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Original article

Is there any support for the humped-back model in some steppe and semi steppe regions of Iran?

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ABSTRACT

One of the famous theories in ecology is the humped-back model (HBM) which explains that habitats with intermediate productivity and disturbance support the most species. Most studies on HBM patterns have been conducted for herbaceous species. Knowledge about this theory in arid and semi-arid communities is still weak, especially with severe environments and disturbances containing woody plants. In this study, an analysis is presented on species richness–productivity relationship along a gradient of disturbance and stress in some steppe and semi steppe rangelands in Iran. A nonlinear curve-fitting approach was used that fitted a three-parameter Gaussian curve between species richness and productivity across 180 plots (1 m^2). Mitchell-Olds and Shaw 's test (MOS) was used to assess the significance of the humped-back curve. Data were collected from six rangelands, including all life forms of species (grasses, forbs and small shrubs) with litter. Fitted Gaussian curve showed a positive trend between productivity and species richness across a decreasing gradient of disturbance in which species richness was increased. Maximum values for species richness correspond to values of plant productivity in undisturbed sites with a moderate stress. The MOS test showed a significant positive trend in the curve which means that the observed shape in the species richness–productivity relationship covers the mechanisms located in low to medium productivity in the left-hand side of the humped-back model. In other words, this research did not detect a full unimodal curve. This is because of less productivity in the arid and semi-arid ecosystems with abiotic stress. However, there was a partial support for the humped-back model in this study. Hence, more studies to test the existence of a humped-back model in such areas, would be required to reveal all aspects of this relationship.

1. Introduction

Ecologists have been trying to understand the major force which drives and controls the species richness; therefore, many theories were introduced throughout the years. For conservation of biodiversity, enough knowledge about prediction of ecosystem responses to various strategies of management is necessary. These goals can be achieved by developing ecological theories and testing them more and more as they provide the information for decision-makers and ecosystem managers. The humped-back model (HBM) (Grime, 1973a) is an explanatory theory based on the experimental results of Grime (1973b) for British communities. This theory is about the statistical relationship between species richness and productivity of standing crop in herbaceous vegetation. The HBM assumes that the relationship between productivity and species richness is unimodal or bell-shaped. This model explains that in low biomass and litter (<350 g m^{-2}) species richness is decreased because of the existence of high stress or disturbance. In the intermediate biomass and litter (350–700 g m^{-2}) the highest levels of species richness can be seen. This is due to a moderate range of intensities of stress or disturbance and incidence of adaptive strategies. In the high density biomass and litter (>750 g m^{-2}), the species richness decreases due to competitive exclusion (Grime and Pierce, 2012). Al-Mufti et al. (1977) measured aboveground biomass

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plus litter of herbaceous plants in 13 plant communities such as woodlands (<400 g m^{-2}) with about 10 species per 0.25 m^2, grasslands (400–800 g m^{-2}) with over 20 species per 0.25 m^2 and tall herbs (800–2600 g m^{-2}) with about five species per 0.25 m^2. Results showed the strong evidence of the existence of a humped-back curve between total standing crop plus litter versus the species richness in herbaceous species. Grime (1977) divided the factors that limit plant productivity as stress and disturbance. Stress or lack of resources is defined as severe condition in plant community such as deficiency of light, water, temperature and soil nutrients. Stress restricts the production and limits the number of species that can survive. Disturbance is defined as natural or humanistic mechanism, causes low to high destruction in plant biomass such as grazing, frost, soil erosion and fire. HBM focused on competition (negative interactions) as the main factor structuring plant communities and determining diversity in benign environmental conditions (Pugnaire, 2010). Michalet et al. (2006) revised the HBM and proposed a modification in Grime's original model. It includes facilitative processes in structuring plant communities in arid ecosystems with environmental severity involving competitive and stress-tolerant species. Michalet et al. (2006) explained that original HBM claims that in very stressed or disturbed sites, species richness is maintained by the species' physiological tolerances not by biotic processes. Hacker and Gaines (1997) proposed a model where facilitation increases community richness in highly constrained environments in a way that decreases physical disturbance or stress for less tolerant species. The HBM, also called the "Intermediate Productivity Hypothesis" (Huston, 2014), is one of the most challenging and controversial issues in ecology (see Adler et al., 2011; Fridley et al., 2012; Pan et al., 2012; Grace et al., 2012, 2014; Pierce, 2014). To examine the HBM in arid and semi-arid ecosystems, some studies have been performed such as the deserts of Arizona (Guo and Berry, 1998), arid-zone grazing lands (Oba et al., 2001), arid sub-alpine grassland (Bhattarai et al., 2004), Mediterranean wetlands (Espinar, 2006), northern steppe rangelands of Jordan (Noor Alhamad, 2006), Eurasian steppe (Bai et al., 2007), alkali and loess grasslands (Kelemen et al., 2013). Several new empirical studies concluded that there are linear increasing (Bai et al., 2007), unimodal (Virtanen et al., 2013) and non-significant (Šímová et al., 2013) curves between productivity and species richness. Fraser et al. (2015) provided evidence in support of the HBM pattern at both global and regional extents throughout grasslands worldwide. Several meta-analyses about HBM (Gillman and Wright, 2006; Mittelbach et al., 2001; Pärtel et al., 2007; Whittaker, 2010) showed contradiction of many studies in support or refusal of this theory. Fraser et al. (2015) explained that this conflict arises from a lack of general method for testing HMB. According to the earlier studies, the accuracy of the humped-back curve depends on sample size (Oksanen, 1996), area or volume of the sampling units used to study the biota (Whittaker and Heegaard, 2003), the period of the investigation or temporal scales (Al-Mufti et al., 1977; Laughlin and Moore, 2009), spatial scale of study (Mittelbach et al., 2001; Moore and Keddy, 1988; Šímová et al., 2013; Zhang et al., 2011), collecting litter (Al-Mufti et al., 1977; Kelemen et al., 2013), selection of various plant communities from low to high range of productivity (Guo and Berry, 1998) and statistical method performed on a dataset (Guo and Berry, 1998; Whittaker and Heegaard, 2003). Most studies on HBM patterns were conducted on herbaceous plants but knowledge about this theory in steppe and semi steppe communities containing woody plants (shrubs) is still not sufficient. More studies which use a set of standardized methods to test the existence of HBM in these areas would be required to reveal more aspects of this relationship. Therefore, this paper investigates the relationship between species richness and total aboveground productivity in some steppe and semi steppe communities in Iran. The aim of this research is to answer this question "is there any support for the HBM pattern in some steppe and semi steppe regions of Iran in a gradient of stress and disturbance?".

2. Materials and methods

2.1. Study areas

The present study was conducted on six different rangelands in steppe and semi steppe regions of Iran with 1 ha area (200 m × 50 m) ranging from 1400 to 2900 m in height. All sites are under the management of Research Institute of Forests and Rangelands around Tehran province and many different researches are conducted on these sites. Therefore, six sites were selected as representatives in all areas. The climate of the region is arid to semi-arid and semi-humid with a mean annual temperature between 6°C to 19°C and mean annual precipitation from 180 to 408 mm for the period of 30 years (1993–2014). The study sites are covered by grass, forbs and shrubs. Regarding the abiotic parameters such as the rate of soil organic matter (%OC), soil nitrogen (%N) and the effects of fire and grazing, the sites were ranked along a gradient of disturbance and stress (high disturbance by fire and grazing, moderate disturbance with heavily grazing, low disturbance with moderate grazing under management, no disturbance with high stress in an excluded shrub land, no disturbance with moderate stress in an excluded rangeland, and no disturbance with low stress in an excluded rangeland). The six sites are characterized as follows (Table 1, Fig. 1).

Kordan site is located in a mountainous area in the northwest of Tehran. The most abundant species based on relative density percentage in this rangeland are *Poa sinaica, Pimpinella aurea* and *Bromus tomentellus*. On Kordan site, the intensity of disturbance was highest, because the fire occurred on this site in 2009 and all plants destroyed, so, this site was selected as an area with highest disturbance.

Ozineh site is located in northeast of Tehran. The most abundant species based on relative density percentage in this rangeland are *B. tomentellus* and *Agropyron cristatum*. Ozine was near to road and ground cover was removed by sheep grazing heavily, so, in this study Ozine selected as moderate disturbance.

Jashloubar site is located in a mountainous area of north of Semnan. The most abundant species based on relative density percentage in this rangeland are *Acantholimon erinaceum* and *Festuca ovina*. Jashloubar is located at 2500 m that had moderate grazing by sheep under management, so, this site was selected as low disturbance.

Khoshkeroud site is located in northeast of Saveh. The most abundant species based on relative density percentage in this rangeland are shrubs such as *Salsola laricina, Artemisia sieberi* and grasses such as *Stipa hohenackeriana*. Khoshkeroud was excluded from grazing for about eight years and there is no grazing disturbance there, but severe environmental factors like deficiency of rainfall and very poor soil nutrients like organic matter and nitrogen with alkaline soil (pH = 8) are the reasons making this site as no disturbance with high-stress area.

Salafchegan site is located in southwest of Qom province. The most abundant species based on relative density percentage in the fenced rangeland are *Boissiera squarrosa* and *S. hohenackeriana*. Salafchegan was excluded from grazing for about eight years. This site, with moderate stress conditions, was selected as no disturbance with moderate stress.

Lazour site is located in a mountainous area in northeast of