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Drought and grazing combined: Contrasting shifts in plant interactions at species pair and community level

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ABSTRACT

The combined effects of drought stress and grazing pressure on shaping plant–plant interactions are still poorly understood, while this combination is common in arid ecosystems. In this study we assessed the relative effect of grazing pressure and slope aspect (drought stress) on vegetation cover and soil functioning in semi-arid Mediterranean grassland–shrublands in southeastern Spain. Moreover, we linked these two stress factors to plant co-occurrence patterns at species-pair and community levels, by performing *C*-score analyses. Vegetation cover and soil functioning decreased with higher grazing pressure and more south-facing (drier) slopes. At the community level, plants at south-facing slopes were negatively associated at no grazing but positively associated at low grazing pressure and randomly associated at high grazing pressure. At north-facing slopes, grazing did not result in a shift in the direction of the association. In contrast, analysis of pairwise species co-occurrence patterns showed that the dominant species *Stipa tenacissima* and *Anthyllis cytisoides* shifted from excluding each other to co-occurring with increasing grazing pressure at north-facing slopes. Our findings highlight that for improved understanding of plant interactions along stress gradients, interactions between species pairs and interactions at the community level should be assessed, as these may reveal contrasting results.

1. Introduction

How plant interactions change along environmental gradients has been a central theme in plant ecology over the last few decades. First conceptual models focused on competition, hypothesising it would increase with increasing productivity (Grime, 1979), or that it would be invariant along a productivity gradient (Tilman, 1988). Over the last two decades an increasing number of studies have focused on facilitation, i.e. net positive interactions between plants (for review see: Callaway, 2007; He et al., 2013; Pugnaire et al., 2011). Facilitator plant species (i.e. nurse species) can relieve abiotic stress for other plants, for example by protecting them against extreme temperatures and high irradiance or by increasing water or nutrient availability (Callaway, 2007). Next to that, facilitators can lower consumer pressure (i.e. grazing) by protecting other species against herbivores, a process known as associational resistance (sensu Hay, 1986).

A popular conceptual model called the Stress Gradient Hypothesis (SGH) predicts that the frequency of positive interactions will increase with increasing abiotic stress or grazing pressure (Bertness and Callaway, 1994; Callaway, 1995; Callaway and Walker, 1997). Many studies have attempted to test the SGH by experimentally investigating pairs of plant species and calculating the facilitation intensity (i.e. the performance of a plant with a protecting neighbour compared to a plant without) at several stress levels (Goldberg et al., 1999). However, studies from semi-arid ecosystems (e.g. Maestre and Cortina, 2004; Maestre et al., 2005) showed contrasting patterns to the original SGH: plant interactions shifted from competition to facilitation and back to competition along a gradient of high to low rainfall. In parallel, other studies in

List of abbreviations: *C*-score, Checkerboard score; LFA, Landscape Function Analysis; SES, Standardized Effect Size; SGH, Stress Gradient Hypothesis.

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drylands found temporal shifts from facilitation to competition during periods with very low rainfall (Armas and Pugnaire, 2005; Tielbörger and Kadmon, 2000). Also contradicting the predictions from the original SGH, studies in grazed ecosystems have reported an increase in facilitation intensity from low to high grazing pressure but a decrease again with further increases in grazing pressure (Smit et al., 2009). Such collapses in facilitation intensity at high grazing pressure have been observed in both terrestrial (Brooker et al., 2006; Graff et al., 2007; Saiz and Alados, 2012; Smit et al., 2007) and aquatic ecosystems (Bulleri et al., 2011; Le Bagousse-Pinguet et al., 2012; Levenbach, 2009). Plants can protect neighbours by physically sheltering them from herbivore damage, but when grazing pressure becomes very high, facilitative interactions might wane, because the nurse itself gets damaged by grazing or trampling (Michalet et al., 2014), or because consumers might start searching more intensively for resources (Soliveres et al., 2011a). Hence, from the examples above, it is clear that both abiotic conditions (resource and non-resource based, Maestre et al., 2009) and grazing pressure alter plant–plant interactions, but it remains unclear how multiple stressors combined, e.g. drought and grazing, shape plant interactions along combined gradients. Comparing the relative effects of both drought stress and grazing pressure on interaction intensity is important, because both may ultimately result in a decline in facilitative interactions, which may cause rapid degradation of arid ecosystems (Verwijmeren et al., 2013). One of the few available studies to date that tested combined effects of drought stress and herbivory is Soliveres et al. (2011a). This study showed that rabbit herbivory altered plant–plant interactions throughout the year, with positive interactions between *Stipa tenacissima* and *Retama sphaerocarpa* during winter and autumn, but with neutral interactions during summer. Other studies also showed that effects of grazing pressure on plant interactions can depend on water availability (Soliveres et al., 2012; Veblen, 2008), but the interactive effects of drought and grazing on plant interactions is yet surprisingly understudied and therefore unclear. One the one hand, grazing may have a bigger effect on plant interactions under high drought stress, as plants will have lower ability to compensate for herbivory than in lower stressed environments (Gómez-Aparicio et al., 2008). On the other hand, herbivores may play a smaller role in higher drought stressed environments as herbivores density will be less abundant and plants are less palatable due to lower productivity (Smit et al., 2009; Verwijmeren et al., 2013).

Furthermore, the effect of stress on plant interactions is thus far mostly studied by observing one or multiple pairs of species (Soliveres et al., in press). Studies that assess interactions at the entire community level, i.e. considering all species pairs within a community, are still scarce (but see; Saiz and Alados, 2012; Soliveres et al., 2011b, 2012), particularly those that consider multiple (interacting) stress factors. Thus, it still remains unclear how species interact at the community level along an environmental gradient consisting of drought and grazing, and how this relates to changes at species level.

The aim of this study is to investigate how plant interactions shift along a combined gradient of grazing pressure and drought stress. We expected grazing to increase the amount of positive associations, because of increased importance of associational resistance (Saiz and Alados, 2012; Verwijmeren et al., 2013). We performed an observational study in semi-arid grassland–shrubland in southeastern Spain, using aspect (north- vs south-facing slopes, reflecting a drought contrast) and grazing pressure (distance from stable). By performing transects we measured the grazing pressure, the vegetation cover and degradation level and also quantified species co-occurrence from species presence-absence data in quadrats along the same transects. We describe the effect of grazing pressure and aspect on vegetation cover and soil functioning, and indicate how these stressors interact in affecting aggregation and segregation patterns at plant community and at species-pair level.

2. Methods

2.1. Study site

We performed our study at goat grazed semi-arid fields in southeastern Spain (Murcia region 37°57′28.37″N – 1° 0′16.14″W). Average annual rainfall here is 301 mm, with on average 38 rainy days with more than 1 mm of precipitation annually. Highest rainfall occurs during spring and autumn and there is an extensive dry period in summer; average rainfall in August and July is only 10 and 5 mm, respectively. Mean monthly temperature ranges from 10.1 °C in January up till 26.7 °C in August (Agencia Estatal de Meteorología, AEMET).

Altitudes in our field site range from 175 to 302 m above sea level. Soil type consists of loamy sand. We performed our observations on slopes where vegetation mainly consists of a mixture of woody shrubs, grasses and chamaephytes (dwarf shrubs). Most occurring species are (in order of abundance): *Teucrium polium* (chamaephyte), *Rosmarinus officinalis* (unpalatable shrub), *Anthyllis cytisoides* (palatable shrub), *Fumana ericoides* (chamaephyte), *S. tenacissima* (unpalatable tussock grass) and *Brachypodium retusum* (short grass).

The study area has been grazed since April 2009 by a herd of approximately 200 goats of the Murciano Granadina breed. We selected three large zones at increasing distance from the herd shelter; the furthest zone (800–1400 m from shelter) was ungrazed by goats for decades, the middle zone (650–800 m from shelter) was grazed at low pressure since 2009, and the nearest zone (100–400 m from shelter) was grazed at high pressure since 2009. The nearest zone (high grazing pressure) was visited daily by the herd, while the middle zone (low grazing pressure) was visited weekly. The two grazed zones were grazed year-round except for the driest months July and August. We verified the assigned grazing pressure levels by counting droppings (described below). Besides grazing by goats, other – natural – herbivores in our site that may have a significant influence on the vegetation are rabbits (*Oryctolagus cuniculus*).

2.1.1. Study design and data collection

To assess the impacts of grazing pressure and drought stress on degradation and plant–plant interactions, we established a study design with three levels of goat grazing along a range of slopes with aspect varying from north to south, thus differing in drought stress. This is because drought is more intense on sunnier and dryer south-facing slopes, and this is linked to decreased plant performance in semi-arid regions in previous studies (e.g. Gómez-Aparicio et al., 2004).

Within every grazing treatment we measured the perennial vegetation cover, soil functional status, and the species co-occurrence on replicated line transects. We selected 10–12 (1.5 × 30 m) transects within every grazing treatment, with transects following the maximum slope angle and being equally distributed over north-facing and south-facing slopes. The selected slopes varied in aspect and inclination. Aspect (expressed as degrees deviation from north) ranged from 0 (pure north) to 180 (pure south) and did not significantly differ between the three grazing levels (Kruskal–Wallis $\chi^2 = 0.252$; $p = 0.882$). Slope inclination ranged from 20 to 74%, with an average of 42% and did not significantly differ among the three grazing levels (Kruskal–Wallis