[
\text{Species richness} = \sum_{i=1}^{n} f_i
\]

\[
\text{Species evenness} = \frac{1}{H} \sum_{i=1}^{n} f_i \log f_i
\]

\[
\text{Shannon’s diversity} = -\sum_{i=1}^{n} f_i \log f_i
\]

where:

- \(n\) is the number of species per plant growth form within each quadrat.
- \(f_i\) is the relative frequency of species \(i\).

Fig. 1. Conceptual models for the prediction of aboveground biomass in semi-steppe rangelands. Models showing hypothesized relationships of how environmental factors (topographic factors and soil textural properties) and disturbance intensity affect biodiversity, plant coverage and aboveground biomass, and how biodiversity and plant coverage concomitantly affect aboveground biomass. a) Combination of plant coverage and species richness; b) plant coverage and Shannon’s species diversity; and c) plant coverage and latent species diversity.
evenness and Shannon’s species diversity were calculated based on Equations (1) and (2), respectively.

\[
SE = \frac{H_s}{\ln(s)} \quad (1)
\]

\[
H_s = -\sum_{i=1}^{e} p_i \times \ln(p_i) \quad (2)
\]

where \(SE\) is species evenness, \(H_s\) is Shannon’s species diversity, \(s\) is the total number of species while \(p_i\) is the proportion of plant coverage of ith species in a quadrat or per plant growth form within each quadrat.

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 shaded area (i.e. physical space occupied by each species) of a specific species to the total area of a quadrat (Ji et al., 2009). After measurement of plant coverage, we then destructively measured aboveground biomass of each plant growth form (including standing dead plants, i.e. litters) by clipping method. We harvested all plants present in the quadrat, including plant litter, to be dried at 70 °C for 24 h and weighed to the nearest 0.01 g. (Fraser et al., 2015). The summary of biomass of each species of 735 quadrats across 35 study sites are provided in Appendix S1.

2.3. Assessment of disturbance intensities

Studied sites were ascribed to five disturbance levels (hereafter simply referred to ‘disturbance intensity’) based on the grazing intensities of livestock (i.e. low, moderate and high grazing), and soil conditions such as erosion, trampling, percentage of gravel stone, rangeland condition (Parker, 1951), and soil depth. For instance, we ascribed 5 for high disturbance with high grazing intensity, high evidence of soil erosion and trampling, poor range condition, shallow soil depth (lower than 25 cm), and high percentage of gravel fraction (higher than 30%); 4 for moderate disturbance with moderate grazing intensity, moderate evidence of soil erosion and trampling, fair range condition, moderate soil depth (25–45 cm), and moderate percentage of gravel fraction (25–30%); 3 for moderate disturbance with moderate grazing intensity with moderate evidence of soil erosion, good range condition, moderate soil depth (25–45 cm), and intermediate percentage of gravel fraction (25–30%); 2 for low disturbance with low grazing intensity, no evidence of soil erosion and trampling, good range condition, moderate soil depth (25–45 cm), and moderate percentage of gravel fraction (25–30%); and 1 for low disturbance, with low grazing intensity with no evidence of soil erosion and trampling, excellent range condition, deep soils (higher than 45 cm), and low percentage of gravel fraction (lower than 25%). The summary of disturbance intensity of 735 quadrats across 35 study sites are provided in Appendix S1.

2.4. Measurements of environmental factors

To take into account any effects of environmental factors on the relationships of aboveground biomass with plant coverage and biodiversity, we measured the soil textural properties including sand, silt, clay and gravel (particles greater than 2 mm in diameter); and topographical properties 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. 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).

In order to reduce the number of local environmental factors and to avoid the strong correlations among them (see Table S1 for correlations), we ran principal component analyses (PCA) for soil textural properties and topographic factors, separately. In all statistical analyses, we used PC1 for soil textural properties and for topographic factors, separately, to represent environmental conditions (see Table S2). Summary of environmental factors dataset of 735 quadrats across 35 study sites are provided in Appendix S1.

2.5. Statistical analyses

We constructed three SEMs based on known theoretical multivariate causes of aboveground biomass, and combination of plant coverage with each measure of biodiversity (i.e. species richness, Shannon’s diversity, and a latent variable of species richness and evenness) across plant growth forms in natural rangelands (i.e. nine SEMs in total), in addition to the effects of environmental factors and disturbance intensities (Fig. 1). Disturbance intensity was an ordinal categorical variable and was coded as 1, 2, 3, 4 and 5 being treated as a regular numeric variable, as recommended (Roosel, 2012). Bivariate relationships were conducted for each of the hypothesized causal paths according to our hypothesized paths (Fig. 1), using Kendall’s (tau) correlations and simple regressions analysis. One-way ANOVA with Tukey’s test was used for testing the significant differences among levels of disturbance intensity, following Ali and Mattsson (2017). All numerical variables including aboveground biomass, plant coverage and biodiversity indices were natural-logarithm transformed and standardized in order to meet the assumptions of normality and linearity (Grace et al., 2016; Zuur et al., 2009). The complementary Kendall’s (tau) correlations between all tested predictors used in SEMs are shown in Table S3.

Several tests were used to assess the model fit of SEM (Malaeb et al., 2000), i.e. Chi-square (\(\chi^2\)) test, goodness-of-fit index (GFI), comparative fit index (CFI), standardized root mean square residual (SRMR) and Akaike Information Criterion (AIC). We used the \(\chi^2\) test, representing the maximum likelihood estimation, to assess how well the nine hypothesized SEMs fit the data (Table S4). Indicators for a good model fit to the data included a non-significant (\(P > 0.05\)) \(\chi^2\) test statistic, SRMR < 0.05, and both GFI and CFI > 0.90 (Malaeb et al., 2000). Among all acceptable models for each plant growth form, we selected SEM with the lowest AIC as our final model. The indirect effect of a predictor was calculated by multiplying the standardized effects of all paths on one route, from one predictor to mediator, and then to aboveground biomass, while total effect was calculated by adding standardized direct and indirect effects (Ali et al., 2017; Grace et al., 2016). The SEM was implemented using the lavaan package (Rosseel, 2012). For all statistical analyses R 3.2.2 was used [R Development Core Team, 2015]. Summary of variables used in the analyses are provided in Appendix S2.

3. Results

Bivariate relationships showed that aboveground biomass increased with increasing species richness and plant coverage across plant growth forms. Aboveground biomass of shrubs and grasses also increased with increasing topographic factors (PC1), whereas aboveground biomass of grasses decreased with
increasing soil textural properties (PC1). Species richness increased with increasing plant coverage across plant growth forms. Plant coverage of grasses increased with increasing topographic factors but decreased with increasing soil textural properties, whereas opposite relationships observed for forbs. Aboveground biomass and plant coverage of shrubs and grasses, and species richness of shrubs decreased with increasing disturbance intensities. Species richness, plant coverage and aboveground biomass of forbs, and species richness of grasses showed almost humpback shape pattern with increasing disturbance intensities (Figs. 2–4). The bivariate relationships between variables used in the best-fit selected SEMs are shown here (Figs. 2–4), whereas the Kendall’s correlations between pairs of all tested variables are shown in Table S3.

Among all tested SEMs, species richness was selected as the biodiversity index, as this combination (plant coverage and species richness) resulted in the best-fit SEM with the lowest AIC across plant growth forms (Fig. 5). The SEM having combination of plant coverage and Shannon’s diversity for forbs was accepted (Fig. S2), but rejected for shrubs and grasses. The SEM based on combination of plant coverage and a latent variable for species diversity was rejected across plant growth forms (Table S4).

The selected best-fit SEMs explained 75–80%, 22–48% and 3–37% of the variation in aboveground biomass, species richness and plant coverage, respectively, across plant growth forms. Plant coverage had a strong positive direct effect on aboveground biomass across plant growth forms, followed by species richness while accounting for the direct effects of environmental factors and disturbance intensities (Fig. 5). Plant coverage had a strong positive direct effect on species richness, and hence indirect positive effect on aboveground biomass via species richness across plant growth forms (Fig. 5; Table 1). Disturbance intensity had a negative effect on plant coverage, whereas variable effect (positive, negative and/or non-significant) on species richness and aboveground biomass across plant growth forms. Disturbance intensity had a strong negative indirect effect via plant coverage than that via species richness on aboveground biomass of shrubs and grasses, but non-significant effect on aboveground biomass of forbs (Fig. 5; Table 1). There was a positive direct effect of topographic factors on aboveground biomass, but variable effect on plant coverage. Topographic factors had a negative indirect effect, via plant coverage, on aboveground biomass of shrubs and forbs, but a positive effect on grasses. Soil textural properties had a variable direct effect on plant coverage and species richness, and therefore variable indirect effect on aboveground biomass across plant growth forms (Fig. 5; Table 1). Plant coverage had a strong positive total effect on aboveground biomass ($\beta = 0.84$ to $0.88$, $P < 0.001$), followed by a positive total effect of species richness, negative total effect of disturbance intensity, and variable total effect of disturbance intensity on aboveground biomass across plant growth forms (Fig. 5; Table 1). There was a positive direct effect of topographic factors on aboveground biomass, but variable effect on plant coverage. Topographic factors had a negative indirect effect, via plant coverage, on aboveground biomass of shrubs and forbs, but a positive effect on grasses. Soil textural properties had a variable direct effect on plant coverage and species richness, and therefore variable indirect effect on aboveground biomass across plant growth forms (Fig. 5; Table 1). Plant coverage had a strong positive total effect on aboveground biomass ($\beta = 0.84$ to $0.88$, $P < 0.001$), followed by a positive total effect of species richness, negative total effect of disturbance intensity, and variable total effect of disturbance intensity on aboveground biomass across plant growth forms (Fig. 5; Table 1).
topographic factors and soil textural properties across plant growth forms (Table 1).

4. Discussion

We assessed how multiple measures of biodiversity (species richness, evenness, and Shannon’s diversity) and plant coverage drive aboveground biomass across plant growth forms (i.e. shrubs, forbs and grasses) in semi-steppe rangelands. To understand changes in aboveground biomass we tested the effects of biodiversity and plant coverage across shrubs, forbs and grasses, after accounting for the effects of soil properties and topographic factors (Figs. 1 and 5). As hypothesized, we found support for the positive effects of plant coverage and species richness on aboveground biomass across plant growth forms.

4.1. The combination of plant coverage and species richness enhances aboveground biomass

Among the tested measures of biodiversity (species richness, evenness, and Shannon’s diversity), we found that only species richness best predicts aboveground biomass in combination with plant coverage and abiotic factors across plant growth forms in the studied rangelands (Grace et al., 2016; Zhang et al., 2017). Our research outcomes provide support for the niche complementarity hypothesis because plant coverage enhances species richness, and as a consequence increases aboveground biomass across plant growth forms. However, high aboveground biomass is strongly driven by high plant coverage compared to high species richness across plant growth forms. This result indicates that the positive effect of plant coverage is ubiquitous across plant growth forms, whereas the positive effect of species richness depends on available resources for each plant growth form in natural rangelands.

Generally, plant coverage is the proportion of community physical space occupied by plants (Ji et al., 2009). It is therefore plausible that plant communities with high coverage are more likely to efficiently use environmental resources than those with low coverage, and as a consequence plant coverage enhances aboveground biomass (Ji et al., 2009). However, light competition among component plant species or growth forms increases with increasing biomass productivity in a plant community, which is the main cause of competitive exclusion in grassland and rangeland communities (DeMalach et al., 2016; Hautier et al., 2009). Grazing releases species from light competition (Borer et al., 2014), and therefore it can be expected to have a strong positive effect on species richness under high levels of productivity (Borer et al., 2014). In this study, we found that plant coverage had strong positive effects on aboveground biomass and species richness, and that species richness had weak positive effect on aboveground biomass across plant growth forms. This result might be 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 (Bessler et al., 2009).

Our results showed that strength of the effect of species richness on aboveground biomass for forbs and grasses was weaker than that observed for shrubs. This indicates that the strength of positive relationship between species richness and aboveground biomass is dependent on plant growth form and influenced by the available resources (Cardinale et al., 2009). This mechanism might be due to the competitive constraints imposed by shrubs (i.e. woody plants) on annual forbs and grasses because of their size and dominant role over the resources for efficient utilizations (Gioria and Osborne, 2014), since perennial forbs and shrubs are the co-dominant growth forms in the studied rangelands. Increases in shrubs cover and height can also potentially restrict the growth of other plant species by limiting light availability (Isla et al., 2011). Resource filtering, caused by the shrubs, likely reduced the strength of the positive effect of species richness on aboveground biomass of forbs and grasses in the studied rangelands. The lack of a positive effect of forbs species richness on aboveground biomass may be due to their unique life-history traits compared with grasses and shrubs (Craine et al., 2001; Li et al., 2016). However, the positive effect of species richness on aboveground biomass of shrubs and grasses suggests that niche complementarity mechanism is driving the observed positive relationships. It is generally plausible that different plant growth forms might have differential root and leaf properties (e.g. root distribution and leaf density) that affect their sensitivity and fitness in response to environmental conditions such as precipitation and temperature. For instance, grasses compared to forbs are relatively shallow-rooted and primarily rely on near-surface soil water and nutrients (Chen et al., 2003; Ogle and Reynolds, 2004). Therefore, grasses compared to forbs do not differ in their resource niches, but that neutral processes such a demographic stochasticity or dispersal allow them for coexistence (Hubbell, 2001).

4.2. Effects of disturbance intensities on plant coverage, species richness and aboveground biomass

In this study, we found that species richness and aboveground biomass of shrubs were significantly decreased due to the disturbance intensities, whereas species richness, not aboveground biomass, of forbs and grasses were increased. Disturbance intensities had also negative effect on the plant coverage of shrubs and grasses. Shrub species were dominant in those studied sites having high disturbance intensity, and formed the dominant plant community type. Some of grasses species in the studied area such as Bromus tomentellus Boiss., Festuca arundinacea, Festuca ovina, Dactylis glomerata L., Melica persica and Stipa barbata are palatable for livestock, and hence decreasing pattern in grasses coverage may be attributable to livestock grazing (Khojasteh et al., 2013). Annual or biennial plant species are more adapted to overgrazing because they can tolerate disturbance much more than perennials due to their shorter life cycle and their prolific seed production (Grime,
The final best-fit structural equation models (SEMs) relating aboveground biomass to plant coverage and species richness, after accounting for the effects of environmental factors and disturbance intensity while considering the hypothesized path between species richness and plant coverage across plant growth forms. Solid arrows represent significant ($P < 0.05$) paths and dashed arrows represent non-significant paths ($P > 0.05$). For each path the standardized regression coefficient is shown. $R^2$ indicates the total variation in a dependent variable that is explained by the combined independent variables. The model fit statistics summary for each SEM is provided.

Table 1

<table>
<thead>
<tr>
<th>Predictor</th>
<th>Pathway to aboveground biomass</th>
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<th>Model in Fig. 5b</th>
<th>Model in Fig. 5c</th>
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<td>$P$-value</td>
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Grasses and sedges are in general the most grazing tolerant plants (Brown and Bagley, 1986; Mysterud, 2006), and may even increase in response to increased grazing pressure (Brown and Bagley, 1986). However, overgrazing may reduce the dominance of palatable grasses due to high stocking rates (Gaitán et al., 2017), and hence increased the proportion of unpalatable and poisonous weeds and reduced ground cover (Gamoun, 2014). The increasing abundances of some unpalatable annual grasses such as Bromus tectorum L., Bromus danthoniae Trin., Taeniatherum capitum-medusae, Boissiéra squarrosa and Aegilops kotschyi in the studied rangelands were found on highly disturbed study sites.

Increase in aboveground biomass and richness of forbs in response to disturbance intensities may be attributable to unpalatable forb species in studied rangelands, because few of forbs are palatable to livestock (Khojasteh et al., 2013). This factor in turn lead to grazing-induced increases in richness and aboveground biomass of forbs. Grazing resulted in the removal of palatable species, which reduced the abundance of some dominant species (Niu et al., 2010). This reduction has benefited some unpalatable and grazing-resistant species through reduced competition and increased nutrient availability and/or light availability (Li et al., 2013; Zhu et al., 2008).

In the history, the studied rangelands are highly disturbed with free grazing or continuous grazing over a long period of time. Under this grazing system, some areas were overgrazed during the early months of the plant growing season. Therefore, long-term free grazing, overgrazing and overexploitation have drastically caused changes in vegetation composition, biodiversity, and replacement of unpalatable and invasion species in the studied rangelands (Sanaei et al., 2015; Sour et al., 2013). However, rotational grazing systems are more recently developed to improve rangelands conditions by resting one or more paddock for a minimum of one year. Under rotational grazing system, only one portion of rangeland is grazed at a time while the other portions are protected. Hence, protected portions of the rangeland allow forage plants to renew energy reserves, rebuild vigor, deepen their root systems, and provide long-term maximum production (Brunson and Burritt, 2009). Consequently, this study also suggests that proper grazing systems (e.g. rotational system) based on carrying capacity and stocking rate of a rangeland may be helpful for the better management of rangelands.

4.3. Effects of environmental factors on plant coverage, species richness and aboveground biomass

The effects of soil properties and topographic factors on aboveground biomass, species richness and plant coverage varied in magnitude and direction, depending on the plant growth forms in the natural rangelands. The positive response of aboveground biomass to topographic factors is consistent with previous studies in rangelands (Enssslín et al., 2015; Zhang et al., 2016). We found that the responses of the species richness and plant coverage of grasses to soil properties and topographic factors were generally stronger or even in an opposite direction compared to shrubs and forbs. This result suggests the adaptation of plant growth forms to the specific soil and topographic conditions for driving high aboveground biomass in the studied rangelands (Jiao et al., 2017). Therefore, the modulating effects of the environmental factors on the relationships of aboveground biomass with species richness and plant coverage suggest that the magnitude and direction of these relationships are highly dependent on plant growth forms in natural rangelands. Lastly, we anticipate that our findings might encourage further explicit studies on the direct effects of abiotic (gravel, sand, silt, clay, elevation and slope) and biotic (plant coverage, species richness and evenness) factors on aboveground biomass across plant growth forms and at whole-community, in order to better understand that what actually drives aboveground biomass across disturbance levels in semi-steppe rangelands.

5. Concluding remarks

To best of our knowledge, this is the first empirical study to tease apart the direct and indirect effects of plant coverage, multiple measures of biodiversity, soil textural properties, topographic factors and disturbance intensities on aboveground biomass across plant growth forms in semi-steppe rangelands. We found that, first, the combination of plant coverage and species richness rather than Shannon's diversity or species diversity (a latent variable of species richness and evenness) substantially enhance aboveground biomass across plant growth forms. Second, the strong positive relationship between plant coverage and aboveground biomass may be attributable to the efficient utilization of resources by component species within each plant growth form having high coverage rather than those having low coverage. The weak positive effect of species richness on aboveground biomass may be happened due to strong light competition among component species across plant growth forms, but plant coverage enhances species richness, and hence high aboveground biomass. Third, disturbance intensities had altered the structure and composition of the plant community. For instance, negative effects on plant coverage and richness of shrubs, negative effect on plant coverage of grasses but positive effects on species richness of forbs and grasses, and hence differentially altered aboveground biomass across plant growth forms. Therefore, disturbance intensities have strong negative effects on plant coverage rather than species richness, but high plant coverage substantially enhances aboveground biomass across plant growth forms. Lastly, we conclude that strong positive relationship for plant coverage with aboveground biomass is ubiquitous across plant growth forms, but the relationship for species richness is stronger for shrubs than forbs and grasses, depending on the available resources for plant growth forms. This study suggests that proper grazing systems (e.g. rotational system) based on carrying capacity and stocking rate of a rangeland may be helpful for biodiversity conservation, better grazing of livestock, improvement of plant coverage and enhancement of aboveground biomass.

Contribution of the co-authors

AS and MAZC conceived and designed the research. AS and MAZC conducted sampling design, field and lab work. AS and AA designed the conceptual idea, analyzed the data and wrote the paper. All co-authors reviewed and approved the final manuscript.

Conflict of interest

The authors declare that they have no conflict of interest.

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Appendix A. Supplementary data

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