

# Foundation species influence trait-based community assembly

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## Summary

- Here, we incorporate facilitation into trait-based community assembly theory by testing two mutually compatible facilitative mechanisms: changes in the environmental filter, causing either an increase in the range of trait values (i.e. a range expansion effect) and/or a shift in trait distributions (i.e. a range shift effect); and changes in trait spacing, suggesting an effect on niche differentiation.
- We analyzed the distribution of three functional traits – leaf dry matter content, specific leaf area and lateral spread – of plant communities dominated by a cushion-forming foundation species at four sites differing in elevation and aspect.
- We found support for environmental filtering and niche differentiation mechanisms by cushions, with filtering effects (in particular range shifts) increasing with environmental severity at higher elevation. The effect size of cushions on trait distribution was similar to that of environmental gradients caused by elevation and aspect. The consideration of intraspecific trait variability improved the detection of cushion effects on trait distributions.
- Our results highlight the importance of facilitation in the modification of taxonomic and functional diversity of ecological communities, and indicate that facilitation can occur through combined effects on environmental filtering and niche differentiation, with strong environmental context dependence of each mechanism.

## Introduction

Interactions between co-occurring organisms play a vital role in shaping communities. Dominant species, in particular, can have strong effects on subordinate species, thereby influencing community structure and diversity (Grime, 1998). In many ecosystems, a single dominant species acts as a foundation species by modulating ecosystem processes through specific characteristics that have a great impact on the local conditions experienced by other species and, consequently, modifying community structure and diversity to a considerable extent (Ellison *et al.*, 2005). In severe environments, foundation species often ameliorate environmental conditions, thereby facilitating other species and enhancing local diversity (Ellison *et al.*, 2005). The specific effects of foundation species on the local environment and their final effect in terms of local diversity have been widely addressed (Callaway, 2007). Nevertheless, community assembly mechanisms determining the nature and magnitude of facilitative effects on the composition of species and diversity of a community are not well understood.

One approach to the analysis of community assembly is through the assessment of functional trait values within a local community relative to a broader pool of species. This approach has led to a surge of community ecology research in recent years (Shipley *et al.*, 2006; Kraft *et al.*, 2008; Weiher *et al.*, 2011). Although facilitation has been considered in phylogenetically based community assembly

theory (Valiente-Banuet *et al.*, 2006; Sargent & Ackerly, 2008), it has remained conspicuously absent from trait-based community assembly tests so far. Such approaches seek to assess the environmental sorting of species under particular environmental conditions (Weiher & Keddy, 1999), in which traits quantify the responses of species to and their effects on local conditions, that is, the realized niche of the species (Violle & Jiang, 2009). Functional trait methods provide insight into the biotic and abiotic factors that structure plant communities (Kraft *et al.*, 2008). The incorporation of facilitation into trait-based models of community assembly provides the opportunity to explore the mechanisms by which the balance between positive and negative interactions drives community assembly and shapes the diversity of species within an established theoretical and analytical framework (McGill *et al.*, 2006).

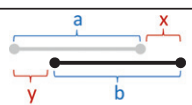
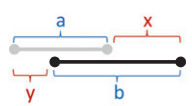
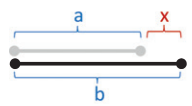
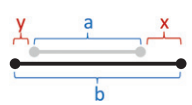
Facilitation may influence community assembly through both environmental filtering and niche differentiation processes. Environmental filtering is the process that determines the limits and range of trait distribution in a community, whereas niche differentiation, in terms of resource partitioning and coexistence, is defined as the process that affects trait distribution within the limits set by the environmental filter (see Supporting Information Fig. S1). A variety of trait metrics have been used to detect these patterns in plant communities (Kraft *et al.*, 2008; Jung *et al.*, 2010). Facilitative foundation species can influence environmental

filtering by shifting the limits of trait distribution relative to the unmodified habitat (Fig. 1). This can be a *range shift* effect, if facilitation changes both tails of the trait distribution in the same direction (i.e. expansion at one tail and contraction at the other), thereby resulting in an at least partially non-overlapping trait distribution between the microhabitat created by the foundation species and the control microhabitat. Furthermore, if the range of traits is expanding or contracting because of the presence of foundation species, facilitation is caused by a *range expansion* effect. However, as changes at the lower and upper tail of the trait distribution by foundation species may result in a partially non-overlapping distribution and a changed range of traits, facilitation can also be caused by combined range shift and range expansion effects. Therefore, range shift and range expansion effects of facilitation are not exclusive, but result in different patterns in the trait distribution and may have different effects on community assembly. For example, in arid and semiarid environments, species acting as nurse plants can reduce light availability whilst increasing water and nutrient availability (Holmgren *et al.*, 1997; Moro *et al.*, 1997). Consequently, neighbors with conservative functional strategies within such a community often benefit from the presence of nurse plants, whereas those with more ruderal strategies usually perform better in the absence of the nurse (Butterfield & Briggs, 2011), probably as a result of a tradeoff between drought and shade tolerance (Holmgren *et al.*, 1997). This effect of the nurse plant on the environment will certainly change the environmental filter and result in a range shift. However, it may also go along with a range expansion effect if the extent of the filter release as a result of improved resources is of a different magnitude than the filter

confinement caused by impoverished light conditions. In another example, spiny or toxic unpalatable species can create favorable environmental conditions for palatable species through protection against herbivory (Callaway *et al.*, 2000). As the novel environment neither positively nor negatively affects habitat conditions for unpalatable species, this facilitative effect creates, but does not eliminate, environmental conditions compared with the unmodified environment, resulting in a simple range expansion effect of the unpalatable plant.

Facilitative foundation species may also create unique habitats suited to particular trait combinations or improve the opportunity for niche differentiation and reduced competition (Lundholm, 2009) without altering the limits of the environmental filter. For example, mature forest trees can provide a wide range of microhabitats that enhance epiphyte diversity through the creation of a complex canopy structure not present in younger forests (McCune *et al.*, 2000). This may result in the creation of unique habitats, but may also enhance spatial niche differentiation of potentially competing species because of the higher availability of spatially differentiated but qualitatively similar habitats.

To test the potential effects of facilitation on trait-based community assembly via environmental filtering and niche differentiation mechanisms, we examined the distribution of three traits of herbaceous alpine species growing inside and outside cushion species. We also considered intraspecific trait variability, which has been shown to be important in trait-based community assembly (Jung *et al.*, 2010; Bolnick *et al.*, 2011). Cushion species modulate the local environment in ways that generally have strong

Facilitation mechanism	Trait distribution	Expansion/contraction	Range	Explanation
Range shift		$x > 0$ $y > 0$ $x = y$	$a = b$	Partially non-overlapping trait distribution of <b>equal range</b> due to <b>equal shifts</b> of the trait limits at both tails of the trait distribution
Range shift and Range expansion		$x > 0$ $y > 0$ $x \neq y$	$a \neq b$	Partially non-overlapping trait distribution of <b>unequal range</b> due to <b>unequal shifts</b> of the trait limits at the two tails of the trait distribution
Range expansion		$x > 0$ $y = 0$ $x \neq y$	$a \neq b$	Overlapping trait distribution of <b>unequal range</b> due to a <b>shift</b> of the trait limit at one tail of the trait distribution
Range expansion		$x > 0$ $y < 0$ $x \neq y$	$a \neq b$	Overlapping trait distribution of <b>unequal range</b> due to <b>opposite shifts</b> of the trait limits at the two tails of the trait distribution

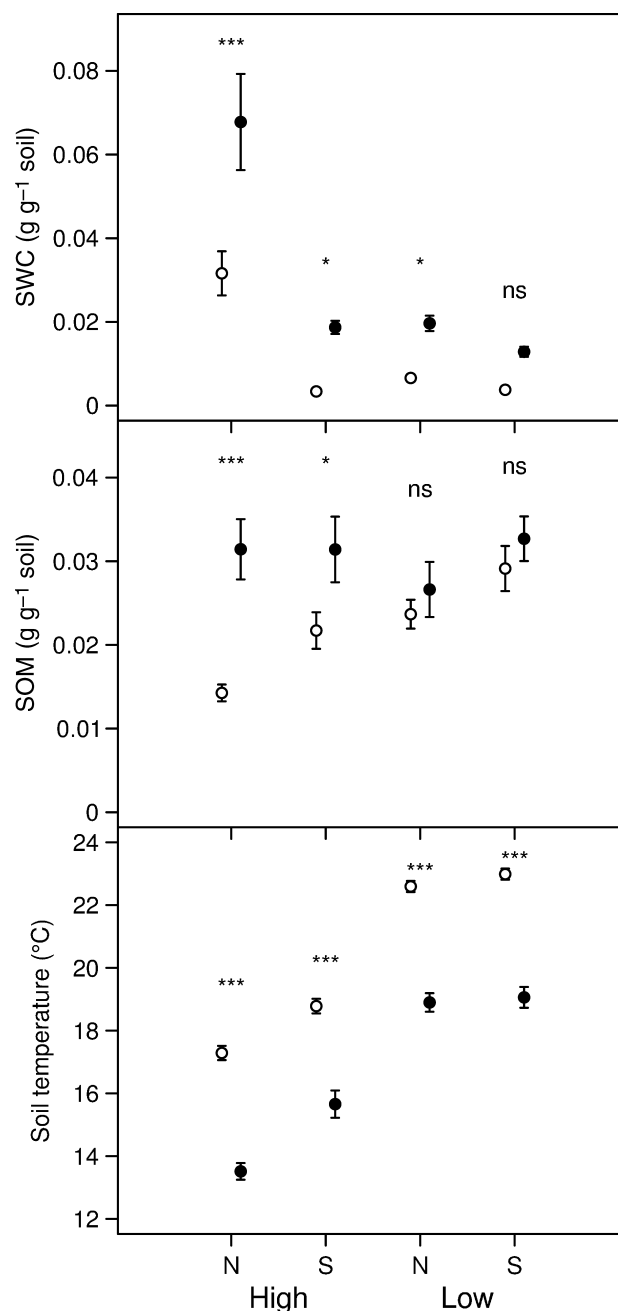
**Fig. 1** Potential changes in trait distributions in response to the presence of foundation species, the corresponding change in the trait metrics (expansion/contraction at the upper and lower tails of the trait distributions ( $x$ ,  $y$ ; in red) and trait ranges ( $a$ ,  $b$ ; in blue)) and their interpretation in terms of environmental filtering effects of facilitation. Gray line, trait distribution in the open microhabitat; black line, trait distribution in the cushion microhabitat;  $a$ , trait range in the open microhabitat;  $b$ , trait range in the cushion microhabitat;  $x$ , expansion/contraction effect of cushions at the upper tail of the trait distribution;  $y$ , expansion/contraction effect of cushions at the lower tail of the trait distribution. Range shift effects are characterized by unidirectional shifts of the trait limits at both tails of the trait distribution ( $x > 0$ ,  $y > 0$ ) in cushions relative to open areas, thereby resulting in a partly non-overlapping trait distribution between the two microhabitats (for simplicity, negative shifts in trait values are not shown). Range expansion effects are characterized by unequal shifts of the trait limits at the two tails of the trait distribution ( $x \neq y$ ), resulting in unequal trait ranges ( $a \neq b$ ) between cushion and open microhabitats. For simplicity, only range expansion effects expanding the trait range are shown ( $a < b$ ).

facilitative effects (Cavieres & Badano, 2009) and act as foundation species (Michalet *et al.*, 2011). We used functional traits of non-cushion species within the community as indicators of biotic responses to the local environment (Violle & Jiang, 2009) generated by cushion plants. Specifically, we tested the hypotheses that the trait composition of subordinate species within cushion plants would show partly non-overlapping ranges (i.e. range shift effect) and greater ranges (i.e. range expansion effect) of trait values as a result of changed environmental filtering in cushions, and an altered spacing of trait values in trait space relative to assemblages growing in unmodified habitats as a result of niche differentiation effects of cushions. We also assessed changes in trait patterns along an elevation gradient at two contrasting mountain aspects to determine the environmental context dependence of facilitative mechanisms. The outcome of biotic interactions is strongly dependent on environmental context (Brooker *et al.*, 2005), and may determine which mechanisms predominate in different communities. For example, even if the net effect of cushions on diversity remains relatively constant along environmental gradients, the underlying mechanisms may shift. The trait-based approach presented here can elucidate such changes, which might otherwise be obscured when simply considering net facilitative or competitive outcomes.

## Materials and Methods

### Study area

Our field sites were in the Sierra Nevada Mountains, Granada province, southeastern Spain. The study area consisted of four sites, two on the northern aspect (N) at elevations of 2720 m (37°05'N, 03°23'W) and 3240 m (37°03'N, 03°22'W), and two on the southern aspect (S) at 2575 m (37°00'N, 03°19'W) and 3110 m (37°02'N, 03°18'W). For simplicity, analyses were conducted with elevation and aspect as categorical variables with two levels (high vs low and north vs south, respectively). In Pradollano (2507 m), on the northern aspect of the Sierra Nevada range close to our low-elevation site, in the 15-yr observation period from 1975 until 1989, the mean annual rainfall was 690 mm and the mean annual temperature was 3.9°C (Rivas-Martinez & Rivas-Saenz, 1996–2009). Study sites were characterized by unproductive alpine gravel habitats on gentle slopes with known differences in soil temperature, water and organic matter content with elevation and aspect (Fig. 2). The rather uniform habitat was dominated by the cushion-forming species *Arenaria tetraquetra* ssp. *amabilis* (Bory) H. Lindb. fil. (Caryophyllaceae). We consider *A. tetraquetra* to be a foundation species because of its creation of locally stable and distinct environmental conditions relative to open areas surrounding cushions (Badano & Cavieres, 2006; Michalet *et al.*, 2011). Spatially discrete individual cushions were haphazardly distributed over the study area and surrounded by large open areas. Cushion cover ranged from 1.2% to 3.5%. Both cushions and open areas were colonized by small annual and perennial grasses and herbs. For plants colonizing cushions, this means growing within the very dense canopy ( $40.0 \pm 2.3$  terminal branches  $\text{cm}^{-2}$ ) formed by *A. tetraquetra* (C. Schöb, unpublished).



**Fig. 2** Soil properties in cushion and open plots at high and low elevation on the northern (N) and southern (S) aspects. Displayed are means  $\pm$  1SE for soil water content (SWC), soil organic matter content (SOM) and soil temperature. Closed symbols, cushions; open symbols, open plots. \*\*\*,  $P < 0.001$ ; \*\*,  $P < 0.01$ ; \*,  $P < 0.05$ ; ns, not significant: indicate results of linear model contrasts testing for differences among microhabitats at each site. At each site, for SWC and SOM,  $n = 20$ ; for soil temperature,  $n = 12$ .

### Sampling design

At three sites, we sampled 100 cushions and 100 paired open areas equal in size within an area of  $c. 500 \text{ m}^2$ , but, at the low site on the northern aspect, the total number of paired samples was 85. For samples of open areas, the border of cushions was simulated with wire and the wire was then randomly placed at  $c. 50 \text{ cm}$  distance from the cushion. Hereafter, we refer to cushion and open areas as

two different microhabitats (cushion vs open) and to each sample as a plot. In July 2010, the number of individuals of all vascular plant species was recorded in each of the 770 plots. We recorded the number of species and individuals per plot because the effects of foundation species on community assembly, in particular through the niche differentiation mechanism, were assumed to potentially influence the composition of species, but also the number of co-occurring individuals of the same and different species. Species richness, that is the number of species within a plot, varied between 0 and 9, and plant density, that is the number of individuals within a plot, varied between 0 and 85. As sampling was carried out on whole cushions, plot size varied with the size of the cushions and had a mean area of  $263 \pm 5 \text{ cm}^2$  (mean  $\pm$  SE). The total number of species found over all four sites was 42.

In 10 plots per site and microhabitat, we determined soil water and soil organic matter content by collecting soil samples underneath cushions and in the open area between the 20th and 29th of July. Samples were kept in sealed containers and fresh weight was determined immediately after sampling in the field. Soil water content ( $\text{g g}_{\text{soil}}^{-1}$ ) was measured gravimetrically as weight loss after drying at  $105^\circ\text{C}$  for 48 h. Soil organic matter content ( $\text{g g}_{\text{soil}}^{-1}$ ) of the same samples was determined by mass loss after ignition at  $400^\circ\text{C}$  for 20 h. In six plots per site and microhabitat, we recorded soil temperature 3 cm below ground using iButtons (Maxim Integrated Products, Sunnyvale, CA, USA). Temperature sensors were cross-calibrated in early July before field measurements. For subsequent analysis, we used the daily mean temperature measured every 10 min between the 20th and 28th of July 2010.

### Trait data

We assessed variation in three functional traits relevant to environmental variation and niche differentiation in alpine plant communities: leaf dry matter content (LDMC), measured as the ratio of leaf dry mass to fully rehydrated fresh mass; specific leaf area (SLA), measured as the ratio of fresh leaf area to leaf dry mass; and lateral spread, measured as the maximum diameter of the plant's canopy. LDMC and SLA are both generally associated with photosynthetic capacity, relative growth rate and leaf longevity (Cornelissen *et al.*, 2003), but are regulated by construction costs related to water and carbon economies, respectively. LDMC generally decreases with higher water availability and lower likelihood of physical damage (Cornelissen *et al.*, 2003), but exhibits no response to temperature variation (Albert *et al.*, 2010). By contrast, SLA increases dramatically in response to increasing temperatures and light availability across a broad range of species (Körner, 2003; Poorter *et al.*, 2009), but may decrease intraspecifically in response to light, as has been shown for evergreen plants (Lusk *et al.*, 2008). Thus, although LDMC and SLA are associated with similar biological processes, they may vary independently in response to different environmental drivers which are known to be influenced by cushion plants (e.g. water availability, temperature; Cavieres *et al.*, 2006). Lateral spread tends to be correlated with total aboveground biomass and foraging strategy, and may be dependent on both resource availability and competition intensity

(Navas & Moreau-Richard, 2005). Lateral spread also tends to be negatively correlated with height in herbaceous plant communities, such as in our focal system, and may be associated with temperature regulation (Körner, 2003). We assumed that changes in the lateral spread of plants growing within the dense canopy of cushions relative to the open area could, in particular, reflect competitive interactions between beneficiary plants and the nurse plant, but also among beneficiary plants. All three traits are therefore probably responding to environmental gradients (in particular LDMC and SLA) and resource partitioning (in particular lateral spread).

We measured plant functional traits between early July and early August, the period of peak biomass. At least five well-grown individuals of each vascular plant species were selected for trait measurements in every site and microhabitat in which the species occurred. In sites in which a species was too rare to accurately estimate functional trait values, the species was omitted from analyses. These cases accounted for  $< 1\%$  of the 7424 recorded individuals. For the determination of LDMC ( $\text{g kg}^{-1}$ ) and SLA ( $\text{m}^2 \text{ kg}^{-1}$ ), we followed Cornelissen *et al.* (2003) and selected one mature and healthy leaf per individual and fully rehydrated it before determining the leaf area and fresh weight. Plant lateral spread (cm) was determined as the maximum canopy diameter of an individual. For subsequent analyses, we averaged the trait values for each species in each microhabitat at each site (i.e. population mean traits), thereby taking into account intraspecific variability caused by aspect, elevation and microhabitat type. To reveal the impact of intraspecific variability relative to species turnover on changes in the observed trait distribution, we further used the mean traits of species by averaging trait values for each species over all microhabitats and sites.

### Data analysis

**Soil conditions, species richness and plant density** We tested for differences in soil water content, soil organic matter content and soil temperature between elevation, aspect and microhabitat type using linear models and, to test for differences between microhabitats per site, we used orthogonal contrasts. Soil water and soil organic matter content were log-transformed to meet normality assumptions.

Differences in species richness and plant density between microhabitats for each site separately were tested with generalized linear models with a Poisson error structure and a log-link function. Tests among sites, that is the effects of elevation and aspect on species richness and plant density, were omitted as a result of unequal plot sizes (i.e. different sizes of cushions).

**Functional trait metrics** For each functional trait, we calculated four metrics in cushion and open plots at all sites. We used the two limits (lower and upper) of trait distribution values, as well as the range of trait values within each plot, to detect environmental filtering, and trait spacing (measured as the coefficient of variation in the distance between two successive neighboring species in trait space) to detect niche differentiation (Fig. S1; Kraft *et al.*, 2008; Kraft & Ackerly, 2010; Jung *et al.*, 2010). Differences in trait limits between cushion and open microhabitats were assumed to



indicate range shift effects (if both limits changed in the same direction) and/or range expansion effects (if one limit changed towards higher and the other towards lower trait values, or if changes at the lower and upper limits were of unequal extent) of the environmental filter (Fig. 1). Range shift and range expansion effects on trait distributions are therefore mutually compatible effects of foundation species (Fig. 1). The change in trait limits in cushions relative to paired open plots, that is the expansion/contraction effect of cushions at the two tails of the trait distribution, was quantified as the difference between the lower limits of paired open and cushion plots (i.e. the expansion/contraction at the lower tail of the trait distribution) and the difference between the higher limits of paired cushion and open plots (i.e. the expansion/contraction at the upper tail of the trait distribution). For the calculation of expansion/contraction effects of cushions at the two tails of the trait distribution, all paired samples with plots with no plants (except the cushion) were excluded, resulting in 309 paired samples of cushion and open plots. Trait range was calculated for each plot ( $n = 679$ , all plots with no plants except the cushion were excluded) as the difference between the lower and upper limits of the trait values within a plot. Expansion/contraction effects of cushions at the tails of the trait distribution were assessed with  $t$ -tests. The relationship of expansion/contraction effects of cushions with elevation and aspect were tested with analysis of variance (ANOVA). The relationship between trait range and elevation, aspect, and microhabitat type was tested with ANOVA using log-transformed values of trait range in order to achieve normality.

Trait spacing was quantified as the coefficient of variation of differences between successive trait values of neighbors within a plot (CV\_NND). Low CV\_NND values indicate even spacing of traits among co-occurring species, whereas high values indicate clumping of species in trait space. CV\_NND is not affected by changes in either trait limits or trait range, because it is calculated using relative distances between traits (Jung *et al.*, 2010). Trait spacing is assumed to indicate micro-scale environmental heterogeneity and resource partitioning, and was used to assess niche differentiation effects of cushions. For CV\_NND calculation, all plots with less than three species (except the cushion) were excluded, resulting in 389 plots included in the analysis. The dependence of CV\_NND on elevation, aspect and microhabitat type was tested with ANOVA, and differences between microhabitats per site were revealed with orthogonal contrasts.

The effects of intraspecific trait variability on the observed trait metrics were tested with repeated-measures ANOVA, including trait metrics based on population and species mean traits (de Bello *et al.*, 2011). Elevation, aspect and microhabitat type (for trait range and CV\_NND) are fixed factors, whereas trait metrics based on population mean traits (i.e. with intraspecific variability) and those based on species mean traits (i.e. without intraspecific variability) represent repeated measures. Consequently, intraspecific trait variability and its interactions with the fixed factors are tested as within factors in the repeated-measures ANOVA.

All calculations of trait metrics and statistical analyses were performed with R software version 2.14.0 (R Development Core Team, 2011). The R-code for calculation of the trait metrics and

the data files, including species names, abundances and corresponding values for all traits at all sites and microhabitats, are provided as Supporting Information (Notes S1).

## Results

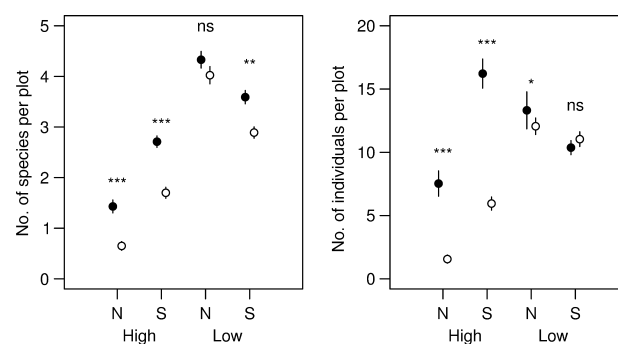
### Soil properties, species richness and plant density

Cushion microhabitats had, on average, higher soil water content than open areas ( $0.030$  vs  $0.011$  g g<sub>soil</sub><sup>-1</sup>), higher soil organic matter content ( $0.031$  vs  $0.022$  g g<sub>soil</sub><sup>-1</sup>) and lower soil temperature ( $16.8^{\circ}\text{C}$  vs  $20.4^{\circ}\text{C}$ ), with similar trends at all sites (Fig. 2). Differences in soil properties were particularly high at high-N and particularly low at low-S sites. On the latter site, we found no significant difference in soil water and soil organic matter content among microhabitats.

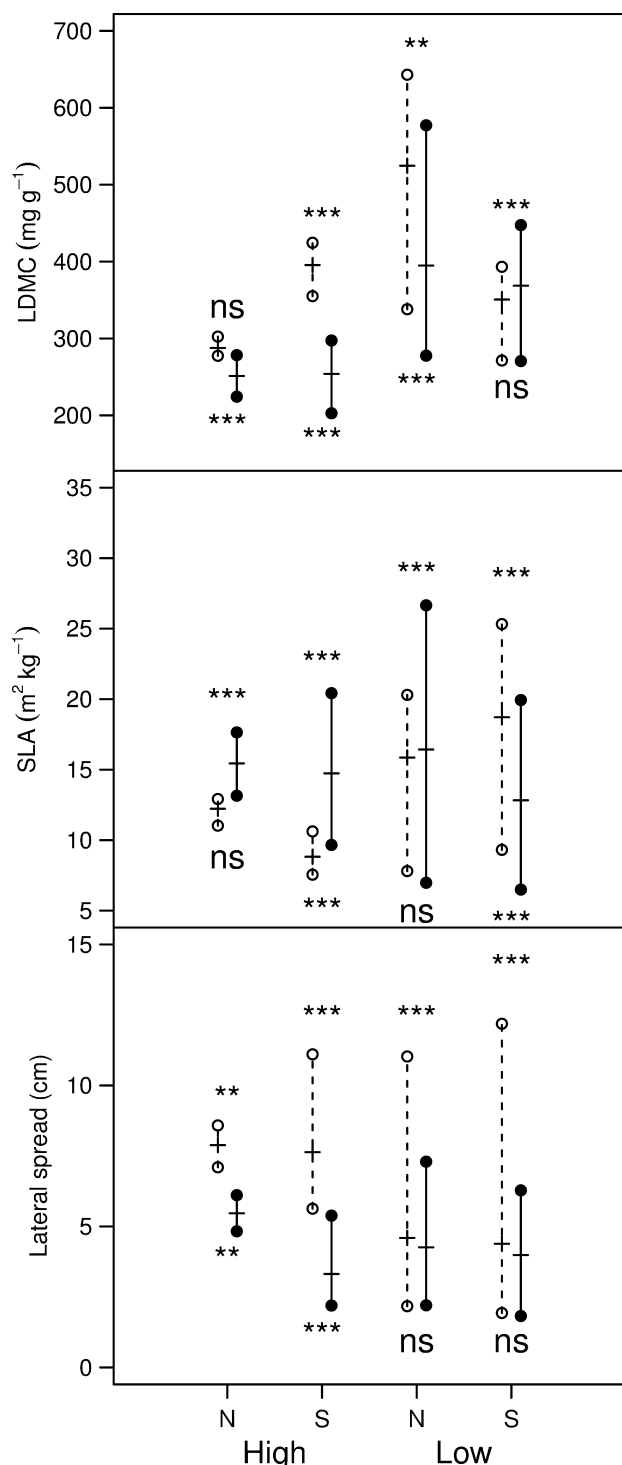
Cushions supported 30% more species than open plots and 58% more individuals on average, with cushion effects on species richness and plant density being significantly higher at high relative to low elevation (Fig. 3). There were no significant differences between microhabitats for species richness at the low-N site and for plant density at the low-S site. At low elevation, 20 (51%) species were more abundant in cushions, 14 (36%) were more abundant in the open and one species (3%) was equally abundant in cushion and open microhabitats. At high elevation, 18 (75%) species were more abundant when growing in cushions, three (12.5%) species were more abundant in the open and another three (12.5%) species were equally abundant in cushion and open microhabitats.

### Trait metrics

**Trait limits and trait range** Shifts in the range of traits caused by cushions (i.e. unidirectional changes in lower and upper trait limits in cushions relative to open plots) were observed for LDMC at all sites, except low-S, for SLA at the two sites on the S aspect and for lateral spread at the two high-elevation sites (Fig. 4). Trait range



**Fig. 3** Species richness and plant density in cushion and open plots at high and low elevation on the northern (N) and southern (S) aspects. Species richness and plant density are displayed as the mean ( $\pm$  1 SE) number of species and individuals per plot, respectively. Closed symbols, cushions; open symbols, open plots. \*\*\*,  $P < 0.001$ ; \*\*,  $P < 0.01$ ; \*,  $P < 0.05$ ; ns, not significant: indicate results of generalized linear models with Poisson error structure testing for significant differences in species richness or plant density between microhabitats at each site. For all sites,  $n = 200$ , except N-low, where  $n = 170$ .



was wider in cushions than in open microhabitats for LDMC at all sites, except low-N, and for SLA at all sites, except low-S (Fig. 4, Table S1). For lateral spread, trait range was significantly narrower at the two low-elevation sites.

The effect of elevation on expansion/contraction effects of cushions at the tails of the trait distributions was significant (except for the upper tail of lateral spread; Table 1), being more pronounced at high-elevation sites (Fig. 4). Similarly, there was a significant interaction effect between elevation and microhabitat

**Fig. 4** Trait limits and trait ranges of leaf dry matter content (LDMC), specific leaf area (SLA) and lateral spread in cushion and open microhabitats at high- and low-elevation sites on the northern (N) and southern (S) aspects. Displayed are trait distributions based on population mean trait values, with the mean upper and lower limits displayed as dots (open circles, open; closed circles, cushions) and community-weighted mean trait values as a cross. For high-N,  $n = 38$  pairs of samples; for high-S,  $n = 84$ ; for low-N,  $n = 87$ ; for low-S,  $n = 100$ . \*\*\*,  $P < 0.001$ ; \*\*,  $P < 0.01$ ; ns, not significant: indicate results of  $t$ -tests testing significant differences of expansions or contractions by cushions at the lower and upper tails of trait distributions from zero. Statistical tests of changes in expansions and contractions at the tails of the trait distributions by cushions with elevation and aspect are shown in Table 1. Statistical analyses relating trait ranges to elevation, aspect and microhabitat type are shown in Table 2.

type for the change in range of all traits, with the larger changes at high-elevation sites (Fig. 4, Table 2). In addition, expansion/contraction effects of cushions at the tails of the distributions, as well as changes in trait range, were rather constant among aspect (with the exceptions of LDMC range and the upper limits of SLA and lateral spread). Nevertheless, at the low-S site, both expansion/contraction effects and changes in trait range by cushions were different from those at the other sites for LDMC and SLA (Fig. 4), as shown by significant interaction terms between elevation and aspect for expansion/contraction at the tails of the trait distributions (Table 1), and between elevation, aspect and microhabitat type for trait range (Table 2).

Repeated-measures ANOVAs, including trait metrics based on population and species mean traits, revealed significant effects of intraspecific trait variability on expansion/contraction effects and trait range for all traits (Table S2). Intraspecific trait variability was particularly important for expansion/contraction effects of cushions at the lower and upper tails of the distributions (significance of the within-factor intraspecific trait variability:  $P < 0.001$  for all three traits). Expansions/contractions at the two tails of the distributions of all traits (except the lower tail of SLA at the low-N site and the upper tail of SLA at the low-S site) were larger when considering intraspecific trait variability relative to those based on species mean traits (Fig. 4 vs Fig. S2). Changes in the range of trait values caused by cushions were significantly larger when considering intraspecific trait variability for SLA and lateral spread ( $P < 0.001$ ), whereas changes in LDMC range caused by cushions were not significantly different based on species relative to population mean traits ( $P = 0.07$ ).

**Trait spacing** We recorded more even spacing of traits among neighbors in cushions relative to open areas for LDMC at the low-S site and for SLA at high elevation (Fig. 5), whereas traits were more clumped for LDMC at the high-N site and for SLA at low elevation. Cushions had no significant effects on trait spacing of lateral spread.

The effects of cushions on spacing of LDMC changed significantly with aspect (from more evenly spaced traits in cushions relative to open microhabitats in S to more clumped spacing in cushions than open plots in N), and with 'elevation  $\times$  aspect' (Table 3). In addition, cushion effects on spacing of SLA changed particularly with elevation and were more pronounced in N relative to S sites (Table 3, Fig. 5).

**Table 1** ANOVA tables of the relationships of expansion/contraction effects of cushions at the lower and upper tails of the distributions of leaf dry matter content (LDMC), specific leaf area (SLA) and lateral spread with elevation and aspect

		Lower tail			Upper tail		
	df	SS	F	P	SS	F	P
LDMC							
Aspect	1	13 196	1.5	0.21	13 769	1.2	0.28
Elevation	1	624 046	73.2	< 0.001	658 381	56.4	< 0.001
Aspect × elevation	1	447 889	52.5	< 0.001	1 035 553	88.7	< 0.001
Residuals	305	2 601 245			3 560 863		
SLA							
Aspect	1	11.9	0.4	0.51	1278	23.5	< 0.001
Elevation	1	1134	42.5	< 0.001	5733	105.4	< 0.001
Aspect × elevation	1	124	4.7	0.032	4737	87.1	< 0.001
Residuals	305	8132		16 593			
Lateral spread							
Aspect	1	31.1	3.7	0.057	396	4.5	0.035
Elevation	1	539	63.4	< 0.001	47.6	0.5	0.46
Aspect × elevation	1	1.21	0.1	0.71	10.2	0.1	0.73
Residuals	305	2593			27 046		

For each trait,  $n = 309$ . SS, Sums of Squares. Values in bold are statistically significant at  $P < 0.05$ ; values in italic are marginally significant at  $P < 0.1$ .

Intraspecific trait variability contributed significantly to the observed changes in CV\_NND in cushions relative to open areas by revealing a more even spacing of SLA at high sites and a more clumped spacing of SLA at low sites (Fig. 5 vs Fig. S3).

## Discussion

Our data show that abiotic environmental conditions (elevation and aspect) and the presence of cushions affected trait distributions through both environmental filtering and niche differentiation. Cushion effects on environmental filtering, as well as their effects on soil properties and their positive effects on species richness and plant density, were stronger at high-elevation sites. Elevation and aspect had significant and varied effects on several components of trait distributions (Fig. 4). Thus, the overall effect on trait distributions of a 500 m difference in elevation and contrasting aspects was similar to the effect of cushions, resulting in similar impacts on species richness and plant density.

## Environmental filtering mechanisms

Cushion plants strongly influenced community assembly through environmental filtering mechanisms, which is particularly notable given the small spatial scale ( $< 1$  m) over which the paired samples were collected. The effects of cushions on the environmental filter were twofold: a shift and an expansion effect. For example, LDMC at the low site in the northern aspect showed a simple range shift effect, indicating a shift of the environmental filter, whereas, at the low site in the southern aspect and at the high site in the northern aspect, we observed a simple range expansion effect, indicating a relaxation of the environmental filter. However, at the high site in the southern aspect, we found a combined range shift and range expansion effect. A range shift effect goes along with the creation of new opportunities for some species to occur locally, whilst reducing

**Table 2** ANOVA tables of the relationships of the ranges of leaf dry matter content (LDMC), specific leaf area (SLA) and lateral spread with elevation, aspect and microhabitat type

Factor	df	SS	MS	F	P
<b>LDMC</b>					
Elevation	1	812	812	297.0	<b>&lt; 0.001</b>
Aspect	1	4.7	4.7	1.7	0.19
Microhabitat	1	78.4	78.4	28.7	<b>&lt; 0.001</b>
Elevation × aspect	1	269	269	98.4	<b>&lt; 0.001</b>
Elevation × microhabitat	1	24.6	24.6	9.0	<b>0.003</b>
Aspect × microhabitat	1	15.1	15.1	5.5	<b>0.019</b>
Elevation × aspect × microhabitat	1	1.2	1.2	0.4	0.52
Residuals		671	1834	2.7	
<b>SLA</b>					
Elevation	1	274	274	392.7	<b>&lt; 0.001</b>
Aspect	1	9.8	9.8	14.1	<b>&lt; 0.001</b>
Microhabitat	1	41	41	58.8	<b>&lt; 0.001</b>
Elevation × aspect	1	35.8	35.8	51.3	<b>&lt; 0.001</b>
Elevation × microhabitat	1	25.6	25.6	36.7	<b>&lt; 0.001</b>
Aspect × microhabitat	1	0.00	0.03	0.05	0.83
Elevation × aspect × microhabitat	1	13.6	13.6	19.5	<b>&lt; 0.001</b>
Residuals		671	468	0.7	
<b>Lateral spread</b>					
Elevation	1	170	170	272.4	<b>&lt; 0.001</b>
Aspect	1	5.3	5.3	8.6	<b>0.004</b>
Microhabitat	1	1.6	1.6	2.5	0.11
Elevation × aspect	1	15.3	15.3	24.5	<b>&lt; 0.001</b>
Elevation × microhabitat	1	16.2	16.2	25.9	<b>&lt; 0.001</b>
Aspect × microhabitat	1	0.6	0.6	0.9	0.34
Elevation × aspect × microhabitat	1	1.4	1.4	2.2	0.14
Residuals		671	418	0.6	

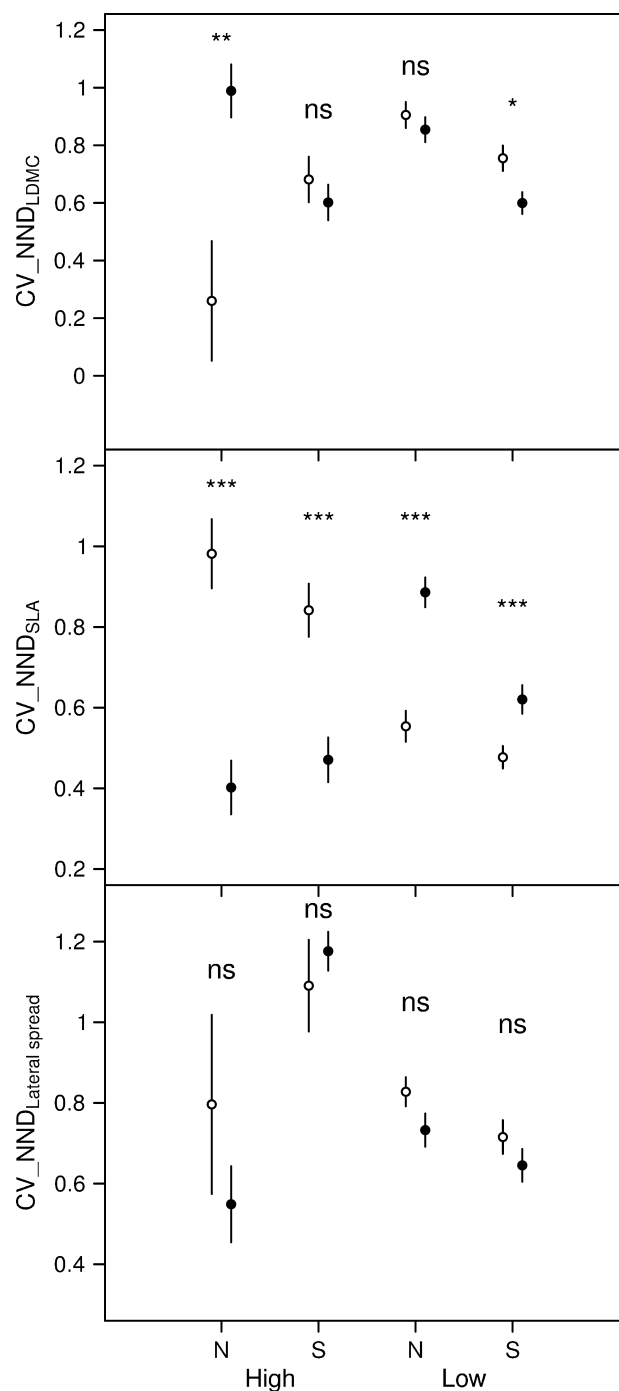
For each trait,  $n = 679$ . SS, Sums of Squares; MS, Mean Squares. Values in bold are statistically significant at  $P < 0.05$ .

**Table 3** ANOVA tables of the relationships of the coefficient of variation of differences between successive trait values of neighbors within a plot (CV\_NND) of leaf dry matter content (LDMC), specific leaf area (SLA) and lateral spread with elevation, aspect and microhabitat type

Factor	df	SS	MS	F	P
<b>LDMC</b>					
Elevation	1	0.84	0.84	5.8	<b>0.017</b>
Aspect	1	4.17	4.17	28.5	<b>&lt; 0.001</b>
Microhabitat	1	0.48	0.48	3.3	<i>0.071</i>
Elevation × aspect	1	0.03	0.03	0.2	0.64
Elevation × microhabitat	1	0.28	0.29	1.9	0.16
Aspect × microhabitat	1	0.65	0.65	4.4	<b>0.036</b>
Elevation × aspect × microhabitat	1	0.95	0.95	6.5	<b>0.011</b>
Residuals	381	55.8	0.15		
<b>SLA</b>					
Elevation	1	0.79	0.79	7.5	<b>0.006</b>
Aspect	1	1.55	1.55	14.8	<b>&lt; 0.001</b>
Microhabitat	1	1.24	1.24	11.8	<b>&lt; 0.001</b>
Elevation × aspect	1	0.77	0.77	7.4	<b>0.007</b>
Elevation × microhabitat	1	5.55	5.55	52.9	<b>&lt; 0.001</b>
Aspect × microhabitat	1	0.43	0.43	4.1	<b>0.043</b>
Elevation × aspect × microhabitat	1	0.30	0.30	2.9	<i>0.090</i>
Residuals	381	39.9	0.11		
<b>Lateral spread</b>					
Elevation	1	7.43	7.43	58.3	<b>&lt; 0.001</b>
Aspect	1	0.02	0.02	0.2	0.68
Microhabitat	1	0.44	0.44	3.5	<i>0.064</i>
Elevation × aspect	1	5.57	5.57	43.7	<b>&lt; 0.001</b>
Elevation × microhabitat	1	0.18	0.18	1.4	0.23
Aspect × microhabitat	1	0.07	0.07	0.5	0.47
Elevation × aspect × microhabitat	1	0.18	0.18	1.4	0.23
Residuals	381	48.5	0.13		

For each trait,  $n = 389$ . SS, Sums of Squares; MS, Mean Squares. Values in bold are statistically significant at  $P < 0.05$ ; values in italic are marginally significant at  $P < 0.1$ .

the habitat suitability for other species. The environmental filter shift caused by cushions was greater at high elevation than at low elevation, but showed no obvious pattern between aspects. Cushions are known to positively affect soil resources, such as water availability, thereby creating favorable environmental conditions for plant growth (Cavieres *et al.*, 2006). This is in line with our results for soil water content and the range expansion at the lower tail of LDMC by cushions. However, they also reduced soil temperature (Cavieres *et al.*, 2006), which may have negatively affected the performance of some species with higher temperature optima (e.g. species with high SLA at low elevation on the southern aspect). Such relationships between trait metrics and environmental conditions suggest how cushion effects on abiotic conditions may affect community assembly mechanisms. However, as traits reflect plant responses to both abiotic and biotic variation (Violle & Jiang, 2009), a shift towards smaller lateral spread in cushions relative to open microhabitats at high elevations may, for example, indicate increased competition intensity between beneficiary species and nurses (Tielbörger & Kadmon, 2000) or among beneficiary plants because of the higher density of individuals



**Fig. 5** Trait spacing (measured through the coefficient of variation of the distance of two successive trait values of neighboring plants (CV\_NND)) of leaf dry matter content (LDMC), specific leaf area (SLA) and lateral spread in cushion (closed circles) and open (open circles) microhabitats at high- and low-elevation sites on the northern (N) and southern (S) aspects. Displayed are means  $\pm$  1SE,  $n = 389$ . Statistical tests of changes in CV\_NND with elevation, aspect and microhabitat are shown in Table 3. \*\*\*,  $P < 0.001$ ; \*\*,  $P < 0.01$ ; \*,  $P < 0.05$ ; ns, not significant: indicate results of linear model contrasts testing for differences among microhabitats at each site.

(Soliveres *et al.*, 2011). This process could potentially reduce suitable habitats for poor competitors. Consequently, positive effects of nurse plants may often coexist with negative effects. Negative effects of nurses on beneficiary species can include



reduced light availability (Holmgren *et al.*, 1997), secretion of allelopathic substances (Callaway *et al.*, 1991) or inhibition of seedling emergence as a result of litter accumulation (Moro *et al.*, 1997). All the above-mentioned studies support our range shift effect of facilitation, which results in positive effects for some species and negative effects for others.

Beyond range shifts, the general expansion of SLA and LDMC range in cushions indicates less restrictive environmental filtering relative to open areas, and provides support for the range expansion effect of cushions. The less restrictive environmental filtering is likely to be primarily a function of improved soil resources and an increased variety of micro-environmental conditions (Fig. 2), which result in enhanced, and spatially more variable, resource availability relative to the open. Furthermore, the wider SLA range in cushions may reflect an amplified range of potential functional strategies, for example, as a result of improved and more stable growth conditions through time in cushions (Cavieres *et al.*, 2006), extending the growing season length relative to the open. Published examples which can be attributed to a range expansion effect of facilitation exist, in particular, with regard to indirect facilitative effects, such as protection against herbivory (Callaway *et al.*, 2000; Schöb *et al.*, 2010), attraction of pollinators (Poole & Rathcke, 1979) or colonization by mycorrhizae (Casanova-Katny *et al.*, 2011; Martínez-García & Pugnaire, 2011). In addition, as the two mutually compatible effects on environmental filtering, that is range shift and range expansion, can occur individually or combined, an expansion of the environmental filter can also result in a shift, which means that one mechanism may change over time into another. For example, a thorny shrub may facilitate a tree which ultimately shades it out, so that herbivore protection can change from a range expansion to a range shift effect, as reflected in phylogenetic analyses of some plant communities (Valiente-Banuet & Verdú, 2008).

### Niche differentiation mechanisms

The effects of cushion plants on trait spacing also provide support for our second proposed facilitative mechanism including niche differentiation effects. Trait spacing of SLA responded most strongly to differences between cushion and open microhabitats, with successive neighbor trait distances being more evenly spaced in cushions at high elevation and in the open at low elevation relative to the other microhabitat. One possible mechanism of this change in trait spacing may be competition between subordinate species within the more productive environments associated with open areas at low elevations and cushions at high elevations. Alternatively, even spacing of traits may be a result of partitioning of micro-scale environmental heterogeneity, which is compatible with the observation that species occupy varied microhabitats within cushions (e.g. plants that root in the cushion canopy, in the soil, live on the edge vs the middle of the cushion). This micro-heterogeneity may not be as large in cushions at low elevation. Environmental heterogeneity in space and time is known to promote niche differentiation (Lundholm, 2009), and is a likely cause of facilitative effects via niche differentiation mechanisms. However, the relatively large number of plots with less than three species (i.e. 381 of 770 plots) also indicates that niche differen-

tiation may not have been very relevant in our study system overall. Studies with the nurse shrub *Retama sphaerocarpa* (L.) Boiss. in semiarid environments, for example, showed small-scale spatial heterogeneity of nutrient and water availability within the area of influence of the nurse (Moro *et al.*, 1997). Heterogeneity of soil resources in space and time provided by foundation species could be an important driver of resource partitioning (Araya *et al.*, 2011). Therefore, enhanced niche differentiation among co-occurring subordinate species, in response to increased small-scale environmental heterogeneity caused by the foundation species, is a valuable potential mechanism of facilitation.

### Environmental context dependence of facilitation mechanisms

The positive effect of cushion plants on habitat conditions for other species via environmental filtering and niche differentiation mechanisms increased species richness and plant density in cushions more strongly at high elevation than at low elevation, even though the cushion effect on diversity was positive overall. If more restrictive environmental filtering (e.g. reduced trait range) is indeed an indicator of increased environmental severity, our data support models predicting increased facilitation under more stressful conditions (Bertness & Callaway, 1994; Brooker & Callaghan, 1998) and provide the underlying facilitative mechanisms. The improved soil resource conditions in cushions, for example, soil water and soil organic matter contents, which are more pronounced at high elevation, could be part of the cushion effect on environmental filtering, that is, in particular, the range shift but also the range expansion effects. They led to more favorable growth conditions in cushions and could explain an increasing effect size of facilitation with increasing stress at high elevation in our study system. These results also indicate that the importance of the different mechanisms of facilitation may change with environmental conditions in space and time, and that a trait-based community assembly approach can reveal such changes which could be obscured when studying only the outcome of facilitation (e.g. species composition or plant fitness). This is in line with previous investigations comparing trait-based with nomenclature-based studies of community assembly, which have shown that traits are generally more sensitive than species to deterministic niche-based processes, such as environmental filtering and niche differentiation (Kraft & Ackerly, 2010; Helsen *et al.*, 2012).

### The importance of intraspecific variability

The significant contribution of intraspecific variability to the observed effects of cushions on trait distributions highlights its importance for trait-based community assembly studies, as suggested by Jung *et al.* (2010). Although effects of cushions were qualitatively similar with or without the inclusion of intraspecific trait variability, the consideration of intraspecific trait variability significantly improved the detection and amplified the observed cushion effects on trait distributions relative to the analyses based on species mean traits. Facilitation of foundation species may therefore increase the intraspecific variability of beneficiary species

by either local genetic adaptation or phenotypic plasticity. This may imply an expansion of the environmental niche of the beneficiary species, as suggested in theoretical models of facilitation (Bruno *et al.*, 2003; Travis *et al.*, 2005). Finally, higher intraspecific variability may contribute to the higher species richness and plant density in cushions, because it has been shown to promote species coexistence (Jung *et al.*, 2010).

### Facilitation and niche theory

On a more theoretical level, the integration of facilitation into niche theory has, until now, focused primarily on the expansion of niche space by the facilitator (Callaway, 2007). As functional traits reflect the realized response of a species to the local abiotic and biotic conditions (McGill *et al.*, 2006; Violle & Jiang, 2009), they can actually be used as a quantitative surrogate of the realized niche of the species (Violle & Jiang, 2009; Weiher *et al.*, 2011). Based on this assumption, our study reveals that the expansion of niche space by the range expansion effect on environmental filtering is just one of several potential mechanisms by which facilitation can affect community assembly. In our system, the effects of foundation species on environmental filtering seemed to be particularly important, but here a shift of the available niche space, as indicated by the range shift effect, may be at least as important as the generally acknowledged niche expansion effect. In addition, an improved level of niche differentiation between co-occurring species within the available niche space could play a far under-appreciated role in facilitation. In this respect, our study can contribute substantially to a successful inclusion of facilitation into niche theory by taking different mechanisms of facilitation explicitly into account.

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## Supporting Information

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

**Fig. S1** Trait metrics and their interpretation for trait-based community assembly.

**Fig. S2** Trait limits and trait range of leaf dry matter content (LDMC), specific leaf area (SLA) and lateral spread using species mean trait values.

**Fig. S3** Trait spacing of leaf dry matter content (LDMC), specific leaf area (SLA) and lateral spread using species mean trait values.

**Table S1** Expansion/contraction at the lower and upper tails of the trait distributions and trait range effects of cushions

**Table S2** Repeated-measures ANOVAs to test the significance of intraspecific trait variability for each trait metric of each trait

**Notes S1** R-code for the calculation of the four trait metrics of all traits, together with the corresponding trait data files and abundance data for each species in each plot.

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