



## Original Articles

# Plant coverage is a potential ecological indicator for species diversity and aboveground biomass in semi-steppe rangelands



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## ABSTRACT

The relationships between species diversity and aboveground biomass remain highly debated in contemporary ecology. Here, we proposed the following three hypotheses by evaluating three different paths between species diversity indices (species richness, evenness, Shannon's species diversity, and a combination of species richness and evenness) and plant coverage for explaining variation in aboveground biomass, in addition to the influences of abiotic factors and disturbance intensities: 1) plant coverage increases species diversity through light capture and use in the vertical physical space; 2) species diversity increases plant coverage through species coexistence; and 3) species diversity and plant coverage may provide positive response to each other, and as a consequence enhance aboveground biomass in natural rangelands. We used structural equation models to explicitly test these hypotheses using biophysical data from 735 quadrats in semi-steppe rangelands in Iran. In all tested models, plant coverage possessed strongest positive effect on species richness and Shannon's species diversity but not on species evenness, and hence strongly determined aboveground biomass as compared to species diversity indices. Disturbance intensity decreased aboveground biomass directly and indirectly via plant coverage than that via species diversity, indicating that plant coverage is sensitive to disturbance intensities for driving aboveground biomass. Species richness or Shannon's diversity substantially enhanced aboveground biomass indirectly via plant coverage, indicating that plant coverage is a linking mechanism for the positive relationships between biodiversity and aboveground biomass. Practically, this study suggests that rotational grazing system might be a suitable choice for the enhancement of plant coverage and aboveground biomass while conserving biodiversity. Theoretically, this study suggests that plant coverage is a sustainable ecological indicator or linking mechanism for high species diversity and aboveground biomass in studied rangelands and other ecosystems in general.

## 1. Introduction

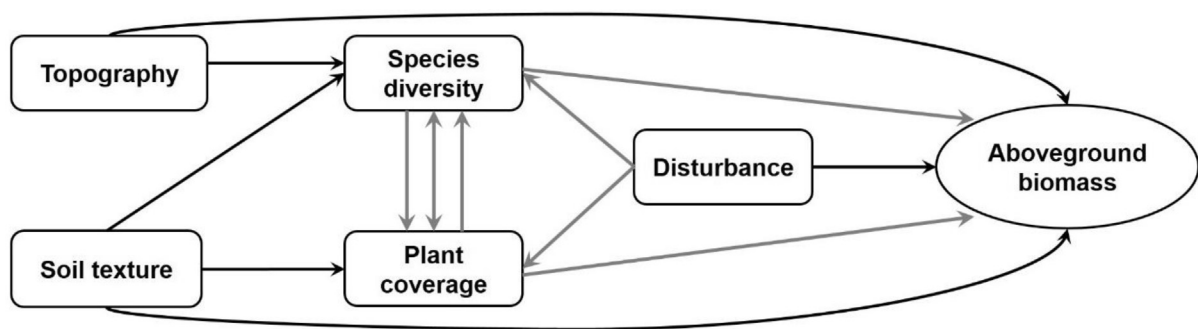
Higher biodiversity and ecosystem functioning are crucially important to assure the existence and persistence of an ecosystem and thereby the quality of life of many organisms – including humans (Grace et al., 2016; Millennium Ecosystem Assessment, 2005). It is, therefore, insightful that high species diversity, plant coverage and aboveground biomass are potential ecological indicators for the sustainable management of an ecosystem (Ji et al., 2009; Qin et al., 2018). The prominent ecological theories such as the niche complementarity hypothesis (Tilman, 1999), the intermediate disturbance hypothesis (Connell, 1978) and the dynamic equilibrium hypothesis (Huston, 1979) together suggest an important theoretical framework for biodiversity conservation, management, and ecosystem functioning (Fig. 1). The ecological integrity, in terms of biodiversity conservation, maintenance of the vegetation structure and enhancement of the ecosystem

function, of the natural communities may require investigating the simultaneous influences of abiotic and biotic drivers of an ecosystem. Therefore, the integrative modeling may help to inform the sustainable strategies and potential ecological indicators to the policymakers for the better management of the natural ecosystems (Grace et al., 2016; Sanaei et al., 2018a).

In rangelands and grasslands, previous studies have suggested that plant coverage and species richness are the main predictors of aboveground biomass (Ji et al., 2009; Qin et al., 2018; Sanaei et al., 2018b). Species diversity can be simply defined by species richness and evenness, or the combination of both such as Shannon's species diversity (Maurer and McGill, 2011). Despite the importance of species richness on aboveground biomass or productivity (Grace et al., 2016; Tilman et al., 1996), species evenness is also very important for the structure, diversity and function of plant communities (Drobner et al., 1998; Mulder et al., 2004). Although species richness and evenness are the

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**Fig. 1.** A conceptual model for the prediction of aboveground biomass in semi-steppe rangelands. Model showing hypothesized relationships of how environmental factors (topographical and soil textural properties) and disturbance intensity affect species diversity, plant coverage and aboveground biomass, and how plant species diversity and coverage concomitantly affect aboveground biomass. Three conceptual models were constructed based on different direct effects of species diversity and plant coverage on each other (gray paths), i.e. plant coverage → species diversity; species diversity → plant coverage; and species diversity ↔ plant coverage.

two main aspects of species diversity, they both respond in a different way to disturbance intensities and environmental factors (Hanke et al., 2014; Svensson et al., 2012). In addition, plant coverage has recently been recognized as an important driver or proxy for aboveground biomass or productivity (Grace et al., 2016; Ji et al., 2009). Yet, it remains unclear whether changes in the interrelationships between species diversity and plant coverage influence the patterns and magnitude of aboveground biomass across local environmental conditions natural rangelands recovering from disturbances (see a conceptual model in Fig. 1).

The relationships between species richness or diversity (such as Shannon's species diversity) and aboveground biomass or productivity are attributed to the four main conflicting predictions of the primary competing ecological theories (Grace et al., 2016, and references therein). However, most of the previous empirical and theoretical studies have ignored or overlooked the effects of species evenness on aboveground biomass but often considered as an aspect of Shannon's species diversity. The positive relationships between species diversity and aboveground biomass are often attributed to the niche complementarity hypothesis (Tilman et al., 2001). As such, plant coverage has been theorized to increase the light capture and use by the component species through the complementarity-use of the physical vertical space within a community (Grace et al., 2016; Yachi and Loreau, 2007). In this background, we propose the following three hypotheses by evaluating three different paths between species diversity (i.e. species richness, species evenness, Shannon's diversity, and a combination of species richness and evenness) and plant coverage for driving aboveground biomass: 1) plant coverage increases species diversity through the efficient utilization of resources and physical space, and as a result enhances aboveground biomass; 2) species diversity increases plant coverage through species coexistence in the vertical physical space, and in turn may increase aboveground biomass; and 3) species diversity and plant coverage may provide positive response to each other for driving high aboveground biomass in natural rangelands (Fig. 1).

The relationships between species diversity and aboveground biomass depend to a large extent on environmental conditions in terms of resource availability (e.g. water and light) (Haferkamp, 1988; Liu et al., 2014). In addition, disturbances such as local grazing disturbances through livestock grazing may strongly influence plant coverage and species diversity, by removing aboveground biomass and opening up the vegetation canopy (Grace et al., 2016; Larreguy et al., 2017). As a result, leading to an increased light availability, and hence enhanced rates of biomass gain in the remaining vegetation due to the competitive exclusion (Dyer et al., 1991) and by compensatory growth (Oba et al., 2000). For example, the intermediate disturbance hypothesis predicts that highest species diversity occurs at intermediate disturbance intensity, and hence the humped-back type of relationship exists between species diversity and ecosystem function (Connell,

1978). The dynamic equilibrium hypothesis suggests that a strong disturbance at a high level of productivity is helpful to respond competitive exclusion, whereas a relatively weak disturbance at a low level of productivity is required to prevent competitive exclusion (Huston, 1979). Yet, it remains unclear whether disturbance intensities strongly influence plant coverage or species diversity indices, and consequently what is the form of interrelationships between plant coverage and species diversity for driving aboveground biomass. Here, we predict that disturbance intensities would strongly influence plant coverage rather than species diversity because plant coverage determines vegetation quantity and productivity (Larreguy et al., 2017; Sanaei et al., 2018a), and in turn would indirectly influence the relationship between species diversity and aboveground biomass via plant coverage (Fig. 1).

We have previously reported that the positive relationships between plant coverage, species richness, and aboveground biomass are ubiquitous across plant growth forms (Sanaei et al., 2018a), whereas few dominant species may affect these relationships in addition to abiotic factors at whole-community level in semi-steppe rangelands (Sanaei et al., 2018b). Consequently, in this study, we aim to assess the main ecological indicator for higher biodiversity and aboveground biomass at the whole-community level. For this purpose, we constructed a theoretical conceptual model (Fig. 1), and then employed the structural equation models (SEMs) to test the proposed hypotheses and the following three main questions. 1) How do plant coverage and species diversity indices influence each other for driving aboveground biomass? 2) What is the main ecological indicator – species diversity or plant coverage – for higher aboveground biomass? 3) Which biotic variable – plant coverage or species diversity indices – is most sensitive to the disturbance intensities? How do plant coverage and species diversity indices are related to environmental factors for driving aboveground biomass?

## 2. Materials and methods

### 2.1. Study area, sites, and quadrats

The research area is located in the middle part of Taleghan, (36°08'10"N 50°43'10"E), in Alborz Province, Iran (Fig. S1a). Based on FAO system of classifications for agroecological zones, Iran has been broadly divided into ten agroecological zones based on the climatic conditions and the types of cultivated crops (FAO, 2005). Our study area is placed within the central agroecological zone in Iran. The soils of the study area are generally classified into Regosols and Cambisols in the FAO systems of classifications for soils (World Reference Base for Soil, 2006). The region is characterized by a semi-arid climate having a distinct dry season between June and October. The mean annual, minimum, and maximum temperature of the study area is 7.5 °C, 4 °C, and 26 °C, respectively. The mean annual precipitation of the studies

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