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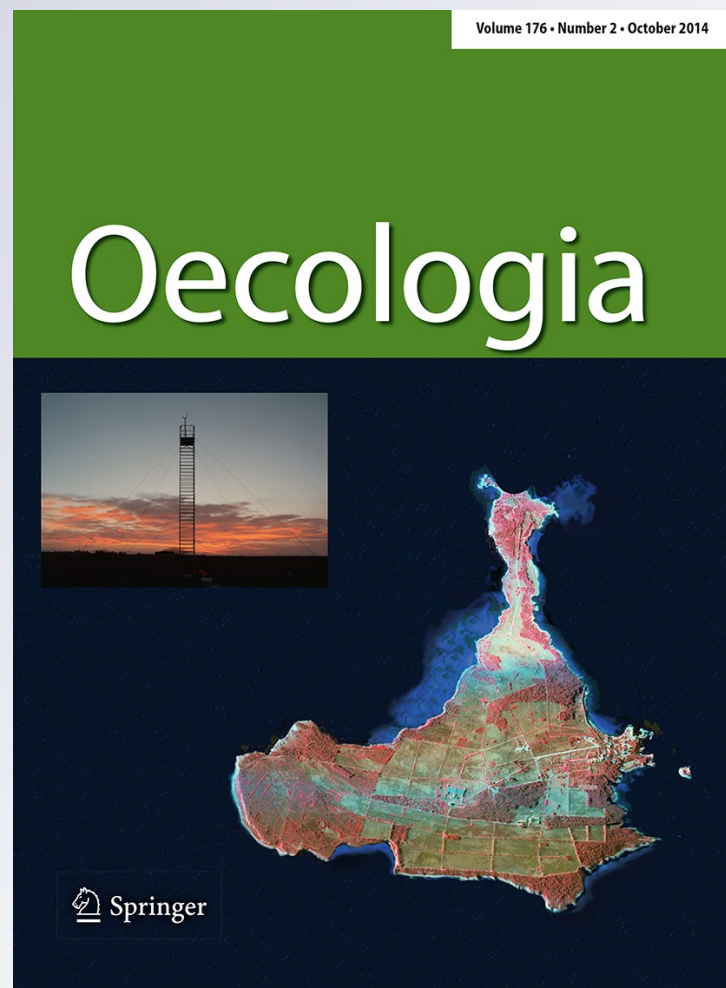
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# Phenotypic differentiation within a foundation grass species correlates with species richness in a subalpine community

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**Abstract** Few studies have examined consequences of ecotypic differentiation within alpine foundation species for community diversity and their feedbacks for the foundation species' fitness. Additionally, no study has quantified ecotypic differences in competitive effects in the field and in controlled conditions to disentangle genetic from plasticity effects in foundation/subordinate species interactions. We focused on a subalpine community of the French Pyrenees including two phenotypes of a cushion-forming species, *Festuca gautieri*: tight cushions in dry convex outcrops, and loose cushions (exhibiting high subordinate species richness) in wet concave slopes. We assessed, with field and shadehouse experiments, the genetic vs. plasticity basis of differences in: (1) cushion traits and (2) competitive effects on subordinates, and (3) quantified community feedbacks on foundation species' fitness. We found that trait differences across habitats had both genetic and plasticity bases, with stronger contribution of the latter. Field results

showed higher competition within loose than tight phenotypes. In contrast, shadehouse results showed higher competitive ability for tight phenotypes. However, as changes in interactions across habitats were due to environmental effects without changes in cushion effects, we argue that heritable and plastic changes in competitive effects maintain high subordinate species diversity through decreasing competition. We showed high reproduction cost for loose cushions when hosting subordinates highlighting the occurrence of community feedbacks. These results suggest that phenotypic differentiation within foundation species may cascade on subordinate species diversity through heritable and plastic changes in the foundation species' competitive effects, and that community feedbacks may affect foundation species' fitness.

**Keywords** Biotic interactions · Competition · Phenotypic plasticity · Facilitation · Feedback effects

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## Introduction

The evolutionary processes of local adaptation and ecological speciation in alpine environments have been largely addressed through the study of genetic differentiation in adaptive traits, which is likely because of the steepness of the environmental gradients (Billings 1974; Körner 2003; Choler et al. 2004). Many mountain ranges have provided numerous examples of ecologically differentiated plant taxa at a very small scale of environmental variation, in particular along topographic and soil gradients (Choler and Michalet 2002; Michalet et al. 2011; Lekberg et al. 2012; Liancourt et al. 2013). For example, Liancourt et al. (2013) showed, in the Mongolian steppe, differences in stress tolerance within the dominant grass species *Festuca lenensis*

along a topographic gradient with a more stress-tolerant phenotype occurring in steep and dry upper slopes and a less stress-tolerant phenotype occurring in wetter and more productive lower slopes. Heterogeneous soil environments are considered particularly prone to sympatric phenotypic differentiation, probably due to increased reproductive isolation (Sambatti and Rice 2006; Lekberg et al. 2012).

Of particular interest, from an evolutionary ecology perspective, is genetic differentiation within foundation species (Ellison et al. 2005), because of increased chances of consequences at the community and ecosystem levels (Whitham et al. 2006; Gibson et al. 2012). Genetic effects have been shown to translate at higher complexity levels through biotic interactions (review by Whitham et al. 2006), as demonstrated by many studies of interactions across trophic levels. In contrast, studies of interactions within trophic levels (e.g. within plant communities) remain scarce (Bailey et al. 2009; but see Adams et al. 2011; Michalet et al. 2011; Gibson et al. 2012) compared with across trophic-level studies, likely due to the diffuse nature of plant–plant interactions and the rarity of feedback effects (Bronstein 2009; Michalet et al. 2011; Schöb et al. 2014). Plant community genetic studies have mainly focused on competition or allelopathy (Lankau and Strauss 2007; Bossdorf et al. 2009; Silvertown et al. 2009), while evolutionary questions associated with positive interactions among plants (i.e. facilitation) such as nurse plant effects remain less documented (but see Valiente-Banuet et al. 2006; Liancourt and Tielbörger 2011; Michalet et al. 2011; Thorpe et al. 2011; Butterfield et al. 2013). Facilitative interactions are known to have strong effects on community and ecosystem properties, including diversity, structure, productivity and stability (Michalet et al. 2006; Callaway 2007; Brooker et al. 2008; Le Bagousse-Pinguet et al. 2014a). Thus, there is a high potential for exploring how phenotypic differentiation within foundation plants may affect community structure through facilitative interactions, and in particular along local soil gradients known to be particularly prone to genetic differentiation.

Michalet et al. (2011) showed that variation in competitive and facilitative effects among phenotypes of *Geum rossii* had strong consequences on species diversity for alpine communities in Northern Arizona, and that beneficiary species had feedback effects acting as selective pressure for the cushion plant. In highly physically disturbed concave volcanic slopes, they observed a phenotype of *G. rossii* characterised by loose stem morphology and strong facilitative effects on other species, and in adjacent more stable convex slopes they found a competitive phenotype, characterised by dense stem morphology. However, because the very low growth rate of this alpine cushion plant did not allow them to manipulate adults in reciprocal transplantations or in common garden experiments,

Michalet et al. (2011) only compared the effects of each phenotype on other species in their own environment. Thus, they could not clearly separate heritable from environmental effects in the foundation/beneficiary interactions, and thus fully address the genetic basis of the processes driving changes in community diversity and composition. Indeed, an increase in facilitation from stable convex slopes to disturbed concave slopes may be due to either genetically based variation in nurse effects, or to nurse trait plasticity induced by changing environments, as well as direct environmental effects on target beneficiary species (Michalet et al. 2014).

We conducted our study in subalpine grassland communities of the French Pyrenees. Alpine communities are particularly prone to positive interactions (Callaway et al. 2002), thus are suitable systems with which to explore how phenotypic differentiation within foundation plant species may affect community structure through facilitative interactions. Competition and facilitation co-occur in the studied system along a natural soil moisture gradient and are directly related to species richness (Le Bagousse-Pinguet et al. 2014b). Also, phenotypic variation within a foundation grass species (*Festuca gautieri* subsp. *scoparia* Hackel and Kerner) has been observed along a soil moisture gradient (Le Bagousse-Pinguet et al. 2014b). A ‘tight’ phenotype with dense cushions with short stiff leaves occurs on dry soils in convex topographical positions (high-stress habitat), and a ‘loose’ phenotype with cushions characterised by open stem morphology and long soft leaves occurs on wetter soils in concave topographies (low-stress habitat). Le Bagousse-Pinguet et al. (2014b) showed that the tight *F. gautieri* phenotype was more drought tolerant than the loose phenotype. In the same subalpine system they transplanted tillers of each phenotype along a complex gradient of soil water availability. They showed that the probability of survival of the loose phenotype was reduced by over 50 % when soil moisture decreased from 40 to 15 %, whereas there was no change in survival of the tight phenotype. Considered together, the contrasting habitat distribution and experimental evidence suggest that the two phenotypes correspond to sympatric ecotypes. Both phenotypes can reach an adult size in a very short time in a shadehouse, allowing an assessment of a potential heritable component of differences in competitive and facilitative effects.

Here, we assess whether changes in subordinate species diversity among habitats and phenotypes are driven by heritable changes in foundation/subordinate species interactions, and thus, evaluate the genetic basis of the ecological processes acting in this subalpine community. Additionally, we assess the potential evolutionary feedbacks of these changing interactions by quantifying the effects of subordinates on the phenotypes’ fitness. Specifically, we aimed to answer these main questions, each related to one of the

three fundamental premises of a full community genetics perspective (Whitham et al. 2006):

1. What are the relative contributions of genetic differentiation and phenotypic plasticity in the morphological trait divergences?
2. To what extent do heritable differences in foundation species' morphological traits between phenotypes contribute to changing cushion effects on subordinate species across habitats?
3. Do subordinate species have feedback effects on the fitness of the foundation species?

Variation in phenotypic traits was first measured both in the field and in a shadehouse in order to assess the heritability of field phenotypic variation. In the shadehouse, morphological traits of both phenotypes were measured under contrasting water stress conditions mimicking natural environmental variation, in order to also quantify the contribution of plasticity in changing traits among phenotypes and environments (see Online Resource 1 for the design). Second, we quantified changes in foundation/subordinate species interactions among phenotypes, both across habitats in the field and in the shadehouse in constant environmental conditions, in order to assess the likely heritability of changes in interactions (Online Resource 1). Third, the potential feedback effects of subordinate species on the cushion species' fitness were quantified in the field (Online Resource 1).

## Materials and methods

### Study system and target species

The experimental site is located in the western Pyrenees, 100 km from the Atlantic ocean at La Pierre Saint-Martin pass (42°58'N, 0°45'W, altitude 1,744 m a.s.l., Pyrénées-Atlantiques, France). The climate is temperate oceanic; the mean winter temperature is  $-2.2$  °C and the mean summer temperature is  $11.5$  °C; the mean annual precipitation is 2,850 mm with the highest rainfall occurring in winter. *Festuca gautieri* is a very distinctive dwarf grass forming circular to elliptic cushions of thin bright green leaves with yellowish-green inflorescences. Flowering occurs from July to August. It is a foundation species typical of subalpine and alpine grasslands on rocky calcareous soils in the entire Pyrenees chain (Saule 1991). This species only dominates grasslands on steep scree slopes under low grazing conditions in the studied communities, likely because of its low grazing tolerance. Two distinct phenotypes of cushions occur in the system, under contrasting topographical and soil conditions (Le Bagousse-Pinguet

et al. 2014b). A tight phenotype dominates convex topographical habitats with shallow, stony (stone cover =  $73.6 \pm 3.7$  %,  $n = 30$ ) and relatively dry soils [soil volumetric water content measured with a ML3X ThetaProbe (Delta-T Devices, Cambridge, UK) 3 days after a rain event,  $13.10 \pm 1.28$ ,  $n = 15$ ]. A loose phenotype dominates concave topographical habitats with deep, less stony (stone cover =  $53.0 \pm 3.4$  %,  $n = 30$ ,  $t$ -test  $P < 0.001$ ) and relatively wet soils (soil volumetric water content,  $27.73 \pm 1.74$ ,  $n = 15$ ,  $t$ -test  $P < 0.001$ ). The scale of habitat heterogeneity was less than 1 m, which allows both phenotypes to exist side by side. Cushions with intermediate traits are also observed in intermediate ecological conditions, but they are less frequent than the two extreme phenotypes [cushion frequency measured in ten 10-m-long transects, 10.4 % for intermediate cushions vs. 66.7 % for tight phenotypes and 22.9 % for loose phenotypes; our field phenotype classification was based on a leaf pungency index varying between 0 (not pungent) and 5 (very pungent); see Online Resource 2]. We also observed contrasting patterns of association with other species along with contrasting flower productions of the cushions. Loose phenotypes had a high cover of other species and a low flower production, whereas tight phenotypes had a low cover of other species and a very high flower production, suggesting a potential reproductive cost for loose phenotypes (see Online Resource 1, 2 for the method). Most frequent subordinate species (i.e. species associated with a community dominant and with a lower abundance) of the community were *Agrostis capillaris* L., *Galium pumilum* Murray, *Campanula rotundifolia* L., *Alchemilla conjuncta* Bab., *Lotus corniculatus* L., *Festuca rubra* L. and *Trifolium pratense* L.

### Differences in cushion traits between *F. gautieri* phenotypes

In order to quantify field variation in cushion traits across phenotypes and habitats, we measured maximum leaf length, cushion penetration [an index of cushion compactness and interference (R. M. Callaway, unpublished data)], leaf thickness and number of inflorescences on a total of 60 cushions (30 tight and 30 loose phenotypes) from our site (see Online Resource 1). In July 2012, cushion penetration was measured by loosely introducing a metal ruler vertically within the cushion. Leaf thickness was measured to a precision of 0.01 mm using a digital micrometer (TEST-WELL, Saint-Ouen, France). Measurements were done on three fresh leaves per cushion, and on the middle length of the leaves. Number of inflorescences was counted on the whole cushion surface.

A shadehouse experiment was set up to quantify the contribution of heritability and plasticity in changing

traits among phenotypes and environments (see Online Resource 1). The shadehouse was located at the INRA station of Cestas-Pierroton, France (44°44'N, 0°46'W; 60 m a.s.l.). Replicates of the two phenotypes were grown for 26 months in contrasting environmental conditions mimicking the two natural habitats. In November 2010, we collected 15 *F. gautieri* cushions (hereafter 'genotypes') of each phenotype at our site. We chose mature and discrete cushion individuals in order to increase the probability of selecting genetically different cushions. Each cushion was planted in a 4-L pot with a soil-less mix of peat moss, perlite, and gravels in a 1:1:0.5 proportion. Pots were stored during the first winter in an unheated greenhouse. In late April 2011, i.e. at the beginning of the treatments, the experiment was set up in a shadehouse transmitting 50 % of light without intercepting precipitation, protecting plants from direct sunlight and air desiccation. Each cushion was separated into 20 individual tillers of from five to ten leaves. Each tiller was standardised by cutting the roots to a length of 5 cm and planted into a separate pot (total  $n = 600$ ). Pots were then randomly placed on benches within the shadehouse before treatments.

We applied a watering treatment with ten replicates of each genotype in each treatment combination (phenotype  $\times$  watering) to assess the potential plastic responses of phenotypes to varying soil moisture conditions. It is important to note that our goal was not to exactly mimic the environmental conditions of the natural habitats of each phenotype, but rather to assess the response of the two phenotypes to the occurrence of a weak drought stress. The watering treatment was applied in 2011 and 2012 from late April to late September and in 2013 from late April to the end of the experiment (late June 2013) by irrigating half of the pots with 1 L of tap water (watered pots) three times a week and the other half once a week only (dry pots). Survival and five cushion traits were recorded for all pots at the beginning and the end of each growing season (in April and October—intermediate measurements) in 2011 and 2012, and at the end of the experiment, late June 2013 (final measurement). As survival was very high in all treatments, only final growth measurements are presented here. Maximum leaf length, cushion penetration and cushion leaf thickness were measured as in the field. We also quantified cushion surface simplified as an elliptic surface by measuring cushion length and width, and cushion leaf density by counting all leaves within a circular ring of 6 cm<sup>2</sup>. Cushion surface is a proxy of cushion growth rate as all cushion individuals had a similar size at the beginning of the experiment and there was very low leaf mortality during the experiment, even during winter (P. Al Hayek, personal observation).

#### Differences in cushion effects between *F. gautieri* phenotypes

A field cushion-removal experiment was conducted to quantify the potential variation in cushion facilitative and/or competitive effects on subordinate species across phenotypes and habitats (Online Resource 1). Three target species with contrasting drought-tolerance abilities and habitat distributions were used to encompass a large and representative panel of possible responses to neighbours (Brooker et al. 2008). We chose two drought-intolerant target species, i.e. the loose fescue phenotype itself and *A. capillaris* (its most frequent subordinate species), and a drought-tolerant target, the tight fescue phenotype itself. Both fescue phenotypes were chosen as targets to also assess responses to neighbours, since both the effect of a neighbour on a target individual and the response of a target individual to the effect of a neighbour are important components of species competitive/facilitative abilities (Goldberg 1990; Liancourt et al. 2009; Le Bagousse-Pinguet et al. 2013). We used naturally occurring individuals for *A. capillaris* and transplants for the two *F. gautieri* phenotypes. In June 2011, we selected five sites in a northern slope with a distance of at least 100 m between sites. In each site, six cushions of each phenotype that included one discrete individual of *A. capillaris* were selected. For half of the cushions (three tight and three loose at each site), we removed by hand the above-ground parts of *F. gautieri* cushions within a circular area of 15 cm in diameter centred on the target individual of *A. capillaris*. Then, one individual of each *F. gautieri* phenotype was transplanted at 5 cm from the *A. capillaris* individual, both within removed and control cushions of both phenotypes. Transplanted individuals of both *F. gautieri* phenotypes were randomly collected at the site in at least ten cushions of each phenotype. Each transplanted individual had from five to ten leaves. All target individuals were tagged with metal rings. Thus, there were five replicates of each combination of the three treatments (cushion phenotype, removal and target species). In late July 2012, we recorded survival, measured height and leaf number of all target individuals. All target individuals were harvested for aboveground biomass measurements. Harvested target individuals were dried for 2 days at 70 °C and weighed. Survival was expressed in percentages (0, 33, 66 or 100 %) per treatment combination (cushion phenotype and removal) and per site, and growth data were averaged per treatment combination and per site before statistical analyses.

To quantify heritable differences in competitive/facilitative effects and responses among phenotypes, a pot experiment was set up in the shadehouse, from early April to late November 2012 (Online Resource 1). We manipulated cushion presence and phenotypes (neighbour treatment) and target identity. The neighbour treatment was

applied by planting targets either within a tight cushion phenotype or within a loose cushion phenotype, or alone without a cushion. We used six different genotypes of each cushion phenotype with six replicates per cushion genotype and one cushion per pot (a total of 36 pots per phenotype plus 36 pots with no cushion). Pots were randomly distributed on benches in the shadehouse at the beginning of the experiment and watered three times a week. The 72 cushions were prepared before the experiment by growing them in separate pots from small tillers of from five to ten leaves to a cushion size of 15 cm in diameter between late April 2011 and early April 2012. As in the field competition experiment, we planted the three different targets—the tight and the loose phenotype of *F. gautieri*, and *A. capillaris*—in each pot. In each with-neighbour pot, the three target individuals were planted within the cushion canopy with an equal distance between them (5 cm). For the two fescue phenotypes transplanted as targets within and without cushions, we used six different genotypes per phenotype with six replicates per genotype. A replicate of target genotype was planted in each cushion genotype. This genotypic sampling was done in order to maximise differences in competitive ability within phenotypes, but was not used as a statistical treatment because of insufficient replication. Survival was recorded at the end of the experiment in late November 2012. All target individuals were harvested for aboveground biomass measurements. Harvested plants were dried for 2 days at 70 °C and weighed. Survival was expressed in percentages (0, 16.7, 33.3, 50, 66.7, 83.4 or 100 %) per target genotype and treatment combination. Biomass measurements were averaged per target genotype in each treatment combination before statistical analyses. In order to quantify responses of the three target species to both cushion phenotype effects, we calculated the relative interaction index (RII) for survival and biomass performances, following Armas et al. (2004):

$$\text{RII} = \frac{P_{+\text{neighbour}} - P_{-\text{neighbour}}}{P_{+\text{neighbour}} + P_{-\text{neighbour}}}$$

where  $P_{+\text{neighbour}}$  and  $P_{-\text{neighbour}}$  represent target performances (survival and biomass) in the presence and absence of cushions, respectively. This index is symmetrical around zero (no significant interaction), and has defined limits between  $-1$  and  $+1$ . Negative values indicate competition whereas positive values reflect facilitation.

#### Community feedbacks

We assessed the potential cost of hosting subordinate species for *F. gautieri* cushions by conducting a removal of subordinate species experiment to test the hypothesis that subordinate species reduce the inflorescence production of loose cushions. In late June 2011, we randomly selected 40

loose cushions and removed all subordinate species growing within a circular area of 20 cm in diameter (surface 314 cm<sup>2</sup>) in half of the selected loose cushions. In late June 2012, regrowth of subordinate species was again removed in the 20 loose treated cushions. In late July 2012, we counted the number of inflorescences produced by all cushions within the delimited circular plot.

#### Statistical analyses

To analyse field differences in cushion traits among phenotypes (tight and loose), we conducted a Student's *t*-test with cushion phenotypes as treatment and the four field traits as response variables. Differences in cushion traits in the shadehouse experiment were analysed using a two-way ANOVA model with phenotype and watering as treatments and the five cushion traits as the response variables. For the removal of *F. gautieri* field experiment and for each target species separately, we conducted a two-way ANOVA with phenotype and removal as treatments, and percentage of target survival and leaf number as dependent variables. For the shadehouse competition experiment, we conducted separate analyses per target species for survival and growth data, and one analysis grouping target species for RII data. We conducted one-way ANOVAs (followed by Tukey tests when necessary) on target percentage of survival and biomass with neighbour presence and identity as treatment (no neighbour, tight phenotype and loose phenotype), and a two-way ANOVA on the RII for survival and aboveground biomass with cushion phenotype and target as treatments. We used one-sample *t*-tests to detect significant deviation of RII values from zero (i.e. no cushion effect on target performance). For the removal of subordinate species experiment we compared the inflorescence production of control and removed loose cushions with a Student's *t*-test. Dependent variables were checked for normality and log (cushion traits and target growth) or arcsine root transformed (target survival) before parametric tests. All statistical analyses were done using R (R Development Core Team 2012).

#### Results

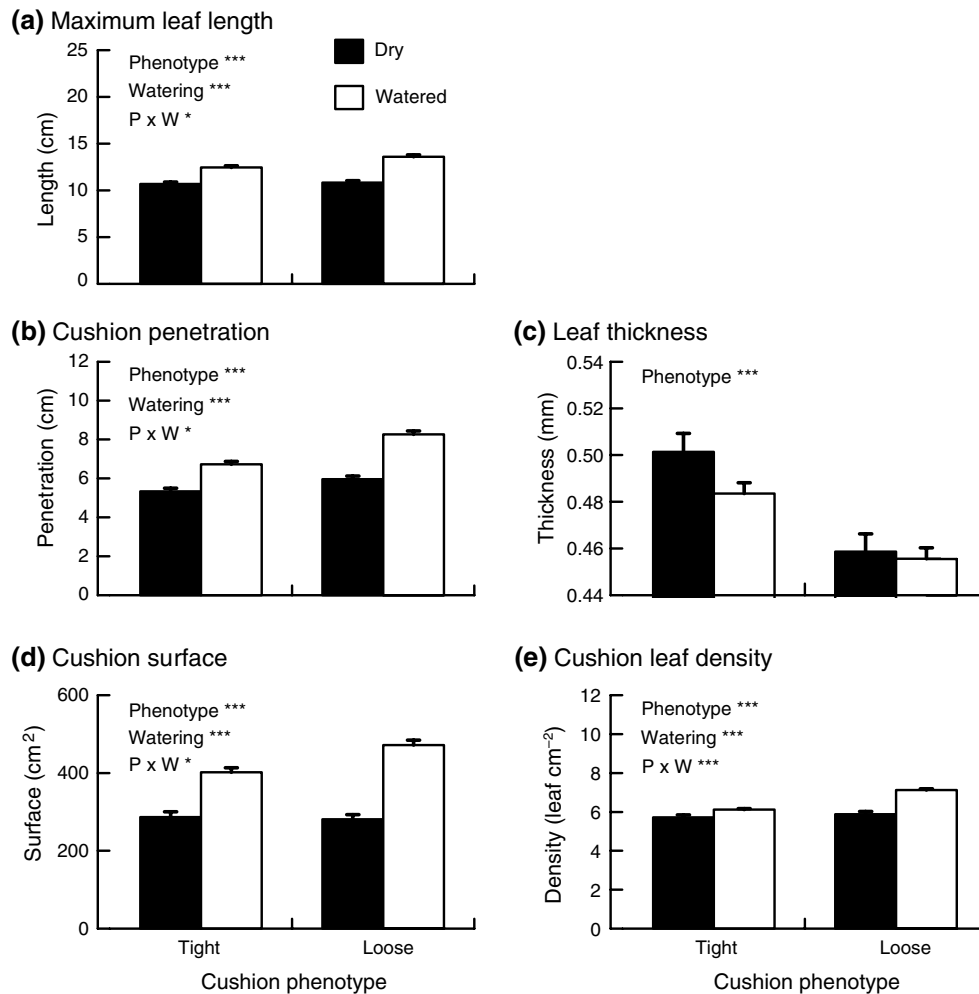
Differences in field traits between the two cushion phenotypes were highly significant for all measured traits ( $P < 0.001$ ; Table 1). Loose phenotypes had 25 % longer leaves, and 100 % higher cushion penetration than tight phenotypes, whereas the latter had ten times more inflorescences and 20 % thicker leaves than the former.

In the shadehouse, after two growing seasons, *F. gautieri* maximum leaf length, cushion penetration, cushion surface and cushion leaf density were highly significantly affected by both the phenotype and watering treatments (Fig. 1a, b,

**Table 1** Mean trait values of the two phenotypes (tight and loose) of *Festuca gautieri* measured in the field ( $n = 30$ ) and significance of phenotype effect determined by *t*-tests

Variables	Trait values		Phenotype effect <i>P</i>
	Tight (SE)	Loose (SE)	
Maximum leaf length (cm)	5.99 (0.31)	7.58 (0.23)	<0.001
Cushion penetration (cm)	4.25 (0.17)	8.05 (0.33)	<0.001
Number of inflorescences (inflorescences cm <sup>-2</sup> )	0.18 (0.03)	0.02 (0.01)	<0.001
Leaf thickness (mm)	0.48 (0.01)	0.40 (0.01)	<0.001

Significant effects are indicated in *italic*



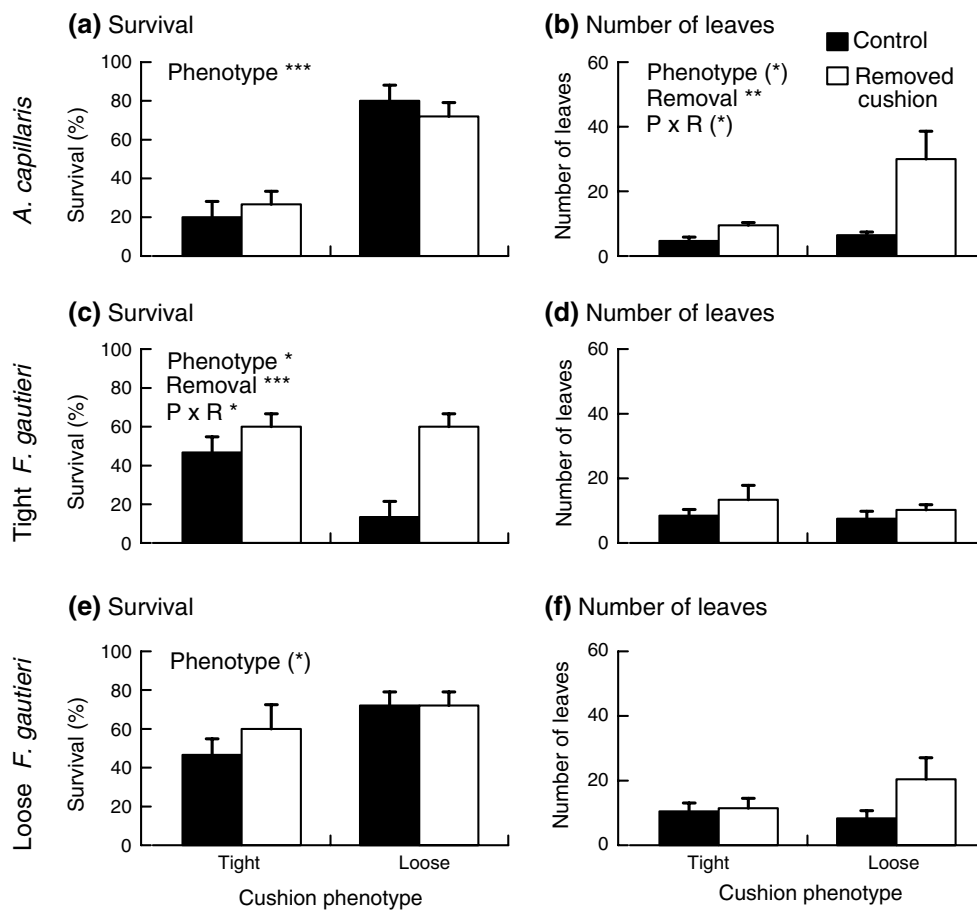
**Fig. 1a–e** Shadehouse trait measurements of tight and loose phenotypes of *Festuca gautieri*, with and without watering. Data shown are means + SE ( $n_{\text{loose-watered}}$  and  $n_{\text{tight-watered}} = 15$ ,  $n_{\text{loose-dry}} = 13$ ,  $n_{\text{tight-dry}}$

$= 14$ ). Significant results of two-way ANOVAs on the effects of phenotype (*P*), watering (*W*) and their interactions are shown for each trait. \* $P < 0.05$ , \*\*\* $P < 0.001$

d, e, respectively). Leaf thickness was highly affected by the phenotype treatment only (Fig. 1c), but for all other traits the effect size was stronger for the watering treatment than for the phenotype treatment. For example, leaves were 5 % longer for loose phenotypes compared to tight ones, whereas watered cushions had 17 % longer leaves than dry

ones. Penetration was 15 % higher in loose cushions than in tight ones, but 25 % higher in watered cushions than in dry ones. Similarly, cushion surface was 8.5 % larger for loose than for tight cushions, but 20 % larger for watered than dry cushions. Leaf density was 9 % higher for loose cushions than for tight ones, whereas watered cushions had





**Fig. 2** Effect of cushion removal, survival and leaf number of **a, b** *Agrostis capillaris*, **c, d** tight *F. gautieri* phenotype, **e, f** loose *F. gautieri* phenotype in the habitats of the two phenotypes of *F. gautieri*. Data shown are means + SE ( $n = 5$ ). Significant results of

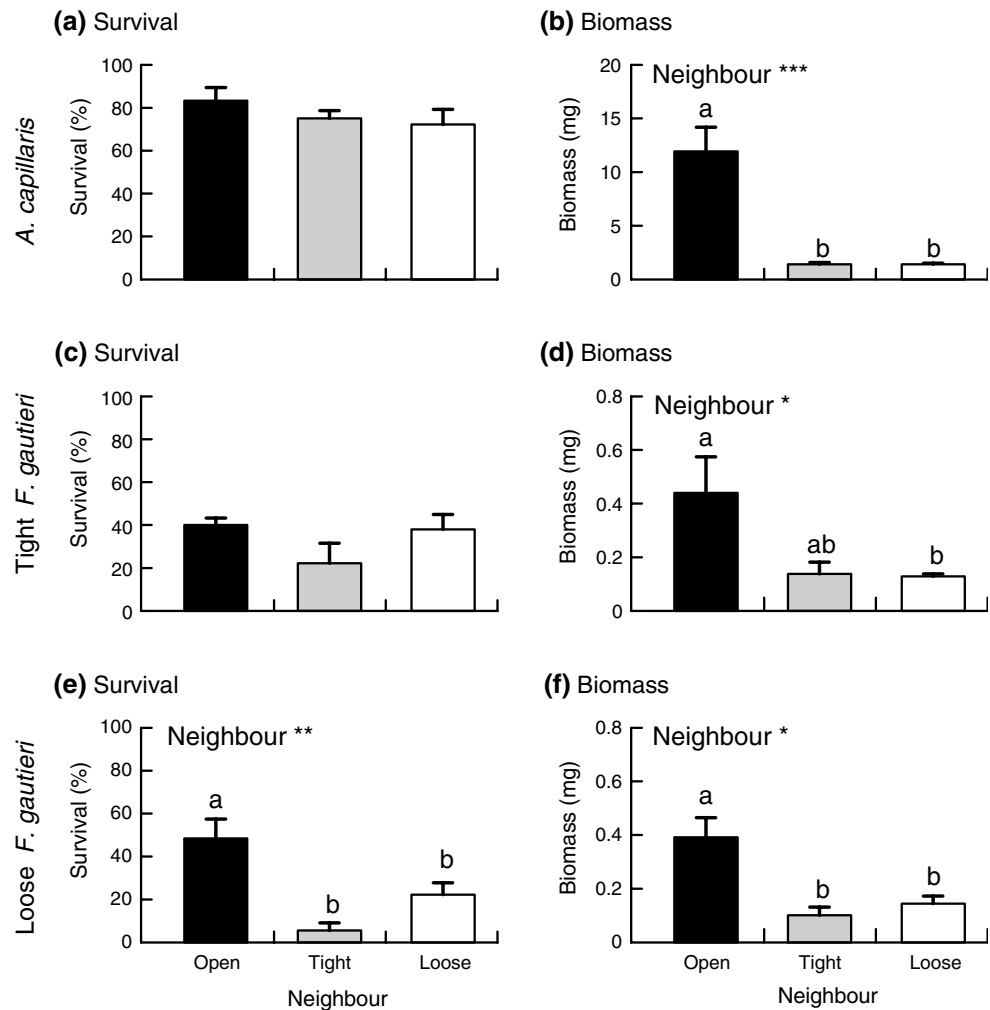
two-way ANOVAs on the effects of phenotype ( $P$ ), removal ( $R$ ) and their interactions are indicated. (\*)  $P < 0.1$ , \*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$

12 % higher leaf density than dry ones. In contrast with the other four traits, tight cushions had 7 % thicker leaves than loose cushions, but there was no difference between watered and dry cushions. Nevertheless, there was a significant phenotype  $\times$  watering interaction ( $P < 0.05$ ) for cushion leaf length, penetration and surface, and this interaction was even highly significant for leaf density ( $P < 0.001$ ). This interaction was due to a higher effect of watering on those traits for the loose cushions than for the tight ones, showing that loose cushions were more plastic than tight ones. Even so, this interaction was not observed for leaf thickness (Fig. 1c). To summarise, trait differences between phenotypes were explained by both genetic and plasticity effects, but with a stronger contribution of the latter.

In the field cushion-removal experiment, target survival was higher in the loose cushion habitat than in the tight one for both *A. capillaris* and the loose target fescue (phenotype effect; Fig. 2a, e). The phenotype effect was very strong for *A. capillaris*, with survival in the tight cushion habitat three times lower than in the loose one. The tight fescue target

survived less in the loose cushion habitat than in the tight cushion, and also less with neighbours than without neighbours (significant phenotype and removal effects; Fig. 2c). Additionally, there was a significant phenotype  $\times$  removal interaction because the negative effect of neighbours on the tight fescue target was much stronger in the loose cushion habitat than in the tight one (Fig. 2c). For target leaf number there was a marginally significant higher performance in the loose cushion habitat than in the tight one for *A. capillaris* (Fig. 2b), but no differences among habitats for both tight and loose fescue targets (Fig. 2d, f, respectively). For *A. capillaris* there was also a significant removal effect and marginally significant phenotype  $\times$  removal interaction. Competition was higher for *A. capillaris* in the loose cushion habitat than in the tight one, with a much higher leaf number without neighbours in the former than in the latter but no difference with neighbours across habitats (Fig. 2b). To summarise, these results show that the tight cushion habitat was more stressful for *A. capillaris*, and that the loose cushion habitat was more competitive for both the tight fescue and *A. capillaris* targets.

**Fig. 3** Survival and biomass of **a, b** *A. capillaris*, **c, d** tight *F. gautieri*, and **e, f** loose *F. gautieri* targets in the three neighbouring conditions: no neighbour (*Open*), within tight *F. gautieri* cushions (*Tight*), and within loose *F. gautieri* cushion of the shadehouse competition experiment (*Loose*). Data shown are means + SE ( $n = 6$ ). Results of Tukey tests are shown at the top of error bars when a significant neighbour effect occurs. Significant results of one-way ANOVAs on neighbouring effects are indicated. \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$



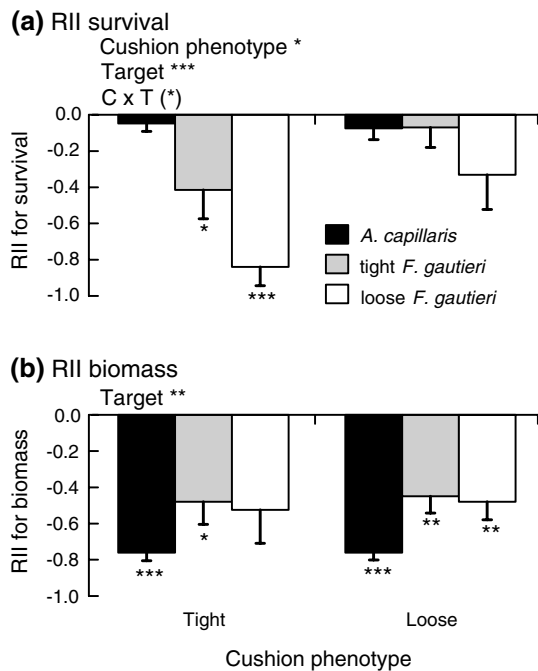
In the shadehouse competition experiment, there was a significant neighbour effect for the survival of the loose fescue target with a higher survival without neighbour than with neighbour (Fig. 3e). Additionally, RII results showed that competition for survival was more intense within the tight fescue cushions than within the loose ones (significant cushion phenotype effect; Fig. 4a). There were also significant differences in competitive responses among the three targets (highly significant target effect for RII survival). The loose fescue phenotype was the worst response competitor for survival and there were no significant differences between the two other targets [Tukey test for the target effect—*A. capillaris* (a), tight *F. gautieri* (a), loose *F. gautieri* (b); Fig. 4a]. However, this effect was mostly found in the tight fescue cushions as shown by the marginally significant cushion phenotype  $\times$  target interaction (Fig. 4a). For biomass there was a significant neighbour effect for the three targets due to a strong decrease in target biomass when grown within cushions (Fig. 3b, d, f). However, in contrast to survival, the worst response competitor was *A. capillaris*, which had the lowest RII values (target

effect; Fig. 4b) and there were no differences in competitive effects between both fescue phenotypes. To summarise differences in competitive abilities between the two fescue phenotypes, results on survival showed that the tight phenotype was the strongest effect competitor and the loose phenotype the weakest response competitor.

The removal of subordinate species within loose cushions evidenced a substantial cost of hosting other species for loose cushions, because loose cushions with subordinate species removed produced almost twice as many inflorescences as controls ( $0.42 \pm 0.09$  and  $0.23 \pm 0.05$  inflorescences  $\text{cm}^{-2}$ , respectively;  $P = 0.04$ ). However, loose cushions with subordinate species removed produced 75 % less inflorescences than tight cushions ( $1.84 \pm 0.25$  inflorescences  $\text{cm}^{-2}$  for tight cushions;  $P = 0.002$ ).

### Discussion

Our shadehouse trait measurements showed that field morphological differences between phenotypes had both



**Fig. 4** Relative interaction index (RII) for **a** survival ( $RII_{\text{survival}}$ ) and **b** biomass ( $RII_{\text{biomass}}$ ) of the three targets (*A. capillaris*, tight *F. gautieri* and loose *F. gautieri*) calculated for both cushion phenotypes as neighbours. Data shown are means + SE ( $n = 6$ ). Significant results of two-way ANOVAs on cushion phenotype (C), target (T), and their interactions are indicated *above panels* and results of one-sample *t*-tests are shown *below error bars*. (\*) $P < 0.1$ , \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$

genetic and phenotypic plasticity bases, with an overall higher contribution of the latter. Our shadehouse competition experiment showed that heritable differences in cushion traits drove contrasting interactive effects and responses, with the highest competitive ability for the tight fescue phenotype. However, our field competition experiment provided opposite results, with higher competition found in the loose (low-stress habitat) rather than in the tight habitat (high-stress habitat). Together, these results suggest that field differences in cushion traits and interactions with other species have both genetic and phenotypic plasticity bases, but that heritable interactions contribute to changes in subordinate species diversity across habitats in a complex way. Finally, our removal of subordinate species experiment showed that loose phenotypes pay a cost for hosting other species.

#### Phenotypic differentiation within *Festuca gautieri* cushions

The five measured traits remained significantly different between both *F. gautieri* cushion phenotypes at the end of the 2-year shadehouse experiment, suggesting that intraspecific morphological variation observed across natural

habitats may have partly a genetic basis. This is consistent with the experiment of Le Bagousse-Pinguet et al. (2014b) who found that young transplants of the two phenotypes of *F. gautieri* had contrasting survival responses along a soil moisture gradient occurring in the same field system. Both genetic variability and phenotypic plasticity are known to explain trait variation in heterogeneous environments (Pigliucci 2001; Byars et al. 2007; Grassein et al. 2010) and we acknowledge that reciprocal transplant experiments conducted in field conditions are necessary to reach straightforward conclusions on the heritability of adult trait differences suggested by our shadehouse experiment. Although common gardens are commonly used to experimentally separate genetic from phenotypic plasticity effects (Clausen et al. 1940; Schmid and Dolt 1994), maternal effects may persist in short-term experiments (Schmid and Dolt 1994). We used cuttings of *F. gautieri* in our shadehouse experiments, which did not clearly allow the ruling out of maternal effects. However, maternal effects on offspring phenotypes—which are generally more prevalent in juvenile life history stages relative to adult life history stages (Roach and Wulff 1987)—are likely to be reduced by selecting mature individuals (Ravenscroft et al. 2014). Thus, trait differences among phenotypes are likely in part due to genetic effects.

In our shadehouse experiment, watering also had a highly significant effect for all traits except leaf thickness, with watered cushions having longer leaves, and higher penetration, surface and leaf density than dry ones. Thus phenotypic plasticity also contributes to the observed morphological variation across habitats. Additionally, the significant phenotype  $\times$  watering interaction for maximum leaf length, cushion penetration, surface and leaf density showed that loose cushions are more plastic than tight ones. Interestingly, genetic and phenotypic plasticity effects acted in the same direction, with overall the strongest trait differences observed between dried tight phenotypes and watered loose phenotypes. Additional heritable and environmental effects were also found by Vitasse et al. (2009) in the Pyrenees mountain range for phenological traits of an oak and an ash species. In contrast, they found counteracting heritable and environmental effects for a beech species.

#### Effects of *F. gautieri* phenotypes on subordinate species and consequences for diversity

The shadehouse trait measurements and competitive experiment suggest that a heritable component may also explain differences in competitive ability among phenotypes. Tight cushions had a higher competitive ability (higher competitive effect-likely through interference mechanisms-and response) than loose cushions under the same

environmental conditions. Contrasting penetration between tight and loose cushions is mainly related to higher leaf thickness and stiffness. Thus tight, thick and stiff leaves of tight cushions can impede the recruitment of other species. Previous studies have shown that phenotypic architectural variation in foundation species may induce contrasting competitive and facilitative effects on other plant species (Callaway et al. 1991; Pugnaire et al. 1996; Rudgers and Maron 2003; Michalet et al. 2011). Our results are consistent with Michalet et al. (2011) who showed that heritable differences in the tightness of two phenotypes of the alpine cushion species *Geum rossii* were related to differences in their effects on subordinate species, with also a higher competitive effect for the tight than for the loose phenotypes. Similarly, Callaway et al. (1991) have shown in Californian oak savannah that differences in root density among phenotypes of *Quercus douglasii* induced contrasting interference effects on their herbaceous understories. However, to our knowledge, our study is the first to show differences in competitive effects among different phenotypes of a foundation species in controlled similar environmental conditions.

Because we did not mimic field variation in water availability in our shadehouse competition experiment, we were not able to directly assess the plasticity of competitive effects across phenotypes' habitats. However, results of the shadehouse trait measurements allow us to predict that with increasing water availability from the tight phenotype's habitat to the loose one, the competitive effect ability of both phenotypes should decrease since both showed an increase in cushion penetration with watering. This effect should be even stronger for the loose phenotype because it showed higher trait plasticity than the tight one. With watering, cushions had softer leaves allowing a higher cushion penetration and thus a decrease in interference effect.

The results of the two shadehouse experiments suggest the prediction that in the field, the highest cushion competitive effect should be observed for the tight phenotype in its dry habitat and the lowest for the loose phenotype in its wet habitat, and thus, that competition should likely decrease from the former to the latter habitat. However, our field competition experiment provided an opposite result. Competition significantly increased for the survival of tight fescue targets only, and weakly increased for leaf number only for *A. capillaris*. Additionally, we did not find any facilitation in this experiment for these two response variables. An increase in competition from the dry convex habitat of the tight phenotype towards the wet concave habitat of the loose phenotype is consistent with Grime (1974) and the stress gradient hypothesis (Bertness and Callaway 1994), models that predict an increase in competition with decreasing stress. Thus, should we conclude that varying

interactions and species richness across habitats in natural conditions are not influenced by heritable and plastic differences in competitive effects among phenotypes?

In order to answer this crucial question, we need to disentangle changes in cushion effects from changes in target responses across habitats. Michalet et al. (2014) have recently proposed a conceptual framework to partition net interactions along stress gradients. They showed that the switch from competition to facilitation that has been recurrently demonstrated from subalpine to alpine communities (e.g. Callaway et al. 2002) was due to two different processes that needed to be disentangled. The increase in competition from low alpine to subalpine communities is due to a neighbour trait effect, defined as a decrease in the target response with neighbours with decreasing stress due to an increase in the competitive effect of the neighbours [consistent with Grime's (1974) model]. In contrast, the increase in facilitation from low alpine to high alpine communities is due to an environmental severity effect, defined as a decrease in the performance of the target species without neighbours with increasing stress, without changes in the facilitative effect of the neighbours. In our field experiment conducted in subalpine conditions we showed that the increase in competition from the stressful convex habitat of the tight phenotype towards the more benign concave habitat of the loose phenotype was either due to neighbour trait or environmental severity effects depending on the target species and the response variable. For leaf number, for which there was only a marginally significant increase in competition from tight (high stress) to loose (low stress) cushion habitats for *A. capillaris*, this increase in competition was due to an environmental severity effect (see Fig. 2b), with no changes in the three targets performance with neighbours. For survival, the increase in competition was significant only for the tight fescue target and was due to a neighbour trait effect, whereas for the two other targets performance with and without neighbours increased towards the loose cushion habitat, due to decreasing environmental severity (i.e. evidence of an environmental severity effect). Thus, we conclude that for the two target species naturally abundant in the loose cushion habitat, where species richness was the highest within cushions, there were only environmental severity effects. This result is not consistent with Grime's (1974) model and the meta-analysis of Michalet et al. (2014), which predicted or showed, respectively, that an increase in competition in subalpine habitats with decreasing stress is due to an increase in the negative effect of the dominant competitor (i.e. a neighbour trait effect). We argue that competitive effects did not increase in the field from tight to loose cushion habitats because of both the counteracting heritable and plastic effects that were evidenced in the two shadehouse experiments (decrease in competitive effects due to

phenotypes and watering). In other words, in the absence of these heritable and plastic effects inherent to this foundation species, competition should have increased more strongly from the stressful habitat of the tight phenotype to the benign habitat of the loose phenotype, consistent with Grime's (1974) competition theory and the meta-analysis of Michalet et al. (2014). However, this hypothesis remains to be tested in reciprocal transplant experiments including neighbour removal. Finally, the decrease in competition due to these genetic and plastic effects suggested by our results likely contribute to the high species richness occurring in the loose cushions.

#### Feedback effects of the subordinate species on the foundation species' fitness

We found evidence of a cost of hosting other species for *F. gautieri*. The removal of subordinate species within loose cushions significantly increased the flower production of *F. gautieri*. Loose cushions in which we removed subordinate species produced twice the number of inflorescences as control loose cushions. Negative feedback effects of subordinate species have been found on water status, growth, and reproductive output of their host nurse shrub *Ambrosia dumosa* in the Mojave Desert (Holzapfel and Mahall 1999). Negative feedback effects of recipient species have also been found on the reproductive output of nurse cushion plants *G. rossii* (Michalet et al. 2011) and *Silene acaulis* (Cranston et al. 2012). In contrast, in semi-arid Spain, Pugnaire et al. (1996) found a benefit for the nurse shrub *Retama sphaerocarpa* of hosting *Marrubium vulgare*. Shrubs hosting the forb had higher biomass and nitrogen contents in branches than shrubs alone. In an evolutionary context, it is crucial to quantify not only the costs but also the benefits of hosting other species (Bronstein 2009). Using an individual-based model, Michalet et al. (2011) showed that the inclusion of a benefit of hosting other species strongly increased the selective pressure of feedback effects for the alpine cushion foundation species' genetic differentiation. However, like in this study, they did not find evidence for this benefit that was only hypothetical in their model. However, a benefit may exist for other traits than flowering output, which was not explored in both studies. For example, Schöb et al. (2014) found in an intercontinental study assessing feedback effects of alpine beneficiary species on their benefactors that the richness of cushion-associated species had positive effects on seed density, although the dominant effect was parasitic with a decline in cushion seed production with increasing cover of beneficiaries.

We showed in our study that phenotypic differences in cushion traits within the foundation cushion grass species, *F. gautieri*, had both heritable and environmental bases. We

also showed that these trait divergences induce contrasting competitive effects for other species that counterbalanced the strong increase in competition, which has been recurrently shown to exist from dry to mesic subalpine habitats. Thus, heritable and plastic effects strongly contribute to maintain high subordinate community diversity through decreasing competition. The high diversity of other species within cushions had feedback effects on the fitness of the loose cushion. Further experiments are needed to also eventually detect a benefit for loose cushions to hosting other species in order to test the hypothesis that these contrasting competitive effects have evolutionary consequences for the foundation grass species. Our study brought additional support to the emerging perspective that diffuse within-trophic level biotic interactions might have important evolutionary consequences at the community level.

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