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

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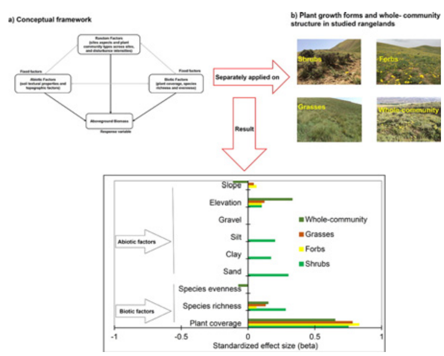
HIGHLIGHTS

- 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



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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 abiotic 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 coverage, 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 coverage, 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

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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.

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 quality and quantity, 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, topo-edaphic 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, 2000; 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 (Schoonover 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