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 Bagoussé-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 feedback starts up (Carson and Peterson, 1999; 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
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 (Hille Ris Lambers et al., 2012; Le Bagoussé-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 (Comes 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 Bagoussé-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 (Aarsen 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 (Kelenen et al., 2013).

We sampled nine stands of dry alkali grasslands dominated by Festuca pseudoovina 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. pseudoovina 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. pseudoovina.

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 (Kutscher 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:

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

where $S$ is the number of species in the sample; $d_{ij}$ is the relative difference between the $i$th and $j$th species: $(|t_i - t_j|/(t_{\text{max}} - t_{\text{min}}))$. 
where $t_i$ and $t_j$ is the value of the particular trait in species $i$ and $j$, $t_{\text{max}}$ is the maximum, $t_{\text{min}}$ is the minimum value of particular trait in all of our samples; $p_i$ and $p_j$ the relative abundances of $i$th and $j$th species in the given sample based on green biomass scores. Thereafter the functional diversity (FD) of multiple traits for each sample was calculated as the average of Rao indices of the traits (Leps et al., 2006).

We used univariate GLM (Zuur et al., 2009) to explore the effects of two predictors (in same model), the green biomass of Festuca and total litter on dependent variables (range of canopy height, range of lateral spread, range of rooting depth, range of seed weight; WM of canopy height, WM of lateral spread, WM of rooting depth, WM of seed weight; Rao of canopy height, Rao of lateral spread, Rao of rooting depth, Rao of seed weight and FD of multiple traits). We controlled for grassland stands in the regression, the grassland stand was included as a random weighting factor.

We used linear regression, where the predictor variable was the species richness and the dependent variables were the Rao indices of each trait (canopy height, lateral spread, rooting depth, seed weight) and the FD of multiple traits, respectively. We controlled for grassland stands in the course of regression. All statistical analyses were calculated based on the 20 cm × 20 cm biomass samples (altogether 270 samples). The partial correlations were calculated using STATISTICA 10.0 (StatSoft Inc., Tulsa, OK, USA). GLM and linear regression were calculated using SPSS 20.0.

3. Results

In line with our former expectations, the partial correlations revealed that each biomass fraction (green biomass of Festuca, total litter and green biomass of subordinate species) was positively correlated with species richness, while the $r$-values ranged from low to moderate (Fig. 1).

The green biomass of Festuca influenced positively the range of canopy height, rooting depth and seed weight, the WM of seed weight, the Rao of canopy height, rooting depth and seed weight, and negatively the WM of lateral spread and rooting depth of subordinate species (Table 1). Green biomass of Festuca had also a positive effect on FD (Table 1). The effect of total litter was weaker than the effect of green biomass of Festuca on most of the trait indices. We detected a significant positive litter effect in case of range of rooting depth, WM of canopy height, lateral spread and rooting depth, and Rao of lateral spread (Table 1).

The species richness affected positively the Rao indices of each of the four functional traits (canopy height: $p < 0.001$, $r = 0.24$; lateral spread: $p < 0.001$, $r = 0.47$; rooting depth: $p < 0.001$, $r = 0.53$; seed weight: $p < 0.001$, $r = 0.35$) and FD ($p < 0.001$, $r = 0.44$; Fig. 2).

![Fig. 1. Partial correlation between green biomass of Festuca pseudovina (Festuca), total litter, green biomass of subordinate species (subordinate biomass) and species richness controlled for stands. Notations: **p < 0.001; ***p < 0.01.](image1.png)

![Fig. 2. Relationship between species richness (species/20 cm × 20 cm biomass sample) and functional diversity of subordinate species.](image2.png)

### Table 1

<table>
<thead>
<tr>
<th>Range</th>
<th>Festuca</th>
<th>Total litter</th>
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<tr>
<td>Canopy height</td>
<td>17.15</td>
<td>4.14</td>
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<tr>
<td>Lateral spread</td>
<td>0.80</td>
<td>0.90</td>
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<tr>
<td>Rooting depth</td>
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<tr>
<td>Seed weight</td>
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<tr>
<td>Weighted mean</td>
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<tr>
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<tr>
<td>Rao</td>
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<tr>
<td>Canopy height</td>
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<tr>
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<td>Rooting depth</td>
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<tr>
<td>Seed weight</td>
<td>1.23</td>
<td>1.46</td>
</tr>
</tbody>
</table>

4. Discussion

4.1. Biomass fractions and species richness

The detected positive correlations between the main biomass fractions are in line with the findings of former studies in stressed habitats (Foster, 1999; Willms et al., 1986). The amount of total litter is usually positively determined by the biomass production of dominant grasses (Facelli and Pickett, 1991; Odum, 1960); moreover, the presence of low amount of litter can facilitate the perennial grasses (Fowler, 1986). These mechanisms explain the detected positive correlation between green biomass of the dominant grass and total litter in stressed grasslands with moderate litter accumulation.

The presence of litter and green biomass of dominant species jointly shift the abiotic conditions to a more favourable state in stressed habitats (Eviner, 2004). Neighbouring plants generally facilitate germination and seedling survival; thereafter, this facilitation can shift to competition and decrease the biomass production of subordinate species (Leroux et al., 2013; Liancourt et al., 2005). The main reason for this ontogenetic shift is the
above-ground competition for light (Butterfield and Callaway, 2013; Grime, 1973; Lepš, 1999). Dry alkali grasslands are characterised by open vegetation, where light is not likely a limiting factor (Soliveres et al., 2010). Besides the facilitated germination and seedling survival, the net effect of biotic interactions can remain positive during the whole lifespan of individuals. This latter assumption was also indicated in the present study. The green biomass of Festuca and the amount of total litter correlated positively with the species richness, and also with the green biomass of subordinate species. Dominant species and total litter can facilitate the coexistence of subordinate species via improved environmental conditions (Isbell et al., 2009; Wang et al., 2011). There are generally positive relationship between species richness and niche complementarity, therefore higher number of coexisting species often leads to overyielding (Loreau and Hector, 2001; Roscher et al., 2004; Wang et al., 2011) as we detected in the present study, where the green biomass of subordinate species positively correlated with species richness.

4.2. Functional traits

We detected positive effects of green biomass of Festuca on the ranges of three traits (canopy height, rooting depth and seed weight). The increased green biomass of the dominant Festuca facilitated the establishment of subordinate species with a wider range of traits. The shading effect of the aboveground parts of the Festuca can protect several subordinate species and facilitates their establishment by ameliorating soil moisture and microclimate in a stressed community like dry alkali grasslands (see also Maestre and Cortina, 2004; Soliveres et al., 2010). The well-developed root system of F. pseudovina can facilitate the neighbouring plants also by hydraulic lifting of water and preventing soil erosion (see Butterfield and Callaway, 2013). Via these ways the dominant species can expand the available niches compared to niches offered by abiotic environment solely and it can also create new niches (see McIntire and Fajardo, 2013).

We found that the effects of green biomass of Festuca and total litter on weighted means of functional traits were different. The effect of Festuca was positive only in case of seed weights. The shading of Festuca can improve the microclimate which is suitable for species with various seed size, but the tolerance of shadow is the most sufficient with relatively large seeds (Csontos, 1998). The weighted means of lateral spread and rooting depth were negatively affected by the amount of Festuca. The small-scale coexistence of species with effective lateral spreading and deep rooting system is hampered by the tussocks and large root system of F. pseudovina (Fitter, 1982; Huber and Stuefer, 1997).

In contrast, total litter affected positively the weighted means of all functional traits except for the seed weight. The detected low amounts of total litter did not act as a biotic barrier which can hamper root growth and clonal spreading. We detected no effect of total litter on weighted means of seed weight. However, in an experimental study, we demonstrated seed-weight-dependent response to different amounts of litter (Miglécz et al., 2013). The litter layer affected negatively the germination when the amount of litter exceeds 300 g/m² in case of small-seeded species and there were no effect in case of species with larger seeds (Miglécz et al., 2013). The present study, the lack of litter effect on seed weights is likely caused by that the litter values remained under 300 g/m² in all studied dry alkali grassland stands.

The effect of green biomass of Festuca was positive on Rao indices of three traits (canopy height, rooting depth and seed weight) and on the functional diversity (FD). The increasing Rao indices mean an increasing degree of niche differentiation based on differences in trait values and abundances of species (de Bello et al., 2013b). In case of dominant species the intraspecific competition is usually higher than the interspecific competition (McIntire and Fajardo, 2013). Therefore, the individuals of dominant species cannot grow too close to each other; thus, it provides an opportunity for the establishment of subordinate species (McIntire and Fajardo, 2013). Moreover, the dominant species can ameliorate the abiotic environment at small-scale and the small subordinate species can utilise even these relatively small resource patches (Aarssen et al., 2006). Thus, co-occurrence and utilisation of resources are easier to a set of species with different traits which lead to increased trait dissimilarity and functional diversity of subordinate species (Cornwell and Ackerly, 2009; Schamp et al., 2008). Thus, fine-scale limiting similarity supports the coexistence of subordinate species which passed the community filter facilitated by dominant species (see Laliberté et al., 2013; Schamp et al., 2008). Our results suggest that facilitation and limiting similarity shape together the coexistence of subordinate species in the open vegetation of dry alkali grasslands.

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