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# Large herbivores change the direction of interactions within plant communities along a salt marsh stress gradient

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**Keywords**
Facilitation; Grazing; *Juncus maritimus* Lam.; Macro-detritivores; Multiple stressors; *Orchestia gammarellus* Pallas. 1766.; Plant traits; Plant–plant interactions; Salt marsh; Stress gradient hypothesis; Trampling

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## Abstract

**Question:** How multiple abiotic stress factors combined with herbivory affect interactions within plant communities is poorly understood. We ask how large herbivore grazing affects the direction of plant–plant interactions along an environmental gradient in a salt marsh.

**Location:** Grazed (cattle) and ungrazed salt marshes of the Dutch Wadden Sea island Schiermonnikoog. Here, patches of tall plant communities, dominated by the tough, unpalatable species *Juncus maritimus* Lam., are found alternating with low-statured, intensively grazed plant communities.

**Methods:** Along the inundation gradient, we measured plant species composition and plant species traits (specific leaf area, specific root length, maximum height and abundance) inside and outside *J. maritimus* patches in grazed and ungrazed areas. In addition, we measured soil structure parameters (bulk density, soil porosity, clay depth), multiple limiting conditions for plant growth (soil salinity, soil redox, plant canopy light interception), plant biomass, presence of herbivores and abundance of soil macro-detritivores.

**Results:** Under grazing, the palatable grasses *Elytrigia atherica* (Link) Kerguélen and *Festuca rubra* L. were positively associated with *J. maritimus*, while shade-intolerant *Puccinellia maritima* (Huds.) Parl. and *Juncus gerardii* Loisel. were negatively associated with this species. Furthermore, macro-detritivore presence was higher inside *J. maritimus* patches. In ungrazed areas *E. atherica* and *F. rubra* were negatively associated with *J. maritimus*, while *P. maritima* and *J. gerardii* were rare. In both grazed and ungrazed conditions the directions of species associations were independent of the inundation gradient. Analysis of species traits and abiotic conditions suggested that associational resistance (a facilitation type) was important in grazed areas. In ungrazed areas, light competition was the likely dominant process.

**Conclusions:** The direction of species associations within these salt marsh communities was strongly affected by grazing, not by the underlying stress gradient. Measurement of species traits indicated that plant–plant interactions shifted from competitive to facilitative under grazing. Besides grazing, cross-trophic facilitation of soil disturbing macro-detritivores may play an important – thus far ignored – role in structuring plant communities.

## Introduction

Detecting universal mechanisms that predict patterns and responses of plant communities along environmental gradients remains a central goal in ecology (Lawton 1999; Grime 2006; McGill et al. 2006). The nature of plant interactions is a key determinant of plant community structure and ecosystem functioning (Tilman 1990; Bruno et al. 2003). A plant community is comprised of many interacting individual plants, where the intensity and direction of their interactions are key mechanistic structuring forces determining which species may or may

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not co-occur (Bertness & Callaway 1994). Classical studies have focused on competitive plant interactions, where all plants compete for the same resources (Grime 1977; Tilman 1990). Recent studies focus increasingly also on interspecific facilitation, i.e. positive interactions between plant species where one species (beneficiary) profits from the presence of another (benefactor) by ameliorating abiotic conditions or protecting against herbivory (Soliveres et al. 2014 for recent review on facilitation research). It is now widely accepted that these two fundamental types of interaction – competition and facilitation – occur simultaneously in natural communities and that it is the net outcome that determines the direction of the overall interaction between species pairs (Olofsson et al. 1999). However, it is still unclear how these species interactions change along an environmental gradient consisting of multiple (often interacting) abiotic stressors and biotic stressors (herbivory or consumer pressure, i.e. disturbance *sensu* Grime (1979)).

Until now much insight has been gained from pair-wise studies: one benefactor hosting one or a few beneficiaries along single environmental gradients (McGill et al. 2006; He et al. 2013). However, naturally occurring plant communities are comprised of multiple interacting species, safe site requirements, dispersal mechanisms and cope with a multifaceted environment where physically limiting factors may interact (Maestre et al. 2009; Soliveres et al. 2014). He & Bertness (2014) argue that multiple environmental gradients are often not correlated across the landscape and therefore lead to more normally distributed patterns in interactions, where interactions are measured along more than one stress gradient. However, in other situations, such as elevation gradients (e.g. mountains and salt marshes), multiple environmental factors can also be strongly interdependent (thus confounded) (Deák et al. 2014; Valkó et al. 2014), where the strengthening of one physically limiting stress may depend strongly on the weakening of another due to changes in underlying physical processes. For example, in salt marshes decreased flooding leads to more oxic soil conditions and higher plant productivity and hence increased competition for light (Olff et al. 1997; Kelemen et al. 2013). In these cases the disentangling of the driving factor of the direction of species interactions is important.

Plant traits play a crucial role in the configuration of the plant community (Westoby et al. 2002). For instance, plants adapted to withstand harsh environmental conditions typically grow slowly, with high root:shoot ratios and low specific leaf area (SLA; Poorter & Nagel 2000; McGill et al. 2006). Such species can ameliorate locally harsh conditions (shading, improved soil moisture; Ungar 1998), facilitating establishment of species with different sets of traits (Langlois et al. 2003). Recent studies show that the traits of such benefactor plants may vary along abiotic stress gradients, and so importantly impact the outcome of plant–plant interactions (Michalet et al. 2011; Schöb et al. 2013). So far, very few have studied how biotic stress – incurred by herbivory – affects the variation in plant traits and resulting outcome of interactions (but see Suzuki & Suzuki 2012). Studies have shown how plant interactions are altered by the presence of consumers (Crain 2008; Smit et al. 2009; Verwijmeren et al. 2014). Benefactor species may offer refugia to less grazing-tolerant species through physical defence (Smit & Ruifrok 2011) and decrease plant presence, i.e. beneficiary species persist in close proximity to plants that are avoided by consumers (Louthan et al. 2014). In the absence of large consumers the benefactors may become strongly competitive and outcompete the beneficiary that may only persist further away (Boughton et al. 2011). Hence, we expect that alterations of species interactions by consumers are quantifiable by variation in plant traits associated with different stress types.

Salt marshes in Northwest Europe present a unique opportunity to research the effects of multiple interacting abiotic stressors, grazing herbivores and the role of plant traits on the direction of plant–plant interactions. Salt marsh plant communities are relatively species-poor, which therefore makes such integrated studies more feasible (Minden et al. 2012). On a salt marsh, the vegetation is exposed to salinity and anoxia (Davy et al. 2011). In addition to these limiting factors herbivores may also induce physical stress through defoliation, trampling (i.e. physical damage) and soil compaction (i.e. increasing anoxia; Milchunas et al. 1988; Olff & Ritchie 1998; Mikola et al. 2009; Schrama et al. 2012b). Where large herbivores (cattle) graze, distinct patches of tall *Juncus maritimus* Lam.-dominated plant communities alternate with short grazing lawns (Appendix S3a,b; Looijen & Bakker 1987). *J. maritimus* is a patch-forming, strongly clonal species spreading through vegetative underground rhizome structures. The leaves are physically defended against herbivory through heavy structural investment and sharpened leaf tips (Fitter & Peat 1994), and as a result are evergreen and long-lived. We used these *J. maritimus* patches to investigate (1) how the spatial associations of five dominant plant species differed between grazed and ungrazed areas inside and outside *J. maritimus* patches along an environmental gradient of increasing elevation and decreasing flooding frequency, and (2) how these differences are reflected by the variation in plant traits under different stress types. We expected that cattle grazing would alter the direction of species interactions with *J. maritimus* along the environmental gradient, and that this change is reflected by variation in plant traits of the five most commonly occurring plant species, as well as of the patch-forming benefactor *J. maritimus*.

## Methods

### Study site

Schiermonnikoog is one of the Dutch West Frisian coastal back barrier islands situated on a sandy substrate within the geographic extent 53°30′ N, 6°10′ E (Olff et al. 1997). The island vegetation is distinctly zoned along the elevation and inundation gradient (Bakker et al. 1993, 2010). Daily temperatures average 10.2 ± 0.72 °C (±SD) (Schrama et al. 2012a) and annual rainfall is approximately 800 mm (www.climate-data.org). On the late successional salt marsh position, cattle are permitted to graze at a density of 0.5 au·ha$^{-1}$ (Bos et al. 2002), annually between 1 May–31 Oct. Cattle are prevented from entering the marsh extending eastwards by a cattle-proof electrified fence (Looijen & Bakker 1987).

### Data collection

Fieldwork on the salt marsh of Schiermonnikoog was conducted on 30 paired plots, each 10 m × 10 m (60 in total), situated on either side of the cattle-proof fence (Appendix S3), following the environmental gradient from low to high marsh 130–227 cm +NAP (Normaal Amsterdams Peil), where 100 cm +NAP is mean high tide, and with a tidal inundation range between 2.29–0.08 h·d$^{-1}$. The plots were located within homogeneous vegetation inside and outside of patches dominated by *J. maritimus*, ranging in size from 10–300 m$^2$. Since age and elevation of the marsh strongly determines which plant communities are present (Bakker et al. 1993; Olff et al. 1997), the location of the grazed and ungrazed paired plots (inside/outside patches) were placed parallel to each other on either side of the cattle-proof fence (Appendix S3c). Parallel plots were placed at a minimum of 80 m and a maximum of 300 m apart to ensure measurements taken were spatially independent and captured the main characteristics of the elevation gradient. Measurements were conducted within subplots located within the 60 main sampling plots.

### Abiotic conditions

Mean inundation hours per day were calculated from the preceding 10 yr of sea level data (01 Jan 2003 to 31 Dec 2013), collected by Rijkswaterstaat (live.waterbase.nl). A transgression curve was then calculated using the cumulative frequency. The data were then averaged over 10 yr to give an estimate of inundation duration (mean hours per day). An exponential model was fitted to the data to obtain the model parameters.

Electrical conductivity (mS·cm$^{-3}$) was measured as a proxy for soil salinity (Mills et al. 2009) in May 2012, Mar 2013 and May 2013. Soil redox (mV) was measured as a proxy for soil oxygen (Davy et al. 2011) in May 2012, Mar 2013 and Jun 2013. Canopy light interception was measured in May 2013, using a leaf area index meter (Harguindeguy et al. 2013).

For soil structural parameters we measured soil bulk density (g·cm$^{-3}$) and soil moisture (%). Moisture measures were repeated in May 2012, Mar 2013 and May 2013. Soil water infiltration (mm·s$^{-1}$) was measured by double-ring infiltrometer (Bower 1986). We measured soil air porosity by maximally compressing 10 × 10 cm Ø soil cores using a technique following Jafarzadeh (2006).

### Vegetation survey

A comprehensive vegetation survey was conducted in May 2012, where we recorded the percentage cover of all species, including bare ground, within 1 m × 1 m quadrats subdivided into a grid of 10 cm × 10 cm cells and placed inside and outside *J. maritimus* patches. From this survey we calculated the frequency of occurrence and cumulative contribution of all species encountered (Appendix S1). The five most frequently encountered plant species were selected for the detailed trait variation inside and outside the benefactor species *Juncus maritimus* Lam. *Elytrigia atherica* (Link) Kerguélen., *Festuca rubra* L., *Juncus gerardii* Loisel., *Puccinellia maritima* (Huds.) Parl., *Artemisia maritima* L. For each of these five plant species and in addition the benefactor species (*J. maritimus*), during May 2013, we measured the following traits averaged from at least ten individuals per quadrat: maximum species height (cm), resource allocation was estimated from shoot biomass (g), separating alive and dead material within a 10 cm Ø sample per plot, and specific leaf area (SLA; mm$^2$·mg$^{-1}$; Harguindeguy et al. 2013) as indicator of environmental stress (McGill et al. 2006). Root biomass (g) was washed from a soil core of 10 cm Ø and 10-cm deep (Jackson et al. 1997). The roots of *J. maritimus* and *E. atherica* could reliably be distinguished from other roots. The remaining fine root biomass was classified as 'Unidentified' fine root material. Specific root length (SRL; cm·g$^{-1}$) was calculated using the methods described in Tennant (1975).

### Herbivore and soil macro-detritivore presence

Within the same sampling plots we quantified large herbivore (cattle) presence by scoring the presence of fresh dung piles (Looijen & Bakker 1987) within 10 m × 10 m quadrats. Soil macro-detritivore presence [*Orchestia gammarellus* Pallas. 1766. are most abundant (Schrama et al. 2012a)] was quantified by counting holes or individuals along 2-m strip transects divided into 20 cm × 10 cm blocks, and presence was calculated as a proportion (*n*/20).

### Data analysis

#### *Plant associations*

To calculate the association of the five focal plant species with the presence of *J. maritimus* we used the relative interaction index (RII) as specified in Armas et al. (2004), RII = Bw − Bo/Bw + Bo, where Bw is the abundance within the patch and Bo is the abundance outside the patch. Values range from 1 to −1, where positive values indicate that a species is positively associated with the patch, negative values indicate that the species is negatively associated with the patch and zero indicates a neutral interaction. Paired *t*-tests (R Foundation for Statistical Computing, Vienna, AT) were used to quantify the differences in distribution of species between grazed and ungrazed plots.

#### *Vegetation height, herbivore presence and abiotic conditions*

Differences between inside and outside *J. maritimus* patches, in the grazed and ungrazed plots, in plant canopy light interception, plant biomass allocation (alive and dead above-ground and below-ground biomass), cattle and soil macro-detritivores presence, and variation in abiotic conditions (salinity, soil redox, soil moisture) were analysed using ANCOVA (Crawley 2005) with mean inundation hours per day as a covariate. Where the covariate was not significant, model simplification was used (Zuur et al. 2009) and two-way ANOVAS or one-way ANOVAS were used. Post-hoc Tukey HSD were used to separate significant differences between groups. Species richness was calculated over all quadrats.

#### *Analysis of trait variation using multivariate techniques*

For data analysis of the plant trait responses, we used canonical correspondence analysis. To fully disentangle how trait variation responds to interacting environmental stressors, the data were divided into three groups: (1) response variables: maximum species height, SLA, log specific root length and abundance of each species; (2) active predictor variables: constrained grazing treatment grazed/ungrazed inside/outside *J. maritimus* patches, and unconstrained continuous: inundation hours per day; and (3) passive predictor variables namely: conductivity (separating between measures May 2012, Mar 2013 and May 2013, soil redox (separating between measures May 2012, Mar 2013 and Jun 2013), plant canopy light interception, percentage bare ground cover, soil bulk density, clay depth, soil infiltration rate, soil air porosity, above-ground biomass (alive and dead), below-ground biomass, plant species richness, presence of herbivores (cattle) and soil macro-detritivores.

The response and active predictor variables were used to ordinate the data in multivariate space to test our hypothesis that the responses of each of the six species would be different among grazing treatments and inside/outside *J. maritimus* patches. The passive predictor variables were fitted as a function of the ordination model, using 999 permutations (Jongman et al. 1995). Significance values were calculated for each passive predictor variable and used to assess the importance of fluctuating environmental gradients (conductivity and redox) and to distinguish between correlated and independent measures along the main axes. Centroid ellipses were added to delineate the different groups in the data representing the grazing treatments, grazed outside and inside *J. maritimus* patches, and ungrazed outside and inside *J. maritimus* patches. A Monte Carlo permutation test (199 permutations) was used to test whether the first and second ordination axes explained significantly more of the variation within the data set than expected by chance.

## Results

### Abiotic conditions

Within the elevation range (50–250 cm + NAP), a tight exponential relation was found between elevation and mean inundation hours per day (GLM: $F_{(1,198)} = 59\,640$, $R^2 = 0.997$, $P < 0.001$). At lower elevation, inundation hours are exponentially longer due to the on and off flow of tidal waters. Locations below 50 cm + NAP are inundated 24 h a day. Salinity (Fig. 1a) showed strong variation between sampling dates and was in most cases not significantly related to the underlying elevation/inundation gradient. However, the soil sampled within *J. maritimus* patches showed the strongest fluctuations [ANCOVA: $F_{(5,174)} = 15.29$, $P < 0.5$ (Mar 2013), $P < 0.01$ (May 2013), $P < 0.001$ (Grazed), $P = 0.58$ (Elevation, Patch)]. Soil redox (Fig. 1b) showed strong fluctuations, especially within the grazed *J. maritimus* patches, but again no strong association of decreasing redox along the elevation gradient [ANCOVA: $F_{(5,174)} = 17.61$, $P < 0.05$ (Mar 2013), $P < 0.001$ (Jun 2013), $P < 0.001$ (Grazed), $P = 0.49$ (Inundation, Patch)]. Canopy light interception (Fig. 1c) showed consistently very high light interception within *J. maritimus* patches and ungrazed marsh compared to the grazed outside *J. maritimus* patches [ANCOVA: $F_{(2,57)} = 16.59$, $P < 0.001$ (Grazed, Patch), $P = 0.40$ (Inundation)]. Soil air porosity (Fig. 1d) was significantly higher on the ungrazed marsh compared to the grazed marsh [ANCOVA: $F_{(2,57)} = 41.25$, $P < 0.01$ (Grazed), $P = 0.44$ (Inundation)]. However, no significant differences were

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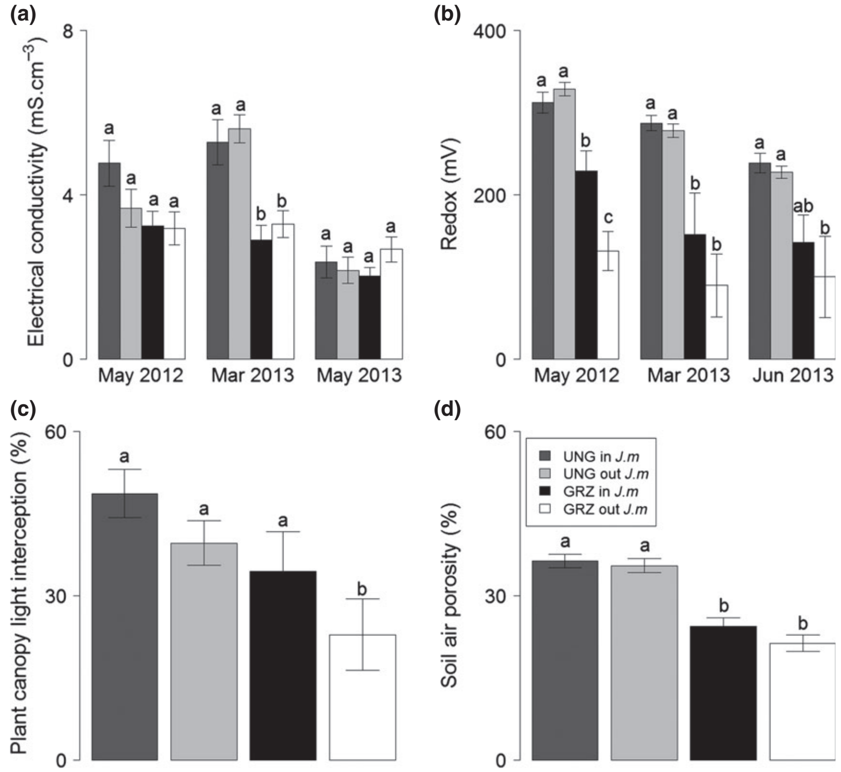

**Fig. 1.** Differences in limiting abiotic stressors between grazed and ungrazed areas inside and outside *Juncus maritimus* patches. (**a**) Electrical conductivity (mS.cm$^{-3}$) as a proxy for soil salinity, measured over time (2012–2013). (**b**) Soil redox potential (mV), as a proxy for soil oxygen, measured over time (2012–2013). (**c**) Plant canopy light interception. (**d**) Soil air porosity. Different letters indicate significant differences within each sampling period (Tukey HSD, $P < 0.05$).

found between soil air porosity inside and outside of the *J. maritimus* patches [$P = 0.84$ (Patch)], despite the expected lower grazing intensity inside the patches.

## Vegetation associations

Using relative interaction indices, we found that *E. atherica* (Fig. 2a) and *F. rubra* (Fig. 2b) were positively associated within the *J. maritimus* patches on the grazed marsh (*E. atherica*: 0.90 ± 0.27; *F. rubra*: 0.23 ± 0.73) and negatively associated with *J. maritimus* patches on the ungrazed marsh (*E. atherica*: −0.20 ± 0.50; *F. rubra*: −0.64 ± 0.59), with significantly different distributions. *J. gerardi* (Fig. 2c) and *P. maritima* (Fig. 2d) were negatively associated with *J. maritimus* patches on the grazed (*J. gerardi*: −0.74 ± 0.53; *P. maritima*: −0.93 ± 0.14) and ungrazed (*J. gerardi*: −0.90 ± 0.04; *P. maritima*: −0.94 ± 0.7) marsh and these distributions did not differ significantly. The spatial association of *A. maritima* (Fig. 2e) with *J. maritimus* appears to be neutral and was not different between the grazed (0.09 ± 0.76) and ungrazed (−0.41 ± 0.67) marsh. Finally, also the patch-forming *J. maritimus* showed differences in absolute abundance within the patch between the grazed marsh (16.8 ± 14.16) and ungrazed marsh (39.5 ± 15.16; paired *t*-test: $P < 0.001$). Plant distributions were not related to the inundation gradient (Fig. 2a–e).

## Vegetation height, herbivore and soil macro-detritivore presence

Vegetation height (Fig. 3a) was not related to the inundation gradient ($P = 0.19$). Vegetation height was lowest outside *J. maritimus* patches on the grazed marsh and highest inside *J. maritimus* patches in the ungrazed marsh (two-way ANOVA: $F_{(3,56)} = 67.01$, $P < 0.001$, post-hoc Tukey HSD). Cattle dung (Appendix S4) was more abundant outside *J. maritimus* patches than inside *J. maritimus* patches (ANOVA: $F_{(1,28)} = 21.55$, $P < 0.001$) and independent of the inundation gradient ($P = 0.59$). Soil macro-detritivores (Fig. 3b) were overall significantly less abundant in the grazed marsh compared to the ungrazed marsh (two-way ANOVA: $F_{(3,56)} = 229.7$, $P < 0.001$, post-hoc Tukey HSD) and the distribution was not related to the inundation gradient ($P = 0.09$). In the grazed marsh, soil macro-detritivore presence was significantly higher inside than outside

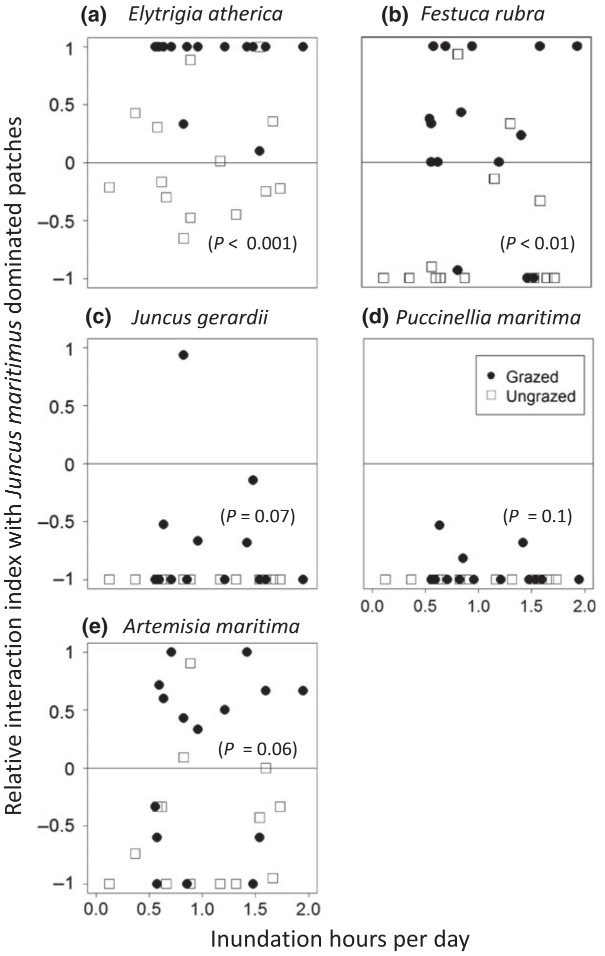

**Fig. 2.** Individual species associations with the benefactor species *J. maritimus* between grazed and ungrazed areas and in relation to mean hours inundated per day, (**a**) *E. atherica*, (**b**) *F. rubra*, (**c**) *J. gerardii*, (**d**) *P. maritima* and (**e**) *A. maritima*. *P*-values indicate the difference in distribution within a plant species between the grazed and ungrazed areas ($N = 30$).

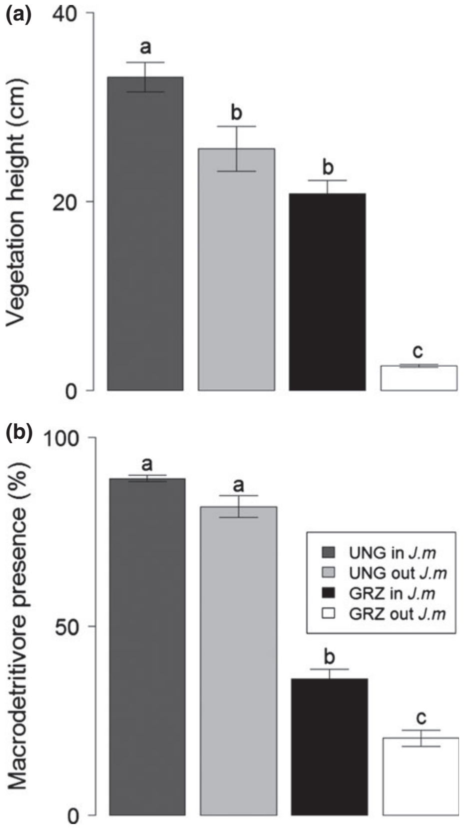

**Fig. 3.** Differences between (**a**) vegetation height averaged all species and (**b**) abundance of soil macro-detritivores, inside and outside *Juncus maritimus* patches on the grazed and ungrazed (by cattle) salt marsh. Different letters indicate significant differences within each sampling period (Tukey HSD, $P < 0.05$).

*J. maritimus* patches ($P < 0.01$), but in ungrazed marshes soil macro-detritivore presence did not differ significantly between inside and outside *J. maritimus* ($P = 0.06$).

## Multivariate analysis of plant trait variation

The CCA yielded four ordination axes, of which axes 1 and 2 explain 96% of the variation within the data. The biplot (Fig. 4) shows the plant traits and abundance, in relation to constrained predictors (shown as centroid ellipses) and unconstrained predictors (inundation gradient) with fitted passive predictor variables with 999 permutations (showing only significant passive predictor variables $P < 0.05$). The overall ordination accounted for significantly more variation than expected by chance (Monte Carlo permutation test: $F_{(1,51)} = 18.39$, $n = 199$, $P < 0.01$), as did the first three axes (Appendix S2). The first axis separated the inside and outside grazed *J. maritimus* patches, however also showed that patches dominated by *J. maritimus* were grouped closely together between the grazed and ungrazed areas. Ungrazed *J. maritimus* patches was positively correlated to a higher abundance and taller *J. aritimus* individuals. However, grazed *J. maritimus* patches differed from ungrazed patches in that they were correlated to higher SLA for *J. aritimus* and both higher SLA and abundance of *E. atherica* and *F. rubra*. In general *J. maritimus* patches were correlated to higher soil anoxia, higher salinity, higher light interception due to increased plant biomass, higher soil porosity, higher abundance of macro-detritivores and lower SLA (Table 1). Outside the *J. maritimus* patches on the grazed marsh, *P. maritima* and *J. gerardii* were more abundant with highest SLA and plant height positively correlated with more compact soil, higher below-ground biomass, plant species richness, higher abundance of cattle and

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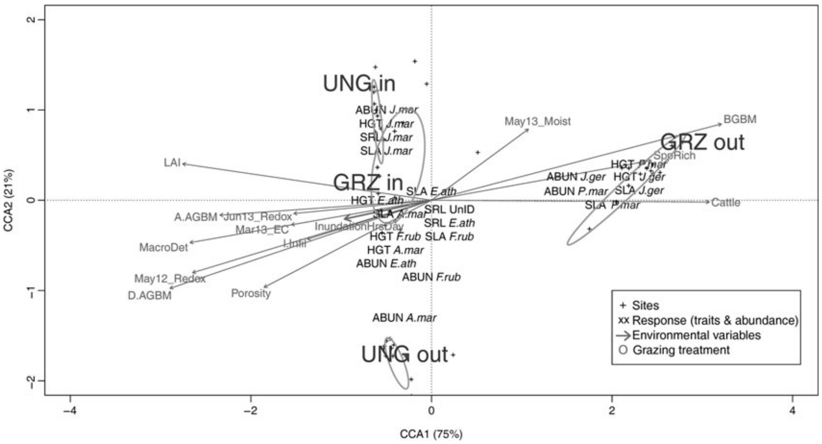

**Fig. 4.** Biplot showing the scores for six focal plant species (*E. atherica, F. rubra, J. gerardii, P. martima, A. maritima* and the patch-forming species *J. maritimus*) response traits (SLA, SRL, height) and abundance in relation to constrained predictors (shown as centroid ellipses: grazed/ungrazed, inside/outside *Juncus* patches) and unconstrained predictors (shown as a gradient: inundation hours per day) with passive environmental predictors (only predictors with $P < 0.05$ are shown), see Table 1 and Appendix S2 for detailed score and statistical summary. SLA, specific leaf area; SLR, specific root length; Hgt, plant height; Abun, % cover; InundationHrsDay, mean inundation hours per day; EC, electrical conductivity (soil salinity); Redox, potential (soil oxygen); Moist, soil moisture; LAI, leaf area index; SppRich, plant species richness; A.AGBM/D.AGBM, alive/dead above-ground biomass; BGBM, below-ground biomass; Cattle, presence; MacroDet, soil macro-detritivore presence; l.Infil, log-transformed infiltration rate; Porosity, soil air-filled porosity.

higher soil moisture. The second axis separates inside and outside *J. maritimus* patches and was independent of environmental variation. Variation in SRL did not show strong patterns and was centrally situation in the CCA analysis.

## Discussion

In the grazed area, we found significantly less cattle dung inside compared to outside the *J. maritimus* patches, indicating how much time these large herbivores spend in different locations (Looijen & Bakker 1987). We can therefore infer that grazing (and trampling) was lower inside *J. maritimus* patches than outside patches. *J. maritimus* tends to be avoided by large herbivores as the plant is physically defended, both by sharpened leaf tips and heavy structural investments (Fitter & Peat 1994) that are hard to digest (Iason & van Wieren 1999). Two species seemed to profit from an association with *J. maritimus* under grazing: *E. atherica* and *F. rubra*, which are stoloniferous palatable grasses without physical or chemical defence traits and actively selected as forage by cattle. Hence, for these two species, protection against large herbivore grazing (i.e. associational resistance) appears to be the main mechanism behind the spatial association with *J. maritimus* under grazing. In contrast, *A. maritima* contains aromatic oils within the vacuoles of the leaves that makes this species salt-tolerant as well as unpalatable to herbivores (Abdelmajeed et al. 2013). This species showed a neutral (no positive or negative) association with *J. maritimus* in our study, both in the grazed area and in the ungrazed area. The short-statured *J. gerardii,* and *P. maritima* were strongly negatively associated with the *J. maritimus* patches in the grazed and ungrazed areas. Studies of *J. gerardii* and *P. maritima* reveal that these species are particularly shade-intolerant (Richards & Clapham 1941; Gray & Scott 1977), therefore largely absent from the tall vegetation. Defoliation by large herbivores decreases the canopy height and thus more light is able to penetrate to the soil surface. In addition, trampling by large herbivores damages above-ground plant parts, especially of tall plants with rigid above-ground structures, resulting in reduced density of leaves and flower stalks of tall-growing plants (Milchunas et al. 1988), and thus promoting conditions for these short-statured species to thrive. It is therefore important to realize that shading highly restricts the distribution of these two species and that they are well adapted to abiotic stress (Jakobsen 1954; Langlois et al. 2003). From our study, it is clear that cattle grazing affected the direction of species interactions, which is well reflected by interspecific trait variation of the dominant plant species.

Grazing by cattle also induced strong intraspecific trait variation. Most notably, several traits of *J. maritimus*, the focal patch-forming species, were affected by grazing. *J. maritimus* was shorter and less abundant in patches under grazing than in the ungrazed area. As a result, the growing conditions differ within *J. maritimus* patches between the grazed and ungrazed areas, and so affected the interactions with other plants. This result forms an interesting parallel with the studies of Michalet et al. (2011) and Schöb et al. (2013) showing that abiotic stress can affect the intraspecific traits of a benefactor species, with consequences for its beneficiary effects. In addition,

**Table 1.** Regression/canonical ordination scores for (a) response traits and abundance, (b) active predictors and (c) passive environmental predictors used to test trait and abundance variation in relation to grazing by large herbivores inside and outside *Juncus maritimus* patches along a continuous inundation duration gradient.

| (a) | Response Traits and Abundance | CCA1 | CCA2 |
|---|---|---|---|
| Specific Leaf Area | SLA *E. atherica* | 0.146972 | 0.022616 |
| | SLA *F. rubra* | 0.151415 | −0.06642 |
| | SLA *J. gerardii* | 2.160447 | 0.113632 |
| | SLA *P. martima* | 2.164024 | 0.149668 |
| | SLA *A. maritima* | 0.07416 | −0.07151 |
| | SLA *J. martimus* | −0.45601 | 0.577683 |
| Specific Root Length | log.SRL *E. atherica* | 0.276989 | −0.07679 |
| | log.SRL Unidentified | 0.238924 | −0.06995 |
| | log.SRL *J. maritimus* | −0.47329 | 0.600823 |
| Height | Hgt *E. atherica* | −0.24466 | −0.11223 |
| | Hgt *F. rubra* | −0.24533 | −0.13608 |
| | Hgt *J. gerardii* | 2.161023 | 0.119427 |
| | Hgt *P. maritima* | 2.161862 | 0.127888 |
| | Hgt *A. maritima* | −0.09453 | −0.09058 |
| | Hgt *J. maritimus* | −0.48563 | 0.623863 |
| Abundance | Abun *E. atherica* | −0.43077 | −0.34579 |
| | Abun *F. rubra* | 0.014318 | −0.48489 |
| | Abun *J. gerardii* | 1.621151 | 0.157576 |
| | Abun *P. maritimus* | 2.075412 | 0.138365 |
| | Abun *A. maritima* | −0.19988 | −0.76056 |
| | Abun *J. maritimus* | −0.52312 | 0.714548 |

| (b) | Active Predictors | CCA1 | CCA2 |
|---|---|---|---|
| Grazing | Grazed in | −1.3417 | −0.52853 |
| | Grazed out | 2.1615 | 0.1238 |
| | Ungrazed in | 0.5976 | 0.8702 |
| | Ungrazed out | −0.384 | −1.806 |
| Gradient | Inundation hours per day | −0.06301 | −0.00336 |

| (c) | Passive Environmental Predictors (999 Permutations) | CCA1 | CCA2 | $R^2$ | *P*-Value | Signif |
|---|---|---|---|---|---|---|
| Abiotic | May 2012 Conductivity | −0.9127 | 0.40864 | 0.0474 | 0.22 | n.s. |
| | Mar 2013 Conductivity | −0.98497 | −0.17275 | 0.1407 | 0.013 | * |
| | May 2013 Conductivity | 0.81628 | −0.57766 | 0.0135 | 0.665 | n.s. |
| | May 2012 Redox potential | −0.95688 | −0.29048 | 0.4337 | 0.001 | *** |
| | Mar 2013 Redox potential | −0.65692 | −0.75396 | 0.0961 | 0.048 | * |
| | Jun 2013 Redox potential | −0.99536 | −0.09617 | 0.1331 | 0.011 | * |
| | May 2012 Moisture | 0.07408 | 0.99725 | 0.0326 | 0.378 | n.s. |
| | Mar 2013 Moisture | −0.11365 | 0.99352 | 0.0139 | 0.675 | n.s. |
| | May 2013 Moisture | 0.80611 | 0.59176 | 0.1007 | 0.038 | * |
| | Light interception | −0.98944 | 0.14493 | 0.4403 | 0.001 | *** |
| Soil Structure | Bare ground | 0.99957 | 0.02929 | 0.014 | 0.711 | n.s. |
| | Bulk density | 0.75256 | 0.65853 | 0.0314 | 0.394 | n.s. |
| | Clay depth | 0.71797 | −0.69608 | 0.0022 | 0.936 | n.s. |
| | (log) Infiltration | −0.95397 | −0.2999 | 0.1179 | 0.026 | * |
| | Porosity | −0.88684 | −0.46209 | 0.2479 | 0.001 | *** |
| Flora | Alive – Above-ground biomass | −0.99753 | −0.07028 | 0.3131 | 0.001 | *** |
| | Dead – Above-ground biomass | −0.94757 | −0.31956 | 0.5303 | 0.001 | *** |
| | Below-ground biomass | 0.96705 | 0.25458 | 0.6258 | 0.001 | *** |
| | Species richness | 0.984 | 0.17815 | 0.3472 | 0.001 | *** |
| Fauna | Cattle | 0.99998 | −0.00652 | 0.5375 | 0.001 | *** |
| | Macro-detritivores | −0.98491 | −0.17304 | 0.4183 | 0.001 | *** |

*$P < 0.05$, ***$P < 0.001$, n.s. = not significant.

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our study adds that biotic stress enhanced by herbivore grazing impacts the intraspecific traits of a benefactor and so alters species interactions.

Grazing by large herbivores was not detrimental for all plant species. Interspecific trait differences between plant species permit different species to dominate under different stress types. We found continuous vegetation dominated by the low-statured *J. gerardii* and *P. maritima* outside of the *J. maritimus* patches, and both species showed an increase in SLA with increased grazing pressure. Likewise, the SLA and SRL of *J. maritimus* and *E. atherica* increased under grazing, which indicates that plants experienced improved growing conditions despite the negative impacts of grazing. In the ungrazed area, we found that SLA and below-ground biomass of the dominant plant species decreased. This indicates that plants in the ungrazed situation grow more slowly, where our measures show a significantly higher canopy and lower light penetration. This finding is in line with Boughton et al. (2011) who also found that *Juncus effusus*, a similar physically defended patch-forming plant species, benefits less grazing-tolerant species in the presence of large grazers and competes with other light competitive plant species where large grazers are absent.

The environmental abiotic gradient (inundation duration) did not result in the expected changes in species interactions. We expected that positive interactions would predominate at long inundation zones (resulting in high salinity and low soil redox) and negative interactions would predominate where the inundation intervals were short (resulting in low salinity and high soil redox), independent of the grazing. However, both salinity and soil redox were not related to the underlying elevation/inundation gradient. Instead, we found that grazing was the dominant driver of alterations of species interactions, with more foraging outside than inside *J. maritimus* patches, inducing locally high stress from defoliation and reduced soil porosity and anoxia through trampling. We did find a remarkable variability in salinity that was most pronounced inside *J. maritimus* patches and on the ungrazed marsh, but in most instances, the salinity was unrelated to the underlying inundation gradient. Only once in our study period did we find the characteristic steady decrease with increasing elevation as usually mentioned in salt marsh studies (De Leeuw et al. 1990; Bakker et al. 1993; Olff et al. 1997). A possible explanation for this is that within the low-growing plant community outside *J. maritimus* (on the grazed salt marsh) the first 10 cm of soil profile contains a very high density of root biomass compared to within the *J. maritimus* patches and compared to both inside and outside patches of the ungrazed marsh (twp-way ANOVA: $F_{(3,56)} = 68.53$, $P < 0.001$). Plant material is less likely to absorb salt than soil due to the high osmolarity of the internal plant constituents preventing the influx of salt (Parida & Das 2005). Increased soil content within the topsoil may readily absorb increased soil moisture and salt, therefore plant communities that contain lower root:soil ratios would experience higher fluctuations in local salinity. Soil redox potential was also not related to the inundation gradient in this study. It is possible that trampling by cattle grazing compacted the soil, reducing drainage and reducing soil aeration (Abdelmagid et al. 1987; Schrama et al. 2012b), whereas on the ungrazed marsh soil redox potentials were consistently higher than the (compacted) grazed marsh. This is possibly due to the increase in soil porosity induced by the bioturbation activities of soil macro-detritivores (Dias & Sprung 2003).

An important and novel finding of this study was evidence for cross-trophic facilitation of the benefactor *J. maritimus* for soil macro-detritivores, notably *Orchestia gammarellus*, the most abundant soil organism within the late successional stage (Andresen et al. 1990; Schrama et al. 2012a). Soil macro-detritivores, integral in soil regeneration processes and whose bioturbation activities promote nutrient mineralization (Wilkinson et al. 2009), are essential in the renewal and functioning of ecosystems (Meysman et al. 2006). Grazing significantly lowers the abundance of macro-detritivores through trampling since they are small soft-bodied organisms (Dias & Sprung 2003). However, we found that the soil macro-detritivores were more abundant inside compared to outside *J. maritimus* patches. This is probably due to the higher availability of dead plant biomass, on which these decomposers feed, and lower grazing intensity. Thus, under grazed conditions the beneficiary effects of *J. maritimus* may cascade through to other trophic levels. Such cross-trophic facilitative interactions via macro-detritivores have not received much attention in the literature (Soliveres et al. 2014), but may be more important for the structure and functioning of ecosystems than thus far acknowledged. In conclusion, our study shows that for an advanced understanding of interactions and spatial organization of plant communities along environmental gradients, it is crucial to include multiple stressors, consumers and their indirect effects.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Appendices S1 and S2.** Provide the frequency distribution of different plant species sampled and the canonical correspondence model parameters.

**Appendices S3 and S4.** Photographs and map of the study system, and a plot showing the presence of cattle inside and outside *of Juncus maritimus* patches on the grazed (by cattle) salt marsh.

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