

Cushions of *Thylacospermum caespitosum* (Caryophyllaceae) do not facilitate other plants under extreme altitude and dry conditions in the north-west Himalayas

Francesco de Bello*, Jiří Doležal, Miroslav Dvorský, Zuzana Chlumská, Klára Řeháková, Jitka Klimešová and Leoš Klimeš

Institute of Botany, Czech Academy of Sciences, Dukelská 135, CZ-379 82 Třeboň, Czech Republic

*For correspondence. E-mail fradebello@ctfc.es

Received: 25 February 2011 Returned for revision: 19 April 2011 Accepted: 26 May 2011 Published electronically: 3 August 2011

• **Background** Cushion plants are commonly considered as keystone nurse species that ameliorate the harsh conditions they inhabit in alpine ecosystems, thus facilitating other species and increasing alpine plant biodiversity. A literature search resulted in 25 key studies showing overwhelming facilitative effects of different cushion plants and hypothesizing greater facilitation with increased environmental severity (i.e. higher altitude and/or lower rainfall). At the same time, emerging ecological theory alongside the cushion-specific literature suggests that facilitation might not always occur under extreme environmental conditions, and especially under high altitude and dryness.

• **Methods** To assess these hypotheses, possible nursing effects of *Thylacospermum caespitosum* (Caryophyllaceae) were examined at extremely high altitude (5900 m a.s.l.) and in dry conditions (precipitation < 100 mm year⁻¹) in Eastern Ladakh, Trans-Himalaya. This is, by far, the highest site, and the second driest, at which the effects of cushions have been studied so far.

• **Key Results** In accordance with the theoretical predictions, no nursing effects of *T. caespitosum* on other alpine plants were detected. The number and abundance of species were greater outside cushions than within and on the edge of cushions. None of the 13 species detected was positively associated with cushions, while nine of them were negatively associated. Plant diversity increased with the size of the area sampled outside cushions, but no species–area relationship was found within cushions.

• **Conclusions** The results support the emerging theoretical prediction of restricted facilitative effects under extreme combinations of cold and dryness, integrating these ideas in the context of the ecology of cushion plants. This evidence suggests that cases of missing strong facilitation are likely to be found in other extreme alpine conditions.

Key words: Alpine plants, *Thylacospermum caespitosum*, Caryophyllaceae, biodiversity, competition and facilitation, stress, nurse plant, Tibet, Ladakh, Himalaya.

INTRODUCTION

It is often assumed that the distribution and abundance of species in high-elevation communities is enhanced by the presence of neighbours, where interactions are predominantly facilitative (Callaway *et al.*, 2002). In these high-altitude regions, positive interactions involve nurse plants facilitating the establishment of other species within their canopy by offering microhabitats that are more favourable for seed germination and/or seedling recruitment than the surrounding environment (Cavieres and Badano, 2009).

Cushion plants are expected to be among the most effective nurse species in alpine habitats (Arredondo-Núñez *et al.*, 2009) and have long fascinated ecologists (Rauh, 1939; Körner, 2003). Their low and compact growth form acts as an efficient heat and water trap and represents a clear model of evolutionary convergence across phylogenetically unrelated taxa in different regions of the world (Körner, 2003; Sklenář, 2009). It has been repeatedly reported that cushion plants act as nurse species in different alpine conditions, where

significantly more plant species grow within cushions than outside their canopy. For example, a literature search of studies assessing potential nursing effects of cushions on other plants resulted in 25 key publications (Table 1), all showing predominantly facilitative effects. Much of this evidence comes from high-Andean communities (but see Antonsson *et al.*, 2009; Haussmann *et al.*, 2010; Yang *et al.*, 2010). The positive effects of cushions were greater with increased environmental severity (Arredondo-Núñez *et al.*, 2009; Badano *et al.*, 2010), i.e. at higher altitudes (Cavieres *et al.*, 2002; Fajardo *et al.*, 2008; Antonsson *et al.*, 2009; Yang *et al.*, 2010) and under drier conditions (Cavieres *et al.*, 2006).

The greater nursing effect under more severe habitats supports the hypothesis of increased facilitation under more stressful conditions (Callaway *et al.*, 2002). At the same time, ecological theory on species interactions alongside the cushion-specific literature also suggests that the importance of facilitative effects could ultimately decrease under extreme stressful conditions (Michalet *et al.*, 2006). Recent

TABLE 1 List of studies assessing facilitative effects from cushion species on other plants

Study	Year	Species	Altitude	Region	Rainfall	Effect
Pyšek and Liška	1991	<i>Sibbaldia tetrandra</i>	3800	Pamiro-Alai, 42°N	2500	+
Nuñez <i>et al.</i>	1999	<i>Mulinum leptacanthum</i> , <i>Oreopolus glacialis</i>	1550–1600	Andes, 41°S	1000	+
Badano <i>et al.</i>	2002	<i>Oreopolus glacialis</i>	1900	Andes, 37°S	2300	+ but species specific
Cavieres <i>et al.</i>	2002	<i>Bolax gummifera</i>	700–900	Andes, 50°S	900–1000	+ more evident in higher altitudes
Arroyo <i>et al.</i>	2003	<i>Azorella monantha</i>	700–900	Andes, 50°S	900–1000	+
Cavieres <i>et al.</i>	2005	<i>Azorella monantha</i>	3100–3300	Andes, 33°S	943	+
Acuña-Rodríguez <i>et al.</i>	2006	<i>Laretia acaulis</i>	2800	Andes, 33°S	400–900	+
Badano <i>et al.</i>	2006	<i>Azorella monantha</i>	3580–3630	Andes, 33°S	>900	+
Badano and Cavieres	2006a	<i>Azorella monantha</i> , <i>Azorella madreporica</i> , <i>Adesmia subterranea</i>	3200–4000	Andes, 30–33°S	242–900	+
Badano and Cavieres	2006b	<i>Pycnophyllum bryoides</i> , <i>Azorella madreporica</i> , <i>Adesmia subterranea</i> , <i>Azorella monantha</i> , <i>Laretia acaulis</i> , <i>Mulinum leptacanthum</i> , <i>Oreopolus glacialis</i> , <i>Discaria nana</i>	1600–4400	Andes, 23–41°S	No data	+
Cavieres <i>et al.</i>	2006	<i>Laretia acaulis</i>	2800–3200	Andes, 33°S	445–943	Increased facilitation at lower (drier) site
Zoller and Lenzin	2006	<i>Eritrichium nanum</i>	2170–3320	Alps	2170–3320	+
Cavieres <i>et al.</i>	2007	<i>Laretia acaulis</i> , <i>Azorella monantha</i>	2800–3600	Andes, 33°S	400–900	+
Badano and Marquet	2008	<i>Azorella monantha</i>	3580–3630	Andes, 33°S	>900	+
Fajardo <i>et al.</i>	2008	<i>Azorella madreporica</i>	3580–3630	Andes, 33°S	943	Both + and –
Antonsson <i>et al.</i>	2009	<i>Silene acaulis</i>	1150–1447	Scandes, 68°N	839	+ above a given altitudinal threshold
Arredondo-Núñez <i>et al.</i>	2009	a meta-analysis	700–4400			+
Badano and Marquet	2009	<i>Azorella madreporica</i>	3400	Andes, 33°S	>900	+
Cavieres and Badano	2009	<i>Mulinum leptacanthum</i> , <i>Discaria nana</i> , <i>Bolax gummifera</i> , <i>Azorella monantha</i> , <i>Pycnophyllum bryoides</i> , <i>Azorella madreporica</i> , <i>Adesmia subterranea</i> , <i>Laretia acaulis</i> , <i>Oreopolus glacialis</i>	900–4400	Andes, 23–50°S	42–1117	Always + but lower effects at both extremes of the environmental severity gradient.
Quiroz <i>et al.</i>	2009	<i>Azorella madreporica</i>	3200–3580	Andes, 33°S	400	+ but changes with altitude
Sklenář	2009	<i>Azorella dicranoides</i> , <i>Azorella corymbosa</i> , <i>Eudema nubigena</i> , <i>Hypochoeris</i> sp., <i>Xenophyllum humile</i>	4650	Andes, 0°S	No data	+
Badano <i>et al.</i>	2010	<i>Azorella madreporica</i> , <i>Laretia acaulis</i>	2700–3600	Andes, 33°S	400–900	+ increases with stress
Hausmann <i>et al.</i>	2010	<i>Azorella selago</i>	300	Marion Island, 46°S	2000	+
le Roux and McGeoch	2010	<i>Azorella selago</i>	10–500	Marion Island, 46°S	2000	+ increases with stress (– only at lower elevation)
Yang <i>et al.</i>	2010	<i>Arenaria polytrichoides</i>	4500–4700	Himalayas, 28°N	680–790	+ and increases with altitude
Present study		<i>Thylacospermum caespitosum</i>	5900	Trans-Himalaya, 33°N	100	–

For each study, the table indicates the cushion species that was studied, the altitudinal range considered (in m a.s.l.), the study region, the approximate mean yearly rainfall (mm year⁻¹) and the effect detected ('+' indicates facilitation, '-' indicates negative effects).

studies suggest that the outcome of interspecific interactions should be positive only at intermediate levels of environmental severity or, at least, not increase constantly with growing abiotic stress (Kaway and Tokeshi, 2007). Under extreme abiotic conditions plants could derive little benefit, and still incur a cost, from growing in close proximity to neighbours (Maestre *et al.*, 2005). Such theoretical predictions suggest that the combination of multiple stress factors, particularly cold and dry conditions, could override any advantage originating from facilitation (Maestre *et al.*, 2009). These hypotheses remain, however, mostly theoretical (Kaway and Tokeshi,

2007), and sometimes controversial (Gross *et al.*, 2010), probably due to the lack of field evidence from really extreme environmental conditions. Specifically, the real outcome on species interactions under the combination of extreme cold and dry conditions largely remains to be demonstrated. There is some evidence that facilitation in extremely dry environments may be limited (Maestre *et al.*, 2005). Similarly, in the context of the cushion-specific literature, Cavieres and Badano (2009) showed the first evidence indicating less positive effects of cushions under drier environmental conditions. le Roux and McGeoch (2010) tested for a possible

decrease in the facilitation of cushions with increasing altitude and wind exposure. They never found negative nursing effects in the conditions with the greatest stress, possibly because the region receives high precipitation (Table 1). We hypothesize that the absence of negative effects with increasing habitat severity in the cushion-specific literature may have been caused by the lack of studies under a combination of both extremely cold and dry conditions.

The region of Ladakh, in the westernmost part of the Tibetan Plateau (Trans-Himalaya), offers particularly suitable environmental conditions for testing these hypotheses. Ladakh is often referred to as a ‘cold desert’, presenting a combination of extremely cold conditions and marked water scarcity. Compared with other Trans-Himalayan regions, Ladakh lies in the rainshadow of the Himalayas. Owing to its position, which poses a barrier to seasonal monsoons, the whole area receives very low precipitation ($<100 \text{ mm year}^{-1}$; Dvorský *et al.*, 2011). The dominant cushion species in the study area is *Thylacospermum caespitosum* (Caryophyllaceae). It occupies the highest vegetation belts at the upper vegetation limits in the region (Klimeš and Doležal, 2010; Klimešová *et al.*, 2011) and it is basically the only species with a sufficiently large canopy to host other plant individuals. This species is phylogenetically related to another cushion species, *Arenaria polytrichoides*, with a demonstrated nursing effect in the Himalayas, due to improved soil resources (Yang *et al.*, 2010). Here, the hypothesis that *T. caespitosum* is a nurse plant for other alpine species was studied. The possible effects of this cushion species depending on its size were also assessed assuming that effects of cushions could be detected by different species–area relationships within and outside cushions (Cavieres and Badano, 2009). A location was chosen which is at the highest distribution of *T. caespitosum* in the region (at 5900 m a.s.l.), close to the upper altitudinal limits of vascular plants, in what is probably the most stressful combination of environmental conditions under which cushion species effects have been assessed so far. Our results show that the role of cushion species as nurse species might not be as general as expected, especially under very extreme environmental conditions.

MATERIALS AND METHODS

The survey was carried out in the Lunglung valley, on the western slope of the Chalung Mountains east of Lake Tso Moriri (33°05′N, 78°27′E), in the same study site as described in Klimeš and Doležal (2010). The highest peaks in the area are 6400 m a.s.l. and the upper vegetation limit in the valley is at 6030 m. However, most species, including *Thylacospermum caespitosum*, do not often occur above 5900 m. *Thylacospermum caespitosum* accounts for most of the vegetation cover in this vegetation type (Dvorský *et al.*, 2011), which totals around 10%. The mean air temperature at the soil surface was around -8°C (with the minimal and maximal temperatures ranging between -22°C and $+9^\circ\text{C}$; Klimeš and Doležal, 2010).

Sampling was carried out at a homogenous site with a gentle slope where 50 well-spaced, not rotten, *T. caespitosum* cushions of varying size (diameter of 2 cm up to 72.5 cm) were randomly selected. No water sources or brooks were detectable at the site. For each cushion, species composition (occurrence

and number of individuals) within, at the edge of and outside each cushion was surveyed. A similar area was sampled for the three positions considered for each cushion (i.e. within, at the edge of and outside cushions). For the ‘outside’ position, a ‘belt’ was defined surrounding the sampled cushion plant, with the belt having the same area as the cushion (using the formula of circular rings, i.e. the outer radius of the belt was equal to $r \times \sqrt{2}$, with r being the cushion radius). For the edges, a similar approach was followed where for each belt an approximately similar area was sampled within and outside the cushion. A total of 150 sampling units were surveyed (50 cushions \times 3 positions). For tussock species, such as *Poa attenuata*, each tussock was considered to be a separate individual.

For the data analyses two parallel approaches were followed. First, to test the effect of cushions on other plants, resampling techniques were used, as commonly applied in studies considering nursing cushion effects (Cavieres *et al.*, 2002, 2006; Yang *et al.*, 2010). We used the Friedman test, with post-hoc comparisons, based on 9999 Monte-Carlo resamplings (Hollander and Wolfe, 1999). This is a non-parametric test assessing symmetry of responses across treatments for repeated measurements. The three positions (i.e. within, at the edge of and outside cushions) were considered as repeated measures for each individual cushion. The test was applied to assess if the total number of species and the total number of individuals were associated with any specific position. The same test was applied to individual species (in terms of both species occurrence and number of individuals). Then, to assess the possible effects of this cushion species depending on its size, we fitted linear models explaining the number of species and the number of individuals with the size of cushions, the sampling position and their interaction. The three positions were again considered as repeated measures for each individual cushion. Parametric and non-parametric (i.e. permanova; Anderson, 2001) models gave largely similar results. The interaction of size \times position in these models indicated different slopes of fitted regression lines using a standardized major axis (Warton *et al.*, 2006). The linear models described above were also applied to test the effect of cushion size on individual species. All analyses were run in R (R Development Core Team, 2009).

RESULTS

A total of 13 species (Table 2) were found in the 150 sampling units considered. In terms of diversity, the number of species and individuals increased (as expected) with sample area (Fig. 1). The increment was, however, stronger outside cushions (higher variance explained outside cushions and a significant shift in regression slopes according to standardized major axis regressions). The numbers of species and individuals were never higher within a given cushion; they were higher either outside (more frequently) or on the edge of cushions (Fig. 1).

None of these species was positively associated with the cushion species, in terms of either occurrence or number of individuals found. On the contrary, nine out of 13 species were negatively associated with *T. caespitosum*, being more frequently found outside the cushions. For each individual cushion, species generally reached lower abundance inside it

TABLE 2. Species found and their distribution inside, at the edge of and outside cushions of *T. caespitosum*

Species	No. of sampling units present			No. of sampling units × cushions with highest abundance			Mean relative proportion of individuals (%)			Occurrence			No. of individuals			Preferred position	
	Inside	Edge	Outside	Inside	Edge	Outside	Inside	Edge	Outside	Inside vs. edge	Outside vs. edge	Outside vs. inside	Area	Inside vs. edge	Outside vs. edge		Outside vs. inside
<i>Aphragmus oxycarpus</i>	1	4	14	0	3	14	0.4	2.8	3.9		*	*			*	*	Outside > edge > inside
<i>Draba altaica</i>	4	30	40	0	7	36	12.6	29.9	41.5	*	*	*	*	*	*	*	Outside > edge > inside
<i>Draba oreades</i>	0	9	12	0	2	11	0.0	9.1	7.0	*	*	*	*	*	*	*	Outside & edge > inside
<i>Eritrichium hemisphaericum</i>	0	2	12	0	1	12	0.0	0.4	1.5	*	*	*	*	*	*	*	Outside > edge > inside
<i>Poa attenuata</i>	7	30	38	0	12	30	15.9	26.4	19.0	*	*	*	*	*	*	*	Outside > edge > inside
<i>Saussurea glacialis</i>	6	5	8	4	1	6	20.0	4.6	3.5								NS
<i>Saussurea gnaphaloides</i>	1	0	0	1	0	0	4.3	0.0	0.0								NS
<i>Saussurea</i> sp.	8	26	33	3	12	24	28.1	14.9	13.3	*	*	*	*	*	*	*	Outside > edge > inside
<i>Saxifraga cernua</i>	0	0	1	0	0	1	0.0	0.0	0.0				*				NS
<i>Saxifraga nanella</i>	0	2	2	0	2	2	0.0	0.4	0.4				*				NS
<i>Saxifraga stella-aurea</i>	0	0	4	0	0	4	0.0	0.0	0.3		*	*	*	*	*	*	Outside > edge + inside
<i>Stellaria decumbens</i>	0	7	14	0	3	14	0.0	3.1	3.1	*	*	*	*	*	*	*	Outside > edge > inside
<i>Stellaria depressa</i>	5	10	10	1	1	10	18.4	7.9	6.5	*		*	*	*		*	Outside & edge > inside

Resampling with post-hoc comparisons was used to define the preferred position of a species (*indicates $P < 0.05$; NS = $P > 0.05$). 'Area' effects indicate increase of species occurrence with sample size.

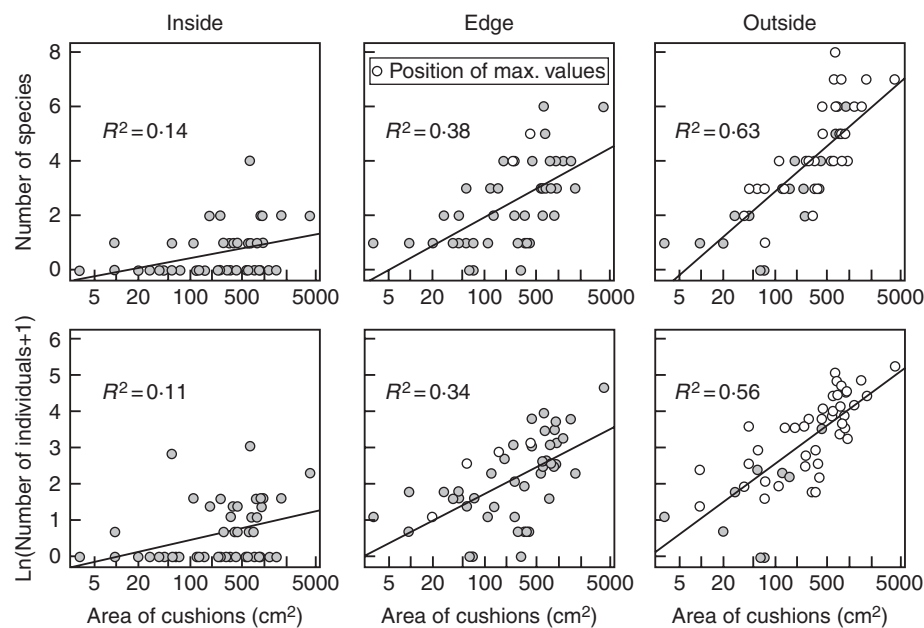


FIG. 1. Variation in the number of species and individuals (after log-transformation) with sample size within, at the edge of and outside cushions of *T. caespitosum*. Open circles refer to the position, for each cushion, where the maximum number of species or individuals was reached (see text for detail). For both number of species and number of individuals there was a significant effect of position ($P < 0.05$), with post-hoc tests between positions indicating outside > edge > inside. The R^2 values of fitted lines are given for each panel.

(Table 2 and Supplementary Data Figure S1). Only four species, i.e. three *Saussurea* species and *Stellaria depressa*, showed, in some cases, the highest abundance within individual cushions. These cases were rather occasional for *Saussurea* sp. (possibly a previously undescribed species) and *Stellaria depressa*. The other two species did not show clear associations with any position. Only *Saussurea gnaphalodes* was limited to the cushions, but with one individual in 150 sampling units.

DISCUSSION

Our study provides a concrete example of no nursing effect of a high-elevation cushion plant (*T. caespitosum*) growing under extreme environmental conditions. Compared with the existing literature on cushion species (Table 1), and on facilitation in general, we selected a site presenting the most stressful conditions, particularly possessing the most extreme combination of cold and dry conditions. In such extreme conditions, we did not find any evidence of positive effects of *T. caespitosum* on other plants, supporting the theoretical predictions advocating for a decrease of facilitation under extreme stressful conditions (Michalet *et al.*, 2006; Maestre *et al.*, 2009). Negative, or non-positive, effects of cushion species have rarely been reported (Table 1) and, as far as we know, never so clearly. Cavieres and Badano (2009), for example, did not find any location with negative effects of cushions on local diversity, while negative effects of cushions are generally observed on a minority of species at a given site (Arredondo-Núñez *et al.*, 2009; Yang *et al.*, 2010). Fajardo *et al.* (2008) found an equal number of positive and negative associations at their lowest site, but almost exclusively positive associations at their highest site. Similarly, le Roux and McGeoch (2010) found

some negative associations, but only at their lowest site. As such our results provide new evidence that needs to be taken into account when generalizing existing theories, and testing new hypotheses, on nursing effects of cushions under extreme alpine conditions. As the entire gradient of stressful conditions on high mountains throughout the world has probably not been studied so far (Table 1), cases of missing facilitation in extremely stressful conditions are likely to be found elsewhere. Although the present study is based on a single cushion species, it is unlikely that the results are due to specific features of this particular cushion species, especially because *T. caespitosum* is phylogenetically and morphologically related to *A. polytrichoides* which has demonstrated a positive nursing effect in the Himalayas (Yang *et al.*, 2010). In comparison with Yang *et al.* (2010), our site does not receive summer monsoons, is characterized by much lower precipitation (approx. 700 mm year⁻¹ vs. approx. 100 mm year⁻¹ in our site) and is situated at a much higher altitude (>1200 m higher).

Why were facilitative effects by cushions not developed under these extreme conditions? It is possible that in these extreme environments all species in the species pool are stress tolerant, i.e. they might be sufficiently adapted to the harsh conditions they inhabit, even without nursing effects (Michalet *et al.*, 2006). In extremely arid habitats in particular, stress-tolerant species do not necessarily profit from facilitative effects from other species but compete for limited resources (Maestre *et al.*, 2009). Ameliorative effects of cushion plants are said to include improved temperature conditions, an increased growing season and greater availability of resources (Yang *et al.*, 2010). However, soil crusts, instead of cushion species, can provide microhabitats that are favourable for seed germination and/or seedling recruitment (Gold and

Bliss, 1995), with the additional advantage of not having to compete with cushions. Soil crusts are frequent in alpine and sub-nival zones of different Ladakh regions and often occupy areas devoid of vascular plants (Reháková *et al.*, 2011). Moreover, in contrast to other regions of the world, the growing season in the study area is extremely short (<2 months; Klimeš and Doležal, 2010) and cushions probably cannot help much in prolonging it. Finally, although the effect of cushions on species with different traits has been considered (Arredondo-Núñez *et al.*, 2009; Yang *et al.*, 2010), little is known about the effects of cushions with different traits on species interactions. Thus, although *T. caespitosum* is largely similar to many other studied cushion species, the extreme compactness of its branches could partially inhibit settling of other plants. Considering the life histories of the interacting species (Maestre *et al.*, 2009), together with the effect of different cushion growth forms (e.g. Rauh, 1939), could provide new insights to generalize cushion effects on other alpine species. However, this may be limited, at present, by two constraints. First, as far as we know, besides the preliminary work by Rauh (1939), a common set of traits for cushion species has not been agreed. Secondly, given the preponderance of positive associations found in the literature (Table 1), meta-analyses of existing data probably cannot reveal any effect of the growth form of cushions on other species.

In conclusion, our results provide evidence that cushion plants do not act as nurse species in extreme alpine conditions, suggesting that cases of missing strong facilitation are likely to be found elsewhere. More generally, our study brings new evidence of the emerging theoretical predictions that the outcome of plant interactions can strongly depend on the combination of temperature and water stress. As such, this study supports the theoretical prediction that facilitation should not hold under extreme combinations of these two factors (Maestre *et al.*, 2009), integrating these emerging ideas in the context of the ecology of cushion plants.

SUPPLEMENTARY DATA

Supplementary data are available online at www.aob.oxfordjournals.org and consist of Figure S1: variation in the number of individuals (after log-transformation) with sample size within, at the edge of and outside cushions of *T. caespitosum*.

ACKNOWLEDGEMENTS

This study was funded by the Institute of Botany, Academy of Sciences of the Czech Republic (AV0Z60050516, GD206/08/H044) and by the projects GAAV-IAA600050802, CNRS-PICs4876 and GAJU-138/2010/P. We thank Petr Šmilauer, Marta Carboni and two anonymous reviewers for their help with the manuscript, and Jan W. Jongepier for language correction.

LITERATURE CITED

- Acuña-Rodríguez IS, Cavieres LA, Gianoli E. 2006. Nurse effect in seedling establishment: facilitation and tolerance to damage in the Andes of central Chile. *Revista Chilena de Historia Natural* **79**: 329–336.
- Anderson MJ. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* **26**: 32–46.
- Antonsson H, Björk RG, Molau U. 2009. Nurse plant effect of the cushion plant *Silene acaulis* (L.) Jacq. in an alpine environment in the subarctic Scandes, Sweden. *Plant Ecology and Diversity* **2**: 17–25.
- Arredondo-Núñez A, Badano EI, Bustamante EO. 2009. How beneficial are nurse plants? A meta-analysis of the effects of cushion plants on high-Andean plant communities. *Community Ecology* **10**: 1–6.
- Arroyo MTK, Cavieres LA, Peñaloza A, Arroyo-Kalin MA. 2003. Positive associations between the cushion plant *Azorella monantha* (Apiaceae) and alpine plant species in the Chilean Patagonian Andes. *Plant Ecology* **169**: 121–129.
- Badano EI, Molina-Montenegro MA, Quiroz C, Cavieres LA. 2002. Effects of the cushion plant *Oreopolus glacialis* (Rubiaceae) on species richness and diversity in a high-Andean plant community of central Chile. *Revista Chilena de Historia Natural* **75**: 757–765.
- Badano EI, Cavieres LA. 2006a. Impacts of ecosystem engineers on community attributes: effects of cushion plants at different elevations of the Chilean Andes. *Diversity and Distributions* **12**: 388–396.
- Badano EI, Cavieres LA. 2006b. Ecosystem engineering across ecosystems: do engineer species sharing common features have generalized or idiosyncratic effects on species diversity? *Journal of Biogeography* **33**: 304–314.
- Badano EI, Marquet PA. 2008. Ecosystem engineering affects ecosystem functioning in high-Andean landscapes. *Oecologia* **4**: 821–829.
- Badano EI, Jones CG, Cavieres LA, Wright JP. 2006. Assessing impacts of ecosystem engineers on community organization: a general approach illustrated by effects of a high-Andean cushion plant. *Oikos* **115**: 369–385.
- Badano EI, Marquet PA, Cavieres LA. 2010. Predicting effects of ecosystem engineering on species richness along primary productivity gradients. *Acta Oecologica* **36**: 46–54.
- Callaway RM, Brooker RW, Choler P, *et al.* 2002. Positive interactions among alpine plants increase with stress. *Nature* **417**: 844–848.
- Cavieres LA, Badano EI. 2009. Do facilitative interactions increase species richness at the entire community level? *Journal of Ecology* **97**: 1181–1191.
- Cavieres L, Arroyo MTK, Peñaloza A, Molina-Montenegro M, Torres C. 2002. Nurse effect of *Bolax gummifera* cushion plants in the alpine vegetation of the Chilean Patagonian Andes. *Journal of Vegetation Science* **13**: 547–554.
- Cavieres LA, Quiroz LC, Molina-Montenegro MA, Muñoz AA, Pauchard A. 2005. Nurse effect of the native cushion plant *Azorella monantha* on the invasive non-native *Taraxacum officinale* in the high-Andes of central Chile. *Perspectives in Plant Ecology, Evolution and Systematics* **7**: 217–226.
- Cavieres LA, Badano EI, Sierra-Almeida A, Gomez-Gonzalez S, Molina-Montenegro MA. 2006. Positive interactions between alpine plant species and the nurse cushion plant *Laretia acaulis* do not increase with elevation in the Andes of central Chile. *New Phytologist* **169**: 59–69.
- Cavieres LA, Badano EI, Sierra-Almeida A, Molina-Montenegro M. 2007. Microclimatic modifications of cushion plants and their consequences for seedlings survival of native and non-native plants in the high-Andes of central Chile. *Arctic, Antarctic and Alpine Research* **39**: 229–236.
- Dvorský M, Doležal J, de Bello F, Klimešová J, Klimeš J. 2011. Vegetation types of East Ladakh: species and growth form composition along main environmental gradients. *Applied Vegetation Science* **14**: 132–147.
- Fajardo A, Quiroz CL, Cavieres LA. 2008. Spatial patterns in cushion-dominated plant communities of high Andes of Central Chile: how frequent are positive associations? *Journal of Vegetation Science* **19**: 87–96.
- Gold WG, Bliss LC. 1995. Water limitation and plant community development in a polar desert. *Ecology* **76**: 1558–1568.
- Gross N, Liancourt P, Choler P, Suding KN, Lavorel S. 2010. Strain and vegetation effects on local limiting resources explain the outcomes of biotic interactions. *Perspectives in Plant Ecology, Evolution and Systematics* **12**: 9–19.
- Hausmann NS, McGeoch MA, Boelhouwers JC. 2010. Contrasting nurse plants and nurse rocks: the spatial distribution of seedlings of two sub-Antarctic species. *Acta Oecologica* **36**: 299–305.
- Hollander M, Wolfe DA. 1999. *Nonparametric statistical methods*, 2nd edn. New York: John Wiley & Sons.

- Kaway T, Tokeshi M. 2007.** Testing the facilitation–competition paradigm under the stress-gradient hypothesis: decoupling multiple stress factors. *Proceedings of the Royal Society B: Biological Sciences* **274**: 2503–2508.
- Klimeš L, Doležal J. 2010.** An experimental assessment of the upper elevational limit of flowering plants in the Western Himalayas. *Ecography* **33**: 590–596.
- Klimešová J, Doležal J, Dvorský M, de Bello F, Klimeš L. 2011.** Clonal growth forms in eastern Ladakh, Western Himalayas: classification and habitat preferences. *Folia Geobotanica* **46**: 191–217.
- Körner C. 2003.** *Alpine plant life – functional plant ecology of high mountain ecosystems*. Heidelberg: Springer.
- Maestre FT, Valladares F, Reynolds JF. 2005.** Is the change of plant–plant interactions with abiotic stress predictable? A meta-analysis of field results in arid environments. *Journal of Ecology* **93**: 748–757.
- Maestre FT, Callaway RM, Valladares F, Lortie CJ. 2009.** Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *Journal of Ecology* **97**: 199–205.
- Michalet R, Brooker RW, Cavieres LA, et al. 2006.** Do biotic interactions shape both sides of the humped-back model of species richness in plant communities? *Ecology Letters* **9**: 767–773.
- Núñez C, Aizen M, Ezcurra C. 1999.** Species associations and nurse effects in patches of high-Andean vegetation. *Journal of Vegetation Science* **10**: 357–364.
- Pyšek P, Liška J. 1991.** Colonization of *Sibbaldia tetrandra* cushions on alpine scree in the Pamiro-Alai Mountains, Central Asia. *Arctic and Alpine Research* **23**: 263–272.
- Quiroz CL, Badano EI, Cavieres LA. 2009.** Floristic changes in alpine plant communities induced by the Cushion plant *Azorella madreporica* (Apiaceae) in the Andes of central Chile. *Revista Chilena de Historia Natural* **82**: 171–184.
- Rauh W. 1939.** Über polsterförmigen Wuchs. *Acta Nova Leopoldina* **7/49**: 267–508.
- R Development Core Team 2009.** *R: A language and environment for statistical computing*. Vienna, Austria: <http://www.R-project.org>.
- Řeháková K, Chlumská Z, Doležal J. 2011.** Soil cyanobacterial and microalgal diversity in dry mountains of Ladakh, NW Himalaya, as related to site, altitude, and vegetation. *Microbial Ecology*, in press. doi:10.1007/s00248-011-9878-8.
- le Roux PC, McGeoch MA. 2010.** Interaction intensity and importance along two stress gradients: adding shape to the stress-gradient hypothesis. *Oecologia* **162**: 733–745.
- Sklenář P. 2009.** Presence of cushion plants increases community diversity in the high equatorial Andes. *Flora* **204**: 270–277.
- Warton DI, Wright IJ, Falster DS, Westoby M. 2006.** Bivariate line-fitting methods for allometry. *Biological Reviews* **81**: 259–291.
- Yang Y, Niu Y, Cavieres LA, Sun H. 2010.** Positive associations between the cushion plant *Arenaria polytrichoides* (Caryophyllaceae) and other alpine plant species increase with altitude in the Sino-Himalayas. *Journal of Vegetation Science* **21**: 1048–1057.
- Zoller H, Lenzin H. 2006.** Composed cushions and coexistence with neighbouring species promoting the persistence of *Eritrichium nanum* in high alpine vegetation. *Botanica Helvetica* **116**: 31–40.