

MECHANISMS AND CONSEQUENCES OF FACILITATION IN PLANT COMMUNITIES

Beneficiary feedback effects on alpine cushion benefactors become more negative with increasing cover of graminoids and in dry conditions

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Summary

1. In facilitative interactions, the beneficiary feedback effect (BFE) has been defined as the effect of beneficiary species (facilitated species) on their benefactor. BFEs have been shown to be dependent on environmental conditions and the composition of the beneficiary community. In alpine cushion systems, BFEs are more negative with more abundant, diverse and phylogenetically aggregated communities of beneficiary species.

2. We tested the hypothesis that the functional composition of the beneficiary communities correlates with the direction and strength of BFE received by alpine cushion benefactors and specifically that a more negative BFE would occur with increasing density of graminoids and a more positive BFE would occur with increasing density of forbs and legumes. Additionally, we predicted that the negative BFE of graminoids would increase with increasing summer aridity.

3. We used a data base of alpine cushion communities from 30 sites throughout the world to assess the overall relationship between the composition of beneficiary communities and the total flower density of cushion benefactors, and its variation with increasing drought. Additionally, in order to assess more precisely the role of the functional composition of the beneficiary communities on BFE in a very dry site with cushion benefactors exhibiting contrasting functional compositions of beneficiary communities, we also designed a field study in the Qilian Shan mountain range (China). At this site with a highly continental climate, we compared the number of flowers and fruits of different phenotypes of the alpine cushion species *Thylacospermum caespitosum* hosting numerous graminoids, numerous forbs or very few beneficiary species.

4. In the intercontinental study, we found a negative relationship between graminoids and cushion benefactor flower density but no effect of other functional groups. The negative BFE of graminoids increased with increasing summer drought. In the dry Qilian Shan range, we found both a negative effect of graminoids on total flower density and a positive effect of forbs on flower density and fruit set.

5. Our study indicates that the context dependence of BFE may be partially explained by the composition of beneficiary communities and in particular the negative effect of graminoids.

Key-words: alpine communities, beneficiary feedback effect, community feedbacks, competition, cushion plants, drought, facilitation, functional composition, graminoids

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Introduction

A complete understanding of the evolutionary consequences of interactions among species depends on knowing how each interacting species affects the other. For example, if two interacting species each have a positive effect on each other, there is the potential for the evolution of a long-term stable mutualism. In contrast, if one of the interacting species has a positive effect and the other a negative effect, then an evolutionary stable state is unlikely (Bronstein 2009). In addition, the relative strengths of reciprocal positive and negative effects affect how long-term evolutionary relationships may play out. However, facilitation has generally been studied as the positive effect of one species, the 'benefactor', on a second 'beneficiary' species, with limited exploration of feedback effects of beneficiaries on benefactors. Thus, the potential evolutionary consequences of facilitation are poorly understood (Bronstein 2009). In fact, since the beneficiary feedback effects (hereafter called BFEs) can be either negative, neutral or positive (Callaway 2007), there may be different scenarios of evolutionary consequences of facilitation, depending on sign and intensity of the BFE.

Beneficiary feedback effects can be positive. For example, Pugnaire, Haase & Puigdefábregas (1996) demonstrated mutualistic interactions between the shrub *Retama sphaerocarpa* and the understorey species *Marrubium vulgare* in semi-arid Spain. Sortibrán, Verdú & Valiente-Banuet (2014) found that the tree benefactor *Mimosa luisana* had higher seed output when facilitating other species. However, many antagonistic reciprocal effects of beneficiaries on benefactors have been described in arid systems (McAuliffe 1984, 1988; Valiente-Banuet, Vite & Zavala-Hurtado 1991; Flores-Martínez, Ezcurra & Sánchez-Colón 1994; Holzapfel & Mahall 1999). These latter findings have questioned the evolutionary stability of facilitation (Bronstein 2009) and have likely contributed to the emergence of an interest in the community ecology literature for the evolutionary consequences of facilitation (Thorpe *et al.* 2011; Liancourt *et al.* 2012; Al Hayek *et al.* 2015; Soliveres, Smit & Maestre 2015).

The resurgence of interest in these reciprocal interactions has led to several studies of BFEs on the reproduction success of their benefactors, and in particular in alpine cushion communities (Michalet *et al.* 2011; Cranston *et al.* 2012; Al Hayek *et al.* 2014; Schöb *et al.* 2014a,b,c). In these studies, reproduction success was chosen rather than survival or growth of the cushion benefactors, because reproduction is recognized as good indicator of fitness (Tielbörger & Kadmon 2000). Negative BFEs on the reproduction success of their benefactors have been found predominantly, although there can be substantial variability depending on the performance trait measured (McIntire 2014; Schöb *et al.* 2014a). For example, in their intercontinental study conducted on 34 alpine sites dominated by cushion benefactors, Schöb *et al.* (2014a) found a negative

effect of beneficiary species cover and number of individuals for the flower density and seed set of the cushion benefactors, but a neutral BFE for their fruit set and seed quality. Therefore, a compensatory increase in the number of flowers producing fruits could actually minimize the cost of a reduced flower density (McIntire 2014).

Schöb *et al.* (2014b) demonstrated the context dependence of BFEs on cushion benefactor species. They showed that the effects of beneficiaries became more negative with increasing both beneficiary species richness and facilitation intensity. Additionally, increasing phylogenetic diversity counterbalanced the negative effects of species richness on the BFE and high-productivity sites showing a weaker negative BFE for cushion benefactors. Schöb *et al.* (2014b) argued that the interplay between the positive effect of phylogenetic diversity and the negative effect of species richness on the BFE suggests that a species-rich community of closely related species imposed significant costs in terms of reduced flower production by the benefactor. Alternatively, the dominance of particular functional groups of beneficiary species might have negative effects on the benefactors. This effect of the functional composition of the beneficiary communities on BFE has been hypothesized by Schöb *et al.* (2014b) but has, to our knowledge, never been tested. This is the major novelty of our contribution, as compared to previous BFE studies conducted in alpine communities (Michalet *et al.* 2011; Cranston *et al.* 2012; Al Hayek *et al.* 2014; Schöb *et al.* 2014a,b,c).

Plant–plant interactions are highly dependent on the traits and functional strategies of the interacting species (Liancourt, Callaway & Michalet 2005; Navas & Violle 2009; Navas & Fayolle 2012; Soliveres *et al.* 2014). Differences in species traits and strategies of both the benefactor and the beneficiary species between communities may lead to substantial changes in plant–plant interaction dynamics, as shown in particular in dry conditions (Gómez-Aparicio *et al.* 2004; Michalet 2007; Gómez-Aparicio 2009; Maestre *et al.* 2009; Forey, Touzard & Michalet 2010). For example, because of their high allocation to roots, grasses are more likely to also compete for water than shrubs or forbs (Davis, Wrage & Reich 1998; Michalet 2007; Gómez-Aparicio 2009). In contrast, forbs may be more likely to have positive indirect effects through increasing pollinator visitation rates (Moeller 2004; Callaway 2007; Sargent & Ackerly 2008; Reid & Lortie 2012; Hegland 2014; Seifan *et al.* 2014). Leguminous forbs exert positive effects on other species through nitrogen inputs (Pugnaire, Haase & Puigdefábregas 1996; Pugnaire, Armas & Valladares 2004; Callaway 2007). Thus, the mediating role of the phylogenetic diversity of the beneficiary community on BFEs found by Schöb *et al.* (2014b) study might be related in part to the functional composition of beneficiary communities. Higher relative cover of beneficiary grasses might enhance negative BFEs, whereas higher cover of forbs and legumes might increase positive BFEs.

In this study, we reanalysed data from an intercontinental study reported by Schöb *et al.* (2014a,b) in order to assess how the functional composition of the beneficiary communities affects the strength and direction of their effects on the flower production of cushion benefactors and how these effects vary with increasing drought. However, because with this data base we could not easily separate functional composition effects from total cover effects, we additionally designed another study specifically addressing the influence of the functional composition of the beneficiary community on its feedback effect on the benefactor. For this purpose, we selected a site where we expected strong BFEs and where naturally occurring, striking differences in the functional group composition of the beneficiary communities were available in constant conditions of total cover. Based on these criteria, we have chosen a site in the Qilian Shan Mountains of China. The site is characterized by a very dry climate, that is climatic conditions from which most published studies showing a significant BFE originate (McAuliffe 1984, 1988; Valiente-Banuet, Vite & Zavala-Hurtado 1991; Flores-Martínez, Ezcurra & Sánchez-Colón 1994; Pugnaire, Haase & Puigdefábregas 1996; Holzapfel & Mahall 1999; Michalet *et al.* 2011; Schöb *et al.* 2014b,c; Soliveres *et al.* 2014). Furthermore, the study site was dominated by the alpine cushion species *Thylacospermum caespitosum* that had some individuals hosting almost no beneficiary species and others hosting either a high number of graminoids or a high number of forbs. For both the intercontinental study and the Qilian Shan study, we focused on four main predictions: (i) graminoids will have a negative effect on the total flower density of benefactors; (ii) forbs and legumes will have a positive effect on the total flower density of benefactors; (iii) the negative effects of graminoids will increase with increasing drought; and (iv) forbs will have a positive effect on fruit density.

Materials and methods

DATA

For the intercontinental study, data on cushion benefactor flower density and the abundance of beneficiary species were taken from Schöb *et al.* (2014a,b), with the addition of two sites sampled in 2014 in Lebanon and one site in the White Mountains of California (Table 1). At 30 sites dominated by plants with cushion morphologies, between 20 and 160 cushions were randomly selected within an area of c. 0.3 km². The identity and number of all individuals of all species that were inside of cushions were counted, the size of cushions was measured, and the flower density of cushions was recorded (see Schöb *et al.* 2014a for further details). Beneficiary species were combined into the following functional groups: graminoids, legumes, shrubs and other forbs. For each site, we also extracted data on actual summer evapotranspiration from the Global Land Data Assimilation System (GLDAS). Data were extracted as monthly sums for the years 2001–2009 and then averaged over the summer months (June–August in the Northern Hemisphere and January–March in the Southern Hemisphere). Actual summer evapotranspiration is the climatic variable most strongly related to plant diversity patterns in alpine systems

(Cavieses *et al.* 2014) and thus suitable as an indicator for climatic effects on plants in cushion-dominated alpine habitats.

At one of the driest sites in the intercontinental study, we assessed more deeply the relationship between the functional composition of the beneficiary community and the reproduction success of a cushion benefactor, *T. caespitosum*, exhibiting a high variation in relative cover of graminoids and forbs (R. Michalet, personal observation). *Thylacospermum caespitosum* is one of the most drought-tolerant alpine cushion species occurring in the highly continental mountain ranges of Central Asia (Dvorský *et al.* 2013; Chen *et al.* 2015). This species has been shown to have a strong phenotypic variation with tight convex cushions hosting very few beneficiary species and loose flat cushions hosting lots of beneficiary species (Dvorský *et al.* 2013 in the north-west Himalayas and R. Michalet, personal observation at our Chinese site). In mid-August 2014, at the Qilian Shan site in China (latitude: 39.590°, longitude: 96.420°, altitude: 3680 m), we selected 90 cushions of *T. caespitosum* that contrasted substantially in either the cover or the functional composition of associated beneficiary species. We selected 30 cushions with a high relative cover of graminoids (>75%) and 30 cushions with a high relative cover of forbs (>75%). And in this case, both groups had a high absolute cover of beneficiary species (>25%). We also selected 30 cushions with a low absolute cover of beneficiary species (<10%). This design allowed us to analyse separately the effect of the functional composition from the effect of the total cover of the beneficiary community. We measured the length and width of each cushion and randomly selected within each cushion a circular area of 20 cm diameter (314 cm²) in which to count flowers and fruits of *T. caespitosum*. With these data, we could, apart from the net number of flower and fruits produced, also estimate fruit set (i.e. the percentage of flowers turning into fruits) and the ratio of unfertilized flowers (i.e. the percentage of flowers not turning into fruits). Fruits were harvested and weighed after drying them for 2 days at 65 °C. We also counted within the same area the number of individuals of all associated beneficiary species and estimated the total cover (%) of each functional group of associated beneficiary species (graminoids and forbs, including very few legumes and young individuals of other cushion species).

STATISTICAL ANALYSES

In the intercontinental study, we tested the relationship between the abundance of beneficiary species in total, and the abundance of each functional group, to the number of flowers of the cushion benefactors in order to assess sign and intensity of the BFE. The relationships were tested with linear mixed models with sites included as random term and cushion benefactor size included as a covariate. The response variable, that is the density of flowers produced by cushion benefactors, was standardized for each site by zero mean and unit variance, whereas the predictor variables, that is the number of individuals of beneficiary species in total, or the number of individuals per functional group, were square root transformed to reduce the impact of extreme values. The random term controlled for site-specific mediators of the BFE of beneficiary species on cushion benefactors, such as climate or productivity (Schöb *et al.* 2014b). We used cushion benefactor size to control for size- and age-specific variation in reproduction (Samson & Werk 1986; Schöb *et al.* 2014a). Significance of the predictor variables and the covariate were tested by a type II Wald chi-square test.

In order to check for context dependence in the effect of graminoid species and forb species on cushion benefactor flower density, we first repeated the analysis relating cushion benefactor flower density to the abundance of beneficiary functional groups for each site separately and extracted the corresponding regression coefficients. For this, we used linear regression models with the same response and predictor variables and the covariate as described

Table 1. The 30 sites dominated by cushion benefactor plants. For each site, we determined cushion benefactor flower density and the abundance of beneficiary functional groups (graminoids, shrubs, legumes and other forbs) and assessed their relationship. Actual summer evapotranspiration data were extracted from the Global Land Data Assimilation System. Coef. graminoids = regression coefficient (slope) of the relationship between the abundance of graminoids and cushion benefactor flower density. NA = no graminoids present

Country	Site	Species	Longitude (°)	Latitude (°)	Elevation (m a.s.l.)	<i>n</i>	Evapo-transpiration	Coef. graminoids
Canada	Cathedral Lake	<i>Saxifraga oppositifolia</i>	−120.218	49.051	2510	39	84.9573	−0.80
Canada	Pink Mountains1	<i>Silene acaulis</i>	−122.864	57.061	1754	32	93.1878	−1.94
Canada	Pink Mountains2	<i>Silene acaulis</i>	−122.866	57.061	1757	59	93.1878	−0.23
Canada	Red Mountain	<i>Silene acaulis</i>	−122.562	51.209	2191	31	70.8703	2.16
Canada	Whistler Mountains, N	<i>Silene acaulis</i>	−122.571	50.032	2100	99	87.1147	1.15
Canada	Whistler Mountains, S	<i>Silene acaulis</i>	−122.571	50.032	2100	141	87.1147	0.69
Chile	Franciscano	<i>Azorella madreporica</i>	−70.26	−33.319	3600	34	34.8139	−8.03
Chile	Tres Puntas, low	<i>Azorella madreporica</i>	−70.239	−33.325	3394	27	34.8139	−12.02
China	Qilian Shan	<i>Thylacospermum caespitosum</i>	96.303	39.302	4239	90	22.2620	−4.13
Ecuador	Volcano Antisana, high	<i>Azorella aretioides</i>	−78.159	−0.472	4700	46	43.3237	9.93
Lebanon	Lebanon	<i>Onobrychis cornuta</i>	35.848	33.975	2222	50	32.7092	−5.62
Lebanon	Lebanon, high	<i>Onobrychis cornuta</i>	35.848	33.975	2200	160	32.7092	−6.87
Lebanon	Lebanon, low	<i>Onobrychis cornuta</i>	35.848	33.975	2000	160	32.7092	−6.27
Spain	Sierra Nevada, N-high	<i>Arenaria tetraquetra</i> ssp. <i>amabilis</i>	−3.371	37.051	3239	46	57.1119	−1.44
Spain	Sierra Nevada, N-low	<i>Arenaria tetraquetra</i> ssp. <i>amabilis</i>	−3.381	37.081	2750	42	57.1119	−5.43
Spain	Sierra Nevada, N-low	<i>Plantago holostium</i>	−3.381	37.081	2750	85	57.1119	−3.12
Spain	Sierra Nevada, S-high	<i>Arenaria tetraquetra</i> ssp. <i>amabilis</i>	−3.313	36.997	3110	20	57.1119	NA
Spain	Sierra Nevada, S-low	<i>Arenaria tetraquetra</i> ssp. <i>amabilis</i>	−3.303	37.036	2575	20	57.1119	3.96
Switzerland	Gemmi1	<i>Silene acaulis</i>	7.629	46.425	2297	20	87.5867	−2.10
Switzerland	Gemmi2	<i>Carex firma</i>	7.628	46.423	2305	20	87.5867	−8.78
USA	Piegan Pass	<i>Silene acaulis</i>	−113.682	48.725	2143	21	94.7583	−1.15
USA	San Francisco Mountains, high	<i>Geum rossii</i>	−111.682	35.343	3800	50	24.3641	−9.84
USA	San Francisco Mountains, low	<i>Geum rossii</i>	−111.684	35.341	3650	50	24.3641	−7.19
USA	Swiftcurrent, high	<i>Silene acaulis</i>	−113.767	48.784	2515	77	101.4587	4.05
USA	Swiftcurrent, low	<i>Silene acaulis</i>	−113.767	48.78	2273	67	101.4587	−1.55
USA	White Mountains	<i>Eriogonum gracilipes</i>	−118.224	37.551	3726	80	18.1813	1.89
USA	Windy Pass	<i>Dasiphora fruticosa</i>	−113.332	48.479	2241	77	84.9573	1.77
Venezuela	Piedras Blancas1	<i>Arenaria venezuelana</i>	−70.868	8.887	4210	35	57.8711	−2.83
Venezuela	Piedras Blancas2	<i>Arenaria venezuelana</i>	−70.867	8.885	4210	35	57.8711	0.77
Venezuela	Piedras Blancas3	<i>Arenaria venezuelana</i>	−70.871	8.893	4356	35	57.8711	−8.19

above. Negative regression coefficients indicate a negative effect of an increasing number of graminoid or forb plants on cushion benefactor flower density and vice versa, with higher values indicating steeper slopes and stronger effect sizes (see also Schöb *et al.* 2014b). The regression coefficients were then related to actual summer evapotranspiration. This relationship was tested by linear regression analysis followed by an ANOVA *F*-test. One site (Volcano Antisana high, Ecuador) showed an extreme value for the relationship between the graminoid effect on flower density and evapotranspiration, so we repeated this analysis with and without this site.

For the study at Qilian Shan, differences in cushion benefactor area, graminoid and forb covers, fruit set and fruit dry weight were analysed with one-way ANOVA with cushion benefactor type (high cover of graminoids, high cover of forbs and low beneficiary species cover) as independent variable. The number of unfertilized flowers, the number of fruits and total number of flowers were analysed using the same independent variable but with a generalized linear model using a Poisson distribution of error terms. Linear contrasts were used when a significant cushion benefactor class effect was observed.

All statistical analyses and plots of the intercontinental study were done with R (R Core Team 2013) using the packages *car* (Fox & Weisberg 2011), *effects* (Fox 2003) and *lme4* (Bates *et al.* 2014). Analyses on the Qilian Shan data were done using JMP software 10.0 (SAS Institute, Cary, NC, USA).

Results

In the intercontinental study, as the number of beneficiary plants increased, the flower density of cushion benefactors decreased (Fig. 1a, Table S1, Supporting information). This negative effect of beneficiary species on cushion benefactor reproduction was correlated with a negative effect of graminoids, whereas the abundance of shrubs, legumes and other forbs showed no significant relationship with cushion benefactor flower density (Fig. 1b, Table S2).

The strong negative relationship of graminoids on cushion benefactor reproduction, however, varied among sites

and was significantly correlated with actual summer evapotranspiration, as did the relationship of forbs and cushion benefactor reproduction (Table 2 and Fig. S1). Increasing actual summer evapotranspiration was associated with lower negative graminoid BFEs, and in some cases positive impacts of graminoids on cushion benefactor flower density.

At Qilian Shan, the three cushion benefactor classes did not differ in size ($P > 0.05$, data not shown), but as designed, there were striking differences in cover of graminoids and forbs. Mean relative covers of graminoids and forbs were $40.1 \pm 2.2\%$ and $4.8 \pm 0.9\%$, respectively, for the high graminoid class, vs. $3.1 \pm 0.4\%$ and $30.5 \pm 2.8\%$, respectively, for the high forb class. For the cushion benefactor class with low beneficiary species cover, the cover of graminoids was slightly lower than the cover of forbs ($0.6 \pm 0.1\%$ and $3.1 \pm 0.6\%$, respectively). There were highly significant differences in number of unfertilized flowers, number of fruits and total number of flowers among the three cushion benefactor classes (Table 3, Fig. 2). Unfertilized flowers were four times less abundant in the high graminoid cushion benefactor class than in the two other cushion benefactor classes, whereas cushion benefactors with high cover of forbs had four times more fruits than the two other cushion benefactor classes. Thus, the highest total number of flowers was in cushion benefactors with high cover of forbs (62.6 ± 5.1), the lowest in the cushion benefactors with high cover of graminoids (16.9 ± 3.1), while cushion benefactors with low cover of beneficiary species had intermediate values (43.8 ± 4.6 , Fig. 2). Cushion benefactors with forbs had significantly higher fruit set ($30.5 \pm 6.6\%$) than cushion benefactors with low cover of beneficiary species ($10.8 \pm 4.1\%$, $P = 0.0321$), with intermediate values for cushion benefactors with grasses ($16.1 \pm 5.1\%$). There were no significant differences in mean individual fruit weight across cushion benefactor types (mean fruit weight: 2.4 ± 0.1 mg).

Discussion

Consistent with our first prediction, we found both in the intercontinental study and at Qilian Shan a significant negative effect of graminoids on total flower density.

Table 2. Statistical results for the intercontinental study on the relationships between the effects of either graminoids or forbs on cushion benefactor flower density and actual summer evapotranspiration rate

Factor	d.f.	SS	MS	F	P	R ²
Graminoid effect						
Actual summer evapotranspiration	1	102	102	4.87	0.036	0.12
Residuals	27	566	21			
Graminoid effect (without site Volcano Antisana high)						
Actual summer evapotranspiration	1	139	139	9.77	0.004	0.25
Residuals	26	370	14			
Forb effect						
Actual summer evapotranspiration	1	136	136	12.25	0.002	0.28
Residuals	28	310	11			

Consistent with our third prediction, the negative effect of graminoids increased with decreasing actual summer evapotranspiration and, thus, with increasing drought stress. In the intercontinental study, there was no effect of legumes or forbs on the density of flowers produced by benefactor cushions. In contrast, and consistent with our second and fourth predictions, in the Qilian Shan Mountains there was a significant positive effect of forbs on flower density and fruit set of *T. caespitosum*. Together, our results show that the high context dependence of BFEs on alpine cushion benefactors found in previous BFE studies may partially be explained by the functional composition of the beneficiary communities and in particular the abundance of graminoids.

THE NEGATIVE EFFECT OF GRAMINOIDS AND ITS VARIATION WITH DROUGHT

The overall effect of beneficiary species on benefactor's flower production was negative in our intercontinental study, supporting results reported by Schöb *et al.* (2014a, b). But here, we demonstrate that this negative BFE was driven primarily by the negative effect of graminoids. This negative effect of graminoids on cushion benefactors was

Fig. 1. Relationship between cushion benefactor flower density and the density of beneficiary plants in total (a) and for each functional group separately (b). Displayed are predicted relationships (mean, 95% CIs for significant relationships only) based on linear mixed models with standardized number of cushion benefactor flowers per cm^2 as response variable and square root-transformed numbers of beneficiary plants per cm^2 as explanatory variables. $n = 1697$, sites (30) included as random factor. Stars give the level of significance of the relationships: *** $P < 0.0001$.

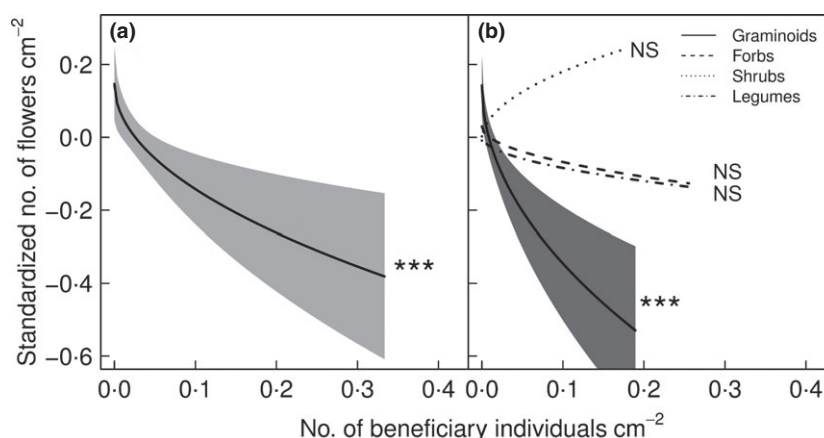
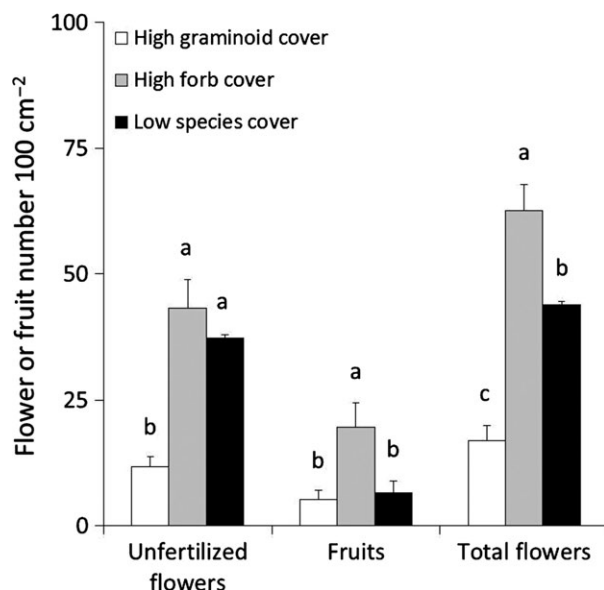


Table 3. Results of the GLM analysis on the effect of the cushion benefactor class treatment on the number of unfertilized flowers, number of fruits and total number of flowers at the Qilian Shan site (China)

Source of variation	d.f.	Unfertilized flowers		Fruits		Total flowers	
		χ^2	<i>P</i>	χ^2	<i>P</i>	χ^2	<i>P</i>
Benefactor cushion class	2	636.3	<0.0001	336.8	<0.0001	846.4	<0.0001

**Fig. 2.** Mean (± 1 SE, $n = 30$) number of unfertilized flowers, number of fruits and total number of flowers in the three cushion benefactor classes (white bars: cushion benefactors with high graminoid cover, grey bars: cushion benefactors with high forb cover and black bars: cushion benefactors with low beneficiary species cover) of *Thylacospermum caespitosum* at the Qilian Shan site. Letters above bars are the results of the linear contrasts for the cushion benefactor class effect in the GLM analysis ($P < 0.0001$ for all the three analyses).

also highly significant in the Qilian Shan study. Most of the species included in our graminoid functional groups were in the Poaceae in both the intercontinental and Qilian Shan studies. The high competitive ability of grasses compared to other functional groups has been demonstrated in several experiments (Davis, Wragge & Reich 1998; Maestre & Cortina 2004; Picon-Cochard, Coll & Balandier 2006; Maalouf *et al.* 2012; Noumi *et al.* 2015) and is likely due to their higher root investment and ability to take up soil resources as compared to other functional groups (Köchy & Wilson 2000; Michalet 2007; Gómez-Aparicio 2009; Gross *et al.* 2009). However, other studies have found both positive and negative effects of grasses on forbs, depending on the forb species, with both effects likely to balance each other at the community level (e.g. Greenlee & Callaway 1996; Michalet *et al.* 2015a).

Armas & Pugnaire (2005) directly assessed the BFE of grasses and revealed counterbalancing positive and negative effects of *Stipa tenacissima* on its shrub benefactor *Cistus clusii* in semi-arid Spain, resulting in net neutral

feedback effects of the grass on the shrub. However, in other studies where beneficiary communities were dominated by graminoids, negative BFEs were observed in general (Holzapfel & Mahall 1999; Michalet *et al.* 2011; Al Hayek *et al.* 2014, 2015). For example, Holzapfel & Mahall (1999) showed in the Mojave Desert (USA) that annuals (of which at least 60% were grasses) had simultaneously strong negative and weak positive effects on the water status, growth and reproductive output of their shrub benefactor, *Ambrosia dumosa*.

Schöb *et al.* (2014b) found that BFEs depended on beneficiary species composition, with diverse beneficiary communities of low phylogenetic diversity having most negative BFEs. They concluded that the negative species richness effect may result from the overall negative impact of a specific phylogenetic group of common beneficiary species, such as grasses. The significant negative effect of graminoids we report here supports their prediction and helps to explain the influence of the phylogenetic structure of the beneficiary communities on the direction and strength of BFEs.

In the intercontinental study, we found that the BFE of graminoids became more negative with decreasing actual summer evapotranspiration and thus that increasing drought stress correlated with an increase in the negative effect of the graminoids. This negative relationship between BFE and actual summer evapotranspiration also held for forbs, although the forbs' BFE was not significant (see Table S2) and, thus, of low ecological importance. These results are consistent with Schöb *et al.* (2014b) who reported that BFEs were more negative in arid than in mesic alpine climates. Schöb *et al.* (2014b) also found that the negative effect of beneficiary species increased with increasing facilitation, while Cavieres *et al.* (2014) found that facilitation increased with increasing stress. Thus, the cushion benefactor's effect became more positive with increasing stress, consistent with the SGH (Bertness & Callaway 1994), while the BFE of graminoids became more negative with increasing drought stress in our study. However, most authors who observed the occurrence of negative BFEs in facilitation studies argued that these effects were due to competition for water (McAuliffe 1984; Valiente-Banuet, Vite & Zavala-Hurtado 1991; Schöb *et al.* 2014c) and several experiments conducted in dry environments have shown that competition from grass species increases with decreasing water availability (Davis, Wragge & Reich 1998; Maestre & Cortina 2004), consistent with the resource supply/demand model of Taylor, Aarssen &

Loehle (1990) and the recent refinement of the SGH proposed by Michalet *et al.* (2014).

THE POSITIVE EFFECTS OF LEGUMES AND FORBS

Results of the Qilian Shan study suggest that the abundance of forbs had a positive effect on fruit set, whereas benefactor flower production was primarily negatively affected by graminoids. Multiple-species floral displays can facilitate pollination and fruit set by attracting a greater number and/or diversity of pollinators, although this effect is highly context dependent (Moeller 2004; Callaway 2007; Sargent & Ackerly 2008; Reid & Lortie 2012; Hegland 2014; Seifan *et al.* 2014). In particular, facilitative effects on pollination are conditional with the density and evenness of the floral mixture and may switch to competition with increasing density of floral resources (Ghazoul 2006; Hegland 2014; Seifan *et al.* 2014). This high context dependence of facilitative effects through shared pollinators may explain why we did not observe an overall significant positive effect of forbs in the intercontinental study. Additionally, the forb functional group is very likely too coarse and heterogeneous to be significant at large scales. Future studies may therefore separate insect- and wind-pollinated forb species into different functional groups of beneficiary species.

The absence of a forb effect in the intercontinental study as compared to the Qilian Shan study might also be due to the different methods. The dominant grass effect might have blurred a secondary forb effect in the intercontinental study because cushion benefactors with particular amount of forbs might have included very different abundances of grasses. Indirect interactions among beneficiary species can influence the species composition within cushions benefactors (Schöb, Armas & Pugnaire 2013) and therefore affect BFEs. The direct positive effect of cushion benefactors on grasses is likely to induce indirect competitive effects of grasses on forbs. For example, Michalet *et al.* (2015a) found that the dominant shrub *Dasiphora fruticosa* induced strong indirect competitive effects on several forb species through its direct facilitation of grasses (and see Michalet *et al.* 2015b for similar results in a *R. sphaerocarpa* community from semi-arid Spain). These indirect interactions are very likely to lead to different functional compositions in cushion benefactors, with some cushion benefactors facilitating mostly grasses and others mostly forbs. The abundance of legumes had also no significant effect on the flower density of cushion benefactors in the intercontinental study. One likely explanation is that the abundance of the legume functional group was very low at most sites, as was the case at Qilian Shan.

Conclusion

We found that the context dependence of BFEs on alpine cushion benefactors was highly correlated with a negative effect of graminoids. This negative effect may be due to the high root investment of grasses and thus to their ability to

compete for soil resources, in particular water. This negative effect increased with increasing water stress, consistent with the resource supply/demand model of Taylor, Aarssen & Loehle (1990). We found a positive BFE induced by forb beneficiaries on the cushion benefactor fruit set at Qilian Shan. This effect, potentially due to indirect facilitation through shared pollinators, was not detected in our intercontinental study. However, a more straightforward definition of the functional groups of forbs is needed to really assess the importance of indirect positive BFEs through shared pollinators. Future studies should also assess the contribution of indirect interactions among contrasting functional groups of beneficiary species to the BFE and their likely evolutionary consequences for the cushion benefactors.

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Data accessibility

Data for this paper are deposited in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.qn2p9> (Michalet *et al.* 2015c).

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Supporting Information

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

Fig. S1. Relationships between the graminoid and forb effects on cushion benefactor flower density and actual summer evapotranspiration.

Table S1. ANOVA table of the linear mixed model testing the relationship between the total number of individuals of beneficiary species and the number of flowers produced by cushion benefactor plants.

Table S2. ANOVA table of the linear mixed model testing the relationship between the number of individuals of each functional group of beneficiary species and the number of flowers produced by cushion benefactor plants.