Journal of Environmental Management 205 (2018) 308–318

Contents lists available at ScienceDirect

Journal of Environmental Management

journal homepage: www.elsevier.com/locate/jenvman

Research article

# The positive relationships between plant coverage, species richness, and aboveground biomass are ubiquitous across plant growth forms in semi-steppe rangelands

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A R T I C L E I N F O

*Article history:*
Received 16 June 2017
Received in revised form
25 September 2017
Accepted 30 September 2017
Available online 12 October 2017

*Keywords:*
Biodiversity
Disturbance intensity
Environmental factors
Plant coverage
Rangelands
Structural equation model

A B S T R A C T

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 is 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.



## 1. Introduction

Positive relationships between biodiversity and ecosystem functions (e.g. aboveground biomass and productivity) have widely been reported in natural ecosystems (Ali et al., 2017; Prado-Junior et al., 2016; Wang et al., 2011; Zhang et al., 2017), and remains hotly debated in ecology for more than four decades (Grace et al., 2016). Previous studies in natural rangelands or grasslands have focused mainly on the relationships between biodiversity and ecosystem functions at whole-community level (Grace et al., 2016; Zhang et al., 2017). However, our understanding regarding whether and how the combinations of plant coverage and measures of biodiversity (i.e. species richness, evenness, and Shannon's diversity) drive aboveground biomass across plant growth forms in natural rangelands remains unclear.

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https://doi.org/10.1016/j.jenvman.2017.09.079
0301-4797/

Empirical studies typically provide evidence 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 positive relationship 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 (Casanoves 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 (Olff 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; Malaeb 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 have 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 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 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 quadrates were established at 10–600 m apart, depending on the area of the site (Fig. S1b). Each quadrat size was