Both facilitation and limiting similarity shape the species coexistence in dry alkali grasslands

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ABSTRACT

Facilitation is an important driver of community assembly, and often overwhelms the effect of competition in stressed habitats. Thus, net effect of biotic interactions is often positive in stressed grasslands, where dominant species and litter can protect the subordinate species. Besides facilitation, niche partitioning can also support species coexistence leading to limiting similarity between subordinate species. Our aim was to provide a detailed analysis of fine-scale biotic interactions in stressed alkali grasslands. We supposed, that there are positive relationships between the main biomass fractions and species richness. We expected the expansion of trait ranges and the increase of trait dissimilarity with increasing biomass scores (total litter, green biomass of dominant species) and species richness. We studied the relationships between main biomass fractions, species richness, functional diversity and functional trait indices (ranges, weighted means and Rao indices). We used fine-scale biomass sampling in nine stands of dry alkali grasslands dominated by *Festuca pseudovina*. The detected relationships were always positive between the main biomass fractions (green biomass of dominant species, total litter and green biomass of subordinate species) and species richness. We found that the green biomass of dominant species and total litter increased ranges and dissimilarity of functional traits. Our results suggest that in dry alkali grasslands facilitation is crucial in shaping vegetation composition. The green biomass of dominant species and total litter increased the biomass production of subordinate species leading to overyielding. We found that mechanisms of facilitation and limiting similarity were jointly shaping the species coexistence in stressed grasslands, such as alkali grasslands.

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1. Introduction

The study of community assembly and biotic interactions like facilitation and competition are hot topics in plant ecology (see le Roux et al., 2013; McIntire and Fajardo, 2013; Rees, 2013). Facilitation is an important driver of community assembly, and often overwhelms the effect of competition in stressed habitats (Eckstein, 2005; Le Bagousse-Pinguet et al., 2014; le Roux and McGeoch, 2008). Accumulated plant material (in form of green biomass and litter) generally mitigates extremities of temperature and protects individuals from direct solar radiation and desiccation (Eviner, 2004; Holmgren et al., 2012; Maestre and Cortina, 2004; Xiong and Nilsson, 1999). Thus, dominant species and litter can provide favourable environmental conditions for plant establishment (germination and survival of young individuals), especially in stressed habitats, while in benign habitats this effect is relatively reduced (see Eckstein, 2005; Schumacher and Roscher, 2009).

The green biomass of dominant species composes later a major part of total litter causing a generally positive relationship between these two biomass fractions (Facelli and Pickett, 1991). However, this relationship can also be negative, especially in productive habitats when the amount of litter exceeds a critical value and a negative feed-back starts up (Carson and Peterson, 1990; Deák et al., 2011; Kelemen et al., 2014). In stressed habitats a slight increase of total litter or green biomass of dominant species can lead to an increase of species richness and green biomass of subordinate species (Kelemen et al., 2013; Schumacher and Roscher, 2009; Xiong and Nilsson, 1999).

Besides facilitation which can increase species richness; niche partitioning also supports species coexistence (MacArthur and

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Levins, 1967; Schamp et al., 2008). Niche partitioning between species can lead to effective niche complementarity potentially resulting in more utilised niches; thus, can cause higher productivity (i.e. overyielding) in species-rich communities than that of in species-poor ones (Loreau and Hector, 2001; Wang et al., 2011).

Abiotic filtering is important in shaping the species pool even in stressed communities, which leads to the functional similarity of species within a community (Grime, 2006; Laliberté et al., 2013). As an opposite effect, the limiting similarity between species which passed into a respective community supports species coexistence via the effective niche partitioning and resource partitioning (Cornwell and Ackerly, 2009; Weiher and Keddy, 1995). Facilitation can smooth the effects of abiotic community filtering supporting a wider range of species to pass into the assemblages, however the limiting similarity is necessary to stabilise the species coexistence (HilleRisLambers et al., 2012; Le Bagousse-Pinguet et al., 2014).

We can analyse the effects of the above-mentioned mechanisms using ranges, weighted means and Rao indices of respective species traits (Cornwell and Ackerly, 2009). In the present study four functional traits (canopy height, lateral spread, rooting depth and seed weight) were selected; the increasing values of each trait indicate an increasing competitive ability of the respective species (Coomes and Grubb, 2003; Lamb and Cahill, 2006; Schenk and Jackson, 2002; Violle et al., 2009).

Several papers draw attention to the importance of facilitation in stressed habitats (see Butterfield, 2009; Le Bagousse-Pinguet et al., 2014; le Roux and McGeoch, 2008), but trait-based analyses are rather scarce, and for alkali grasslands are still missing. The use of specific biomass data provides the most reliable estimation of species abundances; thus, it can be useful for the trait-based studies of biotic interactions (Chiarucci et al., 1999). Field studies are crucial to test the findings of experimental and model-based studies in 'real world' conditions (Cornwell and Ackerly, 2009). Our aim was to provide a detailed analysis to understand the role of biotic interactions in alkali grasslands using fine-scale biomass sampling. We studied the relationships between main biomass fractions, species richness and the distribution of functional trait indices via the following questions. (i) What are the relationships between the main biomass fractions (green biomass of dominant species, total litter and green biomass of subordinate species) and species richness? We expected that there are positive relationships between the main biomass fractions and the relationships are also positive between the main biomass fractions and species richness (ii) What are the effects of total litter, green biomass of dominant species and species richness on the functional trait indices of subordinate species? We expected the expansion of trait ranges by facilitation with increasing biomass scores (total litter, green biomass of dominant species) in dry alkali grasslands (see Bertness and Callaway, 1994; Laliberté et al., 2013). Low competitive ability of species and diverse functional traits in the community support species coexistence (Aarssen et al., 2006; Cornwell and Ackerly, 2009). Therefore, we expect decreasing means and increasing dissimilarity of functional traits (expressed with Rao indices) with increasing biomass scores (total litter, green biomass of dominant species) and species richness.

2. Materials and methods

2.1. Study area and sampling

Our study area is located in Hortobágy National Park on the eastern part of Great Hungarian Plain. The moderately continental climate of this region is characterised by 9.5 °C mean annual temperature and 550 mm mean annual precipitation. Species-poor, dry alkali grasslands with a pronounced mosaic structure are typical

in this area (Deák et al., 2014). Dry alkali grasslands harbouring a unique flora are endangered communities in Europe; thus, they are included in the Habitats Directive of the Natura 2000 system as priority habitats (Török et al., 2012). Alkali grasslands are generally characterised by high fluctuations in groundwater level (Deák et al., 2014). They are usually wet in early spring, due to snowmelt, thereafter become dry during springtime (Valkó et al., 2014). Intense evaporation and high groundwater level with a high salt content cause salt-accumulation in the upper soil layers (Török et al., 2012). These characteristics jointly lead to high levels of abiotic stress in alkali grasslands (Kelemen et al., 2013).

We sampled nine stands of dry alkali grasslands dominated by *Festuca pseudovina* in the Hortobágy within a 15-km radius (coordinates for centre: 47°28′N, 21°04′E). In the study sites, total soil salt content was 0.07–0.1 m/m%, humus content was 3.16–3.97 m/m% and the soil water content was 14.6–20.51 mg/kg on studied grasslands in late June 2011. The dominant species was *F. pseudovina* which formed at least 50% of green biomass in each stand. In these grasslands there are several salt- and drought-tolerant species as subordinate ones (Valkó et al., 2014); we considered all species as subordinate except for *F. pseudovina*.

We collected 30 randomly selected above-ground biomass samples (20 cm × 20 cm) in each stand (in total 270 biomass samples) in late June 2011, close to the peak of biomass production. Samples were dried (65 °C, 24 h), then sorted to total litter (standing dead and litter layer of all species including also the litter of *Festuca* and subordinates) and green biomass of each vascular plant species separately. Dry weights were measured with 0.01 g accuracy in order to precisely measure species abundances at the actual scale of biotic interactions (see Laliberté et al., 2013).

2.2. Retrieval of plant trait data

We used respective functional traits (canopy height, lateral spread, rooting depth and seed weight) of subordinate species in the trait-based analyses. Canopy height (cm) data were obtained using LEDA database (Kleyer et al., 2008). For lateral spread data we used the CLO-PLA database (Klimešová and de Bello, 2009) and we classified the species into four categories based on potential distance of clonal spreading (m/year): (1) no clonal spreading, (2) <0.01 m/year, (3) 0.01–0.25 m/year, and (4) >0.25 m/year. We assigned species to five rooting depth categories (Kutschera et al., 1982, 1992), these were: (1) 1–24 cm, (2) 25–49 cm, (3) 50–74 cm, (4) 75–99 cm, and (5) >100 cm. Seed weight (g/1000 seeds) data were based on the measurements published in Török et al. (2013).

2.3. Data analysis

We used partial correlations to reveal the relationships between the main biomass fractions (green biomass of dominant species, total litter and green biomass of subordinate species) and the species richness, controlled for stands.

We calculated the ranges of each trait for each sample. The weighted means (WM) of traits for each sample were also calculated; for weights we used the proportions of each species in green biomass. We calculated range-standardised Rao indices for each trait (Rao, 1982; Botta-Dukát, 2005; de Bello et al., 2013a; Lepš et al., 2006) in each sample using the following way:

$$\sum_{i=1}^{S-1} \sum_{j=i+1}^{S} d_{ij}\, p_i\, p_i,$$

where S is the number of species in the sample; d_{ij} = the relative difference between the ith and jth species: $(|t_i - t_j|/(t_{max} - t_{min}),$