



## Research article

## Strain and vegetation effects on local limiting resources explain the outcomes of biotic interactions

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## ABSTRACT

Positive interactions are hypothesized to increase with stress (stress-gradient hypothesis, “SGH”), which is defined in terms of standing biomass at the community level. However, recent evidence suggests that facilitation may decrease or remain constant as stress increases. Several reasons for this discrepancy are possible: (i) the outcomes of biotic interactions depend on the component of the fitness considered; (ii) they are influenced by how vegetation affects local limiting resources; (iii) within a particular community, only species that are deviated from their physiological optima are likely to be facilitated. In a removal experiment, we quantified the deviations of species in subalpine grassland from their physiological optima, defined here as species-level “strain”, and examined whether strain and vegetation effects on local resources can explain the outcome of biotic interactions. The experiment was performed along a gradient of standing biomass driven by contrasting land use and resource availability, and used five grass species with contrasting traits and ecological optima. Strain for each species was estimated by comparing growth without vegetation (target species only submitted to local abiotic factors) to growth in optimal conditions (under controlled conditions in an experimental garden). The outcomes of biotic interactions, recorded in terms of survival and growth, could be predicted from the data about strain and vegetation effects on local limiting resources (light and water). Only highly strained species were affected by facilitation, which occurred when the surrounding vegetation alleviated the constraining factors. On the other hand, standing biomass was poorly related with the outcomes of biotic interactions. The “SGH” was only partially validated with growth data when strain and vegetation effects co-varied with standing biomass. As a consequence, strain (at species level) represents a mechanistic basis which could improve the prediction of the outcomes of biotic interactions along ecological gradients.

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## Introduction

Positive interactions are recognized to play a major role in shaping plant communities, especially in severe environments (Choler et al., 2001; Callaway et al., 2002; Olofsson, 2004; Olofsson et al., 2004; Brooker et al., 2007). By ameliorating the harshness of the environment, vegetation cover can have positive effects upon a particular target species (Bertness and Callaway, 1994; Greenlee and Callaway, 1996). Although net facilitation is commonly observed in harsh environments, both negative and

positive interactions usually co-occur along ecological gradients (Walker and Chapin, 1986; Wedin and Tilman, 1993; Pugnaire and Luque, 2001; Maestre et al., 2003). The factors affecting the balance of positive and negative interactions along stress gradients has been synthesized in the “stress-gradient hypothesis” (“SGH”) (Brooker et al., 2005), which posits that competitive effects are more intense in relatively benign environments whereas facilitation increases in intensity with stress (Callaway and Walker, 1997). While the “SGH” has been largely supported by studies in several environments (e.g. Bertness and Hacker, 1994; Choler et al., 2001; Callaway et al., 2002; Maestre et al., 2003; Liancourt et al., 2005), recent work has called the established theory into question (Maestre and Cortina, 2004; Maestre et al., 2005; Cavieres et al., 2006; but see Lortie and Callaway, 2006). Thus, across studies, net facilitation has been found to increase, remain constant or even decrease along stress gradients (Michalet et al., 2006; see Brooker et al., 2007 for a review).

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There may be several reasons for these discrepancies. First, the outcome of biotic interactions depends on the fitness components used to measure interactions (survival, growth, reproduction) (Goldberg et al., 1999; Lortie and Callaway, 2006). Second, even in stressful environments, vegetation can have positive (Liancourt et al., 2005) or negative effects on local limiting resources (Schwinning and Sala, 2004; Padilla and Pugnaire, 2006), leading either to apparent facilitation or to competition. Finally, the concept of stress, as considered in most plant interaction models, is defined at the community level in terms of a decrease of productivity, with standing biomass being commonly used as a proxy (Grime, 1977; Bertness and Callaway, 1994; Michalet et al., 2006). However, gradients of standing biomass are often complex and many limiting factors may co-vary (Rajaniemi, 2003; Michalet, 2006; Gross et al., 2008); thus, using community-level measurements (e.g. standing biomass) to estimate stress for an individual plant may be misleading. In fact, species vary in their environmental tolerance, and facilitation is only likely to be important for those species that are stressed under the conditions prevailing in a particular community (Hacker and Bertness, 1999; Choler et al., 2001; Liancourt et al., 2005). Accordingly, to predict the outcomes of biotic interactions it might be relevant to estimate how far the species present deviate from their physiological optima in the field; i.e. how they deviate from their fundamental niche optima (*sensu* Hutchinson, 1957; Choler et al., 2001; Liancourt et al., 2005). For this purpose, Welden and Slauson (1986) proposed to distinguish “stress”, which refers to productivity at the community level (*sensu* Grime, 1977), from “strain”, an individual-level response to local abiotic factors estimated without biotic interactions.

In this study, we examined the linkages among strain, vegetation effects on resources, and the outcomes of biotic interactions measured at individual-level. We hypothesized that (i) the outcome of biotic interactions is a function of strain measured at the individual-level and the effect of vegetation on local limiting resources; (ii) strain is a more accurate predictor of the outcomes of biotic interactions than stress measured at community-level in terms of standing biomass. For this purpose, we used co-occurring target species of subalpine grasslands that differ in their ecological optima and dominance patterns along a complex ecological gradient driven by contrasting land use and resources availabilities (Quetier et al., 2007; Gross et al., 2008). We estimated strain by comparing the growth of target species under non-limiting conditions in a common garden to their growth in the field without neighbors. Finally, we conducted a removal experiment along the gradient to determine the outcomes of biotic interactions (i.e. whether neighbors exert competitive or facilitative effects on target species growth). These data were combined in order to build a predictive model of biotic interactions.

## Methods

### Field site

The study was performed on the south-facing slope of the upper Romanche River valley, in the central French Alps (Villar d'Arène, 45.04°N, 6.34°E, elevation, 1950 m). The climate is subalpine with a pronounced continental influence. Mean annual precipitation is 956 mm and mean monthly temperatures range between  $-7.4^{\circ}\text{C}$  in February and  $19.5^{\circ}\text{C}$  in July. Only 18% of annual precipitation occurs in the summer, and most precipitation in the cooler months falls as snow.

We numbered our experimental sites with respect to the amount of standing biomass ( $\text{g}/\text{m}^2$ ), here measured at the peak of

the vegetation season. The gradient of standing biomass in the study area is influenced by both land use and resource availability, e.g. soil moisture, and by interactions between these factors. The effect of mowing or grazing on community biomass is mainly indirect. Grasslands are usually only lightly grazed at the end of the growing seasons. Mowing occurs at the end of August, after the period of peak biomass when plants are mostly senescent. Its effect is mainly mediated by its long-term effect on N availability and by litter removal (Robson et al., 2007; Quetier et al., 2007). Thus, our field sites are distributed along a complex gradient of standing biomass, with water availability varying independently from nutrient availability (see Quetier et al. (2007) and Gross et al. (2008) for a more detailed description of the communities, land use history and associated environmental factors). An unmown and unterraced grassland dominated by *Festuca paniculata* (tall slow-growing species, > 70% of the community biomass) (site I) had the highest amount of standing biomass ( $3430\text{ g}/\text{m}^2$ ); a fertilized terraced grassland dominated by *Dactylis glomerata*, *Trisetum flavescens*, *Agrostis capillaris*, *Heracleum sphondylium* and other fast-growing species (site II) was intermediate (standing biomass= $2040\text{ g}/\text{m}^2$ ); a mown *F. paniculata* grassland (site III) had a lower amount of standing biomass ( $1511\text{ g}/\text{m}^2$ ), and was dominated by *F. paniculata*, *Meum athamanticum* and *Trifolium alpinum*; finally, a grassland dominated by *B. erectus*, *S. caerulea* and other short slow-growing species was the lowest on our scale (site IV) (standing biomass= $1210\text{ g}/\text{m}^2$ ).

### Field experiment

Five C3 perennial grass species differing in their abundance across our experimental sites were selected as target species: two fast-growing species, one tall, *D. glomerata* (L.) (vegetative height, H: 21.05 cm; specific leaf area (SLA):  $21.2\text{ m}^2/\text{kg}$ ; leaf dry matter content (LDMC): 26%) and one short, *A. capillaris* (L.) P. De Beauvois (H: 12.23 cm; SLA:  $23.2\text{ m}^2/\text{kg}$ ; LDMC: 25%), which dominate in site II, two short slow-growing species *Sesleria caerulea* (L.) Arduino (H: 8.23 cm; SLA:  $14.89\text{ m}^2/\text{kg}$ ; LDMC: 39%), *Bromus erectus* (L.) (H: 15.33 cm; SLA:  $13.25\text{ m}^2/\text{kg}$ ; LDMC: 35%) which dominate in site IV, and one tall, slow-growing species *F. paniculata* (L.), Schinz et Thellung (H: 20.65 cm; SLA:  $9.85\text{ m}^2/\text{kg}$ ; LDMC: 32%) which is dominant in sites I and III (all species traits were measured under non-limiting conditions, see Gross et al. (2007) for data source and more information on species traits and species tolerances to abiotic factors). Tillers of each species were collected from the field sites in early September 2003. Plants were propagated in a greenhouse at the Joseph Fourier Alpine Research Station (5 km away from field sites, Villar d'Arène, elevation 2100 m).

During May 2004, we established a field experiment to quantify biotic interactions. Each of the four sites was fenced (1 m high fence with  $10 \times 10\text{ cm}^2$  mesh) to protect it from herbivory (small mammals such as marmots, wild ungulates and domestic sheep) and delimited into six blocks ( $24\text{ m}^2$ , i.e.  $6 \times 4\text{ m}^2$ ). For the removal experiment, we randomly defined 30 circular areas (60 cm – diameter) within each block. Aboveground vegetation was removed from half of these areas (15 areas) using a chemical non-selective herbicide (Glyphosate<sup>®</sup>, Monsanto Agriculture France SAS, 69 Bron). Dead vegetation was removed by hand, and roots were cut (25 cm deep) around the edge of the neighbour-removal areas. Then, one randomly selected individual plant (one tiller) was transplanted into the centre of each area. There were three replicates per competition treatment and the five species were arranged randomly within each block (i.e. five species  $\times$  two competition levels  $\times$  three replicates per species and per competition level  $\times$  six blocks  $\times$  four sites).

Each tiller was trimmed – to 3 cm in length for shoots and 5 cm depth for roots – and planted. In total, 720 homogeneous target plants were planted between 5 and 15 May 2004, just after snowmelt. During the experiment, the no-neighbour areas were kept free from vegetation by hand weeding. Periodic inspections and subsequent cutting of any roots entering into the areas were also performed. We mowed each experimental site at the end of the first growing season (end of August 2004).

The field experiment was harvested on July 30, 2005, at a time corresponding with peak-season biomass. At the end of the experiment, plant survival was measured, and the aboveground plants parts were then harvested, washed, dried for 72 h at 60 °C and weighed. The loamy texture of the soil prohibited harvesting and separation of belowground biomass.

### Environmental variables

To assess vegetation effects on abiotic resources, we quantified abiotic factors in each site with and without vegetation in three plots (12 m<sup>2</sup>) per site, interspersed between pairs of blocks used to quantify biotic interactions. Consequently, two blocks (used for measuring strain and biotic interactions) were paired with one plot (used for abiotic factors measurements). To quantify abiotic factors in the absence of vegetation, all plant material was removed at the beginning of the experiment from half of each plot using the same methods as for the biotic interactions experiment, resulting in one subplot with, and one without vegetation.

**Soil moisture** – Soil moisture was quantified at each site with time domain reflectometry (TDR) probes (TRASE system 1 Soil Moisture Equipment Corporation, Santa Barbara, USA). In each plot, three probes were placed (15-cm depth) randomly in areas with and without vegetation at the beginning of the second growing season (May 20, 2005). Soil moisture was measured weekly throughout the growing season between 11 a.m. and 3 p.m. for day to day comparison. Detailed methods and results for these measurements are described in a companion study (Gross et al., 2008).

**Light availability** – Canopy stature at peak biomass was measured within each plot at three randomly located points for each of the vegetated and unvegetated subplots. Light interception was calculated by measuring photosynthetically active radiation (PAR) above and below the vegetation canopy at 30 randomly selected locations per plot (90 locations per community) using a LI-190 (LI-COR Inc., Lincoln, NE, USA).

**Soil N concentration** – At the end of the experiment 3 soil cores (15 cm depth, 4.5 cm diameter) were taken within each plot from the subplots with and without vegetation. Each core was sieved and frozen until extraction. Nitrate and ammonium concentrations were measured by colorimetric reaction (Fiastar 5012 Flow Injection Analyser, Foss Tecator AB, Sweden) following extraction from a 30 g soil subsample (equivalent dry mass) in 2 M KCl. These measurements were assumed to be representative of differences across sites and treatments throughout the growing seasons, as these have been shown to be reasonably stable for the same sites (Robson et al., 2007). Because soil ammonium concentrations did not differ in the subplots with and without vegetation (data not shown), we only used the nitrate data to quantify effects of vegetation on N pools.

**Standing biomass** – Standing biomass was measured at the peak of biomass at the end of July 2005 before the mowing event. Aboveground biomass was harvested from a area of 0.5 × 0.5 m<sup>2</sup> in each plot, and green and dead biomass were separated, dried for 72 h at 60 °C and weighed.

### Deviation from non-limiting conditions

For strain calculations, we measured the growth of the target species under non-limiting conditions (Suding et al., 2003), by ensuring a surplus of resources, the presence of mutualisms and absence of negative interactions. To do this, we grew each species under the same climatic conditions in an experimental garden at the Joseph Fourier Alpine Research Station. One tiller of each species per pot (coming from the same source location as tillers used in the field experiment) was planted in a 15 l pot (33 cm diameter) during early June 2003, with eight replicates per species. We chose tillers of homogeneous initial size, and each of them was cut to 3 cm in length for shoots and 5 cm depth for roots. The soil was composed of 2/3 of sand, 1/4 of clay and 1/12 commercial potting compost (Fertiligène®). Plants were grown from July 5, 2003 to August 15, 2004. We added 15 g of a commercial slow release fertilizer NPK (N, 12%; P, 12%; K 17%; Mg, 2%) to each pot per year. As we used tillers from the field, we assume that root symbioses such as mycorrhizae were conserved. All the pots were watered daily during the two growing seasons. They were randomly located in the experimental garden and rotated regularly throughout the experiment. During winter, we buried them to protect roots from freezing and they were covered by snow during this period. At the end of the experiment plants were harvested, dried at 60 °C for 72 h and weighed.

### Data preparation

#### Vegetation effects on abiotic resources

Water availability for plants (AW) was estimated in each subplot and for each measurement date using:

$$AW(\%) = (\text{soil moisture between 0 and 15 cm depth} - \text{wilting point})$$

Wilting point was estimated for the four sites indirectly from the soil texture, organic matter and stoniness using equations from the Soil Plant Air Water model (SPAW; US Department of Agriculture; Saxton, 1982; Gross et al., 2008).  $AW < 0$  implies that the community was water limited during the growing season, and  $AW > 0$  means that no water limitation was detected.

The effects of vegetation on light, soil nitrate concentration and water availability were quantified using the natural log response ratio (LnRR):

$$\text{LnRR}(\text{resource}) = \ln(\text{resource with neighbors} / \text{resource without neighbors})$$

$\text{LnRR} < 0$  implies a negative effect of vegetation on resources, whereas  $\text{LnRR} > 0$  indicates a positive effect on resource availability.

#### Strain and biotic interactions

We calculated strain for each target species as the deviation of plant growth in the field from unlimiting conditions, using the natural log response ratio:

$$\text{LnRR}(\text{strain}) = \ln(\text{individual biomass production in the field without neighbors} / \text{mean biomass production in non-limited conditions})$$

As strain becomes more negative, target species growth is depressed compared with non-limiting conditions.

The responses of target species to biotic interactions were quantified for survival and growth using the natural log response ratio (LnRR) (Hedges et al., 1999). For survival, one value was calculated for each block as the percentage of survival of three individual targets for each species and each competition treatment. Similarly, one mean aboveground biomass value per block and per target species was calculated in each competition treatment. As a result, six measurements of survival and growth

were obtained for each species and for each site with and without vegetation. Using these data, the log response ratio was calculated for each species as

$\text{LnRR}(\text{interaction}) = \ln(\text{individual target response with neighbors in block } i / \text{mean target response without neighbors for block } i)$ .

When  $\text{LnRR} > 0$  the outcome of biotic interactions is positive, which indicates net facilitation; in contrast,  $\text{LnRR} < 0$  indicates net competition. Because of the high mortality rate of *A. capillaris*, no  $\text{LnRR}(\text{interaction})$  was calculated for growth of this species.

### Statistical analysis

All statistical analyses were conducted at block level where the outcomes of biotic interactions and strain were calculated (six replicates per site and treatment). To incorporate into the analyses standing biomass (as a proxy for stress) and vegetation effects on abiotic resources, we averaged species value of strain and biotic interactions ( $\text{LnRR}(\text{survival})$  and  $\text{LnRR}(\text{growth})$ ) for each pair of blocks (used for biotic interactions measurement) located on either side of one plot used for abiotic factors measurements. As a result, three replicates per species were available in each site for analysis.

### Abiotic factors and vegetation effects

One-way ANOVA models were used to assess whether there were differences among sites for vegetation height, soil nitrate concentration and effect of vegetation on light and nitrate concentration ( $\text{LnRR}(\text{resource})$ ) (see Appendix). For soil moisture, a repeated-measures ANOVA was conducted to test for significant differences among sites throughout the growing season in the effect of vegetation on soil moisture ( $\text{LnRR}(\text{resource})$ ) (analysis are detailed in Gross et al., 2008). *Post hoc* analyses were used to assess differences between sites using Tukey-HSD.

### Strain and abiotic factors

The relationships between strain and abiotic factors (soil moisture, soil nutrient concentration and standing biomass) were investigated for each species using linear regression. Additionally, we calculated linear regressions using the data for all species to test whether there was any general relationship between strain and stress.

### Vegetation effects and the outcomes of biotic interactions

To examine the relationship between the vegetation effect on abiotic factors and the outcomes of biotic interactions, we performed multiple regressions for each species between vegetation effects on abiotic factors (water, nutrient and light) and  $\text{LnRR}(\text{interaction})$  calculated with survival and growth data.

### Strain and biotic interactions

Individual responses to abiotic conditions ( $\text{LnRR}(\text{strain})$ ) and responses to biotic interactions ( $\text{LnRR}(\text{interaction})$ ) were analyzed using a one-way ANOVA per site. We then tested whether each  $\text{LnRR}$  variable (i.e.  $\text{LnRR}(\text{interaction})$  on survival and growth and  $\text{LnRR}(\text{strain})$ ) was significantly different from zero using one-sample *t*-test. Within each site, *post hoc* analyses were used to assess differences between species using Tukey-HSD. The relationship between strain ( $\text{LnRR}(\text{strain})$ ) and  $\text{LnRR}(\text{interaction})$  measured on survival and growth at the block level was tested using linear regression.

To investigate the combined effects of vegetation on resources and strain on the outcomes of biotic interactions calculated with growth and survival data, we constructed a model using stepwise regression (mixed) with the following form:

$\text{LnRR}(\text{interaction}) = f(\text{LnRR}(\text{strain}), \text{LnRR}(\text{resource}), \text{limiting resource})$ .

To measure the goodness of our statistical model, we used the Akaike Information Criterion (AIC), and selected the model with the lowest AIC. Additionally, autocorrelation among variables was tested using the Durbin–Watson test.

### Standing biomass and the outcomes of biotic interactions

The relationship between standing biomass (proxy of stress) and  $\text{LnRR}(\text{interaction})$  measured on survival and growth at the block level was tested using linear regression. In this analysis, we considered all species. Additionally, we used linear regression to examine the relationship between standing biomass and vegetation effects on resources ( $\text{LnRR}(\text{resource})$ ). Finally, we tested whether the effects of standing biomass and vegetation on local limiting resources could explain the outcomes of biotic interactions using the following general linear model:

$\text{LnRR}(\text{interaction}) = f(\text{LnRR}(\text{stress}), \text{LnRR}(\text{resource}), \text{limiting resource})$ .

All statistical analyses were performed using the software JMP 5.0.1 (The SAS Institute, Cary, NC, USA).

## Results

### The effect of abiotic conditions on individual species strain

Strain intensity was both species- and site-specific (Fig. 1). At site I, *B. erectus* and *S. caerulea* were not strained whereas *A. capillaris* was the most strained (Fig. 1a). At site II, *B. erectus* was not strained whereas *F. paniculata* and *A. capillaris* were the most strained (Fig. 1b). At site III, all the target species grew less than they did under non-limiting conditions. *A. capillaris* was the most strained, *B. erectus* and *F. paniculata* were slightly strained, and strain was intermediate for the other two species (Fig. 1c). Finally, the five target species were significantly strained at site IV. Strain was stronger for *A. capillaris*, with the four others being equally affected by abiotic conditions (Fig. 1d). For all species, strain increased as nutrient availability and standing biomass decreased (Table 1) and all species generally experienced less strain as standing biomass increased (Fig. 2).

### Outcome of biotic interactions

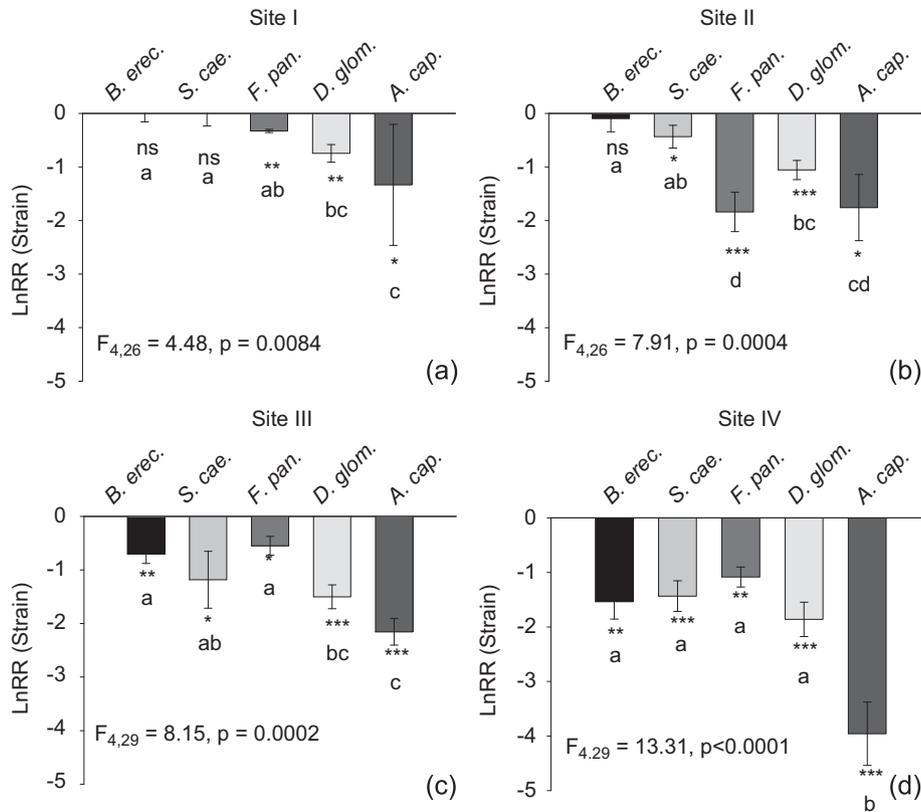
The outcomes of biotic interactions were species-specific and the ranking among species changed depending on the site and the component of the fitness considered, i.e. biomass or survival (Fig. 3).

### Survival

In site I, the outcomes of biotic interactions for survival were not significantly different from zero for any species except for *A. capillaris*, which experienced competition (Fig. 3a). In site II, *F. paniculata* and *A. capillaris* were facilitated whereas *S. caerulea* experienced competition (Fig. 3b). In site III, there was no significant difference among species. However, *D. glomerata* tend to be facilitated, *A. capillaris* experienced competition (Fig. 3c). Finally, in site IV, the two dominant species *B. erectus* and *S. caerulea* were facilitated, whereas all other species experienced competition (Fig. 3d).

### Growth

Effects of neighbors on growth were always negative (Fig. 3e–h) ( $\text{LnRR}(\text{growth})$ ), indicating a predominant influence of competition upon growth in our field sites. In all sites *F. paniculata* was the species least affected by competition (Fig. 3e–h). At site I, all other species experienced a higher competitive intensity (Fig. 3e). At site II, *S. caerulea* had the second best competitive response, *D. glomerata*

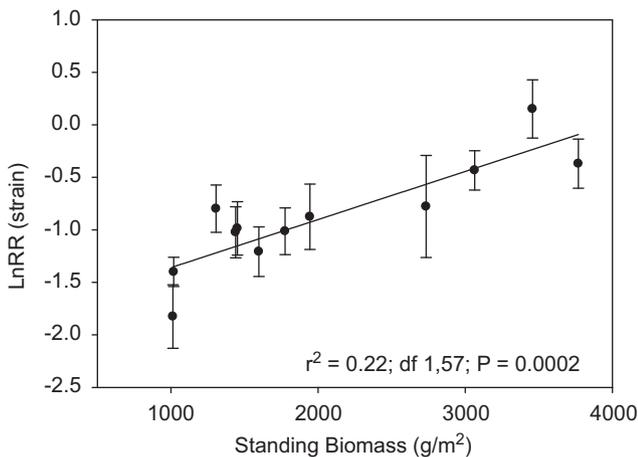


**Fig. 1.** Strain intensity for species in each field sites (six replications per species and site). Different letters indicate that means differ significantly between species in each site (Tukey HSD). We indicate for each site results of the one-way ANOVA testing the species effect. Significant differences from zero are tested by one-sample *t*-test and indicated by asterisks: ns indicates no significant difference from 0, \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ .

**Table 1**  
Relationship between soil resource availability (water and nutrient), standing biomass and strain for each species.

	<i>B. erectus</i>	<i>S. caerulea</i>	<i>D. glomerata</i>	<i>A. capillaris</i>	<i>F. paniculata</i>
Water	ns	ns	ns	ns	0.94***
Nutrient	0.54**	0.75***	0.70**	0.55**	0.44**
Standing biomass	0.55**	0.62**	0.52**	0.54*	ns

Three replications per species and sites were considered. Values listed are  $r^2$  and symbols indicate significance: ns, non-significant relationship, \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ .



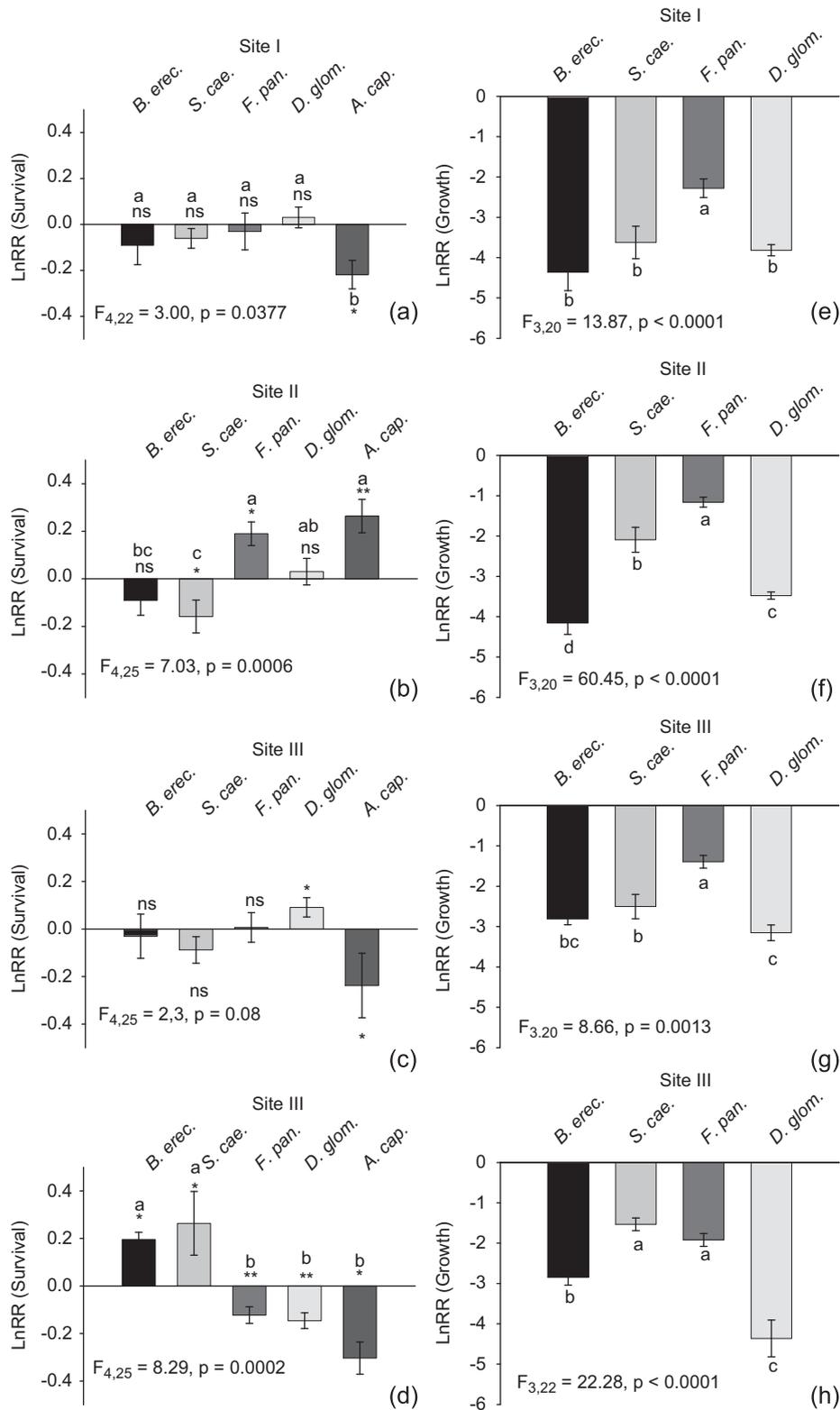
**Fig. 2.** Relationship between standing biomass (g/m<sup>2</sup>) and strain. Three replications per species and site were considered. Each point represented one block where species strain has been averaged for each level of standing biomass. We indicated regression parameter including  $r^2$ , degree of freedom (df) and *p*-value. Error bar represent the variance of species responses at each level of standing biomass.

was intermediate, and *B. erectus* had the worst competitive response (Fig. 3f). At site III, *S. caerulea* and *B. erectus* had an intermediate competitive response and *D. glomerata* was the most affected by neighbors (Fig. 3g). Finally, at site IV, *S. caerulea* had the same competitive response as *F. paniculata*, *B. erectus* had an intermediate competitive response, and *D. glomerata* had the worst competitive response (Fig. 3h).

*Vegetation effects on abiotic factors and the outcomes of biotic interactions*

*Survival*

Biotic interactions (LnRR(survival)) for *B. erectus* and *S. caerulea* became more positive as vegetation had more negative effect on water (LnRR(resource) < 0) (Table 2). For other species, the drying effect of vegetation increased competition intensity. Biotic interactions for *B. erectus* and *F. paniculata* were not related to the vegetation effect on soil nitrate concentration. Biotic interactions for survival of *B. erectus* and *S. caerulea* became more negative as light interception increased. The opposite relationship was observed for *A. capillaris* and *F. paniculata* (Table 2).



**Fig. 3.** Response ratio of the five species to biotic interactions in different field sites (LnRR) calculated with survival (a–d) and biomass data (e–h) (six replications per species and sites). Statistical conventions are as in Fig. 1. When LnRR > 0 net facilitation is observed, LnRR < 0 implies net competition. Statistical conventions are as in Fig. 1.

#### Growth

For *F. paniculata*, competition increased when drying effects of vegetation increased (Table 2). *B. erectus* experienced less competition when the vegetation effect on soil nutrient concentration became more negative. Finally, the intensity of competition increased for all species with increasing light extinction (Table 2) with the exception of *F. paniculata*.

#### Strain and the outcomes of biotic interactions

The outcomes of biotic interactions were predicted by strain, local limiting resources, and vegetation effects on these limiting resources (Table 3). No direct relationship between strain and LnRR(survival) was observed, and positive interactions appeared only for high values of LnRR(strain) (Fig. 4a). However, when

**Table 2**

Relationship between to the outcomes of biotic interactions (Ln RR calculated with survival and growth data) and vegetation effect (veg. effect) on water, nutrients and light availability for each target species.

	<i>B. erectus</i>		<i>S. caerulea</i>		<i>D. glomerata</i>		<i>A. capillaris</i>		<i>F. paniculata</i>	
	Growth	Survival	Growth	Survival	Growth	Survival	Growth	Survival	Growth	Survival
Overall $r^2$	0.33**	0.60**	0.60***	0.73***	0.17*	0.51**	0.73***	0.50**	0.42*	
Interception	-3.10***	0.19**	1.11***	0.19*	-3.41**	-0.13**	-0.12 ns	-1.49***	-0.01 ns	
<b>Veg. effect</b>										
Water	-0.16 ns	-0.24**	-0.22 ns	-0.44***	0.33 ns	0.18**	0.36**	0.87**	0.20*	
Nutrient	-0.64*	0.10 ns	0.55 ns	0.14*	-0.27 ns	-0.14**	0.25**	-0.08 ns	0.08 ns	
Light	0.53***	0.05*	0.35***	0.05*	0.13*	0.00 ns	-0.15***	0.00 ns	-0.08*	

Three replications per species and sites were considered. Values shown are estimated regression parameters, Model  $r^2$ , interception at  $x=0$  and coefficient for each parameter. A separate multiple regression was performed for each species: ns, non-significant, \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ .

**Table 3**

Predicting the outcomes of biotic interactions with strain and vegetation effect on local limiting resource.

<b>(A) Ln RR survival</b>				<b>(B) Ln RR growth</b>					
	df	estimate	F-ratio	p		df	estimate	F-ratio	p
Overall model $r^2=0.40$	7			4.42***	Overall model $r^2=0.25$	7			2.9*
Strain	1		-0.49	7.26**	Strain	1		2.33	6.89*
Water	1		0.01	0.83 ns	Biomass	1		-0.0015	4.27*
Effect water	1		-2.50	13.56***	Effect light	1		1.10	3.92*
Strain $\times$ water	1		0.02	6.34*	Strain $\times$ biomass	1		-0.0012	4.45*
Water $\times$ effect water	1		0.09	11.29**	Biomass $\times$ effect light	1		-0.0003	4.68*
Strain $\times$ effect water	1		-1.55	11.34**	Strain $\times$ effect light	1		0.89	4.06*
Strain $\times$ water $\times$ effect water	1		0.06	7.77**	Strain $\times$ biomass $\times$ effect light	1		-0.0003	6.69*
Error	51				Error	47			

(A) Ln RR (survival) was predicted by soil moisture (water) vegetation effect on soil moisture (effect water) and strain; (B) Ln RR (growth) was predicted by standing biomass (biomass) strain and vegetation effect on light (effect light).

Three replications per species and sites were considered. We indicated multiple regression parameter including overall model  $r^2$ , degree of freedom (df) estimate of parameter, F-ratio and p-value, ns,  $p > 0.05$ , \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ .

strain increased, the intensity of biotic interactions increased either positively or negatively. In site IV, where vegetation had negative effect on soil moisture, highly strained species (*A. capillaris* and *D. glomerata*) were negatively affected by neighbors. On the other hand, where vegetation had a positive effect on soil water availability (sites III and IV), highly strained species (e.g., *F. paniculata*, *A. capillaris* and *D. glomerata*) were positively affected by neighbors. Therefore, as strain increased, species could experience competition or facilitation depending on the vegetation effect on water and species-specific tolerances (Table 3a). A negative relationship between LnRR(growth) and standing biomass was found (Fig. 4b). Hence, overall competition intensity in terms of growth decreased when strain increased. A combination of strain, stress and vegetation effect on light could predict biotic interactions for growth (LnRR(growth)) (Table 3b). As strain and standing biomass increased, species could experience more or less competition depending on vegetation effects on light.

We also tested the relevance of vegetation effects on the other environmental factors (soil nitrate and ammonium, soil moisture and light), and only variables reported in Table 3 were found significant to explain the outcomes of biotic interactions (additional results not shown). Both models (including all variables and their interactions) for LnRR(survival) (Table 3a) and for LnRR(growth) (Table 3b) showed the lowest value for the Akaike Information Criterion (AIC = -190 for LnRR(survival) and AIC = -6 for LnRR(growth)). For LnRR(survival), the Durbin-Watson statistics (DW) was  $< 1.4$ , which indicates no correlation among variables of the model (Table 3a); in contrast, DW was

$> 1.4$  for LnRR(growth), indicating some correlation among variables (see Fig. 2 and analysis below).

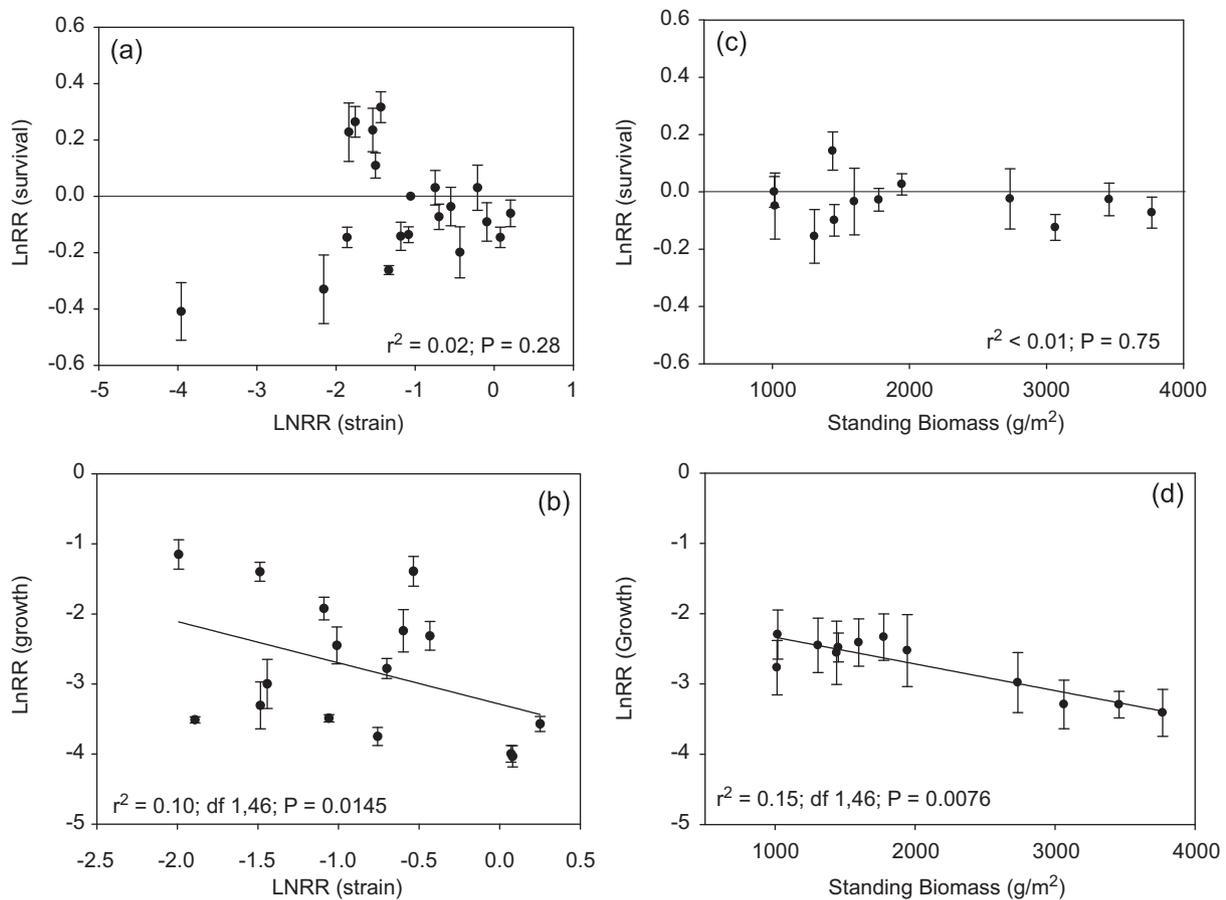
#### Standing biomass and the outcomes of biotic interactions

Similarly to strain, contrasting relationships were found between standing biomass and the outcomes of biotic interactions. No relationship between standing biomass and LnRR(survival) was observed (Fig. 4c), whereas competition intensity measured with growth data (LnRR(growth)) decreased with decreasing standing biomass (Fig. 4d).

Vegetation effects on light (LnRR(light)) and on soil nitrate concentration (LnRR(nutrient)) increased as standing biomass increased (Fig. 5a and c). However, there was no link between community standing biomass and vegetation effect on soil moisture (LnRR(soil moisture)) (Fig. 5b). Finally, standing biomass, vegetation effects on resources and their interactions were not related to the outcomes of biotic interactions estimated with survival data (no significant model, data not shown).

#### Discussion

Strain – estimated by comparing growth in non-limiting conditions to growth in the field without neighboring vegetation – can be viewed as a measure of the deviation of a plant from its fundamental niche optimum. Overall, our results support the “imperfect world” point of view, which posits that individuals in their natural habitat are often limited by abiotic environmental



**Fig. 4.** Relationship between standing biomass ( $\text{g/m}^2$ ) (a and b),  $\text{LNRR}(\text{strain})$  (c and d), and the outcomes of biotic interactions calculated with survival data ( $\text{LNRR}(\text{survival})$ ) (a and d) and growth data ( $\text{LNRR}(\text{growth})$ ) (b and d). Three replications per species and site were considered. We indicated regression parameter including  $r^2$ , degree of freedom (df) and  $p$ -value. Error bar represent the variance of species responses at each level of strain (a and b) or stress (c and d).

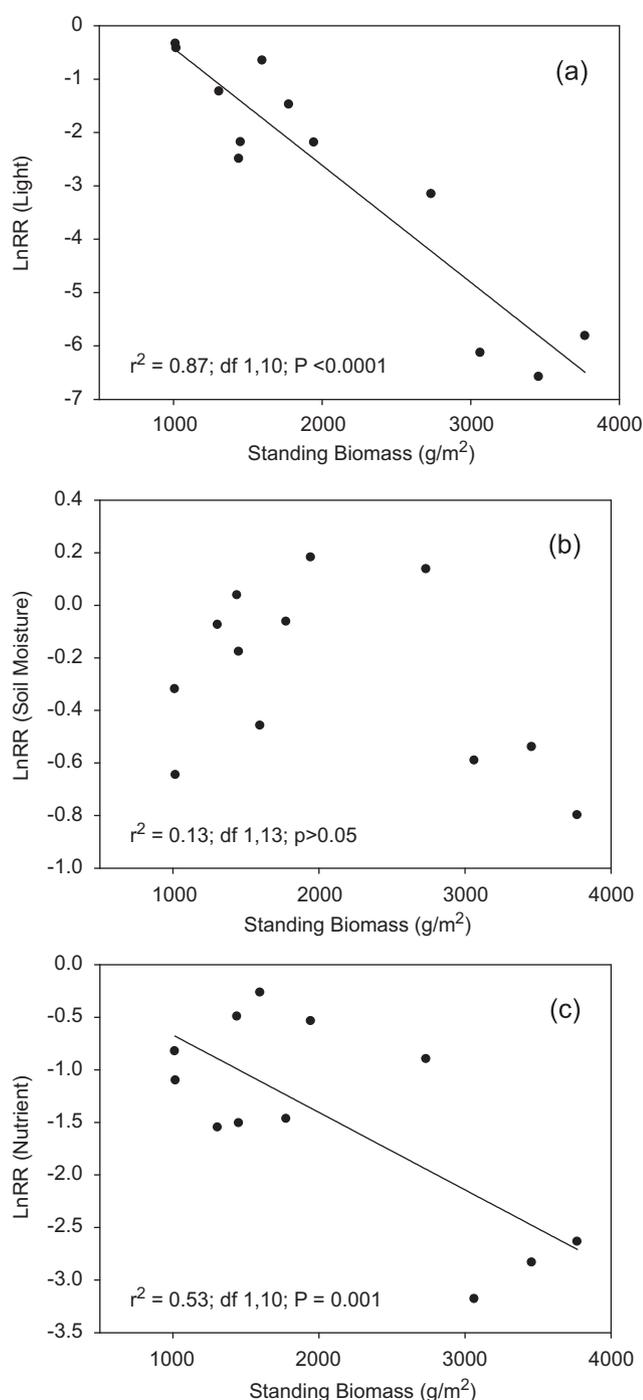
conditions (Korner, 2003, 2004; Lortie et al., 2004). All target species grew less in the field than in non-limiting conditions, although strain differed in magnitude depending on the species considered (Fig. 1). Thus, strain appeared to be species-specific and to depend on particular species tolerances (Liancourt et al., 2005; Michalet et al., 2006). As we had hypothesized, strain and vegetation effects on local limiting resources could be used to predict the outcomes biotic interactions (Table 3). However, contrasting relationships were found depending on the fitness component considered (survival and growth).

#### Strain and the outcomes of biotic interactions

The outcomes of biotic interactions for survival were predicted by strain and vegetation effects on soil moisture (Fig. 4a and Table 3a). Species which deviated greatly from their niche-optimum experienced facilitation or competition depending on vegetation effects on local limiting resources (Table 3) (Padilla and Pugnaire, 2006). As a result, the relationship between strain and the outcome of biotic interactions depended on a cost-benefit relationship (Choler et al., 2001; Liancourt et al., 2005; Cheng-Jin et al., 2008). Target species were likely to be facilitated if they maximized the benefits of having neighbors (low stress-tolerance) (Pennings et al., 2003), minimized their cost (high competitive response ability) (Liancourt et al., 2005), and if neighboring vegetation was able to alleviate constraining abiotic factors (facilitative effect) by which the beneficiary target species were strained (Padilla and Pugnaire, 2006). For instance, site IV

was strongly water limited and vegetation further desiccated the soil – i.e. increased competition for water (Fig. A1, Appendix). In this case, the drought-sensitive species *D. glomerata*, *A. capillaris* and *F. paniculata* (Dixon, 1986) were highly strained, and were negatively affected by neighboring vegetation (Fig. 3d), probably due to competition for water (Table 2). In contrast, *A. capillaris* and *F. paniculata* were facilitated in site II. This site had the driest bare soil in the experiment (Fig. A1, Appendix), and these species deviated strongly from their optimal niche (Fig. 1 and Table 2). It seems that in this community, drought-sensitive species were more likely to benefit from habitat amelioration due to the presence of other plants. This community also had a strong negative effect on light availability (Fig. A1(b)), but it may have been compensated by the better competitive response of *F. paniculata* (Fig. 3) and the shade tolerance of *A. capillaris* (Gross et al., 2007) (Table 2). Finally, both *B. erectus* and *S. caerulea*, which dominated site IV, are drought tolerant (Dixon, 1986; Corcket et al., 2003; Liancourt et al., 2005) and thus, they were able to tolerate competition for water from the surrounding vegetation (Table 2). These species must have been facilitated through amelioration of another abiotic factor. For instance, they might have been protected from frost during winter by surrounding vegetation (Choler et al., 2001; Olofsson, 2004) because snow cover was often absent in winter 04–05 at this site (personal observation).

Overall, our findings show that, depending on their effect on abiotic factors, plant communities are able to positively or negatively modify the realized niches of species (Booy et al., 2000; Choler et al., 2001; Callaway et al., 2002; Bruno et al., 2003;



**Fig. 5.** Relationship between standing biomass ( $\text{g/m}^2$ ) and vegetation effect on light ( $\text{LnRR}(\text{light})$ ) (a), soil moisture ( $\text{LnRR}(\text{soil moisture})$ ) (b) and soil nutrient concentration ( $\text{LnRR}(\text{nutrient})$ ) (c).

Liancourt et al., 2005). When vegetation increases the supply of resources that constrains a particular species, the realized niche of the species will be broader than its fundamental niche (Bruno et al., 2003). Conversely, competitive interactions could lead to a smaller realized niche, even in harsh environments (Walker and Chapin, 1986; Wedin and Tilman, 1993; Pugnaire and Luque, 2001; Maestre et al., 2003). In our experimental communities, positive interactions were strong enough to influence dominance status, and in some cases even dominant species could be facilitated (especially in dry sites II and IV, Figs. 1 and 2). Facilitation is

generally hypothesized to increase biodiversity in harsh environments (see humpback model in Michalet et al., 2006; Mulder et al., 2001; Callaway et al., 2002) as it promotes species outside their fundamental niche and allows them to persist with a subordinate status (Choler et al., 2001; Callaway et al., 2002; Bruno et al., 2003; Liancourt et al., 2005). In our case, facilitation may have an effect on whole community processes as it benefits the most to dominant species (see Grime, 1998; Garnier et al., 2004 for the biomass ratio hypothesis).

#### *Standing biomass and the outcomes of biotic interactions*

Community standing biomass is usually used as a metric for environmental severity in the “SGH” (Michalet et al., 2006; Brooker et al., 2007). In our study, it was not related to the outcomes of biotic interactions estimated with survival data (Fig. 4c). Species experienced competition or facilitation for survival independently from the amount of standing biomass, as water availability and the vegetation effect on soil moisture was not linked with standing biomass and nutrient availability in our study (Fig. 5b) (Gross et al., 2008). For instance, negative and positive effects on soil moisture were observed in a communities characterized by high standing biomass (sites I and II, respectively, Fig. A1), and a strong drying effect was even observed in the community with the lowest standing biomass (site IV, Fig. A1).

The limited predictive power of the “SGH” in our study is not surprising, as resources availability gradients considered in the “SGH” are rather simple gradients where limiting resources and vegetation effects co-vary (Bertness and Callaway, 1994; Michalet et al., 2006). The independence between vegetation effect on soil moisture and standing biomass (Padilla and Pugnaire, 2006; Gross et al., 2008) may explain why the “SGH” is sometimes not supported (see Maestre et al., 2005 for a review). Positive and negative outcomes of plant–plant interactions along aridity gradients are linked with complex mechanisms such as the dynamics of pulses of water availability (Novoplansky and Goldberg, 2001), strain (Table 3a, this study) and local vegetation effects on soil moisture (Sala et al., 1989; Schwinning and Sala, 2004; Padilla and Pugnaire, 2006).

In contrast, our results are partly consistent with the “SGH” when considering growth data as competition intensity decreased as standing biomass decreased (Fig. 4d). This result confirms previous studies within our study area, which found that facilitation did not occur for growth in subalpine grasslands and appeared only at higher altitude (Choler et al., 2001; Callaway et al., 2002). Co-variation between standing biomass and competition for growth is likely to be explained by vegetation effect on light and species strain. Indeed, these two variables both co-vary with standing biomass (Grime, 1977; Rajaniemi, 2003) (Figs. 5a, 2 and Table 3b). Under low stress levels, community biomass is high and strongly decreases light availability. In this case, competition intensity is generally high and is linked with competition for light (Grime, 1977; Wedin and Tilman, 1993). Conversely, when stress is high, species strain is generally high but vegetation effects on light are weak (Michalet et al., 2006). Hence, competition intensity observed for growth is generally small (Bertness and Callaway, 1994). Positive interactions might be observed for growth in harsher condition such as alpine grasslands (Choler et al., 2001) where vegetation effect switch from negative to positive (e.g. protection from frost or UV) (Callaway et al., 2002). Altitudinal gradients correspond typically to a complex gradient where strain and vegetation effects on light co-vary with stress (Choler et al., 2001; Michalet et al., 2006). This may explain why the “SGH” was validated in this context (Choler et al., 2001; Callaway et al., 2002).

## Conclusion

In this study, we showed that strain and vegetation effects on local limiting resources provide a mechanistic basis for the observed variations of outcomes of biotic interactions along ecological gradients. Under low levels of strain, the outcomes of biotic interactions are negative for all species. However, as negative abiotic effects on species increase (strain), the direction of biotic interactions appears to depend upon vegetation effects on resources (positive and negative) (Fig. 4 and Table 3). Facilitation occurs only when strain is high and vegetation alleviates the constraining factors. Moreover, species differ in their ecological optimum and could be adapted to harsh conditions. To investigate the relationship between the outcomes of biotic interactions and community-level measurement of stress (*sensu* Grime, 1977) along larger ecological gradients, it would be important to understand how species-level strain and vegetation effects on local limiting resources co-vary with community-level biomass. In addition, it is necessary to explicitly test the effect of resource additions in the field on how vegetation affects limiting resources and species-level strain (see for instance, Liancourt et al., 2005). Future analyses are also needed to link observed interactions on individual target plants to species abundance patterns. The fact that strain was not related with species status within communities (dominant species were not always the least

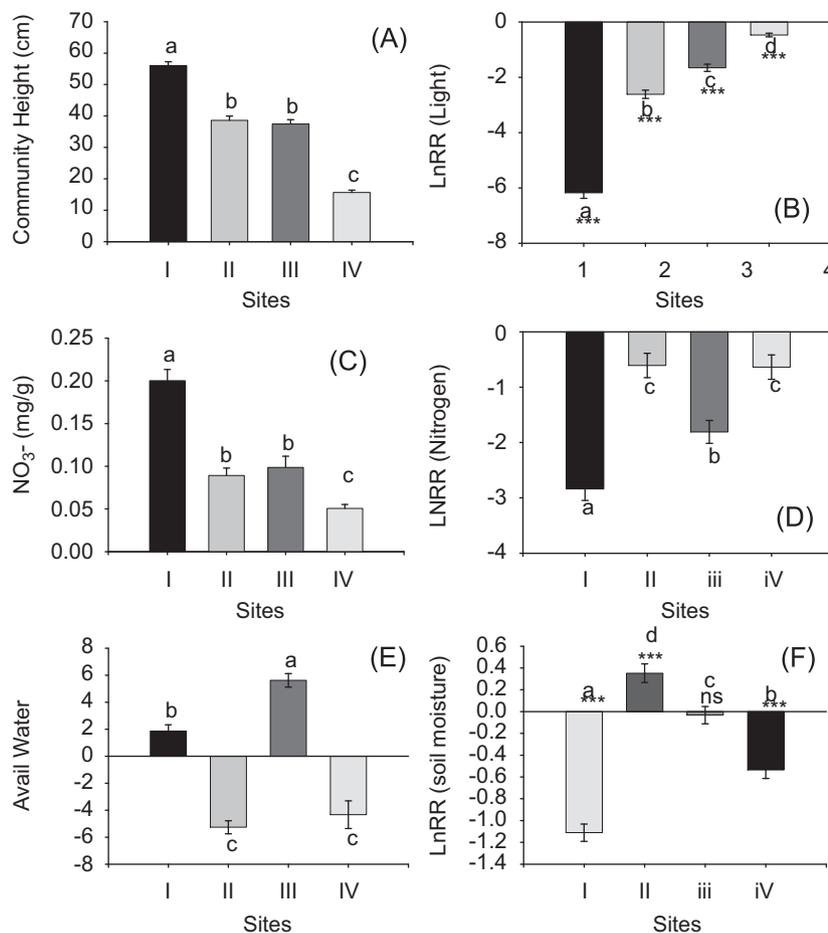
strained, Fig. 1) and that the intensity of biotic interactions increased as strain increased (Fig. 4) may explain why biotic interactions might need to be considered as a key parameter to explain species abundance, community structure and their dynamics in harsh environments.

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## Appendix

See Fig. A1.



**Fig. A1.** Measurement of resource availability and vegetation effect in the four fields sites for light, nitrate and water, light: community height (A), light interception (B); nitrate: NO<sub>3</sub><sup>-</sup> concentration (C) in mg/g of soil, effect of vegetation on nitrate measured with log response ratio (LnRR) (D); available water for plants without vegetation (differences from wilting point (%)) (E), effect of vegetation on soil moisture measured with log response ratio (LnRR) (F). For water availability (%) (E) and vegetation effect on soil moisture (F), the annual mean value for the second growing seasons were presented. Different letters indicate that means differ significantly among sites (Tukey-HSD). We test whether each LnRR(soil moisture) was significantly different from zero using one-sample *t*-test: ns indicate non-significant difference from 0, \*\*\*, *p* < 0.0001.

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